PHYSICO-CHEMICAL ENVIRONMENT, PHYTOPLANKTON BIOMASS AND PRODUCTION IN OLIGO-TROPHIC, SOFTWATER LAKE KALGAARD, DENMARK

Morten SØNDERGAARD & Kaj SAND-JENSEN

Botanical Institute University of Aarhus, 68 Nordlandsvej, DK 8240 Risskov; Freshwater Biological Laboratory University of Copenhagen, 51 Helsingørsgade DK 3400 Hillerød, Denmark.

Received January 5, 1978

Keywords: Oligotrophic Lake, water chemistry, phytoplankton, biomass, primary production

Abstract

Water chemistry of Lake Kalgaard in 1976-77 was characterized by low concentrations of total-CO2 and inorganic nutrients. The ionic composition resembled that of precipitation (Na > Ca > Mg > K and Cl> SO₄> HCO₃). The seasonal pattern of total-CO₂ and PO4 was regulated by internal processes and maximum concentrations as a result of decomposition processes occurred during summer stagnation. NO3 concentrations showed the opposite pattern and were relatively high from late autumn through spring and were extremely low during summer. Total-P and PO4 increased during summer due to release from the sediment. The phytoplankton biomass of surface water was low. The water chemistry suggested a shift from N-limitation of phytoplankton during summer to P-limitation at other seasons. Maximum algal concentrations occurred at 6 m during summer, probably due to a supply of nutrients (especially NH₄) from deeper layers. Phytoplankton productivity was often bimodal, with an upper maximum at depths of 0 or 2 m and a second maximum at 6 m.

Introduction

Nutrient dynamics and phytoplankton production has been investigated in many alkaline, eutrophic lakes in Denmark (reviewed by Jørgensen *et al.*, 1977; Riemann & Mathiesen, 1977), but only a few investigations from softwater lakes exist. Nygaard (1965) made an extensive study of the carbon dioxide system in softwater Grane Langsø, in which he emphasized that alternations between maxima and minima of total- CO_2 were related to

Dr. W. Junk b.v. Publishers - The Hague, The Netherlands

phytoplankton production. Investigations in softwater Canadian Shield lakes have demonstrated that N and especially P regulate the phytoplankton biomass (Schindler & Fee, 1973). In artificially enriched (N, P) lakes CO_2 may be an important factor limiting the rate of production, but its effect on the phytoplankton biomass was negligible.

The present study describes the physico-chemical environment and the biomass and production of phytoplankton in softwater, oligotrophic Lake Kalgaard, Denmark. Special emphasis has been placed on seasonal variations of N, P and total-CO₂ as related to phytoplankton biomass and production. Earlier papers have described the production and physiological adaptation of the extensive macrophyte vegetation of isoetid species (Sand-Jensen & Søndergaard, 1978, Sand-Jensen, 1978).

Lake description

Lake Kalgaard is a small lake (10.5 ha) situated in central Jutland $(56^{\circ} 1'\text{N}, 9^{\circ} 27'30''\text{E}, 74.7 \text{ m}$ above sea level). Maximum depth is 11 m and mean depth 4.6 m (Fig. 1). The water column between depths of 0 and 6 m, which is approximately equal to the epilimnion during summer (Fig. 2), is in contact with about 62% of the bottom area and contains about 85% of the lake volume. The lake formed as a kettle in a subglacial stream trench during the Baltic Glaciation. The geological substrata are carbonate-poor deposits of sand and gravel mixed with morainic material (Hansen, 1958).



Fig. 1. Morphometric map of Lake Kalgaard. Contour intervals measured by T. Høy, 1974. Contour interval is 1 m. Sampling station indicated (x).

To the west and south-west the lake is sourrounded by low hills covered by heath vegetation. These provide little protection from the prevailing winds blowing from the west and south-west. The eastern and southern shores are covered by a coniferous plantation.

Materials and methods

Sampling

Seasonal variations of temperature, transparency, and nutrients (N, P) were followed during 1976 and 1977. Total-CO₂, pH, phytoplankton production, and major elements (Na, Ca, Mg, K, Fe, Mn, Cl) were determined during 1976, and chlorophyll a during 1977 only. All water analyses were duplicated except for chlorophyll a and total-P, which were analyzed in triplicate and quadruplicate, respectively. Samples were taken at noon at 5 or 6 depth with a perspex Ruttner water sampler at the deepest part of the lake (Fig. 1).

Methods

The temperature of water samples were measured at once with a thermometer accurate to 0.1° C. For pH and total-CO₂ measurements separate subsample were transferred to darkened Pyrex bottles (130 ml, completely filled and capped) and measured on the day of collection. A vacuum distillation technique (Krogh & Rehberg, 1931) was used for the total-CO₂ analysis due to its high sensitivity. The proportions of free CO₂ and of HCO₃ were calculated from total-CO₂, ionic strength, pH, and temperature according to Rebsdorf (1972). The amount of free CO_2 in equilibrium with a CO_2 content of 0.033 vol. % of the atmosphere was calculated at the actual temperatures according to Hutchinson (1957, p. 654).

