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MAXIMS - A Computer Program for Estimating the Food Consumption of Fish

by

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Abstract

A user-friendly computer program for IBM/MS-DOS PCs and compatibles is presented that allows for the estimation of daily ration and population food consumption of fish and invertebrates based on a diel cycle of stomach contents weights. This software incorporates estimation of daily ration (i) from mean stomach contents and evacuation rate, (ii) from evacuation rate and the observed differences in stomach contents at the sampling times, and (iii) from an integrated approach accounting for one or two feeding periods per day, where ingestion and evacuation rates as well as feeding times are estimated simultaneously using a nonlinear least-squares algorithm. The software allows to chose between various ingestion and evacuation models. The food consumption of a population (per unit biomass and time) can be estimated based on estimates of daily ration of different size groups and the parameters of von Bertalanffy growth and exponential mortality. Graphic outputs of 24-hours-cycles of stomach contents, and of gross food conversion efficiency or daily ration *vs.* weight are also available.

Introduction

One of the requirements of a multispecies model is knowledge on the amount of food consumed by the species or species groups involved, which, apart from investigations of filtration rate, bite size, respiration or anatomy of the fish, can most directly be derived from analyses of stomach contents.

A variety of methods has been introduced for the estimation of size-specific daily ration as well as population-based food consumption. No effort is being made in the present contribution to decide on the general appropriateness of the various theoretical approaches. The purpose of the present paper is to introduce the software "MAXIMS" that has been developed in order to facilitate the quantitative analyses of stomach contents, based on a few common theoretical approaches, and to give some application examples. Three case studies are presented that show some advantages of an integrated approach of data analysis over those based mainly on the estimation of evacuation rate.

Theoretical background

Estimation of daily ration from mean stomach contents and evacuation rate
Starting with Bajkov (1935), and modified e.g. by Eggers (1979), the product of an instantaneous evacuation rate (E) and mean stomach contents (avg(S_t) over a 24 hours period has become a formula widely used for the estimation of daily ration (Rd), i.e.,

$$R_d = avg(S_t) \cdot E \cdot 24 \text{ hours} \quad (1)$$

This formula is referred to as the "modified Bajkov formula" in the present contribution.

Pennington (1985) generalized the above equation by showing that if the decrease in stomach contents during nonfeeding is proportional to a power B of the stomach contents, i.e., if it follows the model

$$dS/dt = -E \cdot S_t^B \quad (2)$$

the daily ration can be computed from the following equation

$$R_d = avg(S_t^B) \cdot E \cdot 24 \text{ hours} \quad (3)$$

For this equation, called "generalized Bajkov formula" in the following, a variety of values for the parameterization of B has been suggested, e.g., B = 0.5 (volume-dependent model; Hopkins 1966; Jobling 1981), B = 0.67 (surface-dependent model; Fänge and Grove 1979). The simple exponential model (B = 1) has found wide application (e.g., Tyler 1970, Brett and Higgs 1970, Elliott 1972, Eggers 1977, Elliott and Persson 1978, Persson 1986) and was recommended in a review by Jobling (1981) for estimation of food consumption of species feeding on relatively small prey, such as plankton or small benthos.

Estimation of daily ration from evacuation rate and the observed differences in stomach contents
In order to explicitly account for an observed feeding periodicity, it is possible to first estimate the evacuation rate from a nonfeeding phase, and then to add

the differences in stomach contents weights actually observed at the sampling times to the estimate of the content evacuated during the corresponding period. In this case, the evacuation is based on the mean stomach contents of that period, i.e.,

$$R_d = (S_{t2} - S_{t1}) + E \cdot (t_2 - t_1) \cdot ((S_{t2}^{B} + S_{t1}^{B}) / 2) \quad (4)$$

This equation was referred to as "linear course of stomach contents" (LCSC) by Temming (1986) and will be referred to as "point-to-point approach" in the present contribution.

