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Władysława WOJCIECHOWSKA

Institute of Natural Basis of Plant Production, Academy of Agriculture, Akademicka 15, 20-934 Lublin, Poland

CORRELATION BETWEEN BIOMASS, CHLOROPHYLL-A, PHOTOSYNTHESIS AND PHYTOPLANKTON STRUCTURE IN A LAKE

ABSTRACT: Investigations were carried out over one growing season (April-November) in 16 series, each lasting 3 consecutive days. Biomass, chlorophyll-a concentration and primary production were measured every day. The following have been found: (1) lack of an unequivocal correlation between these three parameters, (2) variation in the proportion of chlorophyll-a in phytoplankton biomass in relationship to phytoplankton structure, cell age and light, (3) daily variation in phytoplankton populational structure, (4) limitation of photosynthesis by light, depending on phytoplankton structure.

KEY WORDS: Lake, phytoplankton biomass, primary production, chlorophyll-a, dominant species, *P* : *B*.

1. INTRODUCTION

The relationship between phytoplankton biomass, chlorophyll concentration and primary production has often been presented in the literature (Kalff 1972, Munawar and Burns 1976, Desortová 1981, Rai 1982). The quantity of phytoplankton biomass has also been estimated on the basis of chlorophyll-a concentration, but the fact is not always taken into account that the concentration depends on many factors (Micheeva 1970, Pyrina and Elizarova 1971).

Some investigators think the correlation between phytoplankton biomass and production is a direct one (Nauwerck 1963, Findenegg 1964), while others (Vollenweider 1969, Micheeva 1970) maintain that the intensity of phytosynthesis is not always proportionate to phytoplankton abundance.

Presented in this paper are data from measurements of phytoplankton biomass, chlorophyll-a concentration and primary production, all assessed simultaneously and with a high frequency to record daily variations. Subsequently a trial was made to establish the relationships between the quantities analysed, and whether a certain measurement frequency throughout the growing season is needed to reveal these relationships.

2. LAKE DESCRIPTION

The research was carried out in Lake Bikcze, in the Łęczna – Włodawa Lakeland (middle-eastern Poland), a polymictic water body 85 ha in surface area and 3 m in maximum depth (Wilgat 1953). Originally defined as a eutrophic lake (Brzęk et al. 1975), it is now known (Wojciechowski 1976) to have been undergoing a gradual de-eutrophication since 1969. The de-eutrophication process started after the lake had been embanked. Its embankment has reduced the impact of the catchment area and the neighbouring acid, ombrophilous peat bogs.

3. METHODS

All the investigations were carried out over one growing season (1 April – 6 November 1979) during 47 periods at one mid-lake station with a depth of 2.25 m. Every month investigations were made in two series (for 3 consecutive days followed by a 4-day break and then another 3 consecutive days), exceptionally in May and September three 3-day series were carried out.

In the plankton two fractions were distinguished – nannoplankton (< 60μm) and net plankton, that is, microplankton (> 60 μm). For the assessment of chlorophyll concentration and primary production the nannoplankton was isolated prior to measurements by filtering the water through bolting cloth. In the microscopic estimation of phytoplankton biomass the fractions were distinguished on the basis of micrometric measurements of individuals of algae.

Water samples for all the investigations were collected with a 2 dm^3 Patalas (1954) type sampler. Samples to be used for microscopic analyses of the phytoplankton, biomass estimation, and for chlorophyll-a content measurements, taken from three layers: 0.5, 1.0 and 1.5 m (because of the sediments suspended below), were pooled to form one joint sample. This was subsequently sampled for chlorophyll examination (each sample consisted of 2 dm^3 water), and a separate sample (0.25 dm^3) for microscopic examination of the phytoplankton and for biomass measurements.

Plankton photosynthesis (primary production) was measured by the oxygen method (Vollenweider 1969) in light and dark bottles (of the volume of 175 ± 5 ml) exposed for 24 h (from sunset to sunset) at the depths of 0.7 and 1.2 m, i.e., in the euphotic layer, from which the water in bottles came. Measurements were made in two replications, separately for total phytoplankton and nannoplankton. Since no significant differences were found between the two depths, 0.7 and 1.2 m, the final result was obtained by calculating the mean for both depths and both replications.

Chlorophyll analyses were always started on the sampling day. A specified amount of each sample (from 0.5 to 2 dm^3, depending on the natural phytoplankton concentration) was filtered through GF 82 glass fibre filters (Whatman) and then extracted in 90% acetone (for 12 h at 4°C in darkness). Light absorption by the supernatants was measured with a spectrophotometer (Spekol). The final chlorophyll-a concentration per dm^3 water was calculated by using Lorenzen's formula (according to Vollenweider 1969).

Phytoplankton abundance was determined with the inverted microscope, using Utermöhl's method (following Vollenweider 1969). In each sample the numbers of every algal species were determined, as was also the volume by comparisons to the appropriate geometrical solids. The volume of twenty individuals of each species was calculated (only in the case of low-abundance species was a smaller number taken into account). Algal volume was expressed in biomass, assuming that the specific weight of all plankton algae equals 1.0.

Gross primary production was expressed as the amount of carbon assimilated or energy fixed, on the assumption (following Vollenweider 1969) that 1 g oxygen released corresponds to 0.312 g carbon, or 15 J energy. Chlorophyll-a concentration was presented in weight units of its total quantity, and for comparing it with the production or biomass – as the amount of carbon contained in it (calculated stoichiometrically). Phytoplankton biomass (total and of nannoplankton) was presented in wet-weight units or in carbon units, assuming (following Vollenweider 1969, Micheeva 1970) its constant proportion equal to 9.5% of algal wet weight. All data concerning primary production, chlorophyll-a concentration and phytoplankton biomass were referred only to water volume unit (dm^3).

At all sampling dates the water transparency (with Secchi's disc), light transmission (%/m) (with selenium photocell, according to Matusiak and Wojciechowski 1975) and isolation (with Stoke's heliograph) were measured. Data from the measurement of the last two factors have been used for the calculation (using Angström's formula) of the amount of luminous energy in the range of photosynthetically available radiance or PAR (on the basis of tables and Simmer's nomographs indicating PAR proportion in the total luminous energy, depending on the latitude and cloudiness – unpublished data) on the surface of the water and at the depths of 0.7 and 1.2 m. PAR was expressed in $J \cdot cm^{-2} \cdot d^{-1}$.

4. RESULTS

4.1. VARIATION IN BIOMASS, PROPORTION OF FRACTIONS AND PHYTOPLANKTON TAXONOMIC STRUCTURE

Total phytoplankton and nannoplankton biomass quantities in all the study periods have been presented in Figure 1. The lowest biomass throughout the growing season was recorded in April, October and November, the highest in the first ten-day

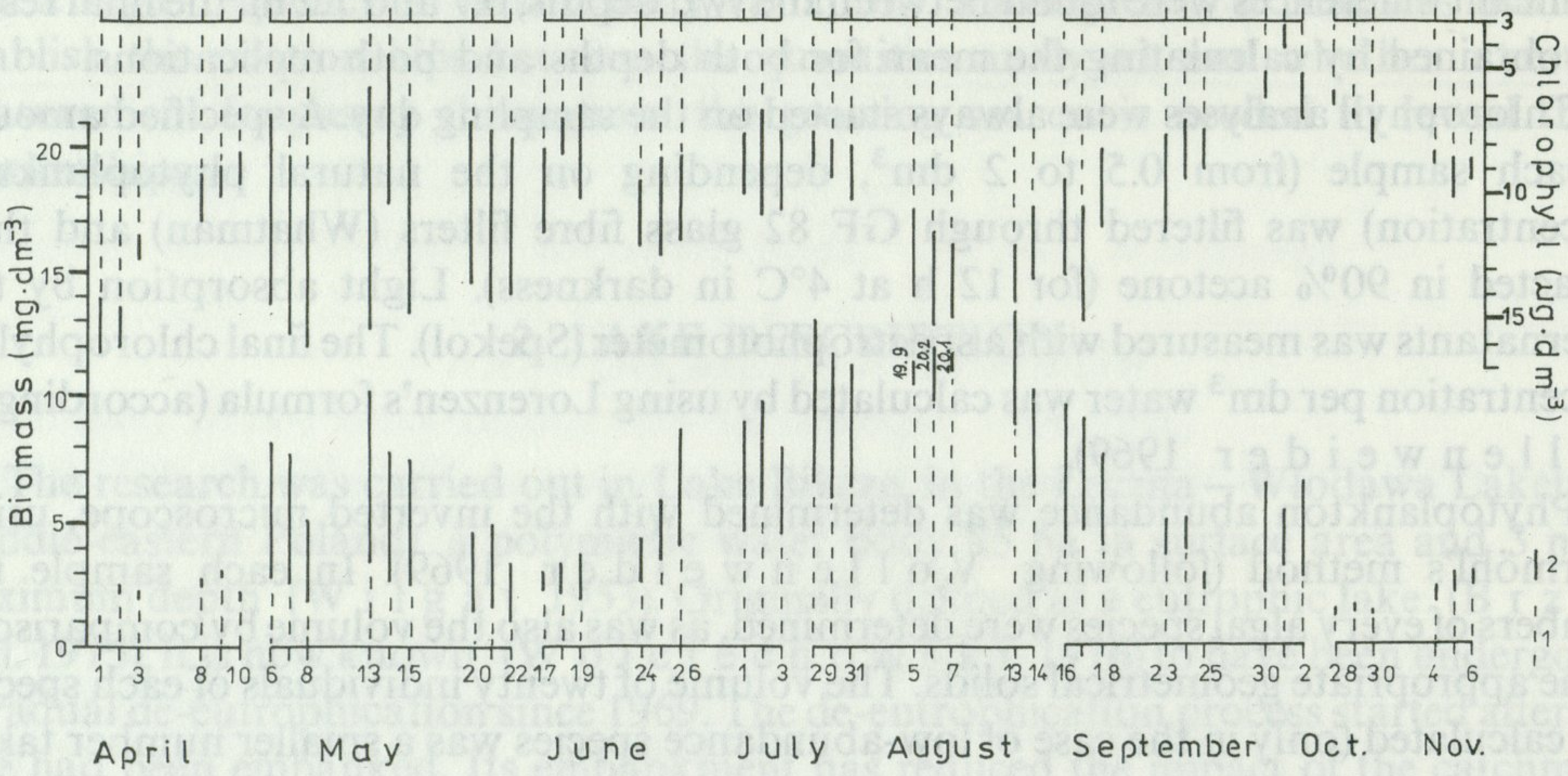

Fig. 1. Daily variation in phytoplankton biomass and concentration of chlorophyll-a in different study periods

1 — nannoplankton (< 60 μm), 2 — microplankton (> 60 μm), 1 + 2 — total phytoplankton

period of August. All-season variation in these values ranged from 1.1 to 20.2 mg·dm^{-3}. Variations between days also showed a generally small amplitude, not exceeding 25% during 24 h. Greater changes were recorded only between June 25th and 26th (47%) and between September 24th and 25th (45%). In many 3-day series a steady increase or decrease in biomass was observed. There also the variation over 48-hour periods was mostly equal to or below 25%, and only between June 24 and 26 was an increase by 100%, and between September 23 and 25 a decrease by 45% recorded.

