EKOLOGIA POLSKA (Ekol. pol.)	23	3	393–415	1975

Grzegorz Jan SOSZKA

Department of Hydrobiology, Institute of Zoology, University of Warsaw, Warsaw

ECOLOGICAL RELATIONS BETWEEN INVERTEBRATES AND SUBMERGED MACROPHYTES IN THE LAKE LITTORAL

ABSTRACT: The invertebrates inhabiting four species of submerged macrophytes (*Potamogeton perfoliatus* L., *P. lucens* L., *Myriophyllum spicatum* L. and *Elodea canadensis* Rich.) have been analysed. The *Lepidoptera* larvae, *Phryganea grandis* L. and *Limnephilus* sp. are the most strongly connected with macrophytes, whereas the numerous *Naididae* are only loosely connected with macrophytes. The macrophytes are used by invertebrates more as a life substrate than as food. The relations of the majority of invertebrates to the macrophytes are not permanent. The macrophytes can be substituted by another kind of substrate. *P. perfoliatus* and *P. lucens* are much more used by fauna than *E. canadensis* and *M. spicatum* and the latter are much less destroyed due to the activity of invertebrates.

Contents

1. INTRODUCTION

The ecological relations between the invertebrates and submerged macrophytes are reciprocal and manifold. The fauna uses the macrophytes directly as a place for living or as food. The macrophytes are damaged by fauna mainly due to animal grazing. Quite significant is also the indirect effect such as change of the environment as a result of different life processes of macrophytes and invertebrates. The complicated character of these relations has been pointed out by many authors (Gurzęda 1959, Gaevskaja 1966, N. Wolnomiejski – unpublished data).

The variety of animal communities, the environmental conditions of the littoral and thus the difficulties in research are responsible for the scarce data on the quantitative relations between submerged macrophytes and invertebrates.

In the majority of cases only some selected relations are analysed such as the use of macrophytes as a life substrate of fauna, invertebrates feeding on plant tissue or losses of macrophytes due to animal grazing. But the main interest is the feeding of fauna on macrophytes. A review of the literature on this subject includes the paper by Gaevskaja (1966). In the majority of papers the grazing by fauna on macrophytes is analysed according to laboratory experiments and therefore they are not relevant to the trophic relations in the natural environment.

Among the very few papers on reciprocal relations between invertebrates and macrophytes the paper by McGaha (1952) can be mentioned.

The ecological relations between the invertebrates and submerged macrophytes in the lake littoral are the subject of this paper. Special attention has been paid to: (1) feeding of invertebrates, (2) use of macrophytes by fauna during reproduction and development, (3) influence of invertebrates on submerged macrophytes.

2. AREA AND METHODS

The study was carried out between 1966 and 1971 in Mikołajskie Lake. Mikołajskie Lake is a eutrophic, holomictic water body of a surface area of 460 ha. Its mean depth is 11.0 m, maximum depth 27.8 m and the littoral covers 19% of the lake surface, and the development of shore line is 1.7.

Three main sites were situated along the south-western shore. These were characterized by various species of submerged plants (1 – *Myriophyllum spicatum* L., *Elodea canadensis* Rich., *Potamogeton lucens* L., *P. perfoliatus* L., 2 – *E. canadensis*, 3 – *P. perfoliatus* and *P. lucens*), different bottom (1 – mud with a large amount of plant detritus, 2 – mud, 3 – sand), and variously exposed to wave action (1 – weak wave action, 2 – medium wave action, 3 – strong wave action). On all sites the depth was similar, approximately 0.5–0.7 m.

A detailed characteristics of the area investigated is given in another paper (G. J. Soszka 1975b).

Use of macrophytes by invertebrates during reproduction and development. The egg-masses on leaves and stems were counted. Also the numbers of organisms mining in submerged macrophytes were estimated.

Grazing of invertebrates on macrophytes. The contents of alimentary tracts and the faeces of main representatives of invertebrates were analysed, the animals being previously decapitated and dissected (the kind of dissection depended on the structure of the alimentary tract). The dissections were made immediately after bringing the material from lake (sometimes the material was kept in cold storage for several hours). In the contents of alimentary tracts and in the faeces the following fractions were distinguished: tissue of macrophytes, algae, detritus, calcium deposit and animals. The faeces were sometimes analysed to estimate the food composition of invertebrates, especially when examining the food composition of molluscs.

In order to analyse in detail the feeding of invertebrates on the tissue of macrophytes laboratory experiments were carried out. This will be described further in the paper.

Experimental substrates. In order to analyse some relations between invertebrates and submerged macrophytes a field experiment was carried out in which experimental substrates were introduced into the lake littoral. The experimental substrates (resembling macrophytes – *Potamogeton perfoliatus* – Figure 1), made of polyvinyl chloride, were placed close to various species of submerged macrophytes. On a nylon string five leaves, each of a surface 16.5 cm^2, were placed (on top of the "plant" there was a cork and at the bottom a stone). The "artificial plants" retained the vertical line, typical for natural ones and were subjected to water movements. The experimental substrates were exposed for three weeks. Over that period the "artificial plants" were colonized by periphyton similar to that found on macrophytes. The invertebrates inhabiting these substrates were sampled and analysed similarly as in the case of fauna living on macrophytes. The numbers of fauna were calculated per 100 cm^2 of leaf surface.

The method of experimental substrates is commonly used for periphyton (Cooke 1956, Sladečkova 1960, 1962, Pieczyńska 1964 and others). It is sporadically used for fauna associated with macrophytes (Macan and Kitching 1972, G. J. Soszka 1975a and others).

The destruction of macrophytes. The leaves and stems were analysed. The contribution of leaves and stems being eaten and the percentage of losses in leaf surface (approximately it corresponds to the losses of leaf biomass) were determined.

In order to estimate the production of losses in tissues of submerged macrophytes the new losses on marked leaves of *Potamogeton lucens* were observed in the field. The changes of the already eaten up surfaces were recorded by measuring every two days their size during three weeks.

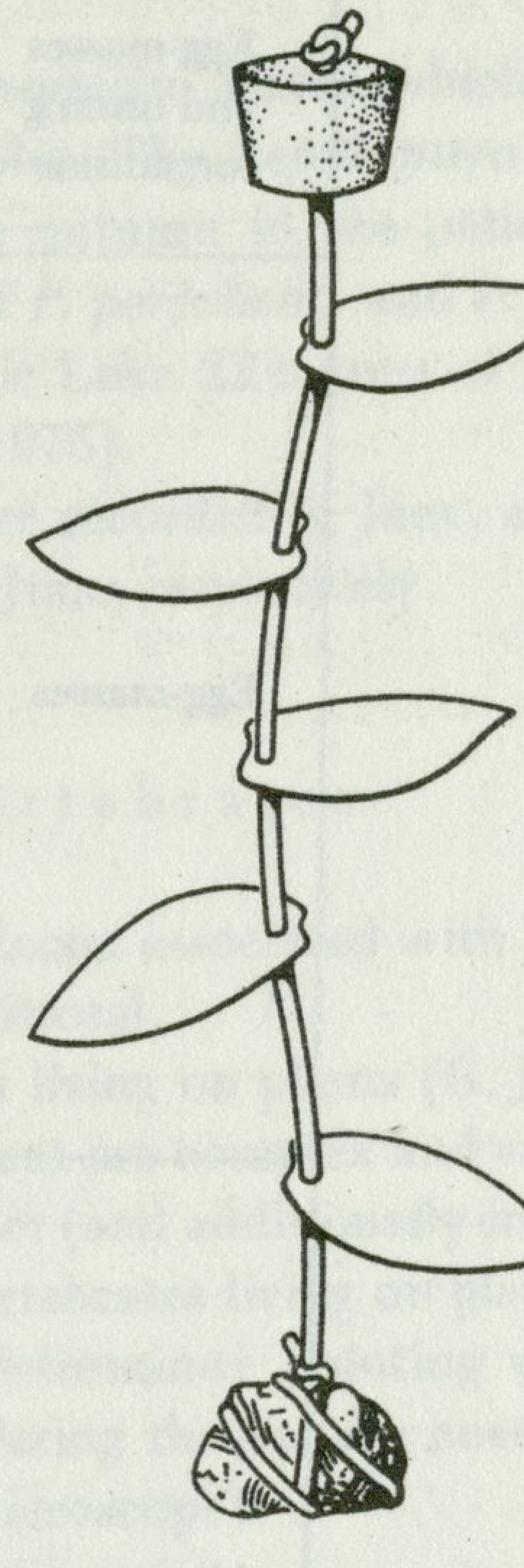

Fig. 1. Experimental substrate

3. RESULTS

3.1. Submerged macrophytes as breeding place, material for cases and a place of mining for invertebrates

The material was collected in Mikołajskie Lake from June to October in 1969 and 1970 and additionally in winter (December 1970, January, February, March 1971). The extent to which submerged macrophytes were used by invertebrates for egg-laying was determined by analysing the plants on three main sites. The eggs of invertebrates were found on *Potamogeton perfoliatus*, *P. lucens* and on *Elodea canadensis* (Tab. I). On main sites they were not found on *Myriophyllum spicatum*, whereas they occurred sporadically in other parts of the lake. The eggs were also found on other submerged substrates, e.g., on stones and branches.

On leaves and stems of *P. perfoliatus* and *P. lucens* about 90% of eggs belonged to *Gastropoda* [most abundant were eggs of *Bithynia tentaculata* (L.) and *Radix ovata* (Draparnaud), *Limnea stagnalis* (L.), *Coretus corneus* (L.), *Planorbis planorbis* (L.), *Physa acuta* (Draparnaud)], *Hirudinea* (Herpobdella sp.) and *Hydracarina*. On *E. canadensis* almost 100% of eggs were of *Herpobdella* sp. and *Bithynia tentaculata* (the latter were twice as many). Other, sporadically occurring ones belonged to *Chironomidae* and *Odonata*.

Tab. I. Number of egg-masses and mining organisms (per 100 g of fresh plant weight) on *Elodea canadensis*, *Potamogeton perfoliatus* and *P. lucens* in Mikołajskie Lake (June-October 1969 and 1970)

Egg-masses and mining organisms	Months and years		Plant species		
			Elodea canadensis	*Potamogeton perfoliatus*	*Potamogeton lucens*
Egg-masses	June	1969	13	613	53
		1970	24	432	84
	July	1969	21	238	37
		1970	79	282	68
	Aug.	1969	158	132	86
		1970	210	338	114
	Oct.	1969	–	–	–
		1970	–	–	–
Mining organisms	June	1969	–	128	11
		1970	–	172	7
	July	1969	–	93	11
		1970	–	150	9
	Aug.	1969	–	66	187
		1970	–	119	147
	Oct.	1969	–	22	31
		1970	–	57	59

The largest number of eggs was on *P. perfoliatus* and they were less numerous on *P. lucens* and *E. canadensis* (on *E. canadensis* as compared to *P. lucens* in June there were almost four times smaller numbers, approximate in July and two times larger in August). The egg-masses on macrophytes analysed were the most numerous in August 1970. In October there were no eggs on these plants. In samples from under the ice they occurred rarely and belonged to *Limnaeidae* and *Theodoxus fluviatilis*.

