Environmental and seasonal influences on lake phytoplankton community structure

A Thesis Submitted For the
Degree of Master of Science
In The
Faculty of Science

By

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October, 1993

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Dedication

To my father

Who was encouraging me to continue my study

but unfortunately he had not the chance to see my

first achievement

Acknowledgements

I thank my supervisor Dr. Kevin Murphy, Department of Botany, firstly for his help and support to get this scholarship and secondly to all his advice and moral support all through my study.

I am very grateful to my supervisor Dr. Roger Tippett, Department of Zoology for his guidance and advice through the course of this thesis. His patience and understand was very greatly appreciated. Special thanks for him for providing the facilities and equipment necessary to conduct this study.

I am indebted to Professor Richard Codgell, Department of Botany, and Professor Graham Coombs, Department of Zoology, for the use of the facilities of both departments of Glasgow University.

Special thanks to Dr. Colin S. Reynolds, Dr. Elizabeth Haworth and all the members of Freshwater Biological Associations for their help during my visit in 1991 and for making my stay a pleasant and productive one.

I also thank Dr. Peter J. Dominy, Department of Botany, for all his help. I thank Dr. Azra Meadow, Department of Zoology for letting me using her computer program for diversity index. Thanks also to. Drs. A. C. Taylor, K. H Locky and S. Lindsay, Department of Zoology for their helpful comments during the interview of first and second year reports,and to Mrs Lesley Drysdale, Computer services, for all her help and kindness with Axum and Cricket graph programs.

Special thanks to Mr.Rab. McMath, chief Technician, for his assistance and helpful suggestions in field sampling and keeping all the equipment in good conditions. I thank all the University Field Station's staff whom made my stay there such a pleasant and unforgottable.

I am very grateful to Anna Simpson for all her help and moral support all through my stay. Special thanks to Ms. Delloula Rouag for her help with computer program, her faithful support and encouragement. I thank Mr. Abd El Hamid Kheder for his help with TWINSPAN and CANOCO programs. I thank Fiona Stewart and Belen Calvo for everything they have done to me throughout my stay.

I would like to thank Mr. Mohamed Makkawy Yacoub, the chairman of the High Dam Lake Development Authority, for his help. Special thanks to Mr. Safwat Gattas Abdul Malek, Under Secretary of State for Fisheries and Mr. Mohamed El Shahat, the General Director of Fishery Management Centre, for their approval to get study leave to do my Master.

I am very much grateful to my colleges Mr Mohamed Shehata and Mr. Ibrahim Omar and my assistants Mr. Rabie Saied Ahmed and Mr. Ahu El Wafa Hassan at the Fishery Management Centre for all their helps, encouragement and moral support.

I would like to express my appreciation to all my friends at Aswan Regional Planning for their moral support.

Special thanks to my Japanese supervisors Professor Y. Aruga, Associate professor T. Ioriya and K. Kihara of Tokyo University of Fisheries for all their helps in the last few years and their moral support.

Special thanks to my mother, sisters, sister in law, brothers, brothers in law, nieces and nephews for their love and faithful support.

I would like to thank Mrs Margaret McCallum and Mrs Anne Marie Lamont for checking the grammar of my thesis.

I gratefully acknowledge financial support from the British Council. I thank Mr. Peter Llewellyn science officer of the British Council in Egypt 1991 for his help and sincere support. I would like to thank my programme officers Ms. Joan Barry and Ms Isobel Mitchell.

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Summary

This is an investigation into the effects of the environment on seasonal changes of phytoplankton community structure and production, contrasting the north and south basins of Loch Lomond, Scotland. It commenced in mid January 1991 and continued until late May 1993.

The north basin of Loch Lomond is a warm monomictic type, showing a single circulation period and is clearly stratified during summer. The south basin is polymictic because it stratifies only for a short period.

In the north basin the effect of incident radiation is reduced by the small surface area to volume ratio and the greater amount of cloud cover. The south basin is wide and open with a larger surface area and consequently receives more light energy per unit volume of the water than the north.

Dissolved oxygen in the water at both sites never showed significant depletion and is typical of oligotrophic waters. The vertical distribution of oxygen in both basins of Loch Lomond tends to be slightly clinograde during summer and orthograde in winter. Dissolved oxygen concentrations were at nearly saturation and supersaturation levels through the period of isothermal conditions and declined to the minimum in the hypolimnion after several weeks of thermal stratification.

The annual range of pH in Loch Lomond is similar in both basins. Alkalinity showed a small annual range generally being high in spring and low in winter.

Conductivity shows that there is a much larger dissolved mineral concentration in the south than the north.

The pattern of seasonal nutrient variation in Loch Lomond showed a maximum abundance of phosphate, silicate and nitrate occurring in winter and the lowest concentration in the summer. Silicate and nitrate were always detectable.

The chemical oxygen demand in the south basin is on average 33% higher than in the north basin.

The seasonal succession of phytoplankton in Loch Lomond exhibited a pattern of domination by diatoms in winter and spring. In general, the south basin retained a higher standing crop than the north basin and the growing season usually started earlier and extended over a longer period of time.

The chlorophyll *a* peak always preceded or coincided with the peak of phytoplankter numbers. Although the largest peak for chlorophyll in the south basin was in autumn, the largest peak for numbers was at the end of June.

From the TWINSPAN classification and CCA ordination for both basins of Loch Lomond, it was clear that the phytoplankton community in winter and spring was dominated mainly by diatoms, with some blue-greens. At this time nutrients are at their maximum level. Silicate appeared to be more important than nitrate and phosphate as a potential environmental control on phytoplankton at this time of year. The summer and autumn species were probably favoured by increasing temperature and tolerance of lower nutrient availability.

Both basins retain 42 species. Diversity is slightly higher in the north than in the south basin except during spring and early summer when values are more or less the same.

Melosira italica, considered to be a plankton characteristic of nutrient-rich lakes, was the most dominant species in the south basin during spring and autumn.

The oligotrophic *Cyclotella kutzingiana* , presented the main constituent in the north basin from early spring to early autumn.

The decline in phosphate concentration, was correlated with the spring algal increase but it is unlikely that this reached growth limiting levels for diatoms before silicate depletion occurred.

Blue-green algae, particularly *Merismopedia glauca,* an indicator of oligotrophic waters, were more important in the north than the south basin.

Dinobryon divergens occurred more in the north basin than in the south basin: this species also prefer nutrient-poor conditions.

Both in terms of standing crop and primary production there was a difference in the state of algal population growth during spring between the north and south basins. In the south basin growth started 4-6 weeks earlier than in the north, and reached a peak 3.5 times as high.

The seasonal zooplankton pattern displayed marked variations in relation to phytoplankton composition and concentration. The general dominance of rotifers through most of the year was related to their faster rate of reproduction compared with

cladocera and copepoda. The seasonal variations of rotifers were also likely to be influenced by temperature and possible supplementary food sources.

1. Introduction

1.1. Aims of the study

1. To quantify the seasonal changes of phytoplankton in Loch Lomond and compare the results with previous data to discover any changes with time.
2. To relate these changes to the physical and chemical features of the loch.
3. To gain a broad understanding of algal interactions with the second trophic level, zooplankton (primary consumer) in the loch.
4. To assess the heterogeneity of plankton abundance (related to the distribution of plankton in different parts of the loch).
5. To compare Loch Lomond (a temperate lake) the Aswan High Dam Lake, Egypt (a tropical lake).

1.2. Limnological background

Phytoplankton biomass measured as chlorophyll *a* or by other measures of primary production, is a variable of great importance in limnological investigations. These variables are often taken to characterise the present trophic state of a water body and to describe its temporal changes. The key to water quality management is the identification of those factors which control these variables and the manner by which this is accomplished.

Until recently it was not easy to distinguish between the effects of the chemical and physical factors which together control the dynamics of phytoplankton productivity and further trophic levels in the community (Harris *et al.*, 1980). Nitrogen, phosphorus and

silica (for diatoms) are generally considered to be the major elements which limit algal growth.

The main source of phosphorus for phytoplankton is orthophosphate. Some algae produce large populations in water containing little phosphorus. This is due to their ability to store phosphorus in excess of their immediate needs (Golterman, 1975).

Algae and photosynthetic bacteria (*Cyanophyta*) may use nitrates, ammonium salts or gaseous nitrogen as sources of nitrogen. Nitrate is the commonest source of inorganic nitrogen in freshwater but when the total content of nitrates and ammonia in the water is very low some *Cyanophyta*, which fix elemental nitrogen are common in the water blooms. Lund (1965) in his review of the ecology of freshwater phytoplankton pointed out that the development of large populations of diatoms is accompanied mostly by a marked decrease in the amount of silicon in the water. There is strong evidence that the sizes of the maxima in some water are determined by the supply of silica. Dokulil *et al.*, (1990) found that dissolved silicate and phosphorus concentrations were critical for the summer situation in their study of Mondsee-Austria. In a study of Lough Corrib, Western Ireland, Mooney (1989) found that the spring diatom crop was limited by either silicate or nitrogen. Vincent (1983) in a study of two oligotrophic lakes, in New Zealand, mentioned that winter circulation usually brings an increased supply of phosphorus and nitrogen which, later controlled the amount of algal growth in the euphotic zone. Pettersson (1990) in his study of Lake Erken (Sweden), reported that phosphorus was the limiting nutrient at the end of the spring bloom. In 1990, Hunter *et al.*, in their study of Lake Tahoe (California-Nevada) pointed out that low phosphorus concentrations were responsible for changes in the phytoplankton community structure. Wood and Gibson (1973) in a study of Lough Neagh came to a conclusion that phosphorus was the key factor which limited the growth of algae. Munawar *et al.* (1988) found that the levels of total phosphorus, nitrate, nitrite and soluble reactive silica were depleted during the stratified period.

In 1976 Munawar and Burns in their study of Lake Erie used factor analysis to show that in the spring, primary production correlated with the phosphorus and nitrogen soluble nutrients only. During summer, primary production correlated with biomass, chlorophyll *a*, the major phytoplankton groups (*Cyanophyta, Chlorophyta, Chrysomonadinae* and *Diatomeae*) and phosphorus. In autumn, production was positively correlated with phytoplankton biomass and with *Chlorophyta* in particular.

The general seasonal succession of species can be related to the interaction of light (solar radiation) and temperature, though other factors are important. Temperature is important due to its effects on the rates of photosynthesis and growth, density changes in the water column and uptake of nutrients. Its effects are correlated with light, wind, the rate of supply of nutrients and grazing.

Some limnologists divide temperate lakes into categories: ultra-oligotrophic, oligotrophic, mesotrophic, eutrophic and hypertrophic. These categories from a series of fertility and though it is not difficult to define the extremes, everyone has a different view where the boundaries lie between categories. Ultra-oligotrophic lakes have very clear water, almost no phytoplankton and hypolimnia saturated with oxygen; hypereutrophic lakes have turbid water, dense algal growths and anaerobic hypolimnia (if they are deep enough) (Moss, 1984).

Ecologists use the adjective 'eutrophic' to describe biological systems into which there is a high input of otherwise limiting nutrients, and which therefore support a high level of organic production. 'Oligotrophic' describes the opposite nutrient-deficient condition. The same applies to freshwater systems: eutrophic waters receive relatively high nutrient loading and can be distinguished from oligotrophic ones by their larger than average standing crops of organisms (not just primary producers), and by other metabolic characteristics (Reynolds, 1984). Perhaps the most important characteristic of a eutrophic lake is that oxygen concentration in the hypolimnion becomes significantly reduced during summer: the greater the epilimnetic production per unit area, the more intense the

hypolimnetic reduction. Although all the contributory factors were not fully appreciated at the time, it was soon realised that the deep, soft-water lakes of mountainous areas were generally oligotrophic; on the other hand, eutrophic lakes were frequently shallow, hard-water and located in lowland districts (Reynolds, 1984).

In 1991 Vaquer and El Hafa reported that the reservoir of Sainte Croix (Province, France) was oligo-mesotrophic during the 1985-1986 period. They found that the seasonal development and vertical distribution of phytoplankton depended typically on temperature and irradiance during the mixing period and on nutrients and biological factors during the thermal stratification (Lund 1965, Foy *et al.* 1976, Vincent 1983, Allott 1986).

Water movements play an important part in the vertical and horizontal distribution of phytoplankton and sometimes in the replenishment of nutrients from the hypolimnion or underwater sediment.

Many algae are tolerant of the range of pH usually found in water, but very acid or very alkaline waters have a restricted flora, though production may be large. The effect of pH is intimately connected with the carbon dioxide-bicarbonate-carbonate system. A high pH in waters rich in ammonium compounds may lead to toxicity from the relatively high concentration of ammonia present or the large uptake of ammonium ions (Lund, 1965).

The spatial and seasonal distribution of phytoplankton biomass expressed as wet weight of phytoplankton is widely studied. In 1978 Munawar and Munawar reported homogeneous distribution with very low biomass concentration (0.1-0.2 g m^{-2}) in an ultra-oligotrophic lake. For oligotrophic lakes Munawar *et al.*, (1988) and Eloranta (1986) recorded a range of seasonal variations between 0.2 to 0.52 g m^{-3} with a single peak during stratified conditions. In the case of mesotrophic lakes, Eloranta (1986) recorded 1.23 g m^{-3} and Sprules and Munawar (1991) reported an average biomass of 586 μg l^{-1}. The mean phytoplankton biomass of an oligo-mesotrophic lake ranged between 0.17 and 1.18 g m^{-3} with high values recorded during spring (May, June) compared with summer (Munawar *et*

al., 1991). For eutrophic lakes, the phytoplankton biomass ranged between 0.6 and 6.0 g m^{-3} and the highest value recorded was 13.2 gm^{-3} in April (Munawar and Munawar, 1976, Eloranta 1986). According to Abdul-Hussein and Mason (1988) and Pettersson (1990), the mean annual phytoplankton biomass ranged between 8.3 and 40.8 mg l^{-1}. The maximum value was recorded in August. The total phytoplankton biomass an acid oligotrophic lake ranged from 10 μg l^{-1} wet weight in winter to 750 μg l^{-1} in spring and summer averages of about 400 μg l^{-1} (Lyden and Grahn, 1985).

Chlorophyll *a* concentration is also used as an index of total algal biomass. The relationship between phytoplankton (biovolume) biomass and chlorophyll *a* was studied in Lake Superior. This study showed a strong positive relationship but which varied with season. The most significant correlation was found during June (El-Shaarawi and Munawar, 1978). Vertical and seasonal distribution of chlorophyll *a* is widely studied in most of the lakes around the world. The chlorophyll *a* concentration fluctuated according to the type of lake (trophic level of the lake) or period of the year. For most of the oligotrophic lakes the chlorophyll *a* concentrations ranged from 0.1 to 4.6 mg m^{-3} in spring (late May). The maximum concentration were measured between 2.5 to 10 m depth from January to June (Mariazzi *et al.*, 1991, Vaquer and El Hafa 1991, Eloranta and Palamaki 1986). But in some of them the concentration increased in late July to reach 8.5 mg m^{-3} (Brooks and Torke, 1977). According to Brooks and Torke (1977) in their study of Lake Michigan, during autumn overturn chlorophyll *a* concentration was uniformly distributed at approximately 1 mg m^{-3} and remained at this level throughout the winter. For the meso-oligotrophic lake 16 μg l^{-1} was recorded in the epilimnion during spring growth of the diatoms in a deep stratifying lake, Mondsee-Austria (Dokulil and Skolaut 1986). Pettersson (1990) and Bailey-Watts (1987) pointed out that the chlorophyll *a* concentration of eutrophic lakes ranged from 30 μg l^{-1} to 35 μg l^{-1} during spring and autumn maxima. In 1988 Abdul-Hussein and Mason recorded high chlorophyll *a*

concentration up to 98 mg m^{-3} in Ardleigh Reservoir. For highly eutrophic or hypertrophic lakes the minimum chlorophyll *a* concentration was recorded in winter (3-10 mg m^{-3}) but started to increase in spring and the summer peak soon developed (80-500 mg m^{-3}) (Osborne 1991, Gibson *et al.* 1971, Priddle and Happey-Wood 1983). Stirling and Dey (1990) recorded 189 $\mu g\ l^{-1}$ at the surface of Loch Fad in August.

The dynamics of algal succession are of fundamental importance in the ecology of freshwater lakes.

The phytoplankton community in the ultra-oligotrophic lake (Lake Tahoe, California-Nevada) is dominate by diatoms, *Chrysophytes* and *Cryptophytes* (Hunter *et al.*, 1991). The phytoplankton data indicated the presence of 79 taxa with the *Bacillariophyceae, Cyanophyta and Chlorophyta* alternatively dominant in Ezequiel Ramos Mexia Reservoir, Argentina (Mariazzi *et al.*, 1991). The species composition of the oligotrophic lake was dominated by phytoflagellates (53 %) and diatoms (38 %) with the blue greens contributing the rest. Among the phytoflagellates, *Cryptophyceae* (26 %), *Chrysophyceae* (21 %) and *Dinophyceae* (5 %) were the main contributors. Approximately 285 taxa were identified in Lake Superior during a study period from May to November/December 1973 (Munawar and Munawar 1978, Munawar *et al.* 1988). In oligotrophic-mesotrophic lakes, Munawar *et al.* 1991, Maulood and Boney 1980, found that in the spring the phytoplankton was dominated by diatoms followed by *chrysophyceae* and *Cryptophyceae.* But during the summer the diatoms showed a decreasing trend due to the relative dominance of *Chrysophyceae, Cryptophyceae* and *Chlorophyta.* The densities of cells which recorded ranged between 15,000 to 900,000 algal units l^{-1}. The phytoplankton community of the acid lake was composed mainly of *Chrysophyceans* and *Dinophyceans* (Lyden and Grahn, 1985). In case of the eutrophic lakes, the recorded taxa ranged between 58 and 109. The phytoplankton communities in eutrophic lakes (central Finnish lakes) were characterised by blue-green algae (21.2 % of total biomass) and green algae (18.7 % of total biomass).

Bacillariophyta dominated during winter and early spring. But during June the phytoplankton composition consisted of a mixture of *Chlorophyta* and *Cyanophyta* (Eloranta, 1986, Abdul-Hussein and Mason, 1988).

Primary production is one of the most important sources of energy input to freshwater ecosystems and has been studied largely to obtain basic information on carbon transfer. The primary production can be measured through carbon uptake as well as the oxygen production or the formation of organic compounds. The classic procedure for determining the oxygen content (oxygen production) of a natural water is known as the 'Light-dark' bottle technique. For carbon uptake, a radioactive trace (^{14}C) is widely used. The choice between the previous two methods depends upon the kind of water (Vollenweider, 1969). There are different ways to express the result such as mg or g C m^3 day^{-1} (if in different layer) or mg or g C m^2 day^{-1} (if the data are integrated to be expressed as production per unit of surface area).

For the oligotrophic lake, Eloranta and Palamaki (1986) recorded 104 mg C m^{-3} day^{-1} at 5000 LX and 20 C and the total phytoplankton primary production during the growing season was 12.5 g C m^{-2}, but Vaquer and El Hafa (1991) and Gulati (1972) reported a range for an oligotrophic lake from 7.8 to 722 mg c m^{-2} d^{-1} . In some Dutch lakes Gulati found about 70% of the production took place in the upper 2m. Mariazzi (1991) in his study of one lake poor in nutrients in Argentina, recorded 13.9 mg C m^{-3} h^{-1} in February at 2.5 m depth. In mesotrophic lakes, Bayne *et al.*, 1983 found that the mean value reached 684 mg C m^{-2} d^{-1} and also found the primary productivity varied greatly both temporally and spatially. Different scientists have studied eutrophic lakes, the annual primary production recorded varies from 170 to 270 g C m^{-2} y^{-1} (Stadelmann *et al.*, 1974, Parparov 1990, Riemann 1983). Lyden and Grahm (1985) recorded 10 g C m^{-2} y^{-1} or 2.0-3.1 t C yr^{-1} for the whole lake. But Pettersson (1990) reported a maximum value of 2200

mg C m^{-2} d^{-1} and the average production for two months during the spring varied from 30 to 64 mg C m^{-3} d^{-1} in an eutrophic lake. Osborne (1991) in his study of one nutrient-enriched lake, using the oxygen method, reported 247- 1,250 mg O_2 m^{-3} h^1 (111-563 mg C m^{-3} h^1) in winter but it increased markedly during spring and the highest recorded value in summer was 6,850 mg O_2 m^{-3} h^{-1} (3,083 mg C m^{-3} h^{-1}). There are many factors affecting the rate of primary production firstly related to temperature and secondly to irradiation (Berger, 1989). The photosynthesistic process may be inhibited by ultra-violet light at the surface (Moss, 1988). Vaquer and El Hafa (1991) found that the vertical profiles indicated a light inhibition of photosynthetic activity at the top of the water column and maximum values always in the upper 2.5-10 m. Lund (1965) pointed out that the photosynthesis is usually insignificant at intensities of light less than 1% of that at the surface.

Phytoplankton as a food source has a determining role in the development of the size of the zooplankton population. However, phytoplankton may also influence the behaviour of zooplankton, e.g. diel vertical migration. In all aquatic ecosystems the role of phytoplankton as a major food source for a larger part of the zooplankton is evident. Peaks in zooplankton numbers commonly occur when primary production is high. The main factors responsible for the timing and growth of the zooplankton population are temperature and food. Dokulil *et al.*, (1990) in a study of Mondsee-Austria found that during summer algal abundance is largely affected by the grazing of zooplankton, but no clear-water phase was observed at the end of the spring peak of phytoplankton. Elser and Goldman (1991) in their study, which was carried out in three lakes of strongly contrasting trophic states to evaluate the effects of zooplankton on phytoplankton, demonstrated that zooplankton-phytoplankton interaction is strongest in lakes of intermediate productivity. Crumpton and Wetzel 1982 observed that losses due to sedimentation and /or grazing are important in many lakes and that interspecific competition may be important in actually

controlling seasonal succession. Sager and Richman (1991) studied the functional interaction of phytoplankton and zooplankton along the trophic gradient in Green Bay of Lake Michigan, the conclusions were:

1- Growth-grazing difference increased with trophic conditions.

2- Eutrophic conditions produced dominance of growth by large size *Cyanobacteria* and low grazing rates by microcrustaceans.

3- Small and occasionally negative growth grazing differences in the meso-oligotrophic region were associated with dominance of larger Cladocerans and Calanoid Copepods and small algal species.

Munawar *et al.* (1991) recorded mean zooplankton biomass which ranged from 173.0 to 1306.0 mg l^{-1} dominated by cladocerans (Bosminids) in an oligotrophic- mesotrophic lake. For a mesotrophic lake Sprules and Munawar (1991) recorded average biomass 663 μg l^{-1} with small bosminid Cladocera being the most abundant organisms. Gulati 1972 recorded between 2 and 44 individuals l^{-1} of *Bosmina* in summer and were the dominant Cladocerean. It is similar to Loch Lomond.

1.3. Previous relevant work on Loch Lomond and other Scottish freshwater lochs

Maulood and Boney (1980) carried out both quantitative and qualitative studies of seasonal succession of phytoplankton in Loch Lomond and described it as diatom-desmid in nature. The bulk of phytoplankton was found in the southern region of the loch. They indicated that the appearance of *Anabaena circinalis* is an indication of the changing trophic status in this region, which may be an indication of the onset of eutrophication.

Maulood *et al.* (1978) studied the diurnal variation of phytoplankton for 48 hours in Loch Lomond. They observed that the maximum abundance was recorded between 4.00 and 6.00 h in surface water and on that occasion the phytoplankton population was dominated by the diatom *Tabellaria fenestrata.* A distinct diurnal variation in cell numbers was also recorded. Moreover, Chlorophyll *a* values showed a regular pattern of variation with a single peak between 10.00 and 14.00 h each day.

Maulood and Boney (1975) through their study of standing crop of the phytoplankton of Loch Lomond, found that the southern basin was the more productive with 900,000 algal units l^{-1} (=cell or colony or filament) in the 1972 spring peak compared with less than 250,000 algal units l^{-1} in the middle region and 150,000 algal units l^{-1} in the north.

In 1981 Bailey-Watts and Duncan reviewed the ecology of Scotland's largest lochs (Lomond, Awe, Ness, Morar and Shiel) in a comparative study. Loch Lomond (north basin) occupied the fourth position (among the other lochs) based on the chlorophyll maxima and yearly means levels of algal biomass. Loch Lomond was also considered one of the two relatively richer waters with 42 phytoplankton species. *Oscillatoria spp* are well represented in Loch Lomond. The period of algal increase correlated with the development of thermal stratification.

Maulood (1974) studied Loch Lomond and five neighbouring lochs north and south of the Highland Boundary Fault. Loch Achray and Loch Ard are thus Highland Lochs and are surrounded by areas of blanket peat bogs, poor hill grazing and forests. Of the two Lowland Lochs, Lake of Menteith is bordered by fertile arable land while Loch Rusky lies a poor peaty district. Loch Achray is situated north of the Highland Boundary Fault at the entrance of the Trossachs and lies in a mountainous area.

Maulood and Boney (1981) carried out a seasonal ecological study carried out on the phytoplankton of the Lake of Menteith which lies to the south of the Highland Boundary Fault (which crosses Loch Lomond from Balmaha in the north-east to Arden in the south-west). All the measured nutrients reached maximum levels during the winter, particularly silicate which showed high concentrations (up to 85 μg at Si l^{-1}). But during the summer period phosphate, nitrate and silicate were almost completely exhausted in the surface waters. The lake was alkaline with pH never <7.0.

Maulood and Boney (1981) presented the results of the first seasonal study of phytoplankton to be carried out in Loch Ard (which lies to the north of the fault). The loch is a typical warm monomictic lake, the water temperature ranged from 18.6 to 4.4 C during the period of study and oxygen saturation from 68 to 112 %. Stratification lasted from May to November. Phosphate was generally very low and almost undetectable. Dissolved silica recorded a regular seasonal pattern range from 9 to 21 μg at Si l^{-1} . Nitrate never showed sign of complete exhaustion (4.0-21.0 μg at N l^{-1}). The loch was described as diatom-desmid in nature.

Information given by Bailey-Watts (1976 a, 1976 b, 1978, 1990) and Bailey-Watts *et al.* (1990) represented a nine-year study of the phytoplankton of shallow, eutrophic and non-stratifying Loch Leven. This study revealed marked seasonal and annual differences in species-composition and population densities. The results showed decreasing concentration of chlorophyll *a* and increasing total dry weight and volume of phytoplankton. Also, increasing the size of dominant algae and decreasing the total numbers of individuals. Moreover, the observed changes can be explained in terms of light regimes and the concentrations of nutrients. Dense populations of planktonic diatom crop were often produced and rates of increase and decrease were high but the relations with dissolved silica did not appear always to be simple.

In 1976 Bindloss discussed the seasonal changes in incident irradiance and underwater light penetration at Loch Leven from 1968 to 1971 in relation to the photosynthetic behaviour and crop density of phytoplankton. The recorded light extinction was highest in the blue and lowest in the orange spectral regions. Euphotic depth varied between 1.2 and 7.4 m. The underwater light extinction depended mainly on phytoplankton crop density (estimated as chlorophyll *a*).

In 1987 (a, b) Bailey-Watts reviewed the phytoplankton succession and ecology of small, not continuous stratifying eutrophic Coldingham Loch. The loch exhibited spring and autumn maxima of about 35 μg l^{-1} chlorophyll *a*. The data showed that nitrogen in summer, phosphorus in spring and silica at various times of the year limited the growth. The loch stratifies intermittently in summer. Generally, oxygen concentrations fluctuations were correlated with mixing and stratification and the bottom recorded low value of 10 % of saturation.

1.4. Description of Loch Lomond and sampling sites

Loch Lomond lies about 30 km north east of Glasgow at a latitude of 56º N. The Loch has a surface area of approximately 70.97 km^2. The Loch has three basins, north, mid and south. The north basin is a typical highland loch: deep, narrow, steep sided and extending along a north south axis for 20.9 km with a mean width of 1 km and a maximum depth of 183m (table 1) (Murray and Pullar, 1910).

The surrounding land is typically nutrient-poor with rock types igneous and metamorphic which is mainly mica-schist, schistose grits and quartzite resulting in a fairly nutrient poor runoff. The surrounding land use is mainly softwood forest with little (sheep) farming. The south basin in contrast is wide and shallow with numerous islands. The maximum

width recorded for this basin is about 8 km. The geology of the south basin is sedimentary and extrusive igneous rocks. The rock is mainly sandstone which is relatively rich in nutrients. The surrounding landuse is mainly pastoral grazing and forestry with some arable land. The middle basin lying 1 km north-east of Luss. The hills in this region rise more gently and the loch is much broader. The mid basin is intermediate in all particulars (Maulood and Boney, 1980).

Table (1) Morphometric data for Loch Lomond

Length (km)	36.44
Mean breadth (km)	1.95
Maximum breadth (km)	7.77
Water surface area (km^2)	71.10
Mean depth (m)	37.0
Maximum depth (m)	189.9
Volume $m^3 \times 10^9$	2.628
Elevation (altitude) (m)	7.92
Shoreline length (km) including islands	153.48
Shoreline length (km) excluding islands	102.69
Area of islands (ha)	466.8
Distance from the sea (km)	30
Catchment area (km^2)	750

There is a unique geological structure characterising the Loch: the Highland Boundary Fault, which divides the Highlands from the central Lowlands of Scotland, cuts across the loch about 8 km from the south end running through a string of islands from NE to SW.

Loch Lomond is a particularly suitable subject for study because of the range of trophic status within the three basins.

The field work was started in January 1992. Samples were taken monthly during the winter (January, February) when conditions where stable and plankton production low, but the sampling was increased to every fortnight in March to follow the rapid physical and chemical changes in spring. This increased sampling frequency was started earlier than planned (April, May) due to the mild winter in 1991-1992. The samples were taken from two stations, one in the north (NN 344 011)and one in the south basin (NS 382 896) (Figure 1).

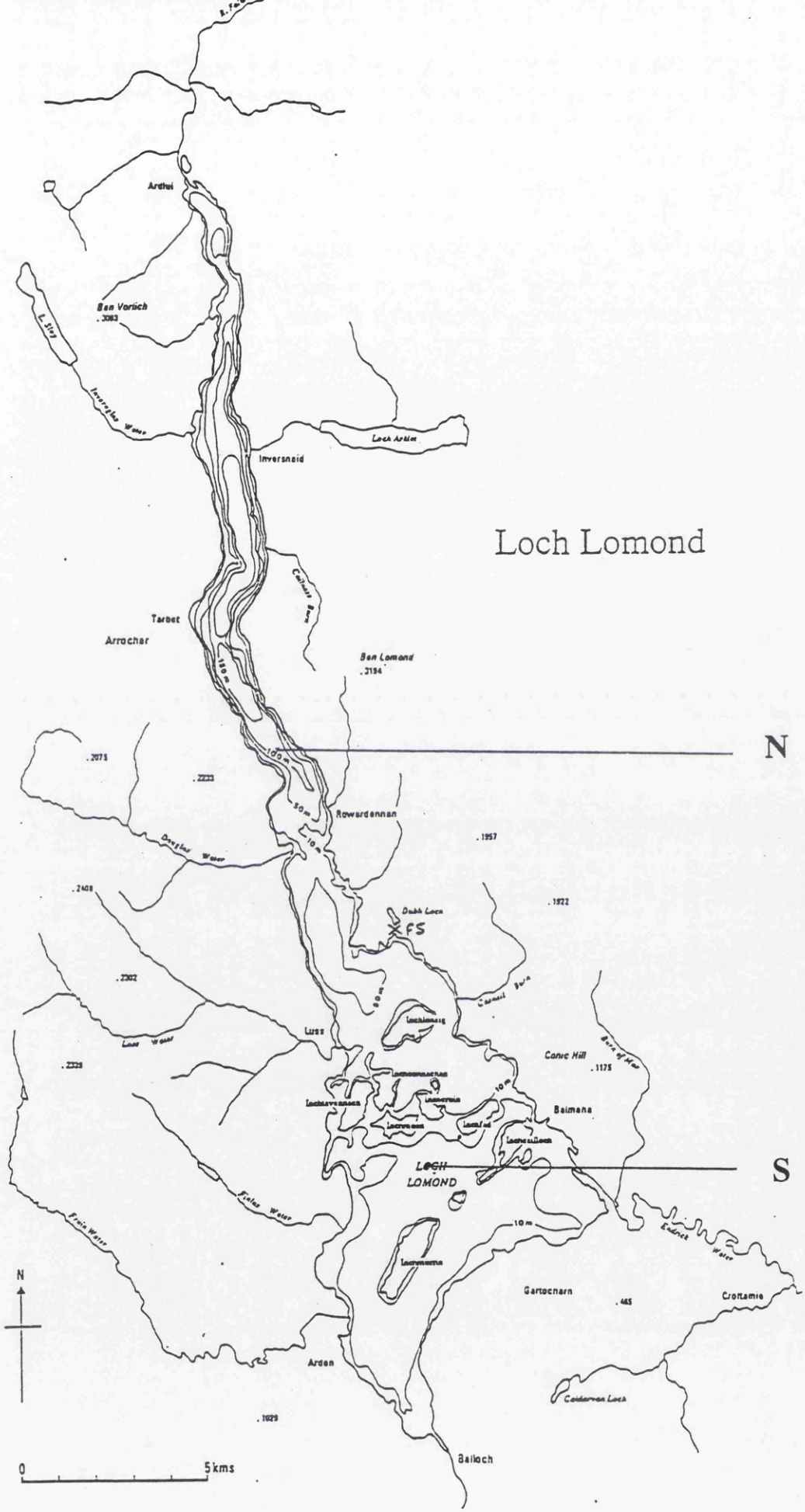


Figure 1. Location of Loch Lomond and position of sampling sites

(N= north basin, S= south basin)

2. Phytoplankton ecology of Loch Lomond:

2.1. Physicochemical environment

2.1.1. Introduction

The major source of energy in most freshwater enters as solar radiation. The total amount of radiation reaching the surface of a water depends on time of year, geography, altitude, state of the atmosphere and several other (usually local) factors.

Light falling on water undergoes changes which depend on both the angle at which it meets the surface and the nature of the water itself. Some of the light reaching the surface will be reflected and the rest transmitted. The amount reflected depends on the angle of incidence and increases as it moves from the perpendicular. Thus, both diurnally and annually, the amount of energy reflected from the surface of lakes varies greatly according to the height of the sun. The radiant energy passing through the water column is further altered: part is absorbed by the water, by its suspended materials and solutes, and transformed to heat, and part is dispersed. Quite apart from the effects of impurities, such as suspended and dissolved materials which may affect transparency, there are variations in the transmissions of different wavelengths of light (Maitland, 1990).

Temperature is one of the most important factors in an aquatic environment. In fact it is possible that no other single factor has so many profound influences and so many direct and indirect effects (Welch, 1952). The effects of an increase in temperature on the density of water are of significance biologically. Density changes much more rapidly at higher temperature than lower; thus a 1C change in temperature at 24C decreases the density many times more than the same change at 4C. This is important for buoyancy, as planktonic organisms, for instance, will tend to sink more rapidly at higher temperatures than lower ones. This factor is also relevant to the development of stratification.The

density of water at constant temperature varies with pressure, and increases slowly in a linear fashion with depth (Maitland, 1990).

Several factors influence the nature and extent of water movements. Because of the importance of winds in producing movements in standing waters and gradients in causing currents in running waters, local topography is of considerable significance. The nature of the basin is also important. The wind can produce currents in two ways: (a) by driving action at the surface and (b) by driving surface water towards one end of the lake, thus inducing sub-surface currents in the opposite direction (Maitland, 1990).

Oxygen and carbon dioxide are of major importance in aquatic systems, and where variations in concentrations occur they normally show an inverse relationship. The respiration processes of plankton and the oxidation processes of breakdown lower the amount of oxygen and increase the carbon dioxide. With sufficient light, the process of photosynthesis by phytoplankton produces the opposite effect- an increase in the amount of oxygen and decrease in carbon dioxide. Temperature is also closely associated with the consumption of oxygen since respiration and other metabolic processes are temperature dependent (Maitland, 1990).

The hydrogen-ion concentration of water is one of those environmental factors that is very strikingly linked to the species composition of communities and their life processes. Because of its effect on pH, the bicarbonate content is (quit apart from its value as the source of the most important nutrient) of prime importance in many problems in limnology. The pH is determined by the relation between CO_2 and carbonate, or more precisely the H^+ ions arising from the dissociation of H_2CO_3 and the OH^- ions arising from the hydrolysis of the bicarbonate (Ruttner, 1963).

As a component of nucleic acids and of adenosine triphosphate (the basis of enzyme synthesis and intracellular energy transfer systems), phosphorus is essential to the function and growth of all plants (Reynolds, 1984). One expects phosphorus, more than any other major biological element, to be of most importance to the ecologist, since it is the one most likely to be deficient in the environment, and therefore to limit the biological productivity. There are different forms of phosphorus: soluble, sestonic and acid-soluble phosphate, organic soluble and sestonic phosphorus. Orthophosphate is considered the most important form in limnology (Hutchinson, 1957). In general, amounts, are low, firstly because the element is naturally scarce, and secondly because of the capacity of many plants to absorb and store many times their immediate needs of it (Maitland, 1990). The total quantity depends largely on geochemical considerations, usually being greater in waters derived from sedimentary rock in lowland regions than in waters draining the crystalline rocks of mountain ranges. The soluble phosphate usually is found in a small fraction, of the order of 10 per cent of the total (Hutchinson, 1957).

Although all phytoplankton have a requirement for the small amounts of silicon involved in protein and carbohydrate synthesis, it is among the chrysophyte genera (and among the diatoms in particular), which obligately strengthen their cell walls with amorphous silica polymers, that the requirement becomes ecologically important (Reynolds, 1984). The most obvious source of silica is the solution of rocks in the drainage basin under the influence of CO_2. Though much silica must be brought into lakes by influents, there is evidence from quantitative studies of the silica in the entire water mass of certain lakes that silica must enter the water from the lakes sediments. There is some indication that this occurs most easily from epilimnetic mud at high temperature. The silica concentration is usually increased in summer stratification in the anaerobic deep water of lakes having clinograde oxygen curves. The development of diatom blooms constitutes the most

important mechanism by which silica is removed from lake waters. The frustules of dying diatoms appear to lose silica to the water (Hutchinson, 1957).

The principal requirement of 'algae' for nitrogen in the synthesis of amino-acids and proteins, where in it constitutes about one-eighth to one-sixth by weight; the minimum nitrogen content of cells is about three to four percent of dry weight (Reynolds, 1984). Nitrogen is an important component of the cells of living organisms and the amounts available in a water, though often small, are of significance to the ecosystem (Maitland, 1990). Unlike the other minor elements or compounds, nitrogen occurs in molecules at several different oxidation states in lake water. The following forms are quantitatively of importance: N_2, NH_3, NO_2, NO_3 and organic N either in dissolved state or as particulate nitrogen. The concentration of all nitrogen compounds vary considerably in different waters, the range being between hardly detectable traces and several mgl^{-1}. Nitrogen enters water from very different sources. The nitrogen content of igneous rocks is only 46 p.p.m., although that of certain sedimentary rocks may be ten times higher. Larger quantities come from erosion of both natural and artificially fertilised soils (Golterman, 1975). In the majority of natural aerobic waters, most nitrogen occurs as nitrate (Maitland, 1990).

Conductivity is a numerical expression of the ability of a water sample to carry an electric current. This number depends on the total concentration of the ionised substances dissolved in the water and the temperature at which the measurement is made. The mobility of each of the various dissolved ions and their actual and relative concentrations affect conductivity (Anon., 1976).

The alkalinity of a water is its quantitative capacity to neutralise a strong acid to a designated pH. The measured value may vary significantly with the end point pH used in

the determination. Alkalinity is a measure of a gross property of water and can be interpreted in terms of specific substances only when the chemical composition of the sample is known. The alkalinity of many surface waters is primarily a function of carbonate, bicarbonate, and hydroxide content, the alkalinity is taken as an indicator of the concentration of these constituents (Anon., 1976).

The chemical oxygen demand (COD) determination is a measure of the oxygen equivalent of that portion of the organic matter in a sample that is susceptible to oxidation by a strong chemical oxidant (Anon., 1976). Thus it is a measure of total organic matter, including that which is not susceptible to biological oxidation. In natural waters many of the constituents are pigmented (brown) dissolved matter and so influence the absorption of light in the water column.

2.1.2. Field methods

Sampling was started from the catamaran "Fiona" but subsequently a Sea Rider inflatable was used.

Water samples were collected using a 0 to 5m integrating water-column hose-pipe sampler (long tube sampler) made of polythene weighted at one end (Kindly provided by Dr. C. S. Reynolds of the Freshwater Biological Associations) (Lund, 1949; Heany, 1976; Eloranta and Palamaki, 1986; Abdul-Hussein and Mason, 1988; Munawar and Munawar, 1988; Lund and Talling, 1957; Munawar and Munawar, 1978; Talling, 1971; Reynolds and Reynolds, 1985; Munawar *et al.*, 1987). The 2 l sample was collected in a clean bucket and divided into 1l plastic bottles. In total 12 l water was collected at each site.

2.1.2.1. Secchi depth

Secchi depths were measured using a 20 cm diameter disc with alternating black and white quadrants. The disc was lowered into the water on a graduated rope, the depth at which it disappeared was noted, it was lifted and the depth at which it reappeared was noted. The average of these two readings on the graduated rope was recorded as a measure of visibility (Welch, 1952).

2.1.2.2. Light

The attenuation of light irradiance (as Photosynthetically Active Radiation: PAR) in the water column was measured with a PAR light meter (LICOR) simultaneously with sampling except in July, August, October and December due to a fault in the LICOR meter.

2.1.2.3. Water temperature and dissolved oxygen

Water temperature and dissolved oxygen (percentage saturation) were measured using a Mackereth Mark II temperature/oxygen probe manufactured by pHOX. Readings were recorded at 1m intervals throughout the water column until 25m and then in the case of the deeper north basin the intervals were increased to 5m to a depth of 65m. From September 1992 onwards the top 6 m only were examined due to a fault in the long cable.

2.1.3. Laboratory methods

Immediately on arrival in the laboratory:

2.1.3.1. pH:

The pH of an unfiltered sample was measured using a Jenway pH meter and / or a Whatman pH A400.

2.1.3.2. Conductivity:

This refers to the ability of a solution to conduct an electric current. Since electricity is carried in a solution by migration of ions, the conductivity under standard conditions bears a relationship to the total ionic concentration. This was measured using a Jenway conductivity meter.

2.1.3.3. Filtration method for chemical analysis

Water sample were filtered through a "Millipore" filter apparatus with Whatman GF/C glass fibre filter paper. The filtrate was used for the following chemical analysis. Details of the methods used are presented in Appendix 1

2.1.3.4. Soluble reactive phosphorus (ortho-phosphate)

In a suitably acidified solution, phosphate reacts with molybdate to form molybdo-phosphoric acid, which is then reduced to the intensely coloured molybdenum blue

complex. The concentration of phosphate is related to the absorbance of this complex which is determined spectrophotometrically at 690 nm. Increased sensitivity can be obtained by extracting the blue complex into an organic solvent (Hexanol) (Mackereth *et al.*, 1978).

2.1.3.5. Soluble reactive silicon (Dissolved silica=silicate)

In acid solution silicic acid (silicate) and some derivatives react with molybdate to form yellow heteropoly (molybdosilicic acids, which are then reduced to intensely coloured silicomolybdenum blue). The resulting absorbance was measured spectrophotometrically at 810 nm (Mullin and Riley, 1955).

2.1.3.6. Nitrate

Two methods were applied:

1. Phenoldisulphonic acid (PDSM) method

This method requires that the sample must be dried completely. The residue was allowed to react with phenoldisulphonic acid (PDSA). After the addition of magnesium sulphate, the addition of sodium hydroxide resulted in an alkaline solution and precipitated magnesium hydroxide. A definite yellow colour appeared. This yellow colour is measured in the spectrophotometer at 410 nm (Mackereth, 1963).

This first method was used at the beginning before the cadmium-copper columns for the second method were available.

PDSA refers to the first method on the graph.

2- Cadmium column method

2-In the second method nitrate was quantitatively reduced to nitrite by passing the sample through a cadmium-copper column in alkaline buffered solution, and estimated as nitrite. This nitrite reacted with sulphanilamide in a strongly acid medium to form a diazonium compound which reacted with N-(1-naphthyl) ethylene diamine dihydrochloride to form a pink /red azo dye. The intensity of this colour is determined spectrophotometrically at 530 nm (Wood *et al.*, 1967) and was proportional to the amount of nitrite present.

2.1.3.7. Chemical oxygen demand (COD)

This measures the organic matter in the sample which is susceptible to chemical oxidation. In this method potassium permanganate was used as the oxidation agent and estimated by iodine-thiosulphate titration (Mackereth, 1963).

2.1.3.8. Alkalinity

Alkalinity is the concentration of weak acid salt, largely bicarbonate, in natural water. The hydrolysis in solution of the bicarbonate ion results in the production of hydroxyl ions.
By titrating the sample with standard acid (thereby removing the hydroxyl ions) using BDH 4.5 indicator, the concentration of bicarbonate in solution can be determined (Mackereth *et al.*, 1978).

2.1.4. Results

2.1.4.1. Light (PAR) extinction

Figure 2 shows the attenuation coefficient at 1m depth of the north and south basin calculated according to Moss (1988).

Highest values were recorded during winter and summer in 1992 and winter and spring 1993 in the south basin, ranging from 0.71 to 0.88. This means that at these times about 70 to 90 % of the light was absorbed at the first metre. During winter phytoplankton did not record a bloom so it must be due to other factors such as increased non-living suspended matter from the inflow of Endrick and re-suspended matter from the sediment of the shallow basin.

The north basin recorded generally lower values compared with the south basin, fluctuating from 0.23 to 0.64 in late February and at the end of June 1992. No general trend was observed.

2.1.4.2. Secchi depth

Secchi disc depth ranged from 2.5 m in early September 1992 to 5.0 m at the beginning of June 1992 in the south basin (Figure 3). Low values were recorded during winter and early spring which were more likely to be non living suspended matter from the inflow of the Endrik water, and re-suspended matter from the sediment in the shallow south basin. It then increased during summer followed by a slight fluctuation in autumn and winter.

The north basin exhibited more or less the same seasonal variations with higher values than the south basin. Secchi disc depth ranged from 4.5 to 6.7 m in early October 1992 and early November 1992 respectively in the north basin.

