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THE INFLUENCE OF THE FISH POPULATION ON THE BIOCENOSIS
OF A POND, USING *ROTIFERA* FAUNA AS AN ILLUSTRATION*

A fish population (carp fry) increases the abundance and the duration of occurrence of plankton rotifers during the four months growing season of the ponds. This is due to the increase in the abundance of detritus and bacterioplankton due to transformation of the pond habitat by fish.

Within the *Rotifera* fauna, the fish population increases the abundance of two small species of *Rotifera*: *Keratella cochlearis* (Gosse) and *K. quadrata* (O. F. Müller).

Fish culture in the ponds results in the littoral species of *Rotifera* disappearing as the result of the elimination of mosaic character of the littoral habitat.

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I. AIM AND POSTULATES OF THE STUDY

The subject of the present study is formed by the description of successional changes taking place in newly-formed fish ponds, using euplankton and littoral *Rotifera* for purposes of illustration. The aim of the study is to attempt to explain both the spontaneous successional variations, connected with the formation of the biocenosis in the newly-formed pond, and also variations due to the influence of the fish population.

The effect of fish on the pond biocenosis is twofold in character:

1) direct influence exerted as a predator constituting the final link in the main food chain and feeding on invertebrate plankton and benthos organisms,

2) indirect – as an organism which can basically modify and transform a habitat, and thus exert an indirect influence on the functioning of the remaining components of the ecosystem of the pond.

The problem of the food and feeding of the fish and their influence as predators on food organisms is one frequently investigated, chiefly on account of its importance in practical fishery management. The following studies may be cited as examples of this – by Vaas and Vaas van Owen (1954), Gurzęda (1960), Grygierek (1962) in which a population of carp was found to have an inhibiting effect on the abundance and dynamics of crustacean plankton and benthos *Tendipedidae*.

Contrary to the problem of the direct influence of fish as predators – the problem of their indirect influence through the transformation of the habitat is represented in literature to an extent so small as to be completely out of proportion to its theoretical and practical ecological importance.

The problem of species strongly influencing and transforming the biocenosis and habitat has been raised by Clements and Shelford (1952), who termed them “dominants” (species influencing the habitat) or “major-influents” (species directly controlling the biocenosis, e.g. large predators). The transforming effect of the fish on the habitat and biocenosis of the body of water has been described in addition to the above mentioned authors, by Cahn (1929) and Dineen (1953). Charin, Šutenko and Myšenko (1954), Hrbaček and others (1959), Hrbaček (1962), Grygierek (1962) drew attention to the considerable changes in the whole pond biocenosis, and therefore also to changes among organisms not directly connected by food relations with the fish.

The influence of fish has been considered in the present study, using *Rotifera* fauna as an illustration. It must be assumed that plankton *Rotifera*, as one of the mass components of the pond plankton, will “reflect” the changes introduced into the ecosystem of the pond by the fish population depending on the intensity of its effect i.e. of population density.

The problem of the direct influence of fish as possible predators of *Rotifera* can be omitted from the present study since, as shown by data in

literature (Vaas and Vaas van Owen 1954, Kosova 1960), carp fry over 2 cm in length do not feed (or at any rate not to any considerable extent) on such small organisms as *Rotifera*. In my own investigations (Hillbricht-Ilkowska 1963) I did not find any distinct limitation of the abundance of even the larger species of *Rotifera* by dense carp fry stock.

The ponds chosen for the investigations are young newly-formed ponds, and therefore like every young biocenosis pass through successional changes. This type of pond makes it necessary to take into consideration the very considerable variability of the object studied, irrespective of any possible variations due to the influence of the fish. It is therefore essential to treat the anticipated changes in the *Rotifera* plankton as a whole over the period of the first few years of existence of the ponds as an "overlapping" of two sources of variations:

- 1) the natural successional changes referred to above, independent of the fish stock,
- 2) variations due to the influence of the fish stock.

II. STUDY AREA AND METHODS

The investigations were continued over a period of four years (1957–1960) on a group of experimental ponds belonging to the Experimental Fishery Station of Institute of Inland Water Fishery at Żabieniec. These ponds are similar in size (area 0.20 ha) and depth (about 1 m) and are of uniform construction. They form a compact group with relatively equal geological and hydrological conditions, since their water is supplied from one source (the river Jeziorka) led into and out of each pond separately¹.

The experimental ponds at Żabieniec were built between 1955–1957 and the first group of them was filled in June 1957. 1957 is therefore the first year of the activity of these ponds – a sort of "trial" activity under hydrological conditions which varied considerably. Technical filling tests caused great fluctuations in the water level, leading in certain of the ponds to a permanent partial state. The activity of the ponds in the three succeeding years (1958, 1959, 1960) took place under relatively stabilised hydrological conditions – all the ponds were kept completely filled throughout the whole growing season².

The period of activity of the ponds (the growing season) lasted about four months in each year (Tab. I). Some of the ponds were stocked with fish the first year. The smallest fish stocks were introduced into the ponds (2,500 fish/ha) in the I and II year, while in the III and IV year the fish stocking was

¹For a sketch of the ponds and further data on them see: Wołny (1962a), Grygierek (1962).

²Owing to the considerable permeability of ground the inflow of the water was continuous.

wider in scope (2,500–30,000 fish/ha). Carp fry (K_1) weighing about 1 gramme and from 2–3 cm in length were used for stocking each year. The fry were introduced into the ponds about seven days after the day on which the ponds were filled. The initial stock, allowing in such case for possible losses during the growing season, was taken as a basis for distinguishing between different variants of stocking. In some of the ponds, particularly in those with dense fish stocking, the fish were given rough-ground barley as supplementary food.

Samples were taken by a 1 l Patalas type of water sampler and strained through a net of 50–60 μ diameter of mesh. A sample contained 10 or 20 litres of water taken 1 litre at a time from places distributed at random within the pond. Intensity of sampling varied in different ponds. In some of the ponds samples were taken every 3–5 days (Tab. I. N – “normally”) throughout the whole period of activity of the ponds. In the remainder of the ponds chosen for investigations “probe” samples were taken (Tab. I. P) that is every 10–14 days. Three 10-litre samples were taken each time from the three “zones” of the pond: “pelagial”, 25–50 cm below the surface of the water, near-bottom – 20–30 cm above the bottom, inshore³, or 2 samples (from the inshore zone – 10 litre sample, from the “pelagial” and near-bottom zones together – 20 litre sample), or one 20–litre sample (only from the “pelagial” and near-bottom zones together).

The inshore and near-bottom zones of the pond from a habitat similar as regards the presence of land plants covering the bottom of the pond before it was filled in June: the “pelagial” zone represents the free body water.

The number of ponds examined frequently (N) and less often (P) and those represented by 1, 2 or 3 samples taken each time, differed in different study years, and is illustrated by the table below.

Year	No. of ponds examined every:				Joint number of ponds examined
	10–14 days		3–5 days		
	1 sample	1 sample	2 samples	3 samples	
1957	–	–	–	6	6
1958	–	–	–	8	8
1959	7	–	6	4	17
1960	17	4	–	–	21

The majority of the ponds in the group of those examined every 3–5 or 10–14 days were of the same age, i.e. in each year of the study period they were all filled for an equal number of years.

The ponds examined every 3–5 days and every 10–14 days will be considered separately in the present paper. The difference in the frequency of sampling has an important effect on the value and scope of such data as the

³The depth of water in the inshore zone was about 50 cm, this part of the pond being formed by a raised shelf.

Basic information on the ponds studied

Tab. I

Year	No. of ponds	Pond no. ¹	Dates of complete filling and emptying of ponds		No. of days of growing season of ponds	Intensity of examination ²	Consecutive year of complete filling	Fish stock		Remarks
			June	October				fish/pond	fish/ha	
1957	4	15	15	28	135	N 3	I	500	2,500	Frequent fluctuations in water level from Sept. marked decrease in water level
		17	28	28	122	N 3	I	500	2,500	
		18	28	28	122	N 3	I	500	2,500	
		21	15	28	135	N 3	I	500	2,500	
	2	27	15	28	135	N 3	I	0	0	
		37	28	28	122	N 3	I	0	0	
1958	2	20	25	27	124	N 3	II	0	0	Up to Aug. - depth about 1 m
		37	25	27	124	N 1-3	II			
	2	27	20	27	99	N 1-3	II	0 ³	0 ³	
		34	20 (July)	27	99	N 1-3	II			
	4	15	25	27	124	N 3	II	500	2,500	
		17	25	27	124	N 3	II			
18		25	27	124	N 3	II				
21		25	27	124	N 3	II				
1959	2	22	18	18	122	N 2	III	0 ⁴	0 ⁴	
		37	18	18	122	P 1	III			
	3	17	18	18	122	N 3	III	500	2,500	
		19	18	18	122	P 1-2	III			
		27	18	18	122	P 1	III			
	3	21	18	18	122	N 2	III	600	3,000	
		23	18	18	122	N 2	III			
		24	18	18	122	N 2	III			
	2	18	18	18	122	N 3	III	600 ⁵ -1,200	±4,500 ⁵	
		20	18	18	122	N 3	III			
	2	16	18	18	122	N 2	III	1,500	7,500	
		39	18	18	122	P 1	II			
	2	30	18	18	122	N 2	III	3,000	15,000	
		38	18	18	122	P 1	II			
3	15	18	18	122	N 3	III	4,500	22,500		
	34	18	18	122	P 1	II				
		36	18	18	122	P 1	II			
1960	3	19	17	(24) ⁶	(130) ⁶	P 1	IV	0	0	
		40	17	24	130	P 1	III			
		46	17	24	130	P 1	III			
	2	17	17	(24) ⁶	(130) ⁶	N 1	IV	500	2,500	
		22	17	(24)	(130)	P 1	IV			
		16	17	(24)	(130)	P 1	IV			
	6	18	17	(24)	(130)	N 1	IV	1,500	7,500	
		25	17	(24)	(130)	P 1	IV			
		26	17	(24)	(130)	P 1	IV			
		39	17	24	130	P 1	III			
		53	17	24	130	P 1	III			
		15	17	(24)	(130)	N 1	IV			
	6	21	17	(24)	(130)	N 1	IV	3,000	15,000	
		20	17	(24)	(130)	P 1	IV			
		24	17	(24)	(130)	P 1	IV			
		30	17	24	130	P 1	IV			
		38	17	24	130	P 1	III			
		29	17	24	130	P 1	IV			
4	35	17	24	130	P 1	III	6,000	30,000		
	47	17	24	130	P 1	III				
	56	17	24	130	P 1	III				

¹ Acc. to standardised numbering of the ponds at Zabieniec (see Wolny 1962a).

² N - "normally" - every 3-5 days, P - "probing" - every 10-14 days, I - one sample taken each time (10 l from below the surface, i.e. from "pelagial" + 10 l from the near - bottom zone, treated jointly), 2 - two samples taken each time (one 10 l from the inshore zone and a second as above), 3 - three samples taken each time (one 10 l from the inshore zone, the second - 10 l from the "pelagial", the third - 10 l from the near - bottom zone).

³ Stocked towards the end of the growing season (Oct. 4th); treated as a control pond in comparison with the rest of the ponds stocked at the beginning of the growing season.

⁴ Very scanty fish stock (about 100 fish in the pond) composed of fish accidentally introduced from neighbouring ponds. Treated as control pond.

⁵ Both ponds were initially stocked with 600 specimens of fry. They were found to contain a considerable amount of fish, probably introduced accidentally, discovered during fishing operations. They were therefore treated as ponds stocked with an amount of fry greater than the initial number, assuming a middle number between the two extremes.

⁶ The so-called two-season ponds, were left fully filled for the winter. For purposes of comparison with one-season ponds Oct. 24th was accepted as the agreed date ending the 4-month growing period (this was the day on which the one - season ponds were emptied).

number of species found, the character of their dynamics, proportions between the abundance of each species (Hillbricht-Ilkowska in press). Certain regularities are, however, illustrated similarly both by data from the ponds examined frequently and from those examined less often. In these cases the results of investigations of both groups of ponds are placed near each other on one graph. In cases in which data from ponds examined every 10–14 days proved to be very fragmentary and differed greatly, this group was omitted.

A total of 2,500 samples was taken over the study period of four years.

III. GENERAL REMARKS ON THE OCCURRENCE OF EUPLANKTON AND LITTORAL *ROTIFERA* IN THE PONDS INVESTIGATED

A total of 85 species and forms of plankton *Rotifera* were found (Tab. II, III). They do not form a homogeneous ecological group – although they lead a plankton way of life in principle similar. The source of their ecological difference is primarily the type of habitat proper to them. Littoral species (48 in number – Tab. II) occur most frequently among water plants, or moving freely between plants, or keeping to the surface of the plants. Certain of them may be included in the composition of the periphyton as its active and non-settled component, e.g. *Scaridium longicaudum* (Pawłowski 1958). There are therefore species, the proper habitat of which is the littoral part of the body of water occupied by plants: they are treated as a tychoplankton element in the pelagial. Euplankton species (37 in number – Tab. III) occur in principle in the body of water free of plants, in the pelagial part of the body of water. The respective habitat – littoral or pelagial, as being characteristic of each plankton species, is noted in every modern key (Voigt 1957, Bartoš 1959, Rudescu 1960) and in monographs (Wiszniewski 1953, Pawłowski 1958). In the group of ponds examined both habitats of plankton *Rotifera* are relatively well separated in space. These are young ponds, not as yet possessing their own water plants⁴, but with inshore zone and bottom covered by land plants, forming a habitat imitating a littoral. This vegetation, which is renewed every year in the ponds and every year submerged again, often continues in good condition up to the end of the period of activity of the ponds. The mass of water beyond the inshore zone, which is not in direct contact with the bottom of the ponds, forms the “pelagial” habitat of these ponds.

The character of the occurrence in different zones of the ponds of littoral and euplankton *Rotifera* is different (Fig. 1). These differences are maintained in each of the successive years during which the ponds are kept filled, which confirms that the division of the plankton *Rotifera* into two different habitat groups is fully justified.

⁴During the study period the appearance of a small number only of stations of water plants was confirmed, in the form of small patches of *Elodea canadensis* Rich., *Phragmites communis* Trin., *Typha*, sp. and water moss.

