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LAKE MACROPHYTES AS THE FOOD OF ROACH (*RUTILUS RUTILUS* L.) AND RUDD (*SCARDINIUS ERYTHROPHTHALMUS* L.)

II. DAILY INTAKE OF MACROPHYTE FOOD IN RELATION TO BODY SIZE OF FISH*

ABSTRACT: Different methods have been used to estimate the daily intake of submerged macrophytes by roach and rudd in some eutrophic lakes. The daily rations decrease linearly with the increasing size of fish. For the probable version, under natural conditions, it is a decrease from 15.5% for fish of a body length 11 cm to 7.7% fresh body weight for fish of a body length 24 cm.

KEY WORDS: Lake littoral, fish, *Rutilus rutilus*, *Scardinius erythrophthalmus*, macrophytes, daily ingestion, size of fish.

Contents

1. INTRODUCTION

This is the second part of research on the significance of submerged macrophytes as the food of lake fish. The aim has been to estimate the daily ingestion of macrophytes for roach and rudd which belong to the main plant consumers in the littoral. There are no data on the subject apart from the fragmentary material of K a r z i n k i n (1955) and "semi-quantitative" results of K l i m c z y k - J a n i k o w s k a (1975).

2. AREA, MATERIAL AND METHODS

Field work and laboratory experiments were carried at about 20°C.

The material was collected by means of seine net and electric shocker in three lakes of the Masurian Lakeland (northern Poland).

L a k e B e ł d a n y. An eutrophic, holomictic lake of a surface area 940.6 ha, maximum depth 46.0 m and mean depth 10.0 m. The littoral covers 247.2 ha, i.e., 26% of the lake area.

M i k o ł a j s k i e L a k e. An eutrophic, holomictic lake of a surface area 460 ha, maximum depth 27.8 m and mean depth 11.0 m. The littoral covers 87.9 ha, i.e., 19% of the lake area.

L a k e W a r n i a k. An eutrophic lake of natural pond type, of a surface area 38.4 ha, maximum depth 3.7 m and mean depth 1.5 m. The macrophytes cover about 34 ha, i.e., about 89% of the lake area.

The daily rations of macrophytes were obtained using the passage rate method and by means of direct measurements under laboratory conditions.

Field material was the base for studies on daily ration by the passage rate method. Thus the daily ration (D) was calculated according to the modified B a j k o v' s (1935) formula:

$$D = A K$$

where: A — weight of macrophytes in the gut expressed as a per cent of body weight of fish, K — food turnover rate or coefficient for daily renewal of gut content.

Here, the weight of all macrophytes introduced to the gut in time required by the food ration to pass the whole gut length, was determined. Putting it otherwise, value A covered the part of macrophytes in the gut and the part of macrophytes already assimilated.

The fish, guts of which were used to study food turnover rate and the weight of macrophytes, were caught in Mikołajskie Lake and Lake Warniak. The fish were immediately weighed, measured (longitudo corporis) and the guts were preserved in separate containers in 75% ethanol and 40% formalin (ratio 25 : 1). The length and diameter of the majority of guts examined were also measured.

The amount of macrophyte food ingested was calculated in terms of fresh and dry weight. Only guts filled with food in at least 75% of their length were taken into consideration. The weight of macrophyte remains in guts was determined for 22 specimens of roach and 73 specimens of rudd. All roaches used in this analysis were caught in Lake Warniak and the rudds — in Mikołajskie Lake and Lake Bełdany in the possibly shortest time interval. All fish had over 11 cm of body length which allowed to treat them according to the results of P r e j s and J a c k o w s k a (1978) as definite macrophyte feeders.

In order to determine the K value (food turnover rate) the diurnal rhythm of feeding activity was determined. This material consisted of 38 roaches of body length 18.5—21.0 cm weighing 125—190 g, and of 62 rudds of body length 14.5—24 cm weighing 60—340 g.

Under laboratory conditions direct measurements were made of daily ration of macrophytes and the passage time of macrophytes was investigated — one of the indispensable elements for calculations of daily ration by the passage rate method.

The fish used in laboratory experiments were caught in the littoral of the Mikołajskie Lake. The fish were transferred to aquaria filled with lake water of $20 \pm 1°C$. In all experiments the natural diurnal rhythm of light changes was preserved. Altogether there were 38 specimens of rudd of body length 10.2—16.4 cm weighing 21.5—122 g and 4 roaches of body length 12.8—14.5 cm weighing 34—48 g. The fish were fed with *Lemna trisulca* L. or *Elodea canadensis* Rich. in excessive amounts. The plants were attached to frames with nylon net, and placed at the bottom of the aquaria. It can be assumed that in order to ingest plants under these conditions the fish had to make an effort similar to that of pulling off fragments of macrophytes growing in the lake. The frames were also a kind of false bottom. And thus the faeces fell to the bottom of the tank being protected against possible attempts to consume them.

3. RESULTS

3.1. DAILY RATION BASED ON DIRECT MEASUREMENTS UNDER LABORATORY CONDITIONS

Eighteen rudds of body length 11.0—14.6 cm weighing 28—48 g were divided into groups of 2—4 fish. It was done mainly because of the lower feeding activity of single rudds in aquaria which was observed in some preliminary experiments.

The fish having at disposal *Elodea canadensis* fed irregularly, usually consuming a small amount at a time. *Lemna trisulca* was, as a rule, ingested in 24 hours independently of the light conditions. The fish fed with great eagerness and regularity — usually with short intervals between successive meals. The food rations when feeding on *Elodea canadensis* (dominant species in the food of rudd in Mikołajskie Lake — P r e j s and J a c k o w s k a 1978) were very low: 0.2—4% (Table I). Such results were recorded independently of the order in which the food was given, e.g., group III was given first *Elodea canadensis* and then *Lemna trisulca*, whereas group IV the other way round. Daily rations when feeding the fish with *Lemna trisulca*, rather of little significance in the natural food (P r e j s and J a c k o w s k a 1978), were much higher: 8—18% of body weight.

It is difficult to find out the reason for such a change in the food habits of fish in aquaria in relation to natural conditions. Undoubtedly this may be connected with the changes in the availability of given food. It may be assumed that the small significance of Lemnaceae in the fish food in Mikołajskie Lake is because they occur usually in places not easily accessible for the fish. Nevertheless, *Lemna trisulca* being fully available in the aquarium for the fish was eagerly consumed. On the other hand, the strikingly poor ingestion of *Elodea canadensis* (one of the most available species in the lake) could be due to its distribution in the aquarium very little resembling the natural conditions.

Table I. Daily rations (D — per cent of body weight) of rudd under laboratory conditions ($T = 20 \pm 1^{\circ}C$)
Groups of fish: I, III — 2 fish; IV, V — 3 fish; II, VI — 4 fish

Food	Group of fish	Average length (cm)	Average weight (g)	D in succeeding experiments		
				1	2	3
Elodea canadensis	I	12.0	32.0	1.0	—	—
	II	12.5	34.0	1.5	—	—
	III	13.5	44.5	0.2	4.0	—
	IV	11.5	25.5	2.5	—	—
Lemna trisulca	III	13.5	44.5	14	10	11
	IV	11.5	25.5	18	12	—
	V	12.5	33.0	8	—	—
	VI	13.0	40.5	8	—	—

3.2. DAILY RATION BASED ON "PASSAGE RATE" METHOD

3.2.1. Amount of macrophyte food in the guts

In order to obtain these data is was necessary to determine the mean relation between the digested and non-digested part in different sections of the gut. The food in the gut is a sum of rations digested to a different extent which can be determined by integrationg the curve describing the distribution of the weight of the non-assimilated part in the time necessary for the passage of the whole food through the gut:

$$a = \int_{0}^{1} f(t)\,dt$$

where: a — weight of food found in the gut (non-assimilated part), $f(t)$ — function describing the changes in the weight of the part not assimilated at the time it remains in the gut (t) and expressed in per cent of the time required for food passage through the gut and assumed as 1.

Because the weight of food decreases in time, for easier calculation, function $f_1(t)$ was taken instead of function $f(t)$, the former is a reflection of the latter in relation to the perpendicular to axis y and passing during $t = \frac{1}{2}$. Thus:

$$a = \int_{0}^{1} f_1(t)\,dt$$

Assuming that the decrease in weight of non-assimilated food is a linear function of time, determining by k — the non-assimilation degree and by kA — the part of not assimilated food:

$$f_1(t) = At + kA(1 - t)$$

that is,

$$a = \int_0^1 [At + kA(1 - t)] dt = \frac{At^2}{2} + kAt - \frac{kAt^2}{2} \Big|_0^1 = \frac{A}{2} + kA - \frac{kA}{2} =$$

$$= \frac{A}{2} - \frac{kA}{2} = A \frac{1 + k}{2}$$

And therefore

$$A \frac{1 + k}{2} = a$$

that is,

$$A = \frac{2a}{1 + k}$$

Assuming that roach and rudd assimilate 30% of macrophytes ingested (P r e j s 1976) k equals 70% or 0.7 and then $A = 1.18\,a$.

