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The relationships between zooplankton and biotic/abiotic factors

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Abstract — Changes in the composition and numbers of phyto- and zooplankton were analysed against the background of environmental conditions in three ponds. In the control pond primary production proceeded in the total profile to 1.2 m, in the fertile pond in a layer of about 60 cm, and in the very fertile one in a layer of 20 cm. The succession of zooplankton species was rapid but the law of crop constancy was fulfilled. The abundance of populations of numerous species of zooplankton significantly decreased with increasing concentration of oxygen and chlorophyll.

Key words: zooplankton, population dynamics, biotic/abiotic factors, statistical relationships.

1. Introduction

Some time ago it was observed (Davidson, Andrewartha 1948, Began, Mortimer 1981) that it did not matter whether the factors regulating the abundance or limiting the numbers of populations were of biotic or abiotic nature. In the literature the role of these factors is approached from two aspects: as information concerning the condition of the environment and as their way of action in the environment.

Of the biotic factors which play an important role in the dynamics and seasonal succession of zooplankton, food should be mentioned in the first place, followed by competition, predation, and allelopathies

(Gilbert 1967, Hutchinson 1967, Hofmann 1972, Halbach 1973, Dumont 1977, Gliwicz 1977, Sommer 1989). Chemical components dissolved in the water and their effect on the population of rotifers and crustaceans were studied by numerous authors, among them Bogatova 1962, Pourriot 1965, De Costa 1975, Grygierek et al. 1977, De Costa and Janicki 1978, Boswell et al. 1980, and Ruttner-Kolisko 1980. Numerous observations showed a coincidence or succession in the development of different zooplankton species with maxima in the development of bacteria (Bogatova 1971, Ramsay 1976, Gophen 1977) or algae (Anderson et al. 1955, Angino et al. 1973, Gliwicz 1977, Foran, King 1982, Langeland, Reinertsen 1982). The studies mentioned above very frequently concerned natural environments, not modified by human activity. The problem of the causes of seasonal succession and the successful development of different species has already been comprehensively elaborated by Kerfoot and Sih (1987), De Mott (1989), Gliwicz and Pijanowska (1989).

In analysing the dependence of the abundance of various species on biotic or abiotic factors, numerous hydrobiologists used the method of multiple regression/correlation. For example, Włodek (1954) applied the method of multiple regression in a description of carp populations, solving equations by the Cracovian method. The same method was used by Antipchuk (1977) in a study on relations between bacterioplankton and phyto- and zooplankton. Using multiple regression, Gliwicz (1977) investigated the dependence of the daily production of eggs by *Daphnia cucullata* upon numerous variables. Pliński and Jóźwiak (1989) applied this method in prognosticating the blooms of blue-green algae, and obtained a high conformability with the observations. It was also used by Habib and Rahman (1992) in analysing the dependence between the number of rotifers and 13 chemical parameters of ponds.

The aim of the present work, based on a field investigation was to determine the relation in the summer season between the numbers of different zooplankton species and chemical factors, numbers of heterotrophic bacteria, and different groups of algae. Besides, relations between the abundance of populations of different plankton species and physical, chemical, and biotic factors were analysed.

2. Study area

The investigations were carried out in the natural environment of three ponds of 1500 m² each from the complex of 24 experimental ponds at Gołysz (49°52′ N, 18°48′ W). The ponds differed in the size of carp stock, agrotechnological operations, and the resulting degree of eutrophication (pond 7 — control, 9 — medium fertility, 8 — high fertility). The fishery characteristics of the ponds were given by Wróbel (1971) and a description of the bottom and physicochemical condition by Pasternak (1958, 1965). Agrotechnological operations carried out in the ponds and the fish stocks are listed in Table I.

Table I. Some data about investigated ponds

Parameter	Number of pond	7	8	9
	Kind of pond	control	very fertile	fertile
Fish stock (indiv. ha^{-1})		300	3868	900
Fish stock (indiv. $pond^{-1}$)		45	580	145
Mean weight (g)		255	248	248
Feeding		—	commom granulate	—
Fertilization kg ha^{-1} (in 6 doses to the end of investigations)		—	400 NH_4NO_3+280 superphosphate	400 NH_3NO_3+280 superphosphate

3. Material and methods

Investigations were carried out from June to August 1973. 30 samples were collected every 2—3 days. Methods used in chemical analyses and in determining phyto- and zooplankton are given by Lewkowicz and Żurek (1991). Counted algae were divided into three groups: small, medium, and large. The sum of average length and width of algae was accepted on the criterion of division. It seems that this criterion better expresses the "relative" size of the algae than, e.g., the coefficient equal to the product of length and width. The value below 100 µm was arbitrarily accepted for small algae, 100—250 µm for medium sized ones, and over 250 µm for large species.

Statistical analyses were carried out by calculation of stepwise regression, using a commercial computed program. All equations were calculated in linear multiple form:

$$Y_i = a + bX_1 + cX_2 - \ldots\ldots + NX_n$$

where:

Y — a dependent variable, numbers of i-th species,
X_n — independent variables.

The authors used 14 independent variables. Each equation was computed in two forms differing in one feature: in the first variant, turbidity was expressed as the amount of ash whereas in the second the turbidity was expressed in SiO_2. For each independent variable the t test and its probability were also calculated. For the full regression coefficients of determination r^2 and r^2 adjusted to degrees of freedom were calculated. The standard error of estimation Y, F test, and its probability were also calculated. In analysis of residuals standardized and nonstandarized values of skewness and kurtosis were also calculated. However, for each datum the Mahalanobis distance was calculated; equations were computed with all data and only one example contained two variants: with all observations and with observations without the highest Mahalanobis distance. The equations were calculated by a backward method, i.e. by manually or automatically removing the nonsignificant variables. After selecting the requested variables for the final model, fitting results were computed once more, using Graham-Schmidt algorithm.

All dependent variables (Y_i) were coded as in Table II from 1 to 35. Codes for independent variables (X_i) are given in Tables III and IV.

3. Results

3.1. Chemical parameters

Table II contains basic data concerning chemical parameters in each the three ponds. The highest average concentrations of dissolved oxygen and the largest range of their variation were found in pond 9. In pond 7 (control) oxygen concentrations did not fall below 6 mg dm^{-3} and the range of variation was uniform. The poorest oxygen conditions were found in pond 8. In all ponds similar tendencies were observed in the changes of oxygen concentration. In periods of homothermy (fig. 1) the distribution of oxygen concentrations was also homogenic, with a tendency to a slight decrease in the zone near the bottom. The concentration of oxygen was slightly correlated with the content of chlorophyll in the experimental model of pond 8 ($r = -0.34$, $P < 0.064$).

The detailed dictribution of temperature in the ponds is given in fig. 2. The pattern of changes in average temperatures was similar in all ponds. In pond 8 the tendency of stratification to occur was stronger and the variation of temperatures wider than in pond 7. The occurrence of a slight thermic stratification was favoured by frequent calms and light winds with an average velocity of 1—2 m s^{-1}. The more frequent winds of 3—5 m s^{-1}, blowing in the second part of July and lower air temperatures contributed to the total mixing of water and homothermy in all the ponds.

