

A surface-dependent gastric evacuation model for fish

A. G. V. SALVANES, D. L. AKSNES AND J. GISKE

University of Bergen, Department of Fisheries and Marine Biology, Bergen High
Technology Centre, N-5020 Bergen, Norway

(Received 30 August 1994, Accepted 2 January 1995)

A gastric evacuation curve expresses how fast prey disappear from the stomach, and empirical models are used generally for the relationship between weight of prey remaining (W_t) and time (t) after a meal. Unfortunately, empirical models are likely to have restricted applicability because their parameters often represent limited biological mechanisms. This paper develops a simple digestion model. The simplest form of the model has four parameters; the digestion velocity (expressing enzymatic breakdown of prey), prey length, initial prey radius and the density of the prey. Two more parameters are included in an extended version; a time-delay before digestion starts and environmental temperature. The approach is based on the assumption that prey digestion is a surface process in that digestive enzymes attack progressively deeper into a prey of known size and shape so that the average digestion rate is proportional to the prey radius r (m). This process is characterized by the digestion velocity d_s (m s^{-1}). Unknown parameters are estimated with uncertainty using the maximum likelihood technique. Model evaluation using published data sets demonstrated that the new model is flexible. Prey geometry is incorporated into the model and temperature effects upon gastric evacuation are linked directly to the digestion velocity. © 1995 The Fisheries Society of the British Isles

Key words: gastric evacuation model; surface-process; prey geometry; digestion velocity; temperature-dependent.

INTRODUCTION

During the last few years there has been an extensive theoretical development of ecological models (Tyler & Rose, 1994) with some emphasis being placed upon an improved understanding of trophic dynamics (Giske *et al.*, 1992; Rose *et al.*, 1993). However, while much effort has been invested in understanding the mechanisms of predator–prey encounters (Eggers, 1977; Luecke & O'Brien, 1981; Dunbrack & Dill, 1984; Aksnes & Giske, 1993), models for gastric evacuation and prey digestion are still mainly empirical (Jobling, 1986, 1987; Bromley, 1994). In this paper we develop a simple surface-dependent prey digestion model which is more flexible than the classical models. It may be used in simulation alternatives for quantification of food consumption in the field. It may also be useful both for evaluation of optimal prey selection and trophic flow in multispecies fisheries models.

GASTRIC EVACUATION—BACKGROUND AND MODEL DEVELOPMENT

Models for gastric evacuation express the relationship between weight of prey remaining in the stomach (W_t) and time (t) after a meal. Experimental analyses of gastric evacuation of fish have been combined generally with stomach content data from field studies to estimate prey consumption in natural environments

(Jobling, 1981; Durbin *et al.*, 1983; Jobling, 1986; Bromley, 1994). Gastric evacuation patterns of fishes can be affected by factors including those related to predator physiology and prey characteristics. One predator factor may be that distension of the stomach modifies the rate at which food is evacuated (Hunt & MacDonald, 1954; Jobling, 1981). The prey characteristics that influence gastric evacuation include surface-to-volume ratio, friability and energy content (Elliott, 1972; Persson, 1981; Jobling, 1987; Elliott, 1991; Bromley, 1994). In the absence of sufficient information about all the predator and prey factors that may influence gastric evacuation, it has been common practice to fit to the data mathematical expressions with a few parameters (Elashoff *et al.*, 1982).

The parameters of the various empirical models which have been fitted to experimental data are likely to have restricted applicability because they often represent limited biological mechanisms (Dos Santos & Jobling, 1991*b*; Bromley, 1994), although the rationale behind the parameters of some models has a biological origin (Jobling, 1981). It has been emphasized, however, that both prey surface-to-volume ratios and temperature, respectively, affect the shape of the gastric evacuation curve and gastric evacuation rate and time (Tyler, 1970; Elliott, 1972; Fänge & Grove, 1979; Persson, 1979; Jobling, 1981; Persson, 1981; Durbin *et al.*, 1983; Jobling, 1986, 1987; Dos Santos & Jobling, 1991*b*). Following a re-analysis of many published data sets, Jobling (1987) concluded that an exponential model gave the best fit to the gastric evacuation pattern for small and easily digested prey, and that a linear expression was more suitable if the consumed prey were large fish, whereas Persson (1979, 1981) and Elliott (1991) and Elliott *et al.* (1993) reported that the exponential model give good fits also to large prey.

In this paper we investigate these ideas further. Based on the fact that differences in surface-to-volume ratios are related to differences in prey shape and size, we outline a surface-dependent model for W_t as a function of time t after a meal and of prey geometry. The simplest form of the model has four parameters; the digestion velocity (expressing enzymatic breakdown of prey), prey length, initial prey radius and the density of the prey. Two model parameters are included in an extended version; a time-delay before digestion starts and environmental temperature. The approach is based on the assumption that prey digestion is a surface process in that digestive enzymes attack progressively deeper into a prey of known size so that the average digestion rate is proportional to the prey radius r (m). This process is defined by the digestion velocity d_s (m s^{-1}). From this it follows that the gastric digestion and evacuation process depends upon the prey surface area and thus on prey geometry. In the following we refer to our new model as 'the surface model'. Unknown parameters are estimated with uncertainty using the maximum likelihood technique. The surface model is evaluated by a re-analysis of some published data and by comparisons with earlier models for the relationship between W_t and t fitted to the same data sets. A relationship between the digestion velocity and temperature is also examined.

DIGESTION AS A SURFACE PROCESS

If digestion of a prey is regarded as a surface process (Tyler, 1970; Fänge & Grove, 1979; Jobling, 1981) where digestive enzymes attack progressively deeper

TABLE I. Explanations of parameters and variables used in the equations

Symbol	Description	Unit
<i>Surface model</i>		
t	Time after a meal	h
T	Temperature	°C
r_0	Radius of a fresh prey	cm
r	Prey radius at any time after a meal	cm
d_s	Digestion velocity	cm h ⁻¹
d_{s0}	Digestion velocity at 0° C	cm h ⁻¹
ρ	Density of prey mass	g cm ⁻³
π	The ratio of the circumference of any circle to its diameter	
W_0	Initial prey weight	g
W_t	Weight of prey remaining at time t	g
L_0	Length of a fresh prey	cm
t_D	Time delay before digestion starts	h
a	Temperature coefficient per degree for digestion	°C ⁻¹
Q_{10}	Temperature rate constant per 10° for digestion	°C ⁻¹
$\hat{\sigma}_e$	Standard error of the equation	g
<i>Classical models</i>		
W_0	Initial prey weight	g
t	Time after a meal	h
g	Specific gastric evacuation rate	g g ⁻¹ h ⁻¹
d_l	Evacuation rate in linear model	g h ⁻¹
d_{sq}	Evacuation rate in square-root model	*
H	Half-life parameter of the power-exponential model	*
s	Shape-coefficient of the power-exponential model	*

*Indicates that although the parameter is commonly used in statistical analysis, it is impossible to express the unit in simple terms because of equation complexity.

into the prey with an average rate d_s , the digestive process can be expressed as a velocity, i.e. the thickness of the prey layer that is digested per unit time. Hence the time t needed for digestion of a homogeneous prey item will be proportional to the thickness of the prey r :

$$t = \frac{r}{d_s} \tag{1}$$

The weight of a newly ingested prey W_0 may be considered as being related to prey volume. Since most prey taken by a fish predator (e.g. gobies, herring, juvenile gadids etc.) would have a shape similar to an ellipsoid, W_0 may be expressed as:

$$W_0 = \frac{4}{3} \rho \pi \frac{L_0}{2} r_0^2 = \frac{2}{3} \rho \pi L_0 r_0^2 \tag{2}$$

where ρ represents the density, r_0 initial radius of the prey and L_0 the prey length. Note that a spherical shape would be a special case of an ellipsoid in which $L_0/2=r_0$. All symbols used in the equations are explained in Table I.

