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Some mathematical considerations in estimating daily ration in fish using food consumption models

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Abstract

The field of stomach content modelling can be broadly divided into evacuation models, which are used to determine evacuation rates under carefully controlled conditions, and consumption models, which apply these evacuation rates to field data to estimate food consumption. In the past, four main forms of evacuation model have been investigated, namely (a) the linear, (b) square root, (c) surface area and (d) exponential forms, with other models related relatively closely to these. Four consumption models are considered in the present work, namely the Bajkov, Elliott–Persson, MAXIMS and Olson–Mullen models. It was attempted here to develop concise mathematical functions for all those of the 16 combinations of evacuation and consumption model for which this has not been done in the past. It was found that no arithmetic solution exists for the Elliott–Persson and MAXIMS models in conjunction with square root and surface area evacuation although in the case of the Elliott–Persson model, a converging process could theoretically be applied. The Olson–Mullen model presents difficulties unless exponential evacuation is assumed and the assumptions which would have to be made in order to implement the model may not be justified. It was concluded that the Bajkov model represents the most universally applicable model in mathematical terms. However, analyses based on simulated data sets highlighted severe problems when this model assumed forms of evacuation other than the exponential. These problems were associated with the fact that the linear, square root and surface area models allow stomach fullness to drop to zero, after which they have to be mathematically constrained to prevent the model from arithmetically assuming evacuation that does not realistically take place. If the fish species analysed shows diel feeding periodicity and the feeding times are known, the errors could be eliminated by basing the analysis only on that part of the feeding cycle when stomachs have at least some contents, providing the full feeding period is covered. In fish populations where fish with empty stomachs are likely to be found at any time of day, it is not possible to truncate the data, concentrating the analysis on those periods when all stomachs have at least some contents. A simple correction factor was devised whereby fish with empty stomachs are excluded from the analysis and the daily ration estimate is corrected for their omission. This factor may be applied regardless of the feeding behaviour of the fish species analysed.

Keywords: Fish feeding; Food consumption models; Stomach evacuation models; Trophic ecosystem models

1. Introduction

The quantification of food consumption by fish is a parameter central to fish ecology, both for the assessment of wild fish stocks, where food availability may limit growth and reproduction, as well as in aquacul-

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ture, where it is often desirable to maximise feed intake without wasting expensive feed in order to maximise profit. Consumption estimates often constitute important parameters in aquatic ecosystem models, such as the ECOPATH model (Christensen and Pauly, 1992), where they help to govern energy flows between compartments or trophic levels. Fish food consumption has mostly been estimated either with the use of bioenergetics models (Arrhenius and Hansson, 1994; Owen et al., 1998; Haertel and Eckmann, 2002) or by investigating the change in stomach fullness over time. The former method relates fish growth to energy flows into and out of the fish while the latter technique models the flow of food into and out of the stomach. Since fish weight increases gradually and it generally takes days or weeks for noticeable changes to occur, sampling for bioenergetics models is generally done at weekly or monthly intervals over a year. In contrast, the weight of the stomach contents tend to fluctuate strongly over the daily cycle and in those cases where the fish show marked feeding periodicity, tend to be more or less the same at the same time of day between different sampling days so that sampling is generally spread at intervals of a few hours over a few consecutive sampling days. Of the two methods, stomach content models are generally rather more frequently used since they only require one item of base information before application to field data, namely the evacuation rate under the prevailing conditions.

The requirement for an estimate of the rate of stomach evacuation prior to the calculation of food consumption has led to two distinct forms of what may loosely be described as "stomach content models" which will hereafter be referred to as "(stomach) evacuation models" and "(food) consumption models". The first class of model is used to determine the evacuation rate, which often takes place in carefully controlled laboratory studies in which the main factors on which the evacuation rate depends (water temperature, fish size, meal size, food composition) are altered to investigate their effect. The second then applies this rate to stomach content data collected in the field in order to estimate the food consumption of the "average fish" in the population investigated.

There is more than one model for each model class, but the reasons for this differ between evacuation and consumption models. In evacuation models, the multitude of models reflects the fact that the physiological basis of stomach evacuation is poorly understood so that the modelling process generally consists of trying to determine which form of equation best fits the data in question. The different types of consumption model, on the other hand, have been conceived because ingestion is controlled rather more by environmental and behavioural than physiological factors so that a specific model has been developed for each type of feeding pattern (irregularly intermittent, diel feeding periodicity, continuous feeding). There has, however, also been some debate as to whether feeding models may be suitable for fish with feeding patterns other than the type they were designed for (Boisclair and Marchand, 1993; Heroux and Magnan, 1996). The principal models used in the study of fish feeding are briefly described below; for more detailed presentations, the reader is advised to consult the original sources.

