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THE INVERTEBRATES ON SUBMERGED MACROPHYTES IN THREE MASURIAN LAKES

ABSTRACT: The composition and number dynamics of invertebrates on 4 species of submerged macrophytes (*Potamogeton lucens* L., *P. perfoliatus* L. *Myriophyllum spicatum* L. and *Elodea canadensis* Rich.) have been analysed. *Chironomidae*, *Oligochaeta* and *Mollusca* dominated. The numbers of invertebrates change noticeably in time, space, and on different species of macrophytes. The species composition, and numbers of invertebrates on macrophytes are different than those of the littoral benthos which is usually less abundant.

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1. INTRODUCTION

The ecology of invertebrates of littoral zone of lakes is not very well known. Usually qualitative studies are being carried out. Less frequent are quantitative studies in which various methods are applied and therefore in the majority of cases the data cannot be compared.

For example, the fauna numbers are given in relation to the following units: plant surface (Entz 1947, Rosine 1955), plant volume (Giziński 1958, Matlak 1963, Kuflikowski 1970, 1974), cut of plant association of a maximum density (Karassowska and Mikulski 1960), dry plant weight (Andrews and Hasler 1943), fresh plant weight (Zimbalevskaja 1966, Bownik 1970, Pieczyński 1973), shoot length (Krecker 1939), surface area of littoral bottom overgrown with vegetation (Macan 1949, 1965, Gerking 1957, Gromov 1960, Ščerbakov 1961, 1967,

Sokolova 1965, Gillespie and Brown 1966, McLachlan 1969, Kořinkova 1971, N. Wolnomiejski – unpublished data), etc. Several authors discuss the range of application of particular methods (Gurzęda 1959, Karassowska and Mikulski 1960, Edmondson and Winberg 1971, Kořinkova 1971, Pieczyński 1973, N. Wolnomiejski – unpublished data, and others).

The aim of this study was to analyse the composition and number dynamics of invertebrates inhabiting submerged macrophytes and their comparison with littoral benthos.

2. AREA AND METHODS

The study was carried out between 1966 and 1971 in three lakes of the Masurian Lakeland: Mikołajskie, Śniardwy and Warniak (Tab. I). The Mikołajskie Lake was the main object of investigations. A description of these lakes is given by Olszewski and Paschalski (1959), Szostak et al. (1961), Mikulski (1966), Szostak (1967), Bernatowicz, Pieczyńska and Radziej (1968), Bernatowicz (1969), Pieczyńska (1972) and others.

Tab. I. Characteristics of the lakes

Lake	Surface area (ha)	Depth (m)		Development of shore line	Area of littoral (in percentage of total lake surface)	Limnological type
		maximum	mean			
Mikołajskie	460	27.8	11.0	1.7	19	eutrophic, holomictic
Śniardwy	10,970	23.4	5.8	2.2	34.5	eutrophic, polymictic
Warniak	38.4	3.7	1.2	1.1	≈100	eutrophic, polymictic

In Mikołajskie Lake the quantitative material was systematically collected over a year on three main sites. These sites were situated along the south-western shore. There were various species of submerged plants, different bottom and different exposure to wave action (Tab. II). During the summer additional material was collected in the littoral of the whole lake. In lake Śniardwy samples were taken in summer in 1966 and 1970 on 22 sites, and in lake Warniak – in summer 1970 on 5 sites.

The methods of collecting and analysing the material were as follows:

Macrophytes. Quantitative samples of macrophytes up to 1 m deep were taken using a frame of a surface area 0.25 m² or 1 m². At greater depths Bernatowicz (1960) sampler of a surface area 0.16 m² was used. In some cases the material was collected by a diver. Afterwards fresh biomass of macrophytes per 1 m² of the littoral was determined.

Fauna associated with macrophytes. Animals living on macrophytes and selected without a microscope were taken into account. The animals were collected together with the macrophytes. The sample was a gently pulled plant placed under the water into bags,

Tab. II. Characteristics of sites in Mikołajskie Lake

Site	Plant species	Bottom	Depth (m)	Wave action
1	<i>Myriophyllum spicatum</i> <i>Elodea canadensis</i> <i>Potamogeton lucens</i> <i>P. perfoliatus</i>	mud with plenty of plant detritus	0.5–0.7	weak
2	<i>E. canadensis</i>	mud	0.5–0.7	medium
3	<i>P. lucens</i> <i>P. perfoliatus</i>	sand	0.5–0.7	strong

plastic boxes or jars. In laboratory the fauna was selected macroscopically and the plants were weighed. In order to compare the composition and numbers of the invertebrates on various plant species, on different sites and in different periods the numbers of fauna were calculated per 100 g fresh weight of plants and per 1 m² of the bottom (with regards to the biomass of plants on 1 m²). The latter was also used for comparisons of the invertebrates on plants and benthic fauna. In order to compare the numbers of fauna on macrophytes and on experimental substrates they were calculated per 100 cm² of leaf surface.

Benthic fauna. Samples of bottom fauna were taken in the neighbourhood of submerged plants. The apparatus of Morduchaj-Boltovskoj (1958) type of a surface of 50 cm² was used. The material was sieved through a sieve of a mesh size 0.4 × 0.4 mm. In laboratory the fauna was selected macroscopically. The numbers of benthic fauna were calculated per 1 m² of the surface area of the bottom.

3. RESULTS

3.1. Macrophytes and the periphyton

The three lakes under study differ in the area occupied by submerged macrophytes and in their species composition and biomass.

In lake Śniardwy submerged macrophytes cover 3,027,7 ha (27,6% of lake surface and 80.0% of the littoral). The *Charales* dominate, and quite abundant are: *Ceratophyllum demersum* L., *Potamogeton compressus* L., *Elodea canadensis* Rich., *Fontinalis antipyretica* L. and *Potamogeton lucens* L. The submerged plants are most abundant at the depth of 3.5–4.5 m. The maximum depth of their occurrence is 6.5 m (Bernatowicz, Pieczyńska and Radziej 1968).

In lake Warniak submerged macrophytes cover 29.1 ha (75.8% of lake surface). *Ceratophyllum demersum* dominates. Quite abundant are: *Stratiotes aloides* L., *Potamogeton compressus* and *Elodea canadensis*. The mean depth of occurrence of submerged macrophytes is 1.2 m and the maximum 3.5 m (Bernatowicz 1969).

In Mikołajskie Lake submerged macrophytes cover 48.0 ha (10.4% of lake surface, and 55% of littoral surface). The maximum depth of occurrence of submerged plants is 6 m. *Charales*,

Ceratophyllum demersum, *Elodea canadensis*, *Fontinalis antipyretica* and *Potamogeton perfoliatus* L. dominate in the lake (Pieczyńska 1972, Kowalczyński — in press).

Four species of macrophytes: *Potamogeton perfoliatus*, *P. lucens*, *Elodea canadensis* and *Myriophyllum spicatum* L. were the main object of study. They were very abundant and especially in the shallow littoral. The changes in biomass of these species were analysed in an annual cycle in Mikołajskie Lake, on three sites, in 1967, 1969 and 1970. 210 quantitative samples of macrophytes were taken.

Potamogeton perfoliatus. It occurs between April and November. In May the biomass of *P. perfoliatus* did not exceed 32 g of fresh weight per 1 m². The highest biomass values were recorded in the successive years in August or September (225–600 g of fresh weight per 1 m²). In October *P. perfoliatus* occurred in small quantities and died in November (Fig. 1).

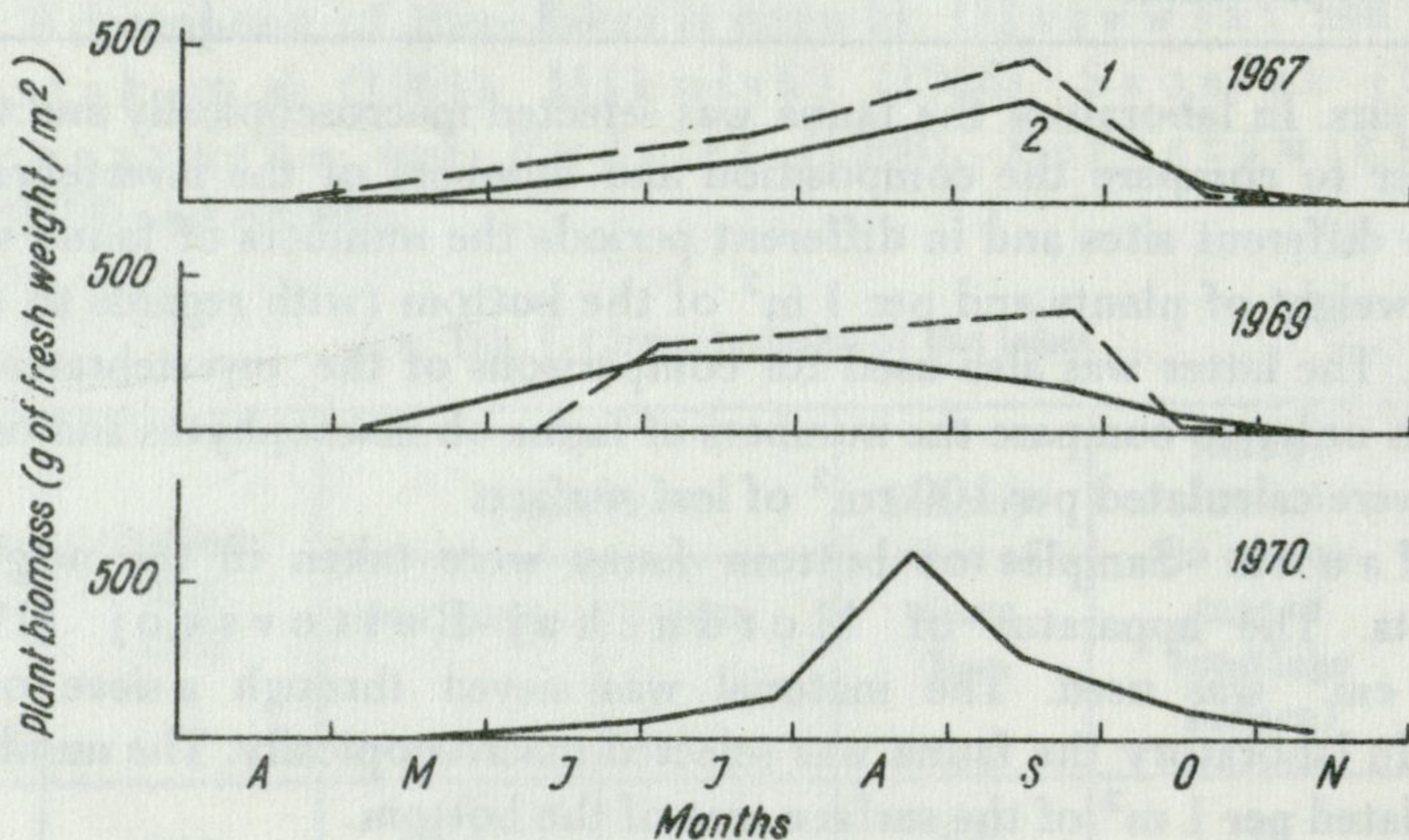


Fig. 1. Changes in biomass of *Potamogeton perfoliatus* in Mikołajskie Lake in 1967, 1969 and 1970
1 — site 1, 2 — site 3

Potamogeton lucens. It occurs between April and November — slightly earlier than *P. perfoliatus*. Its numbers and dates of the appearance of first plants differed on the sites examined and each year. In different environments these plants either do not occur in May or attain 50 g of fresh weight per 1 m² of the littoral bottom. The highest biomass is attained by this plant in different years and parts of the lake in July, August or September. The highest biomass in successive years ranges from 300 to 1,740 g of fresh weight per 1 m². *P. lucens* dies in November and at that time its biomass does not exceed 11 g of fresh weight per 1 m² (Fig. 2).