GASTRIC DIGESTION AND EVACUATION OF ELLIPSOID PREY

For an ellipsoid prey the 'radius' in the length direction, $L_0/2$, and radius of the prey r_0 decrease during digestion with the rate d_s assuming that there is a linear relationship between the initial enzyme concentration in the predator stomach and the surface of a prey (i.e. no enzymatic constraint due to meal size). This is consistent with the assumption behind the surface-area dependent models reviewed by Jobling (1981). However, note that the assumption that enzyme activity is solely responsible for the disintegration of prey may not be strictly true. In some fish species, there may also be a mechanical breakup (e.g. Jobling, 1987 and references therein). The following equation predicts the weight of the remaining prey, W_t , as a function of time:

$$W_t = \frac{4}{3} \rho \pi \left(\frac{L_0}{2} - d_s t \right) (r_0 - d_s t)^2. \quad (3a)$$

For comparison we mention the relationship between the digestion velocity d_s of our surface model and the parameter C of the surface-area dependent models reviewed by Jobling (1981): $dW/dt = -CW^{2/3}$ which becomes:

$$C = \left(\frac{4}{3} \pi \rho \right)^{1/3} d_s \left[2 \left(\frac{L_0/2 - d_s t}{r_0 - d_s t} \right)^{1/3} + \left(\frac{r_0 - d_s t}{L_0/2 - d_s t} \right)^{2/3} \right]$$

and which for the special case of spherical prey shape becomes: $C = (36\pi\rho)^{1/3} d_s$.

If n similar prey items are digested independently, the 'radius' in the length direction, $L_0/2$ and radius of each prey r_0 would decrease during digestion with the rate d_s according to:

$$W_t = \frac{4}{3} \rho \pi n (L_0/2 - d_s t) (r_0 - d_s t)^2. \quad (3b)$$

Delay time before digestion begins

If there is a time delay t_D before digestion enzymes start to attack the prey surface, equation (3a) may be formulated as:

$$W_t = \frac{4}{3} \rho \pi (L_0/2 - d_s(t - t_D)) (r_0 - d_s(t - t_D))^2 \quad (3c)$$

showing that at any time $t > t_D$ the digestion velocity has had effect for t_D time units less than if no delay time occurred.

Temperature dependent digestion velocity

Because the digestion velocity represents an enzymatic process, which is known to be related to temperature, it may be convenient to express the temperature effect in the model. As expressed in the general Q_{10} -concept, enzymatic processes often increase exponentially with temperature. With this relationship the digestion velocity may be expressed:

$$d_s = d_{s0} e^{aT} \quad (4)$$

where d_{s0} is the digestion at 0°C , $a = \ln(Q_{10})/10$ and T is temperature. Substituting (4) into equation (3c) gives the following general equation which expresses the weight of prey remaining W_t as a function of time t :

$$W_t = \frac{4}{3} \rho \pi (L_0/2 - d_{s0} e^{aT}(t - t_D))(r_0 - d_{s0} e^{aT}(t - t_D))^2 \quad (5)$$

If the parameters d_{s0} , Q_{10} and t_D are estimated for a particular predator-prey interaction, one may use equation (5) to predict gastric digestion and evacuation in field studies as well as in simulation models for temperatures within the normal temperature range for the predators.

Specific gastric evacuation rate

The specific evacuation rate g which is defined as the exponent in an exponential model can be expressed also based on the surface model. For the exponential model g is given by:

$$g = \frac{1}{W_t} \frac{dW_t}{dt} \quad (6a)$$

or by taking the derivative of equation (3a) and dividing by W_t :

$$g = \frac{1}{W_t} \frac{dW_t}{dt} = \frac{d_s(2L_0/2 + r_0 - 3d_s t)}{(L_0/2 - d_s t)(r_0 - d_s t)} \quad (6b)$$

When incorporating a time delay parameter the relationship between temperature and digestion velocity g becomes:

$$g = \frac{1}{W_t} \frac{dW_t}{dt} = \frac{d_{s0} e^{aT}(L_0 + r_0 - 3d_{s0} e^{aT}(t - t_D))}{(L_0/2 - d_{s0} e^{aT}(t - t_D))(r_0 - d_{s0} e^{aT}(t - t_D))} \quad (6c)$$

The unit of g expresses the prey weight digested per weight of prey left in the stomach per unit time (i.e. $g \text{ g}^{-1} \text{ s}^{-1}$). Equation (6b) then shows how the specific gastric evacuation rate depends on prey size for a known time delay and temperature and equation (6c) shows how g depends on prey size, temperature and time delay.

Estimation

We have used the maximum likelihood principle to estimate the unknown parameters and have applied the software SHAZAM (White *et al.*, 1990). The maximum likelihood estimator (MLE) is asymptotically unbiased, it is consistent, it is asymptotically efficient, and it is distributed asymptotically normally (Kennedy, 1992). The error term is assumed to be normally distributed. The MLE is analogous to the ordinary least square estimator (OLS), which is the most commonly used estimator in regression analysis, but differs in that the MLE is an iterative approach. The MLE of the specified

