A review of the fish feeding model MAXIMS

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Abstract

A review of the ICLARM fish feeding model MAXIMS is presented, including a literature review of previous publications using the model. This model calculates feeding period, ingestion and evacuation rates and daily ration from sets of 24-h stomach content field data without the need for laboratory studies to determine any of these parameters. The best fit to the data is determined by means of a lowest sum of squared residuals (SSR) approach. The model has four main routines, giving the option of either one (Model 1) or two (Model 2) feeding periods and ingestion rates that are either constant (Models 1.1 and 2.1) or inversely dependent on the level of stomach fullness (Models 1.2 and 2.2). When both the constant and inversely dependent model are fitted to the same data set, nearly the same fit and a slightly lower SSR value is obtained using the latter model; the mathematical reasons for and statistical significance of this phenomenon are discussed. The authors attempt to give biological guidelines on the choice of model for different fish species depending on feeding type and environmental circumstances, as well as a mathematical way to test the goodness of fit of the Models 1.1:2.1 curves against that of the Models 1.2:2.2 curves so that these biological consideration may gain statistical support. An improved version using the software package SAS for Windows is also presented, calculating confidence limits for the various parameters so that curves for different data sets may be compared against each other. © 1999 Elsevier Science B.V. All rights reserved.

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1. Theoretical background

One of the more important factors in fisheries biology is the food consumption of a species since it may contribute towards limiting production. In addition, this parameter is of great significance in a variety of ecological models, such as those dealing with carbon flows in ecosystems or the bioaccumulation of toxic substances. This factor has previously been estimated in several ways, including laboratory experiments under conditions simulating those in the field as closely as possible, studies of the growth rates and energy budgets of species to determine this figure indirectly and quantitative analysis of the stomach contents over time in conjunction with knowledge on the gut evacuation rates of the species concerned.

The latter approach was first put forward by Bajkov (1935) who estimated daily ration by mul-
tipplying the average stomach contents over a time period (in this case 24 h) with a constant evacuation rate, obtaining:

$$R_d = S_{avg} \cdot E \cdot 24 \text{ h}$$  \hspace{1cm} (1)

The symbols used in this equation ($R_d$, $S_{avg}$ and $E$) are explained in detail in Table 1, as are all those used in subsequent equations modelling stomach contents or daily ration.

Pennington (1985) later demonstrated the validity of this approach even if the evacuation rate was not constant but instead dependent on the stomach contents, provided it was not dependent upon any other factors, so that:

$$\frac{dS}{dt} = -E \cdot S$$  \hspace{1cm} (2)

There has been some debate on the precise nature of the dependency of the evacuation rate on the stomach contents, which should more generally be expressed by:

$$\frac{dS}{dt} = -E \cdot S^B$$  \hspace{1cm} (3)

so that:

$$R_d = 24(S_{avg})^B \cdot E$$  \hspace{1cm} (4)

Eq. (4) is generally known as the ‘generalized Bajkov formula’. Some workers (e.g. Moriarty and Moriarty, 1973; Harbott, 1975) have used a value of $B = 0$, assuming linear evacuation ($dS/dt = -E \cdot S$).

Table 1
Explanation of symbols used in the various stomach content and daily ration equations

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Explanation and comments</th>
<th>Units</th>
<th>Pertains to Models:</th>
</tr>
</thead>
<tbody>
<tr>
<td>$S$</td>
<td>Stomach contents</td>
<td></td>
<td>Bajkov: 1.1, 2.1, 2.2</td>
</tr>
<tr>
<td>$S_{avg}$</td>
<td>Average stomach contents over period analysed</td>
<td></td>
<td>Bajkov</td>
</tr>
<tr>
<td>$S_m$</td>
<td>Maximum stomach content — hypothetical value; ingestion in dependent model is represented by the product of ingestion rate and the difference between this value and stomach contents at that point in time</td>
<td>1.2, 2.2</td>
<td></td>
</tr>
<tr>
<td>$S_e$</td>
<td>Equilibrium stomach content — reached when ingestion equals evacuation so that $dS/dt = 0$</td>
<td>1.2, 2.2</td>
<td></td>
</tr>
<tr>
<td>$S_i$</td>
<td>Residual stomach contents</td>
<td>1.1, 2.1</td>
<td></td>
</tr>
<tr>
<td>$S_{r1}$</td>
<td>Residual stomach contents, first feeding period</td>
<td>1.2, 2.2</td>
<td></td>
</tr>
<tr>
<td>$S_{r2}$</td>
<td>Residual stomach contents, second feeding period</td>
<td>1.2, 2.2</td>
<td></td>
</tr>
<tr>
<td>$R_d$</td>
<td>Daily ration — total quantity of food consumed over the 24-h period</td>
<td>Bajkov: 1.1, 2.1, 2.2</td>
<td></td>
</tr>
<tr>
<td>$J_1$</td>
<td>Ingestion rate (constant ingestion models only)</td>
<td>Wt. h$^{-1}$ or % BME h$^{-1}$ (see above)</td>
<td>1.1, 1.2, 2.2</td>
</tr>
<tr>
<td>$J_2$</td>
<td>Ingestion rate (dependent ingestion models only)</td>
<td>h$^{-1}$</td>
<td>1.2, 2.2</td>
</tr>
<tr>
<td>$E$</td>
<td>Instantaneous evacuation rate</td>
<td>h$^{-1}$</td>
<td>Bajkov: 1.1, 2.1, 2.2</td>
</tr>
<tr>
<td>$T_r$</td>
<td>Beginning of feeding period</td>
<td>In all cases time of day, e.g. 19:30 h, or hours since midnight, e.g. 19.5 h; the latter used for calculations</td>
<td>1.1, 2.1</td>
</tr>
<tr>
<td>$T_{e1}$</td>
<td>End of feeding period</td>
<td>1.1, 2.1</td>
<td></td>
</tr>
<tr>
<td>$T_{r1}$</td>
<td>Beginning of first feeding period</td>
<td>1.2, 2.2</td>
<td></td>
</tr>
<tr>
<td>$T_{e2}$</td>
<td>End of first feeding period</td>
<td>1.2, 2.2</td>
<td></td>
</tr>
<tr>
<td>$T_{r2}$</td>
<td>Beginning of second feeding period</td>
<td>1.2, 2.2</td>
<td></td>
</tr>
<tr>
<td>$T_{e2}$</td>
<td>End of second feeding period</td>
<td>1.2, 2.2</td>
<td></td>
</tr>
</tbody>
</table>
The three other types of evacuation model, the ‘simple exponential’ \((B = 1)\), the ‘square root’ \((B = 0.5)\) and the ‘surface area’ \((B = 0.67)\) models were reviewed by Persson (1986); the ‘simple exponential model’ is the one most commonly applied and is also the one used in the MAXIMS software so that the constant \(B\) may be ignored in the formulae.

