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MODELLING GASTRIC EVACUATION IN COD

A NEW GASTRIC EVACUATION MODEL APPLICABLE FOR THE ESTIMATION OF THE DAILY RATION OF COD IN THE FIELD

by

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ABSTRACT

In this paper data on gastric evacuation of cod from the International Data Base on Gastric Evacuation Experiments have been reanalysed.

A general evacuation model was fitted to the data by means of nonlinear regression techniques, which allowed for various curve shapes, including linear and exponential. The degree of curivilinearity of the evacuation curves was by this estimated from the data and not predefined by the model.

Special attention was given to the formulation of an evacuation model, which does not include the experimental meal size as a parameter.

INTRODUCTION

The international database of gastric evacuation experiments was set up following a suggestion of the ICES workshop on stomach evacuation rates in fish, held in 1989 (Anon. 1989). The participants of this workshop could, however, not agree on a gastric evacuation model, which they felt could be applied with confidence to a wide range of species and feeding situations. In particilar, there was no clear consensus if gastric evacuation is either linear or curvilinear.

The compilation of an extended international data base and the subsequent analysis by different workers was considered to give more general insight into the nature of the gastric evacuation process.

Since this database was set up, only Bromley (1990) has analysed the total data base, which constists almost exclusively of data on cod, but also includes some data on whiting. He analysed the data by the techniques of general linear modeling based on the analysis of variance (ANOVA). This technique, however, predefines a linear evacuation model, and can therefore not be used to estimate the 'best' type of model. However, in this analysis meal size turned out to be positively related with gastric evacuation rate.

Dos Santos (1990) has analysed the large subset of cod evacuation data, which he has contributed to the data base. He fitted a power exponential model to these data, which allows the shape of the curve to vary to some extent. The curves fitted can be either S-shaped or concave. The exponential decay function is included as a special case, the other concave shapes are more curvilinear than the exponential function.

He concludes than the data may be adequately described with a negative exponential function. The final model however, depends on experimental meal size as a parameter. This makes the model inapplicable to the estimation of consumption of cod in the field, because meal sizes in the field are unkown.

This study concentrates on two main questions:

1) What is the degree of curvilinearity of gastric evacuation and its variability in quantitative terms.

2) Is the experimental meal size a necessary parameter in gastric evacuation models?

MATERIAL

Only the data from dos Santos experiments with cod fed on capelin, herring and prawns (Pandalus borealis) have been included into the analysis, because these form the largest homogeneous subset of the data base with respect to experimental conditions. For each of the three food types several experiments with some variation of the key parameters predator weight, meal size and temperature were available. Table 1 summarizes the data structure, on which the analyses is based. The analysed data set consists of 905 stomachs in 43 experiments, the total data base contains information on 55 experiments with 1576 stomachs including data on whiting and mackerel.

Data series were cut off at times of first occurrence of empty stomachs, to avoid bias due to censored observations.

METHODS

The estimation of the degree of curvilinearity from experimental results requires a mathematical model, which does not predefine the parameter, which decribes the degree of curvilinearity. In prior analyses either a linear (Bromley 1989, 1990) or an exponential model (Tyler 1970) was predefined, and only the parameters of these models were estimated.

Dos Santos power exponential model has some flexiblility in shape, but the curves are restricted to either S-shape or strongly bent concave forms. Among the concave curves, the negative exponential is the one, which has the lowest degree of curvilinearity.

Following a suggestion of Tyler (1970) and Jones (1974) in this study a model is used, in which the instantaneous evacuation rate is a power function of the instantaneous stomach content. This model includes convex, linear, exponential and intermediate curve types, with a degree of curvilinearity between linear and exponential:

$$\frac{dS}{dt} = - R * S^{B} \qquad (1)$$

The shape of the curve is defined by the value of B:

B < 0: curvilinear, convex curve with increasing negative slope

B = 0: linear, negative slope

0 < B < 1: curvilinear, concave curve with decreasing negative slope

B = 1: curvilinear, exponential decay curce

B > 1: curvilinear, concave curve, the dependence of evacuation rate on the stomach content is stronger than in the exponential case. That implies higher rates at high and lower rates at low stomach contents, when compared with an exponential model.