Estimation of daily ration from an integrated approach
-Simple exponential evacuation

Sainsbury (1986) proposed an alternative approach, wherein daily ration is estimated from a cycle of stomach contents data (of arbitrary duration) as part of an integrated estimation process involving ingestion and evacuation rates, asymptotic stomach contents and feeding times. Based on Elliott and Persson (1978) he developed two models, one (Model I) assuming a constant feeding rate, and the second (Model II) assuming a feeding rate inversely proportional to stomach contents. Both models assume that evacuation follows the simple exponential model. The rate of stomach contents change dS/dt during the feeding period is described by the differential equation

$$dS/dt = J_1 - E \cdot S_t \quad (5)$$

for Model I, where J1 is the ingestion rate in units of stomach contents weight per unit time. For Model II,

$$dS/dt = J_2 \cdot (S_m - S_t) - E \cdot S_t \quad (6)$$

where J_2 is an instantaneous rate of ingestion and S_m the maximum stomach contents.

Both differential equations can be solved analytically, the parameters can be estimated by a multivariate optimization algorithm, and the daily ration is obtained by integrating food ingestion over the duration of the feeding period. Jarre *et al.* (1991) explicitly implemented this approach for a feeding cycle of 24 hours duration, and extended the model to explicitly account for two feeding periods per day.

- The generalized model of ingestion and evacuation in the integrated approach

Accounting for the necessity to use the proper evacuation model for a reliable estimate of daily ration (see, e.g., Temming 1986), the generalized Bajkov model was incorporated into the integrated approach (Jarre-Teichmann 1992) such that both ingestion and evacuation rates may be made proportional to powers of the stomach contents, thus generalizing Eq. (6) to

$$dS/dt = J_2 \cdot (S_m - S_t)^{B1} - E \cdot S_t^{B2} \quad (7)$$

Whereas the corresponding equation for the nonfeeding period can be solved analytically, a numerical solution must be obtained for the above equation. Consequently, the integration for the estimate of daily ration has to be carried out numerically as well.

Estimation of population food consumption

Estimates of daily ration usually pertain to the size of the fish sampled. In order to be able to extend such size-specific estimates to estimates of the food consumption of an entire population, the age-structure of this population has to be considered. This requires estimates of the growth parameters of individual fish as well as estimates of the total mortality of the population. Pauly (1986) derived a model for the estimation of population food consumption per unit biomass and unit time (Q/B) from growth parameters of the von Bertalanffy growth equation, total mortality (Z), and gross food conversion efficiency K_1 (Ivlev 1945). Simplified by Palomares and Pauly (1989), this equation reads

$$Q/B = \text{Food consumption / biomass}$$

$$= \int_{t_r}^{t_{max}} (dW/dt \cdot N_t) / K_{1(t)} dt \quad / \quad \int_{t_r}^{t_{max}} W_t \cdot N_t dt \qquad (8)$$

where t_r is the age at entry into the population in question, t_{max} the age of exit from that population, and N_t the number of animals of age t in the population.

Implementation in MAXIMS

MAXIMS has been developed for IBM/MS-DOS Personal Computers and compatibles. It comprises a data handling subprogram, several approaches for estimating daily ration (Exh. 1), and various estimates related to estimation of population food consumption (Exh. 2). In addition to a user-friendly interface, graphic outputs of diel stomach contents trajectories of the integrated models, and of daily ration or gross food conversion efficiency *versus* weight are available. Nonlinear least squares iteration is performed based on the AMOEBA downhill simplex method (Press *et al.* 1986), and numerical integrations are performed following the Runge-Kutta method or the trapezoidal rule, for differential equations or functions, respectively.

MAXIMS is available at a modest fee for diskettes and postage from the Software Project, c/o The Director, Capture Fisheries Management Program, International Center for Living Aquatic Resources Management (ICLARM), MC P.O. Box 1501, Makati, Metro Manila 1299, Philippines.