While the Bajkov method works well for species with more or less constant levels of stomach fullness (i.e. those species feeding more or less continuously or having very slow evacuation rates), the main problem is that it can be very difficult to reliably estimate average stomach contents if the fish show clear diel feeding periodicity unless many samples are taken over a 24-h period. Another problem is that the evacuation rate usually has to be determined separately from laboratory experiments which may not accurately reflect conditions in the field. Sainsbury (1986) therefore developed a method, based on an approach by Elliott and Persson (1978), by which the evacuation rate could be calculated from the non-feeding period using a set of stomach content data collected over 24 h, which could then be used to estimate the ingestion rate from the feeding period of the same data set. Following this approach, the International Centre for Living Aquatic Resource Management (ICLARM, Manila, Philippines), developed a computer model which they named MAXIMS (Jarre-Teichmann et al., 1990), which essentially computes the various parameters from field data through a process of non-linear regression.

The model is based on the following assumptions:

1. There are one (Model 1) or two (Model 2) distinct feeding periods per 24 h cycle, separated by clear non-feeding phases.
2. The ingestion rate during the feeding period(s) is constant (Models 1.1 and 2.1) or inversely proportional to stomach fullness (Models 1.2 and 2.2).
3. Stomach evacuation takes place constantly and its rate is inversely proportional to the level of stomach fullness (simple exponential decay).

The general equation modelling the evacuation rate is the same as in Bajkov’s approach, (Eq. (3)) also assuming simple exponential evacuation \((B = 1)\) to give Eq. (2). For a non-feeding period following a feeding period in a cycle of ingestion and fasting, Eq. (2) may then be integrated to:

\[
S = S_i \exp(-E(T - T_f))
\]

As stomach evacuation is a continuous process, this equation must be incorporated into that modelling the feeding period which, if the ingestion rate is constant (Models 1.1 and 2.1), then runs as follows:

\[
dS/dt = J_i - E \cdot S
\]

The integral of this equation is:

\[
S = S_i \exp(-E(t - T_f)) + J_i/E(1 - \exp(-E(t - T_f)))
\]

where:

\[
S_i = (J_i/E)(1/(1 - \exp(-24E)))(1 - \exp(-E(T_f - T_i)))
\]

for Model 1.1

and:

\[
S_{i1} = (J_i/E)(1/(1 - \exp(-24E)))(1 - \exp(-E(T_{f2} - T_{i2})))(1 - \exp(-E(T_{f1} - T_{i1})))
\]

and:

\[
S_{i2} = (J_i/E)(1/(1 - \exp(-24E)))(1 - \exp(-E(T_{f1} - T_{i1})))(1 - \exp(-E(T_{f2} - T_{i2})))
\]

for Model 2.1

In Models 1.2 and 2.2, the ingestion rate is inversely proportional to the stomach contents, i.e. the fuller the stomach, the less is ingested, and
is therefore described in terms of a proportion of
the maximum stomach contents, \( S_m \) (a hypotheti-
cal measure of the maximum possible level of
stomach fullness). While Eqs. (5) and (6) still
apply to the non-feeding periods, the feeding pe-
riod may in this case be described by:

\[
dS/dt = J_2(S_m - S) - E \cdot S
\]

(11)

Note that the two ingestion rates, \( J_1 \) and \( J_2 \), are
not directly comparable with each other, even
when the same data sets are analysed with the aid
of the two different types of model. It should also
be noted that, although \( S_m \) represents an ideal
maximum level of stomach contents at which
ingestion becomes zero, due to the effect of evacu-
ation, the stomach contents never reach this level
but stabilise at a lower level, described as \( S_\infty \) in
Jarre-Teichmann et al. (1990, 1991) where \( dS/ dt = 0 \) so that:

\[
S_\infty = (J_2 \cdot S_m)/(J_2 + E)
\]

(12)

Eq. (8) then has the integral:

\[
S = S_\infty \exp(- (E + J_2)(t - T_i)) + S_\infty(1 - \exp(- (E + J_2)(t - T_i)))
\]

where:

\[
S_t = S_\infty (1/(1 - \exp(- 24E - J_2(T_i - T_t))))
\]

\[
\exp(- E(24 + T_t - T_t))
\]

\[
(1 - \exp(- (E + J_2)(T_i - T_t)))
\]

for Model 1.2

(14)

and:

\[
S_{t_1} = S_\infty (1/(1 - \exp(- 24E - J_2(T_{t_1} - T_{t_1}))))
\]

\[
\exp(- E(24 + T_{t_1} - T_{t_1}))
\]

\[
(1 - \exp(- (E + J_2)(T_{t_1} - T_{t_1})))
\]

\[
(1 - \exp(- (E + J_2)(T_{t_1} - T_{t_1})))
\]