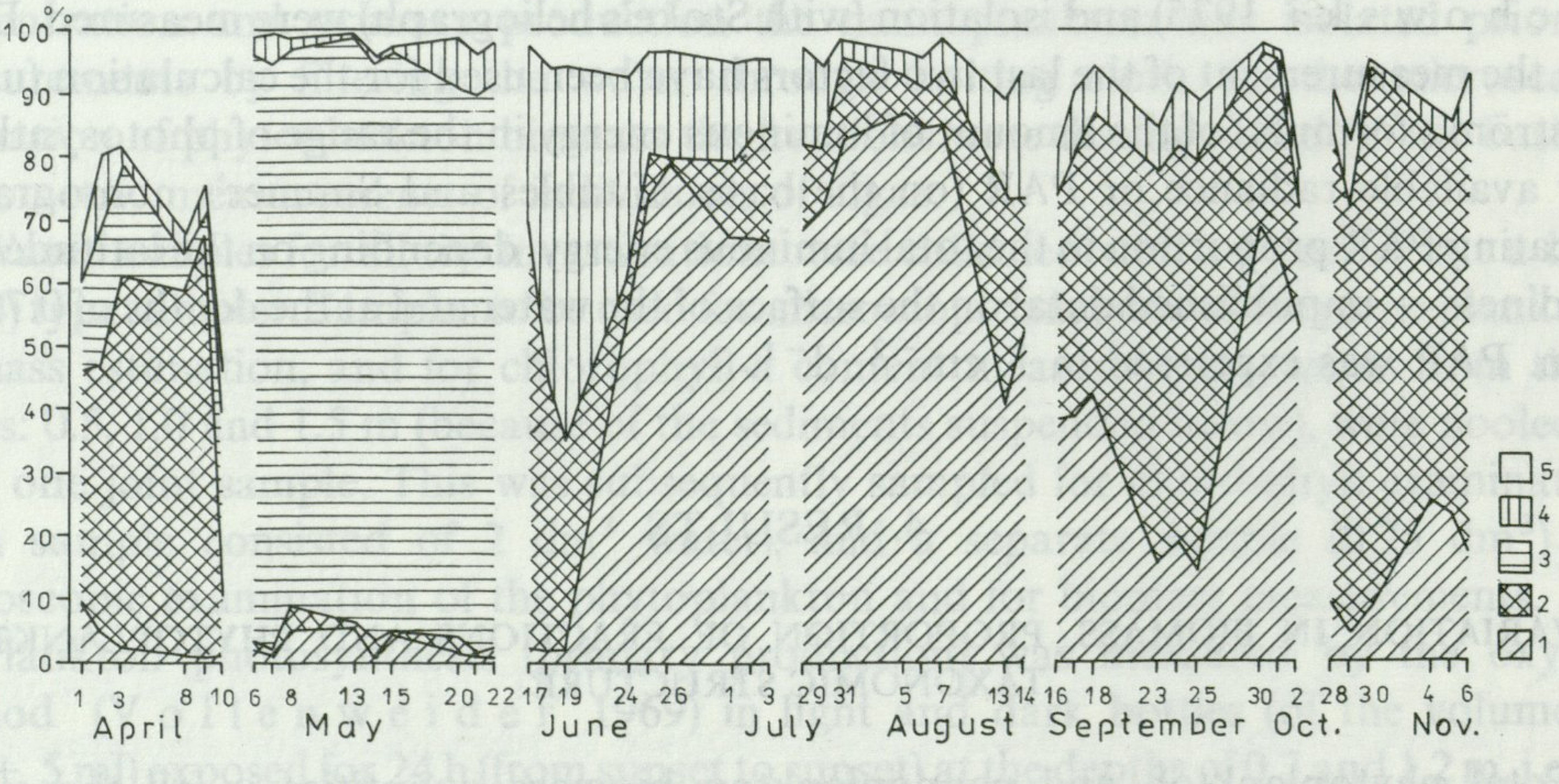

Fig. 2. Daily variation in the percentage of more abundant taxonomic groups in the total phytoplankton biomass in different study periods

1 — Cyanophyta, 2 — Cryptophyceae, 3 — Chrysophyceae, 4 — Chlorophyta, 5 — other groups

Variations in the phytoplankton qualitative structure have been presented in Figure 2 as per cent contributions of the most abundant taxonomic groups to the total phytoplankton biomass. Four taxonomic groups have been distinguished: Cyanophyta, Cryptophyceae, Chrysophyceae and Chlorophyta, whereas Euglenophyta, Dinophyceae and Xanthophyceae, representing small percentages – have been included in the common "others" group. Of the "others" group Bacillariophyceae attained the highest proportion in the total phytoplankton biomass – 30% in April, and about 20% in some periods in September and October. From May to August (inclusive of) their proportion was negligible.

Over the growing season the phytoplankton structure appeared to the most diversified in April. In May *Dinobryon divergens* Imh. formed blooms, which resulted in a dominance of Chrysophyceae (90%) in the phytoplankton biomass. In mid-June, with a clearly lower biomass level than in earlier and later periods, in the species composition of the phytoplankton a transient state between its spring and summer aspects was noticeable. In the last 10-day period of June, in July and in August Cyanophyta constituted the largest proportion in the biomass, while in September, October and in November the highest was the percentage of Cryptophyceae. Only at the turn of September was a temporary decrease in cryptomonad biomass recorded, due to the growth of blue green algae. This may have been a sign of succession after the break-up of the summer phytoplankton that had taken place a week earlier. From September 22 onwards there occurred a conspicuous decrease – from day to day – in the light (PAR) on the surface of the water (on September 18 – 571 $J \cdot cm^{-2} \cdot d^{-1}$, September 22 – 215 and on the following days 204, 207 down to 183 $J \cdot cm^{-2}$ on September 25), and a steady fall of phytoplankton biomass, chlorophyll concentration and primary production in the water. There occurred a fairly rapid growth of Cyanophyta, found between September 25 and 30, with a water temperature fall from 15.25°C to 13°C, and probably a further temperature decrease (down to 12.7 and 12.1°C on the following days) was the cause of the subsequent, rapid retreat of the blue-green algae.

Besides the transition periods between spring and summer (in mid-June), and between summer and autumn (in the second half of September), changes in the phytoplankton structure, noticeable "from day to day" (in the 3-day study series), were usually manifested by a steady decrease in the biomass (in the absolute value and in the proportion in total phytoplankton biomass) of one group and a simultaneous increase of another. For instance, during the first days of April a gradual decrease in the biomass of Cyanophyta was accompanied by a simultaneous increase of the biomass of Cryptophyceae, Chrysophyceae and Bacillariophyceae. Dominant in these groups were: *Cryptomonas* sp., *Mallomonas caudata* Iwanoff and *Cyclotella comta* (Ehr.) Kütz, respectively. A slightly different phase of phytoplankton dynamics was observed in the 8 – 10 April series. An insignificant biomass growth of Cryptophyceae in the period 8 – 9 April (from 1.6 to 1.95 $mg \cdot dm^{-3}$) was followed during the next 24 h (9 – 10 April) by a decrease in biomass (down to 0.2 $mg \cdot dm^{-3}$) due to a rapid decrease in numbers of Cryptomonas with a simultaneous increase in the biomass of Chrysophyceae caused by the growth of *Dinobryon divergens* and Bacillariophyceae (due to a growth in numbers of *Cyclotella comta*). A marked fall of the biomass of Cryptophyceae was also recorded in the period 17 – 19 June (1.5, 0.8 and 0.7 mg · dm^{-3}) which resulted from a growth of the biomass (0.9, 1.6 and 2.3 mg · dm^{-3}) of the developing species of green algae. On June 17 the dominant species in this group was *Pseudosphaerocystis lacustris* (Lemm) Nov., on the following day the highest, almost equivalent biomass values were recorded for two species – *Pseudosphaerocystis lacustris* and *Coenocystis planctonica* Korsch., and on June 19 green algal species could be ordered, according to descending biomass values, as follows: *Botryococcus braunii* Kütz, *Pseudosphaerocystis lacustris, Coenocystis planctonica*, *Pediastrum borgyanum* (Turp.) Menegh., *Scenedesmus quadricauda* (Turp.) Breb., *Oocystis lacustris* Chod. and *Chlorella vulgaris* Beijer. All these species were present in the phytoplankton on each of the three study days, while their biomass changed from day to day due to changes (usually growth) in individual size.

In these periods in which blue-green algae dominated in the total phytoplankton biomass the dominant species was always *Aphanothece clathrata* W. et G. S. West, and in the autumn, particularly at the turn of September, the growth of *Fragilaria pinnata* Ehr. resulted in a high contribution (about 20%) of diatoms.

4.2. VARIATION IN CHLOROPHYLL-A CONCENTRATION AND ITS RELATIONSHIP TO PHYTOPLANKTON BIOMASS

Changes in chlorophyll-a concentration and biomass between successive study periods are presented in Figure 1.

Shown in Figure is also the proportion of nannoplankton in the total chlorophyll concentration and in the biomass of the phytoplankton. At almost all the study dates the proportion of nannoplankton in the biomass and chlorophyll was high, often above 50%. Only in May, when there occurred *Dinobryon divergens* waterbloom, was the percentage of nannoplankton in both quantities clearly lower.

Over the study season variation in chlorophyll concentration ranged from 5.1 to 16.5 μg · dm^{-3}. Chlorophyll concentration and biomass quantity did not in general rapidly change from day to day. An exception was a fall by 35% during the 24 h of 13 – 14 May, and an increase by 40% on the following day, and a similar decrease followed by an increase by about 40% on June 17 – 19.

In the day to day variations in biomass and chlorophyll concentration one of three interrelationships was found: (a) a simultaneous growth or decrease in biomass and chlorophyll concentration in most study periods, (b) a noticeable biomass increase with a nearly stable chlorophyll level (e.g. June 24 – 26), (c) a fall in biomass quantity accompanied by a rise in chlorophyll concentration (May 6 – 8, July 29 – 31).

Calculated for the whole study period, the coefficient of correlation between the total phytoplankton biomass and total chlorophyll was $r = 0.45$ ($n = 47$), statistically significant at the level of < 0.01.

