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Rates of gastric evacuation in brown trout, *Salmo trutta* L.

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Summary

Brown trout of similar length and weight were fed a standard meal which contained a known number of food organisms of the same size-group and taxon (seven taxa were used). The weight of digestible organic matter in a trout stomach decreased exponentially with time, i.e. at a constant relative rate. At a particular water temperature, the food organisms were either evacuated from the stomach at similar rates (Group 1: *Gammarus pulex*, *Baëtis rhodani*, Chironomidae, Oligochaetes) or at progressively slower rates (Group 2: *Protonemura meyeri*, *Hydropsyche* spp., *Tenebrio molitor*). Rates of gastric evacuation were not significantly different for food organisms of different size groups of the same taxon, or for different sized meals, or for different sizes of trout (range 20–30 cm), or for mixed and multiple meals (three meals over 16 h). Times are given for the gastric evacuation of 50%, 75%, 90% and 99% of the digestible organic matter in a meal.

Starvation periods of 1, 2, 3, 4 and 5 days prior to feeding did not affect evacuation rates. The rates were slightly, but not significantly, slower for starvation periods of 6 and 7 days, and were often significantly slower for starvation periods of 10, 15 and 20 days.

Evacuation rates increased exponentially with increasing water temperature. It was possible to estimate both the rate and time for the gastric evacuation of different meals at water temperatures between 3·8°C and 19·1°C.

Introduction

In a study of the food of brown trout, *Salmo trutta* L., samples of fish were taken to discover if the stomach contents reflected the nocturnal increase in invertebrate drift (Elliott, 1967, 1970). Samples were taken at least 4 h after sunset and it was assumed that most of the day food had passed out of the stomach by this time. The validity of this assumption depends upon the rate of gastric evacuation, and the paucity of relevant information on gastric evacuation was the chief reason for the present study. As it avoids any implication of absorption and includes the passage of undigested material through the stomach, the term 'gastric evacuation' is used throughout this

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paper. Several workers have erroneously used the terms 'gastric digestion' and 'digestion rate' to describe gastric evacuation.

Windell (1967) surveyed the literature on gastric evacuation and digestion in fishes, and stressed the relevance of this work to studies of fish production. There is very little information for salmonids, but rates of gastric evacuation have been examined in brook trout, *Salvelinus fontinalis* Mitchill (Hess & Rainwater, 1939), and in rainbow trout, *Salmo gairdneri* Richardson (Reimers, 1957; Windell & Norris, 1969). Although these studies are not very detailed or statistically reliable, they do suggest that the rate of gastric evacuation is affected by water temperature and may vary with different food organisms. Brett & Higgs (1970) recently studied the effect of temperature on the rate of gastric evacuation in young sockeye, *Oncorhynchus nerka* Walbaum. This is the only study in which a mathematical model was used to analyse the results, and the same model is used in the present study.

Materials and methods

(1) *Food organisms*

Taxa used in the feeding experiments are listed in Table I. All the aquatic invertebrates are common foods of trout, and oligochaetes (Lumbricidae obtained from soil) and mealworms (larvae of *Tenebrio*) were chosen to represent foods of terrestrial origin. Live mealworms were used in the experiments and oligochaetes were cut into lengths of 1 cm. All other food organisms were killed by pinching the thorax with forceps.

Definite size-groups of each taxon were used in the experiments, and each size-group contained individuals of the same length (to nearest mm). Samples of each size-group were placed on filter paper to remove surface moisture, then weighed (all weights to nearest 0·1 mg), and finally dried in a vacuum oven for at least 3 days at 65°C until a constant dry weight was obtained. A low temperature was necessary to ensure a minimum loss of volatile, especially lipoid, constituents. The dried material was transferred to a muffle furnace, heated for 24 h at 600°C, and the remaining ash was weighed. Chitin was estimated by the method given by Richards (1951), who also emphasized the errors in this method. Therefore the percentages for chitin in Table 1 are probably only rough approximations.

Rates of gastric evacuation were measured in terms of dried digestible organic matter (Windell, 1966, 1967). Digestible organic matter was defined as dry weight of food organisms minus ash weight and chitin weight. As chitin is generally considered to be indigestible (references in Windell, 1966), a correction for chitin content was made in all estimates of organic matter.

(2) *Fish and feeding experiments*

Brown trout from a hatchery were kept in large circular tanks (described by Bagenal, 1969) and were usually fed twice a day with a commercial pelleted food. Trout with a mean length of 20 cm were used in most experiments (Table 2) and the results from the experiments with larger fish were analysed separately. After they had been weighed and measured, the trout were transferred to large rectangular tanks (165 cm × 90 cm × 60 cm), made of glass-reinforced polyester resin. Partitions of woven wire mesh divided each tank vertically into four compartments and a false bottom of wire mesh was about 10 cm above the true bottom. The tanks were partially covered with black polyethylene so that a fish in each compartment was able to retreat to a zone

Table 1. Number of food organisms, live weight, dry weight, dry weight of digestible organic matter (Y_0), water content and chitin content in each standard meal (weights are mean values (±95% confidence limits) of fifty samples and all percentages refer to live weight)

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	Length (mm)	Number in meal	Live weight (mg)	Dry weight (mg)	Organic matter (Y_o mg)	Water (%)	Chitin (%)
Gammarus pulex L.	3	20	19·4±2·2	5·0±0·4	3·8±0·4	74·2	2·5
	9	20	314·0±24·2	69·0±6·4	51·5±4·0	78·0	2·4
Baëtis rhodani (Pictet)	4	20	18·8±2·4	4·8±0·4	4·1±0·5	74·5	1·6
	8	20	156·4±13·6	36·4±3·2	31·3±2·7	76·7	1·5
Chironomidae	3	30	9·9±0·9	1·2±0·1	1·0±0·1	87·9	0·8
	6	20	66·2±5·6	8·0±0·6	6·8±0·6	87·9	0·8
Oligochaetes (Lumbricidae)	10	10	290·2±21·1	41·1±3·8	34·2±2·5	85·8	0·5
Protonemura meyeri (Pictet)	7	20	168·4±15·2	38·4±1·5	32·5±2·9	77·2	1·6
Hydropsyche spp.	12	10	271·2±18·4	52·8±4·8	41·8±2·8	80·5	1·9
Tenebrio molitor L. (larvae)	15	10	702·1±45·8	280·8±18·2	252·8±16·5	60·0	1·8

Table 2. Lengths and weights of trout used in the feeding experiments, and water temperature (arithmetic mean ± range) in each experiment

	July 1966				January 1967			March	April
Length (cm) mean	20	25	30	20	20	25	30	20	20
range	18–21	23–27	28–31	17–21	19–22	24–27	29–31	19–22	18–22
Weight (g) mean	90	178	298	91	90	180	301	92	91
range	86–94	161–196	211–343	85–98	82–97	158–205	241–358	87–93	86–95
Temperature (°C)	12·1±0·3	12·1±0·3	12·1±0·3	15·0±0·2	5·2±0·4	5·2±0·4	5·2±0·4	7·6±0·3	9·8±0·4

of low light-intensity. There was a continuous flow of water through each tank, and the water temperature remained fairly constant during each series of experiments (Table 2). Water temperatures in the large circular tanks and the experimental tanks were similar.

