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EVALUATION OF THE INTENSITY AND EFFICIENCY OF BLEAK *ALBURNUS ALBURNUS* (L.) FEEDING IN TAJTY LAKE, MASURIAN LAKELAND, POLAND. COMPARATIVE ANALYSIS OF METHODS

ABSTRACT: Daily food rations, annual consumption and food utilization for increment of body weight in bleak were determined in a 3–year study. Two simplest methods: of Bajkov and Vinberg, were applied. Moreover, during one 24-h cycle, the daily rations were determined by several other methods based on measurements of the 24-h variation of food content in the alimentary canal; the results were closely similar to those obtained by Bajkov's method. Comparison of the results obtained by the methods of Bajkov and Vinberg showed that according to Bajkov's method annual food consumption was much lower and food utilization for increment of body weight was much higher than those obtained according to Vinberg's method.

KEY WORDS: bleak, passage period, index of fullness, daily food ration, annual consumption, feeding coefficient.

1. INTRODUCTION

Because of its mass occurrence in nearly the whole of Europe, bleak represents an essential link in matter turnover in water bodies, both as a food consumer and predators prey.

Ichthyological literature comprises many papers dealing with the determination of the amount or energy value of food consumed by bleak, as well as of food utilization for increment of body weight (Mann 1965, Rudenko 1976, Mel'ničuk et al. 1978, Tichomirova 1980). In all these papers the energy balance equation of Vinberg (1956) is used for calculations. However, there are no

studies in which the calculations would be based on the real weight of food present in the alimentary canal.

The aim of the present studies was to determine in bleak, by several methods, the daily food rations, annual consumption and food utilization for increment of body weight, as well as to comparatively analyse the results.

2. MATERIAL AND METHODS

Studies were performed in eutrophic Tajty Lake in Masurian Lakeland. The surface area of the lake is 251 ha, maximal depth in 34 m and mean depth is 7.5 m. In the ichthyofauna of the lake, cyprinid fish are dominant. The numbers of bleak population are very high.

Bleak material was collected during three yearly cycles, on seventeen dates between July 1978 and June 1981. In summer months the material was collected at ca. 1-month intervals, and in the remaining seasons — less often. At the first bleak collection time (in July 1978), in order to determine the 24-h variation alimentary canal fullness, during one 24-h period fish were caught six times. At the remaining sixteen bleak collection times, catches were performed at ca. 11 a.m. A drag net (5 mm mesh) was used.

Samples comprising ca. 50 individuals were taken at random from a greater number of fish caught. About 1/3 of the sample was immediately preserved, whereupon wet body weight (in g) and indices of fullness of alimentary canal with wet weight of food in per mill (‰) of wet body weight were determined. The remaining part of the samples was placed in basins fed filtered water from Tajty lake, and then — irrespective of bleak size, age or sex — the time total gastric emptying was measured. For these estimations, autopsies of several fish, performed at regular time intervals, were carried out.

In samples collected in spring and late summer (i.e. in periods before reproduction and after its completion) the sex and wet weight of fish gonads were also determined; from the scales taken, the age, the increments of body length and body weight, as well as the annual increments of body weight were specified (Table 1).

The range of body weight of all fish collected during the 3-year period of studies was from 0.8 to 19.5 g, with a mean value of 4.8 ± 0.4 g. The group of fish, in which the age and annual increments of body length and body weight were determined, was fully representative of the overall material. In fact, in this group the body weight range was somewhat smaller (from 1.0 to 15.0 g, with a mean value of 4.7 ± 0.4 g), but the distribution of the values was very similar to that in the overall group (Fig. 1). Both mean values did not differ significantly.

Fish age remained within the range of $1+$ to $4+$ (Table 1). Individuals aged $2+$ and $3+$ were definitely dominant. The small contribution of the older year classes probably resulted from natural mortality of the stock; the absence of fish aged $0+$ and the low numbers of those aged $1+$ were due to the selectiveness of the drag net. Annual body weight increments rose with age from 1.5 do 3.5 g. Weighted mean of

Table 1. Characterization of bleak size and body weight increments in different age classes N — numbers of fish, *l.c.* — body length without caudal fin, *WW* — wet body weight, *AIWW* — annual increment of wet weight

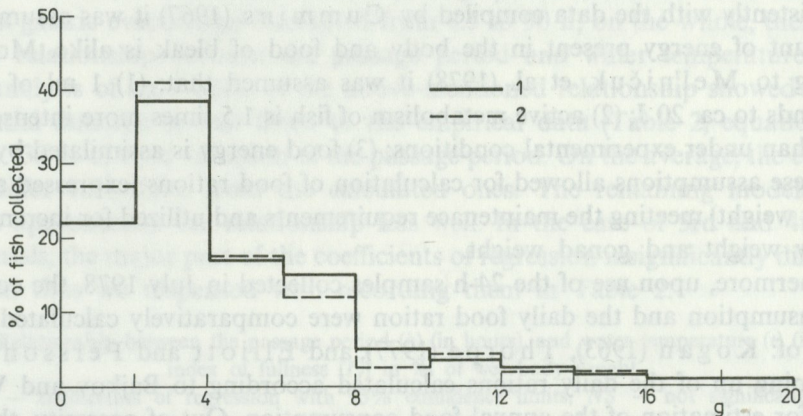| Age class	N	*l.c.* (cm)	*WW* (g)	*AIWW* (g)
1+	20	5.6 + − 0.4	2.2 + − 0.3	1.5
2+	72	6.8 + − 0.2	3.7 + − 0.3	2.9
3+	49	8.1 + − 0.3	6.6 + − 0.7	3.5
4+	5	9.6 + − 0.7	10.1 + − 3.5	
Weighted mean		7.1 + − 0.2	4.7 + − 0.4	2.1

*Mean with 95%CL.

Fig. 1. Percentile distribution of bleak wet body weight in the total material (1) and in the sample used for growth determinations (2)

the annual increments was 2.1 g, this accounting for 46% of mean body weight (Table 1).

In Tajty Lake, bleak matures at the age of 2 +. The weight of sexually mature fish represented 93% of the weight of all fish. In the prespawning and postspawning period, the mean wet weight of gonads of females and males accounted for 6.8 and 0.4%, respectively, of wet body weight. The sex ratio was nearly one. According to Mann (1965), during spawning bleak females excrete (in the form of eggs) an average of 8.1% of body weight, and males excrete (as sperm) an average of 3.9% of body weight. It may thus be assumed that the mean annual production of gonads accounts for ca. 6% of fish body weight.

