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Role of Unionidae and Sphaeriidae (Mollusca, Bivalvia) in the Eutrophic Lake Zbęchy and its Outflow

key words: number, biomass, production, respiration, filtration, flow of phosphorus

Abstract

The abundance, biomass, respiration, and filtration rate of the Unionidae and Sphaeriidae and their significance to the phosphorus cycle was estimated in an eutrophic lake in Poland, situated in an agricultural area, and in its outflow canal. A decrease in Unionidae biomass was compensated for the Sphaeriidae in terms of both biomass and filtration rate. Depending on the developmental state of the Unionidae and Sphaeriidae populations, the volume of pumped water, the amount of removed and assimilated seston and the phosphorus excretion changed significantly.

Contents

1. Introduction

In order to evaluate the importance of Mollusca in aquatic ecosystems it is necessary to know their resources and share in the density and biomass of the invertebrate macrofauna in a given environment. Due to their high density of occurrence, Unionidae sometimes constitute as much as 99 per cent of the total zoobenthos (ØKLAND 1963). As macrofiltrators they play a significant role in the processing of seston both in standing and running waters (LEWANDOWSKI and STAŃCZYKOWSKA 1975, KASPRZAK 1985).

2. Methods and Material

a) Study area

The mussels were collected in Lake Zbęchy and in the outflowing drain-canal. Lake Zbęchy, located at 16° 55′ E longitude and 52° 00′ N latitude some 40 km to the south of Poznań, is part of a group of lakes in an agricultural area (Krzywiń Lake District). The surface area of the lake is 108.9 ha, maximum depth 7.5 m, mean depth 4.2 m, shore-line development 1.88 and volume $4636.6 \cdot 10^3$ m^3. It is an eutrophic, alkalotrophic lake and has no thermal stratification. Lake Zbęchy is polymictic, not only due to its small depth, but also to its location in a flat and open terrain. Emergent plants (in the main Phragmitetum connections) cover approximately 11 % of its surface. The area of the bottom, covered with submerged plants, is about 14.2 ha (corresponding to 13 % of the lake area). The littoral zone (to a depth of 1.5 m) where the Unionidae predominate covers 19.3 ha. Intensive farming is carried out in the drainage basin. The drain canal has a sandy bottom and a very scarce vegetation, it joins a system of drainage ditches and flows into the River Obra Canals located in a typical lowland landscape of intensive agriculture in W Poland (Wielkopolska Region). The studied area was a 1063 m long part of the canal (average depth 0.5 m), 7 km downstream the place where it flows out of the lake. In the vegetation season the mean discharge was 0.11 m^3/sec, the velocity of flow 0.3 m/sec. In drainage basin loamy-sand soils dominate. Their permeability is not much differentiated, usually average. Soils of plough-lands were fertilized by 115 kg/ha nitrate, 96 kg/ha phosphate, 145 kg/ha potassium and 182 kg/ha lime fertilizers. Mean outflow per unit of drainage basin area is 3.5–4.8 dm^3/sec · km^2, thus being very little differentiated. The load of phosphorus to lake from the drainage basin usually did not exceed several g/m^2 year (particular data absent). Mean annual precipitation on the whole area is about 450 mm. The annual average amount of seston (phytoplankton and suspended organic matter and inorganic substances) was 450 mg dry weight per dm^3 water corresponding to 2086.2 t dry weight of seston suspended in the total volume of the lake water. In the studied canal area, the average amount of seston was 350 mg dry weight per dm^3 water corresponding to 817.3 t dry weight of seston suspended in the water which passes 1 m^2 of the canal bottom within one vegetative season (seston concentration data according to unpublished data of Department of Agrobiology and Forestry Polish Academy of Sciences in Poznań). The visibility of Secchi disc in summer was 0.4–0.5 m for lake and 0.3 m for canal. Organic remnants, and dissolved mineral and natural fertilizers get into the lake and the canal from the surrounding completely treeless agricultural areas, which are chiefly occupied by meadows and plough-lands, and from one village with about 150 inhabitants. The shore of the lake near the village received small disperse outlets of sewage. The water there contained considerable amounts of ammonia nitrogen (up to 20 mg N_{NH_4}/dm^3) and also of chlorides (K^+, Na^+, Ca^{+2}), its oxygen consumption was high thus proving a considerable inflow of organic substances accompanied by oxygen deficits. Particular data on the theoretical mean residence time of the water in the lake and on the load of phosphorus to the lake from the atmosphere are absent.

b) Collection and processing of samples

Samples were collected in 1977 and 1978 at 8 stations of the lake littoral, and at 3 stations in the canal from April to November for Unionidae and all year round for Sphaeriidae. In the lake, the Unionidae were sampled at depths of 0.5, 1.0 and 1.5 m from areas of 0.25 m^2 by hand and with the use of a small rake on a framed surface chosen at random at the bottom. At each station 5–10 samples were taken (total 1450 samples). Sphaeriidae were sampled in the canal with a tubular sampler (Kajak, Kacprzak and Polkowski 1965) with a surface of 11.9 cm^2. At each station and date a series of 10 samples was taken along a transverse section through the canal (total 720 samples). In the lake the Sphaeriidae were collected from the following habitats: *Caricetum acutiformis* associations in the eulittoral zone, sand-gravel-muddy bottom amongst the Phragmitetum associations, sandy bottom at depths of 0.2, 0.5 and 1.0 m as well as muddy bottom at depths of 2,3 and 5 m. For the shallow depths a metal frame with a surface of 225 cm^2 and a small net was used, for the remaining habitats an Ekman-Birge sampler with a surface of 218 cm^2. In each habitat a series of 4 samples was collected (total 768 samples). The samples were washed out on a 0.3 mm mesh sieve. As a rule the permanent sampling stations were sampled eight (Unionidae) or twelve (Sphaeriidae) times a year.

c) Calculations

The following quantitative parameters were taken into account: number, biomass, production, respiration, filtration rate, seston consumption, and quantity of stored phosphorus.

The Unionidae biomass was determined on the basis of the following regression equations (Lewandowski and Stańczykowska 1975): for *Anodonta piscinalis* Nilss. – $W_1 = 0.0013\,L^{2.39}$, $W_2 = 0.0000019\,L^{3.3366}$, $W_3 = 0.00000052\,L^{3.1425}$; for *Unio tumidus* Philip.: $W_4 = 0.0018\,L^{2.3086}$, $W_5 = 0.0001\,L^{2.77}$, $W_6 = 0.0000016\,L^{2.9650}$; where: L length of individual with shell in mm, W_1 and W_4 wet biomass of individual with shell in g, W_2 and W_5 dry weight of shell in g, W_3 and W_6 dry biomass of individual without shell in g. Equations valid for *Unio tumidus* Philip. (W_4, W_5, W_6) were used also to calculate the biomass of *Unio pictorum* L.

The biomass of Sphaeriidae was estimated on the basis of weight measurements by the author, and Alimov's (1965a) and Desyatnik's (1968) equations, describing the relation between shell length (L in mm) and body fresh weight (W in g): $W = 0.0002\,L^3$. It was assumed that dry weight amounts to 4 per cent of fresh weight.

The age of individuals belonging to various species of Unionidae was calculated on the basis of the relation between age and length of individuals of specific age groups (Lewandowski and Stańczykowska 1975).

