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**Bailey-Watts, A.E., 1974 The algal plankton of Loch Leven, Kinross. In: *Proceedings of The Royal Society of Edinburgh Section B (Biology)* vol.74 135-156.**

## 9.—The Algal Plankton of Loch Leven, Kinross. By A. E. Bailey-Watts,* The Nature Conservancy, Edinburgh. (With 9 text-figures and 2 tables)

### SYNOPSIS

The species composition and succession of the algal plankton are described. Population density changes, as indicated by chlorophyll *a*, cell volume and numbers are discussed in relation to physical, chemical and biological factors in the environment.

The quality and the amounts of the plankton vary considerably from year to year. However, for most of the period reviewed it has been dominated by dense developments of nanno and other small algae belonging to the diatom and blue-green groups.

Factors of particular importance affecting the high observed biomass and production include the water depth, adequate mixing and a rich supply of nutrients from the inflows and the sediments. Competition from other green plants appears to be low. Utilisation of living algal cells in the plankton by crustacean and protozoan grazing and fungal parasitism is rarely important.

The composition of the phytoplankton is discussed in relation to the eutrophic nature of the loch.

### INTRODUCTION

This paper is a general account of the phytoplankton from 1968 to 1971, although brief reference is made to other years. The treatment differs from that previously adopted; Bailey-Watts, Bindloss and Belcher (1968) and Bailey-Watts and Lund (1973) deal in detail with the ecology of selected dominant algal populations.

The following matters are briefly described. Firstly, qualitative and quantitative seasonal changes in the algal plankton. Secondly, the influence on these changes, of some physical, chemical and biological factors. The main findings of the investigations are highlighted and summarised. Fuller results and discussion are in Bailey-Watts (1973).

Shallow lakes, particularly those that remain unstratified, have not been studied as extensively as deeper dimictic lakes, so even general information on the Loch Leven plankton is of interest. The features outlined concern a community adapted to environmental conditions within a water body that is somewhat unusual in the area to depth ratio (Smith 1974), the rich supplies of dissolved inorganic nutrients in the inflows and the sediments (Holden and Caines 1974), the relative unimportance of macrophytic vegetation (Morgan 1970; Jupp, Spence and Britton 1974) and the feeding nature of the dominant zooplankters (Morgan 1970; Walker 1970; Johnson and Walker 1974).

### METHODS

Methods of sampling, cell enumeration and the estimation of cell volumes and chlorophyll *a* are described in Bailey-Watts and Lund (*loc. cit.*) and Bindloss *et al.* (1972). Water was collected with a tube to obtain an integrated sample extending from the surface to within 25–50 cm of the bottom deposits at a 4 m open water station north-east of Castle Island. Plankton chlorophyll *a* values presented here were estimated on methanol extracts. They are not corrected for pheophytin content, but from a variety of tests (Bailey-Watts *loc. cit.*) it seems clear that pheophytin was not a major component of the estimated pigment. However, chlorophyll *a* in

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the benthos was estimated on acetone extracts according to the method of Moss (1967*a, b*) which incorporates a correction for pheophytin as this is important in the deposits of the loch.

Determination of algal species has been made, as far as possible, using the works of Hustedt (1930), Fritsch (1935, 1945), Skuja (1948), Cleve-Euler (1952), Korshikov (1953), Komárek and Ettl (1958), Desikachary (1959) and Bourrelly (1966, 1968, 1970). Numerous specialist papers have also been consulted and the 'pictorial herbarium' of pictures of freshwater algae, the Fritsch Collection (see Lund 1971) at the Windermere Laboratory of the Freshwater Biological Association.

Methods for the estimation of other parameters referred to in this general paper are described in full elsewhere (Bailey-Watts *loc. cit.*).

## QUALITATIVE NATURE OF THE PHYTOPLANKTON

The approximately 150 species listed in Appendix I have been recorded during the routine activities of counting, searching for fungal parasites and protozoan grazers, etc. Cell enumeration techniques determine the minimum population densities
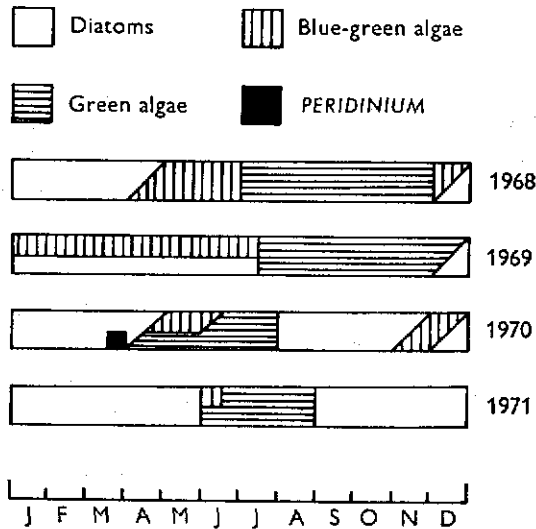


TEXT-FIG. 1.—A diagrammatic presentation of the temporal distribution of the three main algal classes and of *Peridinium* in the plankton of Loch Leven.

below which an alga may not be recorded, and many species present in the lake thus pass undetected. For this reason Appendix I is not a complete algal flora for the loch.

Diatoms probably contribute the major proportion of algal production in freshwater and marine plankton (Fritsch 1935) although other algae may predominate in some aquatic situations (Fritsch 1931; Lund 1942). In Loch Leven diatoms have contributed more to the high biomass and production than any other group. They also predominate in the benthos (Appendix II).

Nevertheless, in the plankton blue-green algae have been very important and they have dominated it for various periods in each of the 4 years reviewed. Certain taxo-

nomic difficulties arose in determination of the 2 major species. That related to *Synechococcus* n.sp. (Chroococcales) will be dealt with elsewhere. The typical form of *Oscillatoria redekei* Van Goor (Nostocales) with triangular gas vacuoles at the ends of the cells (see Lund 1960; Whitton and Peat 1969 and Meffert 1971) was the one most frequently observed. However, morphological types resembling *O. limnetica* Lemm., *O. planctonica* Wolosz., and *O. acuminata* Gomont were also seen (Whitton and Peat *loc. cit.*).

Two green algae *Steiniella* sp. (near *graevenitzii* Bernard, see Lund 1960) and *Dictyosphaerium pulchellum* Wood, dominated a few of the dense crops. In addition,

TABLE 1

*The temporal distribution of the important species of algae in the plankton of Loch Leven, 1968–71*

| | 1968 | 1969 | 1970 | 1971 |
|---|---|---|---|---|
| Jan to Mar-May (increase to major max.) | Centric diatoms, Diatoma elongatum, Asterionella formosa, Synedra ulna | Cyclotella pseudo-stelligera, Oscillatoria redekei D. elongatum | Centric diatoms, Steiniella sp., Synechococcus n.sp., Peridinium cinctum | C. pseudostelligera, Synechococcus n.sp. (maximum) |
| May to Jun (max. except 1971) | Synechococcus n.sp. | O. redekei, D. elongatum | Steiniella sp. | Synechococcus n.sp., Steiniella sp. (post-maximum) |
| Sep to Dec (second max.) | O. redekei, C. pseudostelligera | Dictyosphaerium pulchellum | Stephanodiscus rotula, Synechococcus n.sp. | A. formosa |

a large number of species (see Appendix I) belonging to the Chlorophyta have been important not usually in terms of biomass but because they provide background information to the data on the dominant forms. As Rawson (1956) points out, the numerically less important forms may characterise a water rather more definitely than the few dominant species; the latter are often very cosmopolitan (cf. however the Loch Leven dominants) and therefore presumably less exacting than the rarer forms in their environmental requirements.

