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EXPERIMENTAL AND FIELD STUDIES ON ECOLOGICAL ENERGETICS OF *ASELLUS AQUATICUS* L. (*ISOPODA*)

I. ASSIMILABILITY OF LIPIDS, PROTEINS AND CARBOHYDRATES*

ABSTRACT: Analysis was made of food and faeces composition of *Asellus aquaticus* L. distinguishing ash, lipids, proteins, carbohydrates and lignin contents. Calculated percentages were applied to absolute values of consumption and defecation rates assessed earlier (P r u s 1971) for various groups of these animals. Absolute values of components of assimilated food obtained by difference ($C - F = A$) were then expressed as per cent of dry weight or ash-free dry weight. Efficiencies with which nutritional components of food were assimilated by various groups of these animals are also given.

Contents

1. INTRODUCTION

In ecological bioenergetics, majority of data are finally converted to common units of the heat energy. Such approach is by all means right one especially in studies of trophic levels or more complex ecological units such as biocenoses or ecosystems. However, when studying simpler ecological units such as species or population, a great deal of information on its

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physiology is lost when the approach is purely energetic. Such data are most valuable since they fall between two disciplines, namely bioenergetics and physiology. They can be used both for interpreting the obtained picture of energy flow through a species or population and for broadening our knowledge on physiology of such processes as feeding, digestion, respiration and excretion of animals.

The present paper pertains to digestion and assimilability of food by *Asellus aquaticus* L. It aims at defining assimilability of main nutritional components such as lipids, proteins and carbohydrates of plant material by animals kept as singles or in groups; females (ovigerous and non-ovigerous) and males studied in summer and in winter[1] at a temperature of 10°C. Assimilability of these components by an average individual being a representative of a natural population inhabiting the New Hinksey Stream (the River Thames influent) in spring 1970 was also estimated.

2. MATERIAL AND METHODS

Material for chemical analyses of main components of food and faeces was collected near Oxford from January to June 1970 when the author was carrying out experiments on assimilation efficiency by *A. aquaticus* in Animal Ecology Research Group, University of Oxford, Oxford, Great Britain. The animals brought from the New Hinksey Stream to the laboratory were acclimated to 10°C and fed with leaves of alder, *Alnus glutinosa* (L.) Gaertn. for at least a fortnight. Then the material was sexed and divided into two size classes. These groups corresponded in weight to the animals which were used in the assimilation efficiency experiments (P r u s 1971) aiming at learning about the density effect (large individuals) and that of sex and reproductive state (individuals of average size) on percentage assimilation.

Thus the following groups of animals were distinguished: large males, large females, individuals of average size and large individuals (about 100 specimens in each), and introduced into 4 beakers each holding 200 ml of the stream water. The animals were fed with alder leaves stored in autumn and kept in water at a room temperature for several months. About ten half-leaves were given to the animals in each container, the other half-leaves being dried in oven at a temperature of 100°C and used later for chemical analyses of food. After 48 hrs food remains were removed from the containers and discarded. The faeces were collected by means of a pipette, rinsed in distilled water (for reasons – see P r u s 1971), dried at 60°C, and used for chemical analyses of faeces. The chemical determinations of contents of ash, lipids, proteins, carbohydrates and lignin in food and faeces were carried out later, in the Department of Energetics and Biological Production of Nencki Institute of Experimental Biology, Warsaw, Poland.

Ash was determined by ignition in a muffle furnace at 550°C. Total lipids were determined after S t e r n and S h a p i r o (1953). The apparent fatty acid equivalent weight as high as 780 was obtained by calibrating the method with a preparation of leaf lipids isolated by solvent extraction (for references see D o w g i a ł ł o 1975). Crude protein was estimated from Kjeldahl nitrogen multiplied by a factor of 6.25.

The determinations of carbohydrates were carried out according to methods by H i n d e r m a n and B i e r l i n g (1968), the level of lignin being obtained by direct weighing the residue after hydrolysis with the mixture of Halse (H_2SO_4 + HCl) or as the difference after subtracting the sum of ash, crude protein, carbohydrates and lipids.

[1] In winter group experiments and in summer single experiments were carried out.