Table 1. Oxygen consumption ($R = a \cdot W^{0.75}$) for Unionidae and Sphaeriidae (re-calculated by the author according to Alimov (1981) data; for the temperature 20° C).
R oxygen consumption (respiration); W live body weight with shell in g

Taxons	Index of oxygen consumption rate a (mg O_2 individual/h)
Unio	0.057
Anodonta	0.082
Unionidae	0.096
Sphaeriidae	0.179

The mean value of respiration was calculated according to equations re-calculated by the author according to Alimov (1981) data (Table 1), with our own corrections of temperature coefficients and the duration of the vegetative season (180 days) and of the research period (8 months). We used the following conversion energy units (1 g O_2 = 3.51 Kcal = 14.69 kJ). Following Alimov (1981) we used $Q_{10} = 2.51$ Unionidae and $Q_{10} = 1.68$ Sphaeriidae (for the temperature range 15–20° C). The average caloric value for Unionidae (1 g dry weight of body = 4.43 Kcal = 18.54 kJ) and Sphaeriidae (1 g dry weight of body = 3.77 Kcal = 15.78 kJ) was based on Alimov's (1981) findings.

The annual production of Unionidae was calculated with the method described by Greze (1965) and used for the estimation of biomass production of various zoobenthos invertebrates (Kajak and Rybak 1966, Kajak 1972, Negus 1966, Tudorancea and Florescu 1968, Tudorancea 1968, 1969, Magin and Stańczykowska 1971, Lewandowski and Stańczykowska 1975). We assumed that the theoretical density of individuals belonging to the youngest age is equal to the highest density of individuals from older age classes. Such a calculation is necessary because with the sampling method used the density of young individuals was relatively low. For verification of the data obtained by using Greze's (1965) regression equations for relation between production (P) and respiration (R), we also used the following equations: for Mollusca (Humphreys 1979): $\log P = 1.033 \log R - 0.717$ (in cal/m² · year); for poikilothermic animals (McNeil and Lawton 1970): $\log P = 0.8233 \log R - 0.2367$ (in Kcal/m² · year).

The annual production of Sphaeriidae, especially *Pisidium casertanum* (Poli) and *P. henslowa-*

num (Shepp.) was calculated according to the Boysen-Jensen method. The annual production of species different from *P. casertanum* and *P. henslowanum* was estimated using the annual production/biomass ($P/\bar{B}$) ratio of 1.3.

The filtration rate was calculated on the basis of equations describing the exponential relation between body weight of individuals and volume of filtrated water per unit time (Table 2). In

Table 2. Relation between filtration rate and biomass for Unionidae and Sphaeriidae according to Alimov (1969, 1981).
F filtration rate (µl/individual · h), W wet biomass with shell (g/m²); for 20 °C

Taxons		Range of biomass (g)	Equations of filtration rate
Unionidae:	*Anodonta piscinalis*	1.25 – 65.00	$F = 84.14\ W^{0.49}$
	Unio pictorum	0.80 – 32.72	$F = 90.36\ W^{0.58}$
	Unio tumidus	0.80 – 32.72	$F = 66.80\ W^{0.53}$
Unionidae		0.043 – 156.00	$F = 85.50\ W^{0.605}$
Sphaeriidae:	*Sphaerium*	0.0070 – 0.4030	$F = 10.38\ W^{0.60}$
	Pisidium	0.0016 – 0.2610	$F = 16.07\ W^{0.60}$

this case, the diversity of the biomass of individuals belonging to various taxons or age groups and the length of the vegetative season were taken into account. Following Alimov (1981) for calculation of filtration rate we used $Q_{10} = 3.11$ (for the temperature range 10 – 15 °C) and $Q_{10} = 2.78$ (for the temperature range 20–25 °C). The filtration rate F_I was calculated as follows: $F_I = V_t : V_0$ where V_t–water filtrated per unit time, V_0–total volume of water.

It was assumed that the average food intake for Unionidae is 20.6 mg dry weight per individual and day and the defaecation–4.2 mg dry weight/ind. day. Food assimilation in summer is 79.6 % of the food which has been ingested (Lewandowski and Stańczykowska 1975). We assumed that the average food intake for *Sphaerium corneum* (L.) is 10.7 mg dry weight per individual and per day and for *Pisidium* 4.5 mg dry weight. It was assumed that in summer 80 % of the ingested food was assimilated.

The phosphorus content of Unionidae was estimated to be 1.0 % of the weight without shell (Stańczykowska 1983), and the phosphorus content in the shells 0.02 % (Kuenzler 1961). Similar values were used for Sphaeriidae.

The Shannon-Weaver diversity index was calculated according to the formula:

$$H' = -\sum_{i=1}^{S} p_i \ln p_i$$

where p_i is, for the i-th species, the ratio: average specific numerical abundance (or biomass)/total abundance (or biomass). S is the number of species present.

3. Results

a) Species composition, diversity, density and biomass

In both the lake and the drain canal three species of Unionidae occurred (*Anodonta piscinalis* Nilss., *Unio tumidus* Philip., *U. pictorum* L.). However, the average density of Unionidae per m² was seven times higher in the canal whereas the average dry biomass (without shells) was eight times higher (Fig. 1, Table 3). The largest number of Unionidae in the lake occurred in April (41.2 in d/m², 647.1 g wet wt with shell/m², 149.1 g dry wt of shell/m², 7.0 dry wt without shell/m²), and in the canal–in October (0.8 ind/m², 12.7 wet wt with shell/m², 2.5 g dry wt of shell/m², 0.1 g dry wt without shell/m²) (Fig. 1). In both the lake and canal the dominating species was *Unio tumidus* (lake 69 %, canal 71 %). It was the dominating species also in the canal in terms of biomass (46 %). In the lake, *Anodonta piscinalis* dominated in terms of biomass (60 %) (Fig. 1, Table 4).

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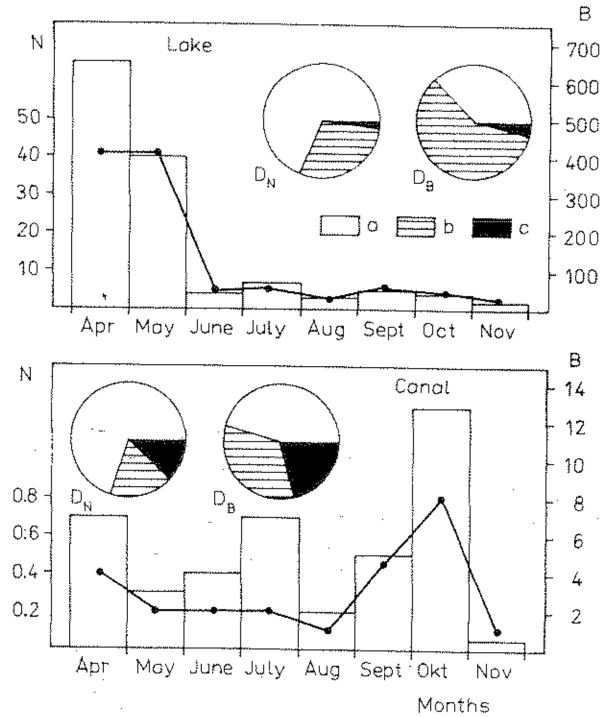

Figure 1. Domination structure and changes of the density and biomass in vegetative season of the Unionidae in Lake Zbęchy and drain canal.
N number (individuals/m²); B wet biomass with shell (g/m²); D_N domination structure with regard to number; D_B domination structure with regard to biomass; *a Unio tumidus, b Anodonta piscinalis, c Unio pictorum.*

Table 3. Average density and biomass of Unionidae.
A density (individuals/m²); B wet biomass without shell (g/m²); C shell weight (g/m²); D dry biomass without shell (g/m²)

	Lake*				Canal			
Species	*A*	*B*	*C*	*D*	*A*	*B*	*C*	*D*
Anodonta piscinalis	4.8 (0.9)	106.62 (18.90)	14.19 (2.51)	1.24 (0.22)	0.07	1.06	0.15	0.02
Unio tumidus	11.3 (2.0)	64.88 (11.50)	42.31 (7.50)	1.93 (0.34)	0.27	1.39	0.75	0.04
Unio pictorum	0.04 (0.01)	6.27 (1.11)	0.13 (0.02)	0.004 (0.0007)	0.04	0.53	0.37	0.01
Total	16.1 (2.9)	177.77 (31.51)	16.63 (10.03)	3.17 (0.56)	0.38	2.98	1.27	0.07

* Average density and biomass (arithmetic means): data in brackets. This value was calculated by multiplying the density and biomass values by the constants (weights) reflecting the ratio of the zonal surface between isobathes to the total lake area. Such calculation allowed to compare the obtained densities in the lake with those in the canal.

