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Evidence of violation of a basic assumption in models currently used for food consumption estimation in fish*

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Abstract

The quantification of food consumption in fish is essential for the development of quantitative trophic models of aquatic ecosystems and in aquaculture. Four models and their derivatives have mainly been used to estimate daily ration by modelling change in stomach contents over time, namely the Bajkov, Elliott-Persson, Olson-Mullen and MAXIMS models. In spite of their widespread application, none of these models have so far been adequately tested to ascertain whether the assumptions they are based on are fulfilled and the daily ration predictions are accurate. Two original datasets, one obtained from milkfish, the other from tilapia hybrids, were used here to apply these four models and compare the consumption estimates with the quantities known to be ingested. In both species, all the model predictions were close together (1.76 to 1.81 % Body Mass Equivalent (% BME) for milkfish; 0.79 to 0.82 % BME for tilapia) but distinctly lower than the known consumption levels (3.15 % BME for milkfish, 1.90 % BME for tilapia). A comparison of the stomach contents observed in the feeding phase with those expected on the basis of the evacuation rate calculated in the non-feeding phase and assuming complete consumption of the food provided strongly suggested that the rate of stomach evacuation in the feeding phase was significantly higher than that when the fish were no longer feeding. When the consumption estimates were recalculated with all models on the assumption that the evacuation rate doubles in the feeding period compared to the non-feeding phase, the model predictions increased to 2.73 to 3.58 % BME for milkfish and 0.98 to 1.58 % BME for tilapia, supporting the validity of this assumption. The present findings cast doubt on one of the fundamental assumptions of all food consumption models and therefore also on the results obtained with the aid of these models.

Kurzfassung

Nachweis der Verletzung einer fundamentalen Annahme in gegenwärtigen Modellen zur Abschätzung der Nahrungsaufnahme bei Fischen

Die Quantifizierung der Nahrungsaufnahme von Fischen ist für die Entwicklung von Modellen zur Beschreibung der Trophie in aquatischen Ökosystemen und in der Aquakultur unbedingt nötig. Um die tägliche Aufnahme von Nahrung bei Fischen beschreiben zu können, wurden in den letzten Jahren hauptsächlich vier Fressmodelle und ihre Ableitungen (Bajkov, Elliott-Persson, Olson-Mullen und MAXIMS) verwendet. Trotz ihrer weitverbreiteten Anwendung wurde bisher keines dieser genannten Modelle auf die Richtigkeit der mathematischen Annahmen, auf denen die Modelle basieren, adäquat

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getestet. Zwei originale Datensätze, einerseits von Milchfischen aus Beckenhaltung und andererseits von Tilapien-Hybriden aus einer Teichwirtschaft, wurden zum Test der genannten vier Modelle angewandt, um die berechnete Nahrungsaufnahme mit der tatsächlich aufgenommenen Nahrungsmenge zu vergleichen. Bei beiden Fischarten variierten die errechneten Werte nur geringfügig (1,76 bis 1,81 % der Körpermasse bei Milchfischen; 0,79 bis 0,82 % bei Tilapien), waren aber eindeutig geringer als die tatsächlich aufgenommene Nahrungsmenge (3,15 % bei Milchfischen und 1,90 % bei Tilapien). Ein Vergleich der Mageninhalte aus der Fressphase mit den zu erwartenden Werten, die auf Basis der Ausscheidungsrate in der Nicht-Fressphase unter Annahme einer vollständigen Nahrungsaufnahme berechnet wurden, lässt auf eine signifikant höhere Ausscheidungsrate während der Fressphase verglichen mit der Ausscheidung in der Nicht-Fressphase schliessen. Nachdem die berechnete Nahrungsaufnahme bei allen Modellen mit einer veränderten Ausscheidungsrate (verdoppelt während der Fressphase) erneut kalkuliert wurde, ergaben die Vorhersagen der einzelnen Modelle bei Milchfischen (2,73 bis 3,58 %) und bei Tilapien (0,98 bis 1,58 %) erhöhte tägliche Rationen und stützen damit die Richtigkeit dieser veränderten Annahme. Diese neuen Ergebnisse wecken Zweifel an einer fundamentalen Annahme aller bisherigen Mageninhaltsmodelle und daher ebenfalls an den mit Hilfe dieser Modelle berechneten täglichen Nahrungsaufnahmen.

Introduction

In recent decades, a large volume of literature has been devoted to the quantification of feed intake in fish (*e. g.* Staples 1975: Thorpe 1977: Lane *et al.* 1979: Persson 1982: Garcia and Adelman 1985: Macdonald and Waiwood 1987: del Norte-Campos and Temming 1994: Shepherd and Mills 1996: Amundsen *et al.* 1999). This reflects the fact that this parameter is of enormous practical relevance to both fisheries and aquaculture. In capture fisheries, the depletion of important fish stocks has forced scientists to look at ecosystems and the interaction of different species within these systems by predation and competition. The modelling of systems requires detailed knowledge not only on the food spectrum but also on the respective quantities of food ingested. In aquaculture, the quantification of actual feed intake, especially in semi-intensive systems, becomes increasingly important in order to make rational use of expensive and principally limited resources. In attempting to determine this parameter, however, one major problem is that direct consumption estimates obtained in “cafeteria” experiments where fish are given food under controlled conditions and the difference in food mass at the start and end of the experiment is assumed to be the amount consumed (Dempster *et al.* 1993; Keshavanath *et al.* 1994; Toguyeni *et al.* 1997) cannot emulate conditions in the wild. Thus, since the fish are often presented with a surfeit of food, the results usually reflect the maximum possible ration rather than that actually consumed in the field. Bioenergetics and nitrogen balance models (Rudstam *et al.* 1994; Hansson *et al.* 1996; Karjalainen *et al.* 1997; Owen *et al.* 1998) relate more closely to field conditions but require a considerable amount of initial work, which again needs to be conducted in the laboratory, with all inherent experimental biases, before growth rates of wild fish can be translated into a consumption estimate.