After a large number of laborious and often futile feeding trials, the following procedure was found to be most satisfactory. Ten trout were transferred to the rectangular tanks, and one fish was placed in each compartment. The trout were not fed for 72 h, and this interval ensured that the stomachs were empty before the start of an experiment. Food organisms of the same size group and taxon were dropped into the tank until each trout had taken a definite number (usually 10 or 20, see Table I). A trout consumed this 'standard meal' in about 5 min. As all food organisms except mealworms were dead, they remained on the bottom of the tank when they passed through the false bottom, and were thus unavailable to the trout. The number of food organisms in a meal was the maximum number which would be taken by a large number of trout, and was determined in preliminary experiments in which the fish were fed to satiation. These experiments also conditioned the trout to voluntarily consume organisms as well as pellets. Although most of the trout consumed a standard meal in the feeding experiments, several fish refused to take the required number of food organisms and were therefore replaced.

After 3 h, the trout were removed from the tank and a small pump was used to empty their stomachs. The stomach contents were transferred to a crucible and the dry weight of digestible organic matter was determined. The whole procedure was repeated with different samples of ten trout, but the time interval was increased at 3-h intervals until less than 1 mg dry weight of digestible organic matter was recovered from each stomach. If the food organisms were mealworms, the feeding experiments ended when the organic matter in a stomach was less than 1% of the digestible organic matter in the standard meal.

The design and operation of the stomach pump are described in detail by Robertson (1945), and its efficiency was checked by killing a trout immediately after the pump was used. One fish was killed in each group of ten and the stomachs were always empty. The stomach pump did not appear to affect adversely the trout and they rapidly recovered in the large circular tanks.

Different meal-sizes were used in some feeding experiments and the trout were forcibly fed for meal sizes greater than the standard meal. A trout was held in a net, a tube was inserted into the oesophagus, and the food organisms in the tube were forced into the stomach by means of a plunger. The trout were returned to the rectangular tank and rapidly recovered. Several fish regurgitated part of the meal and were therefore replaced. Ten trout were used in each experiment and were fed with either *Gammarus pulex* (9 mm) or *Tenebrio molitor*. The fish were killed after 6 h or 15 h, their stomach contents were transferred to a crucible, and the dry weight of digestible organic matter was determined.

Mathematical model for the analysis of the experiments

The geometric mean of dry weight (ordinate, Y_x mg) of digestible organic matter in the stomachs was plotted against the time interval (abscissa, X h) between the consumption of a standard meal and the removal of the stomach contents. Each geometric mean was calculated from a sample of dry weights. The mean values lay close to a linear regression line on a semi-logarithmic scale and close to an exponential curve on

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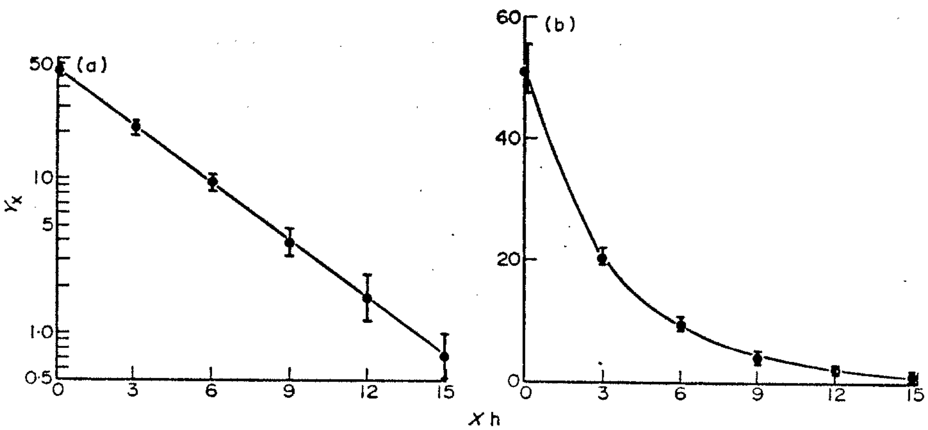

Fig. 1. Relationship between the geometric mean (±95% confidence limits) of dried digestible organic matter (Y_x mg) in the trout stomachs and time (X h). Standard meal was twenty *Gammarus pulex* (9 mm), and water temperature was 15·0°C. (a) On semi-logarithmic scale with linear regression line. (b) On arithmetic scale with exponential curve.

an arithmetic scale (Fig. 1). This relationship between Y_x and X is defined by the regression equation:

$$\log_e Y_x = \log_e A - RX \quad \text{or} \quad Y_x = Ae^{-RX} \tag{1}$$

where $e = 2{\cdot}718$ is the base of natural logarithms, A is the value of Y_x at the intercept of the regression line and the ordinate, R is the sample regression coefficient and is also the exponent for the exponential curve. Therefore R is the constant relative rate of gastric evacuation in terms of dried digestible organic matter, and the actual amount of digestible organic matter leaving a stomach in unit time is proportional to the amount remaining in the stomach. This relationship is expressed by calculus thus:

$$(dY)/(dX) = -RY,$$

which leads to the relation

$$\log_e Y_x = \log_e Y_0 - RX \quad \text{or} \quad Y_x = Y_0\, e^{-RX} \tag{2}$$

where Y_0 is the dry weight of digestible organic matter in a standard meal (see Table 1). If the exponential law is a suitable model for the data, constant A in eqn 1 should be equal to Y_0 in eqn 2. The mean time ($\bar{X}$) for the gastric evacuation of the digestible organic matter in a standard meal is given by

$$\bar{X} = \int_0^\infty \frac{Y_0\, e^{-RX}\, dX}{Y_0} = \frac{1}{R}. \tag{3}$$

The time taken (X_p) for $P\%$ of the digestible organic matter to be evacuated from the stomach is given by

$$X_p = \frac{\log_e 100 - \log_e (100-P)}{R} = \bar{X} \log_e \left(\frac{100}{100-P}\right). \tag{4}$$

Values of X_p were calculated for $P = 50\%$, $P = 75\%$, $P = 90\%$, $P = 99\%$.