In one sample of food and two samples of faeces carbohydrates were analysed in more detail by determining contents of hexose and pentose. Content of lignin in food was assessed gravimetrically and compared with that obtained by subtraction. Each analysis of a sample has two replicates and a mean value was calculated.

Paralelly, material of food and faeces was burned in Phillipson bomb microcalorimeter in order to compare the calorific content assessed directly by ignition with that obtained by summation of calorific equivalents of each component determined by chemical analysis.

3. RESULTS

From the complete chemical analysis it results that the dry matter of decaying alder leaves contains 4.5% of ash, 14.3% – lipids, 21% – crude protein, and 61.7% – carbohydrates (lignin included). Carbohydrates of hexose and pentose type expressed as glucan and xylan amount to 11.1% and 8.8%, respectively, 19.9% in total, the remaining 41.8% is lignin (Table I). The dry matter of *A. aquaticus* faeces consists of 11.6% of ash, 14.7% – lipids, 20.2% – protein and 53% – carbohydrates (lignin included) with lower carbohydrates constituting 8.6% and lignin the remaining 44.4% (Table I).

Table I. Complete analysis of nutritional components of food (*Alnus glutinosa* decaying leaves) and faeces of *Asellus aquaticus* in per cent of dry matter

Components	Food		Faeces	
Ash		4.5		11.6
Lipids		14.3		14.7
Proteins		21.0		20.2
Carbohydrates		19.9		8.6
heksosan	11.1		5.3	
pentosan	8.8		3.3	
Lignin		41.8		44.4
		61.7		53.0
Total		101.5		99.5

When comparing main components of faeces with those of food it becomes evident that the percentage of ash in faeces doubles and the incidence of lower carbohydrates decreases more than by half. This would suggest a very intense assimilation of lower carbohydrates by this species.

The complete analysis of composition of food and faeces verifies to a certain degree the adequacy of the methods applied; the recovery is 101.5% and 99.5% of dry weight of the materials (food and faeces, respectively) which points to a high accuracy of these methods. Therefore, by accepting the content of lower carbohydrates to be 19.9% and 8.6% in food and faeces, respectively, for the whole material, it was possible to calculate the content of lignin as a complement to 100% (Table II).

Despite of the fact that the chemical analyses were carried out on the analogous material as that used in the assimilation efficiency experiments (P r u s 1971), considerable differences were found in the per cent of ash. Determinations of ash content carried out in Oxford always yielded higher values (both in food and faeces) than those obtained at chemical analyses carried out in Warsaw. This difference is considerable, especially when comparing the winter experiments. It has a seasonal character and is connected with a variable balance of minerals in this species (P r u s 1971).

When recalculating the budgets based on dry weight units (P r u s 1971) into budgets of nutritional components (Table III) real values of ash content found in the assimilation efficiency experiments were accepted both for food and faeces, since they were integrally connected with these budgets. Nolens volens the percentage contents of lignin as compared with the complete chemical analyses of food and faeces (Table II) must have been adequately fitted to form 100% (Table III).

Table II. Percentage incidence of nutritional components in food and faeces of *Asellus aquaticus*

Nutritional components		Sex or size					
		large males	large females	mean	average males and females	large males and females	mean
Ash	food	4.5	4.9	4.7	5.9	6.1	6.0
	faeces	12.7	11.2	11.9	12.2	10.5	11.3
Lipids	food	19.3	18.5	18.9	19.0	16.6	17.8
	faeces	15.0	15.9	15.4	13.6	14.3	13.9
Proteins	food	21.0	21.8	21.4	19.2	20.6	19.9
	faeces	19.3	21.3	20.3	20.2	20.1	20.2
Carbohydrates*	food	19.9	19.9	19.9	19.9	19.9	19.9
Lignin**		35.3	34.9	35.1	36.0	36.8	36.4
		55.2	54.8	55.0	55.9	56.7	56.3
Carbohydrates*	faeces	8.6	8.6	8.6	8.6	8.6	8.6
Lignin**		44.4	43.0	43.8	45.4	46.5	46.0

*Accepted from Table I; **complemented to 100%.

