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PRIMARY PRODUCTION AND CHLOROPHYLL CONTENT IN THE BALTIC SEA. PART I. PRELIMINARY EVALUATION OF DIURNAL CHANGES IN THE GDAŃSK BAY

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ABSTRACT

Studies were made on diurnal fluctuation of chlorophyll content and of primary production in sea water. The smallest concentrations of chlorophyll were found before sunrise. The highest ones were observed in early p.m. hours. Sinking of phytoplankton as well as grazing of phytoplankton by zooplankton are considered as main causes of the observed decrease in chlorophyll concentration. The mean ratio of the chlorophyll increase to the carbon increase in phytoplankton was ascertained. During summer, under favourable insolation conditions this ratio had a constant value of approximately 0.034 mg chl/mg C. The effective sinking rate of phytoplankton was estimated as 2 m/hr. The phytoplankton grazing rate for morning hours amounts to obout 3.5% hr.

1. INTRODUCTION

It is well known that pigment content in terrestrial plants changes depending on living conditions of plants. Yentsch, Ryther (1957) and Yentsch, Scagel (1958) studied the similar problem in marine phytoplankton. Further studies in connection with measurements of concentration of nutrients were carried out by Lorenzen (1963) in inshore waters and by Ryther et al. (1961) in offshore waters. The studies revealed that this phenomenon is very complex (Ryther, Menzel 1959), it can result from adaptation of phytoplankton to physical and chemical conditions of the environment (Jörgensen, Steemann--Nielsen 1965) as well as from grazing the phytoplankton by zooplankton (McAllister 1963 and Steemann-Nielsen et al. 1962). Adaptation of phytoplankton to light conditions affects also the intensity of photosynthesis (Yentsch, Reichert 1963). Doty, Oguri (1957) observed that maximum rate of photosynthesis occurred before noon, whereas minimum rate was observed at about 7 p.m. Jitts (1969) and Newhouse et al. (1967) when studying photoassimilation of carbon in incubators, found that assimilation of carbon in the samples of water with phytoplankton taken during daytime was more intense than that in the samples taken at night. Since the properties of the Baltic Sea water are different from those of other oceanic waters, it may be expected that diurnal changes both in chlorophyll content in plankton and in primary production in the Baltic Sea will be slightly different from those studied in the oceanic water. Changes in chlorophyll content and primary production in the Baltic Sea were not investigated in detail, however they had been observed by Lassing, Niemi (1971).

Recently, studies of biological productivity in the Baltic Sea gain especial significance both on account of its role for fishery and protection of marine environment. Since there is a tendency to elaborate a model describing the productivity or hydrobiological position of the Baltic Sea, including such parameters as chlorophyll content and primary production, it is necessary to learn about diurnal fluctuations of these parameters, as well as the controlling factors. The aim of this paper is to show such fluctuations in chlorophyll content and in primary production.

2. MATERIAL AND METHODS

Observations of diurnal changes in chlorophyll concentration and in primary production were carried out during 9 cruises of research vessel "Birkut" in 1971. Studies on chlorophyll were performed at the following stations located in the Gdańsk Bay: J (18°45′E, 54°35′N, depth 54 m), ZP (18°37′E, 54°37′N, depth 28 m), G_2 (19°20′E, 54°50′N, depth 110 m) and at one station in the North Sea (1°30′W, 56°00′N, depth 86 m). In order to study chlorophyll content, samples of water were taken by means of bathometer usually every 3–6 hr at the following depths: 0.5, 5, 10, 20, 30, and 50 m. The water was immediately filtered through membrane filters H. A. "Millipore" which were later stored in a dark desiccator over the drying substance at a temperature of −1°C. The filters were analysed in the laboratory according to the method described by S t r i c k l a n d, P a r s o n (1960) i.e. chlorophyll was extracted by 90% acetone and extinction of the extract was measured at the wave length of 750, 663, 645, and 630 mµ. The chlorophyll content was calculated from formula of R e p o r t of SCOR-UNESCO Working Group (1964).

By "chlorophyll concentration" we understand the amount of chlorophyll-a extracted from plankton that was filtered out of 1 m³ of sea water. The chlorophyll content in the top water column (e.g. 50 m) denotes the amount of chlorophyll contained in the water under the surface of 1 m² from the surface to a given depth (50 m).

Primary production was measured by ¹⁴C radioisotope method (S t e e m a n n - - N i e l s e n 1952) at depth of 0.5, 5, 10, 15 and 20 m by carrying out incubation in situ twice a day from the sunrise until noon, and from the noon until sunset. Primary production in the top water column under the surface of 1 m² was calculated by graphical integration of the curve expressing the primary production as a function of the depth. A total radiant energy was measured by means of a solarimeter fastened to a special mast on the ship.

The details on methods are described in another paper (R e n k 1972). Simultaneously control measurements were taken of temperature, salinity, and phosphate content of water. These results are omitted here since they did not bring any substantial information to the problem discussed below.

3. RESULTS

DIURNAL CHANGES IN CHLOROPHYLL CONCENTRATION

The results of chlorophyll-a measurements made in the Gdańsk Bay at station J from 14 to 17 Dec., 1971 are presented in Fig. 1. Relative values of the same measurements, as related to mean value of chlorophyll-a at a given depth for the whole period of measurements, i.e. from Dec. 14, 3 p.m. to Dec. 17, 4 a.m. are presented in Fig. 2. It can be seen from Fig. 2 that the relative deviations of chlorophyll concentration from the mean value range from 0.8 to 1.5, depending on the time of observation. On the average, the smallest chlorophyll values were observed in euphotic zone before sunrise and the greatest value — in early p.m. hours. It can be also seen that the extreme concentrations of chlorophyll
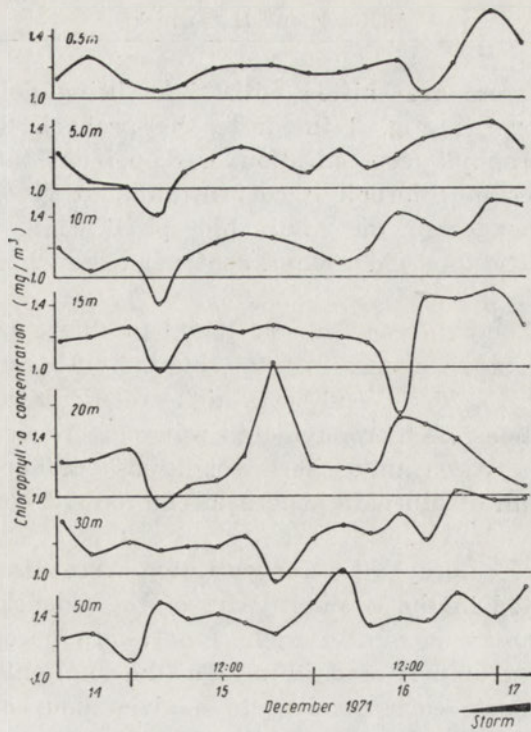
Fig. 1. Concentration of chlorophyll-a in water at different depths on station J
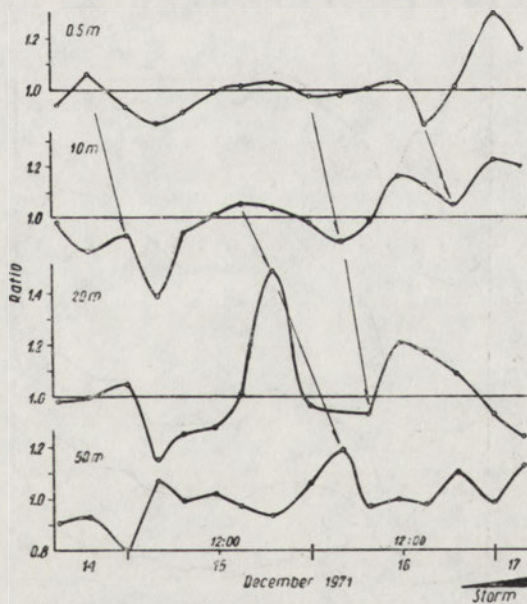(the Gdańsk Bay)

Fig. 2. Relative concentrations of chlorophyll-a as related to the mean for the
whole period of measurements at different depths at station J. The arrows illustrate
the probable sinking of chlorophyll agglomerations

in subsequent layers are shifted with time, being delayed in deeper layers. The arrows in Fig. 2 illustrate the probable lowering of the "clouds" of chlorophyll (concentration or dispersion of phytoplankton). The time changes in chlorophyll concentration at given depths result ultimately in changes of the total chlorophyll content in the water column (Fig. 3). The total chlorophyll content in the whole water column decreases at night.

The diurnal fluctuations were also found in chlorophyll-b content in plankton at station J. Changes in total chlorophyll-b content in the top water column 10, 15, 20, 30, and 50 m high are presented in Fig. 4. The lowest concentrations of chlorophyll-b in water layers were also observed in morning hours. When atmospheric conditions became worse (growing storm), the rhythm of diurnal changes in chlorophyll content was becoming disturbed.

The studies of chlorophyll-a concentration were also carried out at station G_2, situated in the southern part of the Gdańsk Deep. Table I comprises, besides the dates of sampling, the total chlorophyll-a contents in the top water column 10, and 30 m high (the total chlorophyll content is given in the spots corresponding to a given hour of measurement, written in the first line of the Table).
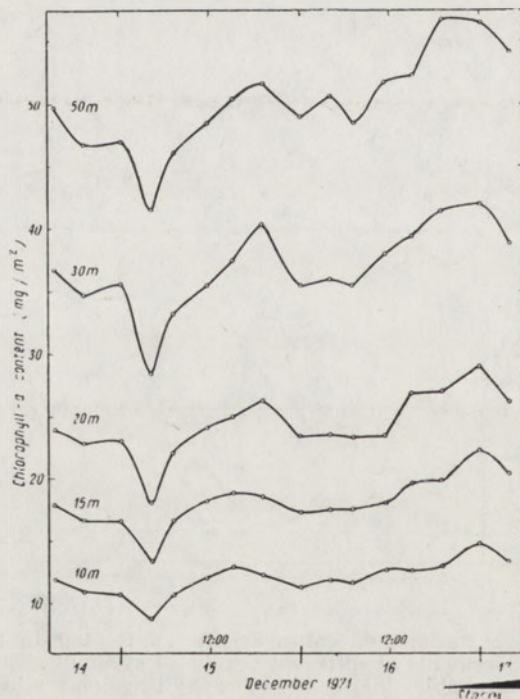

Fig. 3. Total chlorophyll-a content under the surface of 1 m² in the top water column at different depths at station J
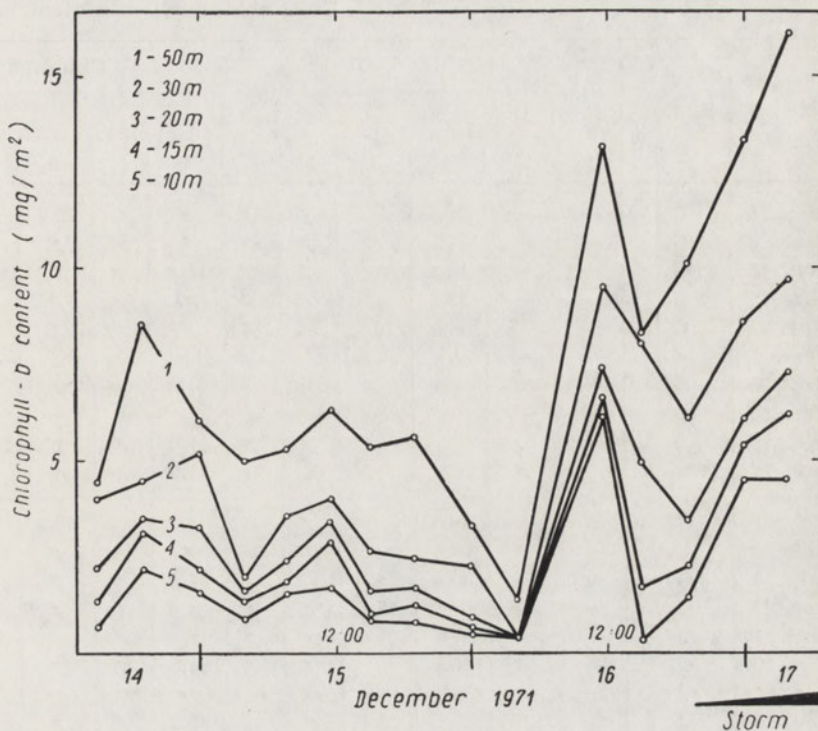
Fig. 4. Total chlorophyll-b content under the surface of 1 m² in the top water column at different depths at station J

It can be seen from Table I that in almost all measurements taken in a.m. hours an increase in chlorophyll concentration was observed, followed by a decrease in p.m. hours and at night. Exceptions to this rule were observed in the periods of rough sea, e.g. Nov. 20 at station G_2 or Sept. 1 and Dec. 16 at station J. These deviations from a general pattern of changes in chlorophyll content can be explained by considering an example of station J on Sept. 1. In the surface layer, down to 10 m, losses of chlorophyll in a.m. hours were probably brought about by the wave action and mixing of the surface water with that of deeper layers, where phytoplankton is generally less abundant. A proof of continuous mixing of water reaching that day down to 10 m can be the fact that concentrations of chlorophyll and phosphate were equal at depths oi 0.5, 5, and 10 m, whereas at depth of 20 they differed from those in the surface layer. On the other hand, the sum of chlorophyll for 30 m layer showed similar changes as in stormless weather.

Similar changes in the chlorophyll concentration were also observed on the cruise made in October to the North Sea. Figure 5 illustrates changes in chlorophyll-a concentration in waters of a chosen station at depth of 1, 10, 25, 30 m. In the surface layer 10 m deep the smallest

Table 1. Total chlorophyll-a content in top

	Date	Station	Chlorophyll-a									
			a. m. hours									
			1	2	3	4	5	6	7	8	9	10
10 m	May 21	G₂	—	—	20.4		↗	↗	↗	↗	22.1	↗
	June 8	G₂	--	—	17.1		↗	↗	↗	↗	↗	↗
	July 15	G₂	—	—	13.4		↗	↗	16.3	↗	↗	↗
	July 19	G₂	—	—	22.9		↗	↗	↗	↗	↗	↗
	Aug. 27	G₂	—	—	—	16.7	↗	↗	↗	↗		18.2
	Sept. 1	J	—	—	—	35.1		↘	↘	↘	↘	30.3
	Nov. 20	G₂	—	60.6		↗	↗		61.6		↘	↘
	Dec. 14	J	—	—	—	—	—	—	—	—	—	—
	Dec. 15	J	↘	↘		8.7	↗	↗	11.0	↗	↗	↗
	Dec. 16	J	↗	↗		11.8	↘	↘	11.6	↗		
30 m	May 21	G₂	—	—	40.0		↗	↗	↗		50.2	
	June 8	G₂	—	—	37.3		↗	↗	↗	↗	↗	↗
	July 15	G₂	—	—	30.9		↗		34.2	↗	↗	↗
	Aug. 27	G₂	—	—	—	45.1	↗	↗	↗	↗	↗	
	Sept. 1	J	—	—	—	81.6		↗	↗	↗		94.9
	Nov. 20	G₂	—	—	175.5		↗	↗	181.5	↗	↗	
	Dec. 14	J	—	—	—	—	—	—	—	—	—	—
	Dec. 15	J	↘	↘		28.4	↗	↗	33.6	↗	↗	↗
	Dec. 16	J	↗	↗		35.9	↘	↘	35.4		↗	↗

↗ — an increase in chlorophyll content, ↘ — a decrease in chlorophyll content, — — no

chlorophyll concentration was observed in a.m. hours, followed by an increase in chlorophyll concentration during the day until 7 p.m. (Fig. 6). The second minimum was found in a deeper layer at 6 p.m.

MEASUREMENTS OF PRIMARY PRODUCTION

In order to draw attention to diurnal differences in photosynthesis four series of measurements of primary production were carried out at station G₂ in different seasons; each time measurements were taken twice a day: in a.m. and p.m. hours. The results are presented in Table II. During observations run in May primary production was lower in a.m. than in p.m. hours. These differences were, however, caused by large differences in insolation. The energy efficiency of photosynthesis was that day higher in p.m. hours than in a.m. hours. In July and August the energy efficiencies of photosynthesis were higher in p.m. hours than in a.m. hours.

July 19th was a very sunny day. In a.m. hours the highest primary production was found at a depth of 5 m. In the surface layer, in spite of high concentration of phosphate, the primary production was lower.

water columns of 10 and 30 m high

content (mg/m²)													
						p. m. hours							
11	12	1	2	3	4	5	6	7	8	9	10	11	12
↗	23.8	↘	↘	20.5	↘	↘	↘	↘		19.0	—	—	—
↗	↗	↗	↗		19.8	—	—	—	—	—	—	—	—
	17.6	—	—	—	—	—	—	—	—	—	—	—	—
	24.5		↘	↘	↘	↘	18.4	↘	↘	↘	↘		18.1
↗	↗	↗	↗		18.4		↘	↘	↘		18.0	—	—
↘	↘	↘	↘	↘	27.1	↘	↘	↘	↘		24.8	—	—
61.0	↘	↘		57.4	—	—	—	—	—	—	—	—	—
—	—	—	—	12.0		↘	↘	11.1	↘	↘	↘	↘	10.6
12.0	↗	↗		12.8		↘	↘	12.2	↘	↘	↘		11.3
12.8		↘		12.6		↗	↗	13.1	↗	↗	↗		14.7
↘	↘	↘		40.4		↗	↗	↗		46.3	—	—	—
↗	↗	↗	↗		38.2	—	—	—	—	—	—	—	—
	35.4	—	—	—	—	—	—	—	—	—	—	—	—
↗	↗	↗	↗		48.4		↘	↘	↘		47.7	—	—
	↘	↘	↘	↘	66.0	↘	↘	↘	↘		65.8	—	—
184.8		↘		174.9	—	—	—	—	—	—	—	—	—
—	—	—	—	36.8		↘		34.6		↗	↗		35.6
35.5	↗	↗	↗	37.4	↗	↗		40.3		↘	↘		35.4
38.0	↗	↗	↗	39.3	↗	↗	↗	41.3	↗	↗	↗		42.0

measurements.

Thus it should be supposed that the lower primary production at the surface was caused by an excess of light. Inhibitory effect of excessive light on photosynthesis was more conspicuous in p.m. hours. A decrease in chlorophyll occurring clearly after 12:00 was also the result of excess of light that day. In November no solar energy measurements were taken, however, according to subjective evaluation, the doses of solar radiation during the a.m. and p.m. incubations were similar. In spite of this primary production during a.m. hours was 3 times as high as that in p.m. hours. The differences in the amount of primary production in a.m. and p.m. hours at given depths are illustrated by Fig. 7.

4. DISCUSSION

PRIMARY PRODUCTION AND CHLOROPHYLL INCREMENT

Primary production depends, besides other factors, on the amount of active chlorophyll. Some methods of quantitative measurements of primary production are based on estimates of chlorophyll-a content (R y t h e r, Y e n t s c h 1957). In the light of observations performed
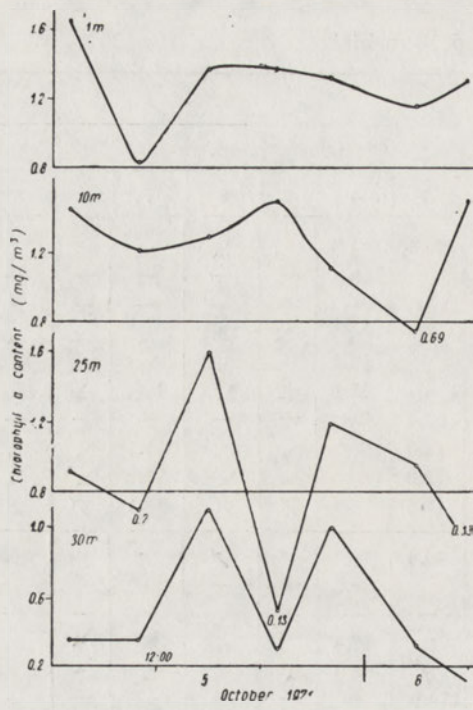
Fig. 5. Concentration of chlorophyll-a in waters at different depths at the station on the North Sea
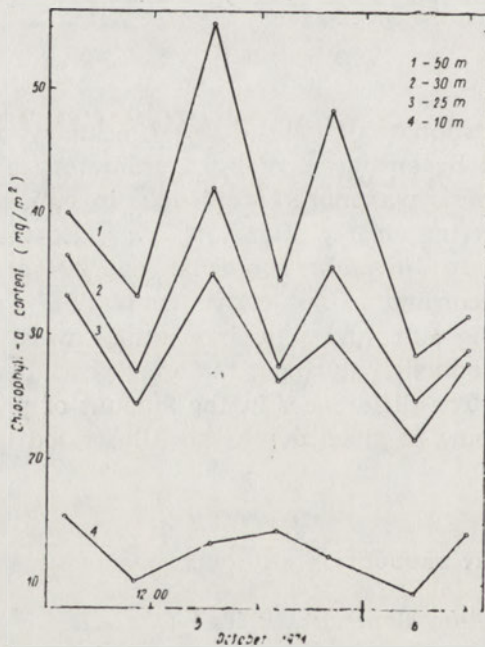

Fig. 6. Total chlorophyll-a content under the surface of 1 m² in the top water column at different depths at the station on the North Sea

Table II. Results of measurements of primary production (1971)

Date	Mean temp. of surface water (°C)	Mean chlorophyll content for 10 m (mg/m³)	A.m. measurements			P.m. measurements		
			E (cal/cm²)	P (mg C/m²)	P/E (mg C/cal·10⁶)	E (cal/cm²)	P (mg C/m²)	P/E (mg C/cal·10⁶)
May 21	11.4	2.1	62	27.2	0.44	281	106.0	0.38
July 19	13.7	2.1	266	247.0	0.92	205	239.0	1.16
Aug. 27	17.5	1.7	105	68.7	0.65	55	98.5	1.79
Sept. 20	8.4	5.7	—	109	—	—	33.8	—

E – total solar energy in solar half-day, P - total primary production in the top water column in solar half-day

on changes in chlorophyll concentration, the method of estimation of primary production from the chlorophyll content gives results that differ one from another depending on the time of the day when measurements of chlorophyll were taken. At present, it seems not possible to find out a close relationship between chlorophyll content and the factors which

Fig. 7. Dependence of primary production on the depth at station G_2 in three seasons of 1971: spring, summer, autumn
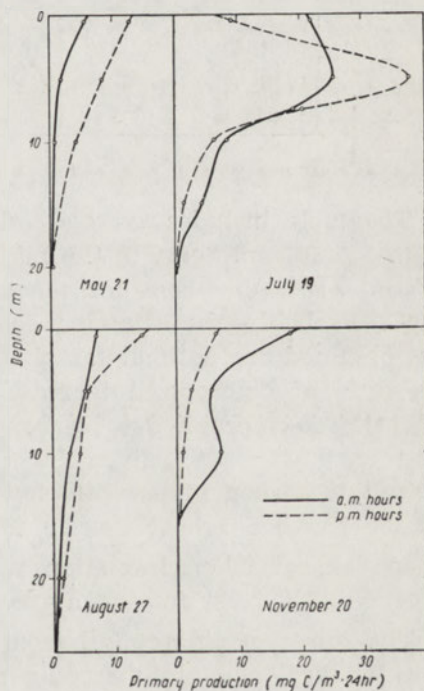
affect the diurnal changes of chlorophyll. Production of chlorophyll is a secondary process following the photoassimilation of carbon. Thus the increase of chlorophyll depends on primary production. On the other hand, the augmentation of chlorophyll content depends on radiation

conditions under which a plant exists. With intense insolations "degradation" of chlorophyll occurs. This could explain a decrease in the amount of chlorophyll in p.m. hours on July 19, 1971. However, substantial losses of chlorophyll at a given depth in diurnal cycle are caused by grazing of phytoplankton by phytophagous zooplankton, and also by sinking of phytoplankton.

A trial was made to find the relationship between the increase in chlorophyll in a.m. hours and the primary production. The results of those calculations are given in Table III. The value $\Delta B_h/P_h$ denotes a ratio of chlorophyll-a increase in top water colum 30 m high to the total primary production in this volume of water.

Table III. Ratio of chlorophyll increase to primary production (1971)

Date	Station	Insolation per hr (cal/cm²·hr)	$\Delta B_h/P_h$ (mg chl/mg C)
May 21	G_2	7.2	0.529
July 15	G_2	20.6	0.033
Aug. 27	G_2	14.4	0.029
Sept. 1	J	31.1	0.034
Sept. 20	G_2	15.0	0.034
Dec. 15	J	3.1	0.264
Dec. 16	J	3.9	0.382

The table includes average values of $\Delta B_h/P_h$ calculated for the period of one a.m. hour. In the period from July 15 to Nov. 20, the ratio $\Delta B_h/P_h$ was rather constant, amounting approximately to 0.032 mg chl/ /mgC. Probably the summer conditions for which minimum $\Delta B_h/P_h$ was obtained are optimal for photosynthesis. For the period mentioned, the ratio of chlorophyll increase to assimilated carbon can equal to the ratio of chlorophyll to carbon in a cell. This value falls within the limits of 0.021−0.045 given by E p p l e y (1968) for the ratio of chlorophyll to carbon in natural phytoplankton. The same value estimated for the North Sea by S t e e l e , B a i r d (1962) amounts to 0.042.

In 3 cases when insolation was below 7 cal/cm²·hr, the ratio of chlorophyll increase to carbon grew clearly.

The losses of chlorophyll from euphotic layer by sinking of phytoplankton are taken into account in the calculated ratio of $\Delta B_h/P_h$ by the fact that ΔB_h was calculated for 30 m layer, thus, practically exceeding by 10 m the euphotic zone. On the other hand, the losses of chlorophyll caused by grazing of phytoplankton by zooplankton will be presented below. After taking into account the correction for grazing the ratio $\Delta B_h/P_h$ is 0.034 mg chl/mg C.

SINKING OF PHYTOPLANKTON

No direct measurements were taken on sinking rate of phytoplankton, however, the presented results allow to draw conclusions concerning this problem. In Figure 2, maxima of chlorophyll in a deeper layer correspond to some maxima of chlorophyll in a given layer, but they are delayed. If arrows in Fig. 2 are to "identify" the same chlorophyll cloud after some time at a greater depth, the probable sinking rate of chlorophyll clouds can be easily estimated; it amounts to about 2.5 m/hr (apart from the period of full day insolation). The observed velocity at which the chlorophyll "clouds" sink can be hardly considered as the sinking rate of phytoplankton cells. We will try to prove that the sinking rate of some (large) cells of phytoplankton in the Baltic Sea is higher than in the oceanic water. The sinking rate of the cells of various species of phytoplankton in the oceanic water, given by different authors, range from 0.05 m/24 hr to 22.7 m/24 hr (A n d e r s e n 1957—1959, E p p l e y et al. 1967, S m a y d a, B e l e y n 1966, S t e e l e 1956). The average rate of cell sinking is of an order of 0.2—0.5 m/hr, which is by one order smaller than the observed sinking rate of chlorophyll agglomerations in the Baltic Sea.

Let us compare the sinking process of the identical cells in the Baltic water and in the oceanic water. The movement of a sinking cell can be described by an equation expressing the equality of forces affecting the cell: the Stockes [1] force on one hand, and the force being the difference between the weight of the cell and the force of water displacement, on the other:

$$A \cdot 3\pi\mu D \, w_B = V \, (\delta_c - \delta_B) \, g \tag{1}$$

where: δ_c — density of cell substance, δ_B — density of the Baltic water, μ — the coefficient of water viscosity assumed at the moment to be equal for the Baltic and oceanic water, D — "effective diameter" of cell, w_o, w_B — the sinking rate in oceanic and Baltic waters, respectively, V — total cell volume, g — gravity acceleration.

Suppose we take that the cell mass can be presented as two elements:

$$V\delta_c = m + V_2\varrho_B \tag{2}$$

where: m — mass of dry matter, which is supposed to be identical in the Baltic and oceanic environment, V_2 — volume of aquatic solution in the cell, ϱ_B, ϱ_o — densities of body fluids in the cell in the Baltic Sea and in the ocean, respectively.

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[1] In general the Stockes' law concerns the falling ball, then the shape coefficient $A = 1$. Application of Stockes' law seems to be justified when introducing a concept of the so-called cell "effective diameter" and coefficient A (E p p l e y et al. 1967).

Taking into account equation (2), equation (1) for the Baltic and oceanic environments will be as follows:

$$A \cdot 3\pi\mu D\, w_B = (m + V_2\varrho_B - V\delta_B)\, g \qquad (3)$$

$$A \cdot 3\pi\mu D\, w_o = (m + V_2\varrho_o - V\delta_o)\, g \qquad (4)$$

where δ_o — density of oceanic water.

Dividing the equations, by their parts one obtains:

$$\frac{w_B}{w_o} = \frac{m + V_2\varrho_B - V\delta_B}{m + V_2\varrho_o - V\delta_o} \qquad (5)$$

Since $V_2 < V$ and $\varrho_o - \varrho_B \leqslant \delta_o - \delta_B$, i.e. the difference in densities of body cell fluids in the ocean and the Baltic Sea is not higher than the difference in densities of oceanic and Baltic waters, one obtains:

$$V_2\varrho_B - V\delta_B > V_2\varrho_o - V\delta_o$$

thus: $w_B > w_o$, i.e. the sinking rate of the same cell of phytoplankton in the Baltic Sea is higher than in the oceanic water. If one considers the fact that with the increase of salinity, its viscesity also increases, inequality $w_B > w_o$ would be still greater.

From equation (1) it is evident that the rate of sinking of a cell is proportional to the square of its diameter. In the surface layer of the sea, viz. euphotic zone, the smallest cells accumulate since they sink very slowly, and on the contrary, the larger cells accumulate in deeper layers. Some tendencies of the sinking rate of "chlorophyll clouds" to increase with depth can be also seen in Fig. 2. Moreover, E p p l e y et al. (1967) found that the sinking rate of dead cells is about 3 times higher than that of living cells. On the other hand, phytoplankton collected from the depth of 30 m shows a considerably lower photosynthetic activity which is supported by our observations as well as by those of N e h r i n g, F r a n c k e (1971) on photoassimilation of ^{14}C in incubators. It can be, then, assumed that in the Baltic Sea a part of phytoplankton below the depth of 30 m is dead, thus according to E p p l e y et al. (1967) data it should sink faster. Therefore, it is very probable that the sinking rate of chlorophyll agglomerations of an order of 2 m/hr found from Fig. 2 is a mean effective sinking rate of the phytoplankton cells.

GRAZING OF PHYTOPLANKTON

Large losses of chlorophyll, especially in summer, are due to the grazing of phytoplankton by zooplankton. Let us consider the changes of chlorophyll in the water column under 1 m² of the sea surface. The following denotations are needed:

B — the biomass of phytoplankton per unit volume at depth x,

$B - dB$ — the biomass of phytoplankton at depth $x + dx$,

P — the primary production per unit volume and hr,

G — the amount of biomass of phytoplankton grazed by zooplankton per unit volume and hr.

