

# STUDIES ON THE VEGETATION AND HYDROCHEMISTRY OF SCANIAN LAKES

## III. DISTRIBUTION OF MACROPHYTES AND SOME ALGAL GROUPS

INAUGURAL DISSERTATION

BY

*ASTA LUNDH*

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## Preface.

The present investigation is a continuation of a previous work (LUNDH 1951 b) treating the macrophyte vegetation in some Scanian lakes. Moreover it deals with macroscopic algae, phytoplankton and epiphytic diatoms in these lakes and here it is based upon a part of the algal material collected in the years 1946 to 1950.

As regards the extent of the investigated area the reader is referred to the introduction in the paper cited above.

The studies were commenced as a link in the investigation of the Scanian Flora directed by Professor H. WEIMARCK and thus they have a completely phytogeographical bearing. The ecological problems arising from the different distribution of the plants are also discussed on the basis of the available field ecological material and the experimental results given in the literature.

To my teacher in botany, the previous Director of the Institute of Systematic Botany Professor emeritus N. HERIBERT NILSSON, I wish to express my respectful appreciation for his never-failing interest in my studies. I am also deeply indebted to the present chief of the same institute, Professor H. WEIMARCK, who suggested this research problem, for his cordial advice and ready assistance.

Professor H. BURSTRÖM, Director of the Botanical Laboratory, has very kindly given me a place to work and the necessary equipment for the determination of the algal material. For these facilities and for his great willingness to discuss actual problems in connection with the treatise I am exceedingly grateful.

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nological Institute, for acquainting me with the elements of freshwater research and his many helpful suggestions.

In addition, I should like to express my sincere gratitude to the many specialists, both in Sweden and abroad, whom I have consulted for their valuable advice and friendly assistance.

In the field work I have been assisted in an excellent way by my mother, Mrs. G. LUNDH, Miss ANNA GRETA JÖNSSON, my fiancé, Fil. mag. ARTUR ALMESTRAND and Fil. stud. MARGARETA NORLIN.

To all my colleagues in the Botanical and Limnological Institutes I am greatly obliged for splendid collaboration and valuable discussions.

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## Macrophytic vegetation.

### Distribution of the species.

In the following the designation macrophytes is used for aquatic vascular plants, mosses, and charophytes, but not for other macroscopic algae. The latter will be treated in a special section.

In a previous report by the author (LUNDH 1951 b), tables of the macrophytes encountered in the lakes investigated are to be found (with the exceptions there reported).

Isoetids, nymphaeids, lemniids, and elodeids (LUNDH *l.c.*, table 6, pp. 120 to 121).

If the lakes are arranged according to the similarity of the composition of species (table 1), it is apparent that three groups of lakes can be distinguished. The largest group (=group A) is composed of the lowland lakes, the next largest one (=group B) of Archaean lakes situated in a transitional area with traces of lime in the soils, and the smallest one (=group C) of Archaean lakes on the ridge Hallandsåsen. Thus the groupage is completely in agreement with what might have been expected from the geological conditions (*cf.* LUNDH *l.c.*, p. 14 *et seq.*).

The lakes within group A vary greatly as regards conditions of size and depth, as well as transparency and lake colour. They are all situated in the part of Scania which has sedimentary bedrock. The soils are of various types, but a high lime content as compared with the Archaean moraine is common to them all. In this group of lakes the elodeid layer is very well developed.

The lakes of group B are small and rather shallow. They very seldom have gently sloping shores (with the exception of Finjasjön). The transparency is medium high and the lake colour is yellow-brown to brown. Cretaceous material is intermingled here and there in the soils, which are otherwise made up of Archaean material. Finjasjön deviates in several respects and it is not as well studied as the other lakes of this group. As far as the macrophyte vegetation is concerned it largely agrees qualitatively with group B and there-







fore it has been included in this group. The helophytes predominate in group B (except Finjasjön).

Group C comprises medium large, deep lakes with clear water and very often gently sloping minerogeneous shores. The lake colour is similar to that of group B. In group C the isoetids form the most dominating component of the vegetation.

More extensive descriptions are given in the earlier paper mentioned above (LUNDH *l.c.*).

In table 1 the eulimnic species have been arranged according to their different distribution within the area investigated. First come the species restricted to group A (=type I), then those more or less regularly distributed within the whole area (=type II) and finally species mainly restricted to group C or to the groups B and C (=type III).

Some species from table 6 in LUNDH (*l.c.*) recorded from only few localities have been excluded here. The sign + indicates very old findings or those made before a lowering of the lake was carried out. Broken lines indicate findings from the Nineteen Twenties. As far as Araslövssjön is concerned there is some uncertainty as to the findings from this period. Exact information on possible lowerings of the lake is not available. The different parts of Ringsjön have been united. The records from Krankesjön are from the summer 1944.

Group A forms a type completely separated from the other two with several characteristic species *e.g.*, *Myriophyllum spicatum*, *Potamogeton Friesii*, *P. lucens*, *P. pectinatus*, and *Ranunculus circinatus*. Most of them are elodeids.

Group B lacks the species mentioned above which are specific for A. A few species with their main distribution in A have been found in some localities in group B, namely *Hydrocharis Morsus-ranae*, *Lemna trisulca*, and *Potamogeton crispus*. *Lemna minor* is common in both groups. The group has some species in common with group C, *e.g.*, *Juncus bulbosus* and *Myriophyllum alterniflorum*. The group is to be considered rather as a transitional type between A and C, characterized by a deficiency in species.

Group C contains in addition to the ubiquitous some elements unfamiliar to most of the lakes of group A, *e.g.*, *Isoetes* spp., *Juncus bulbosus*, *Lobelia Dortmanna*, *Myriophyllum alterniflorum*, *Pilularia globulifera*, and *Subularia aquatica*. Two of these species are, as mentioned before, not uncommon in group B. The *Isoetes* and *Lobelia* mats are completely absent in all the remaining lakes.

As is evident from the table the groups are connected by transitional species. The species with their principal distribution in group A may

thus be found in group B in some cases, and several of the characteristic species of group C occur both in A and B.

The lakes of group A characterized by species from group C are in the table placed at the end of the group. They comprise Fjällfotasjön, Tunbyholmssjön, Hammarsjön, Araslövssjön, and Ringsjön. Some + signs indicate that other lakes have also previously contained Archaean elements. These findings originate from the last century, except that of *Lobelia* at Vombsjön, which is registered in the Nineteen Twenties. It belongs, however, to the period before the last radical lowering. The information on *Lobelia* at Havgårdssjön is obtained from the register of Skånes Flora.

Fjällfotasjön differs from the adjacent lakes by its surroundings which *i.a.* are composed of vast poor fens (*e.g.*, Trobergamyren). The aberrant vegetation in the lake is probably correlated with differences in the soils which are composed of Shale-Archaean moraine. The whole area towards Romeleåsen is characterized by low soil pH values (WALDHEIM 1947).

Tunbyholmssjön is to be considered rather as a pond, edged in the north by large fen grounds. It is situated in the area of sandstone moraine.

Araslövssjön and Hammarsjön are shallow lakes, forming widenings of the Helgeå. Thus they are fed by water from the Småländska Högländ and the spread of Archaean elements into the lakes is facilitated.

Ringsjön is situated on the border between Archaean rock and the Silurian region. The fault between these runs through the southern part of the lake. Of the Archaean species *Myriophyllum alterniflorum* has a wide distribution, *Isoetes* is limited and *Lobelia* probably extinct. Apart from these species the composition of the vegetation agrees with any lake in group A.

All the lakes discussed above deviate geologically or in some other manner from the typical lakes of group A. Also in the water-chemical conditions some deviations are reflected (ALMESTRAND 1951). In the table below the contents of calcium and bicarbonate of the discussed lakes are compared with the averages of the groups A and B.

| p.p.m.                 | Fjäll | Tun | E.Ri | W.Ri | Aras | Ham | Average of group A | Average of group B (except Finjasjön) |
|------------------------|-------|-----|------|------|------|-----|--------------------|---------------------------------------|
| Ca .....               | 31    | 26  | 36   | 33   | 9    | 34  | 45                 | 18                                    |
| HCO <sub>3</sub> ..... | 124   | 42  | 92   | 106  | 54   | 54  | 133                | 54                                    |

It is apparent that all the lakes have values below the average of group A, but generally higher than the average of group B.

### Helophytes (LUNDH *l.c.*, table 7, pp. 122 to 123).

In table 7 the helophytes are divided into two groups, *viz.* the non-ubiquitous and the ubiquitous ones. In the former group two types of distribution can be distinguished, namely one including species limited to group A and one including species growing in groups A and B. Thus also among the helophytes the three lake groups A, B, and C can be recognized. At the transition from A to B some species disappear and at the transition from B to C still others. Fjällfotasjön and the other slightly divergent lakes of group A (see p. 11) do not differ pronouncedly as regards the helophytes.

### Charophytes (LUNDH *l.c.*, table 8, p. 126).

The distribution of the stoneworts shows a marked limit between the lake group A on one side and B and C on the other. In A all species recorded are to be found, even if the number varies in the different lakes. Tunbyholmssjön and Fjällfotasjön differ from the majority of the lakes of A by supporting only the three species *Chara aspera*, *Ch. fragilis*, and *Nitella* sp. (*Ch. aspera* is not found in Tunbyholmssjön), and in this regard they agree with Kvesarumssjön and Finjasjön. Several other lakes *e.g.*, Häckebergasjön, Svaneholmssjön, Snogeholmssjön, Sövdeborgssjön, and Sövdesjön, however, also lack more or less completely all vegetation of charophytes. The cause in this case may probably be another. The *Characeae* are apparently very sensitive to pollutions and similar culture effects (*cf.* HASSLOW 1931 and JAAG 1949). Gaps in the present distribution can thus sometimes be attributed to such environmental changes. *Cf.* Krankesjön, which after 1944 has entirely lost the immense *Chara* meadows (LUNDH *l.c.*) out in the lake.

As is the case with the helophytes Västersjön and Rösjön have also as regards the charophytes the smallest number of species (*Ch. fragilis* and *Nitella* sp.). Curiously enough *Ch. fragilis* has not been encountered in group C in shallow water, which otherwise is the most common habitat. It is likely that on the whole it has a very limited distribution within the group. Group B forms a transition between the two other groups.

### Bryophytes (LUNDH *l.c.*, table 8, p. 126).

The number of lake-mosses proper is small. Those present generally are also quantitatively slightly developed except in Västersjön. Only

*Fontinalis*, *Riccia* and *Ricciocarpus* have been recorded from so many localities, that it is possible to obtain an idea of their distribution within the different lake groups. *Fontinalis* is a ubiquist, whereas the others seem to be restricted to group A.

### Ecological discussion.

#### Isoetids, nymphaeids, lemnids, and elodeids.

The macrophytes are generally classified according to their different biological life forms. The divisions vary somewhat (*e.g.*, ARBER 1920, IVERSEN 1929, DU RIETZ 1930, and FASSETT 1930), but they are consistent on the whole. In table 1 the plant sociological terminology of DU RIETZ has been employed on the basis of table 6 in LUNDH (1951 b).

In ecological discussions species having different possibilities of absorbing nutrients and gases must be kept apart. DAUBENMIRE's (1947) morpho-ecological groups are established along these lines. His groups are: 1. floating hydrophytes (=lemnids, except *L. trisulca*), 2. suspended hydrophytes (in this case=*L. trisulca*, *Ceratophyllum* and *Utricularia*), 3. submerged anchored hydrophytes (=elodeids except *Ceratophyllum* and *Utricularia*), 4. floating-leaved anchored hydrophytes (=nymphaeids), and 5. emergent anchored hydrophytes (=helophytes). DU RIETZ includes rootless elodeids in the rooted ones, as they together form a common layer. It is evident that the two systems otherwise agree very well.

The suspended elodeids were separated by LOHAMMAR (1938) from the remaining elodeids and placed together with some other species in the group hydrotrophs, the common property of which is the poor development of the roots. The hydrotrophs are among themselves ecologically differentiated as they are able to satisfy their gas requirements in variant manners.

*Stratiotes Aloides* is in table 1 included in the nymphaeids, though it occupies a unique position. It is sometimes suspended and sometimes provided with roots, which penetrate the bottom mud. *Hydrocharis Morsus-ranae* should probably be considered a lemnid, since it is very often free-floating. LUNDH (1951 b) includes it in the nymphaeids.

#### Rooted plants (submerged anchored and floating-leaved anchored hydrophytes).

No extensive investigations on the dependence of the aquatic plants on the composition of the lake water and the lake bottom have hitherto been performed. Furthermore most of the works available are rather



old (*cf.* the exhaustive survey in LOHAMMAR 1938, pp. 197 to 207). Later studies are very few (*i.a.* GESSNER 1951, and WILSON 1947).

The present available information on the nutrition of the submerged rooted water plants can be summarized much in the following manner. It seems probable that the roots are the most important organs for the absorption of nutrients. This statement is supported by two facts, namely, 1. the plants studied seem to have an ascending water stream, which is maintained by the root pressure and 2. the plants thrive best, if the roots are fixed in the soils. The absorption which possibly takes place through the shoots is probably of less importance also due to the fact that the concentration of nutrients in the water is generally less than in the bottom. Rooted plants which are in contact with the air naturally must also have a transpiration stream.

As there are strong grounds for assuming that the plants absorb the main part of the salts through the roots, it is of little value to try to explain the heterogeneous occurrence of the plants on the basis of the varying concentrations of the different nutrients in the water, *e.g.*, phosphorus and nitrogen. These elements can be present in the bottom in entirely different concentrations than in the water. The conditions in the soils are on the whole highly complex. The lime content, for example, has other physiological effects in the soil than in the water, and plants react differently for varied hydrogen ion concentrations, if cultivated in soil or in water (OLSEN 1942).

On the other hand, it cannot be doubted that appreciable differences in the water quality in different lakes are correlated with differences in the properties of the soils. For this reason some parallelism between the varied distribution of the plants and the different concentrations of salts in the water can be expected.

As is seen from table 1 there are in the lakes studied two different groups of species, which are generally mutually exclusive. The distribution of these groups should reasonably correspond to an equally apparent difference in the ecological conditions of the lakes.

The important nutrients, nitrogen, phosphorus, and iron vary irregularly and considerably in one and the same lake (ALMESTRAND 1951, table 4). Several other ions, however, exhibit definite differences in their concentrations. It is true of them all that group A has the highest amount and group C the lowest one. Potassium, magnesium, chlorine, and sulphate show rather slight differences. The most pronounced ones are to be found as regards the calcium and bicarbonate ions. If the greatest differences between the lakes originate from differences in the

calcium bicarbonate concentrations, it may be assumed that even the bottom materials in the respective lakes deviate most significantly from one another in regard to their lime contents. If this is the case, the different composition of species in the lakes may be attributed primarily to the varying lime content of the bottoms, and the species considered "calciphilous" respectively "calciphobous". A discussion of the intricate "lime problem" is, however, beyond the scope of this paper.

The plants are naturally also more or less dependent upon the physical properties of the soils (*cf.* PEARSALL 1921). Observations in the field indicate that some prefer minerogeneous and other organogeneous soils. The differences in the distribution of these bottom types, however, are as great within the groups as between them.

The rooted submerged aquatics are, however, not completely independent of the water for their life processes, even if they provide themselves with mineral nutrients preferably from the bottom. They are restricted to the water for their requirements of carbon dioxide for photosynthesis and oxygen for respiration.

The concentration of oxygen seems to be sufficient for the requirements of the plants. The water of the surface layers, where the plants grow, is almost always in movement. The lakes on account of their location are exposed. In enclosed bays with stagnant water, where an extensive decomposition of organic material takes place, the conditions are naturally different.

It may not be assumed *a priori* that the content of carbon dioxide plays a selective role in the lakes studied, as it is theoretically determined by the equilibrium between the water and the air. It has been established, however, that several higher aquatic plants can directly utilize the bicarbonate as a carbon source for photosynthesis (ARENS 1933 and 1936, RUTTNER 1947 and 1948, STEEMANN-NIELSEN 1947 and 1951). All phanerogams investigated have proved to be capable of assimilating bicarbonate. Only few plants have been studied, however, and many of the investigations are only qualitative. It may be assumed that different species have different capabilities of utilizing bicarbonate. If this holds true, those having the highest capacity would easily suppress the remaining species in a water rich in bicarbonate.

Most of the rooted submerged elodeids recorded belong to the bicarbonate-rich waters. Type I comprises eleven species, while type III has only one. Five are ubiquitous. As regards the isoetids, which can also be completely submerged, the distribution is another. One species is limited to group A, six prefer the groups B and C and three are ubiqui-

tous. The isoetid belts are always narrow in the lowland lakes in comparison with those in Västersjön and Rösjön. They do not extend into deep water, nor do they grow on organogeneous bottom. In the latter case a possible oxygen deficiency can play a role. Otherwise their inability to compete seems to be the most important restricting factor, a condition already pointed out by STEEMANN-NIELSEN (1944). The isoetids with slow growth become surpassed by other more rapidly growing species, which are favoured by the richness in bicarbonate. The isoetids have difficulties in holding their own in the struggle for light (IVERSEN 1929).

Rooted, not submerged plants naturally absorb carbon dioxide and oxygen from the air and are therefore independent of the water for their gas exchange. To this group belong floating-leaved plants, which also exhibit a ubiquitous distribution. The latter fact might indicate that the supply of free and combined carbon dioxide in the water may actually play a decisive role in the distribution of the submerged plants in nature.

#### Rootless plants (floating hydrophytes and suspended hydrophytes).

The lemnids, except *Lemna trisulca*, are restricted to the water for their nutrient requirements but not for their supply of gases. In spite of this fact the lemnids are not ubiquitous. Two species extend into group B but not farther. The lemnids prefer sheltered habitats and are characteristic of the quiet water formed by the thick, high reeds. In the open lake they are very seldom met with. The *Lemna* species seem to have a luxuriant growth, when the other higher plants have wilted. Especially in spring they can be observed intermingled with the reed remains in calm places or washed up by the waves on exposed shore stretches.

It is clear, that the water quality in some way governs the distribution of the lemnids. Owing to their occurrence in special microhabitats it is difficult to discuss the factors possibly involved. The chemical factors were studied in the open lake.

The dividing line between suspended hydrophytes and submerged rooted hydrophytes must naturally be somewhat diffuse. Of the species recorded *Lemna trisulca*, *Ceratophyllum demersum* and *Utricularia vulgaris* belong to the former. It is more uncertain whether the *Potamogeton* species with relatively slightly developed roots should be included

here. The rhizoid systems of the charophytes may hardly be more effective, but nevertheless they are considered to obtain the nutrients from the soil.

The suspended hydrophytes are as phytoplankton and other micro- and macroscopic algae only in contact with the water. The most significant difference between these groups is probably their variations in size. The microalgae having the largest contact surface in relation to their mass can be expected to react more rapidly than the others to small changes in the environmental conditions. Only three true suspended hydrophytes occur in the lakes studied. Two belong mainly to group A and one is a ubiquitous. If *Potamogeton Friesii*, *P. obtusifolius* and *P. zosterifolius* are added (*cf.* LOHAMMAR 1938), there will be six species in all. Two of these are ubiquitous and the others are mainly restricted to group A.

The concentration of calcium bicarbonate, as already mentioned, shows the greatest variation among the chemical factors analyzed. The bicarbonate ion may be of importance in photosynthesis as stated above. It also affects the hydrogen ion concentration, the effect of which on the plant growth certainly has not been fully elucidated (*cf.* p. 96). It seems to be rather assumable that there are also species among the suspended water plants with various pH optima, as has been established by OLSEN (1936 and 1937) as regards land plants. The calcium ion is also likely to be selective. Higher plants need apparently larger amounts of calcium than microorganisms, but their specific requirements are naturally unequal. Furthermore the calcium ion has indirect effects, *i.a.* ionantagonistic. It checks, for example, the absorption of potassium (LUNDEGÅRDH 1950).

The calcium bicarbonate content thus must have far-reaching consequences in regard to the ability of plants in absorbing other nutrients. Even if the concentration of potassium is greater in lime-rich lakes than in lime-deficient this fact does not necessarily mean that plants can utilize larger quantities. The calcium bicarbonate also affects the availability of nutrient substances, for example iron. As the calcium bicarbonate can have so many direct and indirect effects, it is probably one of the most important factors governing the distribution of suspended aquatic plants.

As far as the possible limiting effects of other chemical factors on the occurrence of water plants is concerned very little is known. Field studies have shown that there are correlations between the distribution and

certain edaphic factors. The exact relations, however, cannot be clarified from these results. Experiments are necessary for obtaining such information.

#### Ecological conditions in the lakes studied.

In the lakes under consideration there is a definite correlation between the species included in type I and high concentrations of calcium, magnesium, potassium, sulphate ions among others, *i.e.*, on the whole with a high content of electrolytes. This correlation is evident also from the fact that Kvesarumssjön, which in size, location and other properties is similar to the other lakes in group B, exhibits some aberrations in its flora, at the same time as it has a higher content of electrolytes. As distinguished from the adjacent lakes the following hydrophytes are observed here: *Hydrocharis Morsus-ranae*, *Epilobium parviflorum*, *Eupatorium cannabinum*, and *Glyceria maxima*, and of the algae with a similar distribution *Chara aspera* and *Cladophora*. *Cf.* also the conditions in Finjasjön. Since the magnitude of the specific conductivity is determined above all by the lime content, it is possible that this factor is solely responsible for the correlation mentioned.

A correlation, even if not so marked, seems to be found between the species belonging to type III and a low content of electrolytes. This does not throw any light upon the factors controlling the distribution of these plants, however.

The light has been shown to have a very great limiting effect on the quantitative and vertical development of the aquatics (PEARSALL and ULLYOTT 1933 and 1934, PEARSALL and HEWITT 1933 and MEYER and HERITAGE 1941). The lack of light may also be a contributory cause of the general paucity of species in turbid lakes. Thus in such a turbid lake as Ellestasjön the vegetation is both quantitatively and qualitatively poor, while Levrasjön is characterized by an abundant under-water vegetation. It does not seem probable, however, that light differences can be responsible for regional qualitative differences, as the lakes of group A contain the same species, although their transparency is very varying. Nor does the various colours of the water seem to play any decisive role, for the variation of this factor is great even in group A.

The competitive factor acts together with the other limiting conditions. This must be of very great importance in natural environments. If a species grows under unsuitable conditions it is likely to be easily elimi-



nated by a species favoured by the prevailing conditions. A species capable of tolerating without difficulty a supraoptimal concentration of a substance may keep another more sensitive species away. On the other hand a species may show a high quantitative development in the absence of competition, even if the conditions otherwise are not optimal.

Table 1 gives no information as to the abundance of the plants. A comparative study of the quantitative development of the plants would not be of any great value for this investigation, the aim of which is to discover possible regional differences in the distribution of the plants. The quantitative growth of the plants varies with local factors, which naturally are not necessarily identical even in adjacent lakes.

Besides the factors discussed in the foregoing there is still one, which, no doubt, has had and has a great influence on the development and composition of the aquatic vegetation, especially in the lakes belonging to group A. This is the effect of culture. Table 1 contains some + signs, which indicate that the species in question have not been observed in the lakes during the last decades. In many cases they must be regarded as extinct. The most probable cause of this change of the flora is the human interference, directly and indirectly influencing the natural development of the lakes, for example lowering of the water-level, outlet of polluted water and manure-water and other changes. Among the species apparently extinct there are some, which are not common in group A and, therefore, may be supposed to constitute forms which cannot assert themselves in the competition with the typical species of the group.

### Helophytes.

The distribution of the helophytes within the area investigated agrees with that of the floating-leaved plants, that is, no species are restricted to group C or the groups B and C. All species in the groups B and C appear also in group A. Many helophytes thus have an apparently wide amplitude in relation to the submerged water plants. This is possibly due to the fact that the helophytes, as the nymphaeids, have a direct gas exchange with the surrounding atmosphere.

The number of species decreases from group A to C as does the electrolyte content of the water. Probably also the soil properties vary parallelly with the water quality.

All the species to be found in group C can, as already mentioned, also grow in the other groups. This fact must indicate that they are not

especially favoured by the edaphic environments of group C, but their relative abundance in this group is likely the result of the absence of competition. The same explanation might also be applied to the occurrence of typical Archaean elements in the lowland lakes. They are able to grow in these lakes as long as the competition is inhibited in any way. This can be the case in Fjällfotasjön, Tunbyholmssjön and others which deviate somewhat from the typical lakes (*cf.* p. 11). The old findings in the table designated with + can also be explained in this manner. Through the strong influence of culture in recent times the characteristic species of group A have been favoured quantitatively and therefore obtained an opportunity of suppressing such species as *Lobelia* and *Myriophyllum alterniflorum*. JAAG (1949) has pointed out that *Potamogeton lucens*, *P. pectinatus*, and *Myriophyllum spicatum*, that is, the typical plants of group A, increase after pollution. Plants occurring on electrolyte-deficient soils grow slowly according to LUNDEGÅRDH (1949). If so they would seem to be easily ousted by the more favoured plants.

The occurrence of *Isoetes echinospora* in Hammarsjön shows that even such a characteristic Archaean species is able to grow on non-Archaean material. The bottom of Hammarsjön bears helophytes and also several other eulimnic species of the type of group A. *Isoetes lacustris* grows in Ringsjön which also contains many plants of type I. *Rumex acetosella*, which is normally found on acid soils, is also equally well developed on neutral or slightly alkaline soils when the competition is eliminated (OLSEN 1936). ROLL's experiments (1939 a) with *Littorella*, *Lobelia*, and *Isoetes* showed that all three species can grow in alkaline water, although in nature they have their most abundant development in acid, lime-deficient lakes. Curiously enough, *Isoetes* grew best, although in nature it seems to be the most pronounced stenotope.

Some facts indicate, however, the improbability of all Archaean species being excluded from the electrolyte-rich lakes solely because of the strong competition. *Lobelia*, for example, thrived rather badly in ROLL's tests. It is possible that this species is sensitive to the hydrogen ion concentration and MOYLE (1945) has tried to prove that *Lobelia* does not tolerate a high pH value. It is well-known that as regards terrestrial plants different species require different pH for optimal growth (OLSEN 1936 and 1937). Thus some Archaean species may be especially adapted for living in an electrolyte-deficient or acid medium. *Cf.* also the changes in metabolism of plants with lime-induced chlorosis studied by ILJIN (1951).

### Charophytes.

It is presumable that the occurrence of the charophytes to a large extent is determined by the same factors as that of the remaining higher water plants. They exhibit namely a similar tendency in their distribution.

The correlation between the distribution of water plants and the content of calcium bicarbonate in the water has been emphasized several times above. As far as the stoneworts are concerned the correlation is at least equally marked. Like the root-carrying hydrophytes the *Characeae* are apparently primarily restricted to the soils for their nutrition (VOUK 1929, VOUK and BENZINGER 1929). The bottom sediments in the lakes maintaining the both quantitatively and qualitatively most abundant development of charophytes are very often lime-rich and sometimes consist of pure lake-marl. This fact supports the assumption that the lime content in some way influences the occurrence of charophytes in nature. Öland for example with its lime-stone bedrock is famous for its rich *Chara* flora. Of course the fact that the *Chara* species apparently prefer limy habitats does not absolutely imply that they require an especially high concentration of calcium ions for their nutrition, but may instead mean that they are better adapted than many other plants to endure the special conditions accompanying a high lime content. Their photosynthesis is possibly favoured by the large content of bicarbonate in the water (*cf.* DAHM 1926). It is possible that also factors other than lime may have a restrictive effect on the distribution of charophytes. In the extreme habitats of the alvar-lakes on Öland only *Chara aspera* occurs. If other species appear the water is contaminated (HORN AF RANTZIEN 1951).

Some *Characeae* are so-called euryhalinuous species, that is they grow both in salt and fresh water. Such a species is *Ch. tomentosa*, which is recorded from some of the lowland lakes (Ellestasjön, Heljesjön, Kranke-sjön, Råbelövssjön, Oppmannasjön, and Levrassjön), and *Ch. aspera*, which is one of the most common charads in group A and is also found in Kvesarumssjön and Finjasjön. Halophytes very often have a wide range as to the salt content and can grow in water of low salt concentration (DAUBENMIRE 1947, LUNDEGÅRDH 1949 and 1950). Thus they cannot be closely dependent upon the amount of sodium chloride. The most plausible interpretation of their occurrence on salt-rich substrata seems to be that they, as distinguished from other plants, have the capability of adaption to the special conditions prevailing there, *e.g.*, with

respect to the water conditions. They react in a similar manner to high concentrations of several salts other than sodium chloride (*cf.* LUNDEGÅRDH 1949). The high concentrations of certain ions also have a toxic effect, which is unequally strong for different species (MAGISTAD 1945 and BURSTRÖM 1949).

Attempts have been made to explain the occurrence of halophytes in fresh water by postulating that the high lime content can substitute the absence of sodium chloride (SAMUELSSON 1934). This is not supported by any kind of evidence, however (*cf.* MAGISTAD 1945). Such an explanation is not satisfactory either, as the lime content of fresh water does not generally seem to be higher than that of the brackish water. HALME (1944) reports a calcium concentration of 60 mg. per litre from his area, that is about the same order of magnitude as in the lakes of group A.

The foregoing discussion can be applied to the distribution of SAMUELSSON's (*l.c.*) so-called brackish-water species, of which *Potamogeton pectinatus*, *Zannichellia palustris*, *Scirpus maritimus*, and *Sc. Tabernaemontani* are to be found in the lakes under consideration. They are restricted to group A as *Chara tomentosa*. *Sc. Tabernaemontani*, however, has been recorded in Scania also from Western Sorrödssjön, where it forms some small clumps (LILLIEROTH 1950 b). As this lake is very similar to the lakes of group B, the plant thus seems to have a rather wide amplitude. Therefore it is surprising that this *Scirpus* is not more frequent in the province (it can, however, be somewhat more common than is seen from the known localities as it is very easily confused with *Sc. lacustris*). The most luxuriant patches are to be found on recently exposed shores. It is one of the dominants on the sandy shores at Vombsjön, where moreover *Sc. maritimus* has increased in abundance. After the last lowering of Krankesjön it has increased in density also here. On the other hand, it has in the last decades disappeared from some localities, *e.g.*, Häckebergasjön and Ringsjön. Its disappearance from these old localities and abundance on virgin soils may be explained as a result of the fact that the species probably has a low power of competition and is slightly resistant to grazing. A similar lack of competitive ability might also be at least a contributory cause of the limited distribution of the other brackish-water plants in the fresh waters in the area. Especially *Zannichellia* seems to have decreased considerably in distribution in fresh water (SAMUELSSON 1934).