Also the use of submerged macrophytes as material to case building has been observed. *The Lepidoptera* larvae [*Paraponyx stratiotata* (L.) and *Acentropus niveus* (Oliv.)] roll and glue the leaves of pondweeds into "tubes" or cut parts of leaves and stick them to the other part of the leaf; in both cases the larvae use the leaves as dwelling cases. The *Trichoptera* larvae of families: *Phryganeidae*, *Limnephilidae* and *Leptoceridae* use plenty of plant material to build cases (e.g., *E. canadensis*, *M. spicatum*, *P. lucens* and *P. perfoliatus*), the fragments of live plants (e.g., parts of stems and leaves) and the dead plant remains. An analysis of the material used for case building by *Limnephilus* sp. and *Phryganea grandis* L. in winter shows the contribution of green stems and leaves of *E. canadensis.*

All over the investigated period the larvae of mining insects were found in leaves and stems of *P. perfoliatus* and *P. lucens* (Tab. I). The material from main sites showed no mining organisms in *E. canadensis* and *M. spicatum,* although they sporadically occurred in stems of these macrophytes in other parts of the lake.

Among the mining fauna the most abundant are the *Chironomidae* larvae which settle mainly in the stems and are less abundant in leaves and petioles. The *Lepidoptera* larvae (*Paraponyx stratiotata* and *Acentropus niveus*) occur mainly in autumn in the petioles of *P. perfoliatus* and *P. lucens.* The larvae of *Donatia* sp. in stems of *P. perfoliatus* and *P. lucens* occur sporadically in the part touching the bottom. In Mikołajskie Lake 22 taxons of mining invertebrates were found in the analysed macrophytes (U r b a n 1975).

The largest numbers of mining organisms in *P. perfoliatus* were recorded in June, and the smallest in October, whereas in the case of *P. lucens* in August and June, respectively.

3.2. M a c r o p h y t e s a s t h e f o o d o f i n v e r t e b r a t e s

Tissue of vascular plants, detritus, plankton, periphyton, and fauna associated with macrophytes and benthos are potential food for the invertebrates in the littoral.

The variety of potential food and variety of groups of fauna living on plants (G. J. S o - s z k a 1975b), suggest that the trophic relations in this environment are complex and variable.

In Mikołajskie Lake, between 1968–1970, from June to October (and additionally in March 1969), the food composition of dominant representatives of invertebrates living on plants was analysed. The contents of alimentary tracts and faeces were determined pointing out the frequency of occurrence of various food and its quantity (considering the surface covered by particular food fractions in relation to the whole food under the microscope).

The food composition of the examined invertebrates is as follows:

Chironomidae. 150 alimentary tracts of the following species have been examined: *Endochironomus* ex gr. *tendens* F., *E.* ex gr. *dispar* Meig., *Cricotopus* ex gr. *silvestris* F., *Tanytarsus* ex gr. *lauterborni* Kieff. and *Glyptotendipes gripekoveni* Kieff. As the food composition is greatly similar the results are given jointly. In 17% of alimentary tracts fragments of fresh and dead tissue of vascular plants were found. Several fragments of pondweeds were identified. In all alimentary tracts the periphytic algae (including attached forms: *Cocconeis* sp., *Synedra* sp. and *Gomphonema* sp.) and detritus with calcium deposit contributed mostly (Figs. 2–3). In 10% of alimentary tracts there was a small contribution of animal remains: *Oligochaeta*, *Cladocera* and *Rotatoria.* An analysis of food composition of *Chironomidae* larvae in winter (in March 1971) shows that the contribution of periphyton is smaller and of detritus greater as compared to the vegetation period. Generally, the *Chironomidae* species feed mainly on periphyton (periphytic algae and detritus of periphytic origin) and the tissue of vascular plants only slightly contributes to the food.

Stylaria lacustris L. The contents of 200 alimentary tracts of *S. lacustris* were examined. No remains of plants tissues were found. *S. lacustris* is a typical periphyton eater (Figs. 2–3). The alimentary tracts contain periphytic algae, detritus and particles of calcium deposit. In 5% of guts there are very few remains of animal origin: *Rotatoria* and *Cladocera.*

Radix ovata and *Bithynia tentaculata.* The composition of 120 faeces of *Radix ovata* and 150 faeces of *Bithynia tentaculata* was analysed. The remains of fresh and dead plant

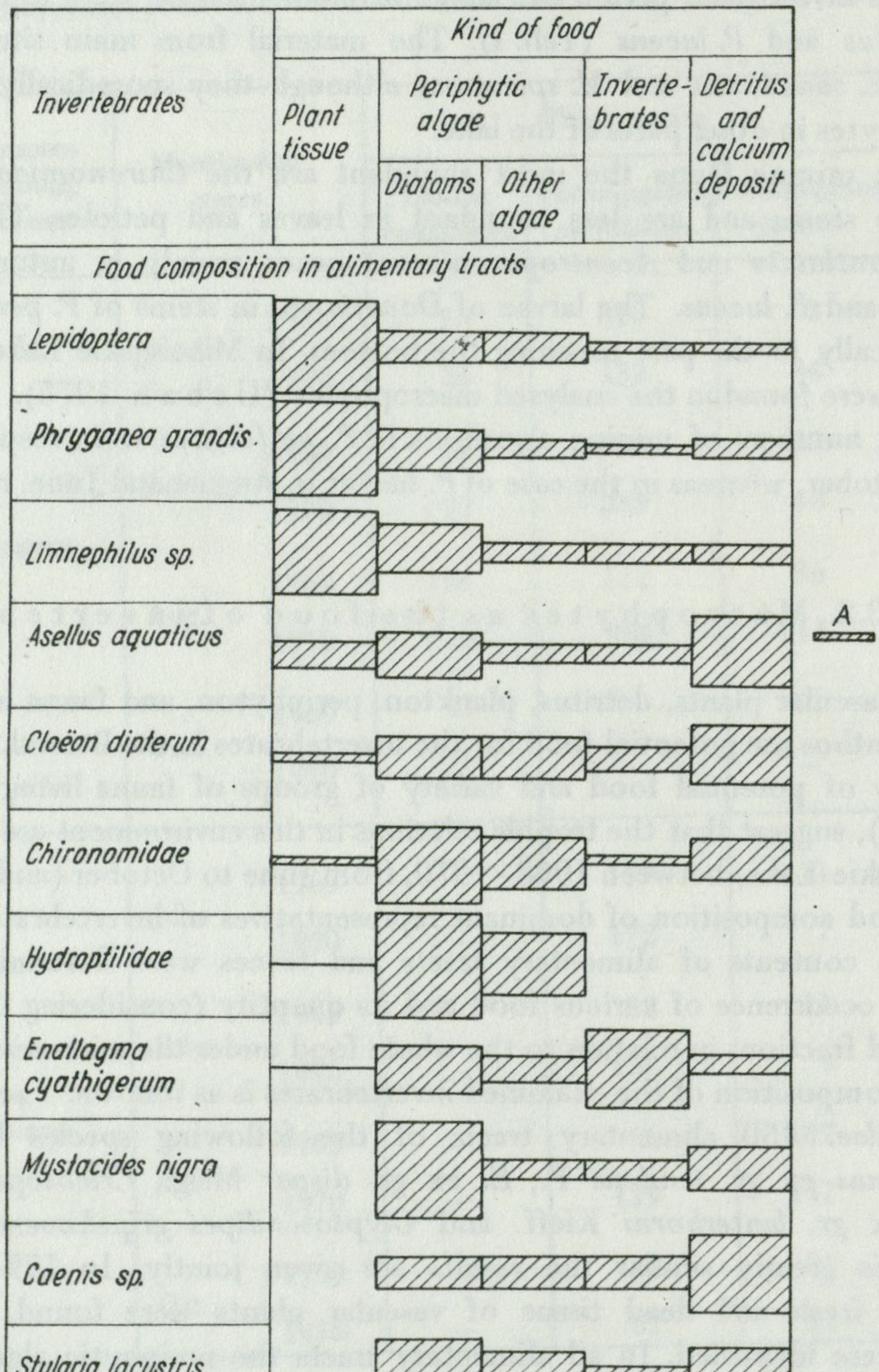

Fig. 2. Contents of alimentary tracts and faeces of dominant invertebrates in Mikołajskie Lake (June, October 1968–1970)

***A* – 3% of surface area (under the microscope) occupied by a particular food component in relation to the area occupied by all food**

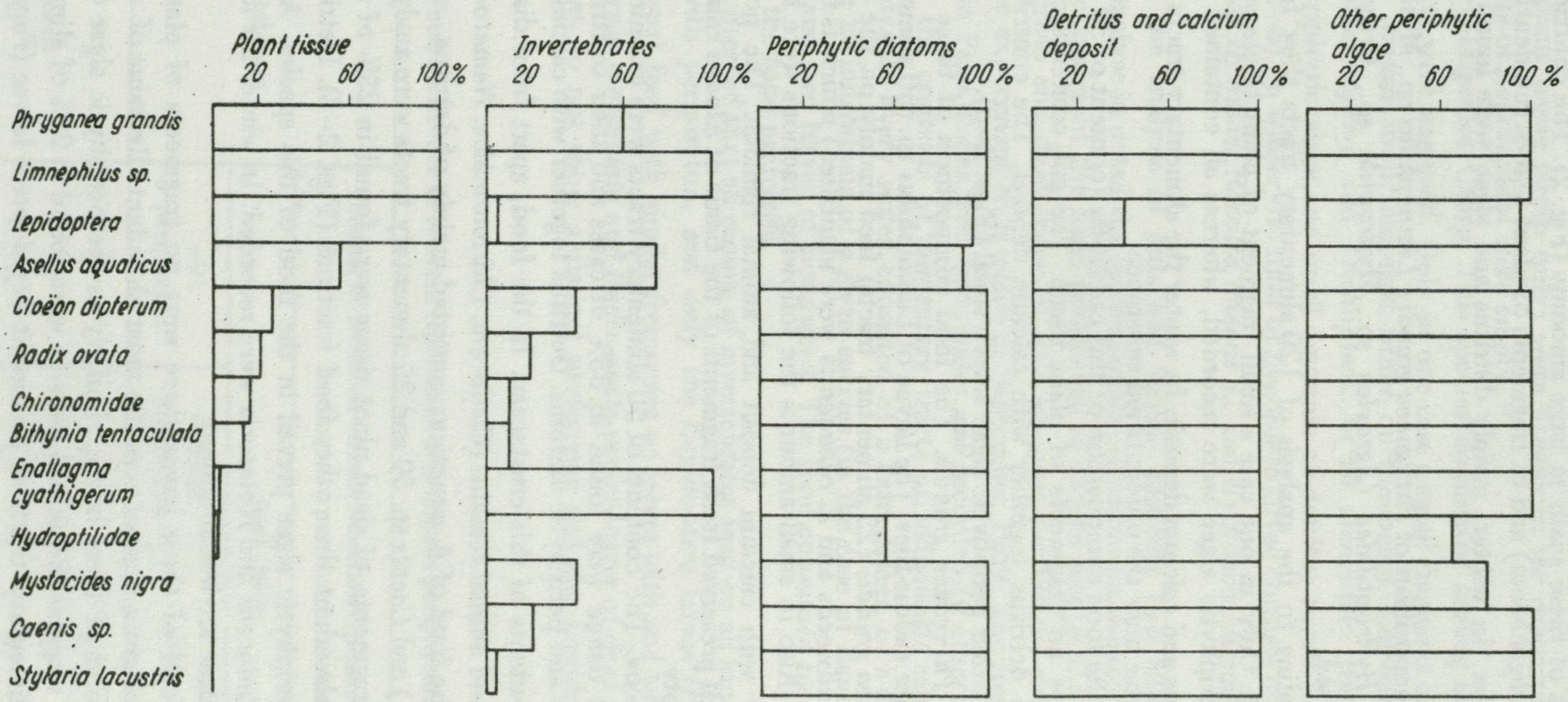

Fig. 3. Percentage of alimentary tracts and faeces of dominant invertebrates with various kinds of food components in Mikołajskie Lake (June-October 1968–1970)

tissue were found in 20% of faeces of *R. ovata* and dead plant tissue was found only in 15% of faeces of *B. tentaculata* (Fig. 3). The periphytic algae, detritus and particles of calcium deposit were found in all faeces of these snails in large amounts (Fig. 2). The contribution of animal remains (*Rotatoria* and *Oligochaeta*) and of fragments of plant tissues (unidentified macrophyte species) was much smaller. In winter, mainly detritus and algae were found in the faeces of these snails.

