ACTA HYDROBIOL.	27	1	63—73	KRAKÓW 1985

Density, biomass, and respiration of phytophilous macrofauna of associations of *Potamogeton perfoliatus* L. of a polymictic, eutrophic lake*

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Manuscript submitted December 15, 1983, accepted April 24, 1984

A b s t r a c t — In a eutrophic and polymictic lake situated in an area of intense agriculture the numbers, biomass, and respiration of phytophilous macrofauna of *Potamogeton perfoliatus* L. associations were investigated. The mean total biomass of macrofauna on the investigated plant communities was 13.5 g dry weight · m^{-2}. Predators constituted the greatest share in the biomass (79%) and phytophages in density (76%). Predators were also characterized by an intensive metabolism reaching up to 75% of the mean macrofauna respiration of *P. perfoliatus* associations during the vegetation season (1682 kJ · m^{-2}).

K e y w o r d s: lake and canal ecosystems, phytophilous macrofauna.

1. Introduction

Invertebrates inhabiting aquatic plant associations, occur usually in great density and constitute a large part of all heterotrophes of numerous aquatic ecosystems. They are also an important component of the biocenose as far as metabolic processes (production and destruction processes) are concerned, and an essential component of fish feed. Within the scope of complex ecological investigations, carried out in surface waters of the central part of Wielkopolska (Great Poland) on territories of

* The investigations were carried out within Project MR. II/15.

intensive agriculture, the numbers, biomass, and respiration of phytophilous macrofauna of *Potamogeton perfoliatus* L. associations were investigated in the eutrophic, polymictic Lake Zbęchy. The present investigations were a continuation of previous research carried out on phytophilous macrofauna of the melioration canal effluent from this lake (K a s p r z a k, B a n a s z a k 1982).

A large part of the shores of Lake Zbęchy (surface area 108.9 ha, mean depth 4.2 m), lying in the Krzywin Lake District is overgrown with emerged vegetation (mainly *Phragmitetum communis*), covering about 11 per cent of the surface area of the lake. Investigated associations of *Potamogeton perfoliatus,* a component of associations of the class *Potametea,* overgrow to greater part of the surface area of the lake. In the investigation period the maximum surface area of the lake overgrown with associations of the class *Potametea,* reached 14.2 ha, this being 13 per cent of the total surface area of the lake, and 50 per cent of the surface area of the bottom of the littoral zone up to a depth of 2.5 m (28.5 ha) (H. P r z y b y s ł a w s k a - G o ł d y n oral information). The water of the lake is taken off by a melioration canal connected with the canals of the River Obra.

2. Methods

Density of phytophilous macrofauna was estimated during the vegetation season from April till September in the years 1981 and 1982. Samples were collected at 5 stations at 3 to 4 week intervals depending on the period of plant development. Each station, of about 16 m^2 surface area and 0.8 m mean depth, was located in a place where the bottom was overgrown uniformly and densely with plant patches homogeneous with regard to species. Plants were excised from an area of 490 cm^2 and preserved in situ in 4 per cent formalin solution. The plant sample of a surface area delineated by a frame was cut out under water with a knife, the plants then being transferred to a container with the utmost care so as to prevent as far as possible the escape of animals. Depending on the size of the plant patches, the number of collected samples varied from 5 to 25, sampling places being distributed at random on the bottom. Altogether, 12 series of samples (a total of 120 samples) were collected during these two years. After drying on very hard blotting paper, the preserved material was weighed with accuracy to ± 0.1 mg and the biomass of the macrofauna determined. In order to determine the variability of density and occurrence of various groups of phytophilous macrofauna, in August additional sample series were collected at three stations at short time intervals during four consecutive days. The mean, minimum, and maximum number of animals was determined and

the standard deviation calculated. Variability of number and biomass was determined by calculating the index of variability (standard deviation: mean). Dry weight was calculated assuming that it constituted for molluscs and all the other groups 4 and 15 per cent of body weight respectively. The mean density of phytophilous macrofauna was calculated per m^2 of bottom surface of the lake, taking into account the relation of the area occupied by associations of the class *Potametea* to the total surface area of the lake (weighed mean). The mean value of respiration was calculated on the basis of Ryszkowski's equation (1975) and Hemingsen's equation (1960) according to Winberg (1976), taking into consideration corrections for temperature and the length of the vegetation season based upon the author's own measurements and applying conversion into units of energy (1 dm^3 O_2 = 20.112 kJ). The significance of differences between calculated means of respiration values was estimated by Student's "t" test.