Myriophyllum spicatum. In comparison to the previously discussed macrophytes it has a longer vegetation period; in winter under the ice cover a small amount of green shoots of rooted plants has been recorded. The highest biomass is in July or August and in different years it is 940–2,625 g of fresh weight per 1 m². In both years the biomass of *M. spicatum* decreased since September (Fig. 3).

Elodea canadensis. It is different from the other species of macrophytes by having perennial shoots which are also green in the winter. It occurred all the time during the investigations. The biomass differed in all three years of the study and also on two sites in the same year. The highest biomass was observed in different months between April and October (460–1,980 g of fresh weight per 1 m²) (Fig. 4).

The comparison of biomass of these species of submerged plants in Mikołajskie Lake shows that *M. spicatum* and *E. canadensis* have a much higher biomass than *P. perfoliatus* and

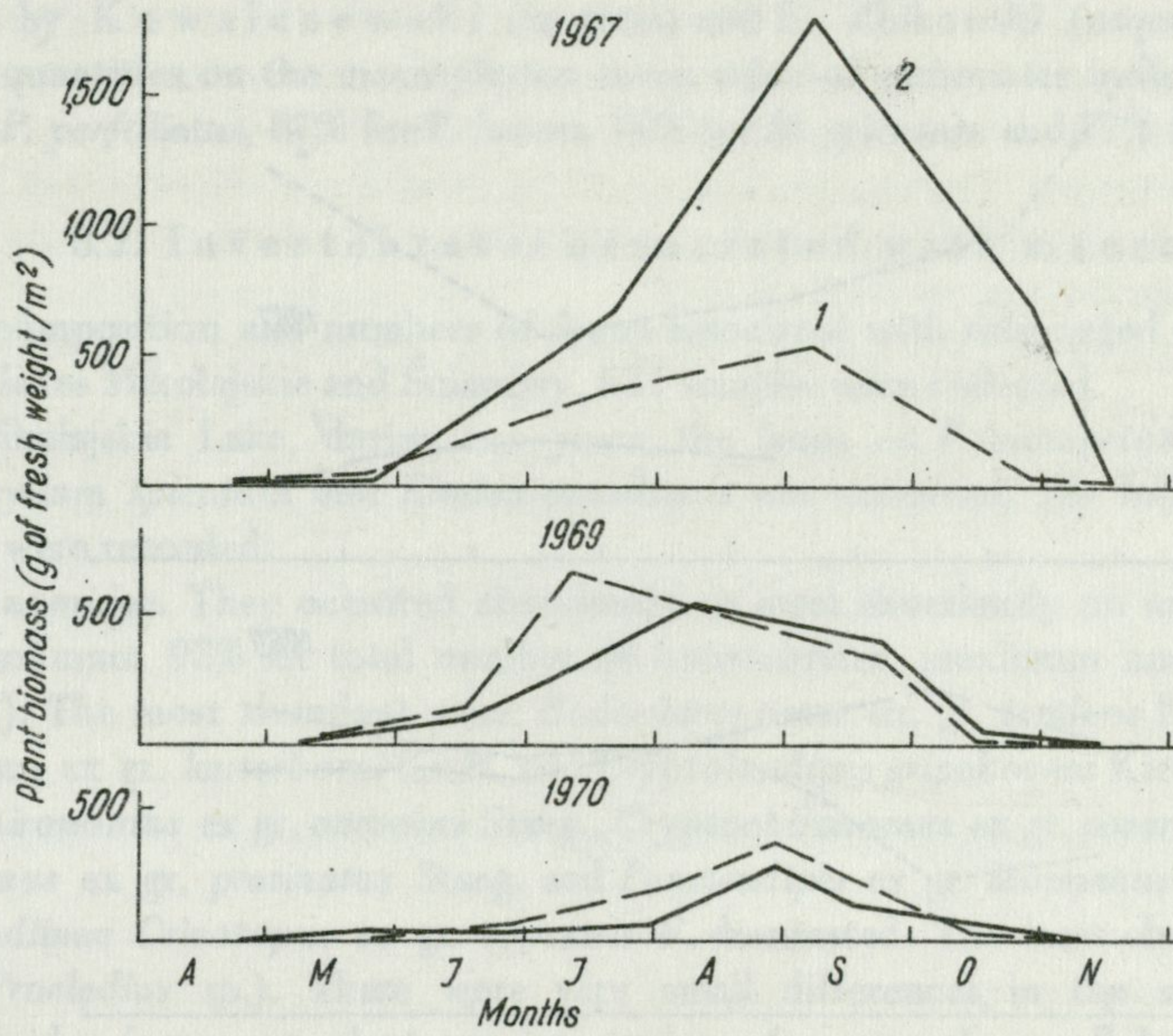


Fig. 2. Changes in biomass of *Potamogeton lucens* in Mikołajskie Lake in 1967, 1969 and 1970
1 – site 1, 2 – site 3

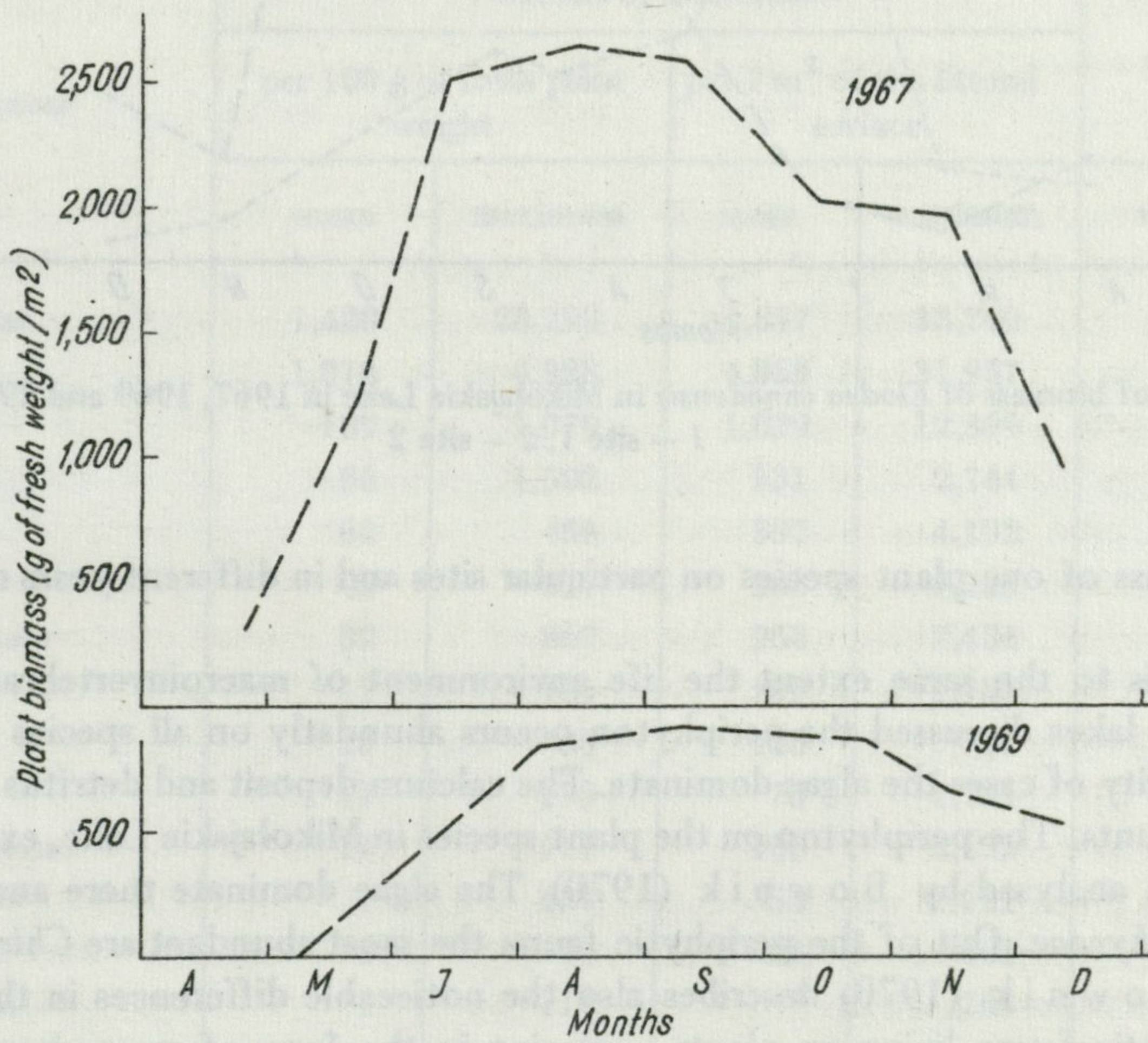


Fig. 3. Changes in biomass of *Myriophyllum spicatum* in Mikołajskie Lake in 1967 and 1969 (site 1)