Rates of gastric evacuation

Feeding experiments were performed at five different water temperatures (Table 2), and food organisms of the same size-group and taxon were used in each series of experiments (Table 1). The results of these experiments were always expressed in terms of dried digestible organic matter and were analysed for agreement with an exponential model (e.g. Fig. 1). Values of the constant A in eqn 1 and the relative rate of gastric evacuation ($R \pm 95\%$ confidence limits) were calculated for each series of experiments (Table 3). Both the correlation coefficients (modal value $-0{\cdot}99$, range $-0{\cdot}92$ to $-1{\cdot}00$) and F-values from the variance ratio (comparing mean square due to regression with residual variance) were highly significant ($P<0{\cdot}001$). Therefore the regression lines were a good fit to the data and the weight of digestible organic matter in a stomach decreased exponentially with time. This exponential decrease is illustrated for one food organism at different water temperatures (Fig. 2). Although the value of A in eqn 1 often departed from the expected value of Y_0 (cf. Tables 1 and 3), the discrepancy was always small and was never significant ($P>0{\cdot}05$).

The relative rates of gastric evacuation (measured by R) were used to divide the food organisms into two groups (Table 3). No significant differences ($P>0{\cdot}05$) were found at each temperature between the values of R for taxa in group 1. The evacuation rate was not affected by variation in the size of the food organisms (cf. values of R for small and large *Gammarus*, *Baëtis*, Chironomidae). At the same water temperature, the values of R for taxa in group 2 were significantly lower ($P<0{\cdot}05$) than those for

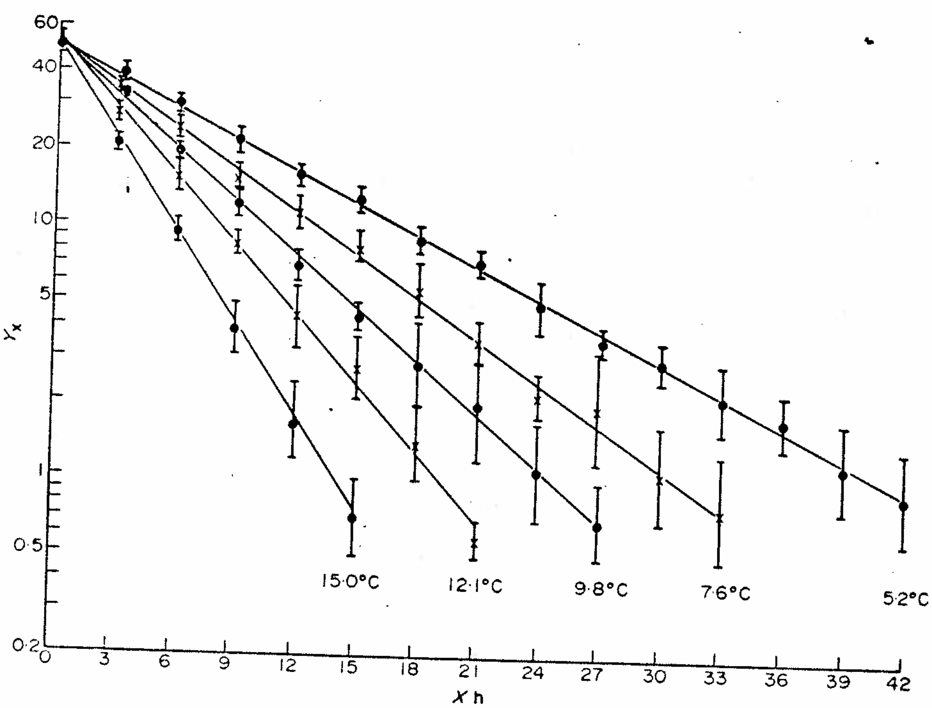

Fig. 2. Examples of the relationship between the dry weight of digestible organic matter (Y_x mg) in the stomachs and time (X h) at different water temperatures. Standard meal was twenty *Gammarus pulex* (9 mm). The points are geometric means ($\pm 95\%$ confidence limits) and a regression line is fitted for each temperature (note that Y_x is on log scale).

Table 3. Values of the constant A and regression coefficient $R(\pm 95\%$ confidence limits) for eqn 1 (mean length of trout was 20 cm)

Table 3. Values of the constant A and regression coefficient R($\pm$95% confidence limits) for eqn 1 (mean length of trout was 20 cm)

			Water temperature (°C) 5·2	7·6	9·8	12·1	15·0
Group 1							
Gammarus	3 mm	A	3·8	—	—	3·9	—
		R	0·094±0·008	—	—	0·203±0·013	—
Gammarus	9 mm	A	51·5	51·8	50·5	53·1	50·5
		R	0·096±0·002	0·126±0·004	0·159±0·003	0·206±0·010	0·284±0·005
Baëtis	4 mm	A	4·1	4·1	—	4·2	4·2
		R	0·094±0·009	0·122±0·008	—	0·204±0·012	0·281±0·011
Baëtis	8 mm	A	31·3	31·4	31·3	31·9	31·6
		R	0·095±0·005	0·124±0·007	0·161±0·005	0·211±0·007	0·287±0·008
Chironomidae	3 mm	A	1·0	—	1·0	—	—
		R	0·096±0·010	—	0·158±0·005	—	—
Chironomidae	6 mm	A	6·8	6·8	6·8	6·6	6·9
		R	0·094±0·008	0·125±0·010	0·160±0·007	0·203±0·014	0·283±0·007
Oligochaetes	10 mm	A	34·2	34·8	34·0	34·9	35·0
		R	0·096±0·010	0·124±0·011	0·157±0·009	0·210±0·011	0·286±0·009
Group 2							
Protonemura	7 mm	A	32·3	32·4	32·8	31·1	32·0
		R	0·085±0·011	0·109±0·010	0·138±0·011	0·178±0·014	0·241±0·014
Hydropsyche	12 mm	A	41·2	41·9	40·8	—	39·6
		R	0·070±0·009	0·092±0·010	0·118±0·012	—	0·209±0·014
Tenebrio	15 mm	A	251·7	250·9	253·8	248·8	249·3
		R	0·042±0·002	0·056±0·003	0·072±0·004	0·093±0·004	0·126±0·004

taxa in group 1, and the value of R decreased significantly from *Protonemura* to *Hydropsyche* to *Tenebrio*.

