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BOTTOM FAUNA OF DEAD VISTULA

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ABSTRACT

The environmental factors in Dead Vistula (salinity, oxygen content, temperature of water and character of bottom) were investigated. The qualitative species composition of macrobenthos was analysed. Special attention was paid to the dependence of the occurrence of common species in Dead Vistula on salinity. Seasonal investigations of the dynamics of numbers and biomass allowed to distinguish the dominant groups in the overgrown parts and in the parts without plants in three regions in various seasons. Considerable differentiation of the bottom fauna was found along Dead Vistula, and also great seasonal changes.

1. INTRODUCTION

The information on the environmental conditions of Dead Vistula can be found in the papers by Kaptur (1965—1966 — unpublished, 1967) and in the materials of the State Hydrometeorological Institute (1969 — unpublished).

Biological investigations connected with Dead Vistula are mainly on the morphology and physiology of inhabiting it organisms. Particularly, the papers deal with embriology, endocrynology and neurosecretion of *Rhitropanopeus harrisi subsp. tridentatus* Maitl. (Ławiński, Węglarska 1959, Szudarski 1963, Ławiński, Pautsch 1963 and others), *Nereis diversicolor* O.F.M. (Konopacka, Szańkowska 1962) and with the cytochemistry and histology of *Cordylophora caspia* Pallas (Osuchowska-Bielańska 1959).

However, there is not much of the ecological publications from this region. The occurrence of several species is discussed in some papers: Decapoda — *Rithropanopeus harrisi subsp. tridentatus* Maitl. (Michalski 1957, Żmudziński 1961, Pautsch et al. 1969), *Paleomonetes varians* (Leach) (Ławiński, Szudarski 1960), Amphipoda (Jażdżewski 1967) and Nudibranchia — *Embletonia pallida* Alder Hancook (Ławiński 1968). The distribution of the secondary hard soil fauna was presented by Arndt (1965).

The macrobenthos studied in this paper supplements the ecological investigations of Dead Vistula. Present paper analyses the species composition, numbers dynamics and changes of the biomass of benthic invertebrates taking into consideration hydrological conditions. The mention of these investigations was already published (Klekot 1968).

2. MATERIALS AND METHODS

Benthic samples and water samples for the chemical analyses were collected in winter (6–7 March), spring (1–2 May), summer (18–21 August) and autumn (10–14 November) 1965.

The chosen sampling stations represented various environments. The changes of the water level, character of bottom, salinity and the distribution of emergent and submerged vegetation were taken into consideration. The sampling stations were unevenly distributed along Dead Vistula (Fig. 1). Five samples were collected from each of them during every sampling except of winter, when only 2 samples were taken. Benthos was sampled with the help of Ekman dredge with the sampling area of 225 cm^2. A total of 240 samples was collected, and 45,195 individuals examined.

The samples were washed at the sieve with the mesh size 0.7 mm^2, and then preserved in 4% formalin. All organisms were taken out from each sample, and then their species composition, numbers, dry weight of each systematic group and dry weight of all organisms at the station were examined. Dry weight was estimated after drying the animals to the constant weight on the blotting papers in 105°C. Mollusca were weighed together with their shells.

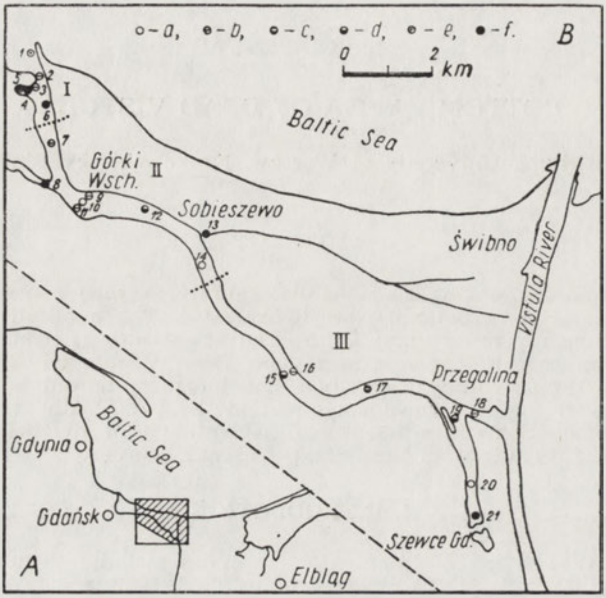

Fig. 1. Map of Dead Vistula. A — general map, B — detailed map and location of sampling stations. I — mouth region, II — middle region, III — east region, ... — boundaries of regions. 1–21 — numbers of sampling stations. Time of sampling: a — winter, spring, summer and autumn, b — spring, summer and autumn, c — winter, summer and autumn, d — winter and autumn, e — spring and summer, f — summer (after Klekot 1968)

The content of the organic matter in bottom samples was determined from one series of samples collected in August 1966. The samples were ashed in 650°C for 4 hr, and the result is a mean from 3 parallel samples.

The samples of water from near the bottom were collected with the help of Pettersen's sampler (Copenhagen model) of 1.7 l capacity. The chlorides were determined according to the Knudsen's method and the oxygen by Winkler's one. The temperature, with the accuracy to 0.1°C, and the depth were measured at each sampling station.

3. TERRAIN DESCRIPTION

Dead Vistula (Fig. 1) is an old bed of the Vistula River. There is no current there since 1895, when the Vistula got a man-made river mouth to the Gdańsk Bay near Świbno. The investigated reach of Dead Vistula, 14,800 m long starts at the jetty in Szewce Gdańskie and finishes at the mouth of Wisła Śmiała near Górki Wschodnie. The width of the reach was from 400 to 600 m, but in the mouth to the sea it was only 58 m. The depth in the previous current is 2–8 m.

The oxygen content in water varied from 4.4 mg/l at 2°C in the SE part (sampling station No. 20 — winter) to 12.3 mg/l at 10°C in the same part (station No. 18 — spring) and in NW part at 6.9°C (station No. 2 — autumn).

The salinity varies greatly vertically and horizontally (Kaptur 1967), and according to the present investigations it was from 3 to 7‰. Dead Vistula is fed with both fresh and sea waters. Fresh water comes from the drains from Żuławy, and periodically small quantities of it get there through the Przegalina lock. Water of the 7‰ salinity get there from the Gdańsk Bay. The salinity of the near bottom water at the times of benthos sampling is shown at the Fig. 2; these data agree with the continuous records of Kaptur (1965—1966 — unpublished). The highest salinity was noticed near the Dead Vistula mouth to the Baltic Sea, and it decreased eastward. The lowest salinity was found during the spring due to the income of fresh water, larger than in the other seasons. High salinity values were noticed during the autumn and winter. This was due to the disgorges of the sea waters during the storms, and at the same time a minimal inflow of fresh water. During the summer the salinity depends mainly on the wind direction. During the winds from the sea the salinity increases, while during the winds from the land — decreases. Generally the salinity of Dead Vistula increases together with the increase of the depth.

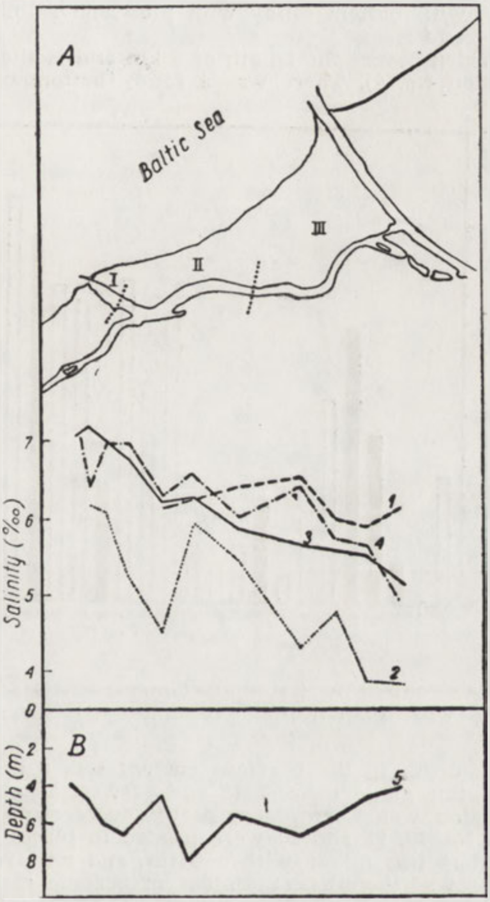

Fig. 2. Salinity changes in Dead Vistula (A) and the depths (B). 1 — winter, 2 — spring, 3 — summer, 4 — autumn, 5 — depth. Other explanations as in Fig. 1

The bottom of Dead Vistula, sandy at the mouth, changes with the distance from the sea to sandy with some quantities of mud, and then to muddy with large quantities of detritus. The percentage content of organic matter in bottom sediments is presented at the Fig. 3. The lowest value, below 1% was found at the stations No. 2 and 21, the highest one — 19.4% — at the station No. 20 with muddy bottom with detritus.

The near bank vegetation is unevenly distributed, and recently strongly reduced due to the conservancy of the banks. *Phragmites communis* Trin., *Juncus sp.* and submerged plants occur there (Pautsch 1965).

Three regions were distinguished within the studied reach on the basis of hydrological conditions and distribution of benthic communities: I — the mouth region, II — the middle one and III — the east one (Fig. 1). In each of them two parts were distinguished: with plants, and without plants.

I. The mouth region covers the mouth of Wisła Śmiała to the Baltic Sea. There was a sandy bottom, maximal depth 6 m, salinity about 7‰ — sampling stations No. 1, 2 and 6. A shallow bay was also included there. It was located at the west bank of Wisła Śmiała, overgrown with submerged vegetation surrounded from three sides by reeds, with bottom sandy with mud and salinity about 4‰ — sampling stations No. 3, 4 and 5.

II. The middle region covers the length of 5 km and is slightly overgrown with vegetation (only station No. 9). There was a sandy bottom covered with 3–4 cm of mud. The average depth in the previous current was 6 m. The salinity varied from 4.5 to 6‰. Sampling stations No. 7–12 and 14 were located there.

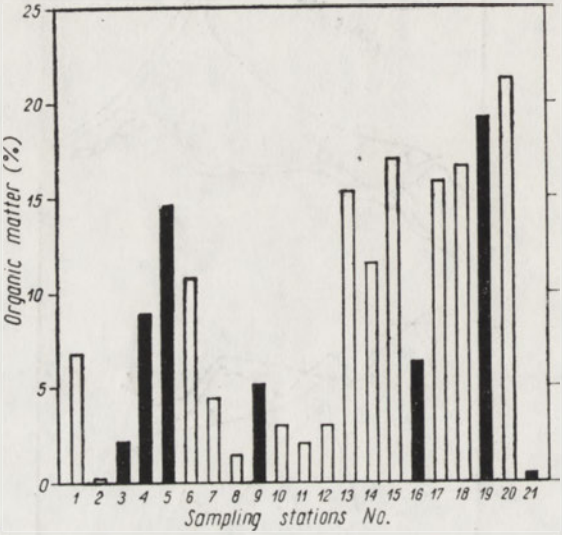

Fig. 3. Organic matter content in bottom sediments of Dead Vistula. Black columns — parts with plants, plain columns — parts without plants

III. The east region was 7 km long, partly overgrown — stations No. 16, 19 and 21. The stations No. 15, 17 and 20 were located in places without any vegetation. Mud at the bottom was mixed with detritus, and its layer at the site No. 19 was 1 m deep. There was the highest content of organic matter in bottom sediments of all investigated regions. The exceptions were only sampling stations No. 16 and 21 located at sandy bottom. The average depth in the previous current was 5 m. The salinity was the lowest among the distinguished regions and it varied from 3 to 6‰.

Two sampling stations, No. 13 and 18 are not included in any of the distinguished regions because of their distinct character. Although the density of fauna on them was very low, an attention should be paid to them due to the species composition there.

4. RESULTS

NUMBERS AND BIOMASS

The benthic invertebrates of Dead Vistula belonged to the following systematic groups: Nemertini (not determined), Oligochaeta (11 species), Polychaeta (5 species), Crustacea (11 species and Decapoda larvae), Insecta larvae (15 Chironomidae species, also Lepidoptera and Trichoptera), Gastropoda (7 species) and Lamellibranchiata (6 species). The occurrence of particular groups in the places with and without vegetation is shown at the Fig. 4.

In the I region, in the part without plants, 96⁰/₀ of the total numbers of benthos consisted of Polychaeta, Crustacea, Lamellibranchiata and Oligochaeta. Lamellibranchiata showed there the highest biomass. Four groups: Chironomidae, Gastropoda, Oligochaeta and Polychaeta were very numerous in the overgrown part. In this part the greatest share in the biomass had Gastropoda, then Chironomidae and Lamellibranchiata. The density and biomass of benthos in the overgrown part of the I region were relatively high.

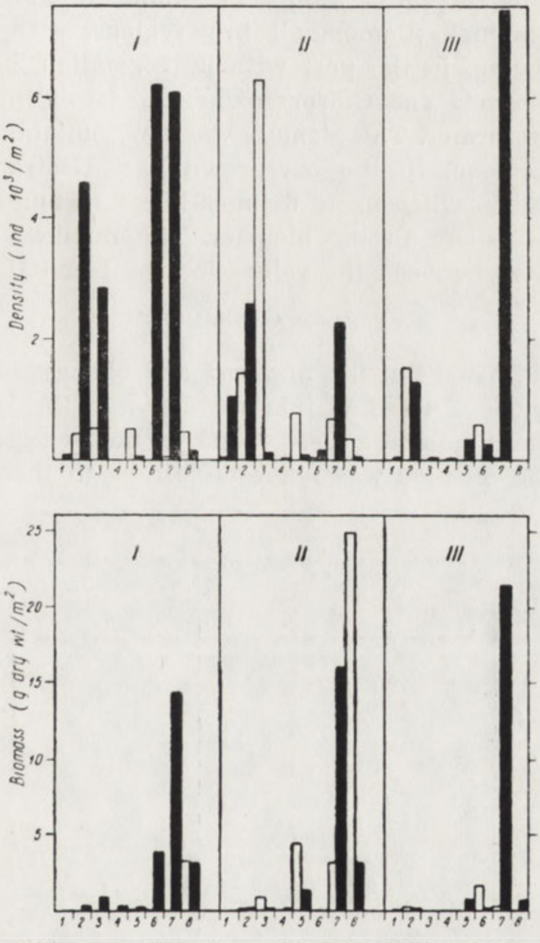

Fig. 4. Numbers and biomass of benthos of Dead Vistula. I–III — investigated regions. 1 — Nemertini, 2 — Oligochaeta, 3 — Polychaeta, 4 — Hirudinea, 5 — Crustacea, 6 — Chironomidae, 7 — Gastropoda, 8 — Lamellibranchiata. Black columns — parts with plants, plain columns — parts without plant

In the II region, in the part without vegetation, Polychaeta occur in the greatest density, then Oligochaeta, Crustacea and Lamellibranchiata, respectively 4, 8 and 9 times less numerously. The Lamellibranchiata dominated in the biomass, and their biomass was several times higher than that of other groups. In the overgrown part of this region, Oligochaeta and Gastropoda are of the highest density. Gastropoda dominated in the biomass, Lamellibranchiata had 5 times lower biomass, and Crustacea half of the latter value. The numbers and biomass in the II region were the highest among all three regions.

In the III region, in the part without vegetation, benthos consisted mainly of Oligochaeta and Chironomidae, the latter in 2.5 times lower density than the former. The biomass was low, but the highest one was this of Chironomidae. In the overgrown part Gastropoda were most numerous, and then Oligochaeta 6 times lower in numbers. Gastropoda had the greatest share in the biomass. The numbers and biomass in the III region was between the values for the I and II one.

SEASONAL CHANGES

The seasonal changes of the numbers and biomass of benthos in the investigated regions of Dead Vistula are shown at the Fig. 5. During all seasons the highest numbers were found in the overgrown part of the I region, but the biomass was not especially high there. The numbers

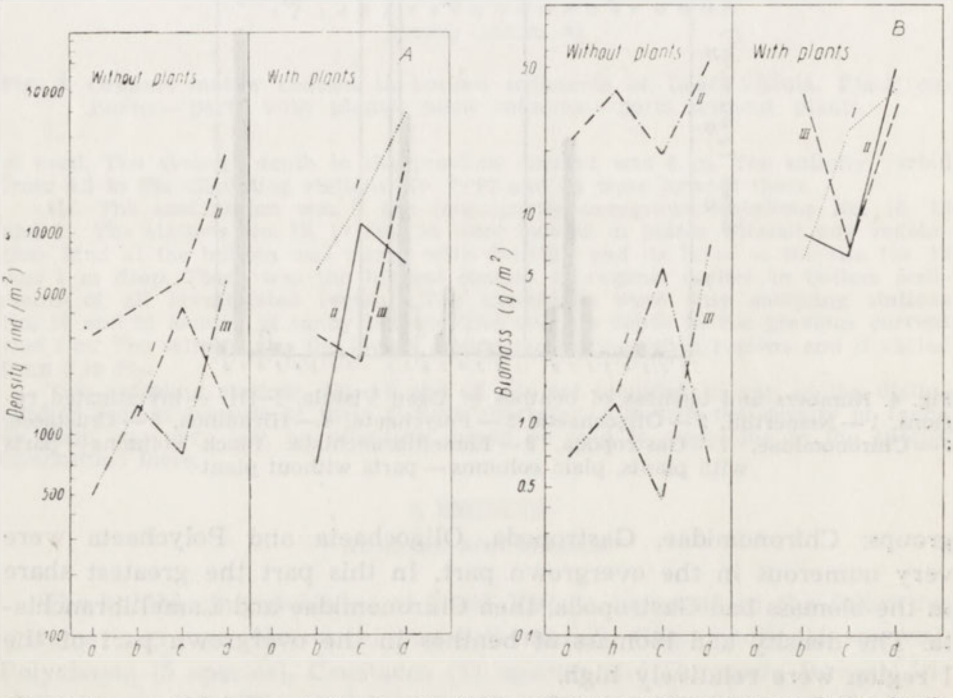

Fig. 5. Seasonal changes of the density (A) and biomass (B) of bottom fauna in the examined regions. Data for bottom without plants and with plants presented separately. I—III — numbers of regions

and biomass maxima were usually found in autumn, with the exception of the I region, part without vegatation, and the II region, overgrown part, where these maxima occurred in summer. In this last part the biomass maximum occurred in autumn, although the numbers were the highest during the summer. A high biomass in the overgrown part of the III region during the spring is also one of the exceptions. Apart from the above exceptions the biomass increases together with the increase of the numbers in particular seasons. However, this dependence is not proportional in the majority of the investigated parts of the water body. E.g. in the overgrown part of the I region a considerable increase of the numbers was observed — from 14,479 individuals/m² in summer to 39,107 individuals in autumn — with only slight increase of the biomass from 25.3 to 39.5 g/m².

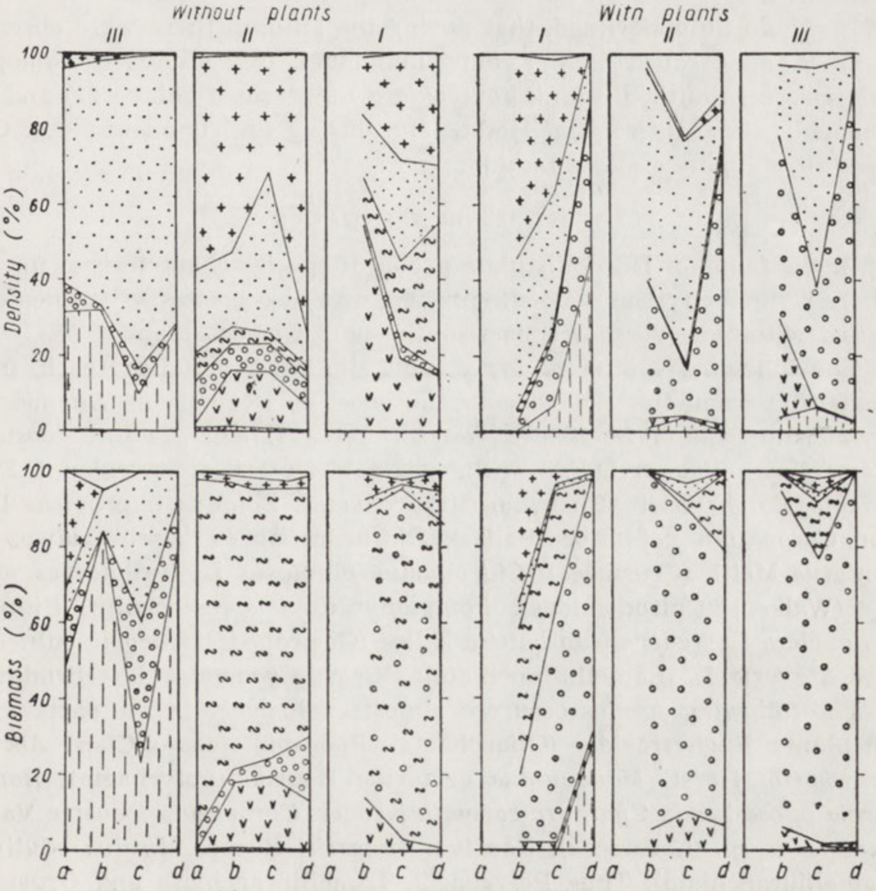

Fig. 6. Annual changes of the percentage share of numbers and biomass of various groups in particular regions. I–III — numbers of regions. 1 — Chironomidae, 2 — Crustacea, 3 — Gastropoda, 4 — Lamellibranchiata, 5 — Oligochaeta, 6 — Polychaeta 7 — others

Annual changes of the percentage share of groups of benthic fauna in particular regions are shown at the Fig. 6. The annual changes of the percentage share of particular groups in total numbers in the parts without plants are quite different in studied regions, and they are different from the biomass changes. The percentage variations of the numbers and biomass in the overgrown parts of the II and III region are, on the other hand, similar. The highest densities were found for Oligochaeta and Gastropoda. The share of Gastropoda in numbers of all animals is large during the spring, smaller in summer, and again large in autumn. These animals dominate during all year in the biomass of benthos in both parts, with and without plants, of all regions, reaching at the average 60% of the biomass. During the summer the percentage share of the biomass of Gastropoda is also smaller. However, the occurrence of fauna in the overgrown part of the I region is different.

It should be underlined, that during the autumn there were observed the mass appearances of the young individuals of Mollusca (*Potamopyrgus jenkensi* Smith, *Bithynia tentaculata* L., *Macoma baltica* L.) and Polychaeta (*Alkmaria romijni* Horst), and during the summer of e.g. Crustacea (*Bathyporeia pilosa* Lind.).

SPECIES DIFFERENTIATION

In the fauna of Dead Vistula a group of species characteristic for this whole water body can be distinguished, and also groups of species connected with the overgrown part or the part without plants.

The following species occurred along the whole studied reach, independently from the presence or absence of vegetation: *Limnodrilus hoffmeisteri* Clap., *Peloscolex heterochaetus* (Mich), *Tubifex costatus* Clap., *Nais elinguis* O.F.M. (Oligochaeta); *Nereis diversicolor* O.F.M., *Streblospio shrubsoli* (Buchanan) (Polychaeta); *Balanus improvisus* Darvin, *Corophium volutator* (Pallas), *Rhithropanopeus harrisi subsp. tridentatus* Maitl. (Crustacea); *Chironomus plumosus* L., *Tanytarsus mancus* (Walker) (Chironomidae); *Potamopyrgus jenkensi* Smith, *Bithynia tentaculata* L., *Radix ovata baltica* Nillss. (Gastropoda); *Macoma baltica* L.. *Mya arenaria* L. (Lamellibranchiata); *Piscicola geometra* L. (Hirudinea).

The following species occurred almost exclusively in the parts without plants: Enchytraeidae (Oligochaeta); *Pygospio elegans* Clap., *Alkmaria romijni* Horst, *Manayunkia aesturina* Bourne (Polychaeta); *Bathyporeia pilosa* Lind., *Cyathura carinata* Kröyer, *Corophium locustre* Vanh., *Gammarus sp.* (Crustacea); *Cardium lamarcki* Reeve, *Mytilus edulis* L. (Lamellibranchiata). Thus Polychaeta, Lamellibranchiata and Crustacea are the characteristic groups for the not overgrown parts.

