THE EFFECTS OF ARTIFICIAL MIXING ON PHYTOPLANKTON GROWTH AND PERIODICITY.

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CONTENTS.

CHAPTER 1. INTRODUCTION.

This research project investigated the phytoplankton ecology of two lowland, eutrophic reservoirs between 1981 and 1983. Staunton Harold reservoir was artificially mixed and the response of the phytoplankton compared to those in a nearby reservoir, Foremark, which was allowed to stratify.

1.1 THE EFFECTS OF MIXING UPON PHYTOPLANKTON ECOLOGY.

Changes in water column stability through stratification and mixing are believed to control the two most important factors in phytoplankton ecology: the perceived light climate and nutrient availability.

Turbulent mixing can affect the size, composition, time and duration of phytoplankton populations. In 1935, Gran and Braarud concluded that phytoplankton growth was poorest in deep mixed waters and richest when stratified conditions became established. They also noted the importance of mixing depths. Riley (1942) discussed this more fully and showed that turbulent mixing had both positive and negative effects on phytoplankton production. Lund (1954 1955) reported that populations of *Melosira italica* (Ehrenb.) Kutz. subspecies *subarctica* O. Müll. increased and became dominant under certain turbulent conditions. Talling (1965) found similar results for populations of *Melosira nyassensis* var. *victoriae* O. Müll. in Lake Victoria, Africa. Lund (1954 1955) also showed that the decline in *Melosira* was a result of a decrease in turbulent mixing. Hutchinson (1967) concluded that species of phytoplankton which were more dense than water sink continuously and that the degree of turbulent water movements played an integral role in the waxing and waning of these species.

Sverdrup (1953) also studied the relationship between physical mixing and phytoplankton and noted that growth was not a direct result of stratification but of changes in the compensation depth (the depth below which net

photosynthesis cannot occur). This interaction of light penetration and mixing depth was more thoroughly investigated by Talling (1957a b 1965 1966 1971).

The phytoplankton community, as a whole, appeared to be very responsive to the degree of vertical mixing (Talling 1957a 1971, Steel 1972, Ganf 1974, Jewson 1976, Reynolds 1976 1980 1984a, Bailey-Watts 1978, Reynolds *et al.* 1983 1984).

The composition of phytoplankton communities and the relative abundance of component species are continuously changing. These changes range from short term alterations in the community structure, in response to mixing processes (Harris and Smith 1977, Harris and Piccinin 1980, Reynolds *et al.* 1983 1984), through annual cycles which are a result of cyclical fluctuations in temperature, solar radiation, nutrients and water column stability (Lund 1965 1981, Hutchinson 1967, Reynolds 1973 1978), to long term changes (Haworth 1980) in response to such factors as nutrient loadings, changes in morphometry and natural eutrophication (Round 1981).

Changes which occur over a time scale of less than a year were investigated by this research. Such variations in the abundance and composition of phytoplankton in any lake are generally repeated year after year (Hutchinson 1967, Round 1971, Reynolds 1980 1984a b).

Researchers in phytoplankton ecology have been trying for the last half-century to explain the relationship between temporal and spatial distributions of phytoplankton communities and environmental factors. Kalff and Knoechel (1978) and Reynolds (1984b) both commented that progress towards understanding and prediction has been slow even though a considerable amount of relevant literature has been published during this period.

However, Reynolds (1980 1984a 1984b) has put forward a hypothesis which explains and predicts the processes which control the seasonal periodicity of phytoplankton in a wide range of lake types. Reynolds (1984a) stated "they [the potentially constraining environmental factors which characterise pelagic systems] offer far more 'niches', in term of stability, temperature, underwater light climate, nutrient availability and biological interactions than is commonly appreciated. The evolutionary adaptations that are required to exploit effectively one range of those 'niches' may be less suitable in another; probably none is adequate under all environmental conditions that may be encountered in open waters." and so selection for the most suited species will occur. But as Reynolds noted, the major difference between terrestrial plant ecology and phytoplankton ecology is that selection as a result of the environmental variables generally operates on much shorter time scales in the latter.

The hypothesis that changes in water column stability was the major influence affecting phytoplankton periodicity (Reynolds 1982) evolved over a number of years from a series of studies. Firstly, from his own studies and the literature, it was found that certain species had different morphological, physiological and behavioral adaptations to survival and growth. No combination of these adaptations appeared to be fully suited to the annual variations in environmental variables. The waxing and waning of different species resulted from the advantageous, or disadvantageous combinations of these adaptations at any point in time.

Analysis of twelve annual cycles of phytoplankton populations (Reynolds 1980) from five different lakes in England revealed that "the patterns discerned among geographically remote but morphologically and trophically similar lakes are often remarkably similar" [Reynolds 1984a]. This suggested

that there are only a few factors, which are common to all these lake types, controlling seasonal periodicity. Reynolds (1980), following Hutchinsons' (1967) review of patterns of seasonal periodicity, proposed 14 species assemblages from the English lakes studied. These assemblages were composed of species which had similar temporal patterns and rates of growth and losses. Five more categories were added (Reynolds 1982 1984a) to include the periodicities reviewed by Hutchinson (1967), Dokulil (1979) and Leah, Moss and Forrest (1980).

The patterns of abundance, growth and decline of these assemblages were found to be closely related to seasonal changes in water column stability (Reynolds 1980).

This hypothesis was experimentally tested (Reynolds *et al.* 1983 1984) and it was shown that an artificially imposed cycle of mixing and restratification affected the seasonal periodicity in a predictable way - species of winter /spring phytoplankton (diatoms) were selected for and became dominant during mixing episodes whilst summer assemblages (colonial Chlorococcales) were favoured and increased during the restratification periods. The growth and dominance of slow growing, late summer species, such as *Microcystis aeruginosa* Kütz. emend. Elenkin and *Ceratium hirudinella* O. F. Müll. which are favoured by stable conditions, were delayed. Reynolds (1980) had also predicted that the average biomass would be maintained below the nutrient carrying capacity and so the peaks of phytoplankton, often troublesome in water management, would not be reached in mixed situations.

Reynolds *et al.* (1983 1984) carried out their experiments in Lund enclosures which have three advantages over whole lake studies. Firstly, the volume of water undergoing mixing was relatively small and so with the

equipment available, they were able to vigorously mix the enclosure. Secondly, the water within the enclosure restratified very quickly and allowed the cycle of mixing and restratification to take place. Thirdly, they were able to minimise the effects of nutrient limitation by artificial fertilisation. Reynolds (1984b) realised this and stated " the applicablity of intermittent mixing to reservoir management depends upon the extent to which the critical physical conditions created in the Lund enclosures can be translocated to much larger volumes of water".

1.2 ARTIFICIAL MIXING OF LAKES AND RESERVOIRS.

The use of artificial mixing in reservoir mangement is not a new idea and experiments have attempted to improve water quality since the early 1950s (Hooper *et al.* 1953). The majority of work has been carried out in the U.S.A. and more recently in Australia and Europe. Many eutrophic reservoirs are now designed with artificial mixing systems (Steel 1972, Tolland 1977). In most cases this has been to prevent stratification and avoid the establishment of an anaerobic hypolimnion and its associated consequences, many of which are troublesome to water management.

Artificial mixing can be split into two categories:-

i) Hypolimnetic aeration, whereby the hypolimnion is oxygenated without breaking down the stratification. This method has been used extensively (Bernhardt 1967, Toetz *et al.* 1972, Dunst *et* al. 1974).

ii) Artificial destratification, whereby external energy from pumps or aerators is used to break down the density gradient of the stratified water body and thus cause complete circulation. Three methods have

been used to carry out artificial destratification:-

a) A compressed gas (usually air) released through a diffuser (Riddick 1957, Fast 1968), a perforated pipe (Schmitz and Hasler 1958, Ford 1963, Tolland *et al.* 1978) or a "Helixor" (Wirth and Dunst 1967, Harper 1978).

b) The mechanical pumping of water from the hypolimnion to the epilimnion (Hooper *et al.* 1953, Symons *et al.* 1967, Steichen *et al.* 1979).

c) The pumping of inflow water into the reservoir through strategically placed jets (Cooley and Harris 1954, Ridley 1964, Harper 1978).

Improvements in water quality of lakes or reservoirs thus treated have been widely reported. These commonly include isothermal conditions, increased dissolved oxygen content (Hooper *et al.* 1953, Irwin *et al.* 1966, Malueg *et al.* 1971, Tolland 1977, Tolland *et al.* 1978), decreased ammonia and sulphide concentrations (Symons *et al.* 1967), decreased iron and manganese levels (Wirth and Dunst 1967, Tolland 1977, Bowles *et al.* 1979).

Over the last two decades, interest in the effects of mixing on phytoplankton has increased, mainly as a result of an increase in the frequency of problems caused by phytoplankton growths in eutrophic lowland reservoirs (Lund 1970, Collingwood 1977).

Results observed during artificial mixing experiments have often been contradictory. They included both an increase and a decrease in algal biomass. Cyanobacteria have sometimes become dominant whilst in other experiments they

have become less abundant. In some experiments there was neither a change in algal biomass nor in the succession whilst in others the seasonal periodicity was altered.

Whether artificial mixing can alter phytoplankton biomass and seasonal periodicity seems to depend mainly upon the timing and intensity of mixing energy, and as Ridley (1971) noted, will be different for each lake. He concluded that continuous mixing at a constant energy would not consistently reduce primary production and there would be times when mixing energy needs to be increased or decreased "thus using the installation as an aid to in-lake quality control, and not as a panacea". Ferguson and Harper (1982) showed that phytoplankton densities were maintained well below the nutrient carrying capacity in Rutland Water where "Helixors" were used continuously during the summer months to prevent stable stratification. Reynolds *et al.* (1984) concluded that continuous operation at a lowered intensity, such as in Rutland Water, may be successful as stable conditions would persist during anticyclonic weather and mixing would occur during windy spells. Thus a pattern of an alternate mixed and stratified water column, which was very similar to that which they had created in the Lund enclosure, would exist.

Ryback (1985) showed that low intensity mixing resulted in a two to four fold increase in phytoplankton biomass but the use of a more efficient mixing system resulted in the inhibition of phytoplankton growth. Steinberg (1983) reported a doubling of biomass but with no corresponding increase in primary production. Shapiro (1981) suggested that such increases in phytoplankton biomass were due to inadequate circulation; the phytoplankton were not thoroughly mixed throughout the water column but as the nutrient concentrations were increased in the euphotic zone, algal biomass increased. In cases where a decreased biomass was observed during destratification, he suggested this was

due to complete circulation, whereby the algal cells spent less time in the photic layer and their production was thus reduced.

Haffner (1974) showed that phytoplankton production and growth in the highly eutrophic Wraysbury reservoir, England was limited by the indirect effects of mixing, which in this case was the continued suspension of seston from the River Thames. Fast (1981) found that primary productivity was approximately three times higher during a year of lake aeration than a control year. Fast believed this was due to the increased circulation of nutrients. Haynes (1971) also studied primary production but unfortunately without control data. He recorded an immediate reduction in production which occured near the surface and was a result of the redistribution of Cyanobacterial cells throughout the water column.

Several mathematical models relating mixed depth to phytoplankton production have been developed which predict the reduction in phytoplankton biomass as mixed depth increases (Talling 1957a, Bella 1970, Oskam 1971, Steel 1973, Lorenzen and Mitchell 1975). The main theme of these models is that phytoplankton cells are fully circulated throughout this mixed depth so as the mixed depth begins to exceed the euphotic depth, algal production decreases. However, Fast (1981) suggested that this was rarely the case and destratification systems, especially air-injection systems, <u>almost</u> caused isothermal conditions with a small thermal gradient persisting in the top few metres. This stratification allowed the phytoplankton to maintain their position in the thermal gradient leading to a decrease rather than an increase in the mixed depth of the phytoplankton and hence to increased production.

Another factor which may have contributed to increased production was that lakes were sometimes destratified when the hypolimnion was anaerobic and rich in nutrients. On mixing, these nutrients were made available to the

phytoplankton and an increase in the biomass was observed (Toetz *et al.* 1972). Also, the temperature at the sediment/water interface was usually increased by artificial mixing and so the rate of release of chemical ions, especially nutrients, from the sediment may have been enhanced (Toetz *et al.* 1972). Brekhovskikh and Korneyev (1984) concluded that hypolimnetic aeration increased the rate of phosphorous release from the sediments, even under aerobic conditions, and its transfer into the photic zone.

The observed changes in the phytoplankton community following mixing have been as varied as the observations of biomass changes. Haynes (1971) attributed a dramatic decrease in *Aphanizomenon flos-aquae* Ralfs *ex.* Born. Flah. to the redistribution of the filaments rather than a decline in the population. Ridley et al. (1966) and Lackey (1973) found that *Anabaena* increased during mixing. Lackey also found that *Ceratium hirudinella* O. F. Müll. became more abundant as a result of mixing. Ryback (1985) reported that species more typical of winter/spring assemblages were favoured by mixing. Hickel (1978) showed that seasonal periodicity did not appear to have been affected by mixing but desmids became more prominent in a eutrophic lake in East Holstein. There are many more examples of the increases or decreases of individual species (see Symons *et al.* 1970, Toetz *et al.* 1972).

The observations of Reynolds et al. (1983 1984) from their experiments in Lund enclosures suggested that the responses of the phytoplankton species and community to changes in water column stability could be explained and predicted more consistantly than previous studies have allowed. The applicability of Reynolds work to whole lake studies depended upon how well the patterns in physical stability achieved during Lund enclosure experiments could be attained in lakes and reservoirs.

This investigation of phytoplankton growth and periodicity, as a response to artificial mixing was carried out between 1981 and 1983 under contract to Severn Trent Water Authority. The research took place at two reservoirs, Staunton Harold and Foremark which lie on the Leicestershire/Derbyshire border some 30 km. to the northwest of Leicester. The results of physical, chemical and phytoplankton data from Staunton Harold, which was artificially mixed for a short period in 1981, and throughout the summers of 1982 and 1983 were compared with contemporaneous data from the nearby, Foremark reservoir which was allowed to stratify in all three years. The decision to use Foremark as a 'control' was based upon data from previous studies, made by the Authority (unpublished), which revealed that physical and chemical variables responded in similar ways and that the growth and periodicity of phytoplankton was also very similar. The chemical data, except for pH, alkalinity and conductivity, was determined and made available by Severn Trent Water Authority.

A report which emphasises certain aspects of this work and the implications for reservoir management has been published by Severn Trent Water Authority (Brierley 1985).

CHAPTER 2. SITES AND METHODS.

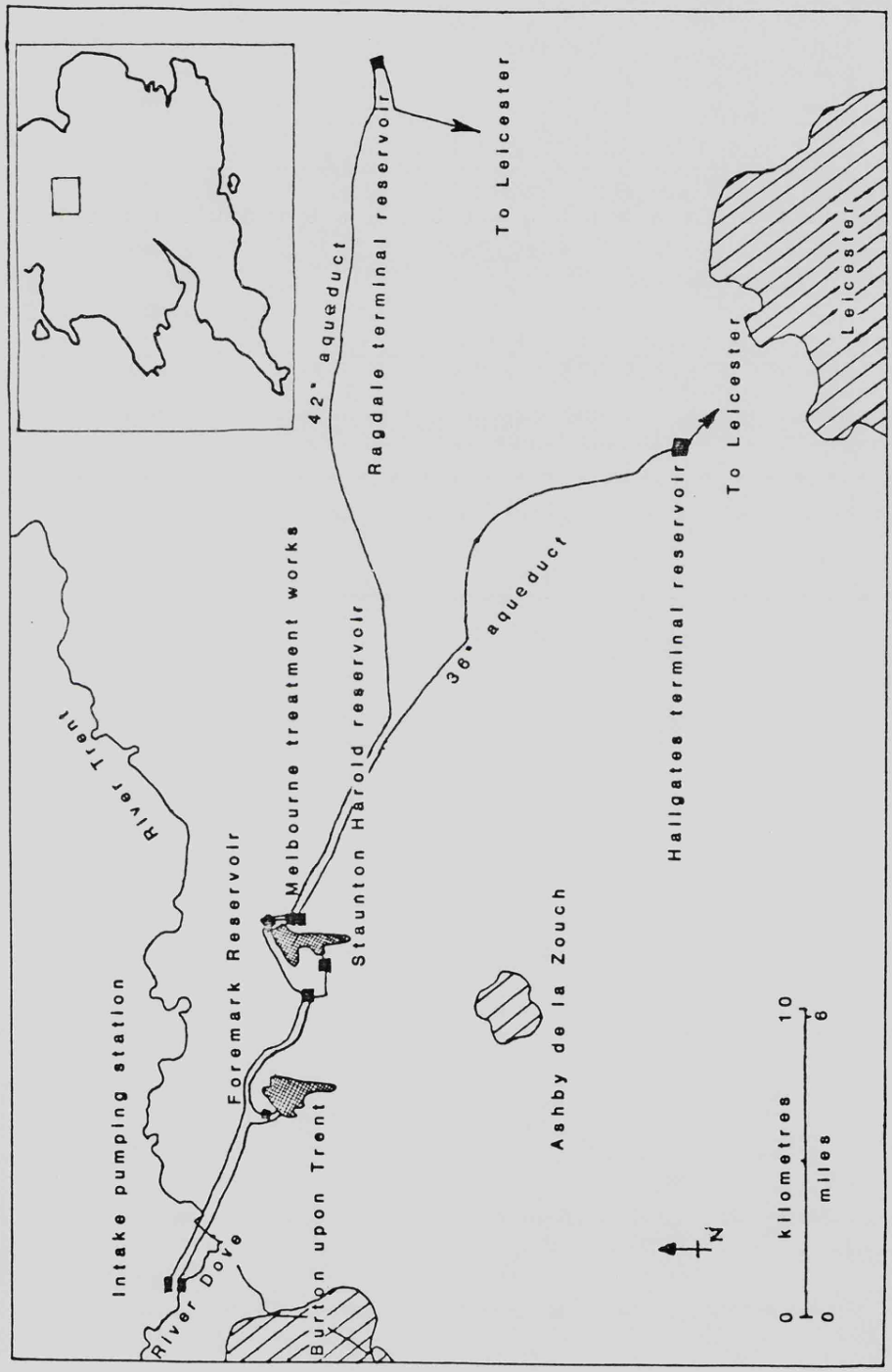
2.1 THE STUDY SITES.

Approximately one third of the water supplied in England and Wales is extracted from impounded storage reservoirs. Many of theses are pumped storage reservoirs, usually situated away from the river channel which is being used as a source, in the case of Staunton Harold and Foremark reservoirs, these basins are impounded tributaries of the lower River Trent, about 13 and 5 kilometres respectively, from their source on the lower River Dove.

The River Dove catchment has an area of 100000 hectares and lies in the centre of England to the north of the main industrial conurbations of the east and west midlands. The geographical position of the Dove scheme is shown in Figure 1.

In the early 1950's, the rising demand for a new water source in Leicester and the county led to the formation of the River Dove Water Board in 1955. The initial stage comprised river pumping stations, treatment works and aquaducts which became operational in 1959. The scheme was extended in 1964 with the completion of Staunton Harold reservoir and again in 1976 when Foremark reservoir was filled.

Figure 1. The location of the reservoirs and major features of the Dove distribution scheme.



2.1.1 The study reservoirs

2.1.1.1 Staunton Harold reservoir.

Staunton Harold is located 30 km to the northwest of Leicester, (Grid SK 3723) (Figure 1). The impounded valley is underlaid by shales with grit bands overlying Carboniferous limestone (to depths of over 90 metres) at the dam site, with limestone outcropping at the upstream end of the reservoir.

Water can be drawn off at three different depths, through draw-off sluice valves and is then pumped from a station below the dam wall, through a short aqueduct to the treatment works (Figure 2).

2.1.1.2 Foremark reservoir.

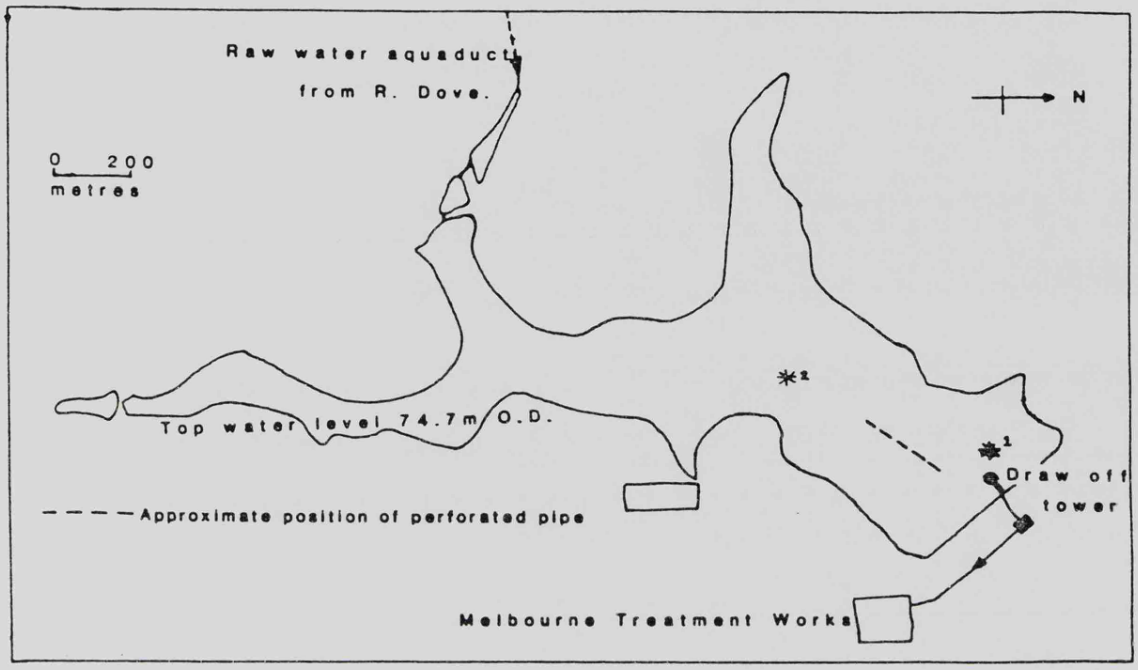
Foremark, also a pumped storage reservoir, was completed in a valley adjacent to Staunton Harold some 7 km from the abstraction station on the River Dove and 5 km from Melbourne Treatment works (Grid SK 3323) (Figure 1).

This valley was far from ideal, geologically, for the siting of a reservoir as fissured Bunter sandstone overlies marl. Where marl was absent, outcrops of Carboniferous sandstone existed. Rolled marl had to be used to seal these permeable strata during construction.

Three siphon draw-off valves, at different depths discharge water into an aqueduct which is then pumped to Melbourne treatment works (Figure 3).

The physical characteristics for both reservoirs are shown in Table 1.

Figure 2. Plan of Staunton Harold reservoir. (* Buoys at which photosynthesis and sedimentation experiments were carried out).



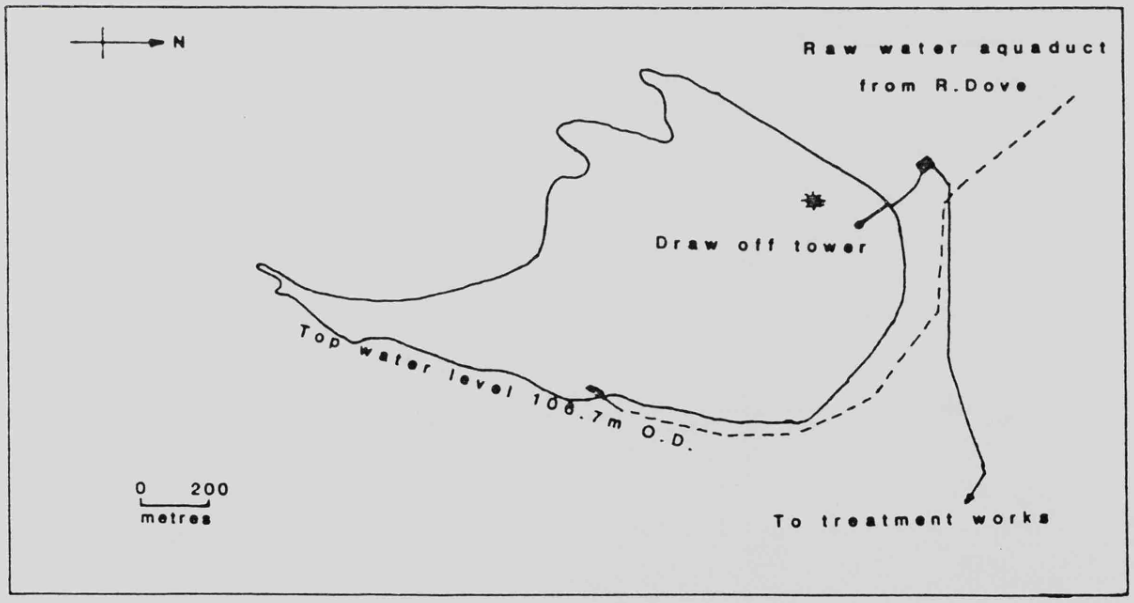


Figure 3. Plan of Foremark reservoir. (* Buoys at which photosynthesis and sedimentation experiments were carried out).

TABLE 1. THE PHYSICAL CHARACTERISTICS OF STAUNTON HAROLD AND FOREMARK RESERVOIRS.

		Staunton Harold	Foremark
Construction completion date		1964	1976
Volume, $10^6 m^3$		6.36	13.4
Area at top water level, ha		85	92
Maximum depth, m		23	32
Mean depth, m		7.9	14.3
Catchment area, ha		2590	295
Average abstraction rate, $m^3 s^{-1}$		0.66	0.84
Top draw off level	m. below T.W.L.	4.6	7.7
Middle draw off level	m. below T.W.L.	10.2	13.7
Bottom draw off level	m. below T.W.L.	16.4	19.7
Nominal retention time, days			
	1980	106	173
	1981	115	159
	1982	102	139
	1983*	108	120

* March to December inclusive, as no readings taken during the water strike in January and Febuary.

2.2 THE DESTRATIFICATION EQUIPMENT.

The destratification system was designed by John Davis of the Water Research Centre for use in Staunton Harold based on previous experience (Davis 1980). It consisted of an electrically powered compressor (Broomwade V85A-F3, CompAir Industrial Ltd. High Wycombe, Bucks.) with oil and particle filters and an after-cooler. These were connected to high density, 40 mm diameter polythene pipework, perforated for the last 150 metres, which ran out into the deepest part of the reservoir at right angles to the dam. In operation, compressed air left the pipe via the holes, and rose to the surface of the reservoir as a curtain of bubbles. This entrained water from the lower layers of the reservoir and brought it to the surface. The system was designed to create local destratification around the pipe, followed by mixing of the whole reservoir and has been shown to be effective elsewhere (Tolland 1977, Tolland *et al.* 1978).

The equipment was installed at Staunton Harold in early 1981, the compressor being housed in the pumping station below the dam wall and the pipe running over the dam wall into the reservoir. The last 150 metres of pipework were perforated with 0.5 mm holes drilled at 0.3 metre intervals and the end of the pipe was closed. The pipe was anchored by tying two house bricks per metre of pipe which held it approximately 0.3 metres above the bed of the reservoir. The destratification equipment was operational in Staunton Harold by the 1st April 1981 and its' effectiveness was tested in September, 1981 (Appendix 7).

In 1981 and 1982 it is estimated that the air flow from the compressor was 28.8 ls^{-1}. In 1983 the air flow was reduced to 27 ls^{-1} which lowered the demand on the compressor.

2.2.1 Operation of the destratification equipment.

Two methods of operation of destratification sytems have previously been used (Tolland 1977). The first is continuous mode whereby the system is run from before the onset of stratification to the time of natural overturn. Here the establishment of stratification is prevented. The second mode is intermittent, whereby stratification is allowed to establish and then the system is operated until the water body is destratified. This is then repeated, as necessary, until the end of the season.

2.2.1.1 Intermittent use.

In 1981 the equipment was used in an intermittent mode. Stratification was allowed to develop but was broken down by strong winds and heavy rain in June and thermal stratification did not develop again. However the reservoir became chemically stratified and was artificially mixed in late summer. The perforated-pipe system was switched on and it ran continuously from September 8th to the 11th (68 hours running) by which time the reservoir was completely destratified (see Appendix 7).

2.2.1.2 Continuous use.

In 1982 and 1983 the perforated pipe-system was operated continuously (except for short periods of stoppage due to power failures or for maintenance) from March 2nd to October 1st (1982) and from April 7th to September 21st (1983).

2.3 METHODS.

2.3.1 Statistical methods.

The statistical methods as stated in Sokal and Rohlf (1969) were used throughout this thesis. The convention of using asterisks representing probabilities was also used throughout. These were as follows:

$* = 0.05 > P > 0.01$, $** = 0.01 > P > 0.001$, $*** = P < 0.001$

2.3.2 Meterological.

Meteorological data were obtained from the Sutton Bonington Agricultural School weather station which is situated 13 km to the east of Melbourne Treatment works. The data used were daily run of wind, maximum and minimum air temperatures, rainfall and solar radiation.

In 1982 and 1983, solar radiation was measured with a CM5 solarimeter (Kipp and Zonen, Delft, Holland) situated on the roof of Melbourne treatment works and the results recorded on a Kipp and Zonen CC2 printing integrator. Variance in the solar radiation measured at the two sites was small except on cloudy days; a regression analysis between the two sites showed a correlation coefficient of 0.97 with 134 df (***). It was therefore feasible to use the Sutton Bonnington data when no records were available from the treatment works.

Daily maximum and minimum air temperatures, rainfall, and daily spot readings (10.00 and 14.00 hours) of wind speed and direction were taken throughout this research by the staff at the treatment works.

Wind speed and direction were measured intermittently during 1982 and 1983

using a AWR-500 portable wind recorder (Vector Instruments, Rhyll, Clywd) which was situated approximately 2 metres above ground level and 10 metres from the dam at the easterly corner of Staunton Harold reservoir.

2.3.3 Physical.

2.3.3.1 Temperature.

Between March and October 1981 and 1982, temperature profiles were taken from nine thermistors (Grant Instruments Ltd., Cambridge) which were attached to the valve towers of both reservoirs. The readings were recorded on Grant continuous temperature chart recorders at three-hourly intervals.

2.3.3.2 Oxygen.

Weekly temperature and oxygen saturation measurements were made with a YSI model 57 combined temperature and dissolved oxygen meter and probe (Yellow Springs Instruments, Ohio, USA) at one metre intervals down the water column at both valve towers.

2.3.3.3 Underwater irradiance.

Irradiance in the reservoirs was measured weekly and during photosynthesis experiments with a LI-185 quantum meter and underwater quantum sensor (LI-192S) (LI-Cor, Lincoln, USA) at half-metre intervals through the water column. This measures photosynthetically active radiation (PAR) in the range 400-700 nm. Irradiance was also measured at various times during the study with a selenium photocell and meter (Lake Instrument Co. Ltd., Windermere) with red (RG2), green (VG9), and blue (BG12) Schott filters (Mainz, Germany) and an opal diffusing filter.

Vertical attenuation coefficients, ε, (In units m^{-1}), were calculated using the results of the irradiance/depth profiles. The euphotic depth, *Zeu*, was defined as the depth at which irradiance (PAR) was reduced to 1% of that penetrating the surface (Talling, 1971).

2.3.3.4 Water transparency.

Water transparency was measured weekly with a 20 cm diameter black and white quartered Secchi disc.

2.3.3.5 Water column stability.

Two measures of water column stability were used in this research; the *Zm/Zeu* ratio and N^2. *Zm*, the mixed depth, was defined as the depth to the top of the thermocline, which was defined as the plane of maximum rate of decrease in temperature (Hutchinson, 1957). In this study the maximum change over a 1 metre depth interval was used. N^2, the Brunt-Vasala frequency, is the natural frequency of oscillation of a vertical fluid column, given a small displacement from equilibrium (Sephton and Harris, 1984). Phillips (1966) and Boyce (1974) gave the following definition:

$$N^2 = \frac{-gd\varrho}{\varrho dz} \ (sec^{-2})$$

where g is the acceleration due to gravity

ϱ is the density of water at $4^{\circ}C$

and $d\varrho/dz$ is the density gradient over a specified depth interval.

A high value of N^2 indicates that density gradients are intense and as a result the resistance to mixing is high. N^2 values were calculated from the weekly temperature depth profiles.

2.3.4 Collection of water samples.

Discrete depth samples were taken weekly between March and October from 1981 to 1983. Samples were taken using either a 2 litre Friedinger bottle (Hans Buchie, Berne, Switzerland) or a 2.5 litre National Institute of Oceanography sampler (NIO, Godalming, Surrey) from the valve towers at the following depths:- Staunton Harold reservoir: 0, 1.5, 3, 8 (1981), or 6 (1982 and 1983), 10 and 14 m below the surface and at Foremark reservoir: 0, 1.5, 3, 8, 14 and 20 m below the water surface. The valve towers were chosen as the regular sampling site due to ease of access under all weather conditions. This was validated by a series of boat surveys. The boat survey described in Appendix 7 illustrates the effectiveness of the destratification system aswell as validating the use of the valve tower in Staunton Harold as the representative sampling site, as does the survey described on page 97 and on page 103 for Foremark.

Between October and March sampling was reduced to fortnightly intervals and a 10 m polythene hose sampler (Lund and Talling 1957) was used. Qualitative samples of phytoplankton were taken by towing a 50 µm mesh vertically through the water column from 10 metres to the surface. These samples were used for identification purposes.

2.3.5 Chemical.

Samples for chemical analysis were taken weekly at the valve towers from the depths noted above. Samples were stored in 2 litre polythene bottles, except those needed for the determination of ammonia which were collected in small (90 ml) glass bottles with ground glass stoppers. On returning to the laboratory (within 3 hours of collection) sub-samples were prepared by filtering a volume of well shaken sample through Whatman GF/C glass fibre

filter papers, previously washed with 700 ml of distilled water. Filtration was carried out under a vacuum with a suction pressure of approximately 100 mmHg. Samples of filtered and unfiltered water were stored in 700 ml polythene bottles in a refrigerator at 3 to 4 ^{o}C prior to analysis. Chemical analysis (except for pH and alkalinity) were carried out by Soar Division staff at the Divisional laboratory, Leicester. The methods of analysis are given in Table 2. Regular checks of unknown standards were made be STWA staff as part of their routine work. Filtered samples were used for silicon from March 1981 to June 1982 but unfortunately due to an error unfiltered samples were used from then on. Filtered samples were used for all ortho-phosphate determinations whilst unfiltered water was used for nitrate, ammonia (precision 5%), pH, alkalinity, conductivity, iron, manganese. All determinations were completed within 4 days of collection (except where repeats of certain analyses had to be carried out). Conductivity was measured with a Chandos conductivity meter and electrode (Chandos Intercontinental, Stockport) and pH using either an EIL 7065 (Kent Industrial Measurements, Chertsey, Surrey) or a Phillips PW 9409 pH meter (Phillips, Cambridge) with a glass and calomel combined electrode. These analyses were always carried out on the same day as collection.

2.3.6 Biological.

Samples for biological analysis were taken at weekly intervals throughout the study from the valve towers. Discrete or integrated samples were taken as described above.

2.3.6.1 Phytoplankton counts.

Samples for algal counting were preserved immediately with acidified Lugol's iodine. Algae were counted with a Wild M40 inverted microscope (E. Leitz, UK Ltd., Luton) and 10 ml Wild sedimentation chambers. The method used

TABLE 2. SUMMARY OF METHODS FOR CHEMICAL ANALYSES.

DETERMINAND	METHOD	REFERENCE
Ammoniacal Nitrogen	Modified Bertholet reaction	ChemLab Instruments Method sheet CW2-008-11, 1981
Nitrate Nitrogen	Azo-dye reaction	Chemlab Instruments Method sheet CW2-066-01, 1978
Silica as SiO_2	Ammonium molybdate Ansa reaction	WRC Laboratory method, 1975
Ortho-phosphate	Modified Denige reaction	Institute of Engineers, 1960, p44.
pH	-	D.O.E. 1972, p47.
Conductivity	-	D.O.E. 1972, p45.
Alkalinity	-	D.O.E. 1972, p52.
Iron, Manganese	Standardised STWA methodology using atomic absorption spectrophotometer.	

was based on that of Utermohl (1931) with the modifications of Lund, Kipling and LeCren (1958). The volume of sample sedimented was dependent on the algal density in the sample and was adjusted accordingly; it ranged from 3 to 10 ml.

Preliminary comparisons and tests of different counting methods were carried out during the early spring of 1981. The results and recommendations are reported in Appendix 1.

The effort involved in attaining the usual degree of accuracy at times of very low algal biomass, either by concentration of samples or the extra time involoved in counting, was found to be prohibitive. It was decided, after preliminary comparisons, tests of counting methods and the time available, that a maximum of 5 transects (large algae) and 50 fields (nanoplankton) would be counted.

Between March and October 1981, algal counts were carried out on all the depth samples from each reservoir. During the winter of 1981/1982 one count for each reservoir was made on the integrated hose-pipe sample. When the reservoirs were mixed with respect to the algae in 1982 and 1983 (as shown by chlorophyll depth profiles) a sub-sample from 0, 6, and 14 m (Staunton Harold) and 0, 8, and 20 m (Foremark) was mixed together and an aliquot of the "integrated" sample used for the count. When the algae were stratified counts were made on the samples from 0, 6 and 14 m (Staunton Harold) and 0, 8 and 20 m (Foremark).

It is not possible to calculate the true growth rate (μ) from cell counts as growth and loss of phytoplankton cells occurs simultaneously. The growth rates can only be approximated in special cases, for instance diatoms, where the frustules of dead cells can be counted which allow estimates of growth and death (Reynolds *et al.* 1982, Sommer 1984). In this study calculations have

been restricted to the net rate of population density change ($kn\ d^{-1}$), which can be calculated from cell counts using the equation given in Sommer (1981):

$$kn = dN / N.dt = \ln N_1 - \ln N_0 / t1 - t0$$

where:

N_0 is the number of cells in the water column at time t_0.

N_1 is the number of cells in the water column at t_1.

2.3.6.2 Chlorophyll analysis.

Samples for chlorophyll analysis were taken at the same times and depths as given above and also during the photosynthesis experiments (see below). The method used was based upon that of Talling and Driver (1963) with modifications as given in Youngman (1978) using boiling 90% methanol as the solvent. The volume of water filtered for the extraction depended on the quantity of algae present in the sample; ranging from 300 ml to 2 litres. The absorbance of the extracted chlorophyll was measured at 665nm on a Cecil CE393 or CE292 spectrophotometer (Cecil Instruments Ltd., Cambridge). All chlorophyll analyses were carried out on the same day as collection.

2.3.7 Boat surveys.

During 1980 and 1982, several boat surveys were carried out to investigate the horizontal and vertical distribution of selected limnological parameters in both the artificially mixed reservoir and the stratified 'control' reservoir. Dissolved oxygen, temperature and chlorophyll were measured at various sites in the main basin of each reservoir.

Chlorophyll was measured either by the extraction of the pigment from

discrete samples (as above) or by the use of *in vivo* fluorimetry (Lorenzen 1966). Water was pumped from the various depths, via a garden hose, using a 12 volt Jabsco "puppy" pump (ITT Fluid Handling Ltd., Hoddesdon, Herts.) powered by a car battery. Chlorophyll fluorescence was measured with an Aminco fluoro -colourimeter (American Instrument Company, Maryland, USA) fitted with a large volume flow-through cell, a blue lamp (405-436 nm), a R136 photomultiplier, a blue primary filter and a red secondary filter. The output was recorded on a Servogor M chart recorder (Goerz Electro, Vienna, Austria).

Both fluorimeter and recorder were powered by a E800 portable generator (Honda Motor Co. Ltd., Chiswick, London). Background fluorescence of the reservoir water was zero-adjusted on the fluorimeter by passing a GF/C filtered sample through the fluorimeter prior to commencing the survey. Output from the fluorimeter was in relative fluoresence units (RFU). A calibration of fluorescence to chlorophyll was made on each occasion, by taking at least five samples of water leaving the fluorimeter and extracting in boiling 90% methanol on returning to the laboratory (see routine monitoring).

This *in vivo* method proved to be quick and allowed a large number of sites to be studied but the fluorimeter was found to be extremely sensitive and great care had to be taken when using the equipment in a boat.

2.4 EXPERIMENTAL METHODS.

2.4.1 Phytoplankton Sedimentation.

Sedimentation was measured in both reservoirs during 1982 and in Staunton Harold only in 1983, using two different types of sedimentation trap. Both types were simple perspex cylinders. Cylinders of type A were 1 m in length

with a diameter of 9.3 cm and an aspect ratio (ratio of length to diameter) of 1:10.7 (Plate 1). Those of type B were 29.5 cm long with a diameter of 10.7 cm and an aspect ratio of 1:2.8 (Plate 2).

The traps were held in pairs on frames and suspended approximately 14 m below the water surface at one site in each reservoir in 1982 and at two sites in Staunton Harold in 1983 (Figures 2 and 3). The mooring system consisted of an anchor weight on the bottom and a rope onto which the trap frame was attached leading to a sub-surface buoy, which kept the the rope stretched and the traps vertical. The sub-surface buoy was attached to a surface buoy. Both types of trap and their mooring systems were designed according to the recommendations of Bloesch and Burns (1980) and Reynolds *et al.* (1980).

The traps were recovered, emptied, refilled with tap water (to avoid contamination of the trapped material when there were high algal numbers in the epilimnion) and replaced usually every 14 days. The trapping periods ranged from 7 to 22 days. The sediment formed a "solid" layer in the bottom of the traps on virtually every occasion. The volume of sample to be returned to the laboratory for analysis was reduced by careful siphoning. If the sediment in the traps was disturbed on recovery, all of the contents were discarded.

The total volume of water and sediment in each trap was estimated in a measuring cylinder and then well-mixed subsamples were taken to estimate algal biomass, measured as chlorophyll a. The volume of subsample filtered varied between 5 and 30 ml.

Qualitative observations of the algal species present was made using the sedimentation tubes and the Wild M40 inverted microscope. The dominant algae were noted on each occasion.

Plate 1. Type A sedimentation traps held by frame in pairs.

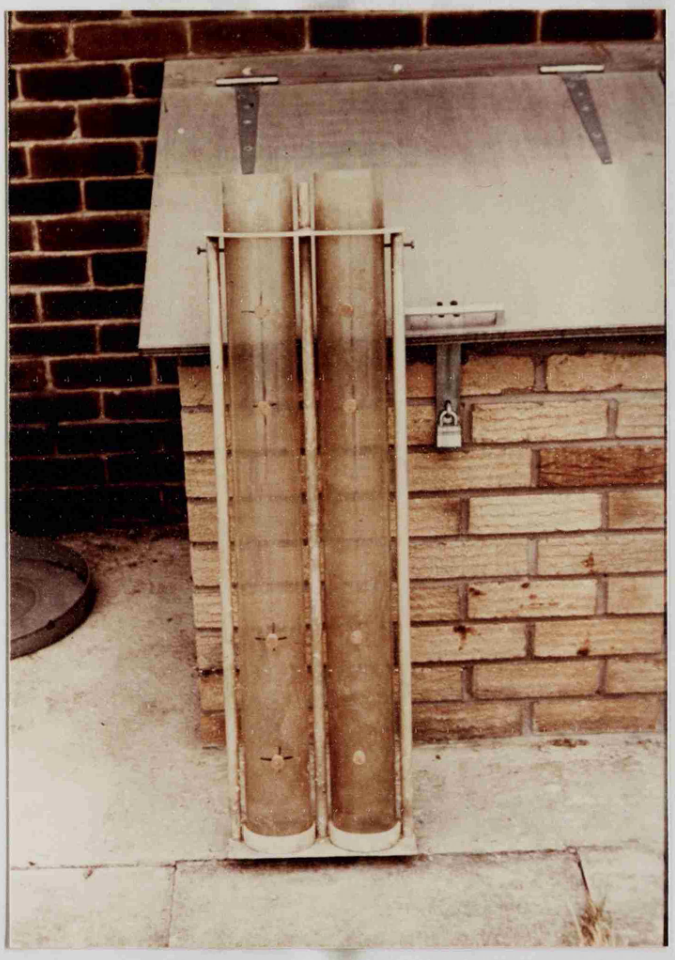


Plate 2. Type B sedimentation traps held by frame in pairs.

The results were expressed areally (cm^{-2} or m^{-2}) and as an accretion rate as follows:-

$$Y = \frac{y \times \text{total volume of water plus sediment}}{\text{area of trap} \times \text{time of exposure}}$$

where Y was the accretion rate

and y was the concentration of chlorophyll a.

2.4.2 Phytoplankton photosynthesis.

Phytoplankton photosynthesis was measured in both reservoirs at intervals varying from a week to a month between March and October in 1982 and 1983 using the oxygen light and dark bottle technique (Gaarder and Gran, 1927).

Reservoir water was taken from different depths using a 2 litre Friedinger bottle or a 5 litre Hydrobios sampler (Hydrobios GmbH, AM Jagersberg, W. Germany).

All precautions and recommendations given in Vollenweider (1969) were adhered to.

Pyrex bottles were filled from the sampler and then suspended in pairs on horizontal frames (Plate 3) at depths throughout the euphotic zone by a vertical length of rope suspended from a buoy. A support frame was constructed from two 1 gallon polythene containers joined by a wooden pole which minimized any shading of the surface bottles. An additional pair of bottles was darkened with a double layer of "Scotch" insulating tape to provide a measure of respiration. The exposure time varied between 2 and 4 hours around midday.

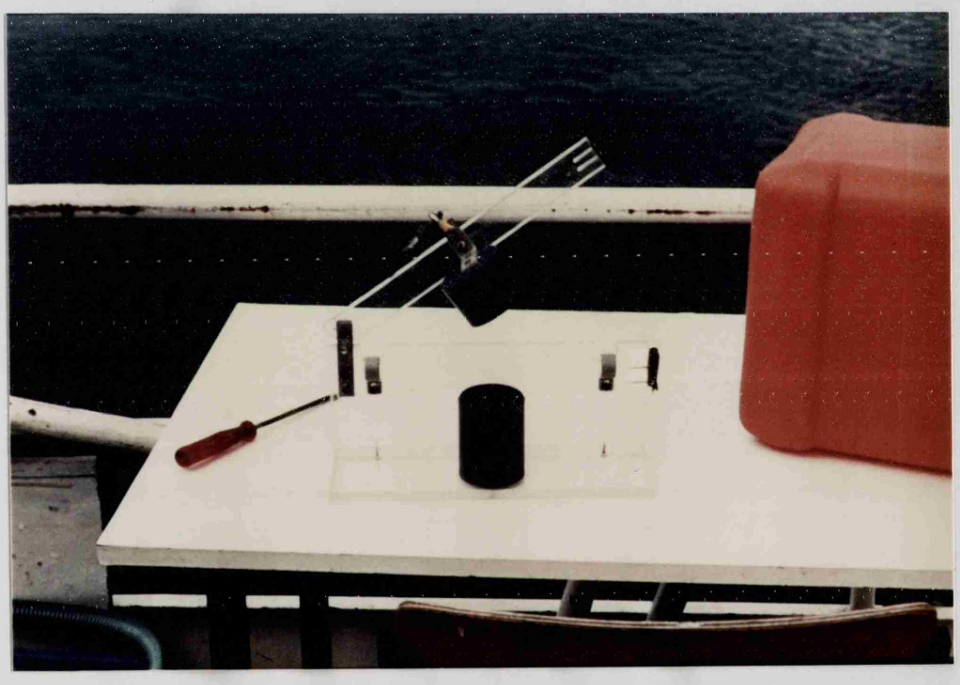
The experiments were carried out at a fixed site in each reservoir (Figures 2 and 3).

The oxygen content of the bottles was determined by the Winkler method, using the reagents given in Golterman (1969). The end point of the back titration was detected amperometrically using the method described by Talling (1973) to an accuracy of +/- 0.03mgl^{-1}. The density of phytoplankton was estimated as chlorophyll a.

Solar radiation for the exposure period was recorded either at Melbourne treatment works or at Sutton Bonnington Agricultural School. All measurements were converted to $\mu Em^{-2}s^{-1}$ (1 $Jcm^{-2}min^{-1}$ = 833 $\mu Em^{-2}s^{-1}$) to make them comparable with current literature.

In 1983, several double experiments were run at the same site. One set of bottles (300 ml capacity +/-5 ml) were exposed *in situ* (ie. they were resuspended at the depth from which the sample had been taken) whilst the other set (125 ml capacity +/-2 ml) were exposed at the same depths as the *in situ* bottles but with the algal suspensions all from one depth. Several experiments were carried out at the beginning of the season to investigate whether bottle size had any significant effect on production rates.

Plate 3. Frame for holding primary productivity bottles in pairs. Light bottles are held horizontally and dark bottles are placed in the vertical chambers. (The dark bottles are held in the grey chamber).



CHAPTER 3. THE METEROLOGICAL, PHYSICAL AND CHEMICAL CHARACTERISITCS.

3.1 METEOROLOGICAL CHARACTERISTICS OF THE AREA.

The meteorological data reported here are those from Sutton Bonnington Agricultural school.

The study area has a climate typical of the Midlands and is not normally subject to any climatic extremes.

The lowest air temperature recorded was -15.8 ^{o}C once during the 1981/1982 winter. Maximum temperatures varied from 26.6 to 30.5 ^{o}C. The annual ranges are shown in Table 3.

Average monthly mean maximum and minimum screen temperatures were very similar between years (Table 4).

Annual rainfall was relatively constant, ranging from 601 mm in 1981 to 680 mm in 1982. However monthly rainfall was highly variable. The lowest rainfall was 4 mm in August 1982 and the highest was 142 mm in July 1982. Monthly rainfall totals for the period of study are given in Table 5.

Annual daily mean of solar radiation was constant around 250 milliWatt hours cm^{-2} (mWhr cm^{-2}). The seasonal pattern, on a monthly basis is shown in Table 6. The lowest mean daily irradiance was 53 mWhr cm^{-2} in December 1982 and the highest was 505 mWhr cm^{-2} in July 1983.

TABLE 3. ANNUAL RANGES OF AIR TEMPERATURE (^{o}C).

	Maximum	Minimum
1980	26.6	-9.2
1981	26.7	-15.3
1982	28.7	-15.8
1983	30.5	-6.9

TABLE 4. Average of the monthly mean maximum and minimum screen temperatures (°C).

	J	F	M	A	M	J	J	A	S	O	N	D
1980	2.3	5.7	4.7	8.3	10.4	13.9	15.5	15.8	14.3	8.8	6.5	5.5
1981	5.7	2.6	7.7	7.2	11.2	13.4	15.7	16.0	14.7	8.1	7.3	-0.6
1982	2.1	4.6	5.9	8.6	11.1	15.3	16.5	15.9	14.0	10.0	7.6	4.1
1983	6.7	1.2	6.6	6.8	10.2	14.0	18.9	17.3	13.8	10.4	n.d	n.d
Monthly mean	4.2	3.5	6.2	7.7	10.7	14.1	16.6	16.2	14.2	9.3	7.1	3.0

TABLE 5. Monthly rainfall totals (mm).

	J	F	M	A	M	J	J	A	S	O	N	D	ANNUAL TOTAL.
1980	68	78	51	18	31	95	49	85	37	83	51	26	672
1981	30	44	76	63	50	23	29	56	92	67	26	45	601
1982	33	27	72	29	20	142	4	136	67	49	55	46	683
1983	59	27	33	88	79	8	29	11	84	40	n.d	n.d	-
Monthly mean	47	44	58	49	45	67	28	72	70	60	44	39	

n.d = no data

TABLE 6. Mean daily solar radiation ($mWhrscm^{-2}$).

	J	F	M	A	M	J	J	A	S	O	N	D	ANNUAL MEAN
1980	132	98	187	343	495	430	379	339	295	173	76	57	250
1981	61	117	162	298	377	440	478	410	348	209	97	79	256
1982	96	101	258	383	531	405	465	307	276	136	73	53	265
1983	70	119	187	328	350	474	505	441	251	174	n.d	n.d	-
Monthly mean	90	109	198	338	438	437	457	374	292	173	82	63	

TABLE 7. Mean daily run of the wind (km).

	J	F	M	A	M	J	J	A	S	O	N	D	ANNUAL MEAN
1980	196	206	251	237	247	224	200	212	238	266	334	341	246
1981	271	249	319	285	221	265	198	163	231	249	264	187	242
1982	235	258	288	195	205	180	225	237	193	193	304	277	233
1983	398	270	274	231	214	219	144	181	269	282	n.d	n.d	-
Monthly mean	275	246	283	237	222	222	192	198	233	247	301	268	

n.d = no data

Monthly means of daily run of wind varied little and ranged from 144 km in July 1983 to 398 km in January 1983 (Table 7). No distinct seasonal pattern was apparent, but there was a tendency for run of wind to be lower in the summer, as shown by the mean monthly figures.

3.2 PHYSICAL CHARACTERISTICS OF THE RESERVOIRS.

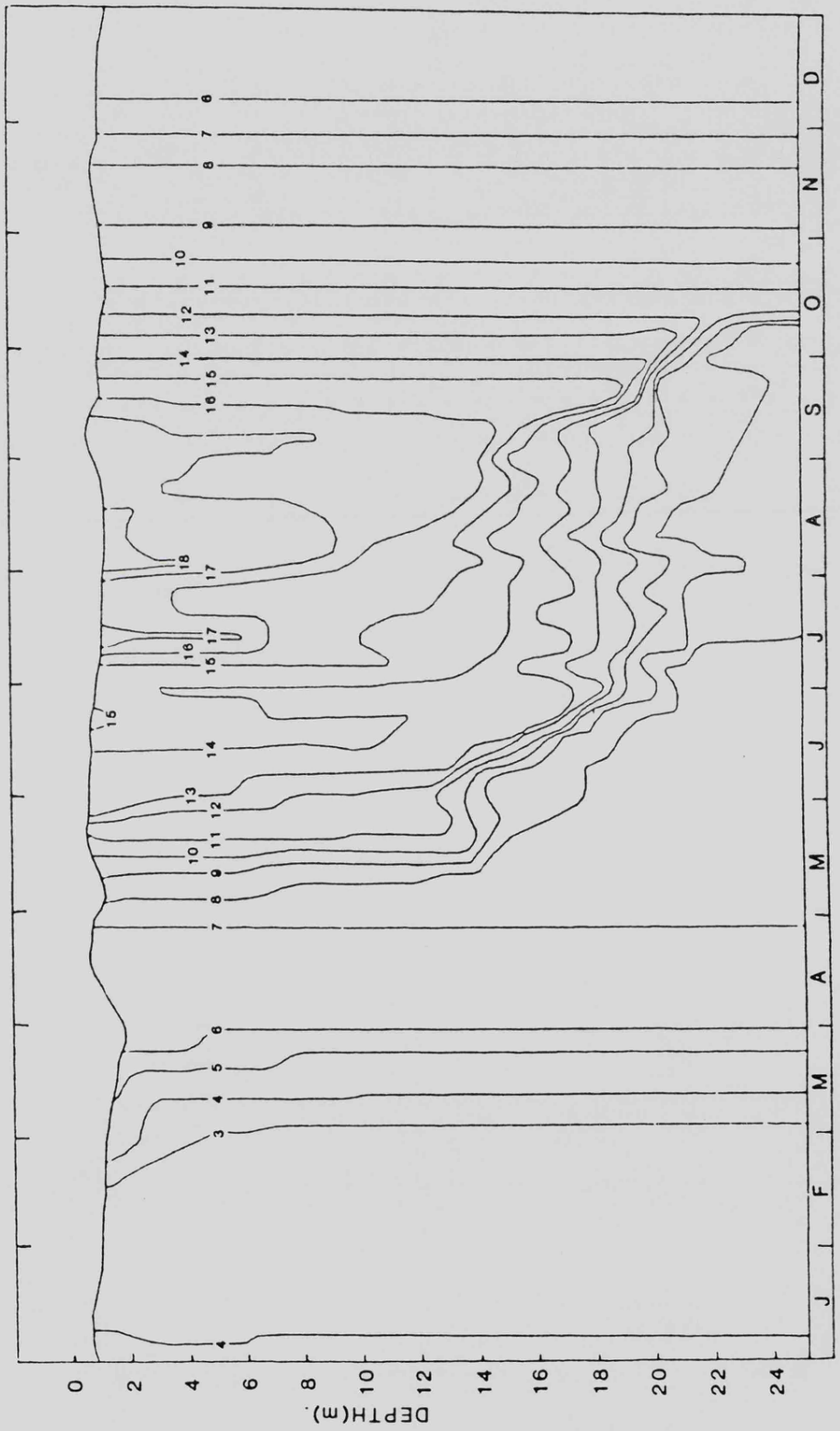
3.2.1 Temperature and oxygen.

3.2.1.1 The normal seasonal pattern.

Previous Severn Trent Water Authority monitoring showed that the study reservoirs followed a dimictic pattern of stratification with a period of thermal stratification occuring between early summer and autumn. This is illustrated during the study period by the variations in temperature in Foremark, 1981 (Figure 4). From January to March the reservoir was fully mixed and the water temperature low. In March surface water temperatures increased and a slight stratification appeared. In late March through to early May the reservoir became isothermal, with water temperatures reaching 7 ^{o}C. In early May, the water temperature increased rapidly and a thermocline started to form at around 12 m below the surface in mid May. At the begining of June the thermocline was depressed by winds and remained between 12 and 18 m below the surface for the rest of the summer. Micro-stratification occurred between 4 and 8m in mid July and August with surface temperatures of 18 ^{o}C as a result of increased input of solar radiation. Water temperatures started to decrease from mid September onwards and the autumnal overturn occurred at the end of September. The reservoir was isothermal by mid October and the water continued to cool to a low of 6 ^{o}C in December.

Maximum summer temperatures of 22 ^{o}C at the surface occurred in Staunton

Figure 4. Variations in the temperature of Foremark during 1981. (Isopleth values are ^{o}C).



Harold and Foremark in 1983 and the minimum was 2 ^{o}C in both reservoirs during the 1982/1983 winter.

Interrelated to this thermal stratification were the variations in dissolved oxygen concentrations. These concentrations underwent a similar pattern of seasonal change and are illustrated here by the changes in Foremark during 1981 (Figure 5). Throughout the winter months the reservoir was well mixed and the water was saturated with dissolved oxygen. The dissolved oxygen in the hypolimnion began to decrease as the summer progressed and thermal stratification developed, until it was below 1% saturation in August and September. The dissolved oxygen at the surface rose to 120% saturation in May and June, 110% in mid July and to 130% in late August and early September. All of these peaks coincided with peaks of high algal biomass and suggested high phytoplankton production. The autumnal overturn in late September resulted in the mixing of water from the anaerobic hypolimnion with well oxygenated water from the epilimnion and by mid October the reservoir was saturated throughout the water column.

The variations of temperature and dissolved oxygen in 1981 are shown in Figures 6 and 7 for Staunton Harold.

The distribution of isotherms and the formation of the thermocline in Staunton Harold during May and June 1981 (Figure 6) was identical to the isotherms for Foremark (Figure 4). Natural destratification took place in Staunton Harold during early June as a result of strong winds and heavy rain and the water column became isothermal. The cool conditions that prevailed for the rest of the summer did not produce stratification. As reported above, stratification continued in Foremark as a result of the greater depth and the thermocline lay between 12 and 18 m below the surface for the rest of the summer.

Figure 5. Variations in the dissolved oxygen of Foremark during 1981.

(Isopleth values are % saturation).

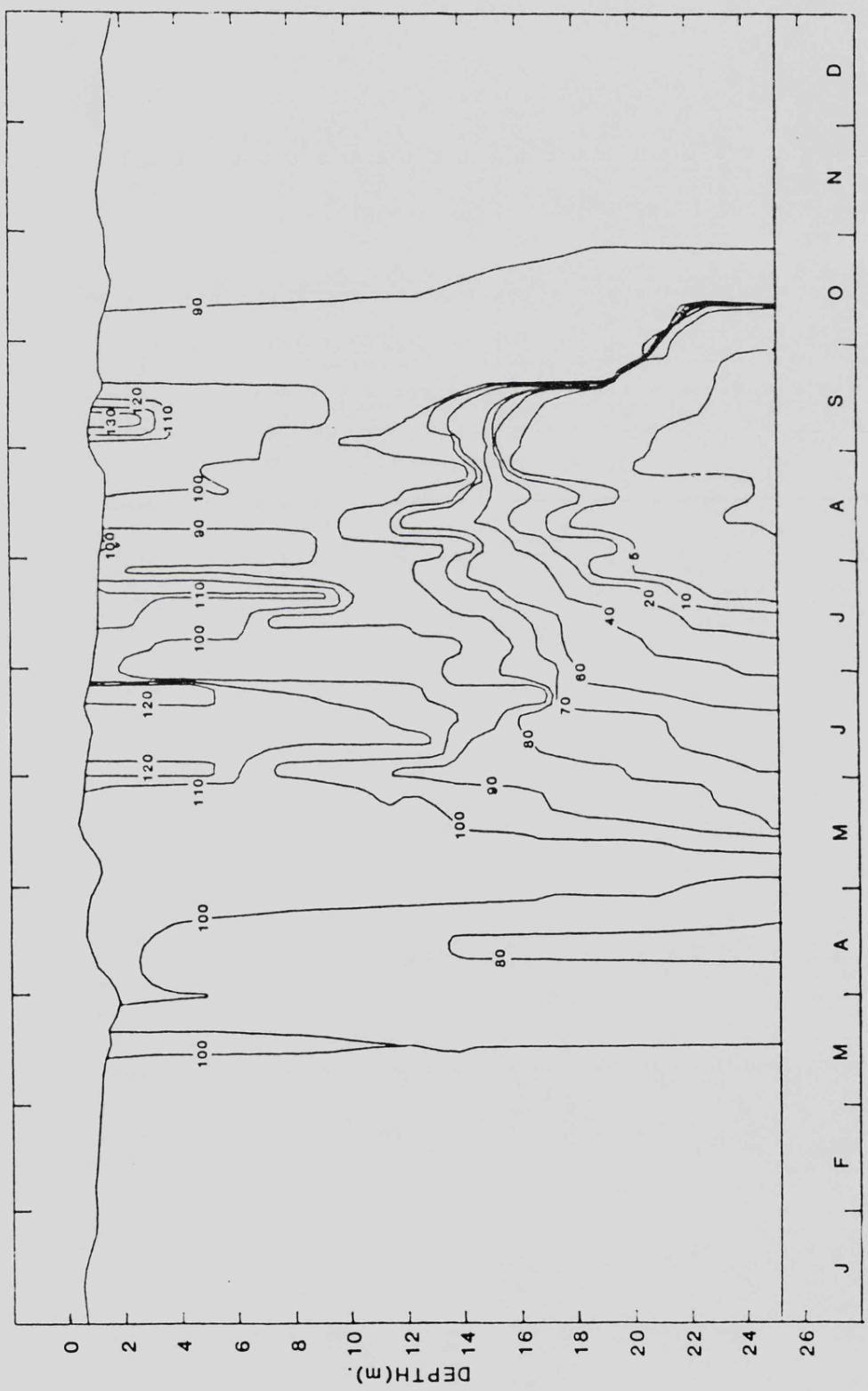


Figure 6. Variations in the temperature of Staunton Harold during 1981. (Isopleth values are ^{o}C). Arrows indicate periods of artificial mixing.

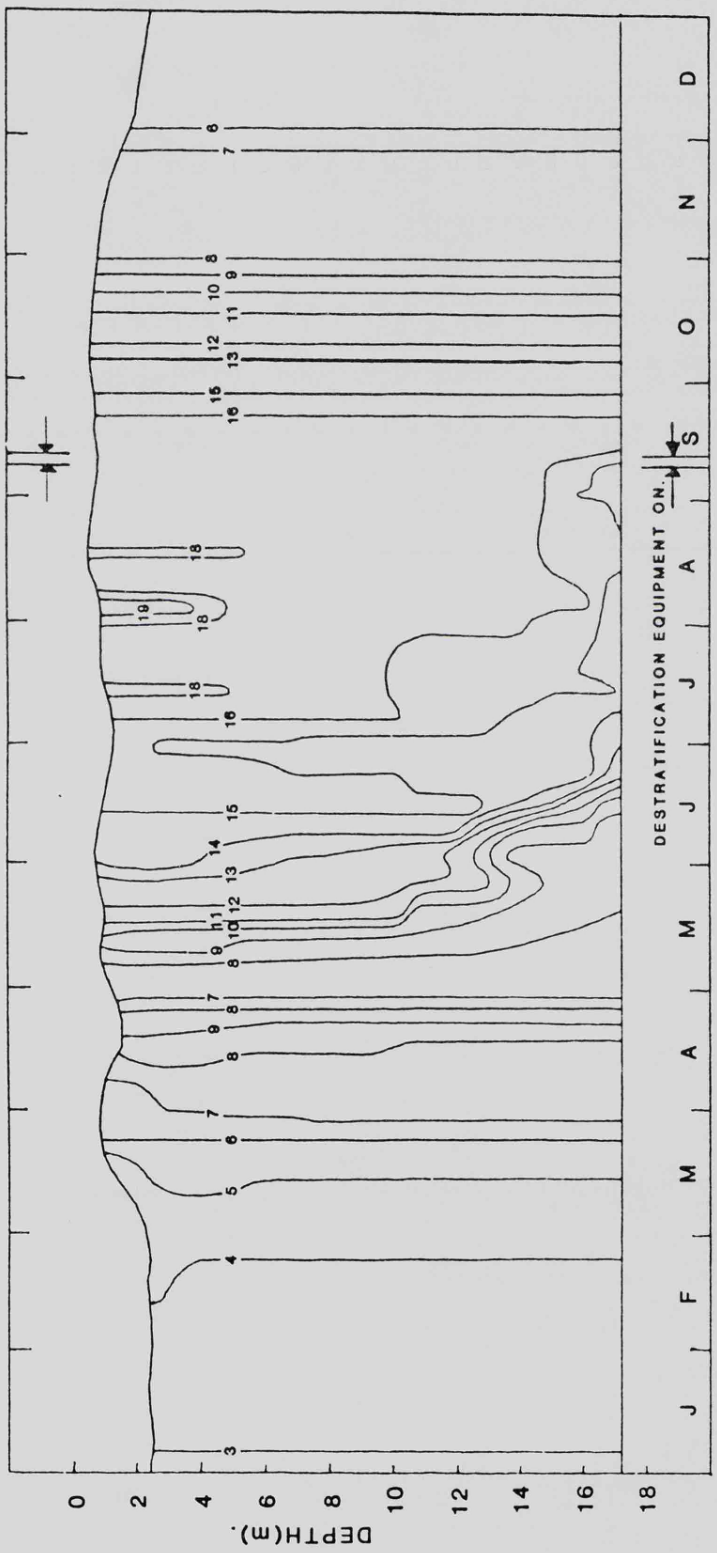
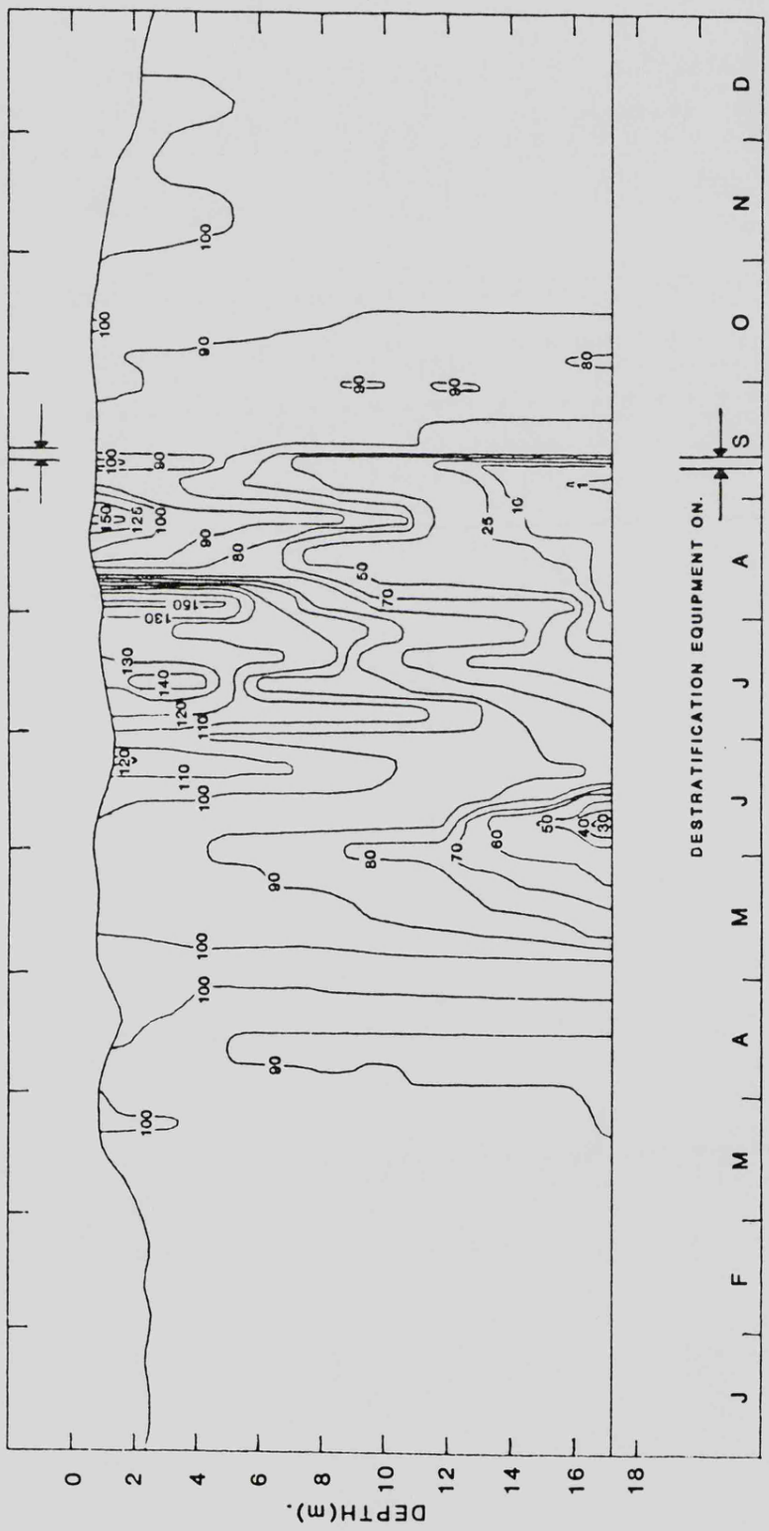


Figure 7. Variations in the dissolved oxygen of Staunton Harold during 1981. (Isopleth values are % saturation). Arrows indicate periods of artificial mixing.