3. Results

3.1. Density and biomass

In the investigated associations of *Potamogeton perfoliatus* 12 groups of invertebrates were found to occur. Among these the most numerous were *Oligochaeta*, mainly *Stylaria lacustris* L. and various species of the genus *Nais* O. F. Müll. (*N. barbata* O. F. Müll., *N. pseudobtusa* Pig., *N. simplex* Pig., *N. christinae* Kasp.) and larvae of *Chironomidae* (together 96 per cent of the mean density in the vegetation season). Larvae of *Chironomidae* and *Hirudinea* also have the largest share

Table I. Average density and biomass of phytophilous macrofauna of Potamogeton perfoliatus L. associations in Lake Zbęchy in the vegetation season (April-September)
N - numbers (individuals $\cdot m^{-2}$),
B - biomass (g dry weight $\cdot m^{-2}$)

Taxons	N	B
Naididae	10661	0.6
Chironomidae	9369	4.4
Gastropoda	461	0.1
Hirudinea	150	8.3
Heteroptera	95	<0.1
Ephemeroptera	56	<0.1
Trichoptera	30	<0.1
Gammaridae	12	<0.1
Coleoptera	15	<0.1
Diptera (others)	14	<0.1
Odonata	10	<0.1
Isopoda	7	<0.1
Total	20880	~13.5

Table II. Average density and biomass of dominating taxons of phytophilous macrofauna of Potamogeton perfoliatus L. associations in Lake Zbęchy and macrophytes of the drainage canal.
N - numbers (individuals . m^{-2}; B - biomass (g dry weight . m^{-2}); x According to Kasprzak and Banaszak (1982) data

Taxons	Lake		x Canal	
	N	B	N	B
Hirudinea	150	8.3	3	0.1
Chironomidae	9369	4.4	34	0.1
Naididae	10661	0.6	-	-
Gammaridae	12	<0.1	411	0.3
Trichoptera	30	<0.1	135	0.2
Simmullidae	-	-	143	0.1
Others	658	0.2	54	<0.1
T o t a l	20880	~13.5	780	~0.7

in the biomass of phytophilous macrofauna, constituting 94% of the mean biomass in the vegetation season (Tables I, II, fig. 1). The occurrence of phytophilous macrofauna in associations of *Potamogeton perfoliatus*, especially of the dominating *Oligochaeta* and *Chironomidae*, is characterized during the vegetation season by very high variability; this is indicated, among other factors, by the range of changes in density. The lowest density of *Oligochaeta* and *Chironomidae* was found in April and May, and the maximum (several hundred times greater than the minimum) in August (fig. 2). The biomass of the whole agglomeration of the phytophilous macrofauna was also lowest in April (0.1 g dry weight · m^{-2} with 145 individuals · m^{-2}) (fig. 3). The index of variability of the biomass was highest in the spring, decreasing considerably dur-

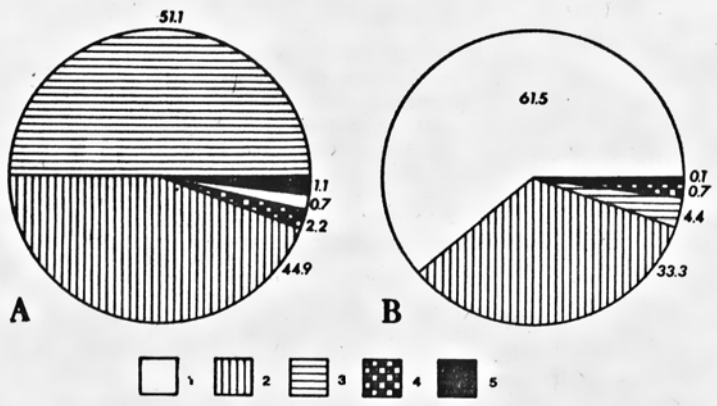

Fig. 1. Domination (in %) of taxonomic groups of phytophilous macrofauna of *Potamogeton perfoliatus* L. associations in density (A) and biomass (B). 1 — *Hirudinea*; 2 — *Diptera*; 3 — *Oligochaeta*; 4 — *Gastropoda*; 5 — others

