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Production and degradation in the trophogenic layer investigation of ecological parameters in the polytrophic rotsee and in the mesotrophic Bay of Horw (Lake of Lucerne)

by Ernst Schegg

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PRODUCTION AND DEGRADATION IN THE TROPHOGENIC LAYER. INVESTIGATION OF ECOLOGICAL PARAMETERS IN THE POLYTROPHIC ROTSEE AND IN THE MESOTROPHIC BAY OF HORW.

ERNST SCHEGG

FRB 2635

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Production and Degradation in the Trophogenic Layer

Investigation of Ecological Parameters in the Polytrophic Rotsee and in the Mesotrophic Bay of Horw (Lake of Lucerne)

by Ernst SCHEGG

Federal Institute for Water Supply, Sewage Treatment, and Water Protection
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Zurich in Dübendorf

TABLE OF CONTENTS

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1. Introduction and Purpose (427)

An organism will grow in a habitat if this latter meets its needs, that is, if a utilizable energy source and nutrients are available.

Only man disregards this law. He has a fast increasing potential of energy which he may apply anywhere, and according to his needs.

The nonhuman world of living beings does not have this potential and, due to its passivity, it is affected by any changes occurring in the energy flow. In order to reverse changes that have occurred involuntarily or carelessly, the ecosystem must be analyzed. A prerequisite for directed action is the knowledge of the qualitative and quantitative interactions. However, this knowledge cannot be obtained only from practical restorative measures; rather, a comprehensive ecological-physiological and experimentally oriented research must be carried out beforehand. Only in this manner, it is possible to find, and establish, standards.

Where there is a utilizable source of energy, the energy flow starts, thus determining the whole substance metabolism. Part of this energy flow passes through organisms; this energy portion which is fixed and converted in organisms may, as OHLE (46) suggested, be called the bioactivity of the waters. In this complex system, there are manifold interactions, with living organisms and the environment facing one another.

The evaluation of these interrelationships will be corroborated by a large number of different parameters which will be included in this investigation.

The present article intends to provide a contribution to the knowledge of these interactions and, particularly, to show the causative interconnections between production and degradation. To a large extent, it takes into account the request for a multiplicity of established parameters.

The set aim was pursued from two different viewpoints, that is: firstly, from the ecological viewpoint, by investigating the natural biotope to determine, in two lakes of different trophicity degrees, particularly the yearly course of the plankton biocoenosis in its interactions with the surrounding water, and

secondly, from the experimental viewpoint, by answering questions about the relationships between bacteria and phytoplankton, which it was possible to investigate only under standardized conditions.

2. Investigated Lakes

Table 1. Orography

See lake	length Länge	width Breite	surface Fläche	max. depth Max. Tiefe	Aver. depth Mittl. Tiefe
Rotsee	2,4 km	0,4 km	0,48 km²	16 m	9 m
Vierwaldstättersee, Lake Lucerne Seeteil Horwer Bucht Bay of Horw	1,5 km	1 km	1, 69km²	72 m	42,6 m

Table 2. Lake types (428)

Lake	Condition of waters	Sewage load	Literature
Rotsee	strongly eutrophic	before 1933, sewage from part of Lucerne discharged non-purified; since 1933, purified mechanically; since the middle of 1959, there is no more load.	DÜGGELI (14) STADELMANN (73)
Bay of Horw (Lake of Lucerne)	mesotrophic	about 9000 inhabitants, sewage discharged non-purified	AMBÜHL (4) GÄCHTER (19)

The graph of Fig. 1 shows the geographical location of the two lakes.

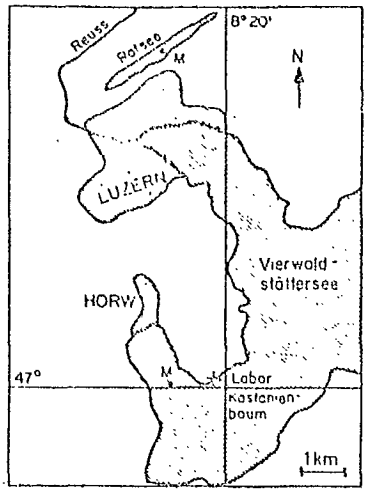

Fig. 1. Geographical location of measuring sites (= M)

3. Methods

During the years 1969/70, the two lakes were investigated once a month, at the following depths:

Table 3. Investigation dates and depths.

	investig.dates Untersuchungsdaten	depth steps Tiefenstufen
Rotsee	1969: 20. 3., 17. 4., 22. 5., 10. 6., 10. 7., 14. 8., 11. 9., 10. 10., 6. 11., 3. 12. 1970: 15. 1., 18. 2., 23. 3.	0, 1, 2,5, 5, 7,5 and 14 m
Vierwaldstättersee Lake of Lucerne	1969: 23. 1., 19. 2., 18. 3., 17. 4., 20. 5., 17. 6., 8. 7., 6. 8., 9. 9., 7. 10., 4. 11., 2. 12. 1970: 6. 1., 24. 2.	0, 2,5, 5, 7,5, 10, 12,5, 15, 25, 45, 60 m

Hereinafter, the above investigation dates will be shortened, (429) to show the month only. The indications regarding the 0 m depth relate to measurements at 0.2-0.3 m below the surface.

For the Lake of Lucerne, this article uses mainly the values of the 0 to 15 m layer (trophogenic layer).

The measuring sites (M) may be seen from Fig. 1; the one in the

Rotsee lies in the middle of the track, the one in the Bay of Horw about in the middle of the bay. This latter was determined with a penta prism, from the shore, by means of auxiliary points.

The samples for chemical analysis were lifted with a Friedinger bottle. Bacteriological samples and water for production measurement were collected with a sterile sampling bottle according to SCHEGG (64).

The formation of a team of investigators pursuing the same investigational object, although with different aims, made it possible to limit the manual effort, while a maximum of information was gained. With the use of a simple correlation plan method (CPM), such teamwork may be further rationalized.

3.1 Physical Determination Methods

1. Temperature: The temperature was determined with AMBÜHL's (3) oxytester.

2. Conductivity: The conductivity was measured with the same instrument as the temperature.

3. Measurement of light conditions: As recommended by SAUBERER (61), the light intensity of various spectral regions was measured with a barrier-layer cell photometer fitted with filters (Firm of Schott and Gen., Mainz, VG 9, BG 12, and RG 2).

4. The visible depth was determined with the Secchi disk.

3.2 Chemical Analysis Methods

1. Oxygen content: The oxygen content was determined according to Winkler, modified according to ALSTERBERG (2).

2. Hydrogen sulfide: The quantitative determination of hydrogen

sulfide was carried out colorimetrically with NN-dimethyl-p-phenylene-diammonium-dichloride and ferric ammonium sulfate (STRICKLAND-PARSONS (76)).

3. Carbonate hardness (SBV): The carbonate hardness was determined according to the directions of the Schweizerisches Lebensmittelbuch (Swiss Food Regulations) (3rd edition).

4. Total carbon (inorganic): From pH value and SBV, the total carbon was calculated according to HARVEY and RODHE (24).

5. Nitrogen components: Nitrate was determined with the sodium-salicylate method according to MÜLLER and WIDEMANN (42), nitrite with sulfanilamide and N-(1-naphthyl)-ethylene-diamine according to STRICKLAND et al. (76), and ammonium according to SCHMID (68). The organically dissolved Kjeldahl nitrogen and the particulate organic Kjeldahl nitrogen were determined according to STADELMANN (73).

6. Phosphorus components: Orthophosphate: Ammonium molybdate - tin chloride method according to Ohle, modified according to SCHMID and AMBÜHL (69). From the difference between the total concentration of the (430) raw water and that of the filtrate, the particulate phosphorus was calculated.

7. Silicic acid: Colorimetric determination with ammonium molybdate (German Standard Methods (15)).

8. Determination of iron: The determination of particulate and dissolved iron was carried out colorimetrically with the orthophenanthroline method (BLOESCH (8)).

All the dissolved components were measured in the filtrate obtained by filtration through a 0.45 μ pore width filter (Millipore HA).

3.3 Biological Investigation Methods

3.31 Qualitative and quantitative investigation of phytoplankton

The plankton samples from the Lake of Lucerne were fixed with Lugol, filled into round-tube compound-chambers (50 ml) and, after 48 hours settling time, counted in the inverted microscope according to UTERMÖHL (79). The samples from the Rotsee were prepared in fivefold dilution, due to their high plankton-cell densities. The biomass was calculated by summing up the single-cell volumes. These latter were determined by measurement, and with the aid of data from literature(PAVONI(53) and NAUWERCK (44).

3.32 Measurement of Primary Production

For the production measurement, the ^{14}C-method established by STEEMAN-NIELSON (75) was used. The ^{14}C ampuls were produced from a sodium-bicarbonate solution (supplied by the Radiochemical Centre, Amersham, England, code No. CFA.3). The production from the solution is safer, since the ^{14}C never appears as $^{14}CO_2$. The ampul activity was determined according to the barium-bicarbonate method (VOLLENWEIDER (81)).

The water collected with the sterile sampling bottle was filled into sterile exposure bottles (Jena G 20, 125 ml), and with the aid of a sterile syringe, 5 μ C-bicarbonate solution was added. The samples were exposed "in situ et loco" for four hours, from 10 A.M. to 2 P.M.. For this purpose, the exposure rack shown in Fig. 2 has proved suitable. In horizontal position, the bottles are exposed to the full light. According to the buttonhole principle, they are slid into a support (Fig. 3). The setting-up therefore requires verylittle time, so that a "light shock" of the algae (GAEMAN et al. (22)) may be prevented. After the exposure period,

the samples were immediately processed. 25 ml each of sample water were filtered through a 0.22 μ pore width filter (Göttinger Membranfiltergesellschaft SM 113 07) with a microfiltration instrument of the firm of Millipore (Code XX1002500). With rubber cement, the filters were glued into an aluminum dish, and exposed for 20 minutes to fuming hydrochloric acid, to remove the adsorbed inorganic ^{14}C.

The measurement took place with a methane flow meter (Firm of Frieseke and Höpfner, FH 407). To calculate the production rate, the correcting factor of 1.06 was used for the isotope effect. The utilization coefficient of the numerator of about 1% was small; yet, it was compensated for during the calculation, since also the ampul activity was determined with the same numerator, and with the same method.

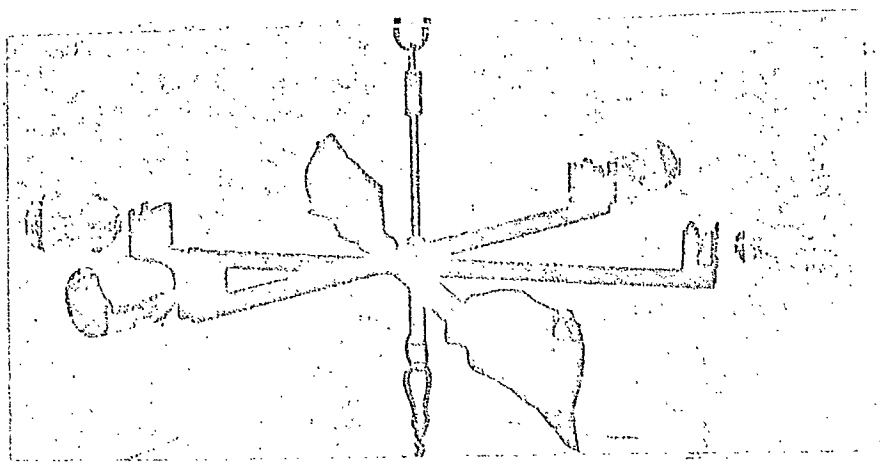

Fig. 2. Bottle exposure rack

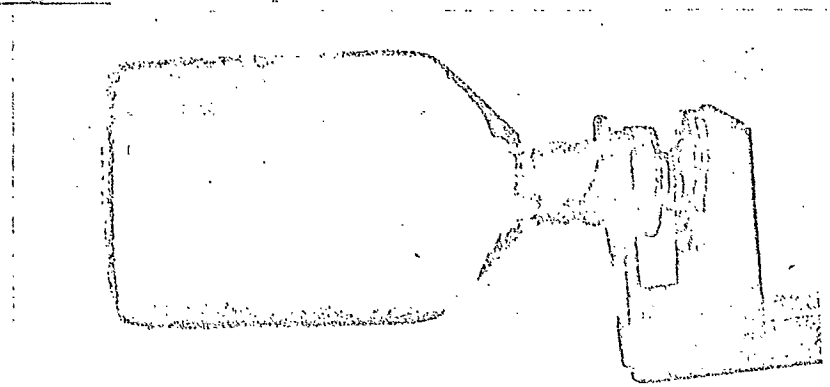

Fig. 3. Support: The bottle is pressed through a foam-rubber plate into the "buttonhole".

3.33 Bacteria

The samples for the bacteriological analysis were processed within 1-2 hours. According to POTTER (56), if the samples are stored in bottles for rather a long time, considerable shiftings may occur in the number of germs and in the species composition. The species number decreases, while the total number increases considerably.

3.331 Plate Method

As medium to determine the number of germs according to Koch's Plate Method, tryptone-glucose extract agar (Difco No. 521983) was used (beef extract 3 g, tryptone 5 g, dextrose 1 g, agar 15 g per 1000 ml of dist. water). The samples were plated in sterile plastic Petri dishes. The medium was poured in liquid form, and care was taken that the sample was mixed with the agar only shortly before the agar solidified. For the samples from the Lake of Lucerne, 0.1 ml of the original sample were plated. The samples from the Rotsee were diluted 1:10, and also 0.1 ml was plated. For each sample, five parallel samples were prepared. After an incubation (432) period of five days, at 20°C, the colonies were counted under the binocular magnifying glass, at 50fold magnification.

3.332 Membrane-Filter Method

The counting results on membrane filters are based on the direct-counting method according to Razumov (from KUZNEZOV (36)). The exact method may be found in SCHEGG and RUSCHKE (65). In some cases, the method according to Razumov and Iwanov (from KUZNEZOV (36) was used to determine the generation time.

Advantages of the membrane-filter method:

Direct microscopical observation and counting provides the best

indications about the number and morphology of bacterial plankton. The actually available number of germs is undoubtedly obtained more accurately in this manner than with the plate method, since a selectively acting substrate determines the number of germs.

Disadvantages of the direct-counting method:

It is often difficult to distinguish the germs on the filters from detritus particles, especially so if they are present in stunted forms.

In strongly polluted waters, particles of young growth, and zoogloeae appear (JANNASCH (32)), that is, bacterial-cell accumulations, the number of which can only be estimated.

According to JANNASCH (31), dead and live bacterial cells may be distinguished by special staining with Acridine Orange and fluorescence-microscopic investigation, in that dead bacteria cells appear red, while live cells appear green. However, DEUFEL (10) arrives at the conclusion that, while all red-fluorescent bacteria are definitely dead, not all dead bacteria are red-fluorescent. Hence, this method was not used. According to KUZNEZOV (35), the percentage of dead bacteria is not more than 10% of the total bacteria present. Kuznezov was also able to prove this order of magnitude by measuring the respiratory intensity in cell suspensions of lake water concentrated by partial filtration.

It may be assumed that dead bacteria autolyze very rapidly, and that therefore the living bacteria that are counted on the membrane filters, constitute the bulk. Nevertheless, the exact percentage of dead bacteria remains unknown.

3.333 Count of Special Species

Isolated species from the Rotsee which, morphologically, were easily recognizable, were observed separately. Particularly Thiopedia rosea, Leptothrix pseudovacuolata, and Chromatium densegranulatum were counted in the inverted microscope of Utermöhl.

3.4 Data Analysis[2)]

The recording of the results and the empirical searching for the correlations were extended by an evaluation and interpretation of the results by means of data processing. GOLDMANN et al. (23) showed how a lake investigation may be consequently evaluated by data processing.

In the present article, the linear correlations among the parameters were calculated ("Korrela" program). Another program ("Profile" program) served to calculate the square-meter numbers (= values below (433) 1 m^2 of lake surface integrated over the depth).

In the Rotsee and in the Lake of Lucerne, at 5 depth steps each, about 30 parameters were determined per investigation. These 5 depth steps showed a complete data sequence over the two investigation years. This met with an essential prerequisite for the use of data processing.

3.41 Calculation of Correlation Coefficients

The value pairs compared in each case are to be considered as normally distributed random variables. The respective correlation coefficients were determined according to the following formula:

---

2) The calculations were carried out on an IBM CPC 6500 of the ETH Zurich computer center.

$$r = \frac{S_{xy}}{\sqrt{S_x \cdot S_y}}$$

r = Korrelationskoeffizient
S_{xy} = Summe $(x - \bar{x})\,(y - \bar{y})$
S_x = Summe $(x - \bar{x})^2$
S_y = Summe $(y - \bar{y})^2$

The correlation coefficient states whether there exists a linear, mathematical relation between the compared input values. GOLDMAN et al.(23) introduce separate parameters, namely growth-dependent values, in logarithmic form. This was intentionally omitted, as it is not possible to apply the criteria of a pure culture to a lake.

The significance limits were set at $2\alpha = p \leq 0.1$ (Dokumenta Geigy (12)). The correlation coefficient r for each lake was determined between all the data; likewise, all equations of the regression lines were always calculated.

The "Korrela" program mentioned in the Appendix provides the following:

1. Writing out of all input data in the block per lake and date.

2. Calculation of all linear correlation coefficients between the input variables in one depth step each, during the investigation period.

3. Indication whether the correlation coefficient is significant, with a 10% error probability ($p \leq 0.1$).

4. Writing out of all significant correlation coefficients in the "intersection diagram".

5. Calculation of the two regression lines between the respective two variables. (In the present article, they were not evaluated).

3.42 Calculation of "Square-Meter Value"

For various parameters, the value per m^2 of lake surface is needed as, for instance, for the primary production. With the "Profile" program

(Appendix), it is possible to calculate the plane under the curve of parameter against depth, in that the respective trapezoid contents, limited by the separate measurements of the parameter, were summed up.

The "Profile" program mentioned in the Appendix provides the following:

Calculation of the value of a parameter per m^2 of lake surface, of the mean value, and of the quotient of mean value to maximum value. This quotient serves to characterize the curve shape; if the curves show only one maximum, the quotient is a direct indication about the stratification conditions.

4. Production (434)

Autotrophic and heterotrophic production by organisms can take place only if the corresponding energy source and nutrients are available. The deterioration in the condition of the waters manifests itself mainly by an increased growth of planktonic algae; however, this often depends directly on the nutrient concentration. GÄCHTER (19) showed experimentally "in situ" for phosphate that not only a single supply of nutrients releases a large production, but rather, that the constant supply of nutrients constitutes the decisive factor.

To the population of organisms belong both producers and consumers. This constant supply of nutrients therefore is not only an external factor, but to a substantial degree an internal factor. With regard to the biological production therefore, it is extremely important to know the quantity and quality of this internal load, recycling or, according to OHLE (48), the "short-circuited cycle". The comprehension of the natural laws and of

the capacity of the "short-circuited cycle" in a lake is the prerequisite for the production evaluation.

In any interpretation and evaluation of results, the dynamics of a body of water is of prime importance. The lake investigation described hereinafter is to serve the enlargement of this knowledge.

4.1 Definition and Limitation of the Trophogenic Layer

"Trophogenic layer" is a term related to biological production. According to RUTTNER (60), during the summer stagnation, a lake is divided into two completely different spaces, a trophogenic and a tropholytic layer. Somehow, the title of the present article is in contradiction to this strict separation; however, the findings of this research work will justify it.

While it may be correct to speak of a trophogenic layer, one should define it from the energy standpoint, for instance as a layer in which the energy balance for the living cells is positive.

4.2 Factors Determining Production

4.21 Physical Bases

4.211 Meteorological Data[3)]

In Figs. 4 and 5, the meteorological data from all the Rotsee and Lake of Lucerne sampling days are listed. The average monthly atmospheric temperatures are shown as stepped diagrams. If the water temperature (0-5 m) is integrated according to the "Profile" program, one obtains the thermal energy content of the water below 1 m^2 for the trophogenic layer. In contrast to the average monthly temperature, a negative value was never obtained,

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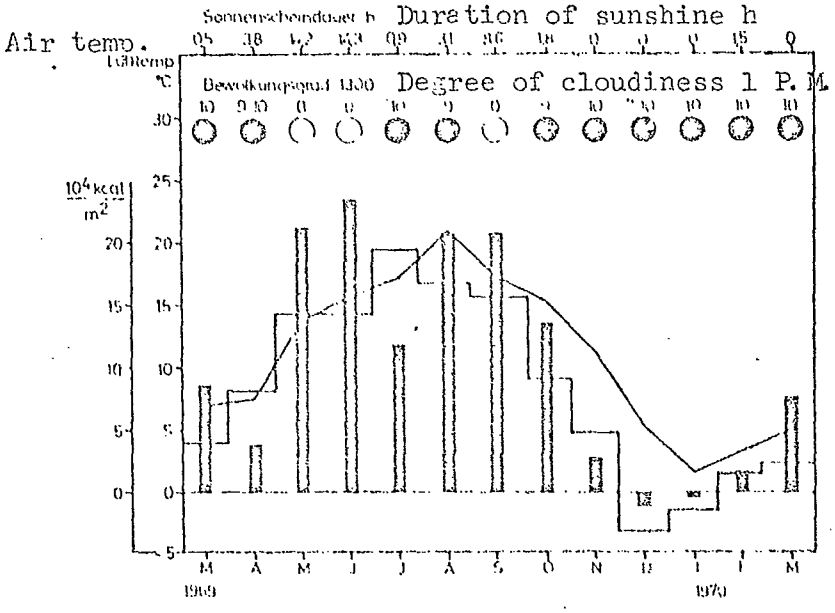
3) Part of these data were kindly made available to the author by the Central Institute of Meteorology in Zurich.

that is, the thermal energy content of the trophogenic layer remained positive over the whole year.

If the two curves are compared with each other, the thermal energy reserve of the lake may be seen directly, in that the curves are mutually displaced in time.



(435)

Fig. 4. Meteorological indications, Rotsee:
Circles: Degree of cloudiness (black = cloudy, white = sunny); separate columns: then air temperatures in °C; stepped diagram: average monthly temperatures in °C, (——): energy content in kcal/m^2 (0-5 m).

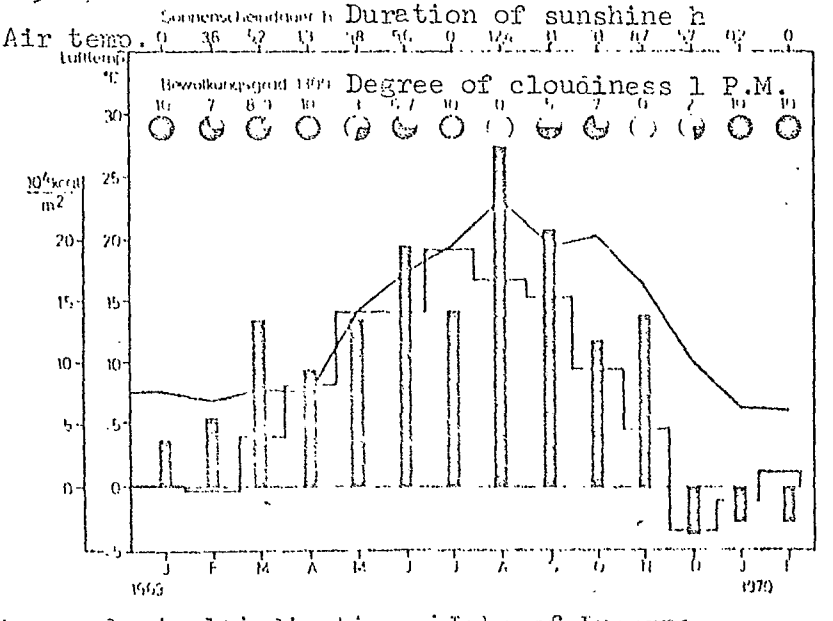


Fig. 5. Meteorological indications, Lake of Lucerne (for explanations see Fig. 4).

In both lakes, heat was stored until August, and then released again. For the lake, the thermal balance was negative again after August. From the respective curve (kcal/m^2), the number of kcal exchanged per m^2 of surface may be read directly. If the energy exchange through 1 m^2 is multiplied by the lake surface, the energy flow between atmosphere and water is obtained. Since this means a parallel shifting for the drawn curve, it was omitted. In the Rotsee, below the total lake surface, the maximum value of the energy content in August, 1969, was about 5×10^{10} kcal, taking into consideration the 0-5 m layer, and the basis of 0°C. (436)

4.212 Temperature

Rotsee: Fig. 5.

The Rotsee was investigated for the first time in March, 1969, when the summer stagnation started forming. In August, 1969, there was a marked thermocline with a maximum surface temperature of 23.5°C, and a sudden change in temperature at the 5 m depth. At the end of November, the autumn circulation started. That this circulation comprised only part of the hypolimnion, resulted from the fact that in December, the temperature of the lower layers was higher, with 6 degrees compared to 5 degrees, than in the epilimnion. This was an inverse stratification. The fact that the circulation did not reach the lowermost layers, was seen also from the chemical analysis values described hereinafter, and from the values of the index organisms (see Thiopedia rosea). It is possible that the salt content of the deep water caused this inverse stratification. In January, a winter stagnation formed, which lasted until the end of February.

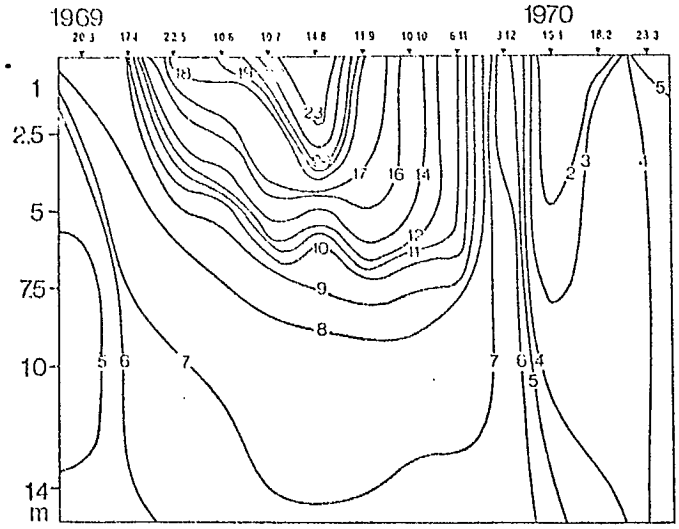


Fig. 6. Rotsee isotherms (°C) (according to STADELMANN, 1971).

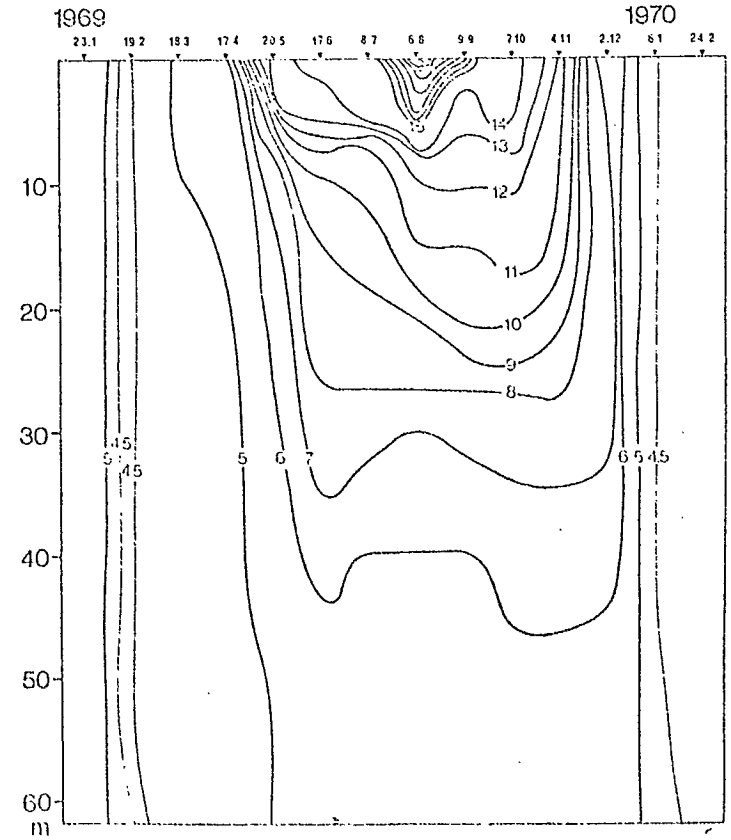


Fig. 7. Bay of Horw isotherms (°C) (according to STADELMANN, 1971).

Bay of Horw

The isopleth graph (Fig. 7) shows the temperature course in the Bay of Horw. In January and February, there was full circulation or turnover, at a temperature of 4.5°C. In April, a stable epilimnetic stratification started forming, which reached its maximum in August (maximum surface temperature 22.7°C). The temperature changes affected the layers down to 50 m; below that point, the temperature remained constant, at about 5°C, throughout the year. For the present research, only the values down to 15 m were taken into consideration, since, for the sake of simplicity, this depth was assumed to be the lower limit of the trophogenic layer.

Stability of Stratification

It is important to find a magnitude that is representative for the momentary stability of the thermal stratification. For one-peak curves, it is possible to form a quotient between maximum value and mean value over the water column. A quotient of 1.0 signifies that there is homothermy; a high quotient signifies a high peak with respect to the mean value, and constitutes the direct magnitude for the stability of the existing stratification.

However, to compare two different lakes, it is important that the (438) same size of water column be evaluated; otherwise, the quotients cannot be compared.

These quotients were calculated with the "Profile" program for all components. For the temperature, they are shown in Fig. 8. It may be seen that the quotient determined from the Rotsee values shows a higher value over the whole year than that from the Lake of Lucerne values. The course of both curves is a result of meteorological conditions. Since, geographically, the two lakes lie close together, the curves proceed mainly parallel.

In the spring of 1969, after an initial ascent in the stratification stability, a collapse occurred in April, due to weather conditions. This was the case for both lakes, in that the temperature stability quotient fell sharply. Then, within one month, a stable stratification built up, which maintained itself until September, and only from October to December, the autumn circulation took place, with the collapse of the stratification stability. The winter stagnation was again clearly seen, particularly the formation of a strong, inverse stratification in the Rotsee.

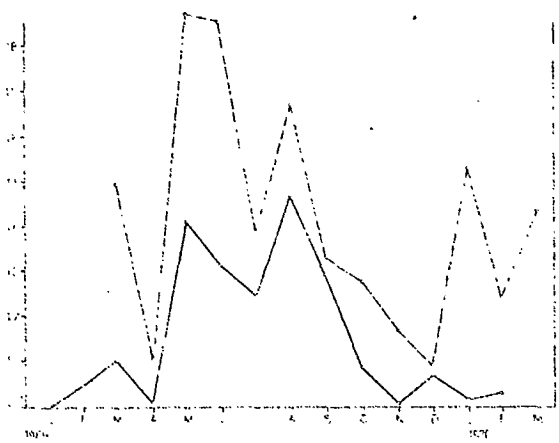


Fig. 8. Stratification stability curves, Lake of Lucerne (——), and Rotsee (----).

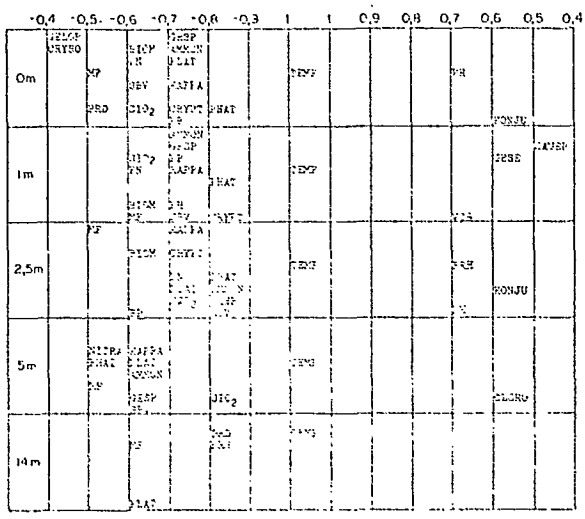
Correlation Analysis

The following manner of representation (Table 4) will constantly be used hereinafter as a basic design. It will therefore be explained briefly:

In the middle of the Table is the parameter against which the correlation is set up, separately for each depth step. Toward the right and the left, the correlation coefficients have been plotted, toward the right in the positive direction, toward the left in the negative direction.

If, for example, ammonium, in the 0 m rectangle, is between -0.7 and -0.8, this means that the correlation coefficient between temperature and ammonium is significant, and has the value of -0.7 etc. From the arrangement within the rectangles, in upward direction, the second decimal point may be estimated in upward direction.

Table 4. K-Analysis to reference parameter Temperature, Rotsee. (439)



In principle, all the parameters used in the correlation analysis were indicated, although it is obvious that part of the correlations are secondary, or have little meaning from the ecological standpoint. To discuss each separate parameter is impossible in this connection; however, essential correlations will be mentioned individually.

All the data used for the correlation analysis are listed in the Appendix.

In the text hereinafter, the following abbreviations are used:

K = correlation

KK = correlation coefficient

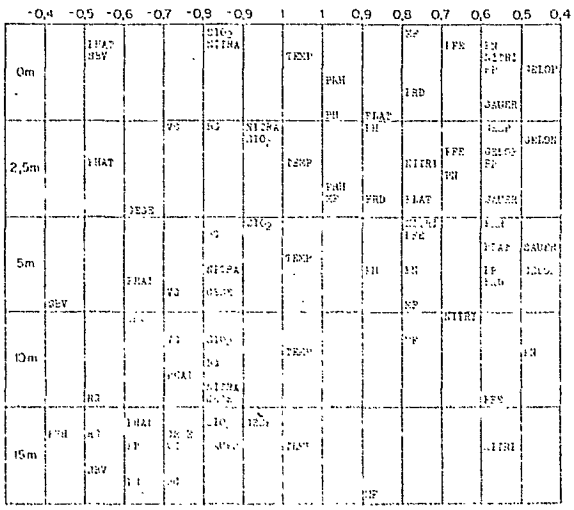
Rotsee (Table 4)

The KK lie mainly in the negative range. These are the production-determining and production-representative parameters. To be specially mentioned is phosphate which correlates negatively with 0.83-0.84. From the total of these correlations, one may conclude that the temperature, that is, the energy content of the lake, is of subordinate importance with regard to biological production, that particularly nutrients, such as phosphate and ammonium, are determinative for the production. This statement does not only apply to the algal population, but rather, as the various negatively correlated bacterial numbers show, also to the bacterial population.

Lake of Lucerne (Table 5)

In the Lake of Lucerne, the K diagram shows a completely different picture. There is a very high KK of more than 0.9 to the primary production in the layer of maximum production (2.5 m). Moreover, there are positive KK for the coefficients characterizing the standing crop, such as PP and PN. The bacterial numbers, both plate and membrane filter counts, correlate

Table 5. K-Analysis to reference parameter Temperature, Lake of Lucerne. (440)



positively with the temperature. It is interesting that the nutrients phosphate and nitrate correlate negatively with the temperature. This is to say that at increasing standing crop and production, the nutrients phosphate and nitrate are consumed.

Further relations will appear more clearly with other reference parameters.

Conclusions from K-Analysis

The Rotsee is a highly productive body of water, the productivity of which is not in the first place temperature-dependent. This statement is confirmed in the corresponding production figures described hereinafter.

The maximum production in the Lake of Lucerne coincides with the summer heating; it is largely temperature-dependent.

4.213 Light conditions

To evaluate the production, one must take into account the light conditions as energy basis of the photo-autotrophic production.

Measurements with a selenium photo-cell provide only relative values in relation to the surface intensity assumed to be 100%.

In the two investigated lakes, the green component (VG 9) penetrates deepest. Figs. 9 and 10 illustrate the penetrating depths of the green light for 1% and 20% of the surface intensity. RODHE (59) defines the magnitude of the productive layer with the 1% penetrating depth of the green light. For data-processing reasons, this very variable limitation of the trophogenic layer was omitted, and the limit for the Lake of Lucerne was set at 15 m, and that for the Rotsee at 5 m.