It is also possible that the species may contain different ecotypes, but the problem is very little discussed.

## Bryophytes.

*Fontinalis* and probably most water-mosses (see RUTTNER 1948, STEEMANN-NIELSEN 1951 and their earlier papers) seem to lack the capability of assimilating bicarbonate. The submerged lake-mosses have a small distribution in the groups A and B. In group C they occupy a somewhat wider space. The difference in distribution can be correlated with the fact that in bicarbonate-rich waters they are not able to compete with the bicarbonate-assimilating plants. *Fontinalis antipyretica* grows partly in the splash zone, which is the most common habitat, partly at a rather great depth, often in the outermost edge of the higher vegetation (*cf.* LUNDH 1951 b, p. 135). In these habitats the soluble carbon dioxide content is likely to be sufficient, in the first case on account of the water movement, in the second on account of decreased photosynthesis and vigorous decomposition of organic material. Because of its low compensation point *Fontinalis* can also be content with less light intensity than other submerged plants, for example, *Elodea* (RUTTNER 1926, LUNDEGÅRDH 1949).

The two other mosses investigated agree in their life form rather with the lemnids as they float on the water and absorb carbon dioxide from the air. (They can also grow on a solid substratum). Like the lemnids they preferably belong to the reed communities.

## Conclusions.

It is necessary to distinguish between plants taking up mineral nutrients and gases in different ways. Plants provided with roots are probably preferably dependent upon the soil for their supply of nutrients. Plants with leaves in contact with the air regulate their gas exchange directly in the air.

The rooted submerged species, termed elodeids, are most frequent in group A. They exhibit an apparent correlation with high concentration of calcium bicarbonate in the water, and their distribution is likely controlled by some factor intimately related to high lime content. Both the lime content of the water and the soils must be regarded to have importance in this case.

The rooted submerged plants, which are called isoetids, have a reverse distribution. In many cases they probably do not avoid *per se* high lime content, but their absence in group A is effected by the strong competi-



tion from elodeids. At least one species, however, is preferably excluded from lime-rich lakes for another reason.

Rooted, non-submerged plants do not show the same dependence on the lime content. The nymphaeids are, for example, ubiquitous. The helophytes have also very often a wide amplitude. Some of them, however, seem to be confined to lakes with lime-rich water.

Rootless, non-submerged plants (=lemnids) are not ubiquitous in spite of the fact that they are supplied with atmospheric oxygen and carbon dioxide. Their distribution is thus governed by some differences in the water quality. These may not be absolutely identical with those obtained from the water-chemical data available from the open lake.

Rootless submerged plants are completely dependent upon the water for their nutrition. The calcium bicarbonate is the factor which primarily can be assumed to be responsible for their distribution, as this compound has very far-reaching direct and indirect consequences. Exact information, however, can only be achieved by experimental investigations.

Most of the charophytes are also closely correlated to high lime content in the water as well as in the bottom. They seem to take their nutrients preferably from the soils, as the rooted hydrophytes. They are also probably capable of assimilating bicarbonate.

Of the bryophytes *Riccia fluitans* and *Ricciocarpus natans* constitute an ecological type reminiscent of that of the lemnids. They have also a similar distribution, which therefore is perhaps regulated by the same factors. The submerged water-mosses are probably not able to assimilate bicarbonate and they have also an inconsiderable distribution in the lowland lakes with the exception of *Fontinalis*.

In nature the competition between the plants is probably the factor which is finally decisive. The most vital species become predominant even if the environmental conditions, disregarding the competition, are not directly inimical to more sensitive species. The competition probably checks the halophytes from asserting themselves in salt-deficient soils.

In the area investigated the climatic differences do not seem to be decisive.

## Macroscopic algal vegetation.

### Distribution of the species.

#### Material.

The following description does not pretend to be a monographical survey of the macroscopic algal vegetation in the lakes investigated. Such a work, if carried out by a single person, should be read with a certain critical attitude towards the reliability of the identifications of species. Many algal genera, for example, *Tribonema*, *Stigeoclonium* and *Ulothrix*, include many forms and are also otherwise difficult to identify. Several are intricate, because they have been insufficiently studied both in their natural habitats and in culture. As regards the blue-green algae there is a recent systematic treatise by GEITLER in RABENHORST's *Kryptogamenflora* (1932). Apart from the fact that the systematics here can hardly be considered as definitive, the great number of species within such genera as *Oscillatoria*, *Phormidium* and others makes the determination of species a difficult task. A monograph of this type would require the assistance of several specialists, if the results were to be fruitful and convenient for comparative phytogeographical and ecological studies. Only a specialist is sufficiently qualified to determine the number of species occurring in the lakes.

The sole aim of the investigation has been to determine, whether there are any marked differences in the composition of the macroscopic algal vegetation of the different lakes, especially the three different groups into which the lakes studied can easily be divided according to the composition of the higher aquatic plants. On account of the range of the investigation the results must be founded mainly upon the material that the author has reliably identified. During the investigation it has proved possible to treat only a small number of species satisfactorily. Unfortunately, at first hand many *Cyanophyceae* must be excluded, as the almost unlimited number of species could only partially be controlled. A study of the blue-greens in the lakes requires a special investigation. A simple examination of the epilithic *Cyanophyceae* within

the littoral zone would probably reveal marked aberrations between the three lake groups here mentioned. In the lowland lakes there generally occurs a calcareous crust on the stones containing blue-green algae, which would seem to be dissimilar to the epilithic blue-greens of the more lime-deficient lakes.

Species belonging to the genera *Tribonema*, *Microspora*, *Mougeotia*, *Spirogyra*, *Zygnema*, *Oedogonium*, *Bulbochaete* and others have only rarely been identified. This is a defect, as they very often constitute a characteristic element of the macroscopic algal vegetation. *Oedogonium*, *Bulbochaete* and the filamentous *Conjugatae* can generally be identified only when fertile. The material collected has mostly included sterile threads. On the whole, it is a rather delicate undertaking for a non-specialist to identify correctly species of all the genera mentioned above.

The report below embraces in the main the algae of the open lake, where the shores are to a greater or lesser extent exposed to winds and waves. The degree of exposition is naturally largely governed by the prevailing directions of the wind (in Scania chiefly westerly to south-westerly) but also by the topographic position of the lake, the shape of its shore-lines and the abundance of forests in the surroundings. The lowland lakes, situated in districts relatively poor in forests, are all appreciably more exposed than the Archaean lakes.

The algal vegetation of the Magnocaricion fens, inundated in spring, has not been closely studied. The dominating forms here are species belonging to the comprehensive genera *Horridium*, *Microspora*, *Mougeotia*, *Spirogyra*, *Tribonema*, *Ulothrix* and *Vaucheria*. The isolated sheltered bays with their often stagnant water afford special milieus (*cf.* SAUER 1937), containing mass development of *i.a.* *Spirogyra* species. Such habitats are not described, if they do not constitute a characteristic feature in the vegetation of the entire lake.

The *Characeae* have already been treated in connexion with the higher aquatic vegetation (LUNDH 1951 b), to which they are most closely related on account of their size and type of growth. They are also generally included in the description of the higher vegetation (*cf. e.g.*, THUNMARK 1931, p. 35).

Samples have regularly been gathered from stones and reeds in the open lake. The stones have been observed from spring to autumn, and the reeds mainly in summer and autumn. Apart from the special spring flora the stone samples have given the best results in summer and early autumn. At this time the algal growth is most abundant both on stones and plants. The reed epiphytes are best developed in dense reedswamps.

The autumn samples are here very often rather valuable for the determination of species, because, for example, the *Gloeotrichia* species at that time form spores. The epiphytes studied have been restricted to those living down to 2 to 3 decimetres below the water-level. For natural reasons the stone flora has been most closely studied in shallow water. By dredging, however, attempts have been made to obtain a slight idea of the occurrence of the most important algae at greater depths. Stones have frequently been transported to the Institute for closer examination. If macroscopic algae other than those mentioned above have been noticed, samples have been collected for microscopic determination.

As soon as the ice has broken up, diatom samples can be gathered. Then the *Ulothrix zonata* zone begins to develop very rapidly. When this green alga is at its prime in April, the water-temperature lies between 6° and 11° C. It may still be present when the temperature rises towards 15° C. This temperature has been established in Västersjön, Rösjön and Råbelövssjön, while the *Ulothrix* border was still beautifully green. *Stigeoclonium* sp. and *Draparnaldia plumosa* grow intermingled in the *Ulothrix* belt. The latter has its maximum from May to the beginning of June, i.e., when *Ulothrix* is dying. At this time it can form a two to three decimetres wide zone on stones, plant remains and other objects, if the conditions are especially favourable. *Stigeoclonium* sp. may be found in blue-green tufts on stones and diverse plants throughout the summer and autumn. Generally a definite species of *Stigeoclonium* predominates in each lake, but it is not probable that it is the same in all lakes. The author is not able, however, to decide the number of the species included. Also *Draparnaldia* can be observed in summer, but more rarely. From the beginning of August it becomes somewhat more common. Tufts of *Cladophora* begin to develop on stones already before the disappearance of *Ulothrix*, and in May they can have a length of several decimetres. In summer *Cladophora* is often coarse and brown from diatoms. Its appearance and abundance during this season change, however, very much from year to year. The autumn maximum is not so wellmarked as that in spring. The free-floating tangles of *Cladophora fracta* can be found as early as in April, but later on they become larger and form thick covers in some localities.

The material has been investigated in fresh condition. In many cases it has proved impossible to work with fixed material, as, among other things, the chromatophores become more or less deformed. The green algae are rather difficult to recognize after fixation, while the *Cyanophyceae* retain their appearance surprisingly well. Furthermore, it is

easier not to overlook a rare form in fresh material, where one has the advantage of the living colours. In the literature (ZIMMERMANN 1928) it is reported that, for example, species of *Chaetophora* have been confused with *Chantransia* on account of the fact that only fixed material had been examined.

### Systematic remarks.

RABENHORST's Kryptogamenflora and PASCHER's Süßwasserflora have been the main literature for the determination of the species. Besides, works by KÜTZING (1854), WOLLE (1887), HAZEN (1901—02), COLLINS (1909 and 1918) and others have been employed. The nomenclature follows PASCHER.

During the attempts to determine the macroscopic algae one encounters rather unexpected difficulties already in a study of the most common species. As a matter of fact, only a few forms are so easily recognizable that there is no risk for incorrect determinations.

The *Cyanophyceae* would have been very valuable subjects for investigation. The study of these, however, requires the knowledge of a specialist. It does not seem to be possible to ascertain the identifications only by using the determination keys in the floras. JAAG has on several occasions (*e.g.*, 1945 a and b) criticized the systematics of the *Cyanophyceae* and by experimental investigations with different light intensities pointed out a surprising variability, including a great number of properties used by taxonomists, for example, colour and ramification. The cell width behaves most constantly (JAAG 1950). Moreover, the humidity and hydrogen ion concentration have a great capability of modifying the appearance of the blue-green algae.

The list (table 2) only comprises a few blue-green species. Of the listed species the two *Tolypothrix* are rather uncertain. The only character which according to the floras distinguishes them is the width of the cells. This quantitative character seems to the author to be too uncertain to base a division of the two species upon, especially as transitional forms are not infrequent. On the whole, this genus like several others among the blue-green algae seems to be in need of a revision. *Gloetrichia Pisum* has been identified according to RABENHORST, where it is supposed to be a collective species. One of the forms examined deviates somewhat, but otherwise the species appears to be rather uniform. The distinguishing character between *Gloetrichia* and *Rivularia*, namely the presence or absence of resting spores, is not

always available, as *Gloeotrichia* often lacks such cells in summer. (There are different opinions regarding the justness of keeping the two genera distinct from a systematic point of view, but this discussion is naturally of no importance in this connexion.)

The author has not been able to identify *Rivularia dura* with certainty. The distinguishing character between *R. dura* and *Biasolettiana* given by the floras as the hardness of the thalli ought to be supplemented with other more conclusive ones, before it seems possible to speak about different species. It would be of great interest here to study the stages of development of the two algae and especially the appearance of the sheath. Characters as, for example, the presence or absence of incrustation in the colonies would seem to be of an insignificant systematic value, *cf.* FRÉMY (1930—31) and BUTCHER (1946).

Like the blue-green algae most *Chlorophyceae* are not easily recognizable. The difficulty of identifying them is largely effected by the fact that the different species are not satisfactorily delimited. They are variously interpreted by different investigators. This holds true of most genera dealt with in this paper. *Chaetophora incrassata*, *e.g.*, does not seem to be a uniform species, but opinions differ as to its delimitation (*cf.* PASCHER and HAZEN). *Cladophora* is very much discussed. The genus *Aegagropila* ought to be brought together to one species (*Cladophora aegagropila*) according to some phycologists (WAERN 1938 and KANN 1940). This is also done in the present work, as the author is in agreement with the algologists mentioned above as to the difficulties in distinguishing the different species. It is not impossible, however, that a thorough investigation may demonstrate the existence of more than one species, *e.g.*, ecologically differentiated forms. *Cladophora basiramosa* (figure 1) has been determined according to WAERN in DU RIETZ *et al.* (1939). The relationship between *Cl. crispata*, *fracta* and *glomerata* is apparently not definitively elucidated (*cf.* KANN 1940, p. 204). At least as far as the two latter are concerned the extremes are easily distinguished (figures 2 and 3), but the transitional forms cannot be equally readily classified. It may seem most expedient to unite them to one species. Experimental investigations, however, must previously have established that the habitually markedly different types really belong to the same species. They generally prefer different habitats. *Cl. glomerata* forms large characteristic tufts on exposed shores rich in stones and boulders, where the water conversion is rapid, whereas *fracta* is found in mass occurrences in calm sheltered habitats with more or less stagnant water, often among high helophytes. The *Cladophora* form





Fig. 1. *Cladophora basiramosa* from Eastern Ringsjön near the sound towards Sätöftasjön. It agrees fairly well with the photomicrograph given by WAERN in DU RIETZ *et al.* (1939). Fresh material. Enl. about 65  $\times$ . 17.9.1948.

which is typical as a reed epiphyte belongs to an environment which considerably deviates from that of *glomerata* and rather agrees with that of *fracta*. BRAND (1906) distinguishes within *Eucladophora* two sessile types: *glomerata* and *crispata*. *Fracta* is considered by him as a detached floating form of *crispata*. This conception coincides on the whole rather well with the opinion obtained by the present author from field studies. Recent culture experiments carried out by E. A. GEORGE, Cambridge, have, however, shown that the three types exist as well-distinguishable species (private communication). Thus it seems necessary to study cultures of the algal material from the lakes before forming a definite conclusion as to the number of species included.

The genus *Draparnaldia*, containing large, readily visible algae, should apparently not offer any difficulties in identification, as the floras only embrace a few species. According to the author's experience,



Fig. 2. Typical picture of *Cladophora fracta* from Oppmannasjön at Kiaby. The branches are always rather strongly curved and fairly deficient in chlorophyll. Fresh material. Enl. about  $30\times$ . 23.5.1948.

however, even this genus seems to require a revision. No monograph has been published since 1901—02 (HAZEN), apart from HEERING's survey in PASCHER (1915). The division of the collected material into two species (table 2) is not well-founded. *Draparnaldia plumosa* only partly includes forms with the typical appearance, which have been found in Gyllebosjön, Heljesjön, Häckebergasjön, Oppmannasjön, and Finjasjön, otherwise the specimens (figure 4) rather resemble *Draparnaldia acuta* according to KÜTZING (1854, Bd 3, tab. 13). As both types may occur in the same lake simultaneously, there are reasons for assuming that they should be brought together into one species. The type given by the figure 5 is the most common in the Archaean lakes.

*Stigeoclonium*, which genus comprises some of the most common lake algae, is not represented in the table. The author has not regarded herself capable of identifying the different species. There is no doubt that the genus requires a systematic revision and a study of the different developmental stages of the species is of importance. It may be possible

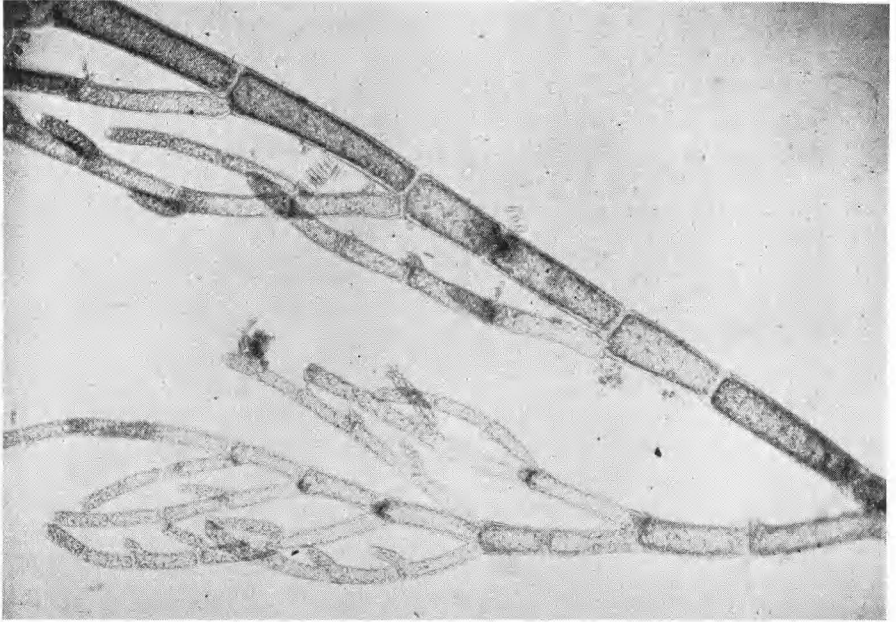


Fig. 3. A small, early, fertile form of *Cladophora glomerata* from Råbelövssjön at Balsvik. This form is attached and the branches are straighter and greener than those of *Cl. fracta*. Later forms deviate still more from *Cl. fracta*. Fresh material. Enl. about 30 X. 23.5.1948.

that young stages of a species are now described as a special species. Such a species as *Stigeoclonium farctum*, for example, judging from the drawings, might just as well be a young form of some other larger species. BUTCHER (1932 a), who closely describes a form of *St. farctum*, mentions that the filaments are hardly distinguishable from those of *St. falklandicum* when the erect system is well developed, which can sometimes occur. He adds (on p. 300) that separate individuals of the two species can be difficult to classify. Some investigations on the life-cycle of *Stigeoclonium* species have been carried out. The reader is referred to the bibliographies given by VISCHER (1933) and GODWARD (1942). It has, however, seldom been possible to follow the complete life-cycle. VISCHER (*l.c.*) also considers the present systematic literature to be of very little value. He has shown a pronounced variability as regards a great number of characters on which the systematics are partly founded, for example, formation of hairs, ramification and cell length. BUTCHER (1951) reports considerable morphological differences

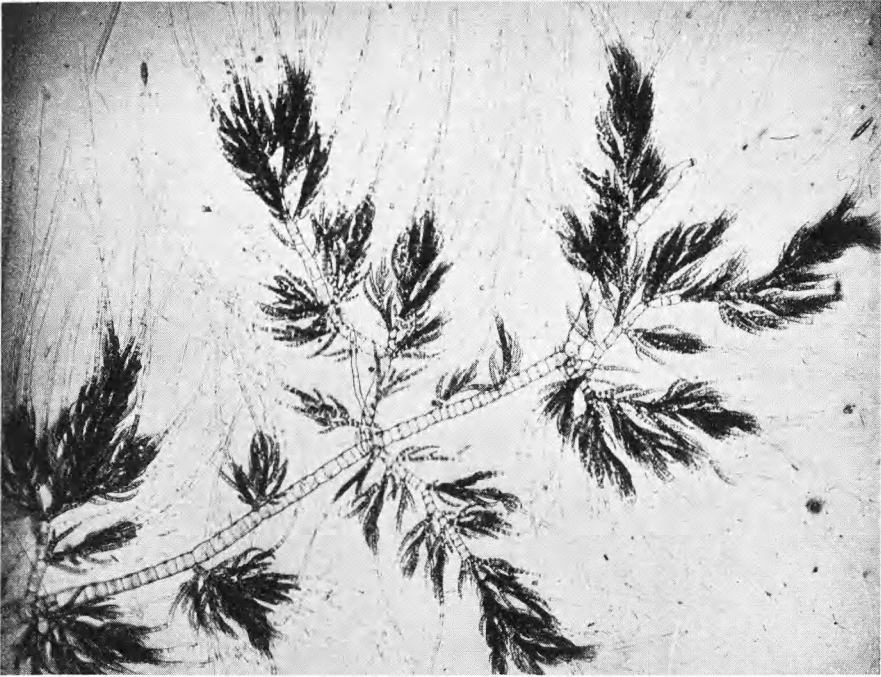


Fig. 4. *Draparnaldia plumosa* from Håckebergasjön. This form of *Dr. plumosa* seems to be the most common one in the lowland lakes. Fresh material. Enl. about 30  $\times$ . 12.5.1948.

in species of *Stigeoclonium*, probably caused by different contents of nitrate and phosphate.

As far as *Ulothrix* is concerned the same seems to be true as has been discussed for the two preceding genera. Especially the small species are poorly studied. The species included in the list as *U. tenerrima* also contains forms with cells narrower than 7  $\mu$ . The floras employ the cell width for distinguishing the species *tenerrima* and *variabilis*, but this can hardly be considered as a sufficiently well-founded character for separating two species. In the same localities there often occur thinner and broader threads which otherwise have a similar appearance. It is, nevertheless, in this case assumable that two different types are present on account of the fact that the individuals collected come from two ecologically different habitats. They grow partly on reeds and underwater plants in the lowland lakes, partly on stones in the Archaean lakes. In the latter case they form green macroscopic coats on the stones

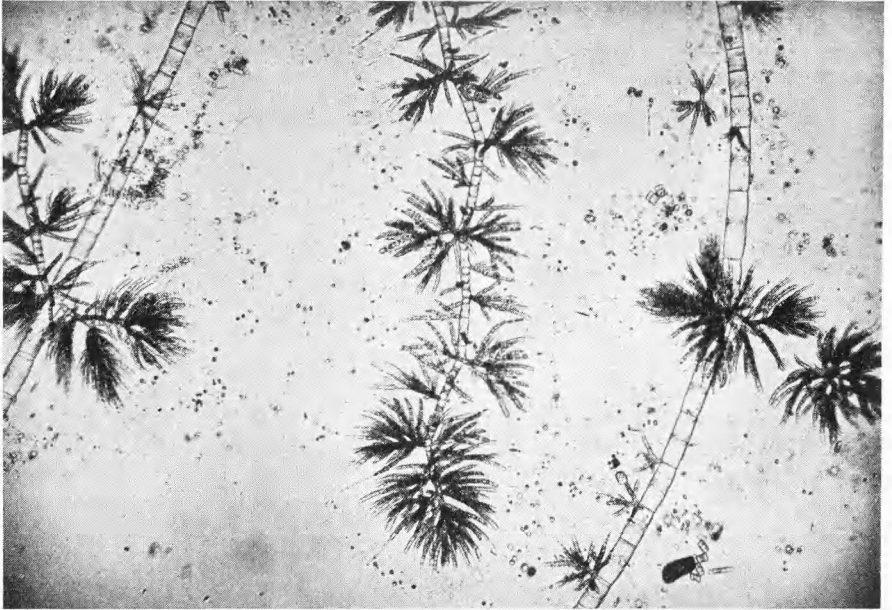


Fig. 5. *Draparnaldia glomerata* from a tributary to Rösjön (Lärkesholmsån). Similar forms have also been found in Västersjön. Fresh material. Enl. about 30 ×. 22.5.1948.

in spring, in the former they are preferably to be found in summer and autumn. Thus, it is just as important here as in many other cases to combine the systematic investigations with ecological observations.

The *Batrachospermum* species have been identified by G. ISRAELSON. The form of *Asterocytis* occurring in the Scanian lakes agrees best with the drawings of *A. smaragdina* REINSCH (*Allogonium smaragdinum* HANSGIRG, *Callonema smaragdinum* REINSCH) given in PASCHER (Heft 11) and GETTLER (1924—25). HAMEL (1924—25) includes in *A. ornata* (AG.) HAMEL, which species DU RIETZ *et al.* (1939) and KANN (1940) have listed from their areas of investigation, also *Callonema smaragdinum* REINSCH. Thus it is possible that the Scanian species and that reported by the authors mentioned are identical.

#### The vegetation of the individual lakes.

Y d d i n g e n. The lake makes a rather sterile impression as to the macroscopic algal growth. Only the calcareous crusts on the stones are visible to the naked eye. Among the blue-green algae forming these



*Rivularia Biasolettiana* may be mentioned. It generally occurs in large coherent crusts. In spring a mass development of *Oscillatoria curviceps* has been observed several times. It has almost covered the water-surface among remains of reeds and other residues in calm water. A macroscopically apparent development of diatoms is to be seen mainly in spring. An attached zone of *Ulothrix* and *Cladophora* is absent. *Draparnaldia plumosa* is to be found in ditches, running into the lake and in the outflow, but has not so far been encountered in the lake. *Cladophora fracta* has been recorded among *Mougeotia* and *Spirogyra* in the bay at Bökeberg under the shelter of reedswamps. The epiphytic growth on reeds is insignificant. The diatoms predominate.

Fjällfotasjön. The macroscopic algal vegetation is somewhat better developed than is that of Yddingen. It gives no impression of richness, however. The abundance of the diatoms is greater in spring compared with Yddingen, but the *Ulothrix zonata* zone is also here apparently absent. *Cladophora glomerata* has been found attached to stones on a small islet, frequented by birds. In shallow water the stones are coated with *i.a.* *Schizochlamys gelatinosa*, *Rivularia Biasolettiana* and *Chaetophora elegans*. The epiphytic growth on reeds is more monotonous than in many of the lakes investigated. *Tolypothrix tenuis*, the most important dominant, is seen in immense quantities. *Coleochaete orbicularis* and *Rivularia Biasolettiana* are also readily visible. *Gloetrichia Pisum* has been found on leaf stalks of water-lilies.

Börresjön. This lake does not either show a marked richness in macroscopic algae. The considerable lowering of the water-level probably disturbed the development of the algae to a certain degree. Those living near the water-surface were obliged to colonize new localities. In spring a greyish yellow cover of diatoms is to be observed. A *Ulothrix* zone only occurs at one place, situated below a spring in the slope. The sessile light green *Cladophora* zone is often well developed, for example on the stone shoals in the southern part and at Sjuttanäbbet. Especially characteristic of the lake are as in Yddingen the calcareous crusts on the stones. *Rivularia Biasolettiana* (figure 6) forms thick extensive crusts. Even in very shallow water (after the lowering *Cladophora aegagropila* grows on the lower parts of the stones, which are otherwise provided with a thick calcareous cover. *Hildenbrandia rivularis* also occurs at similar habitats. After the lowering it has been seen even above the summer water-line. The epiphytes on reeds are very little varied. They mainly include blue-green algae as in Fjällfotasjön. Macroscopically dominant is *Tolypothrix tenuis*.



H a v g å r d s s j ö n. The lake is characterized by an extremely rich macroscopic algal vegetation. In spring the diatoms form large flakes floating on the water-surface. *Ulothrix zonata* is probably widely distributed in the form of microscopic threads, but a macroscopically evident belt has only been found in one locality. *Stigeoclonium* sp. and *Draparnaldia plumosa* occur intermingled with the *Ulothrix* threads. The two latter exhibit in May a pronounced maximum. Especially in 1947 *Draparnaldia* was very widespread, growing on both stones and sandy bottom out to a depth of several decimetres. *Cladophora glomerata* forms thick tufts on the stones, and contrary to the lakes already mentioned it extends to a depth of at least 50 to 75 centimetres. From about 30 centimetres *Cladophora basiramosa* appears in short thick tufts. Its extension downwards is not known. At first the two *Cladophora* species grow together, when *Cl. glomerata* occupies the upper parts of the stones. The light green *Cladophora* was in the water-surface fresh green, but farther downwards it became brown and almost lacked chlorophyll (May 14, 1949). The floating *Cladophora fracta* also attains an abundant development in the lake. *Cl. aegagropila* is probably common on the lake bottom, but does not grow in so shallow water, that it can be reached from the shore as in Börringesjön and several other lakes. The stones near the water-line are mostly covered with a blue-green crust. As epiphytes on reeds the following species occur: *Cladophora*, *Coleochaete orbicularis*, *Chaetophora* cfr *pisiformis*, *Rivularia Biasoletiana*, *Stigeoclonium* sp., *Oedogonium* spp. and *Spirogyra* spp. *Gloeotrichia Pisum* is seen in enormous quantities on submerged plants and reeds. Among the submerged vegetation occupying a considerable area of the lake, masses of filamentous algae at times cover the water-surface. *Cladophora* and *Spirogyra* predominate but otherwise *Mougeotia*, *Zygnema* and *Oedogonium* are included. In 1949 a very thin *Enteromorpha* was found in the algal masses. Two years earlier large tubes were observed probably belonging to the same *Enteromorpha* species. Floating colonies of *Aphanocapsa* sp. and *Tolypothrix lanata* are commonly seen. The latter also grows on stones together with *Chaetophora incrassata*.

B j ö r k e s å k r a s j ö n. The lake is almost completely surrounded by more or less thick reedswamps. This fact causes a rich production of algae, characteristic of stagnant waters, for example *Spirogyra*, *Mougeotia* and *Cladophora fracta*. Open stony shore parts occur very rarely. A *Ulothrix* zone is apparently absent, but the light green *Cladophoras*, both attached and floating, attain an abundant development.



Fig. 6. Börringesjön, eastern shore. The shore was laid bare by the lowering of the water-surface in the summer of 1947. The stones were covered with crust-like *Rivularia* colonies. 5.4.1948.

The stones examined were plentifully colonized by chiefly *Chaetophora incrassata*, *Ch. elegans* and *Schizochlamys gelatinosa*. The reed epiphytes appear in large quantities. In addition to several of the species already mentioned *Tolypothrix tenuis*, *Rivularia Biasolettiana*, *Gloeotrichia Pisum*, *Coleochaete orbicularis* and several blue-green algae, difficult to identify, are also included. *Gloeotrichia Pisum* settles on all types of plant material, particularly on submerged species, e.g., charads and *Potamogeton pectinatus*.

