

Original Research

Seasonal Changes Occurring Over Four Years in a Reservoir's Phytoplankton Composition

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Abstract

In the period 1993-1996, the Maltański Reservoir was found to host 233 phytoplankton taxa, belonging to 9 taxonomic classes. The most numerous were cyanobacteria. After regression of the Cyanobacteria-induced water blooming in the spring, chrysophytes, cryptophytes, green algae or diatoms were dominant. The remaining taxonomic groups were clearly less numerous. Changes in the number of cells and of individual organisms and changes in the phytoplankton biomass were monitored in seasonal cycles. The shares of individual size fractions, i. e., of microplankton ($>60 \mu\text{m}$) and nanoplankton (2-60 μm) in the total numerical force and biomass of phytoplankton were estimated. Considering the size structure of phytoplankton organisms, nanoplankton comprised 50-100%, particularly in the period between November, 1994 and April, 1995, as well as in the early summer (May, June). Microplankton prevailed in total numbers of organisms between April and October, in particular. High correlation were noted between the number of organisms, number of cells and biomass of phytoplankton on one hand and the physico-chemical parameters of water such as transparency, temperature, pH, BOD₅ index, conductivity and total phosphorus on the other. This pointed to the role played by these parameters in the development of algae. On the other hand, dissolved phosphates, nitrite and ammonium nitrogen exerted no limiting effects on the development of phytoplankton.

Keywords: nano-, microphytoplankton, abundance, dam reservoir, species composition

Introduction

This paper reports results of a study on the phytoplankton structure and dynamics in the Maltański Reservoir subjected to biomanipulation. Qualitative and quantitative structure of the phytoplankton was analyzed, as affected by select physico-chemical parameters of water in the reservoir. This paper is an integral part of the comprehensive series of biomanipulation studies conducted on the reservoir in 1993-1996 [1-4]. Data from this research has been published in part [2-4]. During the biomanipulation experiment the reservoir was stocked with predatory fish (for more details see [5]). The develop-

ment of phytoplankton was supposed to be controlled by filter feeders (cladocerans). According to the biomanipulation theory [6], a decreased consumption of macrofilter feeders by planktivorous fish, due to increased predatory fish populations, results in an enhanced potential of cladocerans to control phytoplankton organisms. Because of this, the so-called "clear-water state" should be obtained.

Extensive stocking with predatory fish in order to reduce the pressure of planktivorous fish on zooplankton proved to be insufficient [2-4]. The top-down effect was visible only in the first season, when the number of planktivorous fish was low. In the next years crustaceans and rotifers stimulated the development of microphytoplankton, especially colonial cyanobacteria. The development

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of nanophytoplankton was limited by zooplankton grazing, but usually this did not cause a decrease in total phytoplankton abundance. It could even enhance the growth of cyanobacteria because of nutrients released by zooplankton from grazing nanophytoplankton.

In the Maltański Reservoir, the functioning of the PEG model (Plankton Ecology Group) [7,8] has been largely confirmed. The model explains mechanisms of springtime peaks of small algae biomass and of summertime peaks of large phytoplankton forms. The peaks are separated by the clear water phase appearing as a result of large plankton filtrators pressure [1,2]. The most significant factors that affect phytoplankton dynamics are light and temperature.

The Maltański Reservoir is situated within the limits of the city of Poznań, Poland. The reservoir is a small, shallow water body of 64 ha area, mean depth of 3.1 m, which accumulates water of the lower Cybina river (right tributary of the Warta river) [9]. The catchment area of the Cybina is a typical agricultural region with a definite prevalence of farm fields.

Material and Methods

Phytoplankton samples were collected in the years 1993-1996 every two weeks in spring and summer and once a month in autumn and winter, from a stand situated in the centre of the reservoir, at the surface and at depths of one, two and three meters. Separately, the number of cells and specimens (sum of filaments, coenobia, one-cell organisms, etc.) was counted. The samples were analyzed for the presence of nano- (2-60 µm) and microplankton (60-600 µm). The phytoplankton samples were fixed in Lugol solution, in Utermöhl's modification. They were examined under a light microscope, at $\times 400$ magnification. The biomass was calculated by approximating the organisms to geometric figures and calculating the respective volumes [10]. The taxonomic nomenclature follows that proposed by Hindak, Komarek and Anagnostidis, Siemińska, Starmach, and Uherkovich [11-21]. Within the four-year period the total number of 242 phytoplankton samples were collected and analyzed.

The physico-chemical and biological parameters of water such as: temperature, Secchi disk depth, concentration of chlorophyll *a*, dry mass of seston, primary production, concentration of water-dissolved oxygen (by Winkler's technique), biochemical oxygen demand (BOD_5), water oxygenation, pH, conductivity, the concentrations of ammonium, nitrate, nitrite, organic and total nitrogen levels, dissolved and total phosphorus were analysed.

Results

The main physico-chemical parameters of water in the Maltański Reservoir were examined (Table 1).

In 1993-1996, the nano- and microplankton of Maltański Reservoir exhibited extensive variability, both in

Table 1. Main physico-chemical data in Maltański Reservoir.

	Range
Temperature (°C)	0-27.7
pH	7.1-9.8
Conductivity ($\mu S\ cm^{-1}$)	540-1180
Secchi depth (m)	0.3-2.85
chlorophyll <i>a</i> ($mg\ dm^{-3}$)	0.35-242
seston ($mg\ dm^{-3}$)	0.3-54.2
BOD_5 ($mg\ O_2\ dm^{-3}$)	0.3-22.4
Oxygen ($mg\ dm^{-3}$)	0-25
Total P ($mg\ dm^{-3}$)	0.02-18.62
Nitrate ($mg\ N\ dm^{-3}$)	0-18.6
Nitrite ($mg\ N\ dm^{-3}$)	0-0.06
Ammonia ($mg\ dm^{-3}$)	0.18-2.58
N/P ratio	3.8-462.8

Table 2. Number of taxa in Maltański Reservoir in the course of investigations (1993-1996).

Class	Taxon	Genus	Species	Variety	Form
<i>Cyanobacteria</i>	27	15	18		1
<i>Euglenophyceae</i>	10	3	6	1	
<i>Cryptophyceae</i>	11	2	9		
<i>Chrysophyceae</i>	27	10	20	1	
<i>Bacillariophyceae</i>	35	16	22	3	
<i>Chlorophyceae</i>	102	40	77	6	1
<i>Dinophyceae</i>	4	3	2		
<i>Xantophyceae</i>	5	4	5		
<i>Conjugatophyceae</i>	12	3	9		
Summ	233	96	168	11	2

respect to the number of taxa and phytoplankton abundance. In total, 233 phytoplankton taxa were identified, belonging to 9 classes, 96 genera, 168 species, 11 varieties and 2 forms (Table 2). The numbers of taxa found in the Maltański Reservoir in the four subsequent years of studies within individual phytoplankton classes were similar. The most numerous group of algae, in respect to the number of taxa, were green algae (Table 3). They comprised 44% of the taxa present. The class included 42% genera and 46% species inhabiting the Maltański Reservoir. The *Scenedesmus* and *Monoraphidium* genera were particularly vastly represented. The other groups, represented by a somewhat lower number of taxa, were diatoms (15%), chrysophytes and cyanobacteria (12% each). The remaining classes were much less variable.

