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OCCURRENCE OF GASTROPODA IN THE LAKE LITTORAL AND THEIR ROLE IN THE PRODUCTION AND TRANSFORMATION OF DETRITUS II. ECOLOGICAL ACTIVITY OF SNAILS *

ABSTRACT: Various signs were studied of the activity of snails connected with the production and transformation of detritus by these animals. Most of the species studied were found to prefer feeding on vegetable detritus and periphyton, and to avoid living macrophytes. Preferred food was at the same time better assimilated. The rate of circadian defecation has been determined for different snail species. Submerged-macrophyte-dwelling snails in the Mikołajskie Lake were found to excrete as much as 90% of the total amount of gastropod faeces present there. Food remnants, damaged and discarded during the foraging also appeared to be an important source of detritus.

KEY WORDS: Gastropoda, detritus, feeding, faeces, food decomposition, laboratory experiments.

Contents

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1. INTRODUCTION

There have not been many studies on the importance of snails in freshwater habitats, and these animals have usually been considered from the point of view of their role as intermediate hosts of parasites, or as food for the fishes, less often for other animals. The role of the snails as consumers was much more rarely taken into account. The fact has entirely been ignored that snails, like many other animals, can play an important role in the cycling of matter by participating in the production and transformation of the detritus.

The importance of the detritus in aquatic ecosystems has already been indicated by other authors (literature review — Kołodziejczyk 1980, 1984). It is not only an important source of food for numerous animals, but is also considered a buffer ensuring an environmental homeostasis, by diversifying the environment and permitting a large number of animals to exist. The origin, composition and decomposition of the detritus have been studied, but there have been far fewer studies on its trophical and habitat-forming role. Most papers concentrate on vegetable auto- and allochthonous detritus. Detritus of animal origin is in those studies most often omitted. Some authors (Hargrave 1972, 1976, Berrie 1976, Pavljutin 1979) point out, however, on the basis of their own investigations and data taken from the literature, that fecal detritus may sometimes provide a significant source of food for the invertebrate macrofauna. Attention has also been drawn to the role of animals in the acceleration of detritus decomposition processes (Cummins et al. 1973, Berrie 1976, Gasith and Ławacz 1976, Ostapenja 1979). According to Berrie (1976), the mechanical breaking up of plant remains by animals accelerates their decomposition. It has been found that the passage of various kinds of food through the alimentary tract of many species of aquatic invertebrates causes an increase in the metabolic activity of this material (Hargrave 1976).

In the lake littoral the detritus not only occurs in large quantities (because of the presence of considerable numbers of different macrophyte species and the input of considerable quantities of allochthonous detritus), but it also shows, relative to other parts of a lake, the greatest differences in origin and particle size. Due to this the role of animals in the production and transformation of detritus is very complex and difficult to quantify. The role may, however, be many-sided and very significant. Kołodziejczyk (1980) has pointed to some aspects of the role of the invertebrate macrofauna, therein also of the snails, in the production and transformation of detritus in a lake littoral. Among the few papers discussing the role of animals in the production of detritus in a lake littoral there are studies on the production of faeces and pseudofaeces by *Dreissena polymorpha* Pall. (Stańczykowska 1968, 1975, 1977, Mattice, Stańczykowska and Ławacz 1972) and by Unionidae (Lewandowski and Stańczykowska 1975). The amount was also assessed of fecal detritus input to an environment by the fishes (Prejs 1976, 1984) and by various waterfowl species (Dobrowolski 1973a, 1973b, Halba 1975, Dobrowolski, Halba and Nowicki 1976, Böck

1979, R a m o s 1980). There has also been a narrow-scope study on the production by littoral invertebrates of detritus in the form of food remnants broken up and discarded during foraging (P i e c z y ń s k a 1970, G ł o w a c k a 1976, B i j o k 1981).

In a lake littoral there are many snail species considerably differing in their ecology. An assessment of the role of this large and diverse group may make it easy to understand the processes occurring in the littoral zone. It seems that the role of the snails, and to a large extent also of the whole invertebrate macrofauna in processes associated with the production and transformation of detritus in freshwater habitats has so far been underestimated.

The aim of the present studies was to estimate the role of the snails in the production and transformation of detritus in a lake littoral. The previous paper (K o ł o d z i e j c z y k 1984) presented the numbers, biomass, specific composition and the dominance structure of snails in different habitats in the littoral of the Mikołajskie Lake. For the evaluation of these animals it is necessary also to know the kind and level of the activity of the particular species. The following quantities and phenomena were investigated: food preference, consumption and defecation rates, efficiency of the assimilation of the organic matter ingested with food, and the destruction and discarding of food remains during foraging. The amount was evaluated of the fecal detritus input by the whole snail community to different littoral habitats of the Mikołajskie Lake.

2. STUDY METHODS

To determine the preference of selected snail species, a modification has been used of Gaevskaja's (Ż a d i n 1966) method of enclosures, the same as that applied earlier by S o s z k a (1975), G ł o w a c k a (1976), and K o ł o d z i e j c z y k and M a r t y n u s k a (1980). In the modification the experimental tray was not divided into sectors, but, instead, the occurrences of animals directly on the food were counted. In a single experiment 6 – 40 snails of each of 2 – 4 species were used. Prior to the experiment the snails were starved for 24 hours, whereafter they were placed individually or in groups, depending on their number and body size, in trays or Petri dishes filled with non-filtered lake water. The food provided for them included fresh and dead plants of various species and periphyton. In each experiment 2 – 4 kinds of food were applied. Snails and food were collected simultaneously at the same station. For 6 – 7 hours the occurrences were recorded at 10-minute intervals of snails on the kinds of food offered to them, and the number of occurrences on each of them was totalled. Food selectivity was expressed in per cent frequency of occurrence on the different kinds of food, and by the food preference index computed according to I v l e v (1955), in the same way as presented for laboratory conditions by C i a n c i a r a (1980). According to the value of this index, the food items were divided into three groups: 1 – avoided, 2 – indifferent and 3 – preferred.

For *Lymnaea* (*Lymnaea*) *stagnalis* (L.) and *Planorbarius corneus* (L.) the consumption rate was assessed by the direct method (Żadin 1966) for three kinds of food. The snails were fed with each of them for four 24 hours' periods (three groups, each of which included three individuals of each species per one kind of food), and the food given and its remainder after feeding were weighed. Consumption was assumed to be the difference between the above two quantities expressed in dry weight.

The quantity of faeces produced was also determined and on its basis the efficiency of assimilation was established:

$$\frac{A}{C}\% = \frac{C-F}{C}\cdot 100\%$$

where C = consumption, A = assimilation, F = defecation. Assimilation efficiency was expressed as a percentage of the organic matter assimilated from the food ingested. For this purpose the content was determined of organic matter in food and in the faeces by the method of burning in the muffle furnace. The 5-hour burning time at 550°C was adopted after Rybak (1969). After computing the total amount of organic matter taken up with food and excreted with faeces the efficiency of its assimilation was evaluated by using the above formula.