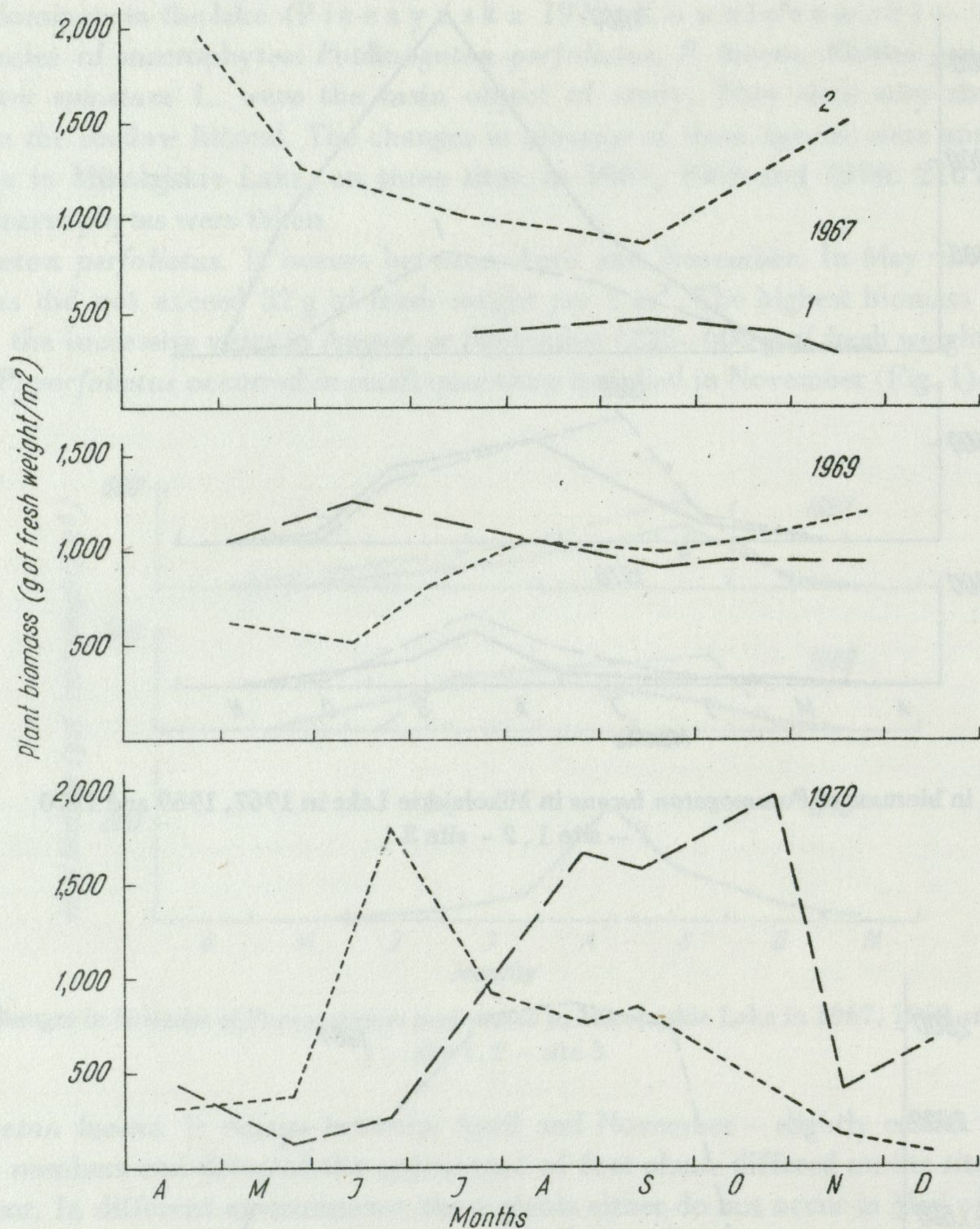


Fig. 4. Changes of biomass of *Elodea canadensis* in Mikolajskie Lake in 1967, 1969 and 1970
1 – site 1, 2 – site 2

P. lucens. The biomass of one plant species on particular sites and in different years may differ considerably.

The periphyton is to the same extent the life environment of macroinvertebrates as the macrophytes. In the lakes discussed the periphyton occurs abundantly on all species of macrophytes. In the majority of cases the algae dominate. The calcium deposit and detritus are found in considerable amounts. The periphyton on the plant species in Mikolajskie Lake, examined in this paper, has been analysed by Bownik (1970). The algae dominate there and amongst them the *Bacillariophyceae*. Out of the periphytic fauna the most abundant are *Chironomidae* and *Oligochaeta*. Bownik (1970) describes also the noticeable differences in the number dynamics of periphytic fauna living on plants wintering in the form of green shoots and on plants of which only the underground parts remain in winter in the lake.

The calcium deposit on these species of submerged plants in Mikołajskie Lake has been analysed by Kowalczewski (in press) and W. Żbikowski (unpublished data). It occurs in large quantities on the macrophytes; mean value of carbonates in dry periphyton weight is 85% for *P. perfoliatus*, 87% for *P. lucens*, 70% for *M. spicatum* and 77% for *E. canadensis*.

3.2. Invertebrates associated with macrophytes

The composition and numbers of fauna associated with submerged macrophytes were analysed in lakes Mikołajskie and Śniardwy. 631 samples were collected.

In Mikołajskie Lake, during two years, the fauna on *Potamogeton perfoliatus*, *P. lucens*, *Myriophyllum spicatum* and *Elodea canadensis* was examined. The following groups of invertebrates were recorded:

Chironomidae. They occurred abundantly or most abundantly on macrophytes (on average 50%, maximum 93% of total number of invertebrates, maximum number 33,740 ind./m²) (Tab. III). The most abundant were: *Endochironomus ex gr. tendens* F., *E. ex gr. dispar* Meig, *Tanytarsus ex gr. lauterborni* Kieff. and *Glyptotendipes gripekoveni* Kieff. Less abundant were: *Limnochironomus ex gr. nervosus* Staeg., *Cryptochironomus ex gr. pararostratus* Lenz., *Pseudochironomus ex gr. prasinatus* Staeg. and *Paratendipes ex gr. albimanus* Mg. Among numerous *Orthocladinae* *Cricotopus ex gr. silvestris* F. dominated. The least abundant were: the *Pelopinae* (*Procladius* sp.). There were very small differences in the species composition of *Chironomidae* larvae on plant species. And so, for example, on *P. lucens* *Cricotopus ex gr.*

Tab. III. Invertebrates on *Potamogeton lucens*, *P. perfoliatus*, *Myriophyllum spicatum* and *Elodea canadensis* in Mikołajskie Lake (1967 and 1970 years)

Taxons	Numbers of individuals:				Percentage	
	per 100 g of fresh plant weight		per 1 m ² of the littoral surface			
	mean	maximum	mean	maximum	mean	maximum
<i>Chironomidae</i>	1,428	28,298	4,557	33,740	50	93
<i>Oligochaeta</i>	1,016	4,928	4,868	31,957	35	85
<i>Gastropoda</i>	139	1,079	1,029	12,369	5	42
<i>Trichoptera</i>	86	1,502	331	2,744	3	54
<i>Heleidae</i>	64	456	387	4,102	2	15
<i>Hydrozoa</i>	43	517	263	4,325	1	33
<i>Ephemeroptera</i>	32	867	268	7,454	<1	23
<i>Lepidoptera</i>	17	181	100	1,180	<1	6
<i>Hirudinea</i>	13	83	108	735	<1	13
<i>Bivalvia</i>	11	199	78	1,711	<1	5
<i>Asellus aquaticus</i>	11	171	106	1,195	<1	5
<i>Zygoptera</i>	7	187	56	1,611	<1	5
<i>Mermithidae</i>	3	47	14	268	<1	2
Other groups	1	114	7	768	<1	3
Total fauna	2,871	32,790	12,172	54,950		

silvestris and *Glyptotendipes gripekoveni* were more abundant than on the other species of macrophytes, and on *E. canadensis* – *Procladius* sp. and *Limnochironomus ex gr. nervosus*.

Oligochaeta. Apart from the larvae of *Chironomidae* the *Oligochaeta* were a very abundant or most abundant group of animals in the majority of cases (on average 35%, maximum 85% of total invertebrates, maximum number 31,957 ind./m²) (Tab. III). In all cases the *Naididae* dominated and amongst them *Stylaria lacustris* L. (frequently over 50% of all *Naididae*). Some *Tubificidae* occurred also (mainly on *E. canadensis*).

Gastropoda. They occurred abundantly, especially on *E. canadensis* (on average 5%, maximum 42% of total number of invertebrates, maximum number 12,369 ind./m²) (Tab. III). Three species dominated: *Bithynia tentaculata* (L.), *Radix ovata* (Draparnaud) and *Physa acuta* (Draparnaud). Also were recorded: *Theodoxus fluviatilis* (L.), *Viviparus viviparus* (L.), *Valvata piscinalis* f. *antiqua* (Sowerby), *V. cristata* (Müller), *Limnaea stagnalis* (L.), *Galba palustris* (Müller), *Amphipeplea glutinosa* (Müller), *Acroloxus lacustris* (L.), *Coretus corneus* (L.), *Planorbis planorbis* (L.), *Anisus vortex* (L.), *Bathyomphalus contortus* (L.), *Armiger crista* (L.), *Gyraulus albus* (Müller), *Segmentina nitida* (Müller) and *Hippeutis complanatus* (L.). The differences in the species composition of *Gastropoda* on macrophytes were very small. And so, for example, *Bithynia tentaculata* and *Valvata piscinalis* f. *antiqua* occurred more abundantly on *E. canadensis*.

Trichoptera. They occurred quite abundantly (on average 3%, maximum 54%, maximum number 2,744 ind./m²) (Tab. III). Very abundant were: *Agraylea* sp., *Hydroptila* sp., *Orthotrichia* sp., *Oxyethira* sp., *Limnephilus* sp., *Mystacides nigra* (L.) and *Leptocerus tineiformis* Curtis. Less numerous were: *Polycentropus* sp. and *Holocentropus* sp. and *Phryganea grandis* L. The larvae of the genera *Phryganea* and *Limnephilus* were more frequently found on *E. canadensis*, *Agraylea*, *Hydroptila*, *Oxyethira* and *Orthotrichia* on pondweeds, and *Leptocerus tineiformis* on *Myriophyllum spicatum*.

Heleidae. Only in some cases they were more numerous (on average 2%, maximum 15% of total invertebrates, maximum numbers 4,102 ind./m²) (Tab. III).

Hydrozoa. A not very abundant group of invertebrates (on average 1%, maximum 33%, maximum number 4,325 ind./m²) (Tab. III).

Ephemeroptera. They occurred in small numbers and only sometimes were more numerous (maximum 23% of total invertebrates, maximum numbers 7,454 ind./m²) (Tab. III). Most abundant were: *Caenis moesta* Bngtss. and *C. macrura* Steph. and *Cloëon dipterum* (L.). Also found were *Proclëon* sp., *Centrophilum* sp., *Caenis horaria* (L.), *C. robusta* Etn., *Ephemera vulgata* L. and *Baëtis macani* Kimmins (the latter was described for the first time in Poland by S o w a 1962). There were no visible differences in the composition of *Ephemeroptera* on the macrophytes. *Ephemera vulgata* and *Baëtis macani* occurred sporadically and only on *E. canadensis*.

Lepidoptera. They were scarce among the invertebrates on all macrophytes, but occurred more regularly on *E. canadensis* than on pondweeds (maximum 6% of total invertebrates, maximum numbers 1,180 ind./m²) (Tab. III). The most abundant were: *Acentropus niveus* (Oliv.) and *Paraponyx stratiotata* (L.). Sporadically occurred: *Cataclysta lemnata* (L.) and *Nymphula nymphæta* (L.).

Hirudinea. They occurred in small numbers on submerged plants (maximum 13% of total invertebrates, maximum numbers 735 ind./m²) (Tab. III). Most frequently occurred: *Herpobdella* sp. and *Glossiphonia complanata* (L.). Also occurred: *Haemopsis sanguisuga* (L.), *Piscicola geometra* (L.) and *Glossiphonia* sp.

Other groups of animals occur quite abundantly in some periods, as for example *Bivalvia* (*Dreissena polymorpha* Pallas dominated, *Pisidium* sp. occurred also), *Asellus aquaticus* Rakov.