The actual weight of organic matter evacuated from a stomach in unit time depends upon the rate of gastric evacuation (R) and also upon the amount of digestible organic matter in a standard meal (Y_0). For taxa in group 1, R was fairly constant but Y_0 varied between taxa (e.g. Fig. 3), whereas both R and Y_0 varied considerably between taxa in group 2 (e.g. Fig. 4). To equate the effects of variations in Y_0, the results were also expressed as percentages of the amount of organic matter in a meal ($Y_0 = 100\%$). The times taken (X_P h) for the gastric evacuation of $P\%$ ($P = 50, 75, 90, 99$) of the digestible organic matter in a meal were calculated from eqns 3 and 4 (Table 4). As there were no significant differences at each temperature between the values of R within group 1, values of X_P were not calculated for each taxon.

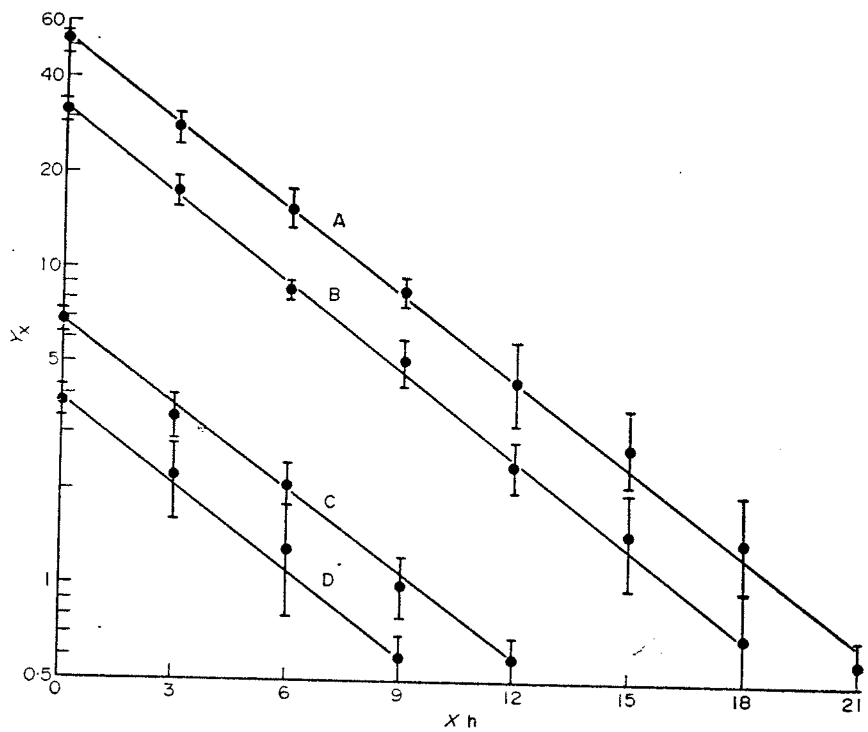

Fig. 3. Examples of the relationship between the dry weight of digestible organic matter (Y_x mg) in the stomachs and time (X h). Water temperature was 12·1°C and standard meals were (A) twenty *Gammarus pulex* (9 mm), (B) twenty *Baëtis rhodani* (8 mm), (C) twenty Chironomidae (6 mm), (D) twenty *G. pulex* (3 mm).

In the experiments with different meal sizes or with different sized trout, there was good agreement between the mean weight of digestible organic matter remaining in the stomachs and the expected weight predicted from eqn 2 (Table 5). X^2 was used to compare actual and expected values, and all X^2 values were not significant ($P > 0{\cdot}05$). Therefore the exponential law was also a good model for these experiments, and the rate of gastric evacuation was not affected by the size of the meal or the size of the trout.

Table 4. Time taken (X_p h ± 95% confidence limits) for the gastric evacuation of 50, 75, 90 and 99% of the digestible organic matter in a standard meal (taxa in group 1 are listed in Table 3)

		Water temperature (°C)				
		5·2	7·6	9·8	12·1	15·0
Group 1	50%	7·3±0·2	5·6±0·2	4·4±0·1	3·4±0·2	2·4±0·1
	75%	14·6±0·3	11·2±0·4	8·7±0·2	6·7±0·3	4·9±0·1
	90%	24·3±0·5	18·6±0·6	14·5±0·3	11·2±0·5	8·1±0·1
	99%	48·5±1·1	37·1±1·2	29·0±0·5	22·3±1·0	16·2±0·3
Protonemura	50%	8·2±1·2	6·4±0·5	5·0±0·4	3·9±0·3	2·9±0·2
	75%	16·3±2·4	12·7±1·1	10·1±0·9	7·8±0·7	5·8±0·4
	90%	27·1±4·0	21·1±1·8	16·7±1·4	12·9±1·1	9·6±0·6
	99%	54·2±8·0	42·2±3·5	33·4±2·9	25·9±2·2	19·1±1·2
Hydropsyche	50%	9·9±1·5	7·5±0·9	5·9±0·7	—	3·3±0·2
	75%	19·8±2·9	15·1±1·8	11·8±1·3	—	6·6±0·5
	90%	32·9±4·8	25·0±3·1	19·5±2·2	—	11·0±0·8
	99%	65·8±9·7	50·1±6·1	39·1±4·4	—	22·1±1·6
Tenebrio	50%	16·5±0·8	12·4±0·7	9·6±0·6	7·5±0·3	5·5±0·2
	75%	33·0±1·6	24·8±1·4	19·3±1·1	14·9±0·7	11·0±0·4
	90%	54·8±2·7	41·1±2·3	32·0±1·9	24·8±1·1	18·3±0·6
	99%	109·6±5·5	82·2±4·7	64·0±3·8	49·5±2·3	36·6±1·2