As a result of this, the modelling of stomach contents over the daily cycle has become increasingly popular in recent decades. While a large volume of literature has been devoted to the modelling of gastric evacuation (Hopkins 1966; Fänge and Grove 1979; Jobling 1981; 1986; Elashoff *et al.* 1982; Basimi and Grove 1985; Persson 1986; dos Santos and Jobling 1992; Salvanes *et al.* 1995) and factors affecting this (Jones 1974; Grove and Crawford

1980; Persson 1982; dos Santos and Jobling 1991; Hölker and Temming 1996; Storebakken *et al.* 1999); the number and variety of methods to determine food consumption based on these approaches has been rather more limited. The principal food consumption models developed are as follows:

1. that of Bajkov (1935) and its modifications (Eggers 1979; Pennington 1985; Temming and Andersen 1994), best suited to continuously feeding fish; hereafter referred to as the "Bajkov model",
2. that of Eggers (1977) and Elliott and Persson (1978), mainly for filter feeders and grazers showing diel feeding periodicity; hereafter named the "Elliott-Persson model",
3. the Sainsbury (1986) and Jarre *et al.* (1991) modification of the Elliott-Persson model, also best suited to grazers and filter-feeders feeding for only part of the day; christened "MAXIMS" by the latter authors and hereafter referred to as such,
4. that of Olson and Mullen (1986), best suited to active carnivores ingesting large-sized prey at irregular intervals; hereafter named the "Olson-Mullen model".

The MAXIMS model was based on the same principles as the Elliott-Persson model but differed in using non-linear regression to calculate average feeding and evacuation rates whereas its predecessor used a point-to-point approach. Richter *et al.* (1999) exploited this fact by using the parameter estimates, standard errors and covariances to devise a method of calculating confidence limits to the consumption estimate from only one set of data.

In spite of the large volume of literature that has been published on the subject of food consumption modelling, no satisfactory attempt has so far been made to verify any of the various models by comparing their daily ration prediction with a known value. Some authors have tried to compare consumption estimates from such models with those of bioenergetics models (Arrhenius and Hansson 1994; Hansson *et al.* 1996; Worishka and Mehner 1998) and have generally found lower estimates from consumption models compared to those of bioenergetics models. It has to be stated, however, that the latter have not been adequately tested with the aid of known ingestion rates either. Elliott and Persson (1978) and Sainsbury (1986) used the data set of Elliott (1975a,b) on brown trout, *Salmo trutta* L.; fed with *Gammarus pulex* (L.), to test the Elliott-Persson and MAXIMS models respectively. Both sets of authors came to the conclusion that their model tended to underestimate the true food consumption a little, but that their predictions were generally in good agreement with the true ration. However, since the overall meal size was not excessive and was consumed within *ca.* 20 minutes, this did not constitute a severe test for a model designed for continuous feeders potentially ingesting a maximum possible ration if confronted by a surfeit of food. Sainsbury (1986) also used Magnuson's (1969) data on skipjack tuna, *Katsuwonus pelamis* L. and that of Joll (1984) on western rock lobster, *Palunirus cygnus* George, but himself expressed dissatisfaction with the fits the model gave to the data sets. Neither the Bajkov nor the Olson-Mullen model have been tested against known food consumption data. The aim of the present work was therefore to test these models by applying them to two feeding scenarios likely to be encountered under aquaculture conditions and comparing their consumption estimates with the quantity of food known to be taken up by the fish.

Mathematical basis of the models used

Bajkov model

Bajkov's (1935) original model depended on an estimate of the average stomach contents over a period of time in conjunction with the gut passage time. Eggers (1979) and Pennington (1985) modified the gut passage time to a stomach evacuation rate which was dependent on the level of stomach contents so that the formula for stomach evacuation was:

$$\mathrm{d}S\,/\,\mathrm{d}t = -E \times S^{B} \tag{1}$$

which, under steady state conditions (constant feeding over 24 hours, evacuation countered by an equal rate of ingestion) may be integrated directly to arrive at the daily ration formula:

$$R_{\mathrm{d}} = \int_{t=0}^{t=24} E \times S^{B}.\mathrm{d}t = 24 \times E \times S_{\mathrm{avg}}^{B} \tag{2}$$

(S = stomach contents, t = time in hours, S_{avg} = average stomach contents over 24-hour period, E = evacuation rate, R_{d} = daily ration, B = dependency constant, usually taken as 1.0)

Elliott-Persson model

Elliott and Persson (1978) retained the idea of stomach evacuation dependent on the level of stomach contents (Equation 1) but did not see this matched by an equal and opposite ingestion rate. Instead, they introduced a new parameter, J (C in their original publication), for this and assumed that B = 1 (simple exponential evacuation), so that the rate of change in stomach contents was expressed as:

$$\mathrm{d}S\,/\,\mathrm{d}t = J - E \times S^{B} \tag{3}$$

which was integrated to give the consumption estimate between successive time intervals:

$$J_{\mathrm{t}} = \left(S_{\mathrm{t}} - S_{0} \times \mathrm{e}^{-E \times t}\right) \times E \times t \,/ \left(1 - \mathrm{e}^{-E \times t}\right) \tag{4}$$

(J_{t} = amount of food consumed in time interval of length t, S_0 and S_{t} = stomach fullness at the beginning and end of the phase analysed respectively, E = evacuation rate, e = Euler's number, base of the natural logarithm). The consumption over the entire sampling period was the sum of all estimates of J_{t}.