The visible depths, on the whole, coincide with VG 9 20%. For practical purposes, this allows for the respective lakes to calculate from

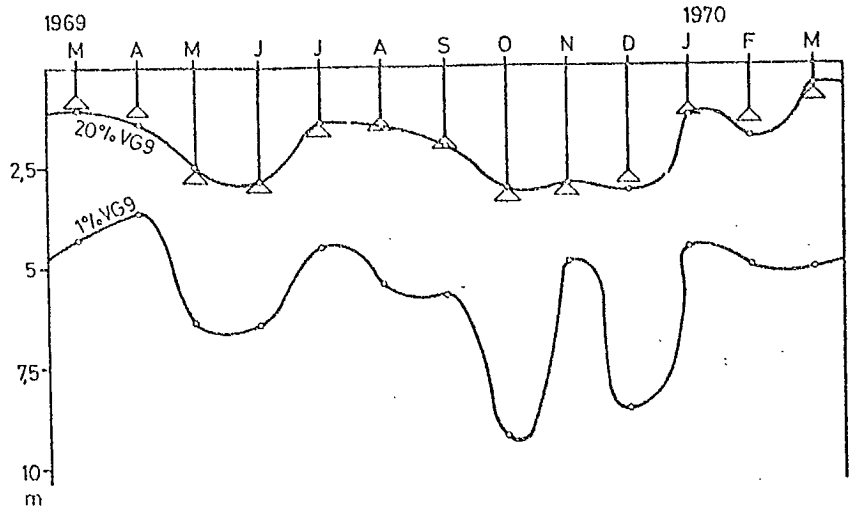


Fig. 9. Penetrating depth of green light (VG 9) in % of the surface intensity and visible depths, Rotsee. (441)

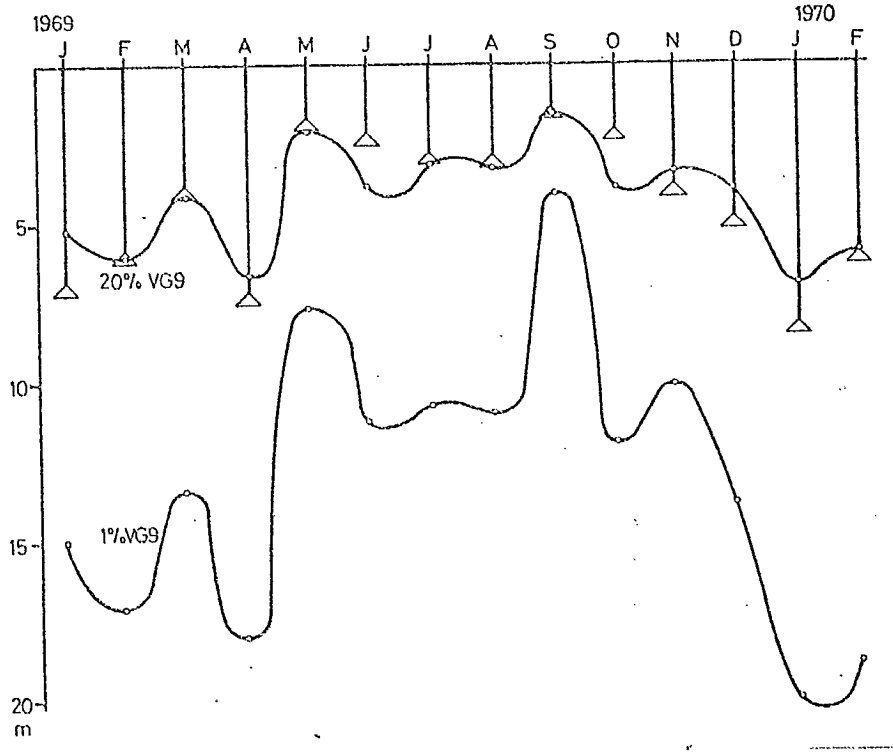


Fig. 10. Penetrating depth of green light (VG 9) in % of the surface intensity and visible depths, Lake of Lucerne.

the visible depth, with reasonable accuracy, the 1% limit of the green light (VG 9).

It is noteworthy that during the summer months, the visible depth shows partly higher values in the Rotsee than in the Lake of Lucerne. Further data on the light intensity may be found in the Appendix.

4.22 Nutrients

To characterize the nutrient situation of the investigated waters, the two most important nutrients, phosphate and nitrate, will be illustrated hereinafter, over the course of the year. A more detailed evaluation of the part nitrogen plays in the nutrient cycle is found in STADELMANN (73). On the importance of phosphorus, BLOESCH (8) will further report in connection with sedimentation measurements. Among the micronutrients, only iron will be mentioned.

The values were calculated per m^2 of lake surface by determining the contents of the trophogenic layer (in the Lake of Lucerne from 0 to 15 m, in the Rotsee from 0 to 5 m) with the "Profile" program mentioned in the Appendix. To each nutrient component, the K to all the other parameters were calculated with the "Korrela" program, and illustrated according to the same pattern as the temperature.

4.221 Phosphate

Rotsee

Fig. 11 shows the phosphate content per m^2 of lake surface in the trophogenic layer of the Rotsee. During the months of August to October, 1959, phosphate was consumed almost completely in the trophogenic layer, while in winter (December), due to full circulation or turnover in the lake,

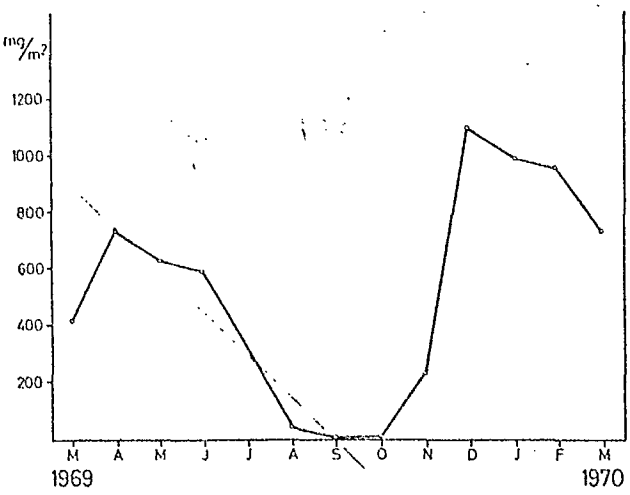


Fig. 11. Phosphate content of the trophogenic layer (0-5 m) in mg of PO_4-phosphorus/m^2, Rotsee.

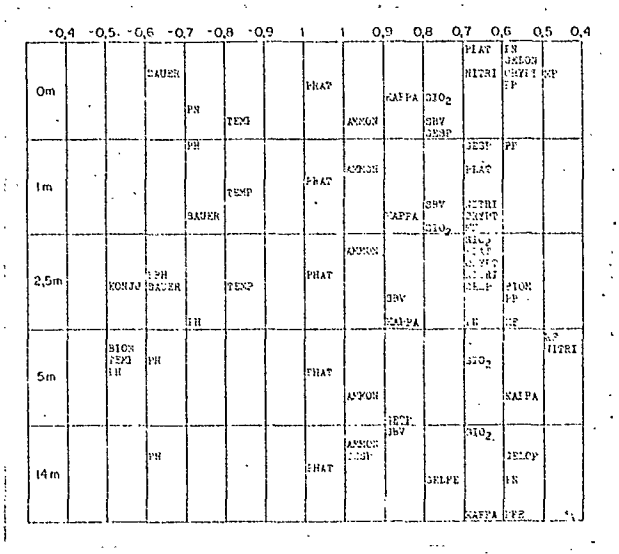


Table 5. K-Analysis to reference parameter Phosphate, Rotsee. (443)

the phosphate content below 1 m^2 rose up to 1 g. Already in May (1969), the consumption of the available phosphate started from the surface down, at decreasing algal population.

The K-Analysis (Table 5) shows that in winter the phosphate concentrations are high, in that there exists a high negative KK relative to the temperature. Moreover, a K may be seen between phosphate and conductivity in the layers down to a 2.5 m depth.

A K to the production parameters may be seen only in the widest meaning (CRYPT, PN, and PP 0.55-0.6). The K to the other phosphorus components are only of secondary nature. However, there is a very close relationship between phosphate and ammonium concentration. This is due to the fact that at turnover, the two components are introduced from the hypolimnion. This assumption is confirmed by the fact that also in the hypolimnion, there exists a K of 0.98 between phosphate concentration and ammonium concentration.

Lake of Lucerne (Fig. 12)

In the Lake of Lucerne, the phosphate concentration below 1 m^2 (0-15 m) is lower than in the Rotsee by a power of ten. It lies, on an average, at 40 mg/m^2.

In the summer months, until the end of the year, a strong phosphate decrease was noticed. An almost complete phosphate consumption took place in September, when no more phosphate was detected between the 2.5 and 15 m depths.

Apparently, due to a more marked turnover in January, 1970, a rather large amount of phosphate was brought back into the trophogenic layer, and the allochthonously supplied amounts were distributed over the profile, so that in February, 1970, the content was much higher than the previous year.

The K-Analysis (Table 7) shows negative correlations between phosphate and the production factors, such as primary production, PN, temperature, and positive correlations between phosphate and nitrate contents of 0.6 to 0.84, at all depths from 0 to 10 m, that is, a constant interdependency exists between the two nutrients.

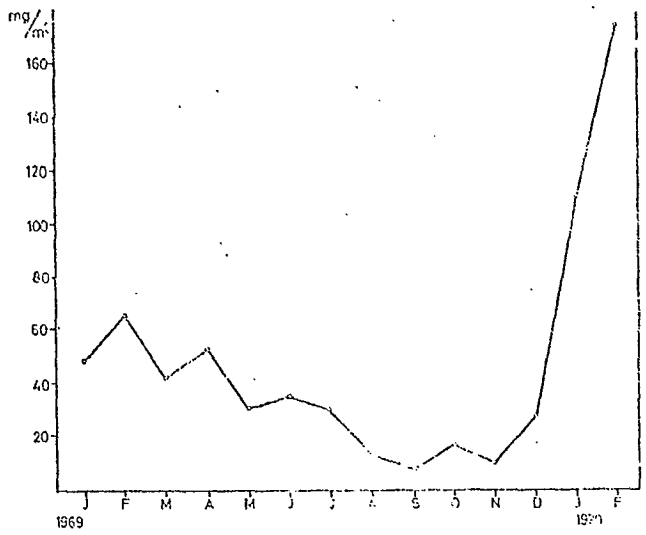
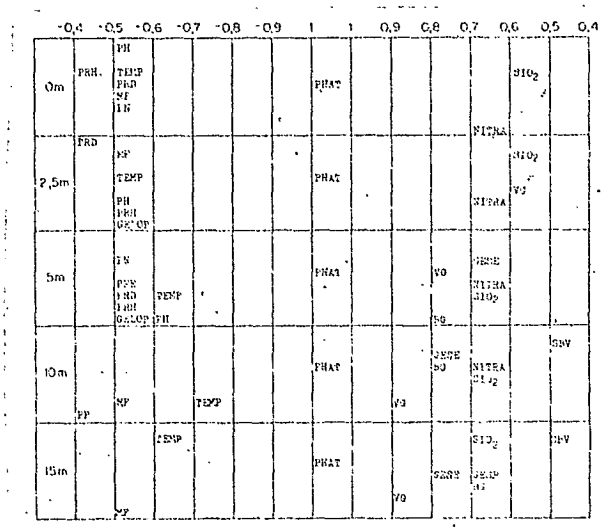


Fig. 12. Phosphate content of the trophogenic layer (0-15 m) in mg of PO_4-phosphorus/m^2, Lake of Lucerne. (444)

Table 7. K-Analysis to reference parameter Phosphate, Lake of Lucerne.



4.222 Nitrogen Components

The nitrogen cycle was investigated in detail by STADELMANN (73). In Fig. 13, the nitrogen components nitrate, ammonium, and nitrite of the Rotsee are listed as square-meter values.

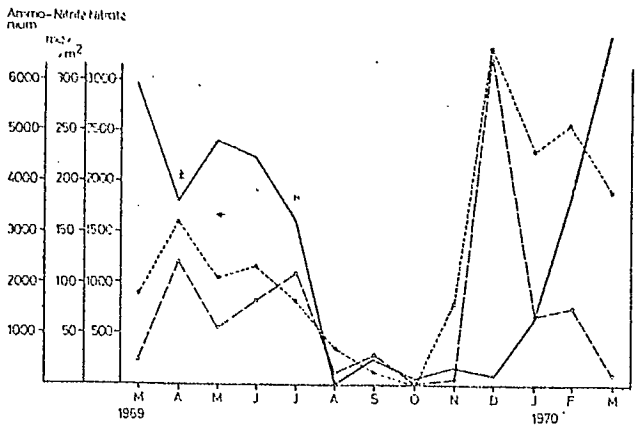
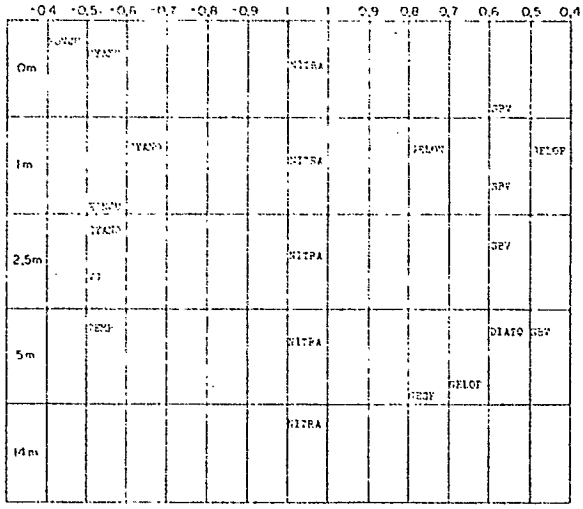


Fig. 13. Square-meter values (0-5 m) of ammonium (----), nitrite (— — —), nitrate (——) in mg/m^2, Rotsee. (445)

Table 8. K-Analysis to reference parameter Nitrate, Rotsee.

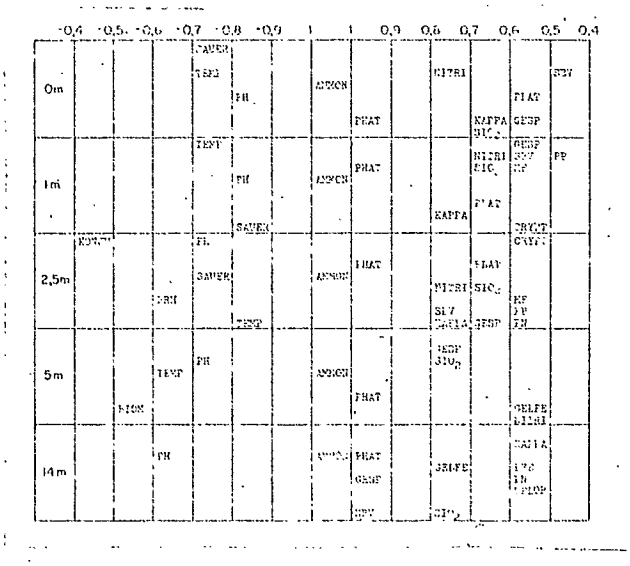


All three nitrogen components show that in the Rotsee the N-consumption is very high, in that from August to November, the values decrease to almost zero. The nitrate concentration increases only after the autumn circulation, from January to May. It may be assumed that this increase originates from the nitrification which starts, due to increasing oxygen concentration.

From the K-Analysis of nitrate (Table 8), it may be seen that in the Rotsee, nitrate as a nitrogen component plays a much lesser part in the yearly regime than ammonium.

This is confirmed by the K-Analysis of ammonium (Table 9). Ammonium correlates very closely with phosphate, and constitutes in the K-pattern a nutrient that partakes in the production. The negative KK to oxygen in the 0 m, 1 m, and 2.5 m depths is another indication therefor.

Table 9. K-Analysis to reference parameter Ammonium, Rotsee. (445)



Lake of Lucerne (Fig. 14)

In the Lake of Lucerne, nitrate, in the course of the year, is never fully consumed in the trophogenic layer as a whole. While in October, 1969, there is, in fact, an almost complete nitrate consumption in the layer of main productivity of 0 to 2.5 m, the nitrate content of the trophogenic layer always remains above 2 g/m^2.

In the Lake of Lucerne, nitrite is of subordinate importance. Two maxima appear, that is, in July and September, 1969, at the lower limit of the trophogenic layer, at about 12 m.

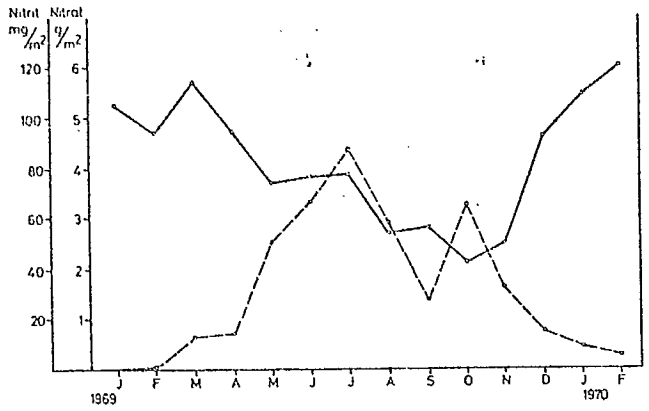


Fig. 14. Square-meter values (0-15 m) of nitrite (---), and nitrate (——), in mg N/m^2, Lake of Lucerne. (447)

Table 10. K-Analysis to reference parameter Nitrate, L.of Lucerne.

	-0,4	-0,5	-0,6	-0,7	-0,8	-0,9	1	1	0,9	0,8	0,7	0,6	0,5	0,4
0m	GELOP		GESF				NITRA			SiO_2		SEV PHAT		
2,5m	GELON GELFE	FFE	GESP SAUER	FF		FRH FRD	NITRA			SiO_2		GESE PHAT		
5m	GELOP		FRD	FF		VP FRH	NITRA			SiO_2		SEV PHAT GESE		
10m	FRH FH	FN		FF		VP FRH	NITRA			SiO_2	GEF	PHAT		
15m							NITRA					PLAT		

Table 11. K-Analysis to reference parameter Nitrite, L.of Lucerne.

	-0,4	-0,5	-0,6	-0,7	-0,8	-0,9	1	1	0,9	0,8	0,7	0,6	0,5	0,4
0m							NITRI				FFE	FRD	FRH PH VP FH	PLAT
2,5m			GESE	SiO_2 NITRA			NITRI		FFE		FRH	FRH FRD FH	FH	
5m				GESE SiO_2			NITRI		FRH			FRD	FH	SAUER
10m	FRH						NITRI						VP	
15m			GESE				NITRI						PLAT	

K-Analysis of Nitrate in the Lake of Lucerne (Table 10)

In contrast to the Rotsee (see K-Analysis Table 8), in the Lake of Lucerne, nitrate appears as antagonist to most production parameters. Particularly, between primary production and nitrate, there is a high negative KK (0.92). Moreover, there are negative K to the PN and PP values of 0.7 to 0.6 which are representative for the standing crop. How close this interrelation is, may also be seen from the fact that at a depth of 15 m, no significant K can be detected between nitrate and the production parameters. Positive K exist to silicic acid with 0.82, and phosphate with 0.63. These K values are surprisingly constant, down to a depth of 10 m. (447)

The K-Analysis of nitrite (Table 11) shows that the denitrification processes at the 10 m depth occur in relation to the bacterial population. In the layer of main productivity, there exist positive KK to the production parameters, and a negative KK to nitrate. One may conclude thereof that at high nitrate assimilation, that is, high photosynthesis, nitrite forms. This is easy to understand, since nitrite forms as the first intermediary product of the nitrate assimilation (STADELMANN (73)). (448)

4.223 Iron

As may be seen from Figs. 15 and 16, both in the Rotsee and in the Lake of Lucerne, the dissolved-iron concentrations calculated for the trophogenic layer, lie in the same order of magnitude. In none of the two examples, the dissolved-iron concentration decreases to 0.

The K-Analyses (Table 12: K-Analysis in the Rotsee) show only in the Rotsee a negative K between the available biomass and the dissolved iron in the trophogenic layer. In the Lake of Lucerne, the K-Analysis

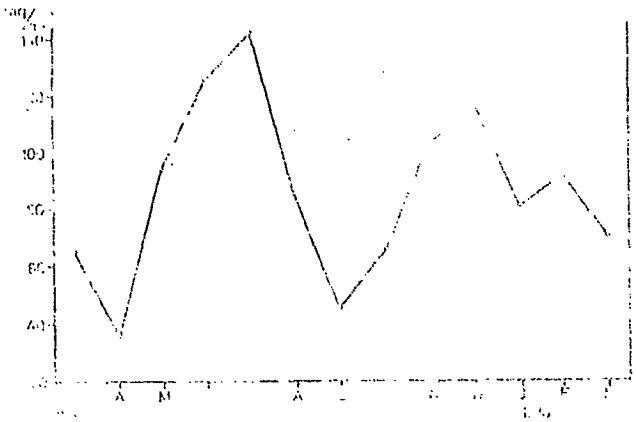


Fig. 15. Square-meter values (0-5 m) of dissolved iron in mg of Fe/m^2, Rotsee.

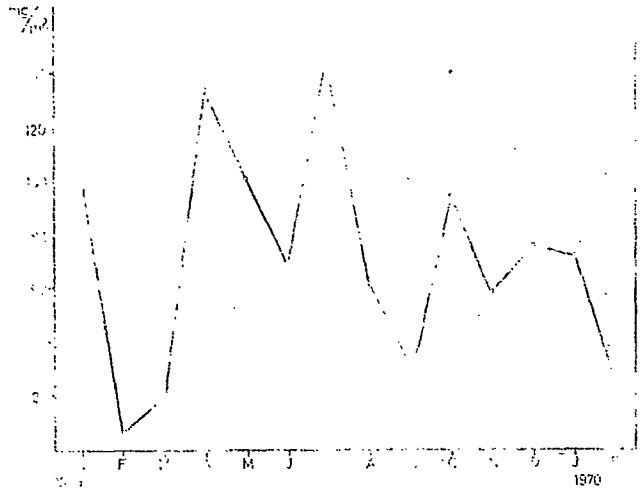
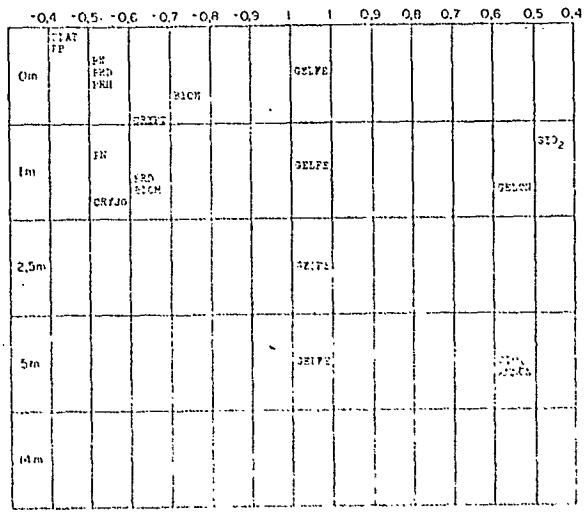


Fig. 16. Square-meter values (0-15 m) of dissolved iron in mg of Fe/m^2, Lake of Lucerne.

Table 12. K-Analysis to reference parameter Dissolved Iron, Rotsee. (449)



values show no relation to the production parameters. An illustration therefore was omitted.

4.224 Total Salt Content

The K-Analysis between the conductivity and the production parameters was carried out in both lakes. For the Lake of Lucerne, it is noteworthy that the conductivity depends exclusively on the alkalinity (SBV). In the trophogenic layer, the KK fall from 0.8, at 0 m, to 0.62, at 15 m, that is to say that below the trophogenic layer, the conductivity may also be influenced by accumulated nutrients. There is no correlation with any of the production parameters. An illustration therefore was omitted.

In the Rotsee (Table 13), this situation is completely different; the conductivity correlates with phosphate with 0.82, at the 0 m, 1 m, and 2.5 m depths. Likewise, significant KK exist between silicic acid, ammonium, and the water hardness (SBV).

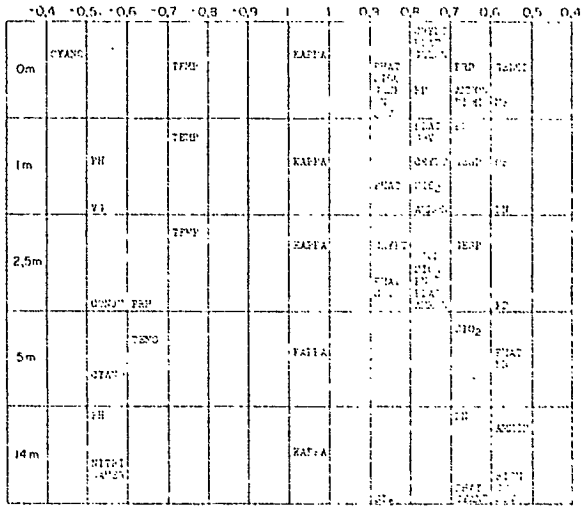
4.3 Production Measurements

The basis for production is a corresponding phytoplankton population. The production volume depends on the population composition, and on the rate of conversion at that time. As shown previously (SCHEGG (63)), the conversion rate may vary substantially, depending on the species composition of the plankton. Phytoplankton investigations therefore serve also for the comprehension of dynamic relations. In this sense, the following detailed phytoplankton investigation in the Rotsee is to be understood.

4.31 Phytoplankton in the Rotsee

The phytoplankton occurrence is described, for one thing, grounwise and, for another thing, by showing the major forms in the space-time diagram.

Table 13. K-Analysis to reference parameter Conductivity, Rotsee. (450)



The algal groups are indicated in biomass, as fresh-weight (= cell volume x specific gravity), the separate forms in cell counts, colonies or number of threads per ml. In the space-time diagrams, shadings are used to show the main vegetational periods more clearly. However, they are not to be understood as isopleths, that is, the delimitations were chosen appropriately in each case, yet not calculated. An isopleth illustration would require a larger basic material. The respective illustration will also be used for other parameters.

4.311 Cyanophyta (Fig. 17)

The blue-green algae showed a rather sharply delimited growth period between September and December, 1969. Compared to the total phytoplankton, their values in the trophogenic layer are relatively low; in the Rotsee, they play a subordinate part.

Only Coelosphaerium Naegelianum reached a very high value in November, 1969, at the 5 m depth. During the whole year, some filaments of Oscillatoria rubescens and Oscillatoria redeckii were always found.

Coelosphaerium Naegelianum (Fig. 18)

The appearance of Coelosphaerium Naegelianum was delimited to the months of October, 1969, to January, 1970, with a maximum in November, 1969. The largest number of colonies (850 colonies/ml) was found at the limit between hydrogen sulfide and oxygen, at a depth of 7.5 m. At the 14 m depth, at a hydrogen-sulfide content of 6.8 mg of S^{2-}/liter, there still were 467 colonies/ml. It was not possible to determine whether these were sunken-down colonies or whether this form grew in the anaerobic range, at extremely weak light intensities.

4.312 Chlorophyceae (Fig. 19)

According to the number of species, the Chlorophyceae were a relatively important group; however, with respect to biomass, they were not in a leading position. Only in April, 1969, they constituted 30% of (452) the biomass. Their appearance was limited mainly to the first half of the year; a growth maximum was observed in April, and a second one in July and August, 1969. The April maximum was caused by Chlamydomonas sp. (Fig.20), the appearance of which was limited mainly to the months of March and April, analogous to the flagellates which will be discussed later on (Fig. 29).

Oocystis lacustris (Fig. 21)

Oocystis lacustris was observed in the months of June to September; it is noteworthy that on 10 July, 1969, there appeared a massive growth at the 5 m depth, at the boundary between hydrogen sulfide and oxygen. One month later, a large number was found at the 14 m depth. This population had obviously sunk down over the anaerobic layer, without dissolving appreciably.

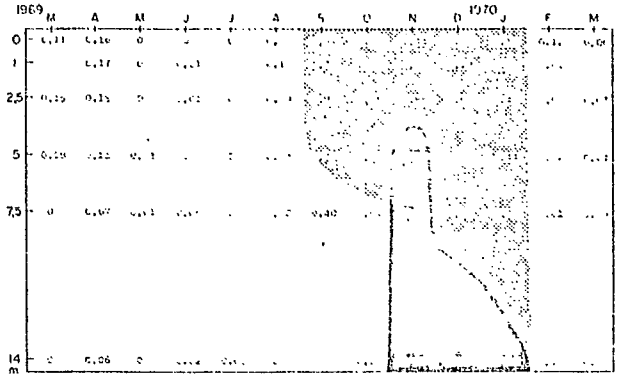


Abb. 17. *Cyanophyceae*, µg/ml, Rotsee.
Fig. 17. Cyanophyceae, µg/ml, Rotsee.

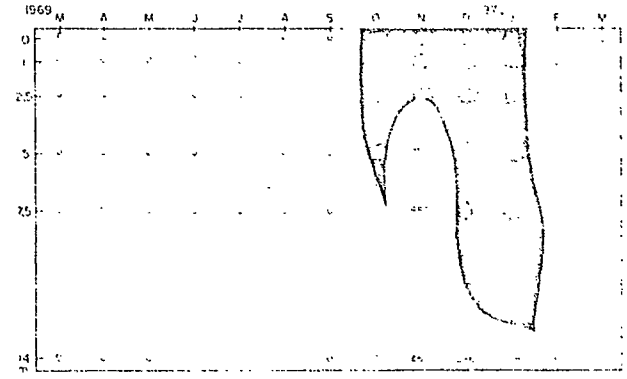


Abb. 18. *Coelosphaerium Naegelianum*, Kolonien zu 30-50 Zellen, Kolonien/ml, Rotsee.
Fig. 18. Coelosphaerium Naegelianum, colonies of 30-50 cells each, colonies/ml, Rotsee.

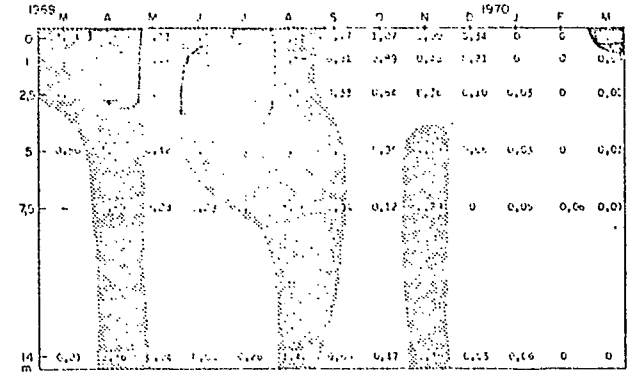


Abb. 19. *Chlorophyceae*, µg/ml, Rotsee.
Fig. 19. Chlorophyceae, µg/ml, Rotsee.

(452)

Fig. 20. Chlamydomonas sp., cells/ml, Rotsee

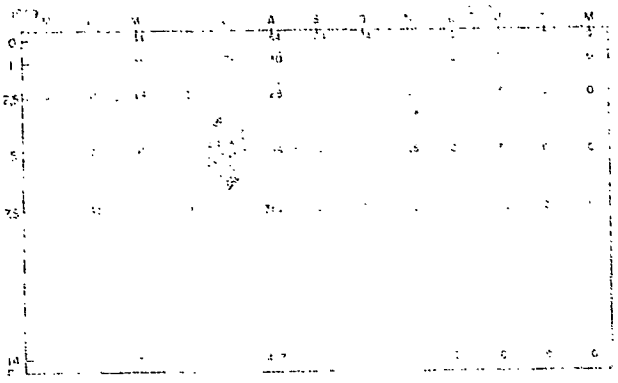


Fig. 21. Oocystis lacustris, cells/ml, Rotsee

It is possible that Oocystis lacustris, the same as (452)
Coelosphaerium Naegelianum described under the Cyanophyceae, belongs to forms which are able to live also under anaerobic conditions or, due to their gelatinous envelopes, remain as cells in the aerobic environment.

Sphaerocystis Schroeteri (Fig. 22) (453)

These colonies were observed in June and November, particularly in the epilimnion.

Characium oreellipes (Fig. 23)

This form appeared in relatively large numbers in May, at the 1 m. depth, and in smaller numbers in November and December, 1969.

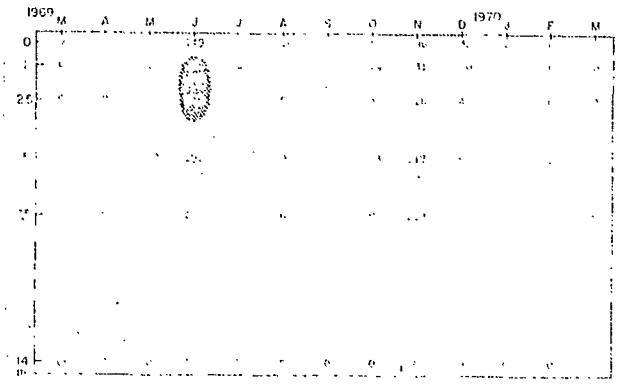


Abb. 22. *Sphaerocystis Schroeteri*, Kolonie zu 10-20 Zellen, Kolonien/ml, Rotsee.
Fig. 22. Sphaerocystis Schroeteri, 10-20 cell colonies, colonies/ml, Rotsee.

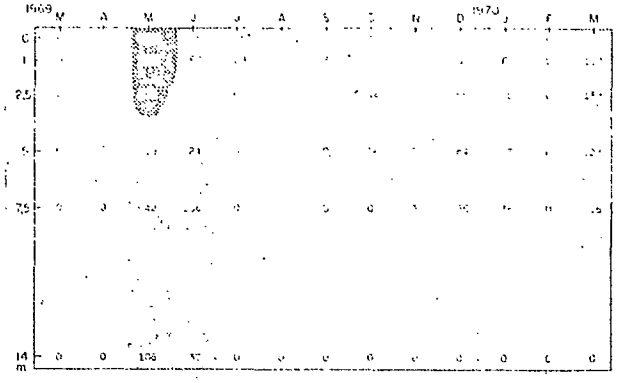


Abb. 23. *Characium gracilipes*, Zellen/ml, Rotsee.
Fig. 23. Characium gracilipes, cells/ml, Rotsee.

Coelastrum microporum (Fig. 24)

Coelastrum microporum showed a massive growth (2549 colonies/ml) on 10 July, 1969. A smaller number of colonies remained until November. Also of this form, very large numbers of colonies were observed in the anaerobic layer; on 14 August, 1969, for example, at the 7.5 m depth, 1444 colonies/ml were counted, at a hydrogen-sulfide content of 1.16 mg of S^{2-}/liter. It would appear that also in this case, the colony form, with solid cell membranes, made life under anaerobic conditions possible.

Scenedesmus quadricauda (Fig. 25)

These colonies appeared sporadically, yet mainly during the summer months, in the epilimnion.

(454)

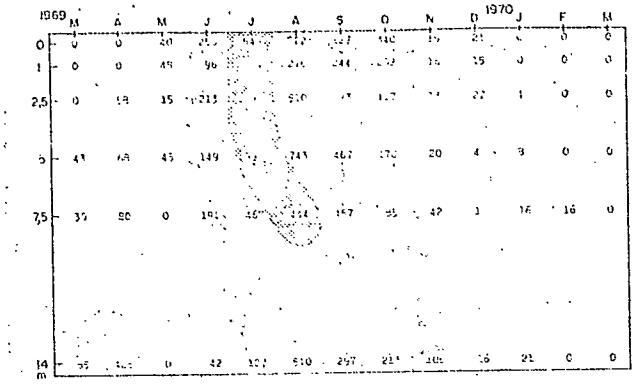


Abb. 24. *Coelastrum microporum*, Kolonien zu etwa 20 Zellen, Kolonien/ml, Rotsee.
Fig.24. Coelastrum microporum, colonies of about 20 cells, colonies/ml, Rotsee.

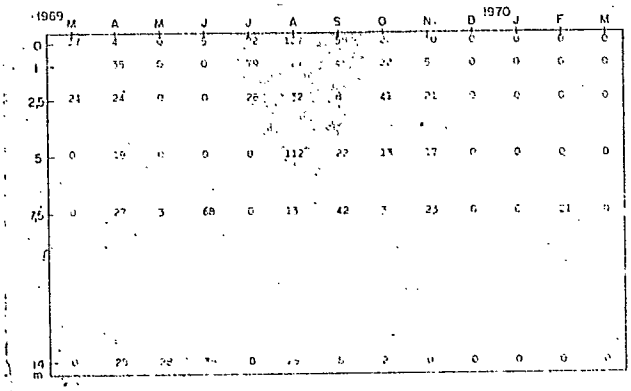


Abb. 25. *Scenedesmus quadricauda*, Kolonien/ml, Rotsee.
Fig.25. Scenedesmus quadricauda, colonies/ml, Rotsee.

Ankistrodesmus convolutus (Fig. 26)

developed mainly during the winter months, December, 1969, to April, 1970; a massive growth was detected in April (4737 cells/ml at the 0 m depth). Due to its smaller cell content, this form is insignificant for the biomass.

4.313 Conjugatae (Fig. 27)

The appearance of this group was limited to the months of August to October. The chief form that appeared was Closterium sp.. Yet, for the total biomass, even this group is insignificant.

(455)

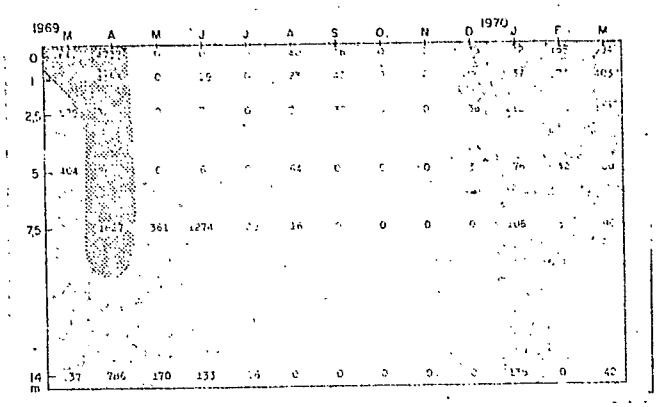


Abb. 26. *Ankistrodesmus convolutus*, Zellen/ml, Rotsee.

Fig. 26. Ankistrodesmus convolutus, cells/ml, Rotsee.

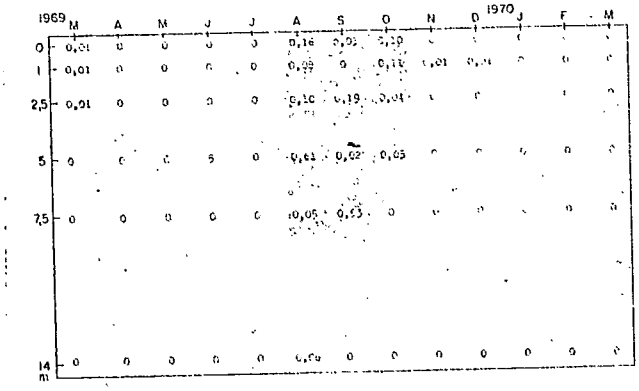


Abb. 27. *Konjugatae*, µg/ml, Rotsee.