(15)

and:

\[
S_{t_2} = S_\infty (1/(1 - \exp(- 24E - J_2(24 + T_{t_1} - T_{t_2}))))
\]

\[
\exp(- E(T_{t_2} - T_{t_1}))
\]

\[
(1 - \exp(- (E + J_2)(T_{t_1} - T_{t_1})))
\]

(16)

for Model 2.2

When data clearly showing two feeding periods
per 24 h are analysed (Models 2.1 and 2.2), each
feeding period is treated separately, although the
ingestion and evacuation rates \( (J_1/J_2 \) and \( E \) )
are assumed to be the same for both periods.

The daily ration, \( R_d \), may then be calculated
from the integrals:

Model 1.1: \( R_d = \int_{t - T_i}^{t - T_i} (J_1 \cdot dt) = J_1(T_i - T_i) \)

(17)

Model 2.1:

\[
R_d = \int_{t - T_i}^{t - T_i} (J_2(S_m - S)dt)
\]

\[
= J_1(T_i + T_{t_1} - T_{t_1} - T_i)
\]

(18)

Model 2.2:

\[
R_d = \int_{t - T_i}^{t - T_i} (J_2(S_m - S)dt)
\]

\[
+ \int_{t - T_i}^{t - T_i} (J_2(S_m - S)dt)
\]

\[
+ ((S_\infty - S_t)/(1 + E/J_2))
\]

\[
(1 - \exp(- (E + J_2)(T_i - T_i)))
\]

(19)

Prior to analysis, the raw stomach content data
must necessarily be transformed to allow for the
fact that bigger fish have bigger stomachs and
that the fish from different subsamples may not
be of the same size, unless a large quantity of fish
are captured which may then be grouped into size classes with small variances (e.g. Moriarty and Moriarty, 1973). The choice of transformation also determines the units which stomach fullness, ingestion rate and daily ration are measured in. The approach suggested by Jarre-Teichmann et al. (1990) involved the determination of the average size of all fish in the sample and the subsequent calculation of the stomach contents compared with those which a fish of that size would have contained at that time of day. Alternatively, the stomach contents may be expressed as a percentage of the total fresh weight of the fish (Richter et al., 1999).

Kühlmann (1998), working on milkfish, Chanos chanos Forsskål, analysed a wide range of sizes over different months and decided to convert stomach contents into contents as a fraction of the metabolic weight of the fish (g kg$^{-0.8}$) in order to allow for the relative decrease in metabolic requirement of fish with age.

Since the MAXIMS software only allows a maximum of 40 data points, the data for each subsample must be averaged in some way; normally, the arithmetic mean is determined. Olson and Mullen (1986), however, pointed out the fact that stomach fullness is not normally distributed at any particular time of day, particularly in the non-feeding period, since it is impossible to have negative stomach fullness, so that data points tend to cluster around zero level. Pauly et al. (1989) attempted to minimise this problem by averaging the first, fifth and ninth deciles for each time of day. This method is only possible, however, if a large number of fish are collected per subsample. Pauly et al. (1989) also transformed their data further by using moving averages over three time intervals to reduce scatter around the regression fit, which helps to produce a clearer curve but leads to data points which are no longer independent of each other.

Typical MAXIMS curves for all four models are shown in Fig. 1. Further explanation of the principles behind the model may be found in Sainsbury (1986) and Jarre-Teichmann et al. (1990, 1991).

2. Previous MAXIMS publications

A recent literature review revealed that MAX-IMS has to date been applied by a number of workers in studies of different scope (Table 2). Earlier literature was mainly based on formerly published data, but more recently, original data has been treated with the aid of the software. Sainsbury (1986) attempted to fit the model to western rock lobster, Panulirus cygnus George, but was dissatisfied with the results; nevertheless, there is no reason why MAXIMS should not be fitted to non-piscian species providing the initial assumptions are met. Sainsbury (1986) also pointed out that the model is additive, i.e. that different stomach content components could be analysed separately and the ration estimates summed over the period in question. This feature was exploited by Kühlmann (1998) on milkfish and Richter et al. (1999) on Nile tilapia, Oreochromis niloticus (L.), who analysed the comparative contribution of natural and supplemental feed to the diet of these species. In addition, Richter and Focken (1998) conducted a mathematical test of the model’s stability when artificial variability was introduced into a perfect data set and found the model to be robust but slightly prone to fitting curves around which the original data were distributed non-randomly.

While MAXIMS is an elegant way of determining daily rations from field data under more ‘natural’ conditions, laboratory studies can be useful in verifying the results. To date, no such study has been published in which ingestion and evacuation rates calculated from MAXIMS field data have been verified in the laboratory. Sainsbury (1986) used laboratory data on brown trout, Salmo trutta L., and skipjack tuna, Katsuwonus pelamis L., to test the model but did not compare the results with field data.