Number of ponds examined every 3–5 days, in which the different species of littoral *Rotifera*¹ were found in consecutive years

Tab. II

No.	Group	Species	Year, no. of ponds examined			
			1957	1958	1959	1960
			6	8	10	4
1	I	<i>Lecane luna</i> (O.F. Müller) 1776	6	8	10	4
2		<i>Lecane lunaris</i> (Ehrb.) 1832	6	8	8	2
3		<i>Euchlanis dilatata</i> Ehrb. 1832	5	8	10	3
4		<i>Trichotria pocillum</i> (O.F. Müller) 1776	5	7	7	2
5		<i>Lecane closterocerca</i> (Schmarda) 1859	6	8	7	3
6		<i>Mytilina ventralis brevispina</i> Ehrb. 1832	5	7	9	1
7		<i>Trichotria tetractis</i> (Ehrb.) 1830	5	8	8	1
8		<i>Lophocharis salpina</i> (Ehrb.) 1834	6	6	4	1
9		<i>Lecane hamata</i> (Stokes) 1896	5	6	7	3
10		<i>Testudinella patina</i> (Hermann) 1783	3	6	10	3
11		<i>Lecane bulla</i> (Gosse) 1886	5	7	6	2
12		<i>Cephalodella gibba</i> (Ehrb.) 1832	5	5	3	1
13		<i>Lepadella acuminata</i> (Ehrb.) 1834	3	7	6	1
14		<i>Lepadella ovalis</i> (O.F. Müller) 1786	3	5	5	1
15		<i>Colurella uncinata</i> (O.F. Müller) 1773	1	1	7	1
16		<i>Euchlanis oropha</i> Gosse 1887	1	3	5	1
17	II	<i>Lepadella patella</i> (O.F. Müller) 1773	5	8	5	—
18		<i>Lecane</i> sp.	2	6	1	—
19		<i>Trichocerca porcellus</i> (Gosse) 1886	5	8	6	—
20		<i>Trichocerca pusilla</i> (Jennings) 1903	4	7	2	—
21		<i>Trichocerca brachyura</i> (Gosse) 1851	3	8	2	—
22		<i>Trichocerca rattus carinata</i> Ehrb. 1830 ²	4	2	3	—
23		<i>Scaridium longicaudum</i> Müller 1786	2	2	1	—
24		<i>Trichocerca rattus</i> (O.F. Müller) 1776	3	1	1	—
25		<i>Colurella uncinata</i> f. <i>bicuspidata</i> (Ehrb.) 1832	1	1	1	—
26		<i>Notommata</i> sp.	4	3	—	—
27	III	<i>Cephalodella gracilis</i> (Ehrb.) 1832	1	2	—	—
28		<i>Colurella colurus</i> (Ehrb.) 1830	4	4	—	—
29		<i>Trichocerca gracilis</i> (Tessin) 1890	1	1	—	—
30	IV	<i>Mytilina ventralis</i> Ehrb. 1832	2	—	—	—
31		<i>Trichocerca longiseta</i> (Schrank) 1802	2	—	—	—
32		<i>Epiphanes senta</i> (O.F. Müller) 1773	1	—	—	—
33		<i>Mytilina mucronata</i> (O.F. Müller) 1773	1	—	—	—
34	V	<i>Adineta</i> sp.	—	8	3	1
35		<i>Platyias quadricornis</i> (Ehrb.) 1832	—	1	1	—
36		<i>Euchlanis triquetra</i> Ehrb. 1838	—	1	2	—
37		<i>Eosphora najas</i> Ehrb. 1830	—	1	1	—
38		<i>Lecane flexilis</i> (Gosse) 1886	—	1	—	—
39		<i>Philodina roseola</i> Ehrb. 1832	—	—	2	1
40		<i>Testudinella elliptica</i> (Ehrb.) 1834	—	—	1	1

Tab. II (con.)

No.	Group	Species	Year, no. of ponds examined			
			1957	1958	1959	1960
			6	8	10	4
41	V	<i>Dissotrocha aculeata</i> (Ehrb.) 1832	—	—	1	—
42		<i>Lecane ungulata</i> (Gosse) 1887	—	—	1	—
43		<i>Platylabus patulus</i> (O.F. Müller) 1786	—	—	1	—
44		<i>Dipleuchlanis propatula</i> (Gosse) 1886	1	—	1	—
45		<i>Trichocerca bicristata</i> (Gosse) 1887	1	—	1	—
46		<i>Trichocerca tenuior</i> (Gosse) 1886	1	—	1	—
47		<i>Trichocerca tigris</i> (O.F. Müller) 1786	2	—	1	—
48		<i>Trichocerca weberi</i> (Jennings) 1903	4	1	—	1

¹ Nomenclature acc. to Voigt (1957).² Acc. to Rudescu (1960).

Number of ponds in which different species of euplankton *Rotifera*¹ were found in consecutive years

Tab. III

No.	Group	Species	Years, group of ponds no. of ponds examined					
			Ponds examined every:					
			3-5 days				10-14 days	
			1957	1958	1959	1960	1959	1960
			6	8	10	4	7	17
1	I	<i>Keratella cochlearis</i> (Gosse) 1851	6	8	10	4	7	17
2		<i>Keratella quadrata</i> (O.F. Müller) 1786	6	8	10	4	7	17
3		<i>Anureopsis fissa</i> (Gosse) 1851	6	8	8	4	1	10
4		<i>Asplanchna priodonta</i> Gosse 1850	6	7	10	4	7	14
5		<i>Polyarthra vulgaris</i> Carlin 1943	6	7	10	4	6	14
6		<i>Brachionus calyciflorus</i> Pallas 1766	5	7	10	4	6	13
7		<i>Filinia longiseta</i> (Ehrb.) 1834	5	7	10	4	6	7
8		<i>Synchaeta pectinata</i> Ehrb. 1832	5	8	10	4	6	12
9		<i>Polyarthra major</i> Burckhardt 1900	5	8	10	4	3	9
10		<i>Brachionus angularis</i> Gosse 1851	5	7	10	4	6	15
11		<i>Synchaeta oblonga</i> Ehrb. 1832	4	8	10	4	7	14
12		<i>Brachionus urceolaris</i> O.F. Müller 1773	6	7	9	2	7	7
13		<i>Asplanchna girodi</i> de Guerne 1888	4	6	8	4	4	9
14		<i>Polyarthra dolichoptera</i> Idelson 1925	3	4	2	1	1	6
15		<i>Polyarthra euryptera</i> Wierzejski 1893	2	5	5	2	3	3
16		<i>Polyarthra longiremis</i> Carlin 1943	2	5	5	1	—	8
17		<i>Hexarthra mira</i> (Hudson) 1871	6	4	1	—	—	3
18		<i>Polyarthra dolichoptera</i> f. <i>aptera</i> Idelson 1925	3	3	1	3	—	—

Tab. III (con.)

No.	Group	Species	Years, group of ponds no. of ponds examined					
			Ponds examined every:					
			3-5 days				10-14 days	
			1957	1958	1959	1960	1959	1960
			6	8	10	4	7	17
19	II	<i>Trichocerca capucina</i> (Wierzejski et Zacharias) 1893	1	2	3	—	—	—
20		<i>Notholca acuminata</i> (Ehrb.) 1832	5	2	—	—	—	1
21		<i>Synchaeta tremula</i> (O.F. Müller) 1786	3	—	—	—	—	—
22	III	<i>Conochilus hippocrepis</i> (Schrank) 1830	—	8	10	4	7	12
23		<i>Brachionus quadridentatus</i> Her- mann 1783	—	4	9	2	—	7
24		<i>Asplanchna sieboldi</i> (Leydig) 1854	—	5	6	1	1	1
25		<i>Brachionus diversicornis</i> (Daday) 1883	—	3	2	2	—	3
26		<i>Filinia brachiata</i> (Rousselet) 1901	—	2	5	1	—	1
27		<i>Notholca labis</i> Gosse 1887	—	3	2	1	—	—
28	IV	<i>Brachionus rubens</i> Ehrb. 1838	—	2	—	—	—	—
29		<i>Notholca squamula</i> (O.F. Müller) 1786	—	1	—	—	—	—
30		<i>Gastropus stylifer</i> Imhof 1891	—	1	—	—	—	1
31		<i>Asplanchna</i> sp. ²	—	—	5	2	1	—
32		<i>Collotheca mutabilis</i> (Hudson) 1885	—	—	2	—	—	1
33		<i>Trichocerca birostris</i> (Miłkiewicz) 1900	—	—	2	—	—	—
34		<i>Trichocerca cylindrica</i> (Imhof) 1891	—	—	—	1	—	1
35		<i>Synchaeta longipes</i> Gosse 1887	—	—	1	—	—	7
36		<i>Asplanchna brightwelli</i> Gosse 1850	—	—	1	—	—	—
37		<i>Argonotholca foliacea</i> (Ehrb.) 1838	—	—	—	1	—	—

¹Nomenclature acc. to Voigt (1957).²Probably *A. intermedia* Hudson 1886, a species new to Poland. Its occurrence will be further investigated.

Littoral *Rotifera* are the most abundant (both the number of species and the mean numbers of individuals) in the inshore zone, and least numerous in the "pelagial" zone. This phenomenon can be observed in all the three years in which the ponds were in operation (Fig. 1).

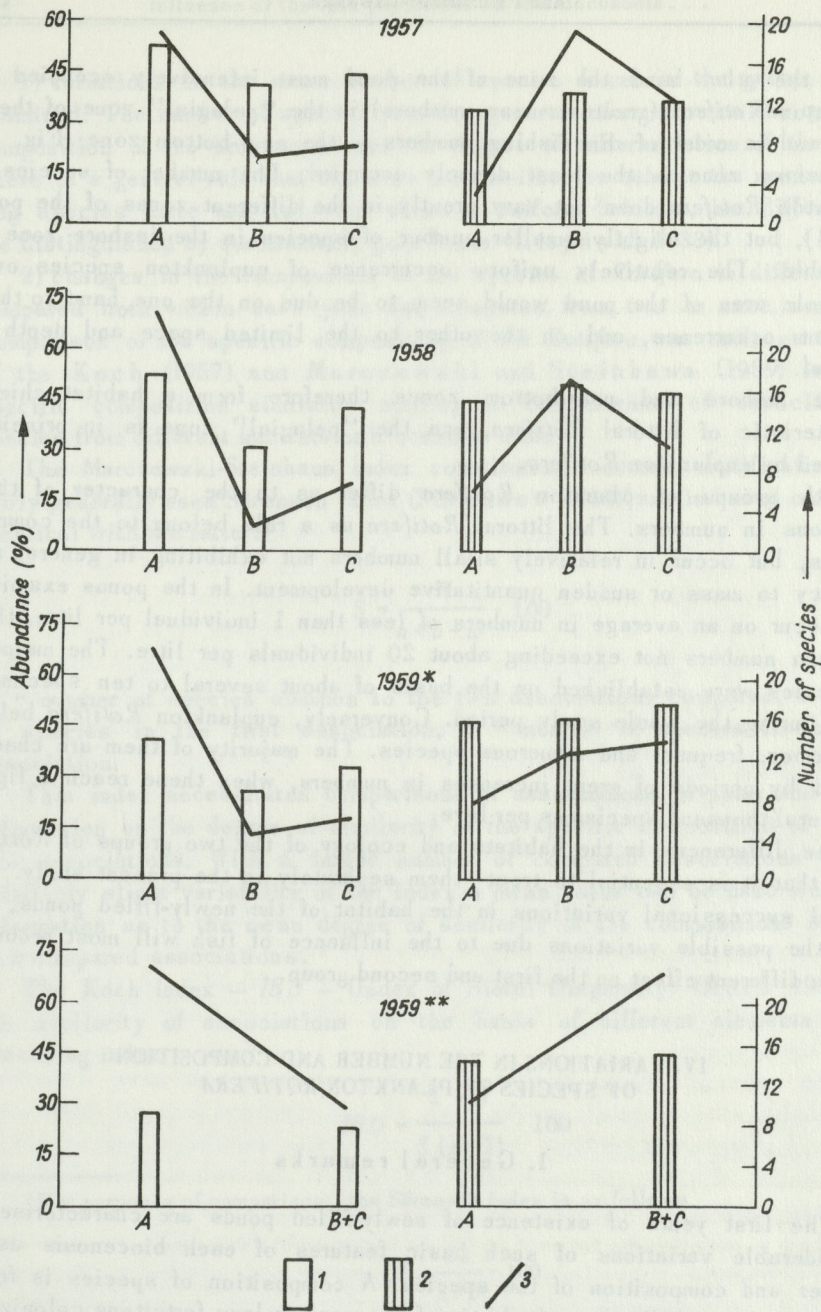


Fig. 1. Number of species and abundance (percentage of mean numbers) of littoral and euplankton rotifers

A - inshore zone, B - "pelagial" zone, C - near-bottom zone; 1 - number of littoral species, 2 - number of euplankton species, 3 - abundance

1959* - ponds from which 3 samples were taken each time, 1959** - ponds from which 2 samples were taken each time

On the other hand the zone of the pond most intensively occupied by euplankton *Rotifera* (greatest mean numbers) is the "pelagial" zone of these ponds and in order of diminishing numbers — the near-bottom zone (Fig. 1). The inshore zone is the least densely occupied. The number of species of euplankton *Rotifera* does not vary greatly in the different zones of the pond (Fig. 1), but the slightly smaller number of species in the inshore zone is noticeable. The relatively uniform occurrence of euplankton species over the whole area of the pond would seem to be due on the one hand to their abundant occurrence, and on the other to the limited space and depth of the pond.

The inshore and near-bottom zones therefore form a habitat chiefly characteristic of littoral *Rotifera*, and the "pelagial" zone is in principle occupied by euplankton *Rotifera*.

Both groups of plankton *Rotifera* differ as to the character of their variations in numbers. The littoral *Rotifera* as a rule belong to the common species, but occur in relatively small numbers not exhibiting in general any tendency to mass or sudden quantitative development. In the ponds examined they occur on an average in numbers of less than 1 individual per litre, their maximum numbers not exceeding about 20 individuals per litre. The majority of species were established on the basis of about several to ten specimens found during the whole study period. Conversely, euplankton *Rotifera* belong to common, frequent and numerous species. The majority of them are characterised by periods of great increases in numbers, when these reach a figure of several thousand specimens per litre.

The differences in the habitats and ecology of the two groups of *Rotifera* show that it is essential to treat them separately in the present study. The natural successional variations in the habitat of the newly-filled ponds, and also the possible variations due to the influence of fish will most probably have a different effect on the first and second group.

IV. VARIATIONS IN THE NUMBER AND COMPOSITION OF SPECIES OF PLANKTON *ROTIFERA*

1. General remarks

The first years of existence of newly-filled ponds are characterised by considerable variations of such basic features of each biocenosis as the number and composition of the species. A composition of species is formed and becomes stabilised on the basis of the more or less fortuitous colonization of species.