The following species occurred almost exclusively in the overgrown parts: *Stylaria lacustris* L., *Ilyodrilus hammoniensis* (Mich) (Oligochaeta); *Erpobdella octoculata* L., *Helobdella stagnalis* L. (Hirudinea) Orthocla-

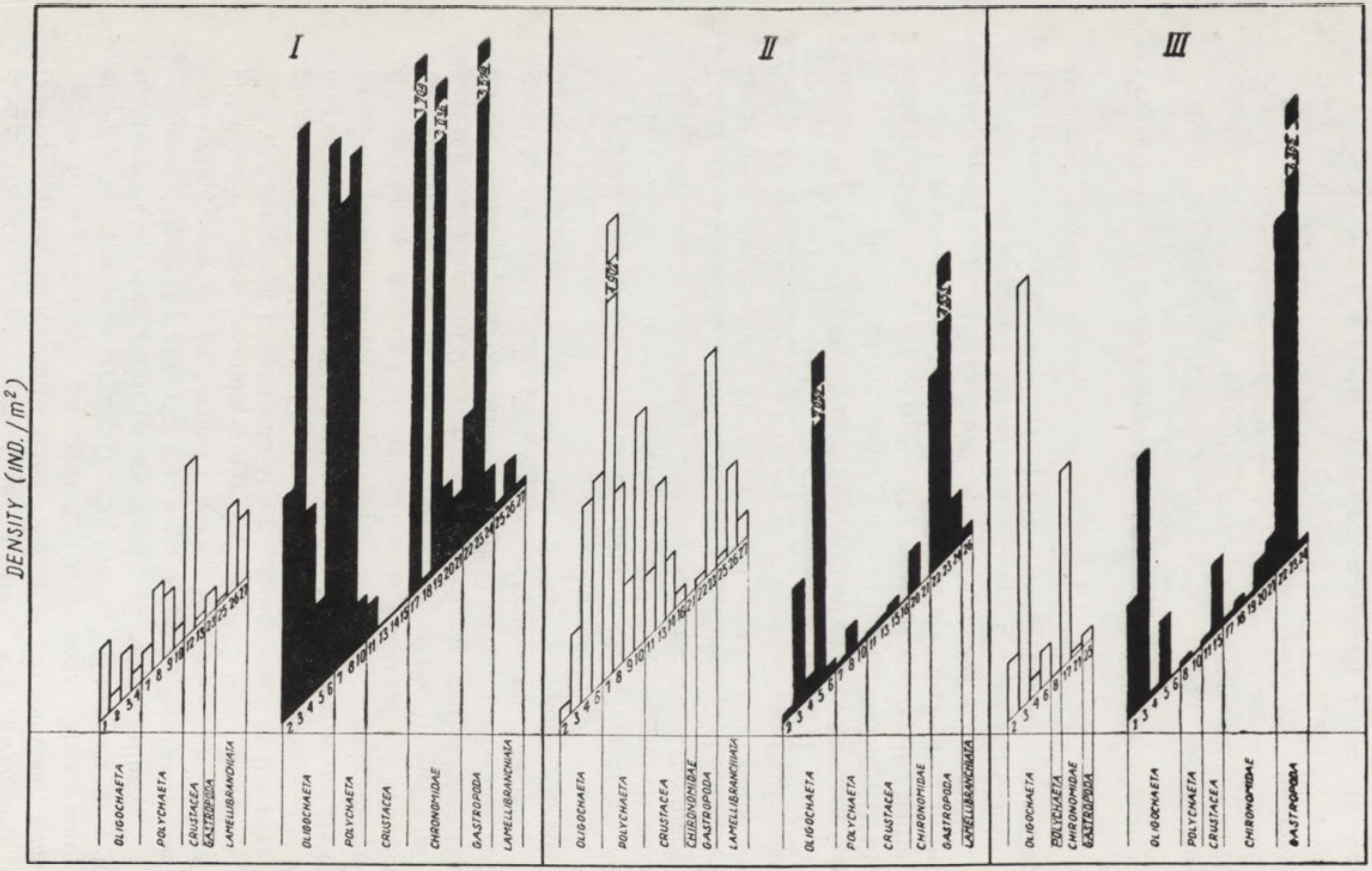

Fig. 7. Density of common species (average values for all investigated regions). I—III — investigated regions, plain columns — parts without plants, black columns — parts with plants. 1 — Enchytraeidae, 2 — *Limnodrilus hoffmeisterii*, 3 — *Limnodrilus* sp. *juv.*, 4 — *Peloscolex heterochaetus*, 5 — *Stylaria lacustris*, 6 — *Tubifex costatus*, 7 — *Alkmaria romijni*, 8 — *Nereis diversicolor*, 9 — *Pygospio elegans*, 10 — *Streblospio shrubsoli*, 11 — *Balanus improvisus*, 12 — *Bathyporeia pilosa*, 13 — *Corophium volutator*, 14 — *Cyathura carinata*, 15 — *Gammarus* sp., 16 — *Rhithropanopeus harrisi*, 17 — *Chironomus plumosus*, 18 — *Endochironomus* sp., 19 — *Glyptotendipes gripecoveni*, 20 — *Orthocladinae*, 21 — *Procladius*, 22 — *Bithynia tentaculata*, 23 — *Potamopyrgus jenkensi*, 24 — *Radix ovata*, 25 — *Cardium lamarcki*, 26 — *Macoma baltica*, 27 — *May. arenaria*

dinae, *Glyptotendipes gripecoveni* Kieffer, *Endochironomus tendens* (Fabr.) and *Endochironomus dispar* Meigen (Chironomidae); *Radix ovata baltica* Nilss., *Planorbis planorbis* L. (Gastropoda). Thus mainly Oligochaeta, Chironomidae larvae, Gastropoda and Hirudinea were found in the parts with vegetation, independently from the salinity.

Several times it was found that various species from the same systematic group dominate in various regions. Changes of the species composition within most common groups from Dead Vistula are shown at the Fig. 7. Among e.g. Oligochaeta the most numerous in the part without plants of the I region are Enchtreaidae, in the II region — *Tubifex costatus* Clap. and *Peloscolex heterochaetus* Mich., and in the III region — *Limnodrilus hoffmeisteri* Clap. apart from the juvenile individuals of *Limnodrilus sp.* Among Polychaeta, *Nereis diversicolor* O.F.M. dominates in the I region and in the overgrown part of the II one, while in the part without plants in the II region — *Alkmaria romijni* Horst is a determined dominant. In the III region Polychaeta nearly did not occur. Among Crustacea, in the part without plants of the I region dominated *Bathyporeia pilosa,* in the same part of the II region — *Corophium volutator* Pallas, and in the last region — *Gammarus sp.*

The species varied more in the parts without plants of the whole studied reach, than in the overgrown parts of the II and III region. The overgrown part of the I region was an exception. Here the highest number of species was found among all the distinguished parts of Dead Vistula. Species characteristic for the I and II region were found here, and the difference between the number of freshwater and Baltic species was the smallest as compared with other regions. In the I region with the highest salinity there is a much higher number of Baltic than freshwater species in the part without plants, while in the III region with the lowest salinity there is an inverse relation between freshwater and Baltic species.

At the two of sampling stations, No. 13 and 18, located in the drainage channel and in the lock between Dead Vistula and the Vistula River the following species occurred, which were not found in Dead Vistula: *Ilyodrilus bavaricus* Oeschmann, *Limnodrilus udekamianus* Clap. and larvae of Heleidae.

INFLUENCE OF SALINITY ON THE DISTRIBUTION OF BENTHOS IN DEAD VISTULA

Figure 8 shows the limits of salinity for several species from Dead Vistula and the comparable literature data. For some freshwater species, as e.g. *Stylaria lacustris* L., *Chironomus plumosus* L., the quoted values of salinity are the highest limiting ones. For the majority of given species the maximal and minimal salinity values from Dead Vistula are within the limits of their occurrence. These are e.g. *Radix ovata f. baltica* Nilss., *Piscicola geometra* L., *Gammarus zaddachi* Sex.

on, *Procladius sp.*, *Balanus improvisus* Darvin, *Cordylophora caspia* Pallas, *Cyathura carinata* Kroyer, *Corophium volutator* Pallas, *Nereis diversicolor* O.F.M., *Potamopyrgus jenkensi* Smith and *Mytilus edulis* L. For some Baltic species as e.g. *Tubifex costatus* Clap., *Alkmaria romijni* Morst, *Streblospio shrubsoli* Buchanan, *Macoma baltica* L., *Mya arenaria* L., *Pygospio elegans* Clap., *Cardium lamarcki* Reeve, *Bathyporeia pilosa* Lind. the found salinity values are the lowest limiting ones.

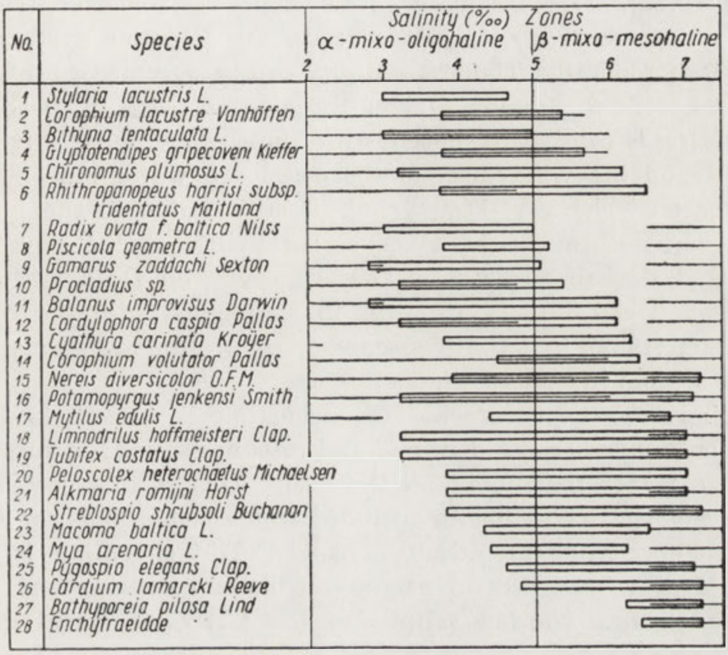

Fig. 8. Limits of salinity for several species from Dead Vistula

Species *Peloscolor heterochaetus* Michaelsen (Oligochaeta), found in Poland for the first time, occurred at the salinity 3.8–7.0$^{0}/_{00}$.

5. DISCUSSION

Dead Vistula is a near Baltic brackish water body. According to the Venetian system it is β-mixo-mesohaline and α-mixo-oligohaline with slightly larger area covered by the latter zone. Among the Polish brackish water bodies it can be placed, as far as the salinity is concerned between Zatoka Pucka (Żmudziński 1967) and Zalew Wiślany (Szarejko-Łukaszewicz 1959). The investigated reach, 14 km long, has a variable environmental conditions similar to that of the parts of the sea bays under the direct influence of Baltic. The mean salinity in Dead Vistula is about 4.5$^{0}/_{00}$. The animals living here are euryhaline, highly tolerant to the changes of salinity, and these were met along the whole investigated reach. Freshwater species are in the minority. Baltic species in the β-mixo-mesohaline zone were not numerous, but the majority of them occurred in α-mixo-oligohaline zone, living in the salinity occasionally lower than $4^0/_{00}$. However, the division between these two zones at $5^0/_{00}$ (acc. to the Venetian system) can be treated more generally. The $4^0/_{00}$ salinity can be assumed as this division for the zones in the major part of the studies reach of Dead Vistula. This lowering is caused by short lasting changes of the salinity, dependent mainly on the wind directions causing the water movements, and on the seasonal changes (low spring salinity is due to the infiltration of fresh water through the river embarkments at the high level of Vistula, and due to thawing of the ice cover on Dead Vistula). The results from Dead Vistula are thus in agreement with the conclusion of Wiktor (1969), that Baltic species occur in β-mixo-mesohaline zone, and more seldom in α-mixo-oligohaline one.

The limits of the occurrence of species No. 7–17 and 24 in Fig. 8 are not continuous, as the maximal and minimal salinity values of these species are larger than given in the table. This results probably from the choice of the water bodies included in the table, but not from the lack of tolerance to the salinity changes. The exception is *Cythura carinata* Kroyer (No. 13) in α-mixo-oligohaline zone, found only by Wiktor (1962) at the low salinity of $0.18–2.18^0/_{00}$ in Kanał Piastowski in Szczecin Bay.

The lower number of freshwater species was found when the salinity was higher. The Baltic species occurred in larger number in Dead Vistula when the salinity was about $5^0/_{00}$ or higher. These observations confirm the conclusion of Remane (1934) that there is a significant decrease of the number of freshwater species in the salinity above $3^0/_{00}$, and a significant decrease of the number of sea species in the salinity below $5^0/_{00}$.

In Dead Vistula an influence of the character of bottom on the occurrence of fauna was noticed. Polychaeta — brackish species, and Chironomidae — freshwater species, were both most numerous in the II region and in the bay of the I region with sand and mud at the bottom, but not in the I or III region, as it could be supposed taking into consideration the salinity. The above dependence caused probably the lack of continuity for certain species in Fig. 8. Although it is known from the literature data (Fig. 8) that these species occur in the salinity higher than that in Dead Vistula, they were not found in the region with the highest salinity. The differentiated bottom of Dead Vistula contains various quantities of the organic matter. Its percentage share in bottom sediments decreases, generally from SE part to the mouth of Wisła Śmiała. Relatively large decrease of this percentage is in the division of Dead Vistula and Wisła Śmiała (station No. 8) and in the mouth to Gdańsk Bay (station No. 2), from where the organic matter is washed out by a strong current. The currents which have place in the mouth, due to the changes of water level, probably deposit the organic matter near the jetty (station No. 1), and on the other side at the front of the back delta, i.e. near station No. 6, where the organic matter content is ten times higher than in the sediments. The organic matter is also deposited in the west side of the river mouth, where the waves action is much weaker. The differentiated quantity of the organic matter along Wisła Śmiała is caused by the every year dredging for the sailing purposes. In the parts with plants the organic matter content in bottom sediments depends on the intensity of water movements. Places more protected against these movements show higher content of organic matter, as e.g. the bay — sampling stations No. 3, 4 and 5. The low organic matter content in the sediments at station No. 21 is the result of waves action which cannot be stopped at the small depth of 30 cm by a poor stand of *Juncus sp*. Thus the distribution of benthos in the distinguished regions of Dead Vistula is limited by two factors: salinity and the character of bottom. As both these factors act simultaneously it is impossible to say which one is more important. The density of bottom fauna of Dead Vistula is twice higher than that of Zalew Wiślany (Żmudziński 1957) and one and a half times higher than the one in Zalew Szczeciński (Wiktor 1962). The larger density of benthos in Zalew Szczeciński as compared with Zalew Wiślany is explained by Wiktor (1962) as resulting from a considerable inflow of fresh water carrying the nutrients. Lack of such data unables such conclusion in the case of Dead Vistula, but it can be assumed that the inflow of drainage waters from Żuławy influences the density of benthos. High content of the organic matter in sediments at station No. 13 and 18 (Fig. 3) in drainage channel and in the lock supports this assumption.

The most typical for the overgrown part of Dead Vistula are Polychaeta, Lamellibranchiata, Crustacea, and as far as biomass is concerned, additionally Gastropoda. Żmudziński (1967) found in the near shore part of Gdańsk Bay extremely high occurrence of fauna, higher than that in the other parts of Baltic. The highest biomass in his investigations was the one of groups which were also present in Dead Vistula. However, because of various methods of the biomass determination, the results are not comparable. In the overgrown parts of Dead Vistula Oligochaeta, Chironomidae larvae and Gastropoda were found independently from the salinity values. The overgrown part is very numerously inhabited with benthos. Such parts in Zalew Szczeciński are also very abundant with benthos, similarly to the shallows. Wiktor (1962) found there Mollusca, Chironomidae and Oligochaeta. However, in Dead Vistula *Potamopyrgus jenkensi* Smith dominates among

Mollusca, while in Zalew Wiślany (Żmudziński 1957) and Szczeciński (Wiktor 1962) — *Dreissena polymorpha* (Pall.), which occurs only sporadically in Dead Vistula. The salinity of the part of Dead Vistula without vegetation is similar to that of the shore parts of Gdańsk Bay, with the exception of the most SE part of the III region. The salinity of the part of III region and of the overgrown parts of Dead Vistula is similar to the salinity of Zalew Wiślany and Zalew Szczeciński.

The investigations of Żmudziński (1957) in Zalew Wiślany showed quite considerable seasonal variations of benthos, and especially of its biomass. In his investigations and in the present ones the highest values were found in summer and autumn. Changes of the percentage share of various groups in the total biomass of benthos in Dead Vistula are not proportional, or even analogous to the changes in their numbers. This results from large differences in the size and weight of individuals of the same species. It is well seen in the case of Mollusca and Crustacea, as their shells have a considerable share in total biomass of these groups. The decrease of the biomass in relation to the numbers is especially well seen at the time of the appearance of young individuals as e.g. in summer of *Bathyporeia pilosa* Lind., and in autumn of *Potamopyrgus jenkensi* Smith, *Bithynia tentaculata L., Macoma baltica* L., and of *Alkmaria romijni* Horst.

6. SUMMARY

The benthic fauna of Dead Vistula was investigated along the 14 km reach during 1965. This water body is connected with Gdańsk Bay through the mouth of Wisła Śmiała and with the Vistula River through the lock (Fig. 1). The environmental conditions, and especially the salinity and the type of bottom are shown at Fig. 2 and 3. The analysis of the benthos species composition is shown at the Fig. 7. Different composition of invertebrate communities was found for the overgrown part and the part without any vegetation. The species of benthos were more changeable in the parts without than with plants. The occurrence of more common species in Dead Vistula were found to depend on the salinity (Fig. 8). Certain species were typical for α-mixo-oligohaline and β-mixo-mesohaline zones, or for one of them. On the basis of the investigations of the dynamics of numbers and biomass and taking into the consideration the salinity and type of bottom there were distinguished parts with plants and without plants in three regions: I — mouth region, II — middle region and III — east region. Various groups of different numbers and biomass dominate in these regions (Fig. 4). The maximum of numbers and biomass have place usually in autumn, but it occurred also in summer. The rise of numbers is not always proportional to the rise of biomass (Fig. 5 AB) due to large differences in the size of animals. A considerable decrease of the biomass in relation to the numbers is characteristic for the periods of mass appearances of juvenile individuals. The yearly changes of the percentage share of particular groups of benthic animals are quite different in various regions. These differences are larger for the parts without plants than for the overgrown ones (Fig. 6). The investigations allowed to state on the basis of an analysis of benthic fauna that the studied reach was highly differentiated, at least during the investigations.

7. STRESZCZENIE

W roku 1965 zbadano faunę denną Martwej Wisły na odcinku ok. 14 km. Zbiornik ten ma połączenie z Zatoką Gdańską przez ujście Wisły Śmiałej i z Wisłą przez śluzę (Fig. 1). Uwzględniono aktualnie panujące tam warunki abiotyczne, a w szczególności zasolenie i charakter dna (Fig. 2, 3). Przeprowadzono analizę składu gatunkowego (Fig. 7). Stwierdzono różny skład zespołów bezkręgowców w części zarośniętej zbiornika i w części pozbawionej roślinności, a większą zmienność gatunkową wzdłuż Martwej Wisły w jej części niezarośniętej niż zarośniętej. Zwrócono uwagę na zależność występowania pospolitszych gatunków Martwej Wisły od zasolenia (Fig. 8). Stwierdzono, że gatunki występujące w Martwej Wiśle są euryhalinowe, typowe dla strefy α-mixo-oligohalinowej i β-mixo-mesohalinowej, lub dla jednej z nich. Na podstawie badań nad dynamiką liczebności i biomasy uwzględniających zasolenie i charakter dna wyróżniono: części zarośnięte i bez roślinności w trzech rejonach: I — ujściowym, II — środkowym, III — wschodnim. Dominują w nich różne grupy o innej liczebności i biomasie (Fig. 4). Badania nad zmiennością sezonową wykazały, że maksimum liczebności i biomasy dla różnych rejonów przypada przeważnie jesienią, a niekiedy latem. Wzrost liczebności nie zawsze jest proporcjonalny do wzrostu biomasy (Fig. 5 AB), co jest wynikiem dużych różnic w wielkości osobników bezkręgowców. Znaczne obniżenie biomasy w stosunku do liczebności jest charakterystyczne dla okresu pojawiania się masowo młodych osobników. Roczne zmiany procentowego udziału poszczególnych grup fauny dennej w różnych rejonach przebiegają bardzo odmiennie. Różnice te są większe dla części niezarośniętych niż dla zarośniętych (Fig. 6). Przeprowadzone badania pozwoliły stwierdzić na podstawie fauny dennej silne zróżnicowanie akwenu, przynajmniej w okresie prowadzonych badań.

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ROTIFERS OF THE NEAR BOTTOM ZONE OF LAKES MIKOŁAJSKIE AND TAŁTOWISKO

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ABSTRACT

Evidence is supplied that near the lake bottom the benthic rotifers species are autochthonous, whereas eurytopic and planktonic ones immigrate from other lake zones chiefly from epilimnion. During the warm season the quantitative and qualitative species composition of rotifers over lake bottom is affected mainly by eurytopic and planktonic species. The number of benthic species does not alter considerably during the research period. The number of species and abundance of individuals in the near-to-bottom zone decreases with increasing depth.

1. INTRODUCTION

Hydrobiological literature comprises papers concerning rotifers, chiefly pelagic ones, from various lakes. It is lacking however in data on profundal rotifers, occurring principally in water overlying the surface of bottom sediments. This is due to technical difficulties in sampling, which constitute an essential obstacle in investigating this habitat. No hermetic samplers are available that would prevent surface water to penetrate into them during the drawing out of a sample towards the surface. Although Pejler (1962) investigated the rotifers of the near-to-bottom zone of a lake, still his interest was limited to depths not exceeding 1 m. This author allows for difficulties in finding a method of sampling in the bottom zone at greater depth. Bigelow (1928) investigated the microfauna communities in various lakes, considering the littoral fauna as poorly known. Wiszniewski (1953) writes that rotifers from littoral and benthic communities remain almost unknown even from the faunistical viewpoint. The lake littoral rotifers were studied by Klimowicz (1964). In connection with plant communities, the occurrence of benthic rotifers at greater depths was however not taken into account. Pawłowski (1958) admits that the bottom composed of muddy soft sediments is very poorly settled by rotifers, particularly in lake profundal.

The present paper aims at investigating the rotifers settling the near-bottom zones of lakes and at establishing their sources of immigration.

2. METHODS

The material was collected in lakes Mikołajskie and Tałtowisko (Mazurian Lakeland) from June 7 to Nov. 15, 1963. Two series of samples were taken every month. Each series of near-bottom samples contained: a sample from the littoral taken from among reeds at a depth 1–2 m, the bottom being for the most part

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sandy, slightly silted; a second one taken from the depth of 3.0–3.5 m, where the bottom was more markedly silted and often covered with under-water meadows. Next samples originated from the bottom covered with grey mud and were taken from the sublittoral up to the deepest parts of the lake (32 m). The distance from the shore to the deepest point was 400 m in Lake Mikołajskie and about 800 m in Lake Tałtowisko. A total of 192 samples were taken from the near-bottom zone.

The samplers widely used for plankton sampling are not suitable for sampling organisms in a thin near-to-bottom layer of water. In the course of present investigation the samples were taken by means of a tube sampler of Łastoczkin type equipped with a lid hermetically covering the top part of the tube, the construction of which was improved at the Institute of Ecology, Polish Academy of Sciences. This modified sampler was further equipped with a set of replaceable sampling tubes up to 50 cm long with apertures of a surface of 10–50 cm^2. The sample taken from the near-bottom zone was composed of a 10–20 cm layer of mud in its lower part and 30–40 cm layer of water in the top part, that underwent further examination. The sampler construction enabled to isolate the material originating from the thin layer of water just above mud surface.

In order to elucidate the sources of immigration of rotifers to the near-bottom zone, additional samples were taken from the pelagial. Over the deepest parts of the lake 24 samples were taken from surface water layer down to 0.5 m and 62 samples every 2 m down from surface to bottom in two series from each lake. These 86 samples from the pelagial were taken using an automatically closed sampler of Bernatowicz type, part of them being preserved with formalin at the sampling station for quantitative examination.

The water samples were filtered through a net of mill gauze No. 25. Most samples were examined in a live state the same day, only few being preserved till the next day in a thermostat at a temperature close to that of lowermost layers of lake water (4–7°C). The examined rotifers were first determined as to species, thereafter the number of individuals was counted in a chamber of 1 ml with the bottom divided into 1000 squares.

3. RESULTS

The number of species and abundance of rotifers in one litre of water of the near-to-bottom layer at various depths are presented on Fig. 1 as average data for the whole research period. As follows from these data, the number of species and abundance of individuals decrease along with increase of depth and distance from the shore. On Fig. 2 numbers are presented of species found at various depths and average numbers of individuals per 1 litre of water found in a water column from surface to bottom, in the deepest parts of the lake. A tendency of decrease of number of species and individuals along with increasing depth is evident. This decrease is less marked (Fig. 2, Tables I, II) in the water layer at the lower limit of occurrence of phytoplankton, in Lake Mikołajskie at 7–8 m, in Lake Tałtowisko 11–12 m. This layer is characterized by high density of phytoplankton, numerous planktonic crustacea and slightly increased abundance of rotifers. A complete list of rotifers, found in lakes Mikołajskie and Tałtowisko is presented on Table III showing the vertical reach of occurrence of species.