The relationship between total phytoplankton biomass and total chlorophyll content is expressed by the regression in Figure 3, and a 95% confidence interval indicates that the relationship is biased by an error. The determinancy coefficient

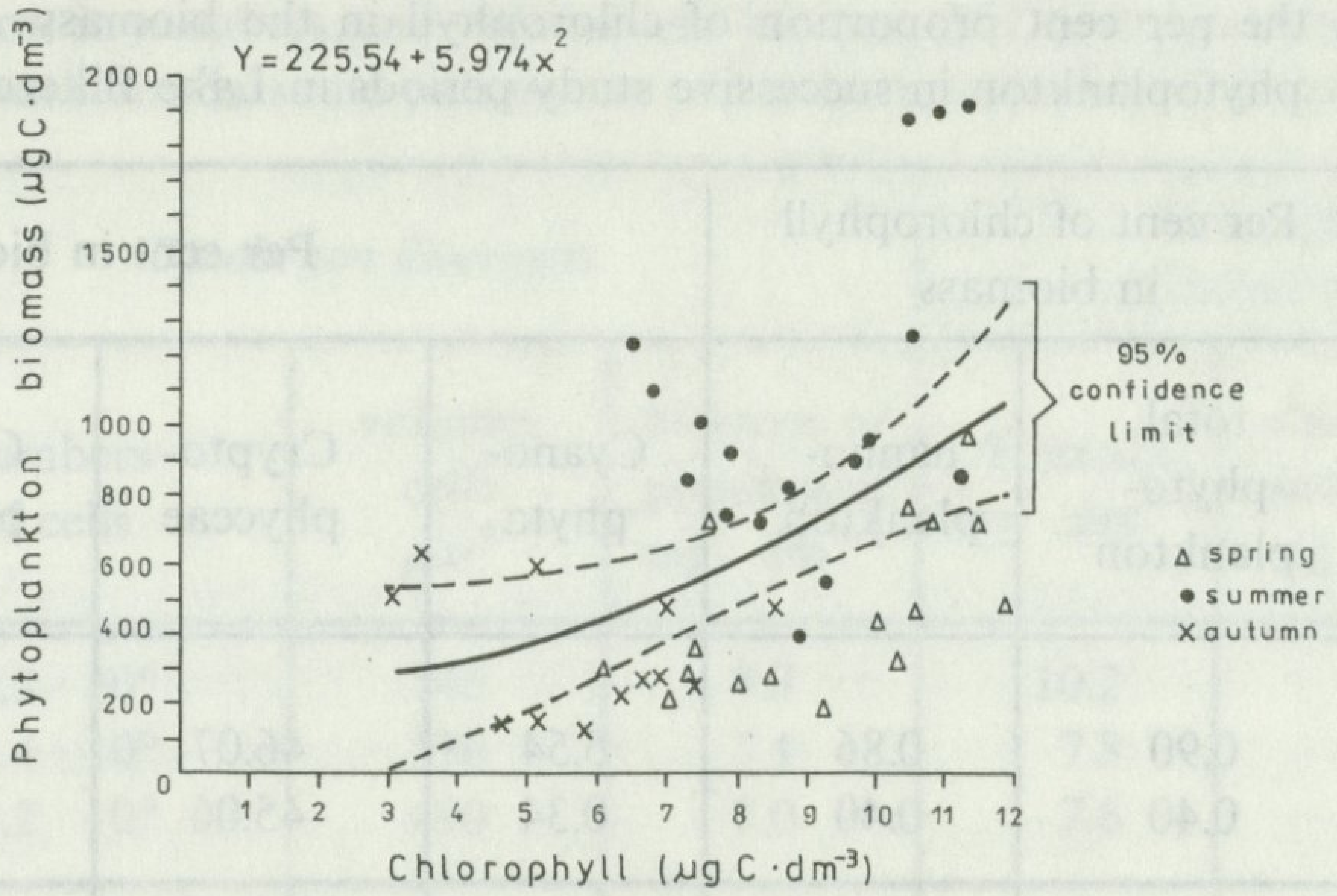

Fig. 3. Relationships between total phytoplankton biomass and total chlorophyll-a concentration, obtained for all (47) study periods

($R^2 = 21.4\%$) that has been calculated indicates that only 21.4% of phytoplankton biomass inferences from chlorophyll concentration can be true.

If of the total of 47 samples all blue-green algae-dominated samples are left out, then the coefficient of correlation between the biomasses and chlorophyll, calculated for samples without blue-green, algae, appears to be highly significant statistically (< 0.001), its value being $r = 0.73$.

The percentage has also been calculated of chlorophyll-a in unit phytoplankton biomass (Table 1). Chlorophyll content in the total biomass of plankton algae on the particular days ranged from 0.07% (29 July and 1 October) to 1.44% (1 April), the average for all (47) days of study amounting to 0.28%. The lowest levels were recorded in July and August (on an average 0.12%) – in the period of the highest levels of total phytoplankton biomass, and the highest in April (on an average 0.65%) and at the turn of October (on an average 0.41%) – when the phytoplankton biomass was at its lowest. The above finding may indicate that an increase in algal biomass causes a decrease in its chlorophyll content.

Chlorophyll content in the nannoplankton biomass was usually (at 33 of 47 dates) higher than in the total phytoplankton biomass. It varied between 0.08 (1 October) and 1.39% (1 April), and the mean for the whole study season was 0.32%. As in the case of total plankton, the lowest values were recorded in July and August (on an average 0.13%), and the highest in April (on an average 0.63%) and at the turn of October (on an average 0.47%).

The taxonomic structure of the phytoplankton was found to have an effect on the content of chlorophyll in its biomass. All those taxonomic groups of algae have been taken into account whose per cent proportion in the biomass at least once exceeded 50%. It was found that chlorophyll content in the biomass was in all periods of dominance of blue-green algae lower than when any of the taxonomic groups dominated.

The effect was analysed of the dominance of one species in the phytoplankton on the content of chlorophyll in relationship to biomass. For this purpose advantage was

Table 1. Variation in the per cent proportion of chlorophyll in the biomass, and the compostion of phytoplankton in successive study periods in Lake Bikcze

Date	Per cent of chlorophyll in biomass		Per cent in biomass			
	total phytoplankton	nannoplankton	Cyanophyta	Cryptophyceae	Chrysophyceae	Chlorophyta
April						
1–3	0.90	0.86	5.54	46.07	17.68	6.91
8–10	0.40	0.40	0.34	45.06	13.03	4.52
May						
6–8	0.23	0.37	2.29	2.05	91.74	3.41
13–15	0.17	0.16	3.48	1.45	91.53	1.15
20–22	0.35	0.48	1.01	1.50	88.06	6.73
June						
17–19	0.32	0.33	19.19	30.77	–	45.15
24–26	0.23	0.27	65.59	3.70	–	22.01
July						
1–3	0.12	0.14	66.74	15.76	–	12.66
29–31	0.08	0.12	74.40	11.56	–	10.53
August						
5–7	0.15	0.11	85.22	6.73	–	4.76
13–14	0.13	0.14	46.05	27.30	–	17.93
September						
16–18	0.16	0.22	39.80	40.84	–	8.32
23–25	0.25	0.27	16.05	63.45	–	8.66
Sept. 30-Oct. 2	0.09	0.17	55.94	31.77	–	2.75
October						
28–30	0.47	0.51	7.84	81.40	–	8.02
November						
4–6	0.35	0.43	21.96	62.19	–	4.60

taken of *Dinobryon divergens* blooms in May when the species represented up to 90% of the total phytoplankton biomass, and variations in its numbers were almost equal to variations in total phytoplankton. Table 2 shows the course of the changes and relationships between them from day to day. An increase in numbers of *D. divergens* cells on May 13–15, with a simultaneous decrease in their volume, indicated cell divisions, which was tantamount to their rejuvenation. This may have caused an increase on those days in the content of chlorophyll in the phytoplankton biomass, as can be seen from Table 2. In the investigation series that followed (20–22 May) *D.*

Table 2. Daily variation in numbers, cell volume and biomass of *Dinobryon divergens* in relationship to variation in some parameters of total-phytoplankton biomass

Dinobryon divergens				Total phytoplankton (including *Dinobryon*)		
Date	numbers of cells	volumes cells μm^3	biomass of population $mg \cdot dm^{-3}$	biomass $mg \cdot dm^{-3}$	chlorophyll concentration $\mu g \cdot dm^{-3}$	per cent. of chlorophyll in biomass
13 May	$12.5 \cdot 10^6$	746	9.3	10.2	16.8	0.16
14 May	$13.4 \cdot 10^6$	530	7.1	7.8	10.8	0.14
15 May	$14.2 \cdot 10^6$	490	7.0	7.6	15.1	0.20
20 May	$8.8 \cdot 10^6$	456	4.0	4.6	14.1	0.31
21 May	$9.9 \cdot 10^6$	435	4.3	4.9	14.7	0.30
22 May	$7.1 \cdot 10^6$	420	3.0	3.4	14.4	0.42

divergens cell volume remained at an almost stable, very low, level, which may have indicated (in spite of a decrease in abundance) a juvenile age of the cells. High also, and almost stable was in that period the total chlorophyll content, in spite of the decrease in total biomass on May 21 – 22, and high too was the percentage of chlorophyll in that biomass (up to 0.42% on May 22) (Table 2).

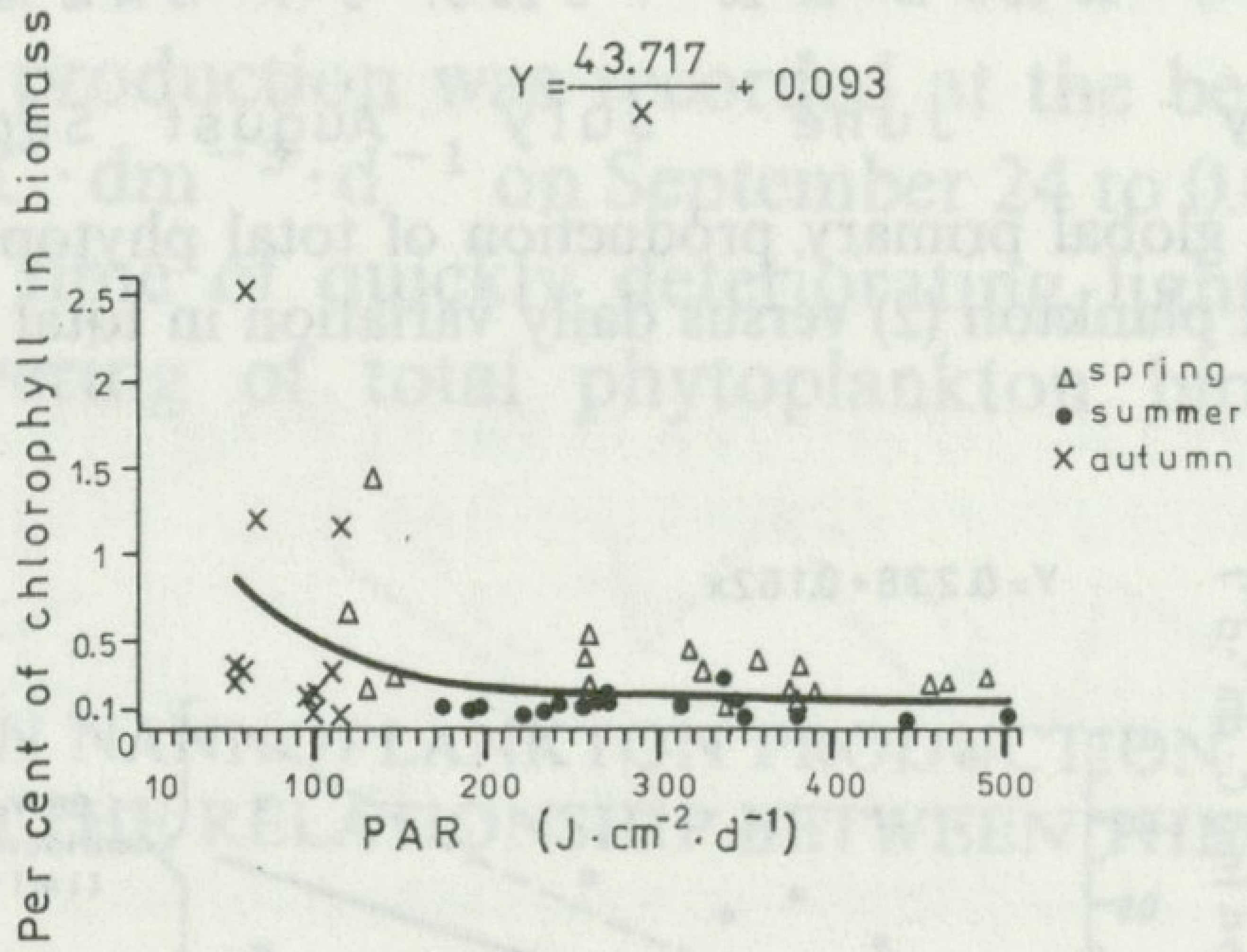

Fig. 4. Relationships between chlorophyll-a percentage in total phytoplankton biomass and PAR at the depth of 0.7 m on the preceding day