Fig. 27. Conjugatae, µg/ml, Rotsee.

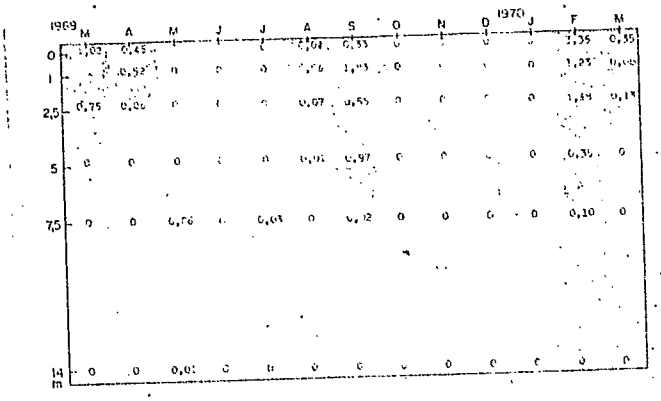


Abb. 28. *Chrysophyceae*, µg/ml, Rotsee.

Fig. 28. Chrysophyceae, µg/ml, Rotsee.

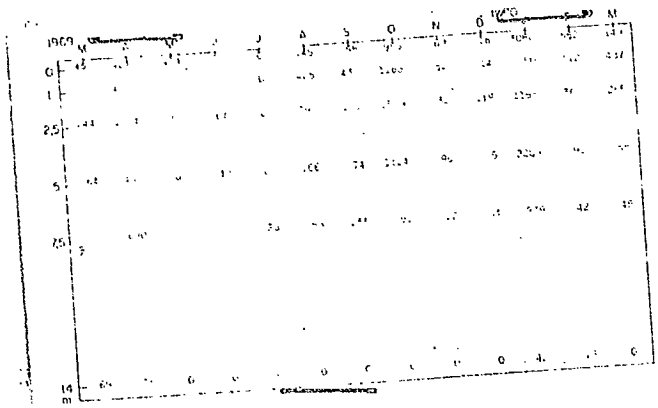


Fig. 29. Various Flagellates, cells/ml, Rotsee.

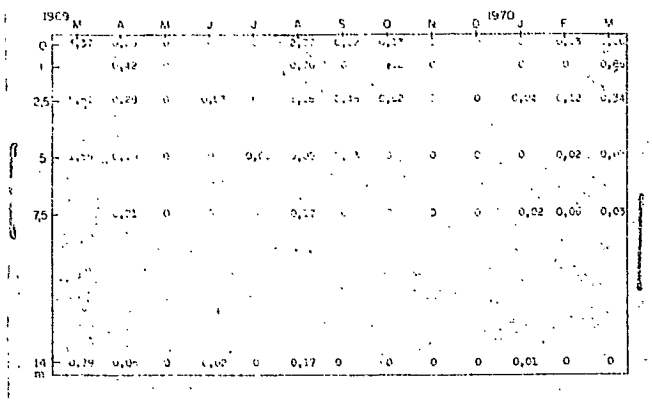


Fig. 30. Diatomeae, µg/ml, Rotsee.

4.314 Chrysophyceae (Fig. 28) (456)

The Chrysophyceae were represented mainly by two forms, that is, in March and April, 1969, by Erkenia subaequiciliata, and in September, 1969, February and March, 1970, by Uroglena americana. Only on 18 February, 1970, at 0 m, they constituted 14% of the biomass. Moreover, more difficultly differentiable flagellates were counted, which are listed in Fig. 29.

4.315 Diatomeae (Fig. 30)

The diatoms developed in vegetational batches, that is, in March and April, 1969, and in February and March, 1970, as well as in August, September and October, 1969.

(457)

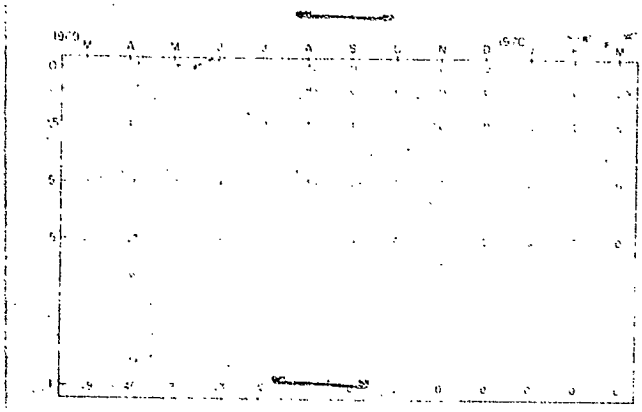


Abb. 31. *Synedra acus*, Zellen/ml, Rotsee.

Fig. 31. Synedra acus, cells/ml, Rotsee.

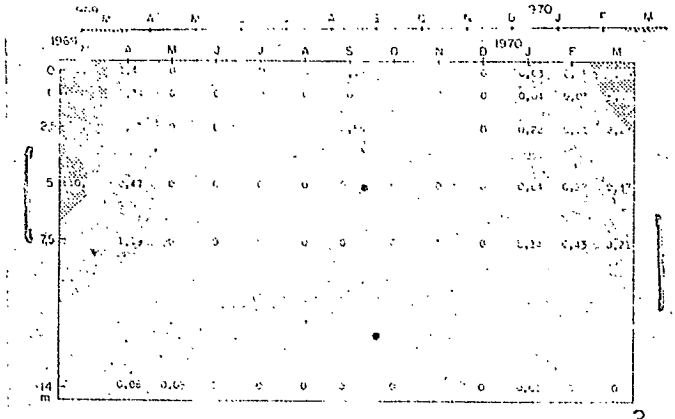


Fig. 32. Stephanodiscus hantzschii, 10^3 cells/ml, Rotsee.

Synedra acus (Fig. 31) (456)

This form determined the Diatomeae biomass in August, while it was hardly present during the other months.

Stephanodiscus hantzschii (Fig. 32) (457)

The most important representative of the diatoms was Stephanodiscus hantzschii, with two winter maxima. In March, 1969, this form reached cell counts of 44,000 cells/ml at the 2.5 m depth. However, due to the small cell volumes, it constituted only 38% of the biomass, even during this massive growth. Interesting was a sporadic appearance of this form on 11 September, 1969, at the 2.5 m depth. This known winter nannoplankton form (NAUMANN (44)) appeared in the Rotsee at a temperature of 18°C.

(458)

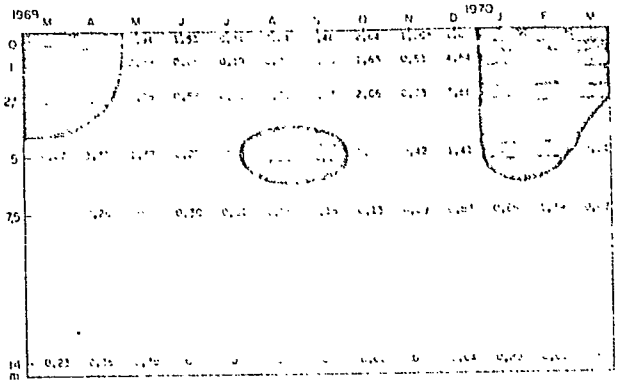


Abb. 33. *Cryptophyceae*, µg/ml, Rotsee.

Fig. 33. Cryptophyceae, µg/ml, Rotsee.

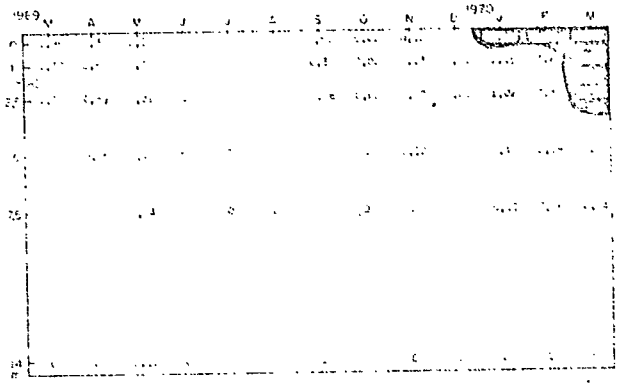


Abb. 34. *Rhodomonas lacustris und lens*, 10^3 Zellen/ml, Rotsee.

Fig. 34. Rhodomonas lacustris and lens, 10^3 cells/ml, Rotsee.

4.316 Cryptophyceae (Fig. 33)

The Cryptophyceae were the dominating algal group in the Rotsee. Their chief vegetational periods were in the winter months, and in August and September (5 m depth). Thus, for instance, the maximum biomass of 34 µg/ml was observed directly below the ice layer (15 January, 1970). During the whole year, no settling of these forms was found; already at the 7.5 m depth, the cell concentrations were negligibly low, compared to the epilimnetic figures, and at the 14 m depth, only isolated forms were found.

Rhodomonas lacustris and lens (Fig. 34)

The massive growths of Rhodomonas were limited to the uppermost water layer of 0 to 2.5 m. The absolute maxima were found at 0 m, from January to March, 1970, (March, 1970: 15,000 cells/ml).

Cryptomonas spp. (Fig. 35)

Cryptomonas spp. were found during the whole year; however, the maximum growths occurred also during the winter months. In January, 1970, 15,290 cells/ml were detected under the ice. An interesting phenomenon was the appearance of Cryptomonas in August and September, 1969, at the 5 m depth, at the boundary between hydrogen sulfide and oxygen.

It is possible that the Cryptomonas bloom, at this boundary line, was caused by the upward diffusion of the ammonium nitrogen. This may be seen in the ammonium distribution, since with the appearance of the Cryptomonas bloom, a very rapid decrease was determined, from 1000 µg/l in June, to 520 µg/l in August, to 200 µg/l in September, and to 0 µg/l in October.

This metalimnetic Cryptomonas bloom also caused an abrupt phosphate (459)
decrease, that is, at the 5 m depth, the phosphate concentration fell from 244 µg/l in July, to 3 µg/l in August.

It is possible that, apart from the nutrient conditions, also the temperature has an influence on this stratification behavior. It was at 13-14°C. FINDENBERG (17) found in Lake Piburg that at the 15 m depth, in the metalimnion, a Cryptomonas bloom appeared at 5°C.

4.317 Peridineae (Fig. 36)

This group appeared only in September, 1969, and in February, 1970. In September, there was a vigorous growth of Peridinium cinctum which, due to its large volume, constituted 80% of the total phytoplankton biomass at 0 m.

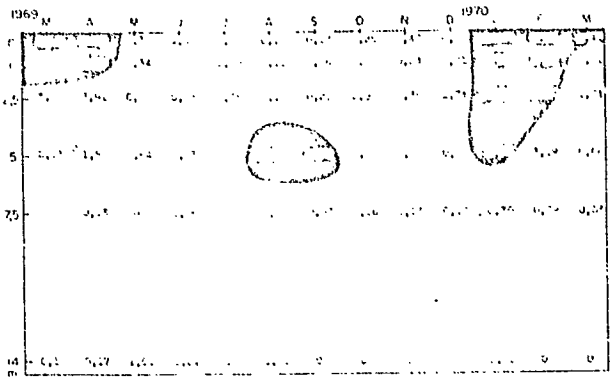


Abb. 35. *Cryptomonas* spp., 10^3 Zellen/ml, Rotsee.

Fig. 35. Cryptomonas spp., 10^3 cells/ml, Rotsee.

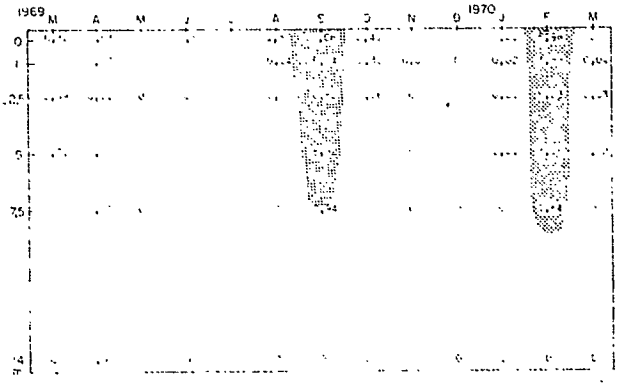


Abb. 36. *Peridineae*, µg ml, Rotsee.

Fig. 36. Peridineae, µg/ml, Rotsee.

In February, 1970, a massive growth of Gymnodinium hantzschii, with over 5000 cells/ml, was found.

During all the other months, the Peridineae were hardly present.

4.318 Phytoplankton Biomass (460)

Fig. 37 shows the space-time diagram of the phytoplankton fresh-weight. In the course of the year, two peaks appeared, at the beginning of 1969 and of 1970. During the summer stagnation period, maximum biomasses were found in the metalimnion, at the boundary between hydrogen sulfide and oxygen.

The absolute figures of more then 30 mg/l of fresh-weight (April, 1969, January, 1970) were extremely high. Thus, according to PAVONI (53),

Fig. 37. Phytoplankton biomass (fresh-weight), µg/ml, Rotsee.

a maximum phytoplankton fresh-weight of 26 mg/l was observed in the Lake of Hallwil. VOLLENWEIDER (80), in his OECD report, indicates phytoplankton fresh-weights that are throughout lower than those found in the Rotsee.

On the amazing fact that also during the summer months, comparatively high plankton densities appeared, at an almost complete consumption of phosphate and other nutrients, will be reported later (see chapter 5.62. Phosphate).

4.319 Population Sequence of Phytoplankton

The phytoplankton populations in the Rotsee developed in rapid succession. Fig. 38 shows these populations, based on the biomass per m^2 of lake surface (0-5 m depth). In March, 1969, there was a Diatomeae maximum (Stephanodiscus hantzschi), and a Cryptomonad maximum. One month later, the Diatomeae had disappeared almost completely, while the number of Cryptomonads went on rising. Simultaneously, large numbers of Chlorophyceae appeared. In May, the total population broke down, except for small remainders of Cryptophyceae. All the other groups remained insignificant, while in June and July, Chlorophyceae were predominant in the plankton picture. In August, Cryptophyceae appeared increasingly; this was essentially the Cryptomonas maximum discussed previously (see page 46), at the 5 m depth. In September,

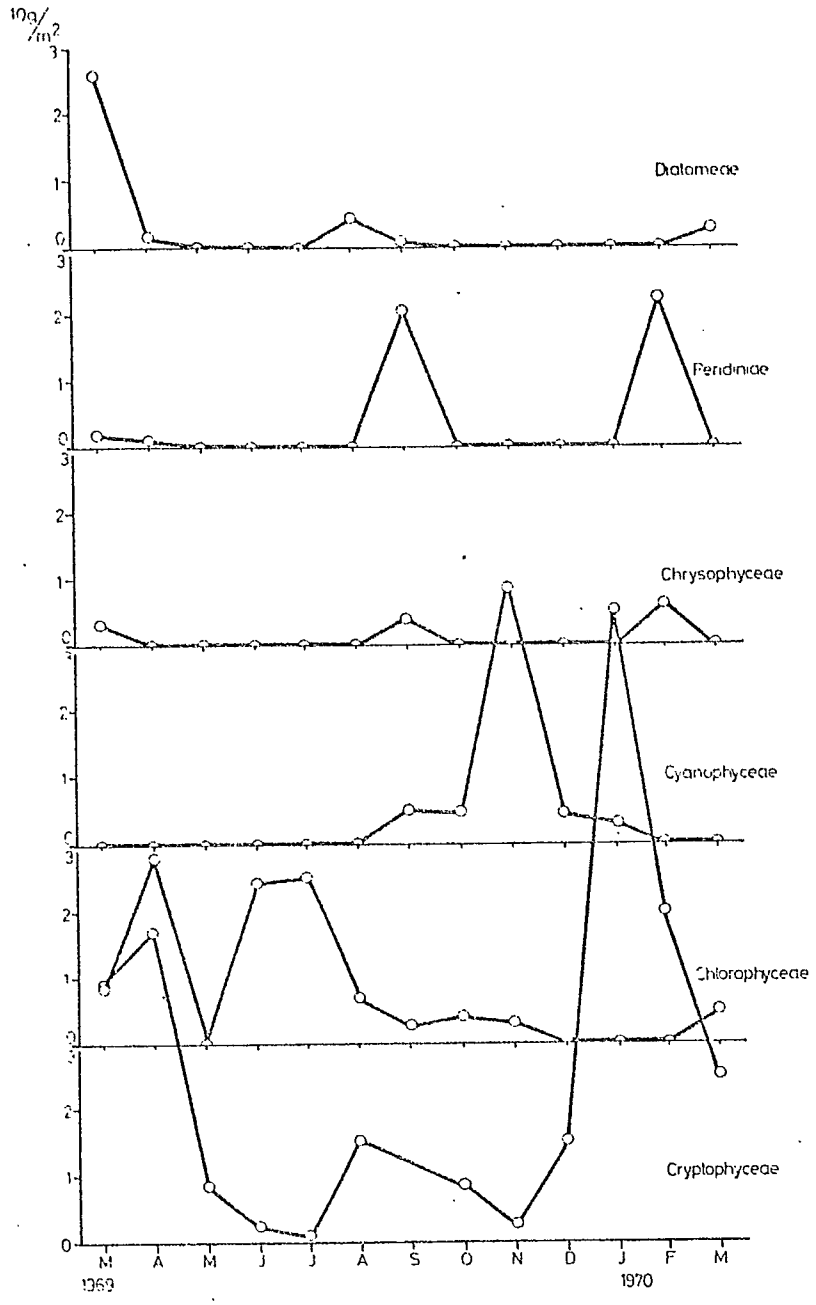


Fig. 38. Population sequence of phytoplankton, square-meter values (0-5 m), g of fresh-weight/m^2, Rotsee. (461)

Peridineae appeared suddenly; the Cryptomonad growth at the 5 m depth (460) decreased considerably. October brought a complete collapse of the populations, yet with a beginning of a Cyanophyceae growth which showed a marked peak in November. This Cyanophyceae peak dissolved at the beginning

of the full circulation or turnover in December, with a simultaneous transfer of the hypolimnetic forms, which will be described later (see Figs. 63 and 64), to the surface. In January, 1970, there was the absolute Cryptomonas maximum under the ice, which completely dominated the plankton picture. In February, a parallel appearance of Chrysophyceae and Peridineae may be seen, while the Cryptomonads still are dominant. (462)

Discussion

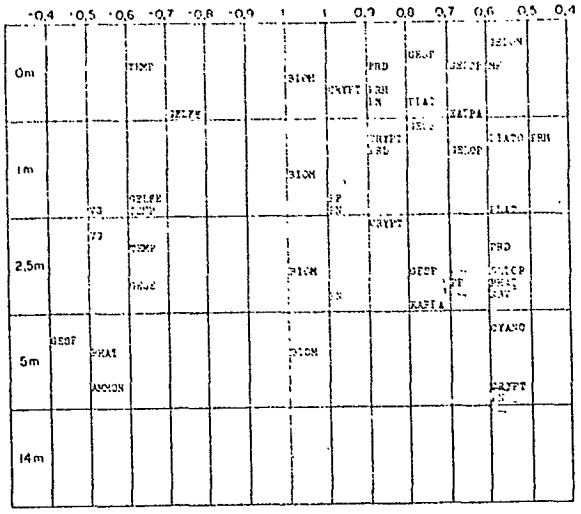
The very dense sequence of different plankton groups (of separate species) shows that the system of the phytoplankton population, in itself, is already highly adaptable, since the population that finds the best conditions, appears to start developing. Apparently, the phytoplankton biocoenosis is very labile, and restricted by many rapidly changing factors. In the yearly regime therefore, one cannot count on the regularity of a continuous culture. In a simplifying manner, a batch-culture pattern may be used for short periods of time.

4.3110 K-Analysis to Reference Parameter Biomass

In the Rotsee, the fresh-weight of phytoplankton (= biomass) (Table 14), in the 0 to 2.5 m layer, is highly correlated with the particulate nitrogen, and in the 1 m and 2.5 m layers also with the particulate phosphorus. For the particulate nitrogen, this relationship was described by PAVONI (54) for separate profiles. A K between the standing crop and the primary production exists only in the 0 m and 1 m layers, while the KK, at 1 m, is as low as +0.48.

In the 0 m layer, there is a KK to the membrane-filter bacteria counts, yet which is smaller than that to the primary production. The highest KK of 0.93 to the Cryptophyceae exists at 0 m, which is to say

Table 14. K-Analysis to reference parameter Biomass, Rotsee.



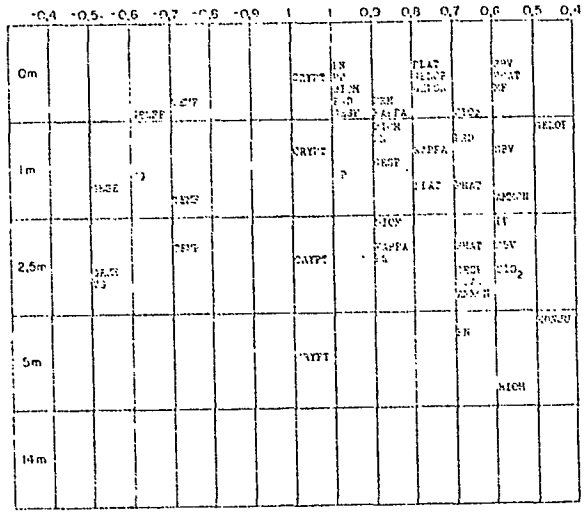
that during the year, phytoplankton in this layer consists mainly of (463) Cryptophyceae. On the relationships between biomass and dissolved organic nitrogen and phosphorus components, there will be reported later (see chapter 5.1). In the Rotsee, it is noteworthy that there are no negative KK to phosphate and nitrate, yet a negative KK to dissolved iron.

The K-Analysis in relation to Cryptophyceae (Table 15) provides a similar picture as for the biomass. With the parameters particulate phosphorus and particulate nitrogen, there exists a very high KK of 0.95 to 0.96 at 0 m. This confirms for the lake the fact that the interrelationships between the particulate components and the biomass appear the more clearly, the closer one gets to a pure culture, as this was described by PAVONI (54).

Conclusions

If at 0 m, one forms a succession of the correlations (K value!) in relation to the biomass, the following results:

Table 15. K-Analysis to reference parameter Cryptophyceae, Rotsee.



Biomass
↓
Individual plankton forms
↓
Production
↓
Particulate P and N contents
↓
Bacteria population

This mathematical joining together reflects directly the ecological causative interconnections of the parameters in the lake.

4.3111 Particulate-Material Components (464)

Fig. 39 shows the square-meter values of the phytoplankton fresh-weight for the trophogenic layer of 0 to 5 m. The maximum value lies above 100 g/m^2.

STADELMANN (73) calculated from the particulate-nitrogen values (according to STURM (77)) the carbon content of the particulate material. This curve is contained in the biomass/m^2 curve. It may be seen that the two curves are not identical; but in their course, and for particular values, they are comparable.

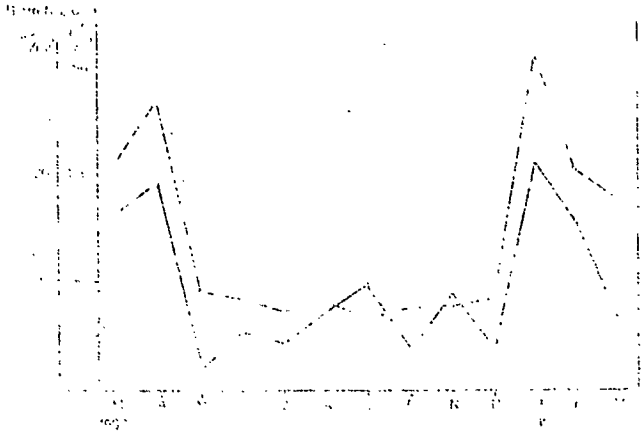


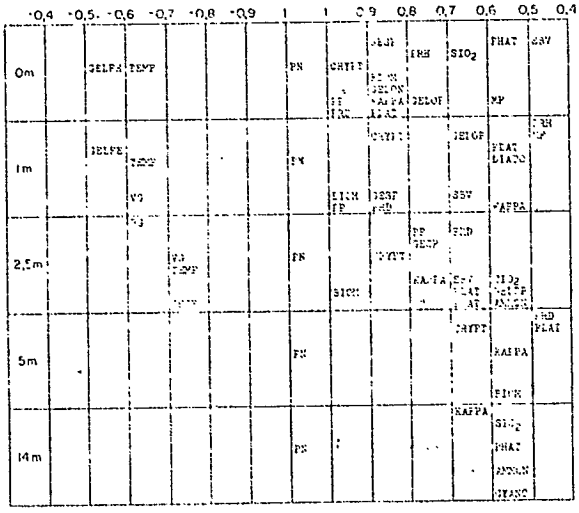
Fig. 39. Square-meter values of phytoplankton (0-5 m), phytoplankton fresh-weight, g/m^2 (= biom F)(——); biomass according to STADELMANN (1971)(Calculation from PN), g C/m^2 (= biom N)(---); Rotsee.

If the percentage is calculated from the relation between fresh-weight and carbon (from the PN values), the carbon values obtained from the fresh-weight are between 25 and 28%. It is true that only the Cryptophyceae maxima were evaluated, since for this group, due to the high KK between biomass and particulate nitrogen, one may be sure to have used but a relatively small portion of detritus erroneously. According to VOLLENWEIDER (80), there is considerable discrepancy in the indications about the carbon content of phytoplankton; it may vary between 3 and 25%. The high value for the C content of phytoplankton fresh-weight from the Rotsee may be explained, according to MULLIN et al. (from VOLLENWEIDER (80)), by the relatively small cell volumes of the plankters.

Fig. 40 shows the square-meter values of particulate phosphorus. In principle, this curve follows that of particulate nitrogen or the conversion to carbon, except for the July value where increased particulate phosphorus was detected in the trophogenic layer. This might be due to the presence of a rather large number of Oocystis lacustris, and the presence at the 5 m depth of Chromatium densegranulatum to be described hereinafter (see Figs. 65 and 66).

Fig. 40. Square-meter values (0-5 m) of particulate phosphorus (mg of P/m^2), Rotsee. (465)

Table 16. K-Analysis to reference parameter Particulate Nitrogen, Rotsee.



For the sake of completeness, the K-Analysis of particulate nitrogen (Table 16) is shown. In the arrangement of the production parameters, it essentially does not differ from that of the biomass. A very high KK exists between particulate nitrogen and particulate phosphorus (more than 0.9 at the 0 to 1 m depth).

(466)

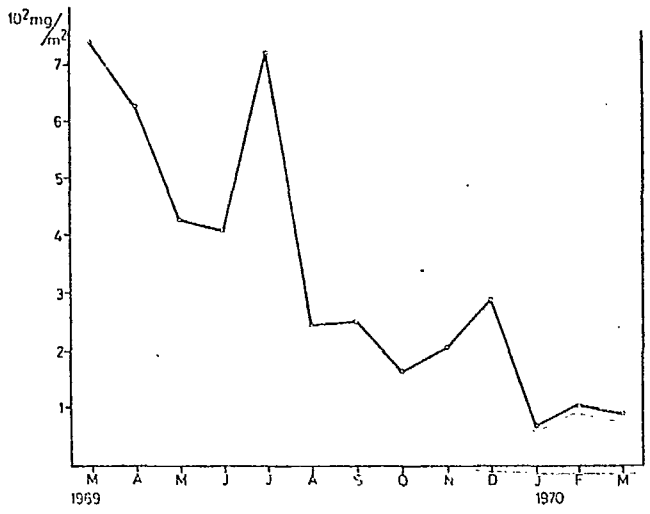
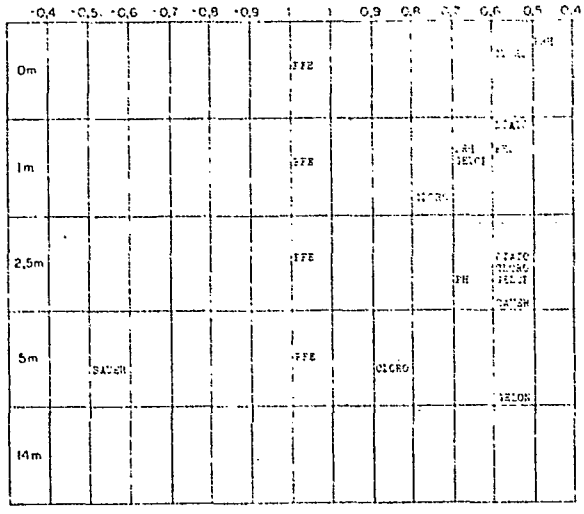


Fig. 41. Square-meter values (0-5 m) of particulate iron (mg of Fe/m^2), Rotsee.

Table 17. K-Analysis to reference parameter Particulate Iron, Rotsee.



Between particulate iron (Fig. 41) and the production parameters, (465) namely the biomass, there exist only extremely scarce relations, as the K-analysis of Table 17 shows; only at 0 m, a KK to the Chlorophyceae may be detected.

In the course of the year, a particulate-iron impoverishment of the trophogenic layer may be found.

Conclusions

In the Rotsee plankton, the Cryptophyceae are predominant. From the fact that practically no intact cells were found in the hypolimnion, one may conclude that a large part of the cells were mineralized already in the epilimnion.

The joining together of the KK relative to biomass results in an ecologically "meaningful" gradation.

4.32 Phytoplankton in the Lake of Lucerne (467)

Based on the findings of the last chapter, regarding the assertive force of the determination of particulate nitrogen, and the fact that phytoplankton in the Lake of Lucerne was researched by STADELMANN (73), and BLOESCH (8), a more detailed illustration may be omitted in this connection.

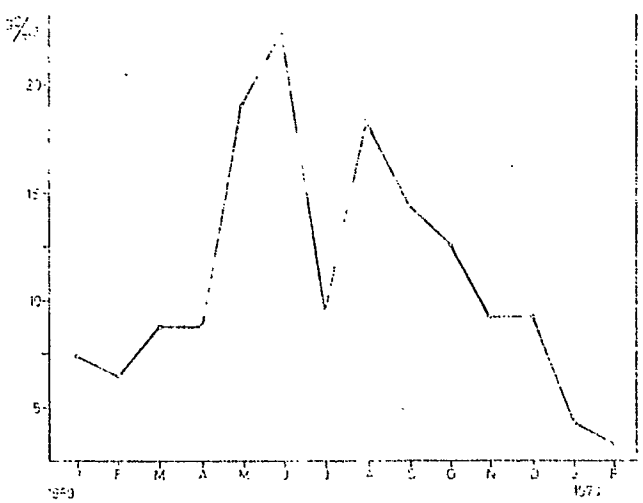


Fig. 42. Square-meter values of phytoplankton biomass according to STADELMANN (1971), g C/m², 0-15 m, Lake of Lucerne.

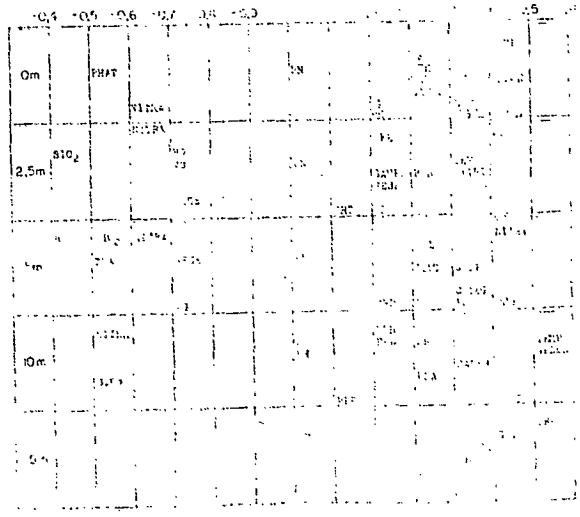
To get acquainted with the conditions regarding biomass in the Lake of Lucerne, Fig. 42 shows the biomass curve calculated by STADELMANN (73) from the C:N values, in the form of g C/m². In the plankton, the

blue-green algae were predominant, that is, Oscillatoria rubescens almost all year round, and in autumn Pseudanabaena catenata. The Diatomeae were represented mainly by Flagilaria crotonensis, Tabellaria fenestrata, Cyclotella spp., and Diatoma elongatum. Among the flagellates, Rhodomonas lacustris and Rhodomonas lens, Cryptomonas ovata, and Cryptomonas erosa were present almost all year round.

K-Analysis

Since the biomass values of the curve, taking into consideration one factor, correspond to those of particulate nitrogen, the particulate-nitrogen value (Table 18) may be used directly for the K-analysis.

Over the whole trophogenic layer, there exist negative KK between particulate nitrogen and the nutrients nitrate and phosphate. Here, the production-determining role of the two nutrients may be clearly seen. There is a close relationship between particulate nitrogen and particulate phosphorus, with a KK of 0.82. Likewise, there exist significant correlations between primary production and particulate nitrogen. The relationship between biomass and bacteria will be shown in chapter 5.4.



(468)

Table 18. K-Analysis to reference parameter Particulate Nitrogen, Lake of Lucerne.

4.33 Primary-Production Measurement

4.331 Daily Rhythm

Each calculation of the primary production for a determined period of time, for instance for the yearly production, requires a conversion based on the hourly production. An essential prerequisite therefor is the knowledge of the daily course of the primary production. The two investigations described hereinafter have only random character; nevertheless, for the investigated lakes, they serve to confirm the calculations of daily and yearly productions, and to evaluate the exposure methods applied.

In the Rotsee (12 August, 1969), and in the Lake of Lucerne (21 May, 1969), on a cloudless day, tests were carried out "in situ et loco", to answer the following questions:

1. Which conversion factor must be used to determine the daily production from a measurement carried out between 10 A.M. and 2 P.M.?

2. Is the production total of a stepwise series of short-term experiments identical with that of a long-term experiment?

3. How does the daily-production curve proceed in comparison to the light curve?

Methods

The sampling depth in the Lake of Lucerne was 2.5 m, in the Rotsee 1 m. At the beginning of the experiment, 20 liters of lake water were filled into a bottle which was stored during the day at the collecting depth. This met the prerequisite that during the investigation, an invariable phytoplankton population be available.

Two series of bottles were formed. At the beginning of the experiment, the first series was mixed with ^{14}C, and exposed. Every hour,

two bottles each were withdrawn and evaluated. Hereinafter, this kind of exposure will be called "long-time". From the second series, two bottles (469) were filled each hour from the 20-liter bottle, mixed with ^{14}C, and exposed for one hour. This kind of exposure will be called "short-time".

With a solarimeter, the number of calories striking one square meter of lake surface was determined, and with the relative light measurement (see Methods), taking into account a 44% reflection at the lake surface, the energy at the respective exposure depth was calculated in kcal per square meter. From these values, it is possible to calculate the quotient of the light utilization (mg of C_{fix}/kcal x m).

Results

1. Lake of Lucerne

Fig. 43 shows the summed-up values of the "long-time" and "short-time" experiments. In the "long-time" experiment, the daily total is 144.9 mg of C/m^3, in the "short-time" experiment, 139.7 mg of C/m^3, that is, in the Lake of Lucerne, the daily total of the "short-time" experiments is identical with that of the "long-time" experiments, within the limit of error of the ^{14}C-measurement, for the 2.5 m depth step. The scattering of the applied method is 3-6% (SCHEGG (62)).

From the ascent of the two curves, it may be seen that the hourly increase in the "long-time" experiment is subject to considerable fluctuations. Its minimum was only 2 mg of C/m^3, between 2 and 3 P.M.. According to OLIE (47), this rest period is due to the inhibitory effect of mainly extracellular accumulation of assimilates, and to the lack of turbulence.

OLIE (47) proved experimentally that the water turbulence, the "washing effect", is of decisive importance. In the "short-time" experiment, these fluctuations do not occur.

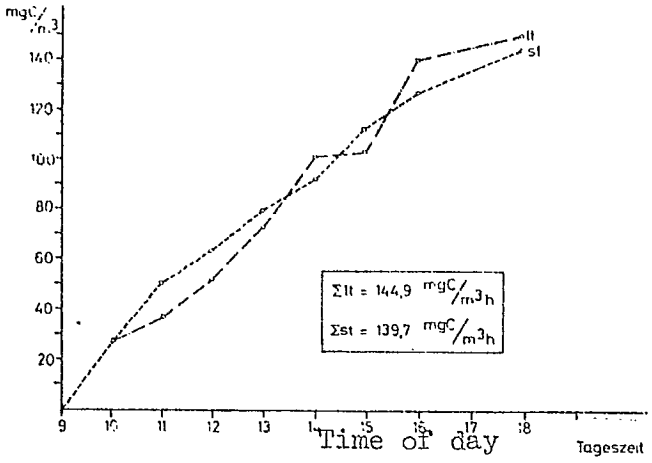


Fig. 43. Summed-up production rates of the "short-time" experiments (---) and the "long-time" experiments (-.-.-) in the Lake of Lucerne (mg of C/m^3).

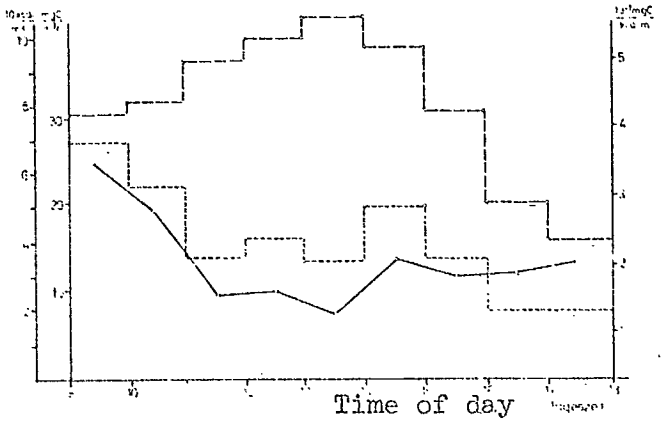


Fig. 44. "Short-time" primary-production measurements (-.-.-), mg C/m^3h, irrediation at 2.5 m (— — —) in kcal/m^2, relative light utilization (———) in mg C/kcal x m, Lake of Lucerne. (470)

In Fig. 44, the "short-time" values of the primary production are plotted against the available energy. Also the quotient of the light utilization is indicated as a curve.

