

Nutrients, biomass and primary productivity of nanoplankton in eutrophic Lake Vombsjön, Sweden

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Seasonal variations of physical and chemical factors were studied in the eutrophic, usually totally-circulated, Lake Vombsjön in South Sweden, 1970 through 1973. Biomass and primary productivity of nanoplankton (< 20 µm) and of the total phytoplankton community were investigated 1971 through 1973. Nanoplankton biomass, estimated as chlorophyll *a*, was highest in early spring (30-40 mg m⁻³) and averaged 20 mg m⁻³ in summer. A 10-fold variation of nanoplankton biomass occurred throughout the year, compared with a 25-fold variation for netplankton biomass. During late summers, when temperature was high and the surface water enriched with nutrients, blue-green algae (netplankton) dominated. Productivity of nanoplankton and of the total phytoplankton community was 3-193, and 8-550 mg C m⁻² h⁻¹, respectively. Correlations between biomass and productivity were established. A significant difference in the photosynthetic capacity of nanoplankton, as compared with netplankton, was found. Mean annual productivity of the total phytoplankton community was 525 g C m⁻² yr⁻¹, of which about 50% was photosynthesized by nanoplankton.

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Сезонные колебания физических и химических факторов исследовались в эутрофном, обычно полностью проточном озере Вомбсьон (южная Швеция) в течение 1970-73 гг. Биомасса и первичная продукция нанопланктона (< 20 мкм) и комплексов фитопланктона измерялась с 1971 по 1973 г. Биомасса нанопланктона, измеренная по хлорофиллу, была максимальной в течение весны (30-40 мг/м³), а летом составляла в среднем 20 мг/м³. В течение года наблюдается 10-кратное колебание биомассы планктона. В конце лета, когда температура высокая, и поверхность воды обогащается элементами питания, доминируют сине-зеленые водоросли. Продуктивность нанопланктона и общей массы планктона составляла 3-193 и 8-550 мгС/м²/час., соответственно. Установлены корреляции между массой и продуктивностью. Найденны существенные различия в фотосинтетической активности нанопланктона и планктона. Среднегодовая продуктивность общей массы фитопланктона 525 г С/м²/год¹, из которой около 50% фотосинтезируется нанопланктоном.

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1. Introduction

Lake Vombsjön is a shallow, nutrient-rich lake in southern Sweden, in a predominantly clayey-limestone area overlain by glacial drift. Since the beginning of the century the lake has been relatively productive, with blue-green algae (*Microcystis* spp.) dominating the phytoplankton community during summer and autumn (Lemmermann 1904, Lundh-Almestrand 1959). About 70% of the catchment area is utilized for agriculture and the lake therefore receives abundant fertilizer. Further details on the lake were given by Gelin (1971). Lake Vombsjön has been used as a reservoir since 1948; water withdrawal increasing from 500 to 1500 l s⁻¹ from 1948 to 1970. Embankments were built along parts of the shore to store spring floods (Fig. 1), and since their completion in 1970, the water level has fluctuated within 2.5 m (Fig. 2).

Phytoplankton makes a significant contribution to the total primary production of the lake. During the study period macrophytes were sparse. Although benthic algae and their productivity were not investigated, they were presumably of less importance due to the turbidity and fluctuations in water level.

This investigation followed the seasonal changes in the biomass and productivity of nannoplankton and total phytoplankton communities in relation to light, temperature, and nutrients during 1971–1973. The photosynthetic capacity of nannoplankton, as compared with netplankton, was studied. The annual productivity of nannoplankton was estimated.

Variations in pH, alkalinity, specific conductivity, temperature, PO₄-P, NO₃-N, NO₂-N, Secchi disc transparency, and light penetration were studied in 1969–1973. The concentrations of the main anions and cations, NH₄-N, total-P, organic N, and SiO₂ were followed during 1970–1973.

In this study, nannoplankton is defined as algae smaller than 20 µm (Dussart 1966). No distinction was made between ultra-nannoplankton and nannoplankton. Quantitative studies on phytoplankton and zooplankton in Lake Vombsjön are reported by Bertilsson (1975) and Berzins (1975), respectively.

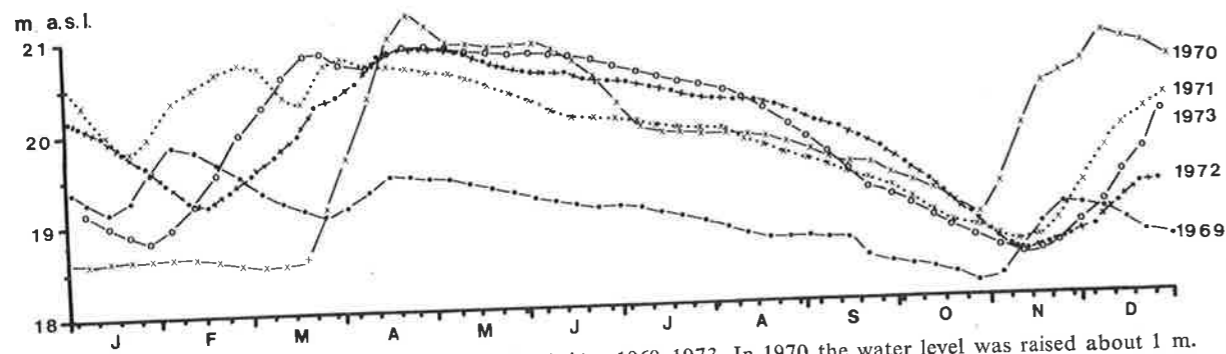


Fig. 2. Fluctuations of the water level in Lake Vombsjön, 1969–1973. In 1970 the water level was raised about 1 m.

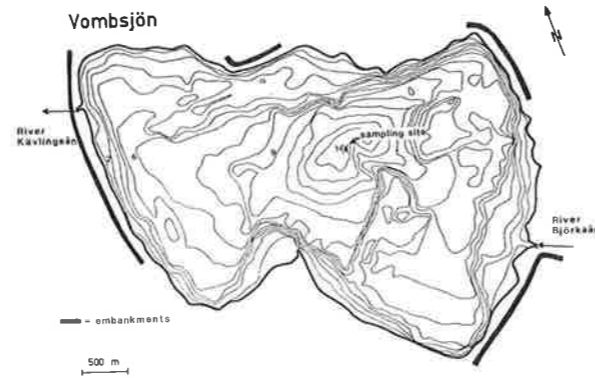


Fig. 1. Morphometry of Lake Vombsjön. (Water level + 19.15 m a.s.l. Underwater contours in metres. Soundings taken by T. Leo 1963).

2. Methods

The physical characteristics of Lake Vombsjön are as follows: maximum length 5.1 km, maximum width 3.1 km, area 12.4 km², shoreline 14 km, shoreline development 1.1, mean depth about 6 m, maximum depth about 15 m, volume 90 Mm³, catchment area 444 km², theoretical replacement time 10 months, and altitude (at mean water level) 20 m a.s.l.

Water samples for chemical analysis were taken with a Ruttner or a Friedinger sampler at the deepest point in midlake (Fig. 1). Samples were taken from six levels (0.2, 2, 5, 8, 12 m depth, and 0.5 m above the sediment surface), usually every third week during the ice-free period.

Phytoplankton productivity was calculated according to Steemann Nielsen (1952, 1965). Water, usually from six depths within the euphotic zone, was transferred to 130 ml glass bottles. After addition of 2 or 4 µCi ¹⁴C-NaHCO₃ they were returned to their respective sampling depths. The ¹⁴C-ampoules were provided by The International Agency for ¹⁴C Determination, Denmark; the analysis also being carried out there (GM-technique). Exposure time was 1.5 h and each experiment was started at noon. Two dark bottles were exposed simultaneously. Filtrations were usually performed

within 2 h following exposure. One subsample from each bottle was directly filtered through a 0.2 µm membrane filter, while another was filtered through a 10 µm plankton net before further filtering through a membrane filter. Examination of the plankton netting under a microscope showed that almost all filamentous algae were retained by the net. Dark-bottle assimilation was subtracted from assimilation in the light-bottles.

Although no measurements on the release of dissolved organic matter from the phytoplankton were made, it was assumed that release of extracellular products is more pronounced in oligotrophic than in eutrophic lakes (cf. Watt 1966). Total carbon dioxide (CO₂ + H₂CO₃ + HCO₃⁻ + CO₃²⁻) was calculated from alkalinity and pH (Buch 1945, Vollenweider 1971). The depth of the euphotic zone was calculated as that corresponding to 1% incident light intensity (Talling 1960a). Primary production rates m⁻² were estimated by planimetric integration of the area enclosed by the axis and the depth-profiles of photosynthesis. During the period 1971–1973 daily rates of primary production were calculated according to Talling (1965).

Penetration of light in the water was measured with a 25 cm diam. Secchi disc and a photocell with red (RG 2, maximum transmission at 630 nm), green (OGr 1, maximum transmission at 530 nm), and blue (BG 7, maximum transmission at 475 nm) filters. The Swedish Meteorological and Hydrological Institute provided data on total incident solar radiation at Svalöv (39 km NW of Lake Vombsjön), Malmö (34 km W of the lake), and Sturup (21 km SW of the lake). Energy available for photosynthesis in the spectral region 400–700 nm was assumed as 46% of the total incoming solar radiation (Talling 1957a). The photosynthetic characteristic (I_K), as defined by Talling (1957a) to express the onset of light saturation of photosynthesis in relation to light intensity, was calculated as the light intensity at which the photosynthetic rate reaches 75% of the light-saturated rate (Talling 1965). The correction for surface-loss was estimated to 10% in this study (Talling 1971).

Phytoplankton biomass was estimated as chlorophyll *a* (Vollenweider 1971). After collection, the water samples were immediately preserved with saturated MgCO₃ and kept in the dark. One subsample was directly filtered through Whatman GF/C glass fibre filter. To calculate the biomass of nannoplankton, another subsample was filtered through a 10 µm plankton net before further filtering through a Whatman GF/C glass fibre filter. Cell pigments were extracted by homogenising the filter in a solution of acetone-water (9:1) and then keeping it in the dark at 4°C for 24 h. The concentration of chlorophyll *a* was calculated according to Lorenzen (1967).

pH was measured potentiometrically with a combination electrode. Alkalinity was determined by titration according to Berger (in Karlgren 1962). Dissolved oxygen was measured by the Winkler procedure. Percentage oxygen saturation was calculated after Trues-

dale et al. (1955). Specific conductivity was measured with a Cambridge conductivity bridge or a "Kemotron Tetramatic". Water colour was measured with a Hellige comparator. The concentrations of Na, K, Ca, Mg were determined with an atomic absorption spectrophotometer (Perkin Elmer, model 303). Chloride was determined by means of an Ag-AgCl electrode and a HgSO₄ electrode in H₂SO₄ medium. Sulphate was analyzed according to Mackereth (1955), phosphate-phosphorus according to Murphy and Riley (1962), and total-P according to Menzel and Corvin (1965). Ammonia-nitrogen was measured after the method of Procházková (1964) until April 1970, after which the method of Chaney and Marbach (1962) was used. Nitrite-nitrogen was measured by the method of Bendschneider and Robinson (1952) and nitrate-nitrogen by the method of Wood et al. (1967). Organic nitrogen was determined by the Kjeldahl digestion method. Samples for determination of nitrate, Kjeldahl-nitrogen, and total-P were preserved with 2 ml 4% HgCl₂ l⁻¹. Silica was determined as "reactive silica" (Mullin and Riley 1955).

