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Some new analytical and comparative methods for estimating the food consumption of fish¹

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Methods of obtaining estimates of daily ration (R_d) and population-weighted food consumption (Q/B) are presented. These include (a) a method for estimating R_d from changes in stomach contents in the course of a 24-h period, which allows either one of two feeding periods per day (i.e. for diurnal, nocturnal, or crepuscular feeders); (b) a method for estimating R_d and Q/B from estimates of gross food conversion efficiency, and growth and mortality parameters of the population; and (c) multiple regression models for predicting Q/B from temperature, asymptotic size, food type, and morphometric attributes of the fish in the population studied, based on species ranging from guppy to tuna, and from temperate to tropical habitats.

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Introduction

Most tropical and subtropical fisheries are based on multispecies resources. Hence, management oriented modelling studies which take multispecies aspects into account require the estimation of vital statistics for a large number of species, often without access to a historic database (Pauly, 1982). For statistics such as growth and mortality, this problem can largely be resolved by giving emphasis to the analysis of easily obtainable length-frequency data (Pauly and Morgan, 1987) and estimates derived from comparative studies of mortality and growth rates (Pauly, 1980; Munro and Pauly, 1983; Pauly and Munro, 1984; Moreau *et al.*, 1986).

A further basic requirement encountered in constructing a multispecies model is knowledge about food requirements of the constituent organisms. Such knowledge is often hard to obtain for individual species and therefore one may be tempted to transfer estimates from one species to the other. However, in order to ensure that the values thus transferred are realistic, it is appropriate to devise general relationships between metabolic

expenditure of populations and their ecological or morphological characteristics (Pauly, 1989).

In this paper, we present (1) an analytical method for estimating relative food consumption by individual fish from diurnal stomach sampling investigations; (2) a model for estimating food consumption in relation to biomass for a fish population; and (3) how some attributes of fishes which are easy to quantify can be used to predict their food consumption.

Estimation of daily ration from the dynamics of stomach contents

Starting with Bajkov (1935), numerous methods have been proposed for estimating the daily ration (R_d) of fish in nature, based on quantitative analyses of their stomach contents (Daan, 1973; Elliott and Persson, 1978; Olson, 1981; Durbin *et al.*, 1983; Gorelova, 1984; Pennington, 1985). Methods which are widely applied emphasize the estimation of stomach evacuation rate, and this had led to a lively discussion as to its proper parameterization (e.g. Jobling, 1981, 1986; Mullen, 1986; Temming, 1986).

Sainsbury (1986) proposed an alternative approach, wherein the estimation of R_d from stomach content data, sampled over a single cycle of arbitrary duration, is

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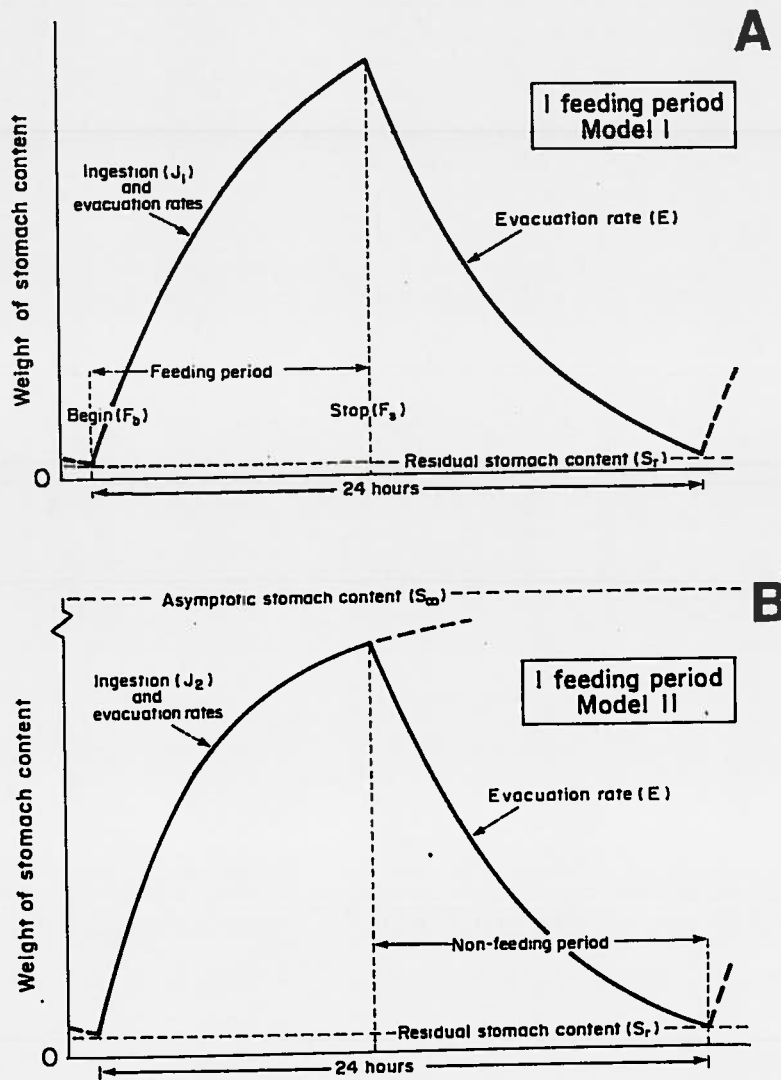