Like many of the green algae observed, species belonging to the Cryptophyceae, Dinophyceae, Chrysophyceae and Xanthophyceae were rarely important. Their sparse intermittent appearances provide a sharp contrast to the prolonged and often dense developments of the diatoms and blue-green algae.

Text-figure 1 illustrates the gross timing of the appearance of the different groups of algae at Loch Leven during the 4 years. The data are restricted to the diatom, blue-green and green algal groups and the peridinian as representatives of these groups dominated the phytoplankton crops for most of the period.

From this general aspect, Loch Leven is characterised by considerable year-to-year variation; although diatoms predominated during the first half of each year (with centric forms commonly but not always followed by pennate forms), their growth extended over different months each year, and in 1969 they were accompanied by blue-green algae. Autumnal growth in the first 2 years was dominated by green algae but by diatoms in the last 2 years. Green algae were important earlier, i.e. during the summers of these latter 2 years, which in 1968–69 had been characterised by Cyanophyceae.

The species dominating the groups represented in text-fig. 1 are included in table 1. This shows the marked annual variation in species which is superimposed on the succession of the groups. Many algae appeared in abundance only once or twice throughout the 4-year period, e.g. *Oscillatoria redekei*, *Steiniella* sp. and *Stephanodiscus rotula* (Kütz) Hendey [formerly *S. astraea* (Ehr.) Grun.].

## QUANTITATIVE FEATURES OF THE PHYTOPLANKTON

### *Chlorophyll* a *Concentration 1968–71*

Yearly differences in the fluctuations of chlorophyll *a* concentration are quite marked (text-fig. 2). However, the increase to the maximum normally occurs in the
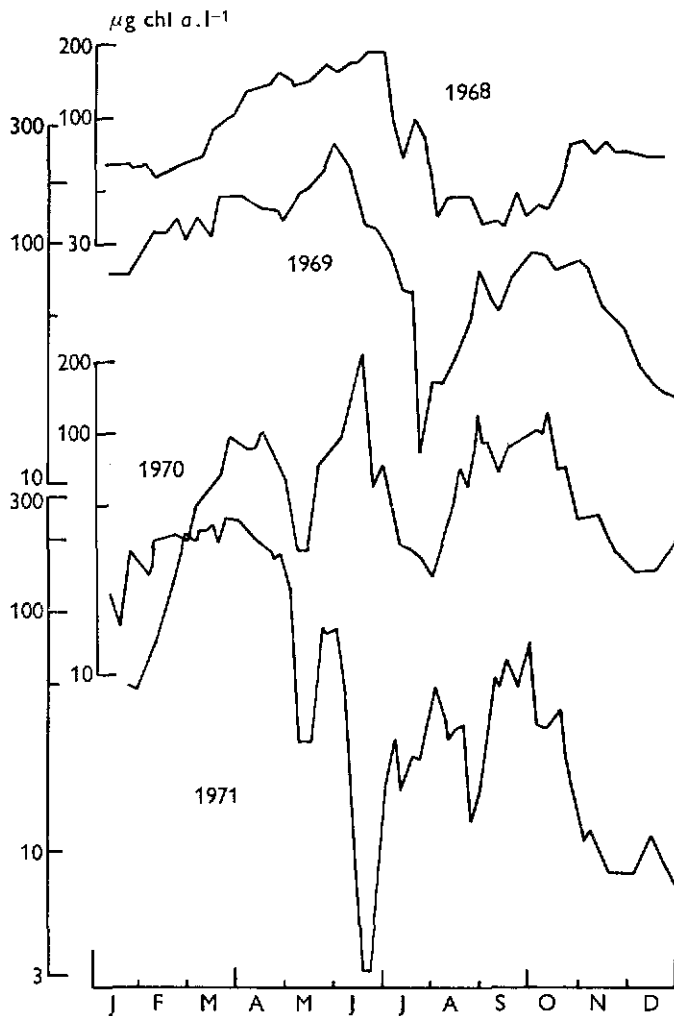


TEXT-FIG. 2.—Changes in the chlorophyll *a* content of the water column (surface to within 0·3 m of the bottom sediments) at Loch Leven, 1968–71. Logarithmic vertical axes vary in length to accommodate different yearly ranges of values.

first half of the year, although high rates of increase can occur at any time. The collapse of populations following the maxima are often as rapid as the increases to those maxima.

The range in values is from 3 to 250 μg chlorophyll $a.1^{-1}$. It is emphasised that in spite of some of the very high levels (cf. Vollenweider 1968) these are representative of the whole water column. At the mean depth of 4 m, therefore, standing crops have reached 1 g chlorophyll $a$ beneath a square metre of loch surface.
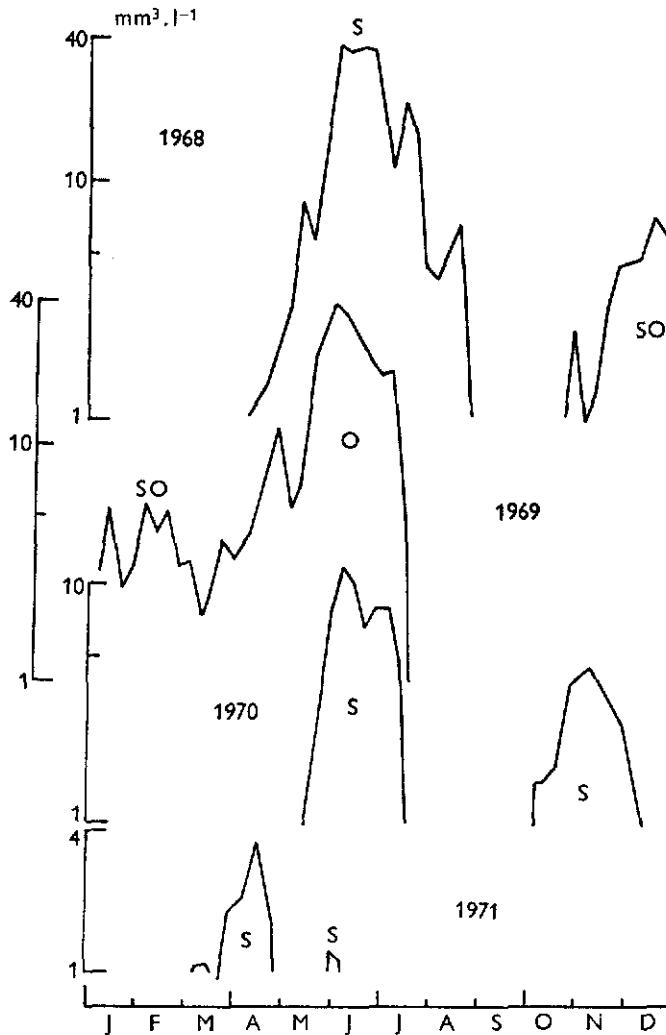
*Algal Volume Biomass*

