EKOLOGIA POLSKA (Ekol. pol.)	24	3	447–459	1976

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BIOMASS DYNAMICS OF DOMINANT SPECIES IN THE PHYTOPLANKTON OF TWO LAKES VARYING IN TROPHY*

ABSTRACT: During two years the biomass dynamics of species dominant in the phytoplankton of a-mezotrophic, holomictic lake and of a eutrophic, polimictic lake were investigated. Species of groups *Cyanophyta* and *Bacillariophyceae* showed marked seasonal maxima, whereas the biomass of species of the group *Dinophyceae* was inversely correlated to the biomass of blue-green algae. All dominant species struggled against water circulation and were unevenly distributed in the vertical cross-section of the lake.

Contents

1. INTRODUCTION

The dynamics of phytoplankton are frequently similar in various lakes, e.g., diatoms frequently have two growth maxima, spring and autumn, and in some lakes there is a third maximum – the summer one. Nevertheless, other species than in spring and autumn decide about the high contribution to the summer phytoplankton (N i k o l a e v 1972). Mass growth of blue-green algae occurs usually in summer periods, which is probably due to the presence of

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*Praca wykonana częściowo w ramach problemu węzłowego nr 09.1.7. ("Procesy decydujące o czystości powierzchniowych wód śródlądowych").

organic substances released in the water after spring phytoplankton blooms. The growth maxima of *Dinoflagellatae* are between May and August. But in several cases seasonal dynamics of phytoplankton are specific for a given lake and depend on many, not always known, factors. According to Round (1971) the autumn and spring cycles of phytoplankton growth depend greatly upon light, temperature and nutrients. Hickman (1974) has also observed a relation between seasonal succession of phytoplankton dominants and the light and nutrients. Another important fact as regards the dynamics of dominants species is pointed out by Hutchinson (1967) who has observed competition for the same elements, apart from the physical and chemical factors. According to McNaughton and Wolf (1970) domination based on species competition occurs when the dominant species occupies the potential niche of other subspecies and this may also happen within the same trophic level. Furthermore, one cannot forget the effect of grazing by zooplankton consumers, especially in the case of nannoplanktonic organisms (Hutchinson 1967, Gliwicz 1967, Gliwicz and Hillbricht-Ilkowska 1972).

The object of this research were observations of the dynamics of dominant species in two successive years.

2. METHODS

The study was conducted in two lakes: a-mezotrophic, holomictic Lake Piaseczno of a max. depth 39 m and in eutrophic, polimictic Lake Bikcze of a max. depth 3 m. Detailed characteristics of these lakes and methods are given in the paper by Wojciechowska (1976). Dynamics of dominant species were recorded observing the changes in their biomass and using Lohmann's spherical curves (Thomasson 1963). On diagrams the species are presented in the order of decreasing frequency, in cases of similar frequency the decreasing abundance decided. The domination of particular species was determined (after Wojciechowski 1972) according to their percentage in total phytoplankton biomass. Species having a contribution $\geqslant 50\%$ are considered as dominants, $\geqslant 25\%-50\%$ as subdominants, others $< 25\%$ as adominants.

3. RESULTS

The biomass dynamics of dominant and subdominant species and the interrelations in the changes of their biomass in the two years of investigations are presented in Figures 1–4. The species examined were either dominants or subdominants in relation to biomass concentration in a water volume unit, which was significant in the case of Lake Piaseczno. Some species subdominated only in one of the thermal layers – e.g. *Mallomonas caudata* Iwanoff and *Tabellaria flocculosa* (Roth) Kütz. in metalimnion – and their biomass in this layer was sufficient to increase their contribution to total biomass in the entire water column up to 25%. Therefore, in Lake Piaseczno there was a smaller number (5) of dominant or subdominant species in the entire water column (under m^2) as compared to the epi- or metalimnion. A systematic list of dominants and subdominants is given in Table I (Lake Piaseczno) and in Table II (Lake Bikcze). The forms in which particular species occur as determined by Starmach (1955) are also indicated in the tables as well as the changes of mean (for 10 specimens) volume of individuals for the two years of study. It is obvious that the volumes