3. Results and discussion

3.1. Physical and chemical factors

Temperature: Lakes in southern Sweden are usually ice-covered for about three months in the year. After the extremely long period of nearly 5 months of ice-cover in 1969/70, the winters 1970 through 1973 were mild and Lake Vombsjön was only occasionally frozen (Fig. 3). Since the lake has a smooth bottom and the lake surface is exposed to the prevailing winds, the water is usually totally circulated during summer and a thermocline is rarely developed. The temperature of the bottom water is usually about 17°C in summer (Fig. 3).

Oxygen: The highest values of oxygen saturation in the surface water occurred in connection with the spring and summer maxima of phytoplankton abundance (Fig. 4). Only twice during the summers of the study period was the oxygen content below 1 mg l⁻¹ in the bottom water. This is a critical concentration for many mud-dwelling organisms (Jónasson 1972). The oxygen consumption of the sediment was 40 ml O₂ m⁻² h⁻¹ at 15°C and 100% saturation (Granéli pers. comm.). Because of the total circulation, good oxygenation is normally found in the bottom water despite the large oxygen demands by the sediment.

Specific conductivity: Marked seasonal variations of specific conductivity occurred in the surface water (Fig. 5). In connection with the rapid melting of snow within the watershed in 1970, specific conductivity initially decreased, but later increased when circulation started after the break-up of the ice. Specific conductivity continuously decreased during the summers due to precipitation of CaCO₃. Thus, the seasonal variation of specific conductivity followed the variation of alkalinity (Fig. 5) and Ca (Tab. 1). Specific conductivity has

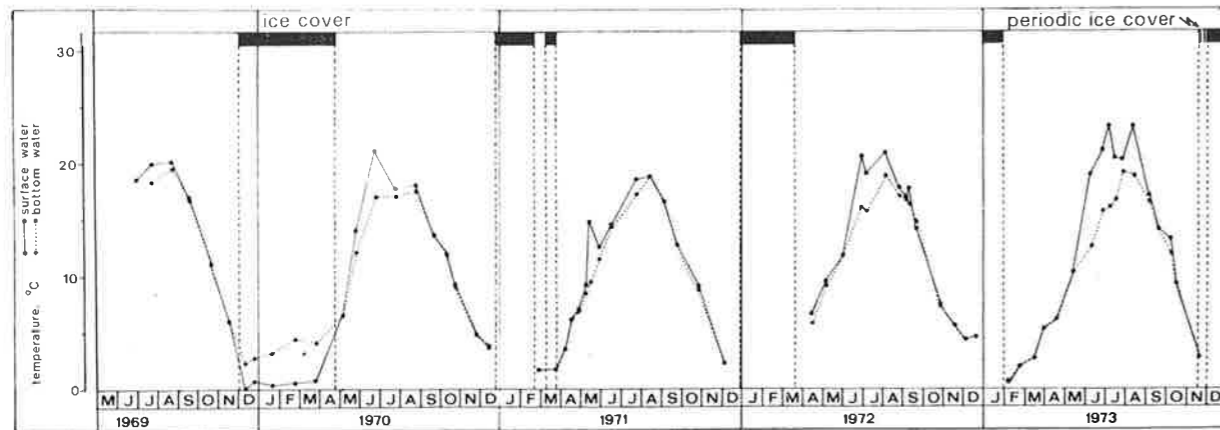


Fig. 3. Temperature of surface and bottom water in Lake Vombsjön, 1969-1973.

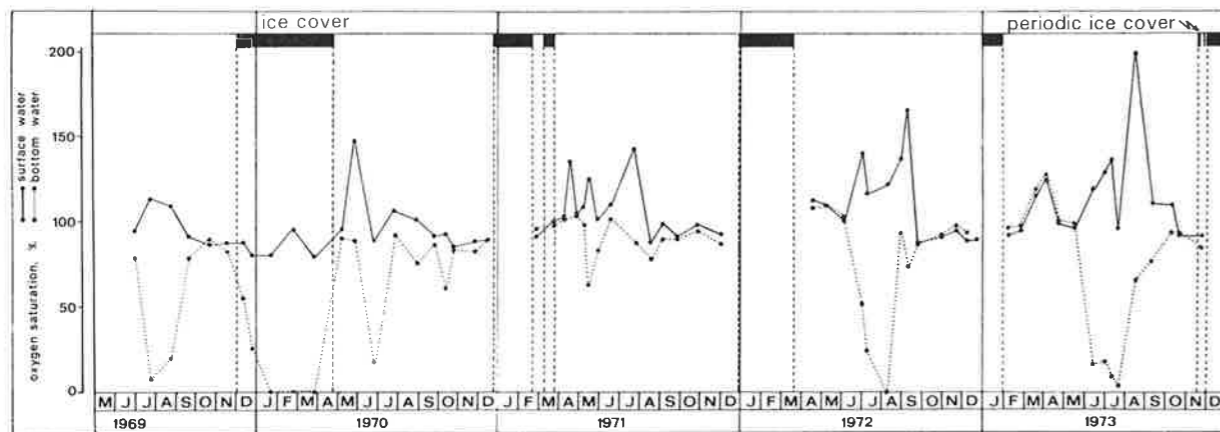


Fig. 4. Percentage oxygen saturation of surface and bottom water in Lake Vombsjön, 1969-1973.

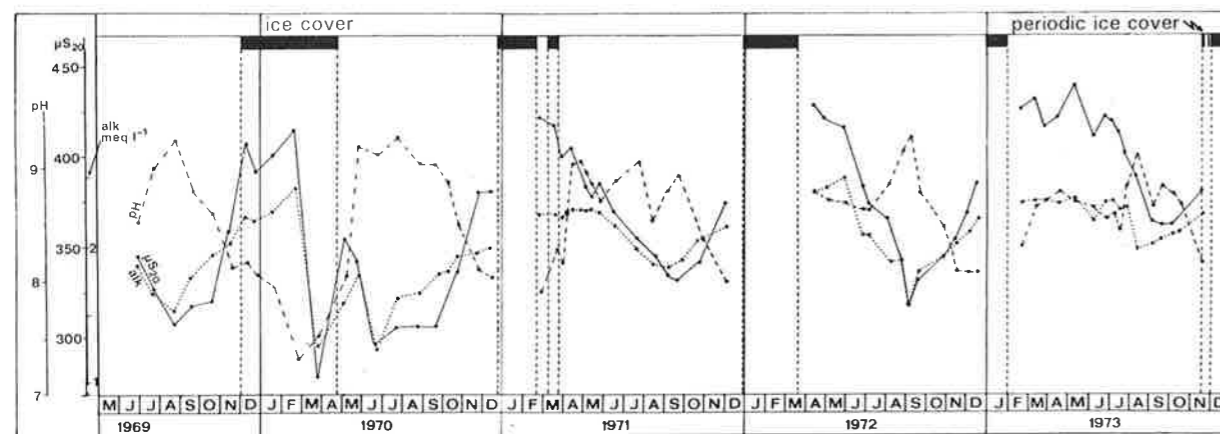


Fig. 5. Seasonal variation of pH, alkalinity, and specific conductivity in the surface water of Lake Vombsjön, 1969-1973.

Tab. 1. Main anion and cation values during maximum and minimum specific conductivity in the surface water of Lake Vombsjön, 1970-1973.

$\mu\text{S}_{20} \text{ cm}^{-1}$	24 March 1970			26 Aug 1970			26 March 1971			4 Sept 1971		
	mg l ⁻¹	meq l ⁻¹	meq l ⁻¹ (%)	mg l ⁻¹	meq l ⁻¹	meq l ⁻¹ (%)	mg l ⁻¹	meq l ⁻¹	meq l ⁻¹ (%)	mg l ⁻¹	meq l ⁻¹	meq l ⁻¹ (%)
Na.....	11.8	0.51	10	9.4	0.41	12	9.4	0.41	9	10.6	0.46	13
K.....	5.9	0.15	3	4.5	0.12	4	4.4	0.11	2	4.0	0.10	3
Ca.....	74.8	3.73	75	48.5	2.42	72	69.3	3.46	78	50.2	2.51	71
Mg.....	6.9	0.57	11	5.1	0.42	12	5.7	0.46	10	5.6	0.46	13
Cl.....	24.9	0.70	14	19.2	0.54	16	20.6	0.58	13	21.8	0.62	17
HCO ₃ + CO ₃ ...	156.2	2.56	50	101.3	1.66	50	137.3	2.25	50	112.2	1.84	50
SO ₄	77.3	1.61	32	52.7	1.10	33	53.7	1.12	25	59.4	1.24	33
NO ₃ -N.....	2.9	0.21	4	0.7	0	0	7.6	0.54	12	0.1	0.01	0

$\mu\text{S}_{20} \text{ cm}^{-1}$	13 April 1972			5 Sept 1972			15 March 1973			3 Oct 1973		
	mg l ⁻¹	meq l ⁻¹	meq l ⁻¹ (%)	mg l ⁻¹	meq l ⁻¹	meq l ⁻¹ (%)	mg l ⁻¹	meq l ⁻¹	meq l ⁻¹ (%)	mg l ⁻¹	meq l ⁻¹	meq l ⁻¹ (%)
Na.....	9.7	0.42	9	10.9	0.47	13	10.8	0.47	9	11.7	0.51	12
K.....	4.5	0.12	2	4.4	0.11	4	8.9	0.23	5	9.3	0.24	6
Ca.....	77.5	3.87	77	48.0	2.40	67	75.5	3.77	75	60.3	3.01	69
Mg.....	7.4	0.61	12	6.8	0.56	16	6.8	0.56	11	7.0	0.58	13
Cl.....	23.5	0.66	14	24.6	0.69	19	26.1	0.74	15	27.0	0.76	18
HCO ₃ + CO ₃ ...	146.4	2.40	49	95.8	1.57	44	142.7	2.34	48	128.1	2.10	50
SO ₄	71.6	1.49	31	62.7	1.31	37	74.5	1.55	32	63.5	1.32	31
NO ₃ -N.....	4.2	0.30	6	0.07	0	0	4.0	0.29	6	0.2	0.02	0

increased from 266 $\mu\text{S}_{20} \text{ cm}^{-1}$ in 1946-1948 to 320 $\mu\text{S}_{20} \text{ cm}^{-1}$ in 1967 (Andersson 1968). Mean values of specific conductivity of surface water (April-September) during the period 1970-1973 were 318, 363, 379, and 406 $\mu\text{S}_{20} \text{ cm}^{-1}$, respectively. Thus, it appears that specific conductivity is steadily increasing.

Relationship between pH, CO₂, and CaCO₃: The buffering capacity of the water is good, and seasonal variations in pH are therefore of a minor nature (Fig. 5). The water was about pH 8.0 in winter when the photosynthetic activity was insignificant, and more than pH 9.0 during the spring and summer maxima of phytoplankton abundance. The diurnal variation of pH during these periods was ± 0.2 .

The alkalinity of the surface water was greatest during the winters (Fig. 5). The lowest alkalinities were usually found in August and during the first half of September when the amount of chlorophyll *a* was about 100 mg m⁻³. The concentration of free CO₂ is low in alkaline Lake Vombsjön, and the dissolved inorganic carbon necessary for photosynthesis is obtained from HCO₃⁻. The decrease in alkalinity and Ca during summer resulted from the photosynthetic precipitation of CaCO₃. The importance of CaCO₃-precipitation in hard-water lake metabolism has been emphasized by several workers (e.g. Hutchinson 1957). Apart from decreasing the amounts of inorganic nutrients by co-precipitation, CaCO₃ can also remove dissolved organic matter by

adsorption (Otsuki and Wetzel 1974). Supersaturation with CaCO₃ seems to be common in hard-water lakes and occurred frequently in Lake Vombsjön (cf. Ohle 1934). In late autumn the alkalinity increased due to dissolution of CaCO₃.