At a relatively low light intensity, in the morning between 9 and 10 A.M., a surprisingly high primary production sets in, with correspondingly high values of light utilization. At maximum light intensity, between

1 and 2 P.M., there is a minimum of hourly primary production, and the minimum of the light utilization. This phenomenon may be explained with a light inhibition. However, it may also be due to the physiological exhaustion of the photosynthesis apparatus (OHLE (47)).

A second maximum of the primary production appears between 2 and 3 P.M., at decreasing light intensity in the exposure layer. Toward evening, the primary production decreases again, in accordance with the decreasing light intensity.

2. Rotsee

On 12 August, 1969, the sequence of the samplings in the Rotsee was further condensed, in that the "short-time" experiments were carried out overlappingly for a half hour. (Immediately after the withdrawal, the samples were filtered on the boat).

The results are shown in Fig. 45. Between 7 and10 A.M., there is a very rapid ascent of the hourly primary production values, which ends up in a plateau between 10 A.M. and 1 P.M..

At highest light intensities, between 12 A.M. and 2 P.M., the inhibitory effect, already observed in the Lake of Lucerne, appears, with a decrease in the hourly primary production by almost half. Likewise, also the ascent of the primary production was observed again, at decreasing light intensities, in the afternoon.

The differences between the "short-time" experiments, shifted by a half hour, showed that the production may undergo considerable fluctuations within short intervals.

Comparison of the daily totals: (471)

"short time":	total, starting at the hour	388.1 mg of C/m^3
"short time":	total, starting at the half-hour	374.6 mg of C/m3
"long time":	during the whole day	384.9 mg of C/m^3

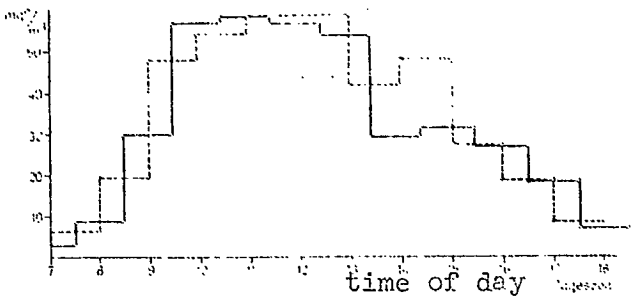


Fig. 45. Overlapping "short-time" experiments, mg C/m^3,
at-the-hour exposures (----),
at-the-half-hour exposures (——), Rotsee.

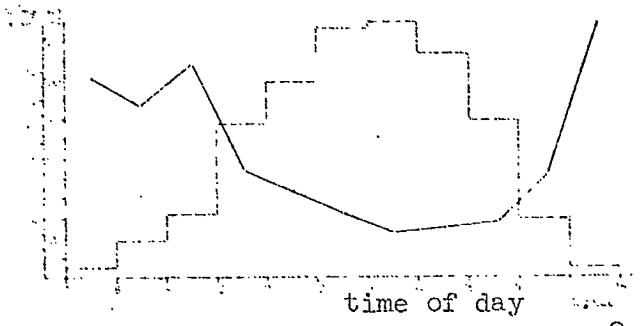


Fig. 46. Light irradiation at 1 m, in $kcal/m^2$ (— — —),
light utilization in mg of C/kcal x m (———), Rotsee.

Taking into account the many separate experiments, the "short-time" values (12 each) are surprisingly close together. As in the Lake of Lucerne, the "long-time" values differ considerably in their hourly increase from that of the "short-time" values; however, the daily totals of both kinds of exposure are again identical.

Fig. 46 shows the values of the irradiated energy of the exposure depth. The maximum irradiation, in time, coincides again with the observed inhibition of the primary production. This results in the least utilization of the irradiated light.

Conclusions

The questions asked at the beginning may be answered as follows:

1. The daily total of hourly experiments corresponds to the values of daily measurements, that is, the productivity for the same plankton population is constant. DOTY et al. (13) also state the same daily totals for long-time and short-time experiments.

2. Considerable daily fluctuations occur, which may be of very (472) short duration, that is, in the order of magnitude of minutes.

3. The daily curve for the primary production of the short-time experiments shows an affinity to the light curve in two directions:
a) the dependency on the light intensity at suboptimal exposure,
b) the inhibition of the primary production by overexposure. Apparently, the physiologically optimal exposure exists only for a very short time in the course of the day.

4. If an exposure takes place between 10 A.M. and 2 P.M., the conversion factor of the hourly production, for the Lake of Lucerne, lies above 9. If the values obtained between 7 and 9 A.M. are interpolated to the daily production, a value of about 10 is obtained for the 2.5 m layer. This factor was used by STADELMANN (73) to calculate the daily production for the values per m^2 of lake surface, that is, for the whole profile.

For the Rotsee, this factor might be lower; at an average production of 52.8 mg of C/m^3h, between 10 A.M. and 2 P.M., it lies at 7.5 - 8 for the 1 m layer.

These values apply to the layer of maximum productivity.

5. The exposure time of 4 hours applied in this research does not constitute the ideal solution, since at the end of the investigation period, it coincides with the light-inhibition period. According to OHLE (47), there

is also an increased release of assimilates during these periods. Better bases of conversion to the daily production would be obtained with a 2- to 3-hour exposure at the optimal time between 10 A.M. and 12 A.M. = 1 P.M., taking into consideration the light curve, or with an exposure over the whole day, from one hour after sunrise to one hour before sunset.

4.332. Primary Production in the Rotsee

Fig. 47 shows the values of the primary production in space and time sequence. In view of the random character of the separate measurements, a real isopleth illustration was omitted. The figures indicated in the Table are the values measured in the clear bottle. The providing of a difference to the dark-values was omitted intentionally, since each incorporation of C atoms into organic substance contributes to an increase thereof.

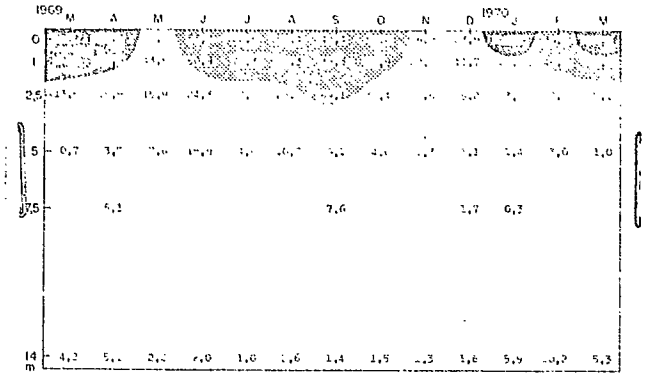
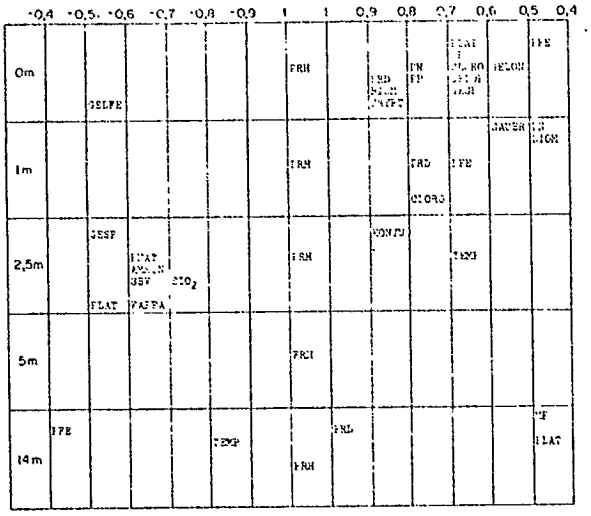


Fig. 47. Primary-production rates (clear-values), mg of C_{ass}/m^3h, in the Rotsee.

The uppermost layer of 0 to 2.5 m is the carrier of the physiologically "highly active" plankton population. In this layer, the bulk of the phytoplankton biomass is built up. The main vegetational periods are in early spring, and to a lesser extent in the summer months. In January, 1970, extreme maxima are found under the ice. However, they show a very small vertical extension. (473)

Table 19. K-Analysis to reference parameter Primary Production (clear-values), Rotsee.



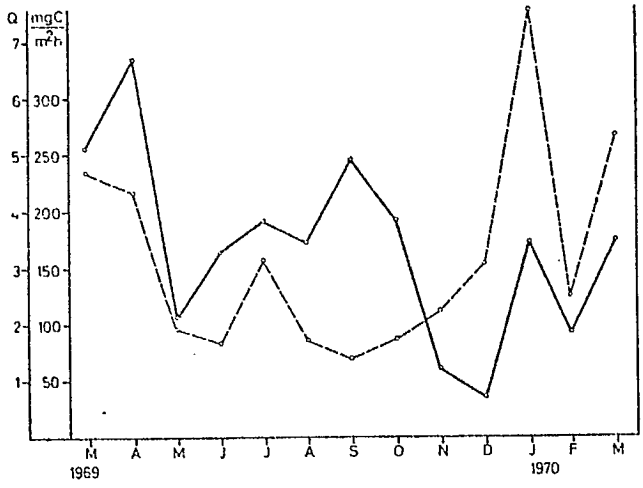


Fig. 48. Square-meter values of primary production (0-5 m), mg C_{ass}/m^2h (——), quotient maximum value by mean value (— — —), Rotsee.

The correlation analysis (Table 19) shows high KK to the biomass, to the dark-values (see Appendix), to the PP and PN values. The relationship to bacteria will be discussed in chapter 5.31. A negative K to phosphate and nitrate exists only in the 2.5 m layer, where also a negative K to ammonium may be observed. Furthermore, a KK of 0.52 to dissolved iron may be detected.

Fig. 48 shows the assimilative performance below 1 m^2 of lake surface (calculated with "Profile" program). It shows a marked peak in the spring of 1969, a smaller peak in the summer of 1969, and another peak in January, 1970. The quotient of maximum value by mean value, which constitutes a measure for the course of the curve, reaches in January, 1970, a value of 7.6, that is, the layer of main productivity shows a low magnitude. For one-peak curves, this quotient is well suited for the lake characterization suggested by FINDENEGG (16), with the vertical distribution of the primary production. (474)

4.333 Primary Production in the Lake of Lucerne

Fig. 49 shows the space-time diagram of the primary production clear-values in the Lake of Lucerne. A marked spring maximum is followed by a minimum in June and July, 1969, and another late-summer maximum. The layer of highest production generally lies at the 2.5 m depth. An isolated high value of 34.8 mg of C/m^3h in August, 1969, at the 10 m depth, was found to be due to the presence of embedded Oscillatoria rubescens.

The primary-production values lie higher than those indicated by GÄCHTER (19). It is true that the measuring site for the present investigation was shifted by some hundred meters, out into the bay. It is also possible that this increase is not due exclusively to an increased sewage load, but rather to a deeper-reaching circulation. That these mixing depths in the Lake of Lucerne are subject to considerable fluctuations, was shown by AMBÜHL (4).

GERLETTI (20) found that in the deep Lago Maggiore the turnover depth in each case plays an important part in the production of the following year.

To draw direct conclusions with respect to trophic growth, a longer period of time would have to be taken into consideration.

The K-Analysis (Table 20) shows a very close interrelationship to the production parameters, especially a high KK to the temperature, which indicates that in the Lake of Lucerne, the temperature plays an important part in the primary production. Negative KK exist to nitrate at 0 m, and to phosphate at all depths down to 5 m, The primary production (clear-values) always correlates Dark with the primary production, down to the 10 m depth.

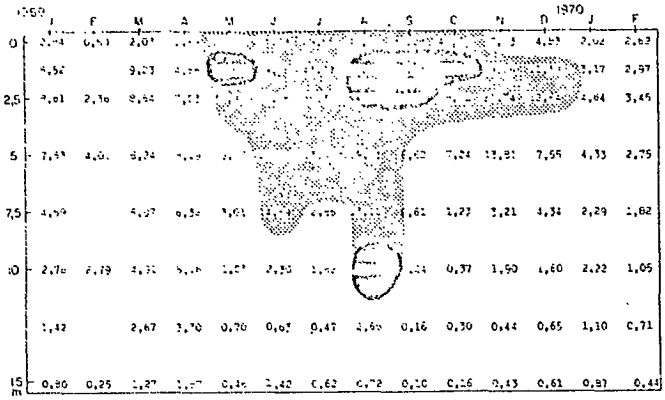


Fig. 49. Primary-production rates (clear-values), mg of C_{ass}/m^3h, in the Lake of Lucerne.

5. Production in Relation to Degradation (475)

Mineralization is the breakdown of energy-rich chemical compounds to energy-poorer ones. This breakdown may be a purely chemical process, or it may involve organisms (degradation). In degradation, part of the broken-down material is used to build up secondary biomass of heterotrophic organisms. The secondary biomass, generally, is smaller than the biomass formed autotrophically. In only slightly polluted lakes, this may be clearly seen PAVONI (54)).

The heterotrophic biomass production may exceed the autotrophic biomass production only if larger amounts of assimilable substrate of allochthonous origin or from the recovery of bottom sediment are available. Such an example was described by KUZNEZOV and ROMANENKO (37) for the dammed-up Rybinsk lake.

In the production biology of lakes, the detecting of relationships, or the setting of values, is possible only if the energy flow is followed, not only to the built-up organism (with energy-rich chemical compounds), but rather, to the remineralization and build-up of secondary heterotrophic biomass. It is therefore not sufficient to merely determine the effects of these processes, such as oxygen deficiency, CO_2 accumulation etc.

The energy basis (substrate) for heterotrophic growth are energy-rich organic compounds. These compounds may occur in a lake in particulate form as standing crop and detritus, or in dissolved form as excretion or autolysis products. For the planktonic bacterial flora, dissolved substrates are of prime importance.

5.1 Phytoplankton Excretion and Autolysis

Many investigations have been devoted to the origin of dissolved organic components, and to their ecological importance (FOGG et al. (18), PROVASOLI (57), HELLEBUST (25), NALEWAJKO (43), and HOOD (29)).

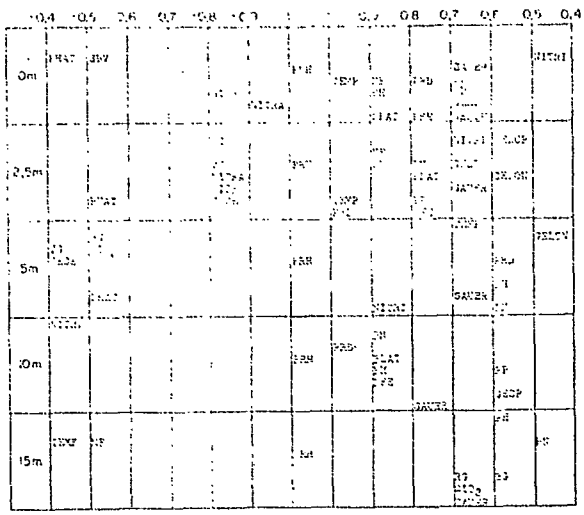


Table 20. K-Analysis to reference parameter Primary Production clear-values, Lake of Lucerne.

According to FOGG et al. (18), plankters excrete organic acids which are easily assimilable for bacteria. For excretion products, such as glucose and acetate, HOBBIE and WRIGHT (27) showed that the assimilative rates are very high. In a body of water, only minute amounts of sugar, for example glucose, may actually be detected.* For amino acids, GOCKE (21) showed experimentally, on bacteria-containing and bacteria-free cultures of Scenedesmus quadricauda, that in the bacteria-containing culture, substantially smaller amounts of free amino acids are accumulated, so that even these occur in relatively low concentrations. However, there exist also more difficultly attackable compounds, mainly humic acids. (476)

In association with particulate phosphorus and nitrogen analyses (RUTTNER (73)), also the dissolved organic components thereof were determined. *as established by ALLAN (1) and WELWOOD (82).

Methodically, the determination of dissolved organic substances in lake water causes some difficulties. It is possible that the relatively high values resulted in part by the bursting of cells during filtration. This might be suspected particularly for the Rotsee, where about 1700 µg/l were found during the January, 1970, investigation. At that time, the planktonic population consisted mainly of flagellates, Rhodomonas, and Cryptomonas, which are known for their pressure-sensitive cell walls (VOLLENWEIDER (80)). A direct proof for losses was provided with the ^{14}C-method by ARTHUR et al. (6). However, the size of error depends on the kind of plankter; it is therefore inconstant.

Figs. 50 and 51 show for both lakes the dissolved organic nitrogen compounds in the space-time diagram.

According to STADELMANN (73), in the Bay of Horw, except for the winter months, the particulate organic nitrogen outweighs the dissolved organic nitrogen per 1 m^2 of lake surface. In the Rotsee, in accordance with production figures, in January to April, 1969, and 1970, particulate nitrogen is higher; during the other months, dissolved organic nitrogen is higher. However, in both lakes, the values of the discussed components lie in the same order of magnitude.

Discussion

In the absence of mineralization and rebuild-up, the dissolved organic substance would have to constitute the sum total of all the excretion and autolysis products yielded during the stagnation. According to OHLE (48), and measurements carried out by BLOESCH (verbal communication), only a minor portion of the available primary production can be collected in the sediment. If a large biomass, with correspondingly large excretion

and autolysis performance, is available in a lake, yet only low sedimentation rates and relatively low values of organically dissolved substance are found, these conditions may be interpreted only by an extremely rapid mineralization and recycling of released organic substance (NALEWAJKO (43)).

If the partly high excretory performance of the algae in the layer of highest production is taken into consideration, then even the dissolved organic components (dissolved organic N and P) would have to show considerably higher differences in the vertical distribution. This is not the case, and it therefore constitutes another indication for the capacity of the bacterial population in the trophogenic layer.

(477)

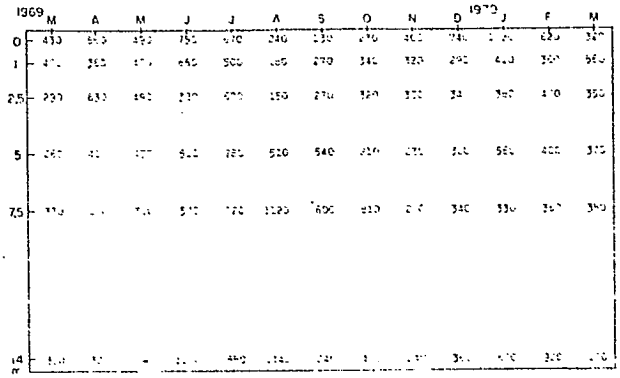


Abb. 50. Gelöster organischer Stickstoff, µg N/l im Rotsee.

Fig. 50. Dissolved organic nitrogen, µg of N/l in the Rotsee.

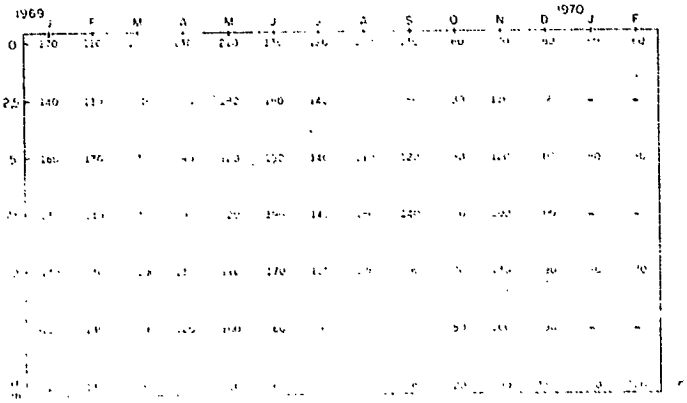


Abb. 51. Gelöster organischer Stickstoff, µg N/l im Vierwaldstättersee.

Fig. 51. Dissolved organic nitrogen, µg of N/l in the Lake of Lucerne.

At first glance, it is disappointing that, in comparison to the bacterial counts, particularly the membrane-filter counts, no KK exist in the yearly cycle of either lake. Regarding plate counts, in the Rotsee, there is a relatively low KK of 0.58 to dissolved organic nitrogen. There are, of course, some exceptions, as, for instance, in October, 1969, when at high membrane-filter counts, the dissolved organic nitrogen showed lowest values.

A similar discrepancy between dissolved organic nitrogen and its utilization by bacteria is found in the marine field where, on an average, 1 mg of C/liter is available in dissolved form (KALLE (33)). For the epilimnion in fresh water, these relatively high dissolved-organic-substrate values may be explained as follows:

According to WEIMANN (82), the bulk of the dissolved organic substance occurs as higher-molecular compounds, mainly as humic acids, which bacteria cannot attack directly. In the lake, there exists a certain level of organic substance which it is difficult to utilize for bacterial mineralization. The relatively high values of dissolved organic substance (478) therefore are the "summed-up" difficultly attackable organic compounds.

The bacterial population obtains its substrate mainly from fresh organic substance, that is, from substance released directly by autolysis and excretion. Only when this latter decreases to small amounts, the available organically dissolved level is reverted to.

5.2 Morphology of Bacteria in the Open Water

To interpret microbiological processes occurring in a lake merely on the basis of chemical measurements would be tantamount to confounding cause and effect. A prerequisite for the comprehension of dynamic relations

is the knowledge of the organisms which co-determine to a large extent the changes in the chemism of the biotope. Apart from the bacterial biomass, also the morphological picture is an "answer" of the bacterial flora to the substrate conditions.

5.21 Planktonic Bacteria

Water, the natural habitat of microorganisms, is suboptimal for their nutrient requirements. The characteristic form of the allochthonous heterotrophic microflora, physiologically, is present in "waiting position" or, as Waksman (from JANNASCH (32)) defined it, as "waiting cells". These latently occurring bacteria which, so to say, metabolize on a "pilot flame", are also called "zymogenic", according to Winogradsky (from JANNASCH (32)).

The population as a whole shows a huge ecological valency, that is, from a multiplicity of physiological groups, the one that owns the enzymatic equipment corresponding to the nutrient supply, is mobilized. WUHRMANN (83) designated this phenomenon as "sociological adaptation". The term "adaptation" is to be understood in relation to the biocoenosis as a whole.

Most aquatic bacteria occur as free swimmers. Shape and structure may vary considerably, depending on the nutrient supply.

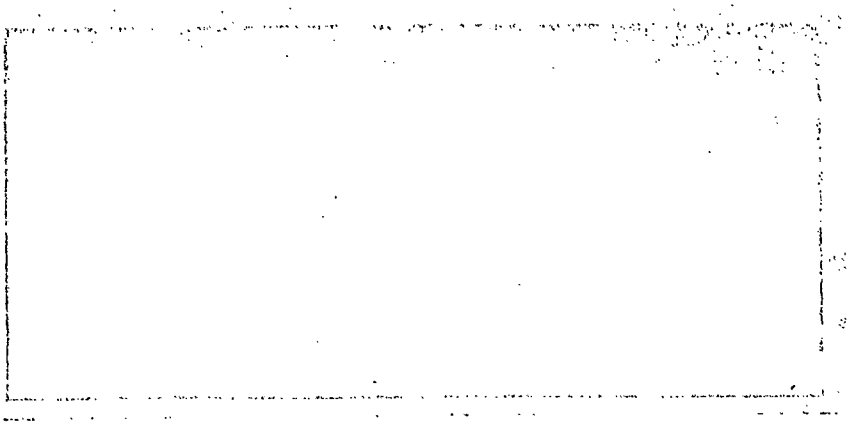


Fig. 32. Cocci and short rod forms on membrane-filter preparation 2.5 m depth) from Lake of Lucerne (magnification about 1000 x, phase contrast).

All the zymogenic germs are small, in the order of magnitude (479) of 0.3 to 1 µ. It is particularly difficult to recognize the "zymogenic" germs in nutrient-deficient waters. Fig. 52 shows a membrane-filter preparation with zymogenic bacteria from the Lake of Lucerne.

To verify these minute forms, an April, 1967, sample from the Lake of Lucerne was examined under the electron microscope. The lake water was fixed with 5% formol, diluted tenfold with membrane-filtered (0.1 µ) water, and 0.02 ml were evaporated on a Formvar film in the water-jet vacuum. The picture from the electron microscope (Fig. 53) shows that the particles in the foreground have the same size as the particles counted on the membrane filters. At 18,000-fold magnification (Fig. 54), one may recognize bacteria with sharply marked cell walls and slightly shrunk plasma bodies. The size of the particles is 0.3 - 0.4 µ.

Electron-microscopic examinations should form a constituent of an extensive morphological clarification about the variability of allochthonous bacterial flora in the headwaters. Such investigations on stalked bacteria were carried out by HIRSCH (26).

A quite different picture was found in the Rotsee, where the bacterial density was considerably higher than in the Lake of Lucerne (see chapter 5.31). In accordance with the higher substrate concentration, the separate cells are larger, and therefore more easily recognizable.

By way of example, Fig. 55 shows a live photograph of the population existing on 17 January, 1970, from 0 m. Compared with the plankton density, the bacterial count is extremely high. It may be seen here how difficult it is to recognize the forms, since only the smallest number of the bacteria lie in one picture plane.

(479)

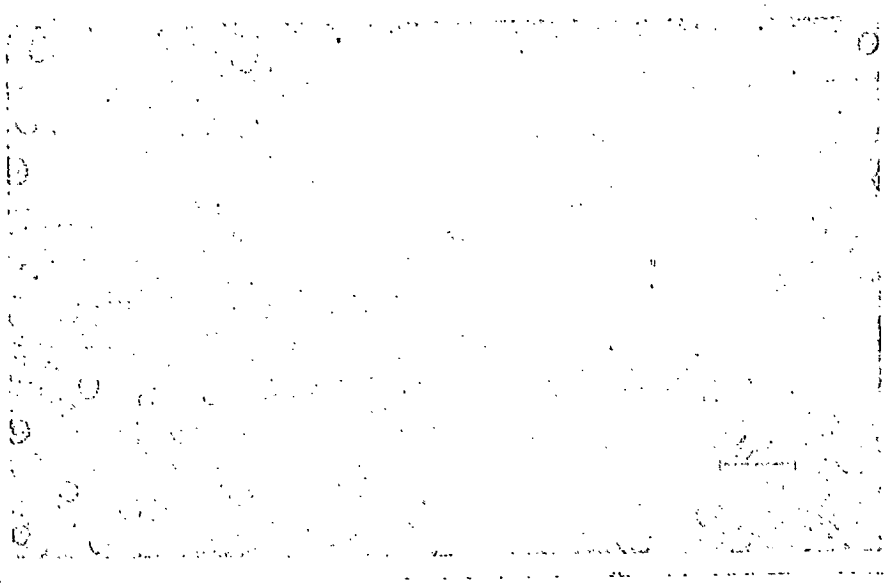


Fig. 53. Zymogenic germs (electron-microscopic photograph, general view, Lake of Lucerne, 0 m depth (magnification about 3000 x).

(480)

Fig. 54. Zymogenic germs: Cocci forms (0.3 µ), Lake of Lucerne, 0 m depth (electron-microscopic photograph, magnification about 18,000 x).

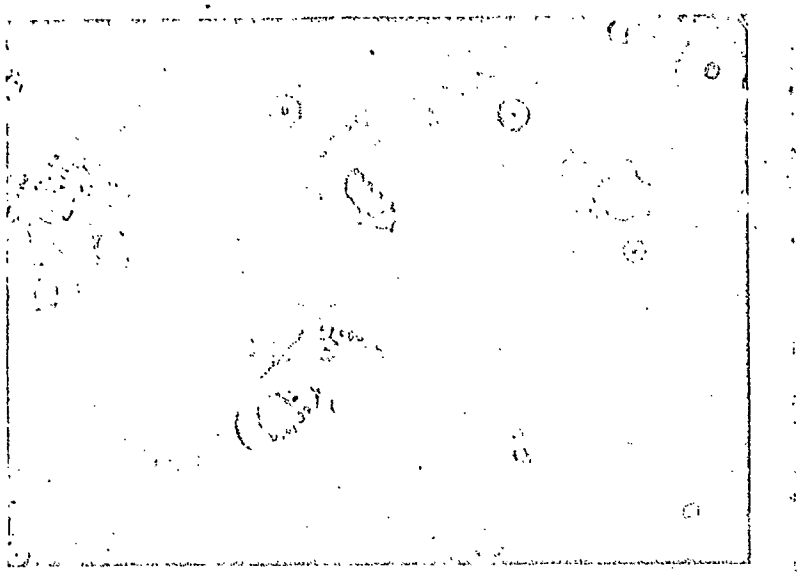


Fig. 55. Live photograph (normal water sample): The two planktonic flagellates are Chlamydomonas sp. (20 µ length). Size of bacteria 1-2 µ, 17 January, 1970, 0 m depth, Rotsee (magnification about 800 x, phase contrast).

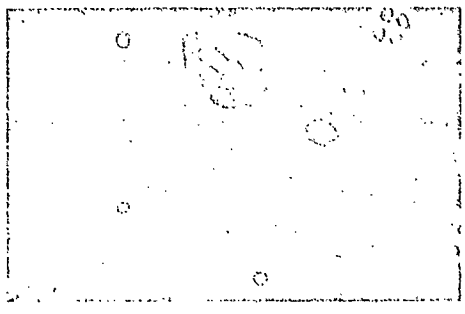


Fig. 56

Fig. 57

Fig. 56. Live photograph: Filamentous bacterium (1). (Length up to over 50 µ, diameter 0.1-0.2 µ). At the right, spirillar forms (2) of very large spiral width may be recognized. April, 1969, 2.5 m depth, Rotsee (magnification about 800 x, phase contrast).

Fig. 57. Live photograph: spirillar forms (1) from the epilimnion, April, 1969, 0 m depth, Rotsee (magnification about 1250 x, phase contrast).

In the Rotsee, extremely thin filamentous bacteria (diameter 0.1-0.2 µ) appeared very often; at the same time, small accumulations of spirilla appeared (Fig. 56). However, in the epilimnion of the Rotsee, also larger spirilla appear (Fig. 57). The very long, thin forms occur also in the hypolymnion, where the bacterial population reaches extremely high values (Fig. 58).

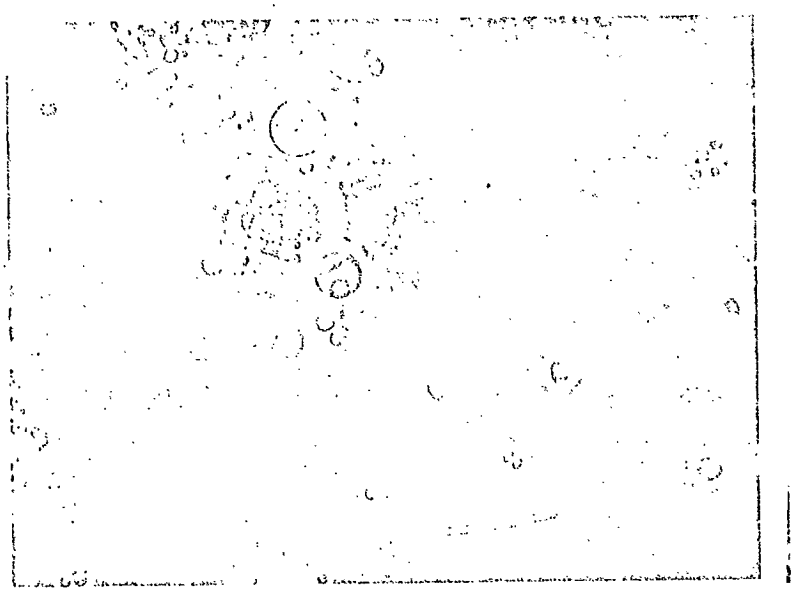


Fig. 58. Live photograph: Bacteria from the hypolimnion (14 m depth), April, 1969, Rotsee (magnification about 1000 x, phase contrast).

5.22 Growth Forms (482)

Growth forms are associations within which rather large organic or inorganic particles may be recognized. Their occurrence may be site-dependent. In lakes with lower substrate concentrations, growth particles are the result of deficiency conditions. The February, 1969, photograph from the Lake of Lucerne (Fig. 59) is an example therefor. However, growth bodies are found also in highly polluted waters, where bacteria settle down on washed-in organic particles.

Bacterial growth on phytoplankton may hardly be observed on intact populations; however, bacterial decomposition of phytoplankton occurs after water bloom, and below the layer of maximum productivity. Fig. 60 is from the Rotsee, at the 5 m depth, in March, 1970. It shows a flagellate cell on which numerous bacteria have settled.

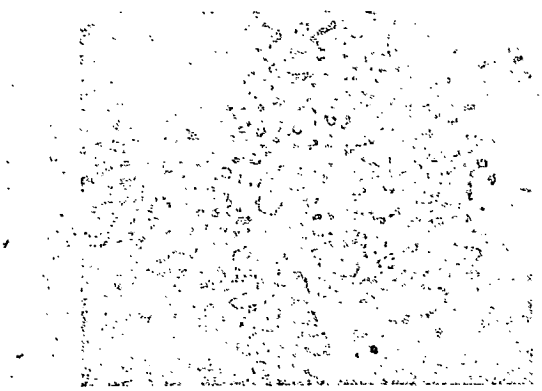


Fig. 59

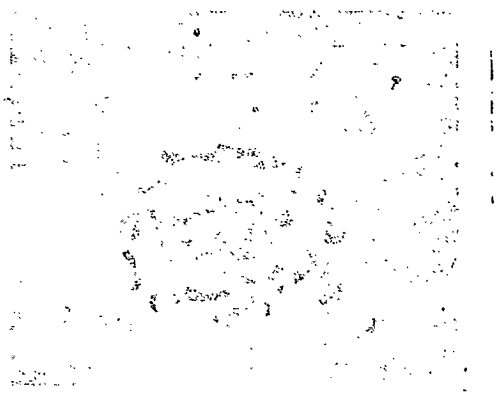


Fig. 60

Fig. 59. Growth particle on membrane-filter preparation. February, 1969, 0 m depth, Lake of Lucerne (magnification about 800 x, phase contrast.

Fig. 60. Bacterial decomposition of a plankter in the metalimnion. March, 1970, 5 m depth, Rotsee (magnification about 1250 x, membrane-filter preparation, phase contrast).

5.23 Zoogloeae

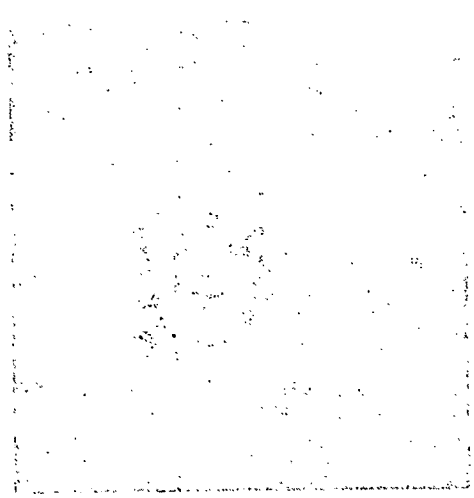
Zoogloeae are cell associations without growth core. Generally, they are species-determined. The occurrence of zoogloeae is typical in waters of high substrate concentration, and in special environments, as the examples from the Rotsee show.

Fig. 61 shows a special zoogloeal form from the Rotsee, beside filamentous bacterial forms.

Further zoogloeae from the Rotsee, such as Thiopedia rosea, Leptothrix pseudovacuolata and Lamprocystis roseopersicina will be discussed later on (see chapter 5.24).

Also in the Lake of Lucerne, special kinds of zoogloeae appeared occasionally. Fig. 62 shows the form Planktomyces bekefii Gimesi, described also by PAVONI (53), a stalked bacterium which may be observed relatively often in the Lake of Lucerne. These star-forming, stalked bacteria are often mentioned, in a great variety of forms, in sea-bacteriological works (KRISS (34)).

(483)



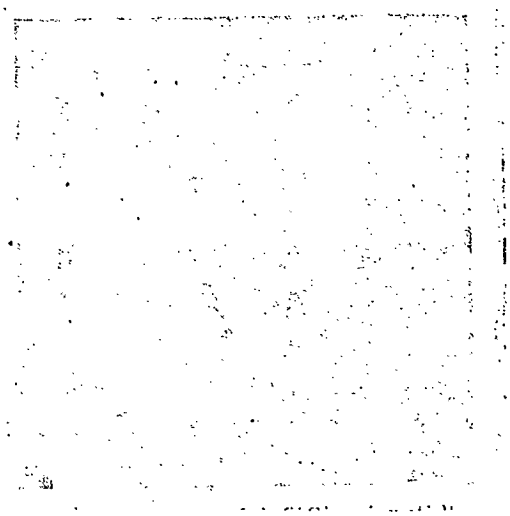


Fig. 61 Fig. 62

Fig. 61. Zoogloeal form, membrane-filter preparation. February, 1970, 5 m depth, Rotsee (magnification about 1000 x, phase contrast).

Fig. 62. Planktomyces bekefii Gimesi, stalked, star-forming bacterium, cell diameter 0.8-1 µ. September, 1969, 7.5 m depth, Lake of Lucerne (magnification about 1500 x, phase contrast, membrane-filter preparation).