Table 3. Abundance and taxonomic structure of phytoplankton in Maltański Reservoir in 1993-1996; abundance [org. x cm⁻³]: •1-100, ••101-1,000, •••1,001-10,000, ••••10,001-1,000,000, + noted only in qualitative tests.

Taxonomic Name	1993	1994	1995	1996
CYANOBACTERIA				
<i>Anabaena affinis</i> Lemmermann (Incl. A. Vigueri Denis et Fremy)		•••	••	
<i>Anabaena flos-aquae</i> Brebisson, ex Bornet et Flahault	•••	•••	••	
<i>Anabaena solitaria</i> Klebahn			•	••
<i>Anabaena spiroides</i> Klebahn	••	•••	•••	•••
<i>Anabaena spiroides</i> f. <i>minima</i> Nygaard		••	••	••
<i>Anabaena</i> sp.		••	••	••
<i>Aphanizomenon flos-aquae</i> (L.) Ralfs	••••	••	••	
<i>Aphanizomenon gracile</i> Lemmermann	•	••	•••	••
<i>Aphanizomenon issatschenkoi</i> (Ussaczew) Proschkina-Lavrenko		••	••	••
<i>Aphanizomenon</i> sp.		•	••	••
<i>Aphanotece clatrata</i> W. et G.S. West	••			
<i>Aphanotece</i> sp.	••			
<i>Chroococcus turgidus</i> (Kutzing) Nageli	•••			
<i>Gomphosphaeria fusca</i> Skuja	••			
<i>Gomphosphaeria</i> sp.	•			
<i>Limnothrix redeckeii</i> (Van Goor) Meffert	••	•••	•••	•••
<i>Lyngbya</i> sp.			•	
<i>Microcystis aeruginosa</i> Kutzning	•••	••	•	••
<i>Phormidium</i> sp.		••	••	
<i>Planktothrix agardhii</i> (Gom.) Anagnostidis & Komarek	••	••••	••••	••••
<i>Pseudanabaena limnetica</i> after Lemmermann from Geitler	••	•••	••••	••••
<i>Pseudanabaena</i> sp.		•		
<i>Synechocystis aquatilis</i> Sauvageau	••			
<i>Synechocystis</i> sp.	•••			
<i>Tetrachloris merismopedioides</i> Skuja			•	
<i>Tetrapedia gothica</i> Reinsch	•			
<i>Trichodesmium iwanoffianum</i> Nygaard	•	•	••	•
EUGLENOPHYCEAE				
<i>Euglena</i> sp.	••	•	•	••
<i>Phacus</i> sp.	••			
<i>Trachelomonas dybowskii</i> Drežepolski	•			
<i>Trachelomonas hispida</i> (Perty) Stein				••
<i>Trachelomonas hispida</i> var. <i>crenulatocollis</i> (Maskell) Lemmermann				•
<i>Trachelomonas intermedia</i> Dangeard	•			
<i>Trachelomonas omphalon</i> Drežepolski			•	
<i>Trachelomonas pulchella</i> Drežepolski		••		
<i>Trachelomonas volvocina</i> Ehrenberg	•	••	••	•••
<i>Trachelomonas</i> sp.	•		••	••

CRYPTOPHYCEAE				
<i>Cryptomonas gracilis</i> Skuja			•••	•
<i>Cryptomonas marssonii</i> Skuja	••	••	•••	•••
<i>Cryptomonas obovata</i> Skuja		••	••	••
<i>Cryptomonas ovata</i> Ehrenberg	•	••	•••	•••
<i>Cryptomonas refleksa</i> Skuja	•	••	•••	••
<i>Cryptomonas rostrata</i> Troitzkaja emend. I. Kiselev		•	•	••
<i>Cryptomonas rostratiformis</i> Skuja	•	••	••	••
<i>Cryptomonas</i> sp.	•	••	••	•••
<i>Rhodomonas lacustris</i> Pascher et Ruttner	•••	••••	••••	•••
<i>Rhodomonas lens</i> Pascher et Ruttner	••	•••	••••	•••
<i>Rhodomonas</i> sp.	•			
CHYSOPHYCEAE				
<i>Bicoeca planktonica</i> Kisselev		••	••	••
<i>Bicoeca</i> sp.	•		•••	•••
<i>Chromulina</i> sp.		••	••	••
<i>Chrysococcus granulatus</i> Hortobagyi		•		
<i>Chrysococcus minutus</i> (Fritsch) Nygaard	•	••••	•••	•••
<i>Chrysococcus rufescens</i> Klebs	•	•••	•••	•••
<i>Chrysococcus skujae</i> Lackey				••••
<i>Chrysococcus triporus</i> Matvienko	•	•••	•••	•••
<i>Chrysococcus</i> sp.	••	••••	•••	•••
<i>Chrysolykos plancticus</i> Mack		+		
<i>Dinobryon divergens</i> Imhof		•••	••	•
<i>Dinobryon sertularia</i> Ehrenberg	••			
<i>Dinobryon sociale</i> Ehrenberg				•
<i>Dinobryon sociale</i> var. <i>americanum</i> (Brunthaler) Bachmann			••	
<i>Erkenia subaequiciliata</i> Skuja	•	••	••••	•••
<i>Kephrion globosum</i> (Czosnowski) Bourrelly			••	••
<i>Kephrion moniliferum</i> (Schmid) Bourrelly	••	•••	•••	••
<i>Kephrion rubri-claustri</i> Conrad		•••		•
<i>Kephrion starmachii</i> (Czosnowski) Bourrelly			•	
<i>Kephrion</i> sp.		••		••
<i>Ochromonas basivacuolata</i> Skuja		•	•	••
<i>Ochromonas globosa</i> Skuja	••			
<i>Ochromonas polychrysis</i> Skuja		••		
<i>Ochromonas</i> sp.	•	••••	•••	•••
<i>Pseudokephyrion pseudospirale</i> Bourrelly	••	••		
<i>Pseudokephyrion</i> sp.		••		
<i>Synura uvella</i> Ehrenberg		••	•••	•••