Stratification of the dissolved oxygen in Staunton Harold during 1981 was maintained even though there was no thermal stratification (Figure 20) and the dissolved oxygen fell to below 10% in the hypolimnion in August and September.

3.2.1.2 Artificially mixed pattern.

Artificial destratification was induced between the 8th and 11th September. Figure 8 shows the changes in temperature at the valve tower over the destratification period and although there was only a temperature difference of 2.5 ^{o}C before the equipment was switched on, after 3 days of continuous operation the reservoir was isothermal. The dissolved oxygen profiles showed a marked stratification before mixing but within 3 days the distribution had become even with depth (Figure 9) and there had been an increase in the total dissolved oxygen throughout the resevoir as a result of oxygenation at the surface. The algal populations were initially stratified, but again within 3 days the chlorophyll was evenly distributed with depth (Figure 10) and an increase was noted which coincided with the artificial mixing. Appendix 7 shows that these observations of temperature and dissolved oxygen, made at the valve tower, reflected those in the main body of the reservoir.

In the summers of 1982 and 1983 stratification in Staunton Harold was prevented by artificial, continuous mixing whilst Foremark was allowed to stratify. Figures 11 and 12 show the temperature difference between the surface and the bottom of the reservoirs. In 1982 the maximum temperature difference was 3.3 ^{o}C on 7th June, compared to 13.25 ^{o}C in Foremark whilst in 1983 the difference reached 2.5 ^{o}C on July 18th in Staunton Harold compared to 13.25 ^{o}C in Foremark. As can be seen in Figures 13 and 14, Staunton Harold remained mixed with regard to temperature throughout both summers and the dissolved oxygen in the hypolimnion never fell below 80% saturation in 1982 and 90% in 1983 (Figures 15 and 16).

Figure 8. The changes in the temperature profiles during artificial destratification in Staunton Harold during September, 1981.

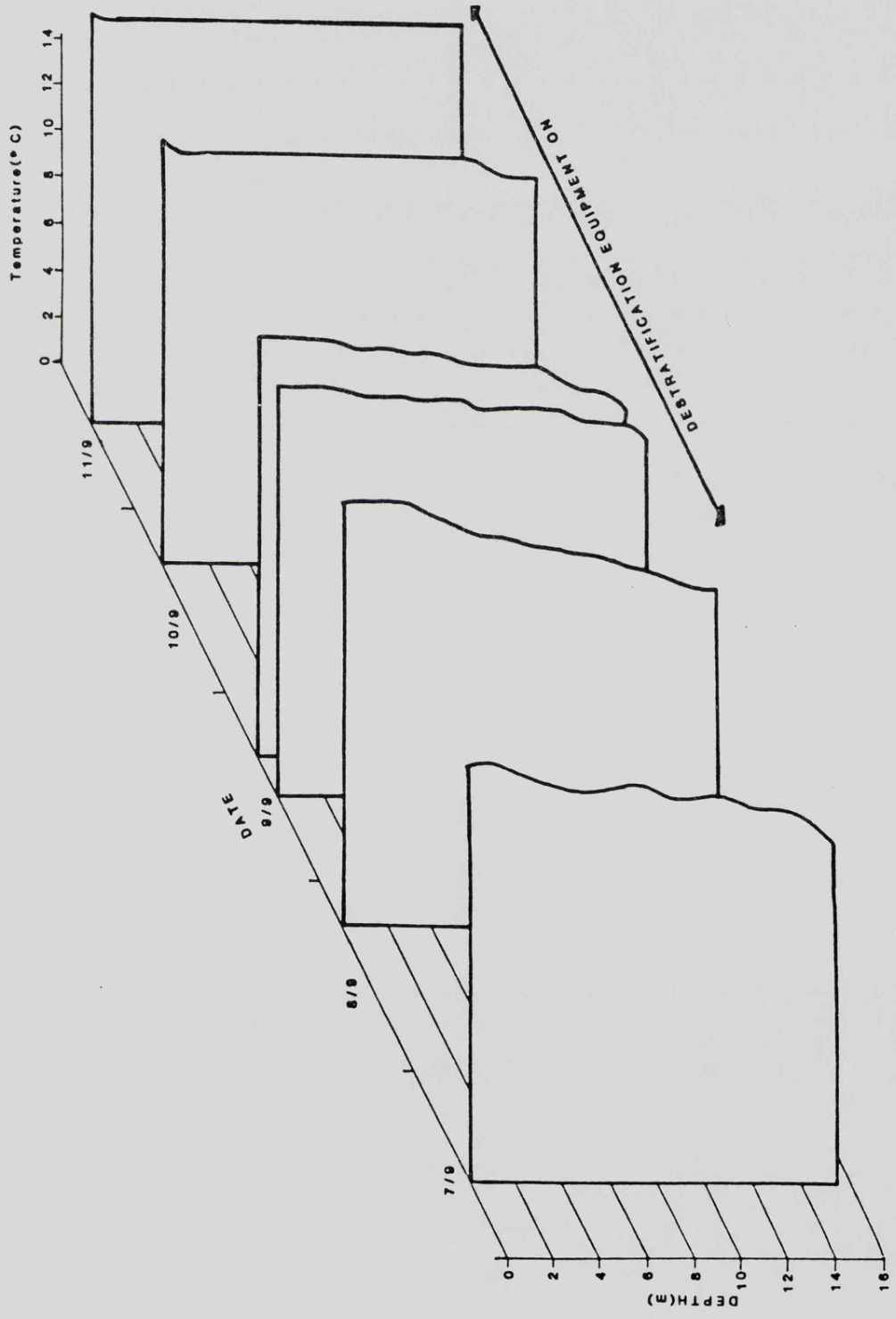


Figure 9. The changes in the dissolved oxygen profiles during artificial destratification in Staunton Harold during September, 1981.

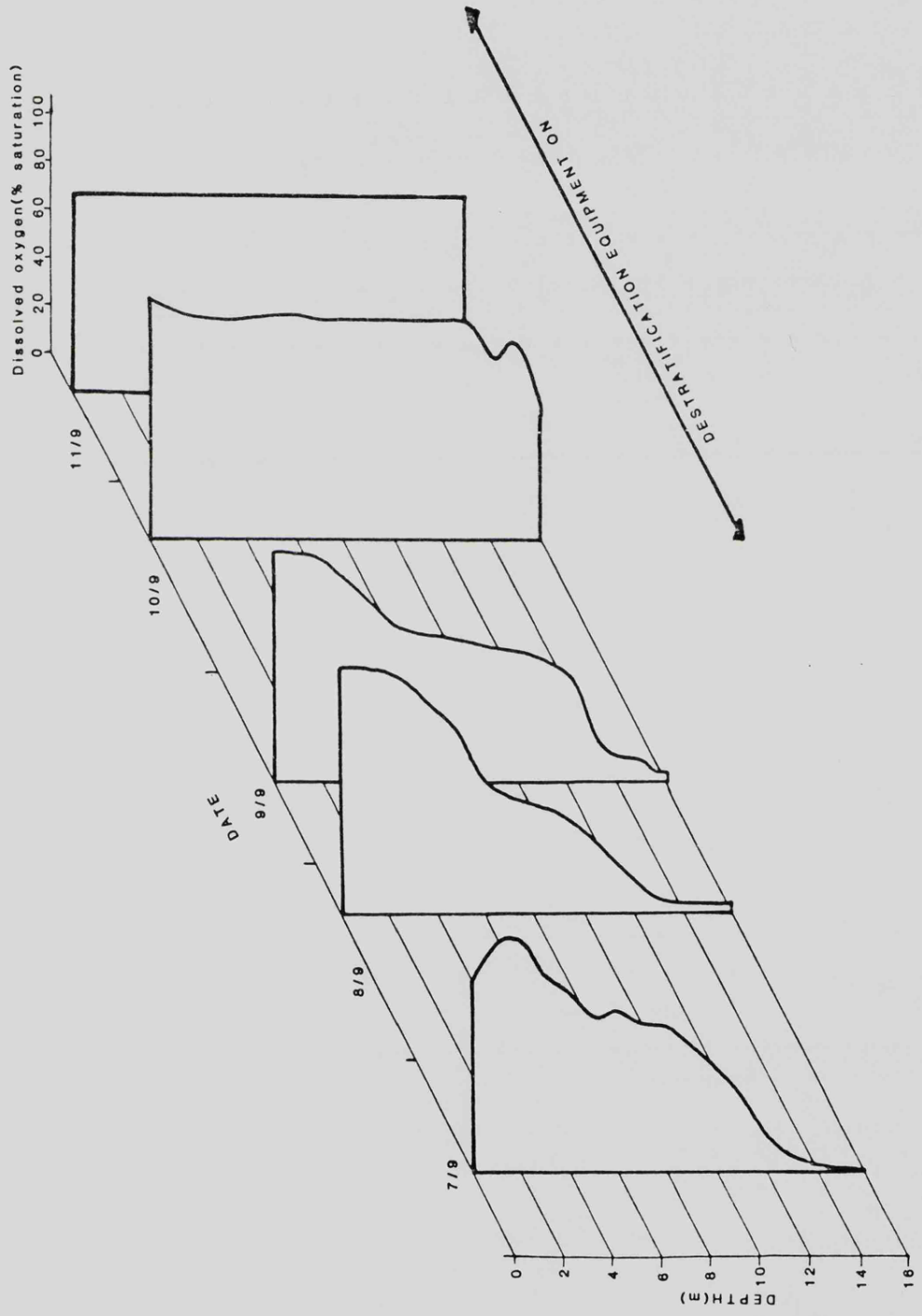


Figure 10. The changes in the chlorophyll a profiles before, during and after artificial destratification in Staunton Harold during September, 1981.

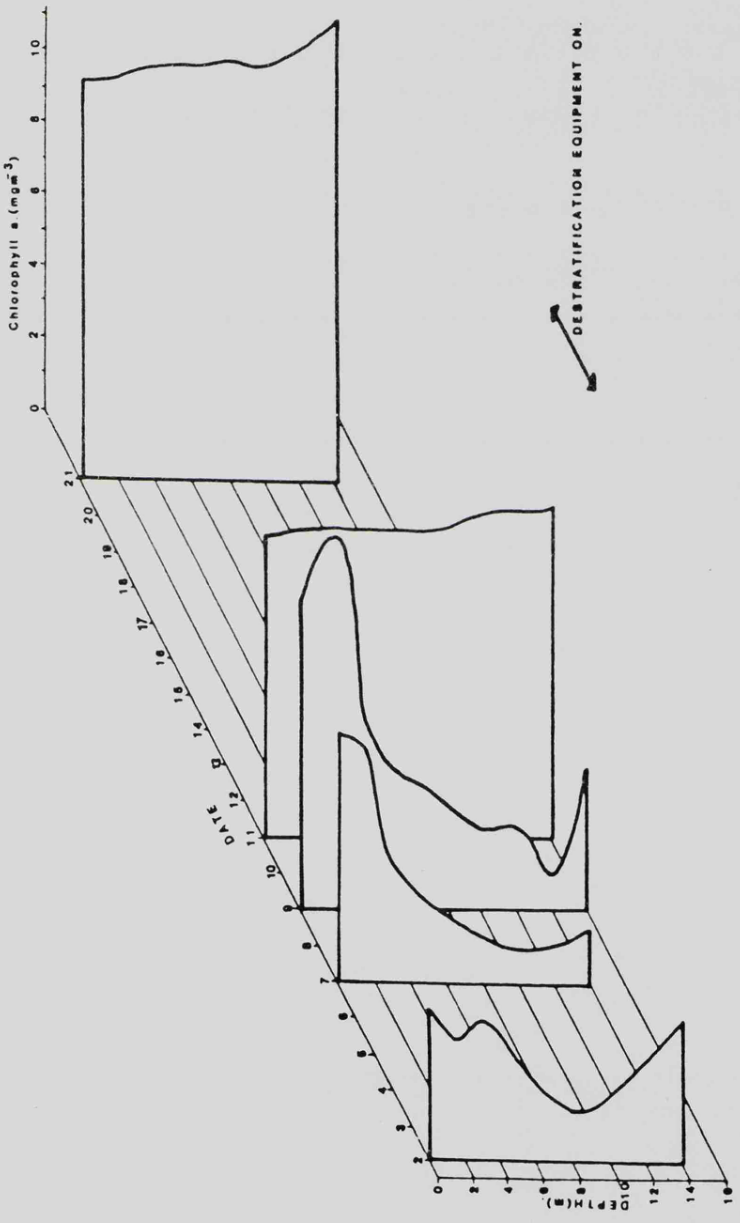


Figure 11. The temperature difference between the surface and bottom of Staunton Harold and Foremark, recorded at the valve towers, during 1982.

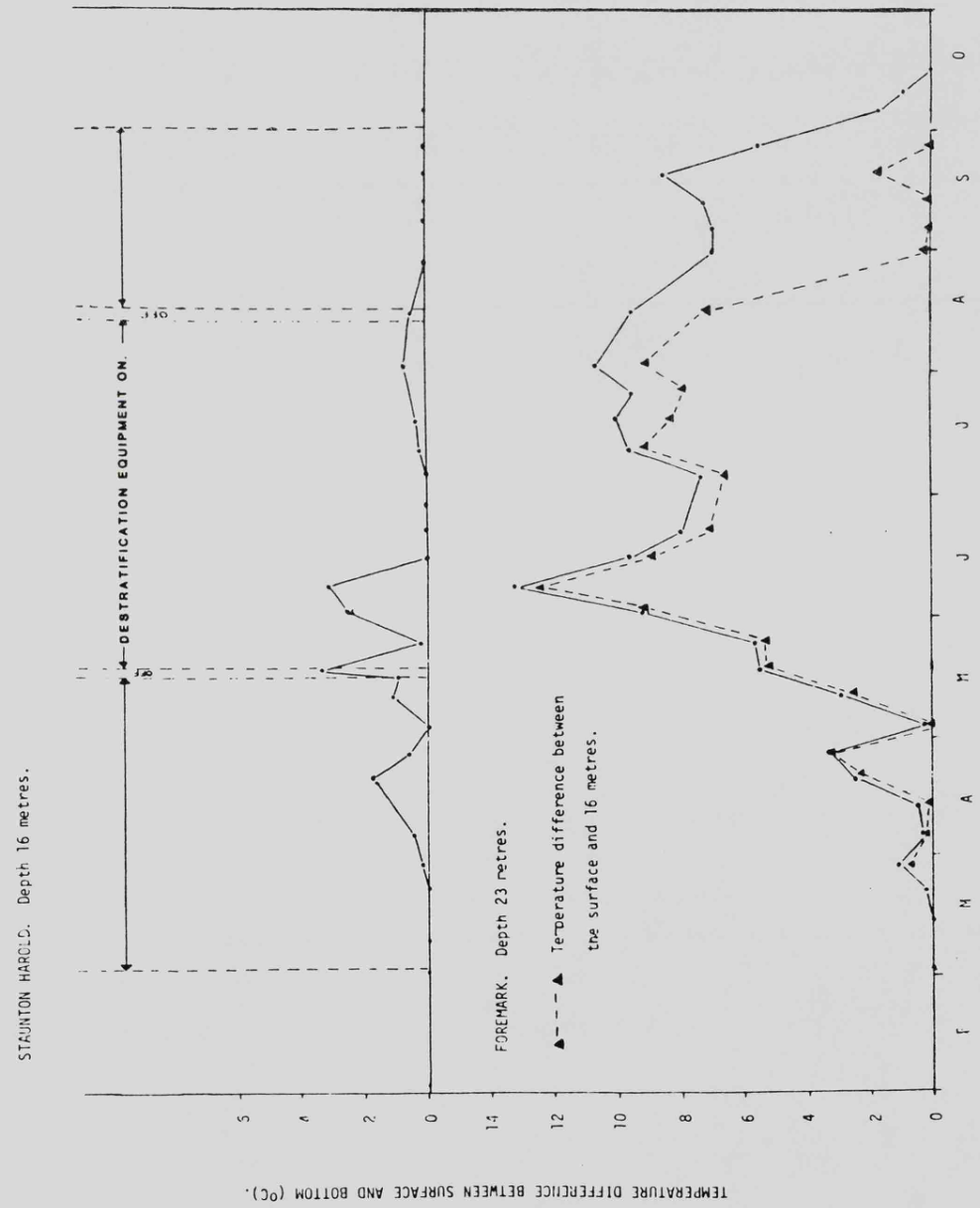


Figure 12. The temperature difference between the surface and bottom of Staunton Harold and Foremark, recorded at the valve towers, during 1983.

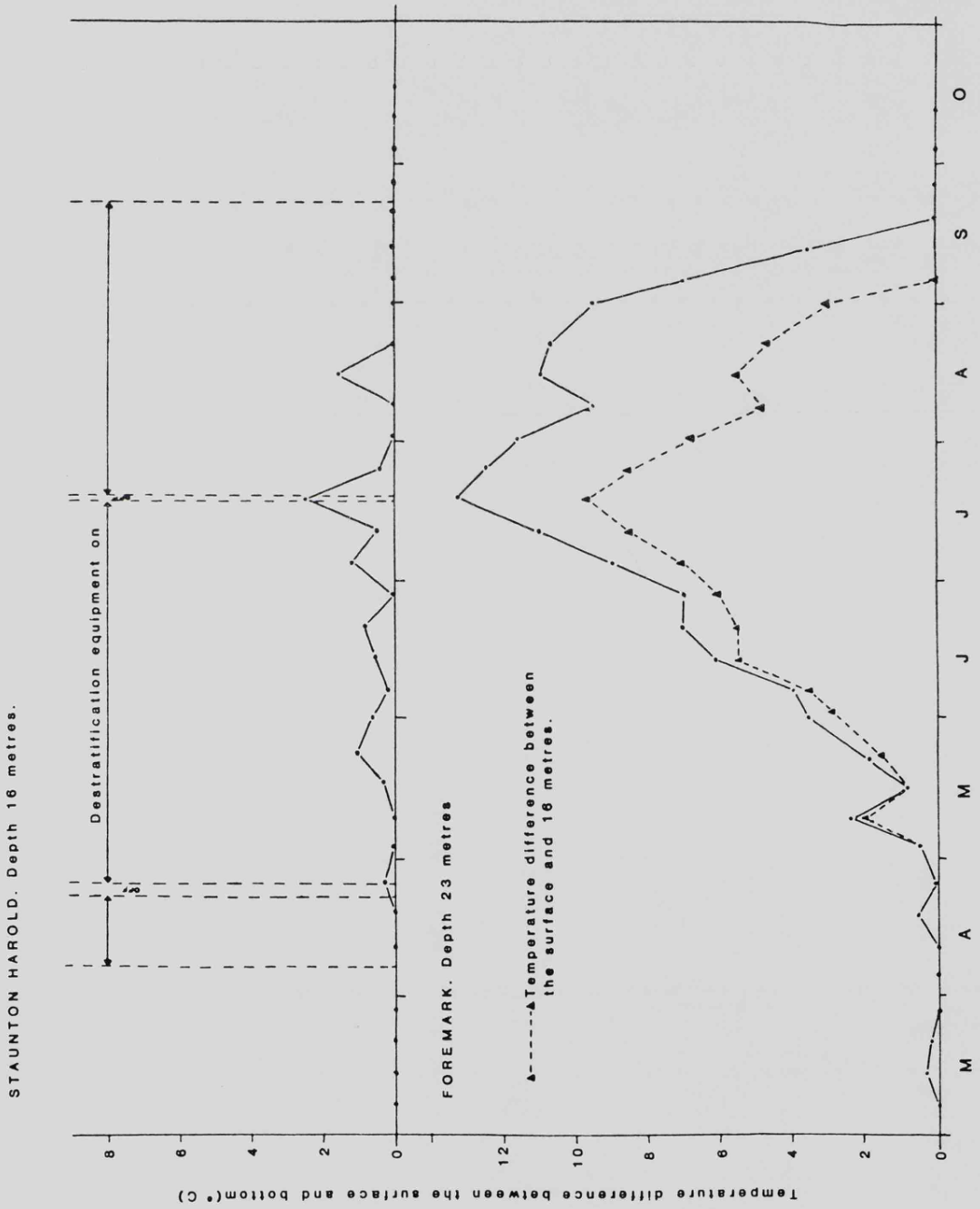


Figure 13. Variations in the temperature of Staunton Harold during 1982. (Isopleth values are ^{O}C). Arrows indicate periods of artificial mixing.

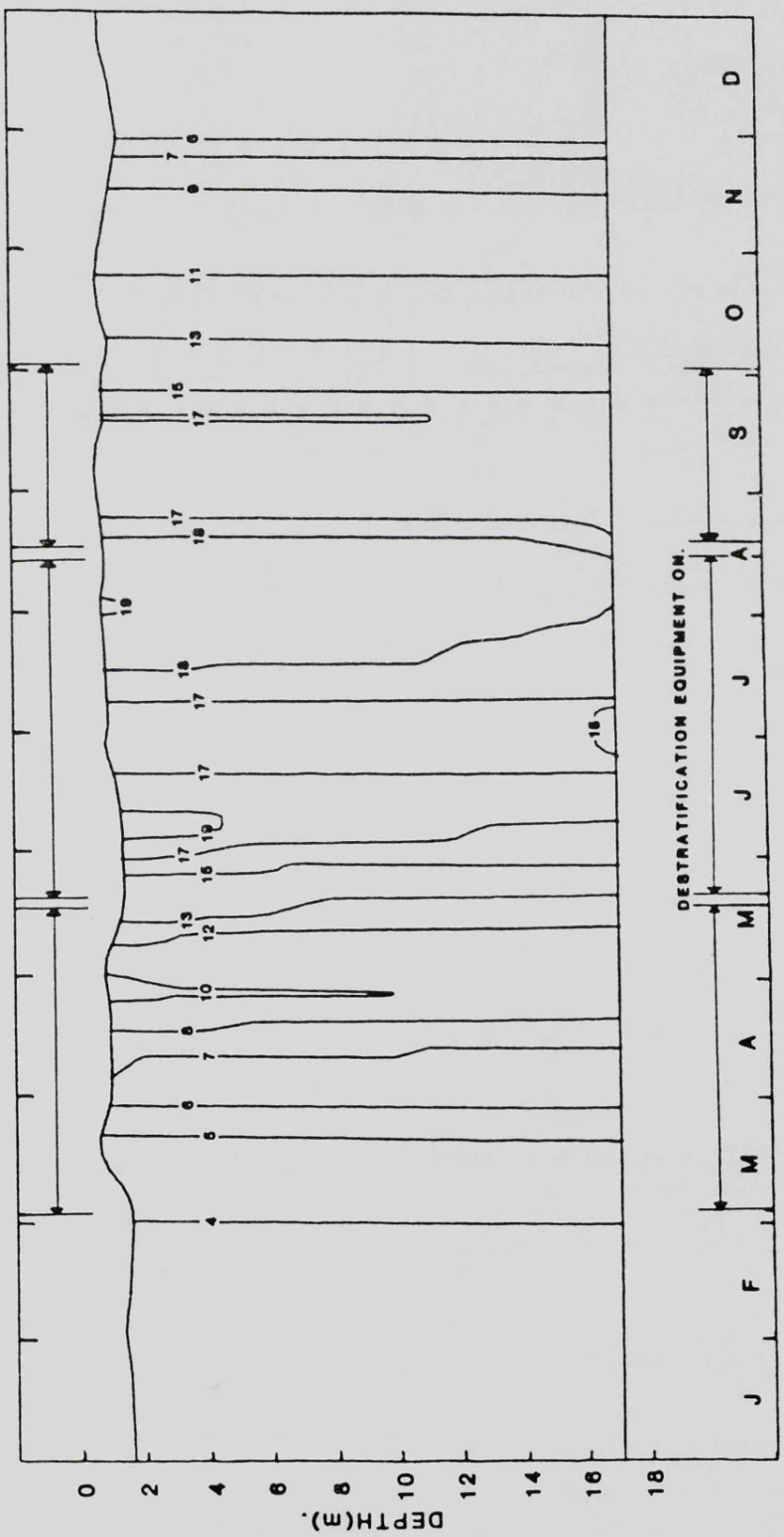


Figure 14. Variations in the temperature of Staunton Harold during 1983. (Isopleth values are ^{o}C). Arrows indicate periods of artificial mixing.

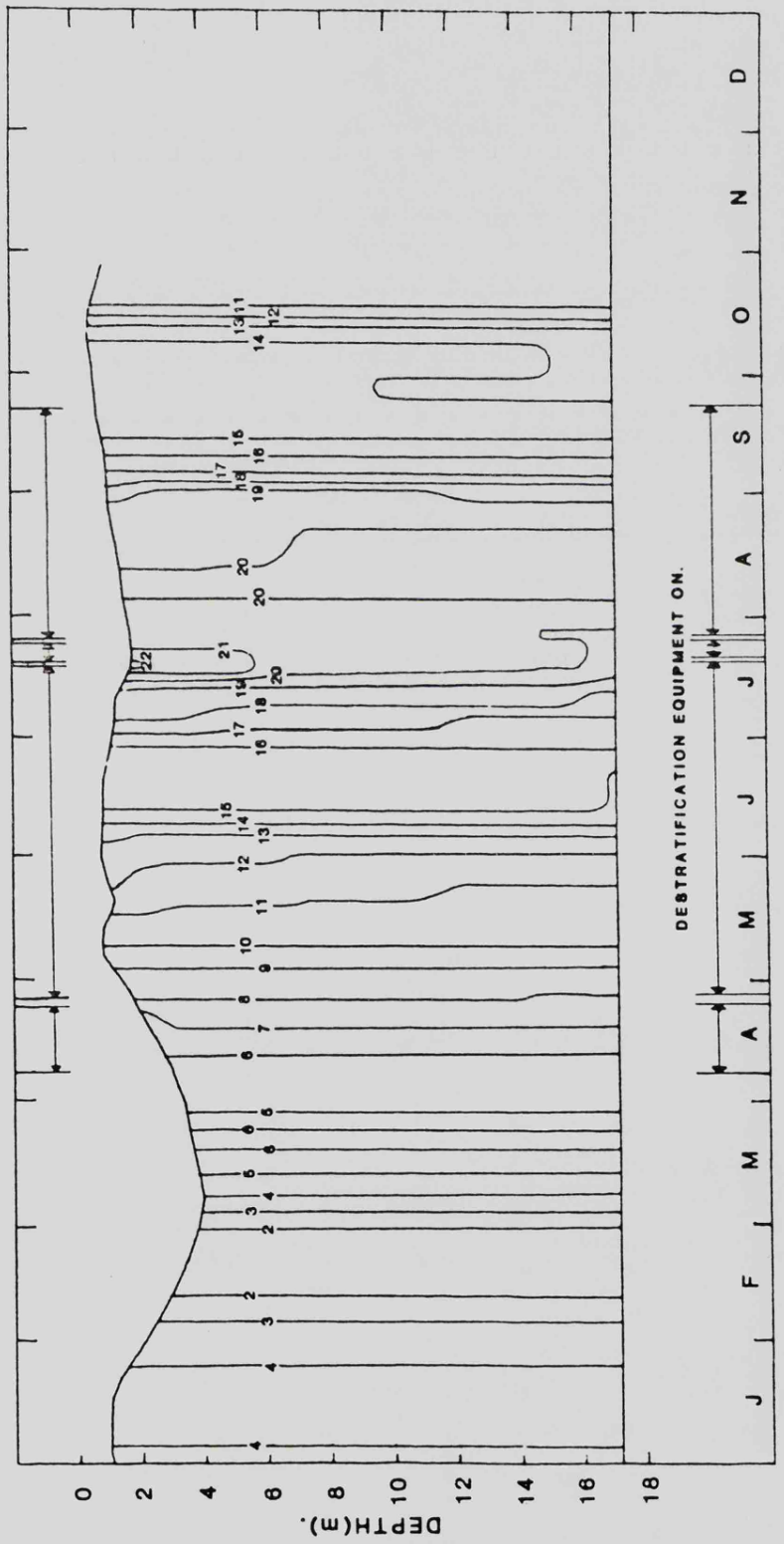


Figure 15. Variations in the dissolved oxygen of Staunton Harold during 1982. (Isopleth values are % saturation). Arrows indicate periods of artificial mixing.

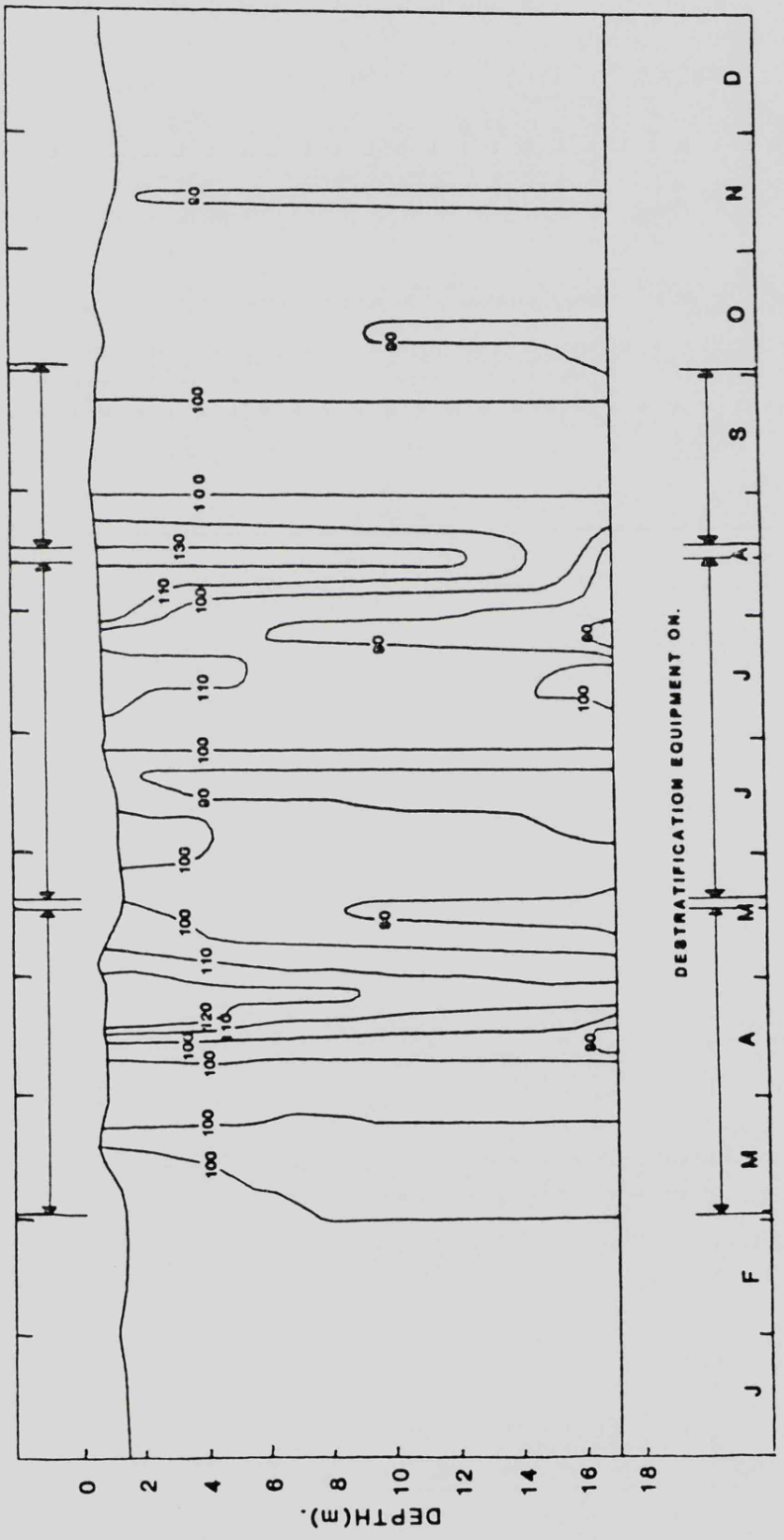
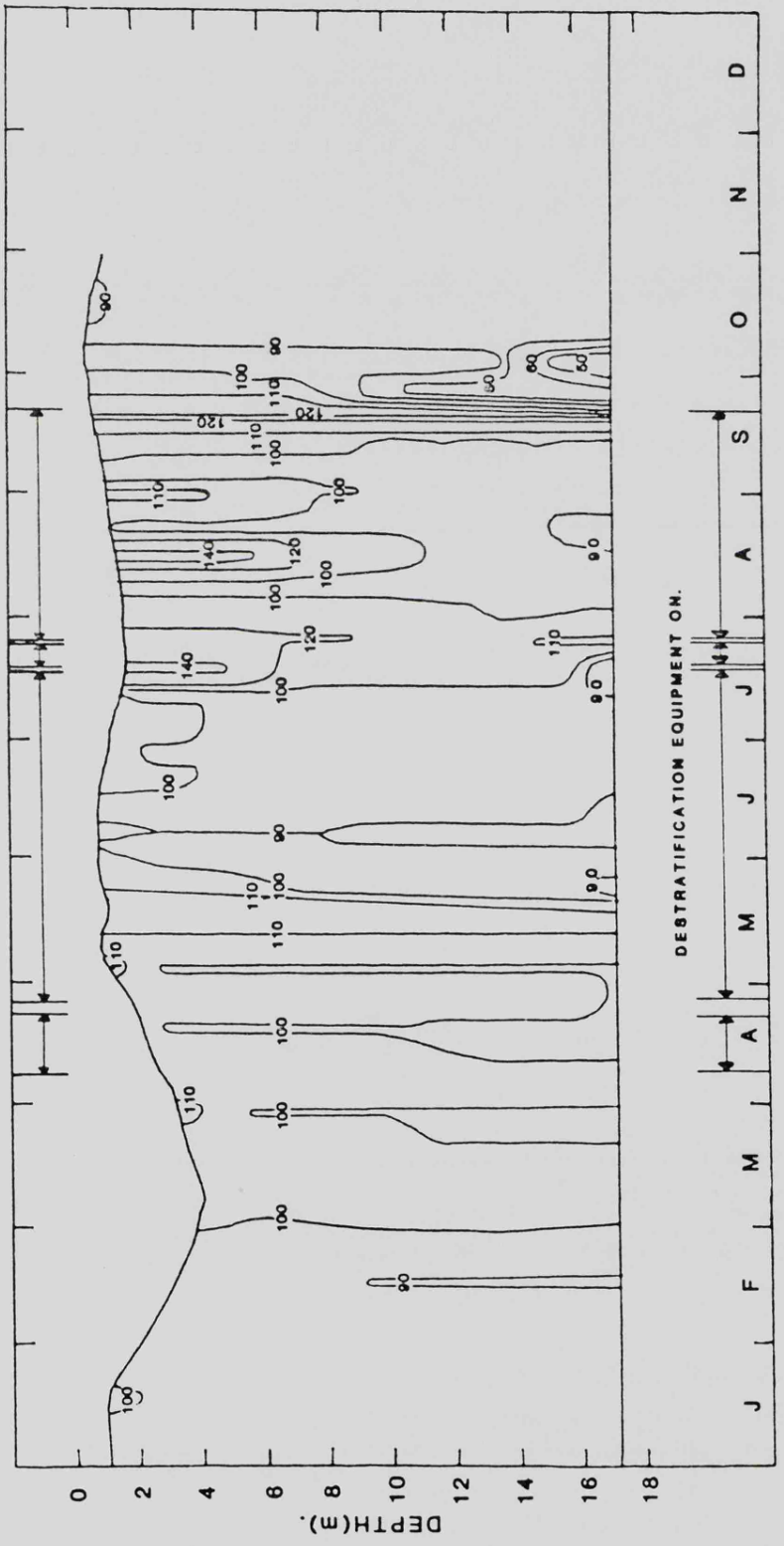


Figure 16. Variations in the dissolved oxygen of Staunton Harold during 1983. (Isopleth values are % saturation). Arrows indicate periods of artificial mixing.



In 1982 and 1983, Foremark became thermally stratified (Figures 17 and 18) and the dissolved oxygen in the hypolimnion fell below 10% saturation in both years (Figures 19 and 20).

On the 15th May, 1982 there was a power failure at the treatment works and the compressor was non-operational between 20.00 hrs on the 15th May to 09.00 hrs on the 17th May. Figure 21 shows the temperature difference between the surface and the bottom of both reservoirs during mid May. A temperature difference of 3.5 ^{o}C developed in Staunton Harold over the weekend of the 15/16th (6.8 ^{o}C in Foremark on the same day). After the compressor had been switched on the temperature difference was reduced to that recorded prior to the failure in five days; the difference continued to increase in Foremark.

3.2.2 Water column stability.

The temporal changes in the Brunt-Vasala frequency, N^2, over 0-5m and 0-15m are shown in Figure 22 for Staunton Harold and Foremark between March and September for the three study years.

1) N^2. In 1981 the oscillations of both N^2 (0-5) and N^2 (0-15) were very similar for each reservoir. In Staunton Harold the cycle of oscillations of the (0-5) values was 3 weeks. The similarity in the fluctuations was a result of the poor climatic conditions which prevented Staunton Harold from stratifying and depressed the metalimnetic layer in Foremark to between 14 and 18m for the majority of the summer.

The effects of artificial mixing on water column stability in Staunton Harold during 1982 and 1983 were very noticeable. N^2 (0-5) in Foremark showed several large peaks in both years. These were related to periods of intense heating of the epilimnion which can also be seen as the much smaller peaks for

Figure 17. Variations in the temperature of Foremark during 1982. (Isopleth values are ^{o}C).

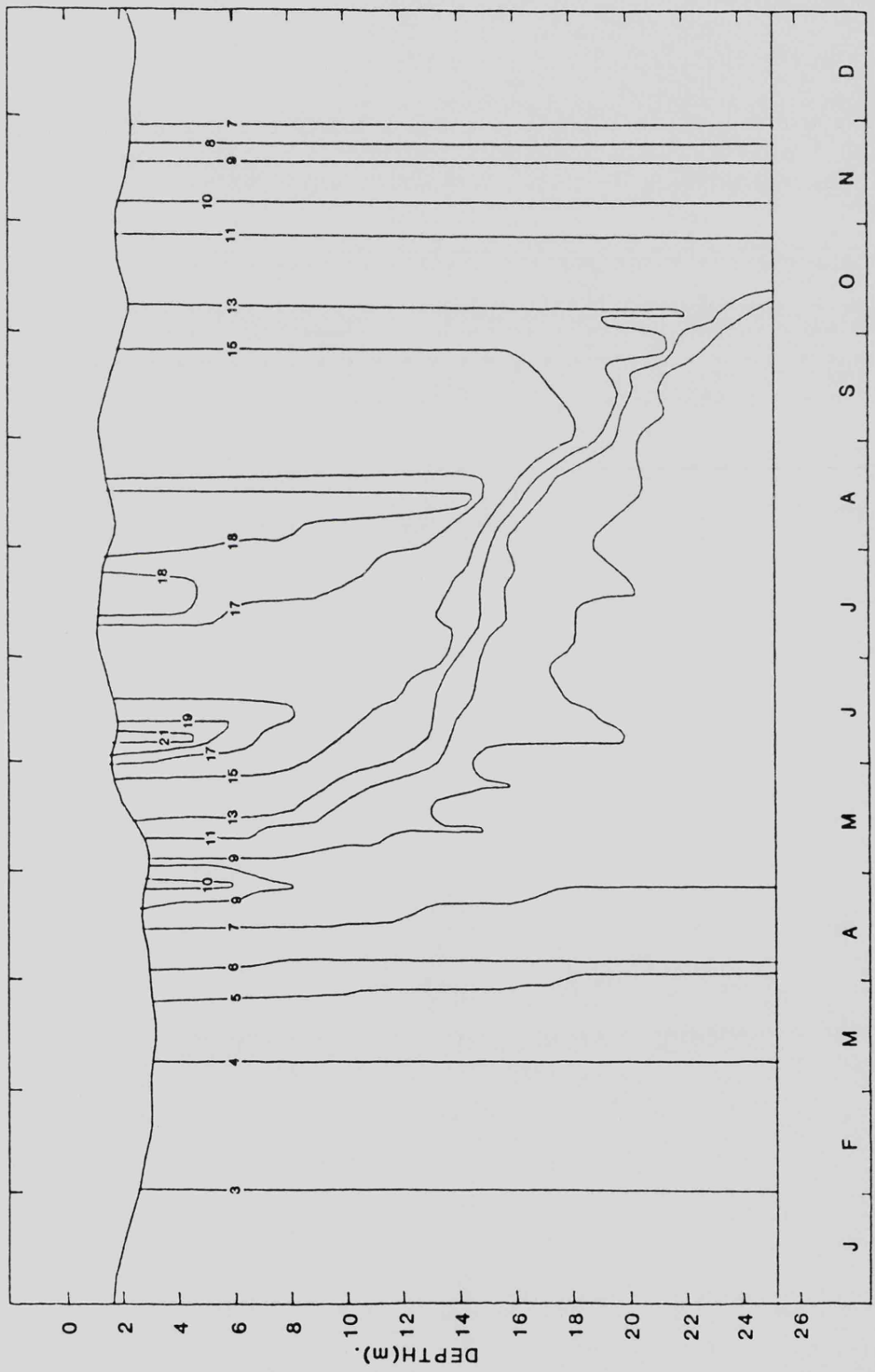


Figure 18. Variations in the temperature of Foremark during 1983. (Isopleth values are ^{o}C).

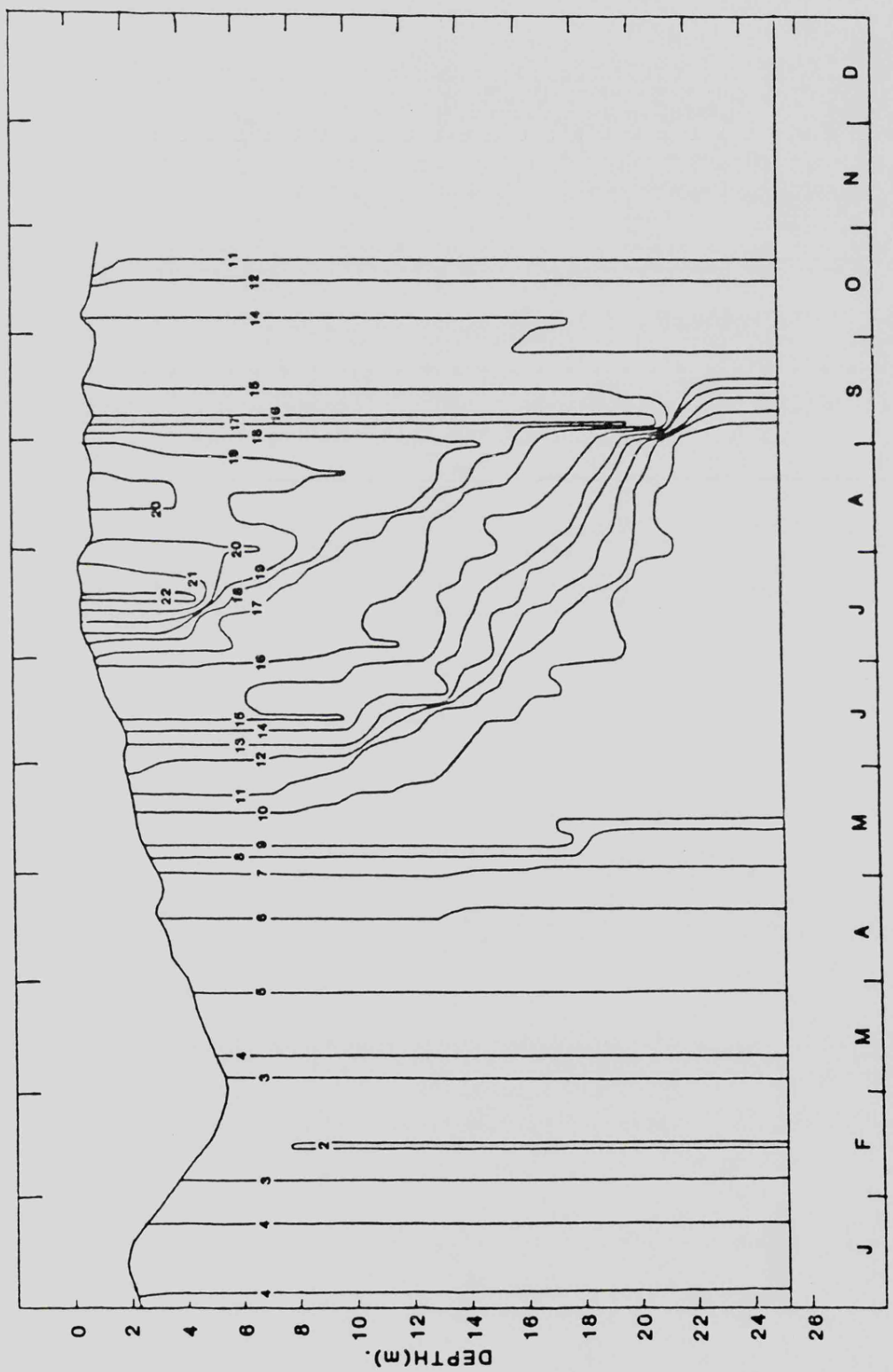


Figure 19. Variations in the dissolved oxygen of Foremark during 1982.

(Isopleth values are % saturation).

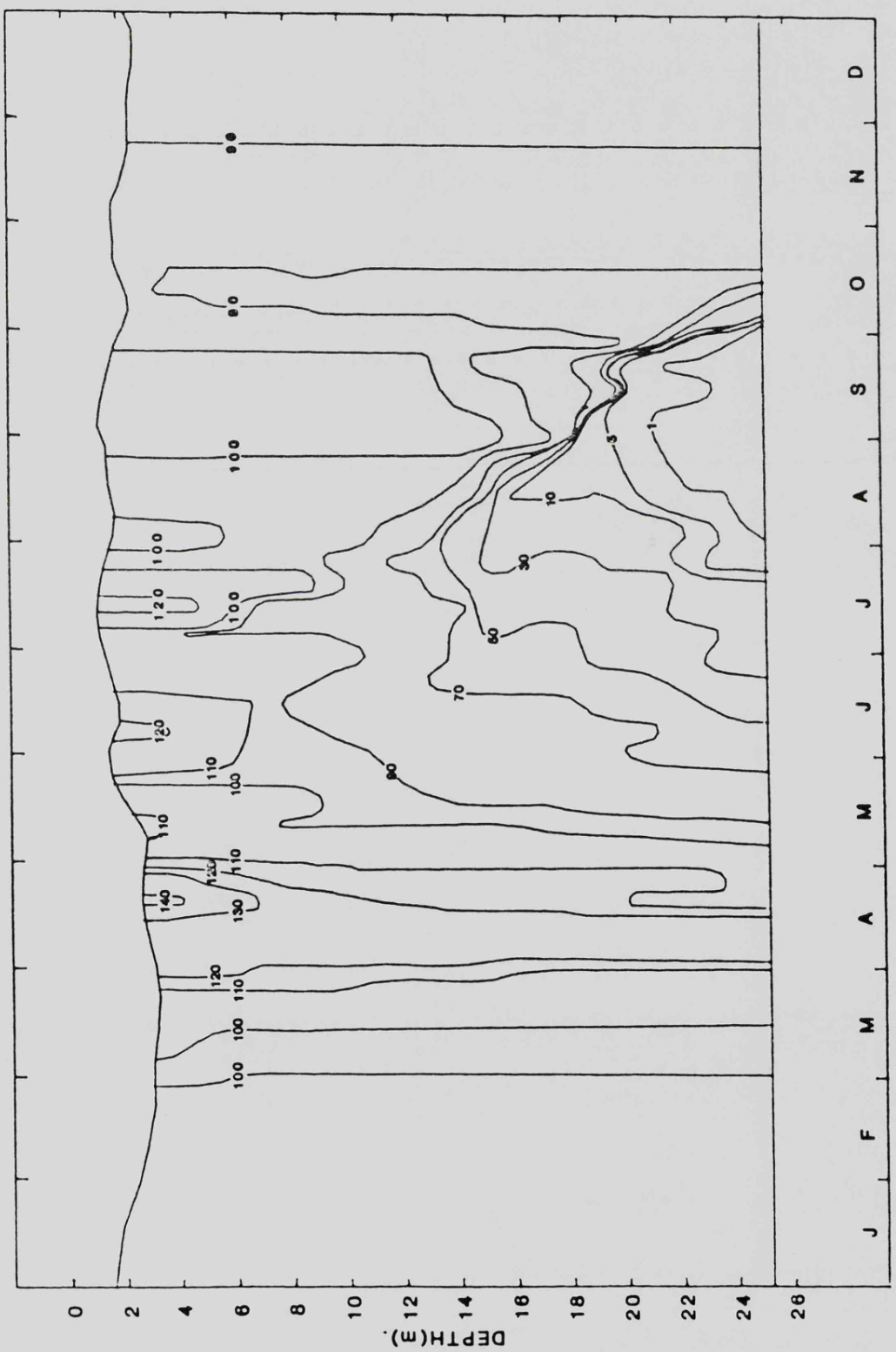


Figure 20. Variations in the dissolved oxygen of Foremark during 1983.

(Isopleth values are % saturation).

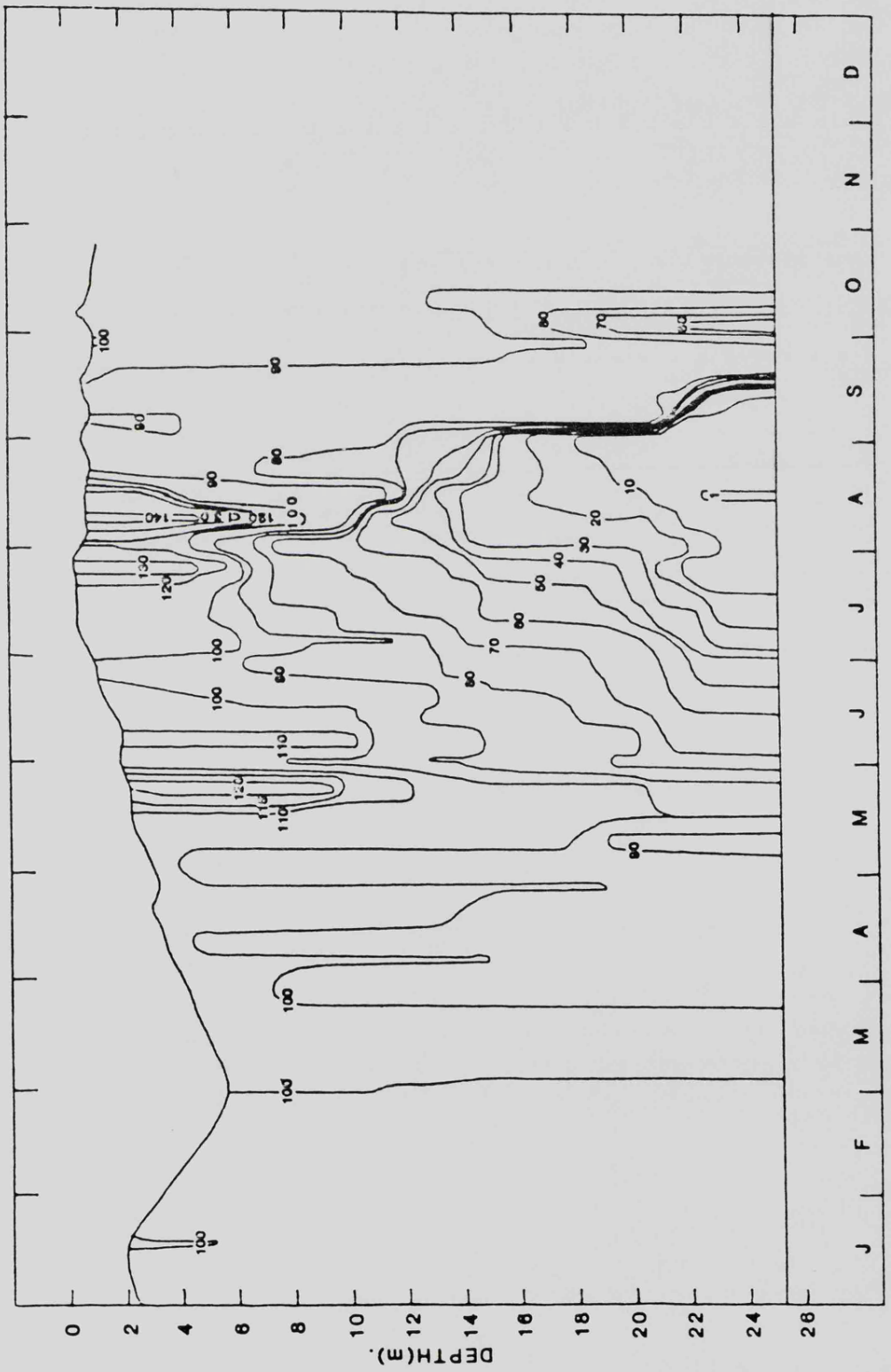


Figure 21. The temperature difference between the surface and the bottom of Staunton Harold and Foremark between the 15th and 17th May, 1982.

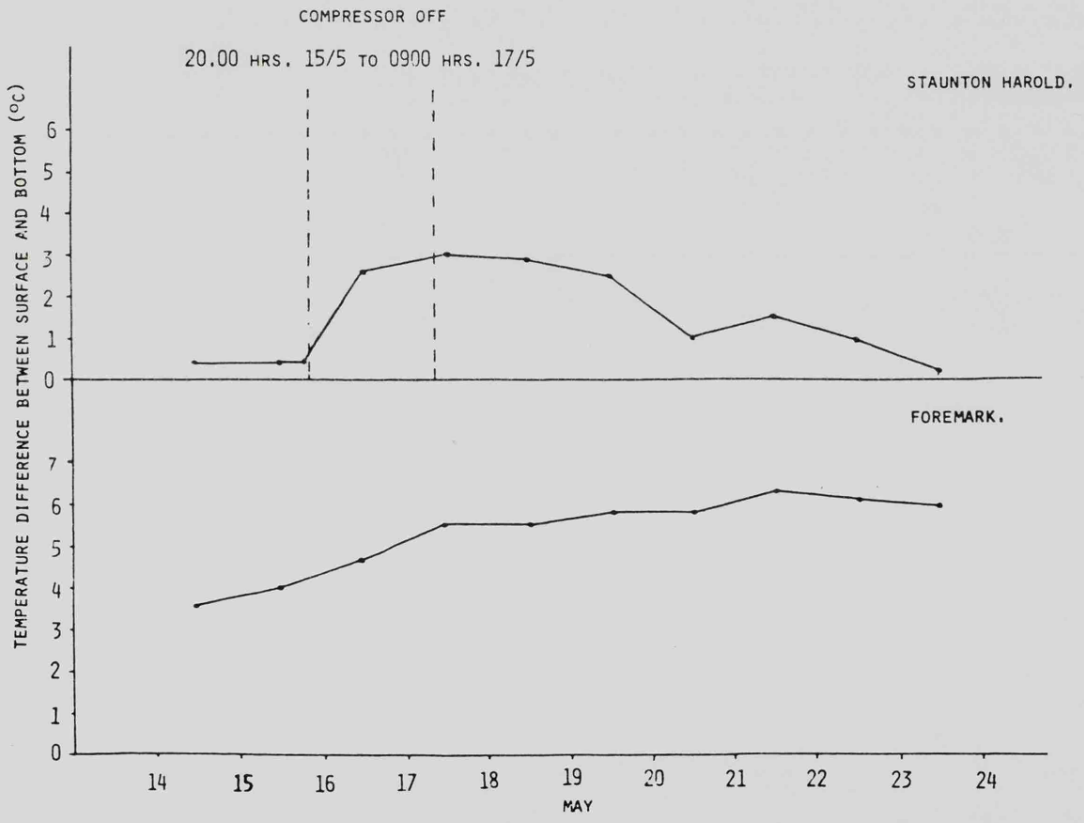
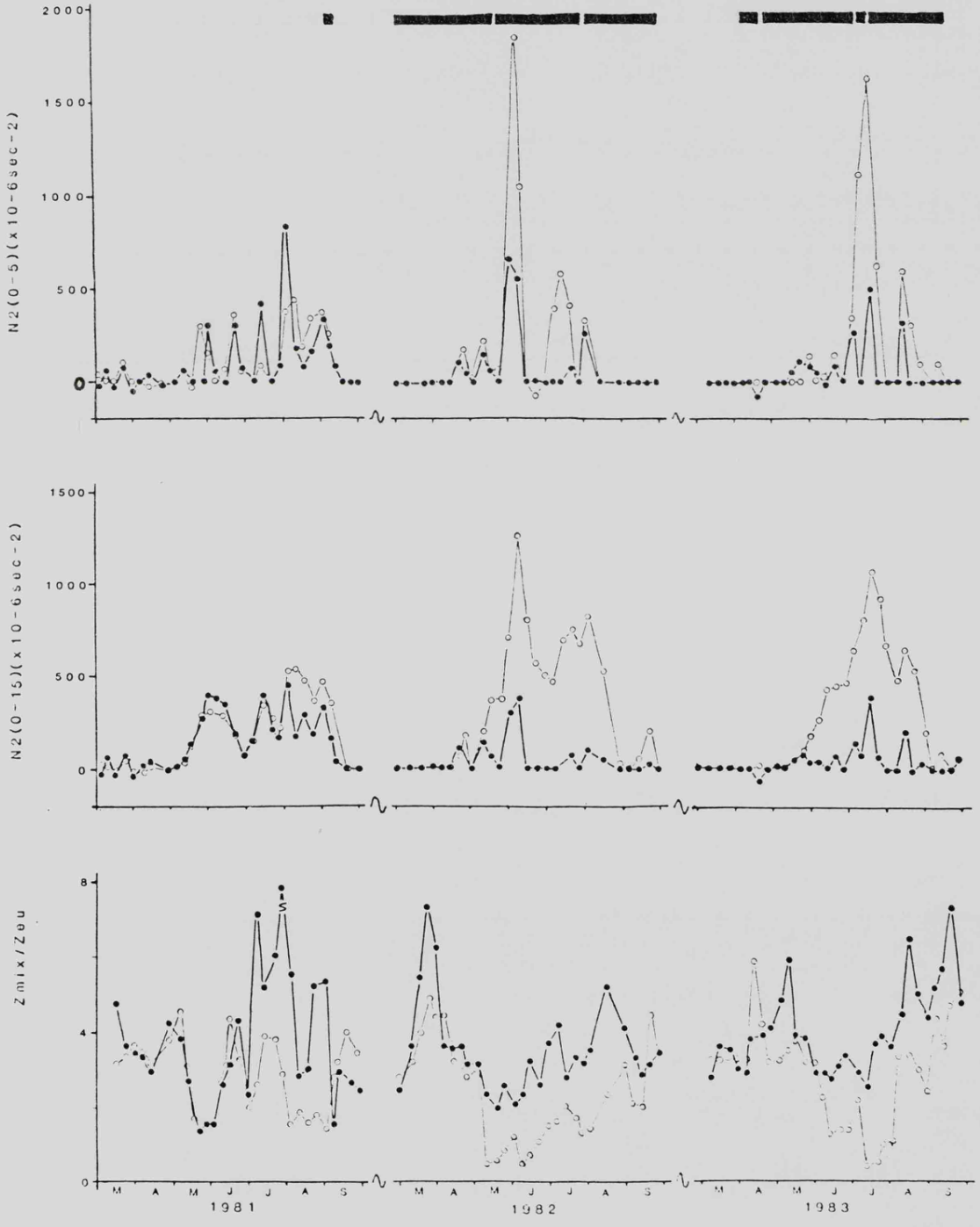


Figure 22. The temporal changes in water column stability, N^2 (0-5) metres and (0-15) metres and the ratio of the mixed depth to the euphotic depth (*Zm:Zeu*) in Staunton Harold (closed circles ●-●) and Foremark (open circles o-o) between March and September in 1981, 1982 and 1983. The solid bar at the top indicates periods of artificial mixing.



Staunton Harold when slight temperature differences were recorded. Generally values of N^2 (0-5) in Staunton Harold were correspondingly lower than those for Foremark.

The values of N^2 (0-15) further emphasise the difference. Low values occured throughout both summers with only small peaks which coincided with much larger peaks in Foremark. The N^2 (0-15) values for Foremark increased in early summer as water temperatures were increasing and remained high until August/September when cooler conditions and stronger winds disrupted the density gradients. Values of N^2 were low throughout the winter months in both reservoirs.

2) *Zm/Zeu.* The ratio of *Zm to Zeu* is shown in Figure 22 for both reservoirs. The whole water column in Staunton Harold was mixed (except for the period between mid-May and mid-June, 1981) and so any changes in the ratio were due to changes in *Zeu.* (Summaries of *Zm, Zeu,* N^2, chlorophyll and vertical attenuation coefficients are given in Appendix 2).

In 1981, there were two peaks in the ratio which correspond to low *Zeu* values. Low *Zeu* values were related to high levels of algal biomass (as chlorophyll a) - see section 3.2.3.5.

The fluctuations of *Zm/Zeu* during 1982 and 1983 in Staunton Harold were all related to oscillations in phytoplankton densities with the exception of the peak in March, 1982. This peak was associated with a low *Zeu* value but chlorophyll levels were not high and the spring diatom peak did not occur until 3-4 weeks later. A smaller peak, in comparison, was also recorded for Foremark at the same time and again this did not appear to be related to high

concentrations of phytoplankton. It is possible that this may have been a result of high turbidity caused either by strong winds or by the input of water from the River Dove.

The fluctuations in the *Zm/Zeu* ratio for Foremark were a result of both changes in *Zm* and *Zeu*. For example in June, 1981 the peak was due to the decreased value of *Zeu* as a result of increased chlorophyll and a shallower *Zm* value resulting from stratification. The peaks early in the year were due mainly to the low *Zeu* values as *Zm* tends to be highest and it was not until June/July that *Zm* started to decrease.

3.2.3 The underwater light climate.

The seasonal variations in the euphotic depth, *Zeu*, secchi depth, vertical attenuation coefficients, ε, (εPAR and the minimum value from the spectral comparison, εMIN) and algal biomass (as chlorophyll a per unit surface area) are shown in Figure 23 for Staunton Harold and Figure 24 for Foremark.

Annual summaries of euphotic depth and Secchi depth data are shown in tables 8 and 9 for Staunton Harold and Foremark respectively. The annual mean *Zeu* values were significantly lower in Staunton Harold (***, paired t-test) whilst the Secchi depth values were not significantly different. This is possibly due to the greater susceptibility to errors in the measurement of Secchi depth as the method is dependent on the observer, time of day, method of observation and on weather conditions (Golterman 1969, Lund and Talling 1957). All but the last factor were kept as constant as possible during this research.

Figure 23. Temporal variations in the euphotic depth, vertical attenuation coefficients and phyotplankton biomass in Staunton Harold between March and September during 1981, 1982 and 1983. The solid bar at the top indicates periods of artificial mixing.

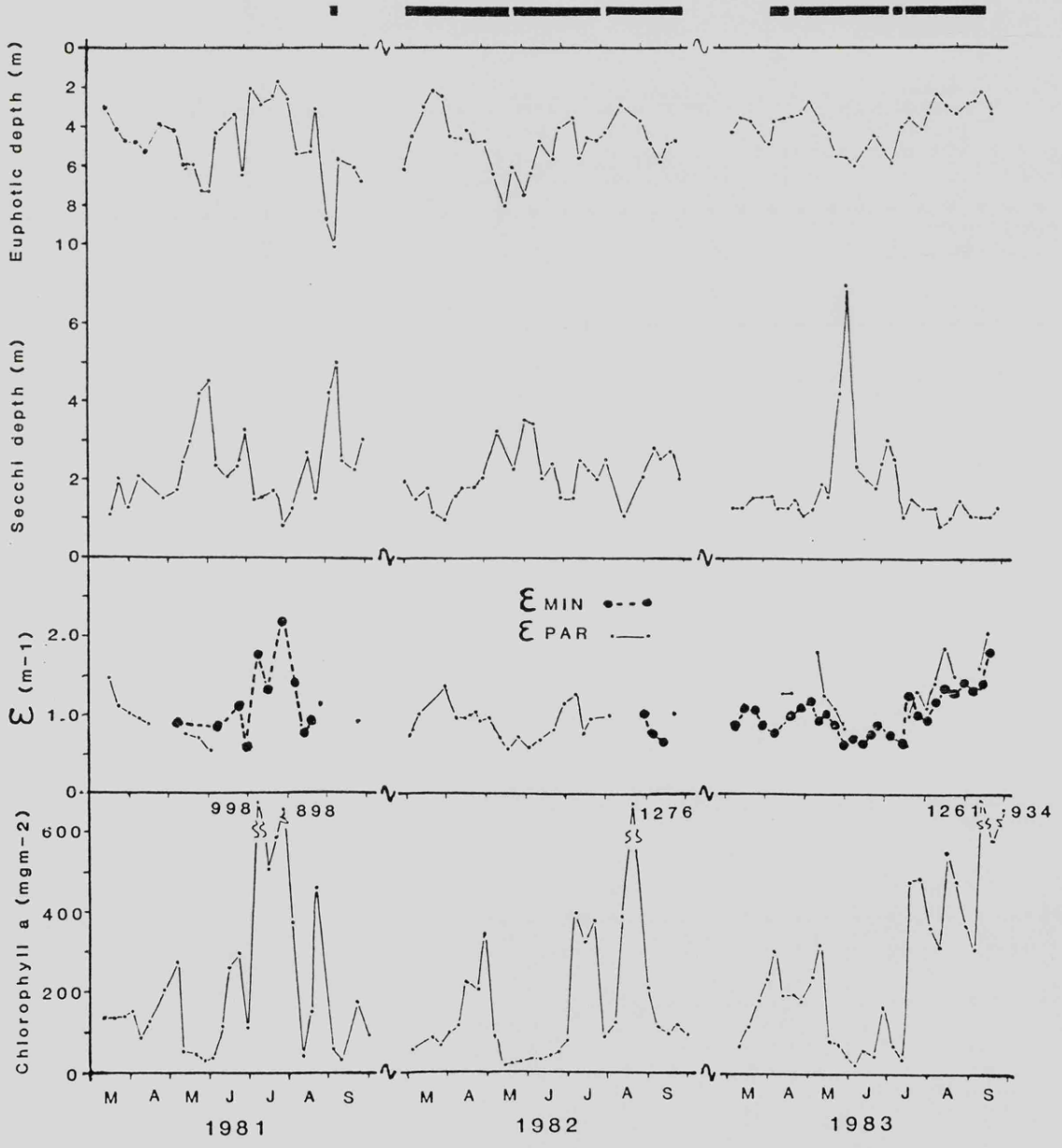


Figure 24. Temporal variations in the euphotic depth, vertical attenuation coefficients and phytoplankton biomass in Foremark between March and September during 1981, 1982 and 1983.

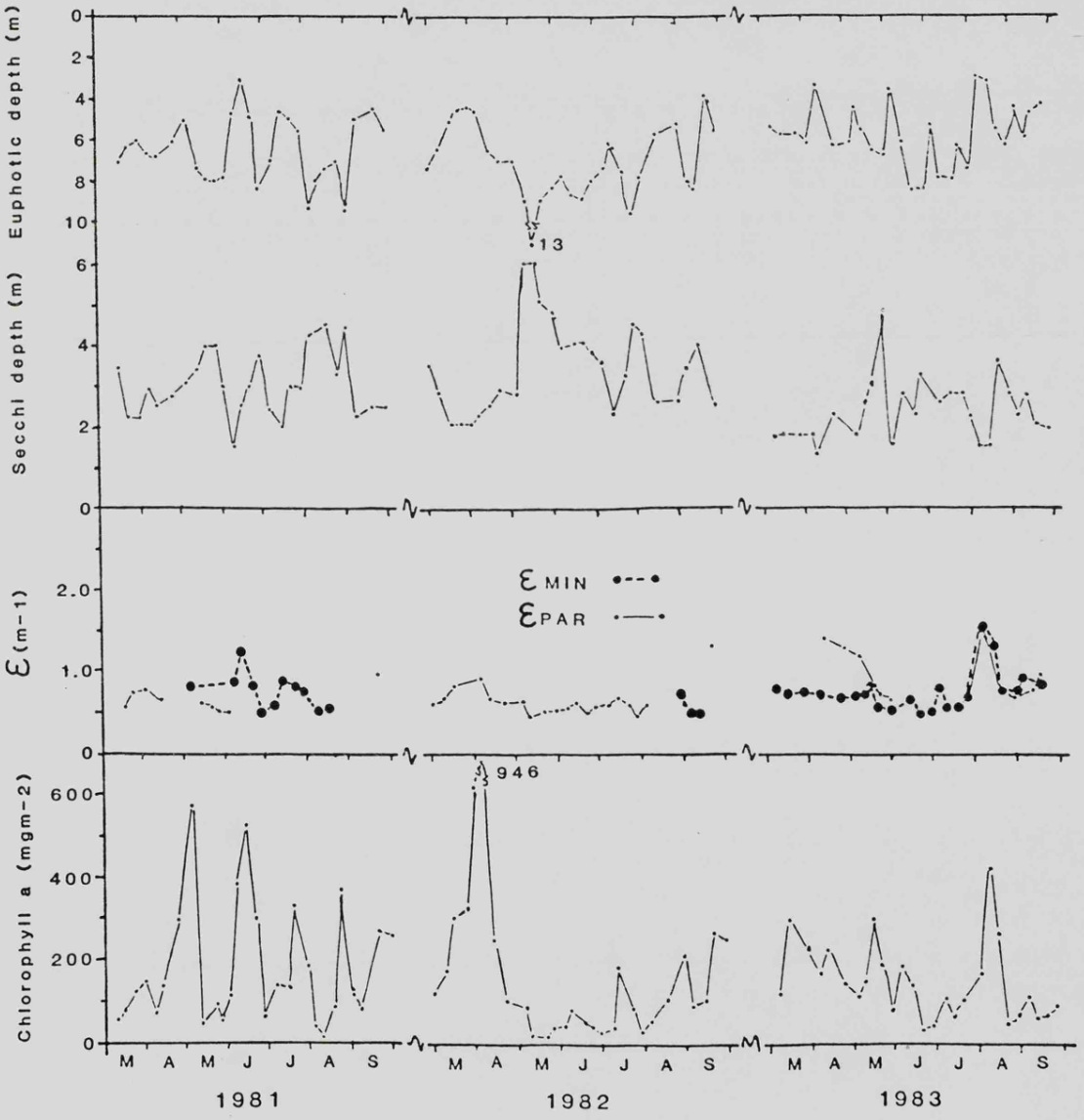


TABLE 8. ANNUAL SUMMARIES OF EUPHOTIC DEPTHS AND SECCHI DEPTHS IN STAUNTON HAROLD.