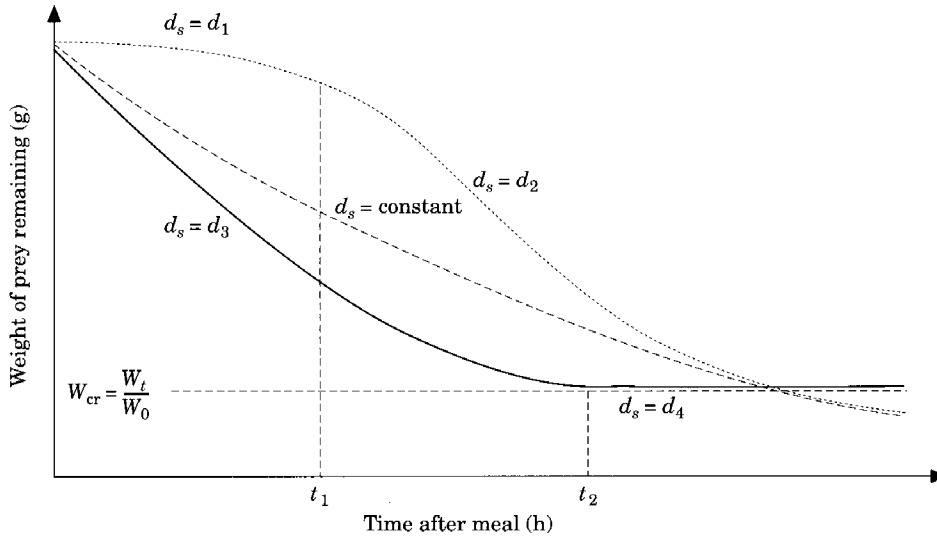


FIG. 1. Conceptual sketch of potential gastric evacuation patterns caused by differences in digestion velocity (d_s) for three hypothetical prey types. For a prey with exoskeleton (\cdots) d_1 represents a slow digestion velocity when enzymes attack the exoskeleton when $t < t_1$. The d_2 represents a faster digestion velocity on the soft tissue for $t > t_1$. For a prey with endoskeleton (—) d_3 refers to a faster digestion velocity as the soft parts are digested ($t < t_2$) and d_4 to a slower velocity when digestion enzymes come into contact with the endoskeleton ($t > t_2$). The $W_{cr} = W_t / W_0$ refers to a hypothetical critical weight of prey remaining when the latter shift from d_3 to d_4 occurs. Gastric evacuation curve for a prey consisting of purely soft tissue (---) is expressed with a constant digestion velocity (d_s).

parameters is the one that gives the greatest probability of obtaining the observed data (i.e. those that result in the best fit through a set of data). To obtain an initial value for the digestion velocity parameter of equation (3a) we have used the polynomial regression as described in Appendix 1. The alternative would be to assume an initial value.

The advantage of the MLE technique is that it allows comparison of differently specified models without having to transform any data set. It makes it thus more easy to judge our new surface model against classical models used for estimating gastric evacuation in fish. Moreover, standard errors are provided directly for the estimated parameters and not for any transformed parameter which is common when OLS are used. However, note that the MLE gives a 'goodness-of-fit' measurement other than r^2 , namely the 'standard error of the equation' $\hat{\sigma}_e$. The lower it is, the better the fit (Kennedy, 1992).

SHIFTS IN GASTRIC EVACUATION CURVES FOR NON-HOMOGENEOUS PREY

The digestion velocity d_s specified in the basic gastric evacuation model [equation (3a)] is assumed to be constant. This is a simplification meant to represent the average velocity at which digestive enzymes attack progressively deeper into the prey. This may be true if the prey is homogeneous. Digestion velocity d_s may, however, change with differences in prey characteristics. For example, prey with an exoskeleton and those with endoskeletons will be expected to have highly variable digestion velocity, whereas prey consisting of purely soft

tissue may have a relatively constant d_s (Fig. 1). The curve for a prey having thick or hard exoskeleton may be dependent upon the shift from a slow digestion velocity (d_1) before the digestive enzymes come into contact with the soft tissues to a faster rate (d_2) following the exposure of the soft tissue. The digestion of a fish prey could, however, shift from fast (d_3) to slow (d_4) as the soft parts are digested and skeletal tissues constitute an increasing proportion of the remaining prey mass. If there exists a shift in the data from experimental studies, then separate estimates of d_s for subdivided time periods will be more accurate than if the entire data are lumped together before estimating the digestion velocity. Such results may easily be incorporated in simulation models by specifying the digestion velocity as a function of time after a meal, or as dependent on the ratio between the weight of prey remaining and initial prey weight. If, however, an apparent shift is due to a delay time before digestion starts, then the d_s and the delay time may be estimated by the maximum likelihood technique on equation (3c).

POTENTIAL PREY SHAPE EFFECT ON GASTRIC EVACUATION CURVE

The effect of prey geometry and size on the gastric evacuation curve was simulated for two hypothetical prey sizes (1 and 30 g), and five prey shapes using constant digestion velocity ($d_s = 0.005 \text{ cm h}^{-1}$). The results show that the smaller and longer the prey is, the faster it will be evacuated (Fig. 2). These results are supported by experimental studies. Large prey fed to freshwater fishes such as perch *Perca fluviatilis* L. and trout *Salmo trutta* L. were evacuated at a faster rate than small prey (e.g. Persson, 1979, 1981, 1984; Elliott *et al.*, 1993). The faster evacuation of small and elongated prey is due to a larger surface area attacked by the digestive enzymes and to the implicit assumption of proportionality between prey surface area and concentration of digestive enzymes. Hence, this suggests that both prey size and prey geometry impel the shape of the gastric evacuation curve. The results of Flowerdew & Grove (1979) and Grove *et al.* (1985) on turbot *Scophthalmus maximus* L. may also be taken as support that the larger the prey surface area, the faster it disappears from a predator's stomach. They fed a fixed 'pellet-length' to small turbot in eight different experiments, but in each experiment the pellet given was subdivided into different number of segments (i.e. 1, 2, 3, 4, . . . 8 pieces). In their Table 4 they report a decrease in gastric evacuation time with increasing subdivisions of the pellet. According to our surface model this may be explained by the increase of total surface area of the food with increasing number of segments as they state that the pellets did not aggregate into a bolus in the predator stomach as judged by X-ray.

EVALUATION OF THE SURFACE MODEL

ATLANTIC COD DATA

To evaluate whether our new surface model expresses realistic gastric evacuation curves for larger fish prey, we chose data sets from experimental studies on cod *Gadus morhua* L. performed by Dos Santos & Jobling (1991b, 1994). Their experiments were standardized (similar experimental conditions) to provide comparable results (for different prey types, sizes, temperatures etc.). In each of the experiments selected for our analysis, one cod (length range 40–50 cm,