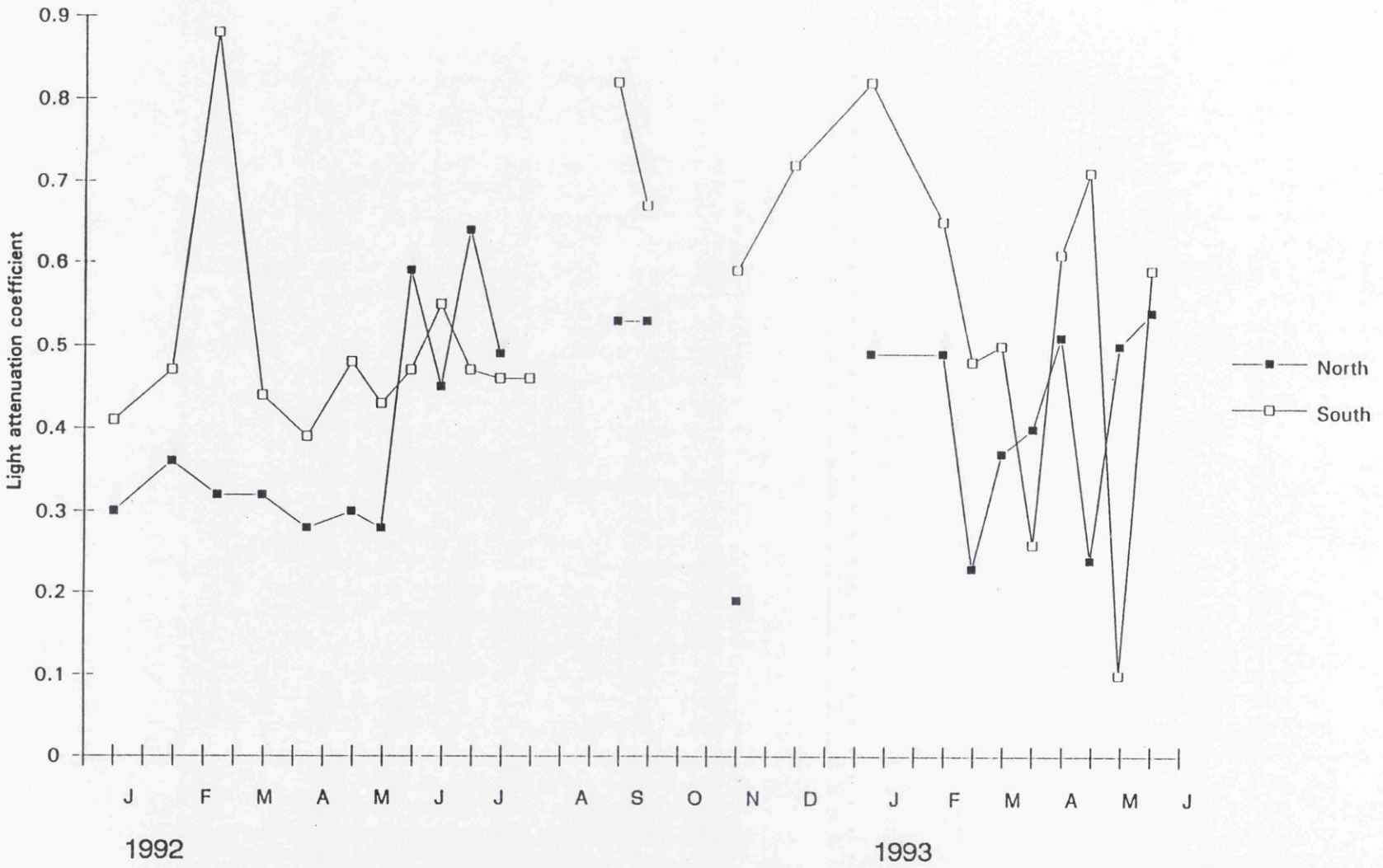


Figure 2. Seasonal variation of light attenuation coefficient for the north and south basin

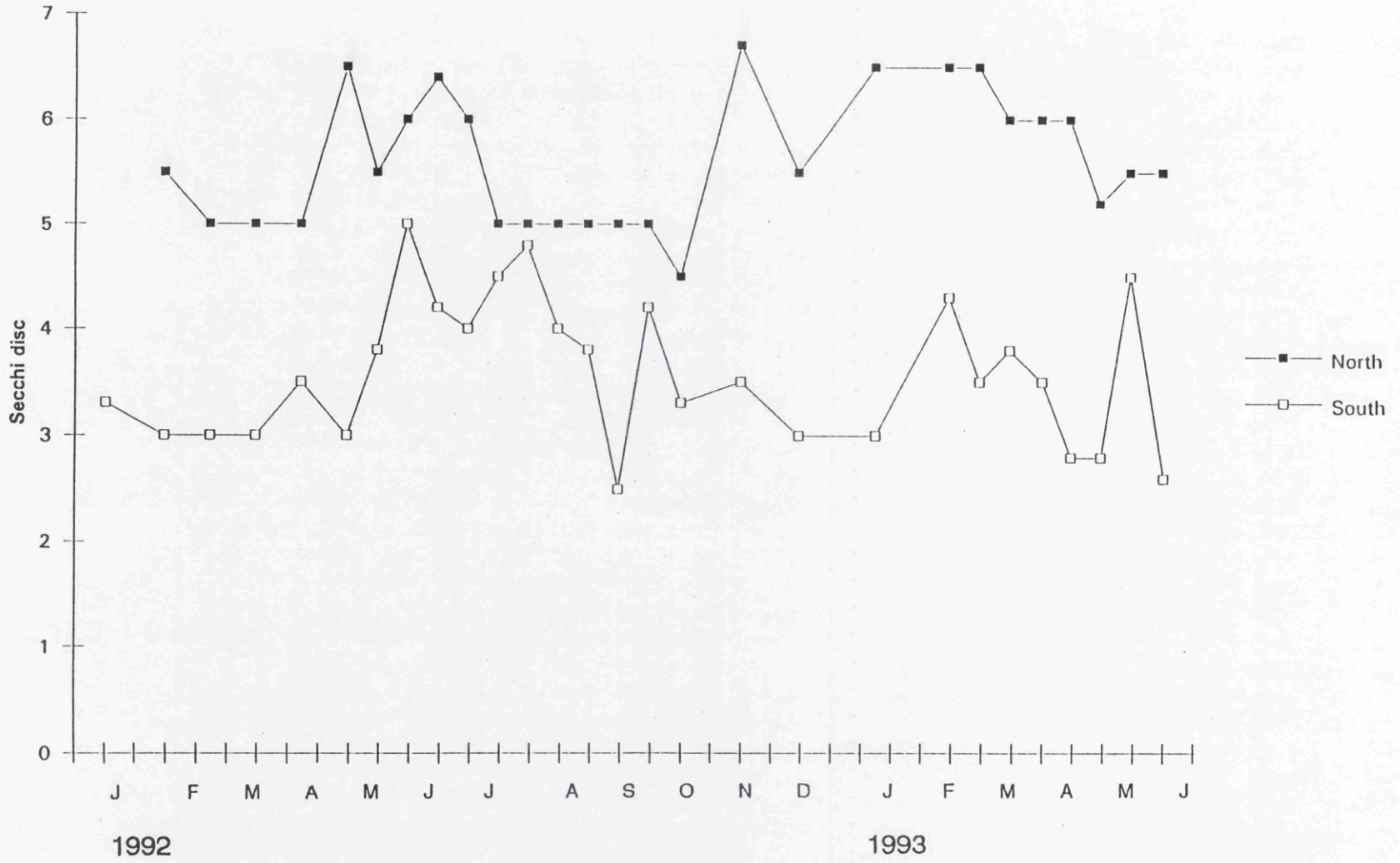


Figure 3. Seasonal variation of Secchi disc readings (transparency) for the north and south basin

2.1.4.3. Water temperature

The surface (mean 0-5m) water temperature in the north basin was higher than in the south basin from January until the beginning of March 1992 and 1993, and warmer in the south from early May until late September 1992 and from beginning of April to May 1993 (Figure 4). From January to early May both basins showed homogeneous water temperature through the whole water column ranging from 5.0 to 8.0 C in 1992 and 4.5 to 9.0 in 1993 (Figures 5 and 6). From the middle of May to the end of June the water temperature increased rapidly from 11.0 to 15.5 C and from 12.0 to 17.0 in the north and south basin respectively.

In the south basin, isothermal conditions were observed throughout the whole sampling programme (January 1992-May 1993), except for 6 weeks from mid June and July 1992 when a temporary thermal stratification was recorded during a period of anticyclonic weather. From August 1992 to May 1993 isothermal conditions were recorded once again with decreasing trend from 14.0 C to reach a minimum of 4.5 in February 1993. From then onwards the temperature started to increase, recording 9.0 C in late May 1993.

In the north basin, isothermal conditions were observed from January to early May 1992, ranging from 6.0 to 7.0 C. From early June to late September 1992 (16 weeks) a structural thermocline was formed. Greatest temperature differential in the water column was 9.5 C (16-6.5 C). From October 1992 to May 1993 temperature was homogeneous through the whole water column cooling from 9.0 to 5.0 C. The heating pattern was as expected because the south basin is characterised by a large surface area to volume ratio, and is less sheltered by the low surrounding mountains and so exposed to more wind. Thus it reaches equilibrium with the atmosphere more rapidly than the north basin.

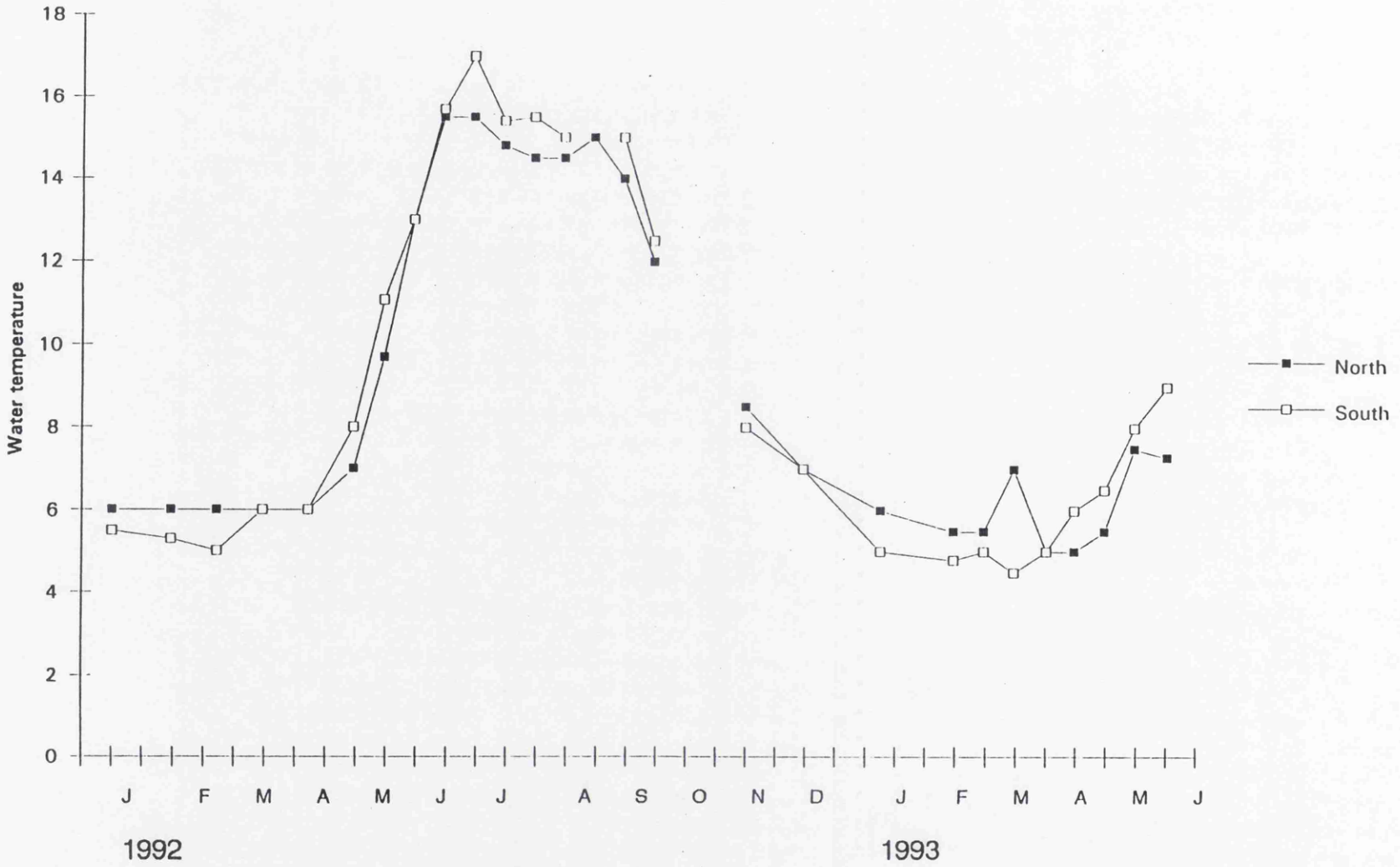


Figure 4. Seasonal variation of mean (0 - 5m) water temperature for the north and south basin

Figure (5) Isopleths of water temperature (C) in the north basin

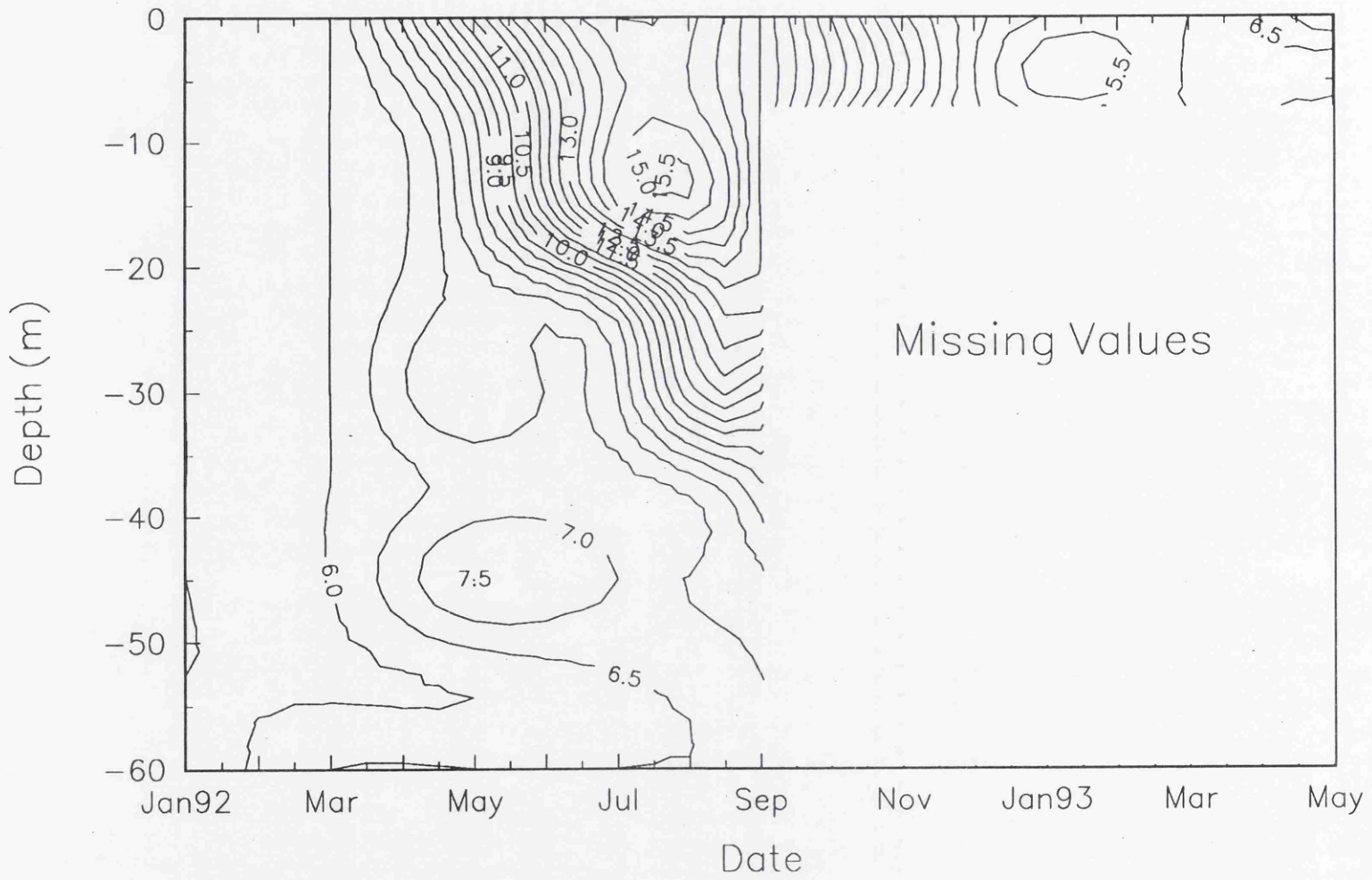
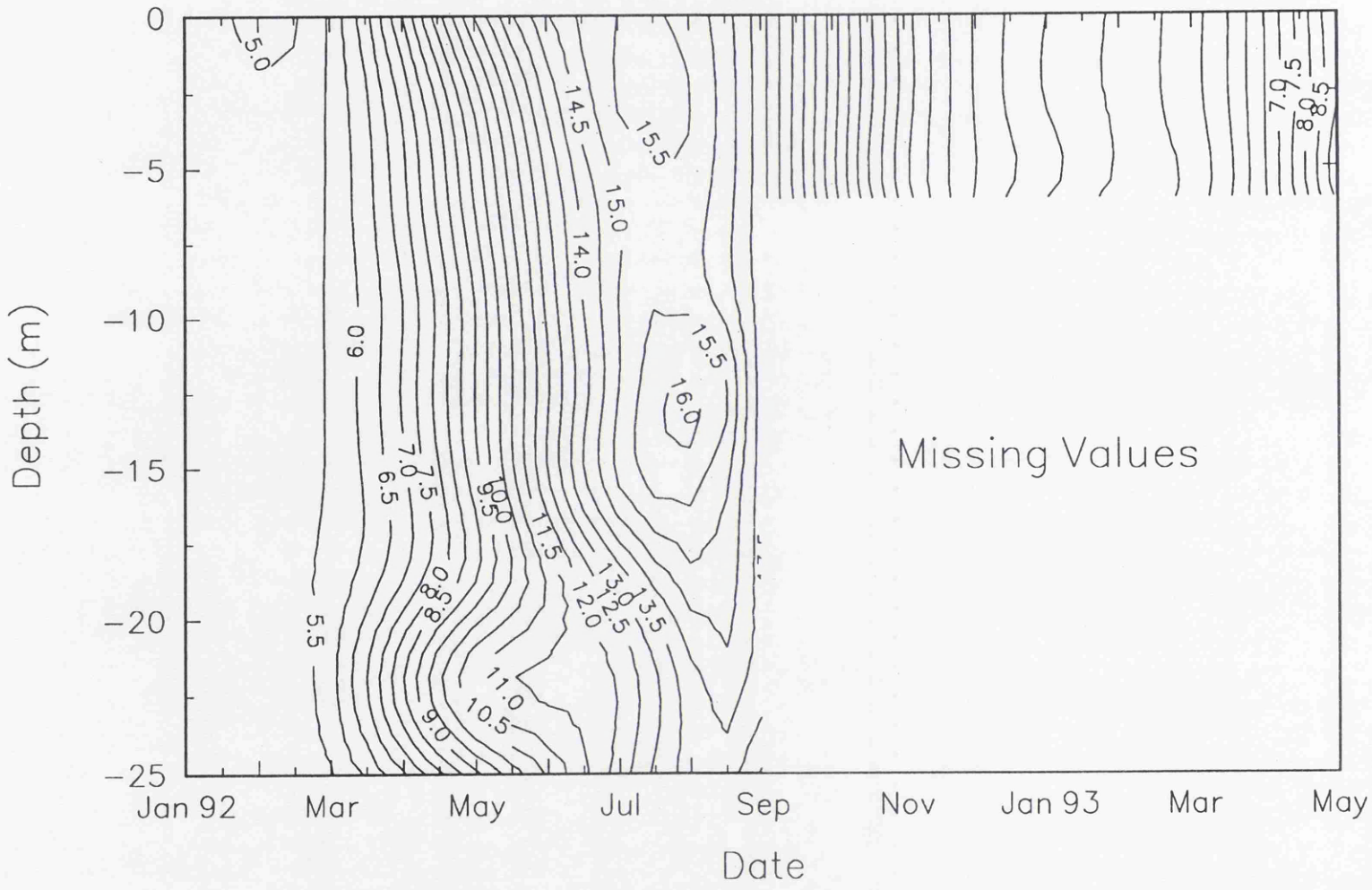


Figure (6) Isopleths of water temperature (C) in the south basin



2.1.4.4. Dissolved oxygen

The surface(mean 0-5 m) dissolved oxygen expressed as a percentage of saturation in the north and south basin are shown in figure 7. Oxygen percentage of saturation ranged from 70 to 100% throughout the water column during the isothermal period from January to March 1992 in both basins. From April 1992, it declined sharply until June 1992. The minimum value recorded during that period was 46 and 40% in the north at 60 m depth and in the south basin at 22 m depth respectively. Oxygen percentage of saturation increased gradually once more from the end of June to reach over 100% during November and December 1992 in the top 6m. The maximum level was 118% in the north and the south basin in early March 1993 and November 1992 respectively. Figures 8 and 9 show the isopleth of oxygen percentage saturation in the water column in the north and south basin. Dissolved oxygen closely paralleled thermal conditions although thermal stratification preceded oxygen stratification by several weeks.

2.1.4.5. pH

The pH of the south basin ranged between 5.85 and 7.65 over the sampling period (Figure 10) with a mean of 6.87. The minimum value was recorded in February 1992 and the maximum in July 1992. In the north basin, pH ranged from 5.7 to 7.41 with a mean of 6.63, slightly lower than in the south basin. The minimum and maximum values were also recorded in February and July 1992 respectively.

The seasonal pattern showed a gradual increase in pH from mid February 1992 to reach a peak in late July 1992 in both basins. A second peak was recorded in late February 1993.

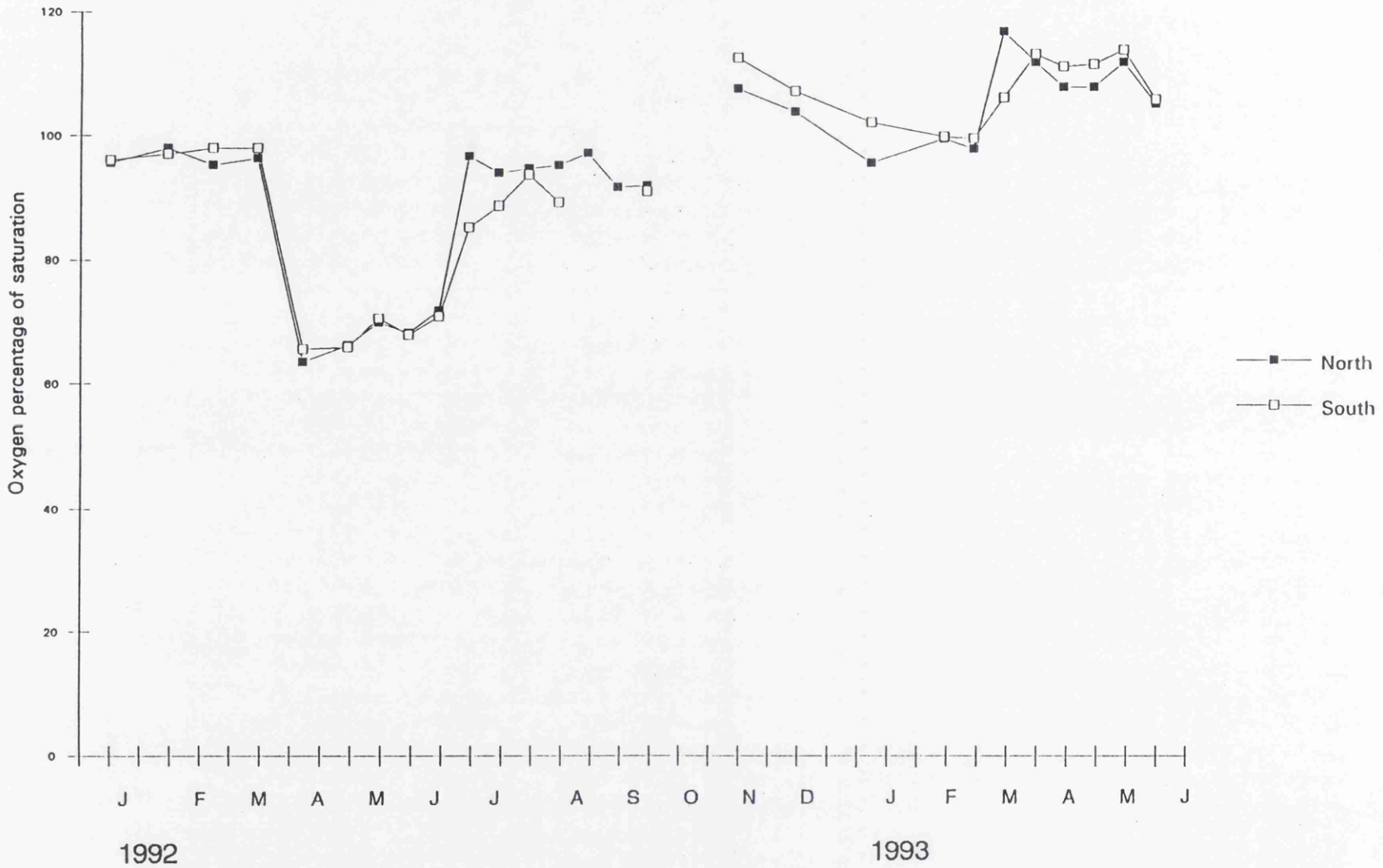


Figure 7. Seasonal variation of mean (0 -5m) dissolved oxygen (percentage saturation) for the north and south basins

Figure (8) Isopleths of dissolved oxygen (percentage saturation) in the north basin

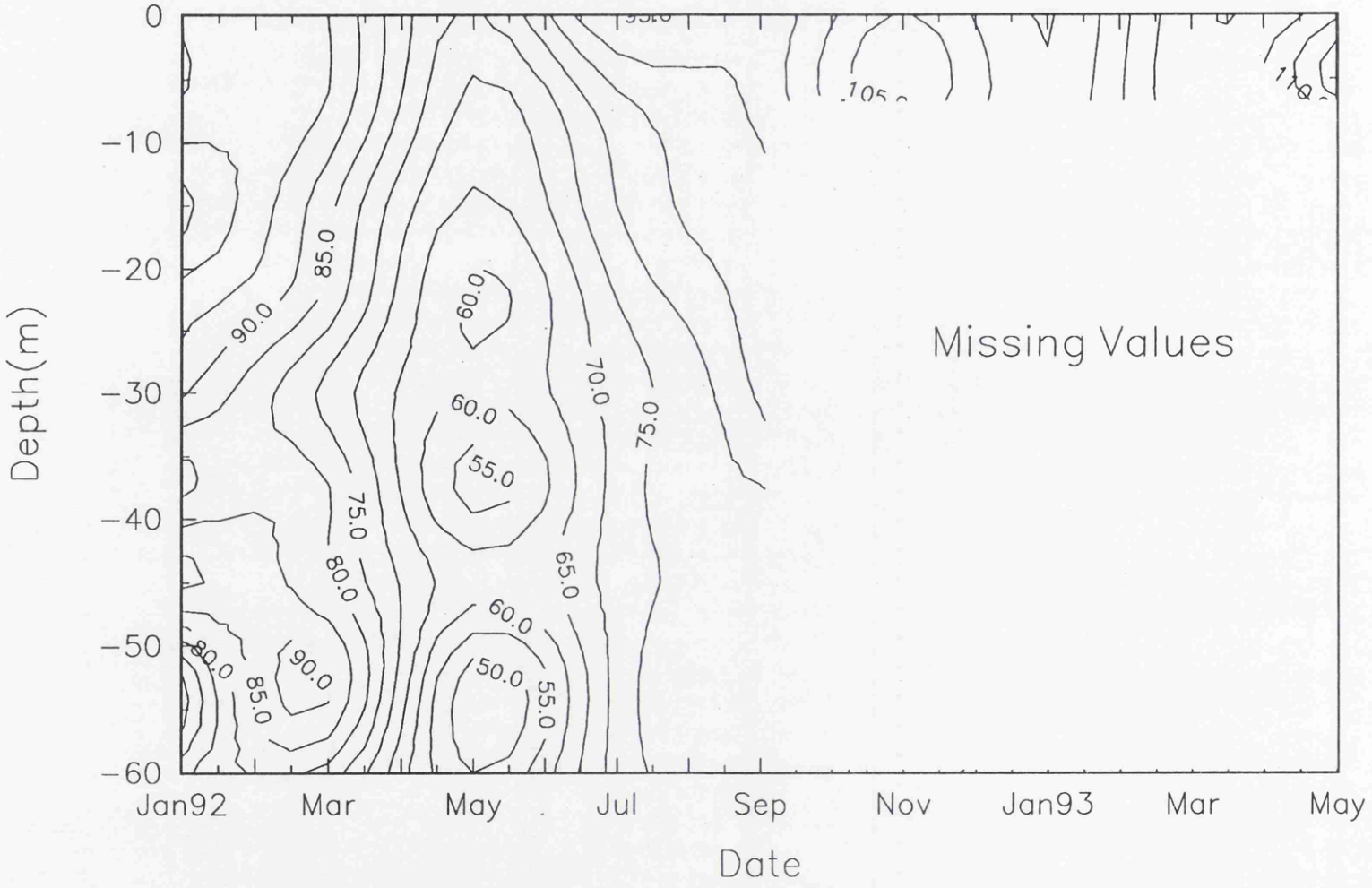
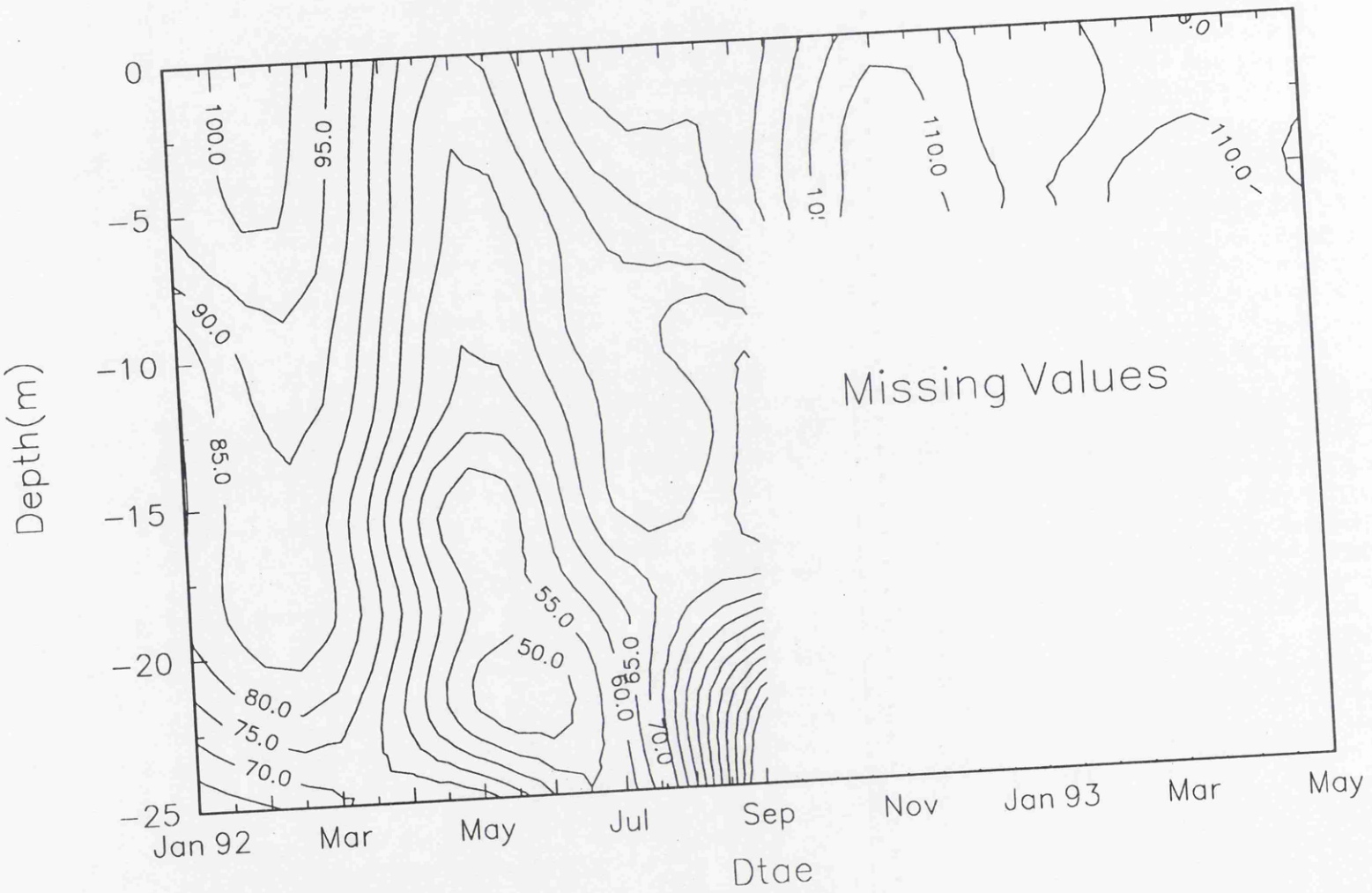


Figure (9) Isopleths of dissolved oxygen (percentage saturation) in the south basin



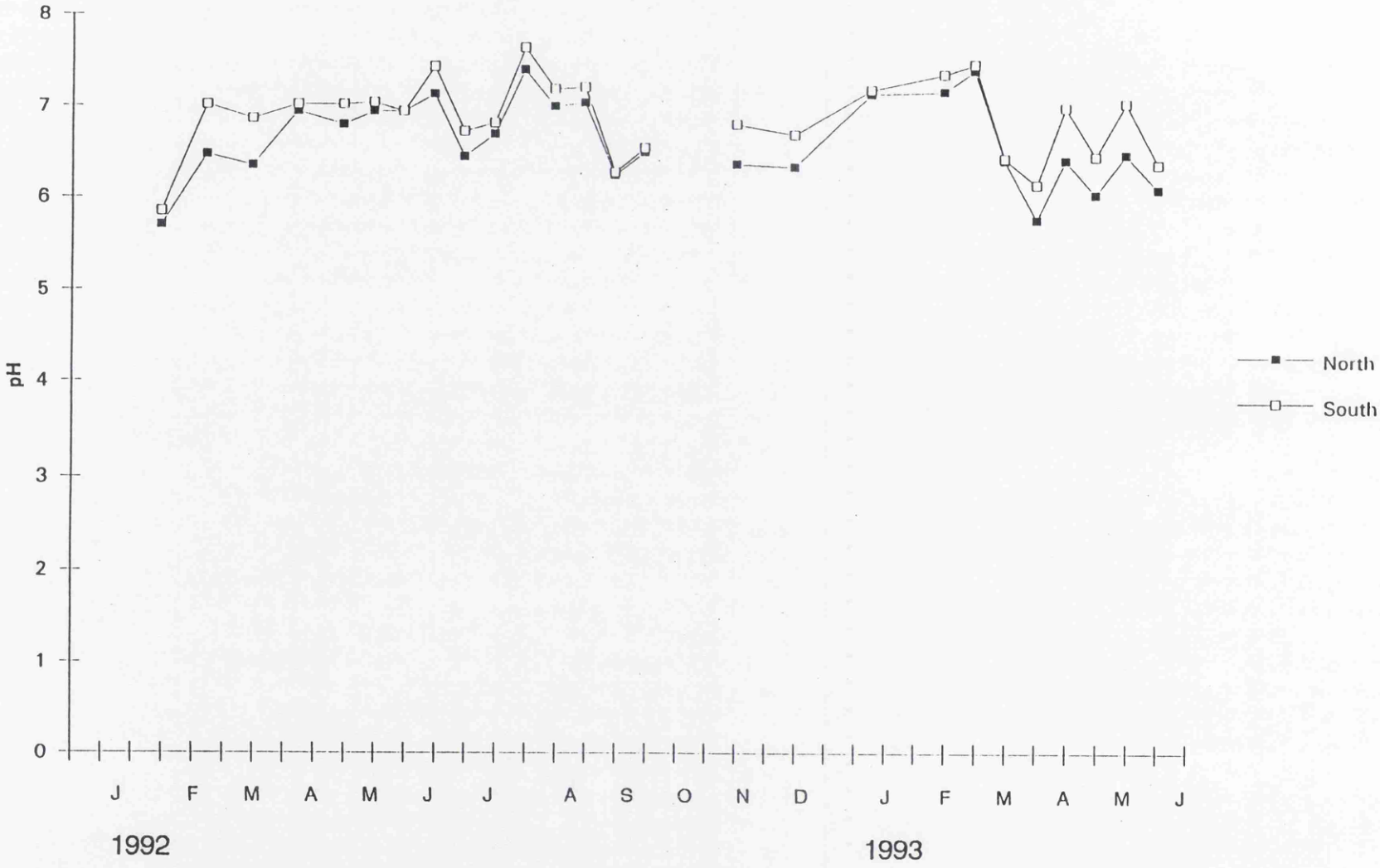


Figure 10. Seasonal variation of pH (Hydrogen ion concentration) for the north and south basin

2.1.4.6. Conductivity

Conductivity is much influenced by geology, edaphic factors (soil), land use and meteorology in the catchment. The major contributors to conductivity (Cl, Na, K, SO_4 etc.) are normally not much influenced by biological activity.

In the south basin, conductivity fluctuated from 6.64 m s m^{-1} as a maximum value in early April 1993 to 5.5 m s m^{-1} as a minimum value in early March 1992 (Figure 11). The north basin recorded lower values than the south basin. It ranged from 4.05 m s m^{-1} in early November 1992 to 5.93 m s m^{-1} in early January 1993.

In general, there was no great variation in the south basin through the whole sampling period with a mean value of 6.16 m s m^{-1}. The north basin, experienced a single peak recorded in early January 1993 with a mean value of 4.62 m s m^{-1}, about 75% of the south basin mean.

2.1.4.7. Alkalinity

On solution, a small part of the CO_2 reacts with water to produce H_2CO_3, which is strongly dissociated to produce hydrogen ions, bicarbonate ions as HCO_3^-, and CO_3^{--}. At pH 7.0, 20.8 % of the CO_2 in a dilute solution is present either as such or as H_2CO_2, 79.2 % as HCO_3.

On all occasions alkalinity was higher in the south basin than the north with the south basin values almost twice as high as those in the north basin, an annual mean basis being 0.192 and 0.108 mmol l^{-1} in the south basin respectively. Both basins showed similar trends of increasing and decreasing. They recorded the maximum and minimum on the same occasions.

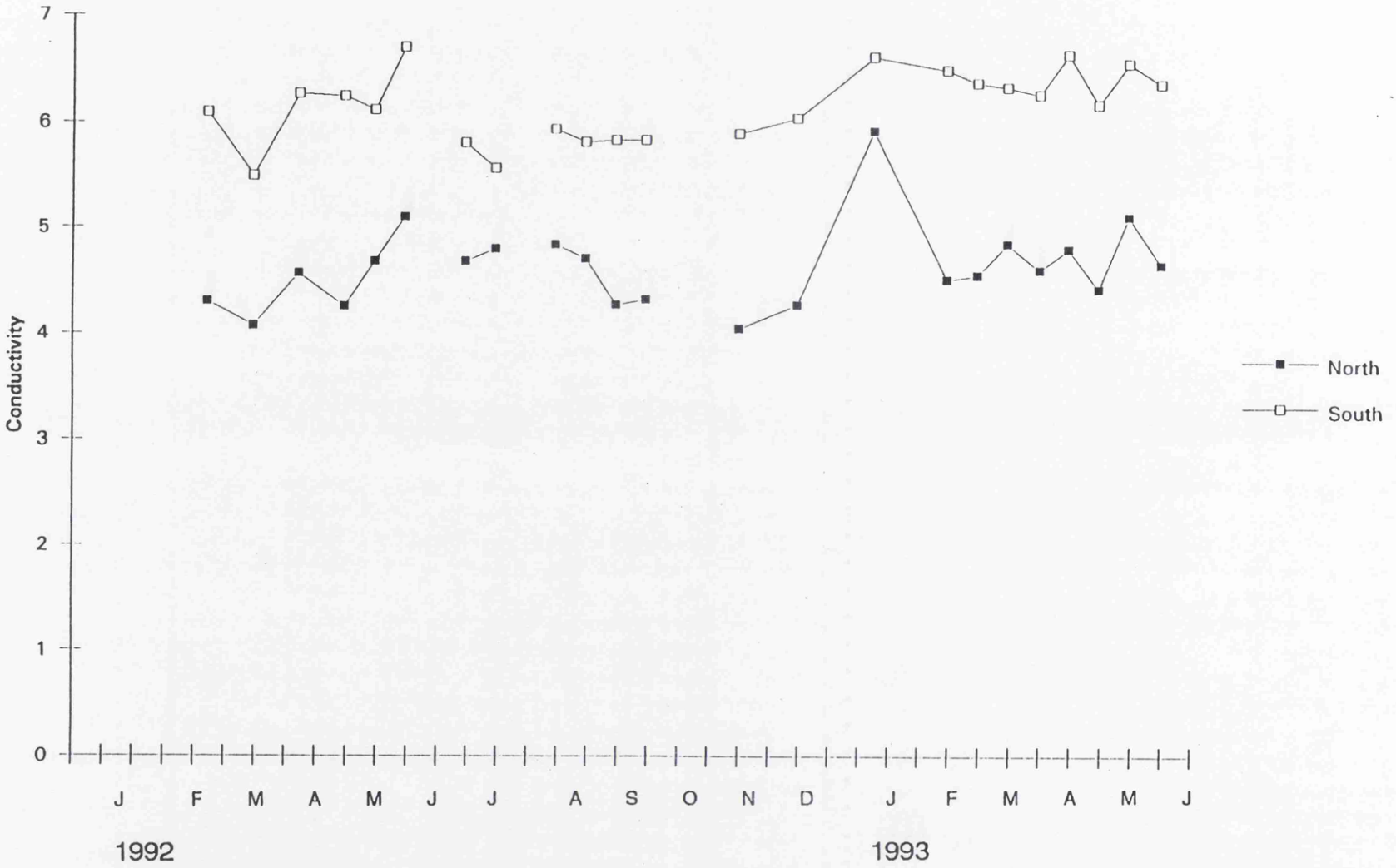


Figure 11. Seasonal variation in conductivity (m S m^{-1}) for the north and south basin

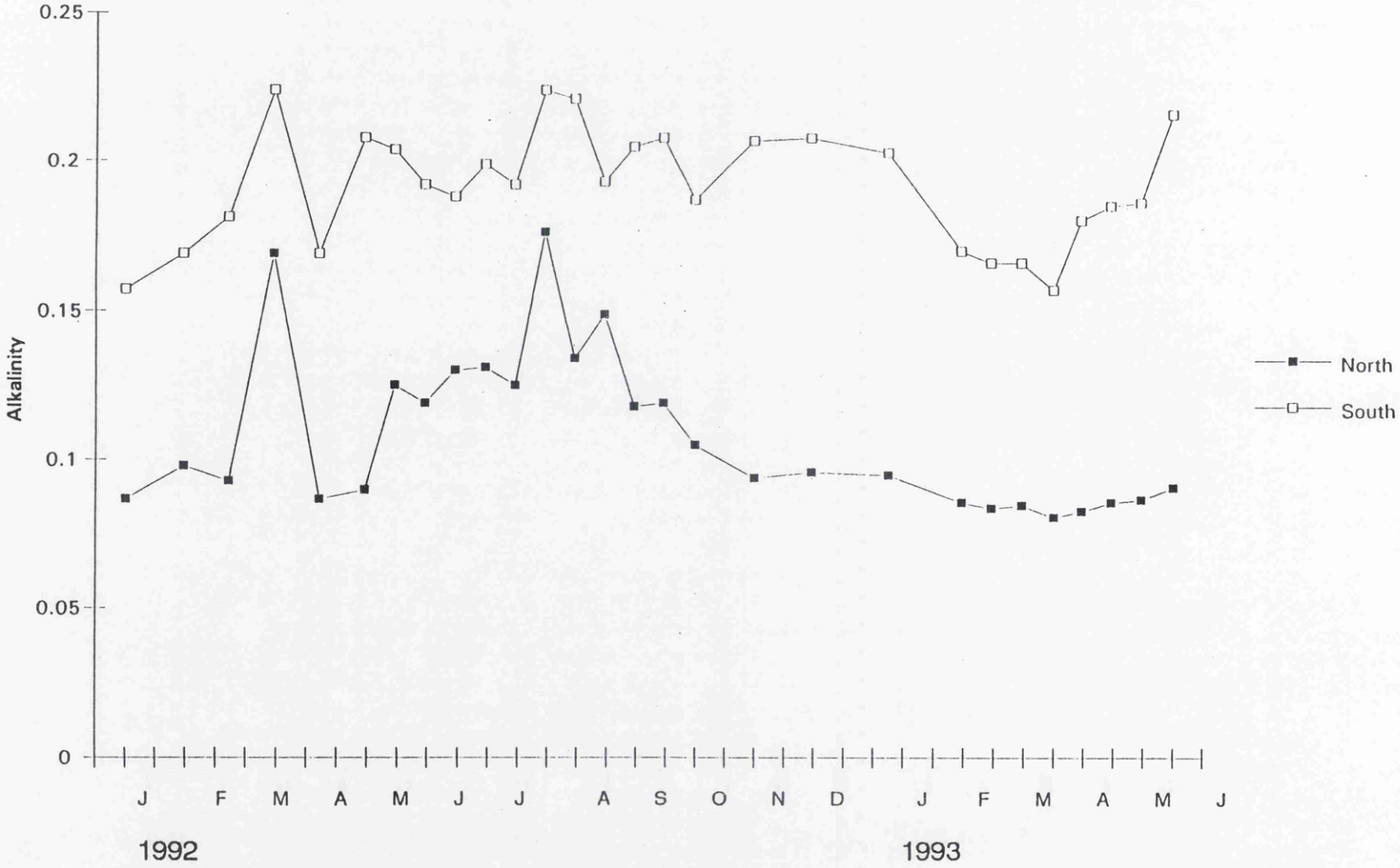


Figure 12. Seasonal variation of alkalinity (m mol^{-1}) for the north and south basin

The seasonal variation in alkalinity in the north basin showed a decreasing trend from the middle of August 1992 towards the end of the sampling period. The south basin showed nearly the same pattern of decrease except it started to increase once again from late March 1993 onward.

In the south basin two peaks were recorded one in late winter (March 1992) and the other in summer (July 1992). These values were 0.224 mmol l^{-1} for both (Figure 12). The same minimum value was recorded in mid January 1992 and late March 1993. It was 0.157 mmol l^{-1}.

The north basin also showed a similar pattern of seasonal variation to the south basin, but with lower values. These values were 0.169 and 0.176 mmol l^{-1} in late March 1992 and at the end of July 1992 respectively. The minimum value was 0.108 mmol l^{-1} in late March 1993.

2.1.4.8. Phosphate

The main source of phosphate for phytoplankton is orthophosphate.

Phosphorus is in many ways the element most important, since it is more likely to be deficient, and therefore to limit biological productivity of temperate region, than are the other major elements. Phosphate in the south basin showed three obvious peaks. They were in winter 1992, winter and early spring 1993. The values were 8.0, 24.9 and 16.9 μg l^{-1} (Figure 13). Apart from these peaks, phosphate concentration ranged from an undetectable level (end of June 1992, late April and May 1993) to 6.9 μg l^{-1} in late March 1993 (On the first two samplings, a different spectrophotometer was used).

In the north basin, one peak only was recorded in spring 1992. It was 4.0 μg l^{-1} in early May 1992. From early March to late September 1992, the phosphate concentration

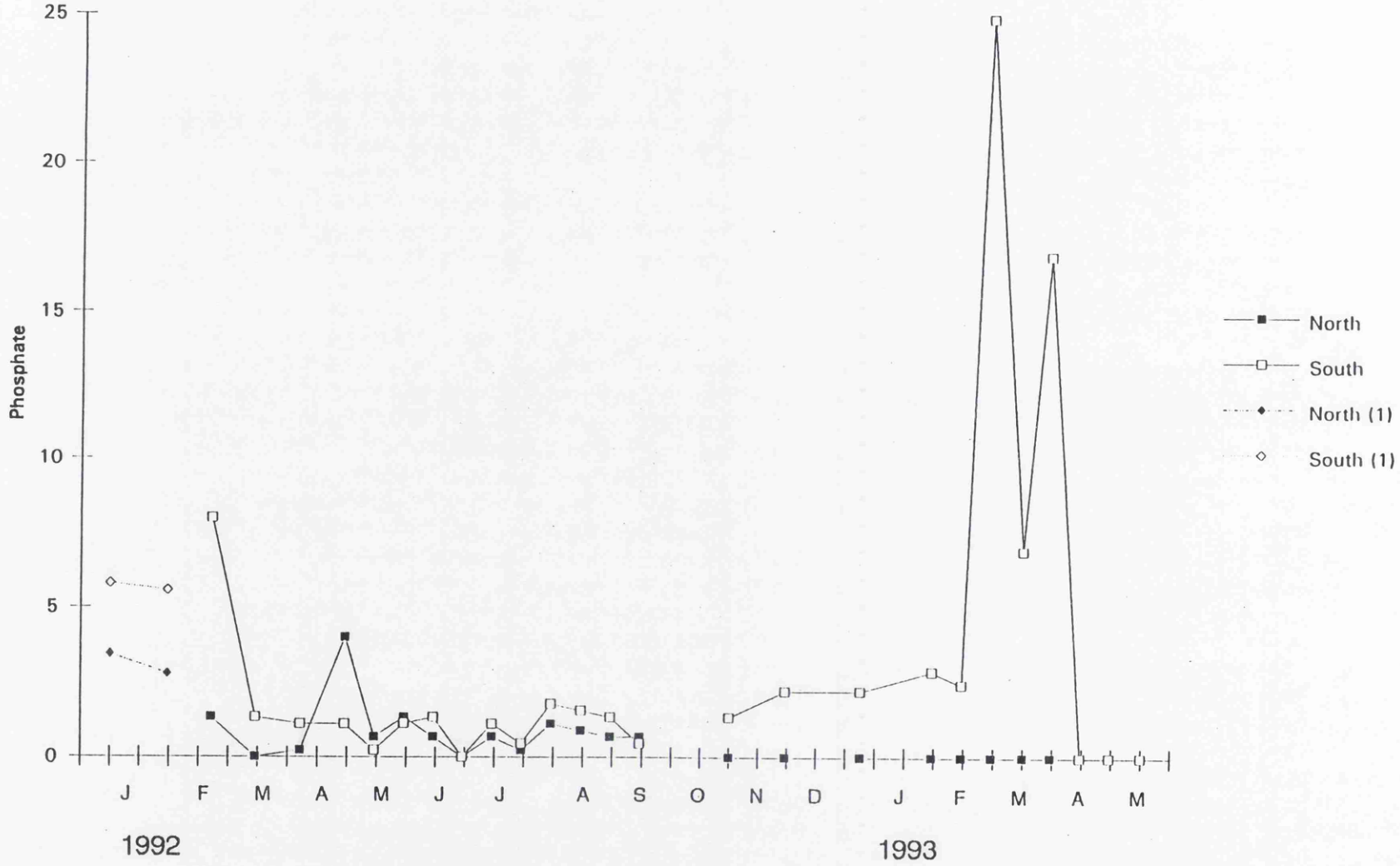


Figure 13. Seasonal variation of phosphate concentration ($\mu g\ l^{-1}$) for the north and south basin

fluctuated from undetectable level to 1.34 $\mu g\ l^{-1}$. From autumn 1992 onward, phosphate was in the undetectable limit.

The changes in phosphate concentration followed the general pattern of nutrient cycling with high levels in winter and low levels in summer.