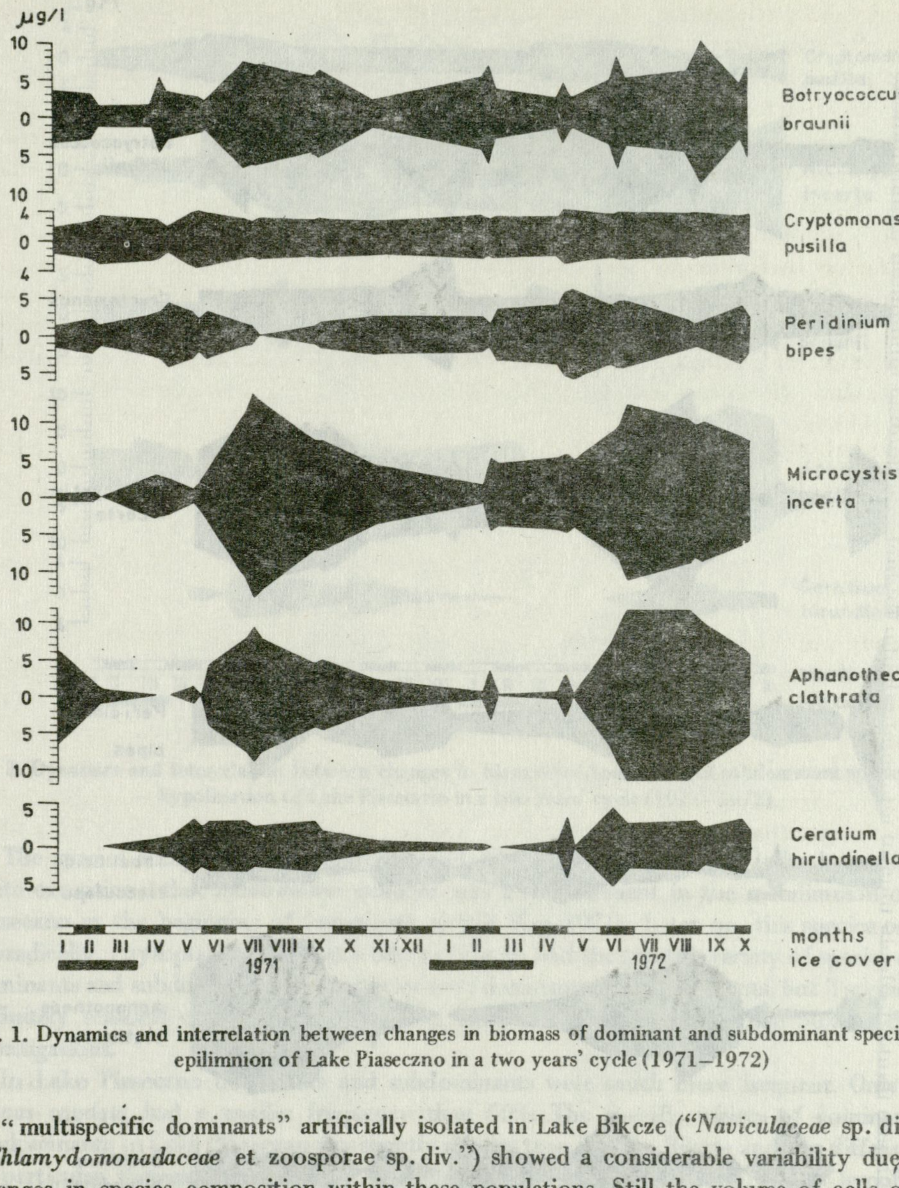

Fig. 1. Dynamics and interrelation between changes in biomass of dominant and subdominant species in the epilimnion of Lake Piaseczno in a two years' cycle (1971–1972)

of "multispecific dominants" artificially isolated in Lake Bikcze ("*Naviculaceae* sp. div." and "*Chlamydomonadaceae* et zoosporae sp. div.") showed a considerable variability due to the changes in species composition within these populations. Still the volume of cells of other species in a unicellular form also varied considerably. The smallest changes were observed in the volume of *Tabellaria flocculosa* cells (Table I). The greatest changes were in the volume of colonies of different species, which could be due to the changes in the size of cells in colonies and to the varying number of cells forming these colonies. No regularity was observed as concerns the changes in the volume of organisms, and even at the same time each year these volumes differed entirely.

Almost all dominant species were typical planktonic species. Only sporadically occurring diatoms in the plankton of Lake Bikcze of the family *Naviculaceae* were accidental. They usually appear at windy weather.