- Data handling submenu
- *Estimates independent of number of feeding periods*
  - Modified Bajkov formula
  - Point-to-point approach

- *One feeding period, integrated models:*
  - Ingestion rate constant, simple exponential evacuation (Model I)
  - Ingestion rate linearly dependent on stomach contents, simple exponential evacuation (Model II)
  - Ingestion and evacuation rates nonlinearly dependent on stomach contents (Model III)

- *Two feeding periods, integrated models:*
  - Ingestion rate constant, simple exponential evacuation (Model I)
  - Ingestion rate linearly dependent on stomach contents, simple exponential evacuation (Model II)

Exhibit 1. Routines implemented in MAXIMS related to estimation of (weight-specific) daily ration.

- Estimation of coefficient ß (Pauly 1986)
- Estimation of Q/B (given ß, growth and mortality parameters)
- Estimation of Daily ration (given ß)
- Sensitivity analysis for Q/B

- Graphic output of R_d and K_1 versus weight

Exhibit 2. Routines implemented in MAXIMS relatied to estimation of population food consumption

Sample applications

For comparison of the results of the modified Bajkov formula, the point-to-point approach and the integrated approach, three examples have been chosen where the data clearly suggested simple exponential evacuation. For this reason, the exponent was fixed to the value of 1.0 for the point-to-point method in all examples.

Diamond turbot

Lane et al. (1979) give a diel cycle of stomach contents weights on diamond turbot (*Hypsopsetta guttulata*) trawled off Southern California. The daily ration obtained by the authors from a cyclic approach using the equations given for Model I above, but using a different estimation routine, was 3.8 % body weight per day for fish of average 96 g. The modified Bajkov formula yielded an estimate of 3.8 % body weight per day, the point-to-point approach an estimate of 3.9 % body weight per day. Model I fitted the data with an estimate of 4.3%, and Model II yielded a very close fit to the data with an estimate of 5.1% body weight per day (Fig. 1).

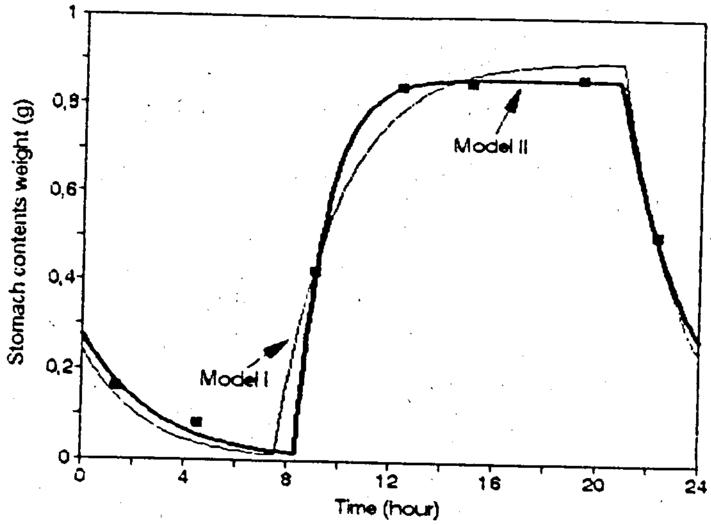

Fig. 1. Diel trajectory of stomach contents of diamond turbot (*Hypsopsettus guttatus*, data from Lane *et al.* 1979) as estimated from the Models I and II of the integrated approach.

Nile tilapia

Data on stomach contents nile tilapia (*Oreochromis niloticus*) from Lake Awasa, Ethiopia from Getachew (1987, cited from Palomares 1991) were used as second application example. The modified Bajkov formula yielded an estimate of daily ration of 37.9 g for fish of average 265 g body weight, the point-to-point approach yielded an estimate of 39.0 g. Model I and Model II gave similarly close fits with estimates of daily rations of 40.0 g and 40.1 g, respectively (Fig. 2).