Ionic composition: Remarkable seasonal variations in Ca, alkalinity, and NO₃-N were found (Tab. 1). The values of Na, K, Mg, and Cl were relatively constant throughout the years. Since 1967 the amount of SO₄ seems to have increased (Andersson 1968). Percentage equivalents of Ca, SO₄, and NO₃ were higher, while alkalinity was lower (Tab. 2) in comparison with other Swedish lakes (Rodhe 1949) and Lake Esrom (Jónasson 1972). NO₃ made a significant contribution to the ionic balance in spring and autumn.

Silica: During the winters the silica concentration was about 8 mg SiO₂ l⁻¹ (Fig. 6), but usually declined sharply in spring because of the diatom blooms. Release of silica from frustules of decomposing diatoms, and from the sediment where the concentration of silica in interstitial solution is high (about 50 mg SiO₂ l⁻¹ in September 1972, Ripl pers. comm.), resulted in an increase of silica in the bottom water. Accordingly, when total circulation occurred, the amount of silica in the surface water rapidly increased. The same seasonal pattern of silica distribution in surface water was reported from the well-mixed Loch Leven, Scotland (Holden and Caines 1974). Due to its sheltered situation,

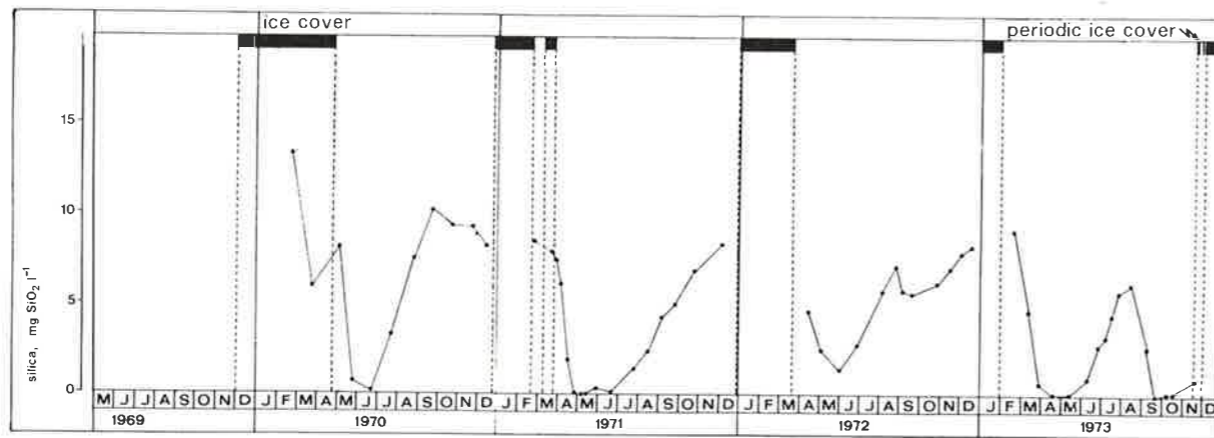


Fig. 6. Seasonal variation of silica in the surface water of Lake Vombsjön, 1970-1973.

Tab. 2. Ionic composition of lake waters. Average values expressed as meq l⁻¹ in %.

	Lake Vombsjön Sweden (n = 8)	Lake Esrom Denmark (a)	Lakes from Uppland Sweden (b)
Na.....	11	17.0	13.6
K.....	4	1.9	2.2
Ca.....	73	66.5	67.3
Mg.....	12	14.6	16.9
Cl.....	16	17.8	9.5
HCO ₃	49	70.5	74.3
SO ₄	32	11.7	16.2
NO ₃	3	0	0
(a) Jónasson (1972)	(b) Rodhe (1949)		

however, a well-developed silica stratification is often observed in Lake Esrom (Jónasson et al. 1974). Granéli (1975), in laboratory experiments with sediment cores from Lake Vombsjön, estimated the mean release during one year as 84 mg SiO₂ m⁻² d⁻¹, at a mean temperature

of 9.3°C, and with renewal each month of overlying water. Similar values are reported for shallow eutrophic lakes in Denmark (Andersen 1974) and West Germany (Tessenow 1966). The release of silica from the sediment was about the same, both under aerobic and anoxic conditions. It is assumed that the release of silica from sediment is little influenced by redox conditions (Tessenow 1966).

Phosphorus: Immediately after the break-up of the ice the concentration of PO₄-P was about 40 µg l⁻¹ within the whole water body, but during the phytoplankton spring outburst PO₄-P rapidly declined to about 5 µg l⁻¹ in the surface water (Fig. 7). Enrichment experiments with addition of PO₄-P alone and PO₄-P + SiO₂ to the natural phytoplankton community during this period showed that P limited phytoplankton growth (Gelin unpubl.).

Thermal stratifications of short duration normally occur every summer during periods of calm weather. Because of the great oxygen consumption of the sediment, the concentration of oxygen decreases and PO₄-P

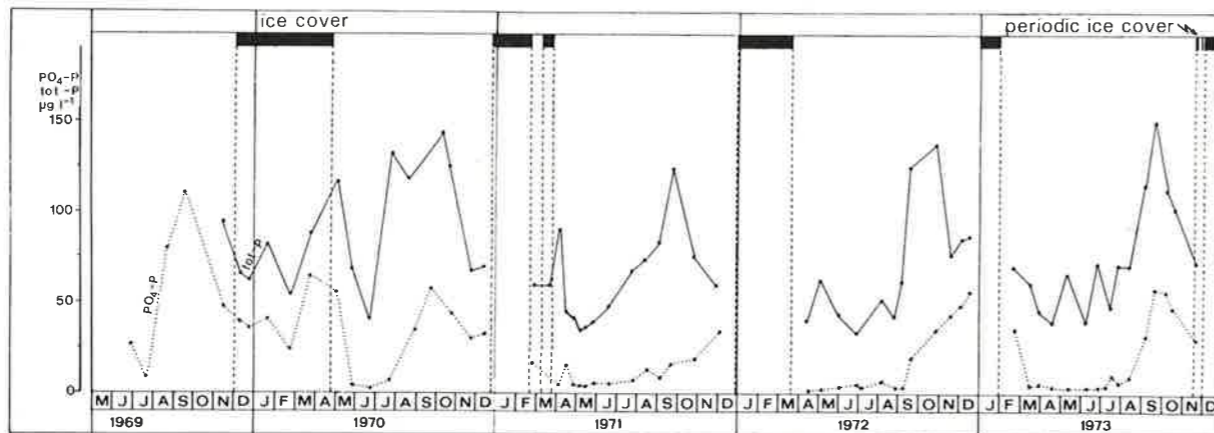


Fig. 7. Seasonal variation of PO₄-P and total-P in the surface water of Lake Vombsjön, 1970-1973.

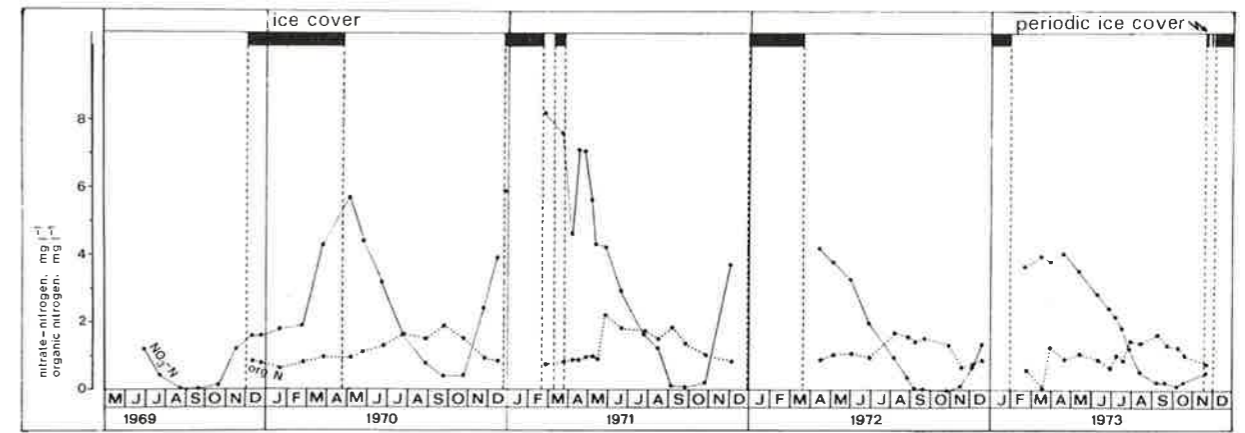


Fig. 8. Seasonal variation of NO₃-N and organic N in the surface water of Lake Vombsjön, 1970-1973.

increases in the bottom water (Fig. 10). Total circulation after such a period provides nutrients for the phytoplankton within the euphotic zone, and probably initiates changes in the phytoplankton community, leading to the dominance of blue-green algae (netplankton). During this period of great phytoplankton abundance the input of PO₄-P via tributaries was small. But PO₄-P continued to increase in the surface water, possible because of high temperatures and high pH which caused intense release of PO₄-P from the sediment (Macpherson et al. 1958). The highest concentration of total-P in the surface water (slightly below 150 µg l⁻¹) usually occurred in August and during the first two weeks of September (Fig. 7). The concentration of PO₄-P in the interstitial water of the sediment surface was 2.78 mg l⁻¹ in September 1972 and 1.19 mg l⁻¹ in February 1973 (Granéli 1975). The sediment of the lake is a calcareous gyttja which contained 170 mg Ca, 19 mg Fe, and 1 mg P g⁻¹ dry weight of sediment in September 1972 (Ripl pers. comm.). The P content of the sediment is comparable to values from oligotrophic lakes.

Laboratory experiments with exchange of P over an undisturbed sediment-water interface showed a much smaller release under aerobic than under anoxic conditions (Granéli 1975). However, high rates of release from the sediment may probably occur, despite the usual aerobic condition of the bottom water, due to wind-induced stirring of the uppermost sediment layer (Andersen 1974).

