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OCCURRENCE OF GASTROPODA IN THE LAKE LITTORAL AND THEIR ROLE IN THE PRODUCTION AND TRANSFORMATION OF DETRITUS
I. SNAILS IN THE LITTORAL OF MIKOŁAJSKIE LAKE – GENERAL CHARACTERISTICS OF OCCURRENCE *

ABSTRACT: In the littoral of the Mikołajskie Lake the occurrence of snails on the commonest substrate types was analysed. The species composition, dominance structure, numbers and biomass of snails were determined, as well as their contribution to the numbers and biomass of the whole invertebrate macrofauna, and also the seasonal variation of these indices. The total abundance of snails in different littoral habitats in the Mikołajskie Lake has been assessed, and differences have been indicated in the use by snails of various substrates, including different macrophyte groups.

KEY WORDS: Gastropoda, occurrence, lake littoral, substrates.

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1. INTRODUCTION

In studies of freshwater ecosystems more and more attention has been given to problems related to the cycling of matter, and particularly to the role of the dead organic matter – the detritus. Many authors (O d u m 1962, O d u m and d e l a C r u z 1963, P h i l l i p s o n 1969, B e r r i e 1976, R i c h and W e t z e l 1978, O s t a p e n j a 1979, P a v l j u t i n 1979, L e C r e n and M c C o n n e l l 1980) consider it one of the most important components of the ecosystem. Relatively little known is the role of invertebrate macrofauna, especially of that which inhabits the littoral zone, in processes connected with the production and changes of detritus (K o ł o d z i e j c z y k 1980). Many data from the literature, as well as the author's own observations indicate that one of the more abundant groups of invertebrate macrofauna in the lake littoral is the snails. It follows from this that the role of these animals in the cycling of matter is considerable. But there have been few studies dealing with this aspect of their importance (e.g., I m h o f and B u r i a n 1972, I m h o f 1973). To assess the role of snails it is necessary, among other things, to know their numbers, biomass, species-composition and dominance structure in their natural habitats, and the temporal and spatial variation of these indices. In the numerous existing studies on the distribution of snails attention has been given to their species-composition, often to their numbers and dominance structure, and far more rarely to their biomass. Quantitative studies were concentrated on one or two of the numerous substrate kinds found in the littoral, and sometimes also on single dominant or particularly interesting species. As a result, a fairly good knowledge has been acquired of many aspects of the ecology of some snail species of the genera *Lymnaea, Viviparus* or *Physa*, as well as species like, e.g., *Bithynia tentaculata* (L.), *Ancylus fluviatilis* 0. F. Müll. and *Potamopyrgus jenkinsi* (E. A. Smith). There have been relatively numerous studies concerned with lake snails (M a c a n 1950, H u n t e r 1957, 1961, B e r g e r 1960, Ö k l a n d 1964, A h o 1966, 1978, S o s z k a 1968, C a l o w 1973, 1974, A h o, R a u t a and V o u r i n e n 1981 among others). In Poland, well studied for the occurrence of snails are, apart from lakes, mainly lowland rivers (P i e c h o c k i 1966, 1969, 1972, 1979). In the Konfederatka, an oxbow lake of the Vistula, various aspects of the ecology of snails have been studied by S t a ń c z y k o w s k a (1959a, 1959b, 1960a, 1960b, 1960c), and by W o j c i e c h o w s k a and T r o j a n (1960). Information on the distribution of snails can also be found in numerous papers dealing with the characteristics of the whole invertebrate macrofauna, but because of the scope of subjects covered, snails are given only a very general consideration, and data on them, dispersed in the literature, often lack taxonomical and numerical accuracy.

The aim of the research presented in this paper was to describe regularities related to the occurrence of snails in various littoral habitats. The author studied the variation in numbers, biomass and dominance structure of the snails living on the most numerous littoral substrates. He determined the proportion of snails in the numbers and biomass of the whole invertebrate macrofauna, and the abundance of snails in different habitats in the littoral of the Mikołajskie Lake.

2. TERRAIN AND STUDY METHODS

The observations and quantitative investigations were carried out in the period 1978–1982, and particularly intensively in the years 1979 and 1980. Samples were collected at three stations in the Mikołajskie Lake, a eutrophic water body of a surface area of 460 ha, located in the Masurian Lakeland (northern Poland). The study sites clearly differed from each other (Fig. 1). At station I there was a belt of stony bottom about 1.5 m broad. This was followed by a belt of sand-mud sediments and farther on a reed belt (*Phragmites australis* (Cav.) Trin. ex Steudel), parallel to the shore and about 3.0 m broad, with few shoots of *Potamogeton perfoliatus* L. At station II the sand-mud sediments began immediately from the shore line, and the reed belt, about 5.0 m broad, at a distance of about 2.0 m from it. At this site more abundant were *P. perfoliatus* shoots. Station III was the most varied of all in respect of both the number of substrates and their spatial distribution. The stony-bottom belt was present there, and so was the belt of sediments overgrown with, among other things, two pond-weed species – *P. perfoliatus* and *P. lucens* L., and there was a large clump of reeds, the free spaces within which were occupied by *P. lucens*, water-lily – *Nuphar lutea* (L.) Sm. and water-soldier – *Stratiotes aloides* L.

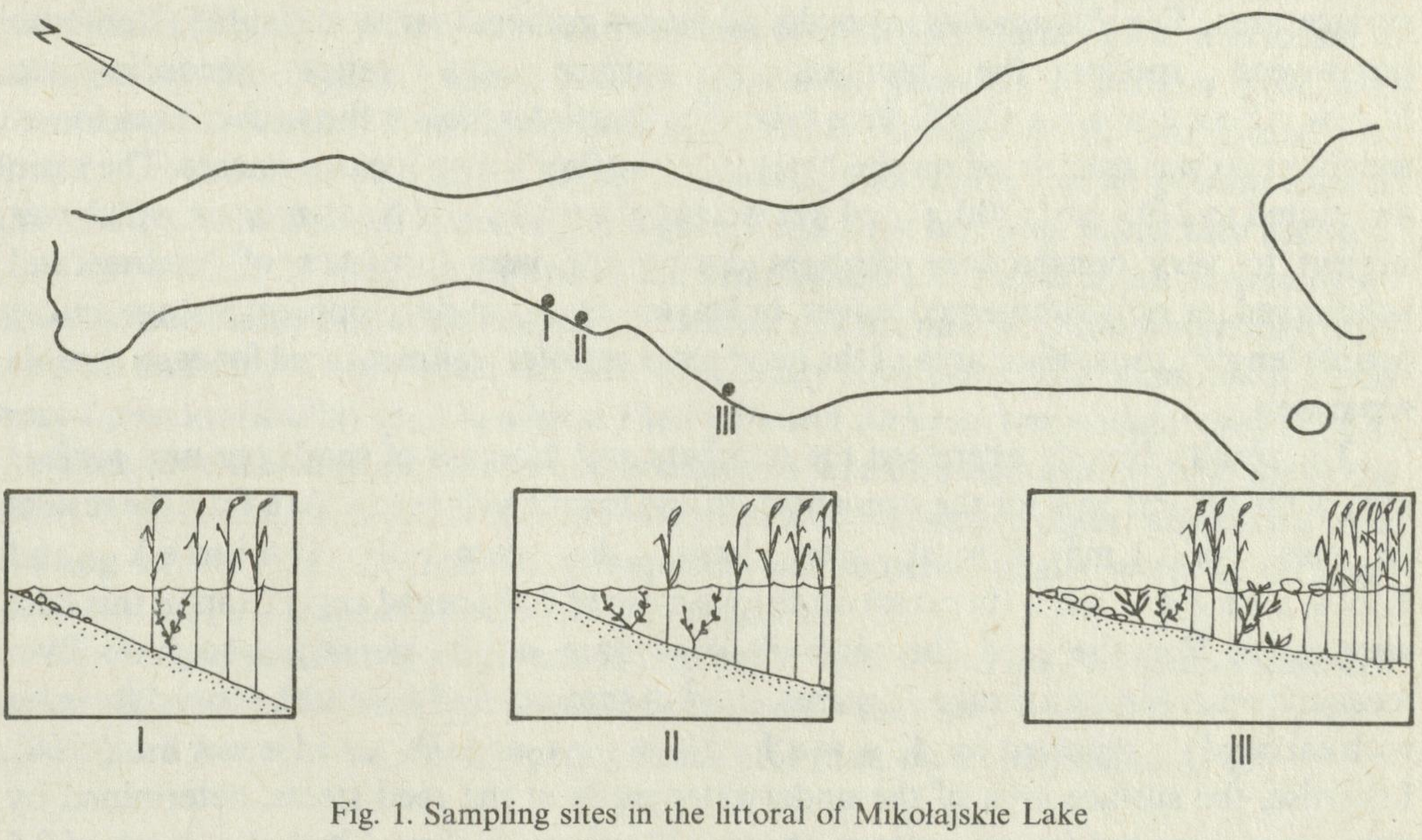

Fig. 1. Sampling sites in the littoral of Mikołajskie Lake
I–III – station numbers

To determine the specific composition, numbers and biomass of the snails in the different habitats of the littoral, as well as the numbers and biomass of the remainder of the invertebrate macrofauna, samples were collected from substrates that were most numerous in the environments under study. Samples were collected in the ice-free period (April to December) at one-month intervals, and once at station III in winter

(January 1982). From the stony bottom and from the sediments samples were collected by means of a small bottom scraper from an area of $\frac{1}{30}$ m^2 delimited with a metal cylinder. A reed sample consisted of the underwater parts of ten stems. A sample of pond-weeds consisted of 5 – 8 shoots, of the water-lily – 5 – 8 floating and underwater leaves along with entire petioles, of the water-soldier – one plant. Each time 5 samples were collected from each of the substrates studied. On two dates, in June 1978 and in September 1980, 10 samples of branches fallen into the water were collected. The specific composition was also determined of snails on different anthropogenic substrates found on the bottom of the littoral of the Mikołajskie Lake. A total of 500 samples were collected containing 5500 gastropod individuals.

Immediately after being collected the material was washed on a sieve, 0.4 × 0.4 mm in mesh-size, isolated and the invertebrate macrofauna was counted and the gastropods were identified. All the organisms were weighed (wet weight) on a torsion balance to the nearest 2 mg. Gastropod egg cocoons contained in the samples were also counted.