The smallest content of organic matter in the water expressed as total chemical oxygen demand (TCOD) and at the same time the smallest

Table. II. Basic statistical data about planktonic species and chemical parameters. Variables from 1 to 34 in indiv. dm^{-3}

No	Variable / Pond No	7			8			9		
		min—max	Average	Skewness	min—max	Average	Skewness	min—max	Average	Skewness
1	Asplanchna girodi	0.0—85.5	13.12	2.917	21.3—72.0	37.56	1.015	3.1—167	64.18	0.72
2	Brachionus angularis	0.0—17.5	4.42	1.543	0.0—144.0	19.81	2.790	0.0—5.4	1.01	1.87
3	— calyciflorus	0.0—52.5	0.0	0.0	22.0—599.0	0.0	0.0	1.6—66.2	0.0	0.0
4	— diversicornis	0.0—125.0	19.14	2.805	0.0—44.5	17.63	0.685	0.0—6.3	1.27	1.91
5	— rubens	0.0—12.5	3.85	1.263	0.0—9.0	3.36	0.496	51—516	174.99	1.77
6	Conochiloides coenobasis	0.0—1560.0	219.285	2.930	0.0—5136	857.6	2.399	7—7028	1165.03	2.15
7	Conochilus unicornis	0.0—209.1	35.14	2.506	0.0—76.5	7.65	3.162	0.0—0.0	0.0	0.0
8	Filinia longiseta	0.0—63.7	7.12	3.122	18.0—927	291.66	1.160	0.0—12.3	1.76	2.72
9	Keratella cochlearis cochlearis	80.0—873.6	403.14	0.366	0.0—113.4	37.22	1.426	2.3—12.3	4.82	2.17
10	— cochlearis tecta	0.0—207.5	3643	2.316	133.6—571.0	316.16	0.583	1.7—72.4	17.22	1.97
11	Sum of K.c. cochlearis + K.c. tecta	166.5—873.6	439.57	0.456	145.7—631.4	353.38	0.741	4.4—75.9	22.04	1.97
12	— quadrata	8.3—55.0	27.54	0.205	0.0—8.0	2.46	0.705	0.0—6.3	2.07	0.69
13	Polyarthra dolichoptera	0.0—214.2	66.37	0.802	0.0—202.4	22.83	3.134	0.0—202.4	22.83	3.13
14	— vulgaris	3.3—99.8	34.24	1.328	0.0—56.7	35.99	—1.022	12.6—478	151.52	1.40
15	Pomoholyx sulcata	0.002—8.5	3.50	0.269	34.6—1939.0	845.97	1.301	0.0—157.5	25.12	2.66
16	Synchaeta sp.	0.0—20.0	3.43	2.200	0.0—0.0	0.0	0.0	0.0—0.0	0.0	0.0
17	Trichocerca sp.	380.0—377.5	104.8	1.550	0.0—137.7	21.06	2.944	0.0—6	1.4	1.67
18	Sum of rotifers	248.52—3061.1	991.179	1.943	1054.6—6122	2945.45	1.185	195.3—7172.1	1466.57	2.13
19	Bosmina longirostris	215.0—215.4	44.13	2.209	107.8—801	366.11	0.691	21.2—122.8	68.58	0.11
20	Ceriodaphnia pulchella	10.8—33.2	24.91	—0.133	0.0—24.3	10.59	0.616	0.0—21.2	7.46	0.69
21	Daphnia hyalina	0.0—0.0	0.0	0.0	0.0—0.0	0.0	0.0	0.0—13.8	5.87	0.76
22	— pulex	1.6—18.2	7.04	1.046	0.0—0.0	0.0	0.0	0.0—2.3	0.57	1.17
23	— longispina	8.3—42.5	22.81	0.631	1.5—49.5	15.85	1.866	0.0—65.3	9.13	2.51
24	Diaphanosoma brachyurum	13.3—105.5	46.15	0.873	0.0—0.0	0.0	0.0	0.0—0.0	0.0	0.0
25	Moina micrura	0.0—57.5	15.55	1.393	8.6—215	91.74	1.072	2.7—54	21.01	1.26
26	Sum of cladocerans	41.4—372.2	160.59	1.158	143—898	488.315	0.262	50.8—163.7	110.72	—0.33
27	Naupli	28.3—262.5	125.51	0.733	247—445	338.61	0.282	90.2—397	226.45	0.39
28	Copepodits	10.0—63.7	39.69	—0.382	22.5—135	52.08	1.642	5.4—73.8	29.35	1.401
29	Cyclops vicinus, adults	0.2—20.0	2.515	2.997	3.8—28.4	13.76	0.610	1.7—28.8	13.88	0.474
30	Thermocyclops crassus, adults	1.5—17.8	9.75	—0.173	4.3—60.3	18.7	2.379	11.5—53.3	26.26	0.957
31	Diaptomus sp.	2.5—20.0	8.58	0.755	3.4—17.2	7.93	1.331	5.2—23.4	11.58	0.935
32	Sum of copepods	43.1—350.2	186.045	0.243	301—589	431.08	0.322	28—478.8	281.52	—0.554
33	Chaoborus crystallinus	1.0—18.0	8.5	0.162	0.0—1	0.2	1.778	0.0—1	0.3	1.035
34	Other	0.0—12.7	4.49	1.150	0.0—23	10.75	0.206	0.0—6.9	1.73	1.414
35	Sedimented volume cm^3	0.01—0.0	0.0347	0.731	0.0—0.5	0.142	1.699	0.025—0.08	0.0447	1.249
36	Bacteria indiv. cm^{-3}	6860—31560	13803	1.741	11610—249000	53088	2.929	6630—61000	17639	2.688
37	Euglenophyceae cells dm^{-3}	0.0—13090	3153.5	1.312	0.0—514080	209202	0.642	0.0—110880	12672	3.051
38	Cyanophyceae cells dm^{-3}	11900—12794900	2622570	2.240	0.0—1113840	329868	1.354	0.0—35700	6201.2	2.117
39	Cryptophyceae cells dm^{-3}	0.0—338675.0	87478	1.549	0.0—514100	149942	1.324	0.0—321100	102857	1.676
40	Chrysophyceae cells dm^{-3}	0.0—17136.0	3617	1.584	0.0—0.0	0.0	0.0	0.0—0.0	0.0	0.0
41	Bacillariophyceae cells dm^{-3}	19040.0—22848	106136	0.311	0.0—104720	26418	1.389	18216—126720	63583.2	0.737
42	Chlorophyceae cells dm^{-3}	273700—814912	1833580	2.324	4.545E6—2.153E7	12654200	0.510	1021250—7259000	3639030	0.483
43	Small aloae cells dm^{-3}	399840—21172500	4543920	2.287	4.76E6—21951900	12956800	0.396	1082930—7389900	3837460	0.555
44	Medium algae cells dm^{-3}	0.0—304640	76481	2.298	23800—1485120	400554	1.766	13708—158400	59645.6	1.368
45	Large algae cells dm^{-3}	0.0—26180.0	3213.0	2.900	0.0—171360	44268	1.425	0.0—92898	23834.2	1.579
46	Temperature °C	17.12—23.73	21.065	—0.762	17.0—23.91	21.114	—0.843	16.8—23.87	20.949	—0.728
47	Oxygen mg O_2 dm^{-3}	6.28—9.23	7.789	—0.059	4.51—8.16	6.633	—0.518	5.87—13.23	9.292	0.251
48	Ash mg dm^{-3}	12.6—22.7	16.66	0.578	41.2—123.2	90.66	—0.621	27.6—120.4	57.22	1.756
49	SiO_2 mg SiO_2 dm^{-3}	53.0—250.0	101.7	1.736	217—1200	544.9	1.217	132—900	295.9	2.618
50	pH	8.45—8.06	8.19	0.38	8.45—7.8	7.97	1.410	9.6—8.05	8.51	—0.06
51	Chlorophyll *a* µg dm^{-3}	12.0—80.0	30.8	1.838	240—440	359	—0.701	65—260	147	0.639
52	Photosynthesis mg O_2 dm^{-3}	0.03—2.47	0.826	1.521	0.93—6.71	4.01	—0.058	—0.47—6.28	2.751	0.111
53	GPP mg O_2 dm^{-3}	0.93—3.80	1.872	1.301	3.44—10.61	7.43	—0.583	1.89—8.81	5.072	0.252
54	TCOD mg O_2 dm^{-3}	16.0—24.0	20.224	—0.1042	49.14—70.4	60.262	—0.256	29.64—41.6	35.032	0.563
55	DCOD mg O_2 dm^{-3}	12.8—22.4	16.804	0.5724	20.8—28.8	25.624	—0.591	12.8—22.4	18.56	—0.265