The dry weight of the food remains discarded onto the bottom during the foraging of *Lymnaea* (*Lymnaea*) *stagnalis* and *Planorbarius corneus* on plants of different species was determined by weighing the broken up food remains collected 24 hours later, and comparing their weight with the weight of the faeces excreted during that time, or with the weight of the eaten food.

To determine the circadian value of defecation, 24 hours' laboratory experiments were carried out. Most of the snail species studied were fed with various kinds of food items found in their natural environment and preferred by these animals. Faeces collected and put in aluminium-foil containers were dried at 105°C and weighed on an analytical balance to the nearest 0.1 mg.

Those snails which excreted fecal pellets that were very small, but of definite shapes (*Theodoxus fluviatilis* (L.), *Bithynia tentaculata* (L.), *Viviparus viviparus* (L.) and *V. contectus* (Mill.)) were, immediately after their catching, placed in sealed jars containing non-filtered lake water and exposed in the littoral for four hours, whereafter the pellets excreted were counted. To express the production of faeces in weight units, for each species several samples (50–100 pellets each) were weighed once and the average weight of a fecal pellet was determined.

The composition was determined of the faeces excreted by the snails immediately after being caught, as well as the size (by means of a microscope with a calibrated eye-piece) of not digested remains in the faeces of snails fed in aquaria with different kinds of food. The proportion of sand in the dry weight was determined in dried and weighed faeces after their crushing in water and subsequent separating of sand grains under a stereoscopic microscope, their drying and weighing. The content was also determined of organic matter in faeces excreted by the snails immediately after being caught, and after the successive culture days.

The choice of snail species for the particular experiments depended on two factors: the intention to use species differing in their habits, level of activity and body-size, and the availability of large numbers of individuals of the particular species at the study site and time. Most of the snails used in the experiments derived from the Mikołajskie Lake (Masurian Lakeland) and the Powsinkowskie Lake (Warsaw).

3. RESULTS

3.1. FEEDING OF SNAILS

Food preference has been determined for representatives of ten snail taxa (Table I). They did not show preference for living plants, whereas dead plant tissues (detritus) were preferred by many snail species. Allowed a selection of other kinds of food items, *Lymnaea* (*Myxas*) *glutinosa* and *Theodoxus fluviatilis* clearly avoided eating plant detritus. Periphyton appeared to be an indifferent food to representatives of five gastropod taxa, to three taxa it was the preferred food, and was avoided only by *Physa fontinalis*. Thus dead plant tissues (detritus) and periphyton have appeared to be a more suitable food item to snails than living plants.

Table I. Food preference of selected gastropod taxa (averaged values from different experiments)
– – avoided food, 0 – indifferent food, + – preferred food

Taxon	Food given		
	living plants	dead plants	periphyton
Lymnaea (Lymnaea) stagnalis (L.)	0	+	+
L. (Myxas) glutinosa (O. F. Müll.)	0	–	0
Theodoxus fluviatilis (L.)	0	–	+
Lymnaea (Galba) sp.	–	0	no data
L. (Radix) sp.	–	+	+
Physa fontinalis (L.)	–	+	–
Planorbarius corneus (L.)	–	+	0
Bithynia tentaculata (L.)	–	+	0
Anisus (Disculifer) vortex (L.)	–	0	0
Viviparus contectus (Mill.)	–	0	0

The samples in Table II represent in detail the results from one of the experiments concerning the food preference of representatives of seven snail taxa. They were fed simultaneously two kinds of food differing in their mechanical structure: living stems of *Eladea canadensis* with delicate leaves, and detritus consisting of dead but still very hard leaves of *Phragmites australis*. Both items of food in the same form occurred simultaneously in the lake littoral in autumn. It has been found that *Bithynia* *tentaculata, Lymnaea* (*Radix*) sp., *L.* (*Galba*) sp. and *Anisus* (*Disculifer*) *vortex* preferred plant detritus (differences in the per cent frequency of foraging were statistically significant at the level of confidence from $p < 0.001$ to $p < 0.05$). In the case of *Physa fontinalis* and *Planorbarius corneus* the differences in the per cent frequency of foraging on both food items fed appeared not to be statistically significant. In this experiment it was only *L.* (*L.*) *stagnalis* that positively chose green stems of *E. canadensis* as its food. This may have been due to the mechanical availability of this plant to the freshwater snail which, because of its size, can cut off delicate parts of living plants with its chitinous jaws.

Table II. Food preference of several gastropod taxa in relation to living shoots of *Elodes canadensis* Rich. and dead leaves of *Phragmites australis* (Cav.) Trin. ex Steudel expressed in per cent frequency of occurrence on food

The observation was carried out on 6–25 individuals of each taxon

Taxon	Average per cent occurrence on:	
	E. canadensis (living)	*Ph. australis* (dead)
Bithynia tentaculata	10	90
Lymnaea (Radix) sp.	22	78
L. (Galba) sp.	28	72
Anisus (Disculifer) vortex	35	65
Physa fontinalis	32	68
Planorbarius corneus	42	58
Lymnaea (Lymnaea) stagnalis	95	5

If snails were fed with living and dead tissues of the same plant species (in the successive experiment these were leaves of *Nuphar lutea*, both forms of which occur simultaneously in the lake littoral in autumn), then they always preferred the dead form (Table III). For representatives of three taxa differences in the percentage of foraging on the two kinds of food were statistically significant at the $p < 0.001$ level of confidence. From previous detailed studies of *Lymnaea* (*Lymnaea*) *stagnalis* also follows that when allowed to choose between live and dead tissues of five macrophyte species, the snail always preferred the dead form (Kołodziejczyk and Martynuska 1980).

In some experiments *Lymnaea* (*Lymnaea*) *stagnalis, L.* (*Myxas*) *glutinosa, L.* (*Radix*) sp., *Planorbarius corneus* and *Bithynia tentaculata* were divided into two groups differing in body size. Large snails always positively preferred dead vegetable tissues, avoiding the living ones. Individuals of a smaller body-size also most often preferred dead plants, but in this case the preference was less pronounced than in adult individuals.

