Jolanta EJSMONT-KARABIN*, Teresa WĘGLEŃSKA**

*Hydrobiological Station, Institute of Ecology, Polish Academy of Sciences,
Leśna 13, 11-730 Mikołajki, Poland
**Department of Hydrobiology, Institute of Ecology, Polish Academy of Sciences,
Dziekanów Leśny, 05–092 Łomianki, Poland

DENSITIES, STRUCTURE AND THE ROLE OF ZOOPLANKTON IN PHOSPHORUS CYCLING IN LIMNETIC AND LOTIC PARTS OF ZEGRZYŃSKI RESERVOIR

ABSTRACT: Studies conducted in 1982 and 1984 examined structure and densities of zooplankton in a main basin of the Zegrzyński Reservoir, made in 1962–1964 in effect of impounding two rivers.

As compared to limnetic sites, the stations located in the lotic part of the reservoir were marked for a steadier course of zooplankton abundance dynamics, a smaller contribution of Crustacea to zooplankton, a smaller fecundity of the dominating crustacean species, but greater – of rotifers, a smaller share of plant food in zooplankton diet, a weaker pressure of invertebrate predators on small bodied zooplankton and about a two-time longer turnover time of total P and phosphorus contained in food in effect of phosphorus regeneration by zooplankton.

KEY WORDS: dam reservoir, zooplankton density, species structure and diversity, predator pressure, phosphorus regeneration, phosphorus sedimentation.

1. INTRODUCTION

Due to pronounced changes in water level, in flow rate and in the amount of organic and mineral suspended matter inflowing with rivers, biocoenoses of reservoirs differ from the lotic and limnetic water. Unstable water masses, thermally unstratified cause, that typical for deep lakes vertical stratification of plankton is much impeded. Hence a group of organisms characteristic of cool, poorly oxygenated hypolimnion water (Ruttner-Kolisko 1977) is not to be found in dam

reservoirs. This, in turn, should result in a decreased number of species in plankton community in the whole mass of water. The lack of stability of abiotic conditions should further strengthen these effects (Giller 1984). On the other hand, a marked horizontal diversity of the conditions and supplying of nutritive suspended matter would increase species diversity of zooplankton. An attempt to determine the effect of environmental conditions on zooplankton densities and functioning was one of the aims of the present work.

Moreover, the present studies aimed at defining the role of zooplankton in phosphorus cycling. Intensive mixing of reservoir water and, consequently, its relatively good oxygenation, as well as a constant inflow with rivers of organic suspended matter decomposing in stabler water masses, result in the fact that the role of zooplankton in dam reservoirs should differ from its role in lakes.

2. STUDY AREA, MATERIAL AND METHODS

2.1. DISTRIBUTION OF THE STATIONS

The Zegrzyński Reservoir is made in the effect of impounding water of the Narew and Bug rivers, after damming Narew at the locality od Dębe. Impounding of the rivers was begun in the second half of 1962 and ended in spring 1964. The flooded valley had formerly been covered by pastures, meadows and wasteland. Also two lakes had spread in the valley (the Ostrowickie and Białobrzeskie), which merged into reservoir later on.

The Zegrzyński Reservoir occupies 33 km² area, its total capacity amounts to about 100 mln m³, working impounding of water 0.5 m and 11 mln m³. It is a shallow reservoir (3−4 m in depth), being deeper only in the old river beds and at the dam where its depth comes to about 7 m. The time of water retention in the Zegrzyński Reservoir in 1982 varied from 1.9−2.0 days (March-April) to 3−9.3 days (May-September). In 1984 retention time ranged from 3.9−4.8 days (March-April) to 7.9−9.3 days (August-September).

In 1982 and 1984 a series of intensive interdisciplinary studies was conducted in the main basin of the reservoir (Dusoge et al. 1985). In 1982 studies were carried out at 5 stations. The stations A, B, C were located in a limnetic part of the main basin, the stations D and E − near the right bank in the mainstream with imperceptible water flow (Fig. 1). In 1984 6 stations were fixed, the stations I, II, III and IV cross-secting the main basin in the direction from the right to the left reservoir bank. Location of the stations I and IV approximated that of the stations B and D respectively in 1982. In the limnetic part, beyong the cross-section limits, the stations V and VI were situated correspondingly to the stations C and A in 1982 (Fig. 1).

old bed of the Narew river

old bed of the Bug river
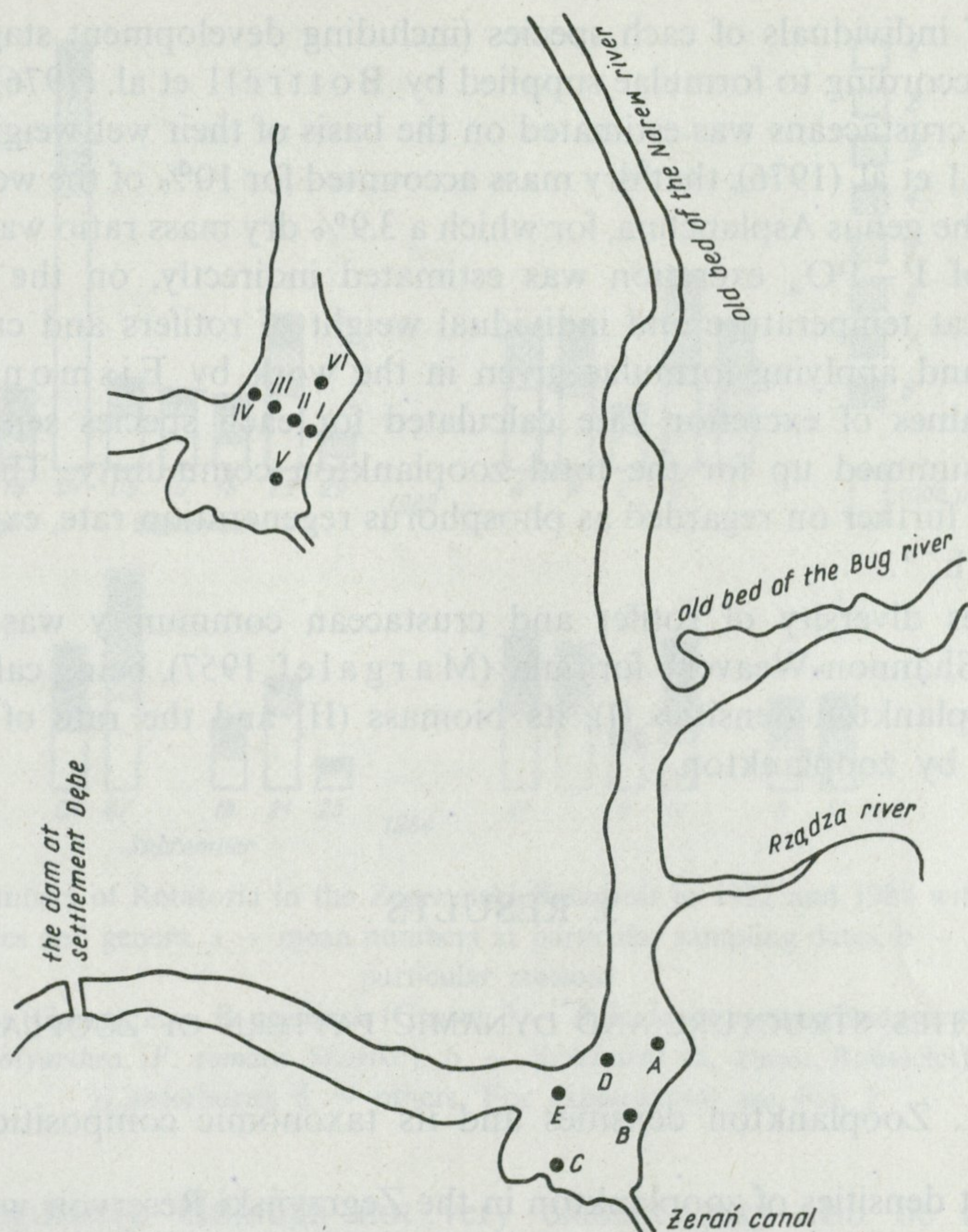
Rzadza river

the dam at settlement Dębe

Żerań canal

Fig. 1. The Zegrzyński Reservoir — distribution of stations in 1982 (A—E) and in 1984 (I—VI). Stations D,E and III, IV — lotic sites, others — limnetic sites

2.2. MATERIAL AND METHODS

Material for further analyses was sampled 8 times in 1982 (since August 4 till September 29) and 5 times in 1984 (in a two times shorter interval, i.e. since 4th to 25th September). Water samples were taken from the surface down to the bottom at every 1 m, using a 5-liter Bernatowicz sampler in such a way, that the amount of filtered water was not smaller than 25 l, which reduced losses in plankton material due to water filtering through a net (Ejsmont-Karabin 1979). In order to condense the zooplankton samples, the use was made of zooplankton screen net of about 30 μm mesh. The condensed samples were fixed in with Lugol's solution and next with 4% formalin.

Zooplankton samples were quantitatively examined according to Hillbricht--Ilkowska and Patalas (1967) and Bottrell et al. (1976). Biomass of rotifers and crustaceans was estimated by an indirect method, basing on a mean body lenght

in a sample of individuals of each species (including development stage in case of crustaceans), according to formulae supplied by Bottrell et al. (1976). Dry weight of rotifers and crustaceans was estimated on the basis of their wet weight, assuming, after Bottrell et al. (1976), that dry mass accounted for 10% of the wet one, except for rotifers of the genus Asplanchna, for which a 3.9% dry mass ratio was considered.

The rate of $P-PO_4$ excretion was estimated indirectly, on the basis of the recorded habitat temperature and individual weight of rotifers and crustaceans of each species, and applying formulae given in the work by Ejsmont-Karabin (1984). The values of excretion rate calculated for each species separately, were subsequently summed up for the total zooplankton community. The value thus calculated was further on regarded as phosphorus regeneration rate, expressed in μg $P-PO_4 \cdot 1^{-1} \cdot h^{-1}$.

Also species diversity of rotifer and crustacean community was exammined according the Shannon-Weaver's formula (Margalef 1957), being calculated with respect to zooplankton densities (I), its biomass (II) and the rate of phosphorus excretion (III) by zooplankton.

3. RESULTS

3.1. DENSITIES, STRUCTURE AND DYNAMIC PATTERN OF ZOOPLANKTON

3.1.1. Zooplankton densities and its taxonomic composition

The greatest densities of zooplankton in the Zegrzyński Reservoir were recorded in summer, i.e. since June till August, its densities decreasing since September on. A relatively great zooplankton densities were recorded in the studied period in the two years.