Nitrogen: The nitrogen cycle is characterized by changes in nitrate concentrations. Large amounts of nitrate enter the lake as a result of intense fertilizer usage within the catchment area. There is usually a decrease from 5-6 mg NO₃-N l⁻¹ in late winter to a minimum of 0.1-0.3 mg l⁻¹ in September (Fig. 8). This decrease was not always associated with algal blooms. After the phytoplankton spring outburst there was no evidence for release of nitrate. As the lake is nearly always well-mixed, nitrate is available to benthic species, as well as to plankton. Because of the great oxygen consumption by sediment there are intervals when the environment at

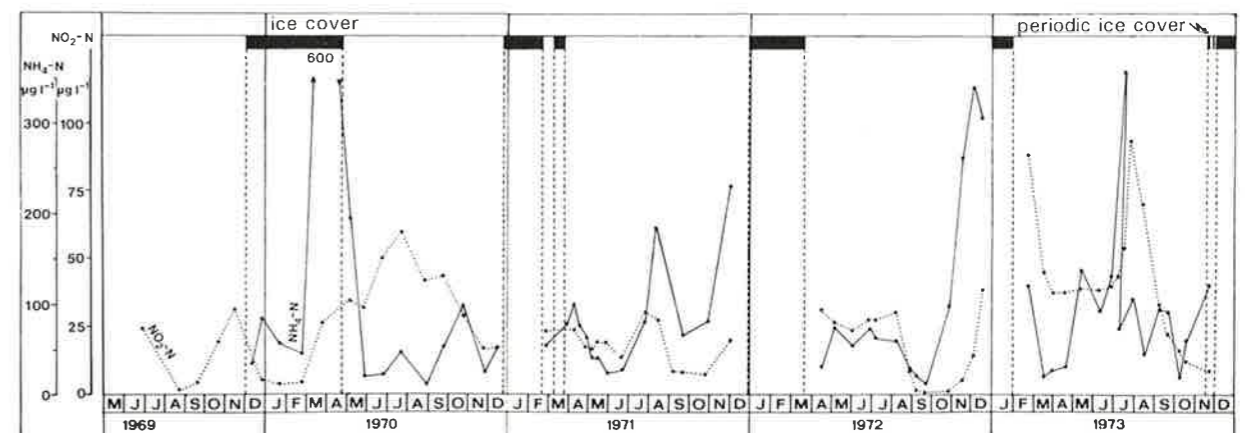


Fig. 9. Seasonal variation of NH₄-N and NO₂-N in the surface water of Lake Vombsjön, 1970-1973.

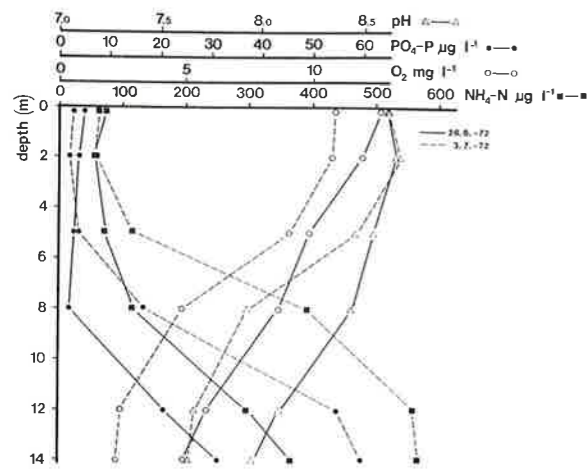


Fig. 10. Vertical distribution of pH, PO₄-P, O₂, and NH₄-N in Lake Vombsjön from 28 June to 3 July 1972.

the sediment-water interface is suitable for denitrification (cf. Johnston et al. 1974). Increasing nitrate concentration from October to March during the study period 1970–1973 was mainly accounted for by allochthonous nitrogen sources.

Maximum values for organic nitrogen in the water (1.7–1.9 mg l⁻¹) usually occurred during the development of blue-green algae in late summer (Fig. 8). The amount of ammonia-nitrogen in the surface water was 62, 91, 109, and 91 µg l⁻¹ in 1970–1973, respectively (mean values during the ice-free period). Corresponding concentrations of nitrite-nitrogen were 36, 19, 18, and 43 µg l⁻¹, respectively. During short stagnation periods in summer the concentration of NH₄-N in the bottom water increased considerably (Fig. 10). Mixing of the water after such stratifications results in peaks of NH₄-N and NO₂-N, often close in time, indicating rapid nitrification (Fig. 9). This nitrification may occur within the water column due to resuspended material, including

bacteria from the sediment. The permanently and relatively high values for NH₄-N and NO₂-N in the surface water may thus indicate rapid nutrient recycling.

3.2. Biomass of nanoplankton and total phytoplankton

The greatest biomass of nanoplankton, estimated as chlorophyll *a*, was 30–40 mg m⁻³, and this was observed at the beginning of the spring outburst (Fig. 12). At that time nutrient content was high and the abundance of zooplankton low. During the summer nanoplankton biomass was about 20 mg m⁻³. Netplankton was most abundant during August and the beginning of September when the surface water was again enriched with nutrients after the spring depletion, due to circulation of the water following periods of stratification. The biomass of nanoplankton in Lake Vombsjön showed substantially less temporal variation than netplankton. Thus, the biomass of nanoplankton showed a 10-fold variation throughout the year while netplankton varied 25-fold (mean values 1970–1973).

Nanoplankton biomass increased during 1971 and 1972 in relation to 1970 (Gelin 1971). This may have been caused by the significant decrease in the numbers of herbivorous zooplankton in these years (Berzins 1975). In 1973 the numbers of filtering zooplankton species increased again and nanoplankton biomass declined. Investigations with a 22 µm Nytex-net disc (Malone 1971) and a 35 µm net (Seliger et al. 1971) have shown that the biomass of algae able to pass through these nets was relatively constant throughout the year in marine environments. The size-selective grazing by zooplankton is thought to be responsible for the dampened fluctuations in nanoplankton abundance (Seliger et al. 1971). Welch et al. (1975) reported that netplankton were utilized relatively little by zooplankton compared to nanno- (5–50 µm) and ultranannoplankton (< 5 µm). However, great differences in the seasonal abundance of nanoplankton were reported by Kalf

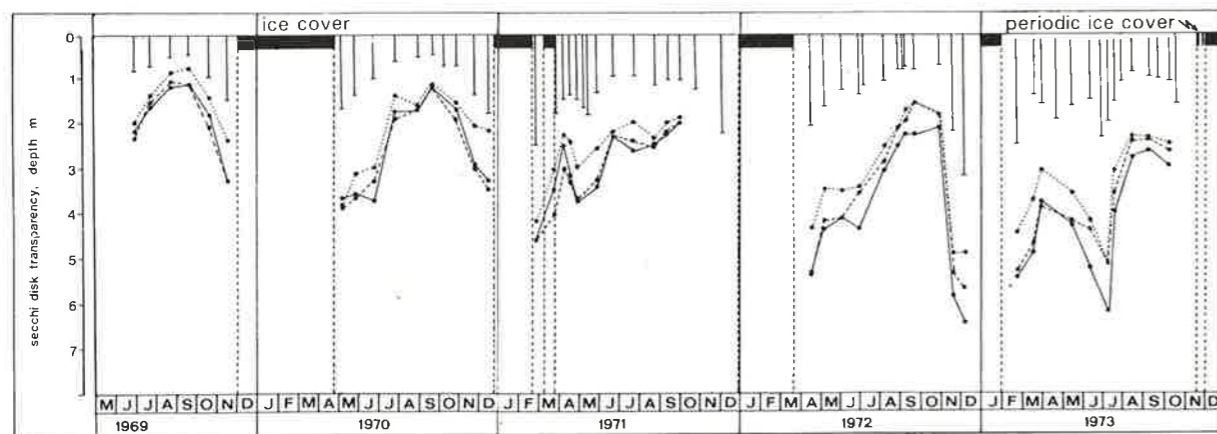


Fig. 11. Seasonal variation of Secchi disk transparency and the depth of penetration of 1% of the surface irradiation in Lake Vombsjön 1969–1973 (.... blue, ---- red, — green light).

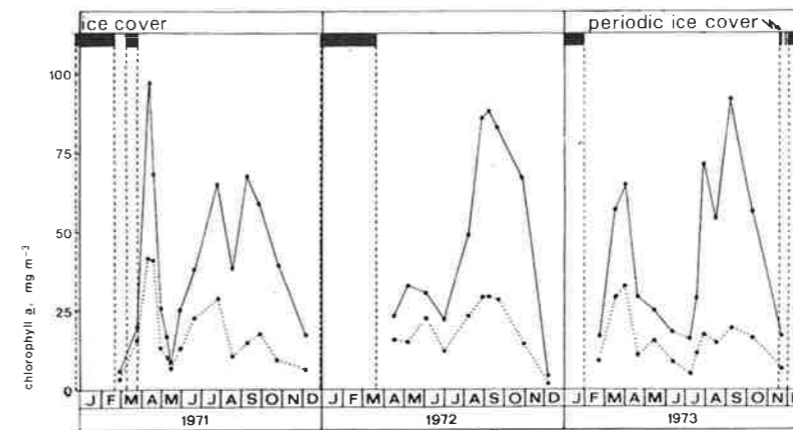


Fig. 12. Seasonal variation of chlorophyll *a* content of the total phytoplankton community (—) and that of the nanoplankton community (....) in the surface water of Lake Vombsjön, 1971–1973.

1972) and Manny (1972) from two eutrophic lakes. Gliwicz and Hillbricht-Ilkowska (1972), using a 50 µm net, stated that nanoplankton was more effectively utilized as food by zooplankton in oligotrophic than in eutrophic lakes.

3.3. Light penetration

Water colour varied slightly about 20 mg Pt l⁻¹ during this investigation. The Secchi-depth during the ice-free periods is determined by phytoplankton abundance and also by the amount of suspended organic and inorganic material caused by the circulation. During winters without ice-cover, transparency was 2.5–3.5 m (Fig. 11). The greatest transparency observed, from the ice, was 4.4 m in January 1970. During the spring maximum of phytoplankton, the Secchi-depth was usually reduced to 1.5 m or less. Transparency increased slightly in May or June and the lowest values were recorded in August and during the first two weeks of September during the maximum of blue-green algae.

Secchi disc transparency plotted against chlorophyll *a* (Fig. 14) and linear regression analyses gives the equation

$$\log Z_{\text{Secchi}} = -1.09 \log \text{chl } a + \log 1.68 \quad (1)$$

when $r = -0.49$ and $n = 45$. This equation can be written

$$Z_{\text{Secchi}} = \frac{1}{0.60 \text{ chl } a^{1.09}} \quad (2)$$

This differs from the equation of Vollenweider (1960):

$$Z_{\text{Secchi}} = \frac{1}{0.04 \text{ chl } a^{0.6}} \quad (3)$$

and that of Ahlgren (1973):

$$Z_{\text{Secchi}} = \frac{1}{0.091 \text{ chl } a^{0.59}} \quad (4)$$

Equations (3) and (4) were derived from measurements of stratified lakes. The hatched line in Fig. 14 is derived from eqn (3) using chlorophyll *a* values from Lake Vombsjön. The two regression lines show the difference of chlorophyll *a* content at corresponding Secchi-depths in an unstratified lake and a stratified lake. This difference may also be influenced by suspended material entering Lake Vombsjön from tributaries, since the water retention time of the lake is only about 10 months.

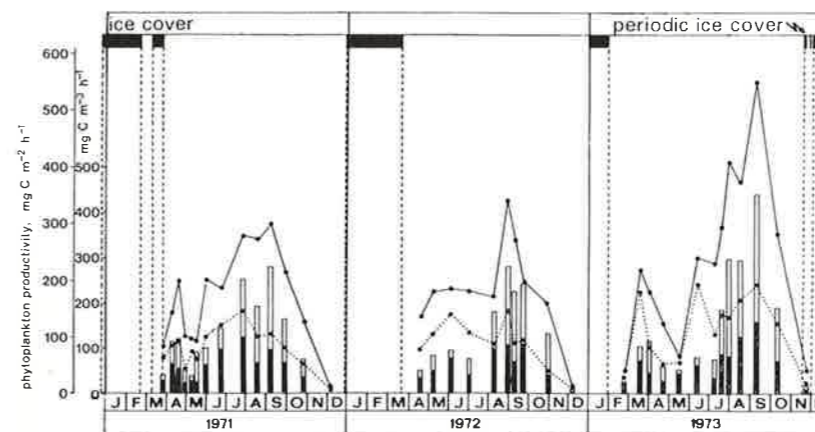


Fig. 13. Seasonal variation of hourly rates of photosynthesis per unit area (ΣA) and per unit volume of water (A_{max}) measured at noon in Lake Vombsjön, 1971–1973. (Total phytoplankton community is denoted by —, nanoplankton by, black columns denote A_{max} of the nanoplankton and whole columns A_{max} of the total phytoplankton community).