In order to describe this aspect of succession the following were taken as bases:

1) variations in the mean number of species found in the group of ponds examined. The number of species provides general information on the qualitative composition of the biocenosis and the degree of differentiation of the habitat. There is a general rule that the more mosaic-like the habitat the more co-occurring species there are and vice versa – uniform habitats, not differentiated, are distinguished by qualitatively poor fauna (Lityński 1938).

2) changes in the composition of the species of *Rotifera* in different ponds compared both within each year and compared from two or more such years. Comparison of the specific composition of the *Rotifera* was made on the basis of the Koch (1957) and Marczewski and Steinhaus (1959) indices of specific composition similarity applied to comparisons of associations of species from different habitats or biocenotic units.

The Marczewski-Steinhaus index constitutes a certain modification of the fairly generally used Sørensen index (Sørensen 1948)⁵ and is based on elements identical with the latter:

$$S = \frac{w}{a+b-w} \cdot 100$$

w = number of species common to the two associations compared, a = number of species in the first association, b = number of species in the second association.

This index necessitates comparisons of associations in pairs and provides information on the degree of similarity of the specific composition of the given two associations. With a larger number of compared associations and with relatively slight variability of the index a mean value can be used which gives information as to the mean degree of similarity of the compositions of species in n compared associations.

The Koch index – *IBD* – (Index of Biotal Dispersity) (Koch 1957) treats the similarity of associations on the basis of different elements from the preceding index:

$$IBD = \frac{T - S}{S(n-1)} \cdot 100$$

⁵For purposes of comparison: the Sørensen index is as follows

$$QS = \frac{2c}{a+b} \cdot 100$$

where $c = w$ in the Marczewski and Steinhaus index, a and b as above.

In my material the Sørensen index exhibits variations completely parallel to the variations in the Marczewski-Steinhaus index. The Marczewski-Steinhaus index is identical with the old Jaccard index. I decided to use it in the present study in the form described by Polish authors.

T = arithmetical sum of species occurring in n compared associations, S = total number of species (list of species) found in n compared associations, n = number of associations compared.

This index gives the way in which S species are distributed in n habitats examined. If a quite different group of species occurs in each habitat, then the degree of their dispersity equals 0 per cent, which means that each habitat has a different specific composition and each species from the joint list of S species is limited to one place. If, conversely – all the habitats have an identical specific composition ($S_1 = S_2 \dots = S_n = S$) then the index of dispersity equals 100%. This index has the advantage over the former in that by using it more than two associations can be compared at one time.

These indices were calculated for: 1) one-year ponds. In this case the index gives information as to similarity, that is, the degree of equalisation of the specific composition of *Rotifera* in a given year, 2) of ponds from different years (e.g. of "neighbouring" years). Ponds investigated in two or more years were combined in one group and the index calculated for the whole group. The index calculated in this way provides information as to the specific composition similarity of ponds within the years compared, that is, indirectly as to variations in the composition of the *Rotifera* species, which took place in the unit of time compared. Considerable differences in the composition of the *Rotifera* fauna will be reflected in the low indices of similarity, while an equalled and similar composition of species of *Rotifera* will accompany high indices.

The use of two indices to describe one phenomenon is intended to eliminate any possible deformations which each index might introduce separately.

Only data from ponds inspected every 3–5 days were used in calculating the above indices. The ponds "probed" (every 10–14 days) were omitted from this analysis on account of the very scanty and varied material. When samples were taken as infrequently as every 10–14 days, 30–50% of the species, especially the rarer and less numerous ones, were not found (Hillbricht-Ilkowska in press).

In the case of littoral *Rotifera* it proved necessary to make a parallel, double analysis – separately on the basis of data obtained from all three zones of the pond represented by three or two samples taken each time, and separately on the basis of data obtained from one sample (or two combined as one) representing two zones of the pond – the near-bottom and "pelagial" zones. This makes it possible to include in the analysis data from 1960, when samples were taken from two zones only of the pond (represented jointly by one sample) and to compare them with data from the previous years, when samples were taken from all three zones of the pond.

This type of differentiation of the material would not, on the other hand, appear to be essential in the case of euplankton *Rotifera*, at least not as far

as the composition of their species is concerned, since the number and composition of euplankton species found in samples from the inshore, near-bottom and "pelagial" zones were not observed to differ greatly (Fig. 1).

2. Variations in the number of species

Variations in the number of species of littoral and euplankton *Rotifera* take a different, even opposite, course in consecutive years (Fig. 2).

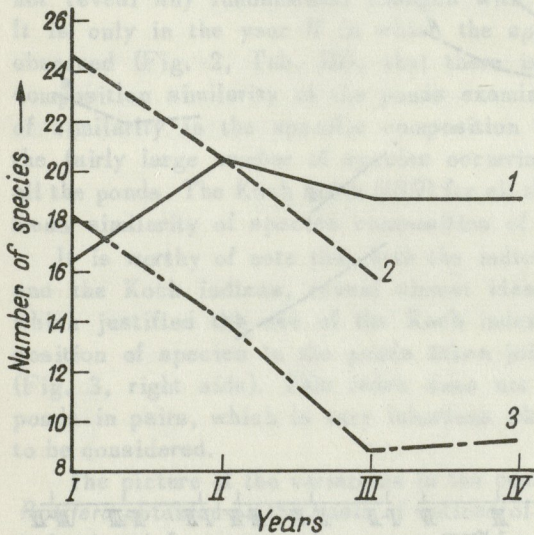


Fig. 2. Variations in the mean number of species of rotifers in successive years

1 - euplankton species, 2 - littoral species (on the basis of data from all the zones of the pond), 3 - littoral species (on the basis of data from the "pelagial" and near-bottom zones)

The number of littoral species decreases with the passage of years; a particularly distinct decrease occurs in the years II and III. The number of euplankton species, on the other hand, increases in the year II, after which it is maintained at a constant level. Two periods may therefore be distinguished from the aspect of variations in the number of species - the first (years I and II) which is characterized by sharp variations both within the littoral *Rotifera* (decrease in numbers) and within the euplankton *Rotifera* (increase in numbers) and the second (years III and IV) which is characterized by the relative stabilisation of a large number of euplankton species and a small number of littoral species.

The disappearance of littoral species would seem to depend on intensity of the use of the ponds examined for fishery purposes, since particularly few species occur in the years III and IV in which the ponds were stocked with fish populations differing greatly in density. The fish population destroying plants most probably eliminates the original mosaic-like cha-

acter of the pond habitat formed by vegetation and thus narrows down the variety in the habitat conditions of littoral *Rotifera*.

The stabilised conditions in the free body of water (constant inwards flow and relatively slight fluctuations in water level) most probably constitute, beginning with the *II* year, the factor favouring permanent occurrence by euplankton species.

3. Variations in the composition of species

Variations in the composition of the species forming the two groups of *Rotifera* "measured" by indices of species composition similarity are different for euplankton and littoral species (Fig. 3).

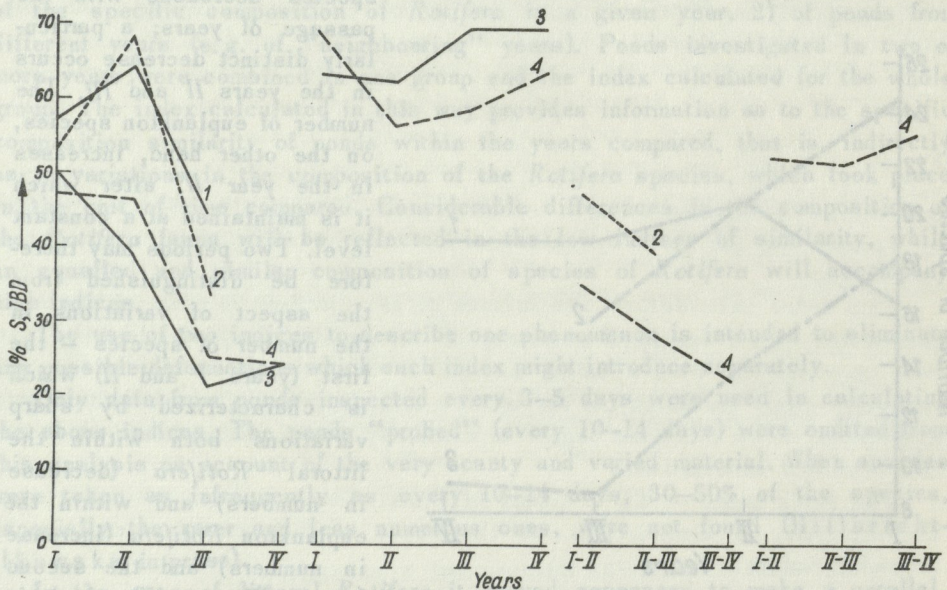


Fig. 3. Variations in indices of similarity of specific composition: Marczewski-Steinhaus (S) and Koch (IBD) of littoral and euplankton rotifers, for ponds in consecutive years and "pairs" of years

1, 2 - on the basis of data from all the zones of the pond, 3, 4 - on the basis of data from the "pelagial" and near-bottom zones

In the case of littoral *Rotifera*, ponds in the year *I* and year *II* exhibit greater similarity in the composition of species than in the *III* and *IV* years (Fig. 3). This same regularity can be seen when comparing the specific composition of ponds from "neighbouring" years (Fig. 3). Therefore years *I* and *II* constitute a period of relatively uniform occurrence of littoral *Rotifera*. A relatively large number of species occur everywhere in the group of ponds

studied during this period. Fundamental changes would appear to take place during the III year, when the number of species decreases and as a result of their disappearance the specific composition of ponds becomes increasingly different. The Koch index (*IBD*) for all the ponds in the years I, II and III (on the basis of data from the inshore, "pelagial" and near-bottom zones) is 37.2%, while it is 21.8% for all the ponds in all the years (on the basis of data from the two latter zones). This is evidence of the relatively small mean similarity of species composition of all the ponds during the study period.

The similarity of the specific composition of littoral *Rotifera* is smaller when we analyse "pelagial" and near-bottom samples, and increases when data from the inshore zone are added to the analysis — that is, from the zone most densely occupied by the littoral rotifers (Fig. 3).

The specific composition similarity of euplankton *Rotifera* is considerable both for ponds in the following year and from "neighbouring" years, and does not reveal any fundamental changes with the passage of the years (Fig. 3). It is only in the year II in which the appearance of many new species was observed (Fig. 2, Tab. III), that there is a slight decrease in the specific composition similarity of the ponds examined. The high values of the indices of similarity in the specific composition of the euplankton *Rotifera* point to the fairly large number of species occurring continuously in all the years and all the ponds. The Koch index (*IBD*) for all the ponds in all the years, that is the mean similarity of species composition of the ponds, is 54.3% for this group.

It is worthy of note that both the indices used — the Marczewski-Steinhaus and the Koch indices, reveal almost identical variations (Fig. 3, left side), which justified the use of the Koch index only for a description of the composition of species in the ponds taken jointly from different "pairs" of years (Fig. 3, right side). This index does not make it necessary to compare the ponds in pairs, which is very laborious when there is a large number of ponds to be considered.

The picture of the variations in the composition of species in both groups of *Rotifera* obtained on the basis of indices of species composition similarity, filled in by data informs as to the occurrence of each species (Tab. II, III). The species were arranged in order of degree of continuing and common occurrence in the group of ponds examined. Group I of littoral *Rotifera* (Tab. II) includes 16 species occurring in all the study years, only one species of which, *Lecane luna*, occurs in all the years and all the ponds. This is the most numerous and commonest species of all the littoral species. This group constitutes only 32% of the list of littoral *Rotifera* found in the group of ponds examined. Group II of littoral rotifers includes 10 species occurring only during the three first study years, and in general only in some of the ponds. Group III includes three species encountered only in the first two study years, and group IV — 4 species encountered only in the first year. As a rule these are species found only in one or two ponds. The remaining 14 species (group V)

were found in numbers from one to approximately five specimens in one or two ponds.

Of the 37 euplankton species found during the study period as many as 18 (Tab. III – group I), that is, about 50% of the list of species found, occur in all the years, and of this number 11 species – in all or almost all the ponds examined. A relatively small number of species – only 3 (group II) occur in years I, II and III, or I and II, or in year I. Six species (group III) which appeared in the year II, including such common species as *Conochilus hippocrepts* and *Brachionus quadridentatus*, generally participate continuously in the composition of the biocenosis of each pond and continue up to the end of the study period. Sporadic species, appearing in the later study years, were included in group IV.

4. Fish stock and the number and composition of Rotifera species

In the foregoing consideration ponds examined in consecutive years were treated jointly regardless of their fish stock. This is justified by the absence of a connection between the size of the fish stock and variations in the number

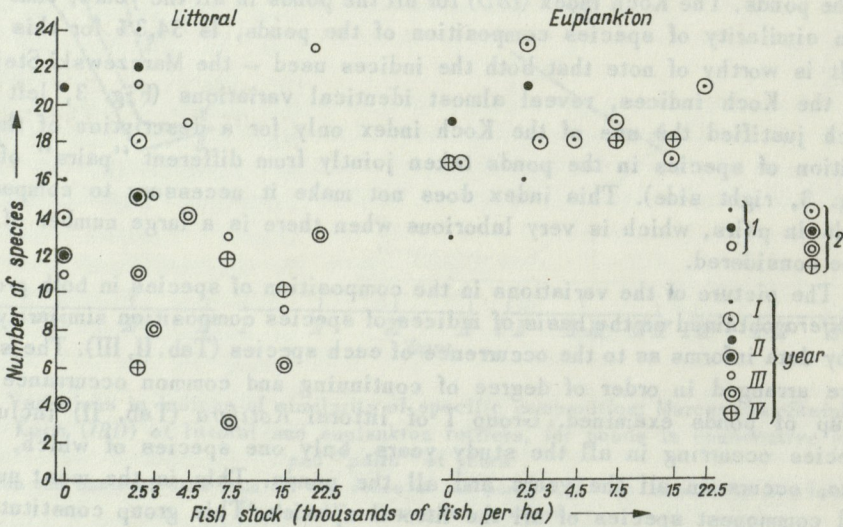


Fig. 4. Number of species of littoral and euplankton rotifers in ponds with different density of fish stocking

1 – on the basis of data from all zones of the pond, 2 – on the basis of data from the “pelagial” and near-bottom zones

and composition of the *Rotifera* species in ponds in one year (Fig. 4). Within the ponds of the same year the littoral species exhibit generally greater

variations, and the euplankton rotifers considerable similarity in the number of species. The absence of indicator species for different stocks would seem to be understandable; since *Rotifera* belong chiefly to eurytopic and ubiquitous species and generally there are no species among them with so narrow an ecological tolerance that it could indicate habitat differences caused by fish stock of different density. The species found in the group of ponds studied are generally characteristic of fertile, eutrophic habitats. One fact is worthy of note, that certain species known from fertile habitats (Pejler 1957) such as *Brachionus diversicornis*, *B. quadridentatus*, *Conochilus hippocrepis*, *Trichocerca birostris*, *Tr. cylindrica* appear in the later study years – the year III or IV (Tab. III), that is, during a period of advanced fish culture.