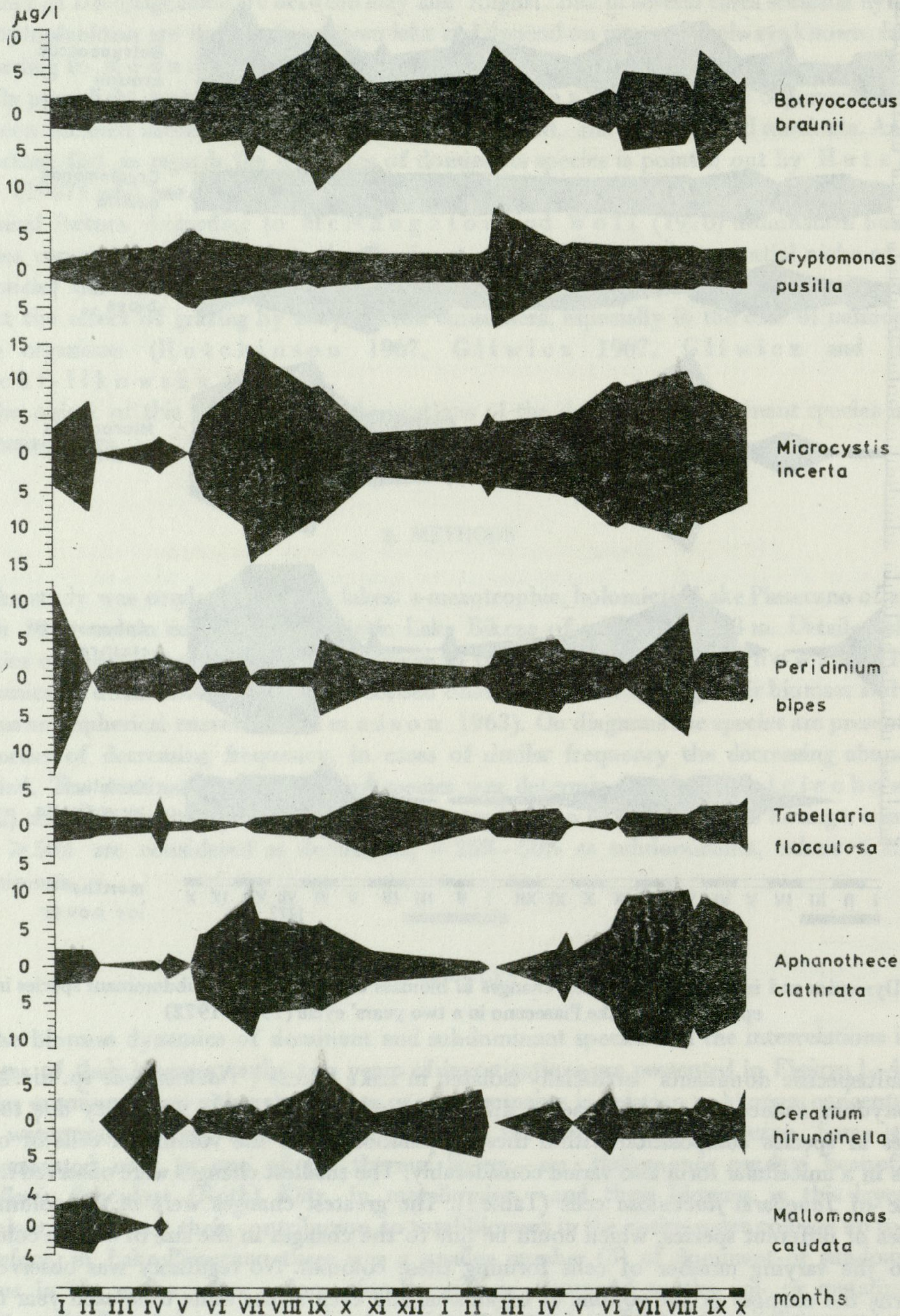

Fig. 2. Dynamics and interrelation between changes in biomass of dominant and subdominant species in the metalimnion of Lake Piaseczno in a two years' cycle (1971–1972)