Figure 1. Schematic representation of different models of stomach content dynamics: A. One feeding period per day, feeding rate constant; B. One feeding period per day, feeding rate proportional to stomach content; C. Two feeding periods per day, feeding rate constant; D. Two feeding periods per day, feeding rate proportional to stomach content.

part of an integrated estimation process which also involves other parameters, particularly feeding and evacuation rates, duration of the feeding period, and asymptotic stomach contents. He developed two models, one ("Model I") assuming a constant feeding rate and another ("Model II") assuming a feeding rate inversely proportional to stomach contents. Both models assume a simple exponential evacuation rate. Slightly modified, the time trajectories and the computations are given in the Appendix. A schematic representation of the trajectories is provided in Figure 1.

The two models fit the same type of curve, but differ in the parameters involved in the computation of the slope

of the trajectory and the asymptotic stomach content weight, as explained in the Appendix. Assuming steady-state conditions, the residual stomach content before the beginning of the feeding period can be directly calculated from the other parameters. The stomach content at the end of the feeding period is readily computed from the time trajectory. Finally, the daily ration R_d is integrated from the food ingestion over the duration of the feeding period.

Sainsbury's (1986) approach allows for the estimation of either parameter set for a feeding period covering a cycle of 24 h, or the estimation of several sets of parameters (one for each of the feeding cycles within a day).

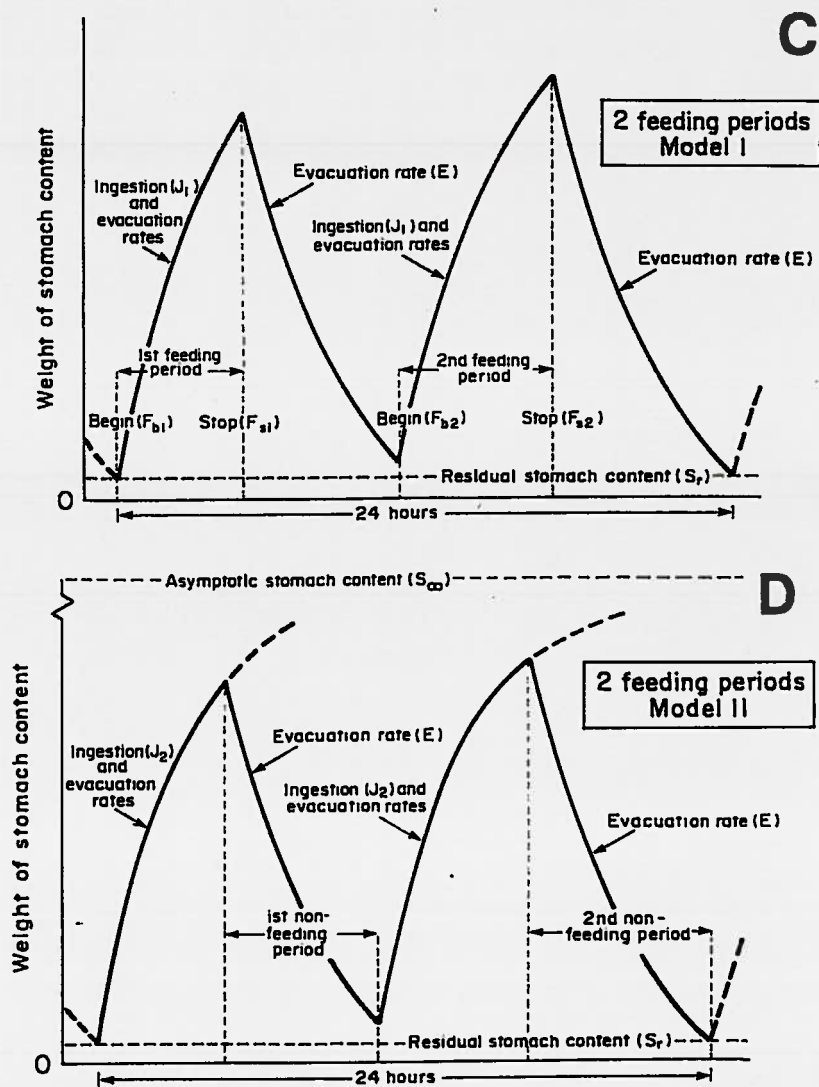


Figure 1. (C) and (D).