V. VARIATIONS IN THE QUANTITATIVE OCCURRENCE OF PLANKTON *ROTIFERA* AS THE RESULT OF NATURAL SUCCESSIONAL CHANGES AND OF THE INFLUENCE OF THE FISH POPULATION

The quantitative occurrence of both groups of plankton *Rotifera* exhibits directional changes with the passage of years and with the increase in density of the fish population.

1. The quantitative occurrence of littoral *Rotifera*

The mean abundance of littoral *Rotifera* in the ponds examined is in general low – being approximately several individuals per litre (Fig. 5). This the result

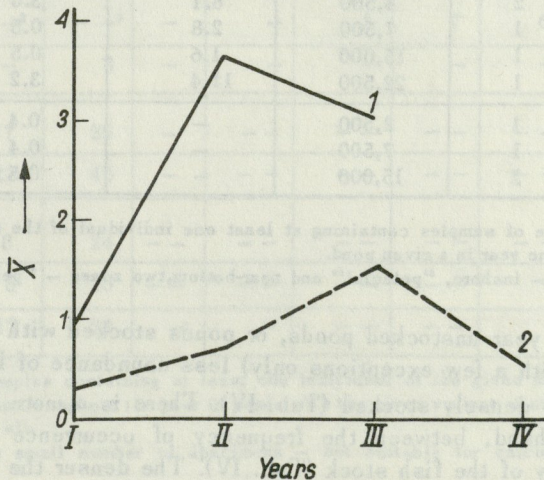


Fig. 5. Variations in mean numbers (\bar{X} – specimens/litre) of littoral rotifers in consecutive years (data from ponds examined every 3–5 days)
1 – inshore zone, 2 – “pelagial” zone

of the very sporadic and scanty occurrence of the species in the group⁶. The numbers of these species do, however, exhibit variations with the passage of time – in the “pelagial” zone continuous increase is observed in the three first years and a decrease in the year *IV*, in the inshore zone a very marked increase in the second year, followed in the year *III* by a slight drop in numbers (Fig. 5). As no data are available for the inshore zone during the year *IV* it is difficult to state whether the decrease observed in the “pelagial” zone affects the inshore zone as well. It would, however, seem probable, judging by the general disappearance of the littoral species, that their numbers decrease in the inshore zone as well in the study year *IV*.

Mean numbers (\bar{X}) and mean frequency¹ of occurrence in time (*F*)
of littoral *Rotifera* in ponds containing different fish stocks

Tab. IV

Year	No. of ponds	Fish stock, fish per hectare	\bar{X} – specimens per litre		<i>F</i> – per cent
			three zones of pond ²	two zones of pond ²	
<i>I</i>	2	0	–	0.5	57
	4	2,500	1.5	0.7	83
<i>II</i>	2	0	4.1	2.5	55
	4	2,500	5.2	1.4	86
<i>III</i>	1	0	0.5	0.1	27
	1	2,500	3.2	1.2	67
	3	3,000	3.3	1.1	53
	2	4,500	8.1	3.0	64
	1	7,500	2.8	0.5	53
	1	15,000	1.6	0.5	79
	1	22,500	11.4	3.2	84
<i>IV</i>	1	2,500	–	0.4	10
	1	7,500	–	0.4	28
	2	15,000	–	0.5	31

¹As percentage of samples containing at least one individual of the total number of samples taken throughout one year in a given pond.

²Three zones – inshore, “pelagial” and near-bottom, two zones – “pelagial” and near-bottom.

Within one year unstocked ponds, or ponds stocked with a smaller number of fish exhibit (with a few exceptions only) less abundance of littoral *Rotifera* than the ponds more densely stocked (Tab. IV). There is a more distinct correlation, on the other hand, between the frequency of occurrence of littoral *Rotifera* and the density of the fish stock (Tab. IV). The denser the fish stock, the more often the littoral rotifers appear in samples, which means that their occurrence

⁶On this account data for the ponds “probed” were omitted from this analysis.

is more continuous during the period that the pond is being used. Of course the absolute values for the given size of fish stock differ every year, for instance density of fish stocking of 2,500 fish per hectare in the year II corresponds to a frequency of occurrence of littoral rotifers like that in the year III – when the stock is 10 times larger. Frequency several times smaller than in the year III corresponds to fish stocks of 7,500 fish per hectare and 15,000 fish per hectare in the year IV. In 1960 (year IV) the frequency of encountering littoral rotifers is in general several times smaller than in the preceding years, which would seem to be the reflection of the decrease in their numbers referred to above. Despite the fundamental differences in the absolute values of frequency of occurrence of littoral rotifers, however, the above relation is present in each year in which a different fish stock is introduced.

Dependence of the frequency of occurrence (in percentages)¹ of several of the more numerous littoral species on the size of the fish stock

Tab. V

Species	Year, fish stock – (fish per hectare)								
	II		III						
	0	2,500	0	2,500	3,000	4,500	7,500	15,000	22,500
<i>Lecane luna</i>	21	54	15	15	19	33	22	25	34
<i>Euchlanis dilatata</i>	26	39	9	39	25	20	37	25	31
<i>Testudinella patina</i>	2	16	3	21	17	24	12	54	37
<i>Colurella uncinata</i>	— ²	— ³	—	—	3	7	6	3	9
<i>Colurella colura</i>	—	8	—	—	—	—	—	—	—
<i>Lecane closterocerca</i>	17	25	—	—	—	—	—	—	—
<i>Lecane lunaris</i>	23	46	—	—	—	—	—	—	—
<i>Mytilina ventralis brevispina</i>	8	24	—	—	—	—	—	—	—
<i>Lecane hamata</i>	6	10	—	—	—	—	—	—	—
<i>Adineta</i> sp.	17	24	—	—	—	—	—	—	—

¹As per cent of samples containing at least one individual of the given species, of the total number of samples taken throughout the year in ponds with the given variant of stocking.

²Does not occur at all.

³Found only in a small number of specimens – not suitable for calculating frequency of occurrence.

This regularity is also observable when analysing different (more numerous) species (Tab. V). Data from 1957 and 1960 can be overlooked since they are

very fragmentary in the light of data on particular species (numbers below 1 specimen per litre). The species given (Tab. V) in general prove the above rule that the fish stock increases the frequency of occurrence of littoral *Rotifera*.

2. The quantitative occurrence of euplankton *Rotifera*

The character of the quantitative occurrence of euplankton rotifers differs completely from that of the occurrence of littoral rotifers, and is distinguished primarily by a tendency to intensive quantitative development.

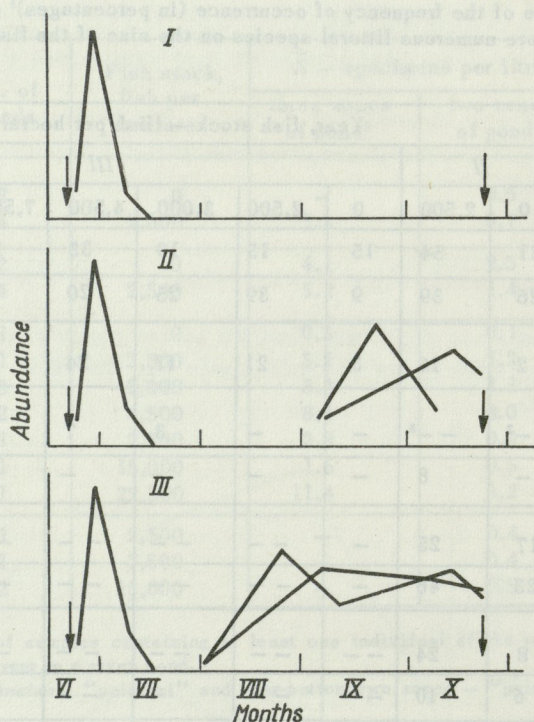


Fig. 6. Types of variations in numbers (I–III) of euplankton rotifers during a four-month period of activity of the ponds (periods in which rotifers occur in numbers of at least twenty-seven tens individuals per litre and create a distinct peak of abundance have been taken into consideration)

– filling or emptying the pond

Three types of variations in numbers of the euplankton *Rotifera* of the ponds can be distinguished within each year (Fig. 6). Type I – one peak of abundance

is observed at the end of June or beginning of July, a few days after the ponds are filled. This period of mass development is generally of short duration, lasting at most only to mid-July. This is the spring peak of the abundance of the rotifers. Type II – two peaks of abundance are observed – the one described above – the spring one, and also the autumn peak occurring during the September-October period. Type III – three peaks of abundance are observed. In addition to the peaks described above there is a third during the period between the end of July and August, which may combine with the autumn peak. This is the summer peak.

An element common to all three types of variations in numbers is the spring peak. This means that in all the study years the *Rotifera* appear in great numbers in the ponds a short time after the latter have been filled. The mass occurrence of rotifers in temporary bodies of water, refilled with water every year during the spring, is a fairly common phenomenon (Mirošničenko 1955, Bragin-skiĵ 1957a, 1957b, Kosova 1960) and a typically spring aspect of the life of these waters. The fish stock is introduced into the ponds examined every year about 7 days after the ponds have been filled, which means that the spring mass development of *Rotifera* takes place de facto in a pond not as yet stocked with fish.

Variations in the abundance of euplankton *Rotifera* taking place during the spring period in consecutive study years may therefore be considered as a manifestation of natural successional changes, not controlled (or at least not directly so) by the current fish stock. The quantitative development of euplankton *Rotifera* outside the spring period – in August, September and October, takes place in a pond fully utilised by the fish population and any possible successional changes will be concealed by the influence exerted by the current fish stock. Data from this period may therefore be used only to illustrate the “fish population-euplankton *Rotifera*” correlation.

The length of the period from the time at which the pond is filled to the time of numerous appearance of *Rotifera* is subject to relatively small variations with the passage of time (Tab. VI). *Rotifera* occur abundantly in all ponds each study year as early as the 4th-6th day after filling the ponds, regardless of the calendar date of filling (Tab. I).

In the year I in two of the six ponds studied, the rotifers did not occur in the form of a distinct peak in numbers. Differences of this kind during the year I following the filling of the ponds, when hydrological conditions were not as yet stable, would seem to be completely understandable. In years II and III almost complete equalisation of the duration and time of the spring appearance of rotifers was observed. This is probably an expression of the relatively uniform conditions prevailing in the ponds at the start of their annual growing season.

It would also appear that the drop in the abundance of rotifers after the spring development period is not hastened by the fish stock, since otherwise

we should observe a more rapid decrease when fish stocks were larger and as a result a shorter period of the mass development of *Rotifera*.

The abundance of euplankton rotifers during the spring peak period is, on the other hand, characterized by a continued increase in every consecutive year (Tab. VI). These variations would seem to indicate that the initial fertility of the annually renewed pond increases with the lapse of time.

Calendar time, duration of appearance (t) and mean numbers (\bar{X}) of euplankton *Rotifera* during the spring

Tab. VI

Group of ponds	Year	No. of ponds	Period from pond filling to appearance of <i>Rotifera</i> (in days)	Calendar time	t in days	\bar{X} specimens per litre
Examined every 3-5 days	I	4 ¹	(5) ²	(July 3 - 30)	(3- 4 weeks)	106.0
	II	6 ³	6	July 1 - 15	9-15	196.0
	III	10	4	June 22-July 1	10	274.7
	IV	4	6	June 24-July 18	18-24	541.5
Every 10-14 days	III	7	4	June 22-July 4	10-13	176.8
	IV	17	6	June 24-July 14	11-21	420.2

¹Two ponds, in which *Rotifera* did not occur in the form of a distinct peak of numbers, were omitted.

²Data in brackets are not exact for this year. During this year the ponds were filled at different times (Tab. I), while the first samples were taken in the first days of July, that is, from 5-21 days after the ponds had been filled. The ponds from which samples were taken after 5 days from date of filling contained *Rotifera* occurring in large numbers. Data in brackets refer to these ponds.

³Two ponds omitted (Tab. I) which were filled a month later than the others.

The duration of the periods of abundant⁷ occurrence and the numbers of euplankton rotifers beyond the spring period, that is, during the remaining three months (August-October) is positively correlated with the size of the fish stock (Fig. 7). A similar correlation, although not so regular, is exhibited by variations in average abundance (Fig. 8). In this case also, however, ponds with a stock of 2,500 fish per hectare have a smaller mean abundance of euplankton rotifers than ponds with a stock of 3,000-15,000 fish per hectare, and these latter, a smaller mean figure than ponds with a stock of 22,500 fish per hectare.

Rotifera do not appear in any large numbers up to the end of the growing season in the ponds left in each study year as control ponds⁸, that is, not

⁷Periods in which rotifers occur at least in numbers from approximately ten to several scores of individuals per litre, and form a distinct peak in numbers, have been taken into consideration.

⁸An exception here is the one pond "probed" out of the 17 ponds examined in the year III.