In further calculations it was assumed that — irrespective of age or sex — a model bleak individual has a mean body weight of 4.7 g, with annual body weight increment of 2.1 g; this annual body weight increment accounts for 46% of mean body weight, and the annual production of gonads — for over its 6%.

Daily food rations were calculated from the modified B a j k o v's equation (1935):

$$R_d = 24 I_f 2 h^{-1} \tag{1}$$

where R_d — daily food ration (in ‰ of wet body weight) I_f — index of fullnes (in ‰ of wet body weight), h — passage period (in h).

The amount of energy utilized by fish for basal metabolism was determined by V i n b e r g's method (1956) on the basis of water temperature and of the results of M e l'n i č u k et al. (1978):

$$R = 0.37 W^{0.95} \tag{2}$$

and on the basis of the results of M a n n (1965):

$$R = 0.336 W^{0.8} \tag{3}$$

where R — oxygen consumption by fish under the experimental conditions (in ml $O_2 \cdot h^{-1}$), W — wet body weight of fish (in g).

Consistently with the data compiled by C u m m i n s (1967) it was assumed that the amount of energy present in the body and food of bleak is alike. Moreover, according to M e l'n i č u k, et al. (1978) it was assumed that: (1) 1 ml of oxygen corresponds to ca. 20 J; (2) active metabolism of fish is 1.5 times more intense under natural than under experimental conditions; (3) food energy is assimilated by fish in 80%. These assumptions allowed for calculation of food rations (expressed as ‰ of wet body weight) meeting the maintenace requirements and utilized for increments of fish body weight and gonad weight.

Furthermore, upon use of the 24-h samples collected in July 1978, the course of daily consumption and the daily food ration were comparatively calculated by the methods of: K o g a n (1963), T h o r p e (1977), and E l l i o t t and P e r s s o n (1978).

Summing up of the daily rations calculated according to Bajkov and Vinberg allowed for estimation of the annual food consumption. Out of necessity, the daily food rations were assumed to remain unchanged for long periods. It was assumed that the constant-food-ration period comprises one half of the period elapsed from previous sample collection plus one half of the period elapsed until subsequent sample collection. Annual consumption calculated according to Vinberg (by assumption, meeting only the maintenance requirements of fish) was augmented by the amount of food utilized annually for body weight increment and for the production of gonads.

Division of the consumption by the mean annual body weight increment afforded the value of the feeding coefficient; its reciprocal referred to as coefficient K_1 is a measure of food utilization for fish body weight increment.

The results of measurements and calculations were treated statistically by the methods reported by R u s z c z y c (1981) and B a l i c k i and J u r e w i c z (1985). Analysis was made of the following relationships: (1) between passage period, and water temperature and index of fullness; (2) between the weight of food remaining in the alimentary canal and gastric evacuation time; (3) between the index of fullness, and water temperature and fish body weight; (4) between the daily food ration, and water temperature and index of fullness.

Linear, exponential, power and semilogarithmic functions, polynomials of the second to the fourth order, as well as multiple regression (simple and with combination of logarithmic transformations of variables) were used. For logarithmic transformation, natural logarithms were applied.

The results were evaluated statistically on confidence level of 0.95. This allowed for elimination of nonsignificant or poor significant variables, and for selection of the functions best illustrating the investigated relationships.

3. RESULTS

3.1. FOOD PASSAGE

As a result of 17 experiments performed during 3 years within a temperature range of $3-24°C$, it was found that the passage period (assumed to be the time of complete gastric evacuation) fluctuated from 8.5 to 90 h; on the whole, there was a negative relationship between the passage period and water temperature.

An analysis of six models of the above-mentioned relationship showed that the exponential function is best fitted to the empirical data (Table 2, equation 3). It explains 73.9% of total variation of the passage period. On the average, the empirical values differ 1.34 times from the calculated ones. The remaining models of the function approximate the relationship less well. In the case of 3rd and 4th order polynomials, the major part of the coefficients of regression insignificantly differ from zero, and thus we dispensed with recording them in Table 2.

Table 2. Relationship between the passage period (h) (in hours), and water temperature (t) (in °C) and index of fullness (I_f) in ‰ of wet body weight
$b_0 - b_2$ — coefficients of regression with 95% confidence limits, NS — not significant on 95% confidence level, e — base of natural logarithm, SE — standard error of estimation of the passage period, $R^2\%$ — coefficient of determination

Model of function	b_0^*	b_1^*	b_2^*	SE	$R^2\%$
(1) $h=b_0+b_1t$	59.7+ −13.7	−2.08+ −0.89		+−11.9	62.5
(2) $h=b_0t^{b_1}$	132.9 x: 1.83	−0.656+ −0.239		x: 1.37	69.6
(3) $h=b_0e^{b_1t}$	66.9 x: 1.40	−0.062+ −0.022		x: 1.34	73.9
(4) $h=b_0+b_1t+b_2t^2$	71.0+ −24.3	−4.56+ −4.55	0.096+ −0.113 NS	+−11.7	66.0
(5) $h=b_0t^{b_1}I_f^{b_2}$	156.1 x: 1.62	−0.876+ −0.236	0.200+ −0.131	x: 1.28	82.8

*Mean with 95% CL.

The measured values of the passage period, with the plotted curve of the exponential function (with 95% confidence limits) and with Krogh's curve plotted on the basis of the tabulated data of Vinberg (1956) are presented in Figure 2. Krogh's curve has a greater slope than the plot of the exponential function, and within the temperature range of $3-19°C$ it runs higher than all the values measured. The wide confidence limits of the exponential function, formed as a result of considerable dispersion of the measured values, comprises — however — the
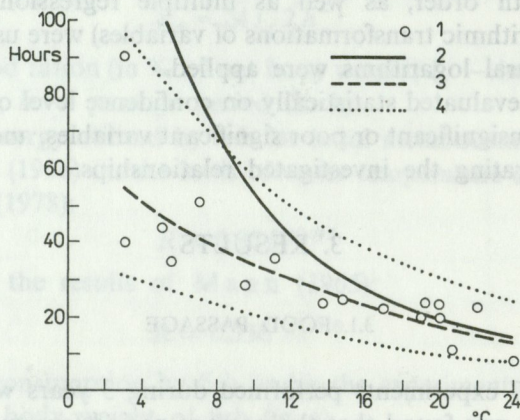
Fig. 2. Relationship between food passage period and water temperature
1 — empirical values, 2 — Krogh's curve according to Vinberg (1956), 3 — plot of exponential function
(Table 2, equation 3), 4 — 95% confidence limits of exponential function

predominant part of Krogh's curve. Therefore, the evaluation of the suitability of the compared curves is not fully reliable.