A detailed survey of the literature concerned with fish stomach evacuation reveals that by no means all the different combinations of evacuation and feeding model have been considered, let alone applied. In view of the diversity of both digestive tract physiology and feeding behaviour between fish species, this seems strange since one would think that there would be at least one species for any given model combination. However, this is probably more a reflection of the fact that from a mathematical view, few models have been put forward. Most workers have presented their model either as a general concept with no specific equations (Olson and Mullen, 1986; Hall et al., 1995) or have combined only one evacuation function with various types of feeding regime (Eggers, 1977; Elliott and Persson, 1978; Sainsbury, 1986; Jarre et al., 1991). Although other workers have been quite innovative in the development of new stomach evacuation functions (Elashoff et al., 1982; Salvanes et al., 1995) or the modification of existing ones (Temming and Andersen, 1994; dos Santos and Jobling, 1995), few food consumption models based on different evacuation forms have been put forward. As a result, most workers simply rely on what is available without questioning the appropriateness of either part of the model (evacuation function or feeding regime) to the species being investigated. This work, therefore, aims to develop specific mathematical functions for the main feeding models in combination with each form of evacuation curve or else determine why specific combinations are not possible. In addition, the most widely used food consumption model is investigated on a theoretical basis using computer simulations in order to test the universal applicability of this model.

2. Stomach evacuation models

Four main types of evacuation model have been proposed: the "linear model" (Olson and Mullen, 1986), the "square root model" (Hopkins, 1966), the "surface area model" (Fänge and Grove, 1979) and the "simple exponential model" (Eggers, 1977; Elliott and Persson, 1978). All are based on the same equation which assumes that the fish are not feeding during the analytical period:

$$\frac{dS}{dt} = -ES^{B} \tag{1}$$

where, S is the stomach contents, t is time, E is the evacuation rate, B is a proportionality constant.

The models differ with respect to the value of B which is zero in the linear, 1/2 in the square root, 2/3 in the surface area and 1.0 in the simple exponential model. These models have been developed further by various other workers who have mainly split up the parameter E to create multivariate models allowing mainly for water temperature, fish size and meal size (Jones, 1974; Basimi and Grove, 1985; dos Santos and Jobling, 1995; Andersen, 1998, 1999). Elashoff et al. (1982) extended the simple exponential model to allow for a delay period at the start of digestion while Salvanes et al. (1995) presented a model based on the penetration of digestive juices in to the food particle which is so closely related to the surface area model that it need not detain us here. In addition, Eq. (1) has also been applied with B as a parameter (Temming and Andersen, 1994) but this will not be considered further since most of what is said here about the surface area and square root models applies to this version too. The above equation may then be integrated for the various models to give:

$$S = S_0 - Et \qquad \text{for the linear model} \tag{2}$$

$$S = \left(S_0^{(1/2)} - \frac{1}{2}Et\right)^2 \qquad \text{for the square root model} \tag{3}$$

$$S = \left(S_0^{(1/3)} - \frac{1}{3}Et\right)^3 \qquad \text{for the surface area model} \tag{4}$$

$$S = S_0\,\mathrm{e}^{-Et} \qquad \text{for the exponential model} \tag{5}$$

where, S_0 is the stomach contents at time $t = 0$, e is Euler's number, base of the natural logarithm.

There are two slight but important mathematical differences between the exponential and the other three models. The first is that the exponential model is multiplicative whereas the others are additive, that is to say that in the linear, square root and surface area models, the reduction in stomach content is subtracted from the initial value, S_0, whereas in the exponential model, S_0 is reduced by multiplication by e^{-Et} (equivalent to division by e^{Et}). The second difference is that the exponential model is the only one in which the stomach contents mathematically never reach zero whereas in the linear model, this takes place at time $t = S_0/E$, in the square root model at time $t = (2S_0^{1/2})/E$ and in the surface area model at time $t = 3S_0^{1/3}/E$, after which the stomach fullness drops further or rises again. This makes it necessary to introduce conditional statements into these models, defining $S = 0$ after these time points.

3. Food consumption models

A number of models have been proposed for the calculation of food consumption, of which only a few have been widely used. The oldest is that of Bajkov (1935), hereafter referred to as the Bajkov model, which was modified by Eggers (1979) to such a considerable extent that it is often referred to as the Eggers model. This model is one of the most widely applied (e.g. Doble and Eggers, 1978; Garcia and Adelman, 1985; Amundsen and Klemetsen, 1988; del Norte-Campos and Temming, 1994), either in the modified form of Eggers (1979) or in its generalised or extended versions (Pennington, 1985; Temming and Hammer, 1994; dos Santos and Jobling, 1995). Elliott and Persson (1978) presented two models of which the simpler one, based on an approach by Eggers (1977), assumed constant feeding rate over the analytical period and has been used probably as frequently as the Bajkov model (e.g. Worobec, 1984; Macdonald and Waiwood, 1987; Worishka and Mehner, 1998; Mazzola et al., 1999) and hereafter referred to as the Elliott–Persson model. This model was modified by Sainsbury (1986) and later by Jarre et al. (1991), hereafter referred to by the name chosen by the latter set of authors, MAXIMS. Olson and Mullen (1986) designed a model primarily for predators intermittently consuming large food items of variable size, hereafter referred to as the Olson–Mullen model. These four models are the ones which will be considered in the present work. Other methods include that of Hall et al. (1995) based more on probability theory and apparently not applied except by the original authors, as well as older approaches by Moriarty and Moriarty (1973) and Thorpe (1977) which appear to have fallen into disuse.