2.1.4.9. Silicate

The south basin recorded two clear peaks of silicate in winter 1992 and 1993 (on the first two samplings, a different spectrophotometer was used). The first peak was higher than the second one. They were 661.3 and 619.8 $\mu g\ l^{-1}$ in March 1992 and February 1993 (Figure 14). The silicate level dropped suddenly and sharply from the middle of April to early May 1992 followed by a gradual decrease.

In 1993, the rate of silicate depletion was gradual but more sever than in 1992 which was related to the higher phytoplankton standing crop in this year.

On the contrary, the north basin showed a gradual increase, recording a peak in spring 1992 lower and about two months later than the south basin. It was 424.9 $\mu g\ l^{-1}$ in early May 1992. A gentle increase was recorded during winter or spring 1993. The lowest concentration was 217.3 $\mu g\ l^{-1}$ in late August 1993. There was not much difference between the two basins during the period from July to September, although the rate of depletion was consistently higher in the south than in the north basin.

The general pattern of seasonal variations of silicate in Loch Lomond especially the south basin showed a winter maximum and a marked summer minimum.

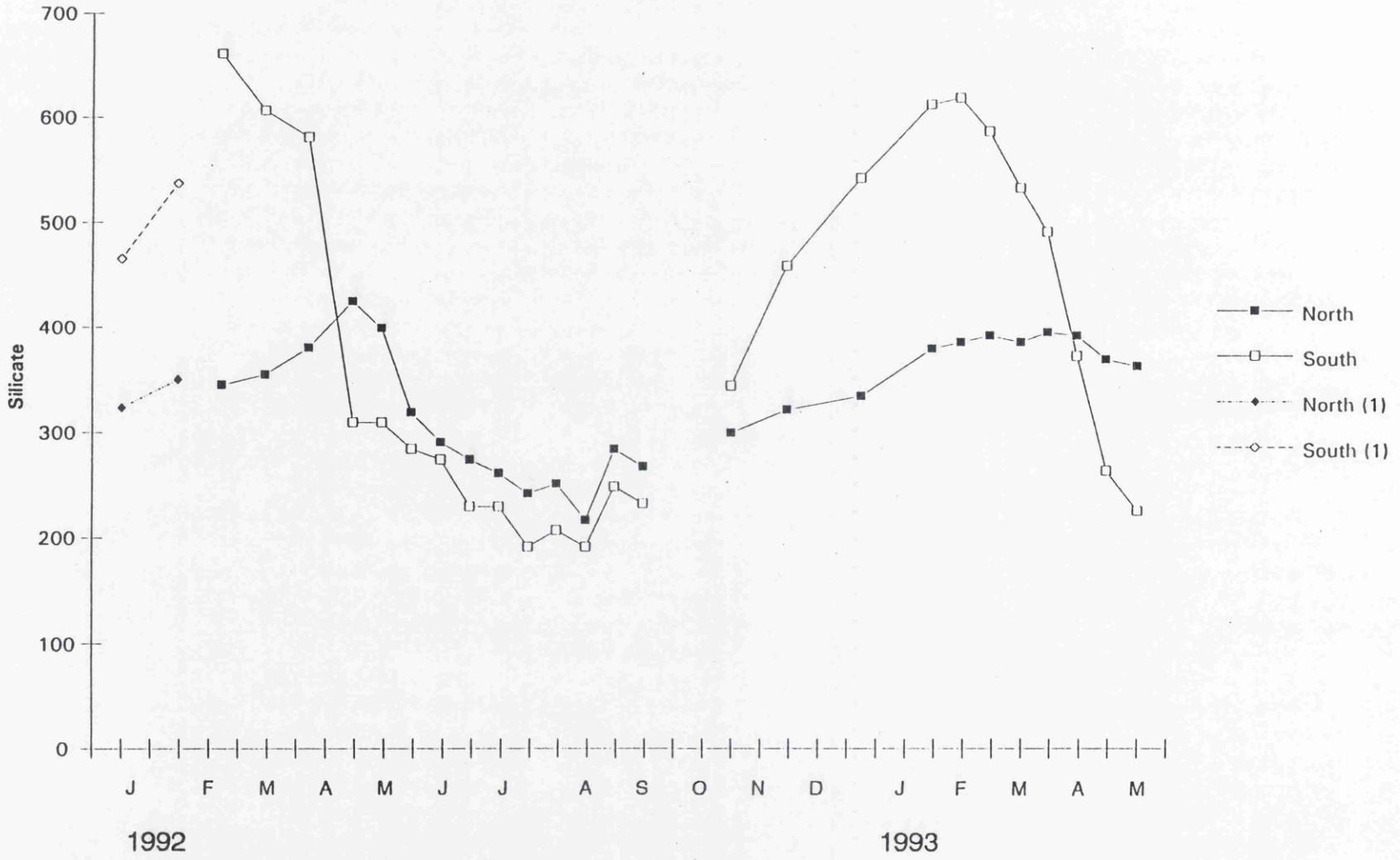


Figure 14. Seasonal variation of silicate concentration ($\mu g\ l^{-1}$) for the north and south basin

2.1.4.10. Nitrate

Nitrate is the commonest source of inorganic nitrogen in most freshwater with NH_4 being important only in anoxic waters and nitrite as transitional ion.

Two methods were used, the first was the Phenoldisulphonic acid (PDSA) method which was applied at the beginning before the cadmium-copper column for the second method was available. There was not a bad agreement between the two methods, on average cadmium-copper column gave reading about 6% higher than PDSA.

The south basin showed three peaks, the first one was in late winter 1992, the second was in late spring 1992 and the third was in winter 1993. They were 292.3, 228.0 and 250.4 $\mu g\ l^{-1}$ in late March 1992, early June 1992 and January 1993 respectively (Figure 15). The south basin showed a gradual decline in nitrate concentration followed by an almost steady state with very slight difference to reach a minimum concentration 186.0 $\mu g\ l^{-1}$ in late summer. Another decline period was recorded from early February 1993 onward recording a slightly lower concentration compared with 1992.

The north basin showed two peaks only in late March 1992 (170.6 $\mu g\ l^{-1}$) and in early June 1992 (181.8 $\mu g\ l^{-1}$). No peak was recorded in 1993. The north basin demonstrated nearly the same decline period of nitrate concentration in the south basin but for shorter period. The minimum concentration was recorded in late September 1992. The south basin demonstrated higher nitrate levels than the north with a mean value over the period of sampling of 211.5 $\mu g\ l^{-1}$ compared with 157.9 $\mu g\ l^{-1}$. The annual variation showed greater levels for winter and autumn and lower in summer.

In general, maximal amounts of nitrate tend to be present at the end of winter or at the vernal circulation.

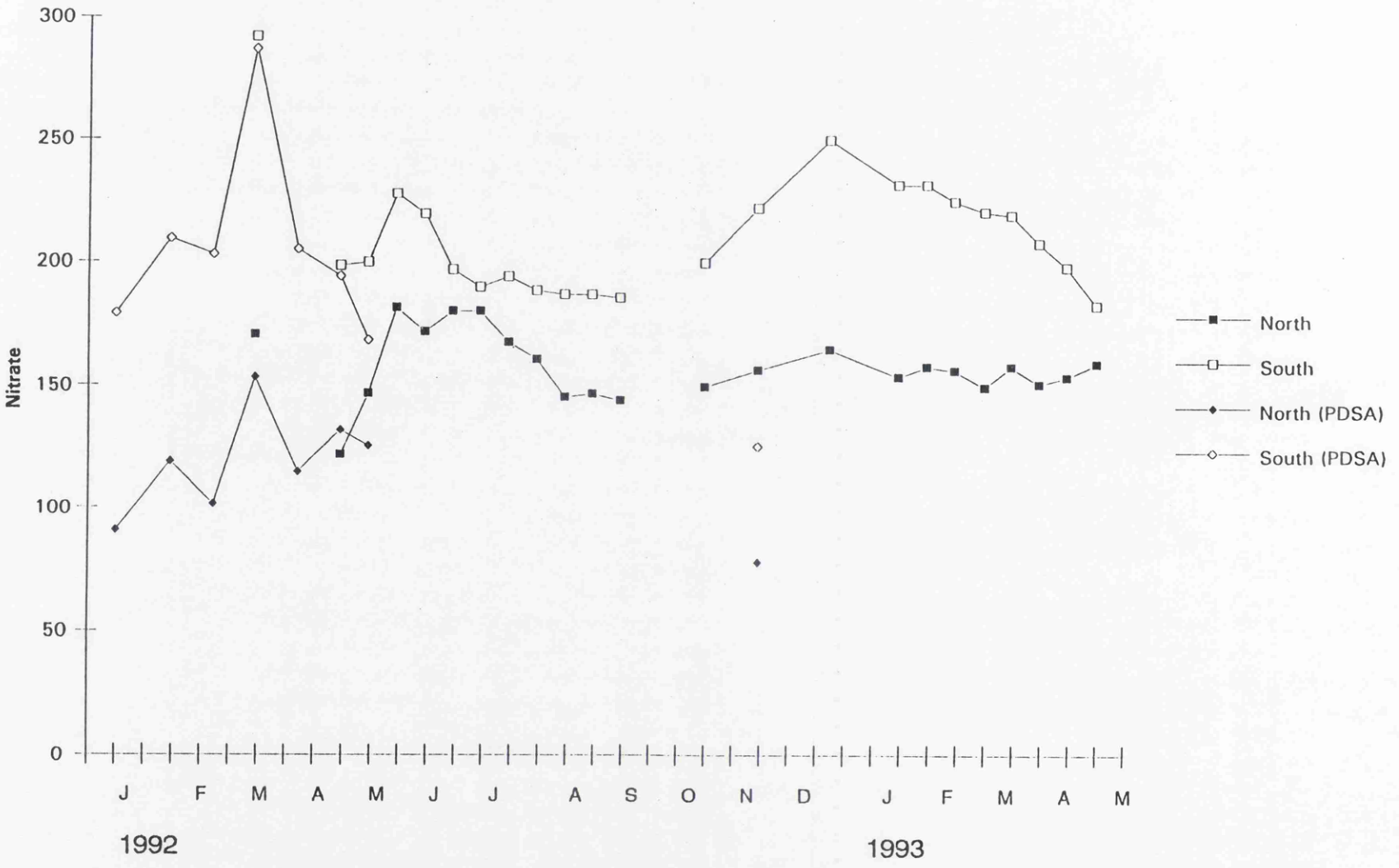


Figure 15. Seasonal variation of nitrate concentration ($\mu g\ l^{-1}$) for the north and south basin

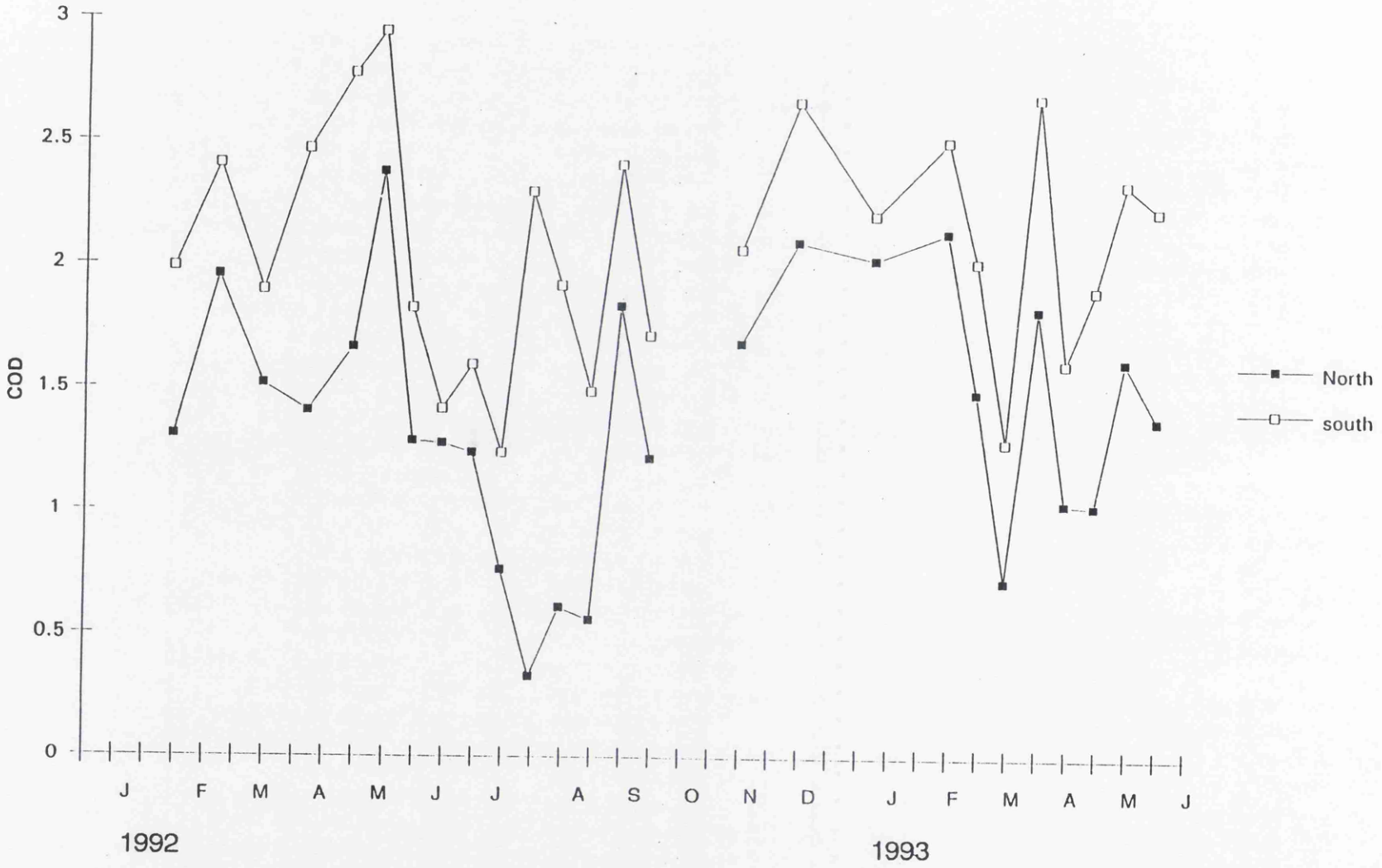


Figure 16. Seasonal variation of chemical oxygen demand (mg O_2 l^{-1}) for the north and south basin

2.1.4.11. Chemical oxygen demand

Chemical oxygen demand reflects the amount of dissolved organic matter in water which can be an approximate measure of the allochthonous material received into the loch. In fact most of it is pigmented which affects the penetration of light.

The north basin consistently had a lower chemical oxygen demand compared with the south. It fluctuated from 0.33 to 2.38 mg O_2 l^{-1} in late July 1992 and the middle of May 1992 respectively with a mean value of 1.4. In the south basin it was 1.24 and 2.95 mg O_2 l^{-1} in mid July and mid May 1992 respectively with a mean value of 2.08 (Figure 16).

In general, both basins showed erratic fluctuation through the sampling period except in late July 1992 when the north basin reached its lowest value, but levels were maintained in the south. No clear seasonal trend was recorded through the sampling programme.

2.1.5. Discussion

The results of the present investigation clearly demonstrate that the north basin of Loch Lomond is of a warm monomictic type, showing a single circulation period and is clearly stratified for four months (June to September). For the remainder of the year the water mass is completely mixed. According to Welch (1952) and Hutchinson (1957) such bodies of water can be classified as a tropic lake of the second order since it has a single circulation period in the winter with a water temperature always remaining above 4 C.

The south basin of Loch Lomond could be defined as polymictic according to the classification of Paschalski (1964); this applies to lakes in which the water mass may be mixed several times in one summer, with only short period of stratification. In the present investigation, the south basin stratified for six weeks only from mid June to mid July.

Light was directly related to phytoplankton growth and temperature, constituting the limiting factor for algal development during winter, whereas increasing day length and solar elevation promoted the outburst in spring (Lund, 1965).

Radiation reaching the loch surface is modified by atmospheric conditions, particularly cloud cover, which as indicated by rainfall, is by no means uniform over the surface of Loch Lomond. For example, mean annual rainfall at Inveruglas (representative of the north basin) was 279.7 mm in 1992, nearly twice the 151.8 mm in 1992 at Portnellan Farm (representative of the south basin) (CRPB annual report). Thus, the north basin receives considerably less radiation than the south basin. This effect is enhanced particularly in winter, by the surrounding mountains shading the water surface from direct radiation from the sun at the beginning and end of the day. This can have the effect of reducing the energy supply by up to 25% in a day in the north compared with the south.

According to Tilzer (1988) Secchi depth is to a great extent a function of beam attenuation of light which depends on the inherent optical properties of the water and is highly sensitive to light scattering from particles. Euphotic depth, by contrast, is a function of the vertical light attenuation coefficient which also depends on absorption and scattering but is less sensitive than beam attenuation to the latter . Algal cells and other particulate matter both absorb and scatter light and therefore influence both Secchi depth and euphotic depth, but in different fashions.

Certain lakes were chosen for comparison with Loch Lomond as they were known to resemble it in one or more aspects.

The principal factor controlling algal growth is the intensity of light. Depending on light attenuation in the water the thickness of the productive zone varies. The attenuation of light is caused by the absorption by water itself and by dissolved and particulate matter in the water. Some of the particulate matter consists of the algae itself and its by-products but this is normally of less importance unless the lake is very eutrophic (Hellstron, 1985). Dissolved and particulate matter are introduced into a lake by inflowing streams or are

blown into the lake. Another source is bottom material, which is eroded and resuspended. Such erosion and resuspension is normally caused by waves (Bengtsson *et al.*, 1990). The currents generally have little importance.

Dokulil and Skolaut (1986) in their study of Lake Mondsee, Austria, found that the Secchi disc transparency varied from 10 m in winter to 2 m in September; the north basin data is compatible because this lake is considered as an oligotrophic lake. Vaquer and El Hafa, 1991, obtained a value of 5.4 of Secchi disc transparency in their study of Sainte Croix Reservoir, France, which is considered a typically mesotrophic lake. The value they recorded is similar to the south basin's data. In Lake West Okoboji, Iowa, Bachmann (1990) recorded average summer Secchi disc transparency ranging from a low 2.5 m to high of 5.5 during the study. His data resemble Loch Lomond data, especially that of the south basin. Campos *et al.* 1990 demonstrated a high mean Secchi disc (10.2 m) in the temperate oligotrophic Lake Todas Los Santas. Stauffer (1985) pointed out that Secchi disc transparency is often high by mid to late summer in Green Lake, Wisconsin.

The distinctive thermal characters of the two regions could be explained by the topography of the surrounding areas, morphology of the basin and the ratio of the surface area to volume. The south basin has the larger surface area to volume ratio and consequently receives more radiant energy than the north basin which has a smaller surface area to a large volume. The greater wind exposure of the shallow southern part of Loch Lomond allows mixing at almost any time of the year.

The north basin only showed a positive correlation between light and temperature ($p < 0.05$). It is a direct correlation as one would expect.

Gulati (1972) in his study of Wijide Blik Lake, North Holland, pointed out that the lake exhibits only temporary thermal stratification on warm days, since the lake surroundings are open and flat, wind and nocturnal cooling destroy such a stratification. Also, there is

continuous circulation from autumn through to spring. This work is similar to the north basin of Loch Lomond. Pettersson *et al.* 1990, in their study of Lake Erken (Sweden), pointed out that summer stratification starts in May and lasts until the beginning of September which resembles to the north basin stratification period. Bindloss (1976), pointed out that shallow lakes, without wind shelter, tend to remain unstratified which resembles to the south basin. Campos *et al.* 1990, in their study of Lake Todos Los Santas, found thermal stratification in summer and winter circulation in that oligtrophic temperate lake.

The oxygen distribution in the water column in Loch Lomond with concentration never showing significant depletion is typical of oligotrophic areas according to Hunter (1970). In the present survey the lowest recorded values were 46% which was lower than that of Slack (1957) who recorded a minimum percentage saturation of 62 and Maulood (1974) who recorded lowest value of 63.6%. Values were obtained in the hypolimnion for the north basin. At the south basin the persistence of high oxygen levels throughout the year is consequence of the period of circulation and the relatively short period of stratification combined with greater exposure to the wind. The vertical distribution of oxygen at both basins of Loch Lomond tend to be generally clinograde during the summer and orthograde in winter. These data are similar to Maulood's. The absence of stagnation at the north basin which is stratified for about one third of the year is attributed by Slack (1957) to the very large volume of hypolimnion making any significant degree of deoxygenation difficult. McColl (1972) gave a similar explanation for the lack of deoxygenation in the deep lakes of New Zealand. In addition, the factor responsible for clinograde oxygen distribution (e. g. decomposition of organic matter) operates at a lower rate, than the low temperature found in the hypolimnion in the north basin. Animal respiration is also of less importance here since the number of animals per square metre of mud surface is less than in the south station (Weerekoon, 1956).

A highly negative correlation was found between temperature and dissolved oxygen ($p < 0.001$) in both basin. It is a direct correlation as one would expect.

Dissolved oxygen concentrations were at nearly saturation and supersaturation levels through the period of isothermal conditions and declined to the minimum in the hypolimnion after several weeks of thermal stratification. The rate of oxygen depletion depends on the total amount of oxygen present, in relation to depth and amount of sinking decaying organic matter originating in the epilimnion (Golterman, 1975).

The rise in temperature through the spring and summer reduced the capacity of the water to dissolve oxygen, and algal production produced supersaturated levels in the upper layers. Mixing conditions due to wind induced turbulence and the shallowness (specially the south basin) afforded isothermal and uniform oxygen saturation levels throughout the water column of most of the year.

Gulati (1972) in his study of Wijde Blik Lake (North Holland) demonstrated that oxygen percent of saturation in the upper water varies from 70 to 120 and the bottom waters were never anaerobic (lowest values 10% oxygen saturation) which is resemblant to this data.

pH in this study paralleled biological activity and was closely related to alkalinity since both are involved in the carbonate equilibrium (Mackereth *et al.*, 1978). To a some extent an increase in alkalinity is associated with an increase in pH.

The annual range of pH in Loch Lomond is similar in both basins. This is in accordance with the small range exhibited by most large lakes (Welch, 1948). The minimum pH values were found in winter and could be related to the high rainfall which effectively reduces the pH. According to Welch (1952), who stated that in some instances, increased rainfall makes striking changes in pH. There is also a relationship with the overturn period (Welch, 1952) which leads to a reduction in pH. A slight increase in pH observed in summer could, to certain extent, be related to the phytoplankton (Prescott, 1969). It is well

known that a heavy growth of phytoplankton can raise the pH of the environment, when the increased photosynthetic demand reduces the carbon dioxide of the water (McCombie, 1953).

Tippett (1985) made a comparison over a period of 17 years and found a steady decline in pH for both basins of Loch Lomond; he added that the decline is more noticeable in the south basin (17%) than in the north (13%). In the present data, pH in both basins fall in the range of the previous work. Only a small proportion of rain lands directly on the loch surface, but the rest falls on the catchment, where the geology and vegetation can modify the effects.

The influence of rainfall is an important factor in the determination of pH and alkalinity. In this study both basins showed a negative correlation (but not very significant <90%) between pH and rain, this means seasons of high rainfall (autumn-winter) lead to a lowering of pH whereas alkalinity rose to the seasonal maximum (Appendix 3). The south basin showed a positive correlation (but not very significant) between rain and alkalinity while the north basin recorded a negative correlation (Appendix 4).

The measurement of pH in poorly buffered waters is very difficult, but this trend appears to be real, and is confirmed by a steady decline in bicarbonate concentration.

Alkalinity, likewise, showed a small annual range generally being high in spring and summer and low in winter. According to Lund (1965) the pH reflects either high concentration of bicarbonate or carbonate (alkalinity) or low alkalinity, which indicates that there is little carbon dioxide in solution.

Conductivity is a general measure of the total ionic matter in solution, and clearly shows that there is a much larger dissolved mineral concentration in the south basin, mainly entering via the Endrick Water. This results in a conductivity in that region on average 25% higher than the north basin. Sodium, Potassium, Calcium and Magnesium could account for much of this difference but they were not measured in this study or previous

ones Maulood (1974) and Tippett (1985). Maulood 1974, did not measure the conductivity but Tippett (Unpublished) recorded similar values to this thesis for both basins.
Conductivity showed a negative correlation with rain ($p < 0.05$) in the north basin only.
Bayne *et al.* 1983, in their study of the West Point Reservoir Albama, Georgia, demonstrated low conductivity of 7.5 μ S m^{-1} which is of considerable similarity to the south basin data.

The seasonal distribution of nutrients in lake water can be ascribed to many different factors, both internal and external to the body of water. Within the loch itself the winter rise in all nutrients is associated with the annual mixing cycle (Hutchinson, 1957). Nevertheless, nutrient release to the overlying water from the sediment is negligible because of the high oxygen saturation at the sediment surface and in the over lying water (Mortimer, 1941). In winter the water and its contents are most likely to be nearly at equilibrium with the environment and unmodified by biological activity. The phosphate distribution in natural waters is determined by the behaviour of other substances, (Reid, 1961) such as iron (which was not measured in this study or Maulood's) which has been shown to occur in the sediment of Loch Lomond (Slack, 1957). Nitrate results from the process of nitrification (Martin and Goff, 1972). External sources of supply are also of considerable importance both from natural and artificial sources. Each year large quantities of dissolved inorganic nitrogen compounds are supplied in the rainfall (Allen *et al.*, 1968) whereas the most important natural source of silicate and phosphate is from the erosion of rock mineral (Golterman, 1973). Moreover, the farm run off (fertiliser) may get into the loch, the south basin is more likely to be greater in this respect than the north basin and also may have sewage inflow, but there is little in the Loch Lomond catchment in general.
The pattern of seasonal nutrient variation in Loch Lomond showed a maximum abundance of phosphate, silicate and nitrate occurring in the winter and the lowest concentration in the

summer. This is in accordance with the general pattern described for many temperate bodies of water (e. g. Heron, 1961; Duthie, 1965; Stewart and Markello, 1974; Maulood, 1978). In Loch Lomond silicate and nitrate were always present and never fell to undetectable levels, even during the summer periods.

Vincent (1983), in his study of Lake Taupo, New Zealand, pointed out that winter circulation brought an increased supply of phosphorus and, more importantly nitrogen. Dokulil *et al.* 1990, found dissolved silicate and phosphorus concentrations are critical for the summer situation in Lake Mondsee, Austria. In a study of the Green Lake, Stauffer (1991), demonstrated that the lake is phosphorus rather than nitrogen limiting. Stauffer (1985), pointed out that the Green Lake (Wisconsin) is actually nutrient-limited by mid to late summer.

Ecologically phosphorus is often considered the most critical single factor in the maintenance of biochemical cycles particularly in temperate freshwater. The deficiency of phosphorus could lead to the inhibition of phytoplankton growth, resulting in the decline in the productivity of aquatic ecosystems (Reid, 1961). Because of its relative insolubility, it is normally available from the environment in very small quantities compared to other nutrients in relation to demand, so often limiting. The luxury uptake of phosphorus is well documented for phytoplankton (Moss, 1988) which can enable algae to grow in waters where one would expect production to be limited by phosphorus availability. The slight increase of orthophosphate during autumn and winter could be related to repressed biological activity (Moss, 1973).

Phosphate distribution was greatly influenced by biological activity within the lake when this decreased, orthophosphate concentrations increased (Moss, 1988). Phosphate showed a winter maximum due to the turnover and depletion trends from spring to summer in both basins to undetectable levels. This depletion was due to the increasing algal production.

The north basin only showed a highly negative correlation between phosphate and dissolved oxygen percentage of saturation ($p < 0.001$). This correlation is an indirect relationship because during the winter season the temperature is low, the percentage of oxygen is high and phosphate is high due to isothermal condition of water.

Dokulil and Skolaut, (1986) in their study of Lake Mondsee, Austria demonstrated that prior to the onset of stratification phosphate-phosphorus concentration was 4 $\mu g\ l^{-1}$, decreasing to undetectable values thereafter. Pettersson (1990), pointed out that phosphorus was shown to be the limiting nutrient at the end of the spring bloom in Lake Erken, Sweden. Daley and Pick (1990), recorded that Lake Kootenay (British Columbia) was nitrogen limited in early 1970's but is now more phosphorus limited. In a study of Lough Neagh, Wood and Gibson (1973), found that phosphorus appears to be the key factor which limits the growth of algae.

The seasonal pattern of silicate was similar to that for phosphate and nitrate. The seasonal depletion of silicate in the water was primarily the result of diatom productivity and growth (Hutchinson, 1957; Lund, 1965). Silicate was highly negatively correlated in both basins with temperature. This indirect relationship is as one would expect because during winter, the water column became isothermal and overturn occurs, and with increasing temperature all the favourite factors encourage the phytoplankton to grow (especially diatoms) which consume the silica. Reynolds (1984), stated that Pearsall carried out a series of field studies on the composition of the phytoplankton in relation to dissolved substances in lakes in N. W. England. *Inter alia*, he concluded that: diatoms increased when the water was richest in dissolved silica; that development of chrysophytes (especially *Dinobryon*) was favoured at low silica levels and high ratios of nitrogen to phosphorus.

Gulati (1972), pointed out that SiO_2-Si decreased from February (400 $\mu g\ l^{-1}$) to June when diatom increased in Lake Wijde Blik, North Holland.

Silicate showed a highly negative correlation with temperature ($p < 0.001$) in both basins. This correlation is probably an indirect rather a than direct relationship, it is due to the growing season of phytoplankton (spring, summer) which in turn consume silicate from the water.

The proportions of each nitrogen compound is related to oxygen concentration, with high oxygen levels favouring nitrate and very low levels of ammonia (Mortimer, 1941). Nitrification is a source of nitrate within a lake. This can take place in freshwater and mud whenever oxygen is present. Nitrification appears to proceed most rapidly in winter and is sensitive to low pH (Hutchinson, 1957). Surface runoff and acid rainfall could both also be important sources of nitrate to a lake system (Golterman, 1975).

Maximal amounts of nitrate were presented in the loch at the end of winter when mixing conditions, high rainfall and a slight increase in pH took place. The north basin showed a high negative correlation with rainfall ($p < 0.05$). The south basin showed a negative correlation as well, but this was not highly significant. This is as one would expect due to the high amount of rain received in the north basin compare with the south basin.

Dokulil and Skolaut (1986), recorded dropping levels of nitrate-nitrogen from 590 $\mu g\ l^{-1}$ to about 100 $\mu g\ l^{-1}$ from prior to the onset of stratification to thereafter in their study of Lake Mondsee, Austria.

The south basin showed a highly positive correlation between nitrate and silicate ($p < 0.001$) which is considered an indirect correlation.

The more a nutrient is limiting the more closely it will have a negative correlation with production. The nutrient, for instance, correlates negatively with the standing crops in the south basin but not in the north basin. So, these results suggesting that phosphorus is most important in the north basin but silicate and nitrate are more important in the south basin.

Chemical oxygen demand can be an approximate measure of the allochthonus material received into the loch. In fact most of it is pigmented which affects the penetration of

light. The chemical oxygen demand the in south basin is on average 33% higher than in the north basin. Tippett (1985) recorded a higher chemical oxygen demand in the north basin, about 16% on average higher than in the south. Maulood did not analyse this parameter.

There was a negative correlation (not significant) between COD and chlorophyll in both basins but it was more significant in the north than in the south. This could be explained by in the north basin all COD is from pigmented material whereas in the south basin it is a mixture of pigmented and coloured (non-living) suspended matter.

2.2. Phytoplankton standing crop

2.2.1. General introduction

Water quality affects the abundance, species composition and diversity, stability, productivity and physiological condition of indigenous population of aquatic organisms. Therefore, an expression of the nature and health of the aquatic communities is an expression of the quality of the water. Biological methods used for measuring water quality include the collection, identification and counting of aquatic organisms; biomass measurements; measurements of metabolic activity rates, measurements of the toxicity; bioaccumulation, and biomagnification of pollutants; and processing and interpretation of biological data (Anon, 1976).

Because of their short life cycles, phytoplankton respond quickly to environmental changes, and hence the standing crop and species composition indicate the quality of the water mass in which they are found. Also, because of their small size and often great numbers, they not only strongly influence certain non-biological aspects of water quality (such as pH, colour, taste and odour), but in a very practical sense, they are a part of water quality. Certain taxa often are useful in determining the origin, or recent history, of a given water mass.

One way of expressing the standing crop of phytoplankton is as numbers of organisms per unit volume. However, since phytoplankton cells or colonies vary greatly in their size distribution, numbers alone do not give a complete picture of population dynamics and the diversity structure of the ecosystem (Anon, 1976).

Phytoplankton data derived on a volume-per-volume basis are often more useful than data given as numbers per millilitre. Determine the volume of a cell by using the simplest geometric configuration that best fits the shape of the cell being measured (such as sphere, cone, cylinder). Cell sizes of an organism can differ substantially in different waters and

from the same waters at different times during the year; therefore, it is necessary to average measurements from 20 individuals of each species for each sampling period. Calculate the total biovolume of any species by multiplying the average cell volume in cubic micrometers by the number per millilitre (Anon, 1976).

The term "phytoplankton succession" is commonly used to explain the duration of the whole cycle of growth and decline followed by maximum successive population of other species which may grow and then decline at various periods through the year. Because successions of particular groups of species occur during particular seasons, the species composition and order in the sequence often remain the same for many years. This constant reappearance year after year of similar algal blooms in many lakes is a very impressive phenomenon (Golterman, 1975).

Chlorophyll *a* is an algal biomass indicator and has been widely used as a convenient correlation of biomass in estimations of phytoplankton biomass and productivity. It is also useful in comparing results from different habitats. Moreover, it is also used as the basis for a number of so-called lake classifications. No overview of the cellular composition of phytoplankton would be complete without some examination of the relationship between chlorophyll content and dry-weight or volume. Generally, chlorophyll *a* is considered to account for between 0.5 and 2% of dry weight (Reynolds, 1984).

A phytoplankton species may be present in the lake throughout the year but usually only in very small numbers, or the cells may be washed a new into the lake with inflow water or from sheltered bays or perhaps they may be resuspended from the bottom deposits or grow from resting (over wintering) stages. The factors that control spring and other maxima can be put into three groups: physical (light, temperature and turbulence), chemical (nutrients) and biological (parasitism, predation and competition). Every algal bloom is the result of

several favourable factors and it is rare for one factor alone to be recognised as the cause of a bloom. Increasing irradiance and temperature are often the dominant factors controlling the onset of the spring outburst of diatom growth, but the absence of predation cannot be neglected (Golterman, 1975).

2.2.2. Material and methods

2.2.2.1. Chlorophyll *a*

The main photosynthetic pigments from algae can be extracted from the cells dissolved in various organic solvents. The concentrations of the various pigments can be estimated spectrophotometrically.

5 l of loch water was filtered through Whatman GF/C glass fibre filter paper in a membrane filter apparatus. A small amount of magnesium carbonate was added to the sample prior to filtering to prevent the degradation of chlorophyll. The filter paper was folded and kept in aluminium foil in the freezer for later analysis. Hot methanol was used to extract the pigments. The absorbency was measured at 665 and 650 nm (Hipkins and Baker, 1986). No correction were made for pheophytin interference (Bucher, 1991). Details of methods are presented in Appendix 2.

2.2.2.2. Sedimentation and enumeration

A 1 l water sample was fixed with 10 ml Lugol's iodine solution and left to settle in a measuring cylinder for 2 weeks after which time 900 ml of the supernatant was carefully siphoned off. The residue was transferred into a 100 ml cylinder and left to settle again for 4 days. The supernatant was again siphoned off, the final volume of the sample made up to 25 ml, shaken and transferred to a counting chamber.

Enumeration was made using a Zeiss inverted microscope with a mechanical stage and recorded using a counting programme (Place and May 1986), and a BBC computer. The programme was designed to record average size of colonial species, common species, less common species and zooplankton.

One traverse was counted at x 250 magnification. On most occasions in excess of 400 individuals were enumerated. Results are expressed as number of algal units per litre.

Algae were identified with various taxonomic texts: Bourrelly (1966, 1968, 1970) and Prescott (1962) for all groups, Lind and Brook (1980) for desmids, Hustedt (1961-1966); Patrick and Reimer (1966) and Barber and Haworth (1981) for diatoms.

2.2.3. Results

2.2.3.1. Seasonal changes in algal biomass (chlorophyll *a*)

Chlorophyll levels in the north basin were smaller than the south throughout the sampling programme, on average throughout the whole set of data the south basin levels were 2.1 times greater than in the north .

In the south basin, there were 4 peaks in chlorophyll *a* concentrations in May, June, early September 1992 and April 1993. At 5.81 $\mu g\ l^{-1}$, the biggest was in September and the smallest (4.54 $\mu g\ l^{-1}$) in June (Figure 17). The north basin showed a slower increase from March to the end of June recording a first peak of 3.3 $\mu g\ l^{-1}$. A second peak of 3.08 $\mu g\ l^{-1}$ was in August but none was recorded in September.

Both basin showed the same trend of seasonal variation recording a gradually increasing peak during spring and summer followed by a gradual decrease through autumn and winter. From March 1993 onwards, the chlorophyll *a* levels started to increase in both basins but the increase was much greater in the south than in the north basin.

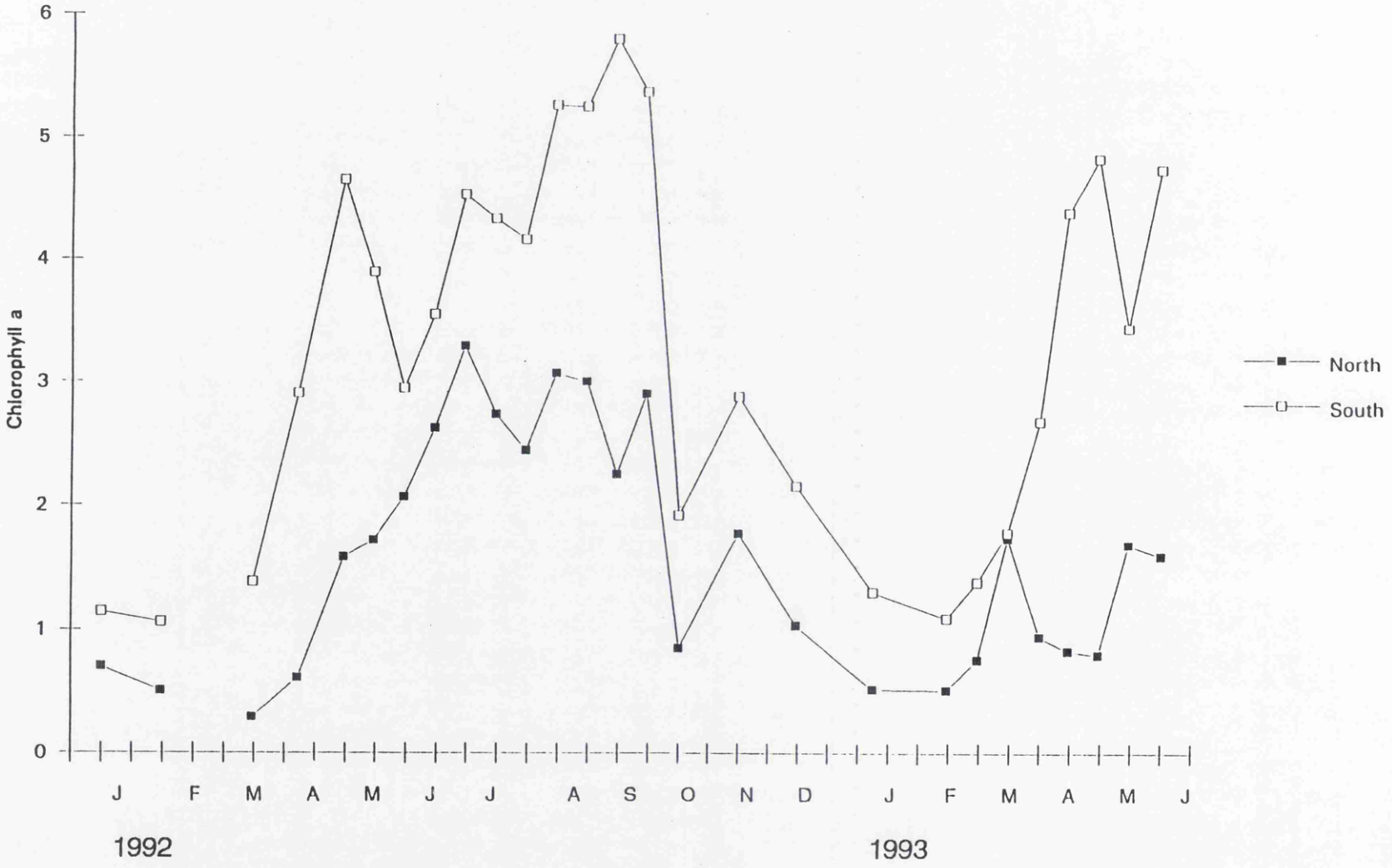


Figure 17. Seasonal variation of chlorophyll *a* concentration ($\mu g\ l^{-1}$) for the north and south basin

2.2.3.2. Seasonal changes in the total number of individuals

During winter 1992, both the north and the south basins recorded low phytoplankton number, but the size of community in the south basin was three times greater than in the north basin. The average number during this period was 1.67 x 10^4 and 0.65 x 10^4 algal units l^{-1} for the south and the north basin respectively.

In spring 1992, phytoplankton in the south basin started to grow 6 weeks before the north basin recording the first peak 8.67 x 10^4 algal units l^{-1} in mid April 1992 (Figure 18 a). The south basin then recorded a second peak in the middle of May which was slightly higher than the first one 13.76 x10^4 algal units l^{-1}. The north basin showed a gradual increase from late May reaching a peak in late June (20.17 x10^4 algal units l^{-1}).

During summer 1992, both basins showed an irregular pattern of small peaks. The average number during this period was 6.88 x 10^4 and 5.38 x 10^4 algal units l^{-1} for the south and the north basins respectively.

Both the north and the south basins recorded a sharp decrease in numbers in autumn 1992 reaching a minimum at the beginning of December.

In winter 1993, the north basin supported a slightly larger community than in the pervious winter (mean 0.89 x10^4 algal units l^{-1} compared with 0.65 x10^4 algal units l^{-1}). The south basin also supported a larger community (about 2.5 times) than winter 1992 (mean 4.15 x 10^4 algal units l^{-1}).

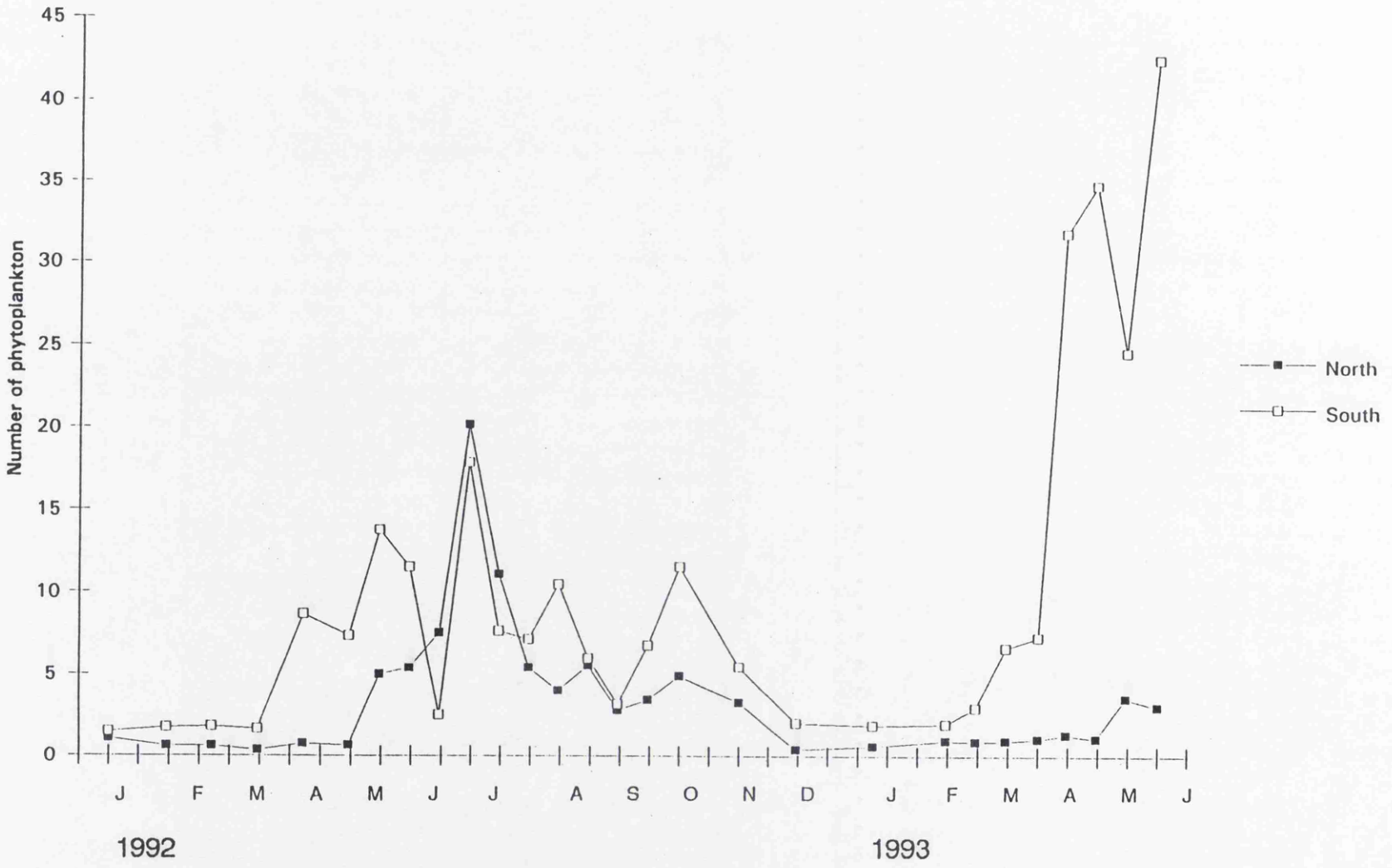


Figure 18a. Seasonal variation of total number of phytoplankton (algal units l^{-1}) for the north and south basin

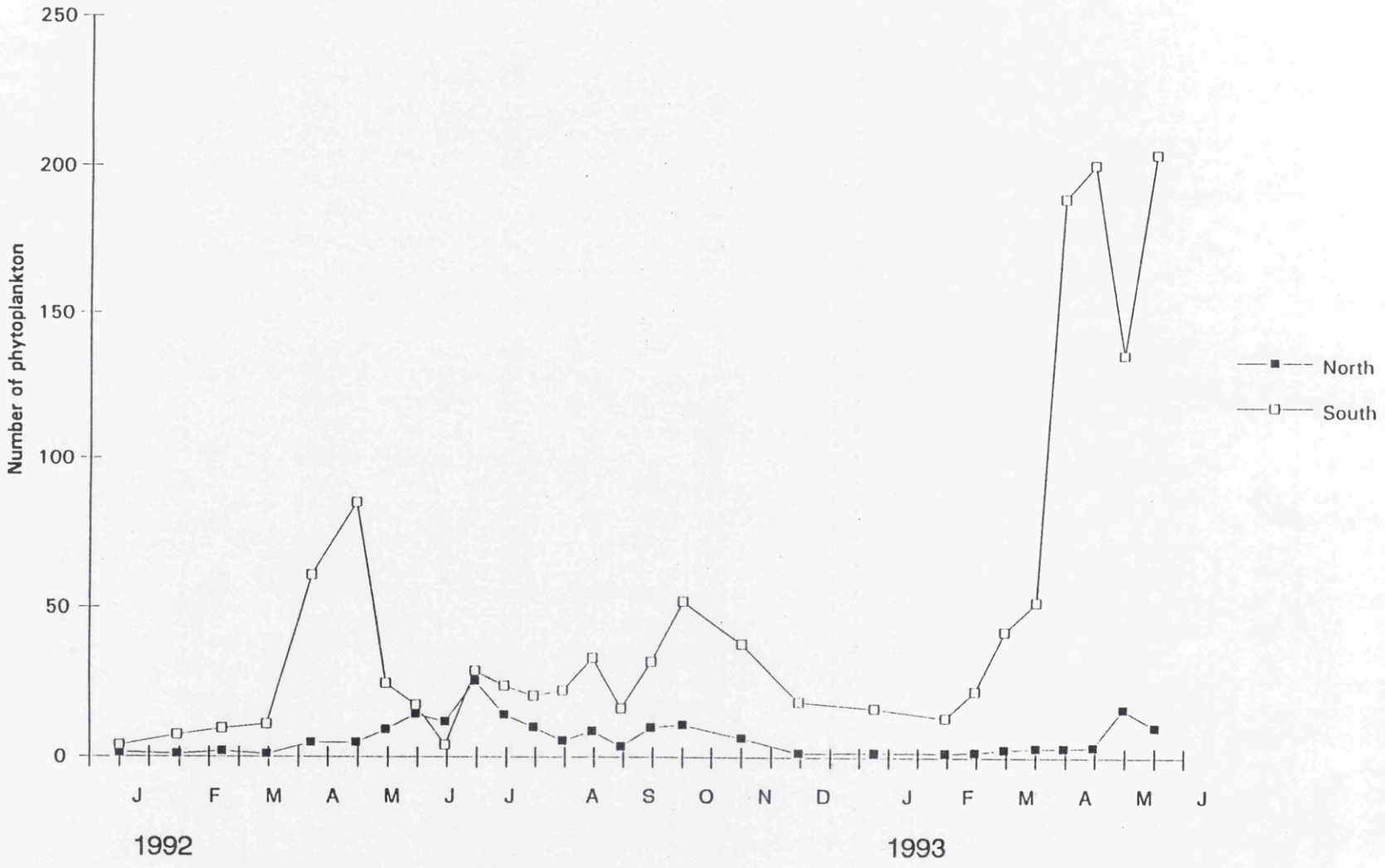


Figure 18b. Seasonal variation of total number of phytoplankton (cells l^{-1}) for the north and south basin

Table (2) Species composition of the phytoplankton

Bacillariophyceae

Melosira italica subsp. subarctica O. Muller

Asterionella formosa Hassall

Tabellaria fenestrata var. intermedia Grunow

Tabellaria floculosa (Roth) Kuetzing

Fragilaria crotonensis Kitton

Cyclotella kutzingiana Thwaites

Eunotia pectinalis var. minor (Kuetz.) Rabenhorst

Synedra tenera W. Smith

Navicula sp

Cymbella sp

Frustulia sp

Surirella robusta Ehr

Cocconeis sp

Cyanophyceae

Oscillatoria agardhii Kufferath

Merismopedia glauca (Ehrenb.) Naegeli

Coelospherium naegelianum Unger

Anabena circinalis Rabenhorst

Oscillatoria sp (c.f. Oscillatoria angustissima) West &West

Chlorophyceae

Staurastrum cingulum (W. and G. S. West) G. M. Smith

Cosmarium depressum (Nag.) Lund

Closterium toxon W. West

Oocystis sp

Scenedesmus quadricauda (Turp.) de Brebisson

Dictyospherium pulchellum Wood

Pediastrum boryanum (Turp.) Meneghini

Staurodesmus spencerianus (Mask.) Teiling

Botryococcus braunii Kuetzing

Spondylosium planum (Wolle) W and G. S. West

Gontazygon sp

Spirogyra sp

Coelastrum sp

Xanthidium antilopoeum var depauperatum W. and G. S. West

Ankistrodesmus falcatus (Corda) Ralfs

Unknown species (c. f. *Ankistrdesmus convalutus*) Corda

Dinophyceae

Ceratium hirundinella (O. F. Muell.) Dujardin

Peridinium willei Huitfeld-kass

Gymnodium caudatum Prescott

Chrysophyceae

Mallomonas acaroides Perty

Dinobryon divergens Imhof

Cryptomonadaceae

Cryptomonas ovata Ehrbg.

