

In situ determination of food daily ration in fish: review and field evaluation

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Synopsis

A literature review showed that numerous studies have dealt with the estimation of fish daily ration in the field. Comparisons of results from different studies are often difficult due to the use of different approaches and methods for parameter estimations. The objective of the present study was to compare the most commonly used approaches to estimate fish daily ration and to propose a standardized procedure for their estimation in the field. Comparisons were based on a field experiment specifically designed to investigate these questions and on data and theoretical considerations found in the literature. The results showed that (1) the gut fullness computed with entire digestive tract content is preferable to the stomach content only, supporting recent research done on other fish species; (2) it is important to consider the data distribution before estimating parameters; (3) estimates of experimental evacuation rates should be used rather than maximum evacuation rate for species showing no feeding periodicity; (4) it is necessary to exclude parasites from gut content in the computation of daily ration as they may significantly decrease daily ration estimates (by an average of 29.3% in this study); and (5) the Eggers (1977) model is as appropriate as, and less complex than, the Elliott & Persson (1978) model for estimating fish daily ration in the field, again supporting recent experiments done on other fish species.

Introduction

A review of literature from the past 20 years shows that numerous studies have been conducted to describe daily ration in fish (Godin 1981, Garcia & Adelman 1985, Brodeur & Pearcy 1987, Amundsen & Klemetsen 1988, Booth 1990, Sagar & Glova 1988, Walsh et al. 1988). The estimation of fish daily ration was widely used to investigate questions such as the relation between ration and growth (Walsh et al. 1988, Boisclair & Leggett 1989, Parrish & Margraf 1990a, Walh & Stein 1991), predation pressure on prey species (Boisclair & Leggett 1985, Ruggerone 1989, Vigg et al. 1991), profitability of different

habitats (Swenson 1977, Héroux 1990), impact of environmental modifications (Borgström et al. 1992), food limitations during the season (Ensign et al. 1990), and competition (Parrish & Margraf 1990a). Recently, the estimation of fish daily ration has been used to test bioenergetic models in different species (e.g. Fox 1991, Walh & Stein 1991, Boisclair & Sirois 1993, Trudel & Boisclair 1993).

Daily ration in fish can be estimated using many different approaches. Food daily ration can be determined completely from laboratory experiments (Walh & Stein 1991), from in situ experiments (Thorpe 1977, Boisclair & Leggett 1985, 1988, 1989, Garcia & Adelman 1985, Kolok & Randorf 1987,

Booth 1990, Sagar & Glova 1988, Walsh et al. 1988), and often with a combination of both approaches (e.g. daily variations of food content weight determined in the field and food evacuation rate estimated in laboratory; Swenson 1977, Godin 1981, Brodeur & Pearcy 1987, Amundsen & Klemetsen 1988, Ruggerone 1989, Brodeur et al. 1992).

There are also many different ways of estimating fish daily ration within each of these general approaches. First, several models have been proposed to estimate fish daily ration (Swenson & Smith 1973, Eggers 1977, 1979, Thorpe 1977, Elliott & Persson 1978, Pennington 1985, Sainsbury 1986, Hayward et al. 1991). Among these, two models have been widely used, those of Eggers (1977) and Elliott & Persson (1978). Although some attempts have been made to compare the accuracy of both models in terms of absolute differences and variability of estimated parameters (Amundsen & Klemetsen 1986, Boisclair & Leggett 1988, Ruggerone 1989, Hayward 1991, Boisclair & Marchand 1993), there is still no clear evidence showing which model gives the more accurate results.

Second, the estimation of food content weight (W) required for the computation of daily ration can be made considering stomach content only or the content of the entire digestive tract (stomach + intestine; Boisclair & Leggett 1988, Boisclair & Marchand 1993). Because evacuation rates based on digestive tract content are slower than those computed with stomach content only (Grove & Crawford 1980), it has been suggested that the use of the former would decrease the probability of missing a meal between two successive sampling periods (Boisclair & Leggett 1988, Boisclair & Marchand 1993).

Third, the instantaneous evacuation rate of food (R), also needed for the computation of fish daily ration, can be based on estimations from either tank experiments or from the maximum evacuation rate between two consecutive sampling period. In tank experiments, the instantaneous evacuation rate corresponds to the slope of the relation between food content (ln-transformed) and time for fish evacuating food during a complete evacuation cycle in field or laboratory experiments (e.g. Persson 1979, Amundsen & Klemetsen 1988, Boisclair &

Leggett 1988) while the maximum evacuation rate corresponds to the highest evacuation rate observed over all the time intervals under consideration (e.g. Boisclair & Leggett 1985, Fox 1991). Although the assumptions of these two approaches differ substantially (see next section), no attempt was made to compare their relative accuracy.

Fourth, the estimation of W values can be based on raw, back log-transformed, or median data, depending on the structure of the data, its effect on the central tendency, and the parameters of interest. Although some analyses have included data transformation, no specific rules were suggested to standardize fish daily ration estimations and thereby facilitate comparison between different studies.

Finally, another source of variation in estimation of daily ration in a given species is the inclusion or exclusion of parasites in the stomach or digestive tract content weight determinations. We found no indication in the literature that stomach or digestive tract contents were examined before weighing; moreover, there is no evidence that, if present, parasites were excluded from weight determinations. Nevertheless, parasites may represent a significant part of the stomach and digestive tract contents.