H ä c k e b e r g a s j ö n. Open shores are more common here than in Björkesåkrasjön, but sheltered sections with almost stagnant water are predominating and in summer characterized by thick algal tangles. *Spirogyra* and *Cladophora* are the chief components. On the stones at the more or less open stretches no *Ulothrix* zone is to be found in spring, but a green coat is formed by *Draparnaldia plumosa* out to a depth of two decimetres. The attached *Cladophora glomerata* zone is well developed on suitable substratum. It preferably occurs on stones, but

it can also be seen on other submerged objects, for instance, wood. The epiphytic vegetation is always visible to the naked eye and abundantly developed. Especially conspicuous is the enormous occurrence of *Gloeotrichia Pisum*, growing on all types of plant stalks. Otherwise the following species have been recorded: *Coleochaete orbicularis*, *Symplocamus muscorum*, *Tolypothrix lanata*, *Chaetophora elegans*, *Spirogyra*, *Mougeotia* and *Oedogonium*. In summer many floating colonies of *Aphanothece* sp. are to be seen. At the eastern shore stones have been collected, the tops of which were covered with *Cladophora glomerata* and the lower parts with isolated threads of *Cl. basiramosa*. On the same stones red thalli of *Hildenbrandia rivularis* and a *Trentepohlia*-like alga could be observed. They were both rather common.

S v a n e h o l m s s j ö n. The entire lake can be said to constitute a lenitic environment for the algae (cf. THIENEMANN 1912). Open shore free from reeds is only to be found in a limited area at the eastern side, where the bottom is gravelly near the water-line. In spring a macroscopically visible but slightly conspicuous algal vegetation grows here, comprising *Ulothrix zonata* and *Draparnaldia plumosa*. The light green *Cladophora* species are early developed. An attached form as well as a floating form have been observed. The former occurs on stones, piles and boats. On stones and plants of variant types there is a rich growth of *Chaetophora incrassata*. *Batrachospermum moniliforme* is also often met with. Furthermore, the following species have been noticed on reeds: *Zygnema*, *Tolypothrix lanata*, *Spirogyra*, *Chaetophora elegans*, *Mougeotia*, *Coleochaete orbicularis*, *C. pulvinata*, *Gloeotrichia Pisum*, *Cladophora et al.* In summer a considerable part of the water-surface is covered with floating algae, e.g., *Spirogyra*, *Cladophora*, *Zygnema*, *Mougeotia*, *Oedogonium*, *Ulothrix tenerrima* and *Tribonema*. Mass development of *Oscillatoria princeps* has often been seen.

K r a g e h o l m s s j ö n. Strangely enough, no *Ulothrix* zone has been found in the lake. In May *Draparnaldia plumosa* has been gathered from stones close to the water-surface. At the same time *Chaetophora incrassata* forms a green coat on stones and dead plant remains. Where large stones are to be found, they are near the water-surface provided with a light green *Cladophora* zone, one to two decimetres wide. *Cl. fracta* lies in large quantities among aquatics in shallow water. On the stones close to the water-line several epilithic species may occur, e.g., *Chaetophora elegans*, *Ch. incrassata*, *Tolypothrix tenuis*, *Rivularia Biasolettiana* and *Schizochlamys gelatinosa*. Also *Pleurocladia lacustris* has been recorded from a similar location. Probably this brown alga is

more widespread in the lake than is as yet known. *Schizochlamys gelatinosa* sometimes forms a mass development of floating colonies, which may cover the water-surface in calm localities. At a depth of some decimetres *Hildenbrandia rivularis* and *Cladophora aegagropila* often appear on the stones, the latter not seldom below the former. They have both a wide distribution. On large stones at the eastern shore there occurs a green mucilaginous zone, which is very conspicuous. It consists of an alga, that resembles *Stigeoclonium farctum* according to descriptions and figures in the literature. In the same localities *Stigeoclonium tenue* is also often to be seen. The epiphytic vegetation on reeds is very rich in species, for example, *Gloeotrichia Pisum*, *Chaetophora elegans*, *Ch. incrassata*, *Coleochaete orbicularis*, *Stigeoclonium farctum* and *Cladophora*.

Ellestasjön. As to macroscopic algae the lake is very monotonous. The development of diatoms is even in spring very insignificant. The diatom cover has as in Börringesjön a greyish yellow colour. In spite of the presence of exposed stony shores the *Ulothrix* zone is slightly developed. *U. zonata* has been observed as a thin cover on stones in a very small area at the northern shore below springs, dry in summer. *Draparnaldia plumosa* and *Stigeoclonium* sp. is to be found near the mouth of a covered drain. *Cladophora* does not seem to form any typical sessile zone on the stones. Only rarely has it been seen attached. *Cladophora fracta*, however, occurs, even in masses, in sheltered localities. The stones are throughout furnished with a calcareous crust, probably to a large extent formed by blue-green algae. These stones, otherwise poor in epilithic algae, recall the conditions in Yddingen and Börringesjön. *Hildenbrandia* colonizes as in Börringesjön the underneath of the stones in shallow water. Its total distribution is not known. The locality noticed is situated on the southern shore, lined by beech-forest. *Rivularia Biasoletiana*, which is very frequent in Yddingen and Börringesjön, has not been found in Ellestasjön. Instead *Gloeotrichia natans* forms small brownish colonies on the stones. *Tolypothrix* sp. is also gathered from similar substrata. The reed epiphytes are poor in species. One sample proved to contain masses of *Tolypothrix tenuis*. On the whole the blue-greens dominate. Otherwise only *Coleochaete orbicularis*, *C. scutata*, *Oedogonium*, *Mougeotia*, *Bulbochaete*, *Spirogyra*, *Stigeoclonium farctum* and *Cladophora* have been listed. On the bottom in the Verlandung bays there often appears a mass development of blue-green filamentous algae, e.g., *Phormidium*.

Snogeholmsjön. The lake has in spring quite another appear-

ance than Ellestasjön. The epilithic algal vegetation is very abundant. *Ulothrix zonata* forms a brightly green or nearly blue-green belt on all sorts of substrata close to the water-line. Especially below the castle the zone is very well marked. When *Ulothrix* has disappeared, a vegetation of *Stigeoclonium* sp. and *Draparnaldia plumosa* is to be seen in very shallow water at the same locality. The abundance varies from year to year. At this time *Cladophora* also begins to grow. The attached form *glomerata* is usually well represented on the stones round the lake and remains the whole summer. *Cl. fracta* is also common. *Cladophora aegagropila* probably occurs on stones outside the most shallow zone, although the author has not succeeded in finding it attached. In August 1949, however, large algal masses drifted around in the northern part of the lake, which contained chiefly *Cl. aegagropila* and *Rhizoclonium hieroglyphicum*. In summer the macroscopic algal vegetation on the stones is insignificant apart from encrusting forms. In autumn a green *Spirogyra* zone may be observed on the stones near the water-line. *Hildenbrandia* is met with only on the western side of the lake. The number of reed epiphytes is both quantitatively and qualitatively insignificant.

Sövdeborgssjön. The lake has a sheltered position and no typical exposed shore exists. A *Ulothrix* zone is also absent. *Cladophora* occurs attached to piles intermingled with *Spirogyra*. In the calm bays one can find thick algal tangles consisting of, among others, *Mougeotia*, *Spirogyra* and *Zygnema*. The epiphytic vegetation on reeds is rich. The following species are dominants: *Gloeotrichia* cfr *Pisum*, *Tolypothrix tenuis*, *Stigeoclonium* sp., *Chaetophora elegans*, *Ch. incrassata*, *Schizochlamys gelatinosa*, *Rivularia Biasoletiana* and filamentous *Conjugatae*.

Sövdesjön. The *Ulothrix* zone is well marked in that part of the lake situated at the village Sövde and the hill Salsbjer. Already in the early spring *Stigeoclonium tenue* is found among the *Ulothrix* threads. Later on the species becomes very dominating with a prominent maximum in autumn. Both the attached forms and the floating form of *Cladophora* (*Eucladophora*) are commonly seen. At Salsbjer *Cl. glomerata* can attain an appreciable length (more than 40 centimetres). Sövdesjön can with good reason be called a *Cladophora* lake. *Cl. glomerata* remains throughout the summer, even if the quantity varies from year to year. *Cl. fracta* has its greatest maximum during the hot season. In a depth of 5 to 6 decimetres the stones in the southern part of the lake are coated with *Cladophora aegagropila*. *Hildenbrandia* occurs at the



same depth. The epiphytic vegetation on reeds is apparently monotonous and insignificant. *Stigeoclonium tenue* and *Stigeoclonium* cfr *farctum* are to be found in enormous masses. Otherwise mainly microscopic blue-green algae difficult to identify are present. Sometimes *Oedogonium* sp., *Coleochaete orbicularis* and *Gloeotrichia Pisum* have been recorded. The latter may occur in large quantities on submerged plants, preferably *Potamogeton pectinatus*.

H e l j e s j ö n. The main part of the algal studies were carried out in 1949, when the lake had already been considerably lowered. Of course, the change in the water-level caused a disturbance in the development of the littoral algae. The normal shores were dried up and did not afford suitable conditions for the algae concerned. Consequently, the information of the normal algal flora is somewhat imperfect.

Probably the *Ulothrix* zone has not been especially prominent. It seems to have developed later than is generally the case in the lakes studied. At the end of May 1948 *Ulothrix zonata* as well as *Draparnaldia plumosa* grew on the stones at a depth of 0 to 10 centimetres, whereas in April none of the species were present. *Cladophora fracta* and *Cladophora glomerata* were recorded at the same time in May, likewise a rich development of *Chaetophora elegans*. In 1949 the algae mentioned were lacking with the exception of isolated tufts of *Ulothrix zonata*. In the bare-laid sandy shore zone, which was still wet, there was a rich algal growth of *Zygnema*, *Spirogyra* and *Ulothrix tenuissima* in the puddles. The submerged aquatic plants are in summer tangled in algal masses, containing the usual species of *Spirogyra*, *Zygnema*, *Oedogonium*, *Mougeotia* et al. *Spirogyra* cfr *communis* may at times have an immense distribution. The lake is also distinguished by an abundant epiphytic vegetation on reeds: *Tolypothrix tenuis* (frequent), *Coleochaete orbicularis*, *Rivularia Biasoletiana*, *Gloeotrichia Pisum*, *Chaetophora elegans*, *Ch. incrassata* and other macroscopic algae.

V o m b s j ö n. The lake has not yet been stabilized after the radical lowering in 1944 and will probably not be so completely, as the water-level can be regulated at will by the waterworks of Malmö. The conditions for the algal vegetation in the shallow zone have been changed. An investigation of this zone can only give an idea of the composition of the species present and very little of their natural distribution in the lake.

No *Ulothrix zonata* zone has been definitely established in the parts of the lake, visited in spring. *Stigeoclonium tenue* is, however, in April widely spread on stones and plants along the northern shore at the



boathouse of the Malmö Sportfiskeklubb. At this time and later on in May one can also find *Draparnaldia plumosa*. Usually the development of diatoms is immense. At the mouth of a small brook there is a green belt of *Ulothrix aequalis* on the stones. The alga has another maximum in autumn. Already in April *Cladophora* forms appear, floating as well as attached. They attain an abundant development. *Cladophora aegagropila* has a wide distribution. By the lowering it has been brought near the water-surface, and at exceptional low water it is laid bare. *Hildenbrandia* has been noted at the stony shore along the railway in the north. The reed epiphytes, hitherto studied, have been poorly developed and comprise only few species. Dominating are diatoms and *Stigeoclonium* spp. (*i.a. farctum*).

K r a n k e s j ö n. The algal vegetation was not investigated before the lowering in 1944. No *Ulothrix* zone has been observed. *Cladophora fracta* may cover large areas among the higher aquatic plants. *Cladophora aegagropila* occurs on stones, now situated only one or two decimetres below the water-surface. The stones close to the water-line are covered with a thick blue-green calcareous crust. Moreover, on these stones also *Rivularia Biasoletiana*, *Tolypothrix tenuis*, *Chaetophora incrassata* and *Spirogyra* sp. are to be found. The sessile algae of the reeds do not include many species. *Spirogyra* constitutes a common element. Other components are *Coleochaete orbicularis*, *Bulbochaete*, *Chaetophora elegans*, *Cladophora*, *Mougeotia* and *Oedogonium*. Among the large quantities of submerged plants, chiefly *Ceratophyllum demersum*, *Potamogeton crispus* and *Myriophyllum spicatum*, which inhabited the lake in 1948 and 1949 there was an important growth of filamentous algae. *Spirogyra* and *Cladophora fracta* were dominants, but many others were included, *e.g.*, *Oedogonium*, *Mougeotia*, and *Zygnema*. In 1944 and 1945 a considerable part of the bottom towards Silvåkra was covered with a mat of *Oscillatoria princeps* f. *maxima*.

G y l l e b o s j ö n. When a thin ice covers the surface, the *Ulothrix* zone begins to develop. It remains to the end of April. During the early growth period (January to February) filaments, the cells of which contain only one pyrenoid, are to be found together with typical *U. zonata*. When gathered, they were considered to be young forms of the latter. It is however, possible, that they may belong to *U. rorida*, discussed by LIND (1932). According to this investigator that species mostly occurs together with *U. zonata*. In the *Ulothrix* zone *Draparnaldia plumosa* and a *Stigeoclonium* with long seta (*longipilum* ?) often grow. The former had in May 1949 a very pronounced maximum and colonized diverse

substrata in large beautiful individuals. In May the *Cladophora* zone begins to develop on stones and walls. *Cl. fracta* drifts about in summer as rather large tangles. The calcareous cover on the stones in shallow water is very important. *Hildenbrandia rivularis* is common along all the stony shores. On the north-western shady shore the red crusts are to be seen even on the upper side of the stones close to the water-surface. Along the north-western shore as well as on the shoal near the hospital stones have been collected by dredging which have been coated with *Cladophora aegagropila*. In this coat also *Rhizoclonium hieroglyphicum* is intermingled. On the shoal mass occurrence of *Tolypothrix lanata* and a *Nostoc*-like *Aphanothece* has been encountered. The reed epiphytes are abundant. The following species are frequent: *Tolypothrix tenuis*, *Chaetophora incrassata*, *Gloeotrichia Pisum*, *Rivularia Biasoletiana*, *Coleochaete orbicularis*, *Stigeoclonium* sp., *Oedogonium* and *Spirogyra*.

T u n b y h o l m s s j ö n. Only in a small area, south-east of the castle, there is an open shore stretch, eroded by the waves. No *Ulothrix zonata* zone has been observed in the lake. The diatom cover in spring is very prominent. On the submerged stones a green-shimmering cover, which proves to be formed by *Ulothrix tenerrima*, grows at the same time and extends out to a depth of at least one to two decimetres. Neither *Cladophora* nor *Draparnaldia* have been noticed in the lake. *Dr. plumosa* occurs in the outflow. The epiphytic growth is plentiful on reeds as well as on water-lilies. Among the reed epiphytes the following species may be mentioned: *Chaetophora elegans*, *Tribonema*, *Oedogonium*, *Coleochaete pulvinata*, *Hapalosiphon intricatus*, *Nostoc*, *Coleochaete orbicularis*, *Microspora*, *Tolypothrix lanata* and *Gloeotrichia Pisum*.

R i n g s j ö n. As far as the macroscopic algae are concerned, no division of the lake into the three parts is necessary. In the large area of the lake the winds move more freely than is the case in the remaining lakes. The open shores become strongly exposed to wave action. The *Ulothrix* zone has an extensive horizontal distribution in all parts of the lake, but most well marked in Eastern Ringsjön (figure 7). It disappears, however, rather rapidly. As early as in the beginning of May there is very little left. Probably this fact is due to the sudden lowering of the water-level, which must be especially pronounced on the gently sloping shores of Ringsjön (cf. LUNDH 1951 a). After desiccation the blue-green *Ulothrix* belt passes over into a white calcareous zone (figure 8), which probably has the same origin as that of the lakes in Holstein (SAUER 1937, ROLL 1939 b, KANN 1940 *et al.*). Similar white zones may be



Fig. 7. Eastern Ringsjön at Fogdarp. The stones are covered with a belt of *Ulothrix zonata*. Below the water-level the algae are still living but are discoloured by brown diatoms. Above the water the zone is dry and white coloured. 15.5.1948.

seen in several other lakes, for example Börringesjön, Råbelövssjön and Levräsjön, but nowhere is it so marked as in Ringsjön. *U. zonata* extends rather deeply out to at least 4 decimetres. *Stigeoclonium* sp. and *Draparnaldia plumosa* are at times seen together with *U. zonata*. They remain for a longer time. The diatom production in spring is abundant. *Cladophora glomerata* as well as *Cl. fracta* occur in large quantities. The best developed attached patches of *Cladophora* are to be found in strongly exposed stony shores, for example at the points.

On the stones some decimetres below the surface and probably also much deeper *Hildenbrandia* is frequent. *Cladophora aegagropila* apparently does not appear until a greater depth, as it has only been collected by dredging. It seems, however, to be fairly widespread. At the same depth as *Cl. aegagropila* *Cl. basiramosa* is found. It has so far been seen only in sparse filaments on the stones. *Rhizoclonium hieroglyphicum* grows rather frequently together with *Cl. aegagropila*. The alga observed in the drifting *Cl. fracta* tangles is probably the same *Rhizoclonium* species.



Fig. 8. View from Eastern Ringsjön at Fogdarp illustrating the white belt of limy remains of *Ulothrix zonata*. 18.5.1947.

On the stones at such a great depth as 60 to 70 centimetres it is possible to find *Chaetophora elegans*, *Coleochaete orbicularis* and *Rivularia Biasoletiana*, that is species, which in the turbid lowland lakes only colonize the most shallow zone. *Nostoc sphaericus* and *Hildenbrandia* are seen in a similar situation. Many other epilithic algae occur in shallow water, for example, *Tolypothrix tenuis*, *Chaetophora incrassata*, *Schizochlamys gelatinosa*, *Stigeoclonium* sp. and *St. farctum*. The stones are often coated with a thick calcareous crust, containing several blue-green algae, e.g., *Rivularia* and *Calothrix*. A sterile *Spirogyra* sometimes forms a green belt on the stones at the same depth as *Cladophora glomerata*. As the reedswamps are relatively few and thin, only a small number of samples of the epiphytic vegetation has been collected. *Stigeoclonium* spp. (i.a. *farctum*) are very widespread, and in addition the following typical species are frequent: *Coleochaete orbicularis*, *Gloeotrichia Pisum*, *Chaetophora elegans*, *Ch. incrassata* etc.

The most striking feature of the algal vegetation is the mass development of filamentous algae on the bottom and among submerged plants.

In summer all higher vegetation is at several places entangled in choking algal threads. In Western Ringsjön *Cladophora* is the chief component, but the genera *Oedogonium*, *Spirogyra* etc. are also represented. In Eastern Ringsjön and especially in Sätöftasjön *Oedogonium* plays the greatest part, even if also *Cladophora* and *Tolypothrix lanata* are included in the offensive algal masses.

D a g s t o r p s s j ö n. *Ulothrix zonata* is absent, but in early spring the stones are covered with a beautifully green-shimmering mat of *U. tenerrima* out to a depth of about 2 decimetres. *Chaetophora elegans* grows in small cushions on stones and reeds at that time. On the shady southern shore the algal growth is insignificant with the exception of diatoms. In May *U. tenerrima* disappears leaving no trace. In the diatom coat on the stones a *Stigeoclonium* species is to be found. On the northern boulder-rich shore *Draparnaldia glomerata* grew in May 1948 at the mouth of a runnel. No *Cladophora* species have been encountered. In summer the stones are provided with a thick green zone of *Spirogyra*. The epilithic vegetation in summer comprises *i.a.*, the following species: *Tolypothrix tenuis*, *Rivularia borealis*, *Tribonema* sp., *Chaetophora elegans* and *Coleochaete orbicularis*. The reed epiphytes are readily seen to the naked eye. Several species are included, *e.g.*, *Coleochaete orbicularis*, *Gloeotrichia Pisum*, *Stigeoclonium farctum*, *Chaetophora elegans*, *Stigeoclonium* sp. and *Coleochaete pulvinata*.

K v e s a r u m s s j ö n. As in the preceding lake a macroscopical *Ulothrix zonata* zone is absent. Single microscopic filaments have, however, been found. In April the stones are covered with a short coat of *U. tenerrima*. The development of diatoms is very rich at this time. *Chaetophora elegans* is also a frequent epilithic alga. Later on *Cladophora fracta* is rather common among the higher plants in shallow water together with *Oedogonium*, *Mougeotia* and *Spirogyra*. In summer a belt of *Spirogyra* appears on the stones out to a depth of a few decimetres.

By dredging it has been established that *Cladophora aegagropila* grows on the stony bottom in the northern part of the lake. It is also to be found on shells of *Anodonta*. The epiphytic vegetation on reeds is not especially conspicuous. The following species are the most dominant components: *Chaetophora elegans*, *Coleochaete orbicularis*, *Batrachospermum moniliforme*, *Stigeoclonium farctum*, *St.* sp., *Bulbochaete* and several filamentous green algae.

T j ö r n a r p s s j ö n. Also here a *Ulothrix zonata* zone is absent. It is replaced by a green cover of *U. tenerrima*. A mucilaginous *Stigeoclo-*

nium sp. and *Chaetophora elegans* are also easily observed in spring. *Batrachospermum moniliforme* is on account of its grey-brown colour more difficult to distinguish from the diatom cover. *Tetraspora gelatinosa* sacks are frequent at a depth of about one decimetre. In summer the stony shores are provided with a *Spirogyra* belt, which to a certain extent resembles the *Cladophora* zone in a lowland lake.

*Cladophora aegagropila* has probably a wide distribution in the lake, but does not occur in the shallow zone. In the calm bays large masses of algae cover the water-surface. They are composed of filamentous *Conjugatae*, *Oedogonium*, *Tolypothrix lanata* etc. In samples from these algal communities *Nodularia spumigena* var. *maior* has been recorded. This blue-green alga is not listed from the other lakes investigated. The epiphytic vegetation on the reeds is abundant. Among others the following species occur: *Tolypothrix* sp., *Chaetophora elegans*, *Coleochaete orbicularis*, *Coleochaete pulvinata*, *Gloeotrichia Pisum* and *Stigeoclonium farctum*.

B o s a r p s s j ö n. The lake is poor in species of macroscopic algae as well as macrophytes on the whole. In spring a green algal cover is never developed. Diatoms are present but not in apparently large quantities. In brooks and ditches running into the lake one can find such species as *Draparnaldia glomerata*, *Tetraspora gelatinosa* and *Ulothrix tenerrima*, but on the lake shores no macroscopic green algae have been observed at all at this time. As in the three last-mentioned lakes a green thick coat of *Spirogyra* is present in summer. The alga has never been seen fertile. In the hot season the lake is also characterized by a high production of *Oedogonium*, which may sometimes entirely cover the higher aquatic vegetation in shallow water. The epilithic vegetation is poorly developed. Only *Chaetophora elegans*, *Tolypothrix* sp. and *Hormidium* sp. have so far been encountered. The number of epiphytes on reeds is also small.

F i n j a s j ö n. The description is founded upon a hasty investigation. As the lake has not been visited in spring, it is not known, whether or not a *Ulothrix zonata* zone occurs. *Cladophora fracta* is included in the floating algal masses, similarly as in Kvesarumssjön. A form attached to reeds has also been found. The main part of the drifting algae consists of *Oedogonium* as in Bosarpssjön. In deeper water *Cladophora aegagropila* seems to have a rather wide distribution. *Cladophora basiramosa* may occur on the same stones as *Cl. aegagropila*.

R å b e l ö v s s j ö n. *Ulothrix zonata* forms in spring a green belt on the exposed shore at the limestone quarry Balsvik. Otherwise the alga



is not especially macroscopically apparent. *Stigeoclonium* sp. is often intermingled. As early as in April small brown tufts of *Cladophora glomerata* are to be found below the *Ulothrix* zone, which is about 1 to 2 decimetres wide. On the large stones at Ekestad no distinct *Ulothrix* zone is to be seen at this time, but *Cladophora* may be well developed. The dark-brown diatom cover also strikes the eye. In May the *Ulothrix* zone is generally still green, especially in the vicinity of the large spring at Balsvik. Below the *Ulothrix* zone the *Cladophora* tufts are developed still more. *Draparnaldia plumosa* and *Chaetophora incrassata* are now intermingled in the algal vegetation. At Ekestad *U. zonata* begins to degenerate, and a rather distinct *Draparnaldia* zone is to be seen just above the *Cladophora* zone. At the western shore near Balsberget, fringed by beeches, no *Ulothrix* has been observed, and *Cladophora* forms only a narrow belt, which downwards is replaced by *Spirogyra*. A similar *Spirogyra* zone is also noted at Ekestad. Generally *Cladophora* remains throughout the summer but becomes brown from diatoms.

On the stones at a depth of more than 2 metres masses of *Cladophora aegagropila* have been found. At Balsvik it may also grow in so shallow water, that it can just be reached by hand. In turbid lakes it occurs mostly still nearer the water-surface. *Hildenbrandia* on the other hand is to be found close to the water-surface, even on the upper parts of the stones.

In summer a rich epilithic vegetation inhabits the stones in shallow water. Cushion-like algae are very common, for example, *Rivularia Biasclettiana*, *Pleurocladia lacustris*, *Chaetophora elegans* and *Nostoc sphaericus*. The reeds are also characterized by an abundant algal vegetation. Among others the following species have been listed: *Gloetrichia Pisum*, *Coleochaete orbicularis*, *Chaetophora* cfr *pisiformis*, *Pleurocladia lacustris*, *Rivularia Biasclettiana*, *Chaetophora incrassata* and *Ch. elegans*.

O p p m a n n a s j ö n. The two localities most investigated are Kiaby and Norregård.

At Kiaby a *Ulothrix zonata* zone is developed in spring close to the water-line on stones, twigs, wood and so on. *Draparnaldia plumosa* and *Stigeoclonium* sp. are also included in the vegetation at this time, preferably colonizing living plants. A strong production of diatoms is also typical for April. In May the algal flora is immensely rich qualitatively as well as quantitatively. *U. zonata* is still partly there, and *Cladophora glomerata* and *fracta* occur in large quantities. *Draparnaldia* attains now its maximum, and *Stigeoclonium* is also frequent. *Tetraspora*

*gelatinosa* forms large green sacks on the bottom and plants. In the low reedswamps near a brook the plants are covered with a blue-green coat of *Ulothrix tenuissima*.

Below the farm and the starch factory at Norregård the green *Ulothrix* zone is visible in April at a distance. It is about 2 decimetres wide. Also here a mass production of diatoms is to be seen. In May a *Draparnaldia* zone is added below the *Ulothrix* belt. *Cladophora fracta* as well as *glomerata* are common.

At a depth of 20 to 30 centimetres *Cladophora aegagropila* begins to appear accompanied by *Hildenbrandia* on the lower parts of the stones at Norregård. Somewhat deeper the same alga grows at Kiaby together with long threads of *Rhizoclonium hieroglyphicum*.

In summer the stones close to the water-line are covered with calcareous crusts, especially conspicuous at Norregård. The most common epilithic algae are *Schizochlamys gelatinosa*, *Rivularia Biasolettiana*, *Stigeoclonium farctum*, *Chaetophora elegans* and *Ch. incrassata*. The composition of species is very much the same at the two localities. At Norregård also *Pleurocladia lacustris* is noticed.

The reeds are likewise coated with a gelatinous greyish yellow calcareous covering containing diatoms. The number of other macroscopic epiphytes is surprisingly small. At Norregård the epizoic species predominate. Among the most constant epiphytes the following may be mentioned: *Coleochaete orbicularis*, *Tolypothrix tenuis* and *Chaetophora elegans*.

Levräsjön. On the exposed eastern shore there occurs in spring a well marked *Ulothrix* zone. In May it disappears gradually and is now intermingled with *Stigeoclonium* sp. The dry *Ulothrix* zone stands out as a white belt. Next below comes a *Draparnaldia plumosa* zone, 1 to 2 centimetres wide. *Draparnaldia* may occur in large quantities and grows on stones, wooden pegs and other dead objects. Tufts of *Stigeoclonium* sp. are also widespread at this time. A *Cladophora* zone is present below the *Draparnaldia* belt. Sometimes *Spirogyra* is to be seen below the *Cladophora* zone.

The stones in shallow water are covered with calcareous crusts and colonized by several algal species, e.g., *Rivularia Biasolettiana*, *Pleurocladia lacustris*, *Chaetophora elegans*, *Ch. incrassata*, *Schizochlamys gelatinosa*, and moreover, long *Schizochlamys*-like gelatinous colonies of diatoms. By dredging stones and *Anodonta* shells have been collected, bearing *Cladophora aegagropila*. At a depth of 2 metres *Cl. basiramosa*

grows very sparsely and is hardly visible on stones, which on the top are coated with *Cl. glomerata*.

The submerged plants, for example the *Characeae*, are woven over with algal masses containing *Cladophora*, *Rhizoclonium et al.* On the western shore large algal tangles float on the water-surface, sheltered by the reedswamps. They are composed by *Spirogyra*, *Zygnema*, *Cladophora et c.* On the bottom made up of lake-marl blue-green algae, for example *Anabaena cylindrica*, form mats.

The epiphytes on reeds are abundant. *Pleurocladia* is very dominant, and in addition the following species may occur: *Tolypothrix tenuis*, *Chaetophora elegans*, *Coleochaete orbicularis*, *Cylindrospermum* cfr *stagnale*, *Gloeotrichia Pisum* and *Rivularia Biasoletiana*.

S i e s j ö n. On the whole no typical exposed shores are to be found in the lake because of its sheltered position. Therefore, the absence of algal zones characteristic of such habitats is not surprising. *Ulothrix zonata* occurs only in microscopic threads. *Cladophora glomerata* has a very limited distribution. *Draparnaldia plumosa* has only been observed at one locality, where it, however, in May—June 1948 exhibited an abundant development.

As could be expected, *Cladophora fracta* is a common algal species. Characteristic is also a mass occurrence of *Chaetophora incrassata*. During the summer 1948 gelatinous colonies of *Aphanothece prasina* the size of plums, floated among water-plants at the water-line. Also *Tetraspora gelatinosa* was a frequent species in the late spring this year.

The epilithic algae include the common species, typical for the majority of the lowland lakes (table 2). The epiphytic vegetation on reeds is very abundant. The species recorded are the same as in the other lakes with a similar location. *Batrachospermum moniliforme* occurs on both stones and plants. In the calm sections with rich submerged vegetation the development of filamentous algae is enormous. *Spirogyra* predominates in the algal masses, which otherwise include *Cladophora*, *Mougeotia*, *Zygnema* and *Tolypothrix tenuis*.

V ä s t e r s j ö n a n d R ö s j ö n. Stony and exposed shores are common. In both lakes *Ulothrix zonata* belts are to be found in spring, but they are most extensive in Västersjön. In Rösjön the macroscopic occurrence is restricted to a short part of the northern shore on both sides of a runnel. Single microscopic threads are probably intermixed in the algal vegetation even at other localities. When the water-surface is lowered at the end of May the *Ulothrix* zone may be recognized as a

grey to white border. The most common followers of *Ulothrix* are even here *Draparnaldia* and *Stigeoclonium*. (They also constitute important elements in the vegetation of the brooks.) In spring the stones are covered in many places with a green coat of *Ulothrix tenerima*.