The passage period is not exclusively dependent on water temperature. It may be influenced, among others, by the starting index of fullness. For example, at 3°C in November 1979 the passage period was 90 h, with the index of fullness amounting to 3.3‰. At the same temperature in March 1981 the passage period was markedly shorter (40 h), but the index of fullness was also lower (0.2‰). A similar regularity was found also for other water temperatures. The analysed material did not allow, however, for finding a significant direct relationship between the two variables. Only calculation of the equation of multiple regression showed that the passage period really depends on both water temperature and index of fullness. Among many equations of multiple regression, this relationship is best approximated by the equation of the power function (Table 2, equation 5). It explains 82.8% of variation of the passage period. The empirical values differ but slightly from the calculated ones (Fig. 3). Thus, taking into account the index of fullness greatly improved the precision of calculations. According to the equation, the passage period is influenced by water temperature strongly negatively, and by the index of fullness positively. The presented equation may be used for the determination of the bleak food passage under similar conditions, without labour consuming experimental measurement of this period.

The course and rate of gastric evacuation were analysed with the use of the empirical data collected in July 1978, at water temperature of 24°C. Seven models were applied for calculating the relationship between the weight of food remaining in the alimentary canal and time of emptying this canal.

During 8 h virtually the total content of the alimentary canal was eliminated. The course of gastric evacuation is best described by the equation of 2nd order polynomial (Table 3, equation 5, Fig. 4), which explains as many as 95.5% of total
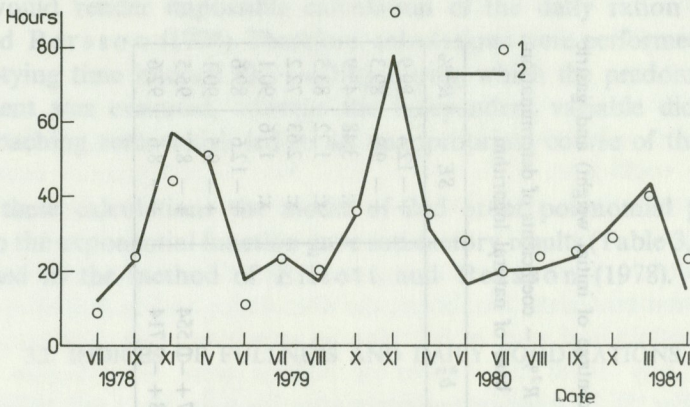
Fig. 3. Variation of food passage period
1 — empirical values, 2 — values calculated from power equation of multiple regression (Table 2, equation 5)
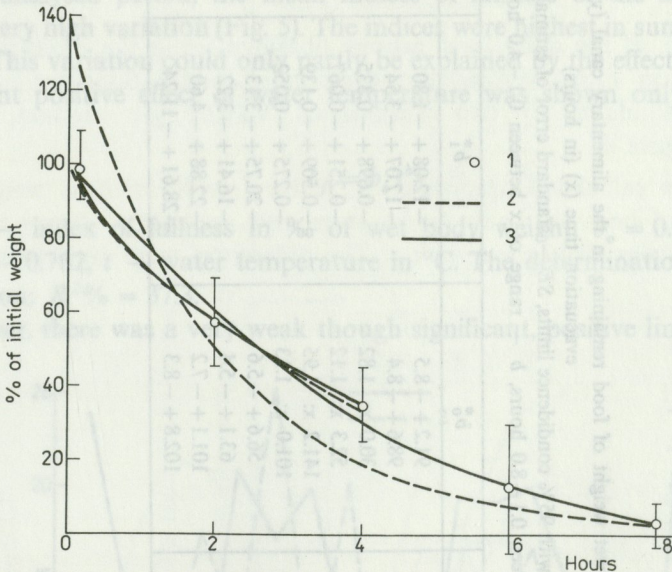

Fig. 4. Course of gastric evacuation at 24°C during the first 4 and 8 hours
1 — empirical values, 2 — plots of exponential functions (Table 3, equation 3), 3 — plots of 2nd order polynomials (Table 3, equation 5)

variation of the weight of food remaining in the alimentary canal, and affords only slight differences between the calculated and measured values (Fig. 4). The linear, exponential, power and semilogarithmic functions (Table 3, equations 1−4) afford values evidently departing from the empirical ones. On the other hand, polynomials of higher orders (not presented in Table 3) very well approximate the empirical values, but their regression coefficients in most cases differ from zero insignificantly.

Poor fitting of the exponential function to the empirical data (Table 3, equation 3, Fig. 4), i.e. a lack of a reliable index characterizing the exponential rate of gastric

Table 3. Relationship between wet weight of food remaining in the alimentary canal (y) (as percentage of initial weight) and gastric evacuation time (x) (in hours)

$b_0 - b_2$ coefficients of regression with 95% condidence limits, SE — standard error of estimation of y; $R^2\%$ — coefficients of determination, a — range of x between 0.1—8.0 hours, b — range of x between 0.1—4.0 hours, e — base of natural logarithm

Model of function		b_0^*	b_1^*	b_2^*	SE	$R^2\%$
(1) $y = b_0 + b_1 x$	a	91.2 + −8.5	−12.08 + −1.80		+ −12.4	89.9
	b	98.6 + −8.4	−17.07 + −3.54		+ − 9.9	89.3
(2) $y = b_0 x^{b_1}$	a	30.0 x: 1.82	−0.698 + −0.335		x: 3.48	45.9
	b	52.3 x: 1.12	−0.251 + −0.067		x: 1.22	83.5
(3) $y = b_0 e^{b_1 x}$	a	141.2 x: 1.95	−0.509 + −0.139		x: 2.63	72.2
	b	101.0 x: 1.13	−0.275 + −0.052		x: 1.16	90.1
(4) $y = b_0 + b_1 \log x$	a	56.6 + −5.6	−20.75 + −3.13		+ −12.6	89.6
	b	63.1 + −5.4	−16.41 + −3.22		+ − 9.5	90.1
(5) $y = b_0 + b_1 x + b_2 x^2$	a	101.1 + −7.2	−22.88 + −4.60	1.347 + −0.554	+ − 8.5	95.5
	b	102.8 + −8.3	−28.61 + −11.24	2.898 + −2.714	+ − 8.6	92.6

*Mean with 95% CL.

emptying, would render impossible calculation of the daily ration according to
Elliott and Persson (1978). Therefore, calculations were performed for another,
shorter emptying time interval (0.1−4.0 h), during which the predominant part of
gastric content was evacuted, whereas the independent variable did not assume
values approaching zero, which led to an unappropriate course of the exponential
function.