YEAR	*Zeu*(m)			Secchi depth(m)		
	mean	n	s.e.	mean	n	s.e.
1981	5.13	34	0.33	2.43	33	0.18
1982	4.77	36	0.21	2.10	34	0.10
1983	4.05	36	0.19	1.80	36	0.19
1981-1983	4.64	106	0.15	2.10	103	0.098
	range 1.7 to 10.1			range 0.75 to 7.0		

TABLE 9. ANNUAL SUMMARIES OF EUPHOTIC DEPTHS AND SECCHI DEPTHS IN FOREMARK.

YEAR	*Zeu*(m)			Secchi depth(m)		
	mean	n	s.e.	mean	n	s.e.
1981	6.54	35	0.25	3.09	31	0.14
1982	6.99	36	0.30	3.32	35	0.18
1983	5.77	32	0.26	2.38	30	0.14
1981-1983	6.46	103	0.17	2.95	96	0.098
	range 2.9 to 13.0			range 1.5 to 6.0		

3.2.3.1 Spectral variation of underwater light.

Vertical attenuation coefficients (ε) of blue green and red light were measured at irregular intervals throughout the research. Blue light always had the highest ε values, indicating that it was the attenuated most rapidly. This has also been recorded for many other inland freshwaters (Jewson, 1976; Bindloss, 1976).

There was little difference between the attenuation coefficients of red and green light and the minimum value (εMIN) varied between the two regions (Appendix 2).

The spectral variation of underwater light attenuation found in both Staunton Harold and Foremark reservoirs was typical of productive waters with high concentrations of either algal or inorganic particulate matter (Bindloss, 1976; Ganf, 1974; Jewson, 1977; Jones, 1977b; Kirk, 1983).

3.2.3.2 The relationship between *Zeu* and εMIN.

The seasonal fluctuations in *Zeu* were inversely related to the fluctuations in εPAR and εMIN. Talling (1965, 1971) found that for a wide range of lakes, *Zeu* could be approximated by the relationship $Zeu = b/\varepsilon MIN$ where *b* was a constant with a value of 3.7. From all available data in this study, a comparison of *Zeu* and εMIN gave values of *b* of 3.88 (95% confidence limits 2.56-5.20) for Staunton Harold and 4.22 (95% confidence limits 2.92-5.52) for Foremark as provided by the data in Appendix 2. This allowed *Zeu* to be calculated from εMIN values when εPAR was not measured.

3.2.3.3 The relationship between *Zeu* and Secchi depth.

Variations in Secchi depth showed seasonal trends similar to those of *Zeu*. Regression analyses of *Zeu* versus Secchi depth for Staunton Harold gave the relationship:

$$Zeu = (\text{Secchi depth} - 0.592)/0.553 \qquad (r = 0.89,\ n = 48,***)$$

and for Foremark:

$$Zeu = (\text{Secchi depth} - 0.128)/0.471 \qquad (r = 0.82,\ n = 39,***)$$

3.2.3.4 The relationship between εPAR and εMIN.

There have been very few published reports of the relationship between measured, rather than calculated, values of εPAR and εMIN. Talling (1965) found that εPAR could be approximated by the relationship $\varepsilon PAR = a\varepsilon MIN$ where *a* had a value of 1.33 for a wide range of lakes. In this study it was possible to make a direct estimate of *a* as both εPAR and εMIN were measured. The average value of *a* was 1.18 with a range of 1.09 to 1.29 for Staunton Harold and 1.1 with a range from 0.93 to 1.7 for Foremark. These values are similar to published values which have been calculated from estimated values of εPAR, eg. Ganf (1974) estimated a value of 1.21 for Lake George, Jewson (1977) 1.15 for Lough Neagh and Jones (1977b) 1.2 for Kinnego Bay, Lough Neagh.

3.2.3.5 Factors affecting light attenuation.

There are two major components which affect the attenuation of light underwater; algal and non-algal (inorganic) material. James and Birge (1938) showed that:

$$\varepsilon total = \varepsilon s + \varepsilon q$$

where εs is the attenuation coefficient due to phytoplankton

and εq is the attenuation coefficient due to non-algal material

(a) Algal material. The seasonal changes in chlorophyll a concentration in the water column were synchronised with changes in light attenuation in both reservoirs as shown in Figures 23 and 24.

The relationships between the vertical attenuation coefficients (εPAR) and the mean chlorophyll a concentrations in the euphotic zone for Staunton Harold and Foremark between 1981 and 1983 are shown in Figure 25a and 25b. Both regression lines are significant at the *** level although the significance relies heavily upon the values at high chlorophyll concentrations. The regression equations of εPAR versus mean chlorophyll a for Staunton Harold and Foremark calculated for the individual years are given in Tables 10 and 11.

The self - shading coefficient, εs, (which is equal to the slope of the regression line (Talling 1960)) was variable between years - Table 10 and 11. This was most likely to have been a result of the different species of the phytoplankton community and their physiological states. There is now evidence, both theoretical and practical, that this variablity in the relationship between chlorophyll concentration and light attenuation is believed to be due mainly to cell size (Talling, 1971; Steel, 1972; Kirk, 1975a, b) and pigment content and composition (Steemann-Nielsen *et al.* 1962; Kirk, 1975a, b) and the difficulties of obtaining a reliable coefficient from mixed species populations in the field.

(b) Non-algal material. Light attenuation by non-algal material is indicated by the intercept, εq, of the regression of εPAR versus chlorophyll and the values from Staunton Harold and Foremark are shown in Tables 10 and 11.

Figure 25a. The relationship between the vertical attenuation coefficient, (εPAR), and the mean concentration of chlorophyll a in the euphotic zone of Foremark between 1981 and 1983.

Figure 25b. The relationship between the vertical attenuation coefficient, (εPAR), and the mean concentration of chlorophyll a in the euphotic zone of Staunton Harold between 1981 and 1983. Note change of scale.

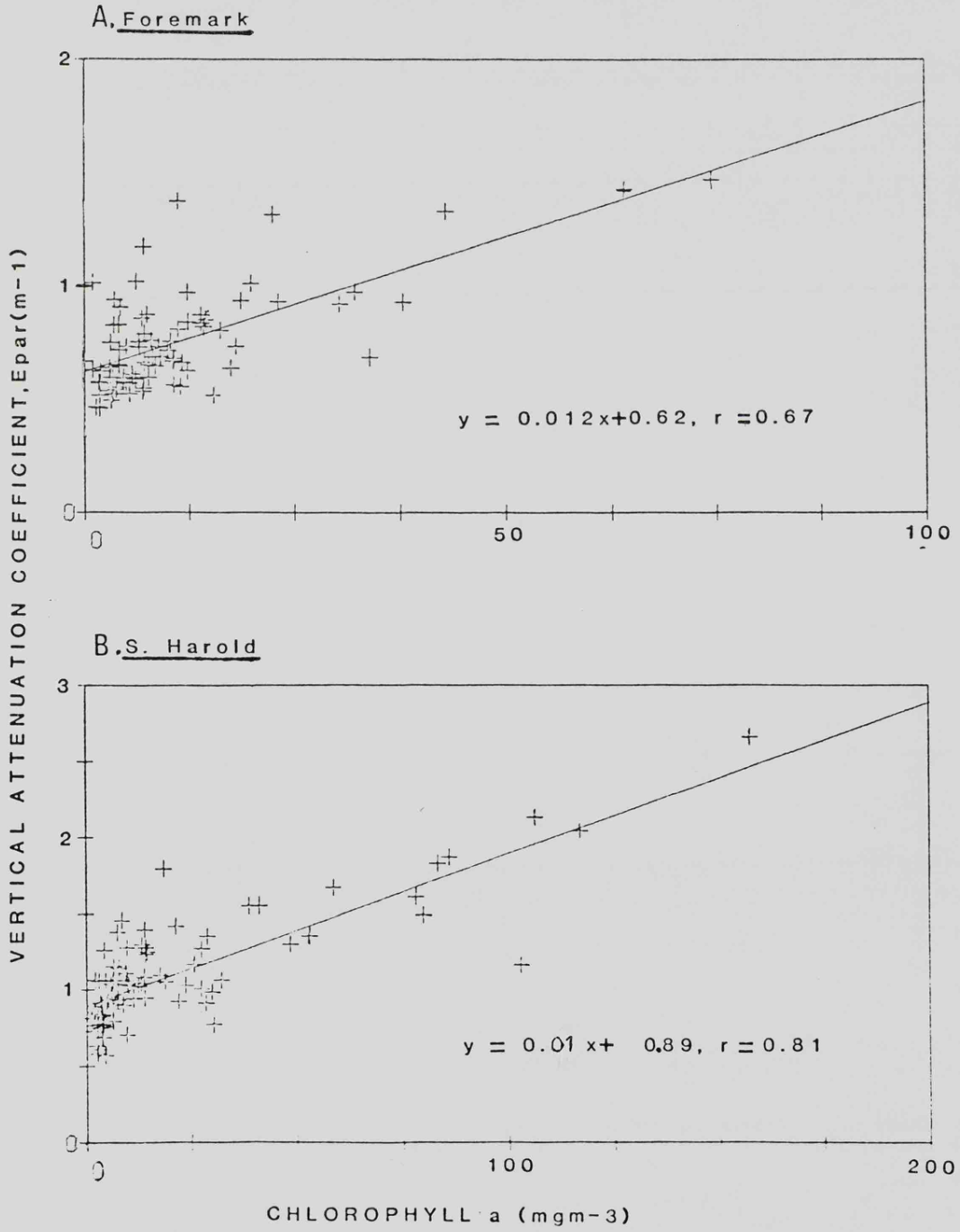


TABLE 10. THE RELATIONSHIP BETWEEN THE ATTENUATION COEFFICIENT (εPAR) AND THE MEAN CONCENTRATION OF CHLOROPHYLL A. IN THE EUPHOTIC ZONE IN STAUNTON HAROLD.

Year	Regression equation	n	r	p
1981	εPAR = 0.011 Chl a. + 0.82	28	0.889	***
1982	εPAR = 0.006 Chl a. + 0.878	27	0.288	NS
1983	εPAR = 0.009 Chl a. + 1.01	30	0.773	***
1981-1983:				
	εPAR = 0.0098 Chl a. + 0.89	86	0.810	***

TABLE 11. THE RELATIONSHIP BETWEEN THE ATTENUATION COEFFICIENT (εPAR) AND THE MEAN CONCENTRATION OF CHLOROPHYLL A. IN THE EUPHOTIC ZONE IN FOREMARK.

Year	Regression equation	n	r	p
1981	εPAR = 0.0125 Chl a. + 0.602	27	0.786	***
1982	εPAR = 0.0121 Chl a. + 0.563	28	0.590	**
1983	εPAR = 0.0105 Chl a. + 0.706	27	0.632	***
1981-1983:				
	εPAR = 0.0119 Chl a. + 0.619	82	0.672	***

The 'background coefficient', εq varied from 0.82 to 1.01 in Staunton Harold and 0.56 to 0.79 in Foremark between 1981, 1982 and 1983.

There are three main components which affect εq:

$$\varepsilon q = \varepsilon w + \varepsilon g + \varepsilon p$$

where εw is the attenuation by the water itself

εg is the attenuation by gilvin substances

εp is the attenuation due to particulate non-algal material (tripton).

In this study, the individual components of εq were not investigated but it was most probable that εp played a major role. εw is usually low in freshwater (Kirk 1983) and the attenuation due to gilvin or yellow substances (which is usually associated with peaty waters with a high concentration of humic acids from plant breakdown) was likely to be low as the River Dove flows through a mainly limestone catchment.

3.2.3.6 The amount of chlorophyll a. in the euphotic zone.

In terms of phytoplankton growth, the maximum chlorophyll concentration in the euphotic zone is of major importance and as mentioned above, it can be high enough to limit growth by self-shading.

Talling (1960 1965) showed that the theoretical maximum chlorophyll concentration (ΣB_{max}. mgm^{-2}) could be calculated from the coefficient, εs. The values of εs for Staunton Harold were 0.011, 0.006 and 0.009 and for Foremark they were 0.0125, 0.0121 and 0.105 in 1981, 1982 and 1983 respectively. If the lower limit of the euphotic zone is defined as $b/\varepsilon par$, the upper limit of chlorophyll (ΣB_{max} mgm^{-2}) below unit area of the euphotic zone is equal to $b/\varepsilon s$ (Talling 1965). Using the εs values given, the theoretical limits for Staunton Harold were 353, 647 and 431 mg chlorophyll m^{-2} in 1981, 1982 and 1983 respectively. For Foremark, the limits were slightly lower at 338, 349 and 402 mgm^{-2} in 1981, 1982 and 1983. The observed concentrations of chlorophyll in the euphotic zone ranged from 8 to 324 mgm^{-2} in Staunton Harold and from 9 to 199 mgm^{-2} in Foremark (Appendix 2).

These εs values are lower than that estimated by Talling (1960). He estimated an average εs value of 0.02. Using Tallings' higher value would suggest that the theoretical maximum chlorophyll concentration in the euphotic zone was 194 and 211 mgm^{-2}, respectively. Thus the upper limit in Staunton Harold would have been exceeded on ten occasions and the phytoplankton would have been completely self-shaded. I believe that on certain occasions, usually when phytoplankton biomass was very high, that the populations were self-shaded and that if the εs values could have been calculated for the dominant species at these times then they would reveal this.

3.3 CHEMICAL CHARACTERISTICS OF THE RESERVOIRS.

3.3.1 The seasonal fluctuations of nutrients.

The concentrations of ortho-phosphate, nitrate and dissolved silica in both reservoirs fluctuated annually. The temporal changes in surface samples and those at the bottom (if different to the surface) between March and September are shown in Figure 26 for Staunton Harold and Figure 27 for Foremark. High concentrations were generally found in the winter months which declined to low values in late summer. This was followed by replenishment in the autumn to high winter concentrations.

Nutrient budgets were not calculated because flow data and nutrient concentrations for the reservoir inflow streams were not measured at regular intervals. Total phosphorus (TP) in reservoir samples were not determined by Severn Trent Water Authority and the effort involved in the extra analyses was considered to be too high and beyond the scope of the main research area. However, in 1977 and 1978, Severn Trent Water Authority had measured total phosphorus (TP) and ortho-phosphate (PO_4) in both reservoirs. Although the percentage ortho-phosphate component of total phosphorus varied throughout the annual cycle, regression analyses allowed TP to be estimated (from PO_4) which could then be used in the determination of trophic state. The regression analyses gave the following equations:

Staunton Harold

$$PO_4 = 0.43\ TP + 0.041 \quad (r = 0.76, n = 126, ***)$$

and for Foremark

$$PO_4 = 0.32\ TP + 0.087 \quad (r = 0.62, n = 140, ***)$$

Figure 26. The temporal fluctuations in the N:P ratio, nitrate, ortho-phosphate and silica concentrations in Staunton Harold between March and September during 1981, 1982 and 1983. (closed circles ●-● represent surface values whilst open circles o-o represent the bottom (14 m) values, if different to the surface). The solid bar at the top indicates periods of artificial mixing.

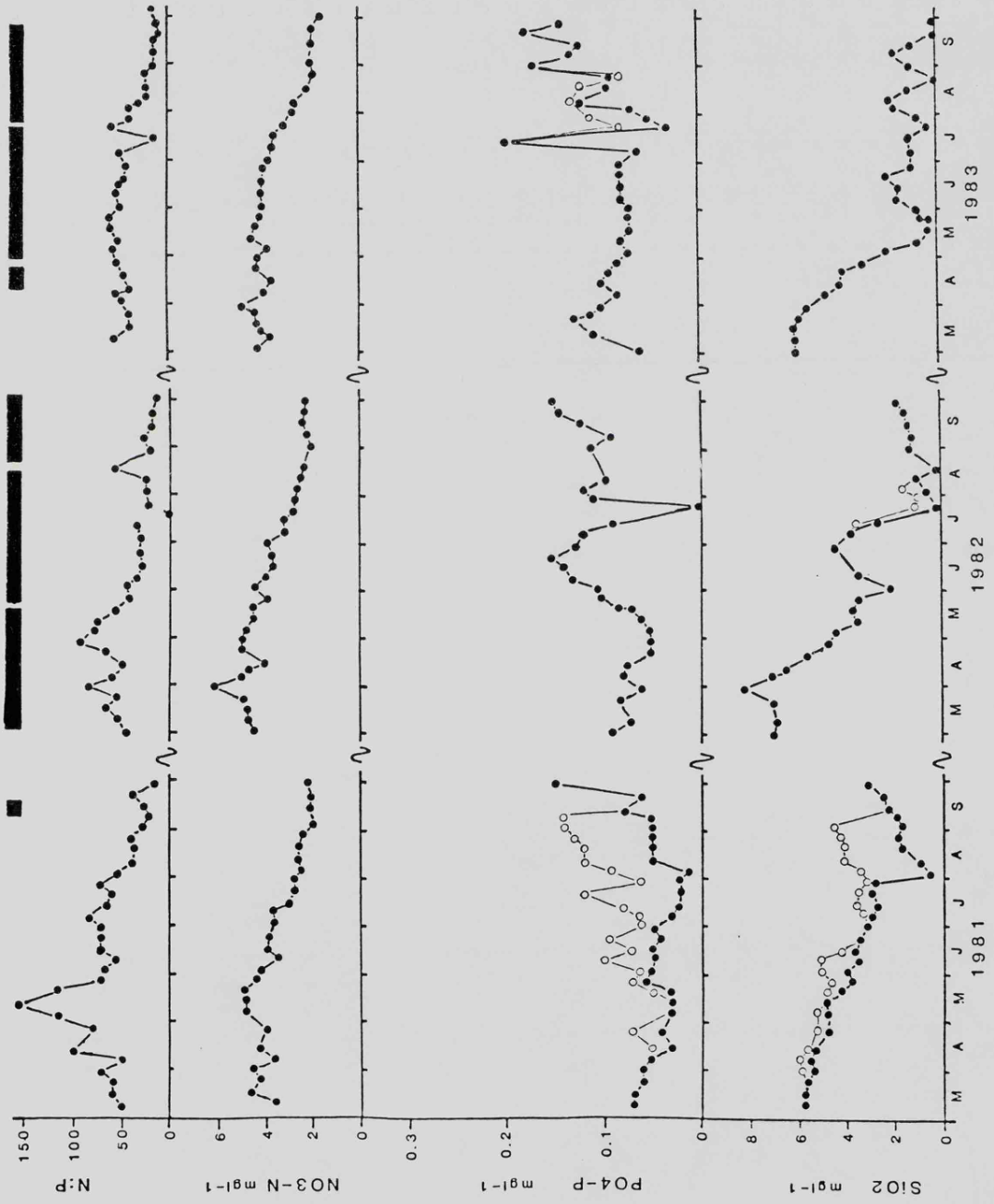
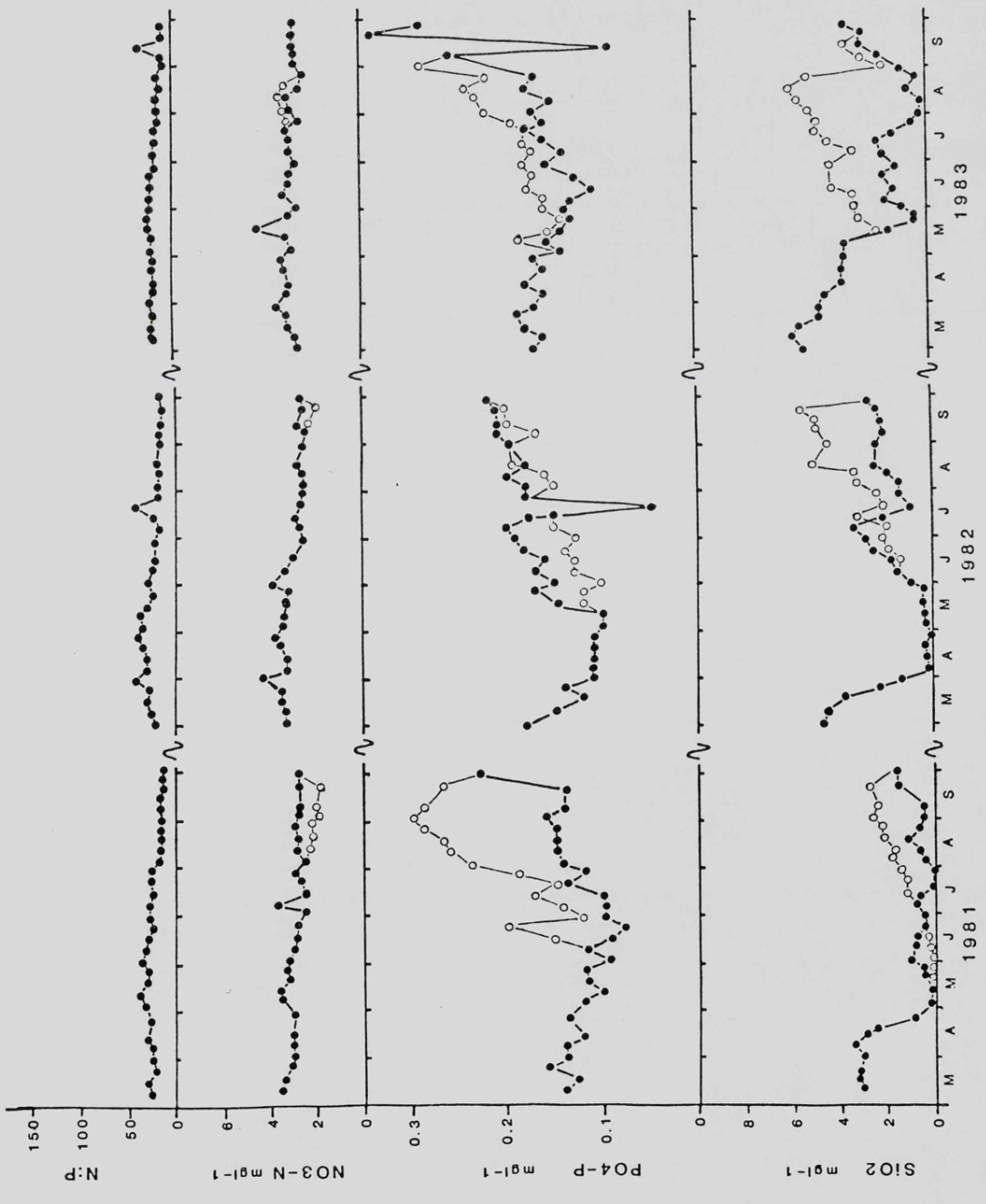


Figure 27. The temporal fluctuations in the N:P ratio, nitrate, ortho-phosphate and silica concentrations in Foremark between March and September during 1981, 1982 and 1983. (closed circles ●-● represent surface values whilst open circles o-o represent bottom (20 m) values, if different to the surface).



3.3.1.1 Nitrate and ammonia.

Nitrate concentrations in Staunton Harold between March 1981 and June 1983 ranged from 1.7 to 6.3 mgl^{-1} with a mean of 3.6 (Table 12). The levels in Foremark were lower with a range from 1.9 to 4.3 with a mean of 3.0 mgl^{-1}. This difference is believed to be due to the larger catchment area of Staunton Harold (2600 ha - Staunton Harold and 295 ha - Foremark) and thus the greater importance of local drainage which is predominantly from arable farmland.

Nitrate reduction probably occured in both reservoirs during all three summers of the study, as shown by the decline in concentration (Figures 26 and 27). Youngman (1975) found that approximately 50% of nitrate pumped into Farmoor reservoir (Oxon) was lost during storage. This was a result of uptake by phytoplankton, bacterial and fungal growth which is termed assimilatory nitrate reduction. The nitrate incorporated into the phytoplankton, bacterial and fungal cells eventually ends up in the sediments where denitrifying bacteria use nitrate instead of oxygen as an electron acceptor at low oxygen concentrations. This process is called dissimilatory nitrate reduction. Nitrate reduction is a continuous process (Hutchinson 1957) but is most rapid in the summer months when uptake by bacteria and phytoplankton in the epilimnion exceed the rate of external supply (Reynolds 1984b) and oxygen concentrations in the hypolimnion are low (O'Neill and Holding 1975).

Anaerobic conditions, which favour denitrification, were present in Staunton Harold even in the years when mixing was taking place. The perforated pipe situated in Staunton Harold was suspended aprroximately 0.3 metres above the bottom (see Chapter 2) and it was noted that on lowering the dissolved oxygen probe that as soon as it touched the sediment, the dissolved oxygen fell rapidly. This indicates that the pipe did not aerate the reservoir to the

TABLE 12. SUMMARY OF THE CHEMICAL DATA FOR STAUNTON HAROLD AND FOREMARK RESERVOIRS, MARCH 1981 TO JUNE 1983

		Maximum	Minimum	Mean
Staunton Harold.				
Alkalinity	$mgCaCO_3l^{-1}$	166	104	146
pH		8.8	7.0	8.2
Conductivity	µS	571	437	519
NH_4-N	mgl^{-1}	0.6	<0.01	0.11
NO_3-N	mgl^{-1}	6.3	1.7	3.6
PO_4-P	mgl^{-1}	0.22	<0.01	0.08
SiO_2	mgl^{-1}	8.1	0.08	3.5
Fe	mgl^{-1}	0.58	0.02	0.13
Mn	mgl^{-1}	0.38	<0.01	0.04
Foremark.				
Alkalinity	$mgCaCO_3l^{-1}$	178	146	161
pH		8.8	7.5	8.3
Conductivity	µS	575	463	533
NH_4-N	mgl^{-1}	0.39	<0.01	0.05
NO_3-N	mgl^{-1}	4.3	1.9	3.02
PO_4-P	mgl^{-1}	0.31	0.05	0.16
SiO_2	mgl^{-1}	6.9	<0.1	2.0
Fe	mgl^{-1}	0.25	<0.01	0.06
Mn	mgl^{-1}	0.71	<0.01	0.04

bottom but left an anaerobic zone just above the sediment. Anon (1963) and O'Neill and Holding (1975) have shown nitrate reduction at the sediment/water interface can take place even when the overlying water is saturated with oxygen.

The rate of decline of nitrate reduction was greater in Staunton Harold, (Figure 26) when compared to the rate in Foremark (Figure 27) but it does not appear to have been affected by continuous mixing in 1982 and 1983. The increased rate of nitrate reduction observed in Staunton Harold was most probably due to the increased temperatures at the sediment surface which would have allowed increased rates of denitrification. In Staunton Harold the temperatures at the sediment/water interface (Figures 8, 13 and 14) were generally about the same as those at the surface due to natural mixing in 1981 and artificial mixing in 1982 and 1983. During the June to September period of all three years the temperature rarely dropped below 15°C. However in Foremark (Figure 4, 17 and 18), stratification developed in all three years and the temperature at the sediment surface between June and September did not rise above 10°C. In a review of denitrification, Knowles (1982) reported that in published work on aquatic environments there was suprisingly little variation in the rate of nitrate reduction with temperature. However O'Neill and Holding (1975) showed a stong temperature dependence under laborarory conditions with cores at 4°C showing nitrate reduction and ammonia appearance at about 20% of the rates recorded at 19°C.

Nitrate concentrations showed little depth variation in either of the reservoirs and this was most likely to be a result of both nitrate reduction processes - nitrate in the surface waters was used by phytoplankton, bacteria and fungi whilst in the bottom layers near the sediments was reduced by denitrifying bacteria.

Ammonia concentrations were low, ranging from <0.01 to 0.6 mgl^{-1} (mean 0.11) in Staunton Harold and from <0.01 to 0.39 mgl^{-1} (mean 0.05) in Foremark (Table 12). In Staunton Harold during 1981 and Foremark during 1981 and 1983, higher values were recorded in the hypolimnion (Figures 28 and 29). These increases can be seen to coincide with decreasing nitrate levels (Figures 26 and 27) which indicates that denitrification was probably the main process.

Artificial mixing in Staunton Harold during 1982 and 1983 eliminated the build up of ammonia in the lower layers and maintained an even distribution with depth.

Variations in ammonia levels have been found to be the result of direct assimilation by some phytoplankton and by decomposition in or near the sediments (Hutchinson 1957). Ammonia is also reported to decrease in the epilimnion and increase in the lower layers of the hypolimnion of productive lakes as the summer progresses (Hutchinson 1957). Increases in the hypolimnion are a result of denitrification at the sediment/water interface and the decomposition of sedimenting plankton and faeces.

3.3.1.2 Ortho-phosphate.

Ortho-phosphate concentrations ranged from below detectable limits (<0.01 mgl^{-1}) to 0.22 mgl^{-1} with a mean of 0.08 in Staunton Harold and from 0.05 to 0.31 mgl^{-1} with a mean of 0.16 in Foremark (Table 12). It was most probable that the higher levels in Foremark were due to a higher rate of re-solution from the anaerobic sediments. Staunton Harold had a median depth (50% volume) of 4.95 m whereas in Foremark it was 7.95 m and the mean depths were 7.9 and 14.3 m respectively. As the surface areas were approximately the same it was apparent that the surface area of the sediment bottom in Foremark which could become anaerobic during the summer months was higher than in Staunton Harold.

Figure 28. The temporal variations in alkalinity, pH, conductivity, ammonia, manganese and iron between March and September during 1981, 1982 and 1983 in Staunton Harold. (Closed circles ●-● represent surface values and open circles o-o represent bottom (14 m) values if different to the surface). The solid bar at the top indicates periods of artificial mixing.

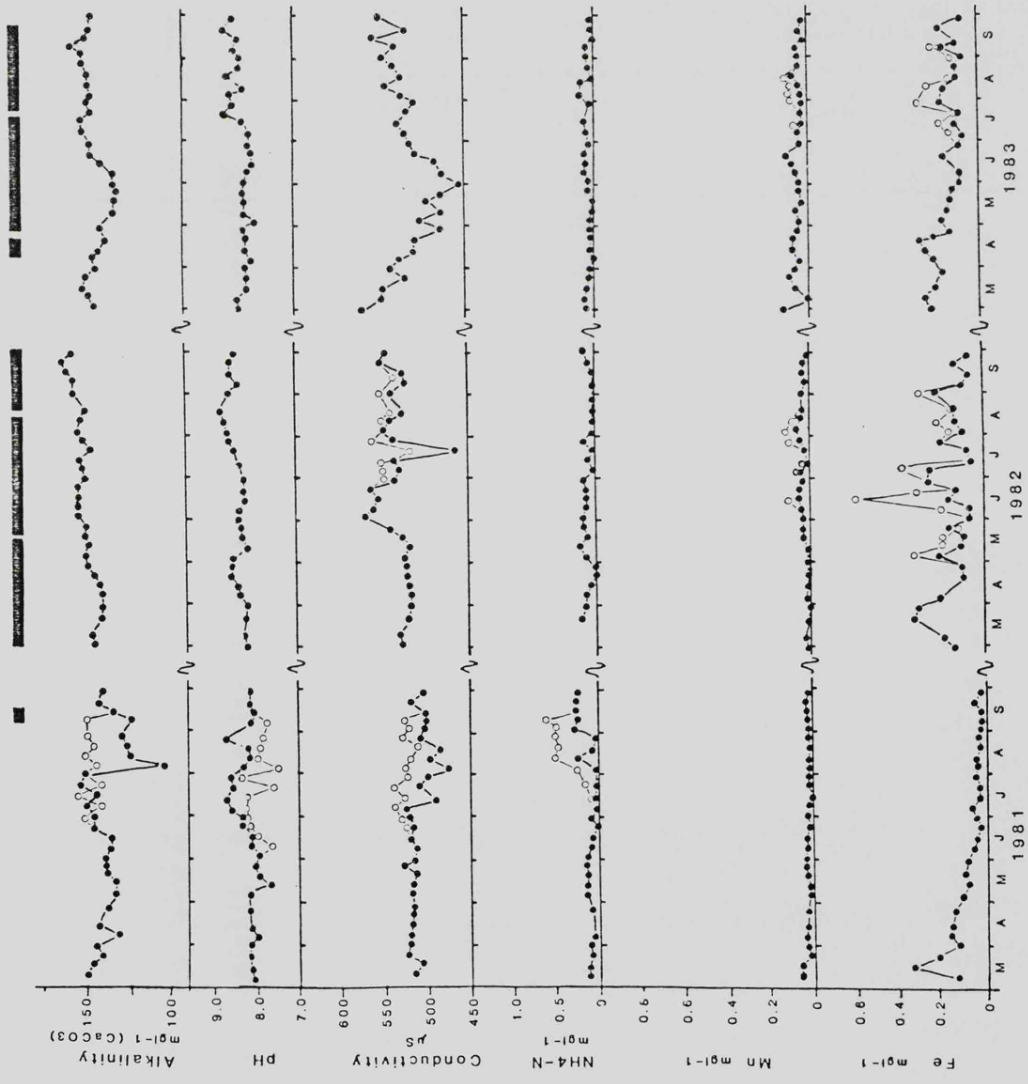
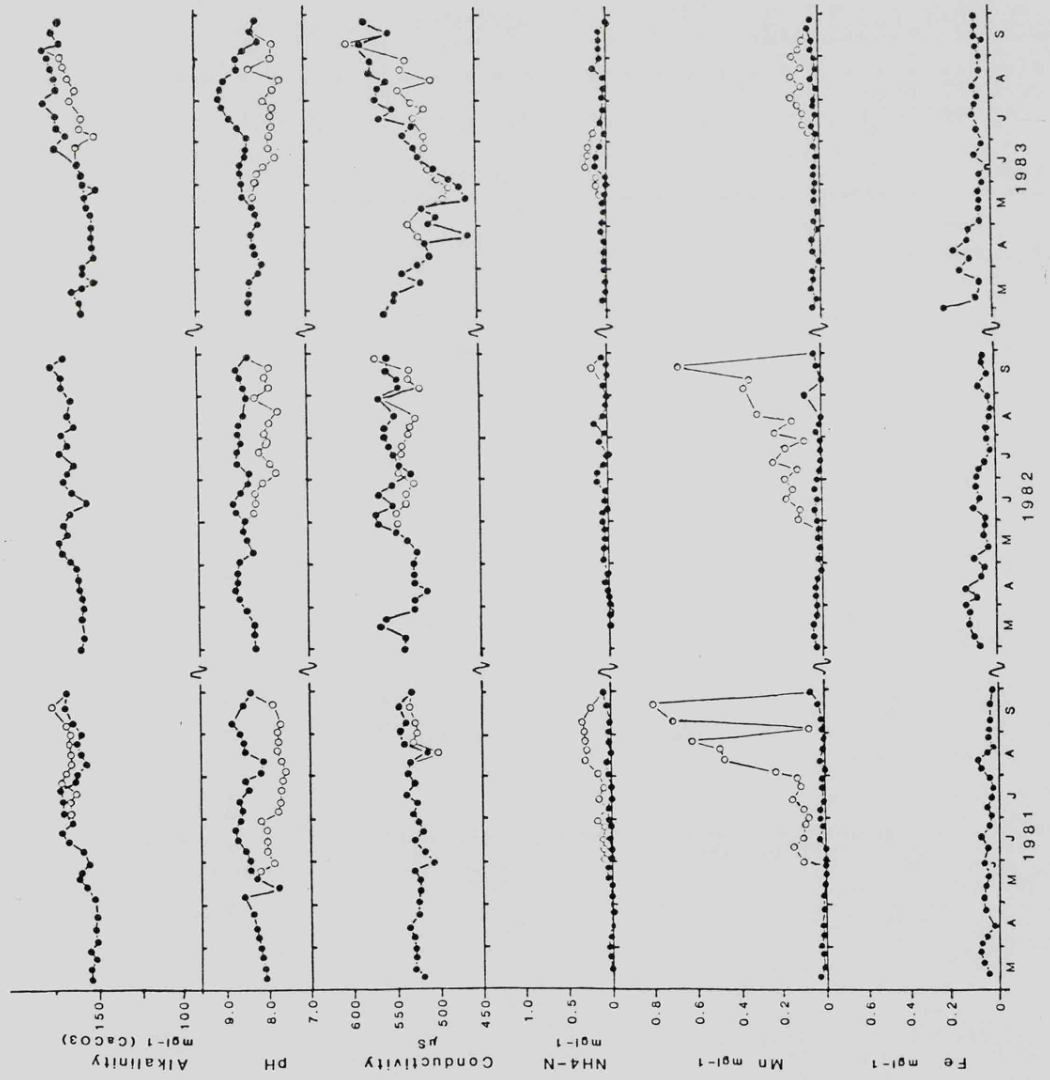


Figure 29. The temporal variations in alkalinity, pH, conductivity, ammonia, manganese and iron between March and September during 1981, 1982 and 1983 in Foremark. (Closed circles ●-● represent surface values and open circles o-o represent bottom (20 m) values if different to the surface).



The larger surface area would have allowed a greater amount of ortho-phosphate release from the sediments under anaerobic conditions and this could have led to the higher concentrations overall.

Ortho-phosphate did not show a clear annual pattern as nitrate did because large fluctuations were superimposed on the general pattern. The cycle of phosphorus in lakes is very complex and hard to measure (Hutchinson 1957) as turnover times at some stages of the cycle are very short. Fluctuations in ortho-phosphate concentrations are due largely to biological activity, mainly phytoplankton growth (Hutchinson 1957, Lack and Johnson 1983, Reynolds 1984b) and are discussed in the next chapter.

Sudden, large decreases in phosphate levels as observed in Staunton Harold and Foremark in mid-July, 1982 cannot be accounted for entirely by phytoplankton growth. These crashes were found to coincide with decreases in iron concentrations (see Appendix 8) and it is possible that the ortho -phosphate precipitated out as an iron phosphate compound. Golterman (1976) stated that phosphate can precipitate out as iron or calcium phosphate. Stumm (1973) and Lack and Johnson (1983) found that under increased pH conditions, phosphate bonds onto calcium and forms a calcium phosphate compound known as hydroxyapatite which then precipitates out. Lack and Johnson (1983) believed this to be caused by increased phytoplankton productivity. In these reservoirs it was unlikely that this was the cause of the crash as pH values and phytoplankton activity were not enhanced.

In Staunton Harold during 1981 and Foremark in 1981 and 1983, clinograde distributions (ie. increased levels in the anaerobic hypolimnion) were observed. Hutchinson (1957) states that this is the most common depth distribution for ortho-phosphate in productive lakes. This is due partly to the decomposition of sinking plankton, but mainly from the release of

ortho-phosphate at the sediment/water interface by reduction under anaerobic conditions (Mortimer 1942).

An unusual distribution of phosphate was found in Foremark throughout most of the summer of 1982. The phosphate concentrations increased with depth to a maximum value at 8 metres during June, the maximum then moved to approximately 14 metres from July to mid August. Below these maxima, concentrations declined again with depth. The most likely explanation for this continued inverse pattern is that water being pumped from the River Dove, which had high ortho-phosphate concentrations, was not being mixed into the reservoir but was kept in the epilimnion due to the density gradients in the metalimnetic layer. It can be seen in Figure 17, which shows the distribution of isotherms in Foremark, that during June the thermocline lay around 8 metres deepening to 14 in July and 16 metres in August.

The effect of artificial mixing on ortho-phosphate distribution is illustrated by the mixing episode in September, 1981 when ortho-phosphate became evenly distributed with depth after three days of continuous mixing.

In Staunton Harold when continuous artificial mixing took place during 1982 and 1983, there was very little increase in the ortho-phosphate levels at the bottom. It was noted, as stated in section 3.3.1.1, that the sediments were anaerobic and so phosphate release from the sediments could have continued as normal. The even vertical distribution of ortho-phosphate must therefore have been a result of artificial mixing. The phosphate once released from the sediments was mixed into the water column and available to phytoplankton. It is also most probable that the rate of release from the sediments was increased in the mixed reservoir due to increased temperatures (see section above). Hutchinson (1957) also found that phosphate release was enhanced at higher temperatures in Lindsley Pond, Conneticut.

In all years natural autumnal mixing resulted in the increase of phosphate throughout the whole reservoir as aerobic conditions allowed the release of ortho-phosphate from ferric phosphate (Hutchinson 1957).

3.3.1.3 N:P ratios.

The N:P ratios for Staunton Harold and Foremark between March and September in the three years of study are shown in Figures 26 and 27. N:P ratios ranged from <10 to 157 in Staunton Harold with a mean of 45 and from 9 to 36 with a mean of 19.5 in Foremark. The lower values in Foremark were a result firstly of the higher ortho-phosphate levels and secondly the lower nitrate concentrations.

The nitrate and ortho-phosphate concentrations remained at levels which were not considered to be limiting. Lund (1950) noted that phosphate was limiting for *Asterionella formosa* at levels less than 1 μgl^{-1}. In Staunton Harold the values were up to 220 times greater than this value and it seems unlikely, with the exception of the short period in 1982 when ortho-phosphate levels fell to below 1 μgl^{-1}, that phosphate was limiting. In Foremark the levels were 50 to 310 times greater and so ortho-phosphate as a limiting nutrient seemed unlikely. Lund (1950) also found that *Asterionella* could utilise nitrate at concentrations below 0.1 mgl^{-1} and as the levels were 17 to 63 and 19 to 43 times higher in Staunton Harold and Foremark respectively, it is unlikely that nitrate limited phytoplankton growth.

Work carried out on the interaction of nitrogen and phosphorus has led to the concept that interspecific competition with varying ratios may play an

important part in the composition and succession of phytoplankton (Kilham and Kilham 1980). Rhee (1978) and Rhee and Gotham (1980) have shown that there are different optimum N:P ratios for Chlorophyceae and Cyanobacteria and so these will influence the competition between these groups. Reynolds (1984b) states that the extent to which N:P ratios affect phytoplankton communities is yet to be resolved. The effects of N:P ratios on the phytoplankton community and its periodicity in relation to this research will be discussed in the next chapter.

3.3.1.4 Silica.

Silica (SiO_2) levels ranged from 0.08 to 8.1 mgl^{-1} with a mean of 3.5 and from <0.1 to 6.9 mgl^{-1} with a mean of 2.0 in Staunton Harold and Foremark respectively. The fluctuations in silica between March and September in 1981, 1982 and 1983 are shown in Figure 26 for Staunton Harold and Figure 27 for Foremark. The higher winter values in Staunton Harold were possibly due to the greater maturity of the reservoir and the build up of the silica 'pool' from the catchment soils and the recycling of diatom frustules.

Large fluctuations of silica concentrations occured in both reservoirs during all three years of the study with high values in the winter and during mixing events but decreasing, sometimes to undetectable levels (<0.1 mgl^{-1}), as the summer progressed.

The increases in silica were a result of replenishment from inflow water and internal recycling. The effect of artificial destratification on silica levels in September 1981 showed that within three days of mixing there was an even distribution with depth. In 1982 and 1983, artificial mixing maintained an even depth distribution whilst in Foremark, clinograde distributions developed during the summer months.

The decreases in silica were due to biologocal uptake. Silica is required by the Bacillariophyta (diatoms) to build cell walls (frustules). Diatoms do not have the ability to take up more silicic acid than is required for the next cell division (Lund 1965). Lund's classical work (1950, 1965) on the seasonal periodicity of *Asterionella in* Windemere showed that the population maxima of this diatom was found consistently to coincide with the depletion of silica to a level of approximately 0.5 mgl^{-1}. Concentrations below this level were recorded in both reservoirs, often during the vernal period (see Chapter 4).

3.3.2 The seasonal fluctuations of selected chemical characteristics.

The maximum, minimum and mean values of alkalinity, pH, conductivity, manganese (Mn) and iron (Fe) during the study period for each reservoir are given in Table 12. The fluctuations in these parameters between March and September in all three years are shown in Figure 28 for Staunton Harold and 29 for Foremark.

3.3.2.1 Alkalinity.

Alkalinities, measured as $CaCO_3$, were relatively high ranging from 104 to 166 mgl^{-1} in Staunton Harold and from 146 to 178 mgl^{-1} in Foremark. Fluctuations in both reservoirs were small except during 1981 in Staunton Harold and Foremark during 1981 and 1983. The effect of artificial mixing in September, 1981 and in 1982 and 1983 appears to have maintained an even distribution of alkalinity with depth.

3.3.2.2 pH.

The pH values had a mean of 8.2 with a range of 7.0 to 8.8 in Staunton

Harold and a mean of 8.3 with a range from 7.5 to 8.8 in Foremark during the study period. The fluctuations in both reservoirs were generally small increasing in late summer as a result of phytoplankton production. Clinograde distributions of pH were recorded in Staunton Harold in 1981 and Foremark in all three years. Artificial mixing during 1982 and 1983 eliminated this clinograde distribution and values were similar throughout the depth of the water column.

3.3.2.3 Conductivity.

Conductivity ranged from 437 to 571 µS (mean 519) and from 463 to 575 µS (mean 533) in Staunton Harold and Foremark respectively which indicates that both reservoirs were moderately high in their total ion content. In Staunton Harold during 1981 and part of 1982, conductivity showed a clinograde distribution which according to Hutchinson (1957) are usually reported during stratified periods. An even depth distribution was recorded during the remainder of the study. In Foremark an inverse relationship was noted in all three years and this is further evidence to support the hypothesis that inflow water from the River Dove (with higher ion concentrations than the reservoir) was remaining in the epilimnion (see section 3.3.1.2).

3.3.2.4 Manganese and Iron.

The behaviour of iron and manganese in lakes are very similar (Hutchinson 1957, Mortimer 1942) and so they will be considered together.

Manganese concentrations fluctuated between <0.01 and 0.38 mgl^{-1} (mean 0.04) in Staunton Harold and <0.01 to 0.71 mgl^{-1} (mean 0.04) in Foremark. Iron levels varied between 0.02 and 0.58 mgl^{-1} (mean 0.13) in Staunton Harold and

<0.01 and 0.25 mgl^{-1} (mean 0.06) in Foremark.

In Staunton Harold during artificial mixing, iron and manganese concentrations were found to be evenly distributed with depth except for short periods in 1982 and 1983. It was most likely that iron and manganese continued to be released from the sediments as an anaerobic layer existed at the sediment/water interface (see section 3.3.1.1). The released iron and manganese would then be mixed into the whole water column.

Iron levels fluctuated in Foremark on a small scale and no build up occurred in the hypolimnion even though the water was anaerobic. Manganese levels, however, showed a large increase in the hypolimnion during 1981 and 1982 and to a lesser extent in 1983. This presumably was a result of manganese release from the sediments. At the overturn the high concentration of manganeses in the hypolimnion was mixed with the epilimnetic water and the overall concentration increased.

The variations of iron levels were greater in Staunton Harold than Foremark and this was attributable to two factors; firstly, release from the sediments and subsequent mixing into the whole water column. Secondly, sludge from the treatment process at Melbourne treatment works, which has a very high iron concentration was left to sediment in lagoons. The lagoons often overflowed and water, with high iron levels entered the reservoir on the eastern shore. When the prevailing winds were westerly, the sediments on this side of the reservoir were disturbed and iron was mixed into the water. For example, the peak of iron in early May, 1982 followed a period of three days when the wind was south westerly at a speed of 5-10 ms^{-1}. The very large peak of 0.58 mgl^{-1} in mid -June also followed a period of over a week with south westerly to westerly winds (4-8 ms^{-1}). Again in September of the same year, the peak of iron followed a four day period with average wind speeds of 7.5 ms^{-1} from the

south west. Observations of this process were made during boat surveys.

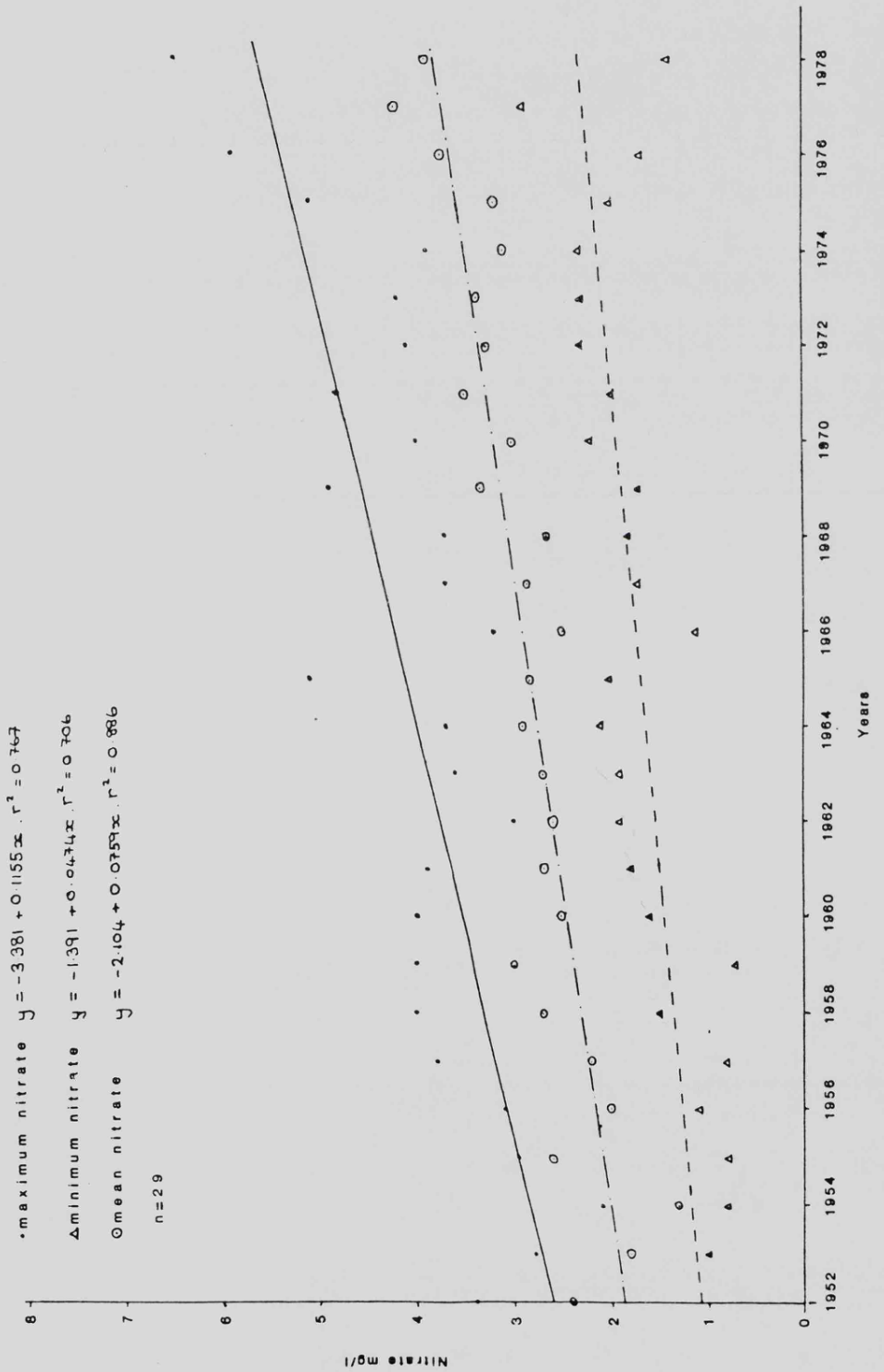
The build up of iron and manganese in the hypolimnion can create severe problems in water management (Brierley 1985). Increases during stratified periods result from increased redox potentials as the water becomes anaerobic (Mortimer 1942). Mortimer's study on Esthwaite in the Lake District showed conclusively that the changes in iron and manganese paralleled the changes in redox potential.

3.4 THE TROPHIC STATE OF THE RESERVOIRS.

The terms oligotrophic, mesotrophic and eutrophic were established by Naumann (1919). This terminology is currently used to describe the fertility of water bodies from the oligotrophic state which is infertile through the mesotrophic to fertile water bodies which are described as being in a eutrophic state. These categories have been extended (OECD 1982) to include ultra -oligotrophic and hypertrophic.

Many water bodies around the world, especially in industrialised countries, have become more fertile over the last few decades. This has resulted mainly from human activities which increase the input of plant nutrients into water bodies. The process is termed 'cultural eutrophication'. The rise in nitrate concentrations of freshwater as a result of the increased use of fertilisers can be illustrated by Figure 30 which shows the changes of nitrate levels in the River Dove during the period 1952 to 1978. Despite year to year oscillations which have not been investigated further, regression analyses confirms that maximum, minimum and mean concentrations have all increased since 1952. Ortho-phosphate levels had not been recorded over this period but the mean and maximum values for 1983 were 250 and 910 mgm^{-3} respectively. These may be compared with a mean concentration of 650 and a maximum of 1560 mgm^{-3}

Figure 30. Changes in the maximum, minimum and mean River Dove nitrate concentrations between 1952 and 1978.



ortho-phosphate in the River Thames which is considered to be hypertrophic (Lack and Johnson 1983).

Increases in plant nutrients usually lead to higher phytoplankton standing crops (Reynolds 1984, OECD 1982). The primary role of phosphorus, and to a lesser extent nitrogen, in eutrophication were realised at an early stage in these studies (Sawyer 1947).

The purpose of the OECD study was to collect together a large amount of data from a wide range of water bodies so that the relationships pertinent to the eutrophication problem could be evaluated. As a result, the study developed an 'open boundary system' which took into account the uncertainty of categorising a lake into a given trophic state. This system enables prediction with an estimate of probablity.

The trophic states of Staunton Harold and Foremark have been evaluated using the open boundary system. Annual mean values of total phosphorus, mean and maximum chlorophyll a and mean and minimum Secchi depths for the three years of study are presented in Table 13a for Staunton Harold and Table 13b for Foremark. The average values (1981-1983) for Staunton Harold (Table 13a) have been fitted into the open boundary system and the results are shown in Figure 31. From these figures the reservoir had the following probabilities of being in any one trophic category:

Total phosphorus		Average chlorophyll	
Oligotrophic	0	Oligotrophic	0
Mesotrophic	0.08 (8%)	Mesotrophic	0.11 (11%)
Hypertrophic	0.32 (32%)	Hypertrophic	0.27 (27%)
Eutrophic	0.60 (60%)	Eutrophic	0.62 (62%)

TABLE 13a. ANNUAL VALUES OF TOTAL PHOSPHORUS, CHLOROPHYLL A AND SECCHI DEPTH IN STAUNTON HAROLD BETWEEN 1981 AND 1983.

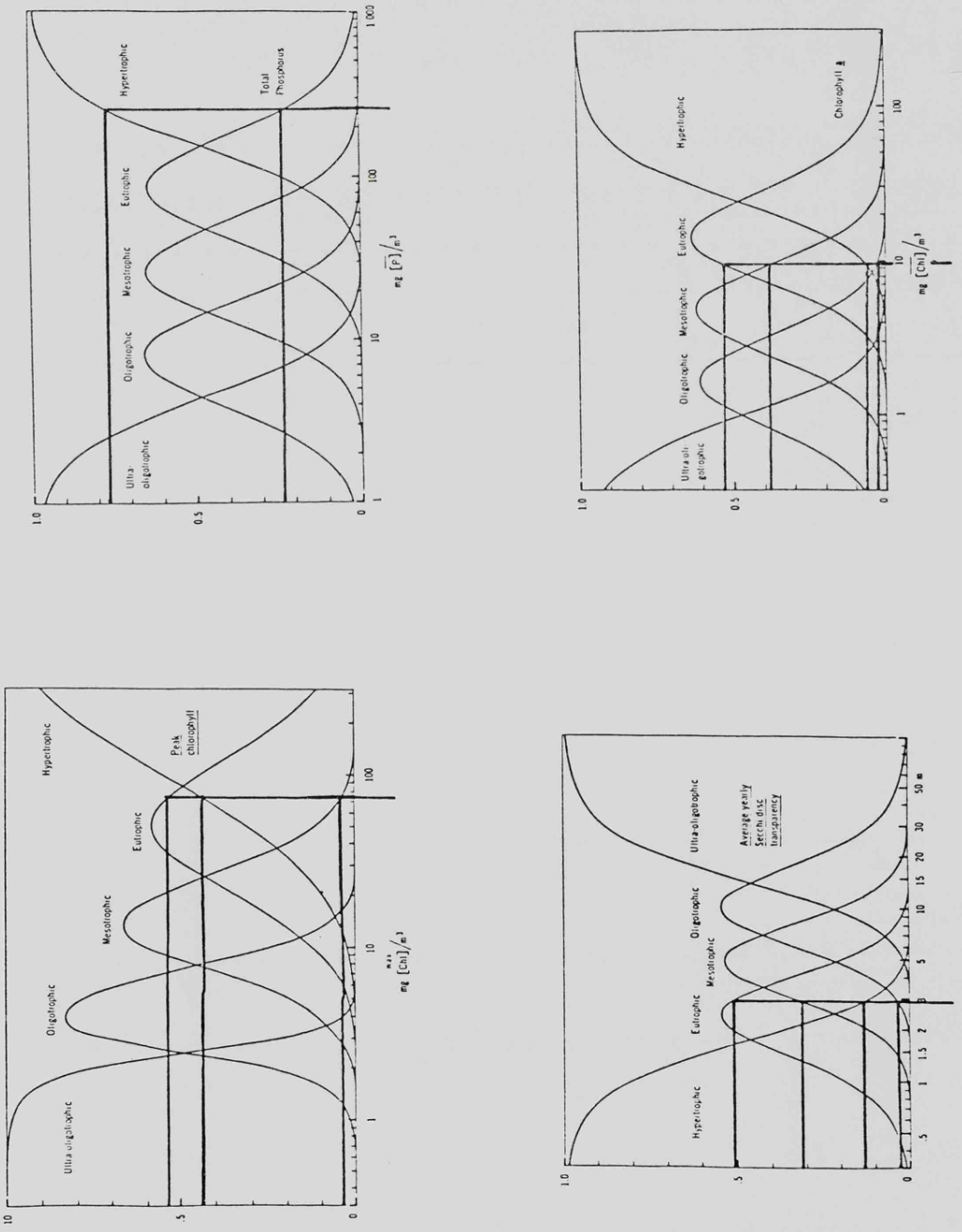
YEAR	MEAN [TP]@	MEAN [CHL]	MAX. [CHL]	MEAN SECCHI DEPTH	MINIMUM SECCHI DEPTH
	mgm^{-3}	mgm^{-3}	mgm^{-3}	m	m
1981	40.0	7.0	176.0	2.4	0.8
1982	140.0	12.0	113.0	2.1	1.0
1983	140.0	24.0$	122.0	1.8	0.75
1981-1983	110.0	17.0$	176.0	2.1	0.75

TABLE 13b. ANNUAL VALUES OF TOTAL PHOSPHORUS, CHLOROPHYLL A AND SECCHI DEPTH IN FOREMARK BETWEEN 1981 AND 1983.

YEAR	MEAN [TP]@	MEAN [CHL]	MAX. [CHL]	MEAN SECCHI DEPTH	MINIMUM SECCHI DEPTH
	mgm^{-3}	mgm^{-3}	mgm^{-3}	m	m
1981	200.0	10.0	66.0	3.1	1.5
1982	230.0	8.0	54.0	3.3	2.0
1983	290.0	9.0$	77.0	2.4	1.25
1981-1983	260.0	10.0$	77.0	2.95	1.25

$ Up to October 1983. @ Mean annual total phosphorus for each year above was estimated from the regression equations calculated from 1978 data on page 71.

Figure 31. The probability distributions for trophic categories based on average concentrations of total phosphorus and chlorophyll, maximum chlorophyll concentrations and average Secchi depths for Staunton Harold during the study period, 1981 to 1983.



Maximum chlorophyll		Average Secchi depth	
Oligotrophic	0	Oligotrophic	0
Mesotrophic	0	Mesotrophic	0.17 (17%)
Eutrophic	0.26 (26%)	Hypertrophic	0.30 (30%)
Hypertrophic	0.74 (74%)	Eutrophic	0.53 (53%)

Using the average data for the three years there was over a 50% certainty (all 4 factors) that Staunton Harold was eutrophic, with maximum chlorophyll showing a 74% probability that Staunton Harold was hypertrophic.

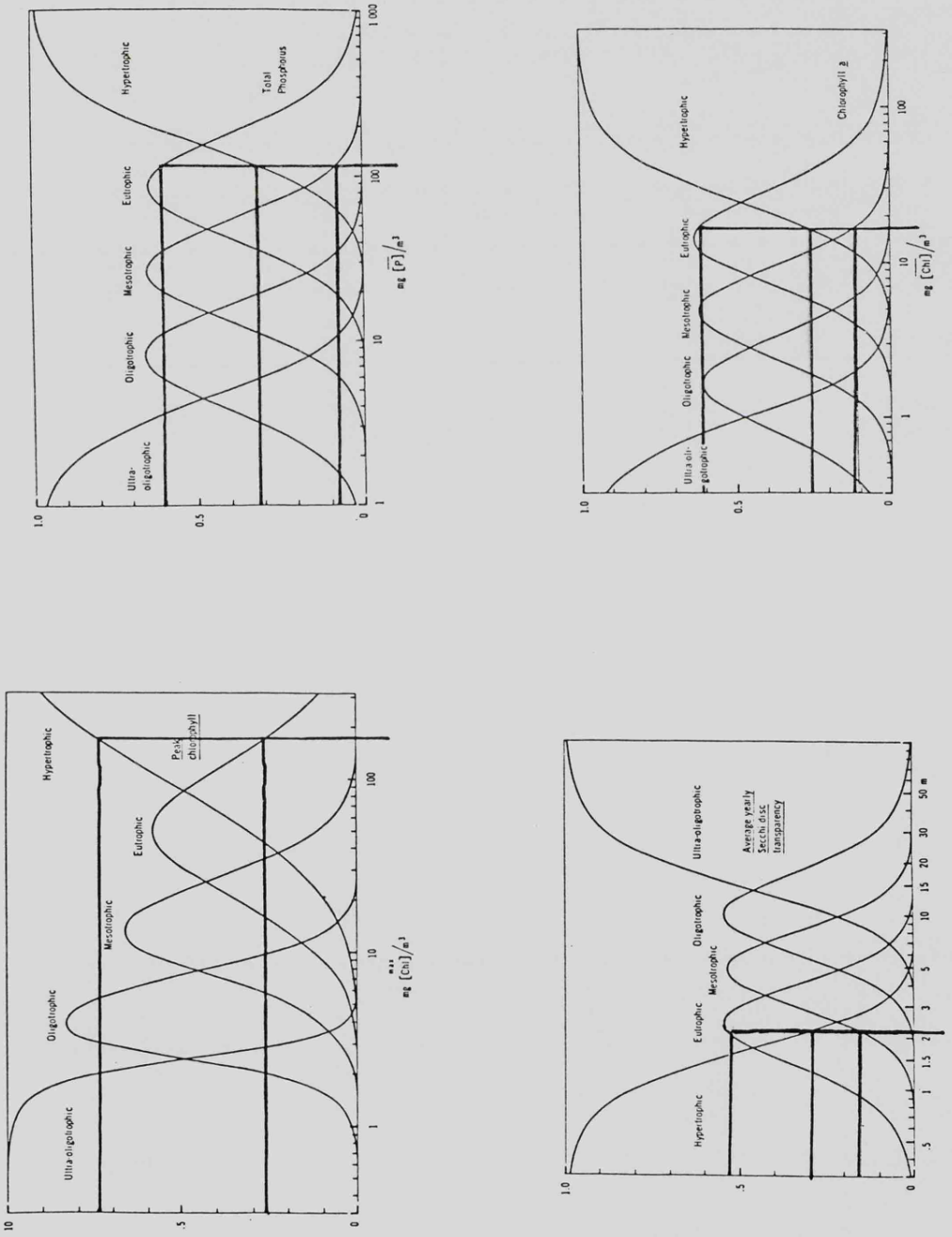
Similarly, for Foremark, the average values (1981-1983) (Table 13b) have been fitted into the open boundary system and the results are shown in Figure 32. From these figures the reservoir had the following probabilities of being in any one trophic category:

Total phosphorus		Average chlorophyll	
Oligotrophic	0	Oligotrophic	0.02 (2%)
Mesotrophic	0	Hypertrophic	0.08 (8%)
Eutrophic	0.23 (23%)	Mesotrophic	0.38 (38%)
Hypertrophic	0.77 (77%)	Eutrophic	0.52 (52%)

Maximum chlorophyll		Average Secchi depth	
Oligotrophic	0	Oligotrophic	0.04 (4%)
Mesotrophic	0.04 (4%)	Hypertrophic	0.14 (14%)
Hypertrophic	0.43 (43%)	Mesotrophic	0.31 (31%)
Eutrophic	0.53 (53%)	Eutrophic	0.51 (51%)

Thus the average data from the three years shows that there was a 50% certainty that Foremark was eutrophic for three out of the four factors. Total phosphorus gave a 77% probability that Foremark was hypertrophic.

Figure 32. The probability distributions for trophic categories based on average concentrations of total phosphorus and chlorophyll, maximum chlorophyll concentrations and average Secchi depths for Foremark during the study period, 1981 to 1983.



Phosphorus concentrations in Foremark were higher than in Staunton Harold but the average chlorophyll concentrations were lower. The relationship between phosphorus and phytoplankton growth has been known for a long time. Lund (1970) showed that there was a good linear correlation between summer maximum chlorophyll and winter maximum phosphate concentration on a log.log scale up to 100 mgm^{-3} phosphate. This relationship was updated by Scott (1975) and Collingwood (1977). The regression was again updated by Lack and Johnson (1983). Data from Staunton Harold and Foremark are included in the relationship (Figure 33) confirming that Lund's observation (1970) that the linear relationship does not hold above 100mgm^{-3} phosphate. Once the ortho-phosphate winter maximum level exceeded this value, no corresponding increase in summer maximum chlorophyll occurred. There must, therefore, be another explanation for the limitation of phytoplankton growth as the potential with respect to phosphorus appears to have been reached in both Staunton Harold and Foremark. There are several possible explanations. Self-shading is one, although as stated above (section 3.2.2.6) there is no concrete evidence for this using the average values of the self-shading coefficients. The most likely explanation, however, is that the release of ortho-phosphate from the sediments in Foremark was higher (see section 3.3.1.2).

Lund (1970) also showed a similar relationship for nitrate, the other major plant nutrient. The relationship between winter maximum nitrate concentrations and summer maximum chlorophyll has also been updated by Scott (1975) and the data from Staunton Harold and Foremark are included in the plot in Figure 34. The data from this project lies around the upper end of Scott's regression line. It is interesting to note that the concentrations of nitrate, unlike phosphate, had not reached a level where phytoplankton growth had become limited and the linear relationship (on a log.log scale) put forward by Lund (1970) still holds.

Figure 33. The relationship between winter maximum ortho-phosphate and summer maximum chlorophyll concentrations.