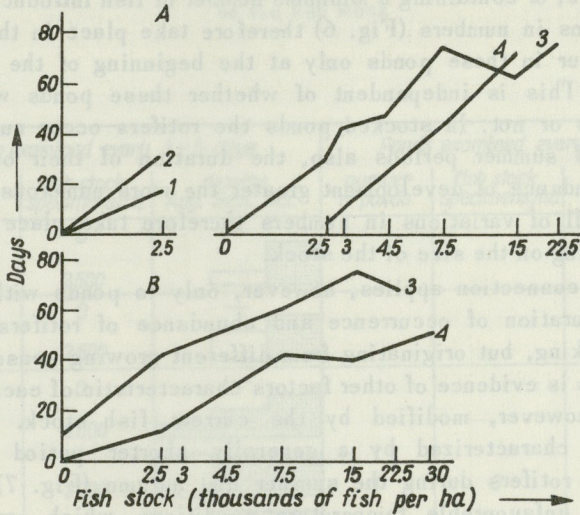


Fig. 7. Dependence of long-continuing abundant occurrence (in days) of euplankton rotifers during the period of August, September and October on the size of the fish stock

A - for ponds examined every 3-5 days; B - for ponds examined every 10-14 days, 1 - I year, 2 - II year, 3 - III year, 4 - IV year

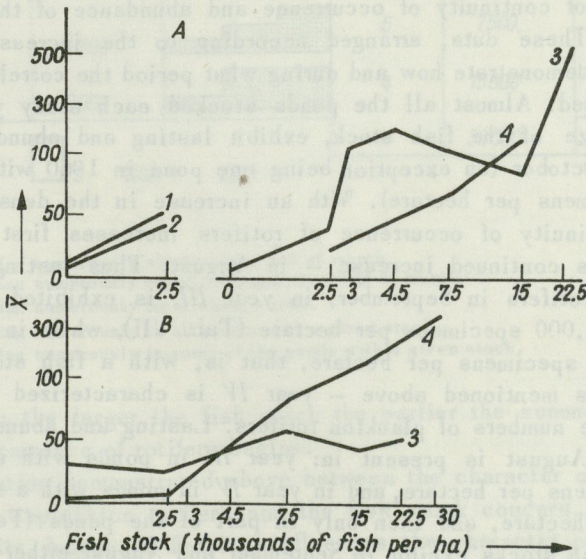


Fig. 8. Dependence of mean numbers (\bar{X} - specimens/litre) of euplankton rotifers during the period of August, September and October on the size of the fish stock

A, B, 1, 2, 3, 4, - see Fig. 7

stocked with fish, or containing a minimum number of fish introduced accidentally. Type I variations in numbers (Fig. 6) therefore take place in these ponds, that is, rotifers occur in these ponds only at the beginning of the growing season of the ponds. This is independent of whether these ponds were stocked in preceding years or not. In stocked ponds the rotifers occur numerously during the autumn and summer periods also, the duration of their occurrence being longer and abundance of development greater the more numerous the fish stock. Types II and III of variations in numbers therefore take place in these ponds (Fig. 6) depending on the size of the stock.

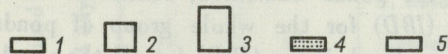
The above connection applies, however, only to ponds within one growing season. The duration of occurrence and abundance of rotifers in ponds with analogical stocking, but originating from different growing seasons, is different (Fig. 7, 8). This is evidence of other factors characteristic of each year, the effect of which is, however, modified by the current fish stock. The year *IV* in particular was characterized by a generally shorter period of quantitative development of rotifers during the summer and autumn (Fig. 7). Probably this is due to the unfavourable temperature conditions which prevailed in 1960 (Wolny 1962a).

The data given in the figure (Fig. 7) represent the summarised number of days of abundant occurrence of rotifers during the period of the three months (August to October), while the table (Tab. VII) represents the detailed description of the quantitative occurrence of euplankton rotifers in these three months. Three degrees of continuity of occurrence and abundance of the rotifers were distinguished. These data, arranged according to the increasing density of the fish stock, demonstrate how and during what period the correlation described above is realised. Almost all the ponds stocked each study year, irrespective of the size of the fish stock, exhibit lasting and abundant occurrence of rotifers in October (an exception being one pond in 1960 with a fish stock of 2,500 specimens per hectare). With an increase in the density of the fish stock the continuity of occurrence of rotifers increases first in September, then — with its continued increase — in August. Thus lasting and abundant occurrence of rotifers in September, in year *III*, is exhibited by ponds with a stock of $\geq 3,000$ specimens per hectare (Tab. VII), while in year *IV*, those with $\geq 15,000$ specimens per hectare, that is, with a fish stock three times greater. As was mentioned above — year *IV* is characterized by a generally low level of the numbers of plankton rotifers. Lasting and abundant occurrence of rotifers in August is present in: year *III* in ponds with a fish stock of $\geq 7,500$ specimens per hectare, and in year *IV* in ponds with a stock of 30,000 specimens per hectare, and then only in part of the ponds (Tab. VII). Ponds with smaller fish stocks exhibit in September and August either non-continuous occurrence of rotifers or the euplankton rotifers occur continuously and numerously only in one or two ponds belonging to these stocks. As the fish stocks increase, however, the ponds become increasingly similar from the aspect of the quantitative character of occurrence of the rotifers.

Dependence of the time of abundant occurrence of euplankton rotifers on the fish stock

Tab. VII

Year	Ponds examined every 3-5 days			Ponds examined every 10-14 days		
	number of ponds	fish stock specimens/ha	months Aug. Sept. Oct.	number of ponds	fish stock specimens/ha	months Aug. Sept. Oct.
I	2	0	—			
	4	2500				
II	2	0	—			
	4	2500				
III	1	0	—			
	1	2500				
	3	3000		1	0	
	2	4500		2	2500	
	3	7500 22500		4	7500 22500	
IV				3	0	—
	1	2500		1	2500	
	1	7500		5	7500	
	2	15000		4	15000	
				4	30000	



- 1 - rotifers occurring numerous shorter than half of month,
- 2 - rotifers occurring numerous equal or longer than half of month,
- 3 - rotifers occurring numerous for a whole month,
- 4 - rotifers occurring numerous in all ponds with a given stock,
- 5 - rotifers occurring numerous in some of the ponds with a given stock.

To sum up: the larger the fish stock the earlier the summer-autumn period of abundant occurrence of rotifers begins.

The correlation demonstrated above between the character of the occurrence of littoral and euplankton rotifers and the fish stock concurs. The fish stock, depending on its degree of density, influences the character of the occurrence of species in the first and second ecological group. This influence is exerted through such a change in habitat conditions in the ponds as permits of the more frequent occurrence of littoral rotifers and of the extension of the period of abundant occurrence and higher quantitative level of euplankton rotifers.

VI. VARIATIONS IN THE STRUCTURE OF SEASONAL ASSOCIATIONS
OF EUPLANKTON *ROTIFERA* AS THE RESULT OF SUCCESSIONAL CHANGES
AND OF THE INFLUENCE OF THE FISH POPULATION

There are differences in the species interrelations of euplankton rotifers occurring during the spring, summer and autumn periods. These differences are evident primarily in the quantitative relations and dominating species, and to a lesser degree, in the number and composition of species. In the spring, summer and autumn period different associations of euplankton rotifers occur which differ as to their domination structure. By domination structure of an association is meant the number of species dominating and their relative abundance. The domination structure of all three associations undergoes directional changes with the passage of years and also changes correlated with the current density of the fish stock. The general trend of both types of changes may be described as follows: a tendency to uniformity and more sharply marked quantitative relations within one association as the result of the quantitative development of a defined species.

1. Variations in the structure of the spring associations

The composition of the species in the spring association is subject to relatively slight changes with the lapse of years. The mean number of species per pond is: year *I* - 12.2 (range 11-14), year *II* - 15.1 (range 14-17), years *III* and *IV* - 14.0 (range for both years 12-17). In year *II* a distinct increase therefore takes place in the number of species, in year *III* a slight decrease and continued stabilisation on a level of about 14 species. Species occurring during this period - commonly occur in the ponds examined, since the Koch index of species composition similarity (*IBD*) for the whole group of ponds examined is about 60% each year. The mean Koch index (*IBD*) for all the ponds in all the study years was 47%, that is, during the spring period, after the ponds have been filled, a relatively large group of the same species appears in all the ponds in all the study years.

The composition and percentage of dominating species which determine the structure of the association during this period, is subject to significant directional changes (Tab. VIII).

With the passage of years the composition of the dominant species in the group of ponds studied tends to become uniform (Tab. VIII). In years *I* and *II* the spring association varied fairly considerably in different ponds: the list of dominating species for the whole group of ponds is fairly long, which means that in general different species dominate in each pond. The mean number of co-dominants in each pond is also fairly large (in comparison with subsequent years), being two or more species. In year *III* the degree of differentiation in the composition of dominants in the ponds examined markedly decreases. The list of dominants is shortened to 1/3 of the original length, while the

List, total number (S) and mean number (\bar{X}) of euplankton species dominating¹ during the spring period in consecutive years

Tab. VIII

Group of ponds	Year	Number of ponds	Species	S	\bar{X}
Examined every 3-5 days	I	4	<i>Anureopsis fissa</i> <i>Asplanchna priodonta</i> <i>Brachionus angularis</i> <i>Keratella cochlearis</i> <i>Polyarthra maior</i> <i>Synchaeta oblonga</i>	6	2.0
	II	6	<i>A. fissa</i> <i>As. girodi</i> <i>As. sieboldi</i> <i>B. calyciflorus</i> <i>Filinia longiseta</i> <i>K. cochlearis</i> <i>Hexarthra mira</i> <i>Polyarthra vulgaris</i> <i>S. oblonga</i>	9	2.6
	III	10	<i>B. calyciflorus</i> <i>K. cochlearis</i> <i>S. oblonga</i>	3	1.8
	IV	4	<i>K. cochlearis</i> <i>P. vulgaris</i>	2	1.2
Examined every 10-14 days	III	7	<i>K. cochlearis</i> <i>S. oblonga</i>	2	1.3
	IV	17	<i>Conochilus hippocrepis</i> <i>K. cochlearis</i> <i>P. vulgaris</i> <i>S. oblonga</i>	4	1.2

¹The abundance of which was more than 20% of the total numbers of euplankton *Rotifera*, at least in one pond.

mean figure falls to < 2.0 . A further reduction both in the list of dominants and in the mean number of dominants per pond is revealed in year IV, in which the dominant is generally one species only in all the ponds examined in the spring period.

One of the dominants during the spring in all the study years is the species *Keratella cochlearis* (Tab. VIII). With the lapse of years its numbers increase, also its percentage in the spring association of euplankton rotifers (Fig. 9). Two periods can be distinguished during this process: in years I and II this species occurs in small numbers and its mean percentage for the whole group of ponds is very small (several per cent), in years III and IV its numbers rise

sharply with a corresponding increase of the percentage. In year *IV* this species dominates in all the ponds, forming on an average 60–70% of the total numbers of rotifers (Fig. 9).

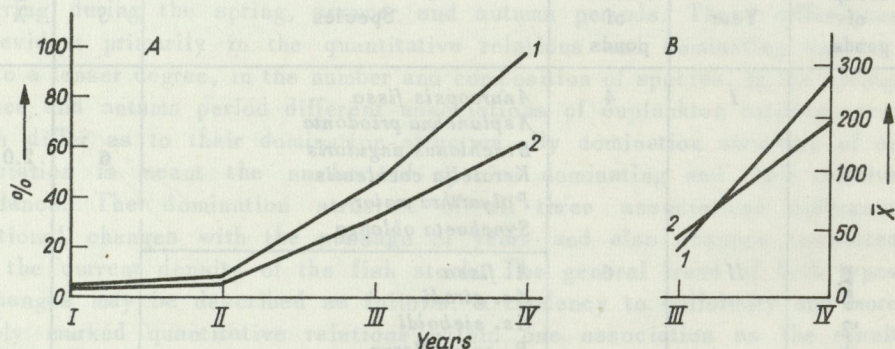


Fig. 9. Variations in mean numbers (\bar{X} – specimens/litre) and mean percentage of *Keratella cochlearis* during the spring in consecutive years
A – for ponds examined every 3–5 days, B – for ponds examined every 10–14 days; 1 – mean numbers, 2 – percentage

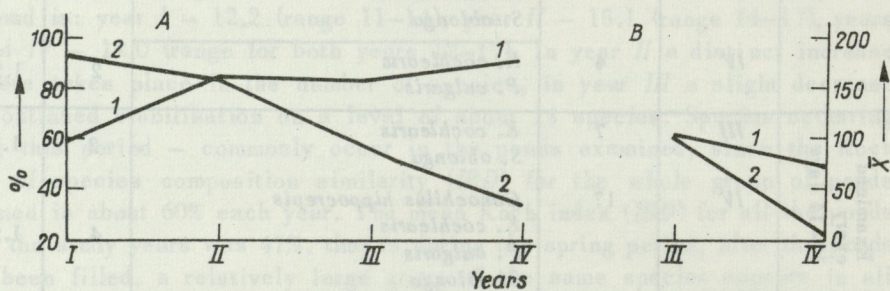


Fig. 10. Variations in mean numbers (\bar{X} – specimens/litre) and mean percentage of dominating species (apart from *Keratella cochlearis* – see Tab. VIII) during the spring in consecutive years
A, B, 1, 2, see Fig. 9

The gradual predomination of *K. cochlearis* in the spring association is accompanied by the disappearance of species from the list of those dominating in years *I* and *II* (Tab. VIII), despite the fact that these species exhibit a slight increase in numbers with the lapse of time (Fig. 10 – data for ponds examined every 3–5 days). The only species which maintains an analogical position to that of *K. cochlearis*, that is, the numbers and percentage of which increase with the passage of time, is a species of the same genus – *Keratella quadrata*

(Fig. 11). Its numbers and percentage, however, are several times smaller than those of *K. cochlearis* (Fig. 11 – a different scale of abundance).

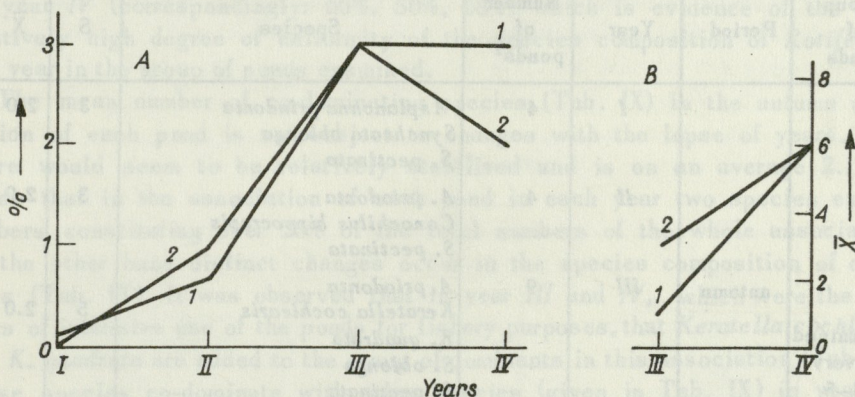


Fig. 11. Variations in mean numbers (\bar{X} – specimens/litre) and mean percentage of *Keratella quadrata* during the spring in consecutive years

A, B, 1, 2, – see Fig. 9

To sum up: the structure of the spring association passes through the following successional changes: maximum differentiation of the composition of dominants occurs in the group of ponds examined during the first two years of their existence. In the following two years in principle one species only dominated in all the ponds.

2. Variations in the structure of summer and autumn associations

The variety of species of euplankton rotifers occurring in the ponds outside the spring period – in August, September and October, is on an average smaller than that of the spring association.

