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ESTIMATING INITIAL STOMACH CONTENT USING STOCHASTIC SIMULATION

by

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ABSTRACT

The stomach evacuation model now in use when quantifying the predation from cod on Barents Sea capelin assumes that the evacuation rate is dependent on the stomach fullness after the last meal, which is not known in the field. The paper seeks to overcome this problem by fitting a simple feeding model for cod to the distribution of stomach contents from field data of individual cod stomachs.

Introduction

The management of the fish species in the Barents Sea is highly inadequate if not species interactions are taken into account. One of the most important of the species interactions in the Barents Sea ecosystem is the predation by cod on capelin. A quantification of this predation has become part of the assessment of the capelin stock (Anon, 1994) and constitutes one of the few elements of multispecies assessment in use in practical management today. Also, the quantification of the consumption of capelin by the cod is a cornerstone in multispecies modeling (Tjelmeland and Bogstad, 1993), (Ulltang, 1994) as well as works aiming at giving general overviews of the ecosystem dynamics (Bogstad and Mehl, 1992), (Mehl, 1989).

The building blocks for the quantification of the cod stock's consumption on capelin are 1) an assessment of the size of the part of the cod stock that preys on capelin, 2) an assessment of the overlap in time and area between the species, 3) an assessment of the stomach fullness, 4) the joint PINRO-IMR stomach content data base and 5) an evacuation rate model. Each of these elements have associated uncertainties, an attempt to quantify which was made at the 1992 meeting of the Atlanto-scandian Herring and Capelin Working Group (Anon, 1993). However, in the present paper only one particular aspect of using the evacuation rate model will be dealt with.

The evacuation rate model is developed at the University of Tromsø (dos Santos and Jobling, 1992) and used in a number of works dealing with the consumption by cod on various of it's prey species in the Barents Sea. The mathematical formulation is given by the following expression, cast into a form slightly different from the original by Bogstad and Mehl (Bogstad and Mehl, 1992):

$$S_t = S_0 e^{-ln2 \frac{t}{He^{-cT}\left(\frac{S_0}{W}\right)^b}} \tag{1}$$

where S_t is the stomach content at time t (hours). c is a constant describing the temperature (T, °C) dependence and b is a constant describing the dependence on the initial meal size. S_0 is the stomach content immediately after the last meal (initial meal size). H is the time for a meal of the same size as the body-size W to be digested to half it's initial size at T=0 °C.

The parameters are estimated by feeding laboratory fish with known amounts of food and measuring the stomach content after some time of digestion. The initial stomach content is known in the experiment. However, for fish caught in the field, the amount of food in the stomach immediately after the last meal is not known. Thus, there is a fundamental uncertainty connected to using this formula on field data.

In practical use, the mean stomach content in an area and during a period has been used in the formula, and the initial stomach content has been set to a scaling factor multiplied with the mean stomach content. A high scaling factor corresponds to a feeding situation in which the cod eats large meals seldomly. A low scaling factor applies in a situation in which the cod feeds small meals with short intervals. The limiting value of 1.0 applies when the cod feeds continuously. It has been customary to use the value 2.0. The scaling factor will in this paper be referred to as "initial stomach content ratio".

The purpose of this paper is to give some indication of which values to use in different feeding situations by fitting a general feeding model to field data. Even if the purpose of the paper is to shed some light upon the value of the initial stomach content ratio, the method of the paper is applicable in all situations where the consumption is not readily calculated from the data, i.e when not a constant evacuation model or an exponential evacuation model with a fixed time constant is assumed.

A feeding model for cod

The basic idea is that the distribution of stomach content reflects the feeding situation of the cod. Thus, the shape of the stomach content distribution gives some information about the feeding situation in addition to the mean content. The purpose of the paper is to utilize this information. This paper is to a large extent inspired by recent Icelandic work (Magnusson, 1992) with a feeding model for cod. Magnusson found the Santos evacuation model to be incompatible with the data. In the present work, the Santos model is found compatible with data, probably because the simulation approach enables a more flexible feeding model than the one used by Magnussons analytical work.

The consumption is viewed as a stochastic process. The field situation of sampling a large number of fish at one instant (which is equivalent to assuming stationary conditions when the real sampling take an extended period of time) is equivalent to sampling one fish many times at random throughout a long period. Thus, in the model fish feed at irregular intervals in time, the size of the meal and the time between meals being stochastic variables. Between each meal the fish evacuates according to formula 1. The stomach content is recorded at stochastic intervals and the consumption is calculated in the same way as when using field data. In this experiment the number of samples is great enough to neglect uncertainty in the consumption estimated from the model data.

It is unrealistic that this simple feeding model should apply in extreme situations. For cod having stomachs of very high content, one might expect the probability of another meal to be lower than the average, if for no other reason it might not be possible to stuff another prey item into an already stretched stomach. In situations of almost emptied stomachs the exponential evacuation rate model is both contradictory to observation and physiological unreasonable. It might be tempting to introduce a new parameter, a value of the stomach content below which the evacuation is linear. However, in the present use of the model empty stomachs are counted. Thus, there is no need to distinguish between empty and nearly-empty stomachs. Stefansson and Palsson (Stefansson and Palsson, 1993) discusses the problems connected to empty stomachs using a parametric approach.