5.24 Special Rotsee Forms

Thiopedia rosea Winogradsky

The most remarkable form among the hypolimnetic bacteria of the Rotsee is Thiopedia rosea Winogradsky (HUBER-PESTALOZZI (30)) (Fig. 63), Thiopedia belongs to the Thiorhodaceae. These are photosynthetizing bacteria which fix carbon by utilizing hydrogen sulfide, thiosulfate or

molecular hydrogen as hydrogen donors. The CO_2 fixation may take place over the Calvin cycle or other carboxylation mechanisms (SCHLEGEL (66)). Apart from the CO_2 fixation, carbon may also be assimilated in the form of strongly reduced organic compounds (fatty acids (SCHLEGEL (67)).

Thiopedia rosea, its yearly curve:

According to Utermöhl (from HUBER-PESTALOZZI (30)), Thiopedia is highly microaerophilous. The space-time diagram shown in Fig. 64 confirms this property. Apparent exceptions (April, 1969, February and March, 1970), where Thiopedia appeared in layers of higher oxygen contents, were due to the circulation of the water masses.

The maximum values "feel", so to speak, the border line between oxygen and hydrogen sulfide all year round (shown in Fig. 64). Metabolic requirements for hydrogen sulfide as H-donor may explain the maximum occurrence in March, 1969, at the 14 m depth, and in June, 1969, at the 7.5 m depth. From June to September, 1969, practically no Thiopedia cells appeared in the hypolimnion. In November, the autumn circulation started, which gave rise to an oxygen transfer to the deep water and, thus, to the appearance of Thiopedia. A particularly interesting situation was found in December, 1969, when a circulation occurred almost over the whole water column. Emerging from the mud (according to Utermöhl from HUBER-PESTALOZZI (30), Thiopedia occurs in large numbers also in anaerobic mud); large numbers of Thiopedia cells were brought up into the epilimnion, unto 0 m. However, the homogeneous distribution that had been expected, did not occur, in that at the 5 m depth, a relative maximum appeared, which reflects the probably optimal light conditions at this depth. In December, over the whole water column, the oxygen values were less than 1 mg/l. (485)

This released this massive Thiopedia growth. In January, 1970, at the very high hydrogen-sulfide value of 13.1 mg/l, the absolute maximum growth of Thiopedia appeared, with 373,000 cells/ml. This sample therefore got colored macroscopically with an intensive blue-red. One month later, in February, the hydrogen-sulfide content had fallen from 13.1 mg/l to 1 mg/l, which pointed to an intensive utilization of hydrogen sulfide as hydrogen donor.

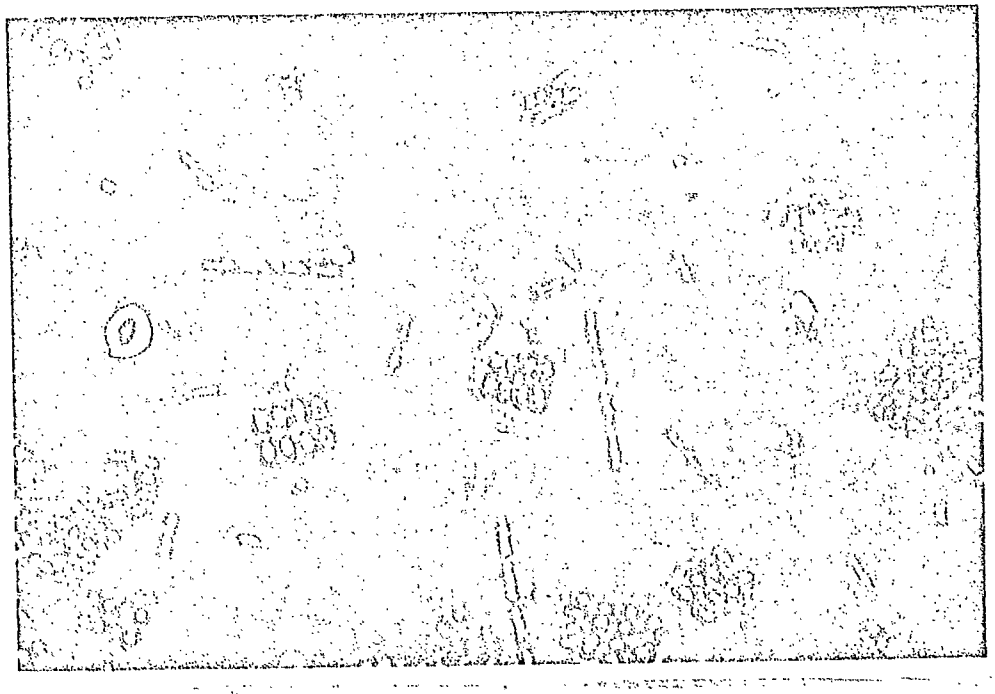


Fig. 63. Thiopedia rosea: accumulation of cells arranged in the form of plates (1). The coloring is relatively weak, and more marked only at the cell periphery. The cells are slightly ellipsoidal, with a diameter of 1.5-2 μ. In some cells, sulfur grains may be observed in the polar caps. (484)

In the center, there is an extremely large spirillar form, with two sulfur grains (2). Live preparation from the hypolimnion. January, 1970, 14 m depth, Rotsee (magnification about 1000 x, phase contrast).

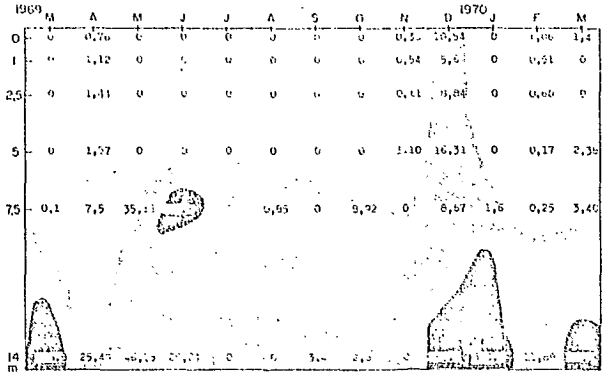


Fig. 64. Thiopedia rosea, 10^3 cells/ml, Rotsee.
Pale-gray shading: oxygen content less than 1 mg/l.
Dark-gray shading: Thiopedia accumulations.

Discussion (485)

The production values of the ^{14}C-measurement at the 14 m depth reflect the appearance of photomyxotrophic bacteria, such as Thiopedia and Lamprocystis (see Figs. 65 and 66). Thus, in March and April, 1969, values of 4 to 5 mg of C/m^3h were found, and in January, February, and March, 1970, 5 to 10 mg of C/m^3h. In January, a sample taken from the 14 m depth, was exposed at the 5 m depth, that is, it was exposed to higher light intensity. It was then found that 34.2 mg of C/m^3h were incorporated in this sample; this is 6 times the value of the production taking place at the 14 m depth. This allows to conclude that in the area of natural occurrence, at the extremely weak light of the 14 m depth, the production is far below the productivity of the organisms.

Amazing is the fact that Thiopedia rosea showed its maximum growth at the 14 m depth, where with the light-measuring means used, no more light was detected. Apparently, Thiopedia is sensitized to extremely low amounts of light. According to SCHLEGEL (67), the Thiorhodaceae are able to absorb, not only infrared light, but with the aid of carotenoids, also light in the

visible range between 400 and 600 nm; thus, they are capable of photosynthetic performance in the wave-length range of which the weak light of deeper layers consists. The green light (1% VG 9 (= 525 nm)) generally penetrated deepest during the months in which hypolimnetic Thiopedia maxima were observed.

It is not probable that these Thiopedia maxima are due exclusively to the utilization of reduced organic compounds, that is, to heterotrophic growth. A corresponding sensitive in-situ light measurement would further clarify this point.

If a priority were to be set on the factors limiting the occurrence of Thiopedia, the hydrogen-sulfide content would have to be placed first. However, with respect to productivity, light in the green range is decisive.

Lamprocystis roseopersicina

Fig. 66 shows the occurrence of Lamprocystis. Also this bacterium belongs to the Thiorhodaceae. Together with the Thiopedia rosea cells, also massive growths of Lamprocystis roseopersicina were observed (Fig. 65). Parallel to the massive growth at the 7.5 m depth of more than 100,000 Thiopedia cells in June, 1969, 19,000 Lamprocystis cells/ml appeared. Another smaller growth was found in October, 1969, with 7800 cells/ml of (486) Lamprocystis, at the 7.5 m depth. Simultaneously with the massive growth of Thiopedia rosea in January, 1970, at the 14 m depth, 26,300 Lamprocystis cells/ml were found. This population showed a considerable metabolic activity, which was evident from the very high primary production value of 10 mg of C/m^3h.

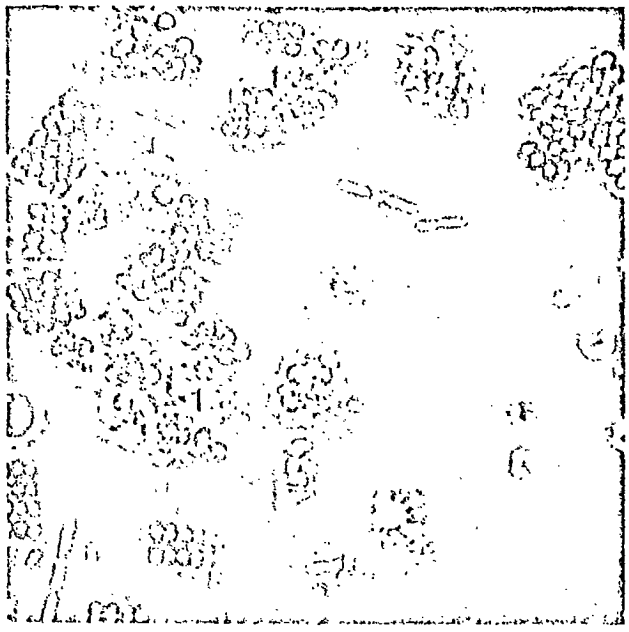


Fig. 65. Lamprocystis roseopersicina: Incoherent cell clusters (1) beside plate-shaped agglomerations of Thiopedia cells (2). January, 1970, 14 m depth, Rotsee (magnification about 1250 x, live preparation, phase contrast).

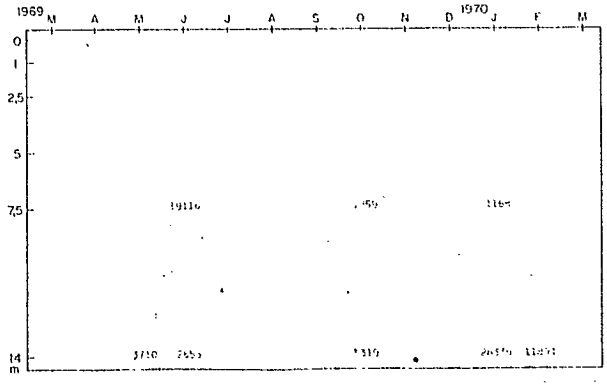


Fig. 66. Lamprocystis roseopersicina, Rotsee.

Chromatium densegranulatum Skuja (Chromatium Linsbaueri Gickhorn)

Fig. 67 shows this Chromatium species described by SKUJA (71). According to Skuja, it is extremely difficult to distinguish the two above mentioned species; probably, they are even identical. The observed cells (487)

were 12-15 µ in length, and 6-8 µ in width. To judge from the granula, they corresponded to the Chromatium densegranulatum mentioned by SKUJA. The color was weak, and the contours appeared only in the phase-contrast picture.

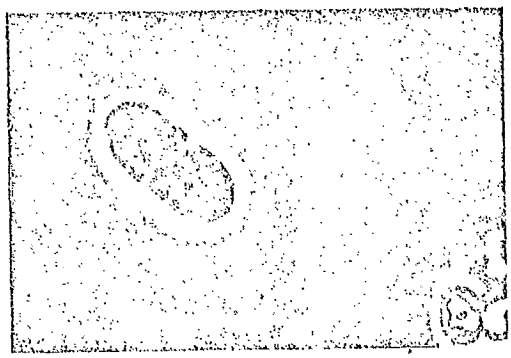


Fig. 67. Chromatium densegranulatum Skuja. Length about 12 µ, width about 6 µ. April, 1969, 5 m depth, Rotsee (live photograph, magnification about 1250 x, phase contrast). (487)

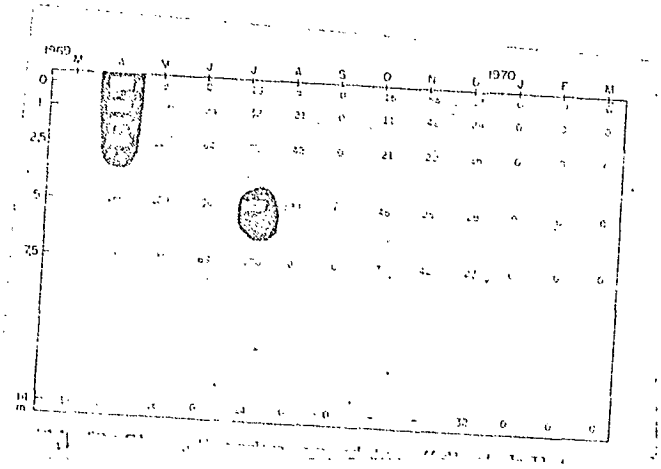


Fig. 68. Chromatium densegranulatum, cells/ml, Rotsee.

The observed cells showed a rather marked small areola. The light-refractive amorphous little spheres ($CaCO_3$) described by HUBER-PESTALOZZI (30) were also detected.

Fig. 68 shows the space-time diagram for Chromatium. Two maximum accumulations occurred in April, 1969, at the 2.5 m depth, and in July, 1969, at the 5 m depth.

If one compares the appearance of Chromatium with the nitrite concentrations (Fig. 69) stated by STADELMANN (73), one may see that the two cell maxima coincide with the epilimnetic nitrite maxima. The nitrite maximum was due to nitrification, since at the same time, high ammonium concentrations existed. From this space-time conformity, one may presume that Chromatium densegranulatum partakes in the nitrification.

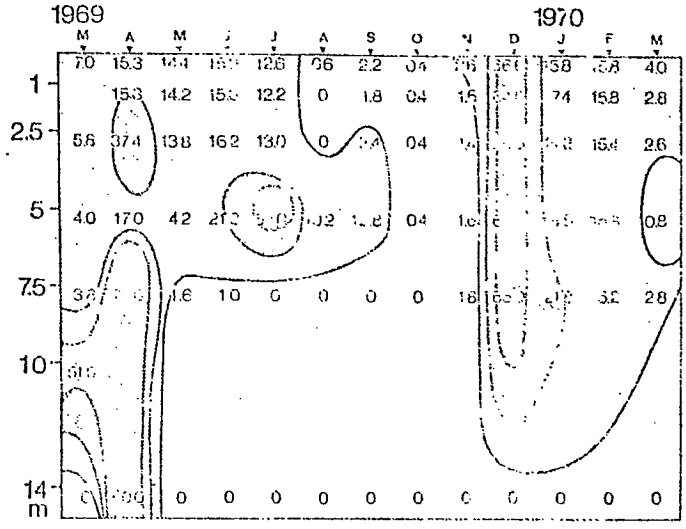


Fig. 69. Nitrite concentration (µg of NO_2-nitrogen/liter) of the Rotsee (according to STADELMANN, 1971). (488)

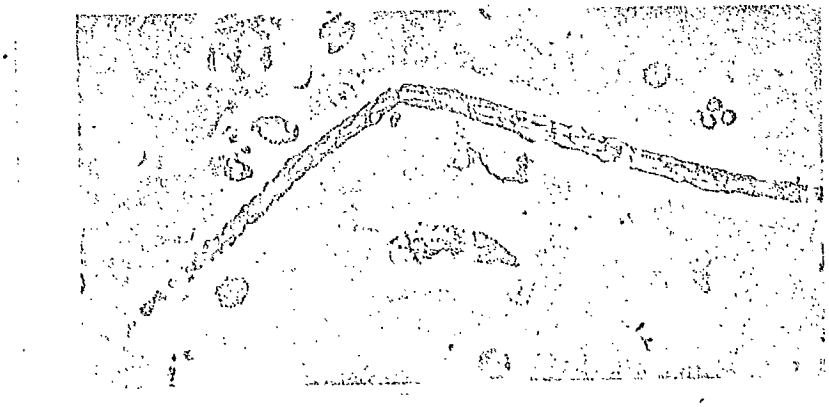


Fig. 70. Leptothrix pseudovacuolata. The formation of sheaths and the emerging of single cells from the sheaths may be seen. February, 1970, 2.5 m depth, Rotsee (magnification about 2000 x, phase contrast).

Leptothrix sp. (cf. pseudovacuolata (Berfiliev) Dorff)

In the Rotsee, this Leptothrix form appeared quite frequently. Fig. 70 shows a Leptothrix filament. The lengths of these filaments varied considerably in the course of the year; thus, in April, 1969, they were very short, while when with incrusted sheath (September and October, 1969), they reached greater lengths. According to SKUJA (71), there are two different species, one appearing in spiral shape, the other one slightly bent. All the Leptothrix pseudovacuolata filaments observed in the Rotsee were straight. The cell size and number of pseudovacuoles may vary considerably. Trichomes without incrusted sheaths are between 1.5 and 1.8 μ in width. Trichomes with incrusted sheaths showed fewer vacuoles than unsheathed trichomes. The vacuoles are always arranged axillarily. Compared to the (489) Leptothrix pseudovacuolata described by SKUJA, the sheaths were surprisingly small; generally, they were only twice the trichome width. The giant cells described by HUBER-PESTALOZZI (30) were not found. The incrustation with iron compounds was recognized only by the reddish-brown coloration of the sheaths.

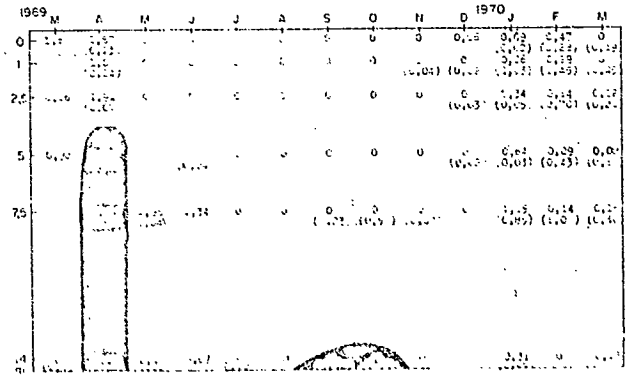


Fig. 71. Leptothrix pseudovacuolata, 10^4 μ thread length/ml, Rotsee. Figures without brackets: Filaments without incrusted sheaths; figures in brackets: filaments with incrusted sheaths.

Fig. 71 shows the space-time diagram for Leptothrix pseudovacuolata in the Rotsee. In April, there was a massive growth in the hypolimnion, with a maximum of 36 x 10^4 µ thread length/ml, at the 7.5 m depth. In the spring, the slightly incrusted trichomes were predominant. The massive growth in spring coincided with that of Thiopedia rosea. The spring circulation caused a distribution through the water column. The maximum was at a very low oxygen tension of 1 mg/l. This is in conformity with the indications of HUBER-PESTALOZZI (30) who described an appearance of Leptothrix in the mud, at low oxygen tension.

A second hypolimnetic bloom occurred in September and October, 1969, at the 14 and 7.5 m depths. This growth consisted exclusively of forms with incrusted sheaths. They appear only at low temperatures of less than 10°C; optimal growths occur at about 7°C. PAVONI (53) also described the appearance of Leptothrix pseudovacuolata in winter and in spring. Leptothrix may appear in both oxygen-enriched and oxygen-deficient zones. Thus, in April, 1969, at 0 m, and at an oxygen content of 12 mg/l, 1.5 x 10^4 µ thread length/ml still were found. Interesting is the appearance of incrusted sheaths at low oxygen contents.

According to HUBER-PESTALOZZI (30), iron and manganese compounds are embedded in the sheaths. It was not possible to detect any clear relationship between particulate iron and the appearance of Leptothrix. Only the April, 1969, investigation might provide an indication, when the particulate iron exceeded 100 mg/l at simultaneous breaking up of the dissolved iron.

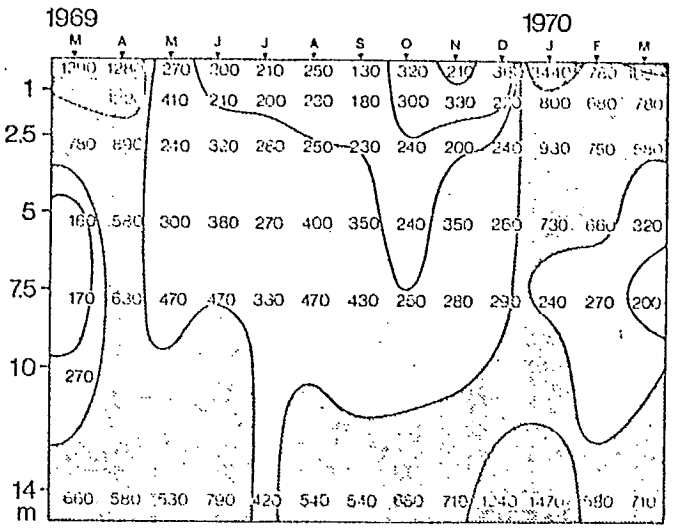


Fig. 72. Particulate Kjeldahl N (µg of N/l) of the Rotsee (according to STADELMANN, 1971). (490)

Discussion

Fig. 72[4]) shows the distribution of particulate nitrogen in isopleth illustration. In the hypolimnion, there were extremely large amounts of particulate nitrogen, the occurrence of which was largely due to the existing hypolimnetic bacterial flora. This hypothesis is confirmed by the fact that parallel to the appearance of Thiopedia rosea, at 14 m depth, in December, 1969, and January, 1970, there was a considerable increase in the particulate-nitrogen figures from 710 µg/l in November, 1969, to 1200 µg/l in December, 1969, and to 1400 µg/l in January, 1970.

It must be emphasized that this particulate nitrogen is fixed by organisms, and appears only to a lesser extent as detritus. This state of affairs will be further dealt with in the summarizing discussion (see ch.7).

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4) The isopleth illustration originates from STADELMANN (73).

5.3 Vertical and Seasonal Distribution of Bacteria

OVERBECK (51) pointed to methods for the descriptive interpretation of vertical profiles, which allowed him to make some essential statements on the dynamics of the substance cycle in the lake.

In earlier research (SCHEGG and RUSCHKE (65)), it was also attempted, from separate profiles of lakes of various trophicity degrees, to detect the dynamics of the substance cycle. Since separate profiles always are a kind of snapshots, which may change again very rapidly, a joining together of these separate profiles, even subject to considerable differences, provides more declarative force for the course of the action.

To cover mathematically the combinations of different isopleth (491) illustrations, the correlation analysis was carried out over the whole year, at each depth step. However, despite the advantages of the space-time diagram, it is suitable to test various parameters on the vertical profile (OVERBECK (51)).

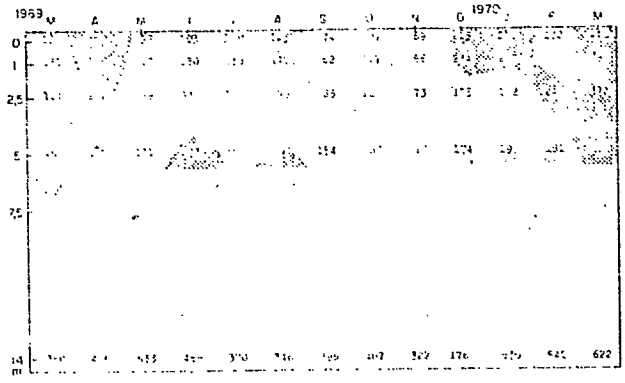


Fig. 73. Membrane-filter bacteria, 10^4 cells/ml, Rotsee.

5.31 Rotsee

Fig. 73 shows the space-time diagram of the membrane-filter bacteria in the epilimnion from 0 to 5 m. The figures were between 600,000 and 4,000,000 bacterial cells/ml of sample water. At the 14 m depth, the bacterial counts were between 1.7 and 8.3 million cells/ml. Thks indication is representative for the hypolimnion.

Maximum bacterial counts coincided with a large primary production, which may be seen both in the spring of 1969, and in the winter and spring of 1970.

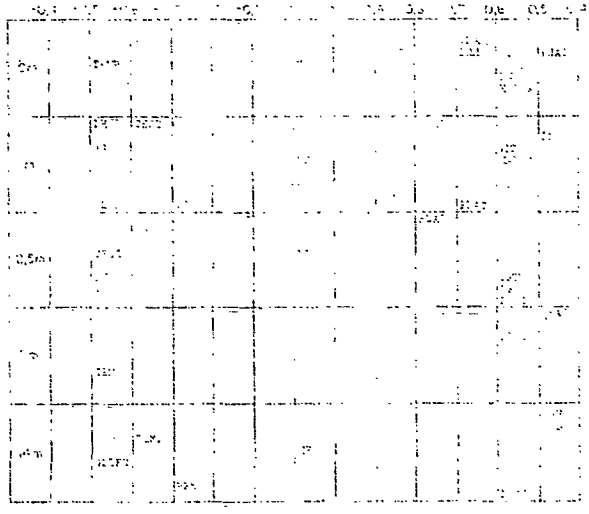
According to WUHRMANN (83), in the physiological reaction rates of psychrophilic and mesophilic microorganisms, there exists a temperature factor of 1.5 to 2.5 per 10°. This value applies to pure cultures. In a biocoenosis (biological mud-clarifying plants), the temperature factor is considerably smaller (about 1.2 per 10° Δ t). This is explained by the "sociological adaptation", in that relatively optimal conditions exist for the population selected in each case. However, size, number, and conversion rate depend exclusively on the easily assimilable substrate available. It may be assumed that a similar plankton population, even at higher temperatures, would not show a substantial increase in the conversion rate and number, at unchanged substrate supply.

On the basis of these reflections, the high germ counts observed in the Rotsee are to be understood at this low temperature. The vertical distribution shows that the maximum growth is generally found at the 0 m or 1 m depth. This is the zone of high photosynthetic activity of the phytoplankton. This distribution in the vertical profile confirms the 1967 findings (SCHEGG (53)).

K-Analysis

At 0 m, the K-analysis (Table 21) shows a KK of 0.87 with the plate figures, that is, one may speak about a constancy of the ratio of membrane-filter counts to plate counts. In a eutrophic water body, the (492)
K of the membrane-filter counts to the plate counts is narrow, since a major portion of the zymogenic germs is adapted to the higher substrate supply of the pour-plates.

Table 21. K-Analysis to reference parameter Membrane-Filter Bacteria, Rotsee.



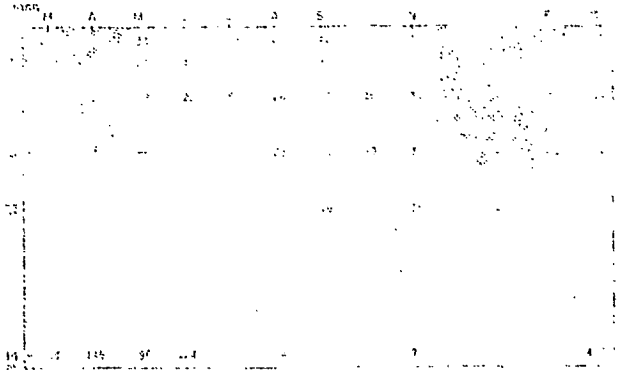


Fig. 74. Plate counts, 10^2 cells/ml, Rotsee.

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At 0 m, there exist further KK of the membrane-filter counts to the primary production, and a somewhat smaller KK to biomass, Cryptomonas, and particulate nitrogen. At the 1 m depth, only a correlation to PN and PP may be observed. Already at the 2.5 m depth, these relationships to the production parameters do no longer exist. The fixed correlation between phytoplankton and primary production, as indicated by OVERBECK (49), must be modified, so that this relation applies mainly to the layer of maximum production.

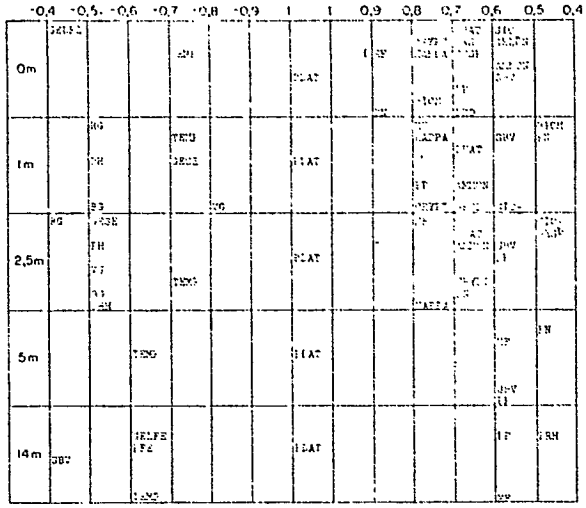
Fig. 74 shows the plate counts in the space-time diagram. During the periods of main productivity, in the spring of 1969 and 1970, there were accumulations of the heterotrophic bacteria growing on tryptone-glucose agar. With this method, only aerobic heterotrophic germs were determined. The measurements at the 14 m depth, in the hypolimnion, therefore provided higher values only where a minimum oxygen tension remained available. Such a minimum oxygen tension existed during the spring, 1969, and December, 1969, circulations. The epilimnetic values coincided essentially with the distribution of the membrane-filter counts (KK + 0.87). The absolute figures were between 1500 and 56,800 cells/ml. (493)

The order of magnitude of the heterotrophic bacteria determined on plates differed but little from those determined by DÜGGELI (14) on Heyden agar. However, the values cannot be compared directly with those of DÜGGELI (14), since the methods and substrate compositions were different.

K-Analysis (Table 22)

There exist more correlations between the plate counts and the production parameters than in the case of the membrane-filter counts, since a higher percentage of heterotrophic germs are adapted to the enriched nutrient medium of the Rotsee than of a less polluted water body. KK exist

Table 22. K-Analysis to reference parameter Plate Counts, Rotsee.



particularly between the plate counts and particulate nitrogen, the biomass, cryptomonads, primary production, particulate phosphorus, and the nutrients phosphate and ammonium. At the 1 m depth, this pattern is obtained, in that the K to the cryptomonads and particulate phosphorus result higher. This points to the degradation processes taking place in the layer of main productivity.

Ciliates (Fig. 75)

Apart from zooplankton (which, unfortunately, cannot be dealt with in this investigation), the ciliates are consumers of bacterial plankton (RUTTNER (50)). They are grouped as a whole. The most frequent forms (494) were Strombidium sp. and Coleps sp.). Their appearance coincided, in space and time, with the bacterial maxima; agglomerations were found particularly in April, 1969, at the 1 m depth, and in January, 1970, from 0 to 2.5 m depth. The first massive appearance reached a maximum in May, 1969, while the bacteria and plankton populations had receded considerably. The distribution over the whole year showed the close interrelationship between ciliates and primary and secondary biomass which serve them as food.

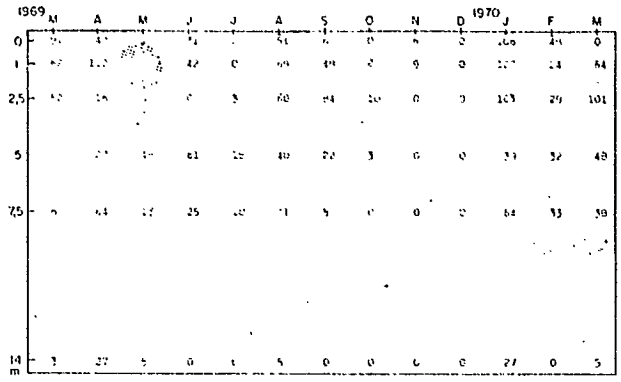


Abb. 75. *Ciliaten*, Zellen/ml, Rotsee.

Fig. 75. Ciliates, cells/ml, Rotsee.

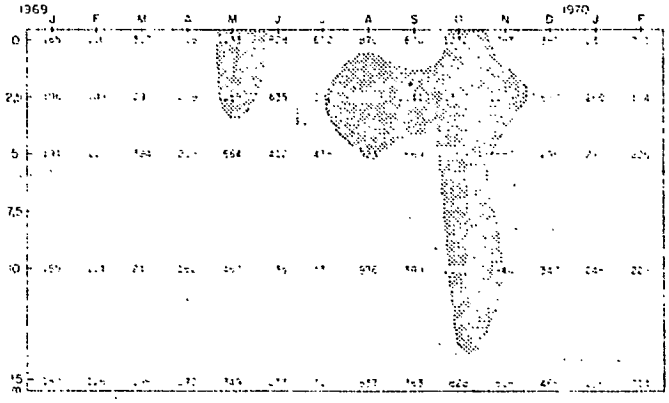


Abb. 76. Membranfilterbakterien, 10^3 Zellen/ml, Vierwaldstättersee.

Fig. 76. Membrane-filter bacteria, 10^3 cells/ml, Lake of Lucerne.

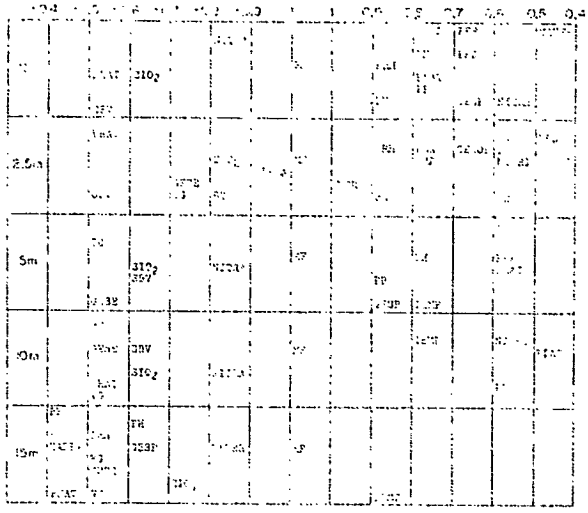
5.32 Lake of Lucerne

Fig. 76 shows the space-time diagram of the membrane-filter bacterial counts from the Lake of Lucerne. The figures varied between 110,000 and 1.8 million cells/ml. They are a "mirror image" of the plankton growth, at the vegetational start in March, 1969, a first maximum in May, 1969, and a second maximum in October, 1969. The October, 1969, increase propagated to deeper layers, down to below 15 m. This increase in the metalimnion coincided with the metalimnetic oxygen consumption illustrated in Fig. 81 and Table 27.

Seen from a dynamical point of view, the bacterial distribution (495) points to the degradation of the organic substance yielded in the trophogenic layer.

A relative maximum arising at the 10 m depth, in August, 1969, was caused by an embedding of Oscillatoria rubescens.

Table 23. K-Analysis to reference parameter Membrane-Filter Bacteria, Lake of Lucerne.



For the membrane-filter bacteria (Table 23), the K-Analysis shows a close relationship to the production parameters, particularly a KK of 0.86 between primary production and membrane-filter bacteria. At the 2.5 m depth, the KK to the primary production is highest with 0.87. The parameters PP and PN, which are representative for the biomass, correlate also significantly with the membrane-filter bacteria. Interesting is the high negative KK, existing over the whole epilimnion, between membrane-filter bacteria and nitrate; in the maximum trophogenic layer, at the 2.5 m depth, it is -0.94. A direct consequence of the bacterial presence is the oxygen consumption in the respective layer. At the 15 m depth, where the assimilative balance is negative, there exists a high negative KK of -0.85 between membrane-filter bacteria and oxygen.

As also in the Rotsee, a KK between plate counts and membrane-filter bacteria may be found; however, it is lower.

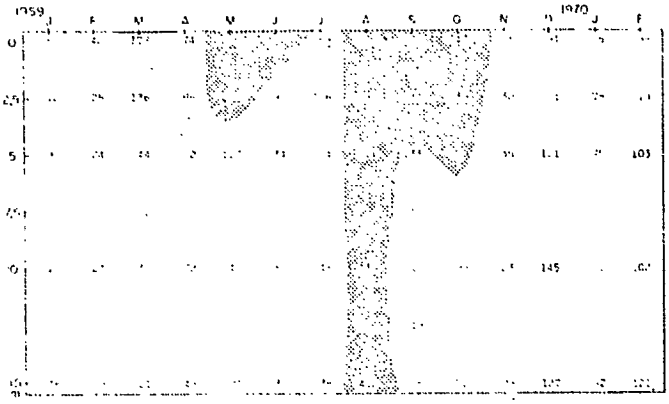


Fig. 77. Plate counts, 10 cells/ml, Lake of Lucerne (496)

Table 24. K-Analysis to reference parameter Plate Counts, Lake of Lucerne.

	-0,4	-0,5	-0,6	-0,7	-0,8	-0,9	1	1	0,9	0,8	0,7	0,6	0,5	0,4
0m														
2,5m														
5m														
10m														
15m														

The distribution of the plate counts (Fig. 77), the same as the distribution of the membrane-filter counts, reflects the two summer accumulations of organic substance by phytoplankton, and a receding during the autumn circulation and the winter stagnation.

The K-analysis between plate counts (Table 24) and investigated values, the same as in the case of the membrane-filter bacteria, shows a close relationship between bacterial flora and production parameters. Particularly remarkable is a KK of 0.82 to the primary production at 0 m, and of 0.73 at the 2.5 m depth.

Conclusions

1. The space-time distribution of the bacteria is largely in conformity with that of the phytoplankton, that is, the yielded organic material brings about higher bacterial counts at the site of its build-up.

It may be deduced therefrom that under natural conditions, the material released by excretion and autolysis is broken down immediately. These findings are identical with those of OVERBECK (49, 50).

2. If the KK are graded, the following bacterial picture is obtained in the layer of main productivity:

Bacteria
↓
Primary production
↓
Biomass
↓
Particulate-P and -N contents (497)

5.4 Bacterial Counts and Primary Production

An earlier report (SCHEGG (63)) showed data on the relationship between primary production and bacterial counts for the two investigated lakes. The curves shown hereinafter are intended, for one thing, as a supplement and completion and, for another thing, as elucidation of the relationships described with the KK.