MAXIMS model

Sainsbury (1986) also used the concept that ingestion did not necessarily equal stomach evacuation (Equation 3) but assumed J to be constant when the fish was feeding. Nevertheless, the model assumed strict diel feeding periodicity so that in those phases when there was no consumption, Equation 1 applied. The parameters were determined by non-linear regression through the data set according to the integrals of Equations 1 and 3 when not feeding and when feeding respectively:

From Equation 1: $$S = S_{\mathrm{s}} \times \mathrm{e}^{-E\times(t-F_{\mathrm{s}})} \tag{5}$$

From Equation 3: $$S = S_{\mathrm{b}} \times \mathrm{e}^{-E\times(t-F_{\mathrm{b}})} + (J / E)\times\left(1 - \mathrm{e}^{-E\times(t-F_{\mathrm{b}})}\right) \tag{6}$$

(S = Stomach contents, S_{b} and S_{s} = stomach contents when the fish begins and stops feeding respectively, J = Ingestion rate, E = Evacuation rate, F_{b} and F_{s} = times when the fish begins and stops feeding respectively, e = Euler's number).

The daily ration, R_{d}, was then calculated as the integral of the ingestion rate over the feeding period:

$$R_{\mathrm{d}} = \int_{t=F_{\mathrm{b}}}^{t=F_{\mathrm{s}}} J.\mathrm{d}t = J \times (F_{\mathrm{s}} - F_{\mathrm{b}}) \tag{7}$$

The model was extended to allow the ingestion rate to decrease with increasing stomach contents and Jarre *et al*. (1991) made further modifications to permit two feeding periods per 24-hour cycle but these need not be discussed here.

Olson-Mullen model

Olson and Mullen (1986) developed a model primarily suited to predatory fish in which the ingestion of a single prey item can cause the stomach contents to increase dramatically within seconds. Fish of the same population can therefore show great variation in the level of stomach fullness. Moreover, the stomach contents can be made up of several different prey types, each with their own evacuation rate, leading to differences in overall evacuation rate between fish depending on stomach composition. The Olson-Mullen model is therefore based on partitioning the stomach contents into their various food types, each of which is modelled separately with the results then combined over the period analysed. It was shown that the average weight of a given type of food in the stomach, $S(i)_{\mathrm{avg}}$ ($W(i)_{\mathrm{avg}}$ in the original publication) over an (extensive) period of duration t is:

$$S(i)_{\mathrm{avg}} = \left(M(i)_{\mathrm{avg}} / T(i)_{\mathrm{avg}}\right)\times \int_{t=0}^{t} \mathrm{f}_i(t).\mathrm{d}t \tag{8}$$

($S(i)_{\mathrm{avg}}$ = mean weight of food type i in the stomach over the sampling period, $M(i)_{\mathrm{avg}}$ = mean weight of items of food type i when ingested, $T(i)_{\mathrm{avg}}$ = mean time interval between ingestion of individual items of food type i, $\mathrm{f}_i(t)$ = 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 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:

$$R_{\mathrm{d}} = 24 \times \sum_{i=1}^{i=\mathrm{N}} \left[M(i)_{\mathrm{avg}} / T(i)_{\mathrm{avg}}\right] = 24 \times \sum_{i=1}^{i=\mathrm{N}} \left[S(i)_{\mathrm{avg}} \Big/ \int_{t=0}^{t} \mathrm{f}_i(t).\mathrm{d}t\right] \tag{9}$$

Materials and Methods

Milkfish sampling

200 milkfish, *Chanos chanos* (Forsskål), (mean weight 9.7 g) were stocked in a 3000 l, 2.5 × 1.5 × 1 m flow-through concrete tank at the Tigbauan Main Station of the Southeast Asian

Fisheries Development Center (SEAFDEC), Philippines, and allowed to acclimatize for ten weeks. The tank outflow consisted of a vertical tube rising from the bottom at one end of the tank with small holes in the upper 10 cm. The tank was cleaned weekly in order to prevent the build-up of *Aufwuchs* and phytoplankton which might have acted as a source of natural food, and was shaded to keep the temperature more or less constant (29.0 to 29.7 °C). Salinity and dissolved oxygen did not fluctuate greatly either (33.3 ‰ and 5.0 to 5.9 $mg{\cdot}l^{-1}$ respectively). Mortality reduced the number of fish to 133 by the time the trial was conducted, but no mass mortality was observed and no fish died in the seven day period immediately preceding the experiment. Two days before the trial, the experimental feed (3 mm pellets, Hohenheim standard formulation: 50 % fishmeal, 42 % wheatmeal, 4 % sunflower oil, 2 % each vitamin and mineral premix; 10 % moisture content) was given in several small doses spread throughout the day and the feeding behaviour of the fish monitored. It was noticed that all the feed was consumed within 2 to 3 minutes; feeding activity ceased and no uneaten food was visible. The last dose of feed was given at 17:00 hours that day and the fish were starved the following day to ensure that their stomachs would be empty at the start of the trial.