(mainly on *E. canadensis*), *Mermithidae* (especially on pondweeds), *Zygoptera* (most abundantly represented by larvae of *Enallagma cyathigerum* Charp., less frequently: *Erythromma najas* Hans. and *Ischnura pumilio* Charp. — most abundant on *E. canadensis*).

Also not very abundant and sporadic were: *Turbellaria* [*Dugesia* sp. and *Dendrocoelum lacteum* (Müller)], *Bryozoa* [*Plumatella fungosa* (Pall.), *P. repens* (L.) and *Cristatella mucedo* Cuv.], *Spongillidae*, *Chrysomelidae* (*Donatia* sp.), *Heteroptera* (*Ranatra linearis*, L. and *Nepa cinerea* L.) and larvae of *Dytiscidae*.

In lake Śniardwy the composition of invertebrates did not differ much from that in Mikołajskie Lake. *Chironomidae*, *Oligochaeta* and *Mollusca* dominated. The study on invertebrates in lake Warniak was carried out by Pieczyński (1973). *Chironomidae*, *Oligochaeta* and *Ephemeroptera* dominated in lake Warniak.

The fluctuations in numbers of invertebrates were analysed on 4 species of macrophytes in Mikołajskie Lake in 1967 and 1969.

Potamogeton perfoliatus. In both years of the study *Chironomidae* and *Oligochaeta* dominated (Fig. 5). On site 3 the fauna numbers were much higher than on site 1 (almost three times). The maximum numbers of invertebrates were in September or November and were due to the considerable increase in the number of *Chironomidae* or *Oligochaeta*. The smallest numbers of fauna were recorded in the spring and at the beginning of summer (Fig. 5).

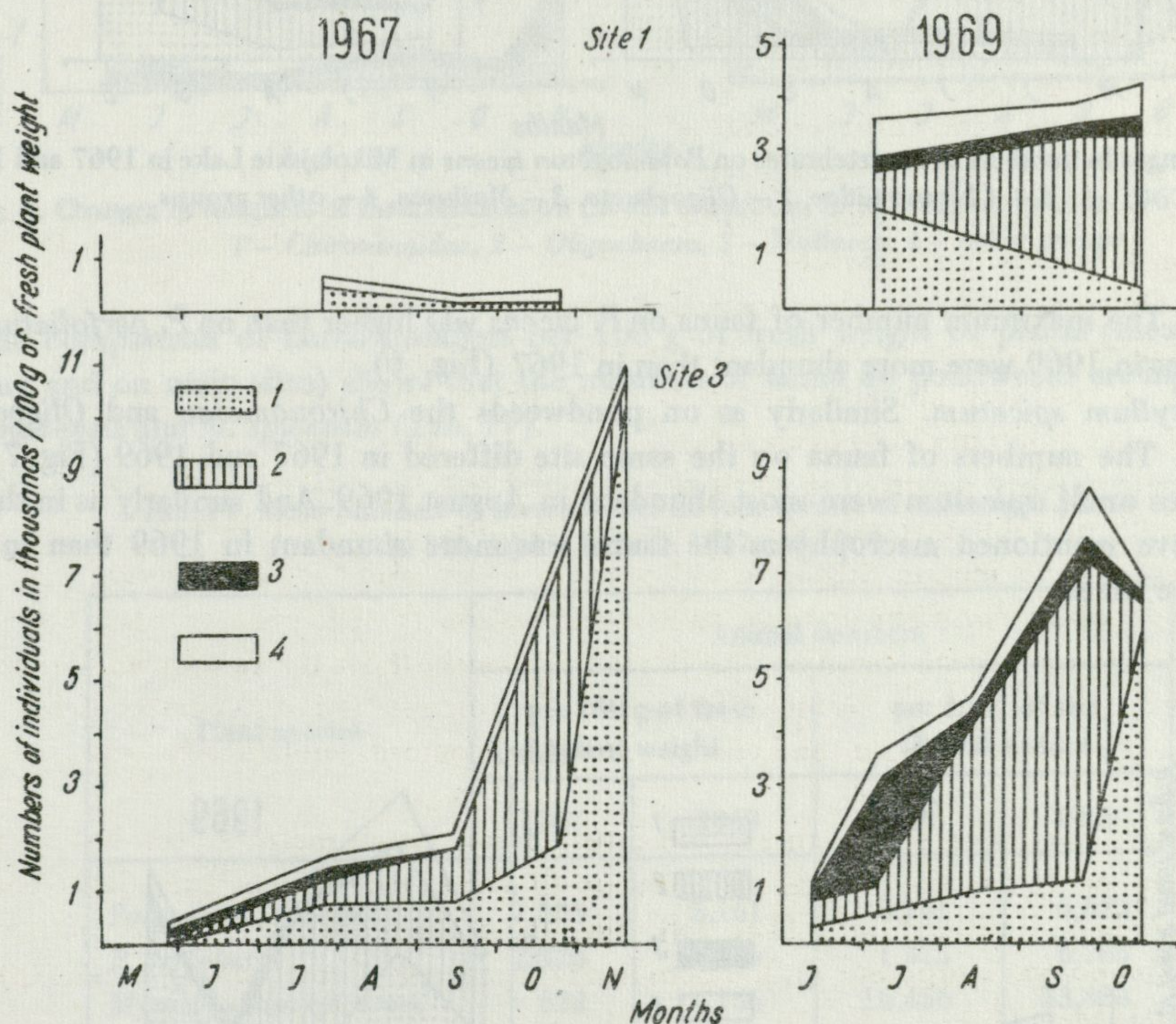


Fig. 5. Changes in numbers of invertebrates on *Potamogeton perfoliatus* in Mikołajskie Lake in 1967 and 1969
1 — *Chironomidae*, 2 — *Oligochaeta*, 3 — *Mollusca*, 4 — other groups

Potamogeton lucens. The composition and changes in numbers of invertebrates on *P. lucens* were similar as in the case of *P. perfoliatus*. In both years the maximum number of invertebrates was recorded on site 3 in October or November. On site 1 this number was smaller and

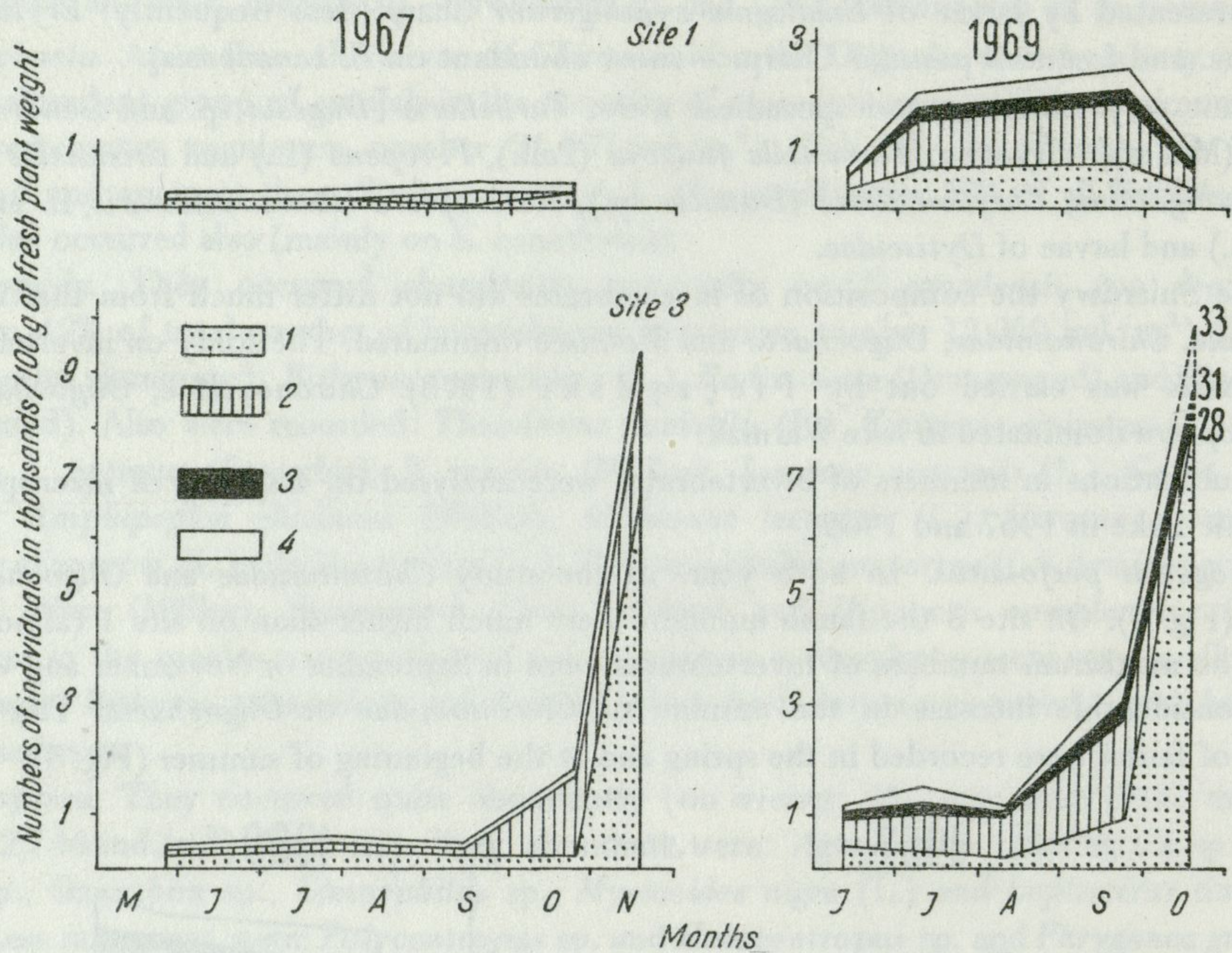


Fig. 6. Changes in numbers of invertebrates on *Potamogeton lucens* in Mikołajskie Lake in 1967 and 1969
1 – Chironomidae, 2 – Oligochaeta, 3 – Mollusca, 4 – other groups

more even. The maximum number of fauna on *P. lucens* was higher than on *P. perfoliatus*. The invertebrates in 1969 were more abundant than in 1967 (Fig. 6).

Myriophyllum spicatum. Similarly as on pondweeds the *Chironomidae* and *Oligochaeta* dominated. The numbers of fauna on the same site differed in 1967 and 1969 (Fig. 7). The invertebrates on *M. spicatum* were most abundant in August 1969. And similarly as in the case of the above mentioned macrophytes the fauna was more abundant in 1969 than in 1967 (about three times).