In text-fig. 3 are shown the fluctuations in the total volume of diatoms. In 3 of the years, spring growth was greater than that in the autumn and in 1969 autumnal
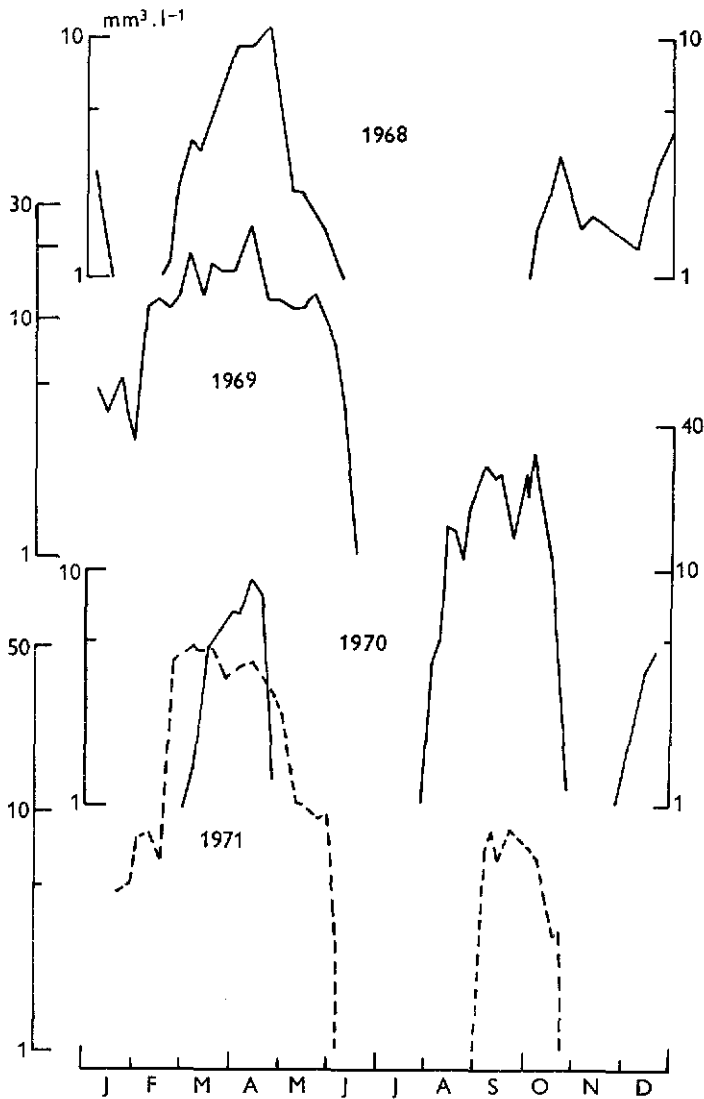


TEXT-FIG. 3.—Fluctuations in diatom volume biomass.

biomass did not exceed 1 mm³. In 1970 the reverse held; a very dense population of *Stephanodiscus rotula* (maximum $30 \times 10^6$ cells.$l^{-1}$) was observed (Bailey-Watts and Lund *loc. cit.*). Approximately twice as many diatoms (maximum $56 \times 10^6$ cells.$l^{-1}$) had developed in the spring but the dominant *Cyclotella pseudostelligera* Hustedt

mm³.$l^{-1}$

1968

S

SO

O

1969

1970

S

S

S

S

1971

J  F  M  A  M  J  J  A  S  O  N  D

TEXT-FIG. 4.—Changes in blue-green algal volume biomass and an indication of the temporal distribution of the two important species *Oscillatoria* (O) and *Synechococcus* (S).

was less than ¼ the size of the *Stephanodiscus*, so it contributed a smaller total biomass. Text-figure 4 shows the changes in total blue-green algal biomass as volume, and the species composition with regard to *Oscillatoria redekei* and *Synechococcus* n.sp. Only during late 1968 and early 1969 did these two algae occur in abundance together. At its peak in June 1969 *Oscillatoria*, with *Diatoma elongatum* Agardh. and centric diatoms, constituted one of the largest crops observed during the 4 years: 47·8 mm³.$l^{-1}$. The blue-green algae here appear to be able to survive under a variety of

environmental conditions. The *Oscillatoria* was abundant throughout a period of nearly 12 months, and *Synechococcus* produced dense populations on 6 different occasions.

Of the numerous algae contributing to the total green algal volume biomass (text-fig. 5), *Dictyosphaerium* caused the growth in autumn 1969 and *Steiniella* with a small
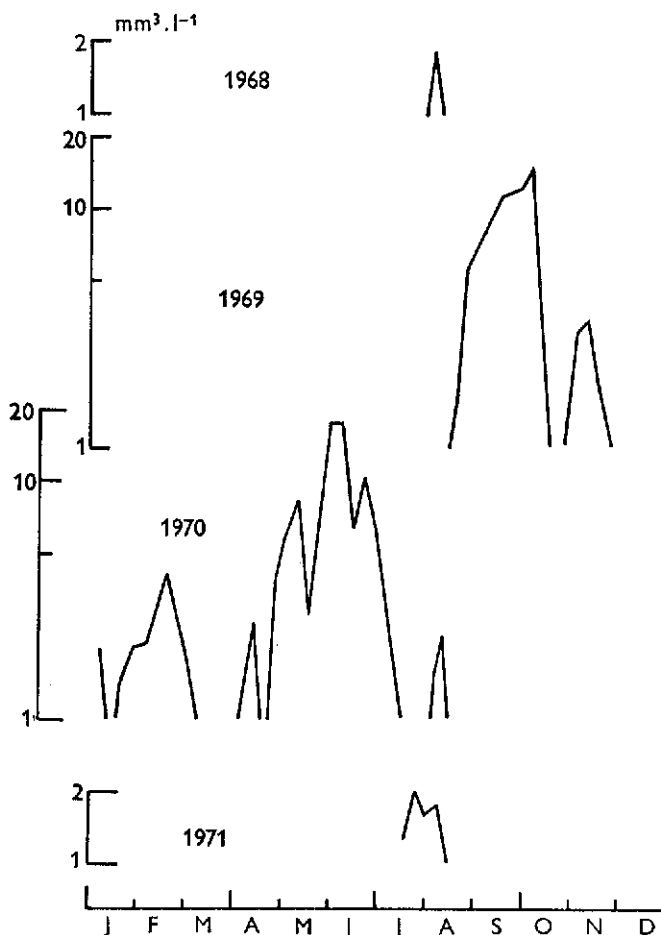


TEXT-FIG. 5.—Changes in total volume biomass of green algae.

amount of *Dictyosphaerium* caused that in the first half of 1970. As indicated on the figure, green algae were not important at other times.