3.1. Bajkov model

The original Bajkov model involved the application of a gut passage time to the average level of stomach fullness over the experimental period to calculate food consumption. Eggers (1979) changed the gut passage time to a stomach evacuation rate, assuming exponential evacuation and Pennington (1985) demonstrated that the model also holds true for other forms of stomach evacuation. The model assumes that the level of ingestion is matched by an equal and opposite level of evacuation over the study period so that, if evacuation is described by Eq. (1), ingestion becomes:

$$\frac{\mathrm{d}S}{\mathrm{d}t} = ES^B \qquad (6)$$

which, assuming sampling is takes place over a 24-h cycle, may be integrated to arrive at the daily ration:

$$R_\mathrm{d} = \int_{t=0}^{t=24} ES^B\,\mathrm{d}t = 24ES_\mathrm{avg}^B \qquad (7)$$

where, R_d is the daily ration, S_avg is the average stomach fullness over the daily cycle.

Eggers (1979) demonstrated that the model also works if there are considerable fluctuations in stomach fullness over the analytical period, providing that the values for the start (S_0) and end (S_{24}) of the period are the same. For those data sets in which this was not the case, he determined the following correction factor:

$$R_\mathrm{d} = 24ES_\mathrm{avg}^B + (S_{24} - S_0) \qquad (8)$$

3.2. Elliott–Persson model

Elliott and Persson (1978) based their model on a point-to-point approach, assuming that evacuation was always exponential and that the ingestion rate would be constant between successive points, i.e. subsamples taken over the daily sampling period. Nevertheless, this model allowed for fluctuations in the ingestion rate over the daily cycle. The model was, therefore, based on the following:

$$\frac{\mathrm{d}S}{\mathrm{d}t} = J - ES^B \qquad (9)$$

with $B = 1$ which, when integrated and solved for J, becomes

$$C_t = Jt = (S_t - S_{t-1}\,\mathrm{e}^{-Et})\frac{Rt}{1 - \mathrm{e}^{-Et}} \qquad (10)$$

where, J is the ingestion rate, C_t is ingestion over time period t, t is the time period between consecutive subsamples being investigated, S_t is the stomach fullness at the subsample at the end of the time period, S_{t-1} is the subsample at the beginning of the time period.

The daily ration is then the sum of all C_t values determined from the field data.

3.3. MAXIMS model

Sainsbury (1986) presented a model based on the Elliott–Persson model but modified to the extent that strict feeding periodicity was assumed. The daily cycle was, therefore, split into feeding and nonfeeding periods, with the former defined by Eq. (9) and the latter by Eq. (1), both with $B = 1$. In contrast to its predecessor, this model was applied by nonlinear regression through the data to estimate the parameters J, E, T_b (beginning of the feeding phase) and T_s (beginning of the nonfeeding phase). The above equations were, therefore, integrated and solved for S to give:

$$\text{when not feeding}: \quad S = S_\mathrm{s}\,\mathrm{e}^{-E(t-T_\mathrm{s})} \qquad (11)$$

$$\text{when feeding}: \quad S = S_\mathrm{b}\,\mathrm{e}^{-E(t-T_\mathrm{b})} + \frac{J}{E}(1 - \mathrm{e}^{-E(t-T_\mathrm{b})}) \qquad (12)$$

where, S_b and S_s are stomach fullness at the start of the feeding and nonfeeding phases, respectively.

Jarre et al. (1991) modified the model by making it cyclic (stomach fullness at the start of the day equal to that at the end of the day, $S_0 = S_{24}$) and allowing for two feeding periods in the 24-h cycle. They also produced a user-friendly software for application to stomach content data and christened the model MAXIMS.

3.4. Olson–Mullen model

Olson and Mullen (1986) produced a more general model which was particularly designed for predators intermittently ingesting large food items of different prey species which might not only be evacuated from the stomach at different rates but even have different evacuation functions altogether. The model arrived at a consumption estimate by the separate modelling of different prey species. The basis of the model was the calculation of the weight of a food item from its original weight a certain period after ingestion using the evacuation function for that food type, $f(t)$:

$$S_t = Mf(t) \tag{13}$$

where, S_t is the stomach fullness at time t, M is the weight of the food item when ingested, $f(t)$ is the proportion of food item remaining in stomach at time t.

It was shown that the average weight of a given type of food in the stomach over an (extensive) period of duration t is:

$$S(i)_{\mathrm{avg}} = \frac{M(i)_{\mathrm{avg}}}{T(i)_{\mathrm{avg}}} \int_0^t f_i(t)\,\mathrm{d}t \tag{14}$$

where, $S(i)_{\mathrm{avg}}$ is the mean weight of food type i in the stomach over the sampling period, $M(i)_{\mathrm{avg}}$ is the mean weight of items of food type i when ingested, $T(i)_{\mathrm{avg}}$ is the mean time interval between ingestion of individual items of food type i, $f_i(t)$ is the evacuation function of food type i.