Samples for nutrient determinations were brought to the laboratory in acid-washed polythene bottles. The samples were filtered (Whatman GF/C filters), stored at 4°C in the dark and analyzed the following day. Riemann & Schierup (1978) have recently shown that unpredictable changes in NH4 concentrations may occur in samples stored for only a few hours. Therefore, NH₄ samples collected during 1977 were treated immediately. A test performed 24 October 1977 showed an increase of NH4 concentrations by about 20 μ g N l⁻¹ when filtration and addition of reagents were put off until the next day. NH4 analyses from 1976 are probably too high, since these samples were stored before analysis. To increase the accuracy of the PO₄ measurements the spectrophotometrical readings were made in 4 cm cuvettes. The analyses accord with the following methods: PO4 (Murphy & Riley, 1962), total-P (Koroleff, 1970), NH4 (Solórzano, 1969), NO3 (Crosby, 1967; Strickland & Parsons, 1968), Cl and O₂ (Golterman, 1969). Na, Ca, Mg, K, Fe, Mn were measured by Atomic Absorption Spectrophotometry. Chlorophyll a was extracted in methanol according to Riemann (1976), and calculated without correction for degradation products.

Phytoplankton production was measured by the ¹⁴Cmethod using GM-counting (Steemann Nielsen & Hansen, 1959, and Goldman et al., 1969). Samples were taken from 5 depths along with parallel samples for total-CO₂ determination and were transferred without air-contact to Jena glass bottles (130 ml). Dark-fixation was measured at the upper and lower depths. Incubation was from midday to sunset. To prevent overestimating production due to an effect of carrier carbon in the CO₂poor water (Nygaard, 1968) only 100 μ l of Na¹⁴CO₃ + NaH¹²CO₃ (20 μ Ci ml⁻¹ and 2.2 μ mol total -CO₂ ml⁻¹) were added to each bottle. This addition normally increased total-CO₂ in the bottles by less than 3%. The reduction of the initial content of total-CO₂ in the bottles during incubation was 8% at a maximum and normally much lower.

Results and discussion

Water economy

The lake is a seepage lake without surface in- and outlets. A small, diffuse inlet at a water depth of 0.5 m is visible



Fig. 2. Depth-time isotherms (°C) during 1976 and 1977. Ice cover drawn to scale.

J

1977

J

М

Period	Р	e ^a	Ew	₽-E _w	۵W	
1 April - 30 Sept.	193	519	604	-411	-400	
l Oct 31 March	445	69	74	374	330	
l April - 30 Sept.	331	463	538	-207	-190	

at the west bank. During 1976-77 this inlet was dry from May to September, corresponding to the period in which the potential evaporation surpasses the precipitation. The water economy is much influenced by the balance between precipitation and evaporation, which creates a characteristically fluctuating water level. In Table 1 precipitation, evaporation, and changes in water level are compared for two summer periods and one winter period of 1976-77. The precipitation (P) was measured at the meteorological stations (Danish Meteorological Institute) in Bryrup 4 km from the lake. The potential evaporation (Ep) is a mean of monthly values measured at 7 stations in central Jutland (Gregersen, 1977, 1978). The evaporation from the lake surface (Ew) has been estimated by multiplying by the factor 1.16 according to Kristensen (1971). The water level in Lake Kalgaard was highest in April and lowest in October. The changes in water level (ΔW) agreed well with the differences between precipitation and evaporation (Ew), which indicate that the groundwater supply was small in proportion to the precipitation (Table 1). Nygaard (1965) reached a similar conclusion for Lake Grane Langsø, situated 200 m north of Lake Kalgaard.

Temperature and major elements

Lake Kalgaard is dimictic (Fig. 2). Summer stratification lasts approximately four months (mid-May to mid-September) during which the deeper layers become anoxic and H_2S develops (Table 2). The period of ice-cover is variable but according to observations from several years may occur irregularly from mid-December to early April. A well defined hypolimnion does not exist. During summer the bottom temperatures increase from about 8-9°C to about 13-14°C. In agreement with the chemical analyses (see below) this warming must be due to a windinduced transport and not to direct solar heating, since the transparency is about 4-6 m (Figs. 8 and 10). Water temperatures during the dry, hot summer of 1976 were appreciably higher than during 1977.