Description of the model

In each unit of time there is a probability p that the cod will have a meal. The distribution of intervals between meals is then exponential with an expectation value of $t = 1/p$, which will be an independent parameter in the model. The size of the meal for the smallest fish in the model is uniformly distributed between m1 and m2, where the latter parameter is transformed to the average consumption rate c for all fish in the model, and the meal size is assumed proportional to body size. The independent parameters in the model are then c, t and m1. The reason for choosing two parameters for the meal size is for the model to comply with the situation that the cod feeds more or less exclusively on capelin. When the cod feeds also on smaller organisms (amphipods), the m1 would be expected to be close to zero.

In practice, in order to obtain a stomach content distribution fish must be sampled within a size interval. To simulate this in the model, the model is run with fish of 1500 g and one fish of 2500 g. The data are recorded between 1000 and 3000 g. The number of fish of 1500 g is calculated from the data assuming that the amount of fish in each size group changes linearly between 1000 g and 3000 g.

A wide size interval gives more fish in the distributions, and thereby more precise estimates. However, then also the body size varies more strongly within the data and this variation needs to be accounted for in the model, giving rise to additional uncertainty. If the method in this paper should be used to estimate consumption of fish, some tradeoff must be found by experimenting with the model.

Sensitivity to model errors

The model described in the previous section will be referred to as the main model.

To investigate how robust the results are to the particular model chosen, also runs using a uniform distribution of feeding intervals and runs where the meal size is independent of the fish body size are performed. Using a simulation approach, the confidence in the consumption rate estimates is related to the confidence in the feeding model applied. There will always be considerable uncertainty as to the appropriate formulation of meal size distribution and feeding interval distribution. In order to quantify how this uncertainty is reflected in the consumption rate estimates, one might try a great number of models, parameterizing each using the data and regard the variance in the consumption rate estimates obtained as a measure of the uncertainty in our knowledge of the consumption rate. The two different alternatives to the main model tried in this paper should be regarded as just an attempt to start such a process.

Feeding interval model

In a uniform feeding interval model there will be fewer very short feeding intervals than in the exponential model. Also, there will be no very long intervals. The uniform feeding interval is not very attractive in terms of biological interpretation, and is chosen simply to have a model that is quite different from the exponential model.

Meal size model

To test the robustness of the model against the assumption that the meal size is in proportion to the body size, also runs where the meal size is independent of body size have been performed. This seems highly unrealistic and the reason for choosing this model is again to test against a model that is quite different from main model.

Estimates of model parameters using real data

The model is fit to data by comparing histograms of stomach content frequencies sampled in 10 g intervals to the corresponding histograms from the data. The multinomial maximum likelihood estimator appropriate for histogram fitting is (Eadie et. al. 1971):

$$ln(L) = \sum Y_i ln(f_i(\underline{\theta}))$$

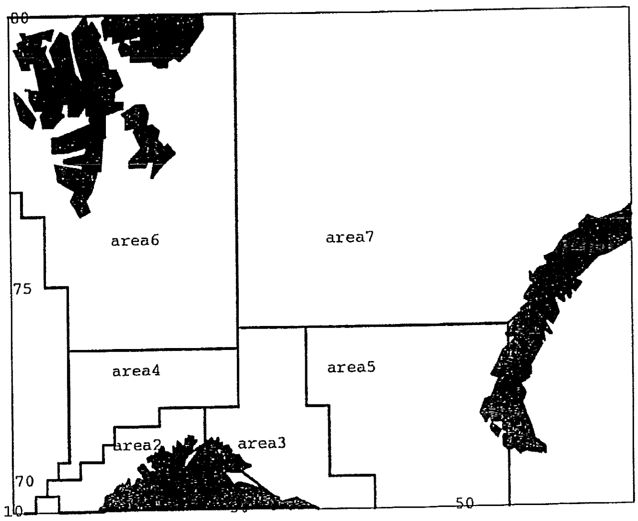
where Y_i is the number of observation in stomach content interval i, f_i is the normalized simulated frequency and θ is the parameter vector.

f_i is the probability of observing a stomach content in stomach content interval i and is calculated from the histogram obtained from the model data. There is no analytic dependence of f_i on the model parameters, rather the functional dependence of the probabilities on the model parameters is found by simulation.

The data used consist of stomach samples from individual cod obtained during January, February and March in the years 1984 to 1992. The stomach data are collected in a joint project between IMR and the Russian research institute PINRO in Murmansk. To get a variety of different feeding situations, the data have been selected from the areas shown in figure 1 separately. This area division is also underlying the multispecies modeling at IMR.

It is assumed that the cod feeds exclusively on capelin.