Such calculated A values, i.e., amount of food in the gut expressed as per cent from the weight of rudd of different body lengths, is shown in Figure 1.
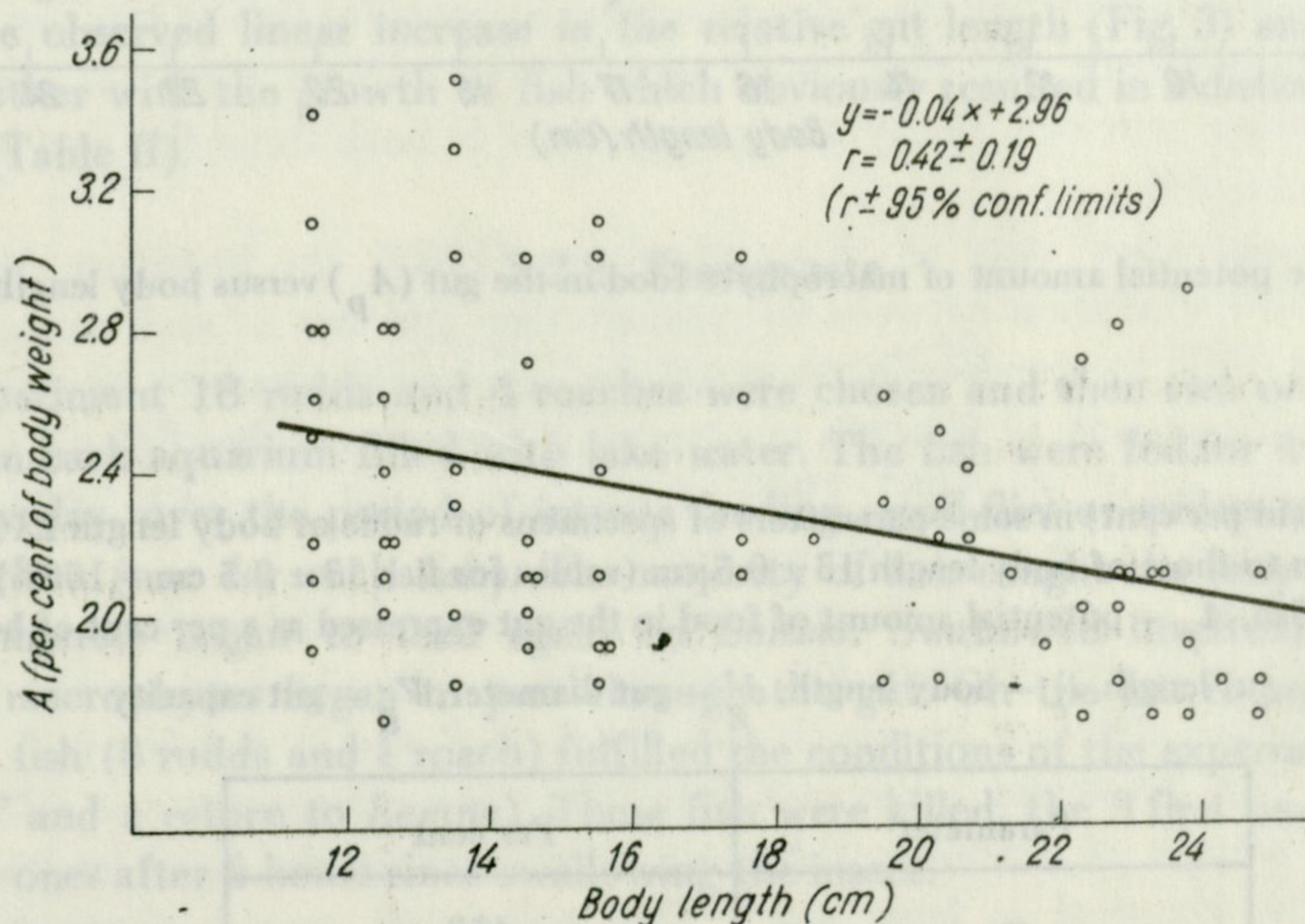

Fig. 1. Relative amount of macrophyte food in the gut (A) versus body length of rudd

As regards the roach it was found, with the probability determined by a smaller number of A measurements, that they do not differ significantly from A values for corresponding sizes of rudd.

The obtained values of the relative amount of macrophyte food in the gut tend to decrease with the growth of fish. This tendency is recorded in the literature as regards the total gut contents (e.g., H u n t 1960, B a c k i e l 1971). Although here it is not so evident ($r = -0.42$) it can be described by the linear regression equation $y = -0.04\, x + 2.96$ (y — average amount of food, x — body length of fish). Several factors are responsible for the fact that despite a considerable number of samples ($N = 73$) the correlation between these properties is not precise.

First of all the large scatter of A values for fish of the same body length should be pointed out (Fig. 1). This was the result of not only the differences in filling particular guts with macrophytes. Frequently the differences in gut capacity of particular fish were more significant. Guts of fish of the same body length similarly filled with food frequently differ in length by 20 and sometimes 30%, and in diameter by 10 to 17%.
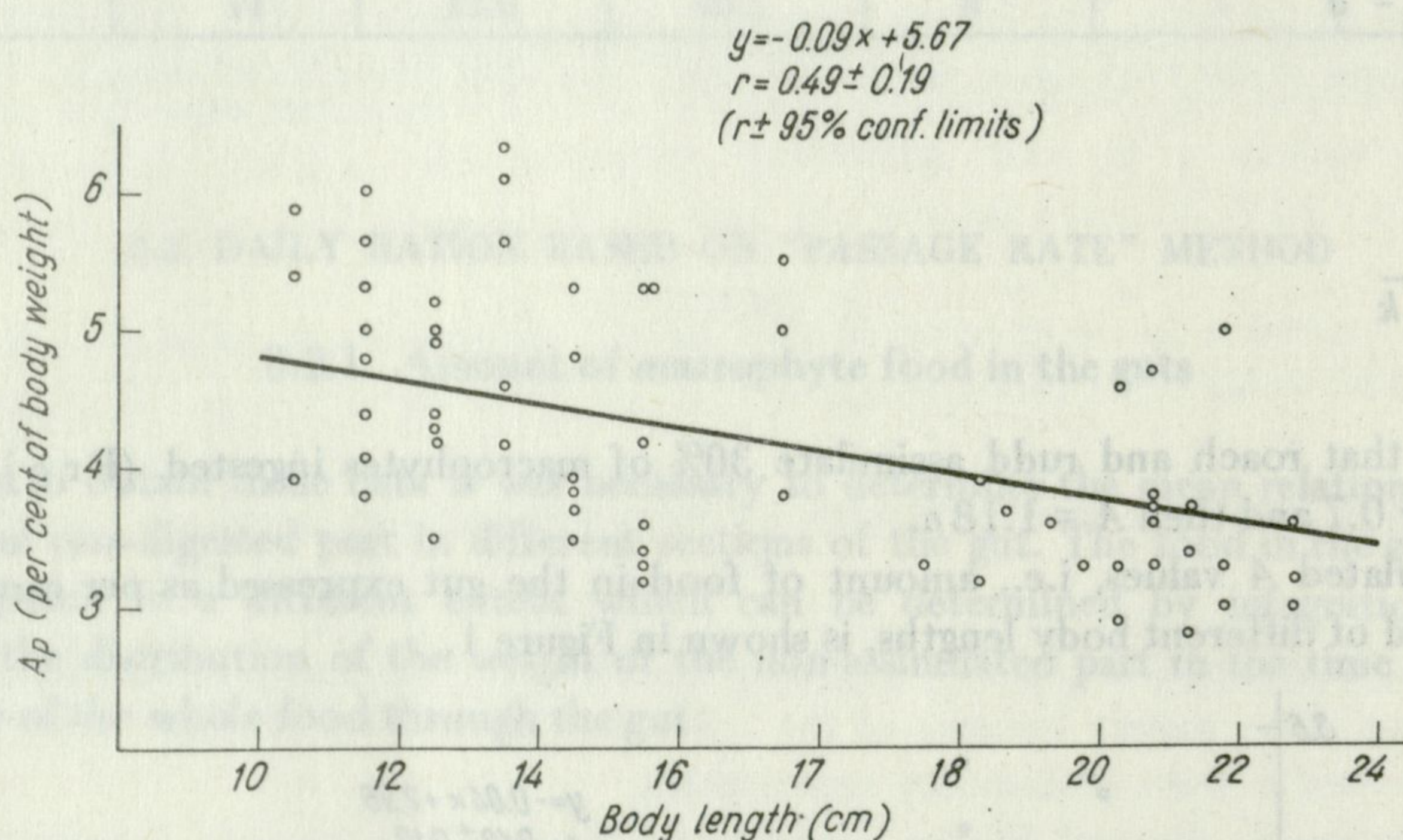

$$y = -0.09x + 5.67$$
$$r = 0.49 \pm 0.19$$
$$(r \pm 95\% \; conf. \, limits)$$

Fig. 2. Relative potential amount of macrophyte food in the gut (A_p) versus body length of rudd