In order to generalize tendencies in quantitative and structural changes in zooplankton recorded both in time and space, the mean numbers of rotifers were computed, both with regard particular sampling dates (the mean from 5 stations in 1982 and from 6 stations in 1984) as well as to particular stations (the mean from 8 sampling dates in 1982 and from 5 — in 1984). In both years of studies stations were diversely denoted and sampling dates were different as well. However, the values recorded at particular stations and dates were arranged in the graph (Fig. 2) in such a way so as to make their display comparable for the two years of studies. This is the reason of numerical irregularity of stations I—IV in 1984. The employed lay-out made it easy to notice that (although sampling dates differed in the two years) rotifer numbers characteristic for particular stations were, on the whole, similar in the two years. The stations A, B and D in 1982 and the corresponding stations VI, I and IV in 1984, were marked for high numbers (from 2678 ind. $\cdot dm^{-3}$ at the station I in 1984 to 3558 at the station D in 1982). On the other hand, in the two years of studies rotifer densities at the station D and the corresponding station V were 2 times smaller than at the other stations (Fig. 2b).
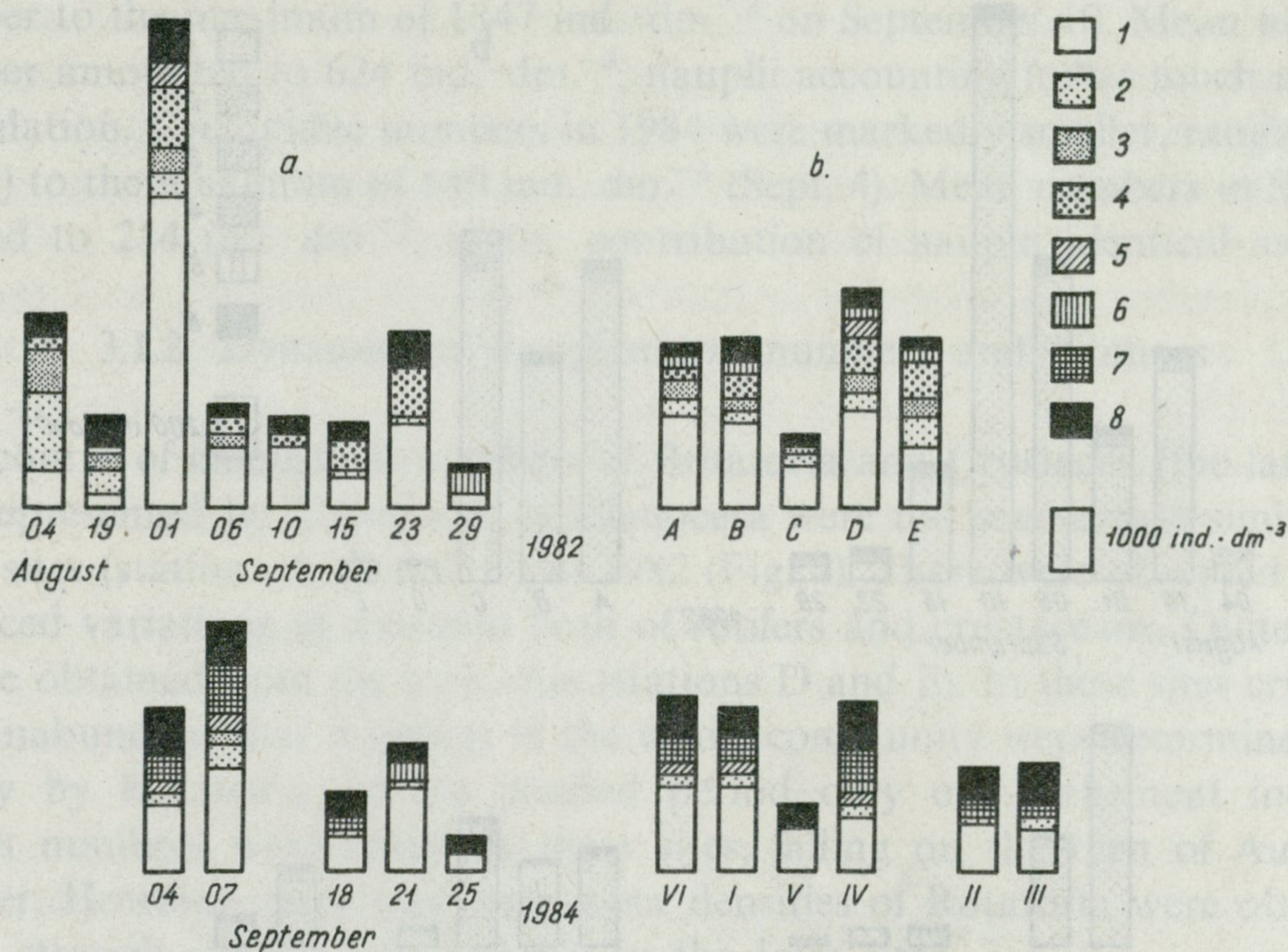
Fig. 2. Mean numbers of Rotatoria in the Zegrzyński Reservoir in 1982 and 1984 with specification of dominating species and genera. a — mean numbers at particular sampling dates, b — mean numbers at particular stations

1 — K. cochlearis (Gosse), 2 — B. angularis (Gosse), 3 — B. budapestinensis (Daday), 4 — B. caliciflorus (Pallas), 5 — Polyarthra (P. remata Skoriko), 6 — Synchaeta (S. kitina Rousselet), 7 — T. pusilla (Lauterborn), 8 — others. For explanations see Fig. 1

Certain regularity, although not very distinct, may also be noticed while analyzing the rotifer number dynamics. A well-marked decrease down to less than 1000 ind. $\cdot$ dm^{-3} was stated by the end of September in both years of studies. In 1982 the highest rotifer density was recorded in September. The mean from 5 stations amounted then to 7995 ind. $\cdot$ dm^{-3}, the value approximating those estimated in hypertrophic lakes (K a r a b i n 1983).

The community of Rotatoria abounded in species. Apart from dominants marked in diagrams (Fig. 2), the following species were fairly numerous: Keratella valga (Ehrenberg), Trichocerca stylata (Gosse), Filinia passa (Müller), F. longiseta (Ehren-berg), F. brachiata (Rousselet), Proalides (probably P. tentaculatus Beauchamp), Cephalodella catellina (Müller). Moreover, the community included numerous accessorial species, which occurred more abundantly only periodically, e.g. Epiphanes macroura Barrois et Daday, which was numerous in the first 10 days of August only.

In the years of studies the rotifer community was uniform with respect to its taxonomic structure, although certain differences were perceived. In 1984 there was a greater contribution of Trichocerca pusilla (Lauterborn), fairly inabundant in 1982, while markedly less numerous were species of the genus Brachionus, which very profuse in 1982. Also Anuraeopsis fissa (Gosse), a species which occurred inabundantly in 1982 (up to 20 ind. $\cdot$ dm^{-3}), was much more numerous in 1984 (up to 200 ind. $\cdot$ dm^{-3}).
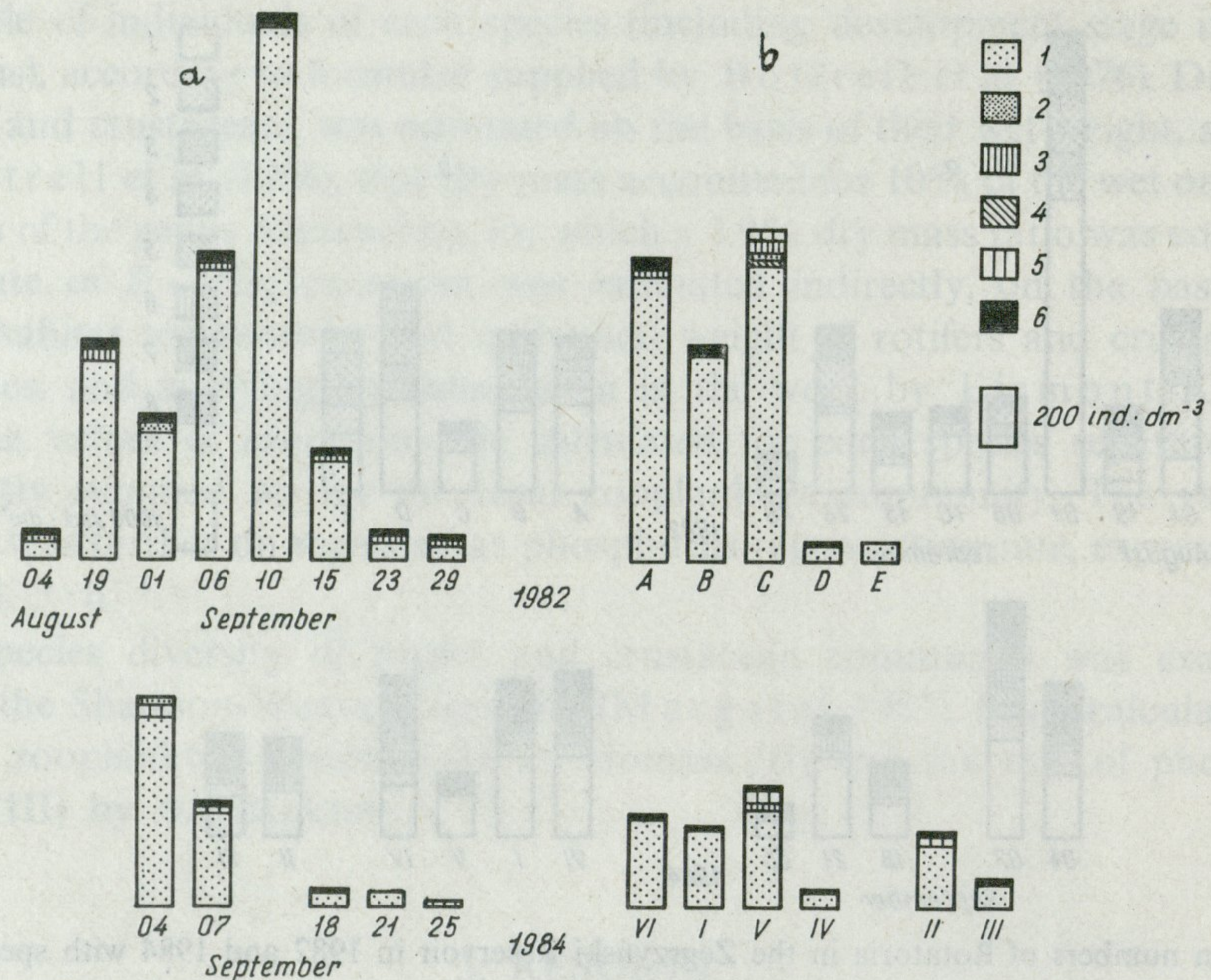
Fig. 3. Mean numbers of Crustacea in the Zegrzyński Reservoir in 1982 and 1984 with specification of the
dominating species and groups
1 — Cyclopidae, 2 — *Moina rectirostris* Leydig, 3 — *Daphnia longispina* (O. F. Müller), 4 — *Bosmina
longirostris* (O. F. Müller), 5 — *Daphnia cucullata* Sars, 6 — others, a, b — see Fig. 2, A—E, I—VI — see
Fig. 1

Alike rotifers, also crustaceans were subject to an alike analysis, which revealed
(Fig. 3) that the recurrent quantitative and structural regularity of the community
noted in the two years in case of rotifers, was also characteristic of crustaceans
(Fig. 3). Although in 1984 mean numbers of crustaceans in the period under
comparison were pronouncedly smaller than in 1982, yet in both years a marked
decrease in the community density was stated to have taken place in the end of
September. Moreover, crustacean numbers at the stations A, B, C and, cor-
respondingly, VI, I and V were greater than at the lotic sites (station D and
corresponding station IV in 1984).

Species composition of crustaceans in the whole study period and in both years
of studies was rather poor, although Cladocera included in total as many as 14
species. However, with respect to quantity, Cladocera were of a little significance in
the studied community, as only 5 species (*Daphnia cucullata,* Sars, *D. longispina* O. F.
Müller, *Bosmina longirostris (O). F. Müller), Moina rectirostris* Leydig, *Diaphano-
soma brachyurum* (Levin) occurred at densities of $10-50$ ind.$\cdot$dm^{-3}, the other
species being only sporadically found.

The most abundant among crustaceans in both years of studies were Cyclopidae,
the prevailing being their youngest stages. In 1982 mean Cyclopidae densities at all
the stations ranged from 48 ind.$\cdot$dm^{-3} in the beginning of August and in the end of

September to the maximum of 1847 ind.·dm^{-3} on September 10. Mean numbers in September amounted to 624 ind.·dm^{-3}, nauplii accounting for as much as 81% of the population. Cyclopidae numbers in 1984 were markedly smaller, ranging from 5 (Sept. 25) to the maximum of 649 ind.·dm^{-3} (Sept. 4). Mean numbers in September amounted to 214 ind.·dm^{-3}, at the contribution of nauplii identical as in 1982.