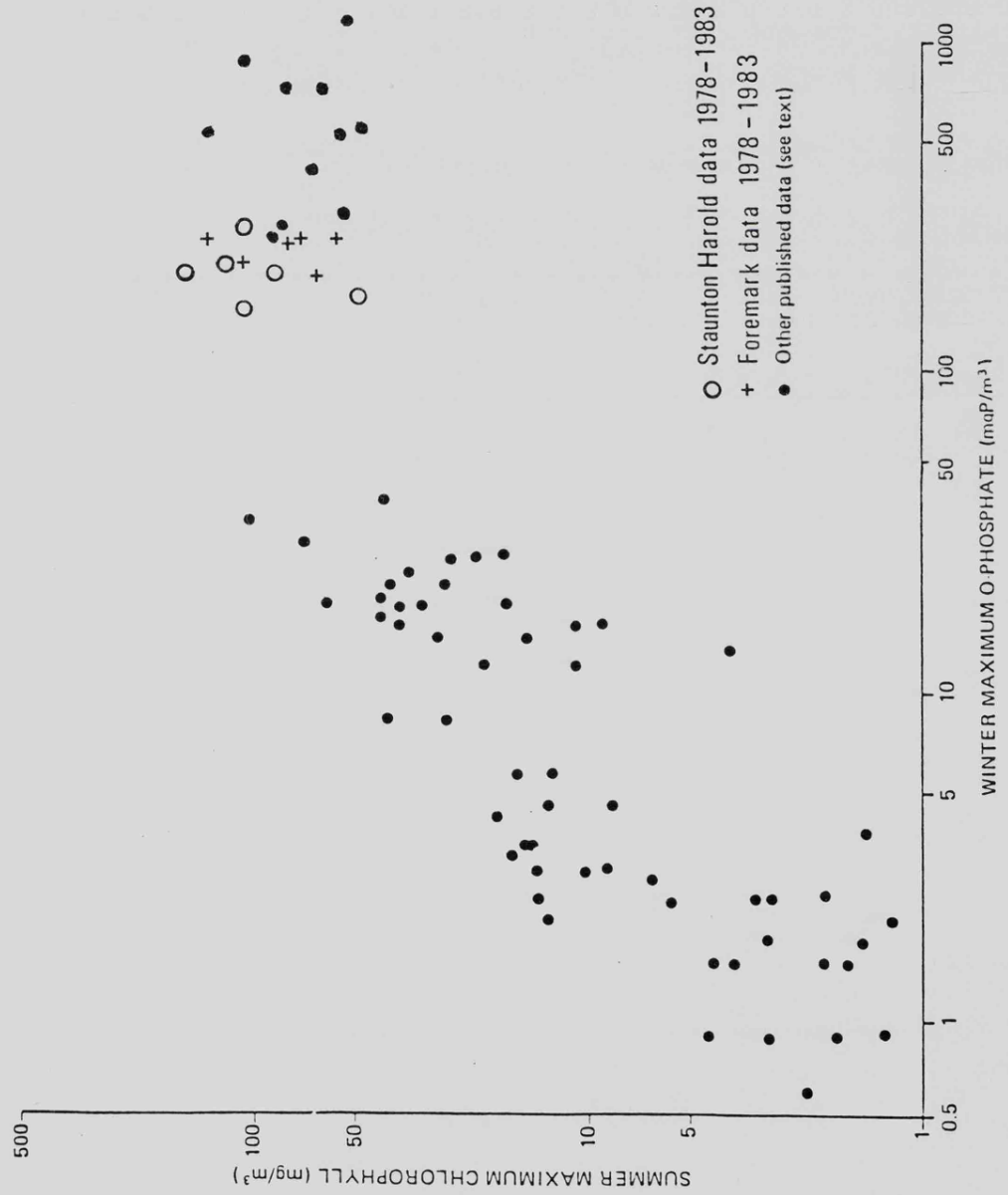
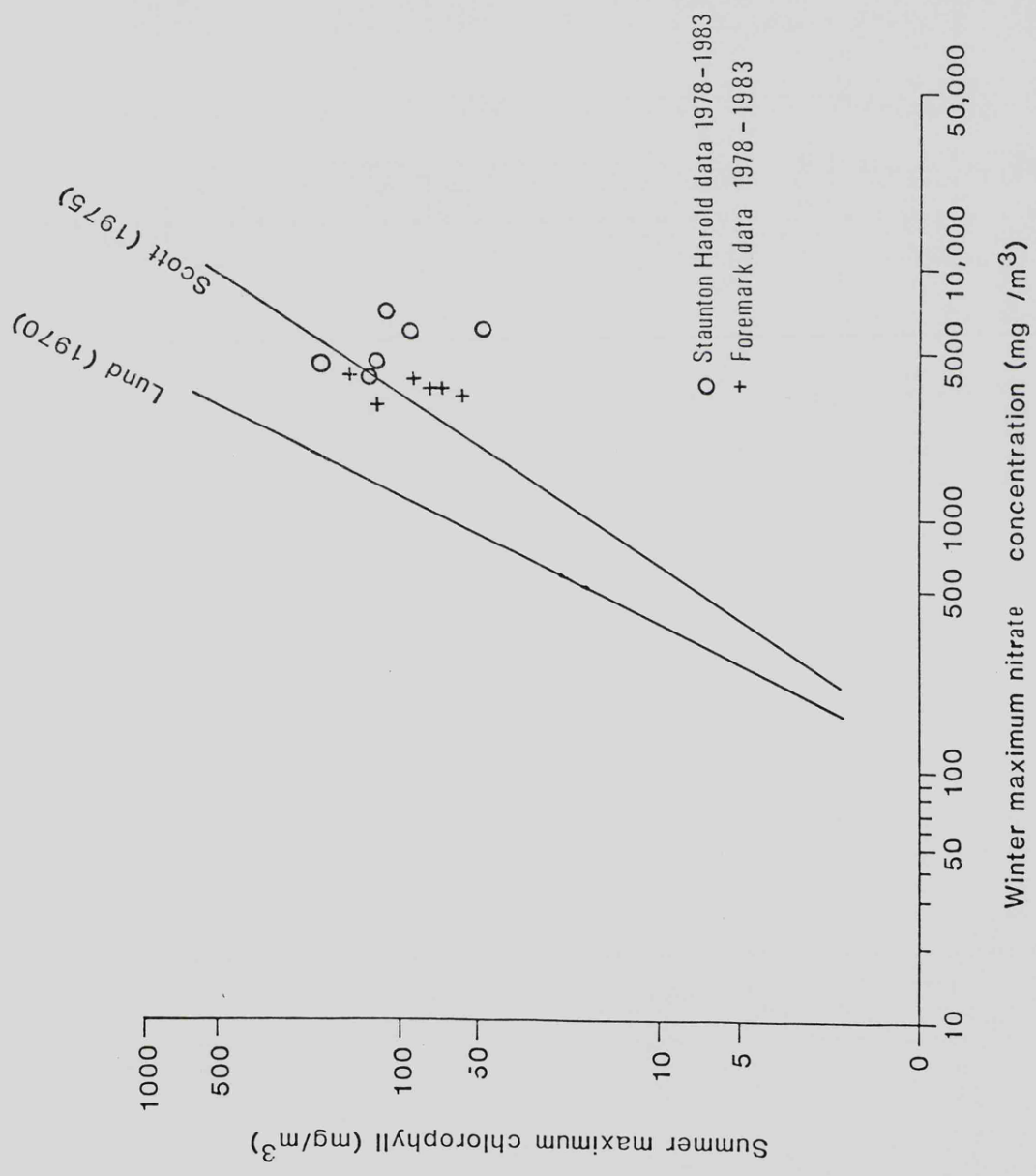


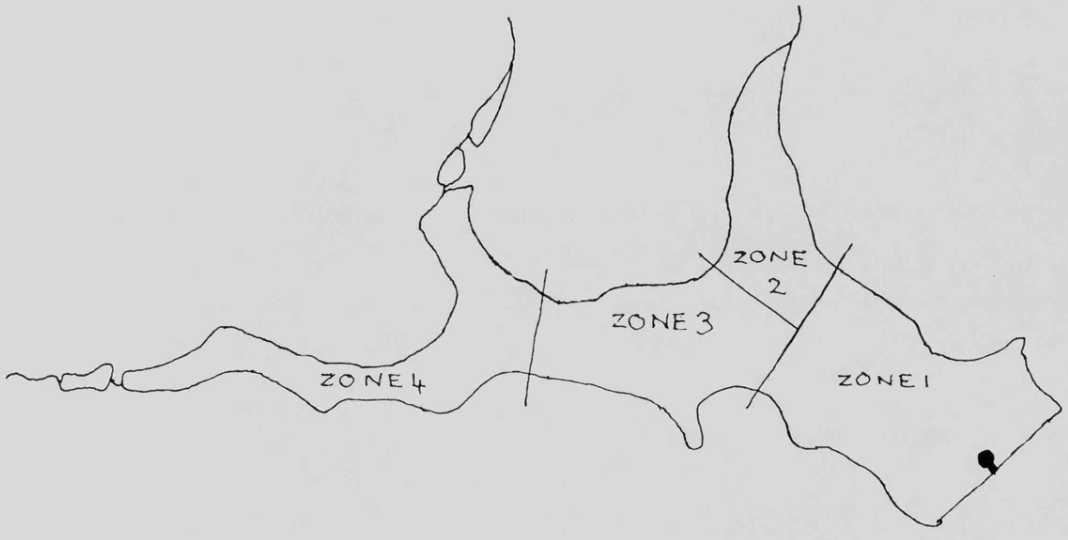
Figure 34. The relationship between winter maximum nitrate and summer maximum chlorophyll concentrations. See text for details of regression lines.



3.5 SPATIAL VARIATION OF TEMPERATURE, DISSOLVED OXYGEN AND CHLOROPHYLL A.

This section identifies the effects of mixing on the distribution of temperature, dissolved oxygen and chlorophyll a in the main basin of Staunton Harold and compares the results with those from the stratified 'control' reservoir. These surveys were carried out to confirm any differences or similarities which may have been noted during the routine sampling from the valve towers. The spatial distribution of phytoplankton in reservoirs (both horizontally and vertically) is very complex and it was considered to be far beyond the realms of this project to study distribution patterns in detail. See also section 2.3.4 and Appendix 7.

Prior to any artificial mixing, in October, 1980, a boat survey was carried out at Staunton Harold. Surface samples from twenty nine random sites - using randon numbers and a grid over a map of the reservoir - and one from the valve tower were taken and analysed for chlorophyll a. As no replicates were taken, the reservoir was divided into four zones for the purpose of analysis, as shown below. The number of samples in each zone were then treated as replicates.



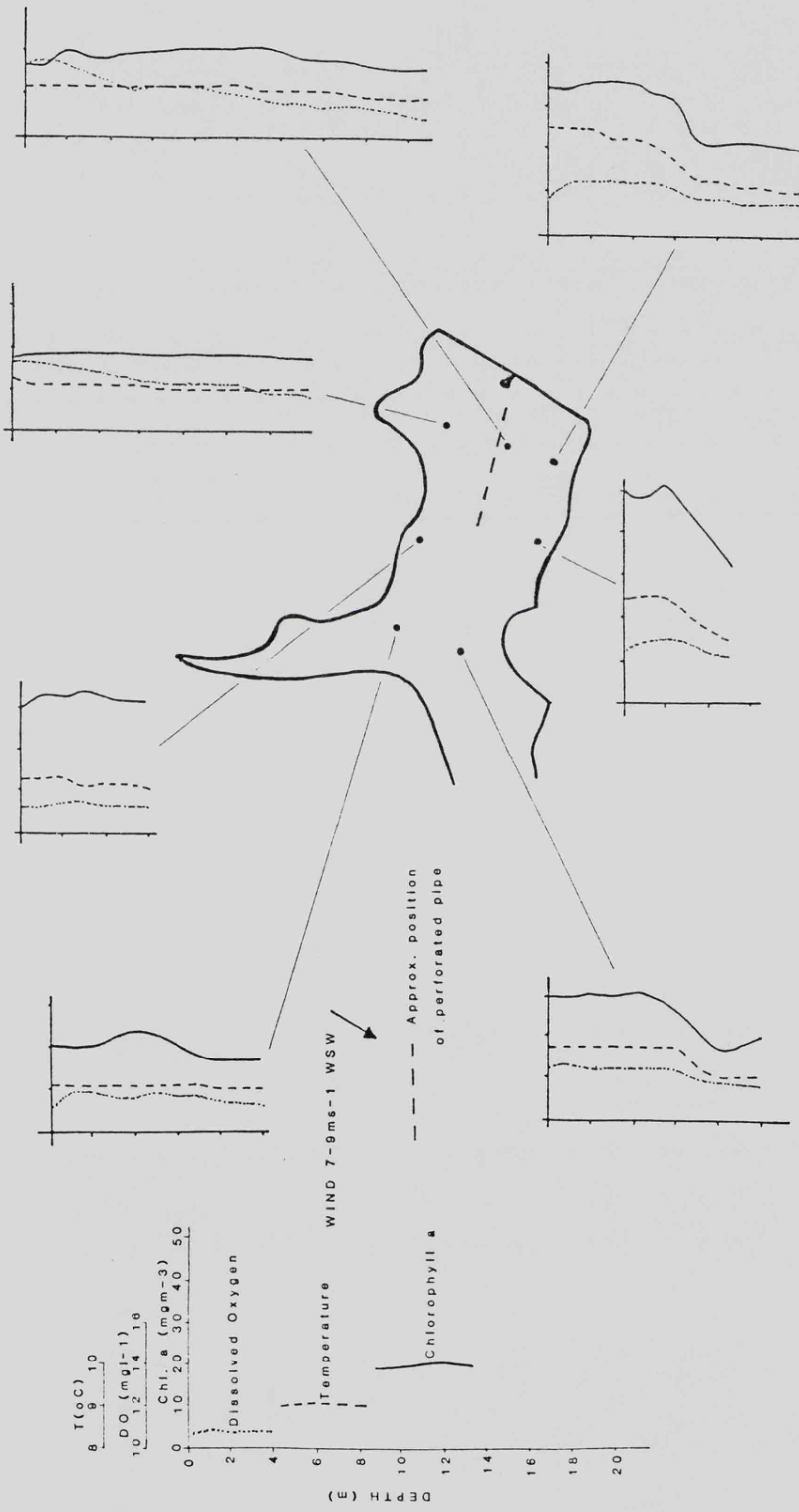
The results from a one-way analysis of variance gave an F value of 2.56 (F_{tab} [0.05] = 3.01) and so there is no significant difference at the 95% level

between the four zones. A test was made to determine whether the valve tower sample was different from the others. The valve tower sample had a chlorophyll a value of 32.9 mgm^{-3}, the mean and 95% confidence limits of the other twenty nine sites was 34.53 +/_ 2.28 mgm^{-3} and so the chlorophyll concentration at the valve tower was within the 95% confidence limits of the mean. Although this is not a statistically rigorous test, when combined with the ANOVA result it shows the homogeneous nature of the surface chlorophyll a.

Problems were encountered with the statistical analyses of boat survey data and the analysis of variance tables (ANOVA) are not presented. The results , although statistically sound, are suspect in terms of the hypotheses being tested. This has resulted from several factors in the experimental design. Firstly, the sites had uneven depths which complicates the analysis and led to the ANOVA being carried out only on data to the maximum depth of the shallowest site. Secondly, replicates could not be taken due to time restrictions and thirdly, because the differences between sites and depths was often very small, any variation would have given a highly significant difference in the ANOVA table. This is well illustrated by the temperature and dissolved oxygen depth distributions in Staunton Harold on the 22nd September, 1982. The ANOVA gave highly significant (***) differences between sites and depths for both parameters whereas a glance at Figure 38 shows that the horizontal and vertical distributions were very similar.

On the 23rd April, 1982, the phytoplankton in Staunton Harold was dominated by the Cryptophytes, *Cryptomonas* spp. and *Rhodomonas minuta* Skuja var. *nanoplanktica* Skuja (1048 and 2860 cells ml^{-1} respectively). In the week preceeding the survey, wind speed had been low at 2 to 5 ms^{-1} from the west. On the day of the survey the wind speed increased to between 7.5 and 9 ms^{-1} and was west north westerly. The results of the survey are shown in Figure 35. It

Figure 35. The horizontal and vertical variations of temperature, dissolved oxygen and chlorophyll a in the main basin of Staunton Harold reservoir on the 23rd April, 1982.



is interesting to note the surface build up of chlorophyll on the windward (eastern) shore was a result of the wind and possibly vertical movements by the motile cells. A second point of interest is that within approximately 30 m of the perforated pipe the chlorophyll was distributed evenly with depth. This showed that even motile phytoplankton could not maintain their optimum depth distribution and were mixed throughout the water column.

The results of a boat survey carried out on the 15th July, 1982 are shown in Figure 36. The phytoplankton were dominated by the diatoms, *Asterionella formosa* and small centrics (3-12μm) (550 and 4530 cells ml^{-1} respectively at the surface) and *Rhodomonas minuta* (722 cells ml^{-1}). The wind during the previous week had been north easterly ranging from 2 to 8 ms^{-1} but on the day of the survey moved round to the south west and ranged from 2 to 4 ms^{-1}. The distribution of chlorophyll again showed a build up on the windward shore. The slight temperature stratification which was recorded was the result of an intense period of heating (Figure 11 shows the temperature difference in Foremark increased dramatically during this period) and possibly the decrease in wind induced turbulence. Dissolved oxygen depth distributions also showed stratification which was probably a result of the change in temperature and also high phytoplankton productivity (see Chapter 5).

The distribution of surface chlorophyll at 12 sites was carried out on the 8th September, 1982. Depth profiles of temperature, dissolved oxygen and chlorophyll were taken at the valve tower. The results are shown in Figure 37. The phytoplankton were dominated by the Cryptophyte, *Cryptomonas* spp. and the Cyanobacterium, *Microcystis aeruginosa* Kutz. emend. Elenkin, both of which can control their depth distribution. The wind had been south westerly and ranged from 0 to 7.5 ms^{-1} prior to the survey but wind speed declined and ranged from 3 to 5 ms^{-1} on the day, moving round to south, south west. Temperature, dissolved oxygen and chlorophyll a showed even distributions with depth at the

Figure 36. The horizontal and vertical variations of temperature, dissolved oxygen and chlorophyll a in the main basin of Staunton Harold reservoir on the 15th July, 1982.

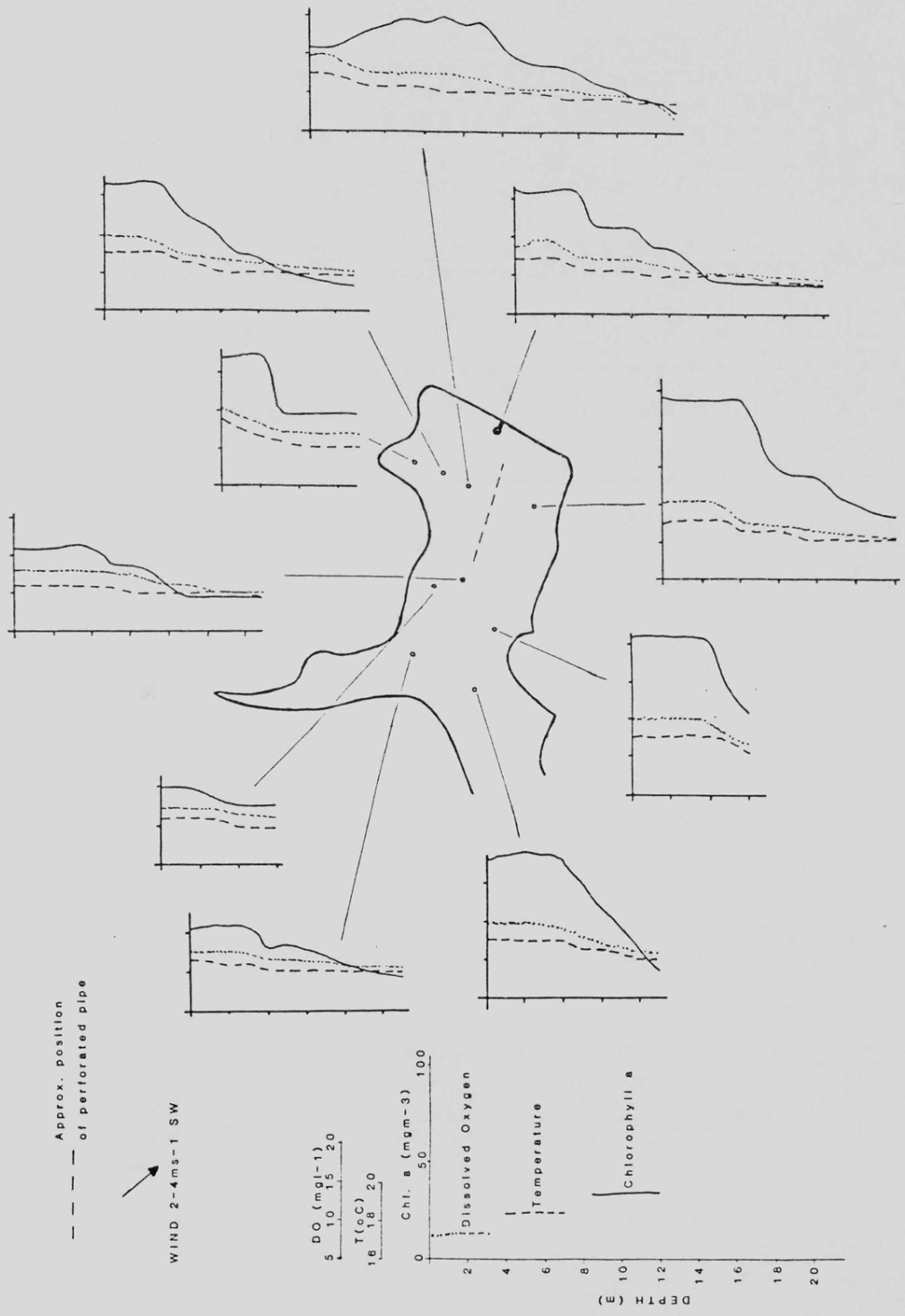
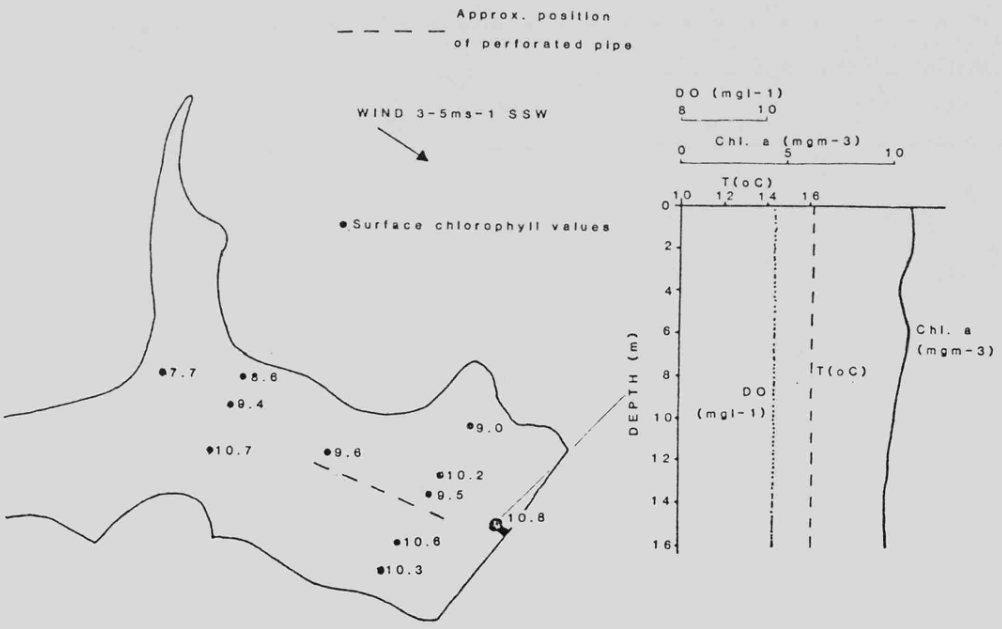


Figure 37. The horizontal variation of surface chlorophyll a and the depth distribution of temperature, dissolved oxygen and chlorophyll a at the valve tower in Staunton Harold reservoir on the 8th September, 1982.



valve tower. The surface chlorophyll value at the valve tower was 10.8 mgm^{-3} and the mean and 95% confidence limits for the other 11 sites was 9.58 +/- 2.08 and so the valve tower is within these limits. The distribution of surface chlorophyll appears not to have been affected by the wind except for the value of 7.7 mgm^{-3} at the south west end of the main basin. Here the sampling site was sheltered from the south, south westerly wind by a hill which lies between the two arms of the reservoir.

Another boat survey at Staunton Harold was carried out on the 22nd September, 1982 (which was at the beginning of the natural autumnal overturn as recorded in Foremark - see Figure 17). The phytoplankton were dominated by *Cryptomonas* spp., *Rhodomonas minuta* and the Cyanobacterium, *Anabaena circinalis* Rabenh. *ex* Born. *et* Flah., all of which are motile. Wind speed on the day was between 0 and 5 ms^{-1}, south westerly and similar to that of the previous week. The results are shown in Figure 38 and all three parameters showed even depth distributions.

Two boat surveys were carried out at Foremark during 1982. The first on the 10th April, recorded the distribution of chlorophyll a only, the results are presented in Figure 39. The dominant phytoplankton at the time were *Stephanodiscus astraea* (Ehrenb.) Grun., *Asterionella formosa* and small centric diatoms. The wind speed was 5 ms^{-1} from a westerly direction. Wind speed had ranged from 5 to 15 ms^{-1} and was south westerly for the week prior to the survey. The even depth distribution of chlorophyll a was not unexpected as the survey was carried out previous to any thermal stratification being apparent and also the species of phytoplankton which were present were non-motile. The slightly higher concentration of chlorophyll a in the lower layers was a result of sedimentation of the diatom cells.

The results from the other boat survey carried out on the 15th September,

Figure 38. The horizontal and vertical variations of temperature, dissolved oxygen and chlorophyll a in the main basin of Staunton Harold reservoir on the 22nd September, 1982.

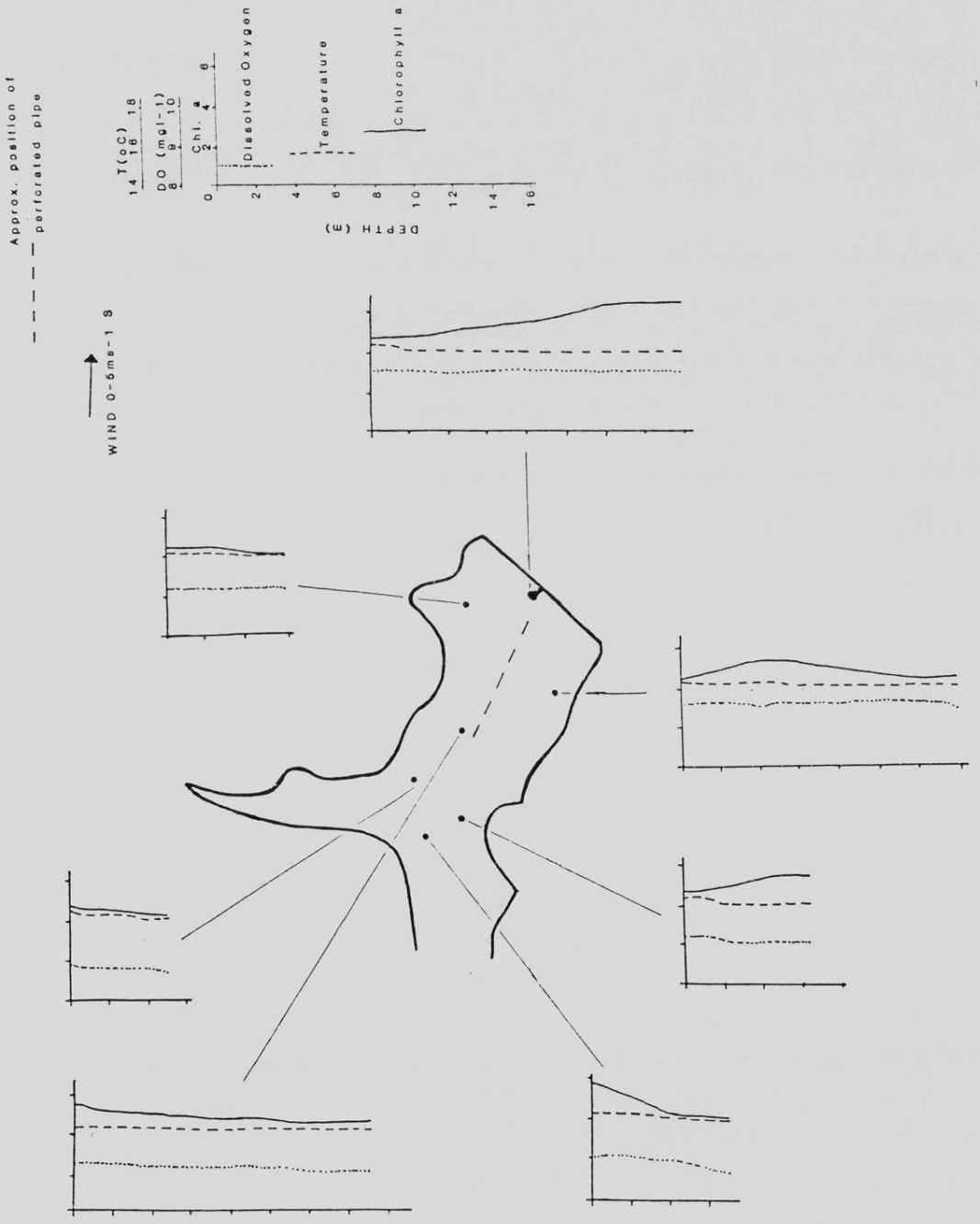
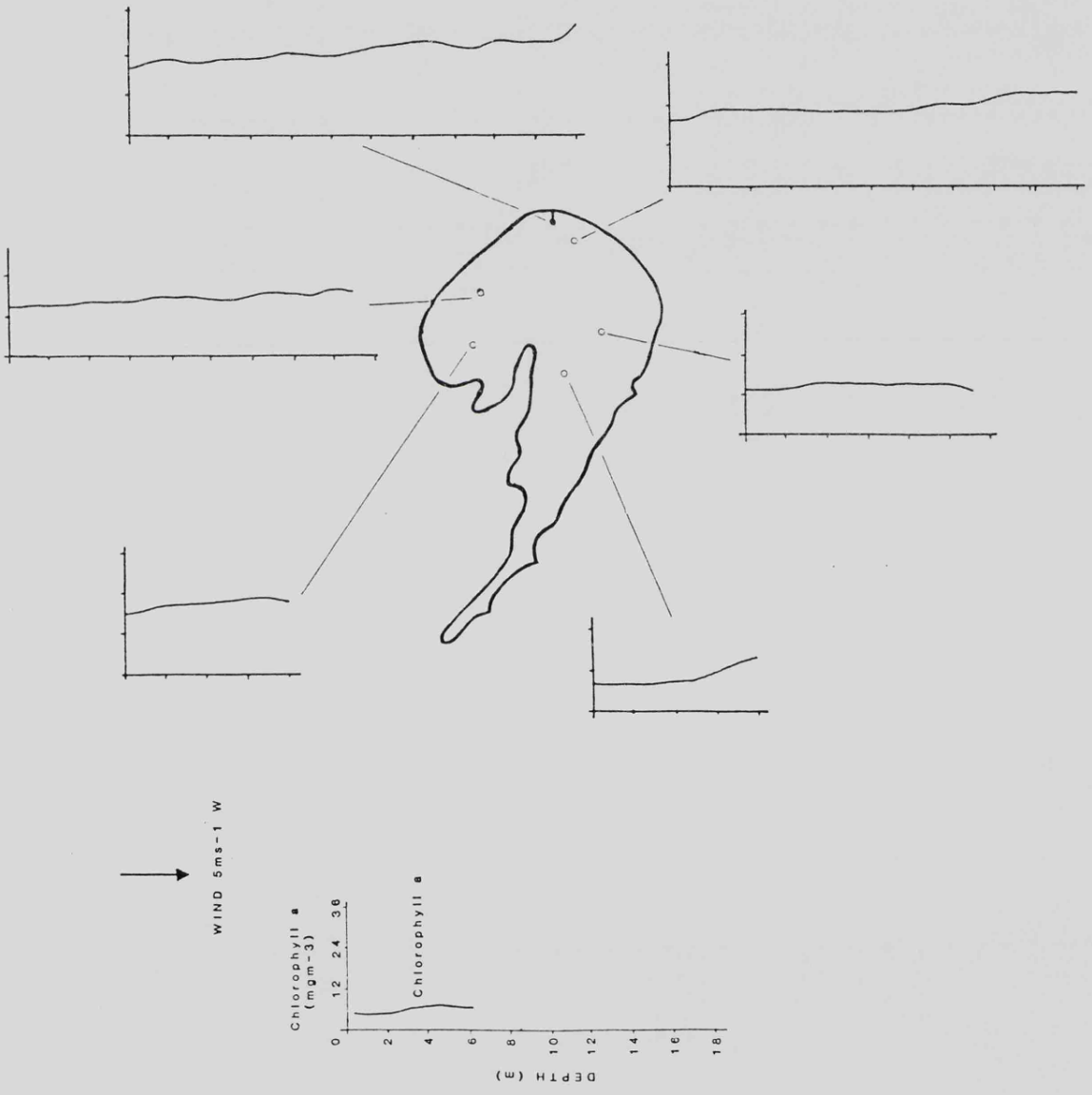


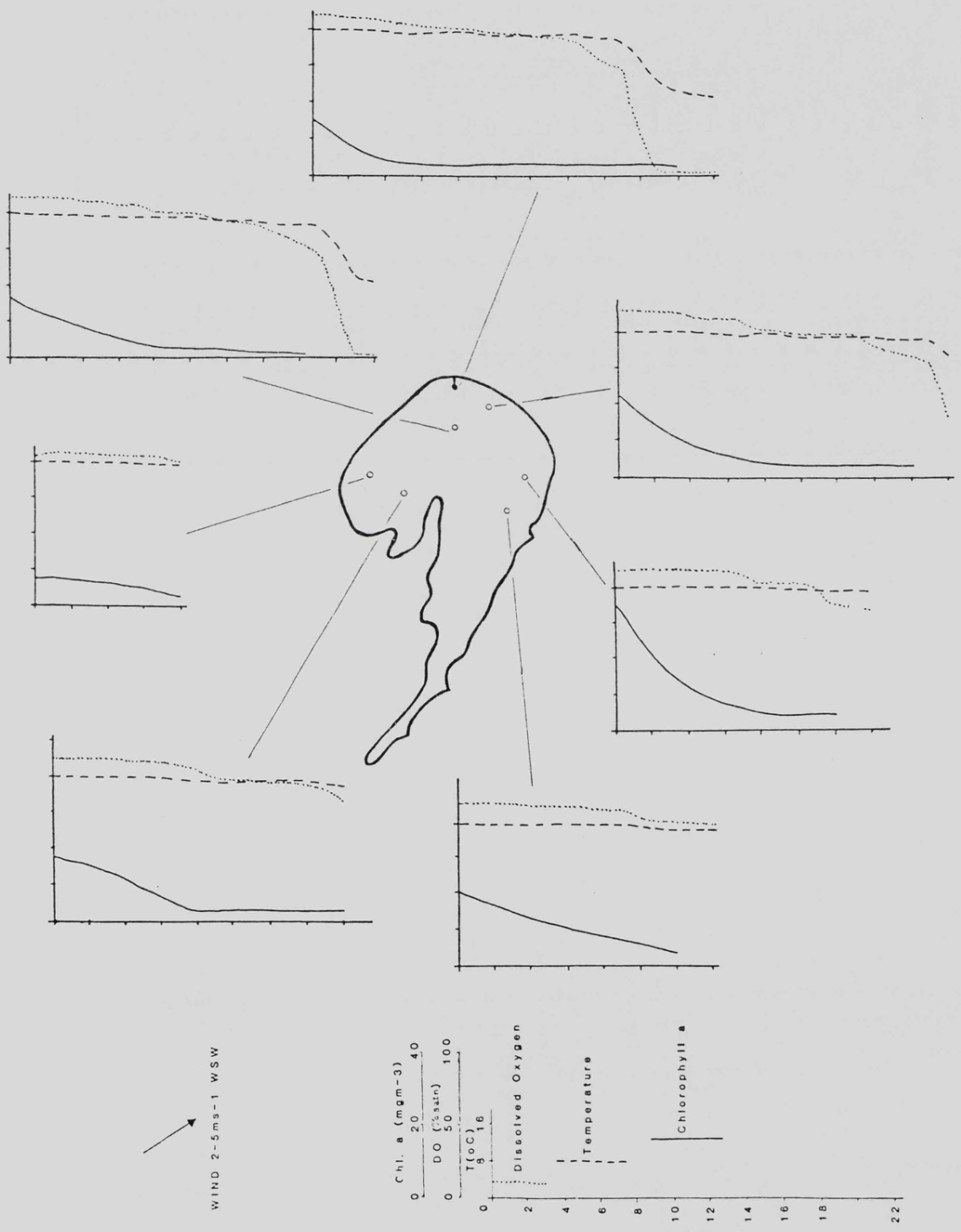
Figure 39. The horizontal and vertical variations of chlorophyll a in the main basin of Foremark reservoir on the 10th April, 1982.



1982 are presented in Figure 40. The wind was west, south westerly and ranged from 2 to 5 ms^{-1}. The phytoplankton standing crop was mainly composed of *Cryptomonas* spp., *Rhodomonas minuta, Microcystis aeruginosa, Pandorina morum* and *Asterionella formosa*. Chlorophyll stratification was apparent and it is suggested that this was due mainly to the presence of motile species of phytoplankton - the temperature and dissolved oxygen also showed stratification but only below 16 metres. This can also be seen in Figures 17 and 18 which show the depth distribution of temperature and dissolved oxygen during 1982. Again there was a build up of chlorophyll on the windward shore and less in the sheltered areas, such as the shallowest site on the western side of the reservoir.

The distribution of phytoplankton in the reservoirs was affected mainly by the interactions of wind-induced water currents and water column stability. Reynolds (1984b) stated that these interactions between two of the major factors determine spatial and temporal distributions. The patchiness of phytoplankton is still not understood but it is now clear that discontinuous distributions are the most common pattern found (Harris and Smith 1977). In terms of the interaction of phytoplankton cells and their environment, short time scale variations are important as the cells can only perceive changes over short periods, usually less than the cell generation time (Harris 1980). The changes in distribution due to interactions of the wind and water column stability can be on very short time scales and thus play an important, if not dominant role in phytoplankton growth and succession (Reynolds 1984).

Figure 40. The horizontal and vertical variations of temperature, dissolved oxygen and chlorophyll a in the main basin of Foremark reservoir on the 15th September, 1982.



CHAPTER 4. PHYTOPLANKTON BIOMASS, GROWTH AND PERIODICITY.

4.1 TEMPORAL AND VERTICAL CHANGES IN PHYTOPLANKTON BIOMASS.

In the previous chapter it was concluded that both reservoirs were eutrophic and could therefore, support large phytoplankton biomasses.

The phytoplankton biomass (measured as chlorophyll a) was very variable in both reservoirs over the study period. Maximum, minimum and mean densities between March and October for each reservoir during 1981, 1982 and 1983 are shown in Table 14. [The standing crop (chlorophyll a per unit surface area) in the whole water column, the mixed and euphotic depth are shown in Appendix 2].

The lowest value recorded in Staunton Harold was 0.1 mgm^{-3} and 0.5 mgm^{-3} in Foremark. The maximum values in Staunton Harold ranged from 122 mgm^{-3} in 1983 to 176 mgm^{-3} in 1981 and in Foremark from 54 mgm^{-3} in 1982 to 77.0 mgm^{-3} in 1983. Higher values were recorded in years previous to this study and also when special surveys were made.

A comparison of the mean and maximum biomass levels in Staunton Harold during years when artificial mixing took place revealed that in one year (1983) the biomass was increased and whilst in another (1982) it was reduced relative to the naturally mixed year (1981). In Formark the biomass levels were lower than those in Staunton Harold but the mean values showed that the highest biomass was achieved in the naturally mixed year (1981) with slightly lower values reached in 1982 and 1983.

TABLE 14. SUMMARY OF THE SPRING/SUMMER CHLOROPHYLL DATA (MARCH TO OCTOBER) FOR STAUNTON HAROLD AND FOREMARK RESERVOIRS, 1981 TO 1983.

	Chlorophyll a (mgm^{-3}).	
	Staunton Harold	Foremark
1981		
Maximum	176.0	66.0
Minimum	0.1	0.5
Mean (+/-s.e.)	17.0 (+/-2.05)	11.0 (+/-0.75)
1982		
Maximum	113.0	54.0
Minimum	0.9	0.5
Mean (+/-s.e.)	12.0 (+/-1.26)	9.0 (+/-0.72)
1983		
Maximum	122.0	77.0
Minimum	1.2	0.8
Mean (+/-s.e.)	24.0 (+/-2.12)	9.0 (+/-0.88)

The changes in biomass (measured as chlorophyll a) between March and October are shown in Figures 41, 42 and 43 for Staunton Harold and 44, 45 and 46 for Foremark. The values plotted are those from surface and bottom (14 m in Staunton Harold and 20 m in Foremark) samples. The seasonal pattern was similar between years and reservoirs and the values fluctuated widely. Generally, values were low throughout the winter, increasing (often rapidly) to form the vernal peak. The decline, again often rapid, of this pulse to low early summer values was followed by several mid and late summer peaks. Values then declined again, usually after the autumnal overturn, and returned to low winter values. This general pattern is typical of many temperate, eutrophic lakes (Hutchinson 1967, Scott 1975, Toms *et al.* 1975, Youngman 1975, Jewson 1976, Jones 1977a, Reynolds 1978, Harris and Piccinin 1980, Bailey-Watts 1978 1982, Ferguson and Harper 1982, Lund and Reynolds 1982, Lack and Johnson 1983).

The depth distribution of phytoplankton biomass, as chlorophyll a, is shown in Figures 47, 48 and 49 for Staunton Harold during the three years of study. Chlorophyll a was found to be evenly distributed with depth during artificial mixing in 1982 and 1983 except when the water column stability increased (Figure 22) and motile species were present (eg. *Aphanizomenon* in August, 1982 and Cryptomonads in late May, 1983). The boat surveys (see chapter 3) showed that this pattern of phytoplankton stratification existed throughout the reservoir except in the vicinity of the bubble plume of the perforated pipe. In Foremark, phytoplankton biomass was stratified throughout the summer months in all 3 years and was concentrated in the top 5m (Figures 50, 51 and 52).

4.2 TEMPORAL AND VERTICAL CHANGES OF DOMINANT SPECIES IN 1981.

A list of the phytoplankton taxa recorded from both reservoirs between 1981 and 1983 is given in Appendix 3. It does not take all taxa to species level

Figure 41. The variations in the chlorophyll levels at the surface and bottom (14 m) in Staunton Harold during 1981. (Numerically dominant phytoplankton species are indicated)

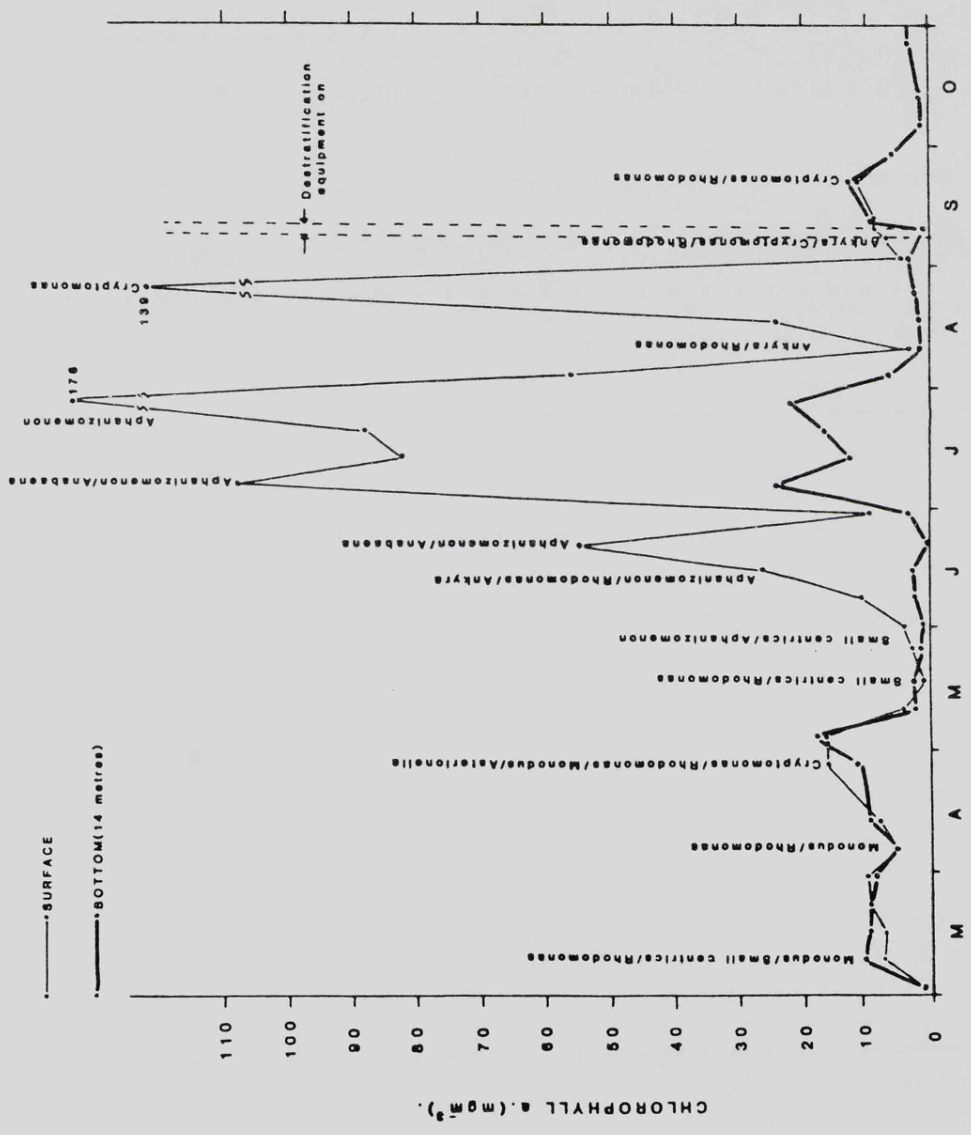


Figure 42. The variations in the chlorophyll levels at the surface and bottom (14 m) in Staunton Harold during 1982. (Numerically dominant phytoplankton species are indicated)

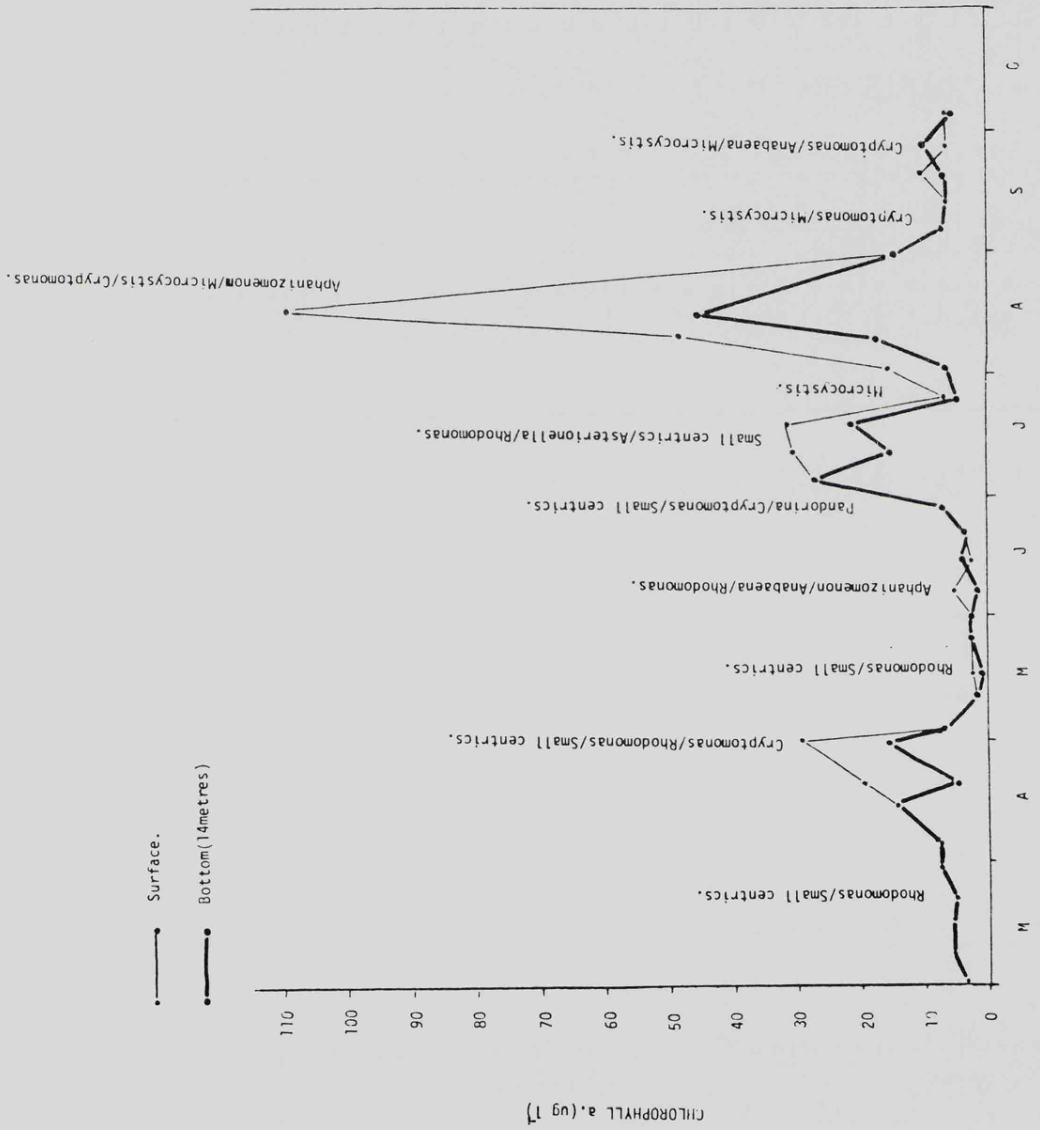


Figure 43. The variations in the chlorophyll levels at the surface and bottom (14 m) in Staunton Harold during 1983. (Numerically dominant phytoplankton species are indicated)

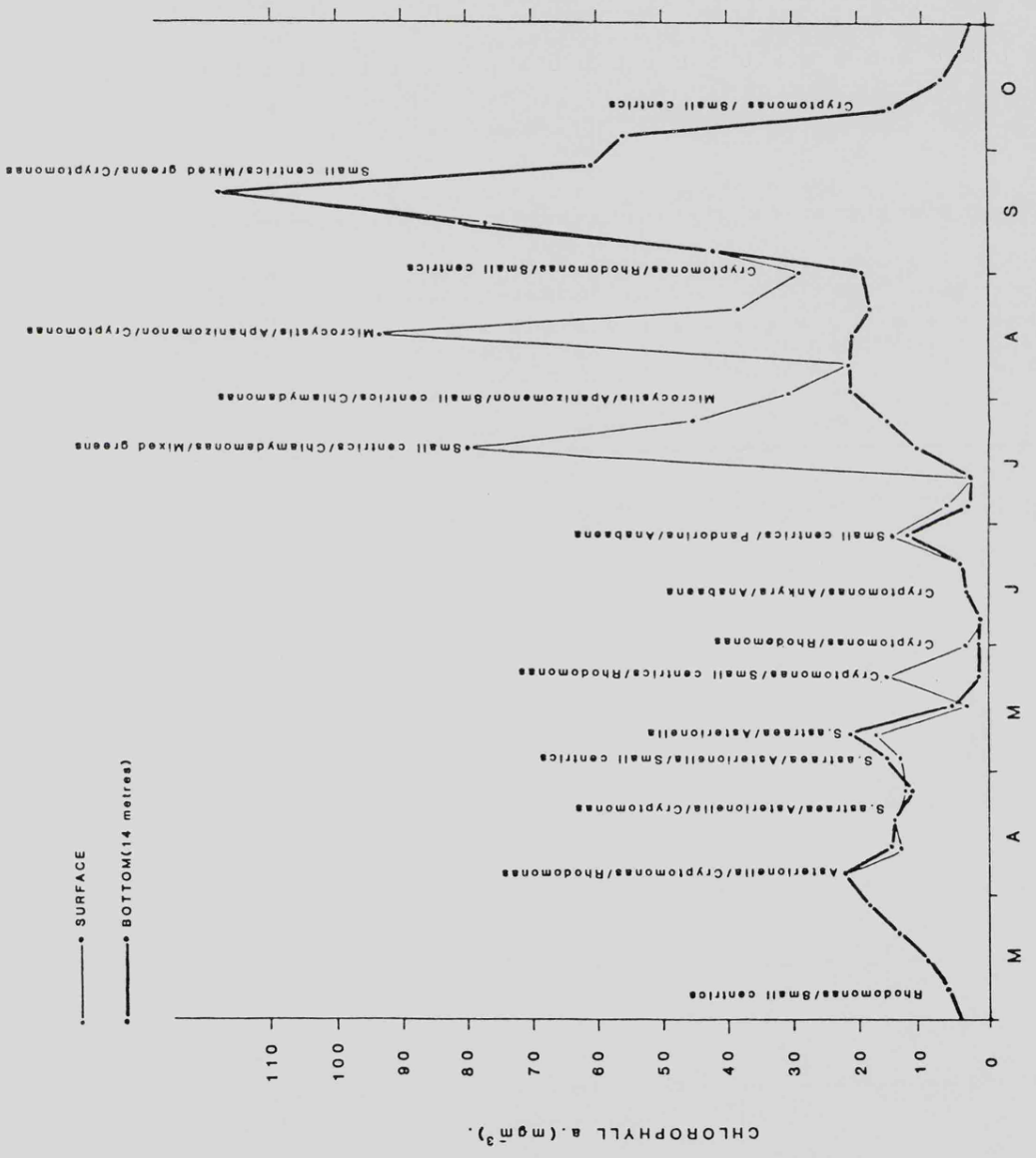


Figure 44. The variations in the chlorophyll levels at the surface and bottom (20 m) in Foremark during 1981. (Numerically dominant phytoplankton species are indicated)

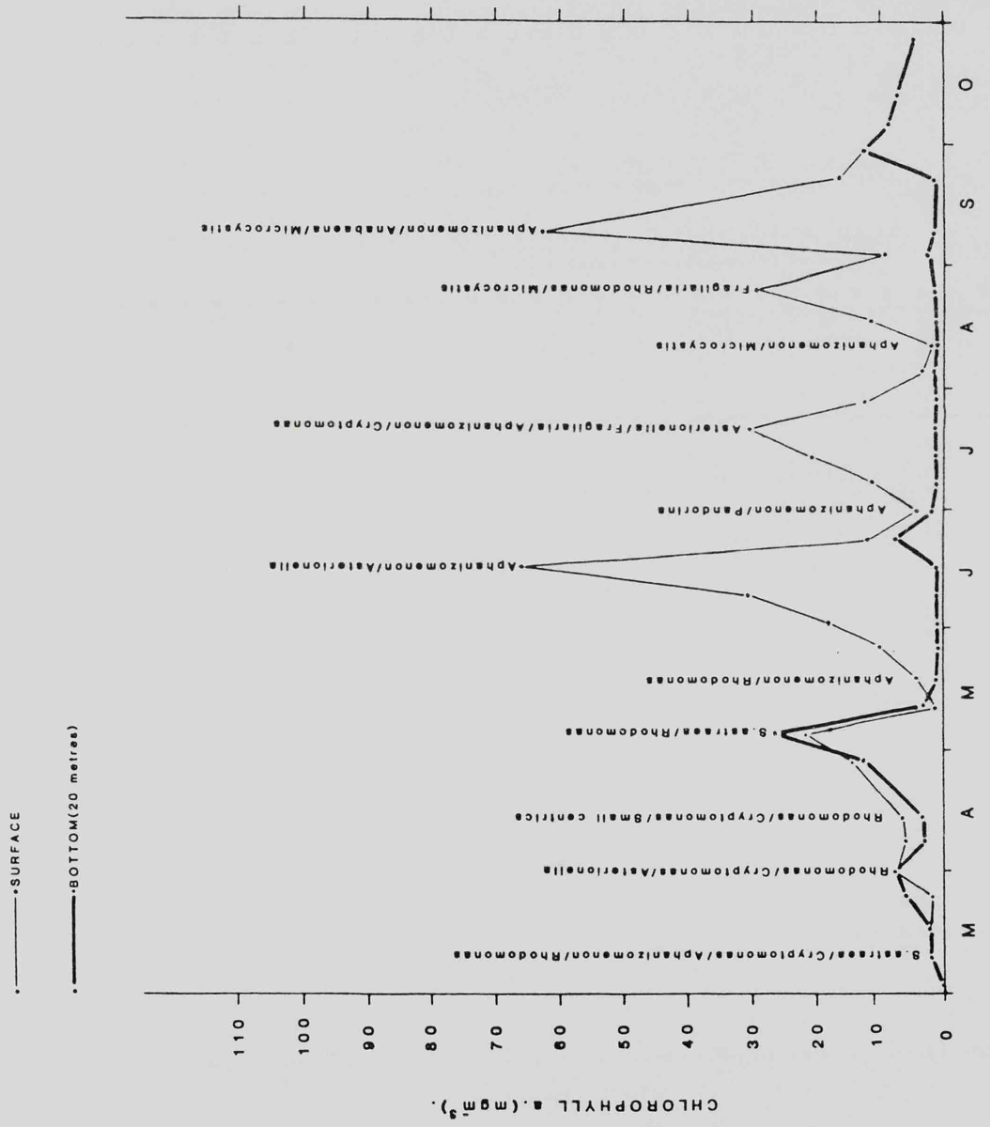


Figure 45. The variations in the chlorophyll levels at the surface and bottom (20 m) in Foremark during 1982. (Numerically dominant phytoplankton species are indicated)

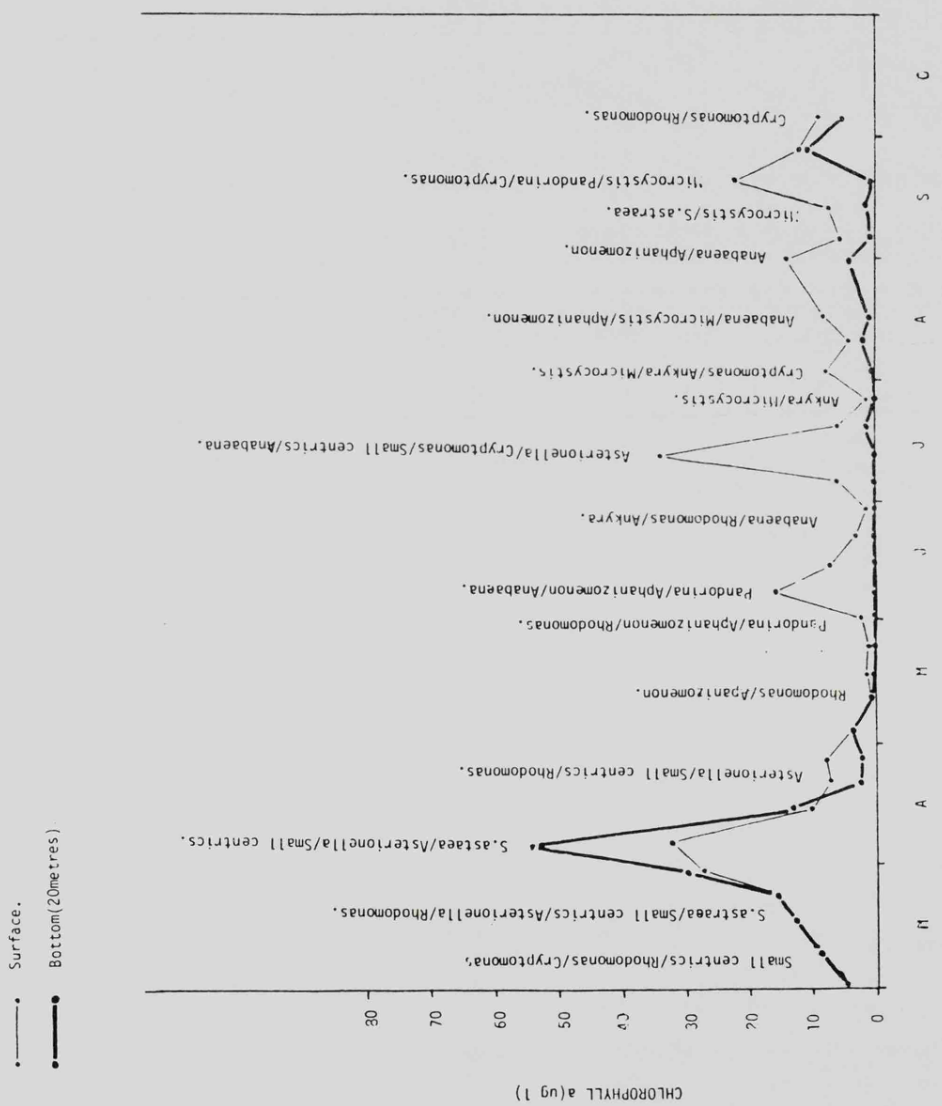


Figure 46. The variations in the chlorophyll levels at the surface and bottom (20 m) in Foremark during 1983. (Numerically dominant phytoplankton species are indicated)

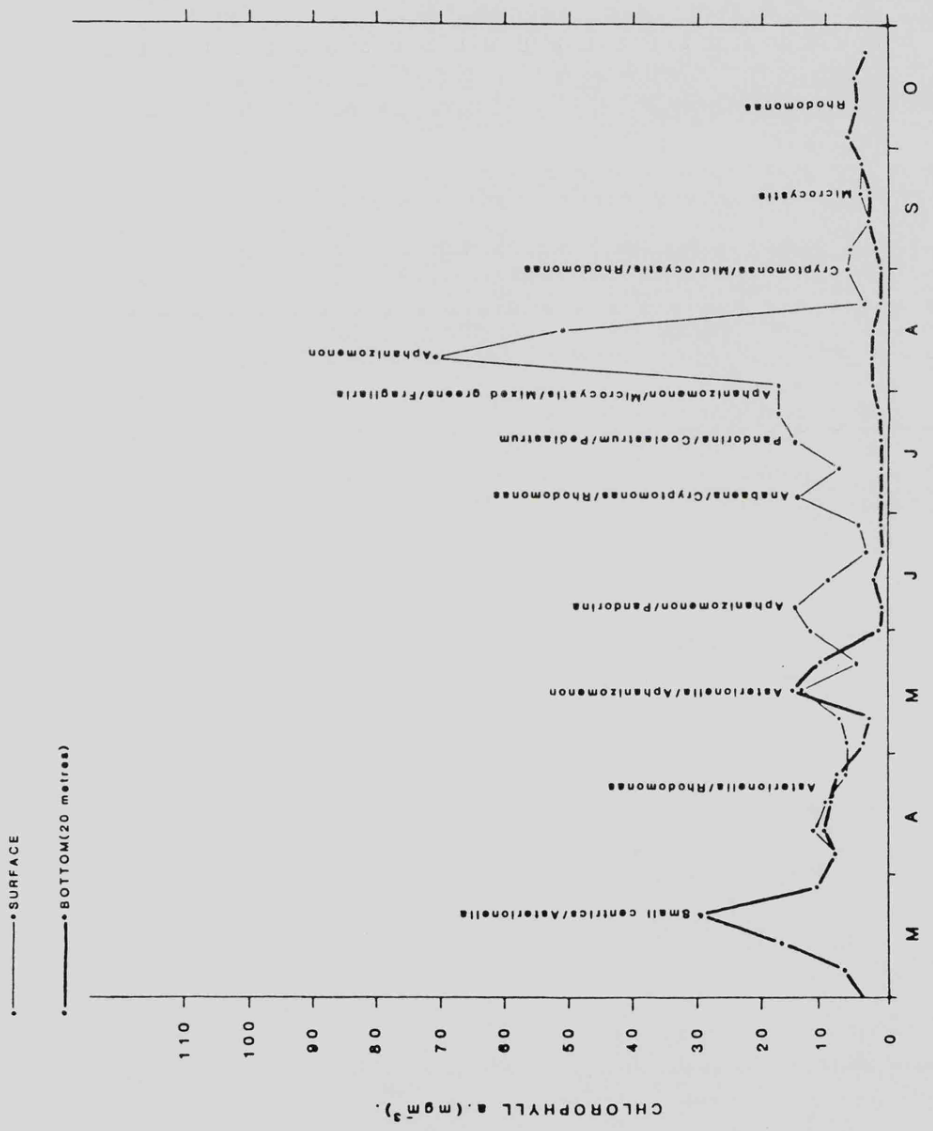


Figure 47. Variations in the vertical distribution of chlorophyll a in Staunton Harold during 1981. Isopleths in mg m^{-3}

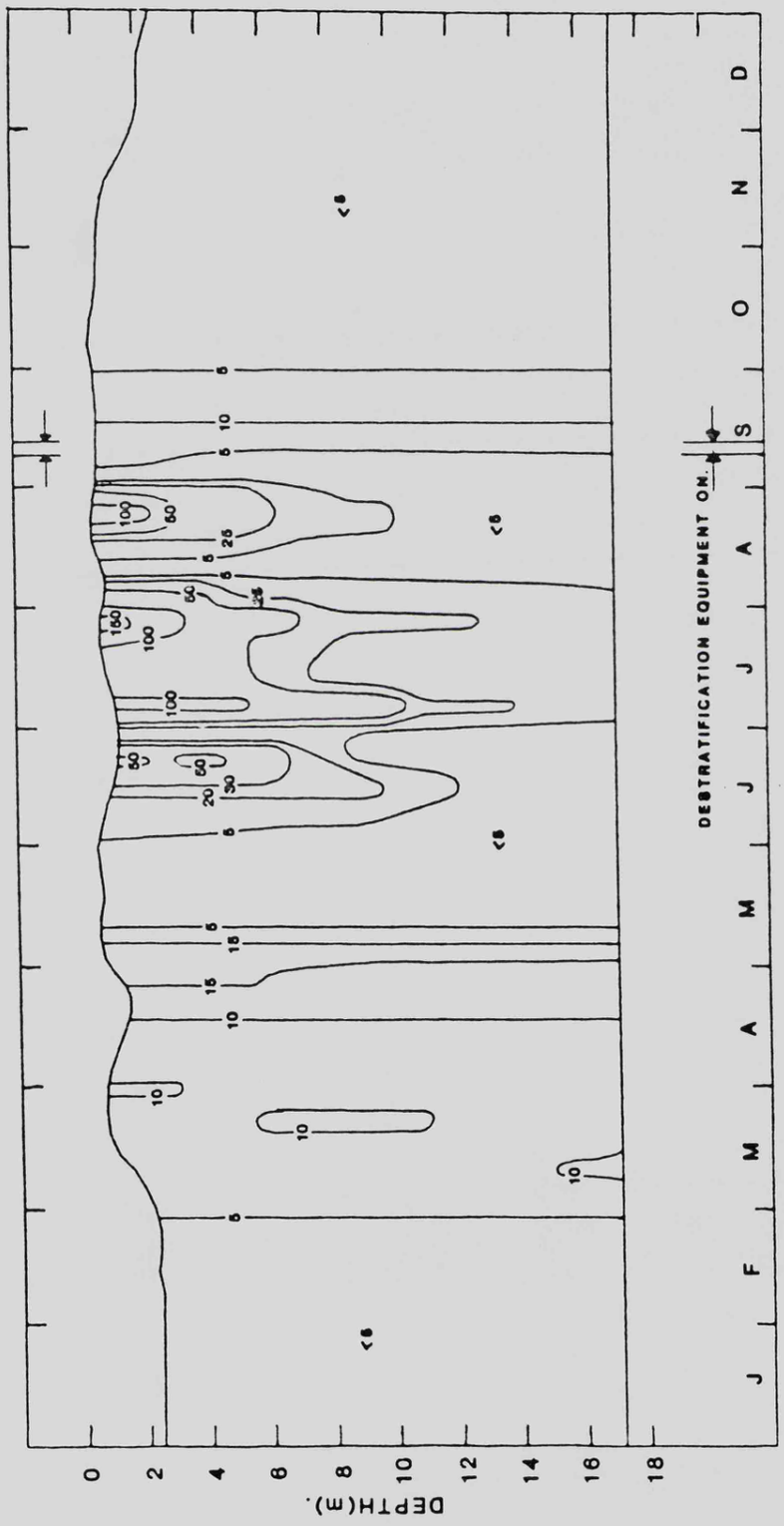


Figure 48. Variations in the vertical distribution of chlorophyll a in Staunton Harold during 1982. Isopleths in mg m^{-3}

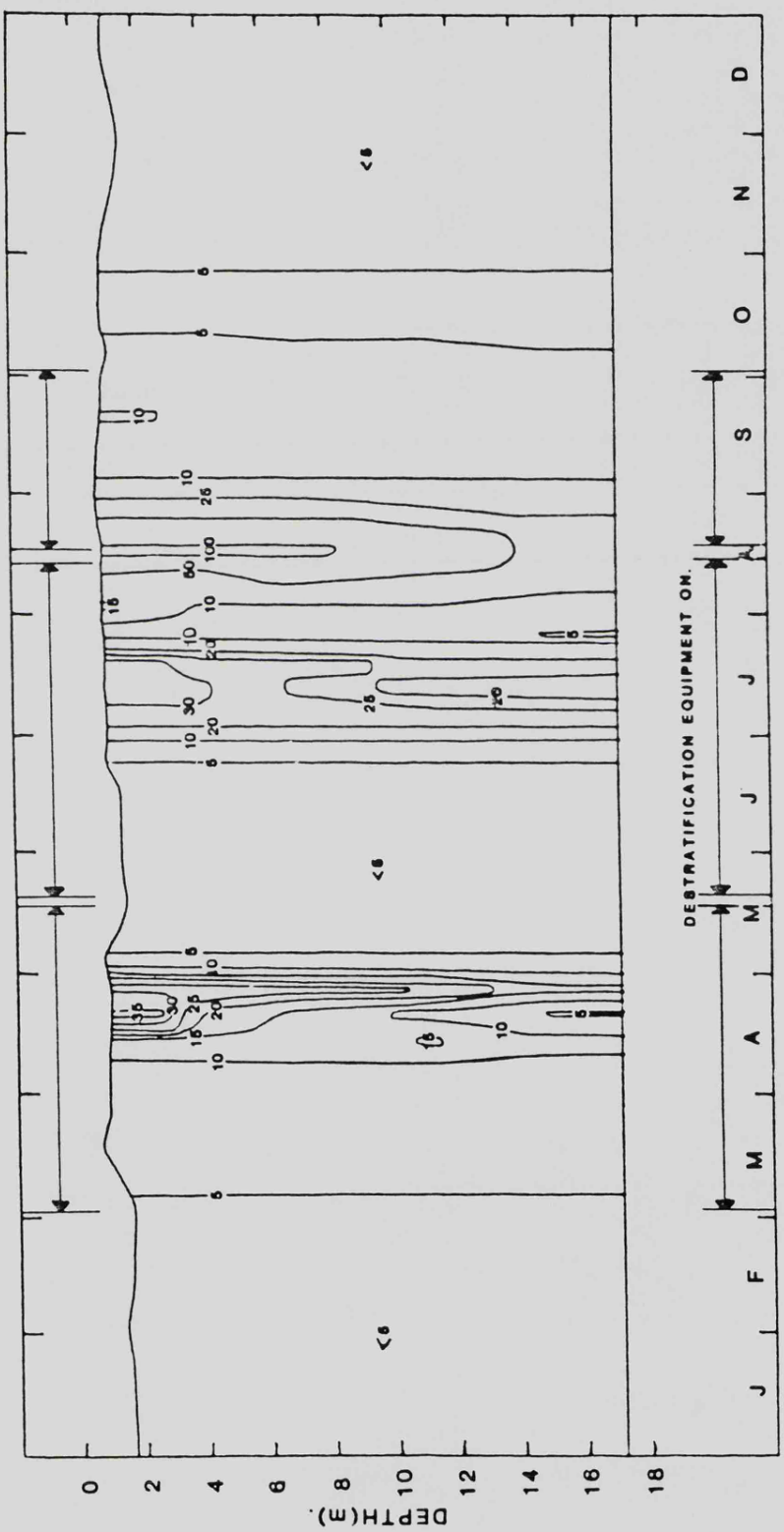


Figure 49. Variations in the vertical distribution of chlorophyll a in Staunton Harold during 1983. Isopleths in mg m^{-3}