Trichoptera. Food composition of *Phryganea grandis*, *Limnephilus* sp., *Mystacides nigra* (L.) and representatives of *Hydroptilidae (Agraylea* sp., *Hydroptila* sp., *Orthotrichia* sp. and *Oxyethira* sp.) was analysed.

Hydroptilidae. According to the analysis of 120 alimentary tracts they feed primarily on periphytic algae (Fig. 2). Only in one case a small fragment of plant tissue was found. In the majority of guts the periphytic algae were recorded, whereas all contained the unidentified substance and no detritus and calcium deposit. In winter the alimentary tracts of *Hydroptilidae* larvae did not contain algae only the unidentified substance.

Mystacides nigra. In the food composition of this caddis-fly (content of 30 alimentary tracts was examined) there are no fragments of plant tissue. The gut contents consist mainly of periphytic diatoms and detritus together with calcium deposit. The contribution of animal remains (*Rotatoria*) and other periphytic algae is very small (Figs. 2–3).

Limnephilus sp. and *Phryganea grandis.* The food composition of these larvae noticeably differs from that of other caddis-flies. The larvae of *Limnephilus* sp. (50 alimentary tracts were examined) and *Phryganea grandis* (25 alimentary tracts) feed mainly on the tissue of vascular plants (fragments of pondweeds and *E. canadensis* were identified) which is found abundantly in all cases (Figs. 2–3). Also in small amounts the following fractions were found: periphytic algae, detritus together with calcium deposit and animal remains. The periphytic diatoms prevailed. In winter, well preserved fresh fragments of the tissue of *Elodea canadensis* occurred; part of the guts was empty.

Asellus aquaticus Racov. The contents of 50 alimentary tracts were examined. Fragments of dead unidentified plant tissue were found in 55% of cases and their contribution was much smaller than of detritus and periphytic diatoms. Detritus together with calcium deposit was the main fraction in gut contents of this crustacean. In the food, apart from diatoms, there were other periphytic algae and animal remains (*Cladocera*, *Chironomidae*, *Nematoda* and *Rotatoria*) (Figs. 2–3). In winter the food of *A. aquaticus* consisted mainly of detritus.

Cloëon dipterum (L.) and *Caenis* sp. 50 and 25 alimentary tracts were analysed, respectively.

Cloëon dipterum. Fragments of dead plant tissue were found in 25% of alimentary tracts. They were much less abundant than other food fractions (Figs. 2–3). Detritus together with calcium deposit and periphytic algae prevail in the food of this species. Among the animal remains *Oligochaeta*, *Cladocera* and *Rotatoria* were recorded. In winter the amount of detritus is greater, whereas the algae are less abundant.

Caenis sp. In the food of these larvae there were no fragments of plant tissue, whereas detritus together with calcium deposit was the most abundant. Remains of animal origin were less abundant in the food of these larvae, similarly as the periphytic algae (Figs. 2–3) which were found in all cases, whereas the animal remains were found in 20% of alimentary tracts.

Lepidoptera. 100 alimentary tracts of dominant *Lepidoptera* larvae (*Paraponyx stratiotata* and *Acentropus niveus*) were analysed. The food composition of both species did not differ. The *Lepidoptera* larvae feed primarily on the tissue of vascular plants (Figs. 2–3). Fragments of tissues of pondweeds and *E. canadensis* were identified. Large amounts of plant tissue were found in all cases. In the majority of alimentary tracts there were small amounts of periphytic algae. In 40% of cases there were also very small amounts of detritus together with calcium deposit and sporadically animal remains (e.g., *Cladocera*, *Oligochaeta* and *Rotatoria*). Fragments of plant tissue (fresh only) were usually in the shape of "morsels". In winter the alimentary tracts of *Lepidoptera* were empty.

Enallagma cyathigerum Charp. This species dominated among the *Zygoptera* larvae. Sixty alimentary tracts were analysed. Only in one case a small fragment of a plant was found. These larvae feed on animal food, amongst other on *Cladocera*, *Chironomidae*, *Stylaria lacustris*, *Copepoda*, *Ephemeroptera* and *Trichoptera*. In all alimentary tracts there are considerable amounts of periphytic algae and small amounts of detritus together with particles of calcium deposit (Figs. 2–3). In winter the food of *Zygoptera* larvae consists of algae and animal remains.

In the guts of *Heleidae*, *Ranatra linearis* L. and *Hydrozoa* fragments of vascular plants were not found.

Apart from the analysis of guts and faeces' contents two laboratory experiments were carried out to analyse in detail the feeding of invertebrates on the macrophyte tissue.

In the first experiment the food preference of chosen groups of invertebrates was estimated in relation to fresh and dead leaves of *Potamogeton perfoliatus* and leaves with and without periphyton. The experiment took place in September 1969. The frequency of feeding on two kinds of food in Petri dishes with lake water was recorded (6 observations every 30 minutes). Simultaneously the contents of alimentary tracts of individuals randomly chosen from each series were analysed. Every series consisted of 5 Petri dishes, of a diameter 10.5cm. On each dish there were 20 individuals of a given species (in the case of *Lepidoptera* larvae there were 10 individuals) and two leaves of pondweed. The food consumed by 60% and more individuals was assumed as the food preferred.

It has been observed that all groups of invertebrates feed on all kinds of analysed food. They prefer leaves with periphyton, and only the *Lepidoptera* larvae (*Paraponyx stratiotata* and *Acentropus niveus*) feed with similar frequency on leaves with and without periphyton. *Asellus aquaticus*, *Bithynia tentaculata* and *Radix ovata* prefer leaves of dead plants, *Chironomidae* and *Cloëon dipterum* do not show a distinct preference and the *Lepidoptera* larvae prefer fresh leaves (Tab. II).

Tab. II. Food preference of selected invertebrates as regards periphyton and macrophytes

Invertebrates	Feeding of fauna on various substrates (percentage of individuals feeding on a particular substrate)			
	plant tissue			
	with periphyton	without periphyton	live	dead
Radix ovata	87	13	27	73
Asellus aquaticus	78	22	24	76
Chironomidae	77	23	47	53
Bithynia tentaculata	76	24	33	67
Cloëon dipterum	75	25	53	47
Lepidoptera	51	49	82	18

In the second experiment the feeding intensity of chosen representatives of invertebrates on leaves of *Potamogeton lucens* was determined. Simlarly as in the previous experiment the Petri dishes with lake water were used. The weight of leaves of *P. lucens* before and after feeding after 4 days of exposure was compared. Each group of invertebrates was represented by several individuals. The amount of consumed food was calculated per weight unit of a consumer and per time unit. The experiment was repeated twice in September 1969.

The *Lepidoptera* larvae (*Paraponyx stratiotata* and *Acentropus niveus*) fed most intensively on fresh tissue – 94 mg of *P. lucens* per 24 hr per 1 g biomass (Fig. 4). *Radix ovata* and *Chironomidae* larvae fed to a much smaller extent on the fresh tissue *Bithynia tentaculata*, *Cloëon dipterum* and *Asellus aquaticus* fed much less intensively and on partly dead leaves (this could be observed not sooner than on the third day). A *Lepidoptera* larva of a mean weight 230 mg consumes daily 21.8 mg of fresh plant tissue, i.e., its daily food ration is almost 10% of fresh weight of animal. Taking into consideration the numbers of *Lepidoptera* larvae on analysed macrophytes in Mikołajskie Lake it was found that the *Lepidoptera* of mean numbers inhabiting 100 g fresh plant weight consume daily about 0.5 g of fresh plant weight, whereas in the case of maximum numbers about 4.0 g fresh plant weight. According to the biomass of macrophytes and numbers of *Lepidoptera* larvae per 1 m^2 the *Lepidoptera (Paraponyx stratiotata* and *Acentropus niveus)* can consume daily about 20 g of fresh plant weight which corresponds approximately to the weight of one pondweed.