The main objectives of the present study were then to compare the estimated *in situ* daily ration in fish from: (1) stomach and entire digestive tract contents, (2) raw, back log-transformed, and median data, (3) instantaneous evacuation rates from tank experiments and from maximum food decline in the gut between two consecutive sampling periods, (4) computations including and excluding parasites from food content weight determinations, and (5) using the Eggers (1977) and Elliott & Persson (1978) models. Comparisons were based on a field experiment specifically designed to investigate these questions and on data and theoretical considerations found in the literature. Two secondary objectives were (1) to suggest standard symbols for future application and (2) to propose what would be the best approach for the *in situ* estimation of daily ration in fish.

The models

The estimation of daily ration requires information on (1) the mean quantity of food found in the gut of fish during a given time interval (e.g. 24 h) and (2) the rate of food evacuation during that interval. In this section, we describe the different approaches used to estimate these parameters and the two most commonly used models to estimate daily ration, those of Eggers (1977) and Elliott & Persson (1978). The symbols used in this section are usually based on their most frequent use in the literature (Table 1).

Instantaneous evacuation rate (R)

Three models have been used to describe the relation between food evacuation and time in fish: the linear, exponential, and square root models. However, recent empirical and theoretical studies have suggested that the exponential model is probably the most appropriate for describing the evacuation of food in most fish species (Persson 1986, Brodeur & Pearcy 1987, Ruggerone 1989). This model is expressed as:

$$W_t = W_0 e^{-Rt}, \quad (1)$$

where W_0 is the amount of food at the beginning of the time interval, W_t is the amount of food at time t , and R is the instantaneous evacuation rate; the relation is computed over a complete evacuation cycle. A semi-logarithmic transformation of this equation gives a linear model that can be fitted with current mean squares procedures as:

$$\ln W_t = \ln W_0 - Rt. \quad (2)$$

(a) R determined from tank experiments ($R_{(exper)}$)

In this form, the instantaneous evacuation rate (R) corresponds to the slope of the relation between $\ln W_t$ and time. The instantaneous evacuation rate is often estimated in the laboratory (Swenson 1977, Godin 1981, Brodeur & Pearcy 1987, Parrish & Margraf 1990b). In these studies, fish captured in the field are acclimated to laboratory conditions with respect to temperature, photoperiod, and artificial feeding (usually with a unique type of prey, comparable or similar to those encountered in the field). Prior to the experiments, the fish are generally starved, then fed ad libitum and sacrificed at regular time intervals until a given group has completely evacuated their meal ('serial slaughter method'; Windell 1967). This approach is based on the assumptions that laboratory conditions, starvation prior to feeding, prey type, and lack of prey diversity do not have any effects on the evacuation rate. One advantage of this procedure is that the fish are presumed to be unstressed following acclimation and during the experiments. There are also studies where the instantaneous evacuation rates were estimated from field experiments (Thorpe 1977, Garcia & Adelman 1985, Boisclair & Leggett 1988, Booth 1990, Walsh et al. 1988, H  roux 1990, H  roux & Magnan unpublished). In these cases, the fish were captured in the field at a selected period of the day and immediately placed in experimental tanks on the shore of the lake or stream. Each experimental tank was supplied by a continuous flow of filtered water coming from the same depth/temperature of capture. The fish are then sampled at regular intervals from the time of capture and processed as in the laboratory experiments. With this approach, one

Table 1. Definition of symbols used in the text.

C	Food consumption
$C_{24(E)}$	Daily ration following the Eggers (1977) model
$C_{24(E)C}$	Daily ration following the corrected Eggers (1979) model
$C_{24(E-P)}$	Daily ration following the Elliott & Persson (1978) model
F	Gut fullness
K	Number of time intervals
R	Instantaneous evacuation rate
$R_{(exper)}$	Experimental instantaneous evacuation rate
$R_{(max)}$	Maximum instantaneous evacuation rate
t	Hour
T	Duration of the time interval
T_i	Time interval i
W	Weight of food in the stomach or digestive tract
W_0	Weight of food at the beginning of a given time interval
W_t	Weight of food at time t
W_{24}	Mean weight of food content over 24 h
W_F	Fish weight

assumes that the stress of capture and holding conditions do not affect the evacuation rate and that the time of capture is representative of the feeding mode of the species. The advantage of this approach is that it better integrates all other field conditions (prey types and diversity, individual variability, and evacuation rate under normal feeding mode, i.e. without any forced starvation period). This type of estimation will hereafter be called the *experimental* evacuation rate ($R_{(exper)}$).