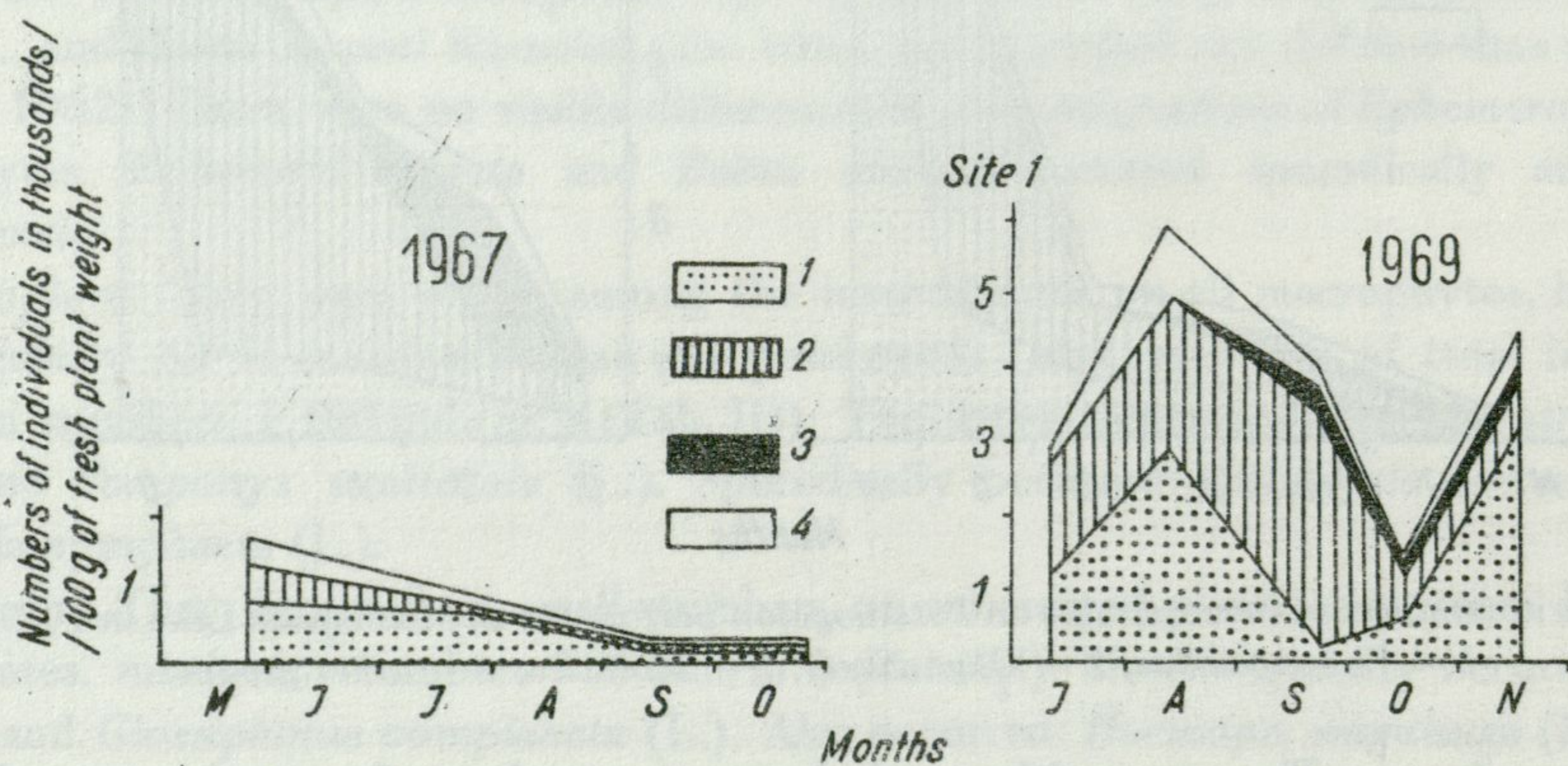


Fig. 7. Changes in numbers of invertebrates on *Myriophyllum spicatum* in Mikołajskie Lake in 1967 and 1969 (site 1)
1 – Chironomidae, 2 – Oligochaeta, 3 – Mollusca, 4 – other groups

Elodea canadensis. In both years of the study the invertebrates were primarily represented by *Oligochaeta*, *Chironomidae* and *Mollusca*. Maximum numbers of fauna were in various months of the vegetation season (Fig. 8). Usually the numbers of *Oligochaeta* decrease in late autumn, whereas *Chironomidae* numbers increase. On both sites the fauna numbers were higher in 1969.

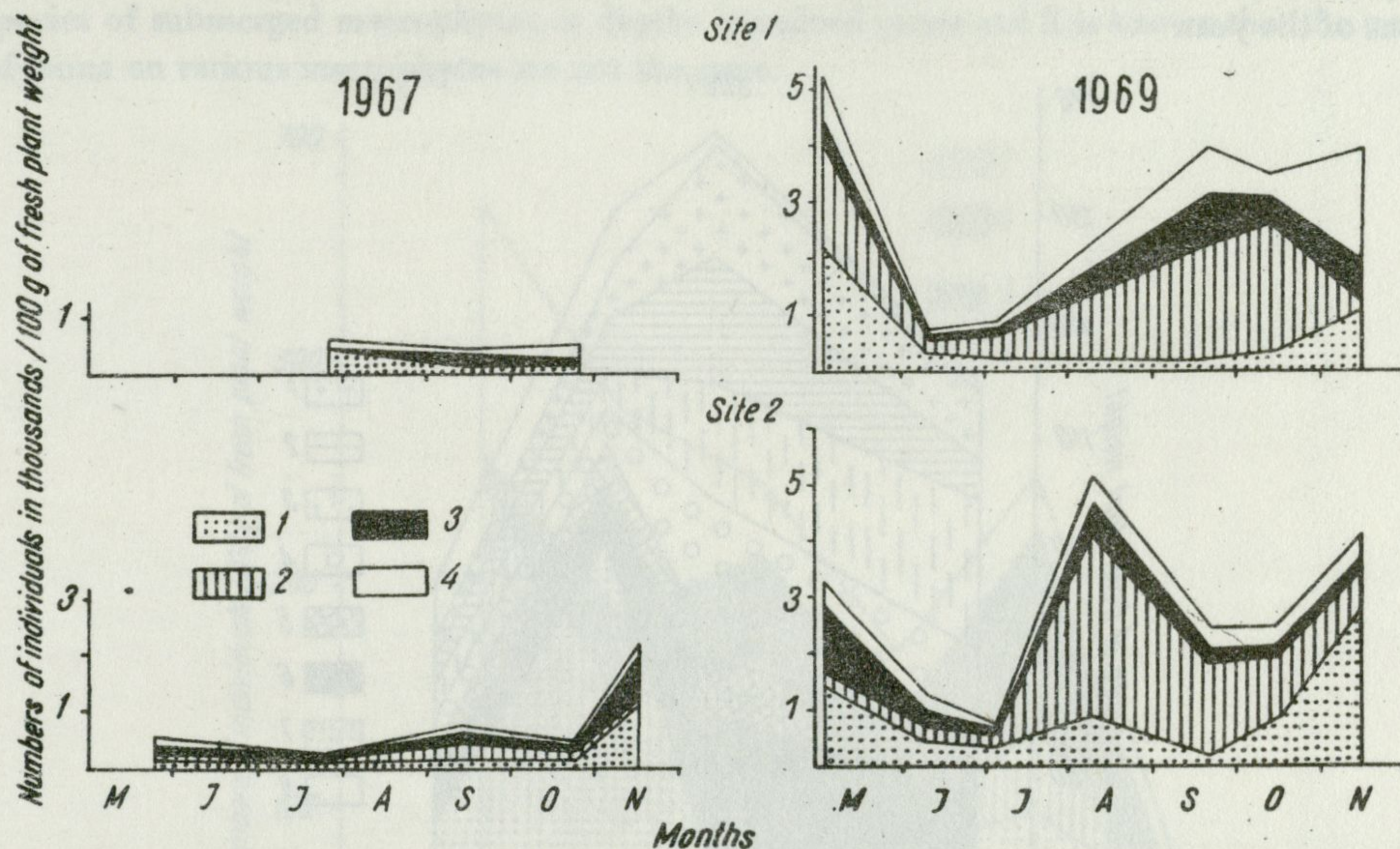


Fig. 8. Changes in numbers of invertebrates on *Elodea canadensis* in Mikolajskie Lake in 1967 and 1969
1 – *Chironomidae*, 2 – *Oligochaeta*, 3 – *Mollusca*, 4 – other groups

The comparison of fauna numbers per 100 g of fresh weight of plants (mean values for 2 years and on main sites) shows that the numbers of fauna on pondweeds are higher than on *E. canadensis* and *M. spicatum* (Tab. IV).

Tab. IV. Mean numbers of invertebrates on four species of submerged plants in Mikolajskie Lake in 1967 and 1969

Plant species	Animal numbers			
	per 100 g of fresh plant weight		per 1 m ² of the littoral surface	
	1967	1969	1967	1969
<i>Potamogeton lucens</i>	1,303	5,161	3,161	6,423
<i>P. perfoliatus</i>	2,320	4,556	1,375	6,788
<i>Myriophyllum spicatum</i>	622	4,156	16,436	33,483
<i>Elodea canadensis</i>	580	3,133	5,590	30,483

Out of macrophytes examined *Elodea canadensis* is the only species occurring abundantly in winter in the form of green shoots. The study on invertebrates on *E. canadensis* in winter (December 1970 to March 1971) has shown that the fauna consisted of all groups of inver-

tebrates typical for summer period. The numbers of fauna over the four winter months vary (Fig. 9). The mean numbers are about 20 times smaller than in the summer period. The numbers of *Oligochaeta* noticeably decrease (in some cases none occurred). The numbers of *Chironomidae* and *Mollusca* decrease less (about 30 and 8 times, respectively), whereas, for example, *Asellus aquaticus* and *Zygoptera* are more abundant in winter than in the other seasons of the year.