BACILLARIOPHYCEAE				
<i>Amphora ovalis</i> Kutzing Rys.	•			
<i>Anomoeoneis exilis</i> (Kutzing) Cl.		•••	••	•
<i>Asterionella formosa</i> Hass.		•••	••	
<i>Asterionella zasuminensis</i> (Cabejsz.) Lundh-Alm.		•••		
<i>Asterionella</i> sp.	•			
<i>Cyclotella commensis</i> Grun.			••	
<i>Cyclotella</i> sp.	••	••		
<i>Cymbella cistula</i> (Hemp.) Grun.	•			
<i>Cymbella</i> sp.	•			•
<i>Diatoma elongatum</i> (Lyngb.) Ag.		•••	•	•••
<i>Fragilaria crotonensis</i> Kitt.	•	•••		
<i>Fragilaria</i> sp.	•	••		•••
<i>Gomphonema angustatum</i> (Kutzing) Rabh.	•			
<i>Gomphonema olivaceum</i> (Lyngb.) Kutzing			••	•
<i>Gomphonema</i> sp.		•		
<i>Gyrosigma acuminatum</i> (Kutzing) Rabh.				•
<i>Melosira granulata</i> (Ehrenberg) Ralfs	••			
<i>Melosira varians</i> Ag.			•	
<i>Melosira</i> sp.	••	••		
<i>Navicula hungarica</i> Grun.	•			
<i>Navicula hungarica</i> var. <i>capitata</i> (Ehr.)		•	•	•
<i>Navicula lanceolata</i> (Ag.) Kutzing		•		
<i>Navicula oblonga</i> Kutzing	•			
<i>Navicula</i> sp.	•	••	•	••
<i>Nitzchia acicularis</i> W.Sm.		••	•••	•••
<i>Nitzchia acicularis</i> var. <i>closterioides</i> Grun.			••	•••
<i>Nitzchia</i> sp.				•••
<i>Rhoicosphenia curvata</i> (Kutzing) Grun.		•		
<i>Stephanodiscus hantzschii</i> Grun.	••	••••	•••	••••
<i>Stephanodiscus</i> sp.	•			
<i>Synedra acus</i> Kutzing	•	•••	••••	••••
<i>Synedra acus</i> var. <i>angustissima</i> Grun.				•••
<i>Synedra ulna</i> (Nitzsch) Ehr.		••	•••	••
<i>Synedra</i> sp.				••
<i>Tabellaria flocculosa</i> (Roth) Kutzing		••		
CHLOROPHYCEAE				
<i>Actinastrum hantzschii</i> Lagerheim	•	••	••	••
<i>Ankistrodesmus gracilis</i> (Reinsch) Kors.				•
<i>Ankistrodesmus setigerus</i> (Schroeder) G.S.West	•			
<i>Ankistrodesmus</i> sp.			•	

<i>Capsochloris</i> sp.	••			
<i>Chlamydomonas incerta</i> Pascher		••		
<i>Chlamydomonas</i> sp.	••	•••	••	•••
<i>Chloromonas</i> sp.			••	••
<i>Chlorella minutissima</i> Fott et Novakova			••	••
<i>Chlorella vulgaris</i> Beij.	••			
<i>Chlorella</i> sp.	•		••	•••
<i>Chlorobion</i> sp.	•			
<i>Closteriopsis acicularis</i> (G. M. Smith) Belcher et Swale	•	•	••	••
<i>Closteriopsis longissima</i> (Lemmermann) Lemmermann		•		
<i>Coelastrum astroideum</i> De Notaris		•••	••	••
<i>Coelastrum microporum</i> Nageli in A. Braun.	•	••	•	••
<i>Coenocystis planctonica</i> Kors.	•••			
<i>Coenocystis</i> sp.			•	
<i>Crucigenia quadrata</i> Morren 1830	••	••	•	••
<i>Crucigenia tetrapedia</i> (Kirchner) W et G.S.West		•		
<i>Crucigeniella quadrata</i> Morren			••	••
<i>Crucigeniella rectangularis</i> (Nag.) Komarek	•		•	
<i>Diacanthos bellenophorus</i> Kors.	•			
<i>Dictiosphaerium</i> sp.			••	••
<i>Didymocystis bicellularis</i> (Chodat) Komarek	••			
<i>Didymocystis planctonica</i> Kors.	••			
<i>Didymocystis</i> sp.		•	••	••
<i>Diplostauron pentagonium</i> (Hazen) Pasher		•		
<i>Elakatothrix bplex</i> (Nygaard) Hindak		••	••	••
<i>Elakatothrix</i> sp.			••	••
<i>Franceja elongata</i> Kors.	•			
<i>Gleotila pelagica</i> (Nygaard) Skuja			••	
<i>Granulocystis</i> sp.	•			••
<i>Keratococcus suecicus</i> Hindak			•••	•
<i>Keratococcus</i> sp.	•			
<i>Keriochlamys</i> sp.	•			
<i>Kirchneriella contorta</i> (Schmidle) Bohlin	•	••	•	••
<i>Kirchneriella irregularis</i> var. <i>spiralis</i> Kors.		•		•••
<i>Kirchneriella</i> sp.	•			
<i>Koliella longiseta</i> (Vischer) Hindak		•••	••	••
<i>Koliella spiculiformis</i> (Vischer) Hindak	•	••	•••	••
<i>Koliella</i> sp.			••	
<i>Lagerheimia ciliata</i> (Lagerheim) Chodat				••
<i>Lagerheimia genevensis</i> (Chodat) Chodat	••	••	••	••
<i>Lagerheimia subsalsa</i> Lemmermann		•		

<i>Mikraktinium pusillum</i> Fresenius		●	●	●
<i>Monoraphidium arquatum</i> (Kors) Hindak		●	●●	●●
<i>Monoraphidium circinale</i> (Nyg.) Nygaard			●●	●●
<i>Monoraphidium contortum</i> (Thur.) Kom.-Legn.	●	●●	●●●	●●●
<i>Monoraphidium irregulare</i> (G. M. Smith) Kom.-Legn.			●●	
<i>Monoraphidium komarkovae</i> Nygaard		●	●●	
<i>Monoraphidium minutum</i> (Nag.) Kom.-Legn.		●●	●●●	●●
<i>Monoraphidium pusillum</i> (Printz) Kom.-Legn.		●●	●	
<i>Monoraphidium</i> sp.	●●		●●	●
<i>Mychonastes</i> sp.	●●			
<i>Oocystis lacustris</i> Chodat	●●	●●	●●	●●
<i>Oocystis marssoni</i> Lemmermann	●●			
<i>Pediastrum duplex</i> Meyen		●	●	●
<i>Pediastrum boryanum</i> (Turp.) Menegh.	●	●	●●	●●
<i>Pediastrum tetras</i> (Ehrenberg) Ralfs			●	●
<i>Phacotus lenticularis</i> (Ehrenberg) Srein	●	●●●	●●	●●
<i>Planktonema lauterbornii</i> Schmidle	●			
<i>Pteromonas angulosa</i> (Carter) Lemmermann		●●	●●	●●
<i>Pteromonas aculeata</i> Lemmermann				●●
<i>Pteromonas cordiformis</i> Lemmermann	●			●●
<i>Scenedesmus abundans</i> (Kirchn.) Chodat		●		
<i>Scenedesmus acuminatus</i> (Lagerh.) Chodat	●	●	●●	●●
<i>Scenedesmus acuminatus</i> var. <i>minor</i> G.M. Smith (Skuja)		●●	●	●●
<i>Scenedesmus acuminatus</i> var. <i>tetradesmoides</i> G.M. Smith (Chodat)				●●
<i>Scenedesmus acutus</i> Meyen		●	●	●
<i>Scenedesmus antennatus</i> Breb. in Ralfs			●	
<i>Scenedesmus bicaudatus</i> Dedusenko	●	●●	●	●●
<i>Scenedesmus bicellularis</i> Chodat	●			
<i>Scenedesmus dimorphus</i> (Turp.) Kutzing		●	●	●●
<i>Scenedesmus disciformis</i> (Chodat) Fott et Komarek		●		
<i>Scenedesmus ecornis</i> (Echrenb.) Chodat	●	●	●●	●●
<i>Scenedesmus helveticus</i> Chodat				●
<i>Scenedesmus obtusus</i> Meyen 1829		●		
<i>Scenedesmus opolensis</i> P. Richter 1896			●	
<i>Scenedesmus opolensis</i> var. <i>bicaudatus</i> Hortobagyi		●		
<i>Scenedesmus opolensis</i> var. <i>mononensis</i> Chodat				●
<i>Scenedesmus opolensis</i> var. <i>opolensis</i> Richter & Hortobagyi				●
<i>Scenedesmus ovalternus</i> Chodat				●
<i>Scenedesmus protuberans</i> Fritsch			●	●●
<i>Scenedesmus quadricauda</i> (Turpin) Breb. sensu Chodat	●	●●	●●	●●●
<i>Scenedesmus quadricauda</i> f. <i>granulatus</i> Hortob	●			