In both lakes, for the depths that showed maximum values for the primary production (in the Rotsee, 0 m, and in the Lake of Lucerne, 2.5 m), the membrane-filter bacterial counts were plotted against the biomass and the primary production.

Fig. 78 shows the values from the Rotsee. The curves of the three parameters are largely parallel. Deviations are found in July, 1969, and in March, 1970, where the biomass shows a different curve shape.

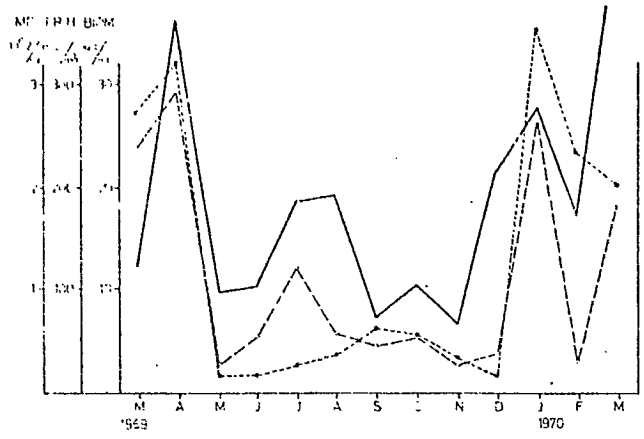


Fig. 78. (——) membrane-filter counts, 10^6 cells/ml,
(— — —) primary production, clear, mg C_{ass}/m^3h,
(-----) biomass phytoplankton, µg/ml,
0 m depth, Rotsee.

The analogous illustration from the Lake of Lucerne (Fig. 79) shows basically the same common course of the curves. In accordance with the plankton curve, there are two maxima, the first one in spring, and the second in late summer. The same observation of two maxima in the bacterial curve was made also by other authors, such as DEUFEL (11), OVERBECK (49), and POTAENKO (55). Also in the Lake of Lucerne, a divergence between the biomass curve and the two other curves may be found in May, 1969.

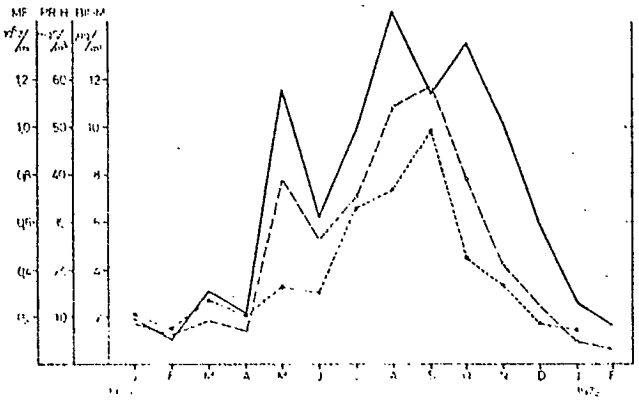


Fig. 79. Membrane-filter counts, primary production, clear, biomass phytoplankton, Lake of Lucerne, 2.5 m depth (for explanations see Fig. 78). (498)

Discussion

In the layer of main productivity, the correlation between primary production and bacterial counts is closer than the relation of the bacteria to the available biomass. This result points to the fact that the current excretion of a plankton population has an important substrate-forming effect. These findings are in conformity with those reported previously (SCHEGG (63)).

The fact that the bacterial population reacts very rapidly to the primary-production performance in the layer of main productivity, points to relatively short generation times of the bacterial population. KUZNEZOV et al. (37) report on the determination of generation times. In the dammed-up Rybinsk lake, KUZNEZOV et al. (37) found values for generation times of between 10 and 110 hours. According to the author's own investigations (SCHEGG (62)), in the Lake of Lucerne, a generation time of 20 to 30 hours may be expected in the epilimnetic range, while in the Rotsee, these figures are somewhat lower, that is, between 6 and 20 hours.

The generation times were determined according to a method where the water was exposed filtered (5 µ) and unfiltered for a certain time "in situ et loco", during which time the bacterial population was observed KUZNEZOV (36)). In part, these investigations are subject to discrepances, since for a bacterial population, the conditions in a bottle change rather rapidly, compared to those of the natural environment. Theoretically, this corresponds to the step from a "momentary flow culture" to a "batch culture". Nevertheless, the orders of magnitude of the generation times, from some hours to some days, might be in accordance with reality. This bacterial growth rate exceeds the growth rate of other organisms in the lake; however, it is far below that of a pure bacterial culture under optimal conditions.

This shows a very essential fact, that is, although the biological processes occurring in a lake follow the known pure-culture growth curve with lag, log, stationary, and dying phases, bacteriological growth in natural waters is constantly limited by various factors, and optimal growth is never reached. In the end effect, growth processes occur, the balance (499) of which no longer shows an exponential, but a more or less linear course. The concentration of the respective limiting factor is always below that of the half-maximum growth, which may explain the extremely differentiated and rapid "response" of the bacterial population to changes in the substrate.

5.5 Bacterial Counts and Degree of Trophicity

THIENEMANN (78) used the oxygen content to characterize a body of water. He thus introduced the results of heterotrophic breakdown of organic substance, namely the oxygen consumption, as criterion. It will now be attempted to establish a trophicity classification, also in relation to the cause of the oxygen consumption, namely the bacterial population.

In the epilimnetic range of the trophogenic layer, the oxygen consumption is overlapped by the autotrophic production, so that it is difficult to show a direct relationship between oxygen consumption and bacterial population.

Table 25 shows the total bacterial counts (determined with the membrane-filter method) from different lakes. These are figures from various authors, obtained from completely different waters. Nevertheless, within wide limits, it is possible to establish a trophicity scale.

Since number and composition of the bacterial population are the effect of the available substrate, it is more appropriate to use the real production parameters for lakes that are not excessively loaded with

allochthonous material, to characterize the trophicity. Hence, the present compilation is to be understood more as a survey of the total bacterial counts to be expected in waters of different trophicity gradations.

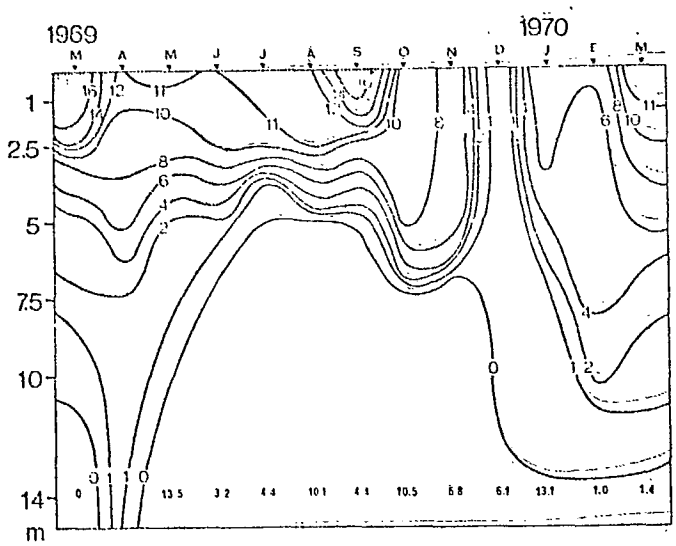


Fig. 80. Oxygen (mg of O_2/l) and hydrogen sulfide (mg of S/l) in the Rotsee. Pale shading: 100% saturation, dark shading = 150% saturation. Hydrogen sulfide is indicated at 14 m (according to STADELMANN, 1971).

5.6 The "Short-Circuited Cycle" (501)

The term "short-circuited cycle" was created by OHLE (45). It means the intrabiocoenotic cycle of substances involved in the production of the trophogenic layer. OHLE (45) proved the relationships experimentally, mainly by means of sedimentation measurements. His investigations are the starting point for a better comprehension of the substance cycles, particularly those of the epilimnion.

5.61 Oxygen

The oxygen conditions in the epilimnion are the result of various processes:

Table 25. Bacterial counts (MF) and degree of trophicity.

Tab. 25. [illegible] (MF) und Trophiegrad

Typus des Sees / lake type	See / lake	[illegible] / production at time of max.	Gesamtbakterienzahl in 10³/ml / tot. germ count: average	Maximum	Grössenordnung / o. of magn.	Autor / author
[illegible]ic	[illegible]-See	[illegible]	[illegible]	7000	1-10 Mio.	[illegible] [36]
	[illegible]	[illegible]	3[illegible]	[illegible]500		[illegible]
	[illegible]	[illegible]	[illegible]	3000		[illegible] 1971
	[illegible]	5[illegible] mg C/m³h		2500		Overbeck [51]
	Schöhsee	37 mg C/m³h		(6000)		[illegible] [11]
	[illegible]gewässer		[illegible]000	2200		Overbeck 1967
	[illegible]see	140 mg C/m²Tag	1100	3200		Overbeck [49]
	Kylinsk-Stausee	[illegible] mg C/m²Tag	1000	2700		Kuznezow and Romanenko [37]
[illegible]ic	[illegible]burger See		1020		0,5-2 Mio.	[illegible] [32]
	[illegible]see l.Luc.	[illegible] mg C/m³h	900	1550		Schegg [63]
	[illegible] l.Luc.	[illegible] mg C/m³h	670	1050		Schegg and Ruschke [65]
	Vierwaldstättersee [illegible]	50 mg C/m³h	[illegible]	1500		Schegg 1971
	[illegible]	7 mg C/m³h	300	[illegible]		Schegg and Ruschke [65]
	Titisee	[illegible] C/m³h	[illegible]	1200		Schegg and Ruschke [65]
	Gr. Plönersee	35 mg C/m³h	1000			Overbeck [49]
oligotrophic	[illegible]see		50	200	0,05-1 Mio.	Kuznezow [56]
	Feldsee	[illegible] mg C/m²Tag	200	500		Schegg and Ruschke [65]

1. Exchange at the interface of water and atmosphere.

2. Photosynthetic excretion of oxygen by phytoplankton.

3. All kinds of respiration processes and chemical oxidations.

The oxygen content reflects the balance of the multiple gas-exchange processes. Only in very particular situations, they allow to make direct predictions regarding processes occurring in the lake. Such a situation appeared in December, 1969, (Fig. 80) in the Rotsee, when due to a circulation down to the hypolimnion, the oxygen content fell, even in the uppermost water layer, to less than 1 mg/l. Soon afterwards, the lake was ice-covered, which eliminated the diffusion between atmosphere and water. Hence, the oxygen content determined in January, 1970, under the ice, is the result of assimilation and respiration processes. The order of magnitude of the assimilation processes may be calculated on the basis of the ^{14}C-measurements.

This allows to estimate the respiration processes. They result in the following values:

oxygen content on 3 December, 1969	28.7 mg of O_2/m^2
oxygen content on 15 January, 1970	376.7 mg of O_2/m^2
oxygen increase in the epilimnion (0-5 m)	348 mg of O_2/m^2

This value constitutes the net oxygen increase.

On 15 January, 1970, the photosynthesis performance was 172.2 mg of C/m^2h. This corresponds to a daily production of about 2400 mg of O_2/m^2 (conversion factor to daily production according to chapter 4.331 = 8).

According to STEEMAN-NIELSON (75), the respiratory intensity is assumed to be about 10% of the optimal photosynthesis. Of the about 2400 mg of O_2/m^2, about 500 mg of oxygen (day and night) must be deducted as phytoplankton respiration. The remaining net oxygen production is 1900 mg of

O_2/m^2 x day. This daily value is 5.5 times the value determined by accumulation during the whole month! There exists here obviously a very large oxygen deficit. This may be explained in two manners:

1. by purely chemical oxidation processes, and

2. by bacterial respiration of the yielded organic substance.

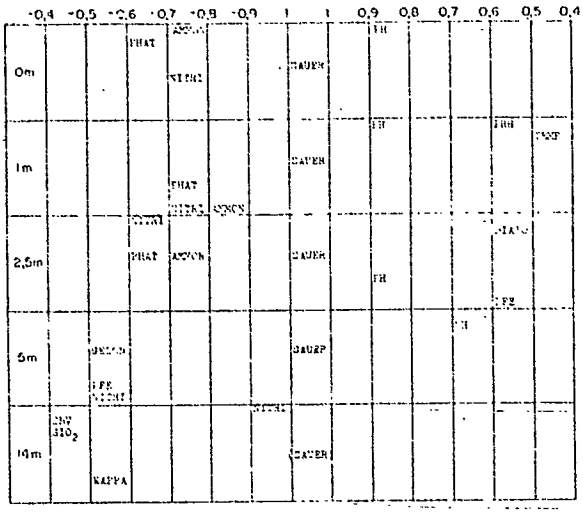
Assuming that the purely chemical oxidation processes constitute half of the oxygen consumption, there results a value of about 850 mg of O_2/m^2 x day for the oxygen utilization of the bacteria. At a bacterial population of 9.17×10^{12} bacterial cells/m^2, there results an hourly respiratory intensity of about 4×10^{-12} mg of O_2/cell and hour. This (502) value is in good conformity with that of KUZNEZOV (36) of 6×10^{-12} mg of O_2/cell and hour.

KUZNEZOV (36) states that in lakes with low humic-acid content, the purely chemical oxidation processes constitute an unimportant percentage. On the other hand, research work carried out by BREHM (9) and GOCKE (21) showed that a major portion is released by purely chemical decomposition. The value of 50% of purely chemical processes, assumed in this connection, might constitute the upper limit.

From the oxygen consumption, by means of the respiration equation, one may also predict the substrate consumption. This results in a substrate consumption of about 7.5×10^{-12} mg of glucose/cell and hour.

When searching for the correlations to the oxygen content in the Rotsee (Table 26), one finds that only few parameters are directly dependent on oxygen. A partial circulation in December, 1969, brought about a change in the oxygen content, which had nothing to do with the production. This affected the oxygen content also during the following months. It is expressed also by the negative KK to phosphate and ammonium which, likewise,

Table 26. K-Analysis to reference parameter Oxygen, Rotsee.



owed their yearly course mainly to the hydrological situation. Hence, this falsifies a K observation over the whole year.

This example points to the limited declarative force of the correlation observations.

In the Lake of Lucerne (Fig. 81), the epilimnetic oxygen contents coincided in time with the periods of main productivity. A maximum of 14 mg of O_2/l in August, 1969, at the 10 m depth, was due to an embedding of Oscillatoria rubescens.

Although a slight increase in the bacterial counts was detected in the vertical profile, it was relatively small. It is possible that (504) Oscillatoria rubescens causes a temporary inhibition of the bacterial growth. In October, 1969, there was a marked oxygen consumption from the 7.5 m depth downward; this change was seen also in the vertical profile of the bacteria, in that in October, 1969, the highest values of bacterial growth were found, and also high figures occurred down to 15 m depth.

For the Lake of Lucerne, the K-Analysis of oxygen (Table 27) shows a basically different picture than for the Rotsee. In the Lake of Lucerne,

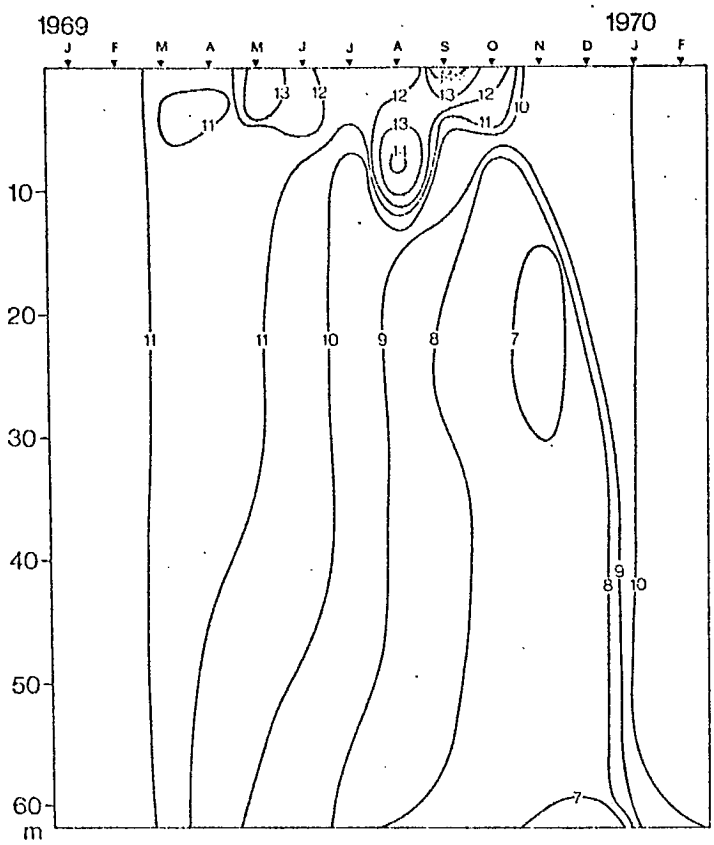
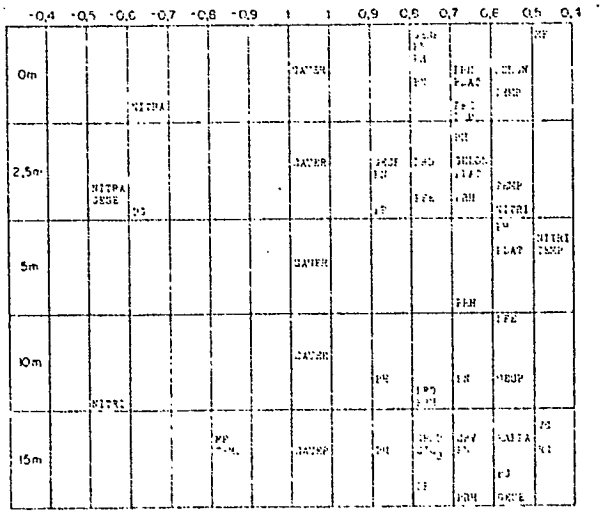


Fig. 81. Oxygen of the Bay of Horw (mg of O_2/l). (503)
Pale shading = 100% saturation,
dark shading = 150% saturation,
(according to STADELMANN, 1971).

Table 27. K-Analysis to reference parameter Oxygen, Lake of Lucerne.



the oxygen content is exclusively production-dependent. However, this relationship is not quite as close as it might be expected; the production parameters correlate between 0.6 and 0.8. This may be explained by the fact that the changes in the oxygen content are caused by a change in the conversion rate of oxygen.

Discussion

As shown in the previous observations, the oxygen content existing at the time, in reality, is only the balance of a quantitatively far greater conversion. In the calculated example, an oxygen atom is converted up to ten times daily in the "short-circuited cycle". Each change in the oxygen content means that the ecosystem, temporarily, performs more on the production side than on the degradation side, or vice versa. An important objection which might be raised against these reflections is the fact that, despite relatively high bacterial counts in the hypolimnion of oligo-mesotrophic lakes, one cannot find a higher oxygen consumption. However, this might be explained by the fact that the bacterial population shows in each layer the activity and conversion rate corresponding to the substrate supply, that in deeper layers therefore, the conversion rate of the bacterial activity decreases. It is therefore possible, already from the oxygen curve and the formation of metalimnetic oxygen minima (for ex. Lake of Lucerne in November, 1969, Fig. 81), to indicate the sedimentation path which the organic, assimilable substance travels, until it is broken down.

On the same basis, the CO_2 values in the water might be calculated. As OHLE (48) showed, from the hypolimnetic CO_2 enrichment, and taking into consideration the sedimentation rates, it is possible to make statements about the production and its degradation.

Conclusions

The oxygen content existing at the time being states little about the processes going on constantly; particularly for the separate processes, it is quantitatively negligible. However, since it constitutes the balance of these processes, it is an extremely sensitive index for qualitative changes in the substance metabolism. Quantitative conversion rates can be calculated only on the basis of biological-production figures.

5.62 Nitrogen and Phosphorus

STADELMANN (73), on the basis of detailed measurements regarding the nitrogen balance of the two investigated lakes (taking into account the natural supply, supply by sewage waters, supply from the atmosphere, consumption of dissolved nitrogen compounds during stagnation, losses by sedimentation, and on the basis of production measurements) arrives at the following results:

Lake of Lucerne: (505)

Primary production	58.7 g of N/m^2
External supply and consumption	19.9 g of N/m^2
Supplied by short-circuited cycle	38.3 g of N/m^2

Rotsee:

Primary production	66.9 g of N/m^2
External supply and consumption	36.9 g of N/m^2
Supplied by short-circuited cycle	30-40 g of N/m^2

According to these values, which apply to the average of the stagnation period, in both lakes about 60% of the nitrogen were supplied by the "intrabiocoenotic cycle".

How effective the "short-circuited cycle" may be in extreme situations, may be seen from calculations from the August, September, and October, 1959, investigations in the Rotsee (Table 28).

Table 28. Calculation of the "short-circuited cycle" regarding nitrogen in the Kotsee. The values apply to the trophogenic layer (0-5 m). E = renewal coefficient (according to STADELMANN (73)).

$$E = \frac{\text{standing crop}}{\text{daily primary production}}$$

	14. Aug. 1969	11. Sept. 1969	10. Okt. 1969
Vorhandener partikulärer N (average)	1,43 g/m²	1,19 g/m²	1,34 g/m²
E	0,22	0,37	0,28
Tageszuwachs (daily increase)	0,31 g/m²	0,440 g/m²	0,375 g/m²
Verh. Ammon-, Nitrite, Nitrate N (avail.)	0,810 g/m²	0,55 g/m²	0,090 g/m²

On 10 October, 1969, more than four times the amount of available dissolved inorganic nitrogen was utilized as particulate nitrogen.

Calculation of the hourly nitrogen conversion rate: By dividing the daily increase (10 October, 1969) by the experimentally determined factor 8.0 (daily production to hourly production), one obtains the amount of nitrogen converted per hour. It was 47 mg of N/m^2. At a bacterial population of 5.29 x 10^{12} cells/m^2, a nitrogen conversion of 8.9 x 10^{-12} mg of N/bacterium and hour is obtained.

Conclusions

During these three days of the summer stagnation, the daily N requirement was met practically completely by the "short-circuited cycle". This was seen also by the fact that the decrease in the dissolved organic nitrogen from 0.8 to 0.09 g of N/m^2, during the two months, corresponded to a daily decrease of 0.012 g of N/m^2. This was 2-3% of the daily requirement. Hence, during the summer months, when nutrients were largely exhausted, 90-95% of the nutrients that served to maintain and increase the phytoplankton population, were regenerated from the "short-circuited cycle".

Similar values were obtained for the Lake of Lucerne. There, the available dissolved inorganic nitrogen was utilized within 2-3 days.

Phosphates (506)

Based on investigations carried out in the Bay of Horw, GÄCHTER (19) states that the phosphate requirement of the trophogenic layer is met, up to two thirds, by the "short-circuited cycle".

In the two investigated lakes, there was a marked phosphate consumption in the summer, in that for three months, the phosphate contents were extremely low. During these months, a similar conversion rate must be expected for phosphorus as calculated for nitrogen.

Table 29. Calculation of the "short-circuited cycle" regarding phosphorus in the Rotsee.

	14. Aug. 1969	11. Sept. 1969	10. Okt. 1969
Particulater Phosphorus	151 mg m²	174 mg m²	175 mg m²
Factor (nach STRICKLAND 1960)	0.22	0.37	0.28
Entspricht P-Umsatz pro Tag	33 mg m²	64 mg m²	49 mg m²
Verh. PO_4-P	43 mg m²	12 mg m²	28 mg m²

In Table 29, the phosphorus requirement per day is calculated for the investigation days on which the phosphate content in the Rotsee was low. On 14 August, 1969, somewhat less than the available dissolved phosphorus was incorporated as particulate phosphorus, while on 11 September, 1969, five times the amount, and on 10 October, 1969, twice the amount was required to form biomass.

At an hourly increase of 8 mg of P/m^2, on 11 September, 1969, this results for the bacterial population present of 3.52×10^{12} cells, in a conversion rate of 2.3×10^{-12} mg of P/bacterium and hour. These conversion rates per bacterial cell are to be considered as order-of-magnitude values, and they apply to the specific case.

Summary

Both the available dissolved inorganic nitrogen and the dissolved phosphate are absolutely insufficient to maintain the primary production during the summer stagnation. During these summer months, the available amount would be utilized within less than one day. The fact that, nevertheless, there was a relatively large phytoplankton population, can be explained only by the high conversion rates of the "short-circuited cycle". It is possible that for the two components nitrogen and phosphorus, also allochthonous influences play a part. However, in comparison to the spatial concatenation of the "short-circuited cycle", these processes are extremely slow, so that for a daily production, this allochthonous influence may be disregarded. For the lake, they become fully effective only if the nutrients of these, generally punctiform, sources are distributed homogeneously over the lake. The balance calculations of GÄCHTER (19) for phosphorus, on the one hand, and those of STADELMANN (73) for nitrogen, on the other hand, for the Bay of Horw, result in both cases in about two thirds of the supplementary supply of required dissolved nitrogen and phosphorus from the "short-circuited cycle".

5.7 Sedimentation, Degradation, and Primary Production (507)

According to calculations by STADELMANN (73) from sedimentation measurements by BLOESCH (8), in the Lake of Lucerne only 8%, in the Rotsee about 30%, of the primary production was collected in the sediment below the trophogenic layer. These figures relate to the nitrogen components and the trophogenic layer. By exhaustive sedimentation measurements carried out in North-German lakes, OHLE (48) showed that only a small percentage of the biomass formed in the epilimnion settles completely down to the bottom.

It may be seen therefrom that also from sedimentation investigations, the existence and capacity of the "intrabiocoenotic cycle" may be demonstrated experimentally. However, also this case is only a balance observation, which does not take into account the amounts converted within the cycle. As shown for oxygen, phosphorus, and nitrogen, these amounts might be substantially higher than the amounts that appear as balance.

Another article on the phosphorus cycle, the primary production, and sedimentation rates from the same investigation series will appear by BLOESCH (8).

6. Experimental Investigations

The relationship between bacteria and phytoplankton in the lake can be covered only deductively and descriptively. To investigate the complex system of a lake, in its interactions and, above all, their rates, experiments with standardized conditions and organisms are required. Hereinafter, two experimental series will be described; in the course of the first one, deviating from lake conditions, a pure culture of algae was used beside a mixed population of accompanying bacteria. Producer and consumer were facing each other, distributed in the same space.

The idea underlying the second experimental series was a separation of the two organism groups, in such a manner that they were not in immediate contact with one another, while the interaction of their extracellular activities remained intact.

6.1 Experiment I

In association with investigations on nutrient-uptake kinetics carried out by KRUMMENACHER (35) on a non-bacteriafree culture of Microcystis sp. (Algothek EAWAG, No. 167, M1), the algal growth, as well as the development of a mixed culture of accompanying bacteria, were observed. One requisite was that in the present inorganic nutrient solution, the bacteria, in fact, had no substrate available. In order to investigate the nutrient-uptake rate, and the growth at different nutrient concentrations, varying ratios of P:N amounts (as phosphate and nitrate) were added. It was attempted to answer the following questions:

1. Are the accompanying bacteria in any relation to the algal culture?

2. Is there a relationship between bacterial and algal growth, and how do the two growth curves proceed?

6.11 Methods (508)

Everything was carried out in a sterile manner. The Microcystis culture was inoculated into an autoclaved P-free and N-free stock solution, and cultivated in a 2-liter G-20 glass flask, under permanent lighting (fluorescence tubes, light intensity 6000 lux), and aeration. The temperature was at 24°C. Into this stock solution, nitrate and phosphate were introduced at the indicated constant ratios, and replaced daily to the starting concentration, in the sense of a semi-continuous nutrient supply.

The algal-cell counts were determined in each case by counting from iodeosine-stained membrane filters. The preparation took place as for membrane filters for bacterial counts, as indicated in chapter 3.332.

Compared with the normal counting method of Utermöhl, this preparation has considerable advantages, in that the membrane filters may be produced currently, in illimited numbers, and stored until counting, and the corresponding preparations are available even later on as proof. Moreover, counting on the membrane filter is extremely simple for uniform algal cultures. The germ counts were determined according to the previously mentioned pour-plate method (see chapter 3.331).

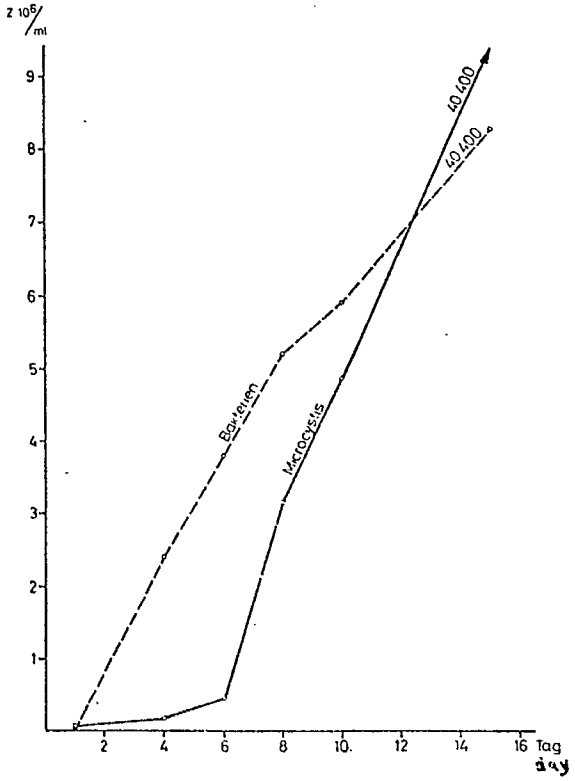


Fig. 82. Growth curve of Microcystis sp. (10^6 cells/ml) (——), growth curve of bacteria (plate counts) (10^6 cells/ml) (---).

6.12 Results and Interpretation (509)

Fig. 82 shows the maximum-growth curves. It is interesting that maximum growth occurred at a P:N ratio of 1:10. This ratio lay closest to the 1:7.2 ratio (STUMM (77)).

The cultures were observed up to the 16th day after inoculation. Initially, the bacterial culture showed a more rapid growth than the algal culture. This changed at the beginning of the log phase of the algal culture.

Fig. 83 shows the growth curves at different nitrate contents and a constant P content of 80 µg/l. In principle, the course of the algal-growth curves was always about the same in the lag phase, up to the sixth day, irrespective of the P:N ratio, while in the following log phase, the different concentrations of the nutrient medium caused substantial differences in the growth rates.

Fig. 84, right side, shows the bacterial-growth curves. Vigorous growth of the bacterial culture started already in the lag phase of the algae. Between the 8th and the 10th days, when the algal cultures underwent the highest increase in cell numbers, an inhibition of the bacterial growth occurred, which was the more marked, the lower the concentration of the available nitrate. With the flattening of the algal-growth curves, the bacterial growth increased again.

In the lag phase of the algae, the nutrient composition is not limitary of the algal growth. Hence, the excretory processes, compared to the algal biomass, are relatively high. This statement was found confirmed by the fact that the bacterial numbers increased more rapidly than the algal population. In the middle of the log phase of the algal culture (between the 8th and the 10th days), a large portion of the substances, (510)

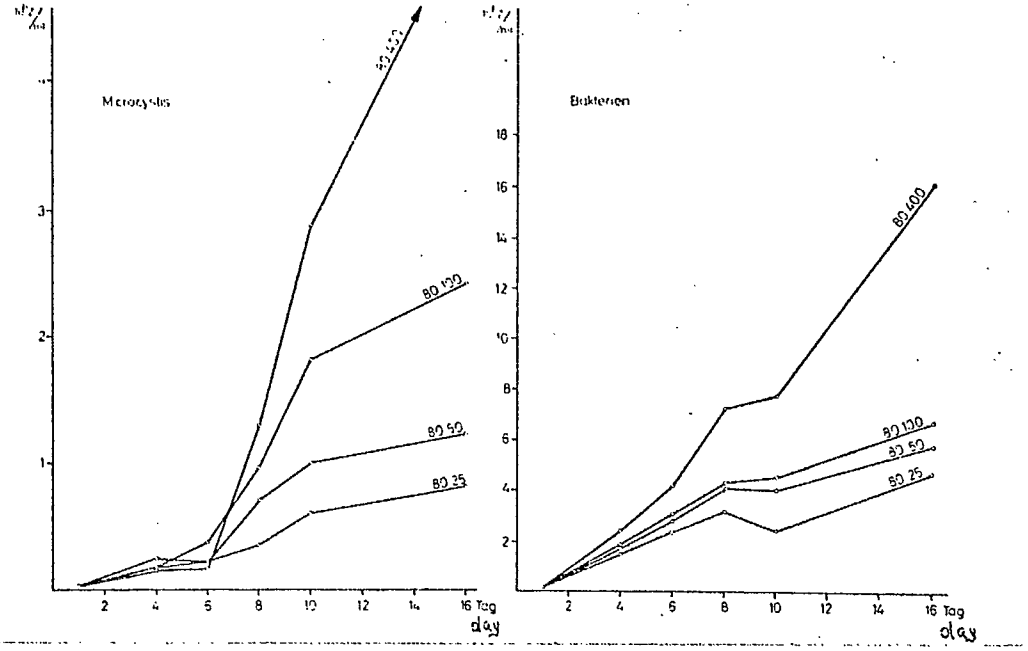


Fig. 83. Growth curves of Microcystis sp. and accompanying mixed bacterial population, at different P:N ratios (phosphate and nitrate) (µg) in the nutrient solution.

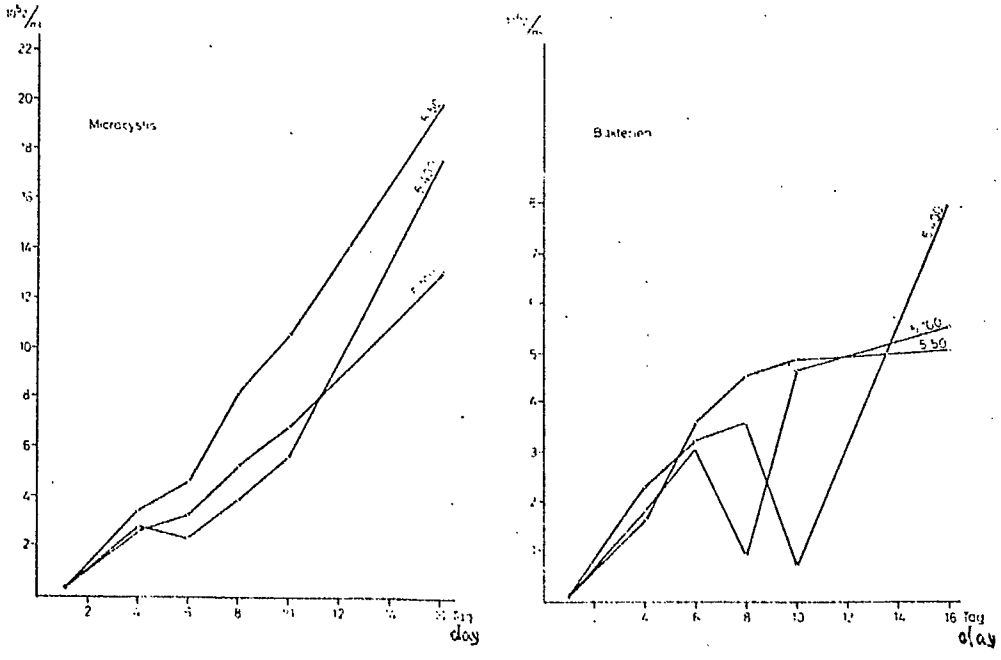


Fig. 84

obviously, was converted intracellularly; growth became optimal in relation to the nutrient concentration; thus, growth was limited by the nutrient concentration. Despite increased algal numbers, excretion decreased. The

clear slowdown until the stagnation of the bacterial growth, between the 8th and the 10th days, confirmed this interpretation.

At the flattening of the growth curves of Microcystis, between the 10th and the 16th days, larger excretory amounts appeared again, which partly were due already to autolytic processes. This substrate enrichment caused a renewed growth of the bacterial numbers.

A considerably more differentiated picture was obtained at a constant phosphorus concentration of only 5 µg/l (Fig. 84). The maximum growth curve was reached at a P:N ratio of 5:50. An increased nitrate addition had no growth-promoting effect on the algal population, either in the lag phase or in the log phase. The same applied to the bacteria. At a P:N ratio of 5:50, the bacteria-inhibitory effect which appeared at the P:N ratios of 5:400 and 5:100, was lacking between the 8th and the 10th days. These growth conditions may be called a balanced system. However, the bacterial-growth curve underwent a limitation from the 10th day on, by the complete utilization of phosphate (KRUMMENACHER (35)). The two minima of the bacterial curves, up to P:N ratios of 5:400 and 5:100, (511) between the 8th and the 10th days, are due to the same reason.

6.13 Conclusions

1. The findings give a clearly positive answer to the first question, since a direct relationship between algal growth and bacterial population was demonstrated. Each bacterial growth was the result of a substrate enrichment by the algal population, since no other organic material was available as energy basis for heterotrophic growth. A nutrient-dependent increase in the algal growth resulted in a substrate-dependent increase in the bacterial growth. Hence, optimal nutrient conditions had a direct and

indirect effect on the bacterial growth. The substrate release of the algal population depended on its physiological condition. At equal physiological condition, the substrate release constituted approximately a linear function of the available biomass.

2. The bacterial population "responds" with increased growth to an increase and production of the algal population. The "response" of the bacterial population is immediate; this may be explained by the short generation times of the bacteria.