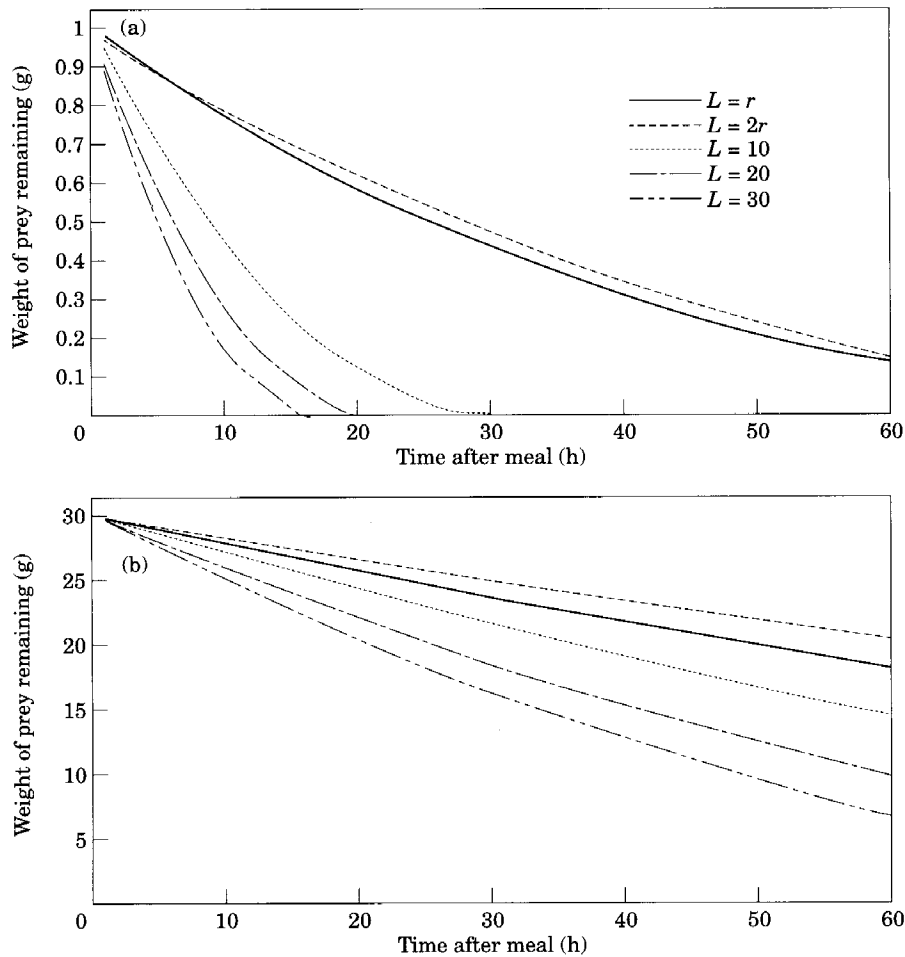


FIG. 2. Simulated effect of prey geometry on gastric evacuation curve using a constant digestion velocity ($d_v=0.005$) for two hypothetical prey weights: (a) 1 g and (b) 30 g for five prey shapes represented by the length (L).

average weight 714 g) was fed one herring *Clupea harengus* L. We estimated gastric evacuation curves for W_t v. t for experiments with different sizes of herring prey—for experiments performed at different temperatures but in which prey size was constant, and also for one and two herring prey in a meal of similar size. For two data sets, one of which appeared curved and the other almost linear, several of the classical models were fitted to the data and compared with our new surface model.

Comparing the surface and power-exponential models for five prey sizes

We estimated gastric evacuation curves for five prey sizes of herring (4, 8, 16, 32 and 48 g) fed to cod [see Table II and Dos Santos & Jobling (1991b) for further details about the data sets] using the MLE technique on our model given by equation (3a) and on the power-exponential function ($W_t = W_0 \cdot 2^{-\frac{(t/H)^2}{2}}$) which Dos Santos & Jobling (1991b) used on these data sets. To convert prey

TABLE II. The maximum likelihood estimates with 95% confidence range (in parentheses) for the parameters of the empirical and theoretical gastric evacuation models

Data set	n	W_0 (g)	\hat{L}_0 (cm)	H (h)	s	\hat{W}_0 (g)	$\hat{\sigma}_s$	r_0 (cm)	d_s (cm h ⁻¹)	$\hat{\sigma}_e$	
32	17	4	9.29	19.20 (2.24-35.96)	0.94 (0.20-1.68)	4.21 (2.23-6.19)	0.43	0.44 (0.40-0.48)	0.0049 (0.0035-0.0063)	0.45	
35	21	8	11.43	35.45 (28.4-42.49)	2.38 (0.32-4.44)	6.26 (5.00-7.52)	0.85	0.57 (0.52-0.62)	0.0059 (0.0041-0.0077)	0.92	
37	20	16	14.04	33.64 (15.30-51.98)	0.95 (0.45-1.45)	18.03 (12.89-23.17)	1.31	0.75 (0.72-0.78)	0.0050 (0.0041-0.0059)	1.37	
39	16	32	17.26	58.13 (42.97-73.29)	1.21 (0.61-1.81)	32.51 (27.03-37.99)	2.47	0.96 (0.92-1.00)	0.0047 (0.0037-0.0057)	2.47	
40	21	48	19.48	63.00 (39.50-86.50)	1.08 (0.66-1.50)	46.99 (37.61-56.37)	3.52	1.05 (1.01-1.09)	0.0041 (0.0035-0.0047)	3.49	
					Weighted average: Coefficient of variation:		Weighted average: Coefficient of variation:				
					1.31 0.85		1.31 0.85				

Data set refers to the experiment number in Dos Santos & Jobling (1994) databases. The empirical curves are estimated from the power-exponential model $W_t = W_0 \cdot 2^{-t/H}$, where W_0 expresses initial prey weight, H the 'half-life parameter' and s the 'shape-coefficient' for the fitted curve (Elashoff *et al.*, 1982; Dos Santos & Jobling, 1991). The n refers to the number of data points, \hat{L}_0 to the initial prey length, \hat{W}_0 to the initial prey weight estimated using the power-exponential model and $\hat{\sigma}_e$ to the standard error of the equation. The parameter r_0 is the initial prey radius and d_s the digestion velocity estimated from equation (3a).

weight to prey length, which was needed as input for equation (3a) due to the lack of prey length in the data, we used an empirical weight-length conversion for herring: $L = e^{(\ln(W_D) + 6.10)/3.358}$ provided by Jens Christian Holst, Institute of Marine Research (unpubl.).

The estimated curves are shown in Fig. 3(a)–(e) together with the data points of weight of prey remaining W_t v. time t . The curves for the specific gastric evacuation rate g for all prey sizes are shown on Fig. 3(f) and the MLE estimated parameters with 95% confidence range are provided in Table II. Table II shows nearly identical standard error of the equation $\hat{\sigma}_e$ for our surface model and for the power-exponential model for each of the five prey sizes. Hence, both models have similar goodness-of-fit to the data set, as also is the intuitive interpretation of Fig. 3(a)–(e). However, the two models differ in another aspect, namely in the stability of estimated parameters. The half-life parameter H of the power-exponential model and the initial prey radius r_0 of the surface model increase as expected with increasing prey size. The digestion velocity d_s of our model is, however, much more stable and is represented with a much narrower 95% confidence range than the analogous parameter (shape coefficient) s of the power-exponential model (Table II). As all the five 95% confidence ranges for d_s for the five prey sizes overlap to a large degree, despite being narrow, we regard d_s as constant. The weighted average of the five estimates of d_s in Table II becomes 0.0049 and the corresponding coefficient of variation is 0.25. For comparison, the 95% confidence ranges for the parameter s of the power-exponential model also overlap broadly. However, their ranges are much wider and the coefficient of variation for an average s becomes large (0.85). We may therefore conclude that the surface model gives a more precise estimate of the parameter expressing the digestion process than the power-exponential model. Moreover, since the digestion velocity parameter of the surface model is nearly constant and independent of prey size, we may also regard the surface model as more general than the power-exponential model. A d_s independent of prey size for a particular prey type (herring) allows us to use one equation to predict the gastric evacuation of several known prey sizes, whereas different equations seem to be required for different prey sizes if predictions are based on the power-exponential model.