The benthic species, that in spite of swimming ability, remain in a permanent contact with a solid substratum, are placed in the upper of Table III (No. 1–7). Next are eurytopic species occurring in the near-bottom zone and among plants even in the shallowest part of the littoral (No. 8–20). The following place in Table III is occupied by species characteristic chiefly for pelagic lake plankton, transported however to near-bottom and littoral zones (No. 21–31). The subsequent species are those never found in habitats most specific for rotifers, that is in the littoral or pelagial, but observed only in deep near-bottom zones of lake (No. 32–35). These are followed by species found only in the epilimnion (No. 36–37) then by those found in littoral and epilimnion (No. 38–42), not observed in deeper near-bottom lake zones. On the last place of Table III are species found only in lake littoral (No. 43–51).

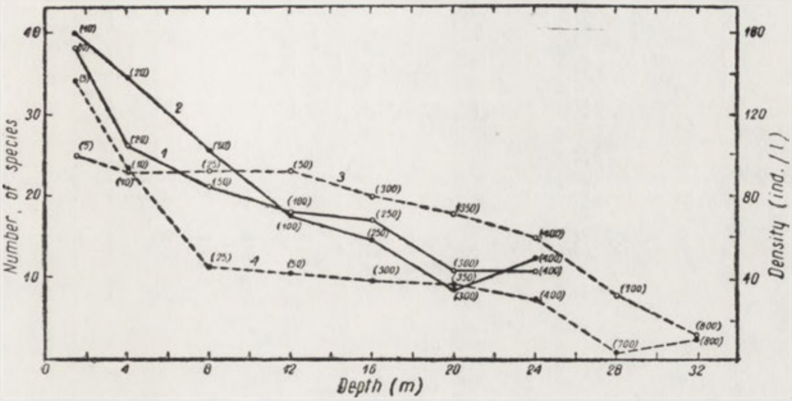

Fig. 1. Number of species and mean density of Rotatoria in the near-to-bottom water layer, in relation to water depth. The distances of sampling stations from the shore are given in brackets. Lake Mikołajskie: 1 — number of species, 2 — density, Lake Tałtowisko: 3 — number of species, 4 — density

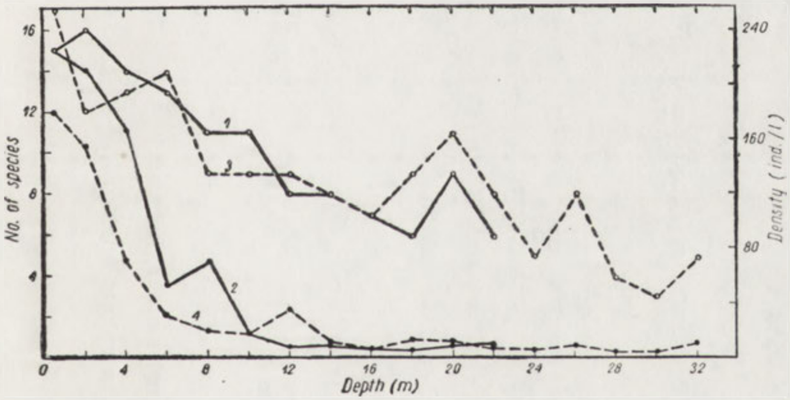

Fig. 2. Number of species and mean density of pelagic Rotatoria in relation to water depth. Lake Mikołajskie: 1 — number of species, 2 — density, Lake Tałtowisko: 3 — number of species, 4 — density

Among rotifers inhabiting the lacustrine profundal near-bottom zones, two groups of species may be distinguished according to Table III: benthic ones, that although capable of floating remain permanently in con-

Table I. Changes of abundance (ind./1) of Rotatoria with increase of depth. Lake Mikołajskie, Aug. 23, 1963

No.	Species	Depth (m)												
		0.5	1	2	4	6	8	10	12	14	16	18	20	22
1	*Keratella cochlearis* (Gosse)	32	38	45	37	10	19	8	2	4	2	2	2	2
2	*Keratella cochlearis tecta (Gosse)*	43	45	32	21	6	10	4	—	—	1	—	1	1
3	*Keratella quadrata* (Müll.)	15	17	18	15	10	15	3	1	2	2	1	2	1
4	*Polyarthra vulgaris* Carlin	20	14	19	16	5	4	2	1	2	—	1	—	2
5	*Asplanchna priodonta* Gosse	22	18	11	10	2	4	1	—	—	1	—	—	2
6	*Synchaeta pectinata* Ehrb.	17	11	16	12	3	2	2	1	—	1	—	—	1
7	*Conochilus unicornis Rousselet*	4	6	7	4	2	1	—	1	—	—	1	2	—
8	*Kellicottia longispina* (Kelli.)	18	16	8	6	1	3	2	1	1	2	—	—	—
9	*Chromogaster ovalis (Bergendal)*	21	8	12	8	2	1	—	2	—	—	—	—	—
10	*Pompholyx sulcata* Hudson	4	5	3	2	1	—	—	—	—	—	—	—	—

tact with solid substratum (No. 1–7); eurytopic ones that find optimum life conditions in deep water and among plants as well as planktonic forms (No. 8–31).

Table II. Changes of abundance (ind./1) of Rotatoria with increase of depth. Lake Tałtowisko, Sept. 5, 1963

No.	Species	Depth (m)																	
		0.5	1	2	4	6	8	10	12	14	16	18	20	22	24	26	28	30	32
1	*Keratella cochlearis* (Gosse)	30	31	36	19	9	7	12	15	9	2	3	3	2	1	3	3	1	4
2	*Keratella quadrata* (Müll.)	15	20	17	12	6	2	1	6	2	1	2	1	2	3	1	1	—	2
3	*Synchaeta pectinata* Ehrb.	17	10	12	11	3	2	—	3	—	2	—	—	—	—	2	—	1	1
4	*Trichocerca cavia* (Gosse)	5	3	4	1	—	2	—	2	—	—	1	2	1	—	1	—	2	2
5	*Keratella cochlearis tecta* (Gosse)	20	18	14	6	7	8	10	10	5	1	1	1	—	—	1	1	—	—
6	*Pompholyx sulcata* Hudson	15	17	10	2	3	—	—	—	—	—	—	1	1	—	1	—	—	—
7	*Anuraeopsis fissa* (Gosse)	9	5	2	—	—	1	—	1	—	—	—	—	2	—	—	—	—	—
8	*Kellicottia longispina* (Kelli.)	22	19	7	1	2	1	—	1	2	—	1	—	—	—	—	—	—	—

A considerable abundance of rotifers in epilimnion (down to 4 m, Tables I, II) is connected with mass occurrence in this zone of eurytopic species (No. 8–11, 13–14, 18; Table III) and of planktonic ones (No. 21, 23–26; Table III). Individuals of eurytopic and planktonic species were found in most cases from surface layers of epilimnion to the bottom throughout the whole water column.

Benthic rotifers (No. 1–7; Table III) occur chiefly in lake littoral. The reach of occurrence of these species in deeper lake zones is variable. In deep layers individuals of these species are found exclusively in the near-bottom zone, except for *Rotaria rotatoria* (No. 1), *Euchlanis dilatata* (No. 3) and *Lophocharis oxysternon* (No. 4). Within this group of species the occurrence of *Rotaria rotatoria* (No. 1) deserves special attention. It is an interesting fact that individuals of *Rotaria rotatoria*, a species requiring usually a solid substratum for creeping, was absent in Lake Mikołajskie from water surface down to 16 m of depth, then it was found in water from 16 to 20 m and in the near-bottom layer. All depths exceeding 6 m *R. rotatoria* was always a dominating species as to number of individuals in the 40 cm layer above the bottom.

Taking into account that in Lake Mikołajskie maximum depth attains 24 m the occurrence of this benthic species also in water column, 8 m above the bottom, is significant. In Lake Tałtowisko individuals of this species were found at the depth 26 m i.e. 6 m above the bottom. In August and next months in most samples from deeper strata of near-

Table III. Rotatoria species found

No.	Species	Mikołajskie			Tałtowisko		
		Littoral (1-2 m)	Depth (m)		Littoral (1-2 m)	Depth (m)	
			Near-bottom zone	Pelagial		Near-bottom zone	Pelagial
1	*Rotaria rotatoria* (Pallas)	+	4–24	16–20	+	4–32	26–32
2	*Rotaria neptunia* (Ehrb.)	+	4–16	—	+	4–28	—
3	*Euchlanis dilatata* Ehrb.	+	4–24	1–2	+	4–24	26
4	*Lophocharis oxysternon* (Gosse)	+	4–8	2	—	4–24	—
5	*Philodina roseola* Ehrb.	+	4–16	—	—	—	—
6	*Dissotrocha macrostyla* (Gosse)	+	4–8	—	—	4–12	—
7	*Itura aurita* (Ehrb.)	+	4–12	—	—	—	—
8	*Keratella cochlearis* (Gosse)	+	4–24	0.5–32	+	4–32	0.5–32
9	*Keratella quadrata* (Müll.)	+	4–24	0.5–22	+	4–28	0.5–32
10	*Trichocerca cavia* (Gosse)	—	—	—	+	4–28	0.5–32
11	*Pompholyx sulcata* Hudson	+	4–24	0.5–6	+	4–24	0.5–26
12	*Keratella quadrata frenzeli* (Eckstein)	+	4–24	0.5	+	4–20	0.5
13	*Anuraeopsis fissa* (Gosse)	—	—	—	+	4–20	0.5–20
14	*Polyarthra vulgaris* Carlin	+	4–16	0.5–22	+	4–8	0.5–10
15	*Trichocerca tenuior* (Gosse)	+	4–8	—	—	—	—
16	*Trichotria pocillum* (Müll.)	+	4	0.5	+	—	—
17	*Brachionus angularis* Gosse	—	—	—	+	4	—
18	*Synchaeta pectinata* Ehrb.	+	4–24	0.5–22	+	4–28	0.5–32
19	*Gastropus stylifer* Imhof	+	4–12	0.5–10	+	4–12	0.5–10
20	*Bipalpus hudsoni* (Imhof)	+	4–8	—	—	—	—
21	*Keratella cochlearis tecta* (Gosse)	+	4–24	0.5–22	+	4–32	0.5–28
22	*Trichocerca pusilla* (Jennings)	—	—	—	+	4–28	20–22
23	*Asplanchna priodonta* Gosse	+	4–24	0.5–22	+	4–24	0.5–20
24	*Kellicottia longispina* (Kelli.)	+	4–24	0.5–16	+	4–24	0.5–20
25	*Conochilus unicornis* Roussel.	+	4–16	0.5–20	+	4–24	0.5–10
26	*Chromogaster ovalis* (Bergandal)	+	4–24	0.5–12	—	4–12	0.5–26
27	*Trichocerca similis* (Wierzej.)	+	4–8	0.5–20	+	4–24	0.5–26
28	*Collotheca mutabilis* (Hudson)					8–20	10–22

in selected zones of examined lakes

No.	Species	Mikołajskie			Tałtowisko		
		Littoral (1-2 m)	Depth (m)		Littoral (1-2 m)	Depth (m)	
			Near-bottom zone	Pelagial		Near-bottom zone	Pelagial
29	*Trichocerca capucina* (Wierz. Zach.)	—	4–16	0.5–8	+	—	—
30	*Synchaeta grandis* Zacharias	+	4	0.5	—	—	—
31	*Filinia limnetica* (Zacharias)	+	4	0.5	—	—	—
32	*Notholca squamula* (Müll.)	—	—	—	—	8–20	—
33	*Rotaria neptunoidea* Harring	—	12–16	—	—	12	—
34	*Synchaeta stylata* Wierzejski	—	—	—	—	8–16	—
35	*Cephalodella sterea dentata* Donner	—	—	—	—	4–12	—
36	*Brachionus calyciflorus dorcas* Gosse	—	—	0.5–4	—	—	—
37	*Brachionus diversicornis* (Daday)	—	—	0.5	—	—	—
38	*Euchlanis triquetra* Ehrb.	+	—	2	—	—	—
39	*Cephalodella gibba* (Ehrb.)	+	—	1	—	—	—
40	*Lecane luna* (Müll.)	+	—	0.5	+	—	—
41	*Monostyla lunaris* (Ehrb.)	+	—	—	+	—	0.5
42	*Cephalodella catellina* (Müll.)	—	—	—	+	—	0.5
43	*Lepadella patella* (Müll.)	+	—	—	+	—	—
44	*Colurella bicuspidata* (Ehrb.)	+	—	—	—	—	—
45	*Cephalodella auriculata* (Müll.)	+	—	—	—	—	—
46	*Trichocerca tigris* (Müll.)	+	—	—	—	—	—
47	*Lepadella ovalis* (Müll.)	+	—	—	—	—	—
48	*Lepadella rhomboides* (Gosse)	+	—	—	—	—	—
49	*Pleurotrocha petromyzon* (Ehrb.)	+	—	—	—	—	—
50	*Philodina citrina* Ehrb.	+	—	—	—	—	—
51	*Lecane stichaea* Harring	+	—	—	—	—	—

-bottom zones of lakes only specimens of *Rotaria rotatoria* were found. During this period of investigations the group of species in profundal near-bottom zones of both lakes was much the same.

Special sampling was carried out from a layer of 40 cm, close to the bottom, to examine its microstratification; it proved that irrespective of the time of research period, the less numerous rotifers fauna was found in a layer of few centimeters above the bottom.

The abundance of benthic species as e.g. *Rotaria rotatoria* in the littoral of Lake Mikołajskie was 0–25 specimens in 1 litre of water, and in the profundal near-bottom zone 5–11 specimens per litre. *Euchlanis dilatata* in littoral 3–18, in profundal 0–2 specimens. *Lophocharis oxysternon* 0–15 and 2–4 respectively, *Philodina roseola* 0–12 in the littoral and 0–2 in the profundal near-bottom zone. An analogical general quantitative situation in benthic species was observed also in Lake Tałtowisko, where the numbers of specimens were lower and not all the species noticed in Lake Mikołajskie were found in Lake Tałtowisko as well. No dependence was observed of the number of benthic specimens in the profundal zone of a lake upon their quantitative development in the littoral.

The fauna of benthic rotifers in profundal zone does not undergo throughout the warm season any considerable changes, as it has been proved by numerous tests, because of stable environmental conditions. During this season in deepest regions of the examined lakes in a layer of less than 1 meter over the bottom the oxygen concentration was 0.0 to 2.4 mg/l and the temperature 4.5 to 9.4°C. Lack of oxygen in water (0.0 mg/l) was observed since the beginning of August. At the same time a distinct decrease in number of rotifers specimens, sometimes down to a dozen per 1 litre of water was noticed in both lakes.

The eurytopic and planktonic rotifers (No. 8–31; Table III) were found in both the pelagial and the profundal near-bottom water layers. Representatives of most species were present in the whole water column from upper epilimnion to the bottom. Despite of the presence of rather numerous specimens of the above mentioned species in the near-bottom layer, yet evidence is given by examples shown on Table I and II that reproduction occurs chiefly in the epilimnion. The abundance of specimens of eurytopic and planktonic species in the near-bottom zone is exclusively dependent on their simultaneous abundance in overlying water layers. Within these species the following ones were represented by the highest number of the individuals: *Keratella cochlearis, K. cochlearis tecta, K. quadrata, Synchaeta pectinata, Kellicottia longispina,* and *Asplanchna priodonta.* From the distinguished euplanktonic and planktonic species (No. 8–31; Table III) the following ones should be selected, that occur in abundance in epilimnion, but are considerably less resistant to conditions of the near-bottom zone: *Polyarthra vulgaris* (No. 4, Table I), *Asplanchna priodonta* (No. 5), *Conochilus unicornis* (No. 7), *Chromogaster ovalis* (No. 10), *Kellicottia longispina* (No. 8; Table I, No. 5; Table II), *Trichocerca cavia* (No. 4; Table II) and *Anuraeopsis fissa* (No. 7, Table II). Specimens of these species are sporadically found in the near-bottom zone. At depths below 5 m these species are found not in every quantitative sample limited to 5 l. They are more numerous in layers of less than 1 meter above the bottom, however not attaining the same abundance as in epilimnion. As follows from examples presented in Table I and II, most individuals of eurytopic and planktonic species certainly sink from the epilimnion to deeper profundal layers. The reach of occurrence of species in the near-bottom zone of deep profundal is not equal (No. 8–31; Table III). Except for individuals of *Trichocerca tenuior* (No. 15), *Trichotria pocillum* (No. 16), *Brachionus angularis* (No. 17), *Bipalpus hudsoni* (No. 20), *Synchaeta grandis* (No. 30), and *Filinia limnetica* (No. 31), all other species attain depths exceeding 10 m.

Species denoted in Table III by No. 43–51, occurring in the reed zone, did not exceed 3.5 m of depth over a firm bottom, but sporadically were found over underwater meadows. No specimens of these species were noticed at the border of underwater meadows or of sublittoral with firm bottom. The reach of these species over lake bottom is particularly distinct. The chances of meeting on underwater meadows individuals of these species decreased clearly together with the decrease of their abundances in the border zone between reeds and the pelagial.

Microscopic examination of surface layers of lake bottom sediments enabled to count dead and decaying specimens of rotifers. Only very few lorica were found, strongly damaged. Dead undamaged specimens were never recorded.

4. DISCUSSION

Pejler (1962) observed only planktonic forms in samples taken from depths exceeding 16 m. This author noticed also, that most rotifers species avoid loose bottom sediments. Only individuals of species *Euchlanis triquetra* and *Lepadella triptera*, that have trigonal cross-section of body with a wide basis, are adapted to reside over loose surface of bottom sediments. Moore (1939) enumerates 28 rotifers species from Lake Douglas, among which in deeper sublittoral and profundal zones occur: *Rotaria rotatoria, R. tardigrada* and *Dissotrocha macrostyla*. Between 14 and 22 m only *Rotaria rotatoria* is observed. After this author the number of rotifers species decreases with increasing depth. Comparing with other seasons, at the same depths in lake profundal, during summer stagnation the microfauna is reduced as to number of species and abundance of individuals.

The main original feature of the present paper is the discussion of origin of rotifers residing in the profundal near-bottom lake zones. As it follows from data presented in Table III, the species occurring in near-bottom zone of a lake and being a special object of the present investigation, are probably born in the near-bottom habitat as well as the pelagic one. The main difference between species in this habitat is their origin, from the near-bottom zone or immigrating species. A less numerous group of species are the autochthonous, benthic ones, that in particular months of the warm season succumb to insignificant changes as to species composition and abundance of individuals. On the contrary, the major group of species are the immigrating ones, eurytopic or planktonic, that undergo changes in species composition and density of individuals throughout the warm season of the year. Their occurrence in the discussed habitat depends on their abundance in the epilimnion (examples — Tables I and II), that determines their abundance in the profundal, over the lake bottom.

The benthic species in lake profundal are indigenous, since they find conditions favourable to reproduction and development in the water layer over lake bottom. These species are often represented by a considerably higher number of individuals in deep water strata, than in the littoral at the same period. Only few specimens may migrate from the littoral to profundal lake zones. Their abundance as to number of individuals is stable in the warm season. The discussed species are presumably resistant to oxygen deficiency and low water temperature. In warm summer days, in the course of examination of samples taken from the near-bottom zones, specimens of benthic species died much faster than specimens of the same species found in samples taken simultaneously from among reeds in the littoral. This fact corroborates also the supposition that specimens of benthic species found in the profundal must reproduce chiefly above the lake bottom, since they are better adapted to lower temperatures and oxygen deficiency than those originating from lake littoral. Benthic species, that dominate in the profundal near-bottom lake zone occur abundantly except for *Rotaria neptunoidea*, also in small water pools in winter, when oxygen concentration is 0.0–2.0 ml/l and water temperature 0.5–4.0°C (Klimowicz 1970).

The abundance of individuals of the group of eurytopic and planktonic species in the near-bottom lake zones is markedly varying during the warm season of the year. This variability is influenced chiefly by the development of these rotifers in lake epilimnion. This conclusion is corroborated by parallel investigations of Hillbricht-Ilkowska (1967) on production of rotifers, taking *Keratella cochlearis* as a model.

It should be mentioned that the generally accepted presumption, of mass deposition on lake bottom of dead specimens of organisms occurring in the water column up to the surface, found no confirmation. According to a justified assumption, the lorica scarcely found in the surface layer of bottom sediments, originate chiefly from population of rotifers occurring near the lake bottom, their number in the samples being too small. Certainly the sinking of dead individuals towards the bottom is very slow and they undergo an advanced decomposition in the water column, so that only few carapaces strongly decayed attain the bottom. In the surface layer of mud eggs of Cladocera were often found in the form of "ephippium", despite of the fact, that dead specimens of Cladocera were very uncommon. Carapaces of *Chydorus sphaericus* were an exception, they were found frequently in samples.

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5. SUMMARY

The settlement of rotifers in the near-bottom profundal lake zone of lakes Mikołajskie and Tałtowisko in the warm season was examined. Samples were taken also from the littoral and from the water column from surface to bottom at the deepest places of the examined lakes. Individuals of benthic species are autochthonous in the near-bottom profundal zone, since no dependence was noticed of their abundance on that in the littoral. On the other hand eurytopic and planktonic species immigrate from other lake zones, chiefly from the epilimnion (Tables I and II). The fauna of Rotatoria over the lake bottom undergo qualitative and quantitative changes, this regards however chiefly eurytopic and planktonic species. The intensity of changes depends on the density of these species in other lake zones, chiefly in the epilimnion (Table I, II). Benthic species were more stable as to qualitative and quantitative changes. Occurrence of particular species and density of individuals in the near-bottom lake zone and in the water column from surface to bottom decreases with increasing depth (Fig. 1, 2). A deviation from this rule was noticed only in the water column from surface to bottom at the limits of phytoplankton reach and a water layer close to the bottom, where the number of species and abundance of idividuals increases.

6. STRESZCZENIE

Badano zasiedlenie wrotków w przydennej profundalnej strefie w ciepłej porze roku jezior Mikołajskiego i Tałtowisko. Pobierano również dodatkowe próby z litoralu oraz z pionu wody od powierzchni jeziora do dna w najgłębszych miejscach badanych jezior. Osobniki gatunków bentosowych w strefie przydennej profundalu są tu autochtoniczne, nie stwierdzono bowiem zależności ilościowego występowania ze spotykanymi w littoralu, natomiast eurytopowe i planktonowe napływają tu z innych stref jeziora, głównie z epilimnionu (Tab. I–II). Fauna Rotatoria nad dnem jeziora zmienia się pod względem jakościowym i ilościowym, zmiany te dotyczą jednak głównie gatunków eurytopowych i planktonowych. Nasilenie zmian jest uwarunkowane liczebnością tych gatunków w innych strefach jeziora, a głównie epilimnionie (Tab. I–II). Gatunki bentosowe nie zmieniały się tak wyraźnie pod względem jakościowym i ilościowym. Występowanie poszczególnych gatunków i liczebność ich osobników w warstwie przydennej jeziora oraz w pionie wody od powierzchni lustra do dna, zmniejsza się wraz z głębokością (Fig. 1, 2). Nieznaczny wyjątek stwierdzono jedynie w pionie wody od powierzchni

do dna na granicy zasięgu fitoplanktonu i w warstwie wody przy samym dnie gdzie zwiększa się liczebność gatunków i osobników.

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PRODUCTION OF CRUSTACEAN ZOOPLANKTON IN MOTY BAY, LAKE JEZIORAK. PART I. THE METHOD OF PRODUCTION ESTIMATION

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ABSTRACT

Formulas of Winberg et al. (1965) for estimation of net production of crustacean zooplankton have been modified. The modifications account for the changes in biomass increase of animals hatching from eggs and transformed into individuals of successive stages before the lapse of the period *T* for which production is estimated.

1. INTRODUCTION

In recent years the estimation of primary and secondary production in water ecosystems has become one of the focal interests of hydrobiologists. Precise understanding of the directions of the flow of energy between the trophic levels of water reservoirs will allow to find out the cause of the rapidly progressing eutrophication of lakes, and eventually to check the process or even to reverse it; this is a long range objective but considering the imminent deficit of clear water it is of paramount importance. The initial stage of the extensive research program ought to involve reliable estimation of production of the predominating animal and plant groups in reservoirs. As it seems, an assessed value of production in a given reservoir, particularly of its secondary production, is likely to approximate reality, provided that the formulas employed for the calculation account for the actual state of the investigated population at every moment of its development. For example, the formulas for the estimation of crustacean zooplankton production, besides accounting for the time of development and the number of individuals in the several stages, must also take into consideration, whether it is the process of development or of ageing which predominates in the investigated population.

2. THE EXISTING METHODS OF ESTIMATION OF ZOOPLANKTON PRODUCTION

The methods of estimation of zooplankton production offered in literature depend on the determination of the increase of the number of individuals during a studied period, or else on the determination of the increase of their weight.

An early attempt at solving the problem was presented by Elster (1954, 1955). He proposed to calculate the number of individuals hatching from eggs from the known number of eggs in the environment and their rate of development. Nauwerck (1963) calculated the production of all the stages of development of *Eudiaptomus gracilis* emploing Elster's (1954) "restoration index". Stross et al. (1961) assessed the number of newly produced individuals of *Daphnia longispina* and of *D. pulex* during *T* days, using a formula similar to that employed by Edmondson (1960), assuming a straight-line increase of the number of individuals. The resulting number of produced individuals was used by these authors to define the period of turnover of individuals which, multiplied by average biomass of the whole population and divided by the length of the period of investigation, rendered the biomass production. Such method of production estimation is exposed to the charge that it requires an additional, not always sound assumption to the effect that the time of turnover of individuals is equal with the time of turnover of biomass. Hillbricht-Ilkowska, Patalas (1967) discuss the merits and failures of formulas and methods of zooplankton production estimation offered in literature of the preceding decade.