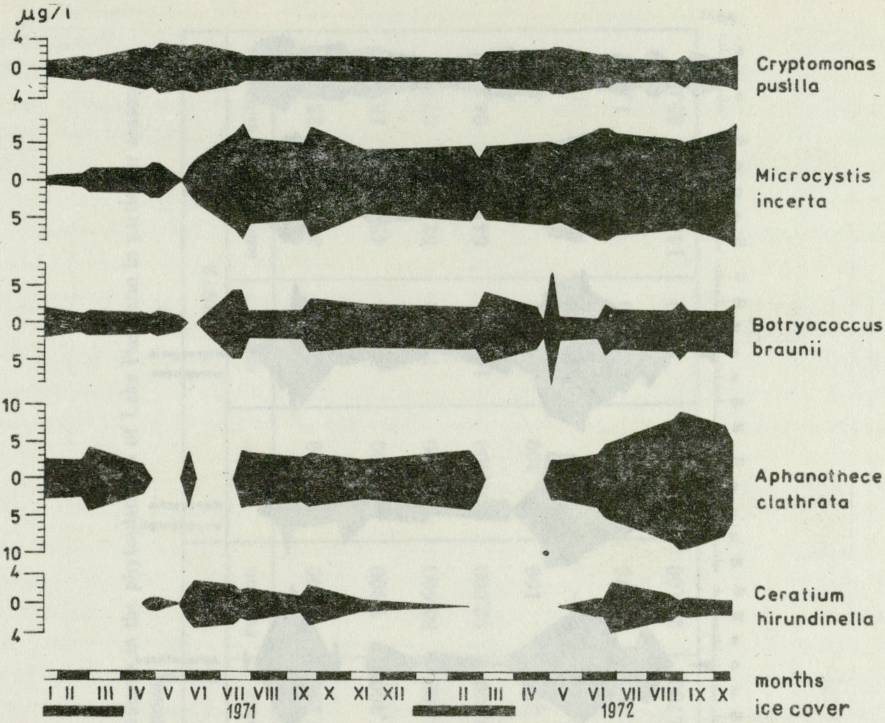

Fig. 3. Dynamics and interrelation between changes in biomass of dominant and subdominant species in the hypolimnion of Lake Piaseczno in a two years' cycle (1971–1972)

The species composition of dominants and subdominants was similar in both years. It was quite exceptional that *Mallomonas caudata* was a subdominant in the metalimnion of Lake Piaseczno at the beginning of investigations (till May 1971). Later on, this species occurred sporadically. Phytoplankton of Lake Bikcze (Fig. 4) had the greatest variety of species of both dominants and subdominants. Then species were dominants or subdominants, but 3 species had a definitely seasonal character of occurrence. They were found on less than 50% of dates of investigations.

In Lake Piaseczno dominants and subdominants were much more frequent. Only *Mallomonas caudata* had a smaller frequency than 50%. The specific variety of dominants and subdominants in Lake Piaseczno was slightly smaller than in Lake Bikcze and was differentiated in particular thermal water layers. The smallest variety was recorded in the hypolimnion (5 species), and the highest in metalimnion (8 species), and all dominant and subdominant species in hypolimnion remained such in higher water layers. In the majority of samples from both lakes the dominants and subdominants decided about the biomass of their superior systematic groups (W o j c i e c h o w s k a 1976). Their biomass was 80–90% of total biomass of corresponding superior systematic groups. Exceptionally in Lake Piaseczno the order of *Chlorococcales* reached in June, both years, higher biomass values than the dominant in this group *Botryococcus braunii* Kütz. The systematic group in Lake Bikcze with a biomass much higher than that of species dominant in this group were diatoms. Such great differences between the biomass of systematic groups and species dominating there were due to the specific variety within systematic groups and low level of species dominance (slightly exceeding 25% of total biomass).