<i>Scenedesmus regularis</i> Swirensko		●		
<i>Scenedesmus sempervirens</i> Chodat		●	●●	●●
<i>Scenedesmus spinosus</i> Chodat			●	
<i>Scenedesmus</i> sp.			●●	●●
<i>Schroederia planctonica</i> (Skuja) Philipose	●			
<i>Schroederia setigera</i> (Schroeder) Lemmermann				●
<i>Siderocelis irregularis</i> Hind.	●			
<i>Siderocelis kolwitzii</i> (Naumann) Fott		●●	●●	●●
<i>Tetraedron caudatum</i> (Corda) Hansgirg		●●	●	●●
<i>Tetraedron minimum</i> (A. Braun) Hansgirg	●	●●	●●	●●
<i>Tetraedron regulare</i> Kutzing		●●		●
<i>Tetrastrum glabrum</i> (Roll) Ahlstr. et Tiff.		●●	●●	
<i>Tetrastrum komarekii</i> Hindak	●	●●	●●	●●
<i>Tetrastrum staurogeniaeformae</i> (Schroeder) Lemmermann	●			
<i>Tetrastrum triangulare</i> (Chodat) Komarek		●●	●●●	●●
<i>Treubaria planctonica</i> (G.M. Smith) Kors.	●		●	●●
DINOPHYCEAE				
<i>Ceratium hirundinella</i> (F.B. Muller) Bergh	●			
<i>Peridinium aciculiferum</i> Lemmermann		●●	●●	●●
<i>Peridinium</i> sp.	●	●	●●	●●
<i>Gymnodinium</i> sp.	●	●●	●●	●●
XANTOPHYCEAE				
<i>Goniochyloris mutica</i> (A. Braun) Fott	●	●	●	●●
<i>Ophiocytium capitatum</i> Wolle	●●		●	
<i>Pseudostaurastrum hastatum</i> (Reinsch.) Chodat			●	
<i>Pseudostaurastrum limneticum</i> (Borge) Chodat			●	●
<i>Tetraedriella spinigera</i> Skuja			●	●
CONJUGATOPHYCEAE				
<i>Closterium ceratium</i> Perty	●			
<i>Closterium gracile</i> Brebisson ex Ralfs	●	+	+	
<i>Closterium incurvum</i> Brebisson	●			
<i>Closterium limneticum</i> Lemmermann				●
<i>Closterium</i> sp.	●	●●	●●	●
<i>Cosmarium bioculatum</i> Brebisson in Ralfs	●			
<i>Cosmarium humile</i> (Gay) Nordst.	●			
<i>Cosmarium</i> sp.	●			
<i>Staurastrum gracile</i> Ralfs		●		●
<i>Staurastrum pachyrhynchum</i> Nordstedt	●			
<i>Staurastrum tetracerum</i> Ralfs		+	+	
<i>Staurastrum</i> sp.	●			

Phytoplankton abundance changed in a dynamic way over 4 years. Within the entire study period, the nano- and microplankton were least numerous in November, 1993 (290 organisms $\cdot \text{cm}^{-3}$). On the other hand, the maximum concentration of organisms was noted in December, 1995 in the subsuperficial layer ($72.1 \cdot 10^3$ organisms $\cdot \text{cm}^{-3}$).