The numbers and biomass of snails were calculated and expressed per 1 m^2 of stony bottom, bottom sediments and submerged parts of the reed, as well as per 100 g of wet weight of submerged vegetation and of plants with floating leaves, and per 1 m^2 of their surface area. For *Phragmites australis* all stems gathered were measured. For both pond-weed species the biomass to surface area ratios according to Kowalczewski (1975) were used. For *Stratiotes aloides* the surface area to wet weight ratio was calculated on the basis of the author's own measurements. The ratio amounted to 2195 $cm^2 \cdot 100\ g^{-1}$ of wet weight of a plant. For *Nuphar lutea*, which was subject to very conspicuous changes during the year (presence of floating and submerged, or only submerged leaves, or leaves varying in developmental stage and in petiole length), the surface area of the leaves and petioles was measured for each sample separately.

The results directly expressed the numbers and biomass of snails per unit surface area of the littoral only for the stony bottom and for the sediments. To adjust the results to the per 1 m^2 littoral area basis, the data of Ozimek and Kowalczewski (in press) on the biomass of submerged vegetation in this lake were used. For the reed the author's own data on its density, based on own measurements (on an average 72 stems $\cdot\ m^{-2}$ in summer and autumn), proved to agree with earlier data reported by Kowalczewski and Wasilewski (1966). Likewise, the surface area of the underwater parts of the reed stems, determined by direct measurement (on an average about 0.72 $m^2 \cdot m^{-2}$ of reed-bed at a depth of 0.5 – 0.6 m), appears to agree with Opaliński's (1971) data.

In the determination of the total number and biomass of snails in the different littoral habitats of the Mikołajskie Lake, data on the number of different substrates inhabited by snails have been used. A reed-bed area of 39 ha (Kowalczewski and Wasilewski 1966 and the author's data), and a submerged-vegetation biomass of 264 tons of wet weight (Ozimek and Kowalczewski – in press) have been adopted. For different growing seasons corrections were applied taking into account changes in the submerged-vegetation biomass (recording of the phenology of the particular species) and in the density of the reed (author's measurements). On the basis of field measurements it has been estimated that in the Mikołajskie Lake the stony bottom occupies a belt of shallow littoral of an average breadth of 0.5 m and a length equal to half the length of the shore line.

When elaborating the materials gathered, the coefficient of dominance was calculated for both the numbers and biomass of snails. A mean value of this coefficient for the entire period of material gathering has been calculated as the percentage of the total number and biomass of all the snails collected. The constancy (frequency) of each of the taxa was expressed in terms of the coefficient of constancy defining the percentage of samples containing a particular taxon in the total number of samples collected.

3. RESULTS

3.1. GENERAL DESCRIPTION OF OCCURRENCE

In the littoral of the Mikołajskie Lake representatives of 23 gastropod taxa have been found (Fig. 2) [1]. Within two of the species collected a different form was found in addition to the "*typica*" form: *Valvata* (*Cincinna*) *piscinalis* f. *antiqua* Sow. and *Potamopyrgus jenkinsi* f. *aculenta* Overton. Within *Armiger crista* two forms were found: *A. crista* f. *nautileus* and *A. crista* f. *spinulosus* Cles. In the further presentation of the results the individual forms of the same species have not been taken into account.

Only 8 of the 23 snail taxa found in the Mikołajskie Lake were characterized by an absolute constancy or a constancy of occurrence at least on one of the seven substrates studied, and only 6 were observed on all the study substrates. The commonest snails were *Lymnaea* (*Radix*) sp., *Theodoxus fluviatilis* and *Bithynia tentaculata*; they were at the same time the constant or absolutely constant taxa on substrates so different as the stony bottom and the sediments, and some species of submerged plants and plants with floating leaves (Fig. 2). The least frequently-encountered snails were *L.* (*Myxas*) *glutinosa, L.* (L .) *stagnalis* and *Viviparus viviparus.*

The largest number of snail taxa (18 on each) were found on *Phragmites australis* and on *Stratiotes aloides* (Fig. 3), and the smallest on the stony bottom (11). They were much more frequent on *Potamogeton lucens* (16) than on *P. perfoliatus* (12).

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[1] Piechocki's (1979) classification has been used. Since the identification was based mainly on conchological features (this was because in later experimental stages the material was dried, sometimes burned and destroyed), identification to the species was impossible in the case of snails of the subgenera *Radix* Montf., 1810, *Galba* Schr., 1803, and of the genus *Gyraulus* Charpentier, 1837. Some individuals of the subgenus *Radix* have been identified on the basis of their sex apparatus. The presence of *Lymnaea* (*Radix*) *auricularia* (L.) was found.

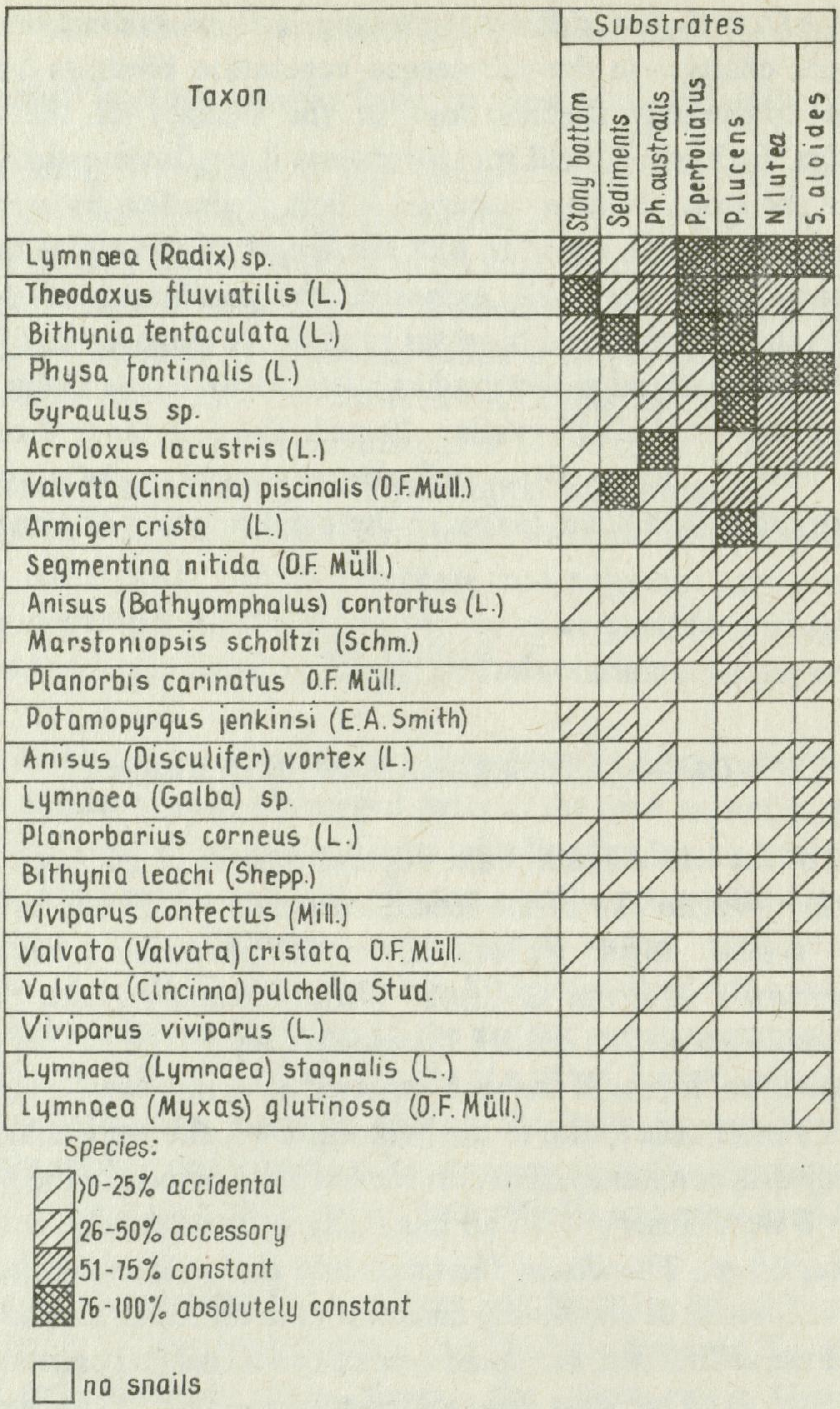

Fig. 2. Frequency of different taxa of Gastropoda in the littoral of Mikołajskie Lake
Data of the years 1979, 1980, stations I, II and III

The percentage has been determined of each of the taxa in the total numbers and biomass of the snails collected throughout the study period. With regard to numbers (Fig. 3), on the stony bottom *Theodoxus fluviatilis* was found to constitute the largest proportion, in the sediments – *Potamopyrgus jenkinsi*, on the reed – *Acroloxus lacustris*. On all the species of submerged plants and of plants with floating leaves under study *Lymnaea* (*Radix*) sp. dominated. This dominance was more marked on the two pond-weed species than on *Nuphar lutea* and *Stratiotes aloides*, where *Physa fontinalis*