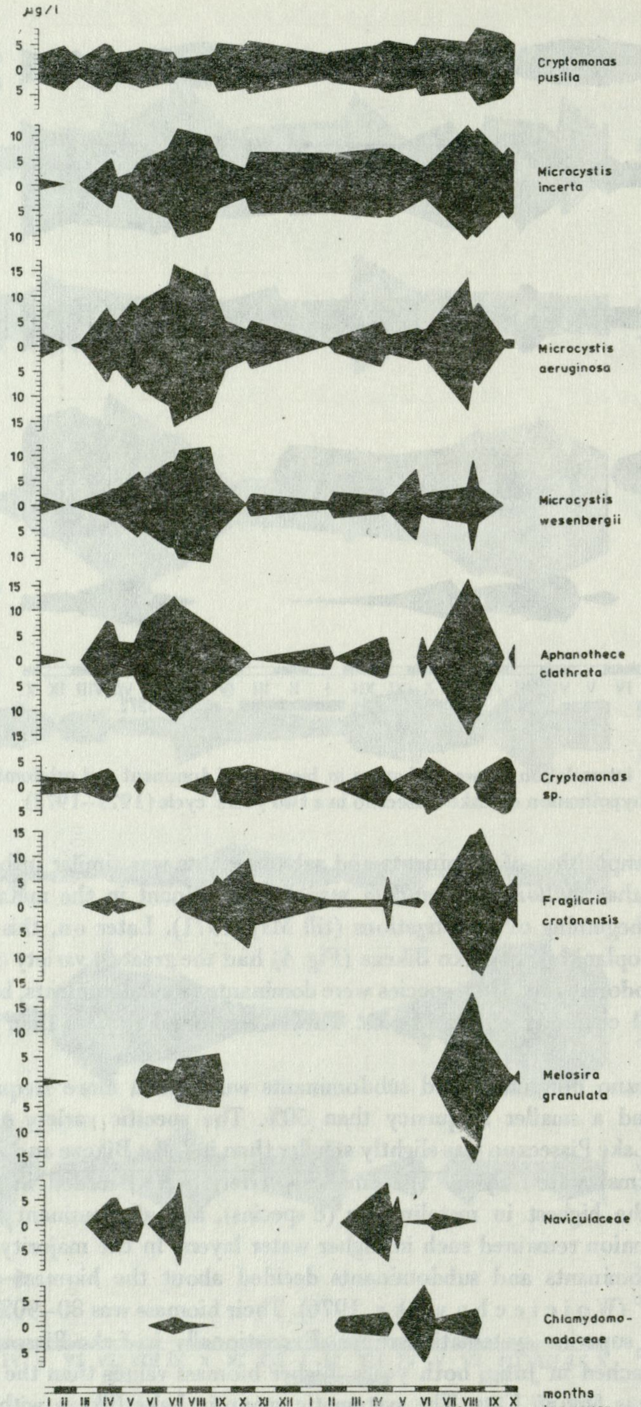

Fig. 4. Dynamics and interrelation between changes in biomass of dominant and subdominant species in the phytoplankton of Lake Bikcze in a two years' cycle (1971–1972)

Table I. Mean volume (μm^3) of cells or colonies of dominants and subdominants in the phytoplankton of Lake Piaseczno in particular seasons of two years of investigations

Systematic unit	Form of occurrence*	1971				1972			
		winter	spring	summer	autumn	winter	spring	summer	autumn
Microcystis incerta Lemm. f. div.	K	4,500	14,720	39,200	5,600	8,200	10,600	33,000	25,000
Aphanothece clathrata W. et G. S. West	K	60,000	28,300	17,300	7,900	29,000	16,800	42,500	18,000
Peridinium bipes Stein	O	84,000	57,300	36,800	80,600	68,300	76,000	52,000	57,000
Ceratium hirundinella (O. F. M.) Bergh	O	–	88,500	68,800	52,000	67,400	126,000	64,000	84,000
Cryptomonas pusilla Bachm.	O	240	740	320	160	300	500	410	270
Mallomonas caudata Iwanoff	O	6,600	2,040	–	–	–	–	–	–
Tabellaria flocculosa (Roth) Kütz. var. div.	O	1,600	1,300	1,300	1,470	1,420	1,430	1,200	1,600
Botryococcus braunii Kütz.	K	1,100,000	110,000	322,700	22,100	392,000	8,600	143,000	86,000

*O – single cells, K – colonies apart from filamentous.

Table II. Mean volume (μm^3) of cells or colonies of dominants and subdominants in the phytoplankton of Lake Bikcze in particular seasons of two years of investigations

Systematic unit	Form of occurrence*	1971				1972			
		winter	spring	summer	autumn	winter	spring	summer	autumn
Microcystis aeruginosa Kütz. f. div.	K	35,500	76,400	67,300	41,000	43,000	57,000	104,000	11,000
Microcystis incerta Lemm. f. div.	K	4,300	5,000	10,400	8,100	5,700	6,600	9,800	16,000
Microcystis wesenbergii Kom.	K	45,800	48,000	110,000	65,900	31,000	86,000	86,000	–
Aphanothece clathrata W. et G. S. West	K	5,700	15,300	28,400	12,900	11,000	49,000	19,300	13,000
Cryptomonas pusilla Bachm.	O	170	630	215	240	220	630	750	700
Cryptomonas sp.	O	2,000	4,000	4,000	3,700	–	6,200	3,000	5,700
Melosira granulata (Ehr.) Ralfs	N	6,000	12,900	26,900	–	–	–	39,000	20,000
Fragilaria crotonensis Kitt.	N	–	5,000	11,900	28,200	5,100	12,000	33,000	18,000
Naviculaceae gen. div.	O	–	51,000	51,000	–	350	5,100	3,900	–
Chlamydomonadaceae et zoosporae gen. div.	O	–	–	150	–	7,600	1,400	600	–

*O – single cells, N – filamentous colonies, K – other forms of colonies.