The data sets listed as '35' and '37' (i.e. 8 and 16 g herring prey) in Table II are chosen for further examination because of their apparently curved and almost linear patterns of gastric emptying. The parameters of four of the classical models provided in Table 1 of Bromley (1994); the linear ($W_t = W_0 - d_s t$), square root ($W_t = W_0 - (2d_{sq}\sqrt{W_0})t + (d_{sq}t)^2$), exponential ($W_t = W_0 e^{-gt}$) and power exponential ($W_t = W_0 2^{-(d_s H t)}$) are estimated using MLE. Figure 4 indicates that all models provide good fits to the data. With the exception of the linear ($\hat{\sigma}_e = 1.20$ and 1.60, respectively for 8 and 16 g prey), similar goodness-of-fit is obtained for the surface model ($\hat{\sigma}_e = 0.92$ and 1.37 respectively for 8 and 16 g prey), for the power-exponential ($\hat{\sigma}_e = 0.85$ and 1.31 respectively for 8 and 16 g prey), square-root ($\hat{\sigma}_e = 0.92$ and 1.37 respectively for 8 and 16 g prey) and for the exponential model ($\hat{\sigma}_e = 0.94$ and 1.31 respectively for 8 and 16 g prey). Thus, it would be difficult to choose one of the classical models over the others at least for these particular data sets by using only the goodness-of-fit measurement as a criterion. Other criteria should also

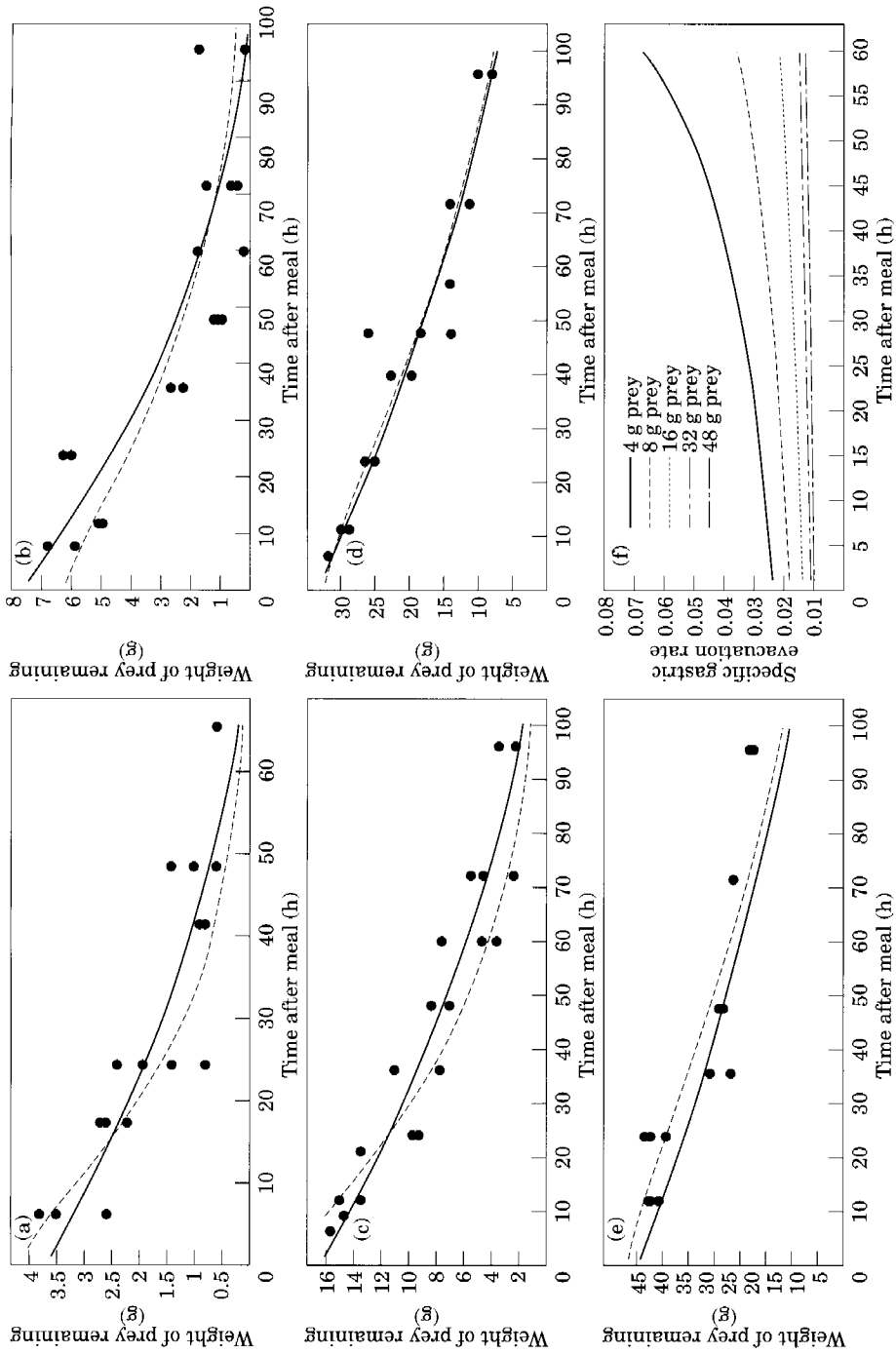


FIG. 3. Comparisons of observed data points, with estimated gastric evacuation curves for cod (size group 40–50 cm, mean weight 714 g) fed one prey of herring (keeping temperature interval narrow) based on the surface (—) and power-exponential (---) models for (a) 4 g prey, (b) 8 g prey, (c) 16 g prey, (d) 32 g prey, (e) 48 g prey sizes and (f) showing how the specific gastric evacuation $g \text{ g}^{-1} \text{ h}^{-1}$ depends on prey size for all five prey sizes. The observations are provided from the databases of Dos Santos & Jobling (1994). Further details of the parameters are given in Table II.