The quantity consumed was determined in the laboratory for two snail species, *Lymnaea* (*Lymnaea*) *stagnalis* and *Planorbarius corneus*, each of which was fed with

Table III. Food preference of three gastropod taxa in relation to living and dead leaves of *Nuphar lutea* (L.) Sm. expressed in per cent frequency of occurrence on food
The observation was carried out on 10–20 individuals of each taxon

Taxon	Average per cent occurrence on:	
	living plant	dead plant
Planorbarius corneus	17	83
Lymnaea (Radix) sp.	22	78
L. (Lymnaea) stagnalis	25	75

three kinds of food differing in freshness and mechanical availability (Table IV). These food items, in the form used in the experiments, were available simultaneously (end of September) in the lake littoral. On account of the variable consumption rhythm [1] of the individuals, only the mean values have been presenten in Table IV. It has been found that in terms of quantities per one individual, *L.* (*L.*) *stagnalis* ate 2.7 – 4.5 times as much of each of the food items given than did *P. corneus*, although the average body-weight of individuals of both these snail species is similar. The two species under study have been found to eat fresh stems of *Elodea canadensis* least readily, and to consume 1.6 – 2.0 times as much *Hydrocharis morsus-ranae* at the initial stage of decomposition. *L.* (*L.*) *stagnalis* ate *Potamogeton perfoliatus* stems at an advanced stage of decomposition in almost twice as large quantities as it ate *H. morsus-ranae*. For *P. corneus* a small increase in consumption was found in the case of this food item (Table IV). Expressed as a percentage of snail body-weight, the value of circadian consumption in *L.* (*L.*) *stagnalis* amounted to 0.42 – 1.31% of the dry weight of the entire snail, and from 1.84 to 5.85% of the dry weight of its tissues, and in *P. corneus* – from 0.11 to 0.25 and from 0.62 to 1.51%, respectively (Table IV). These results point to a different trophic importance of two snail species of a similar body-size and inhabiting similar environments. Simultaneously, they confirm data from previous experiments indicating that snails prefer dead plant tissues as their food. Expressed in mg of organic matter, the value of consumption was also higher in *L.* (*L.*) *stagnalis*, and in both snail species it depended on the kind of food (Table V), as in the case of its description in units of dry weight.

The efficiency of assimilation in the two snail species also has been determined for different kinds of food and expressed as a percentage of the organic matter ingested

[1] A varying consumption rhythm in snails was observed during many hours' experiments on food preference. Acc. to S u š k i n a (1949), *Lymnaea stagnalis* and *Planorbarius corneus* show a clear diurnal consumption rhythm; S t r e i t (1975) reports that *Ancylus fluviatilis* O. F. Müll. feeds very irregularly, whereas acc. to Z. Fischer-Malanowska (personal communication), snails, in comparison with other invertebrates, are characterized by a highly irregular feeding rhythm. A different view is held by C a l o w (1975), according to whom *A. fluviatilis* and *Planorbis contortus* (L.) feed with a fixed frequency.

Table IV. Value of 24 hours' consumption of three food types by two gastropod species (average values from 12 replications)
A – *Elodea canadensis* (fresh), B – *Hydrocharis morsus-ranae* L. (beginning to decompose), C – *Potamogeton perfoliatus* L. (at advanced stage of decomposition)

Species	Mean dry weight of 1 indiv. (mg)		Food given	Average 24 hours' consumption		
				calculated per 1 indiv. (mg d. wt.)	in per cent d. wt. of snail	
	with shell	without shell			with shell	without shell
Lymnaea (Lymnaea) stagnalis	1050	265	A	5.2	0.42	1.84
			B	8.2	0.71	3.14
			C	14.6	1.31	5.85
Planorbarius corneus	1350	230	A	1.5	0.11	0.62
			B	3.0	0.22	1.32
			C	3.2	0.25	1.51

Table V. Efficiency of assimilation of organic matter from three types of food by two gastropod species (average values from 12 replications)
A, B and C – as in Table IV

Species	Food given	Value of consumption	Value of defecation	Assimilation efficiency (%)
		mg org. matter per 1 indiv. per 24 hrs		
Lymnaea (Lymnaea) stagnalis	A	3.50	2.56	26.9
	B	6.87	2.80	59.2
	C	12.44	3.77	69.7
Planorbarius corneus	A	1.08	0.83	23.1
	B	2.51	2.08	17.1
	C	2.64	0.96	63.6

(Table V). Assimilation efficiency was found to be very low when the snails fed on living *Elodea canadensis* (this applying to both snail species) and *Hydrocharis morsus-ranae* at the initial decomposition phase (in *Planorbarius corneus*), and to be the highest (about 60–70%) when they ate dead, decomposing *Potamageton perfoliatus*. A marked difference in the efficiency of organic mater assimilation between the two snail species under study was observed only when they were fed with *H. morsus-ranae*; the efficiency was much higher in *Lymnaea (Lymnaea) stagnalis*. The efficiency of the assimilation of the organic matter derived from the other food items was in this snail only slightly higher than in *Planorbarius corneus* (Table V).

3.2. PRODUCTION OF FAECES AND THEIR IMPORTANCE IN THE ENVIRONMENT

A large proportion of the food eaten returns in the form of faeces to the environment where it increases the detritus pool. The assimilation efficiency value indicates that, depending on the kind of food and snail species, about 30 – 80% of the organic matter ingested with food is expelled in the form of fecal detritus. Presented in Table VI is the average (for the summer period) circadian production of faeces by adult individuals representing ten gastropod taxa. The values have been obtained from field and laboratory experiments. Calculated per an individual, the circadian production of faeces of different snail species varies considerably, amounting on an average to from 0.5 (*Anisus* (*Disculifer*) *vortex*) to 40.8 mg of dry weight (*Planorbarius corneus*). However, if calculated per 1 g of the dry weight of a snail, the values appear to be less variable; the lowest circadian production of faeces has been found in *Theodoxus fluviatilis* (4.3 mg d. wt.) and *Bithynia tentaculata* (12.5 mg d. wt.). In the remaining snail species the average production of faeces ranges from about 65 mg of d. wt. per 1 g of d. wt. of a snail and shell.

Table VI. Circadian production of faeces by adult gastropods in summer (averged values from different experiments, and the range of variation)

Taxon	24 hours' production of faeces (mg d. wt.) calculated per:			
	1 individual		1 g d. wt. of snail with shell	
Anisus (Disculifer) vortex	0.5	(0.3–0.8)	64.8	(45.2–99.0)
Theodoxus fluviatilis	0.7	(0.2–1.0)	4.3	(1.3–6.8)
Bithynia tentaculata	1.3	(0.9–1.7)	12.5	(8.3–16.8)
Planorbis carinatus	4.6	(4.5–4.7)	46.2	(27.4–65.0)
Lymnaea (Galba) sp.	5.1	(4.4–12.5)	29.8	(22.1–52.8)
L. (Radix) sp.	11.0	(4.6–16.4)	43.0	(23.3–77.6)
L. (Lymnaea) stagnalis	17.7	(6.2–38.6)	43.4	(21.2–104.9)
Viviparus viviparus and *V. contectus**	21.0	(1.5–40.6)	28.9	(1.0–100.2)
Planorbarius corneus	40.8	(14.1–65.4)	35.2	(10.2–49.0)

*No difference in faeces production has been found between these species.