The north basin showed only a slight increase during spring 1993 compared with the same period of 1992. In the south basin an obvious increase was recorded reaching 42.54 x 10^4 algal units l^{-1} in mid May.

For interpretation of chlorophyll *a* results and comparison with other work, the number of phytoplankton cells (for diatoms colony only) is presented in Figure 18 b. In this Figure, two peaks were recorded in spring and autumn 1992 with the spring one being higher than the autumn. The spring peak of 1993 was earlier by two weeks and higher by 2 and 2.5 times than 1992 in the north and south basin respectively.

2.2.3.3. Seasonal pattern of major group

Table 2 presents a list of all species encountered from both basins in Loch Lomond during this study.

Figure 19 and 20 show the percentage contribution of each group of phytoplankton to the total in the north and south basins respectively.

During winter 1992 the community was dominated by diatoms in the south basin. The diatoms increased gradually to reach the maximum (96.4%) by late March. The rest of the community was occupied by a small proportion of different groups of phytoplankton.

In spring 1992, the diatoms maintained a high percentage until early May then decreased sharply recording 9.4% by mid May, followed by a slight increase. During the middle of May, the community was dominated by others (unknown algae c.f. *Ankistrodesmus convolutus*). In late spring, cryptomonus and chrysophyceae dominated the community. Blue green algae recorded a moderate percentage from early to mid June.

Diatoms started to increase gradually in summer 1992 reaching a maximum of 85.4% in early September with the rest of community being a mixture of all other groups.

Figure (19) Seasonal distribution of majors phytoplankton groups (expressed as percentage) for the north basin

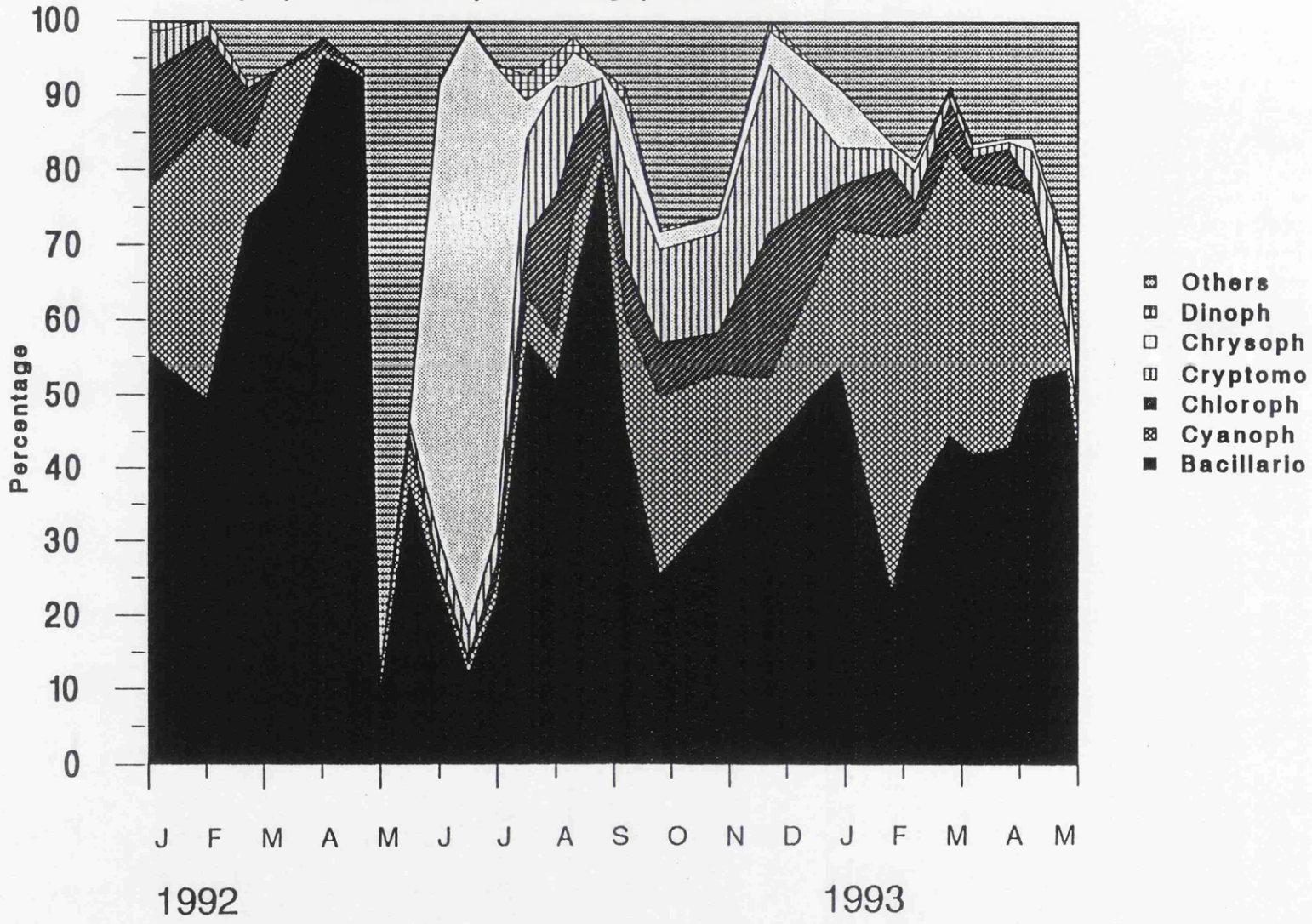
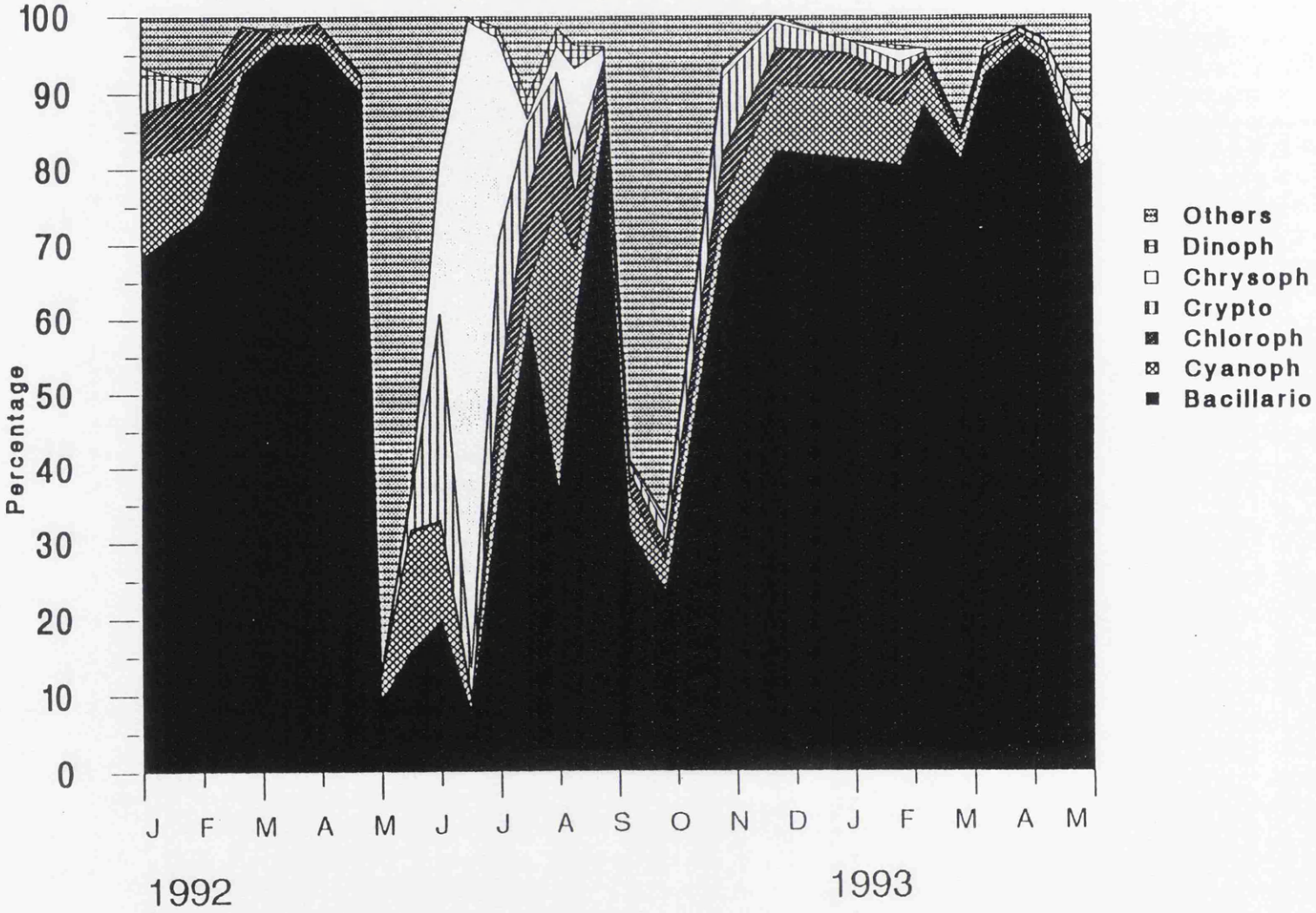


Figure (20) Seasonal distribution of majors phytoplankton groups (expressed as percentage) for the south basin



During autumn 1992, all the groups again showed a marked decline until early October and the community was dominated by others (unknown algae c.f. *Ankistrodesmus convolutus*). From then onwards, the diatoms started to increase and dominate the community. Less than 30% were a mixture of other groups.

In winter 1993, the diatoms continued to dominate the community in the south basin with high proportion, ranging from 80.4% to 91.9%. Blue green algae showed a small proportion never more than 8% of the total during this period. The other groups represented the rest of community.

There was no big difference between winter and spring 1993 in the south basin , in which the diatoms were still the dominant group with a high percentage ranging from 80.3% to 96.2%.

Figure 19 shows the percentage contribution of each group of phytoplankton to the total in the north basin.

As in the south basin, during winter 1992 diatoms were the dominate group in the north basin although the percentages were more moderate ranging from 49.5 to 78%. Blue green algae showed a higher proportion during this period compare with the south basin.

The diatoms continued to dominate the community in the north basin, in early spring 1992. From mid May to early June, others (unknown algae c.f. *Ankistrodesmus convolutus*) took over recording a high proportion. For the rest of spring, chrysophyceae dominated the community with percentage ranging from 61.4 to 80.6.

In the beginning of summer 1992, chrysophyceae continued to dominate the community until mid July in the north basin. Diatoms started to increase gradually from mid July to reach a peak in early September. The rest of the community was a mixture of other groups.

During autumn 1992, diatoms represented a small percentage of the total ranging from 25.5 to 43.3% in the north basin. Throughout this period, blue green algae started to increase to

comprise the second main constituent of the community followed by cryptomonas. Others (unknown algae c.f. *Ankistrodesmus convolutus*) gained an importance during this period.

In winter 1993, blue green algae recorded a high percentage in the north basin dominating the community in early February.

Diatoms maintained their percentage contribution among other group in the north basin during spring 1993, but blue green algae showed a sharp decrease in early May. The community was then dominated by diatoms and others (unknown algae c.f. *Ankistrodesmus convolutus*).

In general, diatoms were more important in the south than in the north basin for most of the year. Whereas, blue green algae were more important in the north than in the south basin especially during winter, early spring and autumn.

Bacillariophyceae

In the south basin, *Melosira italica* was the main constituent genus followed by *cyclotella kutzingiana* and *Asterionella formosa* from January to early May 1992 (winter to early spring). It was the same for the north basin except that *Cyclotella kutzingiana* was followed by *Tabellaria fenestrata* not *Asterionella formosa.*

During late spring and summer, *Tabellaria fenestrata* became the main genus replacing *Melosira italica* in the south basin. In the north basin, *Tabellaria fenestrata* was the only genus to continue throughout the sampling period with percentages ranging from 1.0 to 31.6 (Figure 21). *Cyclotella kutzingiana* was the most abundant genus in the north basin from late spring to early autumn 1992 ranging from 24.9 to 53.2%. It was the second dominant genus in the south basin for the same period, fluctuating from 11.5 to 36.7% (Figure 22). *Fragilaria crotonensis* represented about 1/3 of the total in September and October in the south basin only (28.3%, 31.5%). In the north basin, it showed a very low percentage throughout the sampling period except in September and October reaching 8.0 and 13.0% respectively. In the south basin, *Melosira italica* recorded two obvious peaks,

Figure (21) Seasonal distribution of *diatoms (Bacillariophyceae)* species (expressed as percentage) for the north basin

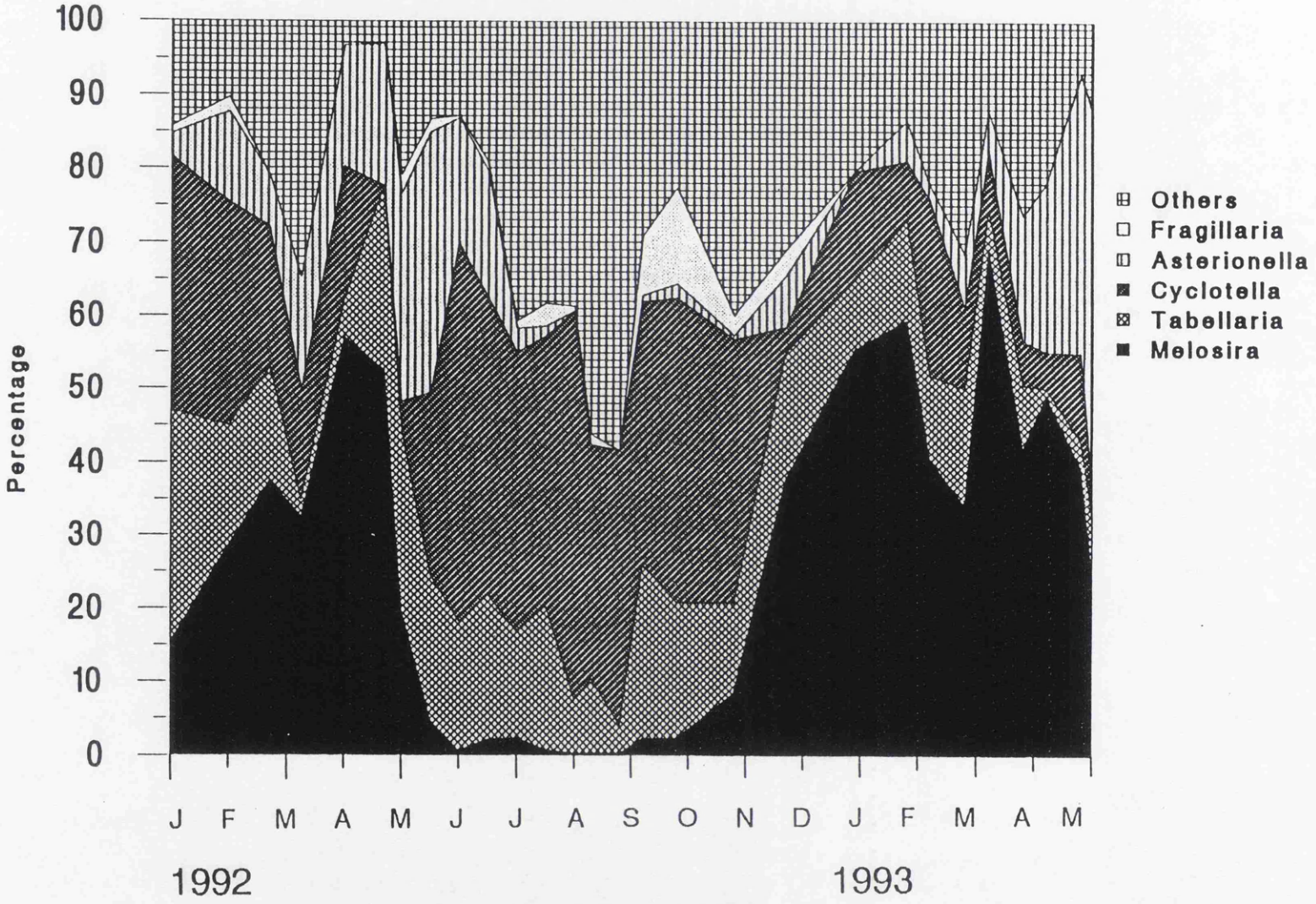
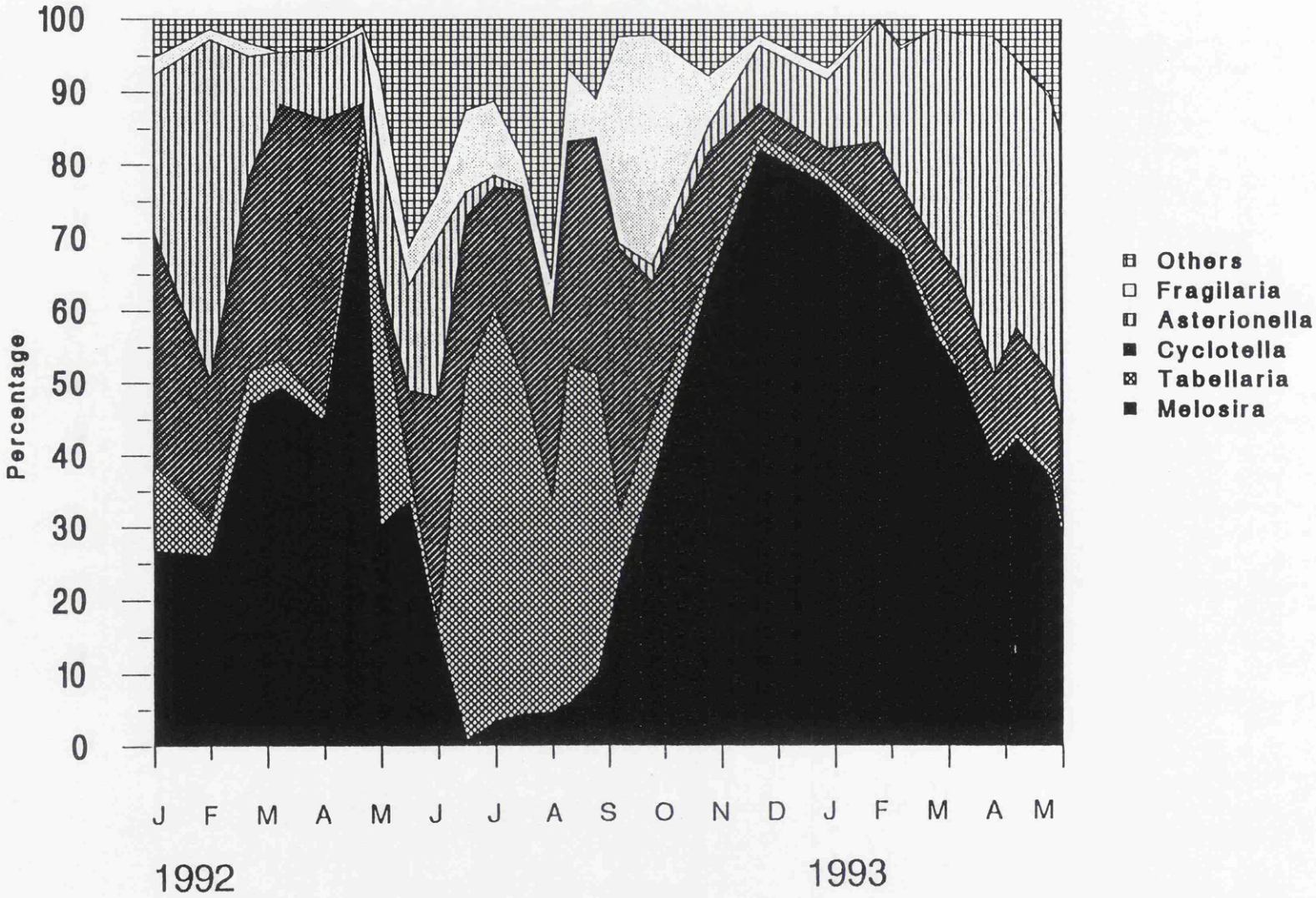


Figure (22) Seasonal diatribution of diatoms species (expressed as percentage) for the south basin



the first one lasted for 6 months (winter and spring) with the maximum percentage in early May 1992 (81.9%). The second one extended for 8 months from autumn 1992 to spring 1993, the peak was 82.1% in the beginning of December 1992. The north basin showed nearly the same story but with a lower percentage than the south.

Cyanophyceae

Oscillatoria agardhii was the main constituent in the south basin throughout the sampling period. It ranged from 30.8 to 100% of the total *Cyanophyceae* (Figure 24). In the north basin it was the second or third abundant genus ranging from 1.9 to 100% throughout the whole set of data (Figure 23).

Merismopedia glauca showed a moderate peak in the south basin ranging from 23.1 to 33.3% during winter 1992, followed by a sharp decline. From late spring and summer 1992, it showed an obvious fluctuation but did not exceed 3.8% then it started to increase gradually and remained steady for a while reaching a peak in early April 1993 of 25% of the total *Cyanophyceae.* In the north basin, *Merismopedia glauca* formed a high proportion of the total blue green algae in late summer and late autumn 1992 ranging from 66.7 to 87.0%. It was the only constituent to continue all along the sampling period except from mid April to mid May 1992 and the middle of July.

Oscillatoria sp (c.f. *Oscillatoria angustissima*) was the main constituent in the south basin during winter 1993 and the second one from late April to the middle of May 1993. It was recorded twice in mid January 1992 (3.1%) and in the middle of July 1992 (33.8). In the north basin, it showed a high percentage from mid January to late March 1992 ranging from 44.5 to 80.5%. It then disappeared thereafter to reappear once again from early January 1993 to the middle of May 1993. It fluctuated from 16.7 to 90.6%.

Coelospherium naegelianum was recorded in the south basin during the winter of 1992 (January and February) and from early October 1992 to late March 1993 (autumn and winter) recording the maximum in late March 20.9%. In the north basin, *Coelospherium*

Figure (23) Seasonal distribution of blue green algae species (expressed as percentage) for the north basin

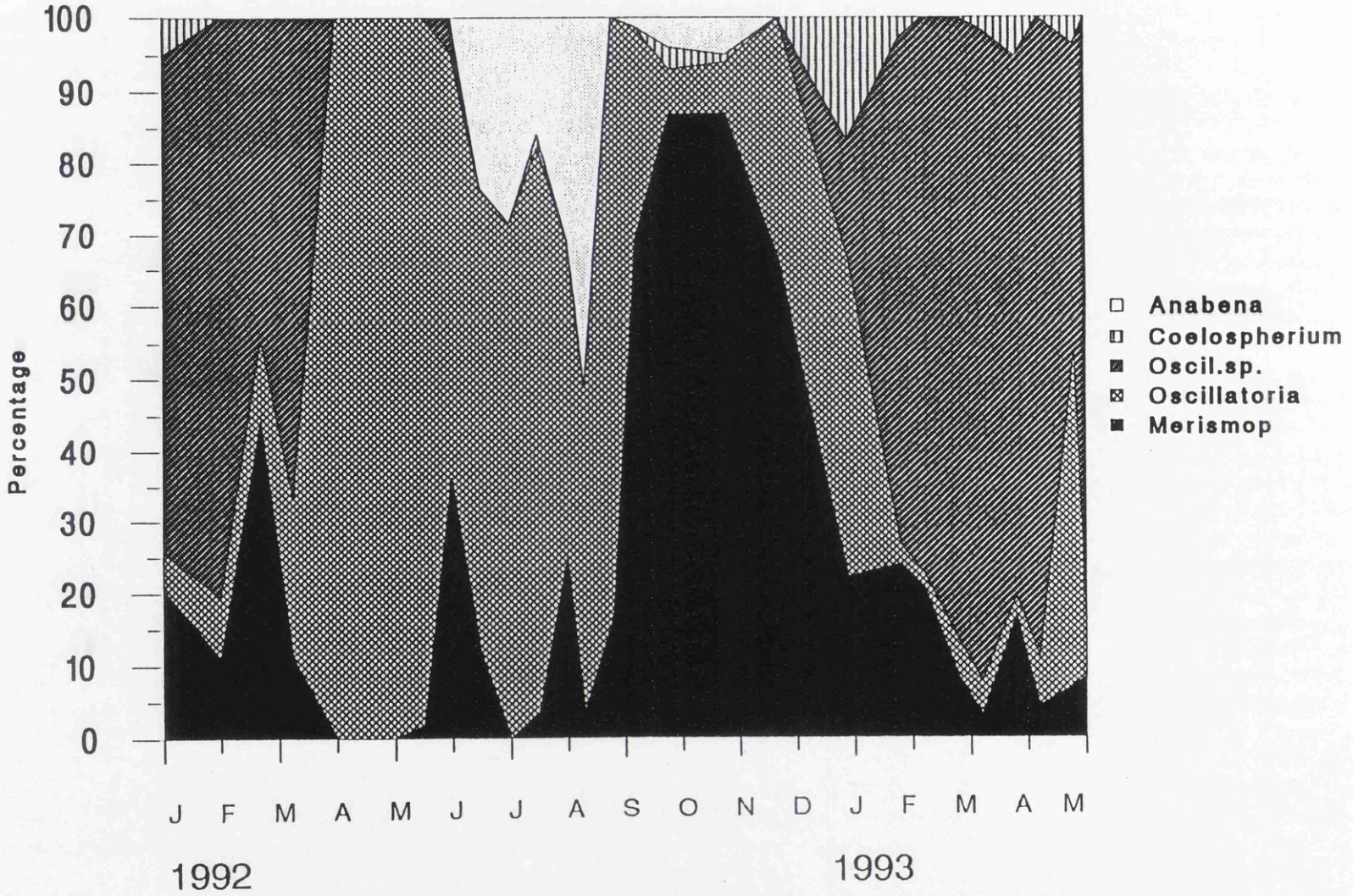
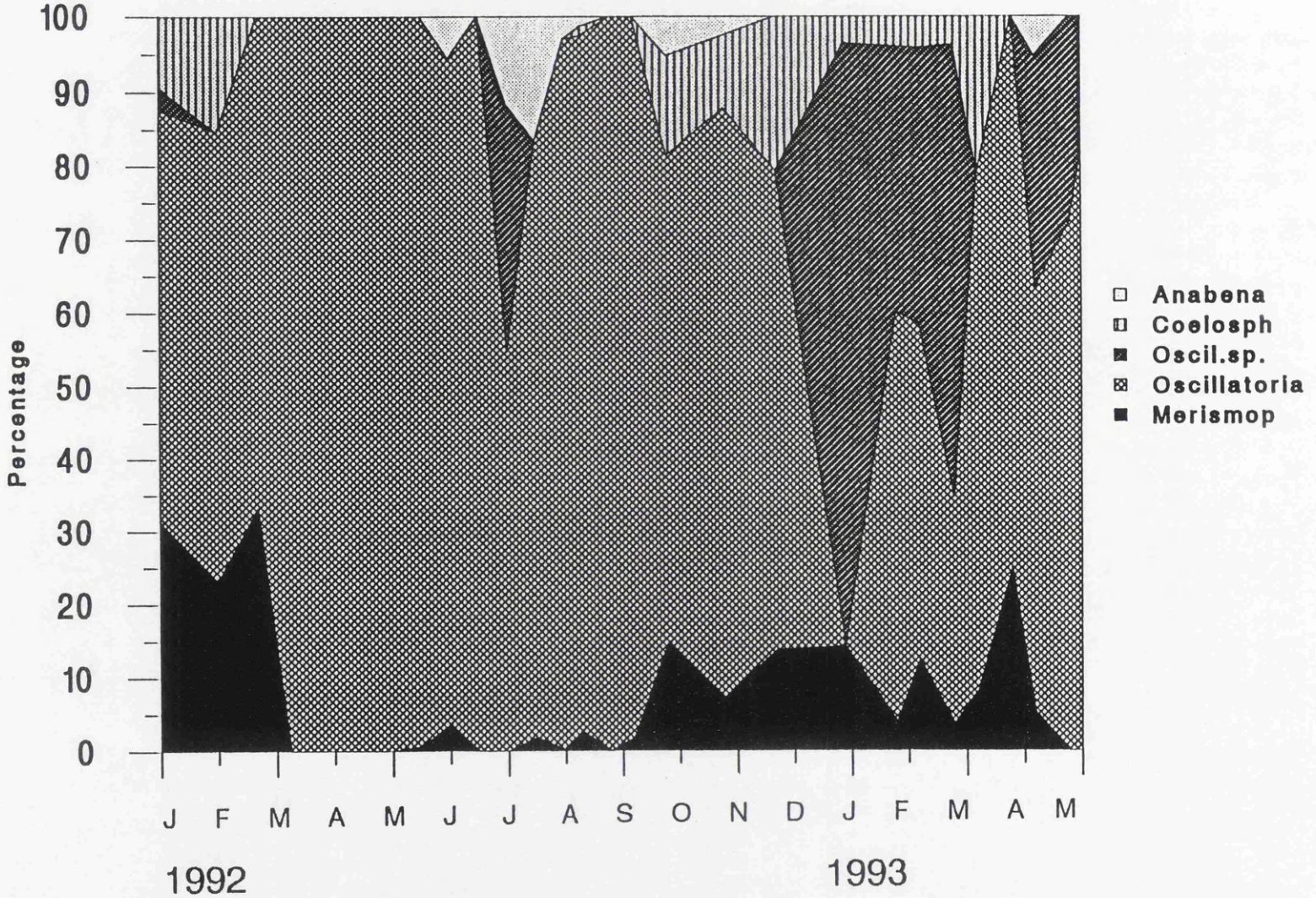


Figure (24) Seasonal distribution of blue green algae species (expressed as percentage) for the south basin



naegelianum was less dominant than in the south. The maximum percentage was in early January 1993 (16.7%).

Anabena circinalis showed a very low percentage of the total in the south basin, it did not exceed 16.6% during summer and early autumn 1992. In the north basin, it showed a high proportion ranging from 1.2 to 51.2% in the same period.

2.2.3.4. Diversity

Species diversity is one of the basic concepts of ecology that has been used to characterise communities and ecosystems. At first glance the concept appears to be rather simple but ecologists and mathematicians have been searching for ways to express the various aspects of diversity since 1922 (Gleason 1922) even though the term did not appear in literature until 1943 (Fisher *et al.*, 1943). Consequently, the concept has been defined in many ways, and several different indices have been developed to express it.

There are three common diversity indices in their sensitivity to the two aspects of diversity: species richness, species evenness and heterogeneity (DeJong, 1975). Species richness is usually thought of as the number of species per sample and makes a valid comparison only between samples of similar size. Species evenness (equitability) is a parameter which indicates relative abundances of the various species in a sample. Equitability increases as species are more evenly distributed in a sample such that a maximum is obtained when all the species are equally abundant. Species diversity is a function of the number of species richness and the evenness with which the individuals are distributed among these species (Margalf 1958, Lloyd and Ghelardi 1964, Pielou 1966). Species diversity increases as the number of species per sample increases and as the abundances of species within a sample become more even (Pielou 1969, Kricher 1972).

Good (1953) and Leti (1965) suggested the term heterogeneity. Margalef and Pielou, two of the strongest advocates of the heterogeneity approach have both stated how they consider diversity should be defined. Margalef (1969) explained that diversity is a statistical function that implies no particular regularity in distribution, and in whose computation the number of individuals in all the species are taken into account. Pielou (1969) wrote "diversity is a single statistic in which the number of species and evenness are confounded".

All diversity indices have some difficulties, but of the common ones available (Margalef, Simpson, Yule and Shannon-Wiener), Shannon-Wiener was chosen for this work and calculations were made using number of algal units (not cells).

Diversity index was calculated using Shannon-Wiener index (1949) and diversity also shown as sample number of species present (Figure 25 b). Figure (25 a) shows the results for the north and south basins. The north basin showed a higher diversity index from January to early May 1992 (winter-spring) and from late September to early March 1993 (autumn-winter) than the south. The south basin demonstrated a high diversity during late spring and summer (mid May-early September 1992). These differences between basins were not shown by a single count of number of species present.

It has been noticed that when biomass increased the diversity decreased. This phenomena was very obvious in the north basin. A highly negative correlation was found between biomass (as number of colonies) and diversity in the north basin only (over 90%), but both basins showed a high positive correlation between the diversity index and number of species, especially the south basin (Table 3 and 4). The north basin exhibited a highly negative correlation between diversity index and the three variables: biomass as number of colonies, biomass as number of cells and chlorophyll. The south basin did not show any correlation with the previous factors.

Table (3) Correlation coefficient between diversity index and other variables in the north basin

Diversity index	vs.	no. of colony	- 0.535	$p < 0.01$
Diversity index	vs.	no. of cell	- 0.545	$p < 0.01$
Diversity index	vs.	chlorophyll *a*	- 0.316	$p < 0.10$
Diversity index	vs.	no. of species	0.458	$p < 0.02$

Table (4) Correlation coefficient between diversity index and other variables in the south basin

Diversity index	vs.	no. of colony	- 0.214	
Diversity index	vs.	no. of cell	- 0.172	
Diversity index	vs.	chlorophyll *a*	0.085	
Diversity index	vs.	no. of species	0.553	$p < 0.01$

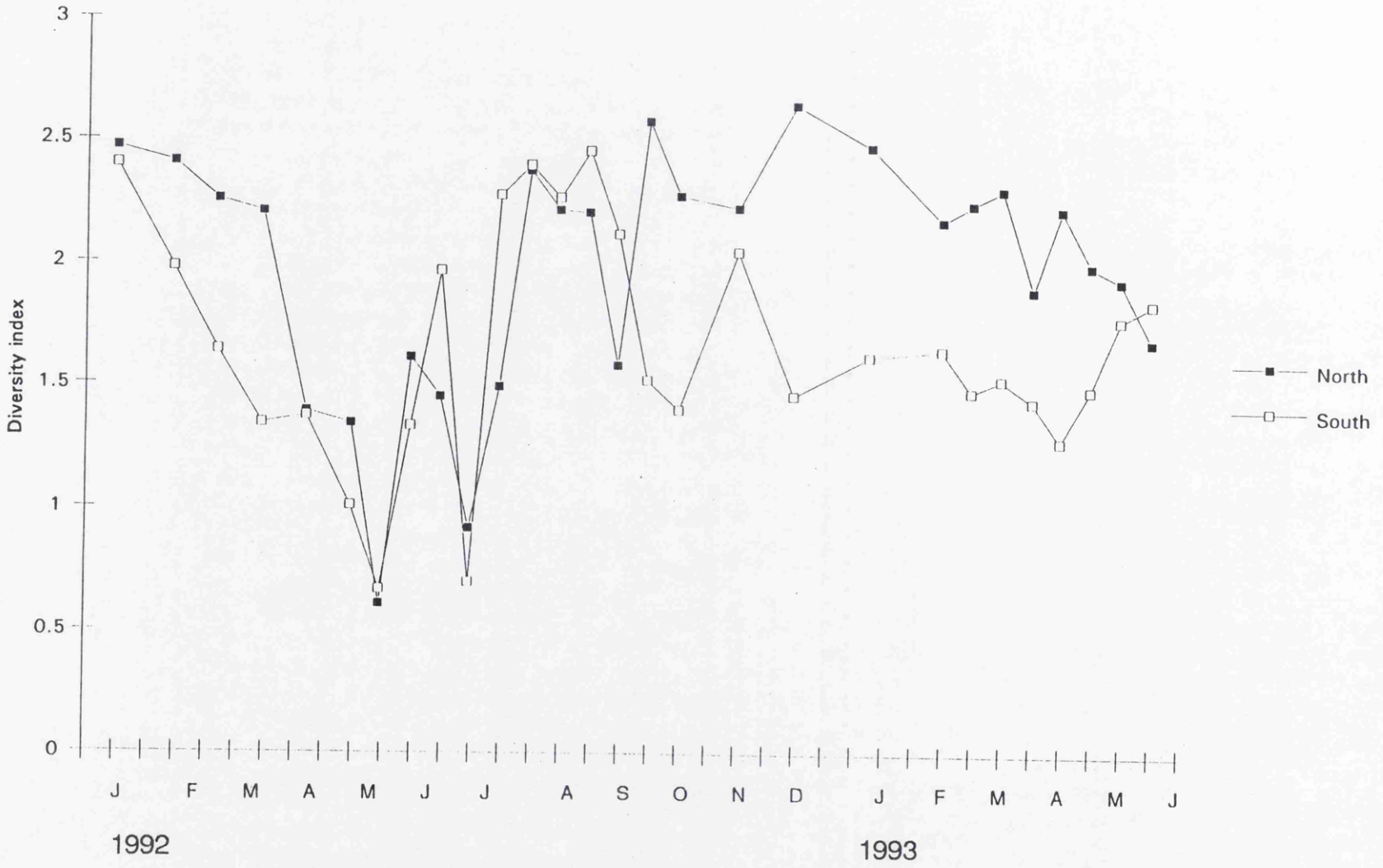


Figure 25a. Seasonal variation of Shannon-Wiener diversity index for the north and south basin

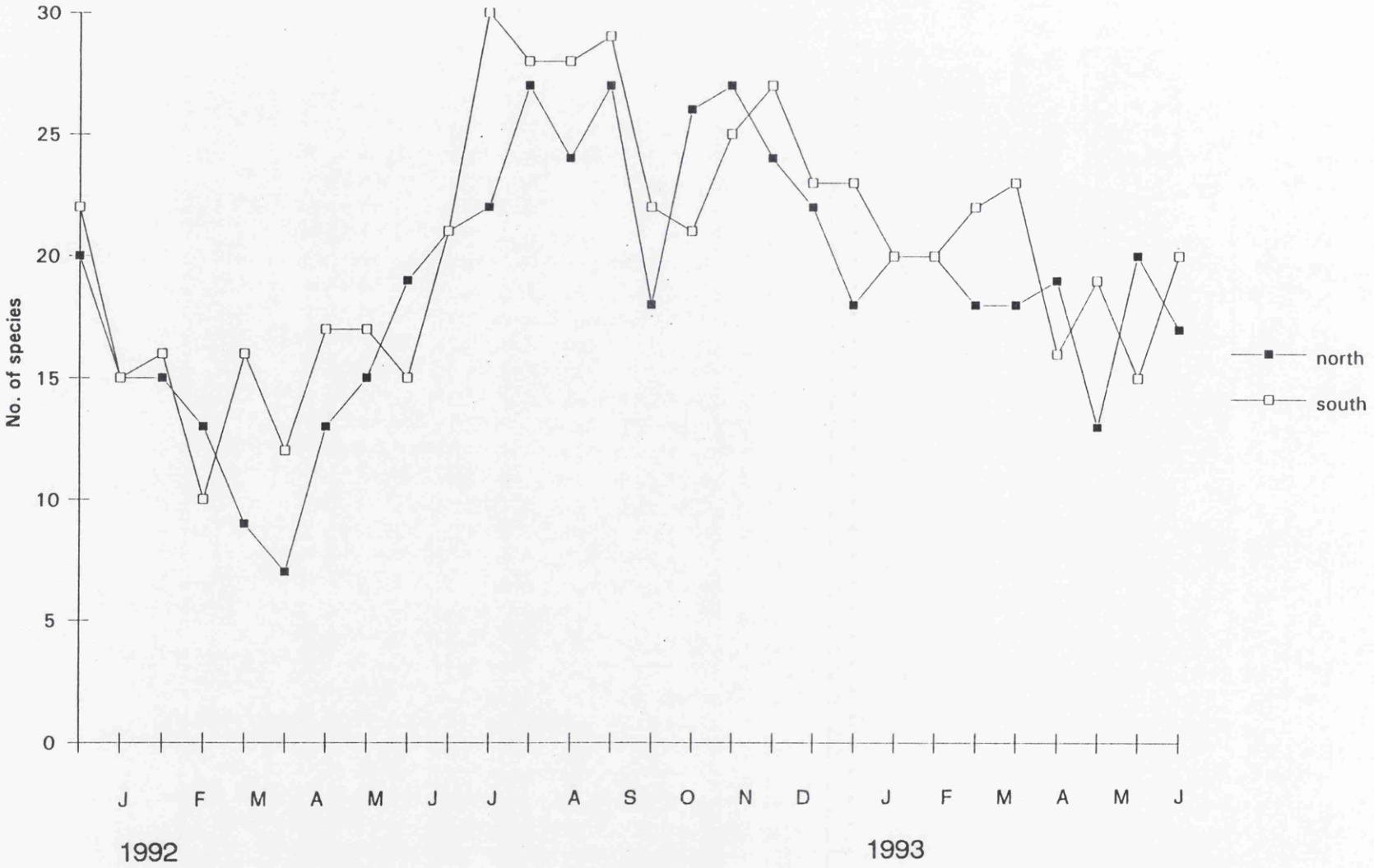


Figure 25b. Seasonal variation of species richness for the north and south basins

2.2.3.5. Correlation between phytoplankton and physicochemical environment

Appendices (3) and (4) show the correlation coefficients between 13 environmental factors and population parameters for the north and south basin respectively.

A matrix of 190 correlations was obtained. In the south basin, 33 correlations were significant but the north basin showed a slightly higher number of 47 correlations. Seven correlations, only, among the previous relations were the same in both basins. Tables (5) and (6) show the most significant environmental factors in the north and south basin respectively.

Table (5) The correlation coefficient of the most significant variables in the north basin ($p < 0.001$)

			r	r^2
Temperature	vs.	DO mg	-0.715	0.51
Phosphate	vs.	DO sat	-0.746	0.56
Silicate	vs.	Temperature	-0.813	0.66
Chlorophyll a	vs.	Temperature	0.899	0.81
No phytoplankton	vs.	Temperature	0.773	0.60
Diatoms	vs.	Temperature	0.886	0.78
Chlorophyll a	vs.	Silicate	-0.694	0.61
No phytoplankton	vs.	Chlorophyll a	0.754	0.57
Diatoms	vs.	Silicate	-0.773	0.60
Diatoms	vs.	Chlorophyll a	0.845	0.71
Diatoms	vs.	No phytoplankton	0.722	0.52

Table (6) The correlation coefficient of the most significant variables in the south basin ($p < 0.001$)

			r	r^2
Temperature	vs.	DO mg	-0.798	0.64
Silicate	vs.	Temperature	-0.817	0.67
Nitrate	vs.	Silicate	0.792	0.63
Chlorophyll *a*	vs.	Silicate	- 0.828	0.69
Chlorophyll *a*	vs.	Nitrate	- 0.781	0.61
Diatoms	vs.	No phytoplankton	0.924	0.85

2.2.3.6. Multivariate analysis of species and environment

Classifying lakes using algae as indicator organisms is well documented in the literature (Brooke, 1959; Holland, 1968; Jarnefelt, 1952; Nygaard, 1949; Rawson, 1956; Round & Brook, 1959; Stockner, 1971; Stoermer, 1978; Teiling, 1955; Thunmark, 1945). Much of this information has been compiled for convenience by Lowe (1974). A system which would classify water bodies independently from the ecological requirements of species would be more desirable and have much wider applications.

TWINSPAN (Two-Way Indicator Species Analysis) a divisive classification technique developed by Hill (1979), is a system which ordinates both samples and species in a two-way cases attributes data matrix. In general, sampling sites (or sampling dates) are considered together initially and then divided hierarchically into groupings and smaller subgroupings. The system also provides a key to the sample classification by listing indicator species which are characteristic of each grouping and subgrouping. This information can then be pooled with physico-chemical data to further characterise and define sampling sites more fully.

The phytoplankton communities were classified using the computer program TWINSPAN (Hill, 1979). TWINSPAN has become a standard method for community classification. The program takes the site (or sampling dates)-species data and divides it into groups, the sites (or sampling dates) in each group being more similar to each other (in terms of their species present) than they are to the sites (or sampling date) in other group. This process is repeated a number of times, resulting in a hierarchical (dendrogram) classification, with a number of groups of sites as the product.

Problems in community ecology often require the inferring of species-environment relationships from community composition data and associated habitat measurements. Multivariate community analysis techniques based on older methods such as multiple linear regression models are often inadequate to define such relationships because these models

assume linear relationships, which in reality are more likely to be unimodal (Ter Braak and Van Dam, 1989).

Detrended Correspondence Analysis (DECORANA: Hill 1979, Hill & Gauch 1980), was until recently a standard method for ordination of survey data. A development of this method is Canonical Correspondence Analysis (CCA), one of the suite of methods in the software package CANOCO (Ter Braak 1985, 1986, 1989). This offers a number of advantages over DECORANA. In particular there are some improvements to the fundamental algorithms employed and the program allows direct (rather than indirect) correlation of environmental axes with site (or sampling date)-species data (Ter Braak 1985).

In common with other ordination programs, CCA extracts from data consisting of the abundance of species at a number of sites (or sampling data), the dominant pattern of variation in community composition. This pattern of variation may then be correlated with the variation in environmental variables. CCA provides a number of options to carry out this analysis. CCA is a correspondence analysis technique in which the axes are chosen in the light of the environmental variables. It was used here to identify the relative positioning (site-date) of assemblages of phytoplankton taxa along environmental gradients in the CCA ordination field.

CCA provides a direct gradient analysis of all species simultaneously in relation to the underlying gradients within the measured environmental variables. Axes are derived that are linear combinations of environmental variables. Individual species are related directly to these axes under the assumption of a unimodal species response to the environmental variables.

Table (7) summarising lists the content of 4 species-groups identified by the divisive TWINSPAN classification (see also Figure 26). The 43 phytoplankton species recorded in the two sampling stations (north and south basins) on each of 28 sampling date (total 56 samples) were used to produce a species classification for Loch Lomond.