On the day of the experiment, three fish were collected from the tank each hour from 7:00 to 21:00 hours inclusive by gently moving a fine meshed seine net from one end of the tank to the other, thereby reducing the free space for the fish, and then collecting the required number of fish with a bag net. This technique was considered to minimise the stress to the fish. After sampling the fish were immediately killed, measured (nearest mm), weighed (nearest 0.01 g) and the stomachs removed and preserved in 70 % ethyl alcohol until further analysis. To simulate an extended feeding period, the fish were given the daily ration in five equal doses at hourly intervals from 7:55 to 11:55 hours inclusive at the end of the tank distal to the outflow. The total quantity of feed given was 3.15 % Body Mass Equivalent (% BME). For the sake of comparison, this figure and all subsequent ones relating to this unit are given as dry mass as percentage of the wet body mass of the fish. Sampling was not carried out until feeding activity had ceased to ensure that all the food given had been consumed by the time fish were collected for analysis.

Tilapia sampling

Tilapia hybrids, *Oreochromis niloticus* (L.) × *O. aureus* (Steindachner) (mean body mass: 80 g) were stocked in 30 cages (1 × 1 × 1 m) in a 1.8 ha fishpond (mean depth: 2 m) used for tilapia-mullet-carp polyculture at the Dor Research Station, Israel. The cages were constructed from 5 mm mesh netting with a solid canvas bottom to prevent uneaten food from dropping through to the bottom of the pond, and were each stocked with 60 fish (mean weight: 80 g). The fish were allowed to acclimatize for 10 weeks, during which time they had access to natural food (phytoplankton) but were also given supplemental feed (3 mm pellets, Zemach Central Feed Mill Corporation Ltd.; Israel: 38 % wheat components, 32.4 % soy components, 19.6 % other plant components, 4 % poultry components, 2 % fishmeal, 2.9 % dicalcium phosphate, 1.1 % oil; 10 % moisture content) at a rate of 1.9 to 2.2 % BME, depending on their body size, according to the feeding table of Zohar (1986). It was observed that, throughout the acclimatization phase, the feed given was consumed quickly and apparently completely. Water quality remained fairly constant and varied mainly with time of day: temperature fluctuated between 28 to 31 °C and dissolved oxygen was around saturation level except early in the morning (2.5 $mg \cdot l^{-1}$) before the fish were fed. Secchi depth remained around 1 m throughout the acclimatization phase and experiment. Mortality rates were negligible throughout the acclimatization period so that water quality levels were not considered to limit fish feeding and digestion.

The sampling date was chosen to coincide with a period of calm weather to prevent having the food washed out of the cages by wave action soon after feeding. Subsamples of twelve fish were collected at two-hour intervals between 5:00 and 23:00 hours inclusive by removing four fish from three different cages. Once a cage had been sampled, no fish were collected from it for the remainder of the experiment to minimise stress to unsampled fish. Following sampling, the fish were killed, measured (nearest mm), weighed (nearest 0.1 g) and the stomachs removed and preserved. During the experiment, the fish were given their daily ration (1.9 % BME) at 9:00 hours in one dose, shortly after sampling the fish for that hour. During sampling, the cages were lifted carefully from the water to avoid the possibility of uneaten feed being washed out of the cage by the swell. However, even during the first sampling after feeding (11:00 hours), no traces of unconsumed feed were observed.

Stomach content analysis

At a later date, the preserved stomachs of both milkfish and tilpaia were dissected and their contents flushed into preweighed vials and further preserved in 70 % ethyl alcohol. In the case of the tilapia, the stomach contents were thoroughly mixed and three representative portions of each fish's contents analysed visually under the microscope to assess the relative contributions of natural food and supplemental feed. The results were combined for each fish to give an average percentage for both components and the three portions recombined with the original sample. The stomach contents of both species were then dried in an oven at 105 °C for five hours and the weight recorded. As in the case of the formulated feed given to the fish, the stomach content weights were converted to % BME (dry:wet basis) for each individual fish. In order to be able to compare the stomach contents with the original feed, a representative portion of the latter was also dried to constant weight and the feeding rates recalculated to the ones quoted throughout this publication.

Bajkov model application

Equation 2 was applied with the parameter B set to 1.0, the evacuation rate E taken from the initial MAXIMS prediction and the average stomach contents S_{avg} determined from the data sets. Since the sampling period did not cover the full 24-hour cycle in either case, the time period multiplier was set to 14 hours for milkfish and 20 for tilapia, assuming each subsample to represent the mean for a full hour.

When the model was reapplied with the increased evacuation rate, parameter E was simply doubled for both species compared to its previous value, thereby exactly doubling the consumption estimate.

Elliott-Persson model application

Equation 4 was applied to the data between all successive time intervals for both species. Although the original idea of Elliott and Persson (1978) was based on an evacuation rate determined from an independent data set, some authors using this model have used that part of the data set when the stomach contents are declining and the fish were presumed not be taking in food to obtain this value (Arrhenius and Hansson 1994, Haroon *et al.* 1998). The evacuation rate E was therefore taken from the MAXIMS analysis. The duration of time interval t in Equation 4 was set to 1 hour for milkfish and 2 hours for tilapia and the estimates of S_b and S_s determined from the data set. When the model was reapplied, parameter E was doubled only for the time intervals in which feed was given, i.e. 7:00 to 12:00 hours and 9:00 to 11:00 hours respectively for milkfish and tilapia.