Some fish species have been reported to exhibit bimodal activity patterns (Hobson, 1972), in particular under twilight conditions during dusk and dawn (Hobson *et al.*, 1981). Therefore, extensions of the above two models were developed for two diel feeding periods, assuming the ingestion rate in these two is the same (Fig. 1 and Appendix).

In this extension, both feeding periods can be treated separately, with an adjustment for the feeding and non-feeding times. The integration to compute R_d is in principle the same as before, with an adjustment for two ascending branches and the appropriate times for the integral limits¹ (Appendix). Examples of application of

¹A user-friendly program for IBM and compatible personal computers implementing this approach and the Q/B model presented below is available upon request.

these models to field data are given in Table 1 and Figures 2 and 3. The general pattern appears to be adequately described by the models, the Peruvian anchovy *Engraulis ringens* (data from Rojas de Mendiola, 1989; Alamo, 1989) clearly showing one diel cycle and the Baltic cod *Gadus morhua* (data from Arntz, 1974) two feeding cycles.

Relating size-specific estimates of daily ration to consumption by an entire fish population

Other methods for estimating daily ration (e.g. Mann, 1978; Olson and Boggs, 1986) share with those presented above the feature that the results are size-specific, i.e. they pertain to the size of the fish sampled in the field or used in the experiments. Box models, how-

Table 1. Parameter estimates for the models of stomach content dynamics for *Engraulis ringens* (data from Rojas de Mendiola, 1989, and Alamo, 1989), and *Gadus morhua* (length class 26–30 cm; data from Arntz, 1974).

	Model I	Model II	Unit
<i>Engraulis ringens</i>			
Beginning of feeding period	12:50	13:15	h
End of feeding period	1:50	1:40	h
Evacuation rate	0.16	0.13	h ⁻¹
Ingestion rate	0.04	0.05	*
Asymptotic stomach content	—	0.27	g
Sum of squared residuals	0.01	0.01	g ²
Daily ration	0.57	0.50	gd ⁻¹
<i>Gadus morhua</i>			
Beginning of 1st feeding period	5:20	5:30	h
End of 1st feeding period	8:05	8:00	h
Beginning of 2nd feeding period	13:50	14:05	h
End of 2nd feeding period	18:35	18:35	h
Evacuation rate	0.25	0.25	h ⁻¹
Ingestion rate	0.67	0.14	*
Asymptotic stomach content	—	2.22	g
Sum of squared residuals	0.08	0.08	g ²
Daily ration	5.02	4.92	gd ⁻¹

*Model I: unit gh⁻¹; Model II: unit h⁻¹.

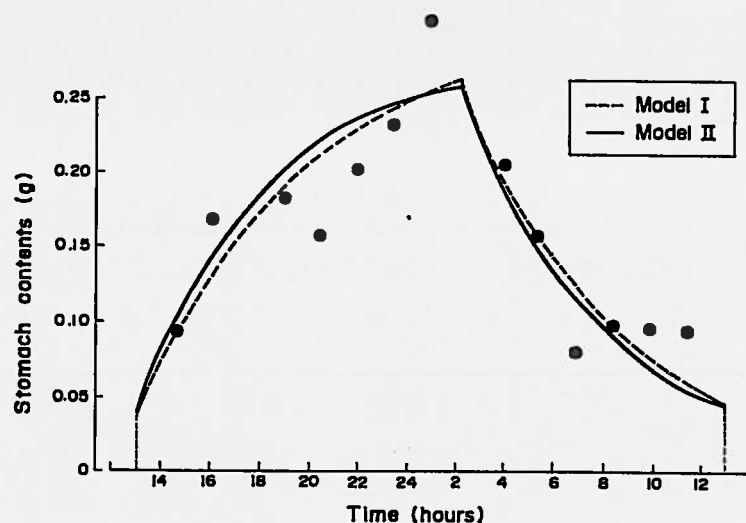


Figure 2. Application of models A and B (cf. Fig. 1) to stomach contents of Peruvian anchoveta (*Engraulis ringens*) (mean live weight = 19.7 g; data from Rojas de Mendiola, 1989 and Alamo, 1989).