It is worth-while to consider the method of Winberg et al. (1965), perhaps the most commonly employed now. In this method, the production value of each development stage is obtained by multiplying the number N_o by the diurnal increase of biomass of the given stage and by the length of the period of investigation *T* in days. The formula expressed in uniform symbols (Hillbricht-Ilkowska, Patalas 1967) for calculating the production of the whole population (exemplified by Copepoda) looks as follows:

$$P_{TW} = \left[\frac{We \cdot N_o e}{De} + \frac{(W_o c - W_o n)\, N_o n}{Dn} + \frac{(W\bar{a} - W_o c)\, N_o c}{Dc} \right] \cdot T$$

where P_{TW} stands for production expressed in weight units, We, $W_o n$, $W_o c$, $W\bar{a}$ stand for initial weight of an egg, nauplius, copepodite and an average mature individual (at the initial moment t_o); De, Dn, Dc symbolize the period of development of an egg, nauplius, copepodite as dependent on the temperature of water during the period of investigation: $N_o e$, $N_o n$, $N_o c$ represent the number of eggs, nauplii and copepodites respectively at the moment t_o.

The formula does not include an element for calculating the increase of biomass of mature individuals, since it has been assumed that Copepoda stop to grow when they attain sexual maturity. After due transformation, the formula can be employed to calculate the production of Cladocera (Hillbricht-Ilkowska, Węgleńska 1970). The application of the quoted formula requires to take for granted the simplifying assumption that every individual remains in the "development stage" in which it has been at the moment t_o until the end of the investigated period T, though its biomass continues to increase. However, we know that young individuals which will increase their biomass, will hatch from eggs sampled at the moment t_o and also from some eggs laid by females during the period of investigation T.

Thus, the biomass produced by eggs can be considered as a sum of the biomass of eggs laid by females and of biomass increases of individuals hatched during the period T.

We face a similar situation when production of larvae in the nauplial stage is calculated. In each sample drawn from the lake there are individuals of various weights. Even though the period T, for which production is assessed, ought to be shorter, or at least not longer than the period of development of the nauplial stage, it is obvious that the largest individuals will be transformed into larvae of the next stage, yielding higher diurnal increases of their biomass, even before the period T elapses. This is illustrated on the example of an individual "a" weighing 0.001 mg (Fig. 1).

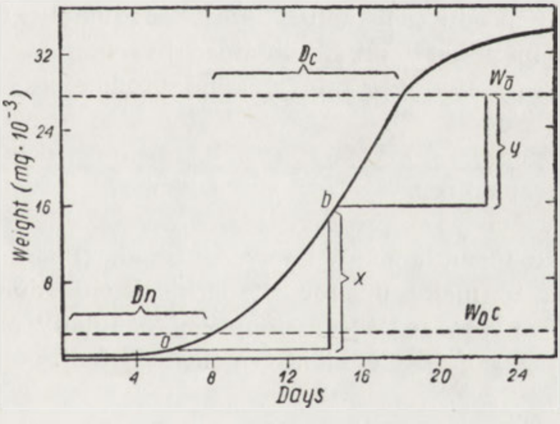

Fig. 1. A graphic method of computing Copepoda production from the curve of development. Dn, Dc — periods of development of a nauplius and copepodite in days; W_0c — initial weight of a copepodite; $W\bar{a}$ — average weight of an adult individual; x — production of an individual a during 8 days; y — production of an individual b during 8 days

Production of this individual for T (8 days) computed by means of the above quoted formula (Winberg et al. 1965) is 0.0024 mg. Actually however, after only two days, the individual will be transformed into the copepodite form which gives higher biomass increases. Its production "X" read from the graph (Fig. 1) is a sum of its biomass increases in the nauplial stage (2 days) and in the copepodite stage (6 days), X =

$= 0.0016 + 0.0142 = 0.0158$ mg. It is thus more than six times higher than the value rendered by the application of the formula.

A different situation arises in the copepodite stage. For example, a big individual "b" (Fig. 1) will attain sexual maturity, i.e. it will stop to grow, before the lapse of the period *T*, and its production "Y" read from the graph is 0.0156 mg, i.e. less than the value given by the formula (0.0197) under the assumption that each individual in this stage continues to increase its weight during the whole period *T*.

It can be seen from what has been said that production for a period *T* computed by means of the formula (Winberg et al. 1965) is underestimated for the egg and nauplius stages, and overestimated for the copepodite stage as compared with the actual values. The formula fails to account for as important a factor as the development stage of an investigated population — whether it is growing or ageing. Two populations with the same initial parameters needed to compute their production, but containing among, e.g., its copepodites, more of younger and smaller individuals in one case and more of bigger and heavier individuals in the other, will actually yield different biomass increases in a definite time instead of equal ones, as given by an application of the formula (Winberg et al. 1965).

It seems that production values most adequately reflecting what actually occurs in nature can be obtained by summing up the results rendered by multiplying the number and production (as read out of a graph) of individuals belonging to all the size or weight classes of an investigated population. This is still impossible since we are lacking a full set of graphs representing the curves of development of the predominating species in different temperatures and food conditions.

However, the formula of Winberg et al. (1965) can be largely improved so as to make up for the critical objections by applying modified formula, based on the assumption that daily production within the several stages of development remains constant.

3. DEDUCTION OF THE MODIFIED FORMULA FOR PRODUCTION ESTIMATION

In the deduction, uniform symbols of Hillbricht-Ilkowska, Patalas (1967) were used. In the final version of the formula, production of a single individual during a period *T* is symbolized for nauplius, juvenile form of Cladocera and copepodite by $Pn \cdot T$, $Pj \cdot T$, $Pc \cdot T$ respectively, where Pn, Pj, Pc stand for daily production. For the deduction, as well as for the application of the formulas, it is necessary to divide an investigated population into small length and weight classes and to know the number of animals in each class.

PRODUCTION OF EGGS

In the sample drawn from the lake at the beginning of the period T there is a certain number of eggs, Ne, in different stages of development, as it is shown by the arrows 1, 2, 3 cut by the vertical line t_o (Fig. 2).

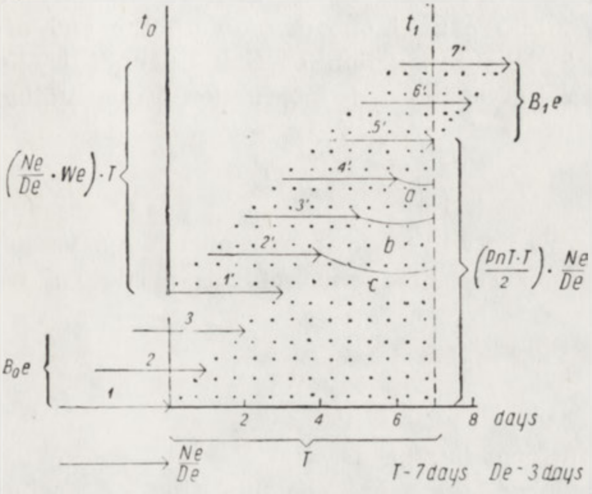

Fig. 2. An auxiliary illustration for the deduction of the formula $PnT \cdot T/2 \cdot Ne/De$, for computing the production of individuals hatched from eggs before the lapse of T. T — the period between two samplings of plankton; t_0, t_1 — the initial and final moments of T; De — the period of egg development; Ne — the number of eggs caught at the moment t_0; B_0e, B_1e — weights of eggs at the initial and final moments of T; $Ne/De \cdot We \cdot T$ — production of eggs during T; a, b, c — the period of growth of an individual from the hatching to the end of T

Since we know how long an egg. develops (De — 3 days), we can assume that 1/3 of eggs (arrow 1) had been laid 3 days before the sampling, 1/3 (arrow 2) two days before the sampling, and the remaining 1/3 (arrow 3) one day before the sampling (Fig. 2). It can be expected that females will lay new eggs, in the amount equal to $Ne/De = 1/3$ of the number of eggs in the sample, every day (arrow 1′ to 7′ on Fig. 2). Each of these will also develop for three days. This number multiplied by the weight of one egg We and by T gives the biomass of eggs laid during the whole period T:

$$\frac{Ne \cdot We}{De} \cdot T \tag{1}$$

This is the well known formula to estimate the production of eggs (Winberg et al. 1965, Hillbricht-Ilkowska, Patalas 1967).

The next step is to trace the development of eggs caught in the sample and of those laid by females in the several days of the period T. Only a part of them will remain in the egg stage by the end of the period T; those are represented by arrows 5′, 6′, 7′, cut by the vertical line t_1 (Fig. 2). They will make up the mass of eggs caught in the next sample. Out of the remaining eggs (arrows from 1 to 4′) nauplii will hatch sooner or later during the period T, which are marked by higher biomass increases. Among them, 1/3 (Ne/De — arrow 4′) will be transformed into nauplii one day before the end of the period T (arch a, Fig. 2); the production of these nauplii is Ne/De (or their number) multiplied by the daily production of a nauplius (Pn_1):

$$\frac{Ne}{De} \cdot Pn_1 \tag{2}$$

1/3 of eggs (arrow 3′) will be so transformed two days before the period T lapses (arch b). The production of this portion of nauplii is given by the formula:

$$\frac{Ne}{De} \cdot Pn_2 \tag{3}$$

Similarly for the remaining eggs.

The production of the nauplii hatched from eggs which are symbolized by arrow 1 can be presented by the formula:

$$\frac{Ne}{De} \cdot PnT \tag{4}$$

After the reiterating part Ne/De is withdrawn, a series of seven terms remains, in which the first term Pn_1 represents the daily production of a nauplius during the whole period T. To find its sum, we have to add the first and the last number and divide the result by 2, according with the familiar mathematical rule:

$$\frac{(Pn_1 + PnT) \cdot T}{2} \tag{5}$$

multiplied by the withdrawn reiterating part Ne/De is the formula for computing the production of nauplii hatched (before the lapse of the period T) from eggs caught in the sample and from those laid by females during T:

$$\frac{(Pn_1 + PnT) \cdot T}{2} \cdot \frac{Ne}{De} \tag{6}$$

The sum of the biomass increases as indicated by (1) and (6) represents the value of production of eggs and of individuals hatched from them during the whole period T (Fig. 2, the dotted space).

As the formula (6) was practically applied, it turned out that the results differed when full days or shorter time spans, e.g. 12 hour periods, were substituted for time symbols. The cause of the error can be most easily explained by means of a graph (Fig. 3).

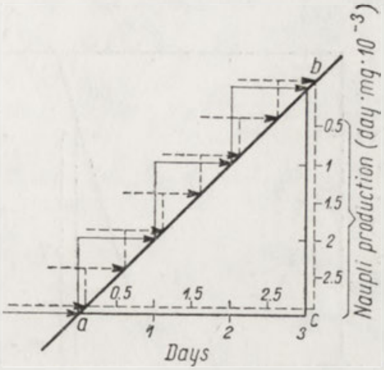

Fig. 3. An auxiliary illustration for the deduction of formula (7). Hortizontal lines define the period *T*, vertical ones the value of production of nauplii, arrows — *N*e/*D*e (continous in days, dotted in half-day intervals)

In Figure 3 horizontal lines define the period *T*, the continuous line in daily intervals and the dotted one in 12 hours intervals; continuous arrows stand for *N*e/*D*e at daily intervals, and dotted arrows represent *N*e/*D*e at half-day intervals.

When values expressed in terms of daily intervals were substituted for the respective symbols in (6), the resulting value of production was identical with that obtained by planimetrics of the field limited by the continuous lines and arrows. This value was higher from that obtained by means of the formula (6) when 12 hours data were employed, or by means of planimetrics of the smaller field limited by the dotted lines and arrows. The real value of production of nauplii hatched from eggs before the lapse of *T* is given by planimetrics of the triangle (*a*, *b*, *c*) in Fig. 3, as expressed by the formula:

$$\frac{P\mathrm{n}T \cdot T}{2} \cdot \frac{N\mathrm{e}}{D\mathrm{e}} \tag{7}$$

PRODUCTION OF NAUPLII

In order to estimate more precisely the production of nauplii, individuals which will remain in that stage until the end of the period of investigation and those which will be transformed into the next larval stage before the lapse of *T* must be considered separately. The population of nauplii must be divided into two classes and the number of individuals in each of them must be determined.

The value of production of a nauplius during period T must be subtracted from the weight of the smallest copepodite in order to obtain the biomass of an individual on the border of the two required classes ($c - PnT = a$, Fig. 4).

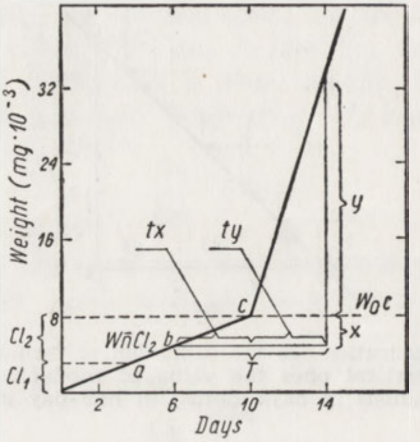

Fig. 4. Production during T of a class 2 nauplius ($W\bar{n}Cl_2$) transforming into a copepodite before the lapse of T. tx — the period of life of the individual b in the nauplial stage, x — production realized by b during its nauplial stage, ty — the period of life in copepodite stage, y — production realized in copepodite stage

All the animals in the nauplial stage weighing more than the border value (class 2) will be transformed into the next larval stage, showing higher biomass increases, before the lapse of the period T. Individuals with lesser weight (class 1) will remain in the nauplial stage until the end of the period T.

The estimated number of class 1 individuals is substituted for the respective term of the formula for computing the production of this class of animals. It is based on the formula offered by Winberg et al. (1965):

$$PnT \cdot NnCl_1 \tag{8}$$

Pn symbolizes the daily production of a nauplius, T the period between two samplings, $NnCl_1$ the number of individuals belonging to class 1.

Production of larvae of class 2 is the sum of biomass increases of individuals (of various weights) during the period of investigation. As a method of estimation of production, such an approach is difficult and toilsome. An approximate value of production can be attained by multiplying the biomass increase of an individual with average weight belonging to class 2 during the period T by the number of individuals in that class:

$$(P\bar{n}\ Cl_2 \cdot T) \cdot NnCl_2 \tag{9}$$

Application of this formula requires a number of mathematical operations. To obtain the production X of an individual "b", an average one in class 2, until the moment of its transformation into a copepodite, its weight should be subtracted from the weight of the smallest copepodite "c":

$$c-b=X \tag{10}$$

The value X from (10) divided by the daily production of a nauplius defines the time tx (Fig. 4) of the development of the individual "b" during its nauplial stage:

$$\frac{X}{P\mathrm{n}}=tx \tag{11}$$

However,

$$T-tx=ty \tag{12}$$

where ty (Fig. 4) defines the time of development of an average class 2 nauplius from the moment of its transformation to the end of the period T (i.e., during its copepodite stage). The time ty (as defined in (12)) multiplied by the daily producion of a copepodite $P\mathrm{c}$ shows the biomass increase "y" of an average class 2 individual from its transformation into a larva of the next stage until the end of the period of investigation (Fig. 4):

$$ty \cdot P\mathrm{c}=y \tag{13}$$

The sum of values rendered by (10) and (13) defines the production of an average class 2 individual "b" during the whole period T:

$$x+y=P\bar{\mathrm{n}}\mathrm{Cl}_2T \tag{14}$$

The value obtained from (14) and the estimated number of individuals in class 2 ought to be substituted for the respective symbols in formula (9).

The weight of an average class 2 individuals is close to the biomass value situated in the middle between points a and c on the graph in Fig. 4, which define the production during T of the smallest individual belonging to class 2. Thus we can assume that an average class 2 individual will be transformed into a copepodite after the lapse of the half of the period T. Its biomass increase before transformation would thus be equal to the half of the biomass increase (during the whole period T) of a nauplius, and after transformation it will be equal to the half of the biomass increase of a copepodite during the considered period.

This reasoning allows to deduce the formula for estimation of production of class 2 individuals in which the calculations from (10) to (14) can be eliminated:

$$\frac{PnT}{2} + \frac{PcT}{2} \cdot NnCl_2 \tag{15}$$

The sum of the values rendered by formulas (8) and (15) is the value of production of all the nauplii during the period T.

PRODUCTION OF INDIVIDUALS IN THE COPEPODITE STAGE

Production of the copepodites ought to be the sum of biomass increases of individuals which will continue their growth during the whole period T (class 1) and of those which will attain sexual maturity (and thus will stop to grow) before the lapse of T (class 2).

The weight of an individual "a" dividing the population into the two classes is obtained by subtracting the production of a copepodite during the period T from the biomass of an average adult individual 'c" (Fig. 5):

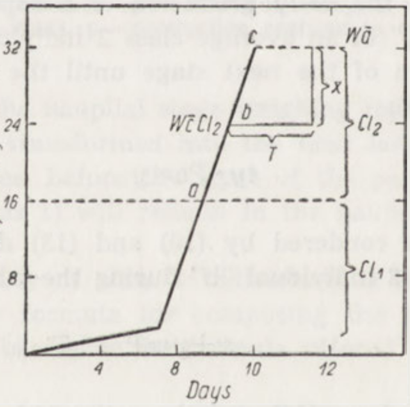

Fig. 5. Production (x) during T of an average weight class 2 copepodite ($W\bar{c}\ Cl_2$) attaining sexual maturity before the lapse of T

$$c - PcT = a \tag{16}$$

The estimated numbers of individual in both classes are substituted for terms of the respective formulas, i.e. the number of animals in class 1 is introduced into the formula defining the production of individuals which continue their growth until the end of the period T:

$$PcT \cdot NnCl_1 \tag{17}$$

where Pc stands for the daily production of a copepodite estimated according to the formula of Winberg et al. (1965), T — the period between two samplings, $NnCl_1$ — the number of individuals in class 1, while the number of individuals in class 2 is introduced into the formula defining the production of copepodites which will attain sexual maturity before the lapse of T:

$$P\bar{c}Cl_2T \cdot NcCl_2 \tag{18}$$

$P\bar{c}Cl_2T \cdot NcCl_2$ symbolizes the biomass increase X of an average class 2 individual during the period T, obtained as the difference between the weight of an average adult individual "c" and the weight of an average class 2 individual "b" (Fig. 5).

Assuming that similarly as in the nauplial stage the weight of an average class 2 individual approximates the biomass value placed on the graph in Fig. 5 in the middle between points a, c, the formula for computing the production of class 2 individuals assumes the form:

$$\frac{PcT}{2} \cdot NcCl_2 \tag{19}$$

The sum of the values rendered by formulas (17) and (19) is the production of all the animals in the copepodite stage during the period T.

In its final version, the formula for estimation of the production of the whole Cyclopidae population during the period T, consists of formulas (1), (7), (8), (15), (17), (19) as its elements.

$$P_{WT} = \left[\left(\frac{Ne \cdot We}{De}\right) \cdot T + \left(\frac{PnT \cdot T}{2}\right) \cdot \frac{Ne}{De}\right] + \left[PnT \cdot NnCl_1 + \left(\frac{PnT}{2} + \frac{PcT}{2}\right) \cdot \right.$$

$$\left. \cdot NnCl_2 \right] + \left[PcT \cdot NcCl_1 + \frac{PcT}{2} \cdot NcCl_2\right] \tag{20}$$

4. DISCUSSION

Production values for eggs and nauplii as computed by means of formula (20) deduced in the present work is higher from those obtained by means of the formula offered in Winberg et al. (1965), while for the copepodite stage the present method gave a lower value.

The formula offered here can be fairly easily handled if a certain sequence of operations is observed. At first, daily production values for individuals in each phase of development must be computed by means of Winberg et al. (1965) formula. The most difficult phase is the estimation of the number of individuals in the several classes (for it is a new operation, not described in extant literature), but it will not be very troublesome if the researcher who applies the present method will have elaborated for himself a table of biomasses corresponding to the lengths of individuals.

After slight modifications, the offered formula can be applied for estimating the production of Cladocera:

$$P_{WT}=\left[\left(\frac{Ne\cdot We}{De}\right)\cdot T+\left(\frac{PjT\cdot T}{2}\right)\cdot\frac{Ne}{De}\right]+\left[PjT\cdot NjCl_1+\left(\frac{PjT}{2}+\frac{PaT}{2}\right)\cdot\right.$$

$$\left.\cdot NjCl_2\right]+\left[\left(\frac{W\bar{a}\cdot W_0a}{D\bar{a}}\cdot Na\right)\cdot T\right] \tag{21}$$

PjT, PaT stand for biomass increases (during the period T) of a single individual of the juvenile (j) and adult (a) forms of Cladocera; W_0a represents the weight of the smallest adult individual; Na symbolizes the number of adult animals and $D\bar{a}$ the period of development of an average adult individual computed by means of the formula offered in Hillbricht-Ilkowska, Węgleńska (1970).

The value of production computed by means of formula (21) will be higher for eggs, lower for juvenile forms, and equal for adult animals than the respective values obtained by application of the formulas (Winberg et al. 1965, Hillbricht-Ilkowska, Patalas 1967). This can be explained by a different shape of the curve of development than in the case of Copepoda, and by the fact that adult Cladocera continue to grow, though at a slower rate than in the earlier stages.

The validity of production estimation is importantly influenced by the length of the period T for which production is computed. Most authors are of the opinion that the period between two samplings should not exceed the time of the nauplial stage (for Copepoda) or the period of development of the juvenile form (for Cladocera). If T is shorter than the periods of development of those forms, the populations of the investigated stages must be divided into two classes. If T is equal or slightly longer than Dn or Dj, all individuals in these stages will belong to class 2, and thus formula (8) can be left out. If T is much longer than Dn or Dj, estimation of production will be complicated or even impossible, since some individuals hatched from eggs will be transformed into copepodites (in case of Copepoda) or into the adult form (in case of Cladocera). Not only computations will thereby be made more complex, but a huge error will be introduced by mortality of animals.

5. SUMMARY

Familiar formulas of Winberg et al. (1965) and Hillbricht-Ilkowska, Patalas (1967) have been modified in order to arrive at a more precise estimation of the net production of plankton crustaceans. The modifications account for the changes in biomass increases of animals hatching from eggs or transformed into the next stage of development before the lapse of the period *T* during which production is estimated. In order to apply the modified formulas, an investigated population must be divided into small classes of size, and the number of individuals in each class must be estimated. Such a classification is helpful in determining the number of larvae which remain unchanged or are transformed into the next stage of development during the period *T*. Formula (20) serves for estimation of Copepoda production, and (21) for Cladocera.

6. STRESZCZENIE

W celu dokładniejszej oceny produkcji netto skorupiaków planktonowych, zmodyfikowano znane z literatury wzory Winberga et al. (1965) i Hillbricht-Ilkowskiej, Patalasa (1967). Modyfikacje te dotyczą uwzględnienia zmian przyrostów biomasy zwierząt wylęgających się z jaj, lub po przeobrażeniu się przechodzących przed upływem czasu *T* (za który jest oceniana produkcja) do następnego stadium larwalnego. W celu posługiwania się zmodyfikowanymi wzorami należy badaną populację podzielić na małe klasy pod względem wielkości osobników i określić liczebność zwierząt w każdej z nich. Podział ten jest pomocny do oznaczania liczebności larw pozostających (w okresie *T*) i przechodzących do następnego stadium rozwojowego. Do oceny produkcji Copepoda służy wzór (20), Cladocera — (21).

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PRODUCTION OF CRUSTACEAN ZOOPLANKTON IN MOTY BAY, LAKE JEZIORAK. PART II. ESTIMATION OF PRODUCTION OF THE PREDOMINATING SPECIES

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ABSTRACT

Crustacean zooplankton production was estimated during five months (May 2—November 7, 1969) in a shallow and slightly eutrophized Bay Moty, Lake Jeziorak. Production was computed by two methods: Winberg et al. (1965), and Winberg's method modified by Zawiślak (1972). The modified method gave higher values of production of the investigated species.

1. INTRODUCTION

Zooplankton constitutes a specific group of animals, providing the link between the trophic levels of producers (phytoplankton) with the successive levels of consumers. Exact assessment of the production of this group of animals is a step towards the knowledge of the energetic balance of water reservoirs. There are several methods now in use for estimating the zooplankton biomass increase. In Zawiślak (1972), the method of Winberg et al. (1965) for computing the crustacean zooplankton production was modified. The modification allows to compute biomass increases of animals hatching from eggs, transformed into the successive larval stage, or attaining maturity before the lapse of the period of investigation. The aim of the present work is to compare the values of production as obtained by the method of Winberg et al. (1965) and by its modified version, and to judge the degree of usefulness of the latter for estimation of production.