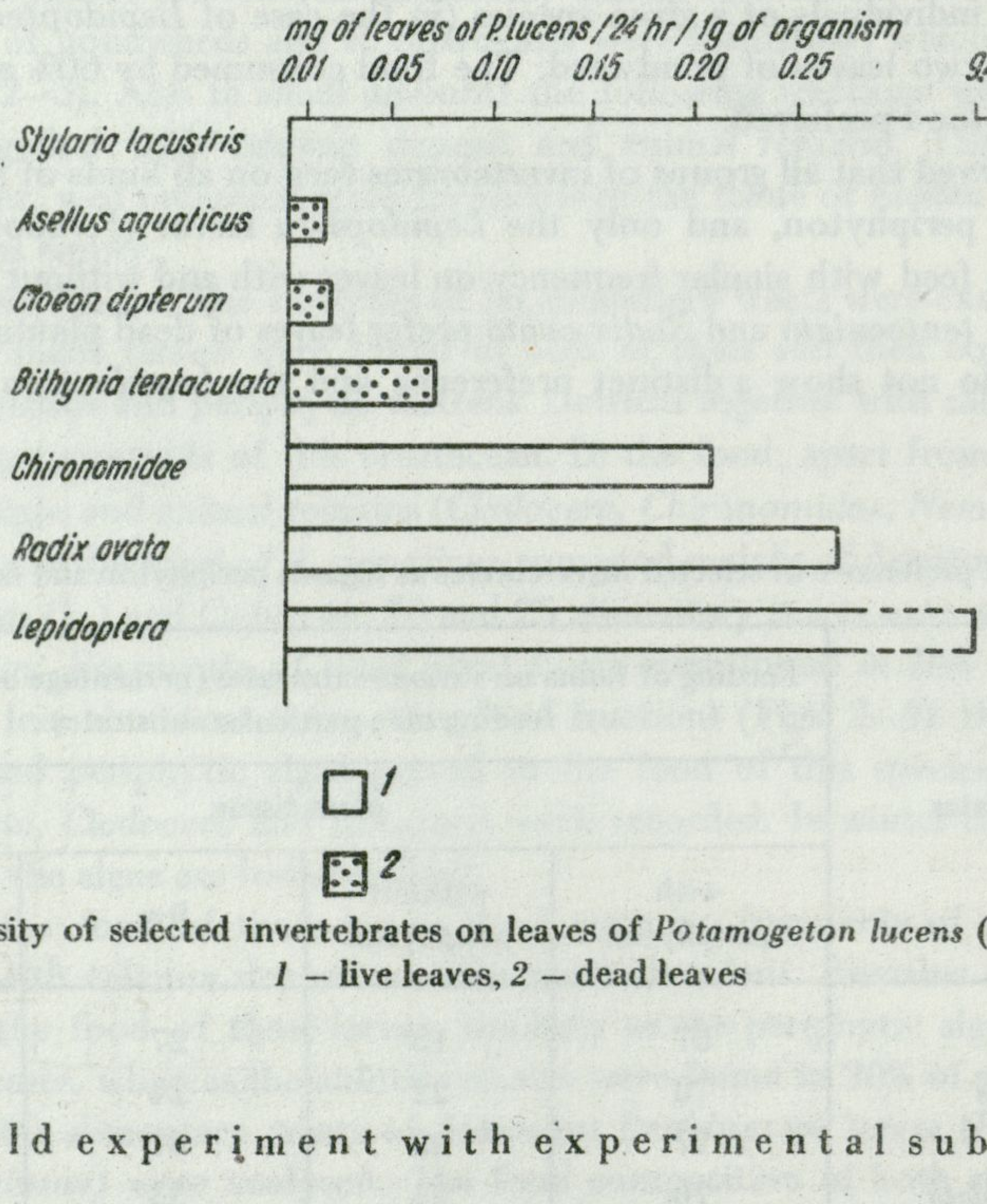

Fig. 4. Feeding intensity of selected invertebrates on leaves of *Potamogeton lucens* (laboratory experiment) 1 – live leaves, 2 – dead leaves

3.3. Field experiment with experimental substrates

The fact that invertebrates use macrophytes as a place for living is beyond any doubt on the ground of previously described material and literature data. It is also known that the littoral fauna associated with macrophytes occurs also on submerged stones, branches and other solid substrates. The literature on periphyton also points to the fact that similar periphytic organisms colonize all natural or introduced by man substrates in water bodies. Therefore, the question is to what extent the macrophytes are one of the many potential substrates and to what extent the specific relations between macrophytes and the fauna occur.

In order to analyse in detail the relations between submerged macrophytes and the littoral invertebrates a field experiment has been carried out where plastic experimental substrates resembling *Potamogeton perfoliatus* were introduced into the littoral (Fig. 1).

The experiment lasted from May to November 1969 and during that time on sites 2 and 3 in the littoral 63 experimental substrates were distributed. The control series showed that the experimental substrates after three weeks of exposure in the lake did not differ from macrophytes with regard to the composition and amount of periphyton colonizing them and the same amount of detritus accumulated there. This similarity of periphyton on experimental substrates and on plants is frequently pointed out in the literature (Cooke 1956, Castenholz 1961, Pieczyńska and Spodniewska 1963 and others).

Composition and number dynamics of invertebrates on experimental substrates and on analysed submerged macrophytes were compared. On the "artificial plants" eggs of invertebrates were recorded.

It turned out that both in the case of colonization by invertebrates and in the case of egg-laying the experimental substrates substitute well the macrophytes. The invertebrates were found on "artificial plants" during the full plant vegetation. Early in spring when there were no aboveground shoots of pondweeds yet – only the plastic plants – the fauna colonized these experimental substrates as well (Fig. 5). At that time, among others, there were *Chironomidae, Gastropoda, Hirudinea, Ephemeroptera, Trichoptera, Asellus aquaticus*, etc. A similar situation occurred in late autumn when the pondweeds were dead. In this case the littoral fauna remained till the end of the exposure of experimental substrates, i.e., till the end of November.

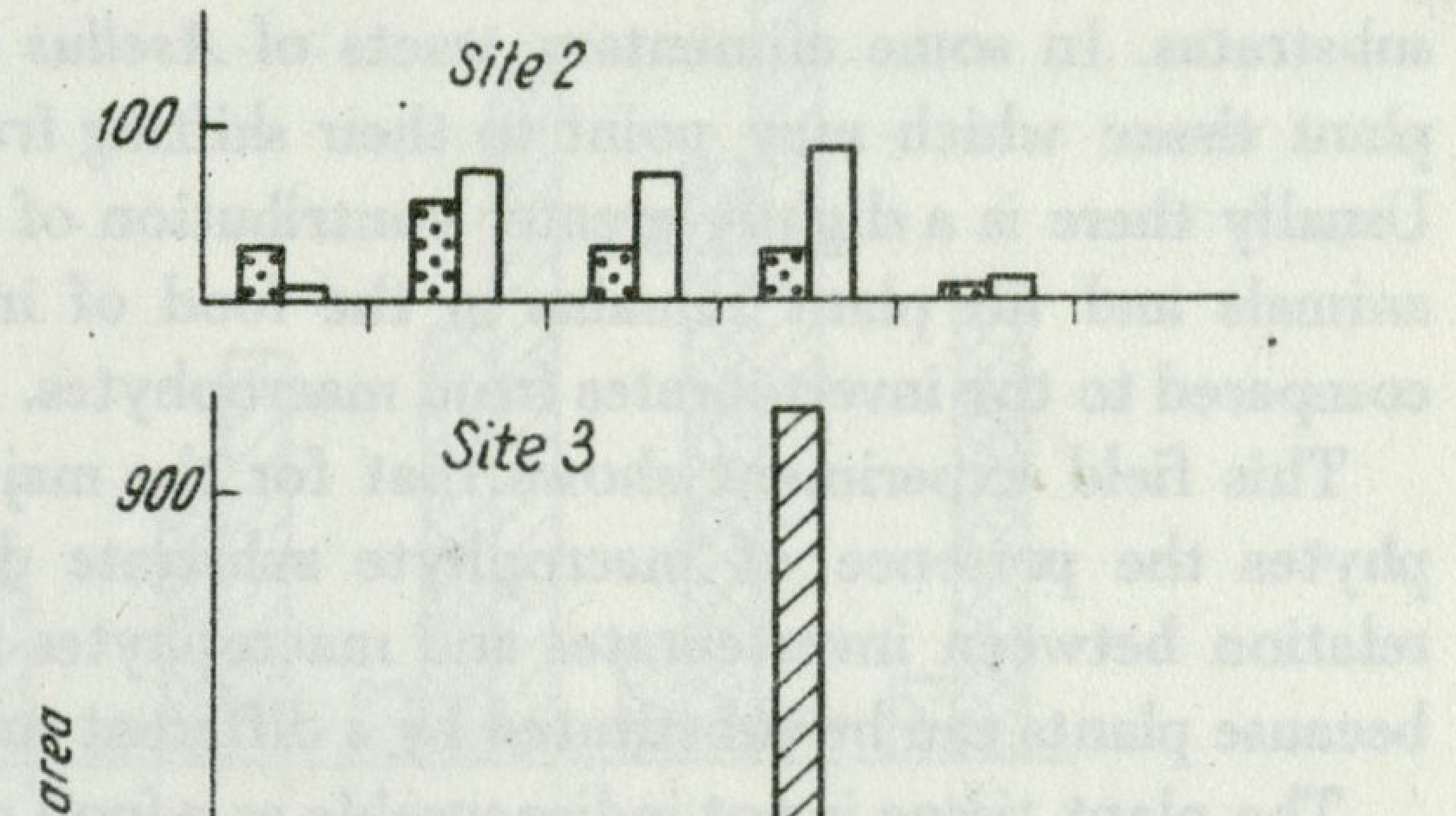

Fig. 5. Comparison of animal numbers on experimental substrates and on three species of macrophytes in Mikołajskie Lake in 1969

1 – experimental substrate, 2 – *Elodea canadensis*, 3 – *Potamogeton lucens*, 4 – *P. perfoliatus*

The composition of invertebrates was almost the same on both kinds of substrate and only the *Lepidoptera* larvae did not occur on "artificial plants". The numbers of fauna on experimental substrates were usually similar as on macrophytes. These numbers were smaller on experimental substrates as compared to *Potamogeton perfoliatus* and *P. lucens* in October and much higher in comparison with the numbers of fauna on *Elodea canadensis* in the whole period with the exception of May, and especially in October and September (Fig. 5).

On experimental substrates eggs of such invertebrates as *Theodoxus fluviatilis, Bithynia tentaculata, Limnaea stagnalis, Radix ovata, Coretus corneus, Physa acuta*, others *Planorbidae*, *Herpobdella* sp., *Hydracarina* and others were recorded. In some cases their numbers on experimental substrates were twice or even three times higher than on macrophytes in spring and in full summer.

The food composition of chosen invertebrates occurring on both substrates was examined. It has been expected that the food composition will be similar in the case of these groups of invertebrates in which the plant tissue is of no great significance as a food component but only the periphyton and detritus.

Usually the food fractions of fauna (e.g., periphyton, detritus and animal remains) from experimental substrates and macrophytes are the same. *Stylaria lacustris, Hydroptilidae, Caenis* sp. and *Mystacides nigra* are examples. The differences in the quantity of periphytic algae in alimentary tracts of these representatives of fauna did not exceed 5%. Greater differences were recorded in several cases. For example, in the food composition of *Chironomidae, Radix ovata* and *Cloëon dipterum* collected from the macrophytes there were small amounts of plant tissue which was not observed in guts of invertebrates from experimental substrates. In some alimentary tracts of *Asellus aquaticus* there were small amounts of dead plant tissue which may point to their shifting from macrophytes onto the "artificial plants". Usually there is a slightly greater contribution of detritus and a slightly smaller contribution of animals and no plant remains in the food of invertebrates from experimental substrates as compared to the invertebrates from macrophytes.

This field experiment shows that for the majority of invertebrates associated with macrophytes the presence of macrophyte substrate does not decide about their occurrence. The relation between invertebrates and macrophytes as their life substrate is not a permanent one because plants can be substituted by a different substrate.

The plant tissue is not indispensable as a food component for the majority of representatives of invertebrates associated with macrophytes even in cases where under natural conditions it was found in the alimentary tracts (e.g., *Radix ovata* and *Chironomidae*). Nevertheless, in some cases, for example the *Lepidoptera*, the plant tissue is indispensable as a basic food component (these organisms did not occur at all on "artificial plants").