Results of chemical analyses of food and faeces produced from it by males and females of different size of *A. aquaticus* are given in Table II. The differences in composition of food replicates result solely from randomness of the material and accuracy of the methods applied. However, the plausible differences in the composition of faeces, besides the above mentioned sources of variation, can depict differentiated assimilability of nutritional components in males and females of different size. Nevertheless the differences in chemical composition of both food and faeces are small and seem to be negligible.

It would be possible to say a little more about the quality of the assimilated food, when the difference between the quantity of food consumed and that of faeces produced (the data

derived from paper by P r u s 1971, Tables 1, 3, 6, 8 and 10) is analysed both quantitatively and qualitatively by taking into account the data of Table II. Such compilation is given in Table III.

Basing on the known percentages of nutritional components of the daily consumption rates (C) of an individual, assessed in mg dry weight (data marked with single asterisks in Table III), were expressed as weights of nutritional components. The same holds for defecation rates (F). The difference between consumed amount of each food component and its remains in faeces was considered as the assimilated amount of this component (A). Thus obtained absolute values of components of assimilated food were again related as per cent of total amount of assimilated food (dry wt, ash free dry wt) resulting in chemical composition of the assimilated food – the information which is inaccessible neither by chemical analysis nor in the other way.

The composition of the assimilated food was calculated for 5 series of experiments carried out on large animals kept in single cultures (*1*) and in groups (*2*) as well as for average-sized animals cultured individually: non-ovigerous females (*3*), ovigerous females (*4*) and males (*5*). By taking into account the proportions between three latter groups of animals (*3–5*) which were found in a natural population of *A. aquaticus* inhabiting the New Hinksey Stream in spring 1970, the composition of the food assimilated by an average representative of this population was calculated. In other words, data (*6*) are a weighed mean of data *3* to *5*.

Besides the percentage composition of the assimilated food the data in Table III allow to calculate the assimilation efficiency for each component (last column in this Table) and compare it with general assimilation efficiency calculated from calorific equivalent of food and faces (marked with doubled asterisks). The compostion of food assimilated by individuals of an average size in spring-to-summer period is rather similar for both sexes and almost identical for ovigerous and non-ovigerous females. Assimilated food consists of 6.5% of ash, 27.3–31.8% of lipids, 16.8–17.7% of crude protein, 37.3–46.6% of carbohydrates and from −2.1 to +11.2% of lignin. The composition of assimilated food calculated for a hypothetical individual of the New Hinksey Stream population (Table III, *6*) pertains to a population in which 34.9% of individuals were non-ovigerous females, 44.4% – ovigerous females, and 20.7% – males (P r u s 1971). Naturally, it can be calculated for any population of this species in an arbitrary way, according to the structure of population. The composition of assimilated food by such arbitrary individual is as follows: 6.3% – ash, 28.7% – lipids, 17.4% – crude protein, 40.2% – carbohydrates of hexose and pentose type and 7.4% – lignin.

The composition of food assimilated by large individuals cultured, both individually and in groups in winter renders interpretational difficulties because of "dissimilation" of minerals, i.e., discarding more ash in faeces that has been taken in food. Negative values of assimilation of minerals (ash) are compensated by the artificially augmented percentage of assimilated lignin. The interpretation becomes more plausible, if percentage composition of ash-free dry weight of the assimilated food is considered (Table III, *1–2*). The percentage composition of organic matter of the food assimilated by large individuals in winter does not differ much from analogous values obtained for individuals of the average size studied in summer (Table III, *3–5*).

Besides chemical composition of the assimilated food the data presented in Table III permitted calculation of assimilation efficiencies ($\frac{A}{C} \times 100$) for various food components, i.e., to estimate what per cents of ash, lipids, crude proteins and carbohydrates that were present in the food became assimilated by different groups of these animals. Efficiencies of assimilation by individuals of the average size range 18.4–22.2% for ash, 49.8–56.6% for lipids, 26.1–36.3%

Table III. Budget of nutritional components, percentage composition of assimilated food and percentage assimilation of these components in various groups of *Asellus aquaticus*
Rate = mg dry wt/ind. per 24 hours