It has been found that the amount of faeces excreted by snails depends on the type of food. After eating their preferred food (decomposing plants, periphyton) *Lymnaea* (*Radix*) sp. individuals excreted on an average about 15 times as much fecal dry weight as they did when fed fresh plants (Table VII). This is probably due to a higher rate foraging on preferred food items, since the differences in the efficiency of assimilation of different kinds of food (up to about 4 times, Table V) were much smaller than the observed differences in the production of faeces; at the same time preferred food items were assimilated with a higher efficiency.

Table VII. Circadian production of faeces by *Lymnaea (Radix)* sp. in relationship to the food given (average values from 3–6 replications, and standard deviation)

Food given	Average weight of 1 snail (mg)	Average 24 hours' faeces production (mg d. wt.) calc. per:	
		1 individual	1 g d. wt. of snail with shell
Potamogeton lucens (fresh)	212	1.1 ± 0.5	5.2 ± 2.0
P. lucens (beginning to decompose)	197	4.6 ± 1.0	23.3 ± 4.9
P. lucens (advanced decomposition)	193	15.0 ± 7.7	77.6 ± 39.9
Periphyton (dominated by filamentous algae)	242	16.3 ± 14.3	67.8 ± 59.1

In *Lymnaea* (*Radix*) sp. circadian faeces production per an individual does not differ significantly. although the range of individual body-weight is very wide (from 3.5 to 5.5 mg d. wt. of faeces for individual body-weights from 16 to 93 mg). Only for the largest snails among those used in the experiment was a clear increase recorded of the amount of faeces (Table VIII). By calculating the circadian faeces production per 1 g of the dry weight of a snail a very high value (265.4 mg d. wt.) was found for the smallest snails; for the remainder of them it ranged from 43.2 to 87.0 mg (Table VIII).

Table VIII. Circadian faeces production by *Lymnaea (Radix)* sp. in relationship to body weight (average values obtained from joint measurements of 10 individuals in each size class)

Mean dry weight of 1 snail (mg)	Average 24 hours' faeces production (mg d. wt.) calc. per:	
	1 individual	1 g d. wt. of snail with shell
16	4.4	265.4
40	3.5	87.0
70	5.5	64.9
93	4.0	43.2
193	8.8	45.6

In snails which excrete faeces in pellets of definite shapes (*Theodoxus fluviatilis*, *Bithynia tentaculata*, both species of the genus *Viviparus*) there was a very wide variation in the number of pellets excreted during an hour. This variation was particularly conspicuous in snails of the genus *Viviparus* – between 0 and 80 fecal pellets. No correlation was found between the body-size of an individual and the number of fecal pellets excreted by it (for *T. fluviatilis* individuals 6 to 12 mm in body-size, and for *Viviparus* sp. 10 to 35 mm). Statistically significant correlation has, however, been found between the body-size of *T. fluviatilis* and individuals of the genus *Viviparus* and the size of fecal pellets excreted by them.

The above-mentioned measurements were made in summer. In *Theodoxus fluviatilis* also the effect was studied of water temperature on the production of faeces. In the period May-October, when the water temperature in the littoral ranged from 9 to 18°C, for this species no relationship has been found between the temperature of the water and the number of fecal pellets. Neither could a regularity be seen in the variation of the number of pellets expelled in the successive months. *Lymnaea* (*Radix*) sp. individuals, collected under the ice cover in January and exposed in situ for several hours, were found to excrete small numbers of faeces. Each of these snails expelled from 0 (35% of individuals) to 24 faeces per 24 hours, while the average for the summer period was 30.

Apart from amounts, significant for the role of snails in the formation and transformation of littoral detritus is the composition of faeces. In the faeces of snails feeding under natural conditions considerable amounts of sand were found. Sand represented on an average 9% of the dry weight of faeces of *Lymnaea* (*Lymnaea*) *stagnalis* individuals collected from submerged vegetation, and 48% of the fecal dry weight of *Planorbarius corneus* individuals collected from a sandy bottom (Kołodziejczyk and Martynuska 1980). The faeces of *Bithynia tentaculata* also were found to contain large amounts of sand, while in *L.* (*Radix*) sp. sand was found in the faeces of individuals collected from different substrates – from the bottom, reeds and from different species of submerged plants. Thus the content of organic matter in the faeces collected from snails immediately after their catching was as a rule small. In spring and summer in *L.* (*L.*) *stagnalis*, *P. corneus* and *L.* (*Radix*) sp. collected from different water bodies it amounted to 15 up to 25%. A larger proportion of organic matter in faeces was seen in autumn (40–60%) in *L.* (*L.*) *stagnalis* and *P. corneus* occurring on decomposing submerged plants. A clear increase in the percentage of organic matter (up to 30–45%) in their faeces was observed also as early as after a 1–3-day feeding of snails with plant food in aquaria without access to sand.

In the faeces of *Lymnaea* (*Lymnaea*) *stagnalis*, *L.* (*Radix*) sp., *Bithynia tentaculata*, *Viviparus viviparus* and *V. contectus* mainly remnants of some brown amorphous detritus were found, and rarely green, periphytic algae, and entirely sporadically fragments of green plant tissues. It has been demonstrated also (Kołodziejczyk and Martynuska 1980 and subsequent studies) that after passing through the alimentary tract of *L.* (*L.*) *stagnalis* (Table IX) the food appears to be broken up to a considerable degree. Irrespective of the size of the food item used in the experiment, the average length of particles in the faeces did not exceed 2.0 mm, and their surface area – 0.4 mm ^{2}. Entirely sporadically were pieces, up to 4.0 mm long, of dead leaves of *Glyceria aquatica* (L.) Wahlb. found in the faeces of this snail. Longer particles of undigested food were observed in the faeces of *Planorbarius corneus* – a considerable number of them attained a length of 2.0 mm, and the longest fragments – 12.5 mm. These data concern the largest-bodied snails excreting large

Table IX. Quantity of vegetable food in the environment and of food remains in the faeces excreted by *Lymnaea (Lymnaea) stagnalis**

Food given	Food	Remains in faeces	Food	Remains in faeces
	average length (mm)		average area (mm^2)	
Lemna minor	2	0.8	4	0.4
Elodea canadensis (leaves)	9	0.5	15	0.1
Filamentous algae	100	0.7	600	0.4
Glyceria aquatica (leaves)	200	2.0	5000	0.3

*According to Kołodziejczyk and Martynuska (1980), completed.

fecal pellets. A high degree of food breaking-up, often even up to 100-fold (in respect of length, Table IX), may be of significance in the process of detritus transformation by snails.

Faeces of snails living on plants and various objects submerged in water can rapidly get into the sediments. The rate of falling of the faeces of *Planorbarius corneus* and *Lymnaea* (*Galba*) sp. has been estimated at about 1.1 $cm \cdot s^{-1}$, and of the faeces of *Bithynia tentaculata* – about 0.4 $cm \cdot s^{-1}$. For *L.* (*L.*) *stagnalis* (Kołodziejczyk and Martynuska 1980) the average falling rate is 3.6 $cm \cdot s^{-1}$, strongly depending on the diet of the snail.