Starting from B = 0 the degree of concave curvilinearity increases with B. The integrated form for all cases except B = 1 reads:

$$St = \left[So^{(1-B)} - R * (1-B) * t \right]^{(1/(1-B))} \qquad (2)$$

with variables	and parameters
St = residual stomach content at time t	So = initial meal size
t = time after ingestion	B = shape parameter
	R = constant, dpendent on temperature, food, predator weight and others

In order to analyse the variability of the estimated exponents (B), this univariate version has been fitted to each of the individual experiments in the data base. The data sets of individual experiments were considered homogenous with respect to temperature and predator weight.

In addition to this univariate model a multivariate version was fitted to the data of three subgroups of experiments, each of these subgroups comprising all experiments with the same food type. The explaining variables in the multivariate model were time after ingestion, weight of predator, temperature and meal size. The full model reads:

$$St = \left[(M * E * E)^{(1-B)} - R' * e^{A*T} * W^{C} * M^{D} * (1-B) * t \right]^{(1/(1-B))}$$

(3)

with Variables and Parameters

M = meal size	A = temeraturecoefficient
T = temperature	B = shape parameter see above
t = time after ingestion	C = predator weight coefficient
W = predator weight	D = meal size coefficient
	E = adjustment parameter, without of this parameter, curves are forced through M at t = 0.
	R' = food type constant

The multivariate model was also applied without the variable meal size (and parameter D), since models, which include the variable meal size, cannot be incorporated in consumption models.

Regression technique

The models were fitted with Non Linear Regression techniques in the computer package SPSS (using a Marquard algorithm). The advantage of this technique is the that the variance structue is not effected by transformations, and the model structure is extremly flexible. Problems occur however, if during the iterative process of parameter estimation, predicted values have to be calculated for data points, which fulfill the following condition:

$$t * (1-B) * R > So^{(1-B)}$$ in the univariate or

$$t * (1-B) * W^{C} * M^{D} * e^{A*T} * R' > (M * E * E)^{(1-B)}$$ in the

multivariate case with the actual set of parameter values. In these cases a negative value has to raised to the power (1/(1-B)), which will cause a system error (No real value solution for roots of negative numbers)

To avoid this error the evacuation model has been extended by a conditional expression:

$$St = \begin{cases} \left[S^{(1-B)} - R*(1-B)*t \right]^{(1/(1-B))} & \text{if } R*(1-B)*t > S^{(1-B)} \\ \text{ZERO} & \text{if } R*(1-B)*t =< S^{(1-B)} \end{cases}$$

(4)

Calculation of consumption

Evacuation models, which were fitted to the data sets exluding meal size as a parameter, have been applied to estimate the yearly consumption of North Sea cod by age group. Data on mean quarterly temperature and mean stomach content of North Sea cod by age group were taken from (Anon 1987). Quarterly consumption for one age group (CQA) was calculated as

$$CQA = R * W^{C} * e^{A*T} * S^{B} * 24 * 91 \qquad (5)$$

S = mean stomach content of a cod age group in the field
T = mean quarterly temperature in the field
The multipliers 24 and 91 refer to hours per day and days per quarter, respectively.

RESULTS

Analysis of individual experiments

Table 2 summarizes the paramter estimates for the univariate evacuation model (Eqn. 2), fitted to the data sets of individual experiments. Curvilinearity is strongest in the capelin data (Mean B = 1.39, Range: -0.65 to 2.86), lower in the herring data (Mean B = 0,90, Range: 0.05 to 2.61) and lowest in the prawn data (Mean B = 0.43, Range: -1.31 to 1.62). The variability of the estimated B values, however, is high (Stand. Dev.: Capelin: 0.93, Herring: 0.59, Prawn: 0.73) and the estimated asymptotic 95%-confidence limits are wide. In capelin the mean lower limit amounts to 0.33, the upper limit to 2.44. The corresponding figures for Herring are 0.02 and 1.77, and for Prawn -0.66 and 1.44.

Analysis of the total data base by food types

The best fits of the multivariate model (Eqn. 3) resulted for all three food types, when meal size was included as a parameter (R-squared: Capelin: 0.934, Herring: 0.944, Prawn: 0.904, all runs with E = 1 fixed, Tab. 3). The estimated exponents (B) in these runs, B = 1.37 for capelin, B = 0.84 for Herring and B = 0.35 for prawn, match more or less the mean estimates from the individual experiments. The meal size exponent D was negatively correlated with the amount of B: Prawn: D = -0.14, Herring: D = -0.57 and Capelin: D = -1.155.

Without the parameter meal size generally lower B values were estimated: Capelin: B = 0.47, Herring: B = 0.43 and Prawn: B = 0.27. In all cases the asymptotic 95%-confidence limits were narrow and zero and and one were not included between lower and upper limits. In case of capelin the exclusion of meal size reduces the explained variance from 0.93 to 0.89 (-0.04), for herring the effect is much less (-0.01) and for prawn the loss is neglectible (-0.005).