The only other algae of note are the cryptophycean *Rhodomonas pusilla* Bachm., which in July 1969 formed a transitory dense population maximum of 8·6 mm$^3$.l$^{-1}$, and the dinoflagellate *Peridinium cinctum* West which was common for a number of weeks, and reached a maximum of 3·4 mm$^3$.l$^{-1}$. At these times they represented approximately 65 and 30 per cent respectively, of the current totals of volume biomass.

A comparison has been made of the pigment and volume estimates of crop density during this study. Where 1, 2 or 3 species constitute the major part of the algal crop, the range of values found has been 2·7–6·8 $\mu$g chlorophyll $a$.mm$^3$ cell volume. No algal species or group seems to be consistently richer in chlorophyll than any other.

*Cell Numbers of Major Species*

Further examples of the dense nature of the algal populations are indicated in table 2. The maximum concentrations of cells are shown along with typical mean cell volumes. In addition to the nanno algae the other important species, e.g. *Oscillatoria redekei*, *Asterionella formosa* Hassall, *Stephanodiscus rotula* are commonly

TABLE 2

*Population density maxima and mean single cell volumes of important algal plankters*

| Alga | Year | Population maxima (cell no. $\times 10^{-6}.1^{-1}$) | Mean single cell* volume ($\mu m^3$) |
|---|---|---|---|
| Asterionella formosa | 1968 | 6·8 | 186 |
| | 1971 (Spr) | 0·2 | 240 |
| | 1971 (Aut) | 15·8 | 460 |
| Cyclotella pseudostelligera | 1968 | 14·0 | 120 |
| | 1969 | 126 | 208 |
| | 1970 | 57·6 | 157 |
| | 1971 | 226 | 250 |
| Diatoma elongatum | 1968 | 13·7 | 274 |
| | 1969 | 41·0 | 260 |
| Stephanodiscus rotula | 1970 | 26·8 | 970 |
| Synedra ulna | 1968 | 3·0 | 396 |
| Oscillatoria redekei | 1969 | 750 | 50–200 |
| Synechococcus n.sp. | 1968 | 5000 | 8 |
| | 1970 | 1100, 480 | 6, 8 |
| | 1971 | 420 | 10 |
| Dictyosphaerium pulchellum | 1969 | 232 | 65 |
| Steiniella sp. | 1970 | 775 | 22 |
| Peridinium cinctum | 1970 | 0·42 | 7900 |

* Filaments for *Oscillatoria redekei*.

larger elsewhere. Nevertheless the range in cell size, within and between species, is still considerable. The relationship between cell numbers is therefore variable; during this study, 1 $\mu$g chlorophyll *a* has at different times been equivalent to as few as $30 \times 10^3$ (*Peridinium*), or as many as $30 \times 10^6$ (*Synechococcus*) cells.

## RELATIONSHIP OF ALGAL PLANKTON TO ENVIRONMENTAL FACTORS

*Physical Factors*

Wind-induced turbulence effects a thorough mixing of the water mass (Smith 1974). Text-figure 6 shows a comparison of chlorophyll *a* concentrations in 0–4 m tube and Ruttner bottle samples taken at 0·5 m for primary production studies (Bindloss 1974).

From these data it appears that vertical differences in plankton density were rarely important.

A similar picture is presented in text-fig. 7, where data comparing the concentrations of pigment in samples from two different stations are shown. These are typical of comparisons made between a number of other stations. Spatial variation in algal population density is therefore insignificant, the major variation being that associated with time.
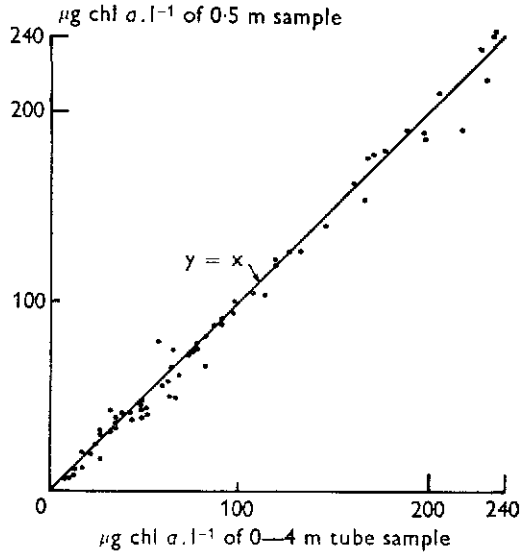


Text-fig. 6.—Comparison of chlorophyll *a* concentrations in 0·5 m and 0–4 m samples.
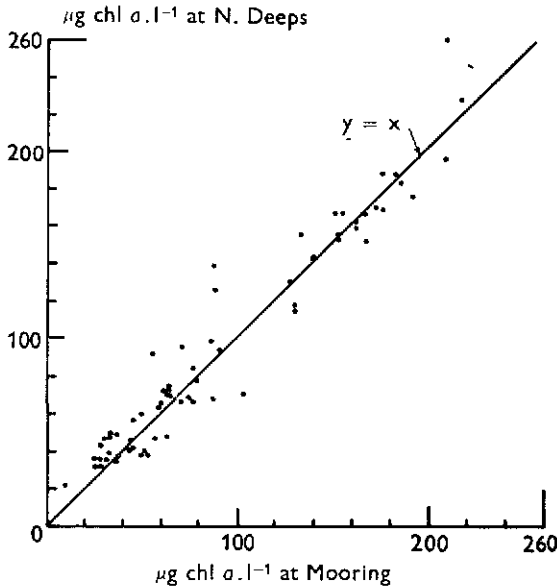


Text-fig. 7.—Comparison of the chlorophyll *a* content of the water at the North Deeps and the Mooring stations.

To some extent at least, temperature must be important in determining algal succession but the results of the present study do not make this clear. Many species (e.g. *Oscillatoria redekei*) were abundant over a wide range of temperatures and some, like *Synechococcus*, achieved good net growth [$G$ (cell doubling time in days, see Fogg 1966) = 5–10] at different temperatures (8–13°C). *Cyclotella pseudostelligera* achieved a high population density in spring 1971 before the water temperature had risen much above 4°C (minimum $G$ = 2·15 days). Also the population, equivalent to around 200 μg chlorophyll $a$.$l^{-1}$, was maintained for a number of weeks during which the temperature did not exceed 7°C (text-fig. 8). The relative absence of this
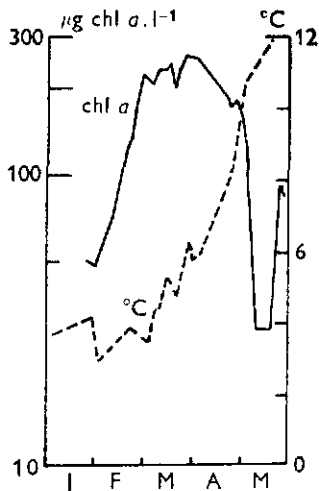


Text-fig. 8.—Chlorophyll $a$ (chl $a$) and temperature (°C) changes during the first 5 months of 1971.

diatom at much higher temperatures in Loch Leven is more likely to be controlled by nutrients than rising temperature. In fact most species listed in Appendix I can be found at any time of the year.