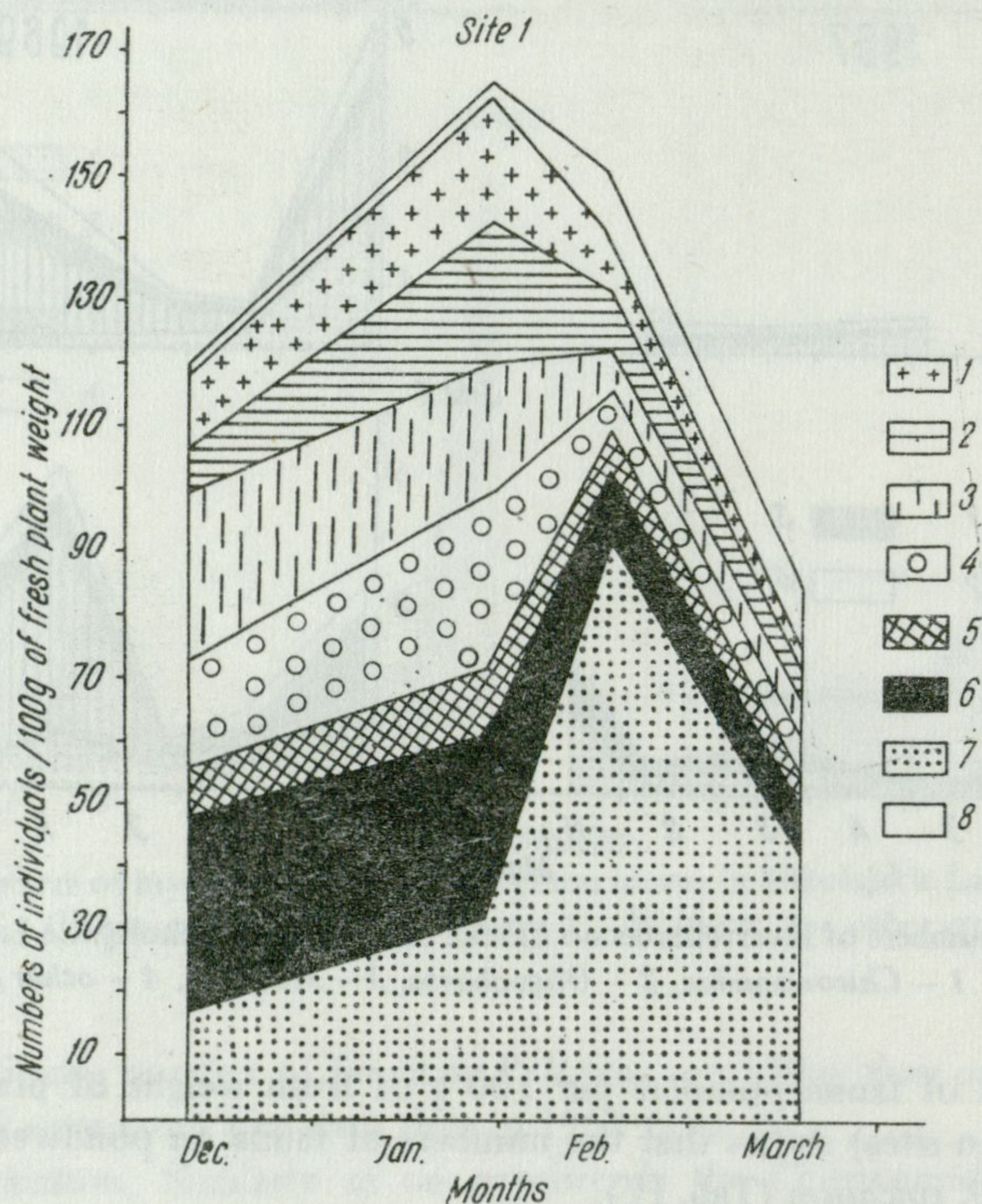


Fig. 9. Changes in numbers of invertebrates on *Elodea canadensis* in Mikolajskie Lake in winter 1970/1971 (site 1)

1 – *Lepidoptera*, 2 – *Odonata*, 3 – *Asellus aquaticus*, 4 – *Ephemeroptera*,
5 – *Trichoptera*, 6 – *Mollusca*, 7 – *Chironomidae*, 8 – other groups

The numbers of fauna on submerged macrophytes in Mikolajskie Lake are on average twice higher than in lake Warniak (Pieczyński 1973) and five times higher than in lake Śniardwy.

In order to analyse the spatial variability of the composition and numbers of the invertebrates in July 1969 samples were taken from 11 additional sites at the depth 0.75–3.0 m. In various environments *Chironomidae*, *Oligochaeta* and *Mollusca* dominated interchangeably. Relatively small differences were observed on particular sites in the case of *M. spicatum* (1,452–3,090 individuals), whereas they were quite considerable on *E. canadensis* (779–6,100) and on pondweeds (*P. perfoliatus*: 1,399–7,899 and *P. lucens*: 974–4,886). The differences in composition and numbers of fauna at various depths are small. The invertebrates are most abundant at the depth of 1 m and the least abundant at the depth of 3 m. The numbers of *Oligochaeta* decrease together with the depth whereas the numbers of *Chironomidae* slightly increase.

The analysis of the occurrence of invertebrates at various depths in lake Śniardwy (material sampled to the depth of 6 m) shows that the numbers of fauna are slightly higher in the shallower littoral than in deeper places. The invertebrates are most abundant at the depth of 1 m and the least abundant at the depth of 6 m (Fig. 10). It is difficult to analyse in detail the relation between the numbers of invertebrates and the depth as the percentage of particular species of submerged macrophytes at depths examined varies and it is known that the numbers of fauna on various macrophytes are not the same.

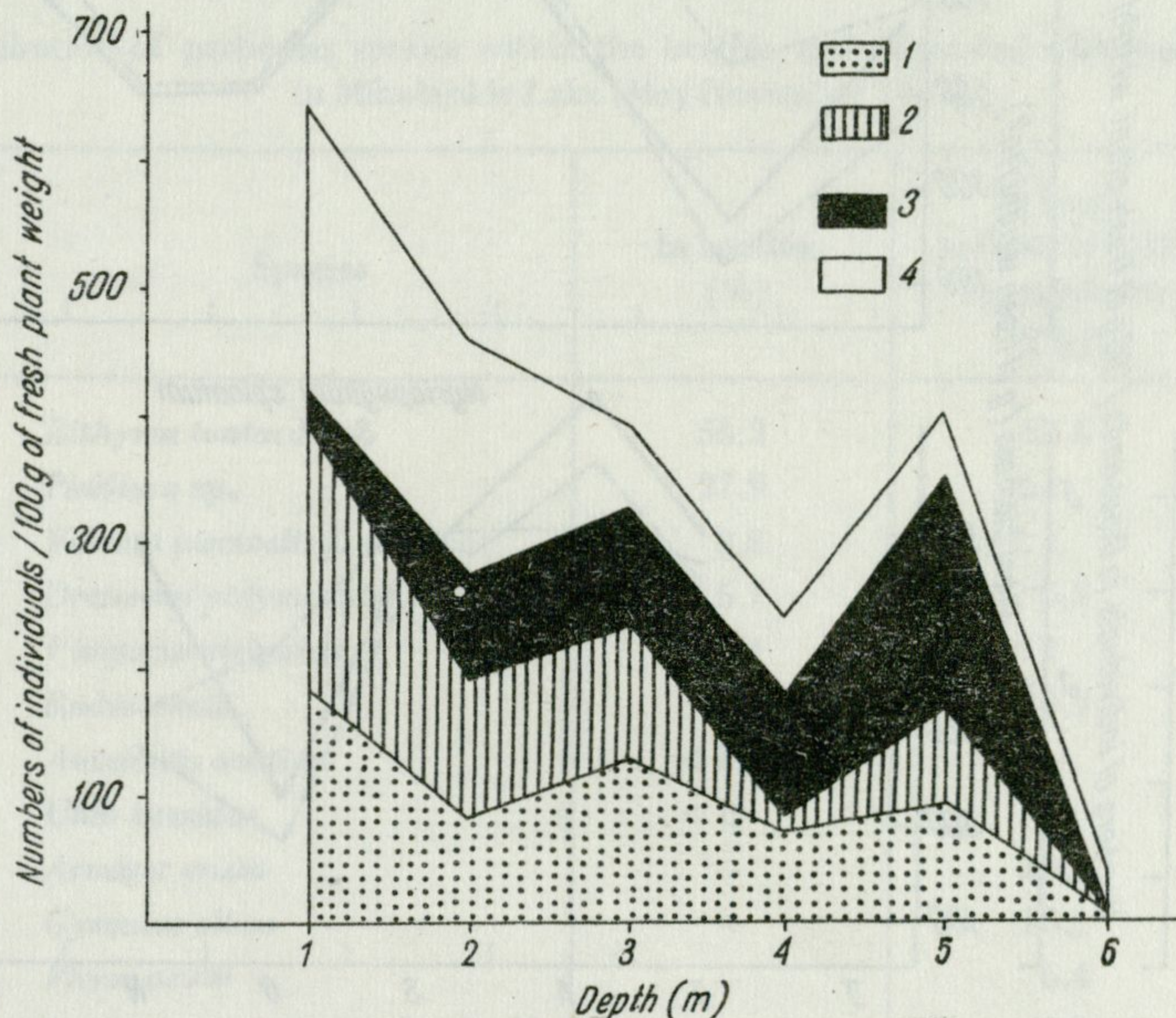


Fig. 10. Composition and numbers of invertebrates at different depths in lake Śniardwy
1 – Chironomidae, 2 – Oligochaeta, 3 – Mollusca, 4 – other groups

Knowing the numbers of fauna related to the weight of plants and the biomass of macrophytes, the number of invertebrates per 1 m^2 of the surface area of the littoral bottom has been determined. And as the number of fauna per 100 g of fresh weight of plants is usually higher on both pondweeds the number of fauna per 1 m^2 of the surface area of the littoral bottom overgrown with *M. spicatum* and *E. canadensis* is noticeably higher than in the environment with pondweeds (Tab. IV). This is due to the much smaller biomass of pondweeds.

An analysis of the changes in numbers of invertebrates per 1 m^2 of bottom overgrown with macrophytes shows a noticeable relation between these changes and the changes in numbers of fauna per 100 g of fresh weight of plants in the case of *E. canadensis* and *M. spicatum* (Fig. 11). Such relation is not observed in the case of *P. perfoliatus* and *P. lucens*.