ever, usually deal with entire populations and not with cohorts characterized by a limited size range. Since small fish consume relatively more food than big fish of the same species (Pauly, 1986), and are also more abundant, estimates of R_d pertaining to a specific size have to be converted into estimates of food consumption (Q) per unit biomass (B) and per unit time of an age-structured population. This requires estimates of the individual growth of the fish in the population, as well as estimates of the instantaneous rate of total mortality prevailing in this population. Pauly (1986) derived a comprehensive model for the estimation of Q/B from growth parameters of the von Bertalanffy growth equation (von

Bertalanffy, 1938; Beverton and Holt, 1957), total mortality (Z), and gross food conversion efficiency K_1 (Ivlev, 1945). A slightly simplified version (Palomares and Pauly, 1989) reads

$$Q/B = \int_{t_r}^{t_{max}} \frac{[dw/dt] \times N_t}{K_1|t|} dt / \int_{t_r}^{t_{max}} W_t \times N_t dt \quad (1)$$

In a sensitivity analysis of this model, Pauly (1986) shows that the output is largely insensitive to changes in age of recruitment (t_r) and age of exit (t_{max}) from the exploited stock. Therefore, these two parameters can be replaced in the integration by 0 and ∞ , respectively.

The number of animals of age t in the population (N_t) is obtained from the mortality equation

$$N_t = N_0 \times \exp(-Z \times (t - t_0)) \quad (2)$$

Assuming constant recruitment, N_0 cancels out in the integration of Q/B , and therefore does not appear as a parameter in the equation set.

The actual weight-at-age (W_t) is given by the von Bertalanffy growth equation and the weight increment (dw/dt) is computed from its first derivative. Conversion efficiency (K_t) is obtained according to its definition from the daily weight increment divided by the daily ration. Pauly (1986) provided a method for computing the conversion efficiency at age ($K_{1,t}$). Palomares and Pauly (1989) give details of a least squares approach of Q/B for cases when several R_d values, pertaining to different fish sizes, are available. It should be observed that the value of Q/B is very sensitive to the parameters which relate body weight to size and conversion efficiency to age. It should further be noted that the assumptions for this model include a steady-state population under constant recruitment.

The model has been applied to the Peruvian anchoveta data shown in Table 1 and Figure 2. The ration estimated from "Model I" is $0.57 \text{ g} \times \text{d}^{-1}$ for specimens with a mean weight of 19.7 g. On the basis of the growth parameters given by Palomares *et al.* (1987), the conversion efficiency is estimated at 0.091. If the total mortality rate is taken as 2.5 yr^{-1} , the integration of Equation (1) then yields $Q/B = 14.0 \text{ yr}^{-1}$. From this, the gross efficiency of Peruvian anchovy can be calculated as the ratio of production and consumption: $GE = 2.5/14.0 = 0.18$.

Estimating Q/B through empirical equations derived from comparative studies

The methods proposed above for estimating R_d and Q/B are associated with data requirements which will often not be met. Empirical models for the prediction of Q/B from easily quantifiable morphometric characteristics of fish, which take the very different metabolic levels of different types of fish into account, might help to overcome this problem (Pauly, 1989). In this contribution, we briefly follow up on three aspects of models recently presented for this purpose by Palomares and Pauly (1989) and Pauly (1989), by (a) relating the aspect ratio of the caudal fin of a fish to its level of activity, (b) accounting for the body depth ratio in the model, and (c) adjusting the linearizing transformation function of temperature.

The models of these authors used the aspect ratio (A) of the caudal fin of fishes as key variable. Figure 4 provides two examples of fish belonging to the "sluggish" and "active" type, both of which types appear to be well characterized by their respective values of A . As shown in Palomares and Pauly (1989) and Pauly (1989), A correlates rather well with Q/B . We show here on the basis of a documented data set (Table 2; Gray, 1954) that, according to physiological expectations, A is also correlated with gill area. Since the available data refer to fish of different weights, we accounted for size by regressing relative gill area (G , in cm^2/g) vs. weight (W , in g). Only species recognized as "intermediate" as regards activity level by Ursin (1967) were included (Table 2). This led to