3. Comparison of Models 1.1/2.1 with Models 1.2/2.2

One of the most common findings is that the constant ingestion and inversely dependent ingestion models give very similar predictions in terms of feeding period, daily ration and SSR. In the absence of laboratory data confirming that inges-
Fig. 1. Theoretical examples of the four cases of the MAXIMS Model (Model 1.1: constant ingestion, one feeding period; Model 1.2: ingestion inversely dependent on stomach contents, one feeding period; Model 2.1: constant ingestion, two feeding periods; Model 2.2: ingestion inversely dependent on stomach contents, two feeding periods).
Table 2
Summary of previous applications of MAXIMS

<table>
<thead>
<tr>
<th>Author</th>
<th>Original source</th>
<th>Common name</th>
<th>Latin name</th>
<th>Locality</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sainsbury (1986)</td>
<td>Elliott and Persson (1978), Magnusson (1969)</td>
<td>Brown trout Skipjack Tuna Katsuwonu pelamis Panulirus cygnus</td>
<td>Laboratory held fish Laboratory held fish</td>
<td>Western Australia</td>
</tr>
<tr>
<td></td>
<td>Joll (1984)</td>
<td>Western rock lobster</td>
<td></td>
<td>Western Australia</td>
</tr>
<tr>
<td></td>
<td>Lane et al. (1979)</td>
<td>Diamond turbot</td>
<td>Hypsopsetta gutulata</td>
<td>Anaheim Bay, CA</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Swamp barb</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Long-snouted barb</td>
<td></td>
<td></td>
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<tr>
<td></td>
<td></td>
<td>Filamented barb</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Striped rasbora</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Palomares et al. (1997)</td>
<td>Original data</td>
<td>Tiger-toothed croaker</td>
<td>Otolithes ruber Stolephorus commersonii Stolephorus indicus</td>
<td>San Miguel Bay, Philippines (all species)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Commerson’s anchovy</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Indian anchovy</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Orangefin ponyfish</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Kühlmann (1998)</td>
<td>Original data</td>
<td>Milkfish</td>
<td>Chanos chanos</td>
<td>Fishponds, Philippines</td>
</tr>
<tr>
<td>Richter et al. (1999)</td>
<td>Original data</td>
<td>Nile Tilapia</td>
<td>Oreochromis niloticus</td>
<td>Laguna de Bay, Philippines</td>
</tr>
</tbody>
</table>

It is either constant or dependent on stomach fullness, workers often attempt to fit both types of model and find that the predictions match closely and that the resulting curves are almost identical (Sainsbury, 1986; de Silva et al., 1996). This, however, is only to be mathematically expected, particularly in those cases where the observed data give a good fit. This is facilitated by the similarity in the equations modelling the feeding period of the two models (Eqs. (7) and (13)), making the constant model merely a special case of the inversely dependent model. In such a case,
the dependent model ingestion rate \( (J_2) \) tends to zero and the asymptotic stomach content value \( (S_{\infty}) \) assumes a value almost identical to its counterpart in Eq. (7) \( (J_1/E) \) so that the two equations, although made up of different components, reach nearly the same end value and similar predictions in terms of times of feeding and non-feeding periods, stomach evacuation rate and daily ration are made.

In spite of the similarity between the predictions made by the two types of model, the SSR value given by the dependent model is usually slightly lower than that produced by the constant model applied to the same data set. While it may be tempting to assume that this implies that the fish species’ ingestion rate is inversely proportional to stomach fullness rather than constant, as pointed out by Ratkowsky (1990), more complex models have an inherent tendency to produce better fits than simple ones due to their greater number of parameters. In the case of the MAX-IMS model, the dependent model has two parameters defining ingestion \( (J_2 \text{ and } S_{\infty}) \) while the constant ingestion model only has one \( (J_1) \).

Nevertheless, it should not be forgotten that in the analysis of the goodness of fit, one extra parameter will result in the loss of one degree of freedom, so that the fit obtained with the dependent model may actually be statistically less precise than that from the constant model, in spite of a lower SSR value.

4. Interpretation of the SSR value

While the best fit to a given data set is calculated by means of a minimum Sum of Squared Residuals (SSR) approach, the SSR value is in itself only relative to the data set it pertains to and the SSR values from different data sets may therefore not be compared with each other directly. If, for example, any given data set is compared with a hypothetical second data set which is based on the first but with all stomach content values doubled, the ingestion rate and daily ration would necessarily double as well, while the SSR value would increase by a factor of four. This also means that different analyses of a set of fish stomach contents will give different SSR values depending on whether the data have been transformed into ‘stomach content of an average fish’ or ‘stomach content as a percentage of fish weight’ or depending on how many data points there are in the set. This demonstrates that almost the only useful function of the SSR value is to arrive at the best fit for a given data set and that a low value for SSR may be related merely to low stomach content values and does not necessarily imply a very good fit to the data.

5. Guidelines on model choice and quality control

In previous studies, some workers have fitted both types of model to their data sets in order to compare the results and usually conclude that the inversely dependent model gives a better fit which may, however, not be statistically any more significant. Nevertheless, this line of thought must be erroneous; a fish cannot have an ingestion rate which is both constant and inversely dependent at the same time. It would therefore seem appropriate to base the choice of model on the biological, physiological and environmental factors specific to the situation.

Generally, the inversely dependent model tends to give a more flattened curve than the constant ingestion model, which has a more peaked function, but personal experience has shown that either model is capable of producing either curve. The shape of the curve is dependent mostly on the evacuation rate, the length of the feeding period and, in the case of the inversely dependent model, the relative value of the asymptotic stomach contents. Peaked curves are characterised by lower evacuation rates, shorter feeding periods and higher asymptotic stomach contents than curves coming to a plateau towards the end of the feeding period.