3.1.2. Dynamics of zooplankton numbers and biomass

The course of changes in numbers of Rotatoria and Crustacea (the latter being mainly represented by Copepoda, as Cladocera were too scarce, was similar in the limnetic sites (stations A, B and C) in 1982 (Fig. 4). There were observed frequent, pronounced variations in densities both of rotifers and crustaceans. Quite different data were obtained from the lotic sites (stations D and E). In these sites crustaceans were so inabundant that numbers of the whole community were determined almost exlusively by Rotatoria. In the studied period only one wehement increase in Rotatoria numbers were noted in these sites, falling on the turn of August and September. However, since mid-September densities of Rotatoria were observed to diminish strongly at the two stations in the lotic sites.
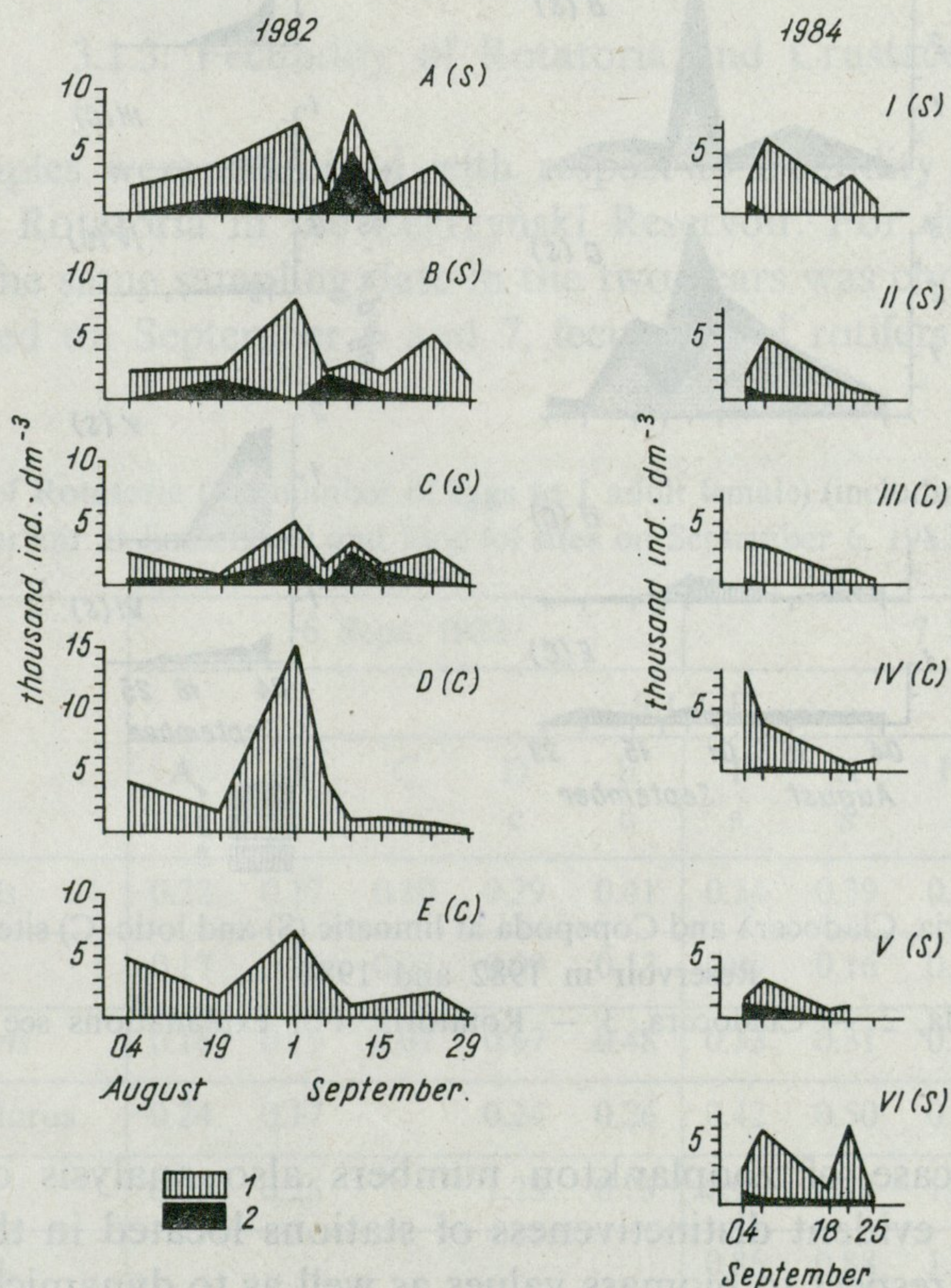

Fig. 4. Number dynamics of Rotatoria and Crustacea at limnetic (S) and lotic (C) sites in the Zegrzyński Reservoir in 1982 and 1984

1 — Rotatoria, 2 — Crustacea (Copepoda). For explanations see Fig. 1

A considerably smaller numbers of crustaceans were observed in the current sites also in September 1984 (Fig. 4). Densities of Copepoda in the limnetic sites (stations I, V and VI) were decidedly greater than in the lotic sites (stations III, IV). However, numbers of rotifers in the lotic sites in the beginning of September were not as high as in 1982. Nonetheless a marked decrease in zooplankton densities in the second half of September was observed in these sites as well. Only in the limnetic sites (stations I and IV) there was noted a distinct increase in rotifer numbers on September 23.

Biomass of zooplankton community was almost exlusively contributed by Crustacea, Copepoda and Cladocera, their shares in the two years of studies being approximately the same (Fig. 5).
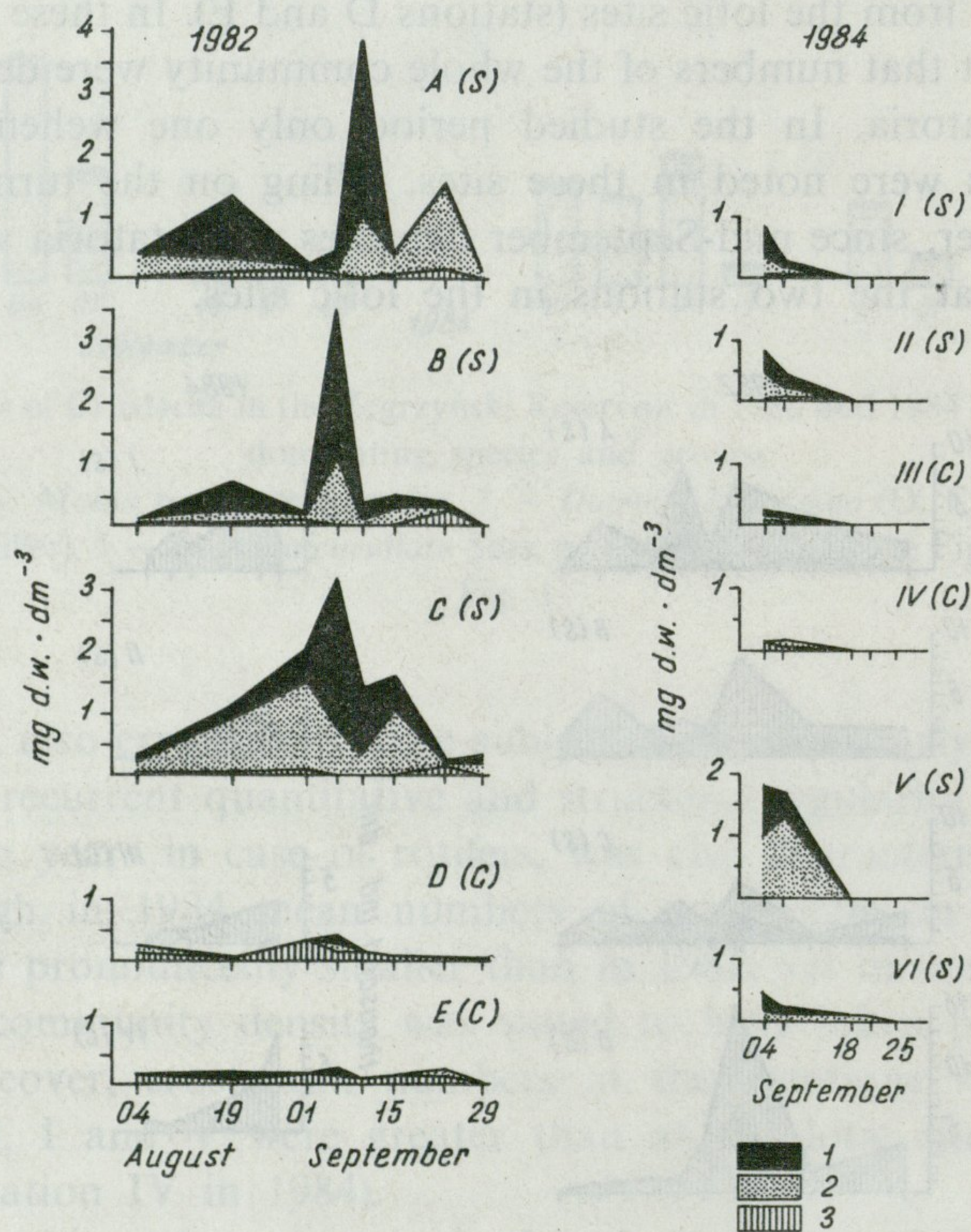
Fig. 5. Biomass of Rotatoria, Cladocera and Copepoda at limnetic (S) and lotic (C) sites in the Zegrzyński Reservoir in 1982 and 1984

1 — Copepoda, 2 — Cladocera, 3 — Rotatoria. For explanations see Fig. 1

Similarly as in case of zooplankton numbers also analysis of zooplankton biomass revealed an evident distinctiveness of stations located in the limnetic and lotic sites, both with respect to biomass values as well as to dynamics of its changes. In 1982 the limnetic sites (stations A, B and C) were marked for a very large biomass of Crustacea and strong changes in biomass values over the examined period of two

months. The course of changes in rotifer biomass was alike at all the three stations, while biomass of Crustacea was subject to changes distinct at each of the three stations in the period of studies, the station C being the most distinct in this respect. The limnetic sites (stations D, E) were noted for such small values of Crustacea biomass (Fig. 5) that total zooplankton biomass was decided by Rotatoria. Since rotifers are very small bodied as compared to crustaceans, therefore total biomass of zooplankton at these stations was very little. Equally paltry were changes in zooplakton biomass over the studied period.

The above tendencies were further confirmed by the data obtained two years later. In 1984 zooplankton biomass was dominated by Crustacea (Fig. 5). Greater biomass values were recorded in the limnetic sites (st. I, V, VI) than in the lotic ones (st. IV). A trend of zooplankton biomass to decrease along with an increase in the rate of water flow was very well captured in the data gathered at stations I to IV located along the section running from the limnetic to the lotic parts of main basin.

The course of biomass dynamics in 1984 differed notably from the one observed in 1982. In September 1984 biomass was noted to diminish constantly and was not subject to any strong growths or drops, as those recorded in the limnetic sites in 1982.

3.1.3. Fecundity of Rotatoria and Crustacea

All the samples were examined with respect to fecundity measured as egg to female ratio of Rotatoria in the Zegrzyński Reservoir. For detailed analysis only material from the same sampling date in the two years was chosen. In the analyzed samples collected on September 6 and 7, fecundity of rotifers was high (Table 1),

Table 1 Fecundity of Rotatoria (the number of eggs to 1 adult female) (including dominating species) in the Zegrzyński Reservoir at limnetic (s) and lotic (c) sites on September 6, 1982 and September 7, 1984.

Species	6 Sept. 1982					7 Sept. 1984					
	SITE										
	A s	B s	C s	D c	E c	I s	II s	III c	IV c	V c	VI c
Keratella cochlearis	0.22	0.17	0.10	0.39	0.41	0.34	0.39	0.42	0.27	0.23	0.34
Keratella valga	0.17	0.26	0.07	0.09	0.13	0.09	0.16	0.18	0.27	0.00	0.14
Brachionus angularis	0.16	0.19	0.07	0.67	0.48	0.33	0.31	0.34	0.22	0.17	0.19
Brachionus calyciflorus	0.24	0.17		0.24	0.26	0.42	0.50	0.16	0.30		0.23
Polyarthra remata	0.25	0.26		1.28	0.73	0.91	0.76	1.21	0.68	3.62	1.86
Trichocerca pusilla						0.85	0.88	1.31	0.70	0.67	0.70
Rotatoria	0.19	0.16	0.13	0.34	0.34	0.44	0.44	0.47	0.32	0.30	0.43

A−E, I−VI − see Fig. 1.

being markedly greater in 1984 than in 1982. The most fecund species was *Polyarthra remata,* a species common in the two years of studies. High fecundity (from 0.67 to 1.31) was also characteristic of *Trichocerca pusilla,* a species laying eggs on colonies of algae. In the peak of density and fecundity, the species was observed in the Zegrzyński Reservoir to lay eggs also on carapaces of rotifers *Brachionus angularis* Gosse, so frequently 6 — 8 (and sporadically up to 11) eggs of *Trichocerca pusilla* were found on an individual *B. angularis.* It would be indicative of good trophic conditions promoting high reproduction of *Trichocerca pusilla* and of the lack of a proper algal substratum for attaching eggs.