The distribution of major elements is shown in Table 3. Concentrations were low, and the specific conductance was only 65-67 μ S cm⁻¹ (20°C). Apart from Fe, Mn and HCO₃ all the elements had small seasonal and vertical fluctuations. From spring (19 April) to summer (16 August) the concentrations of Na and Cl increased. These elements are abundant compared to their small utilization in algal growth and they are little affected by changing redox conditions of the sediments (Wetzel, 1975). Their increase corresponds with the reduction of lake volume due to evaporation (Table I). Fe and Mn are released from sediments under anoxic conditions. These

Table 2. Ammonia and oxygen in Lake Kalgaard during summer stratification of 1976.

Depth (m)	NH4-N	0 ₂ (mg 1 ⁻¹)		
	29 July	16 August	29 July	
0	83	21	8.9	
2	46	22	8.9	
4	38	73	8.9	
6	29	28	8.7	
9	307+)	62 ⁺⁾	0	

+) H₂S development

The relative amounts (weight basis) of cations in surface waters were: Na > Ca > Mg > K > Fe > Mn, and of anions: $Cl > SO_4 > HCO_3$. A comparison with the ionic composition of rain water (Table 3) shows that the lake water is concentrated by a factor of about 2 for Na, Mg, K and Cl, and about 3 for Ca. SO₄ concentrations were about equal in rain and lake water, and HCO₃ does not occur in rain water due to the low pH (4.3-4.4, Jørgensen, 1974). These results suggest that (1) the lake contains rain water in a concentrated state due to evaporation from the lake and from the terrestrial drainage, (2) Ca and HCO₃ become selectively increased due to ionic exchanges with the colloidal systems of the soil and lake mud (Rodhe, 1949), and (3) SO_4 is not concentrated like the other elements because of reduction processes under anaerobic conditions causing a loss of H₂S to the atmosphere or of FeS to the sediments.

The ionic composition of Lake Kalgaard resembles that of neighbouring Lake Grane Langsø (Nygaard, 1965) and of North German lakes (Ohle, 1955). The dominance of Na and Cl is no doubt a consequence of the supply of airborn ions from the North-Sea (about 90 km from the lake) and of the small influence of the well leached, sandy subsoil in the drainage area.

pH and total-CO2

The seasonal variation of pH in surface and bottom waters is shown in Fig. 3. The surface water was near neutrality (6.5-7.0), with the higher values during the summer. A brief extreme maximum (pH 8.3) occurred on a calm day (19 July). During the first period of thermal stratification (until 14 June) pH decreased to 5.6 at 9 m parallel with an increase in total-CO₂ (Fig. 4). In spite of continuously increasing total-CO₂, pH increased to 6.1 in late July. It appears from Tables 2 and 3 that this increase can be explained by an increased bicarbonate alkalinity due to liberation of ferrous, ammonium, and manganous bicarbonate from the sediment during anoxic conditions (Hutchinson, 1957, p. 686). This explanation is supported by the subsequent decrease of these elements and of pH on 16 August.

Total-CO₂ in the surface water was 0.03-0.09 mM (Fig. 4), confirming the classification of Lake Kalgaard as a softwater lake. The minimum was found beneath thin,

Kalga	ard	Na	Ca	Mg	К	Fe*	Mn*	Cl	so ₄ **	нсо _з
Date	Depth(m)				(m	g 1 ⁻¹)			· · · · · · · · · · · · · · · · · · ·	
13.1	0	6.65	3.44	0.91	0.84	0.05	0.00	11.7		1.34
19.4	0 1.3 2.6 5.2	6.50 6.50 6.50 6.50	2.64 2.78 2.80 3.45	0.91 0.91 0.91 0.91	0.84 0.84 0.84 0.84	$0.04 \\ 0.04 \\ 0.04 \\ 0.04 \\ 0.04$	0.00 0.00 0.00 0.00	11.7 11.7 11.7 11.7		2.07
	8.5	6.50	3.62	0.91	0.84	0.04	0.00	11.7		2.07
29.7 0 2 4 6 9	0 2 4 6	6.90 6.85 6.85 6.70	3.00 2.98 2.84 2.78	0.84 0.83 0.84 0.80	0.85 0.85 0.84 0.85	0.00 0.00 0.00 0.00	0.00 0.00 0.00 0.00	12.1 12.1 11.8 11.8	6.6	2.80
	9	6.65	2.76	0.89	1.03	0.90	0.15	11.7		12.63
16.8 0 2 4 6 9	0 2 4	7.10 6.70 6.60	3.32 3.32 3.30	1.10 1.10 1.20	0.80 0.79 0.81	0.00 0.00 0.00	0.00 0.00 0.00	13.3 12.3 12.2		3.35
	6 9	6.50 6.70	3.26 2.98	1.00	0.81 0.82	0.00 0.01	0.01 0.01	12.1 12.2		5.73
Rain'	* *	3.76	1.14	0.44	0.44			6.12	6.73	0

Table 3. Major elements in Lake Kalgaard during 1976 and in rain water.