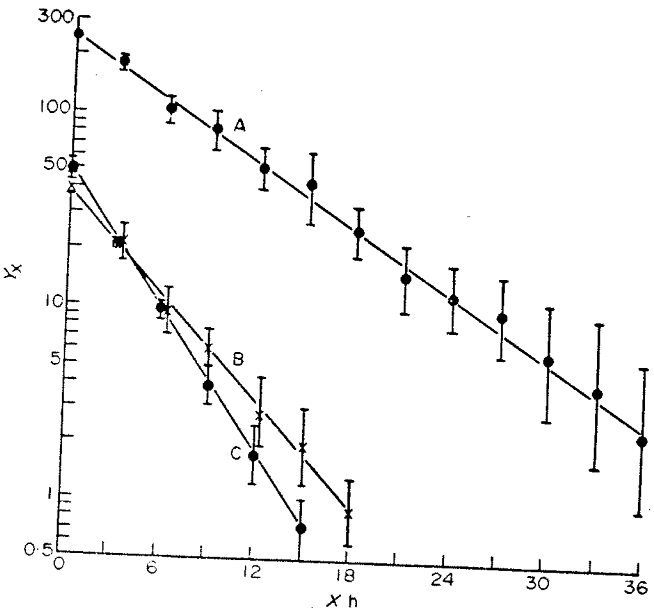

Fig. 4. Examples of the relationship between the dry weight of digestible organic matter (Y_x mg) in the stomachs and time (X h). Water temperature was 15·0°C and standard meals were (A) ten *Tenebrio molitor*, (B) ten *Hydropsyche*, (C) twenty *Gammarus pulex*.

Relationship between gastric evacuation rate and water temperature

It was apparent from the results of the feeding experiments (Tables 3 and 4) that the rate of gastric evacuation increased with increasing water temperature (e.g. Fig. 2). The relationship between evacuation rate (R) and temperature (T°C) was found to be linear on a semi-logarithmic scale (ordinate, log R and abscissa, T°C). This exponential relationship is defined by the regression equation:

$$\log_e R = \log_e \mathrm{a} + \mathrm{b}T \quad \text{or} \quad R = \mathrm{a}e^{\mathrm{b}T} \tag{5}$$

where a and b are constants. The time taken (X_p h) for the gastric evacuation of P% of the digestible organic matter in a meal was related to temperature (T°C) by a similar equation which was easily derived from eqns 4 and 5 thus:

$$X_p = \log_e \left(\frac{100}{100-P}\right)\frac{1}{R} = \mathrm{A}_p e^{-\mathrm{b}T} \tag{6}$$

where the constant

$$\mathrm{A}_p = \log_e \left(\frac{100}{100-P}\right)\frac{1}{\mathrm{a}}.$$

Values of a, b and A_p (for P = 50, 75, 90, 99%) were calculated for group 1 and the three taxa in group 2 (Table 6), and the excellent fit of the regression lines is illustrated by Fig. 5.

Therefore both the rate and time for the gastric evacuation of a meal can be estimated for water temperatures between 5·2°C and 15°C. As a few feeding experiments were performed outside this temperature range, it was possible to examine the

Table 5. Results of feeding experiments with different meal sizes, or with larger trout (mean lengths of trout were 20 cm for experiments with different meal sizes, and 25 and 30 cm for experiments with larger trout)

Mean length of trout (cm)		Number	Y_o (mg)	5·2°C, 6 h: Act. Y_x (mg)	5·2°C, 6 h: (Exp. Y_x) (mg)	5·2°C, 15 h: Act. Y_x (mg)	5·2°C, 15 h: (Exp. Y_x) (mg)	12·1°C, 6 h: Act. Y_x (mg)	12·1°C, 6 h: (Exp. Y_x) (mg)	12·1°C, 15 h: Act. Y_x (mg)	12·1°C, 15 h: (Exp. Y_x) (mg)
20	*Gammarus*	5	12·9	6·1	(7·3)	3·4	(3·1)	4·2	(3·8)	0·7	(0·6)
		10	25·8	16·2	(14·5)	5·8	(6·1)	6·9	(7·5)	1·1	(1·2)
		30	77·2	41·8	(43·4)	17·4	(18·3)	23·8	(22·5)	3·8	(3·6)
		40	103·0	60·2	(57·9)	22·8	(24·4)	29·1	(30·0)	4·1	(4·7)
	Tenebrio	5	126·4	103·7	(98·2)	61·2	(67·4)	76·8	(72·3)	35·6	(31·4)
		15	379·2	276·8	(294·6)	201·8	(202·1)	231·2	(216·9)	92·8	(94·0)
		20	505·6	400·7	(392·9)	256·3	(269·5)	300·8	(289·2)	119·7	(125·4)
25	*Gammarus*	30	77·2	46·1	(43·4)	15·2	(18·3)	22·0	(22·5)	4·1	(3·6)
	Tenebrio	15	379·2	310·4	(294·6)	190·3	(202·1)	229·8	(216·9)	103·3	(94·0)
30	*Gammarus*	30	77·2	47·8	(43·4)	16·7	(18·3)	25·6	(22·5)	3·0	(3·6)
	Tenebrio	15	379·2	288·7	(294·6)	215·3	(202·1)	215·8	(216·9)	106·1	(94·0)

Y_o was the dry weight of digestible organic matter in each meal. Act. Y_x was the dry weight (geometric mean of ten weights) of digestible organic matter remaining in a stomach after 6 h or 15 h at 5·2°C and 12·1°C. Exp. Y_x is the expected value predicted from eqn 2, using values of R from Table 3.

Table 6. Values of the constants b (±95% confidence limits), a and A_p for eqns 5 and 6

	b±95% CL	a	A_p ($P=50\%$)	A_p ($P=75\%$)	A_p ($P=90\%$)	A_p ($P=99\%$)
Group 1	0·112±0·003	0·053	13·0	26·0	43·2	86·4
Protonemura	0·107±0·002	0·049	14·3	28·5	47·4	94·7
Hydropsyche	0·112±0·002	0·039	17·6	35·2	58·5	117·0
Tenebrio	0·112±0·009	0·024	29·1	58·1	96·5	193·0