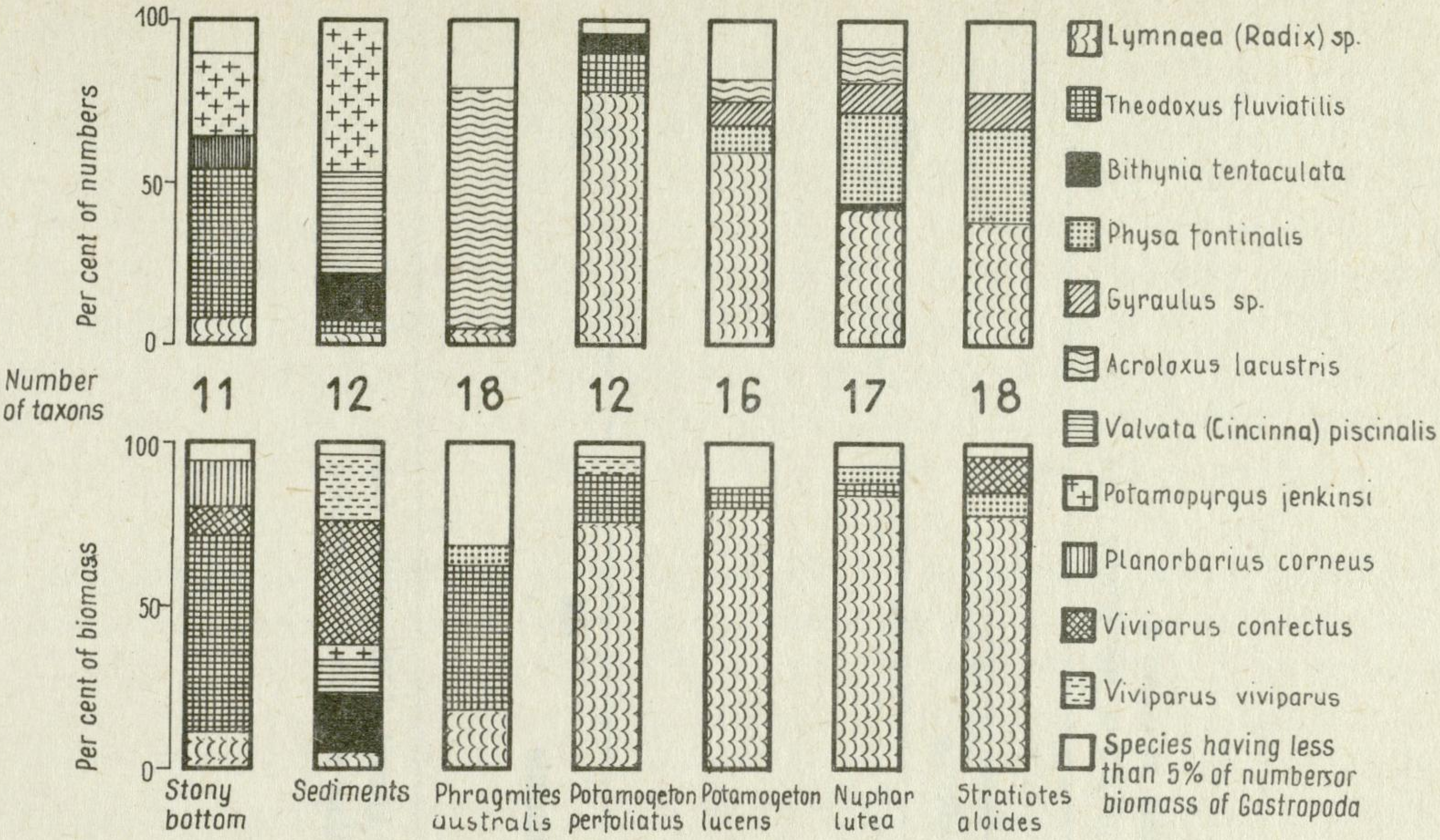

Fig. 3. Percentage of individual taxa in total numbers and biomass of Gastropoda on different substrates in the littoral of Mikołajskie Lake
Data of the years 1979. 1980, stations I, II and III

also represented a high proportion. As regards biomass (Fig. 3), the main difference, in contrast to numbers, consisted in a predominance of *Viviparus contectus* and *V. viviparus* in the sediments, and of *T. fluviatilis* on *Phragmites australis*, and in a very high percentage of *L.* (*Radix*) sp. on *N. lutea* and *S. aloides*.

Although the number of taxa on the particular substrates was considerable, the snail dominance structure was in general very distinct. The most abundant species on each of the different substrates represented (for the whole sampling period) from 40 to 80% of numbers, whereas in the particular months the values of the coefficient of dominance were sometimes much higher. Differences in average body-weight between individuals of different snail taxa, common in the Mikołajskie Lake, are considerable – the average weight of *Acroloxus lacustris* is 6 mg of wet weight, and that of *Lymnaea* (*Radix*) sp. – 111 mg. On many substrates snails of a comparatively large size (e.g., *L.* (*Radix*) sp. and *Theodoxus fluviatilis*) represent a large percentage of numbers, while small-bodied species of the families Planorbidae or Valvatidae occur sporadically (Fig. 3). Due to this, the biomass dominance structure is considerably more distinct than the dominance structure of numbers. This can be seen on the stony bottom, on *Potamogeton lucens*, *Nuphar lutea* and *Stratiotes aloides* (Fig. 3). As a result, the role of a whole snail assemblage on a specific substrate is determined, in spite of the large number of taxa, by only one up to three of them. In some months, however, the biomass

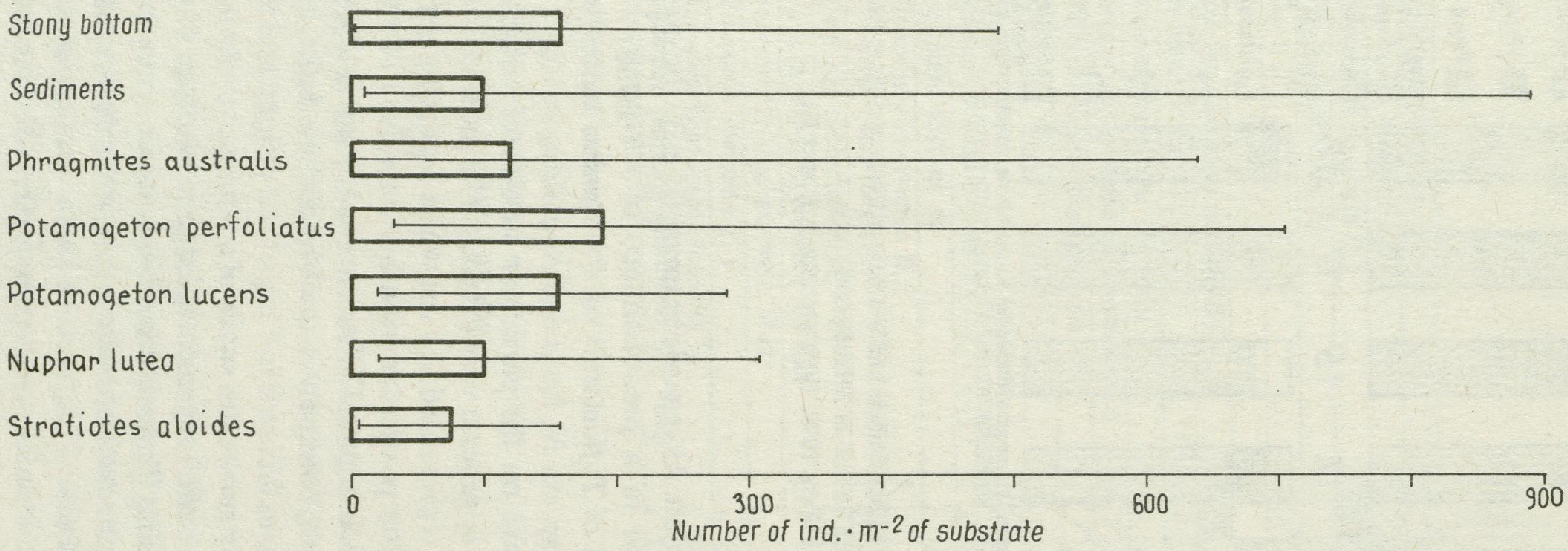

Fig. 4. Numbers of Gastropoda on different substrates in the littoral of Mikołajskie Lake
Data of the years 1979, 1980, stations I, II and III; mean values and range of variation

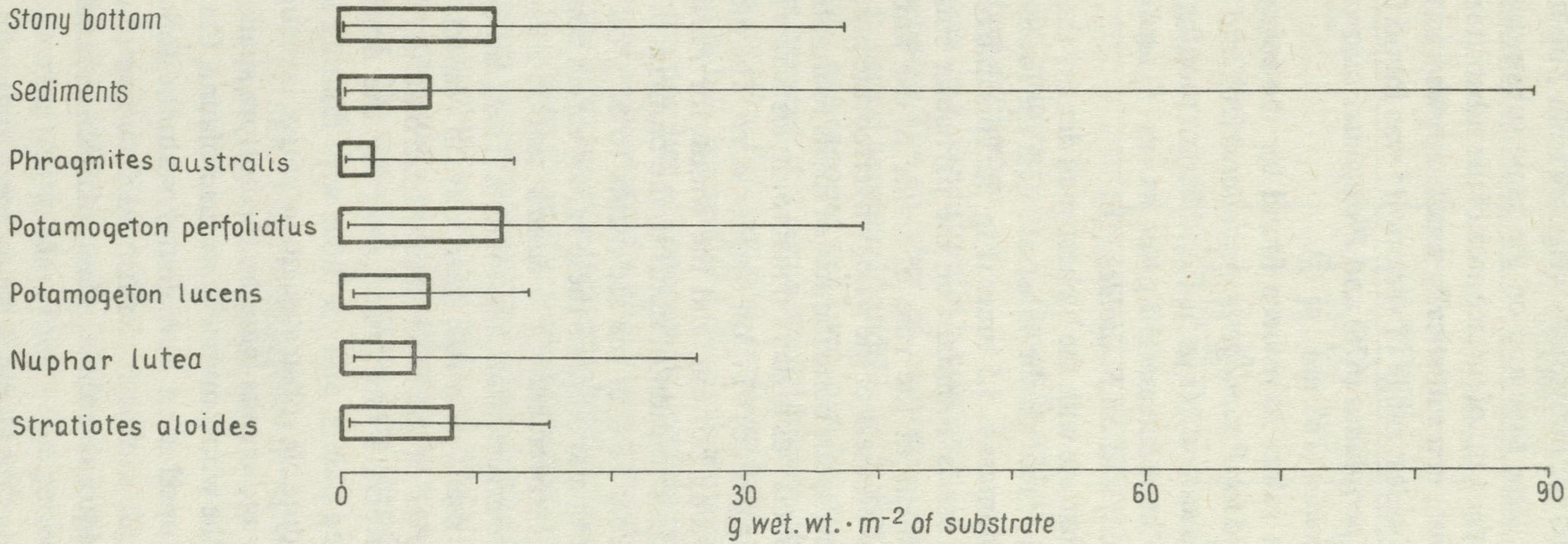

Fig. 5. Biomass of Gastropoda on different substrates in the littoral of Mikołajskie Lake
Data of the years 1979, 1980; mean values and range of variation

dominance structure did not appear to be more distinct than the abundance dominance structure. The cause of this was primarily the great differences in individual body-weight among *Lymnaea* (*Radix*) sp.; individuals weighing from 2 up to 3000 mg of wet weight could be found at the same time and on the same substrates.

Average numbers of snails per 1 m^2 of surface area of the substrate inhabited did not differ, for the whole study period, in a statistically significant way, amounting from 73 to 190 ind. $\cdot$ m^{-2} (Fig. 4). The widest range of variation [2] was found for the sediments (882 ind. $\cdot$ m^{-2}), *Potamogeton perfoliatus* (676) and *Phragmites australis* (638), and the narrowest – for *Stratiotes aloides* (168 ind. $\cdot$ m^{-2}).

The highest snail biomass values have been found for the stony bottom (on an average 11 g wet wt. $\cdot$ m^{-2}) and for *Potamogeton perfoliatus* (10), and the lowest – 2 g wet wt. $\cdot$ m^{-2} – for *Phragmites australis* (Fig. 5). For different months the widest range of variation has been found in the sediments (90 g wet wt. $\cdot$ m^{-2}), and the narrowest on *Ph. australis, P. lucens* (14 each) and on *S. aloides* (16).