- * Detection levels for Mn and Fe were 0.002 and 0.005 mg 1⁻¹, respectively.
- ** Calculated on the assumption that meq cations l^{-1} is equal to meq anions l^{-1} (Nygaard 1965).

*** Mean valves for the area during 1970-1974 (Jørgensen 1974).

transparent ice in late February after the lake had been open to the atmosphere in January. The maximum occurred just before autumn circulation in September. Total- CO_2 increased during summer stratification, both in surface waters (from 0.05 mM in May to 0.08 mM in August) and in bottom layers (0.05 mM to 0.60 mM). Until late July there was a well defined boundary between epilimnion and deeper layers defined by the 0.06 mM isoline at 6 m depth. Afterwards the total- CO_2 that had accumulated in the bottom layers gradually was mixed

into the epilimnion. The depth gradient was established again after mid-December under ice and heavy snow cover, which reduced photosynthetic uptake.

The concentration of free CO_2 in the surface water varied between periods of subsaturation (January-March 1976, July 1976) and supersaturation (August 1976-February 1977, Fig. 5). The quantitative relations of CO_2 exchange between the atmosphere and the lake are unknown. However, an invasion of CO_2 may occur especially during the periods of maximum productivity in



Fig. 3. Seasonal variation of pH in surface water (•—•) and at 9 m (0----0) from January 1976 to February 1977. Periods of ice cover and summer stratification are indicated.

July when about 12-15% of the pool of total-CO₂ in the epilimnion is assimilated in daily gross photosynthesis. The pool of total-CO₂ in the lake increased from 216 kg C in January to 630 kg C in August (Fig. 6). The increase of total-CO₂ especially occurred during July, primarily due to bottom-accumulations. The CO₂ increase may be ascribed to the following sequence of processes: (1) uptake from the atmosphere, (2) assimilation by algae, and (3) release from decaying, sedimented algae in the bottom waters. The increase of total- CO_2 in the lake was only a small part of the phytoplankton production from January to August (about 1900 kg C), thus supporting the suggestion that respiration alone may account for the CO_2 increase. A release of CO_2 to the atmosphere probably occurs during autumn circulation when the CO_2 rich bottom water was mixed into the epilimnion. Thus the pool of total- CO_2 in the lake decreased from 630 kg C (19 September) to 370 kg C (18 October).

Phosphorus and nitrogen

Seasonal and vertical distribution of inorganic P and N are given in Table 2 and Figs. 7, 8 and 9. As discussed already, absolute concentrations of NH₄ from 1976 are too high but they are presented for comparison of relative differences, which are probably real.

Inorganic P and N concentrations were low. During the hot summer of 1976 PO₄ was 10-17 μ g P l⁻¹ but 1-7 μ g P l⁻¹ during 1977 (Fig. 7A). Apart from a single measurement in the bottom layers during winter stratification (February 1977), PO₄ could not be detected between late



Fig. 4. Depth isopleths of total-CO₂ (mM) from January 1976 to February 1977. Ice cover drawn to scale.



Fig. 5. Seasonal variation of free CO_2 in the surface water ($\bullet - \bullet$) and free CO_2 in equilibrium with the atmosphere at the actual water temperatures ($\circ - - - \circ$) from January 1976 to February 1977. Ice cover and summer stratification are indicated.

autumn and spring. This is entirely different from the pattern normally registered in deep, dimictic oligotrophic and eutrophic lakes of low water renewal (e.g. Schindler & Nighswander, 1970; Jonasson *et al.*, 1974). The higher PO₄ concentrations are more usually found in winter and spring, and values are close to zero during summer. NO₃ showed the expected seasonal pattern (Fig. 7B). Maximum concentrations (80-133 μ g N l⁻¹) occurred from autumn to early spring, and low values were found during summer (2-10 μ g N l⁻¹). PO₄ and NO₃ concentrations in the deeper layers (8-10 m) were only slightly different from surface concentrations.

NH₄ showed a variable seasonal and vertical distribution during 1977 (Fig. 8). Undetectable levels occurred in April. During summer a maximum occurred at 0 m on several occasions (16 May, 6 June, 18 July, 15 August),



Fig. 6. Seasonal variation of total inorganic carbon (total-CO₂) in the lake from January 1976 to February 1977. Ice cover and summer stratification are indicated.

and a second maximum developed in the bottom layers (6 and 27 June, 18 July, 15 August). It is apparent that the NH₄ accumulated in the bottom layers occasionally is mixed up into the layers above (18 July, 5 September) a phenomenon also indicated during 1976 (16 August, Table 2). In between the surface and bottom maximum of NH₄ concentrations were often zero.

 NH_4 is generated by bacterial decomposition of organic matter and from zooplankton excretion. At depths, from 2 to 8 m the NH_4 released is quickly taken up by algae or nitrified. The bottom accumulation is a common phenomenon explained by decomposition of sedimented organic matter. The NH_4 maximum at the surface is not easily understood but may be related to increased zooplankton activity, decreased algal uptake or a supply from the atmosphere.