Since $M(i)_{\mathrm{avg}}/T(i)_{\mathrm{avg}}$ represents the mean hourly feeding rate on food type i (assuming that evacuation is also expressed per hour), if the fish is feeding on N food types, the daily ration R_{d} may simply be calculated from:

$$R_{\mathrm{d}} = 24 \sum_{i=1}^{i=N} \frac{S(i)_{\mathrm{avg}}}{\int_0^t f_i(t)\,\mathrm{d}t} \tag{15}$$

4. Other combinations of evacuation and consumption models

The original Bajkov model was modified by Eggers (1979) on the assumption of exponential evacuation but following its generalisation by Pennington (1985), it may be used with any value of B (Eq. (1)). More recently, dos Santos and Jobling (1995) adapted the modified exponential evacuation function of Elashoff et al. (1982) to this model. In conjunction with the correction factor presented by Eggers (1979), this model, therefore, most closely satisfies the demand for a "universally applicable model".

The adaptation of the Elliott–Persson and MAXIMS models to evacuation functions other than the exponential follows similar lines since the two models are based on the same function for the feeding phase (Eq. (9)). Substituting $B = 1/2$ into this formula and integrating gives:

$$\left[2S_0^{1/2} + 2\left(\frac{J}{E}\right)\ln\left(\left|S_0^{1/2} - \frac{J}{E}\right|\right)\right] - \left[2S^{1/2} + 2\left(\frac{J}{E}\right)\ln\left(\left|S^{1/2} - \frac{J}{E}\right|\right)\right] = Et \tag{16}$$

while substituting $B = 2/3$ into this formula and integrating gives the even more complex:

$$\left[3S_0^{1/3} + \frac{3}{2}\left(\frac{J}{E}\right)^{1/2}\ln\left(\left|\frac{S_0^{1/3} - (J/E)^{1/2}}{S_0^{1/3} + (J/E)^{1/2}}\right|\right)\right] - \left[3S^{1/3} + \frac{3}{2}\left(\frac{J}{E}\right)^{1/2}\ln\left(\left|\frac{S^{1/3} - (J/E)^{1/2}}{S^{1/3} + (J/E)^{1/2}}\right|\right)\right] = Et \tag{17}$$

It is clear that these cannot be solved arithmetically for either J (necessary for the Elliott–Persson model) or for S (necessary for the MAXIMS model) since both factors are found inside as well as outside the natural logarithm. Since the MAXIMS model is based on nonlinear regression, making arithmetic solutions to the above equations imperative, it will never be possible to implement this model with surface area or square root dependent evacuation. In contrast, it would be theoretically possible to apply the Elliott–Persson model by using a converging process to determine J once all the other parameters are known. In practice, however, there would be serious mathematical limitations, e.g. the term $(J/E)^{1/2}$ does not permit negative values for J in view of the constant and positive value for E. For a variety of reasons (e.g. deviation between evacuation rate determined in the lab and the true rate in the field, deviation between mean stomach contents of sample and of population), small negative values are frequently recorded using the conventional Elliott–Persson model when ingestion is actually zero. Due to the cyclic nature of the model (stomach contents at $t = 24$ are assumed to be the same as at $t = 0$), the differences cancel each other out over the daily cycle but if the model was to be applied with square root or surface area dependent evacuation, the ingestion rates for certain parts of the study period would be simply unobtainable. The application of the Elliott–Persson model in this form can, therefore, not be recommended either.

The solution to the linear model is rather simpler for both the Elliott–Persson and MAXIMS models. Substituting $B = 0$ into Eqs. (1) and (9), integrating and solving for J gives the following for the Elliott–Persson model:

$$C_t = Jt = (S_t - S_0) + Et \tag{18}$$

while for the MAXIMS model, the equation for the feeding period becomes:

$$S = S_b + (J - E)(t - T_b) \tag{19}$$

and that for the nonfeeding period:

$$S = S_s - E(t - T_s) \tag{20}$$

which can be solved by simple linear regression "by hand" without the need for a special computer programme. There is an important feature of the model pointed out above, making this approach all the more advisable: unlike in the exponential model, the theoretical level of stomach fullness in the linear evacuation function can reach and drop below zero. Any preprogrammed software would have to incorporate a condition to allow for this.

The Olson–Mullen model was originally very loosely defined with no specific equations for the different evacuation functions given, although the authors stated that they applied it to data on yellowfin tuna, *Thunnus albacares* (Bonaterre), feeding on four different food types. The exponential solution to the model was demonstrated by Richter et al. (2002):

$$R_d = \frac{tS_{avg}}{(1/-E)(e^{-Et} - 1)} \tag{21}$$

It is evident that, unless E is very small, an experimental period of 24 h is large enough to reduce the exponent to nearly zero so that the above equation tends towards the exponential form of the Bajkov model (Eq. (7) with $B = 1$ for $t = 24$).