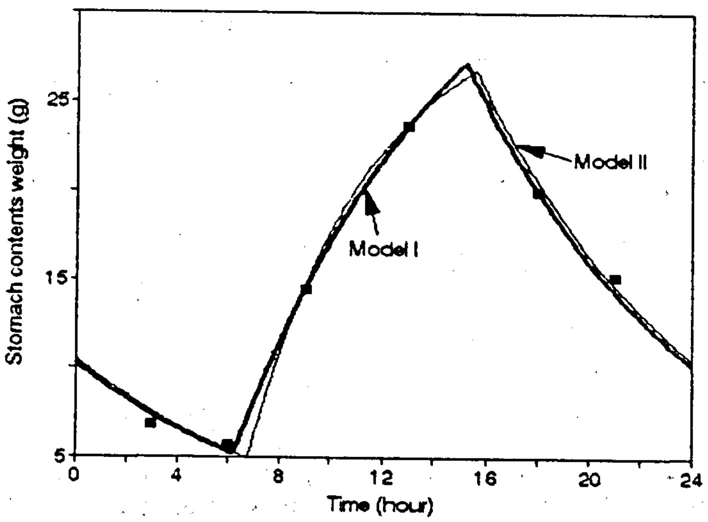

Fig. 2 Diel trajectory of stomach contents of *Oreochromis niloticus* (data from Getachew 1987 cited from Palomares 1991) as estimated from Models I and II of the integrated approach.

Cod

Arntz (1974) collected an extensive data set on food consumption of cod in the Kiel Bight, Western Baltic. The size class 26-30 cm showed a clear bimodal pattern of feeding activity during dawn and dusk. For this data set, a daily ration of 4.9 g was estimated by the modified Bajkov formula, and an estimate of 5.0 g was obtained using the point-to-point method. The integrated approach yielded an estimate of 5.2 g and 4.9 g for Model I and Model II, respectively (Fig. 3). It should be noted that the trajectories can hardly be distinguished from one another in spite of the different assumptions on the intensity of feeding with increasing stomach content.

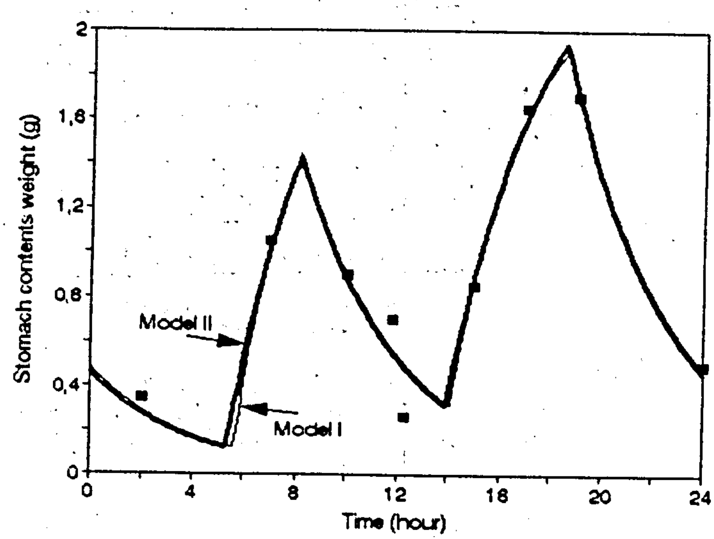

Fig. 3 Diel trajectory of stomach contents of Baltic cod (*Gadus morhua*, data from Arntz 1974) as estimated from Models I and II of the integrated approach.

Case studies with simulated data

As the estimates of daily ration are reasonably close to each other in the three preceding examples, the question arises whether the integrated approach has any advantage at all over the easier computed Bajkov and point-to-point methods. Three case studies have therefore been constructed to illustrate possible shortcomings of the two latter approaches.

All case studies assume fish feeding with a constant ingestion rate during the feeding period, and, for simplicity's sake, with simple exponential evacuation. Sampling is done over an entire 24-hours cycle, however, not in equal time intervals, as is frequently the case in practice. A daily ration of 10.0 g has been set for the fish in each of the three cases. The parameters settings are given in Table 1. A random error (± 10%, "measurement error") was imposed on the stomach contents weights at the sampling times, yielding the samples given in Table 2.