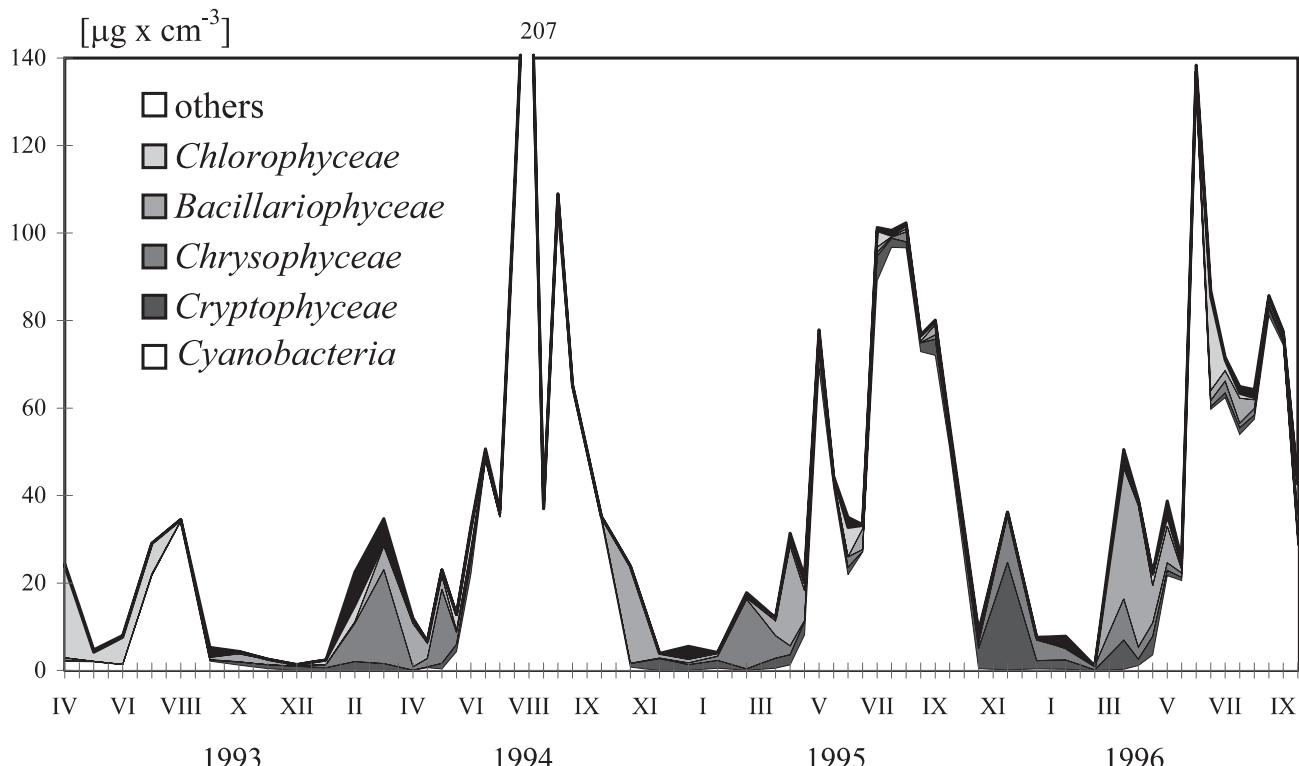


Fig. 1. Changes in phytoplankton biomass in the studied period within individual taxonomic groups (example: water surface layer).

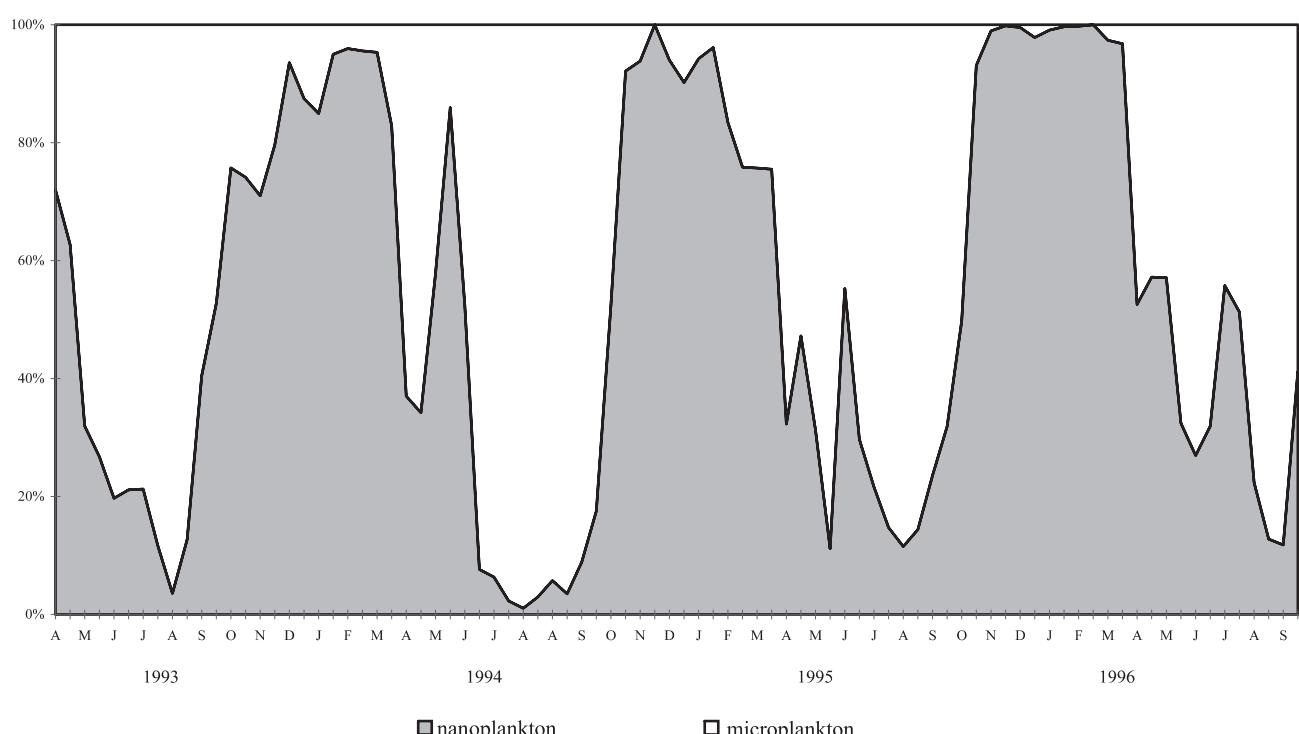


Fig. 2. Shares of nanoplankton and microplankton in total numbers of phytoplankton (example: water surface layer).

Similarly to the abundance, the biomass of the phytoplankton exhibited variations with the season and the depth of the reservoir at which the water sample was collected. The highest densities were noted in July, 1994 on the surface ($207 \mu\text{g} \cdot \text{cm}^{-3}$) (Fig. 1) and the value was fivefold higher than that obtained in 1993 ($40 \mu\text{g} \cdot \text{cm}^{-3}$ at a depth of 2 m),

twofold higher than that observed in August, 1995 at the surface, slightly higher than that noted, in June, 1996 ($170 \mu\text{g} \cdot \text{cm}^{-3}$, at the depth of 1 m).

Upon analysis of algal size structure, a clear domination of nanoplankton (2-60 μm) was noted in the total abundance in the cool months, i.e. between November (1993-1995) to April (1994-1996). In these periods, nanoplankton made between 50% and 100% of phytoplankton. In the remaining periods, microplankton ($>60 \mu\text{m}$, Fig. 2) had the highest share in the numerical force of phytoplankton. Microplankton dominated in par-

ticular between July and September, 1993 and in the periods between April, 1994-1996 and October, 1994-1996.

The Maltański Reservoir phytoplankton was found to include species of 9 classes. Not all of them were equally important in determining general numerical force and biomass of phytoplankton. The most significant group in this respect was cyanobacteria, present in vast numbers between spring and autumn (Fig. 3). The other groups, the participation of which grew in phytoplankton after regression of blooming of cyanobacteria, included cryptophytes, chrysophytes, green algae and diatoms. Repre-