The biomass dynamics of the majority of dominant or subdominant species showed distinct seasonal maxima, particularly in the case of some blue-green algae species. *Microcystis incerta* Lemm. and *Aphanothece clathrata* W. et G. S. West decided about the biomass of this group in both lakes, and in Lake Bikcze also *Microcystis aeruginosa* Kütz. and *Microcystis wesenbergii* Kom. Changes in biomass of each one of these species showed positive intercorrelation and they attained maximum biomass in summer periods of both years.

The diatoms in both lakes examined showed also distinct changes in biomass according to the season of the year. The more important species from this group in Lake Bikcze were *Melosira granulata* (Ehr.) Ralfs and *Fragilaria crotonensis* Kitt. Their occurrence was distinctly seasonal (especially that of *Melosira*) in spring-summer periods and attained maximum biomass at the end of the summer. Changes in the biomass of the family *Naviculaceae* depended on water mixing which introduced these organisms into plankton. In Lake Piaseczno, *Tabellaria flocculosa* was the subdominant diatom species with maximum biomass in the autumn. The changes in biomass of diatom species mentioned (except the family *Naviculaceae*) were usually inversely correlated with the changes in biomass of dominant species of blue-green algae in both lakes.

A less distinct seasonality of biomass changes was displayed by dominant species of the *Dinophyceae* class: *Peridinium bipes* Stein and *Ceratium hirundinella* (O. F. Müll.) Bergh. Their biomass dynamics were high in epi- and metalimnion in both years, but it seemed correlated to a greater extent with the changes in biomass of blue-green algae than with the season. Two maxima of specific biomass can be approximately determined – early in spring and at the turn of summer. However, these maxima decrease as a result of increasing biomass of blue-green algae, and in the metalimnion this was inversely correlated to the biomass of *Tabellaria flocculosa* also. In the hypolimnion the biomass maximum of *Ceratium hirundinella* was much smaller and usually a week later than in higher layers, thus allowing to assume that the reproduction and growth of this species occurs in the epi- and metalimnion, and these organisms find their way to the hypolimnion in the second place.

Botryococcus braunii has been a very dynamic species but its maxima were unevenly distributed in time, still the highest biomass of this species in Lake Piaseczno was in warm seasons of the year. No distinct correlation with the biomass of other species was observed.

The lowest biomass dynamics in both lakes had *Cryptomonas pusilla* Bachm., which remained almost on the same level all year round. Changes in biomass of this species were to a very small extent inversely correlated with those of blue-green algae. This inverse relation was much more distinct in the case of *Cryptomonas* sp. in Lake Bikcze.

Biomass concentration of particular species in different thermal layers in Lake Piaseczno was uneven and depended on the size of organisms. For example, in winter 1971 colonies of *Botryococcus braunii* of a considerable volume (over 0.01 mm^3) but not numerous were found in the epilimnion of Lake Piaseczno. Whereas in meta- and hypolimnion the colonies were much smaller (up to 0.004 mm^3) but much more numerous. Similar vertical differentiation in the size of organisms was observed in the same samples for the green algae *Quadrigula closterioides* (Bohl.) Printz, the mean number of cells in colonies decreased with increasing depth.

Comparison of the biomass of particular species in Figures 1–4 shows that the majority of species attained the highest biomass in metalimnion, and the lowest in hypolimnion. Such characteristic vertical distribution for oligo- or a-mezotrophic lakes is mainly recorded in the warm seasons of the year. In winter 1971, some species (*Cryptomonas pusilla, Botryococcus braunii*) had the maximum in epilimnion. But as in the winter of the following year the lake was not covered with snow and the species had their maximum in metalimnion thus it can be assumed that at least the vertical distribution of these species is conditioned by light. This is confirmed by changes in vertical distribution of *Cryptomonas pusilla* in winter 1971 and described by Lecewicz, Sokołowska and Wojciechowski (1973). In January and February 1971 the biomass of this species gradually increased in all thermal layers of the lake. The snow fall at the end of February slightly decreased the visibility of the ice-snow cover in Lake Piaseczno and the biomass of *Cryptomonas pusilla* rapidly decreased in hypolimnion increasing simultaneously in meta- and especially in epilimnion.