Table III. Regression analysis for *Brachionus calyciflorus*. Variables as follows: X4 — chlorophyll; X5 — bacteria; X6 — Euglenophyceae; X12 — small algae; X13 — medium algae; X-TCOD — total COD; Xph — photosynthesis; a and b — coefficients of regression equations

					ANOVA			
X	a	b	o	Pb	F	P	r	r^2
X4	—50.9	0.753	0.130	0.0000034	33.29	0.0000	0.74	0.55
X5	84.1	—0.000008	0.000641	0.99	0.00015	0.99	—0.00238	0.00
X6	37.0	0.624	0.185	0.0022	11.40	0.0022	0.54	0.29
X7	92.7	—0.00898	0.011	0.4	0.650	0.4278	—0.15	0.02
X12	18.8	0.00914	0.004047	0.03	5.10	0.0319	0.39	0.15
X13	70.5	0.075	0.091	0.4	0.664	0.422	0.15	0.02
X-TCOD	—154.9	6.201	1.116	0.0000006	30.84	0.00001	0.72	0.52
Xph	14.15	27.566	12.185	0.03	5.12	0.032	0.35	0.12
X4, X5, X6, X7, X12, X13					16.04	0.0000	0.898	0.807
X4, X5, X6, X7, X12, X13, X-TCOD					13.28	0.0000	0.899	0.808

range of its variation throughout the investigation period were observed in pond 7. In pond 9 where mineral fertilization was applied, the content of organic matter was considerably greater and slightly correlated with that of chlorophyll (r = 0.57). In spite of the same fertilization, in pond 8 the eutrophication was most advanced, the highest value of TCOD were slightly correlated with changes in chlorophyll content (r = 0.45).

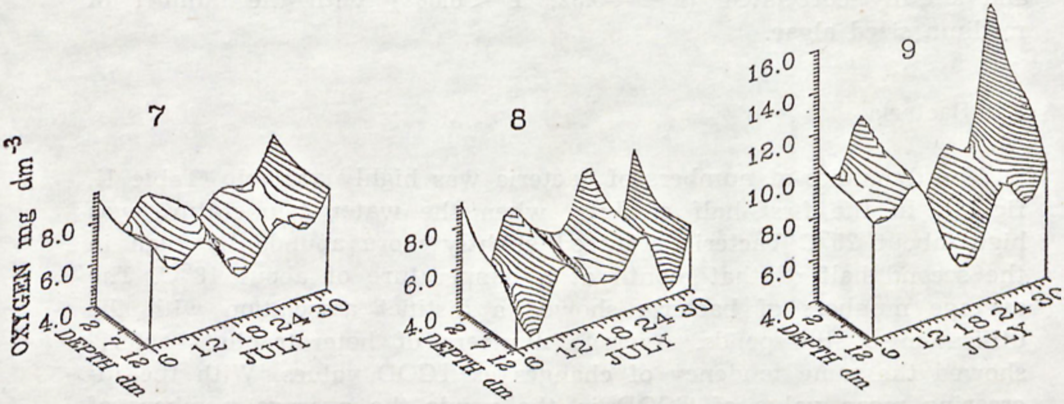


Fig. 1. Time-space distribution of oxygen concentration in the investigated ponds

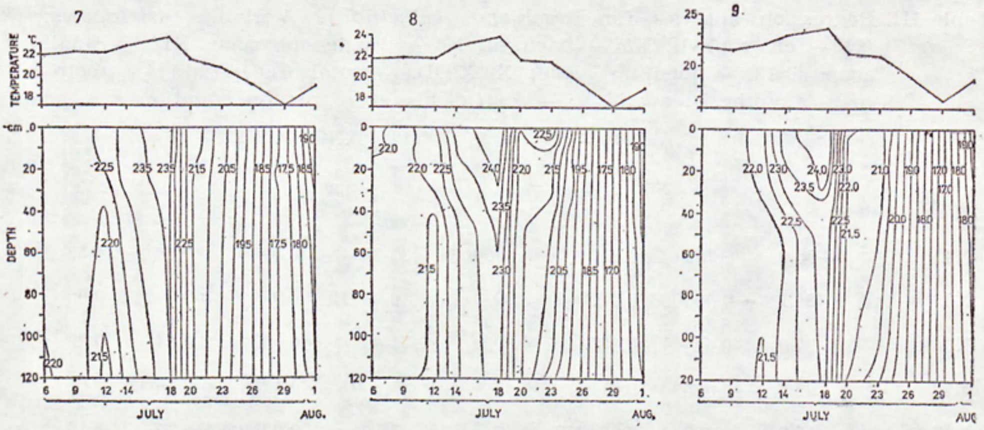


Fig. 2. Temperature ditribution in the investigated ponds

Chemical oxygen demand of dissolved organic matter (DCOD) was stable in all three ponds. The lowest content of dissolved organic matter was found in pond 7, a higher one in pond 9, while in pond 8 it was higher by 38%.