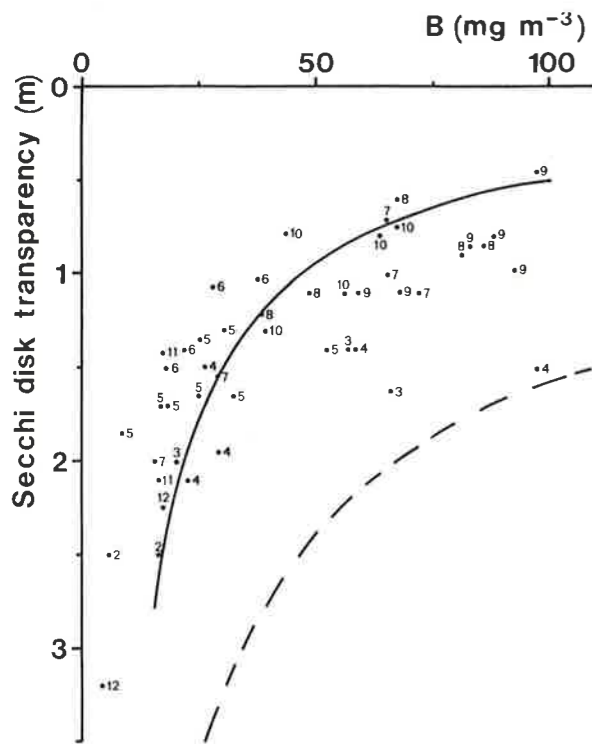


Fig. 14. Relationship between phytoplankton biomass (B), estimated as chlorophyll a , and Secchi disk transparency in Lake Vombsjön, 1970–1973 (solid line). Figures denote months. Hatched line is calculated from the equation of Vollenweider (1960) using chlorophyll a values from Lake Vombsjön.

There was a trend towards increasing transparency from 1970 until 1973 (calculated as mean values during June–September), despite increasing chlorophyll a within the euphotic zone, indicating a decrease in the amount of suspended material.

The most penetrating components within the visible spectrum of light were green and red (Fig. 11). Blue was always least penetrating. A similar situation was reported for Lake Erken and Lake Grosser Plöner See (Rodhe 1965). The minimum vertical extinction coefficient (ϵ_{\min}) varied seasonally between 0.9 and 2.8 \ln units m^{-1} (mean values 1969–1973). The euphotic depth varied between 1.9 and 5.1 m (mean values 1969–1973). The lowest values were recorded in connection with bloom of blue-green algae. On average, the depth of the euphotic zone was 2.5 times the Secchi-depth.

3.4. Phytoplankton productivity

The following symbols are those recommended by Winberg (1971):

A_{\max} = light-saturated rate of photosynthesis per unit water volume ($\text{mg C m}^{-3} \text{ h}^{-1}$).

ΣA = hourly integral photosynthesis per unit area ($\text{mg C m}^{-2} \text{ h}^{-1}$).

B = population density per unit volume of water ($\text{mg chl } a \text{ m}^{-3}$).

P_{\max} = $\left(\frac{A_{\max}}{B}\right)$ = light-saturated rate of photosynthesis per unit biomass ($\text{mg C mg chl } a^{-1} \text{ h}^{-1}$).

ϵ_{\min} = minimum value (over the visible spectrum) of the vertical extinction coefficient (\ln units m^{-1}).

I_0' = light intensity below the water surface, 400–700 nm (i.e. surface light intensity, I_0 , corrected for surface loss).

I_k = light intensity indicating onset of light-saturation of photosynthesis (400–700 nm). This characteristic was introduced by Talling (1957a) and is equivalent to the light intensity at which an extrapolation of the initial linear region of the rate-intensity curve reaches the light-saturated rate.

Distribution of photosynthetic activity with depth: The seasonal variation in the configuration of depth-profiles of photosynthetic activity per unit volume of the total phytoplankton community, and of the nannoplankton community, was the same during 1971 through 1973. On most occasions photosynthesis was inhibited near the surface, usually within the uppermost 0.5 m (Fig. 15). Beneath the zone of light-saturation, photosynthetic rates declined rapidly due to the rapid extinction of light which was influenced not only by the density of the phytoplankton crop but also by the amount of suspended non-algal particulate matter.

Photosynthesis per unit area: In late winter and early spring about 80% of the total productivity per unit area was contributed by nannoplankton (Fig. 13). At this time of year the nutrient content was high, but light intensity and temperature were low. Towards the end of the spring outburst the nannoplankton species were partly replaced by netplankton and the percentage share of nannoplankton productivity, to that of total productivity, decreased. During May and June the phytoplankton productivity declined, mainly due to depletion of $\text{PO}_4\text{-P}$ and SiO_2 . The amount of dissolved silica was usually below $0.6 \text{ mg SiO}_2 \text{ l}^{-1}$, and this limited diatom development (cf. Lund 1971). At the onset of summer, when nutrient content was low, nannoplankton contributed about 80% of the total productivity per unit area (Fig. 15). At the end of summer when the surface water was enriched with $\text{PO}_4\text{-P}$, blue-green algae (netplankton) dominated and nannoplankton productivity per unit area, in relation to total phytoplankton productivity, was the lowest during the year, usually 35–45% (Fig. 13). There was a biannual pattern in the total phytoplankton productivity.

Influence of phytoplankton density on light penetration: The correlation coefficient between phytoplankton density (as chlorophyll a per unit volume) and minimum vertical extinction (ϵ_{\min}) was 0.73 (Fig. 16). As Lake

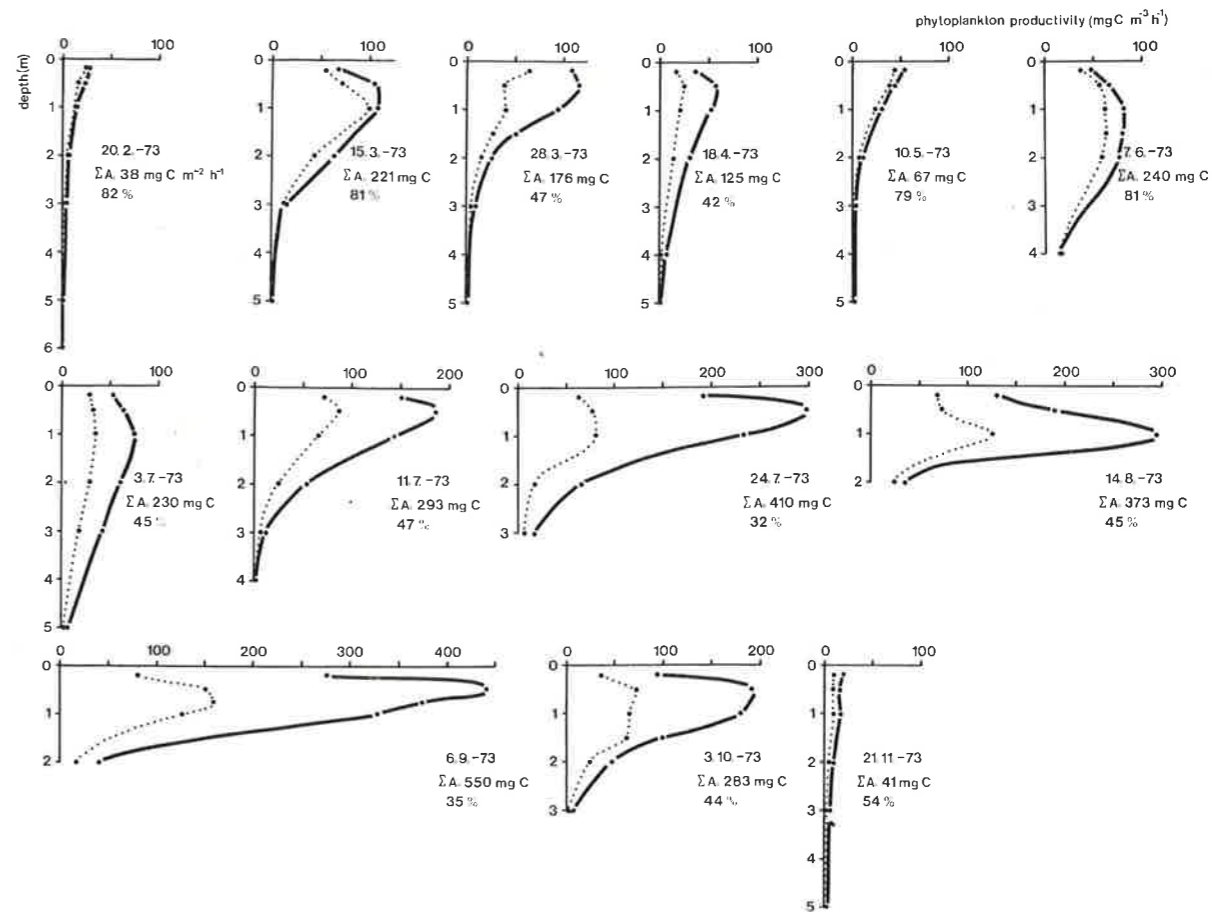


Fig. 15. Depth-distribution of photosynthetic rates per unit volume of water in Lake Vombsjön 1973. (Total phytoplankton community is denoted by —, nannoplankton by Percentage figures denote the productivity per unit area of nannoplankton in relation to the total phytoplankton community).

Vombsjön is usually totally circulated, non-algal particulate matter is thought to be an important factor in reducing light-penetration. The mean increase of ϵ_{\min} in relation to unit increase of phytoplankton biomass, calculated from the linear regression line, was 0.016 (Fig. 16). This increase in ϵ_{\min} per unit algal concentration (ϵ_s in Talling 1960b) in Lake Vombsjön is of the same order, 0.02, as found for Lake Windermere (Talling 1960b) and Lake George (Ganf 1972). Value for ϵ_s is 0.0086 in Loch Leven (Bindloss 1974). Self-shading occurred in Lake Vombsjön, but shading by non-algal particulate matter was pronounced causing a narrow euphotic zone in relation to phytoplankton biomass and water colour.

The intercept of the regression line on the y axis (Fig. 16) indicates a relatively high average background level of non-algal light extinction in comparison with, for example Esthwaite Water, a summer-stratified lake (Talling 1971). During 1970, the first year after the latest regulation of the volume of lake water for increased water storage, the amount of background light extinc-

tion was most important (Fig. 16). This may have been due to overflow in certain areas following the raising of water level, but there was also a massive spring flood in 1970 which probably also increased background light-extinction. On average a phytoplankton biomass equivalent to $50 \text{ mg chl } a \text{ m}^{-3}$ accounts for about 50% of total light extinction in the water column. The equation

$$\Sigma A = \frac{A_{\max}}{1.33 \epsilon_{\min}} (\ln I_0' - \ln 0.5 I_k)$$

for theoretical calculation of the integral photosynthesis per unit area (Talling 1965) cannot be applied to Lake Vombsjön, probably because of the large amounts of non-algal particulate matter influencing ϵ_{\min} in relation to A_{\max} and the ratio $(\ln I_0' - \ln 0.5 I_k)$.