Alternative models with B fixed to either one (exponential) or zero (linear) and meal size excluded generally explain less variance than models with variable B and meal size excluded (-0.03 to -0.14).

All figures presented so far, refer to models, which are forced through the initial meal size (Parameter E = 1 fixed). Comparitative results with variable E are also contained in Table 3. The overall trends are similar, only the explained variance is in some cases a little higher.

Consumption estimates

The highest consumption is estimated with the evacuation model fitted to capelin data, the lowest is based on the prawn data. In all three cases the exponential model gives the highest estimates and the linear model the lowest. The model results give comparable results for predator age groups with a mean weight similar to that of the experimental fish (Fig. 1). The deviations between different model estimates increase rapidly with increasing predator age and weight.

DISCUSSION

Analysis of individual experiments

The large scatter of the estimated exponents and the wide confidence limits show, that it is difficult to decide between alternative models on the basis of data sets with some 10 to 20 observations, even in experiments, where fish feed individually controlled identical meals. In many experiments with low numbers of observations the confidence limits include both zero and one.

This also implies, that in experimental designs with mass feeding the determination of the shape of the evacuation curve is almost impossible. In mass feeding experiments the distribution of meal sizes is skewed with high variance. This leads to a corresponding variance of the data points and to the early occurrence of empty stomachs. In this case censoring effects can not simply be circumvented by cutting off the data series at the time, where the first empty stomach occurs.

The mean exponents over all experiments, however, clearly indicate that gastric evacuation is in this case not a linear process.

Analysis of the total data base by food types, meal size included as a parameter in the models

The finding of a curvilinear evacuation is confirmed by the fits of the multivariate evacuation model (Eqn. 3, meal size included as a parameter), which all yield exponents above zero, and where zero is in all cases excluded from the 95%-confidence intervals.

The results of runs with meal size included as a parameter also show, that the degree of curvilinearity depends on the type of food used. No one of the estimated exponents for one food type is included within the 95%-confidence limits of one of the other two exponents.

An interesting result is the exponent B = 1.36, which has been estimated for capelin as food. The confidence limits also exclude the exponential case (1.19 to 1.55). This type of evacuation, which is characterized by an extremely radid initial decay of the ingested food, has to the authors knowledge not been discussed in the literature so far. It can only be speculated here whether this result has any biological meaning related to the physical and biochemical properties of live capelin, or reflects rather effects of the handling (storage times, freezing and thawing procedure and so on) of the prey items prior to the experiment.

The comparitively low exponent estimated for the prawn experiments may be related with the delaying effect of a robust exoskeleton. This exoskeleton prevents a rapid initial decay of the prey items.

Analysis of the total data base by food types, meal size <u>not</u> included as a parameter in the models

Once the parameter meal size is excluded from the evacuation model, the estimated exponents (B) for the different food types concentrate in a narrow range between zero and one: Prawn : B = 0.27, Herring : B = 0.43 and Capelin B = 0.47. The exponent B for herring now lies within the 95%-confidence interval of the exponent for capelin and vice versa.

This reduction of the exponents B for herring and capelin can be explained based on Figure 3. Here evacuation curves of herring are displayed for experiments with different meal sizes (Fig. 2 D), but with more or less constant predator weight (means: 690 - 781g) and temperature (means: 3.4 - 5.5°C).

It can be seen, that the average slopes of the evacuation curves (linear trends) increase with increasing meal size, and that the curves are also shifted to the right with increasing meal size. The increase of the slopes, however, is less, than what would be predicted with an exponential model with a constant instantaneous rate (R).

This is effect is also visible in the parameter estimates for the exponent D of the meal size in the fits of the full model with meal size as a parameter. The estimated D-values for herring and capelin are large and negative. This means in other words, that with increasing meal size the estimated instantaneous rates (R) are decreasing.

The general evacuation model, with B-values between zero and one, however, is the only one, that can account for the effect of slopes increasing moderately with increasing meal size, without of changing the instantaneous rate (R).

Consumption estimates

The consumption estimates for the different age groups of North Sea cod are extremely sensitive to different prey types on the one hand and choice of an evacuation models on the other hand. It should be noted however, that the differences between the models are less dramatic at ages 2 and 3, where the predator weight matches approximately the weight of the experimental fish. The extreme differences are mainly a result of extrapolation beyond the range of parameter variation in the experiments.