In 1982 rotifer fecundity was, on the whole, higher in the lotic sites, yet various species reacted diversely to an accelerated rate of water flow. A decidedly greater fecundity in the lotic sites was noted among females of the species *Polyarthra remata*
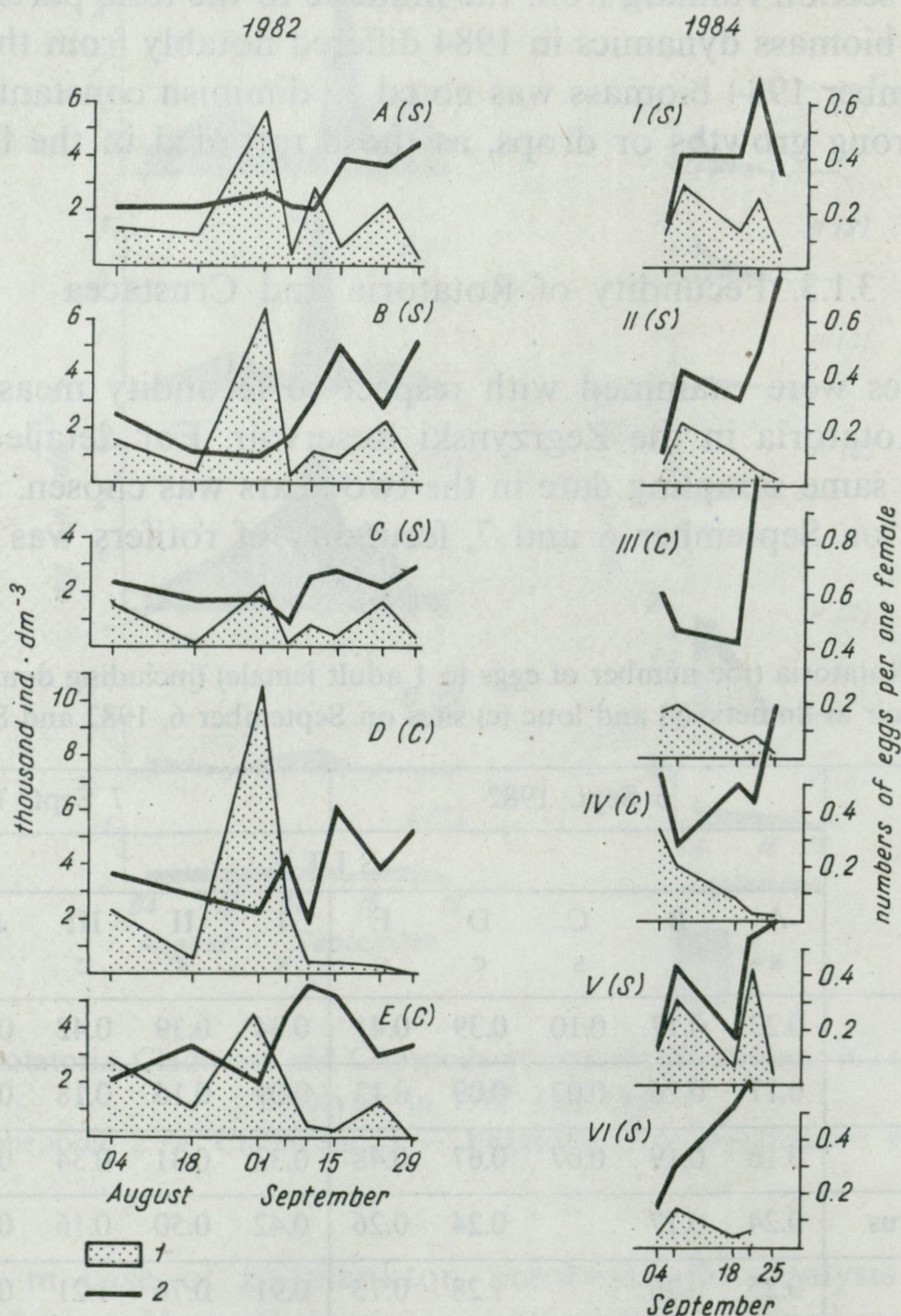

Fig. 6. Changes in fecundity of species positively reacting to accelerated rate of water flow (*Keratella cochlearis, Brachionus angularis, Polyarthra remata*) against their numbers at limnetic (S) and lotic (C) sites in the Zegrzyński Reservoir in 1982 and 1984

1 — numbers, 2 — fecundity (the number of eggs per 1 female). For explanations see Fig. 1

Skorikov, *Brachionus angularis* and *Keratella cochlearis*. Such a tendency was not observed in case of *Brachionus calyciflorus* Pallas and *Keratella valga*. It should be emphasized that the species positively reacting with respect to their fecundity to a higher water flow rate, were also the most abundant in the studied period.

Such greater fecundity of rotifers in the lotic parts of the reservoir was not recorded in 1984 (Table 1).

In order to ascertain whether the species *Keratella cochlearis*, *Brachionus angularis* and *Polyarthra remata* really reacted with increased fecundity to an increase water flow over the whole period of studies, the fecundity values calculated for each of the species separately were summed up to represent the species as one group (Fig. 6). Fecundity of this group of species was analyzed with respect to changes in its numbers.

As it follows from the diagram, an increase in densities of this rotifers group was seldom coupled with an increase in its fecundity. On the contrary, frequently an increased fecundity was recorded at a simultaneous decrease in rotifer numbers. Moreover, changes in fecundity were usually less pronounced than those in numbers, which would point to the fact, that densities of this group of rotifers were affected by factors other than fecundity, e.g. by mechanical factors (rinsing or destroying specimens by a high water flow rate) or, most likely, by predation. The latter reason seems to be proved by the fact that an increase in biomass of Cyclopidae (whose adult forms feed on small bodied rotifers) was accompanied by a decrease in numbers of rotifers of the analyzed group (cf. Figs 5 and 6).

The comparison of fecundity values of the analyzed group in both years showed that a greater fecundity observed in 1984 on the basis of the samples from September 6 and 7, lasted throughout September. Densities of this group of rotifers were also greater in 1984 than in 1982.

Also greater fecundity of the three species in question in the lotic sites than in the limnetic ones lasted over the whole period of studies (Fig. 6). It is well evidenced by mean values of rotifer fecundity estimated for the whole period of studies in the two types of sites. In 1982 mean fecundity of the analyzed rotifer group in the limnetic sites (stations A, B, C) ranged from 0.22 to 0.29, while in the lotic ones (st. D and E) — 0.36 and 0.37. In 1984 in the limnetic sites (st. I, V, VI) mean fecundity amounted to 0.39, 0.35 and 0.32 respectively, the values visibly increasing towards the lotic parts of deep water area, while mean fecundity at the stations I, II, III and IV amounted to 0.39, 0.42, 0.71 and 0.51 respectively.

Fecundity of the species of Cladocera and Copepoda, dominating in the crustacean plankton community in the Zegrzyński Reservoir, was very high in the studied period and comparable to crustacean fecundity in strongly trough flow lakes, e.g. in heated lakes of Konin system (Ejsmont-Karabin and Węgleńska 1988). On the whole — fecundity of crustaceans was greater in 1982, than in 1984. In the two years of studies the most fecundus among Cladocera were *Daphnia longispina* and *Moina rectirostis*. Also high fecundity was recorded of the two dominating Copepoda species, i.e. *Acanthocyclops bicuspidatus* (Claus) and *Acanthocyclops vernalis* (Fischer) (Table 2).

Table 2. Numbers (ind. · dm^{-3}) (1), fecundity (the number of eggs to 1 adult female) (2) and length (mm) of adult (3) of the dominating plankton crustacean species at limnetic (s) and lotic (c) sites in the Zegrzyński Reservoir in 1982 and 1984

Species		6 Sept. 1982					7 Sept. 1984					
		SITE										
		A	B	C	D	E	I	II	III	IV	V	VI
		s	s	c	c	c	s	s	s	s	c	c
Daphnia	1	17.1	10.2	33.5	0.2	1.3	7.7	4.0	9.0	27.5	0.5	
longispina	2	8.1	14.6	10.5		3.0	6.2	1.0	7.5	9.9	0.3	
	3	1.650	1.860	1.900	1.250	1.210	1.670	1.250	1.590	1.700	1.240	
Daphnia	1			21.5	2.3		10.6	5.2	29.0	16.0	3.9	3.7
cucullata	2			5.5	1.0		2.5	2.0	3.6	3.5	2.0	0.5
	3			1.340	1.080		1.380	1.260	1.340	1.550	1.160	1.150
Moina	1	3.9	2.2	1.2	0.6		1.5		21.5			
rectiorostris	2	10.6	8.5	7.9	5.2		4.0		4.0			
	3	0.745	0.770	0.750	0.620		0.630		0.680			
Bosmina	1	11.4	12.5	16.9	4.9	2.7	3.1	1.5	3.2	3.2	2.9	0.6
longirostris	2	1.9	2.4	2.0	1.6	1.7	2.0	1.3	2.3	1.8	1.3	1.0
	3	0.380	0.360	0.460	0.330	0.350	0.430	0.350	0.440	0.380	0.320	0.320
Acanthocyclops	1	980	710	1030	55	65	231	227	470	261	106	88
bicuspidatus	2	9.7	22.0	21.0	22.0	10.0	23.0	10.0	11.0	17.0	18.0	20.0
+ A.verbalis												

A−E, I−VI — see Fig. 1.

Unlike rotifers, fecundity of Cladocera was notably higher in the two years of studies in the limnetic sites than in the lotic ones, although various species reacted differently to changes in water flow rate. The greatest differences in fecundity between the limnetic and lotic sites were recorded at *Daphnia longispina* (from 6.2 do 14.6 in the limnetic sites and from 0.3 to 3.0 in the lotic ones) and at *Daphnia cucullata* (from 2.5 to 5.5 and from 0.5 to 2.0 at the two sites respectively). The smallest differences in fecundity between the limnetic (1.8 − 2.4) and the lotic sites (1.0 − 1.7) were stated for the species *Bosmina longirostis*.

No tendencies of this type were observed at Copepoda. Both in the limnetic and lotic sites, fecundity of the two dominating species, i.e. *Acanthocyclops bicuspidatus* and *A. vernalis*, was very high, approximating the maximal values recorded for each species (Table 2).

Mean for the study period values of fecundity of Cladocera and Copepoda were presented against changes in their numbers and mean body size of adult individuals (Table 2). It follows from this comparison that a generally greater fecundity of Cladocera was coupled with a greater numbers of individuals, this regularity concerning both many years' differences (greater densities of Cladocera in 1982) as well as differences between sites (higher densities in the limnetic sites than in the lotic

ones). Only in case of Copepoda their diminished numbers in the lotic sites were not coupled with fecundity decrease.

It is interesting to compare mean body size of adult cladocerans with changes in their fecundity. In both years of studies body size of individuals of all the dominating cladoceran species was larger in the limnetic sites than in the lotic ones, and positively correlated with changes in fecundity of Cladocera (Table 2).