Table (7) TWINSPAN classification of species into groups (A-D)

Group A (12 species)

1 Mel Spp *Melosira italica*

2 Ast Spp *Asterionella formosa*

8 Eun Spp *Eunotia pectinalis*

9 Syn Spp *Synedra tenera*

10 Nav Spp *Navicula sp*

11 Cym Spp *Cymbella sp*

12 Fru. Spp *Frustulia rhomboides*

13 Sur Spp *Surirella robusta*

17 Coe Spp *Coelospherium naegelianum*

18 Spi Spp

26 Clo Spp *Closterium toxon*

42 Fil Thn *Oscillatoria sp* (c. f. *Oscillatoria angustissima*)

Group B (9 species)

3 Tab Ast *Tabellaria fenestrata*

4 Tab Spp *Tabellaria floculosa*

7 Cyc Spp *Cyclotella kutzingiana*

15 Osc Spp *Oscillatoria agardhii*

16 Hol Spp *Merismopedia glauca*

20 Cry Spp *Cryptomonas ovata*

39 Mal Spp *Mallomonas acaroides*

41 Dia Unk

43 Unk Unk (c. f. *Ankistrodesmus convalutus*)

Group C (9 species)

5 Tab Int *Tabellaria fenestrata*

6 Fra Cro *Fragilaria crotonensis*

24 Sta Spp *Staurastrum cingulum*

25 Cos Spp *Cosmarium depressum*

28 Sce Spp *Scenedesmus quadricauda*

30 Ped Spp *Pediastrum boryanum*

31 Sta Spp *Staurodesmus spencerionus*

32 Bot Spp *Botryococcus braunii*

38 Ank Spp *Ankistrodesmus falcatus*

Group D (13 species)

14 Coc Spp *Cocconeis sp*

19 Ana Spp *Anabena circinalis*

21 Per Spp *Peridinium willei*

22 Cer Spp *Ceritum hirundinella*

23 Gym Spp *Gymnodium caudatum*

27 Ooc Spp *Oocystis sp*

29 Dic Spp *Dictyospherium pulchellum*

33 Spo Spp *Spondylosium planum*

34 Gon Spp *Gonatozygon sp*

35 Spi Spp *Spirogyra sp*

36 Coe Spp *Coelastrum sp*

37 Xan Spp *Xanthidium antilopoeum*

40 Bin Spp *Dinobryon divergens*

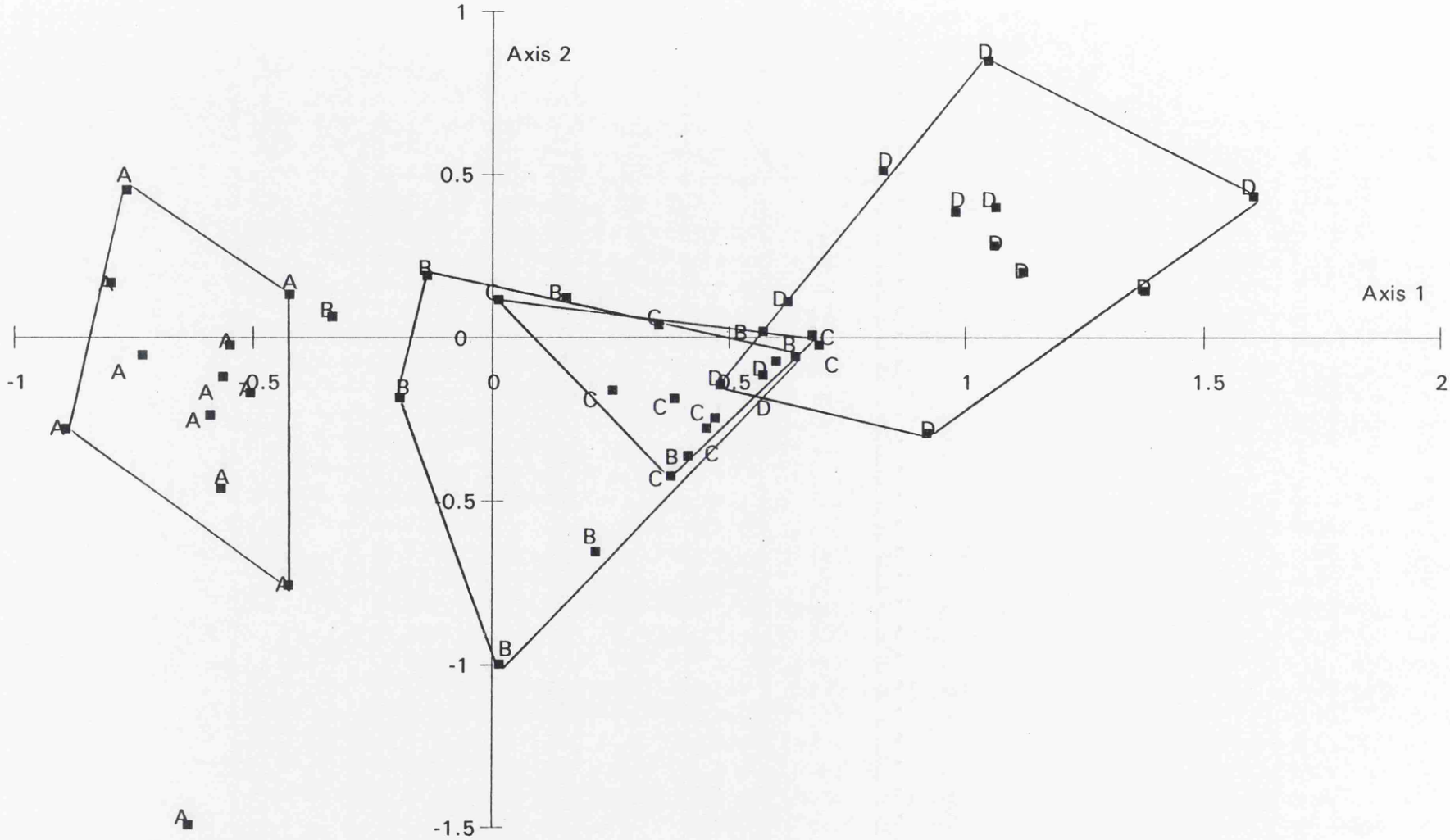


Figure 26 Species ordination using Canonical Correspondence Analysis (CCA) 1992-1993, with TWINSPAN species groups (c.f., Table 7) overlaid on the plot

Because of identification difficulty in the beginning, *Tabellaria inter* (5) was counted alone, but for the final results it was combined with *Tabellaria fenestrata.* Initially taxon 18 was identified as *Spirulina sp* (18), and distinguished from other thin filamentous algae (taxon 42). Subsequently, however, taxon 42 was identified as *Oscillatoria sp* (c.f. *Oscillatoria angustissima*) and specimens of taxon 18 were reassigned to this taxon: for taxon 18 read taxon 42, throughout. The TWINSPAN analysis divided the species initially into two groups of 21 species and 22 species at the first level. It then subdivided each of these groups into two subgroups: subgroup A consists of 12 species, subgroup B with 9 species, subgroup C with 9 species and 13 species within subgroup D.

Group A:

This group includes mainly diatoms, together with two blue green algae and one green alga taxa. *Melosira italica* and *Asterionella formosa* were the dominant almost throughout the data set, but with differing abundances. The rest of the diatoms were rare or occurred occasionally in winter and spring. *Oscillatoria agardhii* was moderately abundant during winter, spring and early summer.

Group B:

This group was a mixture of diatoms, blue green algae and flagellates. *Tabellaria fenestrata, Tabellaria floculosa* and *Cyclotella kutzingiana* were the most important species. They were present almost throughout the year. In general all the species occurred in this group are perennial but with different abundance.

Group C:

This group was dominated by green algae and one diatom species. *Fragilaria crotonensis* is the most important species among this group, it is almost a perennial species. The rest of the group was a rare green algae species and occurred sometimes in low abundance.

Group D:

This group characterised by a mixture of different group of algae like flagellates, green, blue green algae and diatoms. All these species were rare or recorded once or twice only.

Table (8) Abundance values (1-9) used for TWINSPAN analysis showing range of terms of counts of algal units per litre

1 =	1 -60
2 =	61 -100
3 =	101 -200
4 =	201 -500
5 =	501 -1000
6 =	1001 -10000
7 =	10001 -50000
8 =	50001 -150000
9 =	150001 -200000

Table (9) TWINSPAN classification samples into groups (1-4)

Group 1 (25)	Group 2 (15)
1= 15 Jan. 1992, N	7= 19 May 1992, N
2= 11 Feb. 1992, N	8= 2 Jun. 1992, N
3= 3 Mar. 1992, N	9= 16 Jun. 1992, N
4= 24 Mar. 1992, N	18= 4 Nov. 1992, N
5= 14 Apr. 1992, N	29= 15 Jan. 1992, S
6= 5 May 1992, N	33= 14 Apr. 1992,S
19= 1 Dec. 1992, N	34= 5 May 1992, S
20= 6 Jan. 1993, N	35= 19 May 1992,S
21= 9 Feb. 1993, N	36= 2 Jun. 1992, S
22= 23 Feb. 1993, N	37= 16 Jun. 1992, S
23= 9 Mar. 1993, N	46= 4 Nov. 1992, S
24= 23 Mar. 1993, N	53= 6 Apr. 1993, S
25= 6 Apr. 1993, N	54= 20 Apr. 1993, S
26= 20 Apr. 1993, N	55= 4 May 1993, S
27= 4 May 1993, N	56= 19 May 1993, S
28= 19 May 1993, N	
30= 11 Feb. 1992, S	
31= 3 Mar. 1992, S	
32= 24 Mar. 1992, S	
47= 1 Dec. 1992, S	
48= 6 Jan. 1993, S	
49= 9 Feb. 1993, S	
50= 23 Feb. 1993, S	
51= 9 Mar. 1993, S	
52= 23 Mar. 1993, S	

Group 3 (6)

17= 7 Oct. 1992, N

41= 11 Aug. 1992, S

42= 25 Aug. 1992, S

43= 8 Sep. 1992, S

44= 22 Sep. 1992, S

45= 7 Oct. 1992, S

Group 4 (10)

10= 30 Jun. 1992, N

11= 14 Jul. 1992, N

12= 28 Jul. 1992, N

13= 11 Aug. 1992, N

14= 25 Aug. 1992, N

15= 8 Sep. 1992, N

16= 22 Sep. 1992, N

38= 30 Jun. 1992, S

39= 14 Jul. 1992, S

40= 28 Jul. 1992, S

Table (9) summarising the divisive TWINSPAN sample classification scheme is presented in Figure 27. This program divided the sample into two groups of 40 and 16 samples at the first level. Then subdivided each of these groups into 2 subgroups: subgroup 1 consists of 25 samples, subgroup 2 with 15 samples, subgroup 3 with 6 samples and 10 samples among subgroup 4.

Table (8) shows the abundance values (1-9) used for TWINSPAN analysis showing the range of terms of counts of algal units per litre.

Group 1:

This group includes 16 samples of the north basin and 9 samples of the south basin. These samples were mainly in winter and early spring. Two indicator characterised this group: *Oscillatoria sp* (2) (c.f. *Oscillatoria angustissima*) and *Eunotia pectinalis* (1). (The value in brackets after indicators represents pseudospecies, i.e. the species at a given abundance level, as shown in Table 8).

Group 2:

This group was dominated by the south basin sample (11 samples) whereas 4 samples only accounted for the north basin. These samples were mainly in spring except 2 samples of late autumn. *Oscillatoria agardhii* (5), *Fragilaria crotonensis* (2), *Tabellaria fenestrata* (5), Diatom unknown (unidentified) (5) and *Cyclotella kutzingiana* (5) were the indicator for this group.

Group 3:

All the samples in this group were from the south basin except one sample of the north basin. The group was characterised by summer and early autumn samples. The indicators were *Fragilaria crotonensis* (5), *Scenedesmus quadricauda* (4) and *Mallomonas acaroides* (2).

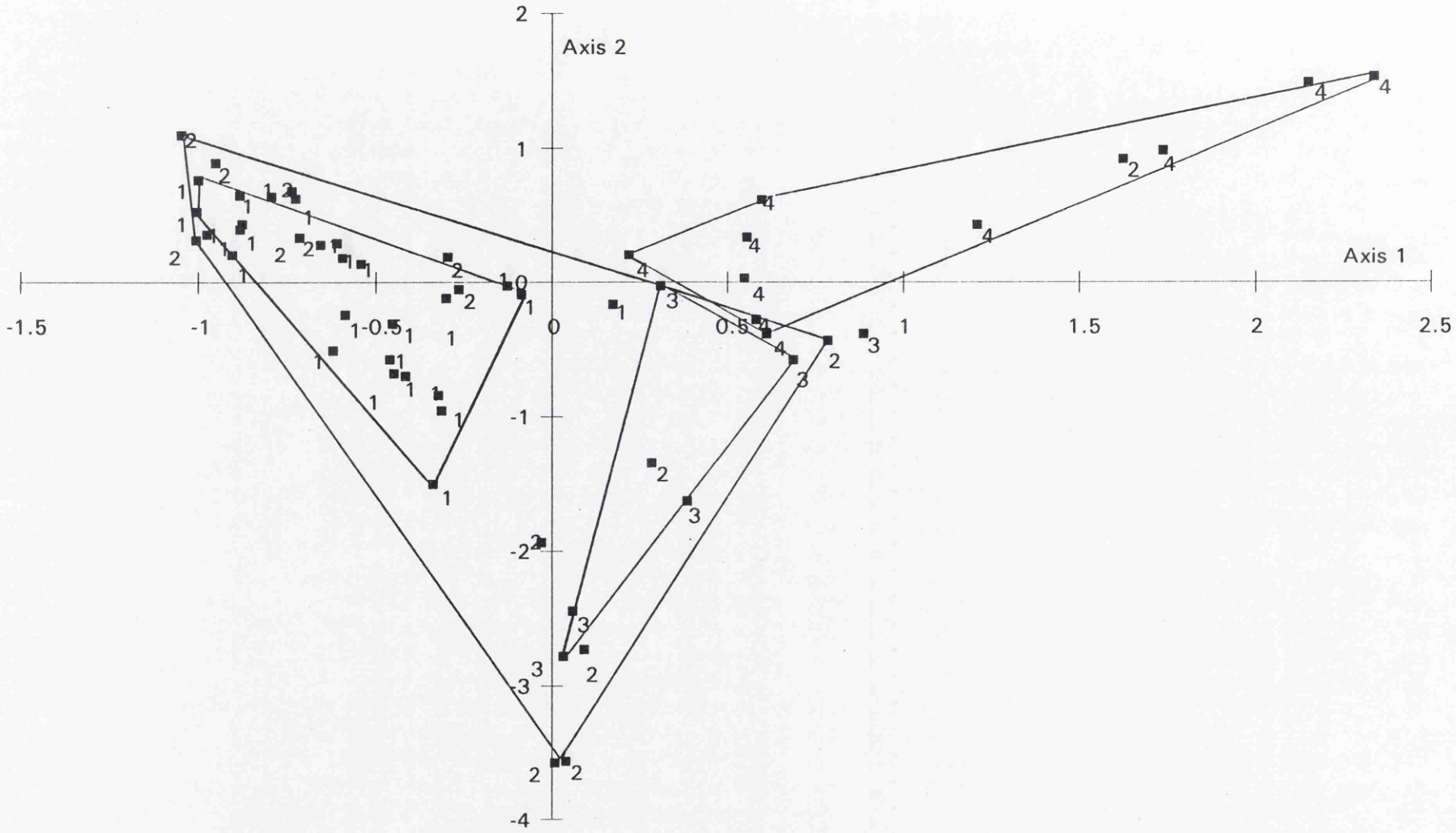


Figure 27 Ordination diagram using CCA with sample score groups, with TWINSPAN samples groups (c.f., Table 9) overlaid on the plot

Group 4:

The north basin samples comprised 70% from the total samples. Most of the samples occurred in summer and early autumn. *Spondylosium planum* (4) was the only indicator for this group.

In general group 1 and 2 could be considered as one group especially because most of the samples occurred mainly in winter and spring. The same would be the case for groups 3 and 4 which are characterised by summer and early autumn samples. Compared with the ordination of species (Figure 26), which showed a clear separation of the 4 main groups identified by TWINSPAN, there is a poorer separation of samples (species assemblage) in Figure 27. Nevertheless, as is shown by Figure 28, was a reasonable separation of samples from the north and south basin.

Application of CCA to the data set from Loch Lomond produced a sample biplot (Figure 29) in which the ordination axes were defined by the environmental variables such that each variable was represented by an arrow pointing in the direction of maximum change within the species set. The length of the arrow represents the importance of that variable. The longer the arrows, the more highly correlated with the axes are the variables. The length is derived from the eigen value of the axes (i.e. which has a value between 0 and 1; the higher the value the more important the ordination axes; the eigen value is also a measure of separation of the species distributions along the ordination axes) and the interest of that variable with the axes.

Species are plotted on the diagram (Figure 29) using the species scores. The point at which the species is plotted represents the centroid of distribution of the species, i.e. the point at which the species is most abundant on the diagram. The closer species (and sites or sampling date if plotted) are to each other, the more similar they are (in this case in terms of environmental variables as well as species composition). If a perpendicular line is

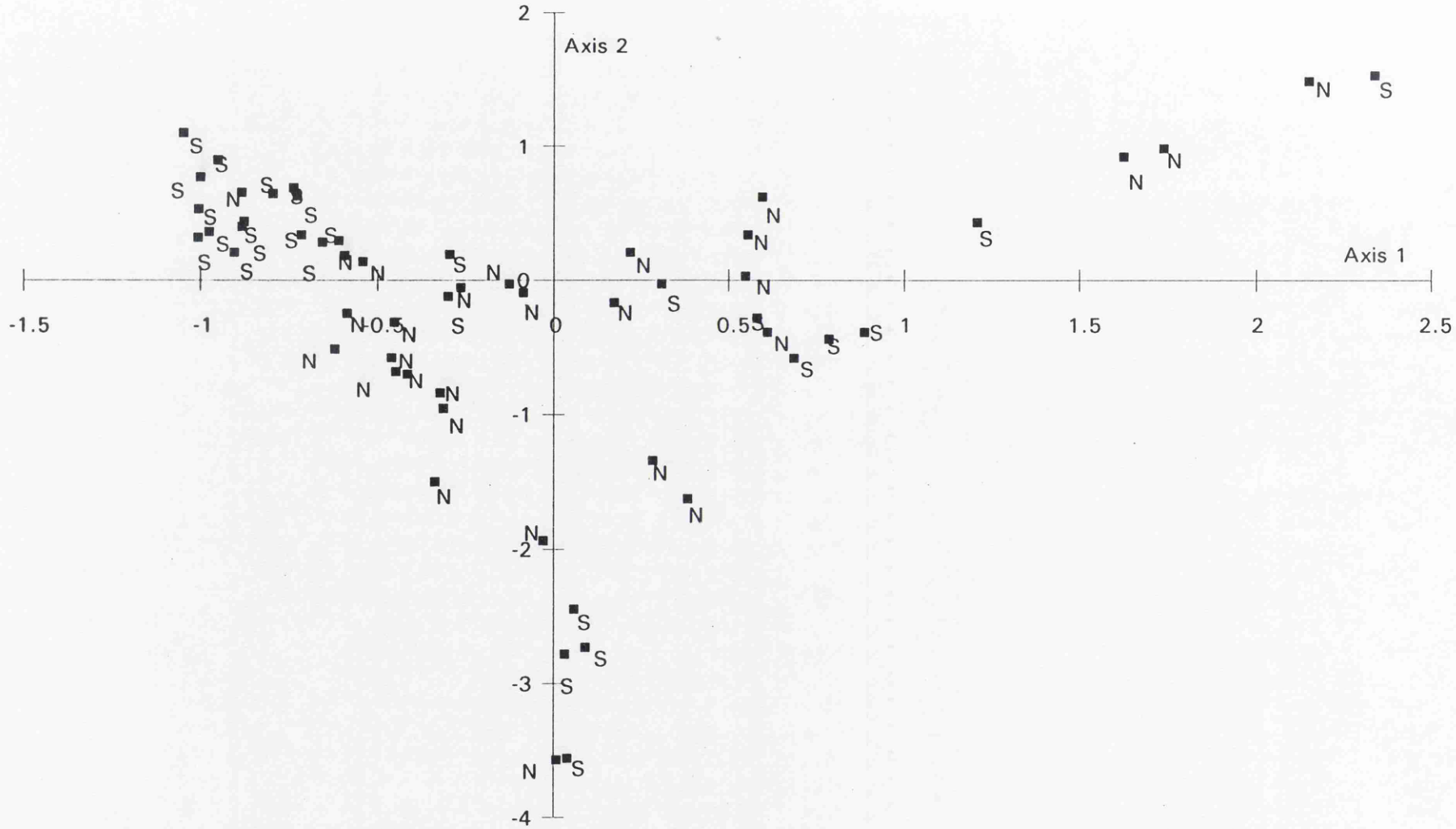


Figure 28 Overlay plots of geographical location (N = north, S = South) on sample CCA ordination

dropped from species points to an environmental arrow the species may be ranked in terms of its relative position along the environmental gradient which the arrow represents. The species points jointly represent the dominant patterns in community composition insofar as these are explained by the environmental variables, and the species points and the arrows of the environmental variables jointly reflect the species' distributions along each of the environmental variables.

Axis 1 was significantly negatively correlated with dissolved oxygen ($p < 0.001$), conductivity ($p < 0.001$), silicate ($p < 0.001$), chemical oxygen demand ($p < 0.001$), nitrate ($p < 0.01$) and phosphate ($p < 0.01$); and significantly positively correlated with temperature ($p < 0.001$) and light penetration (as shown by Secchi disc depth) ($p < 0.001$) (Table 10).

The strong influence of this temperature gradient is seen on the species plot which shows green algae and flagellates (groups C, D) like *Staurastrum cingulum*, *Cosmarium depressum*, *Ceritum hirundinella*, *Gymnodium caudatum* and *Dinobryon divergens* apparently favour by high temperature, while species like *Tabellaria floculosa*, *Cyclotella kutzingiana* and *Mallomonas acaroides* appeared to be favoured by low temperature.

Axis 2 was significantly positively correlated with chlorophyll ($p < 0.01$) and dissolved oxygen ($p < 0.001$). The strong influence of silicate gradient is seen on the species plot which shows diatoms (group A), like *Melosira italica* and *Asterionella formosa*, require high silicate compared with *Cocconeis* which has a low demand of silicate.

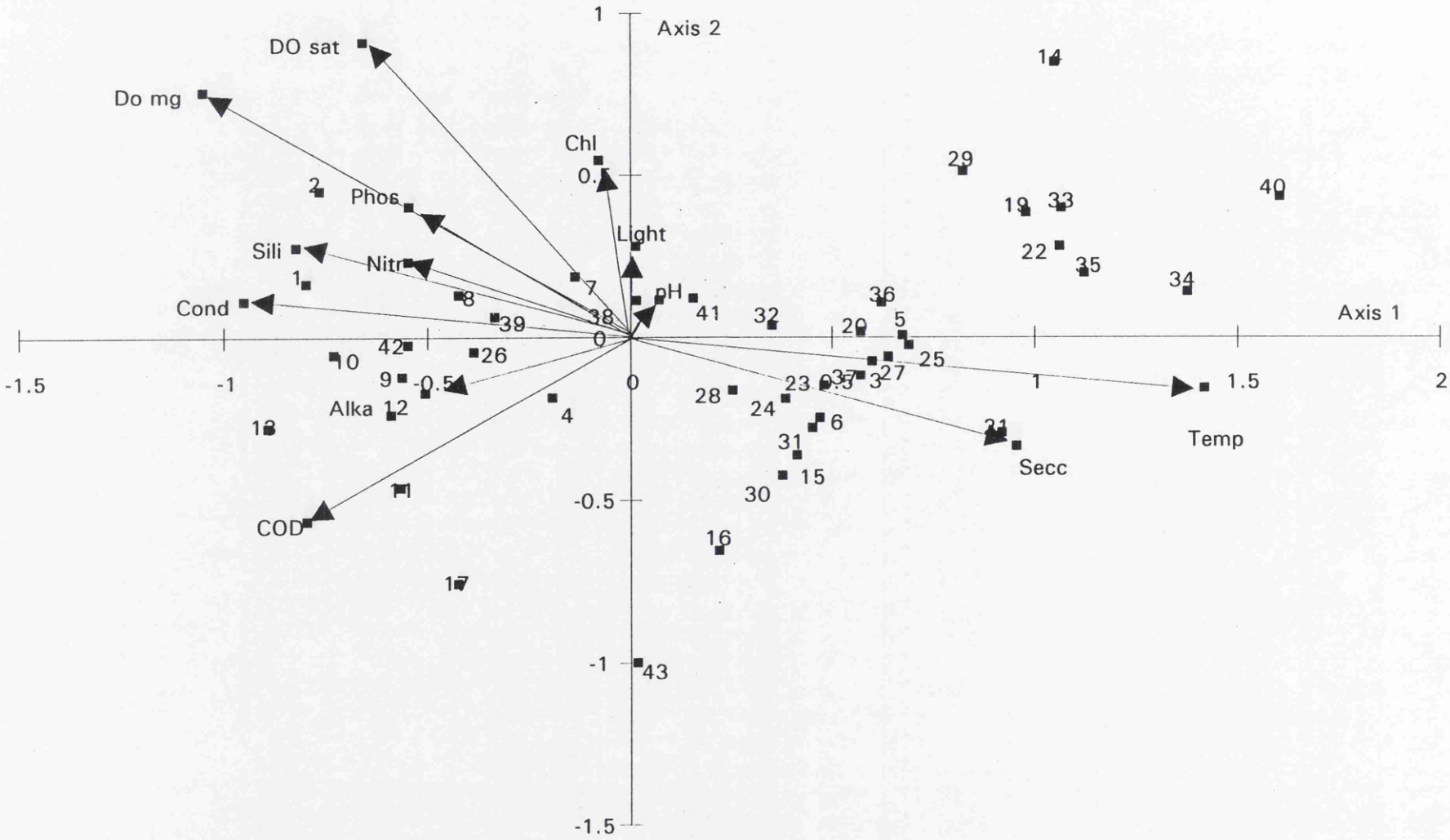


Figure 29 Environmental ordination using CCA for data from Loch Lomond 1992-1993

Table (10) Correlation coefficients between environmental variable and CCA. Level of significance are represented as follows;*** = $p < 0.001$ and ** = $p < 0.01$. Eigen values represent the percentage variation in the data accounted for by the axis.

Variable	Axis 1	Axis 2
DO sat	-0.4391***	0.6065***
DO mg	-0.7001***	0.5025***
Temperature	0.9456***	-0.1040
pH	0.0476	0.0779
Secchi disc reading	0.6362***	-0.2235
Light	0.0084	0.1875
Conductivity	-0.6337***	0.0744
Alkalinity	-0.2571	-0.0294
Phosphate	-0.3638**	0.2687
Silicate	-0.5483***	0.1843
Nitrate	-0.3644**	0.1557
COD	-0.5309***	-0.3766
Chlorophyll a	-0.0526	0.3635**
Eigen value	0.9559	0.7332

2.2.4. Discussion

The annual periodicity of phytoplankton in temperate zones is primarily controlled by seasonal changes in incident light and water temperature levels (Hutchinson, 1967). During winter months, light energy is the main limiting factor for the growth of algae and normally enable nutrient levels to increase over this period (Moss, 1988). These nutrients then decline in spring when the growth of phytoplankton populations takes place under increasing temperatures and insolation levels.

Phytoplankton standing crop in this project was measured in two ways: chlorophyll and cell counts.

In general, the south basin retains a higher standing crop and the growing season usually starts earlier than in the north basin and extends over a longer period of time.

Although both chlorophyll *a* and phytoplankton numbers for the south basin recorded three peaks for the chlorophyll and five peaks for the phytoplankton numbers throughout the whole data set, the chlorophyll *a* peak always either preceded, as at the end of June, or coincided with the peak of numbers.

In the north basin, the chlorophyll *a* peak coincided with the peak number of phytoplankton at the end of June, but the August peak for chlorophyll *a* preceded it.

The range in the amount of chlorophyll *a* was smaller than that in numbers in both basins except during the period from mid June to the end of July in the north where the number of phytoplankton exceeded that in the south basin.

Although the largest peak for chlorophyll *a* in the south basin was in autumn, the largest peak for numbers was at the end of June.

The advantages of using the chlorophyll method lie in the relative quickness of manipulation and the absence of any laborious counting procedure so it is widely used world wide. There are, however, disadvantages. There is uncertainty that all the algal cells

in the filtered material yield their total chlorophyll content to the same extent, and the filtration process may damage the more delicate organisms (Boney, 1978).

The amount of chlorophyll per cell varies according to species, rate of growth, physiological conditions and environmental conditions (Nusch, 1980).

For instance, the amount of chlorophyll in a cell depends on the rate of division (generally speaking there is less per cell at times of rapid cell division) and the type of cell. Some, such as large desmids, have a lot of chlorophyll, whereas others such as flagellates, have very much less. This is in agreement with what was mentioned previously; chlorophyll's peak either preceded or coincided with phytoplankton number.

Nevertheless, chlorophyll estimations can play some part in the seasonal studies of loch phytoplankton. Measured at short time intervals these values can give a quick indication of the short term (diurnal) fluctuations in a population (Boney, 1978).

The disparity between the chlorophyll and cell count results can be explained in two ways. Firstly, the largest peak of chlorophyll *a* (September) is more likely to be affected by the degradation products of phytoplankton during the latter part of the growing season than in spring when populations are growing more actively. No correction was made in this study or Maulood 1974 or Bailey-Watts and Duncan 1981. Bucher (1991) concluded that we should "forget about calculated pheophytin" because potential inaccuracies in the method are more likely to be misleading than useful. Secondly, a simple analysis of cell numbers takes no account of the different sizes of individuals, and whether single cells, colonies or filaments are counted. Figure (18b) shows the total number of phytoplankton as cell l^{-1} (for diatoms colony only) to compare with chlorophyll data. In this Figure, two peaks were recorded in spring and autumn 1992 with the spring one being higher than the autumn. The spring peak of 1993 was earlier by two weeks and higher by 2 and 2.5 times than 1992 in the north and south basin respectively.

Both basins, showed a highly positive correlation between chlorophyll and temperature with different level of significance, for the north basin ($p < 0.001$) and ($p < 0.01$) for the

south basin. The north basin only showed a positive correlation with light ($p < 0.05$). These are direct correlation as one would expect.

Bailey-Watts and Duncan (1981), studied Scottish lochs, Loch Lomond (north basin only) among them. They concluded that the levels of chlorophyll recorded were very low, the highest being only 3.2 $\mu g\ l^{-1}$ in Loch Awe, which occurred in June and preceded the August maxima in all the other lochs. The maximum value for Loch Lomond was 2.9 $\mu g\ l^{-1}$ in mid August 1978 and the minimum was 0.2 $\mu g\ l^{-1}$. These data were in agreement with Bailey-Watts and Duncan's but higher than Maulood's by a factor of 10.

Comparison can be made with other bodies of water which have a similarity to Loch Lomond in one or more aspects. Vaquer and El Hafa (1991) demonstrated that the chlorophyll concentration generally varied between 0.1 and 3.5 $\mu g\ l^{-1}$ in an oligo-mesotrophic lake. In a mesotrophic type of water, Eloranta and Palamaki (1986) recorded average chlorophyll of 4.6 $\mu g\ l^{-1}$. In the North Channel of Lake Huron, Munawar *et al.* 1988 pointed out that the maximum concentration of chlorophyll was 2.9 $\mu g\ l^{-1}$ in May. Compos *et al.* 1990, recorded a range of chlorophyll between 0.04 and 1.03 $\mu g\ l^{-1}$ for the upper integrated layer (0 to 40 m) for oligotrophic water, but this low value could be due to the length of the column of water. In West Okoboji Lake, Bachmann (1990) found chlorophyll concentration ranged from 3 to 4 $\mu g\ l^{-1}$. Miyazaki *et al.* 1989 demonstrate a slightly higher concentration of chlorophyll at 1m, it ranged between 0.4 and 6.5 $\mu g\ l^{-1}$. The maximum value which Dakulil and Skolaut 1986 recorded was higher than any recorded values for Loch Lomond. They found 16 $\mu g\ l^{-1}$ during the spring growth of diatoms in Mondsee, Austria. Pettersson 1990, recorded even higher concentrations than Dokulil and Skolaut, with an average of 30 $\mu g\ l^{-1}$ in the epilimnion. Megard, (1972) demonstrated an average concentration of chlorophyll range from 13 to 35$\mu g l^{-1}$. The last three sets of data were very high compared with both basin of Loch Lomond.

Brylinsky and Mann (1973) noted that chlorophyll *a* concentration showed a strong positive correlation with phytoplankton number. This has also been found to be true of the

marine systems (Ryther and Yestsch 1957, 1958) and it has been suggested that chlorophyll *a* concentration is also a good indicator of nutrient conditions too (Harvey 1953, Yenstsch and Vaccaro 1958). These results support this work, for instance, phytoplankton biomass was closely positive correlated with chlorophyll concentration in the north basin ($P < 0.001$) and in the south basin ($P < 0.01$). Both basins showed a highly negative correlation between chlorophyll and silicate ($p < 0.001$). This correlation is so obvious because diatoms represent the dominant group in Loch Lomond. Nitrate also showed a highly negative correlation with chlorophyll ($P < 0.001$) in the south basin only.

The phytoplankton community consisting of 43 species from each basin of Loch Lomond was analysed in relation to 13 environmental variables. Two multivariate methods were applied: TWINSPAN for classification and Canonical Correspondence analysis (CCA). CCA allows a straightforward display of the locations of species along environmental gradients reflected in phytoplankton composition. Multivariate methods have been used in many studies of phytoplankton community ecology (e.g. Allen and Skagen, 1973; Colebrook, 1982; Kaneta *et al.*, 1985; Tharrington-Smith, 1971) but direct gradient analysis of the type used here appears to be a relatively new approach for this plant community type (Fangstrom and Willen, 1987).

TWINSPAN is based solely upon analysis of species abundance without reference to the environmental variables. CCA on the other hand separates species along compositional axes which are optimally related to linear combinations of those environmental variables for which data are supplied.

When the TWINSPAN species groups are plotted as an overlay on the CCA biplot there is good evidence of a clear separation of Loch Lomond algal species along Axis 1 of the ordination forming, four main groups. The left hand side of the biplot was occupied by Group A which was dominated by diatoms. Groups B and C had a mixture of diatoms, blue-greens and flagellates located the middle. The right hand side of the ordination was

occupied by Group D which was dominated by flagellates, greens, blue-greens and diatoms.

When the TWINSPAN sample classification was overlaid on the CCA ordination there was a less clear separation along the Axis into four groups. In general the left hand side of the ordination was occupied by winter and spring samples, represented by Groups 3 and 4.

The geographical location of samples in the north and south basin showed little evidence for any clear separation into north vs. south when the TWINSPAN plot was overlaid on the CCA ordination. Thus, it seems to be that the temporal variation is more important than spatial variation in determining species assemblage characteristics in Loch Lomond.

The results of CCA ordination produced by CANOCO are broadly in line with what would be expected. In a study of Swedish lakes Fangstrom and Willen (1987) concluded that the position of the various phytoplankton species in the diagram is determined by their relative abundance along the environmental gradients present (e.g. pH). In the present study, phytoplankton species plotted in the left hand side of the diagram are mostly associated with high availability of nutrients (typical winter and spring conditions). Those occurring towards the right hand side of the diagram are mostly associated with low availability of nutrients and higher water temperature species (typical summer and early autumn conditions). Silicate appeared to be more important than nitrate and phosphate.

Bailey-Watts and Duncan (1981) stated that of the five main lochs studied in Scotland Loch Lomond and Loch Awe are considered relatively richer waters holding 42 and 43 species respectively. These results are in agreement with their result which proved that both basin retain 42 species.

The diversity of the phytoplankton communities was measured in this study by the Shannon-Wiener index. The diversity index was higher in the north basin than the south basin most of the time. In the south basin, the maximum growth of phytoplankton coincided with a decrease in the diversity index. No big seasonal difference of the diversity index was recorded in the north basin.

The high diversity index during summer coincided with high number of species of both basins. The coexistence of a relatively large number of species under more limiting conditions in summer (Hutchinson, 1967) seems to be the result of a non-uniform environment in a period of stratification (Moss, 1972). Margalef (1958) stated that diversity increases with time during the spring and summer development of phytoplankton populations in temperate waters. In 1964 and 1965, Margalef pointed out that the cause of the decrease in phytoplankton diversity, when biomass increases, is the richness of nutrients.

The range of diversity in the south basin (between 0.7-2.46 with an annual mean 1.66) was slightly lower than the north basin (between 0.61-2.65, annual mean 1.97). These values are slightly lower than those for pervious work in 1970-1972, when values recorded for the south basin were between 1.5-3 (Tippett, unpublished).

Phytoplankton diversity seems to be lower in spring than during summer and autumn. This seems to be related to the common dominance of diatoms in the phytoplankton after the winter.

Elber and Schanz (1989) stated that high values of diversity, or increase in diversity, were a result of low nutrient availability and grazing pressure. Lower diversity values, or decreases in diversity, were a result of a plentiful nutrient supply, low grazing pressure and grazer selectivity with respect to food organisms.

The greater diversity in the north than the south is in agreement with the observation of Margalef (1964, 1968) who pointed out that phytoplankton communities in infertile waters are more diverse than those in fertile waters.

During winter and early spring, the community was dominated by diatoms in the south basin and the north basin but with a slightly lower percentage. Diatoms are seldom lacking in the plankton community, except in extremely oligotrophic lakes, and they often predominate, especially during the so called spring outburst (Rosen, 1981). Similar results showing that diatoms predominate in winter and spring have been found by many other workers (Mooney 1989, Priddle and Happey-Wood 1983, Munawar *et al.* 1991, Abdul-Hussein and Mason 1988, Munawar *et al.* 1988, Munawar and Munawar 1988, McCombie 1953, Rosen 1981, Munawar and Munawar 1976, Compos *et al.*, 1990, Neale *et al.*, 1991). Hickman (1979) found that growth of diatoms populations was negatively correlated with dissolved silica ($r = -0.54$, $P < 0.05$). These results are in agreement with him, the north basin showed a high negative correlation ($r = -0.77$, $P < 0.001$) but the south basin showed unsignificant negative correlation (Appendix 3 and 4).

Diatoms *Melosira italica*, *Cyclotella kutzingiana* and *Asterionella formosa* dominated in winter and early spring in the south basin and were the first species to grow in springs. This early start was presumably due to the ability of these three species to grow under conditions of weak light and low temperatures which are less suitable for other algae (Lund, 1965). In the north basin compared with the south basin, it was the same except that *Tabellaria fenestrata* replaced *Asterionella formosa* over the same period. The faster rate of increase of *Melosira italica* (Lund, 1954) lead to its forming the first spring peak in April (north basin) or early May (south basin)(Appendix 6). The different optimal temperature conditions of each species influenced on the rate of division (Lund, 1950, 1954) and therefore these successional peaks. *Melosira italica* attained its maximum after a slight increase in winter temperature from 5 C to 8 C and *Cyclotella kuzingiana* at about 11 C.

The small number of cells per colony of *Melosira italica* found throughout spring-summer was likely to be determined by the rate of division and silicate supply (Lund, 1949;

Gardiner, 1940, 1941) (Appendix 6). Hecky *et al.*, 1986, pointed out that the spring algal maximum were dominated by *Melosira italica* and the seasonal cycle of it followed closely by the seasonal cycle of dissolved silica.

The diatoms population was sustained by high nutrient levels (especially silicate), increasing light and temperature levels, and continued suspension in the photic zone by water turbulence in spring. The end of the period of growth in June was presumably set by the depletion of silicate to under 200μg l^{-1} (Pearsall, 1932, Lund, 1950).

Mooney (1989), pointed out that the diatoms reached maximum cell densities at the end of April in Lough Corrib, Western Ireland, when silicate levels were in the order of 200 mg Si m^{-3} at that time.

The restoration of small populations of both species at the time of the autumn overturn is related to turbulence and resuspension of *Melosira italica* filaments from the bottom sediment (Lund, 1954) and the growth of suspended *Asterionella formosa* cells under the increase of circulating nutrients in the tropogenic zone (Lund, 1949; Blanton, 1973).

The decline in phosphate concentration, was correlated with the spring algal increase but is unlikely that this reached limiting growth levels for diatom before silicate became limited.

Through the autumn overturn the algal population continued growing under decreasing light and temperature conditions, at the time when nutrient levels began to increase. Under full autumnal circulation, silicate levels (above 300 μg l^{-1}) were not reached before November, by which time it is likely that low light levels limited the growth of diatoms (Lund, 1965).

Blue green algae were more important in the north basin than the south basin. They comprised the second main constituent in winter and autumn. This autumnal blue green algae peak in the north basin might be determined by special chemical conditions, possibly involving the accumulation of specific organic compounds such as vitamins (Hutchinson, 1967, Pearsall, 1932).

The seasonal succession of phytoplankton in Loch Lomond (south basin) exhibited a classic pattern being dominated by diatoms in winter and spring followed in late spring by *cryptomonas* and *chrysophyceae*, diatoms in summer, an unknown species (possibly *Ankistrodesmus convalutus*) dominated in autumn, blue green algae represented the second constituent sharing diatoms in winter and finally being dominated by diatoms again in spring. In the north basin, the picture was slightly different in winter (January and February) and autumn 1992 where blue green algae represented the second constituent and again mainly in the winter of 1993.

A similar pattern of seasonal distribution of phytoplankton has been found in many lakes in the north temperate zone among them Lake Windermere (Macan, 1970) and Gull Lake (Moss, 1972).

Tabellaria fenestrata and *Fragilaria crotonensis* have been shown to have lower requirement for silicate and phosphate (Macan, 1970). The disappearance of *Asterionella formosa* coincided with the establishment of stratification and the consequent sinking of cells beneath the limit of the photic zone. The absence of turbulence within the water column would prevent re-circulation of *Asterionella formosa* (Reynolds, 1973).

It has been shown that below this concentration (300 μg l^{-1}) silicate become limiting for the growth of *Asterionella formosa* (Lund 1949, Lund 1965, Fogg 1965). Neale *et al.*, (1991), demonstrated that the *Asterionella formosa* population usually decline rapidly once nutrient depletion occurs.

Tabellaria fenestrata produced one clear pulse in summer 1993 when silicate fell below 200 μg l^{-1} in the south basin and almost throughout the whole sampling programme in the north basin. Maulood had reported the same when *Tabellaria fenestrata* continued to increase even when silicate fell to less than 0.2 mg SiO_2 l^{-1}. This shows that *Tabellaria fenestrata* have the ability to utilise silicate at much lower levels in nature than has been previously supposed. This has been indicated by Macan (1970) who stated that *Tabellaria*

fenestrata are able to take up phosphate and silicate at much lower concentration than *Asterionella formosa.*

Cyclotella Kutzingiana presented the main constituent in the north basin from early spring to early autumn but presented the second dominant genus in the south basin for the same period. Munawar and Munawar, 1978 and Rosen, 1981, pointed out that *Cyclotella* is associated with oligotrophy.

Melosira italica showed two peaks, the first was in winter and spring 1992 for six months and the second lasted for 8 months from autumn 1992 to spring 1993 in the south basin and slightly lower percentage in the north basin. Its increase coincided with high silicate levels (Kilham, 1971), increasing daily solar radiation and isothermal conditions, which are necessary for its growth according to Lund (1954). *Melosira italica* has a faster rate of increase (Macan, 1970) than other phytoplankton and consequently formed the first pulse of the year during spring (Appendix 6). The presence of an autumn pulse of *Melosira italica* is known in many other areas (Lund, 1954); the first reading of this was more than 80 years ago by West and West (1912). The periodicity of *Melosira* is due to their relatively high rate of sinking and ability to remain alive on and in the deposits in darkness (Petrova, 1986).

Blue green algae were more important in the north basin than the south basin. It comprised the second main constituent in winter (January and February) and autumn 1992. This autumnal blue green algae peak in the north basin might be determined by special chemical conditions, possibly involving the accumulation of specific organic compounds such as vitamins (Hutchinson, 1967, Pearsall, 1932).

Blue green algae in Loch Lomond was represented by five species only *Oscillatoria agardhii, Merismopedia galauca, Oscillatoria sp* (c.f. *Oscillatoria angustissima*), *Coelospherium naegelianum* and *Anabena circinalis. Oscillatoria agardhii* was the main constituent in the south basin throughout the sampling period but it was the second or third

most abundant species in the north basin. Foy *et al.* (1976) and Priddle and Happy-Wood (1983) pointed out that *Oscillatoria agardhii* was dominant during the summer months. *Merismopedia glauca* formed a high proportion of the total cyanophyceae in late summer and late autumn in the north basin and it was the only blue green alga to continue throughout the sampling period. Hornstrom (1981) demonstrated that *Merismopedia glauca* is very common in the oligotrophic lakes and it is considered to be one of the indicator species. In the south basin, it showed a moderate peak during winter and low percentage in late spring and summer.

Anabena circinalis showed a very low percentage in summer in the south basin but with higher proportion in the north basin. Foy *et al.* (1976) recorded the same. *Anabena circinalis* and *Coelospherium naegelianum* are not important in both basins.

Green algae were not important at all in both basins, this is in agreement with Dokulil (1991), who maintained that the contribution of green algae to total biomass never exceeds 10%. Green algae are almost invariably found in all types of lakes (Happey-Wood, 1988), but are usually more dominant in small or shallow water bodies of higher trophic level (Reynolds, 1984).

Chrysophyceae were presented by two species *Mallomonas acaroides* and *Dinobryon divergens.* In late spring, the community of the south basin was dominated by Chrysophyceae forming a single pulse. In the north basin, Chrysophyceae dominated the community with a higher percentage showing during the first peak and continued to dominate the community in the beginning of summer. The peak was reached between July and August and generally coincided with lowest level of phosphate as indicated by Provasoli (1969), Lund (1965), Hutchinson (1957, 1967), and Wetzel (1975). In the north basin, phosphate was almost undetectable while in the south basin, where the smallest pulse was observed, this nutrient was comparatively higher. Dokulil and Skolaut, (1986) found that *Dinobryon* species occurred in most cases in the epilimnion near the lake surface, which indicating a preference for high irradiance. Rosen (1981) confirmed that from his

results, which illustrated that *D. divergens* prefer nutrient deficient waters. All these works are in agreement that *D. divergens* occur more in the north than in the south basin.

Dinophyceae was presented by three species in Loch Lomond: *Peridinium willei, Ceratium hirundinella* and *Gymnodium caudatum.* In general, *Dinophyceae* was not important in both basins. Dokulil and Skolaut (1986), pointed out that *P. willei* and *G. caudatum* are associated with low temperature. In the north basin, they occurred mainly in the summer with very low numbers but in the south basin they were distributed throughout the sampling programme in moderate numbers. *Ceratium hirundinella* and *Peridinium willei* produced a single pulse in both basins between July and September. Hutchinson (1967) indicated that these are warm water organism and occur when water temperature is between 12 and 15 C as was the case in Loch Lomond. Rosen, (1981) pointed out that *p. willei* is considered an oligotrophic species. Heany and Talling, (1980) stated that *C. hirundinella* had a preference for high temperature and high light. This is in agreement with this set of data which revealed that *C. hirundinella* exhibited a summer pulse in both basins.

Cryptophyceae was represented by *Cryptomonas ovata* only. It occurred throughout the data set with different percentage in both basins. The higher percentages in summer or autumn in both basins are in agreement with the general pattern as described by Osmund (1959) and Hutchinson (1967). Dokulil and Skolaut (1986) stated that *cryptophyceae* occur all the year round but are more important during winter. According to Ramberg, (1979) *C. ovata* species has high growth rates and is able to adapt to a wide range of light-temperature conditions. Moss (1972), added that *C. ovata* grows mainly in summer.

From the study of individual species as trophic indicators, it is evident that *Tabellaria flocculosa,* is a species found to be characteristic of oligotrophic areas (Teiling 1955, Rawson 1956) was almost entirely restricted to the north basin.

2.3. Primary production (phytoplankton productivity)

2.3.1. Introduction

Productivity is defined as the rate at which inorganic carbon is converted to an organic form. The phytoplankton serve as the major primary producers in the lacustrine food chain. Productivity is the rate of production expressed as production, divided by a period of time. Productivity is usually an average of the instantaneous rates over a period such as a day or a year, since natural systems have so many factors causing rapid, frequent, and irregular changes in the instantaneous rates that only average rates can be determined in a normal study (Wetzel, 1975). Photosynthesis results in the formation of a wide range of organic compounds, the release of oxygen, and the depletion of carbon dioxide from the surrounding waters. Primary productivity can be determined by measuring the changes in the oxygen and CO_2 concentration in the water. In poorly buffered waters, pH can be the sensitive property for deleting variations in the system. As carbon dioxide is removed from the aquatic system during photosynthesis, the pH rises. This shift can be used to estimate both photosynthesis and respiration. There are problems in doing this, such as water movement and diffusion, which can affect the measurements, but it has been applied successfully to productivity studies in some lake water (Anon, 1976).

Measuring algal growth means, in principle, measurement of the increase in dry weight or cell numbers with time. In almost all lakes these increases are too small to be measured during periods sufficiently short for natural population not to have changed qualitatively. Moreover, the total particulate matter in the water includes varying amounts of material such as detritus and sediments stirred up from the bottom or freshly transported into a lake by rivers and these will make the determination of algae dry weight unreliable. In practice, therefore, the production of oxygen or the uptake of CO_2 is measured instead (Golterman, 1975).

Two well-established methods of measuring the rate of carbon uptake and net photosynthesis *in situ* are (a) the oxygen method and (b) the carbon 14 method. In both methods, clear (light) and darkened (dark) bottles are filled with water samples and suspended at regular depth intervals for an incubation period of several hours. The basic reactions in algal photosynthesis involve the uptake of inorganic carbon and the release of oxygen, summarised by the equation:

$$CO_2 + H_2O \text{ ——— } CH_2O + O_2$$

Oxygen production is usually measured using three bottles filled with lake water, so-called light-dark method. The first bottle, A, gives the initial O_2 concentration. A second, L, is placed in the light while the third bottle, D, is kept in complete darkness. The increase in oxygen concentration in the light bottle during incubation is a measure of net production (L-A) which, because of the concurrent use of oxygen in respiration, is somewhat less than the total or gross production(L-D). The loss of oxygen in the dark bottle is used as an estimate of respiration (A-D). The elegance and acceptability of the method lies in the fact that the measurements can be made *in situ*, i.e. the bottles are suspended in the lake at certain depths so that measurements are made under as near natural light and temperature conditions as possible (Golterman, 1975). Measurements at various depths should be made to enable photosynthesis-depth curve to be constructed. The concentration of dissolved oxygen is determined at the beginning and end of the incubation period. Productivity is calculated on the assumption that one atom of carbon is assimilated for each molecule of oxygen released.