Also in these calculations the model of 2nd order polynomial proved to be
optimal; also the exponential function gave satisfactory results (Table 3, Fig. 4) which
could be used in the method of Elliott and Persson (1978).

3.2. INDICES OF FULLNESS AND DAILY FOOD RATIONS

In Tajty Lake bleak mainly fed on adult and larval forms of insects and on big
cladocerans.

In the analysed period, the mean indices of fullness of the alimentary canal
displayed very high variation (Fig. 5). The indices were highest in summer and lowest
in winter. This variation could only partly be explained by the effect of temperature.
A significant positive effect of water temperature was shown only by the power
equation:

$$I_f = b_o \, t^{b_1} \tag{4}$$

where I_f − index of fullness in ‰ of wet body weight, $b_o = 0.45$ x: 7.2, $b_1 =
= 1.096 + -0.782$, t − water temperature in °C. The determination coefficient for
this equation: $R^2\% = 37.3$.

Moreover, there was a very weak though significant, positive linear relationship
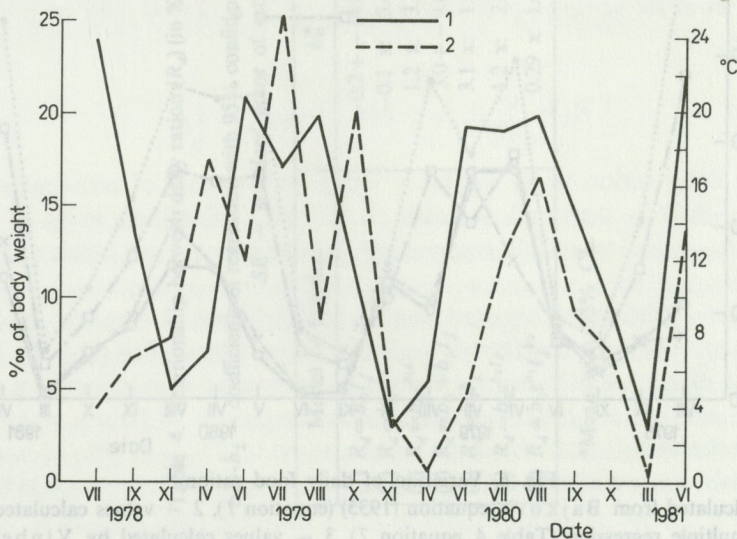

Fig. 5. Variations of mean daily water temperature at a 2-m depth (1) and variation of the index of
fullness (2)

between the index of fullness and wet body weight of all fish for which the initial
index of fullnes was determined:

$$I_f = b_o + b_1 W \tag{5}$$

where $b_o = 4.4 + -1.9$, $b_1 = 0.96 + -0,32$, W — wet weight of fish in g. The
determination coefficient: $R^2\% = 12.6$. This may testify against considering the
index of fullness to be a universal measure of the amount of food present in the
alimentary canal.

It is difficult to explain the remaining variation of the indices of fullness with the
use of the present materials. Doubtless, the abundance and accessibility of food, the
weather or physiological state of fish play an important part. For example, during
spawning (in July 1978) the indices of fullness were low, despite high water
temperature (Fig. 5). In turn, immediately after ice thaw (in April 1979), in spite of
low water temperature the indices of fullness were higher. This does not, however,
directly indicate that fish consumed a greater or smaller food ration during the 24-h
period.

The variation of the daily food rations obtained using the modified Bajkov's
equation (equation 1) as well as the variation of food rations for maintenance
requirements (calculated by two variants of Vinberg's method, 1956) are
presented in Figure 6.

Food rations calculated according to Vinberg, with constant weight of fish,
obviously depend only on water temperature and are nearly always higher than
those obtained from Bajkov's equation. The differences were particularly great in
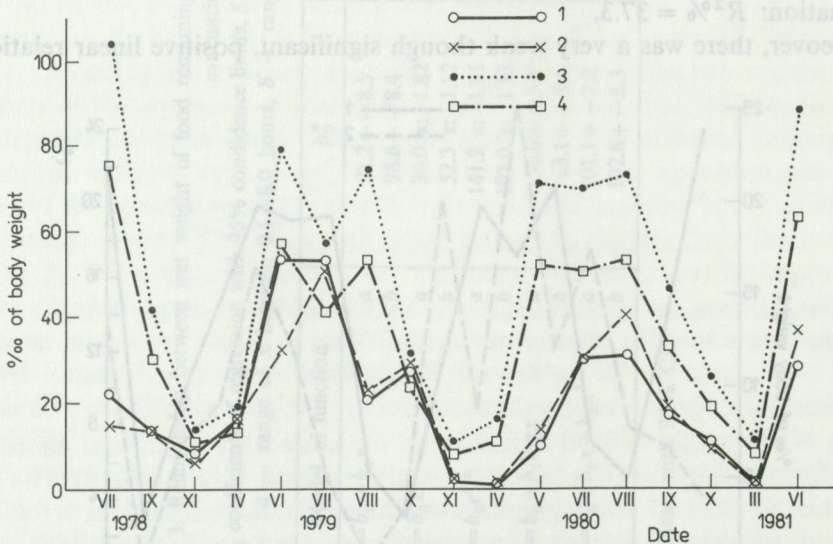

