A seasonal study of the surface biota of the Dubh Lochan

by

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Declaration

I hereby declare that this thesis is composed of work carried out by myself unless otherwise cited or acknowledged and that the thesis is of my own composition. The research was carried out within September 1979 to September 1982. This dissertation has not been previously presented for any other degree in whole or part.

Signed

E. A. McDonnell

Date: 30.11.88

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CONTENTS

Figure Contents

Table Contents

SUMMARY

A seasonal study of the surface biota of the Dubh Lochan was carried out during the period July 1980 to September 1982. Four surface sites were chosen, three in bay areas and one in open water. Samples were collected to a depth of 5mm. These were compared to depth samples collected at the open water site. The following parameters were measured:- water temperature, oxygen content, surface tension, Secchi disc depth, incident solar radiation, pH, alkalinity, acidity, conductivity, nitrate, nitrite, phosphate, ammonia, DOC, TOC (and hence POC), DON, PON (and hence TON), chlorophylls a, b and c, the carotenoids and phaeopigments. Phytoplankton and zooplankton enumeration, heterotrophic bacterial density and ^{14}C carbon fixation rates were determined. Two 24h surveys of the physical, chemical and biological components of the surface layer were carried out. Weather data was kindly provided by the Clyde River Purification Board.

During 1981, wind induced cooling of the surface layer resulted in surface water temperatures of up to 2 ^{o}C cooler than those measured at 0.5m depth.

Surface tension measurements indicated higher surface tension depression in the bay areas, particularly among the *Nuphar* and *Nymphaea*, than in open water. These higher surface tension depressions were linked with the higher POC levels recorded among the *Nuphar* and *Nymphaea*.

The determination of C:N ratios indicated that the organic content of the surface layer is highly refractive in nature, suggesting the positive accumulation of humic substances at the surface film through surface runoff, via the inflows, through turbulence, adsubble processes and the degradation of surface accumulated labile material of autochthonous origin.

A similarity in phytoplankton species composition between the top 5mm of the Dubh Lochan and the subsurface waters was observed. All the species noted, except for *Golenkinia radiata*, were recorded at all the sites and depths sampled and can be considered as either planktonic or

benthic in nature. The relative abundance of those species recorded at the surface layer was observed to vary, both species and temporal differences in the surface accumulation of algae was evident. Positive buoyancy, surface accumulation by entrainment and entrapment in the surface film, positive photoactic responses and wind driven lateral displacement were all implicated as methods for the observed surface enrichments. The variation in the distribution pattern of the species recorded and the lack of any assemblages of unique species of microalgae at the top 5mm of the Dubh Lochan suggested that the phytoplankton communities recorded at the surface layer were the result of constant transient movements of the algae between the surface, subsurface and the benthos.

While surface accumulation of microalgae may occur, this does not give any indication, in terms of their specific primary production rates, of the physiological state of the algae. The productivity data collected in this study suggests that, even when surface enrichment has not been recorded and particularly during overcast conditions, the surface layer exhibits a higher specific rate of photosynthesis. The contribution of the surface layer to the overall production of the lake system may prove to be significant. The responses of open water surface samples to changing light conditions when compared to those measured at 1m indicated the possibility of photoadaptation of the surface populations to higher light intensities. The development of such distinct populations depended upon the weather conditions. They were only observed when the weather was dry and calm. Wind induced mixing of the upper water column did not allow physiologically distinct populations to develop.

The distribution ranges of many of the zooplankton species recorded in the Dubh Lochan extended to the surface layer. Species differences were observed between the open water site and littoral regions but in both areas the cladocerans were numerically the most dominant component. Various members of the zooplankton were observed to migrate to the top 5mm during both day and night to graze upon the phytoplankton. In this way the zooplankton were able to influence the composition of the surface phytoplankton community. Those species capable of grazing at the surface layer may possess a competitive

advantage over other species. They have access to an additional food source in the form of the accumulated detritus.

Chapter 1

Introduction

1 INTRODUCTION

In its broadest sense, the surface layer of a body of water can be considered as that region in contact with or in close proximity to the air/water interface. The term surface layer can be further defined in several ways depending on the definitors judgement of the extent of its physical, chemical and biological parameters. These definitions fall broadly into two categories :

1) The surface layer can be considered as only the top few μm of water. This definition allows one to consider the surface film of water and those organisms dependent upon and associated with this film. 'Surface microlayer' and 'surface film' are usually used as descriptive terms.

2) The surface layer can be considered in a much broader sense i.e. anything from the top few millimetres down to a metre in depth but still, in one way or another, of direct influence to or influenced by the surface film.

In both cases the definition chosen depends upon the parameter or parameters selected for study and upon the sampling techniques used. The air/water interface is subject to direct exposure to radiation and hence to increased u.v. radiation and heat, to impact by rainwater and evaporation and hence fluctuations in salinity, to deposition of airborne anthropogenic substances, to cooling by wind action, to gaseous exchange and to greater turbulence and bubble bursting leading to the formation of aerosols (including, in the seas and oceans, giant salt nuclei). Organisms inhabiting this boundary layer must therefore be capable of coping with the stresses brought about by these fluctuating conditions.

The terms surface layer, surface microlayer and surface film are commonly used when describing the physical and chemical nature of the air/water interface. When defining the biological community within these parameters, which can be used in either marine or freshwater or systemic or microsystemic studies, further terms, with prefixes to subdivide the biocoenosis, are necessary. Banse (1975) has provided an historical review of the terminology and its derivatives.

Historically the term 'pleuston', originally coined by Schröter and Kir˘chner (1896), is used to describe "that part of the biological community associated with the air-water interface." (in Hutchinson, 1967). Naumann (1917) introduced the term 'neuston' to designate that "assemblage of microorganisms associated with the surface film" since Schröter and Kirchner's original definition actually included only the floating plants - both submerged and interfacial - associated with the surface film. These are considered by Hutchinson (1967) to be megaloplanktonic. Gams (1918) used the term pleuston to cover the whole assemblage of organisms associated with the surface film excluding the megaloplankton. He subdivided the pleuston into macropleuston, incorporating, in part, Schröter and Kirchner's definition and micropleuston, incorporating Naumann's definition.

Geitler (1942) suggested that the macropleuston should be termed simply the pleuston while the micropleuston are conveniently called the neuston since these short equivalents permit the use of prefixes. Pleuston are thus macroscopic with an upper dry surface (above the surface film) and a lower wet surface (either below or in contact with the surface film). Neuston are microscopic and can be classified as either epineustonic, being essentially ariel organisms which exist upon the surface film, doing so by means of flotation discs, stalks, 'hairs' and/or the production of lipids as water repellent substances, or hyponeustonic, being associated with the under surface of the film, either free-floating or attached by similar mechanisms as exhibited by the epineuston. This terminology is used by many. The term pleuston can also be subdivided into epi- and hypopleuston. Rapoport and Sanchez (1963) defined those animals capable of walking upon the surface film as epipleustonic since they can use the physical properties of the surface and so be considered as morphologically adapted to interfacial life but they do not occupy the interface *per se*. Carpenter (1928) and Welch (1952) had originally defined these as superneuston.

In marine studies the term neuston is often used to describe both the micro- and macroscopic components of the surface layer, which may extend from a few centimetres to a metre in depth. Hempel and Weikert (1972) subdivided marine neustonic organisms into permanent and

temporary inhabitants using the following categories ;

a) euneuston - those organisms with their maximum abundance in the immediate vicinity of the surface where they stay day and night i.e. permanent dwellers.

b) facultative - those organisms concentrated at the surface only during certain hours e.g. at night as a result of diel migration i.e. temporary dwellers.

c) pseudoneustonic - those organisms whose maximum concentration does not lie at the surface but at deeper layers, the range of their relative distribution reaching the surface layer only occasionally i.e. temporary dwellers.

This terminology has been used in marine neustonic studies by e.g. Cheng (1975), Champalbert (1977), Holdway and Maddock (1983) and Locke and Cory (1986).

Gladyshev and Malyshevskiy (1982) have attempted to clarify the terminology used. Based on Zaitsev's (1970) work and their own studies Gladyshev and Malyshevskiy argued that only the term'neuston' should be used to describe the surface biocoenosis. All other terms, especially epi- and hyponeuston thus become descriptive terms applying to the habit of those organisms found in the neuston. Thus, the term plankton can also be used to describe the life-style of those organisms which, while not attached to the surface film, float just below it. This ranking of terminology thus allows one to consider the surface layer as an entire ecological habitat (the 'neuston'),rather than attempting to subdivide it into small, artificially separated niches (pleuston, neuston, epineuston, hyponeuston etc.).

The sampling methods used in the study of the surface layer are obviously influenced by the definition employed and these also fall into two main categories:

a) Those which are concerned with removing just the surface film with its attendant microorganisms while leaving behind as much of the

underlying water as possible and

b) those which are concerned with removing a pre-determined volume or depth of water with its associated surface film and organisms.

Studies on the chemical and microbiological nature of the surface film usually employ type (a) methods. There are at least eighteen such methods. The most commonly used are the Harvey and Burzell (1972) glass plate method used in field studies by Gallacher (1975), Albright (1980), Mackin *et al* (1980). Berry-Lyons *et al* (1980), Hardy and Valett (1981), Carlson (1982,1983), Danos *et al* (1983), Lion and Leckie (1983), Hardy and Apts (1984) and Hardy (1985); and the Garrett (1965) screen. Screen materials have included Monel, stainless steel, aluminium, polyethylene and Nitex, see Williams (1967), Garrett (1967), Piotrowicz *et al* (1972), Duce *et al* (1972), Pravdić and Vulcović (1976), Eisenreich *et al* (1978), Dragcević *et al* (1979), Elzerman and Armstrong (1979), Bacon and Elzerman (1980), Mitamura and Matsumoto (1980), Barnes *et al* (1982), Danos *et al* (1983) and Knap *et al* (1986). All the methods more or less sample the surface microlayer but the thickness of the surface film that they remove and the efficiency with which they sample it and its chemical constituents varies and this must be very carefully taken into account when comparing the resultant data. The influence of sampling method on the determination of the chemical and biological composition of surface films has been discussed by Danos *et al* (1983), Daumas *et al* (1976), Van Vleet and Williams (1980), Hatcher and Parker (1974) and Garrett (1974).

Surface layer studies which consider the near-by planktonic organisms, such as algal blooms and feeding zooplankton usually employ type (b) methods. Either a net or a surface skimmer is used to remove the top few cm for either qualitative or quantitative studies. These methods allow much larger areas and volumes to be sampled and so are more useful in population studies. Most nets are qualitative and the depth to which they sample varies (David, 1965; Schram, 1981; Ben Yami *et al*, 1970; Derenbach and Ehrhardt, 1975; Matsuo *et al*, 1976; Champalbert, 1977; Locke and Corey, 1986 and Holdway and Maddock, 1983). Quantitative designs tend to be "skimmers", designed to remove as a layer the top few cm of water e.g. Hinton and Boney (1979). These

methods tend to be used at sea and require the use of motorized boats. A simpler design involves a polyethylene tray (Hardy, 1973) which can be lowered to the desired depth and dragged along by hand. By this means the top few mm can be collected. This method is suitable for smaller bodies of water.

Whatever the terminology adopted and parameters used to delimit the area of investigation one underlying physical parameter governs all definitions and descriptions and that is the air/water interface. As previously stated, this boundary is subject to the direct effects of light, heat, precipitation, evaporation, gaseous exchange and wind induced turbulence and as such its chemical and biological composition can be expected to differ quantitatively and qualitatively from that of the underlying water.

Water molecules are attracted to one another by weak electrostatic forces. Hydrogen bonding exists between the molecules in all directions and it is this bonding which is responsible for water's liquid rather than gaseous nature at temperatures between 0 and 100 ^{o}C. At the air/water interface this bonding pattern is disrupted. Molecular attraction becomes unbalanced. The electrostatic forces are directed sideways and downwards. An inward adhesive force is exerted to the bulk liquid. The result is the formation of an interface, surface or film which is under tension. This surface tension is measureable (newtons m^{-1}or dynes cm^{-1}) and for pure water (72.7 dyn cm^{-1}) is higher than that of any other liquid except mercury (472 dyn cm^{-1})

Surface tension is known to decrease with increasing temperature while the presence of dissolved inorganic compounds causes a slight increase. Hardman (1941) made over 100 measurements of surface tension on 40 lakes. She found that the surface tension was depressed by the presence of organic compounds e.g. coloured bog lakes and stagnant water, both high in dissolved organic matter (DOM), exhibited depressions of 6-7 dynes cm^{-1}. Thus pH had little effect unless organic acids were present. During heavy algal blooms surface tension depressions of 10-20 dyn cm^{-1} were measured. In littoral regions, where the growth of floating algae and macrophytes was particularly abundant, surface tension depressions of about 20 dyn $cm.^{-1}$ were also noted. Thus

natural populations of algae and submerged macrophytes which secrete large quantities of organic compounds during active photosynthesis (Fogg, 1977; Hardy and Apts, 1984) as well as during senescence and lysis can affect the surface tension of bodies of water.

Many of the early investigations on the biological components of freshwater surface films have been qualitative. Bacteria, algae, protozoa, fungi and higher plants and animals which possess physical adaptations that allow them to remain in contact with the surface film have been described, e.g. Woronin (1880), Miall (1892), Schröter and Kirchner (1896), Scourfield (1894, 1900, 1901, 1930), Mast and Root (1916), Naumann (1917), Stehle (1923), Korchikoff (1926), Carpenter (1928), Henrici and Johnson (1935), Russel and Ramachandraroa (1941), Pascher (1942), Geitler (1942), Vischer (1943), Gessner (1949), Petersen and Hansen (1958, 1960, 1961), Fott (1954), Valkanov (1968), Babienzen (1966), Jones and Sloof (1966), Maynard (1968), Babienzen and Schwartz (1970), Lukavsky (1971), Niewolak (1971a, 1971b), Ingold (1973, 1975), Bednarz (1974), Caponigro and Eriksen (1976), Frolund (1977) Dudka (1982) and Pentecost (1984). Goldacre (1949), Welch (1952), Ruttner (1973) and Gladyshev (1987) have discussed the biological importance of the surface film in providing mechanical support and a source of food for those organisms adapted for life at the surface.

Quantitative and qualitative analyses of the surface layer of freshwater bodies have indicated that the majority of species found are normally associated with the plankton, benthos and periphyton and may show considerable surface enrichment when compared to subsurface waters, e.g. Stehle (1923), Maynard (1968), Parker and Wodehouse (1970), Danos *et al* (1983) and Pentecost (1984). Parker and Hatcher (1974) in a study of the surface microlayer of Virginian ponds, reported no neustonic algae *per se*. Instead, surface enrichment of typically planktonic species such as *Chlamydomonas*, *Chlorella*, *Trachelomonas* and *Merismopedia* were recorded.

Since the surface layer is subjected to higher light intensities than the underlying waters, it has been postulated that phytoplankton primary production will be inhibited at the surface. Both Niewolak

(1971) and Belay (1981) have recorded surface inhibition of photosynthesis by solar radiation in the surface layer of freshwaters. This subject has been reviewed by Harris (1978).

Algal blooms which accumulate in the surface layer of freshwaters have been well documented, e.g. Griffiths (1939), Prescott (1948), Brook (1957) Reynolds and Walsby (1975), and Reynolds (1984). These blooms can be caused by algae of all the major groups, Cyanophyta, e.g. *Anabaena*, *Aphanizomenon* and *Microcystis* (Reynolds and Walsby, 1975), Chrysophyta, e.g. *Dinobryon* and *Synura*, Bacillariophyta, e.g. *Stephanodiscus rotula* (Bailey-Watts and Lund,1973), Chlorophyta, e.g. *Botryococcus braunii* and *Nautococcus pyriformis* (Pentecost, 1984), Euglenophyta, e.g. *Euglena granulata* (Bednarz, 1974) and Dinophyta, e.g. *Peridinium gatunense* (Hickel and Pollinger, 1988).

Surface layer studies of marine and estuarine waters are more extensive, with several references to the presence of distinct surface layer populations of bacteria, e.g. Dietz and La Fond (1950), Zaitsev (1970), Tsyban (1971), Sieburth (1971a), Bezdek and Carlucci (1972), Crow *et al* (1975), Dietz *et al* (1976), Sieburth *et al* (1976), Norkrans and Sorensson (1977), Von Winckelmann (1980), Syzdek (1982) and Harvey *et al* (1983). Algae and chlorophyll a levels have been described by Norris (1965), Harvey (1966), Harvey and Burzell (1972), Hardy (1973), Gallacher (1975), Wandschneider (1979), Hardy and Valett (1981), Hardy and Apts (1984) and Timpano and Pfiester (1984). Colourless flagellates have been described by Harvey (1966), protozoa by Vucetich (1972) and Sieburth *et al* (1976) and invertebrates by Hempel and Weikart (1972), Champalbert (1973, 1977), Cheng (1975), Hartmann (1976), Holdway and Maddock (1983) and Locke and Corey (1986). Instances of surface inhibition of photosynthesis and depletions of algae, bacteria and chlorophyll and ATP levels have also been reported (Sieburth, 1971b; Dietz *et al*, 1976; Albright, 1980; Bell and Albright, 1982; Carlson, 1982; Souza-Lima *et al*, 1983) while Hardy and Apts (1984) stated that the apparent decrease in ^{14}C photosynthesis measured at the sea-surface microlayer may have resulted from the extracellular release of ^{14}C as glycollate under high light intensities.

The presence of toxic blooms of marine algae, particularly

dinoflagellates, in the surface layer is well known e.g. Grall and Le Fevre (1967), Dale *et al* (1978), Chang and Carpenter (1985) and Miles and Tett (1987).

Stratification and enrichment of organic and inorganic materials in the surface microlayers of both marine and freshwater habitats has been well documented. The presence of organic compounds can be detected visually by their formation of a surface film or slick. These slicks have the property of damping capillary waves such that a calm patch on a body of water is visible during light breezes. In more moderate winds (above 3.4 m sec^{-1}) these slicks will break up and reorientate into long bands, parallel to the direction of the wind (Langmiur,1938). The oldest verifiable record of the effect of surface films on the calming of waves is that of Pliny Secundus (AD 77). Goldacre (1949) detected surface films on practically every body of freshwater that he investigated. Even when slicks were not visible to the naked eye, their presence could be detected by the fact that they caused a depression in the surface tension of the water (detected using the methods of Adam, 1937 and Goldacre, 1949). The lowest depressions were found in rivers and streams, indicating a sparse film of organic material and the highest in stagnant ponds and lakes, indicating the presence of a well developed surface accumulation of organic materials. The nature and origin of natural surface films is a matter of debate. By visual observation of the physical characteristics of these films, Goldacre concluded that they are monomolecular and composed of protein or lipoprotein being derived from decomposing plant tissue of either autochthonous or allochthonous origin. Dietz and Lafond (1950) by experimentation, concluded that sea surface slicks are probably derived from diatoms which can release fatty acids. Pojasek and Zajicek (1978) concluded that surface films and foams in freshwaters were formed from allochthonous surfactants obtained from the leaching of terrestrial materials, such as tree exudates, by rainwater.

Free fatty acids, fatty acid esters, fatty alcohols and hydrocarbons have been identified as components of the surface films of seawater (Dietz and Lafond, 1950; Williams, 1967; Jarvis *et al* 1967; Garret, 1967, 1970; Sieburth *et al*, 1976; Duce *et al*, 1972; Larsson *et al*, 1974; Kattner and Brockman, 1978; Carlson and Meyer, 1980; Knap *et*

al, 1986) but their concentrations suggest that quantitatively fatty acids make up only a small contribution to the composition of the surface layer. Baier (1970, 1974) as a result of extensive studies of freshwater and marine surface films concluded that the microlayer is composed mainly of glycoprotein and proteoglycans with large amounts of uncharacterised organic matter whose nature is similar to that of the organic matter found in bulk water. Some of this is humic in nature. He concluded that surface films are composed of degraded compounds of planktonic, littoral and autochthonous origin with high concentrations of lipids only being found in regions of pollution. Work by Hunter and Liss (1977), Hunter (1977) and Carlson (1982) supports this view.

The controversy that has arisen stems partly from the difficulty of sampling surface films. Duce and Hoffmann (1976) stated that "the thickness of the sea surface microlayer" (and hence the concentration of its components) "is operationally defined by the methods used for its collection". This statement can be further expanded to include the chemical composition of the surface film since several samplers have been shown to selectively remove either the hydrophobic or the hydrophilic components (Daumas *et al*, 1976; Van Vleet and Williams 1980). Chemical characterisation of the surface film is further complicated by the fact that the surface film is not a static layer of fixed chemical composition. It is, rather, a dynamic system where constant removal and replenishment of its chemical species is such that its thickness and composition will vary with time. Physical processes such as wave action, bubble bursting, film compression and solar radiation along with biological activity provide a number of competing processes by which the chemical nature of the surface film can be altered.

Inorganic nutrient enrichment has been reported in the surface layers of both freshwater habitats (Parker and Wodehouse, 1970; Parker and Barsom, 1970; Eisenreich *et al*, 1978; Cavenko, 1979; Danos *et al*, 1983) and marine environments (Goering and Wallen, 1967; Williams, 1967; Barker and Zeitlin, 1972). Berry Lyons *et al* (1980) linked the surface enrichment of phosphate, nitrate and silicate to biological activity, with maximum enrichment at times of maximum phytoplankton growth in the subsurface waters.

These organic and inorganic compounds provide a source of nutriment to both autotrophic and heterotrophic surface-living organisms. Compression of a surface film by, say, wave induced pressure can cause the film to collapse forming particulate material which then sinks, so also providing a food source for benthic and non surface inhabiting plankton. Aerosols may be formed when bubbles pass through the water column and upon reaching the surface film where they adsorb organic and inorganic material, bacteria and algae,become injected into the atmosphere as the bubble bursts (Baylor *et al*, 1962; Blanchard, 1964, 1983; Garrett, 1967; Blanchard and Syzdek, 1978, 1982; Blanchard *et al*, 1981; Schlichting, 1981; Gershey, 1983; Weber *et al*, 1983). Wilson (1959) has implicated such a mechanism to explain the high levels of organic nitrogen and salts in the virgin snows found above the vegetation line in New Zealand. These aerosols seeded rain clouds which were then carried by the prevailing winds.

Besides naturally occurring substances, surface microlayers have been shown to contain substances derived from human activities in much higher concentrations than measured in subsurface waters. Synthetic surfactants such as ABS (alkyl benzene sulphonate) and LAS (linear alkyl sulphonate) have been recorded in the surface films of both freshwater and marine environments (O'Connor, 1963; Tarring, 1965; Parker and Wodehouse, 1970). Sodergren (1978) reported the surface enrichment of chlorinated hydrocarbons such as hexachlorobenzene (a fungicide) and hexachlorobiphenyl (a PCB). Eisenreich *et al* (1978) and Seba and Corcoran (1969) have recorded the presence of the DDT group of pesticides, dieldrin and aldrin in concentrations of up to $x10^3$ that of subsurface waters. Heavy metal enrichment has been well documented (Andren *et al*, 1975; Eisenreich *et al*, 1978; Pojasek and Zajicek, 1978; Owen *et al*, 1979; Bacon and Elzerman, 1980; Pattenden *et al*, 1981; Lion and Leckie, 1982; Barnes *et al*, 1982; Hardy *et al*, 1985). All the trace metals found in the surface film are known to form strong organic complexes. This is a possible mechanism by which they become enriched at the surface microlayer and it is postulated that these materials arrive by dry deposition, carried by prevailing winds from industrial land sites, by surface runoff from agricultural land, rainfall and, in the case of estuarine and coastal waters, from rivers. These materials

may become incorporated into the food chain via the bacteria and plankton in surface films, they may precipitate out on collapse of the surface film under the influence of wind induced pressure or they may become airborne in the form of aerosols.

As stated previously, the majority of studies on the biology of freshwater surface layers have been qualitative. Seasonal quantitative data are sparse and most of these were conducted over short periods of time (Naumann, 1915-1916; Rylov, 1925, 1926; Conrad, 1940; Niewolak, 1971; Parker and Hatcher, 1974; Estep and Remsen, 1984). Frolund (1977) and Danos (1980, 1983) carried out long term studies, each of a year, on the seasonal variation of the bacteria and algae of freshwater lakes. References to zooplankton have only been found in the Russian literature (Nikolayev, 1972, 1979; Gladyshev, 1980, 1981, in Gladyshev, 1987).

The study of the surface biota of the Dubh Lochan, presented in this thesis, was conducted to determine the seasonal fluctuations in the biological components of the surface layer of a dystrophic/oligotrophic freshwater habitat over a two year period. Since a study of the zooplankton associated with the surface layer was to be an integral part of this work a type (b) method was therefore employed to provide integrated, quantitative samples which could then be compared with subsurface samples.

Chapter 2

The Dubh Lochan.

2.1 DESCRIPTION OF THE STUDY AREA.

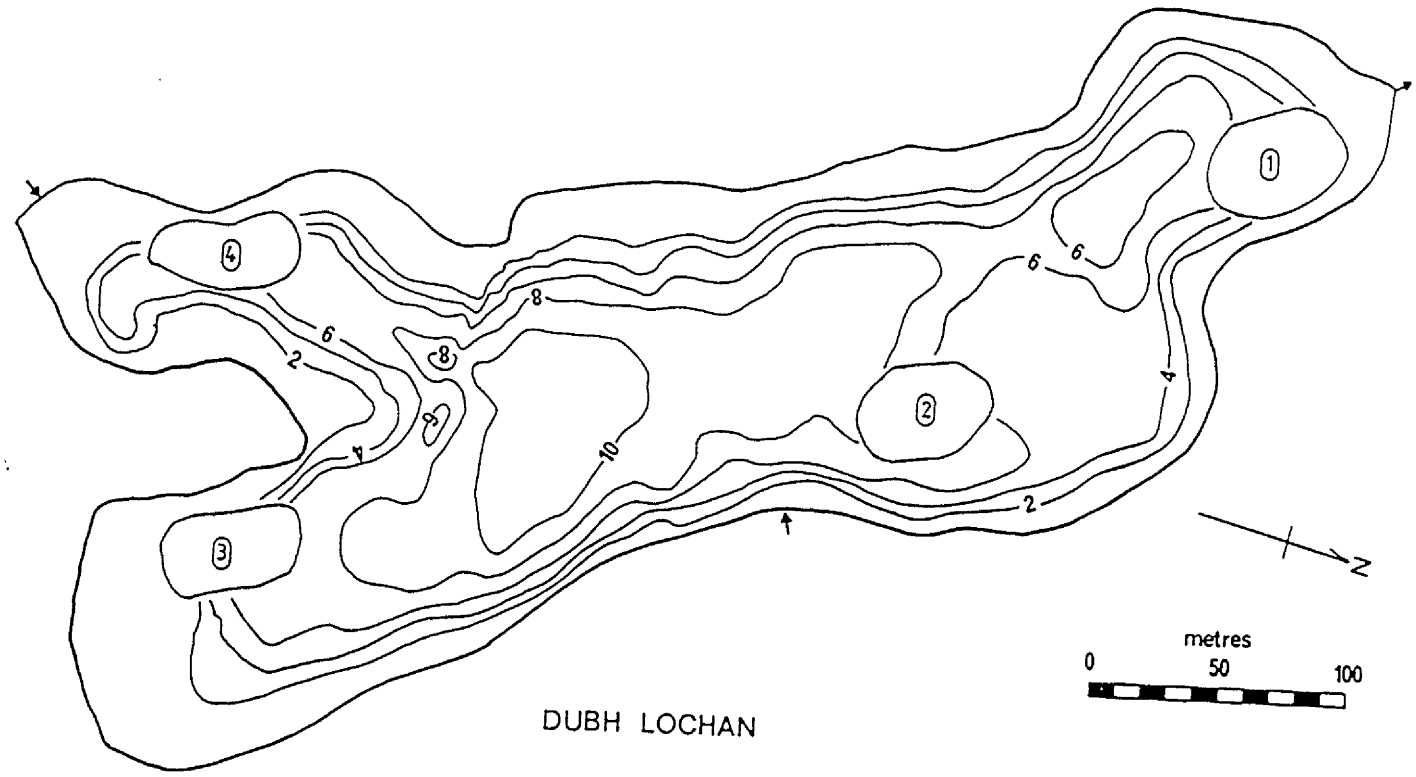
The National Grid Reference of the Dubh Lochan is NS 377964 Lat. 56^{o} $7'$ N, Long. 4^{o} $35'$ W. It is located 10 km. N of the Highland Boundary Fault on the East shore of Loch Lomond on the Ross Peninsula and is separated from Loch Lomond by a small rise of about 200m (Goldspink and Scott, 1971) Klarer (1978) described the Dubh Lochan as a dystrophic, monomictic lake which stratifies in the summer, suffering oxygen depletion in the hypolimnion. He defined its physical characterisics as outlined in Table 2.1.

TABLE 2.1

surface area	$7.06 \times 10^{4} m^{2}$
volume	$3.38 \times 10^{5} m^{3}$
max. depth	11.1 m
av. depth	4.8 m
length	550 m
mean breadth	128 m
shoreline	1550 m
shoreline development	1.645
volume development	1.301
catchment area	1.1 km

The bedrock forms part of the Tay Nappe - a sedimentary Dalradian series deposited in the late Pre-Cambrian or early Cambrian in a deep-water environment (Anderson, 1947). The deposits were metamorphosed into slates, grits and schists during the Caledonian Orogeny and the Carboniferous period. The rock strata lie in vertical bands rather than the horizontal layers in which they were deposited. The oldest layers lie due south of the Dubh Lochan. The southern half of the Loch lies on a band of grit while the northern half lies on a band of schist, the youngest of these layers.

There are two distinct inflow burns. The principal burn flows into the Dubh Lochan along the East shore entering by the central basin (see Fig. 2.1). It is the major source of surface flow but is very low in nutrients. The second inflow arises from the field station's septic



DUBH LOCHAN

Figure 2.1

Morphometric map of Dubh Lochan

Depth contours in 2m intervals.

Sampling areas 1 - 4. Depth samples

collected at site 2.

tank at the southern end of the loch. There is a single outflow into Loch Lomond at the N.W.

The climate is typical of the West coast of Scotland but as the Lomond area is isolated from the coast, the temperature range is more characteristic of inland Britain. Tittensor and Steele (1971) and Klarer (1978) noted that the weekly mean air temperatures illustrated the mildness of the climate, infrequently falling below $0^{o}C$ or rising above $20^{o}C$.

The vegetation surrounding the Dubh Lochan has been described by McVean (1964), Tittensor and Steele (1970), Walker (1975) and Stewart *et al* (1984) as follows :

The Dubh Lochan is surrounded by a semi-natural woodland frequented by *Quercus petraea* Liebl. and *Q. petraea* x *Q. robur* L. hybrids, *Betula pubescens* Ehrh., *Sorbus aucuparia* L., *Larix decidua* Mill., *Fagus sylvatica* L., *Fraxinus excelsior* L., *Populus tremula* L., *Ilex aquifolium* L., *Hedera helix* L., *Rhododendrom ponticum* L. and *Lonicera periclymenum* L.. The field layer is composed of *Pteridium aquilinum* (L.) Khun, *Vaccinium myrtillus* L., *Deschampsia flexuosa* (L.) Trin., *Anthoxanthum odoratum* L., *Dryopteris* spp and *Blechnum spicant* (L.) Roth. The most conspicuous herbaceous plants are *Potentilla erecta* (L.) Rausch., *Melampyrum pratense* L. and *Oxalis acetosella* L.

Above the Dubh Lochan there are several conifer plantations, the area being husbanded by the Forestry Commission. These are composed mainly of *Picea abies* (L.) Karst., *P. sitchensis* (Bong.) Carr. and *Pinus contorta* Loud.

Beyond the forest lies wet moorland, blanket bog and at the highest altitudes, Rhacomitrium heath or short turf with an arctic-alpine flora.

At the north end of the loch lies a fen area, through which the loch's outlet drains. Here can be found *Salix cinerea* L. spp. *atrocinerea* Brot., *S. aurita* L., *Alnus glutinosa* (L.) Gaertn., *Betula pubescens* Ehrh, *Myrica gale* L., *Erica tetralix* L., *Molinia caerulea*

(L.) Moench., *Galium palustre* L., *Ranunculus flammula* L., *Viola palustris* L., *Juncus acutiflorus* Hoffm. and much *Sphagnum* section Palustris. The macrophyte flora is well developed, forming a fringe around the loch and is composed of *Phragmites australis* (Cav.) Trin. ex Steudel, *Carex rostrata* Stokes, *Equisetum fluviatile* L., *Nuphar lutea* (L.) Sm., *Nymphaea alba* L., *Hippuris vulgaris* L., *Juncus bulbosus* L., *Myriophyllum alterniflorum* DC., *Lobelia dortmanna* L., *Fontinalis antipyretica* Hedw., *Littorella uniflora* (L.) Aschers, *Sphagnum* spp and *Isoetes lacustris* L. In the shallows, *L. dortmanna* L., *F. antipyretica* Hedw., *E. fluviatile* L. and *P. australis* (Cav.) Trin. ex Steudel dominate while in deeper waters, *Sphagnum subsecundum* Nees ex Sturm, *Myriophyllum alterniflorum* DC., *Nuphar* sp and *Nymphaea* sp dominate.

2.2 PREVIOUS STUDIES.

The Dubh Lochan has been the subject of several previous studies. Hamilton (1958) conducted a detailed study of the biology of the Cladoceran *Holopedium gibberum* (Zaddach). Shafi (1969) carried out population studies on the perch (*Perca fluviatilis* L.) and pike (*Esox lucius* Linn.). Goldspink and Scott (1971) studied the vertical migration of the aquatic stages of the Dipteran *Chaoborus flavicans* (Meagen). Walker (1975) surveyed the pollen profile of the sediment of the Dubh Lochan as part of a description of the vegetational history of the area. Klarer (1978) studied the seasonal succession of both the phytoplankton and the zooplankton. Those findings most relevant to the present work, can be summarised as follows:

Nanoflagellates dominated the phytoplankton community during much of the year. A spring peak of nanoflagellates was rapidly replaced by *Dinobryon divergens* Imhof. when orthophosphate levels became limiting in early summer. The zooplankton exhibited a population maximum in summer and their grazing pressure caused first a fall in the *Dinobryon* population and then a shift in dominance towards the net phytoplankton. The rise and fall of the Cladocera and to some extent the Rotifera corresponded to changes in the concentration and composition of the phytoplankton. In the late summer and autumn, zooplankton populations declined, permitting nanoflagellates to again assume dominance.

Primary production was highest in spring and autumn and zooplankton consumption was highest in summer. Succession rate determinations demonstrated that the marked increase in photosynthetic efficiency recorded during the autumn was not caused by a rapid shift in species composition but by an increase in efficiency of the existing community. This increase in photosynthetic efficiency immediately after the autumn overturn indicated that during summer low nutrient concentrations limited primary production. During the winter months low insolation levels limited primary production. Net primary production was generally large enough to support the zooplankton community. Only in midsummer and in midwinter was zooplankton grazing greater than net primary production. At both times detritus and bacteria could have provided an alternative source of energy.

Millhouse (1981) studied the seston as a source of energy for the benthic community of the Dubh Lochan.

Islam (1987) studied the role of plankton in the energy flow to the sediment through the detrital pathway. He found great variations in the chemical conditions of the lake since Klarer's study. pH and orthophosphate concentration had declined while nitrate and silicate levels had increased. Phytoplankton biomass showed a single summer peak with green and blue-green algae dominating the population. Zooplankton biomass showed three distinct seasonal peaks in spring, summer and autumn. Seston biomass also showed three distinct seasonal peaks in spring, summer and autumn. He calculated that, on an annual basis, 0.87% of the energy fixed by phytoplankton was transferred to the zooplankton. 77% of the energy was channelled through the seston. Benthos production was independent of primary production in deep water but in shallow water it closely followed primary production. The efficiency of energy transfer from the phytoplankton to the benthos varied between 1.19% and 7.73%.

Klarer (1978) identified 147 species of algae and 52 species of zooplankton while Islam (1987) identified a total of 158 species of algae, adding 12 species of Chlorophyta, 27 species of Chrysophyta, 1 species of Rhodophyta and 5 species of Cyanophyta to the list. 27 species were not recorded. 57 species of zooplankton were

identified, 5 species of Cladocera and 1 Rotifer being added to the list while 4 species were not found.

2.3 THE STUDY SITES.

Four sites (see Fig. 2.1) were chosen for the surface studies. Three can be considered as bays (sites 1,3 and 4) and one as open water.

Site 1 was situated at the northern end of the loch. This area is fringed by *Phragmites*, *Lobelia*, *Equisetum* and *Fontinalis*. These reed beds are used by nesting birds. Sampling took place in open water rather than amongst the reeds so this site can be described as 'semi-littoral'.

Site 2 was situated in open water. This station was also used for depth sampling, taken for comparative estimations.

Site 3, at the SE end of the loch, was shallow, encroached by reeds and some *Nuphar* and *Nymphaea* in the summer. The reed beds often extended through much of this bay. This site can therefore also be described as 'semi-littoral'.

Site 4, at the SW end of the loch, was situated amongst dense *Nuphar* and *Nymphaea* vegetation. Sampling took place within this vegetation. This site can be described as littoral.

Sampling at the four sites was carried out every fortnight from July 1980 to September 1982, weather permitting. Sampling was not normally possible during periods of ice cover in winter. From April 1981 sampling at 1m, 3m and 5m depths at site 2 was initiated. Primary productivity studies were carried out during the period March to September 1982.

Chapter 3

Materials and methods.

3.1 SAMPLING METHODS.

Surface samples were collected by means of an enamel tray with oblique end walls. As mentioned in the Introduction, there are several methods of sampling the surface layer depending on the definition accepted and on whether interest lies in the chemical composition of the boundary layer or the organisms associated with this layer. Since it was the intention of this study to survey the surface biota including the zooplankton associated with the surface film a thicker sample than that collected by the Garret screen was deemed necessary. The depth of sampling was set at 5mm. Hardy (1973), using a plastic box sampled the top 4mm of a lagoon. The tray sampling technique used was chosen since it complied with the following criteria :

1) The technique had to be quick and easy to use.

2) The absolute minimum of equipment maintenance and preparation was required.

3) It was easily transportable.

4) It was of minimum cost.

5) It was capable of repeatedly sampling the top few mm.

This "type (b)" method is not suitable for the collection of surface layers for chemical analysis since it allows considerable dilution of the surface film with the underlying water. The study of possible enrichment effects was therefore limited to the biological components only since any chemical measurements were deemed to be more likely representative of the water body *per se*. Surface samples from sites 1-4 (see Fig. 2.1) were collected for chemical analyses and phytoplankton, zooplankton and bacterial enumeration. Depth samples from site 2 were collected for phytoplankton and zooplankton enumeration and for pH, alkalinity, acidity, conductivity and chlorophyll measurements. Samples from the depths of 1m, 3m and 5m below the surface at site 2 were collected by means of a 6 litre van Dorn sampler.

The tray was lowered obliquely until the leading lip just broke the surface. Water was allowed to flow in over the lip until approximately 1 litre had been collected. This volume was transferred to a carboy. This procedure was repeated until a total volume of 12 l of sample water had been collected. The depth of sampling was determined and maintained by the use of glass rods attached to the sides of the tray in such a manner that when the tray was immersed the markers on the rods were horizontal and at the water surface and at an angle of 90^{o} to the vertical.

Slight foreward motion of the tray was necessary to facilitate filling and to ensure that the samples were collected over a large area. Using this method 1 litre was equivalent to a surface area of 2,000 cm^2 ($0.2m^2$) with a depth of 5mm.

The volumes required for phytoplankton and zooplankton enumeration were based on those used by Klarer (1978). The equivalent surface area was collected to allow comparisons to be made between surface and depth samples.

3.2 CLEANSING of APPARATUS.

All glassware was initially cleaned in 95% chromic acid followed by thorough rinsing in tap water and distilled water. Subsequent washing after use was by soaking in a 2% solution of DECON 90 for 2-24h. Glassware for phosphate analysis was then stored in 2% H_2SO_4/HCL solution until required. All glassware was thoroughly rinsed in distilled/deionised water. All plastic containers were first cleaned in 5% DECON 90 and subsequently cleaned in either 2% DECON or 2% acid. The carboys were filled with 2% acid until required. All plastic ware was thoroughly rinsed in distilled/deionised water before use. The enamel surface sampling tray was cleaned first in 2% DECON and then 2% acid before each field collection. Plankton nets were cleaned by vigorous backwashing with tap water. The incubation bottles used for the ^{14}C studies were cleaned and decontaminated in 2-5% DECON 90 solution for 24 h followed by much rinsing in tapwater and distilled/deionised water. Glassware for organic analyses were cleaned in 95% chromic acid

before and after use. For the determination of organic carbon the ampoules used were then heated to 550^{o}C for at least 3 h in a muffle furnace.

3.3 PHYSICAL MEASUREMENTS.

3.3.1 Temperature and oxygen measurements.

% oxygen saturation and temperature ^{o}C for both surface and depth samples were measured by means of the Mackereth combined thermistor-oxygen meter.

3.3.2 Measurements of surface tension depression.

The surface tension depression measured in dynes cm^{-1}, as defined by Russel and Ramachandraroa (1941), was determined by the method of Adam (1937). This method has been used by Ewing (1950), Gallacher (1975), Goldacre (1949), Hardmann (1941) Hardy (1973) and Elzerman and Armstrong (1979). The importance of this method in determining surface layer structure has long been realised, (see Adam, 1937; Gallacher, 1975; Goldacre, 1941; Hardman, 1941; Jarvis, 1967; Maynard, 1968; Frolund, 1977; Lemlich, 1966; Parker and Barsom, 1976; Pojasek and Zajicek, 1975; Wheeler, 1975 and Zaitsev, 1971). More accurate methods are available such as the vertical plate method, versions of which have been designed by Harkins and Anderson (1937), Jordan and Lane (1964) and Slowinski and Masterton (1961) or the ring method as used by Stahlberger and Guyer (1950) and Yamashita and Yamashita (1970). These methods have the disadvantage of requiring a solid, horizontal working space free of vibration and so cannot be used in the field whereas Adam's method requires the use only of a series of graded oils and a small glass rod. This technique is based on the observation that an oil will just spread against a surface tension depressed by a contaminant. The tension by which the contaminant lowers the "normal" surface tension equals the spreading force or "spreading coefficient" of the oil.

The oils were prepared following the procedure given in Adam (1937). AristaR grade dodecyl alcohol was chosen, as recommended by

Adam (1937) since it is not affected by changes in the acidity of water. Boots PLC mineral oil (medicinal liquid paraffin) provided the base as recommended by Yeo (1980 pers. comm.).

A series of oils of varying concentrations of dodecyl alcohol were prepared as given in Table 3.1

Table 3.1

% dodecyl alcohol in mineral oil	Surface pressure against which slow spreading occurs. dyne cm^{-1}
0.07	1
0.1	2-3
0.2	5-6
0.3	11-12
0.4	14-15
0.5	16
0.6	17-18
0.7	19
0.8	20
0.9	21
1.0	22

Once prepared, the oils were calibrated with a Wilhelmy type Torsion Balance Type E2. The oils were calibrated at $20^{o}C$ against Lochan water. Many surface samples from several sites on the Dubh Lochan were collected over a number of days. These were decanted into acid-cleaned evaporating dishes. The dishes were left loosely covered and undisturbed for 24 h to allow a surface film to develop. The surface tensions of these samples were measured by using the torsion balance. Once the surface tensions of the samples were known the oils could be calibrated by their spreading power upon them. The surface tension or range of surface tensions over which an oil just spread indicated its "spreading coefficient". The oils' spreading powers were found to be very similar to those determined by Adam (1937). A series

of oils which covered the range 1 - 22 dynes cm^{-1} were prepared.

The following procedure was used in the field to measure the surface tension depression:

Once the site had been reached the boat was allowed to drift for two minutes to ensure that wave pressure from the boat did not influence the measurement. At arm's length a drop of oil of known "spreading power" was dropped from the height of about 30cm. The oil droplet was observed for about 30 sec. If the oil just spread against the surface film that oil sample's tension was taken as the surface tension of the water. If the oil stayed as a small drop, an oil of greater spreading power was chosen and tested. If the oil spread immediately forming a large "pool", an oil of lesser spreading power was tested. This was repeated until the surface tension of the water was determined. Care was taken to ensure that the drops were well spaced to avoid cross contamination.

3.3.3 Light measurements.

It had been originally intended to use a Slack light meter to record incident and depth light levels simultaneously in four wave bands; white, blue, green and red, to coincide with ^{14}C primary production measurements. Unfortunately, this machine proved unreliable. A Secchi disc was employed instead. The disc was lowered until it was just observed to disappear. The depth was noted. The Secchi disc was then lowered beyond this point and raised until it was seen to just appear. Again the depth was noted. This procedure was repeated three times and the average of all six readings taken. The extinction coefficient was then roughly determined from the empirical relationship:

$$k = \frac{1.7}{d}$$

where d = the averaged depth in metres at which the disc is just visible and k = the extinction coefficient or the rate of decrease of illumination with depth (where $k \sim k_{\lambda}$).

During 1982 the use of a Kipp and Zonen solarimeter, situated on the roof of the field station, was occasionally made available, providing a measurement of radiation in g cal $cm^{-1}min^{-1}$.

3.3.4 Meteorological data.

Daily data on hours of sunshine, mm of rainfall, wind speed and wind direction, along with a general weather diary were kindly provided by the Clyde River Purification Board from the Meteorological Office's station at Arrochymore, situated 6 km S of the field station. This data has been supplemented with a personal weather diary. Notes were made the day before and the day of sampling.

3.4 CHEMICAL ANALYSES.

3.4.1 Soluble reactive phosphorus (orthophosphate).

The method used was that of Murphy and Riley (1962) as modified by Stephens (1963) with the exception of the replacement of butan-1-ol by hexan-1-ol as recommended in Mackereth *et al* (1978) for the determination of low phosphate concentrations in freshwater.

3.4.2 Inorganic forms of nitrogen: nitrite-nitrogen and nitrate-nitrogen.

The determination of nitrite-nitrogen was carried out using the method of Bendschneider and Robinson (1952) as modified by Shinn (1941) and given in Wood *et al* (1967).

Nitrate-nitrogen determination was by the cadmium-reduction method of Wood, Armstrong and Richards (1967) in which nitrate is reduced to nitrite by a Cd/Cu column. The nitrite so formed could then be measured by the method mentioned above.

3.4.3 Ammonia-nitrogen.

The technique used was that of Chaney and Marbach (1962) as given in Mackereth *et al* (1978).

3.4.4 Soluble reactive silicon.

The technique used was that of Mullin and Riley (1955) as described in Mackereth *et al* (1978).

3.4.5 pH.

pH was measured electrochemically with a pH meter and glass electrode. At the time of the study electrodes suitable for measuring the pH of poorly buffered waters were not readily available. Readings taken in 1980 and 1981 cannot be considered as accurate. In the latter part of 1981 and in 1982 the following procedure was used :-
A 250 ml. BOD bottle with a neck just wide enough to accept the electrode was filled with the sample water. In the laboratory, a small magnetic flea was introduced to the bottle and the pH electrode inserted via the neck. Nescofilm was used to seal around the neck and the electrode to minimise contamination by the air. The contents were gently stirred while the electrode was in place until the meter reading was stable (2-10 min). As stirring can induce a lower than actual reading, the stirrer was switched off and the pH read once the reading was stable (2-3 min). Since this study Davison and Gardner (1986) have recommended a technique for the determination of pH in poorly buffered freshwaters which is, in effect, the same as that given above.

3.4.6 Conductivity.

Conductivity was measured at the field laboratory following the guidelines given in Mackereth *et al* (1978) using a Petercord model PCM1 conductivity meter.

3.4.7 Alkalinity.

The method of titration given in Mackereth *et al* (1978) was used. Alkalinity measurements were very low, often at the limits of detection of the method. Overestimations may have occurred on occasions.

3.4.8 Free carbon dioxide acidity.

The traditional titration method of the APHA (1976) as given in Mackereth *et al* (1978) was used. Mackereth (1963) commented that the end point of the titration was reached when the pink colour remained for 5 min. On observation it was found that this end point could be detected after just 2 min.

3.4.9 Total inorganic carbon (TIC).

Total inorganic carbon was calculated by adding the alkalinity value to the acidity value. This method assumes that:

1) The alkalinity is a measure of the total alkalinity.

2) The acidity is a measure of total free carbon dioxide which cannot be titrated specifically in the presence of interrelated equilibria e.g. sulphate ions and humic acids.

One can assume that the alkalinity measurement is a measure of the total alkalinity since the pH is so low and by calculation from the carbonate equilibrium, carbonate alkalinity is negligible ($< 1 \times 10^{-7}$ meq l^{-1}).

This method was chosen to determine TIC rather than using calculations based on the equilibria constants since it was found that because alkalinity was so low, pH became the main factor in determining TIC concentration i.e. variations in [TIC] were totally dependent on variations in pH e.g.

Alkalinity = .005 meq l^{-1}, acidity = 10mg l^{-1}, temp = $15^{o}C$, conductivity = 100 μS $cm.^{-1}$

At a pH of 5, TIC = 1.64 mg l^{-1}.

At a pH of 4, TIC = 15.84 mg l^{-1}

This tenfold increase in TIC was not considered to be realistic. The addition method which did not involve pH was therefore considered to be a more likely reflection of the levels of TIC.

The calculation was carried out as follows:

$$TIC = (12 \times \text{alk meq } l^{-1}) + (0.273 \times \text{acidity mg } l^{-1}).$$

For the example given, TIC = 2.79 mg l^{-1}.

3.4.10 Dissolved, particulate and total organic carbon (DOC, POC and TOC).

The wet oxidation method of Airey and Hogan (1980) for the determination of DOC and TOC, as based on that of Menzel and Vaccaro (1964) was used. Samples for DOC were filtered through GF/C grade filter paper as defined by Baker *et al* (1974). Unfiltered samples were used for TOC measurements and POC was obtained by subtraction of DOC from TOC. A Grubb-Parsons infra-red gas analyser model SB2 with an Elliot chart recorder was kindly provided by Prof. M.B. Wilkins.

3.4.11 Dissolved, particulate and total organic nitrogen (DON, PON and TON).

The kjeldahl method recommended by APHA (1976) as given in Mackereth *et al* (1978) was used to determine DON and PON. 200 ml of sample water was filtered through GF/C and the filter used for PON analysis. For DON analysis 40 ml of filtered sample was used.

3.4.12 Carbon to Nitrogen ratios.

According to Hutchinson (1957) organic matter allochthonous in origin and hence refractory, contains 6% crude protein with a C:N ratio of 45-50:1. In contrast, autochthonous organic matter produced by the decomposition of plankton and littoral flora contains about 24% crude protein with a C:N ratio of about 12:1. This ratio, therefore, gives an indication of the types of organic matter that were present in the Dubh Lochan.

3.5 PLANT PIGMENT ANALYSES.

Chlorophylls a, b and c, total carotenoids and phaeopigments were determined by the acetone extraction method of Strickland and Parsons (1972), as taken from Richards and Thompson (1952) with modifications by Parsons and Strickland (1963), and Strickland and Parsons (1968). The equations used were those of Parsons and Strickland (1963).

3.6 ENUMERATION OF PHYTOPLANKTON.

The technique used was a modification of the membrane filtration technique of McNabb (1960). At the field station 1 litre samples were placed in 1 litre measuring cylinders to which 2 ml of Lugol's iodine was added. These were left to sediment for two weeks. The supernatant was siphoned off until approximately 10 ml remained above the sediment. The cylinder was gently shaken to stir the contents which were then rinsed into universal vials. Another drop of Lugol's iodine was added to maintain preservation. Upon return to the main laboratory the equivalent of 250 ml. of original sample was gently filtered through 25 mm Millipore HA membrane filter paper (0.45 μm pore size) by low vacuum. The filter and the sides of the filter reservoir were washed with a few ml of distilled water and left under vacuum until almost dry (a few seconds). The procedure as detailed in Maulood (1974) was followed. Briefly, the membrane filter was cleared with UVinert immersion oil. A Nikon binocular microscope model LBR-Ke was used to count and identify the algae found in a minimum of 30 randomly chosen fields at x400 mag. A minimum of 1,000 algae were counted. Occasionally counts were made at x1,000 especially when *Synechococcus* and

Aphanothece dominated. Conversely *Dinobryon divergens* colonies were counted at x100 mag. During periods of algal blooms when one or two algae predominated it was often only necessary to count 10-15 fields to obtain 1,000 cells. Counts of the non-dominant organisms only were then continued until either 30 fields or 1,0000 cells had been counted.

The number of algae per litre were calculated as follows :

$$\text{No. algal}_{\wedge}^{\text{units}}\, l^{-1} = \frac{\text{Area of filter x total counts in the fields.}}{\text{Total area of the fields x Vol sample filtered in l}}$$

3.7 ENUMERATION OF ZOOPLANKTON.

In the field 6 l of tray sample or the 6 l contents of a van Dorn were poured through a fine mesh phytoplankton net. The concentrated zooplankton sample was then rinsed into two universal vials and preserved with 2-3 drops of formalin. Upon return to the field station the samples were allowed to sediment (6-24 h). The supernatant was decanted and the contents of the two vials combined and poured into a 25 ml sedimenting counting chamber. The volume of the chamber was made up to 25 ml and a coverslip placed over the chamber. These samples were allowed to sediment for 6-24 h and counted under low power by an inverted microscope. The entire area of the chamber was counted.

The volume required for counting had previously been determined by Klarer (1978). In winter the volumes filtered were increased to 12 l due to the small numbers of organisms.

3.8 ENUMERATION OF VIABLE BACTERIA.

It was decided that a count of viable heterotrophs rather than total bacteria would be carried out since this was more likely to reflect the numbers which were physiologically active and taking part in biochemical processes at the surface layer. The term 'heterotrophic' will thus be used to refer to that fraction of the bacterial population capable of colony formation on the growth medium used.

Subsamples of water collected by tray were poured into pre-sterilized universal vials. These were overfilled to ensure the collection of a homogenous sample. These vials were kept cool until return to the main laboratory (i.e. refrigerated for approximately 32 h). Upon return to the main laboratory the samples were allowed to stand for 0.5 -1 h to attain room temperature. The vials were then vigorously shaken for 1 minute. 1 ml of each vial was removed using sterile calibrated syringes and serial dilution series prepared. Sterile Ringer's solution was used as the diluent. 8 x 20 μl drops, dispensed from a Pipetman piston pipette, using presterilized tips, were pipetted onto the surface of previously prepared CPS medium plates (Collins and Willoughby, 1962; Jones, 1970; Staples and Fry, 1973). These drops were spaced equidistantly. This is a modification of the method of Miles and Misra (1938) as used by Bousefield *et al* (1973). Four replicates of each dilution were prepared. The plates were incubated at 15^{o}C for 10-20 days. Plates showing about 10 separate colonies per drop were chosen for counting. The total number of colonies on the four plates were counted and divided by the number of drops to give an average value. This figure was then used to calculate the original concentration of viable heterotrophic bacteria. If evidence of inhibition or overgrowing by spreading colonies was observed for a drop, it was ignored when counting.

3.9 MEASUREMENTS OF PRIMARY PRODUCTIVITY.

3.9.1 The ^{14}C light and dark bottle technique for measuring the primary productivity of phytoplankton.

This technique was first introduced by Steeman Nielsen (1952). Descriptions of the basic technique may be found in Saunders *et al* (1962), Vollenweider (1971) and Wetzel and Likens (1979).

The in situ method described by Wetzel and Likens (1979) was used with some following modifications. Two types of incubation bottle were used :

1) Flat 130 ml bottles, 2 cm thick, for the surface samples.

2) Standard 128 ml BOD bottles for the depth samples. Surface samples were collected by tray from sites 1-4. 1m, 3m and 5m depth samples were collected at site 2 using a 6 l van Dorn sampler.

The sample bottles were stored in a compartmentalized dark box before and after incubation.

The depth samples were hung by means of a rope and metal clips from a lifebuoy anchored at site 2. The necks of the 'surface sample bottles' were slotted into Perspex collars, the design of which was based on that of Schindler and Holmgren (1971), as used by Hannah (1979). Polystyrene floats, attached to the collars via wooden sticks ensured that the bottles were positioned just at the water surface. Lengths of rope secured these holders to the buoy while allowing them to float free.

Incubation periods of 4 and 24 hours were used. After incubation the bottles were placed in the dark box in which had also been placed reusable ice blocks. The samples were filtered at the field station so keeping to a minimum the period when ^{14}C loss by respiration could occur. 25 mm HA Millipore membrane filters of pore size 0.45 μm. were used. These were prerinsed with 2 ml of water at pH 2 (distilled water to which HCL had been added) before as much sample as could be filtered was passed through under low vacuum. The filtrate was then rinsed with 5 ml of pH 2 water (Lean and Burnison ,1979) to eliminate residual [^{14}C] bicarbonate activity. 15 ml of Packard 299 liquid scintillant was added to a plastic vial into which the membrane filter was introduced. The vials were left for 24h to allow the filters to clear. They were then shaken to ensure a homogenous distribution of radioactivity and left to settle for 1h to allow any air bubbles to escape. This was facilitated by occasional gentle tapping of the vials. The vials were counted for 10 minutes using a Packard liquid scintillation counter. Quench curves were prepared using two sources of quenching :

1) Concentrated Chlorella culture (green quenching).

2) Dialysed Lochan water which was highly coloured with humic acids (yellow quenching).

By preparing two quench curves the effect of the two possible sources of quenching could be equated and either one or the other was used depending on the colour of the filter. These equations were inserted in a computer programme written to calculate carbon assimilated in $\mu g\ l^{-1}\ h^{-1}$, where TIC was the value calculated as described in section 3.4.8. The algorithm used was that given in Wetzel and Likens (1979) :

$$^{12}C \text{ assim.} = \frac{^{12}C \text{ avail [TIC]} \times {}^{14}C \text{ assim.}}{^{14}C \text{ added}}$$

Specific production rates were then expressed as the photosynthetic capacity measured for each surface sample or depth sample as :

$$\frac{\mu g\ C\ l^{-1}\ h^{-1}}{\mu g \text{ Chlor a } l^{-1}} = \mu g\ C\ (\mu g \text{ Chlor a})^{-1}\ h^{-1}$$

using volume rather than area as the comparator.

3.9.2 ^{14}C light and dark bottle technique to compare the photosynthetic efficiency of a surface sample with a depth sample.

These experiments were carried out to determine :

1) If the photosynthetic efficiency under differing light conditions (depth) of the surface phytoplankton sample differed from that of a phytoplankton sample collected from 1m and

2) whether the samples collected were from the same or different populations.

On the 22/7/82, 29/7/82, 19/8/82, 28/8/82 and 2/9/82 the following experimental procedure was carried out in an attempt to answer the above questions.

A surface sample from site 2 was collected by tray and a depth sample from 1m below was collected by van Dorn. Two light and one dark flat 'surface' bottles and six light and three dark standard 'depth' bottles were filled to overflowing for each sample. These were inoculated with 0.5ml of 2μCi ml^{-1} sodium [^{14}C] bicarbonate. The site 2 and 1m flat bottles were placed in the Perspex collars as previously described. Two light and one dark bottle from each set were hung at 1m, 3m and 5m. The bottles were incubated for four hours. Removal and subsequent treatment was as previously described.

Water was also collected at the same time for pH, conductivity, alkalinity and acidity (TIC) measurements. Secchi disc and temperature and oxygen measurements were also made. Samples were taken for phytoplankton and chlorophyll estimates.

Chapter 4

Physical and chemical features

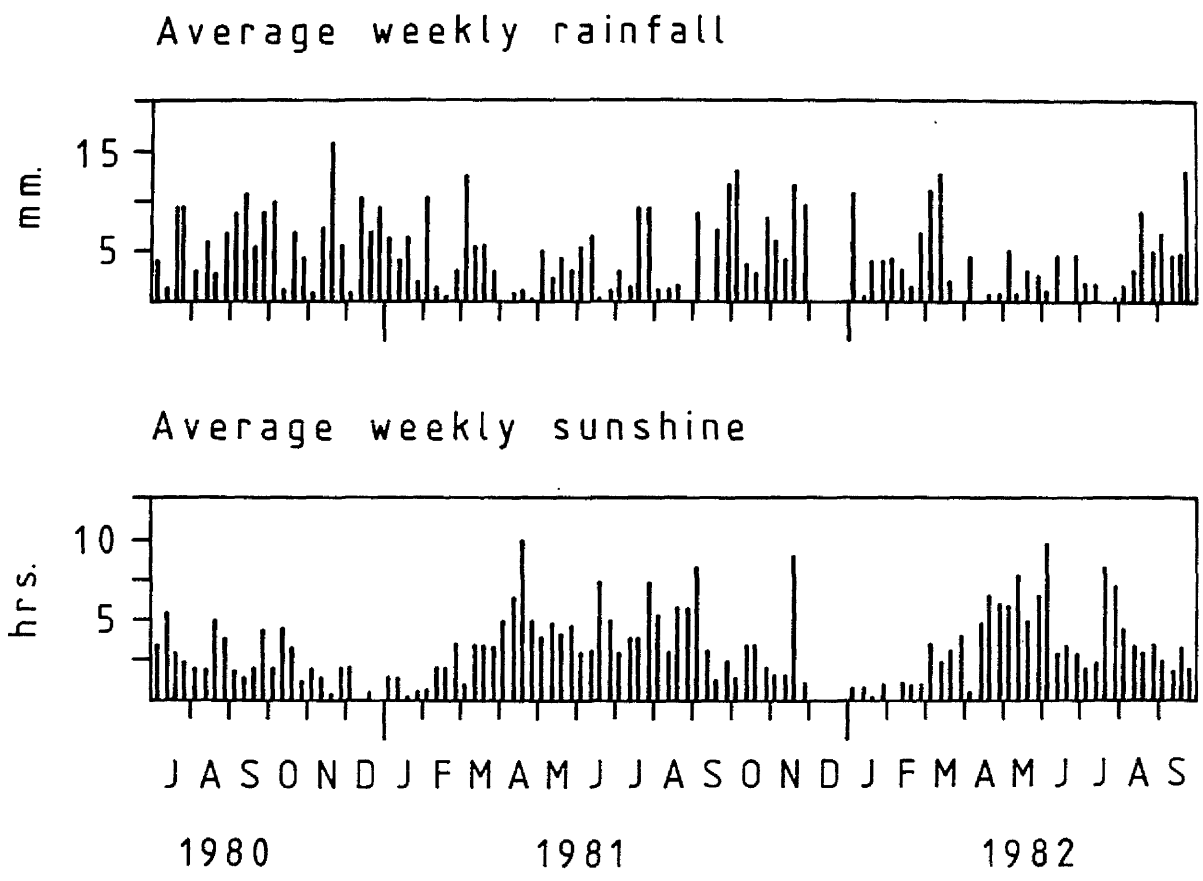

Average weekly rainfall
mm.
15
5
Average weekly sunshine
hrs.
10
5
J A S O N D J F M A M J J A S O N D J F M A M J J A S
1980
1981
1982

Figure 4.1

Average weekly rainfall (mm) and sunshine (h)

July 1980 - September 1982

Data supplied by

Clyde River Purification Board.

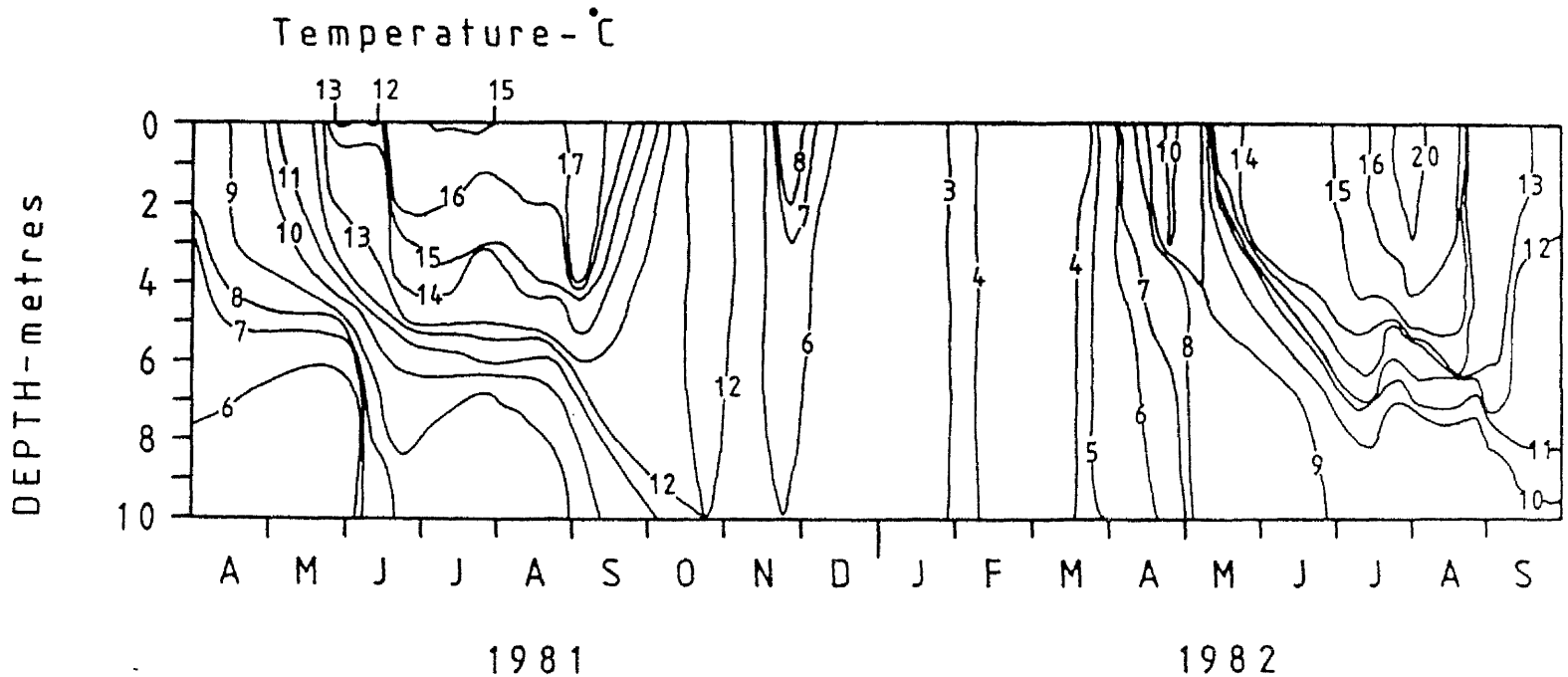

Temperature - °C
DEPTH - metres
0
2
4
6
8
10
A M J J A S O N D J F M A M J J A S
1981
1982

Figure 4.2
Temperature profile in ^{o}C
of Dubh Lochan at site 2
April 1981 - September 1982

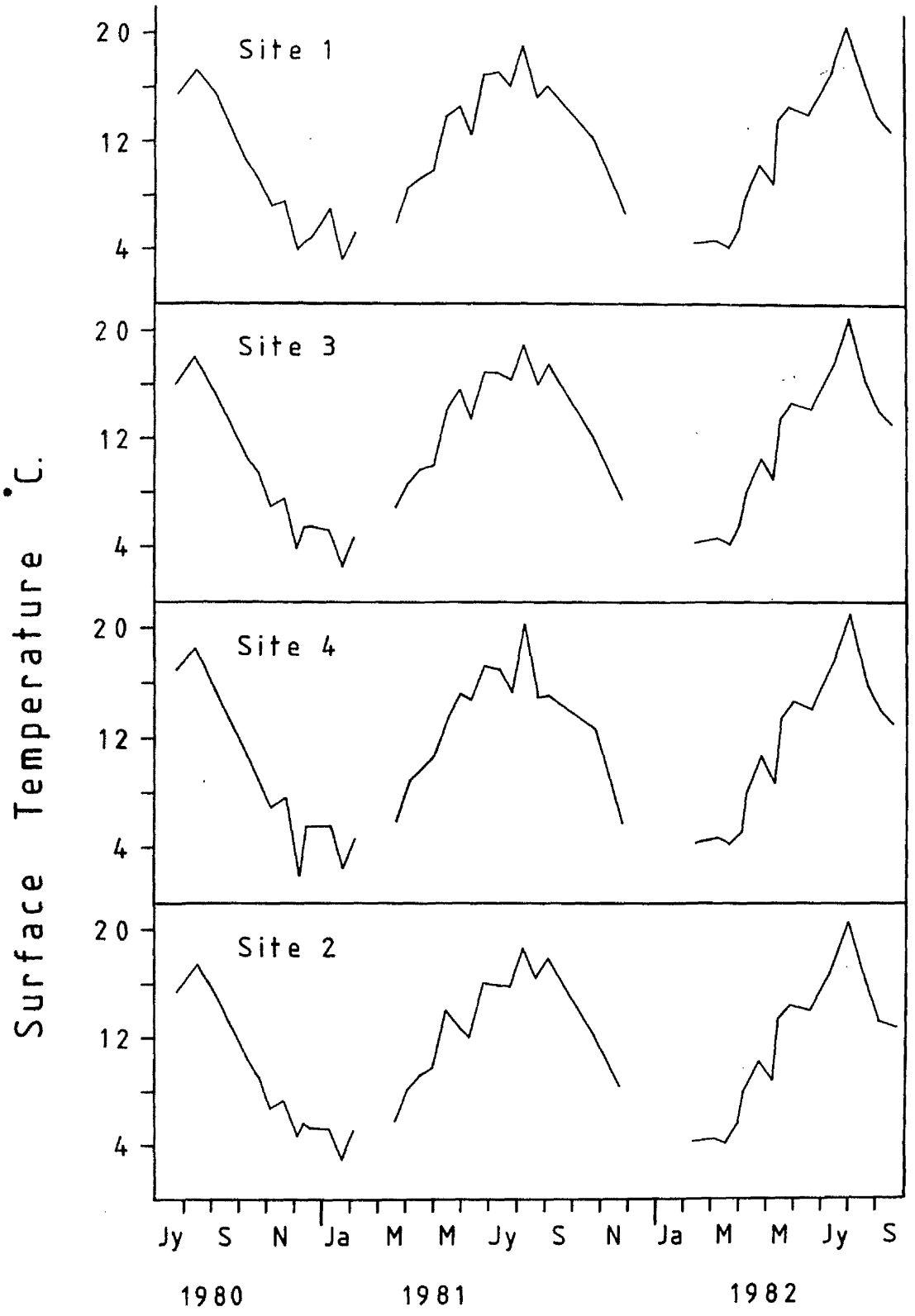

Surface Temperature °C.
Site 1
Site 3
Site 4
Site 2
20
12
4
Jy S N Ja M M Jy S N Ja M M Jy S
1980
1981
1982

Figure 4.3

Surface temperatures

Sites 1 - 4

July 1980 - September 1982

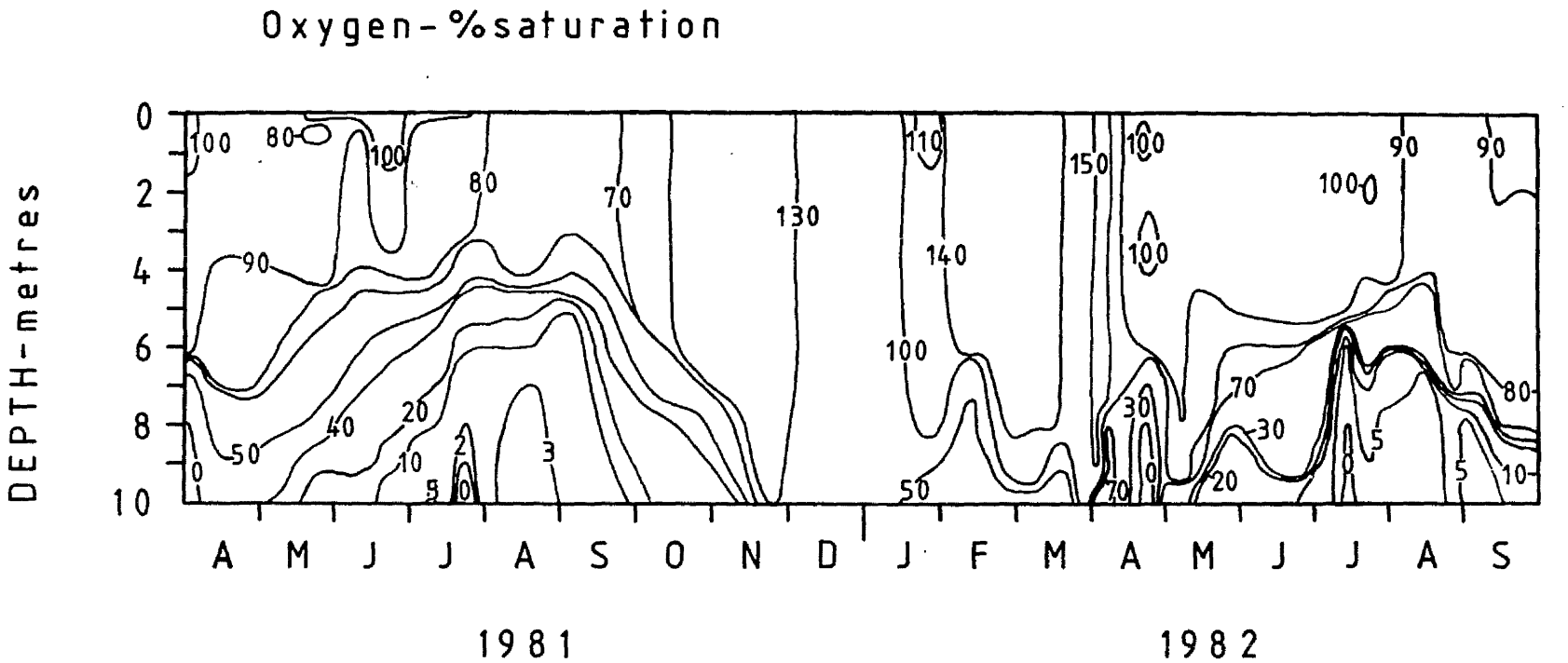

Oxygen - %saturation
DEPTH - metres
0
2
4
6
8
10
A M J J A S O N D J F M A M J J A S
1981
1982

Figure 4.4
Percentage oxygen saturation profile
of Dubh Lochan at site 2.
April 1981 - September 1982

4.1 PHYSICAL FEATURES.

4.1.1 Meteorological data

The average weekly rainfall (mm) and sunshine (h) were calculated from data supplied by the Clyde River Purification Board and are represented in Fig. 4.1. Data for December 1981 were not available.

July to December 1980 was mainly dull with many periods of rain, often quite heavy and accompanied by high winds, particularly in November and December. At the beginning of December the Loch became covered in a thin layer of ice. This thin ice cover persisted until February 1981 when a thicker more complete ice cover, 1-3 inches in thickness, formed over the loch. Sampling was discontinued until ice thaw in late March. April was dry while March through to November was characterised by alternative periods of sunshine and rain. Persistent cloud resulted in low levels of sunshine during May, June, July, September, October and November. During the period September to November 1981 strong winds and heavy rain prevented sampling on several occasions. At the beginning of December, a complete ice cover 3-8 inches in thickness formed over the loch. This persisted until the beginning of February 1982 and prevented sampling from taking place. On the 13th and 27th January 1982 water samples were taken from sites 1 and 2 since during this period the ice was thick enough to walk upon and support a sledge carrying sampling equipment. The end of February and the beginning of March were characterised by heavy rainfall. Showery weather persisted into April. May was dry while overcast conditions resulted in low levels of sunshine in June and July. Increased periods of rainfall were encountered through August and September.

4.1.2 Water temperature

The temperature profile measured at site 2 during the period 1.4.1981 to 16.9.1982 is represented as isopleths in Fig.4.2. The temperature of the loch ranged from $3^{o}C$ in winter to $20.6^{o}C$ in summer. The maximum water temperature in 1981 was $17.85^{o}C$ at the surface, extending to 3m in depth while in 1982 the maximum temperature was

20.6°C, extending from the surface to 2m in depth.

In 1981 thermal stratification extended from the end of May to the end of September. Rapid turnover was stimulated by the high winds noted for that season such that isothermal conditions were recorded in October when the water temperature was 12°C. In 1982 stratification began in the middle of May and by the end of the sampling period in September it was breaking down. Autumn overturn occurred at roughly the same time in both years while during stratification the epilimnion extended to about 5m and the metalimnion to between 5 and 7m. A period of ice cover in 1981/1982 was characterised by isothermal conditions and low temperatures (3°C on 27th January 1982 below ice). Periods of surface cooling were observed in May, June and July 1981 when surface water temperatures at site 2 were lower than those measured at 0.5m. On the 28th May the surface temperature was 12.70°C while that at 0.5m was 14.50°C. On the 10th June, surface temperature was 12.00°C, that at 0.5m was 2.00°C higher. During July a 0.5 to 0.75°C difference between surface and 0.5m depth temperatures was maintained. By August such temperature differences were minimal (0.1-0.2°C). During 1982 any temperature differences recorded were minimal (0.1-0.2°C).