3.4. The effect of life activity of invertebrates on submerged macrophytes

The destruction of submerged macrophytes due to life activity of invertebrates were analysed. The material was obtained from Mikołajskie Lake in different months of the vegetation season in 1969 and 1970. The losses in leaves and stems of submerged macrophytes were determined. The rate of occurrence of new losses and changes in the size of the already existing ones in the leaves were examined:

21,590 leaves and 1,480 stems of four species of macrophytes were surveyed. The comparison of *Potamogeton perfoliatus, P. lucens, Myriophyllum spicatum* and *Elodea canadensis* showed that in both years pondweeds were much more destroyed by the invertebrates (Figs. 6–7). Already in June 1969 the contribution of leaves of *P. lucens* being eaten exceeded 75% and 70% in 1970, whereas in the case of *P. perfoliatus* 60% and 75%, respectively. In autumn these values were almost 100% for both species. The losses of leaf surface due to the destructive activity of invertebrates increased during the season and in

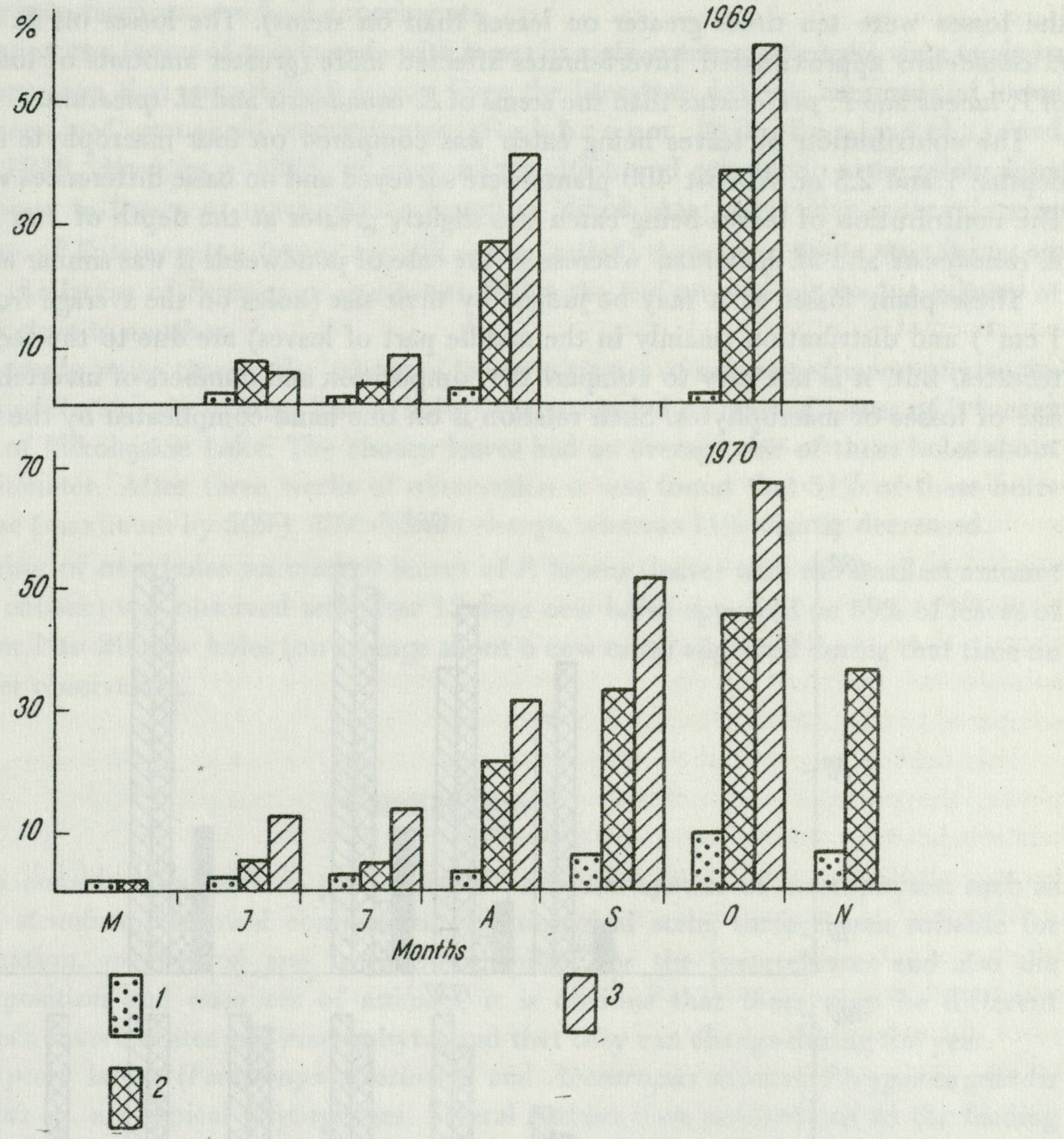

Fig. 6. Losses (due to animal grazing) of surface of three species of macrophytes in Mikołajskie Lake in 1969 and 1970 (percentage of total leaves' surface)
1 — Elodea canadensis, 2 — Potamogeton lucens, 3 — P. perfoliatus

autumn, for *P. perfoliatus*, they attained almost 60% in 1969 and 65% in 1970, whereas in the case of *P. lucens* 40% and 45%, respectively. In some parts of the lake this reduction in autumn was about 90%. In both years of the study *E. canadensis* and *M. spicatum* were much less damaged by the invertebrates. The contribution of leaves being eaten increased during the season, but in the case of *E. canadensis* it did not exceed 20% in autumn 1969 and 35% in 1970, whereas the reduction of leaf surface did not exceed 2% in 1969 and 7% in 1970 (Figs. 6–7). In 1969 40% of leaves being eaten was the maximal in the case of *M. spicatum* (Fig. 7).

In the case of *E. canadensis*, in early spring, the contribution of leaves being eaten on old (last year's) plants was three times higher as compared to young shoots. This characteristic feature of old plants may be explained by their greater mechanical availability. The contribution of leaves being eaten on last year's *E. canadensis* was 36% and on the young one 12%.

The leaves are much more affected by invertebrates than the stems (greater amounts of losses). This is especially noticeable in the case of *P. perfoliatus* and *P. lucens* (e.g., in October the losses were ten times greater on leaves than on stems). The losses on *M. spicatum* and *E. canadensis* approximated. Invertebrates affected more (greater amounts of losses) the stems of *P. lucens* and *P. perfoliatus* than the stems of *E. canadensis* and *M. spicatum.*

The contribution of leaves being eaten was compared on four macrophyte species at two depths: 1 and 2.5 m. Almost 400 plants were surveyed and no basic differences were observed. The contribution of leaves being eaten was slightly greater at the depth of 1 m in the case of *E. canadensis* and *M. spicatum*, whereas in the case of pondweeds it was similar at both depths.

These plant losses as it may be judged by their size (holes on the average from 0.2 mm^2 to 1 cm^2) and distribution (mainly in the middle part of leaves) are due to the feeding of invertebrates. But, it is not easy to compare the composition and numbers of invertebrates with the size of losses of macrophytes. Such relation is on one hand complicated by the movements of

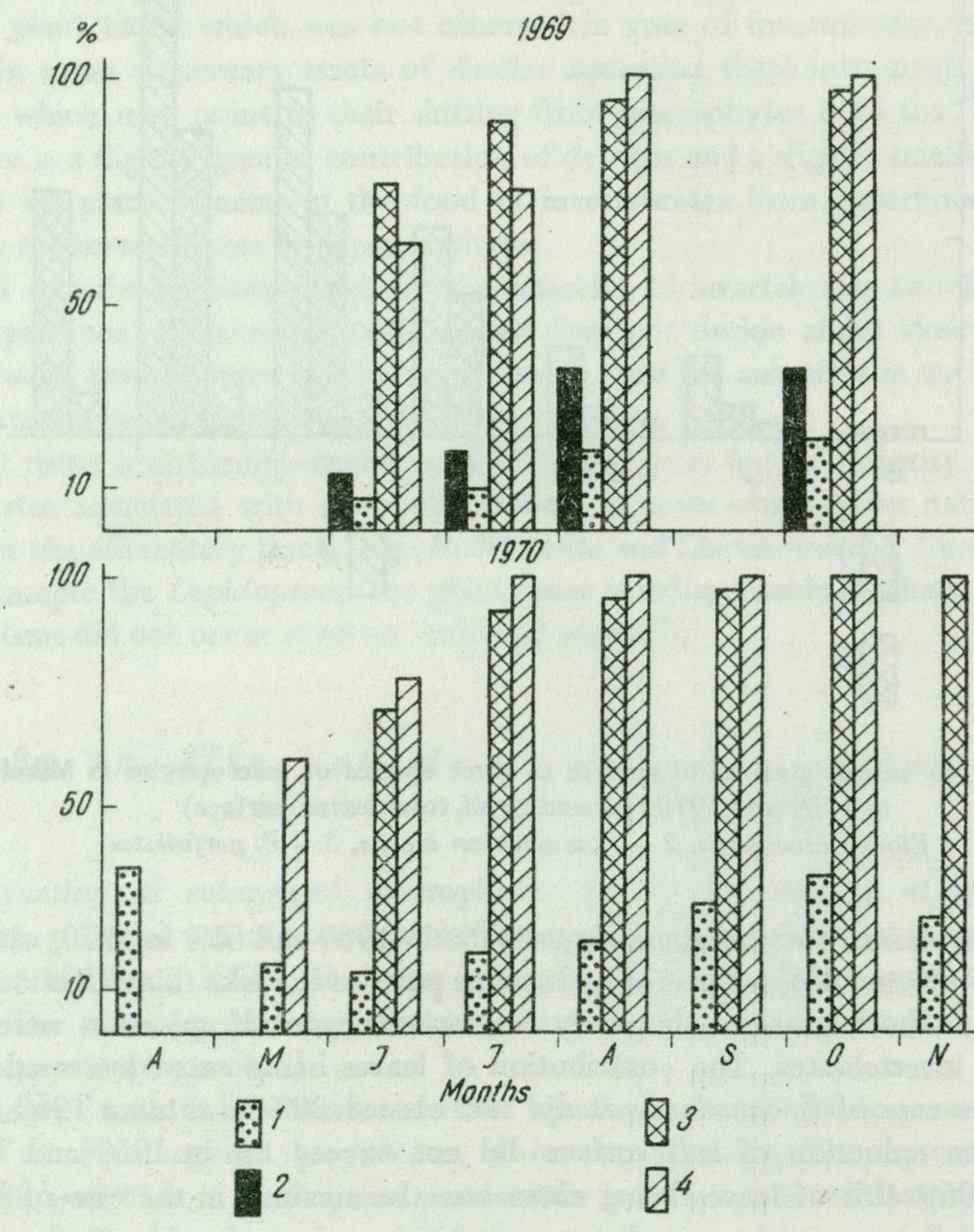

Fig. 7. Contribution of leaves being eaten on four species of macrophytes in Mikolajskie Lake in 1969 and 1970 (percentage of eaten leaves)

1 – Elodea canadensis, 2 – Myriophyllum spicatum, 3 – Potamogeton lucens, 4 – P. perfoliatus fauna and the divergence between places of feeding and living, and on the other hand by the unknown time during which these losses are arised. Most exact analysis of this problem would require further investigations and field experiments.

When analysing the leaves of pondweeds with losses in early autumn, attempts were made to indicate the organism that caused these losses. Even the literature data on the kinds of losses caused by determined groups of invertebrates (Rehbronn 1937, Pavlovskij and Lepneva 1948, Hering 1951, Frömming 1956 and others) do not explain fully the kind of losses in leaves of macrophytes found in Mikołajskie Lake. Only early in spring when the leaves of *Potamogeton lucens* are still young (rolled) there is no doubt that the losses are caused by the larvae of *Paraponyx stratiotata.* When the leaf spreads out the losses form of oval holes, one close to another.