The asymptotic stomach content is to some extent a measure of the maximum holding capacity of the stomach. Personal observation has shown that, for example, milkfish have a smaller capacity than Nile tilapia in terms of stomach contents as a percentage of total body weight, even though they both feed in the same manner
and on much the same food source. MAXIMS curves for milkfish therefore reach a plateau far quicker than those for tilapia (Richter, unpublished data). However, it should be noted that if the curve reaches a plateau, this does not always mean that the stomach cannot physically hold any more than it does at the end of the feeding period: if food availability is very limited (so that ingestion rate is low, but constant) and the feeding period is long while at the same time evacuation rate is high, the stomach would never be filled to any extent before the food is moved into the gut. In such a case, a plateau curve would be arrived at in a constant ingestion rate model. The authors have found this to be true for Nile tilapia in Laguna de Bay (Richter, unpublished data).

Therefore, in the absence of data to confirm the true nature of the fish’s ingestion rate, an assessment should be made as to which parameter is the most limiting. If ingestion rate is high and the feeding period is long so that the stomach is truly filled to maximum capacity, the inversely dependent model is truly more appropriate, e.g. as in diamond turbot, Hypsopsetta guttulata (Girard) as shown in Fig. 2. If, on the other hand, food is limited or the ingestion capacity is low, it is unlikely that the stomach will ever be filled to saturation so that the fish will continue to ingest as much as it can rather than simply keeping the stomach topped up, in which case the constant model is the one to use. This is particularly true for filter feeders which are limited not only by the food source but also by the rate at which they can strain it from the surrounding water. Indeed, it has been suggested that Nile tilapia may not get enough nutrition from the filtered matter in order to satisfy their demands and have to resort to grazing on periphyton in order to avoid weight loss (Dempster et al., 1995). Other fish tend to have high ingestion rates in which they quickly fill the stomach to capacity, after which they do not continue feeding at a reduced rate but simply stop altogether, giving rise to relatively short feeding periods. In these situations, a constant ingestion rate model seems more appropriate too, such as in common cod, Gadus morhua (L.), shown in Fig. 3.

It is, of course, also possible to statistically test which model is more appropriate to any particular data set by means of an $F$-test. Bates and Watts (1988) pointed out that in non-linear re-

![Fig. 2. MAXIMS Model 1.2 curve for diamond turbot, Hypsopsetta guttulata, showing strongly flattened curve better fitted to the dependent ingestion model (data after Lane et al., 1979).](image-url)
gression, when comparing a simple model with a more complicated one (more parameters), the reduction in the SSR value should be proportional to the loss in the number of degrees of freedom. In our case, one may calculate:

\[ F = \frac{(\text{SSR}_1 - \text{SSR}_2)}{\text{SSR}_2} \frac{(\text{DF}_1 - \text{DF}_2)}{\text{DF}_2} \]  

(21)

where SSR1 is the SSR value of constant ingestion model; SSR2, the SSR value of inversely dependent model; DF1, the degrees of freedom of constant ingestion model and DF2, the degrees of freedom of inversely dependent model.

The number of degrees of freedom, of course, depend on how many data points and which model is used and may be calculated as:

\[ \text{DF} = \text{data points} - \text{parameters} \]  

(22)

where parameters = 4, 5, 6 or 7 for Models 1.1, 1.2, 2.1 or 2.2, respectively.

An F value close to 1.0 would indicate that the constant ingestion model is more appropriate. High F values suggest that either the inversely dependent model is more appropriate or that random scatter caused it to fit better. The F value may then be assessed according to its probability level with the null hypothesis that the inversely dependent model is more appropriate (DFnum = (DF1 - DF2); DFdenom = DF2).

An example of an optically better fitting inversely dependent model curve is shown for Nile tilapia, in Fig. 4. In this case, the SSR value and degrees of freedom may be computed as 0.2674 and 4 DF for the constant ingestion model and 0.1830 and 3 DF for the inversely dependent model. This gives an F(1,3) value of 1.384 with a probability level of 0.50 < P < 0.75. This means that the probability that the null hypothesis is incorrect is between 50% and 75% (or rather higher than 5%) so we conclude that, in spite of the higher SSR value, the constant ingestion model should be used. This supports the biological hypothesis that filter feeders such as Nile tilapia are more appropriately assigned constant ingestion rates.

It should perhaps be pointed out that any model is only as good as the data that goes into it and the MAXIMS model is no exception. While it is tempting to believe that the data for the evacuation phase is not as important as that for the
ingestion phase, possibly because in many cases large numbers of empty stomachs are found towards the end of the former period, this part of the feeding cycle is actually more important since the evacuation rate is derived mainly from it. The estimates of ingestion rate and daily ration are, however, highly sensitive to this parameter so that a reliable data set covering all parts of the 24-h period is essential. Previous studies using the MAXIMS model vary considerably in the number of subsamples used to calculate the different parameters as well as their spread over the daily cycle. A simple way of testing whether the data set is sufficient for deriving a reliable daily ration estimate is to omit individual data points from the evacuation phase and to recalculate the parameters. Large differences between the original and subsequent estimates suggest that the data set used for the calculation is close to or even below the lower limit of the model’s requirements.

A further caveat is that, regardless of the mathematical robustness of the model’s predictions, the daily ration estimates do not automatically have to be biologically sound. Worthmann (1982) studied two amazonian sciaenids, both active carnivores, and found that all fish caught in a purse seine had empty stomachs while most fish taken with the aid of a gill net at the same time and in the same area had at least some stomach contents. Thus the daily ration estimate can evidently be influenced significantly by activity patterns of the fish being studied; other plausible sources of bias include (possibly unintended) selection of special age/size classes, sex groups or mainly breeding or non-breeding fish. If, for example, ration estimates of about 1% body weight equivalent on a fresh weight basis are arrived at, depending on the average size of the fish and the composition of the food, further analysis might reveal that this is not even enough to sustain the resting metabolism of the species in question, let alone leave enough for weight increment. In view of this, independent verification of the daily ration estimates with the aid of, e.g. food conversion ratios, prey mortality or production rates wherever possible seems advisable, particularly if the daily ration estimates are to be used in the construction of carbon flow, bioaccumulation or similar models.