Table 4. Number of individuals and biomass of the Unionidae. *A*, *A′* number of individuals (*A* individuals · 10^6, *A′* individuals · 10^3); *B*, *B′* wet biomass with shell (*B* t, *B′* kg); *C*, *C′* dry biomass without shell (*C* t, *C′* kg); *D*, *D′* shell weight (*D* t, *D′* kg)

Species	Lake				Canal			
	A	*B*	*C*	*D*	*A′*	*B′*	*C′*	*D′*
Anodonta piscinalis	0.9	23.3	0.2	0.72	0.3	5.79	0.09	2.7
Unio tumidus	2.2	20.7	0.4	3.59	1.3	10.24	0.19	8.2
Unio pictorum	0.008	1.2	0.0008	1.77	0.2	4.31	0.05	0.03
Total	3.1	45.2	0.6	6.08	1.8	20.34	0.33	10.9

The average annual biomass of Sphaeriidae in the lake amounted to 12.0 mg dry wt/m² (55.6 ind/m²). In the lake *Pisidium ponderosum* Stelf., *P. crassum* Stelf., and *P. henslowanum* Shepp. made up the greatest number (51.2 ind/m²) and biomass (11.3 mg dry wt/m²) of Sphaeriidae. *P. ponderosum* was the most abundant species (10.0 mg dry wt/m²). The highest biomass of Sphaeriidae (Fig. 2) and highest density of dominating species (Fig. 3) was found in a depth about 0.5 m and a depth from 1.5 to 2.0 m. *P. ponderosum* was the most abundant species in 3 m depth. The annual average biomass of Sphaeriidae in the canal (1552.4 mg dry wt/m²) was more than 100 times higher than in the lake (Table 5). In the canal *Sphaerium corneum* (L.), *Pisidium casertanum* (Poli) and *P. henslowanum* (1549.5 mg dry wt/m²) exhibited the highest biomass. The highest average density of Sphaeriidae in the lake and the canal normally was observed in autumn and winter, less frequently in summer (Fig. 4).

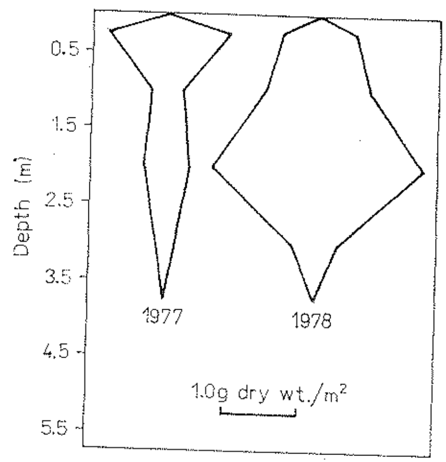

Figure 2. Changes of mean annual biomass of Sphaeriidae in various depth of the Lake Zbęchy.

This species structure of Sphaeriidae is characteristic of European eutrophic lowland lakes (Banaszak and Kasprzak 1980). The diversity of Sphaeriidae showed remarkable differences between the lake and the canal. The fauna in the lake is much more multifarious.This is confirmed by the comparison of the species diversity indices *H′* calculated for the number (H'_n) and the biomass (H'_b) separately in the lake and in the canal (Table 6), as it had to be expected. Though numerically dominant species do not always predominate as regards biomass, the relation between H'_n and H'_b is characterized by a high correlation coefficient ($r = 0.85$; $P < 0.05$). This suggests that both species diversity evaluation indices are equally valid. There is

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Canal		
B'	C'	D'
5.79	0.09	2.7
10.24	0.19	8.2
4.31	0.05	0.03
20.34	0.33	10.9

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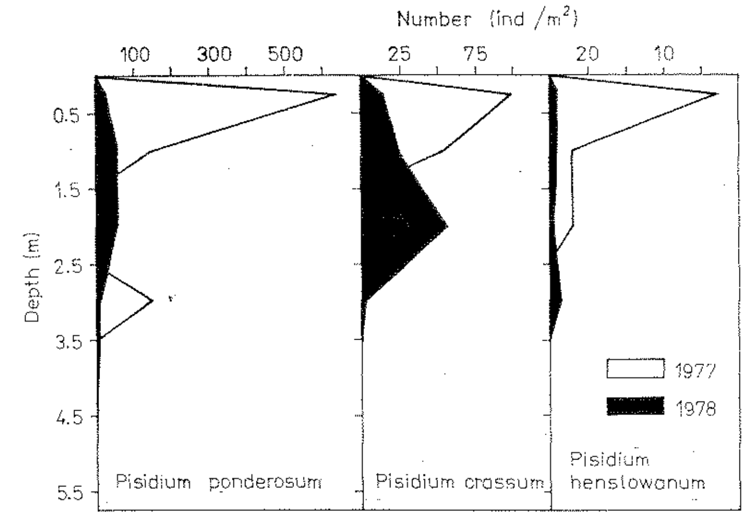

Figure 3. Changes of mean annual number of dominating species of Sphaeriidae in various depth of the Lake Zbęchy. (Read 60 instead of 10 – abscissa *Pisidium henslowanum*.)

Table 5. Comparison of mean annual biomass ($\bar{B}$) and annual production (P) of Sphaeriidae in the lake and the drain canal. The values are expressed as kJ/m² · year

Ecosystems	$\bar{B}$	P	$P/\bar{B}$
Lake	0.19	0.29	1.53
Canal	24.50	33.77	1.38

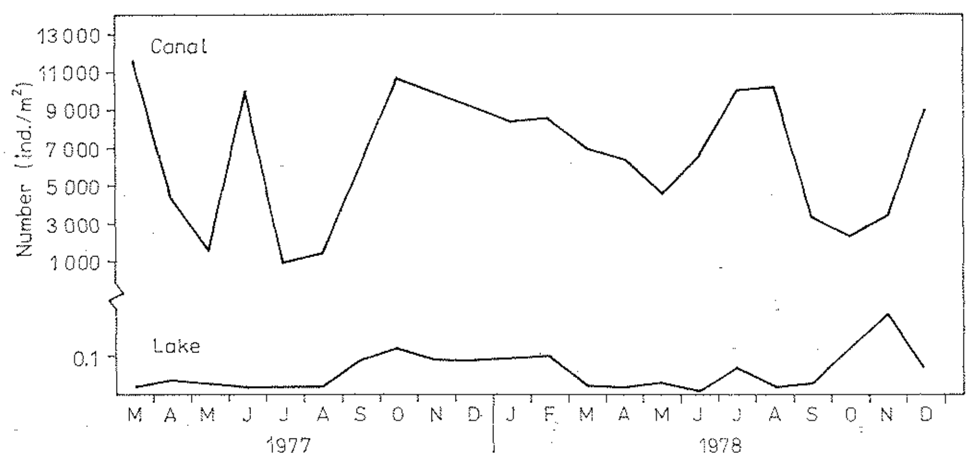

Figure 4. Changes of mean density of Sphaeriidae in the Lake Zbęchy and drain canal during the various months.

a negative correlation between H'_n and the logarithm of density (canal: $r=-0.51$, lake: $r=-0.77$; $P<0.05$) (Fig. 5).