Among the relationships studied was also that between the per cent content of chlorophyll in the biomass and the quantity of PAR in the water. It was of an inverse nature – the amount of chlorophyll decreased as the light increased. However, the coefficient of correlation between these quantities was low and insignificant statistically. The highest correlation ($r = -0.37$ for $n = 47$, statistically significant at the level of < 0.01) was found by using the PAR value of the day preceding the day of collecting the samples for biomass and chlorophyll analyses. This indicates that one day of light can result in a noticeable difference in the content of chlorophyll in algal cells. This relationship has been presented graphically in Figure 4. The probable cause of values dispersion around the regression curve is the seasonal variation in species composition; the most distant from the curve are autumn samples dominated by Cyanophyta and Cryptophyceae.

4.3. PLANKTONIC PRIMARY PRODUCTION AND ITS RELATIONSHIP TO THE BIOMASS

Values of the global primary production of total plankton on individual study days ranged from 0.08 to 0.69 mg C · $dm^{-3} \cdot d^{-1}$, the lowest values having been recorded for the calendar autumn and the highest usually for summer. Presented in Figure 5 are between-day differences in production versus daily biomass variations.

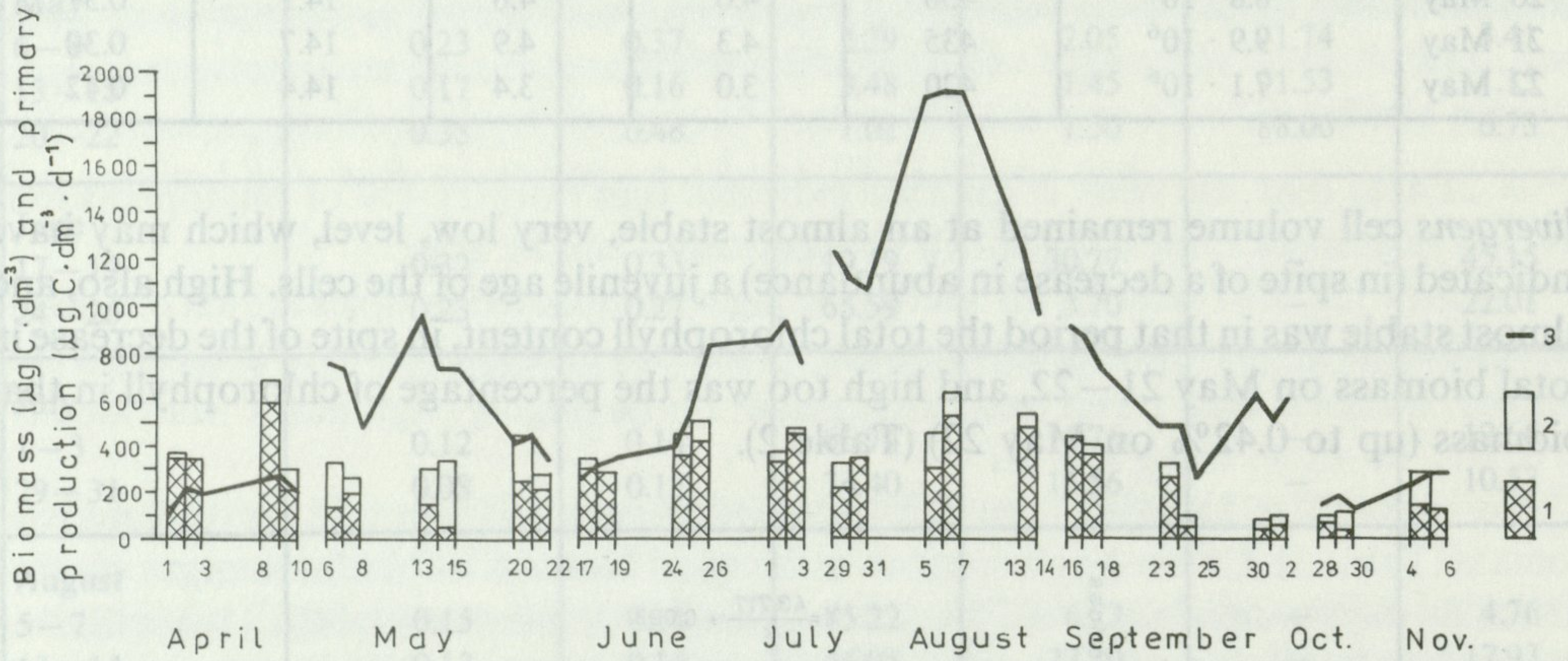

Fig. 5. Daily variation in the global primary production of total phytoplankton (total column height), nannoplankton (1) and net plankton (2) versus daily variation in total phytoplankton biomass (3)

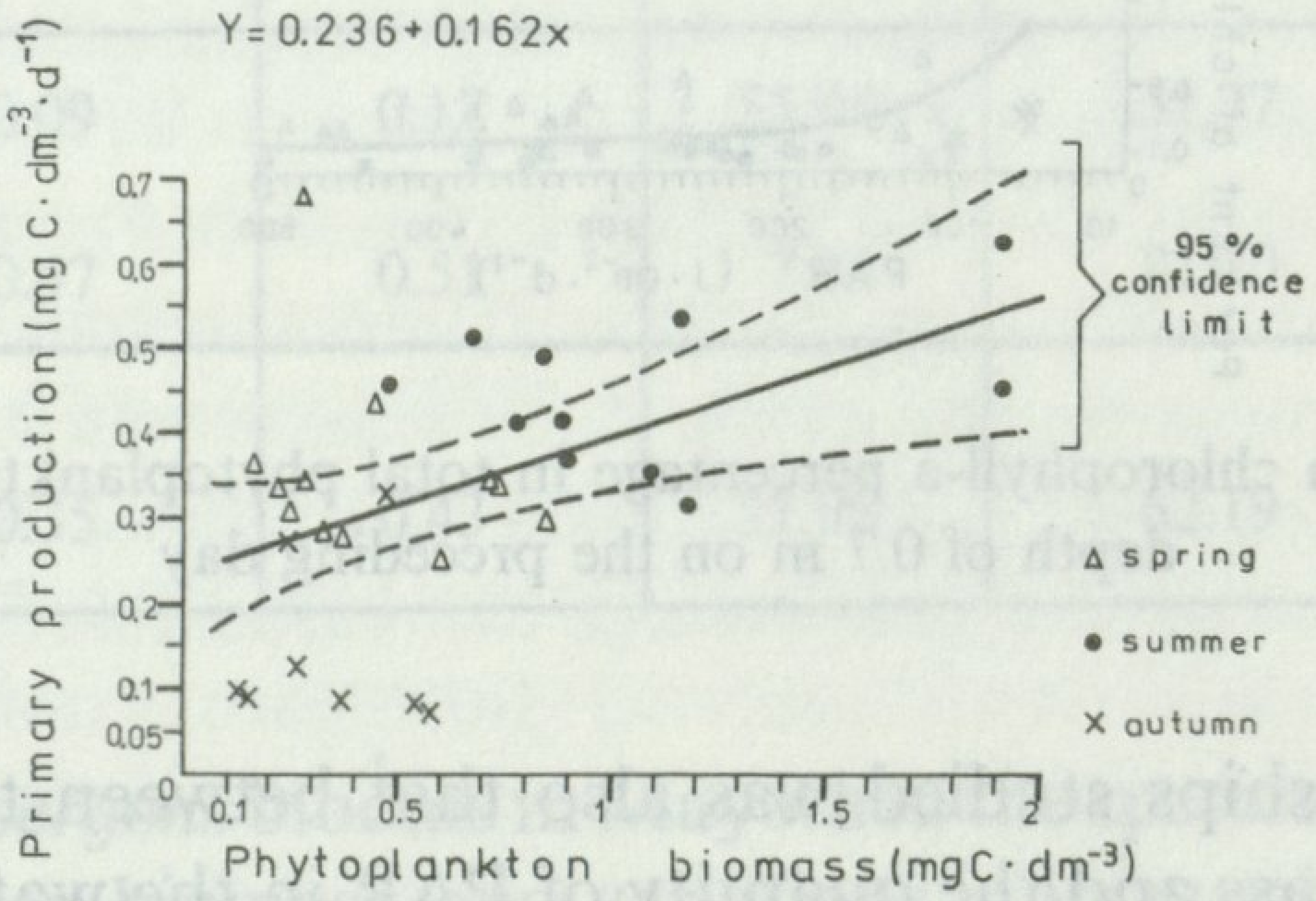

Fig. 6. Relationships between primary production and total phytoplankton biomass recorded for all (47) study periods

The coefficient of correlation between primary production and biomass was $r = 0.50$ ($n = 31$), statistically significant at the level of < 0.01; the course of the regression curve (Fig. 6) indicates a direct relationship between production growth and biomass increase. However, the 95% confidence interval indicates that this relationship is not "close".

A detailed analysis of daily variations in the production and biomass of total phytoplankton has shown that only in full autumn (28 – 30 October and 4 – 6 November) were the lowest values of biomass accompanied by the lowest production. This regularity was also evident, though to a slightly lesser extent, in August when the highest biomass was as a rule accompanied by a high level of production.

A high production was recorded on 9 April, although on the following day the level of production did not differ from the average for that season. That single primary-production peak cannot be attributed to light conditions which were worse, due to cloudiness, on April 9 than on the preceding and on the following day, nor to changes in the total biomass of the phytoplankton or its composition.