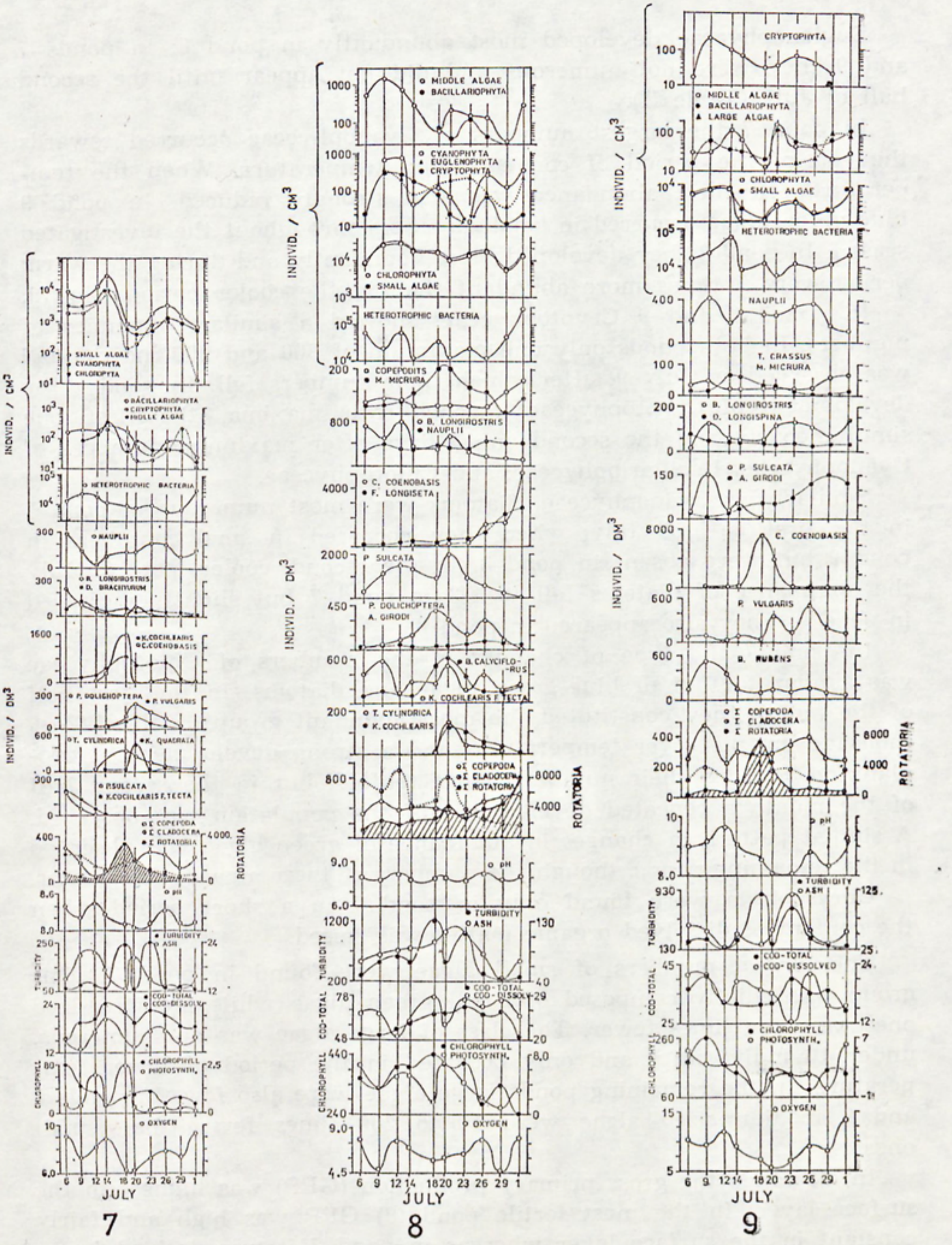
The lowest concentration of chlorophyll *a* was found in pond 7. In pond 9 the content of chlorophyll was 7 times greater, though it decreased strongly in the second decade of July on account of a mass development of cladocerans and then of rotifers. The highest and most stable content of chlorophyll was observed in pond 8.

The least turbidity of the water was observed in pond 7, in pond 9 being 3 times and in pond 8, 5 times greater. In all the ponds a dramatic increase in turbidity was observed during 5 days around 20th July (fig. 3).

In all three ponds the reaction of the water was weakly alkaline and sligthly correlated ($r = -0.32$, $P < 0.082$) with the number of medium sized algae.

3.2. Bacteria

The dynamics of numbers of bacteria was highly variable (Table II, fig. 3). In the first half of July, when the water temperature was high (about 25°C bacteria occurred slightly more abundantly than in the second half of that month at a temperature of about 18°C. The average numbers of bacteria showed a distinct association with the utilization of the ponds. Average numbers of heterotrophic bacteria showed the same tendency of changes as TCOD values. With the increasing mean value of TCOD in the ponds the average numbers of heterotrophic bacteria also rose.



7 8 9

Fig. 3. Changes in the numbers of bacteria, algae, zooplankton, and chemical factors in the investigated ponds. Units of chemical factors as in Table II

3.3. Algae

Euglenophyceae developed most abundantly in pond 8; in ponds 7 and 9 they were not numerous and did not appear until the second half of July (Table II).

In pond 7 the largest numbers of Cyanophyceae occurred towards the end of the period of constant high temperature. When the temperature fell their abundance was also strongly reduced. In pond 9 blue-green algae occurred in small numbers throughout the investigated season. In pond 8 they developed more abundantly and during the warm period were 5 times more abundant than in the cooler period (fig. 3).

In ponds 8 and 9 Cryptophyceae showed a similar dynamics of numbers. In both ponds only one maximum of 300 and 200 indiv. dm^{-3} was observed on July 9, after which their numbers fell. In pond 7 the development of Cryptophyceae reached two maxima, the first one simultaneously and the second one 3 days after maximum numbers of Cyanophyceae, Bacillariophyceae, and Chlorophyceae.

Similarly as Cyanophyceae, diatoms were most numerous in pond 7 in the first half of July, when they occurred in small numbers in pond 9 but were absent in pond 8. In the second, cooler, part of July the abundance of diatoms fell to 1/3 in pond 7 but slightly increased in pond 9. They also appeared in pond 8.

In pond 7 the type of changes in the numbers of Chlorophyceae was similar to that of blue-green algae and diatoms. In the first half of the month they constituted the most abundant group of algae (2—8 thousand cm^{-3}). Lower temperatures and a strong development of zooplankton reduced their numbers about tenfold, but in the second half of the month a repeated development of the population was observed. A similar pattern of changes in abundance of green algae was observed in the remaining ponds, though the numbers of these algae were greater.

Chrysophyta were found only in pond 7 in a short period when the content of dissolved organic matter was raised.

The largest numbers of small algae were found in pond 7. This group was chiefly composed of small green algae while medium-sized ones were ten times fewer. The class of large algae was not numerous, under 10 indiv. cm^{-3}, and only occurred in the period of lower temperature. In the remaining ponds large algae were also few. In ponds 8 and 9 medium-sized algae were 10 to 200 times fewer than small ones.

In all ponds the gross primary production (GPP) was highest in the surface layer. In the most fertile pond (8) GPP was high and fairly constant in the surface layer whereas in pond 7 it was decided lower and uniform in the entire profile. The most variable values of GPP in the surface layer were found in pond 9 where the differences reached

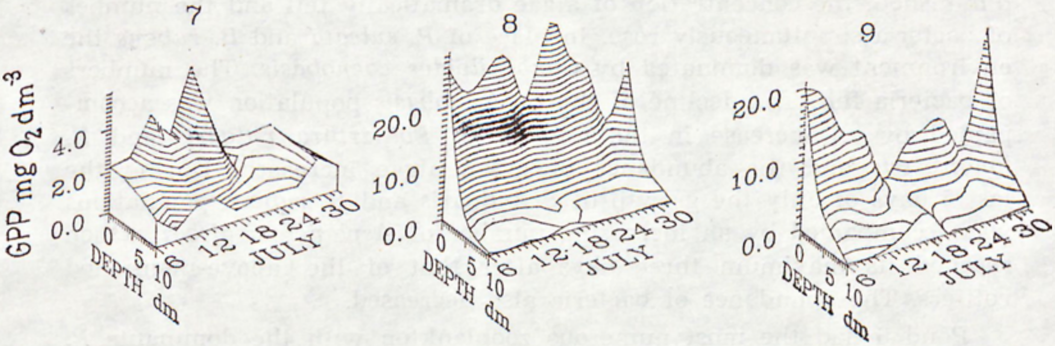


Fig. 4. Time-space distribution of gross primary production (GPP) in the ponds

17 mg O_2 dm^{-3} (fig. 4). In pond 7 photosynthesis usually prevailed over respiration in the whole profile, while in pond 8, in the layer below 50 cm, respiration almost always dominated. In pond 9 the dominance of respiration over photosynthesis was rarely noted at a depth of 50 cm but was always found at a depth of 100 cm.