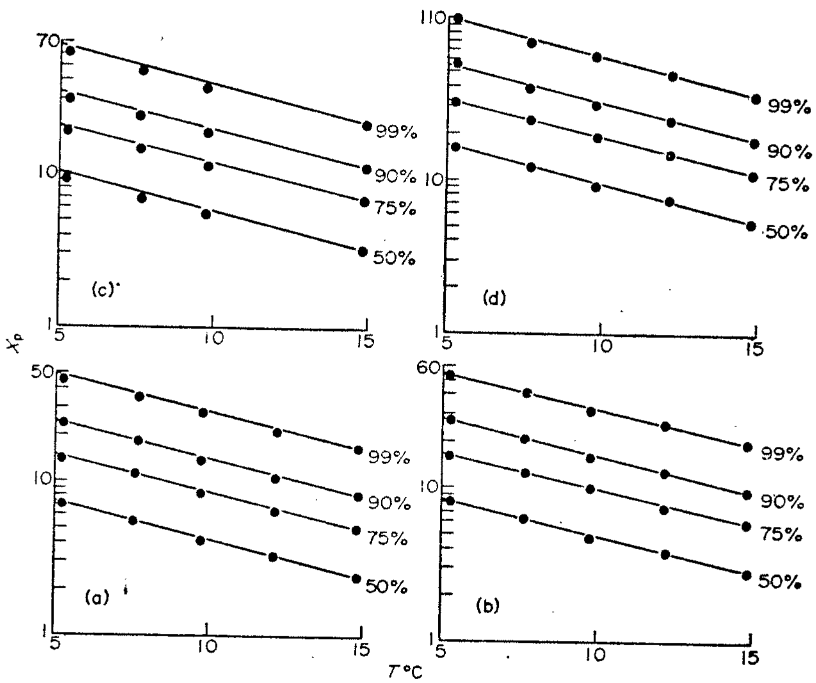

Fig. 5. Relationship between the time taken (X_p h) for the gastric evacuation of 50%, 75%, 90% and 99% of the digestible organic matter in a standard meal and water temperature (T°C). Food organisms were (a) taxa in group 1 (see Table 4), (b) *Protonemura meyeri*, (c) *Hydropsyche*, (d) *Tenebrio molitor*.

validity of using eqn 5 to estimate R for extremes of temperature. In all these experiments, there was good agreement between the mean weight of digestible organic matter remaining in the stomachs and the expected weight predicted from eqn 2 with values of R estimated from eqn 5 (Table 7). X^2 was used to compare actual and expected weights, and all X^2 values were not significant ($P>0{\cdot}05$). Although these experiments were limited to five taxa and only one or two time intervals, they confirmed that the results of the detailed experiments could be extrapolated at least to water temperatures between 3·8°C and 19·1°C.

Effect of different starvation periods on gastric evacuation rates

The trout were usually starved for 72 h before the start of a feeding experiment. As the length of the starvation period may affect evacuation rates, a series of feeding experiments was performed with starvation periods between 1 and 20 days (Table 8).

Table 7. Results of feeding experiments at 3·8, 16·4 and 19·1 °C (ten fish (mean length 20 cm) were used in each experiment)

			Mean temp. ± range (°C)								
			3·8±0·2			16·4±0·2			19·1±0·3		
	X (h)	Y_o (mg)	R	Act. Y_x (mg)	(Exp. Y_x) (mg)	R	Act. Y_x (mg)	(Exp. Y_x) (mg)	R	Act. Y_x (mg)	(Exp. Y_x) (mg)
Gammarus (9 mm)	6	51·5	0·081	30·1	(31·7)	0·333	7·6	(7·0)	0·450	4·8	(3·5)
	15	51·5	0·081	17·4	(15·3)	0·333	0·2	(0·4)	0·450	0·1	(0·1)
Baëtis (8 mm)	6	31·3	0·081	17·6	(19·3)	0·333	5·7	(4·3)	0·450	2·4	(2·1)
	15	31·3	0·081	11·1	(9·3)	0·333	0·3	(0·2)	0·450	0·1	(0·0)
Protonemura	6	32·5	0·074	21·7	(20·9)	0·283	7·1	(6·0)	0·378	5·2	(3·4)
Hydropsyche	6	41·8	0·059	28·0	(29·3)	0·226	11·5	(10·8)	0·301	5·8	(6·9)
	15	41·8	0·059	18·8	(17·3)	0·226	2·0*	(1·4)	0·301	0·5	(0·5)
Tenebrio	6	252·8	0·036	198·6	(203·8)	0·139	115·3	(109·7)	0·185	89·8	(83·4)
	15	252·8	0·036	154·5	(147·4)	0·139	31·6	(31·4)	0·185	18·5	(15·7)

X h was the time interval between consumption of standard meal and emptying of stomach. Y_o was the dry weight of digestible organic matter in each meal. R was the evacuation rate estimated from eqn 5. Act. Y_x was the dry weight (geometric mean of ten weights) of digestible organic matter remaining in the stomach after 6 h or 15 h. Exp. Y_x is the expected value predicted from eqn 2.

Table 8. Results of feeding experiments with different starvation periods (S.P.) (ten trout (mean length 20 cm) were used in each experiment).

S.P. (h)	*Gammarus* 5·2°C 6 h Act. Y_x	*Gammarus* 5·2°C 15 h Act. Y_x	*Gammarus* 12·1°C 6 h Act. Y_x	*Gammarus* 12·1°C 15 h Act. Y_x	*Tenebrio* 5·2°C 6 h Act. Y_x	*Tenebrio* 5·2°C 15 h Act. Y_x	*Tenebrio* 12·1°C 6 h Act. Y_x	*Tenebrio* 12·1°C 15 h Act. Y_x
24	—	—	12·3	3·1	—	—	141·2	65·8
48	27·8	14·6	14·1	2·4	204·6	132·6	156·3	63·3
96	30·3	12·1	17·4	3·0	178·3	143·1	139·5	62·6
120	29·5	14·3	15·2	1·9	184·8	131·8	148·6	66·9
144	33·6	15·5	17·8	3·2	209·9	144·5	155·8	63·7
168	36·8	15·4	22·2	3·8	218·2	148·3	167·2	69·2
240	40·2*	17·2	25·1**	4·1	231·4*	144·6	170·4*	71·3
360	43·5**	18·6	26·2**	4·0	223·1	149·5	173·8*	75·7
480	47·2***	20·3*	28·7***	5·6*	248·1***	162·8*	181·6**	78·9*
	Exp. Y_x	Exp. Y_x	Exp. Y_x	Exp. Y_x	Exp. Y_x	Exp. Y_x	Exp. Y_x	Exp. Y_x
72	28·9	12·2	15·0	2·4	196·4	134·7	144·6	62·7

Act. Y_x was the dry weight (geometric mean of ten weights) of digestible organic matter remaining in a stomach after 6 h and 15 h at 5·2°C and 12·1°C. Exp. Y_x is the expected value predicted from eqn 2, using values of R from Table 3.
A significant difference between actual and expected values is indicated by asterisks thus: $*P<0{\cdot}05$ $**P<0{\cdot}01$, $***P<0{\cdot}001$.