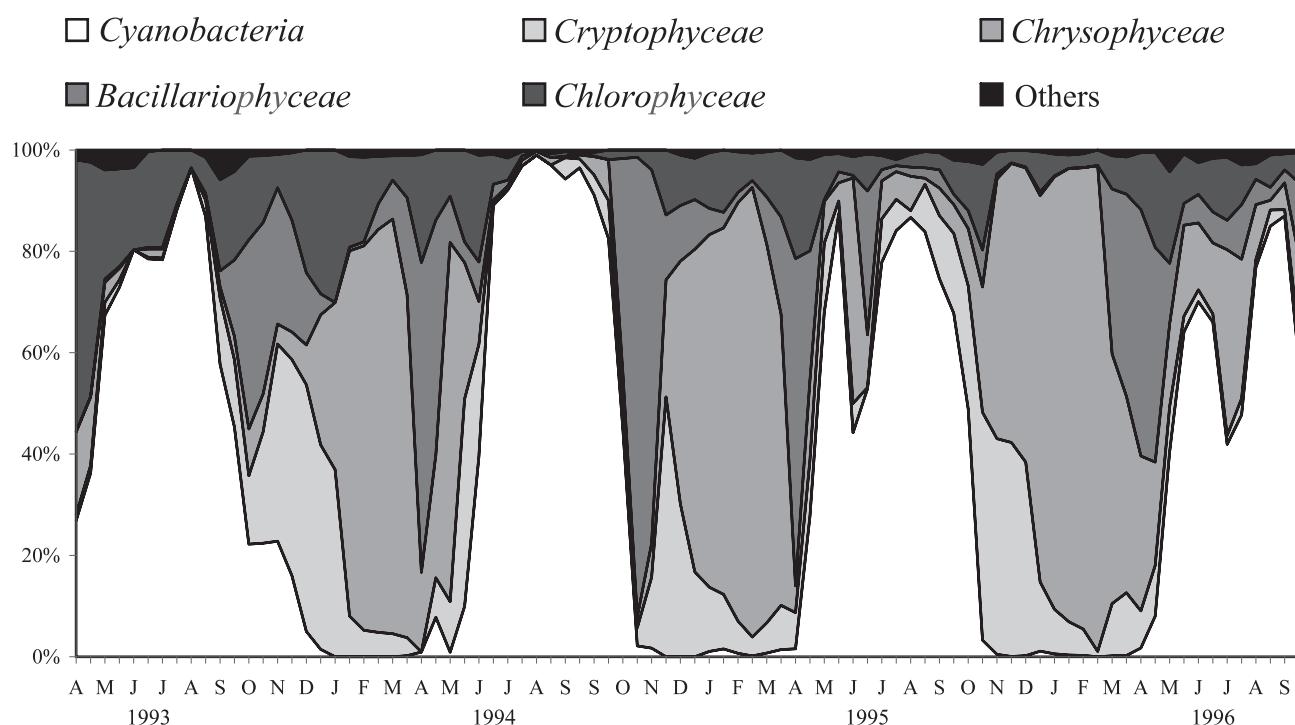


Fig. 3. Shares of principal taxonomic groups in the total abundance of phytoplankton (example: water surface layer).

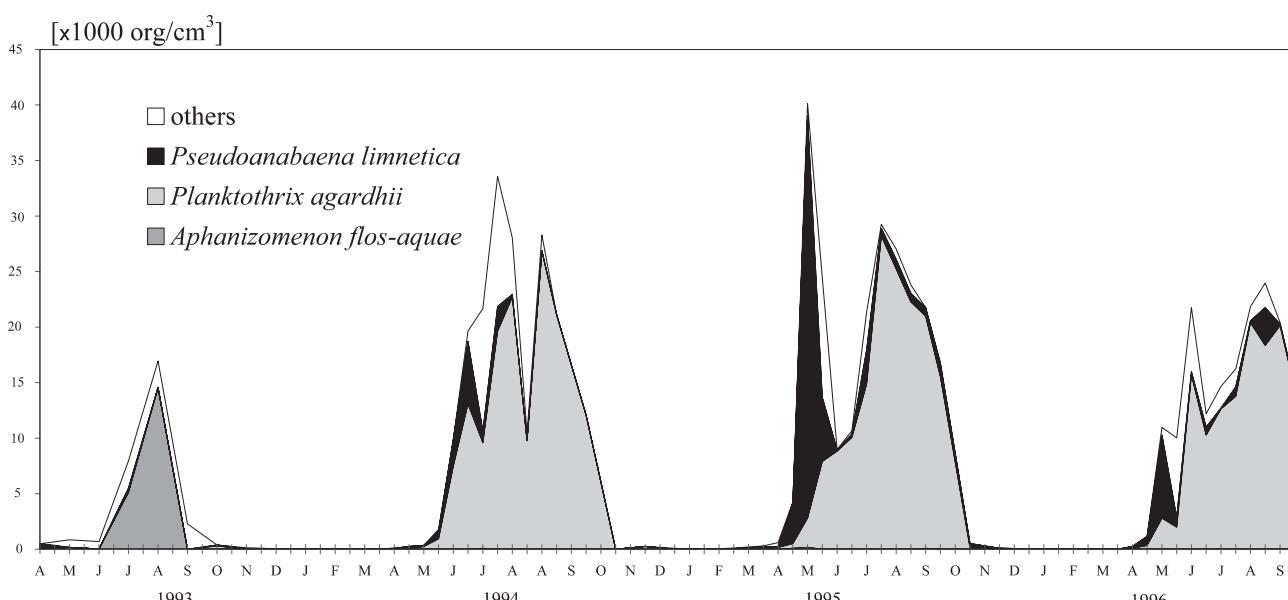


Fig. 4. Shares of most numerous cyanobacteria in total abundance of organisms in the taxonomic group (example: at a depth of 1 m).

sentatives of the remaining taxonomic groups of phytoplankton appeared sporadically.

The most important species of cyanobacteria, which caused or participated in induction of water blooming, included *Aphanizomenon flos-aquae* in 1993 and *Planktothrix agardhi* and *Pseudanabaena limnetica* in the subsequent years (1994-1996; Fig. 4). The numerical force of *A. flos-aquae* was pronounced particularly in July and August, reaching the value of $14.6 \cdot 10^3$ organisms $\cdot \text{cm}^{-3}$. At that time the species was the main component of phytoplankton but in subsequent years its presence was only sporadic. Apart from the above-mentioned species, in 1993 relatively numerous also were *Microcystis aeruginosa*, *Anabaena affinis*, *Anabaena flos-aquae*, *Anabaena spiroides*, *A. spiroides f. minima*, *Chroococcus turgidus* and *Synechocystis sp.*

Chrysophyceae was another vastly represented group. The most frequent were the species of *Ochromonas sp.*, *Chrysococcus minutus*, *Kephyrion moniliferum*, *Dinobryon divergens*, *Synura uvella*, *Chrysococcus rufescens* and *Ch. minutus*. Within the studied period, the highest abundance was noted at the surface in December, 1995, for the nanoplankton species of *Erkenia subaequiciliata*. In April, 1996, a high density of chrysophytes was noted, particularly in the surface water layer, *Chrysococcus skujae*, *Ch. triporus*, *Ch. minutus* and *Chrysococcus sp.*

Among *Cryptophyceae* the prevailing species involved *Rhodomonas lacustris* and *R. lens*. The two species reached the maximum numerical force in December, 1995. Apart from the above-mentioned species, the cryptophytes were represented by *Cryptomonas marssonii* and *Cryptomonas ovata*.

Diatoms were particularly numerous between March (1993) or April (1995, 1996) and May (1995) or June

(1994, 1996). In the remaining months, the species of this group were encountered less frequently. Both in respect of the numerical force of organisms and their biomass, *Stephanodiscus hantzschii* and *Synedra acus* prevailed among diatoms. Apart from the two species, high numerical forces and high biomass values were found of the taxa such as: *Fragilaria sp.*, *Synedra ulna*, *Fragilaria crotonensis*, *Nitzschia acicularis* var. *closterioides* (particularly in 1996) and *Diatoma elongatum*.