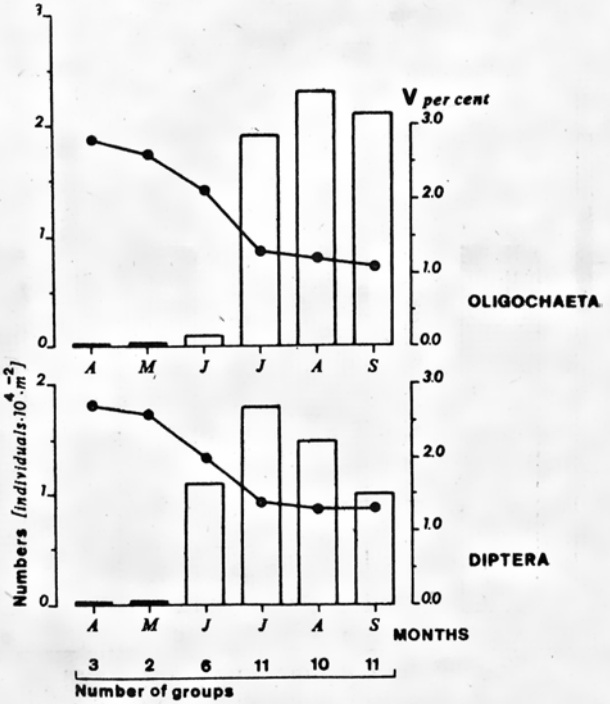

Fig. 2. Variability of density of *Oligochaeta* and *Chironomidae* (*Diptera*), and variability of occurrence of groups of phytophilous macrofauna in the vegetation season in *Potamogeton perfoliatus* L. associations. V — index of variability (ratio standard deviation: arithmetic mean)

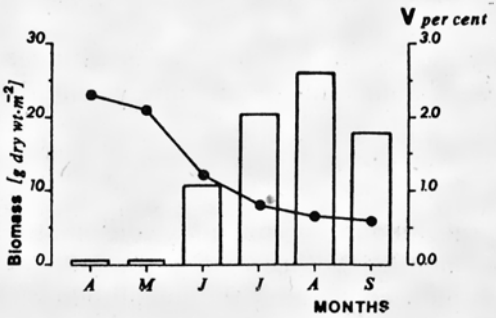

Fig. 3. Variability of biomass of phytophilous macrofauna in the vegetation season in *Potamogeton perfoliatus* L. associations. V — index of variability (ratio standard deviation: arithmetic mean)

ing the vegetation season (fig. 3). This variability results from great changes in the density and occurrence of groups of invertebrates not only in various months of the vegetation season but even in the course of a few consecutive sampling dates, as in shown in fig. 4. As for biomass,