No.	Density	Sex and reproductive state	Mean wet weight of one individual mg	Nutritional components	Consumption *C*		Defecation *F*		Assimilation *A*			Assimilation efficiency
					per cent	rate	per cent	rate	rate	per cent of dry wt	per cent of ash free dry wt	
1	single cultures	mostly males	32.14	ash	13.9	0.0325	29.2	0.0531	–0.0206	–39.5	–	–63.4
				lipids	18.9	0.0443	15.4	0.0281	0.0162	31.2	22.3	36.9
				proteins	21.4	0.0501	20.3	0.0369	0.0132	25.3	18.1	26.3
				carbohydrates	19.9	0.0466	8.6	0.0156	0.0310	59.4	42.6	66.5
				lignin	25.9	0.0606	26.5	0.0482	0.0124	23.7	17.0	20.5
				total	100.0	0.2341*	100.0	0.1819*	0.0522*	100.0		26.3**
2	group cultures of 10	mostly males	28.39	ash	13.5	0.0342	21.5	0.0355	–0.0013	–1.5	–	–4.1
				lipids	18.9	0.0478	15.4	0.0254	0.0224	25.5	25.1	51.0
				proteins	21.4	0.0541	20.3	0.0335	0.0206	23.4	23.1	38.1
				carbohydrates	19.9	0.0503	8.6	0.0142	0.0361	41.1	40.6	71.8
				lignin	26.3	0.0666	34.2	0.0565	0.0100	11.4	11.2	15.3
				total	100.0	0.2530*	100.0	0.1651*	0.0878*	100.0		34.9**
3	single cultures	non-ovigerous females	8.66	ash	11.9	0.0698	14.9	0.0543	0.0155	7.0	–	22.2
				lipids	19.0	0.1115	13.6	0.0496	0.0619	27.8	29.9	55.5
				proteins	19.2	0.1127	20.2	0.0736	0.0391	17.6	18.9	34.7
				carbohydrates	19.9	0.1168	8.6	0.0313	0.0855	38.4	41.3	73.2
				lignin	30.0	0.1761	42.7	0.1556	0.0205	9.2	9.9	11.6
				total	100.0	0.5869*	100.0	0.3644*	0.2225*	100.0		40.8**

4	single cultures	ovigerous females	12.00	ash	13.0	0.0497	17.2	0.0398	0.0099	6.5	–	19.8
				lipids	19.0	0.0725	13.6	0.0315	0.0410	27.3	29.2	56.6
				proteins	19.2	0.0733	20.2	0.0467	0.0266	17.7	18.9	36.3
				carbohydrates	19.9	0.0760	8.6	0.0199	0.0561	37.3	39.9	73.8
				lignin	28.9	0.1102	40.4	0.0934	0.0168	11.2	12.0	15.3
				total	100.0	0.3817*	100.0	0.2313*	0.1504*	100.0		43.6**
5	single cultures	males	11.82	ash	11.2	0.0944	13.0	0.0770	0.0174	6.9	–	18.4
				lipids	19.0	0.1602	13.6	0.0805	0.0797	31.8	34.1	49.8
				proteins	19.2	0.1618	20.2	0.1196	0.0422	16.8	18.1	26.1
				carbohydrates	19.9	0.1678	8.6	0.0509	0.1169	46.6	50.0	69.7
				lignin	30.7	0.2588	44.6	0.2640	–0.0052	–2.1	–2.2	–2.0
				total	100.0	0.8430*	100.0	0.5920*	0.2510*	100.0		33.2**
6	the New Hinksey Stream population	hypothetical individual	10.80	ash	12.2	0.0669	15.5	0.0546	0.0123	6.3	–	18.4
				lipids	19.0	0.1043	13.6	0.0479	0.0564	28.7	30.6	54.1
				proteins	19.2	0.1053	20.2	0.0712	0.0341	17.4	18.5	32.4
				carbohydrates	19.9	0.1093	8.6	0.0303	0.0790	40.2	42.9	72.3
				lignin	29.7	0.1630	42.1	0.1484	0.0146	7.4	8.0	9.0
				total	100.0	0.5488*	100.0	0.3524*	0.1964*	100.0		40.2*

*Data from paper by P r u s (1971); **based on calorific equivalents of food and faeces (P r u s 1971).

for crude protein, 69.7–73.8% for carbohydrates and minus 2.0–15.3% for lignin. All minima were those for males and maxima (except of ash) – for ovigerous females. Efficiencies of assimilation in non-ovigerous females fall between those values.