It was found that on the substrate with the highest snail density the average number of snails was 2.6 times as large as that on the substrate with the lowest density (Fig. 4); the respective ratio for snail biomass is 5.5 times (Fig. 5). This difference is caused by variations in body-size of the snails dominant on the particular substrates.

Significant for the assessment of the role of snails is the knowledge of their percentage in the numbers and biomass of the whole invertebrate macrofauna. On the stony bottom and in the sediments the contribution of snails to numbers (Table I) was not great (on an average 4%), but it was higher on macrophytes where it attained (on an average for the whole sampling period) 41% on *Nuphar lutea*. The narrowest range of variation was found for the stony bottom, and the widest for *Phragmites australis*. Considerably higher was the contribution of snails to the biomass of the invertebrate macrofauna, on an average from 15% in the sediments to 68% on *N. lutea*. In the different months and at the particular stations these values varied considerably (Table I), being sometime very high. In November, on *N. lutea* at station III snails represented 98% of the biomass of the whole invertebrate macrofauna. Thus, although on the stony bottom and in the sediments snails as a rule gave way, in respect of numbers and biomass, to other representatives of the invertebrate macrofauna (like Oligochaeta, Hirudinea, Chironomidae, Bivalvia), they were positively the dominant group on plants, especially on submerged plants, and on those with floating leaves.

Snails also colonize other durable substrates, quantitative investigations of which are difficult. On tree branches and trunks lying on the bottom snails represent on an average 6% of the numbers of the whole invertebrate macrofauna. On those substrates representatives of eight gastropod taxa were found with the following dominant species: *Bithynia tentaculata, Theodoxus fluviatilis* and *Lymnaea* (*Radix*) sp. Objects introduced by man into the littoral (rubber, glass, plastics, ceramics, metals) were

[2] The range of variation of R has been adopted after K a s p r z a k (1981): $R = x_n - x_1 + 1$, where x_n = the highest estimate, x_1 = the lowest estimate.

Table I. Percentage of Gastropoda in the abundance and biomass of the whole invertebrate macrofauna on different substrates in the littoral of Mikołajskie Lake, at stations I, II and III, in the years 1979, 1980 (mean values and range of variation)

Substrate inhabited	Percentage of Gastropoda	
	in numbers	in biomass
Stony bottom	4 (0–12)	24 (0–76)
Sediments	4 (1–28)	15 (2–58)
Phragmites australis	19 (1–81)	39 (2–75)
Potamogeton perfoliatus	13 (1–39)	61 (24–86)
P. lucens	19 (3–32)	61 (43–85)
Nuphar lutea	41 (11–74)	68 (18–98)
Stratiotes aloides	14 (2–35)	43 (2–75)

abundantly inhabited primarily by *T. fluviatilis* and *B. tentaculata*, less often by *L.* (*Radix*) sp. and other snail taxa.

For snails to occur in a lake littoral it is essential that there are suitable substrates for laying egg cocoons. The number of cocoons on *Phragmites australis* varied throughout the study period between 10 and 33 $\cdot m^{-2}$ of stem surface area. Only in June was an average of 163 egg cocoons per 1 m^2 found at station III; the difference in the number of cocoons between this year's reed (146) and last year's reed (179) was not significant statistically. On *Potamageton perfoliatus* the largest number of cocoons (95 $\cdot m^{-2}$) was found in July, whereafter it clearly decreased with the successive months, while on *P. lucens* the number of cocoons attained its peak (15 $\cdot m^{-2}$) in September. *Nuphar lutea* appeared to be covered with the most abundant cocoons (745 $\cdot m^{-2}$) only in June, whereas in the other months their number did not come up to twenty. Similarly low values were found throughout the sampling period on *Stratiotes aloides.* On both plant species gastropod egg cocoons were present during the whole study period from April to November. Dominant among the egg cocoons gathered were those of *Lymnaea* (*Radix*) sp., *Bithynia tentaculata* and *Planorbarius corneus*, the latter being particularly numerous on *N. lutea.* No snail egg cocoons were found on the stony bottom.

3.2. SEASONAL VARIATIONS IN NUMBERS, BIOMASS AND DOMINANCE STRUCTURE

To present the results in a synthetical way, the data obtained for the individual seasons have been merged. Taking into account phenological phenomena in the lake, and particularly the phenological cycles of the macrophytes, the results have been presented jointly for spring (April, May, June – the period from the disappearance of the ice-cover to the abundant appearance of plants with annual above-ground shoots), summer (July, August, September – the period of peak plant biomass) and autumn (October, November, December – the period of dying of plants with annual, and partly of those with perennial above-ground shoots, until the appearance of the ice-cover on the lake). The results for *Potamogeton perfoliatus* and *P. lucens* (plants with annual above-ground shoots) also were presented jointly, and so were the data for *Nuphar lutea* and *Stratiotes aloides*, partially wintering in the form of green shoots.

On the stony bottom, a very conspicuous growth in number of the snails was found in the period from spring to autumn, a clear increase in their biomass in summer, and a slight its decrease in autumn (Fig. 6).

In the sediments, a clear peak of numbers of the snails was observed in autumn. It was caused by an outbreak of *Potamopyrgus jenkinsi*. The spring biomass peak was the result of a mass occurrence of large individuals of *Viviparus contectus* and *V. viviparus* in the shallow littoral in May and June.

On reed, where snail numbers were in general relatively high and the biomass very low, the lowest values of both these indices were recorded in summer (Fig. 6). In the period April-July, the number of snails markedly decreased from month to month at all sites, on an average from 245 to 30 ind. $\cdot$ m^{-2} of stem surface area, and so did their biomass. A rapid decrease in the numbers and biomass of snails was also seen in

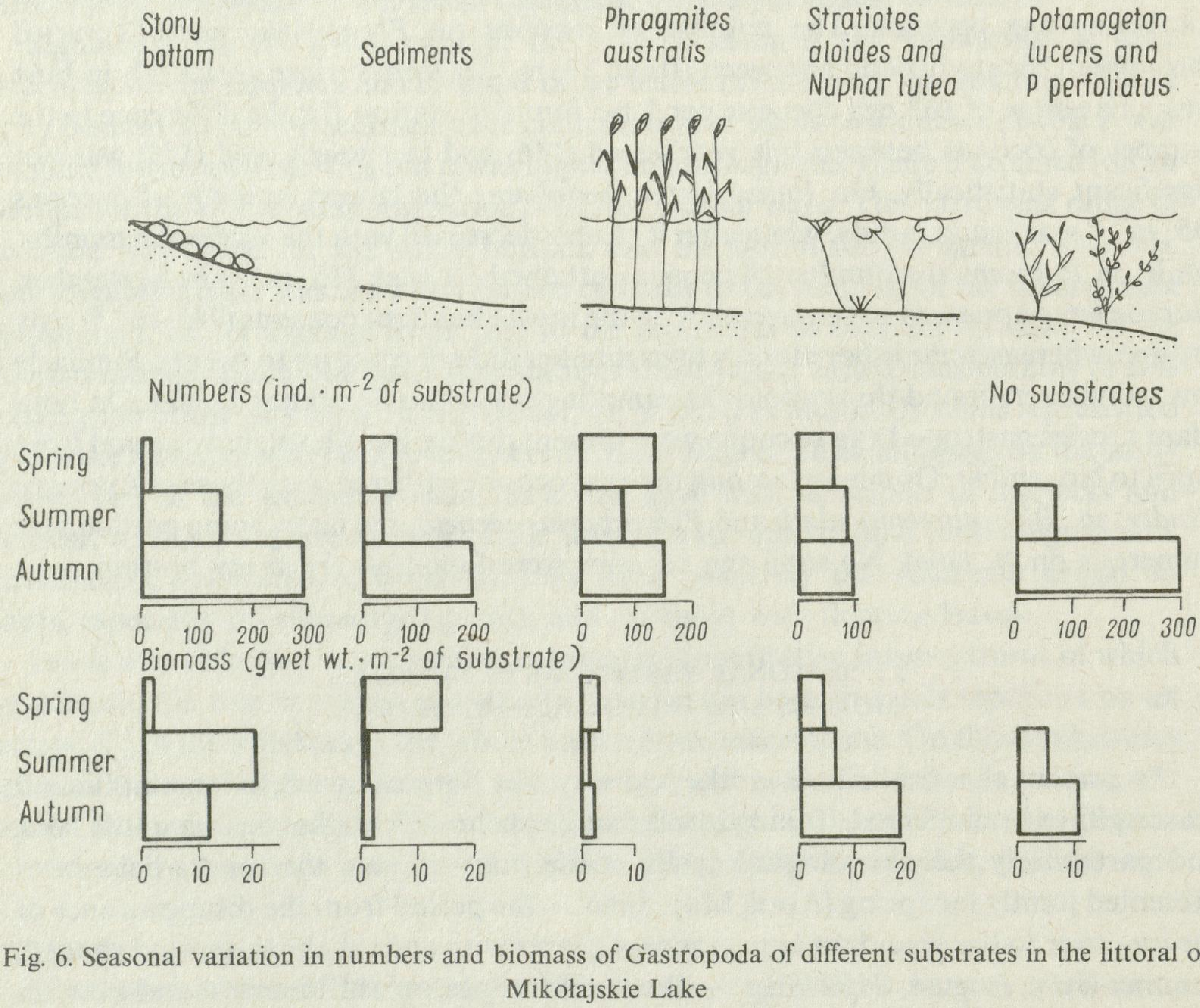

Fig. 6. Seasonal variation in numbers and biomass of Gastropoda of different substrates in the littoral of Mikołajskie Lake
Mean values for stations I, II and III (data of the years 1979, 1980)

November – from 318 ind. · m^{-2} in October to 11 ind. · m^{-2}, followed by a growth in number in December, to 116 ind. · m^{-2}.

On the other macrophytes (Fig. 6) snail biomass increased from spring (*Nuphar lutea* and *Stratiotes aloides*) or from summer (both pond-weed species)[3]. On pond-weeds also a marked growth in the number of snails could be seen, while in the case of *N. lutea* and *S. aloides* the average values for the seasons did not differ significantly.

Specific situations were observed immediately before and after the appearance of the ice-cover. On the stony bottom, in spring immediately after the disappearance of the ice-cover the number and biomass of snails were very low. In this zone a decrease in numbers was seen also immediately before the appearance of the ice-cover, in December, down to 235 ind. · m^{-2}, relative to the higher numbers recorded for October, and particularly for November (436 ind. · m^{-2}).