In order to study more closely the arising of losses in tissues of submerged macrophytes the changes in size of the already existing losses (holes) were recorded on marked leaves of *P. lucens* in the littoral of Mikołajskie Lake. The chosen leaves had an average size of these holes about 1–5 mm in diameter. After three weeks of observation it was found that 51% of these holes increased in size (maximum by 50%), 38% did not change, whereas 11% slightly decreased.

The formation of new holes on marked leaves of *P. lucens* (leaves with the smallest amount of holes were chosen) was observed and after 12 days new holes appeared on 59% of leaves of *P. lucens.* From 1 to 20 new holes (on average about 6 new ones) appeared during that time on the leaves under observation.

4. DISCUSSION

Taking into consideration various properties of particular species of macrophytes, such as morphological structure, chemical composition, physiological state, surface area suitable for animal colonization, mechanical and trophic availability for the invertebrates and also the different composition and numbers of animals, it is obvious that there may be different relations between invertebrates and macrophytes and that they can change during the year.

The *Lepidoptera* larvae (*Paraponyx stratiotata* and *Acentropus niveus), Phryganea grandis* and *Limnephilus* sp. are typical phytophages. Several authors have pointed out to the feeding on plant tissue by the *Lepidoptera* larvae (Berg 1942, Entz 1947, McGaha 1952, 1954, H. Wojtusiak and R. J. Wojtusiak 1960, Kaškin 1961, Kokociński 1963, Hrubý 1964, Gaevskaja 1966 and others), and also by *Phryganea grandis* and *Limnephilus* sp. (Kaškin 1961, Lepneva 1964, Gaevskaja 1966, Hickin 1967 and others). Gaevskaja (1966) ranks these invertebrates as obligatory phytophages. The laboratory experiment presented in this paper has shown that the feeding intensity on macrophytes is the highest in the case of *Lepidoptera* larvae (several hundred times higher than for other representatives of the invertebrates inhabiting plants).

The *Chironomidae* larvae and *Gastropoda* feed less on the live plant tissue. The presence of plant tissue in the food of various *Chironomidae* species is mentioned in several papers (Černovskij 1949, Berg 1950, Walshe 1950, Konstantinov 1958, Gaevskaja 1966, Pankratova 1970, H. Soszka 1974, N. Wolnomiejski – unpublished data, and others). Attention is also paid to the various intensity of feeding of *Chironomidae* larvae on plant tissue. Among others, *Endochironomus ex* gr. *dispar* and *Cricotopus* ex gr. *silvestris* are included among the facultative phytophages and *Endochirono-*

mus ex gr. *tendens* among the obligatory phytophages (G a e v s k a j a 1966). It has been also pointed out that the contribution of plant tissue to the food of *Chironomidae* larvae increases as the macrophytes die (H. S o s z k a 1974). Among *Chironomidae* despite the presence of species *Endochironomus* ex gr. *tendens*, which is an obligatory phytophage acc. to G a e v s k a j a (1966), the contribution of tissue of vascular plants to their food is small. Similarly as in the case of *Chironomidae* larvae it is a generally known that the *Gastropoda* feed on plant tissue (F r ö m m i n g 1956, W i k t o r 1958, K a š k i n 1961, G a e v s k a j a 1966 and others). It has been mentioned frequently that the snails prefer partly decomposed plants than the live ones (S t a ń c z y k o w s k a 1960, G a e v s k a j a (1966). G a e v s k a j a (1966) states that the contribution of plant tissue to the food of *Radix ovata* is smaller as compared to other factions and very small in the food of *Bithynia tentaculata*. An analysis of material from Mikołajskie Lake points to a smaller contribution of plant tissue to the food of *Radix ovata* than one would expect considering the data of G a e v s k a j a (1966). Besides *Bithynia tentaculata* usually feeds on dead plant tissue (in Mikołajskie Lake – exclusively).

In the food of *Asellus aquaticus* and *Cloëon dipterum* the plant tissue is of little significance and these invertebrates usually feed (in the field) on dead tissue of macrophytes. In very few cases the fresh plant tissue has been stated in the food of *Asellus aquaticus* (G a e v s k a j a 1966) and *Cloëon dipterum* (M i k u l s k i 1936, I v a n o v a 1958 after G a e v s k a j a 1966). The results of the present laboratory experiment show that *Asellus aquaticus* and *Cloëon dipterum* very rarely use fresh plant tissues as food.

Some of the examined representatives of invertebrates associated with macrophytes do not feed on plant tissue. These are: *Stylaria lacustris*, *Mystacides nigra*, *Caenis* sp., *Heleidae*, *Ranatra linearis*, *Hydrozoa* and also *Hydroptilidae* and *Enallagma cyathigerum*. According to the literature data, presented in a monography by G a e v s k a j a (1966), these invertebrates are not mentioned as organisms feeding on macrophytes. Thus, very few representatives of invertebrates feed on fresh tissue of macrophytes to a considerable extent under natural conditions, e.g., the *Lepidoptera* larvae (*Paraponyx stratiotata* and *Acentropus niveus*), *Phryganea grandis* and *Limnephilus* sp.

The literature provides plenty of data, frequently contradictory, on the extent of utilization of plant tissue as the food of invertebrates. G a e v s k a j a (1966), on the basis of vast literature and own studies, says that for 72% of estimated organisms the plant food in the form of tissues of vascular plants is of the greatest significance. M c G a h a (1952) has found that out of 61 analysed species of insects 58 belong to phytophages utilizing the tissues of vascular plants to a various extent.

On the other hand, some authors point to the small contribution of tissues of vascular plants to the food of invertebrates. According to O d u m (1957) the main group of phytophages on submerged macrophytes in Silver Springs are invertebrates which feed on periphytic algae. D a r n e l l (1964), in his analysis of food composition of large invertebrates and fishes, points to the great significance of detritus and animals in their food, small significance of algae, and the smallest of submerged macrophytes. K a š k i n (1961), in his study on invertebrates feeding on macrophytes, says that only a few use the tissue of vascular plants as main food. According to G u r z ę d a (1959) in the case of the majority of species inhabiting the macrophytes, there is no direct trophic relation with macrophytes but only to periphyton. R o s i n e (1955), in his analysis of the differentiation of invertebrates associated with macrophytes, points to the fact that invertebrates do not use the tissue of higher plants but the periphyton. W e s t l a k e (1965) says that the majority of phytophagous animals found on periphyton and dead plant material and only for few species of invertebrates the leaves of plants are the only food source. Entz (1947) mentions only two *Lepidoptera* species which fed on the tissue of vascular plants. According to him the most important food is detritus and periphytic algae.

Several field investigations, similarly as the results of the present paper, point to the small contribution of plant tissue to the food of invertebrates (Odum 1957, Kaškin 1961, Darnell 1964, H. Soszka 1974 and others). The death of macrophytes improves the trophic conditions for fauna by making the plant tissue available for the majority of invertebrates. Amongst others, this may be proved by the increase of the numbers of invertebrates on pondweeds in autumn. Bownik (1970) has expressed a similar opinion when analysing the community of periphytic fauna on submerged macrophytes in Mikołajskie Lake.

Usually the algae and detritus of periphytic origin contribute mostly to the food of invertebrates in the littoral of Mikołajskie Lake (Figs. 2–3). Several authors have pointed out the great significance of periphyton in the feeding of aquatic invertebrates (Rosine 1955, Gurzęda 1959, Westlake 1965, Pieczyńska 1970, H. Soszka 1974).

The presented material and the literature data show that the majority of representatives of invertebrates feed mainly on periphytic algae and detritus of periphytic origin. Usually the plant tissue is of little significance in the food of invertebrates, and especially the fresh tissue. Nevertheless, in some cases in which the macrophytes are the main food as, e.g., in the case of *Lepidoptera* larvae the plant tissue is consumed in large amounts.

Some authors are of opinion that the macrophytes are used by invertebrates mainly as a mechanical substrate. Undoubtedly in this way the submerged macrophytes are used by several groups of attached or partly attached invertebrates such as, e.g., *Porifera*, *Hydrozoa*, *Bryozoa*, *Dreissena polymorpha* Pallas and others. Nevertheless, even this obvious kind of relation is not specific for macrophytes. Amongst other things this is shown in experiments with experimental substrates where the macrophytes were substituted by a different substrate for almost all groups of invertebrates (the exception are the *Lepidoptera* larvae not recorded on experimental substrates).

In studies on invertebrates inhabiting macrophytes plants have been rarely substituted by experimental substrates in natural conditions. Macan and Kitching (1972) have used plastic experimental substrates in order to analyse several regularities of the occurrence of invertebrates in the littoral. They have also observed similar regularities to those observed in Mikołajskie Lake: submerged macrophytes can be substituted by experimental substrates, the composition of invertebrates is similar on both substrates and the numbers of invertebrates on experimental substrates are frequently higher. G. J. Soszka (1975a) has used plastic and wooden experimental substrates to analyse the changes in numbers and the biomass of invertebrates in fish ponds with heated water having various temperatures. The numbers of fauna on both experimental substrates exceeded the numbers of invertebrates on *Polygonum amphibium* L. growing in vicinity.

It is a commonly known that the invertebrates use the aquatic macrophytes as their living place environment.

The literature on mining fauna does not contain plenty of quantitative data. *Chironomidae* larvae are found most frequently and abundantly. This is pointed out by Hering (1951), Wolnomiejski (1969 and unpublished data), Urban (1975) and others. In the present research it has been stated that the *Chironomidae* larvae also dominated among the mining fauna.

The relation between invertebrates and macrophytes can be also indirect by means of utilizing the periophyton colonizing plants. The complex relations between submerged macrophytes and invertebrates are mentioned by many authors (Frost 1942, Gorbunov

1955, G u r z ę d a 1959, K a š k i n 1961, G a e v s k a j a 1966, Z i m b e l e v s k a j a 1966, N. Wolnomiejski – unpublished data, and others). Thus it is necessary to examine parallely the factors conditioned by the biology of littoral invertebrates (feeding, reproduction, life cycle), determined by macrophytes themselves (morphological structure, chemical composition and physiological state of plants) and environmental factors (water chemistry, wave action, presence of calcium deposit), etc.

In some papers on the invertebrates of the littoral there are classifications according to the criteria of various relations between them and macrophytes. For example, Z i m b e l e v s k a j a (1966), in her studies on invertebrates associated with macrophytes, has distinguished four groups of invertebrates: littoral-phytophilous, bottom-phytophilous, phytophilous-pelagic and phytophilous. Niewiadomski (unpublished data) gives three groups of invertebrates: phytobiontic, phytophilous and phytoxenic. S t a ń c z y k o w s k a (1960) has given three main groups of snails: typical for plants, typical for the bottom and a medial group. G a e v s k a j a (1966) gives several groups of animals acc. to their intensity of feeding on macrophytes.