In attempting to apply the other forms of stomach evacuation to the Olson–Mullen model, we encounter problems arising from an above mentioned property of the evacuation models, namely that with the exception of the exponential model, evacuation functions are additive. Since the basic equation of the Olson–Mullen model is multiplicative, it is difficult to separate out the factor $f(t)$ from Eq. (13) if the evacuation function is not exponential. This factor is defined in the original publication as "*the proportion of food ... remaining in the stomach t time units after* [ingestion of] *a single meal* [of weight M]", making it equivalent to S/M. A close look at Eqs. (2)–(4) demonstrates that it is not possible to simplify these formulae without leaving M (equivalent to S_0 in Eqs. (2)–(4)) in the function $f(t)$ as follows:

$$f(t) = \frac{S}{M} = 1 - \left(\frac{E}{M}\right)t \qquad \text{for the linear model} \tag{22}$$

$$f(t) = \frac{S}{M} = \left[1 - \frac{1}{2}\left(\frac{E}{M^{1/2}}\right)t\right]^2 \qquad \text{for the square root model} \tag{23}$$

$$f(t) = \frac{S}{M} = \left[1 - \frac{1}{3}\left(\frac{E}{M^{1/3}}\right)t\right]^3 \qquad \text{for the surface area model} \tag{24}$$

This presents the worker with a problem, since M is not only unknown in field data but, worse, is what one is indirectly trying to determine! The only solution would be to obtain meal size specific evacuation rates E when this is determined in laboratory trials by correlating this parameter with fixed powers of meal size (M, $M^{1/2}$ or $M^{1/3}$ for linear, square root or surface area evacuation, respectively) so that M can be eliminated from the function $f(t)$.

As stated above, several workers have used multivariate regression to split up the parameter E to allow

Table 1
Summary of publications in which the various combinations of stomach evacuation and food consumption model have been presented, or of mathematical problems associated with the implementation of these model combinations

	Linear evacuation ($dS/dt = -E$)	Square root evacuation ($dS/dt = -ES^{0.5}$)	Surface area evacuation ($dS/dt = -ES^{0.67}$)	Exponential evacuation ($dS/dt = -ES$)
Bajkov model	Pennington (1985)	Pennington (1985)	Pennington (1985)	Eggers (1979)
Elliott–Persson model	Present work	No arithmetic solution for J, converging method for J subject to limitations	No arithmetic solution for J, converging method for J subject to limitations	Eggers (1977); Elliott and Persson (1978)
MAXIMS model	Present work	No arithmetic solution for S in feeding phase, nonlinear regression not possible	No arithmetic solution for S in feeding phase, nonlinear regression not possible	Sainsbury (1986); Jarre et al. (1991)
Olson–Mullen model	Requires evacuation rate correlated with meal size, M	Requires evacuation rate correlated with square root of meal size, $M^{0.5}$	Requires evacuation rate correlated with cube root of meal size, $M^{0.33}$	Richter et al. (2002)

for variation in water temperature, fish size and meal size. Of these three factors, meal size has been considered least but some information is available. Koed (2001) investigated zander (pikeperch, *Stizostedion lucioperca* (L.)) and found that the square root model gave the best fit but that meal size was little correlated to the evacuation rate ($E \propto M^0$). Pääkkönen and Marjomäki (1997) and Pääkkönen et al. (1999) studied burbot (*Lota lota* (L.)) and concluded that the evacuation rate was correlated with the ratio of fish size:meal size, i.e. equal changes in both these factors would leave the evacuation rate E unaffected. Andersen (1998) fed whiting (*Merlangius merlangus* (L.)) a variety of prey types and found that for fish prey, the surface area model gave the best fit and that the meal size coefficient tended to be negative. Similar results were obtained by Richter et al. (2003) in Nile tilapia given single doses of pelleted feed. On the whole, it, therefore, appears that fixing the relationship between E and M to some positive power of the latter when determining the former in the lab would introduce a certain amount of bias which could lead to significant over- or underestimates of food consumption.

A summary of the various combinations of stomach evacuation and food consumption models is given in Table 1. It seems that only the Bajkov model may be combined without problems with all evacuation functions, supporting the claim that it is simple, robust, easy to apply and widely applicable (Boisclair and Marchand, 1993; Heroux and Magnan, 1996). This will now be tested further.

5. Testing the Bajkov model's universality of application

It has been mathematically demonstrated that the Bajkov model is applicable to fish with any form of stomach evacuation (Pennington, 1985) and may even be used when diel feeding periodicity is found (Eggers, 1979). There is, however, one mathematical aspect which does not seem to have been considered, let alone tested. This is the fact that all evacuation equations derived from Eq. (1) except the one that describes exponential evacuation include conditional statements for time points after the stomach has emptied fully, but that this is not integrated into the feeding model. The correction factor presented by Eggers (1979) provides an adequate means of determining food consumption when initial and final stomach fullness levels differ but what about data sets in which for considerable parts of the study period only empty stomachs are found? It was decided to test the robustness of the model in such cases using computer simulations.

Four data sets were constructed, one each for the linear, square root, surface area and exponential forms of stomach evacuation. In all cases, it was assumed that the fish consumed food at the rate of $10\,\mathrm{g\,h^{-1}}$ for 8 h and ceased feeding for the remainder of the 24-h period. The total consumption was, therefore, 80 g in all data sets. In calculating the level of stomach fullness for S_t, it was assumed that all food ingested during the time interval between S_t and the previous time point, S_{t-1}, was ingested exactly halfway between these time points and had, therefore, been evacuated been evacuated at the normal rate for half that time interval (equivalent to a period of $[t-(t-1)]/2$). At the end of the feeding period, the stomach contents were assumed to evacuate at the rate described by Eqs. (2)–(5). The evacuation rates used were $0.5\,\mathrm{h^{-1}}$, $1.1\,\mathrm{g^{033}\,h^{-1}}$, $1.25\,\mathrm{g^{0.5}\,h^{-1}}$ and $4.5\,\mathrm{g\,h^{-1}}$, respectively, for the exponential, surface area, square root and linear models; as the units imply, these rates are not comparable to each other and were chosen arbitrarily to arrive at curves suitable for a rigorous test of the model.