(b) R determined from periods of maximum food decline in the gut ($R_{(max)}$)

The maximum evacuation rate is computed from fish captured in the field (Boisclair & Leggett 1985, Kolok & Randorf 1987, Sagar & Glova 1988, Fox 1991). One instantaneous evacuation rate ($R_{(Ti)}$) is computed for each time interval (Ti) under consideration:

$$R_{(Ti)} = \frac{\ln W_t - \ln W_0}{T}, \quad (3)$$

where T is the duration of time interval. In a given experiment, the estimated evacuation rate corresponds to the highest rate observed over all the time intervals under consideration as:

$$R_{(max)} = \text{Maximum value of } R_{(Ti)}, \quad (4)$$

It is implicit here that a given value of $R_{(Ti)}$ is computed only when W_0 and W_t are significantly different. This approach is based on the assumptions that food evacuation is constant over a complete feeding cycle and that $R_{(max)}$ is representative of R because it corresponds to a period of minimum or no feeding by the fish (i.e. that reflect food evacuation only). The use of $R_{(max)}$ is also based on the assumption that short-term stochastic events involving decrease of feeding (e.g. storm, strong wind) will not affect the estimation of maximum evacuation rate.

Eggers (1977) model

The estimation of daily ration following the Eggers model ($C_{24(E)}$) is given by the equation:

$$C_{24(E)} = W_{24} \cdot R \cdot 24, \quad (5)$$

where W_{24} is the mean weight of food content over 24 h. This model is based on the assumption that the weight of food in the stomach or digestive tract does not change between the beginning and end of the 24 h cycle. However, Eggers (1979) suggested a modification of his 1977 model that corrects the daily ration estimates when this assumption is not met (i.e. when the weight of food in the stomach or the digestive tract at the beginning and at the end of the 24 h cycle are significantly different) as:

$$C_{24(E)C} = C_{24(E)} + (W_{t=24} - W_{t=0}). \quad (6)$$

Amundsen & Klemetsen (1986) suggested that the corrected Eggers (1979) model is likely to give more robust estimates of food consumption than the Elliott & Persson (1978) model when there is large within-sample variability in the weight of food in the stomach or digestive tract. Hayward (1991) also showed that the corrected Eggers (1979) model gives estimations of daily ration closer to those of the Elliott & Persson (1978) model than the earlier Eggers (1977) one. Although Eggers (1979) reported that his model was not recommended for piscivorous fish that consume large prey periodically and have slow rates of evacuation, the results of Boisclair & Leggett (1988) suggested that it can be applied to species that feed throughout the day on a wide range of prey types, exhibiting occasional feeding peaks, and having no rigid feeding periodicities.

Elliott & Persson (1978) model

The estimation of daily ration following the Elliott & Persson model corresponds to the summation of the amount of food consumed during consecutive time intervals over 24 h, each time interval being preferably 3 h or less (Elliott & Persson 1978). The food consumed during a given time interval (C_{Ti}) is estimated using the equation:

$$C_{Ti} = \frac{(W_t - W_0 e^{-RT}) RT}{1 - e^{-RT}} \quad (7)$$

and the daily ration, with the equation:

$$C_{24(E-P)} = \sum_{i=1}^K C_{Ti} \quad (8)$$

By its nature, the Elliott & Persson model assumes that food evacuation is exponential and that the rate of food consumption within the sampling interval is constant (Godin 1981).

Computation of daily ration

There are two different ways of expressing daily ration: in g food g fish⁻¹ d⁻¹ or in % body weight d⁻¹, from equations 5, 6, 7, and 8. In fact, the two methods determine a meal in g d⁻¹ for a given group of fish. The first way of estimating daily ration is by dividing the daily meal by the mean weight of the fish used in the experiment, what was called appropriately 'a typical fish' by Ruggerone (1989). Second way is to substitute the food content weight (W) in equations 5, 6 and 7, by the gut fullness (F) using the equation:

$$F = (W/W_F) \cdot 100, \quad (9)$$

where W_F is the weight of each corresponding fish. However, one must be cautious in using such a ratio in the computation of daily ration, as well as in any biological parameters (see Packard & Boardman 1988). The standardization or adjustment of any variable by dividing individual values by corresponding measures of body size (or body weight) is based on the implicit assumption that the variable of interest varies isometrically with body size, i.e. that the relation between a given variable and body size (1) is linear, and (2) passes through the origin (Packard & Boardman 1988).

Measure of central tendency

The data distribution may affect both W and R estimations. First, in calculating W, the use of the arithmetic mean is justified when food content weights are normally distributed while the geometric mean is more appropriate when there is heteroscedasticity and the variances are proportional to the mean

values (Amundsen & Klemetsen 1986). Some authors have used the median values in the estimation of food content weight (Clarke 1978, Cochran & Adelman 1982, Garcia & Adelman 1985, Parrish & Margraf 1990b), but this parameter does not integrate the values of all measurements. Second, in the estimation of evacuation rate, the presence of null or very low values in food content weight, especially in the first sampling periods, may bias the R estimations (see Amundsen & Klemetsen 1988). This is mainly due to the fact that some fish emptied their stomachs before sampling, in the field or laboratory. In such cases, the median has been suggested to be a better estimation of central tendency than the arithmetic mean (Amundsen & Klemetsen 1988).

Materials and methods

Study lake

The study was done in Lake Simpson, Mastigouche Reserve, north of Trois-Rivières, Québec, Canada (46°38' N, 73°15' W) between 10 and 12 June 1992. This lake is a typical small oligotrophic temperate zone lake with respect to area (28.5 ha), mean depth (3.3 m), conductivity (12.5 µS cm⁻¹), Secchi disk transparency (2.5 m), dissolved oxygen, and thermal stratification (Magnan 1988). Brook charr, *Salvelinus fontinalis*, and northern redbelly dace, *Phoxinus eos*, are the only fish species in the lake. Lake temperature varied between 17.8–19.0° C in the first 2 m of the littoral zone during the three days of the experiment.