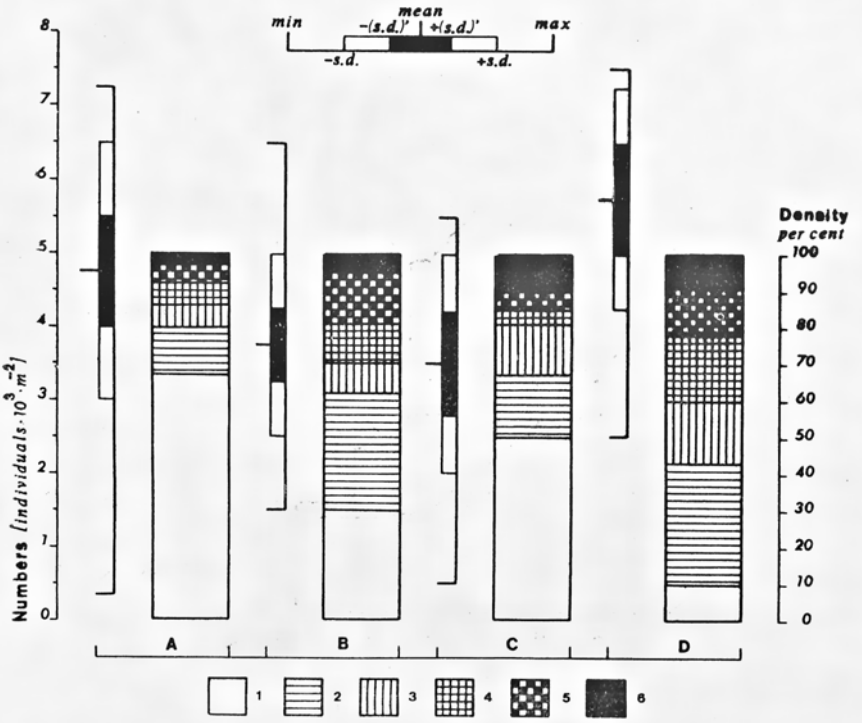

Fig. 4. Composition and variability of density of phytophilous macrofauna colonizing *Potamogeton perfoliatus* L. associations during the first (A), second (B), third (C), and fourth (D) day in August. 1 — *Oligochaeta*; 2 — *Chironomidae* (*Diptera*); 3 — *Hirudinea*; 4 — *Ephemeroptera*; 5 — *Gastropoda*; 6 — *Trichoptera*. s.d. — standard deviation; (s.d.)' — standard error of standard deviation

predators (79 per cent) dominated decisively, whereas numerically phytophagous forms were dominant (76 per cent) (Table III).

3.2. Respiration

Estimation of the amount of oxygen consumption is one of the generally adopted methods of assessing the role of the fauna in an ecosystem, though data concerning the magnitude of respiration do not always give a precise picture of the role played by various groups of invertebrates in aquatic ecosystems. The mean respiration values, calculated by Ryszkowski's and Hemmingsen's equations are very similar for the whole phytophilous macrofauna. The differences between the values calculated by these two equations are statistically non-significant (for $P < 0.05$), this indicating that either equation may be used in order to obtain an estimation of the respiration values of phytophilous macrofauna. In associations of *Potamogeton perfoliatus*

Table III. Average density, biomass, and respiration of functional groups of phytophilous macrofauna of Potamogeton perfoliatus L. in Lake Zbęchy and macrophytes of the drainage canal. N - numbers (individuals m^{-2}); B - biomass (g dry weight $\cdot m^{-2}$); R - respiration (kJ $\cdot m^{-2}$).
x According to Kasprzak and Banaszak (1982) data. 1 - Calculated on the basis of Ryszkowski's (1975) equation: $R = 0.357\ W^{0.813}$ (R - µl $O_2 \cdot$ individual$^{-1} \cdot h^{-1}$, W - live body weight in mg; for temperature 15° C); Q_{10}= 2. 2 - Calculated on the basis of Hemmingsen's (1960) equation according to Winberg (1962); $R = 0.142\ W^{0.751}$ (R - ml $O_2 \cdot$ individual$^{-1} \cdot h^{-1}$, W - live body weight in g; for temperature 20° C); Q_{10}= 2. Note. Calculated with regard to corrections of temperature on the basis of individual field measurements (canal: 16.9° C, lake: 18.2° C).

Functional groups	Lake				x Canal			
	N	B	R		N	B	R	
			1	2			1	2
Predators (1)	5137	10.6	1261	1527	140	0.2	26	31
Phytophages (2)	15747	2.9	421	456	495	0.4	57	62
Filtrators (3)	-	-	-	-	142	<0.1	8	10
Parasites (4)	-	-	-	-	<0.1	<0.1	<0.1	<0.1
Total	20884	13.5	1682	1983	~777	~0.7	~91	~103

(1) Trichoptera, Coleoptera, Chironomidae (part), Hirudinea, Neuroptera, Odonata, Chaetogaster diaphanus (Oligochaeta)
(2) Gammaridae, Ephemeroptera, Chironomidae (part), Gastropoda, Isopoda Heteroptera, Ephydridae, Oligochaeta
(3) Simullidae, Chironomidae (part)
(4) Hymenoptera

in Lake Zbęchy predators constitute a large share in the respiration of the total macrofauna (75 per cent of mean respiration of the whole phytophilous macrofauna) (Table III). Hence the value of respiration develops here in a different way from that in associations of phytophilous

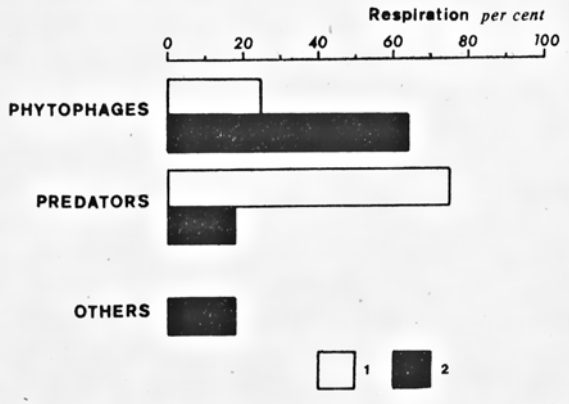

Fig. 5. Comparison of respiration of phytophages and predators of phytophilous macrofauna in *Potamogeton perfoliatus* L. associations in the eutrophic lake and melioration canal. 1 — lake; 2 — melioration canal

macrofauna of the melioration canal effluent from the investigated lake where, during the vegetation season, phytophagous forms show a great participation (64 per cent) in the respiration of the whole phytophilous fauna (fig. 5).