Table II. Changes (in per cent) in some parameters of specimens of rudds of body length 23 ± 0.5 cm in relation to those of body length 13 ± 0.5 cm (values for fish 13 ± 0.5 cm $= 100\%$)
w — fresh weight of fish, A_p — potential amount of food in the gut expressed as a per cent of body weight, l_g — gut length, l_c — body length, d_g — gut diameter, V_g — gut capacity

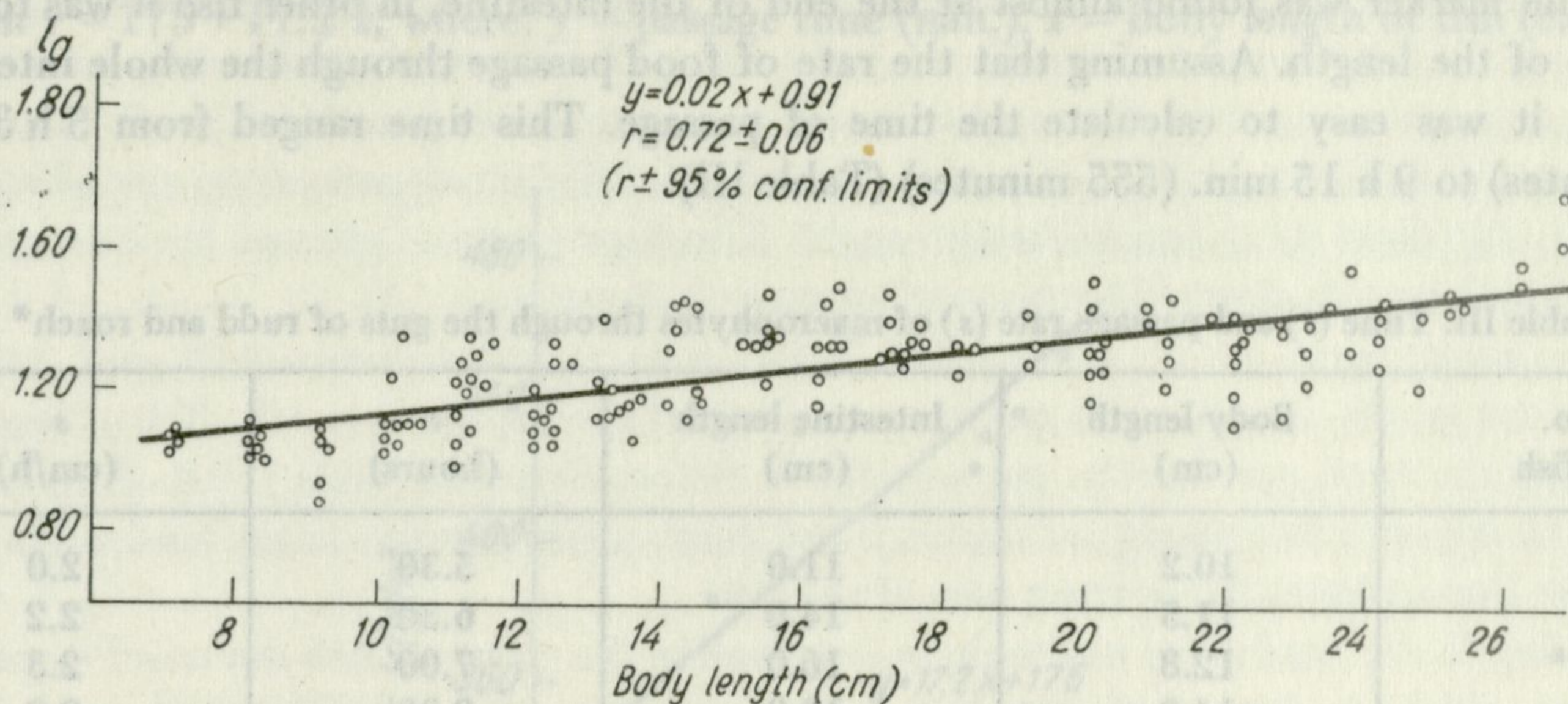| Parameter	Per cent
w	450
A_p	82
l_g/l_c	115
d_g/l_c	110
V_g	330

Fig. 3. Relative length of the gut (l_g) versus body length of rudd

Also the contribution of macrophytes to the total food of different sizes of fish varied. For the smaller fish it usually ranged from 80 to 95%, whereas for big fish it even reached 99% of weight of whole food. Thus the tendency to a decreasing relative potential amount of whole food (A_p)[1] together with the body length (Fig. 2) was slightly more distinct ($r = -0.49$) even at a smaller number of samples ($N = 62$).

Considering the growth rate of body weight and length of fish the relative amount of food decreased relatively slowly. For example, fish of a length 23 cm were over 4 times heavier than fish 13 cm long, but the corresponding A_p value differed only by 18% (Table II). This was caused by the observed linear increase in the relative gut length (Fig. 3) and the relative gut diameter together with the growth of fish which obviously resulted in a distinct increase of the gut capacity (Table II).

3.2.2. Passage rate

In the experiment 18 rudds and 4 roaches were chosen and then two or three individuals were placed in each aquarium filled with lake water. The fish were fed for 4 days with *Lemna trisulca*. Every day, over the period of intense feeding, small flies or spiders were thrown on to the water surface (one for each fish). The majority of fish caught the prey immediately and after some minutes began to feed again on *Lemna*. Swallowed invertebrates marked the moment the macrophytes began to pass through the gut. On the fourth and last day of the experiment 9 fish (8 rudds and 1 roach) fulfilled the conditions of the experiment (ingestion of the "marker" and a return to *Lemna*). These fish were killed, the 3 first ones after 4.5 hours and the 2 last ones after 6 hours since swallowing the insect.

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[1] $A_p = \dfrac{V_g}{w} \cdot 100$

where: V_g — gut capacity, w — weight of fish.

The position of the marker was determined when the guts were dissected and analysed. Only in 2 fish the marker was found almost at the end of the intestine, in other fish it was found in about 3/4 of the length. Assuming that the rate of food passage through the whole intestine is the same, it was easy to calculate the time of passage. This time ranged from 5 h 30 min. (330 minutes) to 9 h 15 min. (555 minutes) (Table III).

Table III. Time (t) and passage rate (s) of macrophytes through the guts of rudd and roach*

No. of fish	Body length (cm)	Intestine length (cm)	t (hours)	s (cm/h)
1	10.2	11.0	5.30'	2.0
2	11.5	14.0	6.30'	2.2
3*	12.8	16.0	7.00'	2.3
4	14.2	19.0	8.30'	2.2
5	14.4	18.8	8.30'	2.2
6	15.2	18.6	5.45'	3.0
7	15.3	18.8	6.15'	3.4
8	15.8	19.5	9.15'	2.1
9	16.4	20.0	8.00'	2.5

Despite the relatively low number and great differentiation the results obtained indicate a tendency to lengthen the absolute time and to increase the passage rate as the fish grow.

This image is mostly disturbed by the differences in the passage rate for fish of a similar body and gut length (cf. Table III — fish 7 and 8). This confirms the earlier observations (P r e j s 1973) that under such situation individual variability may be greater than that connected with the growth. Another example are fish No. 4 and 5 (Table III). Their guts attained a length much higher than the determined mean values for fish of this size[2].

But the greater gut length, and thus longer way of food passage, were not compensated by an increase of passage rate and finally the passage time in both these fish was longer than it might have been expected.

Apart from fragmentary data of K a r z i n k i n (1932) the literature does not have preactically data on the relation between the passage time and size of such stomachless fish as are the Cyprinidae. Still, the tendencies observed, i.e., prolonged absolute time of passage and its rate, as well as the growth of fish, are mentioned in papers on other fish (K i n n e 1960, M e n z e l 1960, P a n a d i a n 1967, 1970, S w e n s o n and S m i t h 1973, E l l i o t t 1975, J o b l i n g, G w y t e r and G r o v e 1977).