The poorest is the composition of species in the summer association, which, as has been shown in the preceding section, occurs only in the ponds with a relatively large fish stock during the period August-September. The mean number of species occurring during this period is, in 1959 – 9.3 (range 8–11), in 1960 – 6.0 (range 6–6). The variety of species of the autumn association, which occurs in all the ponds stocked during the period September-October, is slightly greater: in year I an average of 11.2 species occur (range 10–13), in year II – 12.2 (range 11–14), in year III – 11.4 (range 9–15), in year IV – 10.2 (range 5–17).

List, total number (S) and mean number (\bar{X}) of euplankton species dominating¹ during the summer and autumn period in consecutive years

Tab. IX

Group of ponds	Period	Year	Number of ponds ²	Species	S	\bar{X}
Examined every 3-5 days	autumn	I	4	<i>Asplanchna priodonta</i> <i>Syncheata oblonga</i> <i>S. pectinata</i>	3	2.0
		II	4	<i>A. priodonta</i> <i>Conochilus hippocrepis</i> <i>S. pectinata</i>	3	2.0
		III	9	<i>A. priodonta</i> <i>Keratella cochlearis</i> <i>K. quadrata</i> <i>S. oblonga</i> <i>S. pectinata</i>	5	2.0
		IV	4	<i>C. hippocrepis</i> <i>K. cochlearis</i> <i>K. quadrata</i>	3	2.0
	summer	III	8	<i>C. hippocrepis</i> <i>K. cochlearis</i> <i>K. quadrata</i>	3	1.5
		IV	3	<i>C. hippocrepis</i> <i>K. quadrata</i>	2	2.0
Examined every 10-14 days	summer - autumn	III	7	<i>C. hippocrepis</i> <i>K. cochlearis</i> <i>K. quadrata</i> <i>S. oblonga</i>	4	2.4
		IV	14	<i>A. priodonta</i> <i>K. cochlearis</i> <i>K. quadrata</i> <i>S. oblonga</i>	4	1.9

¹The abundance of which is more than 20% of the total numbers of euplankton *Rotifera*, at least in one pond.

²In which the *Rotifera* appeared in the summer and autumn. These are only stocked ponds.

³Differentiation between the summer and autumn association for ponds examined every 10-14 days is not possible on account of the small number of samples. Hence ponds examined every 10-14 days are described by joint data for the summer-autumn period (August-October).

The degree of distribution of the species in the summer and autumn associations in the groups of ponds investigated, "measured" by the Koch index of species composition similarity (*IBD*), is: for the summer association 50% (in 1959 and 1960), and 48-68% for the autumn association, depending on the year. For the first three years this index is 48-50%, but for year IV - 68%. The above indices are slightly smaller in comparison with the analogical ones for the spring association. This is evidence that the ponds examined are more varied, from the

aspect of the species composition of euplankton rotifers, during the summer and autumn, than during the spring period. In general, however, the Koch index for the spring, summer and autumn associations exhibits relatively high values for year IV (correspondingly: 60%, 50%, 68%) which is evidence of the comparatively high degree of uniformity of the species composition of *Rotifera* in that year in the group of ponds examined.

The mean number of co-dominating species (Tab. IX) in the autumn association of each pond is not subject to changes with the lapse of years. This figure would seem to be relatively stabilised and is on an average 2. This means that in the association of each pond in each year two species exhibit numbers constituting over 20% of the total numbers of the whole association. On the other hand distinct changes occur in the species composition of dominants (Tab. IX). It was observed that in year III and IV, which were the first years of intensive use of the ponds for fishery purposes, that *Keratella cochlearis* and *K. quadrata* are added to the group of dominants in this association (Tab. IX). These species co-dominate with other species (given in Tab. IX) in year III, while in year IV they are the only dominants; *Conochilus hippocrepis* co-dominated with them in one pond only. We therefore observe a distinct concurrence in the trend taken by variations in the domination structure in the spring and autumn association. In both cases, in year III and IV the principal dominants are species of the genus *Keratella*.

The summer association occurs, as shown in the preceding section, only in ponds with a relatively large fish stock, hence it is noted only in year III and IV, when such stocks were introduced. In this association both species of the genus *Keratella* appear at once as co-dominants with *Conochilus hippocrepis* and maintain this dominance for both the study years (Tab. IX).

Percentage of cases of domination¹ during the autumn period of *Conochilus hippocrepis*, *Keratella cochlearis* and *K. quadrata* in ponds with fish stocks greater or lesser than 7,500 specimens per hectare, examined every 3–5 days

Tab. X

Species	Year and fish stock — specimens/hectare			
	1959		1960	
	< 7,500 ≤	≤ 7,500 <	≤ 7,500 <	< 7,500 ≤
<i>K. cochlearis</i>	9	50	33	50
<i>K. quadrata</i>	41	50	33	50
<i>C. hippocrepis</i>	—	—	33	—
Others ²	50	—	—	—

¹ As per cent of the number of dominating species (exhibiting abundance $\geq 20\%$ of total numbers) found in the given period and year in the group of all the ponds examined.

² Other species from the list of dominating species — see tab. IX. Chiefly: *Asplanchna priodonta*, *Synchaeta oblonga*.

The analysis so far made shows that the expansion of both species of the genus *Keratella* is connected with fish stocking. The question therefore arises as to what the behaviour of these species is when we compare ponds with different fish stocks within one study year, that is, 1959 and 1960, when a wide range of sizes of fish stocks was used.

Percentage of cases of domination¹ during the summer – autumn period of *Keratella cochlearis* and *Conochilus hippocrepis* in ponds with fish stocks greater or less than 7,500 specimens per hectare, examined every 10–14 days

Tab. XI

Species	Year and fish stock – specimens/hectare			
	1959		1960	
	< 7,500 ≤		≤ 7,500 <	
<i>K. cochlearis</i>	25	44	38	50
<i>K. quadrata</i>	25	44	38	50
<i>C. hippocrepis</i>	25	12	—	—
Others ²	25	—	24	—

Explanations see Tab. X.

Percentage of cases of domination¹ of *Keratella cochlearis*, *K. quadrata* and *Conochilus hippocrepis* during the summer period in ponds with different fish stocks, examined every 3–5 days

Tab. XII

Species	Year and fish stock – specimens / hectare			
	1959		1960	
	< 4,500 ≤		≤ 15,000	
<i>K. cochlearis</i>	—	50	—	—
<i>K. quadrata</i>	—	38	50	not examined
<i>C. hippocrepis</i>	100	12	50	—

¹As per cent of the number of dominating species (exhibiting abundance ≥ 20% of the total numbers) found in the given period and year in the group of all the ponds examined.

In each study year both species of the genus *Keratella* dominate in the autumn association in ponds with a fish stock equal to or over 7,500 specimens per hectare (Tab. X, XI); when stocks are smaller *Conochilus hippocrepis* and other species co-dominate with these species. In the summer association (Tab. XII) in 1959 both species of the genus *Keratella* dominate in ponds with fish stocks of over 4,500 specimens per hectare, and where stocks are smaller only *C. hippocrepis* dominates. The following year *K. quadrata* co-dominates with *C. hippocrepis* in all the summer associations.

Therefore in ponds with large fish stocks chiefly *K. cochlearis* and *K. quadrata* dominate in the summer and autumn association.

The above remarks refer to the percentage of species dominating in ponds divided into groups with smaller and larger fish stocks. Having, however, material from a wide range of fish stocks available from two study years, we can trace in detail the variations both in numbers and in the percentage of dominating species with transition to ponds with increasingly large fish stocks.

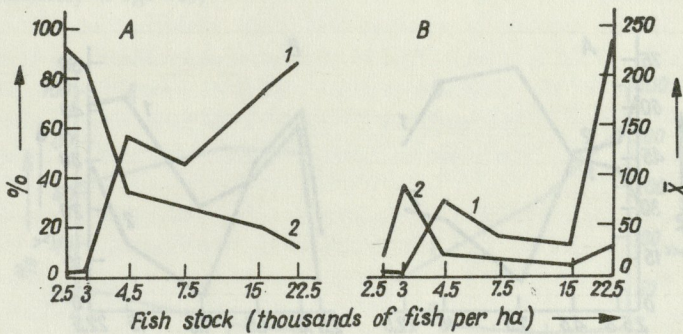


Fig. 12. Dependence of the mean percentage (A) and mean numbers \bar{x} (B) of *Keratella cochlearis*, *K. quadrata* and *Conochilus hippocrepis* on the size of the fish stock (summer, ponds examined every 3–5 days, III year)

1 - *Keratella cochlearis* and *K. quadrata* together, 2 - *Conochilus hippocrepis* - remaining dominating species

Figures 12–15 show the percentage and mean numbers of both species of the genus *Keratella*⁹ and remaining dominating species as the function of the size of the fish stock. All the ponds examined in 1959 and the ponds examined every 10–14 days in 1960¹⁰ were chosen to illustrate this.

In comparing data (Fig. 12–15) it must be stated that:

1) the percentage of both species of the genus *Keratella* increases with an increase in density of the fish stock. An exception to this is the autumn

⁹Relations between both species of *Keratella* will form the subject of a separate publication. These are most probably species constituting a pair of competitors, the numbers and character of occurrence of which, however, exhibit a similar dependence on the size of the fish stock (Hillbricht-Ilkowska 1962a). With an increase in density they become the most abundant species in the summer and autumn associations of the ponds examined. This justifies their being treated jointly for the purposes of the present analysis.

¹⁰Four ponds examined every 3–5 days in 1960 were omitted, as the summer and autumn association is formed only in three of them. These ponds belong to two variants of fish stocking (7,500 and 15,000 specimens per hectare) and do not exhibit significant differences in the percentage and numbers of *Keratella*, which is generally high in the first and second variant.

association in ponds with the largest fish stock (22,500 specimens per hectare) in which a decrease in the percentage of *Keratella* is observed (Fig. 13, 14), while in the summer association the above regularity is fully maintained (Fig. 12);

2) with an increase in density the mean percentage of the remaining dominating species decreases, being greatest in ponds with the smallest fish stock (2,500–3,000 specimens per hectare) (Fig. 12, 13, 14). The percentage of these species increases again in the autumn association in ponds with the largest fish stock;

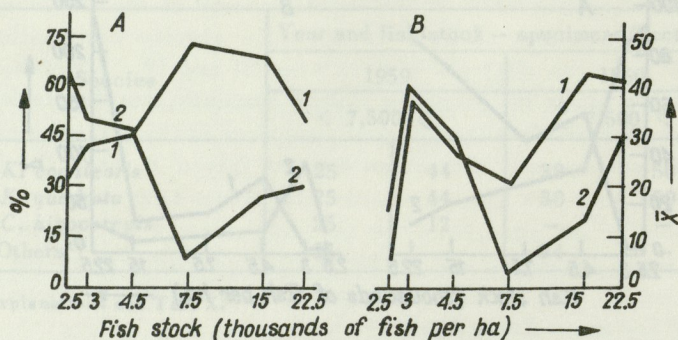


Fig. 13. Dependence of the mean percentage (A) and mean numbers \bar{X} (B) of *Keratella cochlearis* and *K. quadrata* and remaining dominating species on the size of the fish stock (autumn, ponds examined every 3–5 days, III year)

1 – *Keratella cochlearis* and *K. quadrata* together, 2 – remaining dominating species (see Tab. IX) together

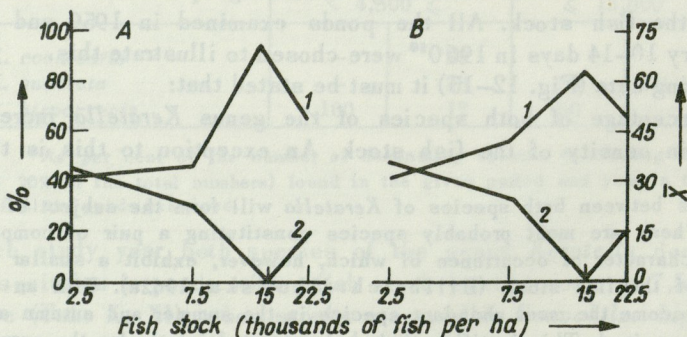


Fig. 14. Dependence of the mean percentage (A) and mean numbers \bar{X} (B) of *Keratella cochlearis* and *K. quadrata* and the remaining dominating species on the size of the fish stock (summer-autumn period, ponds examined every 10–14 days, III year)

1, 2, see Fig. 13

3) parallel to the variations in the percentage changes take place in the mean numbers, i.e. the mean abundance of *Keratella* increases with increasing density, while that of the remaining species decreases. This regularity can be observed most distinctly, however, in data for the joint summer-autumn period, i.e. for data from ponds examined every 10–14 days (Fig. 14 and 15). and partly for the summer period (data for ponds examined every 3–5 days – Fig. 12). On the other hand variations in the numbers of *Keratella* and the other dominating species for the autumn period take a parallel course, although on different levels, which in effect causes the percentage of *Keratella* to increase gradually (Fig. 13);

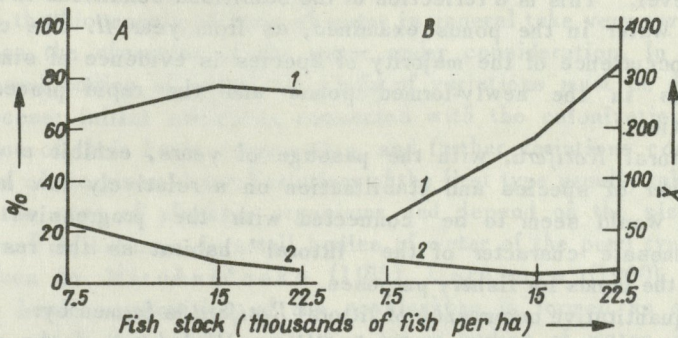


Fig. 15. Dependence of the mean percentage (A) and mean numbers \bar{X} (B) of *Keratella cochlearis* and *K. quadrata* and the remaining dominating species on the size of the fish stock (summer-autumn period, ponds examined every 10–14 days, IV year)

1, 2 – see Fig. 13

4) in all the graphs (Fig. 12–15) a tendency is observed to a slight increase in numbers and percentage of the remaining dominating species in ponds with the largest fish stocks in comparison with ponds with smaller stocks. Despite this, however, these species participate in numbers several times smaller than those of *Keratella*.

In general it must be said that when comparing ponds within the same growing season that with an increase in density of fish stock the role of both species of *Keratella* increases in the summer and autumn association. This conclusion is therefore identical with the result obtained from comparison of the percentage of cases of domination (Tab. X–XII) in ponds divided into two groups of size of stock.