Let us express the increment of the phytoplankton biomass in the water volume of 1 m² · dx in time dt as $\delta B \cdot 1$ m² · x. This increment is controlled by the following factors:

$P \cdot dt \cdot 1$ m² · dx — the increase resulting from primary production,

$R \cdot dt \cdot 1$ m² · dx — the energy losses due to respiration of phytoplankton,

$Gdt \cdot 1$ m² · dx — the losses of phytoplankton due to grazing by zooplankton,

$B \cdot 1$ m² · dt — the increment of phytoplankton mass due to sinking from the upper layer,

$(B-dB) \cdot 1$ m² dt — the decrement of phytoplankton mass due to sinking.

Irrespective to the so-called "bleaching" of phytoplankton the following equation can express the phytoplankton budget for the water volume of 1 m² dx for morning (a.m.) hours.

$$\delta B \cdot 1 \ \text{m}^2 \cdot dx = (P-R-G) \ dx \cdot 1 \ \text{m}^2 \cdot dt + dB \cdot w \cdot dt \cdot 1 \ \text{m}^2 \qquad (6)$$

Equation (6) can be simplified to:

$$\delta B = (P-R-G+w \ \frac{dB}{dx}) \ dt \qquad (7)$$

accepting $\dfrac{dB}{dx} = $ grad B, the last equation takes form:

$$\delta B = (P-R+w \cdot \text{grad} \ B - G) \ dt \qquad (8)$$

Precise solving the above equation can be only possible if we know the dependence of the functions in the equation upon the time. Assuming that in time $\varDelta t = 1$ hr the particular values are constant, we obtain another expression for the approximated amount of grazed phytoplankton per hr:

$$G = P - R + w \cdot \text{grad} \ B - \frac{\varDelta B}{\varDelta t} \qquad (9)$$

grad B can be obtained from the graph expressing the dependence of phytoplankton biomass on depth, and value $\varDelta B/\varDelta t$ from Fig. 1. Table IV contains the results of grazing of phytoplankton by zooplankton at the stations in question. Calculations pertain to morning hours. Primary production per hr was approximated by dividing the value of primary production obtained during half day incubation by number of hours of incubation. The value of energy losses for respiration was accepted after R y t h e r (1956) $R \approx 0.1 \ P$. Besides, the previously calculated value for $\varDelta B_h/\varDelta P_h = 0.034$ mg chl/mg C was used in these calculations.

Table IV. Grazing of phytoplankton

Date	Station	Depth (m)	G (mg chl/m³·hr)	G/B·100 (%)
July 15	G₂	5	0.03	1.8
		10	0.02	1.3
July 16	ZP	5	0.05	1 6
		10	0.06	1.8
Aug. 27	G₂	5	0.15	9.4
		10	0.03	1.9
Sept. 1	J	5	0.25	7 6
		10	0.30	10.0
Nov. 20	G,	5	0.04	0.7
		10	0.15	2.4
Mean				3.8

G—amount of grazed chlorophyll per 1 m³ of sea water per hr,
$G/B·100$ – percentageous loss of chlorophyll per 1 hr due to grazing.

The calculated mean value of grazing of phytoplankton in the morning hours, amounting to 3.8% of chlorophyll mass per hr is high and probably burdened with an error. The sources of this error are the following:

a) less precise estimation of grad B,

b) approximated estimation of primary production per hr,

c) less precise estimation of sinking rate,

d) approximated estimation of energy loss for respiration,

e) omission of the phytoplankton 'bleaching" effect (Y e n t s c h, S c a g e l 1958),

f) omission of the factors connected with dynamics of the sea, which can also affect phytoplankton,

g) omission of the heliotropic properties of phytoplankton (E p p l e y et al. 1968).

Acknowledgements

5. SUMMARY

The paper contains results of diurnal changes in chlorophyll content of plankton and in intensity of photosynthesis. Measurements of chlorophyll were carried out at 3 stations in the Gdańsk Bay as well as at one station of the North Sea. The lowest concentrations of chlorophyll were observed before sunrise. The highest concentrations of chlorophyll were found in early p.m. hours. Primary production

was measured in the Gdańsk Deep. Considerably large differences in primary production were observed between a.m. and p.m. hours. The ratio of chlorophyll increment to primary production was calculated. It amounted to 0.034 mg chl/mg C for summer period with good light conditions.

The sinking rate of phytoplankton was estimated to be 2 m/hr. A trial was also made to calculate the rate of grazing the phytoplankton.

6. STRESZCZENIE

W pracy podano wyniki badań nad fluktuacjami dobowymi zawartości chlorofilu w planktonie oraz nad wahaniami intensywności fotosyntezy. Pomiary chlorofilu przeprowadzono na trzech stacjach w Zatoce Gdańskiej oraz na jednej stacji na Morzu Północnym. Zaobserwowano występowanie najmniejszych koncentracji chlorofilu przed wschodem słońca. Największe koncentracje chlorofilu notowano we wczesnych godzinach popołudniowych. Pomiary produkcji pierwotnej przeprowadzono na Głębi Gdańskiej. Zaobserwowano stosunkowo duże różnice produkcji pierwotnej za okres przedpołudniowy i okres popołudniowy. Obliczono stosunek przyrostu chlorofilu do produkcji pierwotnej, który dla okresu letniego przy dobrych naświetleniach wynosi 0,034 mg chl/mg C.

Skalkulowano szybkość opadania fitoplanktonu na około 2 m/godz. Podjęto także próbę obliczenia szybkości wyżerania fitoplanktonu.

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J. DONNER

BERICHT ÜBER FUNDE VON RÄDERTIEREN (ROTATORIA) AUS DER ANTARKTIS

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Ausgezeichnete und zusammenfassende Arbeiten über die Mikrofauna (darunter die Rädertiere) der Antarktis haben wir von S u d z u k i (1964 ab), S u d z u k i, S h i m o i z u m i (1967), hier such weitere Literatur. Erinnert sei an eine kleine russisch geschriebene Abhandlung von K u t i k o v a (1958), ferner an mehrere Berichte von D o u g h e r t y (1964 ab), D o u g h e r t y et al. (1960), D o u g h e r t y, H a r r i s (1963), die antarktische Rädertiere erwähnen.

Im Jahr 1962 erhielt ich zur Bestimmung der Rotatorien einen "**Al**genfilz" ('algal felt") vom Ross Island, gesammelt von L. G. H a r r i s in Zusammenarbeit mit E. C. D o u g h e r t y. Darin waren die Arten *Adineta grandis* Murray (Abb. 1), *Habrotrocha constricta* (Dujardin) und *Macrotrachela insolita* de Koning var. (Abb. 2). Vorher schon war mit im gleichen Material begegnet *Philodina gregaria* Murray (Abb. 3). Diese Art sowie *Adineta grandis* und *Macrotrachela insolita* var. sind beschrieben nach den antarktischen Funden bei D o n n e r (1965) (200—202 mit Fig. 147 a; 273 mit Fig. 200 a und 132 mit Fig. 98 1—m).

Schliesslich bekam ich im Jahr 1970 durch Herrn Profesoren Dr R. Z. K l e k o w s k i aus Nencki Institut für Experimentale Biologie in Warszawa eine Probe aus einem kleinen See vom Haswell Island (66°31'S 93°00'E, Queen Mary Land), nahe der Sowjetischen antarktischen Station "Mirnyj". Diese Probe wurde durch polnische Biologen, Dr S. R a k u s a --S u s z c z e w s k i und Mgr K. W. O p a l i ń s k i, im Jahr 1969 in der Antarktis gesammelt und nach Warszawa in lebendem Zustand gebracht.

Die Probe enthielt: *Adineta gracilis* Janson, *Adineta grandis* Murray, *Habrotrocha elusa elusa* Milne, *Philodina gregaria* Murray, und die monogononte Art *Ephiphanes senta* (O. F. Müller).

Alle bdelloiden Tiere waren karotinrot gefärbt, ausser einigen Individuen von *Habrotrocha elusa*.
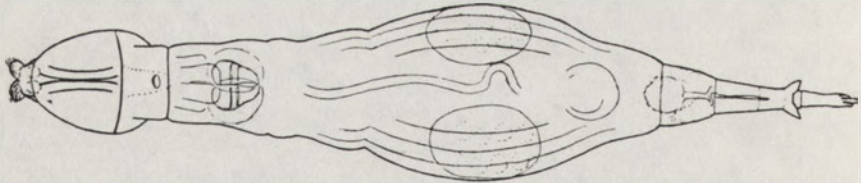
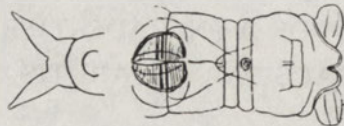Abb. 1. *Adineta grandis,* total (aus D o n n e r 1965)

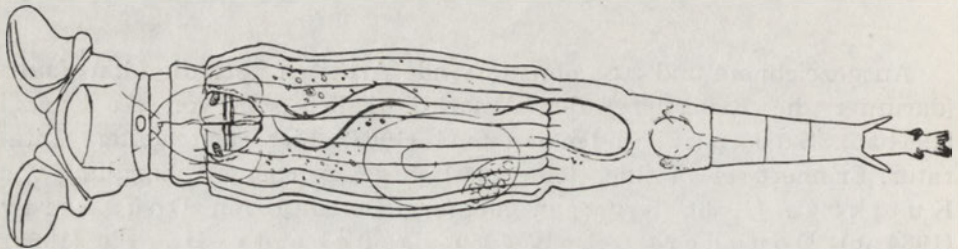Abb. 2. *Macrotrachela insolita* var., Kopf und Sporen (aus D o n n e r 1965)

Abb. 3. *Philodina gregaria,* total beim Rädern (aus D o n n e r 1965)

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A. HILLBRICHT-ILKOWSKA

MORPHOLOGICAL VARIATION OF *KERATELLA COCHLEARIS* (GOSSE) (ROTATORIA) IN SEVERAL MASURIAN LAKES OF DIFFERENT TROPHIC LEVEL

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ABSTRACT

The abundance and period of occurrence of *Keratella cochlearis f. tecta* is extending with the increase of degree of eutrophy of the water body. The average individual size is smaller in August (period of maximal abundance of phytoplankton) in comparison to that in June and in the epilimnion in comparison to meta- and hypolimnion. The vertical differentiation on individual size is maintained in the circadian cycle.

1. INTRODUCTION

Keratella cochlearis (Gosse) is one of the most cosmopolitan and abundant species of planktonic rotifers. It is characterized also by a greatest morphological variation among Rotatoria. This variation regards the following features: length of spines of the lorica, particularly of posterior spine, size of the lorica, form of structural elements of the lorica and their ornamentation, form of the lorica. The size of lorica and length of posterior spine undergo the greatest variation (Fig. 1). Variation of these features served L a u t e r b o r n (1901) to distinguish forms with decreasing size of lorica and length of posterior spine, arranged in a so-called "tecta" series. This series is initiated by the form macracantha, the largest one and with the longest spine (Fig. 1 A), followed by forms with smaller lorica and shorter posterior spine — *f. typica* (Fig. 1 BCD) and *f. micracantha* (Fig. 1 EF). This series is closed by a minute form, devoid of posterior spine, so called *f. tecta* (Fig. 1 GH).
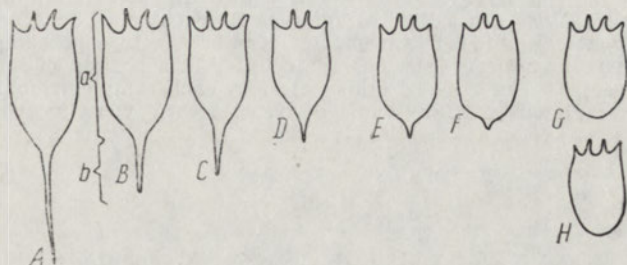

Fig. 1. "Tecta" series of *Keratella cochlearis*: A — *f. macracantha* (after Voight 1957); B, C, D — *f. typica*; E, F — *f. micracantha*; G, H — *f. tecta* (after P e j l e r 1957). a — length of lorica, b — length of posterior spine

The degree of development of particular forms and their occurrence in a population of *K. cochlearis* in a given water body, may be various. Most frequently the simultaneous occurrence of two forms (e.g. *f. typica* and *f. tecta*) is observed, occasionally several forms with varieties exhibiting intermediate features.

The analysis of morphological variation of *K. cochlearis* population leads to a distinction of two general patterns (P e j l e r 1957, 1962). First one concerns interhabitat variation that results in morphological individuality of the whole *K. cochlearis* population occurring in a water body. The second one relates to seasonal variation, manifesting itself by a directed tendency of changes in size of individuals in the population of a given water body. As regards the first type of variation, it has been generally found that in fertile water bodies, e.g. eutrophic and hypertrophic lakes (like those polluted with sewage) and in ponds the average individual size of *K. cochlearis* is smaller and their posterior spines are shorter, in comparison with individuals occurring in less fertile water bodies, like meso- and oligotrophic lakes. P e j l e r (1962) found a positive correlation of individual size with transparency of a dozen of Swedish lakes he investigated. This may suggest that the abundance of phytoplankton and seston is the factor influencing a local morphological variation of *K. cochlearis* population.

The second type of variation, the seasonal one, is a widespread phenomenon, particularly as regards populations occurring in larger water bodies, including lakes. During the time from spring to autumn the average individual size decreases and at the same time the occurrence of *f. tecta* is being intensified (C a r l i n 1943), so that at the end of summer and in autumn the share of this form is high and it may dominate in the population of *K. cochlearis*. This in turn points to a thermic and/or trophic factor as possibly controlling the cyclic changes of size and shape of individuals of *K. cochlearis*.

As follows from the foregoing, the character of variation of *K. cochlearis* (analogically to some other species of Rotatoria) is in some measure opposed to environmental and seasonal variation of planktonic crustaceans as Daphnia or Bosmina. In these genera the improvement of trophic conditions results in an increase of body size, whereas the cyclic variation connected with water temperature and density (cyclomorphosis) consists in an enlargement or lengthening of certain body elements (head, antennae) (M a n u j l o v a 1964), but not in a decrease, as in the case of *K. cochlearis*.

The present investigation aims at analysing the occurrence of *f. tecta* in several lakes of a various morphological and trophic character, as well as analysing in details the seasonal and vertical variation of all individuals of *K. cochlearis* in Lake Mikołajskie, a typical eutrophic one.

2. TERRAIN DESCRIPTION AND METHODS

The investigations were carried out on the following lakes: Warniak (pond-like, maximum depth 3.7 m), Jorzec (strongly eutrophic, bradymictic, maximum depth 11 m), Flosek (dystrophic, maximum depth 8 m), North Mamry (α-mesotrophic, maximum depth 44 m), Tałtowisko β-mesotrophic, maximum depth 39.5), Mikołajskie (eutrophic, maximum depth 27.8 m), Śniardwy (eutrophic, polymictic, maximum depth 21.2 m). On lakes Mikołajskie and Tałtowisko the investigations were carried out during two succeeding years, on the remaining ones during one season. Samples for quantitative examination were collected every 5—14 days from April till November (except for the Lake Mamry North where the investigations were carried out only in summer) using a 5-litre sampler of B e r n a t o w i c z type (B e r n a t o-w i c z 1953). A net was used with meshes of 50 microns. In each sample the *K. cochlearis* individuals and forms (Fig. 1) were counted in a portion of sediment corresponding to at least 0.5 l of filtered lake water. In each sample from Lake Mikołajskie at least several tens of individuals of *K. cochlearis* were moreover measured, separately the length of lorica and of posterior spine (scheme of measurement — Fig. 1).

3. RESULTS

In the examined water bodies the species *K. cochlearis* is one of most numerous components of zooplankton (numbers from several hundreds to several thousands per litre), particularly in strongly eutrophic lakes

(Hillbricht-Ilkowska 1967). It appears at the beginning of April and occurs incessantly till the end of November. Almost exclusively two forms are present — *typica* and *tecta*, both *f. macracantha* and *micracantha* were encountered sporadically and in small numbers.

Analysing the occurrence of *f. tecta* in the examined populations of *K. cochlearis* (Table I) one can state, that the duration of occurrence of this form (in relation to occurrence of the species), its mean share in the population and mean abundance during its occurrence, are in general

Table I. The duration of occurrence, abundance and the share of *K. cochlearis f. tect*} in whole population of *K. cochlearis* in the epilimnion of several lakes of differena morphometry and trophy

Max. depth	Lake (type, year)		Period of occurrence of *f. tecta*	Duration of occurrence in relation to whole population (%)	Mean number *f. tecta* (ind./1)	Share of *f. tecta* in whole population (%)
above 20 m	Mikołajskie (eutrophic)	1963	15 June − 15 Nov.	70	90	36
		1964	1 July − 10 Nov.	65	43	28
		1965	15 June − 10 Nov.	65	72	30
	Tałtowisko (β-mesotrophic)	1963	1 July − 15 Nov.	65	51	22
		1964	1 Aug. − 1 Oct.	30	41	23
	Mamry North (α-mesotrophic)	1967	1 July − 1 Sept.	−	4	5
below 20 m	Warniak (pond-like)	1967	1 June − 20 Sept.	71	35	16
	Jorzec (eutrophic)	1967	1 Aug. − 1 Oct.	41	15	10
	Śniardwy eutrophic)	1966	20 July − 20 Oct.	48	11	14
	Flosek (dystrophic)	1966	1 July − 1 Sept.	46	2	3

greater in deeper lakes (over 20 m) in comparison to shallower ones, whereas within lakes similar as to their morphometry, these values are greater in more fertile lakes (eutrophic) in comparison with less fertile ones (mesotrophic, distrophic). Consequently e.g. these values are in

general greater in an eutrophic Lake Mikołajskie in comparison with β-mesotrophic one Tałtowisko and α-mesotrophic North Mamry; in the last one the share of this form in *K. cochlearis* population amounts to merely a few per cent. In the group of shallower lakes (below 20 m) — this form occurs most persistently and abundantly in a pond-like Lake Warniak, but less abundantly and during a shorter period in eutrophic lakes represented by lakes Śniardwy and Jorzec, and only sporadically in a dystrophic Lake Flosek.

The above said differences in the character of occurrence of *K. cochlearis f. tecta* in the chosen lakes, seem to point to its limnetic character on the one hand, i.e. more abundant and persistent occurrence in deeper lakes, and on the other to its indicatory character as for trophy of the water body. These differences do not appear accidental, i.e. connected with specificity of the given vegetative season (investigations in particular lakes were carried out in different years) which is proved by results from lakes Mikołajskie and Tałtowisko (Table I) obtained in several successive years.
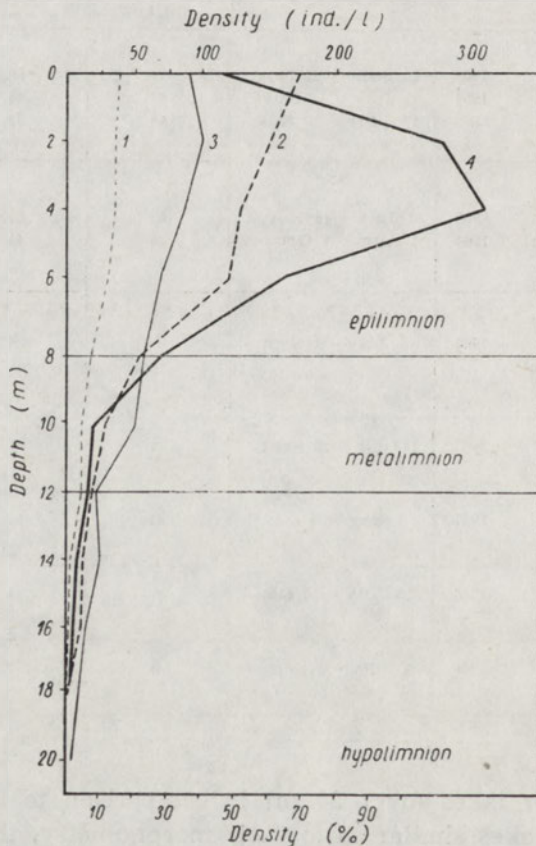

Fig. 2. Vertical distribution of the number of *Keratella cochlearis* and the percentage of *f. tecta* in July and August in Mikołajskie Lake. Percentage of *f. tecta* in July (1) and August (2), number of *K. cochlearis* in July (3) and August (4)

K. *cochlearis* f. *tecta* occurs mainly in surface layers (Fig. 2). In these layers the share of f. *tecta* in July (low density of population) attains 20⁰/₀, whereas in August (numerous population) it rises even to 70⁰/₀. The share of f. *tecta* in meta- and hypolimnion of this lake does not exceed in any of these periods 10⁰/₀ of the whole population. It is even lower in meta- and hypolimnion of the remaining lakes of lower trophy and in Lake North Mamry this form was not found at all in meta- and hypolimnion.

A detailed analysis of the course of seasonal changes in abundance of K. *cochlearis* f. *tecta* (Fig. 3) in surface layers of Lake Mikołajskie induces to the statement, that this form appears in the population K. *cochlearis* not before mid-June, when the epilimnion temperature is at least 16°C. The discussed form is encountered in the lake till the end of autumnal circulation, when the temperature of lake water falls to about 9°C. The highest percentage of form tecta in epilimnetic population of K. *cochlearis* is observed in August and September (Fig. 3).
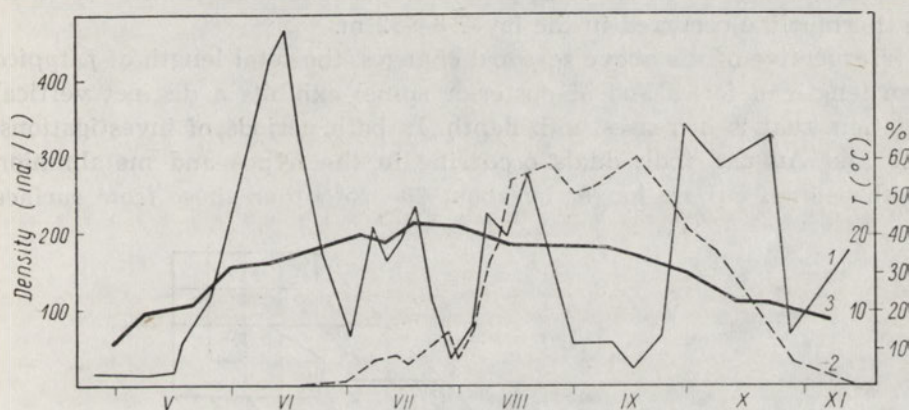

Fig. 3. Seasonal changes of the number of K. *cochlearis* (1), percentage of f. *tecta* (2) and temperature (3) in epilimnion of Mikołajskie Lake (1964)

Beside the seasonal and vertical changes of occurrence of K. *cochlearis* f. *tecta*, the size of f. *typica* as well as the size of the f. *tecta* itself undergoes also seasonal and vertical changes (Table II).

The mean total length of individuals of f. *typica*, occurring in the population K. *cochlearis* of the Lake Mikołajskie in mid-June, is in all thermic layers greater in comparison with specimens of the same form occurring in mid-August (Table II). And so, mean total length of individuals occurring in epilimnion (0—7 m) in June falls within the range 150—180 μ, while in August 140—160 μ; for deeper layers (8—20 m) the ranges are 180—200 μ and 160—190 μ, respectively. On an average

Table II. The variation in the dimensions of *K. cochlearis f. typica* and of f. *tecta* as related to depth (means from 20—40 measuremants)

Depth (m)	f. typica						f. tecta
	lorica		posterior spine		total length		lorica
	June (μ)	August (μ)	June (μ)	August (μ)	June (μ)	August (μ)	August (μ)
0	112	100	40	36	151	140	98
4	112	105	43	44	154	145	100
8	128	110	56	50	179	160	101
12	125	115	59	54	187	175	105
16	133	125	57	60	185	183	112
20	135	127	63	60	196	187	120

the specimens occurring in the epilimnion in August are shorter by 15%/o than those occurring in June. This difference, as it follows from Table II, consists of length reduction of the lorica as well as of pesterior spine. It should be added, that the thermal stratification in both months of the year of investigation was similar: the epilimnion (0—8 m) temperature was about 19°C, that of hypolimnion (deeper than 12 m) — 8—9°C; the thermocline occurred in the layer 8—12 m.

Irrespective of the above seasonal changes, the total length of f. *typica* (both length of lorica and of posterior spine) exhibits a distinct vertical variation, that is increases with depth. In both periods of investigations, June and August, individuals occurring in the hypo- and metalimnion (depth below 8 m) are longer by about 20—25%/o than those from surface
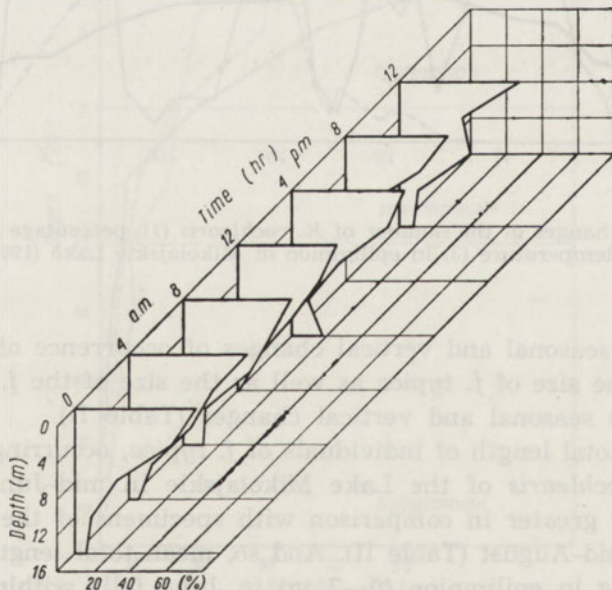

Fig. 4. Diurnal changes in vertical distribution pattern of *K. cochlearis f. tecta* (in percentage of the total number of *K. cochlearis*) in August, Mikołajskie Lake

layers. The changes of dimensions of lorica and of spine in *K. cochlearis* from Lake Mikołajskie seem to be proportional, since the ratio of spine length to total length is similar in all individuals from different thermal strata and amounts to about 1/3.

The vertical variation of lorica size of *f. tecta* is analogical to this variation of size of *f. typica* (Table II). Although the decided majority of individuals of *f. tecta* occurs in epilimnion (Fig. 2) the few ones found in the hypolimnion are by 20—25% longer than those from the epilimnion.

The morphological differentiation of populations from various layers persists in the circadian cycle. This is indicated by: lack of changes in
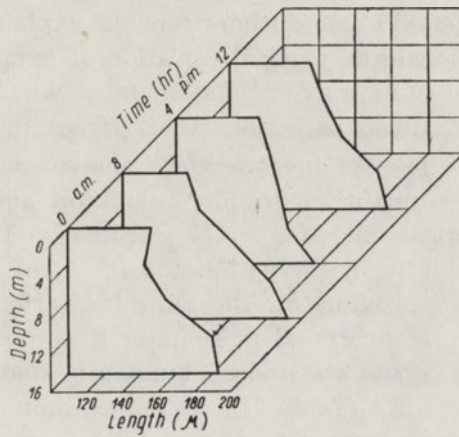

Fig. 5. Diurnal changes in vertical distribution of the mean size of *K. cochlearis f. typica* individuals; August, Mikołajskie Lake
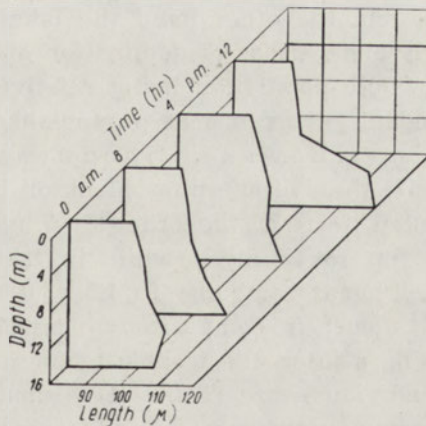

Fig. 6. Diurnal changes in vertical distribution of the mean size of *K. cochlearis f. tecta* individuals; August, Mikołajskie Lake

vertical stratification of *f. tecta* in circadian cycle (Fig. 4) and results of measurements of individuals of *f. typica* and *f. tecta* sampled at various depths and various hours in mid August (Fig. 5, 6), at a time most strongly manifested thermal stratification in Lake Mikołajskie. This seems to prove the lack of circadian migrations crossing the borders of thermal strata and lack of mixing of populations of various morphological character.

4. DISCUSSION

The above observations concerning both the character of occurrence of *Keratella cochlearis f. tecta* and the character of size changes in *f. typica* and *f. tecta*, corroborate the results of other authors (C a r l i n 1943, C o m i t a, M u n r o 1960, P e j l e r 1957, 1962, B u c h n e r et al. 1957, P o u r r i o t 1964). These authors tend to explain the variation of *K. cochlearis* by seasonal and vertical variation of temperature or by the trophic factor. However no univocal statement of what factor is decisive and what is its mechanism of action results from these investigations.

The results of the present investigation seem to point to the trophic factor, connected presumably with phytoplankton abundance, as deciding over morphological variation of *K. cochlearis*. The tecta form of this species occurs chiefly in the epilimnion (0—7 m), the average temperature of which is approximately the same for various deep lakes (Mikołajskie, Tałtowisko, Mamry) and in summer it is most often 17°C, nevertheless this form occurs the more abundantly and persistently, the higher is the lake fertility (Table II). In the epilimnion of Lake Mikołajskie the maximum occurrence of *f. tecta* falls on periods of both high temperature (August) and low one (September) (Fig. 3). Individuals of *K. cochlearis* occurring in June and August differ as to morphology and size despite of similarity of mean temperature for the respective thermal strata in both periods. On the other hand the lakes in which *f. tecta* occurs most abundantly and periods of domination of this form, the size of individuals of the whole population being relatively small, both are characterized by abundant occurrence of phytoplankton. And so according to H i l l b r i c h t - I l k o w s k a, S p o d n i e w s k a (1969) and S p o d n i e w s k a (1967) the average phytoplankton biomass in the epilimnion of Lake Mikołajskie is of the order 5—7 mg/l with a distinct maximum in August (up to 15 mg/l) while in lakes Tałtowisko and Śniardwy the average biomass amounts to 1.5—3.0 mg/l with summer maximum significantly lower in comparison to an analogical period in Lake Mikołajskie. Basing also on the trophic factor one can explain the vertical variation of individual size (Table II) — smaller ones and with the excess of *f. tecta* display the most abundant occurrence in surface layers, that is not only the warmest layers, but also those with the highest phytoplankton concentration. Analogical differences between in-

dividuals from various thermal strata were noticed by B e r z i n s (1958) for the species *Kellicottia longispina.*

Thus in the case of this species, analogically to other rotifers, the possible indicator of favourable food conditions would be the occurrence of individuals of smaller size as well as of *f. tecta,* as a small morphological form. In another rotifer species, *Brachionus calyciflorus,* R a u h (1963) have found that individuals cultured either in better food conditions, or in higher temperature, are smaller than those cultured in worse food conditions or at lower temperature. These experimental results demonstrate that the effect of both trophic and thermal factors may manifest itself in a similar variation. Nevertheless in the case of the species *K. cochlearis,* in compliance with the present results, its morphological variation — occurrence of a minute form and a decrease of individual size — seems to be chiefly depending on the trophic factor. Such explanation of causes of variation in this species is admitted also by P e j l e r (1962).