Easier to interpret is the production fall recorded on 10 April down to the average level, in spite of improved light conditions and only a slightly lower level of total biomass. Between the evening of April 9 and the evening of April 10 there occurred fairly significant changes in phytoplankton structure – the biomass of Cyanophyta, Chrysophyceae and Bacillariophyceae increased slightly (jointly by 0.08 mg $C \cdot dm^{-3}$), the biomass of Cryptophyceae decreased slightly more noticeably (by 0.18 mg $C \cdot dm^{-3}$), while the biomass of the whole nannoplankton fraction decreased in that time almost twice (from 0.27 to 0.14 mg $C \cdot dm^{-3}$). This was manifested by a rapid decrease in the per cent contribution of nannoplankton to the total phytoplankton biomass, and may have been connected with a lowering of the rate of phytosynthesis of the whole community.

Another rapid fall of production was recorded at the beginning of the calendar autumn – from 0.34 mg $C \cdot dm^{-3} \cdot d^{-1}$ on September 24 to 0.09 mg $C \cdot dm^{-3} \cdot d^{-1}$ on 25 September – at the time of quickly deteriorating light conditions and water temperature, and a lowering of total phytoplankton biomass and chlorophyll concentration.

4.4. VARIATION IN NANNOPLANKTON PRODUCTION AND BIOMASS AND THE RELATIONSHIP BETWEEN THEM

Values of the global photosynthetic production of the nannoplankton on particular study days varied between 0.03 and 0.47 mg $C \cdot dm^{-3} \cdot d^{-1}$, and on an average throughout the study period nannoplankton production represented about 60% of the primary production of total plankton. Daily variations in nannoplankton production versus daily variations in the production and biomass of total phytoplankton have been presented in Figure 5.

The coefficient of correlation between nannoplankton production and biomass was equal to $r = 0.49$ ($n = 31$), and was statistically significant at the level of < 0.01, and very similar to that for total phytoplankton.

Being almost permanently high, the proportion of nannoplankton in the primary production of total plankton appeared to be conspicuously lower in May and October. In May, the lower nannoplankton production and its proportion in total biomass were most likely caused by the dominance in the phytoplankton of *Dinobryon divergens* which formed large colonies. In October, the low production of nannoplankton and of total phytoplankton could probably be attributed to a "gap" between the summer and autumn aspect of the phytoplankton community. As late as the end of October and beginning of November, a multiplication could still be seen in the proportion of cryptomonads and diatoms leading on to a gradual growth of nannoplankton and net plankton production.

A particularly high proportion (on an average about 96%) of nannoplankton in the primary production of total plankton in April was obvious with a high percentage of Cryptophyceae in the total biomass of the phytoplankton. In summer nannoplankton accounted for over 70% of the primary production of total plankton, although *Aphanothece clathrata* dominated in the biomass. During the filtering of samples some colonies, less than 60 µm in size, of this species passed through the net meshes.

4.5. SEASONAL RELATIONSHIPS AND CORRELATIONS BETWEEN PLANKTON PRIMARY PRODUCTION AND CHLOROPHYLL CONCENTRATION

In most of the successive study periods values of the overall primary production of total plankton and of total chlorophyll-a level increased or decreased simultaneously (Fig. 7). The most conspicuous disagreement – an increase in production accompanied by a chlorophyll concentration fall – was recorded in the period 3–9 April, although as early as the following day both quantities diminished. This irregularity has already been analysed (in Section 4.3).

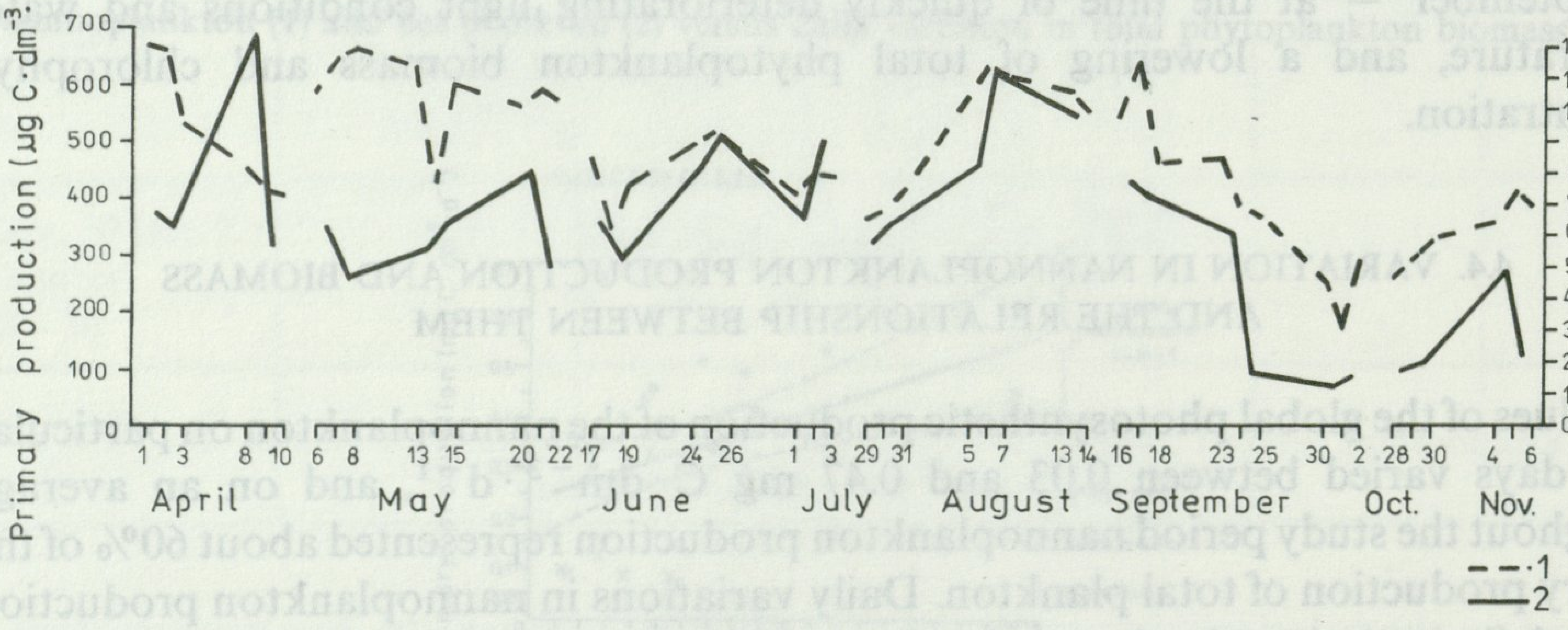

Fig. 7. Course of seasonal variation in total chlorophyll-a concentration (1) and total-plankton primary production (2)

Calculated for the whole study period, the coefficient of correlation between variations in the primary production of total plankton and total chlorophyll level, was equal to $r = 0.62$ ($n = 31$); it was statistically significant at the level of < 0.001, and had a similarly high value ($r = 0.65$) for the nannoplankton fraction, being statistically significant at the level of < 0.001.

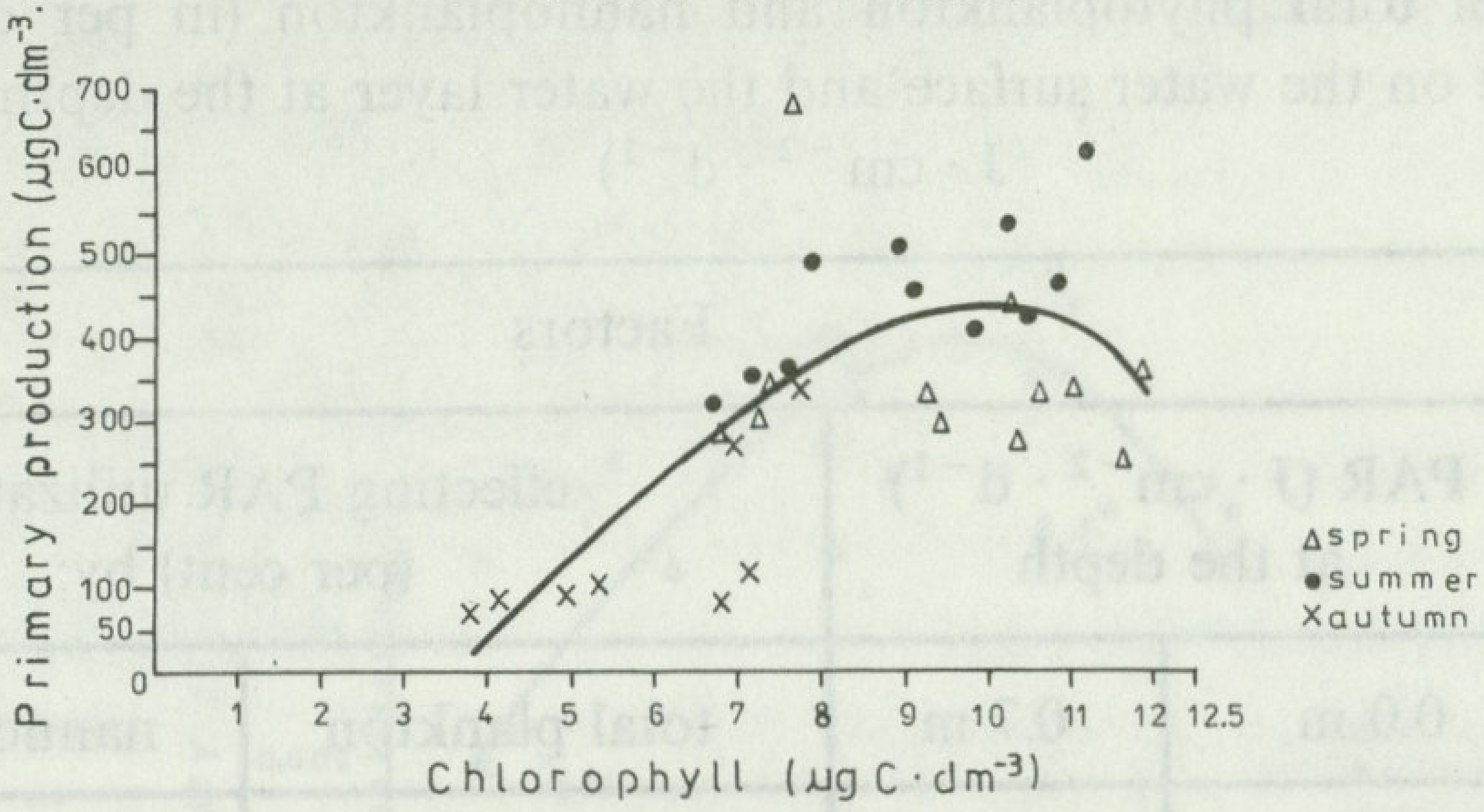

Fig. 8. Relationships between total-plankton primary production and total-chlorophyl-a concentration recorded for 47 study periods

The regression function, presented in Figure 8, may confirm a high correlation between these parameters. The course of the function indicates, however, that there exists a direct, linear and proportionate relationship only to a production level of about 0.45 mg $C \cdot dm^{-3} \cdot d^{-1}$, and a chlorophyll concentration equal to about 10 μg $C \cdot dm^{-3}$. With a further increase in chlorophyll content primary production drops, probably due to self-shading. Values most distant from the regression line were usually found in spring and summer, that is, in periods with the highest level of both primary production and chlorophyll concentration, and with a range of variation of these quantities narrower than in autumn. In spring the primary production of total plankton varied between 0.26 and 0.69 mg $C \cdot dm^{-3} \cdot d^{-1}$, in summer 0.32–0.63, and in autumn 0.08–0.34, and chlorophyll concentration 7.1–12.0 μg $C \cdot dm^{-3}$, 6.5–11.2 and 3.0–8.5, respectively.