$$\ln G = 2.632 - 0.180 \times \ln W \quad (3)$$

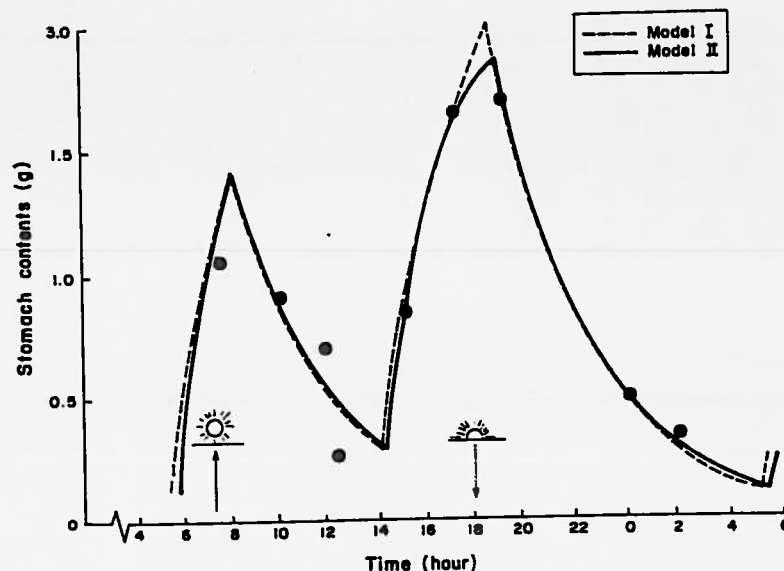


Figure 3. Application of models C and D (cf. Fig. 1) to stomach contents of Baltic cod (length class 26–30 cm; data from Armtz, 1974).

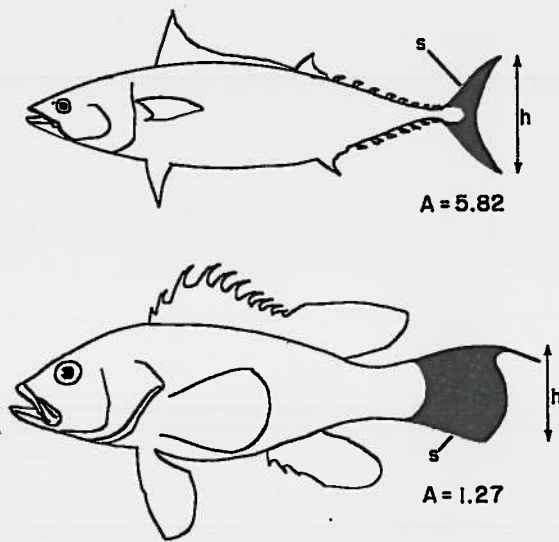


Figure 4. Examples of the variation in the aspect ratio ($A = h^2 s^{-1}$) of the caudal fin: top *Euthynnus alleteratus*, an "active" species; bottom *Centropristis striatus*, an "intermediate" species (see text).

Applying this equation ($r = 0.547$; d.f. = 17) to all fish of Table 2 for which A could be computed yielded predicted values of G. These were subtracted from the observed values and the residuals (Res) when plotted vs. A led to the significant ($r = 0.627$; d.f. = 26; $\alpha = 0.01$) relationship.

$$\text{Res} = -1.749 + 5.337 \times \ln A \quad (4)$$

Aleev (1969) noted that high values of A occur both among streamlined, active fishes and among less active fishes when they are deep-bodied. In the latter case, the reason is that the propulsive effect of the caudal fin is strongest for those parts of the fin which are outside the zone of vortices in the wake of the swimming fish (shaded areas in Fig. 5). Therefore, deep-bodied fish tend to have caudal fin lobes that are spread wide apart, and hence high values of A even if they are not particularly active (Aleev, 1969). The empirical model of Palomares and Pauly (1989) did not account for this effect; the model of Pauly (1989) does include depth ratio (D, standard length/maximal body depth) as a variable, but the rationale given here was not stated.

The empirical models of Palomares and Pauly (1989)

Table 2. Mean body weight, relative gill area, aspect ratio of the caudal fin, and Ursin's activity code for various species. (Mean weights and gill area from Table 1 in Gray, 1954; activity codes from Ursin, 1967; A = "active", S = "sluggish", U = "intermediate".)