The abundance dynamics of gastropods was compared more exactly on *Potamageton perfoliatus, P. lucens, Nuphar lutea* and *Stratiotes aloides* (Fig. 7). On both species of plants with annual above-ground shoots the number of snails increased in the period

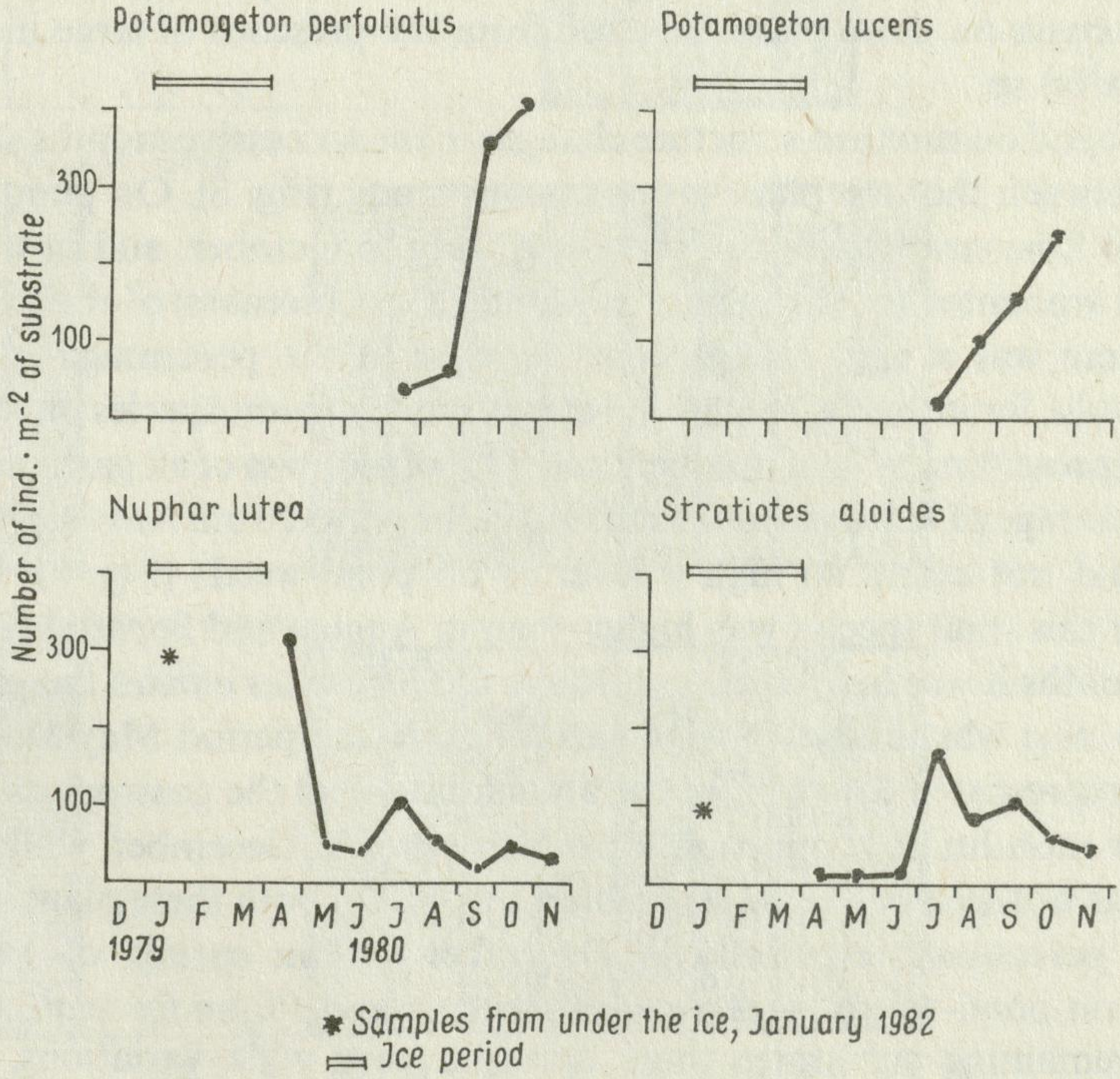

Fig. 7. Variation in numbers of the Gastropoda found on four macrophyte species in the littoral of Mikołajskie Lake
Stations I, II and III

[3] In the study period the presence of pond-weeds was only found at the beginning of June, but since their shoots were in that month very small and few in number, the first quantitative samples were collected only at the beginning of July.

July-October, the process being particularly noticeable on *P. perfoliatus*. Within a month (August-September) the number of snails increased from 67 to 366 ind. $\cdot$ m^{-2} of the surface area of this plant. The increase in number (and biomass) progressed during the growth and dying of both pond-weed species.

The course of changes in numbers of the snails on plants with perennial above-ground shoots was different (Fig. 7). On *Nuphar lutea* the highest numbers of snails were recorded in April; high numbers were recorded also in December and January. From May until November the average number of snails did not exceed 50 ind. $\cdot$ m^{-2} of plant surface area, the differences between successive values being statistically insignificant. On *Stratiotes aloides* snails appeared to be most abundant in December, whereas very low numbers – below 10 ind. $\cdot$ m^{-2} of plant surface area – were seen in spring (Fig. 7). Snail biomass on *N. lutea* was very high in periods of the highest abundance, and in October and November (15 – 26 g wet wt. $\cdot$ m^{-2}), whereas in the other months it did not exceed 5 g of wet weight. On *S. aloides* a high snail biomass level was found in the autumn period and partially in summer (from 12 to 15 g wet wt. $\cdot$ m^{-2}), while in the remainder of the months it did not even come up to 2 g of wet weight. The high snail biomass on these plants resulted from the presence of large individuals of *Lymnaea* (*Radix*) sp.

The gastropod dominance-structure changes in the successive months showed clear differences between the two plant groups under study (Fig. 8). On ponds-weeds the proportion of *Lymnaea* (*Radix*) sp. grew from July to October, and in the period of plant dying it amounted to 90% of numbers (and 98% of biomass) of all the snails living on them. There was a very conspicuous decrease in the percentage of *Theodoxus fluviatilis*; in July, for instance, at station I it was the dominant species on *Potamageton perfoliatus* (representing 54% of numbers and 79% of biomass of all gastropods). On *N. lutea* the percentage of *L.* (*Radix*) sp. increased in the period from August to November, but here it did not attain so high a level as on pond-weeds (Fig. 8). In July, the percentage of this snail species was higher than in August and September, and in the remaining months it was low, or absent (May). On *Stratiotes aloides* the percentage of *L.* (*Radix*) sp. also was subject to wide variations. In the period May-November this snail species represented 33 – 67% of the abundance of all the gastropods collected in the successive months; its proportion was much lower in December, while in April *L.* (*Radix*) sp. was not seen on the water-soldier (Fig. 8). On both these plant species there was a large percentage, especially in December and in spring, of species rarely encountered on pond-weeds – *Acroloxus lacustris* and *Physa fontinalis*.

On the remaining substrates there occurred very wide variations, along with changes in numbers, in the gastropod dominance structure in the successive months, but no regularities could be noticed. On the stony bottom the dominant species, in addition to *Theodoxus fluviatilis*, were *Potamopyrgus jenkinsi*, *Lymnaea* (*Radix*) sp. and *Bithynia tentaculata*. In the sediments, in addition to *P. jenkinsi*, in different months very numerous were *Valvata* (*Cincinna*) *piscinalis*, *B. tentaculata* and *L.* (*Radix*) sp. On reeds, apart from *Acroloxus lacustris*, the dominants were: *T. fluviatilis* and *L.* (*Radix*) sp.

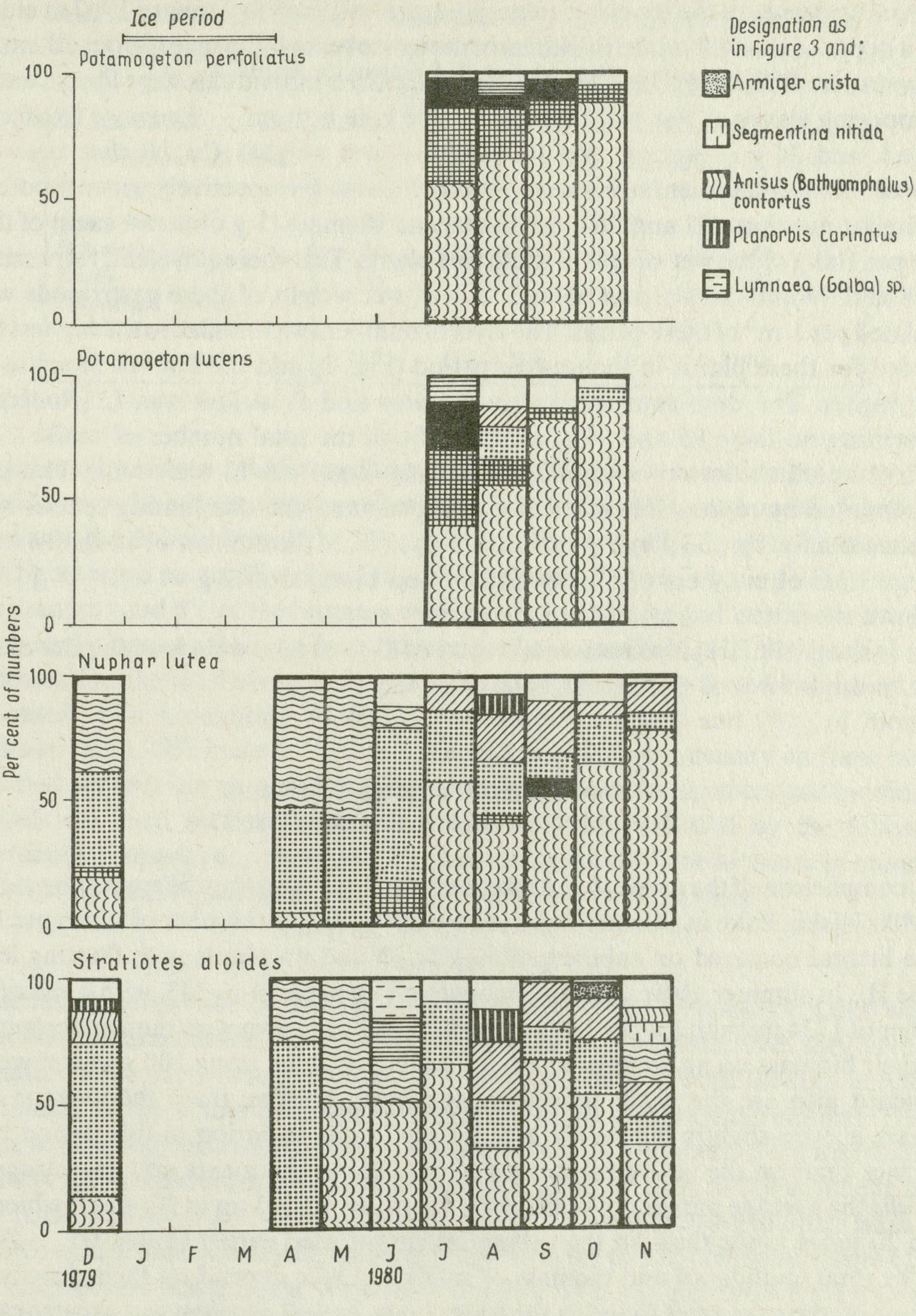

Fig. 8. Changes in the dominance structure of the Gastropoda found on four macrophyte species in the littoral of Mikołajskie Lake
Stations I, II and III

From underneath the ice-cover materials were collected in January 1982 at station III at a depth of about 1 m, the thickness of the ice-cover coming up to about 30 cm. On *Phragmites australis* stems only few *Acroloxus lacustris* individuals were found, and on decomposing leaves of this plant species on the lake bottom – *Lymnaea* (*Radix*) sp. (120 ind. and 24 g of wet wt. per 100 g of leaf wet weight). On *Nuphar lutea* and *Stratiotes aloides* representatives were found of 3 and 4, respectively, gastropod taxa, and similar numbers (22 and 26 individuals) and biomass (5 g of w. wt. each) of these snails per 100 g of the wet weight of these two plants. This was equivalent, respectively, to 298 and 99 individuals, and 66 and 24 g of wet weight of these gastropods when calculated per 1 m^2 of these plants. The level of numbers was similar to the highest level recorded for these plants in the ice-free period (Fig. 7), and the level of biomass was much higher. The dominant species on *N. lutea* and *S. aloides* was *L.* (*Radix*) sp., representing on them 95 and 99%, respectively, of the total number of snails.