Biomass in relation to production rates: The relation between biomass and the light-saturated rate of photosynthesis of the total phytoplankton community is shown in Fig. 17 ($r = 0.90$) (4 observations strongly deviating in early spring 1971 and 1973 were not included, since these were influenced by algae adapted to low-light

intensity). The corresponding correlation for nannoplankton was lower ($r = 0.74$, Fig. 18). The biomass per unit volume was a good index of productivity per unit area ($r = 0.76$, Fig. 19). The productivity per unit area was determined by the ratio $\frac{A_{max}}{\epsilon_{min}}$, of which both components A_{max} and ϵ_{min} were dependent on the population density, but ϵ_{min} was also influenced by the amount of non-algal particulate matter. The average relationship between ΣA and $\frac{A_{max}}{\epsilon_{min}}$, when $r = 0.96$, can be written

$$\Sigma A = \frac{A_{max}}{\epsilon_{min}} \times 2.3 \text{ and is denoted by a solid line in Fig. 20. The same relationship applies to nannoplankton,}$$

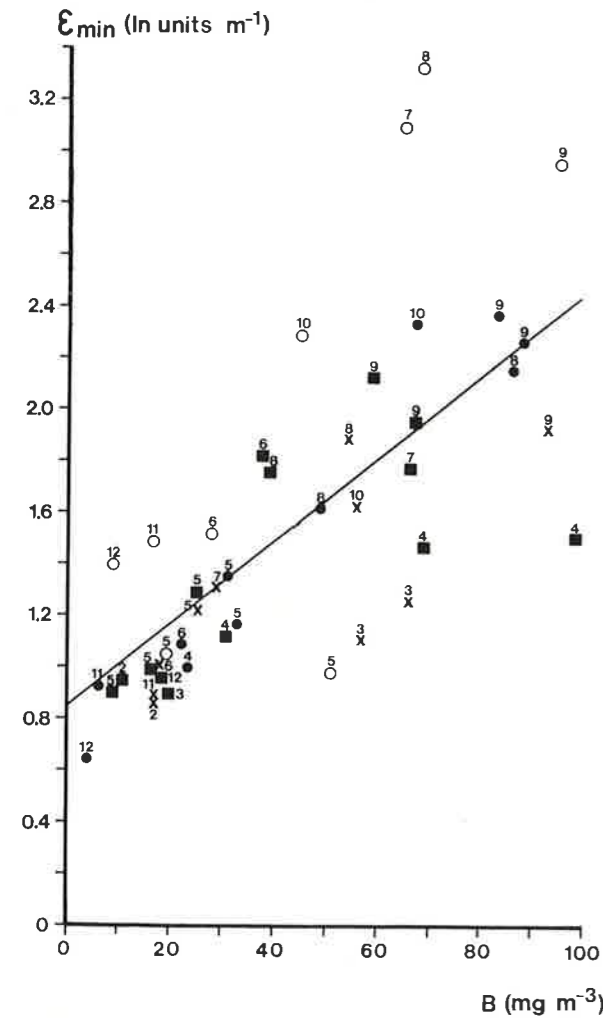


Fig. 16. Relationship between the minimum vertical extinction coefficient (ϵ_{min}) and the concentration of chlorophyll a (B , surface water) in Lake Vombsjön 1970–1973. \circ = 1970, \blacksquare = 1971, \bullet = 1972, \times = 1973. Figures denote months.

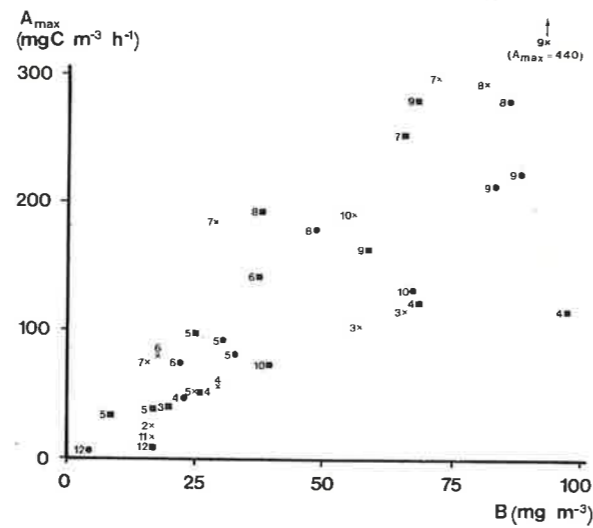


Fig. 17. Relationship between light-saturated rate of photosynthesis of the total phytoplankton community per unit volume of water (A_{max}) and phytoplankton biomass (B), estimated as chlorophyll a , in Lake Vombsjön 1971–1973. \blacksquare = 1971, \bullet = 1972, \times = 1973. Figures denote months.

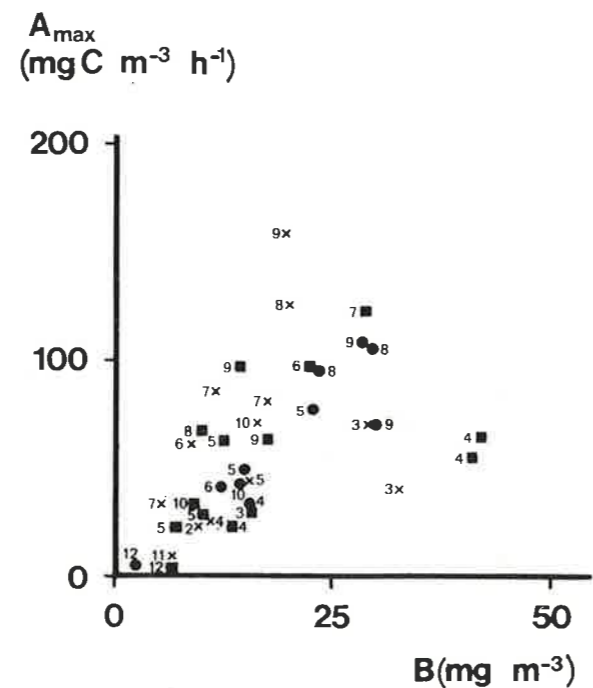


Fig. 18. Relationship between light-saturated rate of photosynthesis of nannoplankton per unit volume of water (A_{max}) and nannoplankton biomass (B), estimated as chlorophyll a , in Lake Vombsjön, 1971–1973, \blacksquare = 1971, \bullet = 1972, \times = 1973. Figures denote months.

when $r = 0.92$ (Fig. 21). Values reported in the literature are $\Sigma A = \frac{A_{max}}{\epsilon_{min}} \times 1.9$ (Bindloss 1974), $\Sigma A = \frac{A_{max}}{\epsilon_{min}} \times (2.4 \text{ to } 2.7)$ (Rodhe et al. 1958), and $\Sigma A = \frac{A_{max}}{\epsilon_{min}} \times 2.6$ (Talling 1965).

Due to circulation in Lake Vombsjön the phytoplankton is usually distributed uniformly with depth. The total amount of chlorophyll a per m^2 in the euphotic zone (ΣB) was calculated from the concentration of chlorophyll a per m^3 multiplied by the depth of the euphotic zone. During the period 1971–1973 the chlorophyll a content of the total phytoplankton community within the euphotic zone varied between 28 and 297 $mg\ m^{-2}$. The highest values were recorded in early spring and late summer. The corresponding range of nannoplankton was 8–144 $mg\ m^{-2}$, with the peak in early spring. When the euphotic zone is defined according to Talling (1965), $z_{eu} \approx 3.7 \epsilon_{min}^{-1}$, ΣB can be calculated from $3.7 \times B \times \epsilon_{min}^{-1}$. The theoretical upper limit of ΣB will be equal to $3.7 \epsilon_s^{-1}$, i.e. 230 $mg\ chl\ a\ m^{-2}$ using the average

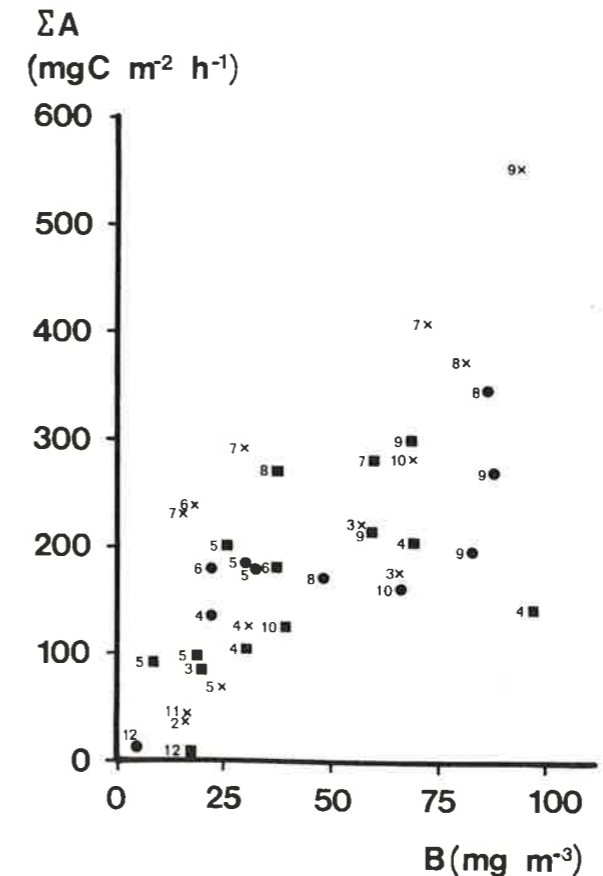


Fig. 19. Primary productivity of phytoplankton per unit area (ΣA) in relation to chlorophyll a concentration per unit volume water (B) in Lake Vombsjön, 1971–1973. \blacksquare = 1971, \bullet = 1972, \times = 1973. Figures denote months.

$\epsilon_s = 0.016$. This value was only exceeded during the phytoplankton spring outburst. Steemann Nielsen (1962) determined experimentally the maximum amount of ΣB in the euphotic zone as 800 $mg\ m^{-2}$. This referred only to chlorophycean plankton algae, but was 400 $mg\ m^{-2}$