Each trout was fed a standard meal of either twenty *Gammarus pulex* (9 mm) or ten *Tenebrio molitor*, and the stomachs were emptied after 6 h or 15 h. For starvation periods between 24 h and 120 h (1–5 days), there was good agreement between the mean weight of digestible organic matter remaining in the stomachs and the expected weight predicted from the results of the experiments with the usual starvation period of 72 h. Therefore a starvation period of less than 6 days had no apparent effect on evacuation rates. The rate of gastric evacuation was slightly, but not significantly, slower for starvation periods of 144 h and 168 h, and was often significantly slower for longer starvation periods (significance levels indicated by asterisks in Table 8). As there were only a few experiments for starvation periods longer than 7 days, it was not possible to quantify the relationship between evacuation rate and the length of the starvation period.

The adequacy of the mathematical model for mixed and multiple meals

The estimates of evacuation rates were all obtained from experiments in which each trout was fed one standard meal with food organisms of the same taxon. As trout in a stream usually feed more than once a day and take a variety of food organisms, the evacuation rate of mixed and multiple meals was investigated in a series of experiments. At 08.00 hours, 14.00 hours and 20.00 hours, ten trout (mean length 20 cm) were each fed a meal of five *Gammarus pulex* (9 mm), five *Baëtis rhodani* (8 mm), five chironomids (6 mm), and three oligochaetes (10 mm). The dry weight of digestible organic matter in this meal (Y_o) was estimated to be 32·7 ± 2·5 mg. Therefore one fish consumed three meals with a total organic matter content of 98·1 ± 7·5 mg. At 24.00 hours, the stomachs were emptied and the dry weight of digestible organic matter in each stomach (Act. Y_x)

was determined. The expected weight of organic matter in each stomach (Exp. Y_x) was calculated from the exponential model thus:

$$\text{Exp. } Y_x = Y_o(e^{-RX_1}+e^{-RX_2}+e^{-RX_3}) \quad (7)$$

where $X_1 = 16$ h, $X_2 = 10$ h, $X_3 = 4$ h and R is the mean value for group 1 (from Table 3).

At each water temperature, there was good agreement between the actual and expected weights of organic matter per stomach (Table 9). Therefore the exponential model and estimates of evacuation rate were perfectly adequate for these feeding experiments. The probable changes in the amount of organic matter in a stomach are illustrated by Fig. 6 which showed the exponential decrease between meals and a final value of 38·3 mg after 16 h and three meals.

Table 9. Dry weight (Act. Y_x mg) of digestible organic matter remaining in the stomachs of ten trout which were fed with three meals of mixed food organisms

		Water temperature (°C)		
		7·6	12·1	15·0
		Act. Y_x	Act. Y_x	Act. Y_x
Trout number	1	103·6	61·3	37·1
	2	98·2	63·9	40·8
	3	104·3	54·7	35·8
	4	105·1	58·5	36·4
	5	93·8	59·2	41·2
	6	108·4	62·8	40·8
	7	101·5	63·2	42·1
	8	99·2	60·7	38·2
	9	94·6	57·2	35·1
	10	102·3	58·6	39·2
Geometric mean		101·0	60·0	38·6
		Exp. Y_x	Exp. Y_x	Exp. Y_x
		101·6	59·3	38·3

Exp. Y_x is the expected weight predicted from eqn 7.

Discussion

The exponential model developed in eqns 1–6 is an excellent model not only for rates of gastric evacuation in trout, but also for the relationship between evacuation rate and water temperature. If the amount of digestible organic matter (Y_x) remaining in a stomach after X h at T°C is expressed as a percentage of the total amount of organic matter in a meal ($Y_o = 100\%$), then a general equation for the relationship between Y_x and T is easily derived from eqns 2 and 5 thus:

$$\log_e Y_x = \log_e Y_o - RX = \log_e 100 - Xae^{bT} = 4{\cdot}6052 - Xae^{bT} \quad (8)$$

where a and b are constants from eqn 5 (see Table 6). Values of $Y_x\%$ can be either calculated from eqn 8 or estimated directly from Fig. 7 for all water temperatures between 4°C and 19°C.

The general relationship described by eqn 8 and illustrated by Fig. 7 assumes that the relative rate of gastric evacuation is not affected by the size of the trout, the size

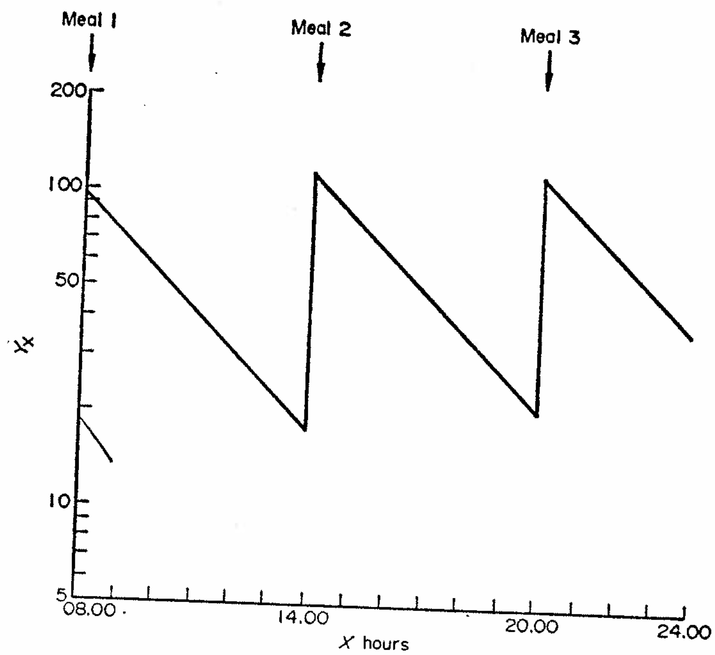

Fig. 6. Expected changes in the dry weight (Y_x mg) of digestible organic matter remaining in the stomachs of trout which were fed with three meals over 16 h at 15·0°C.

of the food, the size of the meal, short starvation periods (< 7 days), or the frequency with which meals are taken. These assumptions were all confirmed by the results of the feeding experiments. Barrington (1957) suggested that fish digest small meals more rapidly than large meals and small prey more quickly than large prey. The results of the present study and those of other workers (Hunt, 1960; Windell, 1966; Kitchell & Windell, 1968; Tyler, 1970) do not support these suggestions, and show conclusively that the amount of food evacuated in unit time is increased as the size of the meal is increased (e.g. Fig. 3).