Therefore, in order to describe the probable character of relation between the time of macrophyte passage and size of both fish species the results obtained on the passage time (Table III) were divided into two groups (I: fish No. 1, 2, 3, and II: fish No. 6, 7, 8, 9) leaving out the results for fish No. 4 and 5. For each group the mean passage rate was calculated. Then the measured gut lengths of particular fish were substituted by the mean lengths of guts for large groups of fish identical in body size[3]. Thus calculated passage times showed highly significant correlation ($r = 0.96$) with the body length of fish examined (Fig. 4). The character

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[2]These values calculated from Figure 3 are for fish No. 4: 17.1 cm, and for fish No. 5: 17.5 cm.
[3]Mean values calculated from Figure 3.

of the increase in passage time together with the growth of fish is described by linear regression equation $y = 175 + 17.2 x$, where: y — passage time (min.), x — body length of fish (cm).
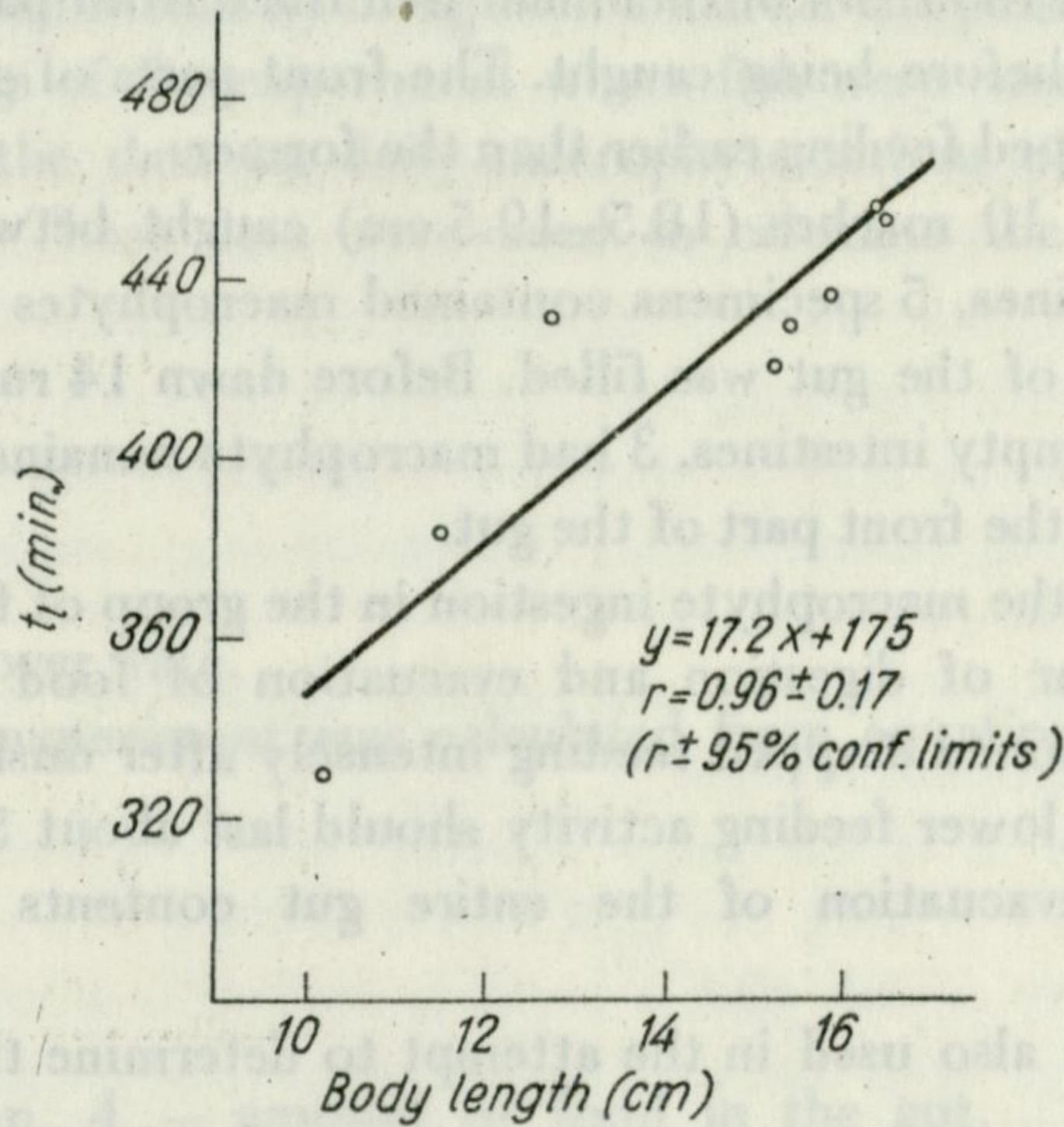

Fig. 4. Time of passage of macrophytes through the gut under laboratory conditions (t_1) versus body length of roach and rudd

Data were also obtained on the probable passage time of macrophytes through guts of roach and rudd under natural conditions.
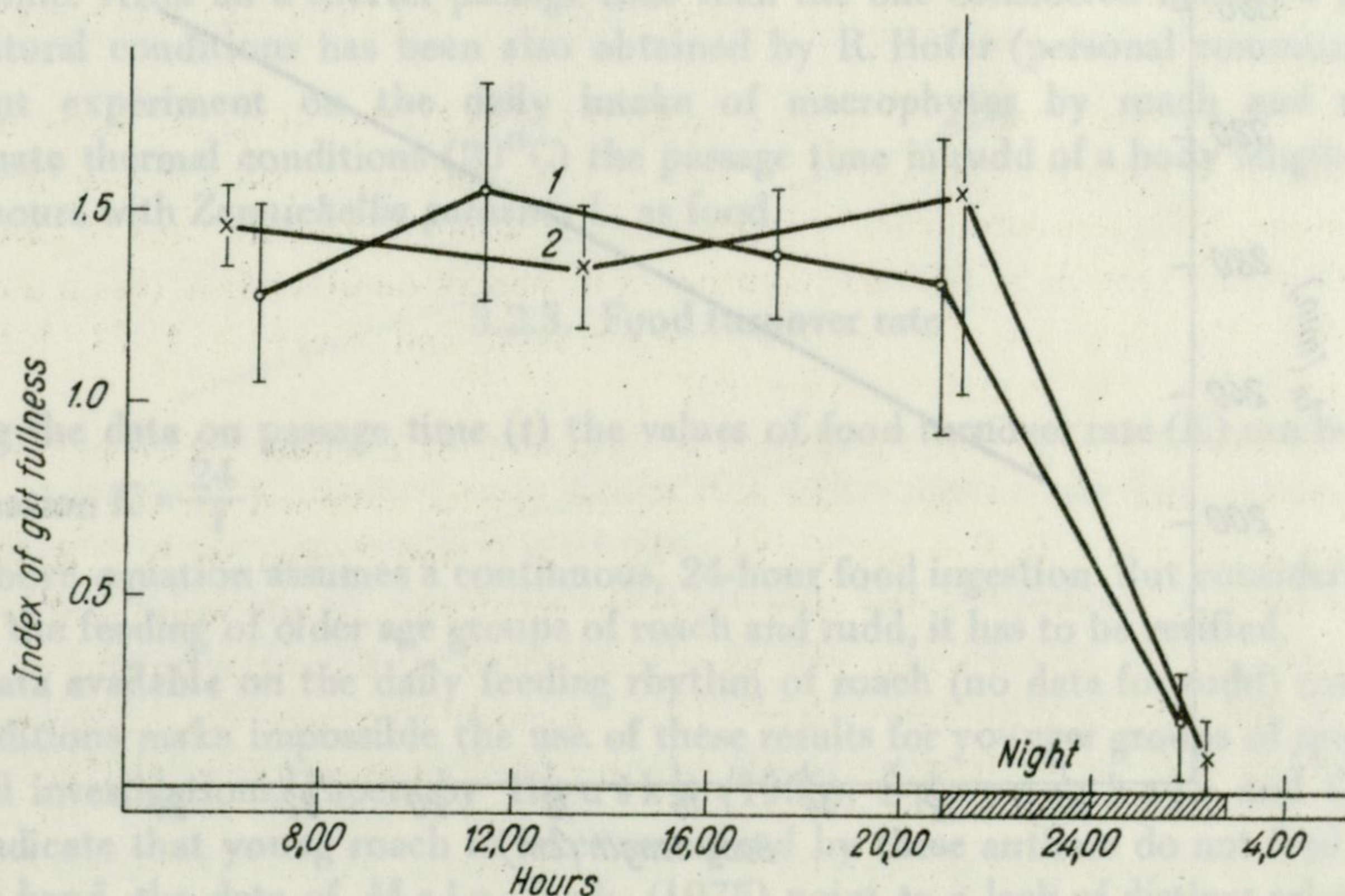

Fig. 5. Diurnal rhythm of feeding activity of roach (1) and rudd (2) expressed as an index of gut fullness (mean ± standard deviation)

Therefore, the material on the diurnal rhythm of feeding activity of the part of roach and rudd population mainly feeding on plant food, was used (Fig. 5). The filling of intestines over the day remained on a well balanced level, the number of individuals with empty intestines did not exceed several per cent. Intestines of 8 rudd specimens (body length 14.5–19.5 cm) caught at dark were also filled with food. Six of them had well filled front part of the gut which means that they consumed a lot before being caught. The front parts of guts of the two other fish indicate that these fish stopped feeding earlier than the former.