The extrapolated consumption estimates for larger fish depend on the effect of predator weight on evacuation rate in all models, and, additionally, on effects of stomach content on evacuation rate in curvilinear models. In curvilinear models the rate is dependent on the amount of food in the stomach. This effect can be quantified even if predator weight is not varied at all, if the shape of the evacuation curve is curvilinear. The weight effect on evacuation rate in the linear evacuation model, however, can only be estimated, if the predator weight is varied to some extent.

It may not be excluded, that the weak weight effect of predator weight on the linear evacuation rates (Prawn: C = 0.2, Herring: C = -0.02, Capelin: C = 0.3) is due to the limited variation of predator in the experiments analysed here. Bromley (1989) has estimated this exponent to be C = 0.59, based on predator weights ranging from 6 - 3600 g in feeding experiments (Assuming that feeding rate on average equals evacuation rate) and 800 - 3000 g in evacuation experiments.

Conclusions

Three main conclusions may be drawn from the results presented here:

1) The evacuation process in the experiments studied here is curvilinear. The degree of curvilinearity depends on the food type.

2) The effects of increasing meal size on exponential and linear gastric evacuation curves is accounted for by a negative (exponential model) or positive (linear model) exponents to the parameter meal size, which decreases (exponential model) or increases (linear model) the instantaneous rate of evacuation with increasing meal size.

3) Evacuation/Consumption models without meal size as a parameter explain at worst 4% less of the total variance, compared with a model that includes meal size. These models take account of the changing curve shapes due to increasing meal size by choosing exponents B between 0.27 (Prawn) and 0.47 (Capelin).

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Table 1: Summary the the experiments with cod in the International Data Base of Gastric Evacuation Experiments performed by dos Santos

Exp. Nr.	Nr. of Fish	Temerature Mean C	Std.dev. C	Pred.weight Mean g	Std.dev. g	Prey code *)	Nr.of prey	Meal size g
8	14	7.2	0.4	341	48	2	8	16
9	11	7.1	0.3	327	90	2	4	16
10	32	7.2	0.4	306	69	4	1	16
11	12	7.3	0.5	726	102	2	8	16
12	11	7.3	0.5	691	120	2	4	16
13	18	7.1	0.2	690	118	4	1	16
14	52	1.9	0.5	373	69	4	1	16
15	19	1.9	0.5	358	72	2	4	16
16	18	1.3	0.2	418	62	3	1	16
17	48	1.9	0.5	691	141	4	1	16
18	56	2.0	0.4	683	145	2	4	16
19	19	1.2	0.2	634	137	3	1	16
20	22	2.0	0.5	697	144	1	40	16
21	19	1.8	0.6	690	172	2	2	16
22	28	1.6	0.4	724	146	4	3	48
23	13	2.5	0.0	738	201	2	4	32
24	26	1.9	0.5	1533	371	4	1	16
25	13	1.8	0.6	1478	277	2	4	16
26	28	5.6	0.2	673	129	1	40	16
27	19	5.7	0.1	822	174	2	8	16
28	22	5.6	0.1	721	158	2	4	16
29	23	5.7	0.1	765	186	2	2	16
30	27	5.6	0.1	658	81	3	1	16
31	29	5.6	0.2	650	113	4	1	16
32	29	5.2	0.2	770	126	4	1	16
33	17	4.8	0.1	765	143	2	8	16
34	24	4.9	0.1	751	120	3	1	16
35	21	5.3	0.2	765	121	2	2	16
36	22	4.9	0.2	739	115	1	40	16
37	24	2.6	0.4	712	145	4	1	16
38	19	3.7	0.2	722	143	4	1	16
39	20	3.4	0.6	708	140	3	1	4
40	21	4.2	0.2	692	170	3	4	16
41	16	3.6	0.2	695	175	3	8	32
42	21	5.2	0.4	691	158	3	1	8
43	17	5.1	0.4	646	103	3	2	16
44	20	4.3	0.2	709	139	3	1	16
45	15	4.1	0.3	744	156	3	2	32
46	16	4.0	0.3	746	159	3	1	32
47	24	5.5	0.9	782	167	3	1	48
48	21	6.3	0.5	654	121	2	1	2
49	17	7.5	0.1	696	140	4	1	16
50	23	8.3	0.0	698	134	4	1	16
51	65	3.9	0.4	858	122	3	1	16
52	18	5.9	0.3	776	96	3	1	16
53	20	5.1	0.1	832	117	2	4	8