Fig. 4. MAXIMS Models 1.1 and 1.2 curves for Nile Tilapia, *Oreochromis niloticus*, showing a closer fit for the dependent ingestion model which, upon statistical analysis, is found to be mathematically inferior due to the loss of more degrees of freedom, making the constant ingestion model more appropriate. For details, see text (data after Richter et al., 1999)
6. Mathematical problems and improvements

Despite the fact that MAXIMS is a useful tool which has already been employed on several species, there remains scope for improvement. The MAXIMS software will only accept 40 data points or less, necessitating the use of averages for different times of day which may then be non-normally distributed. Furthermore, Richter and Focken (1998) demonstrated that in some cases, the software tends to give non-randomly distributed fits, probably because the evacuation rate is calculated separately from both periods so that in case of a large discrepancy in the two estimates, an average value is taken which doesn’t necessarily fit the evacuation phase very well. In the feeding phase, the inclusion of a good estimate for the ingestion rate will probably improve the fit so that this phenomenon is not so marked. This problem could very likely be mitigated or eliminated by giving more weight to the data points in the evacuation phase.

One problem which the authors have encountered repeatedly while using the ICLARM software but for which no logical explanation can be found is the fact that the programme will not readily deviate from the original estimate for the end of the feeding period. This can obviously be a serious stumbling block in the quest for a true minimum SSR and should be eliminated from future versions of the software. A further drawback of the programme is the fact that no confidence limits are given for the calculated parameters. This makes it difficult to statistically test the difference between different curves obtained for the different species in the same habitat, the same species from different habitats or times of year, etc.

In order to overcome at least some of these shortcomings, the authors set out to reconstruct the MAXIMS model using a variety of softwares carrying out non-linear regression and have succeeded in writing routines using the analytical package SAS for Windows (Version 6.11 or higher) for each of the four models (1.1, 1.2, 2.1 and 2.2), details of which are given in the appendices. By this approach, confidence limits may be obtained to compare different sets of results; moreover, tests on data collected in the field have confirmed that the software performs as well as the original MAXIMS programme and is also less prone to reach a merely local minimum while all parameters, including the end of feeding period, are varied equally readily. A further advantage is the fact that more than 40 data points are accepted, eliminating the need for averaging the data for any particular time of day, so that less biased data points may be used. In addition, if confidence limits are required, the use of moving averages (e.g. Pauly et al., 1989) must be cautioned against, since the data points will no longer be independent of each other.

7. General advice on using SAS 6.11 to calculate MAXIMS curves

The following routines given in the appendices are based on the example for segmented non-linear regression in the SAS user’s guide manual (SAS Institute Inc., 1989). The equations have been adapted to those given in Jarre-Teichmann et al. (1991) and the data sets and their parameters are taken from Richter et al. (1999); all figures in bold italics are data or parameter estimations pertinent to that data and will have to be substituted by users wishing to fit the curves to their own data. All other parts of the routines should be copied verbatim.

The original MAXIMS programme requires only estimates for start and end of feeding period(s) and attempts to calculate estimates for the remaining parameters by itself. The SAS routines are not as user-friendly and the user will have to calculate these estimates himself. The start and end of feeding period(s) should be easy enough to estimate optically by graphing the data. General guidelines for the remaining parameters are discussed below.

7.1. Ingestion rate, J

In constant ingestion models (1.1 and 2.1), calculate:

\[ J = \frac{Y_{(x_2)} - Y_{(x_1)}}{X_2 - X_1} \]  

(23)

where \( Y_{(x_1)} \) is the stomach content value of the first
data point in the feeding period; $Y_{(X_2)}$, the stomach content value of the second data point in the feeding period; $X_1$, the time of the first data point in the feeding period and $X_2$, the time of the second data point in the feeding period.

If this does not give a reasonable estimate, the first and third data points in the feeding period may be used.

In inversely dependent ingestion models (1.2 and 2.2), calculate:

$$J = \frac{(Y_{(X_2)} - Y_{(X_1)})/(X_2 - X_1)}{(Y_{\text{max}} - Y_{\text{min}})}$$

where $Y_{\text{max}}$ is the highest stomach content value of data set and $Y_{\text{min}}$ is the lowest stomach content value of data set.

### 7.2. Evacuation rate, $E$

In all models, calculate:

$$E = \frac{(Y_{(X_3)} - Y_{(X_4)})/(X_4 - X_3)Y_{(X_3)}}{(X_4 - X_3)}$$

where $Y_{(X_3)}$ is the stomach content value of the first data point in the non-feeding period; $Y_{(X_4)}$ is the stomach content value of the second data point in the non-feeding period; $X_3$ is the time of the first data point in the non-feeding period and $X_4$ is the time of the second data point in the non-feeding period.

Again, if this does not give a reasonable estimate, the first and third data points in the non-feeding period may be used.

### 7.3. Asymptotic stomach contents, $S_\infty$

Enter the highest stomach content value in the data set. If the curve stops short of a plateau, it is adviseable to multiply this figure by 1.25; if the curve is very peaked (probably due to rather short feeding periods), multiply by 1.5.