As with temperature, the length of day is undoubtedly important in determining some of the gross features of algal succession in the loch, but specific effects on the observed growth of individual species are not clear and have not been investigated. Within the water column, light penetration varies with the amounts of algae present. To some extent the euphotic depth and thus the euphotic to mixed (= total) depth ratio is determined by the abundance of algal particles (Bindloss *et al.* 1972; Bindloss 1974). Secchi disc readings are commonly <1 m but rarely <0·5 m. Relationships between this parameter and algal density vary according to which measure of the latter is used, i.e. chlorophyll $a$, cell volume or dry weight. Other factors are also naturally important, e.g. presence of non-algal seston, type of dominant algae, etc., but generally the higher Secchi disc readings (>2 m) are observed at low algal crop densities (<20 μg chlorophyll $a$.$l^{-1}$).

The mean retention time of the loch is 5·2 months (Smith 1974). As he implies, dilution by the inflowing water and loss of cells in the outflow normally have little effect on population density within the loch. This has been illustrated also in a short-term study to assess the effects of these factors on the loch concentrations of silica and diatoms (Bailey-Watts *loc. cit.*).

Observations on the decline of some of the algal populations in Loch Leven suggest that losses of cells to the sediment may be significant. Rates of disappearance of cells are higher than could be accounted for by grazing in the plankton, transport to the outflow, or dissolution (in the case of diatom frustules). Although calm conditions allowing maximum rates of passive sinking are rare, it is possible that cells could be transported to the sediment by other mechanisms. Such mechanisms might effect losses comparable to those calculated from experimentally-determined sinking rates, e.g. 1·75 and 0·65 $\mu.\sec^{-1}$ for centric diatoms and *Synechococcus* respectively.

*Chemical Factors*

Algal relations with the chemical environment have been investigated by comparing the population data with firstly those of Holden and Caines (pers. comm. and 1974) on dissolved and particulate nitrogen and phosphorus, and dissolved silica, and secondly seston analyses of carbon, nitrogen and phosphorus (made by Mr S. E. Allen, Merlewood Research Station, the Nature Conservancy, England) and of amorphous (biogenous) silica (author). In addition, experiments have been carried out involving nutrient (nitrate, phosphate and silicate) enrichment of natural populations suspended in the loch for 1-, 2- or 3-week periods.

Inferences drawn from the different types of data vary. However, in some cases the relations implied from the raw field observations are confirmed by the results of both the seston analyses and the enrichment experiments. Nevertheless, the relations between algal abundance, the amounts of nutrients incorporated in their cells and the concentrations of these nutrients in the surrounding water vary considerably from year to year.

Quite marked increases in algal biomass often commence when dissolved concentrations of nitrate and phosphate would appear to have precluded them. The same commonly applies to the growth of diatoms in relation to dissolved silica. At other times algal growth is observed to have little effect on the concentrations of the dissolved nutrients. Indeed, nutrient levels may increase during periods of quite vigorous algal growth. At population maxima achieved under these conditions of varying nutrient supplies, the cells may be expected to contain different amounts of N and P etc.: the various analyses have given the following ranges in $\mu$g per mm$^3$ cell volume of a number of different populations; 4·9—45 N and 1·5—8·5 P.

Other results suggest utilisation of e.g. nitrate, either by planktonic algae at rates far in excess of those indicated by the biomass changes, or by agencies other than planktonic algae or in addition to them, e.g. benthic algae. Early in 1971 the decline in phytoplankton density from the large maximum referred to earlier was accompanied by a disappearance from the water of nearly 1·2 mg $NO_3.N.l^{-1}$. To indicate the magnitude of this it is worth considering that the nitrogen incorporated into the crop at the time of the maximum was considerably less than this amount, i.e. 900 $\mu$g.$l^{-1}$. In 1968 and 1969 the late spring algal maxima coincided with the attainment of nitrate minima as did the second algal maximum in 1970. From these data it was generally concluded that the algal growth in the plankton was the prime cause of the inorganic nitrogen decreases; the 1971 observations, however, show that more work on this aspect of the algal-chemical relations is necessary.

During periods of apparently low algal activity, the increases of silica and occasionally of nitrate in the water column occur at rates greater than can be attributed to the

inflows alone. With silica some indication has been gained of the importance of sediment release and other factors.

An attempt has been made to quantify the relations between the dissolved and particulate forms of this element by studying the gains via the inflows, interchanges between the sediments and the water within the loch, dissolution of diatom frustules, and losses via the outflow. Diatom growth has produced biomass levels equivalent to 10 mg silica.$l^{-1}$. Thus although the maximum concentrations of dissolved silica (in the loch and the inflowing streams) approach this, levels within the loch may be reduced to less than $0 \cdot 1$ mg.$l^{-1}$. The silica incorporated into the cells varies according to species and the nature of the cells with regard to size, sculpturing and thickness of wall, etc., but values in the range $0 \cdot 1$–$0 \cdot 2$ mg$\times 10^{-9}$.$SiO_2$ per $\mu m^2$ of cell surface or $\mu m^3$ of cell volume have been common for the dominant small centric diatoms. The silica represents between 30 and 50 per cent of the total dry weight.

It is for these silica demands to be met that a source additional to the inflows appears to be necessary. Concentrations of silica dissolved in the sediment interstitial water are often considerably higher than those measured in the overlying water; values up to 20 times the latter are not uncommon and concentrations tend to increase with depth in the sediment. Maxima ($30$–$60$ mg $SiO_2.l^{-1}$) have been found at 5 cm below the sediment surface in sand and at 25 cm in mud which tends to be richer. In the more fluid sediments these high concentrations represent a large reservoir of the element.

Experiments with cores indicate that dissolved silica can be released into the overlying water at rates similar to those calculated from the observed changes in the levels of silica in the loch (Holden and Caines 1974) during periods of low diatom activity. These rates approximate to 470 mg $SiO_2.m^{-2}.d^{-1}$. Crystalline silica as sand, and silicates in clays are abundant in the Loch Leven sediments and may be potential contributors to the silica cycle there. However, the impression is that these forms are inert relative to the most abundant amorphous, and thus the most soluble form of silica, i.e. the diatom frustule. Experiments on frustule dissolution are still in progress. Preliminary results confirm the suspicion that they are an important source of dissolved silica.

### Biological Factors

Included here are grazing, parasitism and competition. The magnitude of grazing of planktonic algal cells by benthic animals is not known (but see Discussion) so the following remarks are restricted to the zooplankton.