Vertical distribution of species in stagnating lake can be the result of different intensity of growth and reproduction and grazing of algae in particular water layers. In order to find whether planktonic algal species can move actively or at least struggle against vertical water movement attention was paid to vertical distribution of species during seasonal water cycling in Lake Piaseczno. The only abiotic factor which is different is the light which in case of species struggling against vertical movement may determine the light requirements of these species.

During the period investigated the water cycling in Lake Piaseczno was on 26th of April and 3rd of May in 1971, and on 10th of November 1971. In 1972 homothermy was recorded only on the 23rd of February but this was not connected with full cycling of water.

Table III. Vertical distribution of biomass (μg/l) of dominant and subdominant species in water layers of Lake Piaseczno during seasonal water cycling in 1971

Species	Water layer	26 IV	3 V	10 XI
Microcystis incerta	epi-	67	50	267
	meta-	67	25	102
	hypolimnion	50	42	292
Aphanothece clathrata	epi-	0	0	36
	meta-	0	0	36
	hypolimnion	0	0	73
Peridinium bipes	epi-	130	324	66
	meta-	130	65	33
	hypolimnion	12.6	97	22
Ceratium hirundinella	epi-	8	12	2
	meta-	4	50	7
	hypolimnion	2	3	2
Cryptomonas pusilla	epi-	139	20	42
	meta-	136	75	29
	hypolimnion	62	148	22
Mallomonas caudata	epi-	0	0	0
	meta-	14	0	0
	hypolimnion	0	0	0
Tabellaria flocculosa	epi-	2	2	113
	meta-	2	0.7	347
	hypolimnion	4	3	173
Botryococcus braunii	epi-	499	14	23
	meta-	15	18	200
	hypolimnion	7	13	100

Total phytoplankton biomass in cycling periods was approximate in all thermal layers and increased only slightly together with the depth. But all species, mentioned in this chapter, to a smaller or greater extent struggled against water cycling and were unevenly distributed in the vertical cross section of pelagial (Table III). This observation was both true for species with locomotive organelles (*Peridinium bipes*, *Ceratium hirundinella*, *Cryptomonas pusilla*, *Mallomonas caudata*) and the nonflagellated species. Thus the mechanism of shifting of these species must have been based on another principle, probably on the change of specific weight. In the majority of cases (9) the maximum biomass of particular species were observed in the epilimnion, whereas it was very rare (3 cases) in the hypolimnion.

4. DISCUSSION

The size of phytoplankton organisms is variously determined by different authors (Nauwerck 1963, Goldman et al. 1968, Ruttner after Goldman et al. 1968, Findenegg after Vollenweider 1969). For example, the volume of the cell of *Ceratium hirundinella* is from 23.640 μm^3 (Goldman et al. 1968) to 75.000 μm^3 (Nauwerck 1963). Volumes of individuals of various species, dominant, subdominant (Tables I, II) and adominants, are usually approximate to values given by other authors, although never identical. For example, the volume of cells of *Ceratium hirundinella* in Lake Piaseczno ranges from 52.000 to 126.000 μm^3. It seems thus necessary when giving the phytoplankton biomass to determine each time the numbers and the volume of organisms because of the varying size of organisms in different lakes and the seasonal and several years' variability of size in one lake.

The criteria for estimating the abundancy have been originally determined on the basis of phytoplankton numbers (Wojciechowski 1972). Here, biomass indicates the dominant species. Finding the dominant species is essential in most ecological papers. Assuming the biomass as equal to volume as a dominance criterion is in agreement with the definition of McNaughton and Wolf (1970) and is better than the numbers (Wojciechowski 1972).

According to Odum (1963) the highest productivity distinguishes the dominants within a given trophic level. Thus only nannoplanktonic species as most productive (Findenegg 1965) should be considered as dominants regardless of their biomass. According to McNaughton and Wolf (1970) nannoplanktonic species should considered as "essential species" which considerably contribute to energy and metabolic rate but do not have to be dominants.