It remains to be explained what adaptative significance may have in this species the shortening of body dimensions in favourable food conditions, when at the same time in the case of planktonic organisms as crustaceans, particularly Cladocera, the opposite is common — individuals living in favourable food conditions, e.g. fertile water bodies, are characterized by greater dimensions of the body. In this point the hypothesis of E r m a n (1962) on the role of posterior spine and of the lorica as a some sort of adaptation enabling a better utilization of nutritive suspension, seems interesting although controversial. *K. cochlearis* is a typical sedimentator, that is it drafts the food particles to the mouth by means of water currents raised by movements of the trochal disc. According to analyses of stomachs carried out by this author, *K. cochlearis* feeds mainly on very fine detritus (order of $1-2\,\mu$), bacteria and very fine nannophytoplankton. This explains the occurrence of the discussed species in periods of phytoplankton abundance (spring) as well as in periods of summer blooms composed mainly of Cyanophyceae, when the abundance of detritus and bacteria is high. According to the suggestion of E r m a n (1962), the posterior spine acts as a sort of stabilizer, making the functioning of the trochal disc more effective, that enables the animal to provide against lack of food in conditions of its low concentration. On the other hand in conditions of high food concentration the increase of effectiveness of functioning of trochal disc is not necessary, hence in such conditions the small forms may occur, or forms devoid of posterior spine like *f. tecta.* In compliance with this hypothesis both forms would then differ in velocity of movement and rate of filtration, the values being higher for *f. typica* (with spine-stabilizer) and lower for the form tecta (without spine). In fact H a l b a c h (1971) carrying out experiments with *Brachionus calyciflorus* — a species of a variation analogical to *K.*

cochlearis, has noticed that individuals with posterior spines exhibit a higher filtration rate and move faster than those devoid of posterior spines [1].

Although *K. cochlearis f. tecta* seems to be an indicatory form for trophic conditions of the water body, since it occurs the more persistently and abundantly, the higher is the eutrophy, however its share in the population of *K. cochlearis* in deeper lakes is higher than in shallower ones. This may lead to a supposition that in deeper water bodies exist general possibilities of a marked and persistent environmental differentiation of pelagic strata (thermal, light, food stratification, thus creating conditions that stimulate the species variation and coexistence of various forms to a higher degree than shallower lakes, characterized generally by greater homogeneity of the water column. In a lake where the water level was rapidly lowered, shifting the conditions towards the littoral ones, P a r i s e (1961) established, that the population of *K. cochlearis* that exhibited before the lowering wide range of variation of individuals, after the lowering showed a narrower range and smaller average size of individuals. Analogically P e j l e r (1957) and C a r l i n (1943) suggest, that in shallow water bodies one form is found in general, exceptionally coexisting two forms, whereas in conditions of great lakes the coexistence of several forms is encountered more frequently, the occurrence of two forms being very common.

5. SUMMARY

The occurrence of *K. cochlearis f. tecta* in several water bodies, differing morphologically and trophically, was analysed, and the occurrence of this form and morphological variation of individuals *K. cochlearis* in an eutrophic Lake Mikołajskie was examined in detail.

It has been found, that *f. tecta* occurs chiefly in the epilimnion, more abundantly and persistently in deeper lakes in comparison to shallower ones, whereas within lakes morphologically similar — it is more numerous in fertile ones.

The average size of individuals of *K. cochlearis* occurring in Lake Mikołajskie is smaller in August than in June, at similar thermic conditions, but different phytoplankton abundance, that attains its maximum in August (biomass about 15 mg/l). The size of individuals of *K. cochlearis,* including tecta forms occurring in the epilimnion is smaller by 20–25% than that of individuals found in the metalimnion and hypolimnion.

The differentiation of individuals is maintained during the whole summer season (comparison was made of results from mid-June and mid-August) and during the twenty four hours cycle.

An assumption is put forward of a trophic factor, connected presumably with the abundance of phytoplankton and seston, as decisive for the morphological variation of *K. cochlearis.*

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[1] After the opinion of this author these results do not agree with the hypothesis of E r m a n (1962), since he admits that after this hypothesis individuals devoid of posterior spines should move faster and filter more effectively than those with spines.

6. STRESZCZENIE

Analizowano występowanie *K. cochlearis f. tecta* w kilku zbiornikach różnych morfologicznie i troficznie oraz szczegółowo przebadano występowanie tej formy oraz zmienność morfologiczną osobników *K. cochlearis* w eutroficznym jeziorze Mikołajskim.

Stwierdzono że *f. tecta* występuje głównie w epilimnionie, licznej i trwałej w zbiornikach głębszych w porównaniu z płytszymi, zaś w obrębie podobnych morfologicznie jezior — liczniejsza jest w jeziorach żyznych.

Przeciętna wielkość osobników *K. cochlearis* występując w jeziorze Mikołajskim jest mniejsza w sierpniu w porównaniu z czerwcem przy podobnych warunkach termicznych, ale różnej obfitości fitoplanktonu, którego maksymalny rozwój (biomasa rzędu 15 mg/l) przypada na sierpień. Wielkość osobników *K. cochlearis*, w tym *f. tecta* występujących w epilimnionie jest około 20—25% mniejsza od osobników przebywających w meta- i hypolimnionie.

To zróżnicowanie osobników utrzymuje się w całym sezonie letnim (porównywano połowę czerwca i połowę sierpnia) oraz w cyklu dobowym.

Wysunięto przypuszczenie o decydującym dla zmienności morfologicznej *K. cochlearis* czynniku troficznym związanym prawdopodobnie z obfitością fitoplanktonu i sestonu.

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THE DYNAMICS OF GROWTH OF EXPERIMENTAL POPULATIONS OF THE ROTIFER *BRACHIONUS RUBENS* EHRBG

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ABSTRACT

Demographic processes of *Brachionus rubens* populations were investigated in cultures with either *Aerobacter aerogenes* bacteria or *Chlorella vulgaris* algae as food, differing in volume and in initial densities of animals. Biologically most vital were the populations fed with algae, with low initial densities. Unfavourable environment conditions stimulate an increase of the level of micticity, a shift of reproduction pattern from parthenogenetic to sexual and, in effect, a decrease of the extent of a population. Mictic females of *B. rubens* can be impregnated only before they start to produce eggs. Copulation after haploidal eggs had been produced does not cause impregnation nor change the type of eggs.

1. INTRODUCTION

We know little about rotifers as a link in the chains of matter and energy transformations in trophic biocenoses. However, many authors believe that because of their speed of reproduction and their large amounts, rotifers are apt to play an important role both as consumers and as food for other trophic levels (E d - m o n d s o n 1960, 1962, 1965, G a l k o v s k a j a 1965, G r y g i e r e k 1963, H i l l - b r i c h t - I l k o w s k a 1964). Plankton Rotatoria are particularly important in fish farms, since they are the basic food for fry of e.g. *Cyprinus carpio* during the first period of its life (T r z o c h - S z a l k i e w i c z 1971).

As the role of rotifers in a reservoir is determined by the size of a population, the dynamics of growth of natural and laboratory populations are studied by many authors and in many aspects.

The materials here presented are an introductory part of a bioenergetic study of *Brachionus rubens*, a plankton microphiltrator.

The species was selected because of its mass appearance, usually during the whole vegetation season, in strongly eutrophized reservoirs, such as fish ponds and sedimentary ponds in sewage clearance systems.

The cycle of development of Brachionidae is marked by metagenesis (Fig. 1). Parthenogenetic generations of amictic females lay diploidal oocytes (without meiosis) from which females only develop, either amictic or mictic. The oocytes of mictic females undergo meiosis, i.e. they are haploidal. Males devolop from unimpregnated haploidal eggs of mictic females. Impregnated oocytes are resting eggs from which the first generation of amictic females would be born in spring.

The appearance of mictic females and sexual reproduction is stimulated by unfavourable changes of the environment (B i r k y, G i l b e r t 1971, R u t t n e r - - K o l i s k o 1964), e.g. by a sudden fall of temperature or a change of the diet.
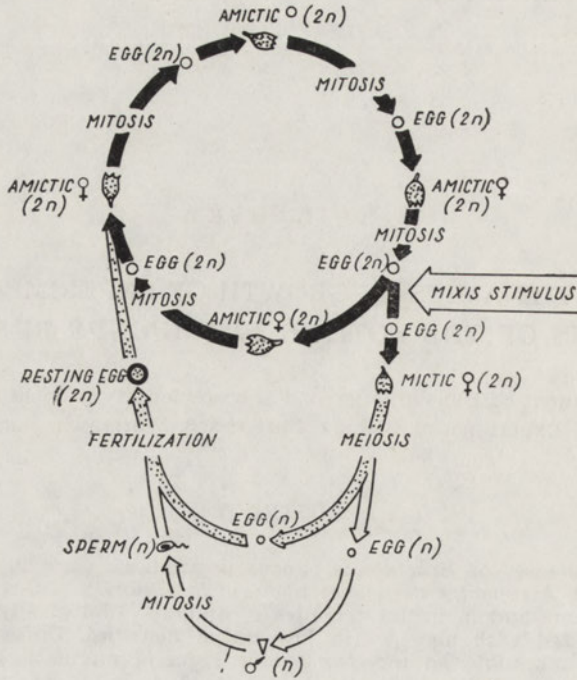
Fig. 1. Life cycle of the monogonont rotifers. "Mitosis" and "meiosis" refer to the oocyte maturation divisions in amictic and mictic females, respectively (from B i r k y 1964)

The aim of the present work was to investigate the parameters of individual development and the demographic patterns of experimental populations of *B. rubens* fed with two types of food: the algae *Chlorella vulgaris* and the bacteria *Aerobacter aerogenes*.

2. MATERIAL AND METHODS

Brachionus rubens was taken for the experimental cultures from sedimentary ponds of a yeasts factory at Józefów near Błonie in which they were very numerous (about 2000 individuals per liter) during the whole season of vegetation. The initial material were resting eggs drawn with mud and stored in a refrigerator at about +4°C. The cultures were initiated by transporting portions of about 1 g of mud to Petri plates; they were drowned with water kept still for some time and placed in thermostats (21 ±0.2°C). During the hatching period (from the second until the fifth day after the drowning of mud) the plates were inspected twice a day and the rotifers were transported into small vessels with pure food suspension.

Two kinds of food were applied: suspensions of *Chlorella vulgaris* algae and suspensions of bacteria *Aerobacter aerogenes*. *A. aerogenes* was cultivated on skewes (broth solidified with 2% agar) from which bacteria were taken daily and suspended in physiological salt. The algae were drawn from a monoculture ran on Prat's medium. Bacteria concentration was defined by means of a nefelometer, and algae concentration by counting their cells in a Thoma-Zeiss chamber.

In all the cultures the rotifers were transported once a day to fresh environments in which the concentration of food was always 10^6 cells of *C. vulgaris* or $15 \cdot 10^7$ cells of *A. aerogenes* (about 30 µg dry weight per 1 ml).

The experiment was carried out at 21±0.4°C.

In order to establish the life time, fecundity and time of embryo devolopment of *B. rubens*, 588 individuals 0—2 hr old were isolated and cultivated in 1 ml suspension of algae or bacteria, each one separately. Those cultures were examined

every 2 hours in order to record the time of egg laying and of the hatching of young which were isolated.

Death rates in the consecutive phases of development of the rotifers were also investigated in individual cultures. 100 resting eggs and 276 eggs from which mictic females developed had been picked for observation. A half of the latter were cultivated individually and the females laid haploid eggs; to each of the remaining females 4 males were introduced. The death rates were expressed in percentages of the initial number of the eggs selected for observation.

The dynamics of development of the *B. rubens* population was investigated in cultures differing with respect to the kind of food, volume of the environment and initial number of amictic females, as it is indicated in Table I.

Table I. The scheme of population experiments

Food	Capa-city (ml)	Initial num-ber	Num-ber of tests
A. aerogenes	0.2	1	27
		5	23
		10	21
	0.5	1	30
		5	30
		20	24
C. vulgaris	0.5	1	10
		5	10
		20	10

The cultures were examined every 24 hr; numbers of amictic and mictic females and eggs were recorded and dead individuals and eggs were withdrawn. As the period of development of parthenogenetic eggs from their laying to the hatching is shorter than 24 hr, the actual numbers of eggs laid between two controls were computed as a difference between the total number of rotifers plus their eggs and their number on the previous day.

The data collected in this way permitted to calculate the following demographic indices of the populations:

fecundity rate — the number of eggs (in per cent) laid by a statistical female during a time unit (24 hr),

death rate — the percentage of dead individuals,

intrinsic rate of population increase r_m — an actual rate of population increase per one individual in definite, constant circumstances, without food and space limitations,

net reproduction rate R_o — the multiple of population increase during one generation time T.

The above indices were computed by means of formulas from A n d r e w a r t h a, B i r c h (1954).

The indices (except the first one) were also calculated for populations cultivated in 20 ml suspensions of *C. vulgaris*.

3. RESULTS

The data on lifetime, fecundity and embryo devolopment time are presented in Table II.

It can be seen that the females fed with bacteria live shorter, start to lay eggs later and produce less eggs during their lifetime than the females fed with algae.

The lifetime of males is the same in both nutritional environments; they do not take food at all.

Table II. The parameters of individual development of *Brachionus rubens*

Group	Fo-od	No. of tests	Lifetime (days±S.E.)	No. of eggs (±S.E.)	Embryo development time (days±S.E.)	Postembryo development time (days±S.E.)	Frequency of the laying eggs (days±S.E.)
Amictic females	a	104	10.5±1.2	13.6±2.9	0.51±0.11	1.8±0.3	0.45±0.10
	b	99	7.3±1.3	6.4±4.1	0.55±0.13	2.5±1.0	0.68±0.13
Mictic unim-pregna-ted fe-males	a	86	7.9±1.7	19.4±3.3	0.31±0.05	2.0±0.5	0.33±0.04
	b	70	6.9±1.8	12.8±5.9	0.32±0.06	2.3±0.7	0.34±0.02
Mictic impreg-nated females	a	71	7.5±1.1	7.2±2.1	2.46±0.21	2.3±0.6	0.68±0.15
	b	69	6.1±1.3	5.7±3.2	2.53±0.46	2.4±0.5	0.72±0.16
Males	a	42	2.0±0.8	×	×	×	×
	b	47	2.1±0.6				

a — algal food, b — bacterial food.

In Fig. 2 graphs of death rates of three groups of females are shown: amictic (Fig. 2 A), mictic unimpregnated (Fig. 2 B) and mictic impreg-
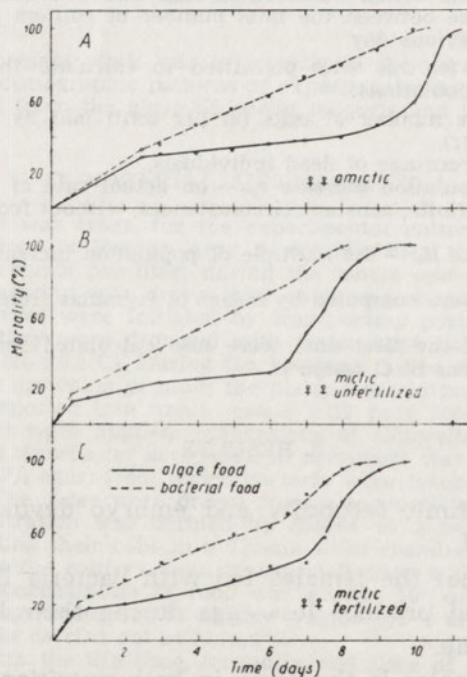

Fig. 2. Death rates curves of *Brachionus rubens* fed with various food. A — amictic females, B — mictic unfertilized females, C — mictic fertilized females

nated (Fig. 2 C), fed with bacteria or with algae. It can be seen that when algae are used as food, the initial death rates are low and they increase suddenly only two or three days before the complete extinction of a cohort, while the death rates of females fed with bacteria are essentially uniform. For all groups the percentages of individuals surviving at any given moment are lower in bacteria cultures.

In the generation of mictic females hatching from resting eggs the death rate during embryo development and hatching is about 50% (during 2.5 days), while for the mictic generation of females it is lower and amounts to 17—23% during a half of a day. The final sections of the death rate lines for all the investigated groups of females are very little slanted to the time axis.

The quantitative dynamics of *B. rubens* populations in cultures of various capacity and initial number of females is represented in Fig. 3.
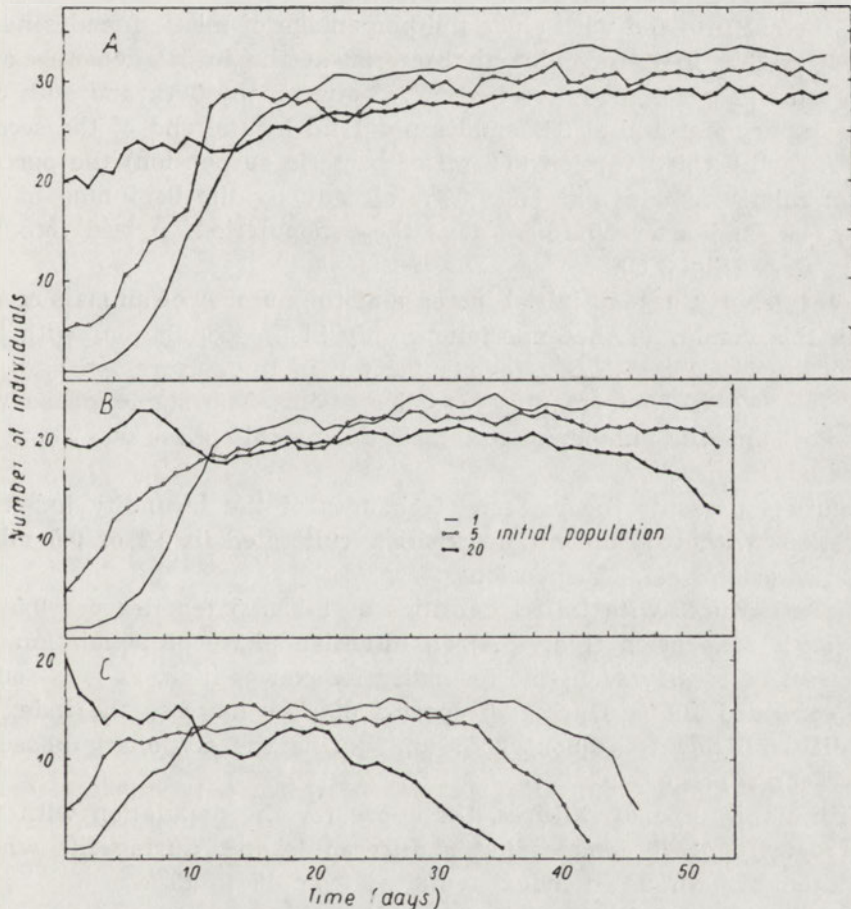

Fig. 3. Dynamics of growth of *Brachionus rubens* populations in cultures: A — with 0.5 ml of *C. vulgaris* suspension, B — with 0.5 ml of *A. aerogenes* suspension, C — with 0.2 ml of *A. aerogenes* suspension

The curves of the sizes of the populations cultivated in 0.5 ml of
C. vulgaris suspension in which the initial densities of Rotatoria were
1 and 5 individuals, are S-shaped. During the logarithmic growth (until
about the 12th day) the curves are parallel; later the changes in amo-
unts of rotifers are virtually identical.

In the populations with the initial density of 20 females per 0.5 ml
the increase of their number is slow and uniform. In this version of
feeding and capacity the stationary size of the population was 31 indi-
viduals.

In cultures of the same capacity (0.5 ml) but fed with bacteria (Fig.
3 B) the period of rapid increase was remarkably shorter; at the highest
initial density the number of individuals fell down during the first two
days, went up during the subsequent four days to the maximum and
then decreased again. During the stable phase the number of individuals
was about 22 in all the three initial densities.

In the cultures fed with algae the percentage of mictic females never
exceeded 12%; in those fed with bacteria, at the initial densities of 1
and 5 females per 1 ml it reached 50% between the 30th and 40th day
of the experiment and at 20 females per 1 ml by the end of the second
decade. In the third version (0.2 ml of bacteria suspension) the percen-
tage of mictic females exceeded 50% already by the beginning of the
first week, and after 30 to 50 days these populations passed into the
resting stage (Fig. 3 C).

A very short phase of initial increase of the number of animals occur-
red, in this version of the experiment, only in the populations with ini-
tial densities of 1 and 5 females per 0.2 ml; in the cultures with 20 fe-
males per 0.2 ml their number was decreasing. The stable phase was
very short and the number of Rotatoria during this phase was about 13
individuals.

Figure 4 presents the pattern of changes of the fecundity index of
populations with varying initial densities, cultivated in 0.2 or 0.5 ml of
either bacteria or algae suspensions.

In the cultures with initial densities of 1 and 5 females per 0.5 ml
C. vulgaris suspension (Fig. 4 A) an intensive phase of population in-
crease can be clearly seen; the fecundity index was high, as it is some-
times exceeded 100%. During the period of slow increase the index of
fecundity fell down to about 20% and during the stationary phase it
was 30% in average.

Within this type of cultures, the curve for the population with the
initial density of 20 females has a different shape; during the whole
experiment the discussed index oscillated from 17 to 23%.

In the cultures fed with bacteria, with similar capacities of the envi-
ronments (Fig. 4 B), high values of the fecundity index were characte-
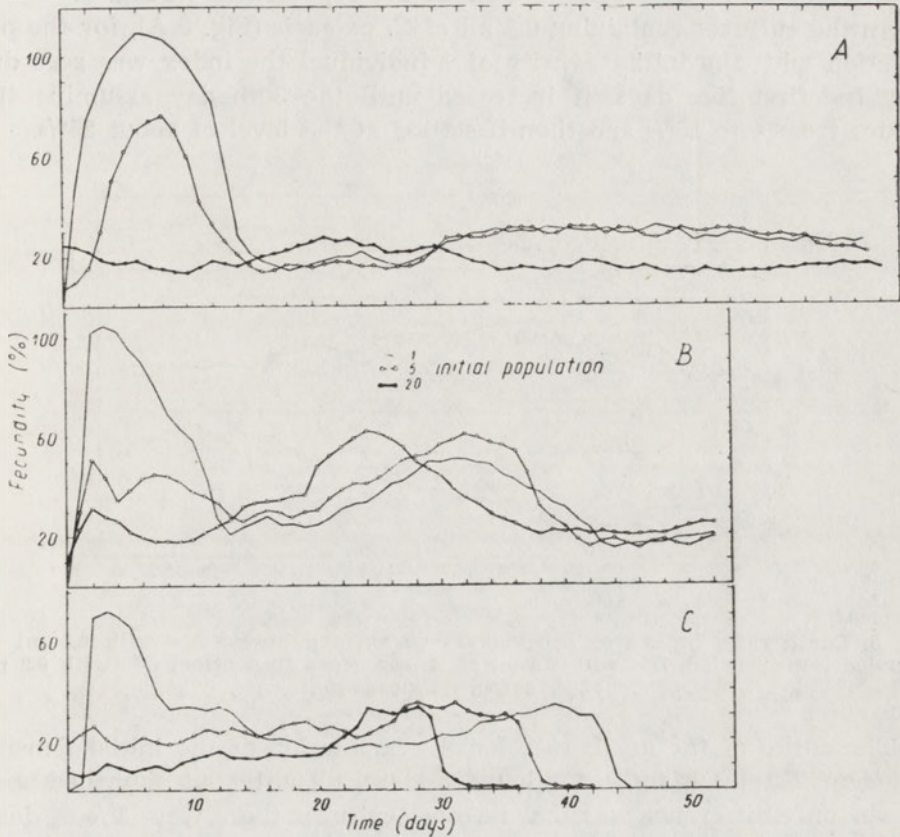ristic for the early period of development of populations with the smal-

Fig. 4. Fecundity indices of *Brachionus rubens* in cultures: A — with 0.5 ml of *C. vulgaris* suspension, B — with 0.5 ml of *A. aerogenes* suspension, C — with 0.2 ml of *A. aerogenes* suspension

lest initial densities. Another period of high fecundity occurred during the fourth decade and it was related to the production of eggs by mictic females.

Similarly, in the cultures with initial densities of 5 and 20 individuals the increase of the fecundity index was related in time to an increase of the number of mictic females. The values of the index during the initial period of development of those populations were in reversed proportion to the prearranged densities (similarly as the latter were related to the intensity of increase).

In the cultures 0.2 ml in volume (Fig. 4 C) high values of the fecundity index for the early phases of growth were recorded only in the populations with the lowest initial density. However, in all the three series of initial densities the fecundity index values were increasing up to 30—40% during the period before the extinction of the whole population, when haploidal and, above all, resting eggs were laid.

The curves of the death rate index are represented in **Fig. 5.**

In the cultures containing 0.5 ml of *C. vulgaris* (Fig. 5 A), for the population with the initial density of 1 individual the index was zero during the first five days, it increased until the 30th day assuming the values from 4 to $16^0/0$ and then it settled at the level of about $25^0/0$.
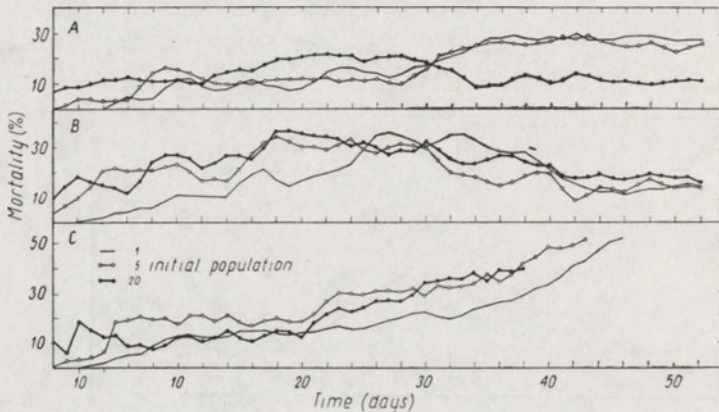

Fig. 5. Death rates indices of *Brachionus rubens* in cultures: A — with 0.5 ml of *C. vulgaris* suspension, B — with 0.5 ml of *A. aerogenes* suspension, C — with 0.2 ml of *A. aerogenes* suspension

The curve of the death rate for the population of the initial density of 5 females per 0.5 ml was virtually identical with that described above; the only difference was that in those cultures there were $2^0/0$ of dead animals as early as the second day.

In the populations with the initial density of 20 females per 0.5 ml of algae suspension the death rate index was $10^0/0$ during the first 14 days and since the 35th day until the end of the experiment; between these dates it was somewhat higher, nearly $20^0/0$.

In the populations cultivated in 0.5 ml of *A. aerogenes* suspension (Fig. 5 B) the patterns of change of the discussed index were similar for all the three initial densities; the curves mounted up during the first 20 days from zero (for 1 and 5 individuals) or from $10^0/0$ (for 20 individuals) to about $30^0/0$. During the subsequent 20 days they oscillated within the range of $20—30^0/0$ and during the last decade they fell down again to about $10—20^0/0$.

In the third version of the experiment (Fig. 5 C) three periods can be distinguished in the patterns of changes of the death rate index: during the initial five days it was less than $5^0/0$ for the initial densities of 1 and 5 females, or $15^0/0$ in average for 20 females. During the subsequent 15 days the index was stable at the level of 15 to $20^0/0$. Since the 20th day until the ultimate extinction of the adult individuals within the population the death rate index increased to $40—55^0/0$.

Besides, the population of *B. rubens* was characterized demographically by the indices of intrinsic rate of natural increase — r_m, net reproduction rate — R_o and generation time — T. The results are plotted in Table III.

Table III. The demographic parameters of *Brachionus rubens* populations (r_m calculated for the generation time T)

Food	Capacity (ml)	Initial number (ind.)	Intristic rate of increase r_m	Generation time T (days)	Net reproduction rate R_o
Algae	20	10	1.140	3.5	10.12
	0.5	1	0.688	3.4	6.18
		5	0.365	3.5	3.74
		20	0.248	3.6	1.35
Bacteria	0.5	1	0.407	3.5	4.20
		5	0.172	3.7	1.71
		20	0.032	3.7	1.10
	0.2	1	0.116	3.8	1.38
		5	0.017	3.8	1.56
		20	—	4.0	0.20

It can be seen that the values of r_m and R_o are higher in populations with lower initial densities of the rotifers (greater volumes of the vessels or lesser numbers of animals) and higher in populations fed with algae than in those fed with bacteria. The generation time T is practically the same for all the types of cultures.

It was observed in individual cultures that the mictic females which started to produce haploidal eggs, did not change the type of eggs laid by them in spite of copulation. Resting eggs were produced by those females only which had copulated before the laying of their first egg. This phenomenon was observed for the first time.

4. DISCUSSION

In the described experiment the type of food — either *C. vulgaris* algae or *A. aerogenes* bacteria — influenced the lifetime, the number of the produced eggs, the time of embryo and postembryo development of *B. rubens;* the influence of algae food was positive and that of bacteria was negative (Table II).

It should be supposed that the results obtained in artificial cultures, fed with both types of food, were lower from the potentialities of the studied organisms because of the use of uniform food and of the cumulation of metabolic products in the environments.

Since in both series of cultures the resources of energy supplied in food were similar, the stronger limiting influence of bacterial food can be accounted for by a lesser physiological utility of *A. aerogenes* administered as the only nutrition. This seems to be confirmed by the fact that the survival time of the fasting females was the same in both feeding environments (Table II).

However, the main cause of the poor results of *B. rubens* cultures fed with bacteria is perhaps the stronger negative impact of the products of metabolism of bacteria. This suggestion can be supported by the observation that the Rotatoria in bacteria cultures survived longer and laid more eggs (by 10 to 13%) if the environment was changed every 8 hours. In algae cultures the results deteriorated by a comparable value if the environment failed to be changed during 2 or 3 days.

It can be well understood that such a detrimental influence of the bacteria environment also impaired the demographic characteristics of *B. rubens* populations.

For example, in the cultures fed with bacteria, the death rates indices were always higher (Fig. 5), fertility was lower (Fig. 4), the intristic rates of increase and net reproduction rates were also lower (Table III), and so was the number of Rotatoria in the stable phase (Fig. 3) — in comparison with the respective values for the algae cultures.

On the other hand, demographical processes were also negatively affected by the density of populations, working as a self-regulatory mechanism which limited the increase of a population by influencing the fecundity and survival.

According with the theory of logistic growth, every new individual added to the population limits its intrinsic rate of increase by a certain constant value. This assumption is valid if a young individual is from the outset identical with the perental animals. This can be taken for granted in case of rotifers, since the differences between young and adult individuals are "quantitative" only, e.g., related to the amount of food consumed, rather than "qualitative", as both groups occupy the same ecological compartment.

Accordingly, it can be expected that populations which begin to develop starting from higher densities will be continuing the upper parts of logistic curves. A good illustration of such a concept are the experiments in which the initial densities of populations were increased, either by putting more individuals into the cultures (one, five or twenty), or else by limiting the volume of the environments (0.5 or 0.2 ml) (Fig. 3).

Higher densities do not exert direct effect by negative interaction, since the studied species tends to live in swarms. In natural conditions, a few dozens of tightly packed rotifers were frequently observed on a single individual of *Daphnia magna*. In artificial cultures, *B. rubens* also tend strongly to assemble together; usually about 80% of the ani-

mals form a single big swarm, or a few smaller ones. Strong currents produced by such swarms prevent the food from sinking to the bottom and make it more readily available.

It seems that the unfavourable influence of the increasing densities of rotifers is related mainly to the fact that they change the conditions in their environment. E.g., the food concentration is apt to decrease by as much as even 20 to 25% of the administered amount during a day, while the products of the rotifers' metabolism become more and more abundant.