The status of algae in the diet of the copepod *Cyclops strenuus* var *abyssorum* Sars, which was dominant up to June 1971 (Walker 1970; Burgis and Walker 1972; Johnson and Walker 1974) is usually considered to be small as it is generally accepted to be a carnivore (Fryer 1957; Gliwicz 1969a; Monakov 1972). However, as Fryer (1957) points out, there is a need to investigate the feeding of the species in lakes which differ in zooplankton composition from the ones in which his specimens were collected. Occasional gut analyses of *Cyclops* adults in Loch Leven revealed cells of *Diatoma elongatum* and *Dictyosphaerium pulchellum*, i.e. larger Loch Leven algae, when these were abundant. In the absence of more information on this the impression is that grazing by this animal is not a major cause of the observed algal fluctuations, although it is unlikely that the population is not dependent on plant material to some extent,

e.g. during the naupliar stages. For a short period during the summer of 1971, however, when the herbivorous cladoceran *Daphnia hyalina* var *lacustris* Sars became abundant, the situation changed. Gut contents of all individuals examined were packed with algae, and at the time of the recorded population maximum (60 individuals per litre) algal densities and Secchi disc readings were respectively the lowest (3 $\mu$g.l$^{-1}$) and highest (4·75 m) observed during the 4 years reviewed here.

Neither protozoan grazing nor fungal parasitism are very significant in determining the abundance of the algae. On the few occasions these did cause a decline in algal numbers, the growth was also limited by other, i.e. chemical and physical, factors.

Two protozoans which became abundant both belong to the Order Proteomyxa, (Subclass Rhizopoda). One feeding within the colonies of *Dictyosphaerium pulchellum* was not identified but is clearly a vampyrellid which pierces the algal cell to ingest its contents but not its cell-wall. The other is *Asterocaelum algophilum* (Canter 1973) which was first discovered in Loch Leven. It is capable of feeding on a number of different algal species and it ingests the whole cells. However, at the time it was abundant in the loch, autumn 1970 (during which it achieved a population density of 1400.ml$^{-1}$), it appeared to be feeding selectively on *Stephanodiscus rotula* (Bailey-Watts and Lund *loc. cit.*).

Chytrid fungi are commonly observed at Loch Leven and many algal species are infected from time to time. Quite high (e.g. 30 per cent) infections of some of these host populations were recorded, but these commonly arose not by any marked increases in fungal numbers relative to the algae but by the decline of the algae due to lack of nutrients.

Competition between species may be important in determining the success of different algae in the plankton at different times. The ability of one species to grow faster than an other under identical conditions would allow that species to become the more numerous. Commonly, however, environmental factors affect various algae to differing extents; for example, the more prolonged abundance of diatoms in Loch Leven appears to be limited by low silica concentrations, but as other nutrients may not be limiting at the same time, algae which do not require silica can subsequently develop.

Competition for nutrients from other photolithoautotrophs (Fogg 1953) varies. Macrophytes are sparse in Loch Leven (Jupp *et al.* 1974), but high standing crops of benthic algae extend over at least the sandy sediment there. In text-fig. 9 are shown the concentrations of chlorophyll *a* in the uppermost 1 cm of sediment and that in the overlying water column at stations 'M' and 'D' (0·8 and 1·9 m respectively) on the north-east side of the loch. At these stations the benthic algae consisted mainly of epipsammic species, e.g. *Cocconeis placentula* var *euglypta* (Ehr.) Grunow, *Opephora martyi* Heribaud (see also Round 1965), although unattached species of e.g. *Ankistrodesmus, Pediastrum, Scenedesmus* and *Steiniella*, and settled phytoplankton were important, particularly at the deeper station. The epipsammic population densities averaged over 15 months was approximately 300 mg chlorophyll *a*.m$^{-2}$.

Such aggregations would imply that the benthic algae are more important in biomass than the plankton but the latter are of course distributed throughout the loch. However, benthic algal production has not been investigated and may be considerable for in addition to the abundant crops, they also contribute to the diet of Chironomidae and other benthic invertebrates.
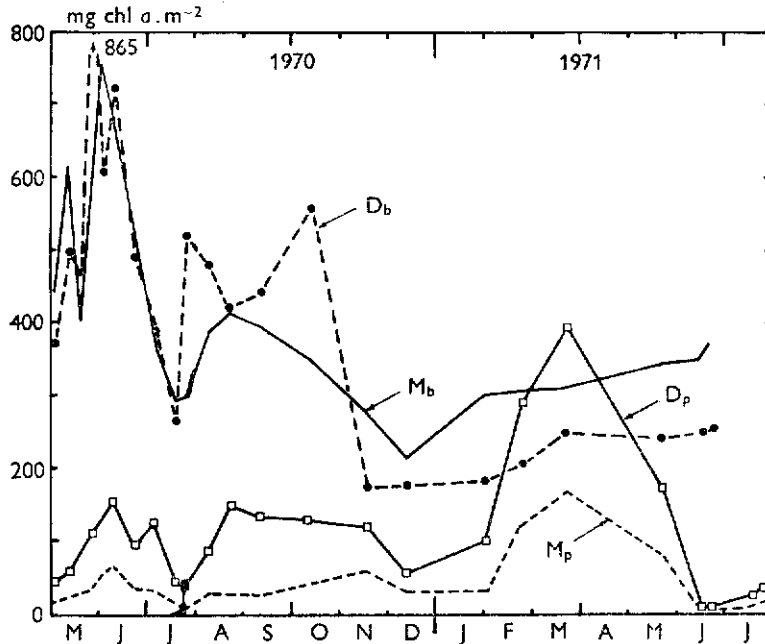
TEXT-FIG. 9.—Areal concentrations of chlorophyll *a* in the uppermost centimetre of sediment (b) and in the overlying water column (p) at stations 'M' and 'D'.

## DISCUSSION

It is possible to identify what appear to be the main environmental factors affecting the nature of the algal plankton in this loch. High rates of population growth are perhaps not surprising in view of the mean depth and the favourable euphotic to mixed (= total) depth ratios (Bindloss *et al.* 1972; Bindloss 1974). A fairly uniform distribution of biomass is adequately maintained due to mixing of the water by wind. However, in part at least, the specific nature of the algal dominants is conducive to homogeneity; large buoyant algae (e.g. colonial gas-vacuolate Cyanophyceae), very dense forms (e.g. large diatoms) and strongly motile species (e.g. large flagellates) were each rarely recorded at Loch Leven during 1968–71. By contrast, *Anabaena flos-aquae* (Lyngb.) Bréb. was extremely abundant in 1972. Then, under calm although isothermal conditions, its population was characterised by aggregation within the uppermost few centimetres of the water column. Under such conditions, the euphotic zone is considerably reduced so that other algae are present in relatively dark water. Thus the surface aggregation of the blue-green alga on the windward side of the loch, by effecting unfavourable conditions beneath it, could explain the poor growth of macrophytes there at that time (see Jupp *et al.* 1974).