Abundance of green algae increased in particular in the spring months. The most numerous were: *Morariaphidium contortum*, *M. minutum*, *Koliella spiculiformis*, *K. longiseta*, *Actinastrum hantzschii*, *Phacotus lenticularis*, *Tetrastrum triangulare*, *Coelastrum astroideum* and *Scenedesmus quadricauda*.

Small abundance of *Euglenophyceae*, *Dinophyceae*, *Xantophyceae* and *Conjugatophyceae* was noted and their presence showed no evident seasonal variation.

A correlation was found between the number of organisms (individuals), number of cells and biomass of phytoplankton on one hand and physico-chemical data on the other (Table 4).

Discussion

In 1993-1996, an evident seasonal variation was observed in the manifestation of individual groups of algae in phytoplankton of Maltański Reservoir. In summer, in conditions of a reduced alimentary pressure of zooplankton, intense development of cyanobacteria took place, similarly as at one of stages of the annual course of plankton succession (PEG model, [7]). In August, 1993, the short-term water blooming was caused by *Aphanizomenon flos-aquae*.

Table 4. Correlation between number of organisms and biomass of phytoplankton on one hand and physico-chemical variables on the other. Only the relations significant at $p < 0.05$ have been presented.

Variables	N	Number of organisms r (p)	Number of cells r (p)	Biomass r (p)
Secchi depth	61	-0.88 (0.001)	-0.83 (0.001)	-0.88 (0.001)
Chlorophyll a	242	0.83 (0.001)	0.73 (0.001)	0.77 (0.001)
Seston	242	0.70 (0.001)	0.77 (0.001)	0.79 (0.001)
pH	235	0.27 (0.001)	0.57 (0.001)	0.53 (0.001)
BOD ₅	235	0.61 (0.001)	0.51 (0.001)	0.59 (0.001)
Conductivity	235	-0.38 (0.001)	-0.54 (0.001)	-0.53 (0.001)
Temperature	235	0.38 (0.001)	0.77 (0.001)	0.66 (0.001)
Ammonia	38	*	-0.41 (0.001)	-0.48 (0.001)
Organic nitrogen	38	*	0.41 (0.011)	0.62 (0.002)
Total N	38	*	-0.33 (0.045)	*
Total P	38	*	0.34 (0.036)	0.51 (0.001)

N — number of data, r — correlation coefficient, p — significance level, * — $p > 0.05$

The species has frequently been inducing water blooming in eutrophic water reservoirs, e. g., in Jelonek lake and Świętokrzyskie lake (Poland) [22,23]. The species also was, noted in numerous polymeric Mazurian lakes [24]. Along with *Microcystis aeruginosa*, it was the dominant species in the Goczałkowicki reservoir (Poland) [25]. *Aphanizomenon flos-aquae* also was, noted in high concentrations in small, subjected to biomanipulation reservoirs in Finland [26], Denmark [27,28] and in Holland [29].

In subsequent years (1994-1996) the phytoplankton was dominated by large, colony-forming species of cyanobacteria, not decreasing in numbers until an evident decrease in temperature took place in the autumn. The most numerous species were *Planktothrix agardhi*, *Pseudanabaena limnetica*, *Anabaena spiroides* and *Anabaena flos-aquae*. *P. agardhi* is supposed to poorly tolerate light deficiency conditions [24]. The species was found to dominate in eutrophic Mazurian lakes and its maximum abundance was noted in summer, although the species may be present in reservoirs all year [24]. The species was also one of co-dominating taxa in the eutrophic reservoir of Arancio [30].

The taxonomic identity also depends on whether N or P is the limiting nutrient. *Aphanizomenon flos-aquae* reported in 1993 was replaced by *Planktothrix agardhii* reported in 1994-1996. The Sommer's [31] hypothesis reports that if N rather than P is in short supply, heterocystous *Nostocaceae* e.g. *Mougeotia thylespora* or *Aphanizomenon flos-aquae* should be the dominant species. If P is more limiting the potential candidate for domination is *Planktothrix agardhii*. However, this hypothesis cannot be fully applied to Maltański Reservoir. Although in the spring (i.e. from March to May of 1994, and from April to May 1995), phosphorus was not detectable in the water of the reservoir, the species *P. agardhii* was abundant in the periods from May to October in the same years.

Only in the first year of the biomanipulation experiment (1993), phytoplankton numbers were low and its development was controlled by zooplankton. Nevertheless, in July a rapid decrease in macrofiltrators and an increase in colonial cyanobacteria were recorded. This was a typical feedback effect, considered one of the most important reasons of the low effectiveness of biomanipulation experiments [32,33].

In the next years (1994-1996) the effect of zooplankton on phytoplankton development was evidently less important. The disappearance of the largest daphnids (connected with an increasing pressure of fish) brought to the ineffectively controlled development of cyanobacteria [34, 35].

Alimentary pressure of cladocerans, which prefer fine phytoplankton, leads to an increasing share of forms which are non-edible for zooplankton (microplankton) [36,37]. In reservoirs subjected to biomanipulation, the so-called feedback effect frequently takes place [34,38-41], which involves the development of diatoms of long cells in the spring or of cyanobacterial colonies in summer. In the Maltański Reservoir, such phenomena have

been observed a few times, e. g., at the end of March, 1994 diatoms of long cells have appeared, including *Synedra acus*, *Asterionella formosa*, as well as *Diatoma elongatum* and *Fragilaria crotonensis* at the verge of May and June. Apart from these species, in 1996 *Synedra acus* var. *angustissima* and *Nitzschia acicularis* var. *closterioides* also manifested in high numbers. Species of the *Nitzschia* genus dominated immediately after regression of the vernal water blooming in the biomanipulation-subjected lake of Zwemlust [42].

Phytoplankton rapidly reacts to alteration of environmental conditions. Its quantitative and qualitative alterations provide examples of organism adaptation to the changing habitat. An analysis of statistical relations between water temperature and the parameters describing phytoplankton have demonstrated that temperature significantly affects increases in the number and biomass of phytoplankton. A positive correlation between the parameters ($r=0.77$; $p<0.001$) has confirmed the dependence of the photosynthetic functions and, thus, the abundance and biomass of algae on temperature. This fact has been explained by a hypothesis of Shapiro [43] who has indicated that cyanobacteria, which dominate among phytoplankton cells, prefer high temperatures ($>20^{\circ}\text{C}$). Water blooming in the warm periods has been induced almost exclusively by representatives of this class.