3.4. Zooplankton

The pattern of changes in numbers and dominance of species was different in each pond (fig. 3). Changes in species composition were rapid. Early in July in pond 7 the populations of *Keratella cochlearis* f. *tecta, Pompholyx sulcata,* and *Bosmina longirostris* died out and the number of nauplii decreased. At the same time, the number of bacteria rose, *K. cochlearis* f. *cochlearis* with cladocerans *Daphnia longispina, Ceriodaphnia pulchella,* and *Diaphanosoma brachyurum,* succeeded in dominating the environment. Two days after the reduction of populations of zooplankton and bacteria, the numbers of small algae, chiefly blue--green and green species, increased. Later, the zooplankton was dominated by *Conochiloides coenobasis* (1600 indiv. dm^{-3}), *K. cochlearis* f. *cochlearis* (850 indiv. dm^{-3}, and *D. brachyurum* (80 indiv. dm^{-3}). In that period the abundance of phytoplankton was reduced 15-fold and that of bacteria halved. Towards the end of July the environment was dominated by *Keratella quadrata* and *B. longirostris* (80 indiv. dm^{-3}).

In pond 9 and in the control one the numbers of rotifers were similar. The abundance of crustaceans markedly increased. Towards the end of the second decade of July bacteria were scarce and *Daphnia longispina* (800 indv. dm^{-3}) prevailed in the zooplankton. The population of *Brachionus rubens* also rapidly increased (over 500 indiv. dm^{-3}). *D. longispina* was them replaced by *B. longirostris*. Three days later, when the abundant populations of *Pompholyx sulcata* and *B. rubens* had diminished, the concentration of algae dramatically fell and the number of bacteria simultaneously rose. In place of *P. sulcata* and *B. rubens* the environment was dominated by *Conochiloides coenobasis*. The numbers of bacteria fell. The decline of the *C. coenobasis* population was accompanied by an increase in the number of *Polyarthra vulgaris* and *B. longirostris* and the abundance of green algae increased. During the last 5 days of July the growth of *P. vulgaris* and *B. rubens* populations was accompanied by an increasing number of *Asplanchna girodi*, which reached its maximum three days after that of the above-mentioned rotifers. The abundance of bacteria also decreased.

Pond 8 had the most numerous zooplankton with the dominants *P. sulcata, Filinia longiseta, C. coenobasis, B. longirostris,* and *Moina micrura*. In the first decade of July the increasing numbers of algae were associated with the growing populations of *P. sulcata* and *K. cochlearis* f. *tecta*. At that time the population of *B. longirostris* fell until the numbers of the above mentioned rotifers had been reduced about fivefold. A repeated increase in the abundance of *K. cochlearis tecta* was accompanied by a decrease in that of *Bosmina* and bacteria populations. In the second decade of July, with a further dominance of *P. sulcata,* the populations of *M. micrura, B. calyciflorus, K. c. tecta,* and *K. c. cochlearis* reached their maxima. Then, within 5 days, the structure of the association radically changed. The species mentioned above died out while green- and blue-green algae, euglenoids, and bacteria developed. Towards the end of July the numbers of copepods and above all of *C. coenobasis* and *F. longiseta* rose.

3.5. Statistical results

The dependence of the numbers of *Brachionus calyciflorus* on 8 single variables was analysed. The values of the obtained correlations ($|r|$) varied from 0.74 for chlorophyll *a* to 0.0024 for bacteria. The best coefficient of determination r^2 was 54.3% at a 5% confidence interval (Table II). Values P for coefficient b varied from 0.00—0.99. The equation of multiple regression with 6 variables simultaneously taken into consideration resulted in 75% of elucidated variability (Table II). Even when TOCD was taken into account the quality of the equation was not improved.

The following example illustrates the consequence of discarding certain observations with the greatest Mahalanobis distance. For *Thermocyclops crassus* the regression equation of its numbers on environmental factors is reduced to a significant dependence on 4 parameters. The calculated equation gave the value 7.4 for the F test and 0.54 for r^2. A high Mahalanobis distance was found for three observations: 114.5,

Table IV. Significancy (P) and sign of relationship between zooplankton density (N dm^{-3}) and independent variables. X1 — temperature; X2 — oxygen; X3 — turbidity as mg ash; X4 — chlorophyll *a*; X5 — bacteria; X6 — Euglenophyceae; X7 — Cyanophyceae; X8 — Cryptophyceae; X9 — Bacillariophyceae; X10 — Chrysophyceae; X11 — Chlorophyceae; X12 — small algae; X13 — medium algae; X14 — large algae

Species / Code of independent variable	X1	X2	X3	X4	X5	X6	X7	X8	X9	X10	X11	X12	X13	X14
Y 1 Asplanchna girodi					—0.08	—0.07		—0.03		—0.05				0.004
Y 2 Brachionus angularis				0.001		—0.0003	0.072					—0.054	0.000	
Y 3 — calyciflorus				0.000	—0.007	0.000	0.014					—0.058	—0.004	
Y 4 — diversicornis												0.02		
Y 5 — rubens		0.0003		0.01				0.002				—0.001		
Y 6 Conochiloides sp.		—0.07			0.004									
Y 7 Conochilus unicornis														
Y 8 Filinia longiseta	—0.0007	—0.001		—0.05	0.06		—0.000	—0.0002			—0.000	0.000		
Y 9 Keratella cochlearis cochlearis		—0.03	—0.04						0.01	0.0003				
Y10 — cochlearis tecta				0.022			—0.05	—0.059			—0.04	0.046	0.002	
Y11 total K.c. cochlearis + + K.c. tecta		—0.004								0.008		0.034		
Y12 K. quadrata			—0.004				0.07			0.0004				
Y13 Polyarthra dolichoptera		—0.01	0.018							0.065		0.09	—0.007	
Y14 — vulgaris											—0.04			0.09
Y15 Pompholyx sulcata				0.0006	—0.0051	0.0001								—0.056
Y16 Synchaeta sp.														
Y17 Trichocerca sp.		—0.042	—0.0129											
Y18 total rotifers		—0.006			0.0108									
Y19 Bosmina longirostris				0.000				—0.028					0.000	—0.004
Y20 Ceriodaphnia pulchella	0.002			—0.004										
Y21 Daphnia hyalina		0.002		0.048			—0.04	0.077			—0.023	0.044		
Y22 — pulex				—0.005				—0.017	0.03		0.069	0.097		0.024
Y23 — longispina				—0.023	—0.033		—0.034	—0.013				0.01		
Y24 Diaphanosoma brachyurum	0.018	—0.008	—0.006	—0.076				—0.021	0.015		0.025			
Y25 Moina micrura	0.002			0.001		0.003							—0.000	
Y26 total cladocerans				0.000				—0.022					0.000	—0.004
Y27 naupli		—0.03					—0.002				—0.005	0.003		
Y28 copepodits	—0.08				0.000									
Y29 Cyclops vicinus, adults	0.02	0.03		0.0005										
Y30 Thermocyclops crassus, adults						—0.0002					0.0001	0.0035		0.0013
Y31 Diaptomus sp.			—0.02								0.02	—0.05		
Y32 total copepods					0.08		—0.05		—0.05		—0.09	0.06		
Y33 Chaoborus crystallinus		—0.01		—0.06								—0.08		
Y34 other	—0.01	—0.0006		—0.01	0.03		—0.01	—0.07			—0.03	0.01		
Y35 sedimented volume				0.0001		—0.003					—0.001		0.000	0.09