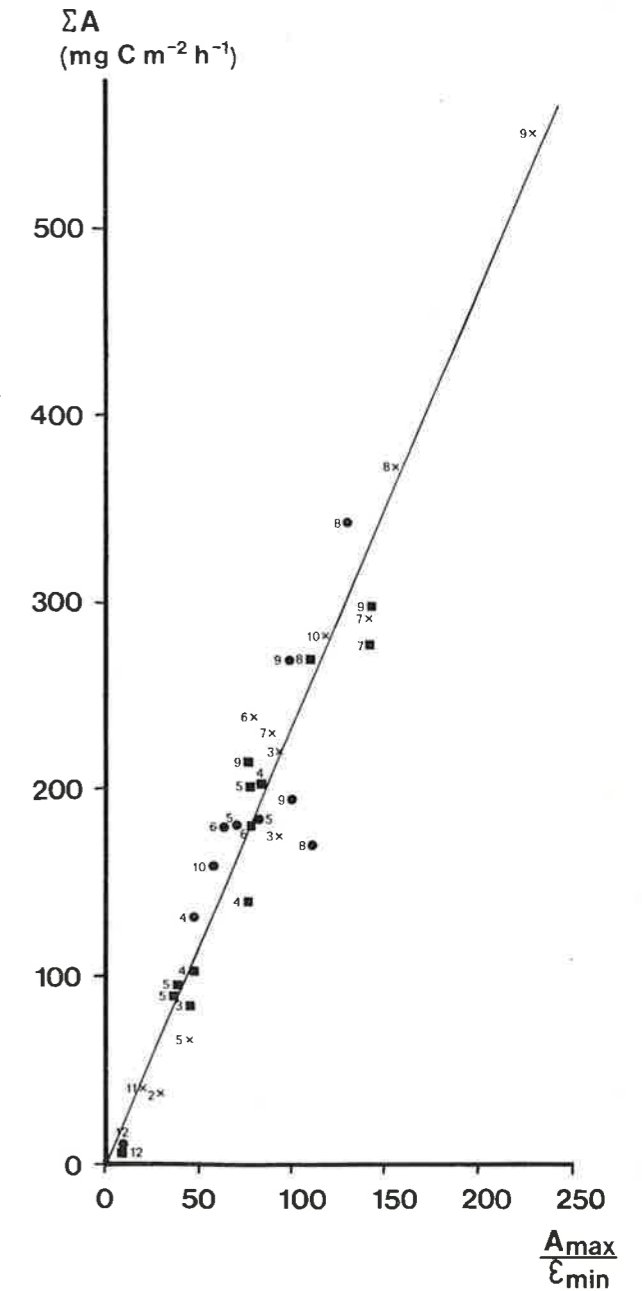


Fig. 20. Primary productivity of the total phytoplankton community per unit area (ΣA) correlated with the ratio $\frac{A_{max}}{\epsilon_{min}}$ in Lake Vombsjön, 1971–1973. \blacksquare = 1971, \bullet = 1972, \times = 1973. Figures denote months. Average relationship is indicated.

if the species were brown (for example diatoms). Steemann Nielsen (1962), on the basis of field data, considered that the upper limit in the photosynthetic layer was about 300 mg m^{-2} . Talling et al. (1973) reported ranges of $179\text{--}325 \text{ mg chl } a \text{ m}^{-2}$ in the euphotic zone of highly eutrophic lakes in Ethiopia, and Bindloss (1974) found an upper limit of $456 \text{ mg chl } a \text{ m}^{-2}$ in Loch Leven. Ahlgren (1970) gave 470 mg m^{-2} (chlorophyll $a + b + c$) as a mean value of five observations from eutrophic Lake Norrviken, Sweden.

In Lake Vombsjön there was a good correlation be-

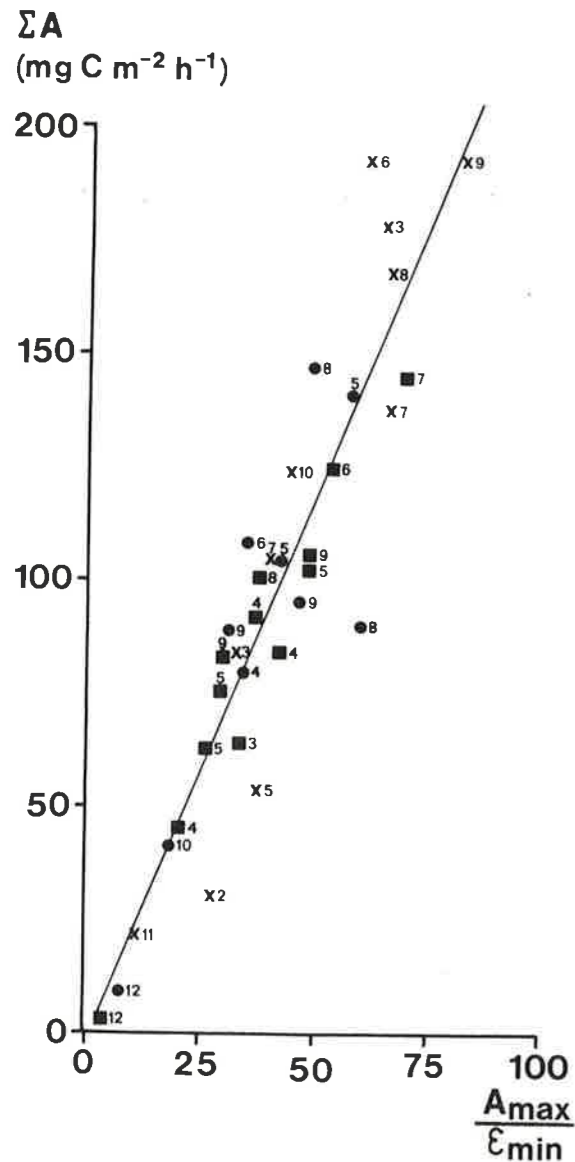


Fig. 21. Primary productivity of nanoplankton per unit area (ΣA) as a function of the ratio $\frac{A_{\max}}{\epsilon_{\min}}$ in Lake Vombsjön, 1971–1973. ■ = 1971, ● = 1972, × = 1973. Figures denote months. Average relationship is indicated.

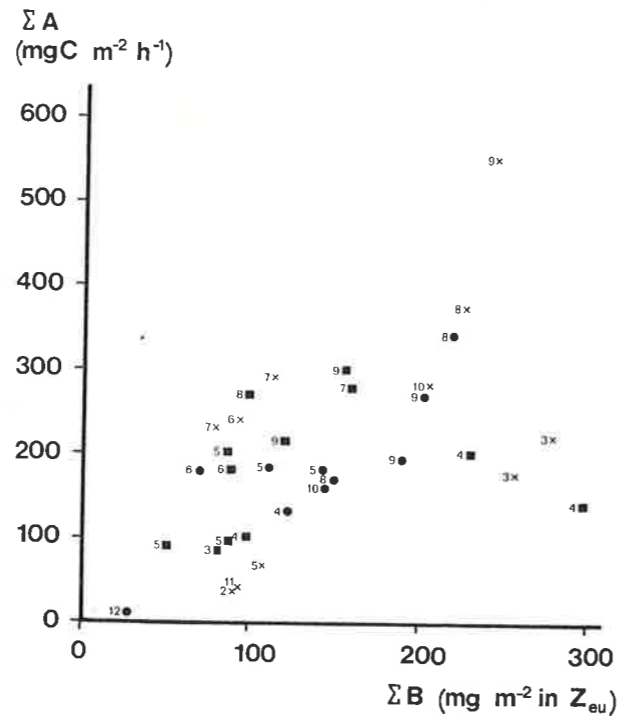


Fig. 22. Primary productivity of phytoplankton per unit area (ΣA) in relation to the chlorophyll a content per unit area of the euphotic zone (ΣB) in Lake Vombsjön, 1971–1973. ■ = 1971, ● = 1972, × = 1973. Figures denote months.

tween ΣA and ΣB ($\text{mg chl } a \text{ m}^{-2}$ in z_{eu}) ($r = 0.77$, $n = 30$ but 4 observations in early spring 1971 and 1973 are not included, Fig. 22).

Photosynthetic capacity: The variation in photosynthetic capacity (P_{\max}) was correlated with temperature, the most significant source of variation (Fig. 23). The calculated linear regression line of the total phytoplankton community gives an average Q_{10} of 1.8. The correlation coefficient between $\log P_{\max}$ and temperature was 0.89. The correlation coefficient was 0.82 for nanoplankton and 0.77 for netplankton. The constant Q_{10} relationship adopted here may be an over-simplification. The temperature coefficient can only be used as a broad summary of the data as the investigated phytoplankton communities in Lake Vombsjön were mixtures of different algae, observed under different environmental conditions (Steemann Nielsen et al. 1962, Jørgensen 1969).

The photosynthetic capacity of nanoplankton was significantly higher ($0.05 > P > 0.01$) than that of netplankton (Fig. 23). Q_{10} values of 2.1 (Talling 1966) and 2.2 (Bindloss 1974) have been reported. Megard (1972) found a lower value of 1.4 for eutrophic Lake Minnetonka, Minnesota.

The seasonal changes of P_{\max} of both the total phytoplankton and nanoplankton communities in relation

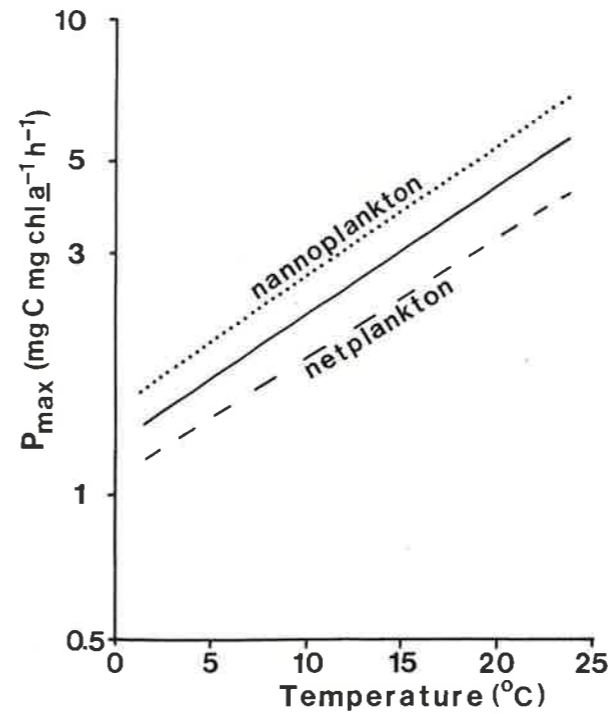


Fig. 23. Relationship between temperature and photosynthetic capacity (P_{\max} , logarithmic scale) of the total phytoplankton community (—) $r = 0.89$, $n = 36$, $Q_{10} = 1.8$, of the nanoplankton community (···) $r = 0.82$, $n = 36$ and of the netplankton community (---) $r = 0.77$, $n = 34$.

to biomass, pH, and temperature were the same during 1971–1973 and are illustrated with values for 1973 (Fig. 24). P_{\max} for total phytoplankton community varied between 0.5 and 6.4, and for nanoplankton community from 0.6 to $8.1 \text{ mg C mg chl } a^{-1} \text{ h}^{-1}$. When temperature was constant there was an inverse relationship between P_{\max} and B at about pH 9.0 or more (Fig. 24). This is shown clearly for Lake George (Ganf 1972) and Loch Leven (Bindloss 1974), possibly due to the greater phytoplankton biomass causing an increase to nearly pH 10, and thereby producing conditions unfavourable for photosynthetic activity.

Another factor limiting the photosynthetic capacity is depletion of nutrients ($\text{PO}_4\text{-P}$, SiO_2) which occurred in Lake Vombsjön mainly at the end of the spring outburst. During this period in 1973, P_{\max} values of the nanoplankton, as well as the total phytoplankton community, varied about $2 \text{ mg C mg chl } a^{-1} \text{ h}^{-1}$, despite increased temperature (Fig. 24). On the other hand, when the surface water was enriched with nutrients in the beginning of September, the value of P_{\max} of the nanoplankton and of the total phytoplankton community increased to 8.1 and 4.8, respectively, despite a temperature decrease during this period (Fig. 24). Consequently, the photosynthetic capacity is influenced by temperature, nutrient concentration, and pH. The va-

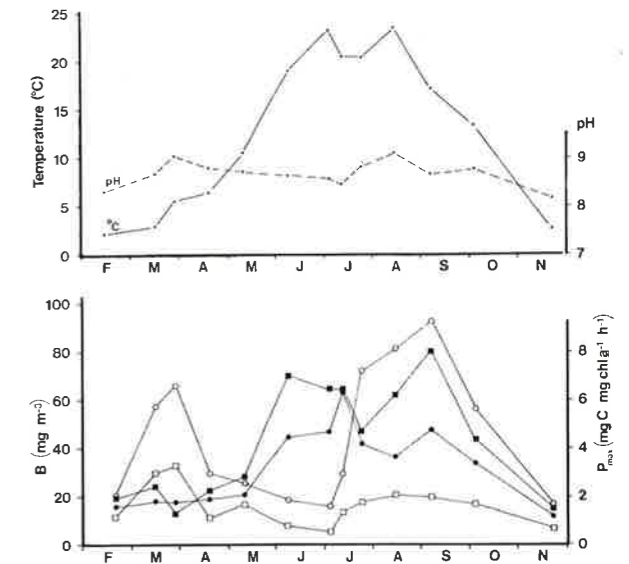


Fig. 24. Seasonal variation of light-saturated rate of photosynthesis per mg chlorophyll a (P_{\max} ; filled symbols), and phytoplankton biomass (B ; empty symbols), estimated as chlorophyll a , in relation to pH and water temperature in Lake Vombsjön 1973. Circles denote the total phytoplankton community, squares the nanoplankton community.

riation of P_{\max} in relation to B throughout 1971–1973 showed a regular seasonal pattern (Fig. 25).