The stomach content trajectories for the various simulations are given in Fig. 1. It is evident that without the conditional statement ($\mathrm{d}S/\mathrm{d}t = 0$ after $S = 0$), fixing stomach fullness to zero after the stomach has been fully emptied, the model predicts negative stomach fullness in the linear and surface area models whereas in the square root model, stomach fullness rises again after this time point. It was now decided to apply the Bajkov model with the evacuation rates used to calculate the trajectories and the average stomach fullness as determined from the generated data. In doing so, three time intervals were considered: (a) the full 24-h period, (b) the first 10 h and (c) that part of the simulated time trajectory in which stomachs had some contents, i.e. from $t = 0$ to the first zero value, whenever this occurred. When considering the full 24-h period, consumption estimates were based on both simulations, one restricted (stomach fullness fixed to zero after full evacuation) and one unrestricted (stomach fullness allowed to rise again or drop below zero). The correction factor of

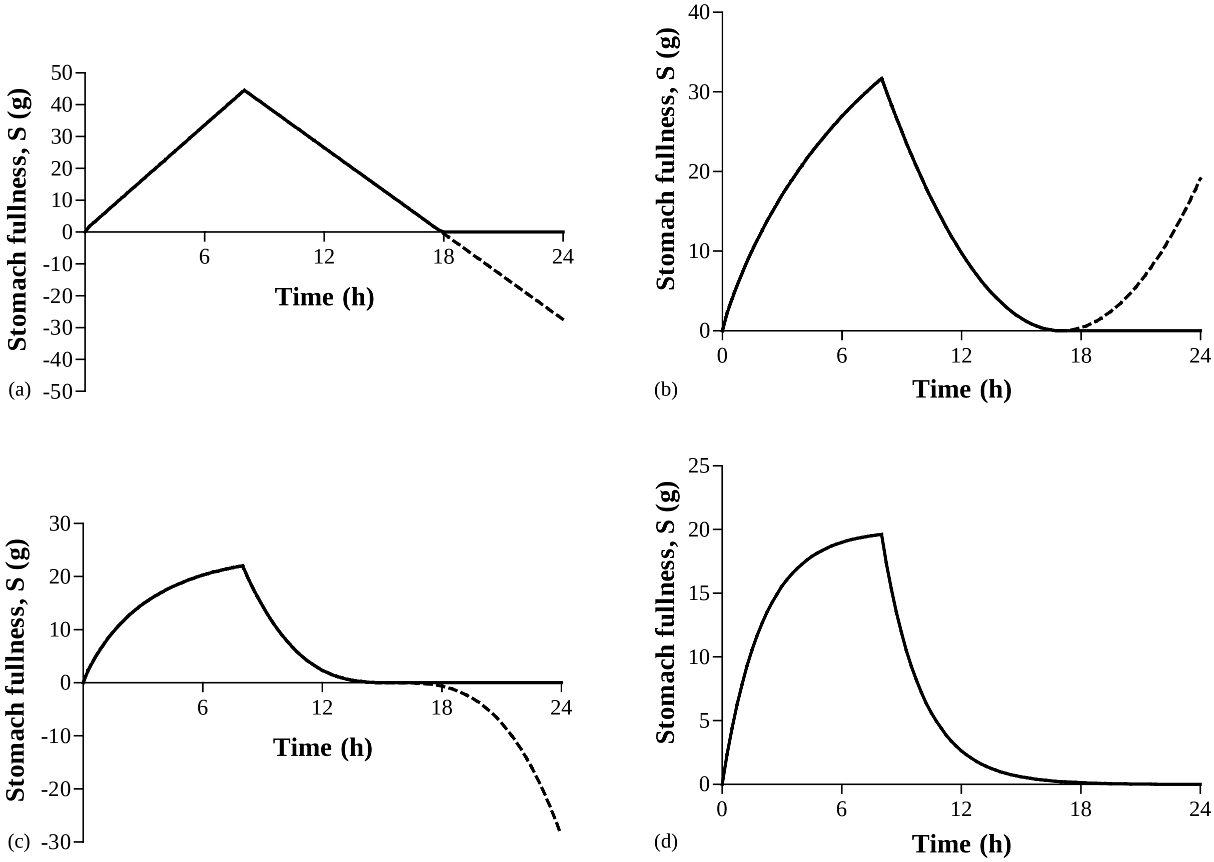

Fig. 1. Trajectories of simulations of stomach fullness over time with the linear (a), square root (b), surface area (c) and exponential (d) evacuation models. Feeding in each case takes place in the first 8 h at the rate of 10 g h^{-1} (total food consumption always 80 g). Linear, square root and surface area models were either restricted (stomach fullness stays at zero after it reached this value, solid line) or left unrestricted (stomach fullness allowed to vary after it has reached zero, dotted line).