*) Prey code: 1 = Krill, 2 = Prawn, 3 = Herring, 4 = Capelin

Table 2: Estimated Parameters from fits of the univariate model to data of individual experiments

Exp. Nr.	Nr. of Fish	R-sqrd	B Estim.	B 95%-conf.limit lower	B 95%-conf.limit upper	R Estim.	So Estim.
			EXPERIMENTS WITH PRAWN				
8	14	0.857	-0.61	-2.10	0.88	0.67926	14.2
9	11	0.829	0.55	(-5E14)	(+5E14)	0.04847	16.7
15	19	0.804	0.26	-1.99	2.51	0.05312	15.2
18	56	0.778	0.43	-0.51	1.37	0.04166	14.2
21	19	0.834	1.60	-0.56	3.75	0.00248	16.7
23	13	0.923	-1.31	-3.83	1.21	10.77885	31.3
25	13	0.912	1.62	0.13	3.11	0.00400	20.3
27	15	0.953	0.92	0.20	1.63	0.04473	18.8
28	18	0.971	0.52	0.14	0.89	0.07959	16.6
29	20	0.937	0.09	-0.45	0.62	0.15748	15.2
33	17	0.934	0.33	-0.17	0.84	0.11652	17.4
35	18	0.928	0.37	-0.21	0.95	0.10213	18.0
48	18	0.878	0.40	-0.26	1.06	0.09518	2.5
53	16	0.970	0.84	0.35	1.33	0.04602	8.2
			EXPERIMENTS WITH HERRING				
16	18	0.906	0.05	-1.02	1.12	0.10263	15.4
19	19	0.923	2.61	1.31	3.91	0.00043	22.8
30	24	0.945	1.11	0.63	1.58	0.02711	18.6
34	21	0.875	1.24	0.36	2.11	0.02160	19.4
39	17	0.821	1.14	-0.10	2.37	0.03127	4.2
40	19	0.819	0.38	-0.61	1.37	0.09259	14.6
41	14	0.944	0.56	-0.20	1.33	0.05858	32.2
42	15	0.836	0.14	-0.84	1.11	0.09936	7.5
43	14	0.913	0.84	-0.04	1.73	0.04216	19.2
44	20	0.906	1.03	0.17	1.90	0.01837	17.7
45	15	0.886	1.33	0.04	2.63	0.00480	37.0
46	16	0.906	0.74	-0.23	1.71	0.02816	33.7
47	21	0.935	0.71	0.08	1.33	0.02897	46.3
51	57	0.900	0.83	0.36	1.30	0.02394	16.0
52	16	0.972	0.73	0.35	1.10	0.07220	17.4
			EXPERIMENTS WITH CAPELIN				
10	28	0.868	-0.65	-1.71	0.40	0.92318	14.4
13	18	0.815	2.85	0.40	5.31	0.00069	57593.6
14	52	0.848	1.42	0.73	2.11	0.00758	16.8
17	48	0.885	1.76	1.16	2.36	0.00464	17.7
22	28	0.918	2.20	1.21	3.20	0.00018	54.4
24	23	0.872	2.86	1.68	4.05	0.00073	59376.9
31	20	0.953	1.34	0.77	1.91	0.02277	20.2
32	22	0.896	1.23	0.56	1.90	0.03436	27.2
37	21	0.932	0.98	0.35	1.60	0.02884	17.1
38	16	0.711	0.84	-1.32	3.01	0.02976	16.0
49	17	0.941	1.25	0.57	1.93	0.02539	19.6
50	16	0.920	0.57	-0.41	1.56	0.23249	16.9