2. TERRAIN DESCRIPTION, MATERIAL AND METHODS

Moty is a shallow (depth up to 1.5 m) and eutrophized bay in the southern part of Lake Jeziorak. It has a well developed coastal line; about 67 species of plants grow in its littoral zone (Bohr 1965). In this part of the reservoir zooplankton consists of an abundant variety of species. On some stations, amounts of individuals were several times greater than the quantities of plankters caught in other zones of the lake (Zawiślak, Bittel in print).

The material for the present work was sampled at 7 days intervals in spring, and at 10 days intervals in autumn. Plankton was drawn on 4 stations, 1.5 m of depth each, arranged along the bay.

On each station water was sampled from the surface and from 0.3, 0.6, 0.9 and 1.2 m with a 5 l dipper (described in Patalas 1954), 25 l in total.

Since there is no stratification in the bay, the material filtered out (gauze No. 25; 74 threads/cm) of 100 l of water from the four stations was poured together and, according with the suggestions of Hillbricht-Ilkowska, Patalas (1967) it was handled as an uniform sample. A part (one tenth) of each fixed sample was surveyed under a microscope to determine the length and species indentity of animals. Individuals in each species population were divided into small classes of body length at 25 μ intervals. The number of animals in each class was determined. Then the lengths were translated into body weights employing the formulas of Pechen (1965) for Bosmina and Daphnia, and those of Klekowski, Shushkina (1966) for Copepoda, and their developmental stages.

Water temperatures were gauged during the whole period of investigations to determine the averages for the several intervals between the samplings. It allowed to define the times of development of the particular stages for various species. The set of graphs from Hillbricht-Ilkowska, Patalas (1967) were used.

6 months production (from May 5 to September 7, 1969) at the temperature of water equal to or higher than 10°C was determined for the predominating species. Production was estimated by means of the modification of Winberg formulas elaborated by the present author (Zawiślak 1972), and for comparison, by means of the original formulas (Winberg et al. 1965; Hillbricht-Ilkowska, Patalas 1967). The production for 6 months was the sum of biomass increases during short, 7 or 10 days intervals. Since there were large differences in the amounts of eggs (particularly in Cladocera) in the consecutive samples, average quantities from two succeeding samples were introduced into the formulas, thereby eliminating the spurious jumps in the fertility of females.

3. RESULTS

Among the identified species the following predominated in quantity: *Mesocyclops leuckarti, M. (Th.) oithonoides,* of the Cyclopidae; *Daph-*

Table I. Production (g/m^3) of Cyclopidae during 6 months calculated by the author's modification of Winberg's formulas. Successive maximal values of production of the several stages are shown within the frames

Date	Stage			Total
	eggs	nauplii	copepodits	
May 2	0.03	0.10	0.26	0.39
May 9	0.10	0.29	1.46	1.85
May 16	0.09	0.39	2.88	3.37
May 23	0.06	0.48	3.94	4.48
May 29	0.11	0.33	.63	4.08
June 6	0.07	0.22	4.94	5.21
June 13	0.17	0.17	3.75	4.09
June 20	0.70	0.96	2.02	3.69
June 27	0.74	1.28	1.92	3.96
July 5	0.07	0.79	1.19	2.05
July 11	0.08	1.62	2.19	3.89
July 18	0.10	1.69	2.67	4.46
July 25	0.04	0.33	1.24	1.61
July 31	0.14	0.76	1.12	1.91
August 8	0.17	0.68	1.30	2.15
August 15	0.20	0.93	1.07	2.19
August 22	0.48	2.03	0.90	3.41
September 1	0.21	1.09	1.34	2.64
September 11	0.10	1.58	2.19	3.87
September 22	0.05	0.37	2.70	3.12
September 30	0.01	0.12	2.43	2.56
October 9	0.01	0.05	2.11	2.17
October 18	0.01	0.05	1.70	1.71
Total	3.75	16.31	49.27	69.33

nia cucullata, *Bosmina longirostris* and *B. coregoni* among the Cladocera. The total biomass of individuals of those species made up 95–100% of the whole crustacean zooplankton biomass in each sample. As the data concerning the periods of individual development and the relation of length to biomass were identical for all the Cyclopidae, while species identification of juvenile forms was difficult, the production of this group of animals was estimated jointly (Table I).

The investigation of the changes in production of the several development stages allowed to distinguish three periods of regeneration of the Cyclopidae population (Table I). In each of the periods, two phases of development were discerned: (1) initial growth, marked by the highest production of biomass by eggs and nauplii, (2) stabilization and ageing of the population, marked by a decrease of its production.

In one of these periods (May 9 to June 13) the first phase was less distinct; the development seemed to start from the stages of nauplii and the smallest copepodites which have survived the winter. Actually, then, the development had started in the preceding autumn and continued during the winter. In general, the production of Cyclopidae was fairly uniform during the whole period of investigation.

Table II. Production (g/m^3) of Cladocera during 6 months calculated by the author's modification of Winberg's formula. Successive maximal values of production of the several species are shown within the frames

Date	Species			Total
	D. cucullata	*B. coregoni*	*B. longirostris*	
May 2	—	—	0.10	0.10
May 9	—	—	1.47	1.47
May 16	0.35	0.11	7.97	8.43
May 23	0.67	0.41	9.10	10.18
May 29	2.12	0.55	7.45	10.13
June 6	1.77	0.36	6.36	8.49
June 13	2.15	0.39	0.18	2.73
June 20	3.12	0.24	0.21	3.57
June 27	4.29	0.14	0.38	4.81
July 5	0.67	0.06	0.23	0.95
July 11	0.40	0.10	0.16	0.66
July 18	0.39	0.12	0.36	0.86
July 25	0.19	0.09	0.37	0.65
July 31	0.48	0.23	1.42	2.12
August 8	0.62	0.40	1.52	2.54
August 15	0.44	0.48	0.78	1.70
August 22	1.42	0.72	0.87	3.01
September 1	1.09	0.34	0.05	1.47
September 11	0.43	0.16	0.02	0.60
September 22	0.46	0.09	0.02	0.57
September 30	0.57	0.08	0.01	0.66
October 9	0.19	0.08	0.01	0.28
October 18	0.19	0.08	0.02	0.29
October 28	0.23	0.08	0.01	0.30
Total	20.22	5.20	39.05	64.47

In opposition to Cyclopidae, the production of Cladocera was diversified (Table II).

Two periods of sudden increase of production were recerded: in May-June and in August, which gave 75 and 15% of the total biomass increase respectively, for the whole season of vegetation. Maximal biomass increases of the particular species of Cladocera (Table II) were observed at various periods and they were separated by periods of decrease in production of equal length. It was remarkable that the maxima occurred in periods directly preceding the highest individual daily increases of biomass in the several species (June 20–July 5 and August 22–September 22).

In sum, the production of Cyclopidae and Cladocera for six months was estimated by means of the modified method as 134 g/m^3, i.e. 69.3 and 64.5 g/m^3 respectively. These values were higher than the values obtained by the original method (Winberg et al. 1965). Differences in production of the particular development stages of Cyclopidae are shown in Fig. 1, where the values obtained by means of the Winberg et al. (1965) formula are represented by the straight horizontal line.

The application of the modified formulas gave higher values of production for eggs and nauplii and lower values for copepodites during the whole period of investigation. Production values for the whole population (Fig. 1) were at different periods either lower or higher than those obtained by Winberg et al. (1965) method. The graph is a good illus-

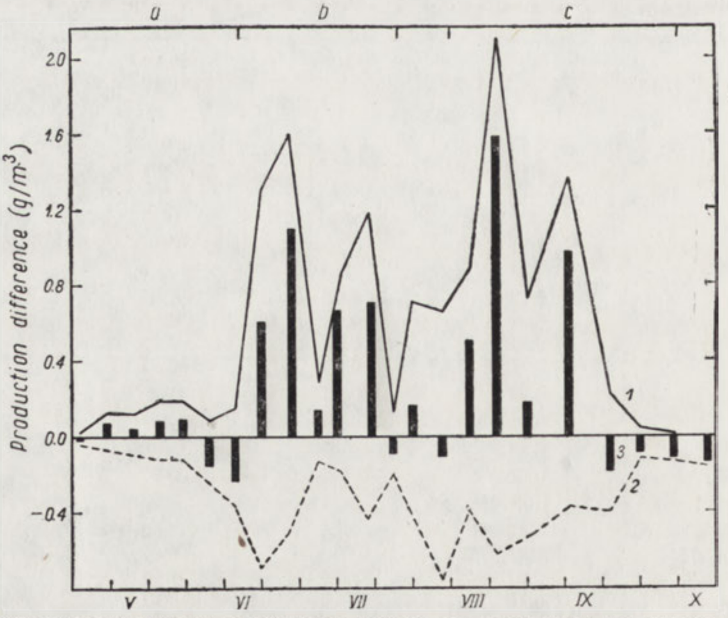

Fig. 1. Differences between production values as computed by means of Winberg's formulas (0 level) and by the author's modification of these formulas. 1 — eggs and nauplii, 2 — copepodites, 3 — the total production. a, b, c — periods of regeneration of the population

tration of how great influence is exerted upon production by an actual state of development of the investigated population. In the phase of growth and stabilization the modified method gave higher values, and in the phase of ageing it gave lower ones than those obtained by the method of Winberg et al. (1965). Figure 1 (the stakes) exactly reflects the phases of development in the three periods of regeneration of the population (Fig. 1 — a, b, c), mentioned above when Table I was discussed. In the period "a", ending on June 13, only the second and third phase were present; the first one had occurred in winter, as we have already remarked.

The value of production of Cladocera (64.5 g/m^3) as computed by means of the modified formulas was higher than that obtained by the method of Winberg et al. (1965).

Similarly as in the case of Cyclopidae, the differences in production of the several stages and of the population as a whole emphasize the influence of the development stages upon the value of production.

Table III. Production of the predominating species as calculated by the two methods. The value given by the method of Winberg et al. (1965) is assumed as 100%

Species	Method		Difference	
	by the author	by Winberg	g/m^3	%
Cyclopidae	69.330	63.812	5.518	8.7
B. longirostris	39.049	30.176	8.873	29.4
B. coregoni	5.204	3.652	1.552	42.5
D. cucullata	20.222	10.943	9.279	85.1
Total	133.805	108.583	25.222	23.2

In Table III the values of production for the whole season, obtained by the modified and by the original method of Winberg et al. (1965), are juxtaposed for comparison.

The percentages of differences between those values for the several species varied from 9% for Cyclopidae to 85% for *Daphnia cucullata*. For the whole of crustacean zooplankton the value of production obtained by means of the modified method was 23% higher.

Table IV. The shares of developmental stages in total production of species populations (%), according with the two methods

Species	Eggs		Juvenile Cladocera, nauplii		Adult Cladocera, copepodites	
	acc. to the author	acc. to Winberg	acc. to the author	acc. to Winberg	acc. to the author	acc. to Winberg
D. cucullata	65.0	29.3	20.7	44.6	14.3	26.1
B. coregoni	73.0	52.1	17.0	33.7	10.0	14.2
B. longirostris	74.0	60.8	16.3	27.0	9.7	12.2
Cyclopidae	5.4	0.6	23.3	10.3	71.3	89.1

The ratio of average daily production of young individuals to average daily production of maturing ones was very low (0.1) for Cyclopidae and high for Cladocera, it was 1.3 for *Daphnia cucullata,* 1.9 for *Bosmina coregoni* and 2.2 for *B. longirostris.* It was this ratio which was decisive for the percentage contribution of the several development stages to the total production of a species population (Table IV).

Since the rate of mortality is lower for younger animals, it seems that the computed value of production for Cladocera is more close to reality than in the case of Cyclopidae. The pattern of results in Table IV clearly suggests that the percentage share of eggs in the total production of a population increases for the species in which females lay bigger eggs in relation to the size of their bodies. Of course, fertility of females plays an important role here.

As the *P/B* coefficient and the turnover rate of biomass can be easily translated into each other, only the T_B was computed (Table V).

Table V. Turnover rate of biomass (days), calculated by the two methods. a — medium for the whole season, b — the ranges of oscillations during the season

Method		*D. cucullata*	*B. coregoni*	*B. longirostris*	Cyclopidae
By the author	a	4.1	5.2	6.6	7.2
	b	1.6–12.3	1.7–11.9	0.6–19.8	2.4–23.7
By Winberg	a	7.3	7.2	8.1	7.2
	b	3.2–19.6	3.2–14.7	1.4–22.4	2.9–22.4

Medium turnover rates of biomass as computed from production values estimated by Winberg et al. (1965) method were, for all the

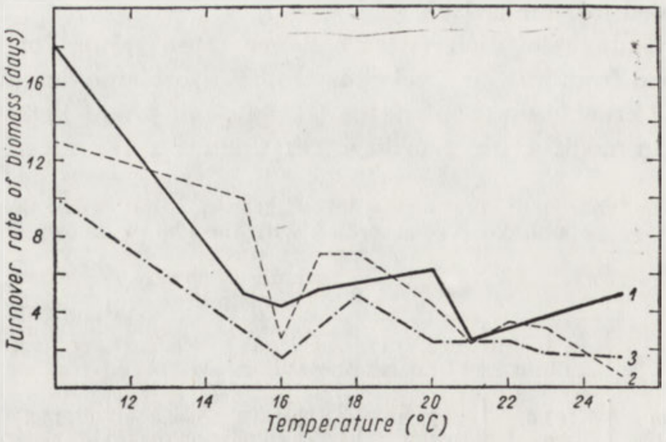

Fig. 2. Turnover rates of biomass as dependent on water temperature (in °C). 1 — Cyclopidae, 2 — *Bosmina longirostris,* 3 — *Daphnia cucullata*

species of Cladocera, equal or longer than the turnover rate of biomass for Cyclopidae.

It was interesting to trace the influence of water temperature upon the turnover rate of biomass (Fig. 2).

Shapes of the curves in Fig. 2 suggest that there were two points of optimal development for all the species of animals, i.e. at 16 and 21°C.

In Zawiślak (1972) it was pointed out that the stage of development of a population influences the validity of production estimations. Obviously, production values should reflect the course of development of an investigated population. An increase of production of young individuals is an evidence of growth of the population, while its decrease accompanied by an increase in production of adult forms reflects a transition of the population to the phase of ageing.

Figure 3 presents the ratio of production values of eggs and nauplii to production values of copepodites as computed by the original method (Winberg et al. 1965) and by the modified one. Each method gave a curve of development different in shape, particularly with respect to the initial and maximal phases of growth.

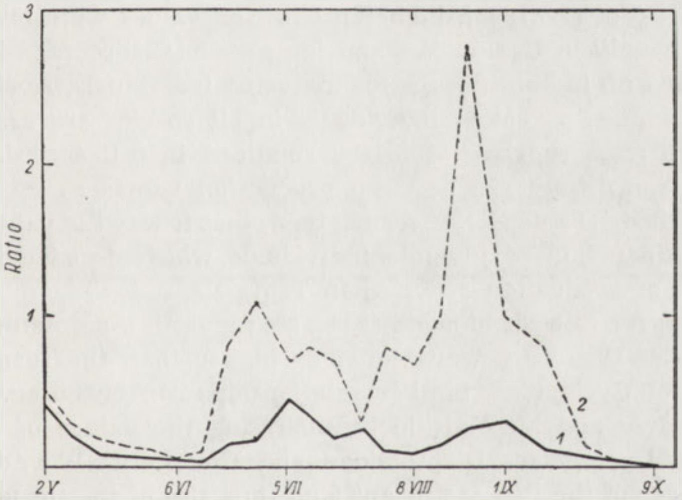

Fig. 3. The relation of eggs and nauplii production to copepodites production, calculated from production values as given by 1 — Winberg's formulas, 2 — the present author's modification

4. DISCUSSION

The production of crustacean zooplankton computed for 6 months as 134 g/m³ was fairly high. Winberg et al. (1965) estimated the production in an eutrophic Lake Batorin as 113.4 g/m³ during 5 months.

Warda (1968) obtained the result of 18.4 g/m^3 in Lake Mikołajskie for July and August; Hillbricht-Ilkowska, Węgleńska (1970) reported 22 g/m^3 during 40 days in Lake Mikołajskie.

Our results recomputed to 1 m^2 basis are close to those reported in literature. We obtained 201 g/m^3. Hillbricht-Ilkowska et al. (1966) estimated the production of Lake Mikołajskie as 296 g/m^2 and of Lake Tałtowisko as 198 g/m^2 (including Rotatoria production) during the whole vegetation season. Warda (1968) estimated the increase of zooplankton biomass in Lake Mikołajskie during two months (July–August) as 174 g/m^2.

It is difficult to explain fully the large range in percentage differences of production values as estimated by the two methods (Table III). The shapes of the curves of development for Cladocera and Copepoda are essentially different. In Cladocera, the highest daily biomass increases are observed in juvenile individuals, while in Copepoda the most efficient producers are copepodites. In comparison with the method of Winberg et al. (1965), higher production values were obtained for eggs [1] and nauplii in Cyclopidae, and for eggs in Cladocera, while lower values turned up in both groups for maturing individuals. Average daily production values of young individuals in all species are arranged (in a succession from the largest to the smallest) in full accordance with the percentage differences between production values as estimated by the two methods (Table III). It seems, then, that it was the value of average daily production of juvenile individuals which decisive influenced the pattern of production reported in Table III.

The turnover rates of biomass (Winberg et al. 1965 method) for all the species of Cladocera were equal or higher than the turnover rate of biomass of Cyclopidae. Similar relationships can be observed in the lakes Śniardwy and Mikołajskie by analysing the values of P/B coefficients for Cyclopidae, Diaptomidae and Cladocera (Warda 1968). Similar values of the P/B coefficient (and thus also of the turnover rates) for Cyclopidae and *Daphnia cucullata* were reported by Winberg et al. (1965) for the lakes Batorin and Miastro.

The long period individual development of Cladocera in comparison with Cyclopidae and the low daily production of their juvenile stages would rather suggest that the turnover rate of this group of animals is likely to be longer than in Cladocera. Such a pattern was obtained in the present research by means of the modified method only (Table V).

Turnover rates of biomass of all the investigated animals, and of Cyclopidae in particular, oscillated during the vegetation season (figures in brackets, Table V).

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[1] Biomass increases of individuals hatched from eggs before the lapse of the period T were considered as biomass produced by eggs (Zawiślak 1972).

Measurements continued during the whole vegetation season proved that the body of *Mesocyclops leuckarti* contracted as water temperature increased (up to 1/4 of its maximal length).

If recomputed to biomass, this gives almost double decrease. Elbourn (1966) observed a contraction of the body of *Cyclops strenuus strenuus* by 1/5 from January to August, when water temperature increased by 20°C. Similar observations on Copepoda of the Black Sea are reported by Kovalev (1964). Seasonal changes in length and biomass of the body of individuals, while weights of eggs almost do not change, make up a favourable situation for a relative (in relation to the initial biomass) increase of production of the Cyclopidae population, and thereby for a shortening of the turnover rate of biomass.

It can be seen from the pattern of the curves in Fig. 2 that there were two optimal periods of development for each of the species. Among Cyclopidae the predominating species were *Mesocyclops leuckarti* and *M. (Th.) oithonoides*. Both were found during the whole research season, but the former predominated when water was cooler, and the latter when it was warmer. Different periods of quantitative predomination of each of these species, and thereby of their production, made the turnover rates of biomass shorter; the effect is visible in Fig. 2. *Bosmina longirostris* occurred in a few forms which formed their optimal conditions of development at different water temperatures. On the other hand, *Daphnia cucullata* showed the greatest changeability of its shape (cyclomorphosis), closely dependent on temperatures of water. As it seems, such changes of Cladocera highly influenced the oscillations in duration of the turnover rate.

5. SUMMARY

Crustacean zooplankton production was estimated by two methods, of Winberg et al. (1965), and by Winberg's method modified by the present author, for short, 7 to 10 days, periods from May 2 to November 7, 1969. Production amounted to 133.8 g/m^3, 64.5 g/m^3 for Cladocera and 69.3 g/m^3 for Cyclopidae according to the modified method (Table III). These values were higher by 23% from those computed by Winberg et al. (1965) formulas.

For all the predominating species the modified method brought higher values (Table III). The differences were 8.7% for Cyclopidae, 29.4% for *Bosmina longirostris*, 42.5% for *B. coregoni*, and 85% for *Daphnia cucullata*.

Medium turnover rate of biomass was estimated as 4.1 day for *B. cucullata*, 5.2 days for *B. coregoni*, 6.6 days for *B. longirostris* and 7.2 days for Cladocera (Table V).

6. STRESZCZENIE

Metodami Winberga et al. (1965) i modyfikacją autora metody Winberga obliczono produkcję zooplanktonu skorupiakowego dla krótkich 7–10 dniowych odcinków czasu w okresie od 2 maja do 7 listopada 1969 r. Za cały okres badań wynosiła ona 133,8 g/m^2, z czego na Cladocera i Cyclopidae wypadło odpowiednio 64,5 i 69,3 g/m^3 (Tab. III). Były to wartości wyższe o 23,2% od wyliczonych

przy pomocy wzorów Winberga et al. (1965). Dla wszystkich gatunków dominujących wyższe wartości produkcji uzyskano metodą zmodyfikowaną (Tab. III). Różnice w wartościach produkcji wynosiły dla Cyclopidae 8,7% *Bosmina longirostris* 29,4%, *B. coregoni* 42,5% i *Daphnia cucullata* 85%. Średni turnover biomasy oceniono na 4,1 dnia dla *D. cucullata*, 5,2 — *B. coregoni*, 6,6 — *B. longirostris* i 7,2 dla Cyclopidae (Tab. V).

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SEDIMENTATION OF SUSPENDED MATTER BY *DREISSENA POLYMORPHA* PALLAS AND ITS SUBSEQUENT UTILIZATION BY CHIRONOMIDAE LARVAE

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ABSTRACT

During the summer months in the Uchinskoye water reservoir *D. polymorpha* Pallas excretes 48.8 tons dry weight per day of the agglutinated seston in the form of faeces and pseudofaeces. The possibility of utilization of this matter by Chironomidae larvae (*Endochironomus albipennis* Mg. and *Chironomus anthracinus* Zett.) was experimentally investigated. The newly born larvae were kept till the 3rd instar on various food which was agglutinated or not by *D. polymorpha*, such as natural suspended matter, mud, detritus originating from *Potamogeton sp.* Pseudofaeces of *D. polymorpha* are more rich in bacteria than the original seston. The suspended matter agglutinated by *D. polymorpha* was the most valuable food source for Chironomidae larvae.

1. INTRODUCTION

The significance of filtrators in the complicated processes of the self-purification of water bodies is commonly known. However, in order to evaluate the significance of particular species in the suspended matter sedimentation process (detritus [1], phyto and zooplankton), and its further transformation, the quantitative approach to these processes is necessary. The experiments to estimate the significance of *D. polymorpha* for the seston sedimentation in the Uchinskoye water reservoir were carried out in 1968—1969. The possibility of further utilization of the suspended matter sedimented by molluscs was investigated in experiments with the Chironomidae larvae: *Endochironomus albipennis* Mg. — littoral species, and *Chironomus anthracinus* Zett — abundant profundal species.

2. MATERIALS AND METHODS

D. polymorpha is the most effective filtrator in the Uchinskoye water reservoir. Its population covers about 40% of the reservoir area at the depth from 1.5 to 8 m. The average biomass in this zone is about 500 g/m², and numbers about 1000 individuals per square metre. The greatest density of these molluscs was at the depth 2–3.5 m, where the free divers found a wide belt of great clumps of *D. polymorpha*, spreading below the zone occupied by macrophytes. The zone of

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[1] By detritus we understand the mineral and organic substances (organic detritus) and microorganisms inhabiting them. This meaning of the term "detritus" was established during the seminar on detritus and its significance in the production processes in water bodies (Sushchenya 1968).

submerged macrophytes occupies about 150 ha of the reservoir bottom surface. The majority of the *D. polymorpha* larvae settle on these macrophytes, which serve as a substratum. The number of settling larvae varies in different years as e.g. in 1966 in the spawning period 1 m^3 contained 30,000 ind., and in 1967 — up to 150,000. After the larvae settlement they grow quickly and measure about 17 mm at the end of the vegetation season. The quantity of detritus and plankton transformed by *D. polymorpha* and sedimented in the form of faeces and pseudofaeces was calculated on the basis of experiments carried out directly in the reservoir. The experimental methods of Mikheev (1967) with some modifications were applied. The experiments were carried out in the funnels of a surface 0.01 m^2, joined with the test tubes by rubber tubings. The funnels contained polystyrol nets, where the animals were placed. These experimental chambers were lowered to the near bottom water layer in the zone most numerously inhabited by *D. polymorpha*, i.e. to the depth 1.5–2.0 m. A total of 15 series of experiments were made. Each series contained 10 funnels with molluscs and 2 control ones to estimate the quantity of the sedimenting suspended matter. Five to twenty individuals of *D. polymorpha* of the same size were placed in each funnel. The sedimented matter was collected once a day and then weighed after drying to constant weight at 105°C.

The filtration rate of *D. polymorpha* was estimated in the laboratory conditions at 20°C on the basis of changes of the suspended matter quantity at the beginning and at the end of the experiment. The clay suspension was used in these experiments. The continously stirred suspension passed through a glass tube with molluscs to the other container below the previous one. The molluscs were weighed, measured, and the filtration rate and the relative filtration rate per one gramme wet weight of mollusc were estimated (Lvova-Katchanova 1971).