VII. COMPARISON OF RESULTS

1) It was found that the species composition, numbers of plankton rotifers, and structure of their associations undergo definite variations during the study period. These are:

a) Directional variations connected with the formation of the biocenosis and stabilisation of the habitat in the newly-formed pond.

b) Variations connected with consecutive years of use of the ponds for fishery purposes.

c) Variations connected with the current density for the given year of the fish stock.

2) Variations in the number and species composition of littoral and euplankton *Rotifera* are connected with the process of their colonisation of the newly-formed ponds, the stabilisation of their habitats and variations in the "littoral" habitat.

a) Euplankton *Rotifera*, with the passage of years, exhibit at first an increase in the number of species and then stabilisation on a relatively high level. This is a reflection of the stabilised conditions in the free body of water in the ponds examined, as from year II. The common and lasting occurrence of the majority of species is evidence of similar habitat conditions in the newly-formed ponds and the rapid process of their colonization.

b) Littoral *Rotifera*, with the passage of years, exhibit a decrease in the number of species and stabilisation on a relatively low level. These changes would seem to be connected with the progressive liquidation of the mosaic character of the "littoral" habitat as the result of the use of the ponds for fishery purposes.

3) The quantitative occurrence of littoral *Rotifera* is formed by:

a) Successional variations in the "littoral" habitat of the ponds. It is true that the numbers of these species were found to increase in year II and partly in year III, but this was followed by a decrease in year IV.

b) The current fish stock in a given year. In each study year the rule was found to apply, that the larger the fish stock, the greater the frequency and abundance of occurrence of littoral *Rotifera*.

4) The quantitative occurrence of euplankton *Rotifera* is formed in different periods of the growing season of the pond by different factors:

a) In all the years and in all the ponds mass, short-lived occurrence of *Rotifera* was found in the spring period, a few days after the ponds had been filled. The abundance of *Rotifera* during this period increased with the passage of years. It would therefore seem that the fertility of the pond habitat in the initial period of the yearly growing season increases successionaly the longer the pond remains in use.

b) The quantitative occurrence of *Rotifera* outside the spring period exhibits a dependence on the current fish stock for the given year and pond. In each study year the rule was found to apply that the larger the fish stock, the earlier and more abundantly the *Rotifera* appear halfway through the growing season.

5) The structure of each association of euplankton *Rotifera* exhibits successional variations and variations dependent on the current fish stock for the given year:

a) With the passage of years the domination structure of the spring associations becomes uniform as the result of the quantitative development of *Keratella cochlearis*.

b) In each year in which a wide range of fish stocks was used the regularity was found to apply that the larger the fish stock, the greater the role played by *Keratella cochlearis* and *K. quadrata* in the summer and autumn associations.

VIII. DISCUSSION

Successional variations in the species composition and quantitative relations in the biocenosis of body of water in general take very varied courses, depending on the character of the water under consideration. In the case of a newly-formed bodies of water two kinds of variations must be distinguished in this process: initial variations connected with the colonization of species and formation of their basic composition, and further variations connected with the evolution of the given water. Variations of the first type usually take place very rapidly in the case of plankton organisms and depend on the size and depth of the water. For instance, in small bodies of water of the pond type, according to data given by Mirošničenko (1955), Baranova (1960), Pidgajko (1961), the basic composition of the zooplankton is formed as early as the 1st year in which the ponds exist. For larger bodies of water, such as, for example, dam reservoirs, Ceeb (1961) and Dzjuban (1957, 1959) give a period of 2-4 years, emphasising that this is a comparatively short time. The short time needed for stabilisation of the basic species composition of plankton in a newly-formed body of water is understandable, when the commonness of the occurrence of the resting forms of these organisms, their predominantly eurytopic character, the great rate of their quantitative development and also the commonness of their occurrence in the body of water from which the newly-formed ponds are filled, are borne in mind. In the group of ponds described the basic group of euplankton and littoral *Rotifera* is formed in year I and II of the existence of the ponds. In later years the appearance of only a few species is observed. In the first years considerable differentiation in the quantitative relations can be observed in the ponds examined. Different species develop in great numbers in different ponds in analogical periods. This would appear to be fortuitous and not due to the simultaneous character of occurrence of the species in each body of water and is peculiar to young biocenoses in process of formation.

Further transformation both of the species composition and of quantitative relations in the plankton of the pond are now connected with the concrete conditions of its evolution.

The food factor is the fundamental successional factor governing the variations in the plankton in different types of bodies of water. By this factor

is meant the resources of those forms of organic matter which are the true food of plankton organisms.

Variations in the plankton correlated with variations in trophism have been observed in bodies of water of different kinds: lakes (Sebestyen 1953, 1958, D'Ancona 1953, Parise 1961, Meschkowa 1961), estuaries (Margalef 1960), dam reservoirs (Dzjuban 1957, Morduchaj-Boltovskaja 1959, Bitjukov 1961, Ceeb 1961), small astatic pools (Voronkov and Korsunskij 1910), ponds (Baranova 1961), experimental aquaria or other water micro-habitats (Woodruff 1912, Kurihara 1960, Hillbricht-Ilkowska 1961, Hillbricht-Ilkowska 1962b). The general conclusion reached from these observations is that with an increase in trophism in the sense of an increase in plankton food (e.g. detritus), the total abundance of plankton increases and small forms of filtrators and sedimentators such as rotifers, protozoic nanno-plankton and small *Cladocera* begin to dominate, while in waters where the amount of organic matter in the pelagial zone decreases, then the larger forms of zooplankton begin to dominate in the plankton, while the abundance of plankton as a whole decreases. This type of phenomenon is typically characteristic of the succession in dam reservoirs and ponds after filling, both in plankton (Dzjuban 1957, Morduchaj-Boltovskaja 1959, Bitjukov 1961, Baranova 1961) and in benthos (Morduchaj-Boltovskoj 1961, Kajak 1962).

The successional variations in plankton rotifers described in the present study are also the expression of directional changes in food conditions understood as the abundance of organic matter available to plankton. These changes would seem to a great extent to be the result of the effect of the fish than of natural succession. Proof of this is provided by the correlation described in this study, between the quantitative occurrence and domination structure of rotifers associations and the size of the fish stock. In order to explain the presumable mechanism and the consequences of this correlation for the whole ecosystem of the pond, it is necessary to examine the question of the food requirements of the rotifers and their place in the economics of the pond ecosystem.

In the biocenosis of a body of water plankton *Rotifera*, like the majority of plankton organisms, are considered as consumers of the first order, i.e. as phytophagous organisms feeding on small phytoplankton. It has been, it is true, found that the small forms of laboratory plankton producers — especially the single-cell *Chlorophyta* such as *Chlorella*, *Lagerheimia* and others, are readily eaten by *Rotifera* (Rezvoj 1926, Pennington 1941, Pourriot 1957, 1958, Vasileva and Okuneva 1961, Erman 1962a and 1962b). Under natural conditions the mass development of *Rotifera* after periods of the appearance of these algae is often observed (Sladeček 1958). The basis of the selection of plant food is, in the opinion of Pourriot (1957), the size and simplicity of form of the algae, e.g. certain *Diatomae* are not eaten for

these reasons. According to Pennak (1946), Edmondson (1957, 1961), Pourriot (1957), Manujlova (1955, 1962) and others, in addition to typical plant food some of the common foods eaten by plankton sedimentators (*Rotifera*) and filtrators (*Cladocera*) are detritus and bacteria. These organisms do not feed only on live plant plankton but also on the products of the decomposition both of plants¹¹ and animals – everything which forms the fine bacteriologically active organic particles in suspension, hence the frequently observed connections between the development of zooplankton and the abundance of bacterioplankton (Jankjavečjus, Baranauskėnė and Vaškjavičjute 1960, Jankjavečjus and others 1961, Manujlova 1962) or the abundance of detritus (Hillbricht-Ilkowska 1961).

Irrespective of the sources of food, the size of a "bite" of food of such small organisms as rotifers cannot exceed 20–26 μ (after Rezvoj 1926 and Pourriot 1957), and in the case of such small rotifers as those of the genus *Keratella* – several μ .

For these reasons the rotifers form a relatively sensitive index of the abundance of fine organic suspension occurring in the free water of a body of water, that is, indirectly, its trophism. This suspension is composed of detritus, nanoplankton (*Protozoa*, phytonanoplankton, bacteria) and organic products of the metabolism (faeces) of all organisms.

For these reasons the mass occurrence, dominating in the plankton, of *Rotifera* in relatively shallow strongly eutrophised waters is often noted, even in waters exhibiting a relatively considerable degree of saprobic character, e.g. in young ponds (Mirošničenko 1955) particularly after they have been filled (Braginskij 1957a, Pidgajko 1957a, Klimczyk 1957, 1958, George 1961) or fertilised (Akatova 1957, Krzeczowska 1961). According to Pidgajko and Radzimovskij (1959) their mass development points to saprobic conditions in the pond. According to Langhans (1936) and Lachnovič (1958), *Rotifera* in general and certain of their species in particular, form an indicator of well fertilized productive ponds. According to Kulamowicz (1956) *Rotifera* form an indicator of the process of the eutrophisation of ponds. According to Hrbáček (1962) *Rotifera* predominate especially in ponds containing a large fish stock. The qualitative and quantitative domination of *Rotifera* even in the total biomass of the plankton, is characteristic of larger bodies of water also, e.g. dam reservoirs, and that during the period of their greatest productivity (Dzjuban 1957, Morduchaj-Boltovskaja 1959, Bitjukov 1961) and also of the inshore zone of these reservoirs after their periodical filling (Morduchaj-Boltovskoj 1958). It is also characteristic of the spring aspect of life in certain lakes (Kiselite 1961, Davis 1962).

¹¹ In the investigations made by Hillbricht (1961) *Rotifera* occurred in aquaria especially numerous during the period of decay of the plants introduced into the aquaria.

In the examples of succession described at the beginning of the section the rotifers occurred in the initial phases, during a period of the relatively high fertility of the habitat. From the above examples it can be seen, however, that rotifers occur very abundantly in situations in which the trophism of the habitat undergoes "refreshment" chiefly from allochthonic sources (fertilisation, soil humus and detritus in the freshly-filled reservoir or pond).

In the case of the ponds examined this source would seem to determine the abundance of occurrence of rotifers only during the short spring period after the pond had been filled.

The period immediately following the filling of the ponds is a period of intensive production of detritus from the decomposing land vegetation and lixiviation of humus in the submerged soil. A fertile bacteriologically active organic suspension then occurs in the free body of water. After a certain time the detritus most probably sinks on to the bottom of the pond or is consumed as the result of the activity of the organisms themselves. The habitat in the free body of water loses its initial fertility, the organic matter content decreases and the euplankton rotifers retreat from the habitat. A phenomenon similar to this was revealed by Dunke (1960) using the filtrator *Bosmina longirostris* as an example. In the unfertilised ponds the largest individuals (those best nourished) occurred for a short time only after the pond had been filled. Erman (1962c) demonstrated by experiment the correlation between nutrition and the cyclomorphosis in the rotifer *Brachionus calyciflorus*. The form without posterior processes occurred in cultures with a considerable concentration of algae, and the form with processes – in cultures with a low concentration of algae. In the ponds examined the first form of *B. calyciflorus* predominated in the first phase of the spring peak period of *Rotifera* – the second form during the period of the reduction, thus indicating deterioration of the food supply¹². It would not, however, seem that the allochthonic¹³ source of trophism remained unaltered in consecutive years, in fact a constant increase in the numbers of euplankton *Rotifera* is observed during the spring period in consecutive year. The allochthonic source is therefore constantly enriched, most probably as the result of the decomposition and mineralisation of plant particles progressing with the passage of time. This process would seem to be hastened by the use of the group of ponds for fishery purposes.

The fundamental factor of the fertility of the ponds (outside the spring period) in the sense of the abundance of food available to plankton, is the autochthonic source.

¹²An exact description of this phenomenon, taking place regularly during the spring period in each year in which the ponds were filled, will form the subject of a separate publication.

¹³The term "allochthonic" is used in the sense "not produced during the growing season of the pond" as opposed to "autochthonic", produced during the growing season of the pond.

The connection described in this study between the quantitative occurrence of rotifers and the fish stock gives grounds for assuming that the autochthonic source of plankton food is in essence regulated by the fish population by enriching it and making it more continuously available during the growing season of the pond.

This correlation applies to other groups of plankton also. In the study by Grygierek (1962), referred to in the introduction, made on these same ponds, the authoress found increased abundance of crustaceans in stocked ponds. This increase was greater where the density of the fish stock was greater. In studies by Hrbaček (1962), Grygierek (1962) and Charin Sutenko and Myšenko (1957), the increase in the abundance of plankton in stocked ponds applied primarily to the smaller forms – in the group of plankton organisms examined. The connection found in this study between *Rotifera* plankton and the fish stock confirms the above results. The rotifers, as stated in the introduction, constitute one of the smaller components of plankton in comparison with crustaceans.

In the light of the results discussed and data in literature we obtain a consistent picture of the changes which an active fish population introduces into the structure of a plankton biocenosis. These changes are expressed in the more continuous and more abundant occurrence of the small elements of one of the trophic levels of the pond, such as constituted by plankton filtrators and sedimentators.

The fish most probably have a stimulating effect on the production and abundance of food available to the food apparatus of these small forms, during the period of the growing season of the pond in which the allochthonic sources of food become exhausted. The results both of the mechanical transformation of the habitat by the feeding carp, and of its biological conditioning probably contribute to this effect. Cahn's description (1929) and my own observations of ponds containing the largest fish stock, draw attention to the considerable turbidity of densely stocked ponds, due to the fish searching and rooting in the bottom, and to the constant mixing of the water. This type of activity therefore favours the constant maintenance of detritus in the free water, prevents it from settling on the bottom of the pond and is favourable to the mineralisation of organic matter both on the bottom and in the free water. Biological conditioning of the habitat most probably takes place through the continual excretion into the pond habitat of fecalia and products of metabolism, which in turn constitute food for bacteria. This biological conditioning of the habitat by the metabolites of a given population (of uniform age and species) would seem to be a fundamental factor¹⁴ under pond conditions, bearing in mind the small dimensions of the ponds, their complete accessibility to

¹⁴ Contrary to large bodies of water, in which this type of effect on the habitat by natural fish populations is difficult to envisage.

the feeding fish and the considerable density of the fish stock. Therefore, as a result of the transformation by the carp stock of the pond habitat, conditions are created for the constant supply of finely pulverised organic matter rapidly assimilated by small filtrators and sedimentators, in the form of a mass of bacteria, detritus and phytonannoplankton. This is confirmed by the data given by Hrbaček (1962) on the increase in the contents of nannoseston with an increase in the density of a fish population. With regard to plant plankton food it must be mentioned that the development of net phytoplankton, as shown in material from these same ponds described by Spodniowska (1962), that is, larger forms (not passing through the mesh of 50μ dimensions) of producers, does not exhibit a correlation with the fish stock, and therefore they cannot be responsible for the development of zooplankton. The increase in the primary production, observed by Hrbaček and others (1959) in stocked ponds should, in the light of data given by Wolny (1962b), and of his own later data (Hrbaček 1962) on the development of nannoplankton in stocked ponds, most probably take place at the expense of the small forms of producers, which among others include *Chlorophyta*.