*Cladophora glomerata* and *fracta* seem to be absent. *Cladophora aegagropila*, gathered by dredge from a depth of some metres, has a wide distribution, especially in Västersjön. *Nostoc Zetterstedtii* sometimes lies on the shores washed up in large quantities.

Among the submerged plants and on the bottom an immense development of *Zygnema*, *Spirogyra*, *Oedogonium* etc. is to be found, which recalls the conditions in Säftasjön and Bosarpssjön.

The epilithic as well as the epiphytic vegetation comprise partly other species than those in the preceding lakes, especially the lowland lakes, only some of which have been identified here. On the stones the blue-green algae predominate, e.g., *Dichothrix* sp., *Stigonema* sp., *Pleurocapsa* sp., *Rivularia borealis*, and *Oscillatoria splendida*. Of the green algae *Chaetophora elegans* is very frequent. The reed epiphytes include some species, well known from the lakes mentioned previously, e.g., *Gloeotrichia Pisum*, *Coleochaete pulvinata*, *C. orbicularis*, and *Stigeoclonium farctum*. Such a mass development of *Chamaesiphon* sp. has, however, never been seen in the other lakes studied.

### Some aspects of the distribution of the algae studied.

In table 2 a survey of the algae best studied are given. In addition to the preponderating macroscopic forms some microscopic algae are also included, but only those readily observed and identified.

Among the Myxophyceae the following species seem to be ubiquitous within the area investigated: *Gloeotrichia Pisum*, *Tolypothrix tenuis* and *Nostoc cuticulare* (?). Some have a distribution showing no distinct tendencies. Others are known from too few localities to be classified. One species, however, is apparently restricted to group A, namely *Rivularia Biasolettiana*. *Rivularia borealis* is possibly confined to groups B and C. *Stigonema* sp. and *Pleurocapsa* sp. belong to group C. On the whole, the number of blue-green algae determined is too small to permit a characterization of the lakes. One can, however, trace a certain groupage of them, as *Rivularia Biasolettiana* disappears as soon as the lakes are situated on Archaean rocks. The blue-green algae are numerous represented in all the lakes, mainly microscopic forms, and







a specialized investigation on their distribution would certainly give elucidating contributions to the characterization of the lake types.

Two fairly large *Nostoc* species have been recorded in the lakes studied, viz. *N. Zetterstedtii* and *N. sphaericum*. The former has long been known from so-called oligotrophic lakes (cf. e.g., THUNMARK 1931 and LILLEROTH 1950 b). It is restricted within the area investigated to Västersjön and Rösjön, where it, however, appears in large amounts. The latter grows as rather small cushions (up to 5 millimetres) on the stones in Råbelövssjön and Ringsjön within a zone below the water-surface down to a depth exceeding 70 centimetres in the first-mentioned lake and 50 centimetres in the last-mentioned. On the other hand, *Nostoc pruniforme* has not been observed. This alga is registered from Swedish localities by, among others, WAERN (1938) and STÅLBERG (1939). KANN (1940) reports it from Grosser Plönersee. According to these authors it can occur both epilithically and epiphytically.

Among the Chlorophyceae the following species are apparently ubiquitous: *Chaetophora elegans* (collective species?), *Cladophora aegagropila* (collective species?), *Coleochaete orbicularis*, *C. pulvinata*, *Hormidium subtile*, *Tetraspora gelatinosa* (probably a collective species in the sense of the author) and *Ulothrix zonata*. *Rhizoclonium hieroglyphicum* is also possibly ubiquitous, but it has been too little observed perhaps on account of the fact that it has been overlooked. *Geminella interrupta* and *Schizochlamys gelatinosa* seem to be confined to group A.

A distinct borderline is to be found between the lakes as far as the green alga-flora is concerned, namely the *Cladophora*-limit. *Cladophora* denotes here *Cl. glomerata* in a wide sense comprising all the species of *Eucladophora*. Generally one can find both attached and floating *Cladophora* forms in the same lake, if otherwise suitable habitats are available. Only in Kvesarumssjön and Finjasjön is it somewhat uncertain whether *Cladophora glomerata sensu strictu* is really to be found. The latter lake is, however, poorly studied. The *Cladophora* limit does not entirely coincide with the distinct macrophyte limit between group A and B, as it is observed in two lakes belonging to group B (Kvesarumssjön and Finjasjön). These two lakes, however, deviate somewhat even as regards the higher vegetation and the hydrochemistry from the others within the group (cf. p. 18, furthermore LUNDH 1951 b and ALMESTRAND 1951).

A distribution on the whole agreeing with that of *Cladophora* discussed above is distinctive of the following algae: *Cladophora basiramosa*, *Chaetophora incrassata* and *Draparnaldia plumosa*. The localities known are, however, not numerous enough for the formulation of

definitive conclusions. A *plumosa*-like *Draparnaldia* has been noted in Rösjön, but otherwise *Dr. glomerata* seems to predominate in the Archaean lakes, if one judges from the somewhat uncertain determinations of the species. It is in any case obvious that the typical *plumosa*, such as it appears in the rivers and brooks of the lowland, does not occur in the brooks debouching in the Archaean lakes investigated.

The epiphytes frequently occurring on *Cladophora*, *Aphanochaete repens* and *Uronema confervicolum*, which have been included in the table 2, as they are easy to recognize, grow also on *Oedogonium*. Therefore, findings are present even from lakes lacking *Cladophora*.

*Ulothrix zonata* may occur in all the three groups. It is notable that within group B it has not been found growing in macroscopic belts (with the reservation for Finjasjön, which has not been visited in spring). In Rösjön it appears as patches visible to the naked eye only at one locality below a runnel. In Västersjön the alga has a rather wide distribution along the northern shore.

*Ulothrix zonata* grows mostly on more or less exposed stretches of stony shore. When it exhibits a maximal development it inhabits not only stones, but also sand grains, water-plants and all kinds of dead objects lying in the water, *e.g.*, bricks, bottles and so on. According to OBERDORFER (1928) the alga seems to be favoured by contaminated water. Its occurrence within the area investigated does not directly contradict this assumption, as most of the lakes are more or less polluted. The lowland lakes, where it is absent, are, however, not at all less contaminated than the others. It is apparent that *Ulothrix* in several cases, where it has a limited distribution, for example in Börringesjön and Ellestasjön, is distinctly restricted to the mouths of runnels (and covered drains). It is rather futile to discuss the possible causes of this fact without knowing the ecological requirements of the alga and without possessing exact analyses of the factors that might be involved. It must then be borne in mind that also other factors than those generally suggested, *e.g.*, the supply of oxygen and the water temperature, may be included. The content of carbon dioxide or the occurrence of minimal amounts of more or less unknown substances may be involved. Such studies, however, are beyond the scope of this investigation. It is in any case clear that flowing water or spring water is in some manner appropriate for the growth of *Ulothrix*, as the tufts remain for the longest time around the very mouth of the runnel or the spring. In 1949 the alga grew throughout the summer close to the spring at Balsvik in Råbelövssjön. In the Scanian lakes the *Ulothrix* belts disappear in May,

but in Vättern (STÅLBERG 1939 and private communication) and Hjälmaren they are still green as late as in July. Information on the occurrence of *Ulothrix* in June is to be found in the literature (BRUTSCHY 1922 and GODWARD 1937).

According to FJERDINGSTAD (1950) *U. zonata* is composed of two ecological strains. As far as the author is aware, the distribution in the Scanian lakes gives no certain proofs of the assumption that two forms are included, but the possibility is not excluded.

Concerning the distribution of the green algal species not mentioned above no reliable conclusions can be drawn on account of the insufficient number of localities.

Only three genera of Rhodophyceae are listed in the table. *Asterocytis* and *Hildenbrandia* are interesting in this connexion, as they are completely confined to group A. The former appears as a common epiphyte on the *Eucladophora* species. It has also been observed on *Cladophora aegagropila*, and probably it can also inhabit other substrata. Thus the alga would not be restricted to the *Cladophora* lakes, if no other factors checked its growth. It may be noted in passing that Börringesjön and Ellestasjön, both on the whole fairly poor in sessile algae, are characterized by a rich growth of *Asterocytis*. Nor as far as the substratum is concerned do there seem to exist any obstacles for the spreading of *Hildenbrandia* within the entire area investigated. *Batrachospermum* is only poorly represented in the lakes studied. *B. moniliforme* shows a ubiquitous tendency, whereas *B. vagum* probably is confined to the lakes on the ridge Hallandsåsen.

Phaeophyceae are rarely seen in the lakes studied. *Heribaudiella fluviatilis*, which has a relatively wide distribution in Central Sweden in flowing water and at least in some lakes (ISRAELSON 1938 and WAERN 1938), is not observed in any lake investigated. ISRAELSON, who has made extensive investigations, has not recorded it from any Scanian locality not even in flowing water, which indicates that it is absent or very little distributed here. *Pleurocladia* does not seem to be so common in the province as might have been expected. According to ISRAELSON (*l.c.*) it occurs within Scandinavia in Uppland and Denmark. KANN (1940) has reported it from North Germany as frequent in Grosser Plönersee, Kellersee and Dieksee. In Scania, however, it will probably not appear to be widespread in the lakes, even if more localities are discovered. In the Kristianstad lakes the alga is now commonly distributed on stones and reeds. The number of localities known is small, but it illustrates rather clearly that the species is restricted to group A.

## Some features of the extra Scanian distribution of the algae confined to group A.

The literature concerning the algae discussed here is not very comprehensive. Only works from areas with a similar climate and geology are considered below. In adjacent regions lake investigations have been performed in L. Ullevifjärden (WAERN 1938), Tåkern (DU RIETZ *et al.* 1939), Vättern (STÅLBERG 1939), Åland lakes (CEDERCREUTZ 1934), Plöner lakes (KANN 1940), Windermere (GODWARD 1937) and Brandenburger lakes (PANKNIN 1941). There are also plant geographical works from the Baltic States carried out by SKUJA (1926—28) and MÖLDER (*i.a.* 1944, 1945 and 1946). Algological works from flowing water are more numerous, for example, CEDERGREN (1938), ANDERSSON-LUNDH (1948), ISRAELSON (1949), FJERDINGSTAD (1950), BUDDE (1930, 1932 and 1935), FRITSCH (1929) and BUTCHER (1932 a and b, 1940 and 1946). The ecological conditions of these two types of water are at least partly of different nature, *e.g.*, as regards the water conversion. For this reason the author has restricted herself to studying the lake literature. Only this can be compared with the results of the present investigation. To the extent that information of the distribution of algae restricted to group A is to be found in the literature, they have generally been noted from calcareous and eutrophic lakes (KANN *l.c.*, WAERN *l.c.* and PANKNIN *l.c.*) or »Potamogeton lakes» (CEDERCREUTZ *l.c.*). As concerns *Geminella interrupta* and *Schizoclamys gelatinosa* information is absent or sparse. The former is registered from Lake Windermere, a lake, which on account of its geological location hardly resembles the Scanian lowland lakes (GODWARD 1937 and PEARSALL 1921). The latter is not listed from any neighbouring lakes, but, on the other hand, it is considered by ISRAELSON (1949) as a differential species for his *Zygnema* type of flowing water. The remaining species discussed here, however, belong to his *Vaucheria* type, which is characterized by a specific conductivity ( $\times 10^6$ ) of more than 60—100. (*Rivularia Biasoletiana* and *Geminella interrupta* are not mentioned.)

*Hildenbrandia*, to which much attention has been given in the last decades, has been observed in many different lake milieus from a depth of 90 metres in Lake Garda (ZIMMERMANN 1928) and 30 metres in Vättern (STÅLBERG 1939) to the most shallow littoral zone in *e.g.*, the Plöner lakes (KANN 1940 and 1945). In brooks and rivers it appears on different substrata and in water of varied qualities (SKUJA 1926, FRITSCH 1929, GEITLER 1932, ISRAELSON 1942 and TARNAVSCHI 1943). The red alga grows, furthermore, also in tropical lakes (RUTTNER 1936). ZIMMERMANN (1928 p. 12) has suggested the possibility that it is a collective species, and STARMACH (1928) has followed this line of thought. The distribution of *Hildenbrandia* in Sweden is apparently confined to electrolyte-rich water (ISRAELSON 1942), thus quite agreeing with the Scanian distribution.

### Results.

The aim of the study of the macroscopic algae has been to establish in what degree the groupage of the lakes according to the composition

of the macrophyte vegetation is substantiated by the algal vegetation. A division of the lakes exclusively according to the algae could not be thought of, as the author is not sufficiently well versed in the algal systematics to be able to identify all the species present. Uncertain determinations should not be published without reservations. A list of species which does not meet this criterion will not make the science richer. As far as these algae are concerned, great experience is required in many instances to be able to determine the correct name of the species. There are probably numerous examples in the literature where different authors have had divergent opinions regarding the same species. (Often most this cannot be proved, as the material is seldom available for re-examination.) Note for example SAUER's and KANN's divergent conceptions of one and the same species (KANN 1945, p. 22). A critical attitude towards one's own determinations as well as those found in the literature is most essential.

In investigations of the foregoing type all material must be classified, even if the specimens are not fully satisfactory or only such stages of development are present that are not furnished with the characters decisive from the systematic point of view. Under such circumstances the defects of the floras available are most obvious. In this case the floras are rather old and their authors often admit that the keys for determination are imperfect. It is very difficult to examine forms, which are not what the taxonomists call typical. A specimen is considered typical by a taxonomist, if it agrees with his idea of the species, which is founded upon the original description once given. To an ecologist a specimen could rather be said to be typical, if it belongs to the form most common in a district, and the typical form of the taxonomist has but a limited value for him. Instead he must know the total variation of the species or rather of the unit with identical ecological requirements.

In ecological investigations it is necessary to work with units with identical ecological requirements (ecotypes according to TURESSON 1922). These do not always coincide with the taxonomical units, the species and its subsections. They must as regards primitive organisms be based preferably upon morphological characters and therefore become to a certain extent subjective. The barrier of sterility cannot be employed. Physiological differences will for that reason be neglected to a large extent.

When trying to arrive at the ecological units in field studies, one must thus, as long as experimental results are not available, not undervalue the importance of slight morphological variations which by the taxonomists are termed, for example, forma or varietas. So-called eurytopic species will possibly

on careful study prove to be composed of two or more ecologically differentiated strains and thus not so indifferent as they appeared.

Even modifications on account of the habitat can also be of value from the ecological point of view. Such morphologically unequal forms should be kept apart, although they are not genetically separated.

It is apparent that several groups of algae are in need of a renewed revision. In this manner the entire related complex of species must be treated at the same time. In addition to the systematic work proper, more importance should be given to the ecological differences which have been observed in field studies, and, furthermore, the possibilities offered by experimental research for the solution of the problem should be utilized. The life-cycle of the species must often be studied by culture experiments. Sometimes a technique has been employed in algological field studies making a certain observation of different stages of development possible. BUTCHER (1932 b) and GODWARD (1934) placed slides in water which were then examined at regular intervals.

An example of the difficulties of the field science in solving an apparently simple species problem is the discussion of the three species belonging to *Eucladophora* (cf. p. 29).

By experimental work it is conceivable that a relationship can be discovered between forms oftenmost habitually well distinguished. USPENSKAJA (1929—30) has, for example, obtained *Stigeoclonium*-like types from *Draparnaldia glomerata* by increasing the nitrate concentration in the nutrient solution.

PRINGSHEIM (1950 a) recommends a co-operation between laboratory and field work. Investigations in Switzerland are also conducted after a similar program. Cf. JAAG (see p. 28) and VISCHER (1950). VISCHER (private communication) emphasizes the importance of trying to obtain ecological units which can be used as indicators of various milieus. It has been proved that habitually very agreeing forms can in agar cultures react in quite different manners and thus are to be considered as ecologically well distinguished types. This coincides completely with the author's opinion that one must carefully differentiate the systematic conception species and the ecological unit, which are not always identical.

The list of species (table 2) comprises not only the species most interesting in this connexion, namely those showing a definitive tendency in their distribution, but also several which have been observed at an insignificant number of localities and therefore are not especially valuable in an eventual groupage of the lakes. They may, however, to a certain extent contribute to a characterization of the lake vegetation



and are perhaps of some interest from a phytogeographical point of view. The algae that have been determined only to the genus, *e.g.*, *Spirogyra* have not been included in the table, as they cannot have either phytogeographical or ecological interest.

It seems, as if there is a special borderline between the lakes of group A on one side and the lakes of group B and C on the other also as regards the macroscopic algae. To group A the following species are almost completely restricted: *Rivularia Biasoletiana*, *Cladophora glomerata*, *Cl. fracta*, *Schizochlamys gelatinosa*, *Pleurocladia lacustris*, *Asterocytis smaragdina* and *Hildenbrandia rivularis*. A similar distribution, but not so well delimited, is characteristic of *Draparnaldia plumosa* and *Chaetophora incrassata*. To group C the following algae seem to be bound: *Pleurocapsa* sp., *Stigonema* sp., *Nostoc Zetterstedtii* and *Batrachospermum vagum*. As among the macrophytes no species are exclusively restricted to group B.

### Ecological remarks.

The macroscopic algae exhibit a groupage of species which in its main features agrees with that of the investigated plant groups previously discussed. The mode of life is similar to that of the rootless submerged macrophytes. Thus they are dependent upon the water for salt absorption as well as for gas exchange. Nutritional physiological studies on these algae seem to be very few. USPENSKI (1927) worked among others with *Cladophora* and concluded that iron is the most important factor determining the distribution of the algae. This fundamental importance of iron has later been doubted (*cf.* p. 94). STEEMANN-NIELSEN (1947) has shown that the photosynthesis of *Cladophora insignis* (?) is badly affected by a slightly acid reaction in the water. Several other plant physiologists have performed investigations on higher algae *i.a.* on the photosynthesis of *Hormidium* and *Cladophora* (VAN DEN HONERT 1930, VAN DER PAAUW 1932, and MANNING *et al.* 1938).

Of the investigations mentioned the experiments by STEEMANN-NIELSEN with *Cladophora* are especially interesting. In the lakes treated other *Cladophora* species are concerned, it is true, but it is possible that the fresh water *Cladophora* species do not differ very greatly. If so, the injurious effect of the acid reaction may explain the distinct *Cladophora* limit within the area studied. The lakes lacking *Cladophora* are those which can have the lowest pH. At the same time they are those most deficient in electrolytes. In conformity with *Myriophyllum spicatum*,

*Potamogeton lucens* and others *Cladophora* is able to utilize bicarbonate for its photosynthesis.

Thus it is possible that a factor related to the calcium bicarbonate content may constitute the limiting factor for the distribution of some higher algae.

### Conclusions.

In spite of the fact that only a small part of the macroscopic algae present has been studied, it has been shown that they seem to be distributed differently in the lake groups. Some species are quite restricted to group A and others exclusively to group C. As regards *Cladophora* experimental evidence indicates that at least this alga is indirectly dependent on the content of bicarbonate in the water. Otherwise the ecological requirements of the algae have been very little studied experimentally.

# Phytoplankton.

## Distribution of the species.

### Material.

The aim of the phytoplankton investigation has been to compare the lakes in order to establish whether or not the differences encountered in their macrophytic vegetation have any correspondence in the plankton

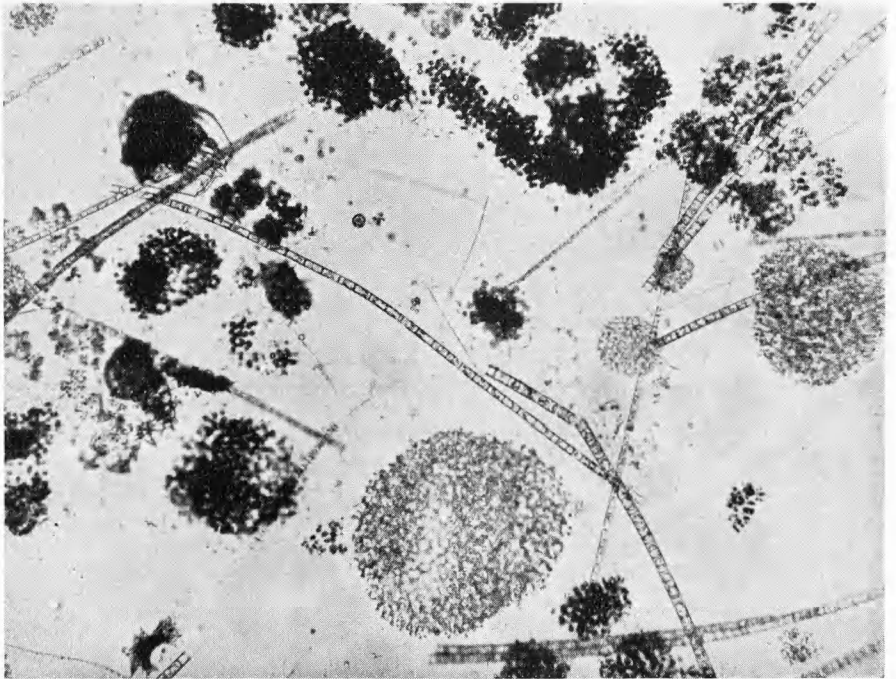


Fig. 9. Plankton from Ellestasjön. The picture is predominated by *Myxophyceae*, especially *Microcystis* species. The narrow, hardly visible threads are *Lyngbya limnetica*. The centric diatom *Melosira ambigua* is also highly frequent. Enl. 115  $\times$ . 6.8.1949.

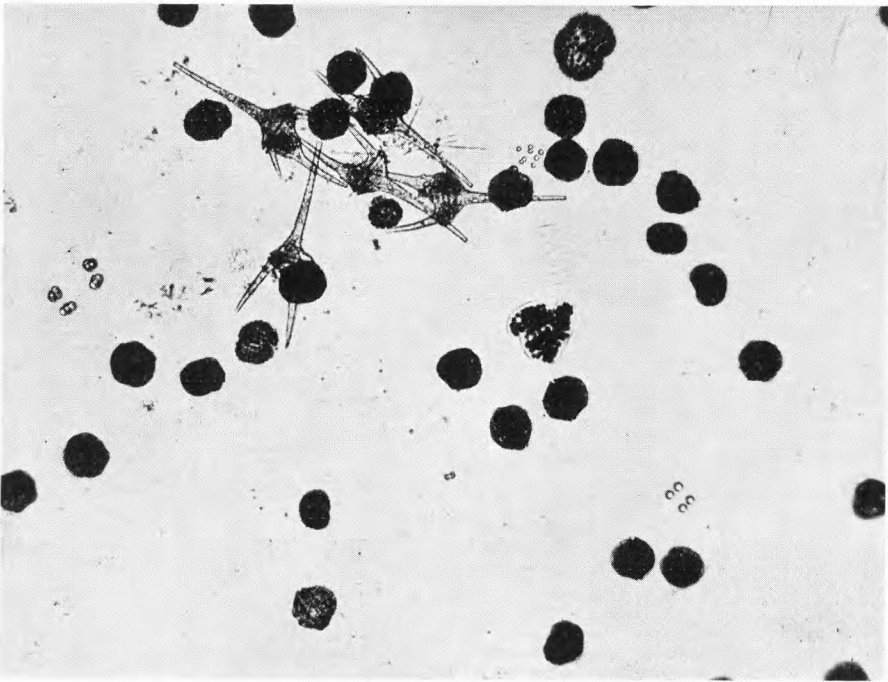


Fig. 10. Plankton from Gyllebosjön. The main components are *Peridineae*, comprising *Peridinium Volzii* and *Ceratium hirundinella*. Enl. 115  $\times$ . 27.8.1949.

vegetation. For this purpose two plankton samples from every lake were treated here, namely one spring sample, gathered in April to May, and one late summer sample, collected during the period late July to early September (with the exception of Havgårdssjön, Heljesjön and Ringsjön), both from the year 1949. A winter sample would have made the list of species more complete, but the sample-collecting has been rather irregular during the winter months. For this reason no winter samples have been examined.

Thus, the samples studied do not contain all the species occurring in the lakes, but they reflect in broad outlines the differences in the composition of the phytoplankton. The species possibly overlooked can naturally reinforce or modify the differences obtained. They cannot, however, completely invalidate the results of the investigation.

The material for examination has been selected so that the samples were as simultaneous as possible. They have been collected from a

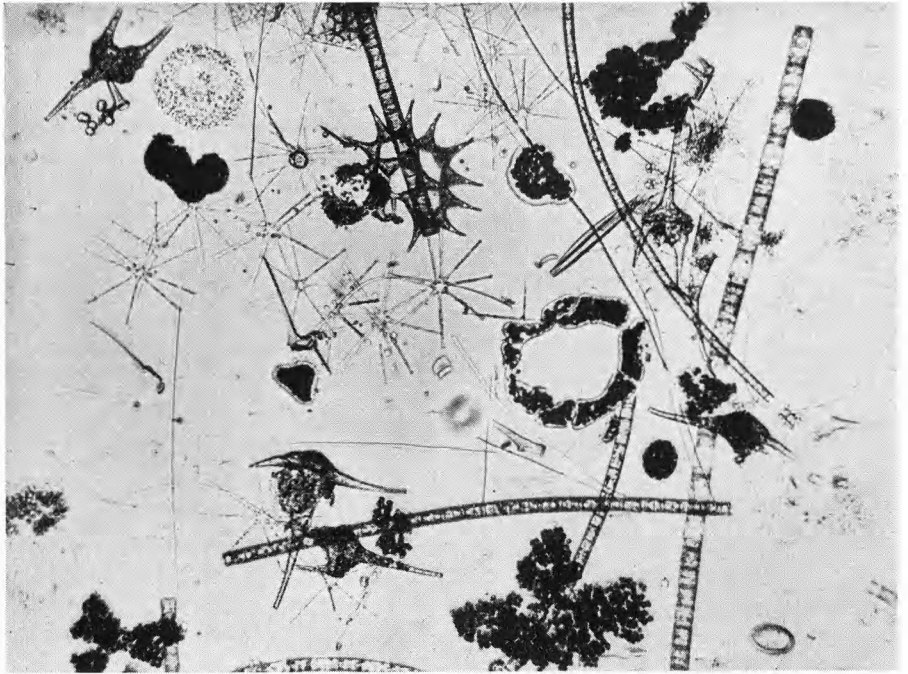


Fig. 11. Plankton from Oppmannasjön at Kiaby. It is very rich in species. The dominants are *Melosira granulata*, *Asterionella formosa* and *Lyngbya limnetica*.  
Enl. 115  $\times$ . 6.8.1949.

boat by a plankton net of Müller silk bolting cloth No. 25 down to a depth of 0.5 metres. Unfortunately it has been necessary to gather them without paying any regard to the weather prevailing. This has brought about a more or less strong contamination by detritus and other suspended matter. In the shallowest lakes the water is always mixed with suspended material, even in calm weather. Such weather is in fact not frequent on the plains. Nannoplankton has not been studied.

In accordance with the plan of the investigation it was important to exclude from the net samples the species which only accidentally occurred there, as these cannot be used in comparative studies. For the same reason it was also necessary to separate under the microscope the organisms that were living at the moment of fixation from dead ones, as far as possible. The diatoms, which often cannot be identified until the cell content has been removed, are probably underrepresented in the sample records, since only those have been listed that have definitely



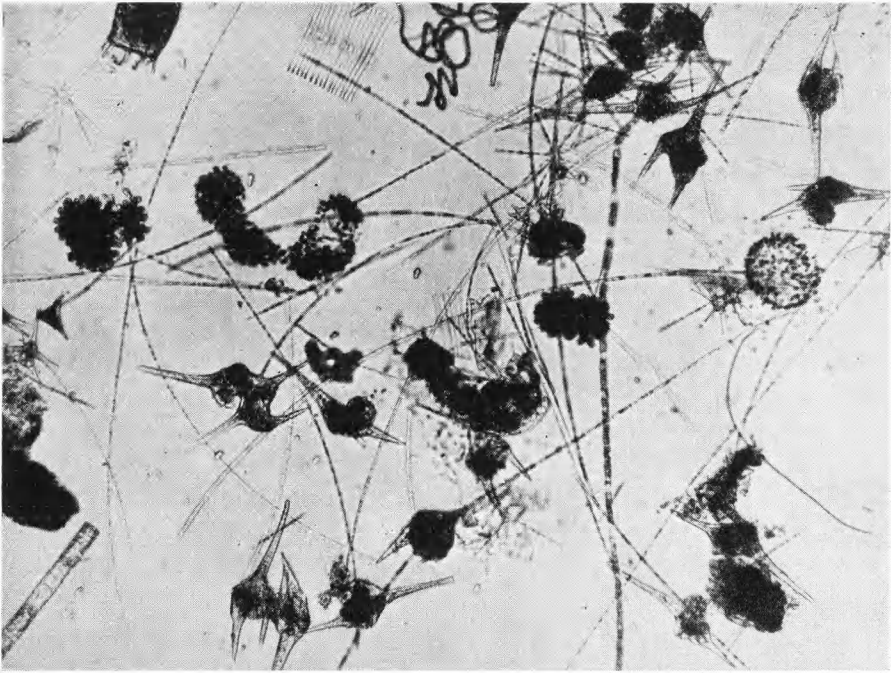


Fig. 12. Plankton from Eastern Ringsjön at Hörby. It is characterized by *Ceratium hirundinella* and a narrow *Melosira* species, *M. granulata* var. *angustissima*. No bundles of the otherwise frequent blue-green alga *Aphanizomenon flos-aquae* can be seen in the picture. Enl. 115  $\times$ . 17.9.1949.

been found living. Rare, small species can in this connexion readily be overlooked.

The samples have been subjected to a preliminary examination before the fixation. The main work has, however, been carried out on fixed material.