MAXIMS model application

Non-linear regression in distinct phases using Equations 5 and 6 was carried out on the data sets. The software used was SAS 6.12 for Windows with the routines derived from those given for MAXIMS Model 1.1 in Richter *et al.* (1999). When the model was reapplied for the increased evacuation rate, this parameter was doubled in Equation 6 (“$2 \times E$”) but not in Equation 5 (“E”). Food consumption was then calculated according to Equation 7 using the values for J, F_b and F_s given in the SAS output.

Olson-Mullen model application

Although the Olson-Mullen model is best suited to fish with several different stomach content components, only compound feed was modelled for both species in the present work so that Equation 9 was applied with N = 1. Again, the time period multiplier was set to 14 hours for milkfish and 20 for tilapia to account for the fact that the experimental phase was less than 24 hours in both cases. The value for S_{avg} was in both cases obtained from the data sets. The function describing stomach evacuation, f(t) (change in stomach contents due to evacuation alone, disregarding increases due to ingestion), was assumed to be the same as in the other models when the fish is not feeding and was adapted from Equation 5. Since in the MAXIMS model, Equation 5 describes the overall change in stomach contents during a non- feeding period whereas in this case, it applies only to the evacuation component regardless of whether the fish is still feeding or not, the start of the non-feeding phase F_s may be substituted with t_0 (start of the period being analysed) so that:

$$\mathrm{f}(t) = \mathrm{e}^{-E \times (t - t_0)} \qquad (10)$$

This may then be integrated over the entire experimental period, for simplicity’s sake disregarding time of day so that t is the length of the analytical period and $t_0 = 0$, to give:

$$\int_{t=0}^{t} \mathrm{f}(t).\mathrm{d}t = \int_{t=0}^{t} \mathrm{e}^{-E \times t}.\mathrm{d}t = \frac{1}{-E} \times \left(\mathrm{e}^{-E \times t} - 1\right) \qquad (11)$$

The food consumption over the entire experimental period of duration t may then be calculated as:

$$R_{\mathrm{d}} = t \times S_{\mathrm{avg}} / \left(\frac{1}{-E} \times \left[\mathrm{e}^{-E \times t} - 1 \right] \right) \qquad (12)$$

with t set to 14 hours in milkfish and 20 hours in tilapia. When the model was reapplied with the increased evacuation rate, the parameter E was doubled.

Results

Ten weeks after stocking, on the day of the respective experiments, the milkfish had grown to an average size of 15.4 g and the tilapia to 182 g. In the case of the tilapia hybrids, microscopic analysis revealed that the stomachs of all fish contained mostly supplemental feed; at no time of day did the proportion of natural food in the stomachs exceed 10 %. This was also true for those fish collected at 5:00 and 7:00 hours, suggesting that some supplemental feed from the previous day had not been evacuated and that the fish had not yet started to feed on natural food on the sampling day to any significant extent. Since, as pointed out by Sainsbury (1986), the model is additive, *i. e.* different stomach content components may be analysed separately, the stomach content weights were corrected by multiplying the values by the proportion of supplemental food for that fish so that only this component was modelled in the analysis.

The observed stomach contents for milkfish and tilapia are shown in Figures 1 and 2 respectively which also include the MAXIMS curves from which the evacuation rates were obtained. Since feed was only given once in the case of tilapia and the feeding period was

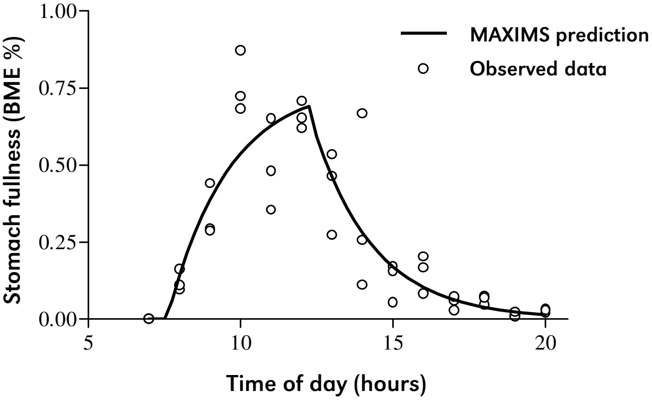

Figure 1: Observed data and MAXIMS prediction for milkfish (% BME: % Body Mass Equivalent).

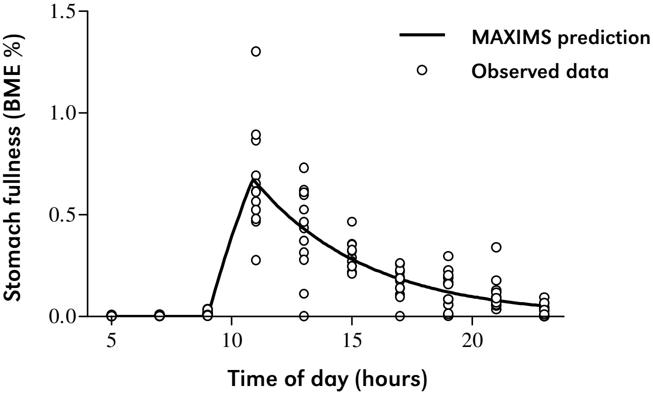

Figure 2: Observed data and MAXIMS prediction for tilapia (% BME: % Body Mass Equivalent).

rather shorter than the interval between fish sampling, it proved difficult to get the model to converge so that the start of the feeding period was fixed to 9:00 hours. There is clearly some scatter around the predicted curves, attributable to the fact that, since fish were not kept individually, dominant individuals would have had access to more of the food than other fish. Nevertheless, the evacuation rate may in both cases evidently be obtained with good accuracy from the non-feeding phase. Some authors (*e. g.* Olson and Mullen 1986) have suggested that stomach evacuation is not exponential but linear and recommend truncating the data immediately prior to the occurrence of the first empty stomachs. The fact that almost all stomachs of both species contained at least some food after feed was given, particularly in the case of milkfish, makes linear evacuation very unlikely.