Surface temperatures taken at the four surface sites are summarised in Fig. 4.3. They exemplify the typical fluctuations of a temperate lake. Temperature ranged from 2°C (on 13th January below ice) to 21°C (on 29th July 1982). On comparison of the temperature data with the meteorological data (section 4.1) it was observed that small increases in surface temperature corresponded with periods of rain, while small decreases corresponded with increased wind speeds (personal weather diary).

4.1.3 Dissolved oxygen.

Both seasonal and vertical variations in the percentage oxygen saturation were observed (see Fig.4.4). During the study period the dissolved oxygen content varied from 0% (above the lake bed in April and July) to 150% (in spring during isothermal conditions and mixing of the water column). Summer stratification of the oxygen levels were associated with thermal stratification with an epilimnion of between 5

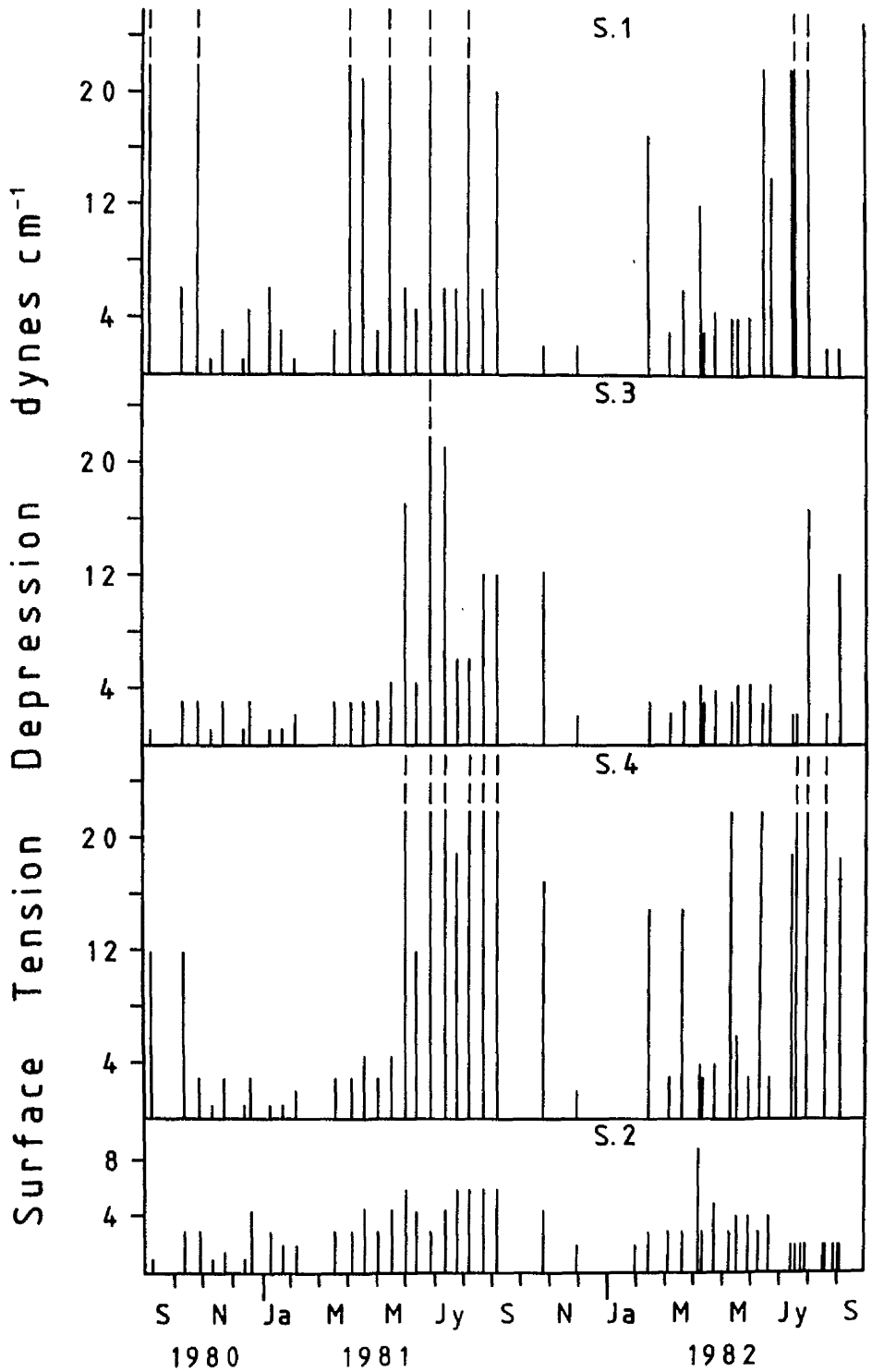

Surface Tension Depression dynes cm⁻¹
S.1
S.3
S.4
S.2
20
12
4
20
12
4
20
12
4
8
4
S N Ja M M Jy S N Ja M M Jy S
1980
1981
1982

Figure 4.5

Surface tension depression measurements, dynes cm^{-1}.

September 1980 - September 1982

and 6m, a clinograde vertical profile and overturn occurring in late September. During the summer, surface oxygen fluctuated between 90 and 100%. In both 1981 and 1982 two periods of deoxygenation were recorded in the hypolimnion. The first, in April, resulted in anoxia of the bottom levels. In 1982 this short period of anoxia was accompanied by a short period of heating of the top 3m to 10°C, before the onset of stratification *per se*. By the beginning of May wind-induced mixing had increased the oxygen content of the bottom waters to 40% in 1981 and 30% in 1982. From the middle of May to the middle of July, there was a progressive depletion in oxygen saturation to 0% at the lake bottom. Slight increases in oxygen saturation then occurred in August and September. At overturn, stratification broke down rapidly and isothermal conditions coincided with an increase in oxygen content throughout the lake.

According to Hutchinson (1957) these temperature and oxygen data indicate that the Dubh Lochan is a warm monomictic lake.

4.1.4 Surface tension depression (s.t.d.)

Surface tension measurements (Fig. 4.5) showed both seasonal and site variations. The highest readings were recorded in the 'bay' areas (sites 1,3 and 4) and the lowest in open water (site 2). On all four sites the highest readings were generally obtained in the summer and early autumn months (May to September) and the lowest in the winter months. The dashed lines indicate that surface tension depression was greater than could be measured using the field technique i.e. s.t.d.> 22 dyn cm^{-1}.

At site 2 the highest s.t.d. recorded was of 9 dyn cm^{-1} on the 6th April 1982. Apart from this one record, the s.t.d. varied between <1 (i.e. a clean surface) to 6 dyn cm^{-1}, the highest readings occurring in the summer months.

At site 3 a s.t.d > 22 dyn cm^{-1} was recorded once. Again the highest depressions were recorded in the summer months.

At site 1 s.t.d. measurements > 22 dyn cm^{-1} were recorded on seven occasions. One of these readings occurred outside the summer period on 23rd. October 1980. On 11th. February 1982 a measurement of 17 dyn cm^{-1} was obtained. On this occasion the oil did not spread evenly but rather in a star-shape. Goldacre (1949) has stated that this is indicative of a solid film.

The greatest s.t.d. values were measured at site 4 among the *Nuphar* and *Nymphaea*. S.t.d. values in excess of 22 dyn cm^{-1} were observed on nine occasions in the summer months. Lesser peaks were recorded on 9th October 1980 (12 dyn cm^{-1}), 22nd October 1981 (17 dyn cm^{-1}), 11th February 1982 (15 dyn cm^{-1}) and on the 18th March 1982 (15 dyn cm^{-1}). A star-shaped pattern of oil spread was observed on this latter date and again indicated that the film was solid.

4.1.5 Light measurements.

Secchi disc readings are given with the corresponding productivity measurements in Figs 5.21 to 5.23 and are summarised in Table 4.1 together with their extinction coefficients.

Readings were taken between 10 and 11 am. The bracketed readings were taken between 2 and 3 pm.

Light penetration was highest in spring, summer and autumn and lowest in winter. Strong coloration (turbidity) of the water was noted when light penetration was low. This coloration was caused by yellow humic and fulvic acids.

On those dates marked with an asterisk incident light measurements were available and are summarised in Table 4.2 together with the period over which they were taken.

Table 4.1
Secchi disc readings (S.d.) and extinction coefficient (k) measurements determined at site 2 between 22/7/1981 and 16/9/1982.

Date	S.d. (metres)	k
22.7.81	4.20	0.405
20.8.81	4.43	0.384
25.8.81	3.93 (4.70)	0.433 (0.362)
3.9.81	4.53	0.375
22.10.81	3.18	0.535
25.11.81	3.35	0.507
27.1.82	3.83	0.444
11.2.82	3.98	0.427
4.3.82	3.89	0.437
18.3.82	3.59	0.474
31.3.82	4.30 (4.20)	0.395 (0.405)
6.4.82	4.13	0.412
7.4.82	4.125	0.412
22.4.82	4.025	0.422
13.5.82 *	4.025	0.422
26.5.82 *	4.35	0.391
17.6.82 *	4.00	0.425
14.7.82 *	4.15	0.410
22.7.82 *	4.125	0.412
29.7.82 *	4.125	0.412
18.8.82	4.25	0.40
19.8.82	4.15	0.410
26.8.82 *	4.00	0.425
1.9.82 *	4.05	0.420
2.9.82 *	4.005	0.425
16.9.82	3.20	0.531

Table 4.2
Incident light measurements. Meter positioned on the roof of the field station.

Date	radiation g cal $cm^{-1}min^{-1}$	Period of measurement
13.5.82	19.24	12 noon to 5 pm
26.5.82	100.34	8 am to 2 pm
	24.53	10 am to 2 pm
	42.19	2 pm to 6.30 pm
17.6.82	12.72	11 am to 3 pm
14.7.82	6.49	10.30 am to 2.30 pm
22.7.82	27.65	10.30 am to 2.30 pm
29.7.82	28.74	11 am to 3 pn
26.8.82	14.83	11 am to 3 pm
1.9.82	20.37	11 am to 3 pm
2 9 82	16.48	11 am to 3 pm

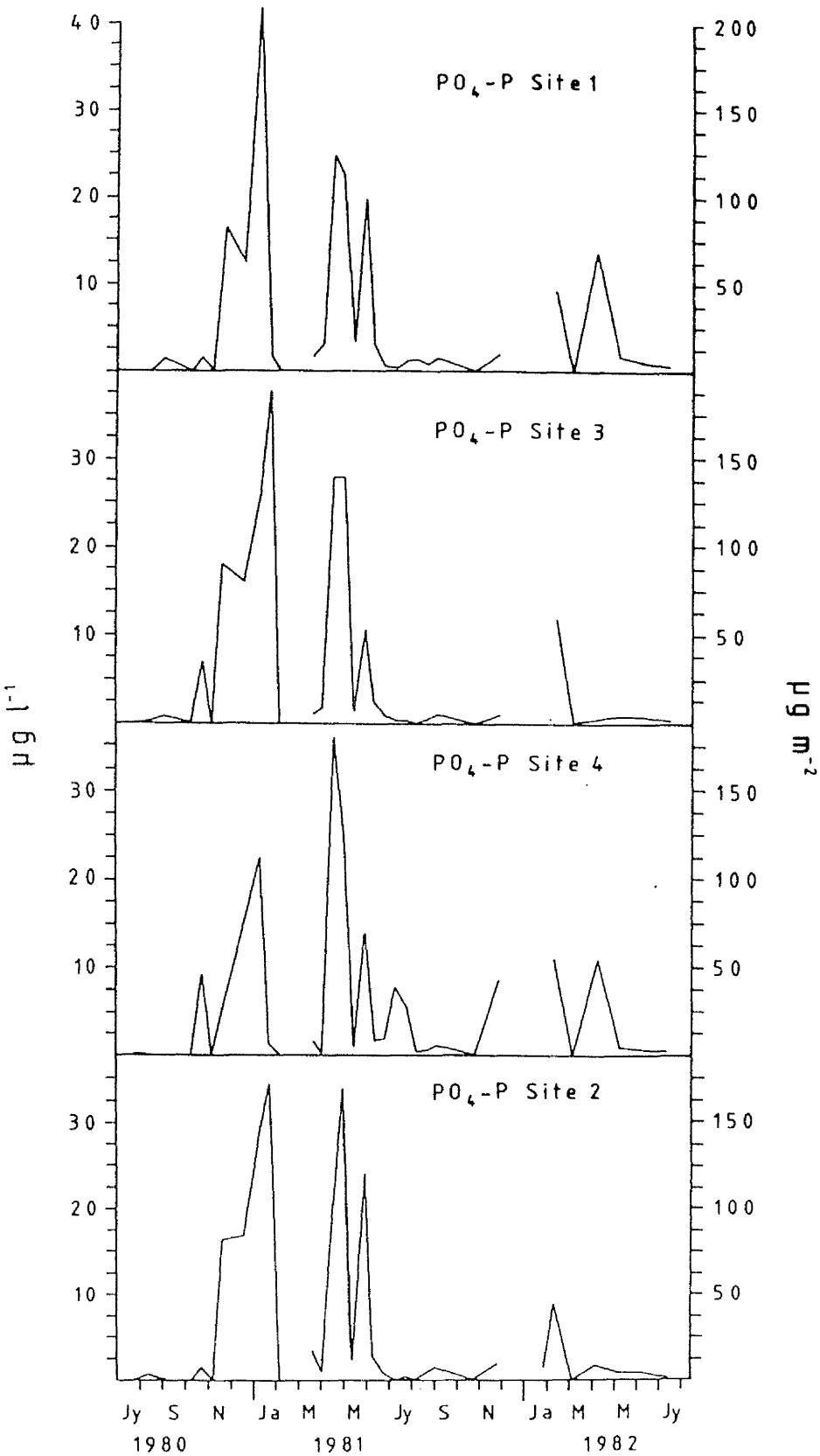

PO4-P Site 1
PO4-P Site 3
PO4-P Site 4
PO4-P Site 2
µg l-1
µg m-2
40
30
20
10
200
150
100
50
Jy S N Ja M M Jy S N Ja M M Jy
1980
1981
1982

Figure 4.6

Soluble reactive phosphorus (orthophosphate) $\mu g\ l^{-1}$

July 1980 - July 1982

4.2 CHEMICAL ANALYSES.

4.2.1 Soluble reactive phosphorus (orthophosphate)

A seasonal variation in orthophosphate levels was noted with values in the range from analytical zero to 41.8 $\mu g\ l^{-1}$(Fig.4.6). Levels were lowest in the summer and autumn and highest in the winter and spring.

The period 24th July to 9th October 1980 was characterised by very low levels of orthophosphate (analytical zero to 0.75 $\mu g\ l^{-1}$). A small rise in orthophosphate on 23rd October preceded the rapid increase in levels to the winter maxima (January 1981). Values peaked at sites 1 and 4 on the 8th January (41.78 and 22.44 $\mu g\ l^{-1}$ respectively) and at sites 2 and 3 on the 22nd. January (34.44 and 37.78 $\mu g\ l^{-1}$ respectively).

Measurements taken on 5th February 1981 were analytical zero. After ice-thaw orthophosphate concentrations rose to their maximum levels in April. Again, concentrations peaked at sites 1 and 4 first (16th April, 24.78 and 36.02 $\mu g\ l^{-1}$ respectively) followed by sites 2 and 3 (30th April, 33.91 and 28.05 $\mu g\ l^{-1}$ respectively). Levels remained high particularly at sites 1 and 4 until the beginning of June when a dramatic fall in concentrations was noted. Except for a small flux in orthophosphate level at site 4 in July (7.42 $\mu g\ l^{-1}$), concentrations remained below 2 $\mu g\ l^{-1}$ throughout the late summer and autumn and until the onset of an ice cover.

After ice thaw in 1982 the increase in orthophosphate, when compared to that obtained in 1981 (Fig 4.6) was much reduced (8.9-11.9 $\mu g\ l^{-1}$ on 11th February). The measured increase in April was also much smaller (0.65 to 11.30 $\mu g\ l^{-1}$) after which orthophosphate levels remained below 2 $\mu g\ l^{-1}$. Samples taken through the ice cover during the winter of 1982 gave the following readings; 13th January site 1 0.98 $\mu g\ l^{-1}$, site 2 2.68 $\mu g\ l^{-1}$, 27th January site 2 0.40 $\mu g\ l^{-1}$, 1m 1.6 $\mu g\ l^{-1}$, 3m 2.8 $\mu g\ l^{-1}$and 5m 3.6 $\mu g\ l^{-1}$.

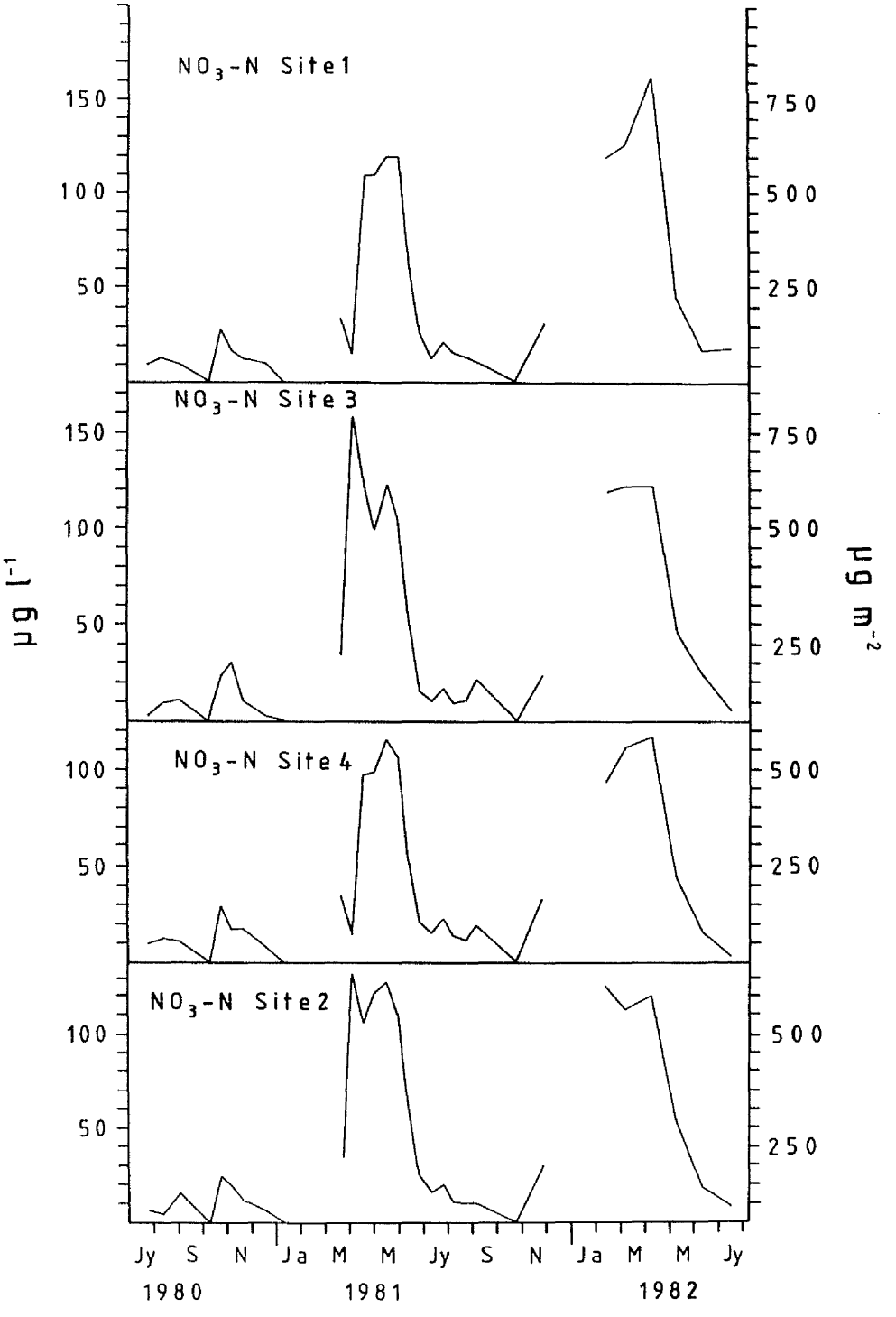

NO3-N Site1
NO3-N Site3
NO3-N Site4
NO3-N Site2
150
100
50
750
500
250
µg l-1
µg m-2
Jy S N Ja M M Jy S N Ja M M Jy
1980
1981
1982

Figure 4.7

Inorganic nitrogen - nitrate-nitrogen $\mu g\ l^{-1}$

July 1980 - July 1982

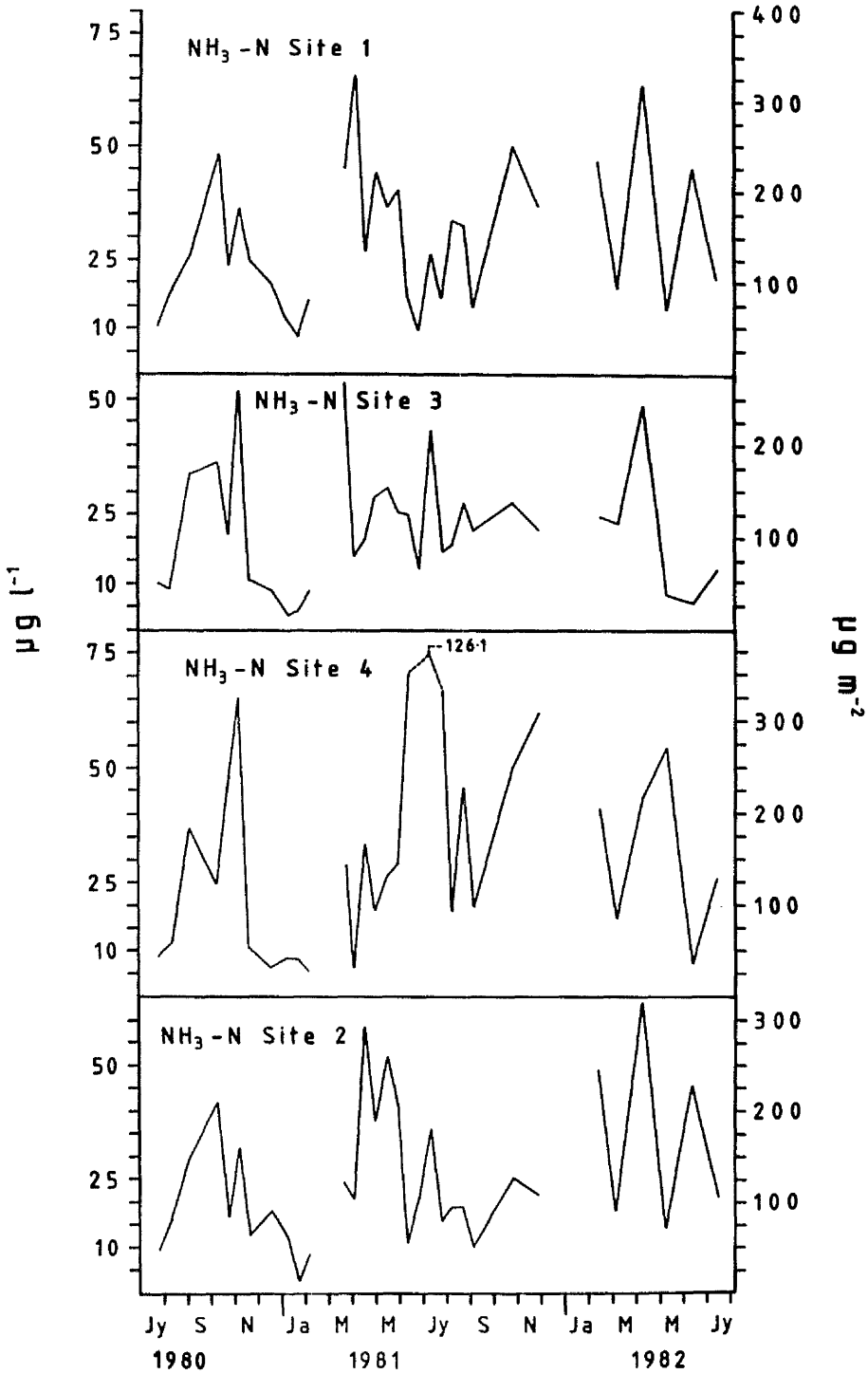

NH3-N Site 1
NH3-N Site 3
NH3-N Site 4
126-1
NH3-N Site 2
µg l-1
µg m-2
75
50
25
10
400
300
200
100
Jy S N Ja M M Jy S N Ja M M Jy
1980
1981
1982

Figure 4.8

Inorganic nitrogen - ammonia-nitrogen $\mu g\ l^{-1}$

July 1980 - July 1982

4.2.2 Inorganic forms of nitrogen; nitrite-nitrogen and nitrate-nitrogen.

Nitrite-nitrogen measurements throughout the experimental period were analytical zero. No graphical or tabular representation of the data has therefore been made.

Seasonal variation and some site variation in nitrate-nitrogen levels were recorded (Fig. 4.7). Values ranged from analytical zero to 186.41 $\mu g\ l^{-1}$. Summer/autumn/early winter minima and spring maxima were observed.

From 24th July to the 9th October 1980 nitrate-nitrogen concentrations were low (less than 15 $\mu g\ l^{-1}$). On the 23rd October at sites 1, 2 and 4 and on the 6th November at site 3, a small increase in nitrate levels was observed (24-30 $\mu g\ l^{-1}$). Nitrate concentration fell gradually to analytical zero (8th January 1981) where it remained at the onset of ice cover. After ice thaw a rapid increase in nitrate levels to their maxima in April was observed, first at sites 2 and 3 (2nd. April, 131.58 and 157.89 $\mu g\ l^{-1}$ respectively) and then at sites 1 and 4 (16th April, 110.17 and 96.61 $\mu g\ l^{-1}$ respectively). These high concentrations were maintained until June when a fall to half their previous maximum values was recorded (55.81-63.57 $\mu g\ l^{-1}$). A gradual decline in the nitrate content of the surface layer was observed throughout the summer with a small increase in levels occurring before the onset of ice cover. As recorded in 1981, after ice melt in 1982 high levels of nitrate-nitrogen were measured (94.08-124.8 $\mu g\ l^{-1}$ on 11th February 1982) remaining high (94.08-161.86$\mu g\ l^{-1}$) throughout March and April. Samples taken through the ice gave the following readings; 13th January 1982 site 1 186.41 $\mu g\ l^{-1}$, site 2 117.39 $\mu g\ l^{-1}$, 27th Janury site 2; 143.20 $\mu g\ l^{-1}$, 1m; 142.77 $\mu g\ l^{-1}$, 3m; 152.43 $\mu g\ l^{-1}$ and 5m; 139 32 $\mu g\ l^{-1}$. Through May, June and July 1982 the gradual fall in nitrate levels observed the previous year, again occurred, such that by the end of the experimental programme, on 13th July, nitrate levels were between 3.20 and 17.26 $\mu g\ l^{-1}$.

4.2.3 Ammonia-nitrogen.

Considerable variation in the ammonia-nitrogen levels of the surface layer was observed throughout the experimental period (Fig. 4.8). The maximum value obtained was 126.10 μg ammonia-nitrogen l^{-1}. and the minimum 3.00 μg l^{-1}. Both sites 1 and 2 displayed similar trends throughout the experimental period. At the start of the programme (24th July 1980) ammonia-nitrogen levels were 10.50 μg l^{-1} (site 1) and 9.50 μg l^{-1} (site 2) rising in September to a peak at the beginning of October (48 and 42 μg l^{-1} respectively) and at the beginning of November (36 and 32 μg l^{-1}). A similar trend was observed at sites 3 and 4. All four sites showed a fall in ammonia-nitrogen levels over late November to early February 1981. After ice thaw in 1981 sites 1 and 2 showed a rapid increase in ammonia -nitrogen with a peak at site 1 at the beginning of April (65.63 μg l^{-1}) and at site 2 in the middle of April (58.83 μg l^{-1}). At site 4 the maximum period did not occur until June (126.10 μg l^{-1}) falling to 18.77 μg l^{-1} by the beginning of August with a second smaller peak on the 20th (45.72 μg l^{-1}). Ammonia-nitrogen levels at site 3 were much lower than those measured at sites 1, 2 and 4. A peak in March (53.13 μg l^{-1}) was followed by two lesser increases in May and July (30.74 and 43.09 μg l^{-1} respectively). Further fluctuations at all four sites were observed for the rest of the year. Before the formation of ice cover levels were higher than those measured in 1981 (21.9 to 61.98 in November 1981 as opposed to 10.7 to 24.7 μg l^{-1} in November 1980).

Samples taken through the ice cover gave the following readings; 13th January 1982 site 1, 26.50 μg l^{-1}; site 2, 19.68 μg l^{-1}; 27th January site 2, 63.60 μg l^{-1}; 1m, 31.80 μg l^{-1}; 3m, 40.02 μg l^{-1} and 5m, 30.48 μg l^{-1}. After ice thaw in 1982 surface layer levels were between 24.38 and 46.84 μg l^{-1}. By March these had fallen to between 17.18 and 23.01 μg l^{-1}. An April rise was recorded at all four sites (39.62-63.84 μg l^{-1}) after which considerable variation in ammonia-nitrogen levels was observed at all four sites over the remaining three months.

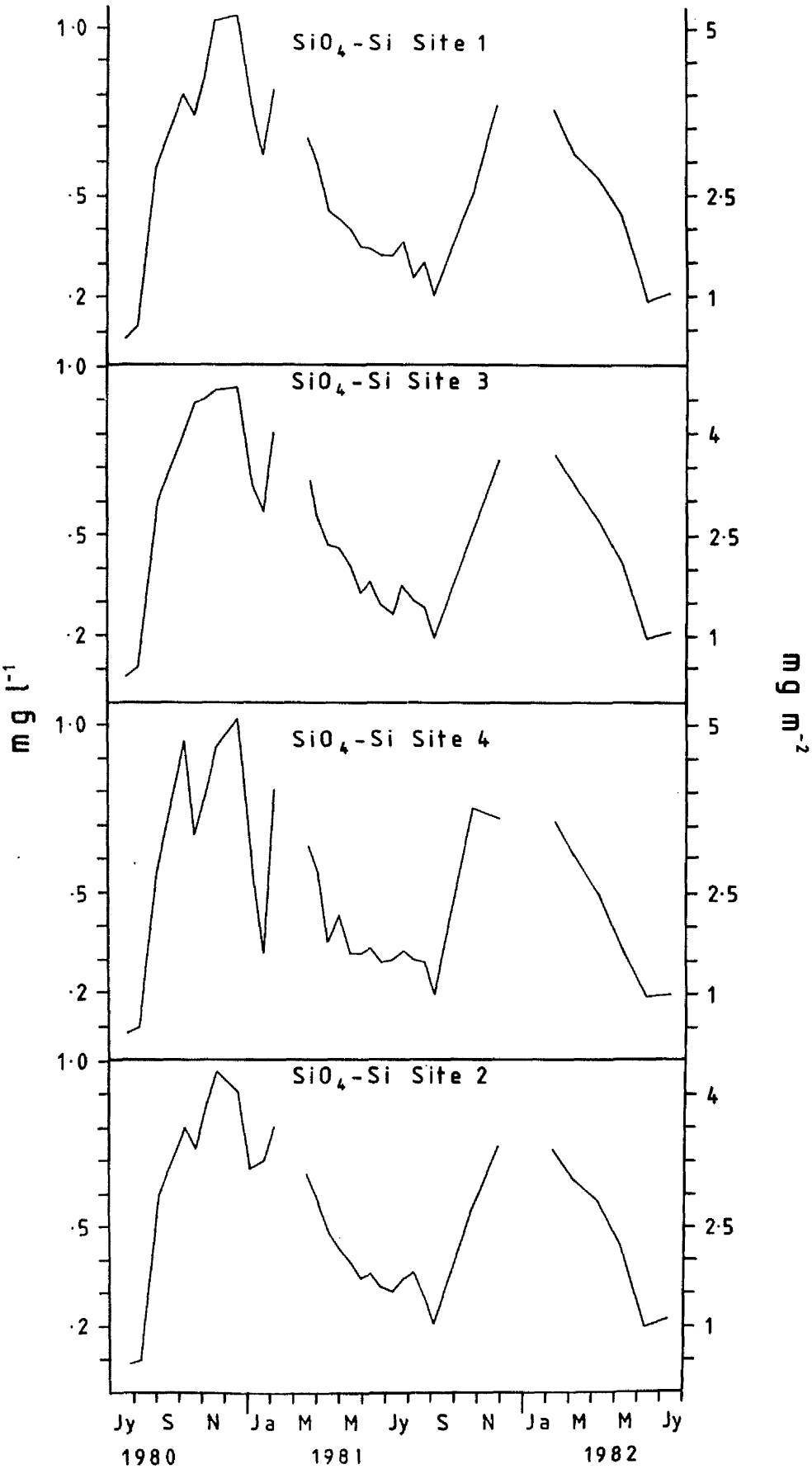

SiO4-Si Site 1
SiO4-Si Site 3
SiO4-Si Site 4
SiO4-Si Site 2
mg l-1
mg m-2
1·0
·5
·2
5
2·5
1
4
Jy S N Ja M M Jy S N Ja M M Jy
1980
1981
1982

Figure 4.9

Soluble reactive silica (silicate) $\mu g\ l^{-1}$

July 1980 - July 1982

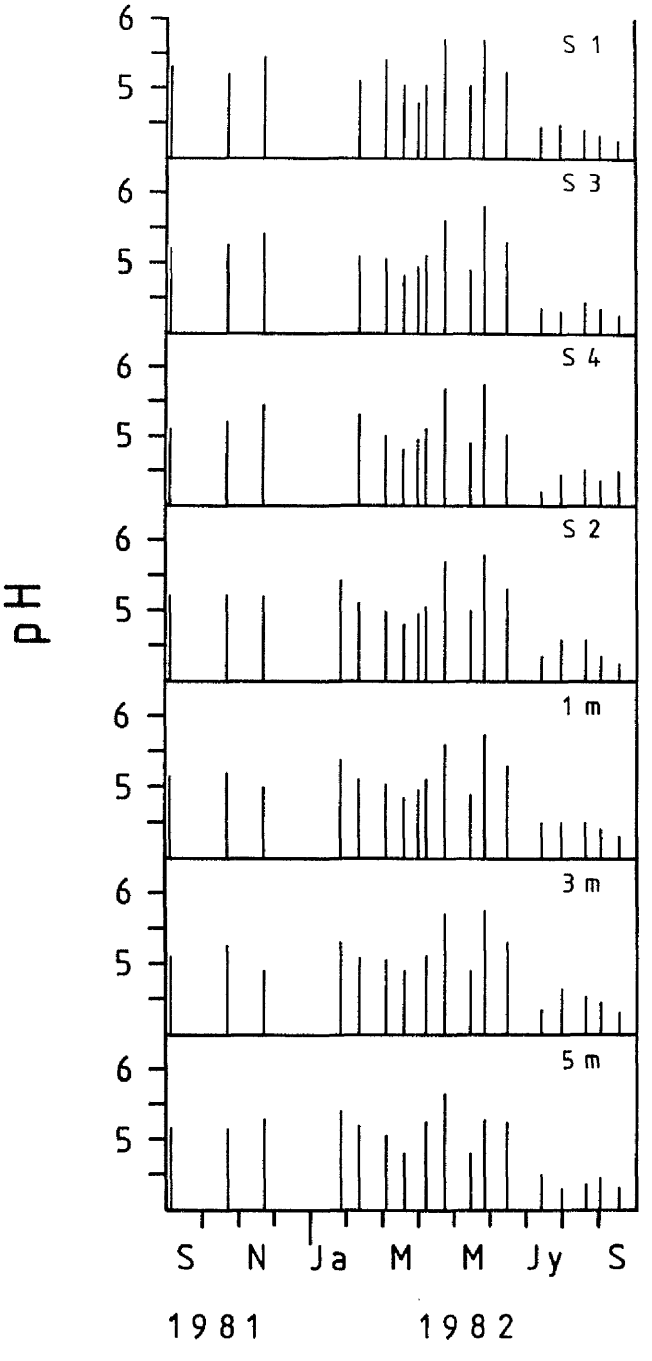

pH
6
5
S 1
S 3
S 4
S 2
1 m
3 m
5 m
S N Ja M M Jy S
1981 1982

Figure 4.10

pH

September 1981 - September 1982

Table 4.3

Conductivity $\mu S\ cm^{-1}$

	Surface				Depth		
Date	Site 1	Site 2	Site 3	Site 4	1m	3m	5m
18.3.82	135.48	127.26	127.26	134.79	131.38	133.20	128.76
31.3.82	102.06	96.75	101.58	103.22	92.34		
7.4.82	108.70	98.66	98.09	95.76	98.66	96.86	98.85
22.4.82	96.31	96.31	99.64	99.64	100.55	99.57	99.57
13.5.82	103.27	101.88	95.81	100.32	95.59	96.93	100.74
26.5.82am	100.46	100.80	96.36	93.38	100.80	100.80	106.67
26.5.82pm	102.90	106.86	104.22	99.84	102.90	102.90	106.91
17.6.82	98.51	90.50	90.52	91.51	93.04	93.04	93.46
14.7.82	92.64	92.64	92.10	93.75	92.10	92.64	96.93
22.7.82		92.89			96.10		
29.7.82	99.86	96.51	95.02	95.66	94.63	101.92	113.95
18.8.82	104.11	97.20	94.34	97.20	103.47	100.24	101.85
19.8.82		86.29			83.42		
26.8.82		97.01			92.77		
1.9.82	98.38	100.55	94.04	94.05	94.40	97.89	95.79
2.9.82		97.23			94.52		
16.9.82	100.29	100.29	100.05	107.57	98.56	102.62	102.71

4.2.4 Soluble reactive silica

Seasonal variations in silicate-silica levels were observed with maxima in autumn and winter, gradually falling through the spring to minima in late summer. Values ranged from 77 $\mu g\ l^{-1}$ to 1.04 $mg\ l^{-1}$ (Fig 4.9).

The lowest levels were recorded at the start of the survey, in July 1980 (77-85 $\mu g\ l^{-1}$). A rapid increase to the winter maxima was observed in November and December (910 -1040 $\mu g\ l^{-1}$) coinciding with the period of temperature minima, isothermal conditions and the mixing of the water column. After ice melt in 1981 a gradual decline in the silicate content was observed to minima in September (195.3-205.1 $\mu g\ l^{-1}$) rising at overturn to between 721-747 $\mu g\ l^{-1}$ before the onset of ice formation. Measurements taken through the ice cover on the 13th January 1982 were 904 $\mu g\ l^{-1}$ at site 1 and 1000 $\mu g\ l^{-1}$ at site 2. On the 27th January, the following readings were obtained; just below the ice; 736 $\mu g\ l^{-1}$, at 1m; 717 $\mu g\ l^{-1}$, at 3m ; 750 $\mu g\ l^{-1}$ and at 5m ; 723 $\mu g\ l^{-1}$. After ice melt the same pattern of gradual reduction of the silicate content of the surface layer was observed, reaching between 199 and 221 $\mu g\ l^{-1}$ at the end of the sampling programme.

4.2.5 pH and conductivity.

pH values ranged from 4.20-5.80 over the period September 1981-September 1982 (see Fig. 4.10). pH readings taken in 1981 ranged from 4.90 to 5.45. After overturn in late September/early October pH was evenly distributed with depth. On the 27th January 1982 samples taken immediately below the ice cover and at 1m and 5m had a pH of 5.40 and at 3m of 5.30. After ice thaw (February) the pH gradually fell from 5.1-5.3 to 4.95-4.8 (end of March). In April a rise in pH at both surface and depth sites to 5.70 occurred. A further peak in pH was measured in late May after which pH gradually fell to below 5 (July) where it remained at the end of the sampling programme.

The vertical distribution of pH for the period 22nd. April to 13th June 1982 displayed the typical oligotrophic pattern i.e. a gradual decrease in pH with depth. After this period the pattern could be

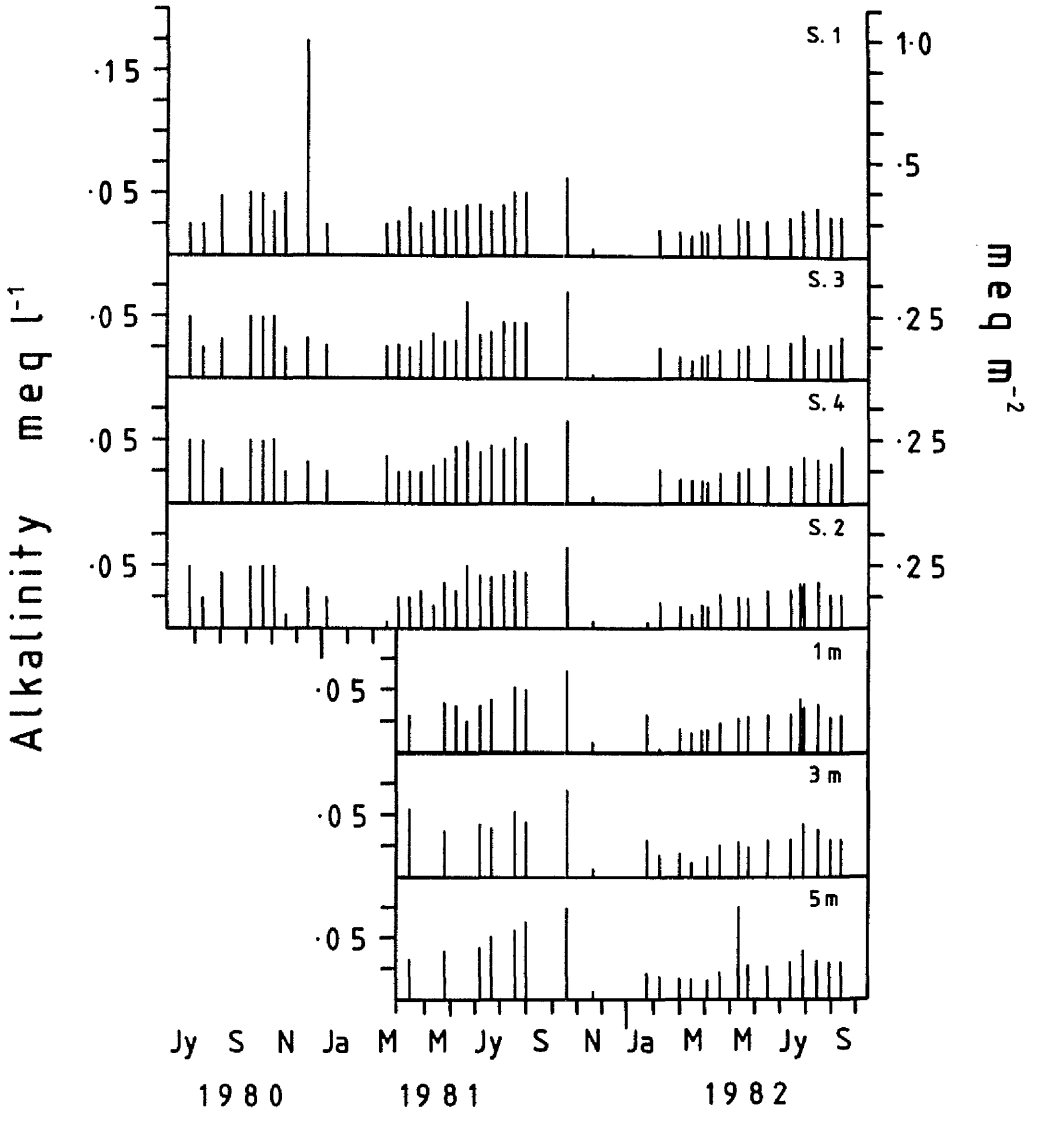

Alkalinity meq l⁻¹
meq m⁻²
S. 1
S. 3
S. 4
S. 2
1m
3m
5m
·15
·05
1·0
·5
·25
Jy S N Ja M M Jy S N Ja M M Jy S
1980
1981
1982

Figure 4.11

Alkalinity meq l^{-1}

July 1980 - September 1982

described as heterograde i.e. maximum pH occurred at varying depths throughout the remaining period.

No correspondence with alkalinity or free carbon dioxide acidity was noted. Comparison with rainfall data indicates that during 1982 pH was depressed during periods of high rainfall.

Conductivity measurements were made between 18th February 1982 and 16th September 1982 to complement nutrient analysis data. The standardized (to 25^{o}C) measurements, in μS cm^{-1} are represented in Table 4.3.

Conductivity measurements ranged from 83.4 to 135.5 μS cm^{-1}. From the higher readings obtained in the middle of March (127.3-135.5 μS cm^{-1}) conductivity fell over the spring and summer coinciding with the gradual depletion of nutrients in the epilimnion. Over this period the average conductivity value was 98.1μS cm^{-1} (s.d. 4.9 μS cm^{-1}).

4.2.6 Alkalinity.

Alkalinity values in meq l^{-1} are represented in Fig.4.11. The exceptionally high value of 0.2 meq l^{-1}, obtained at site 1 on the 18th December 1980, was probably the result of contamination of the sample and so will be ignored in the following description of results.

Alkalinity values ranged from 0.003 to 0.077 meq l^{-1}. These readings are very low as is to be expected since alkalinity is a pH dependent factor at its minimum at pH's below 5.

In general, surface layer levels were higher in late summer/autumn 1980 (0.05 meq l^{-1}), low in spring 1981 (0.025 meq l^{-1}) with a small increase in June (0.041-0.065 meq l^{-1}), increasing again in late summer to a maximum value in October (0.07 meq l^{-1}). During 1982 alkalinity levels were again low in spring (0.015- 0.0185 meq l^{-1}) rising in late April to maxima in July (0.035 meq l^{-1})and September (0.0265-0.0445 meq l^{-1}).

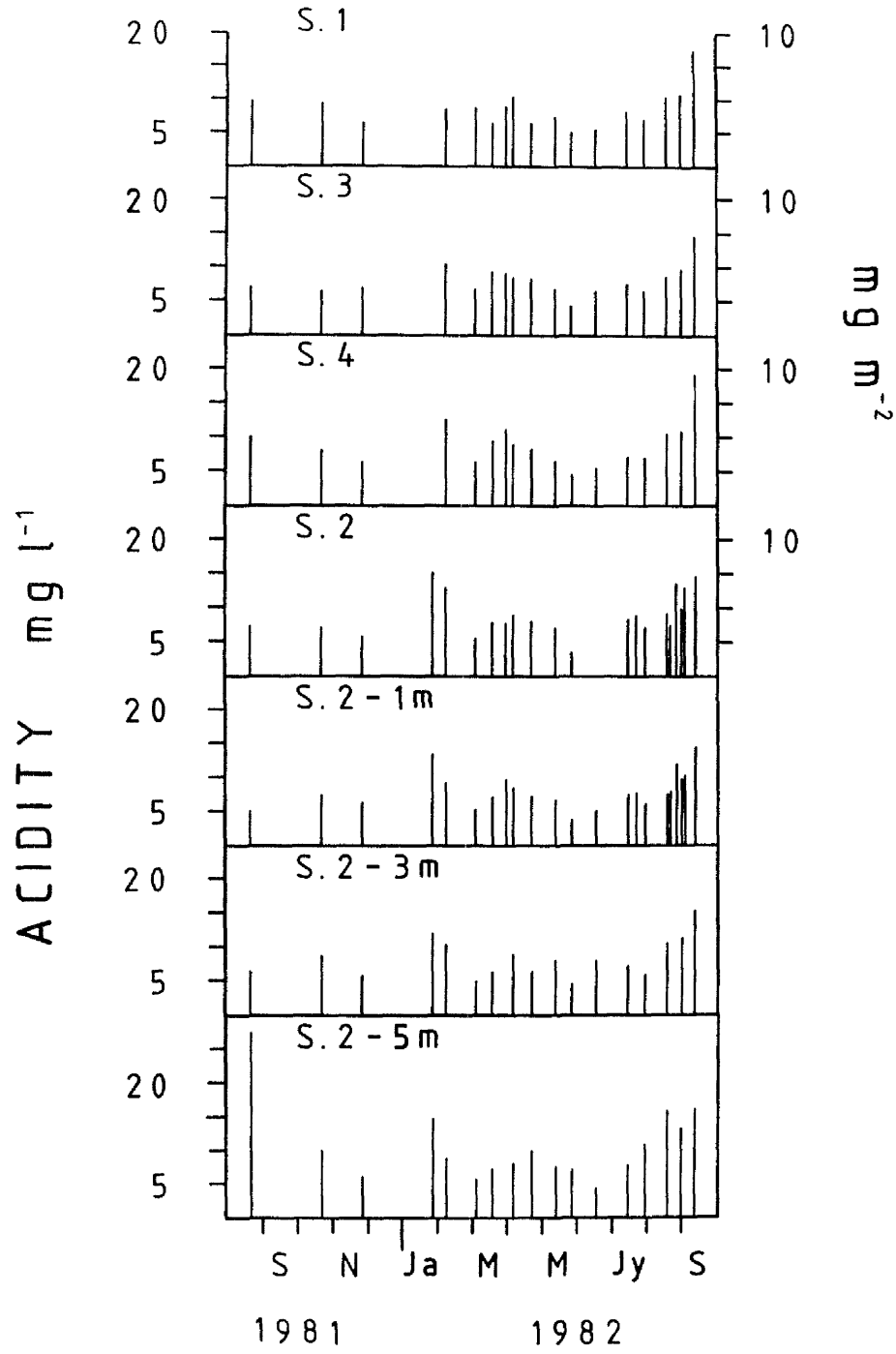

S. 1
S. 3
S. 4
S. 2
S. 2 - 1m
S. 2 - 3m
S. 2 - 5m
20
5
10
ACIDITY mg l-1
mg m-2
S N Ja M M Jy S
1981
1982

Figure 4.12

Free carbon dioxide acidity mg CO_2 l^{-1}

August 1981 - September 1982

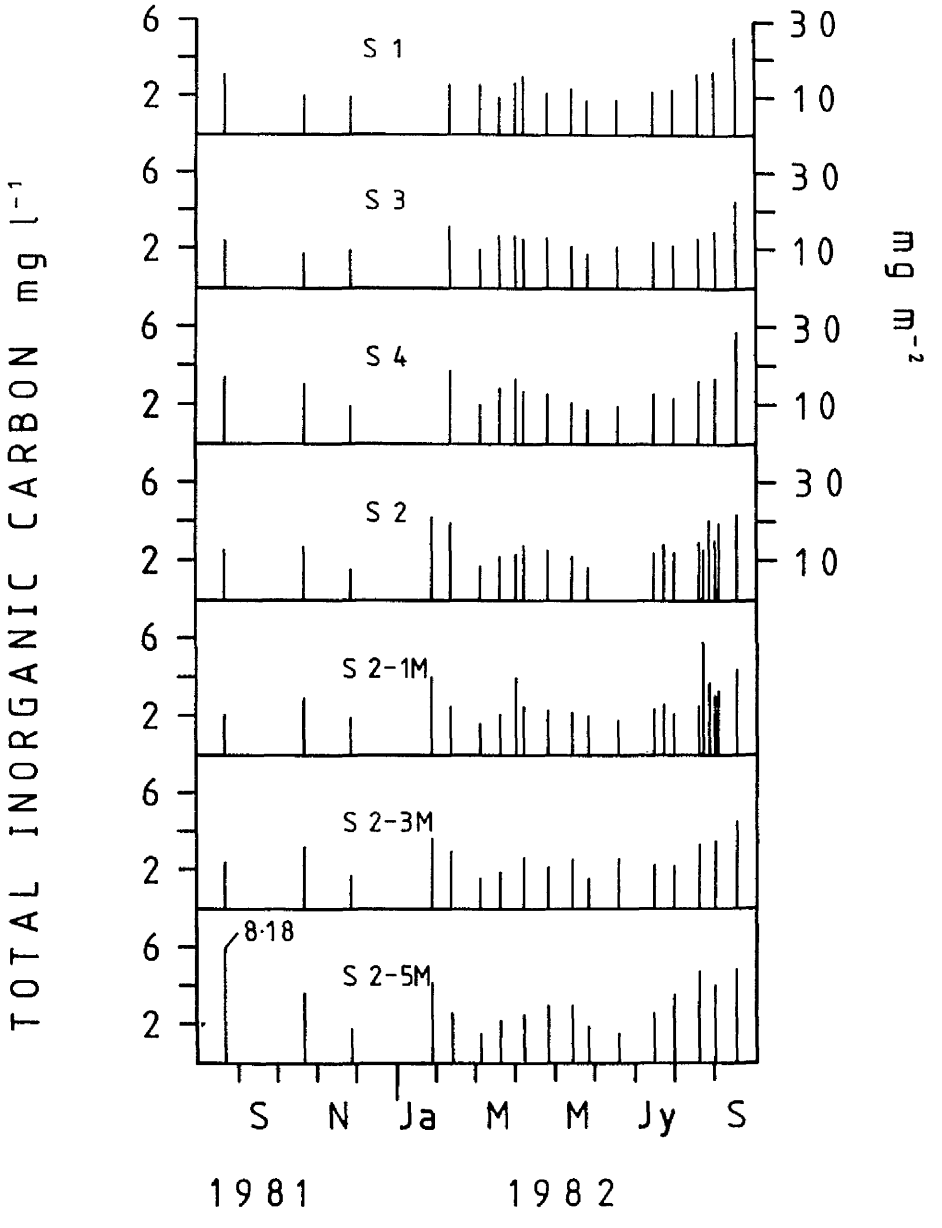

TOTAL INORGANIC CARBON mg l⁻¹
mg m⁻²
S 1
S 3
S 4
S 2
S 2-1M
S 2-3M
S 2-5M
8·18
6
2
30
10
S N Ja M M Jy S
1981
1982

Figure 4.13

Total inorganic carbon TIC mg C l^{-1}

August 1981 - September 1982

Depth samples taken between April 1981 and September 1982 showed variations to this surface layer pattern. At 1m, peaks in alkalinity were recorded in August (0.053 meq l^{-1}) and October 1981 (0.0625 meq l^{-1}). During 1982 a gradual rise in alkalinity occurred to reach a maximum value in July (0.043 meq l^{-1}). At 3m, high alkalinity values were obtained in April (0.055 meq l^{-1}), September (0.0525 meq l^{-1}) and October 1981 (0.070 meq l^{-1}). In 1982 the maximum value recorded occurred on the 29th July (0.0425 meq l^{-1}). At 5 m, a gradual increase in alkalinity from 0.033 meq l^{-1} in April to 0.075 meq l^{-1} in October 1981 occurred. During 1982 maximum values were recorded in May (0.077 meq l^{-1}) and July (0.0395 meq l^{-1}). Comparison of surface layer alkalinities at site 2 with depth alkalinities indicate that at depth alkalinity is greater with the pattern of distribution being heterograde.

Statistical comparison of pH with alkalinity showed no correlation between the two factors ($r = -0.414$, s.e.= 0.88, $t = 4.705$, $p < 0.001$). This was not surprising given the very low levels of alkalinity recorded which were at the limits of the titration method.

4.2.7 Free carbon dioxide acidity.

Acidity measurements ranged from 3.95-27.54 mg CO_2 l^{-1} (see Fig. 4.12) indicating that it is the major component of inorganic carbon in the Dubh Lochan. A seasonal fluctuation in levels was apparent with high acidity in late summer/autumn, spring and after ice melt. Samples taken at site 2 through the ice on 27th January 1982 gave high readings (15.36 mg l^{-1} just under the ice, 13.45 mg l^{-1} at 1m, 11.92 mg l^{-1} at 3m, and 14 67 mg l^{-1} at 5m). Low levels of acidity were recorded in early winter, early spring and early summer. The vertical profiles showed no seasonal profile.

4.2.8 Total inorganic carbon (TIC).

Since free carbon dioxide acidity formed the major component of the inorganic carbon system in the Dubh Lochan, seasonal fluctuations in TIC are a reflection of the acidity levels (see Section 4.2.7). TIC ranged from 1.53 to 8.18 mg l^{-1} with high levels in summer 1981 (8.18

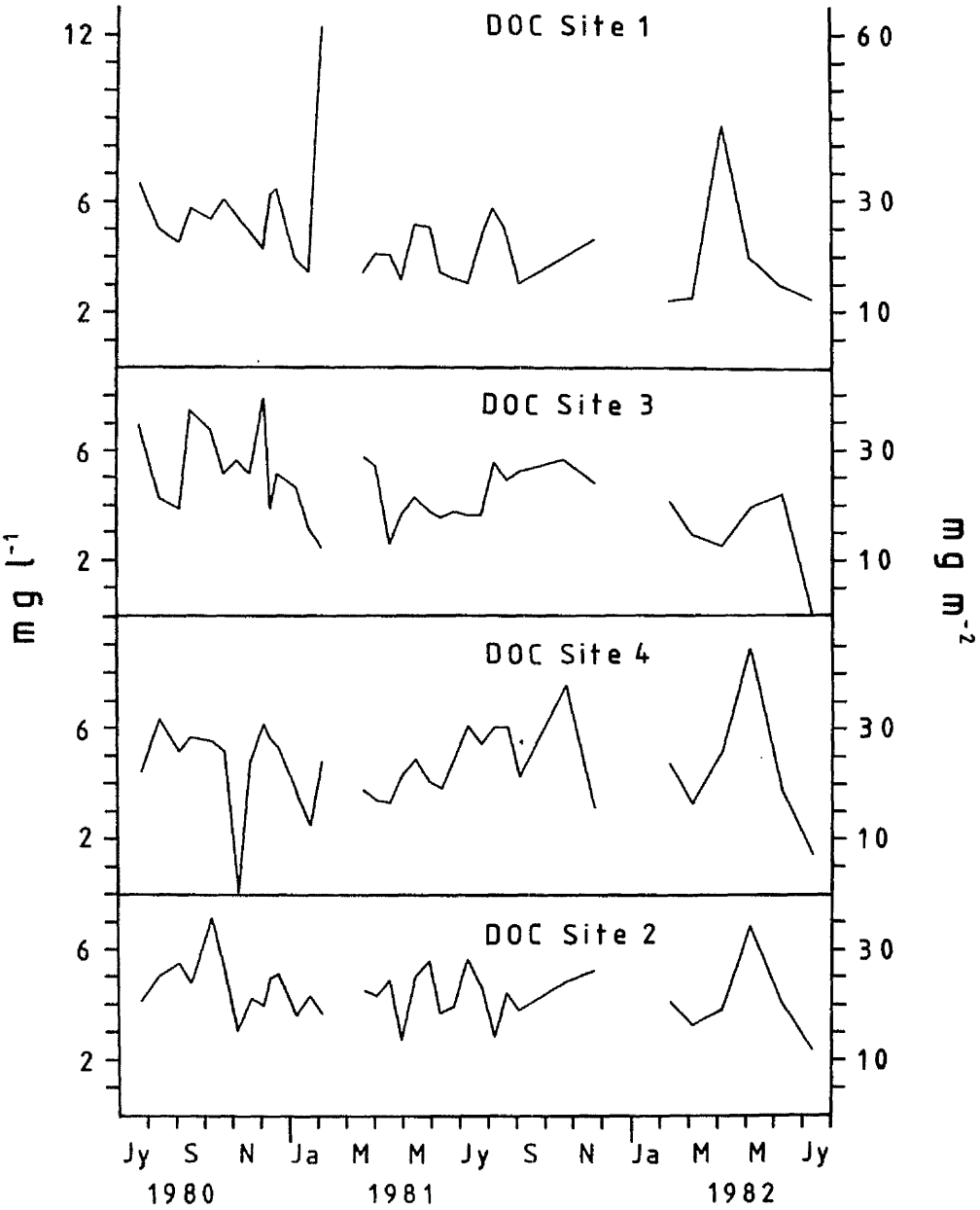

DOC Site 1
DOC Site 3
DOC Site 4
DOC Site 2
12
6
2
60
30
10
mg l-1
mg m-2
Jy S N Ja M M Jy S N Ja M M Jy
1980
1981
1982

Figure 4.14

Dissolved organic carbon DOC mg l^{-1}

July 1980 - July 1982

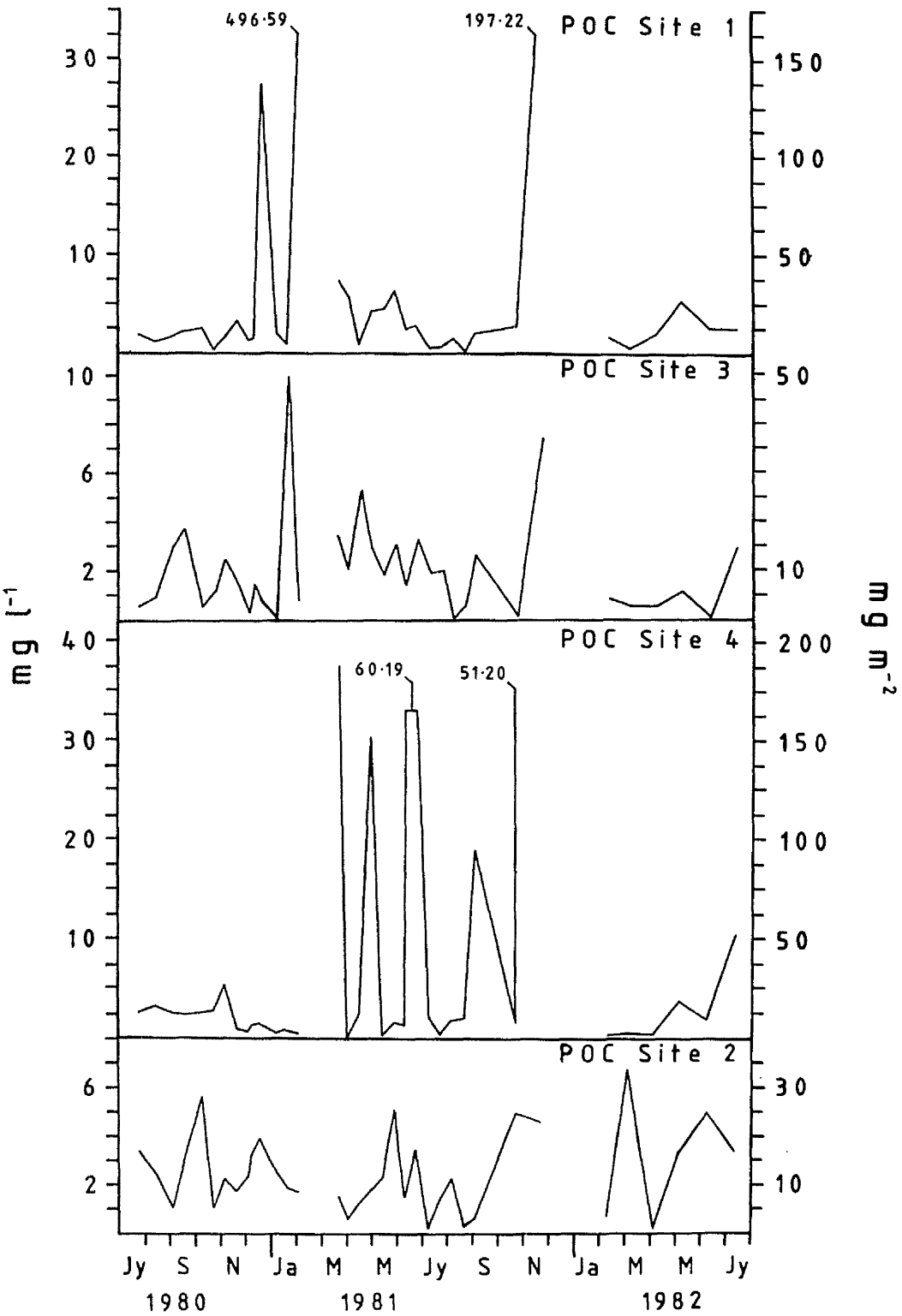

496·59
197·22
POC Site 1
30
20
10
150
100
50
POC Site 3
10
6
2
50
10
POC Site 4
60·19
51·20
40
30
20
10
200
150
100
50
POC Site 2
6
2
30
10
mg l-1
mg m-2
Jy S N Ja M M Jy S N Ja M M Jy
1980
1981
1982

Figure 4.15

Particulate organic carbon POC mg l^{-1}

July 1980 - July 1982

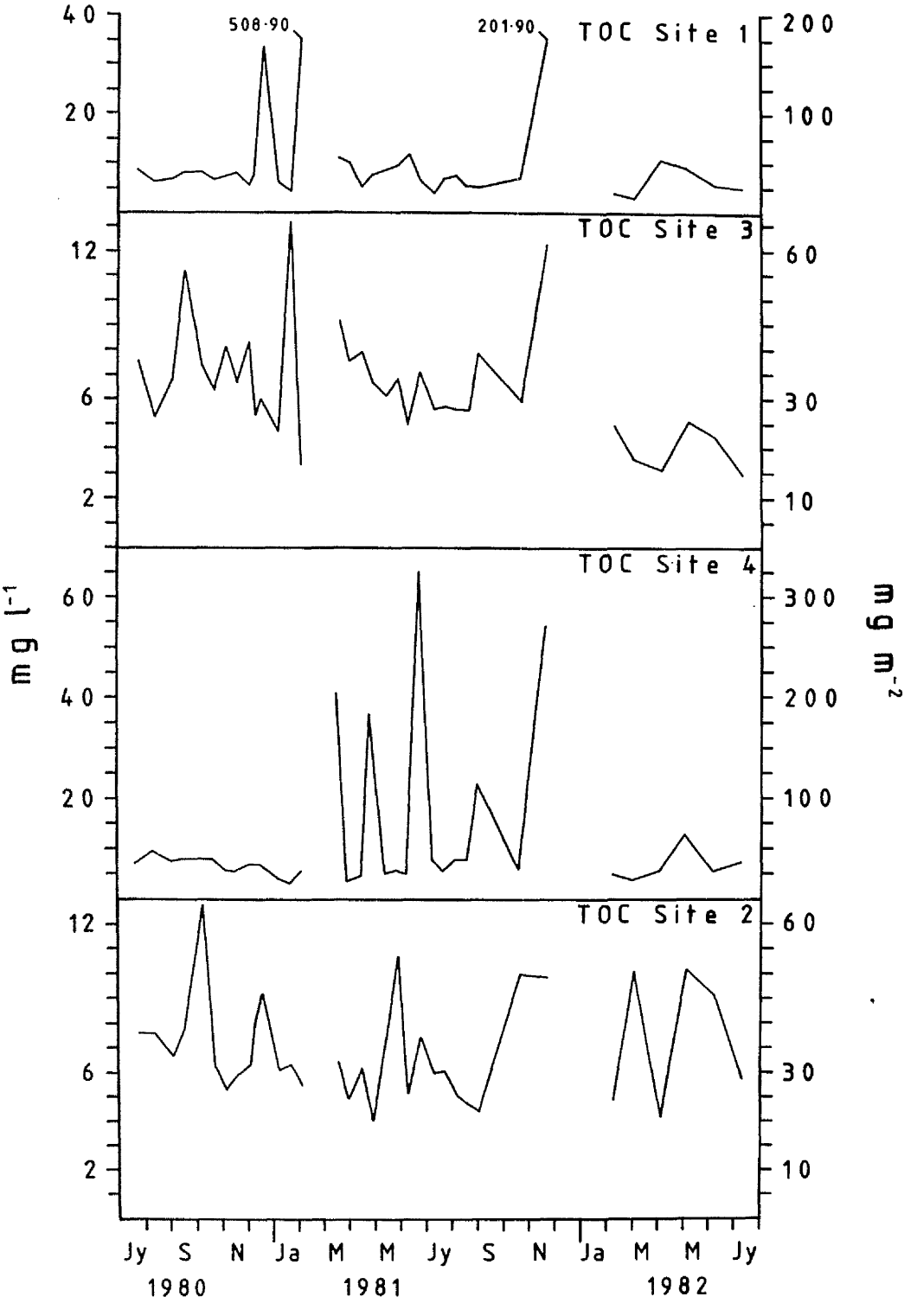

TOC Site 1
TOC Site 3
TOC Site 4
TOC Site 2
508·90
201·90
mg l-1
mg m-2
40
20
12
6
2
60
30
10
200
100
300
Jy
S
N
Ja
M
M
Jy
S
N
Ja
M
M
Jy
1980
1981
1982

Figure 4.16

Total organic carbon TOC mg l^{-1}

July 1980 - July 1982

mg l^{-1}), winter 1982, spring 1982 and summer 1982 (Fig. 4.13).

An even distribution of TIC was not observed during the period of circulation (October to April) and the vertical profile showed no seasonal pattern as such though a comparison of measurements at 1m and 3m with 5m showed that on 13 out of 17 occasions TIC was higher at 5m, just above the metalimnion, than at 1m and 3m.

4.2.9 Dissolved organic carbon, particulate organic carbon and total organic carbon (DOC, POC, TOC).

The fluctuations in organic carbon levels measured throughout the experimental programme reflect the varied origins and composition of organic material.

Dissolved organic carbon (DOC) levels varied from 18.35 μg C l^{-1} to 12.31 mg C l^{-1} with a mean value of 4.78 mg l^{-1} (see Fig.4.14). At site 1 two large increases in DOC were measured; on the 5th February 1981 (12.31 mg l^{-1}) and on the 6th April 1982 (8.73 mg l^{-1}). Otherwise DOC ranged from 2.42 to 6.61 mg l^{-1} with a mean value of 4.74. At site 2 only minor variations in DOC were observed with values ranging from 2.37 to 7.18 mg l^{-1} (mean 4.44 mg l^{-1}).

At site 3 a minimum value of 18.36 μg l^{-1} was measured on the 13th July 1982. Otherwise DOC levels ranged from 2.43 to 7.86 mg l^{-1} (mean 4.61 mg l^{-1}).

At site 4 a drop in DOC to 78.33 μg l^{-1} was recorded on the 6th November 1980 while a peak in DOC was observed on the 6th May 1982 (8.96 mg l^{-1}). Apart from these measurements DOC ranged from 1.49 to 7.55 mg l^{-1} (mean 4.69 mg l^{-1}).

Comparison of DOC data with weekly rainfall show that high DOC levels occurred 3-4 weeks after high rainfall.

Particulate organic carbon (POC) values ranged from analytical zero to 469.59 mg C l^{-1} (Fig. 4.15). Considerable spatial variation in POC concentration was observed with more frequent peaks recorded at

site 4 and low levels recorded consistently at site 2. If one compares this spread of data for 1981 with the measurements of surface tension depression (Section 4.5) one can observe a similar trend i.e. surface tension depressions were higher more frequently at site 4 and low at site 2. No such coincidence was observed between the data for sites 1 and 3 nor was any statistical correlation observed. This was expected since as stated previously, the sampling method used is not suitable for such studies as it allows considerable dilution of the surface film to occur which, in turn, will mask any correlation between surface tension depression and organic carbon levels.

At site 1 three peaks in POC were observed; 18th December 1980 (27.25 mg l^{-1}), 5th February 1981 (496.59 mg l^{-1}) and 22nd November 1981 (197.22 mg l^{-1}). These peaks coincided with autumn overturn, the onset of ice formation and the possible resuspension of surficial sediments. Apart from these high levels POC ranged from 84.62 μg l^{-1} to 7.30 mg l^{-1} (mean 2.38 mg l^{-1}).

At site 2 no such increases in POC were measured. Values ranged from 0.27 to 6.74 mg l^{-1} (mean 2.47 mg l^{-1}).

At site 3 two peaks in POC were observed before the onset of ice formation in 1981; 22nd January 1981 (9.95 mg l^{-1}) and 22nd November 1981 (7.36 mg l^{-1}). POC ranged from 48.62 μg l^{-1} to 9.95 mg l^{-1} (mean 2.04 mg l^{-1}).

At site 4 POC levels during 1980 ranged from 0.60 to 5.69 mg l^{-1}. In 1981 considerable fluctuations in POC were measured. Values ranged from analytical zero to 60.19 mg l^{-1}. Peaks occurred in March, April, June, September and November. During 1982 POC levels were initially low (0.24-3.77 mg l^{-1}) rising in July to 10.57 mg l^{-1} at the termination of the experimental programme.