4. Discussion

Investigations on the composition and density of the whole phytophilous macrofauna have hitherto been carried out mainly in various plant associations of the littoral zone of lakes and dam reservoirs (among others Hillbricht 1953, Karassowska, Mikulski 1960, Wolnomiejski, Dunajska 1966, Kuflikowski 1974, Soszka 1974, 1975a, 1975b, Głowacka et al. 1978) and of fish rearing ponds (Szumiec 1962, Matlak 1963, Kuflikowski 1970, Korinkova 1971, Markošova 1974, Srokosz 1977). There are no precise data on phytophilous macrofauna inhabiting aquatic plant associations in small eutrophic, polymictic lakes and running waters, especially small melioration canals, which makes scrupulous comparisons difficult. Many published results concerning the density of phytophilous macrofauna can also be compared only with difficulty on account of the various methods applied in converting the obtained values of density (Starmach 1954, Karassowska, Mikulski 1960, Gurzęda 1959, Głowacka et al. 1976). Data concerning the amount of biomass and respiration as well as the participation of various functional groups in the density or respiration of the whole phytophilous macrofauna are also lacking.

A comparison of the mean density and composition of communities of phytophilous macrofauna of *Potamogeton perfoliatus* associations in Lake Zbęchy, and their variability, with results concerning the eutrophic Lake Mikołajskie (Głowacka et al. 1976) indicates a great similarity both as far as taxonomic composition and quantitative relations between particular groups of invertebrates are concerned. However, a comparison of phytophilous macrofauna communities of *Potamogeton perfoliatus* of Lake Zbęchy and of the phytophilous macrofauna of all plant communities of the melioration canal, which drains water from the investigated lake, points to the occurrence of considerable differences in biomass and participation of particular functional groups. In plant communities of the canal *Sparganium simplex* Huds. (Kasprzak, Banaszak 1982) associations are most numerously inhabited by macrofauna, among which *Amphipoda* (*Rivulogrammarus roeselii* Gerv.), *Trichoptera*, and *Simullidae* (*Diptera*) dominate, constituting jointly 88 per cent of the total phytophilous macrofauna of the canal with regard to number and biomass (Table II). The mean biomass of the whole macrofauna in

associations of *Potamogeton perfoliatus* of Lake Zbęchy was in the vegetation season 13.5 g dry weight · m^{-2}, whereas the mean biomass in conversion, taking into account the relation of the area occupied by associations of *Potamogeton perfoliatus* to the whole area of the lake bottom, was 1.76 g dry weight · m^{-2}, and was almost six times as great as that of phytophilous macrofauna of all plant communities on an average m^2 of the bottom area of he canal (0.3 g dry weight · m^{-2}) (Kasprzak, Banaszak 1982). The great variability in taxonomic composition and number of phytophilous macrofauna of the investigated associations of *Potamogeton perfoliatus* (fig. 4) should be ascribed on the one hand to considerable undulation of the water and on the other to the agricultural use of the bank. The investigated plant patches were located in places exposed to the wind from the side of the lake in close proximity to a cattle watering place and to where water was drawn for farm use. Among the distinguished functional groups phytophagous forms were dominant in the biomass, i.e. opposite to the behaviour of associations of *P. perfoliatus* in Lake Zbęchy where in this respect predators dominated. These differences resulted, among other reasons, from the fact that among phytophilous predators forms (mainly *Hirudinea*) markedly larger than in the canal (mean individual biomass 2.05 mg dry weight) dominated. The mean individual biomass of predators of plant associations in the canal was 1.4 times smaller (1.54 mg dry weight) than that in the lake, whereas that of phytophages was 4.4 times greater (canal 0.79 mg dry weight, lake 0.18 mg dry weight) (Kasprzak — unpublished data). Phytophagous invertebrates of the association *Potamogeton perfoliatus* in the Lake Zbęchy were characterized not only by a smaller individual weight than phytophages of plant associations in the canal, but also by the highest numerical share of the whole phytophilous macrofauna, this also demonstrating their important role in the decomposition of organic plant matter in the lake. It is not excluded that in various times of the year and of the vegetation season the participation of predators in plant associations in the canal and lake undergoes considerable changes resulting from changes of the feeding grounds of fish hydrological relations, and alterations in the periods of plant development in the canal and in the lake. There are markedly fewer groups of invertebrates and a lower density of *Mollusca, Chironomidae* (*Diptera*), and *Oligochaeta* in the canal than in Lake Zbęchy and other eutrophic lakes (Karassowska, Mikulski 1960, Wolnomiejski, Dunajska 1966, Głowacka et al. 1976). *Rivulogammarus roeselii* Gerv. (*Gammaridae*), a species constituting in the canal 50 per cent of the total biomass of phytophilous macrofauna (Table II) and one of the basic components of fish feed in the canal (Truszkowski, oral information), is in the associations of *Potamogeton perfoliatus* of Lake Zbęchy almost 70 times lower (0.04 per cent of the total