The experiments which allowed to determine the nutritive value of pseudofaeces for the Chironomidae larvae were carried out in the laboratory. In the experiments lasting for 20 to 50 days the development of Chironomidae larvae was being observed from their hatching moment to the 3rd instar at the temperature 17–21°C. The larvae were divided into groups of 10–20 individuals placed in dishes of a diameter 60 mm, filled with the already filtered water. The pseudofaeces of *D. polymorpha* were added there as the food: 1 — these from the natural suspended matter of reservoir water, 2 — from the mud collected at the depth where the larvae inhabited, 3 — from the previously dried and milled *Potamogeton perfoliatus* L. or *P. pectinatus* L. The control groups of larvae were kept on the same food but not agglutinated by *D. polymorpha*. Apart from that the larvae were kept in the filtered water of the Uchinskoye water reservoir without extra food or with yeast suspension added every day. Daily observations were carried out. The nutritive value of food was estimated on the basis of larvae survival, their behaviour, the growth rate, and the time between moultings. Each experimental variant was repeated three times. The number of bacteria was estimated by direct counting.

Changes in the assimilation degree of Potamogeton detritus and its agglutinates, depending on the detritus decomposition degree, were studied by the radiocarbon method (Sorokin 1966, 1968) on *C. anthracinus* larvae in the 4th instar. For this purpose *Potamogeton pectinatus* L. was marked with ^{14}C and dried. Before the experiment Potamogeton was covered with water, milled in a mortar, and then half of it was agglutinated by *D. polymorpha*, while the other half was not. The intensity of food assimilation (the ratio of the assimilated food to the weight of larvae) by larvae was estimated during 8 days. The larvae were placed in both kinds of food every day for 12 hr, then for 6 to 6.5 hr in the not-marked food. Afterwards the larvae were homogenized and mounted on microscopic slides. The homogenate was equally arranged on the circle of a diameter 20 mm. This circle was drawn on 1/3 of the microscopic slide with a wax pencil. Radioactivity was estimated with the help of the end window counter of a window diameter 25 mm.

3. RESULTS AND DISCUSSION

The calculations allowed to estimate the possible effect of filtration by *D. polymorpha* population in the Uchinskoye water reservoir. It was calculated on the basis of the laboratory experiments that during the summer months at the temperature 20°C the average rate of filtration per 1 g wet weight of mollusc is 40 ml/hr. This allows to say that on 1 m^2

of bottom surface the molluscs filtrate during 24 hr 0.48 m^3 of water (40 ml/g · hr · 500 g/m^2 · 24 hr), and the whole population of *D. polymorpha* about 3 milions m^3 which is 1/50 part of the volume of the whole reservoir. The *D. polymorpha* filtration in other reservoirs is also high. Stańczykowska (1968) calculated the time necessary for the *D. polymorpha* population to filtrate the whole volume of epilimnion. This time for various Mazurian lakes was found to vary from 2 days to 2000 days (with the average rate of filtration 35 ml/hr/g wet weight of mollusc). Mikheev (1967) calculated that in the Pjalovskoye water reservoir *D. polymorpha* filtrates during one day 1/20 part of the whole reservoir.

All these calculations give only the idea of the order of magnitude of the discussed phenomenon and they cannot be applied to estimate the quantity of sedimenting suspended matter, as *D. polymorpha* filtrates only the near-to-bottom water layer. Depending on the hydrological conditions in the reservoir and on the density of *D. polymorpha* population the same volume of water can be filtered various number of times. The water passing through the gill apparatus of *D. polymorpha* is almost absolutely deprived of the suspended matter. It was found that in the water from the Uchinskoye water reservoir filtered by *D. polymorpha* 2.2 to 2.4 mg/l of the suspended matter is left (estimated on the Beilis's turbidity-meter, model of Rublev Station of Moscow pipe-line system), which cannot be sedimented by molluscs even after repeated passages through their gill apparatus.

During the filtration the water is sucked into the mantle cavity of zebra mussel by the inhalant siphon, the tentacles of which act as a preliminary filter[2]. The particular of detritus and plankton brought in by the water current are surrounded by mucus excreted by the cells of gill apparatus and agglutinated. The particles of this suspension move along the gill lobes in the direction of the mouth opening, where a food portion is formed. Part of the filtered detritus gets into the alimentary canal and is digested. The not assimilated parts (faeces) in the form of 2 cm long filaments surrounded by mucus leave the mantel cavity through the exhalant siphon and they sediment on the bottom. Part of the suspended matter which does not get into the alimentary canal passes into the back part of the mollusc mantel cavity where it forms larger particles surrounded with mucus, and is thrown out from the cavity through the inhalant siphon and settles also on the bottom. These are the so-called agglutinates or pseudofaeces.

The data obtained by the applied funnel method allow to calculate the average quantity of the suspended matter which sediments in the

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[2] The detailed description of the gill apparatus, filtration process, feeding mechanisms and the excretion from the mantle cavity of *D. polymorpha* can be found in Yonge, Campbell (1968) and Morton (1969).

reservoir due to the activity of *D. polymorpha*. The results can be expressed per various size groups of zebra mussel, in mg/ind. or in mg/g wet weight of mulluscs. For *D. polymorpha* individuals weighing from 0.025 to 3.700 g, 5–32 mm long, the weight of the filtered suspended matter is from 2 to 400 mg per individual, or from 80 to 1 mg/g wet weight of mollusc at 17–21°C. When calculating these data for the average biomass of *D. polymorpha* in its habitat it was found that these molluscs filtered 7 g dry weight of the suspended matter per m^2. The agglutinated suspended matter is gradually transported to greater depths. Assuming that it spreads evenly at the bottom of the reservoir, *D. polymorpha* sediments 2.5 g dry weight/m^2, and 48.8 t in the whole reservoir.

The suspended matter sedimented by *D. polymorpha* is utilized by the Chironomidae larvae and by other organisms.

The growth of Chironomidae larvae from their hatching to the 3rd instar, kept on food agglutinated by *D. polymorpha* or not agglutinated, allowed to determine the nutritive value of pseudofaeces.

The experiments showed that for the Chironomidae larvae the most valuable food are the agglutinates (pseudofaeces) of the natural suspended matter. The agglutinates of milled Potamogeton were also well assimilated. The larvae fed on this food had a quicker growth and the percentage of surviving larvae was higher (Table I, II). Apart from the younger stages of Chironomidae larvae also the *E. albipennis* larvae in the 4th instar were kept on this food. During the experiment the num-

Table I. The growth and development of *Chironomus anthracinus* Zett. larvae fed with varius foods

Date	Food														
	Natural suspended matter in the reservoir water			*D. polymorpha* pseudofaeces from natural suspended matter			The mud of the reservoir bottom			Filtered reservoir water			Filtered water+yeast		
	I	$\bar{l}$	%	I	$\bar{l}$	%	I	$\bar{l}$	%	I	$\bar{l}$	%	I	$\bar{l}$	%
June 9	1	1.00	100	1	1.00	100	1	1.00	100	1	1.00	100	1	1.00	100
June 14	1	1.15	100	1	1.25	100	—	—	—	1	1.00	30	—	—	—
June 17	1	1.50	100	1	1.60	100	1	1.40	100	—	—	20	1	1.50	100
June 20	1	1.50	90	1 2	1.60 1.80	100	×	×	0	—	—	—	1 2	1.50 1.80	100
June 24	1	1.50	80	2	2.10	100	×	×	×	—	—	0	—	—	—
June 26	1	1.50	70	2	2.50	100	×	×	×	×	×	×	—	—	—
June 29	1	1.60	40	2	3.00	100	×	×	×	×	×	×	2 3	3.00 3.50	100
July 4	1	1.50	10	2	3.50	100	×	×	×	×	×	×	×	×	×
July 6	1	1.50	10	3	3.50	100	×	×	×	×	×	×	×	×	×
July 9	×	×	0	3	4.20	100	×	×	×	×	×	×	×	×	×
July 13	×	×	×	3	5.00	90	×	×	×	×	×	×	×	×	×
July 23	×	×	×	3	5.20	40	×	×	×	×	×	×	×	×	×

I — instar, $\bar{l}$ — average length of larvae (mm), % — percentage of larvae living from the beginning of experiment, × — end of experiment, — — no data.

Table II. The growth and development of *Endochironomus albipennis* Mg. larvae fed with various foods

Date	Food																				
	Natural suspended matter in the reservoir water			*D. polymorpha* pseudofaeces from natural suspended matter			The mud of the reservoir bottom			*D. polymorpha* pseudofaeces from mud			Potamogeton detritus			*D. polymorpha* pseudofaeces from Potamogeton detritus			Filtered reservoir water		
	I	$\bar{l}$	%	I	$\bar{l}$	%	I	$\bar{l}$	%	I	$\bar{l}$	%	I	$\bar{l}$	%	I	$\bar{l}$	%	I	$\bar{l}$	%
July 13	1	0.60	100	1	0.60	100	1	0.60	100	1	0.60	100	1	0.60	100	1	0.60	100	1	0.60	100
July 18	1	0.95	30	1	1.10	70	1	×	0	1	0.90	10	1	1.00	50	1	1.10	70	1	×	0
July 22	1	1.05	20	1	1.30	40	×	×	×	×	×	×	1	1.15	40	1	1.20	60	×	×	×
July 25	1	1.10	10	2	1.60	30	×	×	×	×	×	×	1	1.30	30	2	1.50	50	×	×	×
July 28	1	1.10	10	2	1.85	30	×	×	×	×	×	×	2	1.50	30	2	1.70	50	×	×	×
August 1	1	1.10	10	2	2.60	30	×	×	×	×	×	×	2	2.00	30	2	2.50	50	×	×	×
August 4	1	1.10	10	3	3.20	30	×	×	×	×	×	×	2	2.50	30	3	3.00	50	×	×	×
August 8	1	1.15	10	3	3.50	30	×	×	×	×	×	×	3	3.00	30	3	3.40	50	×	×	×
August 11	1	1.15	10	3	3.75	30	×	×	×	×	×	×	3	3.20	30	3	3.60	50	×	×	×
August 14	1	1.15	10	3	4.00	30	×	×	×	×	×	×	3	3.30	30	3	3.90	50	×	×	×
August 18	×	×	0	3	4.50	30	×	×	×	×	×	×	3	3.60	30	3	4.20	50	×	×	×

I — instar, $\bar{l}$ — average length of larvae (mm), % — percentage of larvae living from the beginning of experiment, × — end of experiment.

bers of bacteria were also controlled in the food and in the guts of larvae (Table III, IV). The samples were taken after half an hour, after 48 hr and after 154 hr from the beginning of the experiment. As it could have been expected the bacteria were more numerous in the guts of larvae feeding on the food rich in bacteria, than in the guts of larvae kept on food poor in bacteria (Table IV). While analysing the bacteria numbers in the food, in the guts of the 4th instar, and the rate of growth and development of younger larvae, it is obvious that the normal growth and development of Chironomidae larvae is conditioned by food rich in bacteria (more than 60 milion cells/ml during first 48 hour of the experiment). These data confirm the high nutritive value of the bacterial part of the detritus-bacterial complex (Rodina 1966, Sushchenya 1968, Esipova 1969).

Table III. Numbers of bacteria (millions of cells/ml) in various foods

Food	Time from the beginning of the experiment					
	0.5 hr		48 hr		154 hr	
	mean	*n*	mean	*n*	mean	*n*
Natural suspended matter in the reservoir water	2.3	2	9.8	2	21.6	2
D. polymorpha pseudofaeces from natural suspended matter	9.1	2	68.2	2	100.1	2
The mud of reservoir bottom	2.9	2	12.7	2	17.7	2
D. polymorpha pseudofaeces from mud	4.1	2	20.2	2	25.5	2
Potamogeton detritus	7.7	2	91.0	2	113.7	2
D. polymorpha pseudofaeces from Potamogeton detritus	10.9	2	102.3	2	127.4	2
Filtered reservoir water	0.9	2	5.0	2	13.2	2

The experiments with the utilization of food marked with ^{14}C allowed to discover the changes in the assimilation degree of detritus and

Table IV. Numbers of bacteria (thous. of cells per one gut) in the guts of *Endochironomus albipennis* larvae fed with various foods

Food	Time from the beginning of experiment			
	48 hr		154 hr	
	mean	*n*	mean	*n*
Natural suspended matter in the reservoir water	3.75	2	17.10	2
D. polymorpha pseudofaeces from natural suspended matter	30.60	2	39.50	2
The mud of the reservoir bottom	5.85	2	11.45	2
D. polymorpha pseudofaeces from mud	7.60	2	16.85	2
Potamogeton detritus	34.45	2	43.25	2
D. polymorpha pseudofaeces from Potamogeton detritus	37.85	2	58.25	2
Filtered reservoir water	1.85	2	11.35	2

its agglutinates. *C. anthracinus* larvae in the 4th instar are active and they build their cases when placed in the agglutinates, although their guts are nearly empty during the first 6 days, and the food assimilation is low despite its gradual increase from 0.091% to 0.325%. The assimilation rapidly increased on the seventh day to 3.7%, and it was 6.1% on the eighth day. However, as it can be seen in Table III, the rapid increase of the quantity of bacteria in the agglutinates takes place on the second day, and the food is then potentially easy to assimilate. The lack of food in the guts of larvae can be explained by the fact that the agglutinated parts are hardened by mucus, which softens and gradually breaks up because of the continuous activity of larvae. The detritus sedimentated by molluscs is as if preserved. In our experiments the agglutinates were a well assimilated food while the not-agglutinated detritus was losing its nutritive value to a large extent due to mineralization (the assimilation intensity of this food by the Chironomidae larvae decreased from 9.6% to 0.09%). The suspended matter during the passage through the mantle cavity of *D. polymorpha* is preserved by mucus excreted by the gill cells, but it also becomes richer in bacteria (Table III). Apart from that the mucus itself is rich in acid polymucosaccharides, determined by us with the help of the pas-reaction, and its is probably an additional food source for bacteria. The higher nutritive value of the agglutinated food can be also explained by the fact that the detritus in it is easier to assimilate due to the acid phosphatase which is most probably present in the mucocytes of *D. polymorpha*, as it is so in all mucocytes of *Mytilus sp.* (Pasteels 1969).

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4. SUMMARY

The role of *Dreissena polymorpha* Pallas in the sedimentation of the suspended matter was established as well as the possibilities of the utilization of this matter by Chironomidae larvae: *Endochironomus albipennis* Mg. and *Chironomus anthracinus* Zett. The experiments were carried out in the Uchinskoye water reservoir where the occurrence of *D. polymorpha* is on the average 1000 ind./m^2 and the biomass — 500 g/m^2. In the zone of their occurrence these molluscs sediment per day 7 g of the suspended matter (dry weight per square meter). The population of *D. polymorpha* in the whole reservoir sediments in the form of agglutinates and faeces 48.8 t per day.

The laboratory experiments on the growth of Chironomidae larvae on agglutinated and on not-agglutinated food (natural suspension, mud, detritus from *Potamogeton sp.*) showed that larvae grow and develop in the natural way when kept on food with a large quantity of bacteria (more than 60 million cells/ml for the

first 48 hours of the experiment). The natural suspended matter agglutinated by *D. polymorpha* was found to be the most nutritive food. *D. polymorpha* enriches the agglutinated matter with bacteria, and, probably under the influence of the digestive enzymes of the mucocytes, it changes the organic detritus into a more readily assimilated form.

5. РЕЗЮМЕ

Выяснена роль *Dreissena polymorpha* Pallas в осаждении взвеси и возможность дальнейшего её использования личинками Chironomidae: *Endochironomus albipennis* Mg. и *Chironomus anthracinus* Zett. Эксперименты проводились на Учинском водохранилище. Поселения *D. polymorpha* при средней численности 1000 экз/$м^2$ и биомассе 500 г/$м^2$ в зоне её распространения осаждают за 24 часа 7 г сестона (сухой вес) на 1 $м^2$. Популяция *D. polymorpha* во всём водохранилище осаждает в виде агглютинатов и фекалий 48,8 т ежесуточно.

Лабораторные опыты по выращиванию личинок Chironomidae на агглютинированных и неагглютинированных кормах (естественная взвесь, ил, детрит из Potamogeton) показали, что личинки нормально растут и развиваются на кормах с большим количеством бактерий (более 60 млн. кл./мл через 48 часов от начала опыта). Наиболее питательным кормом оказалась агглютинированная *D. polymorpha* естественная взвесь, так как агглютинируя взвесь *D. polymorpha* обогащает её бактериями и, вероятно, под действием пищеварительных ферментов мукоцитов переводит органический детрит в более усвояемую форму.

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POLSKIE ARCHIWUM HYDROBIOLOGII (Pol. Arch. Hydrobiol.)	19	2	211-213	1972

V. SLÁDEČEK

THE VECTOR OF SAPROBITY AND THE SYSTEM OF WATER QUALITY

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ABSTRACT

A modification of the Gołowin's (1968) vector of saprobity was proposed to suit the general scheme of water quality. All 5 limnosaprobic as well as 4 eusaprobic degrees were included into the half-circle. The vector of saprobity plays here the role of a pointer.

The saprobity of an aquatic habitat was estimated in past times subjectively according to the investigator's knowledge of different organisms applied as indicators of certain saprobic degrees (zones, stages, levels). Pantle, Buck (1955) started the attempts for a more exact expression of results and proposed the saprobic index "S" which proved to be very suitable and is used in many European countries. Zelinka et al. (1959) introduced their concept of saprobic valency expressed in a 10-points-system, which is more exact, but also more laborious. The third way is the vector of saprobity proposed by Gołowin (1968) which requires quantitative data, but the resulting saprobity is achieved by a simple graphical procedure. All these three ways arose from the saprobic system founded by Kolkwitz, Marsson (1902, 1908, 1909) and developed more in detail in recent years by a series of investigators, mainly after the severe critique raised by Caspers, Schulz (1960).

The vector of saprobity is an original and progressive method and can be considered the best Polish achievement in the field of saprobiology.

A half-circle is divided by Gołowin (1968) in such a manner that the angles 0–45° represent polysaprobity, 45–90° α-mesosaprobity, 90–135° β-mesosaprobity and 135–180° oligosaprobity. The lines representing the above named angles are the boundaries between each two degrees of saprobity. The centres of all degrees are marked by additional lines = axes showing the values of 22°30′ for polysaprobity, 67°30′ for α-mesosaprobity, 112°30′ for β-mesosaprobity and 157°30′

for oligosaprobity. The quantitative data of indicator organisms belonging to every respective saprobic degree (according to the revision of Liebmann 1951, 1962) are marked on these axes and considered vectors. The resulting saprobity is then calculated as sum of vectors by a simple graphical procedure and the angle determines the resulting saprobity. Furthermore, applying the surfaces of triangles, Gołowin developed also a graphic way to show the saprobic valency of the whole community under consideration.

A question arises if there is a relation to the general scheme of water quality (Sládeček 1966), where the same half-circle was used and comprised all nine degrees of saprobity, whereas Gołowin applied only four.

It is easy to modify the scheme of Gołowin to suit the general scheme of water quality: The sequence of angles is reversed and we start with 0° in the left as the beginning of xenosaprobity. The angle 90° is the border line between the last limnosaprobic degree polysaprobity and the first eusaprobic degree isosaprobity. It is also a demarcation between the aerobic conditions (on the left) and the anaerobic conditions (on the right). Within the limnosaprobity (x-p) each saprobic degree has now 18° vectorial angle and its axis is situated 9° from both border lines (Fig. 1). Because the eusaprobity has 4 degrees, one degree has 22°30′ vectorial angle and the axis is situated 11°15′ from both border lines. The procedure of the graphical calcula-

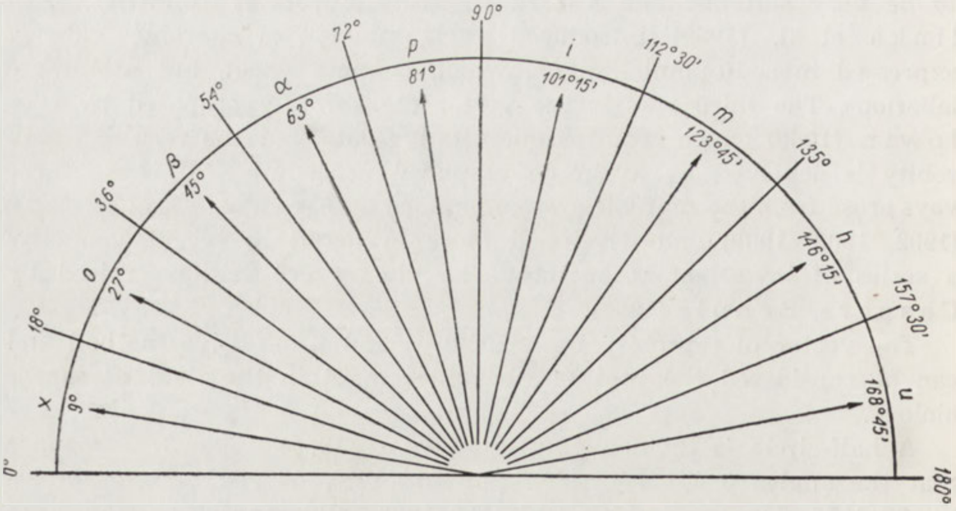

Fig. 1. Modification of the Gołowin's (1968) vectorial calculation of saprobity to suit the system of water quality. Within the limnosaprobity (x, o, *β*, *α*, p) each degree has 18° vectorial angle, within the eusaprobity (i, m, h, u) 22°30′. The sequence of degrees is reversed and the + and — signs neglected. Border lines marked by longer lines than vectors. Abbreviations: x — xenosaprobity, o — oligosaprobity, *β* — *β*-mesosaprobity, *α* — *α*-mesosaprobity, p — polysaprobity, i — isosaprobity, m — metasaprobity, h — hypersaprobity, u — ultrasaprobity

tion is the same as in the original form of Gołowin; we disregard the graphical + and — signs and gain a perfect conformity with the system of water quality in its circle scheme. The vector of saprobity plays here a role of a pointer.

The modification is meant more as a theoretical consideration and effort to keep all modern procedures in a direct relation with the general concept of water quality. In a real case of limnosaprobic communities the original and more simple scheme of Gołowin is preferred.

SUMMARY

After the publication of two methods of calculation of the resulting saprobity by Pantle, Buck (1955) and by Zelinka et al. (1959), the third method was proposed by Gołowin (1968) who introduced a simple graphical solution of the vector of saprobity. Because Gołowin used only 4 degrees of saprobity for his half-circle, which is useful for practical purposes, but inconvenient for theoretical considerations, a modification is proposed in Fig. 1, where 5 limnosaprobical and 4 eusaprobical degrees are included in the same half-circle. This modification is in conformity with the circle scheme of the system of water quality and the vector of saprobity plays here the role of a pointer.

SOUHRN

Po dvou metodách k výpočtu výsledné soprobity (Pantle, Buck 1955, Zelinka et al. 1959) přibyla třetí, velmi exaktní metoda výpočtu vektoru saprobity, kterou navrhl Gołowin (1968). Protože Gołowin rozdělil půlkruh jen na 4 stupně saprobity, což je pro praktické ùčely velmi užitečné, avšak málo vhodné pro teoretické představy jednotného schématu jakosti vody, je v Fig. 1 navržena modifikace s ohledem na teorii: v půlkruhu je zahrnuto 5 limnosoprobních a všechny 4 eusaprobní stupně. Tato modifikace plně odpovídá systému jakosti vody a vektor saprobity tu má ùlohu ukazatele.

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Z. FISCHER

THE ENERGY BUDGET OF *LESTES SPONSA* (HANS.) DURING ITS LARVAL DEVELOPMENT[1]

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ABSTRACT

Energetic balance of Odonata *Lestes sponsa* larvae was estimated for their whole life until metamorphosis. Food was supplied in excess during the whole laboratory experiment (*Daphnia magna, Tubifex tubifex*). Daily food intake, respiration and weight increases were measured and energy conversion indices (K_1, K_2) were computed cumulatively for the whole larval life of the investigated dragonflies.

1. INTRODUCTION

Studies were made on *Lestes sponsa* (Hans.), whose larvae live typically in astatic reservoirs. The life cycle of this species consists of a short period of larval development of 2 months (May—June), coinciding with the existence of periodic small ponds, and a long, 10-month period of embronic development of eggs, coinciding with dry or frozen period of these ponds (Fischer 1964 a, b). The rate of growth in this species is very intensive as compared with that of other dragonflies, occurring in more static environments. Therefore, one would expect a very intensive transformation of energy by this species. In order to obtain the energy budget, the following elements were ascertained: 1. the food intake or consumption (i.e., the weight and calorific value of the food consumed during 24-hr period), 2. the cost of maintenance (the amount of oxygen consumed and its calorific equivalent), 3. the calorific values of the larvae at different age classes which corresponded to subsequent stages of their development.