Table V. Significancy (P) and sign of relationships between zooplankton density (N dm^{-3}) and independent variables. X1 — temperature; X2 — oxygen; X3 — turbidity as mg SiO_2; X4 — chlorophyll *a;* X5 — bacteria; X6 — Euglenophyceae; X7 — cyanophyceae; X8 — Cryptophyceae; X9 — Bacillariophyceae; X10 — Chrysophyceae; X11 — Chlorophyceae; X12 — small algae; X13 — medium algae; X14 — large algae

Species / Code of independent variable	X1	X2	X3	X4	X5	X6	X7	X8	X9	X10	X11	X12	X13	X14
Y 1 Asplanchna girodi	—0.04		0.01			—0.002				—0.055				0.001
Y 2 Brachionus angularis				0.004		—0.000		—0.005					0.000	
Y 3 — calyciflorus			—0.003		—0.0001	0.0001	0.014					—0.058	—0.0042	
Y 4 diversicornis														
Y 5 — rubens		0.0003		0.003				0.0016			—0.0021			
Y 6 Conochiloides sp.			0.003	—0.008	0.002									
Y 7 Conochilus unicornis														
Y 8 Filinia longiseta	—0.0007	—0.001		—0.05	0.06		—0.000	—0.0002			—0.000	0.000		
Y 9 Keratella cochlearis cochlearis		—0.0305		—0.064					0.0306	0.0004				
Y10 — cochlearis tecta	—0.07	—0.03	—0.057	0.000										0.01
Y11 total K.c. cochlearis + + K.C. tecta	0.04	—0.002	—0.02							0.003	0.07			
Y12 K. quadrata				—0.01			0.06			0.0001				
Y13 oPlyarthra dolichoptera		—0.001		0.0008									—0.001	
Y14 — vulgaris														
Y15 Pompholyx sulcata	0.0006		—0.005	0.0001	—0.056									
Y16 Synchaeta sp.				—0.081										
Y17 Trichocerca sp.	0.004	—0.06	—0.05											
Y18 total rotifers		—0.04	0.026		0.008									
Y19 Bosmina longirostris				0.000				—0.028					0.000	—0.004
Y20 Ceriodaphnia pulchella	0.0001	—0.026	—0.0002				0.102							
Y21 Daphnia hyalina		0.002		0.04			—0.04	0.02			—0.04	0.07		
Y22 — pulex				—0.013				—0.034	0.005		0.007			—0.027
Y23 — longispina				—0.042				—0.017	—0.043		0.017			
Y24 Diaphanosoma brachyurum	0.008	—0.004	—0.019	—0.018				—0.032	0.023		0.050			
Y25 Moina micrura	0.002			0.001		0.003							—0.0006	
Y26 total cladocerans				0.000				—0.016					0.000	—0.004
Y27 naupli		—0.039					—0.002				—0.005	0.003		
Y28 copepodits					0.0004		0.086				0.091	—0.091		
Y29 Cyclops vicinus, adults	0.026	0.037		0.0005										
Y30 Thermocyclops crassus, adults	0.01		—0.03	0.06	—0.01	—0.01	0.009	0.02			0.004	—0.005	—0.007	0.0001
Y31 Diaptomus sp.														
Y32 total copepods					0.084		—0.055		—0.056		—0.091	0.065		
Y33 Chaoborus crystallinus		—0.026		—0.0004						0.052				
Y34 other	—0.01	—0.0006		—0.019	—0.03		—0.015	—0.073			—0.037	0.014		
Y35 sedimented volume				0.0001		—0.003					—0.001		0.000	0.096

27.8, and 5.0. After discarding them and recalculating the regression equations, the following form of the equation was obtained:

$$Y = -11.43 + 3.06X_1 - 0.101X_5 + 0.041X_4 - 0.044X_6 + 0.0092X_7 + \\ + 0.027X_8 + 0.011X_{11} - 0.011X_{12} + 0.24X_{14}$$

and the calculated value of $F = 12.892$ had $P<0.00$. The determination coefficient r^2 increased to 0.872 and r^2 adjusted to 0.8045. The equation was enriched with 5 variables.

The results of prognosticating the abundance of populations of different species on the basis of the regression equations and observed values are given in fig. 5. A summary of complete analysis of regression, containing significance levels of the different variables included in the equations, is given in Tables IV and V. A total of 137 significant dependences was obtained in the variant with ash (Table IV) and 140 in that with turbidity (Table V). The variant with turbidity gave 7 more highly significant dependences but on the other hand 3 dependences less in the class of moderately significant dependence. Greater divergences concerned the traits: suspension/turbidity, blue-green algae, and small algal species. The variant with ash gave only 6 significant relations for these traits, 5 of which were negative; the variant with turbidity gave 11 significant dependences, among them 8 negative ones. In the two variants 10 species of animal significantly depended on the number of blue-geen algae. In the variant with turbidity there were 5 negative relations, 7 being found in that with ash. A significant dependence upon the number of small algae was found for 17 variables in the variant with ash (of which 5 were negative), while the variant with turbidity gave 8 significant dependences with 3 negative ones.

The role of different variables in increasing the coefficient of determination is illustrated by fig. 6. In the two variants of expressing the content of suspension, after the introduction of a successive variable the increase in the coefficient of determination was for most species almost identical and the successive variables were selected for the equation in the same order. For the total number of the rotifers *Ceriodaphnia pulchella* and *Asplanchna girodi* the variant with SiO_2 resulted in a more rapid increase in the coefficient of determination after introduction of the successive variables. On the other hand, for *Keratella quadrata* and *Polyarthra dolichoptera* the variant with ash gave a more rapid increase in r^2.