Parameter	Case 1	Case 2	Case 3
Ingestion (g/h)	0.833	1.67	1.25
Evacuation (h^{-1})	0.19	0.23	0.26
Feeding - Begin (h)	6	6	6
Feeding - End (h)	18	12	10
Feeding - Begin (h)	-	-	16
Feeding - End (h)	-	-	20

Table 1. Settings of the three case studies used for illustrating possible advantages of the integrated approach. See text for details.

Case 1		Case 2		Case 3	
Time (h)	Contents (g)	Time (h)	Contents (g)	Time (h)	Contents (g)
4	0.591	1	0.293	1:30	0.828
8	1.710	4	0.151	6:30	2.881
11	2.896	7	1.535	9	2.031
14	3.665	10	4.268	12	0.864
17	4.106	15	2.846	15	2.630
20	2.638	18	1.361	18:30	2.425
24	1.280	21	0.698	21:30	0.757

Table 2. Samples constructed in the three case studies used for illustrating possible advantages of the integrated approach. See text for details.

Figs. 4 - 6 give the (true) time trajectories of stomach contents, as well as the sampling points. The results of the estimations of daily ration by the three different methods are given in Table 3.

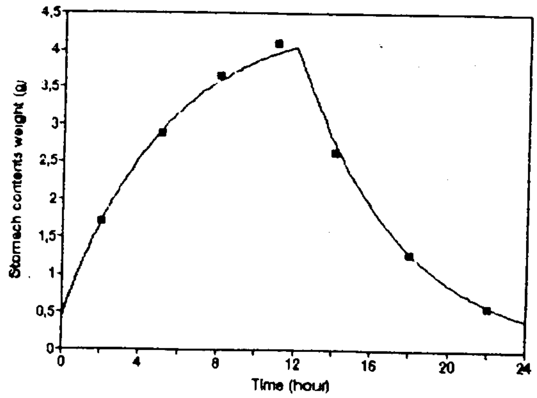

Fig. 4 Diel stomach contents trajectory and sampling points for Case Study No. 1.

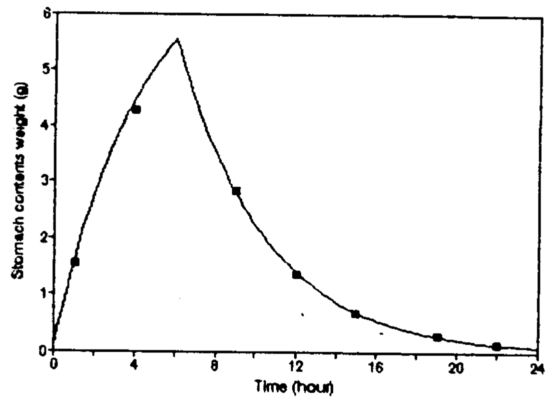

Fig. 5 Diel stomach contents trajectory and sampling points of Case Study No. 2.

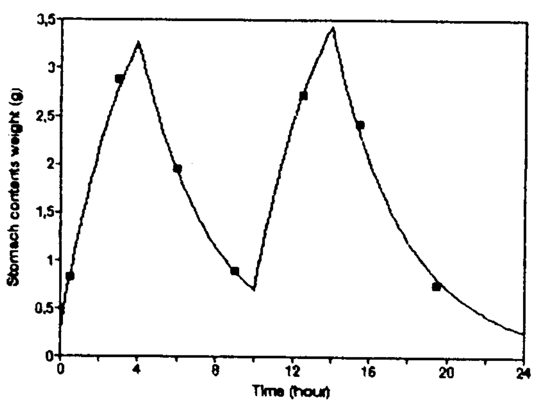

Fig. 6 Diel stomach contents trajectory and sampling points for Case Study No. 3.