3.2. REGENERATION OF PHOSPHORUS BY ZOOPLANKTON

3.2.1. Dynamics of regeneration rate and the role in it of three taxonomic groups of zooplankton

The rate of phosphorus regeneration by zooplankton in the Zegrzyński Reservoir was very high in the studied period (Fig. 7). The maximal values recorded at particular stations ranged from 2 to 4 μg $P-PO_4 \cdot dm^{-3} \cdot h^{-1}$. The values
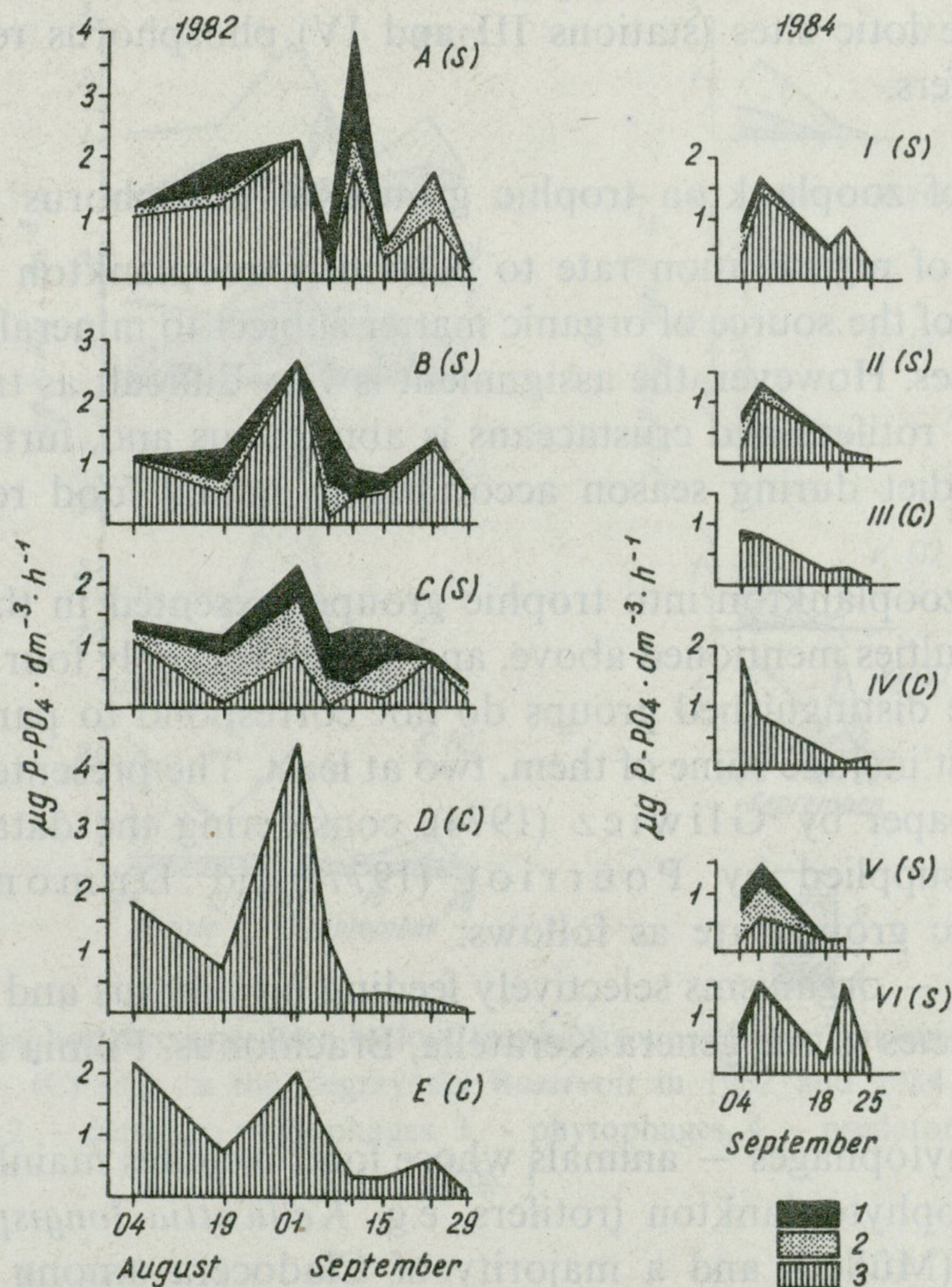
Fig. 7. The rate of phosphorus regeneration by three taxonomic groups of zooplankton at limnetic (S) and lotic (C) sites in the Zegrzyński Reservoir in 1982 and 1984

1 — Copepoda, 2 — Cladocera, 3 — Rotatoria. For explanations see Fig. 1

approximated those recorded in highly eutrophic lakes in summer. The regeneration rate exceeding 3.5 µg $P-PO_4 \cdot dm^{-3} \cdot h^{-1}$ was recorded during studies on lakes in northern Poland only in one case, i.e. in a highly polluted Iławskie Lake (7.8 µg $P-PO_4 \cdot dm^{-3} \cdot h^{-1}$) (E j s m o n t-K a r a b i n 1983a). The range of values of phosphorus regeneration rate at the stations in the Zegrzyński Reservoir recorded in the initial period of studies in 1982, i.e. in the first day of August was $1.1-2.2$ µg $P-PO_4 \cdot dm^{-3} \cdot h^{-1}$. The range of the values estimated for August in lakes in northern Poland varied from 0.3 to 3.5 in shallow unpolluted lakes and from 0.5 to 7.8 µg $P-PO_4 \cdot dm^{-3} \cdot h^{-1}$ in shallow polluted lakes (E j s m o n t-K a r a b i n 1983b). Hence the rate of phosphorus regeneration by zooplankton in the Zegrzyński Reservoir assumed values approximating the upper limit values reported from shallow, strongly eurotrophic (almost hypertrophic and hypertrophic) lakes.

The group which decidedly dominated in the process of phosphorus regeneration in the Zegrzyński Reservoir were Rotatoria (Fig. 7). At the stations A, B and C (the limnetic sites) in 1982 also Copepoda and Cladocera highly participated in phosphorus regeneration (especially at the station C and corresponding in 1984 station V). In the lotic parts (stations D, E) actually the only group regenerating phosphorus to the form assimilated by phyto- and bacterioplankton were Rotatoria. Also in 1984 in the lotic sites (stations III and IV) phosphorus regeneration was dominated by rotifers.

3.2.2. The role of zooplankton trophic groups in phosphorus regeneration

The assignment of regeneration rate to particular zooplankton trophic groups enables the analysis of the source of organic matter subject to mineralization in effect of metabolic processes. However, the assignment is very difficult as trophic status of numerous species of rotifers and crustaceans is abmiguous and, furthermore, many animals alter their diet during season according to actual food resources in the environment.

The division of zooplankton into trophic groups presented in the work is only general, due to difficulties mentioned above, and singles out only four trophic groups of zooplankton. The distinguished groups do not correspond to particular links of the trophic chain, but include some of them, two at least. The presented classification was based on the paper by G l i w i c z (1974), considering the data on particular species of rotifers supplied by P o u r r i o t (1977) and D u m o n t (1977). The distinguished trophic groups are as follows:

I. Detritophages — organisms selectively feeding on detritus and bacteria (small — bodied rotifer species of the genera Keratella, Brachionus, Filinia and *Pompholyx sulcata* Hudson).

II. Detrito — phytophages — animals whose food includes mainly detritus (with bacteria) and nannophytoplankton (rotifers, e.g. *Kellicottia longispina* (Kellicott), *Keratella quadrata* (Müller), and a majority of Cladocera among crustaceans).

III. Phytophages — animals selectively feeding on phytoplankton (rotifers of the genera Polyarthra, Synchaeta, Gastropus, Ascomorpha and crustaceans — younger stages of Cyclopidae and all the stages of Diaptomidae).

IV. Predators — animals selectively feeding on small zooplankton, complementing their diet with larger algae (adult individuals and older copepodites of Cyclopida, rotifers of the genus Asplanchna).

An analysis of changes in the contribution of particular zooplankton trophic groups to phosphorus regeneration at particular stations again brought out a difference between the limnetic and lotic sites (Fig. 8). Although in the two years of studies the group dominating in phosphorus regeneration at all the stations were detritophages, yet the greatest share in this process in the limnetic sites had predators. In the lotic sites, on the other hand, P regeneration by predators was small during the whole period of studies.
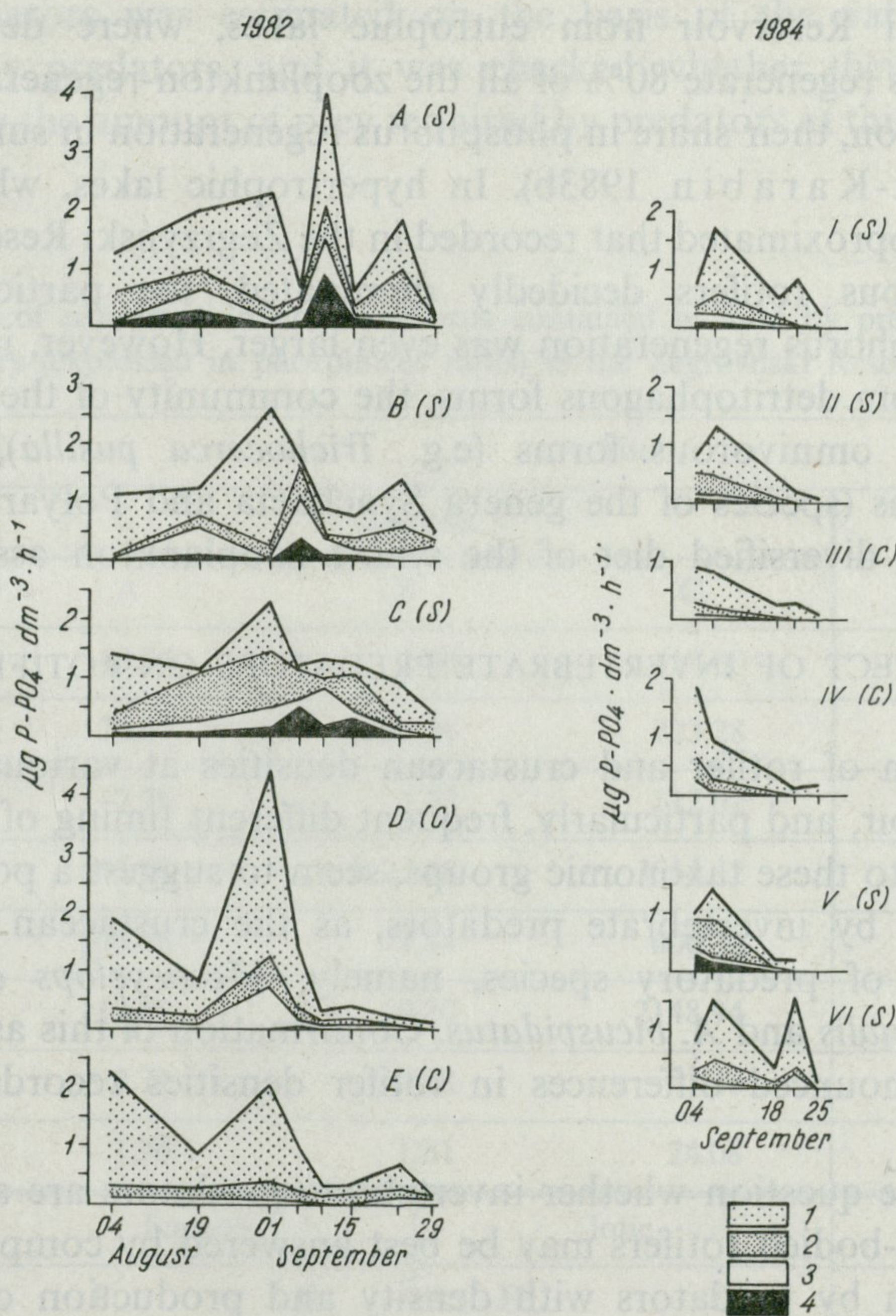
Fig. 8. The rate of phosphorus regeneration by four trophic groups of zooplankton at limnetic (S) and lotic (C) sites in the Zegrzyński Reservoir in 1982 and 1984

1 — detritusophages, 2 — detrituso-phytophages, 3 — phytophages, 4 — predators. For explanations see Fig. 1

Similarly as in case of analysis of zooplankton species structure, also the examination of participation of particular zooplankton trophic groups in phosphorus regeneration strongly accentuated distinctiveness of the station C in 1982 and

the corresponding station V in 1984 from all the other stations in the limnetic sites. The participation in the process of all the four trophic groups was more levelled out at these stations than elsewhere in this site, at a notably higher share of detrito-phytophages.

The analyses of contribution of the zooplankton four trophic groups to phosphorus regeneration revealed that during zooplankton density peak in the Zegrzyński Reservoir, all kinds of organic matter were fairly intensively used, detritus and bacteria in particular, yet also plant food was consumed throughout the study period (Fig. 8). Plant food was the least intensively consumed in the lotic sites, at the station E in particular.

A relatively high share of plant food in zooplankton diet is a feature differentiating the Zegrzyński Reservoir from eutrophic lakes, where detritophages and detrito-phytophages regenerate 80% of all the zooplankton-regenerated phosphorus over vegetative season, their share in phosphorus regeneration in summer being even greater (Ejsmont-Karabin 1983b). In hypertrophic lakes, where phosphorus regeneration rate approximated that recorded in the Zegrzyński Reservoir and where small, detritophagous rotifers decidedly dominated, the participation of detritophages in phosphorus regeneration was even larger. However, in the Zegrzyński Reservoir, apart from detritophagous forms, the community of the smallest rotifers abounded also in omnivorous forms (e.g. Trichocerca pusilla), as well as in phytophagous forms (species of the genera Synchaeta and Polyarthra). It was the reason for a more diversified diet of the whole zooplankton association.

3.3. THE EFFECT OF INVERTEBRATE PREDATORS ON ROTIFER DENSITIES

The comparison of rotifer and crustacean densities at various stations in the Zegrzyński Reservoir, and particularly, frequent different timing of density peaks of animals belonging to these taxonomic groups, seem to suggest a possible regulation of rotifer densities by invertebrate predators, as the crustacean community was composed mainly of predatory species, namely, Mesocyclops oithonoides Sars, Acanthocyclops vernalis and A. bicuspidatus. Confirmation of this assumption would likely explain pronounced differences in rotifer densities recorded at proximate stations.