4.6. SEASONAL RELATIONSHIPS AND CORRELATIONS BETWEEN PLANKTON PRIMARY PRODUCTION AND PAR INTENSITY IN THE WATER

The use of luminous energy in the photosynthesis of total plankton amounted on an average, for the whole study period, to about 3% of the PAR quantity falling on the water surface, and about 7% of that reaching the depth of 0.7 m. The contribution of nannoplankton in both cases amounted to 67% (responsible for the remaining 33% was therefore net plankton). In the study season variations in relative values of the utilization of the PAR reaching deep water layers for the primary production of total plankton ranged from 3.0 to 23.3%, and nannoplankton used about 0.7 to 11.1% of the total amount of PAR in the water. Daily variations in these values have been presented in Table 3. From differences between the values given for total plankton and nannoplankton the amount of PAR utilized by the net plankton can be determined. In most periods nannoplankton dominated over microplankton in PAR utilization, and only at 8 dates (3 in May and 5 in autumn) did net plankton dominate.

A comparison of the variation in the amount of PAR and in its utilization in phytoplankton production in pairs of consecutive days has shown that in the majority of cases (in 11 out of 15) the quantity of PAR increased from day to day, whereas its use

Table 3. Daily variation in energy (PAR) utilization at the depth of 0.7 m in the gross photosynthesis of total phytoplankton and nannoplankton (in per cent) against variation in light on the water surface and the water layer at the depth of 0.7 m (in $J \cdot cm^{-2} \cdot d^{-1}$)

Days	Factors			
	PAR ($J \cdot cm^{-2} \cdot d^{-1}$) at the depth		effecting PAR utilization (per cent) by:	
	0.0 m	0.7 m	total plankton	nannoplankton
2 Apr.	638	258	7.0	6.7
3 Apr.	675	433	3.8	3.8
9 Apr.	474	317	10.4	8.7
10 Apr.	642	417	3.6	2.3
7 May	311	131	12.9	4.5
8 May	313	170	7.4	5.0
14 May	804	392	3.75	1.6
15 May	634	298	5.6	0.8
21 May	927	384	5.6	2.9
22 May	618	265	5.2	3.9
18 June	943	491	3.5	2.9
19 June	984	458	3.0	3.0
25 June	684	265	8.4	6.35
26 June	1039	397	6.3	5.0
2 July	521	198	9.1	8.5
3 July	977	405	5.9	5.2
30 July	890	501	3.1	2.1
31 July	809	368	4.7	4.7
6 Aug.	507	194	11.5	7.3
7 Aug.	919	368	8.2	6.65
14 Aug.	654	308	8.4	7.3
17 Sept.	578	242	8.4	8.4
18 Sept.	571	278	7.2	6.1
24 Sept.	207	112	14.4	11.1
25 Sept.	183	100	4.5	2.5
1 Oct.	168	103	3.6	0.7
2 Oct.	233	128	3.3	1.3
29 Oct.	104	59.5	7.8	3.5
30 Oct.	160	92	5.4	1.3
5 Nov.	97	57	23.3	8.9
6 Nov.	125	74	8.1	7.3

in the production of total plankton dropped. In more than a half of the total number of cases (8 : 15) differences in energy utilization by the two fractions distinguished were opposed, which in general resulted in a reduction of the amplitude of variation in light utilization by total plankton.

The coefficient of correlation between the primary production of total plankton and the amount of PAR at the depth of 0.7 m was $r = 0.55$ ($n = 31$) at the level of

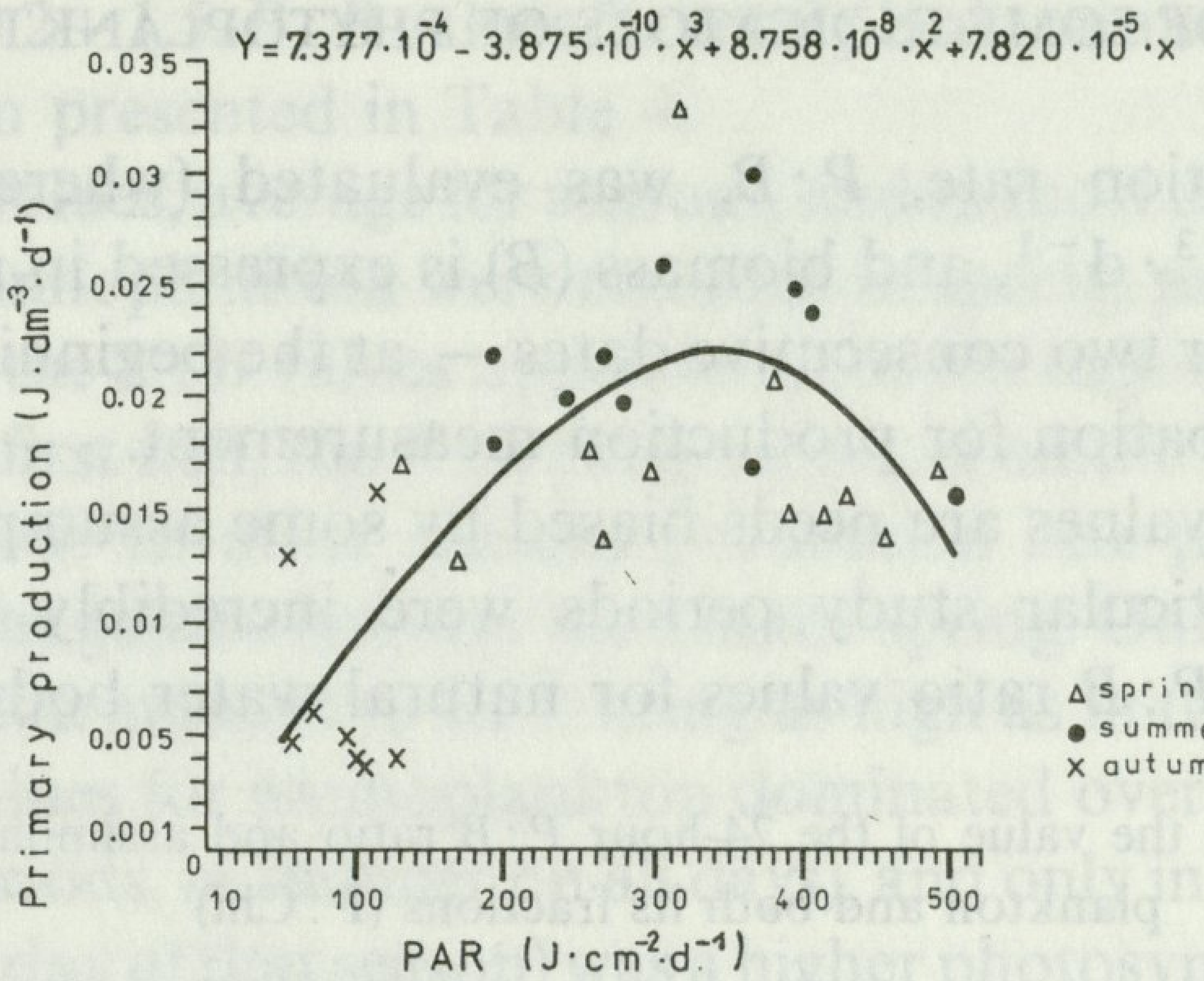

Fig. 9. Relationships between total-plankton primary production and PAR at the depth of 0.7 m recorded for consecutive study periods

significance of < 0.001. The regression function curve (Fig. 9) indicates that the light reaching the depth of 0.7 m limited photosynthesis only to an intensity level of about 250 $\mathrm{J \cdot cm^{-2} \cdot d^{-1}}$, which was manifested by increasing production with growing PAR. Light intensity variations which had no effect on the rate of production (saturation level) ranged from about 250 to 420 $\mathrm{J \cdot cm^{-2} \cdot d^{-1}}$. Above the 420 J value there occurred a state of oversaturation with light, and light inhibited primary production with any further increase in its intensity.

The limitation and saturation ranges covered very similar numbers of points denoting total plankton primary production (13 and 14, respectively), and the smallest number of results (4) were within the inhibition range. But the distribution of the results varied between seasons. All the autumn results were grouped within the limitation range, and most of the spring and summer results — within the saturation range. The distribution of the spring results — with widely varying PAR values and narrow variation in production values (except for April 9) — seems, however, to indicate that throughout that season the phytoplankton was saturated with light.

The highest, also, PAR values in the water (at the depth of 0.7 m) were recorded in spring, although the 24-hour totals of luminous energy falling on the water surface were in many of the summer study periods much higher than those recorded for spring. The cause of the lower light penetration into deeper water layers in summer may have been a higher rate of its absorption by the chlorophyll. The coefficient of correlation between chlorophyll content and light transmission (expressed in per cent per metre) for the whole study period was fairly high, $r = -0.67$ ($n = 47$) and statistically significant at the level of < 0.001. The fact that the high summer chlorophyll concentration was connected with a high biomass of blue-green algae which stayed in the plankton close to the water surface confirms the finding (Steemann-Nielsen and Jorgensen 1968, Tilzer et al. 1975, Reynolds 1982) that blue-green algae were less sensitive than other phytoplankters to the inhibitory effect of high-intensity light.

4.7. ASSESSMENT OF SOME INDICATORS OF PHYTOPLANKTON ACTIVITY

The relative production rate, $P:B$, was evaluated (where production (P) is expressed in mg $C \cdot dm^{-3} \cdot d^{-1}$, and biomass ($B$) is expressed in mg $C \cdot dm^{-3}$) as the arithmetic mean value for two consecutive dates — at the beginning and at the end of a period of sample incubation for production measurement.