Total organic carbon (TOC) levels are represented in Fig. 4.16. Table 4.4 lists the DOC:POC ratios for each sample. These indicate that DOC formed the larger component of TOC. The ratios calculated for the Dubh Lochan showed considerable variation (0.01 -170.49 overall). At site 1 the DOC:POC ratio varied from 0.024-59.91 (mean 4.39, standard

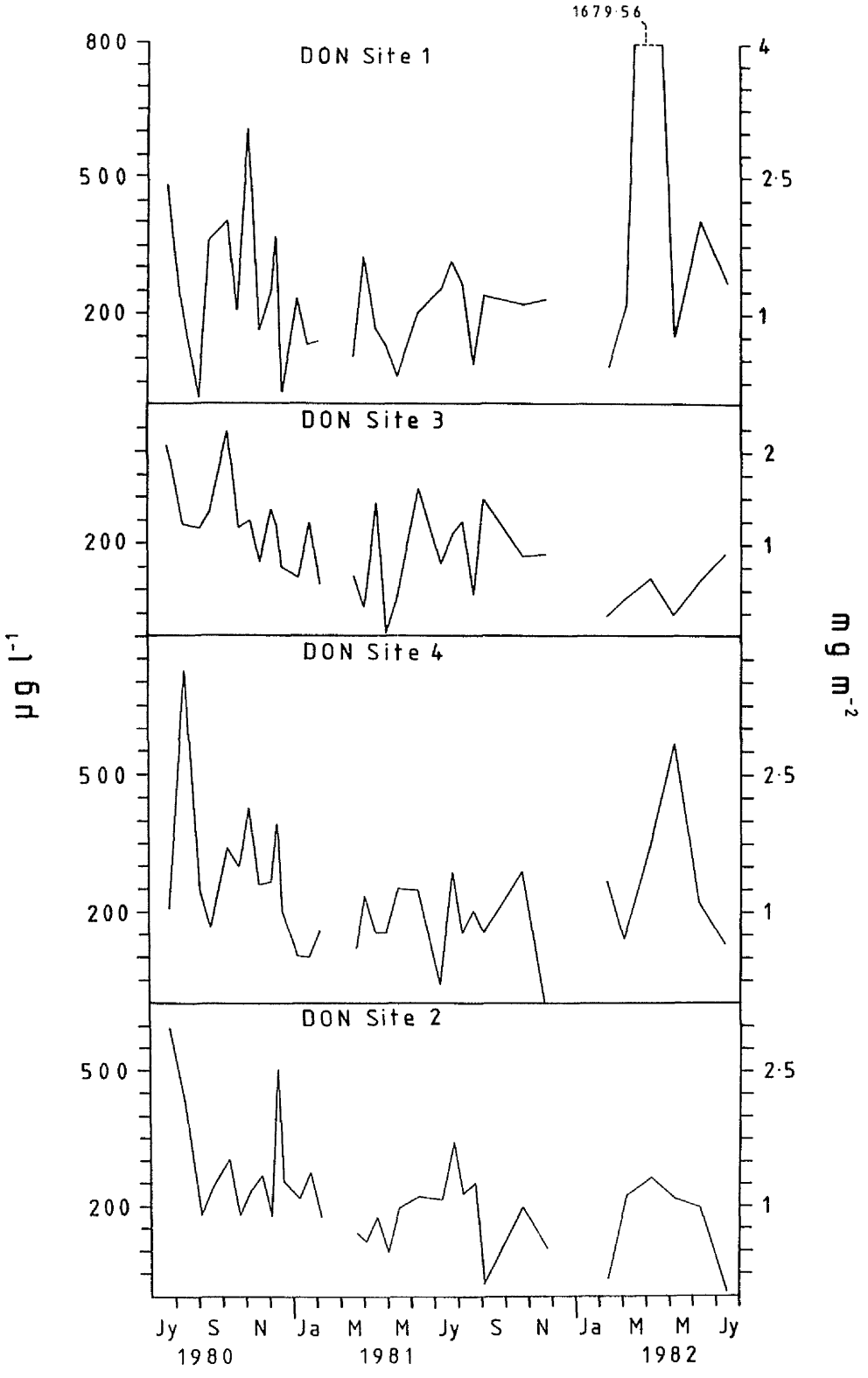

1679·56
DON Site 1
DON Site 3
DON Site 4
DON Site 2
800
500
200
4
2·5
1
2
Jy
S
N
Ja
M
M
Jy
S
N
Ja
M
M
Jy
1980
1981
1982
µg l⁻¹
mg m⁻²

Figure 4.17

Dissolved organic nitrogen DON $\mu g\ l^{-1}$

July 1980 - July 1982

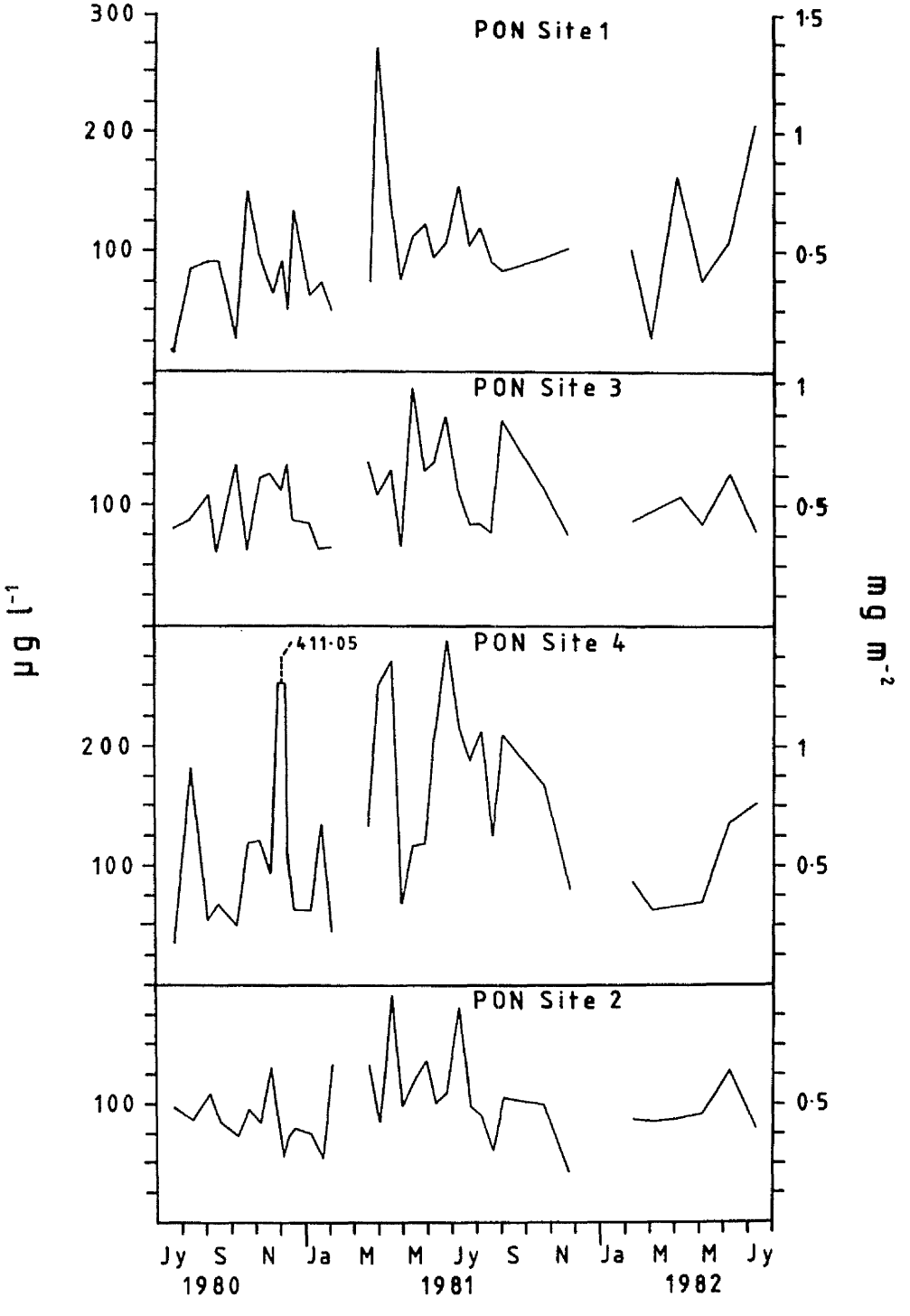

PON Site 1
PON Site 3
PON Site 4
PON Site 2
411·05
300
200
100
1·5
1
0·5
Jy S N Ja M M Jy S N Ja M M Jy
1980
1981
1982
µg l⁻¹
mg m⁻²

Figure 4.18

Particulate organic nitrogen PON $\mu g\ l^{-1}$

July 1980 - July 1982

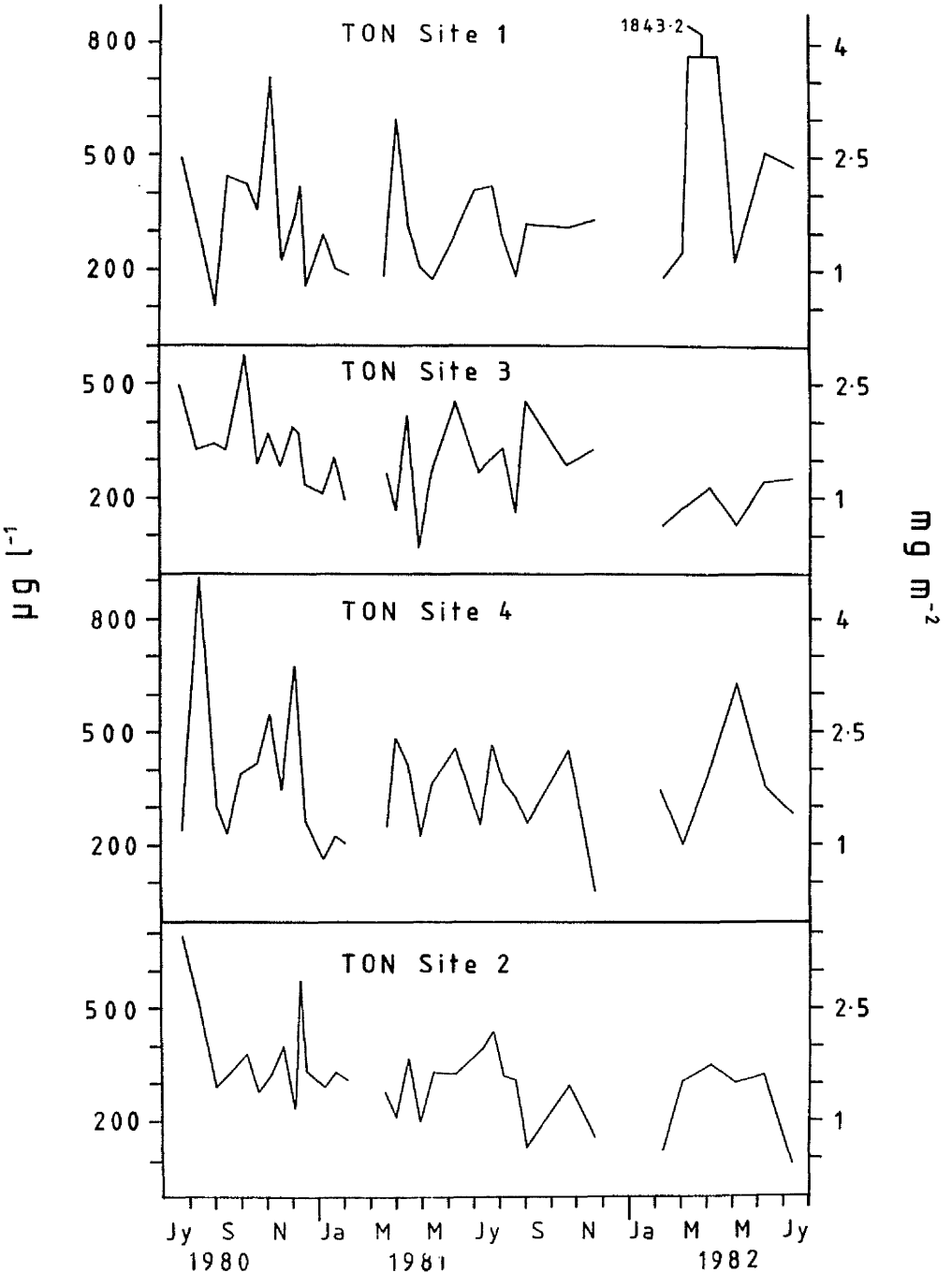

TON Site 1
1843·2
TON Site 3
TON Site 4
TON Site 2
800
500
200
4
2·5
1
Jy S N Ja M M Jy S N Ja M M Jy
1980
1981
1982
µg l⁻¹
mg m⁻²

Figure 4.19

Total organic nitrogen TON $\mu g\ l^{-1}$

July 1980 - July 1982

deviation 9.95). At site 2 the range was 0.49 -17.51 (mean 3.42, standard deviation 3.87). At site 3; range 0.006 -94.65, mean 9.33, s.d. 18.37 and at site 4; range 0.01-170.49, mean 9.78, s.d. 28.58.

4.2.10 Dissolved organic nitrogen, particulate organic nitrogen and total organic nitrogen (DON, PON, TON).

Dissolved organic nitrogen (DON) accounted for roughly half the total dissolved nitrogen of the surface layer of the Dubh Lochan and ranged from 5.1 μg N l^{-1} to 1.68 mg N l^{-1} (Fig. 4.17). At sites 1,2 and 4 fluctuations in DON reflected fluctuations in DOC. Maxima in DON were observed in spring, summer and after overturn indicating that DON levels are linked to productivity.

Particulate organic nitrogen (PON) levels ranged from 15.48 μg l^{-1} to 411 μg l^{-1} (Fig. 4.18).

Total organic nitrogen (TON) levels reflected DON levels (Fig.4.19). Comparison of TON with rainfall indicated that high TON usually occurred about 3-4 weeks after high rainfall.

4.2.11 Carbon to nitrogen ratios.

DOC:DON ratios for the Dubh Lochan gave an overall average of 46.6:1 (Table 4.5). This indicates that the major part of the dissolved organic load was highly refractory, being humic in nature and of allochthonous origin. If the most extreme ratios are ignored, this average falls to 27:1 indicating that there are periods when organic compounds which are autochthonous in origin and so, highly labile, are present in quantity. High C:N ratios were found after ice-melt and in early spring coinciding with high rainfall and high influx through the inlet and land drainage as snow melted on higher ground so bringing in highly refractory allochthonous compounds. High ratios in late summer/autumn are indicative of the gradual degradation of the organic load to more refractive compounds. Low C:N ratios indicated the release of highly labile compounds either as a result of photosynthesis of the macrophyte flora (summer), senescence (late summer and autumn) or wind-induced mixing re-suspending partly degraded organic compounds.

Table 4.4

DOC:POC ratios

Date	Site 1	Site 2	Site 3	Site 4
24.7.80	3.60	1.20	11.57	1.78
13.8.80	4.47	2.03	4.37	2.00
4.9.80	2.61	5.06	1.34	2.12
17.9.80	2.67	1.65	2.01	2.66
9.10.80	2.38	1.28	12.40	2.20
23.10.80	16.37	4.70	4.39	1.94
6.11.80	3.25	1.38	2.27	0.01
20.11.80	1.52	2.39	3.43	6.59
4.12.80	3.21	1.71	23.42	10.26
11.12.80	4.47	1.52	2.73	4.61
18.12.80	0.25	1.34	6.21	3.75
8.1.81	2.14	1.48	94.65	8.26
22.1.81	4.21	2.19	0.32	3.61
5.2.81	0.025	2.13	2.73	8.28
19.3.81	0.48	2.89	1.68	0.10
2.4.81	0.70	7.28	2.63	(POC=0)
16.4.81	3.77	3.90	0.49	3.34
30.4.81	0.71	2.15	1.23	0.14
14.5.81	1.15	2.18	2.28	170.49
28.5.81	0.79	1.09	1.23	2.47
10.6.81	1.40	2.46	2.51	3.24
24.6.81	1.20	1.13	1.16	0.08
9.7.81	4.94	17.51	1.12	3.21
23.7.81	7.34	3.20	1.85	27.74
6.8.81	3.80	1.26	7.33	3.41
20.8.81	59.91	13.60	8.88	3.20
3.9.81	1.50	6.07	2.01	0.23
22.10.81	1.42	0.97	41.23	11.25
22.11.81	0.024	1.15	0.66	0.06

Table 4.4 (continued)

Date	Site 1	Site 2	Site 3	Site 4
27.1.82		1.46		
11.2.82	1.50	5.79	5.03	19.71
4.3.82	4.49	0.49	5.17	7.43
6.4.82	4.37	13.97	4.60	13.51
6.5.82	0.774	2.07	3.54	2.38
9.6.82	1.17	1.61	57.18	2.21
13.7.82	0.98	0.92	0.006	0.14
range				
from	0.024	0.49	0.006	0.01
to	59.91	17.51	94.65	170.49
$\bar{\chi}$	4.39	3.42	9.33	9.78
σ_n	9.95	3.87	18.37	28.58
σ_{n-1}	10.09	3.92	18.63	29.01

Table 4.5

DOC:DON ratios

Date	Site 1	Site 2	Site 3	Site 4
24.7.80	13.81	6.91	16.79	21.29
13.8.80	21.02	11.62	17.75	8.75
4.9.80	368.16	30.39	16.70	20.72
17.9.80	16.06	20.19	27.89	34.16
9.10.80	13.47	23.49	15.25	16.25
23.10.80	29.40	28.01	22.48	17.08
6.11.80	9.01	13.04	22.73	0.18
20.11.80	30.00	15.72	32.06	18.11
4.12.80	17.45	22.11	28.81	23.05
11.12.80	17.20	9.81	16.19	14.42
18.12.80	225.10	20.46	34.77	25.97
8.1.81	17.06	16.79	36.55	35.36
22.1.81	26.15	15.74	13.07	25.47
5.2.81	89.95	21.11	21.39	30.17
19.3.81	33.05	31.46	44.67	31.00
2.4.81	124.37	35.16	90.79	14.34
16.4.81	24.16	27.69	9.02	21.55
30.4.81	24.08	26.95	714.90	27.67
14.5.81	82.58	25.33	55.13	19.30
10.6.81	17.42	16.53	11.26	15.52
9.7.81	12.32	26.08	23.21	142.15
23.7.81	15.35	13.51	16.57	19.06
6.8.81	21.79	12.50	22.45	38.59
20.8.81	56.94	17.43	54.91	29.55
3.9.81	12.94	126.00	17.81	27.46
22.10.81	18.55	24.75	32.70	26.20
22.11.81	20.35	49.78	19.24	1052.00

Table 4.5 (continued)

Date	Site 1	Site 2	Site 3	Site 4
11.2.82	29.05	116.15	95.09	17.54
4.3.82	11.32	14.93	36.71	23.13
6.4.82	5.20	14.53	20.80	14.99
6.5.82	27.38	31.98	84.69	15.78
9.6.82	7.54	21.22	37.98	17.16
13.7.82	9.46	257.82	0.10	11.32
range				
from	5.20	6.91	0.10	0.18
to	368.16	257.82	714.90	1052.00
$\bar{x}$	43.64	34.70	51.83	56.22
σ_n	71.25	46.81	119.30	177.42
σ_{n-1}	72.35	47.53	121.15	180.17

overall mean = 46.60

if excessively high DOC:DON ratios are omitted, overall mean = 27.01

Table 4.6

TOC/TON ratios

Date	Site 1	Site 2	Site 3	Site 4
24.7.80	17.90	10.86	15.28	28.50
13.8.80	18.94	14.44	16.02	10.50
4.9.80	61.30	22.64	19.91	25.03
17.9.80	17.57	23.88	33.99	33.53
9.10.80	18.27	33.71	12.67	20.61
23.10.80	18.15	22.40	21.66	18.55
6.11.80	10.16	16.59	21.87	10.49
20.11.80	35.58	14.96	23.23	15.32
4.12.80	16.63	26.71	21.32	9.96
11.12.80	18.49	14.23	14.26	13.54
18.12.80	208.48	27.39	25.33	25.19
8.1.81	19.66	20.79	22.22	24.76
22.1.81	20.78	19.14	43.03	14.57
5.2.81	2717.76	17.73	16.73	26.38
19.3.81	56.97	23.42	34.75	161.12
2.4.81	16.75	23.65	44.71	6.98
16.4.81	16.26	16.79	18.85	10.42
30.4.81	36.25	20.16	92.92	160.52
14.5.81	55.26	23.12	22.51	13.27
10.6.81	20.25	16.02	11.04	11.04
9.7.81	9.17	15.04	12.45	30.77
23.7.81	15.99	13.78	18.49	11.93
6.8.81	25.68	16.05	16.95	21.17
20.8.81	28.63	15.09	32.94	24.02
3.9.81	15.92	32.62	17.25	86.41
22.10.81	22.07	33.77	20.16	12.89
22.11.81	603.73	65.88	37.16	645.61

Table 4.6 (continued)

Date	Site 1	Site 2	Site 3	Site 4
11.2.82	21.80	39.40	37.93	13.92
4.3.82	12.30	32.79	20.09	18.18
6.4.82	5.82	11.78	13.50	13.49
6.5.82	41.41	33.31	38.95	19.96
9.6.82	11.00	28.23	18.52	15.35
13.7.82	10.75	64.46	11.75	42.26
range				
from	5.82	10.86	11.04	6.89
to	2717.76	65.88	92.92	645.61
$\bar{\chi}$	128.03	24.57	25.10	48.37
σ_n	469.53	12.63	15.19	111.58
σ_{n-1}	476.81	12.83	15.43	113.30

overall mean = 56.52

omitting excessively high TOC:TON ratios, $\bar{\chi}$ = 23.45

TOC:TON ratios (Table 4.6) reinstate the above findings. The overall average ratio was 56.5:1, again reflecting the important contribution of humic compounds to the organic load. If the extreme values are ignored, this ratio falls to 24.5:1. The highest TOC:TON ratios were calculated at those instances when the highest levels of POC were recorded indicating that this highly refractory material was probably allochthonous in origin, having been washed into the lake.

4.3 DISCUSSION.

A comparison of the physical and chemical data for the surface layer with that of Klarer (1978) and Islam (1987) for the main body of the Dubh Lochan indicated the following :

The temperature and oxygen profiles measured in 1981 and 1982 showed little change from those determined by Klarer (1978) and Islam (1987). Anoxia was measured in both years in the hypolimnion. Islam (1987) stated that the development of anoxic conditions in the hypolimnion depended on the time of onset of stratification. When stratification was apparent within the first two weeks of April, anoxia of the hypolimnion occurred. If isothermal conditions persisted beyond the second week in April, anoxic conditions did not develop. In this study, anoxia of the hypolimnion was recorded irrespective of the time of onset of stratification. The development of temporary anoxic conditions in April were linked with the recorded rapid rise in surface temperatures.

The instances of surface cooling recorded in 1981 are an interesting phenomenon of the surface layer and are indicative of wind-induced cooling by evaporation. The weather on those days was cloudy and sometimes breezy. Tovbin (in Zaitsev, 1971) found that on calm sunny days the surface films of small freshwater ponds were slightly warmer than the underlying water mass but in cloudy weather, the temperature of the uppermost 4-5 mm decreased by 0.3-0.4^{o}C as a result of evaporation. The warming of the surface layer on sunny days as measured by Tovbin, Zaitsev (1971) and Hardy (1973) was not recorded in this study. It is probable that the Dubh Lochan is not sufficiently

sheltered for this to occur.

The surface tension depressions measured during September 1980 and September 1982 were indicative of a lake dystrophic in nature, i.e. with a humic acid content, and a well-developed fringe of littoral flora and was obviously linked with biological productivity. Large depressions in the summer coincided with the time of maximum development of the littoral flora and the phytoplankton, particularly at sites 1 and 4 where the organic exudates of the littoral flora were responsible for s.t.d. in excess of 22 dyn cm^{-1}. During the recorded maxima of the phytoplankton in open water, the greatest s.t.d. were only 6 dyn cm^{-1}. These findings are in agreement with those of Hardmann (1941) who measured s.t.d. of between 5 and 20 dyn cm^{-1} among *Lemna*, *Potamogeton* and lilies and s.t.d. of up to 6 dyn cm^{-1} in dystrophic lakes as opposed to only 1 dyn cm^{-1} in clear-water lakes. She concluded that humic acids could depress the surface tension. Goldacre (1949) also reported high s.t.d. among littoral flora and he concluded that the resultant capillary wave damping assisted the flora by reducing lateral movement and hence possible damage.

Nutrient analyses indicated that the seasonal patterns and concentration ranges of silicate-silica and nitrate-nitrogen in the surface layer was similar to that observed by Klarer (1978) for the epilimnion in general. Islam (1987) reported higher levels of both nutrients. While Klarer (1978) reported low levels of nitrite-nitrogen (up to 2 $\mu g\ l^{-1}$) no such observation was made in the top 5 mm during this study.

The surface layer phosphate-phosphorus levels recorded during this survey were higher than those found by both Klarer (1978) and Islam (1987). Also, a seasonal pattern was evident. It is probable that the low phosphate-phosphorus content measured in the spring of 1982 was linked to a lack of an increase in its concentration in the surface layer at autumn overturn the previous year. This, in turn, may have influenced the phytoplankton biomasses measured in 1981 and 1982. Klarer (1978) recorded up to 20 $\mu g\ l^{-1}$ in surface waters with no seasonal pattern and Islam (1987) reported finding only a maximum of 4 $\mu g\ l^{-1}$ in the hypolimnion. It is possible that the surface layer could

be an important source of phosphorus, loosely bound to colloidal organic acids. Hutchinson (1967) indicated that it is associated with brown organic matter and Ohle (1934) has recorded greater levels of soluble phosphate-phosphorus in humic lakes than in clear water lakes.

The non-seasonal fluctuations in ammonia-nitrogen observed in the surface layer during this study were also reported by Klarer (1978) and Islam (1987) in the epilimnion. Both reported that the main bulk of ammonia-nitrogen was to be found in the hypolimnion. Yet, a greater concentration of ammonia-nitrogen was found at the surface layer in this study than previously reported.The maximum level recorded by Islam (1987) was 20 $\mu g\ l^{-1}$. Again, possible surface enrichment associated with the organic nature of the surface layer may have occurred.

The pattern and range of conductivity recorded in this study was similar to that found by Islam (1987). Klarer (1978) reported a much lower range (45-75 $\mu S\ cm^{-1}$). The seasonal pattern of pH change found by both Klarer (1978) and Islam (1987) was not observed in this study. During periods of high biological activity pH was depressed rather than enhanced. One could postulate that errors due to the unsuitability of the electrode were responsible but a comparison of the pH data with free carbon dioxide acidity showed that during periods of biological activity (spring-summer) a high CO_2 content was concurrent with a low pH and visa versa. It therefore seems that during this period, in this poorly buffered system, the pH was more susceptible to changes brought about by external sources e.g. rainfall, inflow via the inlet stream or surface runoff and turbulence effects increasing the free carbon dioxide content, than to changes brought about by internal biological activity. During the spring and summer the lower inputs from the drainage basin and the effective cation exchange mechanism of the littoral flora, *Sphagnum* in particular, combined with high carbon dioxide availablity as CO_2 and the low phytoplankton biomass recorded in 1982 (as compared with 1981) could have led to an overall decrease in pH.

The total inorganic carbon levels determined in this study were of a similar order to those obtained by Klarer (1978) who measured between 2 and 20 mg C l^{-1} throughout the water body. No data is available from

Islam's (1987) study. Klarer (1978) concluded that the gradual decrease in TIC in the epilimnion during the summer months was linked to increased photosthynthetic activity. No such relationship was observed in this study and it is probable that the observed variations in TIC and pH during this period were caused by similar mechanisms, as outlined above.

The dissolved organic carbon content of the surface layer of the Dubh Lochan during this sampling programme was of a similar order to that measured by Islam (1987) (1.9-9.4 mg l^{-1}) for the main body of water but unlike Islam (1987) no seasonal trend was observed. Rather, the data supports Wetzel's (1975) statement that the constancy of the DOC pool measured throughout the seasons is indicative of organic compounds which are primarily refractory in nature. Point increases and decreases were therefore indicative of sudden influxes and efluxes (by e.g. sedimentation) of either labile compounds of autochthonous origin or of refractory humic substances of allochthonous origin. Since the turnover time of labile DOC is less than 48 h (Wetzel, 1975), it is highly unlikely that a fortnightly sampling programme would pick up the rapid oscillation in labile DOC and POC which represent the major C pathways and energy fluxes of lakes. This can be supported by the observation of a general, slight, upward trend in DOC concentration indicative of a gradual build-up of refractory compounds.

The calculated C:N ratios were also indicative of the refractory nature of the DOM and POM of the Dubh Lochan. Islam (1987) measured C:N ratios of 3.29-28.9 in seston collected at 1m and of 2.3-18.9 from seston collected at 9 m, i.e. the nitrogen content of the main body of water was higher than that observed at the surface layer. One could argue that either the surface layer is a site of preferential accumulation of refractory compounds of allochthonous origin or that the degradation of more labile autochthonous matter in the surface layer is much more intense. The humic nature of the Dubh Lochan and the perturbation of the pH suggests that the surface layer is probably influenced more by allochthonous than autochthonous sources. The distribution of POC and PON particularly at site 4 reflects the importance of the littoral community as the main source of autochthonous material. This material may have been lost to the

sediments and later resuspended during overturn and during periods of strong winds (e.g. high PON in December 1980). Yet, the highest POC concentrations coincided with the highest C:N ratios indicative of periods of influx of large amounts of refractory material through surface runoff which then collected at the surface layer. The lower POC and PON levels recorded at sites 2 and 3 reflect the much smaller contribution of the phytoplankton to the organic matter pool of the surface layer.

Chapter 5

Biological aspects : The phytoplankton and plant pigments

Table 5.1

Species composition of the phytoplankton of the Dubh Lochan.

CHLOROPHYTA

Actidesmium hookeri Reinsch. *

Ankistrodesmus falcatus (Corda) Ralfs.

Arthrodesmus bifidus var *lativergens* Breb.

Incus (Breb) Hass. var *minor*

var *Ralfsii*

octocornis Ehr.

triangularis Lagerh. var *subtilis*

Asterococcus limneticus G. M. Smith

Botryococcus Braunii Kutz.

Chaetosphaeridium globosum (Nordst) Klebahn

Characium ornithocephalum A. Br.

Chlamydomonas sp

Dinobryonii G. M. Smith

globosa Snow

Chlorella ellipsoidea Gerneck

Cladophora fracta var *lacustris* (Kutz.) Brand. *

Closterium didymotocum Corda

gracile Breb.

Kutzingii Breb.

setaceum Gronbl.

striolatum Ehr.

toxon W. West

Cosmarium amoenum Breb.

crenatum Ralfs.

contractum var *ellipsoideum* Delp.

depressum var *planktonicum* (Nag.) Lund

margaritiferum Turp.

moniliforme Turp.

Ralfsii Breb.

subtumidum Nordst *

tinctum Ralfs *

Cylindrocystis brebissonii Menegh.

Docidium baculum Breb.

Euastrum bideltatum Nag.

denticulatum (Kirchn.) Gay

didelta (Turp.) Ralfs

pulchellum Ralfs

Golenkinia radiata Chod.

Gonatozygon sp *

Hormodium sp *

Keriochlamys styrica Pascher

Mesotinaeum sp *

Micractinium sp

Micrasterias rotata Grev. *

truncata Bulnh. *

Microspora Willeana Wittr.

Mougeotia sp *

Netrium digitus Ehrg. Itz. and Roth.

oblongum (de Bary) Lutdkem var *cylindricum*

Oocystis lacustis Chod.

rhomboidea Fott

solitaria Wittrock

Pediastrum boryanum (Turp.) Meneghini

Penium cruciferum (de Bary) Meneghini

margaritaceum Ehr. *

Perepyxis sp

Pleurodiscus sp *

Pleurotinaeum coronatum (Breb.) Rabenh.

nodosum Gronbl. *

Pyrobotrys incurvata Arnold

Rhaphalodopsis sp

Scenedesmus denticulatus Lagerheim

quadricauda (Turp) de Breb. *

Schroederia setigera Lemm.

Sphaerocystis schroeteri Chodat

Sphaerozosma vertebratum Breb.

Spyrogyra sp

Spondylosium planum (Wolle) West and West

Staurastrum anatinum forma *paradoxum* Brook
brevispina Breb.
hirsutum Ehr.
inconspicuum Not.
orbiculare Ralfs
planktonicum Teiling
polymorphum Breb.
sebaldi Krieg and Bourr. *
Stigeoclonium tenue Kutz.
Tetraedron duospinum Ackley
minimum (A. Br.) Kutz.
Tetrahymena sp
Xanthidium antilopaeum (Breb.) Kutz. *
Zygnema sp

BACILLARIOPHYTA

Achnanthes flexella (Kutz) Brun.
lanceolata Breb.
saxonica Krasske
Amphora communata Grun.
ovalis Kutz.
Anomoeneis serians (Breb.) Cleve
Ceratoneis Arcus Kutz.
Cyclotella glomerata Bach.
operculata Kutz.
Cymbella aequalis W. Smith
bipartata Mayor
gracilis Rabenh.
prostrata (Berk.) Cleve
ventricosa Kutz.

Eunotia curvata (Kutz.) Langest
exgracilis (W. Smith) A. Cl.
faba (Ehr.) Grun.
lunaris (Ehr.) Grun.
minutisima A. Cl.
monodon Ehr.
parallela Ehr.
pectinalis var *minor* Ralfs
var *undulata* Ralfs
serra Ehr.
tenella (Grun.) A. Cl.
Fragilaria capucina Desmaz.
crotonensis Kitton
virescens Ralfs
var *capitata*
Frustulia rhomboides var *saxonica* (Rabh.) De Toni
Gomphonema acuminatum Ehr.
gracile Ehr.
lanceolatum Ehr.
Hantzschia amphioxus (Ehr.) Grun.
Melosira islandica Otto Muller *
italica Ehr. Kutz. *
Navicula sp
cuspidata Kutz. *
cryptocephala Kutz.
lanceolata (Ag.) Kutz.
oblonga Kutz.
subtillissima Cleve
Neidium affine (Ehr.) Cleve
Nitzschia lanceolata W. Smith
Peroniopsis heribaudii (Brun. and Herb.) Hust.
Pinnularia biceps Greg.
gibba Ehr.
interrupta W. *Smith*
mesolepta (Ehr.) W. Smith
stauroptera (Rabh.) Cl.
viridis (Nitz.) Ehr.
Stauroneis anceps (Kutz.) Cleve

Stenopterobia intermedia (Lewis) Van Heurck *

Surirella elegans (Ehr.) *

linearis W. Smith

ovalis Breb. *

Tabellaria fenestrata (Lyngh.) Kutz. var *intermedia* Grun.

var *lacustris* Meister

flocculosa (Roth.) Kutz.

CYANOPHYTA

Anabaena cylindrica (Lemm.) Fogg. *

spiroides (Lemm.) Elenk. *

sp *

Aphanothece saxicola Naeg.

Calothrix epiphyta West and West

Chondrosphaeria sp *

Chroococcus turgidus (Kutz.) Naeg.

Gomphosphaeria lacustris Chodar

naegeliana Unger

Hapalosiphon intricatus West and West

Merismopedia elegans Braun

Microcystis aeruginosa (Kutz.) Elenk.

Oscillatoria tenuis Ag.

Stigonema ocellatum (Dillw.) Thuret

Synechococcus cedrorum Saur.

major Lagerh.

CHRYSOPHYTA

Dinobryon divergens Imhof

Mallomonas acaroides Perty

longiseta Lemm.

producta Iwan

Pseudokephyron sp

Vaucheria sp *

CRYPTOPHYTA

Cryptomonas erosa Ehr.
Marssonii Skuja
ovata Ehr.
Rhodomonas minuta Skuja

DINOPHYTA

Ceratium hirundinella Mull.
longiseta Mull.
Glenodinium sp
bernardinense Ehr.
Gonyaulax sp
Gymnodimium sp
Peridinium bipes fa. *globosum* Stein
cinctum (Mull.) Ehr.
lubiniensiforme Ehr.
willei Huitfeld - Kasse

EUGLENOPHYTA

Euglena spp
Trachelomonas oblonga Lemm.
volvocina Ehr.

RHODOPHTYA

Batrachospermum moniliforme Roth.

PHAEOPHYTA

One member of the family Ectocarpales

MISCELLANEOUS

On rare occasions the following fungii were observed in surface layer samples and have been identified according to Ingold (1975)

Lemonniera sp
Tricladium sp
Trisulcosporium sp
Trisulcosporium acerinum
Varicosporium giganteum

A microsporidic parasite of *Cyclops* . *Marssoniella elegans* (= *Gurleya elegans*) (Lemm.) Komarek and Vavra. Once thought to be a member of the Cyanophyta of the genus *Gurleya*.

* Found only rarely and in the 61 sedimented samples used for zooplankton enumeration.

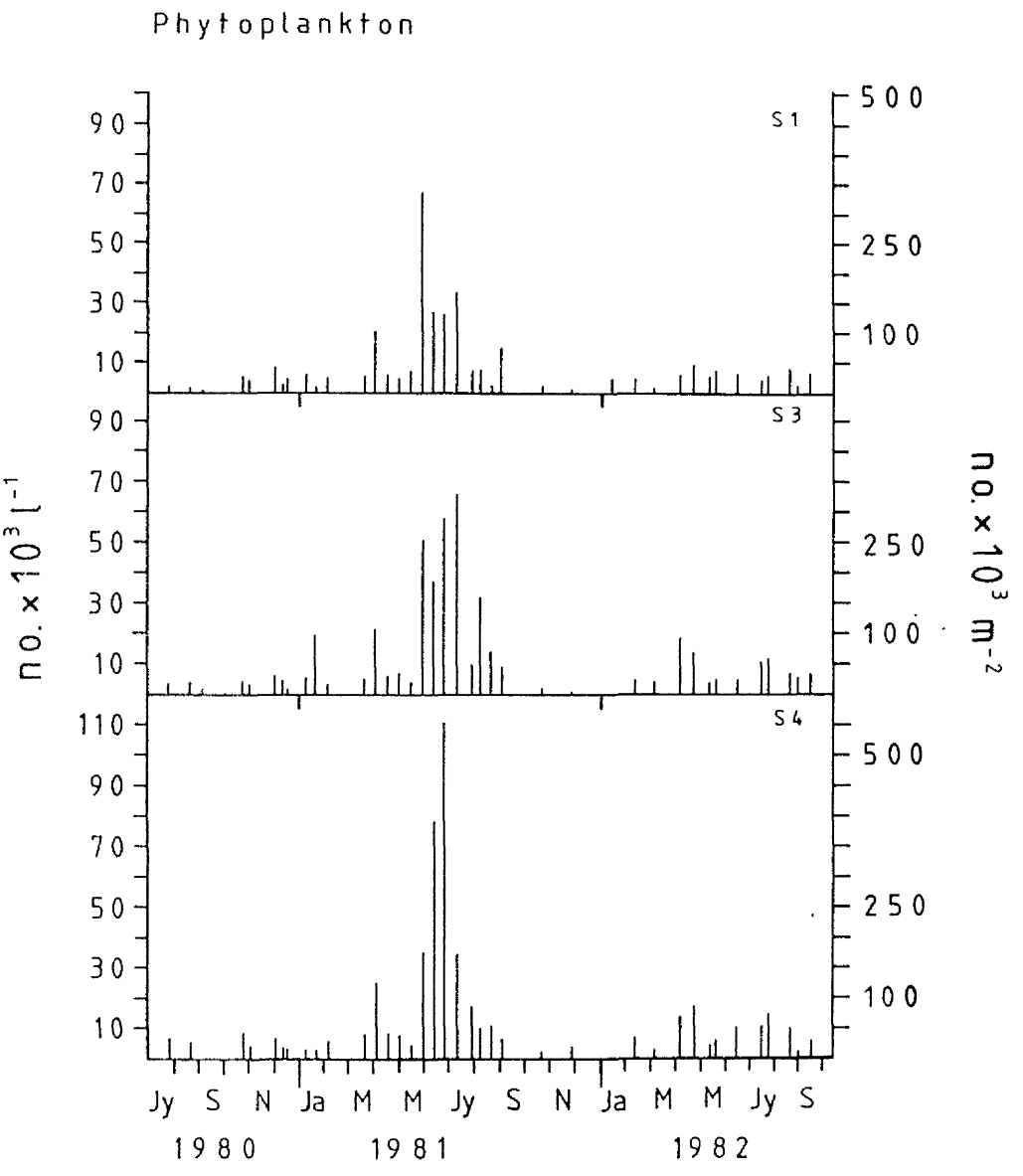

Phytoplankton
S1
S3
S4
90
70
50
30
10
110
500
250
100
no. x 10³ l⁻¹
no. x 10³ m⁻²
Jy S N Ja M M Jy S N Ja M M Jy S
1980
1981
1982

Figure 5.1

Phytoplankton biomass, surface sites 1, 3 and 4

July 1980 - September 1982

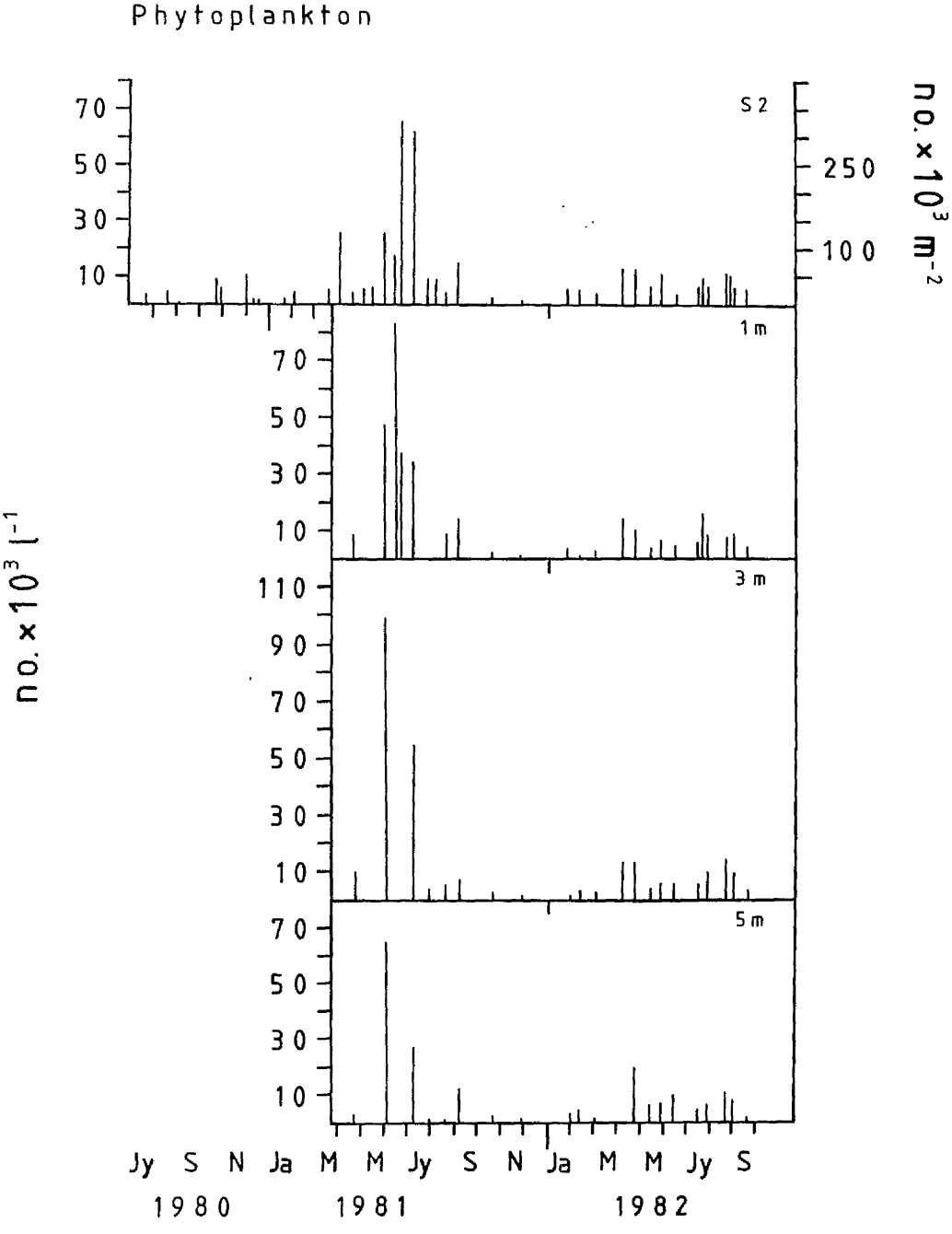

Phytoplankton
S2
1m
3m
5m
70
50
30
10
250
100
110
90
no.×10³ m⁻²
no.×10³ l⁻¹
Jy S N Ja M M Jy S N Ja M M Jy S
1980
1981
1982

Figure 5.2

Phytoplankton biomass, surface site 2 and at depth

July 1980 - September 1982 at surface

April 1981 - September 1982 at depth

5.1 THE PHYTOPLANKTON.

5.1.1 Taxonomic composition.

A species list of those phytoplankton identified in the Dubh Lochan is presented in Table 5.1. In total 182 different algal species and varieties were identified. The distribution among the divisions was as follows; Chlorophyta 82, Bacillariophyta 59, Cyanophyta 16, Dinophyta 10, Chrysophyta 6, Cryptophyta 4, Euglenophyta 3, Rhodophyta 1 and Phaeophyta 1. Added to this list should be unidentified green flagellates (one of which was probably the motile stage of *Sphaerocystis*). 28 species of Chlorophyta, 9 species of Bacillariophyta, 7 species of Cyanophyta, 2 species of Chrysophyta, 1 species of Cryptophyta, 5 species of Dinophyta, 1 species of Euglenophyta and 1 unidentified member of the Phaeophyta were added to the lists of Klarer(1978) and Islam(1987). 34 species of Chlorophyta, 14 species of Bacillariophyta, 10 species of Cyanophyta and 1 species of Rhodophyta listed by Klarer (1978) and Islam (1987) were not observed.

5.1.2 General features.

From July 1980 to December 1980 low phytoplankton counts were measured at all four surface sites (Figs. 5.1 and 5.2). Total phytoplankton density at site 1 varied between 658 units l^{-1} (4th September, high silt load) and 8,649 units l^{-1} (4th December, thin layer of ice).

At site 2 phytoplankton numbers varied between 634 (4th September) and 10,201 units l^{-1} (4th December, open water, ice free). At site 3 the range was from 1,384 (18th December, no ice) to 6,082 l^{-1} (4th December, thin ice).

High silt levels at site 4 prevented counting on the 4th September. The low particulate organic levels on this date (see sections 4.2.9 and 4.2.10), together with microscopic examination, indicated that this particulate matter was siliceous in origin. Phytoplankton numbers varied between 3,495 (18th December) and 7,943

l^{-1} (23rd October).

1981 was characterised by four peaks in phytoplankton biomass (Figs 5.1 and 5.2). The first, on the 22nd January at site 3, occurred under ice (total population 19,241 l^{-1}). The second occurred at all four surface sites on the 2nd April (20,323 - 25,010 l^{-1}). The third was a large increase in algal density which started at the end of May and extended until the beginning of July. At site 1, the maximum phytoplankton population was measured on the 28th May (67,474 l^{-1}). At sites 2 and 4, maxima were measured on the 24th June (65,394 and 119,746 l^{-1} respectively) while the highest level measured at site 3 was on the 9th July (64,923 l^{-1}). Comparison with measurements made for site 2 at 1m, 3m and 5m depths showed a maximum number at 3m on the 28th May (97,897 l^{-1}) and at 1m on the 10th June (64,923 l^{-1}). Due to equipment failure and non-availability of equipment, results were not always available. A fourth increase in phytoplankton populations was measured at sites 1 and 2 on the 3rd September (15,598 l and 15,190 l^{-1} respectively) with a corresponding increase at 1m and 5m depths on that day (13,362 l^{-1} and 12,319 l^{-1}). By the 22nd November, before the onset of ice formation, surface phytoplankton numbers had fallen to between 870 (site 3) and 3,913 l^{-1} (site 4) and at depth, between 842 and 961 l^{-1}.

No large increases in the phytoplankton biomass as measured in 1981, were observed during the summer period of 1982. However the same trend in seasonal population increases was observed. Samples taken through the ice at site 2 on the 27th January showed a small increase in phytoplankton number just below the ice (surface; 5,031 l^{-1}, 1m; 3,763 l^{-1}, 3m; 1,298 l^{-1}, 5m; 2,923 l^{-1}). As in 1981, an increase in phytoplankton density was recorded in April. A peak in numbers was recorded at sites 2 and 3 on the 7th April (12,016 l^{-1} and 18,408 l^{-1} respectively). High silt load at 5m depth on the 7th April prevented counting of that sample.

The highest recorded values for sites 1 and 4 were measured on the 22nd April (9,487 l^{-1} and 17,135 l^{-1} respectively). Comparison with depth samples showed a high density at 1m on the 7th April (14,796 l^{-1}) and at 5m on the 22nd (19,009 l^{-1}). The summer increase in

phytoplankton was fragmented. Large populations were measured at sites 1 and 2 on the 26th May (7,234 l^{-1} and 10,451 l^{-1} respectively), at site 4 on the 18th June (10,686, with an increase at 5m depth to 10,713 l^{-1}) and at sites 3 and 4 on the 29th July (11,724 l^{-1} and 14,945 l^{-1} respectively). The most dense population found at depth was at 1m on the 22nd July (15,894 l^{-1}).

On the 11th August both surface (7, 251 l^{-1} to 11,098 l^{-1}) and depth (9,770 l^{-1} to 13,508 l^{-1}) populations were still high. A fall in surface population was measured on the 1st September (2,308 l^{-1} to 5,522 l^{-1}) but at depth, the populations remained high (8,306 l^{-1} - 9,069 l^{-1}). On the 16th September at the close of the experimental programme, the density of the phyoplankton at depth had fallen to between 2,192 l^{-1} and 4,160 l^{-1} while a slight increase in surface sample measurements was apparent (4,514 l^{-1} - 6,468 l^{-1}).

A comparison of surface populations throughout the experimental period indicated that the greatest densities were found at site 4, fewer at sites 3 and 2 and the lowest at site 1. The determination of the ratio of surface numbers to depth numbers (at 1m) for the period 16th April 1981 to 16th September 1982 indicated that, on occasion, surface accumulation was evident (Table 5.2). Ratios greater than 1.20 were calculated for summer 1981 at sites 2, 3 and 4, at sites 2 and 4 on the 22nd October and at sites 1 and 4 on the 22nd November, when algal numbers were low. The highest ratios were recorded immediately after ice melt, on the 11th February 1982, at all four sites (5.39 at site 1, 6.03 at site 2, 5.74 at site 3 and 7.68 at site 4). The surface accumulation of species throughout the rest of 1982 was much lower, only rising above two at site 4 on the 18th June.

Comparison between these "enrichment factors " at the four surface sites indicated that surface accumulation occurred more frequently at site 4 (on 12 out of 22 occasions), less frequently at sites 2 and 3 (on 9 out of 27 and 22 occasions respectively) and least at site 1 (on 6 out of 22 occasions). Also, on only one occasion did surface "enrichment" exceed two at sites 1, 2 and 3 (11th February) whilst "enrichment factors" greater than two were calculated on five occasions at site 4 (see Table 5.2). These values support the finding that

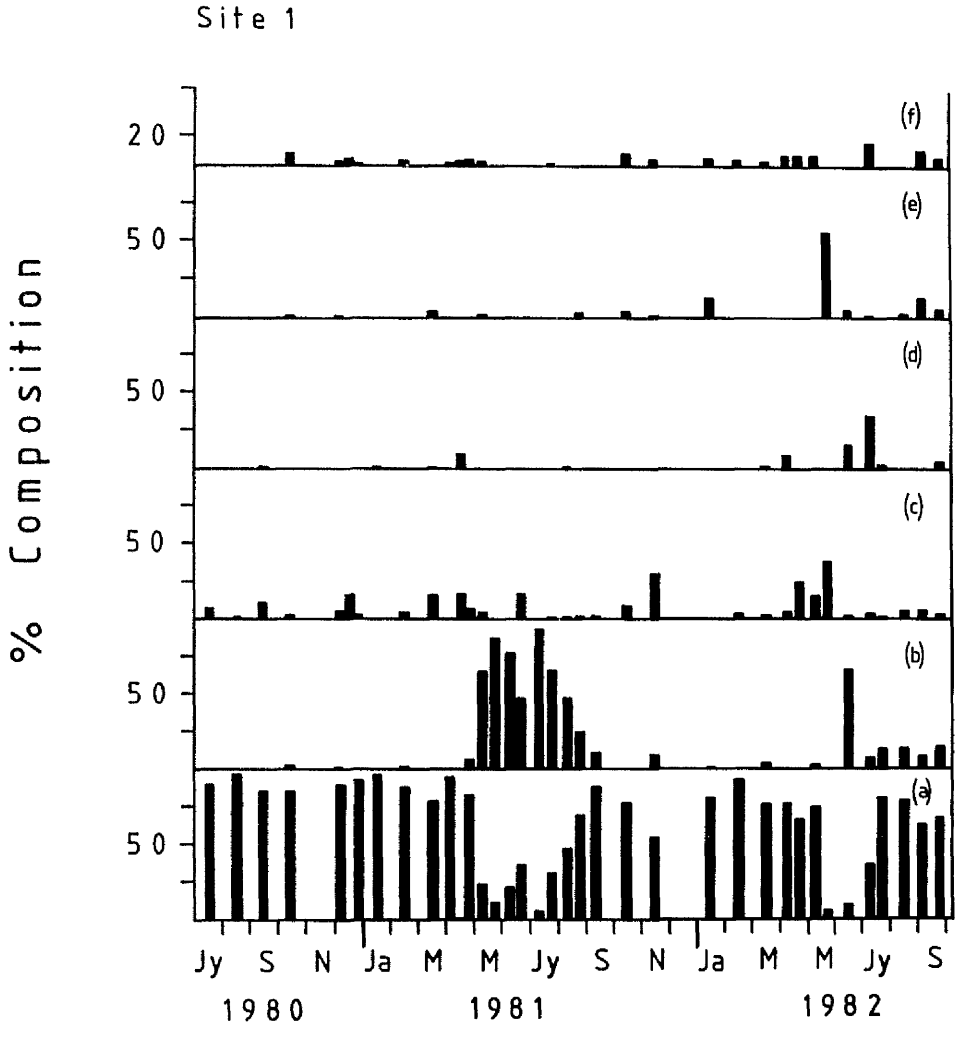

Site 1
% Composition
20
50
50
50
50
(f)
(e)
(d)
(c)
(b)
(a)
Jy S N Ja M M Jy S N Ja M M Jy S
1980
1981
1982

Figure 5.3

Percentage biomass composition of the phytoplankton, site 1.

a) Chlorophyta

b) Cyanophyta

c) Bacillariophyta

d) Dinophyta

e) Chrysophyta

f) Cryptophyta

g) Euglenophyta

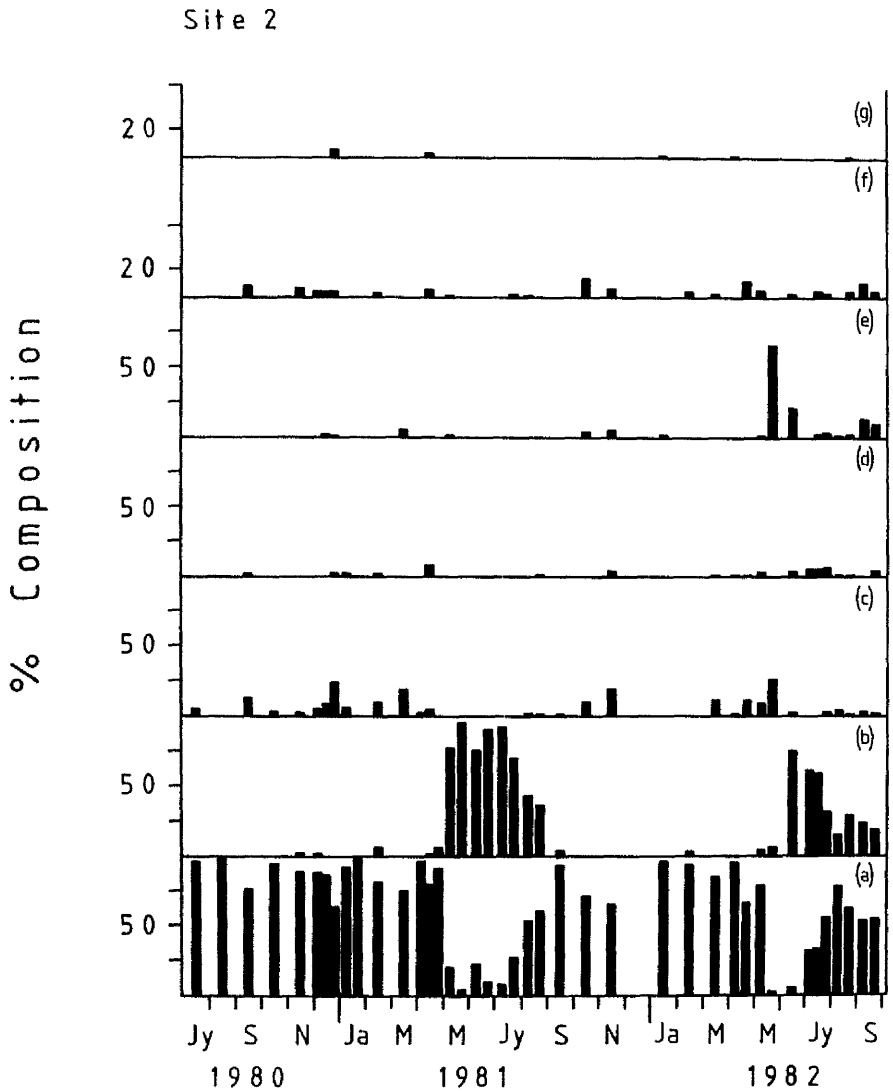

Site 2
% Composition
20
20
50
50
50
50
50
(g)
(f)
(e)
(d)
(c)
(b)
(a)
Jy S N Ja M M Jy S N Ja M M Jy S
1980
1981
1982

Figure 5.4

Percentage biomass composition of the phytoplankton, site 2.

a) Chlorophyta

b) Cyanophyta

c) Bacillariophyta

d) Dinophyta

e) Chrysophyta

f) Cryptophyta

g) Euglenophyta

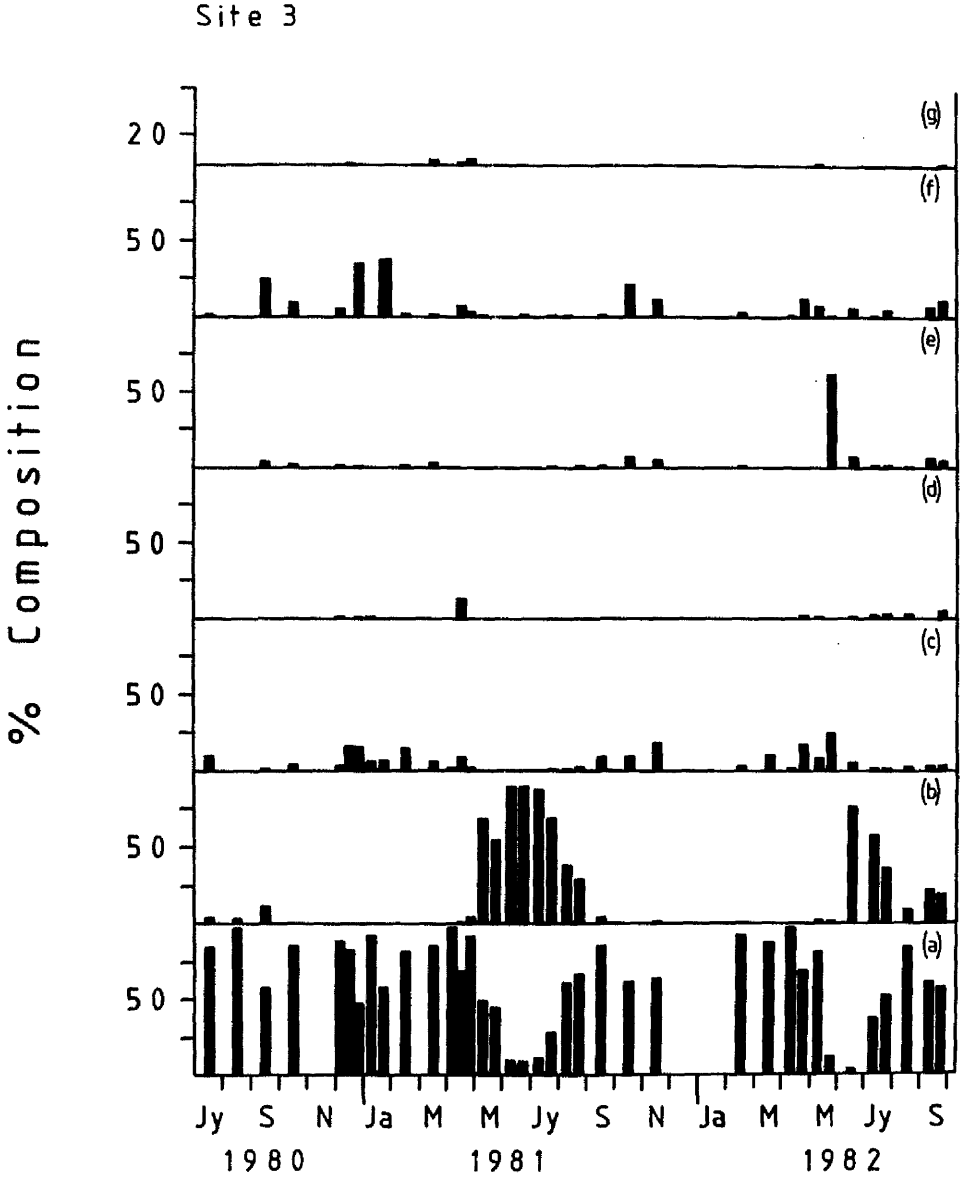

Site 3
% Composition
20
50
50
50
50
50
(g)
(f)
(e)
(d)
(c)
(b)
(a)
Jy S N Ja M M Jy S N Ja M M Jy S
1980
1981
1982

Figure 5.5

Percentage biomass composition of the phytoplankton, site 3.

a) Chlorophyta

b) Cyanophyta

c) Bacillariophyta

d) Dinophyta

e) Chrysophyta

f) Cryptophyta

g) Euglenophyta

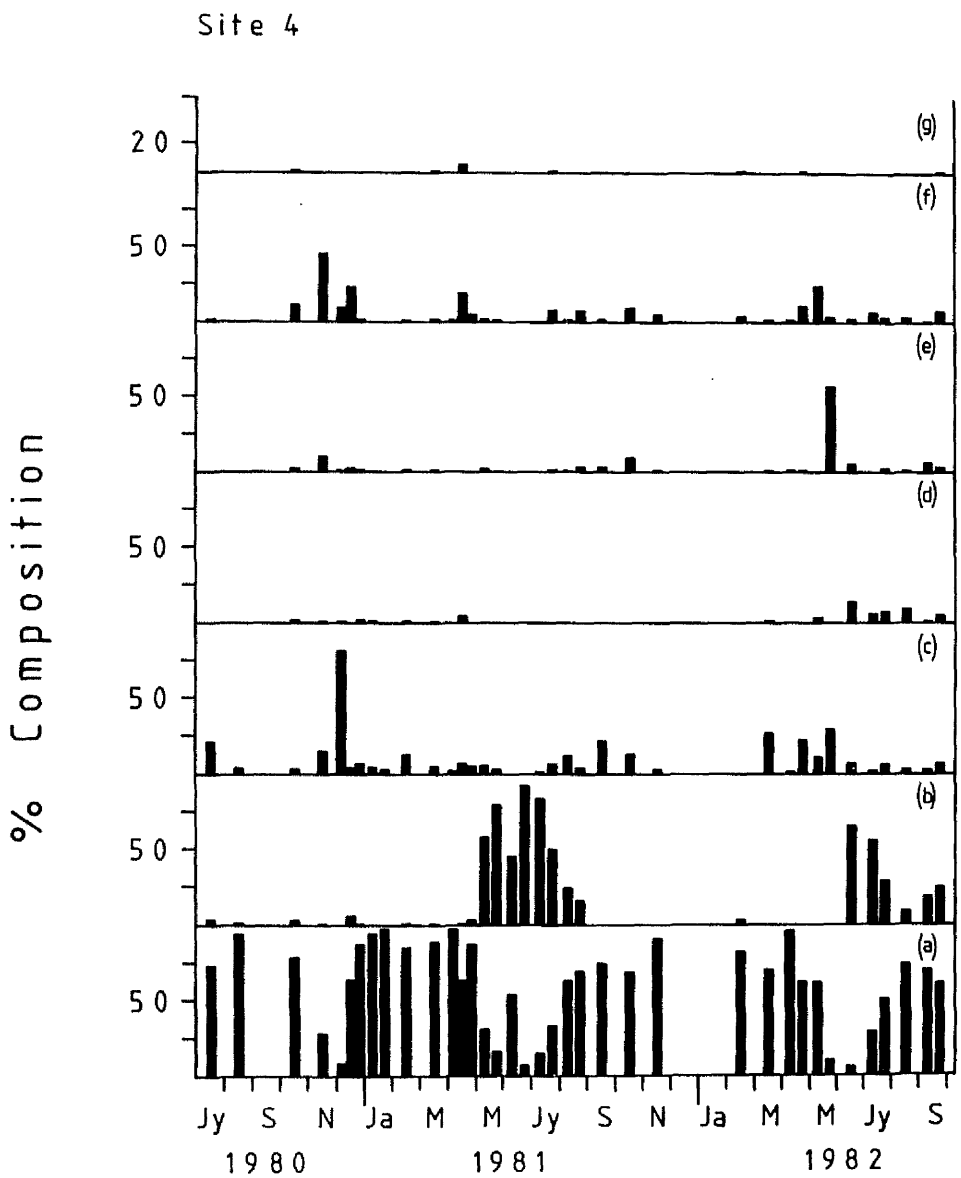

Site 4
% Composition
20
50
50
50
50
50
(g)
(f)
(e)
(d)
(c)
(b)
(a)
Jy S N Ja M M Jy S N Ja M M Jy S
1980
1981
1982

Figure 5.6

Percentage biomass composition of the phytoplankton, site 4.

a) Chlorophyta

b) Cyanophyta

c) Bacillariophyta

d) Dinophyta

e) Chrysophyta

f) Cryptophyta

g) Euglenophyta

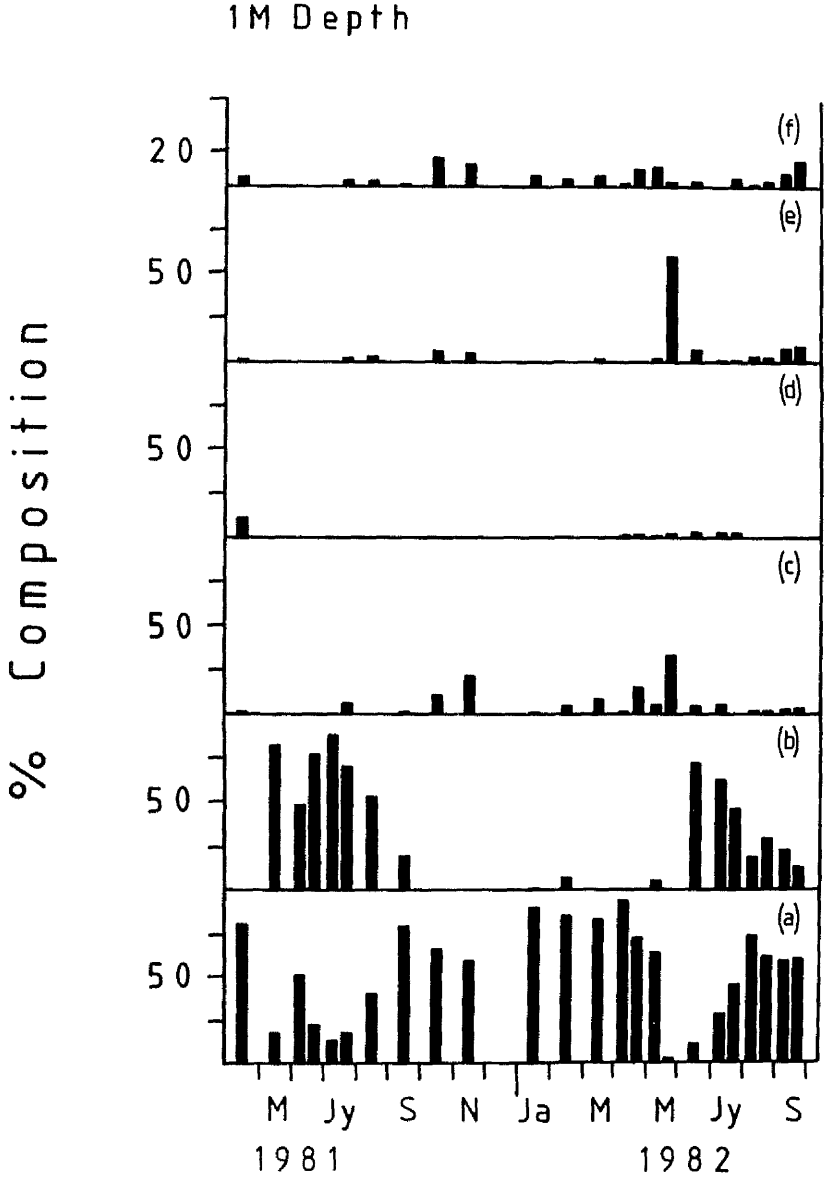

1M Depth
% Composition
20
50
50
50
50
(f)
(e)
(d)
(c)
(b)
(a)
M
Jy
S
N
Ja
M
M
Jy
S
1981
1982

Figure 5.7

Percentage biomass composition of the phytoplankton, 1m depth.

a) Chlorophyta

b) Cyanophyta

c) Bacillariophyta

d) Dinophyta

e) Chrysophyta

f) Cryptophyta

g) Euglenophyta

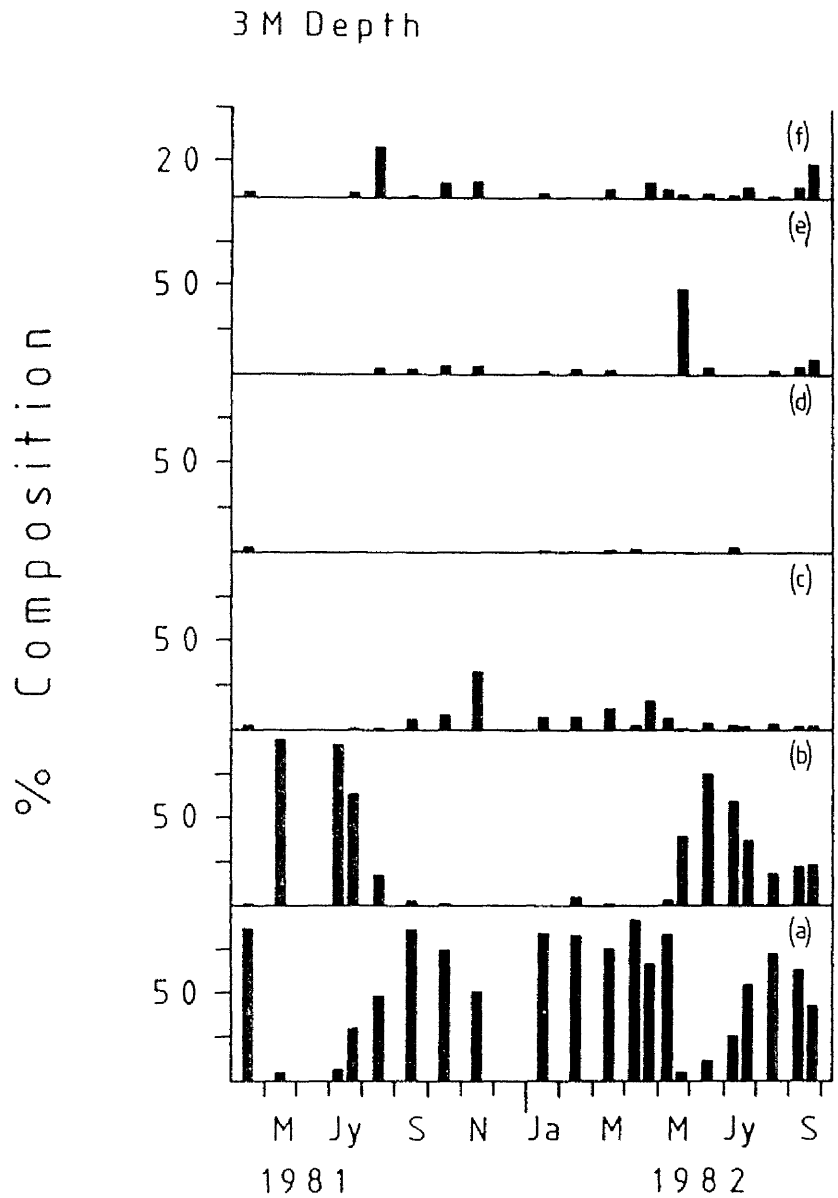

3 M Depth
% Composition
20
50
50
50
50
(f)
(e)
(d)
(c)
(b)
(a)
M Jy S N Ja M M Jy S
1981
1982

Figure 5.8

Percentage biomass composition of the phytoplankton, 3m depth.

a) Chlorophyta

b) Cyanophyta

c) Bacillariophyta

d) Dinophyta

e) Chrysophyta

f) Cryptophyta

g) Euglenophyta

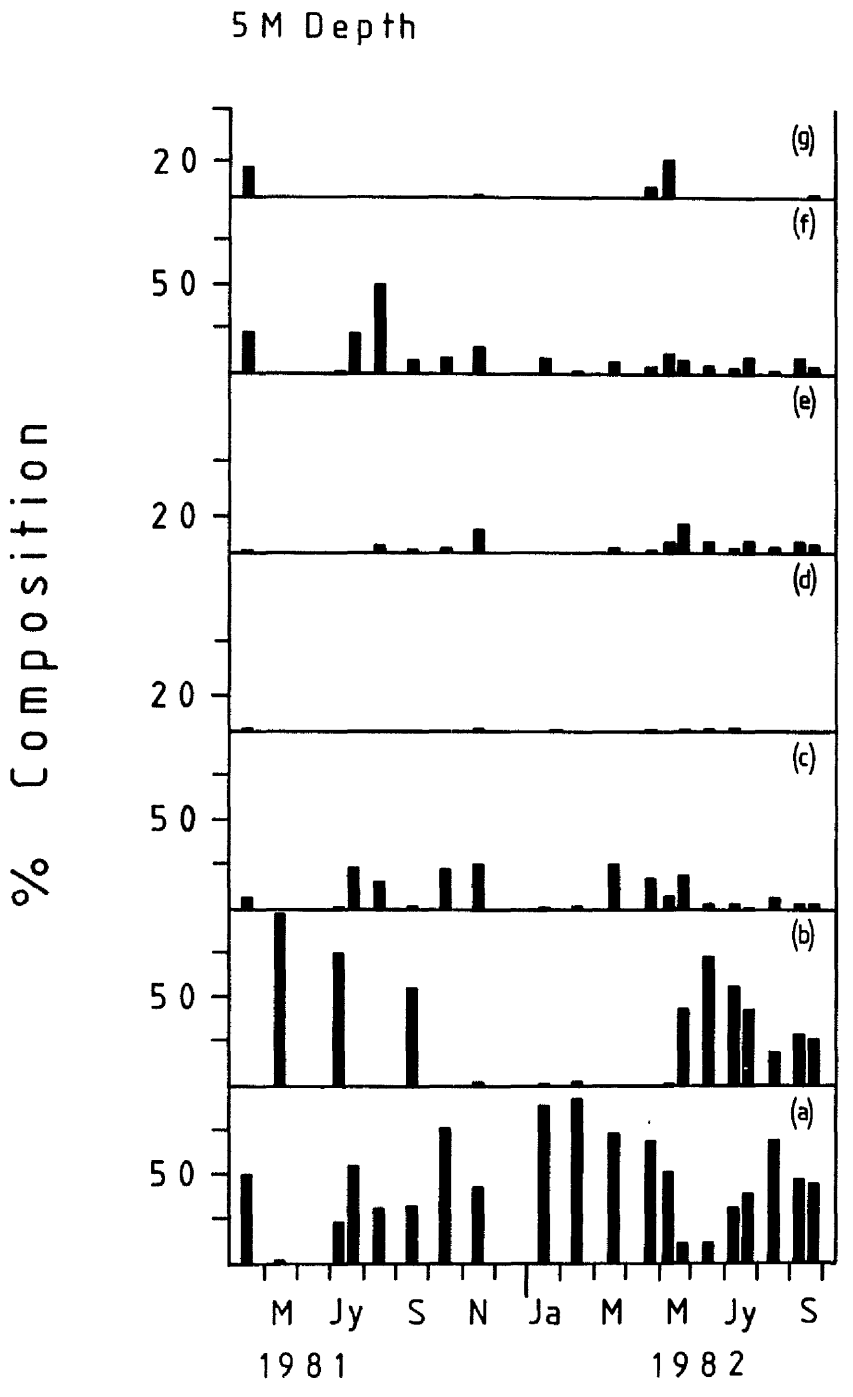

5 M Depth
% Composition
20
50
20
20
50
50
50
(g)
(f)
(e)
(d)
(c)
(b)
(a)
M Jy S N Ja M M Jy S
1981
1982

Figure 5.9

Percentage biomass composition of the phytoplankton, 5m depth.

a) Chlorophyta

b) Cyanophyta

c) Bacillariophyta

d) Dinophyta

e) Chrysophyta

f) Cryptophyta

g) Euglenophyta

surface populations were greatest at site 4 and lesser at sites 3, 2 and then 1.

5.1.3. Biomass composition

Examination of the percentage biomass composition of the phytoplankton indicated that members of the Chlorophyta were the dominant component (Figs 5.3 - 5.9). Only in the summer months did the Cyanophyta assume dominance.This peak in Cyanophyta coincided, in fact, with the peak in *Sphaerocystis* number. The Bacillariophyta, while being taxonomically numerous, were rarely present in numbers great enough to dominate the populations. The Chrysophyta and Cryptophyta though present throughout the experimental programme, were also rarely present in large numbers.

From July 1980 to December 1980 green algae, in particular *Sphaerocystis schroeteri* colonies and cells, were the dominant form. At site 1 (Fig 5.3) between 77.34% and 98.35% of the total phytoplankton population were Chlorophyta. Many diatom species were identified; *Achnanthes saxonica* (Fig 5.13), *Peroniopsis heribaudi*, *Cyclotella glomerata*, *C. operculata*, *Eunotia spp*, *Tabellaria flocculosa*, *T. fenestra*, *Stauroneis anceps*, *Frustulia rhomboides*, *Anomoeneis serians* and *Cymbella* spp. These species were numerically low, comprising less than 16.5% of the total population at any one time.

Only on the 24th July, the 4th September and the 11th December were total diatom counts high enough to comprise 8.52%, 11.60% and 16.46% of the total population respectively (Figs.5.3, 5.13). *Cryptomonas* spp were the most prominent representatives of the Cryptophyta (Fig.5.14). On the 23rd October they provided 7.44% (431 l^{-1}) and on the 11th December, 6.20% (828 l^{-1}) of the total populations. Representatives of the Cyanophyta, Euglenophyta, Dinophyta, Chrysophyta and Rhodophyta together comprised only 6.65% of the total biomass at any one time (23rd October). At site 2 the domination of the population by both *Sphaerocystis* colonies and cells was such that the Chlorophyta comprised between 63.44 and 99.64% of the total (Fig. 5.4). Only on the 18th December did the diatoms (as listed above) form a large part of the population (23.79%). *Cryptomonas* spp

formed between 0 and 6.67% (443 l^{-1} on the 6th November) of the this total. Again, representatives of the Chrysophyta, Dinophyta, Cyanophyta and Euglenophyta together constituted only 8.81% of the population at any one time (18th December).

At site 3, the green algae constituted between 47.54 and 96.64% of the total population (Fig. 5.5). On the 4th September as a result of a fall in the number of *Sphaerocystis* cells (Fig. 5.10) to 52 l^{-1} and an increase in the number of *Cryptomonas* spp. (429 l^{-1}) the Chlorophyta comprised 57.33% of the total population of and the Cryptophyta 25.02%. The diatoms ,as listed above, contributed to 11.42% of the population. On the 18th December only broken *Sphaerocystis* colonies were evident (Fig. 5.10). The green algae constituted only 47.54% of the total . *Cryptomonas* spp provided 35.24% (488 l^{-1}) and the diatoms (*A. saxonica, P. heribaudi* and *Eunotia* spp) 15.57% .

The percentage contribution of the Chlorophyta at site 4 ranged from 8.22% to 93.79% (Fig 5.6). On the 16th of November only broken *Sphaerocystis* colonies were evident (Fig. 5.10). Unicellular green algae (*Sphaerocystis* cells), *Oocystis* spp and *Penium cruciferum* constituted 28.70% of the population. *Cryptomonas* spp provided 45.07% (2,031 l^{-1}) and the diatoms (*A. saxonica, P. heribaudi, F. rhomboides* and *Eunotia* spp) together comprised 14.65% of the total.

The 4th December was noted for a reduction in the number of *Sphaerocystis* colonies and a lack of broken colonies (Fig 5.10). *Oocystis* spp. were the main representatives of the Chlorophyta which, together with a few *Sphaerocystis* , *Chlamydomonas* spp, *Pediastrum boryanum, Asterococcus limneticus* and *Ankistrodesmus falcatus,* made up only 8.22% of the total population. The diatom *Cyclotella glomerata* dominated the population (5,345 l^{-1}, Fig 5.13) and with *T. flocculosa, Achnanthes saxonica, Peroniopsis heribaudi* and *C. operculata* comprised 81.21% of the total. *Cryptomonas* spp provided 8.89%, *Mallomonas* spp 1.17% (Fig 5.6) and the dinoflagellates *Gymnodinium* sp and *Peridinium cinctum* the remaining 0.5% (Fig. 5.6). A gradual increase in the percentage contribution of the Chlorophyta to 87.01% was measured over the remaining part of December.