3. Bacterial growth in a mixed system is basically different from that in a defined substrate system.

6.2 Experiment II

In the following physiological experiment in vitro, it was attempted to verify knowledge gained in the lake. A suitable means therefor constituted the cultivation in common of bacteria and algae, in such a manner that algal and bacterial cells were separated in space, while their extracellular mutual influencing was maintained. In contrast to the previous experiment, in this case, there was operated with a bacteria-free culture of Chlamydomonas sp. (Collection of Göttingen University) and a mixed bacterial culture from the Rotsee. The aim of the investigation was to answer the question:

By excretory processes, an algal culture releases organic compounds into the environment. How much time does a C atom, incorporated in the alga, need until it appears in bacteria-enrichment cultures that proceed parallel?

6.21 Methods

As may be seen from Figs. 85 and 86, there was operated with a "Spinner" flask from the firm of Belcot, as double-culture jar. After sterile inoculation, the Chlamydomonas culture was grown for three days, at permanent lighting, during which time it was shaken for 10 minutes/hour on an agitator. The light intensity was about 2000 lux, and the temperature in the thermostat-controlled room 20-21°C. On the third day, 20 µ $CNaH^{14}CO_3$ in sterile solution was added to the cultures, and the cultures were allowed to grow for another three days under the previously described conditions. As nutrient solution, the modified Z8-solution of Zehnder (according to STAUB (74) was used. On the sixth day, the algal culture was filtered off by means of a sterile filtration instrument, and rewashed (512) twice with sterile Z8-solution (sterile-filtration instrument, Membranfiltergesellschaft, Göttingen SM 165 C).

The bacterial suspension was obtained as follows: Water from the 1 m depth of the Rotsee was plated on tryptone-glucose extract agar (Difco). After an incubation time of five days, 30 colonies were inoculated into a tryptone-glucose extract liquid. The suspension was separated in each case by centrifuging (for 10 minutes at 2000 r.p.m.); the bacterial sediment was rewashed with sterile Z-solution, taken up in Z-solution, and a culture chamber of the "Spinner" flask was inoculated (513) therewith. Into the other culture chamber of the "Spinner" flask, the washed Chlamydomonas culture was introduced. As separating membrane, a purely inorganic "Selas-Silver" membrane filter of 0.45 µ pore width was used.

The cell count of Chlamydomonas was determined in the Utermöhl

inverted microscope, the bacterial counts on tryptone-glucose extract agar, at dilutions of 10^{-5} to 10^{-8}. In each case, three parallel platings were carried out.

Measurement of the radioactive samples on membrane filters as indicated in chapter 3.3.

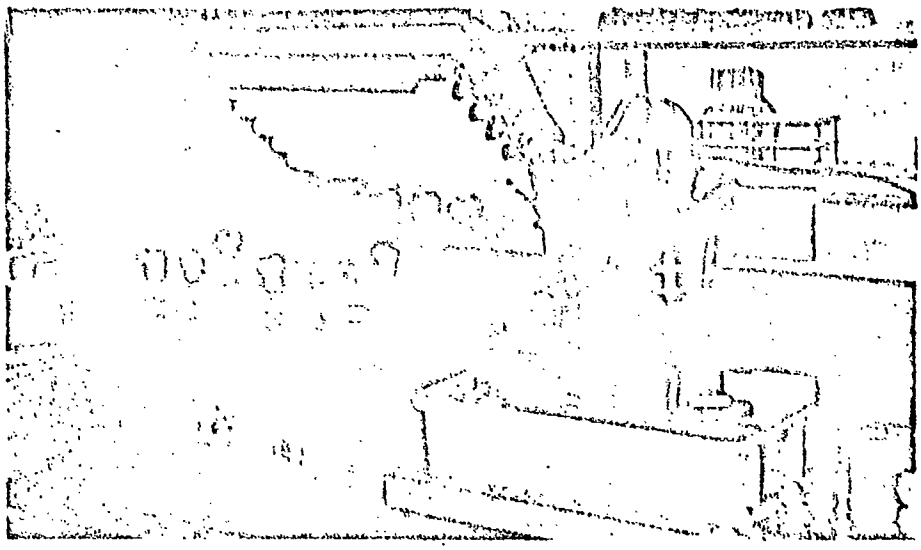


Fig. 85. Test arrangement Experiment II. (512)

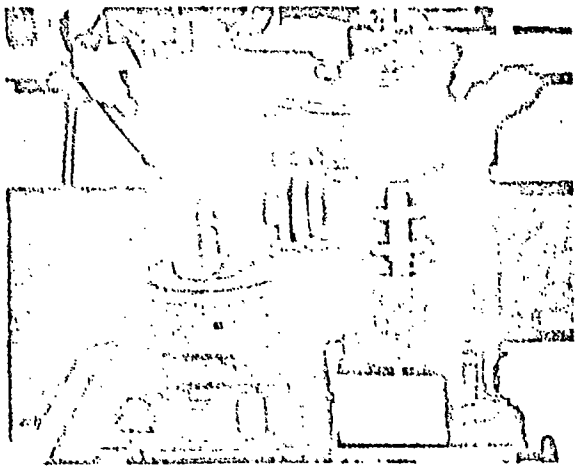


Fig. 86. "Spinner" flask (double-culture jar):
Right side: bacterial suspension,
left side: algal culture, exposed from below.

6.22 Results and Interpretations

Each day, the cultures were examined microscopically, the algal culture for contamination by bacteria, the bacterial culture for algal cells. No infections were ever found. Moreover, samples from the algal culture were plated on the same glucose-agar as the bacteria. Also in these controls, no bacteria were found.

Test I (Fig. 87) was carried out for 20 days. The curves show the following dynamics:

In this Test I, the algae were washed after the marking, and were further grown for one week in unmarked Z-solution; after one week, they were inoculated. In the first three days, the algal cell number doubled, and between the 5th and the 10th days, there was "exponential" growth. After a stationary phase of four days, and a total of 14 days, the population started dying, with a substantial decrease in the cell counts, that is, strong autolysis processes set in. It was not possible to explain the reason for this collapse of the population. Since no new culture solution was ever added, it is possible that the dying was due to the complete consumption of a micronutrient.

By following the algal marking during this period of time, a relatively vigorous excretion was determined, up to the third day, although the cell number rose. This had an effect on the bacterial population, in that the bacteria increased with respect to both cell number and ^{14}C-marking. Subsequently, between the 5th and the 9th days, the algal marking remained almost constant, while the algal cells grew "logarithmically". It may be concluded thereof that in this growth phase of the algal population, the excretory processes were low, an observation which corresponds to that of

Experiment I. The "response" of the bacterial population was a decrease in the cell number by the exhaustion of the substrate, and a stagnating marking. With the transition of the algal population to the stationary phase, the bacterial population started increasing, and this increase was particularly marked at the start of the autolysis processes of the algae. Parallel to the increase in the bacterial cell number proceeded the marking in the bacterial culture. This may be considered as proof that the bacteria obtained their substrate for the higher growth rate from the autolysis production.

In order to explain more accurately the interesting phase between the first and the third days, during which the bacterial growth was due exclusively to excretory processes, a second short-term test was carried out. The algal cells, after the washing-out of the ^{14}C-bicarbonate- (515) containing solution, were inoculated directly into the culture jar. Fig.88 shows that the excretory processes set in very rapidly. Particularly the algal culture, during the first two hours, released a good deal of its marked C atoms into the environment. It is possible that this release was the effect of the preparation, which also explains the reincorporation in the algae (after 4 hours). Seen absolutely, within the first 10 hours, 30 cps/ml of algal suspension were excreted. During this interval, a substantial increase occurred also in the bacterial population, with respect to both the uptake of marked organic material and the cell number. After the 12th hour, the system began to stabilize; the algal excretion diminished, and so did the assimilative rate of the bacterial population. It was seen that the number of bacteria, that is, their growth rate, reacted very sensitively and rapidly to the changes in the algal population. In this sense also the decrease in the bacterial counts, around the 20th hour, was to be understood. After the 25th hour, the effect of photosynthesis was

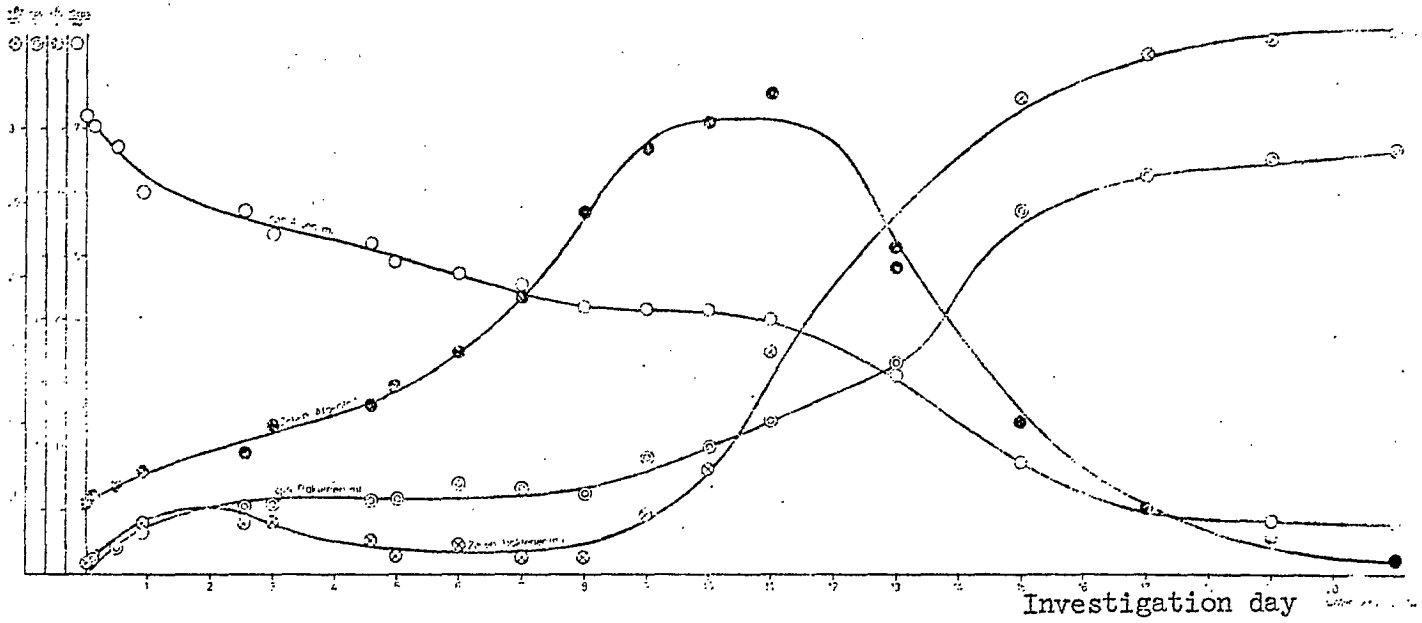


Fig. 87. Growth curves and marking (^{14}C) of the algal and bacterial cultures ("Spinner"-flask experiment).

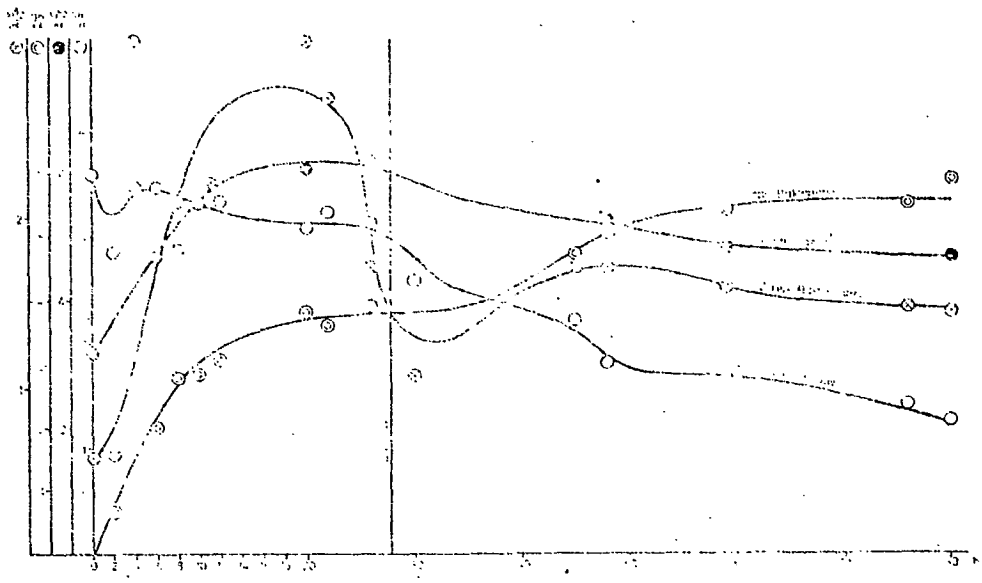


Fig. 88. Growth curves and marking (^{14}C) of the algal and bacterial cultures ("Spinner"-flask experiment). (514)

eliminated by the darkening of the algal culture jar. Unto the 80th hour of the test, the algal cells decreased slightly, due to the interrupted supply of organic material, that is, the propagative rate of the algae was throttled. Simultaneously, there was an increased release of marked material into the medium, due to autolysis and excretion by the algal population. This produced a corresponding increase in the bacterial population, with regard to both incorporation and cell number.

6.23 Conclusions

1. The Chlamydomonas cells excrete constantly. The excretion depends on the physiological condition of the cells.

2. The assimilative rate for excreted material by a bacterial (516) population is extremely high.

3. The mutual effect of different organisms brings about a behavior of the individual organisms which is completely different from that of pure-culture conditions. In the balance, seen over a rather long period of time, these processes occur in the linear range.

7. Summarizing Discussion

7.1 The Trophogenic Layer

Taking into consideration the high degradative intensity of the trophogenic layer, one must desist from the strict division of a lake into trophogenic and tropholytic layers. As Fig. 89 shows, the tropholytic processes extend over the whole profile. If these processes are balanced against one another, the organic substance broken down in the trophogenic layer, in terms of magnitude, may be assumed to be about 60% (see page 111). On the further sedimentation path, another 20-30% is mineralized, and the remaining 5-10% is incorporated into the permanent sediment.

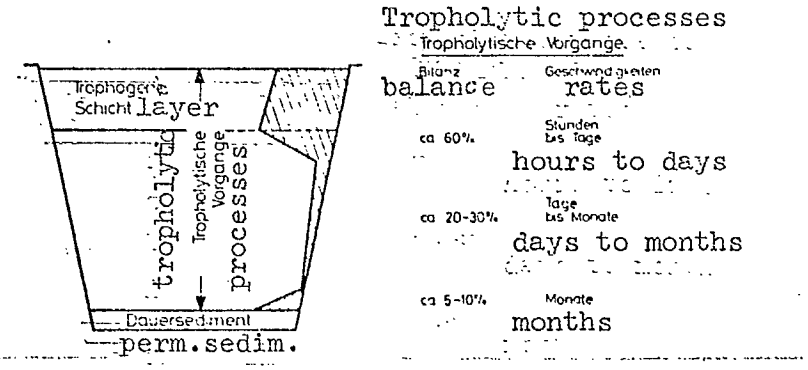


Fig. 89. "Model" of a lake regarding tropholysis. The shaded area shows the tropholytic processes in relative values, in the vertical profile.

However, for comprehension, it is important to evaluate both the balance and the rates of these processes. In the trophogenic layer, in terms of magnitude, the conversion rates may extend from hours to days (see page 110), while below the compensation point, they are considerably slower. This is confirmed by the fact that in the metalimnion, the oxygen consumption never reaches the values calculated for the trophogenic layer (the metalimnetic oxygen consumption, during the summer stagnation, was in

the order of magnitude of a few mg/l). The incorporation into the permanent sediment also requires considerable time (OHLE '48).

As measurements from the polytrophic Rotsee showed, it is also possible for the hypolimnion to become one trophogenic layer. In the Rotsee, during the whole year, the available particulate nitrogen showed higher values in the hypolimnion than in the epilimnion (Fig. 75). As special investigations (5.25) showed, a large portion of this particulate nitrogen occurred as bacterial biomass. Moreover, this finding is confirmed by the measurement of the $^{14}CO_2$ uptake per m^2, below the trophogenic layer. The average ^{14}C-fixation by various carboxylating mechanisms (BACHOFEN (7), SCHLEGEL (66), SOROKIN (72)) resulted in a value of 600 mg of C/m^2 per day, which corresponds to a yearly production of 220 g of C/m^2. The chemosynthetic and heterotrophic C-fixation which proceeds side by side with these processes, exceeds this value by a multiple. According to KUZNEZOV (37), this direct CO_2-fixation, on an average, is only about 6% of the total build-up of heterotrophic biomass. This general value cannot be applied straight away to the present conditions. However, even at cautious assessment, the total production in the hypolimnion (^{14}C-measurement 220 g of C/m^2 per year) should exceed considerably that of the trophogenic layer (381 g of C_{ass}/m^2 and 182 days, according to STADELMANN (73)). (517)

For practical water protection, this results in the following conclusion:

A lake may be considered as irreversibly damaged if the hypolimnion becomes one "trophogenic layer". Its restoration would then be conceivable only if, apart from the known rigorous stoppage of the allochthonous supply, also the productivity of the hypolimnetic "trophogenic layer" could be restricted, for instance by massive leading-off of the water from deeper layers.

7.2 Model of Causative Interrelationship in the "Short-Circuited Cycle"

On the basis of the quantitative-qualitative relations this investigation provided, a revision of the causative interrelationships in the "short-circuited cycle" is suggested. The diagram (Fig. 90) illustrates this causative interrelationship as follows:

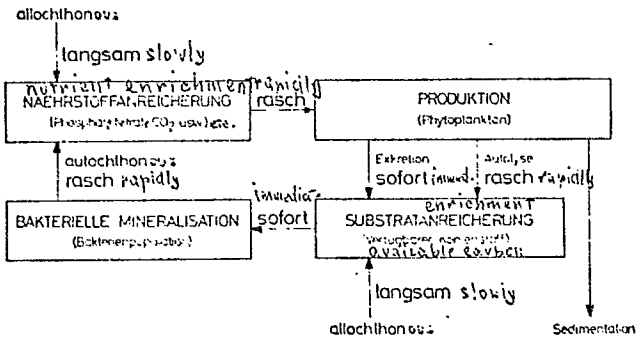


Fig. 90. "Model" of causative interrelationship in the "short-circuited cycle".

The autotrophic phytoplankton builds up a determined biomass. This primary production, except for factors, such as temperature, depends mainly on the nutrient supply. VOLLENWEIDER (80), in the OECD Report on the eutrophication problem, writes the following: "It must be stated emphatically that the key to the eutrophication problem does not lie in the nutrient concentration, but in the nutrient supply".

GÄCHTER (19) showed experimentally for phosphorus, as a nutrient, (518) that the constant addition of small amounts of phosphate releases a higher production than a single addition of a larger amount of phosphate.

As in a commercial investigation, the business situation cannot be expressed merely by a balance sheet; rather, a profit and loss account must also be established, which is far more informative for the respective period

of time; likewise, when considering the effect of nutrients, the conversion rates, and the availability of these nutrients are of extreme importance.

Phytoplankton, essentially, builds up the organic carbon in a body of water. A certain part thereof is available to bacterial heterotrophic assimilation, either by autolysis or excretion.

According to OHLE (verbal communication), the degradation of organic cell components may take place also in a purely chemical manner. Thus, it is possible that even more difficultly attackable compounds are made available to bacteria.

The capability of the bacterial population depends on the substrate supply (HOBBIE and WRIGHT (28)). In Fig. 90, the substrate supply for bacteria is designated as "available carbon". This available carbon may be either of allochthonous origin or formed by phytoplankton production. From the available organic carbon compounds, the bacterial population releases nutrients by mineralization. These nutrients are again available to the phytoplankton for its production. This occurs so rapidly that during the summer months, it is hardly possible to detect the phosphates analytically, while the phytoplankton population showed relatively high values with respect to both biomass and production. It was not possible to explain this exclusively by the influence of the allochthonous nutrient supply, since precisely during the stable summer stratification, the homogeneous distribution of allochthonous, generally punctiform inflows requires very much time, and probably does not take place before the following turnover.

In principle, the described relations are known. However, it is essential in this cycle to evaluate its rates and the availability of the components, that is, again in commercial terms, to produce proof of liquidity.

The process of nutrient addition by allochthonous supply may be called slow. The autochthonous supply of nutrients originates from mineralization, possibly also from the activity of free enzymes, as REICHHARDT et al. (58) showed for the particular case of phosphatase. As the present research work shows, this process, in space, is in closest association with the zone in which the phytoplankton is built up. Nutrients that are mobilized in this manner, are far more rapidly available than those from allochthonous supply.

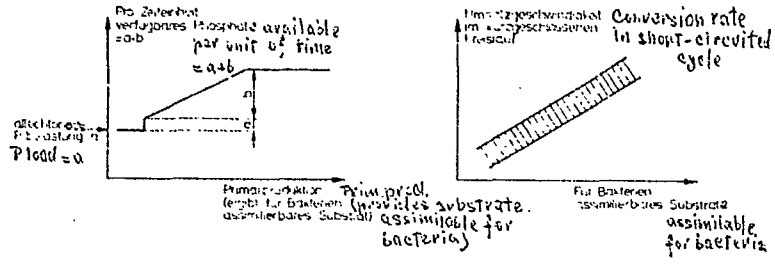
Through bacterial mineralization, both nutrients and CO_2 are released rapidly. It is possible that in microstratifications of phytoplankton populations, at high photosynthesis, CO_2 acts as a limiting factor (KUENTZEL (38, 39)). If the population depended only on diffusion processes, the supply of CO_2 from the atmosphere, etc., then these CO_2 minima would have to be very much higher in the immediate cell surroundings. (519) Through bacterial activity, CO_2 is released, and is immediately available to phytoplankton. According to various experimental investigations, these reflections would appear to be rather obvious (LANGE (40)). Another indication is the washing effect described by OHLE (47).

However, since these processes are microexchanges which, quantitatively, will be difficult to detect, the statements on a CO_2 limitary effect in a body of water, for the time being, must be interpreted with some reservation.

The described causative relations apply to all involved in the substance cycle, particularly to the respective limitary factor.

In various lakes, phosphorus plays this part (VOLLENWEIDER (80)). A phosphorus load in a lake results in the qualitative relations shown in Figs. 91 and 92. An allochthonous phosphate influx causes a higher production

and, thus, an increase in the available carbon. However, this increases the conversion rate in the "short-circuited cycle", and the level of the whole cycle is increased in the sense of a compound-interest calculation (Fig. 91). Thus, the phosphate addition acts as initial factor and "catalyst" for a much higher increase in the production.



Figs. 91/92. "Model" of the mode of action of a phosphate load in the trophogenic layer.

Fig. 92 shows a hypothetical curve of the conversion rate in the "short-circuited cycle", against the assimilable carbon. Under natural conditions, this curve might proceed approximately linearly, since a mixed bacterial culture provides an approximately linear "response function" to a determined substrate supply (see page 118). Due to the "polyvalent" bacterial population, the conversion rate responds very rapidly to a change in the assimilable carbon, even though this latter may vary qualitatively.

In principle, the reflections made for phosphate apply to any growth-limiting factor, if it is involved in the bacterial metabolism.

However, the increase in the level of available carbon may take place also directly by an addition of assimilable carbon compounds; in this manner, the production may be substantially increased, without an increase in the limiting factor.

For practical water protection, it results from the described causative relations that, apart from "production-limitary" factors, the assimilable carbon in the waters is of utmost importance.

SUMMARY

1. Physical, chemical and biological aspects of a one-year cycle (1969-70) in the high eutrophic Rotsee and the mesotrophic Lake of Lucerne (Horwer Bay) in Switzerland were examined. Attention was focused on the quantitative and, to a more limited extent, qualitative determination of the bacterial flora and its ecological influence. (521/2)

2. More than thirty individual components were determined in each sample (see p. 528). Mathematical (linear correlation coefficients) and ecological correlations were sought during the course of the year and at various depths. Two computer programs, adapted to limnological data, were developed to this end (see appendix).

A series of causative relations could be determined mathematically thanks to this program. It is important to note that with regard to the biomass in the Rotsee (Table 14) the following parameters in the lake appear to be the most meaningful causative concatination, ecologically speaking, in this order of correlations: biomass – single plankton form (predominant) – P and N particular content – bacteria population.

3. A detailed examination was made of the phytoplankton population in the Rotsee. Very high values (fresh weight) of over 30 mg/l were noted in April 1969 and January 1970 (see picture 37). The prevailing algal group was the cryptomonades, with peaks in the vegetation development in the winter months (see picture 33).

4. The maximum primary production values (^{14}C-technique) for the Lake of Lucerne in the summer lay around 60 mg C/m³ h and for the Rotsee in the winter around 250 mg C/m³h. Concentrated, overlapping experiments were carried out in situ to study the daily rhythm of primary production. It was found that the total of the many short experiments corresponded to the results of a full-day experiment (see pictures 43 and 45).

5. Most of the bacteria found in a water body appear in a suspended state. They consit mainly of small starved forms called 'zymogenic germs'. The qualitative characteristics of the substrate concentration and the trophic situation can be deduced from morphology. 'Aufwuchs' colonies and zoogloae were also noted. The following specifically hypolimnic forms were found in the Rotsee: *Thiopedia rosea* (picture 63), *Lamprocystis roseopersicina* (picture 65), *Chromatium dense-granulatum* (picture 67), *Leptothrix* sp. (picture 70).

6. High bacterial counts were determined in the levels with maximum primary production (pictures 47 and 73). In the Rotsee the epilimnic bacterial count (membrane-Filter count) was $5 \cdot 10^5$ to $4.4 \cdot 10^6$ germs/ml, in the Lake of Lucerne 10^5 to $1.7 \cdot 10^6$ germs/ml.

7. An ascending series of bacterial counts (MF) can be made with regard to the trophic level (Table 25). But since the bacteria population depends directly on the substrate supply, it seems to be more meaningful to use production parameters for trophic characterization.

8. Tabulations of special situations (for example, almost complete nutrient reduction) were used as a basis to estimate turnover capacity in the intrabiocenotic cycle. It was shown that individual nutrients revealed 4 to 5 intrabiocenotic cycles per day (Tables 28 and 29).

9. Making a distinction between a trophogenic and tropholytic layer is senseless because intense tropholytic processes occur in the trophogenic layer (picture 89).

The hypolimnion as well can become *one* 'trophogenic layer' if photoautotrophic bacteria are predominant as in the Rotsee (see pictures 63 and 72).

10. In order to clarify the mutual influence of phytoplankton and bacteria on each other, two test series were carried out in vitro. A mixed culture of both organism groups on the one hand and separate cultures, on the other hand, were set up. In the latter case both cultures were separated by means of a membrane filter; however, extracellular influencing remained intact (pictures 85 and 86).

The following observations were made:

a) A nutrient-induced increase in algal growth brought about a substrate-induced increase in bacterial growth (picture 83).
b) The bacteria population responded very rapidly to the physiological behavior of the algae (picture 88).
c) Bacterial growth in a mixed system is basically different from that in a defined substrate system.

11. The following conclusions could be drawn on the basis of a synthesis of the results and their evaluation through data processing (picture 90):

a) Primary production is not the direct result of a concentration at a particular time but of the turnover volume and velocity of the 'limiting factor'. (522)

b) The turnover velocity in an intrabiocenotic cycle depends on the performance capacity of the bacterial population, which, in turn, depends on the available quantity of substrate that can be assimilated.

c) Besides having a bearing on the turnover velocity in an intrabiocenotic cycle, an increase of assimilable carbon in the trophic layer leads to more effective utilization of nutrients and greater production (catalytic effect).

12. For practical water pollution control it can be concluded, on the basis of the causative relations mentioned, that not only the production limiting factors but also the amount of assimilable carbon for mixed bacterial population is of pivotal importance.

RÉSUMÉ

(520)

1. Un cycle d'un an (1969 à 1970) du Rotsee, un lac très eutrophe, et du lac des Quatre-Cantons (la baie de Horw), qui est mésotrophe, a été examiné du point de vue physique, chimique et biologique. L'accent a été mis sur la détérmination quantitative et – de façon plus restreinte – qualitative de la flore bactérienne et son influence écologique.

2. Plus de 30 constituants séparés ont été déterminés dans chaque échantillon. Des relations mathématiques (coefficient de correlation linéaire) et écologiques dans les diverses profondeurs ont été examinées au cours de l'année. Deux programmes d'ordinateur adaptés à la limnologie ont été mis au point à cette effet (voir l'appendice).

Grâce à ce programme, une série de relations causales a pu être calculée mathématiquement. Quant à la biomasse du Rotsee (tableau 14), il est important de constater que les paramètres suivants se sont révélés comme étant l'enchaînement écologique la plus évident dans la série des corrélations: biomasse – forme spécifique (dominante) du plancton – teneur en P et en N – population en bactéries.

3. La population du phytoplanction du Rotsee a été minutieusement examinée. Les valeurs très élevées (basées sur le poids de la matière fraîche) de plus de 30 mg/l ont été prélevées en avril 1969 et en janvier 1970 (voir fig. 37). Les cryptomanades ont été prédominants, montrant des poussées de croissance en hiver (voir fig. 33).

4. Des expériences intensives et se recoupant ont été effectuées in situ, afin d'étudier le rythme quotidien de la production primaire. Le résultat de la somme des diverses expériences de courte durée est en accord avec ceux d'une expérience d'une journée entière (voir fig. 43 et 45). En été les valeurs maximales de la production primaire dans le lac des Quatre-Cantons se situaient autour de 60 mg C/m³ h, dans le Rotsee en hiver à environ 250 mg C/m³ h.

5. La plupart des bactéries-dans l'eau sont en suspension. Elles se trouvent sous forme rachitique appelée «bactérie zymogènes». Les caractéristiques qualitatives de la concentration du substrat et de l'état trophique peuvent être déduit de la morphologie. Des colonies de «Aufwuchs» (microorganismes qui poussent sur le substrat solide) et des zoogloca ont également été observées.

Les formes suivantes, caractéristiques du hypolimnion, ont été trouvées dans le Rotsee: *Thiopedia rosea* (fig. 63), *Lamprocystis roseopersicina* (fig. 65), *Chromatium densegranulatum* (fig. 67), *Leptothrix* sp. (fig. 70).

6. Une densité de bactéries très élevée a été relevée dans les couches de production primaire maximale (fig. 47 et 73). Le comptage de bactéries dans l'épilimnion du Rotsee et du lac des Quatre-Cantons (filtre millipore) donnait de $5 \cdot 10^6$ à $4{,}4 \cdot 10^6$ bactéries/ml et 10^6 à $1{,}7 \cdot 10^6$ bactéries/ml respectivement.

7. Une série ascendante de comptes de bactéries (filtre millipore) peut être mise au point pour calculer le degré d'eutrophisation (tableau 25). Mais comme la population des bactéries dépend directement de la disponibilité de substrat il est évident que les paramètres de production soient utilisés pour caractériser l'état trophique.

8. Des bilans de situations particulières (p. ex. disparition quasi-totale de la matière nutritive) ont servi de base de calcul pour évaluer la vitesse de renouvellement dans un cycle intrabiocénotiques par jour (tableaux 28 et 29).

9. Il est inutile de vouloir faire une distinction entre une couche trophogène et une tropholytique, car des processus tropholytiques intenses de déroulent aussi dans la couche trophogène (fig. 89).

Ainsi l'hypolimnion peut devenir *une* couche trophogène homogène si, comme dans le Rotsee, les bactéries photoautotrophes prédominent (voir fig. 63 et 72).

10. Pour étudier les influences réciproques des phytoplanctons et des bactéries deux séries d'expériences ont été effectuées in vitro. D'une part une culture mixte des deux groupes d'organismes, d'autre part des cultures séparées ont été préparées. Dans le second cas les cultures ont été séparées par un filtre millipore; les interactions extracellulaires sont cependant restées intactes (fig. 85 et 86).

Les observations suivantes ont été faites: (520)

a) Une augmentation de la croissance d'algues, influencée par la matière nutritive, a produit une augmentation dépendante du substrat et du taux croissance des bactéries (fig. 83).

b) Les bactéries ont réagi très rapidement au comportement physiologique des algues (fig. 88).

c) L'accroissement des bactéries dans un système mixte est fondamentalement différent de celui d'un système de substrat défini.

11. Les conclusions suivantes ont pu être tirées grace à la synthèse des résultats et leur traitement par ordinateur (fig. 90):

a) La production primaire n'est pas le résultat direct de la concentration du facteur limitant à un moment donné, mais bien de son volume et du taux de son renouvellement.

b) La vitesse de renouvellement dans un cycle intrabiocénotique dépend du rendement de la population des bactéries qui, de son côté, dépend de la disponibilité en substrat assimilable. (521)

c) A part son influence sur la vitesse de renouvellement dans un cycle intrabiocénotique, une augmentation du carbone assimilable dans l'eau riche trophique peut mener à une utilisation plus efficace de la matière nutritive, et à une production plus poussée (effet de catalyse).

12. Dans le but de protéger les eaux on peut déduire des relations de causalité mentionnées plus haut, que non seulement les facteurs limitant la production, mais aussi la quantité de carbone assimilable par la population bactérienne existante sont d'une importance primordiale.