While the SAS routines may be used to calculate the best fit, including confidence limits and other statistics, the graphical output of the programme leaves room for improvement. If a visual estimate of the goodness of fit is required, the following lines may be inserted between the penultimate line (‘end;’) and the last line (‘run;’) of each routine:

```latex
output out = b predicted = yp; run;
proc plot;
  plot y*x yp = *'/overlay vpos = 35;
```

This addition will, however, only plot a predicted value for each data point without connecting these to form a MAXIMS curve. If only few data values are available, the output will therefore not be very clear. In order to get a good idea of the shape of the curve, data points for at least 16 times of day will probably be required.

All of the following routines have been programmed to fit curves to daytime feeding species, so that the first part of the curve is always made up of part of a non-feeding period. While in theory, separate routines could be written for species feeding at night, in practice, it is probably easier to transform the data by adding/subtracting 12 h to each data point time value and readjusting the parameter estimates and results accordingly.

The original MAXIMS software gives the option of fixing parameters to certain values, possibly because they have been determined independently to have that particular value. If the user wishes to implement this in the SAS routine, the parameter should be removed from the parameter list and the value inserted wherever the parameter is declared in the formulae.

It should be noted that both the original MAXIMS software as well as the SAS routines calculate feeding periods in fractions of hours, which may need to be converted afterwards. Thus a time estimate of 6.5 would be equivalent to a time of day of 06:30 h.

### 8. Calculation of confidence limits to the daily rations

The daily ration may be calculated in each of the MAXIMS routines by the equations laid out in the main part of the paper (Section 1, Eqs. (17)–(20)). Sainsbury (1986) demonstrated the calculation of confidence intervals to the daily ration of the first of his two models (equivalent to our Model 1.1) and this approach may be extended to our Model 2.1. As he himself stated,
there is no straightforward way of calculating
the confidence limits to the Models 1.2 and 2.2 daily ratios so that, in case such limits are indispensable, a jackknife method should be used. Our advice is to apply the constant ingestion model also and compare the daily ration estimates between this and the inversely dependent model. If these are similar, the confidence limits for the former may be taken as a first approximation.

While the SAS routines given in Appendices A, B, C and D will calculate standard errors and confidence intervals for the various parameters, the determination of the confidence intervals for the daily ration requires values for the parameter covariances. These are not easily obtainable in SAS without entering more formulae; the output only includes the parameter estimates, their standard errors and the correlation coefficients between the parameters. These are used below to arrive at daily ration confidence limits. The following equations may therefore be calculated by hand or included in the SAS routines; since there is no clear economy of effort in either approach, the necessary programming for the latter option is left to the reader.

9. Model 1.1

The Model 1.1 equivalent developed by Sainsbury (1986) did not include the parameters \(T\) and \(T\) but set the former to zero, thereby featuring total length of feeding period as a different parameter \(T\). The daily ration was then computed as:

\[
R_d = J_1 \cdot T_m
\]  
(26)

and the variance, \(V[R_d]\) given as:

\[
V[R_d] = J_1^2 \cdot V[T_m] + T_m^2 \cdot V[J_1] + 2J_1 \cdot T_m \cdot Cov[J_1, T_m]
\]  
(27)

where \(V[R_d]\) is the error variance for daily ration; \(V[T_m]\) is the error variance for the feeding period; \(V[J_1]\) is the error variance for the ingestion rate and \(Cov[J_1, T_m]\) is the covariance between ingestion rate and feeding period.

As mentioned before, the SAS output includes standard errors, S.E.[parameter], and correlation coefficients, CC[parameter,parameter], for the parameters. The standard errors may be squared to arrive at the respective error variances required. From these, we may calculate \(V[T_m]\), for substitution into Eq. (27), as:

\[
V[T_m] = V[T_1] - V[T_1] + V[T_1] - 2Cov[T_1, T_1] 
\]  
(28)

where:

\[
Cov[T_1, T_1] + S.E.[T_1] \cdot S.E.[T_1] \cdot CC[T_1, T_1] 
\]  
(29)

and similarly obtain \(Cov[J_1, T_m]\) for Eq. (27) from the formula:

\[
Cov[J_1, T_m] = Cov[J_1, T_1] - Cov[J_1, T_1] 
= S.E.[J_1] (S.E.[T_1] \cdot CC[J_1, T_1] - S.E.[T_1] \cdot CC[J_1, T_1])
\]  
(30)

The variance of the daily ration, \(V[R_d]\), is then converted to the standard error of the daily ration, S.E.[\(R_d\)], from which the confidence limits are computed using the Student’s \(t\)-distribution, where the number of degrees of freedom, DF, are calculated from Eq. (22) above.

10. Model 2.1

The basic principle is the same here as for Model 1.1, except that the feeding period, \(T_m\), is defined by four times (Eq. (18)). Different values therefore have to be computed for \(V[T_m]\) and \(Cov[J_1, T_m]\) for substitution into Eq. (27). These are obtained as follows:

\[
V[T_m] = V[T_1] + V[T_1] + V[T_1] + 2Cov[T_1, T_1] 
\]  
(31)

where the covariances between different time points are calculated according to the same principle as in Eq. (29), and:

\[
Cov[J_1, T_m] = Cov[J_1, T_1] + Cov[J_1, T_1] 
- Cov[J_1, T_1] - Cov[J_1, T_1]
\]
认可与致谢