For the first four months of 1981 *Sphaerocystis* again dominated the phytoplankton population. Broken *Sphaerocystis* colonies (10,866 l^{-1}) together with *Asterococcus limneticus* (14 l^{-1}) comprised 56.55% of the population increase noted at site 3 on the 22nd January (Figs 5.10, 5.11). An increase in number of the cryptophyte *Rhodomonas minuta* was noted, such that it contributed to 36.27% of the total (Fig 5.5). The diatoms *A. saxonica, T. flocculosa, Eunotia* spp, *P. heribaudi* and *F. rhomboides* provided 7.15%. An increase in the number of *A. limneticus* (7,957 - 9,055 l^{-1} Fig. 5.11) and *Sphaerocystis* cells (11,518 - 15,092 l^{-1}) was responsible for the peak in phytoplankton number recorded on the 2nd April. These species together with *Closterium Kutzingii, Staurastrum anatinum, Oocystis* spp, *A. falcatus, Chlamydomonas* spp and *Scenedesmus denticulatus* comprised between 96.60 and 96.91% of the total biomass at the surface (Figs 5.3 - 5.6). At 1m, 3m and 5m depths the predominance of *Sphaerocystis* and *Asterococcus* was also recorded, such that the Chlorophyta provided 79.89%, 87.21% and 49.44% of the total populations respectively (Figs 5.7 - 5.9). At 5m *Trachelomonas* spp provided 17.32% and *Cryptomonas* spp 23.46% of the total.

From the end of May to the end of July a dramatic change in the composition of the phytoplankton population occurred; from 71% to 99.35% of the biomass being represented by Chlorophyta to 45.08% to 97.18% being Cyanophyta (Figs. 5.3 - 5.6 and 5.12). *Aphanothece saxicola, Synechococcus cedrorum* and *Synechococcus major* were the most prominent blue - greens (Figs. 5.3 - 5.9, 5.12). At site 1 on the 28th May, When the maximum number of phytoplankton was recorded (67,471 l^{-1}) 87.84% were these blue - greens .While the numbers of *Sphaerocystis* colonies (5,872 l^{-1}) and cells (1,532 l^{-1}) was not low, the green algae made up only 12.01% of the total. The highest levels of *Sphaerocystis* were recorded at site 4 and at 1m on the 10th June during the Cyanophyte "bloom" (35,575 l^{-1} and 38,485 l^{-1} and providing 54.22% and 51.75% of the total biomasses respectively).

On the 24th June, at sites 2 and 4 88.98% and 92.54% respectively were blue-greens. Green algae; *Sphaerocystis* colonies (5,302 l^{-1} and 6,792 l^{-1}) and cells (872 l^{-1} and 38 l^{-1}) together with *Mougeotia* sp, *P. boryanum, A. limneticus, Arthrodesmus* spp, *Chlamydomonas* spp, *Oocystis* spp, *C.Kutzingii, Staurastrum* spp and *Euastrum* spp contributed

9.47% and 7.08% respectively. At site 3, when the phytoplankton biomass was abundant (9th July), representatives of the Cyanophyta formed 87.91% of the population.

Throughout August and into September numbers of blue-greens fell and the green algae again assumed dominance. At 5m an increase in the numbers of *Cryptomonas* spp was recorded in August to the extent that they constituted 50.02% (409 l^{-1}) of the total population.

The increase in numbers measured in September at sites 1 and 2 was due to *Sphaerocystis* cells and colonies such that the Chlorophyta formed 88.10% and 93.23% of the biomass respectively. By the 22nd November, before the onset of ice formation, surface phytoplankton densities had fallen to between 870 and 3,913 l^{-1} and depth samples to between 842 and 961 l^{-1}.This was accompanied by an increase in the proportion of diatoms, *Cryptomonas* spp and Chrysophytes. Many diatom species were identified (*P. heribaudi, Cyclotella* spp, *A. saxonica, Eunotia* spp, *Pinnularia* spp, *Tabellaria* spp, *F. rhomboides, Navicula* spp, *Melosira italica, Ceratoneis Arcus* and *Gomphonema acuminatum*). They provided between 8.87% and 13.37% of the total population of the surface samples. The Chrysophyta (particularly *Mallomonas* spp) contributed between 4.05% and 8.92% and *Cryptomonas* spp provided between 8.33% and 21.17% to the total surface populations. At depth the diatoms constituted between 21.80% and 33.34%, the chrysophytes between 5.83% and 12.76% and the cryptophytes between 8.74% and 15.08%.

During 1982 a similar seasonal pattern in phytoplankton composition was observed. Samples taken through the ice at site 2 on the 27th January showed that *Sphaerocystis* cells dominated, providing 96.17% of the biomass at the surface (just under the ice) 90.11% at 1m, 84.21% at 3m and 88.51% at 5m. *Cryptomonas* spp numbers increased with depth (surface, 27 l^{-1}; 1m, 227 l^{-1}; 3m, 54.5 l^{-1} and 5m, 254 l^{-1}; Fig 5.14). *Mallomonas* spp were more abundant at the surface (surface, 81.7 l^{-1}; 1m, 22.7 l^{-1}; 3m, 18.2 l^{-1} and 5m, 0 l^{-1}) as were *Trachelomonas* spp (surface, 45 l^{-1}; 1m, 27 l^{-1}; 3m, 9 l^{-1}; 5m, 13.6 l^{-1}).

From January and until the middle of May, the green algae again dominated the phytoplankton population contributing between 61.83% and

97.04% to the total number. Diatom level varied between 1.22% and 26.34% of the total. *Cryptomonas* spp provided between 0.11% and 24.04%.

The population increase recorded in April was, as in 1981, attributable to increases in the number of *Sphaerocystis* cells and *Asterococcus* (Figs 5.10, 5.11). This was accompanied by an increase in the number of diatoms, particularly *Cyclotella glomerata* (Fig 5.13) which together with *Achnanthes saxonica, Peroniopsis heribaudi, Eunotia* spp, *Frustulia rhomboides, Tabellaria flocculosa, Navicula* spp, *Stauroneis anceps, C. operculata, Nitzschia lanceolata, Gomphonema gracile* and *Pinnularia* spp, provided between 10.51 and 24.04% of the total population. *Cryptomonas* spp contributed between 8.04 and 12.60% and the dinoflagellates, *P. cinctum, Gymnodinium sp* and *Glenodinium* sp, between 0.34 and 3.87%.

On the 22nd April, at 5m depth, a large number of unicellular green flagellates were observed (9,682 l^{-1}). It is probable that these were the motile stages of *Sphaerocystis*.

On the 13th May, at 5m depth, an increase in the numbers of *Trachelomonas* spp to their highest recorded level was noted (1,241 l^{-1}) such that they constituted 22% of the total population at that depth. On the 26th May an increase in the density of *Dinobryon divergens*, particularly at sites 1 and 2 was recorded to the extent ,with *Mallomonas* spp, that the Chrysophyta made up between 57.12% and 63.95% of the surface populations (Fig 5.14). *Sphaerocystis* numbers were very low ($< 57\ l^{-1}$) and the green algae contributed to only 2.39% and 11.96% of the populations. An increase in the proportion of Bacillariophyta was noted, to the extent that they contributed to between 24.50 and 36.97% of the biomass. At depth, an increase in the density of *Dinobryon* colonies was also noted and they formed 59.49% (3,699 l^{-1}) of the population at 1m and 49.69% (2,746 l^{-1}) at 3m. At 5m, the large number of *Trachelomonas* spp recorded on the 13th May were not found. *Dinobryon*, together with a few *Mallomonas* spp, constituted 16.14% (1,736 l^{-1}) of the population and a rising Cyanophyta population 43.97% .

In June the blue-greens, in particular *Aphanothece saxicola* and *Synechococcus* spp, dominated the population (65.08 to 76.72%) but did not achieve the high numbers recorded in 1981. Maxima of 6,931 l^{-1} at site 4 and 7,837 l^{-1} at 5m were measured on the 18th June, as opposed to 102,484 l^{-1} as recorded in June 1981. An increase in the dinoflagellate, *Gymnodinium,* was also recorded on the 18th June at sites 1 and 4 (1,044 l^{-1} and 1,462 l^{-1} respectively). The largest number recorded at depth was only 36 l^{-1} at 1m.

In July, a high *Gymnodinium* level was still maintained at site 1 (1,709 l^{-1}) but a decline to 595 l^{-1} was recorded at site 4. Low numbers were recorded at sites 2 and 3 (127 l^{-1} and 200 l^{-1}) while the largest number found at depth was 21.8 l^{-1} (3m). An increase in *Glenodinium* (Fig 5.15) was also recorded with the maxima at site 2 on the 18th June (114 l^{-1}) and at 3m on the 14th July (232 l^{-1}). *Gymnodinium* persisted at the surface sites during August, especially at site 4 (946 l^{-1}) with only a few recorded at depth (41 l^{-1} at 1m on the 18th).

A gradual reduction in blue-green algal population characterised July and August along with an increase in the *Sphaerocystis* population to maxima at the end of July and throughout August. As with the blue-greens, greatest densities of *Sphaerocystis* were much lower than those recorded in 1981. Also, the increase in the population occurred much later; June in 1981, late July and August in 1982. On the 29th July the highest number of *Sphaerocystis* was measured at site 4 (6,203 l^{-1}). By the 18th August the number of *Sphaerocystis* was still high (5,855 - 7,728 l^{-1}) but the maximum was recorded at 3m (9,605 l^{-1}).

The decrease in phytoplankton biomass recorded in September was accompanied by an increase in the proportion of cryptomonads and chrysophytes to between 4.84% and 20.10% and between 4.58% and 13.86% respectively.

Comparison of species numbers at the surface sites with those measured at 1m indicated that surface accumulation of some species occurred. This was particularly noticeable among the diatoms, especially *Achnanthes, Peroniopsis* and *Cyclotella*. *Achnanthes* was noted

Table 5.2

Phytoplankton enrichment ratios; surface/1m

Date	Site 1	Site 2	Site 3	Site 4
16.4.81	0.72	0.52	0.76	1.05
28.5.81	1.40	0.53	1.06	0.72
10.6.81	0.33	0.21	0.45	0.94
24.6.81	0.74	1.82	1.62	3.09
9.7.81	0.97	1.79	1.87	0.96
23.7.81	0.93	1.09	1.20	2.06
20.8.81	0.28	0.45	1.63	0.75
3.9.81	1.17	1.14	0.66	0.48
22.10.81	1.08	1.27	0.95	1.24
26.11.81	1.58	1.15	0.91	4.07
27.1.82		1.34		
11.2.82	5.39	6.02	5.74	7.68
4.3.82	0.91	1.63	1.55	1.31
7.4.82	0.52	0.81	1.24	0.93
22.4.82	0.79	0.94	1.14	1.43
13.5.82	1.65	1.43	0.95	1.06
26.5.82	1.17	1.68	0.64	1.01
18.6.82	1.42	0.65	1.04	2.27
14.7.82	0.87	1.10	1.92	1.80
22.7.82		0.52		
29.7.82	0.77	0.78	1.37	1.74
18.8.82	0.83	0.81	0.07	1.14
19.8.82		1.08		
26.8.82		1.31		
1.9.82	0.24	0.34	0.61	0.29
2.9.82		0.67		
16.9.82	1.55	1.09	1.52	1.33

to occur in greater numbers more frequently at site 4 than at the other surface sites. Since the genus *Achnanthes* is generally epiphytic this association with a "littoral" area was not unexpected. *Cyclotella compta* was only recorded in number on the 22nd April 1982. Surface accumulation at site 2 was prevalent.

Gymnodinium was only recorded in any great number at the surface (July 1982). Surface accumulation of *Dinobryon* was measured in 1982 at sites 1 and 2.

Cryptomonas spp were often found in higher numbers at site 4 than at 1m depth or sites 1 - 3. On the 11th February 1982, after ice melt, surface accumulation of *Cryptomonas* spp was such that the numbers were 3 - 6 times higher than those measured at 1m.

Increases in *Sphaerocystis*, in particular broken colonies of *Sphaerocystis* (green unicells), were responsible for much of the measured surface accumulation of phytoplankton. Surface enrichment was measured in May, June, July, August, September, October and November 1981. After ice melt in February 1982 the surface accumulation of *Sphaerocystis* cells was responsible for the large surface enrichment ratios measured at that time . During 1982 surface accumulation of *Sphaerocystis* was also evident in March, April, June, July and September.

Chlamydomonas spp were recorded infrequently yet on the 13th May 1982, a bright sunny day, a large surface accumulation at all four sites was measured. The algae were not found at depth.

When the blue-greens *Aphanothece saxicola* and *Synechococcus* spp were dominant, surface accumulation of these species was measured. During summer 1981, *Synechococcus* spp were found in numbers 1.5 - 2.7 times greater than those measured at 1m. On the 24th June 1981 at site 4, *Aphanothece saxicola* was found at over nine times the number measured at 1m. During summer 1982 enrichment factors of between 1.37 and 2.36 were measured. The surface accumulations of total phytoplankton in the summers of both years were thus mainly caused by the surface accumulation of *Synechococcus* spp and *Aphanothece saxicola*.

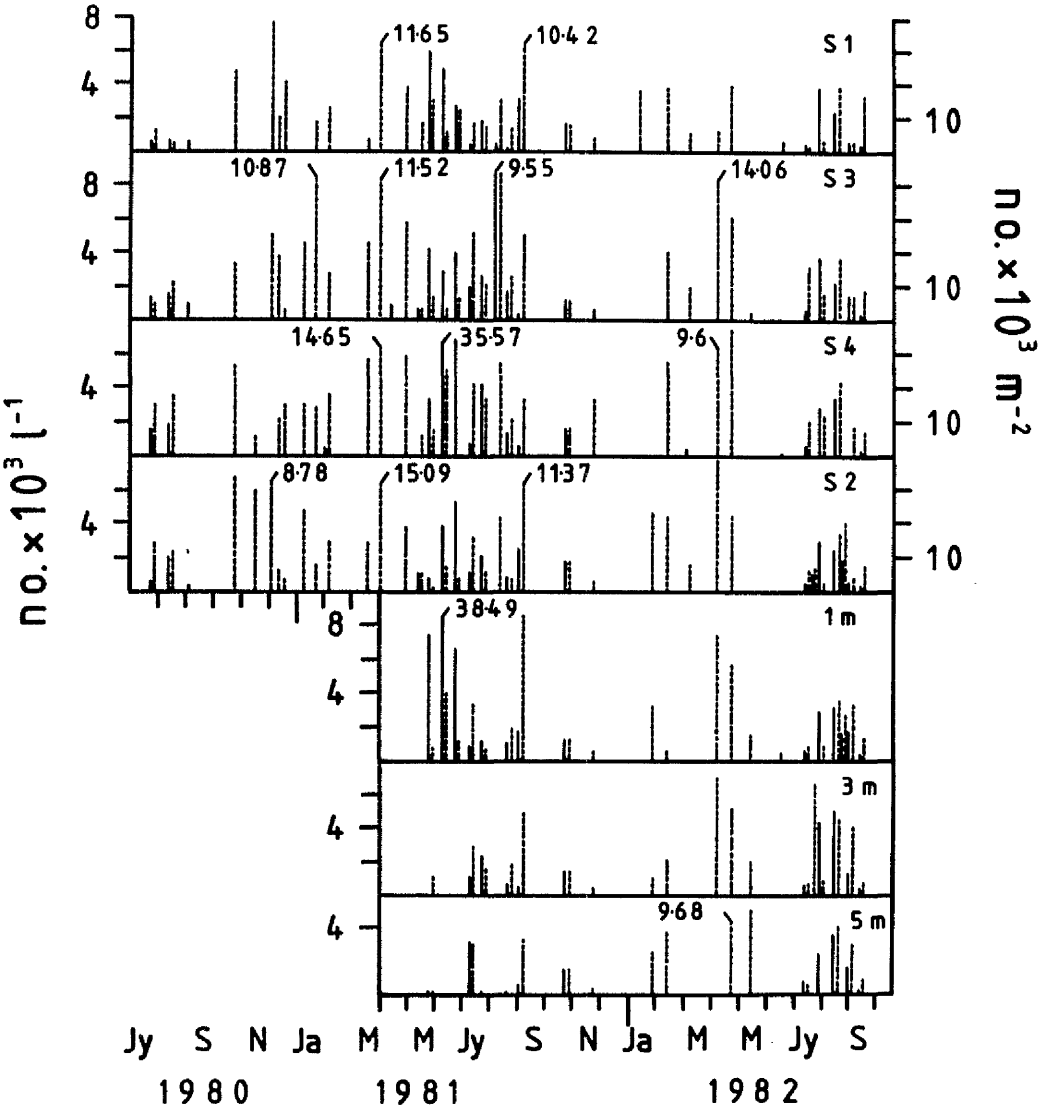

no. x 10³ l⁻¹
no. x 10³ m⁻²
S 1
S 3
S 4
S 2
1 m
3 m
5 m
11·65
10·42
10·87
11·52
9·55
14·06
14·65
35·57
9·6
8·78
15·09
11·37
38·49
9·68
Jy S N Ja M M Jy S N Ja M M Jy S
1980
1981
1982
Sphaerocystis schroeteri
green unicells

Figure 5.10

Sphaerocystis schroeteri and green unicells

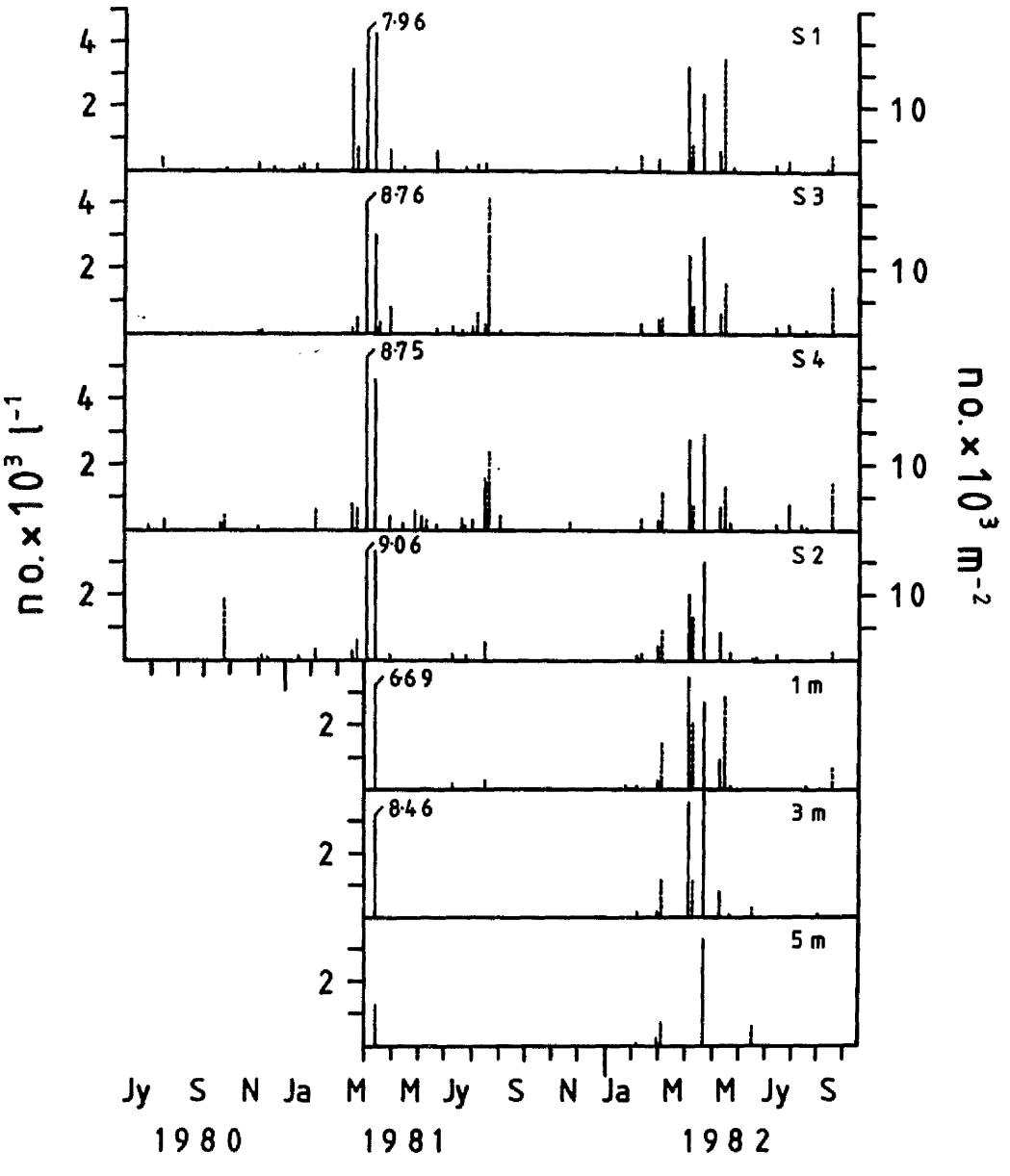
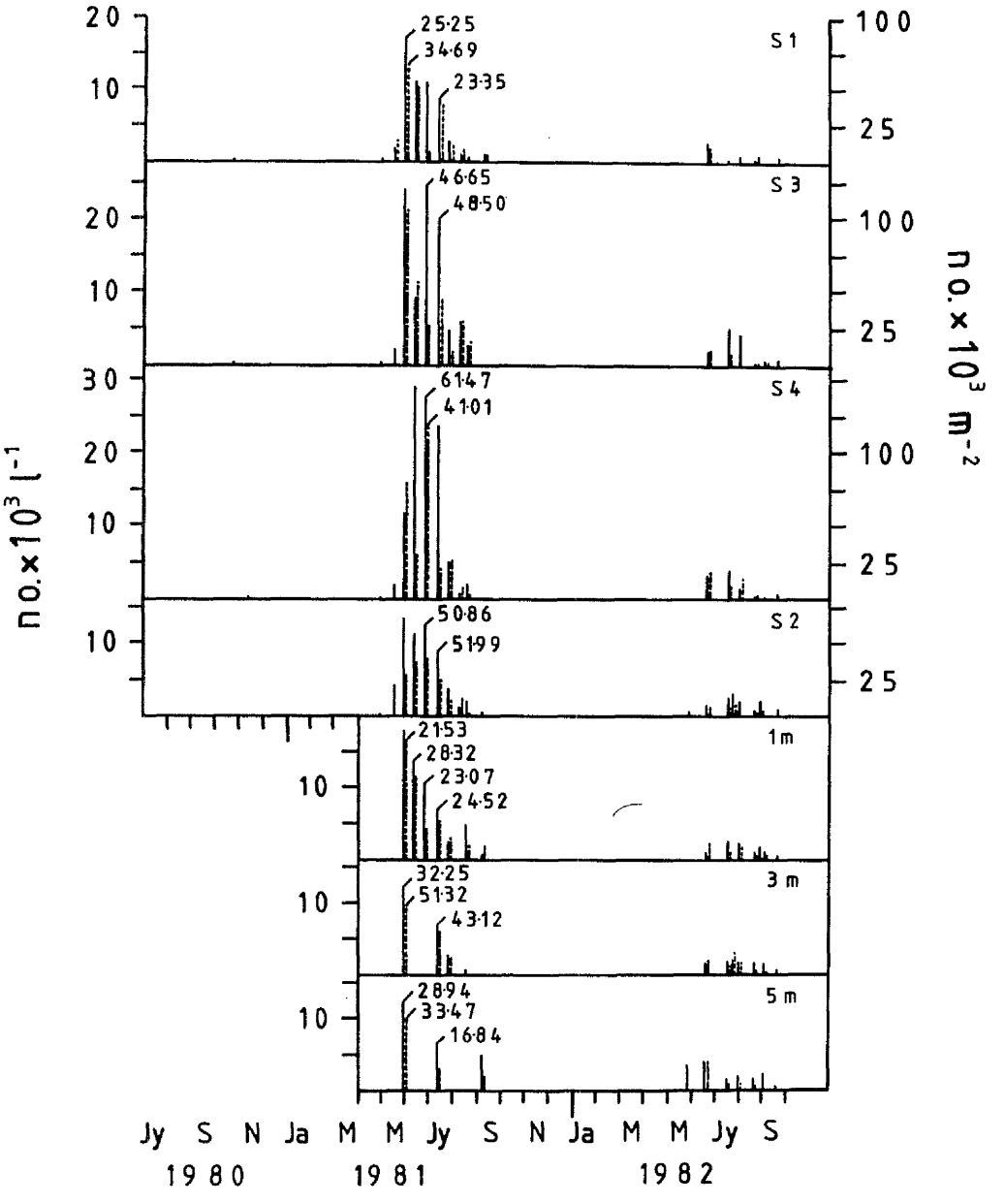

7·96
S 1
8·76
S 3
8·75
S 4
9·06
S 2
6·69
1 m
8·46
3 m
5 m
no.×10³ l⁻¹
no.×10³ m⁻²
Jy S N Ja M M Jy S N Ja M M Jy S
1980
1981
1982
Asterococcus limneticus
Chlamydomonas spp.

Figure 5.11

Asterococcus limneticus and *Chlamydomonas* spp


no.×10³ l⁻¹
no.×10³ m⁻²
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S 3
S 4
S 2
1m
3 m
5 m
25·25
34·69
23·35
46·65
48·50
61·47
41·01
50·86
51·99
21·53
28·32
23·07
24·52
32·25
51·32
43·12
28·94
33·47
16·84
Jy S N Ja M M Jy S N Ja M M Jy S
1980
1981
1982
Synechococcus spp.
Aphanothece saxicola

Figure 5.12

Synechococcus spp and *Aphanothece saxicola*

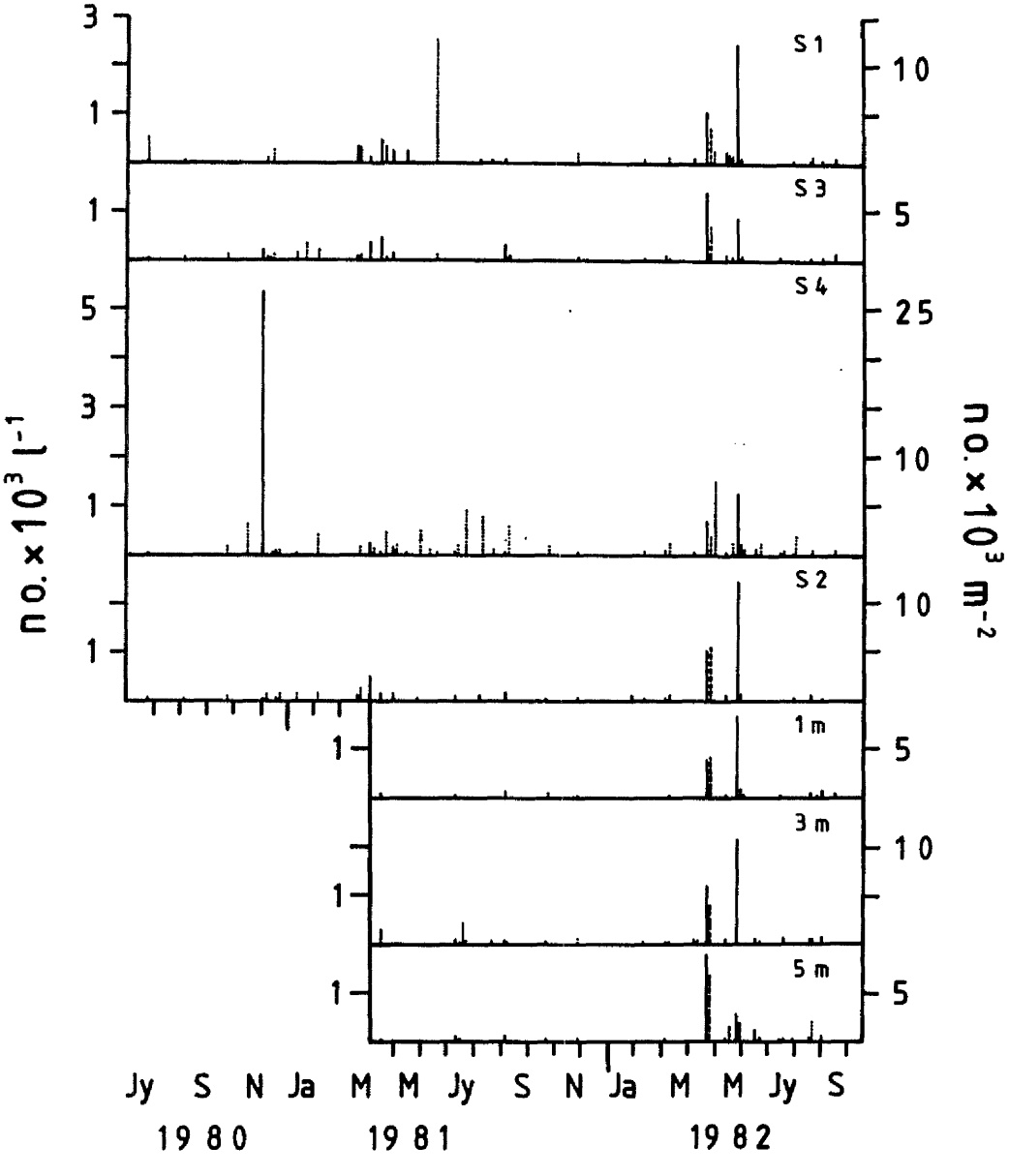

S 1
S 3
S 4
S 2
1 m
3 m
5 m
no. x 10³ l⁻¹
no. x 10³ m⁻²
Jy S N Ja M M Jy S N Ja M M Jy S
19 8 0
19 8 1
19 8 2
Cyclotella glomerata
C. operculata
Achnanthes saxonica

Figure 5.13

Cyclotella glomerata, C, operculata and *Achnanthes saxonica*

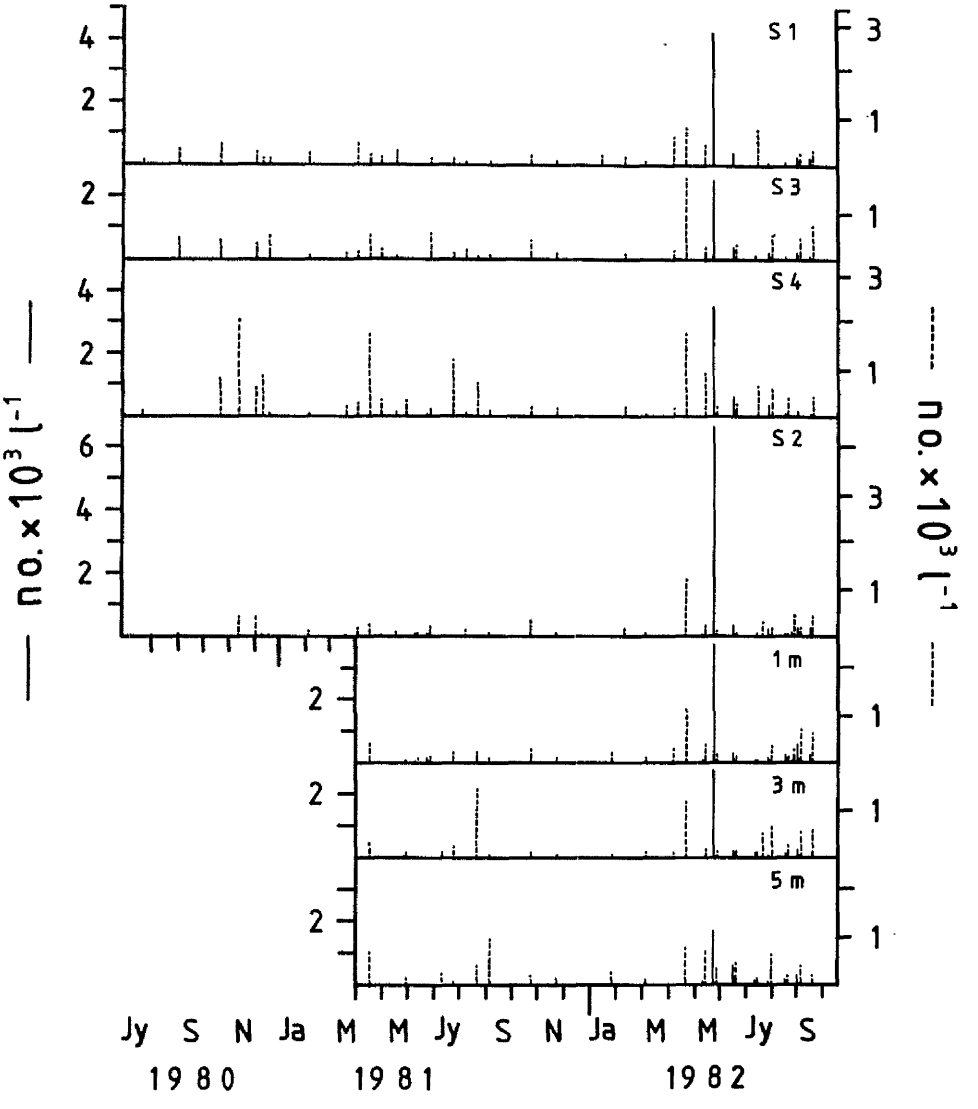

S 1
S 3
S 4
S 2
1 m
3 m
5 m
— no. x 10³ l⁻¹ —
---- no. x 10³ l⁻¹ ----
Jy S N Ja M M Jy S N Ja M M Jy S
1980
1981
1982
Dinobryon divergens ——
Cryptomonas spp. -------

Figure 5.14

Dinobryon divergens **and** *Cryptomonas* **spp**

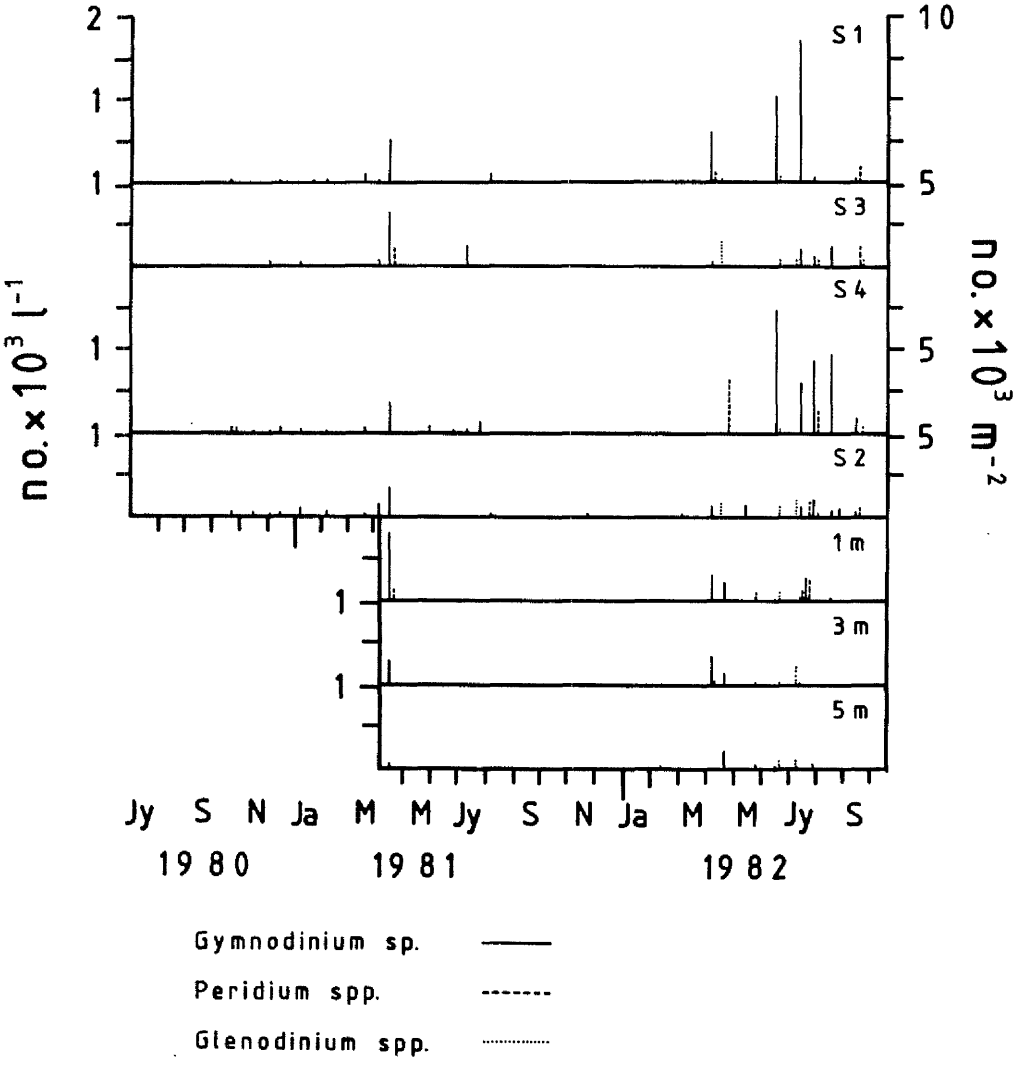

S 1
S 3
S 4
S 2
1 m
3 m
5 m
2
1
1
1
1
1
1
10
5
5
5
no.x10³ l⁻¹
no.x10³ m⁻²
Jy S N Ja M M Jy S N Ja M M Jy S
19 80
19 81
19 82
Gymnodinium sp.
Peridium spp.
Glenodinium spp.

Figure 5.15

Gymnodinium sp, *Peridinium* spp and *Glenodinium* spp

The numbers of *Mallomonas* spp and *Trachelomonas* spp were too low to allow accurate estimation of possible surface enrichment yet there were indications that occasional surface accumulation did occur. In general these species were recorded at 3m and 5m. *Golenkinia radiata* was recorded infrequently and was only found during the summer months of June and July at site 4.

5.2 PLANT PIGMENT ANALYSES.

5.2.1 Chlorophyll a.

Both seasonal, site and depth variations in chlorophyll a levels were observed during the sampling programme (Fig.5.16). Values ranged, in 1980, from 0.42 to 3.86 $\mu g\ l^{-1}$, in 1981, from 0.11 to 18.50 μg l and in 1982, from 0.33 to 8.10 $\mu g\ l^{-1}$.

At the start of the experimental period (27th July 1980) chlorophyll a levels of between 1.18 (site 1) and 3.85 $\mu g\ l^{-1}$ (site 2) were measured at the surface. Chlorophyll a remained within this range until October when decreases in concentration were recorded to between 0.78 (site 4) and 1.08 $\mu g\ l^{-1}$ (site 1). In late November a small rise in chlorophyll a at site 4 was recorded (1.35 $\mu g\ l^{-1}$) and again on the 4th December at sites 4 and 2 (2.96 $\mu g\ l^{-1}$ and 2.75 $\mu g\ l^{-1}$ respectively) coinciding with the formation of patches of ice on the loch and an increase in phytoplankton number. Throughout the remainder of winter levels remained low ($<1.80\ \mu g\ l^{-1}$). After ice thaw in March 1981 the chlorophyll content measured between 0.78 and 1.32 $\mu g\ l^{-1}$. At the beginning of April a peak in chlorophyll a coincided with an increase in phytoplankton (site 1, 5.32 $\mu g\ l^{-1}$; site 2, 5.52 $\mu g\ l^{-1}$; site 3, 2.87 $\mu g\ l^{-1}$ and site 4, 4.19 $\mu g\ l^{-1}$). A second increase was recorded in June, particularly at site 4 (18.59 $\mu g\ l^{-1}$, 24th June) which was attributable to the large numbers of blue-green algae recorded at that time. As blue-green algal levels declined through July, so did chlorophyll a (1.22 $\mu g\ l^{-1}$ -2.62 $\mu g\ l^{-1}$). The beginning of September was marked by a small rise in the chlorophyll a particularly at the surface to 2.05-3.40 $\mu g\ l^{-1}$ coinciding with an increase in *Sphaerocystis*.

Chlorophyll a levels during autumn 1981 and winter 1981/1982 were low, as in 1980 (0.07-1.37 $\mu g\ l^{-1}$). Samples taken at sites 1 and 2 on the 13th January 1982 under the ice cover revealed an increase in chlorophyll a content (2.87 $\mu g\ l^{-1}$ and 3.35 $\mu g\ l^{-1}$ respectively). Samples taken at site 2 on the 27th January did not show this rise (0.43 $\mu g\ l^{-1}$ just below the ice, 0.50 $\mu g\ l^{-1}$ at 1m, 0.47 $\mu g\ l^{-1}$ at 3m and 0.33 $\mu g\ l^{-1}$ at 5m). From the end of March 1982, a rise in chlorophyll a was noted, reaching a small peak by the beginning of April (2.70-3.27 $\mu g\ l^{-1}$) coinciding with an increase in the numbers of *Sphaerocystis* and *Asterococcus*. The highest reading was obtained at 1m. On the 22nd April a peak in chlorophyll a at 5m was noted (3.92 $\mu g\ l^{-1}$) coinciding with an increase in the phytoplankton at that depth which was attributable to green flagellates.

A second, larger, increase was recorded at the end of March (3.95-8.09 $\mu g\ l^{-1}$) coinciding with the recorded increase in *Dinobryon divergens* colonies. Surface values for sites 1 and 2 were higher than those obtained at 1m (8.09 $\mu g\ l^{-1}$ at site 1, 7.05 $\mu g\ l^{-1}$ at site 2 and 5.89 $\mu g\ l^{-1}$ at 1m) as were *Dinobryon* colony numbers. As in 1981 a further, smaller peak in chlorophyll a was recorded at the end of August / beginning of September with surface enrichment occurring at site 4 (3.68 $\mu g\ l^{-1}$ at site 4, 2.75 $\mu g\ l^{-1}$ at 1m on the 18th August). At the end of the experimental programme chlorophyll a levels ranged from 1.69 $\mu g\ l^{-1}$ to 2.48 $\mu g\ l^{-1}$ at the surface and 2.03 $\mu g\ l^{-1}$ (1m) to 1.17 $\mu g\ l^{-1}$ (5m).

Table 5.3 represents the ratios of surface site chlorophyll a concentrations to the corresponding 1m depth concentration i.e.

$$\frac{\text{chlorophyll a at surface}}{\text{chlorophyll a at 1m}}$$

When compared to 1m depth (open water) site 4 ('littoral') exhibited surface enrichment of chlorophyll a (17 samples out of 26 had surface enrichment ratios greater than 1.20). The highest ratios were measured on the 24th June 1981 (6.67, attributable to the abundance of

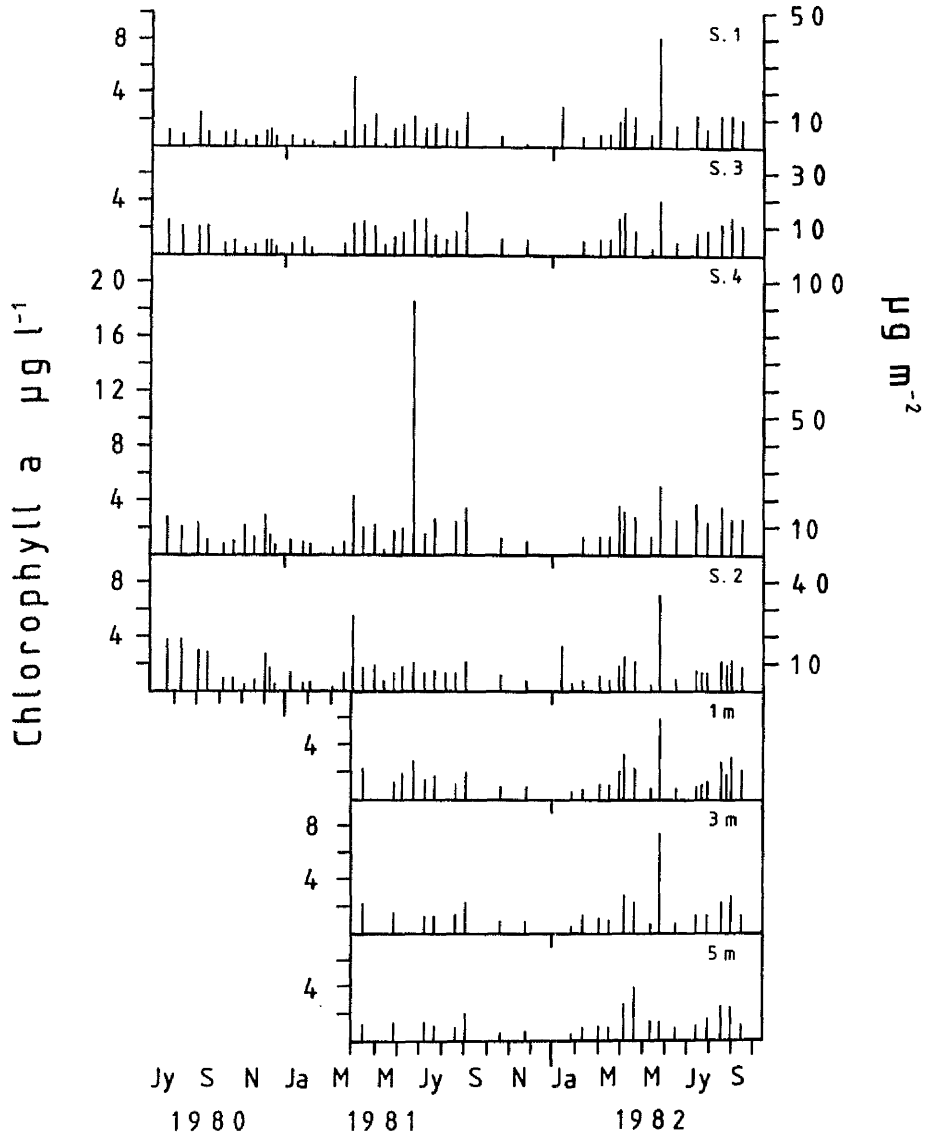

Chlorophyll a µg l-1
µg m-2
S. 1
S. 3
S. 4
S. 2
1 m
3 m
5 m
8
4
20
16
12
50
10
30
100
40
Jy S N Ja M M Jy S N Ja M M Jy S
1980
1981
1982

Figure 5.16

Chlorophyll a levels $\mu g\ l^{-1}$

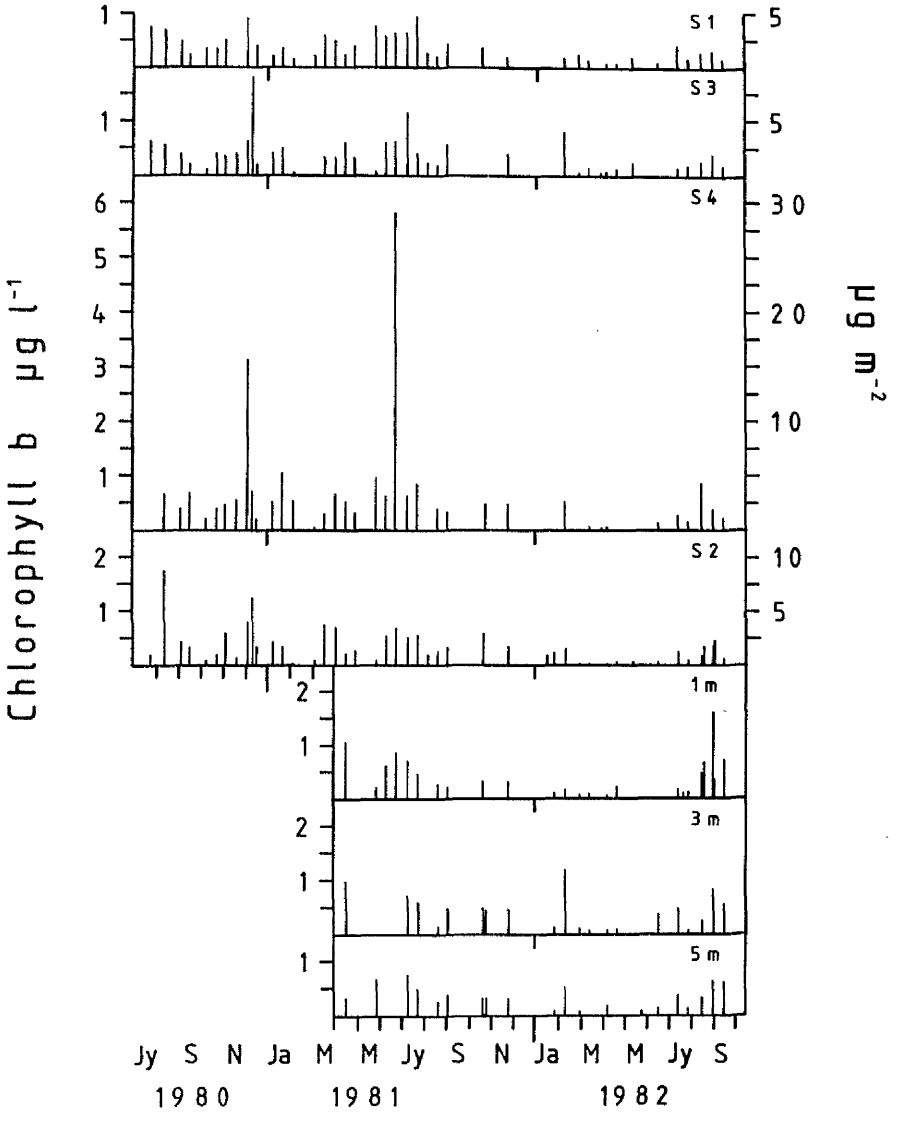

Chlorophyll b µg l-1
mg m-2
S1
S3
S4
S2
1m
3m
5m
Jy S N Ja M M Jy S N Ja M M Jy S
1980
1981
1982

Figure 5.17

Chlorophyll b levels $\mu g\ l^{-1}$

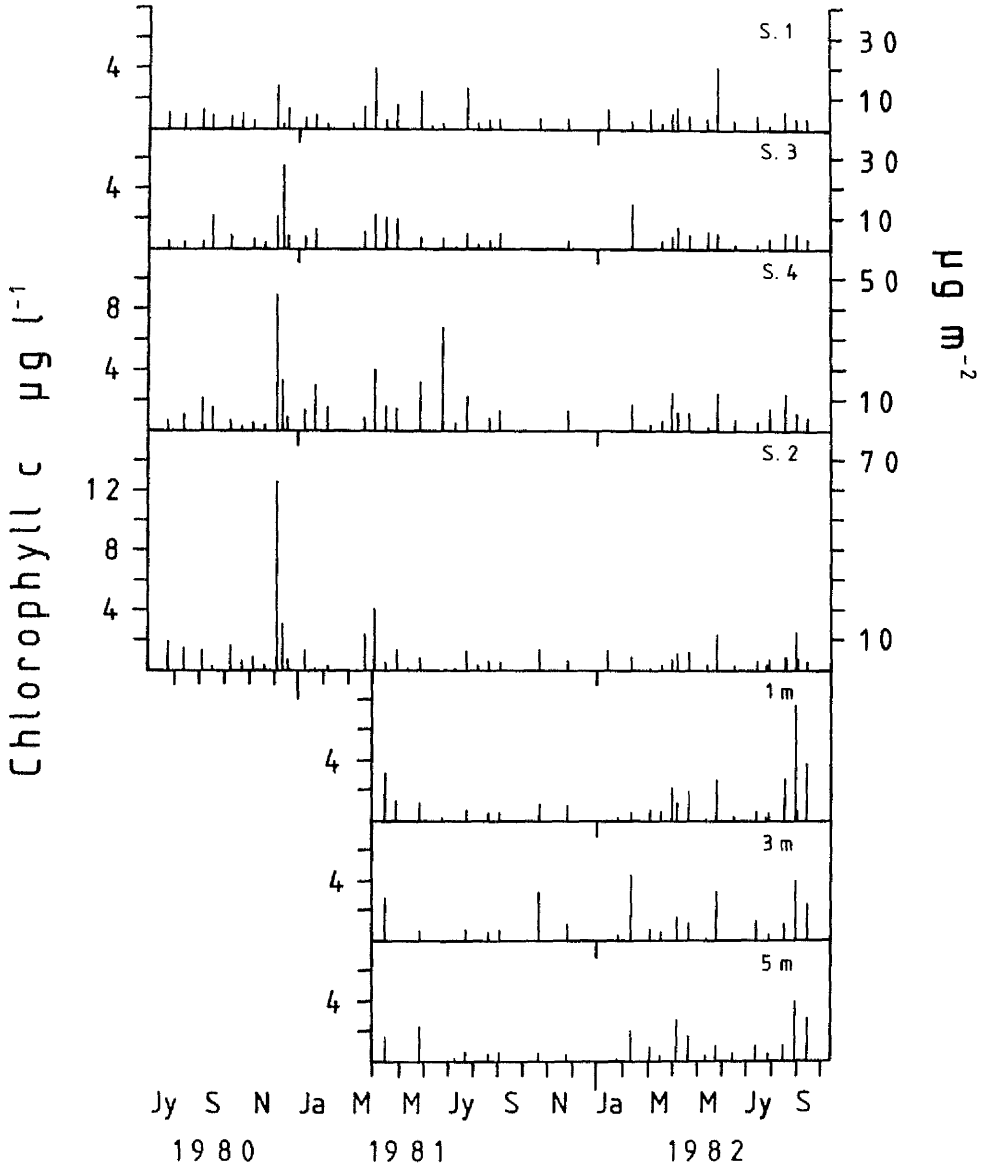

Chlorophyll c µg l⁻¹
µg m⁻²
S. 1
S. 3
S. 4
S. 2
1 m
3 m
5 m
4
8
12
30
10
50
70
Jy S N Ja M M Jy S N Ja M M Jy S
1980
1981
1982

Figure 5.18

Chlorophyll c levels $\mu g\ l^{-1}$

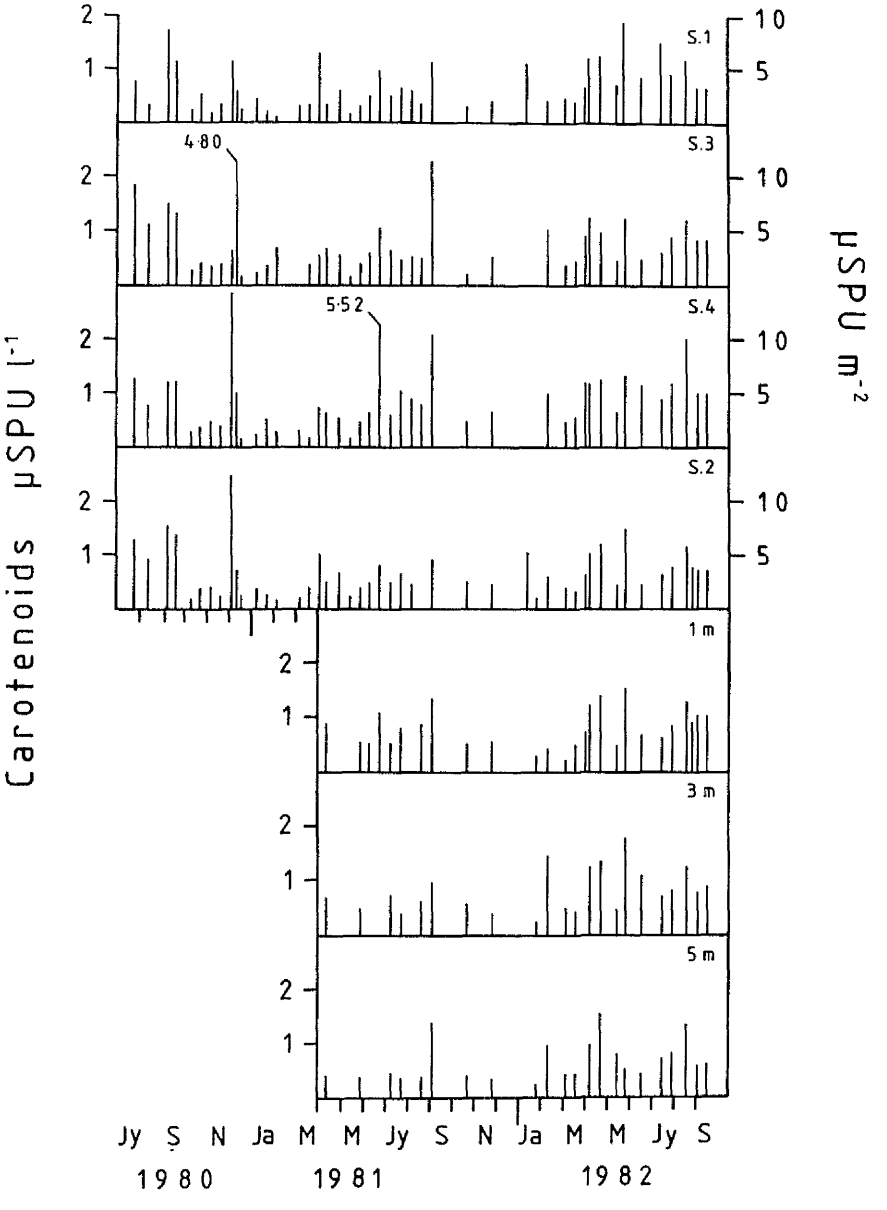

Carotenoids µSPU l-1
µSPU m-2
S.1
S.3
S.4
S.2
1 m
3 m
5 m
4·80
5·52
2
1
10
5
Jy S N Ja M M Jy S N Ja M M Jy S
1980
1981
1982

Figure 5.19

Carotenoid levels μSPU l^{-1}

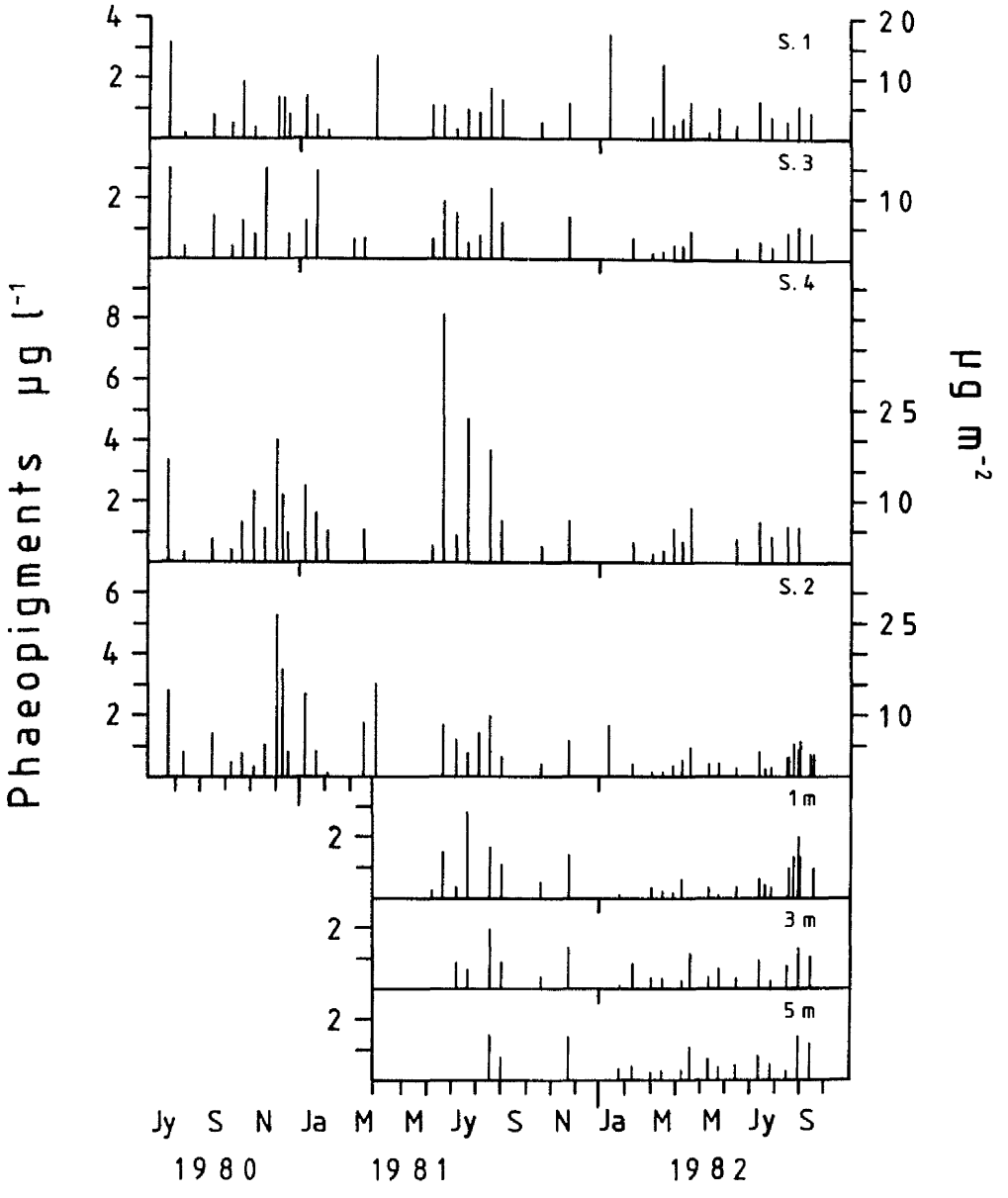

Phaeopigments µg l-1
µg m-2
S. 1
S. 3
S. 4
S. 2
1 m
3 m
5 m
Jy S N Ja M M Jy S N Ja M M Jy S
1980
1981
1982

Figure 5.20

Phaeopigment levels $\mu g\ l^{-1}$

Table 5.3

Chlorophyll a enrichment ratios; surface/1m

Date	Site 1	Site 2	Site 3	Site 4
16.4.81	0.65	0.74	1.04	0.89
28.5.81	1.02	1.08	0.99	1.45
10.6.81	0.79	0.76	0.93	6.67
9.7.81	0.92	1.12	1.85	1.06
23.7.81	0.96	0.84	0.81	1.55
20.8.81	0.99	1.17	1.70	2.27
3.9.81	1.20	1.08	1.59	1.80
22.10.81	0.72	1.17	0.72	1.30
26.11.81	0.08	0.81	1.13	1.00
11.2.81	0.91	0.90	1.29	1.71
4.3.82	0.77	0.97	0.95	1.26
18.3.82	0.84	0.77	1.03	1.25
31.3.82am	0.89	0.89	1.28	1.73
31.3.82pm	0.75	0.91	0.93	0.96
22.4.82	0.95	0.92	0.77	1.17
13.5.82	1.33	0.63	0.60	1.99
26.5.82am	1.38	1.20	0.67	0.85
26.5.82pm	1.93	0.93	0.32	0.93
17.6.82	1.78	0.97	1.10	3.07
14.7.82	2.52	1.49	1.62	1.87
22.7.82		1.20		
29.7.82	0.94	0.99	1.32	1.79
18.8.82	0.82	0.78	0.79	1.34
19.8.82		1.14		
26.8.82		1.04		
1.9.82	0.717	0.732	0.872	0.827
2.9.82		1.06		
16.9.82	0.94	0.83	1.01	1.22

blue-greens), 20th August 1981 (2.27, green algae) and the 17th June 1982 (3.07, blue-greens). Surface enrichment (ratio > 1.20) was measured on seven occasions at site 3, on three occasions at site 2 and on six occasions at site 1.

5.2.2 Chlorophylls b and c.

Chlorophylls b and c levels exhibited similar seasonal and site variations to chlorophyll a, reflecting changes in phytoplankton biomass and composition (Figs 5.17, 5.18). A comparison of chlorophyll c with chlorophyll a concentrations indicated that enrichment of chlorophyll c only occured in late autumn and winter when the green unicells, diatoms, chrysophytes and cryptophytes formed the phytoplankton population.

5.2.3 Carotenoids

Carotenoid levels reflected the large populations of Chlorophyta and Cyanophyta and to some extent, the Bacillariophyta, Chrysophyta and Cryptophyta. The carotenoids followed the same seasonal and site distribution patterns as those for chlorophyll a. Values ranged from analytical zero to 5.52 μSPU l^{-1} (Fig. 5.19).

5.2.4 Phaeopigments

Phaeopigment levels ranged from analytical zero to 8.14 $\mu g\ l^{-1}$ in 1981 and from analytical zero to 1.95 $\mu g\ l^{-1}$ in 1982. These yearly variations reflected the yearly variations found in phytoplankton and chlorophyll a levels (see section 5.1 and 5.2.1). Phaeopigments, being the degradation products of chlorophyll, displayed the same seasonal, site and depth variations as chlorophyll a.

At the start of the experimental period phaeopigment levels were higher than those of chlorophyll a, while in August they only formed between 16.7 and 21% of the measured chlorophyll a. On the 4th September no phaeopigments could be detected. In comparison to chlorophyll a, the phaeopigment content was high on the 17th September (49%-69% of chlorophyll a) and on the 9th October (50% that of

chlorophyll a). On the 23rd October phaeopigment concentrations were again higher than chlorophyll a levels at sites 1, 3 and 4 (1.85, 1.22 and 1.30 $\mu g\ l^{-1}$, compared with 1.08, 0.95 and 0.96 μg Chl a l^{-1}). This finding was repeated at sites 3 and 4 on the 6th November, at sites 2 and 3 on the 20th November, at sites 1, 2 and 4 on the 4th December, at sites sites 1, 2 and 4 on the 11th December and at sites 1, 2 and 3 on the 18th December. These high phaeopigment levels were indicative of both a senescing phytoplankton population and a senesced littoral flora.

During January, February and March, before ice melt, the phaeopigment content was again higher than the chlorophyll content. Throughout April and May phaeopigment measured analytical zero. During June and the first half of July the phaeopigment concentration averaged 50% of the chlorophyll a concentration, indicating a rapid turnover of the phytoplankton population. From the 23rd July to the 26th November phaeopigment levels greater than chlorophyll a concentrations were recorded coinciding with the death of the blue-green algal 'bloom' and the senescence of the algal and macrophyte flora in general. On those dates and sites when phaeopigment level did not exceed chlorophyll a, phaeopigment averaged 43% of chlorophyll a.

Samples taken through the ice on the 13th January gave a high phaeopigment concentration at site 1 (3.42 $\mu g\ l^{-1}$, 2.87 μg Chl a l^{-1}) and a lower reading at site 2 (1.65 $\mu g\ l^{-1}$, 3.35 μg Chl a l^{-1}). The algal population at site 2 was higher than that at site 1 (4,566 l^{-1} at site 2, 1,575 l^{-1} at site 1). Measurements taken on the 27th January under the ice gave the following readings; just below the ice, analytical zero, 1m, 0.90 $\mu g\ l^{-1}$, 3m, 0.10 $\mu g\ l^{-1}$ and 5m, 0.36 $\mu g\ l^{-1}$. The phaeopigment content at 5m exceeded that of chlorophyll a (0.33 $\mu g\ l^{-1}$).

Throughout the remainder of 1982 phaeopigment levels did not exceed those of chlorophyll a. During March and the first week in April they were less than 35% of the measured chlorophyll a content. Coinciding with an increase in *Sphaerocystis* and *Asterococcus* on the 22nd April this proportion rose to between 27% and 67% decreasing to between 0% (no phaeopigment) and 29%, at the surface, on the 13th May.

At depth phaeopigment constituted between 45% and 54% on the 13th, falling to between 7.4% and 28% on the 26th May. During June and the first half of July, coinciding with the measured increase in the number of blue-green algae, phaeopigment averaged 47% of the chlorophyll a indicated a rapid turnover of the phytoplankton population. A further increase in the proportion of phaeopigments was measured at the close of the sampling programme at 3m and 5m depths comprising 80% and 98% of the values of chlorophyll a (1.06 $\mu g\ l^{-1}$ and 1.15 $\mu g\ l^{-1}$ respectively, as opposed to 1.33 μg Chl a l^{-1} and 1.175 μg Chl a l^{-1} respectively).

According to Lorenzen (1967) the ratio,

$$\frac{\text{O.D. 665nm - O.D. 750nm before acidification}}{\text{O.D. 665nm - O.D. 750nm after acidification}}$$

should not exceed a theoretical maximum of 1.7 for 100% 'good' chlorophyll a (0% phaeopigment a).

The acid ratios measured in this programme averaged 1.50, indicating that phaeopigments may have been overestimated by about 12%. If this correction is applied to the measurements obtained it still does not account for the high relative proportion of phaeopigments to chlorophyll a. Rather these high values can be attributed to the following: to the senescence of phytoplankton and macrophyte flora in late autumn and winter, to rapid overturn of the phytoplankton population during the summer maxima, to allochthonous input of leaf material from the surrounding plant population and via the inflow and to a phytoplankton population under some stress from the conditions of low pH and high humic acid content.

5.3 CARBON FIXATION STUDIES.

5.3.1 Carbon fixation rates of phytoplankton.

During the *in situ* measurement of ^{14}C uptake the measurement of gross photosynthesis i.e. ^{14}C uptake only, is impossible. Under certain conditions where glycollate formation is favoured (e.g. under high

Table 5.4

Carbon fixation rates of surface layer and depth samples

18.3.82 - 16.9.82

Date	Site 1		Site 3		Site 4	
	a	b	a	b	a	b
18.3.82	0.013	0.001	0.22	0.002	analytical zero	
31.3.82am	1.60	0.89	2.00	0.77	0.13	0.04
31.3.82pm	2.39	1.54	2.23	1.17	3.55	1.81
" 24h am	0.76	0.42	0.19	0.07	0.92	0.26
" 24h pm	1.58	1.02	1.56	0.82	2.10	1.07
7.4.82	9.60	3.32	9.96	3.22	8.50	2.69
22.4.82	3.34	1.56	4.60	2.64	3.90	1.48
13.5.82	1.70	2.01	1.10	2.88	2.50	1.97
26.5.82am	31.50	3.89	11.33	2.87	15.60	3.10
26.5.82pm	22.50	5.85	14.50	8.45	18.40	3.66
" 24h am	22.50	2.78	10.70	2.71	18.60	3.70
" 24h pm	19.90	1.91				
17.6.82	15.30	10.36	2.87	3.13	5.00	1.96
" 24h	5.35	3.62	2.90	3.17	2.90	3.14
14.7.82	18.60	7.98	6.50	4.33	17.60	10.15
" 24h	7.90	3.39	3.30	2.20	8.00	4.61
29.7.82	4.80	3.90	7.20	4.14	4.80	2.03
" 24h	5.90	4.77	8.00	4.60	6.80	2.88
18.8.82	4.64	2.06	2.60	1.19	6.10	1.66
" 24h	3.34	1.49	4.30	1.97	4.77	1.30
1.9.82	2.26	1.00	2.40	0.88	2.19	0.84
" 24h	0.55	0.24	2.40	0.88	1.20	0.46
16.9.82	9.40	4.96	8.70	4.27	6.90	2.78
" 24h	2.50	1.32	4.60	2.25	3.65	1.47

column heading a :- carbon fixation $\mu g\ C\ l^{-1}\ h^{-1}$

column heading b :- specific carbon fixation $\mu g\ C\ (\mu g\ Chl\ a)^{-1}\ h^{-1}$

Table 5.4 part 2

Carbon fixation rates of surface layer and depth samples

18.3.82 - 16.9.82

Date	Surface site2		1m		3m		5m	
	a	b	a	b	a	b	a	b
18.3.82	0.04	0.05	0.87	0.86	0.68	0.61	0.28	0.26
31.3.82am	3.70	2.05	3.90	1.92				
31.3.82pm	7.60	4.06	6.03	2.93				
" 8h	1.60	0.89	1.90	0.93				
" 24h am	1.10	0.61	0.15	0.07				
" 24h pm	1.09	0.58	1.17	0.57				
7.4.82	1.40	0.55	8.09	2.72	3.70	1.29	0.33	0.12
22.4.82	7.99	3.84	7.40	3.29	5.30	2.39	4.10	1.05
13.5.82	1.20	2.85	4.20	6.58	4.70	7.11	13.90	10.37
26.5.82am	65.00	9.22	52.30	8.88	42.40	5.70		
" 24h am	27.50	3.90	22.10	3.75	17.60	2.37	17.20	12.83
" 24h pm	15.40	3.06						
17.6.82	6.50	8.08	2.50	3.49	2.50	3.49	3.20	3.34
" 24h	4.20	5.22	2.90	3.49	2.90	3.49	1.30	1.36
14.7.82	12.80	9.26	8.10	8.75	8.10	8.74	3.50	3.24
" 24h	1.10	0.80	2.65	2.86	2.65	2.86	0.96	0.89
29.7.82	11.60	8.32	9.80	7.45	9.80	7.45	8.00	4.83
" 24h	7.90	6.10	3.60	2.74	3.60	2.74	2.70	1.63
18.8.82	15.00	6.97	16.50	6.10	16.50	6.10	3.10	1.22
" 24h	7.60	3.53	5.70	2.08	5.70	2.08	0.81	0.32
1.9.82	14.50	6.33	17.00	6.19	11.10	3.97	2.80	1.09
" 24h	5.10	2.23	6.10	1.95	2.70	0.97	0.61	0.24
16.9.82	7.00	4.15	5.30	2.62	0.17	0.14	0.10	0.08
" 24h	3.26	1.93	1.85	0.91	0.19	0.14	0.01	0.008

column heading a :- carbon fixation μg C l^{-1} h^{-1}

column heading b :- specific carbon fixation μg C (μg Chl a)$^{-1}$ h^{-1}

light intensities and hence photoinhibition, nutrient depletion or low CO_2 partial pressure) then glycollate may be excreted or photorespired. Dark respiration of $^{12}CO_2$ from previously fixed carbon sources will occur. Reassimilation of CO_2 then occurs, though to varying degrees (Raven, 1972; incl. in Harris, 1978) such that experiments of approximately 4h duration measure something between gross and net photosynthesis (c.f. review by Harris, 1978). Over a 24h period i.e. including a period of darkness when fixed ^{14}C can become incorporated via the TCA cycle, it is theoretically possible to obtain a closer measurement of net photosynthesis but enclosure of phytoplankton populations for such periods can give rise to 'bottle effects" e.g. nutrient depletion, changes in pH, sedimentation of the algae and increases in the bacterial population. Bearing in mind these states of affairs and to avoid erroneous use of the terms 'gross productivity' and 'net productivity', the terms '4h productivity' and '24h productivity' or '4h fixation' and '24h fixation' will be used where a distinction needs to be made. As stated in section 3.9, incubation periods of 4h were generally used.

The carbon fixation rates, expressed as μg C (μg Chl a)$^{-1}$ h^{-1} of surface and depth samples were measured in situ on the following days during 1982 : 18th March, 31st March, 7th April, 22nd April, 13th May, 26th May, 17th June, 14th July, 29th July, 18th August, 1st September and 16th September.

The results are expressed in tabular form in Table 5.4 and graphical form in Figs. 5.21 and 5.22 together with the corresponding Secchi disc readings (see section 4.15). Note the variation in scale used.

At the start of the experimental programme (18th March), carbon fixation rates were less than 1 μg C (μg Chl a)$^{-1}$ h^{-1} (Fig.5.21), rising gradually through spring and summer to their highest levels recorded on the 17th June (11.38 μg C (μg Chl a)$^{-1}$ h^{-1} at 3m). A gradual reduction in the rate of carbon fixation was then observed and at the end of the experimental programme primary production had fallen to less than 5 μg C (μg Chl a)$^{-1}$ h^{-1} (16th September. Fig. 5.22).

18th March :

The rates of carbon fixation on this date were very low, less than 1 μg C (μg Chl a)$^{-1}$ h^{-1} (Fig. 5.21). At site 4 it was so low as to be unmeasurable. Fixation was greatest at 1m depth. In comparison, the fixation rates at surface sites 1-3 were 10 times lower. The surface water temperature was 4.25 ^{o}C (section 4.12) and the Secchi disc reading was 3.59 m. The weather was dry and bright.

31st March / 1st April :

Five sets of experiments were carried out over this 24h period and the data are represented in Table 5.4. On the morning of the 31st (9am), surface water samples from the four surface sites were collected as well as water from 1m. Each was then divided into three subsamples. The first set of subsamples were treated and incubated for 4h as previously described (section 3.9). The second set were treated as previously described and incubated for 24h. From the third set, subsamples from site 2 and 1m were incubated for 8h. In the afternoon (1pm) water samples from the four surface sites and 1m depth were again collected. These were each subdivided into two sets of incubations, one set for 4h and the other for 24h.

The rate of carbon fixation was greater in the afternoon than in the morning and greatest at site 2 on both occasions. In both the morning and the afternoon, chlorophyll a levels were lower at site 2 than at 1m depth suggesting that the phytoplankton population at the surface was more efficient at fixing carbon than that at 1m. The lowest fixation rate measured occurred at site 4 in the morning (0.04 μg C (μg Chl a)$^{-1}$ h^{-1}) but the chlorophyll a concentration was the highest (3.53 μg l^{-1}).

Over the 8h period the rate of carbon fixation was much lower than that measured during the two consecutive 4h periods (0.88 μg C (μg Chl a)$^{-1}$ h^{-1} at site 2, 0.93 μg C (μg Chl a)$^{-1}$ h^{-1} at 1m). These lower rates suggest that either nutrient limitation, extracellular release of ^{14}C or bacterial degradation may have occurred.

24h incubation samples collected in the afternoon gave higher fixation rates than those collected in the morning (0.57-1.08 as opposed to 0.07-0.6 μg C (μg Chl a)$^{-1}$ h^{-1}). During the morning incubation period the highest rate of fixation occurred at surface site 2 while in the afternoon, samples showed the highest rates of fixation at surface sites 1 and 4. Water temperatures in the morning at sites 1-4 and at 1m were; 5.5, 5.7, 5.7, 5.0 and 5.7 ^{o}C respectively. The weather over the two day period was cold, dry and dull.