2. MATERIAL AND METHODS

Fifty larvae about 24 hr old, with live weight of 0.2 mg each, were captured in a periodic small pond in the Kampinos Forest, near Warsaw. They were brought to the laboratory and put into glass containers, 50 ml in volume, each larva separately to prevent cannibalism (Fischer 1961). The containers were submerged in a water bath of 20°C and illuminated with day light. It was necessary to bring another supply of larvae 6 days later and use them in the experiments on account of a high mortality caused by greater vulnerability of younger larvae (Fischer 1964 b). This material was collected from the same pond as previously, but the larvae were older and weighed about 12 mg. The

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larvae were initially fed with Cladocera (*Daphnia magna*) for one month, later with Tubificidae (*Tubifex tubifex*). The food consumption was measured daily. Every morning, a known number of water fleas was introduced into each vessel. After 24 hr of exposure the numbers of recovered individuals were recorded. The amount of Tubificidae consumed was ascertained by weight. The Tubificidae were weighed before and after the 24-hr exposure. The calorific value of the food was calculated from the lipid and ash contents, which were measured. By subtracting the amount of lipids and ash from the dry weight biomass, the amount of proteins and carbohydrates was calculated. The lipid content was estimated by warm extraction with ethyl ether when the material was abundant, and by a photometric method (Stern, Shapiro 1954) when the material was scarce. The ash content was defined by combustion. The calorific value of proteins and carbohydrates was assumed as 4.3 cal/mg and that of lipids 9.3 cal/mg (Bladergroen 1955), and the calorific value of the food was calculated. The same method was used for defining the calorific value of the dragonfly larvae, four times during the entire experiment. The calorific value of Tubificidae ranged from 4.5091 to 4.7666 cal/mg dry weight, and those of *Daphnia magna* from 3.6603 to 4.8458 cal/mg.

The respiration rate of dragonfly larvae was measured in a constant-pressure respirometer (Klekowski 1967), one larva being placed into each respirometer. During the first week of larval life the measurements were taken daily, later on — 3 times a week.

The energy budget elements were calculated as follows: the food intake — by multiplying the food calorific value by the amount of food eaten during 24 hr; the oxygen consumption was converted into energy units using the calorific equivalent coefficient: 1 μl $O_2=4.840 \cdot 10^3$ cal, or 1 mg $O_2=3.38$ cal (Ivlev 1939, Harrow, Mazur 1958); to assess production, the daily increase in the body weight was multiplied by the calorific value of the larvae in a given stage of development.

The diagrams are based on the moving averages (except for those illustrating the data on the chemical composition and calorific value of dragonfly larvae). Because of high mortality of very young larvae, already mentioned, it was difficult to assess their consumption, cost of maintenance, and production. Thus, the data for the early period of larval life were interpolated (broken lines in Fig. 1). The high mortality of larvae occurred also on 32nd day of the experiment, when the metamorphosis processes began. The survival was then so poor that only one larva reached the adult stage. The data for this final period of development are based on one or two specimens only (Fig. 1).

In order to make all the results comparable, they were related to the time of development and not to the weight of larvae. Otherwise the final period of

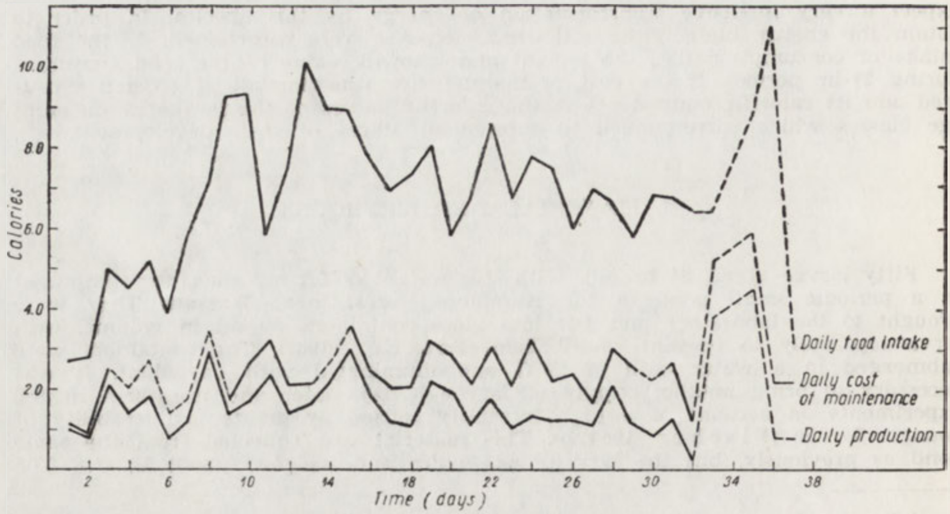

Fig. 1. Food intake, cost of maintenance and production in larval developmental cycle of *Lestes sponsa*

the larval development would be artificially extended in the graphs since the growth rate was very high then. On the other hand, the early larval period would be underestimated because of the very slow growth rate at that time. From the standpoint of biology of this species, the early period of development is at least equally, if not more, important than the remaining periods. An estimation of age was made for the larvae of the second series, brought to the laboratory at the weight of 12 mg. From earlier studies on this species (Fischer 1964 b), it is known that in natural conditions the growth of larvae in the early period of their development is relatively uniform. The following weights correspond to subsequent days of larval life: first day — up to 0.2 mg, second day — 0.8 to 3.0 mg, third day — 0.6 to 0.8 mg, fourth day — 0.8 to 3.0 mg, fifth day — up to 5 mg. From these data the curve was drawn of the age-weight relationship in order to estimate the age of young larvae of the known weight. This refers only to the larvae of the second series, weighing about 12 mg at the beginning of the experiment. Thus, the age of each larva was estimated, and later on the days of the experiment were counted.

3. RESULTS

During their development the larvae of *Lestes sponsa* assimilate less than 50% of energy taken in food. Of the assimilated amount of energy, about 80% is spent for production and about 20% for the cost of maintenance (Fig. 1). The highest assimilation rate was observed during the final 5 days before metamorphosis. In this period, the calorific value of the larvae decreases (Fig. 2). It can be assumed that in dragonflies, similarly as in Holometabola, the amount of lipids decreases in favour of proteins and carbohydrates in the period preceding the metamorphosis since in this period there was no change in the hydration of the larvae: the ratio of wet weight to dry weight was about 6.5.

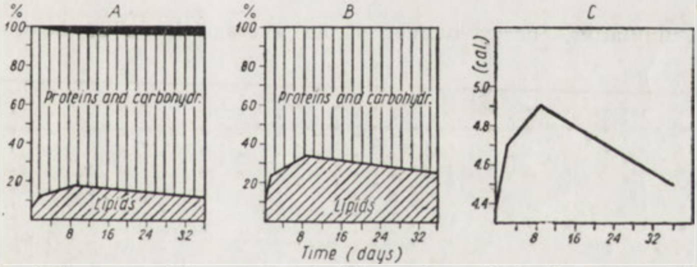

Fig. 2. Chemical composition and calorific value of *Lestes sponsa* larvae. A — dry weight of larvae, B — calorific value of ash free dry weight of larvae, C — calorific value of 1 mg dry weight

The amount of energy used by one larva during its whole development is presented in its cumulative form in Fig. 3. From this graph it is evident that during its whole life an average larva of *Lestes sponsa* consumes 243.8 cal in the food, it stores 56.8 cal in the body, and uses 32.4 cal for the cost of maintenance.

The daily energy budget as percentage of the food intake is presented in Fig. 4. It shows what per cent of the daily food intake is spent for the cost of maintenance, for production, and what proportion of the unassimilated energy is rejected by the organism. During the final 6 days preceding the metamorphosis, there is a conspicuous increase in the assimilation of the energy taken. At this period the daily consumption also increases (Fig. 1). In general, apart from this final period, the assimilation of energy shows a rather constant level during the whole larval development and amounts to about 40% of the daily food intake, although it oscillates greatly (in spite of the application of moving averages).

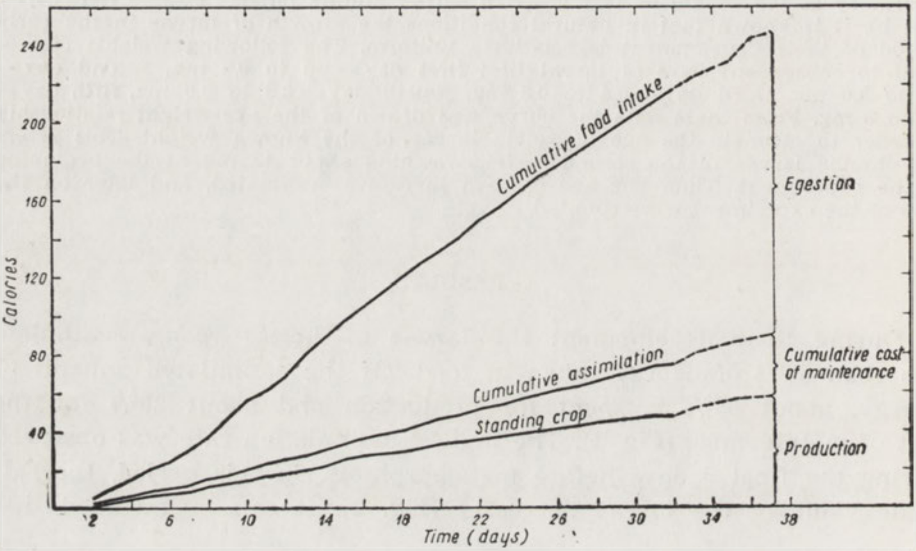

Fig. 3. Cumulative energy budget of an average larva of *Lestes sponsa*

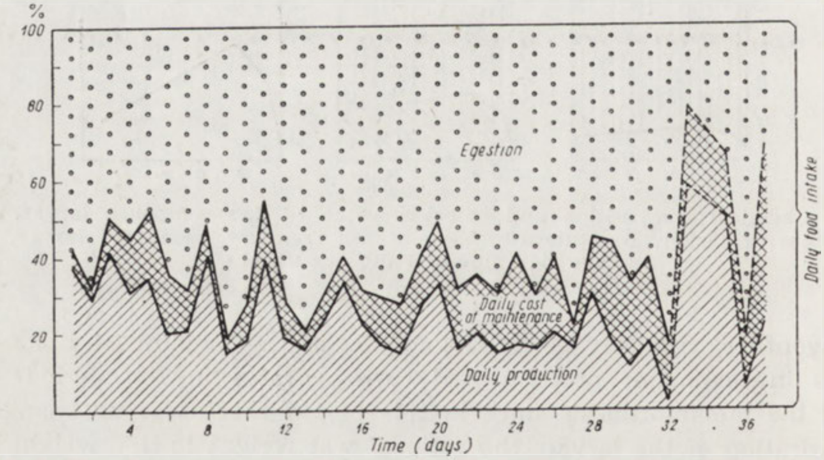

Fig. 4. Daily instantaneous energy budget as percentage of food intake

The changes of assimilation and the gross and net production efficiency indices related to time are shown in Fig. 5. The gross production efficiency index (K_1) is fairly constant during the larval development.

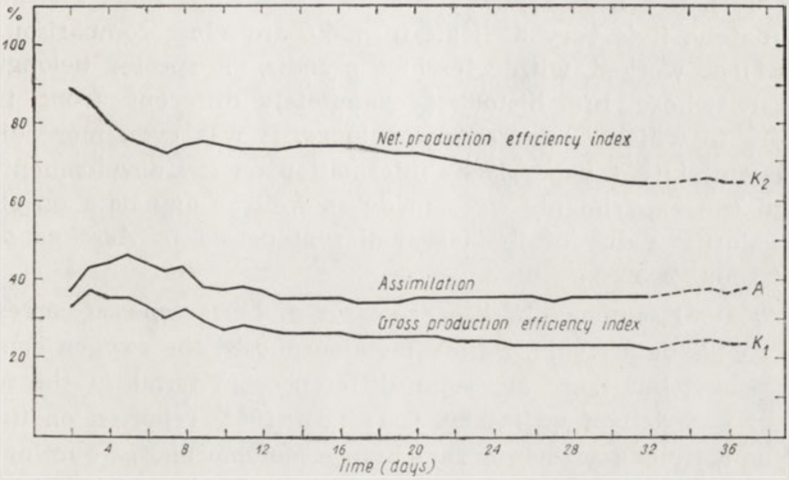

Fig. 5. Gross production and net production efficiency indices and assimilation

After an early period of about 10 days, when it decreases from 35 to 25%, the gross production efficiency index remains constant for the later period. It can be inferred from this index that a relatively large proportion of food consumed is retained as production of body tissues during the whole larval development. The net production efficiency index (K_2) is very high, especially at the early period of about 6 days of the larval development. The high values of K_2 are related with a low metabolic loss due to rather inactive behaviour of these animals and an excess of food in the experiment.

Food assimilation (A) is somewhat higher in the early period of 10 days of larval life, as compared with that of the remaining 28 days of life. In general, it ranges from 35 to the final 46%, in the latest period of larval life.

Water content in the larvae was also studied. It shows conspicuous changes during larval development, especially in the early life period. In very young larvae the water content is 93%, and later on it decreases abruptly to 84.7%. Thus, due to this decreases, the ratio of dry weight to live weight of larvae is doubled. It is most probable that it is during this period that the larvae begin to produce chitin. There are no conspicuous changes in the hydration during the further period of the larval life. Just before metamorphosis takes place, water content decreases to 83.9%. Probably it corresponds to a rapid dehydration of the body at the beginning of metamorphosis. On account of technical difficulties, water content during the metamorphosis was not studied.

4. DISCUSSION

Comparing the present data with the only, as far as they were available, data on the dragonfly larvae and their energetics by Berezina (1957), it can be said that the two sets show some resemblance. Unfortunately, it is very difficult to make any close comparison, since Berezina worked with *Aeschna grandis,* a species belonging to Anisoptera whose life history is completely different from that of Zygoptera to which *Lestes sponsa* belongs. It was even more difficult since Berezina's paper lacks information on the development stage at which the experiments were made as well as any data on changes in the calorific value of the larvae (larval period in *Aeschna grandis* lasts for about 2 years).

The general sequence of life processes of *Lestes sponsa* corresponds to Corbet's data (1962). Before metamorphosis, the oxygen consumption increases, but there are some differences in terms of the feeding behaviour and daily food intake. Corbet (1962) reported on the lack of feeding activity for several days before metamorphosis, quoting *Anax imperator* as an example. He suggested that this phenomenon is typical for other dragonflies. In *Lestes sponsa,* this period is very short, one day or less (Fig. 1). This is obvious, since the larval period in *Lestes sponsa* is much shorter (about 40 days) as compared with that of *Anax imperator* (about 300 days). However, in the period before the emergence occurs, the food requirement increases, the daily food intake being then 11 cal, whereas an average daily consumption during the larval period is around 7 cal per larva. During this final period, the larvae show an increased preference towards organisms of high calorific values (Fischer 1967). The period of fasting which occurs directly before emergence, often called a hunger phase, seems to be completely different from the true hunger. An animal deliberately refuses to take food and its respiration is quite normal or even somewhat increased, whereas at typical starvation the respiration considerably decreases. Thus, the period directly before metamorphosis should not be considered as the stage of hunger, although the larvae do not feed then. The entire organism undergoes such thorough rebuilding during this period that both its morphological structure and the enzymatic system are not able to cope with the functions of feeding, digestion, and assimilation.

The results concerning hydration and its changes during the larval period in *Lestes sponsa* are in accord with general findings for insects (Hoar 1966) as well as with detailed data for *Tribolium castaneum* (Klekowski et al. 1967). Yet, in Tribolium there is a full metamorphosis, and thus too close comparisons should be avoided. Nevertheless, both in Tribolium and in Lestes, hydration is high during the early stages of larval development, followed by a decrease in water content preceding the emergence of an adult.

When comparing the elements of energy budget of *Lestes sponsa* with Richman's (1958) data on *Daphnia pulex*, and Klekowski, Shushkina's (1966) on *Macrocyclops albidus*, a striking similarity can be found between this representative of Copepoda and the species under study (certainly because of the predatory behaviour of these animals), but also a conspicuous difference from *Daphnia pulex*. The assimilation of food in *D. pulex* ranges from 6 to 24% of its food intake, depending on the food concentration, in *M. albidus* — from 40 to 80%, and in *L. sponsa* — from 40 to 45%. The latter values correspond to those for *M. albidus* at the lowest food concentrations. The gross production efficiency index (K_1) in *L. sponsa* larvae (25%) is also similar to that of *M. albidus*; in filtrating *D. pulex* it is much lower, from 3 to 13% (Richman 1958). The net production efficiency index, K_2, indicates that the *L. sponsa* larvae are efficient transformers of energy, as are the copepods (Klekowski, Shushkina 1966). For the dragonfly in the early period of larval life this index amounts to 90%. Similarly, high values of K_2 index were observed by Ivlev (1964) in *Actinia equina* (from 50 to 93.8%). In spite of an important taxonomic difference, there is some resemblance between these two organisms. They are both predatory species and both reveal little mobility. The *L. sponsa* larvae, similarly as marine anemones, are among the heaviest predators of their environments (Fischer 1961, 1967). These dragonflies lead almost sedentary life (Fischer 1964a, 1967), they are not eager to change their position and would stay for days and days passively until a prey gets within the range of their mask. Especially under the circumstances of this experiment, they had no need to move since food was both in excess and access, and the larvae were not compelled to change their position for weeks. With such a mode of living, both in *Actinia equina* and *L. sponsa* larvae the great majority of assimilated food is spent for the growth and only a scant quantity for respiration, which is revealed by the high K_2 index.

Acknowledgements

I wish to express my sincere gratitude to Professor R. Z. Klekowski and to thank him for guidance and help during the preparation of this paper.

5. SUMMARY

In order to obtain an energy balance estimation of Odonata *Lestes sponsa* larvae, daily food intake, respiration and body calorific values of larvae of various ages were measured. It was found that as in this group of animals the metamorphosis is not complete, their cumulative energy balance during development is gradual and reveals no sudden shifts. Food assimilation is fairly small, as it is about 40%; the gross index of ecological efficiency K_1 can be

considered as constant at about 20 do 30%. The net index of ecological efficiency, K_2, is high, particularly during the initial 6 days of life (90–80%) and later on it falls down to as little as 70%. High values of the K_2 index can be probably accounted for by the low assimilation of food and small metabolic losses as the investigated predators move very little under excess of available food.

6. STRESZCZENIE

W celu sporządzenia bilansu energetycznego larwy Odonata *Lestes sponsa* wykonano oznaczenia następujących parametrów: racji pokarmowej, oddychania oraz wartości kalorycznej larw różnego wieku. Stwierdzono, że w związku z przeobrażeniem niezupełnym u tej grupy zwierząt, bilans energetyczny kumulatywny w czasie rozwoju ma przebieg bardzo płynny i nie wykazuje gwałtownych zmian. Wykorzystanie pokarmu jest raczej niewielkie i wynosi około 40%, współczynnik wydajności ekologicznej brutto (K_1) jest stały i wynosi około 20–30%. Współczynnik wydajności ekologicznej (K_2) netto jest wysoki, szczególnie w okresie sześciu pierwszych dni życia (90–80%), w ciągu dalszego wzrostu larw spada do zaledwie 70%. Wysokie wartości współczynnika K_2 są związane najpewniej z niską przyswajalnością pokarmu oraz małymi stratami metabolicznymi związanymi z mało ruchliwym trybem życia drapieżnika przy nadmiarze pokarmu.

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FECUNDITY, SURVIVAL AND HAEMOLYMPH CONCENTRATION OF *PHYSA ACUTA* DRAP. (GASTROPODA, PULMONATA) AND *TUBIFEX TUBIFEX* MÜLL. (OLIGOCHAETA, TUBIFICIDAE) IN RELATION TO SALINITY OF EXTERNAL MEDIUM

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ABSTRACT

Fecundity, survival and haemolymph concentration was investigated in laboratory populations of fresh water species *Physa acuta* Drap. and *Tubifex tubifex* Müll. acclimated to different salinities of external medium (from 1 to 10‰). In salinities surpassing normal (fresh water) osmotic concentration of body fluids, i.e. 4‰ for *T. tubifex* and 4.5‰ for. *P. acuta*, egg laying decreases very rapidly and embryonic development is stopped. Resistance of adult animals is higher, some snails survive even in 10‰, and some tubificids in 9‰. In non-acclimated animals rapid increase of mortality rate is observed in the zone of critical salinity of 5–8‰, being the physiological boundary between marine and fresh water ecosystems. In animals acclimated to brackish media haemolymph concentration is in any case higher than this of the external medium. The curves of osmoregulation in investigated fresh water animals are similar to similar curves for euryhaline brackish water species, probably illustrating the course of osmotic evolution of marine ancestors invading hypotonic media.

1. INTRODUCTION

There is no doubt today that the physiological characteristics of animals influence their eco-geographical distribution. We know that any factor in the environment which changes the physiology of an organism may constitute the ,'threshold factor" limiting the survival of a species in this environment. For the two physiologically different groups of marine and fresh water animals it is the salinity of water medium which appears as the essential limiting factor. The problem of "Arten-Minimum" (Remane 1934, Remane, Schlieper 1958), or of the sudden decrease of the number of species in the range of salinity from 5 to 8‰, i.e. in the transitory area between marine and fresh waters, is familiar to any investigator of brackish waters. The overcoming of this barrier of critical salinity has always been a crucial moment in the evolution of species and their expansion into environments threatening with osmotic stress (Dahl 1956, 1959, Kinne 1964 a, b, Khlebovich 1969).

Eggs, embryos, larval stages and spawning adult individuals tend to be most sensible to environmental changes (Bullock 1960, Kinne 1964 a, Khlebovich 1969). Their response to osmotic stress essentially limits the actual colonization of environments with different salinities even if these can be tolerated by adult individuals with better developed osmoregulatory mechanisms. However, reports of observations concerning this type of sensibility in invertebrates are rather scanty. There are data concerning eggs and larvae of the trematode *Fasciola hepatica* (Styczyńska-Jurewicz 1965) and of *Schistosoma japonicum* (Ito 1955), various aspects of reproduction and development of *Nereis* *diversicolor* (Bogucki 1953, 1954, 1963, Smith 1957, 1964), fresh water molluscs of the genera of Anodonta and Viviparus (Khlebovich 1965), amphibiontic snails *Succinea putris* and *S. pfeifferi* (Petersen 1967) and crustaceans *Acanthocyclops viridis* (Khlebovich 1960) and *Triops cancriformis* (Klekowski, Hempel-Zawitkowska 1968).

The present paper reports the influence of salinity in the range from 1 to 10‰ on reproduction of *Physa acuta* Drap. as a representative of fresh water snails and of *Tubifex tubifex* Müll. as a representative of Oligochaeta group, abundantly occurring in fresh and brackish waters. In addition, sensibility of spawning adult individuals to the transmission from fresh to brackish media is presented. The curves of survival during initial periods of acclimation and of the changes in blood concentration as related to the increased salinity of the medium are put forth.

2. MATERIAL AND METHODS

Salinities of 1 to 10‰ were made by diluting artificial sea water prepared after Hale (1958) with conditioned tap water which was also used as the control medium. Groups of 5 adult spawning snails of *Physa acuta* from laboratory culture were put into small all-glass aquaria 8×8×8 cm, with sand on the bottom, filled with water of a given salinity and covered with glass to limit evaporation. In each salinity there were 10 snails (two vessels), fed with fresh lettuce and dried daphnids. Every second day all the newly laid egg-masses were taken out and the eggs in them were counted. New snails were also substituted for dead ones to keep their number in the vessels constant. Between successive renewals of water in aquaria, salinities were constant or increased insignificantly (0.2–0.3‰).

Experiments were made at a room temperature, in two series: in series I the snails were not acclimated to the respective salinities; losses, occurring however just in 8‰, were replaced by individuals from a fresh water culture. Two experiments were carried out, at temperature ranges from 20 to 22°C in the first, and 17 to 19°C in the second one. In series II, the first experiment was started after 27 days of acclimation of the snails to the respective salinities; only 5 individuals (1 vessel) were examined at each salinity while another 5, likewise acclimated served to replace the losses. The temperature ranged from 19 to 21°C. In the second experiment the snails were acclimated for a longer period (47 days), the temperature ranged from 20 to 21°C. The remaining conditions were similar as in the first experiment of this series.

The material of *Tubifex tubifex* was purchased in a zoological store; for each experiment adult individuals with well developed clitella were selected from a single sample. Laboratory cultures were cultivated according with Lehman (1941) prescriptions. In each full glass aquarium 18 cm in length, 9 cm in breadth and 13 cm in depth, 30 animals were put on a 4 cm layer of pure sand with 5 cm of water upon it. Water was aerated and the worms were fed with yeast. Balls of fresh yeast were dried and pulled deep in sand, 3 in each aquarium, so that there was an abundance or even surplus of food. Losses of water in aquaria caused by evaporation were supplemented each day with distilled water. Cocoons laid deep in sand were collected from it by making them turn up on its surface by rapid stirring. For each salinity there were two aquaria: one with the experimental population and the other for replacing the losses. Two 12 days experiments were carried out. In the first one the temperature ranged from 20 to 22°C; water renewal, collecting of cocoons and replacing of losses were made at 4 days intervals. The worms which had survived after the last collecting of cocoons were left in their aquaria for another 10 days but the daily losses of water due to evaporation were no longer supplemented, so that the concentration of the experimental media increased a little as it was revealed by cryoscopic measurements. After that period, haemolymph was sampled from 4–5 worms and its osmotic concentration was gauged. The freezing point depression of haemolymph was found by a Ramsay microcryoscope as modified by Klekowski (the apparatus and the procedure are described in Klekowski 1963).