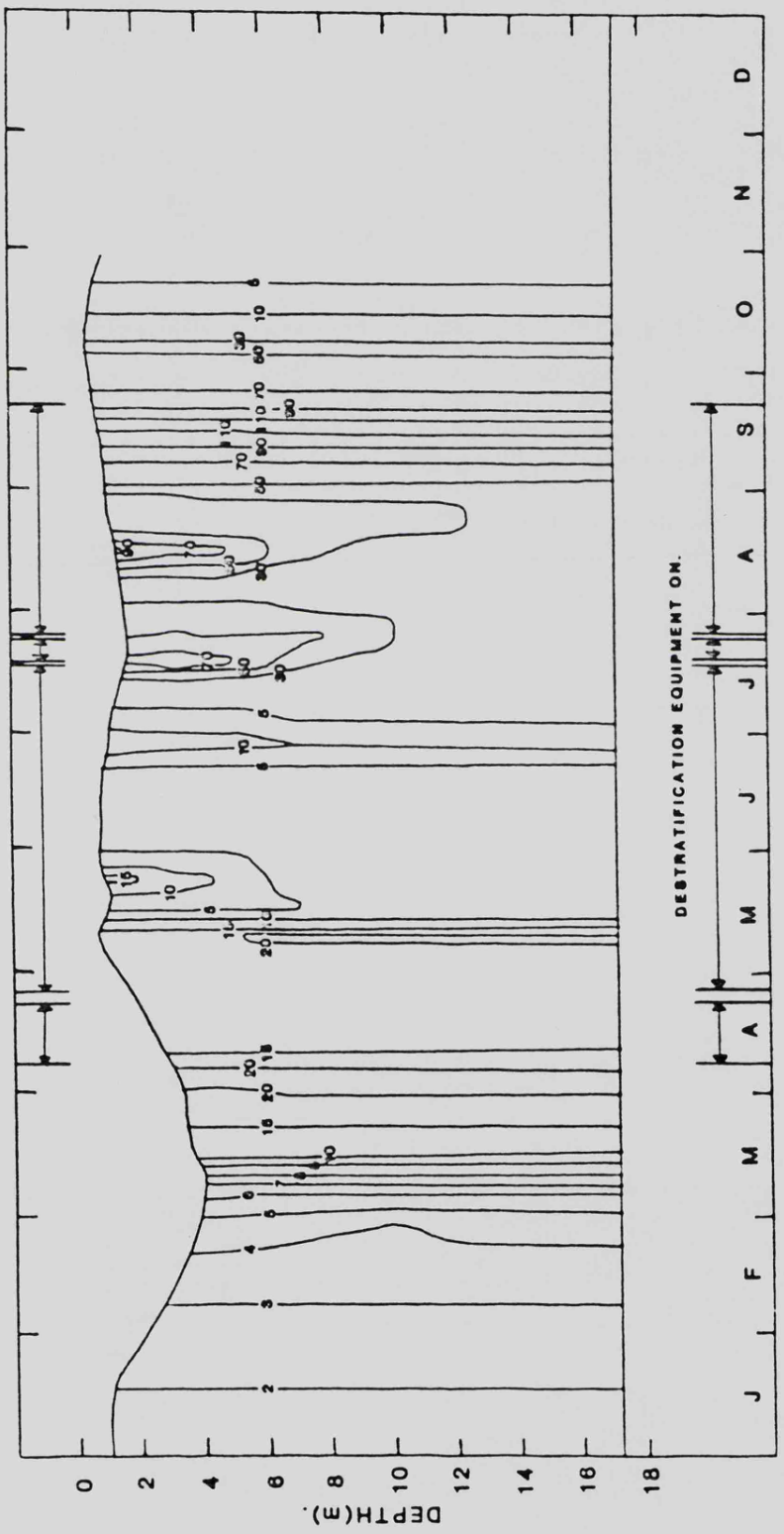


Figure 50. Variations in the vertical distribution of chlorophyll a in Foremark during 1981. Isopleths in mg m^{-3}

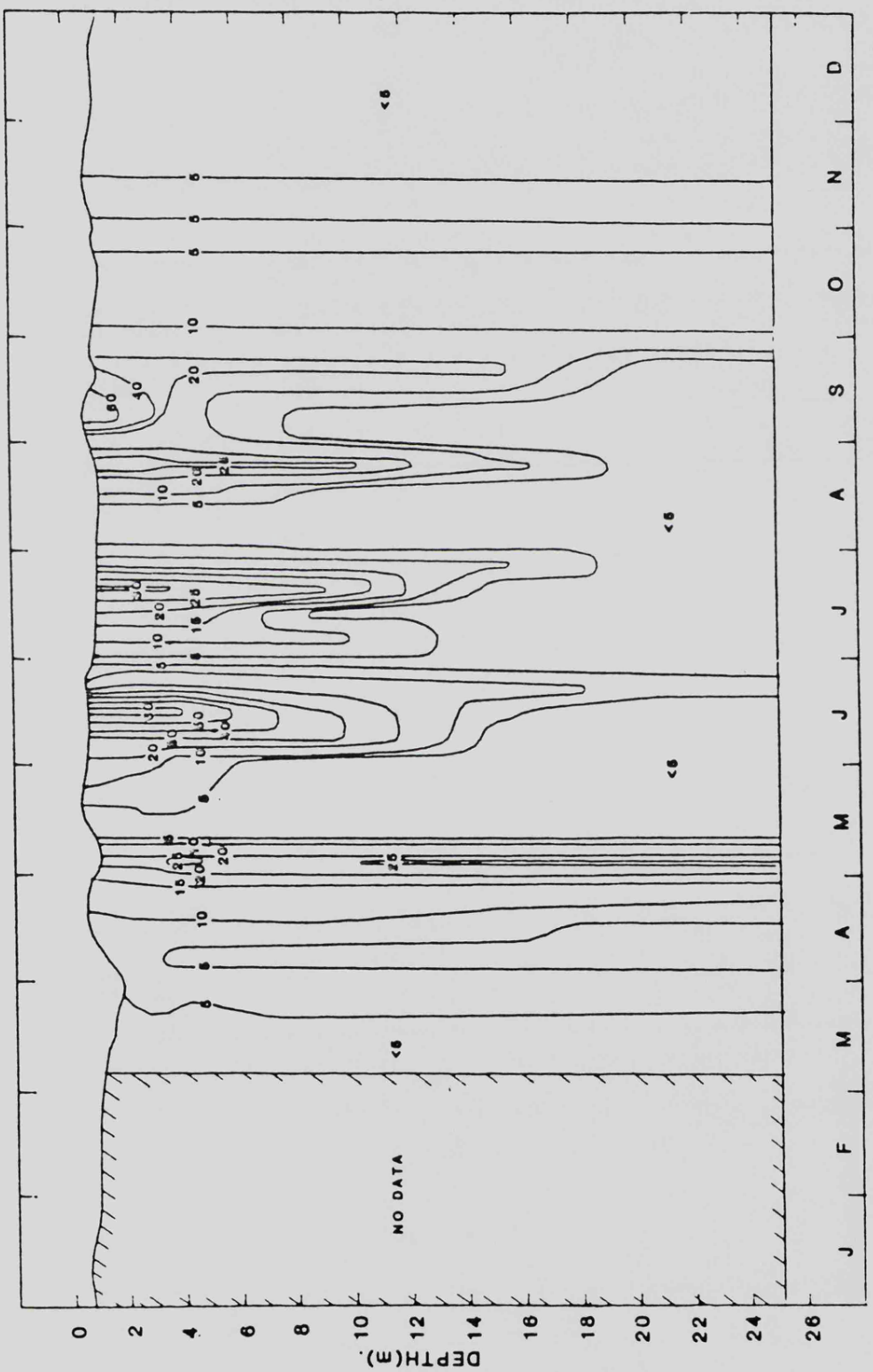


Figure 51. Variations in the vertical distribution of chlorophyll a in Foremark during 1982. Isopleths in mg m^{-3}

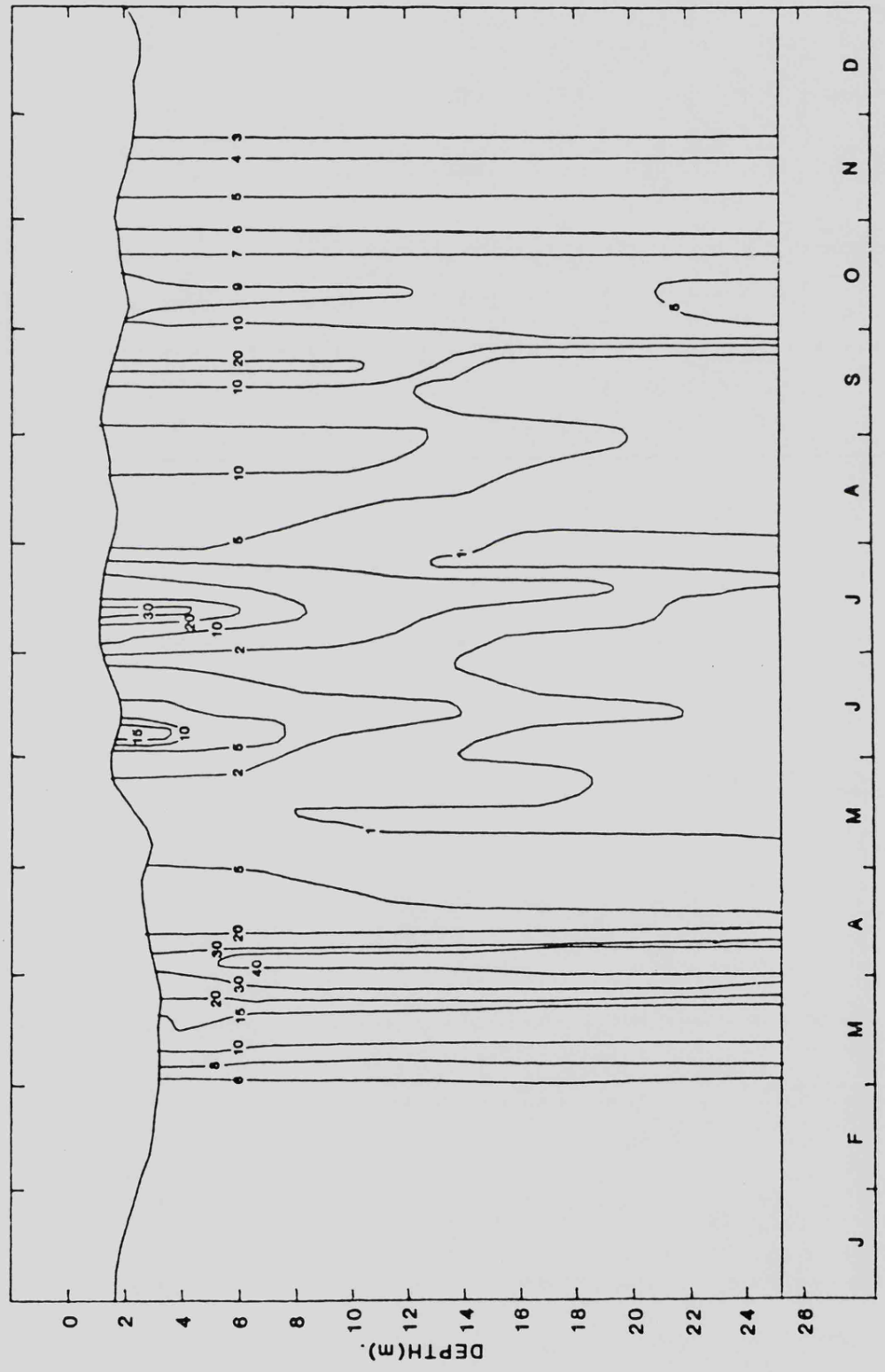
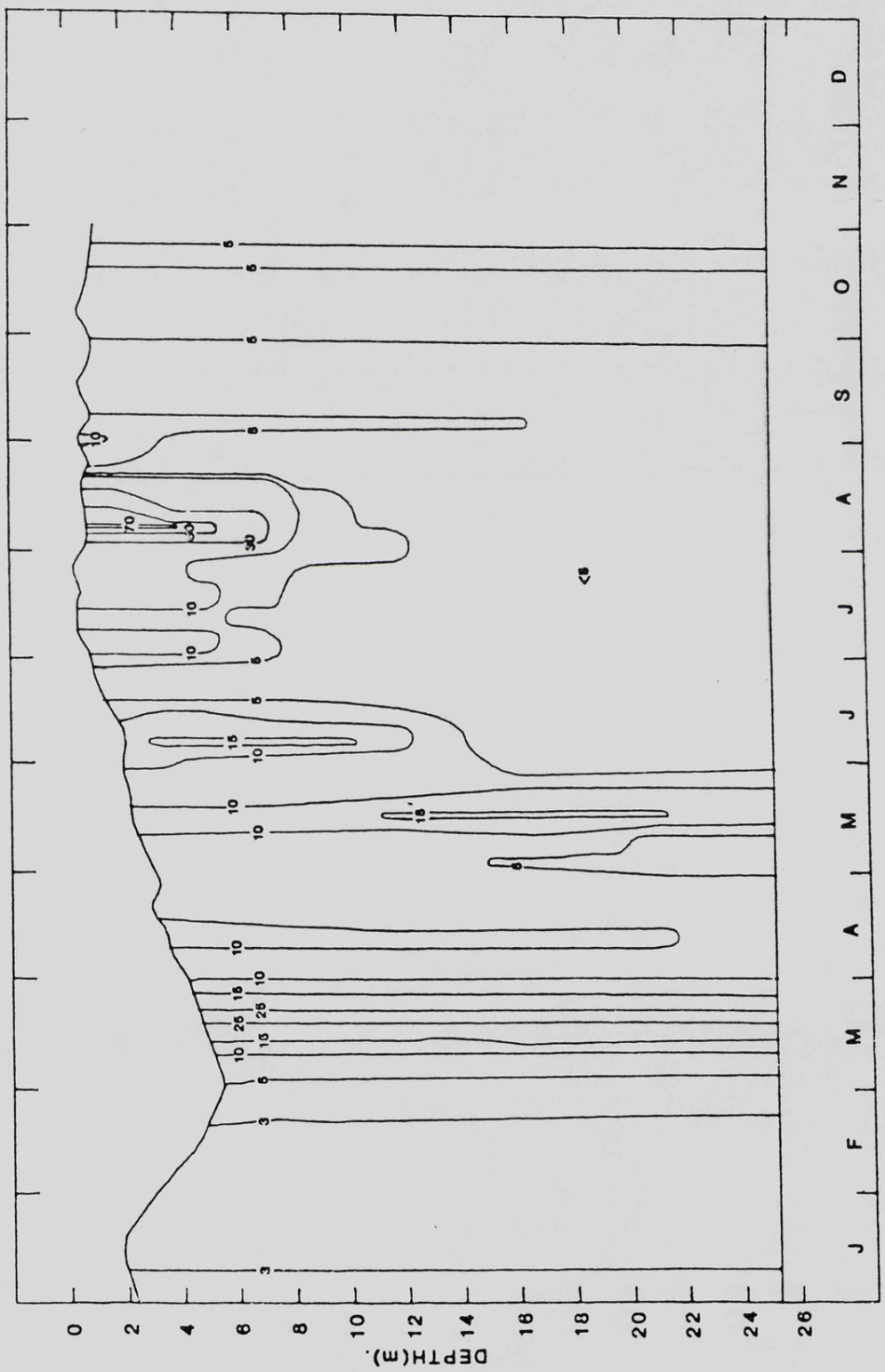


Figure 52. Variations in the vertical distribution of chlorophyll a in Foremark during 1983. Isopleths in mg m^{-3}



because problems were encountered when counting several taxa during the study. The method of treatment of these taxa for analyses are given in Appendix 4.

The seasonal periodicity of phytoplankton in both reservoirs, like the fluctuations in biomass, followed a general pattern which was repeated during each year of the study and was very similar to that found by Hutchinson (1967) and Reynolds (1980 1984a 1984b) for eutrophic, temperate lakes. Spring diatoms formed the first peak of the year, followed by an early summer assemblage dominated by green algae which was overtaken by cyanobacteria in the late summer. Cryptomonads were common thoughout and peaked at times when no other taxa were dominant. The numerically dominant or co-dominant taxa are shown in Figures 41, 42 and 43 for Staunton Harold and 44, 45 and 46 for Foremark.

The following observations and discussion relate the vertical and temporal changes of the main phytoplankton species to changes in environmental variables, especially thermal gradients, ratio of underwater light to mixed depth and water column stability in Staunton Harold and Foremark in 1981. This year is discussed fully because it was the year of study in which natural physical processes dominated both reservoirs.

4.2.1 Staunton Harold.

Monodus increased during the early spring (Figure 53) and reached a population maximum of 20000 cells ml^{-1} at the beginning of March. Its decline paralleled the decrease in *Zmix:Zeu* ratio (Figure 22) and the increase in temperature until, by the middle of April, its density was very low. The population was found to be evenly distributed with depth throughout the period that it was present.

Figure 53. The vertical distribution of *Monodus* (cells ml^{-1}) in Staunton Harold during 1981.

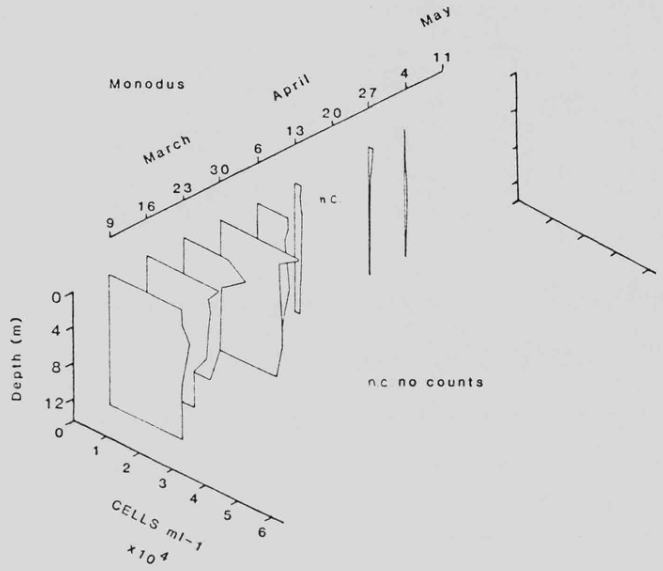
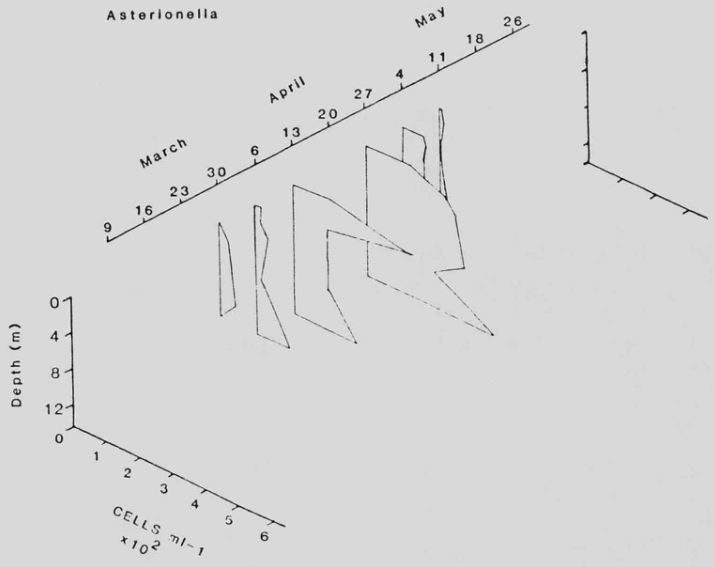


Figure 54. The vertical distribution of *Asterionella formosa* (cells ml^{-1}) in Staunton Harold during 1981.



Cryptomonads were dominant, over diatoms during the vernal period (March to April), perhaps due to reduced grazing pressure. The temporal and vertical changes of *Rhodomonas minuta* and *Cryptomonas* spp. are shown in Figures 55 and 56. The populations of both taxa were abundant throughout the spring and summer and the populations usually increased following increases in stability and during periods when the *Zmix:Zeu* ratios were high (Figure 22). *Rhodomonas* had reached its population maximum (4500 cells ml^{-1}) on the 13th April. The highest density of *Cryptomonas* (2000 cells ml^{-1}) during the vernal peak was observed a fortnight later on the 27th April. Both taxa had declined to low densities by the 11th May. Clinograde distributions occured during these population increases.

Rhodomonas had two more growth phases during the summer. The first, in May/June reached a maximum of 5000 cells ml^{-1} at the surface following an abrupt increase in stability. In early August, it had a brief resurgence with a distinct maxima (3000 cells ml^{-1} at 1.5 metres) on the 3rd August.

Cryptomonas had a second major growth phase during August following an abrupt increase in stability and the *Zmix:Zeu* ratio. The population was concentrated at the surface with 6000 cells ml^{-1} on the 24th. This presumably was a result of vertical migration to the optimum depth.

Diatoms (which usually dominate the vernal period) were subdominant in this year. Small centric diatoms (which were usually evenly distributed with depth) started to increase in early March (Figure 57) and reached a maximum of 1500 cells ml^{-1} at 14 metres, probably as a result of sedimentation, on the 30th March. Subsequent decline was rapid but the population increased again during May and June. Fluctuations in abundance and depth distribution throughout this two month period followed decreases in stability and low *Zmix:Zeu* ratios.

Figure 55. The vertical distribution of *Rhodomonas minuta* (cells ml^{-1}) in Staunton Harold during 1981.

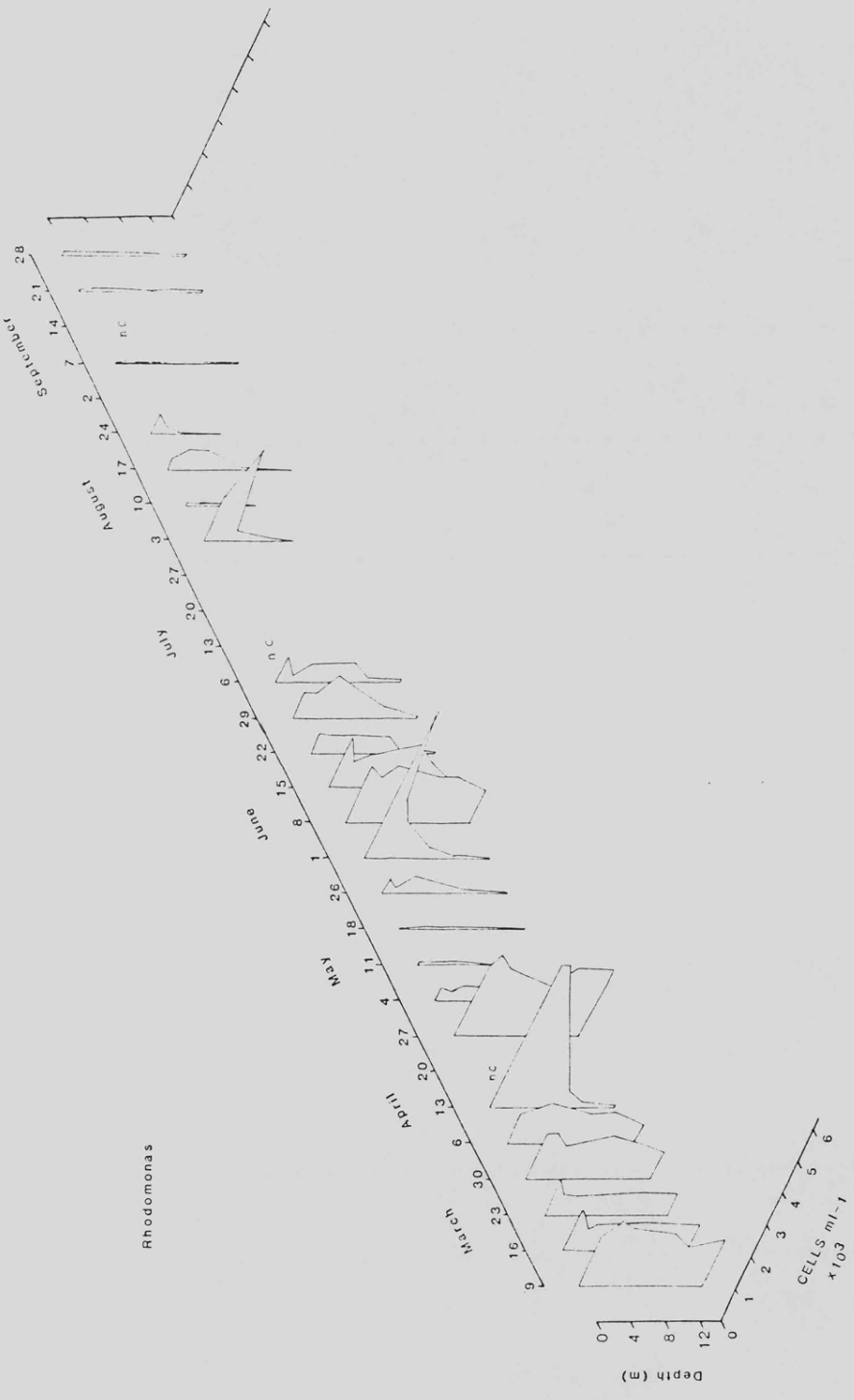


Figure 56. The vertical distribution of *Cryptomonas* spp. (cells ml^{-1}) in Staunton Harold during 1981.

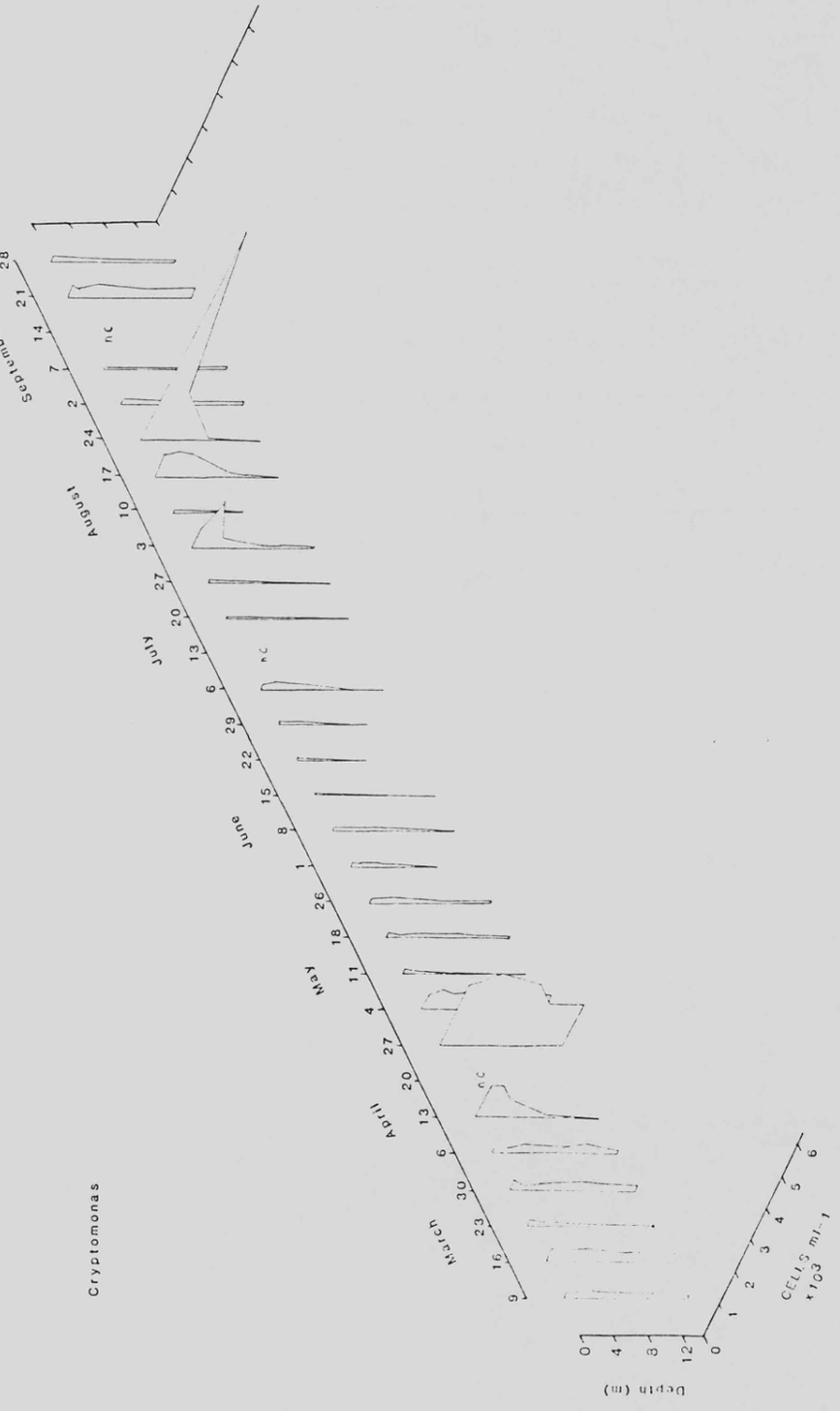
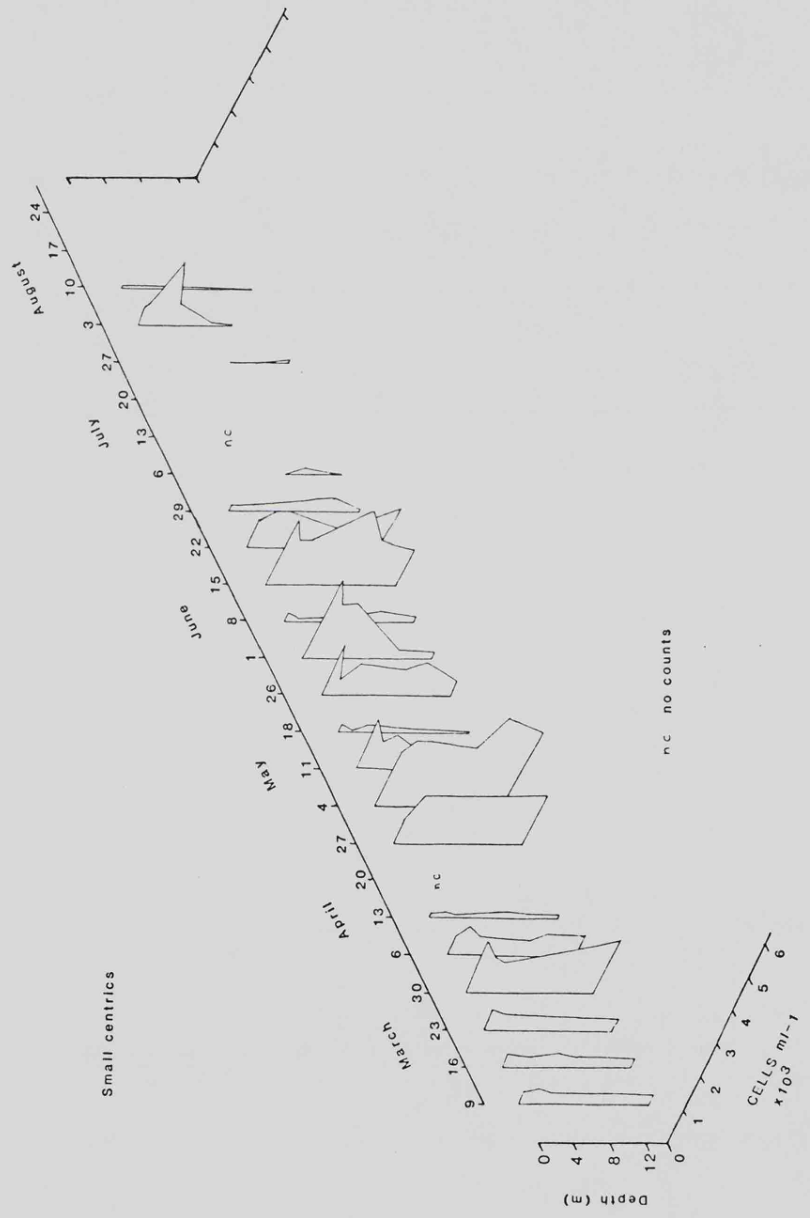


Figure 57. The vertical distribution of small centric diatoms (cells ml^{-1}) in Staunton Harold during 1981.



Asterionella (Figure 54) reached a population maximum of 300 cells ml^{-1} on the 27th April following the demise of the small centrics but itself declined when the small centric population began to increase again during early May. The depth distribution on the 27th April revealed higher densities at the bottom implying that the colonies were sedimenting as a result of the more stable conditions. *S. astraea* (Figure 58) was observed at low densities during the vernal period but increased quickly in June as a result of a sharp decrease in the stability. The population reached a maxima of 300 cells ml^{-1} at the surface on the 3rd August when a distinct depth distribution related to the thermal gradients was observed. The population declined as the stability decreased again.

After the rapid temperature increase in early summer, a number of small Chlorophytes, including *Chlamydomonas* and *Ankyra* dominated the community for short periods. The filamentous Cyanobacteria, *Aphanizomenon* and *Anabaena* (Figures 59 and 60) increased throughout June and July. *Anabaena* reached a maximum density of nearly 20000 cells ml^{-1} on the 6th July and 3 weeks later *Aphanizomenon* reached a population maximum of 540000 cells ml^{-1}. Both populations showed distinct depth distributions which was a result of cell/colony buoyancy. The fluctuations in the populations up to and after their dominance was linked to both water column stability and the *Zmix:Zeu* ratio - the population increased as stability and *Zmix:Zeu* increased and declined or was inter upted when these parameters decreased.

Microcystis concentrations remained relatively low and reached a population maximum, earlier than usual, on the 20th July. Density then declined and remained low for the rest of the summer.

Figure 58. The vertical distribution of *Stephanodiscus astraea* (cells ml^{-1}) in Staunton Harold during 1981.

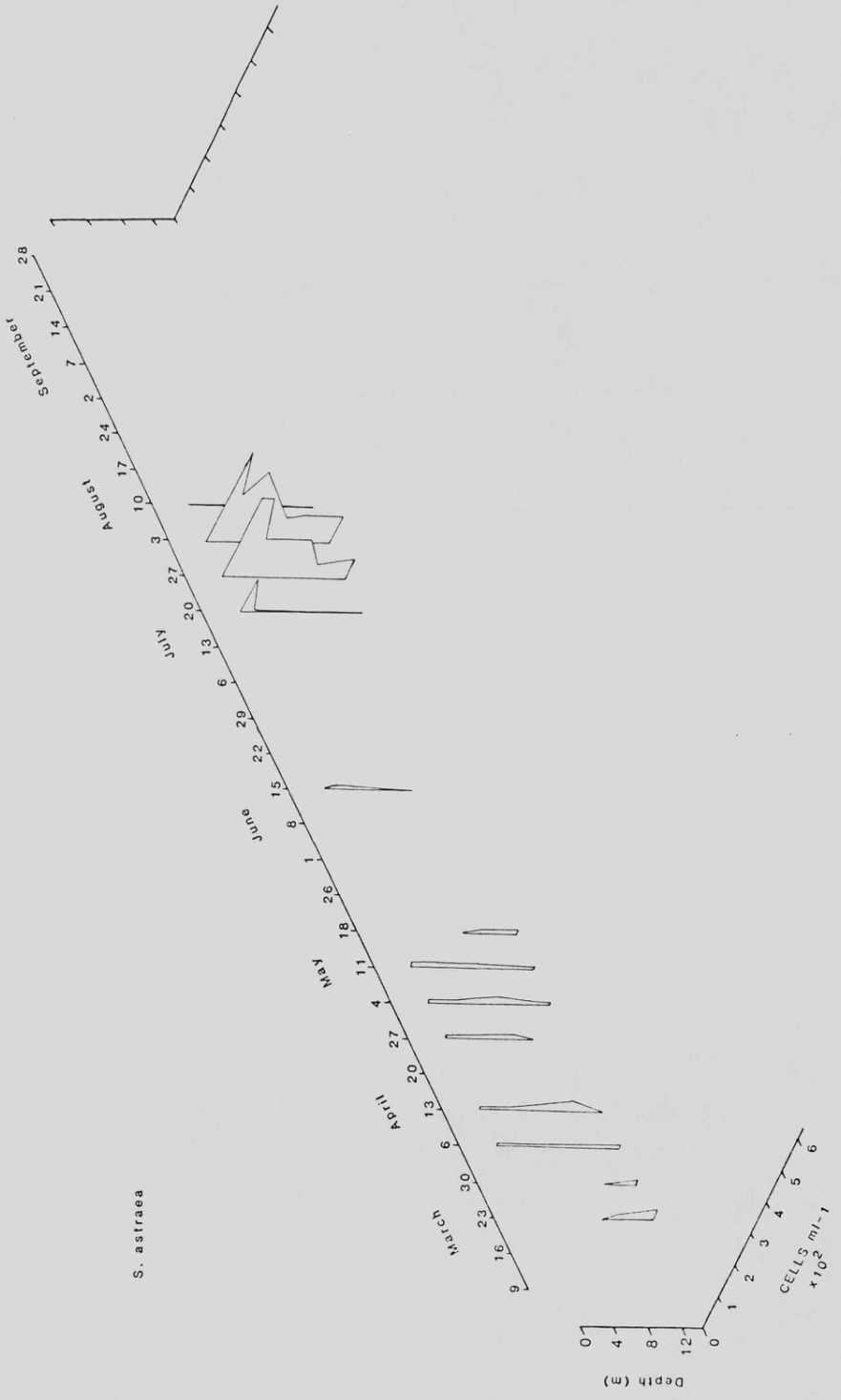


Figure 59. The vertical distribution of *Aphanizomenon flos-aq ua* (cells ml^{-1}) in Staunton Harold during 1981.

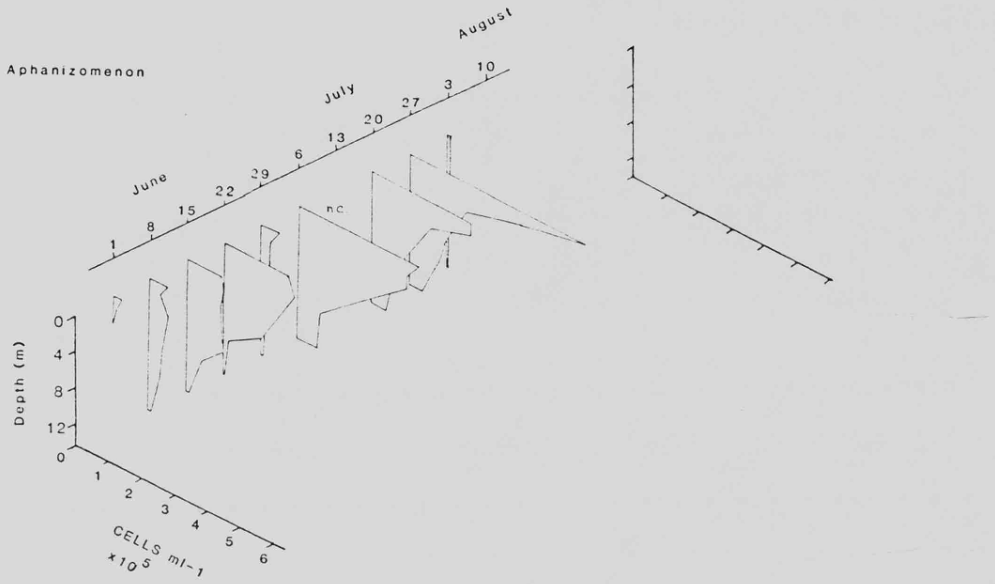
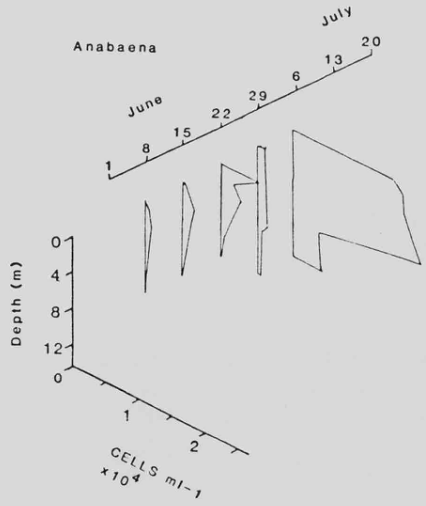


Figure 60. The vertical distribution of *Anabaena* spp. (cells ml^{-1}) in Staunton Harold during 1981.



4.2.2 Foremark.

Cryptomonads were abundant throughout the vernal period (Figures 61 and 62): both *Cryptomonas* and *Rhodomonas* reached population maxima on the 30th March at 200 and 2800 cells ml^{-1} respectively. These taxa, as observed in Staunton Harold, were found to be relatively abundant throughout the rest of the summer and the fluctuations in the populations occured in response to changes in water column stability and *Zmix:Zeu* ratios as described above. *Cryptomonas* reached another maximum in early July and *Rhodomonas* in late May and also early July. The depth distributions shown by these populations were a result of two factors: thermal gradients during very windy spells, and cell motility which allowed migration to preferred depths during calmer periods.

The vernal diatoms included *S. astraea, Asterionella* and small centrics. All reached population maxima in late March and early April (Figures 63 and 64). *S. astraea* reached a population maximum of 312 cells ml^{-1} on the 24th April and *Asterionella* (1400 cells ml^{-1} at 14 metres) a week later. *Asterionella* reached two maxima of 1200 cells ml^{-1} on the 15th June and 3000 cells ml^{-1} at the surface on the 20th July. These responses, as in Staunton Harold were to decreases in the stability and increases *Zmix:Zeu* ratio. *S. astraea* also responded to the deepening of the mixed layer in June and reached a maximum of 130 cells ml^{-1} on the 15th June. The depth distribution of both populations resulted from the thermal gradients with the population maxima above the thermocline. Small centrics were present at low densities throughout the summer.

Aphanizomenon appeared earlier than usual in Foremark (Figure 65) and increased throughout June and July to reach a peak of 800000 cells ml^{-1} at 3m

Figure 61. The vertical distribution of *Cryptomonas* spp. (cells ml^{-1}) in Foremark during 1981.

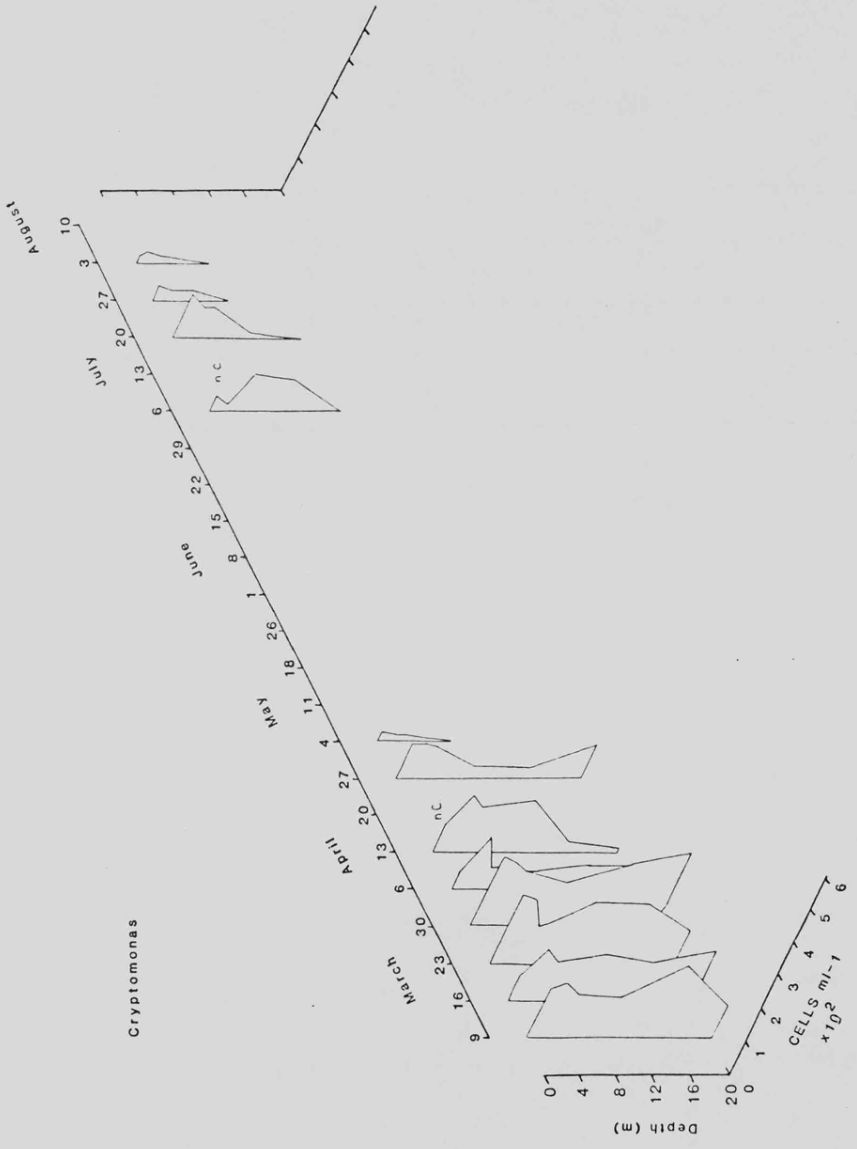


Figure 62. The vertical distribution of *Rhodomonas minuta* (cells ml^{-1}) in Foremark during 1981.

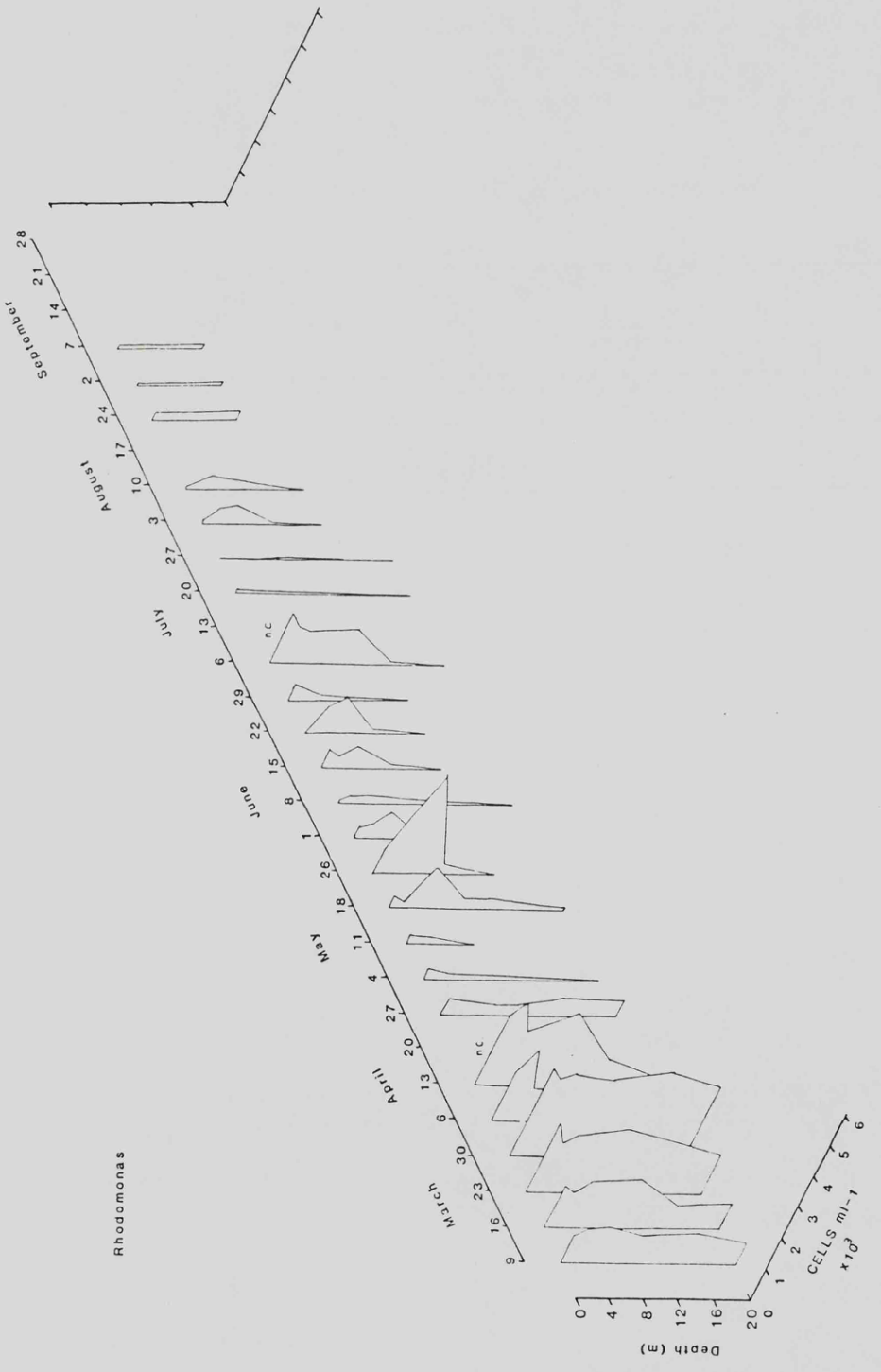


Figure 63. The vertical distribution of *Stephanodiscus astraea* (cells ml^{-1}) in Foremark during 1981.

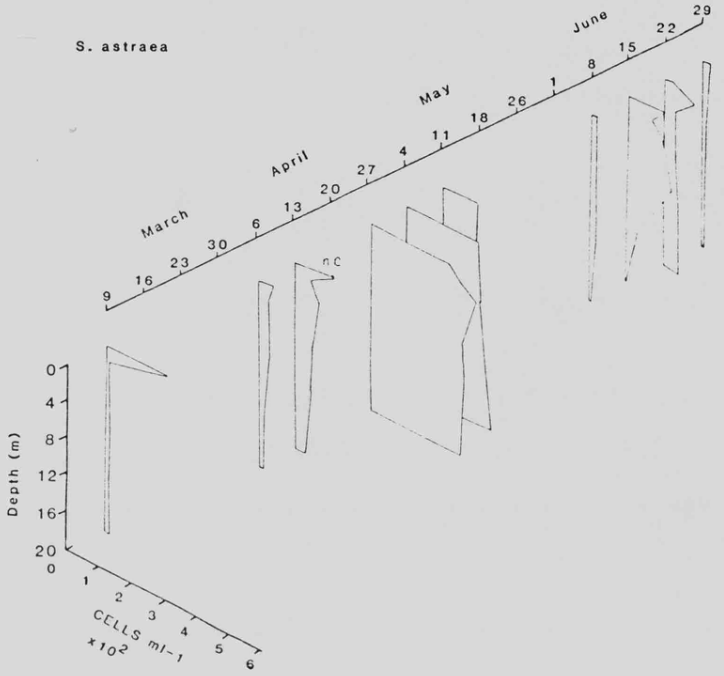


Figure 64. The vertical distribution of *Asterionella formosa* (cells ml^{-1}) in Foremark during 1981.

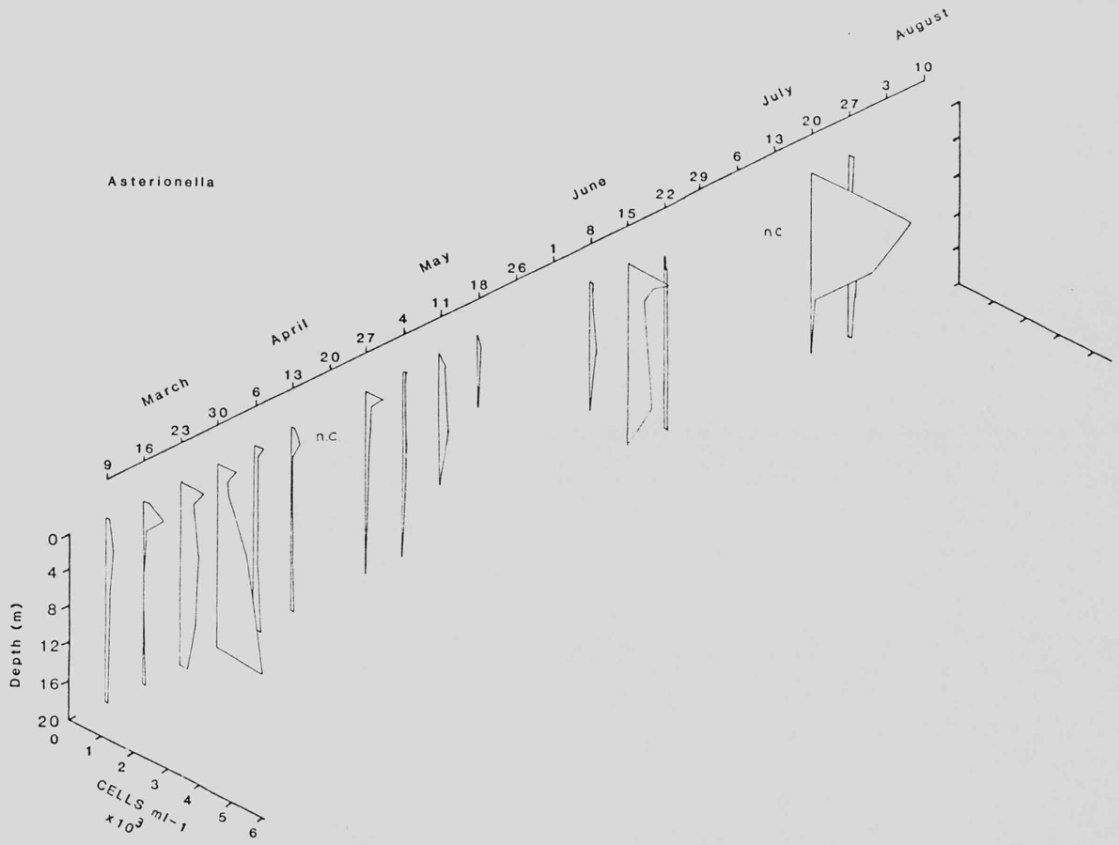


Figure 65. The vertical distribution of *Aphanizomenon flos-aqaua* (cells ml^{-1}) in Foremark during 1981.

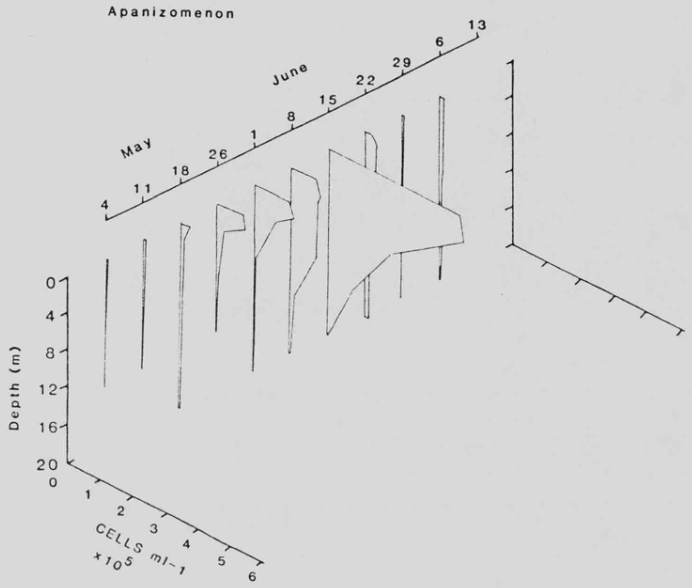
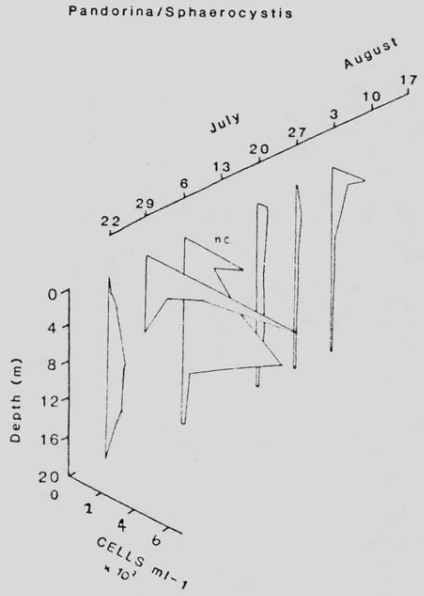


Figure 66. The vertical distribution of *Pandorina/Sphaerocystis* (cells ml^{-1}) in Foremark during 1981.



on the 15th June. This population declined rapidly and only occured at low densities thereafter. The increase followed a decrease in the mixed layer and a subsequent increase in the *Zmix:Zeu* ratio and the decline was concomitant with the epilimnetic deepening which started on the 15th June.

Pandorina/Sphaerocystis, which was one of the typical early summer species in these reservoirs, increased during late June following the abrupt decrease in *Zmix:Zeu* and at the start of a period of increasing stability. The population maximum of 1000 cells ml^{-1} occured at the surface on the 29th June. The population then appeared to sink and decline as the *Zmix:Zeu* ratio decreased.

Fragilaria became dominant during late July (Figure 67) at the same time as *Ankistrodesmus* (Figure 68). They both reached maxima (2400 and 550 cells ml^{-1} respectively) on the 20th July. The marked clinograde distributions were again related to thermal gradients.

Finally, *Microcystis* was more abundant in Foremark than Staunton Harold during 1981. The population increased slowly throughout August and September as the water column stabilised and a maximum of 9300 cells ml^{-1} (0-10 metres integrated) was observed on the 7th September. The population declined slowly as the mixed depth increased to 20 metres by the end of September.

The vertical variations shown by the phytoplankton populations were a result of the thermal/density gradients. Distinct clinograde distributions resulted from either the occurence of motile species such as *Cryptomonas* (Figure 56) and *Aphanizomenon* (Figure 59) which were able to occupy their preferred position in the water column or non-motile species such as

Figure 67. The vertical distribution of *Fragilaria crotonensis* (cells ml^{-1}) in Foremark during 1981.

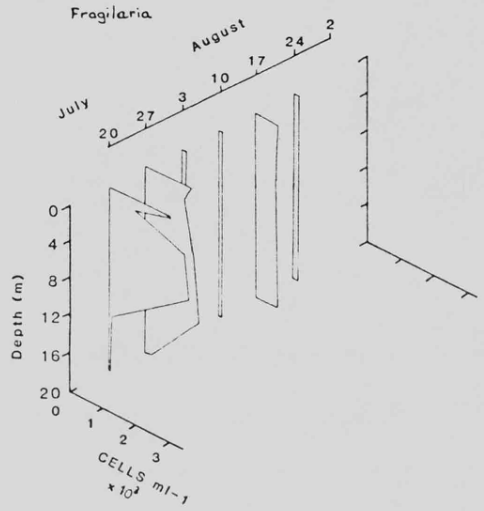
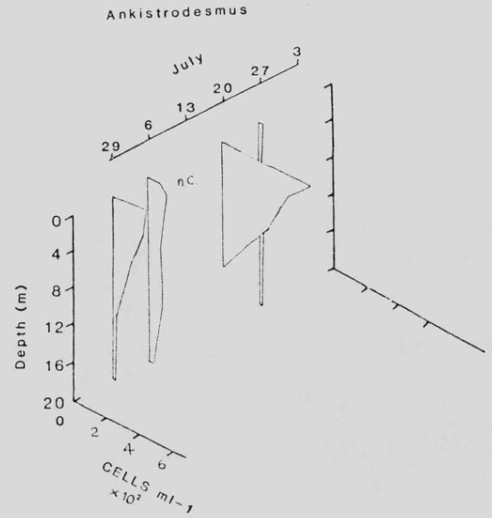


Figure 68. The vertical distribution of *Ankistrodesmus* spp. (cells ml^{-1}) in Foremark during 1981.



Ankistrodesmus (Figure 68) and *Fragilaria* (Figure 67) which rely upon the density gradients and wind induced turbulence to maintain the cells in the epilimnion.

4.3 THE TEMPORAL CHANGES IN THE ABUNDANCE OF DOMINANT SPECIES, 1981 TO 1983.

The seasonal change in phytoplankton species described above was typical of the periodicity in both reservoirs in all three years. The effects of environmental variables on this succession is best explained through an analysis of individual species growth rates. These analyses are carried out below for all three years which include mixed and stratified conditions.

The temporal changes in the densities of dominant species of phytoplankton as a mean for the water column between March and September during 1981, 1982 and 1983 are shown in Figures 69 and 70 for Staunton Harold and 71 and 72 for Foremark. [Repeat copies of nutrients (Figures 26 and 27) and water column stability and *Zmix:Zeu* (Figure 22) have been included to ease comparisons].

4.3.1 The observed rates of phytoplankton density change *(kn).*

Estimates of the net rate of population density changes (*kn*) for the major species were calculated from the phytoplankton densities and Figures 69 to 72. Values of *kn* were calculated from points grouped by eye; the minimum number of points used in the calculation of either increases or decreases was 3. The rates of change have been split into two groups - vernal (March to April) and summer (May to September). The maximum and mean rates are shown for each year of the study in Appendix 5. Maximum rates of increase during the summer period for both reservoirs are given in Table 15. The data have been grouped into artificially mixed years (Staunton Harold in 1982 and 1983), naturally mixed years (Staunton Harold and Foremark in 1981) and stratified years (Foremark in

Figure 22a (repeat). The temporal changes in water column stability, N^2 (0-5) metres and (0-15) metres and the ratio of the mixed depth to the euphotic depth *(Zmix:Zeu)* in Staunton Harold between March and September in 1981, 1982 and 1983. The solid bar at the top indicates periods of artificial mixing.

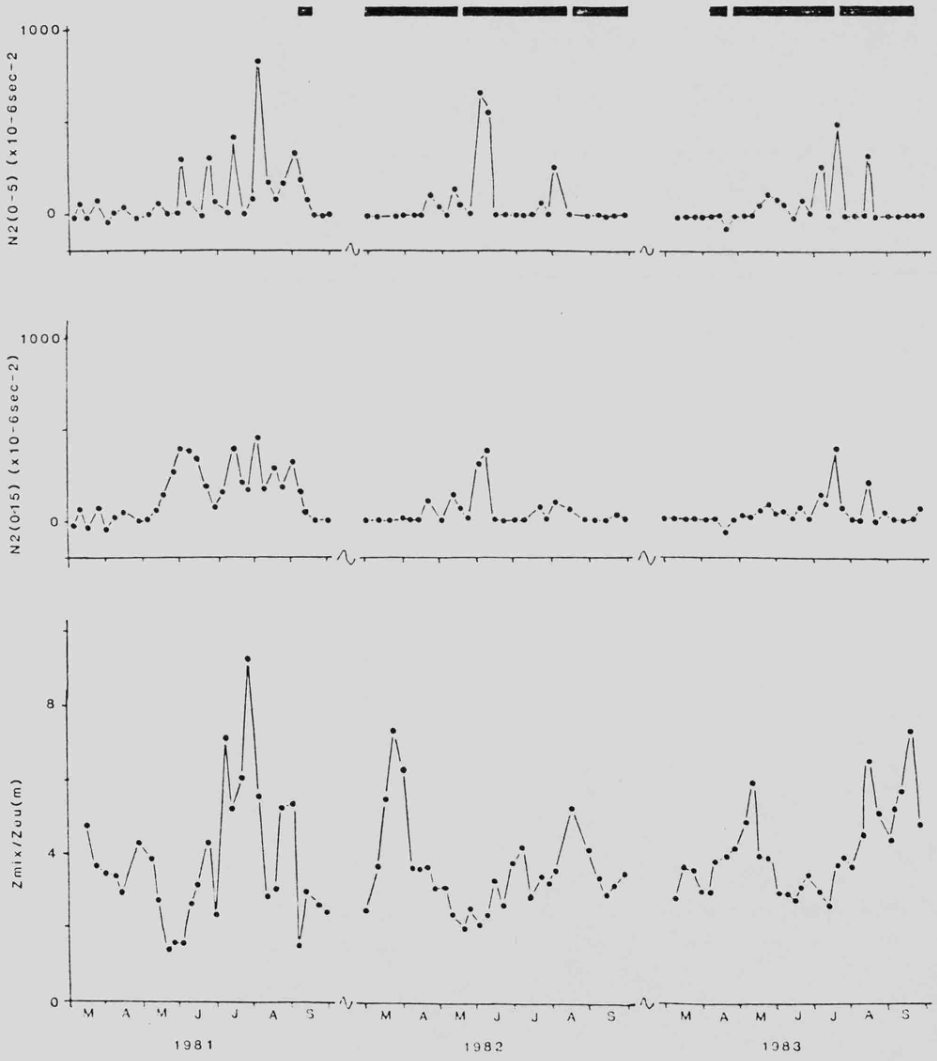


Figure 26 (repeat). The temporal fluctuations in the N:P ratio, nitrate, ortho -phosphate and silica concentrations in Staunton Harold between March and September during 1981, 1982 and 1983. (Closed circles ●-● represent surface values whilst open circles o-o represent bottom (14 m) samples, if different to the surface). The solid bar at the top indicates periods of artificial mixing.

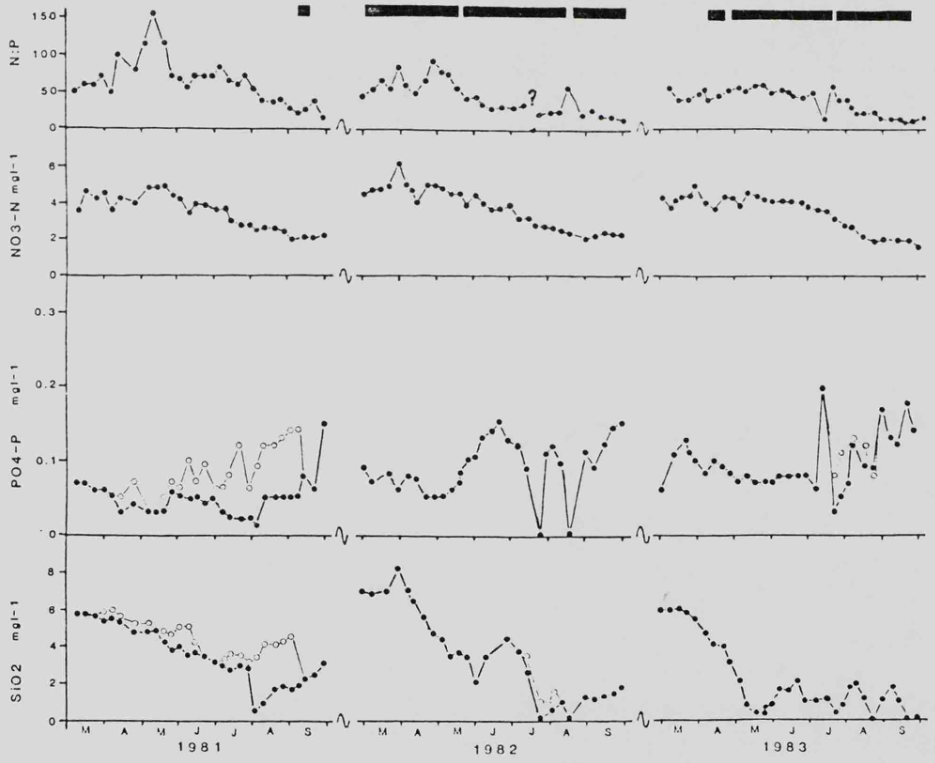


Figure 69. The concentrations in cells ml^{-1} (as natural logarithms) of selected species of phytoplankton (expressed as the water column mean) in Staunton Harold between March and September during 1981, 1982 and 1983.

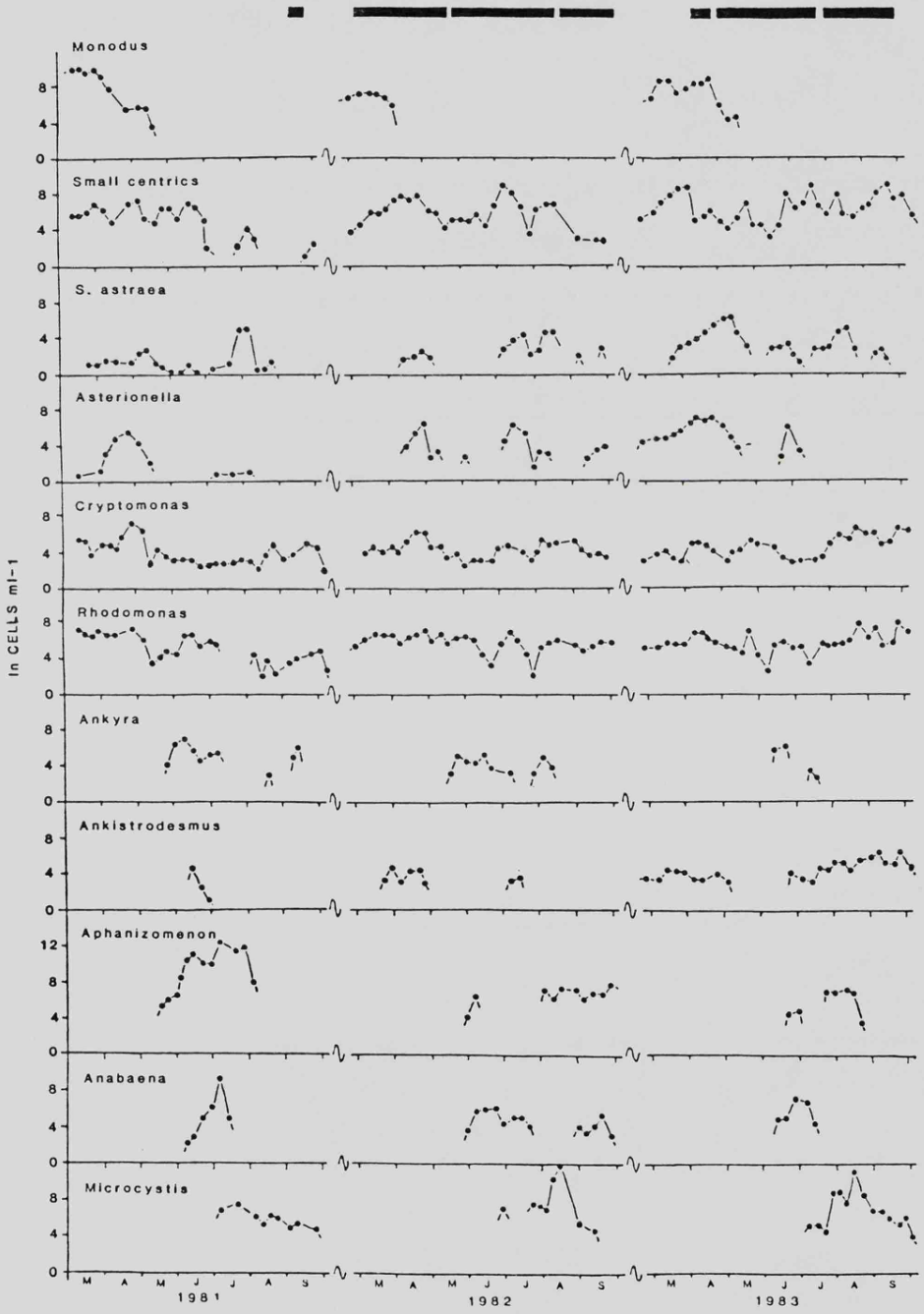


Figure 70. The concentrations in cells ml^{-1} (as natural logarithms) of selected species of phytoplankton (expressed as the water column mean) in Staunton Harold between March and September during 1981, 1982 and 1983.