7th April (Fig.5.21) :

This date was characterised by constant rainfall, at times quite heavy. The water temperatures at surface sites 1-4 and 1m, 3m and 5m depths were; 8.10, 8.10, 8.35, 8.30, 8.10, 7.80 and 6.90^{o}C respectively. Light penetration, as measured by Secchi disc, extended to 4.125m. The highest fixation rates were measured at surface sites 1,3 and 4 (3.32, 3.22 and 2.69 μg C (μg Chl a)$^{-1}$ h^{-1}) and at 1m (2.72 μg C (μg Chl a)$^{-1}$ h^{-1}). A high silt level which prevented estimation of the phytoplankton population was evident at 5m. This may, in part, have been responsible for the low fixation rate measured (0.12 μg C (μg Chl a)$^{-1}$ h^{-1}).

22nd April (Fig. 5.21):

On this day the weather was overcast with extended periods of rain and a continual breeze. The water temperatures at sites 1-4 and 1m, 3m and 5m were ; 10.30, 10.30, 10.55, 10.70, 10.30, 10.00 and 7.25 ^{o}C respectively. The vertical profile of carbon fixation at site 2 showed that fixation was highest at the surface (3.85 μg C (μg Chl a)$^{-1}$ h^{-1}) gradually falling with depth to 1.05 μg C (μg Chl a)$^{-1}$ h^{-1} at 5m. The phytoplankton population and chlorophyll a level at surface site 2 was lower than that obtained at depth suggesting that the surface population was more efficient at carbon fixation. Numerically, the most phytoplankton and chlorophyll a was measured at 5m. Light limitation (S.d = 4.025m) at this depth was probably responsible for the low rate of productivity. The rates at surface sites 1, 3 and 4 were lower than those measured at surface site 2 or at 1m (1.56, 2.64 and 1.48 μg C (μg Chl a)$^{-1}$ h^{-1} respectively).

13th May (Fig. 5.21):

This day was dry and bright with only a thin cloud cover.The water temperatures at sites 1-4, 1m, 3m and 5m were: 13.7, 13.5, 13.4, 13.4, 13.5, 12.4 and 9.5 ^{o}C respectively. Productivity was greater at 1m and at 3m than at the surface. The largest phytoplankton population and chlorophyll a level was measured at 5m on this day. Light penetration, as measured by Secchi disc, extended to 4.025m and the average surface incident light level during the period of incubation was 19.24 g cal $cm^{-1}min^{-1}$. A comparison of the four surface sites showed that the rate of carbon fixation was highest at site 3, where both the phytoplankton population and chlorophyll a level were lowest.

26th May / 27th May (Fig. 5.21):

On this day both 4h and 24h incubations were made both in the morning and the afternoon. Unfortunately equipment loss *in situ* meant that data for the 4h and 24h afternoon incubations were incomplete. The weather was cloudy with a 1.5h period of rain in the afternoon and a continual, cool breeze. Light penetration was 4.35m. The average surface incident light level was 24 g cal $cm^{-1}min^{-1}$ in the morning and 42.19 g cal $cm^{-1}min^{-1}$ in the afternoon. Carbon fixation over both 4h and 24h was highest at surface site 2 (9.22 μg C (μg Chl a)$^{-1}$ h^{-1} and 3.90 μg C (μg Chl a)$^{-1}$ h^{-1}) and at 5m (10.37 μg C (μg Chl a)$^{-1}$ h^{-1} and 12.83 μg C (μg Chl a)$^{-1}$ h^{-1}). At site 2 both the quantities of phytoplankton and chlorophyll a were high (10,451 units l^{-1}, 7.05 μg Chl a l^{-1}). At 5m, though the phytoplankton population was large (7,262 l^{-1}), chlorophyll a was low (1.34 μg l^{-1}). The high efficiency of the phytoplankton population at 5m was probably due to the large number of blue-greens found (43.97% of the population). 24h carbon fixation rates also indicated a high productivity rate for the 5m phytoplankton population (Table 5.4)

Data available for afternoon incubations at sites 1,3 and 4 indicated that primary productivity was higher in the afternoon at the surface, particularly at site 3 (8.45 μg C (μg Chl a)$^{-1}$ h^{-1}) as opposed to the morning (2.87 μg C (μg Chl a)$^{-1}$ h^{-1}). The corresponding

chlorophyll a levels were 1.72 $\mu g\ l^{-1}$ and 3.95 $\mu g\ l^{-1}$ respectively.

17th June / 18th June (Fig 5.21):

On this day the weather was grey and overcast with a NW wind. Light penetration, as measured by Secchi disc was 4.00m. The average surface incident light measurement during the 4h period of incubation was 12.72 g cal $cm^{-1}min^{-1}$. Over 24h it was 10.54 g cal $cm^{-1}min^{-1}$.

4h and 24h carbon fixation rates were highest at surface sites 1 and 2 (10.36 μg C (μg Chl a)$^{-1}$ h^{-1} over 4h, 3.62 μg C (μg Chl a)$^{-1}$ h^{-1} over 24h at site 1, 8.08 μg C (μg Chl a)$^{-1}$ h^{-1} over 4h and 5.22 over 24h at site 2) and at 3m depth (11.38 μg C (μg Chl a)$^{-1}$ h^{-1} over 4h and 4.28 μg C (μg Chl a)$^{-1}$ h^{-1} over 24 h).The lowest 4h carbon fixation rate on the 17th June was measured at site 4 (1.96 μg C (μg Chl a)$^{-1}$ h^{-1}) while the lowest 24h value was measured at 5m (1.36 μg C μg C (μg Chl a)$^{-1}$ h^{-1}). The largest phytoplankton populations were measured at site 4 (10,686 l^{-1}) and at 5m (10,713 l^{-1}) and the highest chlorophyll a level was also recorded at site 4 (2.55 $\mu g\ l^{-1}$). The lower phytoplankton population and chlorophyll a level of site 2 in comparison to 1m depth suggest again that under conditions of cloud cover, the surface population was more efficient at carbon fixation.

14th July / 15th July (Fig. 5.22):

Total cloud cover was evident over this period. There was persistent rain over the night of the 14th and the morning of the 15th with no windy periods. A Secchi disc reading of 4.15m was measured. The average surface incident light level during the 4h incubation period was 12.72 g cal $cm^{-1}min^{-1}$. The water temperatures at sites 1-4, 1m, 3m and 5m were; 16.9, 16.9, 16.9, 16.9, 16.9, 16.9 and 14.4 ^{o}C respectively. The highest rates of carbon fixation were measured at surface sites 2 and 4 (9.26 and 10.15 μg C (μg Chl a)$^{-1}$ h^{-1} respectively). A gradual reduction in the rate of carbon fixation with depth was observed, falling to 3.24 μg C (μg Chl a)$^{-1}$ h^{-1} at 5m. A low rate of carbon fixation was also measured at site 3 (4.33 μg C (μg Chl a)$^{-1}$ h^{-1}) despite the fact that the phytoplankton population was numerically the highest (10,949 l^{-1}). At site 1, despite a lower

phytoplankton population (4,984 l^{-1}), the chlorophyll a concentration was the highest (2.33 $\mu g\ l^{-1}$) as was also carbon fixation (18.6 μg C $l^{-1}h^{-1}$). Over the 24h period carbon fixation rates were lowest at site 2 (0.80 μg C (μg Chl a)$^{-1}$ h^{-1}) increasing at 1m (2.86 μg C (μg Chl a)$^{-1}$ h^{-1}) and decreasing again with depth. The highest 24h rates were measured at surface sites 1 (3.39 μg C (μg Chl a)$^{-1}$ h^{-1}) and 4 (4.61 μg C (μg Chl a)$^{-1}$ h^{-1}).

29th July / 30th July (Fig 5.22):

The weather over this 24h period was dry and sunny with no cloudy periods. Secchi disc depth was measured at 4.125m. The average surface light intensity level over the 4h incubation period was 28.74 g cal $cm^{-1}min^{-1}$. Over the 24h period the average was 9.86 g cal $cm^{-1}min^{-1}$. The water temperature at sites 1-4, 1m, 3m and 5m were: 20.60, 20.60, 21.00, 21.00, 20.60, 19.70 and 15.40 ^{o}C respectively. Previous to this date, the percentage oxygen saturation measured at all sites had been above 90%. On this day the percentage oxygen saturation measured at 5m was 72%. At surface sites 1,3 and 4 it was 87.5%, 88.5% and 83% respectively. At surface site 2 and 1m and 3m depth the oxygen concentration remained above 90% .

4h carbon fixation rates were highest at surface site 2 and at 3m depth (8.32 and 9.51 μg C (μg Chl a)$^{-1}$ h^{-1}) and lowest at surface sites 1, 3 and 4 (3.90, 4.14 and 2.03 μg C (μg Chl a)$^{-1}$ h^{-1} respectively). The lowest rate, at site 4, coincided with the largest phytoplankton population (14,945 l^{-1}) and chlorophyll a content (2.36 $\mu g\ l^{-1}$) recorded for that day. The results of the 24h carbon fixation estimation showed a slightly different pattern. 24h productivity was still higher at the surface site 2 (6.10 μg C (μg Chl a)$^{-1}$ h^{-1}) and at 3m (3.12 μg C (μg Chl a)$^{-1}$ h^{-1}) than at 1m and 5m (2.74 and 1.63 μg C (μg Chl a)$^{-1}$ h^{-1}) but the 24h rates of carbon fixation estimated for sites 1, 3 and 4 were higher than the corresponding 4h rates.

18th August / 19th August (Fig 5.22):

The weather over this 24h period was variable with alternating periods of warm sunshine and rain. A constant breeze blew. On the 19th,

grey cloud cover and rain characterised the day's weather pattern. Light penetration, as measured by Secchi disc extended to 4.25m on the 18th and 4.15m on the 19th. The water temperatures at sites 1-4, 1m, 3m and 5m were: 16.40, 16.10, 16.10, 15.70, 16.10, 16.10 and 15.40 ^{o}C respectively. The corresponding percentages of oxygen saturation were: 90%, 87.5%, 90%, 81%, 86%, 84% and 68% respectively.

4h carbon fixation rates were highest at surface site 2 (6.97 μg C (μg Chl a)$^{-1}$ h^{-1}) falling gradually with depth to 1.22 μg C (μg Chl a)$^{-1}$ h^{-1} at 5m. As on the 29th July, low primary production rates were measured for surface sites 1, 3 and 4 (2.06, 1.19 and 1.66 μg C (μg Chl a)$^{-1}$ h^{-1} respectively). The lower phytoplankton population and chlorophyll a concentration at surface site 2 in comparison to that at 1m depth suggest that the surface population was more efficient at carbon fixation. The greater phytoplankton populations at 3m and 5m were not reflected in higher productivity estimates. 24h carbon fixation estimates also indicated that production rates were highest at surface site 2, falling with depth and low at surface sites 1, 3 and 4.

1st September / 2nd September (Fig. 5.22):

The weather during this 24h period was sunny, with patchy, grey cloud cover and a strong, cold SW breeze. Light penetration extended to 4.05m on the 1st and 4.01m on the 2nd. The average surface incident light level during the 4h period of incubation was 20.37 g cal cm^{-1}min^{-1} while over the 24h period it was 7.22 g cal cm^{-1}min^{-1}. The water temperatures at sites 1-4, 1m, 3m and 5m were: 14.00, 13.30, 14.00, 14.00, 13.30, 13.20 and 13.20 ^{o}C respectively. The corresponding oxygen concentrations were: 86%, 87.5%, 83%, 88%, 87.5%, 85% and 81.5% respectively. The highest rate of 4h carbon fixation was measured at surface site 2 (6.33 μg C (μg Chl a)$^{-1}$ h^{-1}) falling gradually with depth to 1.09 μg C (μg Chl a)$^{-1}$ h^{-1}. As on the 29th July and the 18th August, 4h primary production rates at surface sites 1, 3 and 4 were low (1.00, 0.88 and 0.84 μg C (μg Chl a)$^{-1}$ h^{-1} respectively). The pattern of 24h carbon fixation was similar. The lower phytoplankton population and chlorophyll a content of site 2 in comparison to that at 1m (3,059 units l^{-1} and 2.29 μg Chl a l^{-1} as opposed to 9,069 l^{-1} and 3.14 μg l^{-1}) again suggest that the surface population was more

Table 5.5

Comparison of carbon fixation of surface samples from site 2 with depth samples from 1m.

Date	Surface		1m		3m		5m	
	a	b	a	b	a	b	a	b
22.7.82								
surface	5.80	4.53	6.80	5.31	5.90	4.61	5.39	4.22
1m	3.17	2.96	8.60	8.04	9.40	8.79	7.30	6.82
29.7.82								
surface	11.60	8.32	15.10	11.66	9.30	7.18	7.40	5.71
1m	2.80	2.14	9.80	7.45	10.70	8.14	5.70	4.34
19.8.82								
surface	8.20	3.29	12.20	4.90	3.80	1.53	0.60	0.24
1m	6.20	2.85	7.70	3.54	6.00	2.75	1.25	0.57
26.8.82								
surface	3.60	1.92	19.80	10.58	11.10	5.93	2.50	1.34
1m	3.20	1.77	17.90	9.92	10.00	5.54	2.10	1.16
2.9.82								
surface	2.60	0.98	21.10	7.97	13.10	4.95	2.50	0.95
1m	1.60	0.64	15.30	6.14	7.35	2.95	1.84	0.74

column heading a :- carbon fixation μg C l^{-1} h^{-1}

column heading b :- specific carbon fixation μg C (μg Chl a)$^{-1}$ h^{-1}

efficient at carbon fixation.

16th September / 17th September (Fig. 5.22):

The weather over this 24h period was overcast with grey cloud. Light penetration, as measured by Secchi disc was 3.20m. Water temperatures at sites 1-4, 1m, 3m and 5m were: 12.90, 12.90, 13.00, 13.00, 12.90, 12.40 and 11.85 ^{o}C respectively. The corresponding oxygen concentrations were: 91%, 91%, 92%, 99%, 92%, 83.5% and 82.5% respectively.

4h carbon fixation was highest at the surface sites and showed a gradual reduction with depth. 24h carbon fixation rates showed the same pattern. Of the four surface sites, carbon fixation at site 4 was the lowest (4h; 2.78, 24h; 1.47). The higher rates at the surface sites corresponded with higher phytoplankton populations than at depth.

One can summarise the results obtained for the period 18th March to 16th September as follows:-

1) During 8 out of 11 estimates, the rate of carbon fixation at surface site 2 (open water site) exceeded that at 1m, even when phytoplankton populations and chlorophyll a levels were lower.

2) Only on a very few occasions did carbon fixation at surface sites 1, 3 and 4 (the 'bays') exceed that of surface site 2 or 1m even when, particularly at site 4, the quantities of phytoplankton and chlorophyll a were greater.

5.3.2 Comparison of the photosynthetic efficiency of surface site 2 and 1m depth.

This series of experiments, described in section 3.9.2 are represented in Fig. 5.23 and Table 5.5.

On the 22nd July (dry and sunny) the rate of photosynthesis of the surface population varied little with depth (surface, 4.53; 1m, 5.31; 3m, 4.61 and 5m, 4.22 μg C (μg Chl a)$^{-1}$ h^{-1}). Marked surface inhibition

was noted when the 1m sample was incubated at the surface. Its increased, more efficient rate of photosynthesis at 1m, 3m and 5m indicated that these two samples came from physiologically quite distinct populations.

On the 29th July (dry and sunny) the response of the surface sample to changing light conditions again differed from that obtained from a 1m sample. Surface inhibiton was measured, with an increasing rate of carbon fixation at 1m (surface, 8.32; 1m, 11.66; 3m, 7.18 and 5m, 5.71 μg C (μg Chl a)$^{-1}$ h^{-1}). The photosynthetic efficiency of the 1m sample was less, with marked surface inhibition and a lower rate of photosynthesis at 1m (surface, 2.14; 1m, 7.45; 3m, 8.14 and 5m, 4.34 μg C (μg Chl a)$^{-1}$ h^{-1}). This again suggests that the two populations were quite distinct.

On the 19th August, 26th August and 2nd September, such a variation in response of surface and 1m samples was not observed.

The variation in response to increasing depth of surface and 1m samples on the 19th August (cloud cover) was small, with a slightly greater rate of carbon fixation at the surface and at 1m of the surface sample (surface sample at surface, 3.29 μg C (μg Chl a)$^{-1}$ h^{-1} and at 1m, 4.90 μg C (μg Chl a)$^{-1}$ h^{-1}. 1m sample at surface, 2.80 μg C (μg Chl a)$^{-1}$ h^{-1} and at 1m, 3.54 μg C (μg Chl a)$^{-1}$ h^{-1}). These slight differences suggest that the two populations were similar.

On the 26th August (rain, grey) the responses of the surface and 1m samples to changing light conditions were identical (Fig. 5.23). It is, therefore, highly probable that these two samples were from the same population.

On the 2nd September (patchy, grey clouds, rain) the responses of the two samples were, again, similar. The surface sample was slightly more efficient than the 1m sample (Fig. 5.23) suggesting that these two samples, while they shared a common origin, were in the process of becoming distict populations.

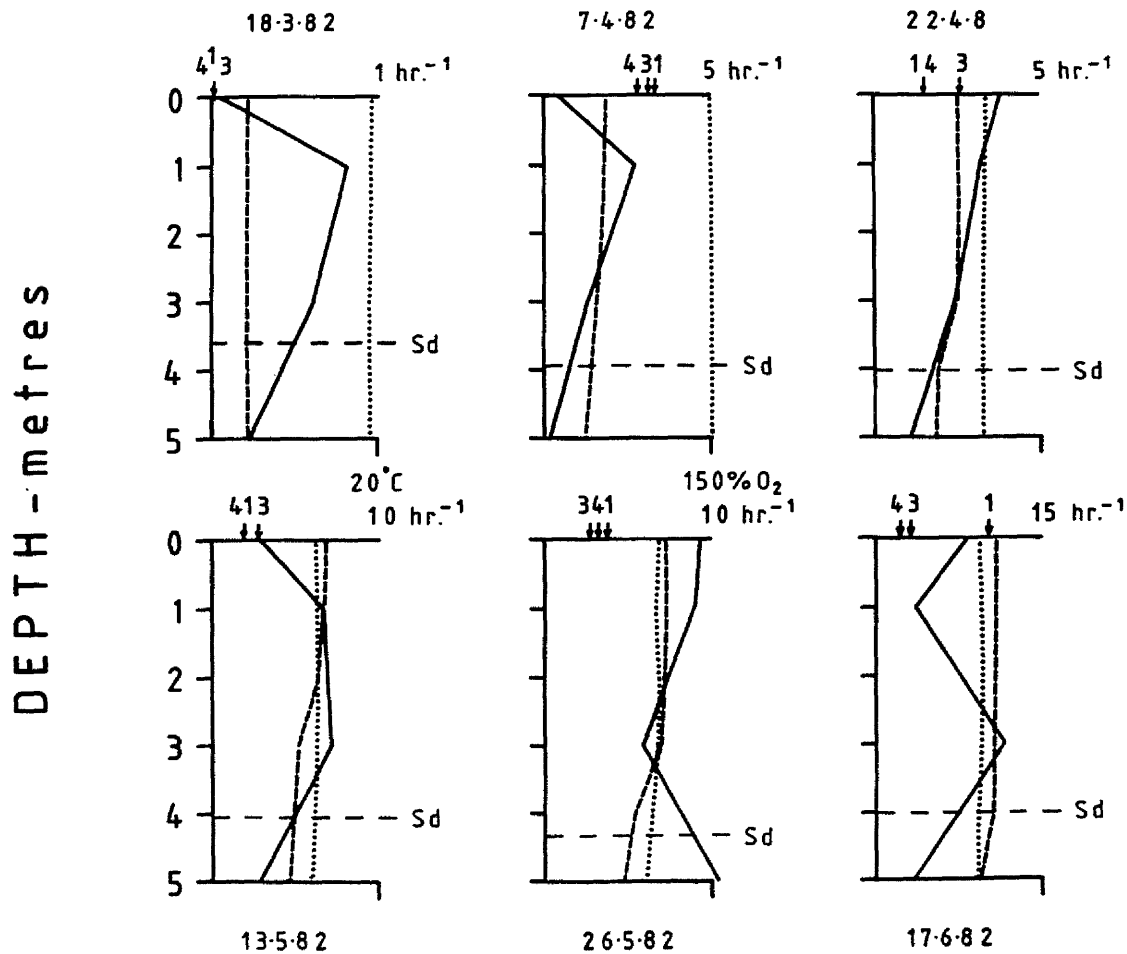

DEPTH - metres
18·3·82
4 1 3
1 hr.⁻¹
7·4·82
4 3 1
5 hr.⁻¹
22·4·82
1 4 3
5 hr.⁻¹
20°C
4 1 3
10 hr.⁻¹
150% O2
3 4 1
10 hr.⁻¹
4 3 1
15 hr.⁻¹
Sd
0
1
2
3
4
5
13·5·82
26·5·82
17·6·82

Figure 5.21

Specific rates of photosynthesis at site 2.

18th March 1982 - 17th June 1982

solid line:- specific photosynthetic rate μg C (μg Chl a)$^{-1}$ h^{-1}

dashed line:- temperature ^{o}C

dotted line:- percentage oxygen saturation

upper scale:- μg C (μg Chl a)$^{-1}$ h^{-1}

lower scale:- temperature ^{o}C and oxygen % saturation

specific photosynthetic rates for surface sites 1, 3 and 4 are indicated by arrow

Secchi disc reading ---Sd

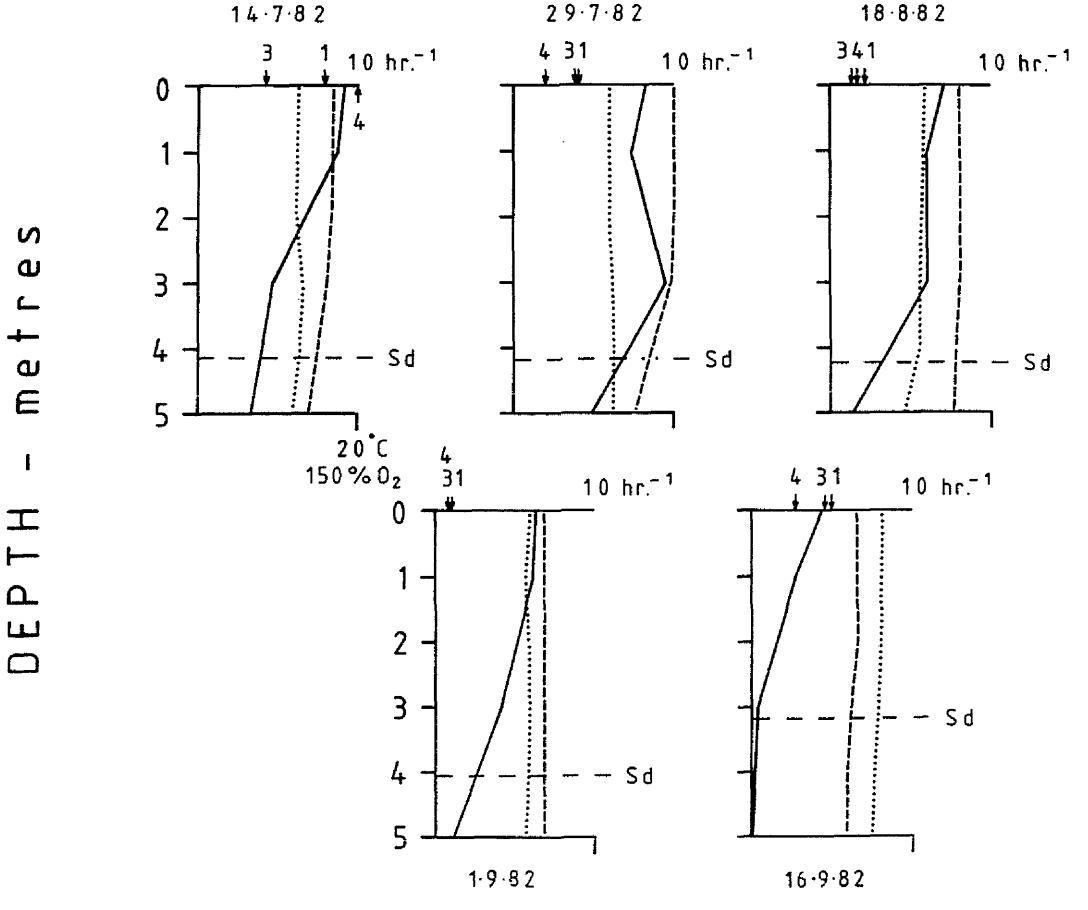

DEPTH - metres
14·7·82
3
1
10 hr.⁻¹
4
29·7·82
4 31
10 hr.⁻¹
18·8·82
341
10 hr.⁻¹
Sd
20°C
150% O2
4
31
1·9·82
16·9·82
0
1
2
3
4
5

Figure 5.22

Specific rates of photosynthesis at site 2.

14th July 1982 - 16th September 1982

solid line:- specific photosynthetic rate μg C (μg Chl a)$^{-1}$ h^{-1}

dashed line:- temperature ^{o}C

dotted line:- percentage oxygen saturation

upper scale:- μg C (μg Chl a)$^{-1}$ h^{-1}

lower scale:- temperature ^{o}C and oxygen % saturation

specific photosynthetic rates for surface sites 1, 3 and 4 are indicated by arrow

Secchi disc reading ---Sd

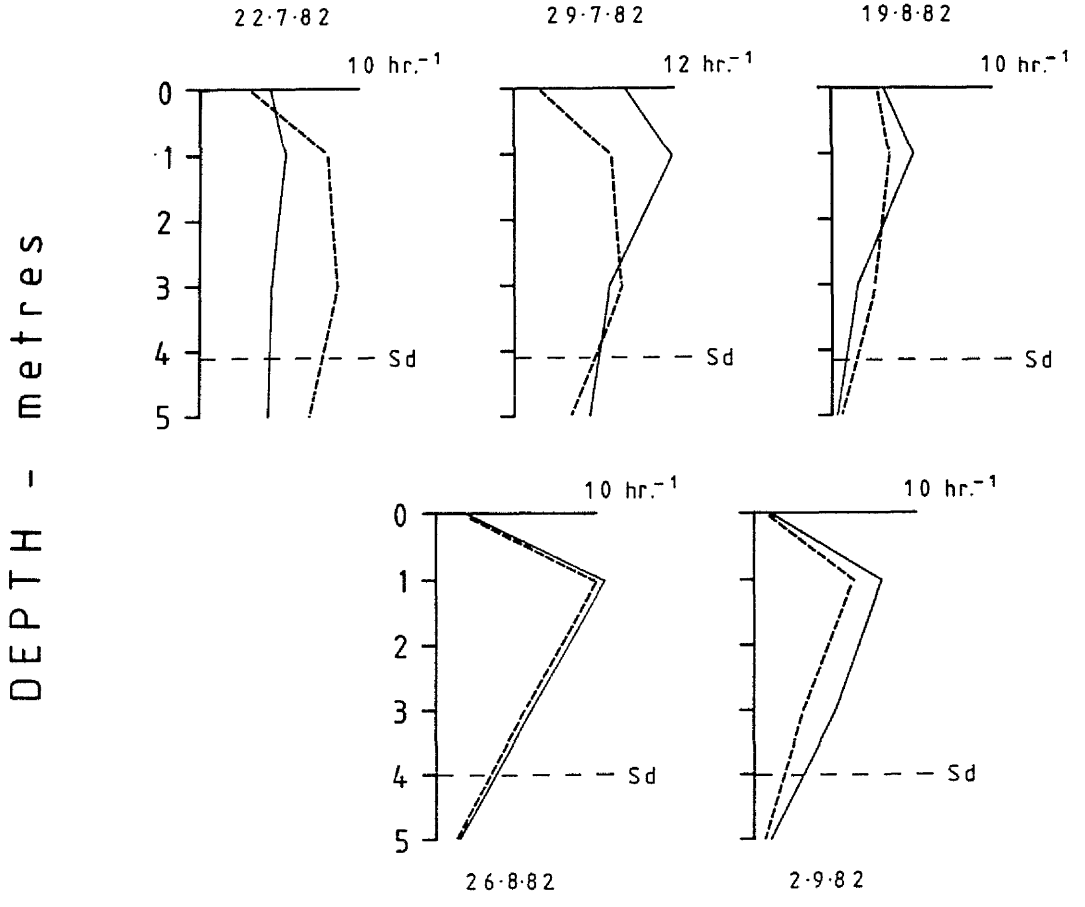

22·7·82
10 hr.⁻¹
29·7·82
12 hr.⁻¹
19·8·82
10 hr.⁻¹
0
1
2
3
4
5
Sd
Sd
Sd
DEPTH - metres
10 hr.⁻¹
10 hr.⁻¹
0
1
2
3
4
5
Sd
Sd
26·8·82
2·9·82

Figure 5.23

Comparative specific photosynthetic rates of surface site 2 and 1m.

22nd July 1982 - 2nd September 1982

solid line:- site 2 suspended at depth sites

dashed line:- 1m depth suspended at depth

upper scale:- specific photosynthetic rate μg C (μg Chl a)$^{-1}$ h^{-1}

An examination of the comparison of phytoplankton populations and chlorophyll a levels revealed that though differences in phytoplankton quantity and chlorophyll a concentration existed, there were no real differences in phytoplankton composition between the two samples on any of the collection dates. This points to the possibility of photoadaptation of the populations. Photoinhibition at the surface was evident for both the surface and the 1m samples but on the 29th July, 19th August and 2nd September the surface sample was better able to utilize the more amenable light conditions at depth, suggesting an ability to respond rapidly to changing light conditions. Such an ability would be a distinct advantage to a surface population.

5.4 DISCUSSION

5.4.1 General community pattern

The general community pattern of the phytoplankton of the upper 5m of the Dubh Lochan during the period July 1980 to September 1982 can be summarised as follows:

During the winter biomass minima of 1980/1981, the green nanoplankton dominated the population together with lower densities of diatoms and cryptophytes. Population maxima under the ice were observed to be dominated by unicellular green algae. Such accumulation of algae under ice cover has been previously reported, for example, in Swedish lakes (Nebaeus, 1984) and is a positive phototactic response to low levels of incident radiation. After ice melt the green algae dominated; the spring increase in the phytoplankton population being composed primarily of green unicellular algae (*Sphaerocystis* cells) and *Asterococcus limneticus*. The peaks in phytoplankton biomass recorded in the summer were caused by an increase in the number of *Sphaerocystis schroeteri* colonies and by a rapid increase the blue-green algal population of *Synechococcus* spp and *Aphanothece saxicola*. The population maxima of the blue greens preceded that of *Sphaerocystis* and during this period the blue-greens were, numerically, the dominant component of the phytoplankton. As the phytoplankton population declined to winter levels the unicellular green algae again assumed dominance and as in the winter of 1980/1981, an increase in the

proportion of diatoms, cryptophytes and chrysophytes was observed. The winter maxima under the ice were again dominated by green nanoplankton.

The community pattern during 1982 differed from that of 1981 in two ways. Firstly the maximum phytoplankton biomass recorded at any site or depth was one seventh of that measured in 1981. Secondly the summer dominance by the blue-green algae was preceded by an increase in the population of *Dinobryon divergens*, which coincided with a decrease in the phosphate content of the surface layer to less than $2\mu g\ l^{-1}$.

This community pattern differs from that recorded by both Klarer (1978) and Islam (1987) who also used a fortnightly sampling programme. Both reported a population in which green nanoflagellates dominated through much of the year, the nanoflagellates being replaced in the spring by *Dinobryon divergens* followed by a summer shift in dominance to *Sphaerocystis schroeteri*. The population decline in autumn was accompanied by a return to dominance by the nanoflagellates.

During this study the green flagellates were only observed in number on one occasion. Instead non-flagellated unicellular algae which could not be distinguished from the colony-bound cells of *Sphaerocystis schroeteri* predominated. It is therefore likely that these cells were the broken remains of *Sphaerocystis* colonies; broken by turbulence, as would happen in autumn, by grazing, as reported by Porter (1976) or during collection and subsequent filtration. *Dinobryon divergens* was only observed in 1982 and in lower numbers than reported by Islam (1987). Also, fewer *Chlamydomonas* spp and *Oocystis* spp were observed with no periodicity to their distribution pattern. Islam (1987) reported that in the summer the phytoplankton biomass was influenced by the rapid growth of *Sphaerocystis*. During this study the rapid growth of blue-greens was responsible for the observed summer biomass. Islam (1987) measured total phytoplankton biomasses in the epilimnion in the range of 1×10^4 to $220 \times 10^5\ l^{-1}$. During this study the total phytoplankton biomasses were much lower, ranging from 634 to $1.1 \times 10^5\ l^{-1}$. The population maxima recorded in 1980 and 1982 were equivalent to Islam's minima. One could postulate that perturbation of the pH during this period was responsible for these observed low phytoplankon populations.

Similarly,the drastic reduction in the total phytoplankton population during 1982 may be linked with the lack of an increase in the phosphate-phosphorus content of the surface layer at overturn in 1981 and hence only the small increase in phosphorus levels recorded in 1982. Though it should be pointed out that the possibility exists that the phytoplankton population increase may have been missed due to a reduced sampling programme in June.

The decline in silicate-silica levels during the summer periods could not be linked with either an increase in diatom biomass or an increase in *Dinobryon* and other siliceous algae. Rather, the observed decline in silica would have been caused by the growth of littoral, epiphytic and benthic diatoms.

5.4.2 The surface layer.

A similarity in species composition between the top 5 mm of the Dubh Lochan and the subsurface waters was observed. All except *Golenkinia radiata* were recorded at all the sites and depths sampled and can considered as either planktonic or benthic in nature. The relative abundance of those species recorded at the surface layer was observed to vary, both species and temporal differences in the surface accumulation of algae was evident.

The most noticeable surface accumulations were of the non-motile diatoms; *Cyclotella glomerata, C. compta, Peroniopsis heribaudi* and *Achnanthes saxonica,* all of which were observed in greater abundance at the surface layer throughout the 2 year survey. *Achnanthes saxonica* by means of mucilage secretion via the raphe, would have been able to attach itself to the surface film. Petersen and Hansen (1960) have observed *Achnanthes minutissima* and *Nitzschia* moving along the underside of the surface film. Both *Cyclotella* spp and *Peroniopsis,* the former by virtue of its small size, the latter by virtue of its lightness, would have been brought to the surface layer and trapped there by means of turbulence and rising bubbles. Such a method of enrichment is known to operate for the bacteria (Blanchard and Syzdek, 1982).

The surface accumulation of *Synechococcus* spp and *Aphanothece saxicola* during their periods of rapid growth can be explained by the possible buoyancy of these algae. Such a mechanism has already been postulated to explain the surface accumulation of blue-green algae during blooms (see e.g. Reynolds and Walsby, 1975). Petersen and Hansen (1960) have also used such an arguement to explain the accumulation of *Botryococcus*, *Aphanizomenon* and *Microcystis* species.

The positive accumulation of the dinoflagellate *Gymnodinium* sp was, since this is a motile species, probably a positive phototactic response to the low level of insolation (total cloud cover) recorded on that sampling date. While both *Gymnodinium* spp and *Peridinium* spp were observed in only low numbers, there was still evidence of some surface accumulation.

Sphaerocystis schroeteri, the green unicellular alga (*Sphaerocystis* cells) and *Asterococcus limneticus* are non-motile algae which were recorded at all the depths sampled. The surface accumulation of both *Sphaerocystis* colonies and *Asterococcus* cells were recorded after their periods of rapid growth. Such an accumulation of algae which are part of a declining population suggests an alteration of their buoyancy mechanism. These algae were no longer able to accumulate preferentially at depth. As in the case of the non-motile diatoms *Cymbella* spp, *Sphaerocystis* cells may have accumulated as a result of becoming trapped, having been brought to the surface layer by turbulence and rising bubbles.

The recorded incident of surface accumulation of the flagellates *Chlamydomonas* spp were probably the result of a positive phototactic response. This same explanation can be used explain the surface accumulation of *Dinobryon divergens* during its population maximum. While *Cryptomonas* spp were recorded preferentially at 3 m and 5 m, higher accumulations at the surface in comparison to 1 m depth were noted, particularly after ice melt and at site 4. Such a preferential distribution of these species suggests a preference for sites of higher nutrient loading. A similar arguement can be applied in the case of *Mallomonas* spp and *Trachelomonas* spp.

The observed higher accumulations of algae at site 4 rather than at sites 1, 2 or 3 were probably caused by wind driven lateral displacement of the open water flora into the bay. The northern end of the loch is exposed and winds were observed to blow preferentially from the north, having been channelled through the Loch Lomond basin. That these populations were the result of wind driven accumulation rather than from development within the littoral flora was supported by the observation that no qualitative differences existed in species composition between site 4 and site 2.

The variation in the distribution pattern of the species recorded and the lack of any assemblage of unique species at the surface layer suggests that the assemblages of phytoplankton recorded at the top 5 mm of the Dubh Lochan were the result of constant, transient movement of the algae between the surface and subsurface waters and the benthos. The presence of an independent, self-reproducing, isolated community, as recorded by Frolund (1977) was highly unlikely. This finding is supported by the fact that, during the periods of stratification, when phytoplankton levels were high, the chlorophyll c concentration was consistently less than that of chlorophyll a. Hardy and Apts (1984) found that the unique assemblage of microalgae recorded at the surface microlayer of Sequim Bay was associated with high chlorophyll c to chlorophyll a ratios. This, they concluded, was an indication of the photoadaptation of the flagellate populations to higher light intensities. The lack of surface enrichment of chlorophyll c in the surface layer of the Dubh Lochan is therefore indicative of the presence of a transient population and the lack of a unique neustonic assemblage. This transience of surface layer populations has also been reported by Hatcher and Parker (1974) and Estep and Remsen (1984). By comparison of the data collected in this study with those of workers mentioned in the Introduction, one can conclude that in large open bodies of water which are subject to wind stress, the development of a stable community of typically neustonic organisms at the surface film is rare. Such communities require the presence of a stable surface film and the lack of wind shear stress. Turbulent conditions do not allow the development of the flotation discs and stalks reported by Naumann (1924), Babienzen (1966), Babienzen and Schwartz (1970) and Frolund

(1977).

While surface accumulation of microalgae may occur, this does not give any indication, in terms of their specific production rates of the physiological state of the algae. The productivity data collected in this study suggests that, even when surface enrichment has not been recorded and particularly during overcast conditions, the surface layer exhibits a higher specific rate of photosynthesis. In temperate regions with an oceanic climate the contribution of the surface layer to the overall production of the lake system may prove quite significant. Also, the responses of surface site 2 populations to changing light conditions differed on two occasions from that measured in 1 m populations, indicating the possibility of photoadaptation of the surface populations. As Harris (1978) has pointed out, photoadaptation of a phytoplankton population *in situ* can take 1 - 2 days i.e. 1 - 2 algal division times. The phytoplankton population must therefore reside at a given depth in the water column for a period of a day or two if any cellular response to depth induced light intensity changes is to be expected. This suggests that when the photosynthetic responses of surface site 2 and 1m populations were identical, that the residence times of the phytoplankton populations at the surface layer were insufficient to allow photoadaptation. These findings further exemplify the transient nature of the surface layer phytoplankton population since distinct surface populations were only recorded during a period of prolonged dry, calm weather. When rain or wind was prevalent no distinction between the surface and 1m populations in terms of their photosynthetic response to changing light levels was recorded together with the presence of marked photoinhibition at the surface.

The photoinhibition exhibited by samples collected from near or in littoral areas and in particular, that shown by samples collected at site 4, under varying light conditions suggests that two possible mechanisms were in effect. The algae may have been exhibiting an allelopathic response to exudates from the macrophyte flora. Since this inhibition was most noticeable at site 4 one could further postulate that *Nuphar* and *Nymphaea* were the sources of this exudate. Or, high light intensities coupled with a large algal population quickly lead to a decrease in pCO_2 and an increase in pO_2 resulting in photorespiration

and the release of ^{14}C as glycollate and $^{14}CO_2$. Both hypotheses would adequately explain the low recorded rates of carbon fixation observed at the bay areas but only by further experimentation could one conclude which, if either, were the main mechanism.

Chapter 6

The zooplankton and other members of the surface biota.

Table 6.1

Species composition of the zooplankton of Dubh Lochan

COPEPODA

Acanthocyclops latipes (Lowndes)
languidoides var *hypnicola* Gurney
Cyclops prasinus Fischer, Schmeil
viridis Jurine
Eudiaptomus gracilis Sars.
laciniatus Lilljeborg
Eucyclops agilis Koch, Sars.
macruroides var *denticulatus* Graeter
macrurus Sars.
Halicyclops aequordus Fischer
Microcyclops bicolor Sars.
Paracyclops fimbriatus Fischer

CLADOCERA

Alona affinis Leydig
costata Sars.
elegans Kurz.
guttata Sars.
Alonella excisa Fischer
nana Baird
Alonopsis elongata Sars.
Bosmina coregoni var *obtusirostris* Sars.
Ceriodaphnia quadrangula O. F. Muller
Chydorus ovalis Kurz.
Diaphanosoma brachyurum Lieven
Eurycerus lamellatus O. F. Muller
Holopedium gibberum Zaddach
Moina brachiata Jurine
Peracantha truncata O. F. Muller
Polyphemus pediculus L.
Sida crystallina O. F. Muller
Streblocerus serricaudatus Fischer

ROTIFERA

Ascomorpha ecaudis Perty
ovalis Carlin
Asplanchna herriki de Guerne
priodonta Gosse
Asplanchnopus multiceps Schrank
Conochilus unicornis Rousselet
Epiphanes macrourus Daday
senta Muller
Euchlanis dilatata Ehrb.
Filinia terminalis Plate
Gastropus sp
stylifer Imhof
Kellicottia longispina Kellicott
Keratella cochlearis Gosse
quadrata Muller
var *testudo*
var *valgoides*
serrulata Ehrb.
Lecane lunaris Ehr.
ploenensis M. Voight
saginata Harr. n. My.
Lecane sp
Lepadella ovalis Muller
Monommata longiseta Muller
Platyias quadricornis Ehrb.
Ploesoma hudsoni Imhof
Polyarthra vulgaris Carlin
Synchaeta pectinata Ehr.
Trichosera longiseta Schrank
Trichotoma tetractis Ehr.

Other members of the surface biota found primarily at site 4.

Protozoa; various amoeboid and ciliated protozoa, including a heliozoan and stalked vorticellids, one of which was free swimming.

Eggs; fish, beetle and snail eggs were observed floating at the surface film at site 4.

Larvae; larval stages of the following groups and genera, observed in low numbers, were found usually at site 4:

Argulus foliaceus	(Copepoda. parasite)	
Atripogon sp	(Perigona)	hyponeustonic
Chironomus sp	(chironomid)	hyponeustonic
Corixidae		hyponeustonic
Culex sp	(Culicidae)	hyponeustonic
Dytisus sp	(Dystiscidae)	hyponeustonic
Isopoda		
Hydrometra sp	(Gerridae)	hyponeustonic
Proisotoma sp	(Isotominae)	hyponeustonic
Thaumalea sp		

Adults; adults of the following groups and genera were observed at the surface layer, mainly at site 4.

Culex sp	(Culicidae)	
Hygrobates sp	(Hydracarina)	
Hydrometra sp	(Gerridae)	epineustonic
Megapus sp	(Hydracarina)	
Proisotoma sp	(Isotominae)	epineustomic
Macrobiotus sp	(Tardigrada)	

Zooplankton

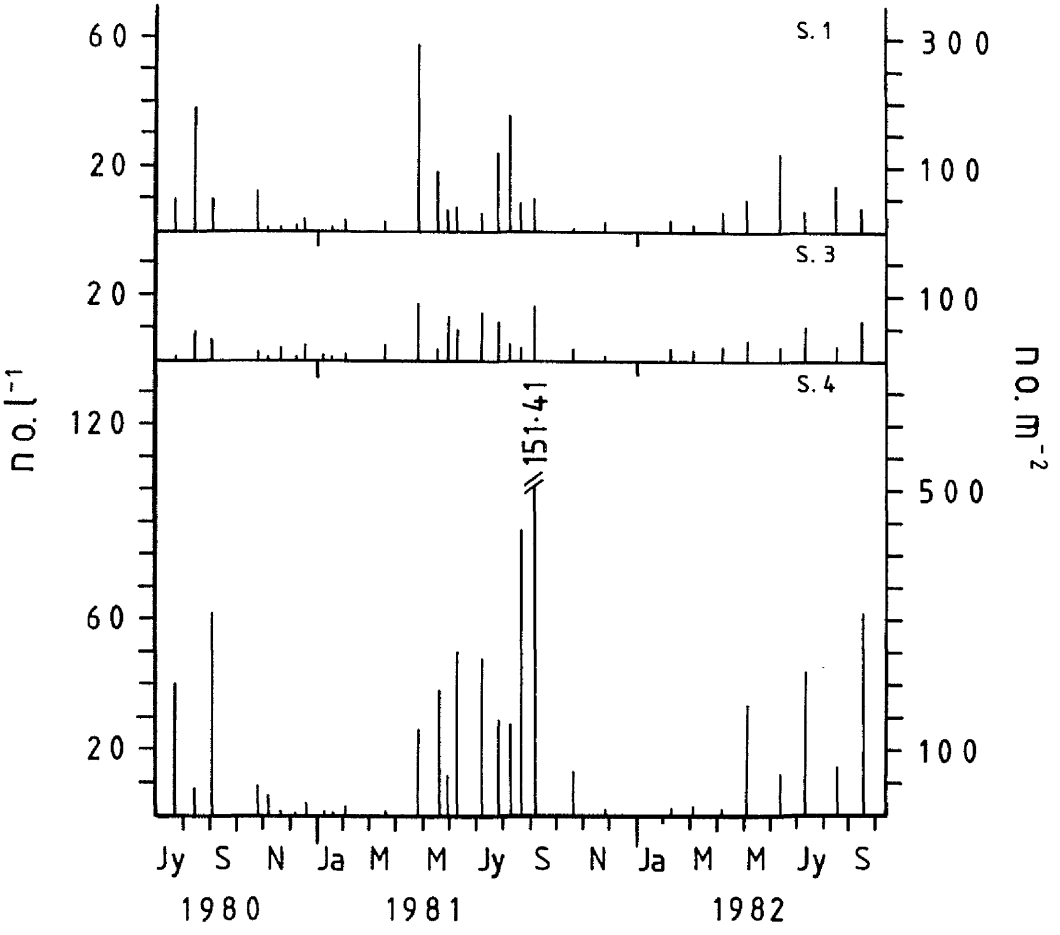


Figure 6.1

Zooplankton biomass, surface sites 1, 3 and 4.

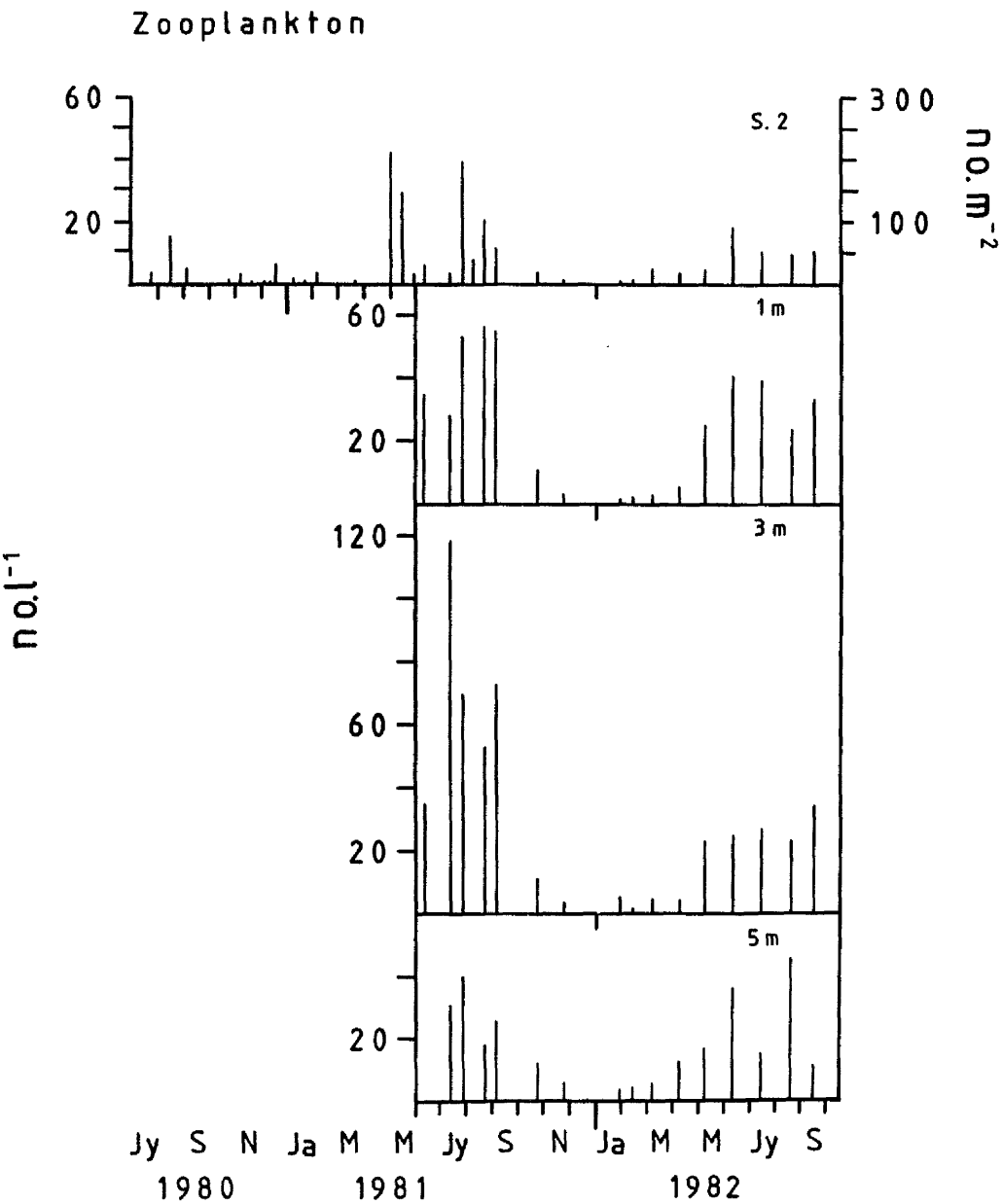

Zooplankton
60
20
300
100
S. 2
no.m-2
1m
60
20
3m
120
60
20
5m
20
no.l-1
Jy S N Ja M M Jy S N Ja M M Jy S
1980
1981
1982

Figure 6.2

Zooplankton biomass, surface site 2 and at depth.

6.1 THE ZOOPLANKTON : TAXONOMIC COMPOSITION (Table 6.1)

12 spp of Copepoda, 18 spp of Cladocera and 30 spp of Rotifera were identified as components of the zooplankton. For these 60 spp in the Dubh Lochan, 7 spp of Copepoda, 6 spp of Cladocera and 2 spp of Rotifera were added to the lists of Klarer (1978) and Islam (1987). One copepod species, 5 spp of Cladocera and 7 spp of Rotifera recorded in previous studies were not found. All the new records, except *Eudiaptomus laciniatus*, were found at littoral site 4. *Eudiaptomus laciniatus* was probably introduced by accident during one of the numerous field courses held at Rowardennan Field Station, from Loch Lomond and was recorded for only a very short time.

Protozoa, various eggs and the larvae and adults of Coleoptera, Hemiptera, Diptera, Collembola, Acarina, Tardigrada and a parasitic member of the Copepoda, *Argulus foliaceus* were also found as components of the surface layer.

6.1.2 The zooplankton; general features.

The zooplankton of the Dubh Lochan exhibited a seasonal distributional pattern (Figs. 6.1 and 6.2). Variations in the zooplankton population between the sites was recorded. Seasonally, maxima were recorded in April/May , July and August/September, corresponding with the phytoplankton maxima reported in sections 5.1.2 and 5.1.3. The greatest numbers of zooplankton measured, were recorded at 3m and at site 4, whilst the smallest quantities of zooplankton measured during this survey were recorded at site 3.

During July 1980 to December 1980, the quantities of zooplankton varied between 0.56 l^{-1} and 37.90 l^{-1} at site 1, zero and 15.20 l^{-1} at site 2, 0.38 l^{-1} and 7.69 l^{-1} at site 3 and between 0.19 l^{-1} and 62.11 l^{-1} at site 4. At the start of the survey (24th July), the largest zooplankton population was recorded at site 4 (39.78 l^{-1}) whilst increases in zooplankton quantity occurred at sites 1-3 in August (37.90 l^{-1} at site 1, 15.20 l^{-1} at site 2 and 8.63 l^{-1} at site 3). A further increase in the zooplankton population at site 4 was recorded

in September (62.11 l^{-1}). During October, a fall in the population was measured at sites 2-4 with a slight increase at site 1 (12.20 l^{-1}). A continued fall in numbers was recorded during November and the beginning of December. On the 4th December, a thin layer of ice was formed, corresponding with low zooplankton estimates (zero to 2.25 l^{-1}). A thaw in the ice cover in the latter part of December was accompanied by an increase in zooplankton to between 3.19 l^{-1} and 6.00 l^{-1}.

During 1981, the zooplankton population varied between 0.71 l^{-1} and 57.41 l^{-1} at site 1, 0.75 l^{-1} and 42.03 l^{-1} at site 2, 0.56 l^{-1} and 17.45 l^{-1} at site 3, 0.19 l^{-1} and 151.41 l^{-1} at site 4, 2.82 l^{-1} and 56.10 l^{-1} at 1m, 3.75 l^{-1} and 118 .01 l^{-1} at 3m and between 5.44 l^{-1} and 40.15 l^{-1} at 5m.

Three zooplankton population maxima were observed in 1981. The first in April/May, the second in July and the third in August/September. These increases in the zooplankton were closely associated with preceding maxima in the phytoplankton populations (sections 5.1.2 and 5.1.3).

Between 0.38 l^{-1} and 4.88 l^{-1} zooplankton were observed, after ice melt, in March. By the end of April the population had risen to between 17.45 l^{-1} and 57.41 l^{-1}. A further increase was recorded on the 14th May at site 4 (37.15 l^{-1}). The second recorded increase in the zooplankton did not occur at all the sites at the same time, rather, the increase was staggered. It was first recorded at site 4 in June (49.34 l^{-1}), then at site 3 on the 9th July (14.07 l^{-1}), at site 2 on the 23rd July (38.47 l^{-1}) and finally at site 1 on the 6th August (35.65 l^{-1}). At depth, zooplankton maxima were recorded on the 9th July at 3m (118.01 l^{-1}) and on the 23rd July at 5m (40.15 l^{-1}). A further increase in the number of zooplankton was recorded on the 20th August at sites 2 (19.89 l^{-1}) and 4 (87.62 l^{-1}). The greatest number of zooplankton recorded at the surface during this survey was measured at site 4 in September 1981 (151.41 l^{-1}), so corresponding with the peak in zooplankton recorded at this site in September 1980. Small increases in the quantity of zooplankton were also recorded at sites 3 (16.51 l^{-1}) and 1 (9.38 l^{-1}) during September. At depth, between 18.39 l^{-1} and

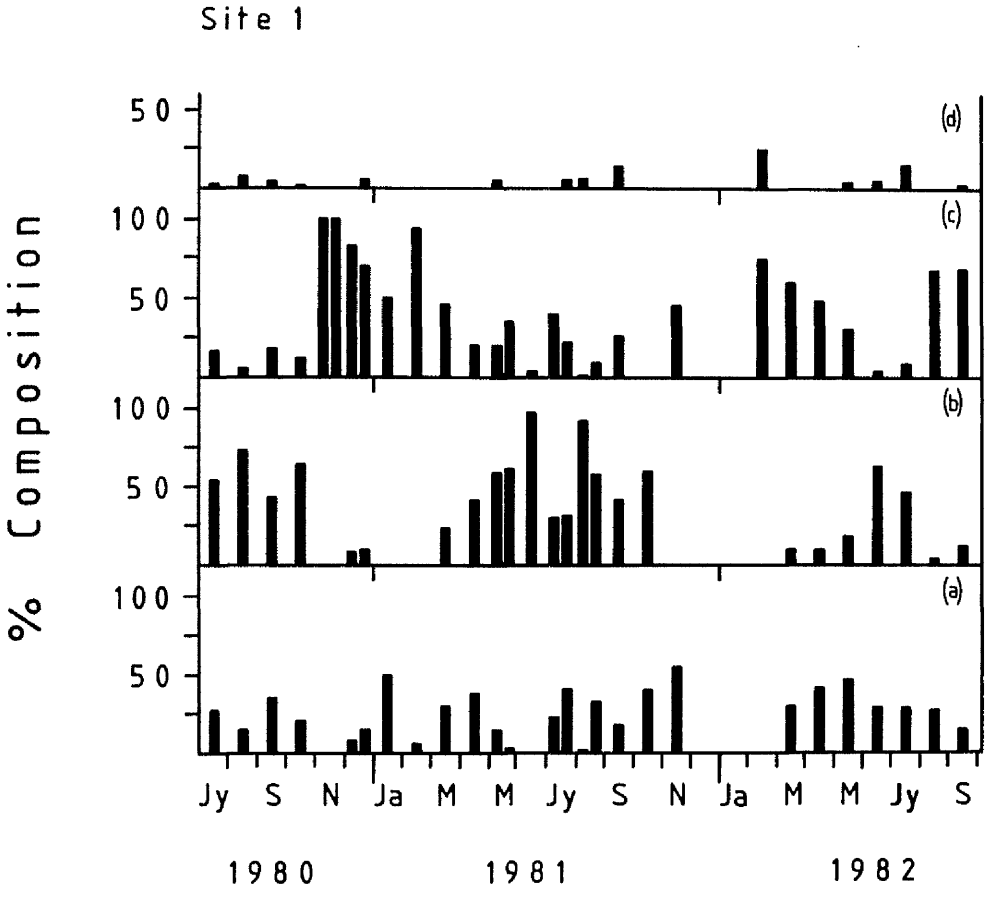

Site 1
% Composition
50
100
50
100
50
100
50
(d)
(c)
(b)
(a)
Jy S N Ja M M Jy S N Ja M M Jy S
1980
1981
1982

Figure 6.3

Percentage biomass of the zooplankton of site 1.

a) Copepoda

b) Cladocera

c) Rotifera

d) Others

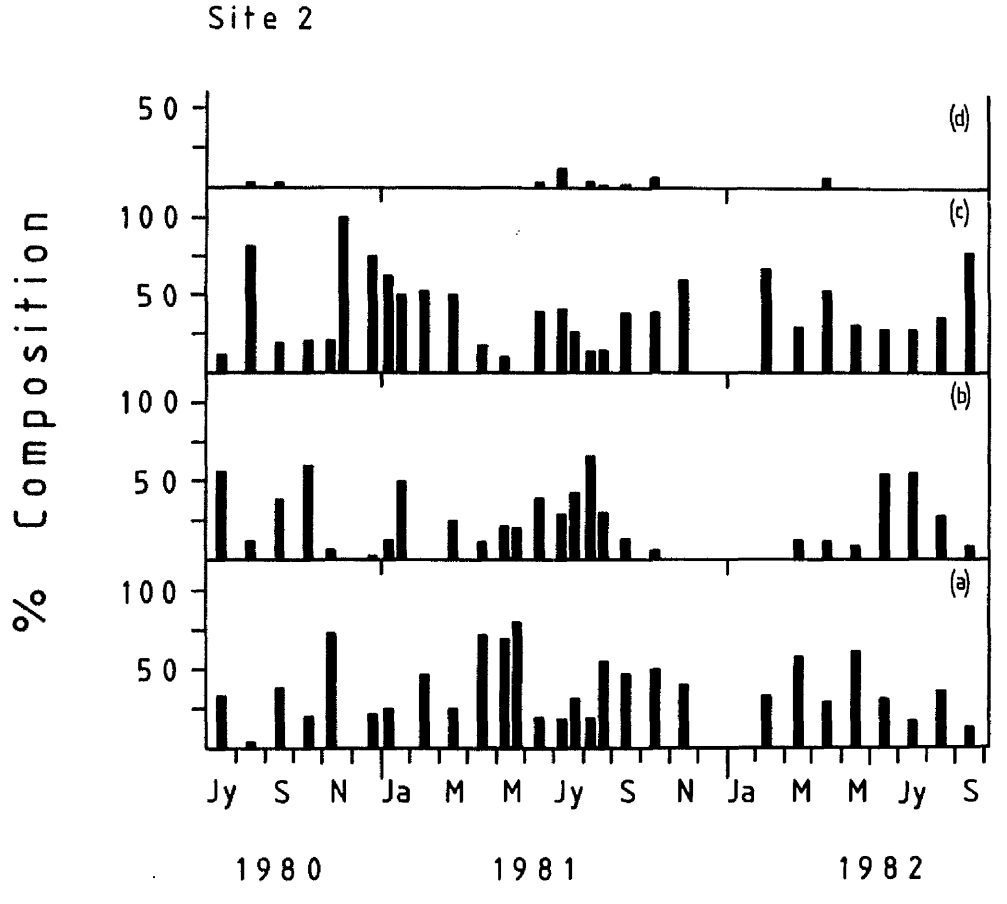

Site 2
% Composition
50
100
50
100
50
100
50
(d)
(c)
(b)
(a)
Jy S N Ja M M Jy S N Ja M M Jy S
1980
1981
1982

Figure 6.4

Percentage biomass of the zooplankton of site 2.

a) Copepoda

b) Cladocera

c) Rotifera

d) Others

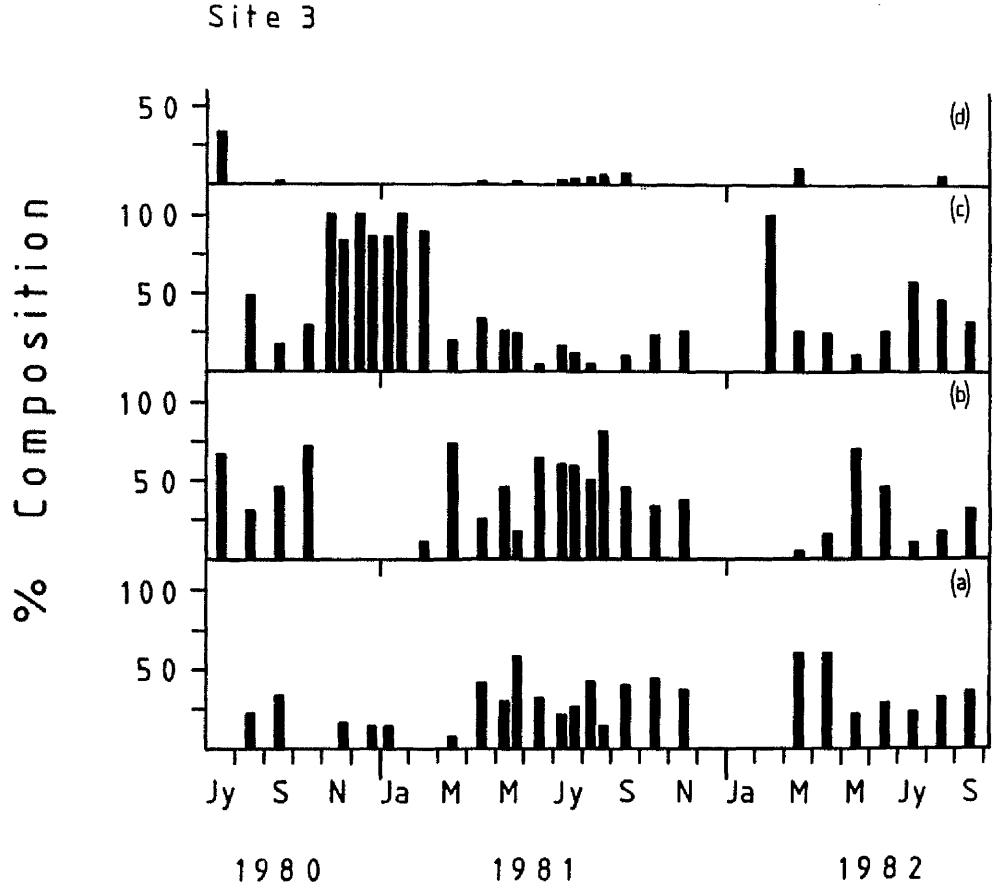

Site 3
% Composition
50
100
50
100
50
100
50
(d)
(c)
(b)
(a)
Jy S N Ja M M Jy S N Ja M M Jy S
1980
1981
1982

Figure 6.5

Percentage biomass of the zooplankton of site 3.

a) Copepoda

b) Cladocera

c) Rotifera

d) Others

Site 4

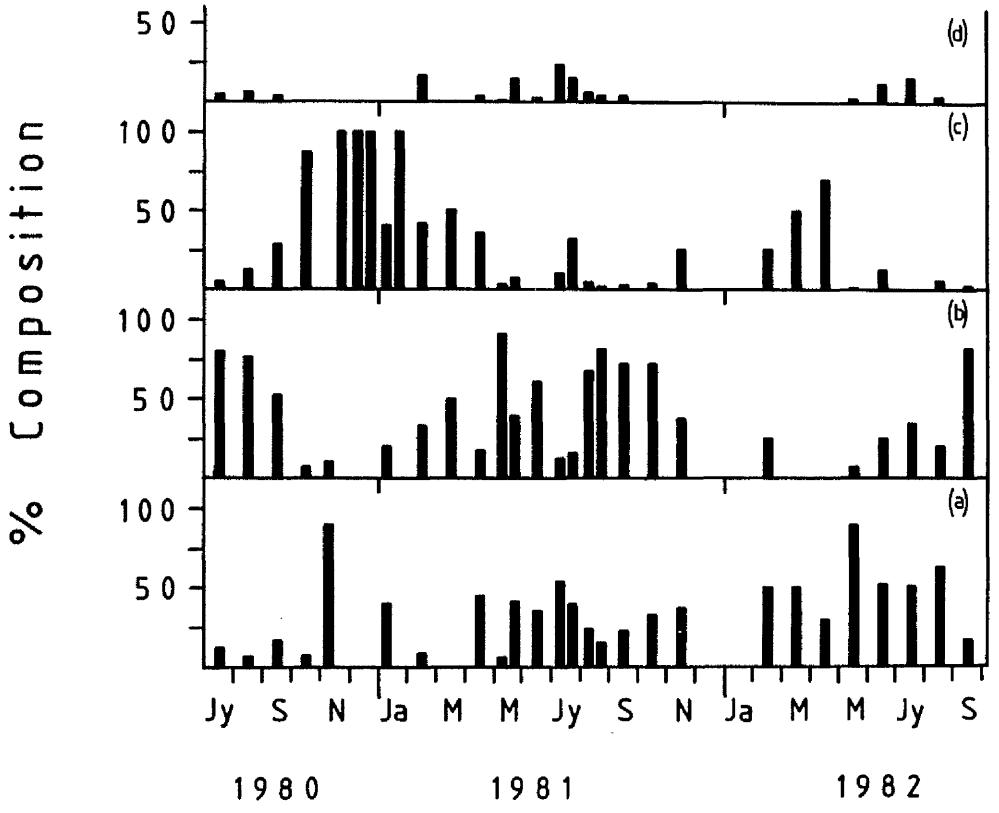

% Composition
50
(d)
100
50
(c)
100
50
(b)
100
50
(a)
Jy S N Ja M M Jy S N Ja M M Jy S
1980
1981
1982

Figure 6.6

Percentage biomass of the zooplankton of site 4.

a) Copepoda

b) Cladocera

c) Rotifera

d) Others

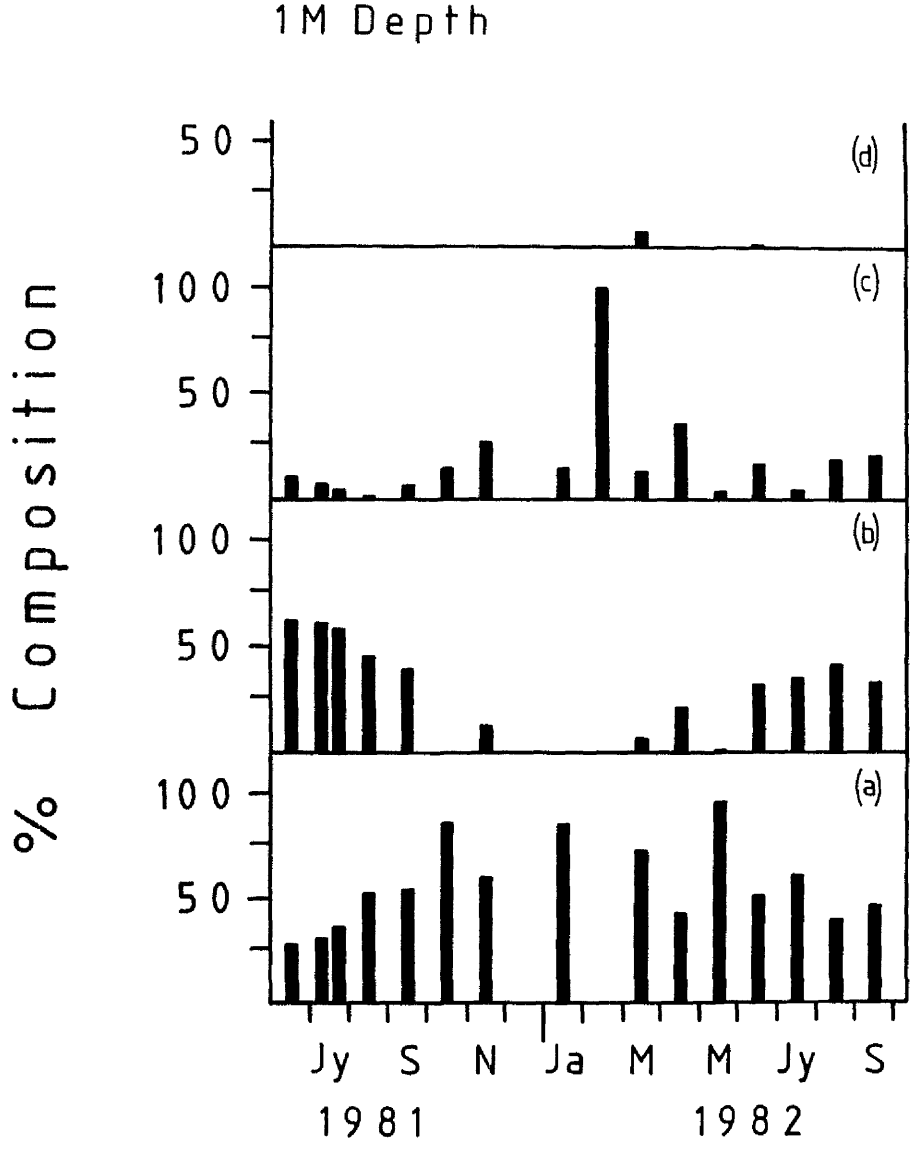

1M Depth
% Composition
50
(d)
100
50
(c)
100
50
(b)
100
50
(a)
Jy
S
N
Ja
M
M
Jy
S
1981
1982

Figure 6.7

Percentage biomass composition of the zooplankton of 1m depth.

a) Copepoda

b) Cladocera

c) Rotifera

d) Others

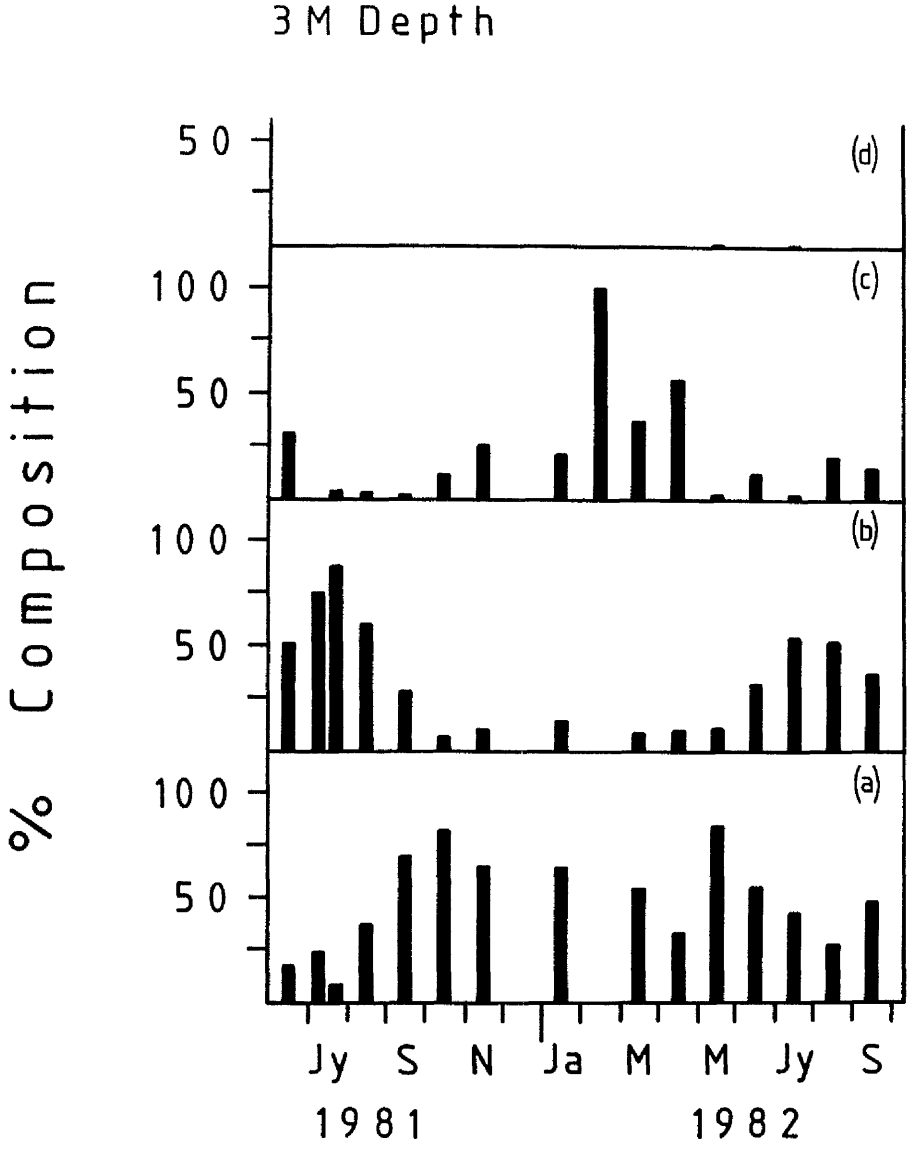

3 M Depth
% Composition
50
100
50
100
50
100
50
(d)
(c)
(b)
(a)
Jy
S
N
Ja
M
M
Jy
S
1981
1982

Figure 6.8

Percentage biomass composition of the zooplankton of 3m depth.

a) Copepoda

b) Cladocera

c) Rotifera

d) Others

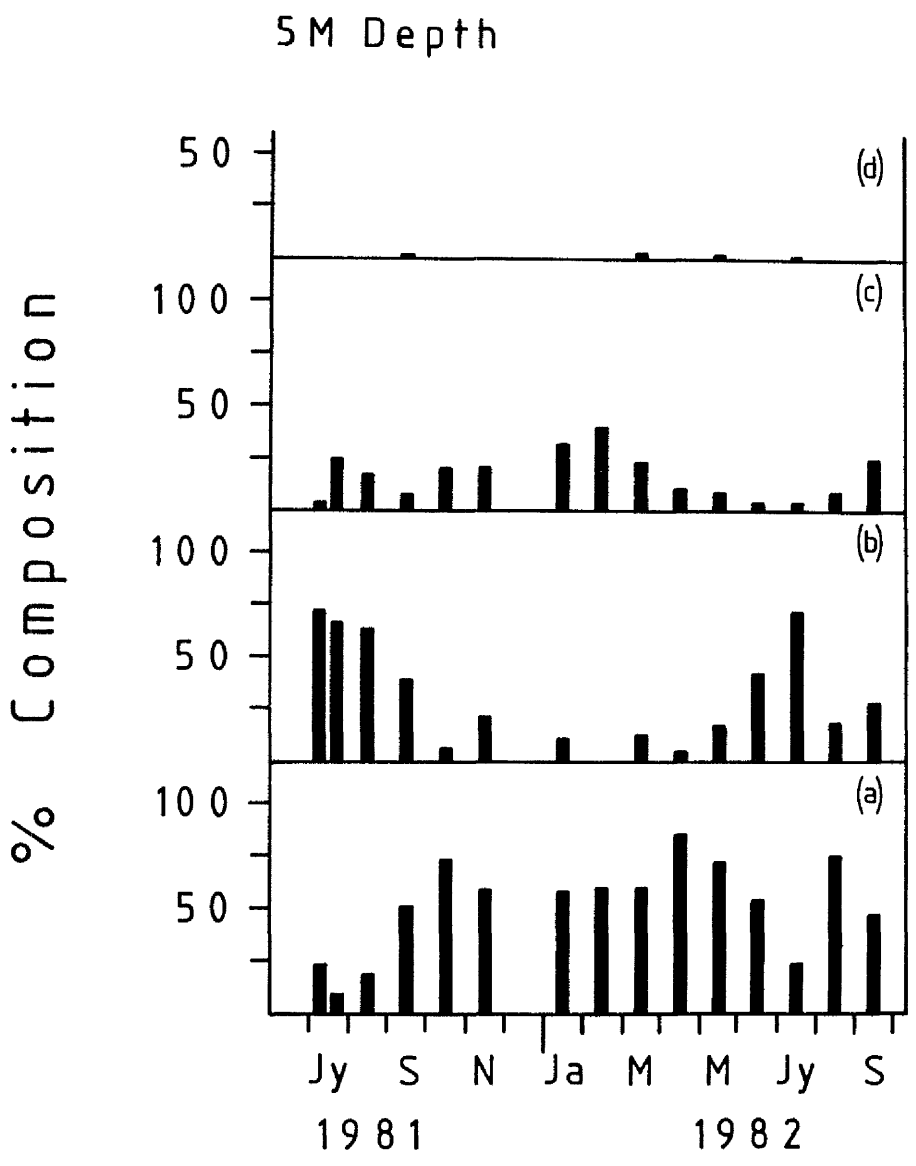

5M Depth
% Composition
50
100
50
100
50
100
50
(d)
(c)
(b)
(a)
Jy
S
N
Ja
M
M
Jy
S
1981
1982

Figure 6.9

Percentage biomass composition of the zooplankton of 5m depth.

a) Copepoda

b) Cladocera

c) Rotifera

d) Others

72.42 l^{-1} were recorded. By October, a dramatic fall in the zooplankton population had been recorded at both the surface sites and depths sites and by November the population ranged between only 2.82 l^{-1} and 5.44 l^{-1}.