These classifications are usually based on one chosen criterion; it maybe the contribution of plant tissue to the food of fauna or the way of utilizing the plant substrate or the occurrence of animals on plants. Although the relations between macrophytes and invertebrates are complex the material presented in this paper has been analysed to estimate the extent of various relations between several groups of invertebrates and macrophytes (Tab. III). The strongest and universal relations to macrophytes are characteristic for *Lepidoptera* larvae (*Paraponyx*

Tab. III. The kind and intensity of using macrophytes by invertebrates in Mikołajskie Lake

Using of macrophytes: +++ very strong, ++ medium, + weak

Invertebrates	Using of macrophytes					
	as food	as a place for egg-laying	as a wintering place	as a mining place	as material for building cases	as a substrate
Lepidoptera	+++	++	+	+	++	+++
Phryganea grandis	+++	++	++		+++	++
Limnephilus sp.	+++	++	+++		+++	++
Radix ovata	++	+	+			+
Chironomidae (non-predatory)	++		+	+++		+++
Asellus aquaticus	+		+++			+
Cloëon dipterum	+		++			+
Bithynia tentaculata	+	+++	++			+
Hydroptilidae			+			+++
Mystacides sp.			+			+
Enallagma cyathigerum			+++			+
Caenis sp .			+			+
Stylaria lacustris						+

Tab. IV. Using of submerged macrophytes by the invertebrates in Mikołajskie Lake
Using of macrophytes: +++ very strong, ++ medium, + weak

Macrophyte species	Using of macrophytes:					
	as food	as place for egg-laying	as a wintering place	as a mining place	as material for building cases	as a substrate
Potamogeton lucens	+++	+++		+++	++	++
P. perfoliatus	+++	+++		+++	++	++
Elodea canadensis	+	+	+++	+	++	++
Myriophyllum spicatum	+	+	+	+	++	++

stratiotata and *Acentropus niveus*), *Phryganea grandis* and *Limnephilus* sp., to a considerable extent for *Chironomidae* (especially the mining ones) and some *Gastropoda* species. It must be pointed out that the numerous representatives of invertebrates, e.g., *Stylaria lacustris*, are connected with macrophytes to a very little extent.

The literature available does not classify the vascular plants according to their mutual relations to the invertebrates. An analysis of these relations in Mikołajskie Lake shows that the submerged macrophytes differ greatly in that respect (Tab. IV). The pondweeds are most intensively utilized during the year, excluding winter because of their life cycle. In the winter the relations between *E. canadensis* and invertebrates are the strongest.

Due to the life activity of invertebrates the macrophytes are greatly damaged. The invertebrates directly affects the submerged macrophytes (feeding, mining) and also indirectly (clearing the way for microorganisms to plant tissue thus speeding up the decomposition of submerged macrophytes).

Taking into consideration the losses of macrophytes caused by the life activity of invertebrates it has been observed that *Potamogeton perfoliatus* and *P. lucens* are much more affected by the fauna than *Elodea canadensis* and *Myriophyllum spicatum*. In the case of pondweeds the losses of leaf tissue are on average 50% of surface area and sometimes even 90%, whereas in the case of *E. canadensis* they do not exceed 10% of leaf surface area. Similarly, the fauna mining submerged macrophytes utilized the pondweeds to a greater extent. It is worth to point out that the parts of plants damaged more as a result of life activity of mining fauna (i.e. plant stems) are less damaged by invertebrates living on plant surface (which feeds mainly on leaves).

U r b a n (1975) when analysing the effect of mining fauna on submerged macrophytes in Mikołajskie Lake has found that the mining invertebrates damage more the stems than leaves and the stems of pondweeds are affected by fauna to a much higher extent than *E. canadensis*. It is characteristic that the mining *Chironomidae* are responsible for losses in leaves and stems of submerged macrophytes in Mikołajskie Lake but not due to the feeding on plant tissue (H. S o s z k a 1974). Comparison of the material from this paper and the data of U r b a n (1975) shows that the fauna living on plant surface damages the macrophytes more than the mining fauna.

The discussed here feeding and mining of invertebrates is only one of the factors responsible for the destruction of macrophytes. The feeding of fish and birds, and wave action are also of considerable significance. In Mikołajskie Lake P i e c z y ń s k a (1972) has observed that considerable amounts of all species of macrophytes have accumulated on the shore due to wave action, whereas J. Nabiałek (unpublished data) has noticed a considerable contribution of macrophytes to the food of roach and rudd. The losses of macrophytes are also due to the decay of vascular plants, indirect effect of invertebrates on plants (e.g., building the cases, disturbing the continuity of plant tissues due to feeding, etc.). Possible fates of macrophytes in lake littoral are discussed by Pieczyńska (1973).

The destructive effect of invertebrates on macrophytes is pointed by several authors. Smirnov (1961) has said that the daily losses in leaves' biomass may reach 7%. Kaškin (1961) estimates the losses in biomass of submerged macrophytes as the tenths and hundredths of a per cent of plant weight for one month. In Mikołajskie Lake the losses of leaves of pondweeds were estimated at the end of vegetation season as 40–50% of leaf surface area (on two *Potamogeton* species examined); the losses in leaves of *E. canadensis* did not exceed 7%. Wesenberg-Lund (1943) in his observations on ponds has found that the *Trichoptera* larvae destroy almost completely the leaves of *Potamogeton natans* in the autumn. According to McGaha (1952) intensive mining by the *Diptera* larvae results so many canals that the leaves are tattered and break at the slightest movement, and sometimes the leaves of aquatic plants are completely damaged by young *Lepidoptera* larvae. Müller-Liebenau (1956) has observed that *Potamogeton perfoliatus* in the lake environment was almost completely destroyed by organisms mining and feeding on leaves. Gaevskaja (1966) mentions that some *Diptera* larvae destroy the macrophytes completely at the end of the season. In Mikołajskie Lake, in late autumn, the leaves of pondweeds were also strongly tattered.

These different forms of destruction of aquatic vegetation have been observed by many authors, but usually no quantitative data are given.

The work has been carried out under the guidance of Dr. Ewa Pieczyńska, Asst. Prof., to whom I am extremely grateful for all the help and valuable criticism throughout this study.

5. SUMMARY

The study was carried out between 1966 and 1971 in Mikołajskie Lake. The use of macrophytes as a place for living, reproduction and development and food of invertebrates was analysed and simultaneously the influence of animals on submerged plants.

The fact that the invertebrates use the submerged macrophytes as a live substrate is not specific for plants. Amongst other things, this is pointed out by experiments with experimental substrates (Fig. 5) which show that macrophytes can be substituted by a different kind of substrate for almost all groups of invertebrates (an exception are the *Lepidoptera* larvae which do not occur on "artificial plants"). Taking into consideration other ways of use of macrophytes by invertebrates it has been observed that pondweeds as compared to *Elodea canadensis* and *Myriophyllum spicatum* are more strongly mined and also used to a greater extent during the reproduction and development of invertebrates. *Elodea canadensis* was the only species on which the invertebrates could winter (in winter the majority of groups of invertebrates were found there).

In the littoral of Mikołajskie Lake the tissue of vascular plants only slightly contributes to the food of invertebrates (Figs. 2–3). Only very few representatives of fauna feed to a considerable extent on fresh plant tissue under natural conditions, e.g., the *Lepidoptera* larvae (*Paraponyx stratiotata* and *Acentropus niveus*) and *Phryganea grandis* and *Limnephilus* sp. To a lesser extent the fresh tissue of macrophytes is the food of some *Chironomidae* and *Radix ovata*. Some representatives of invertebrates feed on dead tissue of macrophytes, for example *Bithynia tentaculata, Cloëon dipterum* and *Asellus aquaticus*. Whereas, some invertebrates associated with submerged macrophytes feed on fresh and dead plant tissue, for example some *Trichoptera* larvae, *Chironomidae* and *Gastropoda*. Usually the algae and detritus of periphytic origin mostly contribute to the food of invertebrates (Figs. 2–3).

The analyses of relations between submerged macrophytes and invertebrates in Mikołajskie Lake allow to draw the following conclusions. Among the invertebrates associated with macrophytes the most strongly

connected with plants are the *Lepidoptera* larvae, *Limnephilus* sp. and *Phryganea grandis*, and to a smaller extent the *Chironomidae* larvae and *Radix ovata*. The *Oligochaeta* which are very abundant on macrophytes are weakly associated with plants. The relations of the majority of invertebrates with macrophytes are not permanent and the macrophytes can be substituted by an another substrate. The majority of invertebrates primarily feed on periphytic algae and detritus of periphytic origin, whereas the fresh tissue of vascular plants slightly contributes to the food of these invertebrates. The invertebrates greatly damage the macrophytes; pondweeds are destroyed due to the life activity of invertebrates to a much greater extent than *E. canadensis* and *M. spicatum* (Figs. 6–7) (losses in leaf tissues of pondweeds are on average 50% and sometimes 90% of leaf surface, whereas in the case of *E. canadensis* they do not exceed 10%). It is worth to point out that the parts of plants which are destroyed to a greater extent by the life activity of mining fauna, i.e., plant stems, are less damaged by fauna living on plants which mainly feeds on leaves. The interrelations between the invertebrates and submerged macrophytes have a dynamic character and chang over the year.

6. POLISH SUMMARY (STRESZCZENIE)

Badania prowadzono w latach 1966–1971 w Jeziorze Mikołajskim. Analizowano wykorzystanie roślin jako miejsca bytowania, rozrodu i rozwoju oraz pokarmu fauny bezkręgowej, a także wpływ fauny na roślinność zanurzoną.

Wykazano, że wykorzystanie makrofitów zanurzonych przez bezkręgowce jako podłoża mechanicznego nie jest specyficzne dla tych roślin. Wskazują na to m. in. eksperymenty z zastosowaniem podłoży eksperymentalnych (fig. 5), z których wynika, że makrofity mogą być zastąpione innym rodzajem podłoży w przypadku prawie wszystkich grup fauny bezkręgowej (wyjątkiem były larwy *Lepidoptera* nie stwierdzone na podłożach eksperymentalnych). Biorąc pod uwagę inne wykorzystanie makrofitów przez faunę bezkręgową, stwierdzono m. in. silniejsze minowanie przez bezkręgowce obu rdestnic, w porównaniu z moczarką i wywłócznikiem, a także silniejsze ich wykorzystanie w czasie rozrodu i rozwoju fauny. Moczarka była natomiast jedynym gatunkiem umożliwiającym zimowanie bezkręgowcow (w okresie zimy byli na niej reprezentowani przedstawiciele większości grup fauny bezkręgowej).

W litoralu Jeziora Mikołajskiego tkanka roślin naczyniowych ma niewielki udział w pokarmie fauny bezkręgowej (fig. 2–3). Tylko nieliczni przedstawiciele fauny w warunkach naturalnych odżywiają się w znacznym stopniu żywą tkanką makrofitów, np. larwy *Lepidoptera (Paraponyx stratiotata* i *Acentropus niveus*), *Phryganea grandis* i *Limnephilus* sp. W mniejszym stopniu żywa tkanka makrofitów jest pokarmem nielicznych *Chironomidae* i *Radix ovata*. Część przedstawicieli fauny bezkręgowej odżywia się obumarłą tkanką makrofitów, np. *Bithynia tentaculata*, *Cloëon dipterum* i *Asellus aquaticus*. Niektóre zaś bezkręgowce, związane z roślinnością zanurzoną, odżywiają się zarówno żywą jak i obumarłą tkanką roślinną, np. niektóre larwy *Trichoptera*, *Chironomidae* i *Gastropoda*. Jak sie okazało, największy udział w pokarmie fauny bezkręgowej mają z reguły glony i detrytus pochodzenia peryfitonowego (fig. 2–3).