Thus we can understand, why the best demographic indices were typical for populations with the lowest densities of rotifers fed with algae (Table III). The values of these indices are lower by only 5 to 7% from those computed by means of E d m o n d s o n (1968) model for optimum conditions of feeding and in 20°C. Biological vigor of the species defined in terms of those indices is high indeed. *B. rubens* can be classified among the organisms which, like some of the Acaridae (S t ę p i e ń 1970) and Protozoa, are able to increase their quantity very quickly, more than ten times during 3.5 days.

Another element of the biology of the species which is vulnerable to environment influences is their peculiar and complex cycle of reproduction. Numerous laboratory studies reveal that changes in this cycle are the response, on the population level, to such factors as a thermic shock, sudden change of the diet, or insufficient supply of some elements in it (B i r k y, G i l b e r t 1971, R u t t n e r - K o l i s k o 1964). In our experiments, too, the conditions of cultivation influenced the reproduction cycle of *B. rubens*. In strongly limited populations (large densities of rotifers, bacterial diet), mictic females appeared quite soon and on mass scale; sexual reproduction set on and resting eggs were produced, while the populations were becoming smaller.

Shifts of the reproduction pattern from parthenogenesis (amictic females) to sexual were also observed, when the rotifers were fed with very low or very high concentrations of food.

Our observations on cultures with individual *B. rubens* seem interesting. When a mictic female had once started to lay haploid eggs, the fact of subsequent copulation did not cause impregnation or bring about the shift in the type of its eggs. Resting eggs were laid only by those mictic females which had copulated before they laid their first egg.

Though this phenomenon is interesting for the physiology of reproduction, it seems to have little significance for the cycle of development of the population. In natural conditions, and indeed in experiments, too, there is a certain percentage of mictic females among the progeniture of the second generation of amictic ones. This happens because the biotic environment is differentiated into micro-environments and because there are individual differences in the vulnerability of amictic females. Thus

the population will not perish even if the prevailing environmental conditions deteriorate suddenly, because a certain number of resting eggs have been produced anyway.

5. SUMMARY

The dynamics of development of *B. rubens* was studied in cultures differing by the type of food (bacteria *A. aerogenes* or algae *C. vulgaris*), the volume of vessels and the initial number of the rotifers. The highest biological vitality is characteristic for populations fed with algae and with low initial densities of the animals (Table II). The deterioration of the demographic indices in populations fed with bacteria and with higher initial densities is perhaps related to the unfavourable influence of the products of metabolism of the rotifers and of the organisms eaten by them.

Less obvious is the influence of the feeding conditions upon individual development, lifetime, fecundity, embryo and postembryo development time of amictic females and of mictic ones, both impregnated and unimpregnated (Table II). However, there are significant differences in the shapes of death rate curves (Fig. 2).

Productive potentialities of *B. rubens* are very large; if food is unlimited and accumulation of metabolits is prevented (cultures of big capacity, low densities of animals, frequent change of medium), the population can be multiplied more than ten times during about 3.5 days.

In such favourable conditions of cultivation, populations are composed in 80 to 90% of amictic females. However, unfavorable conditions cause a change of the reproduction cycle of *B. rubens* from parthenogenetic to sexual (resting eggs are produced), with a parallel reduction of the extent of a population.

Besides, it was observed that mictic females which had started to lay haploidal eggs, do not begin to lay impregnated eggs after copulation. Resting eggs are laid only by those mictic females which had copulated before the laying of their first egg.

6. STRESZCZENIE

Dynamikę rozwoju populacji *Brachionus rubens* badano w hodowlach różniących się typem podawanego pokarmu (bakterie *A. aerogenes* lub glony *C. vulgaris*), objętością środowiska hodowlanego oraz początkową liczebnością wrotków. Najwyższą biologiczną prężność mają populacje karmione glonami o niskich początkowych zagęszczeniach wrotków (Tab. II). Pogorszenie wskaźników demograficznych w populacjach karmionych bakteriami i o wyższych zagęszczeniach wrotków wiąże się prawdopodobnie z niekorzystnym wpływem gromadzących się metabolitów — tak samych wrotków, jak i organizmów pokarmowych.

Mniej wyraźnie wpływają warunki hodowli związane z rodzajem podawanego pokarmu na parametry rozwoju osobniczego — długość życia, płodność, czas rozwoju embrionalnego i postembrionalnego samic amiktycznych, miktycznych niezapłodnionych i zapłodnionych (Tab. II), istotne różnice występują natomiast w przebiegu krzywych śmiertelności (Fig. 2).

Potencjalne możliwości produkcyjne *B. rubens* są bardzo duże — przy braku ilościowego ograniczenia pokarmu i zapobieganiu kumulacji metabolitów (duża objętość hodowli, niskie zagęszczenie wrotków lub częsta wymiana środowiska) w czasie około 3,5 doby populacja może powiększyć swą liczebność ponad 10-krotnie.

W takich warunkach hodowli populacje składają się w 80–90% z samic amiktycznych. Niekorzystne warunkowanie środowiska hodowlanego wpływa natomiast na zmianę cyklu rozmnażania *B. rubens* z partenogenezy na rozród płciowy (produkcja jaj przetrwalnikowych) przy równoczesnej redukcji liczebności populacji.

Zaobserwowano ponadto, że samice miktyczne, które rozpoczęły już produkcję jaj haploidalnych, mimo odbycia kopulacji nie składają jaj zapłodnionych. Jaja trwałe składają jedynie te samice miktyczne, które kopulowały przed złożeniem swego pierwszego jaja.

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THE METABOLIC PRODUCTS OF COPEPODITES OF VARIOUS CYCLOPOIDA SPECIES DURING THEIR RESTING STAGE

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ABSTRACT

The alimentary tracts of Cyclopoida copepodites in their resting stage, isolated from the environment due to the presence of formed bungs, are the place of occurrence of certain forms which are undoubtedly the metabolic products. These are: concretions in the vacuoles of stomach, crystalline bodies in stomach guts and bungs, bungs and shapeless bodies. These formations are typical, as far as their shape and localization are concerned, for particular species of Cyclopoida from both eustatic and astatic water bodies, and thus these formations can be a new systematic feature of juvenile Cyclopoida in their resting stage. The microchemical analyses show that these formations are the derivatives of uric acid. On the return to the active life all these metabolic products are excreted by copepodites through the anus.

1. INTRODUCTION

It has been previously found (Wierzbicka 1966) that during the resting stage of Cyclopoida copepodites IV and V their alimentary tracts are isolated from the environment. The bungs, which are formed on the level of the I and II abdominal segments, close the posterior part of the tract. The bungs are typical for the majority of investigated species. The results of present paper show also that the anterior part of alimentary tract is closed near to the mouth opening. A copepodite stops feeding before its resting stage, therefore the guts are empty. In such a way an alimentary tract completely isolated from the environment accumulates the metabolic products during the resting stage.

The investigations aimed at a thorough examination of the previously observed characteristic bodies in the alimentary tracts of copepodites in the resting stage (Wierzbicka 1966, 1967), i.e., estimation of their number, character, shape and localization in various investigated species. The following species of Cyclopoida were investigated: *Cyclops vicinus vicinus* Ulj., *Cyclops vicinus kikuchii* Smirn., *Cyclops bohater* Koźm., *Acanthocyclops bicuspidatus* (Claus), *Mesocyclops leuckarti* Claus, *Thermocyclops oithonoides* Sars, *Cyclops strenuus* Fischer, *Cyclops furcifer* Claus, *Cyclops insignis* Claus and *Acanthocyclops gigas* (Claus).

2. MATERIAL AND METHODS

The copepodites of investigated species of Cyclopoida in their resting stage were collected in astatic water bodies (located some 30 km from Warsaw, among the fields of Zaborów) and eustatic ones: Lake Kortowskie in Olsztyn and a clay pit in Warsaw (for the descriptions of these water bodies see Wierzbicka 1959, 1960, 1966 and in press., Wierzbicka, Kędzierski 1964).

The samples of mud from the astatic dried up water bodies were collected with the help of a special apparatus constructed by K ę d z i e r s k i (W i e r z b i c k a 1966). The collected mud samples were covered with water in the laboratory (larger samples in aquaria, smaller ones in beakers) for waking the copepodites. The samples from a clay pit were collected with the help of the quantitative K l e k o w s k i sampler (Ż a d i n 1966) to study the vertical distribution of copepodites in bottom sediments, or with a loaded net made of bolting cloth, which was dragged along the bottom (the same method was used by L. S z l a u e r in Lake Kortowskie, to whom I am grateful for providing the material from this lake). The collected mud was sieved through a bolting cloth under the tap water in the laboratory. This helped to select the already awaked copepodites. The observations on metabolic products were carried out for many years (since 1964) and were based on a large material. The observations were made, among the others, during the elaboration of the materials for the following papers: W i e r z b i c k a, K ę d z i e r s k i (1964, 1970, in prep.), W i e r z b i c k a (1966, 1972).

The observation of larger quantities of accumulated metabolic products was possible not only due to the studies of copepodites alimentary tract during the whole resting stage, but mainly due to the investigations of this tract at the end of the resting stage and during the resting stage prolonged for some months in the laboratory conditions.

Various methods of chemical microanalysis were applied for various species of Cyclopoida in order to study the observed metabolic products. The following reagents were applied: for murexid method (M a r c h a l 1889): (1) concentrated HNO_3 and (2) concentrated NH_4OH; for method of C o u r m o n t, A n d r é (1904): (3) 1% $AgNO_3$ and (4) photographic developer; for others: (5) 5% NaOH, (6) 5% $NaHCO_3$, (7) ethyl ether, (8) 0.01 n disodium versenate, (9) 1 n HCl, (10) 0.5% and saturated Li_2CO_3.

3. RESULTS

THE CHARACTERISTIC OF FORMS OF METABOLIC PRODUCTS

The products are located in vacuoles previously connected with the stomach walls and later loosely hanging in stomach, or they are placed anywhere in the alimentary tract.

Concretions

The concretions are a form of metabolic products which can be found in active and resting stages of Cyclopoida. Concretions located in vacuoles in the stomach as small round formations are excreted through the anus during the active life. The number of vacuoles with large concretions in the stomach of *A. bicuspidatus* and *C. strenuus* copepodites IV in resting stage from astatic water body in Zaborów is 13—20 for the former and 12—30 for the latter species. Number of vacuoles in *M. leuckarti* IV and *T. oithonoides* V from a clay pit in Warsaw varies from 11—21 and 12—21, respectively.

At the beginning of the resting stage the last excreted vacuoles are build in the bungs being formed and closing the guts. During the resting stage the concretions become larger, their shape is slightly irregular with a concentric stratification. Sometimes their shape and colour are characteristic for particular species, e.g. in *Thermocyclops oithonoides* V they are brown-rusty contrary to other species where they are mainly green (glaring green and very large in *C. furcifer* IV). After the end of
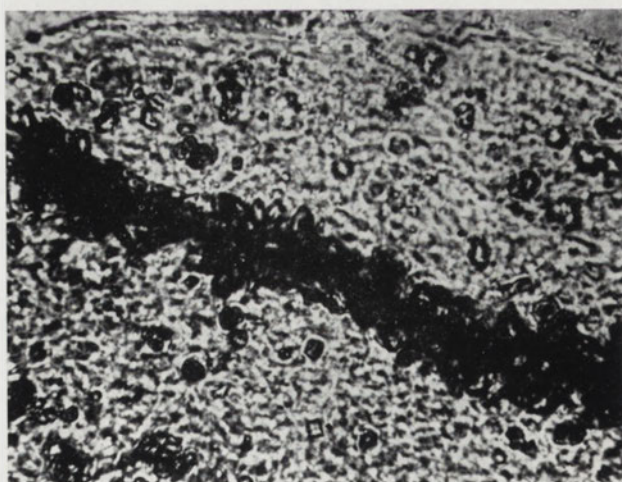
Fig. 1. *Cyclops bohater* V from a clay pit in Warsaw. Crystals in stomach during the prolonged resting stage. A — general view, B — a fragment
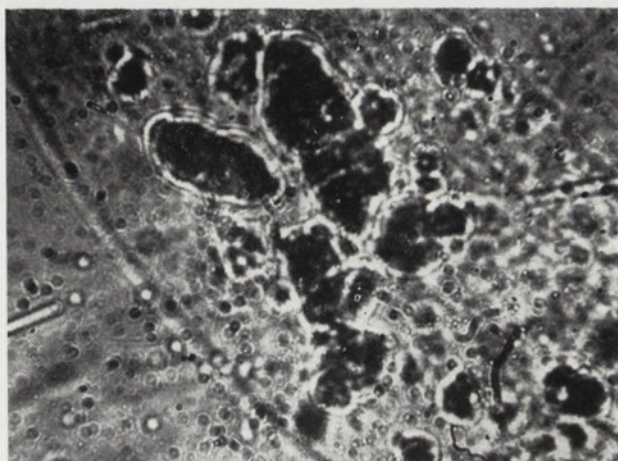

Fig. 2. *Cyclops vicinus kikuchii* V from a clay pit in Warsaw. The shapeless bodies in the stomach of copepodite
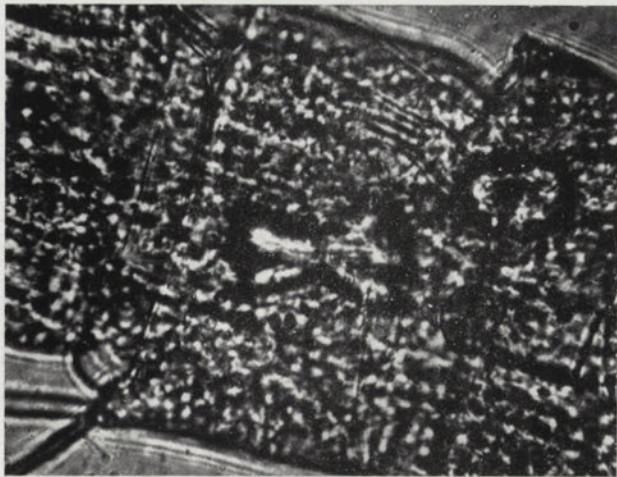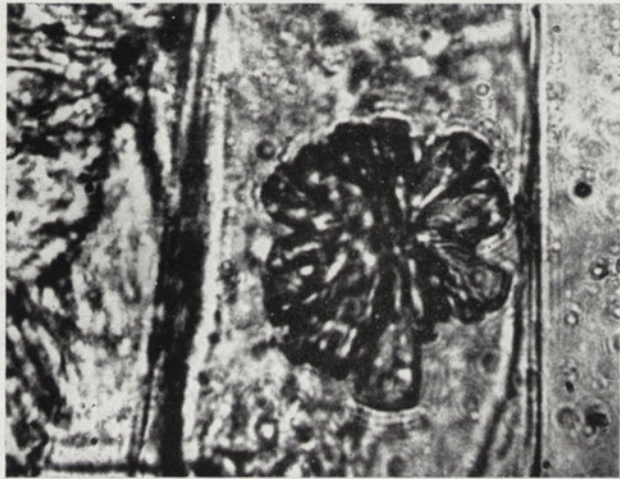
Fig. 3. *Acanthocyclops bicuspidatus* IV from a clay pit in Warsaw. A crystal in gut on the level of the I abdominal segment

the resting stage a copepodite excretes the bung very quickly, followed by the vacuoles with large accumulated concretions. Since then only very small round concretions (with Brownian movements) accumulate in the vacuoles, to be excreted later with the vacuoles during the whole active life of an animal.

Crystalline and shapeless bodies

The crystalline bodies are a very characteristic form of metabolic products (Wierzbicka 1967, Wierzbicka, Kędzierski 1970). The shape of crystals is typical for certain species and can be treated as a systematic feature, similarly as the shape of bungs. Crystals occur in the stomach, guts and in the anterior and posterior bungs. They are sometimes found already in the first months of the resting stage, and are very abundant when prolonging the resting stage for some months in the laboratory conditions (e.g. instead of 4 months in natural conditions — 10—11 months in the laboratory). In the alimentary tract of *Cyclops bohater* V at the end of the resting stage of individuals collected from a clay pit in October, small rectangular and rhomboid crystals were found. After a laboratory prolonged resting stage (next year in May) a great amount of crystals of the same shape in one longitudal formation were found in the stomach (Fig. 1 AB). During the earlier periods of the resting stage, in July and August, shapeless bodies were often observed against the background of numberless microscopic particles vibrating with Brownian movements in the alimentary tract of *C. bohater*. According to the results of the microchemical analysis (see below) these particles are presumably the crystallization centres of metabolic products accumulating there. In the prolonged resting stage large numbers of crystals are also visible against the background of these vibrating particles.

The other two species from the clay pit, *C. vicinus vicinus* IV and *C. vicinus kikuchii* V, also have shapeless bodies (Fig. 2) in their prolonged resting stage. These bodies can be also seen against the background of an enormous quantity of vibrating particles. The shapeless bodies are especially numerous in *C. vicinus kikuchii*. Apart from that, larger and smaller flat rectangle or star-like crystals were also found in *C. vicinus vicinus* stomach and bung in quantities 2, 6, 10 (Fig. 4). The crystals were not found in *C. vicinus kikuchii*.

The fourth species from the clay pit, *A. bicuspidatus* IV, at the end of its resting stage (October), and in the prolonged resting stage has a single crystal typical for this species. It is located in the gut on the level of the first abdominal segment. This crystal is a part of the bung, and it happens to be so large that it shoves aside the gut walls, and even bulges them (Fig. 3, and Fig. 5). Sometimes it is shaped like a double fan with feathers in opposite directions, similar to sodium ura-
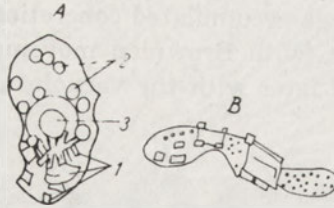
Fig. 4. *Cyclops vicinus vicinus* IV from Lake Kortowskie in Olsztyn. A — a bung with crystals (1), concretions (2) and vacuoles (3), B — a bung with concretions and crystals

Fig. 5. *Acanthocyclops bicuspidatus* IV from a clay pit in Warsaw. A bung with concretions and crystals

te crystal (R a t h e r y 1939). It is interesting that in the same species from the astatic water body in Zaborów such crystal was not found, and the bung was also different, oval (W i e r z b i c k a 1966). The crystals — long narrow rectangles, were placed loosely near the end of the bung. This suggests the presence of physiological differences among the inhabitants of various types of reservoirs, and possibly some taxonomic differences.

Small spindle-shaped or needle-like crystals were observed in bungs and in the stomach of *T. oithonoides* V. The alimentary tract of *M. leuckarti* IV also contained crystals in the bung and stomach. These crystals are sometime large, filling the entire bung, flat, rectangular or polygonal, or star-like (Fig. 6).

Fig. 6. *Mesocyclops leuckarti* V from a clay pit in Warsaw. Bungs with crystals and concretions

The presence of crystals was also noticed in species from astatic drying up water bodies. *C. strenuus* IV was examined very thoroughly. In its stomach and in the bungs numerous crystals were found in quite a variety of shapes: from rectangular, rhomboid, oval, bulgy, to spindle-shaped or claviform narrow rods placed in stars or irregularly. Up to

ten crystals were found in a single stomach. The shapes of these crystals were similar to that of the uric acid crystals as given by R a t h e r y (1939). In *C. strenuus* IV a crystal was seen against the background of particles with Brownian movements, similarily as described above.

After the waking of an animal the crystals were excreted through the anus.

Bungs

The bungs are also a form of metabolic products, simultaneously closing the alimentary tract, thus helping to accumulate these products. The bungs are surrounded by walls (very thick in animals from astatic water bodies), inside which there are visible the shapes of vacuoles, concretions, frequently crystals (Fig. 4, 5) and sometimes of sand grains. After the waking of copepodite the bungs and their content are excreted through the anus.

As mentioned above, the bungs have a characteristic shape for certain species: oval in *A. bicuspidatus* IV, pear-shaped in *A. gigas* V, string of "pearls"-shaped in *C. strenuus* IV from the astatic water bodies; see the pictures and photographs of these formations in W i e r z b i c k a (1966).

The species from lakes and clay pit in Warsaw also have bungs, but their shape is less precise and not so regular as in species from astatic waters, and their walls are more delicate.

It is worth underlining that the bung in *C. bohater* V, a species related in taxonomy to *C. strenuus* according to K o ź m i ń s k i (1934), is also formed of "pearls", as in the latter, which can suggest physiological similarity. In *C. insignis* IV, a species related to *C. strenuus,* from Lake Kortowskie in Olsztyn, a bung formed of 6 "pearls" has been observed (each pearl" is a vacuole with concretions surrounded with walls).

The bungs of *C. vicinus* IV are of various shapes. A large bung with big green concretions in the upper part (Fig. 4) and large irregularly shaped crystals in the lower part were seen on the level of the I abdominal segment. Delicate bungs contained sometimes crystalline formations in the shape of flat rectangles or narrow rods. In individuals awaked after about one month of resting stage (Lake Kortowskie, July) the bungs composed of shapeless formations (up to 8 ones), surrounded by a thin membrane, were seen on the level of the I and II abdominal segments. The concretions were also visible. Apart from these eight formations in the upper part of the alimentary tract, 15 formations were noticed in cephalothorax and thorax segments.

The characteristic bung of *A. bicuspidatus* from a clay pit has been already described among the crystals.

T. oithonoides copepodites V from Lake Kortowskie have delicate frequently elongated or oval bungs. They contain vacuoles with a single

large concretion. The concretions have a typical rusty colour, which makes the entire bung brownish. Small crystals are also present in the bungs. In this so transparent species the bungs were also noticed near the mouth opening. Similarly located bungs were also observed in another transparent species, *M. leuckarti* IV. The bungs in both these species were round or oval, surrounded by a delicate membrane, and they either contained needle-like crystalline formations or the sand grains (as already mentioned the sand grains were frequently found in the alimentary tract of copepodits in their resting stage). *M. leuckarti* IV had a delicate bung on the level of the I and seldom the II abdominal segment (Fig. 6). The bung always contained larger or smaller crystals, from flat rectangles to thin rods, placed in fans or stars; sometimes the crystals were single and large. The sand grains were often found in the bung.

MICROCHEMICAL ANALYSIS OF METABOLIC PRODUCTS

1—4. The microchemical determinations show that these products are purine compounds. The murexid method (reagents (1, 2) see Methods) and method of C o u r m o n t, A n d r é (1904) (reagents (3, 4), see Methods) show the presence of uric acid. The murexid method determining the presence of uric acid shows frequently a ruby colour of concretions (ammonium purpurate). The method of C o u r m o n t, A n d r é (1904) for the determination of uric acid gives an intense black colour of concretions, bungs and crystals. As the presence of Ca compounds gives also the black colour in this method (G o m o r i 1951 after P e a r s 1968), to avoid interference from Ca the aqeuous saturated solution of Li_2CO_3 is applied (10), as it dissolves the derivatives of uric acid. The smallest particles (the possible crystallization centres) with Brownian movements dissolve immediately after the application of Li_2CO_3, then dissolve the characteristic shapeless bodies, and gradually the concretions in stomachs and crystals. The shapeless bodies and the crystallization centres (particles) dissolve also in 0.5% Li_2CO_3. It seems that the dissolving of metabolic products in Li_2CO_3 eliminates the possibility that silver is reduced under the influence of various substances present in the investigated material, similarly as under the influence of uric acid. The above discussed reactions prove the presence of uric acid or its derivatives.

The fact that the concretions are the organic material or the derivatives of uric acid is confirmed by the reactions with reagents (5), (6) and (7) (see Methods).

5. 5% NaOH dissolves completely small concretions in *A. bicuspidatus* V after moulting (from copepodite IV to V). This shows that this material is not only inorganic.

6. $NaHCO_3$ dissolves the concretions (only the shining points were

left). This suggests that these are not inogranic salts of Ca, but they can be the derivatives of uric acid, according to the positive reactions with (1), (2) and (3), (4).

7. The applied ethyl ether dissolves the concretions, leaving only the shining points. Thus the suspection that this is a mineral material can be excluded.

8. An interesting analysis has been the placing of four excreted bungs of *A. gigas* V in versenate. The inside walls were then completely dissolved, while the outside walls of massive bungs remained untouched. The bungs became transparent. Large green concretions in bungs were not dissolved. This analysis showed that the inside wall is incrusted with calcium salts, while the insoluble concretions, according to analyses (1—4), are the derivatives of uric acid.

These analyses (reagents 1—7) showed that mineral calcium salts were not present in concretions, crystals, shapeless bodies, particles with Brownian movements and in bungs. Moreover the reagent (8) dissolving most calcium salts does not dissolve concretions. Thus these formations contained probably the derivatives of uric acid, as suggested by analyses (1—4). The instantaneous dissolving of crystal, and slow dissolving of concretions in reagent (8) was observed only once in the case of excreted bung of *C. vicinus* IV, which might suggest the presence of calcium salts of organic acid there.

9. It is worth mentioning that 1 n HCl immediately dissolves the smallest crystallization centres with Brownian movements, shapeless bodies, crystals, bungs, and after a longer time even the concretions.

Very interesting are the round formations with inside directed rods, found in the stomach of *C. insignis* IV from the astatic water body, which dissolve immediately in 1 n HCl. Their shape is very similar to the crystals of uric acid accumulated in the kidney of *Helix pomatia* during its winter hibernation (K o š t o j a n c 1951).

Summing up, the microchemical determinations showed the presence of uric acid and/or its derivatives in the listed above metabolic products. The majority of physiological processes which end with the formation of these products are specific for particular species. This is confirmed by the differentiation in the character and form of these products occurring in particular Cyclopoida species (crystals, shapeless bodies, bungs), and by the similarity of the related species (shapeless bodies, so typical for *C. vicinus vicinus* and its variety *kikuchii*, bungs shaped like a "pearl" string in *C. strenuus, C. bohater* and *C. insignis,* closely related in taxonomy). The form of the occurrence of metabolic products during the resting stage can be treated as a new systematic feature of juvenile forms (copepodites IV and V) of particular species, thus a systematic feature can be the form of a final product of physiological processes.

4. DISCUSSION

The experimental data on the excretive character of vacuoles of Copepoda are presented in the papers by G u i e y s s e (1907) — Calanoida; L i s o n (1941) and W i e r z b i c k a (1966) — Cyclopoida. L i s o n (1941) said that: "... les granulations jaunâtres présentes dans ces cellules sont le véhicule de produit de déchet". *Colpidium colpoda* Ehrb., a food of copepodites, was placed in methylene blue (W i e r z b i c k a 1966) and their nutritive vacuoles became blue. The homogenate of radish leaves coloured the vacuoles of *C. colpoda* green. The copepodites just after the resting stage fed on such *C. colpoda* contained blue or green vacuoles, and the concretions were intensively navy blue or smaragdine. A faecal pellet filled with excreted vacuoles containing intensively blue large concretions, was also navy blue (after the methylene blue).

The excretive character of vacuoles with concretions is also confirmed by the previously mentioned experiments of W i e r z b i c k a (1966) with cultures of particular starved copepodites awaked from their resting stage. Each copepodite (*C. strenuus*, *C. furcifer* and *A. gigas* were investigated) was placed in a drop of water on a microscopic glass and under the cover glass. Starved copepodites lived even 2 months. Some of them produced in the starvation conditions the bungs once again. The orange lipid balls disappeared, but an orange streak appeared along the whole alimentary tract, and the concretions also became dark orange. The vacuoles with orange concretions moved toward the anus. The faecal pellets with orange concretions were observed in the surrounding water.

Thus after the resting stage the metabolism was intensified, despite of starvation conditions, since the pigment characteristic for lipid balls passed into the alimentary tract, vacuoles and to concretions.

However, credit should be given to the scientists who in the previous century already paid attention to the excretive character of vacuoles in Copepoda and to the analogy of concretions and the "urinary products". to observe the vesical cells with 'concrements" and treated them as According to C l a u s (1858 a), L e y d i g (1854, 1857) was the first one „urinary concrements". In his paper L e y d i g (1860) describes a part of stomach with cells containing small concretions, saying that the processes which in insects take place in Malphigian tubes, in "Cyclopsine" take place in the guts. C l a u s (1858 b) has observed a similarity between the "concrements" of Copepoda and the formations in Malphigian tubes or in the uretic system of molluscs. Both kinds of these formations are excreted. C l a u s (1858 b) observed the concretions of uric acid in a parasite Copepod.

There are numerous data which deal with vacuoles of invertebrates filled with concretions giving them the excretive character. In higher Crustacea (Decapoda) the presence of vacuoles in hepatopancreas was

found. They were characterized as excretive by C u e n o t (1893) and F i s c h e r (1925, 1927, 1928). C u é n o t (1939) wrote that the excretive character of invertebrates "liver" is confirmed by the concretions and vacuoles present in the rectum. He gave several examples from various groups of invertebrates: guanine was found in Arachnoidea (Malphigian tubes connected with liver), the liver tissues contained crytals in cytoplasm of absorption cells. Sodium urate was found in the concretions in Blatta. The concretions become larger in time, and enormous quantities of urate were found in old specimens of *Blatta orientalis* L. The vacuoles with concretions and crystalline needles were also found in the rectum of Sepia. Big purine concretions were found in another Cephalopoda.

D e l a u n a y (1931) wrote that in invertebrates "les bases puriques son excretées en grande partie directement..." without the transformation into the uric acid. Numerous granulations were observed, according to this author, in many invertebrates and especially in Annelida and Mollusca. Urates and uric acid were found in the Zenker's organ in Isopoda (P a r r y 1960). The same organ in Asellus gave a positive murexid reaction. G o o d b o d y (1957) found that small vesicles develop around the alimentary system of Ascidiidae. The vesicles contain single concretions, observed in various species. This author quoted K u p f f e r (1872) who found already then the uric acid in *Ascidia complanata* with the help of the murexid acid test. G o o d b o d y (1957) stated the accumulation of purines and uric acid on the basis of chemical analyses in two species of Ascidia.

The uric acid and guanine are the final metabolic products in molluscs during their hibernation (J e ż e w s k a et al. 1963) when the water supply to the organism is limited. During the active life of these animals when there is enough of water, the urea is the main final product. The authors quote the interpretation of Baldwin, saying that the transformation of excretions from urea to uric acid allows to avoid the increase of osmotic pressure without excretion. These authors criticized the results of D e - l a u n a y (1931). The shift of nitrogenous excretion type towards the purinotelism during the resting stage of the investigated freshwater Cyclopoida is to be underlined.

Summing up, it seems that the presence of vacuoles with concretions and the excretive functions of vacuoles is common among invertebrates. The discussed microchemical analyses showing the presence of final products of nitrogen metabolism — the purine compounds — in concretions, crystals, shapeless bodies and bungs of Cyclopoida, confirm the suggestions and findings of scientists from the previous century. The results (points 5, 6 and 7) on the presence of organic substances in concretions confirm the analyses presented by W i e r z b i c k a (1966), which exclude the presence of phosphates in concretions. The applied incineration

method also confirms the presence of organic substances (the remaining not burned oxides of metals are the components of organic acid salts).

The role of other excretive organs in the resting stages of Cyclopoida, such as maxillary glands or glands located near the basic parts of the III and IV pair of swimming legs is unknown.