The contents of total-P and PO₄ in the lake showed a characteristic increase from late April to August-September 1977 and afterwards declined during autumn circulation (Fig. 9). The increases from minimum to maximum values amount to 8.7 kg total-P and 3.4 kg PO₄-P. The phosphate increases are probably due to internal processes i.e., release from sediments-since the external sources are small. As previously discussed, the subsurface supply in ground water during the summer period can be assumed negligible. The approximate supply by precipitation and dry fallout, calculated from Swedish investigations, is 0.3 kg P (Tamm, 1958, 0.1 kg P ha⁻¹y⁻¹). The phosphate release may occur from both aerobic and anaerobic sediments. The aerobic release is probably very significant because of the greater part of the lake bottom over which it may occur. A significant aerobic PO4 release agrees with the similar PO₄ concentrations observed in the epilimnion and in bottom layers (Fig. 7). Kamp-Nielsen (1974) also found an aerobic and anaerobic PO₄ release of approximately equal size in the chemically similar Lake Grane Langsø. These results may be due to the fact that the major PO₄ fraction in sediments from deeper parts of Grane Langsø and Kalgaard is in organic materials, whereas the amount of Fe-bound PO4 released under anoxic conditions is very small (Kamp-Nielsen, 1974; Jacobsen, 1976). Later experiments by Kamp-Nielsen (1975) in Lake Esrom demonstrated that PO₄ was taken up by the sediment at low temperatures due to sorption processes. At temperatures above 7-10°C liberation of PO₄ increased exponentially with temperatures due to microbial processes. This kinetic could explain the observed increases of total-P and PO₄ in Lake Kalgaard during summer, the higher PO₄ concentrations obtained



Fig. 7. Seasonal variations of mean concentrations of PO₄ (A) and NO₃ (B) at depths of 0-6 m (0----0) and 8-10 m (0----0) during 1976-1977. Measurements were taken at 0, 2, 4, 6, 8 and 10 m. Summer stratification indicated by horizontal lines.

during the hot summer of 1976 and the decline of PO₄ to undetectable values at low temperatures after autumn overturn. The decrease of total-P after autumn overturn may be related to loss of algae by sedimentation.

The importance of aerobic phosphate release in oligotrophic, softwater lakes is supported by data from two shallow Canadian Shield lakes (Armstrong & Schindler, 1971). The nutrient release had little to do with the oxygen regime, since one lake had an anaerobic hypolimnion and the other lake no hypolimnion at all. The high ratio of sediment area to lake volume of shallow lakes was suggested to be more important. The calculated net release during summer stratification in Lake Kalgaard (0.7 mg P m⁻²day⁻¹) resembles that in the two Canadian lakes (0.2 mg P and 1.3 mg P m⁻²day⁻¹, Lake 303 and 304) and the values reported by Cooke *et al.* (1977) from two mesotrophic-eutrophic lakes (0.7-2.7 mg P m⁻²day⁻¹).

Phytoplankton biomass and production

Phytoplankton biomass was measured as chlorophyll *a* during 1977 (Fig. 8). The chlorophyll *a* concentrations of the surface waters (0,2 and 4 m) were less than 10 μ g l⁻¹,



Fig. 8. Vertical distribution of chlorophyll *a* (•—••) and NH₄ (o----o) during 1977. Secchi disc transparency is indicated.

apart from a single maximum of about $45 \ \mu g \ l^{-1}$ on 5 September. The maximum values in April and in July-September coincide with the lower values of Secchi disc transparency. The pattern of transparency and phytoplankton production during 1976 also indicated a spring and summer maximum of phytoplankton biomass (Fig. 10). During the summer period a very conspicuous biomass developed at 6 m (Fig. 8). On 15 August the chlorophyll *a* concentration was 68 $\mu g \ l^{-1}$ at 6 m compared with $5 \ \mu g \ l^{-1}$ at the surface. The populations at 6 m were dominated by the blue-green algae *Coelosphaerium naegelianum* Ungar and the green flagellate *Gonyostomum semen* (Ehr.) Diesing. During winter and spring, diatoms and especially chrysophyceans (Dinobryon, Mallomonas, Uroglena) were more conspicuous. A similar biomass maximum probably developed during 1976, as suggested by the production profiles (Fig. 10, and below). The high chlorophyll a concentrations in the entire water column 5 September were formed by the algal species previously present only at 6 m. Therefore, the increasing concentrations during the period 15 August - 5 September can be explained by an upward transport of algae as the thermocline at the same period was lowered from about 5 m to 7 m (Fig. 2). In addition, growth must have continued



Fig. 9. Content of total-P (\bullet) and PO₄-P (\bullet ---- \bullet) in the lake during 1977.