A more sensitive method for measuring algal photosynthesis is that of Steemann Nielsen, which measures the uptake of labelled CO_2. It has the same advantages as the oxygen method in that measurements can be made *in situ*. Small amounts of ^{14}C-labelled bicarbonate are added to lake water in experimental bottles and the bottles are resuspended in the lake at different depths. High sensitivity is achieved due to the fact that algae from a reasonably large volume of water can be collected on a filter, and that the initial labelled-

CO_2 value is zero, although in practice the background radiation reading from the laboratory is used as the lower limit or "control value" (Golterman, 1975).

Several advantages and disadvantages of both methods need to be considered. The ^{14}C method is certainly the more sensitive one. Expensive counting apparatus is necessary, however, and although bottles may be incubated under field conditions, the counting apparatus must usually be in a laboratory and needs a reliable electricity supply. Determination of O_2, however, can be carried out in the field as accurately as in any laboratory. The ^{14}C method shows a finite rate of dark uptake or fixation. This must not be neglected, as it may be important quantitatively both for algae, and for heterotrophic bacteria. A further disadvantage of the ^{14}C method is that the excretion of products makes results inaccurate if a cell synthesises and then excretes organic molecules, whereas the amount of oxygen produced is not affected by this. A source of inaccuracy in the O_2 method is the assumption, that O_2 utilisation is equal in dark and light bottles. Finally not all the O_2 consumed in the dark is related to the oxidation of algal material, even if zooplankton is absent, since aerobic bacteria may contribute by using dissolved organic matter as a substrate. From ^{14}C data no respiration can be measured, so there is uncertainty whether the method measures net or gross photosynthesis or something between the two (Vollenweider, 1969), whereas the oxygen method provides estimates of gross and net productivity and respiration.

The ^{14}C method is, however, of far greater sensitivity and is the only one that can be satisfactorily used in oligotrophic waters (Vollenweider, 1969).

2.3.2. Methods

Primary production rates were determined every fortnight between March and May 1993 using the ^{14}C tracer technique (Vollenweider, 1969). Water samples were collected at both basins from the surface, 1, 3, 5 and 10 m depths using a 6 l Van Dorn water sampler. The samples were poured in to replicate 110 ml capacity light and dark bottles for each depth. 1 ml radioactive solution containing 2 μ ci ^{14}C was injected into each bottle using a micro pipette. The duplicate sets of light and dark bottles were incubated *in situ* for 4 hours. Dark bottles were used to compensate for any dark uptake of ^{14}C (Strickland and Pearsons, 1972). After the incubation, the samples were transported to the laboratory in a light proof wooden box to prevent further carbon fixation. The whole sample was filtered through HA (0.45 mm) Millipore membrane filters under a weak vacuum so that delicate algae should not be damaged. The filter papers containing the samples were placed in labelled vials containing 15 ml Ecoscint scintillation fluid. The specific activity of the fixed ^{14}C in the samples was determined using a liquid scintillation counter. Vials for original activity and the background were also counted. Great care was always taken during the collection, incubation and filtration to keep the samples away from light as much as possible, particularly the samples from the greater depths (Appendix 2).

The processing was also done as quickly as possible and never took longer than 3 hours. The counting was done on the second day after the experiment. ^{12}C available for photosynthesis was calculated from alkalinity and pH values calculated for each depth (Mackereth, 1963). The calculations were made using a BBC computer using a spreadsheet developed by Mr. T. Bladon.

Results are expressed as mg C fixed $m^{-3}hr^{-1}$

2.3.3. Results

Primary production were only made during the months of April and May 1993, and although they will be continued throughout the rest of 1993 by a different worker, cannot be included in this thesis.

The Vertical distribution of primary production is shown in Figure(30) for the north basin and Figure (31) for the south basin.

Productivity was clearly reduced with depth, so that at 10m depth the level of production ranged from 7.6 to 8.5% in the south basin and from 16.2% to 34.2% in the north of that at the surface or 1m depth.

Most of the production occurred in the top 5 meters of the water column. A photoinhibation was noticed in May (6 Th. and 20 Th.) in the south basin but only in the 20 Th. of May in the north basin.

During early and late April 1993, surface maxima (84.2 and 191.9 mg C m^{-2} h^{-1}) were recorded in the south basin with a gradual decrease with depth to a minimum value at 10m depth. Then, in May there was a great increase in production and the maximum values were recorded at 1m depth. These were 3132.4 mg C m^{-3} h^{-1} in early May and 3422.3 mg C $m^{-3}h^{-1}$. In the north basin, maxima were also observed at the surface during late April and early May, at 46.7 and 292.4 mg C m^{-3} h^{-1} respectively. In May, a value of 1161.1 mg C $m^{-3}h^{-1}$ appeared at 1m depth.

On one occasion (May, 20th) the standing crop was measured as chlorophyll *a* (μg l^{-1}) and as total number of individual (algal units l^{-1}) at the same time as the productivity measurements.

Figure 32 and 33 show the vertical distribution of chlorophyll a, number of phytoplankton and primary production in the north and south basin respectively.

The south basin showed an increase in chlorophyll *a* with depth, recording the highest concentration at 10m depth. In the case of the number of individuals, it showed a slight

Figure (30) Vertical distribution of primary production ($mgC\ m^{-3}h^{-1}$) in the north basin (April–May 1993)

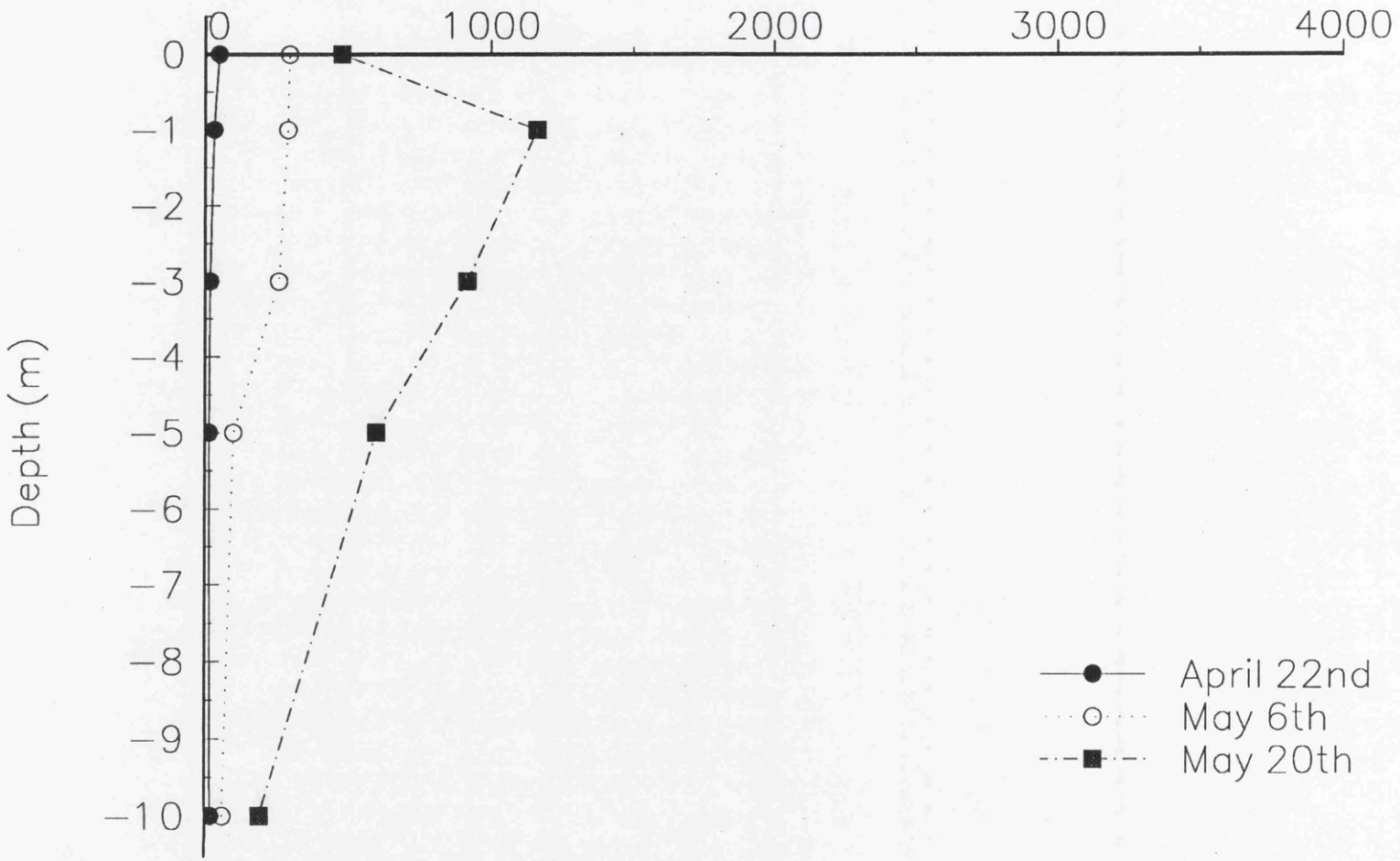


Figure (31) Vertical distribution of primary production (mgC $m^{-3}h^{-1}$) in the south basin (April–May 1993)

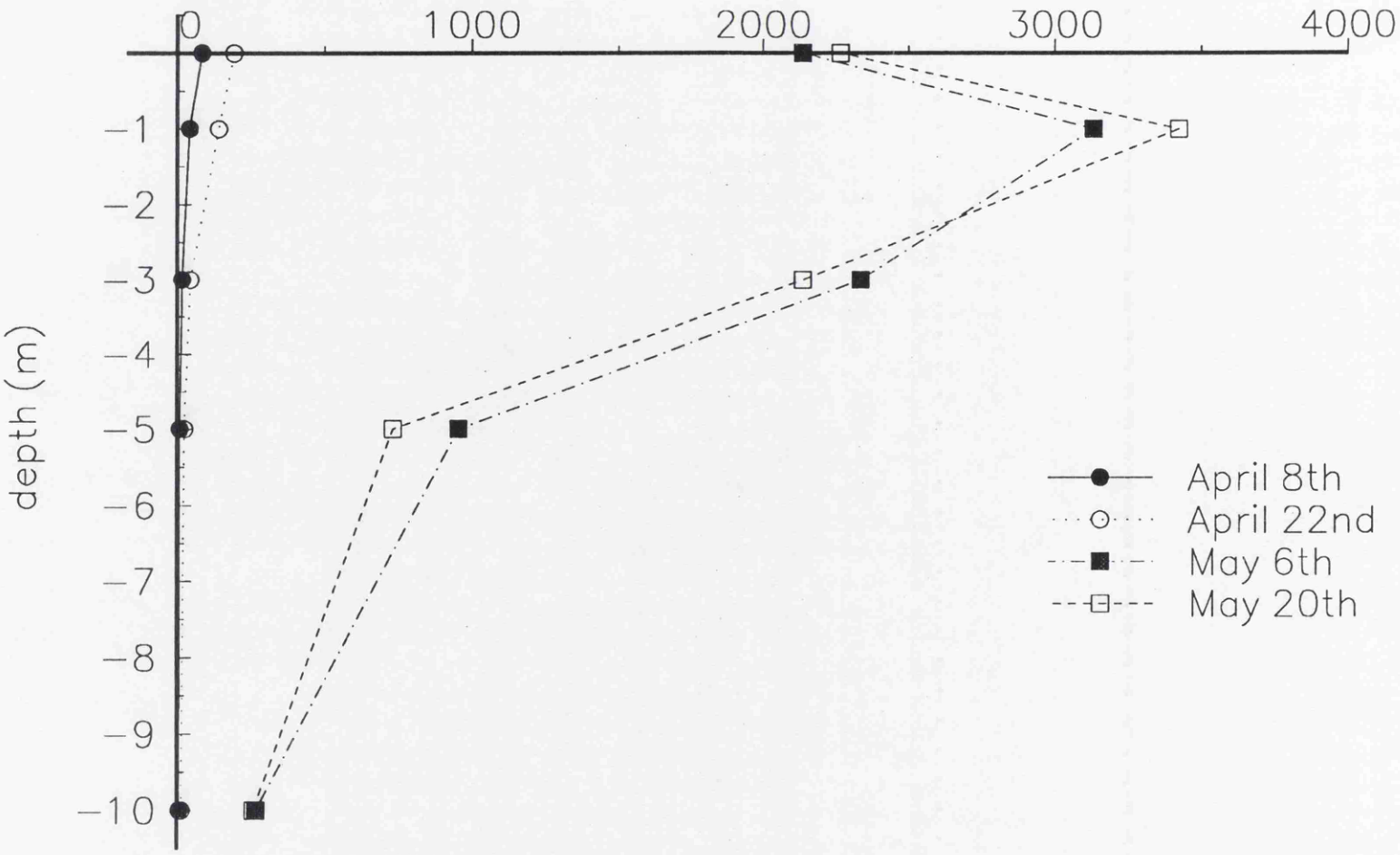
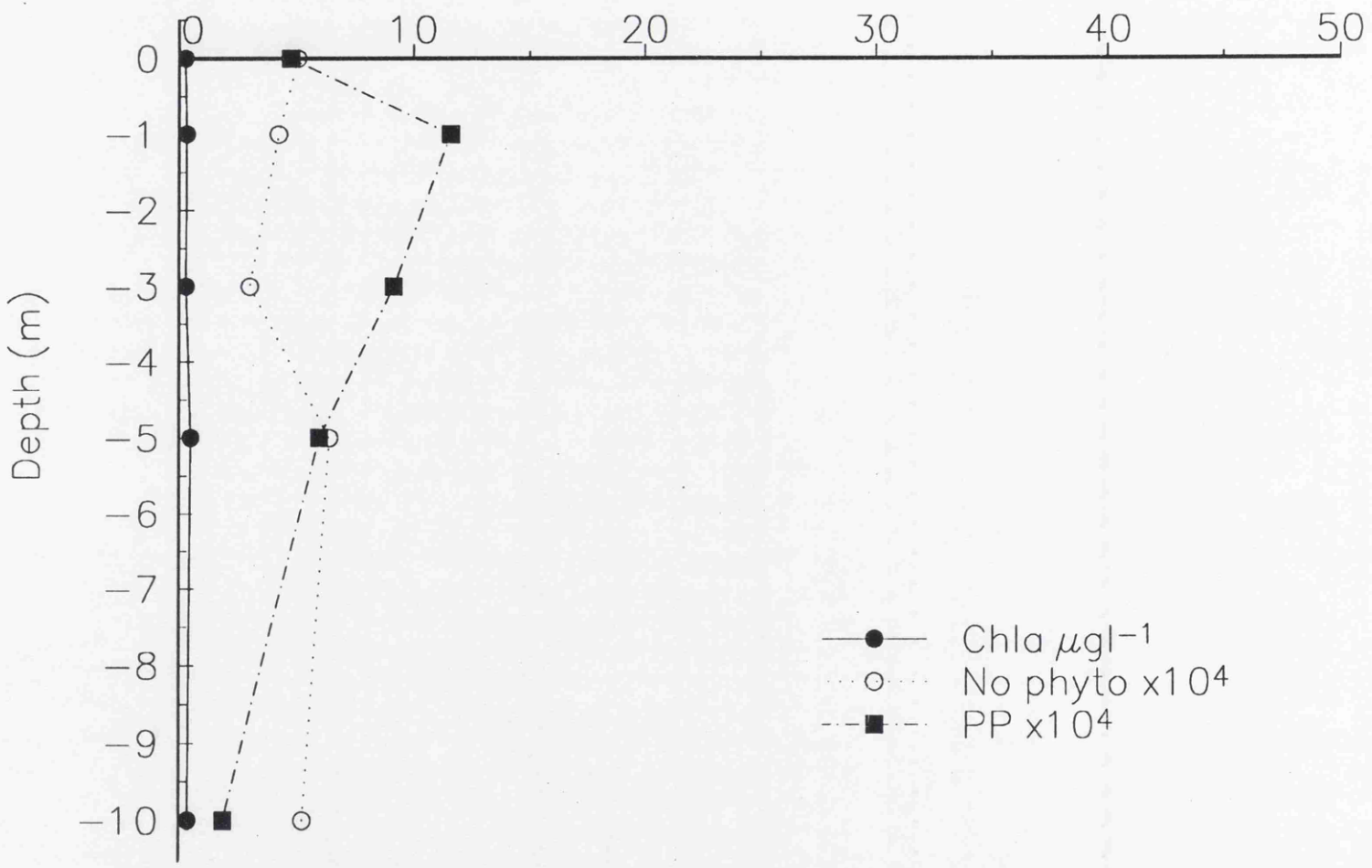
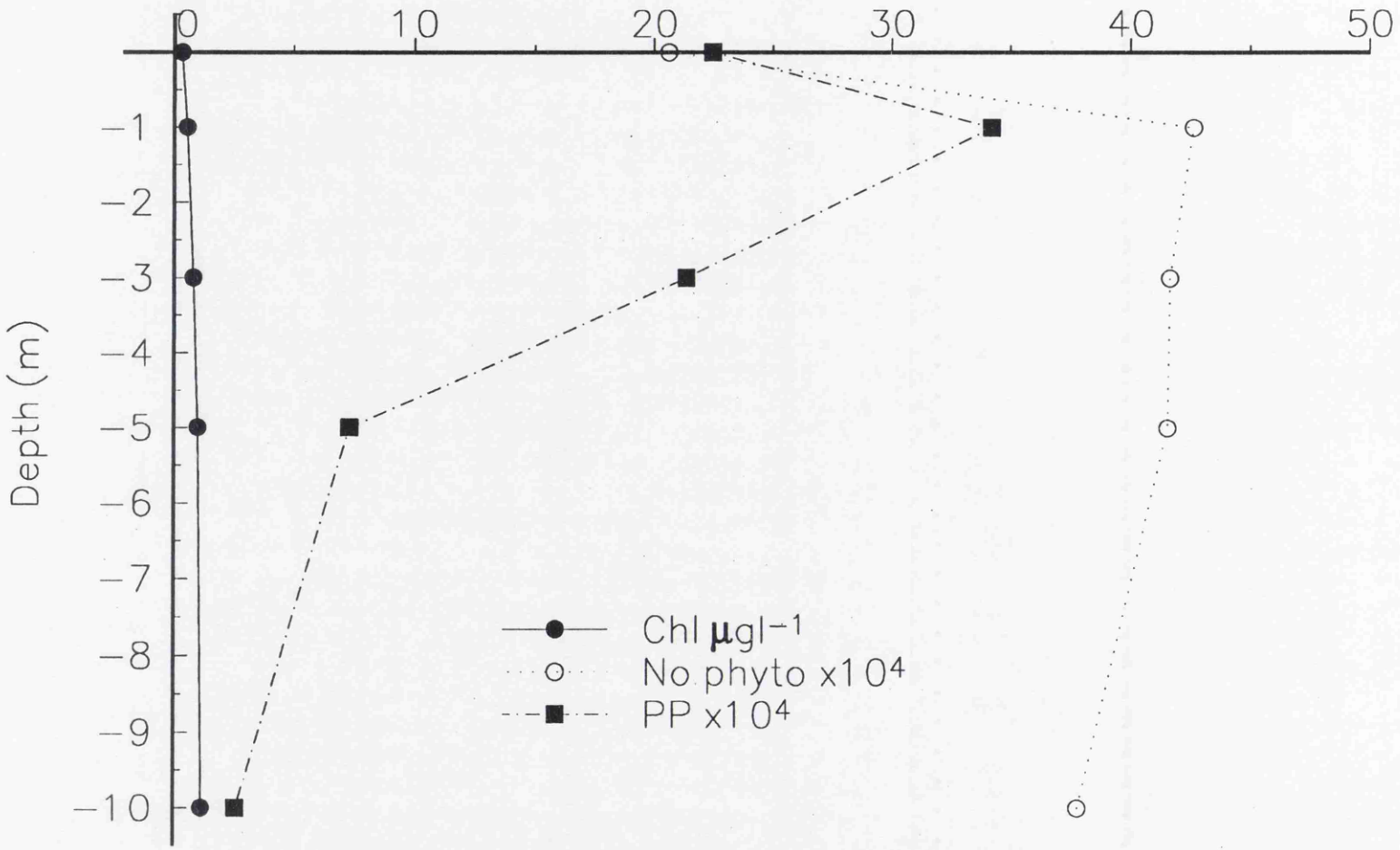


Figure (32) Vertical distribution of chlorophyll, number of phyto-plankton and primary production in the north basin on 20 May 1993



Figure(33) Vertical distribution of chlorophyll, number of phyto-plankton and primary production in the south basin on 20 May 1993



decreasing trend with depth. The maximum cell number was recorded at 1m depth, while the 10m depth recorded the minimum. The highest productivity was recorded at 1m depth. The north basin showed a roughly similar picture to the south basin concerning the chlorophyll *a* except that the maximum concentration was recorded at 5m depth. The number of phytoplankton showed a decreasing trend with depth through the top 3m, then started to increase recording the maximum number of cells at 5m depth. The highest productivity was recorded at 1m depth followed by a gradual decrease.

2. 3. 4. Discussion

Photosynthetic production by phytoplankton is influenced by the complex of factors known as the light-climate. This includes incident solar irradiance, underwater light attenuation and the proportions of illuminated and dark water in the mixed water column (Bindloss, 1976). Phytoplankton productivity was measured using the *in situ* ^{14}C method.

In order to estimate total photosynthesis beneath a unit of water surface one most integrate all the variations of photosynthesis in the illumination gradient with respect to depth and time. The integral may be evaluated directly from measurements of photosynthetic rates between sunrise and sunset at depth intervals (Megard, 1972).

According to Talling (1965) the rate of photosynthesis at any depth is a simple product of population density and the specific rate of photosynthesis by units of the population, which are interdependent; light attenuation increases as densities increase, and photosynthesis therefore decreases rapidly with depth where the population density is high.

For practical reasons it was only possible to measure primary production during the months of April and May 1993. From this set of data, most of the production occurred in the top 5 meters of the water column. Gulati (1972), found that about 70% of the production took place in the upper 2m. A photoinhibation was noticed in May (6th and 20th) in the south

basin but only in the 20th of May in the north basin. On one occasion (May, 20th) a detailed study of the standing crop as chlorophyll a ($\mu g\ l^{-1}$) and as total number of individual (algal units l^{-1}) at the same time as the productivity measurements was made in both basins. From these data, the maximum cell number and highest productivity was recorded at 1m depth. So, it seems that the apparent photoinhibition could be at least in part be accounted by the smaller number of phytoplankton in surface waters comparing with 1m depth. In general, the north basin was less productive than the south basin.

The south basin showed higher total production of carbon in the water column ranging from 2 to 9 times than the north basin.

Comparison with published productivity results can often be difficult because of the ways in which results are quoted, whether production is expressed on a hourly or daily basis. Nevertheless, the values obtained for Loch Lomond are high compared with other bodies of water. The range of the total production for the south basin is from 191.7 to 14.4 g m^{-2} h^{-1} and 180 to 6.4 g m^{-2} h^{-1}.

Gulati (1972) found an average of 380 to 497 mg C m^{-2} d^{-1} primary production during summer. Pettersson (1990) recorded a maximum value of 2200 mg C m^{-2} d^{-1} primary production. Vaquer and El Hafa (1991) stated that daily primary production ranged between 7.8 and 722 mg C m^{-2} d^{-1}. Jewson (1976) recorded a maximum daily rates of gross integral photosynthesis of 11.7 and 15.6 g O_2 m^{-2} d^{-1} (5.3 and 7.0 g C m^{-2} d^{-1}). Megard (1972) stated that the usual limit for integral photosynthesis is 5 g C m^{-2} d^{-1}. In an eutrophic environment, Harris *et al.*, (1980) recorded hourly rates of integral photosynthesis which varied from 25 to 220 mg C m^{-2} h^{-1}.

In a study of Loch Leven, Bindloss (1974) stated that the rate of gross photosynthesis by phytoplankton varied seasonally between 0.02 and 1.59 g O_2 m^{-2} h^{-1} (0.01 and 0.72 g C m^{-2} h^{-1}) and between 0.4 and 21.0 g O_2 m^{-2} h^{-1} (0.18 -9.45 g C m^{-2} h^{-1}).

The results obtained here cover only the period of spring growth when nutrients are not likely to limit production, and when light availability ceased to be limiting (with evidence

of photoinhibition in the most productive sets of results). Under these conditions it is possible that oligotrophic waters could be as productive as eutrophic waters, the difference being that the high levels of production would not be sustainable for a long period. The rest of the season has been sampled by another worker although the results are not yet analysed. The validity of this interpretation will become apparent when these data become available.

It is also possible that there is an error in the spread sheet used for the calculation. This has been looked for but not so far detected.

2.4. Zooplankton

2.4.1. Introduction

A small fraction (less than 0.01) of the radiant energy incident on a lake is converted by the phytoplankton into chemical energy in the form of organic matter. Some of this energy will then be transferred to zooplankton, the so-called primary or herbivorous consumers. Zooplankton growth is expressed mainly as fresh or dry weight per volume or per unit area per unit time.

The animal components of the freshwater plankton are dominated by 3 majors: the rotifers and 2 subclasses of the Crustacea and cladocera (Wetzel, 1975).

The rotifers and crustaceans are the major groups of freshwater zooplankton. The rotifers get their name from the rhythmically beating, apparently rotating 'wheel' of cilia close to the mouth. The cilia direct water with its suspended fine particles into the gut. Some rotifers may have more complicated food gathering mechanisms. Rotifers feed on particles from about 1-20 μm in size, a range shared by the filter feeding Cladocera (crustacean) which can also take food a little larger: up to 50 μm or more in size.

The crustacean zooplankton include the Cladocera which have a carapace which covers the body in most genera. The group includes the well known herbivorous genera *Daphnia* and *Bosmina* and also *Leptodora* and *Polyphemus* which are carnivores on smaller zooplankton. The small particle feeders have thoracic limbs provided with hairs (setae) on which are closely spaced (a few μm) setules which retain small particles as they beat, and eventually convey food to their mouths (Moss, 1988).

Cladocera move through the water more actively than the rotifers, using a rowing action of the large, branched second antennae which gives them their common name, water fleas.

The third important group of zooplankton, also crustacean, is the Copepoda, whose adult members are usually a little larger than Cladocera. They may be small-particle feeding

(mostly the calanoid copepods, like *Diaptomus*) or raptorial, the cyclopoid copepods, which include *Cyclops*. The prey of these may be smaller zooplankton, larger colonies, or masses of phytoplankton. Overall the copepods can tackle a wider range of bigger food particles (5-100 μm) than the non-raptorial Cladocera and rotifers. It seems likely that the calonoid copepods do not filter particles but actively select from those that are brought into the mouth region by the movement of the limbs.

The herbivorous zooplankton feed on phytoplankton, bacteria and aggregates of detritus and micro-organisms.

A comparison of the mean herbivores zooplankton biomass or production against those of the phytoplankton shows a general correlation. The ratio of zooplankton to phytoplankton biomass or productivities tends to decrease as the phytoplankton biomass increases, and this hints at the complexity of the relationship. Not all the phytoplankton is readily available to grazers and the proportion of those that are inedible - usually the larger forms and often the blue-green algae- tends to increase with increasing lake fertility. A better correlation is thus found between zooplankton biomass and biomass of smaller phytoplankton. The implication of these correlation is that zooplankton crops are set by phytoplankton production, much in the same way that the phytoplankton is set by the key nutrients (Moss, 1988).

2.4.2. Methods

Zooplankton were counted using the same samples collected for phytoplankton enumeration. Counts were made using the full 25 ml concentrated sample (see materials and methods of phytoplankton). The whole bottom area of the counting chambers were scanned under the x6.3 objective of Zeiss inverted microscope. The final calculation were expressed as number of individual l^{-1}. Zooplankton were identified using various

taxonomic texts: Pontin (1978) for Rotifers, Scourfield and Harding (1958) for Cladocera, Harding and Smith (1974) for Copepods.

2.4.3. Results

The method of counting is not designed for zooplankton but it gives a general idea about the second trophic level.

Table (11) presents a list of all species encountered from both basins in Loch Lomond during this study.

The zooplankton community is normally small during winter. From January to April 1992, the total number of zooplankton did not exceed 5 to 10 indiv.l^{-1}. in the north and the south basin respectively (Figure 34). Zooplankton abundance started to increase from May to reach a first peak in June 1992 of 195 and 219 indivi.l^{-1} in the south and the north basins respectively. It then decreased rapidly, followed by a large increase forming a second peak in late July 1992 in the south basin (488 indiv.l^{-1}) and in the north in mid August 1992 (367 indiv.l^{-1}). It then declined suddenly and sharply to record 8 and 10 indiv.l^{-1} in the north and south basin respectively.

Seasonal variations were clear showing minimum number during winter and early spring followed by peaks in summer and early autumn.

The zooplankton community was dominated by Copepoda during winter and spring (February-May 1992) in the north and (March-May 1992) in the south basin. It ranged from 75 to 100% in the north and from 63.6 to 100% in the south (Figure 35,36). Table

Table (11) Species composition of the zooplankton

Phylum Aschelminthes

Subphylum Rotatoria

Class Rotifera

Kellicotia longispina Kellicott

Keratella cochlearis Gosse

Trichocera sp

Filina terminalis

Polyarthra sp

Asplanchna priodonta Gosse

Brachionus sp

Phylum Arthropoda

Subphylum Crustacea

Class Entomostraca

Order Cladocera

Bosmina longirostris (O. F. Muller)

Daphnia hyalina Leydig

Leptodora Kindti (Focke)

Order Copepoda

Diaptomus gracilis Sars

Cyclop sp

Nauplius

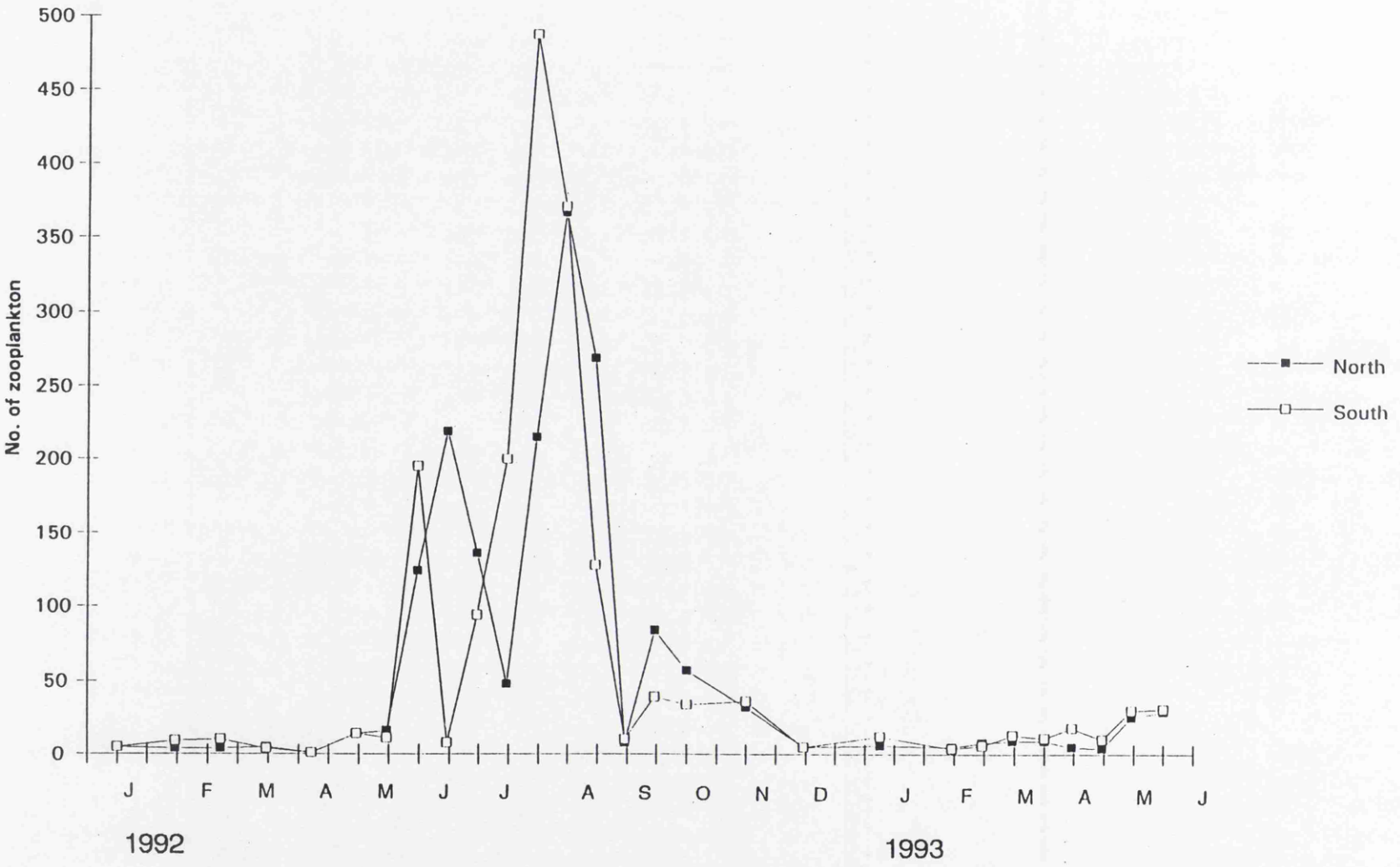


Figure 34. Seasonal variation of the total number of zooplankton (indivi. l^{-1}) of the north and south basin

Figure (35) Seasonal variation of major zooplankton groups (expressed as percentage) for the north basin

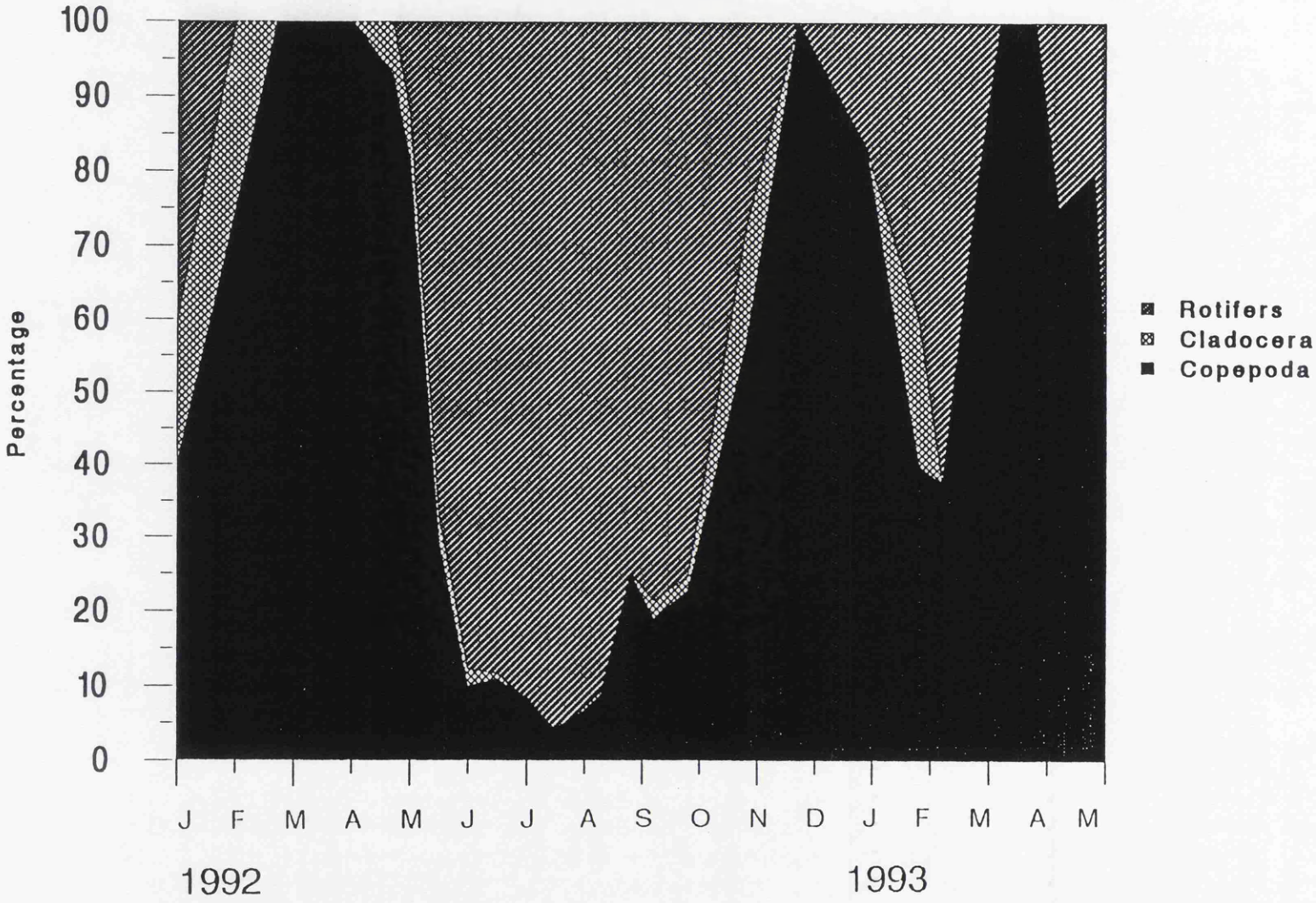
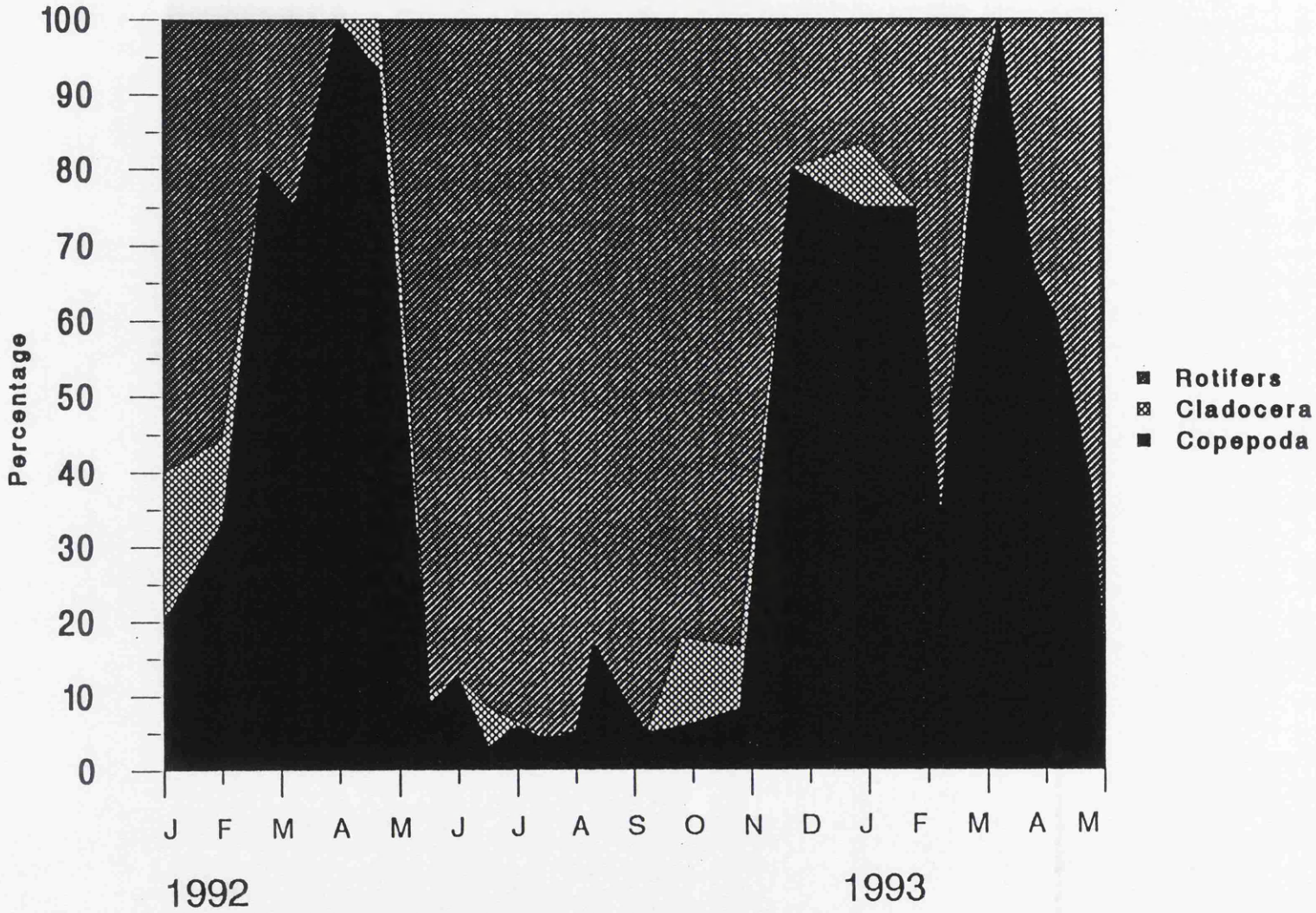


Figure (36) Seasonal variation of major zooplankton groups (expresses as percentage) for the south basin



Rotifera replaced it from early June to early November 1992 in the south basin, but it dominated the north basin from early June to early October 1992. Copepoda reappeared and dominated the community for three months during autumn and early winter (November 1992-January 1993). During February 1993 a sudden pulse of Rotifera was recorded in both basins. From early March 1993 onwards, Copepoda was the dominant group in the north basin but in the south basin they lasted for two months only.

Cladocera was present in small numbers at most times of the year 1992. It fluctuated from 0.2 to 20% and from 0.3 to 25% in the south and north basins respectively.

Seasonal variations were clear, dominated by Copepoda during winter and spring, followed by Rotifera through summer and autumn.

2.4.4. Discussion

The method of sampling and counting was not designed for zooplankton but it gives a general idea about the second trophic level. The sample size was small (only 1 litre) and active animals could avoid the sampling tube.

The seasonal changes of zooplankton for most of the year coincided to those for the phytoplankton in the loch. Zooplankton was recorded a drop in the number of population when the phytoplankton population decline sharply until the middle of June in the south basin and mid July in the north basin.

The community in the north basin has a shorter seasons of growth and is never as large as in the south basin, except on two occasion, mid June which coincided with drop in the phytoplankton numbers and late September. In this it follows the phytoplankton which either directly or indirectly provides its food.

Seasonal variations were clearly in species composition dominated by copepoda during winter and spring followed by rotifera through summer and autumn. These data are in

agreement with Campos *et al.*, (1990) who stated that the highest abundance was observed at the beginning of summer for oligotrophic Lake Todos Los Santos.

The zooplankton results show that rotifers are numerically the most important group, although crustacea (copepods and cladocera) are more important directly in the vertebrate food chain, since they form the major source of food for fish (Powan), the dominant resident fish species (Slack, 1957).

Rotifers are the most diverse and abundant zooplankton group in Loch Lomond for most of the year in the south basin and during summer and autumn in the north basin. Nevertheless, it is possible that during this study copepoda and cladocera populations had been quantitatively under estimated due to the method used for the collection and counting of plankton samples, which was mostly adapted for small organisms such as algae and rotifers (Edmonson and Winberg, 1971). Moss (1988) stated that the crustacean zooplankton move actively, may shoal both vertically and horizontally and often go through vertical migrations, reaching the water surface by night and moving down by day. They are tricky to sample quantitatively.

As with the phytoplankton the rotifer species have a wide distribution in the most of the lochs studied in the west of Scotland, although the dominant species may differ. *Keratella*, however, dominates in other lakes in the region such as Loch Awe (Tippett, 1976).

Over all temperature, rotifers have fastest rate of increase of any zooplankton (Allan, 1976) and this would enable this group to respond quickly to increasing phytoplankton biomass, as was observed in summer and early autumn for the north basin and late spring, summer and early autumn for the south basin.

Some of the variations in both phytoplankton and zooplankton biomass explained by the interactions between the two communities, especially during the spring and autumn when the population numbers were high. During this time, zooplankton populations were relatively high, since phytoplankton the primary food source were moderately high in number.

Moss (1988), concluded that rotifers are mostly suspension feeders, feed on particles from about 1 to 20 μm in size. Starkweather and Bogdan, (1980) stated that *Keratella* prefers dead detritus. The rate of egg production is high, for a new generation of rotifers is produced in only a few days and each female produces up to 25 young in her lifetime of 1 to 3 weeks. This could be account for their abundance in Loch Lomond.

The physical factors that influence the succession of these different species of phytoplankton indirectly influence the growth and development of the zooplankton. Most species of zooplankton are highly selective feeders and can only feed on a limited size range of phytoplankton. Cladocera, such as *Daphnia* feed largely on particles less than 50 μm in size. The small flagellates that typically appear early in the summer are readily consumed, but many of the colonial or filamentous species that appear later in the year are too large to be eaten by *Daphnia* (George *et al.*, 1990).

Maitland *et al.*, (1981), in a study of largest five lochs in Scotland, found six species of Crustacea common in all the lochs, including *Daphnia* and *Bosmina.* The seasonal cycle of *Daphnia hyalina* appeared to be similar in each loch with moderate numbers during winter which dropped to very low levels in spring. Numbers started to rise rapidly in May to reach maxima at different times in each loch (June in Loch Lomond) (Maitland, *et al.*, 1981). This is in agreement with these data.

For *Daphnia* species in Lake Washington, Infant and Litt (1985) found the greatest egg production and biomass production coincided with phytoplankton dominated by the flagellate *Cryptomonas erosa* and a small diatom, *Stephanodiscus hantzshii*, middle range with larger diatoms, *Asterionella formosa* and *Melosira italica* and the lowest production with the small celled *Chlorella* and a thinner variant, *tenuissima*, of *Melosira italica.*

Moss (988), reported that *Daphnia hyalina* was forced in winter to form resting eggs. Lampert (1978) stated that *Daphnia* may at any time be food-limited. The rate of egg production in this species depends on food concentration. Moore (1980) came to a conclusion that temperature and other factors rather than food availability are likely to be

more important. In the recent years there has been much debate as to whether *Daphnia* numbers are controlled "from the top down" by fish predation or "from the bottom up" by food availability (George *et al.*, 1990). Most North American workers have emphasised the importance of fish predation (Brooks and Dodson, 1965; Hall *et al.*, 1976), but more recent studies in Europe suggest that food is often more important (Benndorf and Horne, 1985; Gliwicz, 1985). George *et al.*, 1990, in a study of Esthwaite Water found that the seasonal dynamics of the Daphnia was governed partly by the seasonal temperature cycle, and partly by the periodicity of edible algae.

Both rotifers and Cladocera are parthenogenetic. Females produce broods of eggs asexually which hatch into more females. This allows rapid replacement of the population especially vulnerable to predation.

The third important group of zooplankton, also crustacean, is the copepoda. They may be small-particle feeding (mostly the calanoid copepods, like *Diaptomus*) or raptorial, the cyclopoid, which includes *Cyclops*. The prey of these may be smaller zooplankton, larger colonies, or masses of phytoplankton. Overall the copepods can tackle a wider range of bigger food particles (5-100 μm) than the non-raptorial cladocera and rotifers. It seems likely that the calonoid copepods do not filter particles but actively select from those that are brought into the mouth region by the movements of the limbs (Paffenhafer *et al.*, 1982; Peters, 1984).

Maitland *et al.*, (1981), stated that *Diaptomus gracilis* and *Cyclop abyssorum* were a common members of the zooplankton of all five lochs at all times of the year and in most of them dominated the plankton by number. *Diaptomus* was particularly abundant in Loch Lomond. The seasonal cycle of the *Diaptomus* appeared broadly to be similar in all lochs, with moderate numbers during the winter dropping slightly in spring before rising about April or May to reach maxima in June in Loch Lomond. *Cyclops* occurred with low numbers in all five lochs during the winter, dropped slightly in the spring but started rising in May to reach peak densities in June

in Loch Lomond, after which numbers declined. Nauplius larvae were common in all lochs, especially during summer (Maitland *et al.*, 1981). Nauplius occurred throughout the sampling programme, the highest numbers found in summer 1992 and spring 1993 in either basins.

The present data showed that copepoda was present throughout the sampling programme in both basins but with different percentage. It occurred with high percentage during spring and autumn 1992 and winter and spring 1993 in either basins. This set of data are in agreement with Maitland *et al.*, 1981.

2. 5. Conclusions

Loch Lomond is one of the most important lochs of Scotland, not only because of it is one of Britain's largest water bodies, or because of its importance for tourism and water supply, but also because of its unique geological feature. The Highland Boundary Fault allows comparison between two contrasting basins and so presents an almost unique natural experimental situation, with a deep, narrow, steepsided fjord-like north basin and shallower broad south basin.

Light regime usually influences the thermal regime and primary production with little or no production in either basin in winter (January-March) as would be expected in a temperate lake.

Shape of the basin also influences the thermal regime, thus the north basin is a warm monomictic basin, showing a single circulation period and is clearly stratified during summer, but for the remainder of the year the water mass is completely mixed. The south basin is polymictic because it stratifies only for a short period.

These lead to a seasonal change in the chemical environment with the levels of nutrients in winter being controlled primarily by physical environmental factors. So, all the nutrients are at a maximum at that time. The two most notable features are that phosphate becomes virtually undetectable during the " growing season" indicating that, while nitrate is detectable at all times of the year, as with many other temperate lakes it is phosphate which is most likely to be limiting factor. The other noticeable feature is silicate, where depletion occurs in both basins, but very much more severely in the south basin.