During the period of ice cover in the winter of 1981/1982 samples were collected through the ice and on the 27th January the following quantities were recorded ; just below the ice, 2.63 l^{-1}; at 1m, 1.31 l^{-1}; at 3m, 5.25 l^{-1} and at 5m, 3.57 l^{-1}. As in 1981, the first large increases in the zooplankton populations were recorded at the beginning of May at site 4 (33.77 l^{-1}) and at depth (24.58 l^{-1} at 1m, 22.70 l^{-1} at 3m and 16.51 l^{-1}). Further peaks were recorded in June at sites 1 and 2 (24.21.l^{-1} and 18.20 l^{-1} respectively) and at depth (4.34 l^{-1} at 1m, 24.39 l^{-1} at 3m and 35.83 l^{-1} at 5m). On the 13th July a second increase in the zooplankton population of site 4 was noted (43.53 l^{-1}) The largest number recorded at site 3 also occurred on this date and was only 10.70 l^{-1}. At the close of the survey, further increases in the populations were observed at sites 2-4 (10.73 l^{-1}, 11.28 l^{-1} and 61.27 l^{-1} respectively) and 1m and 3m depths (32.9 $l^{-1}$and 34.11 l^{-1} respectively).

To summarise, the largest populations were continually recorded at depth, surface accumulation of zooplankton was rare. The only surface site at which zooplankton were continually found in large numbers was site 4.

6.1.3 The zooplankton; biomass composition

An examination of the percentage biomass composition of the zooplankton revealed two superimposed cyclic patterns of alternation of dominance (Figs. 6.3-6.9). the most obvous was an alternation of the cladoceran and rotiferan populations. The second was an alternation of the cladoceran and copepod populations, particularly noticeable at depth.

In terms of percentage biomass, the rotifers were dominant in the winter when the zooplankton population was numerically very low, the cladocerans dominated in summer and the copepods dominated in autumn

and winter (Figs. 5.3-5.6).

A spatial distribution of the representative zooplankton was evident. The cladocerans *Alona guttata, A. costata, Alonella excisa, Chydorus ovalis, Peracantha truncata* and *Polyphemus pediculus*, the cyclopid copepods and larval and adult forms of Coleoptera, Hemiptera, Diptera, Collembola, Acarina and Tardigrada occurred mainly in the bay areas, particularly at site 4. The copepod *Eudiaptomus gracilis* and the cladocerans *Diaphanosoma brachyurum, Ceriodaphnia quadrangula,* and *Holopedium gibberum* were found mainly in open water, at depth.

The cyclopid copepoda, dominated by the *Eucyclops* spp,displayed summer maxima, disappearing in winter (Fig. 6.10). They were only found in any great number at site 4, among the *Nuphar* and *Nymphaea* and rarely in open water. During 1980, the largest population recorded occurred in July (4.50 l^{-1}). During 1981, the summer maxima were recorded at site 4 and consisted of two peaks, the first in July (21.76 l^{-1}) and the second in September (7.32 l^{-1}). During 1982 the largest population was recorded at site 4 in July (7.32 l^{-1}), as in 1981.

Polyphemus pediculus is a cladoceran normally associated with the margins of lakes. It was recorded predominantly at site 4 and rarely in open water, with maxima in summer and disappearing in winter (Fig.6.11). During 1980, the largest population was recorded at the start of the survey at site 4 (6.57 l^{-1}). During 1981, three peaks in *Polyphemus* numbers were recorded. The first, in May, was at site 4 (33.40 l^{-1}), with a small rise in the population at site 1 (4.88 l^{-1}) and the second in June (28.33 l^{-1}) together with a small rise in population at site 3 (5.07 l^{-1}). The third increase was measured first at the beginning of August at site 1 (30.96 l^{-1}) and then at the end of August at site 4 (20.08 l^{-1}). Smaller nuumbers of *Polyphemus* were also recorded at sites 1 and 3 (3.57 l^{-1} and 2.25 l^{-1} respectively). During 1982, the population maxima were numerically smaller with peaks at site 4 of only 10.69 l^{-1} in July and 4.91 l^{-1} in September.

The chydorid cladoceran *Peracantha truncata* exhibited the same distributional and seasonal pattern as *Polyphemus*, being found rarely in open water, mainly at site 4 amongst the *Nuphar and Nymphaea* and in

large numbers only in the summer months (Fig. 6.12). During 1980, large populations were observed from July to the beginning of September, particularly at site 4 (maximum 22.89 l^{-1}) and at site 1 (maximum 25.52 l^{-1}). This pattern was repeated in 1981 (maximum 99.06 l^{-1}). During 1982, a large population was only attained in September (41.64 l^{-1}).

Other members of the family Chydoridae: *Chydorus ovalis* (Fig.6.11),*Alona costata, A. guttata* (Fig. 6.13), *A. affinis, A. elegans, Alonopsis elongata*, (Fig. 6.12), *Eurycerus lamellatus*, *Alonella excisa* and *A. nana* (Fig. 6.13) were found rarely in open waters and more commonly at the surface sites in the spring (*Alona costata*) and summer months.

The distribution of both the adult and larval stages of the Coleoptera, Hemiptera, Diptera, Collembola, Acarina and Tardigrada and of the ciliated protozoa also showed a seasonal pattern, being found mainly at site 4 in the summer months (Fig. 6.14). The most common components were the larvae of *Chironomus* sp, the water mite *Hygrobates* sp and free swimming stalked vorticellids. During both July 1981 and July 1982, free swimming vorticellids were numerous (10.70 l^{-1} and 6.00 l^{-1} respectively). Both *Chironomus* lavae and *Hygrobates sp* were found during May to September 1981 and 1982, forming large populations at site 4 in September 1981 (1.88 $l^{-1}$of *Hygrobates* and 3.75 l^{-1} of *Chironomus*).

The copepod *Eudiaptomus gracilis* was found primarily in open water, at depth and rarely at the surface at site 4 (Fig. 6.15).The greatest populations of *Eudiaptomus* were recorded in the summer months, only a few records were made in the winter. During 1981, peaks were recorded for *Eudiaptomus* in late April and May at the surface, particularly at sites 1 (11.82 l^{-1}) and 2 (16.70 l^{-1}) followed by a smaller increase in numbers at site 3 by the end of May (7.51 l^{-1}). Further increases in the *Eudiaptomus* population were recorded in July, particularly at 3m (21.95 l^{-1}) and in September at 1m (21.01 l^{-1}) and 3m (36.96 l^{-1}). During 1982, population maxima were recorded in July (22.51 l^{-1} at 1m) and September (14.91 l^{-1} at 3m) with less than 2.18 l^{-1} being found at the surface sites throughout the year.

Eudiaptomus laciniatus, a common inhabitant of the plankton of Loch Lomond, was recorded on the 9th July 1981 (0.38 l^{-1}) and on the 20th August 1981 at 1m (4.88 l^{-1}) and 3m (5.44 l^{-1}). As stated previously, this species had probably been accidentally introduced during a student field course but was unable to survive in the Dubh Lochan for any length of time. One can postulate that either the adult form was unable to survive in the loch's acidic nature or, more probably, the decreased pH caused a dramatic decrease in the survival rate of it's eggs.

The nauplii of *Eudiaptomus* and *Cyclops* spp were found at both the surface and depth sites with summer maxima and only a very few (< 1 l^{-1}) in winter (Fig. 6.16). The *Eudiaptomus* nauplii were predominant. During 1980, only a small increase in September was observed in the surface populations (maximum 5.82 l^{-1} at site 4). A second smaller increase in November was noted at site 4 (3.94 l^{-1}). During 1981, the first increase in the naupliid population was recorded in April, particularly at sites 2 and 4 (13.70 l^{-1} and 13.13 l^{-1} respectively) At site 3 the population maximum was observed in June (11.26 l^{-1}). The second large increase was recorded in September, particularly at site 4 (15.57 l^{-1}) and at depth (8.44 l^{-1} at 1m, 13.32 l^{-1} at 3m and 7.32 l^{-1} at 5m. During 1982, a rise in the population was first recorded in May (30.21 l^{-1} at site 4, 15.57 l^{-1} at 1m, 11.63 l^{-1} at 3m and 6.75 l^{-1} at 5m) with a further increase in the naupliid population at 5m in June (13.31 l^{-1}). A third peak was measured at site 4 in July (14.82 l^{-1}).

The nauplii of *Eudiaptomus gracilis* exhibited a much wider habitat range than the adult. This may be an important consideration to take into account when conducting population studies in the Dubh Lochan.

The cladocerans *Holopedium gibberum, Ceriodaphnia quadrangula and Diaphanosoma brachyurum* possessed similar distribution patterns i.e. summer maxima, disappearing in winter and more frequent in open water, at depth.

During 1980, the largest number of *Holopedium* occurring at the surface was recorded in September at site 3 (2.63 l^{-1}) (Fig. 6.17). During 1981, a small increase in the number of *Holopedium* was recorded

at site 2 in spring (3.57 l^{-1}). *Holopedium* was most abundant from June to September with large numbers recorded at 3m in July (15.01 l^{-1}) and at 1m in August (16.70 l^{-1}). During 1982, no spring increase in surface numbers was observed. At depth, the maxima occurred from June to September but the population recorded was much lower, reaching only 11.63 l^{-1} at 3m in August.

In 1981 *Ceriodaphnia quadrangula* was found in large numbers at depth only, a peak was recorded in July (1.13 l^{-1} at surface site 2, 1.50 l^{-1} at 1m, 21.39 l^{-1} at 3m and 21.95 l^{-1}at 5m, Fig. 6.18).

Diaphanosoma brachyurum was also found in larger numbers in 1981 than in 1982, with summer maxima in July and August 1981 and in June in 1982 (Fig. 6.19). In July 1981 the largest populations were recorded at 3m (56.10 l^{-1} and 30.40 l^{-1}) with a population of 14.82 l^{-1} at 1m and of 10.51 l^{-1} at the surface. During August, the largest population was again recorded at 3m (14.26 l^{-1}). During 1982, no large surface populations were recorded and the maximum occured in July at 3m (10.32 l^{-1}).

*Bosmin*a *coregoni* was found both at the surface, particularly at site 1, and at depth but not in the large numbers recorded for the previously mentioned cladocerans. Summer maxima were observed. Only a few *Bosminia* were found in autumn, winter and spring. In 1981, the first recorded increase in the population occurred in April at site 1 (17.82 l^{-1}). A smaller increase in numbers was measured in June 1982. Again, the greatest number was recorded at site 1 (12.38 l^{-1}). Large numbers were also recorded at site 2 (5.63 l^{-1}), 1m (6.75 l^{-1}), 3m (2.25 l^{-1}) and 5m (3.75 l^{-1}).

Kellicottia longispina and *Keratella* spp were the most consistent members of the rotiferan zooplankton population but were rarely found in numbers greater than 2 l^{-1}. (Figs. 6.21, 6.22). During December 1980, winter maxima of *Kellicotia* were observed under the thin layer of ice; at site 3 on the 11th December (3.38 l^{-1}) and at all four surface sites on the 18th December (2.06 l^{-1} at site 1, 3.94 l^{-1} at site 2 and 3.19 l^{-1} at sites 3 and 4.). *Kellicottia* were observed in samples collected from under the ice on the 5th February 1981 (2.81 l^{-1} at site

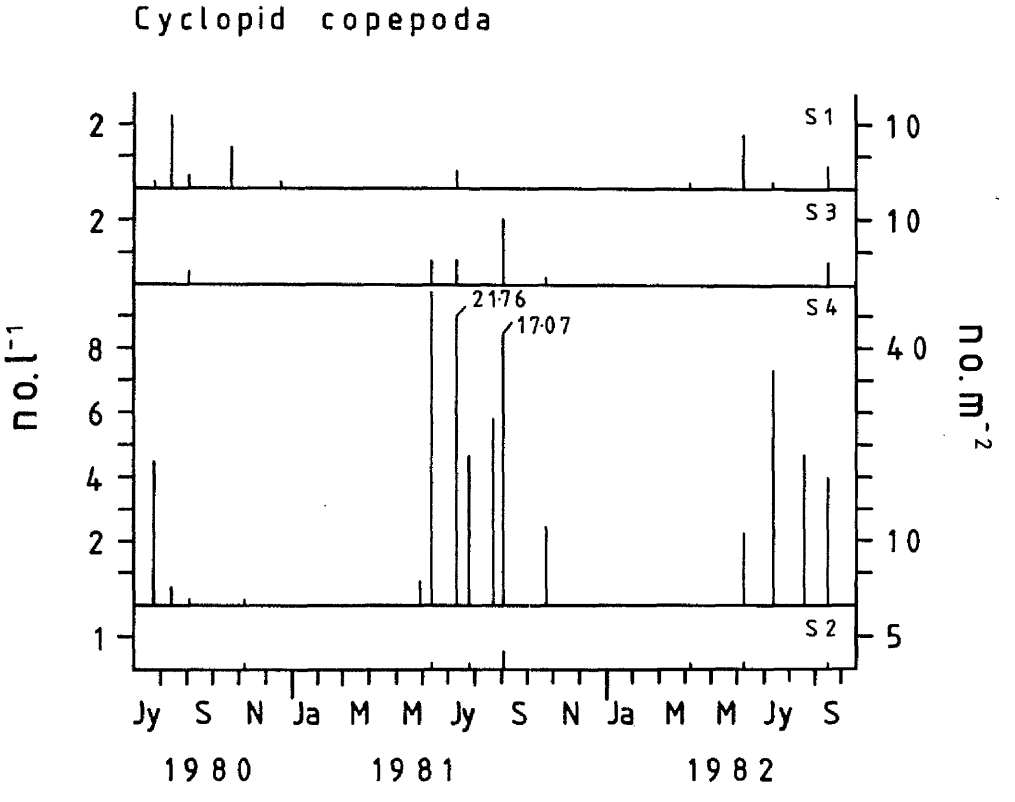

Cyclopid copepoda
S1
S3
S4
S2
21·76
17·07
no.l⁻¹
no.m⁻²
2
2
8
6
4
2
1
10
10
40
10
5
Jy S N Ja M M Jy S N Ja M M Jy S
1980
1981
1982

Figure 6.10

The cyclopid copepoda

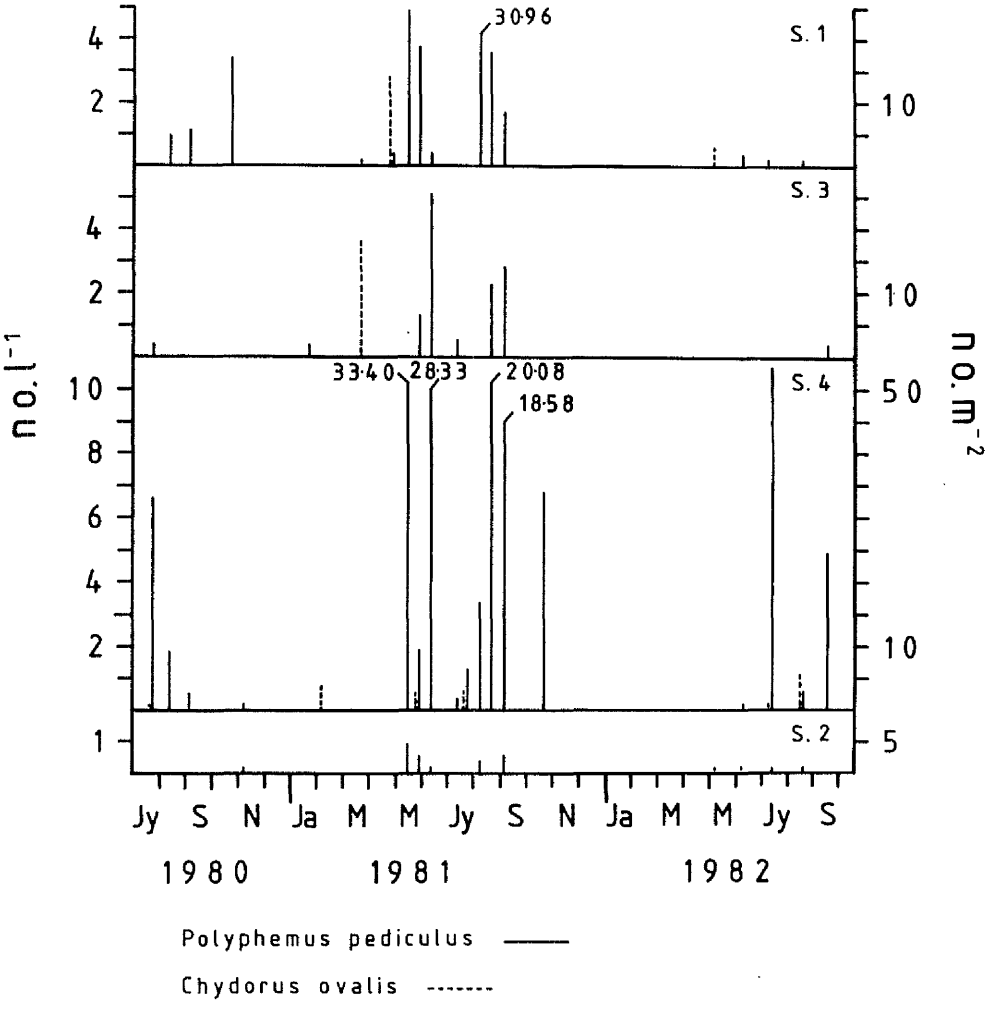

30·96
S. 1
S. 3
33·40
28·33
20·08
18·58
S. 4
S. 2
n o. l⁻¹
n o. m⁻²
Jy S N Ja M M Jy S N Ja M M Jy S
1980
1981
1982
Polyphemus pediculus
Chydorus ovalis

Figure 6.11

Polyphemus pediculus **and** *Chydorus ovalis*

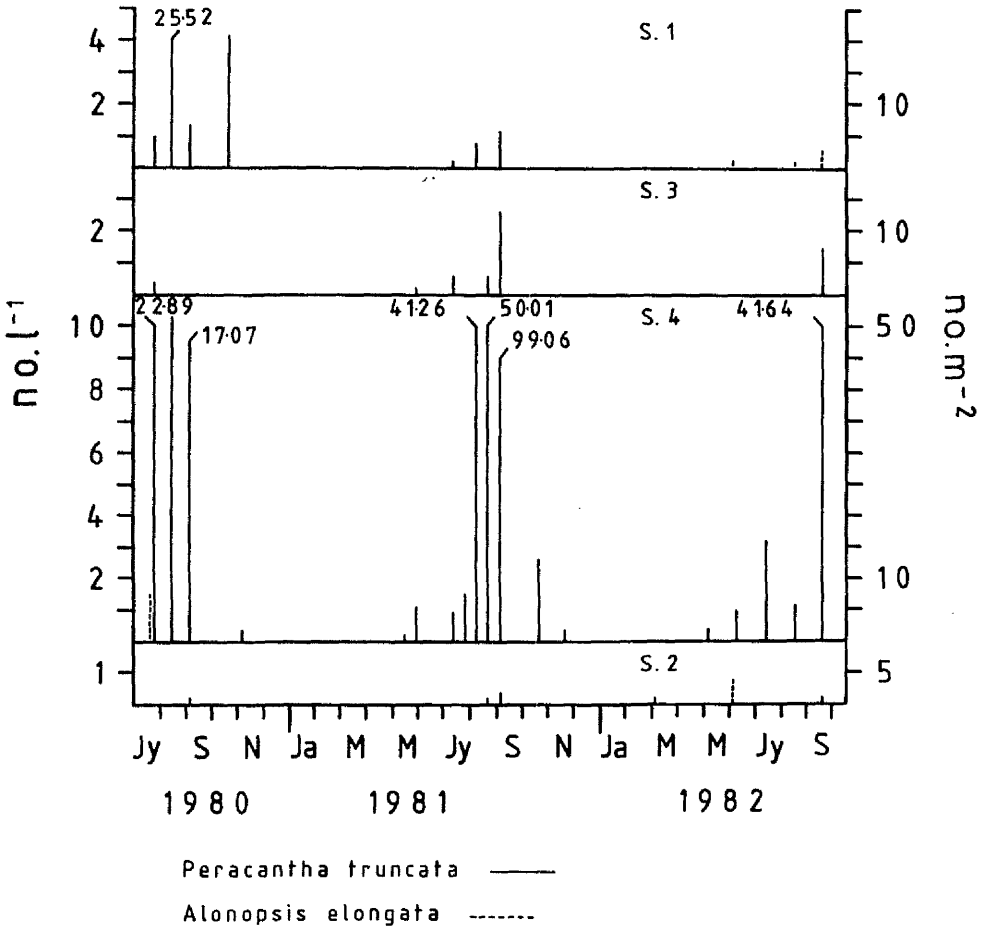

25·52
S. 1
S. 3
22·89
17·07
41·26
50·01
99·06
S. 4
41·64
S. 2
no. l⁻¹
no. m⁻²
Jy S N Ja M M Jy S N Ja M M Jy S
1980
1981
1982
Peracantha truncata
Alonopsis elongata

Figure 6.12

Peracantha truncata and *Alonopsis elongata*

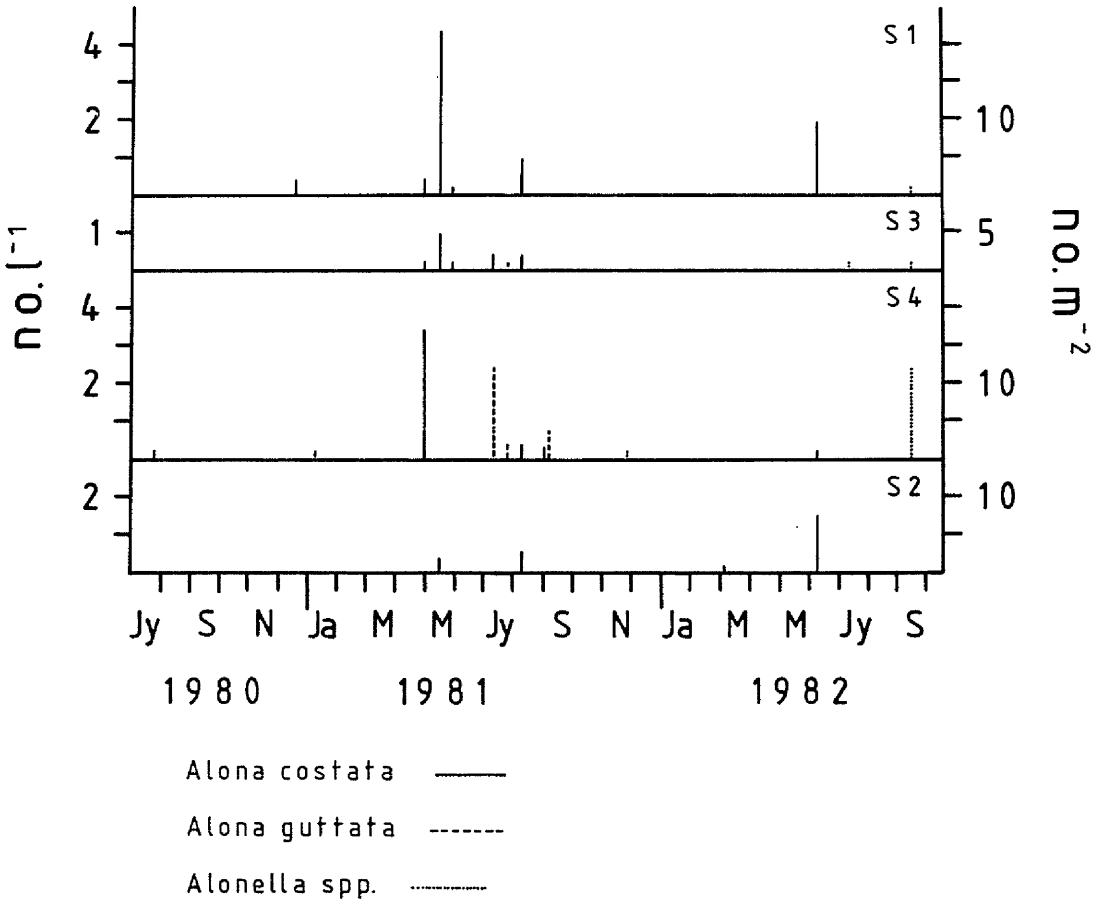

S1
S3
S4
S2
4
2
1
4
2
2
10
5
10
10
no. l⁻¹
no. m⁻²
Jy S N Ja M M Jy S N Ja M M Jy S
1980
1981
1982
Alona costata
Alona guttata
Alonella spp.

Figure 6.13

Alona costata, *Alona guttata* **and** *Alonella* **spp**

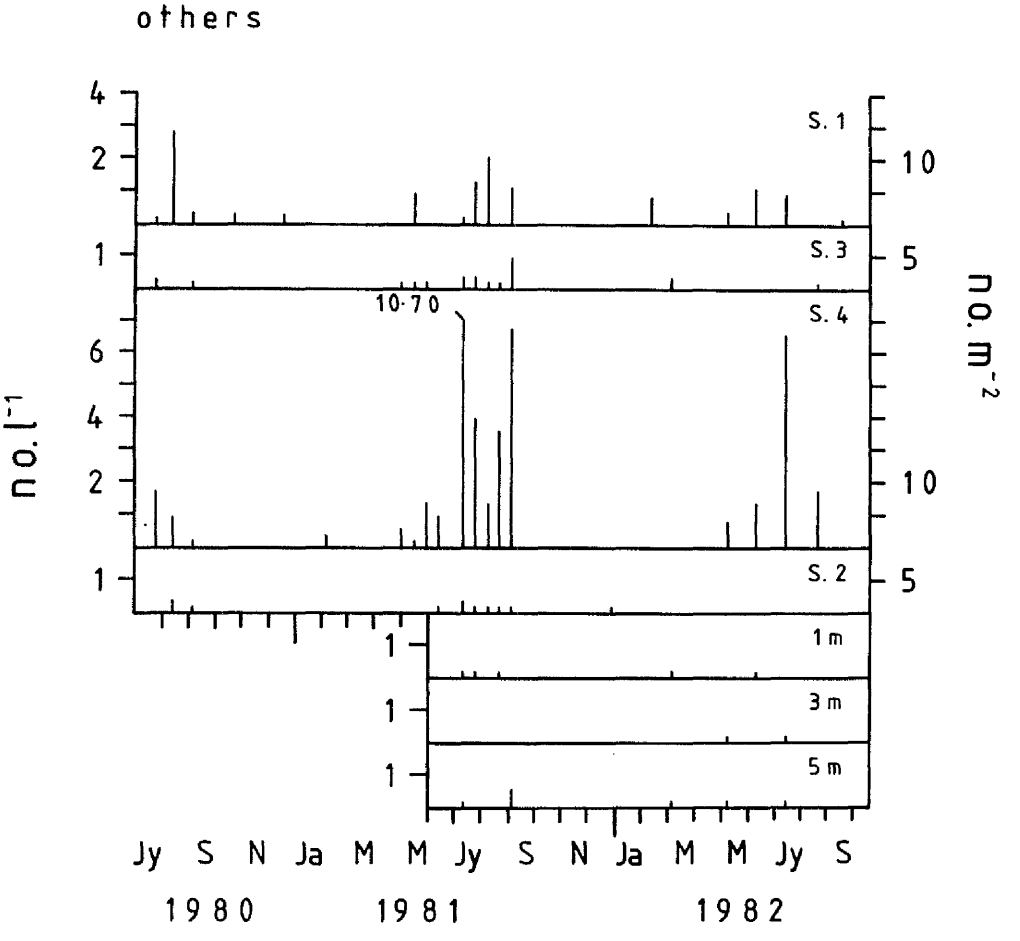

others
S. 1
S. 3
S. 4
S. 2
1 m
3 m
5 m
10·70
4
2
1
6
4
2
1
10
5
10
5
1
1
1
no. l⁻¹
no. m⁻²
Jy S N Ja M M Jy S N Ja M M Jy S
1980
1981
1982

Figure 6.14

Other members of the surface biota

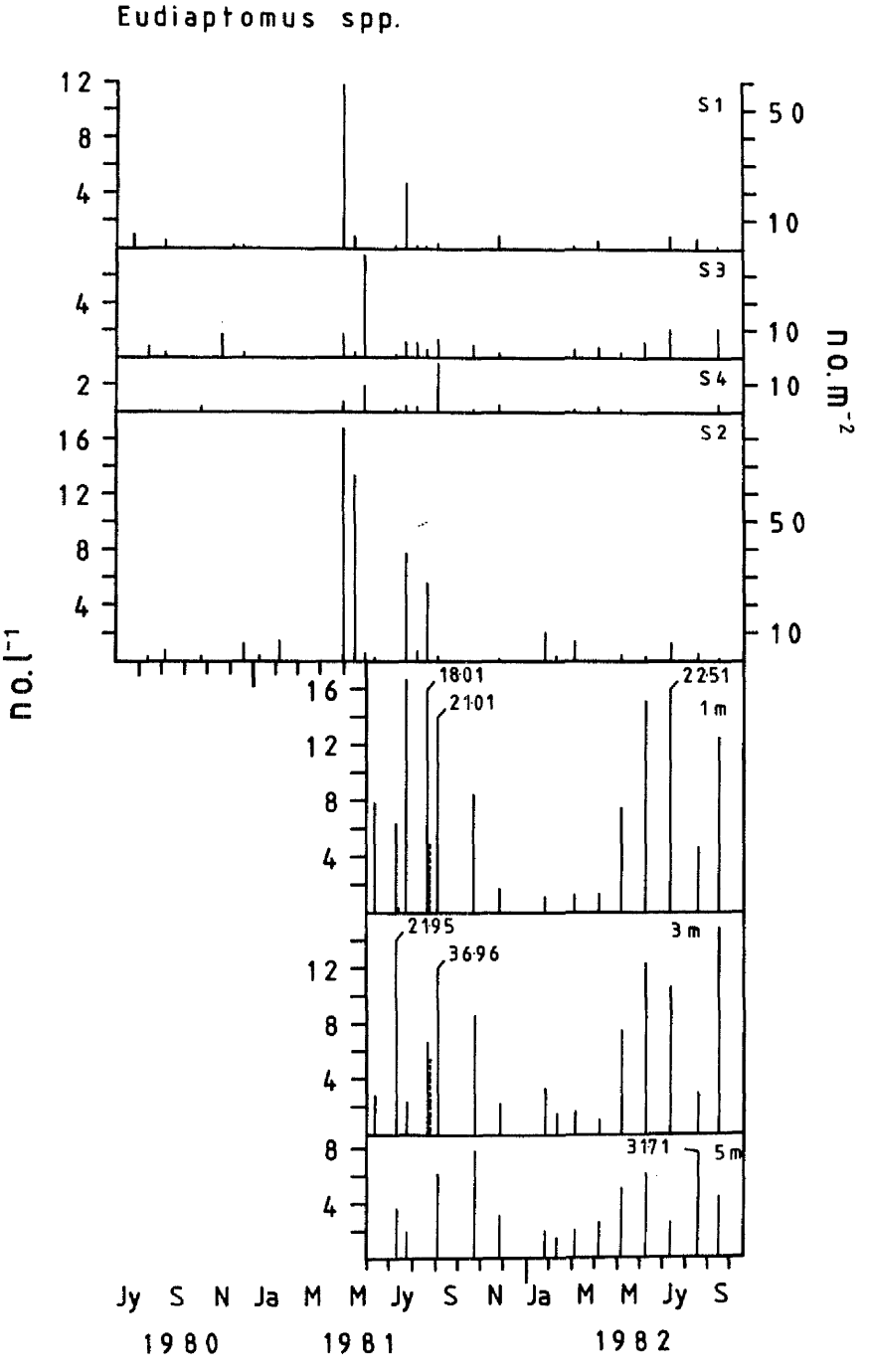

Eudiaptomus spp.
S1
S3
S4
S2
1801
2101
2251
1m
2195
3696
3m
3171
5m
no.l⁻¹
no.m⁻²
Jy S N Ja M M Jy S N Ja M M Jy S
1980 1981 1982
E. gracilis
E. laciniatus

Figure 6.15

Eudiaptomus gracilis **and** *Eudiaptomus laciniatus*

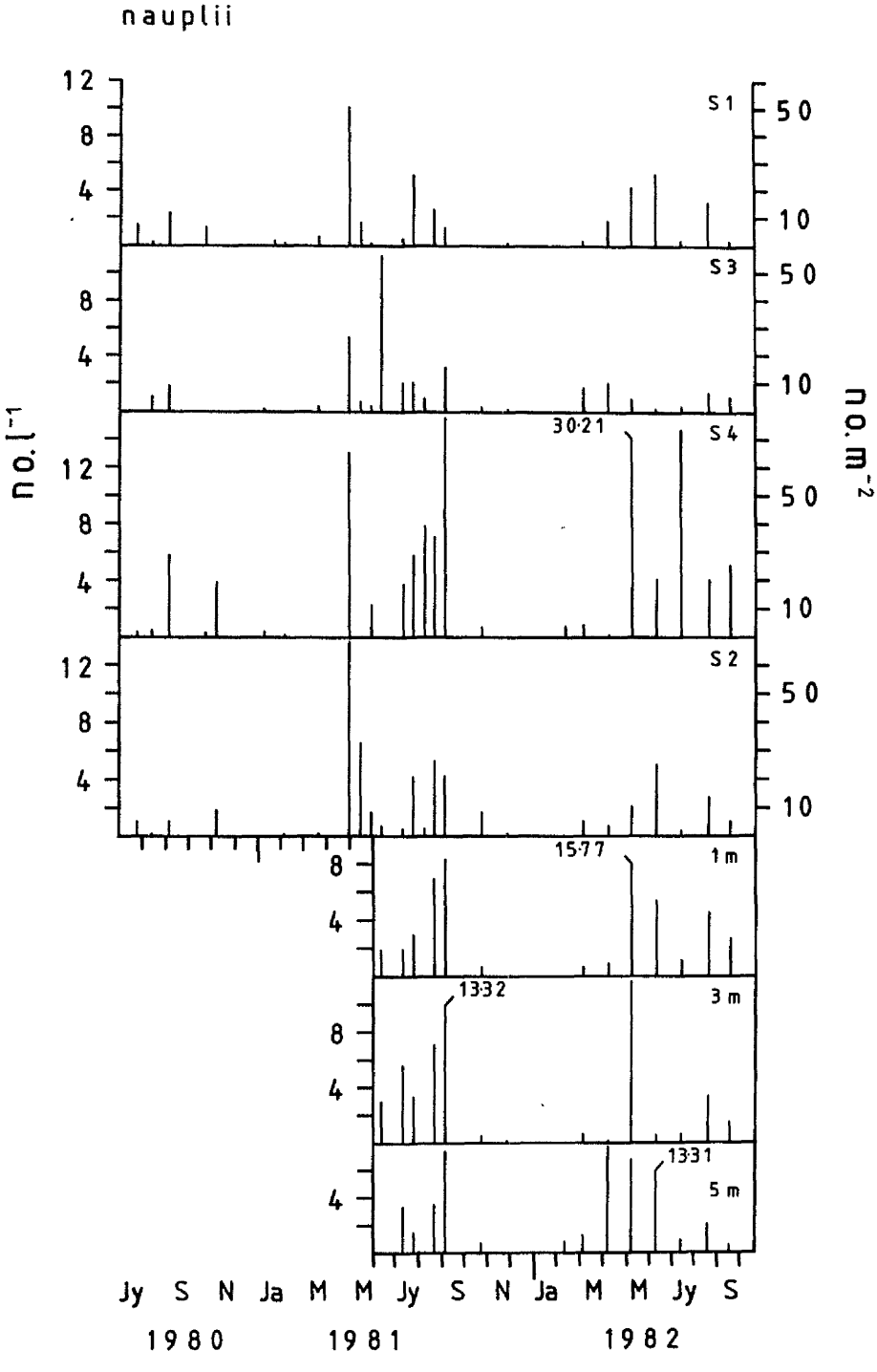

nauplii
no.l⁻¹
no.m⁻²
S1
S3
S4
S2
1m
3m
5m
30·21
15·77
13·32
13·31
12
8
4
50
10
Jy S N Ja M M Jy S N Ja M M Jy S
1980 1981 1982

Figure 6.16

The Nauplii of *Eudiaptomus* and *Cyclops* spp.

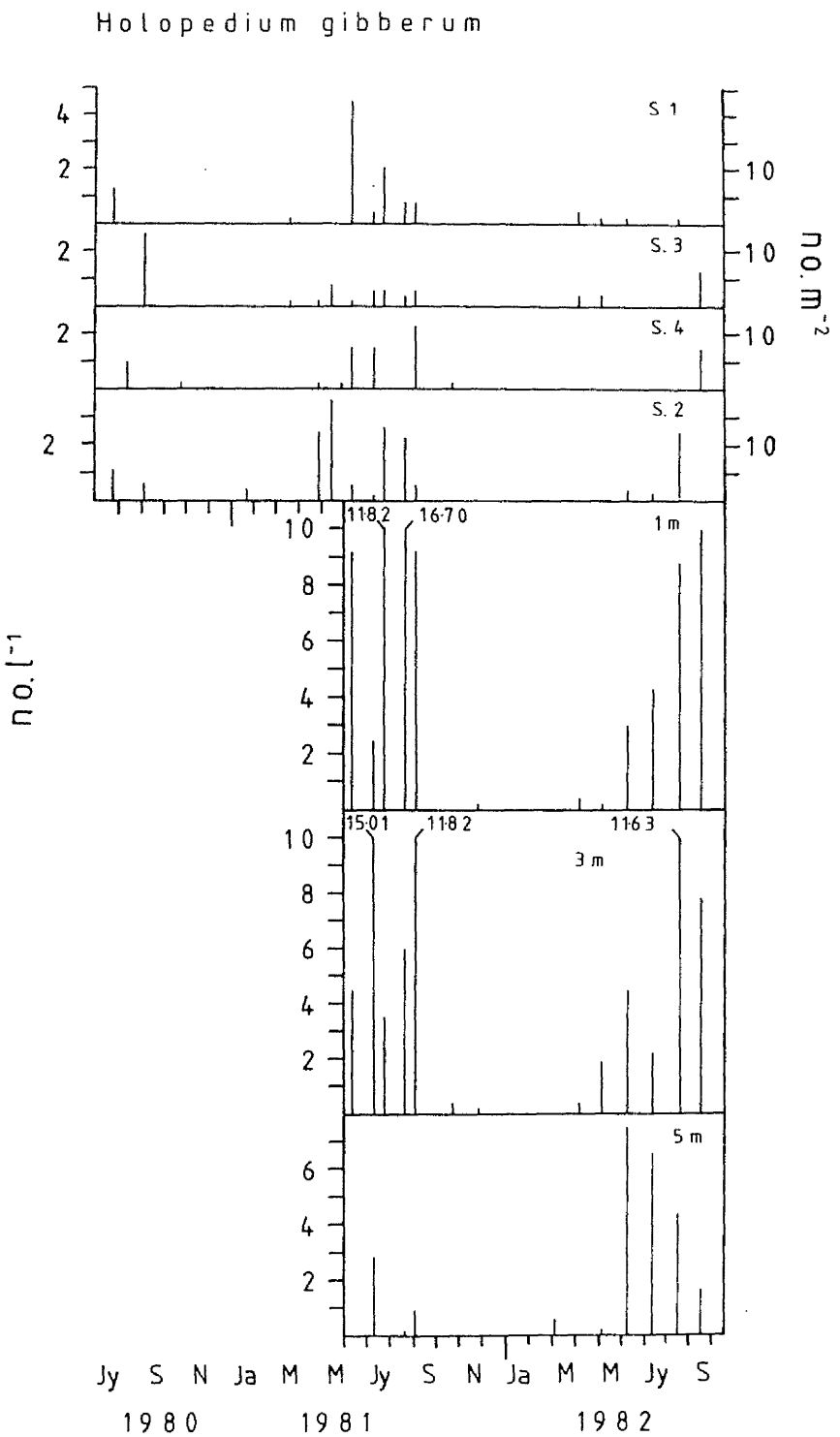

Holopedium gibberum
S 1
S. 3
S. 4
S. 2
n o. m⁻²
n o. l⁻¹
118·2
16·70
1 m
15·01
118·2
116·3
3 m
5 m
Jy S N Ja M M Jy S N Ja M M Jy S
1980
1981
1982

Figure 6.17

Holopedium gibberum

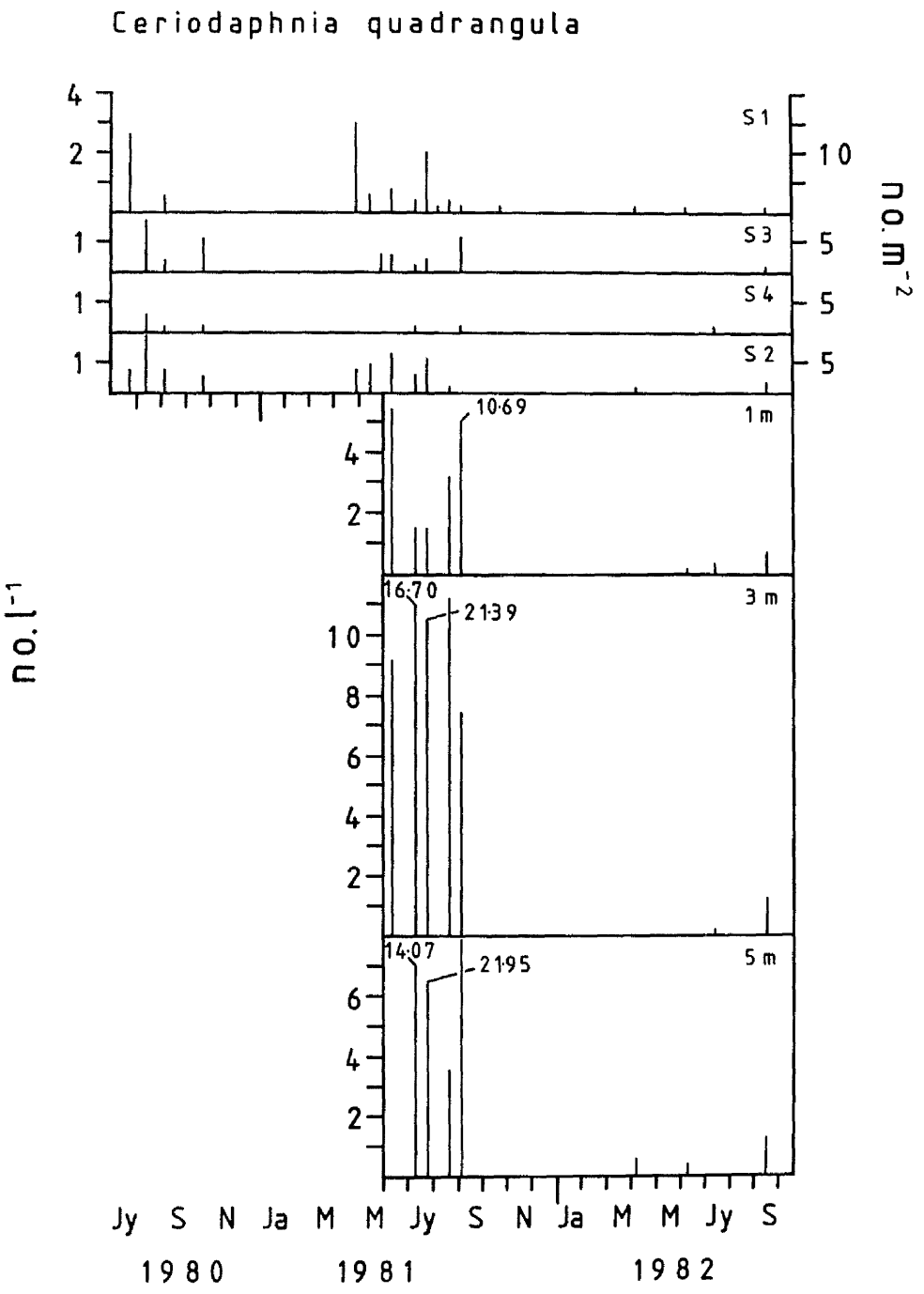

Ceriodaphnia quadrangula
S1
S3
S4
S2
1m
3m
5m
10·69
16·70
21·39
14·07
21·95
no.m-2
no.l-1
Jy S N Ja M M Jy S N Ja M M Jy S
1980
1981
1982

Figure 6.18

Ceriodaphnia quadrangula

Diaphanosoma brachyurum

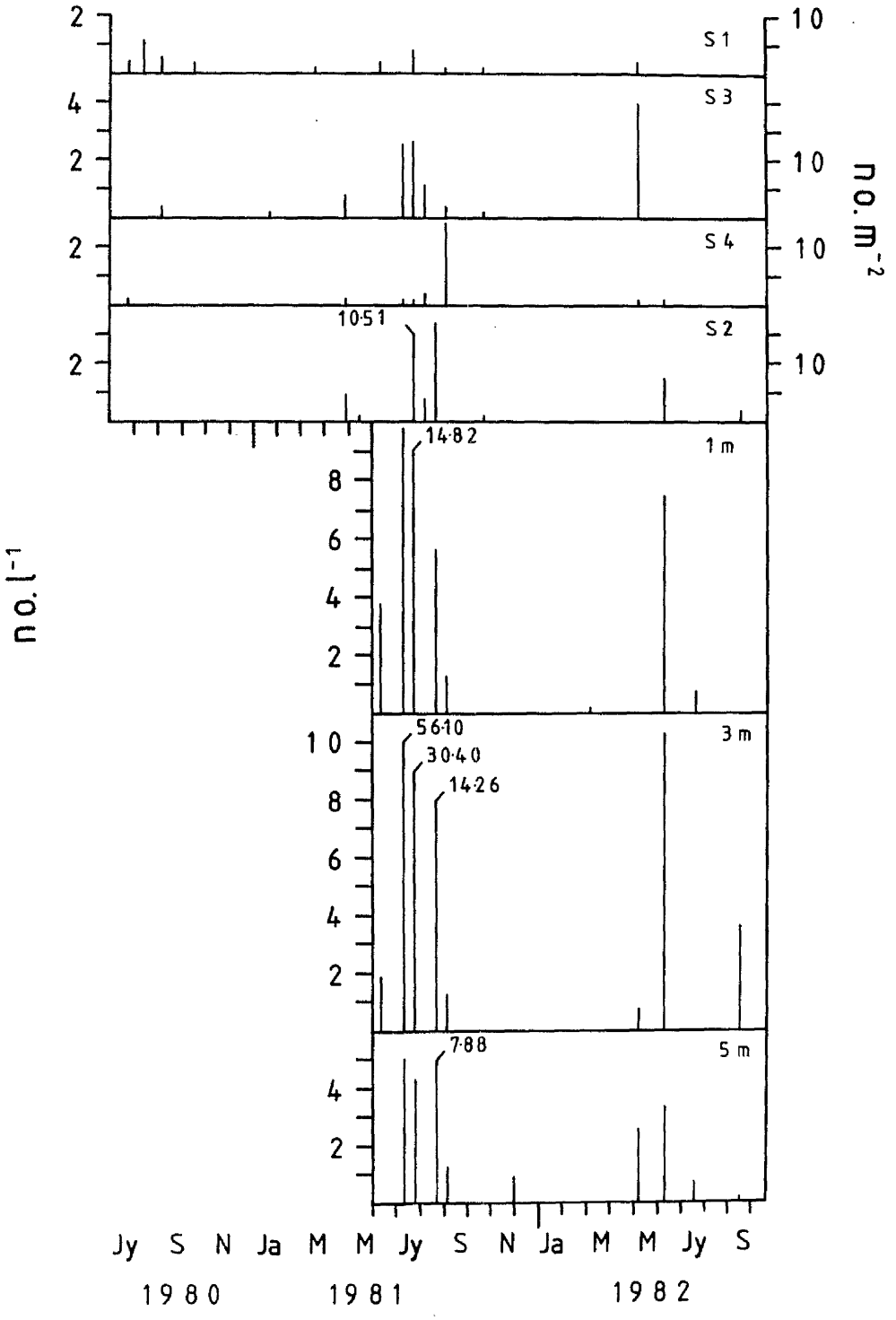


Figure 6.19

Diaphanosoma brachyurum

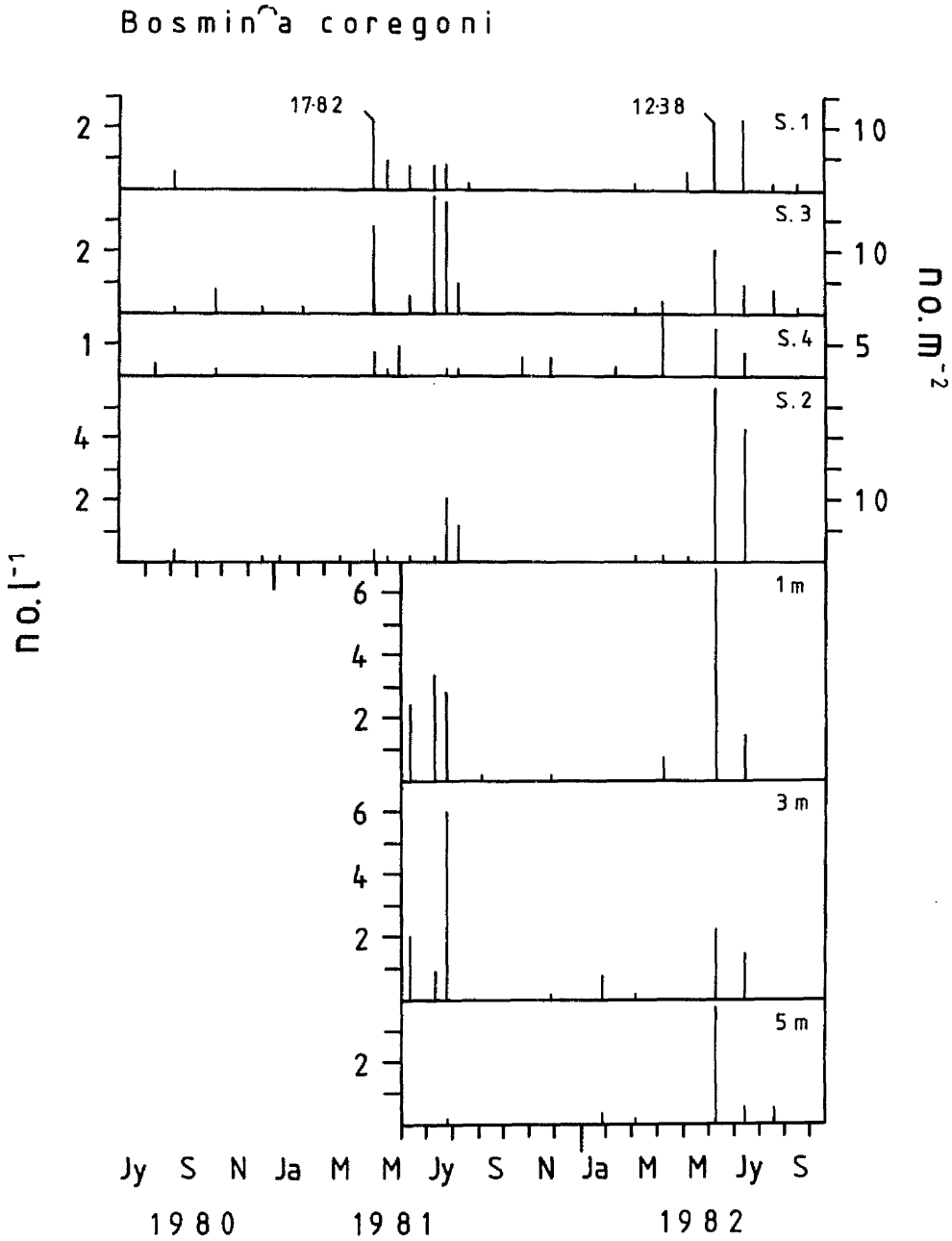

Bosmina coregoni
17·82
12·38
S. 1
S. 3
S. 4
S. 2
1 m
3 m
5 m
no. [-1]
no. m-2
Jy S N Ja M M Jy S N Ja M M Jy S
1980
1981
1982

Figure 6.20

Bosmina coregoni

Kellicottia longispina

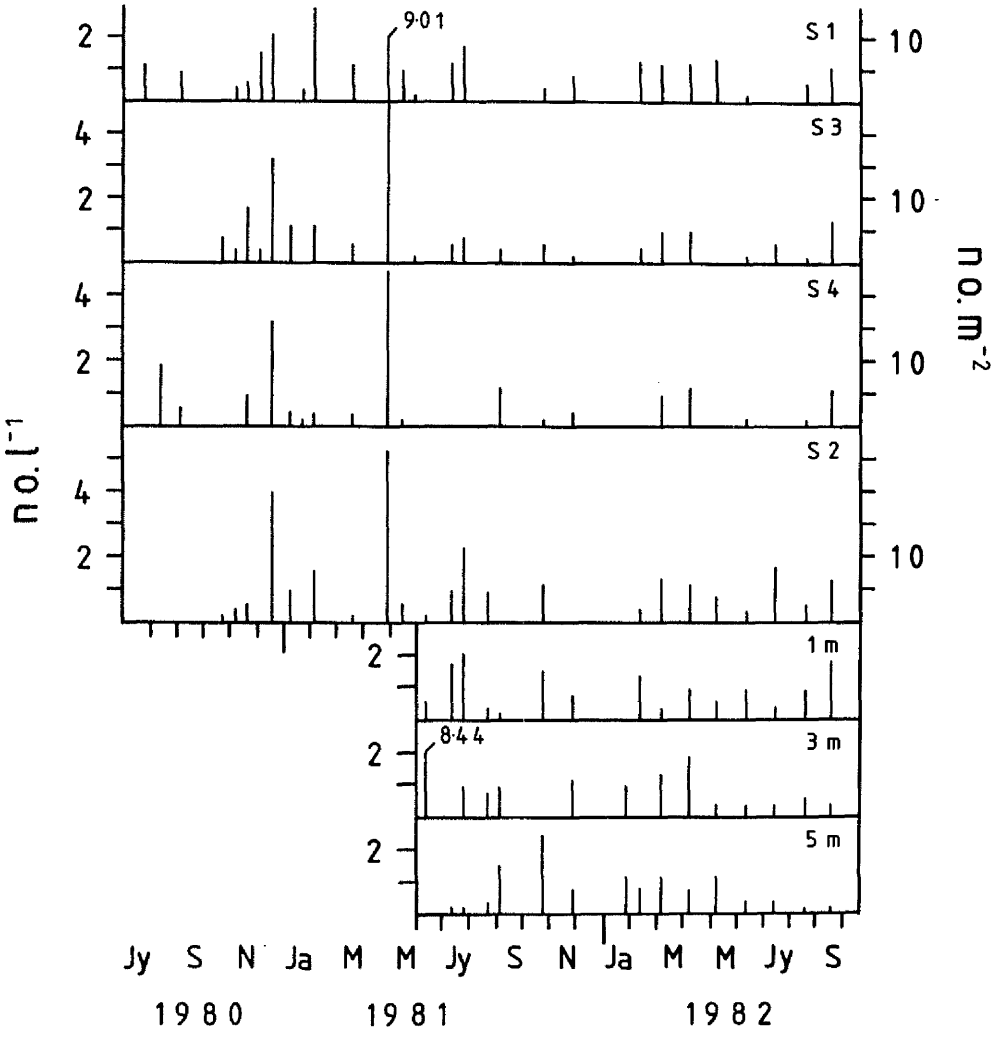
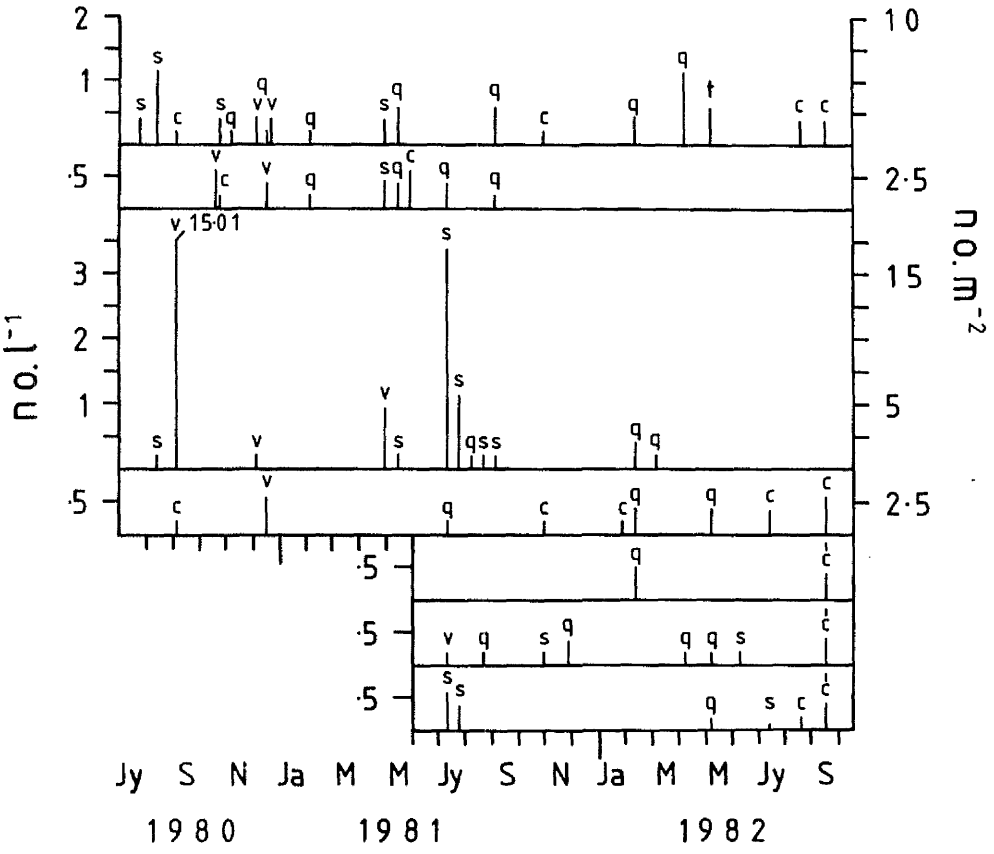


Figure 6.21

Kellicottia longispina

Keratella spp.



q K.quadrata

t " var.testudo

v var.valgoides

s K.serrulata var.curvicornis

c K.cochlearis

Figure 6.22

Keratella spp

1, 1.50 l^{-1} at site 2, 1.13 l^{-1} at site 3 and 0.75 l^{-1} at site 4). During April, spring maxima were recorded (9.01 l^{-1} at site 1, 5.25 l^{-1} at site 2, 4.88 l^{-1} at site 3 and 4.69 l^{-1} at 5m depth). In June, a second large increase in the population was measured at 3m (8.44 l^{-1}).

No increase in the *Kellicottia* population was observed under the ice in the winter of 1981/1982. During 1982, the population remained below 2 l^{-1}.

In general *Keratella* spp were found more frequently at surface site 1 and at 3m depth. . No definite seasonal pattern to their distribution was observed. On only on two occasions did the population exceed 2 l^{-1}, in September 1980 when *K.quadrata* var. *valgoides* predominated (15.01 l^{-1}) and the second in July 1981 when *K.serrulata* var. *curvicornis* predominated (3.38 l^{-1}).

Infrequent records exist for the remaining rotiferan species. Though representatives of this phylum were taxonomically numerous, they were rarely present in any great number. *Asplanchna priodonta, Polyarthra vulgaris, Epiphanes senta, Gastropus stylifer, Euchlanis dilatata* and *Trichosera longiseta* were all recorded predominantly in the summer months together with male rotifera.

6.2 VIABLE HETEROTROPHIC BACTERIA.

Heterotrophic bacterial density varied between 5 x 10^3 l^{-1} and 49.42 x 10^8 l^{-1} (Fig. 6.23). These low densities are typical of a dystrophic lake (Wetzel, 1975). During 1980 and until September 1981, minima were generally observed in the autumn, winter and spring months and maxima in the summer (August), corresponding with the highest recorded temperatures. During 1981, large numbers of bacteria were also recorded in October and November. These increases coincided with the periods of high winds (section 4.1.1) and POC maxima (section 4.2.9). The quantity of bacteria measured after ice melt in 1982 was higher than that measured in 1981 (Fig. 6.23) coinciding with the previous month's proliferation of algae under the ice. An increase in bacterial density was recorded in the spring months followed by a further increase in July.

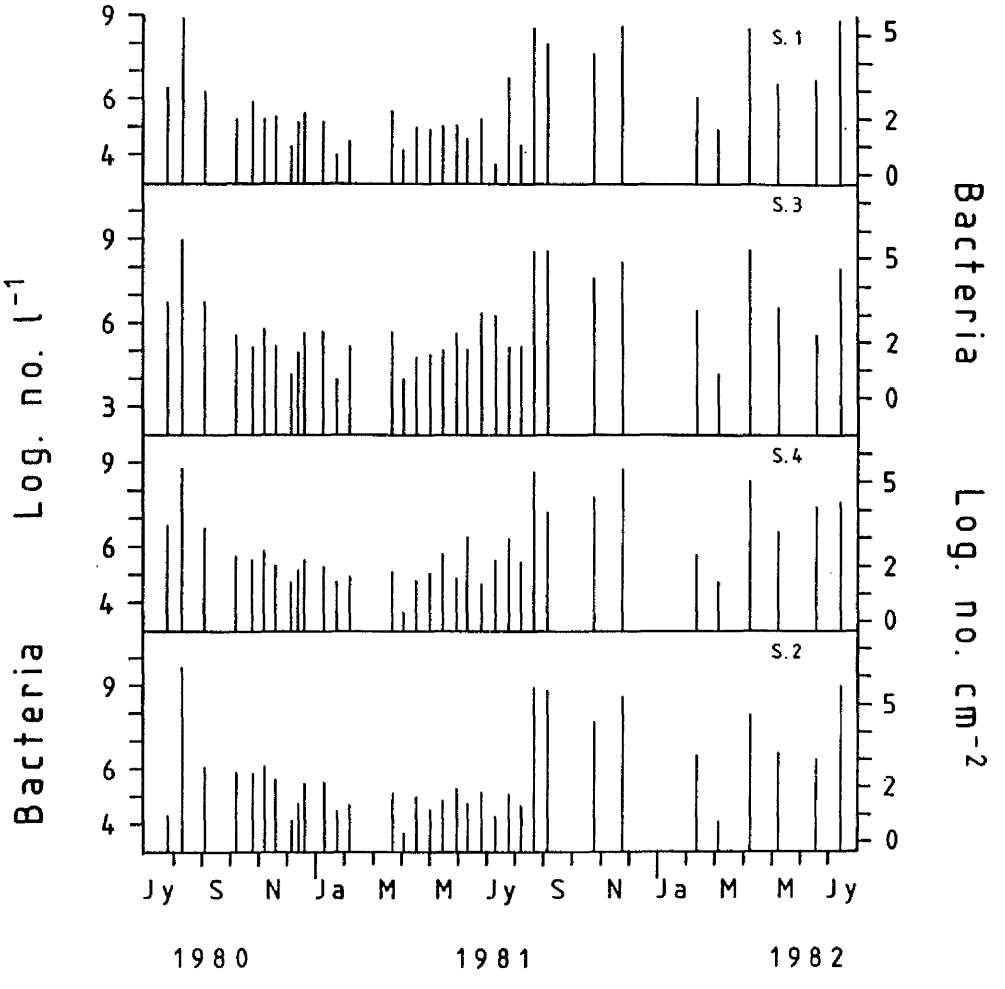

Bacteria Log. no. l⁻¹
Bacteria Log. no. cm⁻²
S. 1
S. 3
S. 4
S. 2
9
6
4
3
5
2
0
Jy S N Ja M M Jy S N Ja M M Jy
1980
1981
1982

Figure 6.23

Viable heterotrophic bacteria

The increase in bacterial density measured in the summer months was probably in response to the previous increase and subsequent lysis of the phytoplankton population and hence was probably a measure of an increase in the autochthonous bacterial population.

No correlation with surface tension, POC, or rainfall was observed. This suggests

1) That the allochthonous bacteria were not an important component of the bacterial population. Any increases in bacterial density were due to autochthonous bacteria and were not a result of sudden influxes from allochthonous sources.

2) The POC was rarely suitable for bacterial growth. This statement can be supported by the fact that C:N ratios were high, suggesting that the highly refractory organic matter was, therefore, unsuitable as a food source to all except specialised bacteria. Only after an algal "bloom" or at the resuspension of particulate matter from the sediments was there enough labile material to support growth. The increased bacterial density measured in October and November may have originated from the hypolimnion and/or the sediment/water interface.

One possible explanation of the proliferation of bacteria measured in April and May 1982 would be a reduction in grazing pressure brought about by a lowering in the number of rotifers and cladocerans measured in 1982 in comparison to 1981 but no general correlation between bacterial density and the cladoceran and rotiferan populations was observed.

6.3 DISCUSSION

Since there was an obvious division of the zooplankton species into "open water" types and "littoral" types, their distribution and bearing on the surface layer will be discussed separately.

6.3.1. General community pattern of the open water. July 1980 to September 1982.

Eudiaptomus gracilis naulpii, the cladocerans,*Holopedium gibberum* and *Ceriodaphnia quadrangula* and the rotifers *Euchlanis dilatata* and *Polyarthra vulgaris* were the main components of the zooplankton community of surface site 2 during July to September 1980. The reduction of the population during autumn was caused by a drastic fall in the number of cladocerans and a gradual reduction in the number of copepods and rotifers. During the winter minima of 1980/1981 when the surface population was occasionally zero, the rotifer *Kellicottia longispina* dominated the community. Adult *Eudiaptomus* and a very few *Bosmin a coregoni* were also present.

During April 1981 rapid increases in both the naupliid and adult *Eudiaptomus* populations were observed such that they dominated the community. The adult *Eudiaptomus* were probably later copepodite stages. An accompanying increase in the cladoceran population caused by *Holopedium gibberum*, and of the rotiferan population caused by *Kellicottia* and *Polyarthra vulgaris*, was observed. The adult *Eudiaptomus* population remained high throughout May as a further increase in the *Holopedium* population occurred. This was accompanied by a decline in the population of *Kellicottia*.

During the supression of the summer cladoceran population at the surface during late May to early July, the rotifers *Trichosera longiseta* and *Polyarthra* dominated the zooplankton community.

During the summer months at 1m, 3m and 5m the cladocerans dominated. The *Diaphanosoma* population formed the main component in July and August, when epilimnion temperatures were at their highest, together with *Ceriodaphnia* and *Holopedium* and, during July only, *Bosmin a.* At the surface *Diaphanosoma* was the most prominent cladoceran. The population maximum of *Diaphanosoma* coincided with the population maximum of *Eudiaptomus* at the surface and at depth and with an increase in the naupliid population. In comparison, the rotifers formed only a small component of the zooplankton community at depth, being composed of *Kellicottia, Asplanchna priodonta, Trichosera* (at the

surface) and *Ploeosoma hudsoni* (at depth).

As the *Diaphanosoma* population declined during September, both *Ceriodaphnia* and *Holopedium* remained and were the most common components of the cladoceran community. This was accompanied by an increase in *Eudiaptomus* to their population maxima.

A rapid decline of the cladoceran and naupliid communities were observed during autumn. Both the adult *Eudiaptomus* population and the rotiferan populations were observed to decline gradually.

During the winter of 1981/1982, the sparse zooplankton community was dominated by *Eudiaptomus* adults and the rotifer *Kellicottia*.

Immediately after ice melt in 1982, the zooplankton population remained low with little change in the composition of said population.

During March and April increases in the populations of *Eudiaptomus* nauplii and adults were measured. These formed the dominant components of the zooplankton population during May and through to September. A further increase in the naupliid population was observed in August but fewer were recorded as compared to 1981.

During summer 1982 the *Ceriodaphnia* population was greatly diminished when compared to that observed in 1981. The initial increase of the cladoceran community was caused by *Diaphanosoma* and *Holopedium* during June and July. As the *Diaphanosoma* population declined in August and September the *Holopedium* population increased and assumed dominance of the cladoceran community.

The observed increase in the rotiferan population during June was caused by *Asplanchna*. Further increases in the rotiferan population were observed during August and September and were caused by *Kellicottia, Keratella cochlearis, Asplanchna* and *Gastropus stylifer*.

During 1982 the surface population was much reduced in comparison to that recorded during 1981, only *Bosmina* was recorded in number together with a few *Keratella* spp, *Kellicottia* and *Eudiaptomus* nauplii.

This seasonal pattern differs from that observed by Klarer (1978) in two ways. Firstly the summer population was dominated by the cladocera, the rotifera formed a much smaller component. Klarer (1978) reported that all three components were present in equal numbers during the period 1974 to 1976. Secondly the seasonal succession pattern of the cladocera differed. An initial increase in the cladoceran community in the summer, during this study, was caused by *Diaphanosoma* which was replaced in September by *Ceriodaphnia* and *Holopedium*. Klarer (1978) reported an initial increase of the cladoceran community in spring caused by *Bosmin̂a*, which was replaced in late spring by *Ceriodaphnia* and *Diaphanosoma*. followed by an increase in *Holopedium* in late June. As recorded in this study, as the population of *Diaphanosoma* declined in August so *Ceriodaphnia* and *Holopedium* became the most common components.

In comparison Islam (1987) reported a reduced copepod community and overall dominance by the rotifers during 1984 to 1986.

This alternation in the zooplankton community during the past twelve years of study is indicative of the feeding competition which exists between the three components and is probably a response to the changes observed in the structure of the phytoplankton community.

6.3.2. Zooplankton/phytoplankton interactions at the surface layer in open water.

The interdependence of the zooplankton and phytoplankton communities of the main body of the Dubh Lochan has been extensively discussed by both Klarer (1978) and Islam (1987). This discussion will, therefore, be limited to the role of the zooplankton in regulating the surface layer phytoplankton community.

Numerically the cladocerans *Holopedium gibberum, Diaphanosoma brachyurum* and *Bosmin̂a coregoni* were recorded most frequently at the surface layer together with both adult and naupliid *Eudiaptomus gracilis* and the rotifer *Kellicottia longispina*; i.e. the

distributional ranges of these zooplankton species extended to the surface layer. *Polyarthra vulgaris, Euchlanis dilatata* and *Trichosera longiseta* were each recorded at the surface layer in number but only very infrequently. *Ceridaphnia quadrangula* was only occasionally recorded.

During 1981 the initial increase in the phytoplankton population, caused by green unicells (*Sphaerocystis*) and *Asterococcus* was followed by an increase in the population of *Eudiaptomus, Holopedium* and *Kellicottia* in May with a concomitant decline in the phytoplankton population. The second large increase in the phytoplankton population during June and July, caused by a rapid increase in the *Synechococcus* population, was followed by an increase in the abundance of *Diaphanosoma* and *Eudiaptomus* adults and, to a lesser extent of *Holopedium, Kellicottia* and *Eudiaptomus* nauplii, during late July. This was accompanied by a rapid decline in the *Synechococcus* population. Thus, at least during the period of rapid growth of the phytoplankton, the zooplankton were able to utilize the surface population as a food source.

During 1982 the depressed phytoplankton population was reflected in a depressed zooplankton population. At the surface only a small increase in the abundance of zooplankton was recorded in June (*Bosmina*), coinciding with the late May increase in *Dinobryon divergens*. The populations of *Sphaerocystis, Synechococcus* and *Aphanothece* recorded during July were not enough to support a large zooplankton population.

The reduced phytoplankton population and hence the reduced food supply would have resulted in increased competition between the zooplankton species for the available phytoplankton. Those able to utilize alternative sources of energy would therefore have an obvious competitive advantage. Porter (1977) has stated that many cladoceran species are non-selective filter feeders, capable of rapidly reproducing but only if there is an abundant food supply. This would explain the observed decline in the *Ceriodaphnia* population and the observed single, reduced peak in the *Diaphanosoma* population. Neither species was able to compete successfully for a limited food supply.

The slower growing *Eudiaptomus* together with *Holopedium, Kellicottia* and *Bosmin̂a* were thus able to compete for and utilize the small phytoplankton population and alternative food sources such as detritus, with its concomitant bacterial flora, more successfully.

6.3.3. General community pattern of the littoral areas. July 1980 to September 1982.

The zooplankton community of the bay areas was dominated by the cladocerans, in particular *Peracantha truncata* and *Polyphemus pediculus* with, to a lesser extent, the cyclopid copepods and the nauplii of both the copepod and *Eudiaptomus* populations.

During July to October 1980, *Peracantha* dominated the community. The cyclopid copepods and the nauplii together with the rotifers *Keratella quadrata* var *valgoides*, *Polyarthra vulgaris* and *Euchlanis dilatata* were also present in number.

The reduction of the zooplankton community during October and November was caused by a drastic reduction in the number of cladocerans and copepods and a gradual decline in the number of rotifers. During the winter minima of 1980/1981, when the surface populations were often zero, the rotifer *Kellicottia longispina* dominated the community. A few *Bosmin̂a coregoni* and nauplii were also present.

During April 1981 a rapid increase in the zooplankton populations at sites 1 and 4 were caused by the nauplii. An accompanying increase in the populations of *Kellicottia* and *Bosmin̂a* were observed.

While the zooplankton populations declined at site 1 and remained low at site 3, a gradual increase in abundance was recorded at site 4 from May to July. This was caused by a rapid increase in the *Polyphemus* population, firstly in May and then in June followed by an increase in the adult cyclopid copepod population (*Eucyclops* spp) in July. This was accompanied by an increase in the population of the rotifer *Keratella serrulata* var *curvicornis*.

The zooplankton population maximum of August and September was caused predominantly by the cladocerans *Polyphemus* and *Peracantha*. This was accompanied by further increases in the naupliid and cyclopid copepod populations. A small increase in the rotiferan population caused by *Kellicottia, Asplanchna priodonta, Ascomorpha* spp and *Epiphanes senta* was also observed. As the zooplankton community rapidly declined during the autumn period the three components were observed to be present in equal proportions.

Immediately after ice melt in February 1982 the zooplankton population remained low.

During May an increase in the zooplankton community caused by the nauplii was observed. They dominated the community during May and June. This was accompanied by an increase in the cyclopid copepod population and of the *Bosmina* population at site 1. A further increase in the naupliid population at site 4 during July was accompanied by a rapid increase in both *Polyphemus* and the cyclopid copepods at site 4 and of the rotifer *Trichosera longiseta* at site 3.

As the naupliid population declined in August and September, the adult cyclopid copepods became the main components of the copepod population. A rapid increase in *Peracantha* led to its dominance. This was accompanied by smaller increases in the populations of *Polyphemus* and *Allonella excisa* at site 4 and of the rotifer population, composed of *Kellicottia, Polyarthra vulgaris, Asplanchna priodonta* and *Gastropus stylifer* (site 1).

6.3.4. Zooplankton/phytoplankton interactions at the surface layer in the littoral regions.

The bay area zooplankton community, dominated by cladocerans of the family Chydoridae, is typical of littoral regions. The differences in species composition observed between the open water and the littoral areas were reflected in the later occurrence of the summer population maximum at site 4 in comparison to that obtained at depth in open water.

In both regions the spring increase in the zooplankton population was caused by the nauplii and this exemplifies their wide habitat range.

The cladocerans dominated both regions, albeit the populations were represented by differing species. The cyclopid copepods, dominated by the raptorial, herbivorous *Eucyclops spp* replaced the filter feeding *Eudiaptomus*.

A comparison of the rotiferan representatives indicated that they were evenly distributed in both regions.

Thus since there was little observed variation in phytoplankton species composition or succession between the open and littoral areas any differences in phytoplankton/zooplankton interactions were caused by the differences in the zooplankton community.

The peaks in zooplankton recorded in July and September 1980 were probably linked with a previous phytoplankton population increase which may have occurred before the onset of this sampling programme.

Over the winter period, the observed increase in the diatom population recorded at the beginning of December at site 4 was followed, in the middle of December, by a small increase in the population of *Kellicottia longispina*. No further corresponding increases in the zooplankton population under ice cover was observed after any other winter phytoplankton increase.