Fig. 10. Vertical distribution of phytoplankton production during 1976. The integral production per unit of surface area (mg C $m^{-2}day^{-1}$) and the transparency are shown.

since the maximum at 6 m was still present and the total amount of chlorophyll a in the lake increased from 9 to 26 kg.

The seasonal and vertical distribution of the phytoplankton biomass is much influenced by the availability of inorganic N and P. Between late autumn and spring nitrate was relatively abundant, whereas PO4 was undetectable and thus probably the major limiting nutrient (Fig. 7). During summer stratification NO₃ became scarce, NH4 was often undetectable between 2 and 8 m, and PO₄ increased although still present at low levels (Figs. 7 and 8). In view of the greater demand of growing algae for N than for P (N/P weight ratio of about 10/ I) N limitation during summer is suggested. Transfer of NH4 from the bottom waters into the photic zone might account for the observed biomass maximum at a depth of 6 m. Transfer of PO₄ is probably less significant, since its vertical gradient is small compared with that of NH₄ (Figs. 7 and 8). CO_2 like NH₄ accumulated in the bottom layers, where elevated Fe and Mn concentrations also were registered (Fig. 4, Table 3). Addition of CO₂, Fe and Mn together with chelating agents can increase productivity in short-term bioassay experiments (e.g. Wetzel, 1966; Sakamoto, 1971), but their importance as biomasslimiting factors seems small (Schindler, 1971; Schindler & Fee, 1973).

The depth-distribution of phytoplankton production during 1976 is presented in Fig. 10. Photoinhibition occurred at all seasons. During summer the production showed a maximum at 0 or 2 m and often a second maximum at 6 m due to increased algal concentrations. Production decreased quickly below 6 m due to increased light extinction by algae in the 6 m layer. Similar curves were described from Canadian Shield lakes (Schindler & Holmgren, 1971) which resembled Lake Kalgaard in being rather shallow, thermally stratified, with small 'hypolimnia' that were anaerobic during most of the summer and rich in at least one nutrient relative to epilimnitic waters. Further, all had euphotic zones extending well into the metalimnion. The explanation by Schindler & Holmgren (1971) of the production profiles is also applicable to Lake Kalgaard: 'The upper production maximum was probably due to optimum light conditions even though nutrients were relatively scarce; the lower maximum was the result of a more favourable nutrient regime (N, P, CO₂), which is an effective stimulant even at low light intensities'.

Production in Lake Kalgaard at 6 m is probably lightlimited and therefore much dependent on the solar radia-

tion during incubation. If the zone of high algal concentrations has a restricted vertical extension, sampling could conceivably 'hit' or 'miss' the major concentrations. Production was indeed variable at 6 m (Fig. 10). Since the production at this depth contributes much to the integral values, the calculated annual production may be somewhat inaccurate. The annual production per unit surface area was 55 g C $m^{-2}y^{-1}$ for the deepest part of the lake. Averaged over the entire lake area the production was 32 g C $m^{-2}y^{-1}$. These values agree with previous results from softwater, oligotrophic lakes in Denmark based upon relatively few determinations by the ¹⁴C method (Riemann & Mathiesen, 1977) or by the oxygen method (Nygaard, 1955). Furthermore, the summer production in Lake Kalgaard resembles those from Canadian Shield lakes showing dichotomic depth-curves of production (Schindler & Holmgren, 1971).

Summary and conclusion

Lake Kalgaard is a relatively shallow seepage lake $(z_{max} = II m, \overline{z} = 4.6 m)$. The lake is rather unsheltered and a well defined hypolimnion is absent. Although CO₂ and NH₄ accumulate in the deeper waters, a wind-induced transport of heat and solutes through the metalimnion occurs.

Chemically the lake is characterized by low concentrations of total- CO_2 and of inorganic nutrients (N, P), and by an ionic dominance of Na and Cl. The ionic composition resembles that of precipitation and is a consequence of the carbonate-poor geological substrata and the proximity to the North Sea (90 km). Total- CO_2 in the lake increased markedly during July, primarily due to bottom accumulations, and afterwards decreased from September to October, when total- CO_2 that had accumulated was mixed into the epilimnion. The changes of total- CO_2 content were ascribed to exchange with the atmosphere.

NO₃ concentrations were relatively high from late autumn through spring and dropped to extremely low values during summer. PO₄ showed the opposite pattern, being detectable only during summer. Total-P and PO₄ contents in the lake increased during summer stratification, probably due to release from sediments (calculated to about 0.7 mg P m⁻²d⁻¹). The similarity of PO₄ concentrations in the epilimnion to those in deeper, anoxic strata indicates that aerobic PO₄ release is significant. Higher PO₄ concentrations occurred during the hot summer of 1976 than in 1977, in accordance with bacterial regulation of PO₄ release. NH₄ concentrations were variable, but the vertical distribution during summer often showed a maximum at the surface, a second maximum at the bottom, and undetectable levels in between.