Table 1: Stomach content data for milkfish (mean of three fish) and consumption estimates determined with the Elliott-Persson model with single evacuation rate (*E*) and evacuation rate doubled between 7:00 and 12:00 hours (2 × *E*). Consumption estimates pertain to the period between the time point for which they are given and that preceding it.

Sampling time (time of day in hours)	Mean stomach contents (% BME)	Consumption estimate with *E* (% BME)	Consumption estimate with 2 × *E* (% BME)
7:00	0.000	–	–
8:00	0.123	0.162	0.205
9:00	0.340	0.338	0.461
10:00	0.760	0.702	0.990
11:00	0.496	0.044	0.329
12:00	0.660	0.456	0.742
13:00	0.424	0.029	0.024
14:00	0.346	0.112	0.108
15:00	0.127	−0.106	−0.108
16:00	0.151	0.094	0.092
17:00	0.053	−0.049	−0.050
18:00	0.063	0.040	0.039
19:00	0.014	−0.031	−0.031
20:00	0.027	0.022	0.021
Mean:	0.256	Total: 1.813	Total: 2.822

Table 2: Stomach content data for tilapia (mean of three fish) and consumption estimates determined with the Elliott-Persson model with single evacuation rate (*E*) and evacuation rate doubled between 9:00 and 11:00 hours (2 × *E*). Consumption estimates pertain to the period between the time point for which they are given and that preceding it.

Sampling time (time of day in hours)	Mean stomach contents (% BME)	Consumption estimate with *E* (% BME)	Consumption estimate with 2 × *E* (% BME)
5:00	0.003	–	–
7:00	0.004	0.003	0.003
9:00	0.011	0.010	0.010
11:00	0.656	0.796	0.974
13:00	0.418	−0.012	−0.008
15:00	0.290	0.020	0.023
17:00	0.177	−0.015	−0.014
19:00	0.119	0.004	0.005
21:00	0.104	0.033	0.034
23:00	0.030	−0.047	−0.046
Mean:	0.181	Total: 0.792	Total: 0.980

The average stomach contents for the (bi-)hourly subsamples for milkfish and tilapia are summarised in Tables 1 and 2 which also contain the Elliott-Persson predictions

Table 3: Parameter and food consumption estimates for milkfish and tilapia obtained with the Bajkov, Olson-Mullen, Elliott-Persson and MAXIMS models.

MAXIMS parameters and consumption estimate with 95 % confidence limits (start of feeding period for tilapia fixed to 9:00 hours). Evacuation rate of MAXIMS model used in applying other three models.

Model	Parameter	Milkfish	Tilapia
All Models	Number of fish (N)	42	120
	Experimental period (hours)	14 hours	20 hours
	Average stomach contents (% BME)	0.26	0.19
Bajkov model	Food consumption, R_d (% BME)	1.79	0.79
Elliott-Persson model	Food consumption, R_d (% BME)	1.81	0.79
Olson-Mullen model	Food consumption, R_d (% BME)	1.79	0.80
MAXIMS model	Ingestion rate, J (% BME·h^{-1})	0.38 (0.25–0.52)	0.43 (0.36–0.51)
	Evacuation rate, E ($hour^{-1}$)	0.50 (0.26–0.73)	0.21 (0.17–0.25)
	Begin feeding, F_b (time of day)	7:35 (7:07–8:03)	9:00 (fixed value)
	Stop feeding, F_s (time of day)	12:05 (11:19–13:03)	10:53 (10:52–10:53)
	Food consumption, R_d (% BME)	1.76 (0.89–2.53)	0.82 (0.68–0.96)

for the time intervals between the subsamples, as well as the overall average stomach contents used to calculate the Bajkov and Olson-Mullen models. The MAXIMS parameters are given in Table 3 which includes the food consumption predictions made by all the models used here. There is evidently some discrepancy between the true and predicted start of the feeding phase (7:55 and 7:30 hours respectively) made by the MAXIMS model for milkfish. More seriously, the consumption estimates for both species given by all models were considerably lower than the amount of feed given and presumably consumed. In the case of the MAXIMS model, this deviation was significant for both species ($p < 0.001$ in both cases).

Discussion

In attempting to find the reason for this consistent discrepancy between predicted and true ration, it is worth reconstructing the true situation in the case of the milkfish. 3.15 % BME was given in five equal doses and this was presumably consumed relatively quickly. The latter point is demonstrated by the fact that the stomach content values at 13:00 hours have already dropped markedly below those at 12:00 when the last dose of food was given, showing that for some time, evacuation without further ingestion had been taking place. The instantaneous evacuation rate may be accurately calculated from the non-feeding phase, so that, on the basis of the above assumptions, the level of stomach contents over time should