C h a m p e a u (1971) has not seen the bungs in all copepodites in the resting stage. The results of present investigations suggest a rather common occurrence of bungs; the author has not observed bungs only in *C. furcifer* IV among the 10 investigated species, and suggested (W i e r z-b i c k a 1966) that in this case the bung was excreted immediately after the waking.

The formation called by C h a m p e a u (1971) a "bouclier" and assumed to close the anterior part of the alimentary tract (this author quotes the description of W i e r z b i c k a 1966) is described by W i e r z b i c k a as a "mud disc" on the cephalothorax. The bungs closing the anterior part of the alimentary tract were described the first time for the transparent species in this paper.

The bung presented by C h a m p e a u (1971) in Fig. 1 (*Diacyclops bisetosus* IV) is very similar to the bung of *A. gigas* (W i e r z b i c k a 1966, photograph 2).

Taking into consideration the taxonomy of R y l o v (1948), used by the author of the present paper, which includes into the genus Acanthocyclops among others such species as *A. gigas, A. bisetosus, A. bicuspidatus*, the similarity of shapes of bungs of species related in taxonomy is confirmed.

Acknowledgements

5. SUMMARY

The alimentary tract of Cyclopoida copepodites IV and V, isolated from the environment by bungs, accumulates during the resting stage various metabolic products. These products are in the form of concretions, crystals, so-called shapeless bodies, the smallest particles — accumulation centres of metabolic products with Brownian movements and the bungs. The concretions are in the vacuoles with an excretive function. The other products are loosely distributed in the alimentary tract. The microchemical analyses and the character of these products, similar to those described by other authors in various animals show that these are purine compounds. The observations of so differentiated forms of metabolic products have been possible due to the investigations of the waked copepodites during the whole resting stage and especialy near its end or during the laboratory prolonged resting stage. The metabolic products are sometimes typical for particular species and can be a new taxonomic feature of juvenile Cyclopoida during the resting stage. It has been found that species closely related in taxonomy have analogous forms of metabolic products, and so apart from the morphological similarity there is also a physiological one. The excretive character of vacuoles was confirmed previously by W i e r z b i c k a (1966) in experiments with the methylene blue and chlorophyll, and by the observations of alive copepodites in the resting stage and in active life.

6. STRESZCZENIE

Układ pokarmowy kopepoditów IV i V Cyclopoida, izolowany dzięki czopom od środowiska zewnętrznego, gromadzi w okresie spoczynku różnorodne produkty metabolizmu. Przybierają one formy konkrecji, kryształów, tzw. utworów nieforemnych, najmniejszych cząstek-centrów akumulacji produktów metabolizmu, podległych ruchom Browna oraz czopów. Konkrecje znajdują się w wakuolach, mających funkcję ekskrecyjną, pozostałe produkty leżą luźno w układzie pokarmowym. Analiza mikrochemiczna oraz charakter form produktów, analogiczny do opisywanych przez innych autorów u różnych zwierząt, wskazują na to, że są to związki purynowe. Obserwacje tak różnorodnych form produktów metabolizmu były możliwe dzięki badaniom obudzonych kopepoditów w ciągu całego okresu spoczynku, a zwłaszcza pod jego koniec lub w czasie znacznie przedłużonego okresu spoczynku w warunkach laboratoryjnych. Wymienione formy produktów metabolizmu są niekiedy charakterystyczne dla poszczególnych gatunków i mogą stanowić nowe cechy systematyczne juwenilnych form Cyclopoida z okresu spoczynku. Stwierdzono, że gatunki blisko siebie stojące w systemie wykazują analogiczne formy produktów metabolizmu, zatem prócz zbieżności morfologicznych zachodzą również zbieżności o charakterze fizjologicznym. Wydalniczy charakter wakuoli został uprzednio potwierdzony przy pomocy eksperymentów z błękitem metylenowym i chlorofilem (W i e r z-b i c k a 1966), oraz na drodze obserwacji żywych kopepoditów po okresie spoczynku i w okresie życia aktywnego.

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Z. STROMENGER

BEOBACHTUNGEN AN WASSERFLÖHEN (CLADOCERA) IN DEN FORELLENTEICHEN BEI DER BIOLOGISCHEN STATION LUNZ (NIEDERÖSTERREICH) [1]

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ABSTRACT

Die Beobachtungen betreffen 4 subalpine, seichte Forellenteiche, die klares, kühles Bachwasser enthalten, nebeneinander liegen und stets durchströmt sind. Insgesamt wurden 7 Cladocerenarten gefunden; am häufigsten waren *Chydorus sphaericus*, *Simocephalus vetulus* und *Scapholeberis mucronata*. Im Vergleich mit der Art- und Individuenanzahl von Cladoceren in den Flachlandteichen ist ihre Häufigkeit sehr gering. In den nacheinander liegenden Teichen nimmt sie im freien Wasser zu, im Litoral dagegen ab. In den besonnten Pflanzenbeständen sind die Cladoceren am zahlreichsten. Ende August—Anfang September ist *Chydorus sphaericus* am häufigsten und in seiner Population kommen zahlreiche Männchen und Ephippienweibchen vor.

1. EINLEITUNG

In den letzten Jahren ist die Cladocerenfauna in den europäischen Fischteichen mehrmals untersucht worden. Da aber die Beobachtungen (auch die meinen, Stromenger-Klekowska 1960) meistens die mehr oder weniger typischen Karpfenteiche des Flachlandes betreffen — schien es mir interessant einen Vergleich dieser Fauna mit der der alpinen Forellenteiche durchzuführen.

Zu diesem Zweck erschienen mir die 4 Teiche bei der Biologischen Station Lunz, Niederösterreich, besonders geeignet. Die Verhältnisse in diesen Gewässern sind ganz anders als in diesen, die ich früher auf der mitteleuropäischen Ebene bei Łódź, Polen, untersucht hatte. Die in Frage kommenden Teiche bei Lunz sind nämlich stark durchströmt, verhältnismässig kühl, das Wasser ist durchsichtig und an Phytoplankton sowie faulende Stoffe arm. Das ziemlich rauhe subalpine Klima und reiche Niederschläge (langjähriges Mittel etwa 1700 mm) schaffen eine zusätzliche Besonderheit der Lebensbedingungen.

Meine Beobachtungen betreffen die Anzahl der Arten und Individuen im freien Wasser und Litoral, deren Änderungen mit der Zeit, sowie die Fortpflanzungszyklen.

2. BESCHREIBUNG DER TEICHE UND METHODE

Die vier Teiche bei der Biologischen Station Lunz, die ich untersucht habe, liegen dicht bei einander, nur durch Dämme getrennt. Sie sind stets durchströmt, am stärksten der Teich No. 1, der, sowie auch der Teich 2, das Wasser unmittelbar

aus der Abzweigung des Seebachs bezieht. Die Teiche 3 und 4 bekommen es erst nachher. Die Lage der Teiche, ihre Numerierung und Grösse sowie die Richtungen des Wasserabflusses sind auf dem Orientierungsplan dargestellt.

Der "Halbdamm" ist ein kaum aus dem Wasser ragender, stark mit Landpflanzen bewachsener Erdwall, der beim Vertiefen der beiden Hälften des Teiches 3 aufgeschüttet wurde.

Der ganze Komplex ist von Bäumen und Gebüsch umgeben und die Damm-hänge sind dicht mit höheren Pflanzen bewachsen, vor allem mit hohem Riedgras (*Carex rostrata*). Ausserdem findet man u.a. auch *Urtica sp.*, *Mentha sp.*, *Myosotis sp.*, *Impatiens nolitangere*, Phragmites und kleine Bestände von *Juncus sp.* und *Equisetum sp.* Der seichtere Boden ist an manchen Stellen mit *Chara sp.*, *Fontinalis sp.*, *Ranunculus aquaticus* und *Potamogeton filiformis* bewachsen. Die zwei letzteren Pflanzen sind im Teich 4 besonders üppig.

Die Tiefe der Teiche beträgt bis etwa 1 m, meistens etwa 60—80 cm. Der Boden ist sehr schlamming, nur an wenigen Stellen etwas mit Schotter bestreut.
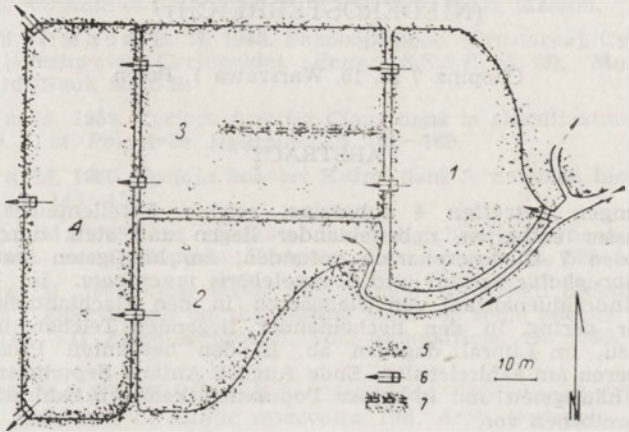

Abb. 1. Plan der Teiche, 1—4 — Nummern der Teiche, 5 — Uferpflanzen, 6 — **Mönch**, 7 — "Halbdamm"

Abb. 2. Teich No. 1 von S—O gesehen

Abb. 3. Teich No. 2 von N—W gesehen

Das Wasser ist sehr klar, nur bei längerem Regen wird es, vor allem im Teich 1 trüb. Sonst ist es durchsichtig bis zum Boden.

Seine Temperatur wurde an den tiefsten Stellen vor den Mönchen am Mittag gemessen.

Die Wassertemperatur im Litoral erreicht viel höhere Werte, besonders im Sommer an den sonnigen Stellen und ist mehr von dem Wetter abhängig. Bei den Hitzen betrug sie stellenweise mehr als 20°C.

In den Teichen züchtet man junge Bachforellen in ihrem ersten Lebensjahr. Das Wasser wird in der zweiten Oktoberhälfte abgelassen; zu dieser Zeit erreichen die Fische die Länge von etwa 5,5—7,0 cm.

Die Proben wurden Ende August bis Ende September 1970 und vom 20 Mai bis 18 Juni 1971 gesammelt.

Im freien Wasser wurde die quantitative Methode angewandt, die auf der Filtrierung des mit einem 10-Liter-Eimer geschöpften Wassers durch ein feinmaschiges Planktonnetz (Müllergaze ca No. 20 d.h. etwa 66 Fäden pro 1 cm) beruhte.

Tabelle I. Wassertemperaturen in den Teichen (°C)

Datum	Haupt-Zufluss	Zufluss zum T. 2	Teich No.				Der See (1 m unter der Oberfläche)
			1	2	3	4	
28.IX.1970	8,4	—	8,6	8,4	9,6	9,7	13,8
26.V.1971	8,9	9,2	9,8	12,7	15,0	16,6	16,3
18.VI.1971	8,6	8,6	10,4	11,6	10,8	11,7	12,8
6.VIII.1971	11,9	11,9	15,1	15,4	16,9	16,6	22,3

Solche Entnahmen wurden am 2 und 3.IX.1970 für jede Probe zehnmal und an allen übrigen Daten fünfmal an verschiedenen, möglichst weit voneinander entfernt liegenden, aber immer etwa denselben Punkten des freien Wassers wiederholt. Die Summe der so gesammelten Tiere wurde wieder pro 1o Liter umgerechnet, woraus sich die Durchschnittszahlen ergaben.

Die Proben aus dem Litoral und den Unterwasserpflanzen wurden nach der qualitativen Methode von der Wasserseite oder vom Ufer her gesammelt, und zwar mit einem Kescher aus Müllergaze (etwa Nr 12, etwa 15 kurze Züge für jede Probe).

Die Angaben über die Cladocerenfauna dieser Gewässer findet man in der Literatur nicht; sie fehlen sogar in der ausführlichen Arbeit von B r e h m, R u t t n e r (1926).

3. DIE ERGEBNISSE

Allgemeine Bemerkungen

Obwohl die Teiche miteinander verbunden sind, unterscheidet sich ihre Cladocerenfauna hinsichtlich der Orte ihres Vorkommens, der Vermehrungszyklen und zum Teil auch der Zusammensetzung nach Arten. Im allgemeinen wurden hier nur sieben Arten von Cladoceren gefunden, nämlich: *Chydorus sphaericus, Simocephalus vetulus, Scapholeberis mucronata, Alona affinis, Alona guttata, Alona costata* und *Ceriodaphnia quadrangula*. Die ersten drei Arten waren die häufigsten, *Chydorus sphaericus* kam in der Mehrzahl der Proben vor und fast stets als Dominat, besonders im Spätsommer. Die Exemplare der drei letzteren Arten kamen in den Proben äusserst selten und nur vereinzelt vor.

Sowohl die quantitativen als die qualitativen Proben zeigten, dass die Zahl der Cladoceren in den nebeneinander liegenden Teichen 1, 2, 3 und 4 im freien Wasser zunimmt, im Litoral dagegen abnimmt. Man sieht dies sehr genau z.B. in den Proben von Anfang September, wo im Teich 1 je 10 Liter Wasser 0,3 Exemplare enthalten waren. Im Teich 2 waren es 19 Exemplare pro 10 Liter, im Teich 3 — 3,8 Ex. pro 10 l, im. Teich 4 — 256 Ex. pro 10 l.

Die Litoralproben bewiesen, dass die Cladoceren im Teich 1 zahlreich vorkommen, in den Teichen 2 und 3 bedeutend weniger zahlreich, im Teich 4 dagegen in recht geringer Anzahl; in einigen Proben von den Teichen 3 und 4 fehlten sie überhaupt.

Auch ist die Häufigkeit der Cladoceren in den verschiedenen Punkten der Uferzone nicht gleich. Massenhaft kamen sie an seichten Stellen nahe an den Ufern, zwischen dichten Beständen des teilweise überschwemmten Landgrases vor (*Chydorus sphaericus* und *Simocephalus vetulus)*. Zwischen den Riedgräsern dicht am Ufer sind sie viel weniger zahlreich, dort aber, wo diese Pflanzen eine mehrere Meter breite Zone des seichten Wassers bewachsen (besonders im Teich 1 und 2 am Zufluss), findet man wieder grössere Mengen von Exemplaren der zwei häufigsten Arten.

In den Proben von Mai—Juni bemerkt man jedoch, dass diese Regel-
mässigkeiten nicht sofort nach der Bewässerung der Teiche eintreten,
sondern sich mehrere Wochen lang entwickeln. Der Teich No. 3 wurde
nach und nach ärmer an Cladoceren, obwohl die Proben von Mitte Juni
viele andere Kleintiere (Heliozoa, Carchesium und Vorticella, Turbellaria,
Rotatoria, besonders Euchlanis, Bryozoa, Insektenlarven usw.) enthielten.
Ab 10—15 Juni wurden die seichten und breiten Regionen der mit
Riedgras bewachsenen Uferzonen, vor allem im Teich 1 schon bedeutend
stärker von Cladoceren besiedelt.

Das Vorkommen der einzelnen Arten

CHYDORUS SPHAERICUS kam, wie gesagt, in der Mehrzahl der
Proben vor. In den ersten zehn Proben von Ende August (27. und 31.VIII.
1970), die noch nicht mit der richtigeren Methode vom freien Wasser
sowie vom Litoral gesammelt worden waren (nur vom Ufer aus, mit
Kescher), war er in sechs vorhanden. Nur im Teich 4 wurden im
Spätsommer Weibchen mit parthenogenetischen Eiern, mit Ephippien
sowie Männchen in derselben Probe gefunden. Ueberhaupt waren die
gefangenen Exemplare recht verschieden an Grösse und Farbe (ihre
Schalen waren glashell bis orangebräunlichen und rötlichen).

Die Tabelle II zeigt das quantitative Vorkommen von *Chydorus spha-
ericus* im freien Wasser in den beiden Untersuchungsperioden.

Tabelle II. Das Vorkommen des *Chydorus sphaericus*
im freien Wasser (ind./10 l Wasser)

Datum	Teich No.			
	1	2	3	4
2—3.IX.1970	0,3	7	2,8	250
8.IX.1970	—	3,2	60,6	186
16.IX.1970	—	1,6	41	8
24.IX.1970	0,2	—	22	22.6
20.V.1971	0,4	—	0.8	6,8
27.V.1971	1,4	—	—	2,4
4.VI.1971	5,0	1,8	0.4	3,0
19.VI.1971	0,4	—	0.4	1,0

Im Litoral (24 Proben im September, 60 im Mai—Juni) kann man
sein Vorkmmen nur im T e i c h 1 als massenhaft bezeichnen, nämlich
am 10.IX und 14.VI im Carex-Bestand, am 18.IX im überschwemmten
Gras und am 28.IX zusammen mit grossen Mengen von *Simocephalus
vetulus*, ebenfalls im überschwemmten Gras; dasselbe am 14.VI im
Riedgras im süd-östlichen Teil.

Am 28.IX fand sich *Chydorus sphaericus* auch im grossen Mengen in
den Chara-Wiesen dicht am Boden. Die letztgenannten Proben wurden
an sonnigen Stellen gesammelt.

Die Probe in unmittelbarer Nähe der oben erwähnten Gräser, die am 18.IX entnommen wurde, enthält bedeutend weniger Exemplare von Chydorus und überhaupt keine anderen Cladoceren.

In den Proben von Mai-Juni kam die Art an verschiedenen Stellen zuerst (26.V und 1.VI) recht selten, an manchen Punkten sogar sehr selten vor. Ab 9.VI begann sie jedoch bedeutend zahlreicher bis nahezu massenhaft zu werden, nämlich in den beiden breiten Litoralzonen (besonders in der südlichen), in den Riedgras-Beständen.

Im T e i c h 2 kam die Art im Litoral im September im allgemeinen häufig vor, im überschwemmten Gras war sie jedoch nicht besonders zahlreich — vielleicht wegen des Dickichts von Fadenalgen. Im Mai–Juni war sie ziemlich häufig, besonders häufig aber in der nord-östlichen Ecke zwischen dem Riedgras bei der Mündung des Zuflusses.

Ziemlich zahlreich war sie auch im September in der Uferzone des T e i c h e s 3, aber nur zwischen überschwemmten Gräsern und an der sonnigen Seite des »Halbdamms«. Im Mai-Juni kam sie an allen 4 Ufern nur in geringer Zahl oder gar nicht vor.

Eher wenige Exemplare dieser Art beherbergte in den beiden Untersuchungsperioden das Litoral im T e i c h 4; in den 8 Proben von 16 und 18.VI kam sie überhaupt nicht vor. Im *Potamogeton filiformis* hingegen, in einiger Entfernung von den Ufern, war sie am 28.IX sogar sehr zahlreich.

Die Maxima der E p h i p p i e n b i l d u n g kommen in den einzelnen Teichen nicht gleichzeitig vor. Als Höhepunkt dieser Erscheinung in der ersten Untersuchungsperiode kann man für den Teich 4 Anfang September annehmen, wo sehr viele Ephippien-Weibchen, Männchen und Paare in copula gesammelt wurden. Im Teich 1 sah man vereinzelte Pärchen schon am 18.IX, zahlreicher jedoch waren sie — ebenso wie die ephippialen Weibchen — erst Ende September zu beobachten. In Proben vom Teich 2 wurden Ephippien-Weibchen nicht beobachtet. Im Teich 3 war ihr maximales Vorkommen am 23.IX.

Im Mai–Juni wurden weder Ephippien-Weibchen noch Männchen gefunden.

SIMOCEPHALUS VETULUS war die zweithäufigste Cladocerenart in den untersuchten Teichen. Im freien Wasser kam er nicht häufig vor. was man auf Tabelle III sehen kann.

Im Litoral war diese Art häufiger, obwohl sie nur zweimal massenhaft vorkam, nämlich im überschwemmten Gras im T e i c h 1 zusammen mit *Chydorus sphaericus* am 18 und 28.IX. Auch am 14.VI kam sie in sehr grossen Mengen vor, und zwar in der breiten süd-östlichen Riedgraszone (mit nahezu massenhaft vorkommendem *Chydorus sphaericus*); viele erwachsenen Weibchen der zweiten Generation hatten zu diesem Zeitpunkt schon Ephippien.

Tabelle III. Das Vorkommen des *Simocephalus vetulus*
im freien Wasser (ind. 10/1 Wasser)

Datum	Teich No.			
	1	2	3	4
2—3.IX.1970	—	0,2	—	0,6
8.IX.1970	—	—	—	4,8
16.IX.1970	—	—	—	0,2
24.IX.1970	—	—	—	0,2
20.V.1971	—	—	—	0,6
27.V.1971	0,2	—	—	—
4.VI.1971	—	—	—	0,2
19.VI.1971	—	—	—	—

Im T e i c h 2 war die Art in den beiden Perioden überhaupt nicht häufig.

In den Proben vom T e i c h 3 waren nur einzelne Exemplare zu beobachten und nur am 28.IX mit Ephippien. In der zweiten Untersuchungsperiode, ab 10.VI fehlten sie in den Proben fast vollkommen.

Im T e i c h 4 war die Art im September, Ende Mai und Anfang Juni viel häufiger, und die Ephippial-Weibchen zeigten sich in den September-Proben ab 10.IX. Zwischen den überschwemmten Landgräsern waren in dieser Periode diese Cladoceren ziemlich zahlreich. Im Juni, ab 11.VI wurden in den meisten Proben Ephippial-Weibchen gefunden.

Bei dieser Art unterscheidet man schon in der zweiten Maihälfte die wenigen, grossen Exemplare der ersten Frühjahrsgeneration, von den viel zahlreicheren, jungen Individuen der zweiten Generation, die sich erst in der zweiten Junihälfte (durch Ephippienbildung!) zu vermehren beginnen. Nach und nach verwischen sich aber die Grössenunterschiede, denn die erwachsenen Weibchen pflanzen sich mehrmals fort, so dass man Mitte Juni in den Proben Tiere von verschiedenem Alter bemerkte.

SCAPHOLEBERIS MUCRONATA stand an dritter Stelle, kam aber eigentlich gar nicht häufig vor. Am zahlreichsten war die Art in den Teichen 2 und 4 und zwar vor allem im freien Wasser oder vor den Abflussmönchen; weniger zahlreich, und nur im September, im Litoral. Am 27.VIII kam sie im Teich 4 vor dem nördlichen Eckmönch im Schatten sogar als Dominant vor. Ueberhaupt waren die Exemplare dieser Art im September nur bis zum 10.IX in den Proben zu finden, später fehlten sie ganz, abgesehen von einem Exemplar, das im Teich 3 in den überschwemmten Gräsern am 28.IX gefunden wurde. Im Mai—Juni wurden sie ausschliesslich in den Proben vom freien Wasser in den Teichen 2 und 4 gefunden.

In den Quantitativproben vom freien Wasser kamen sie (pro 10 Liter Wasser) in folgenden Mengen vor:

Tabelle IV. Das Vorkommen der *Scapholeberis mucronata*
im freien Wasser (ind./10 l Wasser)

Datum	Teich No.			
	1	2	3	4
2—3.IX.1970	—	4,6	0,1	—
8.IX.1970	—	2	—	3,2
16.IX.1970	—	—	—	—
24.IX.1970	—	—	—	—
20.V.1971	—	1	—	0,6
27.V.1971	—	0,2	—	0,4
4.VI.1971	—	3,2	—	1
19.VI.1971	—	—	—	—

Ausserden wurden im T e i c h 1 beim Zufluss nur einmal (am 31.VIII) und auch nur wenige Exemplare gefangen. Es waren grosse Weibchen mit parthenogenetischen Eiern.

Im T e i c h 2 vor dem Abflussmönch waren am 31.VIII diese Cladoceren zahlreich. Vorwiegend handelte es sich um grosse Weibchen mit parthenogenetischen Eiern und Ephippien. Dann, am 10.IX wurde noch ein grosses Weibchen ohne Eier gefunden.

Im T e i c h 3 kam die Art am 31.VIII am Zufluss aus dem Teich 1 in einigen parthenogenetischen Exemplaren und am 10.IX in wenigen weiblichen Exemplaren, u.a. mit Ephippien, vor. Dann wurde, wie erwähnt, noch ein Exemplar am 28.IX in Gräsern gefunden.

Im T e i c h 4, nach dem Maximum am 27.VIII, wurde die Art noch an derselben Stelle vor dem nördlichen Eckmönch in den angeschwemmten faulenden Pflanzenteilen an der Oberfläche in ziemlich grosser Anzahl gefangen, und zwar parthenogenetische Weibchen mit bis zu acht Eiern in der Bruthöhle sowie ephippiale Weibchen.

Am 10.IX wurden noch vereinzelte Exemplare von *Scapholeberis mucronata* (mit parth. Eiern) im Litoral gefangen.

ALONA AFFINIS wurde nur in den Teichen 3 und 4 im September gefunden. Im T e i c h 3 kam sie fast in allen quantitativen Proben vom freiem Wasser vor, und zwar pro 10 Liter Wasser:

Tabelle V. Das Vorkommen der *Alona affinis* im freien
Wasser (ind./10 l Wasser)

Datum	Teich No.			
	1	2	3	4
2—3.IX.1970	—	—	0,9	—
8.IX.1970	—	—	0,4	1♂
16.IX.1970	—	—	0,4	—
24.IX.1970	—	—	—	—
20.V.1971	—	—	—	—
27.V.1971	—	—	—	—
4.VI.1971	—	—	—	—
19.VI.1971	—	—	—	—

Am 16.IX waren etwa die Hälfte der Anzahl Männchen. Vom Litoral wurden nur am 10.IX zwei Exemplare (Weibchen) gefangen.

Im T e i c h 4 wurde die *Alona affinis* ausserdem nur einmal angetroffen, nämlich am 1.IX im nördlichen Eckmönch (ein Männchen). Ueberhaupt ist also diese Art im freien Wassen häufiger.

Die am 28.VIII zum Vergleich gesammelten Proben aus dem Mausrodelteich bei Lunz, erwiesen eine verhältnissmässig grosse Häufigkeit dieser Art im südlichen Teil der Uferzone beim Abflussmönch (Ephippien--Weibchen).

ALONA GUTTATA wurde im September nur am 23.IX in zwei Exemplaren im Teich 3 gefunden: im Riedgras beim Ufer ein Weibchen von forma tuberculata und ein Weibchen mit parthenogenetischen Eiern. Im Juni wurde die Art in den Proben vom Teich 1 (11.VI) und Teich 4 (16.VI), je ein Exemplar, im Riedgras beobachtet.

Im freien Wasser wurde am 4.VI im Teich 4 auch nur ein Exemplar gefunden.

ALONA COSTATA wurde nur einmal gefunden, nämlich im Teich 4 an einer stets schattigen Stelle unter Carex, am 23.IX (zwei Männchen).

CERIODAPHNIA QUADRANGULA wurde im September nur zweimal gefunden: nämlich im Teich 2 am 10.IX im Litoral (drei kleine Exemplare) und im Teich 4 an demselben Tag im Litoral (zwei erwachsene Exemplare).

Im Mai–Juni wurde die Art auch ausschliesslich in der Uferzone gefunden: Teich 2 — 1.VI im süd-östlichen Riedgrasbestand (1 Exemplar) und am 14.VI, ditto (3 Exemplare); Teich 3 — 3.VI am nördlichen Ufer (1 Exemplar); Teich 4 — 11.VI, am nördlichen Ufer (1 Exemplar) und 19.VI, ebenfalls am nördlichen Ufer (1 Exemplar).

4. DISKUSSION

Die fast vollkommene Abwesenheit der Cladoceren im freien Wasser im Teich 1 ist sicher die Folge der Strömung, die hier am stärksten ist (schon im Teich 2 ist sie bedeutend schwächer). Die Tiere werden aus dieser Zone fortgespült und gelangen mit denen von den Teichen 2 und 3 teilweise in den Teich 4, der schon wegen der deutlich schwächeren Durchströmung einen etwas anderen Charakter hat und reichen Unterwasserpflanzenbestand (viel *Potamogeton filiformis*), Phytoplankton und faulende Pflanzenstoffe an der Oberfläche sowie etwas höhere Temperaturen aufweist.

Das häufige und manchmal auch massenhafte Vorkommen der Cladoceren im überschwemmten Gras an sonnigen Stellen ist vermutlich

mit den intensiven Fäulnisprozessen verbunden, die in der erhöhten Temperatur stattfinden, wobei die sich stark vermehrenden Bakterien den Cladoceren als Nahrung dienen. Dasselbe gilt auch für die breiten Carexzonen.

Ueberhaupt scheint die höhere Temperatur für diese Tiere auch hier günstig zu sein, da man sie häufiger an besonnten Stellen des Litorals findet als an den schattigen. So waren an der südlichen, besonnten Seite des »Halbdamms« im Teich 3 die Cladoceren sehr zahlreich, während an der nördlichen, schattigen Seite ihre Häufigkeit in derselben Zeit (am 28.IX) recht gering war.

Die allgemeine Häufigkeit der Cladoceren — im Vergleich mit den mitteleuropäischen Flachlandteichen, die nach meinen Beobachtungen im Spätsommer mehrere Tausende Exemplare pro 10 Liter Wasser enthalten können — ist auch in dieser Jahreszeit äusserst gering.

Die Beobachtungen über *Chydorus sphaericus,* verglichen mit denen an einigen anderen Teichkomplexen (Stromenger-Klekowska 1960, Wawrik 1955, 1960) zeigen, dass diese ubiquistische Art eben in solchen Gewässertypen wie die Lunzer Teiche, besonders günstige Lebensbedingungen findet. Die Periode ihrer bisexuellen Vermehrung ist hier — besonders im Teich 4 — mit ausserordentlicher Intensität ausgeprägt.

Nur die zwei häufigsten Arten: *Chydorus sphaericus* und besonders *Simocephalus vetulus* wurden, in sehr geringer Anzahl, in den Darmkanälen der jungen Bachforellen zwischen Insektenresten gefunden. Ueber die fischwirtschaflichen Aspekte meiner Arbeit an den Lunzer Teichen habe ich ausführlicher schon früher geschrieben (Stromenger 1972 a, b).

Danksagung

5. ZUSAMMENFASSUNG

Die Beobachtungen betreffen die Cladocerenfauna von 4 subalpinen Forellenteichen. Sie bekommen das Wasser entweder unmittelbar aus der Seebach-Abzweigung oder voneinander. Ihr Boden ist schlammig und stellenweise mit Pflanzen bewachsen, ihre Tiefe beträgt durchschnittlich 60—80 cm, sie sind durchsichtig bis zum Boden und ihre Temperatur ist ziemlich tief wegen der ständigen Durchströmung. Es wurden insgesamt 7 Cladocerenarten gefunden, wovon die häufigsten *Chydorus sphaericus, Simocephalus vetulus* und *Scapholeberis mucronata* waren. In den Darmkanälen der dort gezüchteten jungen Bachforellen wurden Reste nur von den zwei ersten Arten gefunden. Im Spätsommer und Herbst wurde die Anzahl der Cladoceren in jedem nächsten der Teiche 1—4 höher — im freien Wasser und niedriger — im Litoral. Im Spätfrühling entwickelt sich diese Regel-

mässigkeit erst nach einigen Wochen nach der Bewässerung der Teiche. Sie ist
wahrscheinlich Nachfolge der abnehmenden Durchströmungskraft in den nacheinan-
der liegenden Teichen und der zunehmenden Häufigkeit von Phytoplankton und
faulenden Pflanzenstoffen. Besonders zahlreich kommen die Cladoceren an den
warmen, sonnigen Stellen zwischen den Ufer- und Unterwasserpflanzen, vor allem
faulenden Pflanzenresten, vor. In diesen Gewässern scheint *Chydorus sphaericus*
besonders günstige Lebensbedingungen zu finden. Ende August erschienen in
seiner Population zahlreiche Männchen. Im Vergleich mit den Karpfenteichen der
mitteleuropäischen Ebene sind die besprochenen Gewässer sehr arm an Cladoce-
renarten und -individuen.