Both from the differentiated assimilation efficiency assessed earlier (P r u s 1971) as well as from a rather constant chemical composition of assimilated food irrespective to the sex and reproductive state of females (present data) it can be inferred that the differences in assimilation efficiency by *A. aquaticus* do not involve the preference of one component of food to the others. For example, if ovigerous females reveal the highest general assimilation efficiency 43.1% they assimilate proportionally more of each nutritional component, i.e., lipids, proteins, and carbohydrates. Similarly males, which show the lowest general assimilation efficiency (33.2%) assimilate proportionally less of each food component, although somewhat higher percentage of lipids in the assimilated portion of food can suggest that they probably are a compensatory source of energy which is necessary to cover a higher loss of energy resulting from higher activity, as evidenced by augmented metabolism in this sex (P r u s – in press).

The assimilation efficiencies in large individuals for main nutritional components are within the limits characteristic for the individuals of the average size. The great differences in percentage assimilation of nutritional components obtained for single and group cultures (Table III, *1–2*) do not allow to infer about the possible effect of size and or season on the efficiency of assimilation of these compounds.

Table IV. Comparison of calorific values (kcal/g dry wt) of food and faeces of *Asellus aquaticus* obtained by two methods

NS – non-significant at 95% probability level, *S* – significant at 95% probability level, *n* – number of replications, *S.D.* – standard deviation

Statistical parameters	Food				Faeces			
	chemical composition	bomb combustion	probability *P*	significance	chemical composition	bomb combustion	probability *P*	significance
n	4	6			4	6		
Mean	5.1824	5.2618	0.05	*NS*	4.7222	4.9004	0.05	*S*
S.D.	0.0931	0.0345			0.0791	0.1814		

Calorific values of food and faeces calculated from chemical composition of the materials were compared with those assessed by means of bomb microcalorimeter. When expressing organic compounds in the form of heat the following relations were accepted after H a r r o w and M a z u r (1958): 9.45 kcal/g dry wt of lipids, 5.65 kcal/g dry wt of proteins, and 4.10 kcal/g dry wt of carbohydrates and lignin. These values were multiplied by incidences of nutritional components determind for 4 groups of individuals (in Table II) to get calorific values of food and faeces. Thus obtained values were then compared with the corresponding values obtained by combustion in bomb microcalorimeter (P h i l l i p s o n 1964) (Table IV). The calorific values calculated from chemical composition were lower than those obtained by direct combustion. The difference between calorific values of food was insignificant, and that between calorific values of faeces – significant one. Lower calorific value of faeces calculated from chemical composition than that obtained by combustion could result from few replicates as well as from higher variance of this material as compared with the variance of calorific value of the food.

4. DISCUSSION

Relatively high content of proteins (about 20%) was found in the alder leaves which were the food of *A. aquaticus*. Kaushik and Hynes (1968) reported that the content of crude protein in autumn shed leaves of related species, *Alnus rugosa* (Du Roi) Spreng, amounts to 10.1% air dry weight and after 50 days washing out in the running stream water it decreases to 7.9%. However, these authors mentioned that "these values would have been greater if the calculation had been made on the basis of oven-dry weight", which was the case in the present work. The other reason of a high protein content in this particular material can be an extremely rich soil in which the alder tree grew, since the fallen leaves were collected from under the alder tree growing in the Botanical Garden of Oxford. This choice was made after failure to find an adequate amount of alder leaves in the natural habitat around Oxford (C. S. Elton – personal communication). The ground under the tree was covered with a sort of fertilizer. Bearing in mind how humid weather can be in this part of England, especially in autumn, it can be easily supposed that the fallen leaves became enriched in nitrogen when staying on the ground. This idea can be supported by findings of Kaushik and Hynes (1971) who found nitrogen content of *A. rugosa* leaves kept in enriched water (N, P) to increase from 2.12% (in controls) to 2.40 at 10°C and 2.54% at 20–23°C. These authors also mention that the results for alder leaves, unlike those for elm, show considerable variation. Similarly Mathews and Kowalczewski (1969) observed that the content of nitrogen of decaying leaves in a river tends to increase.