On the other hand, of 10 roaches (18.5–19.5 cm) caught between 1,00 and 2,00 hours (night), 4 had empty intestines, 5 specimens contained macrophytes in 10–30% of length, and in one case the back part of the gut was filled. Before dawn 14 rudds (19.0–24.0 cm) were caught. The majority had empty intestines, 3 had macrophyte remains in the back parts of guts, 1 had fresh macrophytes in the front part of the gut.

According to the results the macrophyte ingestion in the group of fish discussed stops almost entirely at night in favour of digestion and evacuation of food consumed before. Thus, assuming that the fish examined stopped feeding intensely after dusk and began to feed again about dawn, the period of lower feeding activity should last about 5–6 hours. This would be the time necessary for evacuation of the entire gut contents of fish of body length 19.0–24.0 cm.

The data obtained were also used in the attempt to determine tha passage time in fish of smaller body size.

It has been assumed that the character of the relation between the passage time and the size of fish, resulting from the experiment with fish of body length 10.2–16.4 cm (Fig. 4), also corresponds to that for bigger fish. Assuming a mean passage time for fish of body length 21 cm (i.e., mean for fish 19–24 cm long) as 330 minutes, a line starting from this value has been drawn (Fig. 6) and its slope corresponded to that of the regression line plotted in Figure 4.
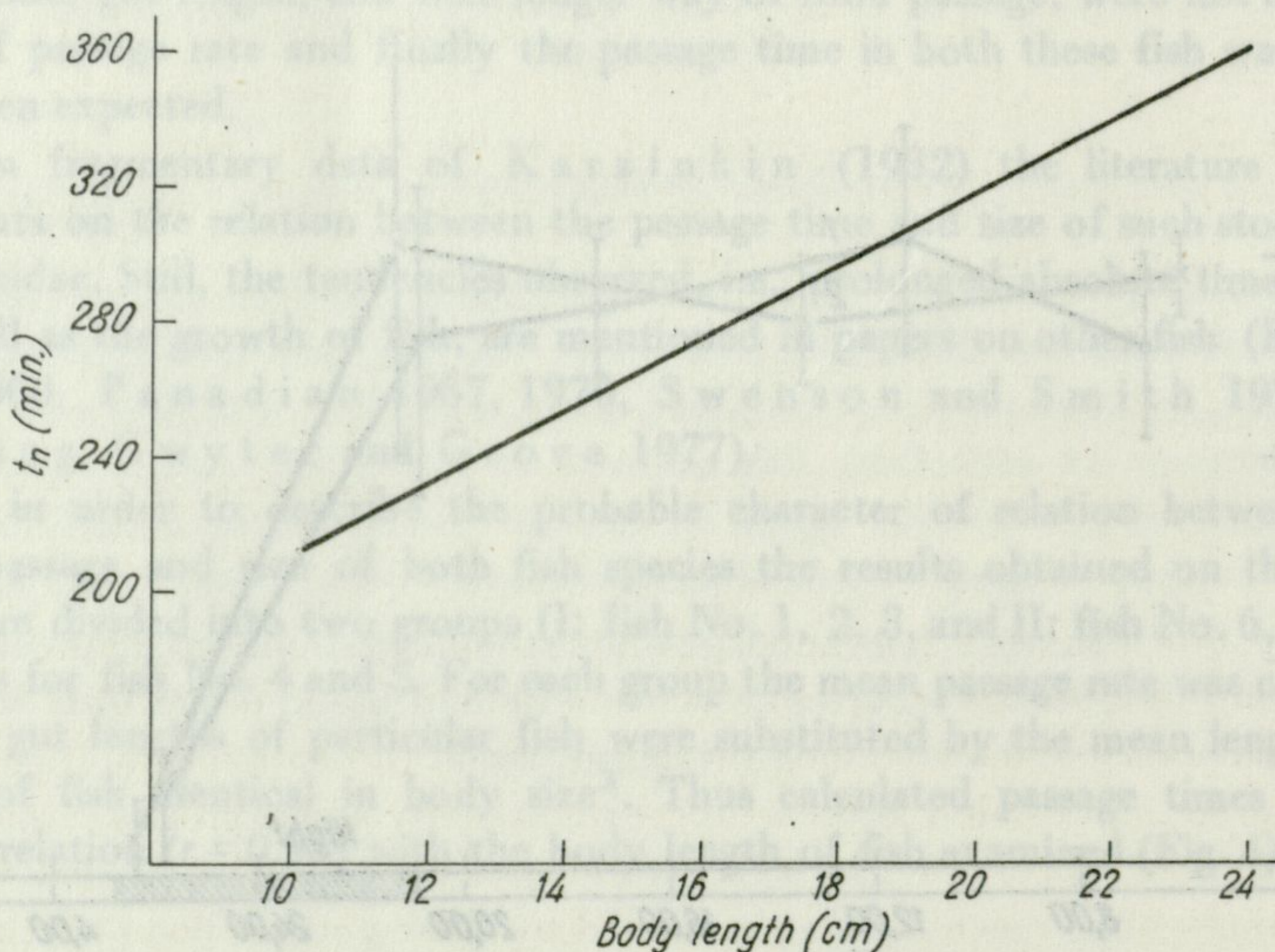

Fig. 6. Possible relation between the passage time of macrophytes through the gut under natural conditions (t_n) and the body length of roach and rudd   .

Thus determined probable time for macrophyte feeders of roach and rudd (i.e., fish over 11 cm in body length) would range from 220 minutes (fish about 11 cm in length) to 360 minutes (fish about 24 cm in length). These values are some 60% lower than the corresponding values from a laboratory experiment where animal food was used as a marker (see Fig. 4). It is quite possible that by using such a marker the passage time could be prolonged as compared to the results of the experiment where fish were constantly fed with plant food. This can be shown by the data on daily macrophyte rations obtained under experimental conditions (see Table I). These data were used to calculate the passage time according to equation:

$$t = \frac{24}{K}$$

where: K — food turnover rate.

The K value for this experiment was calculated from equation:

$$K = \frac{D}{A}$$

where: D — daily ration, A — amount of food in the gut.

Using the maximum values of daily rations (Table I) there were obtained: $t = 205$ min. for fish of a body length 11.5 ± 0.5 cm (group IV) and $t = 250$ min. for fish of a body length 13.5 ± 1 cm (group III). These values approximate the corresponding ones for the probable passage time under natural conditions (Fig. 6). In reality, the time over which the macrophytes pass through the intestines of particular fish (used in the experiment on daily rations) could be even shorter. Considering that the value $D = 18\%$ (Table I) is a mean value for three fish, then at least one of them could exceed it as according to the equations presented this shortens the passage time. After all a shorter passage time than the one considered here as a probable one under natural conditions has been also obtained by R. Hofer (personal communication) in a permanent experiment on the daily intake of macrophytes by roach and rudd. Under approximate thermal conditions (20°C) the passage time in rudd of a body length 10.9 ± 1 cm was 2.7 hours with *Zannichellia palustris* L. as food.

3.2.3. Food turnover rate

Having the data on passage time (t) the values of food turnover rate (K) can be determined using equation $K = \frac{24}{t}$.

The above equation assumes a continuous, 24-hour food ingestion. But considering the night breaks in the feeding of older age groups of roach and rudd, it has to be verified.

The data available on the daily feeding rhythm of roach (no data for rudd) connected with light conditions make impossible the use of these results for younger groups of species without additional investigations. Papers by Hruška (1956), Španovskaja and Grigoraš (1961) indicate that young roach in lakes examined by these authors do not feed at night. On the other hand, the data of Melničuk (1975) point to a lack of distinct relation between the diurnal feeding intensity rhythm of young roach and the change in light conditions. Observations when investigating here the daily ration also do not indicate that the darkness

affects whatsoever the ingestion of macrophytes by roach and rudd under laboratory conditions. This is also confirmed by the results of R. Hofer (personal communication). According to studies of L y a l l (1957), E n g s t r ö m (1963), B a r b u r i n a (1972) the eyes of roach (size, structure of retina, etc.) are adapted to see even then when the light conditions are poor. After all, D i s l e r (1960) points out that the roach while growing learns how to feed in the darkness being guided by sensory skin organs.