#### General survey of the phytoplankton of the lakes.

Almost all the lakes are characterized by a high production of plankton. Svaneholmssjön and Tunbyholmssjön constitute the only real exceptions, and they are also aberrant in other respects (*cf.* LUNDH 1951 b, *i.a.* pp. 31 and 81). In some lakes the strong vegetation turbidity occasionally passes into water-bloom, for example, in Vombsjön, Sövdesjön, Snogeholmssjön, Ellestasjön and Krageholmssjön, which especially in the hot summer of 1947 attained prolonged high production of *Myxophyceae*, preferably species of *Microcystis*. Two of the lakes have in



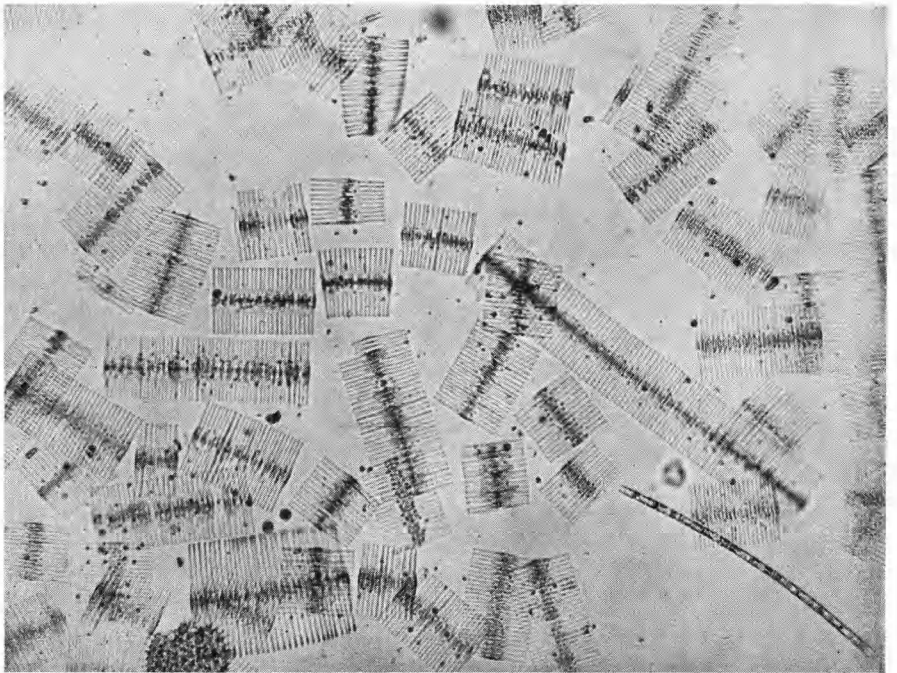


Fig. 13. Plankton from Western Ringsjön. This picture almost resembles a pure culture of *Fragilaria crotonensis*. Another diatom *Melosira granulata* var. *angustissima* also appears highly frequent in the sample. It is impossible to estimate the frequency of the plankters from a single photomicrograph. Enl. 115  $\times$ . 17.9.1949.

summer a rich development of the macroscopically well visible blue-green alga *Gloeotrichia echinulata*, which is otherwise absent in the lakes here discussed. It is, however, recorded from Finjasjön. Water-bloom of *Anabaena flos-aquae* may sometimes occur, e.g., in Kranke-sjön and Råbelövssjön, but it is generally of short duration.

Although the vegetation turbidity is rather well marked in the lakes, there are naturally quantitative variations, which could have been measured by some quantitative method. Such determinations have, however, hitherto not been performed. A more detailed description of the phytoplankton will be given in a later paper.

#### Description of the plankton samples examined.

A net sample was collected from an arbitrarily limited area. In this investigation the area concerned was rather small, and it can therefore

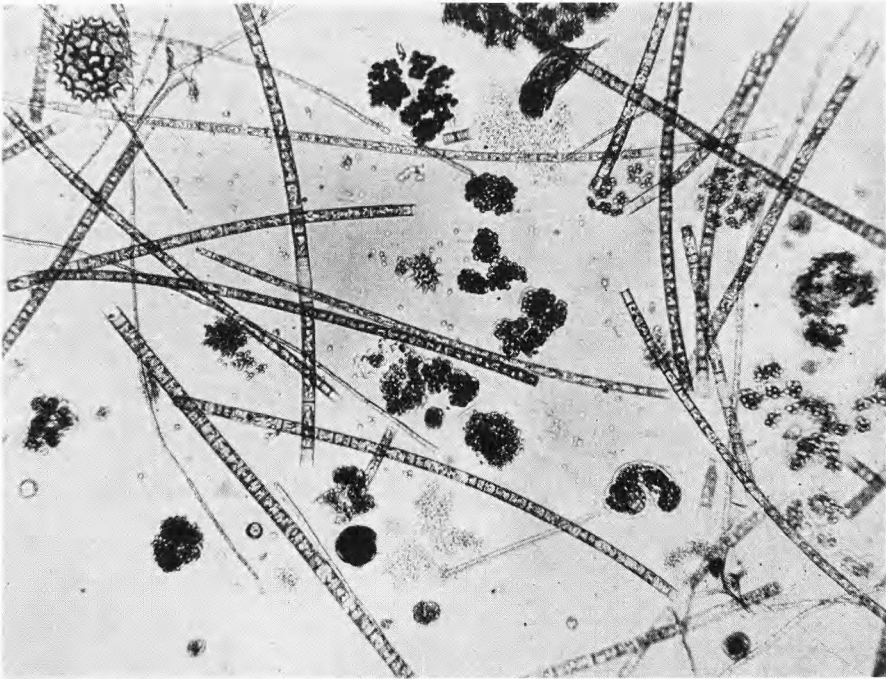


Fig. 14. Plankton from Vombsjön. It illustrates the typical combination of *Melosira granulata* and *Microcystis* species found in many lowland lakes. The narrow threads are formed of *Tribonema* species. Enl. 115  $\times$ . 1.9.1949.

be assumed that its plankton content was nearly homogeneous. The larger the lake surface and the more irregular the shore lines, the greater the probability will be that the plankton content is heterogeneous (*cf.* VERDUIN 1951). The composition of the plankton can be qualitatively as well as quantitatively differentiated in different parts of the lake. Such a large lake as Ringsjön ought to be represented by several net samples. The two samples here dealt with are thus insufficient to afford an adequate picture of the plankton of the entire lake. They give only a preliminary idea of the qualitative composition of the plankton in Eastern and Western Ringsjön. In Oppmannasjön plankton samples are present from two stations, namely Norregård and Kiaby (N. and K. in the tables).

In sociological-planktological literature (THUNMARK 1945 b, NYGAARD 1949 and LILLIEROTH 1950 b) the content of a net sample is considered a plankton community, which is characterized in different manners.

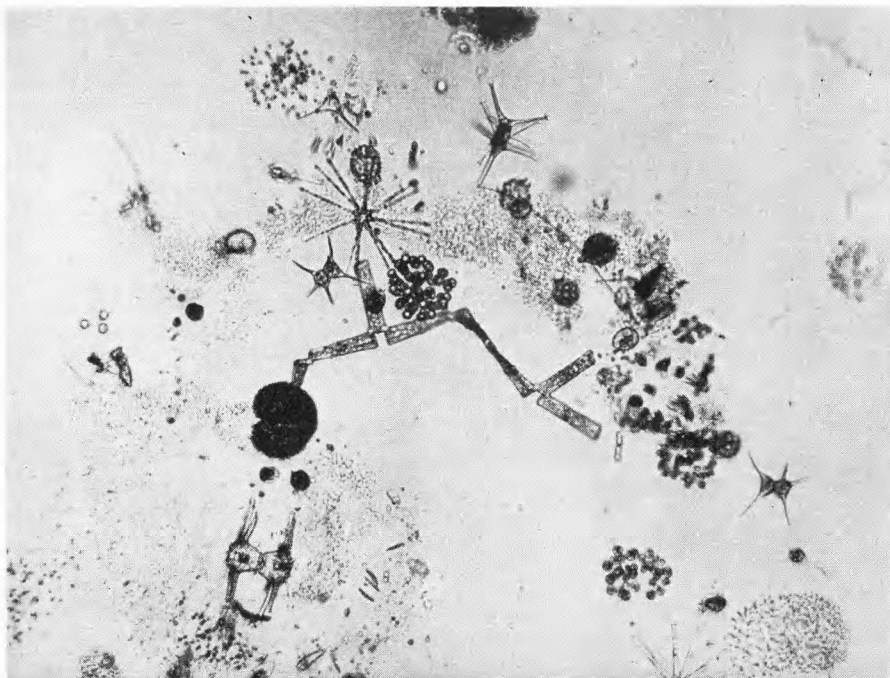


Fig. 15. Plankton from Västersjön. *Coelosphaerium naegelianum* is the dominant species. The plankton in Västersjön and Rösjön is furthermore characterized by several desmid species. A contorted form of *Tabellaria fenestrata* is also typical for the lakes on Hallandsåsen. Enl. 115  $\times$ . 27.8.1949.

THUNMARK and LILLIEROTH characterize the community by naming it after the species with the largest relative volume. This species is termed the dominant. LILLIEROTH reports in addition the species with the highest frequency of individuals, if this is not identical with the dominant. NYGAARD defines the dominant as the species predominating in number. He adds its absolute frequency and, furthermore, possibly the subdominant (s) (*l.c.*, p. 9). Finally these investigators complete the descriptions with one or several so-called phytoplankton quotients, which are based on the qualitative composition of the plankton community.

This characterization seems to be convenient for descriptions of any plankton sample, whether or not it is treated from a sociological point of view. In the short survey below (table 3) the author has endeavoured to characterize the samples on the same lines. The species predominating

as regards the relative volume (dominant according to THUNMARK) and the species with high frequency of individuals are determined by rather rough estimation. The concept of the author as to individuals of colony-forming species agrees with LILLIEROTH's (1950 b, p. 34). The number of species of *Myxophyceae*, diatoms, desmids and chlorococcal are also added in order to give an idea of the general appearance of the samples. The figures do not include, however, the sporadic species, as far as it has been possible to exclude them. It is assumable that the examination of the samples has not been extensive enough to include all the species occurring. Rare species may have been overlooked. The zooplankton is beyond the scope of the present investigation.

No extensive measurements or counts of individuals have thus been carried out. In uncertain cases two alternatives have been given for the dominant or otherwise none at all. The dominant according to THUNMARK is in some respects of interest. It can, for example, play an ecological role by shutting out the light to the disadvantage of other algae (*cf.* TEILING 1916, LUND 1950, p. 17). The frequency of individuals on a single occasion is of limited importance for a comparative investigation, as the number may change very rapidly.

Thus, in this case the qualitative composition of the plankton will be of the greatest value. It is also used by the planktologists for calculation of the quotients. The author has not determined any quotients, even if the number of species has sometimes been great enough. The figures would only be preliminary, since all the species of the samples are probably only rarely detected. Moreover, the diverging definitions of eutrophy and oligotrophy render the value of the quotients rather limited.

Of the lakes investigated as to the macrophytes the following are lacking in the survey below: Håckebergasjön, Björkesåkrasjön, Finjasjön, Hammarsjön and Araslövssjön. From Krankesjön no spring sample is available on account of inconvenient weather on the day for the excursion. R II is a station situated in Western Ringsjön, near the sound between this lake and Eastern Ringsjön. Its plankton probably comes mainly from the latter lake, and there-species. R I lies in the western part of Western Ringsjön. My = Myxophyceae, Di = Diatomeae, De = Desmidiæ, and Ch = Chlorococcales.

Table 3. Description of the plankton samples studied.

| Lake   | Dominant                               | High frequency of individuals   | My | Di | De | Ch |
|--------|--|---|----|----|----|----|
| Bos.   | Mel. ambigua                           | Aphanizomenon fl.-a., Asterionella form., Rhizosolenia long.,<br>Synedra acus var. angust.        | 11 | 11 | 1  | 10 |
| Börr.  | Asterionella form.                     | Attheya Zach., Mel. ambigua, Mel. gran. var. angust. Osc. Agardhii                                | 8  | 9  | 2  | 12 |
|        | —                                      | Lyngbya limn., Mel. ambigua, Aphanocapsa, Aphanothece and<br>Microcystis species with small cells | 25 | 9  | 2  | 17 |
| Dag.   | Micr. aeruginosa                       | Lyngbya limn., Micr. fl.-a.   | 23 | 4  | 3  | 12 |
|        | Mel. ambigua                           | Asterionella form., Nitzschia actularis, Rhizosolenia long., Sy-<br>nedra acus var. angust.       | 5  | 12 | 1  | 6  |
| Ell.   | Cerat. furcoides                       | Dinobryon div., Mel. gran., Peridinium Volzii   | 10 | 8  | 1  | 8  |
|        | Micr. vir. or fl.-a.                   | Mel. ambigua, Synedra acus var. angust.   | 22 | 7  | 2  | 4  |
| Fjäll. | Micr. fl.-a.                           | Lyngbya limn., Mel. ambigua, Micr. vir. (figure 9)  | 24 | 5  | 4  | 9  |
|        | Micr. fl.-a.?                          | Lyngbya limn.   | 16 | 4  | —  | 6  |
| Gyll.  | Micr. fl.-a.                           | Lyngbya limn.   | 20 | 3  | 3  | 12 |
|        | Coel. naeg.                            | Dinobryon div., Frag. crot., Micr. fl.-a., Micr. vir.   | 10 | 7  | 6  | 7  |
| Hav.   | Peridin. Volzii                        | Cerat. hirund. (figure 10)  | 11 | 9  | 7  | 9  |
|        | Diat. elong.                           | Cerat. hirund., Frag. capucina  | 2  | 5  | —  | 2  |
| Helje. | Cerat. hirund.                         | Gloeotrichia echinulata   | 7  | 2  | 1  | 3  |
|        | Dinobryon soc.                         | Cyclotella comta, Synedra acus var. angust., Syn. ulna  | 4  | 7  | 1  | 2  |
| Krag.  | Anabaena fl.-a.                        | Asterionella form., Cerat. hirund.  | 5  | 3  | 3  | 4  |
|        | Asterionella form.                     | Aphanocapsa elachista   | 16 | 12 | 6  | 10 |
| Krk.   | Botryococc. protub.                    | Coel. naeg., Lyngbya limn., Osc. limn.  | 19 | 9  | 8  | 12 |
|        | —                                      | Lyngbya limn.   | 19 | 3  | 4  | 16 |
| Kves.  | Mel. ambigua                           | Mel. Italica  | 10 | 8  | —  | 6  |
|        | Mel. ambigua                           | Asterionella form.  | 24 | 8  | 4  | 15 |
| Levra. | Frag. crot.                            | Asterionella form., Diat. elong., Frag. capucina, Osc. Agardhii                                   | 6  | 8  | 4  | 3  |
|        | Cerat. hirund.                         | Dinobryon soc., var. americanum, var. stipitatum  | 12 | 6  | 4  | 5  |
| Kia.   | Osc. Agardhii                          | Asterionella form., Cyclotella comta, Cycl. quadrijuncta, Synedra<br>acus var. angust.            | 19 | 10 | 5  | 14 |
|        | Mel. gran.                             | Asterionella form., Lyngbya limn. (figure 11)   | 21 | 8  | 10 | 25 |
| Norr.  | Mel. amb. or Syn. acus var.<br>angust. | Cyclotella comta, Cycl. quadrijuncta, Osc. Agardhii   | 14 | 15 | 5  | 14 |
|        | Micr. fl.-a.                           | Lyngbya limn., Mel. gran., Micr. aerug., Micr. vir.   | 23 | 12 | 9  | 22 |
| R. II  | Asterionella form.                     | Mel. gran.  | 5  | 9  | 2  | 7  |



|         |      |                                      |  |    |    |    |    |
|---------|------|--------------------------------------|--|----|----|----|----|
| E. Ri.  | 17/9 | Cerat. hirund.                       | Aphanizomenon fl.-a., Mel. gran. var. angust. (figure 12)                            | 17 | 8  | 4  | 12 |
| R. I    | 22/4 | Dinobryon soc.                       | Asterionella form., Mel. gran., Synedra acus var. angust.                            | 13 | 11 | 3  | 8  |
| W. Ri.  | 17/9 | Frag. crot.                          | Mel. gran. var. angust. (figure 13)  | 15 | 6  | 5  | 9  |
| Råb.    | 22/4 | Asterionella form. or Frag. crot.    | —  | 2  | 9  | —  | 3  |
| Rö.     | 23/8 | Cerat. hirund.                       | Asterionella form., Mel. ambigua   | 12 | 9  | 1  | 6  |
|         | 4/5  | Rhizosolenia long.                   | Asterionella form., Tab. fen.  | 3  | 10 | 1  | —  |
|         | 13/8 | Coel. naeg.                          | Rhizosolenia long.   | 10 | 5  | 11 | 8  |
| Sie.    | 23/4 | Dinobryon soc. var. americanum       | Mel. ambigua, Rhizosolenia long., Synedra acus var. angust.                          | 17 | 11 | —  | 9  |
| Snög.   | 1/8  | Mel. ambigua                         | Asterionella form., Dinobryon soc.   | 20 | 6  | 3  | 17 |
|         | 26/4 | Mel. ambigua                         | Aphanizomenon fl.-a., Micr. fl.-a., Micr. vir., Synedra acus var. angust.            | 22 | 7  | 2  | 9  |
|         | 9/8  | Micr. fl.-a or Aphanocapsa 3.6 $\mu$ | Lyngbya limn., Mel. gran., Osc. limn.  | 19 | 9  | 5  | 14 |
| Svan.   | 6/5  | —                                    | Chroococcus and Pediastrum species   | 7  | 6  | 1  | 7  |
|         | 27/7 | Micr. fl.-a.                         | Asterionella form., Synedra acus var. angust.  | 6  | 4  | 6  | 11 |
| Sö.     | 16/4 | Asterionella form.                   | Mel. ambigua, Mel. gran.   | 12 | 8  | 2  | 10 |
|         | 10/8 | Micr. fl.-a. or Micr. aerug.         | Aphanizomenon fl.-a., Coel. naeg., Mel. gran.  | 20 | 6  | 5  | 11 |
| Söborg. | 26/4 | Mel. ambigua                         | Asterionella form., Cyclotella comta, Mel. gran.                                     | 10 | 5  | 2  | 5  |
|         | 18/8 | Mel. ambigua or Mel. grau.           | Dinobryon soc., Lyngbya limn.  | 13 | 8  | 3  | 10 |
| Tjörn.  | 2/5  | Dinobryon soc. var. stipitatum       | Asterionella form., Mel. ambigua   | 18 | 6  | 2  | 7  |
|         | 17/8 | Tab. fen. or Coel. naeg.             | Lyngbya limn., Mel. ambigua  | 23 | 6  | 6  | 20 |
| Tun.    | 9/5  | Dinobryon sertularia                 | Pandorina morum, Uroglena sp.  | —  | 2  | 5  | 2  |
|         | 22/8 | —                                    | —  | 3  | 1  | 8  | 11 |
| Vomb.   | 26/3 | Micr. vir.                           | Micr. aerug., Micr. fl.-a., Micr. ichtyoblabe, Micr. vir., Tribonema sp. (figure 14) | 12 | 5  | 1  | 7  |
|         | 1/9  | Mel. gran.                           | Asterionella form.   | 19 | 6  | 7  | 21 |
| Vä.     | 4/5  | Tab. fen.                            | — (figure 15)  | 4  | 9  | 4  | 1  |
|         | 27/8 | Coel. naeg.                          | Lyngbya limn., Osc. Redekei, Synedra acus var. angust.                               | 12 | 6  | 18 | 10 |
| Ydd.    | 14/5 | Osc. limn. ?                         | Lyngbya limn., Osc. limn., Osc. sp., Synedra acus var. angust.                       | 24 | 6  | 1  | 12 |
|         | 23/7 | Micr. fl.-a.                         | —  | 20 | 3  | 1  | 12 |



## Survey of the distribution of the species.

### Qualitative differences.

#### *Species discussed.*

On the basis of the records of the two plankton samples from each lake a list of the distribution of most of the species found has been made. (The table is, however, not published.) Some plankton groups are not or only partially treated. Epiphytes and endophytes are completely excluded. They are dependent on the distribution of their host plants, and are thus of little significance in this connexion. Nor are *Eugleninae*, *Cryptophyceae*, *Chlamydomonadales* (except *Eudorina*, *Pandorina* and *Volvox*) and the bulk of *Heterokontae* listed. In the determination of these groups it is generally essential to work with unfixed material. Of the *Chrysophyceae* attention has been paid only to the genera *Dinobryon* and *Mallomonas*, both of which are significant plankton constituents and also rather easily identified. The species belonging to *Synura* and *Uroglena* are not definitively determined, but as far as the author is aware, only one species is to be found in each lake. (Three *Synura* species seem to be included. As the individuals from Yddingen and Vombsjön are not sufficiently examined on account of their rarity, the *Synura* species are not given in the tables 4 to 6.) The taxonomic units of *Ceratium* are on account of their great variation little suitable for ecological studies. No attempts to distinguish different forms of *Ceratium hirundinella* have therefore been made.

The desmids have been identified with the guidance of drawings and descriptions in the plankton literature, as well as the other algae. It has, however, been more difficult for the author to obtain her own idea of the normal amplitude of variation of these species, since they are quantitatively rather infrequent. The species named *Staurastrum cingulum* var. *obesum* is not quite uniform. The individuals from Västersjön are apparently large. A measurement of a small number of individuals from different lakes indicates, however, that there exists a fairly even transition from the smallest to the largest specimens within the district investigated. Even if the size and to some extent also the appearance of the species thus vary somewhat in the different lakes, the author has not found it possible to make a division into different forms. The same holds true on the whole for *Staurastrum planctonicum*. The individuals in Västersjön and Rösjön are somewhat more robust and have a slightly

more elongated body. The experience of the author is, however, still too limited to permit a definite decision.

In some cases it has not been possible to determine the species of the forms, *e.g.*, among the *Myxophyceae*, where it can even be difficult to recognize the genus. *Pediastrum duplex* has been included as one species, but naturally it is a collective species. For that reason it is of little interest in this connexion. Two forms rather like *Pediastrum clathratum* have been noted. They are for the present called *clathratum* a and b. In uncertain cases it is most correct to separate slightly different forms rather than to combine them, as they can be ecologically differentiated. *Tetraedron limneticum* and *planktonicum* are considered by SKUJA (1949, p. 64) to be different stages of development of the same species. In the present plankton list they seem to show a slightly divergent distribution, and therefore there is some reason for distinguishing them, until further studies have been performed.

On the whole the determinations of the plankters are more easily carried out than those of the macroscopic algae. The interest in this pelagic algal group has been great for a long time. Several critical works have been published during the last years not the least by Scandinavian investigators (TEILING *i.a.* 1941, 1942 a and b, 1946 and 1947, SKUJA 1948, and NYGAARD 1949). The subject is also of great practical importance, for example in fishery biology.

Much still remains to be done, however, even as regards net plankton. All-round investigations of so-called critical groups are perhaps most desired. Some characters so far used as taxonomic characters in *Pediastrum* have proved to be of no value in this respect (SKUJA 1948, p. 126 *et seq.*). A revision of the genus is consequently needed. Even other chlorococcal groups require a fresh examination. It is likely and in some cases stated that chlorococcal species appear alternately in single cells and in colonies (*cf.* GRINTZESCO 1902, and PRINGSHEIM 1950 b). Such species are perhaps now considered as two or more different species.

The species are, as previously mentioned, identified by means of descriptions and drawings in the planktologic literature. Hitherto the author has not achieved an independent idea of the quite systematic questions, where conflicting opinions have been put forward.

Besides the literature already cited the following have been employed for the determinations: HUBER-PESTALCZZI (Phytoplankton d. Süßwassers), NYGAARD (1945), PASCHER (Süßwasserflora), RABENHORST (Kryptogamenflora), SMITH (1920, 1924, 1926), TEILING (1944), WEST

& WEST (1904—12), and WEST, WEST & CARTER (1923). Moreover, special works have been studied when necessary.

As has already been mentioned, some algae may occur so rarely, that they have been overlooked in the microscopic examination. This is especially true of desmids and some chlorococcal, *e.g.*, *Lagerheimia* and *Golenkinia*. It is likely, however, that if there exist any significant plankton differences between the different lakes, they will be reflected in the list in spite of its possible defectiveness. Such differences must be based on the occurrence or absence of several species, all of which are not equally infrequent.

Forms found in the plankton without being true plankters have not been listed. It is often very difficult to recognize the euplankters. Species which are termed tychoplankters in the manuals sometimes occur so regularly in the plankton samples, that they must be assumed to be capable of living pelagically for longer periods, *e.g.*, *Amphiprora*. Such species have been recorded in the list. More sporadic forms, as for example *Fragilaria capucina* and *Synedra ulna*, which only sometimes appear regularly and seldom in large amounts, have, on the other hand, not been included. The *Merismopedia* species are considered as fairly occasional plankters, but in these samples they are commonly seen. They are also included in the list.

#### *Species with a limited distribution.*

On the basis of this unpublished list three other lists have been established (tables 4 to 6). Table 4 contains species apparently restricted to the lakes in the macrophyte chapter called group A. Table 5 comprises species belonging to group A and B. Table 6 consists of species which have their widest distribution in the groups B and C or are completely confined to both or one of them.

Findings from only one lake have not been included in the tables 4 and 5. Nowhere have uncertain identifications been listed. In table 6 even single records are given, however. In group C, which is only composed of two lakes, naturally findings from only one lake cannot be omitted. Nevertheless the table can easily become misleading, as far as tycho-plankters are concerned. Such species may happen to be rare or absent in the plankton on the day for the collecting and will therefore not be included in the list. Only few of the species dealt with here can be sporadic forms, but *e.g.*, the species of *Merismopedia* should perhaps be classified as tychoplankters.













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- 2: 3. A. ALMESTRAND and ASTA LUNDH: Studies on the Vegetation and Hydrochemistry of Scanian Lakes. I—II. 1951. 174 p.
- Vol. 3: 1. ASTA LUNDH: Studies on the Vegetation and Hydrochemistry of Scanian Lakes. III. 1951. 138 p., 14 pl.
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*Pris 6: — kronor.*



The table below is a survey of the number of non-ubiquitous species.

| Species confined to         | group A | group A+B | group B | group B+C | group C |
|-----------------------------|---------|-----------|---------|-----------|---------|
| <i>Myxophyceae</i> .....    | 7       | 20        | —       | —         | —       |
| <i>Diatomeae</i> .....      | —       | 6         | 2       | —         | 2       |
| <i>Desmidiæ</i> .....       | 3       | 4         | —       | 2         | 14      |
| <i>Chlorococcales</i> ..... | 10      | 20        | —       | 1         | 1       |
| Total number .....          | 22      | 52        | 3       | 4         | 17      |

It is obvious from the table that the groups A and C differ very much from each other. Both groups have about the same number of species confined to each of them. Group B has very few specific species, of which, neither *Melosira italica* nor *Amphiprora ornata* are considered as euplankters. The latter have, however, not been recorded from epiphytic samples from other lakes. The group has many plankters in common with group A and some with group C. Besides it includes some species (see table 6), which are preferably but not exclusively distributed here and in group C or only here. The plankton of group B thus constitutes a special type by possessing several forms even occurring in group A and at the same time species even occurring in group C. It also differs from the other two groups by lacking the species quite confined to each of them.

While in the groups A and A+B most of the restricted species are blue-green algae or chlorococals, the desmids predominate in group C. It has been a well-known fact for a long time that Archaean lakes contain a plankton richer in desmids than lowland lakes on sedimentary soils (*cf. e.g.*, TEILING 1916, who has proposed the designation caledonic formation for the plankton formation in nutrient-deficient, not polluted lakes, that is characterized by richness in desmids).

Figure 16 illustrates how the four large algal groups are distributed counted in a percentage of the total number of species within the different lakes. The *Myxophyceae* predominate in most of the lakes belonging to group A and in Tjörnarpssjön. In the remainder belonging to the groups A and B the same number or more of chlorococals occur. The diatoms are rather homogeneously distributed in all the lakes. The desmids show a very pronounced increase in group C, the *Myxophyceae* and *Chlorococcales* at the same time a striking decrease in number.

Table 5 includes as mentioned in the foregoing not only species restricted to the groups B and C, but also species, which are spread in some lakes of group A, although they are evidently concentrated to the groups first mentioned. This sporadic distribution within group A is





Fig. 16. The distribution of the planktic blue-green algae, diatoms, desmids and chlorococcal in percentage of the total number of species. The uppermost curve illustrates the bicarbonate concentrations in the lakes obtained by ALMESTRAND (1951, table 4).

distinctive of among others the following species: *Rhizosolenia longiseta*, *Mallomonas elongata*, *Crucigenia rectangularis* and *Dimorphococcus lunatus*. They have been observed preferably in the following lakes: Svaneholmssjön, Tunbyholmssjön, Ringsjön, Oppmannasjön and Sie-sjön. At no time have they been found in that section of group A that is below called *Myxophyceae*-rich lakes. Svaneholmssjön and Tunbyholmssjön have in different connexions been pointed out as being divergent from the others. They are rather to be considered as ponds and are surrounded by vast fen grounds. The algae mentioned are apparently not quite randomly spread in group A, but the causes of their distribution can hardly be discussed with positive result, as long as their ecological requirements are so little known.

By studying the tables one notices a conspicuous difference in the number of blue-green algae between the different lakes. Figure 17 shows the variation of the *Myxophyceae* in the lakes belonging to group A and



B. As the samples are not quite exhaustively examined, the curves must be regarded as preliminary. The solid and the broken curve run on the whole parallelly, which indicates that the number of ubiquitous is about the same in all the lakes. Some exceptions exist, however. In Havgårdssjön there are but few ubiquitous, in Siesjön, Gyllebosjön and Eastern Ringsjön the contrary is the case.

One section of the group A, the *Myxophyceae*-rich lakes, contains about 40 to 60 per cent blue-greens (Ellestasjön, Fjällfotasjön, Yddingen, Siesjön, Börringesjön, Krankesjön, Sövdesjön, Snogeholmssjön). The other section has about 30 per cent (three lakes less than 30 per cent).

The first division consists of shallow lowland lakes, situated in South Scania (except Siesjön). Generally they are small (*cf.* LUNDH 1951 b, table 1). Krankesjön and Börringesjön are rather large, but at the same time they belong to the shallowest ones. Siesjön is situated far from the others, and moreover, it diverges in size and geological conditions. It also has higher transparency. Quantitatively it differs from the others, because it had not attained any high production of *Microcystis* on the days for sampling. Water-bloom of *Microcystis* has never been observed.

The *Myxophyceae*-rich lakes contain some species on the whole confined to them. These algae are enumerated in the table below:

| Species                                  | Ell. | Fjäll. | Sie. | Ydd. | Börr. | Krk. | Sö. | Snog. | Opp. | Krag. | Söborg. |
|--|------|--------|------|------|-------|------|-----|-------|------|-------|---------|
| <i>Coelosphaerium pallidum</i> . . . . . | 1    | 1      | —    | —    | 1     | —    | 1   | 1     | —    | —     | —       |
| <i>Microcystis stagnalis</i>             | 1    | 1      | —    | 1    | 1     | —    | —   | 1     | 1    | 1     | —       |
| <i>Oscillatoria limnetica</i>            | —    | 1      | —    | 1    | —     | 1    | —   | 1     | 1    | 1     | 1       |
| — <i>Redekei</i> . . . . .               | —    | 1      | —    | 1    | 1     | —    | 1   | 1     | —    | 1     | —       |
| <i>Tetraedron caudatum</i>               | —    | 1      | —    | 1    | 1     | —    | —   | —     | 1    | —     | —       |

As is seen from the table, Siesjön differs also in this respect from the other seven lakes. It lacks all the algae listed. These are, on the other hand, to be found in Oppmannasjön, Krageholmssjön and Sövdeborgssjön, which lakes (*cf.* figure 17) have a high number of blue-green algae. On account of the great total number of species the blue-greens cannot show any relative dominance, however.