Fig. 6. Variation of daily food ration

1 — values calculated from Bajkov's equation (1935) (equation 1), 2 — values calculated from power
equation of multiple regression (Table 4, equation 7), 3 — values calculated by Vinberg's method
(1956) on the basis of the data of Mel'ničuk et al. (1978) (equation 2), 4 — values calculated by
Vinberg's method (1956) on the basis of the data of Mann (1965) (equation 3)

Table 4. Relationship between daily ration (R_d) (in ‰ of wet body weight), and water temperature (t in °C) and index of fullness (I_f) in ‰ of wet body weight

$b_0 - b_2$ — coefficients of regression with 95% confidence limits, NS — not significant on 95% confidence level, e — base of natural logarithm, SE — standard error of estimation of daily ration, $R^2\%$ — coefficient of determination

Model of function	b_0^*	b_1^*	b_2^*	SE	$R^2\%$
(1) $R_d = b_0 I_f^{b_1}$	−0.2 + −14.0 NS	1.49 + −0.91		+ −12.1	45.0
(2) $R_d = b_0 t^{b_1}$	−0.1 x: 5.45	1.784 + −0.670		x: 2.41	68.2
(3) $R_d = b_0 e^{b_1 t}$	1.2 x: 3.33 NS	0.157 + −0.078		x: 2.84	55.0
(4) $R_d = b_0 + b_1 I_f$	3.0 + −9.6 NS	1.75 + −0.79		+ −10.4	59.4
(5) $R_d = b_0 I_f$	3.1 x: 1.69 NS	1.125 + −0.235		x: 1.74	87.4
(6) $R_d = b_0 e^{b_1 I_f}$	1.2 x: 2.66 NS	0.157 + −0.081		x: 2.90	53.4
(7) $R_d = b_0 t^{b_1} I_f^{b_2}$	0.29 x: 1.62	0.878 + −0.234	0.826 + −0.130	x: 1.27	97.8

*Mean with 95% CL.

periods when the indices of fullness were low and fish lived at the expense of the accumulated energy store. Food rations calculated using the data of Mel'ničuk et al. (1978) (equation 2) exceeded those obtained from the findings of Mann (1965) (equation 3). Therefore it is evident that the daily food rations obtained from Bajkov's equation cannot meet the maintenance requirements themselves, calculated according to Vinberg.

Daily rations calculated from Bajkov's equation (equation 1) display variation in dependence on water temperature and index of fullness. As demonstrated above, the index of fullness is only slightly related to water temperature. As concerns other factors possibly influencing the magnitude of the daily food rations, only the relationship between the daily rations (expressed in ‰ of fish wet body weight) and this body weight was analysed. The present materials did not, however, testify to a significant relationship between these variables.

The dependence of the daily ration on water temperature is best approximated by the power equation (Table 4, equation 2) which explains 68.2% of variation. The power function (Table 4, equation 5) also best approximates the relationship between the daily ration and the index of fullnes ($R^2\% = 87.4$). On the other hand, the best equation of multiple regression explains as many as 97.8% of total variation of the daily ration (Table 4, equation 7). Daily rations calculated from this equation in most cases hardly differ from the empirical values (Fig. 6). It can thus be attempted, while satisfying the formal statistical requirements, to calculate the daily ration of bleak directly from the presented equation.

As stated earlier, in July 1978 the daily food ration was calculated also by methods based on variation of gastric contents during the 24-h period. In the quoted equations the denotations were made uniform.

Kogan's method (1963) assumes a linear gastric evacuation rate. The method of calculations from six samples collected during the 24-h period may be presented by the equation:

$$R_d = \sum_{i=1}^{6} (t_{i+1} - t_i) b_1 + I_{f_{i+1}} - I_{fi} \tag{6}$$

where R_d — daily ration in ‰ wet body weight, t_i = hours of consecutive catches, $b_1 = 0.88 + -0.39$ — maximal decrease in the index of fullness in ‰ of wet body weight h^{-1}, I_{fi} — indices of fullness in samples from consecutive catches in ‰ of wet body weight.

The indices of fullness fluctuated during the 24-h period from ca. 2 to 6.5‰ of body weight, displaying considerable variation in individual fish (Fig. 7). There was no significant difference between the indices of fullness at 11 a.m. and 1 p.m. as well as at 10 p.m. and 2 a.m. Maximal decrease in the indices of fullnes was between 1 p.m. and 5 p.m.; at this time the drop amounted to $0.88 + -0.39$‰ of body weight per h. The daily ration calculated by Kogan's method was $21.0 + -9.36$‰ of body weight.

The method of Thorpe (1977) assumes an exponential rate, at which the amount of evacuated gastric content depends on the initial weight of this content.
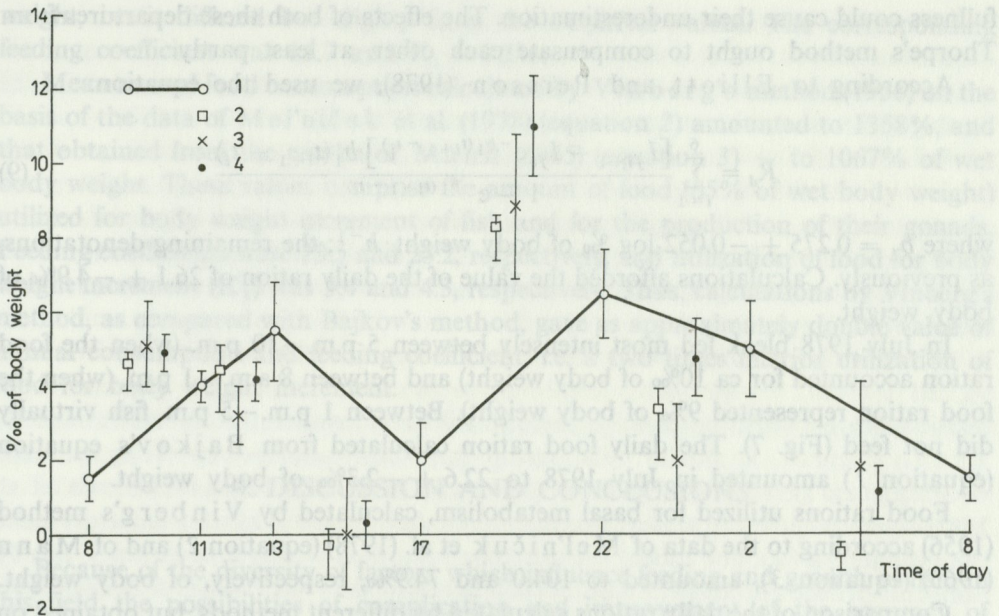
Fig. 7. Daily variation of the index of fullness (1) and of food consumption calculated by the methods of: T h o r p e (1977) — (2), K o g a n (1963) — (3), and E l l i o t t and P e r s s o n (1978) — (4)

Regression analysis of the logarithms of the index of fullness in individual fish between 1 p.m. and 5 p.m. afforded a coefficient of regression of 0.465 + −0.227. It is higher than the coefficient of regression determined experimentally in these studies (0.274 + −0.052). This difference may only be seeming on account of overlapping of the confidence limits of the regression coefficients.