All this allows to assume that both species examined under natural conditions may by elastic as regards the diurnal feeding rhythm. However, usually under natural conditions rapid decrease or even breaks in food ingestion are in periods of total darkness. The observed decrease in feeding intensity together with worsening light conditions does not have to|be|characteristic |of| species as a whole. This relation may be observed in particular populations or age groups and may be the result of existing environmental conditions (e.g., availability and type of food, pressure and period of activity of predators).

What would be the K value if all roach and rudd groups feeding on macrophytes in the lakes examined would stop the ingestion at night?

Under such assumption it is necessary to take into consideration the statements of B o k o v a (1938), P e g e l (1950), K r a j u c h i n (1963), H o t t a and N a k a s h i m a (1966) that the food activity of fish after a break in feeding is usually higher than the average one. B o k o v a (1938) says even that the Caspian roach (*Rutilus rutilus caspicus* (Jak.)) after the night break in feeding fills its empty intestine twice quicker than when feeding without any interruptions.

Considering these data it has been found that a quicker rate of consuming first food rations reduces to a great extent the potential decrease of daily intake due to the night break. For example, when assuming that fish feed with the same intensity over 24 hours the K value is only some 5% higher for fish of a body length about 11 cm and 5–11% for fish of a body length 17–24 cm than the K value calculated when assuming the existence of a night break and the quicker rate with which the first filling of the intestine takes place. Therefore, a possible correction in the equation is omitted.
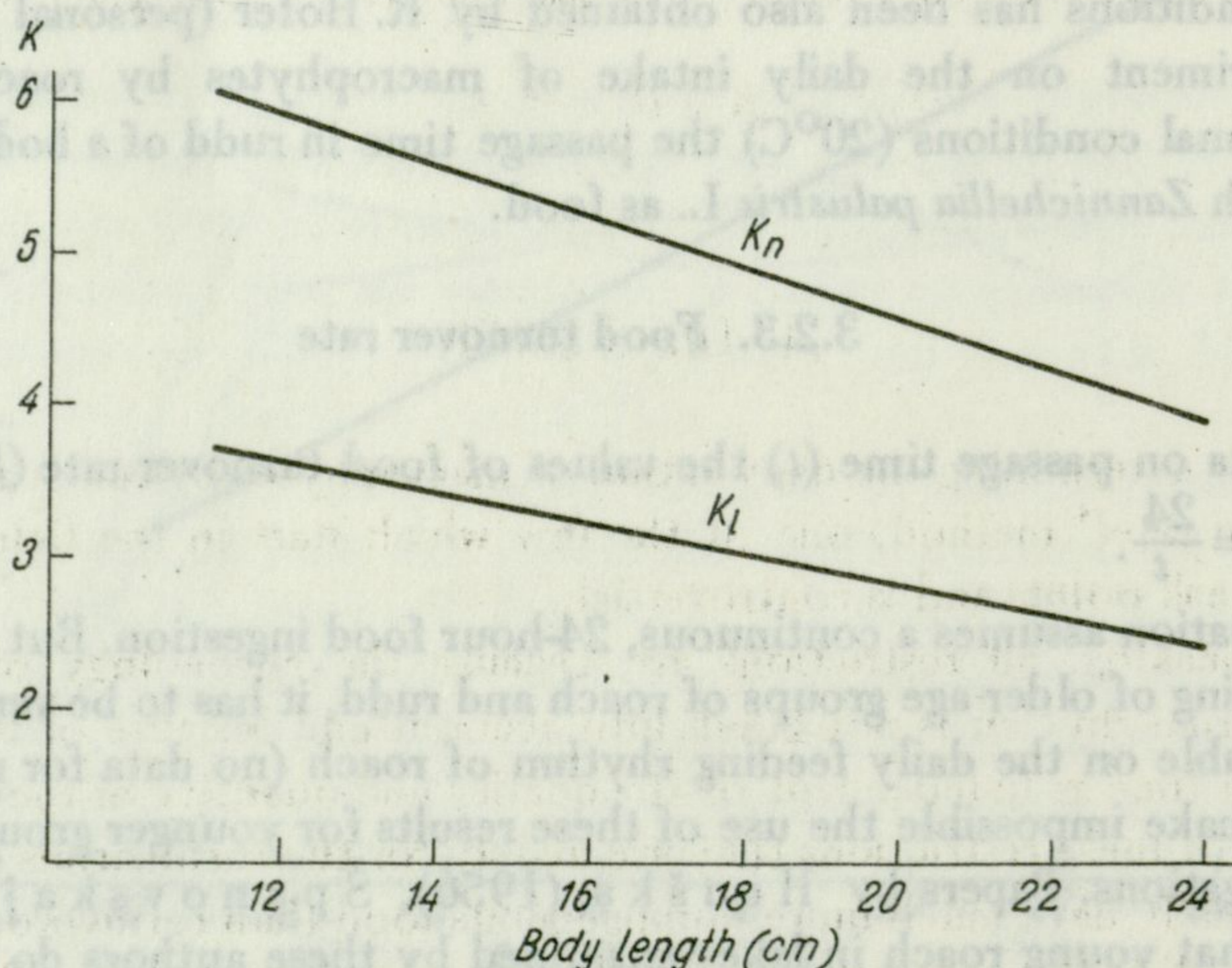

Fig. 7. Possible relation between the food turnover rate (K) and the body length of roach and rudd

$$K_n = \frac{24}{t_n}, \quad K_l = \frac{24}{t_l}$$

The values of food turnover rate calculated on the basis of passage time (Figs. 4, 6) are indicated by the lines in Figure 7.

Having the indispensable data, i.e., the mean amount of food in guts and the food turnover rate the daily rations were calculated. These calculations were made in two versions assuming smaller values of turnover rate (see K_l – Fig. 7) and higher values (see K_n – Fig. 7). In the first variant the daily rations (D_l) decreased by some 9.5% for fish of body length 11 cm to 4.8% fresh body weight for fish of body length 24 cm (4.20–2.15% in terms of dry weight) (Fig. 8). In the second variant the daily rations (D_n) decreased from 15.5 to 7.7% of fresh body weight, respectively (6.9–3.4% in terms of dry weight) (Fig. 8).
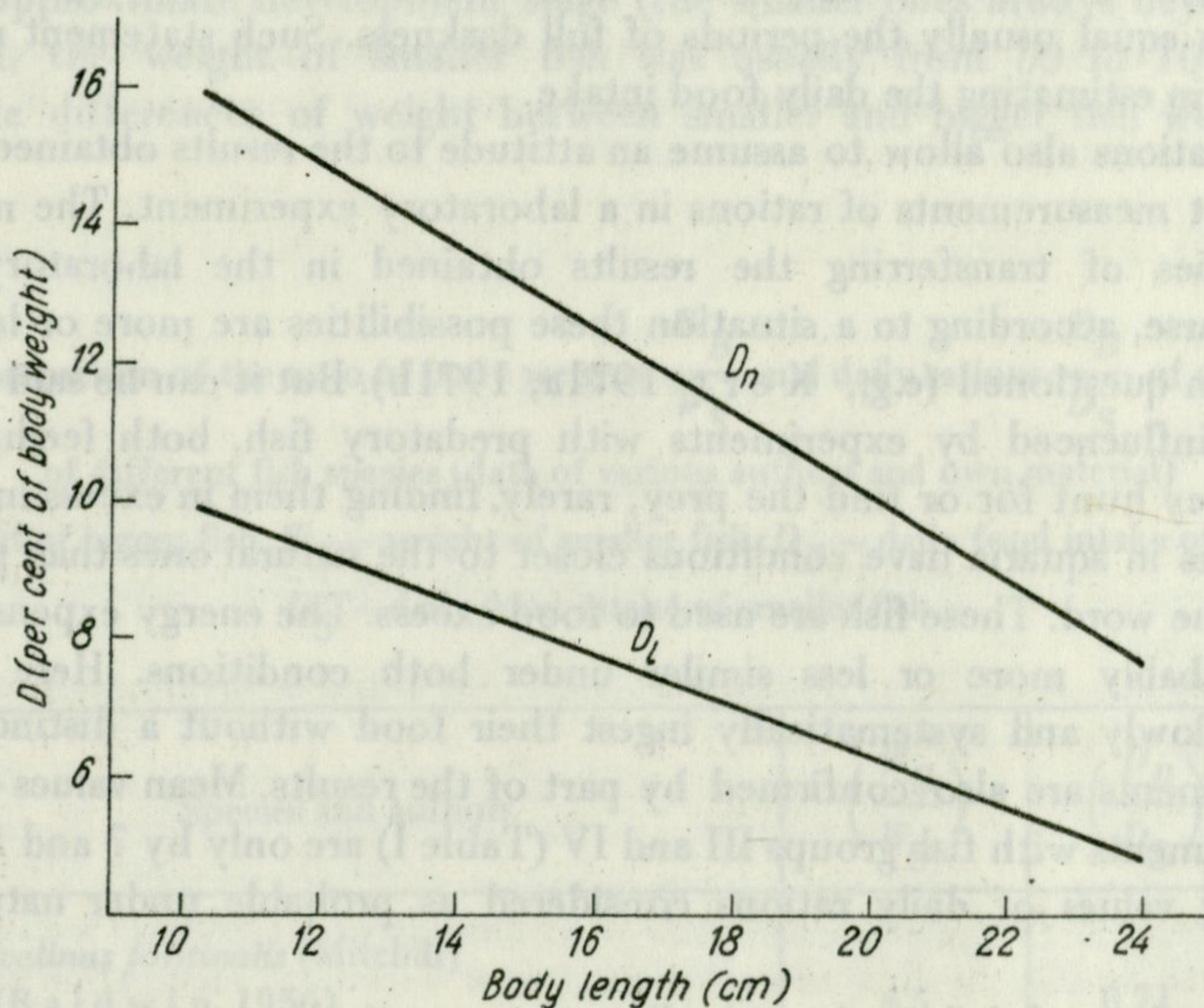