Apart from Siesjön the seven remaining lakes thus constitute a distinct type different from the other more *Myxophyceae*-deficient lakes within group A. Also from a quantitative point of view there is reason for naming them *Myxophyceae*-rich (*cf.* further p. 88).

The second division comprises the *Myxophyceae*-deficient lakes. They are situated on geologically heterogeneous substrata in different parts of the province. Their areas are varying. Disregarding Svaneholmssjön



Fig. 17. The variation of the blue-green algae within the lake groups A and B. The uppermost curve represents the total number of species. The next solid curve shows the total number of *Myxophyceae* and the broken curve shows the non-ubiquitous *Myxophyceae* species in per cent of the total number of species.

and Tunbyholmssjön they are deeper than the majority of the *Myxophyceae*-rich lakes. The visible affluents are rather small in proportion to the water volume of the lakes. Sometimes they are completely absent (cf. LUNDH 1951 b, p. 31). The water is generally more transparent than in the former section. No apparent qualitative plankton differences can be seen (with the exception of the plankton flora in the ponds Svaneholmssjön and Tunbyholmssjön).

If the four lakes within group B are compared among themselves, even here a difference as to the number of blue-green algae is seen (figure 17). Tjörnarpssjön and Kvesarumssjön contain about 30 to 40 per cent *Myxophyceae*. The absolute figures show still more marked differences.

#### *Species with a ubiquitous distribution.*

The following species can be considered ubiquitous within the investigated area:

*Anabaena flos-aquae*  
— *spiroides*

*Aphanocapsa elachista*  
— *elach. var. planctonica*

|                                     |  |
|-------------------------------------|--|
| <i>Coelosphaerium kuetzingianum</i> | <i>Botryococcus Braunii</i>                  |
| — <i>naegelianum</i>                | — <i>protuberans</i>                         |
| <i>Microcystis aeruginosa</i>       | <i>Staurastrum cingulum</i> var.             |
| — <i>flos-aquae</i>                 | <i>obesum</i>                                |
| — <i>viridis</i>                    | — <i>pingue</i>                              |
| <i>Oscillatoria Agardhii</i>        | — <i>planctonicum</i>                        |
|                                     | — <i>tetracerum</i> var. <i>subexcavatum</i> |
| <i>Ceratium hirundinella</i>        |  |
| <i>Peridinium cinctum</i>           | <i>Coelastrum cambricum</i>                  |
| — <i>Willei</i>                     | <i>Dictyosphaerium pulchellum</i>            |
|                                     | <i>Kirchneriella lunaris</i>                 |
| <i>Asterionella formosa</i>         | <i>Oocystis Borgei</i>                       |
| <i>Attheya Zachariasii</i>          | <i>Pediastrum araneosum</i> (?)              |
| <i>Cyclotella comta</i>             |  |
| <i>Diatoma elongatum</i>            | <i>Gemmellicystis neglecta</i>               |
| <i>Fragilaria crotonensis</i>       | <i>Gloeocystis planctonica</i>               |
| <i>Melosira ambigua</i>             |  |
| <i>Tabellaria flocculosa</i>        | <i>Eudorina elegans</i>                      |
|                                     | <i>Pandorina morum</i>                       |
| <i>Dinobryon divergens</i>          | <i>Volvox aureus</i>                         |

*Rhizosolenia longiseta*, *Tabellaria fenestrata* and *Mallomonas elongata* could possibly also be called ubiquitous, as they occur in all three groups. As previously discussed, however, their distribution within group A is, apparently limited in some way, and they attain their greatest development in the groups B and C.

*Total number of species in the individual lakes.*

A survey of the total number of species in the lakes is given below:

|      |       |     |      |       |      |     |     |       |      |      |        |      |    |      |      |
|------|-------|-----|------|-------|------|-----|-----|-------|------|------|--------|------|----|------|------|
| Hav  | Helje | Tun | Råb  | Levra | Svan | Ell | Krk | Fjäll | Gyll | Ydd  | Söborg | Börr | Sö | W.Ri | Vomb |
| 23   | 29    | 35  | 47   | 48    | 48   | 48  | 48  | 50    | 53   | 53   | 54     | 57   | 58 | 60   | 61   |
| E.Ri | Snog  | Sie | Krag | Kia   | Norr |     |     | Dag   | Bos  | Kves | Tjörn  |      |    | Rö   | Vä   |
| 62   | 63    | 69  | 70   | 81    | 91   |     |     | 47    | 55   | 69   | 77     |      |    | 55   | 65   |

The number of species in the phytoplankton is relatively small. It varies between 23 (Havgårdssjön) and 91 (Norregård, Oppmannasjön) within group A, 47 and 77 in group B and 55 and 65 in group C. Group A has the widest variation, but it also includes the majority of the studied

lakes. The corresponding data from lakes in adjacent districts (LILLIEROTH 1950 b) give mostly higher figures. Vårsjön for example contains 160 microphytes, and even if the sum comprises several non-planktic forms here omitted, it is evident that this highly transparent lake slightly affected by culture has appreciably more plankton algae than any of the lakes here treated. Åsljungasjön and Western Sorrödssjön, which have been the most subjected to human interference of the lakes studied by LILLIEROTH, exhibit the lowest values, which seem to be of about the same magnitude as those of the lakes investigated by the author. Thus the insignificant number of species in the latter lakes is likely to be due to the influence of human intervention.

Tunbyholmssjön and Svaneholmssjön are fairly poor in planktic species, but they do not show the lowest number in the group. It is striking that several of the clearest lakes have a plankton deficient in species. The lakes richest in species include the largest ones (Oppmannasjön, Ringsjön and Vombsjön) but also some small ones, *e.g.*, Siesjön.

#### Q u a n t i t a t i v e d i f f e r e n c e s .

Table 7 gives a survey of the highly frequent species in the lakes mainly according to table 3.

The two samples from each lake studied have been gathered at times when the total production of plankton is usually considerable. Maxima of shorter duration appearing at other times have not been exhibited by them, however. The table has therefore been completed with notes from other sampling days in 1948 and 1949. It probably gives information as to the most important highly frequent algae in the lakes.

*Myxophyceae*. — No lake belonging to the groups B and C shows a real high production of *Microcystis* species. Kvesarumssjön and Tjörnarpssjön may develop moderate maxima of short duration. Otherwise, when these lakes attain abundant development of blue-green algae, this is generally produced by *Coelosphaerium naegelianum*. In Bosarpssjön *Aphanizomenon flos-aquae* causes a strong vegetation turbidity, but even *Coelosphaerium naegelianum* may occur in high frequency. High production of *Lyngbya limnetica* is, broadly speaking, confined to group A (and Tjörnarpssjön). Abundant development of the species not named in the table is characteristic of the lakes in group A apart from Bosarpssjön (*Oscillatoria Agardhii*) and Kvesarumssjön (*Anabaena affinis*).

On the whole the *Myxophyceae* thus attain high frequency of individuals only in group A. The most significant exception is *Coelosphae-*

*rium naegelianum*, which gives rise to water-bloom-like high productions in Västersjön, Rösjön, Bosarpssjön and Tjörnarpsjön. This alga, on the other hand, rather seldom appears in greater number of individuals in group A. High production of *Anabaena circinalis* is sometimes to be seen in Västersjön and Rösjön. Otherwise this species is only reported from Ringsjön.

*Peridineae*. — *Ceratium hirundinella*, which is considered a ubiquitous, shows a high individual frequency solely in group A, and here only in the more transparent lakes. High development of this alga has not been recorded from any *Myxophyceae*-rich lake. But a few lakes are characterized by a high individual frequency of *Peridinium* species.

*Diatoms*. — High frequency of individuals of *Melosira granulata* is not distinctive of the groups B and C (except var. *angustissima* from Bosarpssjön). Nor is *Fragilaria crotonensis* highly frequent in these groups, which, on the other hand, seem to be favourable for the development of *Rhizosolenia longiseta* and *Tabellaria fenestrata*. *Asterionella formosa* may occur abundantly in all the groups, and *Melosira ambigua* and *Synedra acus* var. *angustissima* at least in the groups A and B. Of the unnamed species it concerns *Attheya Zachariasii* and *Nitzschia acicularis* in group B and mainly centric diatoms, preferably *Cyclotella comta*, in group A. In Havgårdssjön and Levräsjön there often occurs an abundance of the pennate diatoms *Diatoma elongatum* and *Fragilaria capucina*. (The latter is not considered to be an euplankter in this work.) The unnamed species constitute ubiquitous elements, at least as far as the euplanktic forms are concerned, with the exception of *Stephanodiscus astraea* and possibly *Nitzschia acicularis* and *Cyclotella quadrijuncta*. The latter are, however, recorded from too few localities to be more closely discussed.

*Chrysophyceae*. — Species belonging to the genus *Dinobryon* are often highly frequent. Otherwise *Mallomonas caudata* (Svaneholmssjön) and species of *Uroglena* and *Synura* (the two latter in Dagstorpssjön and Tunbyholmssjön) may occur frequently. High incidence of *Dinobryon* does not appear in the *Myxophyceae*-rich lakes, nor does it seem to be common in group C. Most of the registered *Dinobryon maxima* have been produced by *Dinobryon sociale*. The main species is apparently restricted to the clear lakes in group A. It is to be noted that several of the most highly frequent algae in Tunbyholmssjön belong to *Chrysophyceae* (*Dinobryon bavaricum*, *D. sertularia* and those already mentioned).

As has already been discussed nearly all the lakes may be called high-productive, even if the relative values naturally vary. Svaneholms-

Table 7. Survey of the high-frequent species in the years 1948 and 1949.

|  |  |
|--|--|
| <i>Myxophyceae.</i>  | <i>Fragilaria crotonensis</i> : Gyll., Helje., Levra., R. I, Råb.  |
| <i>Aphanizomenon flos-aquae</i> : Bos., R. II, Snog., Sö., Vomb., Kia.   | <i>Melosira ambigua</i> : Bos., Börr., Dag., Ell., Krag., Kves., Norr., R. II, Sie., Snog., Sö., Söborg., Tjörn., Vomb.            |
| <i>Coelosphaerium naegelianum</i> : Bos., Ell., Gyll., Krag., Kia., Rö., Sö., Tjörn., Vä.  | <i>Melosira granulata</i> : Kia., Norr., R. I, Råb.?, Snog., Sö., Söborg.  |
| <i>Lyngbya limnetica</i> : Börr., Ell., Fjäll., Krag., Krk., Kia., Norr., Snog., Söborg., Tjörn., Ydd.   | <i>Melosira granulata</i> var. <i>angustissima</i> : Bos., Hav., R. II, R. I   |
| <i>Microcystis</i> spp.: Börr., Ell., Fjäll., Gyll., Krag., Krk.?, Kves., Norr., Sie., Snog., Svan.?, Sö., Tjörn., Vomb., Ydd.   | <i>Rhizosolenia longiseta</i> : Bos., Dag., Rö., Sie., Vä.   |
| Other species: Bos., Börr., Hav., Helje., Krag., Krk., Kves., Levra., Kia., Norr., Snog., Ydd.   | <i>Synedra acus</i> var. <i>angustissima</i> : Bos., Dag., Ell., Gyll., Helje., Krag., Kia., Norr., R. I, Sie., Snog., Svan., Ydd. |
| <i>Peridineae.</i>   | <i>Tabellaria fenestrata</i> : Bos., Dag., Rö., Tjörn., Vä.  |
| <i>Ceratium furcoides</i> : Dag.   | Other species: Bos., Dag., Gyll., Hav., Helje., Levra., Kia., Norr., Söborg.   |
| <i>Ceratium hirundinella</i> : Gyll., Hav., Helje., Krag., Levra., R. II, R. I, Råb., Tun.   | <i>Chrysophyceae.</i>  |
| <i>Peridinium</i> spp.: Dag., Gyll., Krag., Svan.  | <i>Dinobryon divergens</i> : Dag., Gyll., Svan.  |
| <i>Diatomeae.</i>  | <i>Dinobryon sociale</i> : Hav., Helje., Levra., Kia., Norr., R. II, R. I, Sie., Söborg.   |
| <i>Asterionella formosa</i> : Bos., Dag., Ell., Gyll., Helje., Krag., Krk., Kves., Levra., Kia., Norr., R. II, R. I, Råb., Rö., Sie., Snog., Svan., Sö., Söborg., Tjörn., Vomb., Vä. | <i>Dinobryon sociale</i> var. <i>americanum</i> : Levra., Sie.   |
|  | <i>Dinobryon sociale</i> var. <i>stipitatum</i> : Levra., Råb., Tjörn.   |
|  | Other species: Dag., Svan., Tun.   |

sjön and Tunbyholmssjön form the only striking exceptions. Their plankton is slightly developed in relation to that of the others. The environmental conditions of these small shallow bodies of water must also be divergent. The major part of the water surface is covered with floating leaves, which exclude large quantities of light (*cf.* TEILING 1916, p. 518), and a great portion of the bottom is inhabited by higher water plants.

In summarizing the results it can be established that there exist evident differences between the three lake groups even as to the quantitative development of the planktic algae. This is especially well marked among the *Myxophyceae* and some diatoms. Group B differs from group A in lacking water-bloom of *Microcystis* and high individual frequency of several other species, *e.g.*, *Melosira granulata*, *Fragilaria crotonensis*, *Dinobryon sociale*, and instead maintaining high production of *Coelosphaerium naegelianum*, *Tabellaria fenestrata* and *Rhizosolenia longiseta*. The group in these respects approaches group C, but it deviates from that group, because it is in some cases characterized



by high frequency of *e.g.*, *Microcystis* species (Kvesarumssjön and Tjörnarpsjön), *Aphanizomenon flos-aquae* (Bosarpssjön), *Lyngbya limnetica* (Tjörnarpsjön) and *Anabaena affinis* (Kvesarumssjön). The lakes of group B form a transition between the two other groups and are not quite uniform among themselves. Nor is group A uniform. The *Myxophyceae*-rich lakes support high frequency of individuals of one or more *Microcystis* species (possibly with the exception of Kranke-sjön) and mostly also of *Lyngbya limnetica*. They lack, however, more abundant development of *Ceratium* and *Dinobryon* species. In the *Myxophyceae*-deficient lakes it is quite the contrary.

### Conclusions.

The division of the lakes into three groups according to the macrophyte vegetation can be maintained even as regards the phytoplankton. The lowland lakes (group A) form a distinct type with several specific species. Rösjön and Västersjön (group C) also constitute a quite separate group with a number of specific species, particularly desmids. Bosarpssjön, Dagstorpssjön, Kvesarumssjön and Tjörnarpsjön (group B) are hardly characterized by specific species but differ from the other lake types, because they contain a mixture of species from them both. It is true of qualitative as well as quantitative data.

As far as the higher plants are concerned, there occur within group A some lakes which can be distinguished from the rather homogeneous main type because of their content of Archaean elements, *viz.* Fjällfotasjön, Tunbyholmssjön and Ringsjön. In the composition of plankton no such deviations common to them all are to be seen.

The plankton of Fjällfotasjön does not show any Archaean (caledonic) species whatsoever. Its character agrees with that of the adjacent lakes Yddingen and Börringesjön. Tunbyholmssjön is characterized by some desmids (*e.g.*, *Xanthidium*) which are often seen in Archaean lakes and otherwise a small number of species. The construction of the lake makes it impossible, however, to compare it directly with any of the other lakes investigated except Svaneholmssjön. The conditions for the planktic forms seem to deviate considerably, which is also reflected in the quantitative development (*cf.* p. 86). The net samples will naturally also usually contain diverse benthic forms. Ringsjön must certainly be considered a rather typical lowland lake. Those of the species mainly occurring in the groups B and C that are found in Ringsjön also appear in true lowland lakes (see table 6).

Of course it cannot be proved whether the plankton of Fjällfotasjön and Ringsjön have previously contained Archaean components or not. It seems, however, rather presumable. If the content of calcium and bicarbonate, *i.e.* those factors showing the most significant differences between the groups (see the table p. 11), is compared with the average within group A, it is observed that the figures for Fjällfotasjön and Ringsjön are lower. They are, however, higher than those of group B.

Fjällfotasjön and Ringsjön are located in old agricultural districts, where the influence of man has been acting for a long time. The absence of Archaean elements in the plankton might be attributed to the fact that the culture-affected water has in some way been harmful to them.

Nor is it impossible that the electrolyte content (*i.a.* also the ions discussed above) has been increased by the supply of manure-water. Thus the chemical deviations from the other lakes in group A might possibly have previously been even more conspicuous than now.

The change has naturally been carried on slowly but at the same time started so early that it has now removed all traces of Archaean components. The lists of species given by LEMMERMANN (1903—04) from the lakes do not indicate that any great changes in the plankton content have taken place since the turn of the century.

Consequently, the plankton algae would appear to be more sensitive than the macrophytes, which is explainable. The latter must, not at least because of their greater volume, be more capable of resisting external influences.

With respect to the composition of plankton another difference is observed in group A. Eight of the lakes are strikingly *Myxophyceae*-rich (absolutely as well as relatively) in comparison to the remaining ones. The first section consists of small shallow lowland lakes with inconsiderable transparency, the second one is composed of lakes of varied area but mostly deeper and with clearer water than the foregoing lakes.

All lakes agree, at least qualitatively, as to the higher plants. Thus it is a likely assumption that also the plankton originally might have been more similar than is now the case. It is plausible that the extensive human intervention might be responsible for the differences mentioned above. It has probably had the greatest effect just on these small lakes with an appreciable supply of surface water in proportion to the water volume. The observations reported in the literature as concerns the influence of sewage fall into line with this suggestion (*e.g.*, TEILING 1916, THUNMARK 1945 a, RODHE 1948 b, and FJERDINGSTAD 1951).

According to PEARSALL (1932) lakes rich in organic substances are beneficial to the blue-green algae. HUTCHINSON (1944) holds that this is not definitely proved, as his own investigations do not speak in favour of it and besides several blue-greens have been cultured in inorganic medium. Even if the *Myxophyceae* can hold their own on inorganic substrata, it is nevertheless not established that in nature they are not promoted more than others by organic compounds and therefore are capable of supplanting other species in organically contaminated water.

More conclusive proofs must wait, until it has been possible to establish the environmental requirements of the individual blue-green algae and their varying reactions in ecologically heterogeneous conditions. It is naturally necessary to attack the problem from two starting-points, *i.e.*, not only by field observations, which has previously been the most common, but by studies of the special requirements of the organisms in experiments under controlled conditions.

In the United States several blue-green algae have been kept for a couple of years in pure cultures partly free from bacteria (GERLOFF *et al.* 1950 a and b). The investigations on the nutrition of *Coccochloris Peniocyctis* have shown that this alga requires a very high content of nitrogen as compared with those of other essential nutrients. This fits in with the fact that the *Myxophyceae* are abundant in sewage-polluted water. One may not generalize, however, since different species may have different requirements. It is to be presumed, for example, that such algae which are able to fix elementary nitrogen (FOGG 1942, 1947 and 1951) can occur in waters with inconsiderable amounts of nitrogen compounds. The real distribution of these algae is not known. FOGG (1947) is of the opinion, however, that they are of great importance for the increase of the content of combined nitrogen in natural waters.

The suggestion put forward above as to the causal factors of the differences between the *Myxophyceae*-rich and *Myxophyceae*-deficient lakes in group A is supported by the fact that the four lakes in group B, which are nearly uniform as far as the higher plants are concerned, show a similar difference in respect to the plankton composition. The two *Myxophyceae*-rich lakes are situated in more cultivated or densely settled districts than the other two. (*Cf.* LUNDH 1951 b, figures 33 and 35. It is not clear, however, from table 2, as the figures of arable land are mean values for that parish or those parishes in which the lake is located.) Kvesarumssjön borders in the south on an agricultural district and Tjörnarpssjön is situated at a station village and surrounded by

summer houses. The shores of Bosarpssjön and Dagstorpssjön have on the other hand hitherto been free from settlement of the last-mentioned kind.

### Ecological discussion of the distribution of the plankters.

It is quite impossible to give an exhaustive explanation of the distribution of the plankton species. The problem has given rise to many investigations and many discussions. In the last years especially American researchers have been interested in such studies. They often lay practical view points on the problem, preferably with respect to the biological production. They have also endeavoured to work out methods for inhibiting the water-bloom, inconvenient in many ways.

The problem must be attacked from two sides. A good knowledge of the natural habitats must be the basis on which the experimental results can be interpreted. By field studies one can arrive at a parallelism between some factors and the occurrence of the organisms. By experiments one has to prove if there is reason for assuming a causal connexion.

The ecological factors are of three types: edaphic, climatic and biotic factors. Under natural conditions all types are always involved, and therefore none may be disregarded in ecological discussions.

It has been proved that the same species which has a high production in one lake may be regularly present in another lake but only in single individuals. Thus different combinations of factors seem to be necessary for the qualitative occurrence of a species and for the maintainance of high production.

### Qualitative occurrence.

**Edaphic factors.** The different qualitative distribution of the plankters has generally been attributed to the edaphic factors. It has been believed that certain so-called »nutrient exacting» (eutrophic, eutrapihent) species require such a high concentration of one or several essential nutrients, that they can only grow in certain waters »rich in plant nutrients» (eutrophic). *Cf.* THUNMARK (1948, pp. 19 to 20) and LILLEROTH (1950 a and 1951). The terms »rich in nutrients» and »deficient in nutrients» seem to bear on the total content of electrolytes, which can easily be determined. Even the land plants are divided into

eutrophic and oligotrophic species according to their supposedly different nutritional requirements (HÅRD AV SEGERSTAD 1924 and ALMQUIST 1929 among others).

*Essential nutrients.* Since phosphorus and nitrogen are present in water in insignificant concentrations, it is plausible to consider them as theoretically limiting factors.

Field studies have also largely established a lower content of phosphorus and nitrogen in electrolyte-deficient lakes, that is in so-called oligotrophic lakes. LOHAMMAR (1938, pp. 180 and 182) states that the total content of nitrogen and phosphorus tends to be somewhat higher in his electrolyte-rich waters (*cf.* RODHE 1951). JUDAY's analyses (1942 p. 108) also give lower values for soluble phosphorus and nitrate in the two electrolyte-deficient lakes. Only an inconsiderable amount of data is available concerning the content of phosphorus and nitrogen in the lake waters compared with the fairly extensive analytical material which is to be found as regards, for example, the specific conductivity, hardness and chloride. Now that exact analytical methods are available it is no longer difficult to obtain accurate values. It is, however, not equally simple to obtain a close correlation between the distribution of the plankters and the concentrations of phosphorus and nitrogen, as long as it is not known exactly how the algae supply their need of the two substances. The same total content of phosphorus can be unequally available for the plants in two lakes, because it may occur in different compounds. Besides, in humic water the phosphate ions are strongly fixed to the humus colloids (OHLE 1937 and 1940, ÅBERG and RODHE 1942). (On the whole the chemical conditions in the humus-rich lakes seem to be rather complex in comparison to those of transparent, colloid-deficient lakes. Among other things the colloids adsorb cations and certain anions and function as protective colloids for *e.g.*, iron and silicon. Even in clayey lakes similar conditions are likely to prevail.) These facts must be taken into consideration when a comparison of the water-chemical data from different lakes is to be carried out. High values of *e.g.*, total phosphorus in humus-rich lakes are naturally not directly comparable with the corresponding phosphorus values from oligo-humic lakes from an ecological point of view.

Some algae can also store phosphorus and nitrogen and thus they do not become completely dependent upon the actual concentration (*cf.* the discussion in RODHE 1948 a and in LUND 1950).

The experimental investigations performed on the effects of the supply of phosphorus and nitrogen on the growth of some planktic



algae have proved that different species have variant optimum requirements (CHU 1942 and 1943, RODHE 1948 a and GERLOFF *et al.* 1950 b). Generally the optimum seems to lie above the conditions in nature, perhaps not always, however (see RODHE's experiments with *Dinobryon* and *Uroglena*). He believes (*l.c.*, p. 91) that the qualitative differences between TEILING's caledonic and baltic plankton types and the different quotients between desmids and chlorococals in oligotrophic and eutrophic lakes will be explained by the different phosphorus requirements of the algae.

The different capability of the plankters in utilizing organic nutrient sources has also been studied experimentally. CHU (1945 and 1946) has shown that certain diatoms, *e.g.*, *Nitzschia palea*, can utilize organic sources of phosphorus. RODHE claims to have confirmed his opinion that *Scenedesmus quadricauda* can utilize such material. ALGÉUS (*e.g.*, 1950) has presented evidence that different algae have different capability in deaminating amino acids.

It seems, however, premature to transfer directly the experimental results to natural conditions. RODHE has shown (*l.c.*) that *Asterionella*, which in culture experiments requires a comparably high phosphorus concentration, can hold its own also in lower concentration if the culture medium is lake water. The algae react to the combined influence of the variant factors and, furthermore, in nature an unknown number of uncontrollable ones are added, the importance of which cannot be estimated. Even the known factors have different effects according to in which combination they are. The optimum requirement of one factor can alter with the concentration of another (LUNDEGÅRDH 1950, p. 270). The ion absorption, which is an active process, is affected by displacements in the ionic balance. Ion antagonistic effects are very often encountered. Thus the concentrations of nutrients in the substratum is not the sole factor governing the ion absorption.

Moreover, in a lake the water volume is much larger than in a culture vessel with a definite volume. Steadily new salts are added to the lakes from rivers and ground water and by replenishment from the bottom mud.

In culture experiments it is also of importance that pure algal material is employed, that is also free from bacteria.

Of other essential nutrients the concentrations common in lake waters are regarded to be sufficient for satisfactory growth (CHU 1942, HUTCHINSON 1944, PENNAK 1946, and RODHE 1948 a). USPENSKI (1927) considered iron to be a factor determining the distribution of plants, as

these require and tolerate variously high concentrations of iron. PRINGSHEIM (1934) and RODHE (1948 a) are sceptical of this opinion. CHU'S (1942) investigations indicate that the algae can hold their own in very low calcium concentrations. Of the *Chlorococcales* *Chlorella*, *Ankistrodesmus* and *Scenedesmus* grow rather well in a calcium concentration 1000 to 5000 times less than the optimal concentration (see further ÖSTERLIND 1949). *Coccochloris* grows well even if the element is completely excluded (GERLOFF *et al.* 1951). Also *Asterionella formosa* requires only a small supply of Ca (LUND 1950).

*Trace elements.* The same trace elements as in the higher plants seem to be essential for the planktic forms (STILES 1946). These elements could thus also be expected to be limiting factors. On one side small concentrations are required, on the other higher concentrations are toxic as is generally the case with heavy metals (GRINTZESCO and PETERFI 1936, GUSEVA 1939 and 1940, and GREENFIELD 1942). By strong fluctuations upwards in pH the solubility of these metals is decreased, at low pH-values the effect is the reverse. Especially in dystrophic waters the manganese concentration can be high (ÅBERG and RODHE 1942). According to PENNAK (1946) there is evidence that copper can be accumulated in the hypolimnion in summer in sufficient quantities to be toxic for the plankton.

Various algae have proved to have different sensitivity to toxic compounds. HERVEY (1949) has found that diatoms seem to be more sensitive to bichromate than the chlorococccals. GUSEVA (1940) has established that the *Protococcus* group is most resistant and the blue-green algae most sensitive to poisoning by copper sulphate. The different sensitivity of the algae is also utilized when lakes are sprayed with this compound (DOMOGALLA 1941 and RODHE 1948 b).

*Growth substances.* It may be assumed that the algae like the higher plants are able to synthesize their growth substances. HUTCHINSON and SETLCW (1946) believe that the plankton algae can produce thiamin. According to HARVEY (1939) a marine diatom studied by him seems, however, to be dependent upon an external organic substance. This is present only in the winter, which fact might cause the appearance of the alga in the winter period. The investigations by HUTCHINSON and SETLOW (1946) on the niacin concentrations in two American lakes prove that this vitamin has its highest concentration in the winter. Compounds of this type thus might sometimes constitute limiting factors. In lakes with low production of plankton it is possible, for example, that the substances in question do not even in the winter occur in

adequate amounts. The periodicity of the algae concerned might also be explained by the periodic appearance of such essential compounds.

Appreciable quantities of soluble organic substances are to be found in the water, 3 to 60 mg. per litre according to PENNAK (1946). The possibility cannot be precluded that some of these substances will be revealed as growth promotors or growth inhibitors. Already in 1932 PEARSALL declared that according to his experience the blue-green algae seemed to require organic compounds for their growth. RODHE (1948 a) thought the same regarding *Gloeotrichia*, as he did not succeed in cultivating it in a completely inorganic substratum. It has for a long time been known that the growth of many algae is promoted if soil extracts are added to the culture medium. *Gloeotrichia* and several other blue-green algae are now cultivated in a pure inorganic nutrient solution (GERLUFF *et al.* 1950 a and b). This does not prove, however, that the blue-green algae are not favoured more than others by organic substances.

There is evidence that *Chlorella* is able to produce an antibiotic, which inhibits its own growth if it is not removed from the medium (*e.g.*, PRATT *et al.* 1940). Chlorellin has not been found to have a disturbing action on the development of other algae. Such algostatic substances are, however, secreted according to LEFÈVRE *et al.* (1948, 1949, and 1951) from several species studied by them. For that reason certain species cannot grow together in cultures, *e.g.*, *Chlorella pyrenoidosa* and *Pediastrum duplex*. It is, however, too early to discuss the significance of these inhibitors excreted in nature where they become strongly diluted. They must be most active when their producers attain maximal development, that is, in connexion with water-bloom.

An example of the fact that natural waters can contain substances essential for the plants in small concentrations is STÅLFELT's discovery (1948 and 1949) of two viscosity changing factors, which are required by the plants without being produced by themselves (at least in sufficient quantities). They exhibit a periodical appearance in nature with a maximum in the autumn after the defoliation. The plasma viscosity is probably of great importance for several physiological processes in the plasma (see the discussion in STÅLFELT 1949). Nothing is known about the special effects of the substances on the water organisms. Like niacin they are most concentrated in the cold season and therefore they could possibly contribute to a periodical appearance of sensitive species. Their organic constitution has not yet been fully elucidated.