Species	Mean weight (g)	Gill area (cm ²)	Aspect ratio	Ursin's code
<i>Gymnosarda alleterata</i>	5216	19.39	5.82	A
<i>Brevoortia tyrannus</i>	613	17.73	2.65	A
<i>Coryphaena hippurus</i>	4015	7.10	2.42	A
<i>Sarda sarda</i>	2192	5.95	4.28	A
<i>Pomatomus saltatrix</i>	1035	6.52	2.12	U
<i>Scomber scombrus</i>	182	11.58	2.65	A
<i>Scomberomorus maculatus</i>	478	7.69	3.38	A
<i>Mugil cephalus</i>	166	9.54	1.44	A
<i>Caranx crysos</i>	129	9.82	4.11	U
<i>Roccus lineatus</i>	3059	3.02	1.99	U
<i>Archosargus probatocephalus</i>	2366	3.28	2.29	U
<i>Chilomycterus chioepfi</i>	316	4.37	0.94	U
<i>Stenotomus chrysops</i>	395	5.06	2.25	U
<i>Tautoga onitis</i>	580	3.92	1.95	U
<i>Prionotus strigatus</i>	460	4.83	1.48	U
<i>Poronotus triacanthus</i>	199	5.98	2.28	U
<i>Cynoscion regalis</i>	807	3.73	1.30	U
<i>Palinurichthys perciformis</i>	199	5.06	1.57	U
<i>Echeneis naucrates</i>	393	5.49	0.77	U
<i>Spheroides maculatus</i>	250	4.70	1.35	U
<i>Centropristis striatus</i>	244	4.58	1.27	U
<i>Lophius piscatorius</i>	6392	1.96	0.85	S
<i>Peprilus alepidatus</i>	71	5.05	2.58	U
<i>Leptocephalus conger</i>	2560	1.35	-	S
<i>Prionotus carolinus</i>	213	3.60	1.48	U
<i>Trichiurus lepturus</i>	116	5.36	-	U
<i>Anguilla rostrata</i>	428	3.02	-	S
<i>Paralichthys dentatus</i>	766	2.42	0.79	U
<i>Pseudopleuronectes americanus</i>	734	2.00	1.56	S
<i>Opsanus tau</i>	233	1.97	1.81	S
<i>Lophopsetta maculata</i>	411	1.88	0.86	S

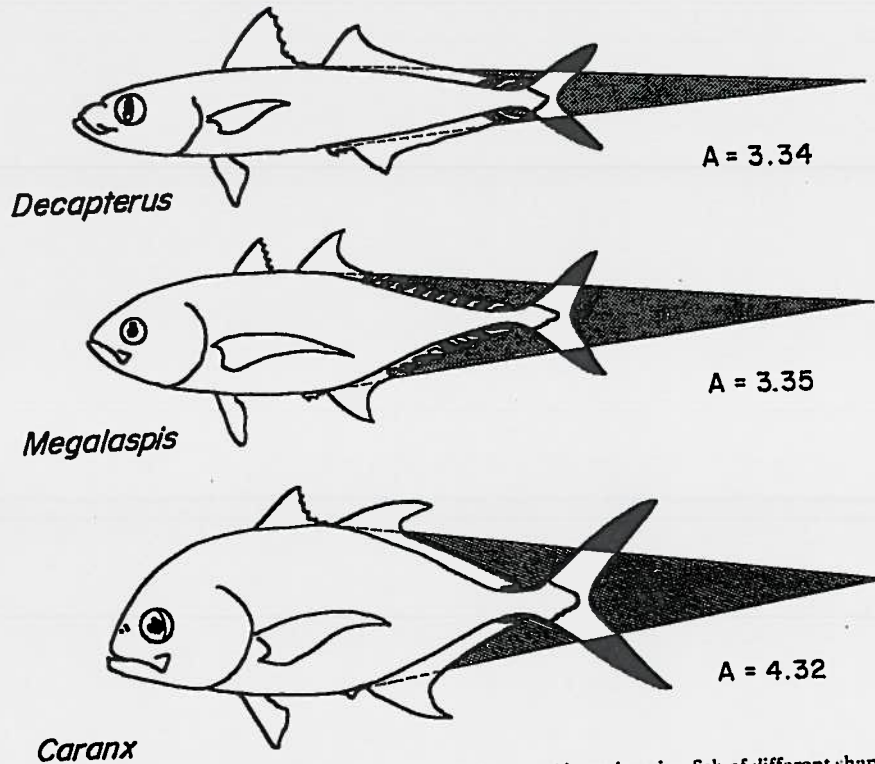


Figure 5. Schematic representation of the turbulent wake (shaded) caused by swimming fish of different shape to show that high-bodied fishes must have a higher aspect ratio of their caudal fin if the lobes are to reach outside the wake (adapted from Figures 80 and 83 in Aleev, 1969; see text).