Underneath the ice-cover also *Ceratophyllum demersum* L. was found. This plant was inhabited by representatives of 11 gastropod taxa, the dominating species being *Lymnaea* (*Radix*) sp. and *Physa fontinalis* (28%, each, of the number of all snails) with a medium level of numbers of 28 individuals, and biomass of 2 g w. wt. $\cdot$ 100 g^{-1} wet weight of the plant.

In January 1982, representatives of a total of 13 snail taxa were found under the ice-cover in the littoral of the Mikołajskie Lake.

3.3. NUMBERS AND BIOMASS OF SNAILS IN DIFFERENT LITTORAL ENVIRONMENTS

A comparison of the number and biomass of snails inhabiting different substrates in the Mikołajskie Lake in summer has shown that the largest number of snails per 1 m^2 of the littoral occurred on submerged vegetation and on plants with floating leaves (Table II). In summer, their number amounts on an average to 343, with a maximum number of 1734 individuals per 1 m^2 of the littoral overgrown with these macrophytes, and their biomass on an average to 19, its maximum value being 100 g of wet weight. Abundant also are the snails inhabiting the stony bottom; there the average snail biomass is even slightly higher (21 g w. wt. $\cdot$ m^{-2}), its variation in this period being narrower than on the above-mentioned plants. In the sediments and on *Phragmites australis* the average number of snails per 1 m^2 of littoral is 3 up to 10, and the biomass 10 to 20 times lower than on the substrates enumerated earlier (Table II).

The total abundance and biomass of snails in a lake depend on their density and biomass on the substrates found in the water body, as well as, often to a greater extent, on the quantity of these substrates. It has been estimated that the total number of snails in the Mikołajskie Lake ranges from about 90 mlln. individuals in spring to about 405 mlln. individuals in autumn (Table III). The total snail biomass varies between about 6 (summer) and about 16 (autumn) tons of wet weight (Table III). In the Mikołajskie Lake, the stony bottom, due to its small surface area, holds a small

Table II. Numbers and biomass of Gastropoda in different habitats in the littoral of Mikołajskie Lake in the summer season (July, August, September), per 1 m^2 of littoral, at stations I, II, and III (mean values and range of variation)

Substrate inhabited	Numbers		Biomass (g w. wt.)	
Stony bottom	150	(61–382)	21	(10–38)
Sediments	34	(10–48)	2	(< 1–6)
Reeds	53	(3–196)	1	(< 1–2)
Submerged plants and plants with floating leaves	343	(26–1734)	19	(1–100)

percentage of the snails inhabiting this water body (Fig. 9). A considerable proportion of snails live in the bottom sediments, especially in spring (60% of abundance and 90% of biomass). Reeds hold from 10 to 23% of the number, and only 4% of the biomass of all snails. Submerged macrophytes and those with floating leaves in spring hold only 15% of the numbers and 6% of the biomass of all snails. In summer and in autumn the total number and biomass of the snails on these plants increase (Table III), and so does their contribution to the total abundance and biomass of all snails in the Mikołajskie Lake, this contribution amounting to 63% of numbers (summer) and 79% of biomass (autumn) (Fig. 9). This increase results from the growth of snail density on these plants (calculated per unit wet weight of the plants, the increase in the numbers and biomass of the snails on them in the successive seasons may be described by the following approximate proportion: 1 : 3 : 6) and from the increase in plant biomass in summer, therein the appearance of plants with annual above-ground shoots.

4. DISCUSSION

The results, presented in this paper, from studies of the Mikołajskie Lake with a littoral zone, characteristic of eutrophic lakes, indicate a considerable, very variable seasonally on the particular substrates, percentage of snails in both the total numbers and biomass of the whole invertebrate macrofauna. In bottom environments (stony bottom, sediments), the average percentage of snails in the numbers of the macrofauna was low (4%), its maximum value sometimes coming up to 28% in the sediment zone (Table I). Data of other authors also indicate that for a stony bottom in other lakes the respective values were also small, on an average from 0.8 to 5.8% of the numbers of the whole invertebrate macrofauna (Ökland 1964, Dusoge 1966, Brittain 1978, Brittain and Lillehammer 1978, Wolnicki 1978). In sediments of different lakes the values were more variable, and sometimes higher – on an average from 0.4 to 54.0% of the abundance of the whole invertebrate macrofauna (Berg 1938, Ökland 1946, Wolnomiejski 1965, Giziński, Tronowska and Widuto 1968, Wolnomiejski and Furyk 1969, Giziński and Kadulski 1972, Giziński and Paliwoda

1972, Giziński and Toczek-Boruchowa 1972). In sediments at the water-land border snails sometimes represented up to 96.0% of the numbers of the whole invertebrate macrofauna (Furyk 1970). The value 5.0% given by Opaliński (1971) for the Mikołajskie Lake included all molluscs (with *Dreissena polymorpha* (Pall.) as the dominant species).

Table III. Total abundance and biomass of Gastropoda on different substrates in the littoral of Mikołajskie Lake in different seasons (data of the years 1979, 1980)

Substrate inhabited	Numbers (thous. indiv.)			Biomass (kg w. wt.)		
	spring	summer	autumn	spring	summer	autumn
Stony bottom	60	500	1000	10	70	40
Sediments	54000	29600	175000	13060	1740	2610
Reeds	21100	20700	41700	550	290	710
Submerged plants and plants with floating leaves	14400	87100	187400	850	4330	12880
Total	89560	137900	405100	14470	6430	16240

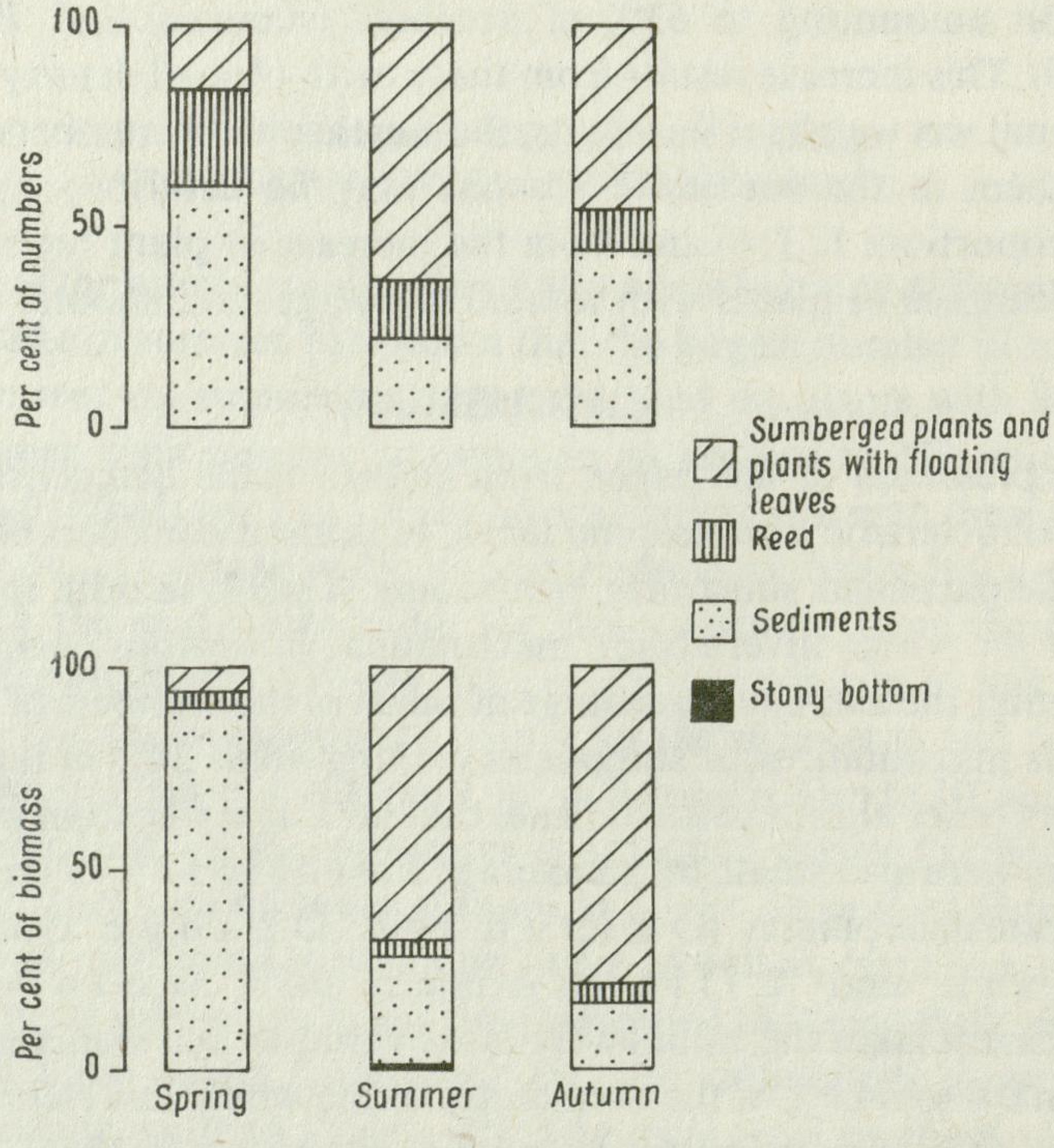

Fig. 9. Percentage of the Gastropoda inhabiting different substrates in the total abundance and biomass of snails in the littoral of Mikołajskie Lake
Data of the years 1979 and 1980

Snails have been mentioned by many investigators as one of the most numerous, besides Chironomidae, Oligochaeta, and sometimes Trichoptera, groups of macrophyte-dwelling invertebrate macrofauna (e.g., Dvořák 1970, Soszka 1975, Dvořák and Best 1982). The average proportion of gastropods in the numbers of the invertebrate macrofauna on reeds in the Mikołajskie Lake was higher than on the bottom (19%), and it showed a very wide variability (Table I). For this substrate in the Mikołajskie Lake Opaliński (1971) gives as low a value as 4% of the abundance of the macrofauna, this including snails and bivalves. The scanty information available from literature, on emergent-vegetation-dwelling fauna in other water bodies indicates that this value may be much higher; according to Dvořák (1970), the proportion of snails on several emergent plant species ranged from 17.4 to 51.7% of the numbers of the whole invertebrate macrofauna. The literature data gathered by that author indicate that in a number of water bodies snails were the dominant group on these plants.