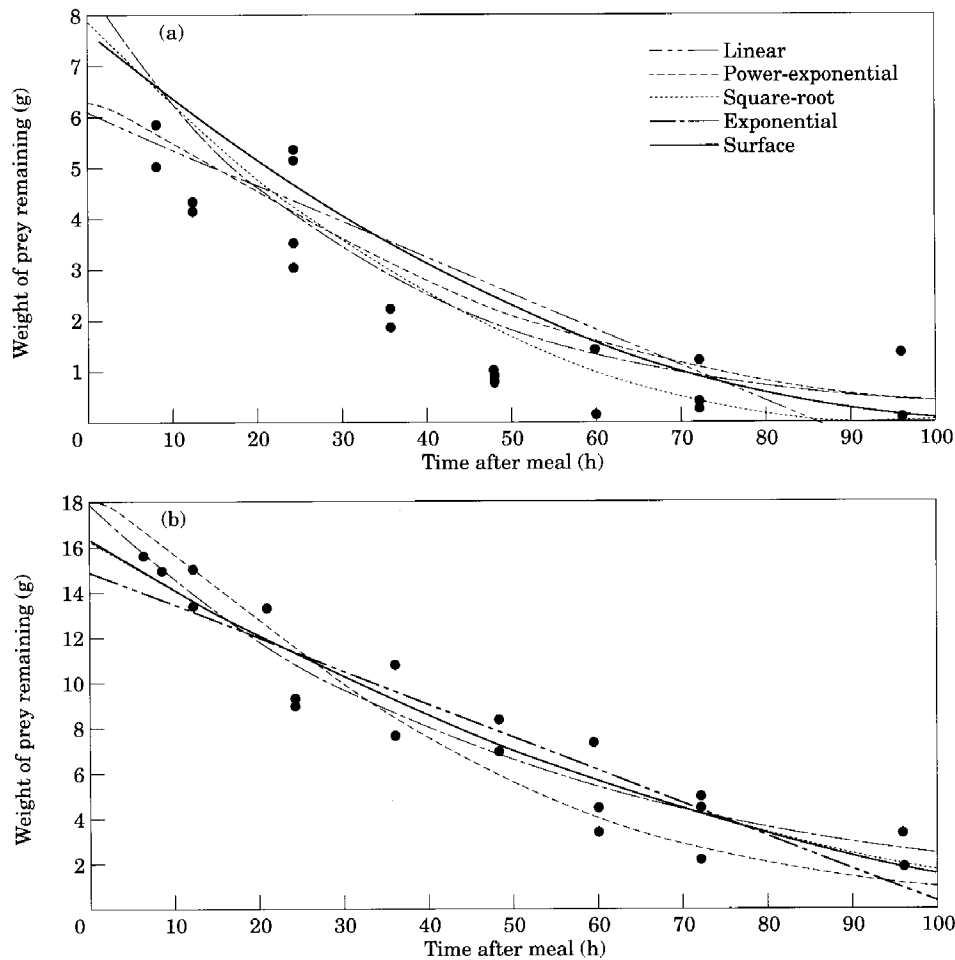


FIG. 4. Comparisons of gastric evacuation curves estimated from the new surface model (ellipsoid) with four classical models: linear, square root, exponential and power-exponential (cf. Bromley, 1994, Table 1), based on two cases 35 and 37 of Table II. Dots refer to observations. (a) 8 g Herring prey (case 35); (b) 16 g herring prey (case 37).

be included. Although the surface model did not indicate strictly the best goodness-of-fit to the data sets examined as judged by the $\hat{\sigma}_e$, it has other qualities that may favour it over the classical models; e.g. that the digestion velocity is independent of prey size.

Examination of time delay

To examine whether there could have been a time delay before digestion started, we also used the MLE technique with the same data sets as above, but with equation 3(c). We obtained similar goodness-of-fit to the data sets as when MLE was applied with equation 3(a) and also the same digestion velocities as in Table II. However, as the 95% confidence range of the time delay parameter t_D for all prey sizes included zero, we may conclude that there were no time delays in these data sets.

Comparison of specific gastric evacuation rate of the exponential and surface models

We have also examined the exponential model in more detail and found similar goodness-of-fit to the same data set as the power-exponential and the surface models ($\hat{\sigma}_e$ was 0.43, 0.94, 1.31, 2.50, 3.53 respectively for herring prey size 4, 8, 16, 32 and 48 g). The estimated gastric evacuation rate g of the exponential model decreased with increasing prey size [$g=0.0341$ (0.0247–0.0435) for 4 g prey; $g=0.0305$ (0.0223–0.0387) for 8 g prey; $g=0.0196$ (0.0161–0.0231) for 16 g prey; $g=0.0130$ (0.0104–0.0156) for 32 g prey; $g=0.0118$ (0.0098–0.0138) for 48 g prey] as there was no or only a slight overlap of most 95% confidence ranges (given in parentheses) for g for two successive prey sizes. Hence, g did not overlap to the same degree as the confidence ranges for the digestion velocity d_s . This is consistent with experimental work (Elliott, 1972, 1991; Persson 1979, 1981) summarized in Fig. 8 of Elliott *et al.* (1993); the gastric evacuation rate for fish prey (representing large prey) fed to trout or perch was lower than if small invertebrates were fed to them. According to equation 6(b) our model expresses, however, how g depends on prey size. This is an additional argument that indicates that our model may be more general than the exponential model which does not express how g depends on prey size.

Independent or bolus digestion of two 16 g herring prey?

We examined if two herring prey were digested independently or aggregated as a bolus by comparing the MLE-estimated digestion velocity for three scenarios of digestion of two 16 g prey. The d_s with 95% confidence range was estimated using MLE with equation 3(a) assuming (i) that the two herring prey were stacked/aggregated to have a common outer surface attacked by the digestive enzymes [$\hat{\sigma}_e=2.90$; $d_s=0.0047$ (0.0036–0.0058)]; (ii) that the two prey were independently digested [$\hat{\sigma}_e=2.91$; $d_s=0.0033$ (0.0022–0.0044)]; (iii) that the two prey were partly stacked (50% had a 'common' outer surface) [$\hat{\sigma}_e=2.91$; $d_s=0.0039$ (0.0030–0.0048)]. The three scenarios had identical goodness-of-fit to the data set, but the estimated digestion velocity differed. The first scenario gave a digestion velocity closest to what we obtained as constant and independent of prey size [$d_s=0.0049$ (0.0047–0.0051), Table II]. Hence, this comparison suggests that the two 16 g herring prey formed a bolus with a common outer surface which was attacked by the digestive enzymes within the cod predator.

Temperature effect on digestion velocity

The effect of temperature T on the digestion velocity was analysed using seven data sets provided by Dos Santos & Jobling (1994). In these experiments individual cod were fed one 16 g herring. According to our analysis the estimated digestion velocity d_s increased with temperature between $T=1.2$ and 6°C , but decreased thereafter. The MLE estimated digestion velocities with 95% confidence ranges were for $T=1.2^\circ\text{C}$, $d_s=0.0033$ (0.0027–0.0039); for $T=3.9^\circ\text{C}$, $d_s=0.0043$ (0.0039–0.0047); for $T=4.3^\circ\text{C}$, $d_s=0.0050$ (0.0041–0.0059); for $T=4.9^\circ\text{C}$, $d_s=0.0073$ (0.0055–0.0091); for $T=5.6^\circ\text{C}$, $d_s=0.0080$ (0.0066–0.0094); for $T=6.0^\circ\text{C}$, $d_s=0.0102$ (0.0091–0.0113); and for $T=9.5^\circ\text{C}$, $d_s=0.0089$ (0.0077–0.0101); and the standard errors of the equation $\hat{\sigma}_e$ were in the range

0.73–1.41. These results suggest an exponential pattern in the digestion velocity–temperature relationship for environmental temperatures between 1.2 and 6° C, but a deviation from such a pattern when temperatures exceeded 6° C. Similar results are also reported for Arctic cod predators by Tyler (1970), but also for juvenile sockeye salmon *Oncorhynchus nerka* (Walbaum) (Brett & Higgs, 1970). Regarding the Arctic cod predators used in the experiments of Tyler (1970) and Dos Santos & Jobling (1994), we expect that the species is not adapted to temperatures as high as 9.5–20° C, as the normal temperature range in Arctic cod habitats will be from about 1 to 6–7° C.