Table 3a: Estimated Parameters from fits of the multivariate evacuation model

	*	R-sqrd	R'	B	C	D	A	E
	Curves forced through the initial meal size							
	1	0.904	0.01570	0.35	0.238	-0.140	0.102	[1]
P	2	0.903	0.01344	0.27	0.229	/	0.105	[1]
	3	0.848	0.00174	[1]	0.244	/	0.131	[1]
	4	0.877	0.03169	[0]	0.199	/	0.094	[1]
	1	0.944	0.06245	0.84	0.018	-0.567	0.173	[1]
H	2	0.931	0.02886	0.43	0.047	/	0.137	[1]
	3	0.880	0.01460	[1]	-0.040	/	0.060	[1]
	4	0.829	0.10076	[0]	-0.016	/	0.193	[1]
	1	0.934	0.00869	1.37	0.487	-1.155	0.098	[1]
C	2	0.895	0.00526	0.47	0.352	/	0.129	[1]
	3	0.846	0.00088	[1]	0.363	/	0.210	[1]
	4	0.757	0.02639	[0]	0.312	/	0.071	[1]
	Curves not forced through the initial meal size							
	1	0.904	0.01480	0.28	0.235	-0.068	0.104	0.993
P	2	0.904	0.01384	0.24	0.231	/	0.105	-0.9908
	3	0.849	0.00183	[1]	0.243	/	0.129	1.01265
	4	0.888	0.02560	[0]	0.211	/	0.097	0.96839
	1	0.945	0.06681	0.92	0.020	-0.650	0.171	1.01253
H	2	0.935	0.02878	0.37	0.053	/	0.147	0.97025
	3	0.880	0.01455	[1]	-0.041	/	0.060	0.9982
	4	0.888	0.08083	[0]	-0.039	/	0.214	0.91948
	1	0.935	0.00953	1.53	0.492	-1.316	0.097	1.02077
C	2	0.916	0.00484	0.36	0.383	/	0.117	0.93649
	3	0.857	0.00052	[1]	0.412	/	0.219	0.94798
	4	0.878	0.01154	[0]	0.371	/	0.080	0.88869

* P = Prawn, H = Herring, C = Capelin
Model type 1: Free exponent B, meal size included
Model type 2: Free exponent B, meal size not included
Model type 3: Exponential, meal size not included
Model type 4: Linear, Meal size not included

Table 3b: Estimated asymptotic 95%-confidence limits for parameters from fits of the multivariate model

*		R' low.	R' up.	B low.	B up.	C low.	C up.	D low.	D up.	A low.	A up.	E low.	E up.
Curves forced through the initial meal size													
P	1	0.00547	0.02594	0.17	0.52	0.155	0.321	-0.380	0.101	0.087	0.118	[1]	[1]
	2	0.00561	0.02127	0.18	0.36	0.150	0.308	/	/	0.090	0.120	[1]	[1]
	3	0.00018	0.00329	[1]	[1]	0.110	0.377	/	/	0.107	0.155	[1]	[1]
	4	0.01560	0.04779	[0]	[0]	0.124	0.275	/	/	0.080	0.109	[1]	[1]
H	1	0.00452	0.12039	0.71	0.97	-0.121	0.158	-0.720	-0.414	0.144	0.201	[1]	[1]
	2	0.00408	0.05365	0.37	0.49	-0.085	0.180	/	/	0.111	0.163	[1]	[1]
	3	-0.00569	0.03489	[1]	[1]	-0.256	0.175	/	/	0.020	0.100	[1]	[1]
	4	-0.00446	0.20599	[0]	[0]	-0.175	0.143	/	/	0.163	0.223	[1]	[1]
C	1	0.00252	0.01486	1.19	1.55	0.382	0.591	-1.368	-0.942	0.078	0.119	[1]	[1]
	2	0.00189	0.00863	0.40	0.53	0.261	0.444	/	/	0.111	0.147	[1]	[1]
	3	0.00003	0.00172	[1]	[1]	0.219	0.508	/	/	0.188	0.233	[1]	[1]
	4	0.01014	0.04264	[0]	[0]	0.220	0.404	/	/	0.053	0.089	[1]	[1]
Curves forced through the initial meal size													
P	1	0.00510	0.02460	0.04	0.52	0.152	0.318	-0.365	0.230	0.088	0.119	0.975	1.011
	2	0.00558	0.02209	0.13	0.34	0.150	0.311	/	/	0.089	0.120	-1.005	-0.977
	3	0.00024	0.00341	[1]	[1]	0.115	0.372	/	/	0.106	0.153	0.992	1.033
	4	0.01126	0.03994	[0]	[0]	0.129	0.294	/	/	0.081	0.113	0.956	0.981
H	1	0.00474	0.12888	0.74	1.10	-0.120	0.159	-0.845	-0.454	0.143	0.199	0.994	1.031
	2	0.00341	0.05415	0.30	0.43	-0.082	0.188	/	/	0.120	0.174	0.958	0.983
	3	-0.00580	0.03489	[1]	[1]	-0.257	0.176	/	/	0.020	0.100	0.978	1.019
	4	-0.01011	0.17177	[0]	[0]	-0.209	0.132	/	/	0.181	0.246	0.906	0.933
C	1	0.00259	0.01646	1.26	1.81	0.386	0.598	-1.613	-1.019	0.077	0.118	0.993	1.049
	2	0.00172	0.00796	0.29	0.42	0.291	0.475	/	/	0.099	0.135	0.923	0.950
	3	-0.00005	0.00109	[1]	[1]	0.250	0.574	/	/	0.194	0.245	0.927	0.969
	4	0.00376	0.01933	[0]	[0]	0.272	0.470	/	/	0.061	0.099	0.875	0.902