Table 6. Mean values of Shannon-Weaver species diversity index (H') for the Sphaeriidae in the lake and in the canal (probability: $0.01 < P < 0.05$, according to Poole (1974))

		Lake	Canal
H'_{number}	1977	1.7654	0.9085
	1978	0.8939	0.5092
$H'_{biomass}$	1977	1.2597	0.9388
	1978	0.6236	0.7469

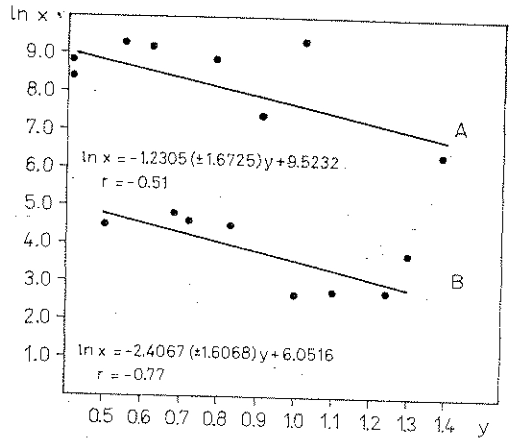

Figure 5. Correlation between Sphaeriidae density and Shannon-Weaver species diversity index H'.
x number (individuals/m^2); y species diversity index H'; A canal; B lake.

b) Age structure of Unionidae populations

Both in the lake and the canal Unionidae from all age groups were sampled (Fig. 6). In the case of *Unio tumidus*, the most numerous individuals are 3 to 6 years old in the lake, and 2 to 5 years old in the canal. With regard to biomass, 6-year-old individuals prevail in the lake and the canal. In the case of *Anodonta piscinalis* the most numerous individuals in the lake are the 4-year-old ones, and in the canal the upto 3-year-old ones. As far as biomass is concerned, the 1 to 3-year-old individuals are much more numerous in the lake and the 5- and 8-year-old individuals in the canal. With regard to both biomass and number, older individuals of *Unio pictorum* prevail in the lake and in the canal (in the lake 6-year-old ones, in the canal 11-year-old ones).

c) Respiration

The energy loss in mussels, due to respiration processes in various aquatic ecosystems, does not exceed 10 % (average 5 %) of the primary production energy of a given ecosystem. Calculations for the Unionidae in Lake Zbęchy and the drain canal showed that the oxygen consumption within 8 months is 40 times higher in the lake than in the canal (Fig. 7). In the lake, the species most significant for the scale of respiration was *Anodonta piscinalis* and in the canal *Unio tumidus*. In the lake Sphaeriidae respiration (40.5 kJ/m^2 · year; *Sphaerium corneum* 55 %, *Pisidium*

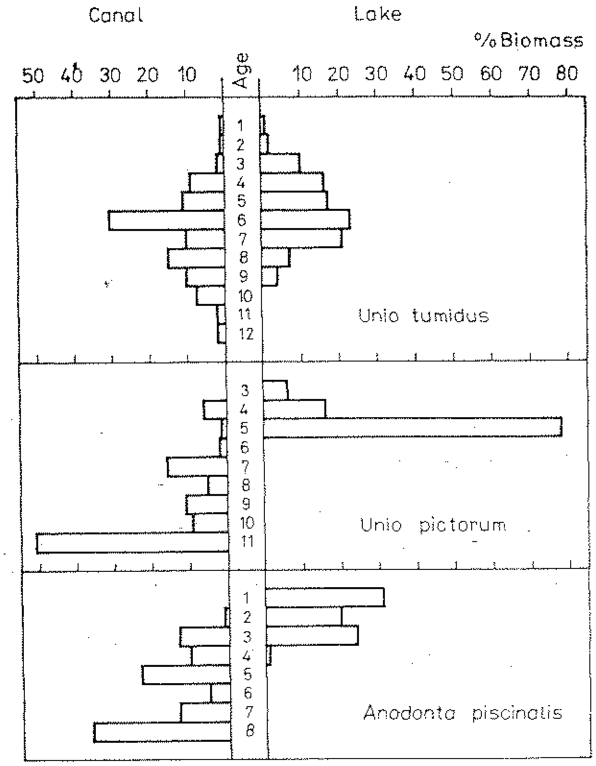

Figure 6. Comparison of the age structure with regard to biomass of the Unionidae in Lake Zbęchy and drain canal.

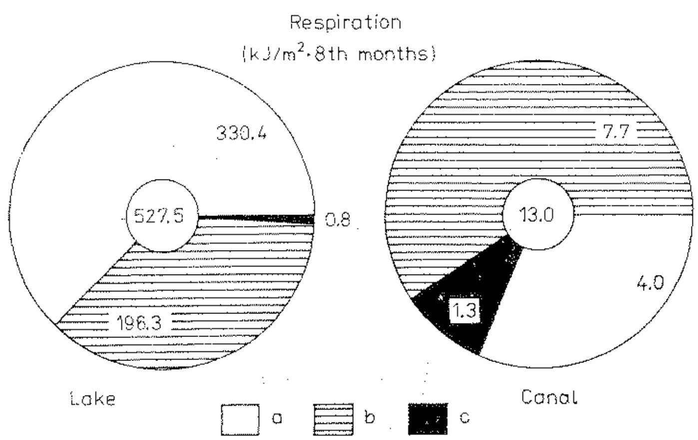

Figure 7. Comparison of the respiration of the Unionidae in Lake Zbęchy and drain canal *a Anodonta piscinalis*; *b Unio tumidus*; *c U. pictorum*.

sp. 45 %) was about 12 times lower than Unionidae respiration. In the canal, oxygen consumption by Sphaeriidae ($47 \cdot 10^3$ kJ/m² · year; *Sph. corneum* 95 % *Pisidium* sp. 5 %) was $3.6 \cdot 10^3$ times higher than the respiration of Unionidae.

d) Production

Table 7. Biomass and annual production of *Anodonta piscinalis* in Lake Zbęchy. A age (years); n density (individuals/m²); b average biomass of one individual (wet weight without shell in g); Δb average increase in biomass of one individual per year in g, $\bar{B}$ average biomass (g/m²), P production (g/m² · year)

A	n	b	Δb	$\bar{B} = n \cdot b$	$P = n \cdot \Delta b$	$P/\bar{B}$
1	1.54*	1.19	1.19	1.83	1.83	1.00
2	1.54*	3.22	2.03	4.96	3.13	0.63
3	1.54*	8.13	4.91	12.52	7.56	0.60
4	1.54	14.38	6.25	22.15	9.63	0.43
5	0.96	19.22	4.84	18.45	4.65	0.25
6	0.22	23.31	4.09	5.13	0.90	0.18
7	1.11	32.96	9.65	36.59	10.71	0.29
8	0.45	48.36	15.40	21.76	6.93	0.32
Total	8.90	–	–	123.39	45.34	–

* Theoretical numbers (non calculated) (= numbers of the 3th and 4th classes of age).

Table 7 shows an example of successive stages of biomass production of *Anodonta piscinalis* in Lake Zbęchy using Greze's (1965) method. The criteria taken into account were: density, average fresh weight without shells, and the average increase in biomass in various age classes. The annual biomass production of all Unionidae in the lake was 638 kg/ha (*Anodonta piscinalis* 71 %, *Unio tumidus* 28.9 %, *U. pictorum* 0.1 %), and in the canal 11.5 kg/ha (*A. piscinalis* 50.9 %, *U. tumidus* 36.0 %, *U. pictorum* 13.1 %). The average productivity index $P/\bar{B}$ (production/biomass) was 0.45 in the lake (*A. piscinalis* 0.46, *U. tumidus* 0.37, *U. pictorum* 0.51), and 0.34 in the canal (*A. piscinalis* 0.44, *U. tumidus* 0.35, *U. pictorum* 0.26). It was highest for younger individuals. The calculation of production is presented in Table 8.