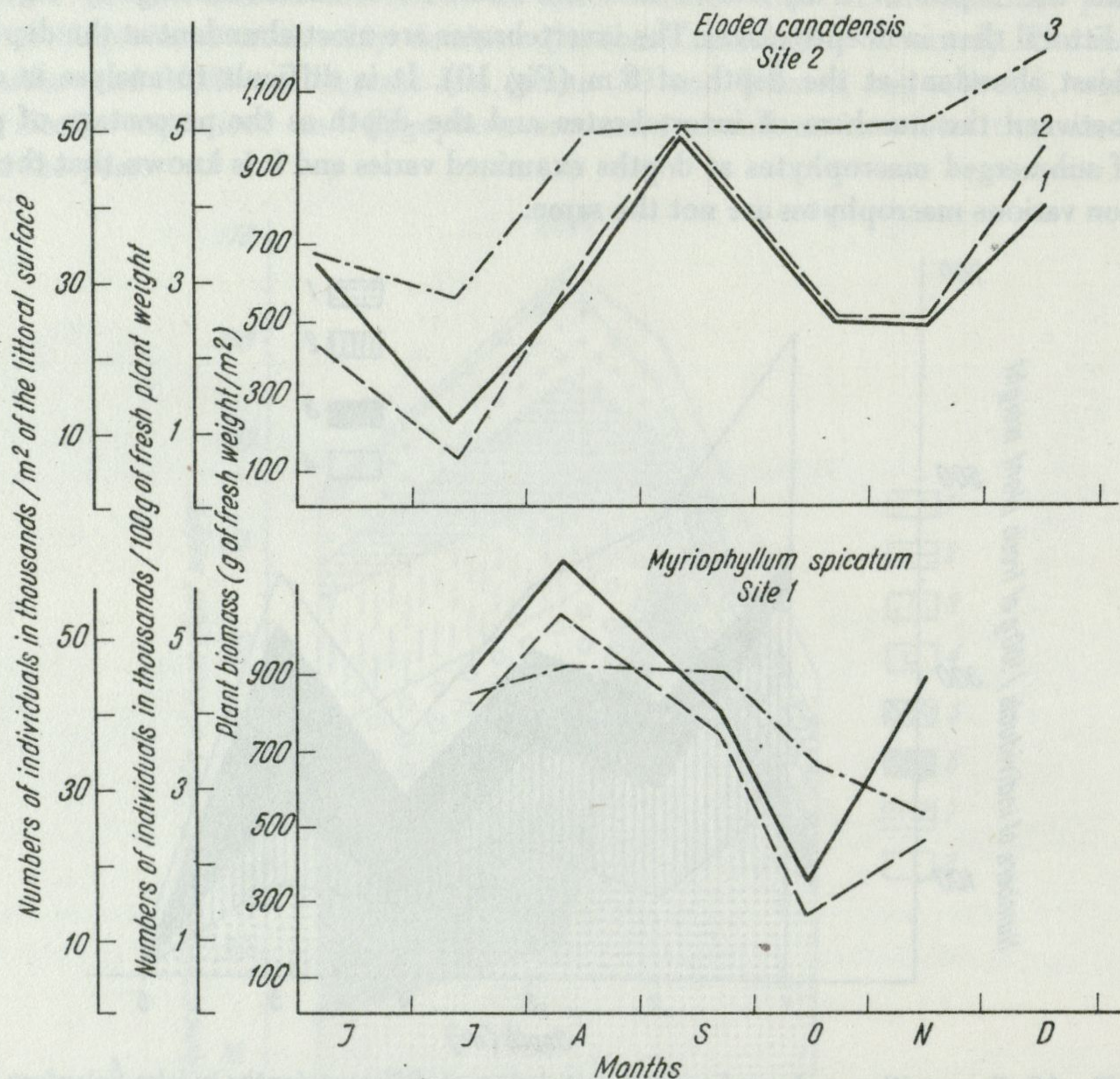


Fig. 11. Comparison in changes of *Elodea canadensis* and *Myriophyllum spicatum* biomass and changes in numbers of invertebrates in Mikolajskie Lake in 1969

1 – numbers of individuals/100 g of fresh plant weight, 2 – numbers of individuals/m² of the littoral surface, 3 – plant biomass

3.3. Comparison of fauna associated with macrophytes and benthic fauna

The benthic fauna was collected in Mikolajskie Lake in 1967 and 1969 (125 benthic samples) on three sites in the vicinity of four plant species: *Potamogeton perfoliatus*, *P. lucens*, *Myriophyllum spicatum* and *Elodea canadensis*.

In the benthos, similarly as amongst the fauna associated with macrophytes, *Oligochaeta* and *Chironomidae* dominate, but the species composition of these groups is different. Among the benthic *Oligochaeta* the *Tubificidae* dominate (on macrophytes – *Naididae*). The following *Chironomidae* species are found exclusively in the community of bottom fauna: *Tanytarsus mancus* v. der Vulp., *T. ex gr. gregarius* Kieff. and *Cryptochironomus ex gr. defectus* Kieff. (among the other larvae: *Orthoclaadiinae* and *Glyptotendipes gripekoveni* occur much more abundantly in the fauna associated with plants). Other *Chironomidae* species occur abundantly both in benthos and on plants. Typical representatives of fauna living on plants, such as for

example *Porifera*, *Hydrozoa* and some *Hydroptilidae* are not found in benthos and such species as *Paraponyx stratiotata* and *Stylaria lacustris* which are common on plants occur sporadically. *Molanna angustata* Curtis, *Tabanidae*, *Anodonta anatina* (L.) and *Unio tumidus* Philipsson are found only in the benthic fauna, whereas *Donatia* sp. and *Ephemera vulgata* are noticeably more abundant in benthos. The contribution of particular *Mollusca* species to both communities varies, amongst other it has been observed that the majority of species is exclusive for one community only (68.4%) (Tab. V).

Tab. V. Contribution of particular species within the benthic and associated with macrophytes *Mollusca* in Mikołajskie Lake (May-November 1969)

Species	In benthos (%)	In fauna associated with macrophytes (%)
<i>Bithynia tentaculata</i>	56.3	28.6
<i>Pisidium</i> sp.	27.9	< 1
<i>Valvata piscinalis</i> f. <i>antiqua</i>	6.8	< 1
<i>Dreissena polymorpha</i>	5.7	5.5
<i>Viviparus viviparus</i>	1.1	< 1
<i>Radix ovata</i>	1.1	10.9
<i>Anodonta anatina</i>	< 1	—
<i>Unio tumidus</i>	< 1	—
<i>Armiger crista</i>	—	18.4
<i>Gyraulus albus</i>	—	18.1
<i>Physa acuta</i>	—	6.4
Young unidentified individuals	—	4.9
<i>Acroloxus lacustris</i>	—	3.2
<i>Theodoxus fluviatilis</i>	—	1.1
<i>Valvata cristata</i>	—	< 1
<i>Bathyomphalus contortus</i>	—	< 1
<i>Anisus vortex</i>	—	< 1
<i>Galba palustris</i>	—	< 1
<i>Amphipeplea glutinosa</i>	—	< 1

The numbers of fauna living on plants are generally higher than in the case of benthos. The maximum differences can be ten times (site 3, September), 40 times (site 1, November) and even 50 times (site 2, November). The maxima of numbers of fauna living on plants and of benthos are in different periods of the vegetation season (e.g., Fig. 12). In 18 comparative analyses of numbers of fauna living on plants and of benthos only in two cases the benthic fauna was more numerous.

The numbers of benthos and fauna on four species of macrophytes were compared when they occurred on one site. This showed that the numbers of fauna on *E. canadensis* and *M. spicatum* were several times higher than benthos numbers as compared to the fauna on *P. perfoliatus* and *P. lucens*. In the case of pondweeds there were periods of more abundant benthos (early spring and late autumn) when the pondweeds were not well developed yet or partly dead and their biomass was very low.

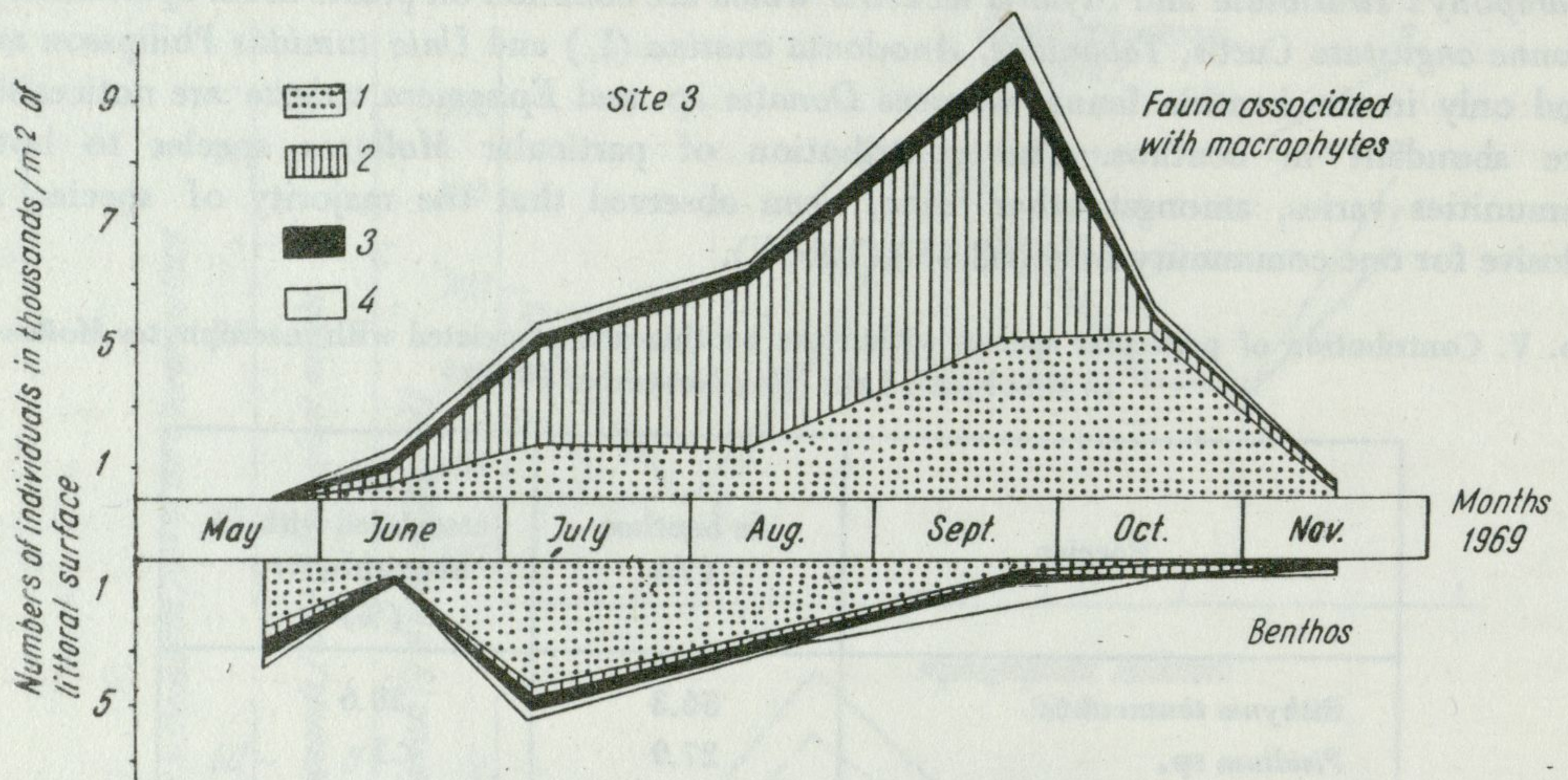


Fig. 12. Comparison of composition and numbers of fauna associated with macrophytes (mean values for two plant species: *Potamogeton perfoliatus* and *P. lucens*) and benthos in Mikolajskie Lake in 1969 (site 3)
1 – Chironomidae, 2 – Oligochaeta, 3 – Mollusca, 4 – other groups

4. DISCUSSION

Potamogeton perfoliatus, *P. lucens*, *Myriophyllum spicatum* and *Elodea canadensis*, apart from other differences, differ in their life cycle and biomass dynamics. The biomass of the same plant species on particular sites and in successive years may differ considerably (Figs. 1–4).

The community of invertebrates inhabiting these macrophytes has a variety of groups of a different biology (most numerous are *Chironomidae*, *Oligochaeta* and *Mollusca*). The numbers of fauna living on plants vary considerably in time, space and on various species of macrophytes (Figs. 5–8). The numbers of invertebrates are higher on *P. perfoliatus* and *P. lucens* than on *E. canadensis* and *M. spicatum* but as the biomass of *E. canadensis* and *M. spicatum* per 1 m² of the littoral bottom is much higher the numbers of fauna per 1 m² of the bottom with these macrophytes is noticeably higher than in the environment with pondweeds (Tab. IV).

The essential differences in the changes in biomass of macrophytes and in the numbers of invertebrates in successive years of the study suggest that one should be careful when comparing the data from different years in such a differentiated and variable environment as the littoral is.