It seems that the question whether invertebrate pradators are able to affect the occurrence of small-bodied rotifers may be best answered by comparing the rate of rotifer consumption by predators with density and production of prey.

The rate of predator feeding may be estimated, among others, on the basis of phosphorus excretion by predators. As consumption comprises assimilation (excretion + production) and defecation, then the values of defecation and production should be calculated so that after summing them up to the value of excretion rate, the consumption rate could be known. Production of predators may be estimated on the basis of their standing crop, applying, after Ivanova (1985), the mean value of P/B for temperatures $11-26°C$ and for Cyclopidae equalling 0.07. Hence the roughly estimated predator production in the Zegrzyński Reservoir in 1982 at all the

stations ranged (in terms of phosphorus units) from 0.0001 to 0.0795 μg $P \cdot dm^{-3} \cdot h^{-1}$. Having added the values of production to the values of the rate of phosphorus excretion by predators, it was possible to estimate the values of the rate of phosphorus assimilation by predators, and, subsequently, to calculate the share of production in it. The share thus calculated varied from 2.8 to 11.3%, the mean amounting to 6.4%. Having considered the excretion to production ratio and having assumed that assimilation of phosphorus from food accounted for about 80% of consumption in case of predators (according to Parsons (1980) it might account even for 90% of consumption, yet the assumed 80% seems more probable), it turned out that phosphorus consumption made up about 1.3 excretion rate (A = 0.8 C, P = 0.64 A). Applying this coefficient, consumption rate (in phosphorus units) of rotifers by predators was estimated on the basis of the values of phosphorus excretion rate by predators, and it was checked whether their environment was feasible to supply the amount of prey required by predators at this consumption rate.

Table 3. Daily ratio of consumption of phosphorus contained in food by predatory zooplankton to production of its prey (expressed in phosphorus units) in the Zegrzyński Reservoir in 1982 and 1984

Date	Site				
	limnetic			lotic	
	A	B	C	D	E
4 Aug. 1982	40.74	1.56	17.80	1.48	0.24
19 Aug. 1982	74.64	229.36	723.28	0.92	3.52
1 Sept. 1982	2.76	1.22	112.02	0.32	0.42
6 Sept. 1982	155.28	1127.46	3564.32	4.00	2.02
10 Sept. 1982	598.46	71.78	600.30	0.92	1.08
15 Sept. 1982	17.62	20.20	2148.94	0.44	0.60
23 Sept. 1982	7.74	0.88	1.46	0.50	1.56
29 Sept. 1982	1.70	1.61	24.08	5.40	10.40

	limnetic		lotic		limnetic	
	I	II	III	IV	V	VI
4 Sept. 1984	200.00	155.56	5.94	0.12	979.60	89.98
7 Sept. 1984	21.04	11.72	4.24	4.74	131.66	4.68
18 Sept. 1984	0.80	1.84	1.74	2.18	2.68	14.26
21 Sept. 1984	0.10	0.00	0.18	1.12	0.00	0.00
25 Sept. 1984	0.00	1.18	0.46	0.40		0.00

A−E, I−VI − see Fig. 1.

The estimated consumption rate of food-bound phosphorus by predators was compared to production and biomass of victims, the values expressed in phosphorus units, assuming, after Makarewicz and Likens (1979) that P accounted for 0.96% of rotifer dry weight. For this purpose rotifer production was estimated for each date and station separately, on the basis of the number of rotifer eggs and the rate of their development in temperatures recorded at that time. The data on relation of development rate of rotifer eggs to temperature were taken from the work by Herzig (1983).

The analysis of the ratio of consumption rate by predators to prey production (Table 3) revealed that in the limnetic sites the consumption frequently surpassed the production output, whereas in the lotic sites consumption of rotifers by predators was smaller than the output of prey production. Hence it may be expected that predators had a decidedly greater effect on standing crop of rotifers in the limnetic sites.

Table 4. Daily ratio of consumption of phosphorus contained in food by predatory zooplankton to summed up values of biomas and production of its prey (expressed in phosphorus units) in the Zegrzyński Reservoir in 1982 and 1984

Date	Site				
	limnetic			lotic	
	A	B	C	D	E
4 Aug. 1982	5.54	0.24	3.02	0.38	0.07
19 Aug. 1982	10.33	20.24	93.86	0.15	0.92
1 Sept. 1982	0.55	0.14	11.69	0.08	0.11
6 Sept. 1982	28.62	206.87	749.77	1.05	0.49
10 Sept. 1982	92.46	12.82	70.25	0.34	0.41
15 Sept. 1982	5.21	5.0	263.25	0.15	0.21
23 Sept. 1982	1.92	0.23	0.35	0.16	0.35
29 Sept. 1982	0.42	0.40	9.53	0.88	1.99

	limnetic		lotic		limnetic	
	I	II	III	IV	V	VI
4 Sept. 1984	25.66	28.57	1.60	0.02	158.05	17.76
7 Sept. 1984	4.76	2.60	0.89	0.87	27.02	1.12
18 Sept. 1984	0.12	0.23	0.26	0.40	0.77	1.92
21 Sept. 1984	0.03	0.00	0.08	0.24	0.00	0.00
25 Sept. 1984	0.00	0.37	0.11	0.10		0.00

A—E, I—VI — see Fig. 1.

Utilization of the habitat food resources is better expressed by the ratio of consumption on the sum of values of prey biomass and their production. Also in this case (Table 4) nutritive requirements of predators frequently exceeded actual food supply. Consumption rate in the limnetic sites was frequently so high that rotifers may have been completely eliminated from the environment over the period lasting from some to several dozen minutes, e.g. on September 6, 1982 (Table 4). It may be assumed that under such an acute food deficiency, predators in question must turn to plant food, providing it occurs in sufficient amounts, or they migrate to other parts of the reservoir area, more profuse in food. The latter assumption seems to be supported by profound changes in the consumption to food supply ratio in the limnetic site e.g. at the station C, where extremely high values of this ratio alternated with much smaller values (Table 5).

Table 5. Phosphorus turnover time (i.e. the ratio of total P in lake water to P excreted by zooplankton) against concentration of total P in the Zegrzyński Reservoir in 1982. TP — concentration of total P (in $\mu g \; P \cdot dm^{-3}$) TT — turnover time (in days)

Date		Site				
		limnetic			lotic	
		A	B	C	D	E
4 Aug.	TP	116	125	109	94	94
	TT	3.8	4.6	3.2	2.0	1.8
19 Aug.	TP	126	146	84	106	98
	TT	2.6	4.9	3.0	5.6	4.8
1 Sept.	TP	lack of	106	76	90	265
	TT	data	1.7	1.4	0.8	6.1
6 Sept.	TP	lack of	90	94	81	90
	TT	data	2.2	3.3	2.4	3.6
10 Sept.	TP	86	88	76	94	92
	TT	0.9	4,1	2.4	14.3	11.4
15 Sept.	TP	106	98	100	76	88
	TT	2.5	5.3	3.3	9.3	10.7
23 Sept.	TP	98	82	120	101	76
	TT	2.3	2.4	5.7	21.0	4.4
29 Sept.	TP	70	88	72	lack of	94
	TT	12.9	7.4	7.9	data	25.8
Mean	TP	100	103	91	92	116
	TT	4.2	4.1	3.8	7.9	8.6

A—E, I—VI — see Fig. 1.

Rotifers in the lotic sites were under a considerably weaker pressure of invertebrate predators, which frequently did not use up the actual production of their prey, and thus the standing crop of the latter was often not disturbed.

On the basis of the analyses presented above it may be assumed that rotifer density in the Zegrzyński Reservoir may have been controlled by invertebrate predators, yet in the limnetic sites rather than in the lotic ones. Furthermore, at the stations where predator pressure on prey populations was particularly strong, it was also subject to strong variations in time (Tables 3 and 4).

An explicit ascertainment of the predator effect on prey abundance is very difficult, as, on one hand, the occurrence of rotifers is determined by all of environmental conditions, including the trophic conditions, while on the other, the occurrence of predators may depend on food availability. In order to detect whether the observed strong pressure of predators on rotifer population was reflected by changes in the standing crop of the latter, the rate of excretion by predators (P) was compared to biomass of rotifers (expressed in phosphorus units) (Fig. 9).

It was found out that at limnetic sites, where predator feeding rate was so high that it could affect the standing crop of rotifers, there was noted a weak inverse dependence, i.e. the higher was the rate of predator feeding (and, consequently, of P regeneration by predators), the smaller was biomass of prey. The correlation coefficient for the two variables expressed in log-log scale was so small ($r = -0.23$, statistically not significant at $\alpha = 0.05$) that only 5% of changes in rotifer biomass could have been explained as caused by predators. Hence it was a very important observation that at lotic sites, where predator pressure on rotifers was so small that predators could hardly affect the population of their prey, dependence between the
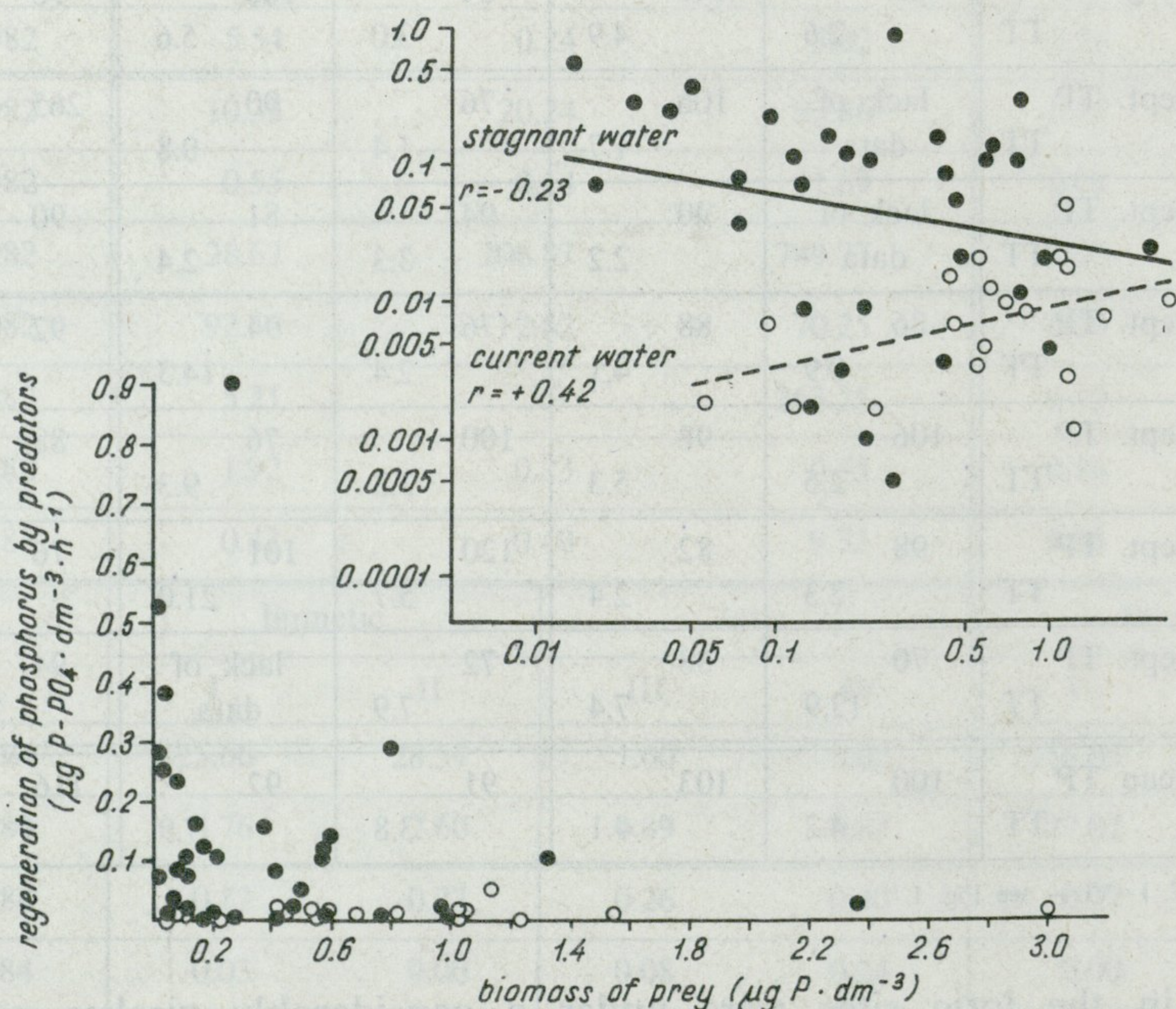

Fig. 9. The rate of phosphorus regeneration by invertebrate predators against the biomass of their prey at limnetic (S) and lotic (C) sites in the Zegrzyński Reservoir in 1982 and 1984

two variables in question was contrary to that noted at limnetic sites, namely, an increase in prey biomass was accompanied by an increase in consumption rate by predators (i.e. in the rate of P regeneration by predators), the correlation coefficient being notably higher in this case (r = 0.42, statistically significant at $\alpha = 0.05$) (Fig. 9).