On the basis of data on the numbers and dominance structure of the snails in different environments in the littoral of the Mikołajskie Lake (Kołodziejczyk 1984), and on the mean circadian production of faeces by representatives of different taxa (Table VI) it has been estimated that in summer these animals input about 1 ton of dry weight of fecal detritus per 24 hours to the environment (Table X). This means that throughout the summer period (July, August, September) the snails living in the Mikołajskie Lake excrete about 88 tons of dry weight of this detritus. Reed-dwelling snails input the smallest amounts of faeces per 1 m^2 of the littoral. As a result, in spite of the fact that there is a considerable dwellable reed surface area in the Mikołajskie Lake (Kołodziejczyk 1984), they excrete as little as 2% of the total amount of the fecal detritus produced by all the snails in this lake. The largest amount of faeces is excreted by snails living on submerged macrophytes, this amount representing as much as 90% of the total quantity. Very low amounts of fecal detritus are expelled by stony-bottom-dwelling snails in the Mikołajskie Lake (Table X), because of both the small area of this environment and the dominance of a species with a very low circadian production of faeces – *Theodoxus fluviatilis* (Kołodziejczyk 1984).

If we assume the average organic matter content in the faeces to be equal to 20%, this means that 195 kg of organic matter per 24 hours, i.e., about 18 tons during the summer, is input by snails to the Mikołajskie Lake.

Table X. Production of faeces by Gastropoda dwelling on different substrates in the littoral of Mikołajskie Lake in summer (July, August, September)
Mean values; in brackets – maximum values

Substrate inhabited	Production of faeces (dry weight)			
	g per m^2 per 24 hrs	g per m^2 per summer season	kg per littoral per 24 hrs	tons per littoral per summer season
Stony bottom	0.37 (0.95)	33.3	1.2	0.11
Sediments	0.09 (0.12)	8.1	78.4	7.06
Reeds	0.06 (0.33)	5.4	23.4	2.11
Submerged vegetation	2.92 (14.75)	262.8	876.0	78.84
Throughout the littoral of Mikołajskie Lake			979.0	88.12

3.3. DESTRUCTION OF FOOD DURING FORAGING

An important source of detritus, beside the faeces, can be the food remains broken up and discarded during foraging. Observations made during cultures of various snails (*Lymnaea* (*Lymnaea*) *stagnalis, L.* (*Radix*) sp. and *L.* (*Galba*) sp.) fed macrophytes have shown that these snails cause injuries to the leaves of several plant species, e.g., *Valisneria* sp., *Hydrocharis morsus-ranae* and *Potamogeton perfoliatus* L., whereas *L.* (*L.*) *stagnalis,* the largest of the snails studied, ate small pleuston plants – *Spirodela polyrrhiza* (L.) Schleiden and *Riccia fluitans* L. in their entirety. In later experiments on *L.* (*L.*) *stagnalis* it has been found that the snail discards food remnants onto the bottom in amounts dependent on the mechanical availability of the food. On fresh leaves of *Nuphar lutea* and dead leaves of *Glyceria aquatica* no injuries were seen; nor were snails found to produce food remnants. The leaves were, most likely, only scraped by the radula and no morsels were cut off. During foraging on the leaves, relatively hard, of *Potamogeton crispus* L. clear injuries could be seen, and the snails left few remnants, on an average 16% of the food eaten. A decaying leaf of *N. lutea* was broken up more intensively – the broken up and discarded fragments represented 33% of the quantity consumed. The delicate leaves of *P. perfoliatus* were eaten in their entirety and no remnants were left.

In a further experiment the production of remains by *Lymnaea* (*Lymnaea*) *stagnalis* feeding on *Elodea canadensis* was studied. It was found that the detritus produced in this way represented on an average 85% of the dry weight of the food eaten, and 124% of the dry weight of faeces excreted (with variations between 10 and 557%). No relationship was found between the amount of detritus discarded during foraging and the body-weight of a snail (over the range of 0.45 – 1.21 g dry wt.), or the quantity consumed or excreted. The size of plant remnants varied over a very wide range, from leaf and stem fragments several millimetres long to stem pieces several centimetres long.

The production was also compared of both types of detritus: faeces and food remnants, by *Lymnaea* (*Lymnaea*) *stagnalis* and *Planorbarius corneus* when fed with three kinds of food (Table XI). The quantity of *Elodea canadensis* remnants discarded during foraging and their ratio to the dry weight of faeces appeared to be much lower here than in the previous experiment. When fed with *E. canadensis, L.* (*L.*) *stagnalis* produced the largest amounts of remnants (on an average 10% of the fecal dry weight). *Spirodela polyrrhiza*, on account of its small body-size, and *Potamogeton perfoliatus* because of the shape of its leaves and stems, were not so much subject to the breaking up by snails. *P. corneus* excreted much less faeces (Table XI), but the quantities of food remnants discarded during its feeding on *P. perfoliatus* and *S. polyrrhiza* were larger than those found for *L.* (*L.*) *stagnalis*, and so was the weight ratio of the remnants to the faeces excreted.

Table XI. Production of faeces and destruction of food during foraging by two gastropod species
In mg of dry weight per 1 individual per 24 hrs; average values from 5 replications, and the range of variation

Kind of food given	*Lymnaea (Lymnaea) stagnalis*			*Planorbarius corneus*		
	food remains	faeces	food remains as percentage of faeces weight	food remains	faeces	food remains as percentage of faeces weight
Potamogeton perfoliatus	0.9 (0–2.4)	26.9 (14.7–36.2)	3.4 (0–10.0)	8.5 (0–41.0)	3.9 (1.1–11.7)	219.5 (0–1863.6)
Elodea canadensis	1.3 (0.2–4.5)	13.3 (10.7–16.7)	10.0 (1.7–26.7)	0.1 (0–0.4)	2.3 (1.3–3.5)	5.3 (0–10.8)
Spirodela polyrrhiza	0.1 (0–0.3)	7.9 (4.0–12.3)	1.3 (0–3.6)	0.3 (0.2–0.5)	2.0 (0.7–4.4)	16.7 (4.3–46.3)

The observation and experiments carried out during the present series have shown that the amount of food remnants discarded by the snails varies over a very wide range, and depends on the kind of food (the ease with which it can be broken up) and on the snail species. This amount can be very large, sometimes approaching the quantity consumed, and sporadically it may even exceed it, sometimes several- to over a dozen-fold.