Fish sampling

Brook charr were captured in the littoral zone with 5 multifilament gill nets (1.5 m in height × 30 m long with stretched mesh of 2.5 cm) at 3 h intervals starting at 15:00 h on 10 June 1992 and continuing for 48 h. The nets were never left more than 60 minutes in the water (mean ± SD: 37 ± 8 min). The sample consisted of 239 brook charr (1+) ranging from 106 to 180 mm total length (TL). Fish were killed with tert-amyl alcohol and placed in a 5% formalin solu-

tion after an incision was made in the abdomen. In the laboratory, charr were measured (± 1 mm) and weighed (± 0.01 g wet). The stomach and intestine contents and parasites associated with each part of the digestive tract were dried separately (24 h at 60°C) and weighed (± 0.01 mg dry). These fish were used to estimate the food content weight at time t (W_t) and the maximum evacuation rate ($R_{(\max)}$).

Another group of fish were seined at approximately 1 hour intervals between 22:00 h on 11 June, and 4:00 h on 12 June 1992 for the determination of experimental evacuation rate ($R_{(\text{exper})}$). This sample consisted of 59 brook charr (1+) ranging from 97 to 172 mm (TL). Immediately after capture, the fish were placed in eight different experimental tanks along the shore. Each tank was supplied with a continuous flow of filtered water (243 μm mesh net) from the littoral zone using a 3.2 cm submersible pump powered with a gasoline current-generator. Water in the tanks was always within 1°C of the mean temperature of the littoral zone. Four to nine charr were then sampled at 3 h intervals for nine

consecutive intervals to follow the progression of food in the stomach and digestive tract. For each period, fish were sampled arbitrarily from the different tanks to randomize the effect of time of capture on their evacuation rate. Fish were processed as previously described.

Food content weight versus gut fullness

We compared the coefficients of variation of mean weight of stomach or digestive tract content (\bar{W}) and gut fullness (\bar{F}) with a variance ratio test (Zar 1984) to assess the suitability of using gut fullness in daily ration estimation. We also tested the null hypothesis that there is no significant relationship between gut fullness and fish weight to determine if gut fullness remove the effect of fish size on food content weight determination (Packard & Boardman 1988). A paired t-test was used to determine if the presence of parasites contributed significantly to the weight of stomach and digestive tract con-

Table 2. Comparison of food content weight (g dry weight) and gut fullness (g dry weight 100 g fish wet weight⁻¹) from fish captured in the gill net experiment for stomach only and entire digestive tract (stomach + intestine). Mean, standard deviation (in parentheses) and coefficient of variation (%). Lake Simpson, 10–12 June 1992.

	Number of sampling periods	Number of observations	Food content weight (W)	Gut fullness (F)	F ratio*	p on C.V.
Stomach content						
Day 1	9	169	0.042 (0.033) 78.5	0.154 (0.113) 73.3	1.110	NS
Day 2	9	70	0.045 (0.045) 100.0	0.172 (0.209) 121.5	1.047	NS
Pooled data	17	239	0.043 (0.036) 83.7	0.159 (0.147) 92.5	1.082	NS
Digestive tract content						
Day 1	9	169	0.078 (0.047) 60.3	0.284 (0.144) 50.7	1.340	< 0.05
Day 2	9	70	0.077 (0.060) 77.9	0.284 (0.232) 81.7	1.145	NS
Pooled data	17	239	0.078 (0.051) 65.4	0.284 (0.174) 61.3	1.259	< 0.01

* ANOVA (Zar 1984).