Thus the rate of phosphorus regeneration (and consumption) by predators may be indicative of a direct effect of predators on populations of their prey. This effect, however, was not so evident in the examined cases, as only 5% of changes in biomass of small-bodied rotifers could be explained as caused by predators.

3.4. ZOOPLANKTON SPECIES DIVERSITY

Zooplankton of the Zegrzyński Reservoir was in the studied period relatively abundant in species. There were recorded 33 Rotifera species (excluding the sporadically occurring species) and 18 Crustacea species. On the average, 39 species
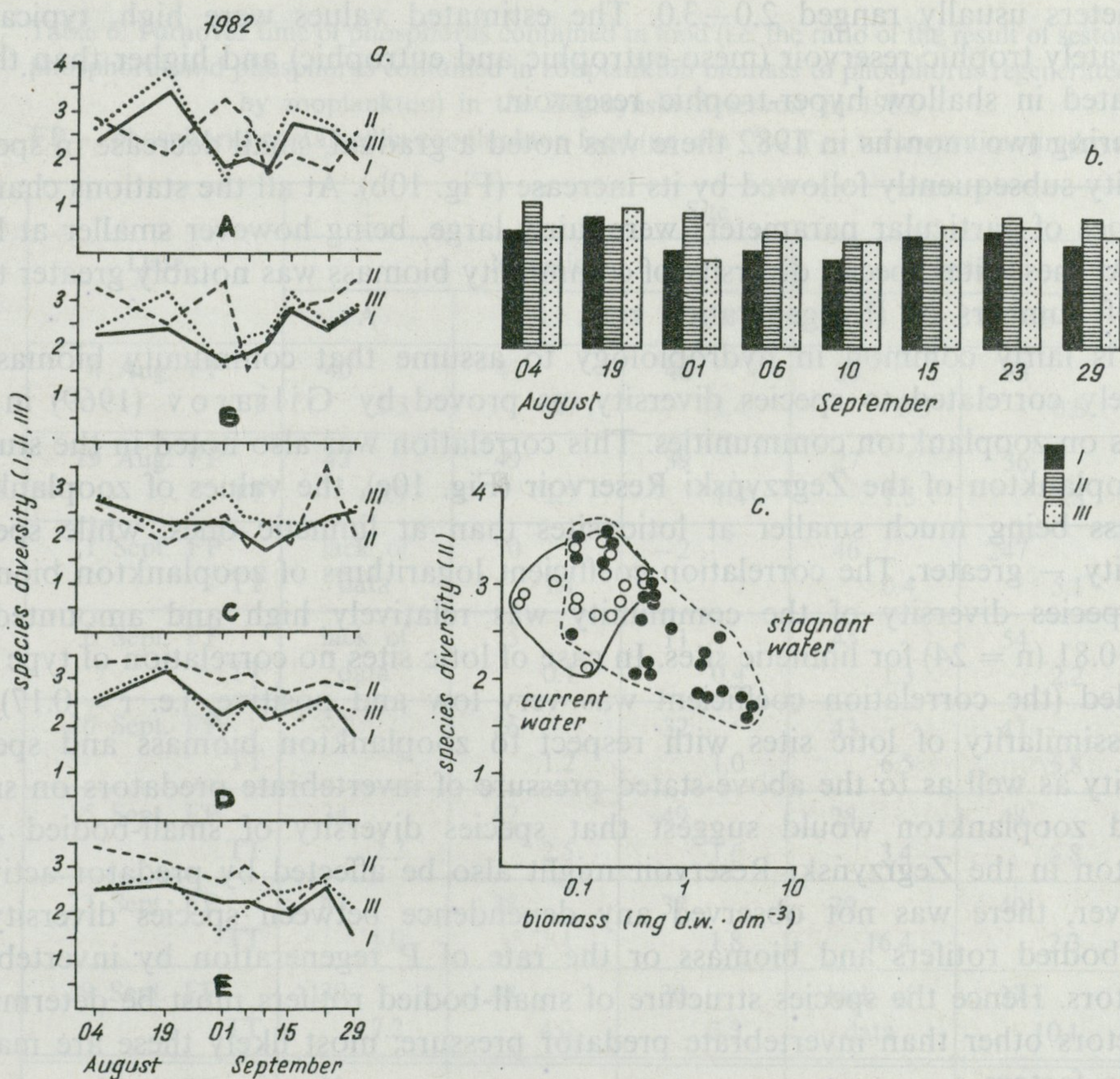

Fig. 10. Changes (a) and mean for particular dates values (b) of species diversity coefficient (I — density, II — biomass, III — the rate of phosphorus excretion). Rotatoria and Crustacea of Zegrzyński Reservoir
A — E — for explanations see Fig. 1

of plankton animals were recorded in a sample in 1982 and 22 species in 1984. If contribution of each species to total numbers or biomass of the community was identical, then at the recorded number of species, (maximal) species diversity would amount to 5.29 in 1982 and to 4.46 in 1984. Obviously, at zooplankton numbers greater than the recorded number of species, entirely even distribution of numbers of particular species in total numbers never occurs in nature, neither did it occur in the studied reservoir. Although two times smaller than the maximal one, species diversity was fairly high throughout the studied period, regardless the parameter upon which it was estimated. Only species diversity of community numbers was slightly smaller than diversity of biomass and of the share in phosphorus regeneration (Fig. 10). Its mean values, estimated for particular dates, were not smaller, however, than 2.0. The values of species diversity in community biomass or in the rate of phosphorus regeneration by the community were only slightly higher. The latter parameter is very significant as it denotes, on one hand, the share of particular species in the process of nutrient regeneration and, on the other, their share in food supply depletion. Mean values of species diversity with regard to the three examined parameters usually ranged 2.0 − 3.0. The estimated values were high, typical of moderately trophic reservoir (meso-eutrophic and eutrophic) and higher than those calculated in shallow hyper-trophic reservoir.

During two months in 1982 there was noted a gradual, small decrease in species diversity subsequently followed by its increase (Fig. 10b). At all the stations changes in values of particular parameters were fairly large, being however smaller at lotic sites. At these sites species diversity of community biomass was notably greater than that of numbers or P regeneration rate.

It is fairly common in hydrobiology to assume that community biomass is inversely correlated to species diversity, as proved by Giliarov (1969) in the studies on zooplankton communities. This correlation was also noted in the studies on zooplankton of the Zegrzyński Reservoir (Fig. 10c), the values of zooplankton biomass being much smaller at lotic sites than at limnetic ones, while species diversity − greater. The correlation coefficient logarithms of zooplankton biomass and species diversity of the community was relatively high and amounted to r = − 0.81 (n = 24) for limnetic sites. In case of lotic sites no correlation of type was recorded (the correlation coefficient was very low and positive, i.e. r = 0.17).

Dissimilarity of lotic sites with respect to zooplankton biomass and species diversity as well as to the above-stated pressure of invertebrate predators on small bodied zooplankton would suggest that species diversity of small-bodied zoo- plankton in the Zegrzyński Reservoir might also be affected by predator activity. However, there was not observed any dependence between species diversity of small-bodied rotifers and biomass or the rate of P regeneration by invertebrate predators. Hence the species structure of small-bodied rotifers must be determined by factors other than invertebrate predator pressure; most likely these are mainly trophic factors.

3.5. ZOOPLANKTON ROLE IN NUTRIENT CYCLING IN THE ZEGRZYŃSKI RESERVOIR

The significance of zooplankton as the community included in phosphorus cycle in water is expressed by turnover time, estimated as the ratio of total phosphorus contained in lake water to phosphorus regenerated by zooplankton. Studies conducted in several dozen of lakes of various trophic conditions (E j s m o n t-K a- r a b i n 1983a) revealed that as concentration of total P in water (and, consequently, the reservoir trophy) increased, the amount of phosphorus regenerated by zoo- plankton increased as well, so, eventually, the turnover time remained steady (or even dropped slightly) at the mean rate of 3 — 7 days. The range of values estimated for particular lakes was wider and spread from 1 to 14 days. Turnover time estimated in this way for the Zegrzyński Reservoir (Table 5) assumed values within the quoted interval, the range of values being notably smaller and turnover time shorter at limnetic sites than at lotic ones, as clearly seen in mean values for particular stations. A noteworthy fact is that, all the same, total P concentration at the two types of sites

Table 6. Turnover time of phosphorus contained in food (i.e. the ratio of the result of seston phosphorus and phosphorus contained in zooplankton biomass to phosphorus regenerated by zooplankton) in the Zegrzyński Reservoir in 1982.
FP — phosphorus contained in zooplankton food ($\mu g \cdot dm^{-3}$) TT — turnover time (in days)

Date		Site				
		limnetic			lotic	
		A	B	C	D	E
4 Aug.	FP	40	47	46	28	33
	TT	1.3	1.7	1.4	0.6	0.6
19 Aug.	FP	43	49	39	27	36
	TT	0.9	1.7	1.4	1.5	1.8
1 Sept.	FP	lack of	70	−2	46	247
	TT	data	1.1	?	0.4	5.1
6 Sept.	FP	lack of	5	11	45	54
	TT	data	0.1	0.4	1.3	2.2
10 Sept.	FP	−2	26	32	43	47
	TT	?	1.2	1.0	6.5	5.8
15 Sept.	FP	34	47	49	28	48
	TT	2.2	2.5	1.6	3.4	5.8
23 Sept.	FP	43	38	37	79	40
	TT	1.0	1.1	1.8	16.4	2.3
29 Sept.	FP	39	48	30	lack of	37
	TT	7.2	4.0	3.3	data	10.1
Mean	FP	33	41	30	42	68
	TT	2.1	1.7	1.4	4.3	4.2

A − E — see Fig. 1.

was approximately the same. It is an evidence that the system of P regeneration by zooplankton at limnetic sites was much more efficient.

The time of phosphorus turnover in metabolic processes of zooplankton is a good indicator of activity of this animal group. It does not inform, however, about utilization of the environmental food supply, i.e. about this part of phosphorus which is contained in zooplankton-devoided seston, yet these data may be acquired by calculating turnover time of phosphorus in suspended food matter, i.e. the ratio of the difference between seston phosphorus and phosphorus contained in zooplankton biomass to phosphorus regenerated by zooplankton. The turnover time estimated in this way (Table 6) was, obviously, much shorter (by 2 — 3 times) than turnover time of total P.

It should be remembered, however, that estimations of this kind are only rough; mistakes may lie in the very assumption that phosphorus concentration in biomass is constant and the same for all the zooplankton organisms (about 1% of dry weight) as well as indirect methods of calculating phosphorus concentration in food may be misleading. Therefore this may be the reason why in two cases of exceptionally abundant occurrence of zooplankton, phosphorus in its biomass was higher than concentration of phosphorus in the entire seston (hence a negative value of P concentration in food — Table 6).

Notwithstanding the possible mistakes in estimates, it is evident that turnover time of phosphorus in food was in many cases very short, lasting several hours only, while at limnetic sites it amounted, on the average, to about 48 hours. Alike turnover time of total P, it was 2 times longer than at lotic sites. It follows from these estimates that trophic relations at the latter site were markedly less than at limnetic sites. Thus the sites of a slow water flow rate seem to act as main "processors" of organic matter by zooplankton associations abounding there. At such a short turnover time, remaining at such a low rate over longer intervals- they are likely to function on a constant supply of organic matter from the outside.