Table 8. Comparison of the production of biomass (in kJ/m²) of Unionidae in the vegetation season in Lake Zbęchy and the drain canal calculated according to Greze (1965) (A), McNeil and Lawton (1970) (B) and Humphreys (1979) (C)

Ecosystems	Method		
	A	B	C
Lake	47.3	139.4	162.8
Canal	0.8	6.2	3.2

The lake and the canal are characterized by a high production of the Sphaeriidae (Table 5). The productivity index $P/\bar{B}$ ranges from 1.38 to 1.53.

e) Filtration rate

The size of seston particles filtrated by Unionidae ranged from 2–4 µm up to 100 µm (Kondratev 1970, Kajak 1979), those filtrated by the genera *Sphaerium* and *Pisidium* was about 1 µm (Rodina 1948). Sphaeriidae are capable to filtrate single bacteria cells. The filtration apparatus of Unionidae and Sphaeriidae is characteriz-

Table 9. Comparison of the biomass of mussels (mainly Unionidae) and filtration rate in the vegetation season in various types of water bodies with different productivity level. P primary production ($kJ \cdot 10^3/m^2$); $\bar{B}$ average wet biomass (g/m^2); F_I index of filtration rate, $F_I = V_t : V_0$ (V_t volume of filtrated water; V_0 water volume)

Ecosystems	P	$\bar{B}$	F_I	Authors
Lake Krasnoe	6.2	1315.0	0.30	ANDRONNIKOVA and DRABKOVA 1976, KUZMENKO 1976
Lake Mikołajskie	13.0	3102.5	1.10	LEWANDOWSKI and STAŃCZYKOWSKA 1975
Lake Drivjaty	7.4	61.0	0.80	GAVRILOV 1970
Lake Krugloe	0.2	15.8	0.21	ALIMOV 1981
Lake Zeleneckoe	0.1	0.1	0.01	ALIMOV 1981
Lake Zbęchy	11.0	177.8	0.79	KASPRZAK 1985
Wołgograd man-made lake	4.7	50.9	0.32	KONDRATEV 1970
Drain canal	0.03	2.9	0.001	KASPRZAK 1985

ed by a high effectiveness of seston removal. It reaches up to 92–100 % of all the particles suspended in the filtrated water (KONDRATEV 1970). ALIMOV (1965b, 1969) described exponential relations between the filtration rate of *Anodonta, Unio, Sphaerium* and *Pisidium* and their body weight. In various types of aquatic ecosystems the filtration rate of Bivalvia is very variable (Table 9) and is particularly high in eutrophic lakes (for example in Mikołajskie Lake) and some artificial lakes. The author's data for Lake Zbęchy and the drain canal show a significant relation between the filtration intensity ($V_t : V_0$) and the total biomass ($\bar{B}$) of Unionidae and Sphaeriidae (Table 10), which is described by a regression equation (Fig. 8). Its slope is in accordance with the data given in the literature, mainly on eutrophic and artificial lakes. For these data, the regression is presented in Fig. 9. In the case of Unionidae there is a distinct relation between filtration rate and production (Fig. 10). In Lake Zbęchy the Unionidae and Sphaeriidae filtrated 80 % of the lake water during the vegetative season. The 4- to 6-year-old *Unio tumidus* and *Anodonta pisci-*

Table 10. Comparison of the filtration rate of the Unionidae and Sphaeriidae in Lake Zbęchy and the drain canal in the vegetation season. $\bar{B}$ average wet biomass without shell (g/m^2); F_I index of filtration rate, $F_I = V_t : V_0$ (see Table 9)

Ecosystems	Taxons	$\bar{B}$	F_I
Lake	Unionidae:	177.8	0.79
	Anodonta piscinalis	106.6	0.37
	Unio tumidus	64.9	0.43
	Unio pictorum	6.3	0.03
	Sphaeriidae:	0.10	0.0059
	Sphaerium corneum	0.03	0.0001
	Pisidium sp.	0.07	0.0059
Canal	Unionidae:	2.98	0.001
	Anodonta piscinalis	1.06	0.0003
	Unio tumidus	1.39	0.0006
	Unio pictorum	0.53	0.0003
	Sphaeriidae:	57.8	0.049
	Sphaerium corneum	42.1	0.015
	Pisidium sp.	15.7	0.034

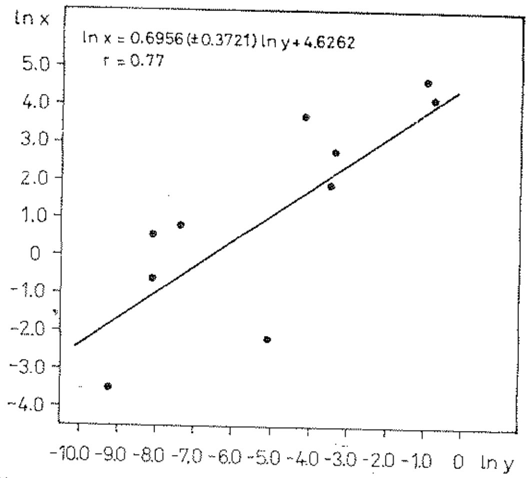

Figure 8. Regression line of relation between biomass and filtration rate for the various species of Unionidae and Sphaeriidae in Lake Zbęchy and drain canal.
x mean annual wet biomass without shell (g/m^2); y index of filtration rate $F_I = V_t : V_0$.

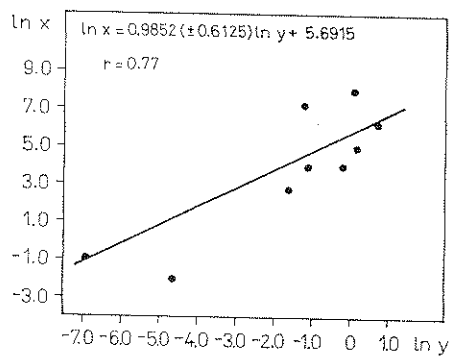

Figure 9. Regression line of relation between biomass and filtration rate for Bivalvia (mainly Unionidae) in eutrophic and man-made lakes according to various literature data.
x mean annual wet biomass without shell (g/m^2); y index of filtration rate $F_I = V_t : V_0$.

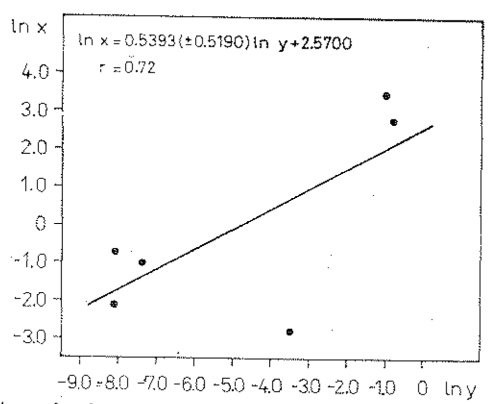

Figure 10. Regression line of relation between biomass production and filtration rate for the Unionidae in Lake Zbęchy and drain canal.
x mean biomass production in vegetative season (g/m^2); y index of filtration rate $F_I = V_t : V_0$.