Calculations were performed according to the equations:

$$I_{fr} = 0.5(I_{fi+1} + I_i)e^{-b_1(t_{i+1} - t_i)} \tag{7}$$

$$R_d = \sum_{i=1}^{6} 0.5(3I_{fi+1} - I_{fi} - 2I_{fr}) \tag{8}$$

where I_{fr} — index of fullness after time $t_{i+1} - t_i$, e — base of natural logarithm, $b_1 = 0.465 + -0.227$ log ‰ of body weight per h; the remaining denotations are the same as in the previous equation. Calculations resulted in a daily ration of 19.9‰ (with dispersion from 14.5 to 22.2‰) of body weight. After discarding the small negative food rations between 1 p.m. − 5 p.m. and 2 a.m. − 8 a.m., the daily ration amounted to 20.7‰ (with dispersion from 16.7 to 22.5‰) of body weight.

In the present studies, we slightly departed from the method of Thorpe. Namely, as b_1 we applied the rate of the decrease in the index of fullness in individual fish at the time of the greatest decrease, instead of using the mean rate of the decrease in the mean index of fullness with different kinds of food. Moreover, we did not trace back the initial index of fullness. Application of the maximal coefficient b_1 could lead to overestimation of the results, whereas the failure of tracing back the initial index of

fullness could cause their underestimation. The effects of both these departures from Thorpe's method ought to compensate each other, at least partly.

According to Elliott and Persson (1978), we used the equation:

$$R_d = \sum_{i=1}^{6} \frac{\left[I_{fi+1} - I_{fi} e^{-b_1(t_{i+1} - t_i)} \right] b_1(t_{i+1} - t_i)}{1 - e^{-b_1(t_{i+1} - t_i)}} \tag{9}$$

where $b_1 = 0.275 + -0.052 \log$ ‰ of body weight $\cdot h^{-1}$; the remaining denotations, as previously. Calculations afforded the value of the daily ration of $26.1 + -4.9$‰ of body weight.

In July 1978 bleak fed most intensely between 5 p.m. -10 p.m. (when the food ration accounted for ca 10‰ of body weight) and between 8 a.m. -1 p.m. (when the food ration represented 9‰ of body weight). Between 1 p.m. -5 p.m. fish virtually did not feed (Fig. 7). The daily food ration calculated from Bajkov's equation (equation 1) amounted in July 1978 to $22.6 + -2.3$‰ of body weight.

Food rations utilized for basal metabolism, calculated by Vinberg's method (1956) according to the data of Mel'nìčuk et al. (1978) (equation 2) and of Mann (1965) (equation 3), amounted to 104.0 and 74.9‰, respectively, of body weight.

Comparison of the daily rations calculated by different methods, but obtained on the basis of the real gastric content weight, points to a striking agreement of the results. Mean daily rations fluctuated only between $20.7 - 26.1$‰ of body weight; the daily ration calculated from Bajkov's equation (with the use of coefficient 2) assumes an intermediate place between the extreme values. It can thus be assumed that this value of the daily ration does not too much depart from its real values.

The presented results concern the period when fullness of the alimentary canal was relatively low and water temperature was high. Therefore, it is difficult to evaluate the reliability of the very high (because of being dependent only on temperature) food rations calculated for this period by Vinberg's method (1956).

3.3. ANNUAL CONSUMPTION AND FOOD UTILIZATION FOR BODY WEIGHT INCREMENT

Summing up of the daily rations for the different seasons (obtained from Bajkov's equation) allowed for estimation of annual food consumption per individual. In the different years of studies, this consumption fluctuated from 381 to 732% of wet body weight. Doubtless, the fluctuations of annual consumption were related, apart from the environmental conditions, to the random factor resulting from the limited number of samples collected during the year, in the presence of high variation of the parameters measured. Therefore, the mean annual consumption for the 3-year period, amounting to 553% of wet body weight, ought to be considered most reliable. In this case, with mean annual body weight increment of 46%, the feeding coefficient amounts to 12.0, and food utilization for body weight increment expressed as K_1 is 8.3%.

Mean annual consumption calculated as the sum of the daily rations obtained from the equation of multiple regression (Table 4, equation 7) was 540% of body

weight, i.e. it differed but slighty from the empirical values. The corresponding feeding coefficient was 11.7 and $K_1 = 8.5\%$.

Mean annual food consumption calculated by Vinberg's method (1956) on the basis of the data of Mel'ničuk et al. (1978) (equation 2) amounted to 1358%, and that obtained from the results of Mann (1965) (equation 3) — to 1067% of wet body weight. These values comprise the amount of food (65% of wet body weight) utilized for body weight increment of fish and for the production of their gonads. Feeding coefficients were 29.5 and 23.2, respectively, and utilization of food for body weight increment (K_1) was 3.4 and 4.3, respectively. Thus, calculations by Vinberg's method, as compared with Bajkov's method, gave as approximately double value of annual consumption and feeding coefficient, i.e. a two times inferior utilization of food for body weight increment.

4. DISCUSSION AND CONCLUSIONS

Because of the diversity of factors which influence feeding and growth of fish, in this field the possibilities of complication and improvement of the accuracy of research methods are nearly unlimited. The tendency for increasing the number of the factors considered is often in conflict with technical limitations, compelling us to apply far-going simplifications which, however, reduce the precision of measurements. Therefore it is difficult to select a research method, even from among methods whose advantages and drawbacks are known.