*Hydrogen ion concentration.* IVERSEN (1929) concluded that the

occurrence of higher aquatic plants was determined by the pH of the water. He also pointed out that the plankton changed with this factor (*l.c.*, p. 295). ALGÉUS (1946) and other authors before him (see ALGÉUS' discussion p. 158 *et seq.*) have shown experimentally that the growth of the algae is affected by the pH. It is naturally difficult to distinguish between the direct and indirect effects of this factor. The pH directly affects the charge of the plasma. In this case very high and very low pH-values are necessary for completely checking the ion absorption (LUNDEGÅRDH 1950). Small organisms can be expected to be more sensitive than larger ones on account of the less effective internal buffer capacity.

The indirect effects are far-reaching and difficult to study. The control of the carbon dioxide content of the water probably belongs to the most important ones. This must be significant for such organisms which are incapable in utilizing the bicarbonate as a source of carbon. The solubility of heavy metals is also altered by variations in the hydrogen ion concentration, as mentioned previously. The iron absorption of the algae is made difficult by a high pH (USPENSKI 1927, ALGÉUS 1946). Free ammonia can also be formed at such pH values and this compound is toxic to the organisms (*cf.* LUNDEGÅRDH 1950). Thus it must not be overlooked that the hydrogen ion concentration of the water may be of decisive importance at least at more extreme values.

*Carbon dioxide.* The bicarbonate content in the water must exert a great influence on the composition of the species in the waters. According to ÖSTERLIND (1951 and the literature there cited) two types as regards the capability of utilizing different carbon sources seem to exist among the algae: 1. The *Scenedesmus* type, which assimilates bicarbonate well if the cultures are young and 2. The *Chlorella* type, which lacks the capability almost completely.

In very high pH, which can easily arise in bicarbonate-rich waters containing an abundant vegetation, only plants capable of utilizing bicarbonate as the source of carbon can live, since free carbon dioxide is practically absent.

*Oxygen.* In the free surface water oxygen deficiency does not generally exist. The plants thus have no difficulty in supplying their need of this gas for respiration, and oxygen cannot reasonably be considered as a limiting factor for the plankton.

As is apparent from the discussion above there is no conclusive evidence that the chemical factors completely control the distribution of the plants in nature. Field ecological studies have not even yielded

concordant results as to the correlation between possible factors and the vegetation (*e.g.*, the phosphorus factor). Sometimes determinable quantities of a probably essential element are lacking, although the plankton is high-productive (*e.g.*, SPENCER 1950). The fact that the correlations are mostly slight, may likely be due to the fact that the influence of the individual factors is modified by the interplay between all the factors involved.

Too little is known about the relation between the plants and their environments. Thus this point must first and foremost be attacked by research. *Cf.* HUTCHINSON's discussion (1944) of physiological adaptation. At present one must rely upon more or less confirmed assumptions of the decisive effects of the factors.

*The chemical conditions in the lakes studied.* The chemical analyses of the lake waters performed by ALMESTRAND (1951) show, as is already mentioned (p. 18), a marked difference in the total electrolyte content. This is caused chiefly by the different calcium bicarbonate contents. Potassium and magnesium among others also decrease gradually like the specific conductivity, as well as the chloride and sulphate concentration. The phosphorus, nitrogen and iron contents vary irregularly and do not seem to follow the total electrolyte curve.

The greatest qualitative plankton differences seem to coincide with the greatest variations in the electrolyte content, that is, between the three lake groups A, B and C. Since the calcium bicarbonate constitutes the most varying element (figure 16), it is possible that this electrolyte exerts a selective influence on the occurrence of the planktic forms.

It is not clear, whether the calcium ion is essential for the algal growth (WINOKUR and ROBBINS 1948). It may, however, have a limiting effect in high concentrations, as different species vary in their tolerance of large calcium amount (CHU 1942). The bicarbonate ion can be supposed to play a decisive role on account of its importance in photosynthesis.

Consequently it is a plausible assumption that the calcium bicarbonate is the most important limiting factor rather than, for example, phosphorus and nitrogen as far as the chemical factors in the lakes investigated are concerned.

Some other controlling factors must, however, also be involved. As is seen from the figure 16 the bicarbonate curve does not show any significant differences within group A, although there is a well marked difference in the plankton composition between the so-called *Myxo-*



*phyceae*-rich and *Myxophyceae*-poor lakes. Nor do the remaining ions determined exhibit any considerable variations within the group. This fact possibly implies that factors other than the common nutrients cause the plankton differences in question. As the lakes discussed are situated in agricultural and densely populated districts it can be supposed that the differences observed have their origin in the organic substances from sewage and other contaminations. The differences in the composition of plankton between the *Myxophyceae*-rich and -poor lakes in group B are not corresponded by any variation in the bicarbonate content. (In Kvesarumssjön slightly higher values of the ions discussed are to be found, but not in Tjörnarpssjön.)

Naturally too great a stress must not be laid on the correlation obtained in this investigation, nor on the absence of any correlation. Both the water-chemical analyses and the plankton determinations should be carried out more regularly with short intervals during the whole year in order to obtain reliable correlations. HUTCHINSON (1944 p. 25) is very doubtful if it ever will be possible to arrive at a solution of the problem of the natural distribution of the species by merely observing the chemical factors of the habitats.

**Climatic factors.** The chemical factors are only a part of the ecological complex of factors regulating the environmental conditions of the plankton. It is a general experience that light and temperature also have an apparent influence on the production of plankton. Thus the plankton bloom is most abundantly developed in hot, calm, sunny days. The summer of 1947 was especially favourable for such phenomena. It is, however, difficult to prove to what degree these factors are of importance for the qualitative distribution.

The light is rapidly absorbed by the water, the more strongly the more coloured the water is. From the investigations by MEYER and HERITAGE (1941) on the photosynthesis in *Ceratophyllum* growing at different depths of water it is evident that the turbidity is of great importance for the vertical distribution of water plants. The compensation point was obtained at low turbidity at a depth of 8 to 10 m. but at maximal turbidity already at 1 to 2 m. In the lakes of group A there is, as already mentioned, a difference in the composition of plankton between transparent and turbid lakes. The rich development of *Myxophyceae*, which float up to the surface, seems to contribute to the low light supply in the turbid lakes. As to fresh water it is still unknown whether the supply of light of different wavelengths can have a qualitatively selective action.

According to FINDENEGG (1943) the various plankters have different requirements of light and heat, which explains their periodic occurrence. He also believes that it is possible to explain in several cases the distribution of the different species within his area by means of these factors.

RODHE (1948 a) is convinced that the cause of the absence of *Melosira islandica* ssp. *helvetica* from Säbysjön and the presence of the same species in the adjacent Valloxen is to be found in the different temperature conditions of these two lakes.

In the lakes under consideration it seems probable that the light does not primarily constitute a limiting factor as regards the qualitative differences in plankton. The discussion in the macrophyte chapter (p. 18) may largely be valid also in this connexion. The differences in the plankton composition between the lake groups A and C cannot be explained as a consequence of various transparency conditions, as group A comprises many turbid lakes as well as the most transparent ones within the whole area.

The temperature conditions of the lakes here studied do not deviate considerably from one another, neither for physiographical nor climatic reasons. Slight differences in the water temperature have naturally been recorded. The temperature rises for example somewhat more slowly in spring in Västersjön and Rösjön. It also changes unequally rapidly in shallow and deep lakes (*cf.* LUNDH 1951 b, p. 23). However, the deviations are probably less than the temperature amplitude of the species occurring in the lakes. No pronounced stratification seems to prevail (with the possible exception of Västersjön and Rösjön, which have not been studied from this point of view).

**Biotic factors.** The great importance of competition in combination with other factors has been discussed previously (*e.g.*, p. 97), as well as the effects of algostatics (p. 95).

### Quantitative occurrence.

The seasonal changes in the plankton production are apparent and they have therefore attracted great attention. The reasons are on the whole unknown, however, perhaps due to the fact that they may vary in different environments.

A species can occur in a lake during the main part of a year only in a few specimens and then it very rapidly increases to high production. The time for this phenomenon is not constant. The pulse can also vary

in abundance or is sometimes completely absent. Everything indicates that a special combination of factors is required.

**E d a p h i c f a c t o r s.** The supply of nutrients is the first causal factor to be considered. When it is exhausted the increase in production must stop naturally. If the supply of nutrients is the sole limiting factor all the plankton pulses should be confined to the periods with the highest concentrations of nutrients and not disappear before the exhaustion of the supplies. This is not the case, however, in reality. The *Myxophyceae* pulses appear when the supplies of nitrogen and phosphorus are lowest (PEARSALL 1932), the pulses can cease although the supply of nutrients is considerable (PENNAK 1946), high productions of the same species can appear at different occasions and with different supply of nutrients among other conditions. The Wisconsin limnologists (see the discussion in WELCH 1935 and HUTCHINSON 1944) have for a long time been of the opinion that phosphorus and nitrogen cannot be limiting factors. The manuring experiments of JUDAY (1942) illustrated that inorganic manure substances had no effects on the plankton production. Nor does OHLE (1934) believe that phosphorus generally is a minimum factor. Some researchers, however, are convinced of the limiting effects of these elements (see WELCH 1935, RILEY 1940 and 1943).

JUDAY's work is the only one carried out in the field. His results have thus the greatest importance for such an ecological discussion as this. RILEY, who made culture experiments, obtained a positive effect by an addition of phosphorus and nitrogen, it is true, but he used concentrations several times higher than those encountered in the lakes studied here.

Investigators which have experimentally tried to obtain an explanation (*e.g.*, RODHE 1948 a and CHU 1943) are inclined to think that phosphorus and nitrogen in several cases are not available in sufficient quantities in the water, and therefore are limiting factors. According to RODHE the phosphorus content can also be too high for some species (*Dinobryon* and *Uroglena*) and thus act as a maximum factor.

As regards *Asterionella* there is reason for assuming that the supply of silicon is of decisive importance for the high production (LUND 1950). Such a correlation is also rather plausible as concerns other diatoms (*cf.* PEARSALL 1932).

It has not yet been proved whether other factors such as minor elements and growth substances can be responsible for the initiation and checking of high production.

**Climatic factors.** The general observation that water-bloom is particularly prominent during warm, dry summers might indicate that climatic factors play a role in the development of high production. RILEY (1943) states that the growth rate of *Nitzschia closterium* is regulated by the weather. CHANDLER (1944) and CHANDLER and WEEKS (1945), who have studied the plankton development in Western Lake Erie, discuss the possible causes of the varying spring and autumn pulses and arrive at that conclusion that phosphorus and nitrogen certainly have a very limited effect on the abundance of the plankton production. According to their opinion the turbidity and water-temperature are primarily responsible for it. Both factors are more or less dependent upon the climate (*e.g.*, solar radiation and precipitation).

**Biotic factors.** RODHE (1948 b) observed that after spraying Lake Norrviken with copper sulphate the *Chlorophyceae* attained high production when the *Myxophyceae* had disappeared. As the copper sulphate addition *per se* cannot have favoured them (RODHE *l.c.*, p. 55) the only remaining explanation must be that the presence of the blue-green algae in some way inhibited their development. In this case the absence of mass production of *Chlorococcales* cannot have its origin in the lack of nutrients or unfavourable climatic conditions. Such substances as chlorellin (*cf.* p. 95) can possibly check high production even in nature. STOREY (1943) states that *Asterionella* seems to have difficulties in growing in lake waters which have contained a bloom of the same alga. HUTCHINSON and SETLOW (1946) could not, however, detect any antibiotic substances in Bantam Lake and Linsely Pond. The effects of such possible growth inhibitors have not been studied in natural conditions and there are still only single observations reported.

### Influence by culture.

The influence by culture which the lakes in cultivated areas are subjected to seems to be of great importance for both the quantitative and qualitative occurrence of the algae. In Switzerland it has been possible to follow the development of lakes affected by culture. The studies have shown that lakes poor in plankton and characterized by oxygen-rich bottom water have passed into a state with high-productive plankton and the bottom layer has become almost deficient in oxygen and rich in hydrogen sulphide (see papers in Verh. Int. Ver. theor. angew. Limnol. X. 1949).

The lakes are supplied with large amounts of electrolytes by sewage

and manure, *i.a.* phosphates, nitrates, and ammonium salts. If nitrogen and phosphorus previously have constituted minimum factors the plankton production will increase considerably. The lake waters are furthermore enriched by organic matter of different kinds, *e.g.*, decomposition products of proteins and growth substances. Some of these compounds will possibly favour the growth, others will perhaps check it (*cf.* the manuring experiments by JUDAY 1942 by which he has proved that the organic substances and not the inorganic ones are responsible for the increased plankton production). A qualitative selection among the plankters can be one of the consequences. Such species must be favoured, for example, which are capable of utilizing organic nitrogen sources (*cf.* ALGÉUS 1950). Substances toxic to the plants even in small quantities can also be transported with contaminated water *e.g.*, metal salts.

By lowering and regulation of the lake surface intervention also takes place in the natural development which must bring about notable consequences. LILLIEROTH (1950 b) has proved that both the macrophyte and plankton vegetation have been changed by human interferences qualitatively and partly quantitatively in the lakes studied by him.

### Conclusions.

It is evident that much remains to be done before the problem of the causes of the different qualitative and quantitative occurrence of the plankton in nature can be regarded as satisfactorily elucidated. At present general conclusions cannot be drawn. Comparative field studies must be restricted to a small area, where only few factors exhibit great variations. Moreover experimental investigations should be conducted to discover the special physiological relations of the individual species to their surroundings.

It has not been proved that the important nutrients phosphorus and nitrogen which are present mostly in small quantities (*cf.* RODHE 1951) give rise to qualitative differences in plankton. These differences are in the area under consideration correlated with changes in the electrolyte content, while no definite connection to phosphorus and nitrogen can be established. The substances concerned must, however, naturally be thought of as minimum factors for high production even if they cannot always be proved to be responsible for their initiation and cessation.

The content of bicarbonate is a chemical factor whose importance

has not been emphasized especially strongly hitherto. Its significance in photosynthesis has not been noticed until the last years. In view of its use as a source of carbon it is likely to determine the composition of species and also the abundance of high production.

The significance of substances toxic in small concentrations must not be overlooked.

Up until now the soluble organic substances have also been neglected. Before any close investigations on their possible effects on the growth of plankton have been carried out, they should not be excluded from that group of factors which can be considered of importance for the development of the plankters.

The numerous field ecological investigations performed have paid attention to many factors which may be regarded as controlling factors. The value of such studies in the future will be greatly increased if the field work is combined to a still higher degree than hitherto with experimental research.



## Epiphytic diatoms.

### Distribution of the species.

#### Material.

Only epiphytic diatom samples from shallow water have been examined, and they are derived from different kinds of plant material according to what was available at the time of the excursion. Most of the samples have been gathered during the spring and autumn of 1948 and 1949. A few samples from a single locality cannot give a representative picture of the diatom flora of a lake. A great number of samples must thus be examined from a lake for obtaining a list of species as complete as that derived from one or two plankton samples. The number of samples investigated in group A varies between three and eleven for every lake (from Sövdeborgssjön only two), in the group B nine and eleven and in group C seven and nine, which numbers must be regarded as fairly insufficient.

Species which are more or less restricted to a definite substratum, for example, *Achnanthes hungarica* to *Lemna*, become recorded very irregularly. Thus *Achnanthes hungarica* has been found only a few times in the samples studied. In pure lemnid samples, however, it is more seldom absent. Species which are strongly restricted to a certain substratum are thus not suitable for these comparative studies, and therefore they can be excluded without hesitation. The summer samples are, as already mentioned, in the minority. Typical summer forms, as for example, *Epithemia* species, would, therefore, have been under-represented if the records had not been completed by examination of some further summer samples.

The material has been cleansed partly by boiling in sulphuric or nitric acid, partly by red-heating. The methods have been described by HUSTEDT *i.a.* in PASCHER H. 10 (1930) and MÖLLER (1944). StyraX prepared by MAX MÖLLER and hyrax have been used for mounting.

The species have been identified mainly after HUSTEDT in PASCHER (*l.c.*) and in RABENHORST's Kryptogamenflora (1930). Furthermore, the

original literature and other literature with drawings have been consulted *e.g.*, HUSTEDT (*i.a.* 1924, 1942, 1945, and 1950), FOGED (*i.a.* 1950 and 1951), MÖLLER (1950), JØRGENSEN (1948), PETERSEN (1950).

### Species discussed.

As regards the genera *Nitzschia* and *Pinnularia* the studies have not yet been completed. For this reason these genera have not been included in the discussion, with the exception of some easily recognizable *Nitzschia* species. The *Pinnularia* species are, moreover, to a large extent bottom organisms and can therefore suitably be treated in connexion with the bottom samples.

As the diatoms have been identified in especially prepared material it has been impossible to distinguish between individuals living at the moment of fixation and dead ones. Thus dead specimens which have not grown on the locality where they have been found but originate from the plankton or the bottom cannot readily be excluded as the dead specimens in the plankton samples. If uncleaned material is examined only some species can be identified. The small forms are, moreover, very often covered by *e.g.*, detritus. The plankton organisms seem to be able to continue living after having adhered to the plants. Therefore, it is a difficult task to separate the normal epiphytes from the other species noted in the samples. It can be assumed, however, that the transported forms are numerically so inferior that they will not generally be included in the lists of species (with the exception of planktic forms).

Some species observed in the slides are termed euplankters by HUBER-PESTALOZZI (Teil 2: 2) and HUSTEDT in PASCHER. A comparison has been made between the findings in the plankton lists and the diatom lists as concerns these species (table 8). Some other species whose mode of life has not been ascertained have also been included in the same list.

*Amphiprora ornata* (litoral form according to HUSTEDT) is in the diatom list represented from two localities in the plankton list from three. The records are too few to obtain a definite idea of its mode of life. It can just as well be a plankter as an epiphyte or both. Nothing indicates that it is preponderantly epiphytic (*cf.* the discussion in plankton p. 80).

*Cyclotella comta* (euplankter according to HUBER-PESTALOZZI and HUSTEDT) is recorded from more localities in the diatom list. This can, however, be due to the fact that it has been overlooked in the plankton

samples, where only the algae living at the moment of fixation have been included. Furthermore a larger number of diatom preparations have been examined.

*Cymatopleura solea* (euplankter according to HUBER-PESTALOZZI) appears only in single specimens and can thus also easily be overlooked in a plankton sample. Considerably more localities are, however, given in the diatom list. This does not speak in favour of its being a typical plankter.

*Diatoma elongatum* (mainly euplankter according to HUBER-PESTALOZZI and HUSTEDT) seems rather to be an eurytopic form.

*Fragilaria crotonensis* (euplankter according to HUBER-PESTALOZZI). It never occurs in larger quantities in the diatom samples. It is, moreover, recorded from several plankton localities without being observed in diatom preparations from the same lakes. It is probably an obligate plankter.

The *Melosira* species *ambigua*, *islandica* and *granulata* are generally regarded as typical plankton forms. They are, however, also abundant in the diatom slides (even in large quantities). This is probably due to the fact that they easily adhere to the plants, as they can also annoy fishermen by clinging to the nets. *Melosira granulata* has been found in the diatom samples from Rösjön, where it has not yet been observed as a plankter. Its occurrence is, however, not surprising. Probably it will also be found in the plankton samples. The *Melosira* species seem to be obligate plankters.

The species of *Stephanodiscus* are considered euplankters by HUBER-PESTALOZZI and HUSTEDT. They are according to the table more frequent in the epiphytic samples. As far as *St. astraea* is concerned it is possible that the plankton material studied has not been comprehensive enough. As regards the two other species this fact cannot be the whole explanation.

The appearance of *Tabellaria fenestrata* in the epiphytic samples does not contradict the opinion that it is an obligate euplankter.

*Tabellaria flocculosa* is by HUBER-PESTALOZZI considered a possible facultative plankter. The table illustrates that it is as frequent in the plankton samples as in the epiphytic ones. Thus it seems to be a normal plankton component in these lakes. Its great dominance in some epiphytic samples indicates that it is an equally normal epiphyte.

The following species have with reference to the above been excluded from the diatom list: *Melosira ambigua*, *M. islandica* ssp. *helvetica*, *M. granulata*, *Cyclotella comta*, *Fragilaria crotonensis*, and *Tabellaria*



*fenestrata*. The pronounced euplankter *Asterionella formosa* has also been omitted.

As the investigation has been carried out in a comparative sense there has been no reason for discussing all species found. Thus in the published tables (9 to 13) only species observed in at least nine localities have been listed except in two cases, namely 1. if the species are restricted to group B or C or one of these, or have their main distribution here and 2. if they seem to be confined to group A. In the first case it ought to be quite justified to include species with few localities. It can hardly be mere chance that they are absent in group A as this group is represented by the greatest number of lakes. In the latter case it is less justified. It is naturally not necessary that species found in few localities in group A will prove to be restricted to this group when closer investigations have been made.

### Distribution of the species discussed.

#### Qualitative occurrence.

The tables 9 to 13 illustrate the distribution of the species studied within the three lake groups.

Table 9 includes species which seem to be confined to group A. On account of the small number of localities the classification is not especially reliable.

Table 10 shows species belonging to the groups A and B and hitherto not recorded from group C. In addition three species are listed here which have been noted so far only from group A but on account of their wide range are likely to be found even in group B.

Table 11 comprises species almost completely restricted to the groups B and C or to one of them.

Table 12 includes species showing an evident concentration to the groups B and C. They have, however, also isolated localities in group A.

Table 13 contains the ubiquitous species.

As is obvious from table 13 conspicuously many epiphytic diatoms are ubiquitous in comparison with the planktic forms (*cf.* the survey below).

| Species restricted to       | Group A | A+B | B+C      | B  | B+C | C  | Ubiquists | Total number of species |
|-----------------------------|---------|-----|----------|----|-----|----|-----------|-------------------------|
|                             | %       | %   | (mainly) |    | %   | %  | %         |                         |
| Epiphytic diatoms . . . . . | 12      | 16  | 9        | 7  | 4   | 9  | 43        | 148                     |
| Plankton . . . . .          | 15      | 35  | 7        | 2  | 3   | 11 | 27        | 150                     |
| Planktic diatoms . . . . .  | —       | 29  | 10       | 10 | —   | 10 | 43        | 21                      |





Table 10. Survey of the species found in the groups A and B but hitherto not recorded in group C.

| Lake   | Råb. | Kiaby. | Norr. | Ste. | Ydd. | Bött. | Havg. | Björk. | Häck. | Svan. | Krk. | Vomp. | Helje. | Sö. | Söborg. | Snog. | Ell. | Krag. | Gyll. | Fjäll. | Tun. | E. Ri. | V. Ri. | Bos. | Dag. | Kves. | Tjörn. | Rö. | Va. |   |
|--|------|--------|-------|------|------|-------|-------|--------|-------|-------|------|-------|--------|-----|---------|-------|------|-------|-------|--------|------|--------|--------|------|------|-------|--------|-----|-----|---|
| <i>Cocconeis pediculus</i> Ehr.              | 1    | 1      | 1     | 1    | 1    | 1     | 1     | 1      | 1     | 1     | 1    | 1     | 1      | 1   | 1       | 1     | 1    | 1     | 1     | 1      | 1    | 1      | 1      | 1    | 1    | 1     | 1      | 1   | 1   |   |
| <i>Cymatopleura solea</i> (Bréb.) W. Smith   | 1    | 1      | 1     | 1    | 1    | 1     | 1     | 1      | 1     | 1     | 1    | 1     | 1      | 1   | 1       | 1     | 1    | 1     | 1     | 1      | 1    | 1      | 1      | 1    | 1    | 1     | 1      | 1   | 1   |   |
| <i>Cymbella lanceolata</i> (Ehr.) v. Heurck  | 1    | 1      | 1     | 1    | 1    | 1     | 1     | 1      | 1     | 1     | 1    | 1     | 1      | 1   | 1       | 1     | 1    | 1     | 1     | 1      | 1    | 1      | 1      | 1    | 1    | 1     | 1      | 1   | 1   |   |
| <i>Epithemia sorex</i> Kütz.                 | 1    | 1      | 1     | 1    | 1    | 1     | 1     | 1      | 1     | 1     | 1    | 1     | 1      | 1   | 1       | 1     | 1    | 1     | 1     | 1      | 1    | 1      | 1      | 1    | 1    | 1     | 1      | 1   | 1   |   |
| <i>Fragilaria brevistriata</i> Grun.         | 1    | 1      | 1     | 1    | 1    | 1     | 1     | 1      | 1     | 1     | 1    | 1     | 1      | 1   | 1       | 1     | 1    | 1     | 1     | 1      | 1    | 1      | 1      | 1    | 1    | 1     | 1      | 1   | 1   |   |
| — <i>construens</i> (Ehr.) Grunow            | 1    | 1      | 1     | 1    | 1    | 1     | 1     | 1      | 1     | 1     | 1    | 1     | 1      | 1   | 1       | 1     | 1    | 1     | 1     | 1      | 1    | 1      | 1      | 1    | 1    | 1     | 1      | 1   | 1   |   |
| <i>Cyrosigma attenuatum</i> (Kütz.) Rabb.    | 1    | 1      | 1     | 1    | 1    | 1     | 1     | 1      | 1     | 1     | 1    | 1     | 1      | 1   | 1       | 1     | 1    | 1     | 1     | 1      | 1    | 1      | 1      | 1    | 1    | 1     | 1      | 1   | 1   |   |
| <i>Navicula anglica</i> Ralfs                | 1    | 1      | 1     | 1    | 1    | 1     | 1     | 1      | 1     | 1     | 1    | 1     | 1      | 1   | 1       | 1     | 1    | 1     | 1     | 1      | 1    | 1      | 1      | 1    | 1    | 1     | 1      | 1   | 1   |   |
| — <i>cincta</i> (Ehr.) Kütz.                 | 1    | 1      | 1     | 1    | 1    | 1     | 1     | 1      | 1     | 1     | 1    | 1     | 1      | 1   | 1       | 1     | 1    | 1     | 1     | 1      | 1    | 1      | 1      | 1    | 1    | 1     | 1      | 1   | 1   |   |
| — <i>cuspidata</i> Kütz.                     | 1    | 1      | 1     | 1    | 1    | 1     | 1     | 1      | 1     | 1     | 1    | 1     | 1      | 1   | 1       | 1     | 1    | 1     | 1     | 1      | 1    | 1      | 1      | 1    | 1    | 1     | 1      | 1   | 1   |   |
| — <i>gracilis</i> Ehr.                       | 1    | 1      | 1     | 1    | 1    | 1     | 1     | 1      | 1     | 1     | 1    | 1     | 1      | 1   | 1       | 1     | 1    | 1     | 1     | 1      | 1    | 1      | 1      | 1    | 1    | 1     | 1      | 1   | 1   |   |
| — <i>gregaria</i> Donkin                     | 1    | 1      | 1     | 1    | 1    | 1     | 1     | 1      | 1     | 1     | 1    | 1     | 1      | 1   | 1       | 1     | 1    | 1     | 1     | 1      | 1    | 1      | 1      | 1    | 1    | 1     | 1      | 1   | 1   | 1 |
| — <i>Reinhardtii</i> Grun.                   | 1    | 1      | 1     | 1    | 1    | 1     | 1     | 1      | 1     | 1     | 1    | 1     | 1      | 1   | 1       | 1     | 1    | 1     | 1     | 1      | 1    | 1      | 1      | 1    | 1    | 1     | 1      | 1   | 1   | 1 |
| — <i>scutelloides</i> W. Smith               | 1    | 1      | 1     | 1    | 1    | 1     | 1     | 1      | 1     | 1     | 1    | 1     | 1      | 1   | 1       | 1     | 1    | 1     | 1     | 1      | 1    | 1      | 1      | 1    | 1    | 1     | 1      | 1   | 1   | 1 |
| — <i>tuscula</i> (Ehr.) Grun.                | 1    | 1      | 1     | 1    | 1    | 1     | 1     | 1      | 1     | 1     | 1    | 1     | 1      | 1   | 1       | 1     | 1    | 1     | 1     | 1      | 1    | 1      | 1      | 1    | 1    | 1     | 1      | 1   | 1   | 1 |
| <i>Nitzschia amphibia</i> Grun.              | 1    | 1      | 1     | 1    | 1    | 1     | 1     | 1      | 1     | 1     | 1    | 1     | 1      | 1   | 1       | 1     | 1    | 1     | 1     | 1      | 1    | 1      | 1      | 1    | 1    | 1     | 1      | 1   | 1   | 1 |
| — <i>gracilis</i> Hantzsch                   | 1    | 1      | 1     | 1    | 1    | 1     | 1     | 1      | 1     | 1     | 1    | 1     | 1      | 1   | 1       | 1     | 1    | 1     | 1     | 1      | 1    | 1      | 1      | 1    | 1    | 1     | 1      | 1   | 1   | 1 |
| — <i>linearis</i> W. Smith                   | 1    | 1      | 1     | 1    | 1    | 1     | 1     | 1      | 1     | 1     | 1    | 1     | 1      | 1   | 1       | 1     | 1    | 1     | 1     | 1      | 1    | 1      | 1      | 1    | 1    | 1     | 1      | 1   | 1   | 1 |
| — <i>recta</i> Hantzsch                      | 1    | 1      | 1     | 1    | 1    | 1     | 1     | 1      | 1     | 1     | 1    | 1     | 1      | 1   | 1       | 1     | 1    | 1     | 1     | 1      | 1    | 1      | 1      | 1    | 1    | 1     | 1      | 1   | 1   | 1 |
| — <i>Rhoicosphenia curvata</i> (Kütz.) Grun. | 1    | 1      | 1     | 1    | 1    | 1     | 1     | 1      | 1     | 1     | 1    | 1     | 1      | 1   | 1       | 1     | 1    | 1     | 1     | 1      | 1    | 1      | 1      | 1    | 1    | 1     | 1      | 1   | 1   | 1 |
| — <i>Rhopalodia gibba</i> (Ehr.) O. Müll.    | 1    | 1      | 1     | 1    | 1    | 1     | 1     | 1      | 1     | 1     | 1    | 1     | 1      | 1   | 1       | 1     | 1    | 1     | 1     | 1      | 1    | 1      | 1      | 1    | 1    | 1     | 1      | 1   | 1   | 1 |
| — <i>Stephanodiscus Hantzschii</i> Grun.     | 1    | 1      | 1     | 1    | 1    | 1     | 1     | 1      | 1     | 1     | 1    | 1     | 1      | 1   | 1       | 1     | 1    | 1     | 1     | 1      | 1    | 1      | 1      | 1    | 1    | 1     | 1      | 1   | 1   | 1 |
| — <i>Synedra parasitica</i> W. Smith         | 1    | 1      | 1     | 1    | 1    | 1     | 1     | 1      | 1     | 1     | 1    | 1     | 1      | 1   | 1       | 1     | 1    | 1     | 1     | 1      | 1    | 1      | 1      | 1    | 1    | 1     | 1      | 1   | 1   | 1 |
| — <i>Vaucheriae</i> Kütz. <sup>1</sup>       | 1    | 1      | 1     | 1    | 1    | 1     | 1     | 1      | 1     | 1     | 1    | 1     | 1      | 1   | 1       | 1     | 1    | 1     | 1     | 1      | 1    | 1      | 1      | 1    | 1    | 1     | 1      | 1   | 1   | 1 |

<sup>1</sup> Probably closely related to *Fragilaria capitellata* (Grun.) Boye P. (FOGED 1951).