* P = Prawn, H = Herring, C = Capelin
Model type 1: Free exponent B, meal size included
Model type 2: Free exponent B, meal size not included
Model type 3: Exponential, meal size not included
Model type 4: Linear, Meal size not included

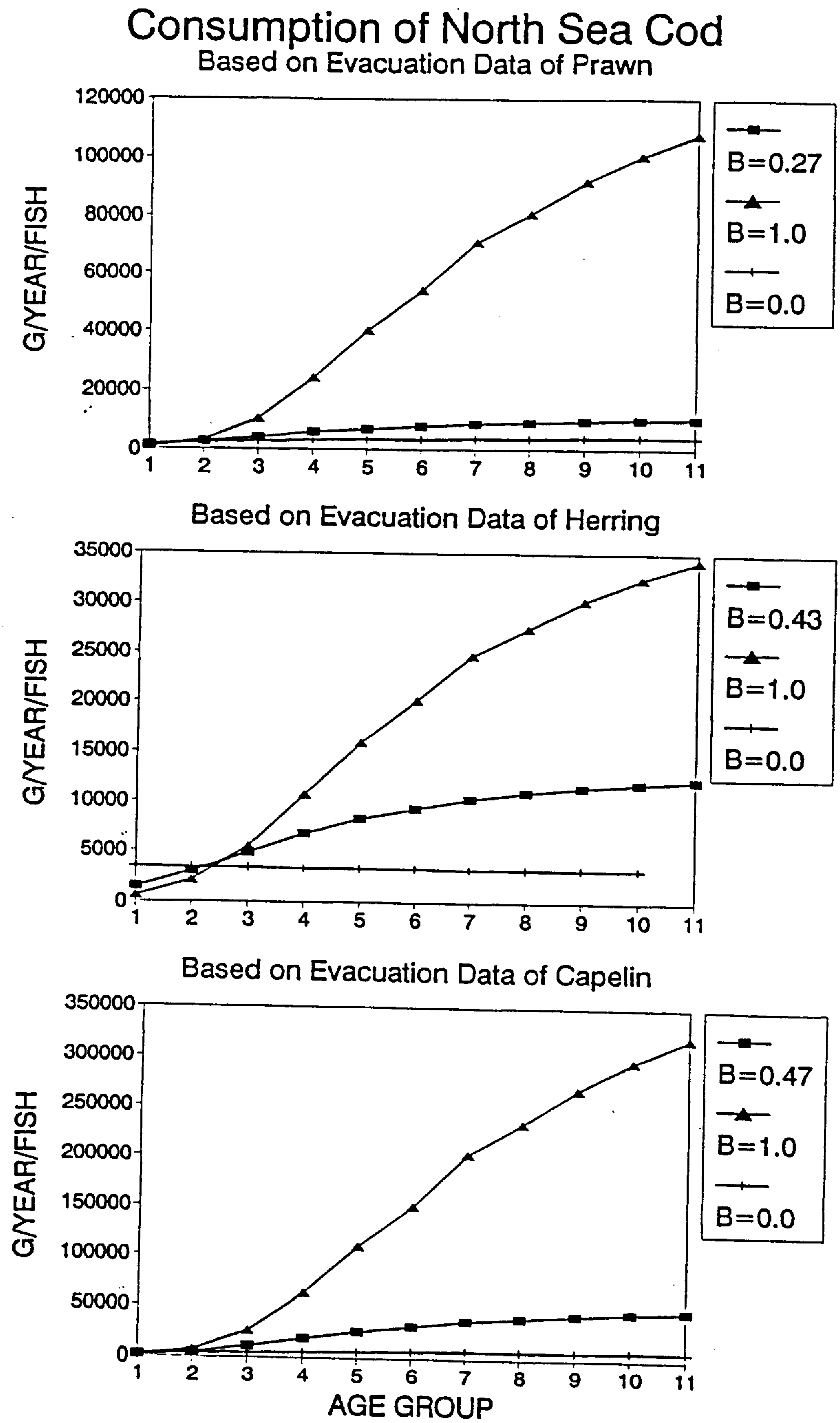

Fig. 1: Consumption of North Sea Cod by age group. Calculations are based on different model types, which were fitted to the same set of experimental data from dos Santos.