Fig. 8. Possible relation between the daily ration (D) of macrophytes and body length of roach and rudd

$$D_n = A\,K_n, \quad D_l = A\,K_l$$

4. DISCUSSION

Two methods for determining the daily ration of macrophytes by roach and rudd were used. One is the "passage rate" method, one of the few which start in the field. As practically all methods it has its weak points and is controversial.

But generally speaking, all restrictions are because the chronology of feeding intensity throughout the diurnal rhythm is not taken into account and because of the assumption that the food evacuation time is independent of the quality and quantity of food ingested. It seems that in all rightness of these restrictions they are mainly for the carnivorous or omnivorous fish. Herbivorous fish usually have much more homogeneous food than carnivorous fish. This food is usually more evenly distributed, more accessible and its standing crop usually is higher than the demands of consumers comparing with animal food. On the other hand, great demand for plant food which is poorly assimilated forces the consumer to ingest it in large quantities and therefore more or less continuously.

If the fact of constant feeding of herbivorous Cichlidae (C. M. M o r i a r t y and D. J. W. M o r i a r t y 1973) is being pointed out then it should be also assumed as probable for the Cyprynidae — fish without a true stomach, functioning as a food reservoir. B o k o v a (1938) and P e g e l (1950) have stated that the time lapse between two meals in several Cyprinidae species (also in roach) equals a certain degree of emptiness of the fore-gut. Considering that this is a very short part of the intestine the breaks in food ingestion should be very short. All this allows to state that the criticized assumptions of the "passage rate" method are best defended in the case of herbivorous fish. Even if the food is not ingested by herbivorous fish with an approximate intensity over 24 hours, it seems, according to the data of H r u š k a (1956), Š p a n o v s k a j a and G r i g o r a š (1961) and to present paper, that the feeding breaks equal usually the periods of full darkness. Such statement allows to avoid some bigger errors in estimating the daily food intake.

Above considerations also allow to assume an attitude to the results obtained by the second method, i.e., direct measurements of rations in a laboratory experiment. The main objections are the possibilities of transferring the results obtained in the laboratory into natural conditions. Of course, according to a situation these possibilities are more or less limited, and sometimes are even questioned (e.g., K e r r 1971a, 1971b). But it can be said again that such fears are mainly influenced by experiments with predatory fish, both feeding on fish and invertebrates as they hunt for or find the prey, rarely finding them in excess in one place. But macrophyte feeders in aquaria have conditions closer to the natural ones than predators in the broader sense of the word. These fish are used to food excess. The energy expense for obtaining only food is probably more or less similar under both conditions. Here and there the herbivorous fish slowly and systematically ingest their food without a distinct division into meals. These arguments are also confirmed by part of the results. Mean values of daily rations obtained in experiments with fish groups III and IV (Table I) are only by 7 and 13% lower than the corresponding values of daily rations considered as probable under natural conditions (Fig. 8).

As regards the values of daily rations the literature practically does not provide comparable data for the herbivorous groups of both species examined. But on the basis of the data obtained an attempt was made to use W i n b e r g's (1956) equation to estimate the ration indispensable for the basic energy requirements of fish. After W i n b e r g (1956) it was assumed that the oxygen uptake during routine metabolism of cyprinids at 20°C is well described by the equation:

$$Q = 0.336 \ W^{0.8}$$

where: Q — uptake of oxygen (ml) per hour, W — fresh weight of fish (g).

It was also assumed that active metabolism is twice the routine metabolism.

The calculations were made for rudd of a body length 18 cm weighing about 100 g, which according to B u d z y ń s k a et al. (1956) should increase its weight over the vegetation season by some 32 g. The accepted by W i n b e r g (1956) value of 80% as the mean digestibility of freshwater animals was substituted by the value 30% as the determined by P r e j s (1976) mean digestibility of macrophytes by roach and rudd. Thus obtained daily ration is equal to 10.7% of body weight, whereas the daily ration (D_n) read from Figure 8 is 11.3%. Despite the obvious reservations as to such a use of W i n b e r g's (1956) equation this convergence may largely confirm the genuineness of results obtained. It also confirms that the D_n rations obtained on the basis of true passage time under natural conditions are closer to reality than the D_I rations.

There still remains the problem of the relation between the daily ration and the size of fish examined. As assumed in the paper the daily ration of macrophytes decreased linearly together with the increasing size of fish. The linear relation between the daily ingestion of algae of two cichlid fishes (*Tilapia nilotica* (L.) and *Haplochromis nigripinnis* Regan) was also found by C. M. M o r i a r t y and D. J. W. M o r i a r t y (1973).

A rough verification of the above-mentioned relation was made. Using the data of different authors the relative food intake of fish varying in size was compared (Table IV). The comparison includes both marine and freshwater fish stomachless and with true stomachs, carnivorous, omnivorous and herbivorous and also the roach and rudd examined. When possible the fish at an approximate development stage (the smaller ones always beyond the fry stage) were compared, the weight of smaller fish was usually from 50 to 100 g, the bigger — 200–300 g. The differences of weight between smaller and bigger fish were 3.5 to 4 times (Table IV).

Table IV. Comparison of the ratio of body weights $\dfrac{W_B}{W_S}$ and daily rations $\dfrac{D_B}{D_S}$ of chosen groups

of different fish species (data of various authors and own material)

W_B — weight of bigger fish, W_S — weight of smaller fish, D_B — daily food intake of bigger fish,

D_S — daily food intake of smaller fish

Species and authors	$\left(\dfrac{W_B}{W_S}\right)$	$\left(\dfrac{D_B}{D_S}\right)$
Salvelinus fontinalis (Mitchill) (B a l d w i n 1956)	4.5	0.71
Lepisosteus platyrchincus (Lacépéde) (H u n t 1960)	3.0	0.66
Salmo trutta L. (E l l i o t t 1975)	4.0	0.72
Tilapia nilotica (L.) (C. M. M o r i a r t y and D. J. W. M o r i a r t y 1973)	4.0	0.87
Urophycis chuss (Walbaum) (V i n o g r a d o v 1977)	3.4	0.83
Abramis brama (L.) (K o z l o v a and P a n a š e n k o 1977)	4.3	0.71
Acerina cernua (L.) (K o z l o v a and P a n a š e n k o 1977)	3.8	0.78
Rutilus rutilus, Scardinius erythrophthalmus (own material)	4.0	0.66

It has been found that despite such a differentiated material the decrease rate of daily rations together with the growth of fish approximated and the value characterizing this property in both species examined remained within the range of fluctuations. This may prove that the described character of changes in the daily ration of macrophytes together with increasing size of fish examined is close to the real one.

5. SUMMARY

The aim of the paper was to determine the daily consumption of macrophytes by roach and rudd which was determined in two ways: direct measurements under laboratory conditions and the "passage rate" method based on data on the amount of food in intestines and the number of intestine fillings in 24 hours.

The daily ration of fish of a body length 11.0–14.6 cm fed with *Lemna trisulca* in the laboratory ranged from 8 to 18% of fresh body weight (Table I).

Information about the amount of macrophyte food in intestines was provided by field material (Fig. 1); the number of intestine fillings over 24 hours (Fig. 7) was determined both under laboratory conditions (investigations of passage time) (Fig. 4) and field conditions (studies of diurnal rhythm of feeding) (Figs. 5, 6). On the basis of these data the macrophyte consumption per 1 g fish body was found to decrease linearly with the growth of fish. In the version considered as probable under natural conditions this means a decrease from 15.5% for fish of a body length 11 cm to 7.7% fresh body weight for fish of 24 cm in length (Fig. 8).