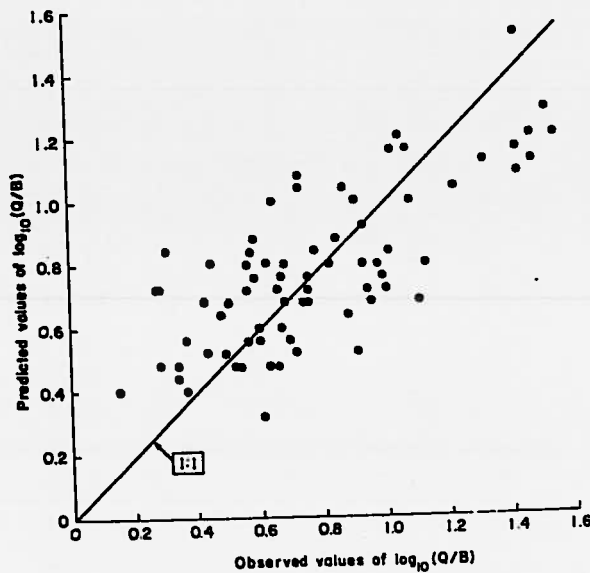


Figure 6. Predicted vs. observed food consumption per unit biomass using the data from Table II in Pauly (1989) and Equation (5) in this paper.

and Pauly (1989) include temperature as a predictor variable. Recently, Regier *et al.* (1990) suggested that it would be physiologically more appropriate to use a transformation of temperature in biological models by $1/T$, where T is the temperature in Kelvin, rather than using $^{\circ}\text{C}$ or its logarithmic transformation. With this transformation, the slopes of the regression lines obtained can be compared across a wide range of biological parameters (Regier *et al.*, 1990). Using the data in Table II of Pauly (1989), we have therefore derived the model ($R = 0.743$, $d.f. = 69$):

$$\begin{aligned} \log_{10} Q/B = & \\ = & 4.885 - 1309.139 \times (1/T) + 0.423 \times \log_{10} A + \\ & + 0.285 \times \log_{10} D - 0.111 \times \log_{10} W_{\infty} - \\ & - 0.445 \times \log_{10} P \end{aligned} \quad (5)$$

where P is the relative height of the caudal peduncle (i.e. caudal peduncle depth/maximum body depth), which distinguishes "burst" swimmers from continuous swimmers (Pauly, 1989). All other parameters are as introduced above. The partial slopes are all significant ($\alpha = 0.01$). Hence, the model appears to be marginally better, both on biological and statistical grounds, than the model of Pauly (1989). A plot of predicted vs.

observed values of food consumption is shown in Figure 6.

Discussion

The examples of estimates of daily ration show that the two feeding models yield very similar results in both cases. Field observations usually do not allow for a precise assessment of feeding periodicity. On the other hand, behavioural changes of captive fishes may bias experimental results on feeding periodicity and associated estimates of ingestion and evacuation rates. Parameterizing the feeding times of fish in nature in addition to the feeding rates may therefore yield more realistic estimates of daily rations than the computation of daily rations from the difference in weight of the stomach contents before and after an arbitrarily defined feeding period. Arntz (1974) used the latter approach, which gives a minimum estimate of $4.4 \text{ g} \times \text{d}^{-1}$. As the models presented here account for evacuation during the feeding period, it is not surprising that the results obtained are slightly higher. With respect to the Peruvian anchovy, Pauly *et al.* (1989) showed that the estimate obtained by applying the method presented here is similar to an earlier, independent estimate by Cushing (1978).

With regard to the empirical models for predicting Q/B, the results suggest that the biological basis for predicting food consumption from shape-related parameters and temperature is sound. However, the model derived by Pauly (1989) as well as the new model presented here (Equation 5) do not lead to very precise estimates. Also, as Figure 6 suggests, predicted values of Q/B tend to be biased upward in the lower range, and downward in the upper range. We attribute this bias to a failure of the logarithmic transformation to linearize the models satisfactorily, a theme that is presently being explored.

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- there are two periods per day, index 1 marks the first and index 2 the second (F_{b1} , F_{s1} , F_{b2} , and F_{s2}). In addition, let: E = instantaneous rate of gastric evacuation (in h^{-1}); $J1$ = ingestion rate (in $g \times h^{-1}$); $J2$ = instantaneous rate of ingestion (in h^{-1}); S_t = stomach contents at time t ; S_r = residual stomach contents; S_f = stomach contents after the feeding period; S_∞ = the asymptotic stomach contents.
- Regardless of the number of feeding periods per day, let the gastric evacuation be described by the differential equation
- $$dS/dt = -E \times S$$
- We consider two models of ingestion. Model I assuming a constant ingestion over time, and Model II assuming that the ingestion declines with increasing stomach contents:
- Model I: $dS/dt = J1 - E \times S$
- Model II: $dS/dt = J2 \times (S_m - S) - E \times S$
- where S_m is the stomach content at which the ingestion becomes zero, and which is related to S_∞ through
- $$S_\infty = J2 \times S_m / (J2 + E).$$