Bajkov's method (1935), together with its later modifications, is relatively simple. It requires the determination of the period of food passage through the alimentary canal and measurement of the initial weight of this food. It is, however, difficult to determine these parameters precisely.

Cyprinid fish (which comprise bleak) mostly begin their next feeding before having completed excretion of remnants of earlier consumed food. Then, during a time equal to the passage period, they consume more food than its amount found in the alimentary canal upon autopsy. Therefore, relying on filling of the alimentary canal with food and on the time of total gastric evacuation may result in substantial underestimation of the food ration values. For avoiding this shortcoming, into the original Bajkov's equation factors have been introduced (Bokova 1961, Nagięć and Martyniak 1974), or the passage period has been determined by food labelling, without interruption of the fish feeding process (Omarov 1970, Noble 1973, Prejs 1978, Okoniewska and Krüger 1979, Białokoz and Krzywosz 1981).

In laboratory studies of perch (*Perca flavescens* Mitchill), Noble (1973) has found that feeding fish digest the same amount of food two times more rapidly than fish which ceased feeding. In not feeding silver carp (*Hypophthalmichthys molitrix* Val.), as compared with feeding silver carp, the passage period has been reported to be 1.5 times longer (Białokoz and Krzywosz 1981). Although we have not found similar data concerning bleak, in the present studies we introduced a factor —

2 into Bajkov's equation (equation *1*); this factor was assumed to eliminate the differences between the real time of food passage through the alimentary canal under natural conditions, on one hand, and the passage period interpreted as the time of total gastric evacuation under experimental conditions.

It is also difficult to exactly determine the gastric evacuation time, primarily because of the differences between individuals in the digestion rate. This differentiation results from individual dissimilarities in food composition and degree of fullness of the alimentary canal, typical of natural conditions. Consequently, the data concerning the passage period are dispersed and display considerable variation which is hard to explain.

Whereas the passage period can be influenced by many factors, it is obviously related to water temperature. According to Backiel (1970), the course of the relationship between the passage period and water temperature is determined by Krogh's curve. A similar relationship has been assumed by Nagięć and Martyniak (1974). Other authors (Molnar et al. 1967, Charitonova et al. 1981) have accepted the power function model. In the case of bleak from Tajty Lake the exponential function model proved to be best fitted (Table 2, equation *3*, Fig. 2), even though the confidence limits of this function were very wide. A considerable part of unexplained variation could be explained upon introducing into the calculations, as an additional independent variable, the index of fullness in the beginning of the passage period (Table 2, equation *5*, Fig. 3).

Grave errors may charge the determination, under natural conditions, of the starting food weight which often changes during the 24-h period. In the present studies it was attempted to overcome this difficulty by catching fish always at ca. 11 a.m.; namely, it has been found previously that in the warmest period of the year, at this very hour alimentary canal fullness approached the mean daily fullness (Fig. 7). The assumptions that mean daily fullness of the alimentary canal always occurred at the same hour and that mean fullness may be regarded as a counterpart of the starting food weight from Bajkov's equation (equation *1*) may be questionable. On the other hand, the errors due to fact that the value of the mean index of fullness is unknown ought to be compensated upon collection of consecutive samples forming no systematic error. The present studies showed that it is possible to calculate by Bajkov's method the daily rations whose values are consistent with those obtained by more accurate methods. Application of Bajkov's method can be simplified, if we succeed in finding a very well fitted model for calculation of daily rations from, exclusively, water temperature and index of fullness (Table 4, equation *7*, Fig. 6). The reliability of the model calls, however, for further confirmation.

Thus, Bajkov's method may be regarded as a procedure for approximate estimation of the food ration, whose accuracy increases with improvement of the precision of the determinations of alimentary canal fullness and real food passage period.

Because of the doubts raised by Bajkov's method, many authors have given up its use, forming other models based on the determination of changes in alimentary canal fullness in the 24-h cycle and gastric evacuation rate (Kogan 1963, Staples 1975, Thorpe 1977, Elliott and Persson 1978).

The method for calculation of the gastric evacuation rate and of the possible changes in this rate is controversial. For determining the gastric evacuation rate in fish with a developed stomach, exponential equation has been used most often (Tyler 1970, Elliott 1972, Thorpe 1977, Persson 1979). Kitchel et al. (1978) and Persson (1982) have applied this equation in studies of cyprinid fish. In studies of trout, Windell et al. (1976) have analysed many models of functions and reported that the relationship under study is best approximated by semilogarithmic equation. Jobling (1981, 1986, 1987) has analysed a number of materials of various authors and found that the shape of the curve of gastric evacuation depends in the first place on the kind of food, which influences the course of the digestion process. Fine food particles, with low energy value, are digested consistently with the model of exponential function whereas big food particles or those with a high energy value are digested according to the linear model. In intermediate cases, the root equation is the best fitted model (Jobling 1987).

In the present studies 2nd order polynomial (Table 3, equation 5), being in fact a transformation of the root equation, proved to be the best model. The exponential model (Table 3, equation 3) well approximated the course of gastric evacuation in the first half of the passage period. These results are consistent with the conclusions of Jobling (1987), as in Tajty Lake bleak mainly fed on medium and fine organisms of medium energy value.

Even when the evacuation model is established, the results must not be univocal. In the exponential equation proposed by Persson (1982) for roach, the coefficient of regression is 0.50 at 24°. A similar value of the regression coefficient (0.51) has been forced by the exponential equation model calculated for the period of total gastric evacuation (Table 3, equation 3); when only the first half of the evacuation period was considered, the value of the regression coefficient decreased nearly twice (0.27). In studies of the evacuation rate in roach at 26°C Kitchell et al. (1978) have obtained a similar coefficients of regression (0.24). The values quoted don't have be a real measure of gastric evacuation in bleak under natural conditions; it can be assumed that they were distorted by the failure of fish to feed during gastric evacuation, and perhaps by the stress due to the experimental conditions.

The disagreement between the results of various authors may also be related to the considerable natural dispersion of the empirical values, and to the multitude of factors left out of account. Thus, assuming a fixed model of the relationship must lead to an increase in the calculation error. The alternative is to each time search again for the best models and to currently modify the methods for food ration determination, e.g. as proposed by Jobling (1981).