The depth (*ca* 2·5 cm) in the sediment to which algae are abundant exceeds the depth to which light penetrates that sediment by a factor of, possibly, 10 (see Hickman and Round 1970; Fenchel 1971). In this respect the sediment algal community is likely to exhibit a smaller net production:gross production ratio than the overlying

water column community all other factors being equal. Moreover, whereas vertical mixing of the whole plankton biomass is rapid and continuous, observations on the sediment suggest that although a thorough mixing of the upper 1–2 cm can occur in a few hours, the occasions on which this happens are rare.

The dense algal crops are supported by a rich nutrient supply from streams and, at least in the case of silica, recycling from the sediments. By virtue of a fairly efficient utilisation, however, nutrients are occasionally reduced to levels which appear to prevent algal populations increasing further at their highest observed rates. The high standing crops of benthic algae may be utilising nutrients similar in source and nature to those required by the plankton. However, the spatial distribution of the benthic communities indicates that much of their nutrient requirements may be met by the interstitial water. In connection with the light relations within the sediment, as mentioned above, many non-motile algae may lie in darkness for considerable periods. A further investigation of these communities would be worth while, particularly in relation to the possibility of heterotrophic growth (Hickman and Round *loc. cit.*).

Utilisation of living algal cells in the water column at Loch Leven by Fungi and Protozoa seems to be insignificant for much of the year. The role of Crustacea is unknown. Thus, a major fate of planktonic algae is likely to be bacterial breakdown or autolysis of the cells either in the water, on the sediment, or, for cells that fall or are transported near or on to the sediment, ingestion by benthic invertebrates. The importance of herbivorous Chironomidae feeding directly on planktonic algae is not known and this link remains a large gap in our knowledge of the Loch Leven ecosystem. However, it is worth comparing the biomass of algae and of larval chironomids on the basis of data available so far. The comparison is made in terms of carbon, and the data refer to March 1971.

The carbon biomass of the plankton in open water was approximately 5 $mg.l^{-1}$ which, calculated for the mean water depth of 4 m, is 20 $g.m^{-2}$. At this time carbon to chlorophyll ratios averaged 25. Applying this relation to the observed benthic algal chlorophyll concentrations, carbon in the uppermost centimetre of the sandy zone amounts to approximately 7 $g.m^{-2}$. From the dry-weight biomass data of the major components of the chironomid fauna (Charles *et al.* 1974 and pers. comm.; Maitland and Hudspith 1974 and pers. comm.), assuming that ash-free dry weight is 90 per cent of the total dry weight and that carbon is 50 per cent of the ash-free dry weight, the carbon incorporated in these animals is approximately 2·4 and 3·4 $g.m^{-2}$ of the sand and mud sediment zones respectively.

Frequent analyses of carbon were made at other times during spring 1971, when the crop growth observed was very largely composed of one algal species, *Cyclotella pseudostelligera*. Over a 33-day period the average rate of biomass accumulation was 122 $\mu g$ $C.l^{-1}.d^{-1}$ or 0·49 $g.m^{-2}.d^{-1}$. As this rate is lower than true net production it serves to illustrate the highly productive nature of the plankton at Loch Leven.

The features so far discussed concern quantities, all of which are perhaps not uncharacteristic of a eutrophic lake. It is the quality, i.e. the species composition that is peculiar: many of the important algae in this lake (e.g. *Steiniella, Synechococcus* and some of the small centric diatoms) are not commonly dominant elsewhere. A comparison of recent algal quality information from some of the better-studied lakes in temperate Europe bears this out; see for example that of Bodensee (Lehn 1969), Erken (Nauwerck 1963), Esrom (Jonasson and Mathiesen 1959), Esthwaite (Lund

1961), Malaren (Bonthron-Willèn 1970), Neagh (Gibson *et al.* 1972), Windermere (Lund 1961) and Zurichsee (Ravera and Vollenweider 1968).

The importance, indeed the predominance, of nannoplankton at Loch Leven is not a character normally associated with a eutrophic lake (see e.g. Lund 1961; Kristiansen 1971). Small algae are characteristic of very rich lakes termed 'hypertrophic' by Pavoni (1963), but in the lakes she studied the major algae were Euchlorophyceae and Euglenophyceae rather than Diatomaceae and Cyanophyceae as found here. Pavoni (*loc. cit.*) did not consider the zooplankton, but the nature of it in Loch Leven is equally unusual for a rich lake (cf. Walker's 1970 data with information presented by Brooks 1969; Gliwicz 1969*b*). The relative paucity of herbivorous Cladocera in the plankton here until 1971 may be a main determinant of the success of small algae and the nature of the energy links from the phytoplankton. However, this success could be effected by the cyclopoids also; the adults may be grazing down larger algae which they can grasp, and the younger stages may be feeding on very small (e.g. <5 μm) algae such as phytoflagellates which are common in the loch but do not dominate the crops there.

In conclusion, the subject of eutrophication should be mentioned. Loch Leven is eutrophic by any quantitative standards, whether these are based on nutrients or algae. Using Holden's data (in Bindloss *et al.* 1972; see also Holden and Caines 1974) Loch Leven appears to be receiving N and P at loading rates of approximately 10 and 4 times respectively, those considered by Vollenweider and co-workers (Vollenweider 1968) to cause eutrophication problems in a lake of a 5 m mean depth. This cultural eutrophication of freshwaters (Hasler 1947; Graham 1968*a*, *b*; Lund 1972) is commonly accompanied by an increase in phytoplankton production although for numerous reasons the relation between nutrients and algal crop densities is not linear (see e.g. fig. 2 of Lund 1970). Such quantitative changes are often manifested in an increased importance of Cyanophyceae (see e.g. Edmondson 1968; Ravera and Vollenweider *loc. cit.*) although diatoms may also be so affected (Davis 1964; Beeton 1965; Schelske and Stoermer 1971).

That cultural eutrophication has been important in the history of Loch Leven is undoubted but the factors constituting natural eutrophication should not be overlooked. Surface blooms of *Anabaena* sp., were noted in Loch Leven as long ago as 1905 (Wesenberg-Lund 1905; Bachmann 1906), and dense populations of other blue-green species have been recorded since that time (Rosenberg 1938; Brook 1958, 1965). The importance, however, of natural factors as opposed to the man-induced ones are difficult to assess (see also Haworth 1972).

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## APPENDIX I

## ALGAE RECORDED FROM THE PLANKTON OF LOCH LEVEN, 1968–71

Species marked with an asterisk have made important contributions to the total phytoplankton biomass.

*Euchlorophyceae*

Actinastrum hantzschii Lagerh.

Ankistrodesmus acicularis A.Br.

A. braunii (Näg.) Collins

A. convolutus Näg.

*A. falcatus (Corda) Ralfs inc. var duplex and mirabile

A. longissimus var acicularis (Chod.) Brunnth.

A. setigerus (Schröd.) G. S. West.

*Ankyra judai (G. M. Smith) Fott.

Botryococcus braunii Kütz.

Carteria spp.

Characium sp.

Chlamydomonas spp.

Chlorella spp.

Chlorococcum sp.

Chlorogonium fusiforme Matwe.