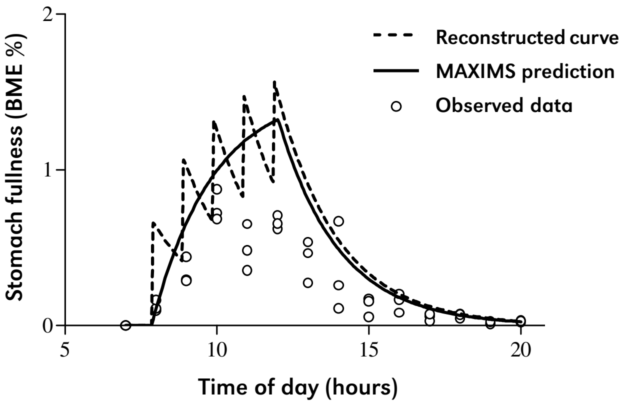

Figure 3: Observed data for milkfish, stomach content curve reconstructed on the basis of 100 % food consumption and equal evacuation in feeding and non-feeding phases and MAXIMS curve averaging the reconstructed curve (% BME: % Body Mass Equivalent).

be described by the function shown in Figure 3. Since the MAXIMS model was programmed to model only one feeding period, the expected prediction should average the true situation in the feeding phase to give the smooth line in Figure 3, the daily ration estimate of which would actually be 3.15 % BME. Practically the entire observed data set consists of stomach content values too low to meet the expected situation. The root of the problem seems to lie in the feeding phase where the difference in stomach contents between successive time points consistently fails to rise to the expected level.

In spite of the differences between the various consumption models, the principle they are based on is common to all. The stomach is assumed to be a compartment with only one entrance and one exit. Food enters as a result of ingestion and leaves by evacuation; there is no assimilation, merely digestion. The difference between the stomach contents at one point in time and a subsequent point therefore reflects the balance between ingestion and evacuation (mathematically equivalent to an equation with two unknown factors). In all applications of any of these models, the evacuation rate (the first unknown factor) is obtained from a period at the start of which the stomach is at least partly full and during which no ingestion takes place (the other unknown factor is zero). This rate is then used in the analysis of a feeding period to calculate the other unknown factor, the ingestion rate, on the assumptions that evacuation takes place at all times, not only when the fish is not feeding, and that the rate at which evacuation takes place is the same in the feeding and non-feeding periods. The consumption estimate is then derived from the ingestion rate, usually by mathematically integrating this factor over the feeding period. This demonstrates that the accurate determination of the evacuation rate is of paramount importance in estimating food consumption with the aid of appropriate models.

The above operational procedure provides two possible explanations for the reduced difference observed in the stomach contents between successive time intervals in the feeding period. Either the true ingestion rate is rather lower than expected, or the real instantaneous evacuation rate must be higher. The evidence suggests that food was consumed completely and relatively quickly after being supplied, in which case only the second reason can apply. The main problem with this explanation is that a higher instantaneous evacuation rate would not provide an adequate fit to the data in the non-feeding phase. This suggests that there is a significant discrepancy between the instantaneous evacuation rate in the feeding and non-feeding period, thereby violating one of the fundamental assumptions made in the application of all food consumption models.

Since the difference between the true and estimated daily ration was in both species a factor of about two, it was decided to reprogramme the MAXIMS model so that whatever the instantaneous evacuation rate was calculated to be in the non-feeding period, this value would be exactly doubled in the feeding period; all other assumptions were kept the same as before. The resulting fit for the milkfish is shown in Figure 4. Evidently, there is little difference between the two models, but the model with the increased evacuation rate is a little more humped, which results in a more accurate prediction for the start of the feeding phase. At the same time, the daily ration estimate increases to 2.73 % BME, which is no longer statistically different from the given ration of 3.15 % BME (Table 4). Evidently, the higher ration estimate is attributable mainly to the increased ingestion rate. All the same, the doubling of the instantaneous evacuation rate is not fully reflected in either the ingestion rate or the daily ration estimate, which increase by only about 60 %.

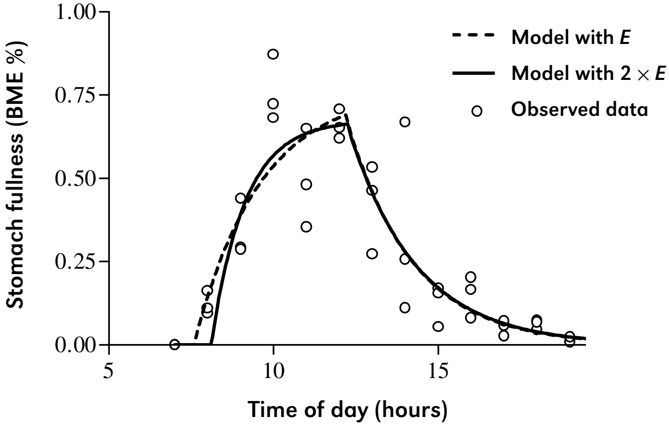

Figure 4: Observed data and MAXIMS models with the evacuation rate in the feeding period set to single (E) or double ($2 \times E$) the evacuation rate in the non-feeding period for milkfish (% BME: % Body Mass Equivalent).

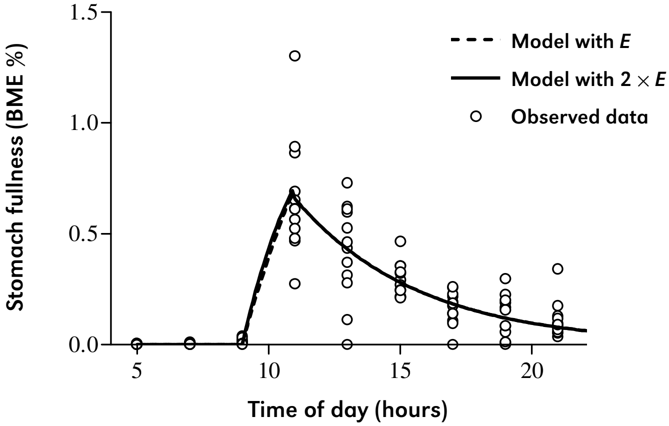

Figure 5: Observed data and MAXIMS models with the evacuation rate in the feeding period set to single (E) or double ($2 \times E$) the evacuation rate in the non-feeding period for tilapia (% BME: % Body Mass Equivalent).