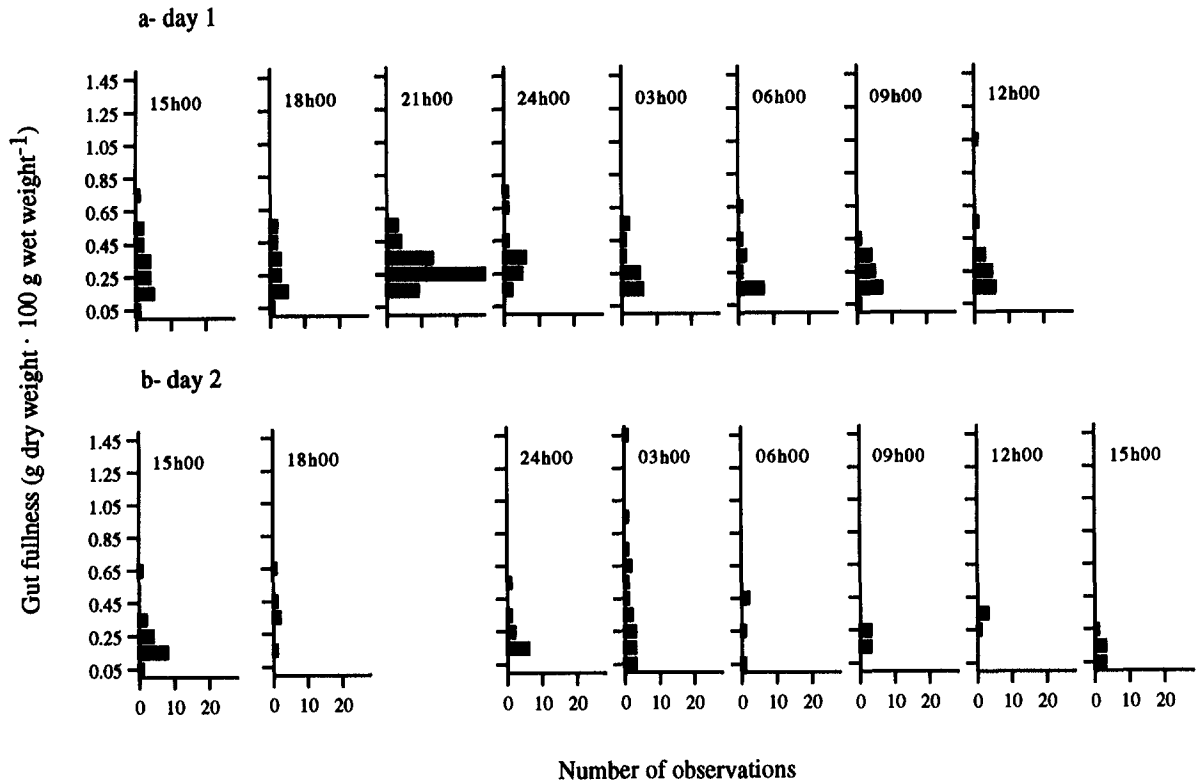


Fig. 1. Distribution of gut fullness data on the two days of experiments: a – 10–11 June 1992; b – 11–12 June 1992.

tent. Furthermore, we compared the use of the arithmetic mean, geometric mean, and median in the computation of food content weight to determine the effect of data distribution on the central tendency and on the parameters of interest.

Statistical analysis

An analysis of variance (ANOVA) followed by an a posteriori Student-Newman-Keuls multiple-range comparison test (SNK) were used to determine if there were any significant differences in the mean food content weight for each sampling period between both days of the experiment and also among the different sampling periods. The homogeneity of variances was tested with an F_{\max} -test (Sokal & Rohlf 1981); when variances were heterogeneous, data were $\log(x)$ transformed prior to analysis. Even though the variance of some data sets were heterogeneous, we assumed that departures from

the assumption of homogeneity of variance had no marked effect on the ANOVA's significance level (Sokal & Rohlf 1981). Linear regression analysis was used to estimate the experimental evacuation rate ($R_{(\text{exper})}$) on \ln -transformed food content weight (F) values.

Bootstrap simulations (Crowley 1992) were used to estimate the standard error of each parameter to be compared ($R_{(\text{exper})}$, $R_{(\text{max})}$, $C_{24(E)}$, and $C_{24(E-P)}$) and to generate a distribution of differences between two given parameters based on their simulated values. For $R_{(\text{exper})}$, values of F were randomly drawn with replacement from the values obtained at each sampling period (tank experiments). These values were then used to compute the slope of the relation between $\ln(F)$ and time (equation 2), which represents one simulated value of $R_{(\text{exper})}$. A total of 5000 simulated values of $R_{(\text{exper})}$ were generated. The standard deviation of 5000 simulated values is considered to be a close approximation of the parameter's standard error (Manly 1991). For $R_{(\text{max})}$, val-

ues of F were randomly drawn with replacement from the values obtained at each of the two consecutive sampling periods yielding the maximum evacuation rate (from gill net sampling). These values were then used to compute one simulated value of $R_{(max)}$ following equation (3). As for $R_{(exper)}$, 5000 simulated values of $R_{(max)}$ were generated to approximate the standard error of $R_{(max)}$. Individual estimations of $C_{24(E)}$ and $C_{24(E-P)}$ were computed following equations 5 and 8, respectively, by randomly selecting (1) values of F for each sampling period from the values obtained at each sampling period (from gill net sampling), and (2) one value of $R_{(exper)}$ within the preceding set of 5000 values generated above. The simulated $R_{(exper)}$ values were used only once in the computation of $C_{24(E)}$ and $C_{24(E-P)}$. In addition, a distribution of the difference between both types of evacuation rate ($R_{(exper)}$, $R_{(max)}$) and both models used to compute daily ration (Eggers 1977, Elliott & Persson 1978) were established using the simulated values computed with the bootstrap method. This distribution was generated as the difference between two simulated values minus the observed difference. Two values were considered significantly different ($\alpha < 0.05$) when the observed difference was outside the central 95% values of the generated distribution of differences (Manly 1991).

Results and discussion

Food content weight versus gut fullness

We found a significant difference ($p < 0.001$) between food content weight including parasites and food content weight excluding parasites, both when computed with W ($t = 9.84$; $df = 122$) or F ($t = 11.98$; $df = 122$) values. Consequently, the analyses of food content weight and feeding periodicity were done excluding the parasites. There was no significant difference ($\alpha > 0.05$) between the coefficients of variation of W and F when using stomach content only (Table 2). However, for the complete digestive tract, the coefficient of variation of F was significantly lower than for W for the first day of the experiment and for the pooled data. In all cases, the coefficients of variation were significantly smaller when using the complete digestive tract than stomach content only ($\alpha < 0.01$). These results suggest that the use of complete digestive tract should be preferred over the stomach content only, supporting the conclusion of Boisclair & Leggett (1988) and Boisclair & Marchand (1993).