Chlorophyll *a* as a measure of the standing crop is always up to twice as high in the south basin as in the north basin, and the spring increase usually occurs about 4-6 weeks earlier. The reason for this are not certain, but there is clear evidence for both higher early season peaks of silica in particular in the south compared with the north basin while the depletion period is approximately 4-6 weeks delayed in the north basin compared with the south basin (c.f. Figure 14). The different nutrient availabilities of the two basins may probably explain the difference in onset of the spring increase. Growth in the south basin starts at a lower temperature than in the north basin.

Standing crop as measured by phytoplankton numbers showed a pattern of growth similar to that of chlorophyll although the relative sizes of the peaks were not always the same. The chlorophyll peak always preceded or coincided with the peak of numbers (for example in the south basin, numbers peaked in the end of June coinciding with the chlorophyll peak). Although the largest peak for chlorophyll in the south basin was in autumn (September, 1992) the largest peak for numbers was at the end of June 1992.

Phytoplankton numbers in the south basin increased earlier than in the north basin and were on average higher than in the north basin, although the autumn decline in numbers coincided in both basins.

The South basin phytoplankton community was dominated by diatoms throughout most of the year with the north basin showing a notably higher proportion of blue greens. This difference is clearly reflected in the different depletion pattern for silicate in the two basins.

Species composition is similar in the two basins, as one would expect, although the relative abundance is different, with *Merismopedia* being much more important in the north basin and *Melosira* in the south basin.

When plotted as an overlay of TWINSPAN species groups on the CCA biplot there is good evidence for a clear separation of Loch Lomond algal species along Axis 1 of the four groups. Group A, which occupied the left hand side of the biplot, was dominated by diatoms. Groups B and C, located in the middle, had a mixture of diatoms, blue-greens and flagellates. Group D occupying the right hand side of the ordination was dominated by flagellates, greens, blue-greens and diatoms.

When the TWINSPAN sample classification was overlaid on the CCA ordination there was a less clear separation along Axis 1 into four groups. Groups 1 and 2, occupying the left hand side of the diagram in general comprised winter and spring samples. Further to the right hand side, Groups 3 and 4 were mainly summer and autumn samples.

Overlay plots of geographical location of samples in the north and south basin on the sample CCA ordination plot showed little evidence for any clear separation into north vs. south categories. It therefore appears that temporal variation may be more important than spatial variation in determining species assemblage characteristics in Loch Lomond.

The results of CCA ordination produced by CANOCO are broadly in line with what would be expected. Species which plotted out towards the left-hand side of the diagram (Figure 29) tend to be associated with a high availability of nutrients. Those plotted towards the right hand side of the diagram (Group D) are mostly associated with low availability of nutrients and higher water temperature (typical summer and early autumn conditions).
Putting all the previous information together, one clear conclusion can be drawn that in both the north and south basins of Loch Lomond, winter and spring are dominated mainly by diatoms, with some blue-greens. At this time nutrients are at their maximum level, and silicate appeared to be more important than nitrate and phosphate. The summer and

autumn species were most probably favoured by increasing temperature and tolerance of lower nutrient availability.

Diversity is slightly higher in the north basin than in the south basin except during spring and early summer when values are more or less the same. This is as one would expect with higher diversity in more oligotrophic waters.

Two months of results confirm the observation from standing crop measurement with production increasing in the south basin about 4 weeks before north basin and maximum production being up to 3.5 times as high in the south as in the north basin.
All the biological results are compatible with the likely controlling nutrient and light regimes in the two basins.

The time of occurrence of maximum numbers of zooplankton coincided in both basins, but population increase started later than for the phytoplankton. The north basin supports more or less the same standing crop as the south basin and there is little significant difference in the composition of the community.
However the sampling method used was designed for phytoplankton so these results are less dependable because of the small sample size, and the more probability that active species could avoid the sampling tube, so the data are probably selective to an unknown degree.

4. The limnology of Loch Lomond, Scotland and High Dam Lake, Egypt: temperate and tropical waters compared

The study of limnology developed in temperate regions of the world, and this has dominated our understanding of the principles of environmental interactions. However, there are some fundamental differences in tropical (and polar) waters which need to be considered before such waters can be understood.

For the purpose of this chapter, tropical lakes are taken as those which are located within the tropics i.e. 23.5^{o} either side of the equator (between tropics of Cancer and Capricorn). According to Lewis (1987), temperate lakes are situated within 30 to 60^{o} latitude.

In this chapter I will as far as possible give examples for two different lakes from my own experience: High Dam Lake, Egypt as an example of a tropical lake and Loch Lomond as a temperate representative. However, it must be understood that each is in someway unrepresentative of its type, the High Dam Lake because it is moderately recent artificial impoundment, and Loch Lomond because it experiences an oceanic climate.

High Dam Lake, Egypt, located between latitudes of 21^{o}N and 24^{o}N (Figure 37, Table 12) and Loch Lomond is at 56^{o}N, so each lies within the region it represents.

A first difference between tropical and temperate lakes we can consider is the possible origins. Tectonic and volcanic lakes are possible in all regions of the earth but in temperate regions many lakes are of glacial origin, whereas in the tropics many are formed in floodplains.

The term tectonic is used to include all lakes formed by movements of the deeper parts of the earth's crust. The actual processes involved in lake formation have been classified as constructive, when the rim is actively built, destructive, when the lake is excavated or obstructive when a pre-existing valley is dammed. It is more convenient, however, to classify according to the general nature of the processes responsible for building, excavation and damming (Hutchinson, 1957).

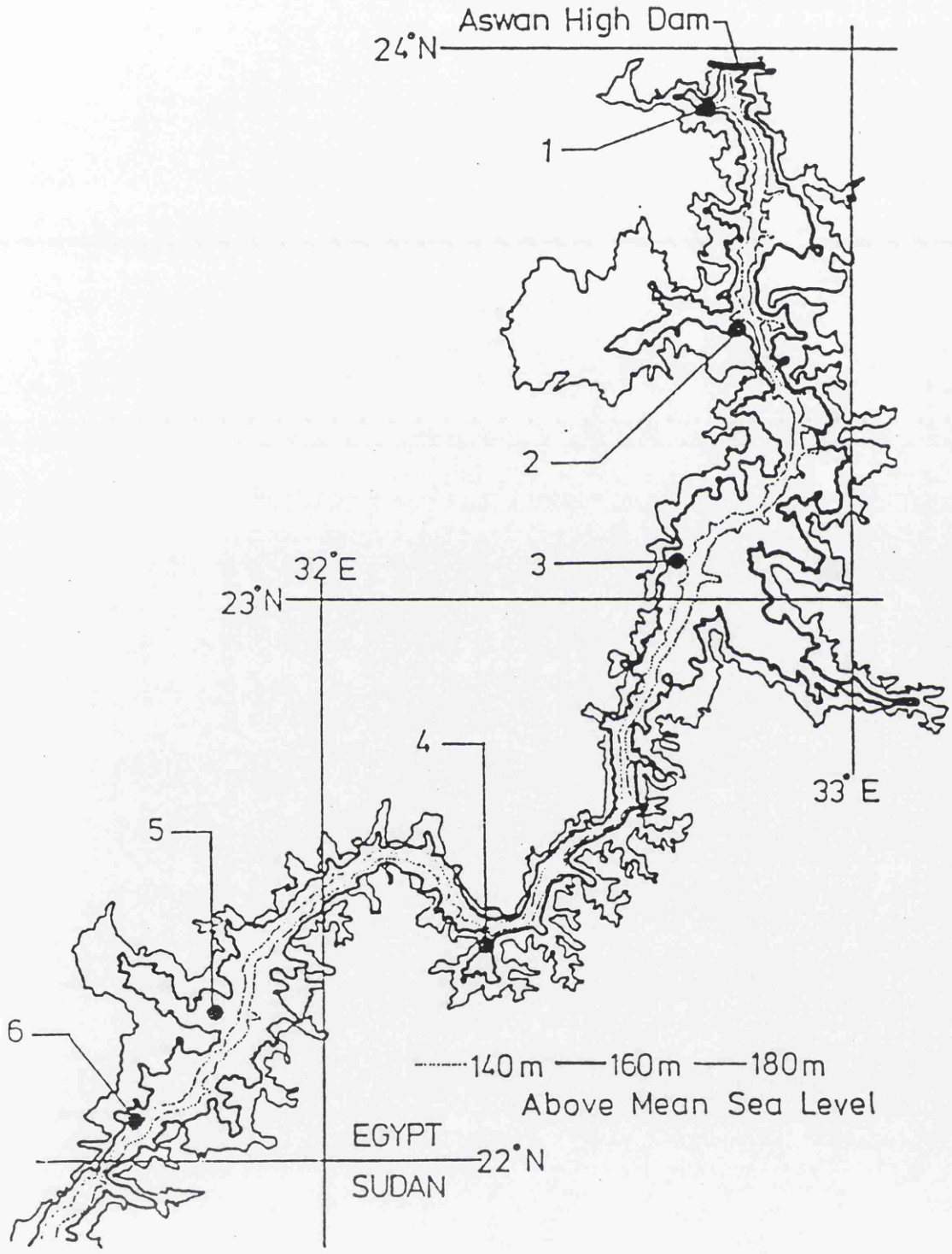


Figure 37. Map of the High Dam Lake, Egypt

Table (12) Morphometric data for the High Dam Lake (Latif, 1974)

	at 160 m	at 180 m
Length (km)	291.8	291.8
Mean width (km)	8.83	17.95
Surface area (km^2)	2,562	5,237
Mean depth (m)	20.5	25
Maximum depth (m)	110	130
Volume (km^3)	53	131
Shoreline (km)	5,416	7,875

Most of the African lakes in the Rift Valley are tectonic e.g. Lake Victoria, Lake Tanganyika.

The High Dam Lake is one of the largest artificial lakes in Africa, it was filled in 1960 after the construction of Aswan Dam (Entz, 1974). So, we can consider it as obstructive.

Loch Lomond is glacial, the north, fjord like basin having been excavated and the south basin being dammed by moraines.

According to Lewis, (1987) the three main latitudinal trends which influence environmental interactions in aquatic ecosystems are:

1- Total annual solar irradiance

2- Annual variance in irradiance

3- Coriolis force

1- Total annual solar irradiance

Annual solar irradiance means the total amount of energy reaching the surface of the earth. Irradiance at the top of the atmosphere can be calculated from solar constant, the latitude, the day of the year, and the time of day.

Figure 38 shows the total annual irradiance at the different latitude (Hutchinson, 1957). On a theoretical basis the tropics receive a higher total irradiance level than temperate regions.

Between the upper atmosphere and the surface of a water body, solar irradiance is reduced in relation to the optical air mass and to the attenuation coefficient, which is influenced by air itself and by atmospheric moisture (clouds) and particles. Although the optical air mass can be predicted from time of year, latitude and elevation, the attenuation coefficient varies in a manner that is difficult to predict.

At the top of the earth's atmosphere, total annual irradiance is distributed around a maximum at 0^{o} latitude. It should be noted that these are average values and individual lakes may well experience near to the theoretical maximum (e.g. in arid region such as The High Dam Lake, or very much less).

A map of global irradiance actually shows the largest amounts of annual irradiance reaching the earth surface near the margin of the tropics, rather than within the central tropics (Landsberg, 1961). This can be accounted for by atmospheric conditions (e.g. cloud accumulating over the tropical rain forests).

From the previous figure, the High Dam Lake receives about 5900 Kcal $cm^{-2}year^{-1}$, whereas Loch Lomond receives a theoretical maximum of 3900 Kcal $cm^{-2}year^{-1}$, reduced by cloud cover.

2- Variation in irradiance

At latitudes higher than 10^{o} N or 5^{o} S, daily irradiances, given a constant attenuation coefficient, would show a single peak near the time of the summer solstice. Between 10^{o} N and 5^{o} S, there would be one irradiance peak near the end of March and a second near the end of September. Very near the equator, the annual minimum daily irradiance for a constant attenuation coefficient would be approximately 85% of the annual maximum daily irradiance.

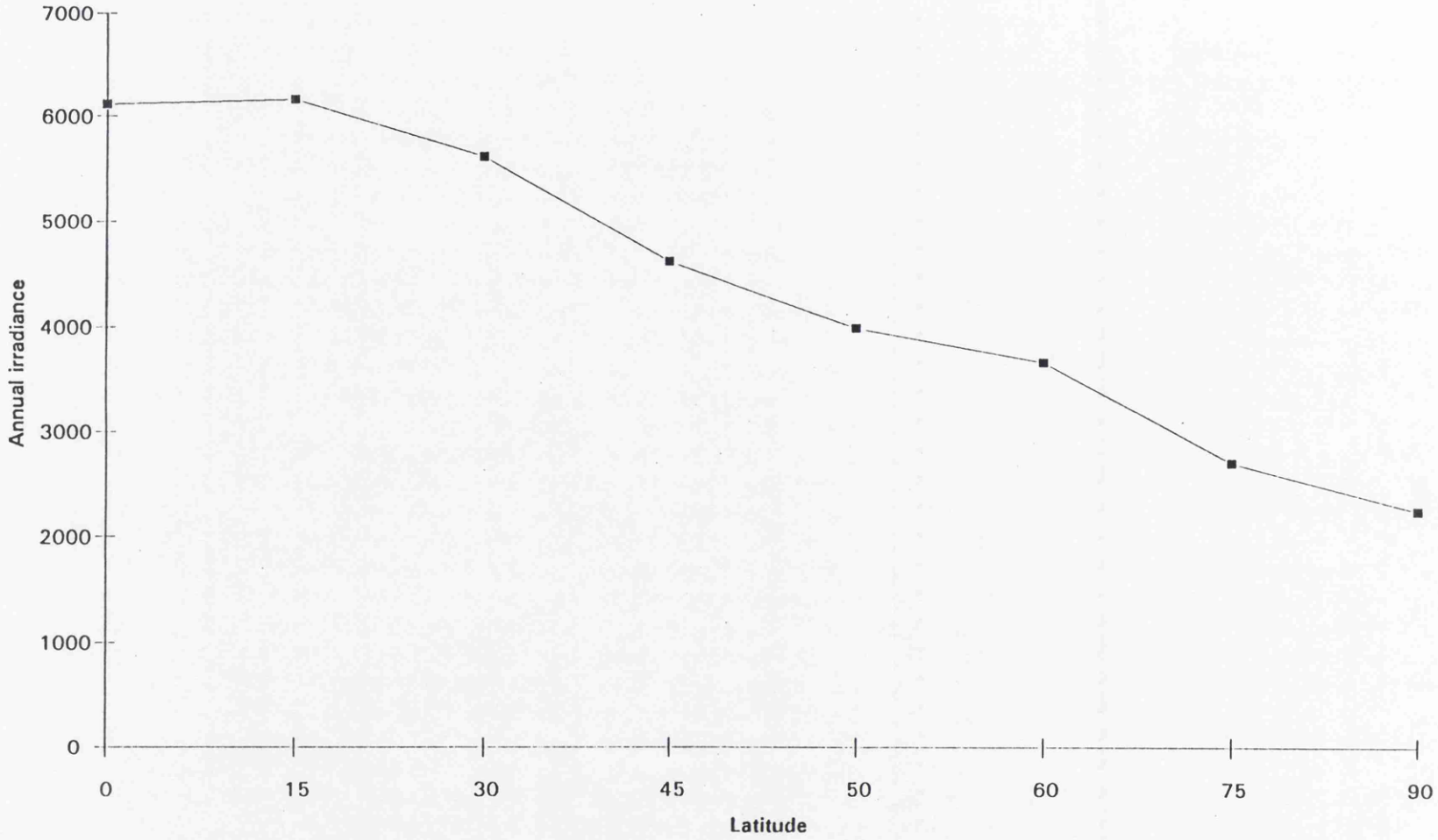


Figure 38. Total annual irradiance at the different latitude (Hutchinson, 1957)

Even within the tropics there is a substantial seasonal change in daily irradiance especially above 10^{o} latitude.

Underlying the variations in daily irradiance through the year are variations in daylength. The annual range in daylength is less than 30 min at the equator, slightly over 1 hour at 10^{o} lat., and slightly over 2 hours at 20^{o} lat. (Brylinsky and Mann, 1973).

Variations in daylength may have some effects on aquatic ecosystems that are separable from the associated variations in daily total irradiance, but the main significant of changing daylength is changing total daily irradiance.

Seasonal change is not only in daylength but also in maximum levels achieved associated with solar elevation- and this may be important when considering photoinhibition.

Figure 39 shows the seasonal variation of irradiation with latitude from Hutchinson (1957). According to this figure there is not much difference all the year round within the tropics but there is very much fluctuation at the higher latitude.

Figure 40 shows the seasonal variation of irradiation for the High Dam Lake and Loch Lomond. It is very obvious that the range of fluctuation is very small for the High Dam Lake comparing with Loch Lomond. Thus, the December level of irradiance in the High Dam Lake is 56% that of the maximum in June, whereas in Loch Lomond the December value is only 6.6% that of June.

3- Coriolis effects:

Coriolis force is explained by the change in the balance between centrifugal and gravitational forces as mass moves over the curved surface of the earth. The force is proportional not only to the speed of movement but also to sin ϕ (where ϕ = true latitude), and it is therefore zero at the equator and maximum at the poles (Van Arx, 1967).

The Coriolis force affects water currents. In lakes, wind stress on the water surface is the predominant cause of water currents. The Coriolis force deflects currents created by wind stress and thus reduces the current velocity than can be maintained by a given wind

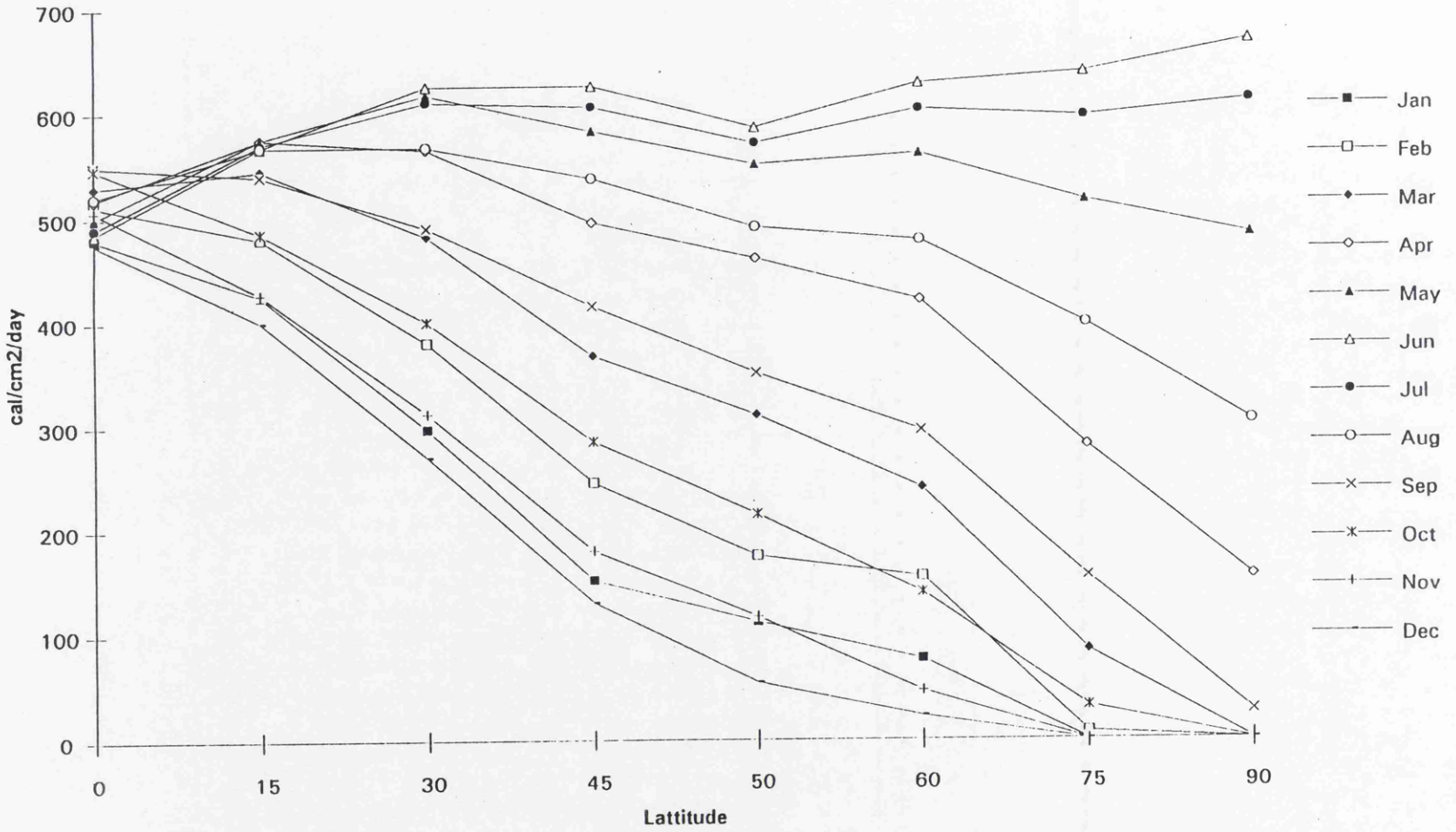


Figure 39. Seasonal variation in irradiance at different latitude (Hutchinson, 1957)

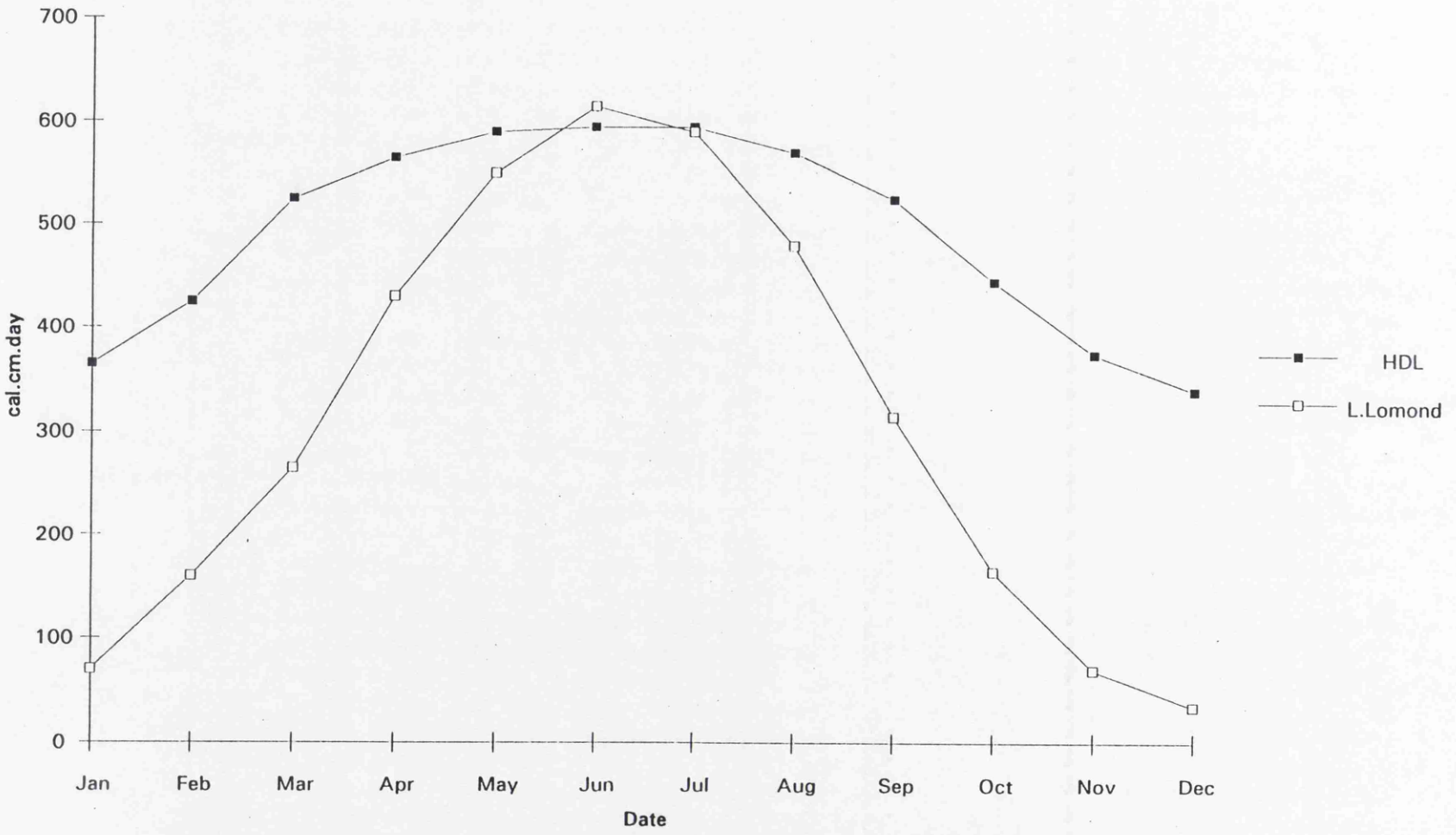


Figure 40. Seasonal variation of irradiance of the High Dam Lake and Loch Lomond (based on information from Hutchinson, 1957)

velocity, which in fact is inversely related to the square root of sin ϕ (Hutchinson, 1957; Munk and Anderson, 1948).

In a lake that contains a vertical density gradient, such as a thermally stratified lake, the depth to which mixing will be realised in response to wind is directly related to surface current velocity. For higher current velocities, greater depth of mixing will be achieved for a given density gradient. Because the Coriolis force influences the current velocity and varies with latitude, the depth of mixing in a stratified lake that can be achieved by a given wind velocity varies inversely with latitude. Mixing in lakes is largely wind induced, so at low latitudes winds are likely to have a greater effect than at high latitudes. For idealised systems, the effect of Coriolis force on mixing depth is quite important and can account for differences in mixing depth as much as two to three fold between low and high latitudes.

Lewis (1987), showed the decline with latitude of relative current velocity in equilibrium with a given wind velocity for fixed conditions of water density and eddy viscosity. The large overall effect of the coriolis force is on current velocities over broad latitude ranges and the steep rate of increase in current velocity toward low latitudes (e.g. about 43% for the High Dam Lake and about 30% for Loch Lomond). For the present purposes, it is best to stop with the conclusion that winds of a given velocity working against a given density gradient will be less effective in mixing at temperate than at tropical as a result of coriolis force.

These three primary causes will each have a number of primary effects and these may be divided into physical and biological effects. Obviously the causes are also likely to interact with each other.

1- Coriolis force:

Coriolis force has less direct biological implication than the other causes and so will be dealt with first. The general effect of this is to increase the effect of wind on the water circulation in the lake which in turn lower the stability of the stratification. This is a

measure of the amount of work required to render the water column of a lake thermally uniform (Idso, 1973). Stability is determined entirely by the distribution of water densities which are related in turn to temperature.

2- High annual irradiance:

High annual irradiance has two effect: firstly physical effects which act directly on the water such as thermal stratification and evaporation and secondly biological effects.

Physical effect:

a) Thermal stratification:

In 1892, Forel classified lakes into 3 categories:

Polar lake which are characterised by a single water circulation within water never rising above 4 C; temperate lakes distinguish by a double water circulation and maximum density twice a year; the third category is tropical lakes which typically have a single circulation in winter, with water never below 4 C. According to this classification all the large lakes (lochs) of Scotland are tropical!

According to my own experience sampling in Loch Lomond during January or February under severe cold (freezing), strong wind and rain or snow, compared with conditions at the High Dam Lake with air temperature around 15C and calm, clear skies, this classic classification seems to be untrue.

Most of the lakes of Africa are either polymictic or warm mononictic. Both the High Dam Lake and Loch Lomond are considered to be a warm monomictic lakes.

Most temperate lakes, have a surface temperature above 4C in summer and below 4C in winter, with a large thermal gradient, and a large seasonal variation. The water temperature of Loch Lomond never falls below 4C throughout the sampling programme. The thermal maximum gradient was 12C and the seasonal variation of water temperature of the top 5m of the water column fluctuated from 5.5 to 15.5 for the north and 5 to 17C

for the south basin. Continental temperate lakes have two circulation periods in spring and late autumn, with reverse stratification in winter (i.e. are dimictic), although in oceanic climates such as Loch Lomond experiences, a single circulation period during winter is more likely (monomictic).

Tropical lakes, with a high surface temperature of 20 to 30 C, have a small annual amplitude of variation, and although only a small thermal gradient may exist, the density difference between the layers may be sufficient to impose considerable stability. Circulation tends to be irregular, but usually occurs only in the coldest time of year.

Within the tropics there are two annual maxima in solar radiation, but in general the variation in the radiation flux is small, and factors other than solar radiation are likely to be of major importance.

Lake Tanganyika is a very large and very deep tropical lake and its thermal regime has been well studied. Beauchamp (1939) found that stratification is permanent and the whole volume of the lake below about 200m is anaerobic and does not circulate. The water below is richer in dissolved salts than is the surface layer. The most important series of temperature observations are those of Capart (1952), the surface water temperature are very variable, values as low as 23.3C and as high as 29.5C have been recorded. In deeper water the corresponding variation is from 26.3 to 26.9C. Below 200m, where the mean temperature is 23.4C, there is a fall to a minimum between 500 and 800m of 23.27C. At depths below 1000m the temperature is found to have risen very slightly, to 23.32 to 23.35C, implying an increase of 0.06C in about 600m.

Though the vast mass of water below 200m appears to be stagnant, it is believed by Kufferath (1952) to undergo a very slow exchange with the surface layers. The first mechanism involved in this exchange is the discharge of warm but saline water from lake Kivu by Ruzizi River at the north end of the lake. This water being denser than the surface water moves along the gentle slope of the shallow north end of the lake, bringing heat,

mineral matter, and oxygen into the monimolimnion. The second mechanism is the falling of heavy showers of cool rain, which may cause some mixing down to 400m.

In a shallow lake (e.g. Lake Victoria), the situation is different. There is no permanent stratification due to the diurnal variation in temperature and very little seasonality in thermal conditions. As we might expect the wind keeps the entire water mass mixed and more or less isothermal during the whole period of heating.

b) High evaporation

This affects the hydrological balance. If the inflow into a system exceeds evaporation then the water will overflow from the lake into the sea. Whereas, if evaporation equals or exceeds inflow then no outflow will occur. If it exceeds inflow, then the system will dry up over a period of years.

The rate of delivery of water into a lake and its loss by evaporation ordinarily varies with the seasons. The influents are usually high in rainy seasons or when ice (not normally important in tropical lakes) is melting; the level of the lake tends to rise at such time.

The key factor of evaporation is temperature. The temperature of the upper mixed layer of a lake will vary as a function of latitude. The maximum surface temperature of a lake often reflects transient daytime heat accumulation and is therefore less useful than a subsurface maximum more typical of the mixed layer.

Minimum water surface temperature, as determined by Straskraba 1980, declines steeply with latitude, this would be expected from the decline in minimum daily irradiance. Elevation has a very strong influence on bottom temperature in tropical lakes and must be considered jointly with latitude. Near the equator, bottom temperature is depressed by 4-5C for each 1000m of elevation (Loffler, 1964, 1968; Lewis, 1973; Kling, 1987). Latitudinal and elevational effects have been expressed on a common basis by reference to the mean normal lapse rate, which varies from 5-10C per 1000m; an empirical average for a selection of tropical land-based weather stations is 6.7C per 1000m of elevation (Lewis,

1973). For broader latitude ranges, the relationship is inaccurate and must be derived empirically rather from the lapse rate. The bottom temperature, latitudes and elevations of an earlier analysis (Lewis, 1973) were supplemented with additional data for lakes of moderate to great depth at latitudes up to 30^{o} (Wood *et al.*, 1976; Allanson, 1979; Huston, 1979; Lewis, 1976).

The bottom water temperature for Loch Lomond ranged from 6 to 8.5C for the north basin and from 5 to 12C for the south basin. For the High Dam Lake, it ranged from 14 to 25C (maximum recorded depth 50m) (Habib *et al.*, 1987, Habib and Aruga, 1988).

There is no significant decrease of maximum temperature within the tropics. However, in temperate regions there is a steep decline in maximum temperatures between 30^{o} and 40^{o} latitude. This corresponds to a steep decline in observed solar irradiance over the same range.

Biological effect:

There is a direct relationship between annual irradiance and temperature on primary production.

In a hypothetical situation with most favourable conditions of nutrients, i.e. no nutrient limitation for production, most favourable light conditions and the thickness of the mixed layer is 5 m. Under this assumption natural phytoplankton population can be expected to have an efficiency close to 0.06 moles of CO_2 per Einstein of photosynthetically active radiation (PAR) absorbed by the cells (Parsons *et al.*, 1984; Bannister and Viedemann, 1984).

The amount of light intercepted by phytoplankton cells in the model lake can be approximated from the amount of PAR entering the water column, the extinction of light by phytoplankton in the water column, and the extinction of light by other means in water column such as dissolved organic matter and non phytoplankton particles. PAR entering the water column is estimated as 46% of the total irradiance (Talling, 1971). For

maximum production, the amount of chlorophyll in the mixed layer should be sufficient to result in the absorption of approximately 99% of the PAR between the top and the bottom of the mixed layer. High stocks of algae will result in higher production near the surface. Lower stocks of algae will have lower production because of the absorption of a higher proportion of irradiance by factors other than algae.

In general, under nutrient sufficient conditions, lakes with thinner mixed layers (e.g. small lakes or very shallow lakes) can have a higher net production because biomass is more concentrated, which allows higher proportional absorption of PAR by the phytoplankton. The relationship between thickness of the mixed layer and maximum production has explored by Uhlmann (1978). According to Uhlmann's calculation of the empirical relationship, maximum potential production would be, if other factors were equal, 25% less for a lake with mixed layer thickness of 10 m and 40% greater for a mixed layer thickness of 2.5 m than in our hypothetical lake with a mixed layer thickness of 5m.

For the model lake with mixed layer thickness of 5m and a chlorophyll concentration of 21μ g l^{-1}, approximately 35% of the irradiance within the mixed layer is absorbed by other means.

For Loch Lomond the chlorophyll concentration ranged from 0.3 to 3.1 μg l^{-1} in the north basin and from 1.1 to 5.8 μg l^{-1} in the south basin. For the High Dam Lake the maximum chlorophyll concentration was 42.4 μg l^{-1} in January 1984 and 36.8 μg l^{-1} in August 1985 (Habib and Aruga, 1988; Habib *et al.*, 1990). Chlorophyll concentrations were generally low during November-March in the High Dam Lake.

One additional important consideration is the light saturation of photosynthesis, which occurs at relatively low light intensities for phytoplankton. Saturating intensities vary according to a large number of factors, but a median value would be in the vicinity of 120 μ E m^{-2} sec^{-1} PAR (Harris, 1978). Except in the winter at high latitudes, surface PAR irradiances can be expected to average as much as 1500 μ E $m^{-2}sec^{-1}$ over approximately

two third of the day. For this reason, light in the uppermost portion of the mixed layer will typically exceed the saturating irradiances.

To discount the absorption of light by phytoplankton in excess of the saturating irradiance, it is convenient to define an effective absorption efficiency. This efficiency is the proportion of PAR at any depth absorbed by phytoplankton up to the minimum of the saturating irradiance. For model lake, this efficiency reaches a maximum of 35% below the depth corresponding to the saturating irradiance and a minimum of approximately 7.5% just at the water surface over the middle portion of the day.

From theoretical considerations, we can draw a production curve based on nutrient sufficient conditions and optimal temperature in the model lake. The hypothetical maximum production does not begin to decline significantly until latitudes exceed 40^{o}.

In accounting for the effect of temperature on primary production under nutrient sufficient conditions, it is necessary to set a temperature for the mixed layer at each latitude and to specify a relationship between maximum growth rate and temperature. The temperature effect on production can be calculated from the mean temperature and a Q_{10} for phytoplankton growth. Work by Eppley 1972 and Goldman and Carpenter 1974 shows that the Q_{10} for growth rate of phytoplankton under nutrient sufficient conditions at optimal irradiance is close to 2.0.

According to Lewis 1987, in tropical lakes ($0\text{-}20^{o}$), cloudiness accounts for a slight suppression from the theoretical maximum. At temperate latitudes ($30\text{-}60^{o}$) a combination of cloudiness and changes in daylength suppresses production from the theoretical maximum by as much as 20%. The temperature effect is quite small in tropical lakes and very large in temperate lakes, where it even exceeds the irradiance effect. The proportion of total suppression accounted for by nutrients is 5 times as high as at low latitudes as at high latitudes, but the total suppression from the theoretical maximum is still significantly greater at high latitudes, primarily because of the temperature effect.

3- Variation in primary production

The greater seasonal effect of turn over is in temperate regions. At the time of turnover, where the temperature is low and annual minimum net production is effectively zero. This situation can last for quite a few months. In tropical regions, production on a temperature and light basis will remain more or less constant throughout the year unless modified by such thing as nutrient availability.

The major factors controlling phytoplankton production are considered to be light penetration, temperature and nutrient supply. The marked contrast between temperate and tropical regions in levels of solar radiation and temperature suggest that energy flow through lakes must differ markedly between these regions and there is evidence that tropical lakes are indeed more productive than temperate ones (Talling, 1965, 1966; Lewis, 1974). Brylinsky (1980) found a significant correlation between gross primary production over a growing season and latitude, indicating that production does tend to be higher in the tropics. Schindler (1978), however, demonstrated that a high proportion of the variance in both annual phytoplankton production and mean annual chlorophyll could be explained by annual phosphorus input (loading) once a simple correction for water renewal time was applied. Furthermore, he showed that there was some evidence for the good correction between latitude and production observed by earlier workers.

Another major difference to be expected between primary production in tropical lakes and their temperate counterparts lies in the degree of seasonality. Ganf (1974) established that an extremely high rate of gross phytoplankton production is maintained at a very constant rate throughout the year in Lake George straddling the equator in Uganda. Conversely, Melack (1979) showed that tropical lakes do exhibit pronounced seasonal fluctuations and that most of these fluctuations correspond with variations in rainfall, river discharges or vertical mixing. Shallow lakes, often with a well-developed littoral vegetation are often more productive than deeper lakes (Ryder *et al.*, 1974) and, particularly in the tropics, are often important subsistence fisheries.

a- Nutrients and nutrient cycling efficiency

Trends in primary production with latitude, when analysed together with trends in other factors that vary with latitude, indicate that more efficient recycling of nutrients occurs at low latitudes. Two of the most important factors influencing recycling efficiency in lakes are: 1- the speed with which a limiting nutrient is released from non living organic matter in a form that can be reabsorbed by primary producers (i.e. recycled within the ecosystem) and 2- the rate at which nutrients are resupplied to the growth zone from deeper water or sediments to offset sedimentation loss (i.e. of allochthonous material).

Moss (1969), working on Lake Malawi and Lake Chilwa, found values of nitrate, phosphate and silicate to be undetectable for the first two nutrients and 0.17 mgl^{-1} for silicate in Lake Malawi. In the case of Lake Chilwa, he found 398 $\mu g\ l^{-1}$, traces and 115 mgl^{-1} for nitrate, phosphate and silicate respectively. In an experiment on the effect of nutrient enrichment of natural waters on the crops of algae expressed as chlorophyll *a* $\mu g\ l^{-1}$ he added nitrate or phosphate or both nutrient together, and found chlorophyll *a* values of 38.3, 750, 47 and 411 $\mu g\ l^{-1}$ for Lake Chilwa and 7.7, 46.2, 7.1 and 37.9 $\mu g\ l^{-1}$ for Lake Malawi for control, nitrate, phosphate and nitrate and phosphate treatments respectively. From this experiment, it appeared that nitrate is more likely to be the limiting factor.

In view of the results of the survey of African lake water chemistry carried out by Talling and Talling (1965), the observed general stimulation of algal growth by nitrate alone, or in combination with phosphate, is of great interest. Seasonal studies in the rivers of the Nile (Prowse and Talling 1958; Talling and Rzoska 1967) and in Lake Victoria where Talling 1966 has carried out comprehensive studies also suggest that nitrate may frequently become limiting to algal growth in East African waters.

The regeneration of nutrients in an usable form from the mixed layer through decomposition is largely a function of metabolic rates of decomposer organisms. From the mean temperature of the mixed layer in relation to latitude, as developed in connection

with the analysis of production, it is possible to estimate the latitudinal trend in nutrient regeneration rates on the assumption that the Q_{10} for decomposition is near 2.0.

In temperate lakes, the return of nutrients from deep water is small because the upper mixed layer does not usually mix with deeper water until seasonal thickening of the mixed layer occurs (i.e. supply is once or twice a year- depending on whether it is mono- or dimictic). In general, throughout the growing season nutrient depletion commonly proceeds steadily without return of major amounts of nutrients from deeper water.

In tropical lakes, the situation can be very different because of large changes in the thickness of the mixed layer. A period of growth in a relatively shallow mixed layer may lead to severe nutrient depletion. However, subsequent thickening of the mixed layer coincident with cool, windy weather returns nutrients from deep water to the mixed layer, thus allowing higher rates of production to be re-established near the surface.

For Loch Lomond, the phosphate concentration falls to undetectable level for several months but it was not the case for nitrogen where the range is from 121.7 to 292.3 $\mu g\ l^{-1}$. In the High Dam Lake, the range of nitrate which recorded ranging from 7.95 to 440 $\mu g\ l^{-1}$ and for phosphate from 9.02 to 254 $\mu g\ l^{-1}$(El-Otify, unpublished). No complete depletion was ever observed.

However, case studies (Talling, 1966; Lewis, 1974; Lewis, 1986) show that variations in the thickness of the mixed layer could easily magnify the primary production of tropical lakes by a factor of two or more in comparison to the productivity of physically similar lakes at higher latitudes.

Fee (1979), said that "one of the few quantitatively well established biological generalities about lakes" is that shallow lakes tend to be more productive than deep ones. According to Kilham and Kilham (1990), this seems to apply to temperate rather than tropical lakes.

Kilham and Kilham (1990) considered the palaeolimnology of African lakes, based on fossil diatom remains from cores from a number of lakes, and they make the following observations:

1- Roughly 9500 years BP most large lakes in tropical Africa were larger and deeper than at present

2- Plankton at that time was dominated by *Stephanodiscus astrea*

3- *Stephanodiscus astrea* species dominate when the supply ratio of silicon to phosphorus (in moles) in the epilimnion is relatively low (Si:P~1). Consequently, lakes dominated by *Stephanodiscus astrea* are often hypereutrophic.

4- As the ratio rises, other genera take over (e.g. recent deposits in Lake Kivu) such as *Synedra* and *Nitzschia.* Lake Kivu has a range of Si:P ratios, from high in an isolated bay (Si:P=420), to moderate in the main body of the lake (Si:P=189), to very low in the southern bay of the lake (Si:P=1.45)

Their hypothesis to explain this is:

1- There is a positive relationship between lake depth and increased phosphorus loading in the epilimnion, possibly because a) Such lakes may have more intense physical mixing (more phosphorus added from below the normal mixing depth) and b) Such lakes have a higher proportion of rainfall in their water budget than by river inflow/outflow. Rainfall, with negligible Si concentration, can dominate the external nutrient input to large African lakes with long water residence times.

2- There is a positive relationship between depth of the mixed layer and the rate of phosphorus regeneration

3- In strongly meromictic lakes there is an accumulation of bacteria at the oxic-anoxic boundary. Strong meromixis tends to lead to lower Si:P ratio because bacterial activity will result in release of phosphorus but leave silica unchanged (Golterman, 1975). Another potential complicating factor is the availability of iron. Phosphate can migrate upwards across the interface into the oxic region unaccompanied by iron and thus remain in solution (Stauffer, 1986). The silicon fluxes in the epilimnion are tightly coupled to the relative loading of phosphorus.

4- Small shallow lakes tend to have high Si:P ratios. One reason is that the hydraulic residence by catchment processes which would supply Si:P ratios in the range of 30-100 or so. The short water column does not allow very much time for nutrient regeneration and reduced conditions are generally confined to the sediments (where the surface remains oxidised) and then phosphorus is unlikely to be released. The relationship between sediment area to epilimnetic volume (Fee, 1979) is probably an important aspect of the Si cycle in small lakes.

5- Surrounding vegetation (usually papyrus) reduces phosphorus loading either by direct uptake and storage or by packaging the phosphorus in large particles that are more easily buried. This process can apparently remove phosphorus from small lakes.

From this example we can see that detailed understanding of tropical nutrient budgeting is little understood and that some of the general concepts propounded for temperate waters may not hold for tropical lakes.

b- Oxygen

For temperate lakes, the oxygen in the water column near the bottom of the lake at the end of the stratification season is related to oxygen concentration at the time of stratification, lake productivity, and lake depth. These factors will also influence oxygen concentrations in the deep water of tropical lakes. In addition, however, two factors will be responsible for latitudinal trends in the occurrence of oxygen depletion in deep water: 1- the effect of temperature on the saturation concentration of oxygen in water, and 2- the sensitivity of biochemical oxygen demand to temperature. It is possible to estimate latitudinal trends in oxygen depletion resulting from the combined action of these two factors.

If we assume that Q_{10} is 2.0 for decomposers, and that decomposers do not exhaust the lower concentration of oxygen held by water at high temperature, the initial oxygen concentration in deep water at the beginning of stratification will be consistently lower at

low than at high latitudes for lakes that achieve full oxygen saturation at the time of mixing.

The trend toward lower oxygen concentration in deep water at lower latitudes is magnified by three other factors which have yet been scarcely explored.

First, the duration of the stratification season in tropical lakes may be longer than in temperate lakes of similar size and shape. This would lead to a longer interval of oxygen depletion and result in more extreme seasonal oxygen depletion in deep water (e.g. Loch Lomond stratifies for 16 weeks, north basin, from early June to late September and for 6 weeks, south basin, from mid June and July, whereas the High Dam Lake stratifies for up to 38 weeks from March to October).

Second, the productivity of tropical lakes of a given amount of nutrient is almost certainly greater than that of temperate lakes. This could magnify the amount of oxygen demand in deep water for tropical lakes generally, although the effect is offset to an unknown degree by the greater tendency in warmer lakes for organic matter to decompose before reaching deep water.

Third, tropical lakes may less readily achieve oxygen saturation during the mixing season than temperate lakes. For a given oxygen concentration at the start of mixing, tropical lakes will deviate less from the saturating concentration and thus will take up oxygen less rapidly.

As foreseen by Ruttner (1931), oxygen depletion will be much more likely in tropical than in temperate lakes. This trend may have profoundly affected the exploitation of deep water by benthos and fishes and may even have influenced the evolution and diversification of these groups in tropical waters.

In the vertical water samples of the High Dam Lake (1987-1988), dissolved oxygen ranged from 1.13 mgl^{-1} (13.95%) to 8.93 mgl^{-1} (105.06%) (El-Otify, Unpublished). In Loch Lomond, the minimum dissolved oxygen recorded was 5.52 mgl^{-1} (46%) and the maximum was 13.81 mgl^{-1} (118%) in 1992-1993.

c- Species diversity

Species diversity is a function of the number of species (richness) and the evenness with which the individuals are distributed among these species (equitability).

In moist terrestrial environments, there is a striking and much discussed increase of species diversity at low latitudes (Connell, 1978; Huston, 1979) and this trend culminates in the remarkably high species diversity of tropical moist forests.

For fish communities, the latitudinal trends are also unclear but Lowe-McConnell (1975), concluded from an extensive survey of tropical fish communities that there is a trend toward higher diversity at lower latitudes.

Achieng (1990) stated that Lake Victoria before introduction of Nile Perch, 30 years ago had 15 commercially important species, *Haplochromis* among them. *Haplochromis* cychlids alone had more than 300 species. Loch Lomond is said to be diverse for a Scottish water with 16 species in total (in addition to 4 recent introductions). Nearly 50 species of fish have been identified in the High Dam Lake.

There is no corresponding trend in the species diversity of freshwater plankton communities. There may even be a minor trend toward lower diversity at low latitudes, although this remains to be confirmed from a larger data base. Zooplankton communities also seem to be of similar complexity across latitudes (Fernando, 1980; Lewis, 1979; Serruya and Pollingher, 1983).

Loch Lomond showed a range of diversity index from 0.61 to 2.65 but the High Dam Lake showed lower diversity index (four occasions only) fluctuated from 0.49 to 0.93.

Hutchinson (1967) called this the "Paradox of the plankton". He stated that, in bounded biotope, in which a number of species are competing with slightly varying efficiency for the same resources which they require in the same proportion, it is easy to show mathematically, provided no commensalism or symbiosis is occurring, that no equilibrium exists when more than one species is present.

The principle involved in a theoretical treatment is commonly referred to as Gause's principle, because experimental confirmation of its validity was first given by G. F. Gause (1934, 1935), following the mathematical investigations of Volterra (1926). The work of Volterra and Gause first brought the competitive exclusion principle before ecologists.

The problem for phytoplankton is that the principle does not appear to hold i.e. the community of apparently directly competing species is too diverse. The question is why?

There are a number of possible answers:

1- It might be argued that the competing species had exactly equal efficiencies in competition.