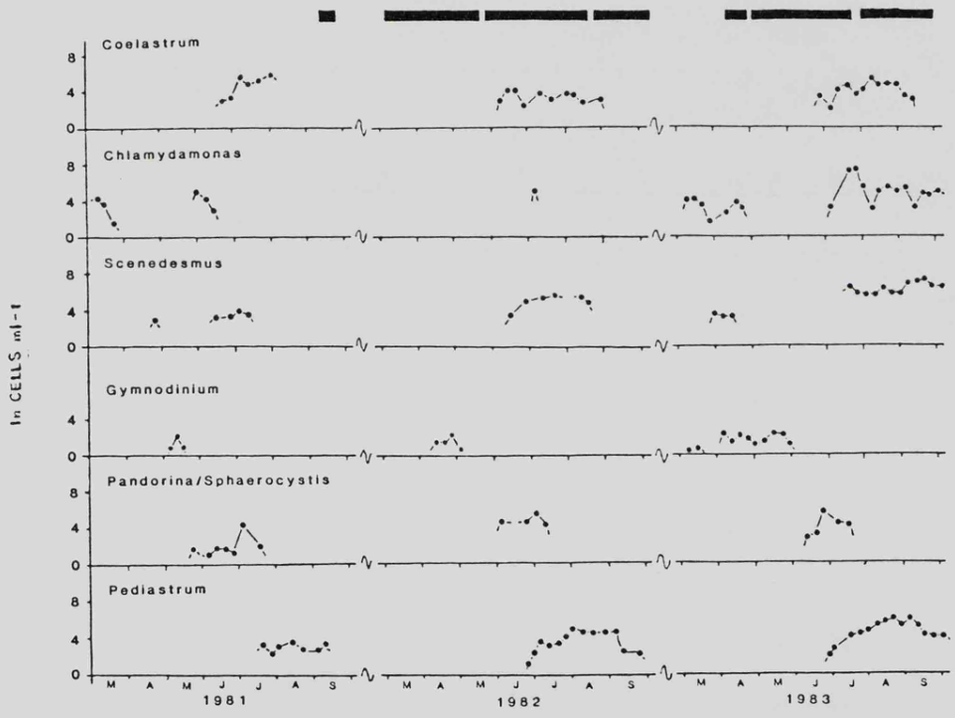


Figure 22b (repeat). The temporal changes in water column stability, N^2 (0-5) metres and (0-15) metres and the ratio of the mixed depth to the euphotic depth *(Zmix:Zeu)* in Foremark between March and September in 1981, 1982 and 1983.

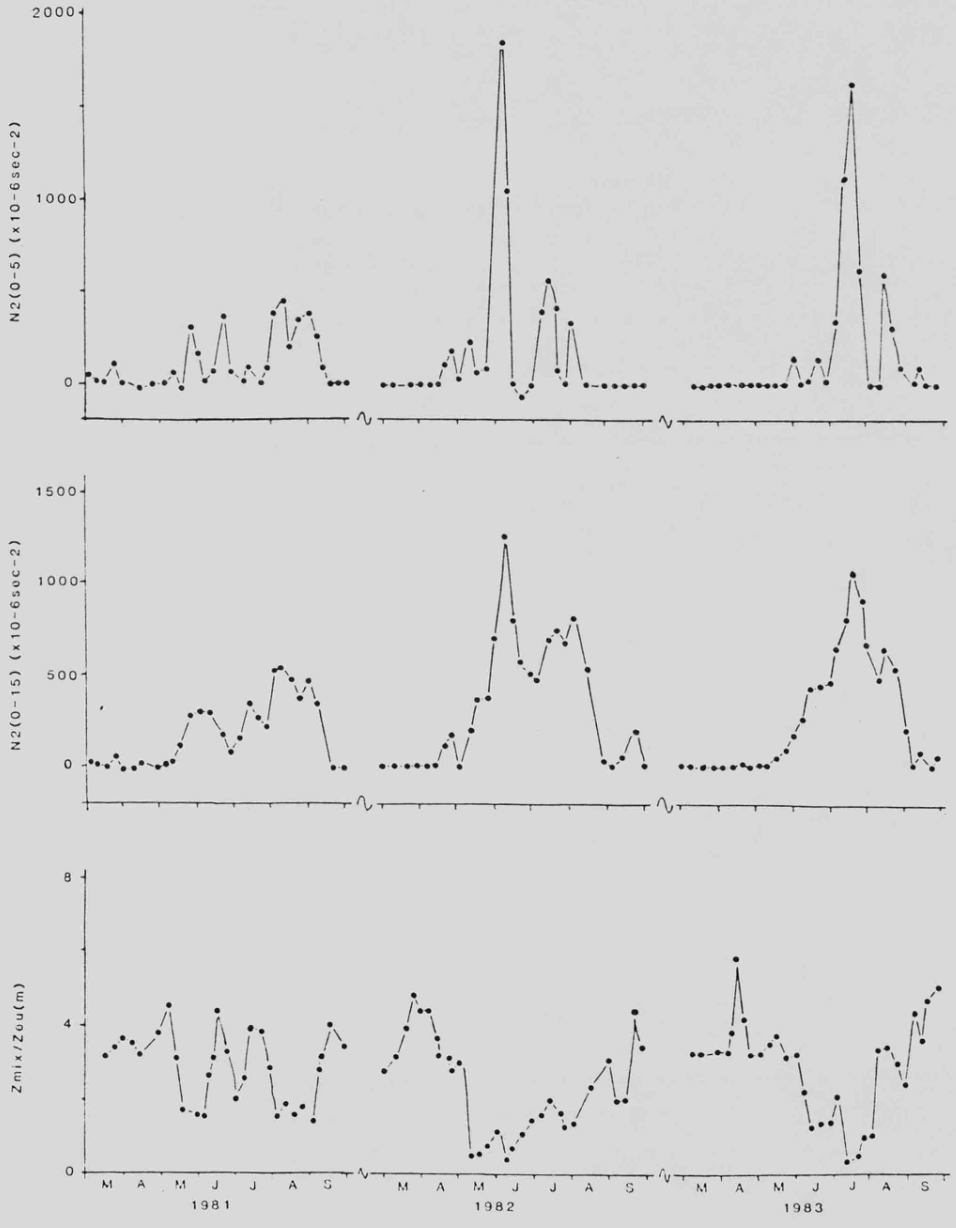


Figure 27 (repeat). The temporal fluctuations in the N:P ratio, nitrate, ortho -phosphate and silica concentrations in Foremark between March and September during 1981, 1982 and 1983. (Closed circles ●-● represent surface values whilst open circles o-o represent bottom (20 m) samples, if different to the surface).

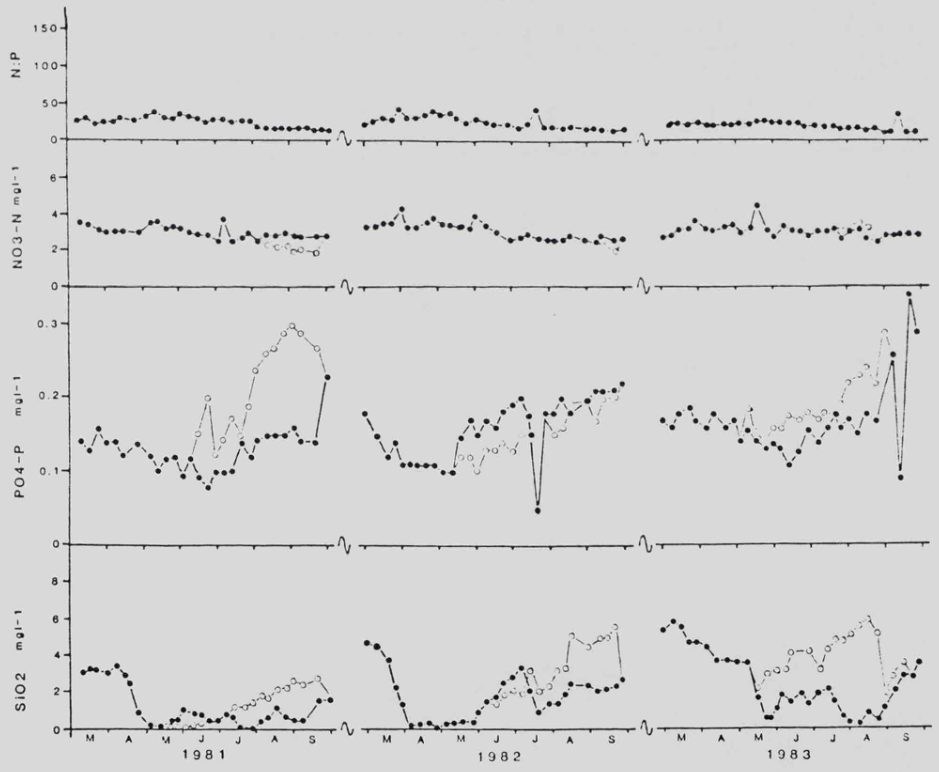


Figure 71. The concentrations in cells ml^{-1} (as natural logarithms) of selected species of phytoplankton (expressed as the water column mean) in Foremark between March and September during 1981, 1982 and 1983.

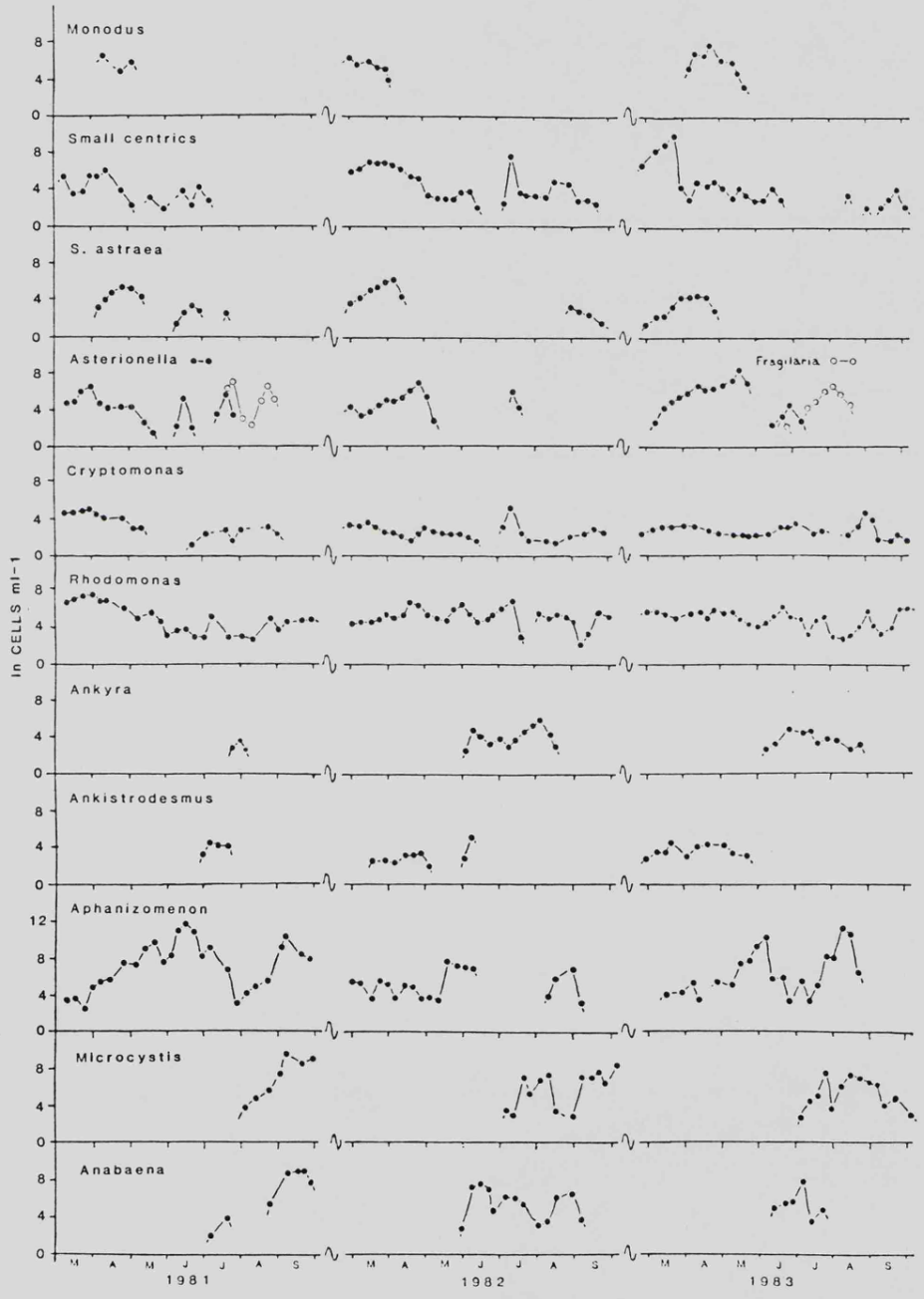


Figure 72. The concentrations in cells ml^{-1} (as natural logarithms) of selected species of phytoplankton (expressed as the water column mean) in Foremark between March and September during 1981, 1982 and 1983.

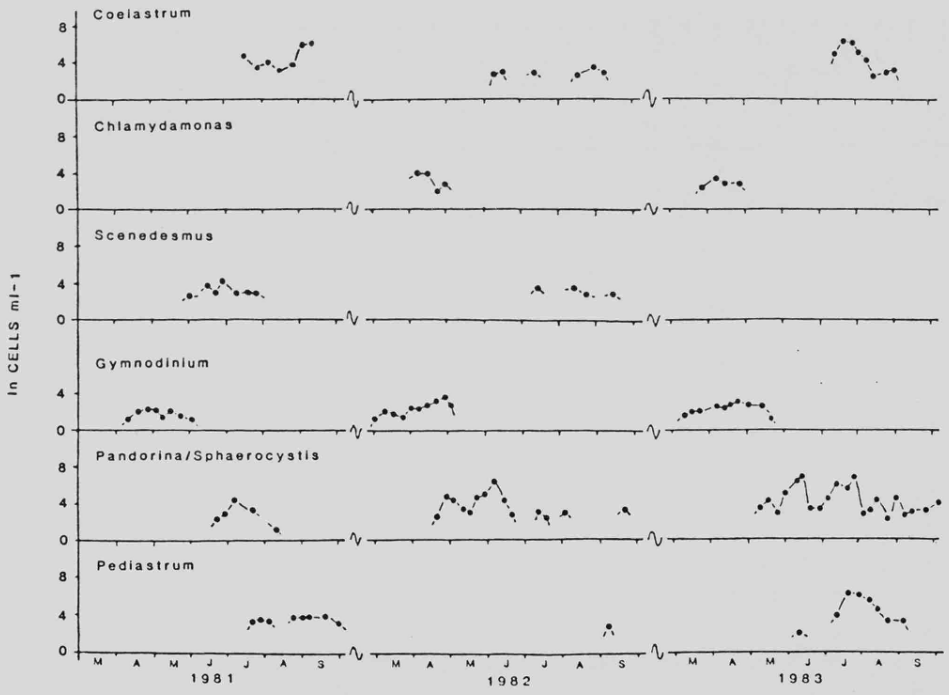


TABLE 15. THE MAXIMUM OBSERVED SUMMER RATES OF POPULATION DENSITY INCREASE (k_n d^{-1}) OF SELECTED SPECIES OF PHYTOPLANKTON FROM STAUNTON HAROLD AND FOREMARK BETWEEN 1981 AND 1983.

	Artificial mixing		Natural mixing		Stratified	
Reservoir	SH	SH	SH	F	F	F
Year	1982	1983	1981	1981	1982	1983
Small centrics	0.38	0.34	0.31	0.30	0.29	0.20
S. astraea	0.15	0.14	0.16	0.17	0.20	-
Asterionella	0.27	0.08	-	0.45	0.15	0.15
Cryptomonas	0.35	0.16	0.20	0.06	0.09	0.16
Rhodomonas	0.29	0.42	0.29	0.34	0.28	0.15
Ankistrodesmus	0.20	0.08	-	-	0.16	-
Chlamydomonas	-	0.30	-	-	0.10	0.04
Aphanizomenon	0.19	0.13	0.20	0.18	0.31	0.29
Anabaena	0.14	0.18	0.26	0.11	0.23	0.14
Microcystis	0.16	0.19	0.16	0.16	0.17	0.26
Coelastrum	0.17	0.07	0.08	0.10	-	0.11
Ankyra	0.34	-	0.40	-	0.11	0.10

1982 and 1983).

Average rates of summer increase from these groupings revealed that small centrics, *Cryptomonas* and *Rhodomonas* had highest rates of increase during artificially mixed years with lower rates in naturally mixed years and lowest rates in stratified years. *Stephanodiscus astraea, Aphanizomenon, Anabaena* and *Microcystis* all had rates of increases which were lowest in the artificially mixed years and highest in the stratified years. The response by *S. astraea* to mixing was not definite as there was only one short period of increase in Foremark during 1982 and 1983 and so the average values for each category of stability (Table 15) were misleading. In contrast, it appears from the increased abundances under both naturally and artificially mixed conditions that this species was favoured by low water column staility. *Asterionella, Chlamydomonas, Ankyra* and *Ankistrodesmus* did not show any clear pattern. In the case of the latter three species it was because the data set was not sufficient to compare the three groups.

4.3.2 The effects of environmental variables on phytoplankton species.

The environmental variables which affect the responses of phytoplankton are numerous and complex. Water chemistry and water column stability have been identified as the major factors controlling the waxing and waning of different species (Lund 1965 1981, Reynolds 1976 1984a b) and are discussed here in relation to growth and decline of the major species in the reservoirs.

4.3.2.1 Nutrients.

The vernal period was usually dominated by diatoms including small centrics, *Stephanodiscus astraea* and *Asterionella formosa*. These species

generally commenced growth during early spring when the water column was well mixed and concentrations of silica, phosphate and nitrate were relatively high. The increase and timing of these species appeared to be controlled by factors other than nutrients and temperature. Reynolds (1973) suggested that increased underwater light was responsible. The silica levels were observed to fall as the diatom populations increased and the rate of uptake exceeded the rate of replenishment from inflows or recycling. For example in Staunton Harold, *S. astraea* increased exponentially during March, 1983 reaching a peak of 500 cells ml^{-1} on the 9th May, 1983 whilst the silica levels had fallen from above 6 mgl^{-1} to 0.6 mgl^{-1}. Lund (1949, 1950) showed that the decline in the *Asterionella* populations in Windermere coincided with the decline in silica levels to below 0.5mgl^{-1}. Silica probably limited the diatom populations in Foremark during the vernal period of 1981 and 1982.

The relationship between silica and diatoms, one of the best studied relationships between environmental chemistry and phytoplankton periodicity (Lund 1949 1950 1964, Reynolds 1973, Bailey-Watts 1976, Lack and Johnson 1983) was observed in both reservoirs during the three years of study.

It is most probable that decreases in phosphate and nitrate levels during the vernal period were partly due to uptake by diatoms. Both phoshate and nitrate levels decreased during the growth phase of *S. astraea* described above. The drop of phosphate from 0.17 mgl^{-1} on the 1st March to 0.11 mgl^{-1} on the 13th April coincided with the increase in *Asterionella* and *S. astraea*.

The early summer phytoplankton were usually dominated by green algae including colonial forms such as *Pandorina/Sphaerocystis* and *Coelastrum.* These taxa appeared to be present when the water columns were begining to stratify and the concentrations of nitrate and phosphate were relatively high (compared

to the late summer levels). *Pediastrum* and *Pandorina/Sphaerocystis* all increased in June and July, for example, after phosphate levels had increased during May and June, 1982 in Staunton Harold. The nitrate levels were decreasing throughout this period. The decline of these species appeared to be related to factors such as water column stability and underwater light which is discussed below. Reynolds (1973, 1978) suggested however, that the growth of these species in Crose Mere was eventually limited by nitrate, although there was no evidence to support nitrate limitation in Staunton Harold and Foremark.

Small centric diatoms were observed throughout the majority of the study in both reservoirs. Increased densities usually followed silica renewal during the summer, for example in Foremark, silica levels increased during June and July, 1982 and small centric diatoms responded by increasing rapidly to a maxima of 3100 cells ml^{-1} on the 12th July, after which both silica levels and the population of small centrics declined.

The mid-late summer period was generally dominated by three taxa of Cyanobacteria. *Aphanizomenon* usually began to develop early in the summer (eg. Foremark during 1981) and continued to increase throughout the summer. The maxima generally occured in July or August. The dominance of the filamentous Cyanobacteria usually followed that of the Chlorophytes and it appeared that the Cyanobacteria became dominant when nitrate levels had dropped to below 3 mgl^{-1}. Reynolds (1978) suggested that *Aphanizomenon* and *Anabaena* were in direct competition with the green algae; green algae predominated whilst nutrients, especially nitrate, were abundant but Cyanobacteria became dominant as the nitrate levels fell. *Aphanizomenon* and *Anabaena* can fix atmospheric nitrogen (Fogg *et al.* 1973) and therefore would have had a competitive advantage when nitrate concentrations are low. The greater abundance of *Aphanizomenon* in Foremark throughout the three years and especially in 1981 may

have been a result of the lower nitrate levels in the reservoir (compared to Staunton Harold) therefore giving it a competitive advantage over the green algae.

Microcystis (which became dominant after the filamentous Cyanobacteria in late summer) appeared to be able to tolerate low nitrate concentrations. This species cannot fix atmospheric nitrogen but conitnued growing at low levels. The decline of this species appeared not to be related to chemical factors.

Summer diatom populations occured in both reservoirs during each year of the study; this is a common feature of eutrophic, temperate lakes (Hutchinson 1967, Reynolds 1973 1980 1984a, Lack and Johnson 1983). The occurence of diatoms usually coincided with the replenishment of the silica supply. However, the silica levels had not crashed in the spring of Staunton Harold during 1981 and 1982 and the populations of diatoms continued to grow (other environmental conditions such as decreased water column stability due to natural mixing were also favourable). The peak of *S. astraea* during August, 1981 resulted in the sudden crash of silica to limiting levels.

Several taxa appeared regularly which were often sub-dominant and became dominant on occasions. These included *Cryptomonas, Rhodomonas, Ankistrodesmus, Scenedesmus and Ankyra*. These species appeared to be tolerant to the wide range of nutrients in the reservoirs and Reynolds (1984a) suggested that the small Chlorococcallean taxa were more typical of hypertrophic systems.

The general pattern of periodicity therefore appeared to be partly controlled by the seasonal availability of nutrients along nutrient gradients (Kilham and Kilham 1980) in a way which has been reported from many studies

(Reynolds 1976, Jones 1977a, Lack and Johnson 1983).

4.3.2.2 Water column stability.

Small centric diatoms and *S. astraea* were found to be more abundant in Staunton Harold during the artificially mixed years when water column stability was low (Figures 69, 71 and Figure 22). However, although the rates of increase were higher for small centrics during artificial mixing, those for *S. astraea* were lower than in the stratified years and this was probably because of the high average value from Foremark (see section 4.2.3.1). In Foremark, small centric diatoms, which were usually present throughout the year became insignificant when the stability was high in Foremark during the summers of 1982 and 1983. Diatoms have been shown to be favoured by turbulent, well mixed conditions (Lund 1949 1950, Ridley 1966, Haffner 1974).

The response of *Pandorina/Sphaerocystis* (Figures 70 and 72) was also related to the degree of water column stability. It has already been noted that this taxa was less abundant in Staunton Harold during artificial mixing and more abundant with higher growth rates during stratified periods in Foremark. A comparison of cell concentration, the *Zmix:Zeu* ratio and N_2 values (Figures 70, 72 and 22) show that the net rates of increase of *Pandorina /Sphaerocystis* occured when the *Zmix:Zeu* ratio was low or decreasing and the stability was high or increasing. *Pandorina/Sphaerocystis* was not eliminated from Staunton Harold during 1982 and 1983 as a result of artificial mixing but occured at lower densities during periods when the *Zmix:Zeu* values were lowest and immediately following periods when N_2 had started to increase.

Filamentous Cyanobacteria (*Aphanizomenon* and *Anabaena)* were more abundant and had higher rates of increase in Foremark under stable conditions than in

Staunton Harold. Natural mixing (and a decrease in stability) in Foremark suppressed the rate of increase (Figure 69, 71 and 22). *Microcystis*, on the other hand, appeared not to have been affected by changes in water column stability.

Cryptomonads were found to be present in both reservoirs throughout the majority of the study and became dominant on several occasions. In Staunton Harold during 1981 and 1982, the vernal peaks were dominated by Cryptomonads, diatoms were sub-dominant: the reverse situation was more usual. Late in 1981, *Cryptomonas* spp. were dominant and formed a large biomass peak in late August after the Cyanobacterial pulse. Cryptomonads have been found to be able to grow under a wide range of conditions (Reynolds 1980 1984a, Sommer 1981, Bailey-Watts 1982) and often become dominant during periods when no other species are numerous. However, they are susceptible to high grazing losses (Reynolds 1980, Reynolds *et al.* 1982 1984) and it was possible that these peaks in spring of 1981 and 1982 were a result of reduced grazing pressure at low temperatures which allowed the population to increase before the diatom populations became established.

4.4 PHYTOPLANKTON GROUPS AND ASSEMBLAGES.

The dominant species recorded above could be divided into three groups according to their responses to changes in water column stability and eight assemblages, each one consisting of species which were usually associated together with similar rates of growth, abundances and losses.

4.4.1 Phytoplankton groups.

Species were grouped according to their responses to changes in water column stability and these are shown in Table 16. Group 1 consisted of the species that had the highest rates of growth under mixed conditions with relatively high *Zmix:Zeu* ratios. Group 2 had the highest rates of increase under stable, stratified conditions with low *Zmix:Zeu* ratios. Finally, Group 3 had growth rates which appeared not to be affected by mixing or the ratio of *Zmix* to *Zeu*.

These groupings in response to changes in water column stability are similar to those recorded by Reynolds *et al.* (1983 1984). However, they found that the Cryptomonads and *Ankyra* were favoured more by stable periods or when *Zmix:Zeu* was low and so included them in the second group. These three species suffer from high grazing losses and the true rates of increase need to be adjusted to include this (Reynolds *et al.* 1984). This adjustment could not be made to the rates from Staunton Harold and Foremark as zooplankton data were not available. Reynolds *et al.* (1984) also observed that the develop ment of *Anabaena* populations was arrested by deep mixing and so they placed them in the third group with *Microcystis* rather than Group 2.

4.4.1.1 Phytoplankton size and *r* and *k* stratgists.

Although these 3 groups were established by their response to water column stability, species within each group were generally similar in size. Group 1, with the exception of *Pediastrum*, tended to be small and unicellular, some of which were motile

TABLE 16. CATEGORIZATION OF PHYTOPLANKTON SPECIES ACCORDING TO THEIR RESPONSE TO CHANGES IN WATER COLUMN STABILITIES.

	Physical conditions favoured.	Reservoir species selected.
Group 1.	Mixed, low stability, relatively high *Zmix:Zeu.*	Small centric diatoms, *Cryptomonas, Rhodomonas, Pediastrum, Chlamydomonas, ? Ankyra, ? Asterionella, ? Coelastrum, ? S.astraea.*
Group 2.	Stratified, stable, low *Zmix:Zeu.*	*Pandorina/Sphaerocystis, Aphanizomenon, Anabaena*
Group 3.	Tolerant of wide range of stability and Zmix:Zeu.	*Microcystis.*

(e.g. *Rhodomonas)* and others with low sinking rates (e.g. *Scenedesmus*) and fast rates of growth. Sommer (1981) and Reynolds et al. (1983 1984) also observed that these species had fast rates of growth. Group 2 phytoplankton were colonial forms either with mucilage (*Pandorina/Sphaerocystis*) or large colonies (e.g. *Aphanizomenon*) which had relatively slow rates of growth, also observed by Sommer (1981) and Reynolds *et al.* (1983 1984). Group 3 were capable of attaining even larger sizes by forming colonies and were shown by Sommer (1981) and Reynolds et al. (1983 1984) to have slow rates of growth but a great deal of motility (Reynolds 1984a). The relationship between cell/colony size and growth rates has been found to be as striking as the differences in responses of species (and assemblages) to environmental variability by many other workers (Sommer 1981, Harris 1983, Harris *et al.* 1983, Reynolds et al. 1983 1984).

Sommer (1981) and Reynolds (1984a b) studied the periodicity of Lake Constance and Lund enclosures, respectively, from the point of view of *r* and *k* selection. Both workers found that species of the same growth and size classes tended to be associated together during seasonal changes. *r* strategists are small with fast growth rates, able to respond quickly but short lived. These were represented in Staunton Harold and Foremark by Group 1 species and were usually present during the early part of the succession. *k* strategists are those which have slow growth rates and are more tolerant to environmental variability. These were represented by Group 2 which are intermediates and were present in the middle of the succession whilst Group 3 (*Microcystis)* and possibly the filamentous Cyanobacteria are extreme *k* strategists and were observed in mid to late summer in the reservoirs.

4.4.2 Phytoplankton assemblages of the reservoirs.

Different phytoplankton species appeared to be associated with each other

and respond in similar ways to changes in both physical, chemical and biotic variables. The phytoplankton assemblages recorded from reservoirs were very similar to the 9 proposed by Reynolds (1984a) for eutrophic lakes. They are as follows:

Reynolds' assemblages	Approximate season	Reservoir species.
Assemblage C.	Vernal period.	*Asterionella, Fragilaria, Stephanodiscus* spp.
Assemblage X.	Vernal period,	*Ankistrodesmus, Scenedesmus, Ankyra, Crucigenia, Tetraedron, Tetrastrum*
Assemblage Y.	Throughout year.	*Cryptomonas, Rhodomonas.*
Assemblage G.	Early summer.	*Pandorina/Sphaerocystis.*
Assemblage H.	Mid summer.	*Aphanizomenon, Anabaena.*
Assemblage M.	Late summer.	*Microcystis.*
Assemblage P.	Mid-late summer.	*Asterionella, Fragilaria.*
Assemblage J.	Mid(-late) summer.	*Pediastrum, Coelastrum.*

4.4.2.1 The effects of environmental variables on phytoplankton assemblages.

In the preceding sections, it has been suggested that the species comprising any one assemblage showed the same approximate response to the interactions of the two major environmental variables. Water chemistry and water column stability are discussed here as the major driving processes of the periodicity in these reservoirs.

The following sequences have been deduced for each reservoir and each year of the study (Figures 69 to 72) using the assemblages described above (dominant

assemblages are noted along with sub-dominants in brackets):

Staunton Harold, 1981; Y (C) -> G (X) -> H -> P -> Y

Staunton Harold, 1982; Y (C) -> G (X H) -> J P -> H M

Staunton Harold, 1983; C (Y) -> Y (X) -> G -> H -> X -> H (J) -> M -> X Y

Foremark, 1981; C (Y) -> H (P) -> G -> P -> H (J) -> M H

Foremark, 1982; C (Y) -> G -> H -> G (X) -> H Y (P) -> M (H)

Foremark, 1983; C (Y) -> H -> G Y -> H -> G (J) -> H (M P)-> Y (M)

A general pattern of periodicity emerges from these sequences and the data from 1978 to 1980 in both reservoirs (STWA unpublished reports). This is C -> G -> H -> M often with P, X, J, or Y included at different stages to various extents.

The occurence of diatoms (assemblage P) during the summer was recorded in both reservoirs and appeared to be a common feature, although the position of this assemblage in the general sequence was not fixed. The reason for this unpredictability was that that the assemblage became dominant in response to decreases in water column stability and this, in turn was a result of the prevailing weather conditions. For example, assemblage P became dominant in Foremark during June and late July, 1981 as the water column stability decreased (repeat Figure 22).

Major disturbances in the sequence of assemblages as a result of artificial mixing were not apparent in 1982 although individual species had been affected (see section 4.3). However, artificial mixing was responsible for a major adjustment in the sequence during 1983. Assemblage (X) consisting of *Chlamydomonas* sp. and a mixture of small chlorophytes (which included

Actinastrum sp., *Tetrastrum* sp., *Tetraedron* sp., *Scenedesmus* spp., *Ankistrodesmus* spp., *Crucigenia* sp. *and Dictyosphaerium* sp.) became numerically dominant in July and September and were more abundant throughout the whole of the summer than in previous years or in Foremark reservoir (Figures 69 to 72). It is probable that the increased abundance and prolonged presence of this assemblage (X) was an indirect result of artificial mixing due, partly to increased nutrient recycling. The even depth distribution of nutrients throughout the water column was an indication of this, although the phosphate and nitrate levels were not higher in 1983 when compared to previous years or Foremark (Figures 26 and 27).

This assemblage was found to be more typical of hypertrophic water bodies (Reynolds 1984a) and it was shown in the previous chapter that Staunton Harold was on the border between eutrophic and hypertrophic.

It is probable that the prolonged presence of assemblage (X) throughout the summer was a response to low intensity mixing which maintained, to a certain degree, the environmental conditions representative of early summer. These included elevated nutrient levels throughout the water column and increased average *Zmix/Zeu* ratios (see chapter 3) which inferred a lowering in the light percieved by phytoplankton cells. Zooplankton densities were not measured and so it is not possible to comment upon any aspect of grazing. Reynolds et al. (1983 1984) found this opportunist assemblage to be less tolerant than other summer assemblages, such as colonial Chlorophytes and filamentous Cyanobacteria, to nutrient depletion and grazing presure.

The effects of changes in environmental factors, especially water column stability, on the general pattern of periodicity were subtle and not as well defined as those observed by Reynolds *et al.* (1983 1984) who found that different assemblages could be repeatably selected for by a sequence of artificial mixing and restratification cycles.

4.5 PHYTOPLANKTON PERIODICITY AND THE PREDICTION OF RESPONSES TO ENVIRONMENTAL VARIABLES.

The responses of phytoplankton species (net rates of density change and abundance) to the fluctuations in environmental factors (chemistry, water column stability and the relationship of underwater light with the mixed depth) were found to be very variable in the reservoirs. The interactions of these environmental and biotic variables was complex and it appears that no one factor is solely responsible for the periodicity observed. There appeared to be a group of factors and these could range from nutrient preferences to different susceptibilities to grazing which selected amongst competing species as suggested by Reynolds (1984a).

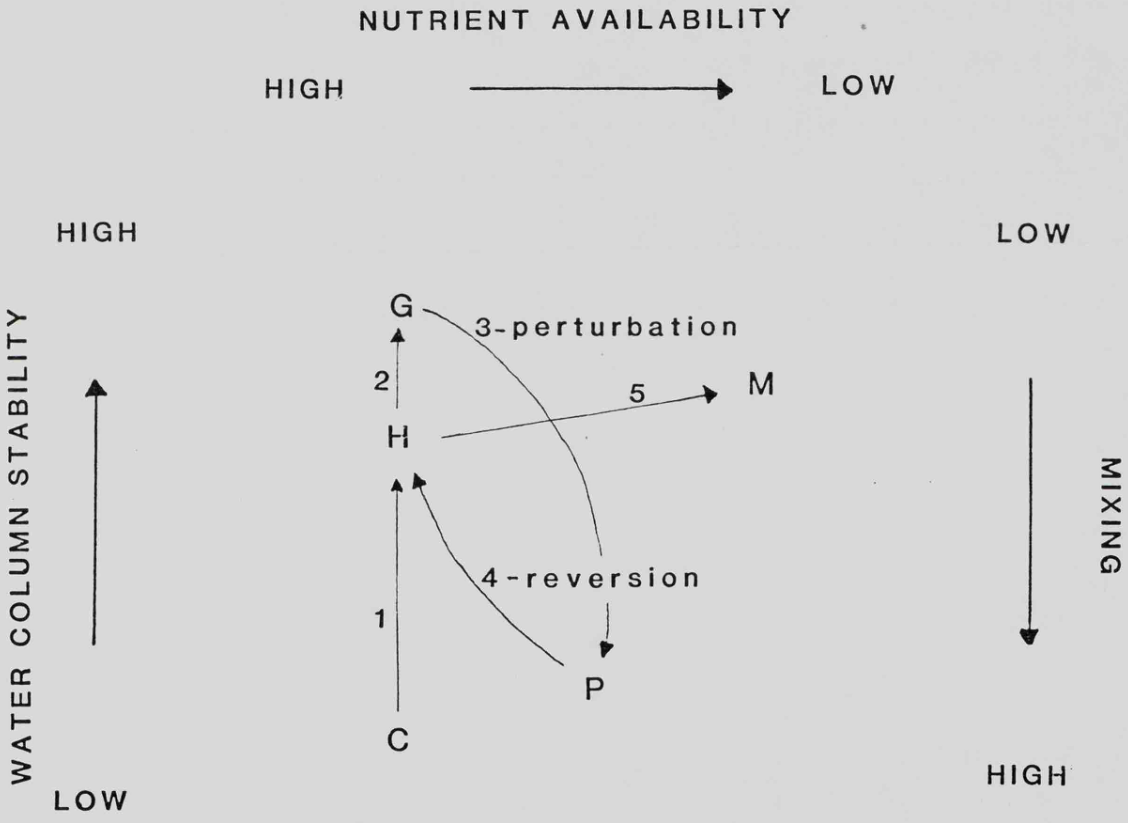
Kilham and Kilham (1980) introduced the idea that competition between species that occured along a resource gradient may influence the composition of communities and play a role in phytoplankton periodicity. Reynolds (1984a) has placed these variables into the following descending order, based on the extent to which the community responds to them. There are physical factors (temperature, mixing and the relative underwater light), chemical (ionic

concentrations, nutrients) and biotic (grazing and parasitism) factors. Reynolds suggests that selection occurs at these major levels and then moves on to progressively finer adaptive criteria.

These environmental variables can be considered as the driving forces of periodicity. They can be split into 'autogenic' processes which are slow, predictable changes in variables (eg. temperature, irradiance, nutrients and water column stability) and 'allogenic' processes which are unpredictable, and often short lived, changes in the variables. The sequence of assemblages can be predicted, loosely, using a matrix bounded on one axis by nutrient availability and on the other the degree of mixing/stability (Reynolds 1980 1984a). 'Autogenic' processes, from any given starting position in a matrix, drive the sequence along the nutrient axis, 'perturbations' which are usually changes in water column stability cause a downward movement to a new position from where a new 'shifted' sequence may start or if the water column becomes stable again, a 'reversion' to the previous dominant may occur. 'Perturbations' and 'reversions' are both 'allogenic' processes.

The periodicity in Foremark generally resulted from 'autogenic' changes. The sequence shown in 1981 (Figure 73), which was typical of the general pattern, started with diatoms in the spring. The water column became more stable, water temperature and irradiance increased and nutrients started to decrease and as a result of the changes in these conditions (step 1), a new assemblage (H) had a competetive advantage over the diatoms and became dominant. Assemblage H was overtaken (step 2) by G as the stability increased. Natural mixing in early June caused a 'perturbation' (step 3) by lowering the stability and summer diatoms (assemblage P) became dominant. As the stability increased again in July (step 4) a 'reversion' to assemblage H occured and 'autogenic' processes (decreasing nutrients and increasing stability) resulted

Figure 73. The phytoplankton periodicity of Foremark, 1981 explained using a matrix bounded by axes of nutrient availability and water column stability. See text for details.

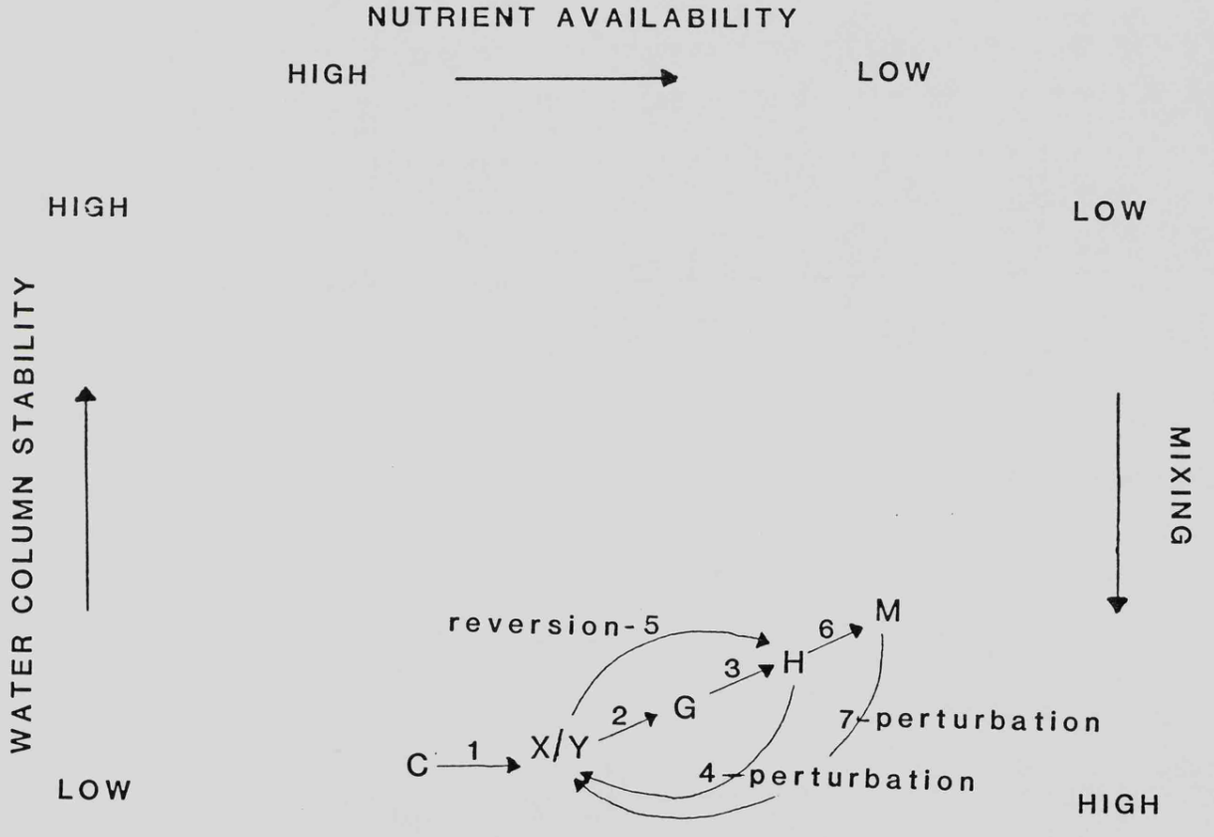


in assemblage M being the final stage of the summer sequence.

In Staunton Harold during 1983 (Figure 74), 'autogenic' processes moved the sequence from the vernal assemblage (C) through assemblage X and Y (step 2) to the early summer assemblage (G) (step 1) and assemblage H (step 3) along the nutrient axis even though the water column was well mixed. It was not until the significant changes in stability during July that a 'perturbation' occured (step 4). The assemblage changed from a developing mid to late summer assemblage (H) to an opportunistic, early summer assemblage (X) comprised of *r* strategists. When the stability decreased to low levels a 'reversion' (step 5) to the previous assemblage (H) and the sequence was then driven by 'autogenic' processes (step 6). Stability during this period fluctuated as a result of the anticyclonic weather producing intense periods of heating, with which the mixing apparatus could not cope, followed by periods of less intense warming when the system maintained stability at low levels (see Chapter 3). These changes in stability were part of the 'allogenic' process which resulted in an alteration of the normal sequence.

The community changes and most likely dominant phytoplankton assemblage at any stage in the sequence can be predicted using this type of matrix with a knowledge of the availability of nutrients, starting point assemblage and water column stability. A matrix such as this which would allow a reasonably definite prediction to be made has great potential in water quality management as well as helping to solve the age old question of why phytoplankton species and communities respond in the ways that they do.

Figure 74. The phytoplankton periodicity of Staunton Harold during 1983 explained using a matrix bounded by axes of nutrient availability and water column stability. See text for details.



CHAPTER 5. PHYTOPLANKTON PHOTOSYNTHESIS AND SEDIMENTATION.

5.1 INTRODUCTION.

Phytoplankton cells need to be able to remain in suspension or be able to move into the euphotic zone so that photosynthetic carbon assimilation and growth can occur.

The balance between the gains and losses of phytoplankton carbon controls the population dynamics. Many workers have observed that much of the carbon fixed does not end up as phytoplankton biomass but is lost (Lewis 1974, Tilzer and Goldman 1978). Forsberg (1985) showed in a recent study of carbon balances in six lakes that production and losses were closely balanced throughout most of the year and in some of these lakes, a considerable proportion of photosynthetically fixed carbon was lost to the sediments. It has been suggested that photosynthetic physiologies and adaptations of different species (Harris 1978 1980, Richardson *et al.* 1983) and the rates of loss of phytoplankton biomass from the water column (Lehman et al. 1975, Reynolds 1984b) were controlling factors in the species succession observed in lakes.

The assimilation of carbon by phytoplankton is dependent upon the amount and quality of light which the cells receive. This, in turn, is controlled by the degree of water column stability which affects the position of cells, including those of motile species if the mixing is strong enough. (The relationship between rates of photosynthesis and growth have not been considered here but the problems associated with such comparisons have been discussed by Harris (1978) and Talling (1984)).

The loss of phytoplankton from the water column results from the processes of death, washout, sedimentation, grazing and parasitism (Lund 1965, Jassby and Goldman 1974, Knoechel and Kalff 1975 1978, Fallon and Brock 1980, Bienfang 1981, Jewson *et al.* 1981, Reynolds and Wiseman 1982, Reynolds *et al.* 1982a b). Sedimentation of phytoplankton cells is inevitable unless they are able to maintain their position by regulating their buoyancy or by swimming (Hutchinson 1967, Reynolds 1984b).

I beleieved photosynthesis and sedimentation would be affected by mixing, an, as they are two of the most important processes controlling community dynamics they required investigating. During 1982 and 1983, experiments were carried out in both reservoirs to investigate the effects of changes in water column stability upon phytoplankton photosynthesis and sedimentation. The results of the photosynthesis experiments (sections 5.2.2 and 5.2.3) are followed by section 5.2.4 which describes some of the prooblems encountered during this work.

5.2 PHOTOSYNTHESIS IN MIXED AND STRATIFIED POPULATIONS OF PHYTOPLANKTON.

5.2.1 Introduction.

Most phytoplankton cells, unlike higher plants, do not remain fixed in space with respect to the light climate but rely upon water movements to remain in the euphotic zone. The cells potentially experience large variations in the light climate as a result of turbulence and it is not surprising that most phytoplankton species are able to adapt to these wide variations. The responses shown by phytoplankton to environmental variations, such as light, operate on time scales from seconds to years and vary from individual cellular and physiological changes (Harris 1978) to population and community changes (Round 1971, Harris 1978, Reynolds 1983, 1984b).

The light regimes experienced by phytoplankton can be divided into two; first order and second order. First order variations are due to the diurnal photoperiod and are manifested in such ways as diel migration in motile algae (Heaney 1976). Second order variations in the light regime are primarily influenced by the vertical position of the cells in the water column (Marra 1978a b). These second order variations are manifested in vertical variations in the biochemical (Gibson 1978a b) or physiological components of the cells (Harris 1978, Richardson *et al.* 1983). Some of these interactions have been investigated by Harris (1973), Harris and Piccinin (1977), Harris *et al.* (1980) and Sephton and Harris (1984).

Photoadaptation of phytoplankton has received a great deal of attention over the last two decades and this is partly because the majority of phytoplankton show a great degree of plasticity in their responses to the changing light climate. This ability of phytoplankton to adapt their photosynthetic physiologies to the light climates which exist in water columns has been demonstrated to play an integral role in the seasonal periodicity of phytoplankton (Harris 1978, Richardson *et al.* 1983 Reynolds 1984a b). A very good resume on the photoadaptive strategies used by phytoplankton was given by Richardson *et al.* (1983) which drew attention to the problems asssociated with analysing data on light adaptation, especially from field data where a description of the phytoplankters' light history and environment is very difficult.

Phenotypic adaptation of phytoplankton to varying light intensities has been studied by many workers. The initial work in this field was carried out by Steemann-Nielsen and his co-workers (Steemann-Nielsen and Hansen 1959, Steeman-Nielsen and Jørgensen 1962 1968, Jørgensen 1969 1970). These early studies suggested that there were two different strategies of photoadaptation. The first was called the '*Cyclotella*' type in which the adaptive response was

an increase in the 'dark' enzymatic reaction. The second was called the '*Chlorella*' type and the adaptation involved an increase in the pigment levels. It is now known that these models oversimplified photoadaptation in phytoplankton but they were the first studies in this field. Falkowski (1980) summarised the phenotypic light-shade adaptation responses as: (a) changes in the photosynthetic pigment content, (b) changes in the ratios of photosynthetic pigments, (c) modification of the photosynthesis/irradiance profiles, (d) changes in enzyme activity and (e) changes in cell volume, respiration rates and chemical compostion.

More recently, Richardson *et al.* (1983) put forward five distinct phenotypic models by fitting data to current hypotheses on photoadaptation. However, they stressed that the models they put forward "are a useful starting point in the study of photoadaptation" but "they cannot explain all of the strategies observed."

Falkowski (1980) stressed the importance of the inter-relationship between mixing rates and adaptation times. Under modelled conditions where the cells were allowed to light-shade adapt by altering the chlorophyll to carbon ratios, Falkowski and Wirick (1981) found that vertical mixing in the euphotic zone probably had little effect on the integrated water column productivity despite this physiological photoadaptation. A reduction in productivity, however, resulted from mixing the whole water column. The empirical models of Talling (1957a), Vollenweider (1965) and Steel (1972) showed that as mixed depth increased productivity decreased. Sakomoto (1966) found that in a series of lakes with a wide range of depths, productivity tended to be lower in the deeper lakes.

In this research, it was possible to study the productivity and photoadaptation of natural phytoplankton populations in both mixed and

stratified water columns. It should be noted that in Staunton Harold reservoir during 1982 and 1983, algal stratification was recorded on several occasions even when the reservoir was being artificially mixed. This allowed experiments to take place in a water column which was fully mixed with respect to physical and chemical parameters, thus eliminating some of the variables which may have affected productivity. The hypotheses that were tested during the research were:

(1) That phytoplankton communities in mixed water columns were light-shade adapted.

(2) As a result of this, the integral primary productivity was lowered in mixed water columns.

5.2.2 Photo-adaptation by mixed and stratified phytoplankton populations.

The depth profiles of photosynthesis in Staunton Harold and Foremark during 1982 and 1983 are shown in Figures 75 to 79, along with the sub-surface irradiance (*I'o*), the algal biomass as chlorophyll a. at each depth and the photosynthetic parameter, *Ik* (Talling 1957a), which defined the irradiance characteristic of the onset of light saturation of photosynthesis. Talling (1957) found that *Ik* was equal to the irradiance at which the rate of photosynthesis reached 71% of the light saturated rate, ie. 0.71 *Pmax*.

The curves are typical of photosynthesis profiles recorded previously (Talling 1957a b, Bindloss 1974 and Jewson 1976) with examples of photoinhibition on several occasions. In Staunton Harold, surface inhibition was only recorded during the experiments carried out on 27th May and 30th June, 1982 whilst in Foremark it was recorded during all experiments except those on 15th June, 1982 and 7th June and 16th August, 1983. It should be noted that when inhibition was recorded, the phytoplankton biomass was

Figure 75. Depth profiles of photosynthetic rates per unit water volume in Staunton Harold during 1982. Values of mean sub-surface irradiance, *I'o*, and *Ik* values ($\mu Em^{-2}s^{-1}$) are given for each profile. The vertical distribution of chlorophyll a. (mgm^{-3}) are given to the right of each profile.

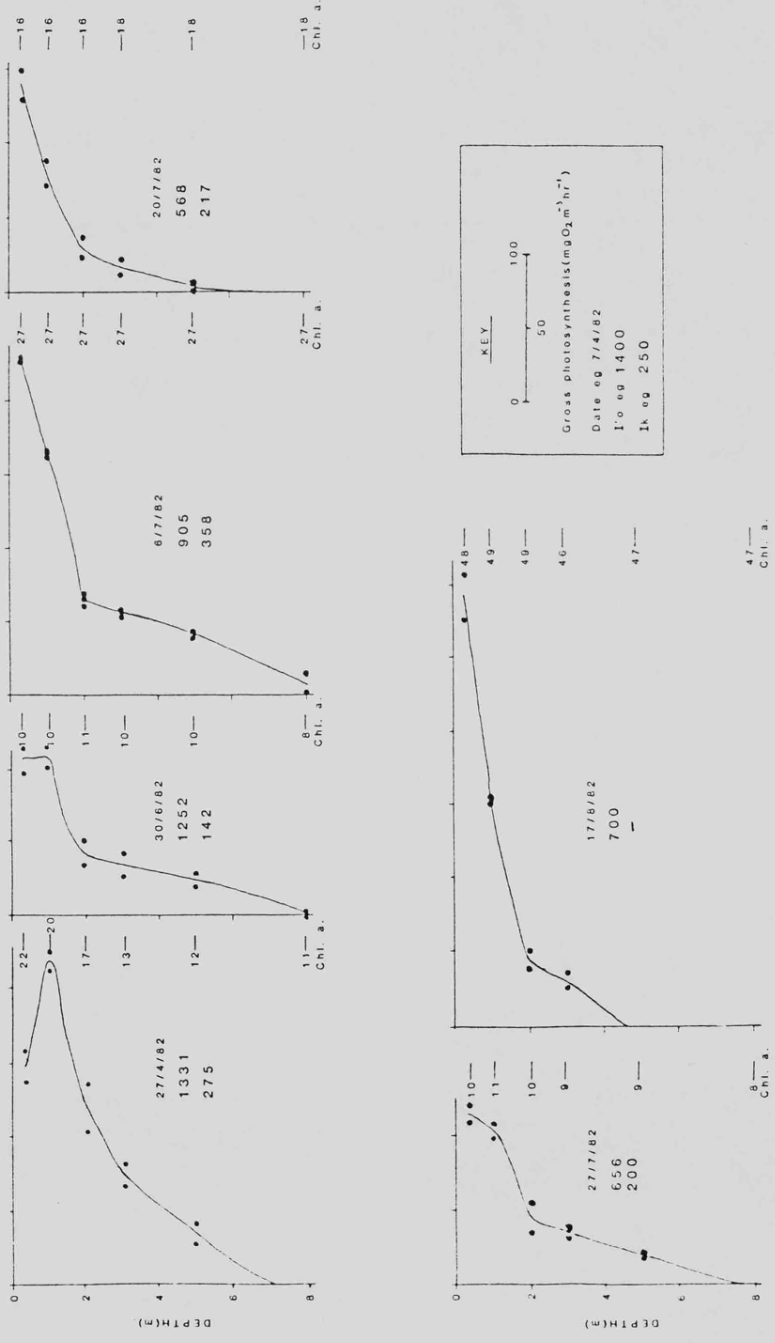


Figure 76. Depth profiles of photosynthetic rates per unit water volume in Foremark during 1982. Values of mean sub-surface irradiance, *I'o*, and *Ik* values ($\mu Em^{-2}s^{-1}$) are given for each profile. The vertical distribution of chlorophyll a. (mgm^{-3}) are given to the right of each profile.

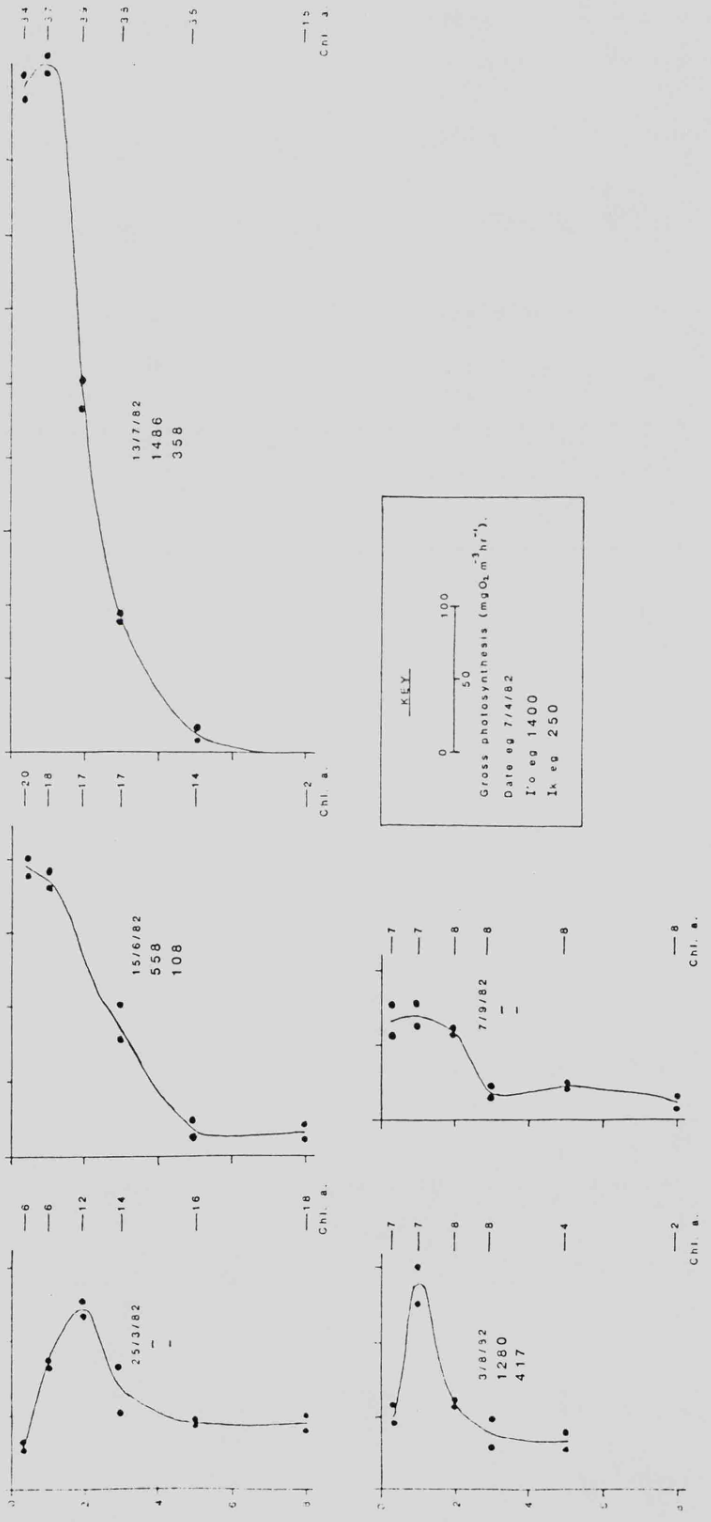


Figure 77. Depth profiles of photosynthetic rates per unit water volume in Staunton Harold during 1983. Values of mean sub-surface irradiance, *I'o*, and *Ik* values ($\mu Em^{-2}s^{-1}$) are given for each profile. The vertical distribution of chlorophyll a. (mgm^{-3}) are given to the right of each profile.

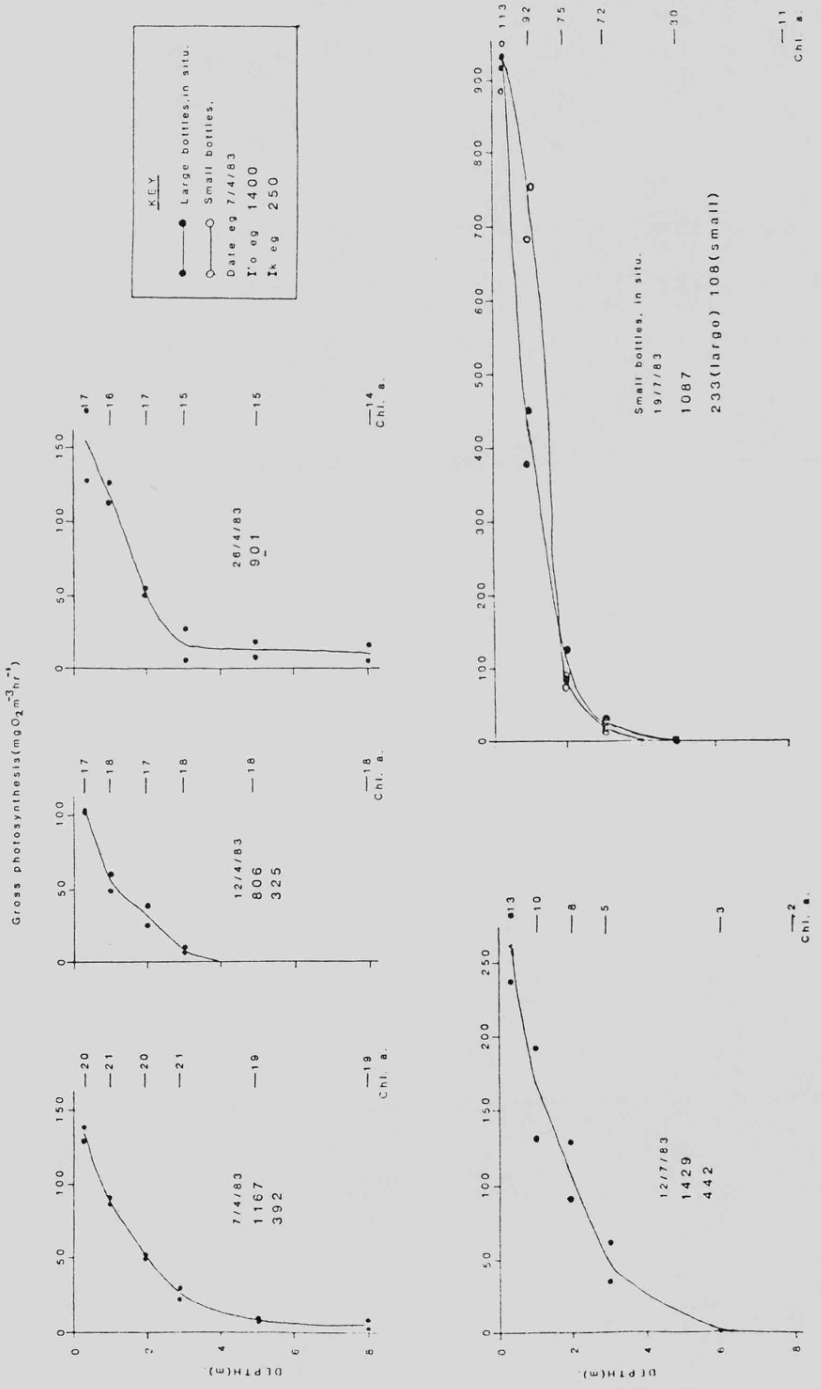


Figure 78. Depth profiles of photosynthetic rates per unit water volume in Staunton Harold during 1983. Values of mean sub-surface irradiance, *I'o*, and *Ik* values ($\mu Em^{-2}s^{-1}$) are given for each profile. The vertical distribution of chlorophyll a. (mgm^{-3}) are given to the right of each profile.

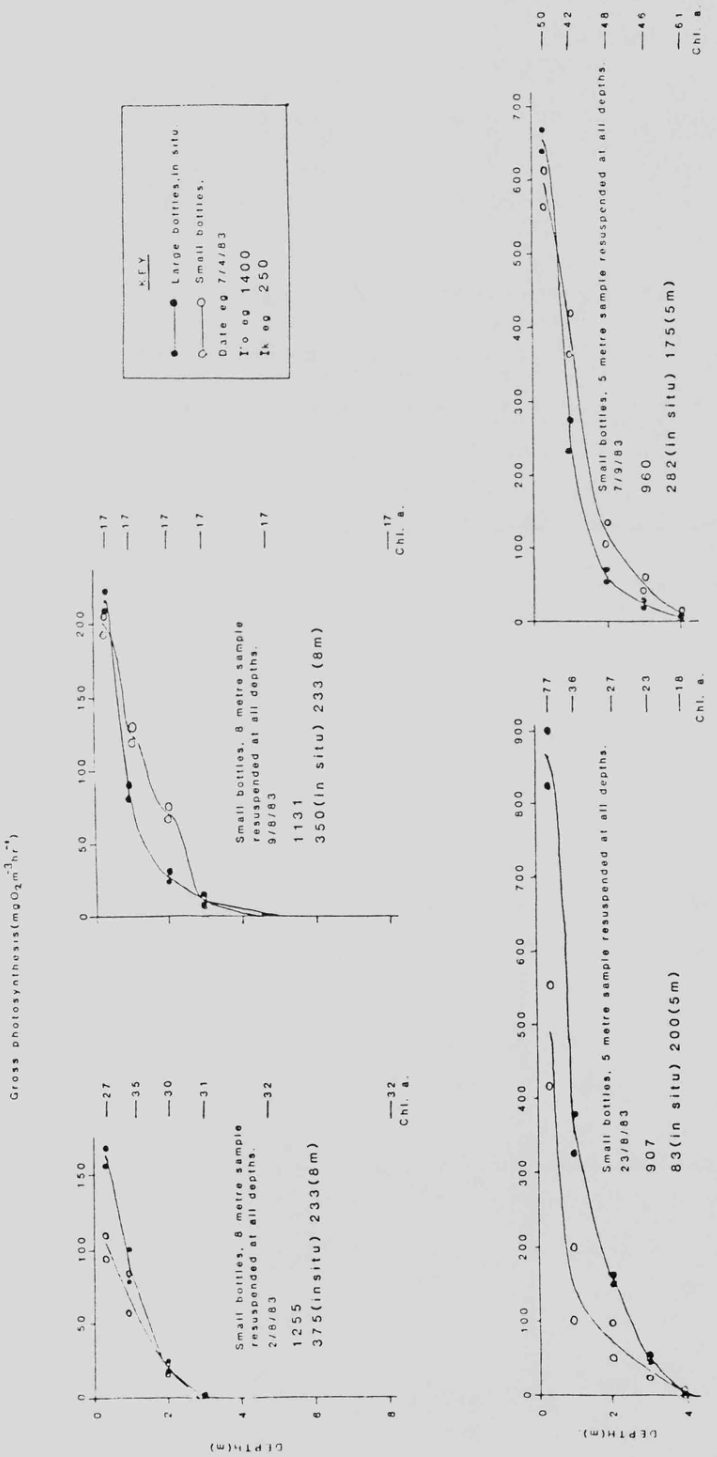
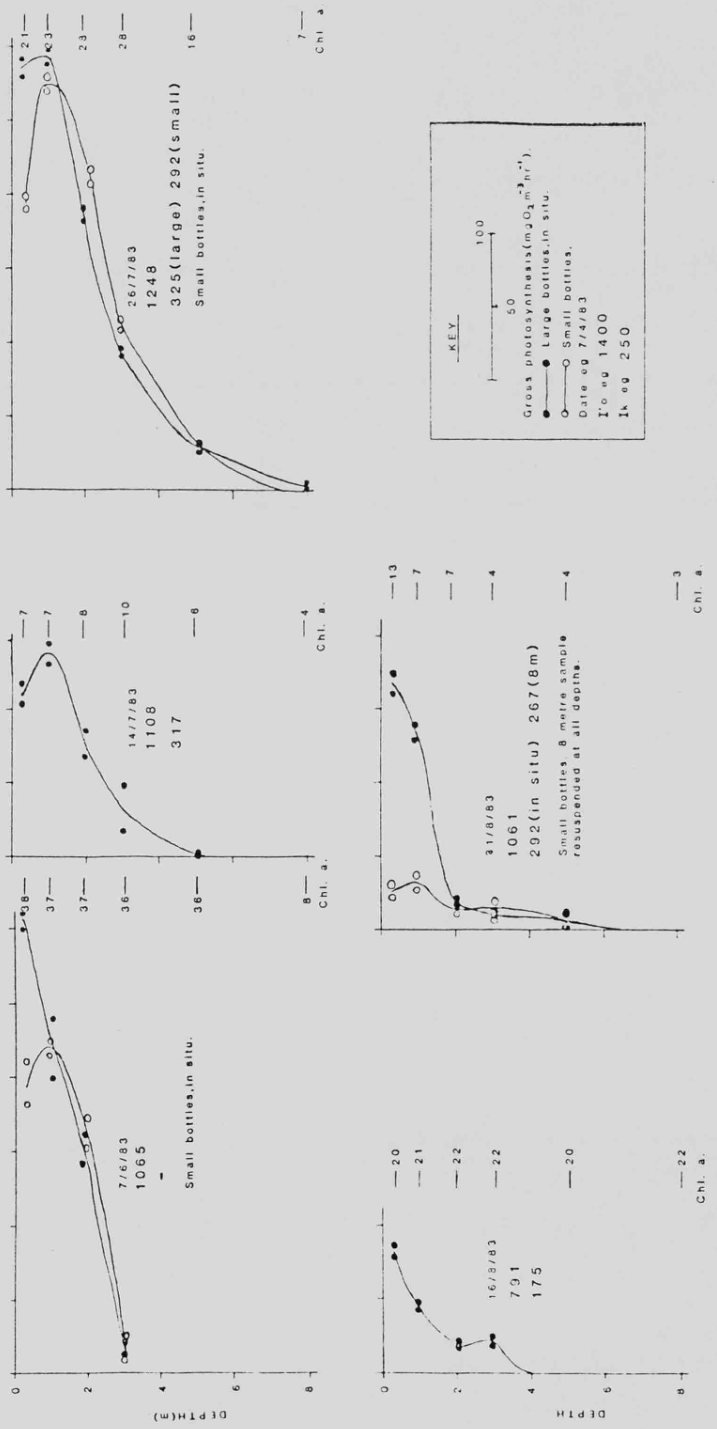


Figure 79. Depth profiles of photosynthetic rates per unit water volume in Foremark during 1983. Values of mean sub-surface irradiance, *I'o*, and *Ik* values ($\mu Em^{-2}s^{-1}$) are given for each profile. The vertical distribution of chlorophyll a. (mgm^{-3}) are given to the right of each profile.



stratified (as shown by the chlorophyll profiles) and when the phytoplankton were well mixed surface inhibition was absent or only just apparent, as on the 7th September, 1982 in Foremark.