The regression analysis showed that gut content estimated from complete digestive tract content was isometrically related to fish body size ($F_{1,237} =$

Table 3. Arithmetic mean (with SD in parentheses), geometric mean (with 95% CI in parentheses) and median values of gut fullness (F ; g dry weight 100 g fish wet weight⁻¹) computed with entire digestive tract content from fish captured in the gill net experiment; Lake Simpson, 10–12 June 1992.

Sampling period	Number of observations	Arithmetic mean	Geometric mean	Median
3	33	0.350 (0.054–0.646)	0.267 (0.066–1.497)	0.265
6	16	0.279 (0.111–0.447)	0.238 (0.085–0.698)	0.201
9	24	0.222 (0.120–0.324)	0.199 (0.056–0.414)	0.214
12	20	0.314 (0.119–0.509)	0.276 (0.117–1.021)	0.274
15	42	0.240 (0.086–0.394)	0.199 (0.053–0.697)	0.203
18	22	0.308 (0.152–0.464)	0.268 (0.086–0.618)	0.310
21	57	0.283 (0.179–0.387)	0.264 (0.104–0.568)	0.274
24	26	0.295 (0.140–0.450)	0.264 (0.135–0.734)	0.266

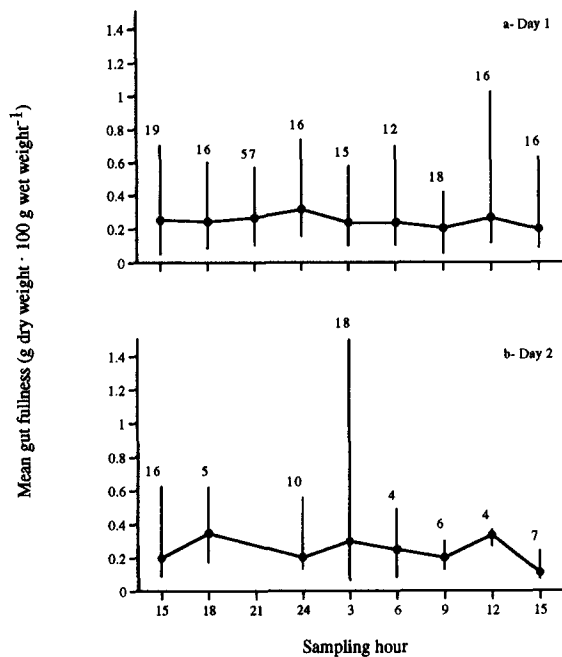


Fig. 2. Mean gut fullness (with 95% CI) for each sampling period for the two days of experiments: a – 10–11 June 1992; b – 11–12 June 1992. Numbers of observations are indicated at the top of 95% CI.

66.28, $p < 0.001$) and that gut fullness (F) remove the effect of fish size on food content weight determination ($F_{1,237} = 0.48$, $p > 0.49$). Considering these results, we calculated gut fullness (F) using the entire digestive tract content in this paper.

Measure of the central tendency in food content weight

For each given sampling period, we found no significant difference in the mean food content weight

between the two days of the experiment ($\alpha > 0.05$) with the exception of 15:00 h ($F_{2,39} = 5.61$, $p < 0.007$) and 24:00 h ($F_{1,24} = 4.70$, $p < 0.041$). We then pooled the data for the two days for each given sampling period for further analysis. The arithmetic means of gut fullness were always higher than the medians (Table 3), indicating that the data were not normally distributed. In fact, the distribution of F values were often skewed to the right (Fig. 1), as Amundsen & Klemetsen (1986) had previously observed with Arctic charr, *Salvelinus alpinus*. Using the arithmetic mean when data are not normally distributed can result in an overestimation of daily ration values, emphasizing the importance of considering the data distribution before computation (Amundsen & Klemetsen 1988). Considering our data set, the geometric mean appeared more appropriate for our calculations (Table 3, Fig. 2); the geometric mean was then used in all subsequent analyses of food content weight.

Feeding periodicity

Our results showed no feeding periodicity during the 24 h period (Fig. 2; $p > 0.05$). We then assumed that fish were feeding continuously, fulfilling the Eggers model assumption for computation of daily ration. Ruggerone (1989) found similar results with coho salmon, *Oncorhynchus kisutch*, while Sagar & Glova (1988) concluded that juvenile chinook salmon, *Oncorhynchus tshawytscha*, showed a diel feeding periodicity when feeding in the drift. Other results suggest that juvenile brook charr (1+) show no feeding periodicity while adults (2+, 3+) are active mainly at dawn and dusk (Bourke, Magnan and Rodriguez, unpublished).

Table 4. Comparison of experimental (R_{exper}) and maximum (R_{max}) evacuation rates for brook charr captured in Lake Simpson, 10–12 June 1992. Values are $R \text{ h}^{-1} (\pm 1 \text{ S.E. in parentheses})$.