The rate of gastric evacuation in trout was found to be affected by long starvation periods (> 7 days), by the type of food organism and by water temperature. Long starvation periods (7, 14, 25 days) also decreased the evacuation rate in bluegill sunfish, *Lepomis macrochirus* Rafinesque, and reduced the size of the pyloric caeca (Windell, 1966). Shrinkage of the pyloric caeca was observed in trout starved for 10, 15 and 20 days in the present study, and this suggests a decrease in enzyme production with long starvation periods (cf. Barrington, 1957). The occurrence of empty stomachs in wild populations of trout indicates that fasting does occur, but the length and frequency of these periods are unknown. In a study of the food of brook trout, Hess & Rainwater (1939) first suggested that the type of food organism may affect evacuation rates and Reimers (1957) found that complete gastric evacuation in rainbow trout took longer for meals of caddis larvae than for meals of oligochaetes and *Gammarus*. Windell (1966) however, found that evacuation rates in bluegill sunfish were very similar for different food organisms and the only major exception was larvae of *Tenebrio molitor*. Evacuation rates in the present study were very similar for the wide variety of food organisms in group 1 (see Table 3) and were not affected by either the degree of chitin-

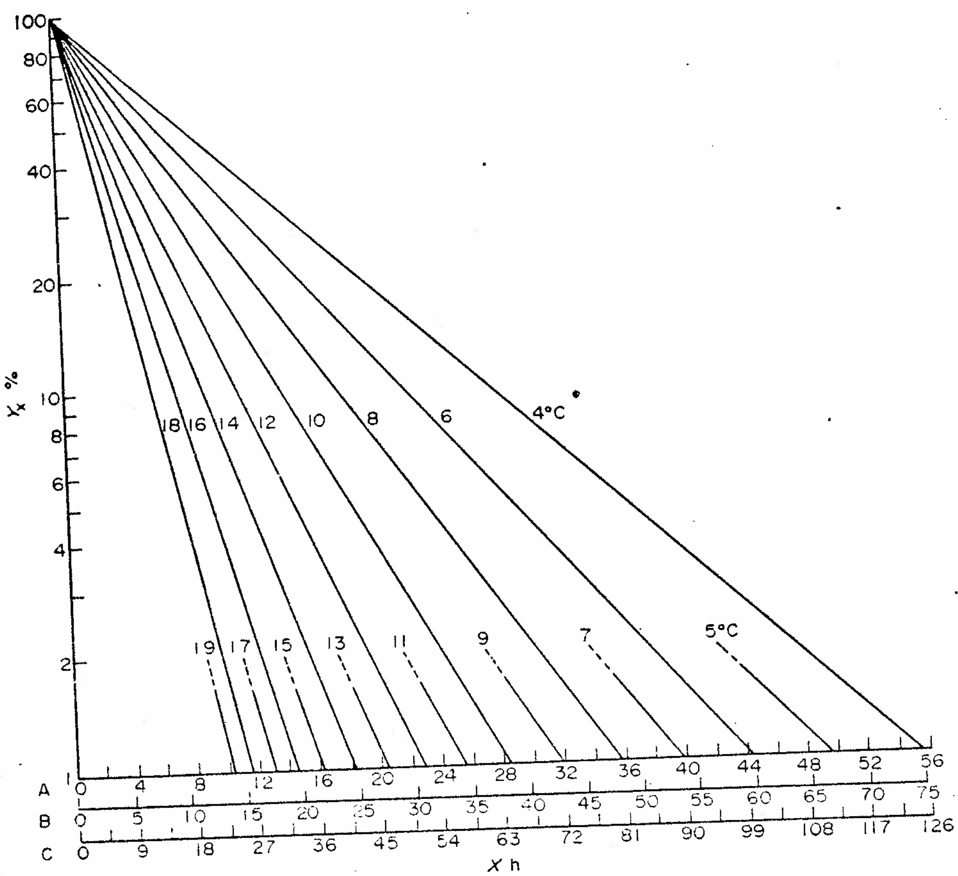

Fig. 7. Percentage of digestible organic matter (Y_x%) remaining in a stomach after X h at water temperatures between 4°C and 19°C. Scales on abscissa are for different food organisms: (A) group 1, (B) *Hydropsyche*, (C) *Tenebrio molitor*.

ization or the water content of the food organisms. The slower evacuation rates for food organisms in group 2 cannot be explained, but may be partially due to the high fat content in larvae of *Tenebrio molitor* and *Hydropsyche*. Fats are known to delay gastric evacuation in other vertebrates (Quigley & Meschan, 1941). Several workers have recorded a positive correlation between water temperature and rates of gastric evacuation in fish, but the only detailed study for salmonids is by Brett & Higgs (1970) who studied the gastric evacuation of a pelleted food in young sockeye salmon. They also found an exponential rate of gastric evacuation, and their results for a pelleted food were very similar to those obtained for *Hydropsyche* in the present study.

Several workers (e.g. Bajkov, 1935; Darnell & Meierotto, 1962; Windell, 1966) have suggested that once the rate of gastric evacuation is known, the daily food consumption can be easily calculated. These methods require several assumptions which are often unrealistic, e.g. the fish are usually assumed to feed continuously. The amount of food found in a fish's stomach at an instant in time depends upon the amount and type of food eaten by the fish, the rate of gastric evacuation, and the length of time since the food was ingested. Therefore knowledge of the size and frequency of meals is required before the daily consumption can be estimated. A trout curtails its feeding after filling its stomach, and does not eat more food even though plenty of food is available (Brown, 1951). This was very obvious in the present study when trout were fed to satiation, but the maximum size of the meal varied with the type of food organism and also between trout of similar length and weight. As complete gastric evacuation of a meal takes longer than 24 h at water temperatures below 11 °C (Fig. 7), a trout can take small meals at frequent intervals or large meals at long intervals, but not large meals at frequent intervals. More information on the frequency of meals is clearly needed before any generalizations can be made.

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