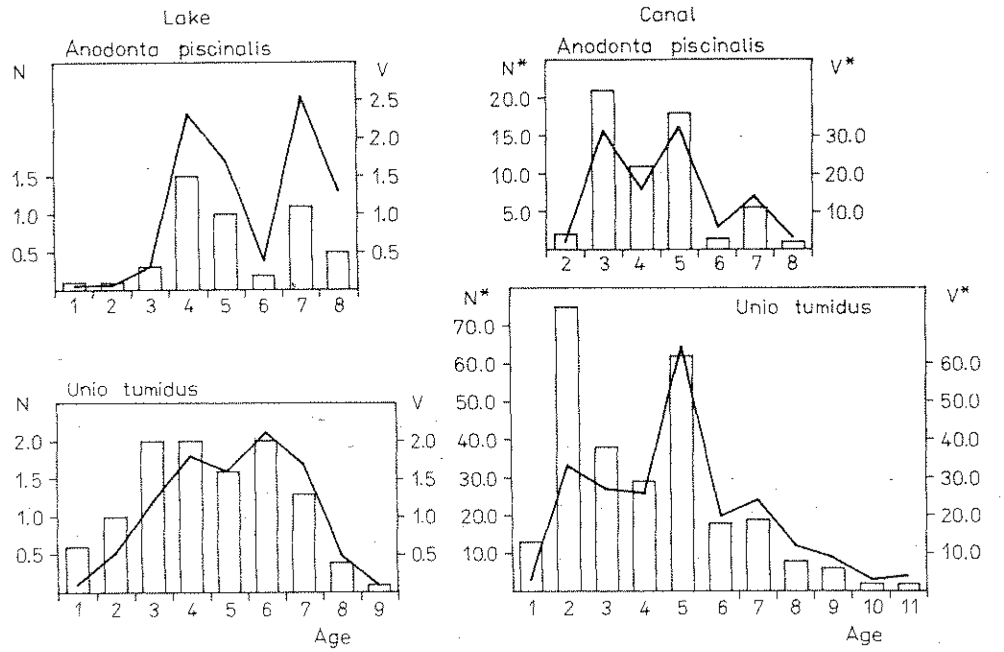

Figure 11. Comparison of the changes of density and volume of filtration rate in vegetative season by members of various age classes (years) of *Anodonta piscinalis* and *Unio tumidus* in Lake Zbęchy and drain canal.
N number (N-individuals/m^2, N^*-individuals $\cdot 10^{-3}$/m^2); V volume of water (V – dm$^3 \cdot 10^3$, V^* – dm^3).

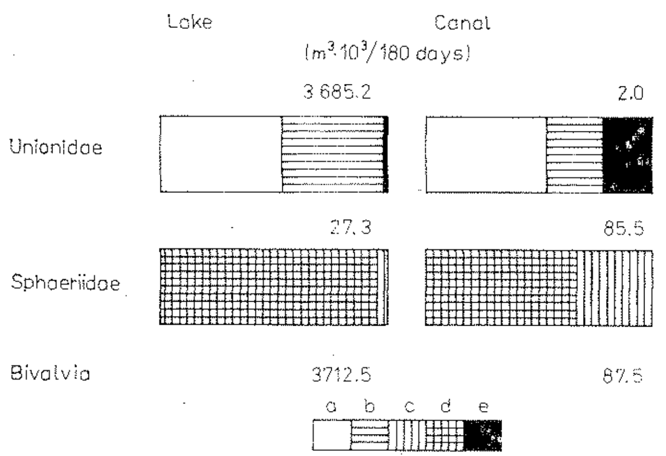

Figure 12. Comparison of the volume of filtrated water in vegetative season by Unionidae and Sphaeriidae in Lake Zbęchy and drain canal, *a Unio tumidus*; *b Anodonta piscinalis*; *c Sphaerium corneum*; *d Pisidium* species; *e Unio pictorum*.

nalis are the most active individuals in this process (Fig. 11). All Unionidae in Lake Zbęchy (about $3 \cdot 10^6$ individuals) can filter water equivalent to 79 % of the volume of the lake in the course of the vegetative season (Fig. 12), removing 11.5 t dry wt of seston from the water, and assimilating 9.1 t dry wt. The Unionidae in the canal remove only 6.81 kg dry wt of seston of which they assimilate 5.42 kg dry wt (Table

Table 11. Comparison of the quantity of seston (in kg dry weight) filtrated in the vegetation season by Unionidae and Sphaeriidae in Lake Zbęchy and the drain canal. S_f filtrated seston; S_a assimilated seston; Fa faeces

Ecosystems	Taxons	S_f	S_a	Fa
Lake	Unionidae:	11476.6	9135.4	2341.2
	Anodonta piscinalis	3402.0	2708.0	694.0
	Unio tumidus	8046.0	6404.6	1641.4
	Unio pictorum	28.6	22.8	5.8
	Sphaeriidae:	12213.3	9769.1	2442.2
	Sphaerium corneum	308.2	246.6	61.6
	Pisidium sp.	11903.1	9522.5	2380.6
Total	Bivalvia	23689.9	18904.5	4783.4
Canal	Unionidae:	6.8	5.4	1.5
	Anodonta piscinalis	1.2	1.0	0.3
	Unio tumidus	4.8	3.8	1.0
	Unio pictorum	0.8	0.6	0.2
	Sphaeriidae:	34425.8	27540.6	6885.1
	Sphaerium corneum	5546.2	4436.9	1109.2
	Pisidium sp.	28879.6	23103.7	5775.9
Total	Bivalvia	34432.6	27546.0	6886.6

11). In the lake the amount of seston assimilated by Unionidae during the vegetative season is, however, only 0.44 % of seston suspended in water. In the canal only 0.00066 % of the amount of seston were removed per m² of the canal bottom. The Sphaeriidae in Lake Zbęchy filtered an amount of water equal to only 1 % of the total volume of the lake (Fig. 12), removing 12.2 t dry wt of seston. At the same time the Sphaeriidae in the drain canal removed 34.4 t dry wt of seston, over $5 \cdot 10^3$ times more than Unionidae. The amount of seston assimilated by Sphaeriidae in the lake during the vegetative season is similar to that of Unionidae (0.46 %). In the canal it is, compared to the lake, almost three times higher (3.4 % of the amount of seston suspended in the water per m² of the bottom).

f) Influence on the phosphorus cycle

The mussels are also of great importance because of the accumulation of phosphorus in their bodies (Stańczykowska 1983). Calculations for the Unionidae in Lake Zbęchy were based on the average number–16.1 ind/m². The average biomass (dry weight and shell) at this density was 59.8 g/m². Thus there was approximately 0.04 g P per m² (Table 12). In Lake Zbęchy the total amount of phosphorus in the Unioni-

Table 12. Comparison of the quantity of total phosphorus accumulative in the Unionidae and Sphaeriidae of Lake Zbęchy and the drain canal

Taxons	Lake (g P/m²)	Canal (g P/m²)
Unionidae	0.04	0.001
Sphaeriidae	0.000004	0.002
Total	0.040004	0.003

dae was about 8 kg P. If we assume that the density is higher, e.g. the actual maximum of 41.2 ind/m^2 (156 g dry wt/m^2), than the amount of phosphorus accumulated in the Unionidae populations in Lake Zbęchy may be as much as 18 kg P. In the drain canal the amount per m^2 was 40 times lower (Table 12). A similar calculation for the Sphaeriidae (32.8 ind/m^2) shows that 4 g P/m^2 were accumulated in the lake, while in the canal with 7,453.5 ind/m^2 the amount of phosphorus is 10 g/m^2. However, if we take into account a higher density of Sphaeriidae, i.e. the maximum in the lake 207.0 ind/m^2 (0.08 g dry wt/m^2) and in the canal 11,850.0 ind/m^2 (2.7 g dry wt/m^2) the amount of phosphorus accumulated in Sphaeriidae populations may reach about 77 g P in the lake, and about 11 g P in the canal. The entire Unionidae population in Lake Zbęchy at the average density of 16.1 ind/m^2 assimilated about 9.1 t dry wt of seston with 36 kg P (Table 13), with the assumption that phosphorus makes up 0.4 % of the dry weight of seston (Stańczykowska 1983). In the canal the Sphaeriidae, whose density is by more than one order lower than that of Unionidae, assimilated over $5 \cdot 10^3$ times more phosphorus (Table 13).