The observed by Wojciechowski (1972) regularities in the structure of phytoplankton numbers in Sosnowickie Lakes were not only true for the phytoplankton numbers in lakes Piaseczno and Bikcze (Wojciechowska 1976), but also for the biomass. Only at some dates the dominance of one species in total phytoplankton biomass did not exclude simultaneous subdominance of another species. But as these values approximated the limit values for dominance (50%) and subdominance (25%) it seems that these irregularities may have been due to methodical errors, eg., mean volume of organisms for the whole season and not the real one for a given sample. The frequency of some species, treated according to their biomass as dominants or subdominants, seemed to contradict Wojciechowski's (1972) thesis about the high frequency of dominants and subdominants. However, this was because of low numbers of these species on some dates of investigations (their presence was not indicated in quantitative analyses of samples). In the deep, stagnating Lake Piaseczno the biomass concentration of particular species was uneven in different water layers. However, the vertical differentiation of biomass of these species had a quantitative character, rather than qualitative. The qualitative similarity of phytoplankton population in the entire vertical section of Lake Piaseczno could be due to the deep penetration of light and considerable oxygenation of hypolimnetic waters.

5. SUMMARY

During two years the biomass dynamics of dominant species were observed. The study was conducted in the pelagial of two lakes: a-mezotrophic. holomictic Lake Piaseczno (max. depth 39 m) and in eutrophic, polimictic Lake Bikcze (max. depth 3 m). The methods are given in the paper by Wojciechowska (1976).

The volume of planktonic species in both lakes was analysed (Tables I, II). There were no regularities in the changes in the volume of organisms; even in the same seasons of the year, in two successive years, the volume differed considerably.

The biomass dynamics of the majority of dominant and subdominant species showed distinct seasonal maxima (Figs. 1–4). This seasonality was the least visible in the case of blue-green algae. All species of this group attained the maximum biomass in summer of both years. Also the diatoms in both lakes showed distinct changes in biomass in relation to the season of the year. The seasonal character of biomass changes was less distinct in the case of species from the class of *Dinophyceae*. Their biomass dynamics was to a greater extent correlated with the changes in biomass of blue-green algae than with the season. *Cryptomonas pusilla* Bachm. had the relatively smallest biomass dynamics in both lakes and remained all the year round almost on the same level.

Attention was also paid to the uneven distribution of biomass of species in the vertical section of the pelagial in Lake Piaseczno (Table III) in periods of circulation. Both species having locomotive organelles and nonflagellated species identically struggled against circulation. The mechanism of movements of these species must be then based on some other principle, and is probably due to changes in specific weight.

6. POLISH SUMMARY (STRESZCZENIE)

Prześledzono dynamikę biomasy gatunków dominujących w ciągu dwóch lat. Badania przeprowadzono w pelagialu dwóch jezior: a-mezotroficznego, holomiktycznego jez. Piaseczno (głębokość maksymalna 39 m) i jez. Bikcze – eutroficznego, polimiktycznego (głębokość maksymalna 3 m). Metody badań podano w pracy Wojciechowskiej (1976).

Przeanalizowano objętości gatunków planktonowych w obu jeziorach (tab. I, II). Nie stwierdzono żadnych prawidłowości zmian objętości organizmów; nawet w tych samych porach roku w dwóch kolejnych latach objętości te były bardzo różne.

Dynamika biomasy większości dominujących i subdominujących gatunków wykazywała wyraźne sezonowe maksima (fig. 1–4). Najwyraźniej zaznaczała się ta sezonowość u sinic. Wszystkie gatunki z tej grupy osiągały maksymalną biomasę w okresach letnich obu lat badań. Również okrzemki w obydwu jeziorach wykazywały dość wyraźną zależność zmian biomasy od pory roku. Mniej wyraźną sezonowość zmian biomasy wykazywały gatunki peridiniów (z klasy *Dinophyceae*). Ich dynamika biomasy była w większym stopniu skorelowana ze zmianami biomasy sinic niż z sezonem. Stosunkowo najmniejszą dynamikę biomasy wykazywał w obu jeziorach *Cryptomonas pusilla* Bachm., utrzymując się w cyklu całorocznym na mniej więcej równym poziomie.

Zwrócono też uwagę na nierównomierne rozmieszczenie biomasy gatunków w przekroju pionowym pelagialu Jeziora Piaseczno (tab. III) w okresach cyrkulacji. Cyrkulacji przeciwstawiały się w jednakowej mierze gatunki posiadające organelle ruchu, jak i bezwiciowe. Mechanizm przemieszczeń tych gatunków musiał więc być oparty na innej zasadzie, prawdopodobnie na zmianach ciężaru właściwego.

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