4. Discussion

The seasonal succession of zooplankton is examined as the state which appears as the result of factors affecting populations from

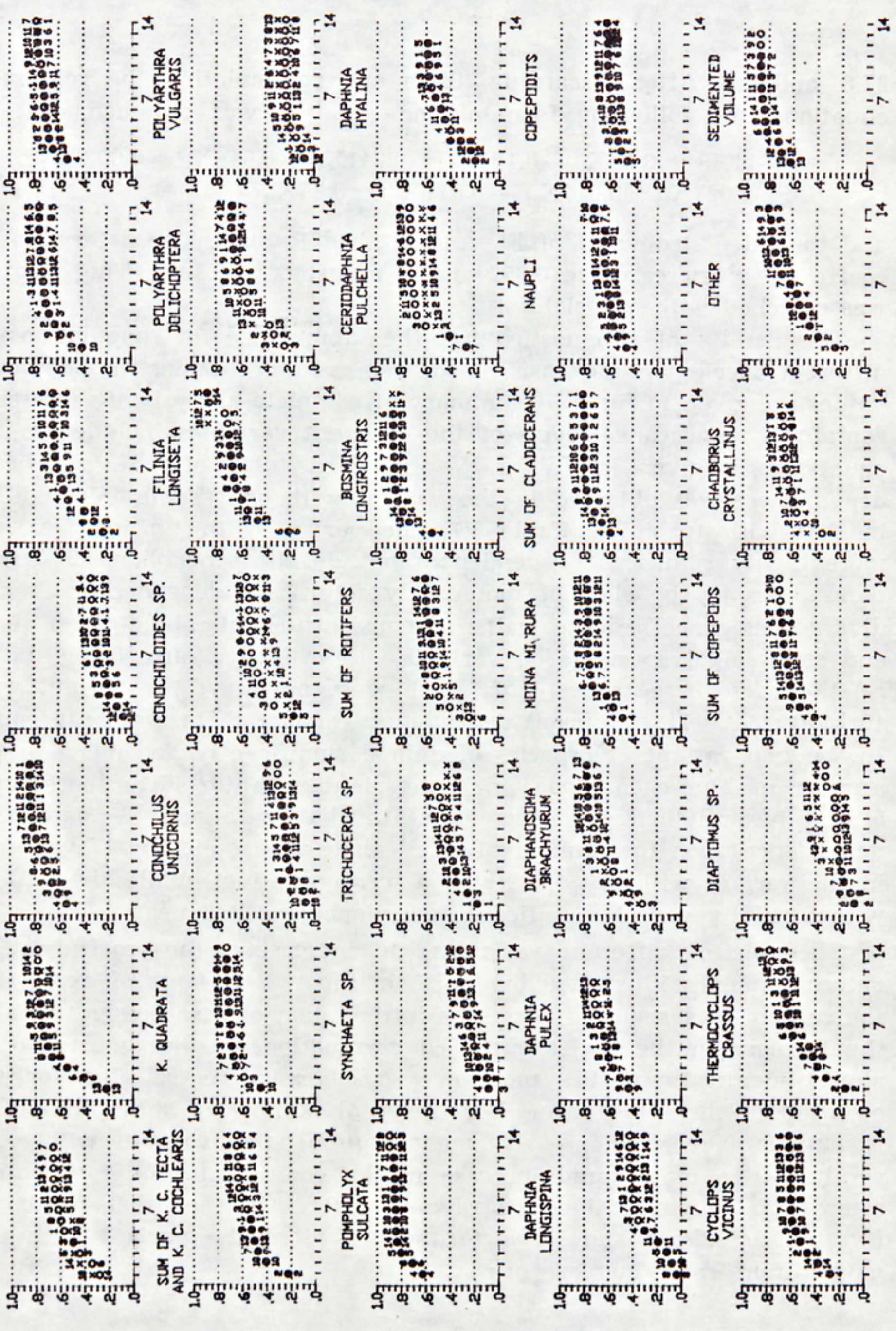


Fig. 5. The role of different variables in increasing determination coefficient r². The variant of equations with ash as a measure of the amount of suspension, is marked x, the figures of variables are given in the lower line. The variant with suspension as SiO_2 is marked o; successive variables are interlined over the symbols

Fig. 6. Agreement of the prognosis concerning the abundance of populations on the basis of regression equations, with recorded data, x — the observed values: - — prognosticated values; bars ± σ

higher (top down) and lower (bottom up) trophical levels, on the one hand, and of the adaptability of the population of the given species on the other. We can now evaluate the result for many species and explain the observed seasonal successions between both the different species and higher taxa (De Mott 1989, Gliwicz, Pijanowska 1989, Gliwicz 1980). Analysis of multiple regression may show the conditions of success or failure of the given species in a concrete environment and, enriched with earlier information, may elucidate numerous relations.

The result of regression analysis will be positive if the investigated factor lies in the range of the lower pessimum; in the range of the optimum no significant relation should be expected, while in the range of the upper pessimum the expected result should be negative. The investigated species may be divided into three groups, their reaction to the given factor (varying within the limit given in Table II) being taken into consideration: the first group consists of species responding with a decrease in the abundance of the population, the second group covers species which increase in number, and the third species neutral with regard to the given factor. For most species temperatures between 17 and 24°C seemed nearly optimal, hence for numerous zooplankters no dependence could be found. If the relations were investigated in a wide range of temperature, the significance of this factor could be confirmed with a different degree of confidence for different species (Edmondson 1964, Moore 1980, Berzins, Pejler 1989a). A frequent lack of dependence upon temperature seems to support the opinion of Buikema (1975), who claims that the successful development of certain species depends more on the amount and quality of accessible food than on temperature and light. On the other hand, Topping (1975) showed that among many chemical and physical factors plankton biomass to a high degree depend on temperature, in up to 88% of the elucidated variation.

In the investigated ponds the range of variation of temperature was narrow, about 5°C, and was found in the zone of optimal temperatures for most species, when the rate of biological processes increased slower than it did with the same change occurring at low temperatures (Kersting 1978, Sushchenva, Trubetskova 1981). Kersting (1978) showed that the growth efficiency of *Daphnia magna* is at its maximum at 10°C and becomes negative above 22°C, i.e. the population did not survive above this temperature. In the same species Sushchenya and Trubetskova (1931) fonud that temperature coefficient (Q_{10}) for the rate of grazing fell below 1 at 25—28°C. Similarly, Lampert (1977) and Lynch (1977) observed that the metabolic requirements of *Daphnia pulex* increased more rapidly than did feeding rates at temperatures above 20°C. For *Filinia longiseta, Asplanchna girodi, Keratella cochlearis tecta*, and copepodits the temperature of the investigated ponds was probably higher than the optimum and hence negatively affected the abundance of the populations. This result confirms the data reported by Horkan et al. (1977), who fonud that an environmental temperature above 22.4°C eliminated *Filinia longiseta*; at a temperature above 25.6°C there appeared a decline in *Conochilus unicornis*, while *Polyarthra vulgaris* disappeared above 26.6°C. Statistical analysis confirmed that the warm stenothermic species *Moina micrura* occurred in the plankton at about 18°C. In Polish ponds it occurs abundantly at temperatures of about 25°C.

Geller and Müller (1981) presented data concerning the ranges of particle filtration by zooplankton species, showing that most cladocerans used particles 1—10 μm in size. Cladocerans may utilize much larger particles, though the strongest competition seems to occur in the above given range of food particles. Numerous species could be easily filtered by cladocerans (*Chlorella*, *Scenedesmus*), but they are nevertheless resistant and less useful than algae with thin cell membranes, bacteria, or detritus. Gophen et al. (1974) showed privileged consumption of bacteria by *Ceriodaphnia reticulata*. Hadas et al. (1982) reported a considerable selectivity of bacteria by *Daphnia magna* from a mixture with *Chlorella* or *Scenedesmus*. Coveney et al. (1977) obserevd the most efficient reproduction of *Daphnia longispina* during the period of maximum abundance of bacteria in the environment. Taub and Dollar (1968) postulated that algae alone could not supply all the substances necessary for the growth of *Daphnia pulex*. A comparison of changes in numbers of Rotatoria, Cladocera, and Copepoda populations (fig. 3) shows that the peaks of their maximum abundance, particularly rotifers, coincide with the minimum numbers of bacteria.