Table 13. Comparison of the quantity of total phosphorus assimilated by Unionidae and Sphaeriidae in Lake Zbęchy and the drain canal

Taxons	Lake (kg P)	Canal (kg P)
Unionidae	36	0.02
Sphaeriidae	39	110
Total	75	110.02

4. Discussion

Numerous studies have shown that mussel biomass in various aquatic ecosystems may attain 75 % of the total benthos biomass, and the production up to 59 % of non-predatory benthos production (Alimov 1981). In the Thames, the Unionidae biomass is over 90 % of the total benthos biomass, twice as large as the fish biomass (Negus 1966). The maximum number per m^2 is several hundred individuals [for example in Kortowskie Lake up to 256 ind/m^2 (Widuto and Kompowski 1968), in rivers from 200 to 400 ind/m^2 (Žadin 1938)]. In oligotrophic and mesotrophic lakes in southern Sweden, the number of *Anodonta piscinalis* is 1.8 ind/m^2, in eutrophic lakes 8.2 ind/m^2, and in extremely eutrophic lakes 20–30 ind/m^2 (Agrell 1949).

The drain canal is characterized by a high density and high production of the Sphaeriidae especially *Pisidium casertanum* and *P. henslowanum.* The density of Sphaeriidae per m^2 may attain some thousand individuals. In the profundal zone of some oligotrophic lakes in Finland the maximum number of *P. casertanum* was 24–319 ind/m^2 (Holopainen and Hanski 1979), in oligotrophic lakes in southern Sweden 100–170 ind/m^2 (Brundin 1949) and in the eutrophic Lake Esröm in Denmark about 5000 ind/m^2 (Berg 1938, Jonasson 1972). The maximum abundance and the maximum number of coexisting species of Sphaeriidae in lakes is reached in the littoral, but there are only one or a few species (with relatively low density) in deep profundity (Holopainen 1979).

In various types of aquatic ecosystems the biomass and the production is very variable (Table 14). The Unionidae biomass in the investigated lake and canal is relatively high—1777 kg/ha in Lake Zbęchy and 30 kg/ha in the drain canal (wet bio-

Table 14. Comparison of the average annual biomass and the average annual production of biomass (in kg/ha) of Unionidae in various water bodies. $\bar{B}$ wet biomass without shell; P production of biomass; $P/\bar{B}$ index of productivity

Taxons	Ecosystems	$\bar{B}$	P	$P/\bar{B}$	Authors
Anodonta piscinalis	Lake Crapina	161.7	50.9	0.32	Tudorancea and Florescu 1969
Unio tumidus	Lake Crapina	116.9	29.9	0.25[1]	Tudorancea and Florescu 1968 b
Unionidae	Lake Mikołajskie	65.6[2]	22.4[3]	0.34	Lewandowski and Stańczykowska 1975
Unionidae	Lake Krasnoe	9400	5640	0.60	Kuzmenko 1976
Unionidae	Thames River	1207.3	193.2	0.16[4]	Negus 1966

[1] The productivity index $P/\bar{B}$ was, similarly as in the case of *A. piscinalis*, higher for young (0.71) then for older individuals (sexual maturity) (0.17).
[2] *A. piscinalis* 84 % [3] *A. piscinalis* 81 % [4] *A. piscinalis* 0.20, *U. tumidus* 0.12

mass without shell). Negus' (1966) findings concerning the high Unionidae biomass in the Thames correspond to our results for Lake Zbęchy. The productivity index $P/\bar{B}$ for Lake Zbęchy is very similar to that for Lake Mikołajskie or Lake Crapina (Table 14). In Lake Zbęchy the productivity index $P/\bar{B}$ for older individuals (5 to 9 years old) of *Anodonta piscinalis* was 0.26, and for the younger ones (1 to 4 years old) 0.67 while the values for *Unio tumidus* were 0.18 and 0.63, respectively. When analysing all the $P/\bar{B}$ values (Negus 1966, Tudorancea and Florescu 1968 b, 1969, Lewandowski and Stańczykowska 1975, Kuzmenko 1976, Kasprzak 1985) it is evident that Unionidae populations are characterised by a low specific production per actual biomass unit. Hitherto studies have indicated that the annual production of the molluscs population is not more than 2.4 % and often less than 0.1 % of the primary production (Alimov 1981). In Lake Zbęchy, the Unionidae production is 0.43 % of phytoplankton primary production.

The average biomass of the Sphaeriidae in the drain canal is relatively high: 388 kg/ha (wet biomass), and the production is 535 kg/ha. In Lake Zbęchy, the biomass is 3 kg/ha, and the annual production is 4.5 kg/ha. The values of the $P/\bar{B}$ ratio for Lake Zbęchy and its drain canal are very similar to those for other oligotrophic and euthrophic lakes. The $P/\bar{B}$ ratio decreased to 1.2 to 1.5 in most cases (Johnson and Brinkhurst 1971); but it is less in deeper regions (Holopainen 1979). The exceptionally low value of deeper regions of Lake Esröm might be due to seasonal oxygen deficiency (Jonasson 1972). The highest value of $P/\bar{B}$ is 4.3, from a river (Madison River, USA) which gets water from hot springs (Gillespie 1969, Holopainen 1979).

The data on Unionidae production based on oxygen consumption are probably too high. Moreover, a comparison of oxygen consumption by Unionidae and Sphaeriidae species indicates that Sphaeriidae are characterized by a specific respiration intensity 2.5 times higher than that of large Unionidae. Oxygen consumption is higher in genus *Anodonta* than in genus *Unio* (Table 1). In mature individuals of *Unio tumidus*, the highest annual oxygen consumption occurs in early spring and in July, and in *Anodonta piscinalis* in April, July and November. An increased respiration in spring is also connected to the beginning of the reproductive seasons and, probably an increased motoric activity following the winter season. Changes of respiration in Sphaeriidae are also connected with their viviparousness. In Lake Zbęchy and the drain canal the estimated energy costs of respiration are 11–16 times higher than the energy expenditure for growth. Similar values of the $P/\bar{B}$ ratio for *Unio tumidus*

nd the average annual pro-
ater bodies. $\bar{B}$ wet biomass
dex of productivity

$P/\bar{B}$	Authors
0.32	TUDORANCEA and FLORESCU 1969
0.25[1]	TUDORANCEA and FLORESCU 1968b
0.34	LEWANDOWSKI and STAŃCZYKOWSKA 1975
.60	KUZMENKO 1976
.16[4]	NEGUS 1966

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0.20, *U. tumidus* 0.12

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r older individuals (5 to 9
ounger ones (1 to 4 years
and 0.63, respectively.
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hot springs (GILLESPIE

sumption are probably
Unionidae and Sphaerii-
pecific respiration inten-
consumption is higher
re individuals of *Unio*
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n increased respiration
seasons and, probably
Changes of respiration
Lake Zbęchy and the
–16 times higher than
ratio for *Unio tumidus*

($P = 7.0$, $R = 97.8$; in kJ/m^2 · year) and *U. pictorum* ($P = 7.8$, $R = 127.2$; in kJ/m^2 · year) have been given by TUDORANCEA and FLORESCU (1968).