The content of lower carbohydrates in alder leaves is also high (about 20%). Although the division of these compounds into lower carbohydrates and lignin does not follow strictly the distinction between structural and non-structural fractions proposed by Smith (1969), considering the lignin as a substance less assimilable made it possible to infer about the degree of assimilability of the remaining carbohydrates. Van Soest and Wine (1967) reported that even animals capable of gastrointestinal fermentation of structural carbohydrates utilize less efficiently food with higher content of structural carbohydrates than that with lower one.

High contents of both crude protein and lipids in food can be of exogeneous (bacterial or fungal) origin. The percentage composition of the food that has been assimilated indicate that the assimilable diet of *A. aquaticus* consists mostly of carbohydrates (40.2%) and lipids (28.7%), and to a lesser degree of proteins (17.4%), lignin (7.4%) and minerals (6.3%). Such composition of the assimilated food seems to be fully justified if one remembers that this animal feeds upon dead or alive organic matter of a plant origin. Gross of the assimilated carbohydrates were sugars of the hexose and pentose type, the assimilated amount of lignin can result either from an error (lignin was calculated as a complement of 100% and the contents of minerals in food and faeces analysed in this paper differed greatly with those found in the assimilation efficiency experiments), or it can also be a fraction of lignin decomposed by microorganisms that is really assimilable by *A. aquaticus*.

Nilsson (1974), basing on the percentage content of protein in food (alder or beech leaves) and faeces of *Gammarus pulex* L., has concluded that this species assimilated proteins less efficiently than carbohydrates. Similar conclusion can be drawn for *A. aquaticus* from the present results. The efficiency with which *A. aquaticus* (the New Hinksey Stream population) assimilates food components is highest for carbohydrates (72.3% of the total carbohydrate content in the food is assimilated) – high for lipids (54.1% of the total lipid content is assimilated) – lower for crude protein (32.4%) and lignin (9%).

By and large, it can be said that besides lower sugars which form a main core of the assimilated food, lipids, because of their high energy content, are also eagerly assimilated. It is interesting to note that the assimilation efficiency varying with sex or reproductive state of females does not depend on a preference to one of the nutritional components, but it affects assimilability of all the components. This may be in support of the idea that the assimilability of food by *Crustacea* depends mainly on the speed with which it passes through the intestinal canal (Watson 1966, White 1968, Hargrave 1970, Nilsson 1974, Klekowski and Duncan 1975 and others).

In order to rank the nutritional components according to their importance in the feeding of *A. aquaticus* one can venture calculation of indices that describe the utilization of food components (they are different from utilization of food sensu, e.g., Nilsson 1974). Such an index could be calculated as a product of the incidence (fraction) of a component in food and the assimilation efficiency (per cent) of this component typical for a given species. Thus utilization of food component (*UFC*) = fraction of this component in food (*FF*) multiplied by percentage assimilation efficiency of this component (*AE*). For shortening: $UFC = FFC \times AE$.

Such indices, calculated for *A.aquaticus* fed with decaying alder leaves, ranked in decreasing sequence, are the following: carbohydrates – 14.3%, lipids – 10.3%, proteins – 6.2%, lignin – 2.7%, ash – 2.2%. They characterize the importance of various components in the feeding of the species, their sum equals to the total assimilation efficiency as calculated on the dry weight basis. When reduced by the index of utilization of minerals (ash) it corresponds to the assimilation efficiency calculated on the ash-free dry weight basis, and in the case of *A. aquaticus* it is lower by about 6.5% from total efficiency assessed from calorific equivalents of food and faeces. To exemplify, an index of 14.3% for carbohydrates says that these compounds which had been assimilated formed 14.3% of dry weight of food consumed. The *UFC*-s are resultants of (1) the incidences of components in food and (2) assimilabilities of these components typical for a given species, thus are a good measure of the role of main organic compounds in nutrition of animals.