4. DISCUSSION

A general survey of features characterizing the structure, densities and significance of zooplankton in the Zegrzyński Reservoir reveal a certain important distinctiveness in functioning of this community as compared to those in lakes of a longer water retention time. Zooplankton of the Zegrzyński Dam Reservoir is under a stronger effect of water flow than in lakes. It was evidenced by a distinct dissimilarity of the zooplankton associations at limnetic and lotic sites. The differences concerned not only the dynamics of occurrence of plankton animals and the structure of zooplankton communities, but also functioning of these communities and their role in phosphorus cycling at particular stations (Table 7).

It would be advisable to examine in details on of the indicators, namely-fecundity of plankton animals (Tables 1 and 2, Fig 6). The values of rotifer and

Table 7. A list of significant features differentiating limnetic and lotic sites in the Zegrzyński Reservoir

Feature	Site	
	Limnetic	Lotic
Zooplankton density dynamics	complicated, vehement changes	more stable and evener
Share of Crustacea in zooplankton community	large	small
Fecundity of the dominating rotifer species	lower	higher
Fecundity of the dominating crustacean species	higher	lower
Length of adult cladocerans	greater	smaller
The share of plant food in zooplankton diet	fairly high	smaller
Invertebrate predator pressure on small zooplankton	strong	weak
Species diversity of zooplankton	high	slightly smaller
Turnover time of total P in effect of regeneration by zooplankton	shorter	2-times longer
Turnover time of phosphorus contained in food in effect of P regeneration by zooplankton	shorter	2-times longer

crustacean fecundity in the Zegrzyński Reservoir were relatively high, comparable to those estimated in lake ecosystems of a high flow rate, e.g. in lakes of Konin system, heating up by power plants (Ejsmont-Karabin and Węgleńska 1988).

Rotifer fecundity was pronouncedly greater at lotic sites due to dominance in the community of three species positively reacting to accelerated water flow. High values of fecundity point to prevalence in this community of the "r" type selection (by way of high reproduction). One of possible explanations may by the hypothesis of "rarefaction", i.e. a constant removal of a part of specimens, which causes a constant unsaturation of the population (Pianka 1974). It would explain a greater fecundity of rotifers at lotic sites, as a strong water current highly rarefies the community either by mechanic damaging weaker individuals or by carrying them away beyond the site borders.

Predator pressure cannot be regarded, on the other hand, as a rarefying factor at these sites. A notably greater invertebrate predator pressure on rotifers was recorded at limnetic sites, where rotifer fecundity was, all the same, markedly smaller. If the removal of individuals from community causing unsaturation of population, was primarily related to predator pressure, than the contrary should be expected, i.e. a greater rotifer fecundity under a stronger pressure of predators.

Nonetheless the effect of food abundance on rotifer fecundity cannot be disregarded. Much better trophic conditions at lotic sites evidenced, among others, by a two-times longer turnover time of phosphorus contained in suspended matter as compared to limnetic sites (Table 6), would favour a greater rotifer fecundity. It is not unlikely that the two factors, i.e. the mechanic and trophic one, affect rotifer fecundity, the trophic conditions being likely to result from water flow rate. The fact that trophic conditions were better at lotic sites seem to be the effect of the inflow of organic matter into the examined part of reservoir.

Considerable differences between lotic and limnetic sites were also noted while examining crustacean fecundity. It is highly questionable whether these differences were caused by various predator pressure and various food supply in the environment. Species composition and dominance structure of the community of plankton crustaceans, i.e. quantitatively equal co-occurrence of large bodied (*Daphnia longispina, D. cucullata, Moina rectirostris*) and small bodied (*Bosmina longirostris*) species, high species diversity and high fecundity of all the crustacean species, according to "size efficiency" hypothesis by B r o o k s and D o d s o n (1965) and "balansed predation" by D o d s o n (1974) and the conception of threshold food concentration by L a m p e r t (1977, 1978), point to a slight pressure of invertebrate and vertebrate predators on crustacean population in the Zegrzyński Reservoir and to abundance of food constantly inflowing from the outside of the system. Thus there must be some other than biological factors determining various fecundity and individual body size of plankton crustaceans. Similarly as in case of rotifers, most likely stronger current at flowing site causes greater elimination of individuals in effect of mechanic destruction of weaker forms or removal of a part of population outside the site. This assumption seems much probable, considering life history strategy of plankton crustaceans with respect to regularity of their growth, development and reproduction.

Out of four cladoceran species dominating in the Zegrzyński Lake in the studied period, three (*Daphnia longispina, D. cucullata* and *Moina rectirostris*) follow the life history and strategy of the "r" type, which consist in a rapid individual development, earlier of first reproduction initiation, somatic growth continuing after maturity and, above all, long life span and maximal reproductive potential (high birth rate and more large clutches) (S t e a r n s 1980, R o m a n o v s k y 1984). At limnetic sites of a slower water flow, specimens of these species have a better chance of surviving the whole life cycle and maximize their growth and reproduction potential. At lotic sites rapid elimination of individuals makes it impossible for them to complete a full life cycle. The shorter life span the smaller is the size at maturity and the smaller is their fecundity rate, as the body size of cladoceran specimens is positively correlated with the number of eggs in clutches a lay (W ę g l e ń s k a 1971).

Small bodied cladoceran species, like *Bosmina longirostris,* are adapted to the life strategy of the "K" type, which consists in a slower rate of development and growth after maturity, short life span and small reproductive pontential (low birth rate and small clutches) (R o m a n o v s k y 1984). At species following this type of life strategy, changes in fecundity (size of clutches) and in individual body size during life

span are much smaller than at species developing according to the "r" life type strategy. Most probably this was the reason why differences in fecundity and individual body size of Bosmina longirostris at limnetic and lotic sites were much smaller than those recorded at species of the genera Daphnia and Moina.

Contrary to Cladocera, the species of the Copepoda group do not grow after maturation and the number of eggs in clutches under optimal trophic conditions, hardly ever depends on the body size of mature females. Even in the first clutch the number of eggs deposited by a female may equal the given species' maximum. Therefore, notwithstanding a quicker elimination at lotic sites and a shorter life span, fecundity of Copepoda was not observed to differ significantly at limnetic and lotic sites. Yet a markedly smaller abundance of Copepoda at lotic sites as compared to limnetic ones, indicates that at such a huge elimination of individuals caused by strong current, high fecundity of Copepoda do not balance the losses resulting from a higher mortality rate or removal of individuals outside the reservoir.

A higher fecundity rate of rotifers at lotic sites coupled with a weak invertebrate predator pressure brought about domination of rotifer biomass production. At limnetic sites zooplankton biomass and the remaining part of seston was relatively quickly transformed into mineral compounds, due to both strong pressure of invertebrate predators on small zooplankton and larger algal cells as well as to a more rapid depletion of food resources by small zooplankton (as evidenced by a very short turnover time of phosphorus contained in food).

An outline of functioning of the two systems differing in water flow rate may be briefly featured as: accumulation of organic matter, produced in time of water flow, less intensively used by zooplankton at lotic sites and zooplankton-affected rapid mineralizaton of organic matter at limnetic sites. Destruction mechanisms are seemingly more powerful at limnetic sites due to an increased rate of defecation of phosphorus compounds by zooplankton, however the products of this process most likely do not reach the reservoir bottom being used up in upper water layers by dominating detritusophagous organisms.

Hence zooplankton activity may be regarded as one of the factors counteracting phosphorus removal in effect of sedimentation in limnetic parts of dam reservoirs. This function of zooplankton in phosphorus removal was already been pointed out by U h l m a n and B e n n d o r f (1979). In their studies the authors noted that zooplankton slackened the rate of phosphorus removal.

"Rarefaction" hypothesis cannot possibly explain another peculiarity of zoo-plankton in the Zegrzyński Reservoir, i.e. its relatively high species diversity, greater than in shallow, much eutrophicated lakes. Summer zooplankton community in the Zegrzyński Reservoir was, on the whole, rather specific, i.e. it was composed of very small organisms, dominated by small bodied rotifers and Cyclopidae (with prevalence of juvenile forms). Although zooplankton of the Zegrzyński Reservoir was dominated by detritusophagous forms, yet this dominance was much smaller than in case of small zooplankton of hypertrophic lakes. For this reason food spectrum of zooplankton in the Zegrzyński Reservoir was relatively wide. The lack of environ-mental stability as well as prevalence of poorly specialized forms in zooplankton

community should result in small species diversity of zooplankton (P i a n k a 1974). However, as compared to shallow, much eutrophicated lakes (G i l j a r o v 1972), species diversity of zooplankton in the Zegrzyński Reservoir was fairly high. A most likely reason of this phenomenon could be plentiful food supply. However, judging by a very short turnover time of phosphorus in food, food abundance resulted not so much from a profuse production of organic matter on the spot, but rather from its constant influx from the outside of the examined sites.

The character of zooplankton occurrence and its activity in the Zegrzyński Reservoir seem to be dominated by mechanic factor affecting either directly the structure, density and fecundity of zooplankton or indirectly, e.g. by way of modifying invertebrate predator pressure on small zooplankton or influencing the amount of food available to zooplankton.

5. SUMMARY

An attempt was made to determine the effect of water flow rate on the character of zooplankton communities and their role in phosphorus cycling in man-made lake. The studies were conducted in limnetic and lotic sites in the main basin of the Zegrzyński Reservoir (Fig. 1), an artificial reservoir made in 1962—1964 in effect of impounding two rivers. The studies were carried out in August and September 1982 and in September 1984.

It was observed that basic quantitative and structural features of zooplankton re-occurred in subsequent years of studies (Figs. 2, 3).

The limnetic and lotic sites were found out to differ notably in a number of aspects (Table 5). Abundance dynamics of zooplankton at limnetic sites was marked for a greater changeability (stronger and more frequent changes in animal densities); furthermore, a greater significance in zooplankton communities in these sites had Crustacea (Figs. 4, 5). There were also recorded differences in fecundity of zooplankton individuals, namely, at limnetic sites fecundity of the dominating rotifer species was considerably smaller, while of crustaceans — greater (Tables 1, 2, Fig. 6). At limnetic sites plant food had a greater share in zooplankton diet (Fig. 8). These sites were also noted for a strong pressure of invertebrate predators on small zooplankton, while in lotic sites the pressure was fairly weak (Tables 3, 4). The two types of sites differed also in turnover time of total phosphorus and phosphorus contained in zooplankton food in effect of P regeneration by zooplankton, namely in lotic sites turnover time was about 2 times longer than in limnetic ones, which means that food conditions in the former site were markedly less tense.

The results of analyses on the state and functioning of zooplankton indicate that due to zooplankton activity in the limnetic sites of the Zegrzyński Reservoir, phosphorus sedimentation should be much lower than in lotic ones. The structure and outcome of zooplankton activity in this type of reservoirs is highly determined by mechanic factors (the rate of water flow), which affect it either directly (e.g. destructing weaker individuals or carrying them away beyond the studied sites), on indirectly (e.g. modifying predator pressure on small zooplankton or food availability to non-predator animals).

6. POLISH SUMMARY

Podjęto próbę określenia efektu szybkości przepływu wody na charakter zespołów zooplanktono-wych i ich rolę w krążeniu fosforu w zbiorniku zaporowym. Badania przeprowadzono na stanowiskach zastoiskowych i nurtowych w rozlewiskowej części Jeziora Zegrzyńskiego (rys. 1), sztucznego zbiornika

powstałego w latach 1962—1964, po spiętrzeniu wód dwóch rzek. Badania prowadzono w sierpniu i wrześniu 1984 roku.

Stwierdzono, iż podstawowe cechy ilościowe i strukturalne zooplanktonu powtarzają się w obu latach (rys. 2, 3).

Porównując stanowiska zastoiskowe z nurtowymi zaobserwowano istnienie między nimi szeregu istotnych różnic (tab. 7). Dynamika liczebności zooplanktonu na stanowiskach zastoiskowych cechowała się większą zmiennością (gwałtowniejszymi i częstszymi zmianami liczebności zwierząt), większe też na nich było znaczenie Crustacea w zespole zooplanktonu (rys. 4, 5). Stwierdzono również znaczne różnice w płodności organizmów zooplanktonowych: na stanowiskach zastoiskowych płodność dominujących gatunków wrotków była wyraźnie niższa, zaś skorupiaków wyższa (tab. 1 i 2, rys. 6). Na stanowiskach zastoiskowych większy też był udział pokarmu roślinnego w diecie zooplanktonu (rys. 8), stwierdzono tam również silną presję drapieżników bezkręgowych na drobny zooplankton.

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