Maximum rates of photosynthesis were either found at 0.3 metres or 1 metre below the water surface. Beneath this photosynthetic rates declined rapidly with depth and it was rarely found that there was any significant photosynthesis below 6 metres.

The data from the double experiments carried out in both reservoirs during 1983 have been replotted in the form of photosynthesis verus irradiance (*P* vs. *I)* curves (Talling 1957b) and are presented in Figure 80 for Staunton Harold and 81 for Foremark.

Two types of result can be distinguished from the *P* vs. *I* curves. Firstly, that where both sets of bottles had approximately the same curves. This included the results from the 2nd and 9th August and the 7th September from Staunton Harold. Secondly, that where the curves from each set of bottles were very different (23rd August in Staunton Harold and the 31st August in Foremark). The two patterns were found to be a result of the differences in vertical distribution of phytoplankton biomass.

In the group with similar curves, the biomass was evenly distributed with depth. It was assumed that the cells had been entrained and carried throughout the mixed depth (this will be discussed in more detail below). The transport of these cells by turbulent mixing would have resulted in their exposure to large and often rapid fluctuations in underwater light. If the rate at which these cells were moved throughout the light gradient was faster than that required for them to physiologically adapt to high ('light') or low ('shade') light then the *P* vs. *I* curves would have been similar for cells

Figure 80. Photosynthesis - Irradiance curves from double experiments carried out in Staunton Harold during 1983. (Open circles, o-o, represent large bottles whilst closed circles, ●-●, represent small bottles).

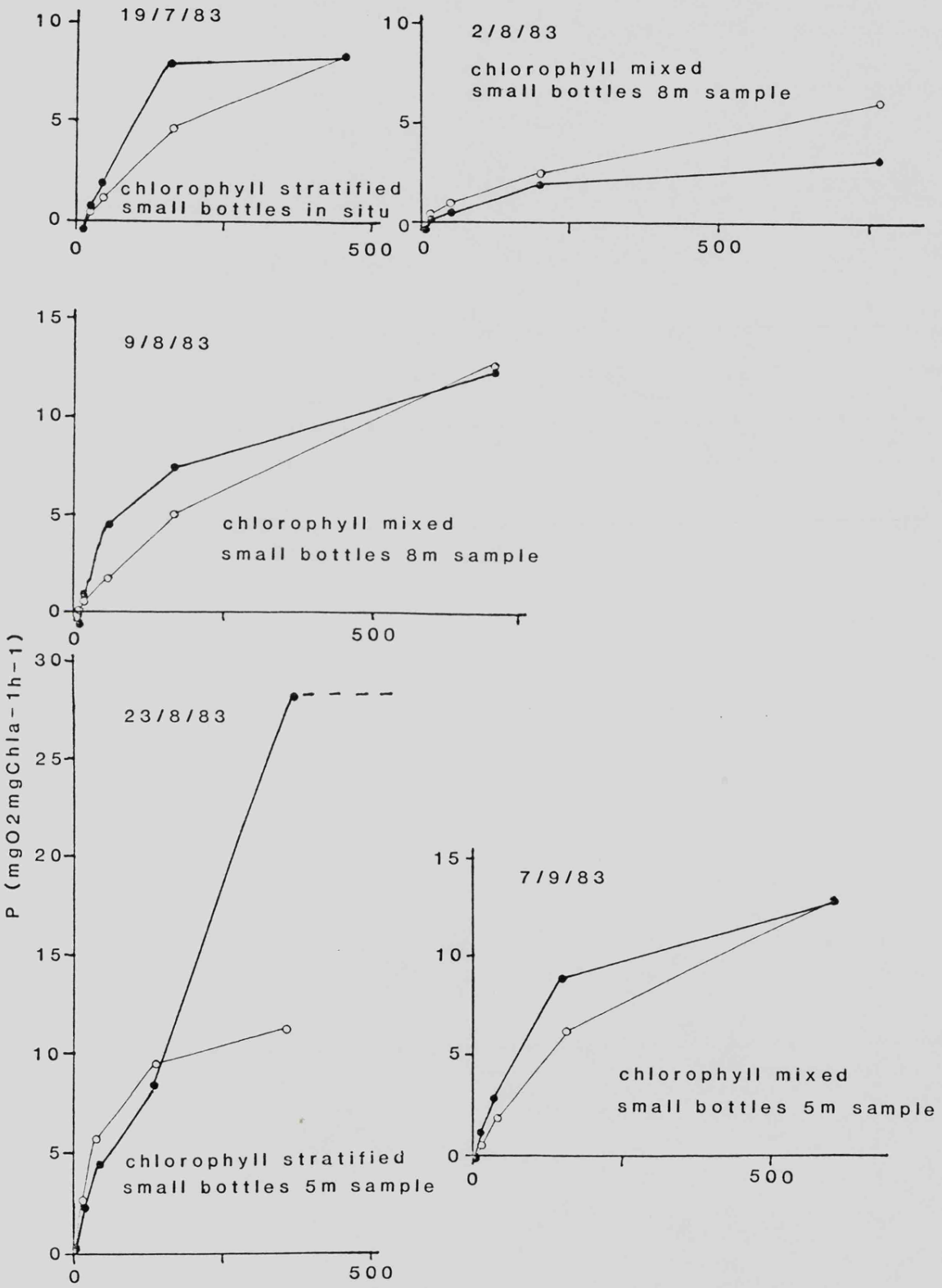
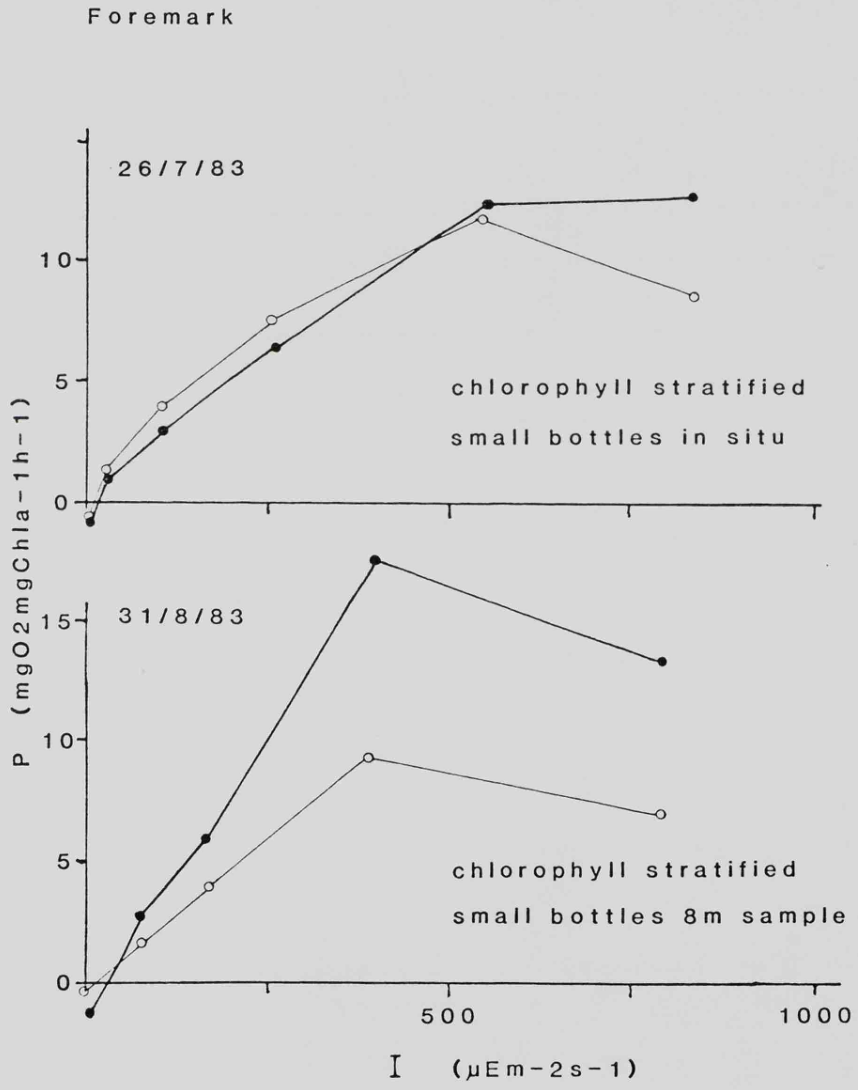


Figure 81. Photosynthesis - Irradiance curves from double experiments carried out in Foremark during 1983. (Open circles, o-o, represent large bottles whilst closed circles, ●-●, represent small bottles).



taken from any depth as observed.

In the group with differences between the *P* vs. *I* curves, phytoplankton populations were stratified. The experiment carried out in Foremark on the 31st August revealed that *in situ* populations had higher maximum photosynthetic rates (*Amax*), photosynthetic capacities (*Pmax*), integral photosynthesis (*ΣA*), *Ik* values and photosynthetic efficiencies (*PE*) than the populations from 8 metres. The *in situ* populations had the characteristics of 'light' adpted cells whilst those from 8 metres appeared to be 'shade' adapted. Similar results of lower *Amax*, *Pmax*, *ΣA*, *Ik* and *PE* values were reported from 'shade' populations by Steeman-Nielsen and Hansen (1959), Yentsch and Lee (1966), Beardall and Morris (1976), Harris (1978), Marra (1978a b) and Falkowski (1980 1983).

The *P* vs. *I* curve for the 5 metre sample in Staunton Harold on the 23rd August was higher than that of the stratified (*in situ*) cells. A probable explanation was that the phytoplankton community comprised of a large number of species including diatoms, small Chlorophytes, Cyanobacteria and Cryptomonads. The Cryptomonads and Cyanobacteria populations were stratified and showed highest densities at the surface whilst the numerous species of small chlorophytes were relatively more abundant at 8 metres. It has been noted that green algae (and dinoflagellates) have slow rates of photoinhibition (Harris 1978). It is therefore possible that when the small chlorophytes from 8 metres were subjected to surface irradiances they became stressed by the high light intensities but did not photoinhibit. This type of phenotypic response has also been recorded by Richardson *et al.* (1983) who proposed that this is a response of the cells by increasing the number of photosynthetic units in response changes in their light climate.

The phytoplankton cells from different depths in the stratified populations appeared to be 'light/shade' adapted whilst those from the mixed populations appeared to be tolerant to rapid and wide variations in irradiance. The following section investigates further these differences in photosynthetic physiologies to assess whether the mixed populations had lower efficiencies and assimilation rates.

5.2.3 Photosynthetic assimilation and efficiency in mixed and stratified phytoplankton populations.

Summaries of the photosynthesis data from both reservoirs are presented in Appendix 6 and the changes during the March to October season are shown in Figure 82 for Staunton Harold and 83 for Foremark along with the major controlling factors.

The aim of this investigation was to deduce any differences in phytoplankton production as a result of artificial mixing. The various parameters measured during those photosynthesis experiments, where *Pmax* was recorded, (see next section) were divided into two groups, depending upon whether the phytoplankton biomass was mixed or stratified (see Figures 47 to 52 and Appendix 6) so that comparisons could be carried out. The Quantum efficiency of cells would have been another method for comparing the mixed and stratified populations but was not attempted during this research as Dubinsky (1980) stressed the difficulty of calculating this parameter from field experiments.

The integrated values of photosynthesis (ΣA) of mixed and stratified populations, which include variation in underwater light with depth, were compared using a t test and showed that the mixed populations had a significantly lower (**) integral. The mean (+/- s.e.) for the mixed population was 296.5 +/- 48.8 $mgO_2 m^{-2} h^{-1}$ and for the stratified populations

Figure 82. Seasonal changes in the rates of photosynthesis and some of the controlling factors in Staunton Harold during 1982 and 1983: The daily surface irradiance, *Io*, expressed as ten day means, the sub-surface irradiance, *I'o* and *Ik* parameter, The maximum photosynthetic rate per unit water volume, *Amax*, the population standing crop, *ΣB*, in the euphotic zone and the water column and integral photosynthesis per unit area, *ΣA*.

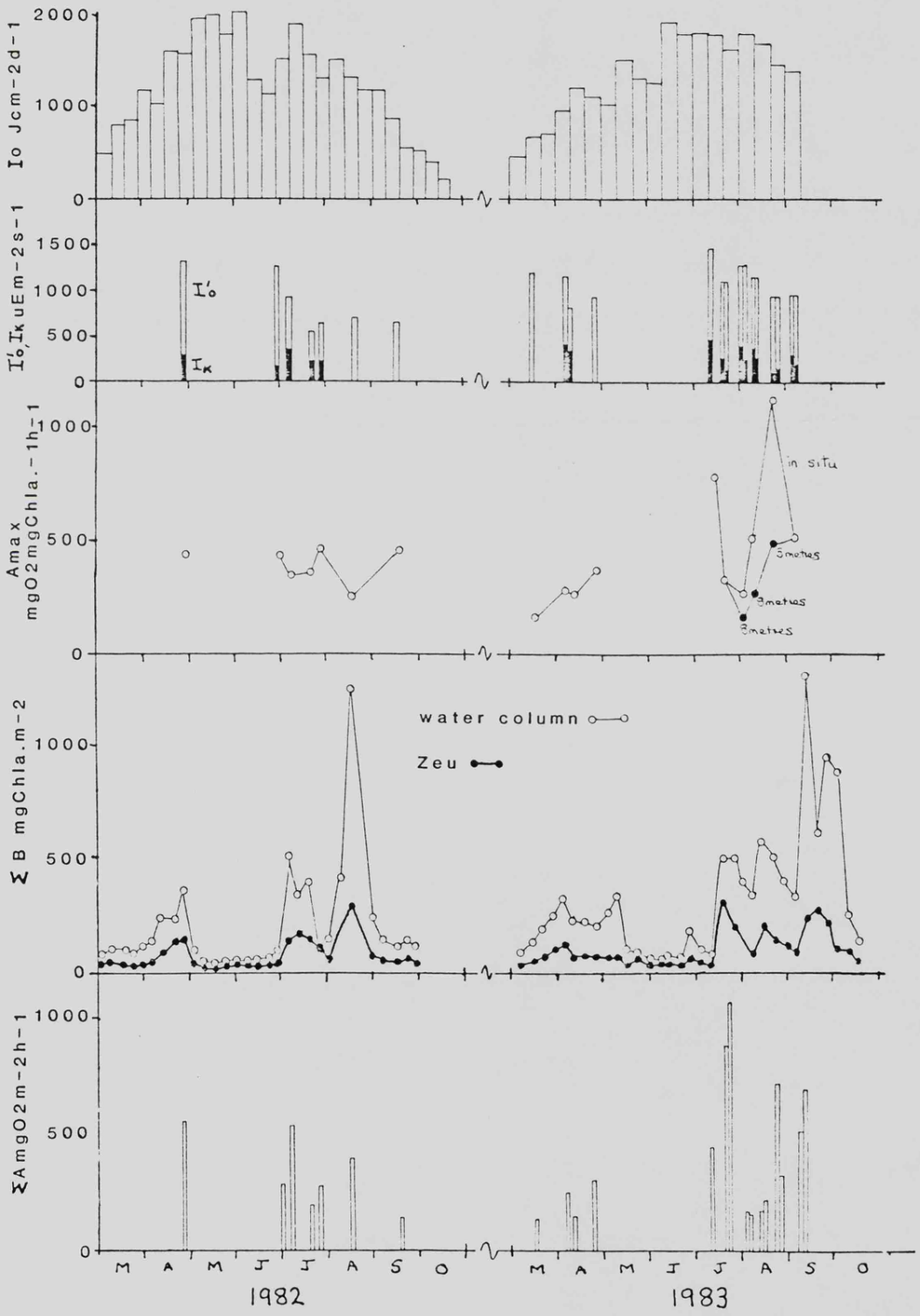
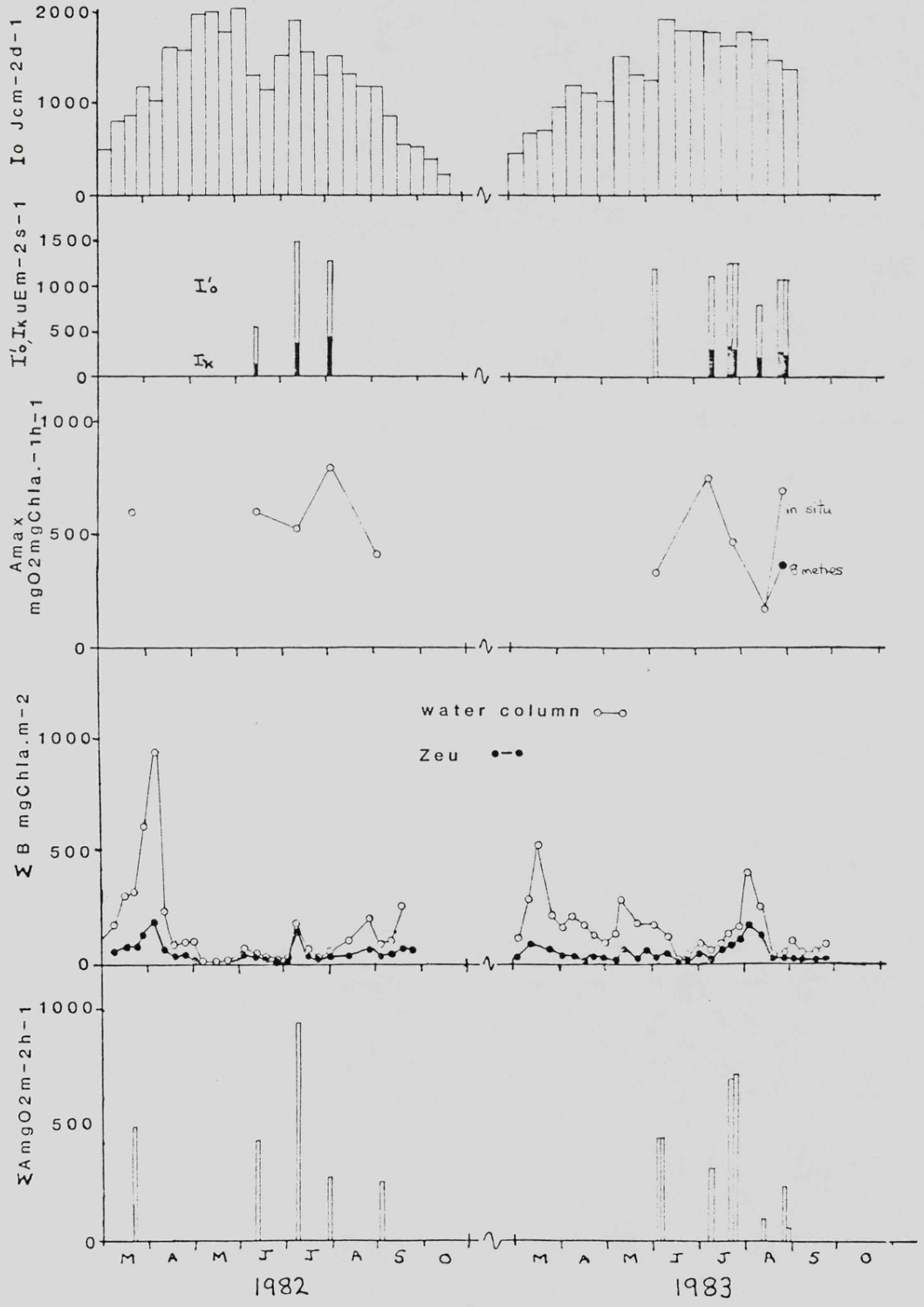


Figure 83. Seasonal changes in the rates of photosynthesis and some of the controlling factors in Foremark during 1982 and 1983: The daily surface irradiance, *Io*, expressed as ten day means, the sub-surface irradiance, *I´o* and *Ik* parameter, The maximum photosynthetic rate per unit water volume, *Amax*, the population standing crop, *ΣB*, in the euphotic zone and the water column and integral photosynthesis per unit area, *ΣA*.

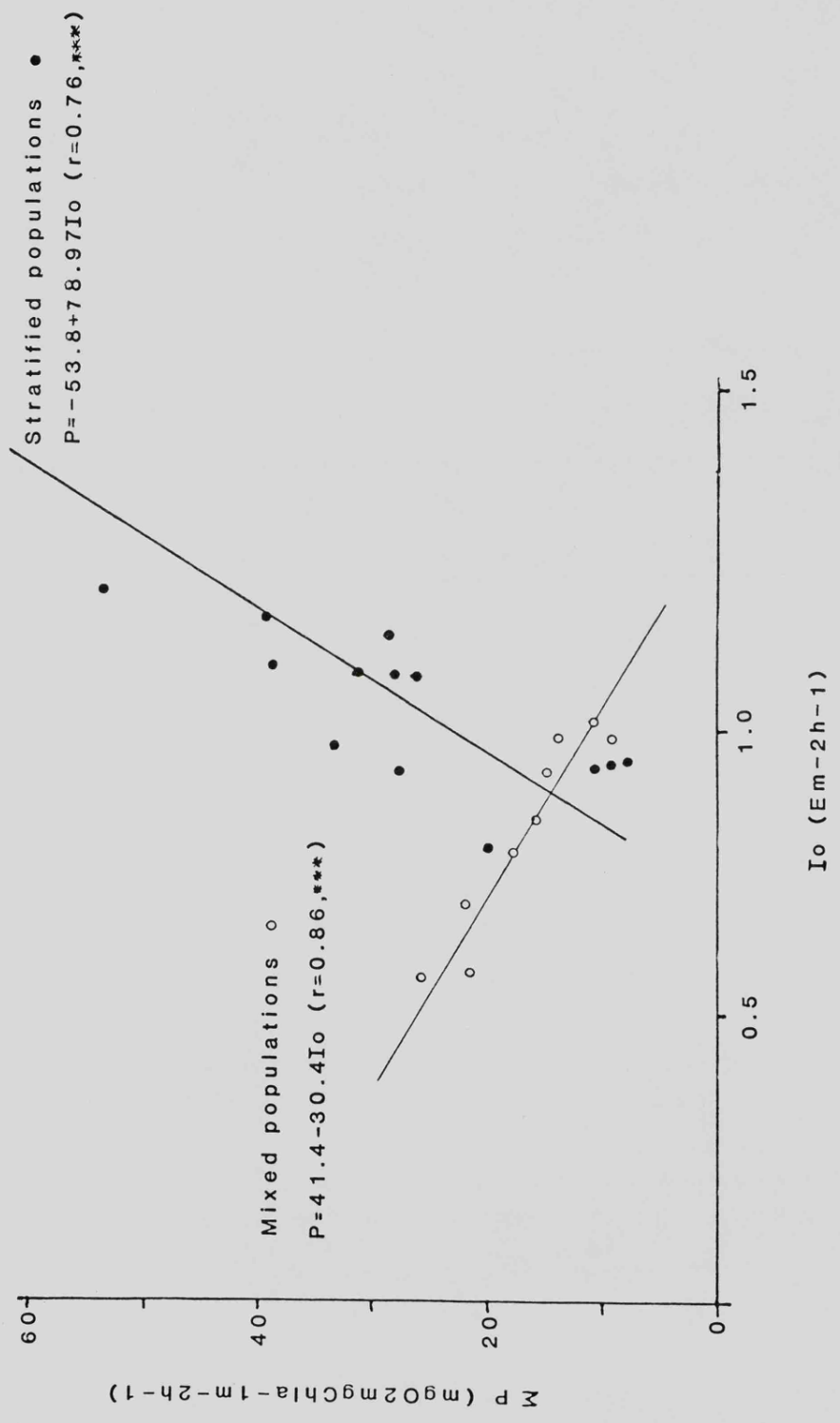


was 596.2 +/- 72.4 $mgO_2m^{-2}h^{-1}$. Much of the variance of integral photosynthesis was reflected by the variation in phytoplankton biomass on the different occasions. This was normalised by integrating the depth profiles of photosyntheis per unit biomass (ΣP). The mean ΣP value (+/- s.e.) for the mixed populations was 17.52 +/- 2.09 $mgO_2mgChl.a.^{-1}m^{-2}h^{-1}$ which was found to be significantly lower (*) than that of 26.68 +/- 3.16 $mgO_2mgChl.a.^{-1}m^{-2}h^{-1}$ for the stratified populations.

The other major controlling factor was the variation due to incident irradiance at the lake surface. Figure 84 shows ΣP values from the mixed and stratified populations plotted against the surface irradiance, *Io*. Only experiments where *Pmax* was recorded have been plotted. In the stratified populations, 58% of the variation of ΣP was accounted for by variation in *Io* and the slope of the line was calculated as 79 $mgO_2mgChl.a.^{-1}E^{-1}m^{-2}$ which is equivalent to an assimilation number that incorporates depth differences in light and biomass and incident irradiance. The regression shows that at higher irradiances, the stratified populations had higher assimilation rates. This value, when converted to carbon (1.25 : 1 O_2 to carbon quotient (Strickland 1960)), of 63.2 $mgCmgChl.a.^{-1}E^{-1}m^{-2}$ was slightly higher but of the same order of magnitude as the value of 43.0 $mgCmgChl.a.^{-1}E^{-1}m^{-2}$ calculated for the New York Bight by Falkowski (1981).

The regression analysis of the mixed population data revealed that 74% of the variation in ΣP could be accounted for by the variation of *Io*. However, the slope had negative value of -30.4 $mgO_2mgChl.a.^{-1}E^{-1}m^{-2}$ which showed firstly that mixed populations had lower assimilation rates than stratified populations and secondly that mixed populations became less rather than more efficient at higher irradiances. This is, I believe, the first record of a negative slope from mixed populations and is probably because other workers have not have not divided their populations into mixed and stratified groups.

Figure 84. Integrated photosynthesis, ΣP, per unit phytoplankton biomass as a function of the surface irradiance, *Io*, in the two reservoirs during 1982 and 1983. Closed circles, ●, represent stratified populations whilst open circles, o, represent mixed populations.



The reduction in assimilation rates agrees with the modelled predictions of Talling (1957a), Steel (1973) and Falkowski and Wirrick (1981). Beardall and Morris (1976) found that the overall effect of growth at lower light intensities resulted in the loss of ability of cells to use higher light intensities. The mixed populations in these reservoirs appeared to conform to the behaviour found by Beardall and Morris (1976) but were not necessarily 'adapted' in the sense of Steeman-Nielsen and Hansen (1959).

The correlation of ΣP and Io appeared to be valid over a wide range of temperatures, biomass levels and nutrient concentrations, but not between the vertical distribution of phytoplankton as was recorded by Falkowski (1981).

The even depth distributions of chlorophyll a indicated that the phytoplankton communities were mixed throughout the depth of the water column. However, the assumption that individual cells within the phytoplankton populations were also mixed throughout the the depth cannot be made without justification. Several methods are available which can determine the previous light history of cells and the mixing regimes of the water mass. Gibson (1978a b) found that the carbohydrate content of cells showed a positive correlation with the dark respiration rate under conditions of nutrient sufficiency. Talling (1957a), Steeman-Nielsen and Hansen (1959), Tilzer and Goildman (1978), Falkowski (1980 1981) and Côté and Platt (1984) have used P vs. I curves from samples taken at known depths to determine 'light/shade' adaptation and the previous light history of the cells. Falkowski (1983) went further and by examining the recent light history of the cells using the molecular ratio of chlorophyll to the P_{700} accessory pigment, he was able to calculate the vertical mixing processes, with good agreement with the physical measurements taken. The use of the double P vs. I curves in the examination of photoadaptation (see previous section) showed that cells from stratified populations were 'light/shade' adapted whilst mixed populations had identical

curves which showed that cells from deep in the water column were adapted in the same way as those from the surface and the whole population therefore had been subjected to mixing.

The phytoplankton communities recorded during the mixed population experiments were varied but in the majority of cases were dominated by a mixture of small Chlorophytes, small centrics and Cryptomonads (see previous chapter). In the previous section it was observed that mixed populations were tolerant to a wide range of light intensities. For each of the three taxonomic groups present, there appeared to be at least one explanation which played a part in the lower assimilation rates found during mixed experiments.

The first explanation was selection of species which are favoured by mixed conditions. Diatoms have been found to exhibit wide tolerances to variations in light intensities in the laboratory and field and are naturally found under turbulent conditions (Lund 1954 1955, Talling 1957b 1965, Harris 1973 1978, Harris and Lott 1973, Haffner 1974, Richardson *et al.* 1983, Reynolds 1984a b).

The second was by control of net cell carbon assimilation. Green algae have been shown to suffer less from photoinhibition than other groups of algae (Richardson *et al.* 1983), can excrete excess photosynthates and photorespire (Raven and Beardall 1981) thus controlling net gains. The small Chlorophytes, which are typical of early summer phytoplankton assemblages, were probably able to regulate their net carbon assimilation and were more efficient at low irradiances and did not photoinhibit at high intensities.

The third explanantion was self-regulation of photosynthesis by motility and regulation of their own light climate (Harris 1978, Richardson *et al* 1983). Cryptomonads and Cyanobacteria were observed to be dominant and sub-dominant in several of the mixed population experiments and both groups

have been recorded to favour low light environments (Richardson *et al.* 1983). It would appear from the results that the overall light environment experienced by the mixed populations was lower than that of the stratified populations and these motile taxa were able to adjust their vertical position when situated away from the bubble plume of the perforated pipe during anticyclonic weather as water column stability was increasing.

To conclude, the mixed populations were found to have lower assimilation rates than stratified populations. The mixed species were shown to have a tolerance to wide ranges in the underwater light and it appeared that this was a result of the selection of species which have either evolved to favour turbulent conditions, or to control carbon assimilation through excretion of photosynthates and photorespiration, or regulation of their own light climate by vertical movement. The stratified populations appeared to be 'light/shade' adapted and had higher rates of assimilation at higher light levels.

5.2.4 Problems encountered during photosynthesis experiments.

Several problems were encountered during these experiments. Firstly, the maximum rate of photosynthesis (*Pmax*) occupies a very narrow depth zone, so on occasions it was most likely that the spacing of the experimental bottles prevented the true maximum rate being recorded. The problem was enhanced when there was rapid attenuation of light. The spacing of the bottles was determined by the light attenuation measured during the weekly sampling which usually took place on the day before.

Secondly, the use of two different size bottles led to several experiments where differences in bottle size were tested by running two separate experiments at the same time (eg. 19th July, 1983 in Staunton Harold and the 26th July, 1983 in Foremark, Figures 77 and 79). These experiments revealed

only small differences in the gross photosynthesis profiles between the two different size bottles. Berger (1984) found that there was no significant difference between primary productivity or respiration measured in 250 ml and 130 ml bottles in a shallow hypertrophic lake. The practical difficulties in suspending two bottles at exactly the same depth were encountered in this research as well as Berger's (1984). During the experiments it proved difficult to suspend bottles at the surface without shading those suspended below. As a result the 'surface' bottles were suspended at 0.3 metres below the water surface and this most probably has had an effect on the photosynthesis depth profiles.

Thirdly, surface photoinhibition was not recorded in many of the experiments (eg. 6th July, 1982 and 12th July, 1983 in Staunton Harold, Figures 75 and 77), even though irradiances were above 200 $\mu Em^{-2}s^{-1}$, which Harris (1978) suggested was the approximate irradiance at which natural populations of phytoplankton started to photoinhibit. Harris (1973) and Marra (1978b) have also recorded occasions when *Pmax* was found at the surface. They assumed that this was a result of the shallow mixed layer which may have selected for species which were adapted to stable light environments. When using stationary bottles, this effect was enhanced as the cells, especially those in the surface bottles, experienced a light climate which was more likely to damage the photosynthetic apparatus. Furthermore, phytoplankton suspensions in the bottles may not have been subjected to the natural light climate. Ohle (1958), Patten *et al.* (1964) and Findenegg (1966) have all demonstrated that the results of productivity experiments depended upon the bottle type used. Quartz or Plexiglass bottles provided a more natural light climate than Pyrex which in turn was more natural than soda-lime bottles. Jones and Kok (1966) in their studies of photoinhibition in spinach chloroplasts found that the main area of the spectrum responsible was the UV-B (290-320nm) region. The effect of UV-B

light on photoinhibition has been clearly demonstrated by the use of quartz, Pyrex and soda-lime bottles in phytoplankton productivity experiments (Harris 1978, Smith and Baker 1980, Worrest *et al.* 1980). Soda-lime bottles have been found to protect the suspensions of cells from high intensities or damaging wavelengths and thus production in these bottles can overestimate that measured in quartz or Pyrex bottles. Worrest *et al.* (1980) showed that productivity in soda-lime bottles was 20% higher than in Pyrex bottles and this in turn was 17% higher than in quartz bottles. This was a direct result of the transmittance of UV-B light by the different types of bottles. Smith and Baker (1980) used the transmittance data from different types of bottles to make a quantitative assessment and calculated the 'biologically effective dose'. This dose is reduced by about 6% in quartz bottles, 13% by Pyrex bottle and 22% by Wheaton bottles at the water surface. In the experiments carried out in this research Pyrex bottles were used and there was no difference in the transmittance of UV-B between the two sizes of bottles.

Attenuation of UV-B light is very rapid in productive waters because of phytoplankton and inorganic material (Smith and Baker 1979). No measurement of the spectral quality in the UV region was made in either reservoir. It is assumed that on most occasions, levels of UV-B, especially at 0.3 metres, were below those which would be damaging to the photosynthetic apparatus of the phytoplankton in the bottles. However on the days when photoinhibition was recorded, the number of sunshine hours was usually considerably higher than the average for the three days previous to the experiment and the water transparency, as Secchi depth, was significantly higher (** t test). This suggests, firstly that cloud cover was low with more UV-B reaching the water surface; and secondly that the UV-B which did reach the surface was attenuated less rapidly so levels at 0.3 metres could have been sufficient to cause photoinhibition.

Photoinhibition of phytoplankton cells is not as frequent a phenomena as was originally thought (Harris 1978). Measurements of production using the bottle technique tend to overestimate photoinhibition (Jewson and Wood 1975, Harris and Piccinin 1977, Marra 1978a b) and the major reasons for this are mentioned above. In their natural environment, phytoplankton cells are not held at the same depth for prolonged periods. Motile forms such as flagellates and some of the Cyanobacteria migrate to a depth where the light climate is optimal. However, as a result of wind action or artificial mixing, most phytoplankton are continuously circulating throughout the mixed layer and will only remain at the same depth during very calm, still periods (Harris and Piccinin 1977).

Vollenweider (1969) listed the limitations of using the oxygen method for productivity experiments. He recommended that the oxygen method was not applicable when the phytoplankton density (expressed as chlorophyll a) was lower than 1 mgm^{-3}. Severe problems were encountered with replication at times when there phytoplankton concentrations were below 10mgm^{-3} chlorophyll a and the results from a number of experiments carried out during the early summers of 1982 and 1983, have been ommitted from the data set.

As a result, the use of Tallings' model (1957a) to calculate seasonal production and therefore detect any difference between annual production in the mixed and stratified reservoirs could not be made as there were gaps in the data set.

Integral photosynthesis was estimated using the semi-empirical model of Talling (1957a) and compared to the experimentally derived values. Even though there was a good agreement (r=0.96 ** for Staunton Harold and 0.95 **

for Foremark) between the values derived from the model and those derived planimetrically from the field experiments, the applicability of the model to this work is questionable. One of the major conditions of the model is that thermal and phytoplankton stratification are absent (Talling 1957a) which was often not the case in these reservoirs. Talling (1984) warned of the dangers of analysing the interactions of the various components which may affect the photosynthesis-depth curves from field measurements. Deduced values can be fitted into the model equation and used to interpret the relationships but this leads to the danger of circular arguments. In some of these experiments, as mentioned above, *Pmax* was not always recorded and to use model on these occasions is questionable. Photosynthesis-depth profiles can only really be used to produce good predictive models in reservoirs and lakes which have well mixed euphotic zones. This has been done in the studies of Talling (1965) on Lake Victoria, Bindloss (1974) on Loch Leven, Ganf (1974) on Lake George, Jewson (1976) on Lough Neagh and Jones (1977b) on Kinnego Bay, Lough Neagh.

5.3 PHYTOPLANKTON SEDIMENTATION.

5.3.1 Introduction.

The physical process of particles sinking in a liquid is complex (Reynolds 1979, Reynolds and Wiseman 1982) but the rate conforms closely to Stokes' Law (Hutchinson 1967, Reynolds 1984b). The measurement of sinking rates is also complex and suffers from many errors especially if multi-species assemblages are being investigated (Bienfang 1980, Reynolds 1984b). Many methods have been employed to estimate sinking rates, some successful others not. These include tracing radioactively labelled cells (Bienfang 1980), calculating the difference between the growth constant based on carbon fixation and that based on change in standing crop (Knoechel and Kalff 1975), fitting regression models to field observations of declining crops (Gibson 1984), by cores taken

of the surface sediment (Reynolds and Wiseman 1982), by artificial sediments (Reynolds and Godfrey 1983) and most commonly by traps (Kirchner 1975, Pennington 1974, Reynolds 1976, Fallon and Brock 1980, Gardner 1980a b, Reynolds and Wiseman 1982 and Reynolds *et al.* 1983 1984).

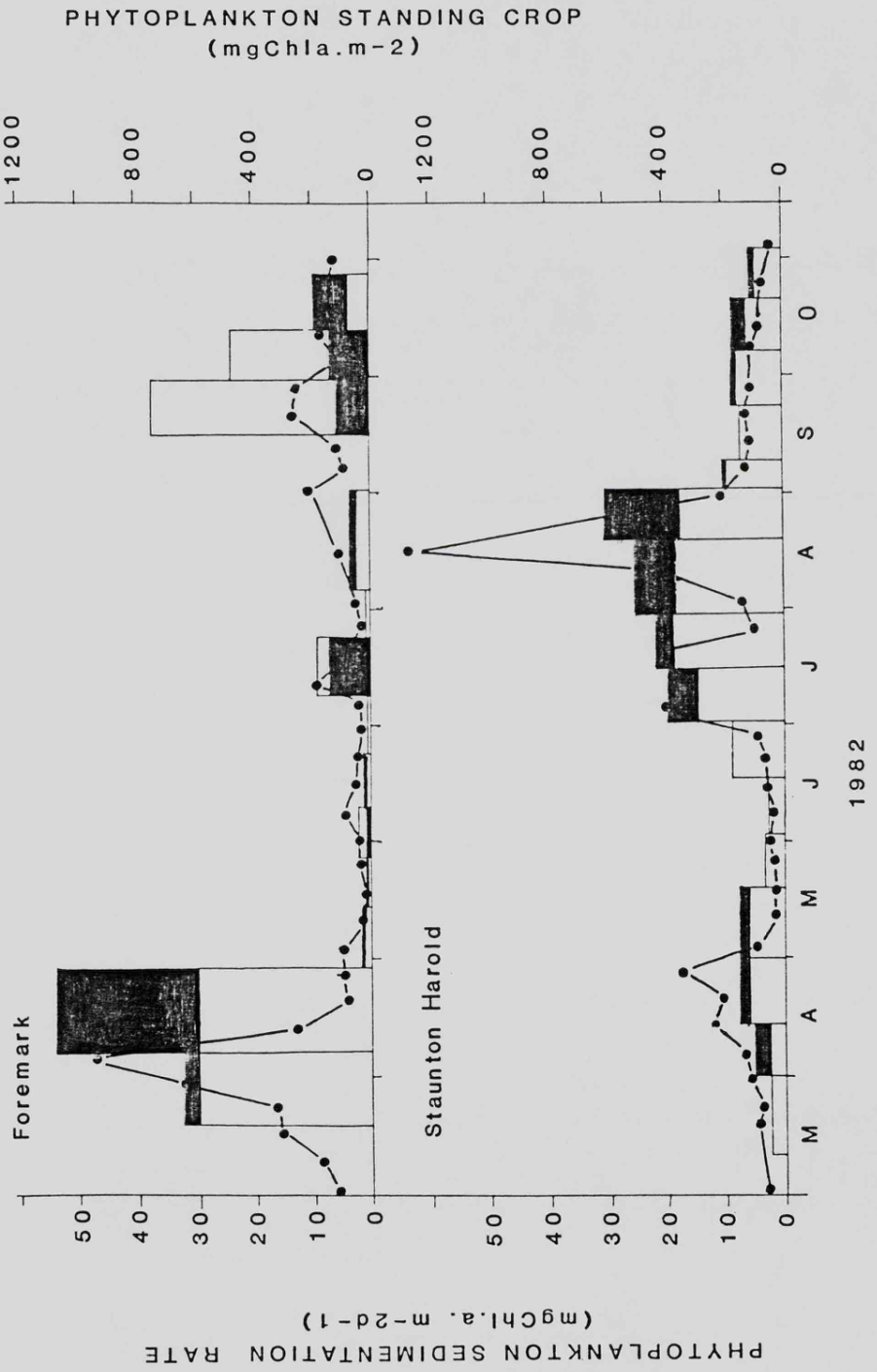
Estimates of the rate of phytoplankton biomass reaching the sediments were made in Staunton Harold and Foremark. A comparison of the rates measured under artificially mixed (Staunton Harold) and stratified (Foremark) conditions was made in 1982 whilst in 1983 the differences between two sites in Staunton Harold were investigated.

5.3.2 A comparison of the rates of sedimentation under mixed and stratified conditions.

There was usually a positive correlation between phytoplankton standing crop and biomass accumulating in the traps in both reservoirs (Figure 85). In Foremark, for example, as the standing crop rose to 946 mg chlorophyll a. m^{-2} on the 5th April and then declined the sedimentation rate followed the pattern. However, differences between the rates measured in each reservoir and thus between mixing conditions could not be detected. The differences between reservoirs are a result of differences in the timing, magnitude and component taxa of the phytoplankton communities which are illustrated by the following examples.

In Foremark, the phytoplankton was dominated by the centric diatom, *Stephanodiscus astraea* which is much denser than water due to its silica frustule. It relies upon turbulence to remain suspended in the water column (Haffner 1974). The daily rate of decline of chlorophyll in the water column was almost exactly matched by the daily rate of increase in the traps (39 mgm^{-2} lost and 38 mgm^{-2} gained) during a calm period in April. However for

Figure 85. A comparison of the rate of phytoplankton biomass accumulation in sediment traps with the water column standing crop in Staunton Harold and Foremark during 1982. (The open bars represent the rates from type B traps and the black bars, those from type A traps, if different, eg. in September, type B traps had higher rates than type A in Foremark.



the comparable period in Staunton Harold, the dominant taxa was *Cryptomonas*, which is motile and less likely to sediment out of the water column. In addition this taxa suffers heavy losses by zooplankton grazing (Reynolds et al. 1983 1984). Only 30% of the loss in standing crop from the water column could be accounted for by that accumulated in the traps and it is most probable that much of the remainder was utilised by zooplankton grazers.

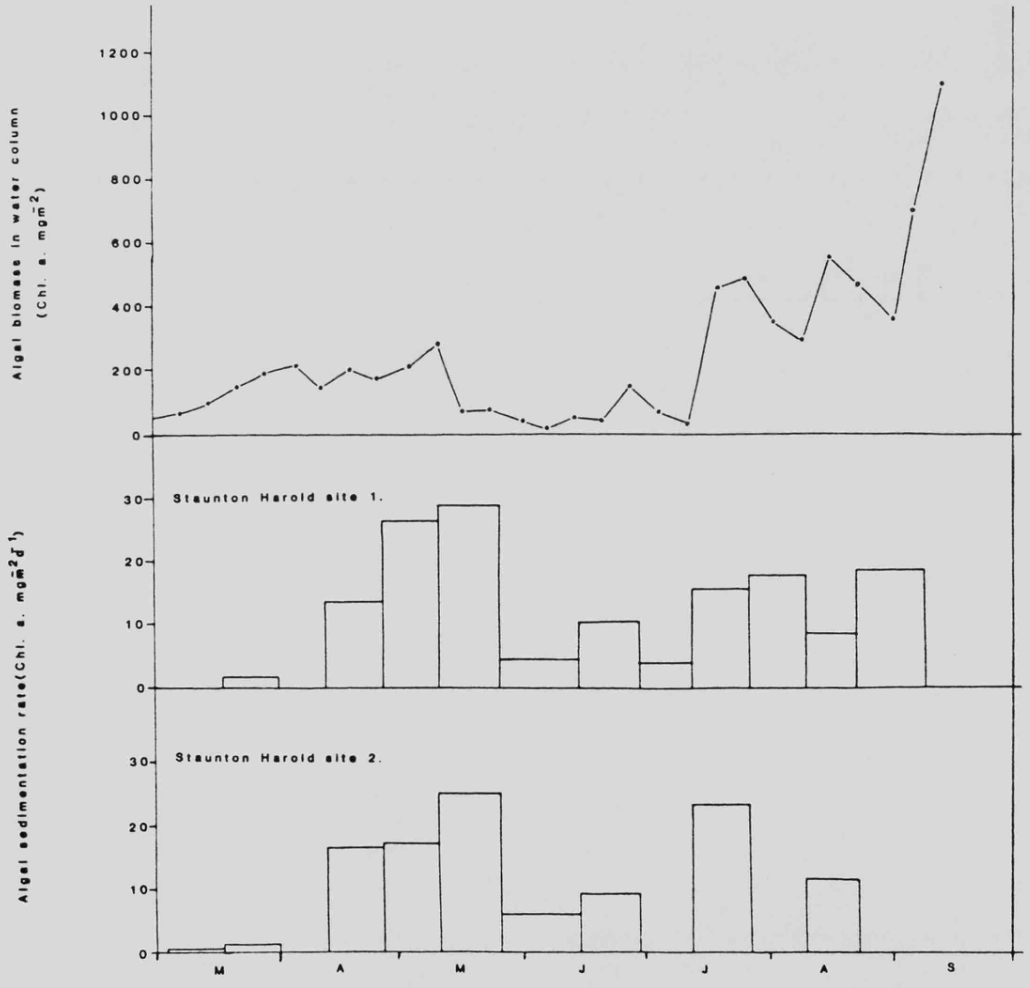
Comparisons of the same species of phytoplankton in each reservoir showed that the percentages of chlorophyll from the water column reaching the sediments were similar. For example, during the decline of the bloom of Cyanobacteria in Staunton Harold in August, 1982 34% of the water column loss could be accounted for by sedimentation, during the decline of a similar bloom in October, 1982 in Foremark, 23% of the water column biomass reached the traps. The decline of bloom forming Cyanobacteria usually resulted in the majority of filaments or colonies rising to the surface where they were subjected to wind and water movements. These scums often ended up blown onto the banks and it is most probable that these accumulations accounted for the low percentage of biomass which reached the traps.

5.3.3 A comparison of sedimentation rates measured at two different sites in Staunton Harold, 1983.

The results of this investigation are shown in Figure 86 along with fluctuations in the standing crop in the water column as for 1982. The observed temporal variations at the two sites was similar and analyses (paired t-test) showed there was no significant difference between replicate traps or between sites.

The fluctuations in the rate of accumulation of phytoplankton biomass to the sediments was strongly correlated with the variations in the standing crop

Figure 86. A comparison of the rate of phytoplankton biomass accumulation in sediment traps at two sites with the water column standing crop in Staunton Harold during 1983.



as in 1982. The high rates measured in April/May, mid July and late August were attributed to the phytoplankton populations present during these periods which consisted predominantly of diatoms (see chapter 4).

5.3.4 A comparison of sedimentation rates measured using two types of traps.

Many workers have noted that sediment traps were efficient at measuring the 'true' sedimentary flux of particles in lakes and experimental tanks under stable stratified conditions but that under turbulent conditions, the results of these measurements need to be treated cautiously (Pennington 1974, Kirchner 1975, Reynolds 1976 1979, Lau 1979, Gardner 1980a b, Reynolds and Wiseman 1982). Kirchner (1975) observed that there were no significant differences between traps of 5 different sizes with aspect ratios ranging from 1:0.6 to 1:7.8 under stable conditions. Gardner (1980b) recommended traps with aspect ratios of between 2 and 3 for use in shallow, turbulent lakes as traps with a higher ratio were found to overtrap. However, in their excellent review of sediment trapping techniques, Bloesch and Burns (1980) recommended that traps for use in turbulent water should have an aspect ratio of 1:10. The two trap types (type A with an aspect ratio of 1:10.7 and type B with a ratio of 1:2.8) were deployed in both the mixed and stratified reservoirs to investigate this problem.

The rates of accumulation of phytoplankton biomass (as mg chlorophyll a. m^{-2} d^{-1}) in the traps along with the fluctuations in the water column standing crop (mg m^{-2}) of Staunton Harold and Foremark during 1982 are shown in Figure 85. A comparison between replicates of each trap type and between the two trap types was made using paired t-tests on root transformed data. There was found to be no significant difference between replicates of either trap type in either reservoir or between trap types in Foremark (excluding the last three trapping periods in September and October). However, there was a

significant difference (**) between rates observed from the two trap types in Staunton Harold.

The difference in accumulation rates measured using traps of varying aspect ratios was not significant under stratified conditions (Figure , May to August in Foremark) whilst under turbulent conditions (spring and autumn in Foremark and throughout most of the March to October period in Staunton Harold) these measurements were significantly different depending upon trap type. Type A traps were giving significantly higher estimates of accumulation rates than type B traps except for the measurements made during September and October in Foremark which are unexplained and rather suspect. It would therefore seem that either type A traps were overtrapping or that type B were undertrapping under turbulent conditions. This problem was not resolvedbut it was believed that the flows due to artificial mixing did not exceed 15 cms^{-1} in Staunton Harold (and this was the value Gardner (1980b) took to be the upper limit for traps of aspect ratios between 2 and 3). It is therefore most probable that the type B traps were giving a more accurate estimate of the rate of accumulation of phytoplankton biomass. However, the problem of which trap type was giving the most accurate estimate of the 'true' rate was considered not to be as important as measuring the differences between reservoirs and between periods when different phytoplankton assemblages were present. The results from this study were not conclusive in resolving the question of whether sedimentation rates were lowered by mixing.

CHAPTER 6. GENERAL CONCLUSIONS.

6.1 PHYSICAL AND CHEMICAL PARAMETERS.

The meterological conditions experienced by the reservoirs is typical of the Midlands and was not subjected to any major extremes during 1981, 1982 and 1983.

The perforated-pipe system was found to be very effective at destratifying Staunton Harold (September, 1981) and prevention of stratification (1982 and 1983). Temperature and dissolved oxygen profiles, water column stability and chemical parameters revealed that this method of artificial mixing was effective and that, with few exceptions, these parameters showed even depth distributions when compared to the 'control' reservoir in all three years.

Comparisons of light attenuation in the PAR region and at blue, green and red wavelengths showed reasonable agreement with published, calculated values and were typical of lowland, enriched reservoirs. The changes in light attenuation and secchi depth were inversely related to phytoplankton biomass. The relationship between *Zeu* and εMIN and *Zeu* and Secchi depth were established and were close to published values.

Artificial destratification in September, 1981 eliminated chemical stratification in only three days and all parameters showed an even depth distribution, although increased in many cases, after mixing.

Artificial mixing in 1982 and 1983 did not stop the release or re-solution of ortho-phosphate, nitrate, ammonia, iron and manganese from the sediments or sediment/water interface. This has resulted from anaerobic conditions which exist in the lower layers even during mixing. These chemical ions once

released into the water are then mixed throughout the whole water column. It was most probable that the rates of release were enhanced by increased temperatures in the lower layers. More research into nutrient recycling and release under artificially mixed conditions is needed to confirm the evidence put forward here.

In the stratified reservoir, chemical parameters behaved as expected with the exception of ortho-phosphate and conductivity. These showed depth distributions which were opposite to those expected. This is believed to be due to water pumped from the River Dove, flowing along the top of the metalimnetic layer and remaining in the epilimnion.

Both reservoirs were classified as eutrophic according to OECD (1982), categories using the 'open boundary system' with Staunton Harold tending towards hypertrophy. The data from this study has been added to the established log/log relationship between maximum winter ortho-phosphate and maximum summer chlorophyll which was first put forward by Lund (1970). The data from these reservoirs showed that the linear relationship found by Lund and other workers only holds up to 100 mgm^{-3} ortho-phosphate, as above this there was no further increase in chlorophyll per unit increase in phosphate. The nitrate data however fit into the linear relationship put forward by Lund (1970) but is closer to the regression equation published by Scott (1975).

The higher levels of nitrate found in Staunton Harold were thought to be due to the larger catchment area and thus greater inflow. Higher phosphate concentrations in Foremark are believed to have been due to the rate of release as a result of a larger anoxic sediment surface. Silica levels which were high in Staunton Harold are believed to have been a result of the increased recycling from the silica 'pool' and input from the catchment.

Nitrate and ortho-phosphate concentrations were found to drop to limiting levels on few occasions. Silica dropped below 0.5 mgl^{-1}, the level which Lund (1950) found to be limiting for *Asterionella*, on many occasions in both reservoirs and was assumed to be limiting further diatom growth.

The boat survey results revealed that phytoplankton distributions were affected predominantly by wind-induced turbulence and that water column stability, although important in some cases, plays a less important role. Stratification of phytoplankton populations occured on several occasions in Staunton Harold whilst it was being artificially mixed. The surveys carried out during these periods of stratification showed that motile or buoyant species were able to maintain their preferred depth distribution or that caused by wind-induced turbulence, away from the perforated pipe. However, in close proximity to the pipe they were not able to do this and were evenly distributed with depth. This is of importance in water management as the phytoplankton species which create the most problems in the treatment process are Cyanobacteria. If the reservoir is mixed so that the anoxic hypolimnion, with all the associated chemical problems, does not form and the nuisance phytoplankton species are stratified then it would be possible to draw water off from below the maximum phytoplankton biomass. The water will be of good quality, chemically and with low phytoplankton numbers.

6.2 PHYTOPLANKTON GROWTH AND PERIODICITY.

A comparison of the mean and maximum biomass levels in Staunton Harold during years when artificial mixing took place revealed that in one year (1983) the biomass was increased whilst in another (1982) it was reduced relative to the naturally mixed year (1981). In Foremark, the biomass levels were lower than those in Staunton Harold but the mean values showed that the highest biomass was achieved in the naturally mixed year (1981) with slighly lower

values in 1982 and 1983.

Phytoplankton biomass was evenly distributed with depth during artificial mixing except for periods when water column stability was increased and/or motile species were present. In Foremark, the biomass remained stratified throughout most of the summers in all three years.

The vertical and temporal distribution of selected taxa from both reservoirs during 1981 showed that the changes in water column stability and the *Zmix:Zeu* ratio were important in determining the abundance of the different species. The vertical distribution patterns were found to be related to either the thermal/density structure of the water column and/or the presence of motile species.

About 60 species of phytoplankton were recorded from the reservoirs during the project but of these, only ten or so became dominant and contributed significantly to the total biomass. The important taxa and the general pattern of periodicity observed in both reservoirs was typical of temperate, eutrophic lakes (Hutchinson 1967, Reynolds 1980 1984a). Diatoms, often accompanied by Cryptomonads comprised the vernal biomass peak and after their demise, *Pandorina/Sphaerocystis* and numerous small Chlorophytes became abundant during early summer. Filamentous Cyanobacteria and *Microcystis*, which usually made up the largest biomass peaks during the annual cycle appeared in early to mid summer and increased slowly. Cryptomonads were common throughout the cycle and often increased when no other species were dominant.

Analyses of the responses of individual species showed that certain species had higher rates of increase under artificially mixed conditions, whilst others responded by having faster rates of increase under stable conditions and others appeared unaffected. Diatoms and the small Chlorophytes were favoured

by decreases in water column stability and increases in *Zmix:Zeu* whilst *Pandorina/Sphaerocystis* and filamentous Cyanobacteria showed higher rates of increase under stable conditions with low *Zmix:Zeu* ratios. The rates of increase of *Microcystis* appeared to be unaffected by either changes in stability or *Zmix:Zeu*. The response of Cryptomonads and *Ankyra* was not as apparent as for many other species and this is thought to be due partly to high loss rates from zooplankton grazing.

The species and assemblages could be classified according to their responses to changes in water column stability. Group 1 which were favoured by mixing and low *Zmix:Zeu* ratios included diatoms and small Chlorophytes. Group 2 included *Pandorina/Sphaerocystis* and the filamentous Cyanobacteria, which were favoured stable stratified conditions and Group 3 appeared to be unaffected by changes in water column stability. *Microcystis* was the only apparent member of this group.

It was observed that these groups (which showed different repsonses to mixing) could also be distinguished by size classes. This enabled the succession to be explained by the *r* and *k* selection hypothesis (Sommer (1981) and Reynolds (1983 1984a b)). The species selected for by decreased stability (group 1) were *r* strategists which were small, often unicellular and had fast growth rates whilst the *k* strategists were those from group 3 (*Microcystis)* were large, had slow growth rates and appeared to be realtively tolerant to environmental variability. The general pattern of periodicity progressed from *r* selected species in the spring to increasingly more *k* selected species in late summer.

Phytoplankton species which had the same rates of growth, abundances and losses were classified into 9 different assemblages (Reynolds 1980) depending upon their responses to changes in water column stability and nutrients. A

general sequence of assemblages from diatoms in the spring through green algae in early summer to Cyanobacteria in late summer was found to be repeated in Foremark in all three years and in Staunton Harold in 1981 and 1982.

Major changes in the seasonal periodicity of phytoplankton assemblages were not apparent as a result of artificial mixing in 1982. However in Staunton Harold during 1983, an assemblage consisting of small centric diatoms and small Chlorophytes was more numerous than in previous years and became dominant in July and September. This response is believed to be due to increased nutrient availability and increased *Zmix:Zeu* ratios which are more 'representative' of early summer when these species usually occur.

The response of the phytoplankton assemblages to environmental variables was found to be predictable and the number of factors which appeared to be important in 'driving' the succession were few. 'Perturbations', either increases or decreases, in water column stability were found to alter the phytoplankton succession. A different assemblage (group 1, *r* strategists in Staunton Harold during 1982 and 1983) was selected for as a result of these 'perturbations'. 'Reversions' then occured as the water column stability returned to the original levels and the previous assemblage continued along the normal sequence.

These types of responses were predicted using a matrix similar to that described by Reynolds (1980 1984b) which has nutrient concentrations along one axis and water column stability along the other.

Rates of density decrease showed that species favoured by mixing (e.g. small centrics) decreased when the water column became stable whilst the response was opposite for those species selected for by stable conditions (e.g. *Pandorina).*

Further intensive short and long time scale studies of the responses of individual species, as well as assemblages, to changes in water column stability are needed so as to increase the predictive power of the generalised hypotheses of Reynolds (1980 1984a) and Harris (1983). I also believe that a large step will be made in understanding the ecology of phytoplankton when the vast amounts of research on phytoplankton physiology and ecology that has been carried out over the last few decades are joined and reviewed together along the lines of Harris (1978), Kilham and Kilham (1980), Richardson *et al.* (1983), Reynolds (1980, 1984a).

6.3 PHYTOPLANKTON PHOTOSYNTHESIS AND SEDIMENTATION.

Investigations into the effects of changes in water column stability on phytoplankton photosynthesis and losses due to sedimentation were carried out in both reservoirs in 1982 and 1983.

The measurement of photsynthesis was used firstly to investigate the physiological adaptations, if any, of mixed and stratified phytoplankton communities and secondly to deduce whether productivity was lowered in mixed water columns as predicted by the models of Talling (1957a) and Steel (1973).

The photosynthesis depth profiles were typical of those recorded from other temperate lakes. Photoinhibition was recorded on several occasions but was observed to be absent when the populations were well mixed.

Photosynthesis versus irradiance curves (P vs. I) from double experiments carried out in 1983 showed firstly that stratfied populations were light-shade adapted and secondly that populations in mixed water columns (except when the phytoplankton were stratified) were being transported through a continuously changing light gradient and were tolerant of the variations in irradiance rather than shade adapted.

An investigation into the effects of this tolerance of productivity revealed that populations which were mixed had significantly lower depth integrated photosynthetic rates per unit water volume (ΣA) and per unit biomass (ΣP) than stratified populations. An assimilation number, which incorporated incident irradiance (Io) and depth differences in light and biomass was calculated from the slope of regression lines between ΣP and Io. The stratified populations had greater assimilation rates at higher irradiances and an assimilation number of 79 $mgO_2 mgChl.a^{-1} E^{-1} m^{-2}$. The mixed populations had a negative assimilation number of -30.4 $mgO_2 mgChl.a^{-1} E^{-1} m^{-2}$, however, which indicated that these phytoplankton had lower assimilataion rates and became less, rather than more efficient at higher irradiances.

There appeared to be three explanations why the mixed phytoplankton communities had lowered assimilation rates. The first was by selection of species which are favoured by mixing and therefore naturally adapted to wide variations in irradiance. Diatoms are such a group which were abundant in the mixed communities. Secondly small Chlorophytes which were also common in these communities have been shown to excrete excess photosynthates and photorespire which would have allowed them control over their assimilation rate. Thirdly,

some species could regulate their photosynthesis through cell motility. Cryptomonads and Cyanobacteria were observed in these mixed communities and were shown to be capable of regulating their vertical position with respect to underwater irradiance.

Further investigations in this area are essential to confirm these findings and study the mechanisms involved in controlling assimilation.

Several problems in the experimental method were investigated during the photosynthesis experiments. These included the use of different bottle sizes and the lack of surface inhibition. Tallings' model (1957a) was not used to calculate the daily and seasonal productivity of the mixed and stratified reservoirs as a result.

The losses of phytoplankton due to sedimentation were compared in the mixed and stratified reservoirs but no differences in the rates under mixed and stratified conditions were distinguished. The temporal variation in the catches of biomass from the traps was related to the magnitude and component phytoplankton taxa in the water column. The loss of biomass from the water column when diatoms were dominant was almost exactly matched by that arriving in the traps whilst during periods when Cyanobacteria were dominant, only 20 to 30% of the water column biomass reached the traps. There was found to be no significant difference between the rates of accumulation of biomass at two sites in Staunton Harold.

A comparison was made using two different types of trap. There was no significant difference between rates measured by the two types in Foremark but in Staunton Harold there was a difference which was believed to be due to the efficiencies of the different types under conditions of increased turbulence. The use of sedimentation traps in turbulent water has been advised against by

several workers for these reasons. The results have been treated with caution and further work is needed in assessing the efficiencies of such traps in turbulent and stratified water under controlled conditions before any conclusions are made about the effect of mixing has upon sedimentation rates.

6.4 THE EFFECTS OF MIXING ON PHYTOPLANKTON ASSIMILATION, GROWTH AND PERIODICITY.

Wide variations in the responses of different phytoplankton species to fluctuations in environmental variables, such as stability, nutrients, light and temperature, are responsible for phytoplankton periodicity. The seasonal patterns of biomass changes and species composition are repeated annually over a wide geographical range of lakes (Hutchinson 1967) because the driving mechanisms of seasonal periodicity are the same from lake to lake and are few in number. It is now generally accepted that variations in water column stability and nutrient availability of water are the dominant variables.

In this research it was found that assimilation rates were lower in communities which were mixed throughout the water column. However some species had higher growth rates whilst others had lower rates as a result of mixing. The mean and maximum biomass levels were lower in one year (1982) of mixing whilst higher in another (1983) when compared to a naturally mixed year (1981). There appears to be a paradox here in that during 1983, assimilation rates were lowered but biomass levels were increased. I think that the loss rates from the mixed water column were lower than from the stratified column which would account for the disparity between assimilation rates and biomass. Losses due to sedimentation cannot be ruled out as a possible cause and investigations into the sedimentation rates of individual species would be worthwhile.

However, I believe that grazing may be the most important of the other loss processes (grazing, washout, death and decomposition) and investigations of the losses due to grazing are necessary. The changes in composition and density of zooplankton species as a result of artificial mixing have been poorly studied but Toetz et al. (1972) reported that the standing crop of zooplankton was reduced by mixing in 2 out of 3 studies. This decrease would reduce the grazing pressure (especially of the more 'palatable' species which in these reservoirs are the small diatoms and Chlorophytes which became more prominent as a result of mixing !) and result in increased phytoplankton biomass.

The generalised hypotheses of periodicity put forward by Reynolds (1980 1984a) allowed the prediction of sequences with some degree of certainty at the assemblage level. It is now necessary to quantify the axes of Reynolds' (1980 1984a) matrix which would allow better predictions to be made. Other controlling factors should be included and the responses of individual species rather than those of assemblages incorporated. Finally, the photosynthetic adaptations and assimilation rates of mixed and stratified field populations in relation to growth rates and losses certainly requires more attention.

GLOSSARY OF SYMBOLS.

A	Rate of gross photosynthesis per unit water volume
Amax.	Value of *A* at light saturation
b	Constant used to calculate εPAR from εMIN. ePAR = *b*εMIN (Talling 1957)
Chl. a	Chlorophyll a.
$d\varrho/dz$	Density gradient over a specified depth interval
g	Gravitational acceleration
Io	Irradiance (PAR) at the water surface.
I'o	Irradiance (PAR) immediately below the water surface.
Ik	Irradiance (PAR) indicating the onset of light saturation of photosynthesis.
kn	Net rate of population density change
N_0	Number of cells in the water column at time t_0
N^1	Number of cells in the water column at time t_1
N^2	The Brunt-Väsäla frequency
PAR	Photosynthetically active radiation, 400-700nm.
P	Specific rate of gross photosynthesis per unit biomass
Pmax.	Value for *P* at light saturation (= the photosynthetic capacity).
Σ*P*	Integral gross photosynthesis per unit biomass
Q_{in}	Annual volume of water pumped into the reservoir
Q_{out}	Annual volume of water pumped out of the reservoir

t	Time
V	Volume of reservoir
Z	Depth
Zeu	Euphotic depth (defined as the depth at which PAR is reduced to 1% of that penetrating the surface).
$Zmix$	Mixed depth (defined as the depth to the top of the thermocline)
ε	Vertical attenuation coefficient
εMIN	Minimum value of ε over PAR spectrum
εPAR	Vertical attenuation coefficient of PAR
$\varepsilon total$	Total vertical attenuation coefficient. εq, εw, εg, and εp are all components of $\varepsilon total$ due, respectively, to non-algal material, the water itself, gilvin (or yellow) substances and particulate non-algal material.
εs	Specific increment in the vertical attenuation coefficient per unit of chlorophyll a.
ϱ	Density of water at $4^{o}C$
ΣA	Hourly rate of gross photosynthesis per unit area
ΣB	Population density per unit area as chlorophyll a
$\Sigma Bmax.$	Theoretical maximum value for ΣB
μ	True growth rate

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APPENDIX 1.

Introduction.

The distribution of phytoplankton populations was reviewed by Ricker (1937). He suggested three types of distribution; a random, a bunched and a spaced distribution. Cassie (1963) found that over-dispersion, or a bunched pattern was the most commonly found form of spatial distibution. When phytoplankton distributions do not approximate to a random pattern, the confidence limits of an algal count can not be applied with any degree of confidence. Over-dispersion has the general effect on sampling programs that a large number of samples need to be taken. In these cases, the calculation of phytoplankton densities and distribution, using microscopic counts, is not always practicable and is often tedious. Therefore a balance needs to be found between accuracy and the effort involved in deducing densities and distributions. This balance depends ultimately on the questions being asked.

Problems encountered in algal counting are similar to those of sampling. The accuracy of a count is proportional to the total size of the count and the precision varies inversely as the square root of the number counted. So to obtain twice the accuracy, four times the number must be counted (Lund, Kipling and LeCren 1958).

In most ecological studies of phytoplankton an error of +/- 20% is accepted which gives the 95% confidence limits

of a count of 100 organisms (Lund, Kipling and LeCren, 1958). In this study at least 100 cells or filaments of the dominant algae were counted to ensure this level of accuracy. The effort involved in attaining this degree of accuracy for the rarer species was considered to be too high.

Preliminary tests of two different counting chambers were made in early spring, 1981 to find the most suitable method of counting both net and nano -plankton during this research.

Net plankton are usually counted in sedimentation tubes using the inverted microscope method of Utermohl (1931) whilst it has been recommended that nanoplankton, or those too small to be counted by the Utermohl technique should be counted in a different type of chamber (Lund 1959). It has been found that the distribution of small phytoplankton within a "Lund chamber" closely approximates a Poisson distribution (Lund, Kipling and LeCren 1958). So it is feasible to count the phytoplankton in a number of random fields and multiply by a conversion factor to calculate the number of cells or colonies per ml.

Methods and Results.