When comparing assimilation efficiencies of *A. aquaticus* calculated for different food components with those for all animals reported by Błaxter (1963) one can conclude that they are generally in a close agreement each other. Crude protein, which was assimilated less efficiently, is an exception.

The assimilation efficiencies for nutritional components of food obtained in this paper are close to those reported by Fischer (1972) for a fish, *Ctenopharyngodon idella* Val. fed with plant food in the case of carbohydrates, with animal food in the case of lipids and in the case of crude protein approach the mean value of assimilation efficiency obtained for both types of food.

To sum up, determinations of chemical composition of the assimilated food permitted to evaluate the importance of main nutritional components in the feeding of *A. aquaticus*.

I wish to thank Dr.A. Dowgiałło for his help in chosing adequate methods of chemical analyses as well as for his invaluable suggestions when preparing this paper. Thanks are also due to Mrs. M. Wątkowska who carried out the chemical analyses of the material.

5. SUMMARY

Percentage contents of ash, lipids, proteins, carbohydrates and lignin in dry weight of food (decaying alder leaves) and of faeces of *A. aquaticus* (cylindrical pellets) were assessed by means of chemical analyses

(Table I, II). Taking into account the obtained percentages of main nutritional components the consumption rates obtained earlier (P r u s 1971) for various groups of the animals (differing in sex, size, and reproductive state of females) were expressed in weights of these components (Table III). Calculated by subtraction amounts of nutritional components that had been assimilated ($C - F = A$, Table III) were then changed into per cents, thus resulting in percentage composition of assimilated food which is as follows: ash – 6.3%, lipids – 28.7%, crude protein – 17.4%, carbohydrates – 40.2%, and lignin – 7.4%.

The assimilation efficiencies of nutritional components were also calculated. Out of the components taken with food the following per cents are assimilated: lipids – 54.1%, crude protein – 32.4%, carbohydrates – 72.3% and lignin – 9%. The differences both in percentage composition of the assimilated food and assimilation efficiencies for its components in relation to sex, size and reproductive state of females are also discussed.

Comparison is also given of the calorific values of food and faeces of *A. aquaticus* with those determined in the bomb microcalorimeter. The differences between the pairs of values were insignificant for food, but significant for faeces (Table IV).

Indices of utilization of food components were proposed in order to characterize the importance of main food compounds in nutrition of this species.

6. POLISH SUMMARY (STRESZCZENIE)

Metodą analiz chemicznych wyznaczono procentowe zawartości popiołu, lipidów, białek, węglowodanów i ligniny w suchej masie pokarmu (gnijące liście olchy) i kału. *A. aquaticus* (tab. I, II). Uwzględniając procenty poszczególnych składników, otrzymane wcześniej dobowe wartości konsumpcji dla różnych grup zwierząt (płeć, wielkość, stan rozrodczy samic) tego gatunku (P r u s 1971) przedstawiono w jednostkach wagowych poszczególnych składników (tab. III). Obliczone ze wzoru: $C - F = A$ ilości asymilowanych składników pokarmowych przedstawiono następnie w procentach, otrzymując w ten sposób procentowy skład asymilowanego pokarmu: 6.3% popiołu, 28.7% lipidów, 17.4% białek, 40.2% węglowodanów i 7.4% ligniny (tab. III).

Wyznaczono również przyswajalność poszczególnych składników pokarmowych. Z pobranych w pokarmie składników asymilowane jest: 54.1% lipidów, 32.4% białek, 72.3% węglowodanów i 9% ligniny. Omówiono różnice zarówno w procentowym składzie przyswojonego pokarmu, jak i w wydajności asymilacji poszczególnych składników w zależnosci od płci, wielkości osobników i stanu fizjologicznego samic *A. aquaticus*.

Porównano kaloryczność pokarmu i kału obliczoną na podstawie składu chemicznego z wyznaczoną za pomocą bomby mikrokalorymetrycznej. Różnica w wartości kalorycznej pokarmu jest statystycznie nieistotna, natomiast wartości kalorycznej kału – istotna (tab. IV).

Obliczono wskaźniki wykorzystania pokarmu charakteryzujące udział głównych składników pokarmowych w odżywianiu się *A. aquaticus*.

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