6. STRESZCZENIE

Obserwacje dotyczą fauny wioślarek (Cladocera) 4 pstrągowych stawków na-
rybkowych rejonu podalpejskiego. Zbiorniki te otrzymują wodę potokową częściowo
bezpośrednio, a częściowo systemem różańcowym. Ich dno jest muliste i miejscami
zarośnięte, średnia głębokość 60—80 cm, przejrzystość całkowita, temperatura dość
niska wskutek stałego przepływu. Napotkano w nich 7 gatunków wioślarek; naj-
liczniej występowały: *Chydorus sphaericus*, *Simocephalus vetulus* i *Scapholeberis
mucronata*. Tylko szczątki dwóch pierwszych z nich znaleziono w przewodach
pokarmowych hodowanych młodych pstrągów potokowych. Na przełomie lata i je-
sieni liczebność wioślarek w każdym następnym stawie od 1 do 4 jest kolejno coraz
większa w śródstawiu, a coraz mniejsza w litoralu. Wiosną prawidłowość ta
rozwija się dopiero w ciągu kilku tygodni po zalaniu stawów. Zapewne jest ona
wynikiem malejącej siły przepływu w kolejnych stawach i wzrastającej obfitości
fitoplanktonu i gnijących szczątków roślinnych. Szczególnie licznie wioślarki wy-
stępują w nagrzanych słońcem rejonach roślinności wynurzonej i zanurzonej,
zwłaszcza gnijącej. W zbiornikach tych szczególnie pomyślne warunki bytowania
zdaje się znajdywać *Chydorus sphaericus*, w którego populacji pod koniec sierpnia
pojawiły się licznie samce. W porównaniu z nizinnymi środkowoeuropejskimi sta-
wami karpiowymi, liczebność gatunków i osobników wioślarek w omawianych
zbiornikach jest bardzo niska.

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M. B. I V A N O V A* and R. Z. K L E K O W S K I**

RESPIRATORY AND FILTRATION RATES IN *SIMOCEPHALUS VETULUS* (O. F. MÜLLER) (CLADOCERA) AT DIFFERENT pH

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ABSTRACT

Studies were made of the effect of different pH of water on filtration, respiration and energy budget of laboratory cultures of *S. vetulus*. The dependence, at pH 7.0, between body length and respiration, filtration and food consumption were expressed by exponential functions. Description is given of changes in values and mutual proportions of resting respiratory rate (RRR), ordinary respiratory rate (ORR) and cost of active locomotion (CAL) under the effect of changing pH. It was found that change in pH in broad range (4.5–9.5) does not affect the RRR, however it causes an increase in ORR, in filtration rate and the share of CAL in ORR. Tentative energy budget was computed and changes of its parameters under the effect of pH are discussed.

1. INTRODUCTION

The problem of physiological optimum in poikilothermic animals was often discussed in literature. A special attention was given to appropriate methods with which it would be possible to determine quickly and with satisfactory confidence an optimum value of a given environmental factor for the animal species investigated. According to F i l i p č e n k o (1932), the irritating action of an environmental factor increases with deviation of its value from the optimum; this action is at its lowest in the optimum zone, but it is the highest when the conditions are close to lethal. Therefore one could expect that animals, being faced with disadvantageous conditions, will try to leave the irritation zone which should be accompanied by an intensified locomotory activity and a corresponding increase in oxygen consumption. I v l e v (1963) has defined the optimum conditions as a zone of the minimum locomotory activity relying on an analysis of distribution of animals in the gradients of several environmental factors as well as of the speed of locomotory movements under different conditions. Thus it seems specially interesting to investigate the energy budget under conditions which are far from optimum for the increase in energy expenditure should be followed by an increase in the amount of energy supplied to an organism as food; without such compensation the animals would die of the energy defficiency.

The effect of temperature on behaviour and physiological features of poikilothermic animals has been most thoroughly investigated, however there is also a great deal of information concerning the effect of active water reaction on aquatic animals. The following problems deserved attention of scientists: the survival boundaries in aquatic animals (S k a d o v s k i j 1928, B o g a t o v a 1962,

Konstantinov 1969), changes in the oxygen consumption rate (Jacenko 1928 a,b, Ivanova 1965, Alimov 1967, Hefco, Miron 1965); Konstantinov 1969), changes in feeding intensity (Ivanova 1965, 1969, Alimov 1967); reproduction rate at different concentration of hydrogen ions (Jacenko 1928 a, b, Ivanova 1963); size of aquatic animals in water bodies of different pH (Manujlova 1949, Salazkin 1966 a,b). It was often found that pH of water which was beyond boundaries of the adaptative ability caused an increase in oxygen demand, in locomotory activity, and in feeding activity of animals used for such experiments. Thus, in the light of the above statement, after Ivlev (1963) the optimum conditions were practically identical with those under which a population has been living and to which it has been adapted.

The present work deals with energy transformation by *S. vetulus* under conditions of rapidly changing active water reaction in short-term experiments. All experiments were carried out with animals which had been acclimated to pH 7.0.

2. MATERIAL AND METHODS

Cladocerans of *S. vetulus* were collected from a large clay ditch near Warsaw, brought to the laboratory and cultivated in aquaria at 22°C; acc. to Krjučkova, Kondratjuk (1966) this is thermal optimum for a number of Cladocera species. *Chlorella sp.* was used as food.

The body length of cladocerans in cultures ranged from 0.7 to 2.5 mm, they reached maturity at the length of 1.1—1.2 mm. Dry weight of animals was ascertained with a torsion balance for each individual separately when the experiments were completed, after drying them at 105°C. Using the least square method, regression was calculated for the body length and dry weight of animals (Fig. 1). This dependence can be described with an appropriate precision by power functions, for immature animals ($L = 0.7$—1.1 mm):

$$W = 10.74 \cdot L^{1.08} \tag{1}$$

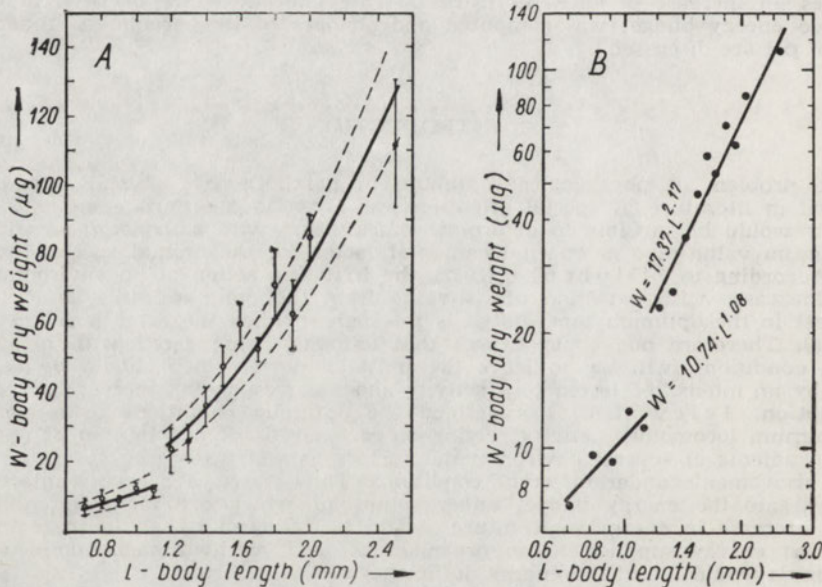and for matured animals:

$$W = 17.37 \cdot L^{2.17} \tag{2}$$

Fig. 1. Dependence between body length and dry weight of *Simocephalus vetulus*. A — regular scale (vertical lines: $W \pm 2\varrho_W$), B — log-log scale

where: W — dry weight of an individual in µg, L — its length in mm. Functions (1) and (2) were calculated from the data in Table I.

Table I. Length and dry weight of *Simocephalus vetulus*

Length (mm)	N	Mean weight (µg)	ρ_w	$\dfrac{w_\rho}{w}$ (%)
0.7	5	7.04	0.81	11.5
0.8	5	9.62	1.05	11.0
0.9	5	9.17	0.56	6.1
1.0	6	12.18	0.54	5.4
1.1	5	11.30	0.61	4.4
1.2	4	23.62	3.24	13.7
1.3	6	25.90	2.52	9.7
1.4	6	35.73	2.89	8.1
1.5	6	47.13	3.71	7.9
1.6	7	59.41	3.48	5.8
1.7	6	52.70	1.59	3.0
1.8	6	71.10	5.02	7.1
1.9	6	62.97	5.15	8.2
2.0	6	84.78	3.54	4.2
2.5	4	111.08	9.48	7.5

The following rates were measured in the experiment: (1) resting respiratory rate (RRR), (2) ordinary respiratory rate (ORR), i.e., active respiratory rate at locomotory movements, (3) filtration rate (*F*). "Cost" of active locomotion (CAL), i.e., energy losses for locomotion, were found by difference between ordinary and resting respiratory rates: ORR—RRR=CAL.

Stoppered cartesian divers after Z e u t h e n (1950) were used for measuring RRR, more detailed description of this model of divers in K l e k o w s k i (1971). This type of divers was used previously in analogous work on bioenergetics of predacious copepod, *Macrocyclops albidus* (K l e k o w s k i, S h u s h k i n a 1966 a, b).

The diameter of head bulbe into which the cladocerans were placed was about 2.5—3.0 mm. Thus the animals were almost immobilized in the divers, from observation of their behaviour it appeared that only filtrating appendages were moving incessantly. This immobilization of animals in divers permits to consider the obtained results as resting respiratory rate (RRR). The duration of the measurement was such that the amount of oxygen in the diver did not decrease more than by 25% of the initial value. As a rule, the measurements lasted about 2 hr.

In order to obtain required pH buffor solutions were used according to D r y l (1961).

The experimental technique was as follows: the animals were placed into 8 divers, one in each, filled with buffor solution of pH 7.0 and their RRR was measured. Later on the animals were removed from the divers and six were transferred to the medium with required pH (cf. Tables IV, V, VI). Two remaining individuals (control) were placed again in a fresh portion of solution with pH 7.0. The animals, in turn, were placed into divers filled with medium of appropriate pH and RRR was measured. The results of two control measurements at pH 7.0 pointed to an effect of handling alone (removal of animals from divers and introducing them again) on the RRR. It appears that the whole procedure of transferring (removing from the diver, washing in a fresh medium, and replacing in the diver) caused a decrease in RRR by 15% on average. RRR in control animals after transferring them amounted to 84.9±5.9% as compared with the first measurement. Thus, appropriate corrections were used in all further calculations of oxygen consumption in the divers.

Ordinary respiratory rate (ORR) was measured in 100—130 ml capacity bottles. Twenty animals were placed into each bottle. The bottles with no animals were used as controls. The bottles were filled with the same buffor solutions as those used for RRR measurements in the divers. The amounts of oxygen in the bottles before and after exposures were determined by means of the Winkler method.

The animals were active in the bottles and swam in water. These active movements were increasing clearly when pH of water in the bottle deviated from 7.0.

The filtration rate was determined in 20 ml containers with suspension of Chlorella. Chemical composition of this suspension and calorific value of its components are shown in Table II[1].

Table II. Chemical composition of *Chlorella sp.* suspension used

Concentration (mln cells/ml)	Protein		Carbohydrates		Lipids		Σ (cal/l)
	(mg/l)	(cal/l)	(mg/l)	(cal/l)	(mg/l)	(cal/l)	
8.0	27.3	125.6	10.7	40.8	8.1	76.7	243.0

The filtration rate (F) was calculated according to G a u l d's formula (G a u l d 1951):

$$F = \ln \frac{C_o}{C_t} - a$$

where F — filtration rate in ml/hr, C_o — initial concentration of Chlorella, C_t — concentration of Chlorella after exposure time, a — correction factor, for sinking of Chlorella. For calculation of filtration rate from G a u l d's formula it is important that the difference in initial and final concentrations was not too large (R i g l e r 1971); in our experiments it did not exceed 15% of the initial concentration. The concentration of Chlorella suspension was measured with Hilger H810-1 Biochem Absorptiometer. In all the experiments concerning the effect of active water reaction on the filtration rate, the initial concentration of Chlorella was 4.5 million cells/ml. The experimental containers were exposed for 3 hr at 22°C.

3. RESULTS

The effect of active water reaction on resting respiratory rate (RRR)

A considerable variation was found in the results of RRR measurements, caused by physiological differences between animals of the same size. It is understandable since the respiratory rate was measured in cartesian divers for a single individual and therefore its individual properties became evident, whereas in each bottle there were 20 animals whose individual properties were levelled. This variation of RRR occurred both in optimum and in non-optimum conditions. One of the factors that affected RRR was moulting during which RRR decreases (Fig. 2).

Dependence between length of animals and their RRR (Table III, Fig. 3) can be described by the function:

$$RRR = 0.083 \cdot L^{1.79} \tag{3}$$

where: RRR — resting respiratory rate (μl/ind. · hr) L — animal's length (mm). The first point of RRR, for animals of $L = 0.7-0.8$ mm, is beyond the confidence limit of equation (3) with the highest variation of individual data (Table III). Perhaps it would be more appropriate to describe the dependence of RRR $= f$ (L) by two functions: for immature *S. vetulus* ($L = 0.7-1.1$ mm) and for matured females ($L = 1.1-2.5$).
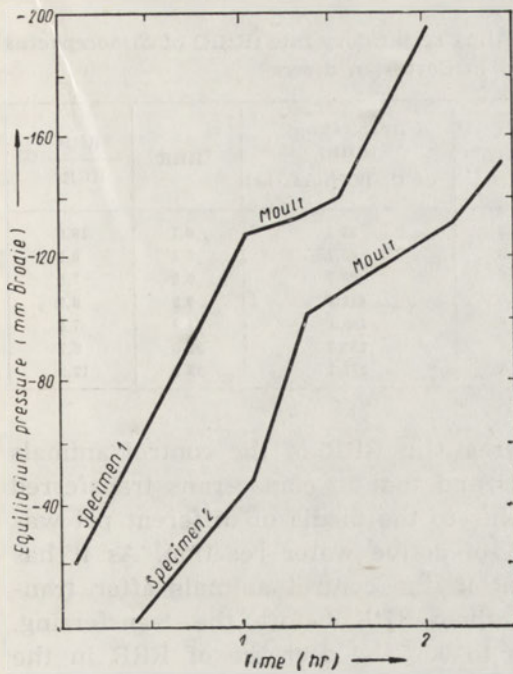

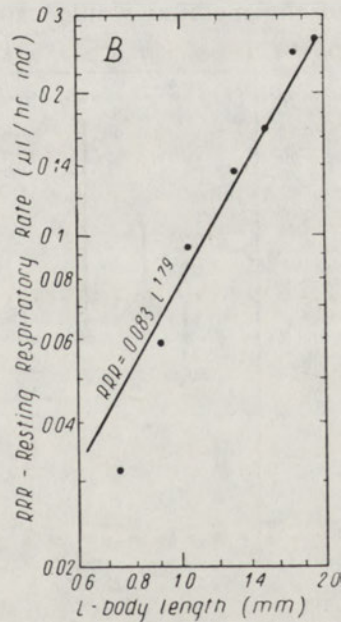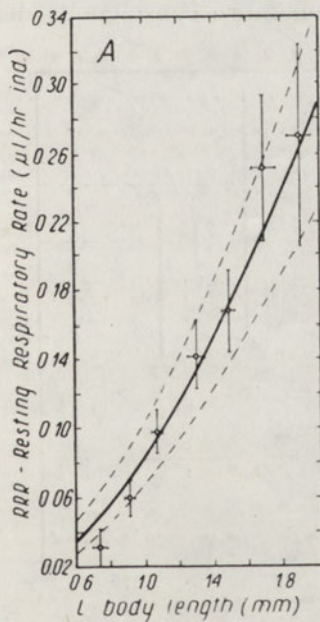Fig. 2. Changing of equilibrium pressure in cartesian divers containing specimens of *Simocephalus vetulus*

Fig. 3. Dependence between body length and resting respiratory rate (RRR) by *Simocephalus vetulus* in cartesian divers. A — regular scale (vertical lines: RRR± $2\varrho_{RRR}$, horizontal lines: L±$2\varrho_L$), B — log-log scale

Table III. Size (length) dependence of resting respiratory rate (RRR) of *Simocephalus vetulus*, measured in Cartesian divers

Length range (mm)	N	Mean length (mm)	$^\rho L$	$\dfrac{^\rho L}{L}$ (%)	Respiration (RRR) ($\mu l\ O_2 \cdot 10^{-3}/\text{ind.} \cdot \text{hr}$)	$^\rho RRR$	$\dfrac{^\rho RRR}{RRR}$ (%)
0.7 —0.8	12	0.744	0.024	3.2	32.1	6.1	18.9
0.81—1.0	31	0.914	0.009	1.0	60.1	5.1	8.5
1.01—1.2	24	1.074	0.011	1.0	98.7	6.9	7.0
1.21—1.4	14	1.295	0.013	1.0	142.7	9.6	6.7
1.41—1.6	14	1.486	0.009	0.6	169.1	11.9	7.1
1.61—1.8	8	1.678	0.030	1.8	252.3	22.0	8.7
1.81—2.0	4	1.888	0.033	1.8	271 7	35.2	12.9

The difference between the decrease in RRR of the control animals in the second series of experiments and that in cladocerans transferred for the second series of measurements to the media of different pH was accepted as an index of the effect of active water reaction. As it has been mentioned (cf. Methods), RRR in the control animals after transferring amounted to ca 85⁰/₀ of their RRR before the transferring. With water pH changing from 4.5 to 9.5, the decrease of RRR in the second series of measurements (after transferring) was identical as in the controls (Fig. 4). When pH was increased to 10.6, a decrease in oxygen consumption was observed. One can suppose that further alkalization of the medium would cause even more conspicuous decrease in
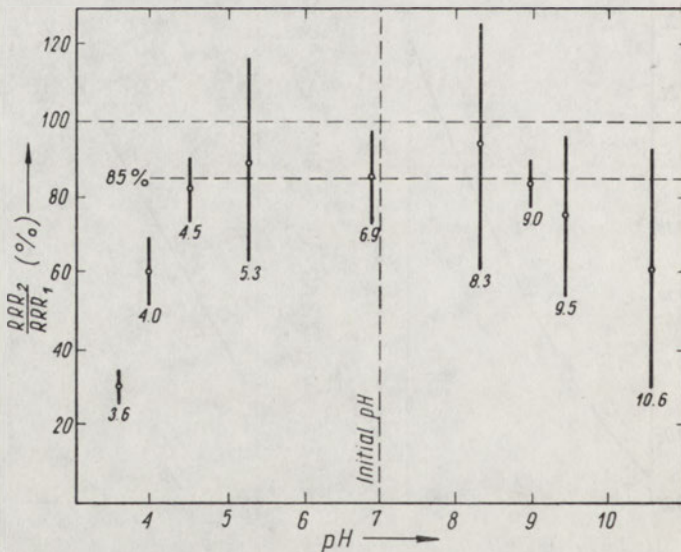

Fig. 4. The effect of transferring *Simocephalus vetulus* from divers with pH=7.0 to new divers at different values of pH on respiration (RRR₂); 100% denotes respiration (RRR₁) by the same individuals in the first series of measurements. Vertical lines indicate variations of the data

RRR. When pH decreased, RRR also decreased which occurred at pH of 4.0 and 3.6. At the latter value RRR was more than twice as low as at pH 6.9. Our results seem to confirm the view by K o n s t a n t i n o v (1969) that aquatic animals endure better alkalization than acidification of the environment.

In general, it can be said that changes within a very broad range of pH did not cause significant changes in RRR.

The effect of active water reaction on ordinary respiratory rate (ORR)

The deviation of pH from the optimum value causes an increase in ORR of cladocerans; the curve for ORR at different pH is bimodal with a depression at the optimum pH value (J a c e n k o 1928 a, b, I v a n o v a 1965, K o n s t a n t i n o v 1969, H e f c o, M i r o n 1965). A similar situation was also found in our measurements of oxygen consumption by *S. vetulus* in bottles, where animals were allowed free movements (Table IV). Since ORR can be considered as a sum of RRR and the cost of active locomotion (CAL) and since RRR does not depend on pH within the

Table IV. Size (length) dependence of ordinary respiratory rate (ORR) measured in bottles (for each length − pH combination, 3 bottles with 20 ind. in each)

Mean length (mm)	pH	Respiration (RRR) (μl $O_2 \cdot 10^{-3}$/ind.·hr)	$\dfrac{ORR}{ORR_{opt.}}$ %
1.9	4.0	630	175
1.9	4.8	520	145
1.9	5.8	430	120
1.9	6.9	360	100
1.7	8.2	420	117
1.7	8.7	450	125

limits at which the investigated cladocerans survive (cf. Fig. 4), one can suppose that with any deviation of concentration of hydrogen ions from the optimum, CAL will increase, which is confirmed by a direct observation of the cladocerans behaviour in the bottles. The smallest ORR by *S. vetulus* was at pH 6.9, whereas any deviation of active water reaction both in acidous and alkaline directions caused an increase in oxygen consumption (Table IV). Under optimum conditions and at an optimum activity in such little mobile form as *S. vetulus*, CAL amounts only to 30% of ORR. Under conditions close to lethal (pH 4.0) CAL can be 3 times as high as RRR (Table V).

Table V. Correlation between ordinary respiratory rate (ORR), resting respiratory rate (RRR) and cost of active locomotion (CAL) at different values of pH (Note: ORR=RRR+CAL)

Mean length (mm)	pH	Respiration (μl $O_2 \cdot 10^{-3}$/ind.·hr)			Respiration as % of ORR		
		ORR	RRR	CAL	ORR	RRR	CAL
1.9	4.0	630	153	457	100	24.2	75.8
1.9	4.8	520	255	265	100	49.0	51.0
1.9	5.8	430	255	175	100	59.0	41.0
1.9	6.9	360	255	105	100	70.5	29.5
1.7	8.2	420	220	200	100	52.5	47.5
1.7	8.7	450	220	230	100	49.0	51.0

The effect of active water reaction on the filtration rate

Rate of filtration under constant physical and chemical conditions of the environment was found to depend on size (or weight) of filtrator and on concentration and calorific value of filtrated suspension (R i c h m a n 1958, M o n a k o v, S o r o k i n 1961, S u s h c h e n y a 1963, 1968, I v a - n o v a 1967, R i g l e r 1971). The rate of filtration is constant and maxi- mal at a small concentration of suspension (approximately up to 1 mg dry weight per liter, or about 5—6 cal/l). At middle range of concentra- tion $F=f(C)$, where F — the filtration rate, C — average food concentra- tion. With an increase of C to over 15 mg dry weight/l, or 80—90 cal/l, the filtration rate reaches again a constant and minimal level.

The results on filtration rate of Chlorella by *S. vetulus* showed defi- nite dependence on the body length of cladocerans (Fig. 5). Using the least square method, the following regressions were calculated from these values:

$$\text{for } C_o=1.8 \text{ million cells/ml, } F=0.040 \cdot L^{3.20} \tag{4}$$

$$\text{for } C_o=4.0 \text{ million cells/ml, } F=0.018 \cdot L^{3.29} \tag{5}$$

where L — body length of cladocerans in mm, F — filtration rate in ml/ind.·hr. Equations (4) and (5) can be pooled together in one:

$$F=a \cdot L^{3.25}, \ a=f(C) \tag{6}$$

With changes in pH of the medium, the filtration rate by *S. vetulus* also changes, increasing in some cases more than twicely (Table VI). The highest filtration rate was observed at pH 5.0—5.5 and 9.0, further alkali- zation or acidification of the medium caused a decrease in filtration rate of the investigated animals. The curve illustrating the filtration rate at different pH of the media (Fig. 6) has two modes, similarly as the oxygen consumption curve for the bottle series, when cladocerans were allowed to move freely. These two curves differ in that with acidification of the
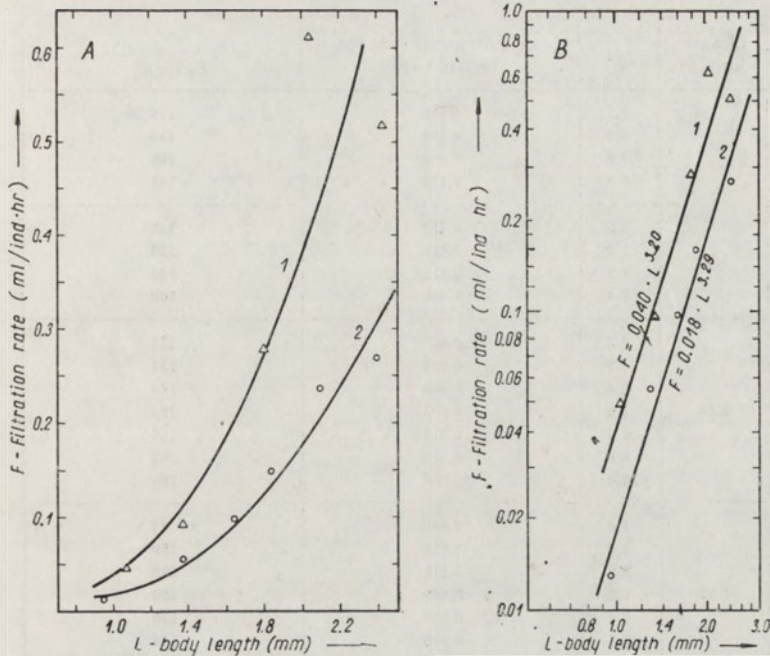
Fig. 5. Dependence between body length and filtration rate by *Simocephalus vetulus* at different initial concentration (C_0) of Chlorella. 1 — C_0=1.8 mln cells/ml, 2 — C_0=4.0 mln cells/ml. A — regular scale, B — log-log scale

medium below pH 5.0 and with alkalization over pH 9.0 — 9.2, the filtration rate decreases (Table VII), whereas the oxygen consumption rate, which reflects the cost of active locomotion (CAL), still increases.

Energy balance of *S. vetulus* at different pH of the medium

For calculation of instantaneous daily energy budget it is necessary to estimate its main parameters: consumption (*C*), respiration (*R*), growth (*P*), and assimilation efficiency of food ($U^{-1}=(R+P)/C$). The consumption rate can be calculated from the following dependence: $\bar{C}=F \cdot c$, where *F* — daily filtration rate, $\bar{C}$ — average concentration of food. At the amounts of algae used in the experiments, the consumption is practically not dependent from the food concentration (Fig. 7), and it is close or even equal to the maximum one. This C_{max} depends, however, on the size of cladocerans, and for the given conditions of the experiment (i.e. at temp. 22°C and pH 7.0) can be expressed as function:

$$C=1.85 \cdot L^{3.34} \tag{7}$$

where: *C* — daily consumption rate (million cells/ind.), *L* — body length

Table VI. Filtration rate in *Simocephalus vetulus* at different values of pH and constant food concentration 4.5 million cells of Chlorella per ml

Length (mm)	pH	Filtration rate (ml/ind.·hr)	$\dfrac{F}{F_{\text{pH7.0}}}$ (%)
1.64	9.2	0.145	176
	8.4	0.103	125
	7.2	0.082	100
	6.5	0.115	141
1.66	6.2	0.127	145
	5.2	0.188	230
	4.2	0.115	140
	3.4	0.089	108
1.50	3.2	0.056	125
	4.2	0.059	131
	5.4	0.065	144
	7.0	0.045	100
	8.0	0.075	166
	8.8	0.118	262
	10.0	0.054	120
1.92	3.0	0.065	94
	4.0	0.110	159
	5.2	0.170	246
	7.0	0.069	100
	8.0	0.090	130
	9.2	0.102	148
	10.0	0.068	98
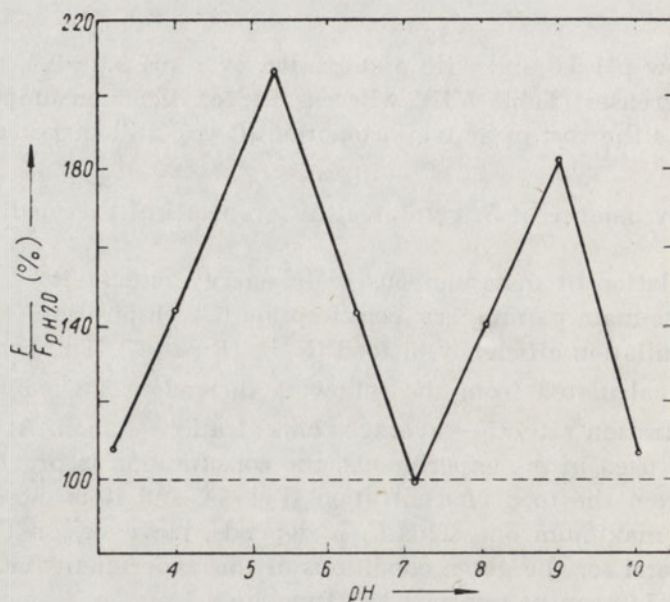
Fig. 6. The effect of active water reaction on the filtration rate by *Simocephalus vetulus*. 100% denotes the rate of filtration at pH=7.0

Table VII. Mean change of filtration rate $F(\%)$ at deviations of pH in medium from its optimal value (F at pH $7.0 = 100\%$)

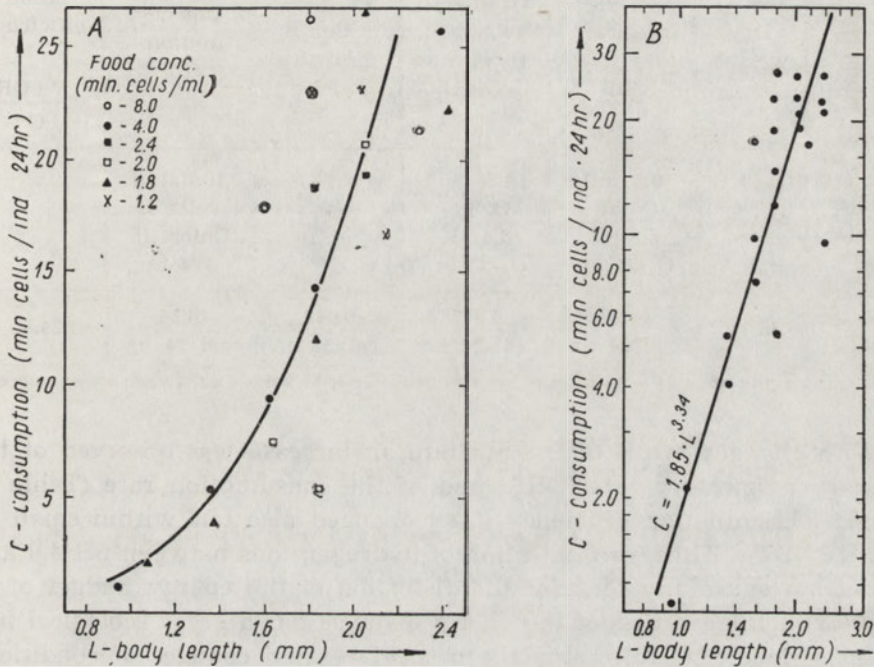| F (%)	pH in medium							
	3.0—3.4	4.0—4.2	5.2—5.4	6.2—6.5	7.0	8.0—8.2	8.8—9.2	10.0
	109	143	207	143	100	140	182	109

Fig. 7. Dependence between body length (L) and daily consumption rate (C) by *Simocephalus vetulus* at different food concentrations. A — regular scale, B — log-log scale

of cladocerans (mm). From our data, equation (7) can be used for calculation of consumption at algal concentrations from 1.2 to 8.0 million cells/ml. A similar dependence was described by S u s h c h e n y a (1968) for an amphipod, *Orchestia bottae*. In other our experiments on energy budget of *S. vetulus* during onthogenesis (K l e k o w s k i, I v a n o v a in prep.) which were also carried out at 22°C and pH 7.0, K_2 was variable from 0.8 to 0.25 with the individual development of cladocerans, which corresponded to change in the body length from 0.4 to 2.15 mm. In experiments presently described on the effect of pH on respiration and feeding rate, the body length amounted to 1.7 mm, on the average. At this body size, K_2 amounted to 0.5, on the average. From formula $K_2 = P/(R+P)$ it follows that $P = R \cdot K_2/(1-K_2)$, and in this particular case with $K_2 = 0.5$, $P = R$. For further considerations we assume $P = R$ at

all pH values since during such short-lasting experiments changes in K_2 are rather less probable. Table VIII presents tentative instantaneous energy budget of *Simocephalus vetulus* calculated for pH 7.0.