4. DISCUSSION

In the previous paper (Kołodziejczyk 1984) the Mikołajskie Lake was used as an example for discussing the species-composition, dominance structure, numbers and biomass of snails in different lake littoral zones which are important, but not the only factors that should be taken into account in an assessment of the role of these animals in the environment. The role of these animals is determined also by their position in the trophical structure of the littoral, and by the ecological activity broadly understood. The problem on which the present study is focussed is the assessment of the role of snails in the production and transformation of detritus in the littoral of a lake. Littoral animals can produce and transform detritus as a result of the different life functions (K o ł o d z i e j c z y k 1980). A particular attention has been paid to feeding, excretion of faeces and food destruction during feeding. The species chosen for the experiments were species occurring in the littoral in large numbers and differing in body-size, way of foraging and dwelling place.

Assimilation efficiency measurements have shown that almost half, and sometimes as much as 80% of the organic matter ingested with food by the snails is returned in the form of faeces to the environment (Table V). The calculated assimilation efficiency values do not differ from those that are most often reported in the literature.For different freshwater, marine and terrestrial snail species feeding on living and dead plants and periphyton, the efficiency of assimilation, most often calculated as a percentage of the energy taken up with food, ranges from 43.0 to 87.5% (M a s o n 1970, P a i n e 1971, G r a h a m e 1973, V i v e k a n a n d a n et al. 1974, R i c h a r d s o n 1975, S t r e i t 1975, K a m l e r and M a n d e c k i 1978, K a l i n o w s k a – in press), the values given by most authors approaching 70%. In two snail species C a l o w (1975) has found a very wide variation in assimilation efficiency, between 9.0 and 76.0%, depending on the kind of food. The low efficiency of assimilation of some kinds of food, including living *Elodea canadensis* (Table V) may be the result of a low assimilability of lignin and cellulose by snails (C a l o w 1975), and by most invertebrates (H a r g r a v e 1970, B e r r i e 1976). Decomposing macrophyte tissues which are a food item preferred by most snails (Tables I, II, III) were at the same time better assimilated (Table V); C a l o w (1975) also observed a better assimilation by snails of food items preferred by them. A high efficiency of detritus assimilation may be due to the presence on it of bacteria that are assimilated very well by invertebrates, sometimes with an efficiency exceeding 90% (H a r g r a v e 1970, 1972, C a l o w and F l e t c h e r 1972, C a l o w 1975, B e r r i e 1976, H a r r i s o n 1977 and others). An extremely high efficiency of food assimilation, amounting to 94% of food dry weight and 98.5% of the organic matter ingested with it, has been reported for herbivorous snails by P a v l j u t i n (1970).

The amount of faeces produced by snails in a lake littoral can be considerable. An example assessment made for the Mikołajskie Lake showed that the snails found in it excreted an average of 2.92 g of dry fecal detritus weight per 24 hours per 1 m^2 of littoral with submerged vegetation (Table X), and during the summer (190 days) in the whole lake – about 88 tons, therein about 18 tons of organic matter. Also compared was the production of faeces by different animals (birds, fishes, *Dreissena polymorpha*, larvae of Lepidoptera, snails) per 1 m^2 of the surface area of the Mikołajskie Lake (Table XII). It has been found that among the above-enumerated animals *D. polymorpha* produces the largest amounts of fecal detritus, but it must be remembered that its numbers in this water body varied considerably from year to year. Moreover, the quantity given for the bivalves is the total of faeces and pseudofaeces, and the latter are, on account of the way they arise, rather similar to food remnants discarded by other animals during their foraging. The roach, the rudd, the coot and the fen-duck produce about twenty times less faeces per 1 m^2 of the lake surface area than do snails (Table XII). Lepidopteran larvae produce still less faeces in spite of the fact that, like most phytophagous insects, they eat very large quantities, as calculated per an individual, of food (Głowacka 1976). When comparing the quantities excreted of organic matter, nitrogen and total phosphorus, it has been found that in this respect, too, the role of snails is particularly important. These quantities are significant and indicate an important role of these animals in the cycling of matter in a lake. The production of faeces by waterfowl also has been assessed for different lakes, therein the Masurian lakes, by Dobrowolski (1973a, 1973b), Dobrowolski, Halba and Nowicki (1976) and Ramos (1980); these authors also have emphasized their importance to the cycling of matter in water bodies.

Table XII. Annual production of faeces by different animal groups in Mikołajskie Lake (calculated from data of different authors)
— no data

Organisms examined	Author	Faeces per 1 m^2 of lake surface area per year			
		dry weight	organic matter	total N	total P
		g	mg		
Dreissena polymorpha	Stańczykowska (1977)	49.78*	–	–	–
Gastropoda	the author's own data	19.12	3820	421	38
Fulica atra L. and *Anas platyrhynchos*	Halba (1975)	1.02	–	10	3
Rutilus rutilus L. and *Scardinius erythrophthalmus* L.	Prejs (1984)	0.96	550	27	2
Acentropus niveus Oliv., *Nymphula nympheata* L. and *Paraponyx stratiotata* L.	Głowacka (1976)	0.17	120	–	–

*A value varying from year to year in connection with wide variations in numbers of *D. polymorpha* in the Mikołajskie Lake (Stańczykowska 1961, 1977, 1978).

It has been found that the content of organic matter in snail faeces is low (usually 15 – 25%), mainly because of a high content of sand, and, probably, calcareous incrustations eaten with the periphyton, and due to a higher efficiency of the assimilation or organic matter relative to the mineral components of the food.

Purchon (1968), Zawieja (1979) and Kołodziejczyk and Martynuska (1980) also indicated considerable amounts of sand in the faeces. A low percentage of organic matter in the faeces of the snail *Tegula funebralis* (Adams) has been found by Paine (1971), whereas for the faeces of *Bithynia tentaculata* Pavljutin (1979) gave much higher values, up to 85.3%. The content of organic matter in faeces seems to be very different from season to season and depend primarily on the kind of food, and also, as noted by Kołodziejczyk and Martynuska (1980), on the dwelling place of the snails (sandy bottom or plants).

Undigested foor remnants found in the faeces are broken up to a great extent (Table IX), relative to the size of the food item given. This may considerably accelerate the decomposition process, as compared with the rate of decomposition of food that has not been crumbled, and facilitate the use of these remnants as food by other microphagous animals. The size of food particles not digested by snails is about 4 times smaller than the food particles found in the faeces of the roach and the rudd (Prejs 1976). Other authors (Soszka 1975, Głowacka 1976) also have indicated a considerable degree of crushing of food remnants in the faeces, or in the contents of the alimentary tract of various invertebrates.

As most of the snails in a lake littoral concentrate on substrates at small distances from the bottom (submerged and emergent vegetation), and faeces fall at a high rate, as has been seen during the present study, and in earlier studies (Kołodziejczyk and Martynuska 1980), they can get into the sediments within several minutes. This means that although the faeces decomposition rate is very high (Kołodziejczyk and Martynuska 1980), they do not decompose in the lake water bulk, so they enter the bottom sediments in their entirety. There they can be used as food by some representatives of the invertebrate macrofauna and as a substrate for the development of microorganisms. It has been found that a number of representatives of the freshwater invertebrate macrofauna can directly utilize the faeces of other animals as food (Ladle 1972, Lammens and van der Velde 1978).