During 1981 the observed increase in the phytoplankton population in April was caused by *Asterococcus* and green unicells (*Sphaerocystis*) and was followed, at the end of April, by an increase in the zooplankton community caused by *Kellicottia longispina* and the nauplii and in May by *Polyphemus pediculus*. The phytoplankton population was observed to decline.

The phytoplankton population maximum of June, caused by the blue-greens *Synechococcus* spp and *Aphanothece saxicola* and the colonial green alga *Sphaerocystis schroeteri* was followed by a rapid increase in the cladoceran population, caused mainly by *Polyphemus pediculus* and *Peracantha truncata* with *Alona guttata* and *Bosmina coregoni* together with the cyclopid copepods and nauplii. An increase in the rotiferan population caused by *Keratella serrulata* var *curvicornis*, *Euchlanis dilatata* and *Epiphanes senta* was also observed.

A further increase in the zooplankton community recorded at site 4 during September was accompanied by a rapid decline in the phytoplankton population. This large zooplankton community was composed primarily of *Peracantha*, *Polyphemus*, cyclopid copepods and nauplii.

During 1982 the recorded increase in the phytoplankton in April, caused by *Asterococcus* and green unicells (*Sphaerocystis*) was accompanied by a rapid increase in the naupliid population.

As recorded in open water, the phytoplankton maxima during the summer months were considerably reduced. This was accompanied by a measured reduction in the total zooplankton population. Only minor increases in the phytoplankton were recorded such as the increase in the population of *Dinobryon divergens* recorded at site 1 in May which was followed by a small increase in the population of *Bosmina* in June and a concurrent rapid decrease in the *Dinobryon* population.

Reduced populations of nauplii, *Peracantha*, *Polyphemus* and cyclopid copepods were observed which indicated that the recorded populations of *Sphaerocystis*, *Synechococcus* and *Aphanothece* recorded during July were not enough to support a large zooplankton population. This reduction in the zooplankton population was particularly noticeable at sites 1 and 3. At site 4, though only single peaks in the populations of *Peracantha*, *Polyphemus* the cyclopid copepods and the nauplii were observed, the total populations were considerably larger than those recorded at sites 1 and 3. This finding is possibly indicative of the larger availability of an alternative food supply, measured as increased levels of POC (section 4.2.9), in the form of the detrital remains of the littoral flora, which these zooplankters could

utilize as an alternative energy source. Those zooplankton able to graze the POC/detritus of the surface film may thus have a competitive advantage over purely planktonic forms by exploiting this additional source of energy.

Chapter 7

Diurnal variation of phytoplankton and zooplankton in Dubh Lochan with particular reference to the surface layer.

7.1 INTRODUCTION

There is much evidence for diurnal periodicity in the photic zone of freshwater habitats (e.g. Ruttner, 1905; (in Hutchinson, 1967); Worthington, 1931; George and Fernando, 1969; Tilzer, 1973; Kairesalo, 1980; Maulood *et al*, 1978; and Frempong, 1981) and while there is considerable evidence of the importance of the role of the marine surface layer in circadian rhythms (see Zaitsev, 1971), little work has been carried out on the diel changes of components of freshwater surface layers (Maulood *et al*, 1978; Freedman *et al* 1982). The majority of studies which mention the surface do not give information on the thickness of the surface sample collected, nor the sampling method used. Since most of these studies have probably used the "bucket method", as in the case of Maulood *et al* (1978), it is unwise to use these data for comparison with observations on fixed thickness surface layers.

The purpose of the two 24h surveys carried out as part of this study were to provide additional information on the nature of the biotic components found at or near the surface layer. Such observations can also indicate the presence of temporary inhabitants at the surface, such as nocturnal migrators. Both surveys were carried out in the summer of 1981, the first on the 15th and 16th of July and the second on the 25th and 26th of August.

7.2 15th AND 16th JULY.

The first survey concentrated solely on the diurnal fluctuations of the surface layer. Over a 24h period samples were collected every 2h at site 2 and the following analyses carried out; enumeration of the phytoplankton and zooplankton, estimates of the chlorophylls and carotenoids and determinations of the surface temperature, surface tension, alkalinity and inorganic nutrients (PO_4-P, NO_3-N, NH_3-N, SiO_4-Si). The willing help of Mr R.Mc Math, particularly with the tedious filtration of samples is gratefully acknowledged. At the start of the survey (7am), the weather was dry with some cloud cover. This persisted until 9 pm when a light rain started which developed into more persistent rainfall at around 1 am. It was still raining at the

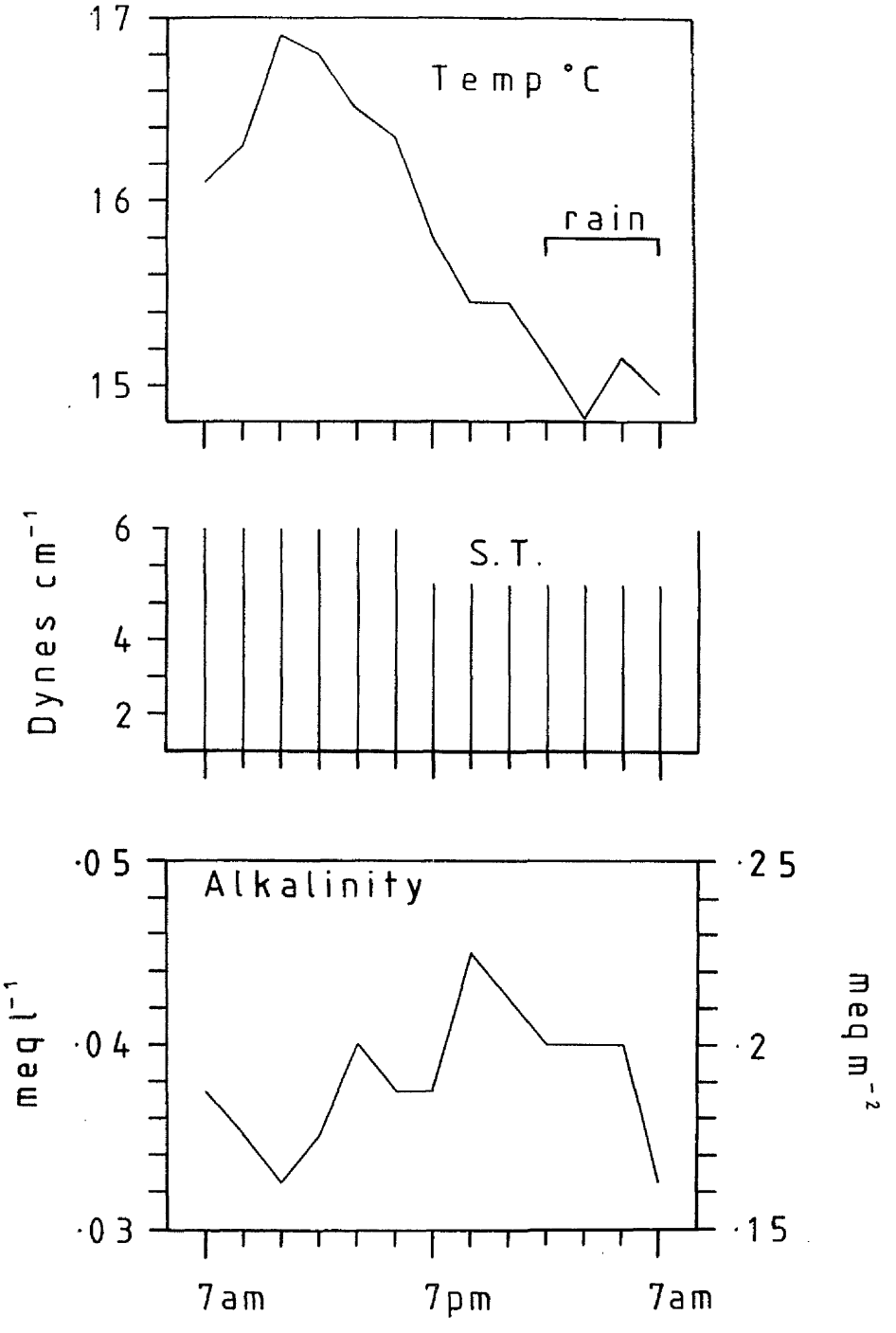

17
16
15
Temp °C
rain
Dynes cm⁻¹
6
4
2
S.T.
·05
·04
·03
Alkalinity
·25
·2
·15
meq l⁻¹
meq m⁻²
7am
7pm
7am

Figure 7.1
Diurnal variation 15/16 July 1981
surface temperature

Figure 7.2
Diurnal variation 15/16 July 1981
surface tension

Figure 7.3
Diurnal variation 15/16 July 1981
Alkalinity meq l^{-1}

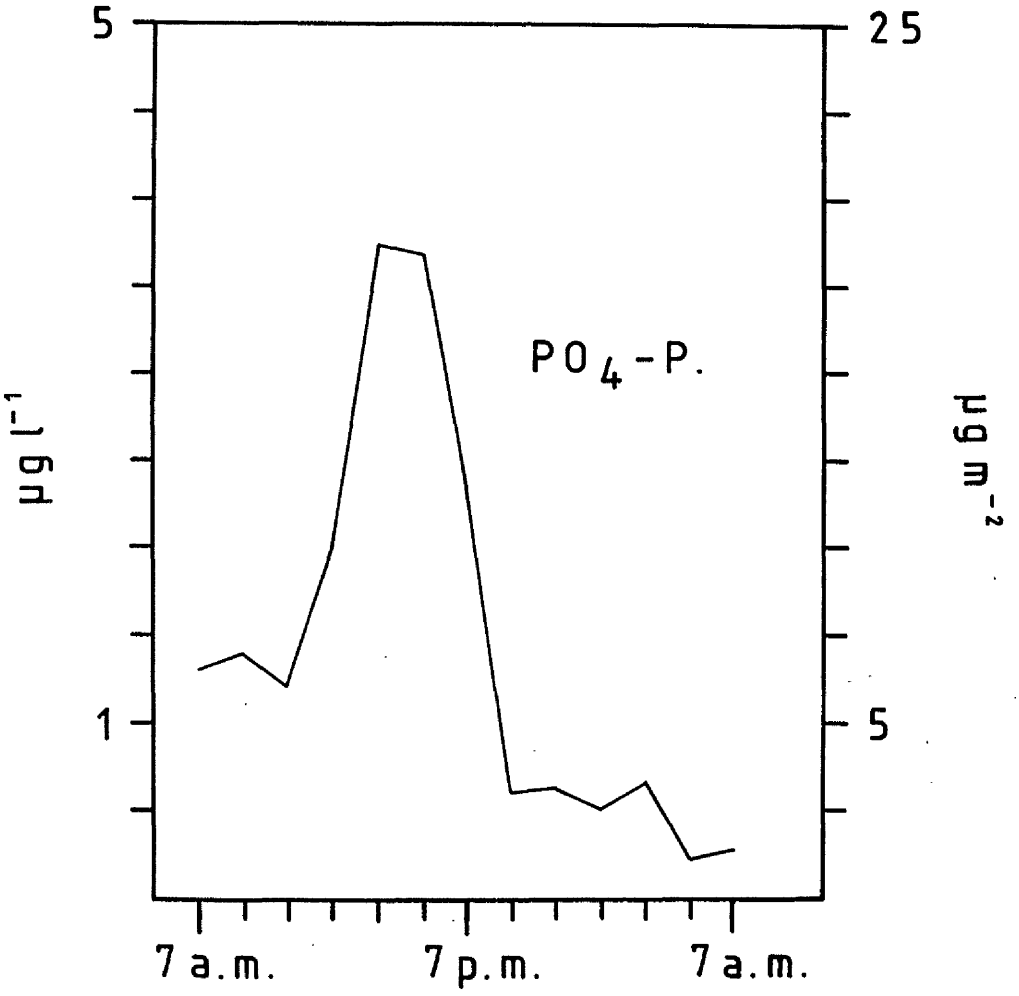

5
25
PO4-P.
µg l-1
mg m-2
1
5
7 a.m.
7 p.m.
7 a.m.

Figure 7.4

Diurnal variation 15/16 July 1981

Phosphate-phosphorus $\mu g\ l^{-1}$

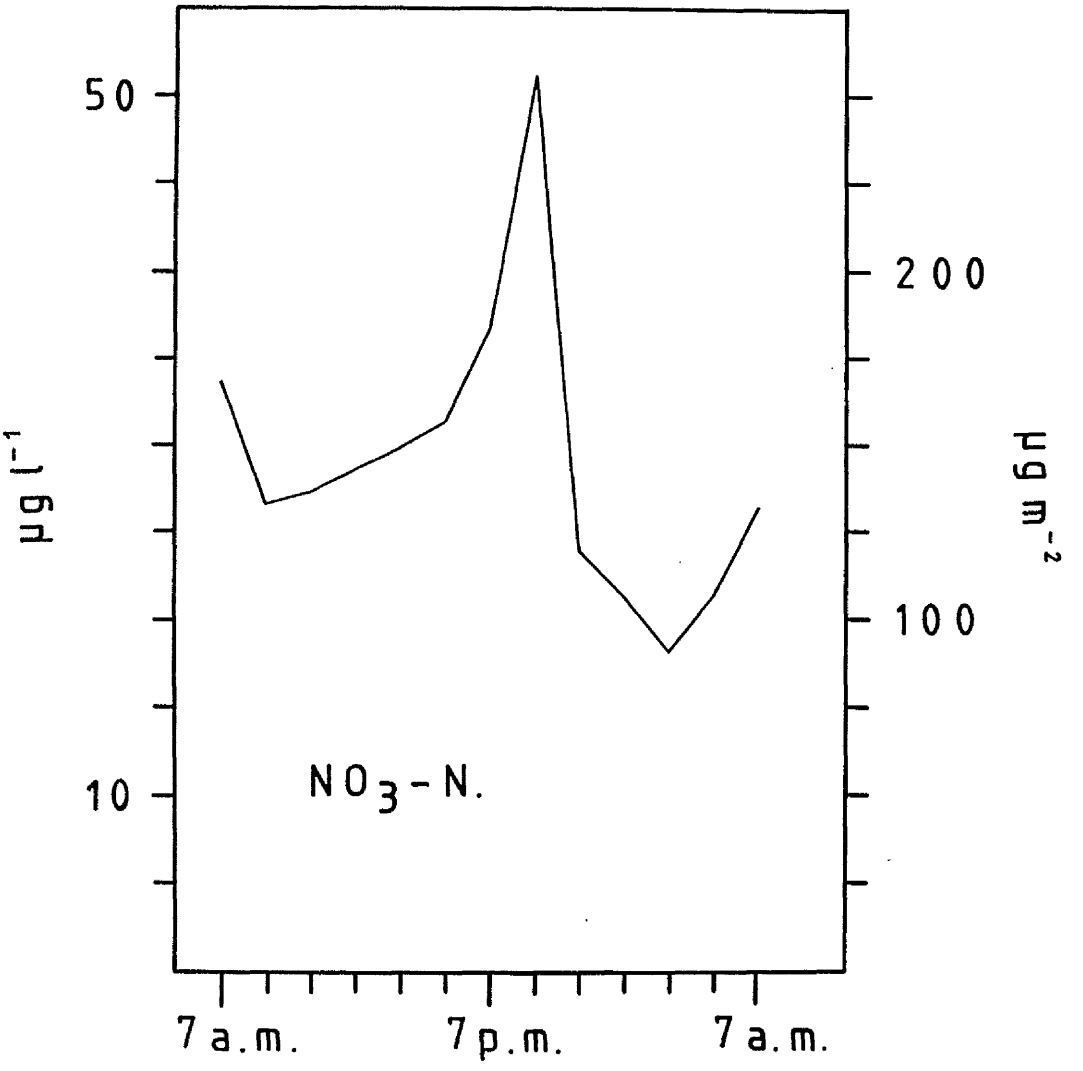

50
10
μg l⁻¹
200
100
μg m⁻²
NO3-N.
7 a.m.
7 p.m.
7 a.m.

Figure 7.5

Diurnal variation 15/16 July 1981

Nitrate-nitrogen $\mu g\ l^{-1}$

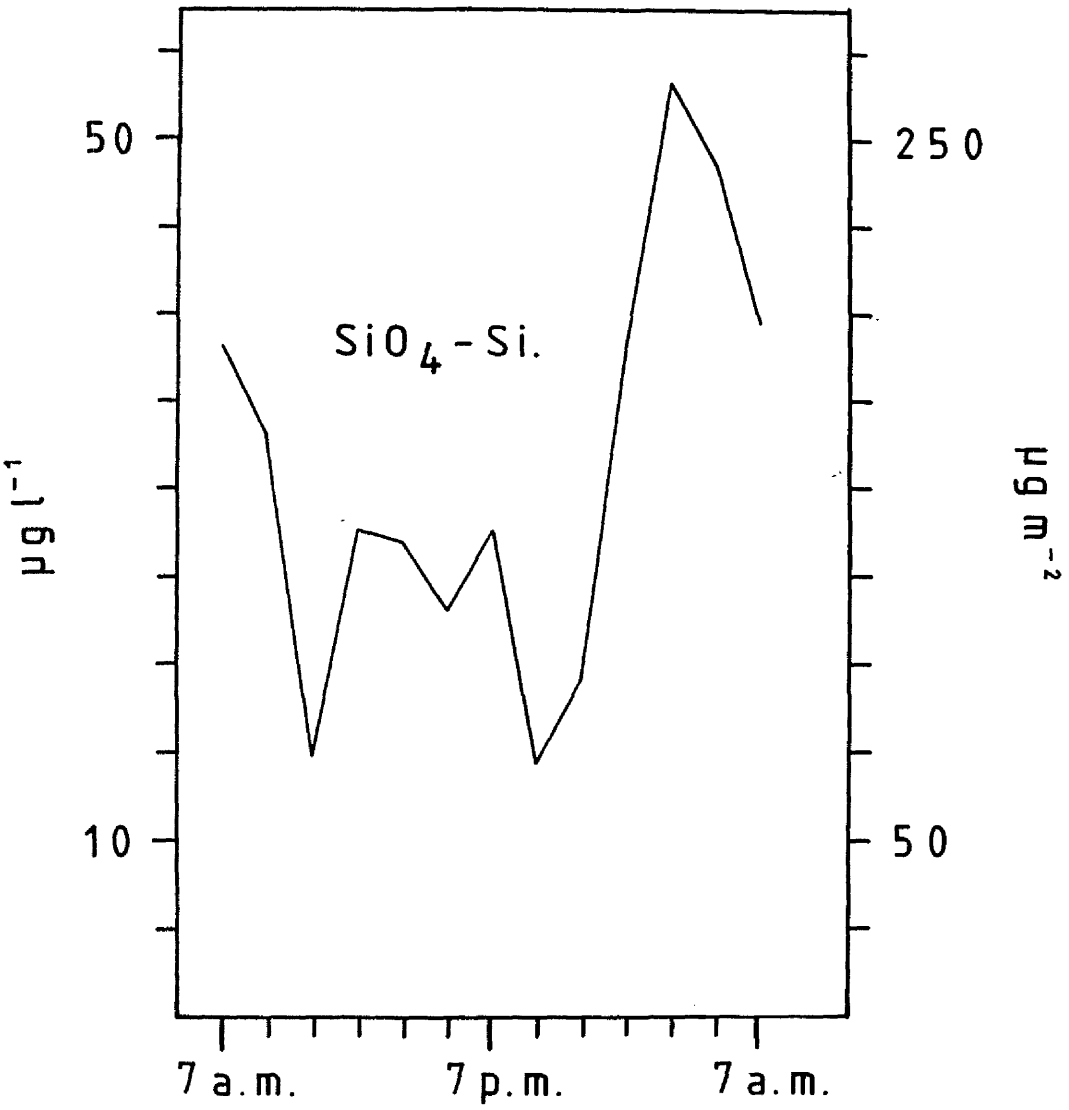

50
10
250
50
SiO_4 - Si.
µg l⁻¹
µg m⁻²
7 a.m.
7 p.m.
7 a.m.

Figure 7.6

Diurnal variation 15/16 July 1981

Silicate-silica $\mu g\ l^{-1}$

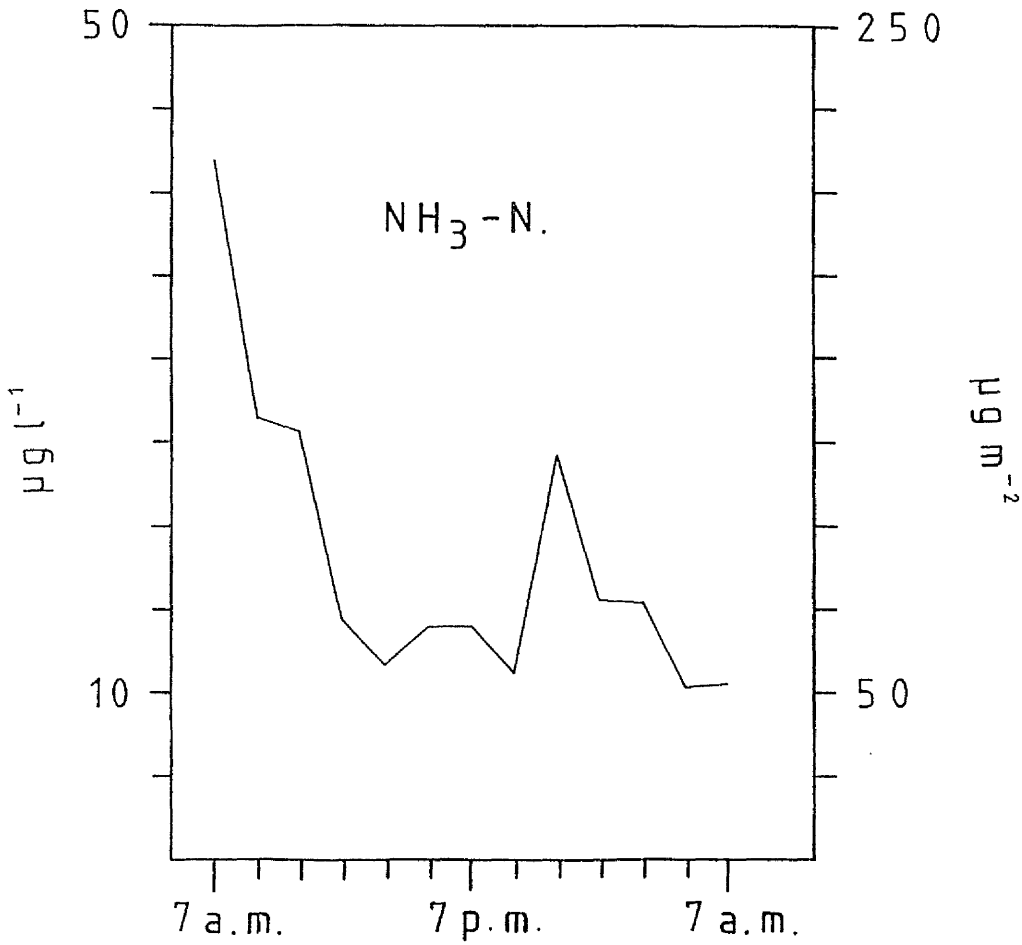

50
250
NH_3-N.
$\mu g\,l^{-1}$
$\mu g\,m^{-2}$
10
50
7 a.m.
7 p.m.
7 a.m.

Figure 7.7

Diurnal variation 15/16 July 1981

Ammonia-nitrogen $\mu g\ l^{-1}$

end of the survey (7 am). Dusk occurred at around 11.15 pm and by 5 am dawn was giving way to full daybreak. The main period of darkness was observed between midnight and just before 3 am.

At the start of the survey period the water temperature was 16.10 ^{0}C (Fig. 7.1) after which a gradual fall in temperature was observed, the lowest level being recorded at 3 am (14.80 ^{0}C). The persistent rainfall probably maintained the depressed water temperature.

Surface tension depression varied little throughout the survey (Fig.7.2). From the beginning of the survey and until 5 pm a reading of 6 dyn cm^{-1} was recorded. Thereafter, the measured surface tension depression lay between two standards. An oil of spreading pressure 3 dyn cm^{-1} spread too quickly and an oil of spreading pressure 6 dyn cm^{-1} not at all. The value has been expressed graphically as 4.5 dyn cm^{-1}. Rain did not seem to alter the surface tension depression.

Alkalinity ranged from 0.0325 meq l^{-1} to 0.045 meq l^{-1} with the minimum recorded at 11 am and the maximum recorded at 9 pm, falling with the onset of rainfall to 0.0325 meq l^{-1} by the end of the survey (Fig. 7.3).

Diurnal fluctuations in the nutrient levels were recorded. Phosphate-phosphorus levels were observed to be low in the morning (1.21-1.40 $\mu g\ l^{-1}$) with a sharp rise in concentration in the afternoon (maximum 3.72 $\mu g\ l^{-1}$) falling again in the late evening and remaining low overnight and the following morning (0.23-0.66 $\mu g\ l^{-1}$, Fig. 7.4). Nitrate-nitrogen levels were observed to fall from a value of 33.69 $\mu g\ l^{-1}$, at the start of the survey, to 26.59 $\mu g\ l^{-1}$ at 9 am (Fig. 7.5). A sharp rise in the nitrate concentration was then measured at 9 pm (51.20 $\mu g\ l^{-1}$) followed by an equally sharp decrease to a minimum of 18.25 $\mu g\ l^{-1}$ at 3 am. By the end of the survey the nitrate-nitrogen level had risen to 26.38 $\mu g\ l^{-1}$ so suggesting a diel periodicity in nitrate-nitrogen with maxima in the morning and evening and minima in the late morning and at night.

Maximum silicate-silica levels were recorded in the morning with smaller maxima occurring in the afternoon (Fig. 7.6). Minima were

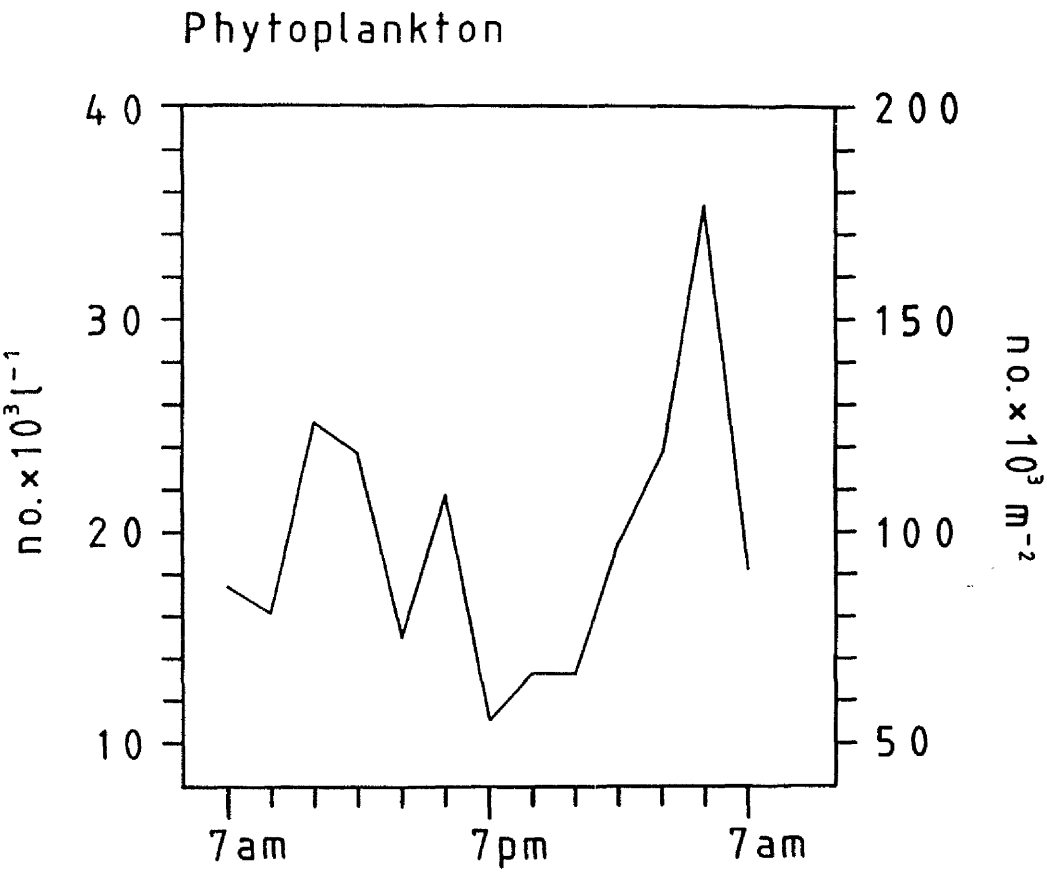

Phytoplankton
40
30
20
10
200
150
100
50
no.×10³l⁻¹
no.×10³ m⁻²
7am
7pm
7am

Figure 7.8

Diurnal variation 15/16 July 1981

Phytoplankton biomass

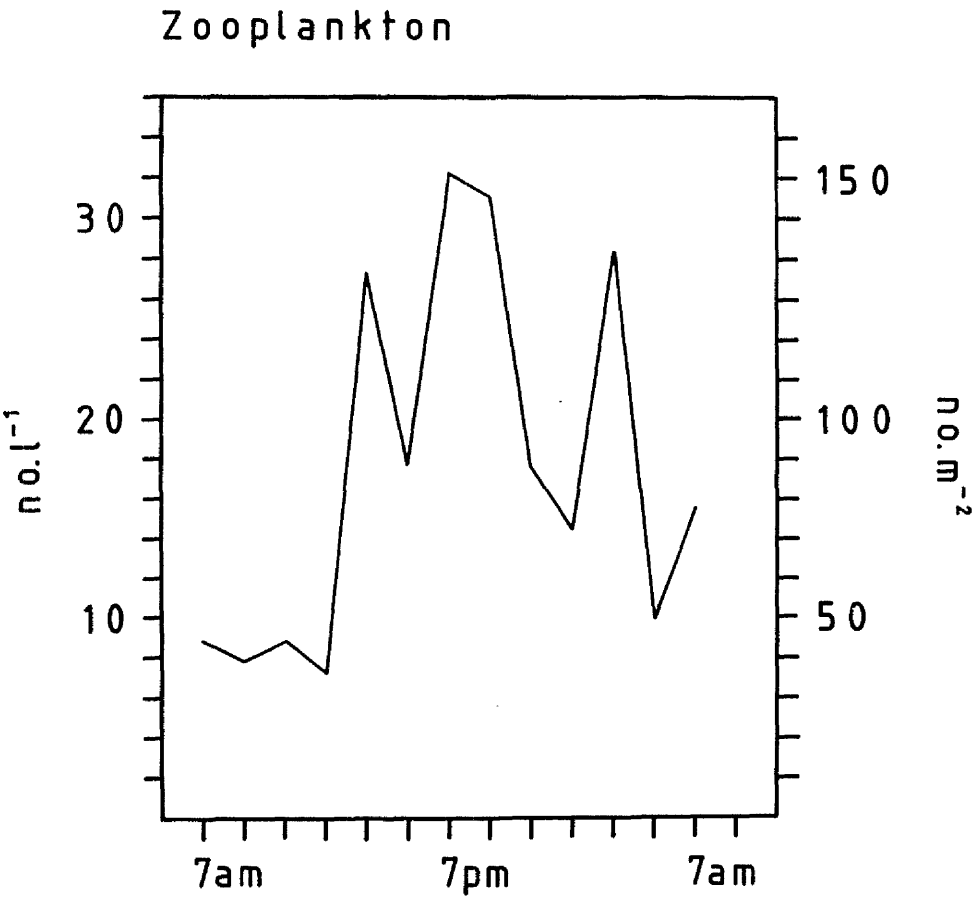

Zooplankton
30
20
10
no.l^{-1}
150
100
50
no.m^{-2}
7am
7pm
7am

Figure 7.9

Diurnal variation 15/16 July 1981

Zooplankton biomass

recorded at 11 am (14.80 $\mu g\ l^{-1}$) and 9 pm (14.47 $\mu g\ l^{-1}$). The highest value was recorded at 3 am (53.29 $\mu g\ l^{-1}$).

From an initially high level of ammonia nitrogen (41.82 $\mu g\ l^{-1}$) a gradual decrease in concentrations were observed during the day to a minimum of 11.71 $\mu g\ l^{-1}$, Fig. 7.7). Only a small rise in the ammonia-nitrogen level was recorded at 11 pm (24.23 $\mu g\ l^{-1}$) after which ammonia-nitrogen levls were again depressed. It is probable that the diluting effects of rain were responsible for this, maintaining low levels and preventing a build-up from occurring during the morning.

An inverse relationship was observed between the phytoplankton (Fig.7.8) and the zooplankton (Fig. 7.9) populations. Three peaks in both the phytoplankton and zooplankton densities at the surface layer were recorded over the 24h period.

The first increase in the phytoplankton population was recorded between 11 am (25,252 units l^{-1}) and 1 pm (23,727 l^{-1}). The zooplankton population at this time was low (7.22-8.88 l^{-1}). The measured decrease in phytoplankton (14,938 l^{-1}) recorded in the afternoon was accompanied by an increase in the zooplankton biomass (27.22 l^{-1}), so suggesting that the observed decline in the phytoplankton was brought about by an increase in grazing pressure. A second smaller increase in the phytoplankton biomass, recorded at 5 pm (21,834 l^{-1}) was accompanied by a decrease in the zooplankton population (17.78 l^{-1}). At 7 pm the phytoplankton density had dropped to the lowest value recorded during the 24h period (11,223 l^{-1}) and it remained low throughout the rest of the evening. The largest increase in zooplankters was also recorded at 7 pm (32.32 l^{-1}). This suggests that the maximum grazing pressure exerted by the zooplankton occurred at this time. Just before dawn, a third rise in the zooplankton population was measured, followed by a rise in phytoplankters to their highest recorded density (35,391 l^{-1}).

The inverse relationship observed between the phytoplankton and zooplankton populations was equally obvious when chlorophyll a levels were compared with zooplankton biomass (Figs. 7.10, 7.9). During this survey chlorophyll a levels were thus a good indicator of phytoplankton biomass. The decrease in algal biomass recorded at 7 pm concurent with

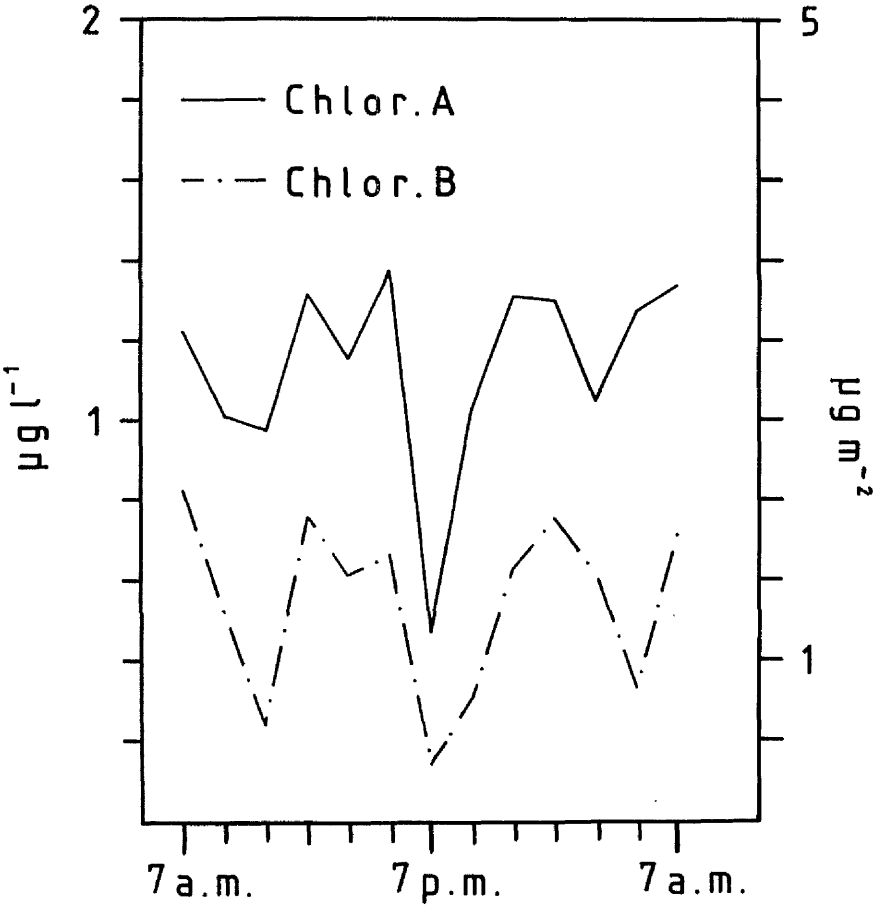

2
5
Chlor.A
Chlor.B
1
1
μg l⁻¹
μg m⁻²
7 a.m.
7 p.m.
7 a.m.

Figure 7.10

Diurnal variation 15/16 July 1981

Chlorophylls a and b

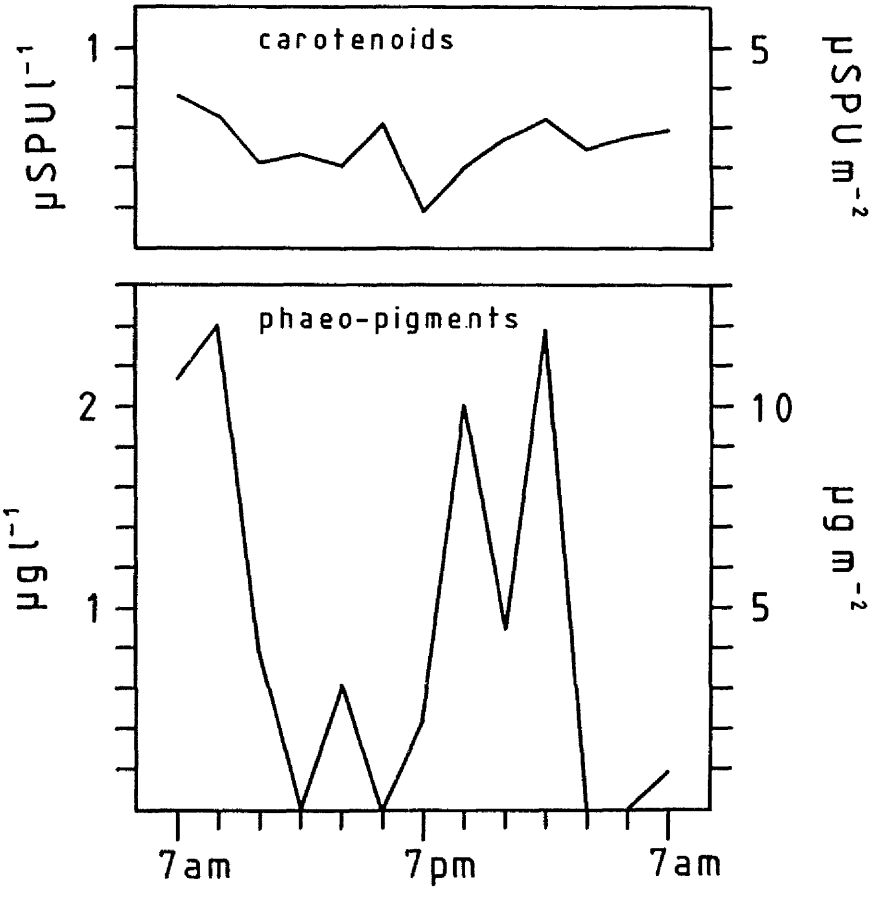

carotenoids
μSPU l⁻¹
1
5
μSPU m⁻²
phaeo-pigments
μg l⁻¹
2
1
10
5
μg m⁻²
7am
7pm
7am

Figure 7.11
Diurnal variation 15/16 July 1981
Carotenoids

Figure 7.12
Diurnal variation 15/16 July 1981
Phaeopigments

the increased zooplankton population was therefore indicative of grazing pressure.

A comparison of phytoplankton number with chlorophyll a level revealed a large rise in chlorophyll a between 9 pm and 1 am while algal levels remained low, suggesting that some synthesis of chlorophylls may have been taking place.

Carotenoid levels were observed to closely follow those of chlorophyll a (Fig. 7.11) while phaeopigment levels exhibited considerable fluctuation (Fig. 7.12). Their concentration varied between analytical zero and 2.42 $\mu g\ l^{-1}$. Phaeopigment concentrations greater than chlorophyll a levels were recorded at 7 am, 9 am, 9 pm and 1 am coinciding with high zooplankton biomass while between 1 pm and 5 pm and 3 am phaeopigment levels were considerably smaller than chlorophyll a levels (analytical zero to 0.63 $\mu g\ l^{-1}$).

The major algal species which contributed to the phytoplankton population were *Synechococcus* spp, *Aphanothece saxicola* and *Sphaerocystis schroeteri* colonies and cells. Also found throughout the survey were *Asterococcus limneticus*, *Cryptomonas* spp, *Cyclotella glomerata*, *Achnanthes saxonica*, *Pediastrum boryanum*, *Trachelomonas* spp *and Mallomonas* spp. 27 other species of algae were also recorded. The phytoplankton increase recorded between 11 am and 1 pm was composed primarily of *Synechococcus* spp (8,885 l^{-1}) and *Sphaerocystis* (8,658 l^{-1} and 6.048 l^{-1}) while the maximum population recorded at 5 am was composed primarily of *Aphanothece* (14,652 l^{-1}) with *Synechococcus* (9,164 l^{-1}) and *Sphaerocystis* cells (10,839 l^{-1}. Figs. 7.12 and 7.13). Thus the *Sphaerocystis* population exhibited surface maxima at midday and after dawn with minima in the evening and early morning. The pattern of diurnal variation exhibited by *Aphanothece* was of an overnight and morning maximum with a depressed surface population occurring during the period of maximum light intensity. The fluctuations in the pattern of *Synechococcus* indicated a possible diurnal pattern with maxima at midday and after dawn and minima during the evening and at night.

A comparison of the population density of *Sphaerocystis* with that

of the zooplankton revealed an inverse relationship between the populations, particularly in the case of the cells of *Sphaerocystis*. Zooplankton maxima coincided with *Sphaerocystis* minima suggesting that grazing pressure, exerted by the zooplankton, was responsible for the observed decline in the alga. Porter (1976) reported that *Sphaerocystis schroeteri* colonies were generally unharmed but often broken up by passage through the gut of *Daphnia*. This breaking up of *Sphaerocystis* would explain why no population increase of the colonies was observed at dawn and would also explain the presence of a large number of *Sphaerocystis* cells. A similar depression of *Synechococcus* during the zooplankton maxima was observed but no such correlation could be found with *Aphanothece*.

The main components of the zooplankton population were *Eudiaptomus gracilis* and its nauplii, *Diaphanosoma brachyurum*, *Holopedium gibberum*, *Bosmina coregoni*, *Kellicottia longispina*, and *Keratella* spp.

A disinct phasing of the periodicity of the cladocerans was apparent (Fig 7.15a). The maxima of the three were temporally distinct. The population maxima for *Diaphanosoma* were recorded at 9 pm (10.74 l^{-1}) and 3 am (13.33 l^{-1}). They were accompanied by a rise in the number of *Eudiaptomus* (6.67 l^{-1} and 5.56 l^{-1}. Fig. 7.16) and *Kellicottia* (9.91 l^{-1} at 9 pm only. Fig. 7.17). The *Holopedium* population maximum recorded at 3 pm (8.33 l^{-1}) was accompanied by an increase in the number of *Bosmina* (5.56 l^{-1}), *Kellicottia* (2.04 l^{-1}) and ciliated protozoa (3.40 l^{-1}). The greatest densities of *Bosmina* were recorded at 7 pm (13.15 l^{-1}) and 11 pm (9.26 l^{-1}). Though *Keratella* spp were recorded throughout the survey their numbers were too low to show any periodicity. The resultant combination of these zooplankters meant that the overall population maximum recorded at 7 pm and 9 pm was composed of two distinct components; the first dominated by *Bosmina* with *Holopedium* and *Eudiaptomus*, and the second by *Diaphanosoma* with *Eudiaptomus* and *Bosmina*.

Numerically the cladocerans were the most important components of the surface layer zooplankton population and so may have exerted a greater influence, in terms of grazing pressure, upon the phytoplankton population.

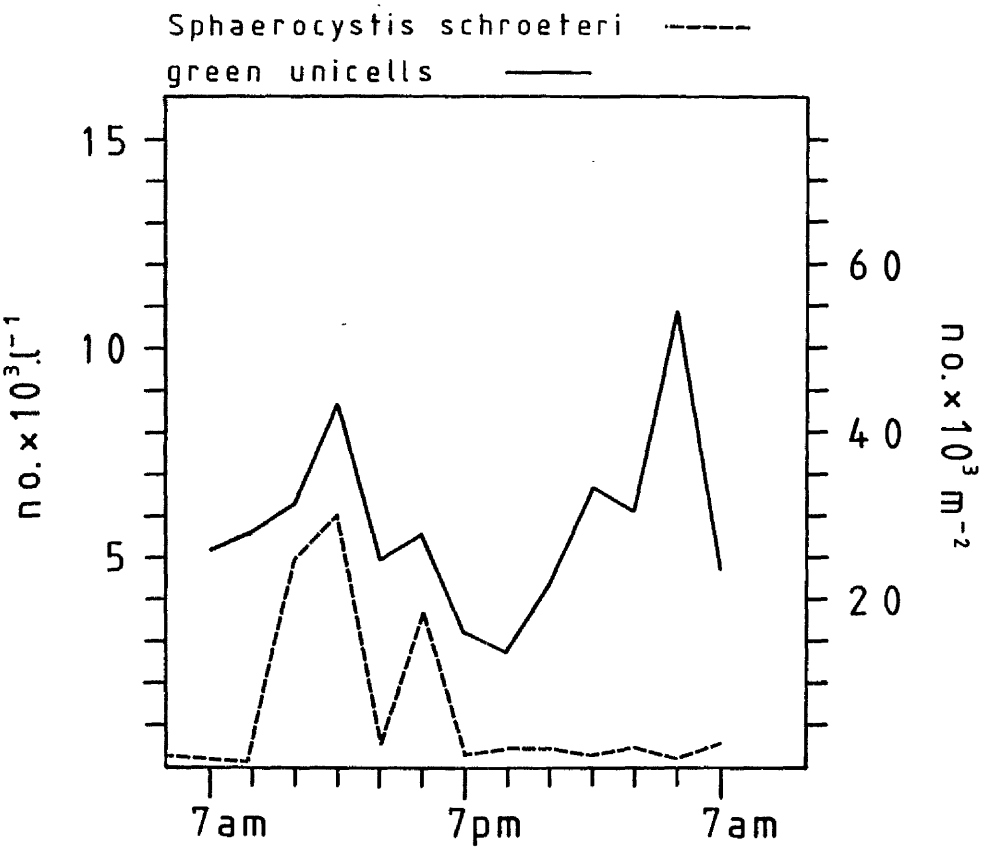

Sphaerocystis schroeteri
green unicells
15
10
5
no. x 10³ l⁻¹
60
40
20
no. x 10³ m⁻²
7am
7pm
7am

Figure 7.13

Diurnal variation 15/16 July 1981

Sphaerocystis schroeteri **and green unicells**

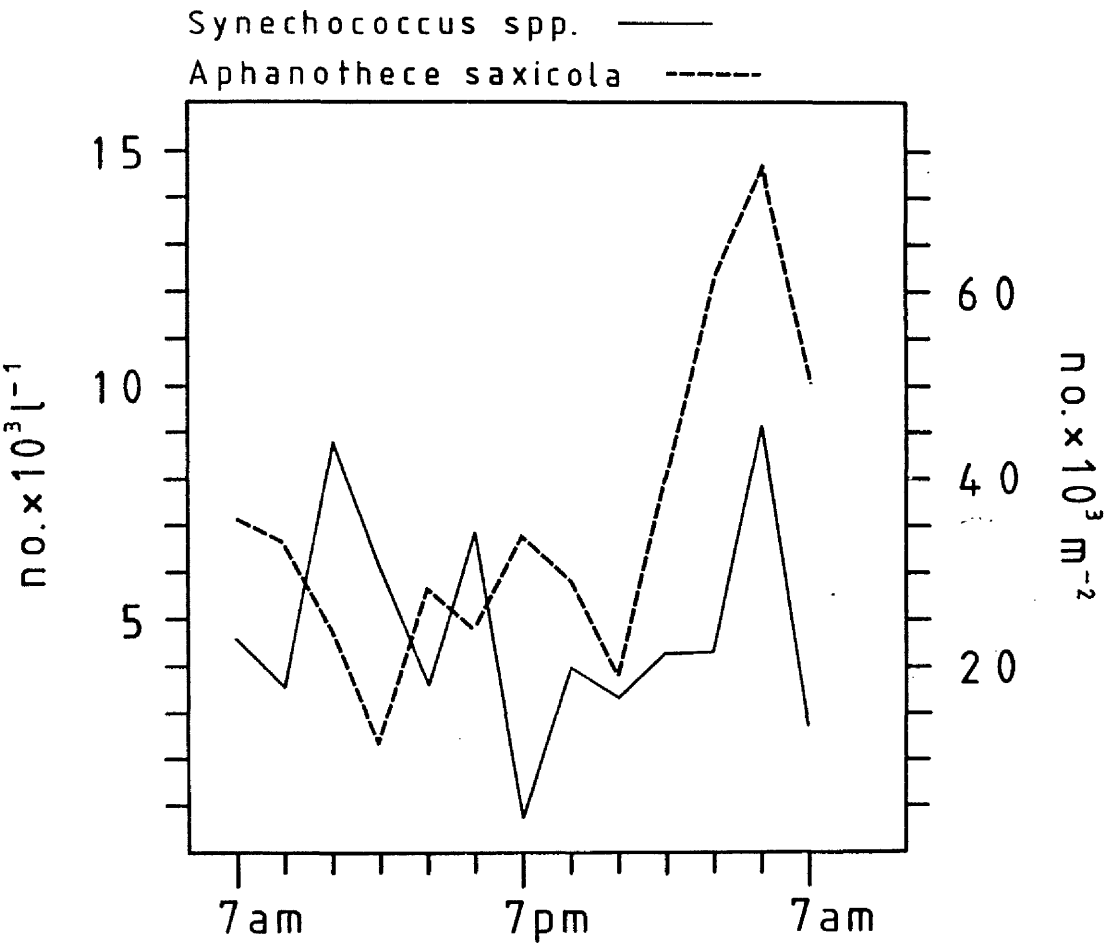

Synechococcus spp.
Aphanothece saxicola
15
10
5
60
40
20
no.×10³l⁻¹
no.×10³m⁻²
7am
7pm
7am

Figure 7.14

Diurnal variation 15/16 July 1981

Synechococcus spp and *Aphanothece saxicola*

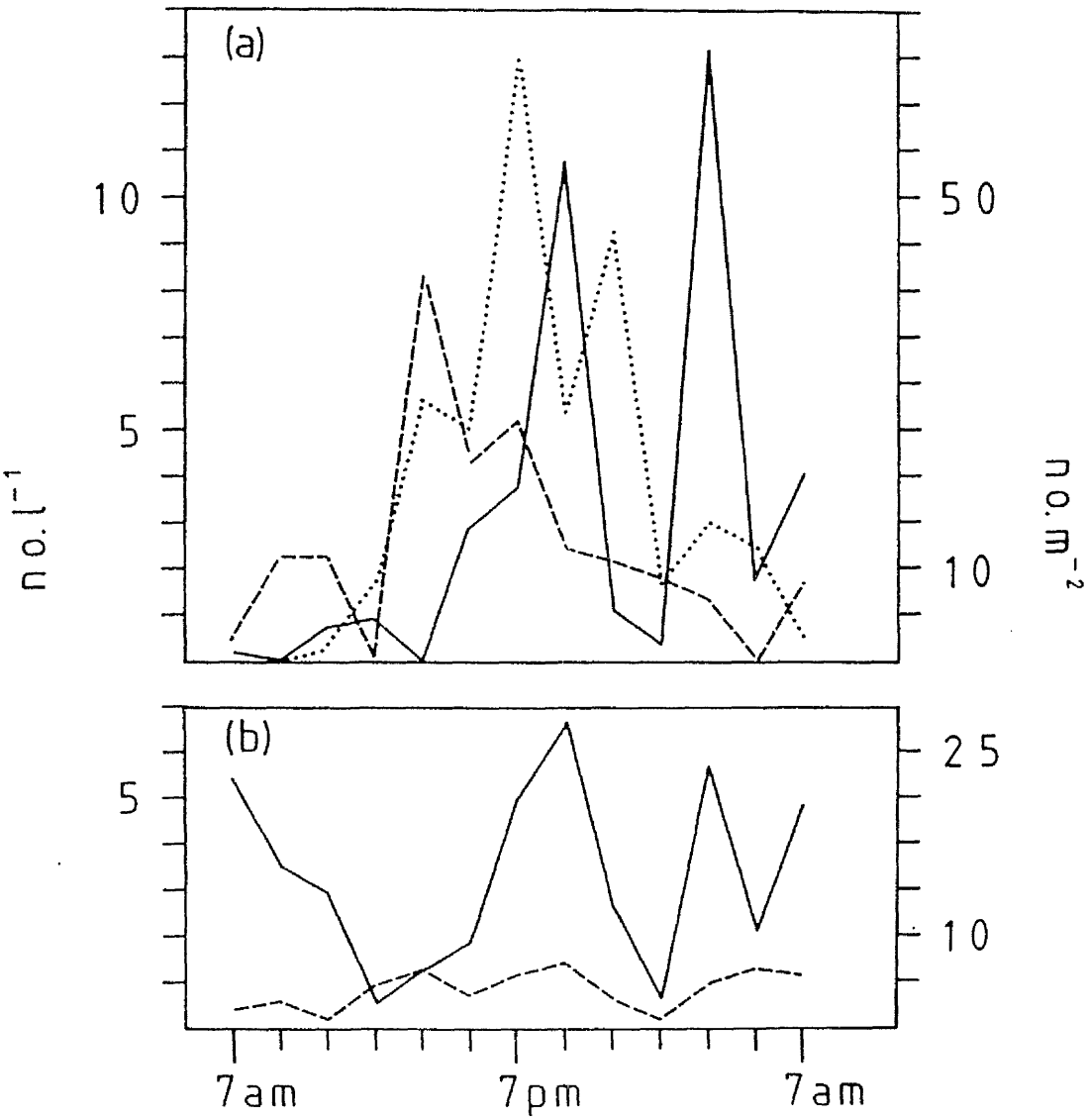

(a)
10
5
50
10
no. l^{-1}
no. m^{-2}
(b)
5
25
10
7am
7pm
7am

Figure 7.15a

Diurnal variation 15/16 July 1981

The Cladocera

solid line:- *Diaphanosoma brachyurum*

dashed line:- *Holopedium gibberum*

dotted line:- *Bosmin^a coregoni*

Figure 7.15b

Diurnal variation 15/16 July 1981

The Copepoda

solid line:- *Eudiaptomus gracilis*

dashed line:- The nauplii

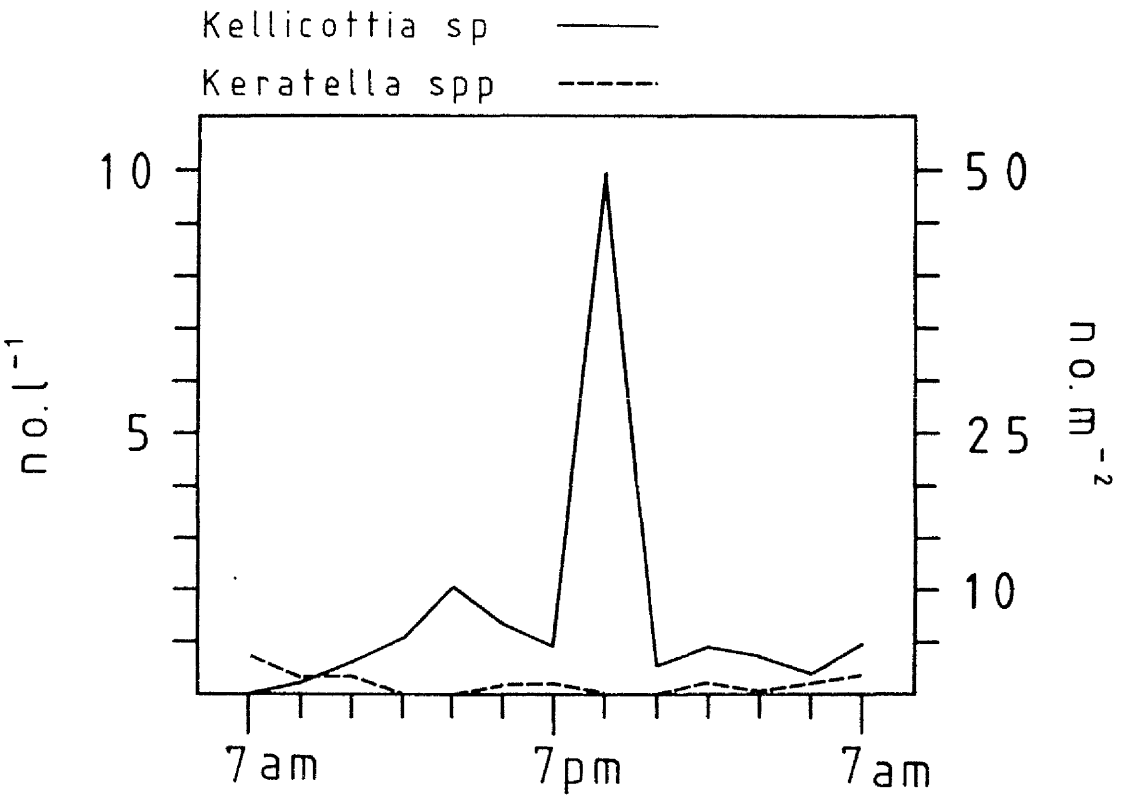

Kellicottia sp
Keratella spp
10
5
50
25
10
no.l^{-1}
no.m^{-2}
7am
7pm
7am

Figure 7.16

Diurnal variation 15/16 July 1981

Kellicottia longispina and *Keratella* spp

7.3 25th AND 26th AUGUST.

During this second survey water samples were collected from surface site 2 and at 1m, 3m and 5m. Between 9 am on the 25th and 9 am on the 26th sampling at all four depths took place every three hours and the following analyses were carried out; enumeration of the phytoplankton and zooplankton, estimates of the chlorophylls and carotenoids, determinations of the water temperature, oxygen content, light penetration by Secchi disc and measurements of inorganic nutrients (PO_4-P, NO_3-N, NH_3-N, SiO_4-Si, alkalinity and acidity). This survey required the coordinated help of six other personnel; Mr R. Mc Math, Grant Scotland, Fiona Mc Rae, Ford Kennedy, Jane Rose and Stuart Brough all of whom carried out their duties unfailingly and without a word of complaint. Dr Roger Tippett placed the field station and its facilities at our disposal.

The weather was mainly dry with some rain at the start (9 am) which cleared up quickly. The sky at night was clear and dawn and dusk were extended. The hours of darkness lay between 10.30 pm and 5 am.

Oxygen and temperature profiles were taken at site 2 at 9am, 3 pm, 9 pm, midnight, 6 am and 9 am together with Secchi disc readings (Fig 7.17). There was sufficient light at 9 pm for a Secchi disc reading to be taken.

At the start of the survey the surface water temperature was slightly lower than that at depth (15.30 ^{0}C at the surface, 15.82 ^{0}C at 1m, 15.55 ^{0}C at 3m and 13.25 ^{0}C at 5m). The oxygen concentration of the surface layer was 85% saturation, decreasing gradually with depth until 4m after which there was a sharp fall in the oxygen content, from 69.5% to 9%, coinciding with a Secchi disc depth of 3.95m. By 3 pm the depth of light penetration had extended to 4.87 m and an increase in the oxygen content at 5m to 64% was recorded. Considerable warming of the water body was recorded with a surface layer temperature of 18.35 ^{0}C. At 9 pm a cooling of the water had occurred with isothermal conditions extending from the surface to 4 m (17.60 ^{0}C). A Secchi disc reading of

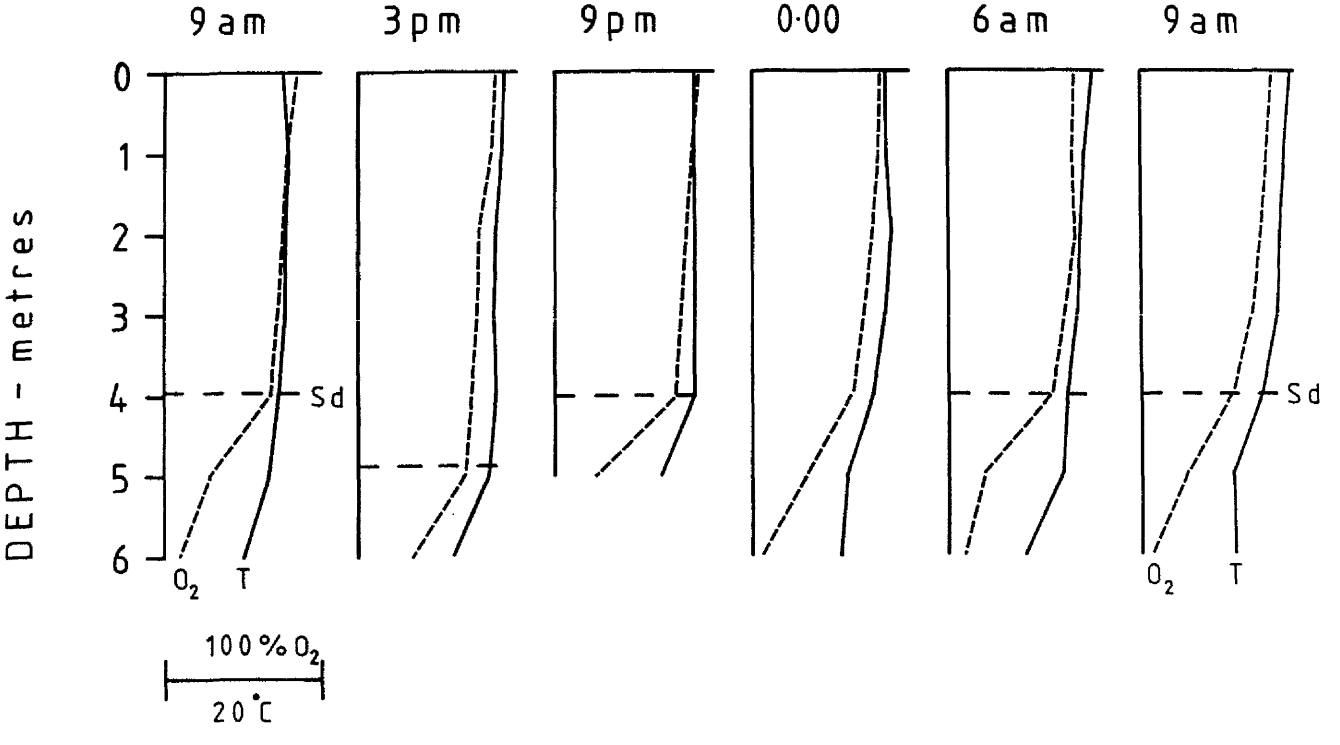

9 a m
3 p m
9 p m
0·00
6 a m
9 a m
DEPTH - metres
0
1
2
3
4
5
6
Sd
Sd
O2
T
O2
T
100 % O2
20 °C

Figure 7.17

Diurnal variation 25/26 August 1981

oxygen and temperature profiles

solid line:- temperature ^{o}C

dashed line:- percentage oxygen saturation

Secchi disc depth:---Sd

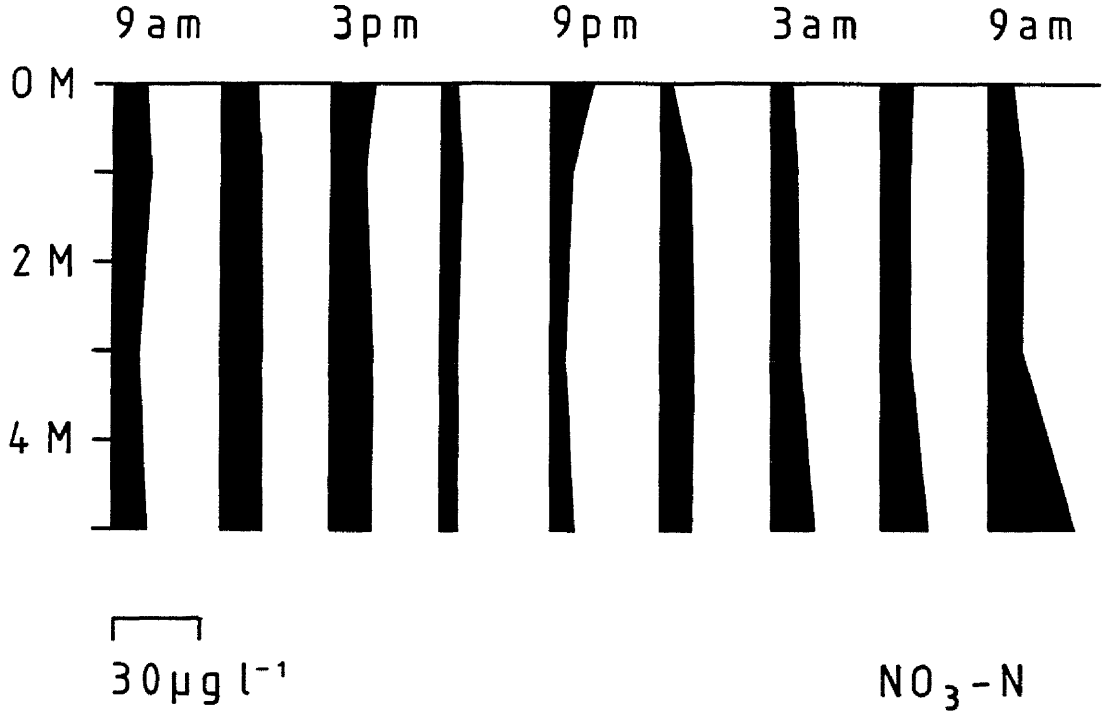

9 a m
3 p m
9 p m
3 a m
9 a m
0 M
2 M
4 M
30 µg l⁻¹
NO3-N

Figure 7.18

Diurnal variation 25/26 August 1981

Nitrate-nitrogen $\mu g\ l^{-1}$

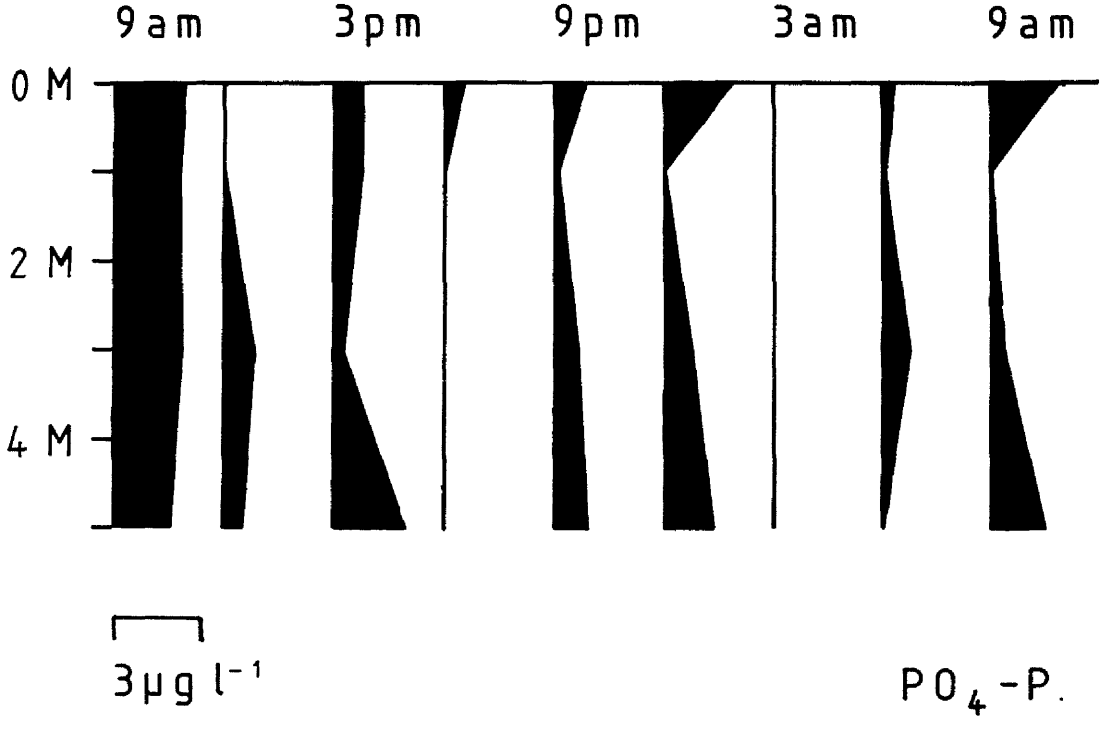

9 a m
3 p m
9 p m
3 a m
9 a m
0 M
2 M
4 M
3 µg l⁻¹
PO4-P.

Figure 7.19

Diurnal variation 25/26 August 1981

Phosphate-phosphorus $\mu g\ l^{-1}$

4.00 m was obtained. Further cooling of the top 1m was recorded at midnight (17.08 ^{0}C). By 6 am the surface layer had become heated to 18.60 ^{0}C with light penetration extending to 4.00 m, corresponding with the depth at which the oxygen concentration was observed to decrease. Further warming of the water body at the close of the survey occurred when a surface temperature of 18.60 ^{0}C was recorded (18.60 ^{0}C at 1m, 17.60 ^{0}C at 3m). Light penetration extended to 4.00 m and coincided with the depth at which both temperature and oxygen were observed to fall rapidly. The use of the Secchi disc thus provided useful additional data on the extent of the epilimnion.

The increase in temperature recorded through the day to an afternoon maximum was also measured on the 15th July as was cooling overnight. It is probable that persistent rainfall on the 15th July prevented warming of the waters after sunrise as measured in this later survey. Similarly the depression of the water temperature measured at the start of this survey in comparison to that obtained 24h later, may have been caused by rainfall over the hours prior to the start of the observations.

The range of nitrate-nitrogen concentration measured at the surface was lower than that obtained in July (3.64 μg l^{-1}-14.88 μg l^{-1}. Fig. 7.18). The pattern of a maximum in late evening and morning minima were not observed. Only small variations in nitrate-nitrogen were recorded throughout the 24h period with an almost uniform distribution with depth. Little change in concentration was observed during 9 am and 3 pm (mean 12.83 μg l^{-1}). At 6 pm a decline in concentration at all depths to between 5.45 and 6.61 μg l^{-1} was recorded. A small rise in the surface content was measured at 9 pm (13.97 l^{-1}), followed by a gradual increase at all depths such that at the end of the survey the nitrate-nitrogen content of the water body was comparable to that recorded at the beginning.

The pattern of phosphate-phosphorus concentration over the 24h period was also dissimilar to that obtained in July (Fig. 7.19). Surface concentrations were lower, ranging from analytical zero to 2.40 μg l^{-1}. Considerable variation in phosphate levels were recorded with depth and time. In general, phosphate concentrations were greater at

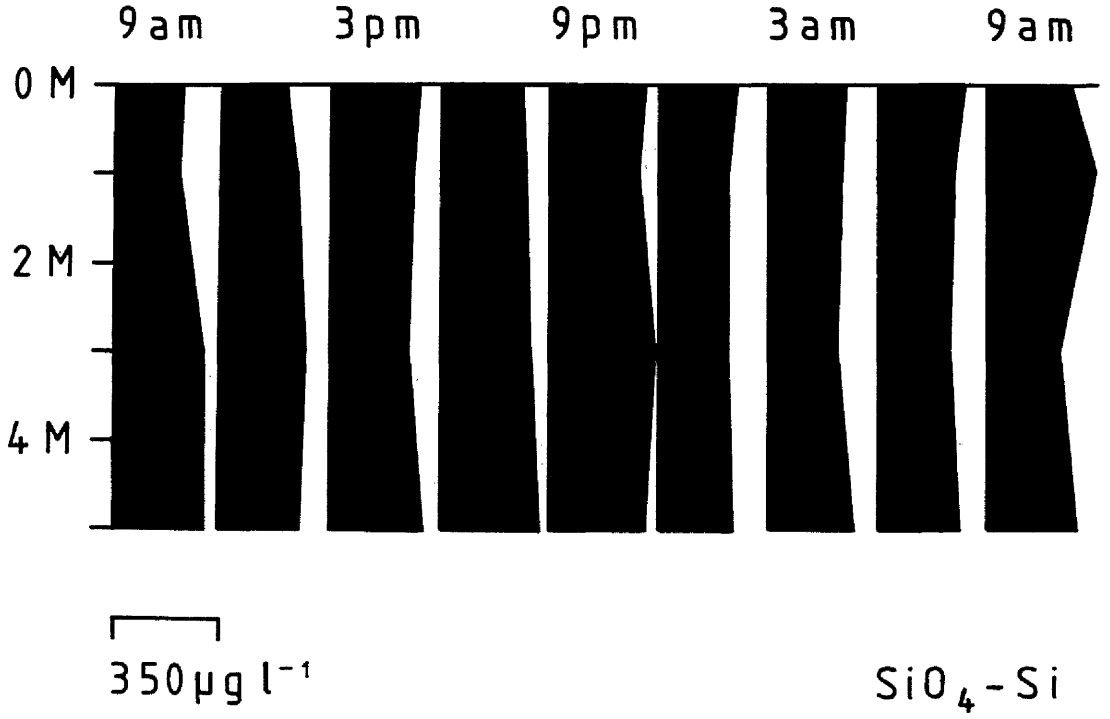

9 a m
3 p m
9 p m
3 a m
9 a m
0 M
2 M
4 M
350 µg l⁻¹
SiO4-Si

Figure 7.20

Diurnal variation 25/26 August 1981

Silicate-silica $\mu g\ l^{-1}$

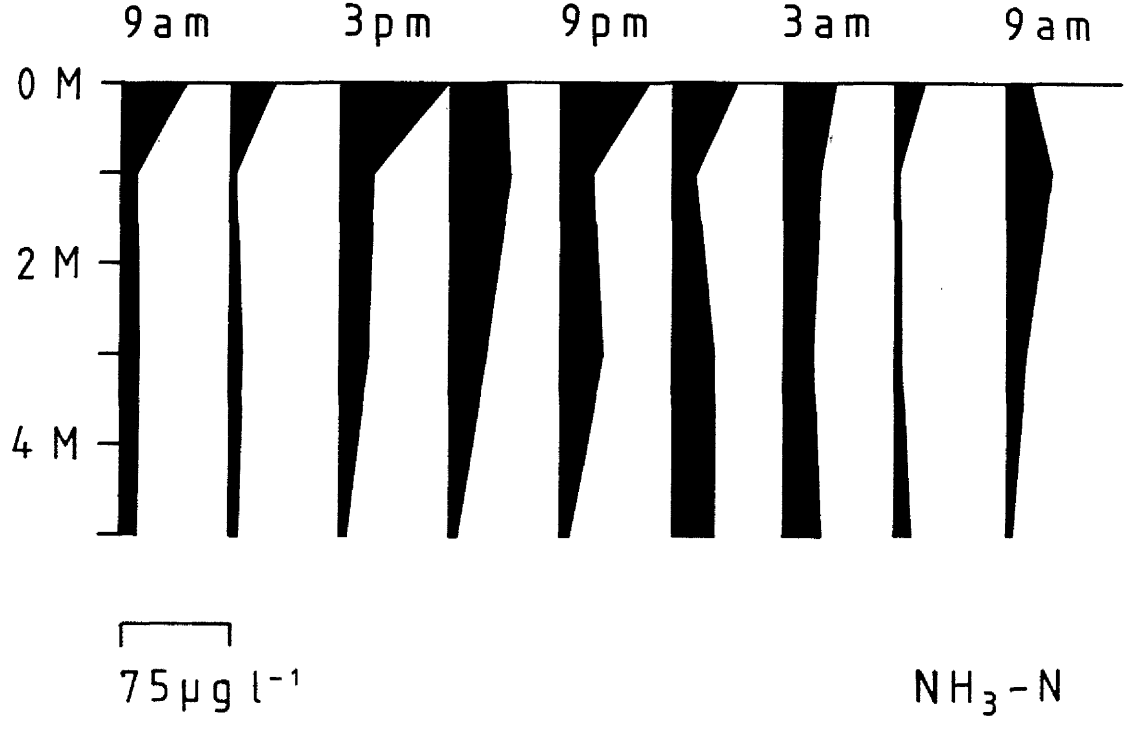

9 a m
3 p m
9 p m
3 a m
9 a m
0 M
2 M
4 M
75 µg l⁻¹
NH3-N

Figure 7.21

Diurnal variation 25/26 August 1981

Ammonia-nitrogen $\mu g\ l^{-1}$

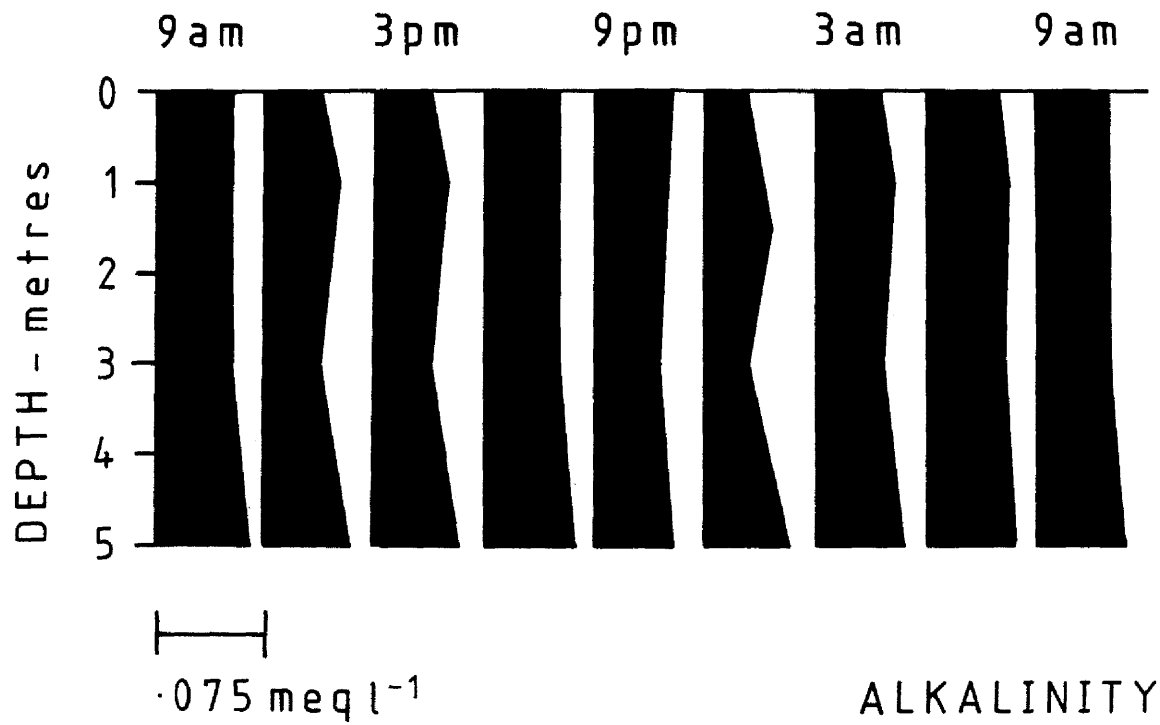

9am
3pm
9pm
3am
9am
0
1
2
3
4
5
DEPTH - metres
·075 meq l⁻¹
ALKALINITY

Figure 7.22

Diurnal variation 25/26 August 1981

Alkalinity meq l^{-1}

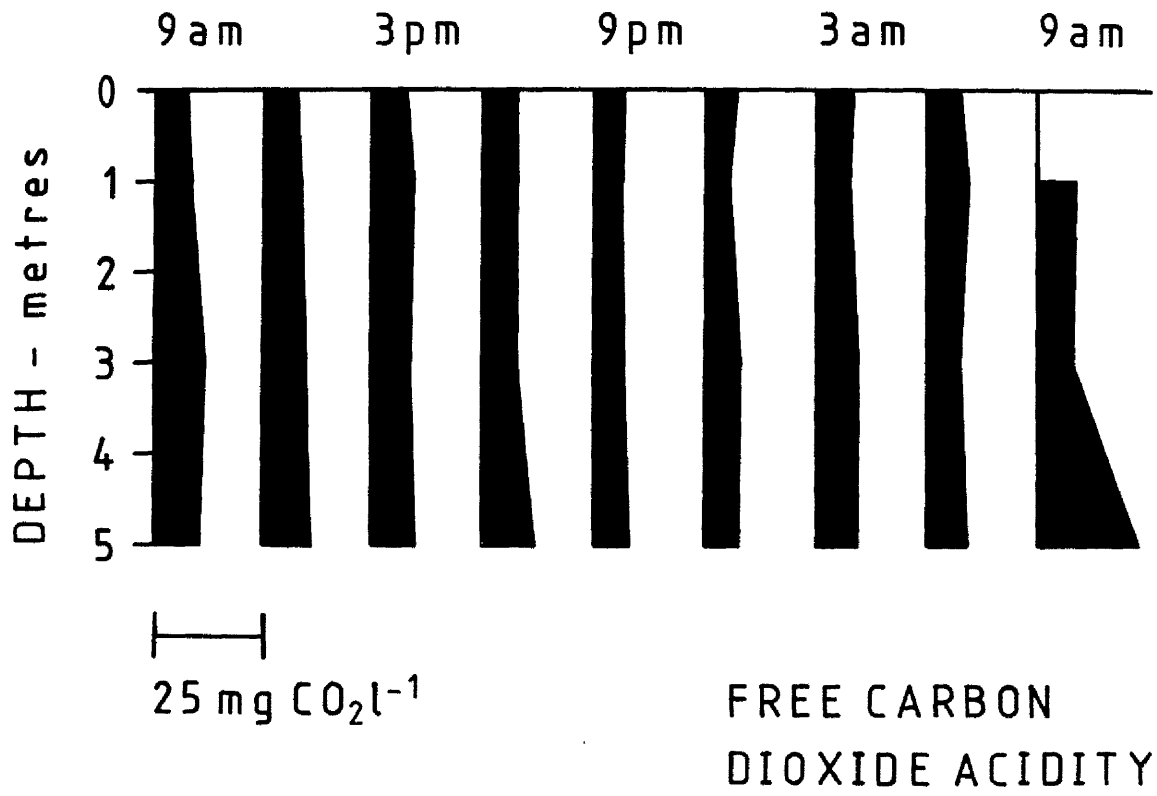

9 am
3 pm
9 pm
3 am
9 am
DEPTH - metres
0
1
2
3
4
5
25 mg $CO_2 l^{-1}$
FREE CARBON
DIOXIDE ACIDITY

Figure 7.23

Diurnal variation 25/26 August 1981

Free carbon dioxide mg l^{-1}

the surface and 5m and lower at 1m. The highest levels were recorded at the start of the survey (1.96-2.40 μg^{-1}), decreasing at noon to analytical zero at the surface and 1m and rising to 2.53 $\mu g\ l^{-1}$ at 5m at 3 am. The lowest levels were recorded at 6 pm and 3 am (analytical zero to 0.7 $\mu g\ l^{-1}$).