Riley (1963) feels that natural selection might operate to increase the efficiency of two species living in essentially identical environments so that these efficiencies approached asymptotically an upper limiting value set by general biology of the organisms. If the organisms then entered into competition, the differences in efficiency might be so small that competitive exclusion would proceed at an undetectably slow rate. This could happen only when the demands of both species on the environment were initially identical and could be met in only one way. It is possible for plankton. This may provide a practical answer.

2- It may be supposed that in spite of appearances to the contrary the environment is not really homogeneous (more diverse) than we are observing. So, there is more one niche in the environment.

There is bound to be detectable temporary thermal stratification near the surface on bright days in any but the most disturbed lake; chemical differences may be associated with the water surface and the horizontal inhomogeneities associated with the langmuir spirals in the wind drift certainly can affect motile and nonmotile organisms differently, leading to a partial separation of population, but it is difficult to believe that any of these effects could be persistent enough to have much significance in the environmental regulation of competition.

It is possible that the requirement that all competition coefficients be positive may not be satisfied, so that commensalism and symbiosis occur. We have seen that some species of the phytoplankton require vitamins and that they are in general small motile forms. The smallness and motility would promote the uptake of mineral nutrients and accessory organic substances.

The tropical terrestrial communities that are so extraordinarily diverse are marked by great abiotic stability and probably also by continuous minor disturbance sufficient to maintain habitat diversity (Connell, 1978; Sousa, 1984). Diversity in plankton communities is probably maintained by continual temporal change rather than physical heterogeneity. Whereas tropical forest communities appear to approach equilibrium in community composition, plankton communities of lakes appear to be almost continually in succession. Succession is probably the main mechanism by which diversity is maintained in plankton communities.

Some empirical evidence indicates that the plankton communities of tropical lakes experience more frequent disturbances, and consequently more numerous discrete successional episodes, than do the plankton communities of temperate lakes (Lewis, 1978a; Lewis, 1986). Sequences of taxa in tropical lakes can even be predicted in some cases *a priori* from the abiotic changes accompanying succession; these sequences are surprisingly similar in temperate and tropical lakes (Lewis, 1986).

More numerous successional episodes will produce greater irregularity in the abundance of individual taxa but will not necessarily broaden the range of taxa because there is a strong element of repetition in separate successional episodes. In fact, frequent truncation of succession by initiation of new episode may reduce diversity somewhat because it prevents the occurrence of taxa that are specialised for late stages of succession. Consequently, it seems quite reasonable, in view of latitudinal trends in abiotic factors and the diversity regulation mechanisms for plankton, that there should be no major trends in diversity with latitude for plankton.

It might be supposed that the assemblage of species in the phytoplankton never really approaches competitive equilibrium so that the prediction of theory implying equilibrium can never be relevant.

The marked contrast between temperate and tropical regions in annual variability of sunlight and temperature leads naturally to the hypothesis that the magnitude, efficiency, and variability of energy flow in biological systems must also differ greatly between these regions.

At the most general level, the key contrast between temperate and tropical lakes is in the seasonal variability of resource supply. As is generally true of temperate lakes, the productivity of tropical lakes appear to be principally limited by two resources sunlight and nutrients.

The contrast between temperate and tropical lakes is thus not in the identity of controlling factors, but rather in their mode of operation.

Solar irradiance (sunlight supply) at the water surface is independent of biological control and in the temperate zone governs the supply of nutrients by determining the timing of interchanges between the trophogenic and tropholytic zone of lakes. A seasonal trend in the tropics toward lower light intensity also forces an opposite trend in nutrient supply, but seasonal variation is much reduced.

The difference in magnitude of variation has two implications 1- both limiting resources will be used more efficiently in the tropics because of the greater equitability of their distribution over time, and 2- nonseasonal effects on resource supply will be more important in the tropics and will tend to uncouple the seasonally-based phasing of resources so that optima of the two resources are more likely to occur together. Thus,

sunlight is used more efficiently in the tropics because high delivery rates are less likely to coincide with extremes of nutrient depletion and nutrients are used more efficiently because of the greater frequency of controlling variations, which distributes them more equitably with regard to sunlight and simultaneously permits them to be cycled more rapidly.

The supply of energy and nutrients to autotrophs as well as some important physical and chemical regulatory mechanisms varies with latitude. These variations are often not intuitively obvious, nor do they conform to some preconceived notions that might be derived from analogies with terrestrial communities. In addition, many effects of higher order resulting from fundamental differences in tropical and temperate freshwater systems are still to be studied. These include such basic phenomena as nutrient regeneration mechanisms, propagation of short-term irregular variation in critical environmental variables through food chains, successional responses of higher trophic levels to environmental variation, and contrasts in adaptive strategies for organisms occupying environments that have different ratios of predictable to unpredictable variation.

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5. Appendices

Appendix (1) Methods used for chemical analysis

Orthophosphate

Almost all methods are colorimetric and most are based on the formation, under acid conditions, of the yellow colloidal phosphomolybdic acid and its subsequent conversion to blue heteropoly compound.

In a suitably acidified solution, phosphate reacts with molybdate to form molybdo-phosphoricacid, which is then reduced to the intensely coloured molybdenum blue complex and is determined spectrophotometrically. Increased sensitivity can be obtained by extracting the blue complex into an organic solvent.

The procedure used in this investigation was according to Mackereth *et al.*, 1978. The analysis of samples were commenced not more than 4 hours after completion of sampling. The samples were not preserved in any way.

Reagents

a) Sulphuric acid solution 14% v/v

140 ml of concentrated A.R. sulphuric acid was added cautiously to 700 ml of distilled water. After cooling make up to 1000ml, this solution can be stored indefinitely in a polythene container.

b) Ammonium molybdate

3.0 gm of finely crystalline A.R. ammonium molybdate $(NH_4)_6MO_7\ O_{24}.4H_2O$ were dissolved in 100 ml of distilled water. This solution was made up freshly before each analysis.

c) Ascorbic acid

5.4 gm of ascorbic acid were dissolved in 100 ml distilled water and store in plastic bottle. This reagent was prepared fresh each time.

d) Potassium antimonyl tartrate

0.34 gm of potassium antimonyl tartrate were dissolved in 100 ml distilled water. This solution is stable for many months whenever stored in a polythene container.

e) Working reagent:

Mix 100 ml sulphuric acid (a), 40 ml ammonium molybdate (b), 40 ml ascorbic acid (c) and 20 ml potassium antimonyl tartrate (d) in this exact order.

f) Hexanol

g) Methanol

Procedure:

200 ml of each sample were dispensed into 250 ml separating funnel. A distilled water blank was similarly prepared. 20 ml of the freshly mixed working reagent (e) were added by bulb pipette. The sample and the reagent were mixed and allowed to stand for 10 minutes. 20 ml of hexanol (f) were added by bulb pipette, shaken well for 1 minute and allowed to stand until the layers have separated. The aqueous layer was run then off and discarded. The solvent layer was run into a 50 ml flask and 1 ml of methanol (g) was added. The solution was centrifuged at about 2000 rev min^{-1} for 1 minute to clear the sample.

The extinction of the blue colour was read at 690 nm against the reagent blank and the concentration of phosphate determined from a calibration graph prepared from samples of known concentration of phosphate.

Results are expressed as $\mu g\ PO_4P\ l^{-1}$

Silicate

The water sample is allowed to react with molybdate at pH 3-4 which result in the formation of the silicomolybdate, phosphomolybdate and arsenomolybdate complexes. A reducing solution, containing metol and oxalic acid, is then added which reduces the silicomolybdate complex to give a blue reduction compound which is determined spectrophotometrically and simultaneously decomposes any phosphomolybdate or arsenomolybdate, so that interference from phosphate and arsenate is eliminated.
Analysis of samples was commenced not more than 4 hours after the completion of sampling.
Allplastic ware was used to eliminate silica contamination from glass.

Reagents

a) Acid ammonium molybdate

2.0 gm of ammonium molybdate $(NH_4)_6\ MO_7\ O_{24}.4H_2O$ was dissolved in 70 ml distilled water, 6 ml of concentrated hydrochloric acid was added. The final volume was made up to 100 ml and was stored in polythene bottle. This reagent was freshly prepared each time.

b) Oxalic acid

10.0 gm of oxalic acid dihydrate $(COOH)_2.2H_2O$ were shaken with 100ml of distilled water. The solution was heated slightly to dissolve the oxalic acid. This solution is stable indefinitely.

c) Sulphuric acid 25% V/V

A 25% V/V solution was prepared by adding 250 ml concentrated sulphuric acid cautiously to 600 ml of distilled water, and the solution cooled and made up to 1 litre with distilled water.

d) Metol-sulphate solution

3.0 gm of anhydrous sodium sulphite Na_2SO_3 was dissolved in 150 ml distilled water followed by the addition of 5.0gm of metol (4-methylaminophenol sulphate). The solution was heated slightly to dissolve metol. This was cooled to room temperature and the volume was made up to 250 ml with distilled water. It was stored in a dark bottle. The solution was freshly prepare each time.

e) Reducing agent

100 ml of metol-sulphite solution (a) were mixed with 60 ml of oxalic acid solution (b), 120 ml of sulphuric acid (c) were then added with mixing and the volume was made up to 300 ml with distilled water.

The reagent was used immediately after preparation.

Procedure:

20 ml of filtrate sample were put in plastic graduated cylinder using bulb pipette A distilled water blank was similarly prepared. 3 ml of acid ammonium molybdate (a) were added to the sample and mix . After ten minutes, 15 ml of reducing agent were added and were made up to 50 ml with distilled water. The samples and the blank were allowed to stand for at least 3 hours. The blue colour was measured spectrophotometricaly at 812 nm against a reagent blank.

The concentration was read off from a calibration graph prepared from samples of known concentration of silicate.

Results are expressed as $\mu g\ l^{-1}$

Nitrate (PDSA)

Reagents

a) Phenoldisulphonic acid

b) Magnesium sulphate solution

10% solution of crystalline $MgSO_4\ 7H_2O$

c) Sodium hydroxide

40% solution approximately

d) Red litmus paper

Procedure

100 ml of the sample were evaporated to dryness in a 200 ml conical Pyrex flask in an oven. A distilled water blank was similarly prepared. 2 ml of phenoldisulphonic acid (a) were added to the residue from graduated pipette. The flask was revolved to wet the residue completely with the acid and was allowed to stand for 10 minute. The acid was washed to the bottom of the flask with not more than 80cc distilled water. 2 ml of magnesium sulphate and a small piece of litmus paper were added to the flask. Sodium hydroxide (c) was added drop by drop until the litmus just stayed blue when the solution was mixed a precipitate of $Mg(OH)_2$ forms which carries with it colloidal organic matter which would otherwise interfere with the reading. The volume was made up to 100 ml exactly. At least 50 ml of the sample was mixed and centrifuged to remove the precipitate. The yellow colour was measured spectrophotometricaly at 410 nm against a reagent blank. The concentration was read off from a calibration graph prepared from samples of known concentration of nitrate.

Results are expressed as $\mu g\ NO_3\text{-}N\ l^{-1}$

Nitrate (cadmium reduction method)

Nitrate is reduced to nitrite when a sample is run through a column containing amalgamated cadmium filings. The nitrite thus produced is determined by diazotizing with sulphanilamide and coupling with N-(1- naphthyl)-ethylenediamine to form a highly coloured azo dye that is measured Spectrophotometrically The method is recommended for the concentration range below 0.1 mg NO_3-N l^{-1}.

Reagents

a) 2 M HCl

12 M (concentrated) HCl was diluted to 2 M

b) Cupric sulphate 2%

20.0 gm Cu SO_4 5 H_2O

a) Preparation of column

5.0 gm cadmium metal filings about 0.5 mm diameter were washed with 25 ml HCl and rinsed with distilled water. 10 ml of cupric sulphate were added. The contents were swirled until the blue colour disappeared. These were used to fill the column. The column was flushed twice with a mixture of 50 ml distilled water and 5 ml buffer solution . The flow was adjusted to about 6 ml per minute.

Buffer solution

100.0 gm NH_4Cl, 20.0 gm $Na_2B_4O_7$ 10 H_2O and 1.0 gm Na EDTA $2H_2O$ were dissolved in distilled water and make up to 1 litre

b) Reduction to nitrate

10 ml of buffer solution were mixed with 100 ml of sample. 30 ml of each buffered sample were allowed to pass through the column and discarded. The remainder of the sample was added to the column, about 10 ml of the next effluent were used to rinse the collecting vessel and discarded. Over 30 ml were collected to use for nitrite determination. For reagent blank, 100 ml distilled water were used.

c) Determination of nitrite

Reagents

a) Sulphanilamide 0.2%

2.0 gm sulphanilamide were dissolved in 1 litre distilled water and kept in a dark bottle. This solution is stable for many months.

b) 6 M HCl

12 m HCl (concentrated) HCl were diluted

c) N-(1-Naphthyl) ethylene diamine di-hydrogen chloride .1%

0.1 gm N-(1-Naphthyl) ethylene diamine di-hydrogen chloride was dissolved in 100 ml distilled water. It was stored in a dark bottle in a refrigerator for up to 2 months

d) Ammonium sulphamate 5%

5.0 gm NH_2 SO_3 NH_4 were dissolved in 100 ml distilled water. It was stored at room temperature.

Procedure:

25 ml of the nitrate samples were diluted to 100 ml. 5 ml of sulphanilamide 0.2% (a) and 2 ml of hydrochloric acid 6 M (b) were added to each sample. After 3 minutes 1 ml ammonium sulphamate 5 % (d) were added and after a further 3 minutes, 1 ml of N-(1-Naphthyl) ethylene diamine di-hydrogen were added (c). The samples were left for the colour to develop for at least 15 minutes and were then measured spectrophotometerically at 530 nm against the reagent blank.

The concentration was read off from a calibration graph prepared from samples of known concentration of nitrate.

Results were expressed as $\mu g\ NO_3$ -N l^{-1}

Chemical oxygen demand (COD)

The chemical oxygen demand (COD) determination is a measure of the oxygen equivalent of that portion of the organic matter in the sample that is susceptible to oxidation by a strong chemical oxidant.

Most types of organic matter are destroyed by a boiling mixture of permanganate and sulphuric acids. A sample is refluxed with known amounts of potassium permanganate and sulphuric acid and the excess permanganate is titrated with sodium thiosulphate. The amount of oxidizable organic matter measured as oxygen equivalent, is proportional to the potassium permanganate consumed.

Reagents

a) Potassium permanganate 0.02 M

3.161 gm K Mn O_4 were dissolved in 1 litre distilled water and was kept in a dark bottle as a stock solution (0.1 M). 0.02 M was made up freshly before use.

b) Sodium thiosulphate 0.02 M

12.41 gm crystalline Na_2 S_2 O_3 $5H_2O$ were dissolved in 1/2 litre distilled water and kept in a dark bottle. This stock solution, concentration 0.1 M, was diluted to 0.02 M immediately before use.

c) Potassium iodide 5% solution

5.0 gm of potassium iodide were dissolved in 100 ml distilled water and kept in a dark bottle.

d) Starch solution

1.0 gm of soluble starch was dispersed in 100 ml distilled water and warm to 90 C with stirring. This solution was prepared freshly before use

e) Sulphuric acid 25% V/V

A 25% V/V solution was prepared by adding 250 ml concentrated sulphuric acid cautiously to 600 ml of distilled water. This was cooled to room temperature and the volume made up to 1000 ml with distilled water

Procedure

100 ml of each sample were dispensed into 250 conical flask.
100 ml of distilled water were used as a blank . 10 ml of potassium permanganate and 10 ml of sulphuric acid were added. The sample and the blank were placed in a boiling water bath for 30 minutes. Then they were removed from the water bath and left to cool. 1 ml of potassium iodide was added and shake. The iodine thus produced in 50 ml sample was titrated aganist 0.02 M sodium thiosulphate in the burette using a starch as indicator.

Calculation:

If (a) is volume of thiosulphate used in titration of the blank
(b) is volume of thiosulphate used in titration of the sample
Then O_2 absorbed sample (C.O.D) = 10 (a-b)/a $mgO_2\ l^{-1}$

Alkalinity (bicarbonate)

In most natural waters bicarbonates, and sometimes carbonates are present. These salts are hydrolysed in solution because of the weakness of carbonic acid (H_2CO_3), with the production of hydroxyl ions and consequent rise in pH

$$M^+ + HCO^-_3 + H_2O \text{ ---------- } M^+ + H_2CO_3 + OH^-$$

The concentration of bicarbonate in solution can be determined by titrating the sample with standard acid (thereby removing OH^-) until the above equation has moved completely to the right, all the carbonic acid then being present as undissociated H_2CO_3 or dissolved as CO_2. Since this occurs when the pH has been reduced to approximately 4.5, an indicator is chosen to give a colour change at this pH.

Reagents

a) 0.01 M hydrochloric acid

0.01 M hydrochloric acid was made up when required from stock solution of M HCl

b) B.D.H. 4.5 indicator

To facilitate recognition of the end-point a standard end point colour was prepared by adding 5 drops of indicator to 100 ml of buffer solution at pH 4.5 (50 ml N sodium acetate + 50 ml N acetic acid) this was kept in a stoppered conical flask

Procedure

100 ml of sample was pipette into conical flask and 5 drops of indicator solution was added. Standard acid was run in from a 10 ml burette with continuous mixing. The titration was completed when the colour of the sample matched that of the standard end point.

Calculation

0.01 M acid contains 0.1 mmol of acid in each ml, so that each ml of standard acid used in the titration corresponds to 0.01 mmol of bicarbonate ion in 100 ml of sample, or 0.1 mmol l^{-1} of sample; therefore if V ml of acid are used in the titration the concentration of bicarbonate in the sample is 0.1 x V mmol l^{-1}

Appendix (2) Methods used for biological analysis

Chlorophyll *a*

Apparatus

1- Millipore filtration apparatus designed to hold 47 mm diameter filters

2- Stoppered plastic tubes of 50 ml capacity

3- Stoppered plastic centrifuge tubes of 15 ml capacity

4- Water bath (temperature 60 C)

5- Bench centrifuge

6- Spectrophotometer

7- Glass fibre filter paper Whatman GF/C 4.5 cm

Reagents

1- Drum methanol

2- Magnesium carbonate suspension:

1 gm of finely powdered was add to 100 ml of distilled water and shaken

Method

1- Five litres of sample were filtered through a millipore filter apparatus with Whatman GF/C glass fibre filter paper. 1 ml of magnesium carbonate suspension was added to the sample prior to filtering to prevent the degradation of chlorophyll due to low pH.

2- After the filtration, the samples were placed in the freezer which has a two fold function of preserving the sample until subsequent chlorophyll extraction and breaking up cells to ease the release of chlorophyll

3- The filter papers were cut into approximately 2mm x 2 mm squares, placed in an aluminium foil coated tube containing a minimal amount of methanol necessary to cover the sample

4- Then, they were placed in a water bath at 60 C for twenty minutes

5- After this time has elapsed, the samples were cooled and transfered to clean foil covered centrifuge tube and centrifuge at 3000 g for five minutes to remove any debrise that may interfere with spectrophotometer readings

6- After centrifugation the chlorophyll / methanol solution was transferred to a 10 ml volumetric flask and made up to volume with fresh methanol

7- The samples were centrifuge for the second time at 3000 g for five minutes to ensure there is no turbidity, then the absorbance at 650 and 665 were measured

For accuracy the spectrophotometer reading should lie between 0.1 and 0.9

8- Chlorophyll was estimated using the following equation

μg Chl *a* /sample = 16.5 (A665) - 8.3 (A650)

9- The extraction procedure was repeated to check that most of the chlorophyll had been extracted. On the whole 90% of chlorophyll was removed in the first extraction. Throughout the extraction procedure the sample should be kept in dim light with all tubes and glassware wrapped in aluminium foil

^{14}C light and dark method of phytoplankton production estimation

In the ^{14}C technique, the incorporation of tracer in the organic matter of phytoplankton during photosynthesis is used as a measure of the rate of primary production.

If the content of total CO2 of the experimental water is known, and if a definite amount of $^{14}CO_2$ is added to the water, then by determining the content of ^{14}C in the plankton after the experiment the total amount of carbon assimilated can be calculated.

Field work

1- Water samples were collected using Van Dorn water sampler from surface, 1, 3, 5 and 10 m depths

2- All water samples from various depths were collected first and filled the experimental bottles immediately after collection. Then they were kept in a dark box

3- 1 ml of radioactive sodium bicarbonate contained 2μ curies per 110 ml sample was injected to the various bottles rapidly

4- Then , they were shaken thoroughly and lowered at once to the selected depths of exposure

5- The bottles were incubated *in situ* for 4 hours, after that they were transported to the laboratory unopend, in the dark and as quickly as possible

Laboratory work

1- Each bottle was gently shaken and filtered through 25 mm membrane filter H.A. Millipore filter under reduced pressure

2- The filter was then placed carefully in a scintillation vial containing 15 ml scintillation fluid, then stoppered and labelled

3- 0.5 ml of the original radioactive solution was also added to a scintillation vial containing 15 ml of the fluid, so that the original activity added can be calculated

4- Liquid scintillation counter LKB Wallac was used to count the activity

The following equation was used to calculate the carbon assimilated

Carbon assimilated = K 1,2,3 .a b / c

Where

a = ^{14}C assimilated = (total counts per minute - background x radiation discrimination factor of 1.06)

b = ^{12}C available = alkalinity (from titration) + dissolved free CO_2 (calculated from nomograph)

c = ^{14}C activity added

K1 = A correction for aliquot factor. If (x) cc were filtered from a bottle of (y) cc capacity and (z) ml of radioactive solution were added, then this factor is y-z/x

K2 = A time factor to convert the results to an hourly basis

K3 = Factor to convert results to standard volume of loch water (This will be 1 to express results per litre, or 1000 to express results per cubic meter)

The calculations were made with a computer using a spreadsheet developed by Mr. T. Bladon

Appendix (3) Matrix of correlation coefficient between 13 environmental factors and population parameters of the north basin

	Do sat	Do mg	Temp	pH	Secchi	Light
Do mg	*** 0.925					
Temp	-0.399	***-0.715				
pH	* -0.495	-0.383	0.006			
Secchi	-0.007	0.153	-0.388	* 0.442		
Light	-0.039	-0.231	* 0.518	-0.049	-0.220	
Conduct	0.025	0.068	-0.089	0.332	0.127	0.395
Alkalinity	-0.412	*-0.543	* 0.549	0.023	*-0.550	0.172
Phosph	***-0.746	**-0.650	0.172	0.207	0.127	-0.084
Silicate	0.053	0.381	***-0.813	0.065	0.341	*-0.483
Nitrate	0.101	-0.059	0.383	0.116	-0.153	* 0.466
COD	-0.326	-0.173	-0.204	0.300	0.293	-0.163
Chloroph	-0.236	*-0.556	***0.899	-0.141	-0.312	* 0.458
No phyto	-0.141	-0.423	***0.773	-0.024	-0.148	* 0.480
Diatom	-0.145	*-0.475	***0.886	-0.175	-0.413	** 0.614
Cyano	0.428	0.356	-0.043	-0.081	0.315	-0.005
Flagel	-0.010	-0.268	**0.631	-0.045	-0.065	0.427
Green	0.052	-0.233	**0.636	-0.048	-0.301	0.276
Unknow	*-0.523	*-0.491	0.254	0.204	-0.114	-0.013
Rain	-0.205	-0.198	0.062	-0.270	0.003	0.269

Conduct	Alkalini	Phosph	Silicate	Nitrate	COD	Chloroph
-0.041						
-0.226	0.034					
0.029	*0.510	0.159				
*0.491	0.439	*-0.471	*-0.477			
0.033	-0.005	0.077	0.216	-0.370		
-0.197	0.305	0.210	***-0.694	0.169	-0.333	
0.028	0.414	-0.056	**-0.604	*0.551	-0.253	***0.754
-0.034	0.340	0.076	***-0.773	0.397	-0.315	***0.845
-0.251	-0.334	-0.392	-0.202	0.097	-0.272	0.107
0.021	0.359	-0.089	*-0.533	*0.520	-0.297	**0.627
-0.278	0.220	-0.057	***-0.814	0.129	-0.291	**0.639
0.122	0.208	0.101	0.067	0.097	0.317	0.194
-0.515	-0.154	0.528	0.073	*-0.553	0.064	0.082

No.phyto	Diatom	Cyano	Flagel	Unknow	Rain
***0.722					
0.058	-0.016				
***0.953	**0.582	0.060			
0.373	**0.583	0.425	0.325		
0.141	0.134	- 0.147	-0.125	-0.188	
-0.113	0.094	-0.335	-0.074	0.045	-0.218

Appendix (4) Matrix of correlation coefficient between 13 environmental factors and population parameters of the south basin

	Do sat	Do mg	Temp	pH	Secchi	Light
Do mg	*** 0.949					
Temp	**-0.574	***-0.798				
pH	-0.283	-0.166	-0.119			
Secchi	-0.366	*-0.450	* 0.516	0.187		
Light	0.072	0.103	-0.141	0.052	-0.423	
Conduct	0.132	0.325	**-0.575	0.334	-0.102	-0.041
Alkalinity	-0.314	-0.401	0.367	-0.008	-0.265	0.268
Phosph	0.308	0.406	-0.420	-0.202	-0.111	0.008
Silicate	0.389	**0.614	***-0.817	0.277	-0.296	0.168
Nitrate	0.127	0.311	*-0.533	0.330	-0.195	0.101
COD	-0.118	0.018	-0.315	0.155	-0.233	-0.111
Chloroph	-0.245	-0.428	** 0.607	-0.415	-0.026	-0.045
No phyto	0.225	0.109	0.128	-0.340	-0.288	-0.059
Diatom	* 0.448	0.389	-0.194	-0.318	*-0.470	0.031
Cyano	* 0.448	-0.428	0.427	-0.060	* 0.478	-0.116
Flagel	-0.193	-0.372	** 0.666	-0.096	0.220	-0.130
Green	0.104	-0.109	* 0.475	-0.158	0.184	0.168
Unknow	*-0.481	*-0.493	0.348	-0.035	0.263	-0.182
Rain	0.238	0.188	-0.071	-0.229	-0.389	0.390

Conduct	Alkalini	Phosph	Silicate	Nitrate	COD	Chloroph
-0.313						
0.283	*-0.522					
0.425	*-0.455	* 0.481				
0.409	-0.030	0.180	*** 0.792			
0.228	0.108	-0.385	0.078	-0.004		
-0.392	0.286	-0.220	***-0.828	***-0.781	-0.143	
0.188	0.053	-0.005	*-0.448	*-0.547	-0.112	** 0.636
0.301	-0.046	0.123	-0.199	-0.301	-0.081	* 0.480
0.265	0.054	-0.224	*-0.485	-0.202	-0.149	0.245
-0.429	0.092	-0.178	-0.395	-0.266	-0.329	0.300
**-0.625	0.094	-0.054	-0.394	-0.428	-0.530	0.346
0.126	0.246	-0.222	*-0.468	-0.320	0.278	0.320
-0.258	0.285	-0.169	-0.047	-0.094	0.264	0.006

No.phyto	Diatom	Cyano	Flagel	Unknow	Rain
*** 0.924					
0.316	0.156				
0.142	-0.128	-0.045			
0.043	0.018	0.049	0.230		
0.304	0.075	** 0.573	-0.149	-0.213	
0.005	0.063	-0.110	0.008	0.039	-0.205

Appendix (5) TWINSPAN ordered two-way table (sitesxspecies) for phytoplankton
samples from Loch Lomond 1992-1993

Order of species including rarer ones.
Relative species number followed by true species number or name.

Rel. number	Name or true no.	*	Rel. number	Name or true no.	*	Rel. number	Name or true no.	*	Rel. number	Name or true no.	*	Rel. number
8	EUN SPP	*	13	SUR SPP	*	18	SPI SPP	*	42	FIL THN	*	12
1	MEL SPP	*	2	AST SPP	*	9	SYN SPP	*	26	CLO SPP	*	10
16	HOL SPP	*	39	MAL SPP	*	43	UNK UNK	*	4	TAB SPP	*	7
15	OSC SPP	*	20	CRY SPP	*	41	DIA UNK	*	6	FRA CRO	*	24
32	BOT SPP	*	5	TAB INT	*	25	COS SPP	*	30	PED SPP	*	31
21	PER SPP	*	27	OOC SPP	*	36	COE SPP	*	40	BIN SPP	*	14
29	DIC SPP	*	37	XAN SPP	*	19	ANA SPP	*	22	CER SPP	*	33
35	SPI SPP	*										

Order of samples
Relative sample number followed by true sample number o name.

Rel. number	Name or true no.	*	Rel. number	Name or true no.	*	Rel. number	Name or true no.	*	Rel. number	Name or true no.	*	Rel. number
2	11FEB92N	*	19	01DEC92N	*	20	06JAN93N	*	21	09FEB93N	*	22
24	23MAR93N	*	25	06APR93N	*	26	20APR93N	*	27	04MAY93N	*	28
4	24MAR92N	*	5	14APR92N	*	6	05MAY92N	*	32	24MAR92S	*	30
50	23FEB93S	*	51	09MAR93S	*	52	23MAR93S	*	47	01DEC92S	*	1
48	06JAN93S	*	54	20APR93S	*	55	04MAY93S	*	56	19MAY93S	*	9
29	15JAN92S	*	46	04NOV92S	*	53	06APR93S	*	7	19MAY92N	*	8
36	02JUN92S	*	37	16JUN92S	*	33	14APR92S	*	34	05MAY92S	*	17
44	22SEP92S	*	45	07OCT92S	*	41	11AUG92S	*	42	25AUG92S	*	10
38	30JUN92S	*	39	14JUL92S	*	40	28JUL92S	*	12	28JUL92N	*	13
16	22SEP92N	*	14	25AUG92N	*							

1Final Table

Samples are columns, species are rows.
Entries in the table are the pseudospecies levels not quantitative values.

Species Rel.	True	Samples, relative numbers.	
		1222222222 3345554 34555 1245 333331444441133411111	
		2901234567834562090127118456989637856734734512018902356 4	
8	EUN SPP	---12221-121---11-211-1-1--3---------1---1---------1----	0000
13	SUR SPP	----------111-11------2----------	0000
18	SPI SPP	4----------	0000
42	FIL THN	5--5555554533----444--5-55551-1----------5------	0000
12	FRU SPP	-1--1------11--------1----4-------1-----1----------	0001
17	COE SPP	--22--13-1------3111332-1----123--------3--4-1-----1----	0010

```
 2 AST  SPP   32-213345553555555665255878515585555553124-1543323--2-  00110
 9 SYN  SPP   -11--311-22-1-----13313-3445-----2-31-32-2-------221----  00110
26 CLO  SPP   22--2----21-----3332234434341155122l-32-3341132-11---1-  00110
10 NAV  SPP   ----------1-------2-11-334-5-132------1----11----1-2----  00111
11 CYM  SPP   ------------------------------22------1------1----------  00111
16 HOL  SPP   3335432422231---3121233133--35424-1-22--6-14123---124252  010
39 MAL  SPP   -22-----222------32332---445-3-34-------3--254-----11--1  010
43 UNK  UNK   ---554555663322354555--2466755455668754565 67-55535555555  010
 4 TAB  SPP   133132121-2232-1--3-222-233322224----15313--223224422122  0110
 7 CYC  SPP   41324333354435-555555455466655556253556455555-6555666556  0110
 3 TAB  AST   32223433145413-443343354255555545555415555555565556655455  0111
15 OSC  SPP   22321222242121-344435522-555435555556555445565555555445 5  0111
20 CRY  SPP   243332224551----232234413565554-514255-25-4555555655545-  0111
41 DIA  UNK   31323435554431-42-334-32266655155454555-5544-55555565656  0111
 6 FRA  CRO   11-------11-----212--31333451335-235433455555*3355542-53  100
24 STA  SPP   3323--21-1-2-2-1-2-112212---33243-3---2-4233443423443344  100
28 SCE  SPP   31---------3----41-21---------333--12-4--444551324--1-22  100
32 BOT  SPP   -2-3131222-------2-323--2--323-4--------3-14-42332344334  100
 5 TAB  INT   -22212---1-------112-22-2-----12--------353455-3-3432344  1010
25 COS  SPP   -2-11-2---------1111211-1----4133--121--422355-132533335  1010
30 PED  SPP   ------------------------1------1----2----12-1----1-----1  1010
31 STA  SPP   --311---------------11------11----------212132----3-2-23  1010
38 ANK  SPP   -----2-3-----------------------------2-3--2----------  1011
21 PER  SPP   ----------------------------3----1-1---11---212--131--21  1100
27 OOC  SPP   ---21--1-------------311--3-222--------33--433424332223  1100
36 COE  SPP   ---------------------1---------------------------2------  1100
40 BIN  SPP   -1312-11-2-------1-1-------363-5--34-5--4334559796353355  1100
14 COC  SPP   ------------1-------------------------2--1-------------5  1101
23 GYM  SPP   -1---1-----------2--1121-3-3-1223--25---2--3443312444-34  1101
29 DIC  SPP   -------------------------3---1------2------121--13--3224  1101
37 XAN  SPP   ------------------------------1-----------------2----1  1101
19 ANA  SPP   -------------------------3---3-1-----2--3--35144-4444-15  1110
22 CER  SPP   ----------------------------3----111----1221543344554133  1110
33 SPO  SPP   ----------------------------------------3------435555445  1111
34 GON  SPP   -------------------------------------------------1-1-----  1111
35 SPI  SPP   -1-----------------------------------------------43-----  1111

              00000000000000000000000000000000000001111111111111111
              00000000000000000000000001111111111111111000000111111111
              00000000000000001111111110001111111111111000011000001111l
              000000001111111100000011   000001111111      0001100001
              000111110001111100000l     011110000011
```

Appendix (6) Seasonal variation in colony size of the most important diatom species

Figure (1) *Melosira italica*

Figure (2) *Asterionella formosa*

Figure (3) *Tabellaria fenestrata*

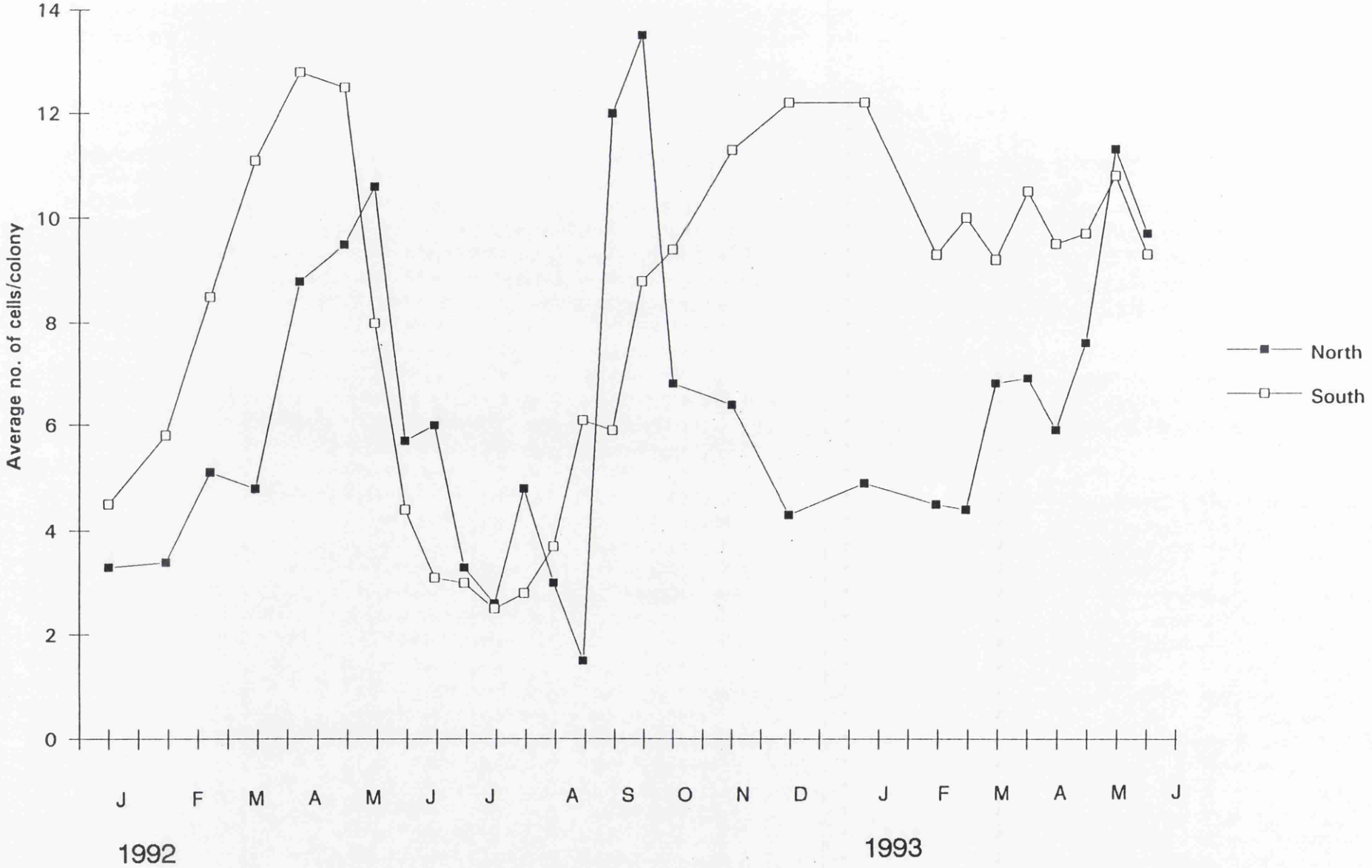

Figure (1) *Melosira italica*

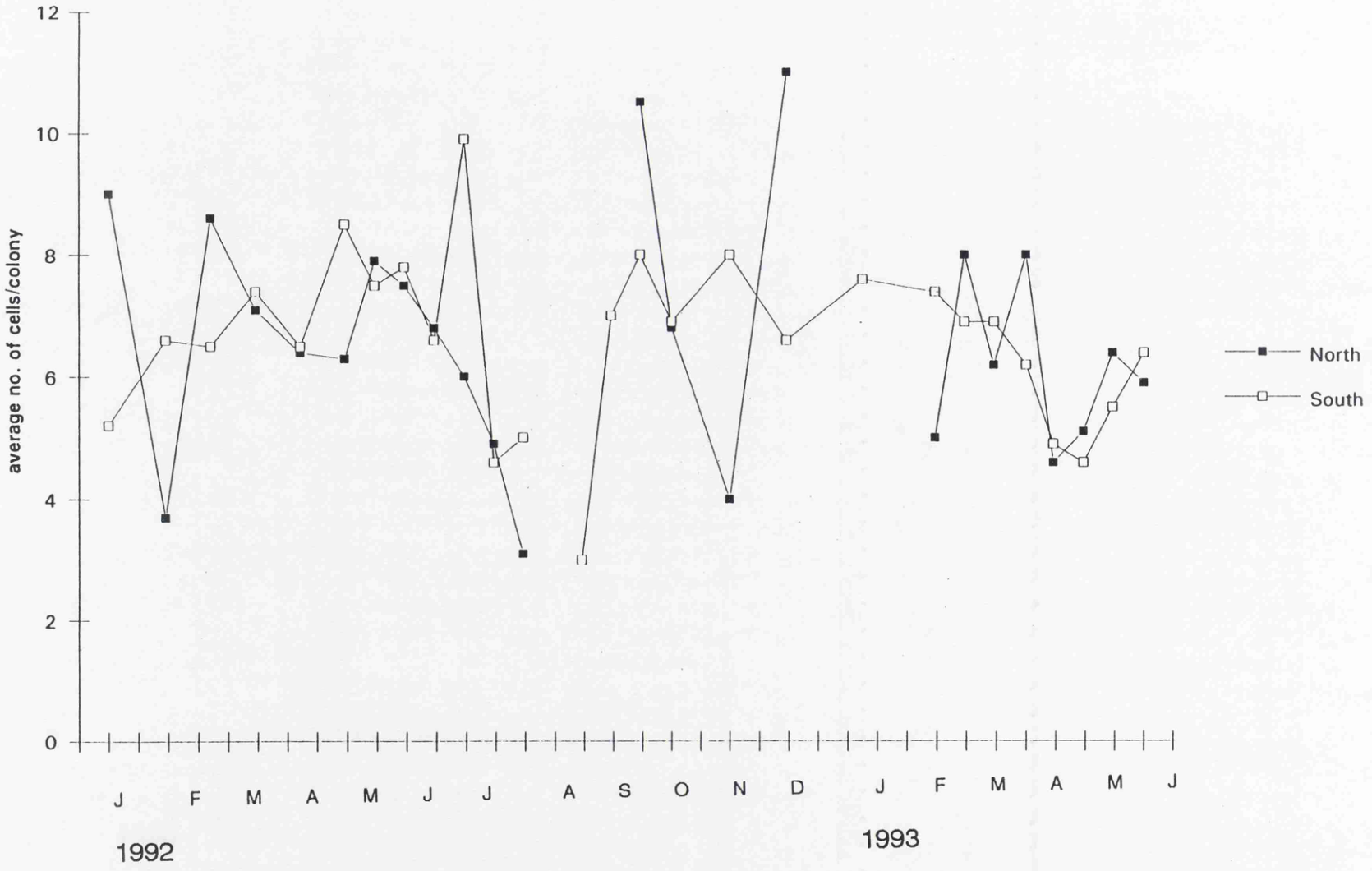

Figure (2) *Asterionella formosa*

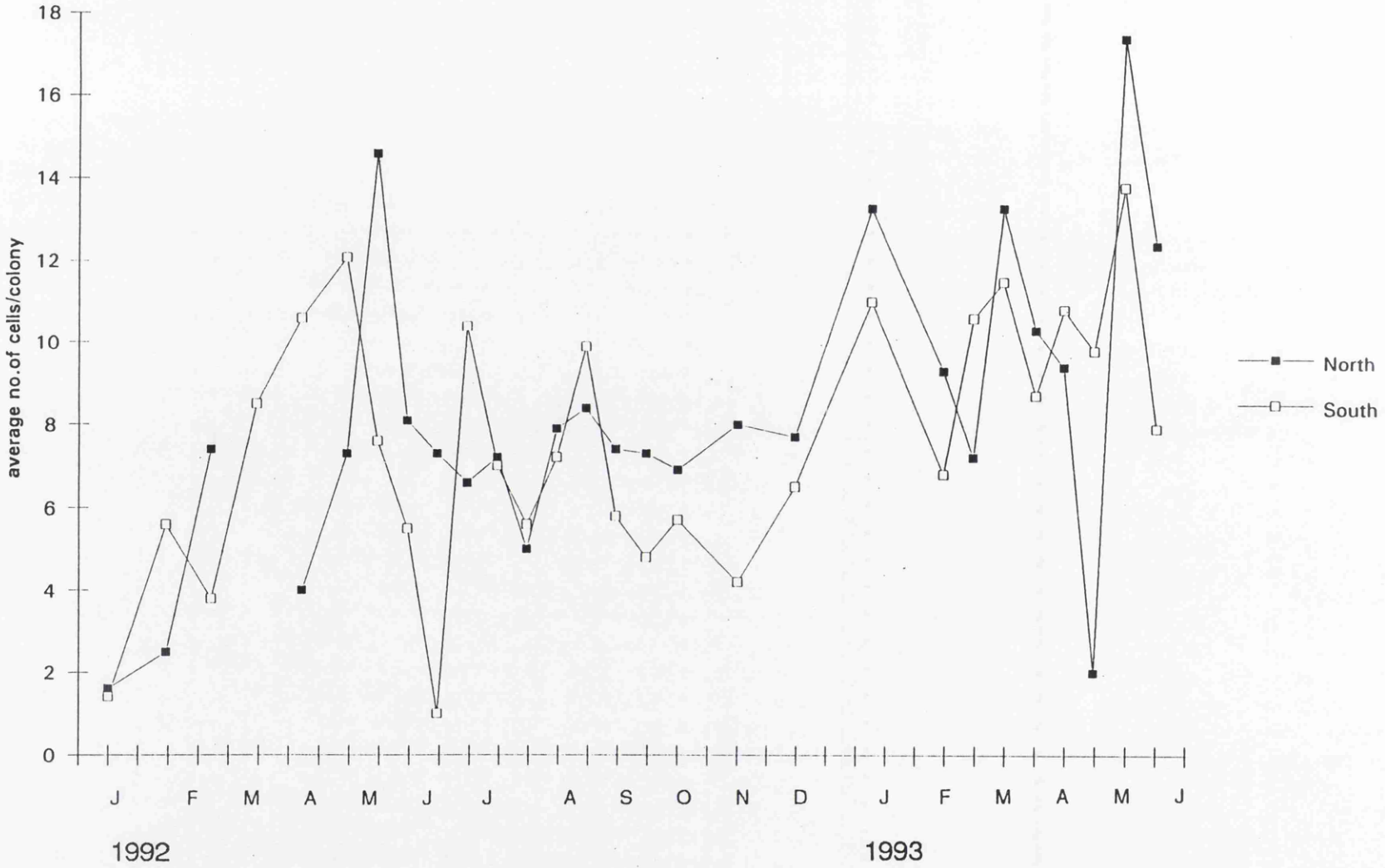

Figure (3) *Tabellaria fenestrata*

Appendix (7). List of Sampling dates (for CANOCO and TWINSPAN)

1- 15 Jan. 1992, N
2- 11 Feb. 1992, N
3- 3 Mar. 1992, N
4- 24 Mar. 1992, N
5- 14 Apr. 1992, N
6- 5 May 1992, N
7- 19 May 1992, N
8- 2 Jun 1992, N
9- 16 Jun. 1992, N
10- 30 Jun. 1992, N
11- 14 Jul. 1992, N
12- 28 Jul. 1992, N
13- 11 Aug. 1992, N
14- 25 Aug. 1992, N
15- 8 Sep. 1992, N
16- 22 Sep. 1992, N
17- 7 Oct. 1992, N
18- 4 Nov. 1992, N
19- 1 Dec. 1992, N
20- 6 Jan. 1993, N
21- 9 Feb. 1993, N
22- 23 Feb. 1993, N
23- 9 Mar. 1993, N
24- 23 Mar. 1993, N
25- 6 Apr. 1993, N

29- 15 Jan. 1992, S
30- 11 Feb. 1992, S
31- 3 Mar. 1992, S
32- 24 Mar. 1992, S
33- 14 Apr. 1992, S
34- 5 May 1992, S
35- 19 May 1992, S
36- 2 Jun 1992, S
37- 16 Jun. 1992, S
38- 30 Jun. 1992, S
39- 14 Jul. 1992, S
40- 28 Jul. 1992, S
41- 11 Aug. 1992, S
42- 25 Aug. 1992, S
43- 8 Sep. 1992, S
44- 22 Sep. 1992, S
45- 7 Oct. 1992, S
46- 4 Nov. 1992, S
47- 1 Dec. 1992, S
48- 6 Jan. 1993, S
49- 9 Feb. 1993, S
50- 23 Feb. 1993, S
51- 9 Mar. 1993, S
52- 23 Mar. 1993, S
53- 6 Apr. 1993, S

26- 20 Apr. 1993, N

27- 4 May 1993, N

28- 19 May 1993, N

54- 20 Apr. 1993, S

55- 4 May 1993, S

56- 19 May 1993, S

Appendix (8). List of Species (for CANOCO and TWINSPAN)

1- Mel Spp	*Melosira italica*
2- Ast Spp	*Asterionella formosa*
3-.Tab Ast	*Tabellaria fenestrata*
4- Tab Spp	*Tabellaria floculosa*
5- Tab Int	*Tabellaria fenestrata*
6- Fra cro	*Fragilaria crotonensis*
7- Cyc Spp	*Cyclotelle Kutzingiana*
8- Eun Spp	*Eunotia pectinalis*
9- Syn Spp	*Synedra tenera*
10- Nav Spp	*Navicula sp*
11- Cym Spp	*Cymbella sp*
12- Fru Spp	*Frustulia rhomboides*
13- Sur Spp	*Surirella robusta*
14- Coc Spp	*Cocconeis sp*
15- Osc Spp	*Oscillatoria agardhii*
16- Hol Spp	*Merismopedia glauca*
17- Coe Spp	*Coelospherium naegelianum*
18- Spi Spp	*Fil thn*
19- Ana Spp	*Anabena circinalis*
20- Cry Spp	*Cryptomonas ovata*
21- Per Spp	*Peridinium willei*
22- Cer Spp	*Ceratium Hirundinella*
23- Gym Spp	*Gymnodium caudatum*
24- Sta Spp	*Staurastrum cingulum*
25- Cos Spp	*Cosmarium depressum*

26- Clo Spp	*Closterium toxon*
27-Ooc Spp	*Oocystis sp*
28- Sce Spp	*Scenedesmus quadricauda*
29- Dic Spp	*Dictyospherium pulchellum*
30- Ped Spp	*Pediastrum boryanum*
31- Sta Spp	*Staurodesmus spencerianus*
32- Bot Spp	*Botryococcus braunii*
33- Spo Spp	*Spondylosium planum*
34- Gon Spp	*Gonatozygon sp*
35- Spi Spp	*Spirogyra sp*
36- Coe Spp	*Coelastrum sp*
37- Xan Spp	*Xanthidium antilopoeum*
38- Ank Spp	*Ankistrodesmus falcatus*
39- Mal Spp	*Mallomonas acaroides*
40- Bin Spp	*Dinobryon divergens*
41- Dia unk	
42- Fil th	*Osillatoria sp (c.f. Oscillatoria angustissima)*
43- Unk Unk	*Unknown alga (c.f. Ankistrodesmus convalutus*