Eggers (1979) was applied whenever initial stomach fullness did not equal final stomach fullness (Eq. (8)). The results of this analysis are summarised in Table 2.

When only nonzero positive values are considered ("zero-to-zero" data set), the model evidently performs quite adequately. The analyses over a 10-h section of the data set demonstrate the importance of applying the Eggers (1979) correction factor when differences in initial and final stomach fullness are observed. This correction factor raises consumption estimates close to the true value, particularly in the case of linear or exponential evacuation. Problems were mainly encountered when linear, square root or surface area evacuation models were applied to data sets over the full 24 h in which stomachs were empty for considerable parts of the analytical period. On the other hand, the exponential model gave satisfactory estimates, when necessary in conjunction with the correction factor, regardless of the length of time analysed.

A closer inspection of the results for the full 24-h period reveals that, based on the data sets restrained by the conditional statement, the consumption estimate was consistently higher than the true value. This reflects that fact that the Bajkov model is based on a consumption rate equal and opposite to the evacuation rate and, in these data sets, overestimates evacuation by assuming it to apply to parts of the daily cycle when it simply does not take place (stomach fullness has reached zero so that there is nothing to evacuate). Nevertheless, the consumption estimates based on the

Table 2
Average stomach fullness (S_{avg}) calculated from simulated curves and consumption estimates (R_d) calculated from these using the Bajkov model

	Linear model ($E = 4.5\,g\,h^{-1}$)	Square root model ($E = 1.25\,g^{0.5}\,h^{-1}$)	Surface area model ($E = 1.1\,g^{0.33}\,h^{-1}$)	Exponential model ($E = 0.5\,h^{-1}$)
24 h—restricted				
S_{avg} (g)	(16.71)	10.41	6.88	–
R_d (g)	**108.0**	**96.8**	**95.5**	–
24 h—unrestricted				
S_{avg} (g)	(13.08)	12.36	4.23	6.66
R_d without CF (g)	**108.0**	**105.5**	**69.0**	**79.9**
R_d with CF (g)	**80.6**	**124.6**	**40.3**	**79.9**
10 h				
S_{avg} (g)	(26.50)	20.73	15.36	14.63
R_d without CF (g)	**45.0**	**56.9**	**68.0**	**73.2**
R_d with CF (g)	**80.6**	**76.1**	**76.9**	**80.4**
"Zero-to-zero"				
S_{avg} (g)	(22.28)	14.70	10.65	–
R_d (g)	**79.9**	**81.5**	**82.5**	–

Correction factors (CF) used when initial stomach fullness differed from final stomach fullness (cf. Eq. (8)). Data sets over 24 h were restricted by fixing stomach fullness to zero once stomachs had emptied fully or left unrestricted, allowing theoretical negative stomach fullness (linear and surface area models) or rises in stomach fullness without feeding (square root model). "Zero-to-zero" and restricted analyses do not apply to the exponential model. True consumption values were 80 g in all cases. S_{avg} values for linear model in parentheses since these were not necessary for calculating food consumption.

unconstrained data sets are no closer to the true value, even allowing for the fact that these trajectories are purely theoretical and will not be found in biological populations. In the linear model, S_{avg} plays no part in calculating food consumption anyway, so that food consumption, R_d, is the same regardless of whether the conditional statement is applied or not. In the square root model, the level of stomach fullness actually rises again after it has intermittently reached zero, effectively simulating ingestion that did not really take place, so that R_d also increases if the conditional statement is not applied. In the surface area model, R_d is in fact reduced by removing the conditional constraint but does not come close the true value so that this method does not solve the problem here either. The application of Eggers's (1979) correction factor only seems to work for the linear model in such a situation.

In the above simulation, clear diel feeding periodicity was assumed, i.e. feeding was restricted to the first 8 h. In such cases, an accurate consumption estimate may be arrived at by only analysing the part of the day when feeding takes place and applying the Eggers correction factor. In fisheries science, such feeding scenarios are rarely encountered. Most of the species on which capture fisheries are based operate at higher trophic levels and these fish encounter prey items at irregular intervals, ingesting them whenever they can catch them and the free space in their stomachs suffices to accommodate the prey. On the other hand, even when feeding is theoretically possible at all times of the daily cycle, the time between such encounters may be long enough for a substantial proportion of the population to have empty stomachs. Hall et al. (1995) observed that in a Scottish sea loch, the proportion of fish captured with empty stomachs ranged between about 50–75% for dab, *Limanda limanda* (L.), about 30–95% for plaice, *Pleuronectes platessa* (L.), and about 20–85% for whiting, *Merlangius merlangus* (L.) over the duration of their 24-h study period. Only in the case of haddock, *Melanogrammus aeglefinus* (L.), did the proportion of empty stomachs drop below 10% for at least part of the study period, in this case nighttime. These figures demonstrate that not only are fish with empty stomachs a real problem when estimating daily ration, but that in most cases there is no clear feeding periodicity so that workers cannot possibly confine themselves to a part of their study period when all or at least most fish have at least some stomach contents.