Since the $P:B$ ratio values are needs biased by some assumptions, certain absolute values for the particular study periods were incredibly high. According to Micheeva (1970), $P:B$ ratio values for natural water bodies in the temperate

Table 4. Daily variation in the value of the 24-hour $P:B$ ratio and assimilation number of total plankton and both its fractions (P : Chl)

Days	Factors					
	$P:B$ coefficient			assimilation number		
	total plankton	nanno-plankton	net plankton	total plankton	nanno-plankton	net plankton
2 Apr.	2.26	2.36	1.11	1.74	1.95	0.50
3 Apr.	1.57	1.68	0	1.77	2.02	0
9 Apr.	2.59	2.30	7.80	4.77	4.70	5.22
10 Apr.	1.29	0.99	2.87	2.28	1.78	4.87
7 May	0.47	0.48	0.46	1.34	1.21	1.42
8 May	0.43	0.87	0.21	0.97	1.34	0.61
14 May	0.36	0.46	0.31	1.42	2.15	1.13
15 May	0.48	0.21	0.62	1.72	0.63	2.415
21 May	0.99	1.57	0.71	1.94	2.22	1.70
22 May	0.73	1.68	0.27	1.23	1.90	0.60
18 June	1.19	1.33	0.78	2.04	2.34	1.24
19 June	0.85	1.43	0	1.72	2.67	0
25 June	0.97	1.25	0.58	2.02	2.36	1.39
26 June	0.75	1.17	0.315	2.27	3.08	1.12
2 July	0.42	0.73	0.06	2.10	3.03	0.40
3 July	0.59	0.93	0.155	2.68	3.94	0.77
30 July	0.28	0.37	0.18	2.23	1.90	3.49
31 July	0.33	0.63	0	2.27	3.02	0
6 Aug.	0.24	0.31	0.18	2.01	1.83	2.46
7 Aug.	0.33	0.52	0.13	2.65	2.91	1.94
14 Aug.	0.48	0.66	0.18	2.51	2.86	1.40
17 Sept.	0.48	1.04	0	2.26	3.49	0
18 Sept.	0.52	0.87	0.16	2.37	3.01	1.08
24 Sept.	0.70	0.76	0.55	2.49	2.47	2.54
25 Sept.	0.25	0.19	0.43	0.79	0.61	1.31
1 Oct.	0.14	0.07	0.19	1.32	0.32	5.92
2 Oct.	0.16	0.13	0.18	1.36	0.74	2.99
29 Oct.	0.66	0.37	1.86	1.49	0.12	12.44
30 Oct.	0.75	0.21	4.105	1.42	0.38	10.46
5 Nov.	1.10	0.59	2.40	3.04	1.26	23.56
6 Nov.	0.45	0.54	0.19	1.33	1.36	1.10

zone are of the range 0.2 – 1.5. $P : B$ values for total plankton and both its fractions at all study dates have been presented in Table 4.

The highest $P : B$ values, average for seasons, and in most cases the highest also for total plankton and nannoplankton were recorded in spring, particularly in April. For the net plankton also the $P : B$ values appeared to be the highest in spring, in April. In May, especially in its first half, the $P : B$ ratio values of all the fractions were low, and their range was narrow. In other seasons production rate per unit biomass of the individual fractions was generally lower than in the spring. Only in the autumn did the average for net plankton amount to 1.24, being as high as in the spring (1.26). In most study periods $P : B$ values for nannoplankton dominated over those for net plankton (in spring in 9 of 12 periods, in summer on all days), and only in the autumn (except the first and the last study day of that season) was a higher photosynthetic activity recorded for the net plankton biomass.

The range of $P : B$ value variation also differed between seasons. The nannoplankton and net plankton showed the highest dynamics in spring (although its variation was very narrow in May) and autumn, and the lowest in summer. Similar was the dynamics of total plankton, but its amplitude was clearly smaller than that of the individual fractions.

Daily variation in $P : B$ values, some times very wide, was often simultaneous with changes in the taxonomic structure of the phytoplankton, or at least in the quantitative proportions of the different phytoplankters.

As one other phytoplankton-indicator the photosynthetic activity of chlorophyll-a unit weight was taken into account. It corresponds to Ichimura's (1958) concept of "assimilation number" or Talling's (in Vollenweider 1969) "average photosynthetic rate per unit of euphotic population", and was calculated according to the formula mg $C_{ass.} \cdot$ mg chl.-$a^{-1} \cdot h^{-1}$ (the chlorophyll quantities here were arithmetic means for two consecutive days). It provides an index that can describe the trophic state of lakes (Ichimura 1958).

A total-plankton "assimilation number", the arithmetic mean for the whole study season (2.0) could indicate a lake status intermediate between the mesotrophic and eutrophic states, but the values found for particular days ranged from values indicative of the oligotrophic status to those of the advanced eutrophic status. Fully unequivocal index values were recorded throughout the calendar summer. Both the mean for that season (2.3) and the values recorded on individual days (2.0 – 2.7) were typical of a low eutrophic state (Ichimura 1958).

The highest mean values of this index for total plankton and nannoplankton were recorded in summer, and the lowest in autumn. In slightly more than half the total number of cases (in 18 of 31) higher "assimilation number" values were recorded for nannoplankton than for net plankton, but estimated for the whole study season, the activity of unit chlorophyll weight was on an average lower for the nannoplankton (2.06) than for the net plankton (3.03).

Day to day variation in the photosynthetic activity of a chlorophyll unit in total plankton was usually narrow (except on 9 – 10 April, or 24 – 25 September), but it was more conspicuous in individual plankton fractions. Daily variations in the "assimilation number", in spite of the dependence of this indicator value not only on production, but also on chlorophyll concentration, usually coincided with $P : B$ variations (in 3/4 of the total number of cases), and to a lesser extent with variation in chlorophyll concentration and light conditions (in about 2/3 of the total number of cases), and the least with changes in chlorophyll percentage in the biomass (in about 1/3 of cases). So even this index probably depended primarily on the taxonomic composition of the community.

5. DISCUSSION

Many papers (e.g. Blaauboer 1982, Reynolds 1982, Škundina 1983, Tilzer 1984a) describe, partly explain, and even forecast phytoplankton population dynamics and seasonal succession of dominants. The seasonal succession, found in Lake Bikcze, of the taxonomic groups that dominated in the phytoplankton was typical of fertile lakes, and agreed with that described in many papers (Vollenweider 1969, Reynolds et al. 1982).

Differences in numeric ratios between the populations, found in Lake Bikcze on successive days usually resulted from (1) changes in numbers of one species (an increase by multiplication, or a decrease, most likely due to zooplankton feeding), or (2) changes in size (volume) of the individuals or colonies of a species.

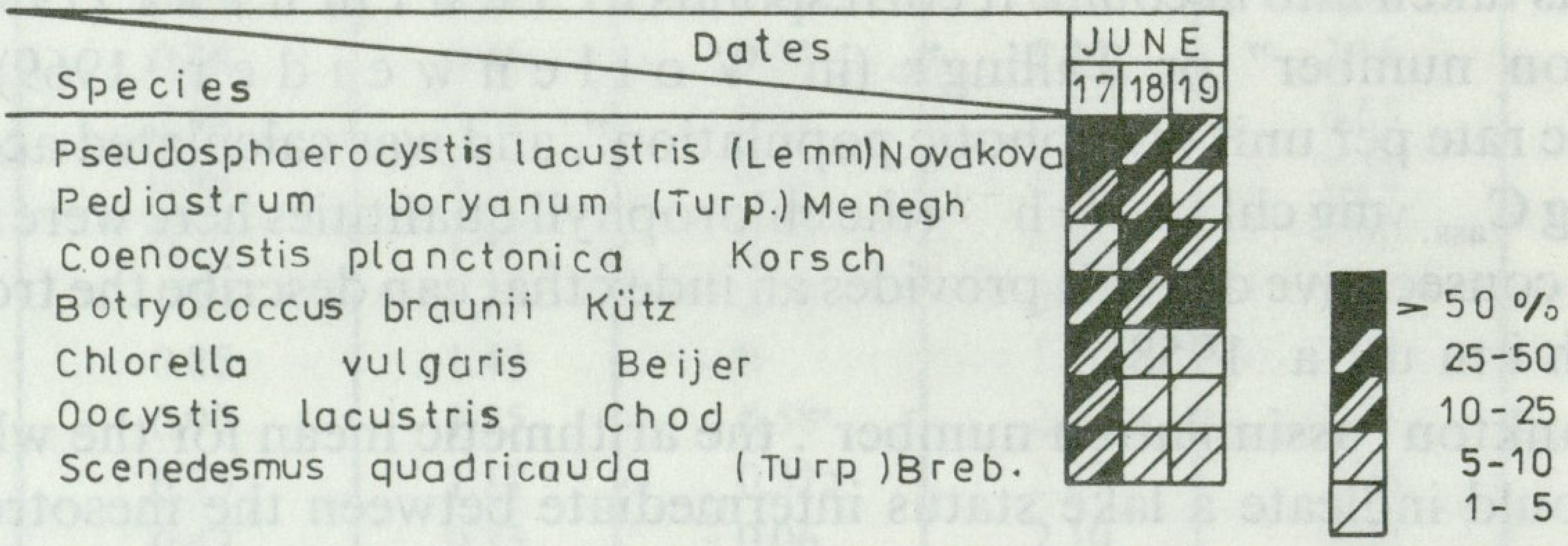

Fig. 10. Changes in species dominance structure in the biomass of planktonic Chlorophyta on three consecutive days in June

Owing to a considerable specific diversity of Chlorophyta and significant biomass levels attained by green algae in June, it was possible to follow the day to day variation of this group. Variations presented in Figure 10, in species dominance in the biomass of Chlorophyta clearly indicated a decrease in the biomass of nannoplanktonic species (e.g. *Chlorella vulgaris*, *Scenedesmus quadricauda*, *Oocystis lacustris*). This resulted, most likely, from the fact that they were fed on by the zooplankton (*Polyarthra vulgaris* Carlin, *Keratella cochlearis* Gosse, *Eudiaptomus graciloides* Lilljebork). In that season, with the rising temperature from day to day (17.8, 19.9, 20.2°C), the activity of the latter (at least their abundance, as recorded for the same lake in June 1971, Brzęk et al. 1975) must have increased.

Biomass decrease of nannoplanktonic species was followed by a growth of the biomass of green-algal net-plankter species (*Botryccoccus braunii*, *Coenocystis planctonica*) due to the growth in size of their cells, which resulted in an increase in the volume of whole colonies. A different kind of daily changes – connected with a growth in numbers (owing to multiplication) of organisms, and a simultaneous decrease in their size (volume) in successive generations – was represented by *Dinobryon divergens* (Section 4.2. and Table 2).

The observation and description of the course of only the above two cases of changes and their mechanisms indicate that they may be frequent, or even common in the phytoplankton, though difficult to notice under natural conditions because they are "masked" by many agents (coincidence of the dynamics of various populations, feeding by zooplankton, sedimentation, horizontal translocations etc.), and their course is fast, due to which an appropriate frequency of daily investigations is needed.

Many authors describe the relationship between biomass and chlorophyll concentration as proportionate (Lund 1970, Elizarova 1974, Desortová 1981), and stress that in deep lakes it is particularly conspicuous in the upper water layers where there is a higher chlorophyll per cent content in the algal biomass (Desortová 1981). It could therefore be expected that in a shallow Lake Bikcze the relationship between biomass and chlorophyll will be very clear. However, calculated for the whole study season, the correlation coefficient between these two parameters showed a low statistical significance ($r = 0.45$ at the level of > 0.01). It became more significant when all glue-green algae-dominated phytoplankton samples were left out ($r = 0.73$, at the level of < 0.001). As a rule, the chlorophyll per cent content in the phytoplankton biomass of Lake Bikcze was also very low in the periods of dominance of blue-green algae. These findings agree with those reported by some authors (Ahlgren 1970, Rott 1978, de Kloet 1982) concerning the relationship between the per cent of chlorophyll in the phytoplankton biomass and the taxonomic composition of the community, and may also indicate that the proportion of blue-green algae in the phytoplankton is of decisive importance to the content of chlorophyll in its biomass.