	Experimental evacuation rate (R_{exper})	Maximum evacuation rate (R_{max})	p-value
Digestive tract	0.104 (± 0.020)	0.110 (± 0.047)	NS
Digestive tract + parasites	0.064 (± 0.010)	0.102 (± 0.044)	NS
p-value	< 0.005	NS	

Table 5. Comparison of experimental ($R_{\text{(exper)}}$) evacuation rates based on mean or median values of gut fullness (F) for brook charr captured in Lake Simpson, 10–12 June 1992. Values are $R \text{ h}^{-1} (\pm 1 \text{ S.E. in parentheses})$.

	$R_{\text{(exper)}}$ based on mean values	$R_{\text{(exper)}}$ based on median values
Digestive tract	0.104 (± 0.020)	0.091
Digestive tract + parasites	0.064 (± 0.010)	0.061

Evacuation rates

Experimental ($R_{\text{(exper)}}$) and maximum ($R_{\text{(max)}}$) evacuation rates did not differ significantly ($p > 0.05$) when using the entire digestive tract contents of brook charr whether we included or excluded parasites from the computation (Table 4). Based on the bootstrap simulation, the standard error is greater when using $R_{\text{(max)}}$ than $R_{\text{(exper)}}$. This result can be explained by the nature of both methods: the experimental evacuation rate ($R_{\text{(exper)}}$) integrates the evacuation of food over a complete 24 h cycle and it is computed through a regression approach that gives the best fit of food evacuation over time. For this reason, $R_{\text{(exper)}}$ is probably more stable and more representative than $R_{\text{(max)}}$, the latter being more subject to short-term variation (or events) as it uses only one time interval i to compute the evacuation rate. The inclusion of parasites had a significant effect ($p < 0.05$) on experimental ($R_{\text{(exper)}}$) but not on maximum ($R_{\text{(max)}}$) evacuation rate. This could also be explained by the nature of both methods. In computing $R_{\text{(exper)}}$, the inclusion of parasites lowers the slope of the relation between food content and time because they stay in the digestive tract as the food is evacuated. In computing $R_{\text{(max)}}$, the inclusion of parasites just added a constant to the equation

and had little effect on the evacuation rate. In addition, the greater variation associated with $R_{\text{(max)}}$ might have prevented the detection of a significant difference between $R_{\text{(max)}}$ with and without parasites. For these reasons, we concluded that $R_{\text{(exper)}}$ is a better estimation of the evacuation rate and used this in our further computations.

Experimental ($R_{\text{(exper)}}$) evacuation rates were not significantly different ($p > 0.05$) when computed with mean or median of ln-transformed values of gut contents for digestive tracts with or without parasites (Table 5). The $R_{\text{(exper)}}$ computed with the median is included in the standard error of the $R_{\text{(exper)}}$ computed with the mean values. When data sets of food content weight are normally distributed, one would expect to get the same experimental ($R_{\text{(exper)}}$) evacuation rate computed either with mean or median values. This is not always the case with such a sample size and with salmonids; for example, our results indicated that with a frequency distribution skewed to the right, it is more appropriate to use the means of ln-transformed values. Therefore, one must be cautious and aware of the data distribution in selecting a specific way of computing evacuation rates. For example, the use of the arithmetic mean or the median of gut fullness may

Table 6. Comparison of the Elliott & Persson (1978) and the Eggers (1977) models for the computation of daily ration with experimental evacuation rate ($R_{\text{(exper)}}$) for brook charr captured in Lake Simpson, 10–12 June 1992. Values of C_{24} are in g dry weight 100 g fish wet weight⁻¹ $d^{-1} \pm 1 \text{ S.E. in parentheses}$.

	Eggers (1977)	Elliott & Persson (1978)	p-value
Digestive tract	0.61 (± 0.12)	0.62 (± 0.11)	NS
Digestive tract + parasites	0.42 (± 0.07)	0.45 (± 0.07)	NS
p-value	$\alpha = 0.0206$	$\alpha = 0.0258$	

have either overestimated or underestimated our $R_{(\text{exper})}$ determination.

Estimation of daily ration

Based on bootstrap simulations, we found no significant difference between the daily ration estimated from the Eggers (1977) or Elliott & Persson (1978) models ($\alpha > 0.05$; Table 6). The impact of including parasites was the same as for the evacuation rate: the inclusion of parasites significantly lowered the daily ration estimates (by an average of 29.3%) using either Eggers (1977) or Elliott & Persson (1978) model. This emphasized both the importance of considering parasites and of evacuation rate estimation in the computation of daily ration.

Conclusion

Some generalities can be emphasized both from the literature and from the results of the present study, which was specifically designed to evaluate different approaches of in situ determination of daily ration.

First, it is possible to use the mean weight of food (W) or the mean gut fullness (F) with both the stomach only or the complete digestive tract content for the computation of evacuation rates and daily rations. Because the variability around the mean is greater when computed with stomach content only, the use of the entire digestive tract is preferred. Boisclair & Marchand (1993) reached a similar conclusion in a study on pumpkinseed, *Lepomis gibbosus*. Their results showed that the choice of using stomach content only or entire digestive tract has a greater influence on the precision of daily ration estimates than the choice to use either the Eggers (1977) or Elliott & Persson (1978) model. However, when using the entire digestive tract, the inclusion of parasites leads to an overestimation of food content weight values (W or F). With fish from the field, it is necessary to remove parasites, if present, before estimating this parameter to avoid overestimation of daily ration estimates. The gut fullness (F) also reduced the variability around estimated values.