The pragmatic solution to the above problem, applying the Bajkov model only in conjunction with the exponential evacuation model, may lead to bias and would certainly deprive the modeller of a great deal of flexibility, e.g. the option of developing meal size independent evacuation models. A rather simpler and more elegant solution, however, would be to ignore individuals with empty stomachs and correct for them afterwards. In the above simulations, when the analysis is confined to that part of the period when stomachs are at least partly full ("zero-to-zero" phase), empty stomachs are being ignored. If the entire data set is randomly mixed with respect to sampling time (effectively simulating irregular intermittent feeding), this will obviously not affect the mean stomach contents value in any way. An consumption estimate based on only the nonzero values would then be the same as that from the "zero-to-zero" analysis once the different time scale had been accounted for. Providing that the subsamples are based on equal numbers of fish, this could easily be achieved by multiplying by the number of fish with some contents and dividing by the entire sample size. This would give rise to the following:

$$R_{\mathrm{d}} = 24 S_{\mathrm{avg}+}^{B} E \frac{n}{N} \tag{25}$$

where, $S_{\mathrm{avg}+}$ is average stomach contents of all fish with nonzero contents, B is stomach content dependency coefficient, n is number of fish with nonzero contents, N is total number of fish sampled.

In the above simulation, for example, the data for the surface area model spans 15.5 h for the "zero-to-zero" analysis and was based on 62 simulated fish (one per quarter-hour) out of a total sample size of 96 for the 24-h period. Multiplying by an extra factor of 62/96 would amount to the same as correcting the results of the "zero-to-zero" analysis for the reduced time interval (62/96 = 15.5/24).

6. Discussion

The present work has demonstrated that a number of combinations between stomach evacuation and food consumption models are mathematically problematic to put into practice or that this is entirely impossible. Most of the possible combinations have already been presented in the literature and applied to field data. Nevertheless, although our initial aim to expand and hopefully complete the repertoire of model combinations failed to cut much new ground, we consider this review useful insofar that it will save other workers time and trouble by preventing them from trying to develop models which are impossible to construct from the mathematical point of view.

When problems of a mathematical nature are encountered in food consumption estimation, this occurs mainly when applying the surface area and square root models (Table 1). The similarity between the surface area model and that of Salvanes et al. (1995) are so great that all of what has been found here with regard to the former probably also applies to the latter. These problems are particularly exasperating since surface area dependent evacuation is practically the only evacuation function based on the physiological aspects of digestion, particularly in the form of Salvanes et al. (1995). Recently, Richter et al. (2003) presented evidence that even in species feeding on small particles, long considered to have exponential evacuation functions (Jobling, 1987; Temming and Herrmann, 2001), the surface area model may well apply. Olson and Mullen (1986) put forward a model based on surface area proportional digestion in conjunction with a limitation in the availability of digestive juices during parts of the digestive process which resulted in a linear evacuation function. Although this model was purely theoretical, if it was tested and found to apply to predatory species, it would strengthen the case for the physiology of digestion being universally dependent on food particle surface area.

In theory, the feeding model best dealing with the issue of empty stomachs is that of Hall et al. (1995), based largely on probability theory. However, this model assumes strictly linear evacuation which often does not apply, so that it would have to be redesigned to a substantial degree in order to be applied to species with stomach content dependent evacuation ($B \neq 0$). Furthermore, the original authors presented more of a modelling concept than a true model and apparently failed to test their approach against known consumption estimates obtained in the laboratory. Our results suggest that the Bajkov model is simple, universally applicable and may give quite reliable consumption estimates as long as the relevant correction factors are used. This does not, on the other hand, mean that other models should be rejected out of hand. One of the main advantages of the MAXIMS model is the fact that the evacuation rate can be determined from field data. Richter et al. (2003) have shown that the trajectories of different evacuation models fitted to the same data set do not differ greatly, making it unlikely that the MAXIMS model would over- or underestimate food consumption to an significant degree if the true nature of evacuation was found the be surface area dependent. When the fish show feeding periodicity, there is a lot to be said in favour of using this model rather than that of Bajkov (1935) and similar arguments in favour of other models might also apply in certain feeding scenarios. The incompatibility of these models with square root or surface area dependent evacuation means that the need for a mathematical correction factor discussed here pertains mainly to the Bajkov model.

The importance of accurate food consumption estimates for ecological models should not be underestimated. In such models, the biomass or energy flows for each fish species is defined by at least one such consumption estimate (to determine production) and usually, except in the case of top carnivores, one more (to determine mortality related to predation). Our simulations, which do not represent in any way unrealistic feeding scenarios, gave rise to overestimates of between 15.7 and 35.2% of the true daily ration. These figures would decline if the feeding period was extended or the evacuation rate lowered, resulting in fewer fish with empty stomachs, but they could equally well rise further if more fish with empty stomachs would be found due to higher evacuation rates or shorter feeding periods. The present work has shown that when one model is integrated into another, in this case the evacuation model into the consumption model, all of the assumptions of the former must also be implemented in the latter for accurate estimates to be obtained.

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