biomass of macrofauna associated with *P. perfoliatus*). As compared with the mean biomass found in rearing ponds, from 15.7 g fresh weight · m^{-2} (Korinkova 1971) to 42.2—66.0 g fresh weight · m^{-2} (Dvořák 1978), the mean biomass of phytophilous macrofauna in the melioration canal was from a few to more than ten times lower (Kasprzak, Banaszak 1982).

5. Polish summary

Zagęszczenie, biomasa i respiracja makrofauny naroślinnej zbiorowisk *Potamogeton perfoliatus* L. śródpolnego jeziora eutroficznego

W eutroficznym i polimiktycznym jeziorze Zbęchy, położonym na terenach o intensywnej gospodarce rolnej, przeprowadzono oceny liczebności, biomasy i respiracji makrofauny naroślinnej, występującej w zbiorowiskach *Potamogeton perfoliatus* L. Wykazano, że średnia biomasa całości makrofauny w badanych zbiorowiskach w sezonie wegetacyjnym wynosi 13,5 g suchej masy · m^{-2} (tabela I, ryc. 1), a największy udział (94%) w wielkości biomasy makrofauny naroślinnej mają *Chironomidae* i *Hirudinea* (tabela II). Zagęszczenie *Oligochaeta* i *Chironomidae* oraz biomasa całej makrofauny naroślinnej charakteryzują się w miesiącach wiosennych największą zmiennością, mierzoną wartościami współczynnika zmienności (ryc. 2, 3); zmniejsza się ona znacznie w ciągu sezonu wegetacyjnego. Zmienność ta spowodowana jest dużymi zmianami w zagęszczeniu i występowaniu poszczególnych grup bezkręgowców nie tylko w różnych miesiącach sezonu wegetacyjnego, ale nawet w ciągu kilku kolejnych dni poboru prób (ryc. 4). Największy udział w zagęszczeniu mają bezkręgowce roślinożerne (76%), natomiast największy udział w biomasie — drapieżniki (79%) (tabela III). Drapieżniki charakteryzują się także wysokim udziałem (75%) w ciągu sezonu wegetacyjnego w wielkości oddychania całej makrofauny naroślinnej (1 683 kJ · m^{-2}) (tabela III, ryc. 5). Porównanie występowania poszczególnych grup i ich zagęszczenia w badanym jeziorze z danymi dotyczącymi kanału odwadniającego wskazuje na występowanie sześciokrotnie większego zagęszczenia całej makrofauny naroślinnej w zbiorowiskach *Potamogeton perfoliatus* L. badanego jeziora i znacznie większego zagęszczenia drapieżników. W jeziorze wśród drapieżników naroślinnych dominują formy (głównie *Hirudinea*) wyraźnie większe (2,05 mg sm.) od drapieżników zbiorowisk roślinnych kanału, których biomasa osobnicza jest w porównaniu z jeziorem 1,4 razy mniejsza (1,54 mg sm.), natomiast roślinożerców 4,4 razy większa (kanał 0,79 mg sm., jezioro 0,18 mg sm.). Bezkręgowce roślinożerne zbiorowisk *Potamogeton perfoliatus* L. odznaczają się nie tylko wyraźnie mniejszym ciężarem osobniczym w porównaniu z roślinożercami zbiorowisk roślinnych kanału, ale charakteryzują się także największym udziałem w zagęszczeniu całości makrofauny naroślinnej tych zbiorowisk.

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