As regards the contribution of snails to the numbers of the invertebrate macrofauna on submerged plants and on plants with floating leaves, in the Mikołajskie Lake values were found ranging from 13 to 41% (average values for different macrophyte species), the maximum value recorded amounting to 74% (Table I). Different authors give for the Mikołajskie Lake values ranging from 5 to 10, and at the most 42% (Ozimek and Sikorska 1975, Soszka 1975), and for other water bodies from 0.4 to 69% (Margolina 1958, Karassowska and Mikulski 1960, Kobuszewska 1973, Pieczyński 1973, Andrikovics 1975 and others). A wide variation in the percentage of snails, similar to that recorded on *Nuphar lutea* (Table I), was observed by Pereyra-Ramos (1981) in Lake Majcz Wielki – where in the successive months snails represented from 1 to 64% of macrofaunal numbers on Characeae.

Far rarer are reports on the percentage of snails in the biomass of the whole invertebrate macrofauna. Ökland's (1964) data indicate that in Lake Borrevann (Norway) snails constituted 18% of macrofaunal biomass on a stony bottom, and from 1 to 12% (depending on the depth) in sediments, thus in both these environments the average values were lower than in the Mikołajskie Lake (Table I). Dvořák (1970) estimated the proportion of snails on emergent macrophytes at 9.0–28.9%, their contribution to the biomass being lower than their contribution to the numbers of the macrofauna (this resulted from the dominance of species of a very small body-size). For submerged plants and plants with floating leaves the average contribution of snails to the macrofaunal biomass in the Mikołajskie Lake (43–68%) was within the range found by Karassowska and Mikulski (1960) for different groups of submerged vegetation in Lake Drużno. According to Pieczyński (1973), this contribution for snails and bivalves jointly on two plant species (*Elodea canadensis* and *Stratiotes aloides*) in Lake Warniak was very low, from 3.7 to 17.0%. In Lake Velence snails on several species of submerged plants represented from 0.1 to 31.4% of the dry weight of the whole invertebrate macrofauna (Andrikovics 1975).

It has been found that on all the substrates under study the percentage of Gastropoda in the biomass of the whole invertebrate macrofauna was always greater (up to 6 times) than their contribution to numbers (Table I). On the particular substrates it attained very high average (up to 68%) and maximum values (up to 98%). The above data indicate a significant role of this group of organisms in the whole community of lake invertebrate macrofauna. Their role may be particularly important in small, shallow water bodies densely overgrown with aquatic vegetation. Comparing the production of different invertebrate macrofaunal groups, Imhof and Burian (1972) and Imhof (1973) stressed the very important role of gastropods in the energy flow in the reed-bed zone of the shallow Lake Neusiedler.

The abundance and biomass of snails vary considerably with time. A clear growth of numbers (Fig. 7) and biomass of snails was observed from summer to autumn on submerged plants with annual above-ground shoots. This seems to be related to the trophical attractiveness of decomposing plant tissues (Kołodziejczyk and Martynuska 1980, Kołodziejczyk 1983). Stańczykowska (1960c) gave a similar interpretation of the growth in numbers of snails on several aquatic plant species in autumn. For other animal groups this phenomenon was observed, e.g., by Bownik (1970) and Soszka (1975).

Quite different was the course of changes in numbers of the snails on plants with perennial above-ground shoots (Fig. 7). On these plants the course of changes in numbers and biomass is fairly complex. High values were found in winter, late autumn and in early spring (only for biomass), and as a rule low ones in spring and summer. *Nuphar lutea* and *Stratiotes aloides* are used by snails as substrates during the ice-cover period. An abundant inhabitancy by the fauna at that time of plants wintering in the form of green above-ground shoots has been demonstrated by Soszka (1975) and Pereyra-Ramos (1981). In view of the considerable reduction of the number of habitats in the littoral in winter, the role of this plant group as substrates for animals seems to be particularly significant.

Very wide variations in numbers of the snails were found on reed. The conspicuous reduction in numbers and biomass of the snails in November 1979 can be related to the violent wind and waves that prevailed during the sampling. The thin, rigid and smooth stems of reed are a substrate, from which animals can be washed off with a particular ease. A limiting effect of waves on snails has been described by many authors (e.g., Klimowicz 1958, Ökland 1964, Soszka 1968, Calow 1973, 1974). The results of experiments with the use of artificial substrates (A. Kołodziejczyk — unpublished data) also indicate a limiting effect of waves on the occurrence of snails.

Changes in numbers of plant-dwelling snails do not probably depend on the abundance of periphyton — a potential food. In the case of both reed, submerged plants and plants with floating leaves no correlation has been found between the volume of periphyton and the number of snails (A. Kołodziejczyk — unpublished data). Estimative calculations of the consumption of reed-dwelling snails have shown that they eat during 24 hours less than 1% of periphyton dry weight. It may thus be expected that this food always occurs in excess. Knecht and Walter (1977) who investigated the feeding of two *Lymnaea* species (*Lymnaea auricularia* (L.) and *L. peregra* (Müll.)) have found a lack of competition between them, and a surplus of food in the habitat.

Variable to a large extent is also the abundance of snails on the bottom. This is connected with a seasonal appearance there of some species in large numbers. The outbreaks, found during the present study, of *Potamopyrgus jenkinsi* in shallower areas in autumn have already been described by different authors (e.g., F u r y k 1970, W o l n o m i e j s k i and F u r y k 1970, K a s p r z a k 1982). A great variability of the spatial distribution of this species and variation in numbers in successive years were also indicated by M a c a n (1970). Concentrations of snails of the genus *Viviparus* at shallow sites in May and June, have been described by Ž a d i n (1928), F r ö m m i n g (1956) and S t a ń c z y k o w s k a (1959a, 1960a, 1960b) and others.

In the Mikołajskie Lake the stony bottom is at a small depth, and it freezes almost completely in winter. The low numbers of snails observed in this habitat before and just after the disappearance of the ice-cover may result from the retreating of snails for winter into deeper parts of the littoral.

Out of the 41 freshwater snail species known to occur in Poland (P i e c h o c k i 1979) 20 have been found to be present in the littoral of the Mikołajskie Lake, and apart from these, also individuals of the genus *Gyraulus* and subgenera *Radix* and *Galba*, not identified to the species (Fig. 2). The longest yet snail species list for this lake (S o s z k a 1975) included 19 plant- and bottom-dwelling snail species; other authors who carried out investigations in this lake (D u s o g e 1966, O p a l i ń s k i 1971, W ł o d a r s k a 1972, M i z i k o w s k i 1974) recorded a much smaller number. B e r g e r (1960) who set out his own results and those of other investigators (since 1861) in his paper on freshwater and terrestrial molluscs of the Masurian Lakeland listed for this area 36 freshwater snails, therein only 14 for the Mikołajskie Lake. B e r g e r (1960) listed several species, not recorded by later investigators, but found during the present research in the Mikołajskie Lake in the years 1978 – 1982. These are: *Viviparus contectus, Marstoniopsis steini* Mart. (= *Marstoniopsis scholtzi*), *Physa fontinalis* and *Planorbis carinatus*. For the Mikołajskie Lake he did not, however, enumerate species which he recorded for other water bodies of that region, and which have been found in the Mikołajskie Lake during the present study. Noteworthy in B e r g e r' s (1960) list of species is the absence of *Acroloxus lacustris* which is very common on reeds in the Mikołajskie Lake.

In 1978, in the Mikołajskie Lake *Potamopyrgus jenkinsi* was recorded – a species never observed there before. In the autumn of 1979 this snail occurred in large aggregations in the near-shore zone, but the following year it was found there only sporadically. In Poland, this invasive species was hitherto described mainly from the Great Poland region (J a c k i e w i c z 1973, B e r g e r and D z i ę c z k o w s k i 1977, K a s p r z a k 1982) and Iława Lakeland (F u r y k 1970, W o l n o m i e j s k i and F u r y k 1970). According to U r b a ń s k i

(1965), this snail occurs on the island of Wolin, and according to Piechocki (1979) – in some water bodies and watercourses of the Pomeranian Lakeland.

Other species not listed so far in the literature concerning the Mikołajskie Lake were *Bithynia leachi* and *Valvata* (*Cincinna*) *pulchella*. *Planorbis planorbis* (L.), whose presence was recorded by Włodarska (1972) and Soszka (1975), has not been found. Nor has been *Hippentis complanatus* (L.) reported by Soszka (1975). According to Włodarska (1972) and Soszka (1975), present in the Mikołajskie Lake also is *Physa acuta* Drap. This species is typical of warmed waters (Feliksiak 1939, Dutkiewicz 1959, Piechocki 1979), so its occurrence in the Mikołajskie Lake is not certain (Piechocki 1979). Berger (1960) mentions for the Mikołajskie Lake *Radix auricularia* L. and *R. peregra* Müll., but they could not be related to the species of the subgenus *Radix* distinguished at present. The same author also found the presence of *Galba corvus* Gmel., whereas Soszka (1975) recorded *G. palustris* (O. F. Müll.) and *Gyraulus albus* (O. F. Müll.). However, *G. palustris* has appeared to be an aggregate species now classified into three separate species: *G. corvus* (Gmel.), *G. turricula* (Held) and *G. occulta* Jack (Piechocki 1979).