In the figures for B, B+C and C those diatom species are also included which outside the groups mentioned are to be seen in Tunbyholmssjön. The number of diatoms in the columns A and B is somewhat uncertain owing to the few localities known. It is to be expected that some species now restricted to group B will also be found in group C. Nor is it improbable that some of the species of group C will be observed in group B, when more samples have been examined. A few identifications in group B are uncertain.

The number of species in the columns A, B+C and C are about the same for epiphytic diatoms and plankton. The number of species common to the groups A and B is, however, less among the diatoms, whereas the number of species restricted to group B is greater.

Each group seems to have some »specific» species. Group B has several species in common with group A but not so many as among the planktic forms, and a greater affinity to group C can be observed. Group A is remarkably uniform as to the composition of species. Only one lake deviates, namely Tunbyholmssjön. This lake is very closely connected to the groups B and C.

#### Q u a n t i t a t i v e o c c u r r e n c e .

The material examined cannot be regarded as sufficiently extensive for studying the possible quantitative differences between the lakes. No thorough estimation of the relative occurrence of the different species after the pattern of FCGED (1947), JØRGENSEN (1948) and MØLLER (1950) among others has been carried out. In the examination of some of the slides the numerically strongly predominating species have been noted, however, if such have been present. Table 14 comprises the observed highly frequent species from 43 slides from group A (including two from Tunbyholmssjön), 13 from group B and 12 from group C.

The groups B and C consist of few lakes, but even in spite of this the number of highly frequent species is notably small. On the whole only the two *Tabellaria* species are concerned. In group A considerably more species have been recorded. All highly frequent species from the groups B and C are found here, but several others are also included, especially species belonging to *Cocconeis*, *Cymbella*, *Epithemia* and *Stephanodiscus*. A negative difference between group A and the two other groups is the fact that the *Tabellaria* species, greatly predominating in the two last-mentioned groups, occur in high-frequency only in three

Table 12. Survey of the species showing an evident concentration to the groups B and C.

| Lake                                  | Rab. | Kibay. | Notr. | Levra. | Ste. | Ydd. | Börr. | Havg. | Björk. | Häck. | Svam. | Krk. | Vomb. | Helje. | Sö. | Söborg. | Snog. | Eil. | Krag. | Gyll. | Tun. | E. Rt. | W. Rt. | Bos. | Dag. | Kves. | Tjörn. | Rö. | Va. |
|---------------------------------------|------|--------|-------|--------|------|------|-------|-------|--------|-------|-------|------|-------|--------|-----|---------|-------|------|-------|-------|------|--------|--------|------|------|-------|--------|-----|-----|
| Achnanthes flexella (Kütz.) Brun      | 1    |        |       |        |      |      |       |       |        |       |       |      |       | 1      |     |         |       |      |       |       |      |        |        |      | 1    |       | 1      |     |     |
| Cymbella naviculiformis Auerswald     |      |        |       |        |      |      |       |       |        |       |       | 1    | 1     |        |     |         |       |      |       |       | 1    |        |        | 1    | 1    |       | 1      |     |     |
| — obtusa Greg.                        |      |        |       |        |      |      |       |       |        |       |       | 1    |       |        |     |         |       |      |       |       |      |        |        |      | 1    |       | 1      |     |     |
| — sinuata Greg.                       |      |        |       |        |      |      |       |       |        |       |       | 1    |       |        |     |         |       |      |       |       |      |        |        |      | 1    |       | 1      |     |     |
| Denticula tenuis Kütz.                |      |        |       |        |      | 1    |       |       |        |       |       |      |       |        |     |         |       |      |       |       |      |        |        |      |      |       | 1      |     |     |
| Eunotia arcus Ehr.                    |      |        |       |        |      | 1    |       |       |        |       |       | 1    |       |        |     |         |       |      |       |       |      |        |        |      |      |       | 1      |     |     |
| — monodon Ehr.                        |      |        |       |        |      | 1    |       |       |        |       | 1     |      |       |        |     |         |       |      |       |       |      |        |        |      |      |       | 1      |     |     |
| — pectinalis var. minor (Kütz.) Rabh. |      |        |       |        |      |      |       |       |        |       |       |      |       |        |     |         |       |      |       |       | 1    |        |        |      | 1    |       | 1      |     |     |
| — tenella (Grun.) Hustedt             |      |        |       |        |      |      |       |       |        |       |       | 1    |       |        |     |         |       |      |       |       |      |        |        |      | 1    |       | 1      |     |     |
| — venteris (Kütz.) O. Müll.           |      |        |       |        |      |      |       |       |        |       |       |      |       |        |     |         |       |      |       |       |      |        |        |      | 1    |       | 1      |     |     |
| Fragilaria virescens Ralfs            |      |        |       |        |      |      |       |       |        |       |       |      |       |        |     |         |       | 1    |       |       |      |        |        |      | 1    |       | 1      |     |     |
| Frustulia vulgaris Thwaites           |      |        |       |        |      |      | 1     | 1     |        |       |       |      | 1     |        |     |         |       |      |       |       |      |        |        |      | 1    |       | 1      |     |     |
| Melosira italica (Ehr.) Kütz.         |      |        |       |        |      |      |       |       |        | 1     |       |      |       |        |     |         |       |      |       |       |      |        |        |      | 1    |       | 1      |     |     |





|   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| — intermedia Grunow <sup>1</sup> .....      | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |   |
| — pinnata Ehrenberg .....                   | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |   |
| Gomphonema acuminatum Ehr. ....             | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |   |
| — acuminatum var. Brébissonii (Kütz.) Cleve | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |   |
| — angustatum (Kütz.) Rabh. ....             | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |   |
| — constrictum Ehr. ....                     | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |   |
| — gracile Ehr. ....                         | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |   |
| — intricatum Kütz. ....                     | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |   |
| — intricatum var. pumila Grun. ....         | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |   |
| — olivaceum (Lyngbye) Kütz. ....            | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |   |
| — parvulum Kütz. ....                       | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |   |
| Gyrosigma acuminatum (Kütz.) Rabh. ....     | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |   |
| Melosira varians C. A. Ag. ....             | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |   |
| Meridion circulare Agardh .....             | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |   |
| Navicula bacillum Ehr. ....                 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| — cryptocephala Kütz. ....                  | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| — hungarica var. capitata (Ehr.) Cleve      | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| — pupula Kütz. ....                         | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| — radiosa Kütz. ....                        | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| — Rotaeana (Rabh.) Grun. ....               | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| — Neidium dubium (Ehr.) Cleve               | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| — iridis (Ehr.) Cleve .....                 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| — Nitzschia angustata (W. Smith) Grun. .... | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| — dissipata (Kütz.) Grun. ....              | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| — palea (Kütz.) W. Smith .....              | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| — romana Grun. ....                         | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| — Opephora Martyi Héribaud .....            | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| — Stauroneis phoenicenteron Ehr. ....       | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| — Stephanodiscus astraea (Ehr.) Grun. ....  | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| — dubius (Fricke) Hustedt .....             | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| — Surirella biseriata Brébisson .....       | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| — Synedra acus Kütz. ....                   | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| — ulna (Nitzsch) Ehr. ....                  | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| — Tabellaria flocculosa (Roth) Kütz. ....   | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |

<sup>1</sup> According to FOGED (1951) Fragilaria Vaucheriae (Kütz.) Boye P.



Table 14. Survey of the high-frequent species in the three lake groups.

|                        |                        |                        |
|------------------------|------------------------|------------------------|
| Group A.               | — helvetica            | Group B.               |
| Achnanthes minutissima | — microcephala         | Cocconeis placentula   |
| Anomoeoneis exilis     | Diatoma vulgare        | Tabellaria fenestrata  |
| Cocconeis placentula   | Epithemia spp.         | — flocculosa           |
| Diatoma elongatum      | Eunotia arcus          |                        |
| Fragilaria intermedia  | Fragilaria capucina    | Group C.               |
| Synedra acus           | Gomphonema spp.        | Achnanthes minutissima |
| Tabellaria fenestrata  | Navicula sp.           | Anomoeoneis exilis     |
| — flocculosa           | Rhopalodia gibba       | Diatoma elongatum      |
|                        | Stephanodiscus spp.    | Fragilaria intermedia  |
| Achnanthes lanceolata  | Synedra ulna           | Synedra acus           |
| Cocconeis diminuta     | — Vaucheriae           | Tabellaria fenestrata  |
| — pediculus            |                        | — flocculosa           |
| Cyclotella comta       | Achnanthes minutissima |                        |
| Cymbella affinis       | Eunotia spp.           |                        |
| — amphicephala         | Tabellaria flocculosa  |                        |

The three last-mentioned species in group A are recorded from Tun.

lakes in group A, if Tunbyholmssjön is left out of consideration. The three lakes concerned are Siesjön (*T. fenestrata*), Håckebergasjön (*T. fenestrata*) and Sövdeborgssjön (*T. flocculosa*). No apparent difference between groups B and C can be established as to the highly frequent species.

## Results.

Judging from the above it can be stated that even as regards the distribution of the epiphytic diatoms differences are revealed, which justify the division of the lakes carried out according to the macrophyte vegetation. Even if many of the common diatoms are ubiquitous, each group has nevertheless several specific species. Both the qualitative and the preliminary quantitative studies indicate a marked limit between group A on one side and the groups B and C on the other. The differences between the two last-mentioned groups are less pronounced.

## Ecological discussion.

The table below gives a survey of the distribution of the studied epiphytic diatoms within the lake groups compared with the main components of the phytoplankton (blue-green algae, desmids, chlorococals and diatoms).

| Species restricted to          | Group A | A+B | (mainly) |    |     |    | C  | Ubiquists | Total number of species |
|--------------------------------|---------|-----|----------|----|-----|----|----|-----------|-------------------------|
|                                |         |     | B+C      | B  | B+C | C  |    |           |                         |
|                                | %       | %   | %        | %  | %   | %  | %  |           |                         |
| Epiphytic diatoms . . . . .    | 12      | 16  | 9        | 7  | 4   | 9  | 43 | 148       |                         |
| Planktic blue-greens . . . . . | 18      | 53  | 3        | —  | —   | —  | 26 | 38        |                         |
| » desmids . . . . .            | 11      | 14  | 4        | —  | 7   | 50 | 14 | 28        |                         |
| » chlorococals . . . . .       | 24      | 49  | 10       | —  | 2   | 2  | 12 | 41        |                         |
| » diatoms . . . . .            | —       | 29  | 10       | 10 | —   | 10 | 43 | 21        |                         |

It is evident that the planktic *Myxophyceae* and *Chlorococcales* have their greatest number of species in column A+B, that is, there seems to be a definite ecological limit between groups B and C, only crossed by a small number of ubiquists. The desmids have on the contrary their maximum development in group C, but a similar ecological limit prevents them growing in groups A and B. The planktic diatoms differ from the foregoing algal groups as regards the type of distribution. Only some of them seem to be restricted by any ecological limit. The greatest difference in the distribution of species is not to be seen between groups B and C but between A and B. The epiphytic diatoms have a distribution very similar to that of the planktic ones.

As is clear from the above, the members of each of the four algal groups are characterized by rather uniform ecological requirements, at least as far as the environmental conditions do not show extreme differences. The planktologists (*cf.* THUNMARK 1945 b, NYGAARD 1949 and others) also base their quotients on the assumption that the groups are composed of species growing under homogeneous ecological conditions. It is likely that the similarity in their distribution is due largely to conformities in their structure.

The diatoms show a similar distribution within the lakes studied independent of the mode of life. This may indicate, that the major factors governing the occurrence of the diatoms in general are those common to them all. The differences owing to their microhabitats are of less importance.

The ubiquitous distribution of many diatoms indicate that all lakes offer on the whole optimal conditions for their growth. There must, however, exist a limiting difference between the extreme lake groups A and C, as they contain several species, which seem to exclude each other.

Extensive results from field studies have been published on the causes of the distribution of diatoms both in salt and fresh water. According to these the factors which preferably have a selective effect on the distri-

bution of the diatoms in nature are the following, namely salt content (especially sodium chloride), pH, phosphorus, and nitrogen.

The diatoms are according to KOLBE (1927 and 1932) divided into different groups on the basis of their occurrence in waters of various salt contents. The cause of the different distribution of the diatoms in nature thus was connected with their assumed dependence on the salt concentration, preferably their requirement of sodium chloride (KOLBE 1932, pp. 265 to 266). To a large extent this was to hold true also for the fresh-water diatoms, possibly with the exception of the halophobous ones (KOLBE *l.c.*, p. 269).

Modern plant physiologists *e.g.*, LUNDEGÅRDH (1950) are sceptical of the assumption that sodium is generally an essential nutrient. CHU (1942) points out that sodium chloride is not essential for the growth of *Pediastrum boryanum*. A difference similar to that prevailing between the vegetation in salt and fresh water can also be recognized between the higher vegetations in soils of various salt contents. See the discussion on p. 22. Several field observations indicate that the same explanation is applicable to the distribution of the diatoms. KOLBE (*l.c.*) stated that sodium chloride can be exchanged with magnesium chloride with the same results. Later on HUSTEDT (1938/39, p. 297) arrived at the conclusion that sodium chloride can be substituted by sulphates of alkalies and alkaline earth metals and bicarbonates of, for example, calcium.

In fresh water the high electrolyte content is mostly caused by calcium bicarbonate and not by sodium chloride. In the lakes here studied the differences in the chloride contents only amount to 13 p.p.m., while the corresponding differences in the bicarbonate contents amount to 205 p.p.m. (ALMESTRAND 1951, table 4). Thus a greater selective effect of the bicarbonate than of the chloride can be expected.

It is apparently rather incredible that the insignificant differences in the chloride contents could create the marked variations in the vegetation which are actually present. JØRGENSEN (1948 p. 43) does not believe that KOLBE'S halophobous species are dependent upon the concentration of sodium chloride. He has found such species in water of fairly high salt content. Their distribution according to his opinion seem to be correlated with pH or some other parallel factor.

A distinct correlation between pH and the distribution of diatoms can be established according to HUSTEDT (1938/39, and 1943). He divides the diatoms after their occurrence at different pH in five classes. The greatest number of species grows at pH=7 to 8.

The pH conditions apparently differ very insignificantly as far as it

can be judged from the analyses available (ANDERSSON 1948, and ALMESTRAND 1951). These determinations cannot be regarded adequate for a careful study of the pH variation within the lakes. For this purpose coherent series from longer periods are required and in addition from different hours of the day and night. It must furthermore be borne in mind that the conditions in free water are not necessarily identical with those in the microhabitats maintaining the epiphytic diatoms. The pH changes in a lake can be considerable (IVERSEN 1929). Already from the data published it is obvious that the pH in Västersjön and Rösjön can fall more than in the remaining lakes. This is also to be expected, as the lack of bicarbonate decreases the buffer capacity of the water. On the other hand, for the same reason the pH cannot rise as greatly as in the lowland lakes. In the lakes rich in humus, it is likely that the amphoteric humic substances have a certain buffer capacity (*cf.* IVERSEN *l.c.*), although it is insignificant in comparison to that of the bicarbonate.

Even if the pH sensitivity of the plants has been exaggerated (*cf.* LUNDEGÅRDH 1950, pp. 470 to 477) the hydrogen ion concentration of the substratum is not unimportant, which fact has been discussed previously (p. 96). In the following lakes according to data in ANDERSSON (*l.c.*) and ALMESTRAND (*l.c.*) pH values of 7.1 and below have been found in Tunbyholmssjön, Dagstorpssjön, Bosarpssjön, Västersjön, and Rösjön. Thus in group B Bosarpssjön and Dagstorpssjön deviate from the two remaining lakes of the group as regards the reaction. None of the other factors studied by ALMESTRAND shows a similar difference in group B. Generally only Kvesarumssjön diverges from the others. If table 11 is studied it is seen that of the 18 species recorded from group B not less than 13 are from Bosarpssjön and Dagstorpssjön. Five of the latter have also been observed in Tunbyholmssjön and group C. Thus there exists an apparent difference between Bosarpssjön and Dagstorpssjön on one side and Kvesarumssjön and Tjörnarpsjön on the other as to those diatoms avoiding the lakes of group A. They prefer thus the two lakes of group B which have the lowest pH values. (It is also possible that pH can rise more highly in Kvesarumssjön and Tjörnarpsjön than in the others, but the analyses only indicate that this can be true of the former.) This fact seems to support the suggestion that pH may have a certain effect on the distribution of diatoms. In this case they appear to react to a slight variation in the hydrogen ion concentration.

The pH is, as previously mentioned, correlated with the bicarbonate

content of the water. Parallely with the latter runs generally the calcium concentration, which has been considered as the more important of these two factors. HUSTEDT has in different papers (*e.g.*, 1938/39 and 1942) emphasized the correlation between the distribution of the diatoms and the lime content. The diatoms are said to be calciphobous, indifferent, calciphilous and calcibiontic according to their occurrence in waters of variant lime concentrations. Later on (1943, p. 258) he has reached the opinion that the bicarbonate and not the calcium is the controlling factor.

Experimental investigations have presented evidence that the calcium content cannot be a minimum factor for the microphytes from a nutritional point of view (*cf.* p. 97). It is, however, very assumable that various species can tolerate different high calcium concentrations (*cf.* CHU 1942). For this reason the calcium ion is likely to have a certain selective effect. The influence exerted by the bicarbonate ion seems to be of still greater importance (*cf.* p. 96).

HUSTEDT (1938/39, p. 310) states that on the basis of his tropical material he has established that the phosphorus and nitrogen standard of the water is of decisive importance for the quantitative and qualitative composition of the diatom flora. Experimentally it is shown that the growth in a natural medium is favoured by an addition of nitrogen and phosphorus (HARVEY 1939, and RILEY 1943). These two elements thus can be expected to be important limiting factors as far as high production is concerned. According to LUND (1950) this is, however, no common rule, for the mass development of *Asterionella* is probably checked by the lack of silicon. Also MELOCHE *et al.* (1938) believe that there exists a correlation between the silicon concentration and the development of diatoms.

It may be that the supply of these nutrients can have a selective action even from a qualitative point of view. It has been proved that different diatoms have different optimal requirements (*cf.* CHU 1942 and 1943). The problem, however, is difficult to solve for field biologists as well as for researchers in the laboratory. The analyses from the lakes investigated given in ALMESTRAND (1951) offer no clue. The determinations of the concentrations of soluble phosphorus and nitrate are not adequate as a basis for a discussion. The capability of the species of utilizing different available nitrogen and phosphorus sources must first be elucidated.

The remaining possible limiting factors such as temperature, supply of organic substances, may be passed over here, as they

have been little or on the whole not at all studied in the lakes discussed here.

Climatic factors, preferably the temperature, may naturally be essential for the composition of the diatom floras when geographically and topographically widely separated areas are considered. The small differences which are to be found between the lakes under consideration must be regarded as completely insignificant (*cf.* HUSTEDT 1942, pp. 167 to 169).

Historical reasons are out of the question as the lakes are situated in a highly limited area. Those located below the highest coast line exhibit no notable deviations in the composition of species.

### Conclusions.

A comparison with the remaining microphytes investigated, represented by different planktic forms, reveals that the distribution of the diatoms is somewhat deviating. Considerably more species are namely ubiquitous, a fact which might mean that the diatoms in general are less sensitive to those factors in the studied lakes which seem to be limiting for the other microphytes.

Some species, however, exhibit a similar groupage as all the other plant groups studied, that is the two lake groups A and C differ as usual strongly from each other. The transitional group B seems to be more related to group C as far as the diatoms are concerned than the other microphytes examined. This may for example be a consequence of a higher sensitivity of the diatoms to pH. The lakes of group B have considerably lower lime content than those of group A, which facilitates rapid fluctuations in the hydrogen ion concentration. (In Tunbyholms-sjön, which also has a low lime content, some diatoms from group B are to be found.)

Thus the bicarbonate content of the water appears to be the most important possible controlling factor, if its direct and indirect effects are considered.

The content of sodium chloride seems to be of less or no importance. The quantities of phosphorus and nitrogen vary irregularly and can hardly be thought of as being responsible for the regional difference in the composition of species.

The climatic factors vary slightly regionally and therefore they cannot be taken into consideration for explaining the qualitative differences of species between the lake groups.



## Some views on the use of the terms oligotrophy and eutrophy.

In lake studies one generally tries to place the lakes in some system of classification as this will facilitate the characterization.

The author has in the above touched lightly one of these systems (p. 91).

The oldest classification in Europe originates from NAUMANN (1919) and THIENEMANN (1921). Both have later discussed the problem in several papers.

NAUMANN distinguished two main types: the oligotrophic and the eutrophic lakes. As a basis he used the quantitative development of the plankton, irrespective of the composition of species. He considered the difference in the content of nitrogen and phosphorus as a possible cause of the various abundance of the plankton.

THIENEMANN divided the lakes according to the supply of oxygen and the bottom fauna which is correlated with this factor, as well as the humus content into three different types: the oligotrophic, dystrophic and eutrophic lakes. In the two former cases the origin of the differences is to be sought in the bottom mud, which is putrefying only in the eutrophic lakes. In the dystrophic lake the oxygen consumption is due to allochthonous humic material. The putrefaction is due to the immense organic material produced which is accumulated in the comparatively insignificant hypolimnion.

The dystrophic lake type is nowadays included by many authors in the oligotrophic one (LILLIEROTH 1951).

The definitions given above are distinct. If they are applied to the lakes investigated all the lakes according to NAUMANN approach to the eutrophic type. This seems to hold true also according to THIENEMANN, even if not so pronounced. The bottom material in all the lakes is composed of gyttjas (LUNDH 1951 b), although with a slight intermixture of dy in Västersjön and Rösjön (and possibly also in group B). The bottom fauna has unfortunately not been studied.

The concepts eutrophic and oligotrophic have, however, not been employed in this paper, because the very meaning of the words refers to the content of nutrients in the water. If this is regarded equivalent to the content of electrolytes there is reason for calling the lakes of group A eutrophic and the remaining more or less oligotrophic. Such a procedure cannot, however, be considered quite justified as long as the importance of the calcium bicarbonate as a nutrient is not fully elucidated. (As previously mentioned this compound is the main component of the electrolytes in the lake waters.)

MÜNSTER-STRÖM (1928, figure 5) states that the most significant difference between what he calls oligotrophic and eutrophic lakes is to be found in the different contents of phosphorus and nitrogen. His definition seems to be rather widely adopted. There is not yet, however, satisfactory evidence of the validity of his suggestion.

It is not even quite clear whether an increase of the production of a lake can be caused by an addition of phosphorus and nitrogen. Such an increase would be *per se* conceivable since both elements have proved to be so-called minor constituents (RCDHE 1951). Some authors define the difference between the oligotrophic and eutrophic lakes as a qualitative variation in the plankton (THUNMARK 1945 a, p. 200 and LILLIEROTH 1950 b, p. 35) and attribute this to changes in the concentrations of phosphorus and nitrogen. There is so far no analytical evidence, however, for this definition (LILLIEROTH 1950 b, table 5).

As the aim of this investigation is to correlate the differences of the lake vegetations with variations in the environmental conditions, there seems to be no reason for discussing lake classifications based upon, for example, types of drainage (*cf.* LUNDH 1951 b, p. 25), stage of evolution (*cf.* PEARSALL 1921) or character of vegetation (*cf. i.a.* SAMUELSSON 1934 and MARISTO 1941). »Potamogeton lakes» can, for example, be caused by variant combinations of factors within different areas, just as a definite species can grow on various substrata in different climatic areas.

## General conclusions.

It is shown that the Scanian lakes can be divided into three groups both as regards macro- and microphytes.

As the climate does not exhibit any greater variations, climatic factors can hardly play any controlling role. The edaphic factors thus must together with the present biotic ones exert the determining influence on the composition of species. A close correlation can be established between the vegetation of the lakes and certain water-chemical factors. As the latter are regulated by the geological properties of the soils it is thus the varying geological character of the area that finally governs the composition of the lake vegetation.

A similar three section of the province has earlier been carried out by WEIMARCK (1947 and 1950) on the basis of phytogeographical investigations of especially the land flora and by WALDHEIM (1947) on the basis of combined plant sociological and ecological studies. WEIMARCK names the different parts the eutrophic, oligotrophic and mesotrophic areas and WALDHEIM calls them the Phascion area, Pogonation area and the transitional area on the ridge Linderödsåsen respectively. Both divisions coincide completely with the one here presented.

According to WALDHEIM the varying lime content and pH are the most important selective edaphic factors. As far as the lakes are concerned the most prominent edaphic variation is constituted by the different concentration of calcium bicarbonate. The correlation between this factor and the vegetation is very marked, not only between the groups but also within group A.

The close relations between the water plants and their environments must be elucidated in connexion with experimental investigations.

## Summary.

The present investigation constitutes a continuation of a previous work in which the macrophyte flora and vegetation of 31 Scanian lakes were described.

I a. In this paper the lakes have been divided into three different groups according to the distribution of the macrophytes. These groups correspond to the different geological character of the area studied.

I b. The limiting effect of possible ecological factors is discussed.

It is necessary to distinguish between plants taking up mineral nutrients and gases in different ways.

Submerged rooted plants must absorb oxygen and carbon dioxide from the water. The content of bicarbonate in the water may here play an important role by forming a direct source of carbon for photosynthesis.

The nymphaeids recorded are ubiquitous, possibly due to the fact that they are independent of the water for their supply of carbon dioxide.

Several helophytes have also a wide amplitude. Some are, however, restricted to lakes with lime-rich water.

The water quality seems to be of minor importance for the distribution of non-submerged rooted plants. The causal factors are probably to be found in the various properties of the soil as far as the area studied is concerned.

The lemnids are not ubiquitous although they are supplied with atmospheric carbon dioxide. Possible causes of their limited distribution cannot be discussed because water-chemical analyses are not available from their special habitats.

The submerged rootless plants are completely dependent upon the water for their nutrition. In this case the calcium bicarbonate, which has far-reaching effects, can be assumed to be a limiting factor. Other water-chemical factors exhibit considerably less variations within the different lakes and cannot thus be expected *a priori* to be of the

same decisive importance for the distribution of the plants. Exact information, however, can only be achieved by experimental investigations.

Most of the charophytes are also correlated to a high lime content in the water as well as in the bottom. Probably they absorb their nutrients mainly from the soil.

Of the bryophytes the floating species constitute an ecological type similar to that of the lemnids. They have also a similar distribution. The submerged water-mosses have an insignificant distribution in the lowland lakes with the exception of *Fontinalis*, possibly due to their inability to assimilate bicarbonate.

On account of the small extension of the area studied and its insignificant changes in level the climatic differences are not pronounced and they seem to have very little controlling action. In nature the competition between the plants is probably the factor which is finally decisive.

II a. The macroscopic algal vegetation in the lakes studied has been described.

The species which have been possible to identify show a distribution indicating that a groupage of the lakes similar to that carried out as regards the macrophytes can also be made here. There is a very marked borderline, the *Cladophora* limit, separating group A from the groups B and C.

II b. According to physiological investigations *Cladophora* seems to be adversely affected by a slightly acid reaction of the water. This fact might indicate that the *Cladophora* limit is determined, at least indirectly, by the concentration of calcium bicarbonate in the water. On the whole very little is known on the nutritional physiology of the macroscopic algae. Their mode of life is reminiscent to that of the rootless submerged macrophytes.

III a. The lake groups A, B and C are characterized by a different content of phytoplankton, which is evident from the two plankton samples examined from each lake. Some lakes investigated in respect to the macrophytes are not included. The difference between the lake groups is exhibited both in the qualitative and quantitative occurrence of the various plankters.

Within group A there is an apparent difference in the composition of species between the so-called *Myxophyceae*-rich and *Myxophyceae*-deficient lakes. This difference may possibly be connected, with a greater or lesser effect of human culture.

A similar variation in the number of *Myxophyceae* has also been observed in the lakes of group B.

III b. Possible ecological causes of the distribution of the plankters are discussed. It has not been proved according to the literature that phosphorus and nitrogen give rise to qualitative differences in the phytoplankton. Such differences are in the area under consideration correlated with changes in the electrolyte content, which is, in its turn, determined mainly by the concentration of calcium bicarbonate. The last-mentioned compound is likely to be a limiting factor. The bicarbonate ion is, for example, probably a direct source of carbon for some plankters and the calcium ion is antagonistic to other essential ions. The bicarbonate also affects the hydrogen ion concentration of the water. Many other causal factors are likely involved, for example, the toxicity of metal ions and the possible inhibiting and promoting effects of organic substances, but further investigations are necessary for elucidating the problem.

The stimulating factors responsible for high productions of phytoplankton are not yet fully clarified. Even if phosphorus and nitrogen must be thought of as minimum factors, a plankton pulse is certainly often initiated by other factors, *e.g.*, climatic ones.

IV a. Epiphytic diatom samples from shallow water have been examined from the majority of the 31 lakes. It can be stated that even as concerns the distribution of the diatoms differences are revealed, which justify a division of the lakes into three groups corresponding to the three macrophytic lake groups. Apparently many diatoms are ubiquitous, however.

IV b. Comprehensive field ecological studies have shown that the calcium bicarbonate content may be a possible controlling factor, *i.a.* because of its effects on the hydrogen ion concentration. The distribution in the investigated lakes might perhaps indicate that the diatoms in some cases are sensitive to changes in pH. No evidence that nitrogen and phosphorus are responsible for the regional differences has been obtained.

V. Some views on the use of the terms eutrophy and oligotrophy are presented.

VI. It is shown that the Scanian lakes can be divided into three groups both as regards macro- and microphytes. The middle group constitutes a transitional type. The edaphic factors seem to exert the controlling influence on the composition of species together with the biotic ones. A close correlation between the composition of species



and some water-chemical factors, particularly calcium bicarbonate, is to be found. The latter factor can thus be assumed to have a limiting action.

Any correlations between the flora and certain ecological factors obtained by field studies cannot offer a solution of the problem as to the close dependence of the plants upon their environments.

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