Both the data on the occurrence of snails (Kołodziejczyk 1984) and the results from experiments on the food preference and value of consumption of different kinds of food, as well as on the quantities excreted by snails when fed with different kinds of food indicate that under natural conditions the main food item of most of the species under study is detritus consisting of decaying plants, and of periphyton. Most of the investigators who analyse the feeding of various snail species have pointed out that their basic food is periphyton (Smirnov 1958, 1959, Stańczykowska 1959, Kaškin 1961, Pieczyńska 1970, Calow 1973a, 1973b, Soszka 1975, Streit 1975, Knecht and Walter 1977, Higashi et al. 1981) and dead, decomposing vegetation (Cichon-Lukanina 1958, Kaškin 1961, Calow 1973a, 1974, Soszka 1975, Kołodziejczyk and Martynuska 1980, Bijok 1981), mud (Heywood and Edwards 1962, Fenchel 1975a, 1975b), and in the case of Prosobranchia – also seston (Cichon-Lukanina 1961, Cichon-

Lukanina and Sorokin 1965). Calow's (1974, 1975) studies have shown that when eating detritus, snails utilized mainly the bacterial fraction of the food. Snails were sometimes seen eating dead animals (Suškina 1949, after Frömming). Living tissues of macrophytes have rarely been mentioned as a food item of some species (Suškina 1949, Frömming 1953, Cichon-Lukanina 1958, Gaevskaja 1966, Vivekanandan et al. 1974, Lammens and van der Velde 1978); some of the authors quoted found, however, that there was a higher rate of consumption of dead than of living macrophytes. Lammens and van der Velde (1978) emphasize that there is a clear phytophagy in adult *Lymnaea stagnalis*, and to a lesser extent also in *Galba palustris* (Müller) and *Radix peregra* (Drap.), despite the opinions held by other investigators.

Contradictory opinions of different authors on the food preference of some snail species have been summarized by Stańczykowska (1959), Gaevskaja (1966) and Kołodziejczyk and Martynuska (1980). It has sometimes been stressed that representatives of many gastropod species are omnivorous (Suškina 1949, Wiktor 1958, Gaevskaja 1966), but the problem requires further investigations to be carried out. It may be assumed that what snails mainly do is transform one form of detritus (dead macrophytes, detritus contained in the bottom sediments and in periphyton) into another form which is further utilized and decomposed. Under natural conditions detritus production from living plants by snails takes place mainly when they feed on the plant fraction of the periphyton, and to a lesser extent when some species eat living macrophytes.

According to Hargrave (1970), the quantity consumed, and according to Frömming (1956), the food preference, too, depend to a large extent on the mechanical structure of the food, although other authors (literature survey – Kołodziejczyk 1980) also indicate different factors affecting it (presence of bacteria and the protein content in the food). Eating of larger amounts of food items that are easier to assimilate was observed in snails, e.g., by Cichon-Lukanina (1958), Gaevskaja (1966) and Kołodziejczyk and Martynuska (1980). On the other hand, Calow (1975) pointed to an increased consumption of inadequate food in order to obtain the required amount of nutrients, whereas according to Vivekanandan et al. (1974), the efficiency of assimilation decreases as the consumption increases. These relationships are very complex. For instance, Dudgeon (1982) who studied the rate of consumption for the freshwater snail *Brotia hainanensis* (Brot) found that the snail ate a larger amount of the preferred food if it was fed with two food items simultaneously. However, when fed with either of them separately, it ate the same amount of each. The data from the author's experiments show that food items, the assimilation of which is poor, are eaten by snails in small amounts. The value of consumption, expressed as a percentage of the dry weight of tissues for *Lymnaea* (*Lymnaea*) *stagnalis* and *Planorbarius corneus*, estimated in the experiment described at 0.60–5.85% is similar to that given in the literature for adult individuals of different snail species – from 0.58 to 5.19%

(M a s o n 1970, G r a h a m e 1973, R i c h a r d s o n 1975, K a l i n o w s k a — in press).

During their feeding snails input to the environment, apart from their faeces, considerable amounts of detritus in the form of food remnants crushed and discarded. The quantity of the detritus thus produced is very variable (Table XI), and seems to depend mainly on the mechanical availability of the food. Similar conclusions have been put forward by B i j o k (1981) who studied the feeding of *Lymnaea stagnalis* on living and dead macrophytes of different species. When estimating the reduction of periphyton by *Radix ovata* Drap. which feeds on it, P i e c z y ń s k a (1970) found that the degree of destruction depended on the structure of the periphyton. Under natural conditions snails have the possibility of choosing food items, the mechanical structure of which is most suitable to them (decomposing macrophytes, periphyton). With many kinds of food present in a habitat the amount of food remnants discarded unconsumed may probably come up to about 100% of the quantity consumed or more. The role of food remnants left during foraging can be very significant to the cycling of matter, because the latter process is accelerated by the breaking up of the food items, and in the case of feeding on living macrophyte tissues — by the direct production of detritus. The importance of these remnants as a source of food for some invertebrates (microphages) has been pointed out by B e r r i e (1976). Destruction and discarding of uneaten food by various groups of freshwater animals have been described, e.g., by D i c k m a n (1968), O p u s z y ń s k i (1972), B e r r i e (1976), P r e j s (1976) and H a r r i s o n (1977), but no numerical data have been given. The relatively numerous assessments of the destruction of periphyton and macrophytes by snails (C a s t e n h o l z 1961, L a m m e n s and v a n d e r V e l d e 1978, U n d e r w o o d 1980, H i g a s h i et al. 1981, U n d e r w o o d and J e r n a k o f f 1981) estimated the total amount of food reduced as a result of consumption, destruction and discarding.

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5. SUMMARY

Selected elements were studied of the activity of various freshwater snail species, related to the role of these animals in the production and transformation of the detritus. For the experiments those taxa were chosen which abundantly inhabited various littoral habitats, the ecology of which varied. Most of the snail taxa under study have been found to prefer plant detritus and periphyton as their food (Tables I, II and III). *Lymnaea* (*Lymnaea*) *stagnalis* was the only species that readily ate living plants with delicate tissues (Table II). A comparison of the quantities consumed during 24 hours of preferred and avoided food items given separately has demonstrated that the former were eaten in much larger amounts (Table IV). The organic matter contained in them also was better assimilated (Table V). About 30—80%, depending on the kind of

food, of the organic matter ingested with food is returned to the environment in the form of fecal detritus. Calculated per 1 individual, the circadian production of faeces by the particular species is very different (Table VI), ranging on an average from 0.5 mg dry wt. in *Theodoxus fluviatilis* to 40.8 mg in *Planorbarius corneus*. If calculated per 1 g dry weight of an animal, the respective values appear to be closer, amounting on an average to about 30 – 65 mg for most of the taxa analysed (Table VI). For snails of the same species the amount of faeces excreted clearly depends on the kind of food (Table VII), but little on the body-size of an animal, over a fairly wide range of this parameter (Table VIII). In *T. fluviatilis* a lack of correlation has been found, over a fairly wide range of temperature values, between it and the number of fecal pellets excreted. In all experiments a great variation in the amount of faeces excreted was observed among individuals of the same species, as well as in the same individuals between successive days. It has been found that snails also excreted small amounts of faeces underneath the ice cover in winter.