The composition of fauna living on plants in lakes Mikolajskie and Śniardwy approximates to the one in the littoral of several other water bodies. *Chironomidae* and *Oligochaeta* are not only the most numerous in lakes Mikolajskie and Śniardwy but also in other water bodies (on the majority of macrophytes) (Krecker 1939, Hillbricht 1953, Matlak 1963, Wolnomiejski and Dunajska 1966, Pieczyński 1973 and others). Other fauna groups, for example *Mollusca* and *Asellus aquaticus* (Karassowska and Mikulski 1960), *Mollusca* (Margolina 1958), *Gastropoda* and *Hirudinea* (Kuflikowski 1970) and others, are rarely the most abundant on some plant species. The species occurring most abundantly within particular groups of fauna living on plants in Mikolajskie

Lake are also mentioned as dominants in other environments, e.g., *Stylaria lacustris* among the *Oligochaeta* (Rehbronn 1937, Müller-Liebenau 1956, Matlak 1963, Kuflikowski 1970), *Endochironomus* ex. gr. *tendens*, *Tanytarsus* ex gr. *lauterborni*, *Glyptotendipes gripekoveni* and *Cricotopus* ex gr. *silvestris* among the *Chironomidae* (Müller-Liebenau 1956, Giziński 1958, Matlak 1963, Kuflikowski 1970), *Enallagma cyathigerum* among the *Zygoptera* (Macan 1965), *Acentropus niveus* and *Paraponyx stratiotata* within the *Lepidoptera* (Müller-Liebenau 1956) and others.

Several authors do not notice great differences in the species composition of fauna living on various macrophytes and other substrates in the same environment. And for example, Matlak (1963) says that on several plant species examined there is no visible specific differentiation of fauna. A similar species composition of *Chironomidae* larvae is given by Frost (1942) for different macrophytes, whereas Gromov (1960) says that the majority of all found *Chironomidae* species occurs on all submerged substrates examined including plants, and Müller-Liebenau (1956) gives the same species of non-mining *Chironomidae* and also *Gastropoda* and *Oligochaeta* in the composition of fauna living on six plant species.

In several other cases considerable differences have been observed in the composition of fauna on different macrophyte species (Krach 1932, Giziński 1958, Karassowska and Mikulski 1960). The occurrence of several representatives of invertebrates only on some species of macrophytes is pointed out by Kreckler (1939), Müller-Liebenau (1956), Harrod (1964), McLachlan (1969) and others. Gurzęda (1959) and N. Wolnomiejski (unpublished data) quote information about the avoidance of specific plants by some fauna groups.

Also the relation between fauna numbers and plant species is pointed out or is being followed from the material of several authors (Kreckler 1939, Andrews and Hasler 1943, Gerking 1957, Giziński 1958, Margolina 1958, Gromov 1960, Karassowska and Mikulski 1960, Stańczykowska 1960, Matlak 1963, Zimbalevskaja 1966, Soszka 1968, Kuflikowski 1970, N. Wolnomiejski – unpublished data, and others).

When discussing the differentiation in composition and numbers of invertebrate fauna on macrophytes the authors rarely explain the causes responsible for this differentiation, and the literature data on the subject are frequently contradictory. Amongst other things, it has been pointed out that the greater leaf fragmentation causes the greater fauna numbers and the differentiation of the species composition (Kreckler 1939, Andrews and Hasler 1943, Entz 1947, Hillbricht 1953, Rosine 1955, Gerking 1957, Stańczykowska 1960 and others). According to some authors the differentiation of fauna depends more on the plant structure than on the chemical composition of water (Kreckler 1939, Harrod 1964), according to others it depends more on the depth (Zimbalevskaja 1966) or on the water chemistry (Frost 1942). In analyses of the occurrence of fauna on plants the authors point out also the significance of chemical composition of plants, differentiation of plant periphyton (Harrod 1964, N. Wolnomiejski – unpublished data) or calcium deposit (Entz 1947).

In Mikołajskie Lake no noticeable differences were observed in the composition and numbers of fauna on plants of different structure. And so, *E. canadensis*, a plant with small leaves, has a great fauna variety, whereas *M. spicatum*, a strongly spiked plant, has a small variety of fauna. The analysis of material from this lake shows that the species composition of fauna is less differentiated on examined species of submerged plants, but the numbers are

greater. Also Entz (1947), Wolnomiejski and Dunajska (1966) and N. Wolnomiejski (unpublished data) point out the greater quantitative than qualitative differences of fauna on macrophytes. In Mikołajskie Lake the numbers of fauna vary on various macrophytes and even on the same species of macrophytes at the same time on different sites. And thus both the character of the plant itself and of the environment condition the composition and numbers of fauna.

A similarly high variability has been also observed by several other authors in the case of other water bodies (Frost 1942, Andrews and Hasler 1943, Rosine 1955, Giziński 1958, Harrod 1964, Macan 1965, Kuflikowski 1970, Pieczyński 1973 and others).

In Mikołajskie Lake there are noticeable changes in numbers of invertebrates on macrophytes with annual and perennial shoots. And the maximum numbers of fauna on *E. canadensis* and *M. spicatum* occur in various months of the vegetation season of plants, including spring, but on *P. perfoliatus* and *P. lucens* they occur usually in the autumn (in this period in several cases the numbers of invertebrates attain much higher values in comparison to the numbers on other macrophytes). As regards the periphytic fauna similar results have been obtained by Bownik (1970). The autumnal increase in numbers of fauna living on some macrophyte species has been recorded by other authors (Hillbricht 1953, Matlak 1963 and Niewiadomski – unpublished data). Some authors suggest that this is due to the better trophic conditions caused by the death of plants (Bownik 1970).

The numbers of invertebrates on submerged macrophytes given by several authors for different aquatic environments are different than in Mikołajskie Lake. Andrews and Hasler (1943), Zimbalevskaja (1966), Pieczyński (1973) and others give smaller numbers of fauna, whereas Frost (1942) and Kořinkova (1971) and others, larger.

An analysis of benthos in the vicinity of fauna associated with macrophytes shows the domination of the same groups of invertebrates: *Oligochaeta* and *Chironomidae*, but the species composition of these groups is different similarly as the number dynamics of both communities and usually the benthos is less abundant (e.g., Fig. 12). Only in some cases the numbers of fauna associated with macrophytes are smaller in comparison to benthos. The very few cases of the presence of representatives more typical for one community in the other one may be, amongst other, due to the moving of invertebrates from the macrophytes to the benthos and vice versa. The contacts between invertebrates inhabiting submerged macrophytes and the bottom fauna are evident (e.g., active moving and passive moving under the influence of wave action). Nevertheless there are visible differences in the composition and numbers of fauna associated with macrophytes and benthic fauna thus showing that these are two different communities as they are treated in the literature (Wolnomiejski and Dunajska 1966 and others). Considerable differences in the composition of benthos and fauna associated with macrophytes are usually confirmed by the material of other authors: Demel (1923), Romaniszyn (1953), Gerking (1957), Stańczykowska (1960), McLachlan (1969), Opaliński (1971) and others.

In some cases the composition of fauna associated with macrophytes and of benthos are similar (e.g., Zięba and Srokosz 1974). Pennak (1953) and Zimbalevskaja (1966) give the classification of the littoral invertebrates according to the more abundant occurrence of fauna representatives on plants or in bottom deposits.

Usually the numbers of fauna on macrophytes are larger in comparison to benthos (Gromov 1960, Gerking 1967, Gurzęda 1959, and Niewiadomski – unpublished data).

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5. SUMMARY

The study was carried out between 1966 and 1971 in three lakes of the Masurian Lakeland: Mikołajskie (main object of the study), Śniardwy and Warniak.

The composition and number dynamics of invertebrates on macrophytes and benthic fauna living among vegetation were analysed (*Potamogeton perfoliatus* L., *P. lucens* L., *Myriophyllum spicatum* L. and *Elodea canadensis* Rich. were estimated).

The macrophytes differ amongst other in their life cycle and biomass dynamics. The community of invertebrates associated with macrophytes consists of a variety of groups having different biology (most abundant are *Chironomidae*, *Oligochaeta* and *Mollusca*). The numbers of invertebrates change noticeably in time, space (Figs. 5–8) and on different species of macrophytes.

The numbers of invertebrate fauna are larger on *P. lucens* and *P. perfoliatus* than on *E. canadensis* and *M. spicatum*, but as the biomass of *E. canadensis* and *M. spicatum* per 1 m² of the littoral bottom is greater, the numbers of fauna per 1 m² of the bottom overgrown with these macrophytes are larger than in the environment with pondweeds (Tab. IV). The analysis of the benthos close to the fauna associated with macrophytes shows that although the same groups of invertebrates dominate (*Oligochaeta* and *Chironomidae*) but the species composition of these groups and the number dynamics of both communities varies and usually the benthos is less abundant (Fig. 12). It is evident that the invertebrates associated with submerged macrophytes and the benthic fauna contact each other. But the noticeable differences in the composition and numbers of fauna associated with macrophytes and bottom fauna show that these are two different communities.

6. POLISH SUMMARY (STRESZCZENIE)

Badania prowadzono w latach 1966–1971 w trzech jeziorach Pojezierza Mazurskiego. Mikołajskie (główny obiekt badań), Śniardwy i Warniak.

Analizowano skład i dynamikę liczebności bezkręgowej fauny związanej z roślinnością i fauny dennej żyjącej wśród roślinności (badano skupienia *Potamogeton perfoliatus* L., *P. lucens* L., *Myriophyllum spicatum* L. i *Elodea canadensis* Rich.).

Badane makrofity różnią się m. in. cyklem życiowym i dynamiką biomasy. Zespół bezkręgowców związany z makrofitami charakteryzuje się różnorodnością grup o odmiennej biologii (najliczniejsze są *Chironomidae*, *Oligochaeta* i *Mollusca*). Liczebność fauny bezkręgowej zmienia się wyraźnie w czasie i w przestrzeni (fig. 5–8). Skład i liczebność fauny bezkręgowej są różne zarówno na rozmaitych gatunkach makrofitów, jak i w badanych środowiskach litoralu. Liczebność fauny bezkręgowej jest wyższa na rdestnicach niż na moczarcie i wywłóczniku; ale – w związku z dużo większą biomasą moczarki i wywłócznika na 1 m² dna litoralu – liczebność fauny w stosunku do 1 m² dna porośniętego tymi makrofitami jest wyższa niż w środowisku porośniętym rdestnicami (tab. IV). Analiza sąsiadującego z fauną związaną z makrofitami zespołu – bentosu – wykazała, że wprawdzie dominują te same grupy bezkręgowców (*Oligochaeta* i *Chironomidae*), ale skład gatunkowy tych grup jest inny, podobnie jak i dynamika liczebności obu zespołów, przy czym z reguły bentos jest mniej liczny (fig. 12). Kontaktowanie się bezkręgowców związanych z roślinnością zanurzoną i fauny dennej jest faktem oczywistym. Tym niemniej stwierdzone wyraźne różnice składu i liczebności fauny związanej z roślinnością i fauny dennej wskazują na to, że są to odmienne zespoły.

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