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APPENDIX

1. In der Arbeit verwendete Abkürzungen Abbreviations used in the present article

		Dimension of input data Dimension der eingegebenen Daten
TEMP	Temperature	Grad Celsius °C
KAPPA	Leitfähigkeit conductivity	Mikrosiemens/cm
MF	Membranfilterbakterien	Tausend Zellen/ml 1000 cells/ml
PLAT	Plattenzahlen plate counts	Zellen/ml cells/ml
SAUER	Sauerstoff oxygen	mg/l
PR H	Primärproduktion Hell clear	mg C_{ass}/m^3h
PR D	Primärproduktion Dunkel dark	mg C_{ass}/m^3h
GELOP	Gelöster organischer Phosphor diss. org. P	µg P/l
GELON	Gelöster organischer Stickstoff diss. org. N	µg N/l
PN	Partikulärer Stickstoff part. N	µg N/l
PP	Partikulärer Phosphor part. P	µg P/l
PH	pH-Wert pH value	
SBV	Alkalinität alkalinity	mval/l
NITRA	Nitrate	µg NO_3-N/l
NITRI	Nitrite	µg NO_2-N/l
AMMON	Ammonium	µg NH_4-N/l
PHAT	Phosphate	µg PO_4-P/l
GES P	Gesamtphosphor total P	µg P/l
GEL FE	Gelöstes Eisen diss. Fe	µg Fe/l
P FE	Partikuläres Eisen part. Fe	µg Fe/l
SI O	Silikate	µg SiO_2/l
GES E	Gesamtenergie tot. energy	Prozent der Oberflächenintensität (= 100%)
VG	Grünlicht (533 nm) green light	Prozent der Oberflächenintensität (= 100%) % of
RG	Rotlicht red light	Prozent der Oberflächenintensität (= 100%) surface
BG	Blaulicht (423 nm) blue light	Prozent der Oberflächenintensität (= 100%) intensity
BIOM	Biomasse, Phytoplankton	µg/ml
CYANO	Biomasse Cyanophyceae	µg/ml
CLORO	Biomasse Chlorophyceae	µg/ml
KONJU	Biomasse	µg/ml
CRYSO	Biomasse Chrysophyceae	µg/ml
DIATO	Biomasse Diatomeae	µg/ml
CRYPT	Biomasse Cryptophyceae	µg/ml
K	Korrelation	
KK	Korrelationskoeffizient	

26)

(527)

2. *Programme* Programs

```
      PROGRAM KORRELA (INPUT,OUTPUT)
      DIMENSION DAT(14,3),KMAX(15),T(7),A(14,7,30),SIG(14)
      DIMENSION MES(30),RK(30,30) ,SEE(2),W(7)
      COMMON X(14),Y(14),N,R
      INTEGER DAT,TEST
      DATA(SIG(I),I=1,15)/
     10.4077,0.4220,0.4354,0.7293,0.6434,
     10.6215,0.5822,0.5494,0.5214,0.4973,
     10.4767,0.4575,0.4409,0.4259,0.4124/
C     TABELLEN NACH LEIGY- IAB, P. 61
C     WERTE FUER 2 ALPHA =0.1
C     DER INDEX I SYMBOLISIERT VERSCHIEDENE DATEN
C     DER INDEX L IST DIREKT EIN CODE FUER ART DER MESSUNG
C     K MAX(I)= ANZAHL TIEFENSTUFEN BEIM DATUM MIT CODE NUMMER I
C     I = DATUM KAN MAXIMAL 14 SEIN
C     K= TIEFE  KANN MAXIMAL  14 SEIN
C     L= CODE, ART DER MESSUNG   KANN  MAXIMAL 30 SEIN
      PRINT 15
 15   FORMAT (1H1)
      I=0
      DO 18 M=1,14
      KMAX(M)=0
      DO 18 K= 1,7
      T (K) = 0.
      DO 18 L= 1,30
 18   A(M,K,L)=0.
 11   I=I+1
      READ 1,SEE(1),SEE(2),DAT(I,1),DAT(I,2),DAT(I,3)
 1    FORMAT (2A10,3I2)
      L=0
      PRINT 16, SEE(1),SEE(2),DAT(I,1),DAT(I,2),DAT(I,3)
 16   FORMAT (1H0,2A10,3(I2,1H.)/)
      TEST =DAT(I,1)+DAT(I,2)+DAT(I,3)
      IF(TEST.EQ.0)  GO TO 13
 8    L=L+1
      READ 2,NI,MES(L),W(1),W(2),W(3),W(4),W(5),W(6),W(7)
 2    FORMAT (I5,A5,/7F8.4)
      IF(NI.EQ.99999)GO TO 111
      IF (NI) 3,9,3
 3    DO 4 J=1,7
      IF (J-1) 6,5,6
 5    T(J)= W(J) $JJ=1
      GO TO 4
 6    IF (W(J))   7,4,7
 7    JJ=JJ+1
      T(JJ)=W(J)
 4    CONTINUE
      KMAX(I)=JJ
      PRINT 17,NI, MES(L),(T(M),M=1,JJ)
 17   FORMAT (1H ,I5,A5,7F10.4)
      L=0
      GO TO 8
 9    CONTINUE
 12   KE= KMAX(I) I LMAX=L
      PRINT 43, MES(L),(W(M),M=1,KE)
 43   FORMAT(1H ,5X,A5,7F10.4)
      DO 10 K=1,KE
 10   A(I,K,L)=W(K)
      GO TO 8
 111  CONTINUE
      PRINT 44,NI
 44   FORMAT(1H ,I5)
      GO TO 11
 13   CONTINUE
      IMAX = I-1
      KM=0
      DO 40 IS=1,IMAX
      IF(KM.GT.KMAX(IS)) 40,42
 42   KM=KMAX(IS)
 40   CONTINUE
      DO 22 K= 1,KM
      PRINT 23, T(K)
 23   FORMAT (1H1,* KORRELATIONEN IN DER TIEFE*F7.1,4X,*METER*/)
      PRINT 24
 24   FORMAT (1H0,*VERGLICHENE  REIHEN*4X,*KORR-KOEF*,3X,*SIGNIFIKANZ-TE
     1ST*/36X,*LEIGY-TAB P.61*/36X*IRRTUMSWAHRSCH. 0,1*/)
      PRINT 200
 200  FORMAT(1H ,5X,1HX,3X,1HY)
      DO 31 MKL=1,30
      DO 31 MKK =1,30
 31   RK(MKL,MKK)=0.
      LXE=LMAX-1
      DO 21 LX= 1,LXE
      LA=LX+1
      DO 21LY=LA,LMAX
      DO 23 I= 1,IMAX
      Y(I)= A(I,K,LY)
 28   X(I) = A(I,K,LX)
      DX=0.
      DY=0.
      DO 60 I=2,IMAX
      DX=DX+X(I)-X(1)
      DY=DY+Y(I)-Y(1)
 60   CONTINUE
      IF(DX)61,21,61
 61   CONTINUE
      IF(DY)62,21,62
 62   CONTINUE
      N = IMAX
      CALL REG
      NU = N-2
      R3=ABS(R)
      IF(R3.GE.SIG(NU))26,25
 25   PRINT 27,MES(LX),MES(LY),R
 27   FORMAT ( 1H ,3X,A5,4X,A5,5X,F 8.5)
      GO TO 21
 26   PRINT 28,MES(LX),MES(LY),R
 28   FORMAT (1H ,3X,A5,4X,A5,5X,F8.5,3X,*SIGNIFIKANT*)
      RK(LX,LY) =R
      RK(LY,LX)=R
 21   CONTINUE
      PRINT 23,T(K)
      IF(LMAX.LE.10)50,51
 50   PRINT32,(MES(J),J=1,LMAX)
 32   FORMAT(1H0,7X,10(A5,5X)/)
      DO33 JS=1,LMAX
 33   PRINT34,MES(JS),(RK(JS,JT),JT=1,LMAX)
 34   FORMAT(1H ,A5,2X,10(F6.4,4X))
      GO TO 22
 51   PRINT 32,(MES(J),J=1,10)
      DO 35 JS=1,LMAX
 35   PRINT 34,MES(JS),(RK(JS,JT),JT=1,10)
      IF (LMAX.LE.20)52,53
 52   CONTINUE
      PRINT 32,(MES(J),J=11,LMAX)
      DO 36 JS=1,LMAX
 36   PRINT 34,MES(JS),(RK(JS,JT),JT=11,LMAX)
      GO TO 22
 53   CONTINUE
      PRINT 32,(MES(J),J=11,20)
      DO 37 JS=1,LMAX
 37   PRINT 34,MES(JS),(RK(JS,JT),JT=11,20)
      PRINT32,(MES(J),J=21,LMAX)
      DO 38JS=1,LMAX
C     DIE ZIFFER 33 SOLL DURCH EINEN GEEIGNETEN  MAXIMALWERT ERSETZT WERDEN
 38   PRINT 34,MES(JS),(RK(JS,JT),JT=21,LMAX)
 22   CONTINUE
      END
```

```
      PROGRAM PROFIL (INPUT,OUTPUT)
      INTEGER SEE,DAT
      DIMENSION SEE(2),DAT(3),KAT(2),X(45),Y(45)
 42   READ 1,SEE,DAT,LEKA
 001  FORMAT (2A10,3I2,3=X,A10)
      PRINT 2,SEE,DAT
 002  FORMAT (1H1,2A10,I2,1H.,I2,1H.,I2,/,X,28(1H*))
      N2=0
      N2 = 2
      NL = 0
      N2 = 0
 3    READ 4,NL,KA
 4    FORMAT(I5,5X,7A10)
      IF(NL.EQ.99999)42,43
 43   CONTINUE
      IF(NL) 41,41,40
 41   CONTINUE
      N2=N2+1
 40   CONTINUE
      IF (KAT(1).NE.LEKA) 5,19
 005  IF (N1.NE.0.AND.NI.EQ.0.AND.NL.EQ.0.AND.N2.EQ.0) 6,15
 006  N1 = N1
      IF (N2.LT.50) 7,9
 007  PRINT 8,NL
 008  FORMAT (///,X,6HPROFIL,I6,/,X,12(1H-))
      N2 = N2+5
      GO TO 11
 009  PRINT 10,NL
 010  FORMAT (1H1,6HPROFIL,I6,/,12(1H-))
 011  PRINT 12
 012  FORMAT (//,X,9HMESSREIHE,6X,7HFLAECHE,7X,12HMITTELWERT,
     1    4X,8HQUOTIENT,6X,1HN,/)
      N2 = 6
      I1 = 1
      I2 = 7
 013  M = 12
      DECODE (70,14,KA) (X(I),I=I1,I2)
 014  FORMAT (7F10.1)
      GO TO 3
 015  IF (N1.EQ.0.AND.N2.EQ.0.AND.NL.NE.0.AND.N2.EQ.0) 16,17
 016  I1 = I1+7
      I2 = I2+7
      IF (I2.GT.49) GO TO 45
      GO TO 13
 017  IF (N1.EQ.0.AND.N2.NE.0.AND.N2.EQ.0) 13,23
 018  N2 = N2
      IF (N1.EQ.K) GO TO 24
      N1 = 0
      N = 3
      DO 19 I = 2,M
      IF (X(I).LE.X(I-1)) GO TO 24
 019  N = I
 020  IF (N.EQ.I) GO TO 25
      I1 = 1
      I2 = 7
 021  DECODE (70,22,KI) (Y(I),I=I1,I2)
 022  FORMAT (7F10.4)
      IF (I2.LT.N) 3,27
 023  IF (N1.EQ.0.AND.N2.EQ.0.AND.NL.EQ.0.AND.N2.NE.0) 24,25
 024  I1 = I1+7
      I2 = I2+7
      IF (I2.GT.49.OR.I2.GT.N+6) GO TO 25
      GO TO 21
 025  PRINT 26,NL,N2,N
 026  FORMAT (/,X,22X,*FEL*,/)
      N2 = N2+3
      GO TO 37
 027  FL = 0
      DO 28 I = 2,N
 028  FL = FL+.5*(X(I)-X(I-1))*(Y(I)+Y(I-1))
      FM = FL/(X(N)-X(1))
      IC = ABS(Y(1))
      DO 29 I = 2,N
      IF (IC.LT.ABS(Y(I))) IC = ABS(Y(I))
 029  CONTINUE
      IF (FM.EQ.0) 30,31
 030  QQ = I.
      GO TO 32
 031  QQ = YE/FM
 032  IF (N2.LT.50) 33,35
 033  PRINT 34,N2,FL,FM,QQ,N
 034  FORMAT (3X,I5,E17.5,F14.6,F12.3,I8)
      N2 = N2+1
      GO TO 38
 035  PRINT 36
 036  FORMAT (1H1,9HMESSREIHE,6X,7HFLAECHE,7X,12HMITTELWERT,
     1    4X,8HQUOTIENT,6X,1HN,/)
      PRINT 34,N2,FL,FM,QQ,N
      N2 = 3
      GO TO I9
 037  NI = 2
 038  N2 = 0
      GO TO 3
 039  CONTINUE
      END
```

```
      SUBROUTINE REG
      COMMON X(14),Y(14),N,R
C     FORMELN LEIGY TABELLEN P. 173,I9
      AN =N
      SX = 0.
      SY =0.
      SXX =0.
      SYY =0.
      SXY =0.
      DO 1 M=1,N
      SX =SX + X(M)
      SY= SY + Y(M)
      SXX  = SXX + X(M)*X(M)
      SYY = SYY + Y(M)* Y(M)
 1    SXY = SXY + X(M)*Y(M)
      BXY=(SXY-(SX*SY)/AN)/(SXX-(SX*SX)/AN)
      BYX=(SXY-(SX*SY)/AN)/(SYY-(SY*SY)/AN)
      AXY=SY/AN-BXY*(SX/AN)
      AYX=SX/AN-BYX*(SY/AN)
      PRINT 10,AXY,BXY
 10   FORMAT(1H ,55X,*REGR.X GEGEN Y = *F15.4,* + *,F15.4,2X,1H* X)
      PRINT 11,AYX,BYX
 11   FORMAT(1H ,50X,*      Y      .X = *F15.4,* + *,F15.4,2X,1H* X)
      SSX = SXX- (SX*SX/AN)
      SSY = SYY - (SY*SY/AN)
      SSXY = SXY - (SX*SY/AN)
      W = (SSX*SSY)**0.5
      IF(W)2,2,3
 2    R=-3.
      RETURN
 3    CONTINUE
      R = SSXY/W
      RETURN
      END
```

3. *Eingabedaten* Input data

ROTSEE 20. 3.69.

I	0.0000	1.0000	2.5000	5.0000	14.0000
TEMP	4.6333	4.2333	4.5350	5.2330	5.2833
KAPPA	250.0333	243.3033	243.0630	265.6330	140.3600
MF	1224.8333	1133.0333	1139.8080	463.6330	3962.2033
PLAT	16927.3333	10532.2833	4147.3590	4747.3329	1317.0333
SAUER	16.0333	15.5850	14.7500	3.4500	3.3333
PR N	237.3253	83.2243	13.5630	.0330	4.3530
PR O	5.5353	4.1443	2.7230	.6153	3.0153
GELOP	352.0330	325.0333	291.0033	219.0333	628.0003
GELON	436.0333	406.0033	743.0000	763.0000	320.0050
P N	1293.0333	1200.0333	753.0350	162.0330	463.0343
P P	142.3333	120.0333	42.0133	14.0333	26.9800
P H	4.6430	8.4395	1.5200	7.4330	6.4403
SAV	2.4430	2.4433	2.4430	2.5400	4.2333
NITRA	550.0333	933.0330	573.3333	613.3034	55.3303
NITRI	7.3333	6.4331	5.4033	4.3333	0.2833
AMMON	90.0330	150.0333	213.3330	930.0030	4440.2030
PHAT	48.3330	55.0333	42.5830	165.5000	1710.3033
GES P	542.0330	433.0033	508.3330	515.0000	2164.0030
GELFE	15.0330	13.5530	12.5300	12.5033	224.0330
P FE	595.5330	142.3330	173.5000	61.5033	221.5300
SI 00	1.7230	1.3030	1.4030	2.1338	4.3370
GES E	100.3330	35.4333	5.0000	.4330	3.3363
V G	100.0333	43.0770	4.5030	.6030	3.3333
BION	27.1930	24.3333	17.0400	2.7600	3.2533
CYANO	.3100	.1133	.1500	.4300	0.3000
CLORO	3.5430	2.1570	1.7048	4.4350	.2450
KONJU	.3100	.0150	.3120	8.0003	3.3330
CRYSO	1.0330	.4730	.7490	8.0333	4.3303
DIATO	3.3660	7.9530	4.6310	1.5459	.7920
CRYPT	18.5780	12.0718	7.3880	.2670	.2270

99999

ROTSEE 17. 6.69.

I	0.0303	1.0000	2.5000	5.0000	14.0000
TEMP	7.5333	7.4333	7.5000	7.0033	5.3330
KAPPA	261.3333	261.0336	265.0030	267.0330	290.3000
MF	3641.3333	2652.3333	2019.0030	1764.0303	4232.3333
PLAT	32938.4128	22330.8833	26731.5033	22963.0330	14503.3330
SAUER	31.3530	10.4330	3.2500	6.1630	.6700
PR N	292.7330	115.8678	13.3380	3.6330	5.1370
PR O	4.4538	5.7458	4.6770	2.2543	5.5470
GELOP	54.0330	73.0039	34.0033	52.0330	1.3303
GELON	883.0300	348.0333	633.3300	414.0030	320.0000
P N	1280.0330	1223.0332	445.0338	593.0030	583.0300
P P	330.3330	100.4333	74.8308	120.0338	47.3300
P H	4.2533	8.1533	5.5530	7.7433	7.2533
SAV	2.5700	2.4230	2.4530	2.4533	2.4000
NITRA	375.0000	330.3330	363.0300	393.8303	56.0030
NITRI	35.3370	15.3333	37.4330	14.0073	60.3303
AMMON	170.3330	513.8000	873.3000	600.3000	2493.3333
PHAT	113.5330	114.0330	174.5300	133.4338	473.3320
GES P	294.0333	307.5000	286.3000	303.0333	560.3303
GELFE	13.5000	8.8300	5.4020	5.8036	6.4400
P FE	152.6300	143.4333	121.3038	184.7333	91.7333
SI 00	1.3033	1.1533	1.5200	3.1530	2.4540
GES E	300.3030	26.3303	3.0033	.1330	6.0330
V G	300.3330	24.3028	4.4333	.2050	3.3330
BION	32.9433	22.7780	14.9208	17.8750	2.3300
CYANO	.3603	.1110	.1500	.3130	.4030
CLORO	10.4440	7.1469	5.5278	3.3540	7.3600
KONJU	4.3390	0.3030	3.4038	7.0333	3.3331
CRYSO	.4460	.5138	.0560	8.0330	6.0300
DIATO	.2041	.4230	.2918	.8330	.3641
CRYPT	19.2153	13.7310	4.4040	3.3140	.3578

-99999

ROTSEE 22. 5.69.

I	0.0010	1.0000	2.5000	5.0000	14.0000
TEMP	10.6333	10.9000	10.4800	6.5330	6.6310
KAPPA	265.3300	260.8033	273.4000	245.3000	322.3030
MF	905.3333	1169.0308	435.0000	1313.0300	5330.0030
PLAT	3286.2333	2143.0350	1763.3033	9542.3330	4653.0033
SAUER	33.4330	10.7233	4.2300	1.4000	0.0033
PR N	20.3073	43.5055	15.3555	7.9643	2.1480
PR O	3.0713	.6320	.5140	1.1453	.1288
GELOP	41.2333	34.2000	23.0000	14.8030	50.3303
GELON	490.0303	453.3303	413.0000	430.8080	316.0030
P N	276.0833	403.0380	249.0000	378.0300	530.0000
P P	17.3333	24.2038	35.0030	96.0333	127.0033
P H	8.4433	4.5420	8.1580	7.4080	7.4100
SAV	2.5201	2.4436	2.4630	2.5510	3.1370
NITRA	500.0333	520.2308	520.0038	380.0030	30.0000
NITRI	14.4330	14.7833	13.8048	4.3333	3.0300
AMMON	3.0830	129.2333	253.3008	1443.0333	3803.0333
PHOS	74.0038	74.0030	107.0000	228.0333	633.0303
GES P	132.3800	134.0330	145.0008	343.0040	720.3303
GELFE	14.5030	26.5230	33.0030	12.0088	43.3033
P FE	71.0333	43.5333	111.0330	81.0300	102.0033
SI 00	2.4538	2.0548	2.1030	1.7530	3.3503
GES E	303.3330	47.3330	14.5800	2.4000	0.5730
V G	100.3030	98.3200	20.0300	4.0330	0.7008
BION	3.0630	3.3500	9.3030	1.8030	.4500
CYANO	0.3010	0.0333	0.0000	.8130	0.0000
CLORO	.0760	.4650	.8568	.4200	.3440
KONJU	0.0030	0.4033	4.0388	0.0300	0.3010
CRYSO	8.0833	0.0200	0.0003	.3540	.0110
DIATO	0.3230	0.7030	0.3030	0.0033	.3243
CRYPT	2.4438	2.0567	1.2450	1.3680	.1830

99999

ROTSEE 10. 6.69.

I	0.7330	1.0070	2.5000	5.0008	14.0828
TEMP	19.5033	17.6330	16.2000	9.3330	4.6033
KAPPA	251.3330	260.3330	262.0000	283.0000	332.0000
MF	1024.3305	3296.3300	931.0000	2724.3338	4694.3000
PLAT	5453.1333	4760.3330	2303.0000	2590.3000	1242.0000
SAUER	11.0333	10.0250	10.3030	1.7800	0.0033
PR N	53.1930	90.3765	24.3158	14.0930	1.3110
PR O	1.5373	.8510	.8203	1.9070	1.4380
GELOP	44.0593	37.3330	33.0000	36.0330	75.3030
GELON	753.2333	668.0033	380.0000	518.0033	1233.0000
P N	280.3330	219.3330	121.0333	378.0330	743.0309
P P	27.8033	51.2000	23.0008	34.0330	17.0033
P H	8.6930	8.6730	8.4233	7.4503	7.1400
SAV	2.5533	2.5000	2.4600	2.6930	3.3330
NITRA	456.0330	470.0000	403.0000	410.0300	56.0030
NITRI	14.3033	15.4000	16.2600	21.7030	0.0350
AMMON	43.0338	320.3200	343.0033	978.0330	3703.3003
PHAT	44.3003	72.2333	79.0033	251.0330	762.3338
GES P	137.2037	140.0038	147.0000	335.3030	463.0300
GELFE	26.0003	25.2033	28.5030	16.5033	53.5330
P FE	72.8033	42.5038	84.0030	45.0000	40.0333
SI 00	1.0530	1.1533	1.6530	1.7333	3.3033
GES E	100.0333	44.3300	17.4300	2.1033	0.3363
V G	100.0333	65.3333	24.3000	3.4033	0.0033
BION	3.2133	5.4138	7.4430	1.1100	.1300
CYANO	0.0833	.0183	.4000	0.0008	.0270
CLORO	1.4310	4.0353	7.7553	1.5810	.2433
KONJU	0.3330	3.3333	0.0030	.0850	1.3303
CRYSO	0.0338	0.0330	0.8030	0.3338	0.3330
DIATO	0.3300	0.0330	.0370	0.0380	.0243
CRYPT	1.5340	.0840	.5883	.2870	0.6710

99999

ROTSEE 14. 7.69.

I	0.0307	1.0000	2.5000	5.0000	14.0007
TEMP	18.1300	18.3033	14.2330	14.0333	7.3000
KAPPA	197.3331	199.3330	200.5300	260.0310	324.1330
MF	1803.3330	1183.3333	1151.0000	1324.0000	3702.3033
PLAT	8450.3830	4493.0000	6143.0303	3443.3300	4210.3040
SAUER	11.7030	11.7033	13.3830	.1330	0.3300
PR N	122.4930	72.2460	17.4050	4.0433	1.0340
PR O	1.7410	1.4453	1.5740	1.7430	1.1663
GELOP	32.0033	25.0830	25.0000	29.0330	29.3300
GELON	673.3303	500.3000	470.0333	740.0030	442.0003
P N	210.0333	200.4008	295.0000	270.0330	426.3140
P P	35.0030	41.0330	43.3333	56.0330	41.6300
P H	8.3030	8.3780	9.3300	7.5130	7.1400
SAV	1.5450	1.7233	1.1030	1.7033	3.4400
NITRA	340.3030	390.8030	403.3333	123.0338	0.0300
NITRI	12.0030	12.2000	13.0420	42.5033	0.3330
AMMON	54.3333	150.0300	91.0330	1000.0030	4462.0000
PHAT	4.3300	3.7000	4.5003	244.3033	444.0000
GES P	71.0330	70.0333	91.0330	323.0330	916.3330
GELFE	30.4000	32.0330	31.5000	15.7033	53.4200
P FE	155.3033	142.1330	145.3033	135.7333	142.3800
SI 00	2.4033	2.3300	2.4300	2.0510	5.1000
GES E	108.0333	26.0330	5.0830	.3330	0.3000
V G	100.0333	30.0830	5.0000	.0033	0.3300
BION	5.5500	5.2300	4.5030	1.6333	.2600
CYANO	4.0033	0.3300	0.0000	0.0333	.0200
CLORO	5.2073	5.0333	4.5600	3.4833	.2040
KONJU	0.3330	0.0030	0.3333	8.0000	0.3030
CRYSO	0.0030	0.3300	0.0000	8.0000	-0.0003
DIATO	0.8333	.0840	0.0430	.3120	0.0000
CRYPT	.3133	.1910	.3130	0.0833	8.0300

99999

ROTSEE 14. 8.69.

I	0.3000	1.0000	2.5000	5.0000	14.0000
TEMP	23.5833	23.4000	22.7630	13.3030	7.2000
KAPPA	183.3313	184.0330	193.0030	241.3330	343.0030
MF	1433.0333	2467.0303	1775.0000	1033.7033	3456.0008
PLAT	2720.0333	1570.3333	2603.0338	2468.3030	3373.8003
SAUER	11.5330	11.7303	11.8000	.0330	4.0330
PR N	53.3330	57.3140	24.5150	10.7359	2.5420
PR O	1.7420	1.7160	1.7030	1.7340	1.0733
GELOP	55.3033	14.3003	12.5000	18.0300	33.3300
GELON	240.3333	140.0338	150.0050	510.3830	3440.3008
P N	254.3333	235.0030	253.0000	403.3330	540.3003
P P	25.3833	21.0000	24.4000	48.4030	27.0000
P H	8.3833	8.4300	9.0400	7.3433	6.3208
SAV	1.3030	1.3700	1.5400	2.7470	3.6480
NITRA	4.0330	8.0333	3.0033	35.4333	10.0000
NITRI	.4330	0.0833	3.0330	10.2330	0.0000
AMMON	6.0330	70.0030	10.0403	520.0330	5080.3330
PHAT	2.7033	1.7300	2.0400	28.0230	46.0030
GES P	42.3090	34.0330	41.2348	44.0328	927.0300
GELFE	11.4300	13.3000	22.4380	13.6233	126.3030
P FE	57.4932	40.0033	35.3000	69.2330	129.4000
SI 00	.7333	.4430	.4008	3.5430	5.3300
GES E	100.0033	15.3030	4.0033	1.0300	0.0000
V G	100.3030	45.3300	13.0000	1.4030	0.0000
BION	7.5133	4.2420	4.5308	14.4330	1.6503
CYANO	.0530	.1020	.0408	.3300	0.0030
CLORO	2.3450	.4640	1.3018	1.8630	1.4218
KONJU	.1570	.0750	.1010	.0040	.3571
CRYSO	.0443	.0640	.3470	.0410	0.0300
DIATO	2.7070	.6951	1.1780	.2830	.1680
CRYPT	.2350	.2440	.2120	11.9150	0.0000

99999

ROTSEE 11. 9.69.

I	0.3000	1.0000	2.5000	5.0038	14.7000
TEMP	17.3330	17.3000	17.0030	15.4330	7.3000
KAPPA	174.0030	173.8300	187.0000	235.0330	370.0000
MF	739.8030	419.0800	450.3030	544.0330	1960.3303
PLAT	3470.0300	3620.8000	2503.0000	1560.4030	1068.3300
SAUER	35.4335	16.7033	4.2083	.4730	0.0000
PR N	47.5430	58.5450	64.8440	9.3270	.4523
PR O	1.5543	1.7823	1.9410	1.3550	.4763
GELOP	4.0333	4.3330	2.0338	14.0338	48.3000
GELON	233.3333	270.8033	273.0000	540.0330	240.0308
P N	130.3433	140.0333	239.0000	350.0330	548.0033
P P	32.3333	23.9333	31.0030	45.7038	25.0300
P H	9.2333	9.1930	8.0508	7.5030	6.5900
SAV	1.3330	1.2800	1.7540	2.3130	4.3300
NITRA	40.3330	48.3330	20.4130	44.0030	0.0300
NITRI	2.2230	1.8033	7.4008	12.8030	3.0330
AMMON	0.3333	0.3300	18.0000	200.0030	6648.0300
PHAT	2.2333	2.1000	1.9008	3.6070	4118.8003
GES P	43.3003	41.0303	43.8000	61.0030	1235.0000
GELFE	18.5330	14.3330	4.0030	4.5333	132.0040
P FE	45.1033	52.5337	53.8000	51.1833	173.6000
SI 00	.7400	.7500	.4500	1.1530	4.2508
GES E	100.3333	16.3033	7.0030	1.5030	0.3000
V G	100.0333	56.4337	15.0300	2.2033	0.0300
BION	12.5330	10.2533	3.5300	17.6600	.8500
CYANO	.4133	1.3433	.0258	1.3100	0.4030
CLORO	.7673	.3110	.1380	.9450	.6503
KONJU	.0433	.0078	.1338	.0230	0.0000
CRYSO	.3120	1.0240	.5480	.9730	0.3000
DIATO	.3140	.0022	.4538	.0320	0.3380
CRYPT	.4530	.1960	.4260	0.4106	0.0008

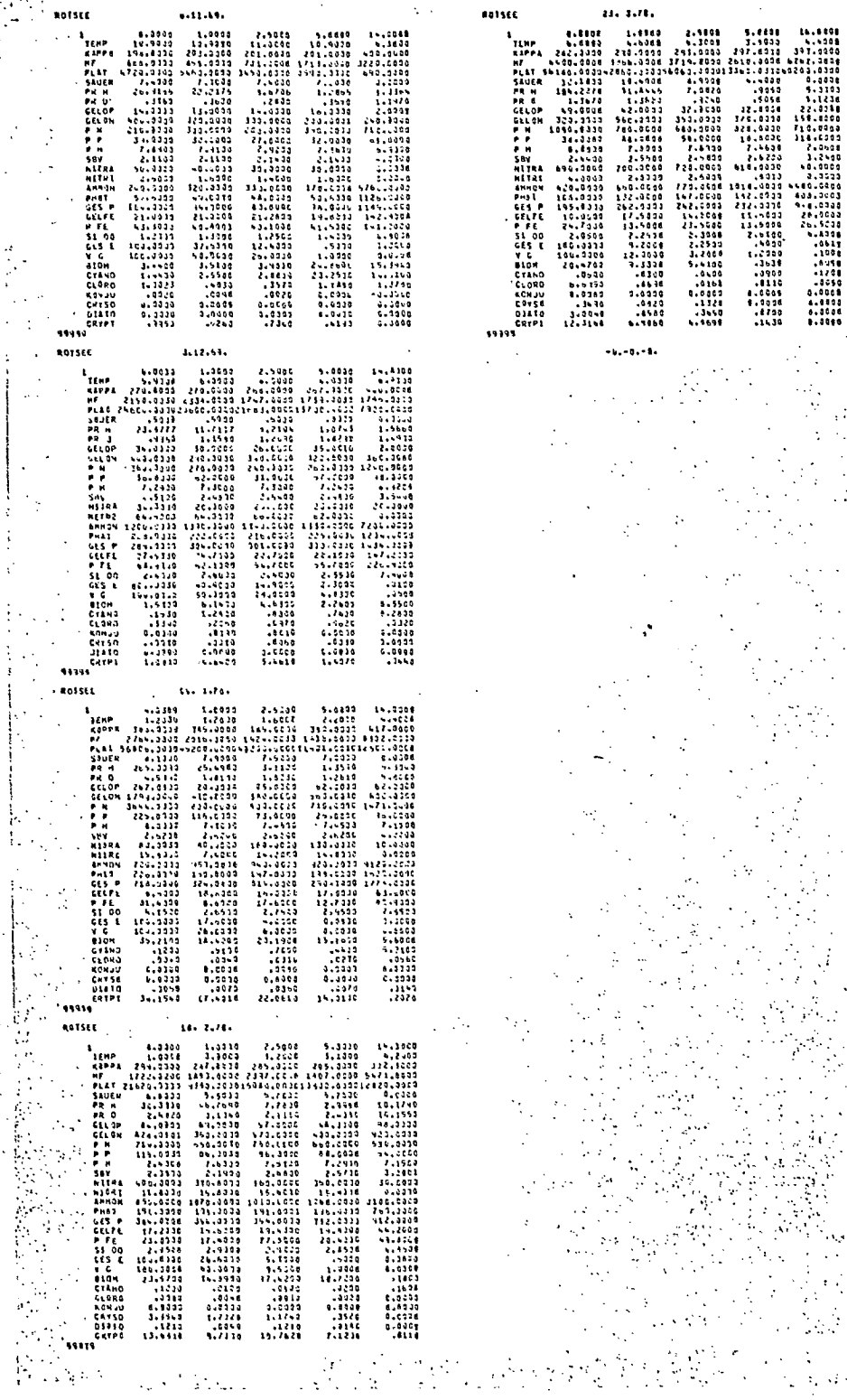
99999

ROTSEE 14.10.69.

I	0.1200	1.0000	2.5000	5.0000	16.3070
TEMP	15.4300	15.4300	15.5030	14.2033	6.8060
KAPPA	205.3230	205.3033	204.0300	263.0330	387.0000
MF	1075.0328	1173.0032	1103.0000	967.0333	4470.0308
PLAT	1750.0300	1303.0000	1020.0000	1350.3300	300.0030
SAUER	4.4333	4.5003	4.4000	4.3330	0.3333
PR N	55.2432	68.9445	36.3734	4.6511	1.4934
PR O	1.2330	1.1910	.6430	.4410	.3376
GELOP	4.3338	4.0030	4.3010	7.3333	48.0000
GELON	230.3300	340.0300	323.0000	213.0333	430.0300
P N	320.0308	303.0303	240.0030	248.3378	480.0300
P P	22.0000	27.3033	32.0003	31.3233	44.0000
P H	8.1033	8.2678	8.3330	8.2730	6.4130
SAV	1.7830	1.4230	1.5333	1.4300	4.2500
NITRA	10.0300	10.0000	10.0000	20.0330	3.3333
NITRI	.4010	.4033	.4033	.4033	0.0300
AMMON	0.0330	30.0030	8.0007	10.0030	8140.3300
PHAT	7.3333	4.3300	4.3330	5.6330	1333.3333
GES P	64.3333	48.0030	47.0033	44.0030	1458.3330
GELFE	21.2333	17.8330	10.3030	4.4378	152.7873
P FE	20.7333	21.4333	47.4028	32.0330	93.2333
SI 00	.8838	.4503	.4300	.3433	7.0038
GES E	100.0330	33.8000	32.0330	1.2030	.3337
V G	100.3333	40.0333	25.0030	8.2033	.1300
BION	5.7433	4.6733	4.3430	3.2330	.4133
CYANO	1.3400	1.2700	.0630	.4134	.0108
CLORO	1.0633	.4493	.8730	.4443	.4750
KONJU	.0370	.1010	.0010	.0438	.0058
CRYSO	0.3333	0.3330	0.0033	0.0330	0.0300
DIATO	.1332	.1203	.7170	0.0330	0.3303
CRYPT	2.4770	1.4300	2.4560	1.2030	.0170

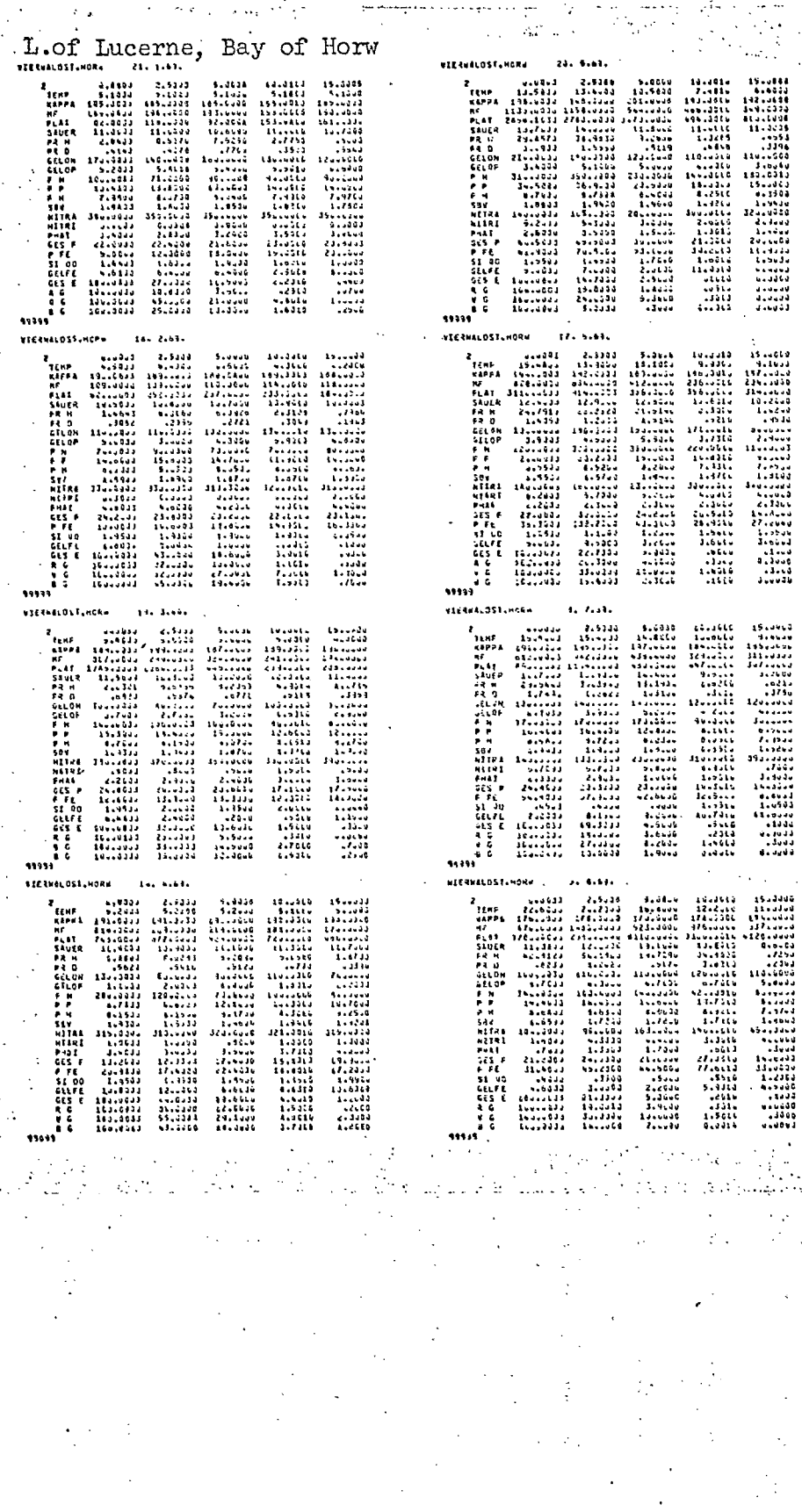
99999

(529)



(530)

L.of Lucerne, Bay of Horw



(531)

L.of Lucerne, Bay of Horw

VIERWALDST.HORW 1. 9.31.

Z					
TEMP					
KAPPA					
AF					
FLAT					
SAUER					
PR H					
PR O					
GELON					
GELOP					
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P P					
P H					
SBV					
NITRA					
NITRI					
PHAT					
SES P					
P FE					
SI OO					
GELFE					
GES E					
N G					
V G					
B G					

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VIERWALDST.HORW 6. 1.70.

Z					
TEMP					
KAPPA					
AF					
FLAT					
SAUER					
PR H					
PR O					
GELON					
GELOP					
P N					
P P					
P H					
SBV					
NITRA					
NITRI					
PHAT					
SES P					
P FE					
SI OO					
GELFE					
GES E					
N G					
V G					
B G					

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VIERWALDST.HORW 7.10.69.

Z					
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KAPPA					
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FLAT					
SAUER					
PR H					
PR O					
GELON					
GELOP					
P N					
P P					
P H					
SBV					
NITRA					
NITRI					
PHAT					
SES P					
P FE					
SI OO					
GELFE					
GES E					
N G					
V G					
B G					

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VIERWALDST.HORW 24. 2.70.

Z					
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KAPPA					
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FLAT					
SAUER					
PR H					
PR O					
GELON					
GELOP					
P N					
P P					
P H					
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PHAT					
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GELFE					
GES E					
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VIERWALDST.HORW 9.11.69.

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P H					
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GELFE					
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VIERWALDST.HORW 2.12.69.

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PR O					
GELON					
GELOP					
P N					
P P					
P H					
SBV					
NITRA					
NITRI					
PHAT					
SES P					
P FE					
SI OO					
GELFE					
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Curriculum Vitae

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1960-1962	Secondary-school teacher instruction St.Gallen
1962	Secondary-school teacher degree for Mathematics and Natural Sciences, St.Gallen
1962-1967	Student at the faculty for Natural Sciences of the Swiss Federal Institute of Technology (ETH), Zurich
1967	Final diploma of Division X for Biology, diploma work in Hydrobiology
1967-1971	Assistant and doctorand at the Hydrobiological Division of the Federal Institute for Water Supply, Sewage Treatment, and Water Protection (EAWAG) of the Swiss Federal Institute of Technology (ETH), Zurich
1969	Diploma for higher teaching at the Swiss Federal Institute of Technology, Zurich