Snail faeces usually contained a small amount of organic matter (15 – 25%), this being connected with the taking up and expelling of considerable amounts of sand with faeces. In the alimentary tract of the snails food is subject to a strong crushing (Table IX), due to which further decomposition of the food remnants expelled with faeces can be accelerated.

On the basis of data on the production of faeces by different snail taxa (Table VI) and information on the numbers and dominance structure of snails in different littoral environments in the Mikołajskie Lake (Kołodziejczyk 1984) the quantity of faeces produced by these animals has been estimated (Table X). Snails inhabiting submerged macrophytes excrete as much as 90% of the total amount of 88 tons of dry weight of snail fecal detritus input to this lake in summer. Snails living on emergent macrophytes produce as little as 2% of the total snail faeces. Very small amounts of faeces are excreted by stony-bottom-dwelling snails. This results from the fact that this environment represents a small part of the surface area of the Mikołajskie Lake, and that the dominant species in this lake is *Theodoxus fluviatilis* which excretes the smallest amount of faeces among the snail taxa studied (Table VI).

The production of faeces by snails was compared with the respective literature data on several other animal groups in the Mikołajskie Lake (Table XII). Snails appeared to be one of the more important groups of fecal detritus producers in this lake.

Apart from this, it has been found that food remnants damaged and discarded by snails during foraging also can provide a significant source of detritus. Many experiments have shown that their quantity which varies considerably depends primarily on the mechanical availability of the food, and that it is sometimes close to, and sporadically even exceeds the quantity consumed.

6. POLISH SUMMARY

Badano wybrane elementy aktywności różnych gatunków ślimaków słodkowodnych, związane z rolą tych zwierząt w procesach produkcji i przekształcania detrytusu. Do doświadczeń wybierano taksony licznie zasiedlające różnorodne środowiska litoralne i charakteryzujące się odmienną ekologią. Stwierdzono, że większość spośród badanych taksonów ślimaków preferowała jako pokarm detrytus roślinny i peryfiton (tab. I – III). Jedynie *Lymnaea* (*Lymnaea*) *stagnalis* zjadała chętnie żywe rośliny o delikatnych tkankach (tab. II). Porównując wielkość dobowej konsumpcji dla podanych oddzielnie pokarmów preferowanych i unikanych stwierdzono, że te pierwsze były zjadane w znacznie większych ilościach (tab. IV). Lepiej była też przyswajana zawarta w nich materia organiczna (tab. V). Zależnie od rodzaju pokarmu, ok. 30 – 80% pobranej w pokarmie materii organicznej powraca do środowiska w postaci detrytusu fekaliowego. Dobowa produkcja fekalii jest, w przeliczeniu na 1 osobnika, bardzo różna u poszczególnych gatunków (tab. VI), wynosząc średnio od 0,5 mg s. m. u *Theodoxus fluviatilis* do 40,8 mg u *Planorbarius corneus*. Bardziej zbliżona jest ona natomiast w przeliczeniu na 1 g suchej masy zwierzęcia, wynosząc średnio dla większości spośród analizowanych taksonów ok. 30 – 65 mg (tab. VI). Ilość wydalanych fekalii jest, dla ślimaków tego samego gatunku, wyraźnie zależna od rodzaju pokarmu (tab. VII), natomiast mało zależna od wielkości zwierzęcia w dosyć dużym jej przedziale (tab. VIII). Na przykładzie *T. fluviatilis* stwierdzono też, że brak jest, w dosyć dużym zakresie temperatur, zależności pomiędzy nią a liczbą wydalanych porcji fekalii. We wszystkich doświadczeniach obserwowano natomiast bardzo dużą zmienność ilości wydalanych fekalii zarówno pomiędzy poszczególnymi osobnikami tego samego gatunku, jak i u tych samych osobników w kolejnych dniach. Stwierdzono, że niewielkie ilości fekalii wydalane są przez ślimaki również w okresie zimowym – pod lodem.

Fekalia ślimaków zawierały na ogół niewielką ilość materii organicznej (15–25%), co jest związane z pobieraniem i wydalaniem w fekaliach znacznych ilości piasku. Pokarm ulega w przewodzie pokarmowym ślimaków bardzo silnemu rozdrobnieniu (tab. IX), co może, po wydaleniu jego resztek w fekaliach, znacznie przyspieszyć dalszy ich rozkład.

Na podstawie danych o produkcji fekalii przez różne taksony ślimaków (tab. VI), oraz danych o ich liczebności i strukturze dominacji w różnych środowiskach litoralu Jeziora Mikołajskiego (K o ł o d z i e j c z y k 1984) oszacowano wielkość produkcji fekalii przez te zwierzęta (tab. X). Z całej ilości 88 t suchej masy detrytusu fekaliowego, dostarczanego w okresie letnim do tego jeziora, aż 90% wydalają ślimaki zasiedlające makrofity zanurzone. Tylko 2% łącznej ilości fekalii produkują ślimaki zasiedlające makrofity wynurzone. Bardzo mało fekalii wydalają ślimaki zasiedlające dno kamieniste, co wynika zarówno z niewielkiej powierzchni, jaką to środowisko zajmuje w Jeziorze Mikołajskim, jak i z dominacji tam *Theodoxus fluviatilis*, wydalającego najmniej fekalii spośród badanych taksonów ślimaków (tab. VI).

Porównano produkcję fekalii przez ślimaki z podanymi w piśmiennictwie analogicznymi danymi dla kilku innych grup zwierząt w Jeziorze Mikołajskim (tab. XII). Ślimaki okazały się jedną z ważniejszych grup producentów detrytusu fekaliowego w tym jeziorze.

Stwierdzono, że istotnym źródłem detrytusu mogą być również szczątki pokarmu, uszkodzone i odrzucone przez ślimaki podczas żerowania. W wielu doświadczeniach wykazano, że ilość ich jest bardzo zmienna, zależna głównie od mechanicznej dostępności pokarmu, niekiedy zbliżona, a sporadycznie nawet znacznie przewyższająca wielkość konsumpcji.

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