A decrease in the content of dissolved oxygen coincided with a mass development of some species, e.g., *Conochiloides coenobasis*, *Brachionus rubens*, and nauplii (fig. 3). Hofmann (1977) observed that changes in the temperature and oxygen content had a striking effect on the dynamics of numbers of rotifers. These factors and food determine the carrying capacity of the environment. The frequently found negative coefficients of dependence on oxygen are associated with the respiration of abundant populations of zooplankton rather than with the negative effect of low oxygen concentration. The concentration of oxygen rather reflects the fertility of the environment and its food resources. The range of oxygen concentration (4.5—13.2 mg dm^{-3}) was sufficiently wide not only for fish but also for zooplankton. Mechanisms of adaptation to low oxygen concentrations are triggered at 3 mg dm^{-3} (Kring, O'Brien 1976) while concentrations below 1.5 mg dm^{-3} might be lethal (Żurek 1992). Most rotifers survive long periods of anoxia (Berzins, Pejler 1989b, Reale et al. (1992).

For many species the concentration o chlorophyll *a* was irrelevant. A large group of species, among them chiefly the predators *Chaoborus* *crystallinus*. *Asplanchna girodi,* and *Synchaeta* sp., negatively depended on this variable on account of their way of feeding. It is interesting to observe the positive dependence of *Cyclops vicinus* numbers on chlorophyll and of *Asplanchna girodi* on large algae. In the first case, the obtained result rather represents a resonance effect, since an increase in the numbers of algae enhances the numbers of victims of the cyclopoid. In the second case the results shows that the diet was supplemented by large algae of various systematic classification. Plankton animals frequently show a preference for some kinds of food. For example, of 7 species investigated by McNaught et al. (1980) only adult *Diaptomus sicilis* and immature cyclopoid copepods were selective specialists and three species of adult cyclopoids and one cladoceran (*Bosmina coregoni*) were generalists in feeding. The above authors found that copepods and adult *D. sicilis* avoided small spined and large sheathed algae.

Many other species which show a negative dependence on chlorophyll and on any other group of algae may utilize other resources of food, for instance, dead organic matter or bacteria (Arndt 1992, Hofmann, Hofle 1992, Vadstein et al. 1992). Angino et al. (1973) also found that the abundance of *Daphnia ambigua* did not depend, among other factors, on the amount of potential food, expressed as chlorophyll *a*. The concentration of chlorophyll elucidated no more than 1.6% of variability. Hazelwood and Parker (1961) found o poor negative correlation (r = —0.286 and —0.306) between the numbers of *Daphnia schødleri* and *Diaptomus leptopus* and chlorophyll. The same authors (1963) obtained a strong negative correlation between the above-mentioned species and potential food defined as dry weight of particles smaller than 0.45 μm or larger than 60 μm. Similarly, Orsi and Mecum (1986) obtained a highly significant and positive dependence of the numbers of *Bosmina longirostris, Cyclops* spp., *Diaptomus* spp., and *Daphnia* spp. populations on rotifers. The investigation carried out by Wynne and Gophen (1981) on different species showed that, e.g., for *Daphnia,* bacteria cannot be the only source of food. Moreover, algae alone (*Chlamydomonas reinhardti* and *Chlorella vulgaris*) also cannot supply all the components necessary for the growth of *Daphnia pulex* (Taub, Dollar 1968). Hadas et al. (1982) observed that in a mixture of bacteria with *Chlorella vulgaris* or *Scenedesmus quadricauda, Daphnia magna* preferred bacteria.

In general, the dependence presented in Tables IV and V agree with those anticipated, on the basis of the knowledge of nutrition of plankton animals, their preferences, competition, fitness etc. Unexpected, difficult to explain dependences may suggest possible study areas, though they also can, with known certitude, indicate them erroneously.

5. Polish summary

Zależności między zooplanktonem a czynnikami biotycznymi i abiotycznymi

Analizowano zmiany dynamiki liczebności 35 gatunków zooplanktonu lub ich grup w zależności od 14 czynników biotycznych, chemicznych i fizycznych.

Badania terenowe przeprowadzono w trzech stawach o różnym sposobie użytkowania (tabela I) i w efekcie różnej trofii. Podstawową charakterystykę statystyczną wszystkich omawianych zmiennych podano w tabeli II.

Produkcja pierwotna brutto (ryc. 4) we wszystkich stawach przebiegała najintensywniej w warstawie powierzchniowej — warstwa ta była najgrubsza w stawie 7 — do dna, cieńsza w stawie 9, żyznym — około 60 cm i najcieńsza w stawie 8, bardzo żyznym — około 20 cm, ryc. 4. Podobnie kształtowały się średnie wartości produkcji pierwotnej brutto. Pomimo wysokiej produkcji w warstwie powierzchniowej, rozkład koncentracji tlenu (ryc. 1), zwłaszcza w okresach homotermii (ryc. 2) był dość jednorodny. We wszystkich stawach obserwowano minima koncentracji tlenu w okresach masowego rozwoju wrotków lub wioślarek (ryc. 3).

Równania regresji liczono w dwóch wersjach różniących się sposobem wyrażania mętności, tzn. mętnością wyrażoną w mg SiO_2 i ilością spopielonej zawiesiny. W tabelach IV i V podano streszczenia obu wariantów analizy w postaci wartości krytycznej prawdopodobieństwa każdej z 14 zmiennych. Obie wersje równań dały niemal dokładnie taką samą liczbę (137 i 140) zależności istotnych. Zgodność prognozy liczebności poszczególnych populacji (Y) otrzymane z równań i wartości rzeczywiste zilustrowano na ryc. 6.

Role poszczególnych zmiennych na przyrost współczynnika determinacji ilustruje ryc. 5. Dla większości gatunków, w obu wariantach przyrost współczynnika determinacji po wprowadzeniu kolejnej zmiennej był niemal identyczny i kolejne zmienne były wybierane do równania w takiej samej kolejności. Od tej zasady było kilka odstępstw. Dla sumy wrotków, *Ceriodaphnia pulchella* i *Asplanchna girodi,* wariant z SiO_2 dawał szybszy przyrost wsp. determinacji po wprowadzeniu kolejnych zmiennych. Natomiast dla *Keratella quadrata* i *Polyarthra dolichoptera* szybszy przyrost r^2 dawał wariant z popiołem.

Sprawdzono jaki wpływ ma na jakość równania odrzucenie najbardziej odstających pomiarów. Przykładowo odrzucenie w równaniu regresji 3 pomiarów o najwyższym dystansie Mahalanobisa spowodowało podwyższenie wartości testu F z 7.4 do 12.89 a współczynnika determinacji z 0.54 do 0.87.

Analizowano także równania jednoczynnikowej regresji/korelacji populacji *Brachionus calyciflorus* od 8 zmiennych niezależnych i następnie regresji wielokrotnej równocześnie od 6—7 tych czynników. Wyniki regresji wielokrotnej od 6 zmiennych dały współczynnik korelacji 0.9 czyli znacznie lepszy niż uzyskany dla zależności pojedynczych (Tabela III).

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