Chlorophyll *a* concentrations were below 10 μ g l⁻¹ in the surface waters (0-4 m) apart from a single maximum by 5 September (45 μ g l⁻¹). During summer stagnation a pronounced chlorophyll *a* maximum (up to 100 μ g l⁻¹) developed at 6 m. This maximum is explained by supply of growth-stimulating substances from deeper layers which are richer in several components (NH₄, CO₂, Fe, Mn), of which NH₄ is probably the major factor regulating biomass. Growth of algae at 6 m is possible since the euphotic zone extends well into the metalimnion, the Secchi disc transparency being about 4-6 m. Based upon the observed seasonal variations of NO₃, NH₄ and PO₄ it is suggested that N was the major factor limiting biomass during summer stratification whereas P was more important at other seasons.

The depth-distribution of production during summer showed an upper maximum at 0 or 2 m, where light conditions were optimal, and often a second maximum at 6 m due to increased algal concentrations. The annual production (55 g C $m^{-2}y^{-1}$ for the deepest part, and 32 g C $m^{-2}y^{-1}$ averaged over the entire lake surface) agrees with results from other oligotrophic, softwater lakes in Denmark as well as with values from shallow, softwater lakes on the Canadian Shield.

References

- Armstrong, F. A. J. & Schindler, P. W. 1971. Preliminary chemical characterization of waters in the Experimental Lakes Area, northwestern Ontario. J. Fish. Res. Bd. Can. 28: 171-187.
- Cooke, G. D., McConas, M. R., Waller, D. W. & Kennedy, R. H. 1977. The occurrence of internal phosphorus loading in two small, eutrophic, glacial lakes in northeastern Ohio. Hydrobiologia 56: 129-135.
- Crosby, W. T. 1967. The determination of nitrite in water using Cleve's adic, 1-naphtylamine-7-sulphonic acid. Proc. Soc. Wat. Treatm. Exam. 16: 51.
- Goldman, C. E., Steemann Nielsen, E., Vollenweider, R. A. & Wetzel, R. G. 1969. The ¹⁴C light and dark bottle technique. In: Vollenweider, R. A. (ed.), A Manual on Methods for Measuring Primary Production in Aquatic Environments. IBP Handbook No. 12, Blackwell, Oxford, pp. 70-73.
- Golterman, H. L. (ed.). 1969. Methods for Chemical Analysis of Fresh Waters. IBP Handbook No. 8, Blackwell, Oxford, 172 pp.
- Gregersen, A. 1977. Nedbør, fordampning og vandbalance 1976. Statens Planteavlsforsøg, Meddelelse: 1314.

- Gregersen, A. 1978. Nedbør, fordampning og vandbalance 1977. Statens Planteavlsforsøg. Meddelelse: 1387.
- Hansen, K. 1958. Landskabsudviklingen i Himmelbjergegnen. Medd. Dansk Geol. Foren. 13: 442-445.
- Hutchinson, G. E. 1957. A Treatise on Limnology. Vol. I. Geography, Physics and Chemistry. John Wiley and Sons, New York, 1015 pp.
- Jacobsen, O. S. 1976. Udtømning af mobilt phosphor fra danske søsedimenter. In: Edberg, N. og Wilander, A. (ed.), Biologisk Omsaetning I Sediment, Fjärde sedimentsymposiet, Norr Malma 1975. Statens Naturvårdsverk, Naturvårdsverkets limnologiska undersøkning, SNV PM 694, Uppsala, pp. 145-159.
- Jonasson, P. M., Lastein, E. & Rebsdorf, A. 1974. Production, insolation, and nutrient budget of eutrophic Lake Esrom. Oikos 25: 255-277.
- Jørgensen, S. E., Kamp-Nielsen, L. & Dahl-Madsen, K. I. 1977. Mathematical modelling in Danish limnology. In: Hunding, C. (ed.), Danish Limnology, Reviews and Perspectives. Folia Limnol. Scand. 17: 59-66.
- Jørgensen, W. 1974. Nedbørens indhold af plantenaeringsstoffer, 1970-74. Statens Forsøgsvirksomhed i Plantekultur, Meddelelse: 1168.
- Kamp-Nielsen, L. 1974. Mud-water exchanges of phosphate and other ions in undisturbed cores and factors affecting the exchange rates. Arch. Hydrobiol. 73: 218-237.
- Kamp-Nielsen, L. 1975. A kinetic approach to the aerobic sediment-water exchange of phosphorus in Lake Esrom. Ecol. Modelling 1: 153-160.
- Koroleff, F. 1970. Determination of total phosphorus in natural waters by means of persulphate oxidation. An inter-laboratory Report No. 3. Cons. Int. pour l'Explor. de la Mer.
- Kristensen, K. J. 1971. Potentiel vandfordampning bestemt ved forskellige metoder. Vannet i Norden 3: 11-28.
- Krogh, A. & Rehberg, P. B. 1931. CO₂-Bestimmung in Flüssigkeiten und Geweben durch Mikrotitration. Biochem. Z. 225: 177-182.
- Murphy, I. & Riley, T. P. 1962. A modified single solution method for the determination of phosphate in natural waters. Anal. Chim. Acta. 27: 21-26.
- Nygaard, G. 1955. On the productivity of five Danish waters. Verh. int. Ver. Limnol. 12: 123-133.
- Nygaard, G. 1965. Hydrographic studies, especially on the carbon dioxide system, in Grane Langsø. Biol. Skr. Dan. Vid. Selsk. 14: 1-110.
- Nygaard, G. 1968. On the significance of the carrier carbon dioxide in determinations of the primary production in soft-water lakes by the radiocarbon technique. Mitt. int. Ver. Limnol. 14: 111-121.
- Ohle, W. 1955. Ionenaustausch der Gewässersedimenten. Mem. Ist. Ital. Idrobiol., Suppl. 8: 221-225.
- Rebsdorf, A. 1972. The carbon dioxide system of freshwater. A set of tables for easy computation of total carbon dioxide and other components of the carbon dioxide system. (Printed booklet: Freshwater Biological Laboratory, Hillerød, Denmark).
- Riemann, B. 1976. Studies on the biomass of the phytoplankton. Rep. Bot. Inst. University of Aarhus. No. 1. ISBN 87-87600-00-5.
- Riemann, B. & Mathiesen, H. 1977. Danish research into phytoplankton primary production. In: Hunding, C. (ed.), Danish Limnology. Reviews and Perspectives. Folia Limnol. Scand. 17: 49-54.