2. Time trajectories¹

The solutions to the differential equations lead to the time trajectories of stomach contents for feeding and non-feeding periods. For each feeding period we get:

$$S_t = S_r \times \exp(A \times (t - F_b)) + B \times (1 - \exp(A \times (t - F_b)))$$

where

$$\text{for Model I: } A = -E \text{ and } B = J1/E$$

$$\text{for Model II: } A = -(E + J2) \text{ and } B = S_\infty$$

We further get for each non-feeding period

$$S_t = S_f \times \exp(-E \times (t - F_s))$$

For the models pertaining to two feeding periods, simple adjustments have to be made by replacing (F_b , F_s , S_r , S_f) by (F_{b1} , F_{s1} , S_{r1} , S_{f1}) and (F_{b2} , F_{s2} , S_{r2} , S_{f2}), respectively.

¹The special case of one feeding period per day is presented in Sainsbury (1986) in a slightly modified version.

Appendix

1. Introduction

Let t be the time (in h) and S the stomach contents (in g). For feeding period F let index b mark the beginning and s the end (F_b and F_s for one feeding period per day). If

3. Computation of S_r

Assuming steady-state conditions, the residual stomach contents can be computed from the other parameters, and hence have not to be estimated independently.

3.1. One feeding period

$$S_r = B \times D \times X_1 \times (1 - X_2)$$

where

$$\text{for Model I: } D = 1/(1 - \exp(-24 \times E))$$

for Model II:

$$D = 1/(1 - \exp(-24 \times E - J2 \times (F_s - F_b)))$$

and

$$X_1 = \exp(-E \times 24 - (F_s - F_b))$$

$$X_2 = \exp(A \times (F_s - F_b))$$

3.2. Two feeding periods

The residual stomach contents before the second feeding period are directly computed from the time trajectory of the first feeding period. For the residual stomach contents before the first feeding period, we obtain

$$S_r = B \times D \times X_1 \times (1 - X_2 \times (1 - X_3 \times (1 - X_4)))$$

where D is defined as above (3.1), and

$$X_1 = \exp(-E \times (24h + F_{b1} - F_{s2}))$$

$$X_2 = \exp(A \times (F_{s2} - F_{b2}))$$

$$X_3 = \exp(-E \times (F_{b2} - F_{s1}))$$

$$X_4 = \exp(A \times (F_{s1} - F_{b1}))$$

4. Computation of daily ration R_d

4.1. Model I, one feeding period

$$R_d = \int_{F_b}^{F_s} J1 dt = J1 \times (F_s - F_b)$$

4.2. Model I, two feeding periods

$$\begin{aligned} R_d &= \int_{F_{b1}}^{F_{s1}} J1 dt + \int_{F_{b2}}^{F_{s2}} J1 dt \\ &= J1 \times (F_{s1} - F_{b1} + F_{s2} - F_{b2}) \end{aligned}$$

4.3. Model II, one feeding period

$$\begin{aligned} R_d &= \int_{F_{b1}}^{F_{s1}} [S_{\infty} \times (E + J2) - J2 \times S_1] dt \\ &= E \times S_{\infty} \times (F_s - F_b) + \\ &\quad + (S_{\infty} - S_r)/(1 + E/J2) \times \\ &\quad \times (1 - \exp(-(E + J2) \times (F_s - F_b))) \end{aligned}$$

4.4. Model II, two feeding periods

$$\begin{aligned} R_d &= \int_{F_{b1}}^{F_{s1}} [S_{\infty} \times (E + J2) - J2 \times S_1] dt + \\ &\quad + \int_{F_{b2}}^{F_{s2}} [S_{\infty} \times (E + J2) - J2 \times S_1] dt \\ &= E \times S_{\infty} \times (F_{s1} - F_{b1} + F_{s2} - F_{b2}) + \\ &\quad + (S_{\infty} - S_{r1})/(1 + E/J2) \times \\ &\quad \times (1 - \exp(-(E + J2) \times (F_{s1} - F_{b1}))) + \\ &\quad + (S_{\infty} - S_{r2})/(1 + E/J2) \times \\ &\quad \times (1 - \exp(-(E + J2) \times (F_{s2} - F_{b2}))) \end{aligned}$$