In the second experiment the temperature ranged from 20 to 24°C; control activities were performed every other day and haemolymph was taken immediately after the experimental period.

An average number of eggs per one individual as the measure of fecundity was computed with account for the mortality rates; i.e. those individuals which have survived a given time interval (i.e. between two tests) plus a half of those which had died during that period were considered.

Survival as related to medium salinity was defined only for unacclimated animals and for those during the first phase of acclimation, i.e. during the initial 10 days for *Physa acuta* and until the first test (after 4 days in the first experiment or after 2 days in the second) for *Tubifex tubifex*. A different approach was technically impossible since the mortality rates of *T. tubifex* in the highest salinities were very high and the reservers of material were insufficient to make up for all the losses.

3. RESULTS

THE INFLUENCE OF SALINITY ON FECUNDITY

As it can be seen in Fig. 1, *Physa acuta* lay eggs intensively up to $5^0/_{00}$. At this level the laying of eggs is checked abruptly, though eggs can be laid sporadically even at $8^0/_{00}$. The snails are much less sensible

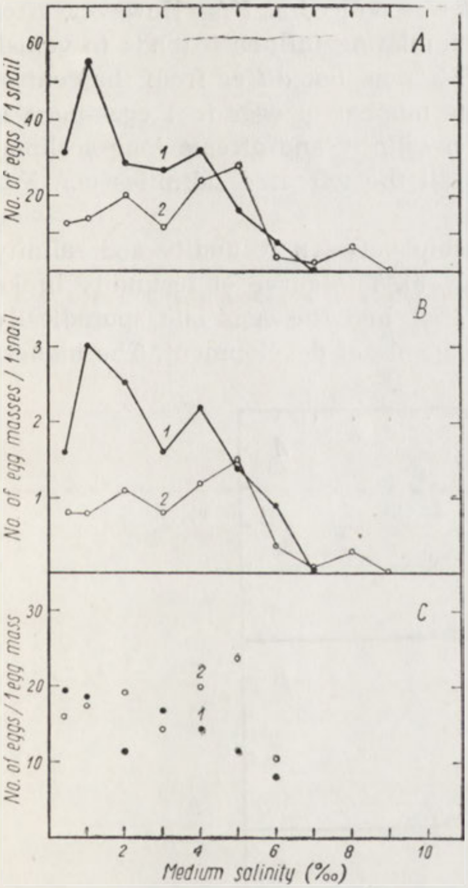

Fig. 1. Effect of medium salinity on fecundity in non-acclimated snails *Physa acuta*. A — mean number of eggs laid by one snail during 10 days experiment, B — frequency of egg laying — mean number of egg masses per one snail, C — mean number of eggs per one egg mass. 1 — first experiment (temp. 20–22°C), 2 — second experiment (temp. 17–19°C)

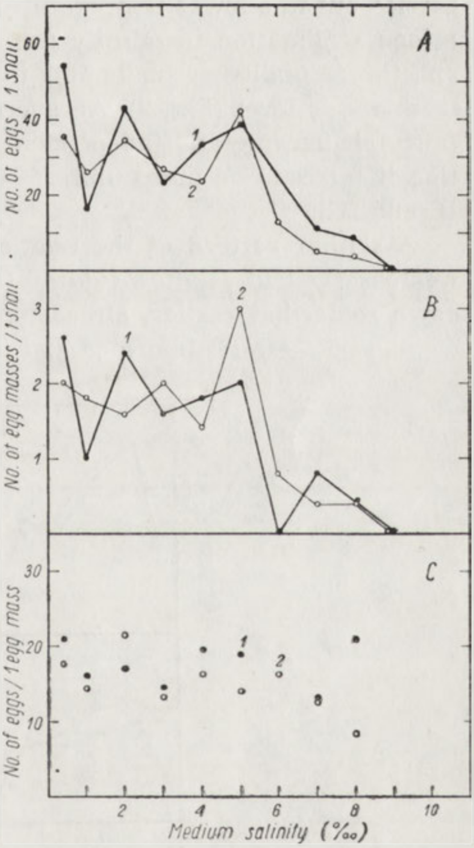

Fig. 2. Effect of medium salinity on fecundity in acclimated *P. acuta*. A — mean number of eggs laid by one snail during 10 days experiment, B — frequency of egg laying — mean number of egg masses per one snail, C — mean number of eggs per one egg mass. 1 — first experiment (temp. 19–21°C) started after 27 days of previous acclimation of snails, 2 — second experiment (temp. 20–21°C) started after 47 days of acclimation

then their process of reproduction, for they can survive even as long as 2 months at 9 to $10^{0}/_{00}$ of salinity. The highest concentration at which the hatching of young snails was observed, was $5^{0}/_{00}$ though at this level many embryos were injured and did not realize their development. The eggs laid at salinities above $5^{0}/_{00}$ were lethally damaged at the beginning of their embryonic development. At $8^{0}/_{00}$ many empty jellies were found with degenerated capsules in them.

In unacclimated snails a stimulating influence of certain salinities upon egg production could be noticed; in the first experiment the highest fecundity was observed at $1^{0}/_{00}$, while in the second experiment, carried out in a lower temperature it was noticed at $5^{0}/_{00}$. However, after a long acclimation to salinity this stimulating influence tends to vanish and the fecundity of snails at 1 to $5^{0}/_{00}$ does not differ from the control fresh water level (Fig. 2). An average number of eggs in 1 eggs-mass is fairly changeable and independent on salinity and after a long acclimation it tends to be more uniform in all the tolerated salinities (c.f. Fig. 1C and 2C).

A similar pattern of the relationship between fecundity and salinity was observed in *Tubifex tubifex* (Fig. 3). The curve of fecundity broke down somewhat earlier, already at $4^{0}/_{00}$, and the eggs laid sporadically at 5 and $6^{0}/_{00}$ were deformed and incapable of development. The highest

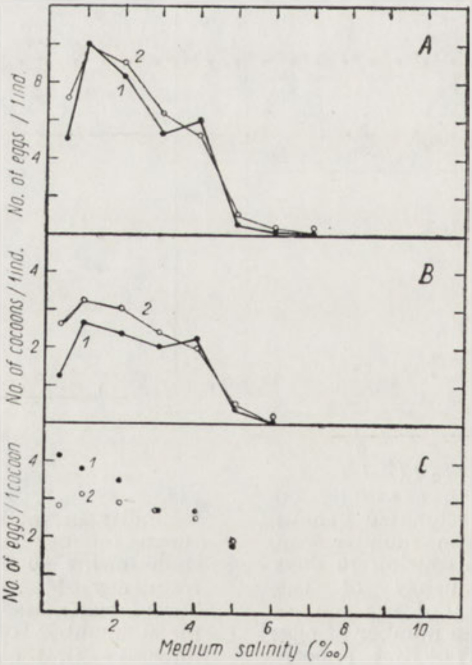

Fig. 3. Effect of medium salinity on fecundity in non-acclimated *T. tubifex*. A — mean number of eggs per one individual, B — mean number of cocoons per one individual, C — mean number of eggs per one cocoon. 1 — first experiment (temp. 20–22°C), 2 — second experiment (temp. 20–24°C)

salinity at which the hatching and survival of *T. tubifex* larvae was observed was $4^0/_{00}$, but when eggs in more advanced stages of embryonic development (embryos elongated in form) were put into salinity of $5^0/_{00}$, normal hatchings did occur (higher salinities were not investigated).

Fecundity at 1 and $2^0/_{00}$ as compared with the fresh water control was higher by 36 and $23^0/_0$ respectively in the first experiment and 97 and $65^0/_0$ in the second one. In opposition to *P. acuta* in which no influence of salinity upon the number of eggs in an egg-mass was observed, in *T. tubifex* this number was changing with fecundity and it fell to the average of 2 eggs in a cocoon in stress environments as compared to 4 in optimal conditions (Fig. 3C).

SURVIVAL OF ADULT INDIVIDUALS

Survival of unacclimated *Physa acuta* was very good, better than that of *Tubifex tubifex*. It was recorded for the whole experimental period of 10 days (Fig. 4B). A high mortality rate of snails occurred only at $10^0/_{00}$, but even then it was quite small in a lower temperature (Fig. 4A — 2). The diagram shows that the mortality rate is highest

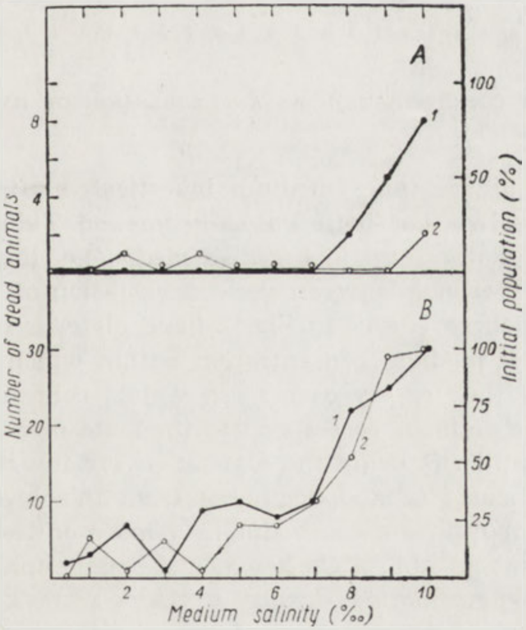

Fig. 4. Mortality rate in the initial phase of acclimation to salinity. A — *P. acuta:* 1 — first experiment (temp. 20–22°C), mortality during 10 days of acclimation, 2 — second experiment (temp. 17–19°), mortality during 10 days of acclimation; B — *T. tubifex*: 1 — first experiment (temp. 20–22°C), after 2 days of acclimation, 2 — second experiment (temp. 20–22°C), after 3 days of acclimation

during the first phase of acclimation and decreases as acclimation continues. This fact permitted to carry out the investigations after a long period of acclimation as discussed above.

In *Tubifex tubifex* cultures a good condition of animals at 1 and 2‰, better than in other salinities and in the control, was remarkable. The animals kept in those concentrations were big and fat and their clitella were well developed, while in higher salinities beginning from 7‰ they were emaciated, the rear segments of their bodies were more frequently rejected, the clitella disappeared, the body fluids became more viscous and their volumes decreased.

The mortality rates of unacclimated *T. tubifex* were much higher than that of the snails and for that reason attempts at prolonged acclimation had failed. At 5‰ the mortality rate was about 25% but at 10‰ it was full 100%. In the latter salinity the worms did not screw into the sand at all but were crawling on it revealing a typical escape reaction and they died during the first 24 hr. The mortality rates were falling down as acclimation continued but they could not be strictly determined in quantitative terms because of small number of worms survived.

HAEMOLYMPH CONCENTRATION AS AN EXPRESSION OF HYPEROSMOTIC REGULATION

The changes in the inner medium investigated after the series of experiments revealed that both *Physa acuta* and *Tubifex tubifex* are hyperosmotic regulators also in brackish media, i.e. they always maintain a positive difference between the concentration of inner and outer medium. All the three curves in Fig. 5 have plateaus corresponding to the range of outer medium concentration within which it does not exceed the original (i.e., observed in fresh water) concentration of inner medium; thus the plateaus correspond to the state of osmotic homeostasis of an organism. In *P. acuta* the plateau covers the range from fresh water to only about 2‰ and beginning from this level the curve of osmoregulation mounts so as to maintain a more or less constant positive difference (about 0.1 Δ°C) between haemolymph and the outer medium (a "hyperosmotic surplus", Styczyńska-Jurewicz 1972).

The changes of the shape of the osmoregulation curve in *T. tubifex* after the prolonged acclimation period are remarkable (Fig. 5B). The plateau which includes the 4‰ level after 12 days of acclimation, is extended to 6‰ after 22 days and hyperosmotic surplus decreases from about 0.15 Δ°C to about 0.08 Δ°C, so that at higher salinities the curve of osmoregulation runs nearer to the line of isoosmosis (Fig 5B — 2).

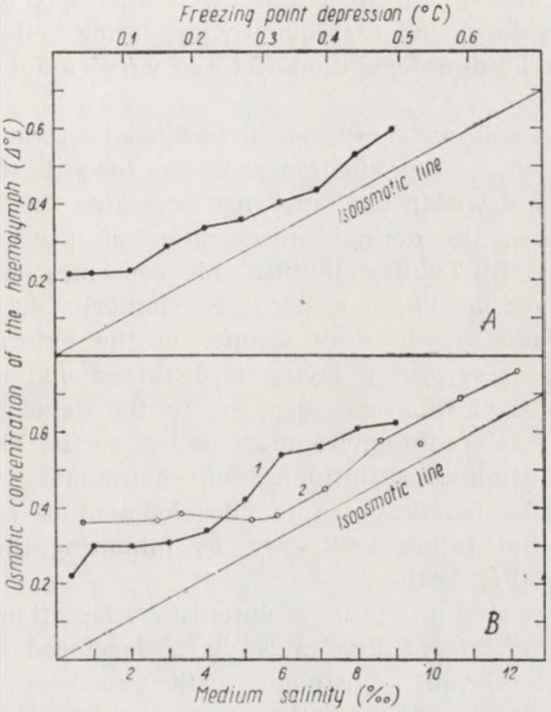

Fig. 5. Changes in haemolymph concentration measured as freezing point depression in relation to salinity. A — *P. acuta* after 10 days of acclimation to salinity; B — *T. tubifex*: 1 — after 12 days of acclimation, 2 — after 22 days of acclimation

4. DISCUSSION

A certain secondary adaptation of fresh water animals to brackish environment, presented in this work, shows the problem of "critical salinity" as having a very important ecological consequences. Khlebovich (1969) analysing the problem in its evolutionary aspect arrives at a notable generalization concerning the way in which marine animals had colonized fresh waters. This was possible because of a development of osmoregulatory mechanisms permitting to maintain the inner osmotic concentration, or the "inner salinity" as he termed it, at a level not below the critical one, i.e. not lesser than 4–5‰. However, because of great sensibility of the processes of reproduction to osmotic stress, various forms of their protection must have developed as the embryos or early larval stages are in general not bestowed with efficient osmoregulatory mechanisms. Such forms are: inner insemination, or in frequent cases hermaphroditism, viviparousness or a shortening of the post embryonic development.

Beside those forms, mentioned by Khlebovich (1969), others can be pointed out, as the structure of eggs of some fresh water animals in which eggs are protected by well developed envelopes with selective permeability, and a frequently appearing colloidal layer also playing its role in osmoregulation (Styczyńska-Jurewicz 1970, 1972).

In the two fresh water species investigated in the present work a full tolerance of the reproduction processes towards the external salinity was observed within the range not exceeding the "inner salinity" of the animals i.e., the normal concentration of body fluids in fresh water conditions. In *Tubifex tubifex* this concentration is 0.22 Δ°C, i.e. about $4^0/_{00}$ and in *Physa acuta* it is, similarly, 0.21 to 0.24 Δ°C, i.e. 4–$4.5^0/_{00}$. When this level of salinity of the external medium is surpassed, the process of egg laying is disturbed and checked in the first place, and then the same happens to the development of eggs still laid to the intolerable environment as by inertia. This proves that the ecologically eliminating influence of environment salinity is not exerted directly by handicapping the development of eggs which had been laid to it but rather undirectly, by inhibiting the fecundity of parent organisms (Fig. 1–3).

It can be supposed that the evolutionary adaptation of species to osmotic changes of the medium must have developed on the similar way and that the relevant adjustments in the processes of reproduction had had to occur as an effect of the changes which the osmotic stress might have caused in the tissues of the parent organisms.

In experimental conditions, the inhibition of egg laying in *P. acuta* and *T. tubifex* in intolerable environment was not immediate; sporadic laids of egg-masses of *P. acuta* could be found even at $8^0/_{00}$ of salinity which was lethal for eggs. Cocoons of *T. tubifex* appeared at similarly lethal salinities of 5 and $6^0/_{00}$.

A similar lowering of fecundity in osmotically stressful medium ($10^0/_{00}$ for succinids) was observed by Petersen (1967) in *Succinea putris* and *S. pfeifferi*, cultivated in media of various salinities.

The stimulated effect of a low salinity upon egg production in unacclimated *P. acuta* and *T. tubifex* (Fig. 1 and 3) seems to be a result of the stimulating influence of such salinity upon the general metabolism and activity of animals (Karandeeva 1966, Klekowski, Duncan 1966). An evidence in favour of such an interpretation is the lack of an obvious stimulating effect in animals after longer acclimation in which metabolism probably returned to the normal (Fig. 2)

SALINITY AND SURVIVAL

An investigation of survival of adult animals was a marginal objective of this work, being mainly an auxiliary tool for a sound assessment of fecundity. However, the curves of mortality of animals during the initial phase of acclimation (Fig. 4), though based on scanty material, obviously point to two regularities: 1. the mortality rate increases within the range of the critical salinity, 2. for adult animals the range of tolerance (up to 9‰ in *T. tubifex* and up to 10‰ in *P. acuta)* are greater than those for eggs (up to 4‰ in *T. tubifex* and up to 5‰ in *P. acuta)*. Of course, a greater tolerance does not mean 100% of survival, while 100% mortality rate means a complete intolerance, but the range of tolerance can be extended by more gradual introduction into stress conditions. Neither does it mean that an animal which succeeds to survive under stress, retains its original homeostasis; on the opposite, the original physiological state always undergoes some modifications, as it is evidenced by the changes of haemolymph concentration in the investigated animals (Fig. 5).

It is remarkable, though scanty material requires care, that the survivals of snails was improved if they were exposed to osmotic stress in a lower temperature (Fig. 4B).

A very good condition of animals in 1–2‰ salinity, noticed mainly in *T. tubifex,* may be an effect of an advantageous decrease of the osmotic tension between an organism and the hypotonic medium. If this was the case, the thermodynamic expenditure for regulation would decrease, according with Pott's (1964) model. This observation can have a practical significance for the cultivation of fresh water animals, which could be probably more efficient if an oligohaline medium of 1–2‰ would be used.

HAEMOLYMPH CONCENTRATION AND THE EVOLUTION OF OSMOREGULATORY FUNCTIONS

The curves of osmoregulation for *P. acuta* and *T. tubifex* (Fig. 5) have a shape which seems to be typical for animals which have accomplished or are still accomplishing the process of evolutionary adaptation to hypotonic environment. Similar in character are the curves of changes in the osmotic concentration in the snails *Coretus corneus* (Klekowski 1963) and *Potamopyrgus jenkinsi* (Duncan 1967) exposed to sea water with ranging degrees of salinity. All of the animals mentioned here, when exposed to salinities above their normal haemolymph concentration (i.e., above the level maintained in fresh water), always show a concentration of their inner milieu which exceeds more (Physa, Coretus, Tubifex) or less (Potamopyrgus) the concentration of the outer environment, so that the curve of osmoregulation always runs above the line of isoosmosis. The mechanism of maintenance of such hyperosmotic surplus is not yet understood. The interpretation by Klekowski (1963) who sees the cause of the increase of the inner osmotic concentration in permeation of ions from the medium to haemolymph, is insufficient. Of course such a process must occur, but it can only equilibre the osmotic concentration of inner and outer medium. The appearance of hyperosmotic surplus must involve biochemical mechanisms of osmoregulation. If hyperosmotic surplus was established by organic molecules for which the body cover is impermeable, its maintenance would not involve thermodynamically expensive mechanisms of active transport, but energetic costs would only have to account for the energy required for the secretion of such osmotically active molecules to the blood. The observed increase of haemolymph viscosity in higher salinities may be an evidence in favour of this hypothesis, although it can also result from a greater dehydration of the whole organism.

Finally, let us point to the similarity, interesting from the evolutionary point of view, of the experimental curves of osmoregulation in fresh water organisms and the corresponding curves for euryhaline brackish animals of marine origin. E.g., similar shapes of osmoregulation curves were found for crustaceans *Gammarus duebeni* (Kinne 1952) and *Rhithropanopeus harrisi* (Kinne, Rotthauwe 1952), with an extensive plateau in the oligo-mesohaline range and with a hyperosmotic surplus from this level toward higher salinities.

It seems that this type of curves, typical for fresh water animals artificially contacted with saline media, illustrates the course of osmotic evolution of their marine ancestors invading hypotonic environments and reflects such evolution in the reversed direction.

Acknowledgements

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5. SUMMARY

1. The investigated species, *Physa acuta* Drap. and *Tubifex tubifex* Müll, reveal normal or even higher fecundity within the range of medium salinities not exceeding the normal osmotic concentration of haemolymph of those animals in fresh water, i.e. up to about 4‰ for *T. tubifex* and 4.5‰ for *P. acuta*.

2. In higher salinities the process of egg laying is inhibited and eggs sporadically laid to the excessively concentrated environment do not develop.

3. Adult organisms are more tolerant to osmotic stress than the embryonic stages; some of them survive even in 9‰ (*T. tubifex*) or 10‰ (*P. acuta*) of salinity.

4. When the salinity of external medium exceeds 2‰ for *P. acuta* and 4‰ for *T. tubifex*, haemolymph concentration of investigated animals increases so that a more or less constant positive difference ("hyperosmotic surplus") between the inner and outer medium is maintained.

5. Such hyperosmotic surplus amounts to about 0.1 Δ°C for *P. acuta* after 10 days of acclimation; for *T. tubifex* after 12 days of acclimation to about 0.15 Δ°C, but after 22 days to only about 0.08 Δ°C.

6. The curves of osmoregulation of freshwater animals acclimated to brackish water are similar in character to the corresponding curves for euryhaline animals of marine origin, illustrating probably the course of physiological evolution of osmoregulatory functions in marine ancestors colonizing hypotonic media.

6. STRESZCZENIE

1. Badane gatunki, *Physa acuta* Drap. i *Tubifex tubifex* Müll., wykazują normalną lub wyższą od normalnej płodność w obszarze zasolenia środowiska zewnętrznego, odpowiadającym swą koncentracją osmotyczną normalnej, tj. przejawianej w wodzie słodkiej, koncentracji osmotycznej hemolimfy tych zwierząt, czyli do około 4‰ dla *T. tubifex* i 4.5‰ dla *P. acuta*.

2. W wyższych od tego zasoleniach proces składania jaj zostaje zahamowany, a jaja składane jeszcze sporadycznie do środowiska zbyt zasolonego nie rozwijają się.

3. Tolerancja osobników rodzicielskich, dorosłych, w stosunku do stresu osmotycznego jest większa niż tolerancja rozrodu, część z nich przeżywa nawet w zasoleniu 9‰ (*T. tubifex*) i 10‰ (*P. acuta*).

4. Gdy zasolenie środowiska zewnętrznego przekroczy 4‰ (dla *T. tubifex*) lub 2‰ (dla *P. acuta*), koncentracja hemolimfy tych zwierząt podnosi się w kierunku utrzymania mniej więcej stałej dodatniej różnicy między środowiskiem zewnętrznym a wewnętrznym.

5. Ta nadwyżka ciśnienia osmotycznego hemolimfy („nadwyżka hyperosmotyczna") w obszarze zasolenia od 4 do 10‰ wynosi dla *P. acuta* po 10 dniach aklimatyzacji około 0.1 Δ°C, a dla *T. tubifex* po 12 dniach aklimatyzacji około 0.15 Δ°C, zaś po 22 dniach aklimatyzacji tylko 0.08 Δ°C.

6. Krzywe osmoregulacji zwierząt słodkowodnych aklimatyzowanych do wód słonawych przypominają swym charakterem podobne krzywe dla zwierząt euryhalinowych pochodzenia morskiego, ilustrując prawdopodobnie przebieg fizjologicznej ewolucji funkcji osmoregulacyjnych u morskich przodków kolonizujących środowiska hypotoniczne.

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Cena zł 39.—

CONTENTS

1. L. Klekot: Bottom fauna of Dead Vistula 151
2. H. Klimowicz: Rotifers of the near bottom zone of lakes Mikołajskie and Tałtowisko 167
3. W. Zawiślak: Production of crustacean zooplankton in Moty Bay, Lake Jeziorak. Part I. The method of production estimation 179
4. W. Zawiślak: Production of crustacean zooplankton in Moty Bay, Lake Jeziorak. Part II. Estimation of production of the predominating species 193
5. E. I. Izvekova and A. A. Lvova-Katchanova: Sedimentation of suspended matter by *Dreissena polymorpha* Pallas and its subsequent utilization by Chironomidae larvae 203
6. V. Sládeček: The vector of saprobity and system of water quality 211
7. Z. Fischer: The energy budget of *Lestes sponsa* (Hans.) during its larval development 215
8. E. Styczyńska-Jurewicz: Fecundity, survival and haemolymph concentration of *Physa acuta* Drap. (Gastropoda, Pulmonata) and *Tubifex tubifex* Müll. (Oligochaeta, Tubificidae) in relation to salinity of external medium 223

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