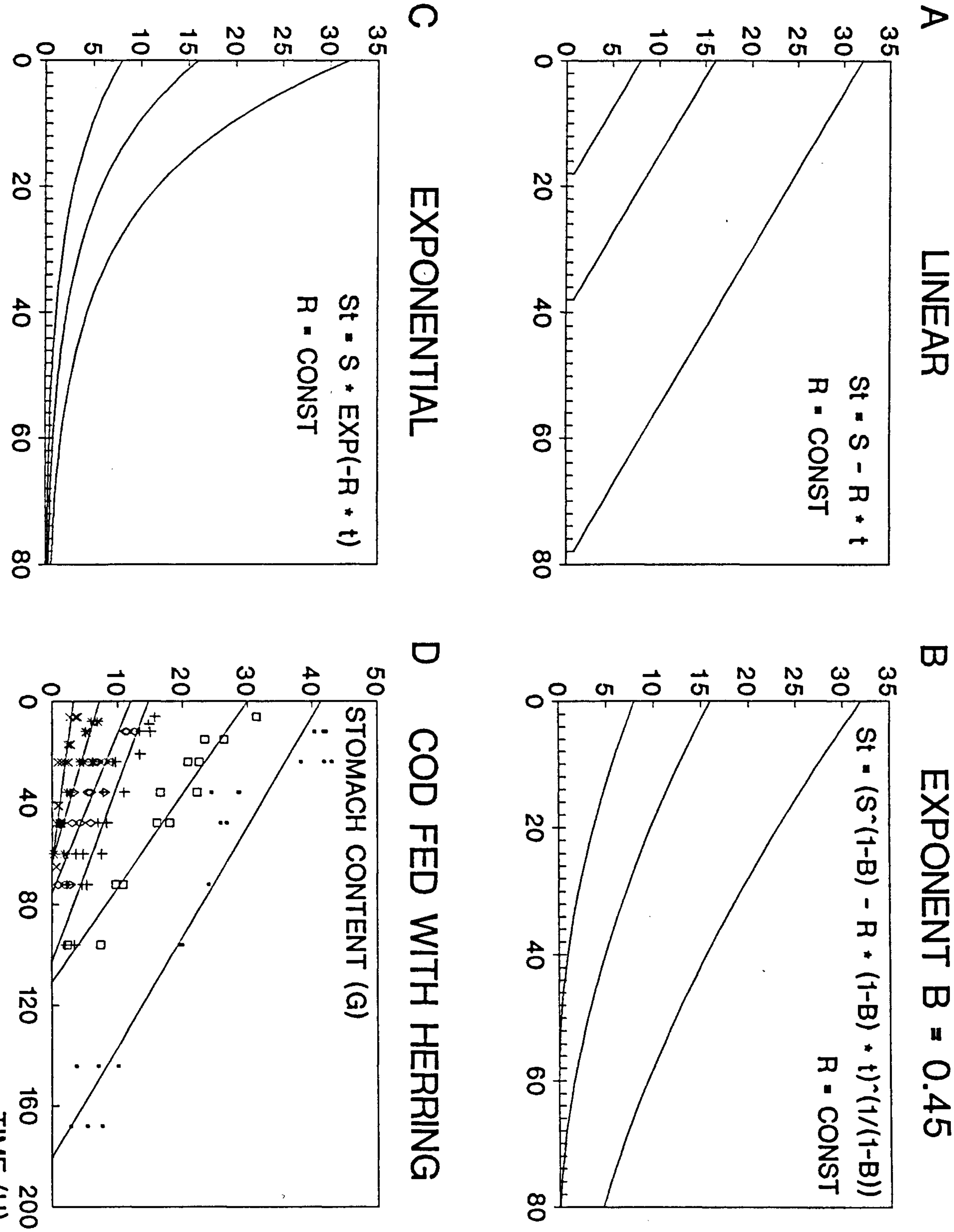

Fig. 2: The effect of variable meal size on gastric evacuation of Herring (D). Data from experiments nrs. 34, 39, 41, 42, 44 and 47 with similar predator size and temperature, but variable meal size (4g - 48g). Linear trends were fitted to the data to visualize changes in overall slope. Figures (A) - (C) display the effect of changing meal size for exponential, linear and 'general' evacuation model, when parameter R is kept constant.