The dominance structure of snails on the particular substrates was found to be usually distinct, especially with regard to biomass (Fig. 3). By collecting samples from the same substrates at different stations it was possible to find that on each substrate type a larger number of taxa was accompanied by a more distinct dominance structure. It is hard to explain this phenomenon, because with a larger number of species the habitat should be shared among them more "fairly". Consequently, the role of gastropods on each of the substrates is determined by one up to three taxa, dominating in numbers and/or biomass of all the snails. On the stony bottom it is *Theodoxus fluviatilis*, in the sediments *Potamopyrgus jenkinsi*, *Valvata* (*Cincinna*) *piscinalis* and *Viviparus contectus*, on reeds – *Acroloxus lacustris* and *T. fluviatilis*, and on the remaining plants under study – *Lymnaea* (*Radix*) sp.

The assessment of the number of snails in the whole littoral of the Mikołajskie Lake, based on information about their density on the different substrates, and about the number of those substrates has demonstrated that the main habitats holding up to 63% of numbers and 79% of biomass are the submerged macrophytes and those with floating leaves (Fig. 9). The stony bottom inhabited by numerous snails in summer and autumn (Table II, Fig. 6), occupies in this lake so small an area that its role as a habitat within the lake as a whole is negligible (Fig. 9). Reed, in spite of the fact that it offers a considerable area, relative to the lake as a whole, of colonizable surface (reed-beds occupy almost half the littoral surface area, and the surface area of the underwater reed stems comes up to 0.72 m^2 of reed-bed), holds small snail numbers and a low biomass. The cause of this probably is the fact that the stem surface is subject to the action of waves, which is particularly unfavourable in the case of species of considerable body size.

The total number of snails may vary from year to year over a wide range, as a result of differences in their density on the substrates, and of changes in the quantity of some of the substrates. Considerable changes in the composition and biomass of submerged vegetation in successive years were found, for example, in the Mikołajskie Lake by Ozimek and Kowalczewski (in press). Snail numbers on submerged plants, both average and maximum, also were much lower in 1979–1980 than the values reported by Soszka (1975). However, on account of the large number of species and the occupation of different ecological niches, changes in the abundance of the whole gastropod community in the lake will probably never be so drastic as those observed, e.g., by Stańczykowska (1961, 1975, 1977, 1978) in *Dreissena polymorpha*.

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5. SUMMARY

Various aspects of the occurrence of snails in the littoral of the Mikołajskie Lake were studied. Most of the materials were collected in 1979 and 1980 on three stations conspicuously differing in the number of substrates available to snails (Fig. 1). Samples were collected from seven kinds of substrates most common in this lake (stony bottom, bottom with sand-mud sediments, *Phragmites australis, Potamogeton perfoliatus, P. lucens, Nuphar lutea* and *Stratiotes aloides*), at one-month intervals during the ice-free season, and once (January 1982) during the ice period. Representatives of 20 species, two subgenera (*Radix* and *Galba*) and one genus (*Gyraulus*) of snails have been found to occur in the Mikołajskie Lake. The commonest among snails were *Lymnaea* (*Radix*) sp., *Theodoxus fluviatilis* and *Bithynia tentaculata*, occurring as constant or absolutely constant species on very different substrates like the stony bottom, sediments or some species of submerged plants and plants with floating leaves (Fig. 2). On each of the substrates a considerable number of snail taxa is found (from 11 to 18), but as a result of a distinct dominance structure (Fig. 3), the role of the snails is determined by only one up to three of them. On the stony bottom it is *T. fluviatilis*, in the sediments – *Potamopyrgus jenkinsi, Valvata* (*Cincinna*) *piscinalis* and *Viviparus contectus*, on reeds – *Acroloxus lacustris* and *T. fluviatilis*, whereas on all the submerged plant species and on plants with floating leaves under study – *Lymnaea* (*Radix*) sp.

In many cases snails were a clearly dominant group among the invertebrate macrofauna, especially with regard to biomass (Table I). This dominance is particularly conspicuous on plants. On different plant species snails represented (on an average for the whole sampling period) from 13 up to 41% of numbers and from 39 to 68% of biomass of the whole macrofauna. In some months this percentage was yet greater, coming up to 98% of biomass. On the remaining substrates the percentage of snails in the numbers and biomass of the whole invertebrate macrofauna was much lower, but there also they were seasonally a clearly dominant group (Table I).

Snails utilize lake macrophytes in different ways. Emergent plants are inhabited throughout the year; the number of snails on them varies, and their biomass is very low (Figs. 5, 6). On plants with annual above-ground shoots, like *Potamogeton perfoliatus* and *P. lucens*, a marked growth in numbers could be seen (Fig. 7), and in biomass as well, in the successive months. They appear to be inhabited by particularly abundant snails in autumn. On plants with perennial above-ground shoots (*Nuphar lutea* and *Stratiotes aloides*), used by animals as a substrate throughout the year, changes in numbers of the snails in successive months are irregular (Fig. 7). Noteworthy is the abundant fauna inhabiting these plants during the ice period and also just before and sometimes immediately after the disappearance of the ice-cover, i.e., when the number of

substrates available to the fauna in the littoral is reduced considerably. For both these plant groups great differences have been found also in the species-composition and dominance structure of the snails inhabiting them (Figs. 3, 8).

In summer, the largest numbers of snails per 1 m^2 of the littoral are found on submerged vegetation and on plants with floating leaves, as well as on the stony bottom (Table II). In sediments and on *Phragmites australis* both the average numbers of snails and their biomass are many times greater than in the habitats mentioned earlier.

It has been estimated that in the ice-free period submerged plants and those with floating leaves hold up to 63% of numbers, and up to 79% of biomass of all the snails in the Mikołajskie Lake. On account of its very small surface area, the stony bottom of this lake, as a substrate, plays a very small role. In spite of its considerable, relative to the whole lake, colonizable surface area, *Phragmites australis* harbours a small number and low biomass of snails. In spring, the main environment where most snails in the Mikołajskie Lake live is the sediment zone (Fig. 9).

6. POLISH SUMMARY

Badano różne aspekty występowania ślimaków w litoralu Jeziora Mikołajskiego. Większość materiałów zebrano w 1979 i 1980 r. na 3 stanowiskach, wyraźnie różnicujących się liczbą rodzajów podłoży, dostępnych dla ślimaków (rys. 1). Próbki pobrano z 7 najpospolitszych w tym zbiorniku rodzajów podłoży (dno kamieniste, piaszczysto-muliste, *Phragmites australis, Potamogeton perfoliatus, P. lucens, Nuphar lutea* i *Stratiotes aloides*), w odstępach miesięcznych w okresie wolnym od lodu, oraz jednorazowo (styczeń 1982) w czasie zlodzenia. Stwierdzono, że w Jeziorze Mikołajskim występują przedstawiciele 20 gatunków, dwóch podrodzajów (*Radix* i *Galba*) oraz jednego rodzaju (*Gyraulus*). Ślimakami najbardziej rozpowszechnionymi były *Lymnaea* (*Radix*) sp., *Theodoxus fluviatilis* i *Bithynia tentaculata*, występujące jako stałe lub absolutnie stałe na podłożach tak odmiennych, jak dno kamieniste, osady lub też niektóre gatunki roślin zanurzonych i o liściach pływających (rys. 2). Na poszczególnych podłożach występuje znaczna liczba taksonów ślimaków (od 11 do 18), ale wobec ostro wyrażonej struktury dominacji (rys. 3) o znaczeniu ślimaków decyduje zaledwie 1 do 3 z nich. Na dnie kamienistym jest to *T. fluviatilis*, w osadach – *Potamopyrgus jenkinsi, Valvata* (*Cincinna*) *piscinalis* i *Viviparus contectus*, na trzcinie – *Acroloxus lacustris* i *T. fluviatilis*, a na wszystkich badanych gatunkach roślin zanurzonych i o liściach pływających – *Lymnaea* (*Radix*) sp.

Ślimaki w wielu przypadkach były grupą wyraźnie dominującą wśród makrofauny bezkręgowej, zwłaszcza w odniesieniu do biomasy (tab. I). Dominacja ta jest szczególnie wyraźna na roślinach. Na różnych ich gatunkach ślimaki stanowiły (średnio dla całego okresu pobierania próbek) 13–41% liczebności i 39–68% biomasy całej makrofauny. W niektórych miesiącach udział ten był jeszcze większy, sięgając 98% biomasy. Znacznie mniejszy był udział ślimaków w liczebności i biomasie całej makrofauny bezkręgowej na pozostałych podłożach, ale i tam okresowo były one grupą zdecydowanie dominującą (tab. I).

Ślimaki w różny sposób wykorzystują makrofity jeziorne. Rośliny wynurzone zasiedlone są przez cały rok; liczebność ślimaków jest na nich zmienna, a biomasa – bardzo mała (rys. 5, 6). Na roślinach o jednorocznych pędach nadziemnych, takich jak *Potamogeton perfoliatus* i *P. lucens*, obserwowano wyraźny wzrost liczebności (rys. 7), a także biomasy ślimaków w kolejnych miesiącach. Szczególnie licznie zasiedlone są one jesienią. Na roślinach o wieloletnich pędach nadziemnych (*Nuphar lutea* i *Stratiotes aloides*), służących jako podłoże dla zwierząt przez cały rok, zmiany w liczebności ślimaków w kolejnych miesiącach są nieregularne (rys. 7). Zwraca uwagę liczne zasiedlenie tych roślin w okresie zlodzenia, a także tuż przed i niekiedy bezpośrednio po zejściu pokrywy lodowej, tj. w okresie, gdy liczba podłoży, dostępnych dla fauny jest w litoralu znacznie ograniczona. Dla obu tych grup roślin duże różnice stwierdzono też w składzie gatunkowym i strukturze dominacji zasiedlających je ślimaków (rys. 3, 8).

W okresie letnim najwięcej ślimaków, w przeliczeniu na 1 m^2 litoralu, występuje na roślinności zanurzonej i o liściach pływających oraz na dnie kamienistym (tab. II). W osadach i na *Phragmites australis* zarówno średnie liczebności ślimaków, jak i ich biomasy są wielokrotnie niższe aniżeli w środowiskach poprzednio wymienionych.

Oszacowano, że w okresie wolnym od lodu do 63% liczebności i do 79% biomasy wszystkich ślimaków w Jeziorze Mikołajskim skupione są na roślinach zanurzonych i o liściach pływających. Dno kamieniste, ze względu na bardzo małą powierzchnię, jaką zajmuje w tym jeziorze, ma jako podłoże minimalne znaczenie. *Phragmites australis*, pomimo znacznej w skali całego zbiornika dostępnej do zasiedlenia powierzchni, skupia niewielką liczbę i bardzo małą biomasę ślimaków. Natomiast w okresie wiosennym zasadniczym miejscem bytowania większości ślimaków w Jeziorze Mikołajskim jest strefa osadów (rys. 9).

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