- Riemann, B. & Schierup, H.-H. 1978. Effect of storage and conservation on the determination of ammonia in water samples from four lake types and a sewage plant. Wat. Res. in press.
- Rodhe, W. 1949. The ionic composition of lake waters. Verh. int. Ver. Limnol. 10: 377-386.
- Sakamoto, M. 1971. Chemical factors involved in the control of phytoplankton production in the Experimental Lakes Area, northwestern Ontario. J. Fish. Res. Bd. Can. 28: 203-213.
- Sand-Jensen, K. 1978. Metabolic adaptation and vertical zonation of Littorella uniflora (L.) Aschers. and Isoetes lacustris L. Aquat. Bot. 4: 1-10.
- Sand-Jensen, K. & Søndergaard, M. 1978. Growth and production of isoetids in oligotrophic Lake Kalgaard, Denmark. Verh. int. Ver. Limnol. 20: 659-666.
- Schindler, D. W. 1971. Carbon, nitrogen and phosphorus and the eutrophication of freshwater lakes. J. Phycol. 7: 321-329.
- Schindler, D. W. & Fee, E. J. 1973. Diurnal variations of dissolved inorganic carbon and its use in estimating primary production and CO₂ invasion in lake 227. J. Fish. Res. Bd. Can. 30: 1501-1510.
- Schindler, D. W. & Holmgren, S. K. 1971. Primary production and phytoplankton in the Experimental Lakes Area, northwestern Ontario, and other low-carbonate waters, and a liquid scintillation method for determining ¹⁴C activity in photosynthesis. J. Fish. Res. Bd. can. 28: 189-201.
- Schindler, D. W. & Nighswander, J. E. 1970. Nutrient supply and primary production in Clear Lake, eastern Ontario. J. Fish. Res. Bd. Can. 27: 2009-2036.
- Solórzano, L. 1969. Determination of ammonia in natural waters by the phenolhypochlorite method. Limnol. Oceanogr. 14: 799-810.
- Steemann Nielsen, E. & Hansen, V. K. 1959. Measurements with the ¹⁴C-technique of the respiration rates in natural populations of phytoplankton. Deep-Sea Res. 5; 222-232.
- Strickland, J. D. H. & Parsons, T. R. 1968. A practical handbook of seawater analyses. Fish. Res. Bd. Can. Bull. 167, 310 pp.
- Tamm, C. O. 1958. The atmosphere. In Ruhland, E. (ed.), Encyclopedia of Plant Physiology. Vol. IV. Springer Verlag, Berlin, pp. 233-242.
- Wetzel, R. G. 1966. Productivity and nutrient relationships in marl lakes of northern Indiana. Verh. int. Ver. Limnol. 16: 321-332.
- Wetzel, R. G. 1975. Limnology. W. B. Saunders, Philadelphia, 143 pp.
- Wium-Andersen, S. & Andersen, J. M. 1972. Carbon dioxide content of the interstitial water in the sediment of Grane Langsø, a Danish Lobelia lake. Limnol. Oceanogr. 17: 943-947.