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附录 A. SAS 荷典 MAXIMS 模型 1.1

```
data a;
input X Y;
cards;
0.50  1.170
3.50  0.950
6.50  0.180
9.50  1.710
12.50 2.430
15.50 2.570
18.50 2.260
21.50 1.420;
proc nlin method = dud;
parms J = 0.5, E = 0.15, Tr = 6, Tf = 17;
file print;
Sr = (J/E)*(1/(1 - exp(-24*E)))
*exp(-E*(24 + Tr - Tf))
*(1 - exp(-E*(Tf - Tr)));
Sf = Sr*exp(-E*(Tf - Tr))
+ (J/E)*((1 - exp(-E*(Tf - Tr)));
S0 = Sf*exp(-E*(24 - Tf))
if 0 < = X < = Tr then do;
model Y = S0*exp(-E*X);
end;
else if Tr < X < = Tf then do;
model Y=Sr*exp(-E*(X - Tr))+(J/E)*(1-
exp(-E*(X - Tr)));
end;
else if Tf < X < = 24 then do;
model Y = Sf*exp(-E*(X - Tf));
end;
run;
```

Appendix B. SAS routine for MAXIMS Model 1.2

```
data a;
input X Y;
cards;
0.50  1.170
3.50  0.950
6.50  0.180
9.50  1.710
12.50 2.430
15.50 2.570
18.50 2.260
21.50 1.420;
proc nlin method = dud;
parms J = 0.2, E = 0.15, Sm = 3, Tr =
6.5, Tf = 17;
file print;
Sr = Sm*(1/(1 - exp(-24*E)))
*exp(-E*(24 + Tr - Tf))
*(1 - exp(-E + J)*(Tf - Tr)));
Sf = Sr*exp(-E + J)*(Tf - Tr))
+ Sm*(1 - exp(-E + J)*(Tf - Tr)));
S0 = Sf*exp(-E*(24 - Tf))
if 0 < = X < = Tr then do;
model Y = S0*exp(-E*X);
end;
else if Tr < X < = Tf then do;
model Y = Sf*exp(-E*(X - Tf))
+ Sm*(1 - exp(-E + J)*(X - Tr)));
end;
else if Tf < X < = 24 then do;
```
Appendix C. SAS routine for MAXIMS Model 2.1

data a; input X Y;
cards;
  0.50 0.140
  3.50 0.000
  6.50 0.510
  9.50 0.460
 12.50 0.940
 15.50 0.860
 18.50 2.650
 21.50 0.980;
proc nlin method = dud;
parms J = 1.5, E = 0.5, Tr1 = 6, Tl1 = 10.5, Tr2 = 15, Tl2 = 19.5;
file print;

Sr1 = (J/E)*(1/(1 - exp( - 24*E)))
   *exp( - E*(24 + Tr1 - Tl2))
   *(1 - exp( - E*(Tl2 - Tr2)))
   *(1 - exp( - E*(Tr2 - Tl1)))
   *(1 - exp( - E*(Tl1 - Tr1))));
Sr2 = Sr1 *exp( - E*(Tr2 - Tl1));
Sf2 = Sr2 *exp( - E*(Tl2 - Tr2))
   + (J/E)*(1 - exp( - E*(Tl2 - Tr2)));
S0 = Sf2 *exp( - E*(24 - Tl2));
if 0 < X < Tr1 then do;
model Y = S0 *exp( - E*X);
end;
else if Tr1 < X < Tl1 then do;
model Y = Sr1 *exp( - E*(X - Tr1)) + (J/E)*(1 - exp( - E*(X - Tr1)));
end;
else if Tl1 < X < Tr2 then do;
model Y = Sf1 *exp( - E*(X - Tl1));
end;
else if Tr2 < X < = Tl2 then do;
model Y = Sr1 *exp( - E*(X - Tr2)) + (J/E)*(1 - exp( - E*(X - Tr2)));
end;
else if Tl2 < X < = 24 then do;
model Y = Sf1 *exp( - E*(X - Tl2));
end;
run;

Appendix D. SAS routine for MAXIMS model 2.2

data a;
  input X Y;
cards;
  0.50 0.140
  3.50 0.000
  6.50 0.510
  9.50 2.460
 12.50 0.940
 15.50 0.860
 18.50 2.650
 21.50 0.980;
proc nlin method = dud;
parms J = 0.15, E = 0.5, Sm = 3, Tr1 = 6.5, Tl1 = 10.5, Tr2 = 15, Tl2 = 19.5;
file print;

Sr1 = Sm * (1 - exp( - 24*E - J*(Tl1 - Tr1)))
   *exp( - E*(24 + Tr1 - Tl2))
   *(1 - exp( - (E + J)*(Tl2 - Tr2)))
   *(1 - exp( - E*(Tl2 - Tl1)))
   *(1 - exp( - (E + J)*(Tl1 - Tr1))));
Sr2 = Sr1 *exp( - E*(Tr2 - Tl1));
Sf2 = Sr2 *exp( - E*(Tl2 - Tr2))
   + (J/E)*(1 - exp( - E*(Tl2 - Tr2)));
S0 = Sf2 *exp( - E*(24 - Tl2));
if 0 < X < = Tr1 then do;
model Y = S0 *exp( - E*X);
end;
else if Tr1 < X < = Tl1 then do;
model Y = Sr1 *exp( - E*(X - Tr1)) + (J/E)*(1 - exp( - E*(X - Tr1)));
end;
else if Tl1 < X < = Tr2 then do;
model Y = Sf1 *exp( - E*(X - Tl1));
end;
else if Tr2 < X < = Tl2 then do;
model Y = Sr1 *exp( - E*(X - Tr2)) + (J/E)*(1 - exp( - E*(X - Tr2)));
end;
else if Tl2 < X < = 24 then do;
model Y = Sf1 *exp( - E*(X - Tl2));
end;
run;
References


Pennington, M., 1985. Estimating the average food consumption by fish in the field from stomach contents data. Dana 5, 81–86.