Podsumowując analizę zależności między badanymi makrofitami zanurzonymi i fauną bezkręgową w Jeziorze Mikołajskim, można stwierdzić następujące fakty.

Wśród bezkręgowców roślinnych najsilniej związane z makrofitami są larwy *Lepidoptera*, *Limnephilus* sp. i *Phryganea grandis* oraz w mniejszym stopniu larwy *Chironomidae* i *Radix ovata*. Bardzo liczne na makrofitach *Oligochaeta* są słabo związane z roślinnością. Związki przeważającej części bezkręgowców z makrofitami nie są trwałe; roślinność może być zastąpiona innym podłożem. Głównym pokarmem większości fauny bezkręgowej są glony peryfitonowe i detrytus pochodzenia peryfitonowego, a żywa tkanka roślin naczyniowych ma niewielki udział w pokarmie tych bezkręgowców. Fauna bezkręgowa powoduje bardzo znaczne niszczenie makrofitów; rdestnice podlegają destrukcji w wyniku działalności życiowej bezkręgowców w wyraźnie większym stopniu niż moczarka i wywłócznik (fig. 6–7) (u rdestnic ubytki w tkankach liści wynoszą średnio 50% i niekiedy dochodzą do 90% powierzchni liści, podczas gdy u moczarki nie przekraczają one 10% powierzchni liści). Wart podkreślenia jest fakt, że te części roślin, które są silniej niszczone na skutek działalności życiowej fauny minującej, tzn. łodygi roślin, są w mniejszym stopniu niszczone przez faunę żyjącą na roślinach, która żeruje głównie na liściach. Wzajemne zależności między fauną bezkręgową i roślinnością zanurzoną mają charakter dynamiczny; zmieniają się w ciągu roku.

7. REFERENCES

1. Berg C. O. 1950 – Biology of certain *Chironomidae* reared from *Potamogeton* – Ecol. Monogr. 20: 85–100.
2. Berg K. 1942 – Contribution to the biology of the aquatic moth *Acentropus niveus* (Oliv.) – Vedensk. Meddel. 105: 59–139.
3. Bownik L. J. 1970 – The periphyton of the submerged macrophytes of Mikołajskie Lake – Ekol. pol. A, 18: 503–520.
4. Castenholz R. W. 1961 – An evaluation of a submerged glass method for estimating production of attached algae – Verh. int. Verein. Limnol. 14: 155–159.
5. Černovskij A. A. 1949 – Opredelitel ličinok komarov semejstva *Tendipedidae* – Izdatel'stvo Akad. Nauk SSSR, Moskva-Leningrad, 185 pp.
6. Cooke W. B. 1956 – Colonization of artificial bare areas by microorganisms – Bot. Rev. 22: 613–638.
7. Darnell R. M. 1964 – Organic detritus in relation to secondary production in aquatic communities – Verh. int. Verein. Limnol. 15: 462–470.
8. Entz B. 1947 – Qualitative and quantitative studies in the coatings of *Potamogeton perfoliatus* and *Myriophyllum spicatum* in the Lake Balaton – Archiva biol. hung. 17: 17–38.
9. Frömming E. 1956 – Biologie der mitteleuropäischen Süsswasserschnecken – Duncker, Humbolt, Berlin, 313 pp.
10. Frost E. W. 1942 – The fauna of the submerged "mosses" in an acid and an alkaline water – Proc. of the Royal Irish Academy of Sciences, 13: 293–369.
11. Gaevskaja N. S. 1966 – Rol vysšych vodnych rastenij v pitanii životnych presnych vodoemov – Izdatel'stwo Nauka, Moskva, 327 pp.
12. Gorbunov K. V. 1955 – Dinamika obrastenij na polojoch nižnej zony delty Volgi i ich rol v pitanii molodi sazana – Trudy vses. gidrobiol. Obšč. 6: 80–103.
13. Gurzęda A. 1959 – Stosunki ekologiczne między fauną bezkręgową a roślinnością zanurzoną – Ekol. pol. B, 5: 139–146.
14. Hering E. M. 1951 – Biology of the leaf miners – W. Junk, New York-London, 283 pp.
15. Hickin E. N. 1967 – Caddis larvae – Hutchinson of London (Hutchinson, CO, Ltd.), London, 477 pp.
16. Hrubý K. 1964 – Prodromus Lepidopter Slovenska – Slov. Akad. Věd, Bratislava, 962 pp.
17. Kaškin N. J. 1961 – O rozmerach ispol'zovanija vysšych vodnych rastenij nekotorymi bezpozvonočnymi fitofagami (na primere Jachranskogo Vodochranilišča kanala Moskva-Volga) – Trudy murmansk. morsk. biol. Inst. 3: 170–184.
18. Kokociński W. 1963 – Uwagi o biologii *Acentropus niveus* (Oliv.) (*Lepidoptera*) (*Pyralidae*) – Polskie Pismo ent. 33: 233–243.
19. Konstantinov A. 1958 – Biologija chironomid i ich rozvedenie – Izdatel'stvo „Kommunist", Saratov, 362 pp.
20. Lepneva S. G. 1964 – Fauna SSSR. Ručejniki. I – Izdatel'stvo Akad. Nauk. SSSR, Moskva-Leningrad, 560 pp.
21. Macan T. T., Kitching A. 1972 – Some experiments with artificial substrata – Verh. int. Verein. Limnol. 18: 213–220.
22. McGaha Y. J. 1952 – The limnological relations of insects to certain aquatic flowering plants – Trans. Am. microsc. Soc. 71: 355–381.
23. McGaha Y. J. 1954 – Contribution to the biology of the some *Lepidoptera* which feed on certain aquatic flowering plants – Trans. Am. microsc. Soc. 73: 167–177.
24. Mikulski J. S. 1936 – Jętki (*Ephemeroptera*) – Fauna słodk. Pol. 15: 1–146.
25. Müller-Liebenau J. 1956 – Die Besiedlung der *Potamogeton* – Zone ostholsteinischer Seen – Arch. Hydrobiol. 52: 470–606.
26. Odum H. T. 1957 – Trophic structure and productivity of Silver Springs, Florida – Ecol. Monogr. 27: 55–112.
27. Pankratova V. J. 1970 – Ličinki i kukolki komarov podsemejstva *Orthocladiinae* fauny SSSR (*Diptera – Chironomidae – Tendipedidae*) – Izdatel'stvo Akad. Nauk SSSR, Leningrad, 341 pp.
28. Pavlovskij E. N., Lepneva G. G. 1948 – Očerki iz žizni presnovodnych životnych – Gosudarstvennoe Izdatel'stvo „Sovietskaja Nauka", Leningrad, 458 pp.

29. Pieczyńska E. 1964 – Investigations on colonization of new substrates by nematodes (*Nematoda*) and some other periphyton organisms - Ekol. pol. A, 12: 185-234.
30. Pieczyńska E. 1970 – Perifiton jako pokarm zwierząt wodnych – Wiad. ekol. 16: 133–144.
31. Pieczyńska E. 1972 – Ecology of the eulittoral zone of lakes – Ekol. pol. 20: 637–732.
32. Pieczyńska E. 1973 – The fate of macrophyte production in lakes – Pol. Arch. Hydrobiol. 20: 77–78.
33. Pieczyńska E., Spodniewska I. 1963 – Occurrence and colonization of periphyton organisms in accordance with the type of substrate – Ekol. pol. A. 11: 533–545.
34. Rehbronn E. 1937 – Beiträge zur Fischereibiologie markischer Seen. II. Das natürliche Nahrungsangebot insbesondere des Aufwuchs und die Ernährung der Fischnährtiere im Litoral eines eutrophen Seen – Z. Fisch. 35: 283–345.
35. Rosine W.N. 1955 – The distribution of invertebrates on submerged aquatic plants surface in Muskee Lake – Ecology, 36: 308–317.
36. Sladečkova A. 1960 – Application of the glass slide method to the periphyton study in the Slapy Reservoir – Sb. vys. Šk. chem.-technol. Praze 4: 403–434.
37. Sladečkova A. 1962 – Limnological investigation methods for the periphyton („Aufwuchs") community – Bot. Rev. 28: 286–350.
38. Smirnov N. N. 1961 – Consumption of emergent plants by insects – Verh. int. Verein. Limnol. 14: 232–236.
39. Soszka G. J. 1975a – Fauna naroślinna w stawach z wodą podgrzaną – Gosp. ryb.
40. Soszka G. J. 1975b – The invertebrates on submerged macrophytes in three Masurian lakes – Ekol. pol. 23: 371–391.
41. Soszka H. 1974 – *Chironomidae* associated with pond-weeds in the Mikołajskie Lake – Bull. Acad. pol. Sci. Cl. II. Sér. Sci. biol. 22: 369–376.
42. Stańczykowska A. 1960 – Charakter występowania mięczaków na kilku gatunkach roślin wodnych – Ekol. pol. B, 6: 333–338.
43. Urban E. 1975 – The mining fauna in four macrophyte species in Mikołajskie Lake – Ekol. pol. 23: 417–435.
44. Walshe B. M. 1950 – The feeding habits of certain *Chironomidae* larvae (subfamily *Tendipediinae*) – Proc. zool. Soc. Lond. 121: 63–79.
45. Wesenberg-Lund C. 1943 – Biologie der Süsswasserinsekten – Verlag von Julius Springer, Berlin, 682 pp.
46. Westlake D. E. 1965 – Some basic data for investigations of the productivity of aquatic macrophytes – Memorie Ist. ital. Idrobiol. 18: 229–248.
47. Wiktor A. 1958 – Z biológii odżywiania się ślimaków – Przegl. zool. 2: 125–146.
48. Wojtusiak H., Wojtusiak R. J. 1960 – Biologia, występowanie i użytkowalność motyli wodnych z podrodziny *Hydrocampinae* w stawach doświadczalnych PAN Ochaby – Pol. Arch. Hydrobiol. 8: 253–260.
49. Wolnomiejski N. 1969 – Obserwacje nad zróżnicowaniem siedlisk i ekologią minujących larw *Chironomidae* – Zesz. nauk. Uniw. Mikołaja Kopernika Toruń, 20: 47–59.
50. Zimbalevskaja L. N. 1966 – Soobščestva bezpozvonočnych v zarosljach vysšej vodnoj rastitel'nosti srednogo Dnepra – Gidrobiol. Ž. 1: 38–48.

Paper prepared by H. Dominas

AUTHOR'S ADDRESS:
Dr Grzegorz Jan Soszka
Zakład Higieny Radiacyjnej
Centralnego Laboratorium Ochrony Radiologicznej
ul. Konwaliowa 7
03–194 Warszawa
Poland.