Kapoor *et al.* (1975) pointed out five ways in which temperature may affect the evacuation rate: (1) feeding rate; (2) hydrolytic activity of digestive enzymes; (3) gastric and intestinal motility; (4) secretory rate of digestive juice; and (5) rate of intestinal absorption. The influence of temperature on gastric juice secretion in the brown bullhead *Ameiurus nebulosus* (Lesueur) was studied by Smith (1967). He showed that acid secretion increased between 10 and 25° C while pepsin secretion was constant. For higher temperatures the acid secretion decreased. Persson (1979) suggests that although the evacuation rate of perch and trout does not deviate from the exponential pattern in the temperature range studied (5–20° C), there may be a deviation at higher temperatures than the species are adapted to. We suggest that the observed differences between perch and trout and the Arctic cod and sockeye salmon are due to different physiological adaptations to environmental temperatures. We presume that the temperature range 1.2–6° C is within the normal temperature range for Arctic cod and therefore assume an exponential relationship between the temperature and the digestion velocity for this range. The parameters of the ln-transformed equation (4) were estimated using regression analysis: $d_s = d_{s_0} e^{(\ln(Q_{10})/10) \cdot T} = 0.0022e^{0.2334T}$; $R^2_{\text{adj}} = 0.84$ resulting in a Q_{10} of 10.32. This value is much higher than Bromley (1994) regarded as normal for fish. However, the obtained Q_{10} should not be used for Arctic cod for a temperature range of 10° C as this species would be adapted to a narrower temperature range. Gastric digestion and evacuation of herring prey fed to Arctic cod may thus be predicted from:

$$W_t = \frac{4}{3} \rho \pi (L_0/2 - 0.0022e^{0.2334T_t})(r_0 - 0.0022e^{0.2334T_t})^2.$$

CONCLUDING REMARKS

Although we assume linearity between prey surface area and concentration of digestive enzymes, this may not be strictly true for all prey types and prey sizes. Earlier studies proposed that distension of the stomach modifies the rate at which food is evacuated from the stomach, and the larger the original volume of the meal, then the greater is the initial rate of emptying of the stomach (Hunt & MacDonald, 1954), but also that gastric distension leads to increased rates of secretion of gastric enzymes and acid (Jobling, 1981 and references therein). We presume that the combination of prey composition, size and shape, environmental temperature and predator physiology influence the gastric evacuation pattern of prey. The purpose of this study has, however, not been to go into details in predator physiology, but to outline a flexible model which has parameters with direct biological interpretation for practical use and for use in

simulation models, but which also can be regarded as an improvement compared with classical models. The overall impression of our analysis is that despite the fact that the classical and surface models give similar goodness-of-fit to the Dos Santos and Jobling data sets, the surface model seems to be more general and flexible than the previous models, particularly because the digestion velocity parameter appears independent of prey size for a certain predator-prey relationship (cod predator-herring prey), but also because the surface model can explain how the specific gastric evacuation rate of e.g. the exponential model depends on prey size as well as on temperature and a potential time delay before digestion starts.

We thank Jorge Dos Santos and Malcolm Jobling for providing data sets needed for model evaluation, but also for critically reviewing a previous version of the manuscript; two anonymous referees for very valuable comments on the manuscript; Jens Christian Holst for providing the length-weight relationship for herring; and Elin Holm for technical assistance with figures. This work has been financed by a grant from the Norwegian Research Council (NFR) to D. L. Aksnes and A. G. V. Salvanes.

References

- Aksnes, D. L. & Giske, J. (1990). Habitat profitability in pelagic environments. *Marine Ecology Progress Series* **64**, 209–215.
- Aksnes, D. L. & Giske, J. (1993). A theoretical model of aquatic visual feeding. *Ecological Modelling* **67**, 233–250.
- Brett, J. R. & Jiggs, D. A. (1970). Effect of temperature on the rate of gastric digestion in fingerling sockeye salmon (*Oncorhynchus nerka*). *Journal of Fisheries Research Board Canada* **27**, 1767–1779.
- Bromley, P. J. (1994). The role of gastric evacuation experiments in quantifying the feeding rates of predatory fish. *Reviews in Fish Biology and Fisheries* **4**, 36–66.
- Castellan, G. W. (1971). *Physical Chemistry*, 2nd edn. London: Addison-Wesley.
- Dos Santos, J. & Jobling, M. (1991a). Gastric emptying in cod, *Gadus morhua* L.: emptying and retention of indigestible solids. *Journal of Fish Biology* **38**, 187–197.
- Dos Santos, J. & Jobling, M. (1991b). Factors affecting gastric evacuation in cod, *Gadus morhua* L., fed single-meals of natural prey. *Journal of Fish Biology* **38**, 697–713.
- Dos Santos, J. & Jobling, M. (1994). *A Database of Gastric Evacuation Observations in Cod Gadus morhua Fed Natural Prey. Experiments Performed in Tromsø, Norway, 1986–1993*. Tromsø: Norwegian College of Fishery Science, University of Tromsø.
- Draper, N. & Smith, H. (1981). *Applied Regression Analysis*, 2nd edn. John Wiley: New York.
- Dunbrack, R. L. & Dill, L. M. (1984). Three-dimensional prey reaction field of juvenile coho salmon (*Oncorhynchus kisutch*). *Canadian Journal of Fisheries and Aquatic Sciences* **41**, 1176–1182.
- Durbin, E. G., Durbin, A. G., Langton, R. W. & Bowman, R. E. (1983). Contents of silver hake, *Merluccius bilinearis*, and Atlantic cod, *Gadus* fed single-meals of natural prey. *Fishery Bulletin* **81**, 437–454.
- Eggers, D. M. (1977). The nature of prey selection by planktivorous fish. *Journal of Fish Biology* **11**, 46–59.
- Elashoff, J. D., Reedy, T. J. & Meyer, J. H. (1982). Analysis of gastric emptying in rainbow trout. *Gastroenterology* **83**, 1306–1312.
- Elliott, J. M. (1972). Rates of gastric evacuation in brown trout. *Freshwater Biology* **2**, 1–18.
- Elliott, J. M. (1991). Rates of gastric evacuation in piscivorous trout. *Freshwater Biology* **25**, 297–305.