Silicate-silica levels ranged from 196.60 $\mu g\ l^{-1}$ to 346.2 $\mu g\ l^{-1}$ (Fig. 7.20). The pattern of distribution of silicate over the 24h period differed from that observed in July. Little variation in surface levels was recorded. High levels were measured throughout the depth of the water column sampled with only slight variation with depth.

The levels of ammonia-nitrogen recorded at the surface were greater than those measured in July and ranged from 17.66 $\mu g\ l^{-1}$ to 73.45 $\mu g\ l^{-1}$ (Fig. 7.21). Only slight similarities were observed between the diel surface patterns obtained in July and August with maxima at the start of the survey, in the afternoon and at 9pm and minima at noon and 6 am. Surface enrichment of ammonia-nitrogen was particularly noticeable over the first 9 h, the decrease recorded at 6 pm being followed again by surface enrichment. The range measured at 1m was 2,26-40.96 $\mu g\ l^{-1}$; at 3m, 3.67-28.25 $\mu g\ l^{-1}$ and at 5m, 4.24-33.90 $\mu g\ l^{-1}$.

Alkalinity levels ranged from 0.03-0.065 meq l^{-1} (Fig. 7.22). Throughout the 24 h period, alkalinity at 5m was greater than that at the surface, 1m, and 3m. The main variations were recorded at the surface and at 3m where at noon, 3 pm and midnight decreases in alkalinity were recorded. Little variation was noted in alkalinity at 1m and 5m.

Free carbon dioxide acidity ranged from 4.81-22.65 mg l^{-1}(Fig 7.23). From acidity concentrations of between 6.89-11.23 mg l^{-1} at the start of the survey, a decline to between 4.81 and 7.24 mg l^{-1} at 9 pm and midnight was observed. A gradual increase in free carbon dioxide acidity was then observed to between 7.68 and 22.65 mg l^{-1} by the end of the survey. In general, the highest levels were recorded at 5m, particularly at 6 pm (11.28 mg l^{-1}) and 9 am on the 26th (22.65 mg l^{-1}).

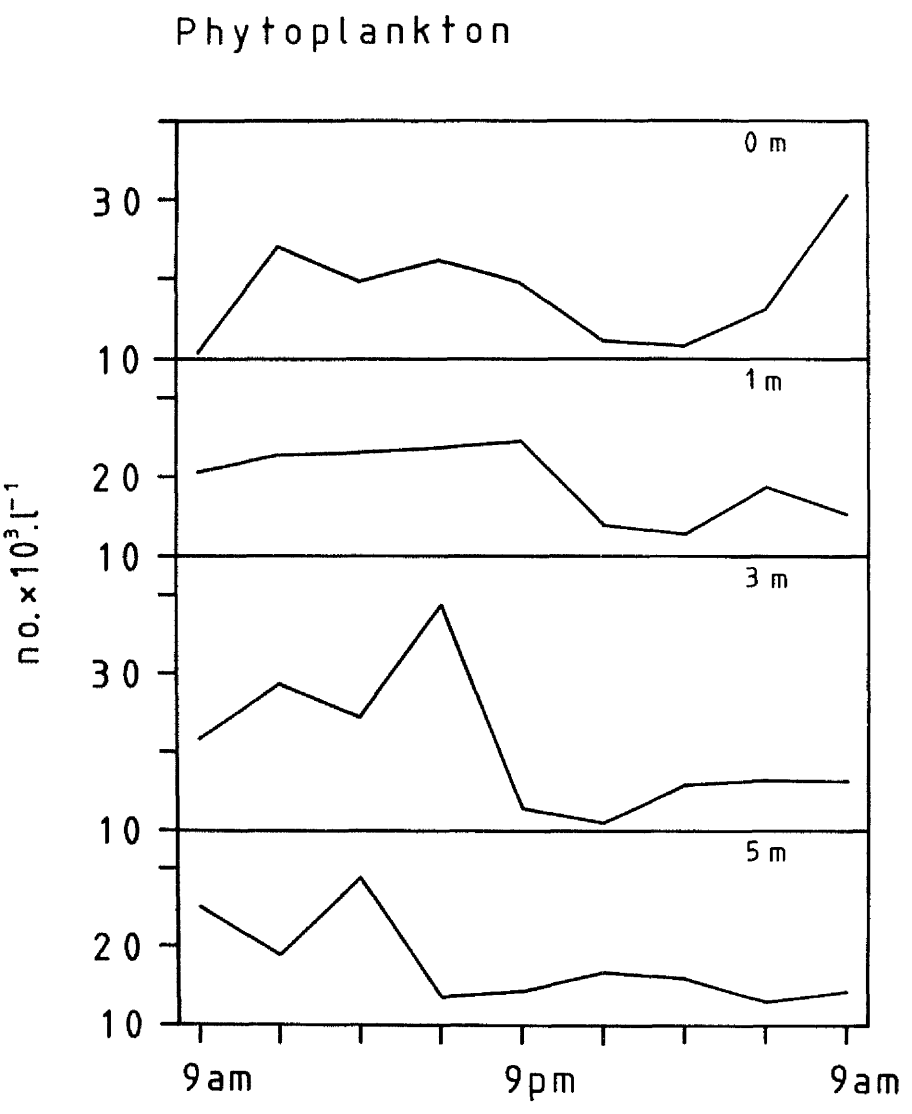

Phytoplankton
0 m
1 m
3 m
5 m
30
10
20
10
30
10
20
10
no.x10³.l⁻¹
9am
9pm
9am

Figure 7.24

Diurnal variation 25/26 August 1981

Phytoplankton biomass

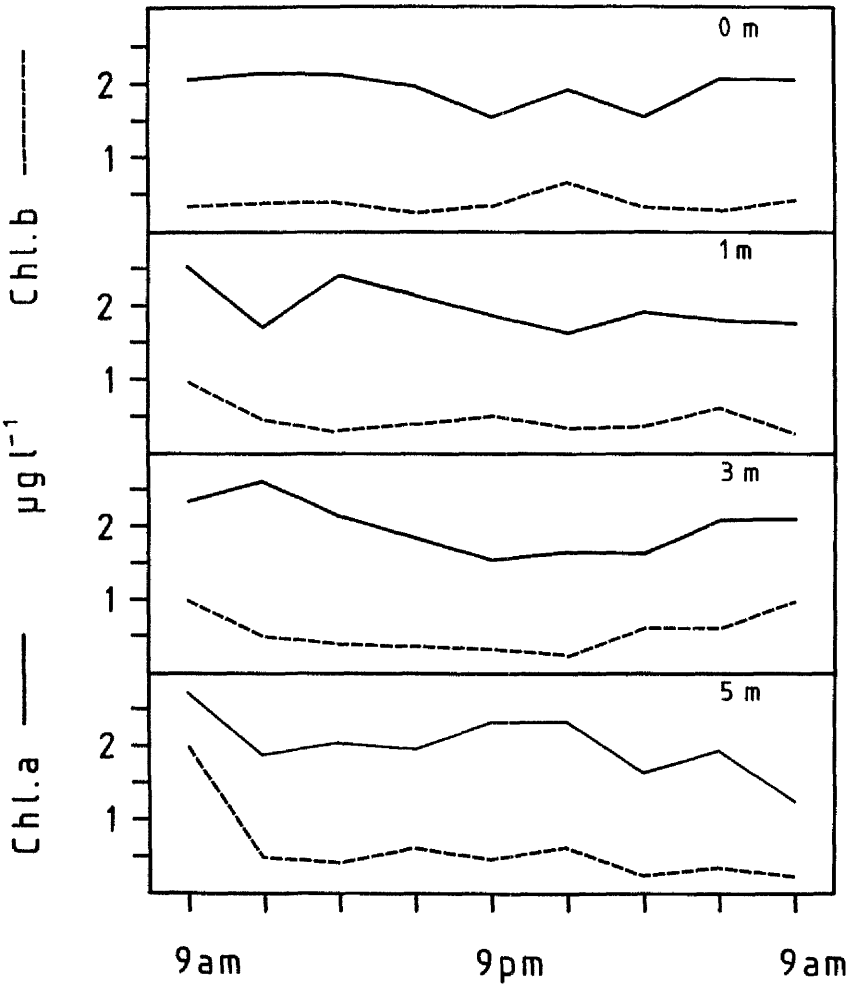

0 m
1 m
3 m
5 m
2
1
Chl.a ——— Chl.b ------
µg l⁻¹
9am
9pm
9am

Figure 7.25

Diurnal variation 25/26 August 1981

Chlorophylls a and b

From an enumeration of the phytoplankton over the 24h period the following pattern emerged: Phytoplankton were observed at the surface layer mainly during the afternoon and early evening (Fig.7.24). Between dusk and dawn a decrease in the population was observed followed by a rapid increase at the end of the survey period. Little change in the phytoplankton population was observed at 1m during the day (20,616 l^{-1}-24.681 l^{-1}). A low population was recorded during the period of darkness (12,885-13,946 l^{-1}) followed by a small increase in quantity at 6 am (18,775 l^{-1}). At 3m the phytoplankton population was again greatest during the day, particularly at 6 pm (38,604 l^{-1}) showing minima at night and low numbers during the morning. The population maximum at 5m was recorded at 3 pm (28,868 l^{-1}) coinciding with the increased depth of light penetration as measured by Secchi disc. The populations recorded at 5m during the rest of 24h period were low with little variation (12,689 l^{-1} to 16,817 l^{-1}). It is possible that vertical migration between 5m and 3m depths occurred during the afternoon. At night the phytoplankton population was evenly distributed with depth and it is possible that the algae sank below 5m. No correlation between phytoplankton periodicity and alkalinity levels could be determined.

An examination of the chlorophylls a and b levels indicated little change in surface concentrations throughout the 24h period (Fig. 7.25). At 1m, slight increases in chlorophyll a were measured at 9 am and at 3 pm. At 3m a gradual decrease in chlorophyll a through the afternoon and evening was recorded, rising slightly in the morning (6 am).At 5m small increases in chlorophyll a were measured at 9 am, 3 pm, 9 pm and midnight. Chlorophyll b levels generally reflected those of chlorophyll a.

A comparison of chlorophyll a concentrations with phytoplankton quantity revealed that chlorophyll a levels did not decrease at night coinciding with the falling phytoplankton population. As observed during the first 24h survey this is probably indicative of the active synthesis of chlorophyll by the phytoplankton population throughout the water column.

Zooplankton

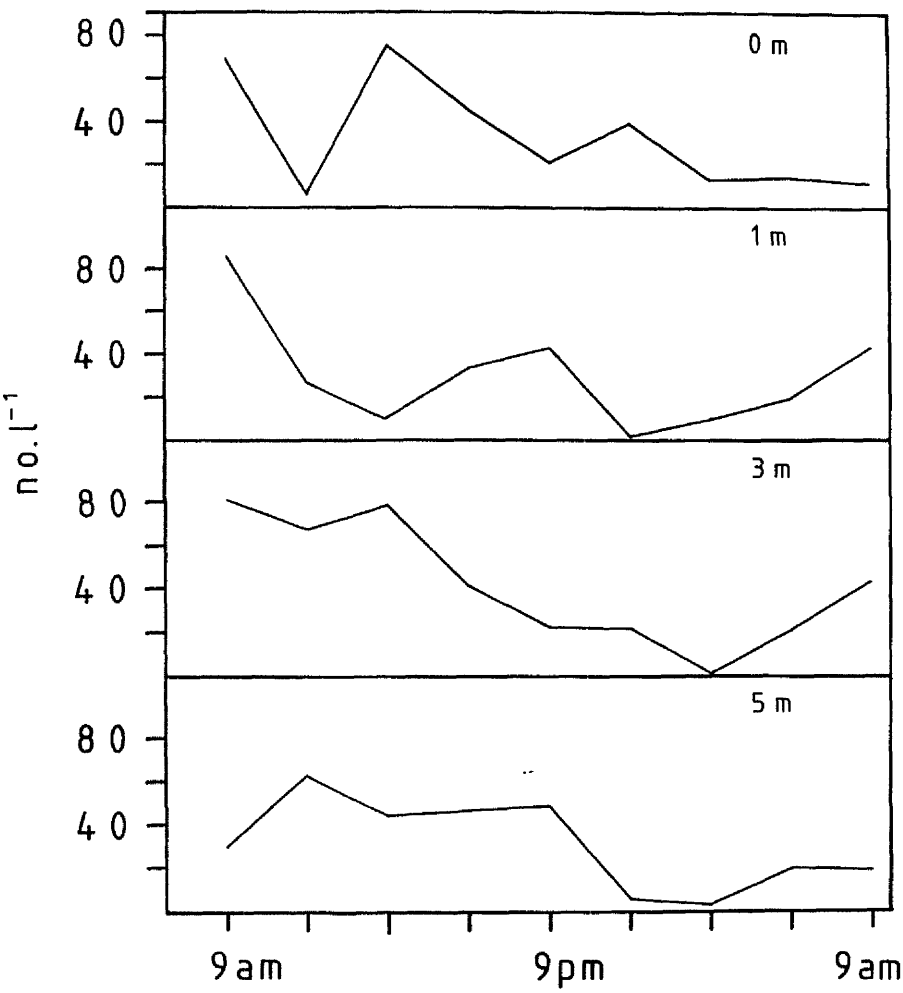


Figure 7.26

Diurnal variation 25/26 August 1981

Zooplankton biomass

It should be pointed out that lateral diffusion of the phytoplankton population may be responsible for some of the observed differences in phytoplankton biomass during the day. At night, it is probable that passive sinking to depths greater than 5m was responsible for the low overall population recorded.

At the start of the sampling programme the zooplankton population was more numerous at 1m and 3m (68.29 l^{-1} at the surface, 86.68 l^{-1} at 1m, 80.68 l^{-1} at 3m and 29.27 l^{-1} at 5m. Fig. 7.26). A noon there was evidence of a sinking of the zooplankton population, particuularly from the surface (6.38 l^{-1}) and 1m (28.14 l^{-1}) accompanied by an increase at 5m (62.66 l^{-1}). The highest surface population recorded during this survey occurred at 3 pm (75.42 l^{-1}). The population at 1m depth was still low (10.51 l^{-1}) while at 3m the maximum population recorded throughout this survey was measured (78.42 l^{-1}). By 9 pm surface and 3m populations had fallen slightly and that at 1m had risen slightly (21.39 l^{-1}, 22.89 l^{-1} and 43.15 l^{-1} respectively). A slight increase in the surface population was recorded at midnight (39.34 l^{-1}) after which little variation in biomass was recorded (11.26 l^{-1}-14.07 l^{-1}). Populations at depth also remained low, rising only at 1m (43.53 l^{-1}) and 3m (43.71 l^{-1}) at the end of the survey.

A comparison of the zooplankton and phytoplankton biomasses revealed that an alternation of the populations occurred at the surface, 3m and 5m but this pattern was not as obvious as that recorded in July such that distinct declines in the phytoplankton population due to grazing pressure were not easy to define.No such pattern was obvious for the data collected at 1m depth.

The smallest zooplankton densities, recorded at the surface at noon, at 1m at midnight, and at 3m and 5m at 3 am occurred when large quantities of particulate matter (siliceous silt) were observed in the samples. It is possible that active avoidance of these depths at these times occurred so resulting in populations of less than 6.40 l^{-1}.

As in July, the phytoplankton population was dominated by *Sphaerocystis, Synechococcus* spp and *Aphanothece* with *Cryptomonas ovata, Mallomonas producta,* and *Pediastrum boryanum, Ankistrodesmus*

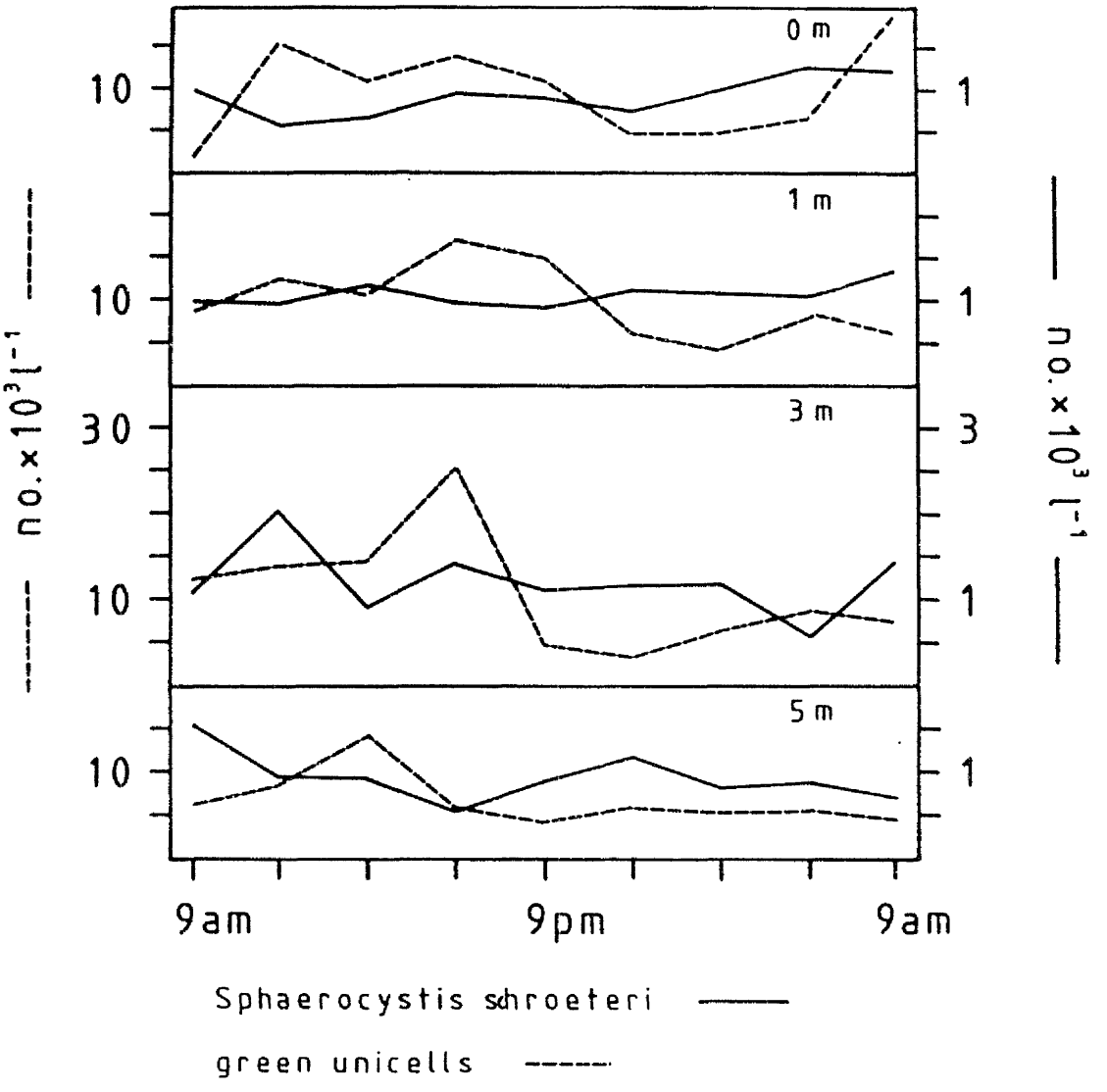

0 m
1 m
3 m
5 m
10
1
30
3
9am
9pm
9am
no.×10³l⁻¹
no.×10³l⁻¹
Sphaerocystis schroeteri
green unicells

Figure 7.27

Diurnal variation 25/26 August 1981

Sphaerocystis schroeteri and green unicells

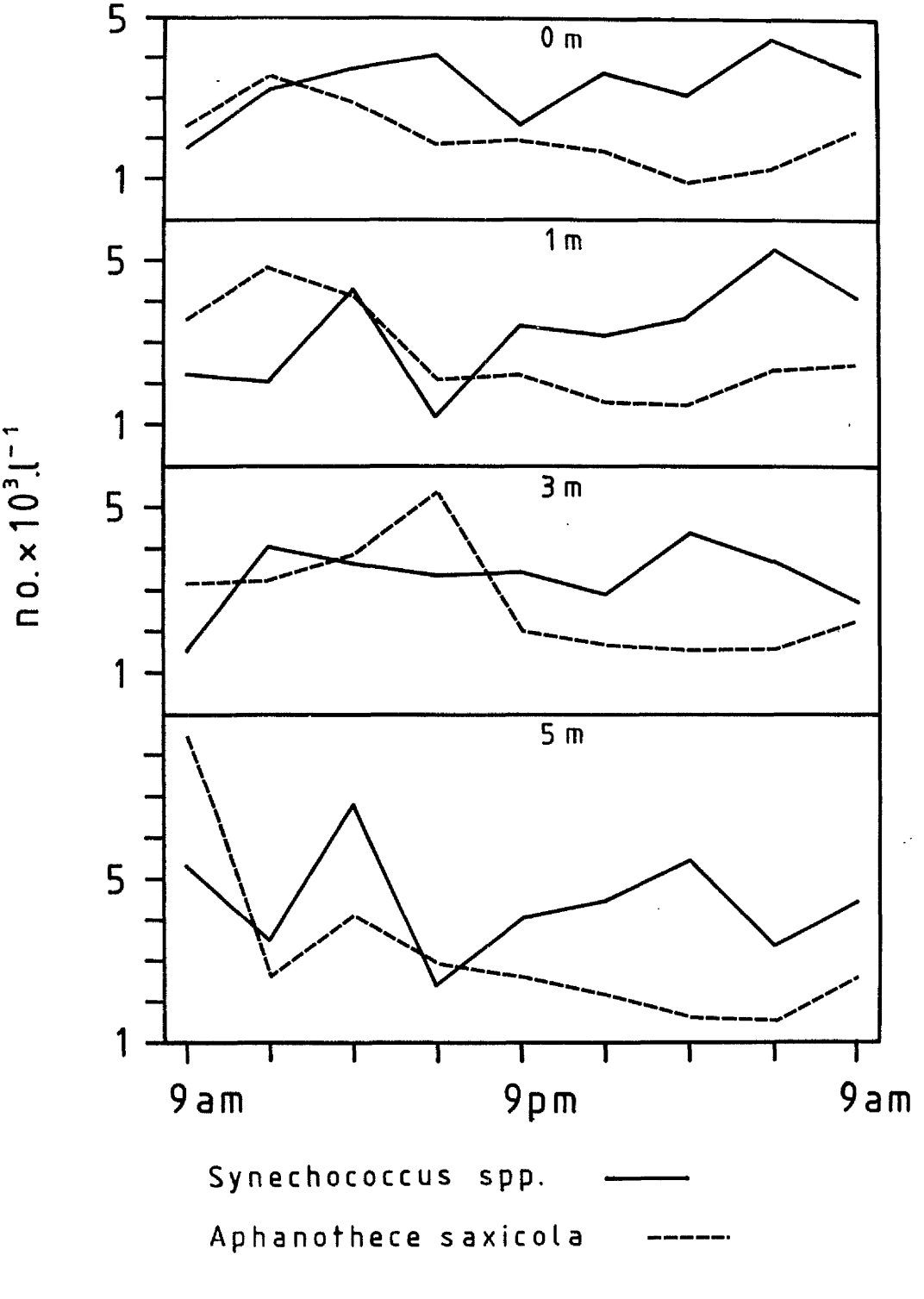

0 m
1 m
3 m
5 m
5
1
no. x 10³.l⁻¹
9am
9pm
9am
Synechococcus spp.
Aphanothece saxicola

Figure 7.28

Diurnal variation 25/26 August 1981

Synechococcus spp and *Aphanothece saxicola*

falcatus, green flagellates, *Rhodomonas minuta* and *Dinobryon divergens*.

Little variation in the population of *Sphaerocystis* colonies at the surface, 1m and 5m was observed (Fig. 7.27). At 3m, a doubling of colony number was recorded at noon (from 2,140 l^{-1} at 9 am to 4,040 l^{-1}). By 3 pm the population had declined (1,770 l^{-1}) after which little variation in the population was observed.

Green unicells which were probably the cells of *Sphaerocystis* colonies were observed at higher levels at the surface during the afternoon and evening than at night and the morning (Fig. 7.27). The largest increase in cell density was recorded at 9 am on the 26th. At 1m depth the population maximum was observed in the evening. A population maximum at 5m at 3 pm, coinciding with the period of greatest light penetration, was followed by an increase in green unicells at 3m at 6 pm. These unicells were thus observed at the surface at noon, to rise from 5m throughout the afternoon and evening to 1m as light levels fell and to be evenly distributed with depth during the period of darkness rising to the surface with increasing light levels in the morning.

At 9 am *Synechococcus* spp were observed in quantity at 5m (5,379 l^{-1}. Fig. 7.28). Population increases at all depths were recorded in the afternoon, particularly at 5m depth at 3 pm (6,809 l^{-1}) coinciding with the deepest Secchi disc reading. While only minor fluctuations were observed throughout the remainder of the survey, a progressive rise in the *Synechococcus* population from 5m during the period of darkness to 1m and the surface at 6 am was apparent.

Aphanothece saxicola was also observed in quantity at 5m depth at 9 am (8,488 l^{-1}.Fig. 7.28), the population rising to the surface and 1m at noon (3450 l^{-1} and 4857 l^{-1} respectively), then sinking to 3m at 6 pm (5345 l^{-1}). Little variation in the *Aphanothece* population was observed over the evening, night and morning periods and any changes in the population were probably the result of slight lateral displacement as opposed to vertical migration.

Mallomonas producta was recorded preferentially at 5m (Fig. 7.29).

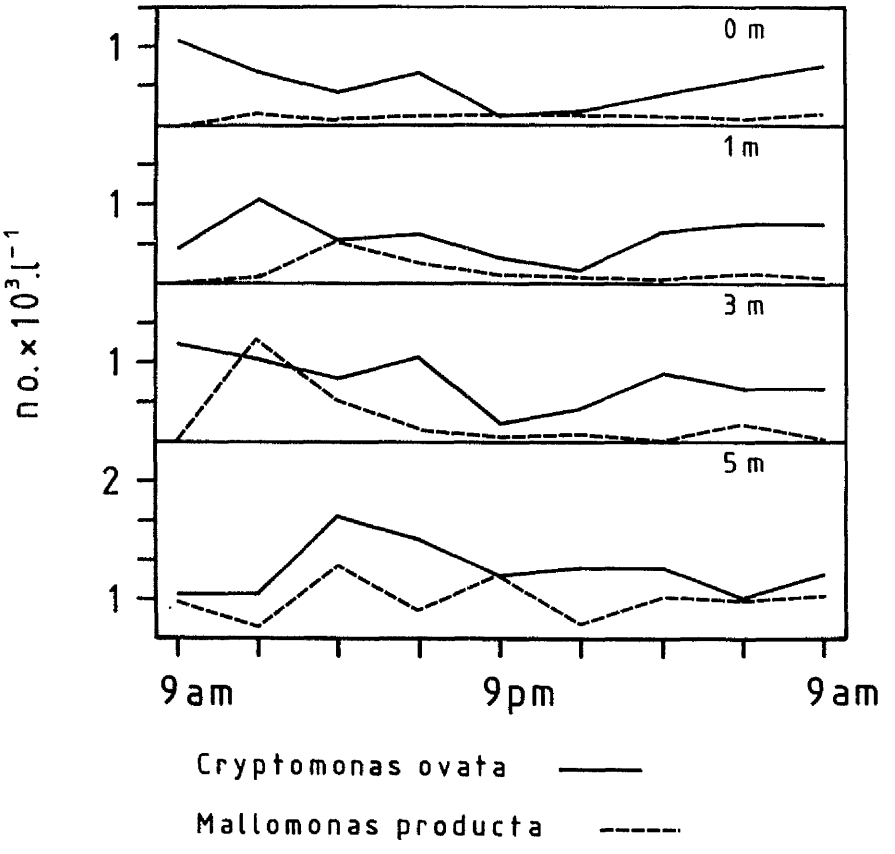

0 m
1 m
3 m
5 m
1
1
1
2
1
no. x 10³.l⁻¹
9am
9pm
9am
Cryptomonas ovata
Mallomonas producta

Figure 7.29

Diurnal variation 25/26 August 1981

Mallomonas producta and *Cryptomonas ovata*

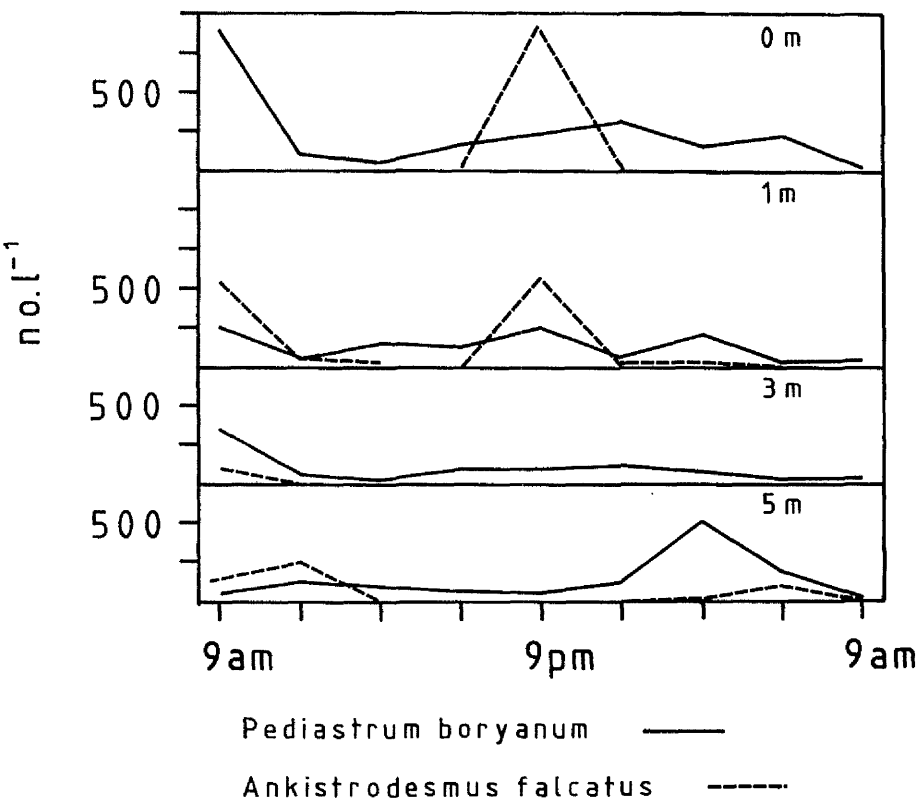

0 m
1 m
3 m
5 m
500
500
500
500
n o.l^{-1}
9am
9pm
9am
Pediastrum boryanum
Ankistrodesmus falcatus

Figure 7.30

Diurnal variation 25/26 August 1981

Pediastrum boryanum **and** *Ankistrodesmus falcatus*

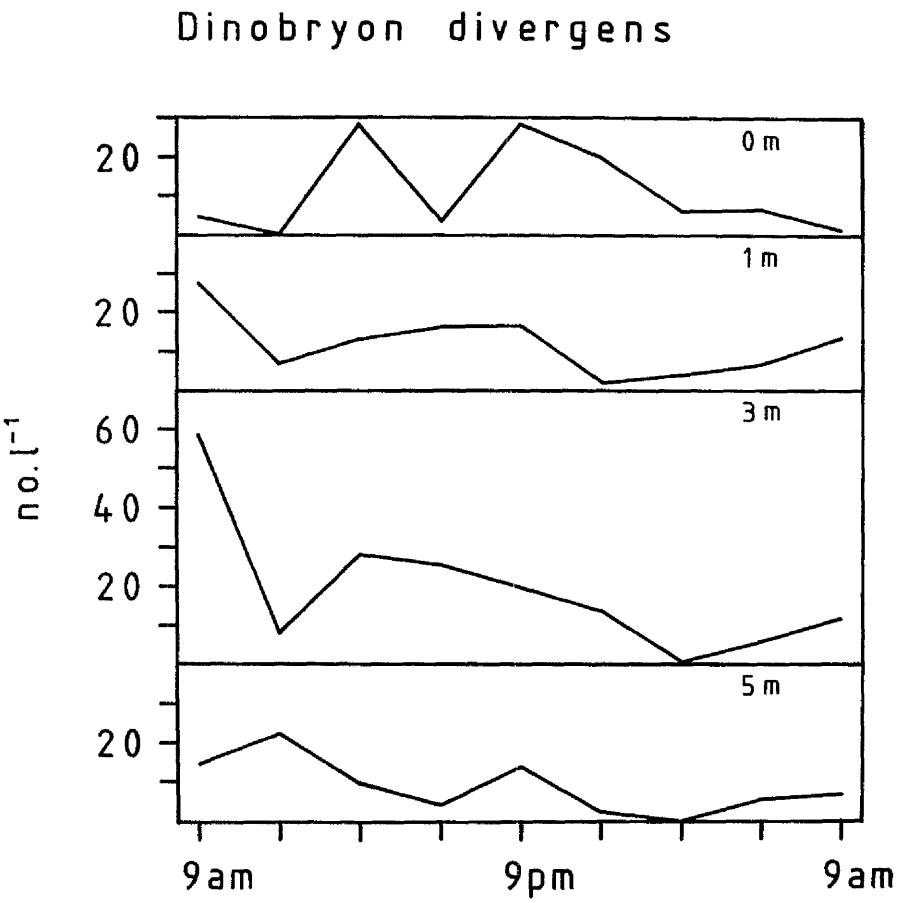

Dinobryon divergens
0 m
1 m
3 m
5 m
20
20
60
40
20
20
n o. l⁻¹
9am
9pm
9am

Figure 7.31

Diurnal variation 25/26 August 1981

Dinobryon divergens

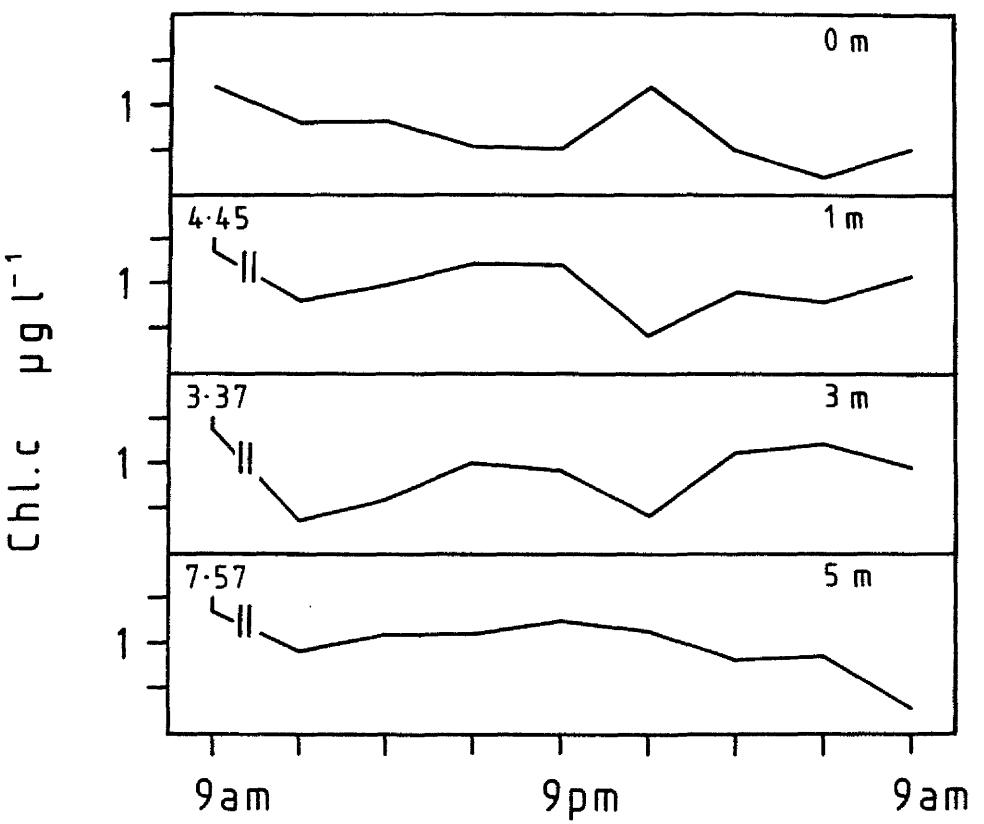

0 m
1 m
3 m
5 m
4·45
3·37
7·57
1
1
1
1
Chl.c µg l⁻¹
9am
9pm
9am

Figure 7.32

Diurnal variation 25/26 August 1981

Chlorophyll c

There was little evidence of vertical migration to the surface and the greatest population recorded during the 24 h period occurred at noon at 3m (1,271 l^{-1}). *Cryptomonas ovata* was also recorded preferentially at 3m and 5m (Fig. 7.29). It was found in quantity at the surface at both the beginning and end of the survey (1,062 l^{-1} and 1,135 l^{-1} respectively). The greatest population was recorded at 5m at 3 pm (1,566 l^{-1}) and preferentially at 5m throughout the evening and at night. After dawn the population was observed to be evenly distributed with depth.

While the *Pediastrum boryanum* population was low in comparison to those algae previously reported, it was observed in the greatest quantity at the surface at the start of the 24 period and again at 5m at 3 am (899 l^{-1} and 499 l^{-1} respectively. Fig. 7.30). *Ankistrodesmus falcatus* was also measured in greater quantities at the surface and at 1m at 9 pm (902 l^{-1} and 562 l^{-1} respectively. Fig.7.30). Mucilage production throughout the day would have increased the buoyancy of this alga and so may have been responsible for its surface accumulation in the evening.

While the numbers of *Dinobryon divergens* colonies were observed to be low (zero-58.88 l^{-1}) these colonies were quite large each being composed of between 20 and 100 cells (Fig 7.31). The greatest population was recorded at 3m at 9 am (58.88 l^{-1}). *Dinobryon* was recorded mainly at 3m throughout the afternoon and evening and at the surface at 3 pm and 9 pm. Since the quantity of *Dinobryon* colonies was so low, it is unwise to conjecture whether vertical migration occurred.

Apart from the high levels of chlorophyll c recorded at the beginning of the survey (1.20-7.57 $\mu g\ l^{-1}$), little variation in chlorophyll c levels were observed (Fig. 7.32). No correlation between the phytoplankton, particularly the chrysomonads and cryptomonads and the initial high value of chlorophyll c were observed. An examination of the raw data revealed anomalous background absorbance between 530 and 630 nm. The high chlorophyll c readings were thus the result of "experimental error" rather than a true representation of the pigment concentration in the field. This highlights one of the problems in using trichometric equations for the determination of chlorophyll c

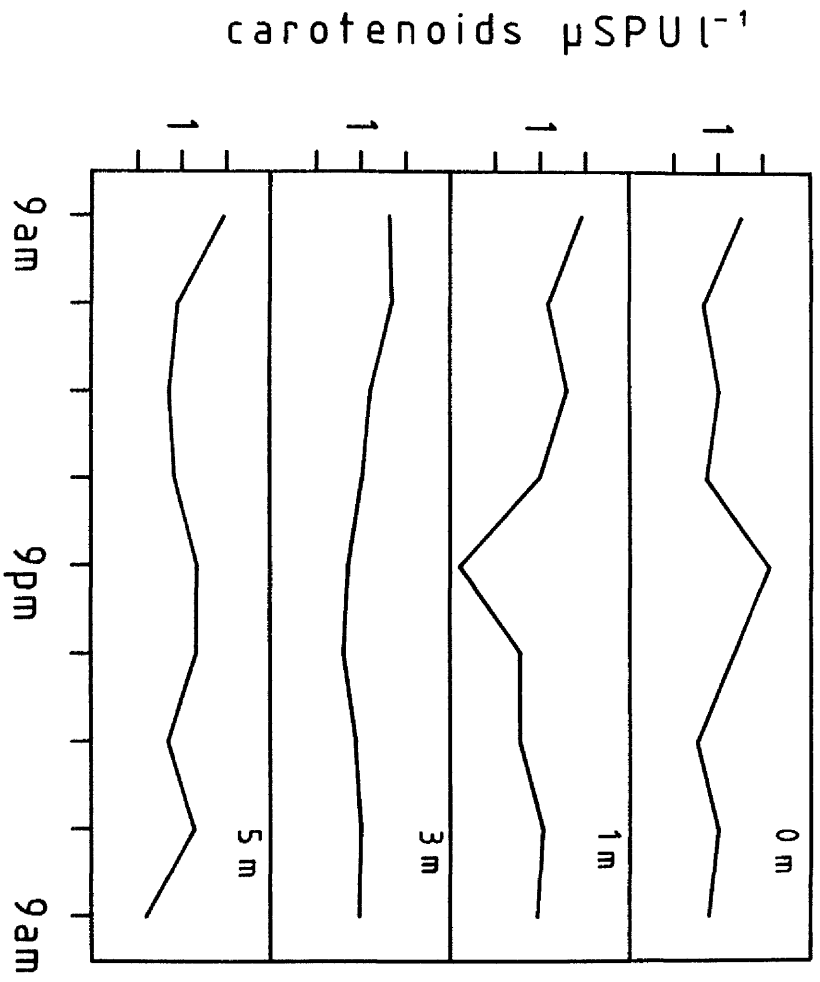

carotenoids µSPU l⁻¹
1
1
1
1
9am
9pm
9am
5 m
3 m
1 m
0 m

Figure 7.33

Diurnal variation 25/26 August 1981

Carotenoids

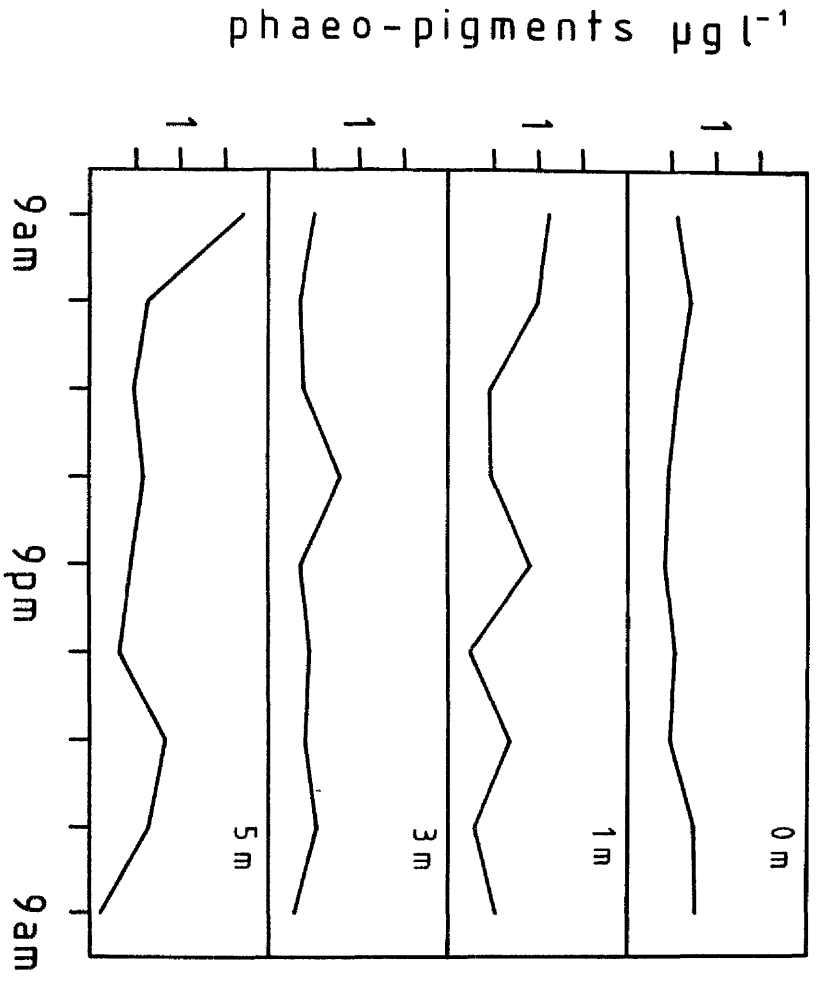

phaeo-pigments µg l⁻¹
1
1
1
1
9am
9pm
9am
5 m
3 m
1 m
0 m

Figure 7.34
Diurnal variation 25/26 August 1981
Phaeopigments

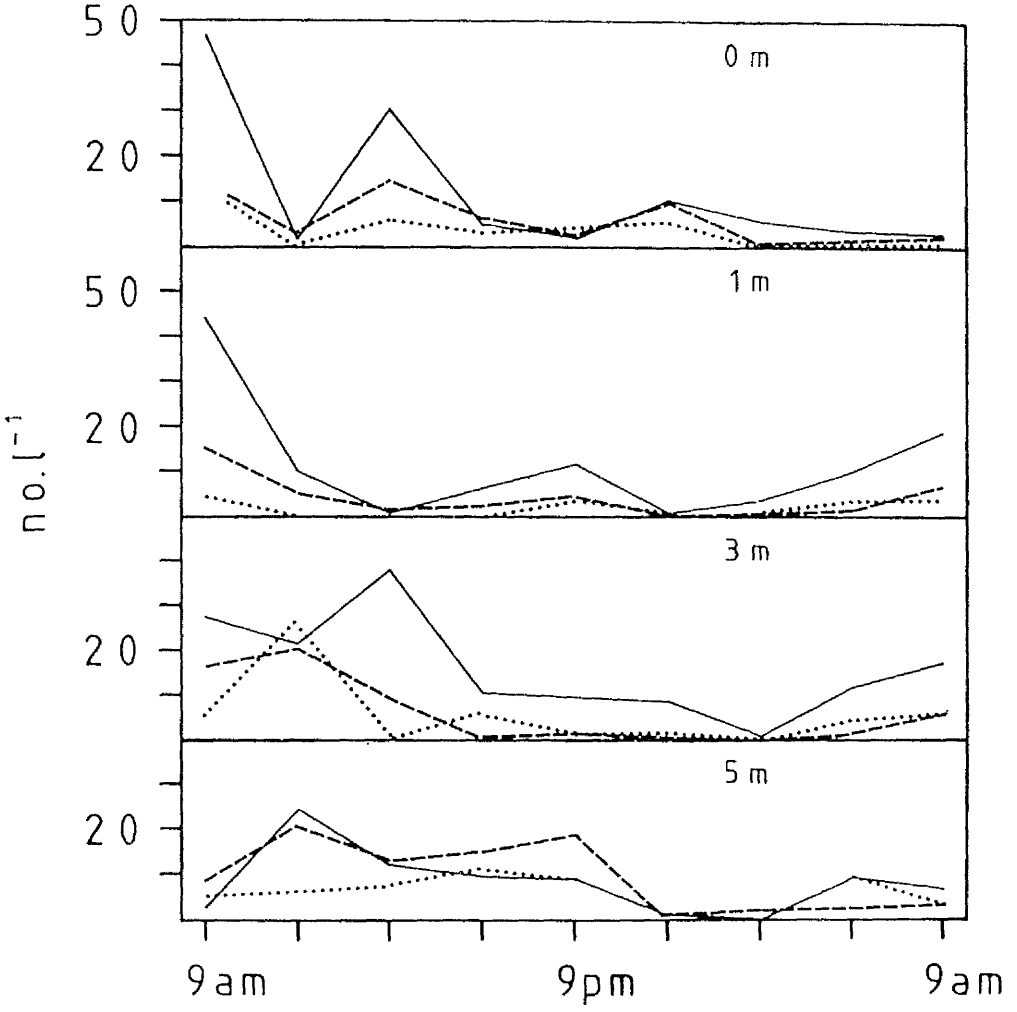

50
20
0 m
50
20
1 m
20
3 m
20
5 m
no. l^{-1}
9am
9pm
9am

Figure 7.35

Diurnal variation 25/26 August 1981

The Copepoda

solid line:- *Eudiaptomus gracilis*

dashed line:- The nauplii

dotted line:- Eggs

since an error in the measurement stage can become over exaggerated at the calculation stage.

The pattern of carotenoid concentrations were similar to that of chlorophyll a at 3m and 5m (Fig. 7.33). Overall, carotenoid levels varied little.

Phaeopigment levels during this 24 h survey were consistently lower than their corresponding chlorophyll a levels (Fig. 7.34). Little variation was observed, particularly at the surface. On average, the phaeopigment levels were 29% of that of chlorophyll a indicating that the phaeopigments were probably algal in origin with little contribution from the littoral vegetation of inflows.

The main components of the zooplankton population during this 24 h period were *Eudiaptomus gracilis*, nauplii, the cladocerans *Diaphanosoma brachyurum*, *Holopedium gibberum* and *Ceriodaphnia quadrangula* and the rotifers *Polyarthra vulgaris* and *Epiphanes senta*.

Eudiaptomus adults were observed particularly at the surface and at 1m at the beginning of the sampling programme (46.53 l^{-1} and 44.28 l^{-1} respectively. Fig. 7.35). A population decrease at noon at the surface (1.50 l^{-1}) and at 1m (10.51 l^{-1}) was accompanied by an increase in the population at 5m (24.02 l^{-1}). At 3 pm *Eudiaptomus* was recorded mainly at the surface (30.02 l^{-1}) and at 3m (37.90 l^{-1}). The population was then observed to decrease throughout the water column sampled and to remain low throughout the evening, overnight and early morning (zero to 11 63 l^{-1}). A small increase in the *Eudiaptomus* population at 1m and 3m was observed at the end of the survey (18.57 l^{-1} and 16.89 l^{-1} respectively).

The majority of nauplii were of *Eudiaptomus*, some calanoid nauplii were observed and so the figures given represent their sum totals (Fig. 7.35). From a surface population of 10.88 l^{-1} and of 15.01 l^{-1} at 1m at 9 am, a decrease in the number of nauplii was observed at noon with increases in the populations at 3m (20.26 l^{-1}) and at 5m (21.01 l^{-1}). During the evening the naupliid population was greater at 5m than at the other depths. A small increase in the surface population was

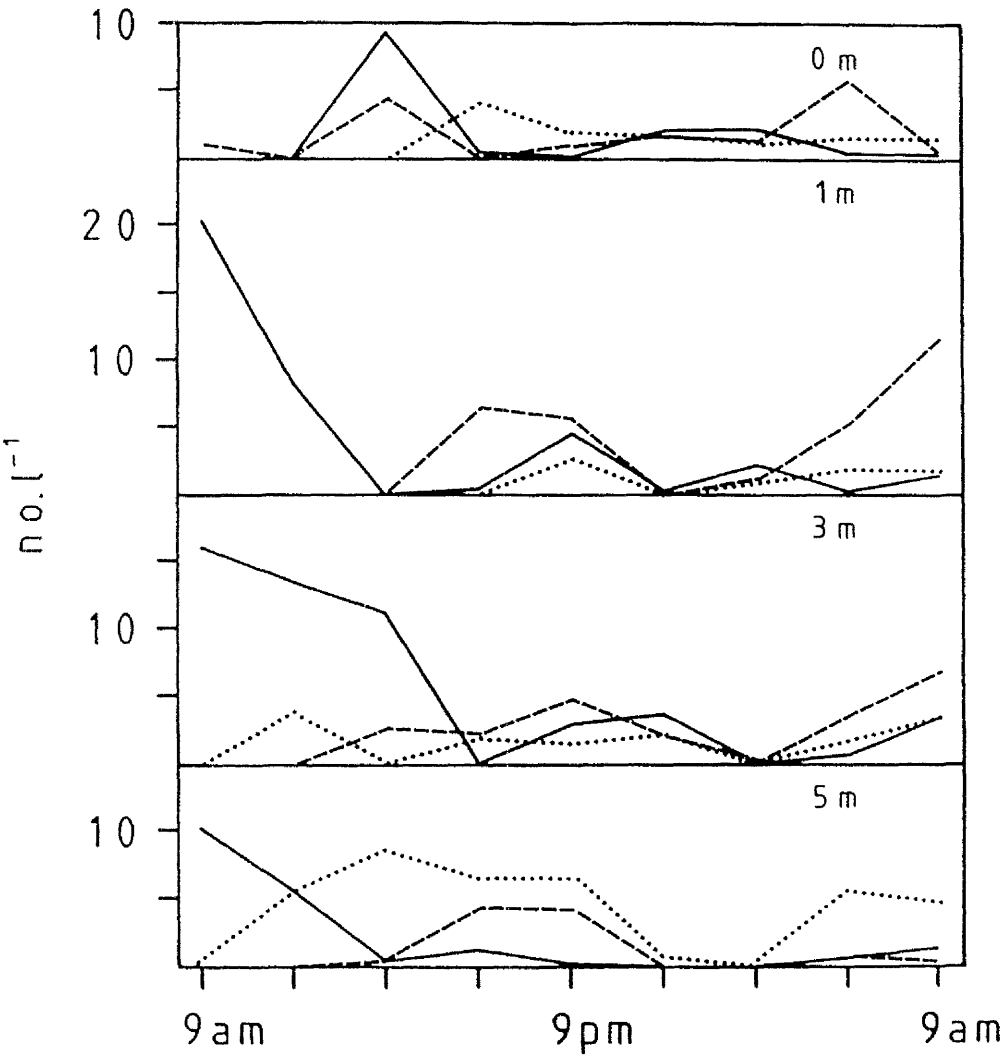

10
0 m
1 m
20
10
3 m
10
5 m
10
no.[-1]
9am
9pm
9am

Figure 7.36

Diurnal variation 25/26 August 1981

The Cladocera

solid line:- *Diaphanosoma brachyurum*

dashed line:- *Holopedium gibberum*

dotted line:- *Ceriodaphnia quadrangula*

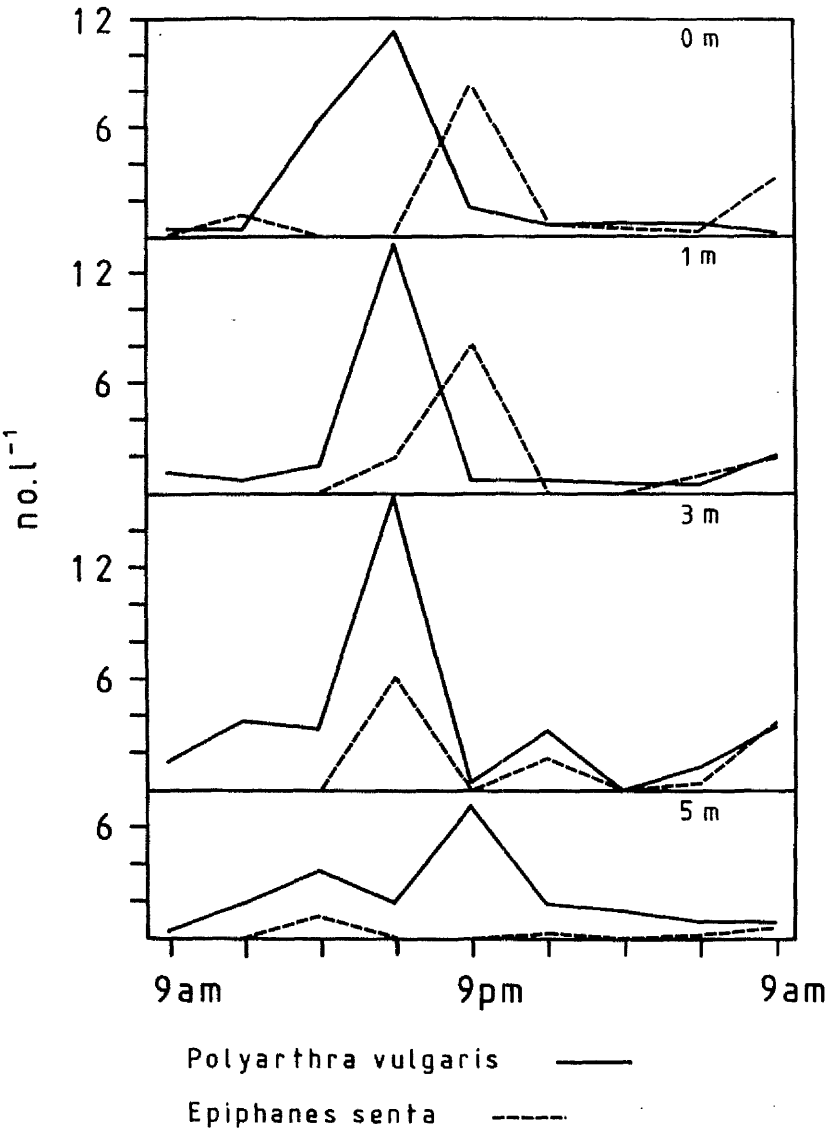

12
6
0 m
12
6
1 m
12
6
3 m
6
5 m
no.l⁻¹
9am
9pm
9am
Polyarthra vulgaris
Epiphanes senta

Figure 7.37

Diurnal variation 25/26 August 1981

Polyartha vulgaris and *Epiphanes senta*

recorded at midnight (9.61 l^{-1}) after which the populations remained below 6.38 l^{-1}.

The number of copepod eggs recorded varied between zero and 27.39 l^{-1} (Fig. 7.35). The maximum was observed at noon at 3m. Apart from this one peak, little variation in the distribution of cladoceran eggs was observed indicating a passive distribution pattern.

The separation observed between the cladoceran population maxima was not as clear cut as that observed in July but was still recognisable at the surface (Fig. 7.36).

Diaphanosoma avoided the surface layer until 3 pm when a population of 9.38 l^{-1} was recorded. Only a few were recorded at night (2.25 l^{-1}). The surface layer was generally avoided. The maximum populations measured during this 24 h period were found at 1m and 3m at 9 am (20.26 l^{-1} and 16.14 l^{-1} respectively). An overall reduction in the population was recorded throughout the 24 h period, to less than 4.50 l^{-1}.

Holopedium was only found in quantity at the surface at 3 pm (4.88 l^{-1}). At 1m the population maxima were observed in the evening and after dawn, rising from 5.25 l^{-1} at 6 am to 11.63 l^{-1} at 9 am, so avoiding the *Diaphanosoma* maximum. At 3m and 5m fewer *Holopedium* were recorded with population maxima at 3m of 4.88 l^{-1} at 9 pm and of 6.94 l^{-1} at 9 am the following day.

Ceriodaphnia were recorded mainly at depth, particularly at 5m. A maximum surface population of only 3.75 l^{-1} was measured at 6 pm, avoiding the maxima of *Diaphanosoma* and *Holopedium*. Minor fluctuations in the *Ceriodaphnia* population were observed at 1m and 3m. The largest quantities were recorded between noon and 9 pm and again after dawn (6 pm) at a depth of 5m.

While the rotifers were not a significant component of the zooplankton population, both *Polyarthra vulgaris* and *Epiphanes senta* exhibited a vertical migration from deeper waters (Fig. 7.37). A dramatic increase in the population of *Polyarthra vulgaris* was observed

at the surface, 1m and 3m at 6 pm followed by an equally sharp decline at 9 pm. At this time a smaller increase in the *Polyarthra* population at 5m was recorded. The vertical migration of *Epiphanes senta* was also recorded from 5m and below at 3 pm to 3m depth at 6 pm and then to 1m and the surface at 9 pm. Both rotifer populations were observed only in low numbers during the morning and overnight.

7.4 DISCUSSION

During the 15th and 16th July only a very slight breeze was evident. It is therefore unlikely that the diel variations measured during this period were the result of wind-induced mixing and strong lateral diffusion. Despite the presence of persistent rainfall during the night and early morning, the surface tension of the site was maintained i.e. the rainfall was not strong enough to break up the surface film or prevent positive accumulation of abiotic and biotic factors for the maintenance of the surface layer. It is therefore unlikely that the observations recorded were the result of rain-driven mixing of the surface layer.

The measured increase in the phytoplankton biomass, and in particular of *Aphanothece*, recorded after sunrise can be accounted for as either a rapid migration from subsurface waters or as a result of cell division. Chlorophyll a was not observed to increase rapidly concomitant with the phytoplankton increase but did so four hours beforehand. It is possible that growth and cell division of *Aphanothece* is regulated endogenously and is fixed to a diurnal cycle. Active synthesis of chlorophyll a and hence synthesis of protein may have been taking place prior to cell division. Once cell division occurred no new synthesis of chlorophyll a and protein would then take place until the next period of growth at night. It is probable that the observed decreases in nitrate and phosphate levels were linked with pre-divisional growth of *Aphanothece*. Since the *Aphanothece* population continued to increase when the zooplankton population was also observed to increase suggests that either *Aphanothece* is unpalatable or its rate of cell division was high enough to compensate for any loss by grazing.

The high phaeopigment levels recorded during this 24h period may thus have been indicative of both grazing pressure and a high turnover rate.

The presence of *Sphaerocystis* colonies at the surface layer between 11 am and 5 pm only suggests either passive sinking during periods of lower light intensities or positive accumulation as a result of increased buoyancy due to mucilage production. Frempong (1981) classifies *Sphaerocystis* as non motile and non buoyant and has explained *Sphaerocystis* accumulations as being the result of wind driven downwelling or upwelling. Since wind-induced effects were observed to be minimal, surface accumulation of *Sphaerocystis* was possible. As stated previously, the recorded decrease of *Sphaerocystis* colonies may be the result of grazing pressure, breaking up the colonies and so increasing the observed population of *Sphaerocystis* cells.

The dramatic increase in the *Kellicottia longispina* population at 9 pm was indicative of active vertical migration. Such diurnal migration in *Kellicottia* has rarely been recorded. Larsson (1971) measured such a population increase at night on only one occasion but it should be pointed out that his findings were based on only two samples per 24h period. As mentioned by Larsson (1971) such diurnal migration is contrary to the observations of Pejler (1957) in northern Sweden.

The temporal distinction observed for the cladoceran population maxima is suggestive of competitive avoidance. Hutchinson (1967) has suggested that such temporal variations in the migration patterns of cladocerans is the result of species specific phototactic and geotactic responses. He also stressed that within a species variations in diurnal behaviour between the sexes and age classes can be observed and this has been well documented for *Eudiaptomus*. This may explain, for example, the bimodal migration pattern of *Diaphanosoma*.

As in July, only a slight breeze was observed on the 25th August, so again, wind induced mixing was unlikely to have had a major effect on the diurnal patterns observed.

During the second 24h survey, diurnal variation in the depth of the epilimnion was recorded with the maximum being observed in the afternoon, coinciding with an increase in water temperature. Convective mixing of the epilimnion may, therefore, have been a factor in determining the distribution pattern of the non-motile phytoplankton species.

The distribution of the phytoplankton population during the 25th and 26th August suggested that active migration or possibly rapid accumulation by convection currents only occurred at the surface at the beginning and end of the sampling programme. Passive sinking rather than active migration was responsible for the observed gradual decline in phytoplankton biomass at the surface layer and at 1m. The observed increase in phytoplankton biomass from 5m at 3 pm to 3m at 6 pm was suggestive of an active response to changing light conditions and epilimnion depth by the blue-greens and by *Sphaerocystis* cells. There was little evidence of active migration of *Sphaerocystis* colonies which were more or less evenly distributed through the top 3m. Internally driven convection currents may thus have been responsible for the observed even distribution pattern.

Surface avoidance by *Mallomonas producta* was evident throughout the 24h survey. Vertical migration was only observed between 3m and 5m during the afternoon suggesting a low-light mediated response.

The gradual decreases and increases in the *Cryptomonas ovata* population at the surface and 1m were not indicative of the strong, active vertical migration pattern observed by Tilzer (1973) and Frempong (1981), though the concentration of *Cryptomonas* above the metalimnion was reported by them. Only the population increase at 5m at 3 pm was suggestive of a light mediated change in vertical distribution.

The lack of a definite relationship between the zooplankton and phytoplankton populations and the resultant difficulty in determining grazing effects was probably the result of the observed quantitative changes in the phytoplankton composition from predominantly unicellular

blue-greens to predominantly green algae. As discussed in chapter 6, a change in the composition of the zooplankton community from the rapidly feeding, non-selective cladocerans to dominance by the selective grazer *Eudiaptomus gracilis* occurred and with it a change in the pattern of grazing pressure.

Hutchinson (1967), George and Fernando (1968) and Frempong (1981) have emphasised the importance of seasonal variations in light, water temperature, oxygen content, weather patterns, community composition and the age of the community in determining the diel variations of lake systems.

The observed diurnal migration of *Kellicottia longispina* in July and of *Polyarthra vulgaris* and *Epiphanes senta* in August indicated, as suggested by George and Fernando (1968) that the vertical migration of rotifers may depend on the water temperature, oxygen content and light regime of lake systems.

The shift in algal composition from a population dominated by rapidly growing blue-greens to one dominated by green algae, with the blue-green population obviously in decline, was accompanied by a shift in the composition of the herbivore community. This change would have been responsible for the observed differences in the diel patterns of the two months.

These surveys exemplified the transient nature of the surface layer phytoplankton population. Surface accumulation occurred during the day with removal by passive sinking at night or reduction by grazing.

The surface layer phytoplankton population could thus be utilized as a food source by both the underlying cladocerans and calanoid copepods. This was observed particularly in the evening and at night when large increases in the zooplankton population of the top 5mm were recorded. Cell division by surface phytoplankton and their positive accumulation at the surface layer was possible.

The majority of the phytoplankton species recorded at the surface layer were non-flagellate. Surface accumulation may thus have occurred by entrapment of near-neutral buoyancy cells or by some positive buoyancy mechanism.

Chapter 8

General Discussion

8 GENERAL DISCUSSION

During this two year study of the surface layer of the Dubh Lochan, a similarity in algal species composition between the top 5mm and the underlying waters was observed. The constant transfer of algae between the surface layer and subsurface waters was responsible for this and for the observed transience of phytoplankton enrichment at the surface layer.

The patterns of stratification of the algal species were observed to vary temporally and resulted in the varied values of surface enrichment and as such, reflected the changes in the composition of the underlying phytoplankton community.

No "neustonic" microalgae *per se* i.e. organisms of either hyponeustonic or epineustonic habit were observed in this study. Such organisms have usually been reported in ponds protected from the effects of wind shear stress and turbulent mixing (e.g. Babienzen, 1966; Babienzen and Schwartz, 1970 and Frolund, 1977). Stable surface films seem to be a prerequisite for the development of an hyponeustonic or epineustonic life style. In more open water sites, which are subject to wind shear stress, a change in the community structure to more planktonic species thus seems to occur.

Surface enrichment of organisms normally associated with subsurface waters have also been observed by Parker and Hatcher (1974) and Estep and Remsen (1984). Their data, too, indicated that while differences in species composition were not observed, the relative proportion of surface layer enrichment varied between species and with time and as such, stress the importance of seasonal variation in the underlying phytoplankton community and of the age of its member components in determining the composition of the surface layer community.

Healthy blue-greens, positively buoyant, may accumulate at the surface, while members of a dying population of *Sphaerocystis schroeteri* or *Asterococcus limneticus* may rise, unable to maintain an

optimum position below the surface layer.

Accumulation by entrapment at the surface layer may occur. Unicellular, non-flagellated algae, such as the diatoms and green unicells, may be brought to the surface by turbulence and rising bubbles.

Alternately, positive accumulation of motile species may be found. *Gymnodinium* sp, *Chlamydomonas* spp and *Cryptomonas* spp were all observed on occasion to accumulate at the surface layer.

Surface enrichment of algae under the ice cover was also reported and as such was probably a response to lowered light levels.

The surface layer community, as observed in this study, may contribute substantially to the overall primary productivity of the lake. Higher specific photosynthetic rates of surface site 2 populations in comparison to those measured at 1m were recorded. The surface layer may, therefore, be an important source of energy, particularly on cloudy days. Evidence for photoadaptation of the surface population was also recorded. For such photoadaptation to occur, as based on Harris' (1978) hypothesis, the existence of stable weather conditions for at least two days may be required. The presence of such distinct populations could not be detected by phytoplankton enumeration or biomass estimation alone. Persistent wind conditions and the resultant continual mixing of the surface waters did not allow such physiologically distinct populations to develop. In future studies the importance of carrying out such comparative experiments cannot be underestimated. Such experiments could provide an additional insight into the habit of the surface layer community, particularly when linked with studies of possible photoinhibition /photorespiration /allelopathy. It is quite possible that allelopathic responses may be more marked at the surface layer than in subsurface waters due to the accumulation and concentration of what are probably organic exudates at the surface film. The observed inhibition of a surface film bacterial population recorded by Sieburth (1971b) and the resultant reduction in response upon dilution of the sample is an example of such a surface-enhanced allelopathic response.

The majority of the zooplankton species recorded in this study possessed distribution ranges which included the surface layer. They were observed to migrate to the top 5mm during the day and at night and to graze upon the phytoplankton. In this way the zooplankton were able to influence the composition of the surface phytoplankton community. It is therefore unlikely that the surface film of the Dubh Lochan could act as a refuge for the more edible nanoflagellates and no evidence for this was observed. Since the majority of epineustonic and hyponeustonic algae possess a flagellate stage (see, for example Catalan, 1987) it is possible that the development of communities of those organisms regarded as neustonic may depend on the absence of a zooplankton community capable of grazing effectively at the surface film.

Those species capable of grazing at the surface layer may have possessed a competitive advantage over those species observed to avoid this region. They would have had access to an additional food source in the form of the accumulated detritus. During periods when phytoplankton populations were low, as observed in 1982, those able to utilize this food source would thus be able to grow and reproduce more effectively.

Species which can be classified as hyponeustonic and epineustonic were not observed among the cladocerans. Hyponeustonic larvae of insects, such as *Culex, Chironomus* and water striders and the springtails and epineustonic adult insects and members of the Collembola were observed only at site 4. The presence of higher surface tensions and capillary wave damping allowed these species to exploit the more stable surface film.

The high refractive content, as indicated by C:N ratios, of the organic matter of the surface layer contrasted with the observations made by Islam (1987) for the seston of the water body as a whole. This is suggestive of the accumulation of humic substances at the surface film. Such accumulation may have occurred as a result of entrainment by turbulent mixing and by adsubble processes, as recorded by Sodergren (1979). Souza-Lima and Romano (1983) recorded the accumulation of "dead", inert organic matter at the surface film of the Bay of Marseilles. Carlson (1982, 1983) reported the surface enrichment of

phenolics, a group of compounds commonly associated with humic acid complexes in aquatic systems. These data suggest that refractory compounds may preferentially accumulate at the surface film, having been brought there through surface runoff, turbulence and adsubble processes and from gradual accumulation as a result of the degradation of surface accumulated labile organic matter. It is also possible that the observed higher concentrations of phosphate and ammonia may be a real phenomenon of surface enrichment. If this is so, then the surface layer of the Dubh Lochan may provide an important additional source of nutrient to those organisms capable of living within its boundaries. Yet the low overall heterotrophic bacterial estimates also indicate that that the surface layer may be a site of perturbation, being directly exposed to the diluting effects of rain, of low pH, to possible inhibition as a result of the surface accumulation by dry deposition of toxic anthropogenic substances and to the inhibitory effects of increased u.v. radiation.

While Niewolak (1971) and Belay (1981) have reported photoinhibition of phytoplankton at the surface layer these studies indicated that this is not always necessarily so. The higher specific photosynthetic rates of the surface site 2 populations in comparison to populations at 1m is not suggestive of a population injured by higher light intensities but rather of one photoadapted to them. The observed low specific carbon fixation rates of the surface phytoplankton populations at site 4 were probably the result of chemical rather than solar inhibition. Surface studies may thus provide much additional data on the role of allelopathy in regulating community structure and function. As stated previously, the future use of comparative experimentation may play a key role in increasing our knowledge of the complex biological and chemical interactions of the surface layer community.

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