The participation of mussels in the destruction of organic matter is 2.0–3.5 times lower than that of larvae of aquatic insects. In the vegetative season the energy-loss by respiration of mussels ranged from 1 to 10 % of primary production (ALIMOV and FINOGENOVA 1975, ALIMOV 1981). The Unionidae are more important in their filtration activity. LEWANDOWSKI and STAŃCZYKOWSKA (1975) found that in Lake Mikołajskie within one season all Unionidae (about 68 · 10^4 individuals) were able to filter about 3 % of the total volume of epilimnion, corresponding to about 2.5 tons dry weight of seston from water. The average volume of water pumped by *Anodonta cygnea zellensis* (GMELIN), 8–10 cm long, was 250–300 ml/h at the temperature of 18–20 °C (DE BRUIN and DAVIDS 1970). MITROPOLSKI'S (1966) experiments showed that *Sphaerium corneum* (only 1,9 cm long) filtered 100 ml/h. In the drain canal the Sphaeriidae are very important since their percentage in the total biomass of invertebrates is fairly high (KASPRZAK, unpublished). The volume filtrated is 50 times higher by Sphaeriidae than by Unionidae (Table 10), and the amount of seston ingested is almost 5 · 10^3 times higher (Table 11). In comparison with the non-predatory zooplankton the amount of seston consumed by Unionidae is 2 · 10^2 times lower in the lake and 2 · 10^3 times lower in the canal than the amount of seston consumed by zooplankton despite the Unionidae biomass in both ecosystems is higher (Table 15). However, in the canal the amount of seston consumed by Sphaeriidae is 6 · 10^2 times

Table 15. Biomass[1] and seston (fresh weight) consumption of various filtrators in Lake Zbęchy and the drain canal in the vegetative season

Ecosystem	Group (species)	Biomass (g/m^2)	Biomass (g/m^3)	Seston consumption (g/m^3 · d)
Lake	Non-predatory zooplankton[2]:	8.7439	1.9431	2.9498
	planktonic crustaceans	8.7088	1.9535	2.9303
	planctonic rotifers	0.0351	0.0078	0.0195
	Unionidae[1,3]:	50.9468	11.3215	0.013704
	Anodonta piscinalis	34.4160	7.6480	0.00407
	Unio tumidus	16.4700	3.6600	0.0096
	Unio pictorum	0.0608	0.0135	0.000034
	Sphaeriidae[1,3]:	0.1013	0.0225	0.0145
	Sphaerium corneum	0.0301	0.0067	0.0003
	Pisidium sp.	0.0712	0.0158	0.0142
Canal	Non-predatory zooplankton[2]:	0.0123	0.0816	0.1237
	planktonic crustaceans	0.0121	0.0803	0.1204
	planktonic rotifers	0.0002	0.0013	0.0033
	Unionidae[1,3]:	0.9973	1.9946	0.0000592
	Anodonta piscinalis	0.4960	0.9920	0.0000014
	Unio tumidus	0.3750	0.7500	0.000057
	Unio pictorum	0.1263	0.2526	0.0000008
	Sphaeriidae[1,3]:	57.8692	115.7384	79.9659
	Sphaerium corneum	42.1234	84.2468	12.8830
	Pisidium sp.	15.7458	31.4916	67.0829

Notes:
1 Wet biomass; for mussels wet biomass without shells.
2 Zooplankton data according to unpublished data of A. KARABIN.
3 For Unionidae data concern 4-, 5- and 6-year-old individuals. It was assumed that the food ratio for crustaceans is 150 per cent and for rotifers 250 per cent of biomass.

higher than in the case of non-predatory zooplankton (Table 15). It should be pointed out that Unionidae ingest seston fractions (also phytoplankton) with a particle size above 30 μm which usually are not utilised by the filtering zooplankton. The proportion of this size fraction in an eutrophic lake is approximately 70 % of all seston (Hillbricht-Ilkowska 1977). Consequently the non-predatory zooplankton and other heterotrophs including Unionidae and Sphaeriidae are alternate consumers of phytoplankton biomass. However, bacteria probably comprise food of a high quality for Sphaeriidae as well (Holopainen 1979).

Consequently, the accumulation of phosphorus in the mussels is much lower than in macrophytes or fishes (Kajak 1978). It cannot be completely neglected in a mass balance of phosphorus. However, the role of Unionidae is not as high as that of *Dreissena polymorpha* (Stańczykowska 1983). In the drain canal, the phosphorus accumulated by Unionidae and Sphaeriidae amounted to 3.4 % of the phosphorus in the seston (3.3 t P) flowing per m^2 of bottom in the vegetative season.

As a result of phosphorus accumulation in various elements of aquatic ecosystems, among others in mussels, the inner resources are beginning to play an important role in eutrophication through the mechanisms and processes within a given ecosystem (Kajak 1979). Naturally, the removal of phosphorus with Unionidae, and with other mussels, as a recultivation procedure, cannot be as effective as the removal of phosphorus with, for example, bottom sediments. The amount of phosphorus removed with Unionidae and other mussels would be very small in comparison with the amount of this element flowing from the basin. It should be also pointed out that the function of Unionidae is not only to accumulate phosphorus but, above all, to be an active element of the ecosystem with a complex role and extensive links.

5. Summary

1. The Unionidae biomass in the investigated ecosystems is relatively high: 1777 kg/ha in the lake and 30 kg/ha in the drain canal (wet biomass without shell). In the lake the $P/\bar{B}$ ratio for older individuals of *Anodonta piscinalis* was 0.26 and for younger ones 0.67 while the values for *Unio tumidus* were 0.18 and 0.63, respectively. The average annual biomass and production of Sphaeriidae in the drain canal is 388 kg/ha (wet biomass) and the production 535 kg/ha. In the lake the Sphaeriidae biomass is 3 kg/ha, and the production 4.5 kg/ha. The $P/\bar{B}$ ratio for Sphaeriidae ranged between 1.38 and 1.53.

2. The diversity of Sphaeriidae measured as Shannon-Weaver index H' shows remarkable differences for the lake and the canal. The values of H' referring to biomass do not correspond to those referring to number since numerically dominant species do not always predominate as regards biomass.

3. The comparison of the respiration of Unionidae populations with the oxygen consumption by the Sphaeriidae populations indicates that in the lake Sphaeriidae respiration (40.5 kJ/m^2 · year) is less than 10 % of the Unionidae respiration, while in the canal oxygen consumption by Sphaeriidae ($47 \cdot 10^3$ kJ/m^2 · year) is $3.6 \cdot 10^3$ times higher.

4. Unionidae and Sphaeriidae in the lake and the drain canal filtrated 80 % of lake water during the vegetative season. In the drain canal the volume of water filtrated by Sphaeriidae is 50 times higher that by Unionidae, and the amount of seston ingested is almost $5 \cdot 10^3$ times higher.

5. In comparison with non-predatory zooplankton, the amount of seston consumed by Unionidae is $2 \cdot 10^2$ times lower in the lake, and $2 \cdot 10^3$ times lower in the canal despite Unionidae biomass in both ecosystems is higher. In the lake Sphaeriidae

consumed $2 \cdot 10^2$ times less seston while in the canal the consumption was $6 \cdot 10^2$ times higher than that of non-predatory zooplankton.

6. In the lake the phosphorus accumulated by Unionidae and Sphaeriidae was 0.90 % of the phosphorus in seston (8.3 t P). In the drain canal the phosphorus accumulated by these mussels amounted to 3.4 % of the phosphorus in the seston (3.3 t P) flowing per m^2 in the vegetative season.

6. References

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