- Elliott, J. M., Elliott, J. A. & Hilton, J. (1993). Sources of variation in post-Chernobyl radiocaesium in brown trout, *Salmo trutta* L., and Arctic charr, *Salvelinus alpinus* (L.), from six Cumbrian lakes (northwest England). *Annals of Limnology* **29**, 79–98.
- Fänge, R. & Grove, D. (1979). Digestion. In *Fish Physiology*, (Vol. 8), (Hoar, W. S., Randall, D. J. & Brett, J. R., eds), pp. 161–260. London: Academic Press.
- Flowerdew, M. W. & Grove, D. J. (1979). Some observations of the effects of body weight, temperature, meal size and quality on gastric emptying time in turbot (*Scophthalmus maximus* (L.)) using radiography. *Journal of Fish Biology* **14**, 229–238.
- Giske, J., Skjoldal, H. R. & Aksnes, D. L. (1992). A conceptual model of distribution of capelin in the Barents Sea. *Sarsia* **77**, 147–156.
- Grove, D. J., Moctezume, M. A., Flett, H. R. J., Foott, J. S., Watson, T. & Flowerdew, M. W. (1985). Gastric emptying and the return of appetite in juvenile turbot, *Scophthalmus maximus* L. fed on artificial diets. *Journal of Fish Biology* **26**, 339–354.
- Hunt, J. N. & MacDonald, I. (1954). The influence of volume on gastric emptying. *Journal of Physiology* **126**, 459–474.
- Hutchings, J. A. (1993). Adaptive life histories effected by age-specific survival and growth rate. *Ecology* **74**, 673–684.
- Jobling, M. (1981). Mathematical models of gastric emptying and the estimation of daily rates of food consumption for fish. *Journal of Fish Biology* **19**, 245–257.
- Jobling, M. (1986). Mythical models of gastric emptying and implications for food consumption studies. *Environmental Biology of Fishes* **16**, 35–50.
- Jobling, M. (1987). Influences of food particle size and dietary energy content on patterns of gastric evacuation in fish: test of physiological model of gastric emptying. *Journal of Fish Biology* **30**, 299–314.
- Kapoor, B. G., Smit, H. & Verighina, I. A. (1975). The alimentary canal and digestion in teleosts. In *Advances in Marine Biology* (Vol. 13) (Russell, F. S. & Yonge, M., eds), pp. 109–239. London: Academic Press.
- Kennedy, P. (1992). *A Guide to Econometrics*, 3rd edn. Oxford: Blackwell.
- Luecke, C. & O'Brien, W. J. (1981). Prey location volume of a planktivorous fish: a new measure of prey vulnerability. *Canadian Journal of Fisheries and Aquatic Sciences* **38**, 1264–1270.
- Persson, L. (1979). The effects of temperature and different food organisms on the rate of gastric evacuation in perch (*Perca fluviatilis*). *Freshwater Biology* **9**, 99–104.
- Persson, L. (1981). The effects of temperature and meal size on the rate of gastric evacuation in perch (*Perca fluviatilis*) fed on fish larvae. *Freshwater Biology* **11**, 131–138.
- Persson, L. (1984). Food evacuation and models for multiple meals in fishes. *Environmental Biology of Fishes* **10**, 305–309.
- Persson, L. (1986). Patterns of food evacuation in fishes: a critical review. *Environmental Biology of Fishes* **16**, 51–58.
- Rose, K. A., Christensen, S. W. & DeAngelis, D. L. (1993). Individual-based modeling of populations with mortality: a new method based on following a fixed number of model individuals. *Ecological Modelling* **68**, 273–292.
- Smith, H. (1967). Influence of temperature on the rate of gastric juice secretion in the brown bullhead *Ictalurus nebulosus*. *Comparative Biochemistry & Physiology* **21**, 125–132.
- Tyler, A. V. (1970). Rates of gastric emptying in young cod. *Journal of the Fisheries Research Board of Canada* **27**, 1177–1189.
- Tyler, J. A. & Rose, K. A. (1994). Individual variability and spatial heterogeneity in fish population models. *Reviews in Fish Biology and Fisheries* **4**, 91–123.
- White, K. J., Wong, S. D., Whistler, D. & Haun, S. A. (1990). *SHAZAM Econometrics Computer Program. User's Reference Manual, Version 6.2*. New York: McGraw-Hill.

APPENDIX 1

ESTIMATING THE DIGESTION VELOCITY PARAMETER BY POLYNOMIAL REGRESSION

For the digestion and evacuation of a fish prey with an ellipsoid shape, the equation for prey remaining W_t v. time t is:

$$W_t = \frac{4}{3} \rho \pi \left(\frac{L_0}{2} - d_s t \right) (r_0 - d_s t)^2 \quad (\text{A1})$$

or:

$$W_t = \frac{4}{3} \rho \pi \left[\frac{L_0}{2} r_0^2 - (L_0 r_0 d_s + r_0^2 d_s) t + \left(\frac{L_0}{2} d_s^2 + 2 r_0 d_s^2 \right) t^2 - d_s^3 t^3 \right]. \quad (\text{A2})$$

Equation (A2) is of a general form, and may be solved if the density of the prey mass g is known, and a data set consisting of weight of prey remaining (W_t) v. time (t) is available and if original prey length L_0 is known. The general form of equation (A2) can be expressed as:

$$W_t = \gamma_0 + \gamma_1 t + \gamma_2 t^2 + \gamma_3 t^3 + \varepsilon \quad (\text{A3})$$

where

$$\begin{aligned} \gamma_0 &= \frac{2}{3} \rho \pi L_0 r_0^2; \\ \gamma_1 &= -\frac{4}{3} \rho \pi d_s (L_0 + r_0^2); \\ \gamma_2 &= \frac{4}{3} \rho \pi d_s^2 \left(\frac{L_0}{2} + 2r_0 \right) \\ \gamma_3 &= -\frac{4}{3} \rho \pi d_s^3. \end{aligned} \quad (\text{A4})$$

We can estimate the γ_i s (where $i=0$ to $i=3$) of equation (A3) by polynomial regression, assuming the error term (ε) to be normally distributed and independent of t (Draper & Smith, 1981). The equations given in (A4) can be solved with respect to d_s (the velocity at which enzymes attach progressively deeper into the prey):

$$d_s = \frac{-3\gamma_1}{4\rho\pi(L_0 r_0 + r_0^2)} = \left(\frac{3\gamma_2}{4\rho\pi(L_0/2 + 2r_0)} \right)^{1/2} = \left(\frac{-3\gamma_3}{4\rho\pi} \right)^{1/3}. \quad (\text{A5})$$

Note that this approach does not provide uncertainty for the digestion velocity parameter. The parameter may also be slightly biased due to correlation between independent variables of the equation (A3). However, the bias in the estimated parameter would not be severe, and it would be useful e.g. as input to the iterative maximum likelihood technique.