6. POLISH SUMMARY

Cel pracy, którym było ustalenie wielkości dobowej konsumpcji makrofitów przez płoć i wzdręgę, osiągnięto dwiema drogami: przez bezpośrednie pomiary w warunkach laboratoryjnych oraz przez zastosowanie metody „passage rate" opierającej się na podstawie danych o ilości pokarmu w jelitach i liczbie napełnień jelit w ciągu doby.

Racja dobowa ryb o długości ciała 11.0–14.6 cm karmionych w laboratorium *Lemna trisulca* wahała się w granicach 8–18% świeżej masy ciała (tab. I).

Informacji o ilości pokarmu makrofitowego w jelitach dostarczyły materiały terenowe (rys. 1); liczbę napełnień jelit w ciągu doby (rys. 7) ustalano zarówno w warunkach laboratoryjnych (badania czasu pasażu) (rys. 4) jak i w warunkach terenowych (badania rytmu dobowego w odżywianiu się) (rys. 5, 6). Na podstawie tych danych stwierdzono, że konsumpcja makrofitów w przeliczeniu na 1 g ciała ryb maleje liniowo wraz ze wzrostem wielkości ryb. W wersji uznanej za prawdopodobną w warunkach naturalnych oznacza to spadek od 15.5% dla ryb o długości ciała 11 cm do 7.7% świeżej masy ciała dla ryb o długości 24 cm (rys. 8).

7. REFERENCES

1. B a c k i e l T. 1971 – Production and food consumption of predatory fish in the Vistula River – J. Fish. Biol. 3: 369–405.
2. B a j k o v A. D. 1935 – How to estimate the daily food consumption of fish under natural conditions – Trans. Am. Fish. Soc. 65: 288–289.
3. B a l d w i n N. S. 1956 – Food consumption and growth of brook trout at different temperatures – Trans. Am. Fish. Soc. 86: 323–328.
4. B a r b u r i n a E. A. 1972 – Razvitie glaz u kruglorotych i ryb v svjazi s ékologiej – Izd. Nauka, Moskva, 131 pp.
5. B o k o v a E. N. 1938 – Sutočnoe potreblenie i skorost' perevarivanija korma vobloj – Ryb. Choz. 6: 86–99.
6. B u d z y ń s k a H., R o m a n i s z y n W., R o m a ń s k i I., R u b i s z A., S t a n g e n b e r g K. 1956 – The growth and summer food of the economically most important fishes of the Gopło Lake – Zoologica Pol. 1: 63–120.
7. D i s l e r N. N. 1960 – Organy čustv sistemy bokovoj linii i ich značenie v povedenii ryb – Izd. Akad. Nauk SSSR, Moskva, 310 pp.
8. E l l i o t t J. M. 1975 – Number of meals in a day, maximum weight of food consumed in a day and maximum rate of feeding for brown trout, *Salmo trutta* L. – Freshwat. Biol. 5: 287–303.
9. E n g s t r ö m K. 1963 – Cone types and cone arrangement in teleost retinae – Acta zool., Stockh. 44: 179–243.

10. H o t t a H., N a k a s h i m a J. 1966 — Experimental study of the feeding activity of jack-mackrel, *Trachurus japonicus* — Biol. Abstr. 50: 108069.

11. H r u š k a V. 1956 — Přispevek k potravni biologii plotice v tuni Poltrubé — Univ. carol., Biologica, 2: 161—207.

12. H u n t .B. P. 1960 — Digestion rate and food consumption of Florida gar, warmouth and largemouth bass — Trans. Am. Fish. Soc. 2: 206—211.

13. J o b l i n g M., G w y t e r D., G r o v e D. J. 1977 — Some effects of temperature, meal size and body weight on gastric evacuation time in the dab, *Limnada limnada* (L.) — J. Fish. Biol. 10: 291—298.

14. K a r z i n k i n G. S. 1932 — K izučeniju fizologii piščevarenija ryb — Trudy limnol. Sta. Kosine, 15: 85—120.

15. K a r z i n k i n G. S. 1955 — Podstawy biologicznej wydajności zbiorników wodnych [Fundamentals of biological efficiency of water bodies] — Państwowe Wydawnictwo Rolnicze i Leśne, Warszawa, 386 pp.

16. K e r r S. R. 1971a — Analysis of laboratory experiments on growth efficiency of fishes — J. Fish. Res. Bd Can. 28: 801—808.

17. K e r r S. R. 1971b — Prediction of fish growth efficiency in nature — J. Fish. Res. Bd Can. 28: 809—814.

18. K i n n e O. 1960 — Growth, food intake and food conversion in a euryplastic fish exposed to different temperature and salinities — Physiol. Zoöl. 33: 288—317.

19. K l i m c z y k - J a n i k o w s k a M. 1975 — Biometric characteristics and food of the rudd (*Scardinius erythrophthalmus* L.) from the reservoir at Goczałkowice — Acta hydrobiol., Kraków, 17: 71—80.

20. K o z l o v a M. F., P a n a š e n k o V. A. 1977 — Godovye raciony i veličina izjatija kormovych organizmov populjacijami lešča *Abramis brama* (L.) i erša *Acerina cernua* (L.) v Kyršskom Zalive — Vop. Ichtiol. 17: 437—444.

21. K r a j u c h i n B. V. 1963 — Fiziologija piščevarenija presnovodnych ryb — Izd. Akad. Nauk SSSR, Moskva, 139 pp.

22. L y a l l A. H. 1957 — Cone arrangement in teleost retinae — Q. Jl microsc. Sci. 98: 189—201.

23. M e l n i č u k G. L. 1975 — Ékologija pitanija, piščevye potrebnosti i balans énergii molodi ryb vodochranilišč Dnepra — Izv. gosud. naučno-issled. Inst. ozer. reč. ryb. Choz. 101: 1—290.

24. M e n z e l D. W. 1960 — Utilization of food by Bermuda reef fish, *Epinephelus guttatus* — J. Cons. perm. int. Explor. Mer, 25: 216—222.

25. M o r i a r t y C. M., M o r i a r t y D. J. W. 1973 — Quantitative estimation of the daily ingestion of phytoplankton by *Tilapia nilotica* and *Haplochromis nigripinnis* in Lake George, Uganda — J. Zool. Lond. 171: 15—23.

26. P a n a d i a n T. J. 1967 — Intake, digestion, absorption and conversion of food in the fishes *Megalops cyprinoides* and *Ophiocephalus striatus* — Mar. Biol. 1: 16—32.

27. P a n a d i a n T. J. 1970 — Intake and conversion of food in the fish *Limnada limnada* exposed to different temperature — Mar. Biol. 5: 1—17.

28. P e g e l V. A. 1950 — Fiziologija piščevarenija ryb — Trudy tomsk. gos. Univ. 108: 1—199.

29. P r e j s A. 1973 — Experimentally increased fish stock in the pond-type Lake Warniak. IV. Feeding of introduced and autochthonous non-predatory fish — Ekol. pol. 21: 465—505.

30. P r e j s A. 1976 — Fishes and their feeding habits (In: Selected problems of lake littoral ecology, Ed. E. Pieczyńska) — Wydawnictwa Uniwersytetu Warszawskiego, Warszawa, 155—172.

31. P r e j s A., J a c k o w s k a H. 1978 — Lake macrophytes as the food of roach (*Rutilus rutilus* L.) and rudd (*Scardinius erythrophthalmus* L.). I. Species composition and dominance relations in the lake and food — Ekol. pol. 26: 429—438.

32. Š p a n o v s k a j a V. D., G r i g o r a š V. A. 1971 — Sutočnyj ritm pitanija nekotorych karpovych ryb — Vop. Ichtiol. 1: 4—15.

33. S w e n s o n W. A., S m i t h L. Jr. 1973 — Gastric digestion, food consumption, feeding periodicity and food conversion efficiency in walleye (*Stizostedion vitreum vitreum*) — J. Fish. Res. Bd Can. 30: 1327—1336.

34. V i n o g r a d o v V. I. 1977 — Sutočnye ritmy pitanija i piščevye raciony serebristogo cheka *Merluccius bilinearis* (Mitchill) i krasnogo nalima *Urophycis chuss* (Walbaum) v rajone Severo-Zapadnoj Atlantiki — Vop. Ichtiol. 17: 677—688.

35. W i n b e r g G. G. 1956 — Intensivnost' obmena i piščevye potrebnosti ryb — Izd. beloruss. Gos. Univ., Minsk, 253 pp.