The above correlation between the way in which the habitat transformed by fish and the development of small filtrators and sedimentators is the stronger where the density of the fish is greater¹⁵. Therefore the strength of the influence of the fish on the habitat is in proportion to their density. This is directly indicated by data on the time at which *Rotifera* appear in the second half of the growing season of the pond habitat. The greater the density of the fish, the earlier the second peak in the numbers of *Rotifera* takes place (the peak after the spring peak). In the investigations made by Grygierek (1962), the greater the fish stock, the earlier the occurrence of the peak numbers of certain species of *Cladocera*.

To sum up: a carp population, under pond conditions, constitutes a factor constantly fertilising the pond habitat. This fertilisation consists in the stimulation of the abundance of finely pulverised organic matter, both live (alga and bacterial nannoplankton) and dead (detritus). This type of organic matter in turn stimulates the quantitative development of small species of pond consumers.

An additional indicator of the above mechanism explaining the variations which a fish population introduces into the plankton is the character of the changes in the domination structure of euplankton *Rotifera* associations. These changes, as has been shown, consist in the increasing domination of two species: *K. cochlearis* and *K. quadrata*. The quantitative development of these species during the summer autumn period is greater when the fish stock is greater.

¹⁵Hrbaček (1962) emphasises that the influence of the fish depends only on their numbers, and not on biomass, i.e. that a large number of small fish exert a stronger influence than a small number of large fish.

Mass occurrence of both species of the genus *Keratella*, and in particular of *K. cochlearis* in ponds, and therefore in relatively fertile bodies of water, is an extremely common phenomenon [Braginskij (1957a), Dunke (1958), Klimczyk (1957, 1958)]. Beach (1960) found large numbers of individuals of the genus *Keratella* in lakes very rich in detritus, in which the water currents maintained the detritus in a state of constant circulation in the free water, retarding its sedimentation and hastening its mineralisation. Edmondson (1957) found that *K. cochlearis* was very sensitive to the bacterial content of food. The number of eggs per female in a population of *K. cochlearis* was 0.33 before the pond was fertilised, and after fertilisation – 0.73. Erman (1962a) found active selection of detritus in the rotifer, while *K. quadrata* was found in addition to feed on the smallest components of the phytoplankton. As has already been mentioned, no eventual food of these species (which do not exceed 200μ in size) can exceed more than a few μ in size.

The quantitative development of species of the genus *Keratella* in stocked ponds is a further expression of the general changes which a fish population introduces into zooplankton by transforming the pond habitat. The fish population not only stimulates the quantitative development of small species of *Crustacea* and *Rotifera* in general, but within the associations of these rotifers stimulates the quantitative development of its small species¹⁶.

The similarity of the direction taken by successional changes, apparent when describing succession, is remarkable [Voronkov, Korsunskij (1910), Sebestyen (1953, 1958), Margalef (1960)], and by changes in the plankton described in the present study and in the studies cited [Hrbáček (1962), Grygierek (1962) and others]. In all these descriptions of succession, increasing trophism is accompanied by great quantitative development of the small plankton forms, and a decrease in trophism – by the domination of the larger forms.

The variations described above in the structure and dynamics of zooplankton introduced by a fish population are undoubtedly of fundamental importance to the structure and to the functioning of the whole pond ecosystem.

The quantitative development of small species from the trophic level of consumers in turn hastens the continued decomposing of organic matter and its mineralisation and increases the rate of the flow of energy through the pond ecosystem.

In addition it creates conditions for the intensive conditioning of the water habitat by the whole of the biocenosis living in it.

The important point in the nutrition of, inter alia, plankton filtrators and sedimentators is, according to Gajevskaja (1958, 1959) and Erman (1956,

¹⁶It must be emphasised that this trend in changes is undesirable from the fishery point of view, as *Rotifera* as organisms of small biomass are not suitable as food for cultured fish. This is expressed in the Skadowski index, Cr/R – the ratio of the biomass of *Crustacea* to the biomass of *Rotifera* defining the suitability of a given body of water as a feeding ground for fish (Zelikman 1960).

1962a) the so-called excessive feeding, that is, the consumption of food far beyond the real needs of the organism. In a given time unit the plankton organism eats an amount of feed greatly exceeding its dry weight, e.g. the rotifer *Brachionus calyciflorus* fed on *Scenedesmus* during the course of 24 hours eats a quantity of food with a dry mass equal to 560% of its own dry weight (Erman 1962a), while another rotifer, *Philodina roseola*, within an hour eats food exceeding in volume 9 times its own weight (Erman 1956). Of this enormous mass of filtered or driven food in the form of fine organic suspension, only a very small part is assimilated. Richmon (after Edmondson 1961) gives the figure as 14–31%, depending on the concentration of the food, for *Daphnia*. In the case of predatory rotifers this value does not exceed 36% (Sorokin, Morduchaj-Boltovskaja, 1962). The remainder of the food, decomposed, saturated with ferments and often even alive (certain algae maintain their structure intact) is excreted into the habitat, and in turn forms food for bacteria. According to Gajevskaja, as the result of the mass development of filtrators and sedimentators “a subtle, unusually bacteriologically active suspension is created in the water” which in turn rapidly becomes the food of these same filtrators and sedimentators. This type of situation is favourable to an increase in the intensity of circulation of organic matter in the pond, and to its mineralisation. First and foremost, however, it encourages the possibility of the biological conditioning of the habitat in the free water by its being continually “passed through” the alimentary tracts of the filtrating organisms. It must be added that the rapidity of filtration of the plankton species is high, e.g. according to Erman (1962d) the rate of filtration of such small organisms as *Rotifera* is of the same order as the larger *Cladocera* and is from 50–150 ml/per day/mg of mass. This figure, according to Edmondson (1961) and Erman (1962d) is relatively constant and does not depend on the concentration of the food (within fairly wide limits). As a result the greater the concentration of algae, the greater the amount eaten by *Rotifera* and *Cladocera*¹⁷. It should therefore be expected that where there is abundance of organic matter and mass occurrence of *Rotifera* and other filtrators, that the intensity of the biological conditioning of the water by means of its passage through the alimentary tracts of these consumers will be high, and the greater the concentration of organic matter and the more numerous the occurrence of these animals, the higher it will be.

The influence of the fish population eliminates from the habitat the larger species from a given trophic group of species and stimulates the quantitative development of small species. Taking as a basis the rule of the reverse connection between the size of biomass and its respiration, or intensity of metabolism: Vinberg (1950), Belackaja (1959), Odum

¹⁷It must be emphasised that this problem is a debatable one, e.g. Suščenja (1958) obtained opposite results. This author also criticises Gaevskaja's rule as to the excessive feeding of these filtrators.

(1956, 1959a, 1959b), it must be stated that the flow of energy through the given trophic level in the presence of species, occurring in great abundance but of small individual biomass, will be greater than the flow of energy through species of greater individual biomass. Therefore the effect of fish in stimulating the development of small organisms in the given trophic level hastens the flow of energy through the ecosystem in which they live. A direct proof of this is provided by the data given by Hrbáček and others (1959) already cited several times, on the increase in production, respiration and *BDO* in stocked ponds.

It would also seem that the influence of the fish is not limited only to their effect on the supply of plankton food. It would seem that in addition to this influence there is a parallel influence on the mosaic character of the pond habitat, particularly on the proportion between habitats of littoral type and pelagial type.

Information is given on the successional changes in the mosaic character of the pond habitat by the variations indirectly described in this study in the composition and abundance of the littoral species. The coincidence of a period of scanty and sporadic occurrence of littoral species with a period of intensive use of the ponds for fishery purposes in year *III* and *IV* is not purely accidental. The disappearance of littoral species in these years cannot be explained only by the natural process of decomposition of land vegetation progressing with the passage of time, as the ponds were filled each year about June 15th-20th, that is, during a period when the meadow vegetation was in full growth. There thus remains the possibility of explaining successional changes in this group of rotifers on the basis of the intensive destruction of vegetation and elimination of the "littoral" habitat as the result of the use of the ponds by fish stocks. We have no direct observations of the spring regrowth of meadow vegetation on the bottom of ponds used the previous year by dense fish stocks, but it must be expected that the intensive rooting of the bottom by the feeding carp hinders the regrowth of plants the following year, before the pond is filled. Cahn (1929) gives a very suggestive description of a pond almost completely deprived of vegetation as the result of the carp searching and rooting in the bottom of the pond. The "qualitative" influence of a dense population of carp on the pond habitat would therefore consist in its being rendered uniform by the elimination of the littoral habitat and formation of uniform "pelagial" conditions in the whole habitat.

In summing up the discussion of results it must be stated that a fish population (a population of carp being used as an example) causes the following changes in a pond ecosystem, which form evidence of the extent of the transforming influence of the fish:

- 1) It renders the pond habitat uniform by destroying the "littoral" habitat and eliminating species connected with this habitat.
- 2) It stimulates the quantitative development of plankton filtrators and sedimentators by increasing the abundance of their food, i.e. detritus, bacterio-

plankton and phytonannoplankton. The development of this food is the result of the increased mineralisation and the biological conditioning of the pond habitat by the fish.

3) As the result of the development of filtrators and sedimentators it hastens the process of mineralisation and decomposing of organic matter and also encourages the biological conditioning of the water by the whole biocenosis of the pond.

4) It introduces important structural changes among consumers of organic matter.

a) It renders uniform the species composition of dominants and sharpens the domination structure of plankton communities.

b) It eliminates forms with large biomass, and stimulates the development of forms with small biomass. Small forms, as the result of the stimulating influence of the fish, begin to dominate and determine the trophic relations in a given trophic level.

5) As the result of the stimulation by the fish population of the mass development of forms with small biomass, the flow of energy is increased through the whole pond ecosystem.

6) As a result of the constant influence exerted by the fish stock on the biocenosis of the pond by constantly supplying its consumers with organic matter, it increases the stabilisation of the functioning of the pond ecosystem during the four months of its growing season.

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WPŁYW POPULACJI RYB NA BIOCENOZĘ STAWU NA PRZYKŁADZIE FAUNY ROTATORIA

Streszczenie

Badania prowadzono w okresie czterech lat na kilkunastu, nowo zbudowanych stawach zarybionych narybkiem karpia o wadze 1 g w ilości od 2 500 do 30 000 sztuk/ha oraz kontrolnych (niezarybionych) (tab. I). Próby ilościowe pobierano w części stawów co kilka, w części co kilkanaście dni, w dwóch lub trzech stref stawu (tab. I i tabelka w tekście – rozdział II) w czteromiesięcznym okresie wegetacji stawów.

Ogółem znaleziono 85 gatunków i form wrotków planktonowych, z czego 48 (tab. II) należy do gatunków związanych z roślinnością – litoralowych, zaś 37 (tab. III) – do euplanktonowych. Stwierdzono trwałe różnice w zasiedleniu poszczególnych stref stawu przez obie grupy gatunków (fig. 1), jak też odmienny kierunek zmian ich liczby w kolejnych latach wegetacji (fig. 2).

Wydaje się, że ustępowanie gatunków litoralowych (fig. 2, 5) związane jest z intensywnością użytkowania rybackiego, które powoduje niszczenie roślinności i zanikanie mozaikowości środowiska stawowego.

Porównanie składu gatunkowego wrotków poszczególnych stawów przeprowadzono

w oparciu o wskaźniki Marczewskiego-Steinhaus'a i Kocha (rozdział IV). Stwierdzono duże i stałe podobieństwo składu gatunkowego wrotków euplanktonowych w stawach, już od I roku wegetacji oraz niskie i malejące z biegiem lat podobieństwo składu gatunkowego wrotków litoralowych (fig. 3).

Stwierdzono brak zależności między liczbą gatunków obu grup a wielkością obsady rybnej (fig. 4), jak też brak gatunków charakterystycznych dla określonych np. wysokich obsad rybnych.

Częstość występowania wrotków litoralowych w okresie wegetacji stawów wykazuje pozytywną korelację z wielkością obsady rybnej (tab. IV, V).

Obfitość występowania wrotków euplanktonowych w okresie wiosennym, tuż po zalaniu stawów, wzrasta w miarę upływu lat wegetacji (tab. VI), co wskazuje na wzbogacenie żywności stawów w początkowym okresie ich corocznej wegetacji.

Obfitość i długość występowania wrotków euplanktonowych w pozostałym okresie wegetacji stawów wykazuje pozytywną korelację z wielkością obsady rybnej (fig. 6, 7, 8, tab. VII) – im większa obsada rybna tym wcześniej i liczniej występują wrotki w okresie: początek sierpnia – połowa października.

W miarę upływu lat wegetacji następuje ujednoczenie składu gatunkowego dominantów w wiosennym zgrupowaniu wrotków euplanktonowych (tab. VIII) z powodu masowego rozwoju *Keratella cochlearis* (fig. 9). Podobne zmiany w kolejnych latach wykazuje gatunek pokrewny – *K. quadrata* (fig. 11). W pozostałym okresie wegetacji rozwój ilościowy obu tych gatunków jest wyraźnie skorelowany z wielkością obsady rybnej (tab. IX, X, XI, XII, fig. 12–15).

Zaobserwowane w planktonie wrotkowym zmiany pozwalają na scharakteryzowanie wpływu populacji ryb, jako kontrolującego siedlisko i biocenozę stawu. Wysłunięto przypuszczenie o wpływie populacji ryb na strukturalność siedliska (jego mozaikowatość) oraz na warunki troficzne zbiornika. Omówiono prawdopodobny mechanizm tego wpływu poprzez niszczenie roślinności i stymulowanie obfitości pokarmu planktonowego (detrytusu, bakterioplanktonu). Wskazano na niektóre konsekwencje kontrolowania siedliska stawu przez ryby dla jego ekosystemu, wyrażające się ogólnie we wzroście tempa obiegu materii i przepływu energii.

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