The two different chambers being tested were Wild sedimentation tubes (10 ml capacity) and Lund chambers (Lund 1959). Several experiments were carried out to find which chamber and method was the most suitable.

Experiment 1. Sub-sampling.

The number of cells of *Monodus* sp. were counted from 5 sub-samples using a Lund chamber.

Sample: Staunton Harold, surface, 16/3/81.
Treatment: Each subsample of 10 mls concentrated by sedimentation, 120 random fields counted.

Total counts from 120 fields:-

104
95 $\chi 2 = 3.7$, $v=4$.
114
120
102

Agreement with the Poisson distribution was accepted at the 95% level (*) and so the method of sub-sampling was found to give samples which agreed with the Poisson distribution.

Experiment 2. Nanoplankton densities estimated using Wild sedimentation tubes and Lund chambers.

Sample: Staunton Harold, surface, 9/3/81.
Treatment: (1) Wild sedimentation tube, 8 mls sedimented, 50 random fields counted.
(2) Lund chamber, 10 mls concentrated by centrifugation, 100 fields counted.

Actual counts

	Wild tube	Lund chamber
Rhodomonas sp.	137	5
Monodus sp.	747	126
Small centric diatoms	27	5

Lund chamber counts were found to be significantly lower than Wild tubes. This result was replicated many times and the same result was found when counting net phytoplankton.

Experiment 3. Methods of concentrating samples for Lund chamber counts.

Sample: Staunton Harold, surface, 16/3/81.
Treatment: (1) 10 mls concentrated by sedimentation.
(2) 10 mls concentrated by centrifugation.
Counting method: Lund chamber.

Monodus sp. count (cells/ml)

Treatment 1	Treatment 2
2785	1783
3022	2618
2730	2117
3175	1838
2723	1560
mean = 2887	mean = 1983.2
S.E. = 90.3	S.E. = 181.8

t = 4.452, v = 8

Samples concentrated by sedimentation gave significantly higher counts of *Monodus* sp. (**, t test). This was found to be due to the brake on the centrifuge which resulted in phytoplankton cells being resuspended when the centrifuge was slowing down.

The low Lund chamber counts found in experiment 2 were possibly due to the pre-treatment of the sample, which was concentrated by centrifugation. Concentration of samples for counts was always by sedimentation.

Experiment 4. Random distribution of nanoplankton in Wild tubes and Lund chambers.

Wild tubes.

Sample: Staunton Harold, surface, 23/3/81.
Treatment: 8 mls sedimented in Wild tube, *Rhodomonas* sp.cells counted in 100 random fields.

Actual counts

195
170
168 $\chi^2 = 5.74, v = 4$
182
153

Agreement with the Poisson series was accepted at the 95% probability level (*) and it was therefore possible that

the distribution of *Rhodomonas* cells was random within the Wild tube.

Lund chambers.

Sample: Staunton Harold, surface, 16/3/81.

Treatment: 10 mls concentrated by sedimentation, *Monodus* sp. cells counted in 70 random fields.

Actual counts

100

124

98 $\chi^2 = 5.14$, $v = 4$

114

98

Agreement with the Poisson series was accepted at the 95% level (*) and it was possible that the distribution of *Monodus* cells was random within the Lund chamber.

It was decided from these experiments that Wild tubes were more suitable for counting than Lund chambers, especially as the phytoplankton biomass was dominated for the majority of the time by net phytoplankton. It was also possible to count nanoplankton in the tubes since the distribution of small cells was found not to deviate from the Poisson distribution. This was done by counting cells or colonies in a number of random fields using a x20 objective.

because it was found, on all but a few occasions, that transect counts did not differ significantly from those covering the complete area with deviations only at low densities.

The major disturbances to the randon distribution of cells or colonies in the Wild tubes was found to be caused by the walls of the chamber. Several complete transects across the diameter of the chamber overcame this problem.

Discussion.

As a result of these experiments the following counting method was used throughout the research:

Wild sedimentation tubes (10ml capacity) were used for counting both net and nano -plankton.

Net phytoplankton were counted at x140 magnification in a number of complete transects across the diameter of the tube, the tube being rotated between each transect.

Nanoplankton were counted at x280 magnification in a number of random fields. The distribution of nanoplankton within the Wild tubes was checked at regular, usually monthly, intervals.

Taxanomic identifications was made at either x700 or x1400 magnification.

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APPENDIX 2. PHYSICAL AND CHLOROPHYLL DATA.

STAUNTON HAROLD.

DATE	Zmix (m)	Zeu (m)	Zmix/Zeu	N^2 ($*10^{-6}$ sec^{-2}) 0-5m	N^2 ($*10^{-6}$ sec^{-2}) 0-15m	Secchi depth(m)	Chlorophyll a.(mgm^{-2}) in water column	Chlorophyll a.(mgm^{-2}) in Zmix	Chlorophyll a.(mgm^{-2}) in Zeu	εPar (m^{-1})	εmin (m^{-1})
05/1/81	14.0										
16/2/81	14.0			-6.9							
23/2/81	14.0										
02/3/81	14.0			-49.1							
09/3/81	15.0			60.8	20.3		138	138			
16/3/81	15.0	3.2	4.7	-47.4	-15.8	1.1	138	138	28	1.4573	
23/3/81	15.0	4.2	3.6	76.1	25.4	2.0	141	141	40	1.1069	
30/3/81	16.0	4.7	3.4	-60.5	-30.3	1.3	152	152	47	1.0257	
06/4/81	16.0	4.8	3.3	0	0	2.1	87	87	25	0.9493	
13/4/81	15.0	5.2	2.9	0	34.9	2.0	130	130	41	0.8994	
27/4/81	16.0	3.8*	4.2	-22.0	-7.3	1.5	203	203	63		
04/5/81	16.0	4.2$	3.8	0	0	1.75	273	273	72		0.9263(Red)
11/5/81	16.0	5.9	2.7	76.7	79.5	2.4	51	51	32	0.7741	
18/5/81	8.0	6.0	1.3	0	201.5	3.0	44	21	13	0.7449	
26/5/81	11.0	7.4	1.5	0	267.5	4.2	31	22	17	0.6327	
01/6/81	11.0	7.4	1.5	336.4	409.7	4.5	33	31	26	0.5685	
08/6/81	11.0	4.3$	2.6	70.2	385.3	2.3	113	91	33		0.8980(Gre)
15/6/81	12.0	3.9$	3.1	0	355.6	2.0	262	248	99		0.9889( )
22/6/81	15.0	3.4$	4.3	312.4	177.3	2.3	303	298	177		1.1481(")
29/6/81	15.0	6.5$	2.3	73.3	94.7	3.25	114	104	56		0.5956(")
06/7/81	15.0	2.1$	7.1	0	173.9	1.5	998	973	214		1.8013(")
13/7/81	15.0	2.9$	5.2	448.6	399.0	1.6	516	516	224		1.3535(")
20/7/81	15.0	2.5$	6.0	0	211.9	1.75	591	571	229		1.5468(")
27/7/81	16.0	1.7$	9.4	84.2	187.1	0.8	898	898	271		2.2516(")
03/8/81	15.0	2.7$	5.5	843.3	448.4	1.25	381	363	172		1.4134(")
10/8/81	15.0	5.4$	2.8	172.8	167.3		42	40	19		0.7905(")
17/8/81	16.0	5.3$	3.0	91.0	283.3	2.75	147	147	114		0.8726(")
24/8/81	16.5	3.1	5.2	172.8	219.3	1.5	470	470	324	1.1619	"
02/9/81	14.0	8.8*	5.3	350.9	328.9	4.25	53	44	26		
07/9/81	15.0	10.1*	1.5	172.8	219.3	5.0	38	37	30		
11/9/81	16.0	5.6*	2.9	85.6	28.5	2.5					
21/9/81	16.0	6.2	2.6	0	0	2.25	183	183	72	0.9402	
28/9/81	16.0	6.7*	2.4	0	0	3.1	95	95	43		
05/10/81	16.0	8.3*	1.9	0	0	4.0	23	23	11		
12/10/81	16.0	5.2	3.1	0	0	2.0	29	29	8	0.8516	
26/10/81	16.0	4.9	3.3	0	0	2.1	50	50	17	0.9104	
09/11/81	15.0	6.6	2.3	0	0	3.0	52	52	26	0.6870	
23/11/81	16.0	5.3	3.0	0	0	2.5	40	40	15	0.8154	
07/12/81	16.0	6.0	2.7	0	0	2.75	25	25	9	0.7620	
MEAN		5.13				2.43	201.3	196.6	78.6	0.893	
+/- S.E.		0.33				0.18	41.4	40.7	15.1	0.06	

* = Zeu calculated from Secchi depth.
$ = Zeu calculated from εmin.

APPENDIX 2. CONTINUED.

STAUNTON HAROLD.

DATE	Zmix (m)	Zeu (m)	Zmix/Zeu	N_2 ($*10^{-6}$ sec^{-2}) 0-5m	N_2 ($*10^{-6}$ sec^{-2}) 0-15m	Secchi depth(m)	Chlorophyll a.(mgm^{-2}) in water column	Chlorophyll a.(mgm^{-2}) in Zmix	Chlorophyll a.(mgm^{-2}) in Zeu	εPar (m^{-1})	εmin (m^{-1})
01/2/82	15.5	4.5	3.4	0	0	2.0				1.0611	
01/3/82	15.0	6.2	2.4	0	0	2.0	63	63	29	0.7534	
08/3/82	15.5	4.3	3.6	0	0	1.5				1.0351	
17/3/82	15.0	2.8*	5.4			1.75	91	91	22		
22/3/82	16.0	2.2*	7.3	0	0	1.1	76	76	18		
29/3/82	15.5	2.5	6.2	0	0	1.0	102	102	20	1.3772	
05/4/82	16.0	4.5	3.6	22.0	14.0	1.5	124	124	34	0.9886	
13/4/82	16.0	4.6	3.5	0	0	1.75	234	234	73	0.9449	
20/4/82	15.0	4.2	3.6	116.8	76.3	1.75	215	215	118	1.0072	
26/4/82	15.0	4.8	3.1	44.1	42.4	2.0	351	351	129	0.9129	
03/5/82	15.0	4.8	3.1	0	0		95	95	28	0.9691	
11/5/82	15.0	6.4	2.3	151.5	81.5	3.25	22	22	7	0.7240	
17/5/82	15.0	8.1	1.9	58.7	296.5		26	26	20	0.5808	
24/5/82	15.0	6.1	2.5	0	22.4	2.25	29	29	16	0.7453	
01/6/82	15.0	7.6	2.0	679.9	304.0	3.5	40	40	22	0.6082	
07/6/82	15.0	6.4	2.3	574.2	394.5	3.4	36	36	21	0.6836	
14/6/82	15.0	4.7*	3.2	0	0	2.0	45	45	14		
21/6/82	15.0	5.7	2.6	0	0	2.4	56	56	21	0.8306	
28/6/82	15.0	4.1	3.7	0	0	1.5	84	84	32	1.1405	
05/7/82	15.0	3.6	4.2	0	0	1.5	401	401	123	1.2704	
12/7/82	15.0	5.6	2.7	0	46.2	2.5	326	326	156	0.7736	
19/7/82	15.0	4.6	3.3	91.0	60.3	2.25	383	383	133	0.9873	
26/7/82	15.0	4.7*	3.2	0	12.1	2.0	88	88	28		
02/8/82	15.0	4.3	3.5	281.1	112.0	2.5	125	125	49	1.0220	
10/8/82							394	394			
16/8/82	15.0	2.9*	5.2	0	62.1	1.0	1276	1276	282		
31/8/82	15.0	3.7$	4.1	0	0	2.0	217	217	55		1.0572(G)
06/9/82	16.0	4.9$	3.3	0	0	2.8	120	120	41		0.7909(R)
13/9/82	16.0	5.8$	2.8	0	0	2.5	101	101	37		0.6701(R)
20/9/82	15.0	4.9	3.1	0	28.1	2.7	124	124	45	1.0354	
27/9/82	16.0	4.7*	3.4	0	0	2.0	101	101	29		
05/10/82	15.0	5.0$	3.0	0	0	2.25	101	101	34		0.7685(G)
11/10/82	15.0	4.9$	3.1	0	20.0	1.75	65	65	22		0.7913(G)
18/10/82	15.0	4.0$	3.8	0	0	2.0	93	93	25		0.9751(R)
01/11/82	15.0	3.6*	4.2	0	0	2.5	60	60	22		
15/11/82	15.0	4.3$	3.5	0	0	2.0					0.8950(G)
29/11/82	15.0	5.8*	2.6	0	0	2.6					
MEAN		4.77				2.1	171.6	171.6	52.3	0.9262	
+/- S.E.		0.21				0.1	39.7	39.7	10.2	0.05	

* = Zeu calculated from Secchi depth.
$ = Zeu calculated from εmin.

APPENDIX 2. CONTINUED.

STAUNTON HAROLD.

DATE	Zmix (m)	Zeu (m)	Zmix/Zeu	N^2 ($*10^{-6}$ sec^{-2}) 0-5m	N^2 ($*10^{-6}$ sec^{-2}) 0-15m	Secchi depth(m)	Chlorophyll a.(mgm^{-2}) in water column	Chlorophyll a.(mgm^{-2}) in Zmix	Chlorophyll a.(mgm^{-2}) in Zeu	εPar (m^{-1})	εmin (m^{-1})
28/2/83	12.0	4.3$	2.8	0		2.5	50	50	19		0.8945(R)
07/3/83	12.0	4.3$	2.8	0		1.25	72	72	28		0.8972(R)
14/3/83	13.0	3.6$	3.6	0		1.25	120	120	36		1.0818(R)
21/3/83	13.0	3.7$	3.5	0		1.5	180	180	49		1.0456(R)
28/3/83	13.0	4.3$	3.0	0		1.5	234	234	81		0.8909(R)
05/4/83	14.0	4.9$	2.9	0	0	1.5	310	310	104		0.7837(G)
11/4/83	14.0	3.7	3.8	0	0	1.25	198	198	51	1.2778	
18/4/83	14.0	3.6	3.9	-76.1	-25.4	1.25	199	199	51	1.2499	0.9713(G)
25/4/83	14.5	3.5$	4.1	0	9.6	1.4	178	178	45		1.0984(R)
03/5/83	16.0	3.3$	4.8	0	0	1.0	240	240	45		1.1834(R)
09/5/83	16.0	2.7	5.9	0	0	1.25	321	321	52	1.7944	0.9253(R)
16/5/83	15.0	3.8	3.9	48.9	16.3	1.9	77	77	18	1.2582	1.0018(R)
23/5/83	16.0	4.25	3.8	109.0	70.5	1.5	75	75	53	1.0836	0.8925(R)
31/5/83	16.0	5.5	2.9	92.6	38.3	4.2	44	44	18	0.8227	0.6468(R)
06/6/83	16.0	5.6$	2.9	51.3	42.3	7.0	20	20	8		0.6876(R)
13/6/83	16.0	6.0$	2.7	0	0	2.25	58	58	22		0.6486(G)
20/6/83	16.0	5.1$	3.1	93.0	61.4	2.0	44	44	18		0.7530(G)
27/6/83	15.0	4.4$	3.4	0	0	1.75	165	165	52		0.8815(G)
04/7/83	15.0	5.2$	2.9	282.5	139.5	3.0	69	69	31		0.7383(G)
11/7/83	15.0	5.9$	2.5	0	61.1	2.5	33	33	14		0.6512(G)
18/7/83	15.0	4.1	3.7	518.6	349.1	1.0	481	481	294	0.9929	1.2622(R)
25/7/83	14.0	3.6	3.9	0	68.2	1.5	483	483	179	1.3005	1.0719(G)
01/8/83	15.0	4.2	3.6	0	0	1.25	366	366	131	1.0645	0.9722(R)
08/8/83	15.0	3.3	4.5	0	0	1.25	313	313	65	1.4184	1.1696(R)
15/8/83	15.0	2.3	6.5	329.5	208.7	0.75	559	559	183	1.8655	1.8070(R)
22/8/83	15.0	3.0	5.0	0	0	1.0	481	481	115	1.5501	1.2844(R)
31/8/83	15.0	3.4$	4.4	0	31.6	1.5	373	373	96		1.1448(R)
05/9/83	15.0	2.9$	5.2	0	0	1.0	308	308	63		1.3147(R)
12/9/83	16.0	2.8	5.7	0	0	1.0	1261	1261	211	1.6056	1.4394(R)
19/9/83	16.0	2.2	7.3	0	0	1.0	586	586	251	2.0385	1.8597(R)
26/9/83	16.0	3.3*	4.8	0	68.7	1.25	934	934	194		
03/10/83	16.0	2.9*	5.5	0	64.4	1.0	858	858	80		
10/10/83	16.0	4.7*	3.4	0	0	2.0	230	230	75		
17/10/83	16.0	2.8*	5.7	0	0	1.75	114	114	30		
24/10/83	16.0	7.4*	2.2	0	15.2	3.5	71	71	33		
31/10/83	16.0	5.2*	3.1	0	0	2.25	47	47	15		
MEAN		4.05				1.8	282.0	282.0	78.1	1.3882	
+/- S.E.		0.19				0.19	46.8	46.8	12.0	0.09	

* = Zeu calculated from Secchi depth.
$ = Zeu calculated from εmin.

APPENDIX 2. CONTINUED.

FOREMARK.

DATE	Zmix (m)	Zeu (m)	Zmix/Zeu	N_2 ($*10^{-6}$ sec^{-2}) 0-5m	N_2 ($*10^{-6}$ sec^{-2}) 0-15m	Secchi depth(m)	Chlorophyll a.(mgm^{-2}) in water column	Chlorophyll a.(mgm^{-2}) in Zmix	Chlorophyll a.(mgm^{-2}) in Zeu	εPar (m^{-1})	εmin (m^{-1})
05/1/81	23.0	4.3	5.3	16.6	5.5					1.0153	
16/2/81	23.0	7.1	3.2	0	0					0.6303	
02/3/81	23.0			33.2	4.1						
09/3/81	23.0			14.9	3.7		59	59			
16/3/81	23.0	7.1	3.2	0	0	3.5	74	74	23	0.5942	
24/3/81	22.0	6.4	3.4	103.2	40.7	2.25	120	120	33	0.7185	
30/3/81	22.0	6.0	3.7	0	0	2.25	147	147	62	0.7909	
07/4/81	23.0	6.6*	3.5	-6.3	-2.1	3.0	67	67	33		
13/4/81	22.0	6.8	3.2	-48.9	13.9	2.5	139	139	51	0.6609	
27/4/81	23.0	6.1*	3.8	0	0	2.75	310	310	86		
04/5/81	23.0	5.0$	4.6	25.5	8.5		577	577	115		0.8467(R)
11/5/81	23.0	7.4	3.1	37.3	75.3	3.4	49	49	13	0.6223	
18/5/81	13.0	7.8	1.7	-47.5	146.1	4.0	97	66	39	0.5708	
26/5/81	12.0	8.0	1.5	291.6	298.7	4.0	53	50	44	0.5322	
01/6/81	12.0	7.8	1.5	126.9	318.9	3.0	112	72	69	0.5166	
08/6/81	12.0	4.7$	2.6	0	297.5	1.5	385	351	152		0.8859(G)
15/6/81	14.0	3.2$	4.4	70.2	298.7	2.5	526	525	199		1.3017(R)
22/6/81	16.0	4.9$	3.3	365.8	189.3	3.0	305	254	131		0.8514(R)
29/6/81	17.0	8.4$	2.0	26.9	70.1	3.75	64	54	33		0.5025(G)
06/7/81	18.0	7.0$	2.6	0	160.4	2.4	138	134	81		0.6009(G)
13/7/81	18.0	4.6$	3.9	85.6	379.5	2.0	131	125	78		0.9197(G)
20/7/81	19.0	5.0$	3.8	0	283.6	3.0	335	331	145		0.8365(G)
27/7/81	16.0	5.5$	2.9	78.8	219.3	3.0	186	181	66		0.7667(G)
03/8/81	14.0	9.3*	1.5	361.4	529.0	4.25	38	28	20		
10/8/81	15.0	8.0$	1.9	441.9	540.6		19	18	9		0.5231(G)
17/8/81	12.0	7.4$	1.6	178.1	467.9	4.5	83	79	73		0.5685(G)
24/8/81	13.0	7.2*	1.8	340.1	364.2	3.25	376	325	191		
02/9/81	13.0	9.5*	1.4	350.9	467.9	4.4	119	101	74		
07/9/81	14.0	5.0*	2.8	261.1	347.2	2.25	87	61	56		
21/9/81	18.0	4.5	4.0	0	0	2.5	276	266	69	0.9740	
28/9/81	19.0	5.6*	3.4	0	0	2.5	263	263	64		
05/10/81	20.0	8.3*	2.4	0	0	3.8	177	165	78		
12/10/81	22.0	5.7	3.9	0	0	3.0	154	154	40	0.7876	
26/10/81	22.0	6.9	3.2	0	0	3.75	95	95	29	0.5776	
09/11/81	22.0	8.2	2.7	0	0	3.9	118	118	46	0.5221	
23/11/81	22.0	6.6	3.3	0	0	2.5	88	88	27	0.6513	
07/12/81	22.0	6.9	3.2	0	0	3.5	63	63	23	0.6388	
MEAN		6.54				3.09	171.5	162.0	68.2	0.6752	
+/- S.E.		0.25				0.14	23.8	23.4	8.4	0.04	

* = Zeu calculated from Secchi depth.
$ = Zeu calculated from εmin.

APPENDIX 2. CONTINUED.

FOREMARK.

DATE	Zmix (m)	Zeu (m)	Zmix/Zeu	N_2 ($*10^{-6}$ sec^{-2}) 0-5m	N_2 ($*10^{-6}$ sec^{-2}) 0-15m	Secchi depth(m)	Chlorophyll a.(mgm^{-2}) in water column	Chlorophyll a.(mgm^{-2}) in Zmix	Chlorophyll a.(mgm^{-2}) in Zeu	εPar (m^{-1})	εmin (m^{-1})
01/2/82	21.0	7.4	2.8	0	0	4.5	66	66	27	0.5963	
01/3/82	21.0	7.5	2.8	0	0	3.5	120	120	40	0.6097	
08/3/82	21.0	6.5	3.2	0	0	2.8	178	178	63	0.6881	
17/3/82	21.0	5.2	4.0	0	0	2.0	304	304	79	0.8222	
22/3/82	22.0	4.5*	4.9	4.8	1.6	2.0	324	324	78		
29/3/82	20.0	4.5*	4.4	21.2	12.5	2.0	618	618	133		
05/4/82	21.0	4.8	4.4	16.4	5.5	2.3	946	946	194	0.9294	
13/4/82	21.0	6.6	3.2	16.5	8.1	2.5	247	247	72	0.6802	
20/4/82	21.0	6.8	3.1	95.7	86.5	3.0	84	84	43	0.6517	
26/4/82	20.0	7.1	2.8	189.3	147.1	2.9	101	101	58	0.6455	
03/5/82	21.0	7.1	3.0	0	0	2.75	96	96	29	0.6464	
11/5/82	4.0	9.0	0.4	288.7	161.4	6.0	20	8	11	0.4635	
17/5/82	6.0	13.0*	0.5	67.1	363.3	6.0	16	9	13		
24/5/82	7.0	9.1	0.8	68.9	379.2	5.0	32	13	17	0.5163	
01/6/82	10.0	8.4	1.2	580.6	720.4	4.75	38	29	26	0.5214	
07/6/82	3.0	7.8	0.4	1854.1	1276.0	3.9	81	48	71	0.5629	
14/6/82	6.0	8.8*	0.7	0	800.4	4.0	51	29	38		
21/6/82	10.0	8.9	1.1	-81.4	575.0	4.0	39	28	24	0.4934	
28/6/82	12.0	7.9	1.5	0	512.2	3.75	26	18	13	0.5716	
05/7/82	12.0	7.5	1.6	0	0	3.5	39	34	26	0.5953	
12/7/82	13.0	6.3	2.1	599.7	691.7	2.25	190	179	164	0.6842	
19/7/82	13.0	7.6	1.7	448.6	752.8	3.25	78	62	43	0.5937	
26/7/82	13.0	9.8	1.3	0	677.0	4.5	25	21	17	0.4592	
02/8/82	11.0	7.9	1.4	333.9	832.9	4.25	54	47	41	0.5885	
16/8/82	14.0	5.8*	2.4	0	530.8	2.6	112	91	43		
31/8/82	17.0	5.3$	3.2	0	25.4	2.6	213	193	71		0.7940(R)
06/9/82	17.0	8.1$	2.1	0	0	3.4	91	82	43		0.5195(G)
13/9/82	17.0	8.4$	2.0	0	66.1	4.0	103	94	56		0.4991(G)
20/9/82	17.0	3.8	4.5	0	211.9		269	260	78	1.3179	
27/9/82	19.0	5.6*	3.4	0	0	2.5	258	209	66		
05/10/82	20.0	6.1$	3.3	0	0	2.6	126	115	50		0.6648(G)
11/10/82	21.0	6.5$	3.2	0	0	3.0	170	170	69		0.6502(G)
18/10/82	21.0	5.3$	4.0	0	0	2.0	156	156	40		0.7949(G)
01/11/82	22.0	6.1*	3.6	0	0	2.75	121	121	34		
15/11/82	21.0	5.1$	4.1	0	0	2.75	107	107	22		0.8245(R)
29/11/82	21.0	5.6*	3.8	0	0	2.5	55	55	15		
MEAN		6.99				3.32	154.3	146.2	53.0	0.6494	
+/- S.E.		0.30				0.18	30.0	30.3	6.7	0.04	

* = Zeu calculated from Secchi depth.
$ = Zeu calculated from εmin.

APPENDIX 2. CONTINUED.

FOREMARK.

DATE	Zmix (m)	Zeu (m)	Zmix/Zeu	N_2 ($*10^{-6}$ sec^{-2}) 0-5m	N_2 ($*10^{-6}$ sec^{-2}) 0-15m	Secchi depth(m)	Chlorophyll a.(mgm^{-2}) in water column	Chlorophyll a.(mgm^{-2}) in Zmix	Chlorophyll a.(mgm^{-2}) in Zeu	εPar (m^{-1})	εmin (m^{-1})
28/2/83	18.0	5.6$	3.2	0	0	2.5	62	62	19		0.7550(G)
07/3/83	18.0	5.4$	3.30	0	0	1.75	120	120	36		0.7804(G)
14/3/83	19.0	5.7$	3.3	0	0	1.8	291	291	94		0.7323(R)
28/3/83	19.0	5.7$	3.3	0	0	1.75	216	216	63		0.7373(R)
05/4/83	20.0	6.1$	3.3	0	0	1.75	156	156	48		0.6914(R)
11/4/83	20.0	3.4	5.9	0	0	1.25	221	221	40	1.3765	
25/4/83	20.0	6.3$	3.2	0	0	2.25	132	132	40		0.6646(R)
03/5/83	20.0	6.1$	3.3	0	16.3		101	101	38		0.6869(R)
09/5/83	15.0	4.4	3.4	0	0	1.75	138	106	29	1.1755	0.6911(G)
16/5/83	21.0	5.5	3.8	0	39.1	2.5	299	299	77	0.8371	0.8027(G)
23/5/83	21.0	6.5	3.2	0	89.8	3.0	184	184	38	0.7343	0.5787(G)
31/5/83	22.0	6.8	3.2	159.4	185.1	4.8	73	73	51	0.6679	0.5625(G)
06/6/83	8.0	3.5*	2.3	0	239.1	1.5	184	129	53		
13/6/83	8.0	6.1$	1.3	29.6	419.5	2.75	135	81	62		0.6884(G)
20/6/83	12.0	8.6$	1.4	150.7	443.0	2.25	32	21	18		0.4862(G)
27/6/83	12.0	8.5$	1.4	0	444.1	3.25	40	31	28		0.4918(G)
04/7/83	12.0	5.4$	2.2	350.9	625.4		104	88	68		0.7759(G)
11/7/83	3.0	7.8$	0.4	1116.3	805.9	2.5	68	21	43		0.5415(G)
18/7/83	4.0	7.9	0.5	1630.6	1061.2	2.75	102	56	79	0.5554	0.5965(G)
25/7/83	6.0	6.3	1.0	628.5	888.2	2.75	144	94	98	0.7337	0.6960(R)
01/8/83	8.0	7.4	1.1	0	632.3	2.25	169	121	117	0.6378	
08/8/83	10.0	2.9	3.4	0	472.5	1.5	423	382	199	1.4713	1.5787(R)
15/8/83	11.0	3.2	3.4	597.9	632.4	1.5	263	241	135	1.3324	1.2969(R)
22/8/83	17.0	5.6	3.0	300.7	515.6	3.5	41	36	18	0.8287	0.7464(R)
31/8/83	15.0	6.3	2.4	188.8	212.5	2.75	66	60	41	0.6865	0.7849(R)
05/9/83	20.0	4.5$	4.4	0	0	2.25	118	105	28		0.9288(R)
12/9/83	21.0	5.9	3.6	91.2	30.4	2.75	61	58	14	0.7507	0.7930(R)
19/9/83	22.0	4.7	4.7	0	0	2.0	69	69	15	0.9405	0.8303(R)
26/9/83	22.0	4.3*	5.1	0	46.4	1.9	99	99	19		
03/10/83	22.0	4.5*	4.9	0	0	2.0					
10/10/83	22.0	7.2*	3.1	0	0	3.25					
24/10/83	22.0	6.6*	3.3	0	0	3.0					
MEAN		5.77				2.38	141.8	126.0	55.5	0.9092	
+/- S.E.		0.26				0.14	16.9	16.7	7.7	0.08	

* = Zeu calculated from Secchi depth.
$ = Zeu calculated from εmin.

APPENDIX 3.

PHYTOPLANKTON SPECIES RECORDED FROM STAUNTON HAROLD AND FOREMARK RESERVOIRS, 1980 TO 1983. (Following the classification given in Round, 1981).

CYANOCHLORONTA (= Cyanophyta).

Chroococcales:

Merismopedia sp.

Microcystis aeruginosa Kütz. emend. Elenkin

Gomphosphaeria sp.

Nostocales:

Anabaena circinalis Rabenh. *ex.* Born. *et.* Flah.

A. flos-aquae Bréb. *ex.* Born. *et* Flah.

Aphanizomenon flos-aquae Ralfs *ex.* Born *et.* Flah.

Oscillatoria limnetica Lemm.

Oscillatoria ? limosa

CRYPTOPHYTA.

Cryptomonadales:

Cryptomonas erosa Ehrenb.

C. marsonii Skuja

C. ovata Ehrenb.

C. ? reflexa/rostrata

Rhodomonas minuta Skuja var. *nannoplanktica* Skuja

CHLOROPHYTA.

Volvocales:

Chlamydomonas spp.

Eudorina elegans Ehrenb.

Pandorina morum Bory

Phacotus sp.

Chlorellales:

Actinastrum sp.

Ankistrodesmus acicularis (A. Braun) Korshikov

A. ? angustus Bernard

A. falcatus (Corda) Ralfs

A. subcapitatus Korshikov

Chodatella ? quadriseta Lemmermann

Coelastrum microporum Näegeli

Crucigenia fenestrata Schimdle

C. ? tetrapedia (Kirchner) W. & G. S. West

Dictyosphaerium pulchellum Wood

Oocystis borgei Snow

Quadrigula sp.

Scenedesmus acuminatus (Lagerh.) Chodat

S. quadricauda (Turp.) Bréb.

Selenastrum ? minutum (Näegeli) Col.

Chlorococcales:

Ankyra ancora (Smith) Fott

A. judayi (Smith) Fott

Coelastrum microporum Näegeli

Oocystis borgei Snow

Pediastrum boryanum (Turp.) Meneghin

P. duplex Meyen

Sphaerocystis schroeteri Chodat

Tetraedron sp.

Tetrastrum sp.

Desmidiales:

Closterium aciculare T. West

Cosmarium ? depressum (Näg.) Lund

Staurastrum spp.

PRASINOPHYTA.

Prasinocladales:

Platymonas sp.

EUGLENOPHYTA.

Euglenales:

Euglena spp.

Trachelomonas sp.

DINOPHYTA.

Gymonodiniales:

Gymnodinium helveticum var. *achroum* Skuja.

Peridiniales:

Ceratium hirudinella O. F. Müll.

Glenodinium sp.

Peridinium cinctum (Müll.) Ehrenb.

XANTHOPHYTA.

Mischococcales:

Monodus subterraneus Boye Petersen

Arachnochloris sp.

CHRYSOPHYTA.

Chromulinales:

Chrysococcus sp.

Ochromonadales:

Mallamonas akrokomos Ruttner

M. ? caudata Iwanoff

BACILLARRIOPHYTA.

Melosirales:

Melosira granulata (Ehrenb.) Ralfs

M. italica (Ehrenb.) Kütz. subsp. *subarctica* Müll.

Thalassiosirales:

? Cyclotella glomerata Bachmann

Stephanodiscus astraea (Ehrenb.) Grun. (= S. rotula (Kütz.) Hendey)

S. hantzschii Grun.

S. hantzschii var. *parva* (Grunow in Cl. & Moll) Stoermer & Hakansson.

Fragilariales:

Asterionella formosa Hass.

Diatoma elongatum Agardh.

Fragilaria crotonensis Kitton

Synedra actinastroides Lemm.

S. acus Kütz.

? Synedra ulna (Nitzsch.) Ehrenb.

Tabellariales:

Tabellaria fenestrata (Lyngb.) Kütz.

Naviculales:

Gyrosigma sp.

Navicula viridula Kütz.

Nitzschiales:

Nitzschia acicularis W. Smith

Nitzschia ? sigmoidea

APPENDIX 4.

PHYTOPLANKTON IDENTIFICATION AND COUNTING PROBLEMS.

Certain phytoplankton taxa caused problems during this research which were avoided by clumping groups together either during counting or for the purposes of analysis.

More than one species of a number of genera of phytoplankton were recorded between 1981 and 1983 in both reservoirs. The individual species were clumped together for the purposes of analysis as in many cases they occured at the same time. In other cases it was not possible to split the species during counting. The genera affected in this way were *Anabaena* (2 spp.), *Ankistrodesmus* (at least 4 spp.), *Ankyra* (2 spp.), *Chlamydamonas* (2 spp), *Crucigenia* (2 spp.), *Cryptomonas* (3 spp.), *Mallamonas* (2 spp.), *Melosira* (2 spp.), *Pediastrum* (2 spp.), *Scenedesmus* (at least 2 spp.) and small centric diatoms.

Several taxa created special problems and are described in more detail below:

(1) Several years ago, Severn Trent Water Authority recorded a small Xanthophycean phytoplankter (2-4 µm) which occured in high densities in early spring. This was identified as *Monodus subterraneus* by the Freshwater Biological Association. This species is very small and was difficult to count and during this study another small Xanthophyceaen genera was recorded. This was identified as *Arachnochloris* sp. Accurate estimations of the individual genera were not possible as the groups were found to occur at the same time and too much time was involved in seperating the genera during counting. They have been recorded and analysed together as *Monodus*.

(2) Identification and counting problems were encountered with small centric diatoms (3-12um). They were seperated by size categories during counting but they have been clumped together for the purposes of analysis. Scanning electron microscopy revealed that there were three species. *Stephanodiscus hantzschii* and *S. hantzschii* var. *parva* have been confirmed (Haworth pers. comm.). The third was a species which resembled *Cyclotella glomerata* and was observed as small chains.

(3) *Cryptomonas* was the third group which caused problems. These were seperated into three groups, mainly divided by size, during counting. They have been clumped together for analyses. These species have been identified and confirmed (Sommer pers. comm.) as *Cryptomonas erosa*, (the commonest form) and *C. marssonii*. The last species has only been tentatively identified and was very similar to both *C. reflexa* and *C. rostrata*.

(4) Another group which caused problems was the colonial green genera. Both *Pandorina morum* and *Sphaerocystis schroeteri* were identified from both reservoirs. They both occured at the same time during early summer. *Pandorina* cells lose their flagella prior to cell division and the cells tend to become more spherical and less well packed within the colony (Smith 1953). These colonies, often with daughter colonies were found to be almost identical to dividing *Sphaerocystis* colonies and unless each was identified seperately at a higher magnification they could not be distinguished. Therefore they have been grouped together for the the purposes of counting and analyses. The number of cells in each colony were counted.

(5) It was not possible to directly count the number of cells of two colonial species encountered during the research. These were

Aphanizomenon and *Microcystis*. The average number of cells per *Aphanizomenon* filament were estimated by measuring the length of thirty random filaments (x140 magnification), counting the number of cells per unit length (ie 50 um) (x700 magnification) of 5-10 filaments, then calculating the average cell length and finally multipying the average filament length by the average cell length. The numbers of *Microcystis* cells were estimated by seperarting the colonies into three arbitrary size classes (x140 magnification) and counting the number of cells in 2-5 randomly picked colonies of each class (x280 magnification).

APPENDIX 5. MAXIMUM AND MEAN (VALUES IN BRACKETS) OBSERVED NET RATES OF POPULATION INCREASE (kn+) AND DECREASE (kn-) FOR SELECTED PHYTOPLANKTON SPECIES IN STAUNTON HAROLD AND FOREMARK RESERVOIRS DURING 1981, 1982 AND 1983. THE TIME OF THE YEAR IS INDICATED (V = VERNAL, MARCH TO APRIL AND SUMMER = MAY TO SEPTEMBER).

STAUNTON HAROLD

	Period	1981				1982				1983			
		kn+		kn-		kn+		kn-		kn+		kn-	
Monudus	V	0.11	(0.08)	0.21	(0.18)	0.10	(0.10)	0.11	(0.11)	0.27	(0.17)	0.27	(0.24)
Small centrics	V	0.13	(0.12)	0.16	(0.16)	0.10	(0.10)			0.12	(0.10)	0.12	(0.12)
	S	0.31	(0.27)	0.33	(0.25)	0.38	(0.36)	0.43	(0.36)	0.34	(0.25)	0.20	(0.18)
Stephanodiscus astraea	V	0.10	(0.10)			0.06	(0.06)	0.09	(0.09)	0.09	(0.09)		
	S	0.16	(0.16)	0.16	(0.14)	0.34	(0.13)	0.34	(0.31)	0.14	(0.13)	0.32	(0.27)
Asterionella	V	0.20	(0.20)			0.17	(0.17)	0.23	(0.23)	0.08	(0.08)		
	S			0.23	(0.23)	0.27	(0.27)	0.33	(0.33)	0.51	(0.51)	0.38	(0.27)
Cryptomonas	V			0.20	(0.19)	0.17	(0.17)			0.14	(0.13)	0.08	(0.08)
	S	0.20	(0.11)	0.13	(0.11)	0.35	(0.21)	0.11	(0.09)	0.16	(0.13)	0.12	(0.10)
Rhodomonas	V					0.08	(0.07)	0.04	(0.04)	0.06	(0.06)	0.07	(0.07)
	S	0.29	(0.16)	0.29	(0.21)	0.29	(0.29)	0.25	(0.20)	0.42	(0.28)	0.31	(0.16)
Ankistrodesmus	V					0.27	(0.27)	0.10	(0.10)	0.04	(0.04)	0.05	(0.05)
	S			0.23	(0.23)	0.20	(0.20)	0.41	(0.41)	0.08	(0.06)	0.24	(0.17)
Chlamydamonas	V			0.19	(0.19)					0.17	(0.13)	0.18	(0.16)
	S			0.15	(0.15)					0.30	(0.21)	0.34	(0.33)
Scenedesmus	V											0.10	(0.10)
	S	0.03	(0.03)	0.05	(0.05)	0.09	(0.06)	0.11	(0.11)	0.16	(0.16)	0.09	(0.06)
Gymnodinium	V					0.10	(0.10)	0.23	(0.23)	0.06	(0.06)	0.10	(0.08)
	S									0.09	(0.09)	0.09	(0.09)
Ankyra	S	0.40	(0.34)	0.36	(0.32)	0.34	(0.32)	0.30	(0.18)				
Aphanizomenon	S	0.20	(0.18)	0.25	(0.17)	0.19	(0.14)	0.17	(0.17)	0.13	(0.13)	0.28	(0.18)
Anabaena	S	0.26	(0.26)	0.52	(0.52)	0.14	(0.14)	0.14	(0.11)	0.18	(0.18)	0.22	(0.22)
Microcystis	S	0.16	(0.13)	0.12	(0.09)	0.16	(0.16)	0.27	(0.27)	0.19	(0.18)	0.33	(0.23)
Coelastrum	S	0.08	(0.08)	0.13	(0.09)	0.17	(0.16)	0.08	(0.08)	0.07	(0.08)		
Pandorina /Sphaerocystis	S	0.20	(0.15)	0.18	(0.12)	0.14	(0.14)	0.21	(0.21)	0.22	(0.22)	0.13	(0.13)
Pediastrum	S	0.09	(0.09)	0.20	(0.17)	0.32	(0.20)	0.15	(0.13)	0.07	(0.07)	0.16	(0.16)

APPENDIX 5 (cont.). MAXIMUM AND MEAN (VALUES IN BRACKETS) OBSERVED NET RATES OF POPULATION INCREASE (kn+) AND DECREASE (kn-) FOR SELECTED PHYTOPLANKTON SPECIES IN STAUNTON HAROLD AND FOREMARK RESERVOIRS DURING 1981, 1982 AND 1983. THE TIME OF THE YEAR IS INDICATED (V = VERNAL, MARCH TO APRIL AND SUMMER = MAY TO SEPTEMBER).

FOREMARK

Period		1981				1982				1983			
		kn+		kn-		kn+		kn-		kn+		kn-	
Monodus	V							0.04	(0.04)	0.12	(0.12)		
	S											0.18	(0.18)
Small centrics	V	0.09	(0.09)	0.18	(0.15)	0.08	(0.08)	0.05	(0.05)	0.14	(0.14)	0.23	(0.18)
	S	0.30	(0.23)	0.26	(0.23)	0.29	(0.18)	0.24	(0.10)	0.20	(0.14)	0.15	(0.09)
Stephanodiscus astraea	V	0.12	(0.12)	0.10	(0.10)	0.07	(0.07)	0.27	(0.27)	0.11	(0.11)	0.17	(0.17)
	S	0.17	(0.17)	0.11	(0.11)	0.20	(0.20)	0.06	(0.06)				
Asterionella	V	0.09	(0.09)	0.18	(0.18)	0.07	(0.07)			0.16	(0.13)		
	S	0.45	(0.45)	0.48	(0.48)	0.15	(0.15)	0.31	(0.28)	0.15	(0.13)	0.24	(0.23)
Cryptomonas	V	0.01	(0.01)	0.07	(0.07)	0.01	(0.01)	0.06	(0.06)	0.05	(0.05)	0.04	(0.04)
	S	0.06	(0.06)	0.12	(0.11)	0.09	(0.08)	0.06	(0.05)	0.16	(0.13)	0.14	(0.12)
Rhodomonas	V	0.05	(0.05)	0.08	(0.08)	0.07	(0.05)	0.09	(0.09)	0.03	(0.03)	0.06	(0.05)
	S	0.34	(0.17)	0.21	(0.15)	0.28	(0.16)	0.17	(0.13)	0.15	(0.05)	0.20	(0.17)
Ankistrodesmus	V					0.07	(0.07)			0.09	(0.09)	0.09	(0.09)
	S					0.16	(0.16)						
Chlamydamonas	V					0.10	(0.10)	0.15	(0.15)	0.04	(0.04)		
Scenedesmus	S	0.06	(0.06)	0.07	(0.07)								
Gymnodinium	V	0.03	(0.03)			0.07	(0.07)	0.05	(0.05)	0.04	(0.04)	0.05	(0.05)
	S			0.04	(0.04)								
Ankyra	S					0.11	(0.11)	0.22	(0.16)	0.10	(0.10)	0.05	(0.05)
Aphanizomenon	S	0.18	(0.14)	0.21	(0.17)	0.31	(0.22)	0.50	(0.20)	0.29	(0.18)	0.33	(0.30)
Anabaena	S	0.11	(0.11)	0.19	(0.19)	0.23	(0.23)	0.23	(0.18)	0.14	(0.14)	0.14	(0.14)
Microcystis	S	0.16	(0.16)	0.13	(0.13)	0.17	(0.17)	0.21	(0.21)	0.26	(0.26)	0.13	(0.09)
Fragilaria	S	0.31	(0.21)	0.34	(0.27)					0.12	(0.12)	0.20	(0.17)
Coelastrum	S	0.10	(0.10)	0.10	(0.10)					0.11	(0.09)	0.15	(0.15)
Pandorina /Sphaerocystis	S	0.14	(0.14)	0.08	(0.08)	0.17	(0.16)	0.27	(0.18)	0.18	(0.14)	0.25	(0.25)
Pediastrum	S	0.02	(0.02)							0.16	(0.16)	0.10	(0.10)

APPENDIX 6.

SUMMARIES OF PHOTOSYNTHESIS DATA FROM STAUNTON HAROLD AND FOREMARK.

STAUNTON HAROLD PHOTOSYNTHESIS SUMMARY

DATE	ΣA	ΣP	ZEU	IO	I'O	AMAX	PMAX	IK	PE	TEMP	ΣACALC	PMAX RECORDED	MIXED /STRAT.
820427	530	28.6	5.9	3215	1331	221	10.6	275	11.0	10.3	655	YES	S
820630	266	25.6	4.1	3025	1252	105	10.8	142	21.1	16.3	291	YES	S
820706	80	11.7	4.9	2186	905	230	2.4	359	6.5	15.3	411	NO	M
820720	174	11.0	3.9	1373	568	140	6.8	217	11.3	18.3	192	NO	M
820727	259	25.7	6.0	1585	656	114	11.4	200	15.8	18.0	295	YES	M
820817	35	5.8		1690	700	291	6.0			18.8		NO	M
820914	104	21.9		1599	662	55	11.4			16.2		YES	M
830315	105	3.1		2905	1203	42	3.7			5.3		NO	M
830407	233	10.9	4.0	2819	1167	132	6.7	392	4.7	5.5	206	YES	M
830412	125	6.8	3.0	1946	806	106	6.2	325	5.3	6.0	109	NO	M
830426	232	18.1		2175	901	154	8.9			9.0		YES	M
830712	421	53.7	7.1	3454	1429	262	19.4	442	12.2	18.5	767	YES	S
830719	861	8.0	3.9	2624	1087	932	8.2	233	9.8	22.0	2215	YES	S
830719	1056	9.3	3.9	2624	1087	925	8.2	108	21.1	22.0	2915	YES	S
830802	184	4.8	3.0	3030	1255	168	6.2	375	4.6	20.9	215	NO	M
830802	105	3.2	3.0	3030	1255	105	3.3	233	3.9	20.8	171	NO	M
830809	176	9.7	3.0	2731	1131	219	12.8	350	10.2	19.3	268	YES	M
830809	232	14.0	3.0	2731	1131	200	12.5	230	14.9	19.3	300	YES	M
830823	798	19.9	3.0	2191	907	665	11.3	63	37.7	20.0	1848	YES	S
830823	324	22.2	3.0	2191	907	491	28.1	117	39.0	20.0		YES	M
830907	523	10.6	3.6	2320	960	657	12.1	282	12.9	17.0	1165	YES	M
830907	731	12.6	3.6	2320	960	592	13.1	175	20.8	17.0	2126	YES	M

FOREMARK PHOTOSYNTHESIS SUMMARY

DATE	ΣA	ΣP	ZEU	IO	I'O	AMAX	PMAX	IK	PE	TEMP	ΣACALC	PMAX RECORDED	MIXED /STRAT.
820325	487	39.9	5.5	3305	1369	122	15.1			4.8		YES	S
820615	434	21.3	5.9	1341	558	192	15.1	106	24.6	13.3	621	YES	S
820713	940	24.0	5.3	3589	1486	465	13.1	358	10.2	18.0	1173	YES	S
820803	276	38.9	8.4	3092	1280	140	13.9	417	13.3	18.9	131	YES	S
820907	266	31.1		2917	1207	68	10.2			15.3		YES	M
830607	440	11.8		2573	1065	306	8.1			13.0		NO	S
830607	444	10.6		2573	1065	222	5.9			13.0		YES	S
830714	333	33.7	6.4	2682	1108	143	18.9	317	16.6	20.0	563	YES	S
830726	709	26.5	6.3	3015	1243	295	13.1	325	11.2	21.5	857	YES	S
830726	722	26.6	6.3	3015	1248	282	12.1	292	11.5	21.5	862	YES	S
830816	96	4.0	3.6	1610	751	95	4.2	175	6.7	20.5	154	NO	M
830831	244	27.6	6.4	2563	1061	168	17.6	292	16.7	19.0	485	YES	S
830831	52	14.9	6.4	2563	1061	33	9.3	267	9.7	19.0	98	YES	M

ΣA mgO2/m2/h
ΣP mgO2/mgCHL.a./m2/h
Zeu metres
Io uE/m2/s
I'o uE/m2/s
Amax mgO2/m3/h
Pmax mgO2/mgCHL.a/h
Ik uE/m2/h
PE mgO2/mgCHL.a./uE/m2
TEMP oC
ΣAcalc mgO2/m2/h

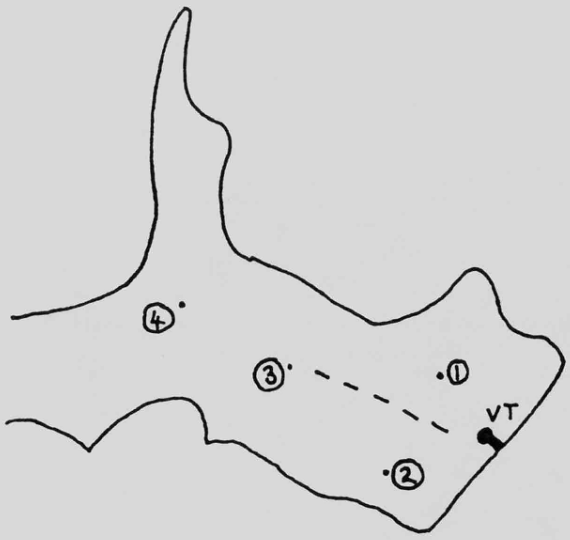
Mixed (M) or Stratified (S) indicates vertical distribution of phytoplankton populations

APPENDIX 7.

THE EFFECTIVENESS OF THE DESTRATIFICATION SYSTEM IN STAUNTON HAROLD RESERVOIR MEASURED DURING SEPTEMBER, 1981.

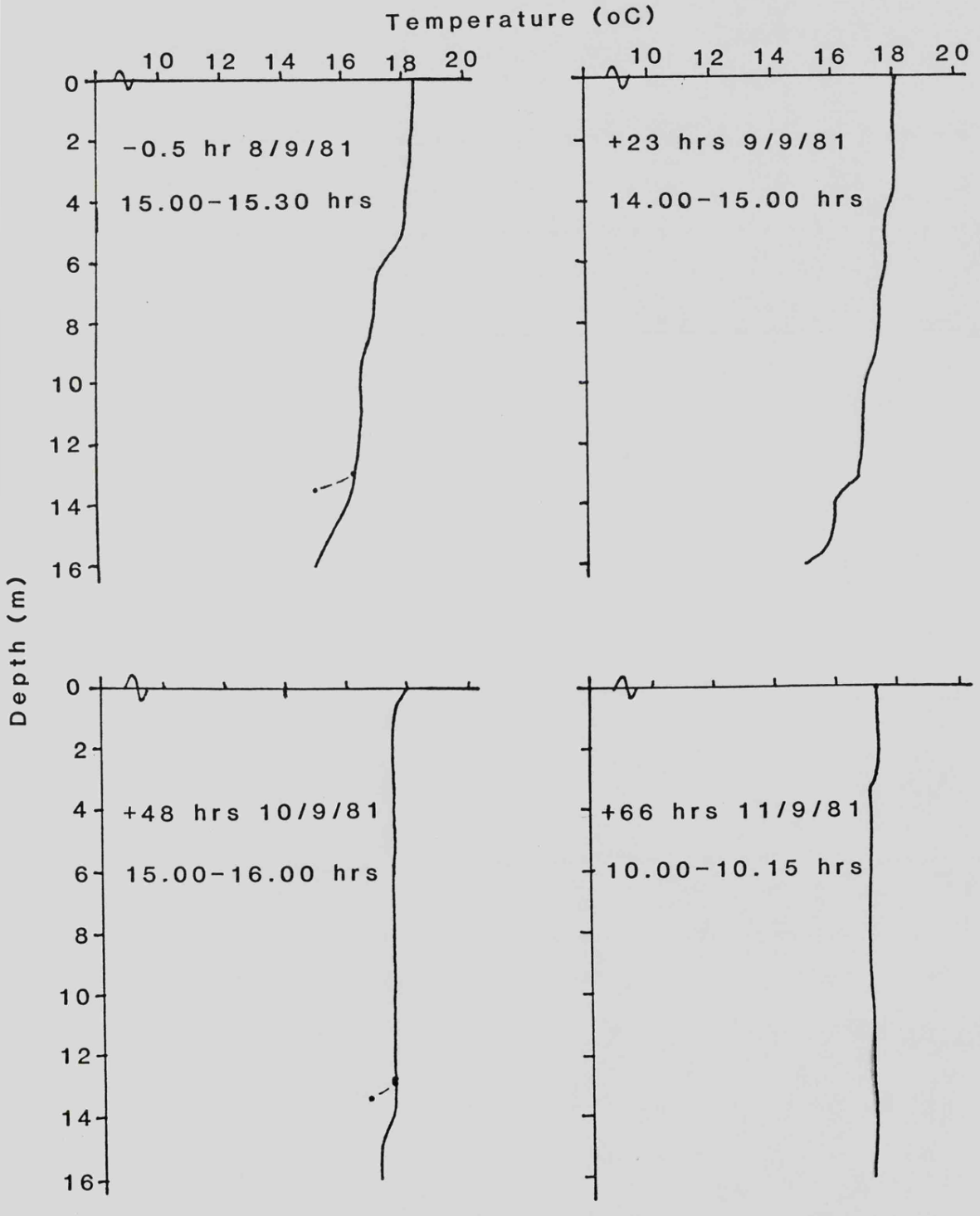
Thermal stratification was not persistent in Staunton Harold during 1981 due to early summer storms. However the reservoir became chemically stratified and dissolved oxygen in the lower layers decreased throughout the summer to less than 10% saturation (below 12 m) by late August. The destratification system was tested between September 8th and 11th (68 hours running) to evaluate its' effectiveness throughout the main basin of the reservoir and also validate the use of the valve tower as the regular sampling site.

Depth profiles of temperature, dissolved oxygen and chlorophyll a were recorded at the valve tower prior to switching on and twice daily until September 11th (see section 3.2.1.2, page 42). Temperature and dissolved oxygen were monitored daily at 4 sites in the main basin:



The temperature profiles from all 4 sites and the valve tower prior to switch on and at different time intervals during the experiment are shown in Figure 1. It can be seen that the destratification equipment was effective

Figure 1. The depth profiles of temperature at the valve tower and 4 sites in the main basin of Staunton Harold reservoir during a destratification experiment (8th and 11th September, 1981). Note than unless the temperature at any depth differs by less than 0.25°C (the accuracy of the meter) then the profile shown is that from the valve tower. Profile 4 (+66 hours) shows only the profile from the valve tower.



and within 3 days of operation, a temperature difference of 2.5^{o}C was eliminated. The valve tower was shown to be representative of the other 4 sites situated in the main basin.

The dissolved oxygen profiles are shown in Figures 2 and 3. The profiles showed that the strong stratification recorded 0.5 hours prior to the experiment was progressively eliminated and the 4th profile (valve tower only), 66 hours after switch on, showed that the dissolved oxygen was evenly distributed with depth. The results again reveal that the valve tower was representative of the other 4 sites in the main basin.

The results of the 68 hour destratification experiment showed that firstly, the perforated-pipe system was capable of mixing the main body of the reservoir and secondly, the valve tower was representative of the other 4 sites which validated its use as the regular sampling site.

Figure 2. The depth profiles of dissolved oxygen at the valve tower and 4 sites in the main basin of Staunton Harold reservoir during a destratification experiment (8th and 11th September, 1981).

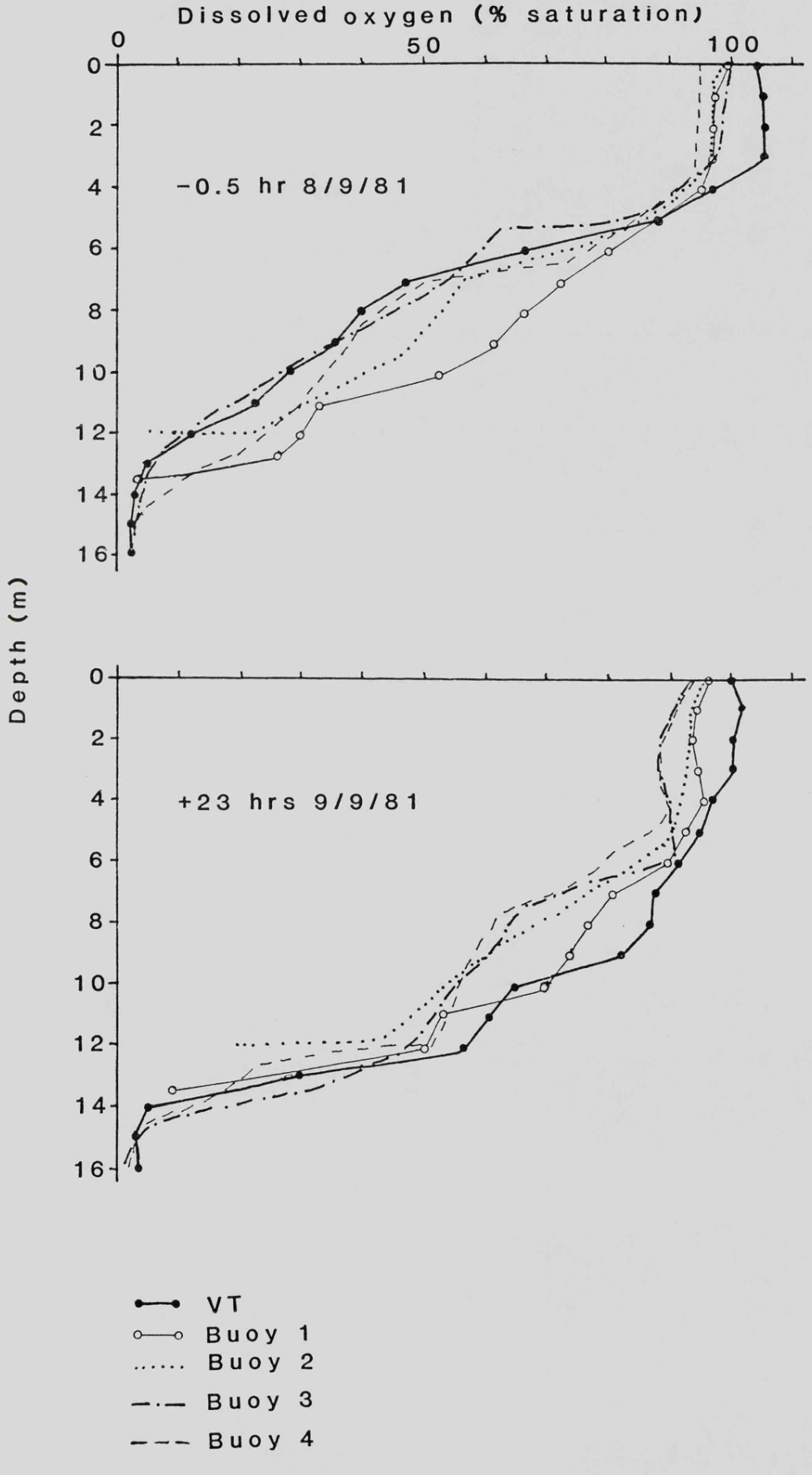
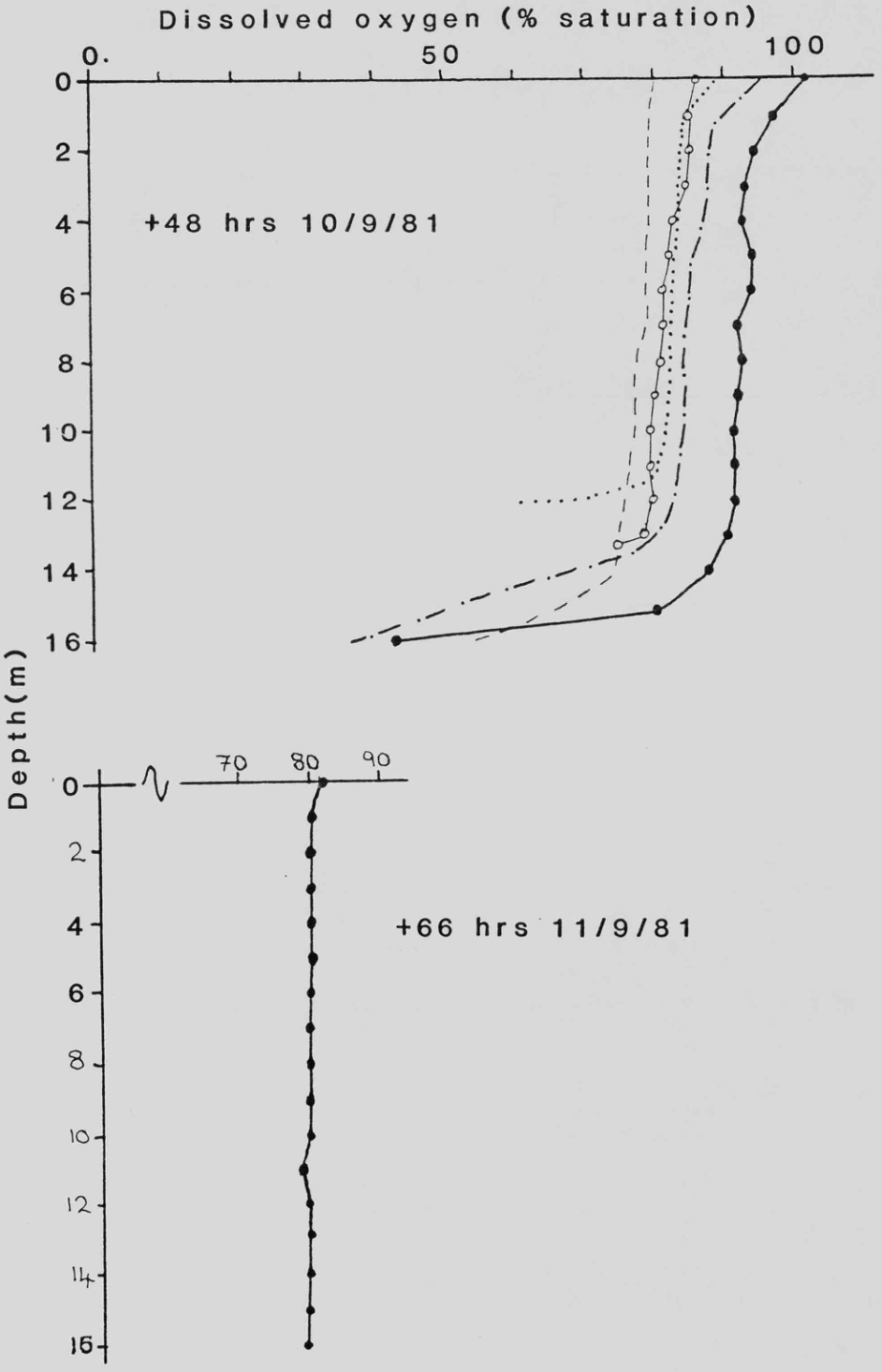


Figure 3. The depth profiles of dissolved oxygen at the valve tower and 4 sites in the main basin of Staunton Harold reservoir during a destratification experiment (8th and 11th September, 1981). Profile 4 (+66 hours) shows only the profile from the valve tower.



APPENDIX 8.

Figure 1. The temporal changes in the concentration of ortho-phosphate and iron in Staunton Harold between June and September, 1982. (Mean values for 6 depths). ⊙ Below detectable limits

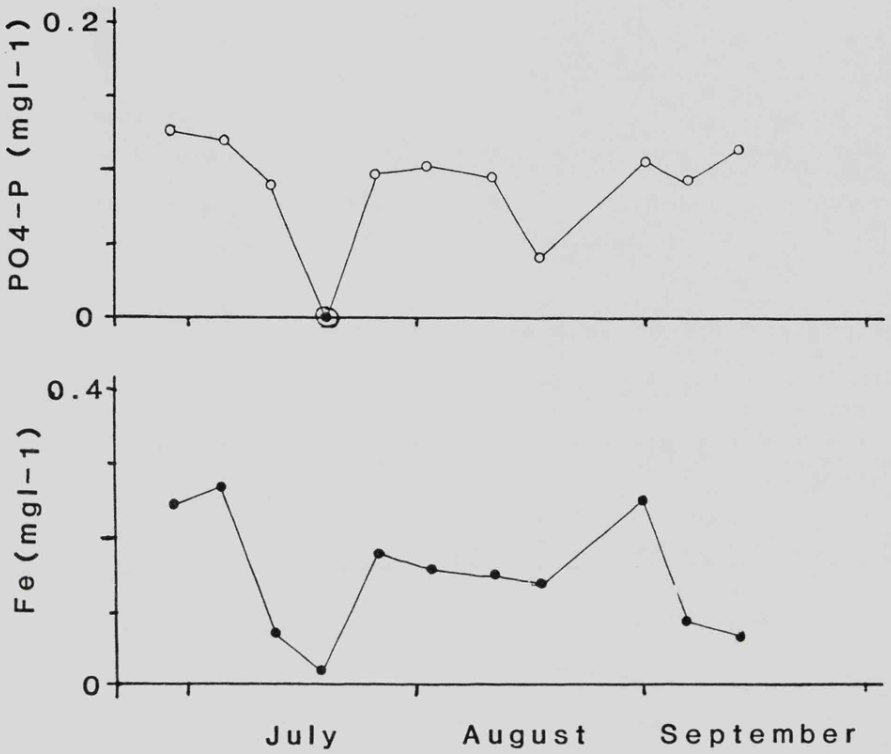
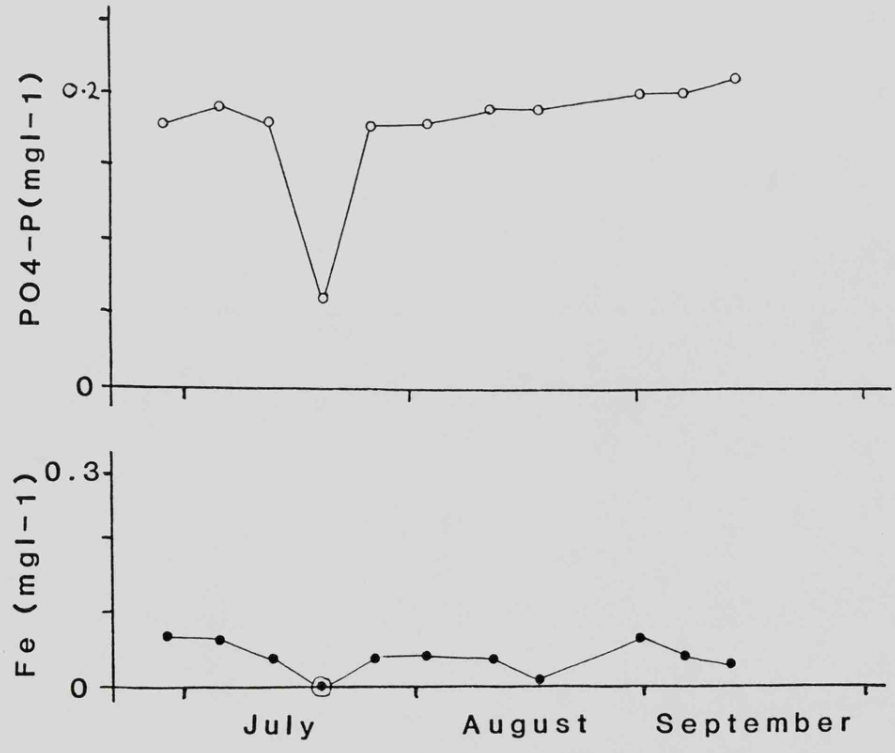


Figure 2. The temporal changes in the concentration of ortho-phosphate and iron in Foremark between June and September, 1982. (Mean values for 6 depths).



ABSTRACT.

THE EFFECTS OF ARTIFICIAL MIXING ON PHYTOPLANKTON GROWTH AND PERIODICITY.

BY S. J. BRIERLEY.

Continuous, low intensity mixing using a perforated pipe system prevented a lowland, eutrophic reservoir - Staunton Harold - from stratifying in 1982 and 1983. Environmental variables were measured and related to the responses of individual phytoplankton species and assemblages. These responses were compared to those from Staunton Harold during a year when natural mixing occurred (1981) and Foremark - a nearby, eutrophic reservoir - which was allowed to stratify in all three years. Diatoms and small Chlorophytes had higher growth rates under mixed conditions whilst colonial Chlorophytes and filamentous Cyanobacteria were favoured by stable water columns. Stratification of phytoplankton communities did occur during mixed years when water column stability was high and/or motile species were present. Nutrient availability and the stability of the water column were found to be the dominant factors affecting the seasonal changes in assemblages. Artificial mixing and a lowering in the stability of the water column in Staunton Harold during 1982 and 1983 did not have major effects upon the periodicity but the perturbations caused by changes in stability could be explained using a matrix whose axes were these dominant factors.

It was also shown that populations of phytoplankton which were mixed throughout the water column were able to tolerate wide ranges of underwater irradiance whilst stratified populations became light-shade adapted. This difference in the photosynthetic physiologies led to the mixed populations having a lower assimilation number and assimilation rates at higher intensties. The stratified populations had a higher assimilation number and assimilation rates at higher irradiances.

Phytoplankton sedimentation was measured in both reservoirs but no differences were found under stratified and mixed conditions.

Although phytoplankton assimilation was lowered by mixing, the mean total biomass was lower in one year of continuous mixing (1982) and higher in another (1983) when compared to the mean biomass in the naturally mixed year and those in Foremark.