Table VIII. Energy budget of *Simocephalus vetulus* at 22°C
and pH 7.0; body length 1.7 mm

	Dry weight	Resting respiratory rate (ORR)	Ordinary respiratory rate (ORR)	Production (growth) (P)	Consumption (C)	Assimilation efficiency $U^{-1} = \dfrac{P+ORR}{C}$
Ordinary units	56 $^{\mu}$g	0.22 µl O$_2$/hr 5.6 µl O$_2$/24 hr	0.36 µl O$_2$/hr 8.6 µl O$_2$/24 hr		10.7 mln cells of Chlorella /24 hr	
Energy units	0.33 cal*	0.027 cal/24 hr	0.042 cal/24 hr	0.042 cal/24 hr	0.34 cal/24 hr	24.8%

Calorific value of body = 3.8 cal/mg dry weight (after K l e k o w s k i, I v a n o v a, in prep.).

With changes in pH of the medium an increase was observed of the ordinary respiratory rate (ORR) and of the consumption rate (Table V, VI). The assimilation efficiency (U^{-1}) changed also but within small limits: 15—25%. Thus, concentration of hydrogen ions between pH 4.0 and 9.0 did not cause any considerable distortion of the energy budget of *S. vetulus*. Such steadiness of the energy balance has a great ecological importance since it enables animals to survive rapid changes of conditions occurring in external environment. As it is evident from the above presented data, the pH range within which there is no clear change of the energy balance coincides with pH values at which the oxygen consumption rate is highest and the RRR is stable. It is interesting to compare these results with the range of survival of aquatic animals at different pH. K o n s t a n t i n o v (1969) reported on survival and oxygen consumption at different pH by three species of Tendipedidae. In all species investigated by this author the maxima of oxygen consumption occurred in these ranges of pH value at which 100% animals survived for 84 hr; further acidification or alkalization of water caused both a decrease in oxygen consumption and death of the animals during 48 hr.

4. CONCLUSIONS

If one accepts the optimum condition definition proposed by I v l e v (1963) and according to this one considers that the optimum conditions

are when a decrease in locomotory activity is observed or there is no unnecessary energy loss for normal development of an organism, then a neutral reaction of water is an optimum for *Simocephalus vetulus*. This optimum zone or according to F i l i p č e n k o (1932) the zone of the minimum of irritation evoked by the environment, converges with those conditions under which the cladocerans have lived. Acidification (to pH 4.0) or alkalization (to pH 9.5) of the environment both create conditions which cannot be considered as optimal, nevertheless they do not bring about any considerable disturbance in physiology of *Simocephalus vetulus*, as it is evident from the fact that the changed conditions did not cause any change in the resting respiratory rate (RRR) and the cost of active locomotion (CAL) is covered from an augmented energy input. One can assume that a longer stay of the cladocerans at these concentrations of hydrogen ions can lead to physiological adaptation. Further changes in the active water reaction (both towards acidity and alkalinity) will change RRR and disturb the overall energy budget. As it appears from the data by K o n s t a n t i n o v (1969), these disturbances are irreversible and the animals which are unable to adapt to new environmental conditions will die.

5. SUMMARY

The experiments on the effect of the active water reaction on filtration, respiration and energy budget, were carried out with laboratory cultures of *Simocephalus vetulus*, adapted to pH 7.0 and temperature of 22°C. The following results were obtained:

1. At pH 7.0 the dependence between body length of cladocerans and the resting respiratory rate (RRR), filtration (*F*) and consumption rates (C) can be expressed by functions: $RRR = 0.083 \cdot L^{1.79}$, $F = a \cdot L^{3.25}$ (at concentration of Chlorella 1.8 million cells/ml, $a = 0.040$; at concentration 4.0 million cells/ml, $a = 0.018$) and $C = 1.85 \cdot L^{3.34}$, where: *L* — body length in mm, RRR — resting respiratory rate in μl O_2/ind. · hr, *F* — filtration rate in ml/ind. · hr, *C* — consumption rate in million cells/ind. · 24 hr.

2. Change in pH from 4.5 to 9.5 does not affect the resting respiratory rate (RRR), however it causes an increase in the ordinary respiratory rate (ORR) and in the filtration rate (*F*). At neutral water reaction the cost of active locomotion (CAL) amounts only 29.5% of the ordinary metabolism rate (ORR), whereas at pH 4.0 this share increases up to 75.8%. The maximum filtration rate was found at pH 5.2—5.4 and at pH 8.8—9.2.

3. With acidification of the medium to pH 4.5 and alkalization to pH 9.5 the total energy budget of cladocerans showed no changes. With further acidification or alkalization of the medium, the resting respiratory rate (RRR) was found to decrease. At pH 4.0 the resting respiratory rate formed only about 60% of that at pH 4.5—9.5.

6. Резюме

Опыты по влиянию активной реакции воды на фильтрацию, обмен и баланс энергии были поставлены на лабораторной культуре *Simocephalus vetulus*, адаптированной к pH 7.0 и температуре 22°C. В результате экспериментов были получены следующие данные:

1. При pH 7.0 зависимости между длиной тела рачков и основным обменом (RRR), скоростью фильтрации (*F*) и рационом (*C*) могут быть выражены функциями $RRR = 0,083 \cdot L^{1,79}$, $F = a \cdot L^{3,25}$ (при концентрации хлореллы 1,8 млн

клеток в мл. $a = 0,040$, при концентрации 4,0 млн кл./мл, $a = 0.018$) и $C = 1,85 \cdot L^{3,34}$ где: L — длина тела в мм, RRR — основной обмен в мкл кислорода/экз. · час. F — скорость фильтрации в мл/экз · час, C — рацион в млн.кл/экз · сутки.

2. Изменение pH от 4,5 до 9,5 не влияет на основной обмен (RRR), но вызывает увеличение активного обмена (ORR) и скорости фильтрации (F). Если при нейтральной реакции воды активный обмен составляет всего 29,5% от общего потребления кислорода, то при pH 4,0 доля активного обмена увеличивается до 75,8%. Максимальная скорость фильтрации наблюдается при pH 5,2—5,4 и при pH 8,8—9,2.

3. При подкислении среды до pH 4,0 и подщелачивании до pH 9,5 общий баланс энергии рачков не нарушается. При дальнейшем подкислении или подщелачивании среды основной обмен (RRR) падает. При pH 4,0 основной обмен составляет всего 60% от основного обмена при pH 4,5—9,5.

7. STRESZCZENIE

Doświadczenia nad wpływem pH na filtrację pokarmu, oddychanie i bilans energetyczny wioślarki *Simocephalus vetulus* prowadzono na zwierzętach z hodowli laboratoryjnej adaptowanej do pH 7.0 i temperatury 22°C. Uzyskano następujące wyniki:

1. Zależność wielkości spoczynkowej racji oddechowej (RRR), racji filtracyjnej (F) i racji pokarmowej (C) od długości ciała zwierząt może być opisana za pomocą funkcji: $RRR = 0,083 \cdot L^{1,79}$, $F = a \cdot L^{3,25}$ (przy koncentracji Chlorella 1,8 mln komórek/ml, $a = 0,040$; przy koncentracji 4,0 mln komórek/ml, $a = 0,018$), $C = 1,85 \cdot L^{3,34}$, gdzie: L — długość ciała (mm), RRR — spoczynkowa racja oddechowa ($\mu l/O_2$ osobn. · · godz.), F — racja filtracyjna (ml/osobn. · godz.), C — racja pokarmowa (mln komórek/osobn. · 24 godz.).

2. Zmiany pH w zakresie 4,5—9,5 nie wpływają na spoczynkową rację oddechową (RRR), powodują natomiast wzrost przeciętnej racji oddechowej (ORR) i racji filtracyjnej. Przy odczynie obojętnym wody (pH 7,0) „koszt" aktywności lokomotorycznej (CAL) wynosi tylko 29,5% przeciętnej racji oddechowej (ORR), lecz w pH 4,0 udział CAL w ORR wzrasta aż do 75,8%. Najwyższe racje filtracyjne spotykano w zakresach pH: 5,2—5,4 i 8,8—9,2.

3. Zakwaszanie środowiska do pH 4,5 i alkalizowanie do pH 9,5 nie powodowało zmian w sumarycznym bilansie energetycznym. Dalsze zakwaszanie lub alkalizowanie środowiska powodowało malenie spoczynkowej racji oddechowej (RRR); przy pH 4,0 spoczynkowa racja oddechowa spadała do ok. 60% w porównaniu do jej wartości w zakresie pH 4,5—9,5.

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THE INFLUENCE OF TEMPERATURE ON THE OXYGEN CONSUMPTION BY *GAMMARACANTHUS LACUSTRIS* SARS (AMPHIPODA)

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ABSTRACT

The aim of this paper was to find the rate of oxygen consumption by coldwater amphipod, *Gammaracanthus lacustris* Sars. It was determined that the highest rate is attained at a temperature of 11°C, at a temperature of 15—18°C the animals consumed less oxygen. The calculated relations between the consumption of oxygen and the weight of the body for three temperature values are as follows: at 4—5°C $Q=(0.778\pm0.0164) \cdot w^{(0.799\pm0.166)}$, at 11°C $Q=(0.1470\pm0.0255) \cdot w^{(0.772\pm0.168)}$, at 15—18°C $Q=(0.093\pm0.010) \cdot w^{(0.770\pm0.041)}$.

Gammaracanthus lacustris is an oligostenotherm relict species and for this reason an experimental study of its ecology, especially its relation to changes in temperature exceeding the normal limits for this species evokes special interest. The material for this work consisted of animals collected from the Krivoye Lake which lies on the shore of the Kandalaksh gulf of the White Sea in the region of the Bay of Chupa. In this lake, *G. lacustris* lives at depths below 20 m, where the temperature of the water during the whole year does not exceed 6.5°C. Three series of experiments were conducted with the aim of determining their reaction to a change in the temperature of the environment. The experiments were done without a preliminary adaptation to the temperature, as this method allows to determine the limits of an ecological optimum, i.e., to show the limiting temperatures at which a physiological compensation of unfavourable external conditions can take place (Ivanova 1969).

The experiments were conducted at the temperature of the normal habitat of the species studied (as such we consider 4.2—5.3°C since the temperature of the lower layers of the lake varies in this range), at a temperature of 11°C which already exceeds the normal temperature for *G. lacustris*, and finally, at a temperature of 15—18°C, which is

significantly higher than the upper temperature limit of the habitat. The temperature conditions during the experiments were kept to constant by the inversion of the experimental vessels in the lake down to a depth with a corresponding temperature, so that the lake was used as a natural thermostat. The series of experiments with the highest temperatures was conducted in the laboratory, and therefore in this series there were the largest fluctuations of temperature during the experiments, namely 15—18°C. At higher temperatures there were no experiments carried out as it was found that 18°C is close to the lethal temperature and in water heated above 18°C the animals died after a few hours.

The consumption of oxygen was determined by the difference in the amounts of oxygen in the closed vessels at the beginning of the experiment and at its end and in the control vessels (in parallelly placed vessels without animals). The volume of the experimental vessels was approximately 140 ml, the length of the exposure was so chosen that the quantity of O_2 consumed by the animals would not exceed 25% of the initial concentration. The amount of the dissolved oxygen was determined by the Winkler's method, for which a part of the water from the respirometers was poured with the help of a siphon into an oxygen bottle of a volume of 30—40 ml.

After the experiments *G. lacustris* were weighed on a torsion balance with an accuracy of 1 mg and their dimensions were measured. The newborn animals were weighed on an analytical balance. Figure 1 shows the body weight as related to its length. As it follows from the obtained results, the length-weight relationship are described by a function $w = qL^b$; where w stands for the weight of the animal (mg), L — its length (mm),
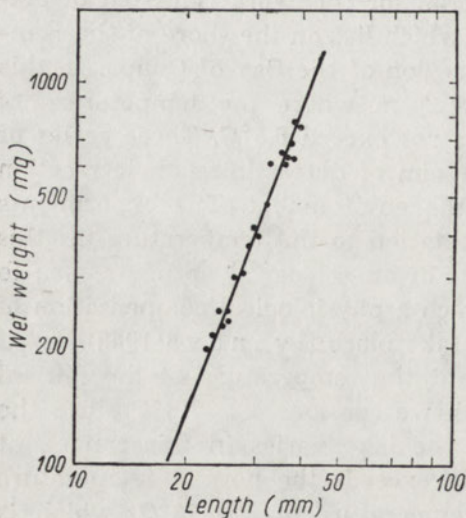
Fig. 1. The relation between the length of the body and the live weight of *Gammaracanthus lacustris*

q and b — empirical constants. Within the limits of length from 3.78 mm (newborn animals) to 38 mm, the coefficients have the following values: $q=0.0113$ and $b=3.11$ (the coefficients were calculated using the method of the least squares). The obtained relation has the following form:

$$w = 0.0113 \cdot L^{3.11} \tag{1}$$

Processing the data on the consumption of oxygen by *G. lacustris* of different weights showed that the correlation between the amount of oxygen consumed, and the weight of *G. lacustris* can be expressed by the function $Q = M_w{}^{a/b}$, where Q stands for oxygen consumption, w — the weight of the animals, M — consumption of oxygen with the weight equal to 1, a/b — constants. The values of M and a/b were calculated using the method of the least squares, statistical errors in the resulting values, and also the confidence intervals were obtained from tables (S t r e l k o v 1966). Using the statistics τ_d D i x o n, M a s s e y (1951), and M i l l e r, K a h n (1962) found that the above curves of the relation between the consumption of oxygen and the weight for *G. lacustris* at temperatures of 15—18, 11 and 4—5°C differ significantly, probability 0-hypothesis being less than 5%. The values of the coefficients are given below:

$$\text{At } 15{-}18°C \quad Q = (0.093 \pm 0.010) \cdot w^{(0.770 \pm 0.041)} \tag{2}$$

$$\text{At } 11°C \quad Q = (0.1470 \pm 0.0255) \cdot w^{(0.772 \pm 0.168)} \tag{3}$$

$$\text{At } 4{-}5°C \quad Q = (0.0778 \pm 0.0164) \cdot w^{(0.799 \pm 0.166)} \tag{4}$$

The consumption of oxygen is expressed in mg of O_2 per hour for 1 specimen, and the live weight of the animals in g. The function was calculated for animals weighing 4—761 mg.

At present, it can be considered certain that the exponent in the given function for all poikilothermal animals varies between the limits 0.6—0.8 (W i n b e r g, P e c h e n 1968). The following values for this coefficient were obtained for the representatives of Amphipoda: 0.78 (Z e u t h e n 1947), 0.81 (W i n b e r g 1950), 0.74 (S u s h c h e n y a 1967). The values given by A r m i t a g e (1962) for the coldwater amphipod *Orchomenalla chilensis* — 0.455—0.652 — differ somewhat from the above cited. Thus, the obtained value of the coefficient a/b agrees with the data of the other authors, except the last one.

As shown above, reliable intervals were found for the values of the exponents at different temperatures (Table I). From the obtained values of the intervals it follows that the temperature of the water did not have any effect on the coefficient a/b. In relation to the temperature the

Table I. Reliable intervals of the coefficients M
and a/b on the probability level of 95%

Temperature (°C)	M	a/b
4—5	0.1144—0.00412	0.965—0.633
11	0.2060—0.0980	1.098—0.445
15—18	0.1160—0.0700	0.8645—0.6855

value of the coefficient M was changed. Comparing equations (2) and
(3) we see that the consumption of oxygen at a temperature of 4—5°C is
by 1.9 lower than that at 11°C; Q_{10} in this temperature interval has been
found equal to 2.89, which is close to Q_{10} according to Krogh's "normal
curve". The consumption of oxygen at temperatures of 15—18°C is lower
than that at 11°C. The coefficient M is approximately 2.4 times lower
than it should be, when calculated according to Krogh's curve. Apparent-
ly such a decline of intensity of respiration was the result of the unfa-
vourable temperature change, exceeding the limits in which a physiolo-
gical compensation was possible.

Figure 2 shows oxygen consumption curves for different representa-
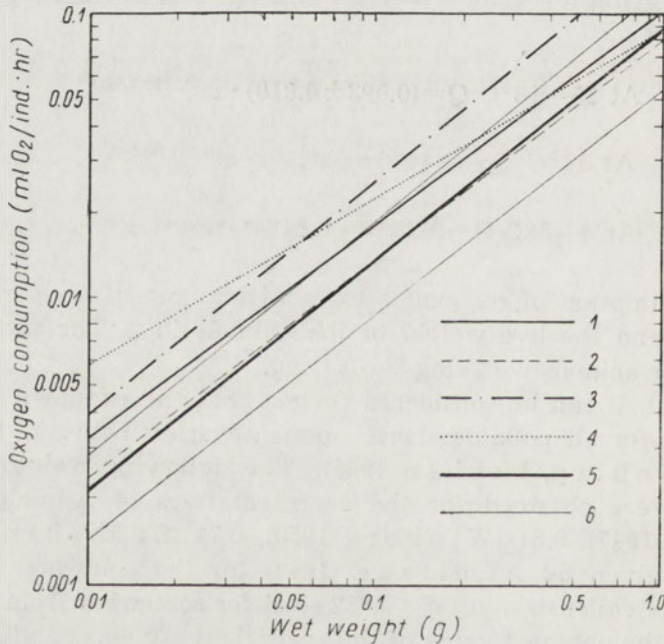
Fig. 2. Consumption of oxygen by amphipods at a water temperature of 11°C. 1 —
Orchestia bottae (Sushchenya 1967), 2 — *Gammarus lacustris* (Winberg 1950),
3 — *Gammarus sp.* (Zeuthen 1947), 4 — *Orchomonella chilensis* (Armitage
1962), 5 — *Gammaracanthus lacustris* (present paper), 6 — the reliable interval on
the probability level of 95% for the respiration curve of *Gammaracanthus lacustris*.
Data on the respiration of 1—4 were obtained at other temperatures and recalcula-
ted for 11°C using Krogh's "normal curve"

tives of Amphipoda at 11°C, the data on respiration from the works of
S u s h c h e n y a (1967), W i n b e r g (1950), Z e u t h e n (1947) and A r-
m i t a g e (1962) brought to 11°C with the help of a "normal curve".
Data, except for the data of Z e u t h e n (Fig. 2 — 3) and A r m i t a g e
(Fig. 2 — 4) recalculated in such a manner lie in a reliable interval of the
obtained curve for *G. lacustris,* so that it can be expected that the respi-
ration level is the same for southern (e.g. *Orchestia bottae*) and northern
(*Gammaracanthus lacustris*) species.

CONCLUSIONS

1. A determination of oxygen consumption by *G. lacustris* at different
water temperatures has shown that the temperature of the water does
not have any influence upon the value of the coefficient a/b in the
function $Q = Mw^{a/b}$ for this species, which means identical influence of
temperature conditions upon the rate of oxygen consumption for diffe-
rent ages.

2. At a temperature of 15—18°C one observes a sharp decline in the
amount of oxygen needed for respiration, which is apparently caused by
the depressing influence of the temperature, exceeding the optimal li-
mits. According to the given physiological exponent *G. lacustris* should
be regarded as belonging to the oligostenotherm forms; this conclusion
is supported by the fact that in the lake it occurs only in the bottom
layer of the deep part of the lake, where the temperature of the water
never exceeds 6.5°C during the summer.

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RESPIRATION OF CARP IN RELATION TO BODY SIZE AND TEMPERATURE

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ABSTRACT

Respiration of carps with wet weight from 1.16 mg to 45.74 g was measured at 10 and 20°C. The relationship between respiration and weight for carps smaller than 1000 mg is described by the formula $QO_2 = 0.595 \cdot W^{0.98}$, and for larger fish the formula is $QO_2 = 1.271 \cdot W^{0.80}$. Different patterns of growth of both size groups of carp are discussed. The Q_{10} values are close to those expected from Krogh's "normal curve".

1. INTRODUCTION

The aim of the present work was to obtain data on respiration of young carps in conditions approaching the natural as a preliminary to a study of the influence of herbicids on their metabolism (K a m l e r 1972). In particular, the employed respirometric methods were controlled by comparing the levels of respiration gauged by our own procedures with data from literature. The relationships between respiration and weight as well as temperature were also tested.

2. MATERIAL AND METHODS

71 measurements of respiration of fish in temperature of $10 \pm 0.05°C$ and 71 in $20 \pm 0.05°C$ were taken during 1969 and 1970. Wet weights of fish were from 1.16 mg to 45.74 g; the fish were supplied by the Institute of Applied Zoology, Agriculture College, Cracow, which cooperated with us. Measurements were taken in rooms with northern windows, without any artifical source of light; the lighting of the constant temperature baths did not exceed 50 lux. Before the measurements fish had been acclimated to the temperatures of 10 or 20°C during 4 (the youngest fish) to 40 (the oldest fish) days. Because of the great range of the size of fish, various methods of oxygen consumption had to be applied. For fish weighing from 1.16 to 1819.0 mg a constant-pressure respirometer described in K l e k o w s k i (1968) was used. Bigger animals were tested in flowing-water respirometers and oxygen contents was determined by Winkler method. Plexiglass respiration chambers were applied, 110 mm long and 45 mm in inner diameter. The biggest fish, from 28.05 to 45.75 g were investigated in another flowing-water respirometer, described in F i s c h e r (1970).

Relations of wet weight to body length were computed for the first year of life of carp, relying on unpublished raw numerical data by M a t l a k (1966), kindly made available by her. 3731 fish were measured, belonging to two families: No. 4 and No. 5, grown in separate ponds on the Experimental Farm of the Laboratory of Water Biology, at Gołysz, Cieszyn District. Since younger fish were weighed in

groups, average lengths and weights found at different drawings were used in the present computations.

3. RESULTS

The relationship between respiration measured at 20°C and wet weight, represented on a double logarythmic scale (Fig. 1, solid circles) is described by two different regression lines. For small fish (weighing
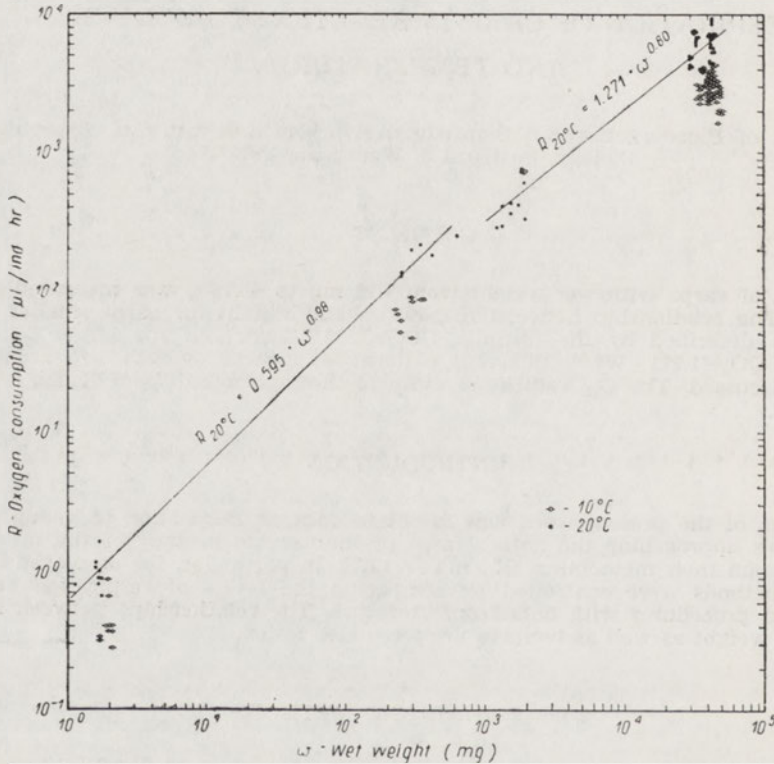

Fig. 1. Oxygen consumption at 10 and 20°C for *Cyprinus carpio* as a function of wet weight

less than about 1000 mg) $R_{20°C} = 0.595 \cdot W^{0.98}$; S.E. of the regression coefficient $(b) = \pm 0.024$; 95% confidence interval: 0.93—1.03; $n = 15$. For large fish (weighing more than about 1000 mg) $R_{20°C} = 1.271 \cdot W^{0.80}$, S.E. ± 0.026, 95% c.i.: 0.75—0.85; $n = 56$. The slopes are significantly different at 0.1% level ($t = 5.031$, B a i l e y 1959).

For the measurements taken at 10°C no such computations were made because of the too narrow ranges of weights, but the pattern of the open circles (Fig. 1) suggests that at 10°C, too, the respiration/weight relationship would be defined by two regression lines and the slope of the curve for smaller carps would also be greater than for larger ones.

It was also found that the weight/length relationship was not identical during the whole period of development; the regression coefficient (slope) was greater in smaller carps ($<$about 1000 mg) than in larger ones ($>$about 1000 mg). The relationships in the two families were similar:

Family No. 4

small: $W = 0.000196 \cdot L^{4.68}$, ± 0.086 (S.E.)

large: $W = 0.0364 \cdot L^{3.00}$, ± 0.035 (S.E.)

Family No. 5

small: $W = 0.000203 \cdot L^{4.59}$, ± 0.080 (S.E.)

large: $W = 0.0434 \cdot L^{2.96}$, ± 0.045 (S.E.)

The determinations of significant differences between the slopes are presented in Table I. It can be seen that during the growth of the youngest carps, from the hatching to the weight of about 1000 mg, the shape of their bodies changes so that they become relatively shorter, while the linear proportions of older fish do not change.

The Q_{10} values are presented in Table II, for both size groups.

Table 1. Determination of differences between slopes of regression of wet weight on length in two size groups of carps from two families

Family	No. 4, large ($n=15$)	No. 5, small ($n=33$)	No. 5, large ($n=27$)
No. 4, small $n=34$	SS t=10.12	NS d=0.70	SS t=13.40
No. 4, large ($n=15$)	✕	SS t=9.03	NS t=0.71
No. 5, small ($n=33$)	✕	✕	SS t=12.28

SS — high significance (0.1% level).
NS — no significance

Table II. Q_{10} values in carps

Size groups	Temp. (°C)	n	Mean O_2 consumption	Q_{10}
Small (<1000 mg)	10	19	0.2452 (µl/mg · hr)	2.37
	20	15	0.5804 (µl/mg · hr)	
Large (>1000 mg)	10	52	0.6139 (µl/mg$^{0.8}$ · hr)	2.18
	20	56	1.3357 (µl/mg$^{0.8}$ · hr)	

4. DISCUSSION

The relationships between oxygen consumption and weight at 20°C are similar to those found out by other authors, both in slopes and positions (Table III). Thus it seems that the slopes are really different for both size groups of carp and thus the discussed relationship cannot be described by a single formula for all carps. It seems, too, that the re-

Table III. A comparison of regressions of oxygen consumption on weight in carps at 20°C as obtained in the present work and by other authors (computed from the original formulas as indicated in S h u s h k i n a et al. 1968)

Size group	Wet wt. (mg) w	n	O_2 consumption (μl/ind. $\cdot$ hr)	$\pm$ S.E. of b
Small carps				
Winberg, Hartova (1953)	2—3800*	123*	$0.600 \cdot W^{0.98}$	—
Present paper	1—600	15	$0.595 \cdot W^{0.98}$	0.024
Large carps				
Winberg (1956)	2500—3487,000	29	$0.967 \cdot W^{0.85}$	0.012
Kausch (1968)	3756—15,702	12	$1.148 \cdot W^{0.816}$	—
Prese..t paper	1235—45,740	56	$1.271 \cdot W^{0.80}$	0.026

— No data available.
* in 115 measurements weights of fish markedly lesser than 1000 mg.

gression coefficient for younger carps is actually close to 1, though W i n- b e r g (1956) was critical about his own still earlier result (W i n b e r g, H a r t o v a 1953). The different relationships between respiration and weight in both size groups may be caused by their different patterns of growth. It was found (Fig. 2) that in smaller carps the length to weight ratio decreases ($b > 3$). If we look at the results of morphometric measurements of the same fishes as presented in M a t l a k (1966), we can see clearly that during the earliest stages of post-embryo development the ratio of body height to body length increases very intensively; e.g., in family No. 5 on hatching day the height was 13.9% of length, while on 41st day it amounted to 41.5%. However, older fish grow uniformly ($b \approx 3$), as we can see in M a t l a k (1966): since 41st day through the first year of life the body height to body length ratio remains constant.