On the other hand, however, the proportion of chlorophyll in Chrysophyceae-dominated biomass (90% of *Dinobryon divergens*, in May), and in phytoplankton biomass with a varied dominance structure (in April and June) did not show any clear dependence on the taxonomic composition of the community, which may confirm the opinion of those authors who do not ascribe any significance to such a correlation (Elizarova 1974, Desortová 1981).

In addition to a clear dependence of the chlorophyll/biomass relationship on the percentage of blue-green algae, and a low significance of its dependence on the proportions of other taxonomic groups in the phytoplankton, this relationship has also been found to depend, to some extent, on the age of individuals in a populations (as exemplified by *Dinobryon*), on the proportion of nannoplankton in total phytoplankton biomass (a higher chlorophyll/biomass correlation has also been found in nannoplankters by Tilzer et al. 1977), and on daily variation in PAR. The above complex of relationships indicates that chlorophyll concentration in the plankton depends on many factors (Pyrina 1963), and restricts the possibility to accurately forecast chlorophyll content in phytoplankton biomass under natural conditions. It also limits the possibility of replacing a direct measurement of biomass with a measurement of chlorophyll concentration.

The level of the global primary production of total phytoplankton was on the whole determined by the production of the nannoplankton fraction. In most study periods the production of this fraction exceeded 50%, and was sometimes close to 100% of the production of total phytoplankton.

Nannoplankton predominance was usually less conspicuous in the biomass than in production. This was reflected in the $P:B$ ratio values, which were in the majority of cases (22/31) higher for nannoplankton than for net (and total) plankton. The cause of a higher photosynthetic activity of unit biomass in nannoplankton must be sought not only in a more favourable surface-area to volume ratio of the organisms, but also in a higher chlorophyll content in that unit biomass. This may also be indicated by a comparison of $P:B$ values and "assimilation number" for particular periods (Table 4), where a coincidence can be seen of the dominance of one or the other phytoplankton fractions in both coefficients (with only 4 exceptions in 31 periods – 7 May, 30 July, 6 August and 24 September), and a higher PAR utilization by the nannoplankton in the majority of study periods (23/31, Table 3).

Coefficients of correlation between production and biomass, calculated for total phytoplankton ($r = 0.50$) and nannoplankton ($r = 0.49$) were very similar, yet low, and of a low statistical significance at the level of < 0.01. A similarly low correlation between production and biomass was found by Munawar and Burns (1976) and by Rai (1982), although Ostrofsky and Peairs (1981) found a direct and unequivocal relationship between these two parameters. In Lake Bikcze primary production has been found to be more strongly correlated (at a higher significance level) with chlorophyll concentration ($r = 0.62$, $P < 0.001$ for total plankton, $r = 0.65$, $P < 0.001$ for nannoplankton).

The regression curve (Fig. 8) indicates, however, that a direct, linear relationship between chlorophyll concentration and plankton primary production only exists up to a certain level (Section 4.4.), above which any further growth in chlorophyll concentration is followed by a decrease in photosynthesis. Reduction in photosynthesis, caused by a chlorophyll concentration growth, similar to that found in Lake Bikcze, has been described by other researchers (Javornický 1980, Meffert and Overbeck 1985). It may be presumed that this phenomenon is caused by the self-shading of algal cells in a planktonic community. Such an explanation seems to be supported by the diminishing water transparency with each successive study period.

Many authors (e.g. Tilzer et al. 1975, Tilzer 1984b) consider the planktonic photosynthesis-light relationship as depending on time (daylight length, sun angular height), or on depth (reduced light penetration). But the dependence of phytoplankton production on light varies with the species composition of the community (Meffert and Overbeck 1985). In Lake Bikcze a directly proportionate relationship between photosynthesis and light intensity was found only to a PAR level of about 250 $J \cdot cm^{-2} \cdot d^{-1}$ (Fig. 9). The inhibition range (above

$420\ \mathrm{J \cdot cm^{-2} \cdot d^{-1}}$) comparised several spring phytoplankton samples – dominated by Cryptophyceae, and two summer samples in which green algae dominated, which may point to a sciophilous nature of the algae of these taxonomic groups.

The correlations presented in this paper indicate that in any ecological studies dealing with phytoplankton it is necessary to take into account the taxonomic composition, at least a roughly-estimated one, and the dominance structure of the community studied.

6. SUMMARY

Presented in the paper is the relationship between phytoplankton biomass, chlorophyll-a concentration and primary production. The investigations were carried out in a shallow (3 m) eutrophic Lake Bikcze. Biomass was estimated by the micrometric method (by counting and measuring individuals with the aid of the microscope), chlorophyll-a concentration – colorimetrically, and primary production – by the oxygen method. Investigations were continued from April to November in 16 series, each lasting 3 consecutive days, due to which it was possible to observe day-to-day variations in the phytoplankton.

The range of variation in phytoplankton biomass, chlorophyll-a concentration and primary production over 24-hour periods has been found to be narrow (Figs. 1, 5). However, in 3-day series significant phytoplankton-structure changes could be seen (Figs. 2, 10), due to (1) changes in numbers of the particular species (an increase caused by multiplication, or a decrease due to being fed on by the zooplankton), or (2) individual size (volume) changes.

No unequivocal correlation has been found between phytoplankton biomass and chlorophyll-a (Fig. 3). The correlation coefficient was equal to $r = 0.45$, $P > 0.01$. When blue-green algae-dominated phytoplankton samples were left out, the coefficient of correlation between biomass and chlorophyll was equal to $r = 0.73$, $P < 0.001$. Chlorophyll-a per cent content has been found to vary considerably, depending on the plankton fractions, taxonomic structure, cell age and light intensity (Tables 1, 2, Fig. 4).

The global primary production of total plankton was determined by nannoplankton production (Fig. 5). Nannoplankton predominance was, however, less marked in the biomass than in production, as indicated by the $P : B$ ratio values which were in the majority of cases higher for the nannoplankton (Table 4).

The coefficient of correlation between production and biomass was $r = 0.50$, $P < 0.01$, and the regression curve (Fig. 6) indicated a direct dependence of production on biomass. Primary production appeared to be more correlated with chlorophyll-a concentration than with biomass (Figs. 7, 8). But the regression function (Fig. 8) shows that there exists a direct, linear relationship between production and chlorophyll up to certain levels, above which any further growth in chlorophyll content is followed by a production decrease, which may be caused by self-shading. The relationship between primary production and light conditions has also been analysed. Daily variations in PAR utilization by total phytoplankton and nannoplankton have been presented in Table 3.

The coefficient of correlation between primary production and the amount of PAR was $r = 0.55$, $P < 0.001$. The regression function curve (Fig. 9) indicates that a directly proportionate relationship between photosynthesis and light intensity was noticeable up to a PAR value of about $250\ \mathrm{J \cdot cm^{-2} \cdot d^{-1}}$. The inhibition range (above $420\ \mathrm{J \cdot cm^{-2} \cdot d^{-1}}$) covered several phytoplanktonic samples in which Cryptophyceae and green algae dominated, which would indicate that they are sciophilous.

All the above-presented correlations indicate that in any ecological studies of phytoplankton it is neccessary to at least roughly determine the taxonomic composition and dominance structure of the community studied.

7. POLISH SUMMARY

W pracy przedstawiono zależności pomiędzy biomasą fitoplanktonu, koncentracją chlorofilu a w wodzie oraz produkcją pierwotną. Badania przeprowadzono w eutroficznym płytkim (3 m) jez. Bikcze. Biomasę obliczano metodą mikrometryczną (licząc i mierząc osobniki przy użyciu mikroskopu), koncentrację chlorofilu a kolorymetrycznie, a produkcję pierwotną metodą tlenową. Badania przeprowadzono od kwietnia do listopada w 16 seriach po 3 kolejne dni, co pozwoliło zaobserwować zmiany zachodzące w fitoplanktonie z dnia na dzień.

Stwierdzono niewielki zakres zmian biomasy fitoplanktonu, koncentracji chlorofilu a oraz produkcji pierwotnej w okresach 24-godzinnych (rys. 1, 5). W trzydniowych seriach zaobserwowano natomiast istotne zmiany w strukturze fitoplanktonu (rys. 2, 10), które były spowodowane albo (1) zmianami liczebności danego gatunku (wzrost – powodowany namnażaniem lub spadek – wyjadaniem przez zooplankton) bądź (2) zmianami wielkości (objętości) osobników.

Nie stwierdzono jednoznacznej zależności pomiędzy biomasą fitoplanktonu i chlorofilem a (Fig. 3). Współczynnik korelacji wyniósł $r = 0{,}45$, $P > 0.01$. Po wykluczeniu z obliczeń prób fitoplanktonu, w których dominowały sinice współczynnik korelacji między biomasą a chlorofilem wyniósł $r = 0{,}73$, $P < 0{,}001$. Stwierdzono dużą zmienność udziału procentowego chlorofilu a w zależności od frakcji planktonu, struktury taksonomicznej, wieku komórek i intensywności oświetlenia (tab. 1, 2, rys. 4).

Poziom globalnej produkcji pierwotnej ogólnego planktonu był na ogół określany przez produkcję frakcji nannoplanktonowej (rys. 5). Natomiast w biomasie przewaga nannoplanktonu była zwykle mniej wyraźna niż w produkcji, co znalazło odzwierciedlenie w wartościach współczynnika $P:B$, które w większości przypadków były większe dla nannoplanktonu (tab. 4).

Współczynnik korelacji między produkcją a biomasą wyniósł $r = 0{,}50$, $P < 0{,}01$, a przebieg regresji (rys. 6) wskazywał na prostą zależność wzrostu produkcji od biomasy. Produkcja pierwotna okazała się jednak bardziej skorelowana z koncentracją chlorofilu a niż biomasą (rys. 7, 8). Jednak funkcja regresji (rys. 8) wskazuje, że prosta liniowa zależność między produkcją i chlorofilem występuje do pewnych wartości, powyżej których w miarę wzrostu koncentracji chlorofilu produkcja maleje, co może być wywołane efektem samozacieniania. Rozpatrzono też zależność między produkcją pierwotną a światłem. Codzienne zmiany wykorzystania wartości PAR przez fitoplankton ogólny i nannoplankton przedstawiono w tab. 3.

Współczynnik korelacji między produkcją pierwotną a ilością PAR wyniósł $r = 0{,}55$, $P < 0.001$. Wykres funkcji regresji (rys. 9) wskazuje, że wprost proporcjonalna zależność fotosyntezy od natężenia światła ujawniała się do wartości PAR ok. 250 $\mathrm{J \cdot cm^{-2} \cdot d^{-1}}$. W zakresie inhibicji (powyżej 420 $\mathrm{J \cdot cm^{-2} \cdot d^{-1}}$) znalazło się kilka prób fitoplanktonu, w którym dominowały Cryptophyceae i zielenice, co wskazywałoby na ich „cieniolubny" charakter.

Wszystkie przedstawione współzależności wskazują, że we wszelkiego rodzaju pracach ekologicznych powinno się przynajmniej szacunkowo określać skład taksonomiczny badanego zbiorowiska i jego strukturę dominacji.

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