Table 4: Parameter and food consumption estimates for milkfish and tilapia obtained with the Bajkov, Olson-Mullen, Elliott-Persson and MAXIMS models assuming evacuation rate in the non-feeding period (E) is doubled in the feeding period (2 × E).

Evacuation rate of MAXIMS model (non-feeding period) used as a basis for the application of other three models. Feeding period in MAXIMS assumed to last from $F_b - F_s$, that in Elliott-Persson model from 8:00–12:00 hours for milkfish and 9:00–11:00 hours for tilapia. Evacuation rate in Bajkov and Olson-Mullen models doubled for the entire experimental period. MAXIMS parameters and consumption estimate with 95 % confidence limits (start of feeding period for tilapia fixed to 9:00 hours). Number of fish, duration of experimental period and average stomach contents as in Table 3.

Model	Parameter	Milkfish	Tilapia
Bajkov model	Food consumption, R_d (% BME)	3.58	1.58
Elliott-Persson mode	Food consumption, R_d (% BME)	2.82	0.98
Olson-Mullen model	Food consumption, R_d (% BME)	3.58	1.58
MAXIMS model	Ingestion rate, J (% BME h^{-1})	0.66 (0.35–0.97)	0.53 (0.41–0.66)
	Evacuation rate, E ($hour^{-1}$)	0.49 (0.24–0.73)	0.22 (0.17–0.26)
	Begin feeding, F_b (time of day)	8:07 (7:24–8:49)	9:00 (fixed value)
	Stop feeding, F_s (time of day)	12:14 (11:19–13:10)	10:50 (10:49–10:52)
	Food consumption, R_d (% BME)	2.73 (1.27–4.18)	0.98 (0.74–1.22)

The same approach was carried out for the tilapia hybrids and here, the predicted feeding curve for the increased evacuation rate model is so close to the original that the two are virtually indistinguishable (Figure 5). In spite of the almost identical fits, the increased evacuation model also gave a markedly higher consumption estimate than the original (Table 4), although in this fish species, the rise was not as pronounced as in the case of the milkfish and the difference between the predicted and true daily ration remains significant ($p < 0.001$). This may have been because the discrepancy between the evacuation rate between feeding and non-feeding phases is greater than a factor of two or because the feeding period was rather shorter here. The latter point is explained by the fact that if evacuation is dependent on the level of stomach contents, which are zero at the start of the feeding phase in milkfish and negligible at this point in time in tilapia, some time is required for the doubling of the instantaneous evacuation rate to have an effect on the ingestion rate.

The other models were also reapplied with the higher evacuation rate. Since the Bajkov and Olson-Mullen models calculate an average ingestion rate from the entire data set, thereby completely eliminating the concept of feeding periodicity, the evacuation rate was doubled for the entire study period. The Elliott-Persson model allows for fluctuations in the ingestion rate depending on the level of stomach contents between successive sampling intervals so that here, the evacuation rate was doubled only for the phases between

8:00 to 13:00 hours. Evidently, the increased evacuation rate exactly doubles the estimate of the Bajkov model, nearly doubles that of the Olson-Mullen model and increases that of the Elliott-Persson model to about the same extent as the MAXIMS model (Table 4).

This is by no means the first time that an increase in the rate of stomach evacuation during a feeding phase compared to when the fish are not feeding has been found. This effect was demonstrated by Rozin and Mayer (1964) in goldfish, *Carassius auratus* L., Moriarty and Moriarty (1973) in Nile tilapia, Noble (1973) in yellow perch, *Perca flavescens* (Mitchill), Jones (1974) in haddock, *Melanogrammus aeglefinus* (L.), cod, *Gadus morhua* L., and whiting, *Merlangius merlangus* (L.), Talbot *et al*. (1984) in Atlantic salmon, *Salmo salar* L., Fletcher *et al*. (1984) in dab, *Limanda limanda* (L.) and Kristiansen (1998) in both brown trout, *Salmo trutta* L., and rainbow trout, *Oncorhynchus mykiss* (Walbaum). The large variety of species studied by these authors suggests that this phenomenon is probably widespread among fish. In addition, the results obtained by Moriarty and Moriarty (1973), whose fish were filter-feeding on phytoplankton in Lake George, Uganda, show that the effect is not restricted to captive fish given pelleted feeds in distinct doses but is also found in continuously feeding species ingesting diets with a higher water content. The study on goldfish, a stomachless fish, also shows that not only fish with stomachs are affected.

Although higher evacuation rates during the feeding phase compared to when fish are fasting have evidently been known about for over 30 years, this is the first time that the serious effect of this phenomenon on daily ration estimation has been shown. When fish consume few, large food items at lengthy time intervals (i.e. predators), they are unlikely to be affected. However, the smaller the prey size and the more items are ingested before the stomach has had time to evacuate fully, the greater the problem is likely to be. In order to develop food consumption models as a useful and reliable tool for daily ration estimation for ecosystem research and modelling as well as for the development of efficient semi-intensive aquculture systems, further work in this field is urgently required. This should aim at both the quantification of these discrepancies in order to reassess past daily ration estimates and at improved models and/or modelling approaches in order to avoid erroneous food consumption estimates in the future.

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