Model	Case 1	Case 2	Case 3
Modified Bajkov			
E (h^{-1})	0.187	0.224	0.201
Daily Ration	10.83	8.58	8.54
Point-to-point			
E (h^{-1})	0.187	0.224	0.201
Daily Ration	10.23	9.20	8.11
Integrated Model I			
Ingestion (g/h)	0.857	1.641	1.389
Evacuation (h^{-1})	0.186	0.232	0.274
Begin 1 (h)	6.03	6.02	6.03
End 1 (h)	17.63	12.20	10.04
Begin 2 (h)	-	-	16.34
End 2 (h)	-	-	20.13
Daily Ration	9.94	10.15	10.83
Sum of sq. residuals	0.0053	0.0049	0.0050
Integrated Model II			
Ingestion (h^{-1})	0.125	0.171	
Evacuation (h^{-1})	0.191	0.229	
Asymptote (g)	3.927	5.564	not applica-
Begin 1 (h)	6.37	6.27	ble:
End 1 (h)	18.37	12.27	too few data
Begin 2 (h)	-	-	points.
End 2 (h)	-	-	
Daily Ration	10.35	9.76	
Sum of sq. residuals	0.1850 (!)	0.0260 (!)	

Table 3. Results of the estimation of daily ration for the case studies.

In the first case (feeding period 12 hours), the daily ration is misestimated by the modified Bajkov formula and the point-to-point approach by 8.3 and 2.3%, respectively. The integrated approach yields a misestimate of 0.6% for Model I, and for 3.5% for Model II. However, the sum of squared residuals is more than one order of magnitude higher for model II, indicating that a better fit is obtained by Model I.

In the second case (feeding period 6 hours), the daily ration is misestimated by 14.2% using the modified Bajkov formula, and by 8% from the point-to-point approach. Model I of the integrated approach yields a misestimate of 1.5%, and Model II a misestimate of 2.4%. Both results are better than those of the two former methods, however, as in the previous case, a comparison of the sum of squared residuals clearly indicates that Model I is more appropriate for fitting the data. This result also corresponds to the case settings.

The third case (two feeding periods of 4 hours each) yields misestimates of 14.6% and 18.9% by the modified Bajkov formula and the point-to-point approach, respectively. Model II of the integrated approach is not applicable, as it has not been found appropriate to fit a set of 7 parameters to 7 data points. The daily ration is misestimated from Model I by 8.3%.

Discussion

The estimates of the evacuation rate (as the major factor in the daily ration estimate) of the modified Bajkov formula and the point-to-point approach are obtained by linear regression, thus minimizing the sum of squared residuals. The estimate of daily ration obtained from the integrated approach, however, is subject to the efficiency of the multivariate search routine used to deal with local minima of the function to be minimized (and on the patience of its user). Whereas strict convergence criteria will improve on the quality of the estimate, this will also imply a rapid increase in computational effort that may not easily be met by personal computers. The implementation of the AMOEBA search routine in MAXIMS is intended as a compromise between desired accuracy of the result and available computational speed. Whereas several restarts of the search with different sets of initial values are required at present to obtain reliable results, a decrease of the convergence criterium may be possible in the future, based on results of further practical application.

One seeming disadvantage of the integrative approaches is the high number of data points required for purely statistical reasons - i.e., the high number of parameters to be estimated from a given data set. However, a complex trajectory of stomach contents will not be adequately accounted for by neither of the models discussed without regular and sufficient sampling over phases of activity and non-activity, as demonstrated Case Study No. 3.

Even if the evacuation rate can be estimated reasonably well from the samples (Cases 1 and 2), the modified Bajkov formula is known to be particularly susceptible to deviations from the true mean of the stomach contents, whereas the point-to-point method may fail if the peaks of the trajectory are not sufficiently covered by the sampling schedule. The errors appear to increase with decreasing duration of the feeding period.If a clear uni- or bimodal feeding activity is apparent from the data, the integrated approach may prove more robust towards gaps in the sampling schedule. Even in cases such as No. 3, where the number of data points is not sufficient to exactly indicate the periodicity of feeding, application of the integrated approach may limit the periods of re-sampling considerably, thus saving ship-time and sampling cost.

Further efort is presently made to include other models for the estimation of daily ration into MAXIMS, e.g., a model alowing for a time-lag in evacuation (Elashoff *et al.* 1982); as frequently observed (e.g., in sharks; Medved 1985), causing a reduction of the maximum possible rate if viewed over the entire feeding cycle.

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