Chodatella ciliata (Lagerh.) Lemm.

C. quadriseta Lemm.

Closteriopsis sp.

Coelastrum microporum Näg.

Cruciginia rectangularis Gay

C. irregularis Wille.

?Dictyochlorella

Dictyosphaerium anomalum Korsch.

D. ehrenbergianum Näg.

*D. pulchellum Wood.

D. regulare Swin.

D. simplex Korsch.

*L. subsalsa Lemm.

L. chodata Bernard.

Micracantha sp.

Micractinium pusillum Fresen.

M. appendiculatum Korsch.

*Nephrochlamys subsolitaria (West) Korsch.

Nephrocytium sp.

*Nephroselmis (= Heteromastix) angulata (Korsch.) Skuja.

Oocystis lacustris Chod.

Pandorina morum Pascher.

*Pediastrum boryanum (Turp.) Meyen and forma glanduliferum Bennett.

P. duplex Meyen.

P. simplex Meyen.

P. tetras (Ehrenb.) Ralfs.

Radiococcus sp.

Scenedesmus acuminatus Chod.

S. arcuatus Lemm.

S. obliquus (Turp.) Kütz.

S. quadricauda (Turp.) Bréb. and var. horridus Kirchn.

Scotiella sp.

Siderocelis (= Amphikrikos) minutissimus (Korsch.) Bourr.

S. ornata Fott.

Sphaerocystis schroeteri Chod.

*Steiniella sp. (near graevenitzii Bernard)

*Didymocystis inconspicua Korsch.
Didymogenes (near palatina Schmidle)
Diogenes sp.
Elakatothrix gelatinosa Wille.
Eutetramorus sp.
Hyaloraphidium contortum Pasch et
    Korsch.
Kirchneriella obesa (West) Schmidle.
K. contorta Bohlin.
Lagerheimia genevensis Lemm.

*Tetraedron caudatum (Corda.) Hansg.
T. minimum (A.Br.) Hansg.
*T. regulare Kütz.
Tetraspora gelatinosa (Wahlb.) Ag.
Tetrastrum staurogeniaeforme (Schr.)
    Lemm.
Treubaria triappendiculata Bernard.
Westella sp. [near botryoides (W. West)
    de Wildeman]

*Ulothricophyceae*

Cladophora sp.
Oedogonium sp.
*Planctonema lauterbornii Schmidle.

Raphidonema berninum Kol.
R. spiculiforme Vischer.
Ulothrix (near zonata Kütz)

*Zygophyceae*

Closterium venus Kütz.
C. intermedium Raifs.
Cosmarium botrytis Menegh.
C. contractum var. minutum (Delp.)
    W. et W.; and var. ellipsoideum Elfv.

Spondylosium planum (Wolfe) W. et
    W.
Staurastrum cingulum (W. et W.) G. M.
    Smith.
S. pingue Teiling.

*Euglenophyceae*

Astasia sp.
Colacium sp.
Distigma sp.

Phacus sp. (Strongylus type).
Trachelomonas spp.

*Cryptophyceae*

*Cryptomonas erosa Ehrenb.
C. marssonii Skuja.
C. ovata Ehrenb.
*Chroomonas (Rhodomonas) minuta var.

nanoplanctica Skuja [? Rhodomonas
    pusilla Bachm.].
Chroomonas (Chroomonas) Nordstedtii
    Hansg.

*Dinophyceae*

Gymnodinium paradoxum Schilling.
G. minimum Klebs.

*Peridinium cinctum West.

*Chrysophyceae*

Chrysochromulina sp.

Mallomonas sp. (very near acaroides
    Perty.).

*Xanthophyceae*

Dichotomococcus capitatus Korsch.
D. curvatus Korsch.
Monodus subterranea B. Petersen.
Nephrochloris sp.

Polykurtos sp.
Pseudostaurastrum (= Goniochloris) sp.
Trachydiscus sp. (near lenticularis Ettl.)

*Bacillariophyta*

Diatomeae (after Hustedt 1930).

[A more comprehensive list than the one which follows is given by Haworth 1972, including planktonic and benthic diatoms found in the recent sediments of Loch Leven.]

*Centrales*

Cyclotella comensis Grunow.
C. comta (Ehrenb.) Kütz.
C. meneghiniana Kütz.
*C. pseudostelligera Hustedt.
Melosira italica subsp. subarctica O. Müller.

M. granulata (Ehrenb.) Ralfs.
*Stephanodiscus hantzschii Grunow.
*S. rotula (Kütz) Hendey.
*S. rotula var. minutula (Kütz) Grun.
*S. tenuis Hustedt.

*Pennales*

*Asterionella formosa Hassall.
*Diatoma elongatum Agardh. (inc. var. actinastroides Krieger)
D. vulgare Bory.
Fragilaria crotonensis Kitton.
Meridion circulare Agardh.
Nitzschia acicularis (Kütz) W. Smith.

N. kutzingiana Hilse.
Synedra acus Kütz inc. var. angustissima Grun.
*S. rumpens Kütz var. scotica Grun.
S. ulna (Nitzsch.) inc. var. danica (Kütz) Grun.

*Cyanophyceae*

Anabaena sp.
[Anabaena flos-aquae (Lyngb.) Bréb., was extremely abundant during 1972 but was not recorded during 1968–71].
Aphanothece (Aphanothece) clathrata W. et G. S. West.
A. (A.) nidulans P. Richt.
A. (Coccochloris) sp.
Gomphosphaeria aponina Kütz.
G. naegeliana (Unger.) Lemm. (= Coelosphaerium naegelianum Unger)

Lyngbya spp.
Marssoniella elegans Lemm.
Merismopedia convoluta Bréb.
Microcystis sp.
Oscillatoria acuminata Gomont.
O. limnetica Lemm.
O. planktonica Wolosz.
*O. redekei Van Goor.
O. splendida Greville.
*Synechococcus n.sp.

APPENDIX II

COMMONER ALGAE (ALL DIATOMS) FROM
THE BENTHOS OF LOCH LEVEN, 1970–71

Achnanthes clevei Grunow
A. grimei Kraeske
A. lanceolata (Brébisson) Grunow
A. lanceolata f. elliptica Cleve

Fragilaria construens var. binodis (Ehrenberg) Grunow
F. pinnata Ehrenberg
Navicula lanceolata (Agardh) Kützing

A. linearis (W. Smith) Grunow
Amphora ovalis Kützing
A. ovalis var. pediculus (Kützing) van
  Heurck
Cocconeis placentula var. euglypta
  (Ehrenberg) Grunow
Coscinodiscus sp.
Cymatopleura elliptica (Brébisson) W.
  Smith
Cymbella ventricosa Agardh

N. radiosa Kutzing
N. reinhardtii Grunow
N. tuscula (Ehrenberg) Kutzing
Nitzschia kutzingiana Hilse
Opephora martyi Heribaud
Pinnularia sp.
Surirella biseriata Brébisson
Synedra acus var. angustissima Grunow
S. parasitica var. subconstricta Grunow