Since the ranges of individual weights of fish in both groups of size, for which Q_{10} values (presented in Table II) were computed, were rather broad (Fig. 1), they had to be reduced to comparable units of metabolic body size (K l e i b e r 1961). For the small fish weighing less than 1000 mg $b \approx 1$, and thus oxygen consumption rates per mg could be compared (Table II). For the large carps, however, the slope differed significantly from 1 and thus oxygen consumption rates per $mg^{0.8}$ had to be used (Table II).
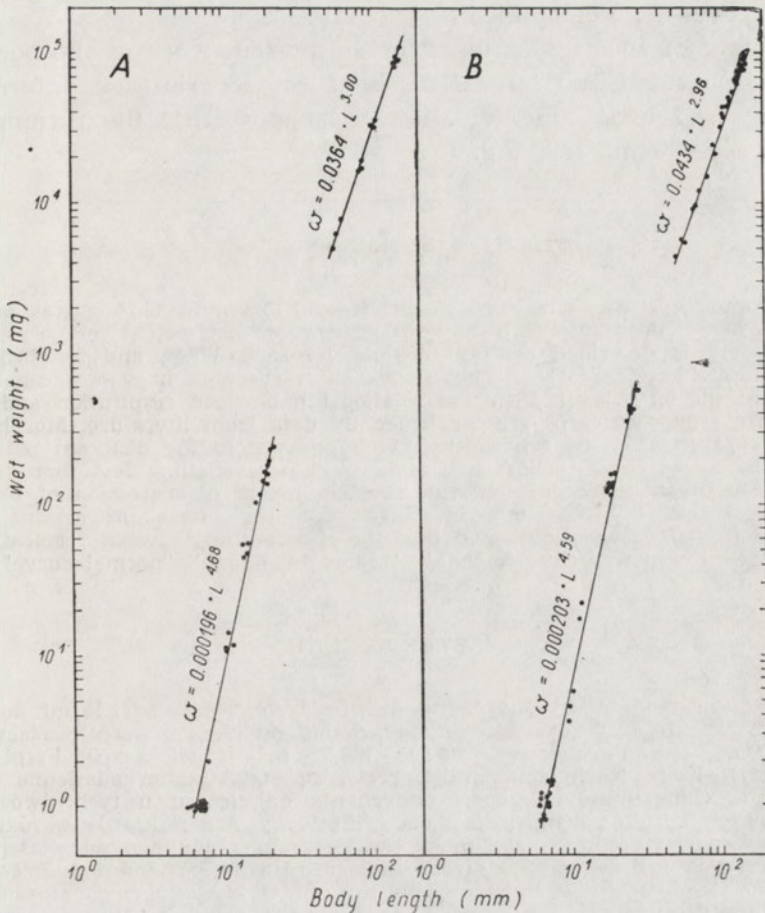
Fig. 2. Wet weight as a function of body length for *Cyprinus carpio*. A — family No. 4, B — family No. 5

The actual Q_{10} values are slightly below that expected from Krogh's "normal curve" for the 10—20°C temperature interval (2.63). It can be seen from W i n b e r g' s (1956) data that the "normal curve" describes fairly well the relation of oxygen consumption rates to temperature for carp. The amounts of oxygen consumed by carp at 10°C ($n=6$) and at 20°C ($n=12$) measured by K a u s c h (1968) yield $Q_{10}=2.43$, i.e. value close to the expected from the "normal curve", though somewhat lower. Recalculating of K a u s c h's data required to account for weight in a manner described above, using of his formula defining the relationship between respiration and weight. It is not surprising that Q_{10} values for carp are similar to those expected from the "normal curve", for carp is an eurythermal species (see Discussion in K a m l e r 1971). Thus to recalculate the oxygen consumption by carp from one temperature to

the other, the method proposed by W i n b e r g (1956) and based on the "normal curve" can be applied.

The limit of 1000 mg assumed in the present work as the borderline between the small and large fish, is of course arbitrary. Informations from Fig. 1, 2 and Table III allow to suppose that the turning point lies between 600 and 1200 mg.

5. SUMMARY

Respiration of carps with wet weight from 1.16 mg to 45.74 g was measured at 10 and 20°C. The relationship between respiration and weight for carps smaller than 1000 mg is described by the formula $R = 0.595 \cdot W^{0.98}$, and for larger fish the formula $R = 1.271 \cdot W^{0.80}$. The slopes of regression lines are significantly different at the 0.1% level. Different relationship between respiration and weight in both size groups of carps are confirmed by data from literature. Morphometric evidence suggests that the differences can be related to the different patterns of growth. In fish in their earliest post-embryo phase (weighing less than 1000 mg) the shape of the body becomes shorter (the coefficient of regression of weight as related to length $b > 4.5$), while in bigger fish the linear proportions remain unchanged ($b \approx 3$). It was confirmed that the relationship between respiration and temperature in carp was close to that described by Krogh's "normal curve".

6. STRESZCZENIE

Przeprowadzono pomiary oddychania karpi o żywej wadze od 1.16 mg do 45.75 g w temperaturze 10 i 20°C. Zależność oddychania od ciężaru karpi ważących poniżej 1000 mg opisano wzorem $R = 0.595 \cdot W^{0.98}$, zaś u większych karpi — wzorem $R = 1.271 \cdot W^{0.80}$. Nachylenia linii regresji są statystycznie odmienne na poziomie 0.1%. Odmienność zależności oddychania od ciężaru u tych dwóch grup wielkościowych karpia potwierdzają dane z literatury. Jak wskazują wyniki badań morfometrycznych, te odmienności mogą być związane z odmiennymi właściwościami wzrostu tych ryb: w najmłodszych stadiach rozwoju postembrionalnego (waga poniżej 1000 mg) następuje zmiana kształtu ciała w kierunku jego stosunkowego skrócenia (współczynnik b dla regresji ciężaru od długości > 4.5), zaś u ryb ważących powyżej 1000 mg nie następuje zmiana proporcji wymiarów liniowych ($b \approx 3$). Potwierdzono, że zależność oddychania od temperatury u karpi jest zbliżona do opisanej przez „krzywą normalną" Krogha.

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PHYSIOLOGICAL EFFECTS OF SODIUM SALTS OF 2,4-D AND MCPA ON *TYPHA LATIFOLIA* L.

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ABSTRACT

The effect of 2,4-D (2,4-dichlorophenoxyacetic acid) and MCPA (2-methyl-4-chloro-phenoxyacetic acid) on transpiration of *Typha latifolia* L. was experimentally investigated during the vegetation season in 1971. Also the influence of these herbicides on chlorophyll and water content and the growth rate of the examined plant was estimated. It was found that 2,4-D and MCPA decrease transpiration, water content and the growth rate of *T. latifolia,* depending on the concentration of applied solutions and the time of acting. High concentrations of 2,4-D and MCPA cause epinastic curling of leaves and the decrease of chlorophyll content.

1. INTRODUCTION

The chemical compounds are recently more and more commonly applied in agriculture for the weed control. The papers on the influence of these chemicals on plant water balance are quite numerous. All more important life processes and the activity of enzymes depend on the water content of a plant cell. Water is also essential for plant growth. Thus a lot of papers deal with the influence of chemicals on plant transpiration (Minshall 1960, Smith, Buchholtz 1964, Allerup 1964, Zelitch 1964, Waisel et al. 1969). Kozinka (1967, 1970) investigated the changes in water uptake by plants due to the action of auxin-like chemical compounds. Several papers deal with the changes which take place in plant cells and in stomatal cells under the influence of herbicides, e.g. Bradbury, Ennis (1952), Maciejewska-Potapczyk (1955).

The majority of researchers conduct their investigations on utilitarian plants. The chemical compounds applied in agriculture are washed out by rains or carried by wind to surface waters. Occasionally they are introduced there on purpose, e.g. herbicides are applied in fish ponds to control aquatic weeds overgrowing the ponds (Solski 1968).

This paper aims at the estimation of the influence of herbicides on aquatic plants, on the example of changes in transpiration, chlorophyll and water content and the growth rate of *Typha latifolia* L.

2. MATERIAL AND METHODS

The herbicides derivatives of phenoxyacetic acid: 2,4-D (2,4-dichlorophenoxyacetic acid) and MCPA (2-methyl-4-chlorophenoxyacetic acid) were used during the investigations. Applied were the commercially available preparations "Pielik" and "Chwastox", in which these compounds are in the form of sodium salts: "Pielik" — about 85%, "Chwastox" — about 80% of pure compound. The solutions were prepared by dissolving the weighed portions of commercial preparations in

unchlorinated tap water. The following solutions were applied: 0, 50, 500 and 5000 mg/l. The plants were cultivated on tap water. The solutions were applied to the roots by means of pouring them on the surface of the plant substrate after pouring out the water. Such application of herbicides is similar as in natural conditions when the preparations used in agriculture reach aquatic or bog plants by surface flow of rain waters.

The experimental plant material was cultivated. The seeds of *T. latifolia* were planted on the mud from eutrophic Mikołajskie Lake. The cuvettes with planted plants were placed in the green-house. After about 3 weeks, when the plants were already about 3 cm high, they were transplanted (also to the lake mud) to plastic pots of capacity 150 ml — 1 seedling per pot, and to plastic buckets of capacity 5 l — 5 seedlings per bucket. In spring the buckets were kept on an experimental open area, and the pots were placed in the green-house.

The investigations were conducted in two directions: I — estimation of the influence of 2,4-D on the intensity of transpiration of *T. latifolia* in various periods of its development during the vegetation season (oppen experimental area), II — estimation of the influence of 2,4-D and MCPA on the intensity of transpiration, chlorophyll and water content and the growth rate (green-house).

The measurements were made in a special experimental chamber, where plants were located 24 hr before them. Inside the chamber a cycle of 16 hr of light and 8 hr of dark was established, and the following were nearly constant: air temperature — $25\pm2°C$, relative air humidity — $65\pm5\%$, light was produced by 3 mercury-vapour filament lamps, 450 W each (produced by Z.W.L. "TELAM").

In the I experiment the measurements were made every 10 days during the entire vegetation season. After the measurements the plants tested with pesticides were destroyed. To estimate the growth rate of *T. latifolia* during the vegetation season the three highest plants in each pot were measured before the application of chemicals. A day before the measurements 1 l of 2,4-D solutions with various concentrations, and 1 l of water to control pots (3 replicates) were added after pouring the water out from the mud surface, after the buckets had been placed in the experimental chamber. Thus each series consisted of plants from 12 pots, and in the next series the plants from other 12 pots were used. Prior to determine the transpiration and the chlorophyll content the plant heights were measured and two first (youngest) well developed leaves were sampled. The youngest leaves were used, as they show best the changes due to chemicals (older leaves can dry as a natural process but not only due to herbicides).

In the II experiment, consisting of short lasting series (about 10 days) the whole above ground parts of plants were used. In this experiment the influence of 2,4-D and MCPA on transpiration, water and chlorophyll content, and the growth rate was estimated before the application of chemicals, and after 24, 48, 96 and 192 hr on application of 20 ml of herbicide solution per pot. A series of measurements of the growth rate of *T. latifolia* was carried out for 10 days in July, when the height of plants was measured every 48 hr. The losses of water during the experiment were made up by adding distilled water to the constant level.

The transpiration intensity was estimated by the method of quick weighing on a torsion balance type WT (range 4000 mg, accurary 1 mg), similarly as in the paper by Królikowska (1971). The pan of the balance was replaced with a special shackle (of the same weight) for hunging the plants.

The chlorophyll content was estimated according to Bray (1960), Carl Zeiss Jena Spektralphotometer VSU was used for the spectrophotometric measurements.

The water content in *T. latifolia* was estimated as the difference between the fresh weight of plants and their weight after drying the samples at 105°C to constant weight.

All series in the II experiment were repeated three times. The transpiration intensity was expressed in mg of water transpired from 1 g fresh weight of plant per 1 hr. The chlorophyll content was calculated in mg per 1 g fresh weight. Water content was estimated as per cent of fresh weight. The results for plants treated with herbicides are expressed in per cent of those for the control ones.

3. RESULTS

The plants growing in plastic buckets on the open experimental area had during the whole season adequate water supply, as the water level

above the mud was maintained at about 15 mm. The growth rate (without herbicide added) during the season can be divided into three stages: the first one of intensive growth, the second with slightly lower growth rate values, and the third one with minimal growth rate, at the end of the vegetation season (Fig. 1).
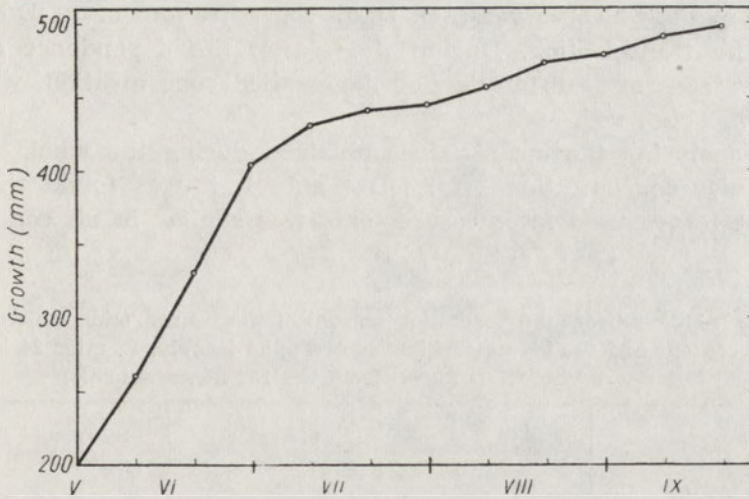

Fig. 1. The seasonal course of growth of *Typha latifolia* L. (means from 9 measurements)
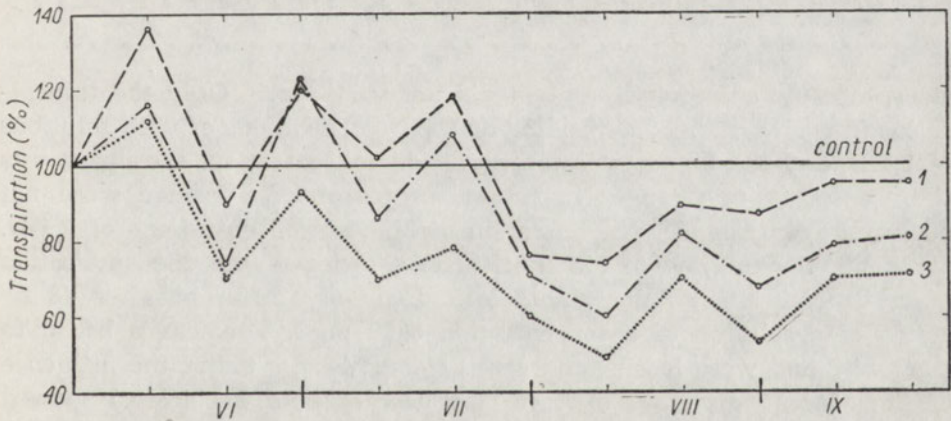

Fig. 2. Effect of 2,4-D on the transpiration of *Typha latifolia* L. in vegetation season 1971, 24 hr after application (means from 9 measurements). 1 — 50 mg/l, 2 — 500 mg/l, 3 — 5000 mg/l

The changes of the transpiration intensity of *T. latifolia* 24 hr after the application of 2,4-D solutions of various concentrations are shown in Fig. 2. The measurements made every 10 days showed that the transpiration of plants treated with herbicides and of control ones varied, what

might have been due to climatic conditions (thus the necessity of expressing the results as per cent of those for the control). The course of the curves in Fig. 2 shows that during the intensive growth of plants, i.e. from June 9 to July 19, 2,4-D stimulates transpiration. After the 9 of June the transpiration of plants in the highest concentration of herbicide was lower than in the control, and after July 29, when parallelly low growth of plants was observed (Fig. 1), all concentrations of 2,4-D clearly reduced the transpiration. During the season the dependence of the rate of decrease of transpiration of the applied concentration of 2,4-D solutions was observed.

When analysing the mean values obtained during the whole season for particular concentrations of 2,4-D (Table I) it was found that the biomass of leaves used for measurements was similar in all concentra-

Table I. Means (from the vegetation season) of the transpiration, chlorophyll content and the biomass of leaves of *Typha latifolia* L. after 24 hr· treatment with 2,4-D (mean from the 132 measurements)

Concentration of 2,4-D (mg/1)	Transpiration (mg/g/hr)	Chlorophyll content (mg/g)	Biomass of leaves (mg)
0	172.9	6.5	588.5
50	170.3	6.7	574.9
500	149.2	6.6	585.3
5000	125.2	6.8	607.1

tions, also the chlorophyll content did not vary much. Only the transpiration intensity changed depending on the concentrations of used solutions of 2,4-D, and the higher was the herbicide concentration, the lower was the transpiration. Changes in colour, turgor and leaf shape were not observed even after the 24 hr action of highest concentrations of 2,4-D.

In the II experiment — in short lasting series — with the application of 2,4-D and MCPA, the plants looked already different after 48 hr action of a solution of a concentration 5000 mg/l. The leaves began to curl, wilt, and were loosing the green colour. Plants under the influence of the concentration 500 mg/l (in the case of both herbicides) showed similar changes only after 96 hr. After 192 hr action of 2,4-D and MCPA in concentrations 5000 mg/l the plants were grey-brown, the leaves showed epinastic responses and very low turgor. The epinastic changes appeared first on the oldest, outside leaves. The leaves of plants treated with 2,4-D curled in rings, while the ones of plants treated with MCPA — curled in spirals.

The longer the plants were under the influence of herbicides, and the higher was their concentration, the lower was the intensity of their

transpiration (Fig. 3). The solution of concentration 50 mg/l at first stimulated the transpiration, but after some time it inhibited this process. MCPA reduced the transpiration to a greater extent than 2,4-D in the same concentrations (Fig. 4). After 192 hr of treating the plants with 2,4-D and MCPA in concentrations 5000 mg/l in certain cases the plants stopped the transpiration and died.

Changes of water content in *T. latifolia* treated with 2,4-D and MCPA were parallel to these of transpiration. The water content in plants
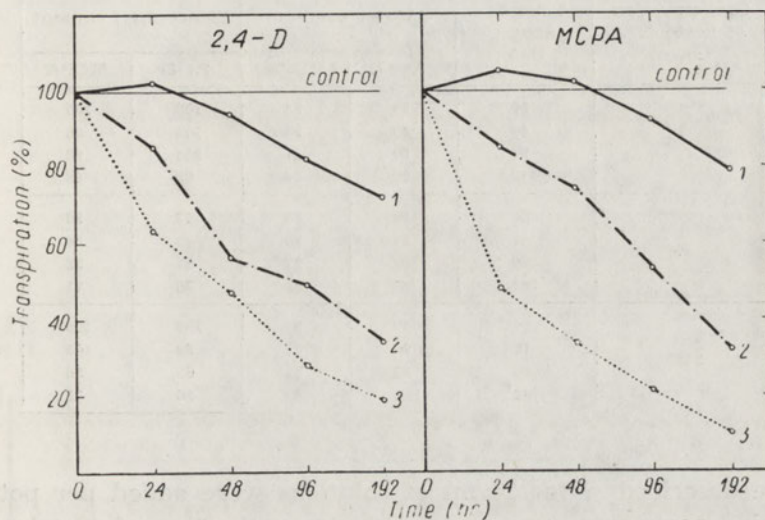
Fig. 3. Effects of 2,4-D and MCPA on the transpiration of *Typha latifolia* L. for a period of 192 hr (means from 9 measurements). 1 — 50 mg/l, 2 — 500 mg/l, 3 — 5000 mg/l
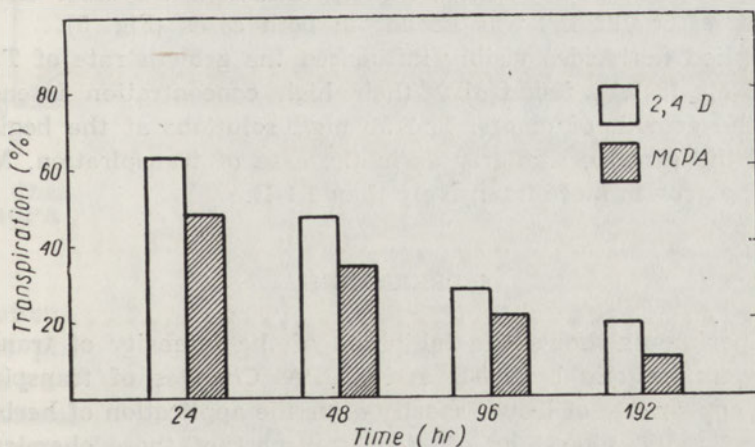
Fig. 4. Changes in the rate of transpiration caused by the various herbicides in the same concentrations (5000 mg/l)

treated with herbicides was lower than in control plants. This was especially clear in the case of the most concentrated (5000 mg/l) solution and the longest time of treatment (192 hr) (Table II). The chlorophyll content also changed, more in the case of 2,4-D.

Table II. Effects of various concentrations and time of action of 2,4-D and MCPA on the water content and chlorophyll content in *Typha latifolia* L. (means from the 9 measurements as % of control)

Concentration of herbicides (mg/l)	Time of action (hr)	Water content		Chlorophyll content	
		2,4-D	MCPA	2,4-D	MCPA
50	24	99	99	100	105
	48	99	98	100	96
	96	99	97	993	88
	192	98	94	52	83
500	24	99	98	103	96
	48	97	98	89	96
	96	99	97	57	92
	192	88	92	39	71
5000	24	99	98	100	100
	48	96	97	69	105
	96	92	91	63	96
	192	61	62	26	71

In the described series 20 ml of solutions were added per pot. Also additional experiments were made with the application of 40 ml per pot of the same solutions as the above described ones. At the beginning (after 24 and 48 hr) it was found that the transpiration intensity in the case of doubled portion of solutions (depending on their concentrations) was inhibited or stimulated more rapidly, although the final effect of experiment (after 192 hr) was similar in both cases (Fig. 5).

The applied herbicides visibly influenced the growth rate of *T. latifolia* (Fig. 6). It was found that their high concentration intensively inhibited the growth of plants. The 50 mg/l solutions at the beginning stimulated the growth, similarly as in the case of transpiration. MCPA inhibited the growth more intensively than 2,4-D.

4. DISCUSSION

The experiments showed an inhibition of the intensity of transpiration of *Typha latifolia* by 2,4-D and MCPA. Changes of transpiration and in the appearance of leaves shortly after the application of herbicides to the plant roots suggest an efficient transport of these chemicals to the leaves, among others due to the transpiration current (C r a f t s 1953). A l l e r u p (1964) found when investigating the beans that the
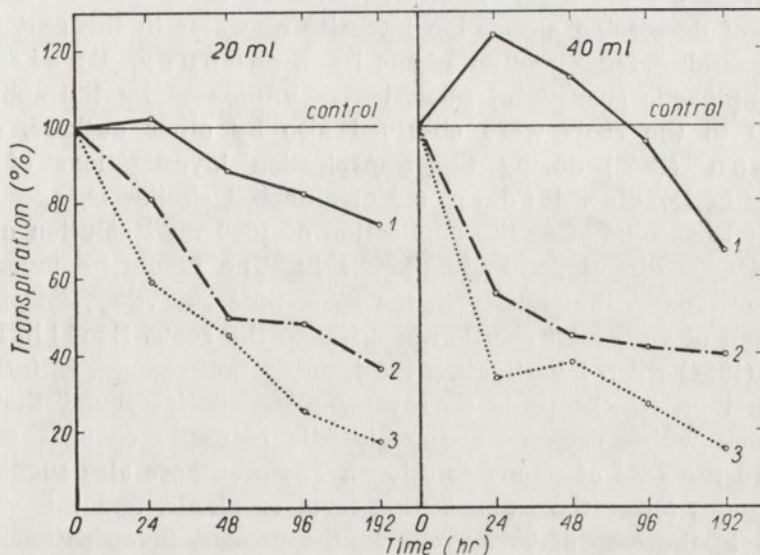
Fig. 5. Effects of the various amounts of 2,4-D solution on the transpiration of *Typha latifolia* L. (means from 9 measurements). 1 — 50 mg/l, 2 — 500 mg/l, 3 — 5000 mg/l
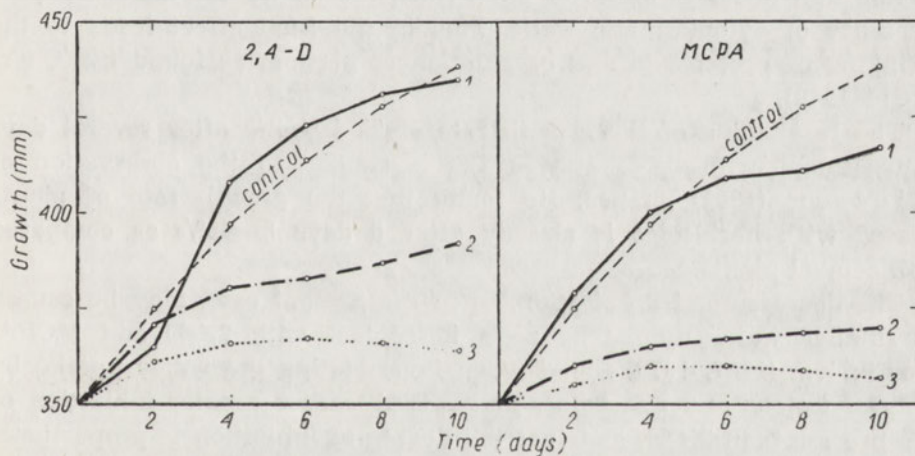

Fig. 6. Changes in the growth of *Typha latifolia* L. induced by application of 2,4-D and MCPA to the root medium for a period of 10 days (means from 9 measurements). 1 — 50 mg/l, 2 — 500 mg/l, 3 — 5000 mg/l

leaf stomata began to close 40 min after the application of herbicide to the plant roots, which makes the transpiration difficult. M a c i e- j e w s k a-P o t a p c z y k (1955) when investigating the action of enzymes of stomatal cells found that plants treated with 2,4-D closed the stomata, their protoplasm became more permeable, and the dehydration of plant cells occurred. This can explain the changes of leaf turgor observed due to herbicides in the present investigation. Permanent wilting of

plants after the prolonged treatment with 2,4-D and MCPA could be a result of decreasing absorption intensity of water in the root system, which was observed for other plants by B r a d b u r y, E n n i s (1952).

The epinastic changes of plant leaves influenced by the application of 2,4-D to the roots were observed also by other authors, e.g. by E l i a s s o n (1965) during the transpiration investigations of young seedlings of Populus. B r o w n (1946) observed similar changes on the leaves of Phaseolus after the application of 1000 mg/l solution of 2,4-D on the leaves directly, already after 1 hr. The plants he investigated died after 7 days, thus nearly in the same time as *T. latifolia* after the application of 5000 mg/l solution of 2,4-D to the roots. S m i t h, B u c h-h o l t z (1964) when investigating the transpiration changes as influenced by more than 30 chemicals on several plant species found that 2,4-D is the one which causes so characteristic epinastic changes of plant leaves (in the case of strong solutions). These authors also suggest that such changes lower the transpiration level of plants, and this was also obtained in the case of *T. latifolia* in the present investigation.

Changes in the water content in the *T. latifolia* leaves after the application of concentrated solutions of 2,4-D can be seen just by leaf curling due to losses of water from cells, caused by the increased permeability of cytoplasmatic walls. This in the final effect leads to the shrinking of protoplasm and coagulation of plasma, as found by C u r-r i e r (1949).

The restraining of the growth rate of *T. latifolia* after several days of treatment with 2,4-D and MCPA is similar to the observation of E l i a s s o n (1961) on pea. He found that the growth rate of plants treated with herbicides is already after 6 days 5—45% as compared with control plants.

The decrease of transpiration, as in the present case, may be caused by smaller water uptake by roots in contact with 2,4-D and MCPA. K o z i n k a (1967, 1970) found when investigating the water uptake by roots of Coleus and Phaseolus, that MCPA causes greater inhibition of this process than 2,4-D, and that the degree of inhibition is proportional to the solution concentration.

The herbicides 2,4-D and MCPA applied in the present paper cause the decrease of photochemical activity of chloroplats, and MCPA is more active in this process (M a s z t a k o w et al. 1971). These authors found that this process is parallel with the inhibition of photosynthesis of plants treated with herbicides, although it depends on the sensibility of plants. In the case of *Zea mays* changes in the chlorophyll content under the influence of MCPA were not quite clear, and even after 168 hr after the herbicide application the chlorophyll content varied only slightly. In the same time 2,4-D caused the decrease of the chlorophyll content (M a s z t a k o w et al. 1971). These results are similar to those

obtained in the present paper. The above mentioned authors also found that the character of the changes of physiological processes in plant depends on its species, resistance to herbicide, and kind of herbicide.

6. SUMMARY

The investigations of the influence of sodium salts 2,4-D and MCPA on *Typha latifolia* L. showed that these herbicides cause changes in the process of transpiration, in the chlorophyll and water content and in the growth rate of examined plants. During the vegetation season 2,4-D stimulates transpiration only during the intensive growth of *T. latifolia* (beginning of the vegetation season), later decreases it. On the average, during the vegetation season, 2,4-D in concentrations 50, 500 and 5000 mg/l decrease the transpiration 2, 14 and 28% relatively (as compared with the control) after 24 hr of treatment. It was also found that the longer was the period of treatment with herbicides, and the stronger were the concentrations applied to the roots, the lower was transpiration of plants. On the average, during 8 days, the solutions of 2,4-D in concentrations 50, 500 and 5000 mg/l lowered the transpiration by 11, 25 and 61% respectively, while MCPA in the same concentrations — 5, 39 and 72%. After 8 days of treatment with herbicides the majority of plants wilted. 2,4-D and MCPA affected also the chlorophyll and water content in plants. In the case of the highest concentrations of herbicides after 8 days the chlorophyll content decreased by about 70% for 2,4-D, and by 30% for MCPA; water content decreased by 40% and by about 40%, respectively.

During 10 days of treatment with 2,4-D and MCPA the growth rate of plants changed depending on the concentrations of chemicals. In the case of the strongest concentration (5000 mg/l) the growth rate of *T. latifolia* decreased as compared with control by about 70% for both herbicides, and at the end the plants were usually dead.

T. latifolia changed morphologically under the influence of both herbicides, the leaves curled epinastically, green colour and turgor were lost.

The low concentrations of herbicides shortly after their application stimulated transpiration and did not cause visible changes in the chlorophyll and water content, also the appearance of plants did not change in this time.

7. STRESZCZENIE

Prowadzono badania nad wpływem soli sodowych 2,4-D i MCPA na *Typha latifolia* L., w wyniku których stwierdzono, że herbicydy te powodują zmiany w procesie transpiracji, zawartości chlorofilu i wody oraz tempie wzrostu pałki. W okresie wegetacyjnym 2,4-D wpływa stymulująco na transpirację tylko w czasie intensywnego wzrostu pałki (początek sezonu wegetacyjnego), w pozostałym okresie działa hamująco. Średnio w ciągu sezonu wegetacyjnego 2,4-D w roztworach o koncentracjach 50, 500 i 5000 mg/l obniża transpirację odpowiednio o 2, 14 i 28% (w stosunku do kontroli) po 24 godz. działania preparatu. Stwierdzono również, że im dłuższy był czas działania 2,4-D i MCPA, i im wyższe było stężenie ich roztworów stosowanych dokorzeniowo, tym bardziej obniżona była transpiracja pałki. Średnio w ciągu 8 dni roztwory 2,4-D o koncentracjach 50, 500 i 5000 mg/l obniżały transpirację pałki odpowiednio o 11, 25 i 61%; natomiast w przypadku tych samych stężeń MCPA o 5, 39 i 72%. Po 8 dniach działania herbicydów w najwyższych stężeniach większość użytych w doświadczeniu roślin była martwa. 2,4-D i MCPA wpływały również na zawartość chlorofilu i wody w pałce, w przypadku najwyższej koncentracji herbicydów po 8 dniach działania zawartość chlorofilu zmniejszała się o około 70% przy 2,4-D i 30% przy MCPA; zawartość wody odpowiednio o 40% i około 40%.

W ciągu 10 dni działania 2,4-D i MCPA tempo wzrostu pałki ulegało zmianom w zależności od stężenia preparatów, w przypadku najwyższego stężenia (5000 mg/l) następowało obniżenie tempa wzrostu pałki w stosunku do kontroli o około 70% dla obu herbicydów, przy czym w końcowym okresie rośliny przeważnie ginęły.

Pałka szerokolistna poddana działaniu 2,4-D i MCPA ulegała zmianom morfologicznym, zaobserwowano epinastyczne skręcanie się liści, utratę barwy zielonej i turgoru.

Niskie koncentracje preparatów w krótkim okresie od aplikacji wpływały stymulująco na proces transpiracji oraz nie powodowały wyraźnych zmian w zawartości chlorofilu i wody, także wygląd pałki nie ulegał zmianie w tym czasie.

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CONTENTS