Ryther and Yentsch (1957) found a mean P_{\max} value of 3.7 in natural populations of marine phytoplankton. Malone (1971), working in neritic and oceanic waters, discussed P_{\max} -values as possible indicators of nutrient deficiency (cf. Curl and Small 1965). Values below 3 indicate deficiency situations while values above 5 indicate nutrient-rich waters. It is difficult to apply these limits to freshwater as other factors influencing P_{\max} vary strongly during the year.

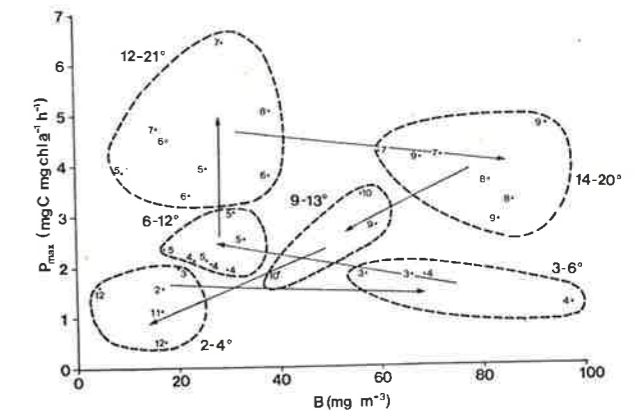


Fig. 25. Yearly cycle of the photosynthetic capacity (P_{\max}) in relation to phytoplankton biomass (B), estimated as chlorophyll a , in Lake Vombsjön 1971–1973. Range of temperature indicated. Figures denote months.

Extrapolation of measured hourly rates of photosynthesis to daily productivity: Vollenweider and Nauwerck (1961) proposed short exposures (1–4 h) to avoid reduction in the rate of photosynthesis with time. Whole day exposures were considered undesirable in the highly eutrophic Lake Vombsjön, so daily rates were converted from hourly rates by applying Talling's (1965) equation:

$$\Sigma \Sigma A = \Sigma A \cdot 0.9 \Delta t \frac{(\log I_0' - \log 0.5 I_k)}{(\log I_0' - \log 0.5 I_k)}$$

where $\Sigma \Sigma A$ = daily integral photosynthesis per unit area.

ΣA = hourly integral photosynthesis per unit area.

I_0' = mean sub-surface light intensity over the daylength (Δt).

I_0' = mean sub-surface light intensity over a 1.5 h exposure period.

Δt = daylength (h).

I_k = photosynthetic characteristic expressing the onset of light-saturation (Talling 1957a).

To make use of this equation the assumption that the photosynthetic activity at a given light intensity remains constant throughout the day must be fulfilled. Due to the turbulence of Lake Vombsjön, gaseous and nutrient exchange between the euphotic and aphotic zones, as well as the gaseous exchange with the atmosphere, must in most cases have been prevented diurnal changes of the photosynthetic activity. The seasonal variation of the daily productivity of the total phytoplankton community and that of the nannoplankton community ranged between 0.05–4.5 and 0.04–2.4 g C m⁻² d⁻¹, respectively (Fig. 26). During June–September the total productivity was nearly always higher than 2 g C m⁻² d⁻¹ while the productivity of nannoplankton varied around 1 g C m⁻² d⁻¹. Low temperatures and low daily light intensities were the main factors limiting the productivity in autumn and winter.

In comparison with the maximum daily production of phytoplankton of lakes in Europe and North America, listed by Vollenweider (1968), the highest value of Lake Vombsjön lies at the upper end of the scale. Talling (1965) recorded 4–6 g C m⁻² d⁻¹ in African lakes and Bindloss (1974) reported 7.9 g C m⁻² d⁻¹ as the maxi-

mum value for Loch Leven. Lakes polluted by industrial and municipal wastes, together with an excess of inorganic phosphorus and nitrogen in summer, seem to have about the same daily production per m² as Lake Vombsjön (Ahlgren 1973, Cronberg et al. 1975, Mathiesen 1971). Phytoplankton communities in these polluted lakes were usually very dense (200–400 mg chl a m⁻³), causing pronounced self-shading and a thin euphotic zone. In comparison, the most productive tropical and sub-tropical oceans yield 0.5–3.0 g C m⁻² d⁻¹ (Stee-mann Nielsen 1954).

In 1971 and 1972, two photosynthesis profiles were measured parallel in Lake Vombsjön on every sampling occasion. One profile of bottles was exposed 1.5 h from noon and the other from noon until sunset. The daily productivity was thus calculated in two ways; the short time exposures by means of eqn 5 (Talling 1965) and the half-day exposures by multiplying these values by 2. An average underestimate of 11% was achieved by multiplying the obtained values for exposures noon – sunset with 2. This percentage is in agreement with estimates by Megard (1972). A 12% underestimate was calculated for nannoplankton. But the ratio A_{max} (nannoplankton)/ A_{max} (netplankton) for every short-term and long-term experiment, respectively, decreased significantly ($0.05 > P > 0.01$), indicating the consequences of greater metabolic activity and of smaller storage capacity in nannoplankton for measurement of primary production (Williams 1964, Odum et al. 1963, Zeuthen 1970), or the partial inhibition of photosynthesis of netplankton algae during long exposures. Long exposures may thus lead to an underestimate of nannoplankton productivity.

The third way of calculating daily productivity from short exposure experiments was to multiply the experimental data by a factor equal to the ratio, "total irradiance per day/irradiance during the exposure time". There was no regularity in the values obtained compared with the in situ values. This method should not therefore be used (Talling 1957, Vollenweider 1971).

Extrapolation of measured hourly rates of photosynthesis to annual productivity: During 1971–1973 the total annual phytoplankton productivity, as estimated by planimetry of the areas under the curves of daily rates, was

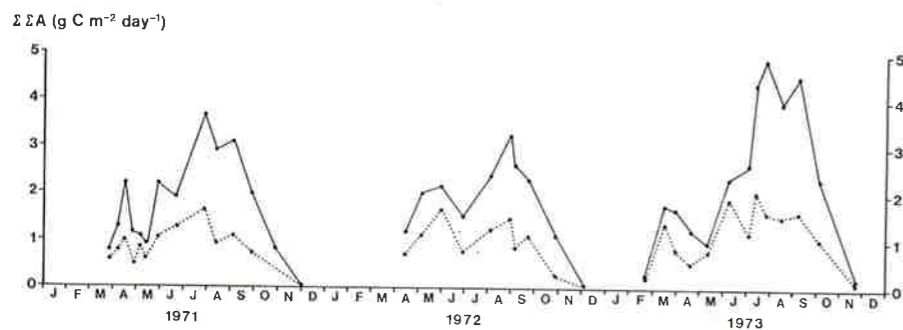


Fig. 26. Seasonal changes in calculated daily photosynthetic productivity ($\Sigma \Sigma A$) of the total phytoplankton community (—) and that of the nannoplankton community (....) in Lake Vombsjön 1971–1973.

Tab. 3. Total incident radiation, annual phytoplankton productivity, and percentage energy conversion calculations for Lake Vombsjön, Sweden, 1970–1973.

	Total incident radiation (J m ⁻² yr ⁻¹)	Phytoplankton productivity		Percentage total energy converted in photosynthesis
		(g C m ⁻² yr ⁻¹)	(J m ⁻² yr ⁻¹)	
1970	374 × 10 ⁷	505	21 × 10 ⁶	0.6
1971	378 × 10 ⁷	485	20 × 10 ⁶	0.5
1972	358 × 10 ⁷	450	19 × 10 ⁶	0.5
1973	399 × 10 ⁷	655	27 × 10 ⁶	0.7

485, 450, and 665 g C m⁻² yr⁻¹, respectively. For the same periods, annual nannoplankton productivity was 225, 230, and 315 g C m⁻². Thus, nannoplankton contributed about 50% of the annual productivity in Lake Vombsjön. In 1970 the total phytoplankton productivity, as calculated from noon-sunset exposures, was 460 g C m⁻², of which 40% was photosynthesized by nannoplankton (Gelin 1971). Mean annual productivity in 1970 through 1973 was estimated to 525 g C m⁻². In comparison with classification schemes of Vollenweider (1968) and Rodhe (1969), Lake Vombsjön should be considered as "eu-polytrophic" or "eutrophic polluted". However, these schemes of classification do not take into account differences between stratified and unstratified lakes. Thus, the mean annual productivity of unstratified Loch Leven was 785 g C m⁻² (Bindloss 1974) while the annual productivity of stratified Lake Esrom, Denmark (Jónasson et al. 1974) and Lake Erken, Sweden (Rodhe 1958) was 240 and 104 g C m⁻², respectively. If Lake Vombsjön had been stratified throughout the summer, productivity would have been much lower, depending on the limiting effects of nutrients.

Assuming 1 g C = 41 900 J (Winberg 1971) the percentage of total energy converted in photosynthesis 1970–1973 varied between 0.5 and 0.7% (Tab. 3). This energy conversion is twice as large as that in Lake Esrom (Jónasson 1972), but lower than reported values from Loch Leven (Bindloss 1974).

4. Summary

1. Biomass of nannoplankton (< 20 μm), estimated as chlorophyll *a*, was greatest in early spring before the grazing pressure by zooplankton began. During summer the variation in abundance of nannoplankton was small. There was a 10-fold variation of nannoplankton biomass throughout the year compared with a 25-fold variation for netplankton biomass.

2. Primary productivity of nannoplankton per unit area in relation to the total phytoplankton community was greatest (about 80%) in early spring when nutrient concentrations were high but light intensity and temperature low, and at the beginning of summer after nutrient depletion. In late summer when surface water was en-

riched with nutrients after short stratification periods and temperature was high, blue-green algae (netplankton) dominated.

3. Good correlation between biomass and productivity per unit volume of nannoplankton, and also for the total phytoplankton community, was observed. The total phytoplankton biomass per unit volume was a relatively good index of productivity per unit area.

4. Significant difference in the photosynthetic capacity of nannoplankton as compared to netplankton was found.

5. Photosynthetic capacity was determined by temperature, nutrient concentration, and phytoplankton biomass, when the latter caused a pH > 9.

6. High background level of non-algal light extinction was observed, caused by total circulation of the water and rapid replacement time.

7. Mean annual productivity of the total phytoplankton community was calculated to 525 g C m⁻² of which about 50% was photosynthesized by nannoplankton.

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