However, it is important to meet the assumptions underlying the use of such a ratio (Packard & Boardman 1988): the weight of food (W) should vary isometrically with body size. A simple way of checking this assumption on a given data set is to regress gut fullness against body size to determine if the ratio remove the effect of body size. Second, it is important to compute all parameters using the same procedure when estimating daily ration. If the evacuation rate is computed using gut fullness, gut content should also be computed using gut fullness, otherwise the daily ration will be under- or overestimated depending on which values was used. For example, Borgström et al. (1992), in a study on brown trout, *Salmo trutta*, estimated the mean stomach content with gut fullness (F) and used the evacuation rate, estimated by Elliott (1972), based on stomach content weight (W) values. If we had estimated our daily ration in this way, we would have obtained 0.64 g dry weight 100 g fish wet weight⁻¹ d⁻¹ instead of 0.61 g dry weight 100 g fish wet weight⁻¹ d⁻¹. When comparing evacuation rate, one must also ensure that all values have been computed with the same parameters, as R computed with W tends to be higher than those computed with F. In a study on Arctic charr, Amundsen & Klemetsen (1988) compared their results of evacuation rate computed with F with those of Elliott (1972) that were computed with W. They concluded that the observed difference was due to an underestimation of their evacuation rate. This difference may also reflect the use of two different parameters in the estimation of evacuation rates. In our study, R computed with W gave a value of 0.110 compared to 0.104 with F. The daily ration estimated completely with either W or F will be similar only if the fish have a similar weight. Our daily ration estimate with W was 0.612 g dry weight 100 g fish wet weight⁻¹ d⁻¹ compared to 0.609 g dry weight 100 g fish wet weight⁻¹ d⁻¹ with F. These examples emphasized the importance of being consistent in the way of using data in computation of daily ration.

Third, as previously mentioned by Amundsen & Klemetsen (1986), it is important to consider the data distribution when estimating daily ration. One should use raw data when it is normally distributed because the mean is a good estimate of the central

tendency. However, data are often skewed when working with fish from the field. With such a data set, we suggest to use the geometric mean for data that are skewed to the right, as in the present study. In experiments where the fish are fed *ad libitum* in the laboratory to determine $R_{(exper)}$, the absence of food in fish stomachs often causes a skewed distribution to the left. In these cases Amundsen & Klemetsen (1988) suggested the use of median value to avoid underestimation of the evacuation rate. The use of median values in our study also led to an underestimation of $R_{(exper)}$ even though our data were skewed to the right. This emphasizes the importance of considering data distribution in the computation of daily ration.

Fourth, the comparison of experimental and maximum evacuation rates showed no significant differences in our study. The absence of significant differences in gut fullness among the different sampling period indicate that 1+ brook charr showed no feeding periodicity. In such a case, the maximum evacuation rate should be theoretically equal to zero, and any observed differences is the result of natural variability, as in our study. As there is no relationship between meal size and evacuation rate (Persson 1981), the use of tank experiments to estimate the instantaneous evacuation rates should then be preferred in these specific cases (i.e. no feeding periodicity). The use of $R_{(exper)}$ is logistically more complex than $R_{(max)}$. A parallel estimate of $R_{(exper)}$ as a validation of the $R_{(max)}$ estimation has been done in some studies (Boisclair & Leggett 1985, Fox 1991). This is a good way to reduce the logistic needs and ensure the validity of the $R_{(max)}$ when the use of $R_{(max)}$ is appropriate (i.e. species showing feeding periodicity). Finally, our results showed that it is necessary to consider the presence of parasites in experimental evacuation rate estimation. Parasites significantly reduced the slope of the relation between mean gut fullness and time ($R_{(exper)}$), leading to significant underestimation of daily ration.

The results of the present study indicate that the use of the Eggers (1977) model is appropriate for daily ration estimates, especially when using the complete digestive tract content, as suggested by Boisclair & Marchand (1993). The advantage of the

Eggers (1977) over the Elliott & Persson (1978) model is that the former is mathematically less complex. In addition, it has been shown that with the Eggers model the time interval between sampling periods can be longer than with the Elliott & Persson model (Boisclair & Leggett 1988). This is another important logistic advantage over the Elliott & Persson model.

In conclusion, this study showed that the use of complete digestive tract should be preferred over that of stomach content only, as recently suggested by Boisclair & Marchand (1993). In estimating the different parameters, it is important to consider the distribution of the data to obtain the more representative estimate of the central tendency of food content weight. Our results also showed that the method used to compute evacuation rate is important in the determination of daily ration. We recommend the use of experimental ($R_{(exper)}$) rather than maximum ($R_{(max)}$) evacuation rate because the latter is subject to greater variability and to stochastic events in the field. It is necessary to consider the presence or absence of parasites in the gut content to avoid underestimation of experimental ($R_{(exper)}$) evacuation rate, as they can have a significant influence on daily ration estimates. Finally, the Eggers (1977) model is appropriate to compute daily ration and has the advantage of being mathematically and logistically less complex than Elliott & Persson (1978) model.

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