In the present studies, three different methods of this type gave − however − similar results of food ration determinations, despite the application of dissimilar, even not very well fitted models of the gastric evacuation rate. It can be assumed that the consistency of the results is due to the concept of basing oneself on changes in the real food weight in the alimentary canal; this concept is common to all three methods. This allowed for elimination of the source of the gravest calculation errors.

The main drawback of the group of methods under survey involves their laboriousness. Probably for this reason the literature of the subject is characterized

by predominance of fragmentary or methodical studies, whereas papers on practical applications of these methods for determining food consumption by fish under natural conditions (particularly in yearly cycles) are nearly nil. For these purposes Vinberg's method (1956), which is an indirect procedure for calculating food consumption, is used most often.

Vinberg's method is based on measurements of oxygen consumption by fish in respirometers, i.e. under conditions greatly departing from the natural ones. Moreover, it requires accepting many assumptions (based on more or less well documented evidence) in calculation of the measurement results, in evaluation of the energy value of fish and of their food, as well as in assessment of the degree of food energy utilization by fish. These assumptions greatly influence the results of calculations, the more so as accepting of inappropriate assumptions leads to a systematic error which accumulates in the final results. For example, in the case of the assumptions accepted in the present studies (cf. "Material and methods"), food utilization for body weight increment in bleak in Tajty Lake amounted to 3.4 or 4.3%, in dependence on the variant of the method. According to Mann (1965), bleak in the River Thames utilizes 6.6% of consumed food weight for body weight increment. The respective index amounts for Krivoe Lake to 5.4% (Rudenko 1976), and for Pel'juga Lake to 4.1% (Mel'ničuk et al. 1978).

The dispersion of the results from 3.4 to 6.2% is mainly due to the fact that various authors accept dissimilar coefficients in the equation of the relationship between bleak respiration and body weight. Resting respiration of fish weighing 4.7 g at 20°C amounts to 1.0 (Vinberg 1956), to 1.2 (Mann 1965), to 1.3 (Rudenko 1976) and to 1.6 ml $O_2 \cdot h^{-1}$ (Mel'ničuk et al. 1978). Additionally, according to some authors under natural conditions active respiration exceeds resting respiration 1.5 times, and according to others — 2 times. Thus, in the case of the above assumptions active respiration of bleak may show a more than double dispersion and may be from 1.5 to 3.2 ml $O_2 \cdot h^{-1}$. In the presence of so great a dispersion caused by the method itself, environmental and genetic differences may be obliterated.

The results obtained by Vinberg's method for bleak from Tajty Lake differ approximately twice from those afforded by Bajkov's method (1935). Unfortunately, the present materials do not allow for full explanation of these differences.

5. SUMMARY

The paper presents the results of 3-year studies of the food passage period, food consumption and food utilization for a body weight increment in bleak from eutrophic Tajty Lake in the Masurian Lakeland.

The amount of food consumed was determined by two different procedures: Bajkov's method (1935) and Vinberg's method (1956). The sources of errors in both methods were evaluated.

The food passage period was related to water temperature and to the index of fullness of the alimentary canal. This relationship was very well approximated by exponential equation of multiple regression (Table 3, equation 5, Fig. 3).

The drop in gastric content weight during the first half of the passage period was of an approximately exponential nature (Table 3, equation 3). This allowed for application of the model of Elliott and Persson (1978) for calculations of the daily rations of bleak. On the other hand, in the case of the total passage period the exponential function failed to well approximate this drop. Second order polynomial was the best fitted function (Table 3, equation 5, Fig. 4).

Because of the curvilinear course of gastric evacuation and in the light of the results of passage period determinations by way of food labelling, it was indisponsable to introduce a corrective coefficient, when using Bajkov's equation (equation 1). In the present studies, a coefficient amounting to 2 was assumed to be correct.

The values of food daily rations in July 1978, calculated by four methods based on the determination of the gastric content weight (including Bajkov's method), were closely similar.

A very significant power equation of multiple regression, describing the relationship between the daily ration (calculated from Bajkov's equation), and water temperature and index fullness was found (Table 4, equation 7, Fig. 6).

Consumption of food utilized for basal metabolism and growth, calculated by Vinberg's method (1956), as compared with Bajkov's method (1935), proved to be much higher (Fig. 6).

6. POLISH SUMMARY

Praca zawiera wyniki trzyletnich badań okresu pasażu, ilości spożywanego pokarmu i wykorzystania tego pokarmu na wzrost przez ukleję w eutroficznym jeziorze Tajty na Pojezierzu Mazurskim.

Oznaczenie ilości spożywanego pokarmu prowadzono dwoma różnymi metodami: Bajkova (1935) i Vinberga (1956). Dokonano również oceny źródeł błędów w obu metodach. Okres pasażu pokarmu zależał zarówno od temperatury wody jak i wskaźnika napełnienia przewodów pokarmowych. Bardzo dobrze zależność tę przybliża równanie potęgowe regresji wielokrotnej (tab. 3, wzór 5, rys. 3).

Spadek masy treści pokarmowej w pierwszej połowie okresu pasażu miał charakter zbliżony do wykładniczego (tab. 3, wzór 3). Pozwala to na zastosowanie do obliczeń racji dobowych uklei modelu Elliotta i Perssona (1978). Natomiast w całym okresie pasażu wykładnicza funkcja źle oddawała ten spadek. Najlepiej dopasowaną funkcją był wielomian drugiego stopnia (tab. 3, wzór 5, rys. 4).

Krzywoliniowy przebieg opróżniania przewodu oraz wyniki oznaczeń okresu pasażu drogą znakowania pokarmu zmuszają, przy korzystaniu z wzoru Bajkova (1), do wprowadzenia współczynnika korygującego. W niniejszej pracy za poprawny uznano współczynnik równy 2.

Racje dobowe pokarmu w lipcu 1978 r. obliczone czterema metodami opartymi o znaczenie masy treści pokarmowej (w tym metodą Bajkova), były bardzo zbliżone. Znaleziono wysoce istotne równanie potęgowe regresji wielokrotnej opisujące zależność racji dobowej wyliczonej wzorem Bajkova od temperatury wody i wskaźnika napełnienia (tab. 4, wzór 7, rys. 6). Oznaczone metodą Vinberga (1956) spożycie pokarmu zużywanego na przemianę podstawową i wzrost okazało się znacznie wyższe niż wyliczone metodą Bajkova (1935) (rys. 6).

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