At lower temperatures, phytoplankton has not been numerous in general and has been dominated by nanoplankton algae, such as fine diatoms, chrysophytes and cryptophytes: *Stephanodiscus hantzschii*, *Erkenia subaequiciliata*, *Rhodomonas lacustris* and *R. lens*. *Stephanodiscus hantzschii* is thought to be an indicator of eutrophic habitats [24]. The small, centric diatoms have prevailed in the phytoplankton biomass of Mazurian lakes [24]. *S. hantzschii* has also been noted in the Sulejowski reservoir [44] and in Jeziorsko [45].

In winter, due to the reduction in the amount of light energy, the abundance and biomass of algae decreased. In the winter months, the dominant species included *Chrysococcus minutus*, *Ch. rufescens*, *Chrysococcus sp.*, *Ochromonas sp.*, *Bicoeka sp.*, *Synura uvella* (in 1995) and *Erkenia subaequiciliata* (1996). When permitted, however, by light conditions (e. g., in December 1995), the phytoplankton developed extensively. At that time the abundance of the organisms was the highest in the entire studied period. The occurrence of the *Chrysophyceae*, *Dinophyceae* or *Cryptophyceae* species has been attributable to their tolerance to low temperatures and to their ability to grow under very low amounts of light. In addition, some flagellates can improve their ability to exploit low light intensity by chromatic adaptation or to grow heterotropically [46].

Relations between the number of cells, organisms and biomass of algae and temperature also was noted in the Rusałka reservoir, but they could not have been confirmed for Strzeszyńskie lake [47, 48].

A strict relation has been detected between the number of organisms, cells and phytoplankton biomass, on

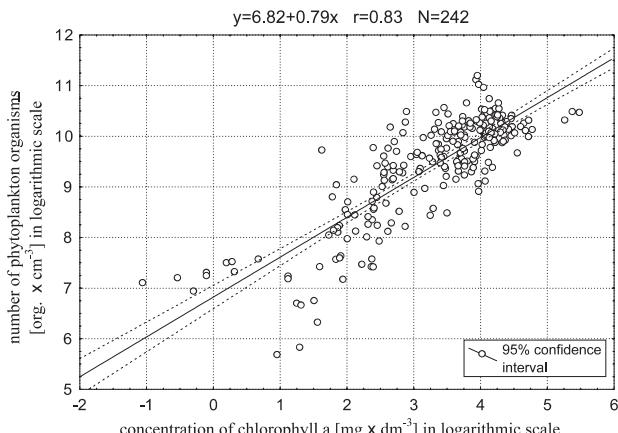


Fig. 5. Correlations between number of phytoplankton organisms and concentration of chlorophyll *a*.

the one hand, and chlorophyll *a* concentration, on the other. The highest correlation coefficient of $r=0.83$ ($p<0.001$) has been found for the relation between the number of phytoplankton organisms and the amount of chlorophyll *a* (Fig. 5). Similar relations, at the significance level of $p=0.01$ and $p=0.05$, have been detected in the Rusałka reservoir and Strzeszyńskie lake, respectively [47, 48]. Similar relations also have been indicated for Vasikkalampi reservoir ($r=0.86$, $N=60$) [49] for Hubenov reservoir ($r=0.83$, $N=32$) [50] and for Volvi lake ($r=0.83$, $N=231$) [51].

Strict relations between phytoplankton biomass and seston ($r=0.79$, $p<0.001$) have reflected the fact that phytoplankton is the main component of seston in Maltański reservoir. A statistically significant correlation between seston and the cells, specimens or biomass of algae also has been noted in Strzeszyńskie lake and Rusałka reservoir [47, 48].

In the Maltański Reservoir, seston has shown strict correlation with the amount of chlorophyll *a* ($r=0.74$; $p<0.001$). Positive relations between seston and the chlorophyll *a* concentration has also been observed by Jones [52] and Kudelska et al. [53].

Increased algae concentration has deteriorated water transparency. In the water blooming periods, e. g. in July, 1994, when chlorophyll *a* level increased to $195 \mu\text{g} \cdot \text{dm}^{-3}$, a Secchi disk was visible only to the depth of 0.3 m. In periods when light access to the deeper layers of the water was negligible, phytoplankton developed mainly in the surface layers of water. Increased concentration of phytoplankton restricted water transparency, which has been confirmed by the negative correlation between these parameters ($r=-0.83$ to -0.88). A statistically significant, negative correlation between water transparency and the biomass of algae has also been noted in Mazurian lakes [54] and in the Rusałka reservoir [48].

In Maltański Reservoir, a significant correlation has also been detected between the numbers of organisms, phytoplankton cells and its biomass, on the one hand, and the BOD₅ index values on the other ($r=0.51$ to

0.61 ; $p<0.01$, $N=235$). A positive relation between these parameters has also been noted by Szelag-Wasielewska in Strzeszyńskie lake and in Rusałka reservoir [47, 48]. This proves that phytoplankton induces deterioration of water purity, described by the values of the BOD₅ index.

In the study reported, development of phytoplankton has also been related to water pH. In general, high water pH has been observed in summer, when cyanobacteria caused water blooming. Several hypotheses have been proposed by Shapiro [55] to explain the dominance of cyanobacteria. According to one of them, the organisms prefer conditions of low CO₂ content and high pH values [43, 55]. The same tendency has been stressed by Bendendorf and Henning [56] and by Bernardi and Giussani [57].

The rich phytoplankton in Maltański Reservoir decreased water concentration of inorganic compounds. This explains marked relations between the cell numbers and the phytoplankton biomass and conductivity ($r=-0.54$, $p<0.001$).

In the studied period, nitrogen did not restrict phytoplankton development (Table 4). In some periods, like in August, 1994 to 1996, nitrates were depleted from the water but ammonium nitrogen was still available, well assimilated by cyanobacteria in particular [58]. Evident relations have been observed between phytoplankton biomass and organic nitrogen ($r=0.62$, $p<0.002$), and total P ($r=0.51$, $p<0.001$). On the other hand, no significant relations have been noted between the nitrogen species mentioned and the number of phytoplankton organisms. A few significant correlations between the amount of phytoplankton and the mineral species of nitrogen and phosphorus have been reported by Szelag-Wasielewska [47] for Strzeszyńskie Lake. Other authors, e. g. Spodniewska [54] in Mazurian lakes, Schwartzkopf and Hergenrader [59] in three American lakes, have confirmed the observations.

In summary, analysis of the results has shown that in the period 1993-1996 the number of 233 phytoplankton taxa was found in the reservoir. The most numerous group of algae, in respect to the number of taxa, were green algae. In determining general numerical force and biomass of phytoplankton the most significant group was cyanobacteria.

The seasonal quantitative and qualitative changes in the phytoplankton were a consequence of physical and chemical changes in the water of the reservoir. The abundance of organisms, cells and biomass of the phytoplankton were found statistically significantly correlated with the physical and chemical characteristics of the reservoir water such as transparency, temperature, pH, BZT5, electrolytic conductivity and total phosphorus content, which confirms the role of these factors in algae development. According to our estimations, the role of the chemical and physical characteristics was greater than that of zooplankton (filter-feeding zooplankton feed ineffectively, allowing the cyanobacteria to develop with decreased competition).

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