Figure 1 Area division

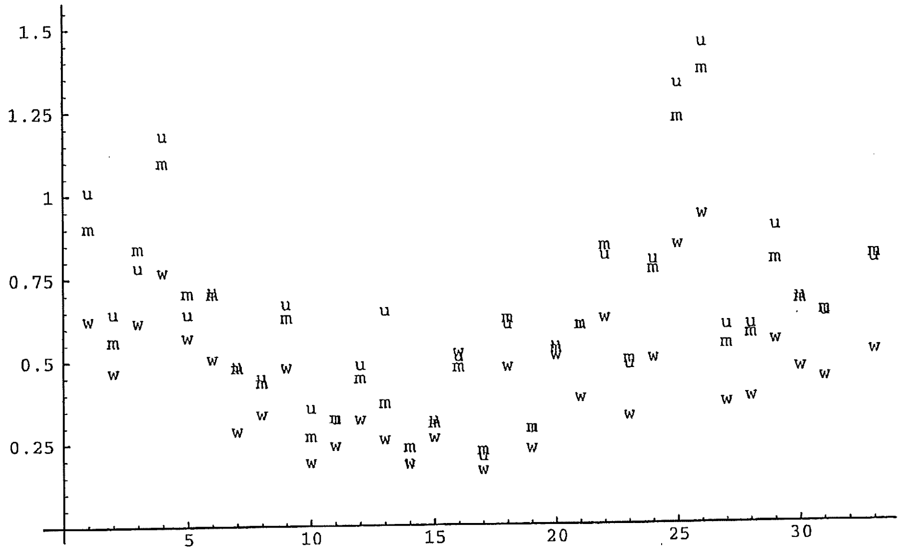


Results

Table 3 gives the estimated model parameters. In those cases where the distribution from the data is wider than 100 g, the contribution from the tail has been taken from the model results. Figure 7 — 9 in the appendix shows the distribution on stomach content along with the model fit for the various data sets. In the majority of cases there seems to be a good fit.

Figure 2 shows the resulting modeled consumption for all 3 models. On the horizontal axis is the experiment number referred to in table 3.

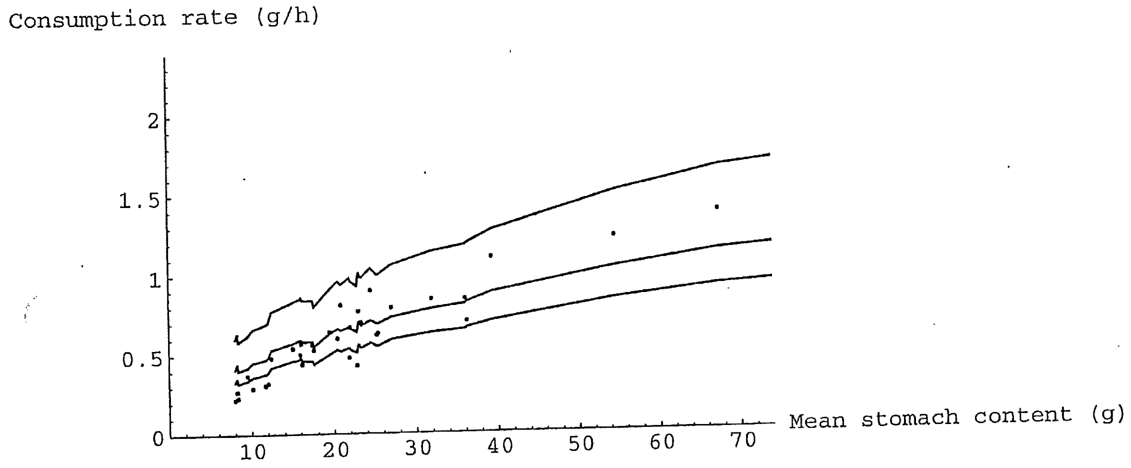
Figure 2 Estimated consumption rate. m: main model, u: uniform feeding interval, w: meal size independent on body size



The consumption rate estimates for the main model and the model using uniform feeding interval follow each other closely in nearly all cases. In case 13, 1988 area 2, the latter model yielded a much higher estimate of the consumption rate, but in this case the model fit to the data was not good. Invariably, the model using meal size independent of body size yields lower consumption rate estimates even if the model fit to the data generally is good.

Using the main model, figure 3 shows the estimated consumption rate as function of model mean stomach content together with the consumption rate calculated from the mean stomach content using a value of the initial stomach ratio of 1.0, 2.0 and 3.0. Each series of points corresponds to a set of the model parameter estimates shown in table 3.

Figure 3 Consumption as function of mean stomach content from the simulation (points) and calculated using an initial stomach content ratio of 1.0 (upper line), 2.0 (middle line) and 3.0 (lower line). Main model.



The humps in the consumption calculated using initial stomach content ratios of 1.0, 2.0 and 3.0 stem from the body size distribution varying from case to case.

For low stomach content, the estimated consumption is below the value calculated using an initial stomach content ration of 2.0, for high stomach content it is higher.

Figure 4 shows the value of the initial stomach content ratio that must be used in each case in order to calculate the true consumption. For cases of low stomach content the appropriate initial stomach content is much higher than the customary value of 2.0 and for high stomach content it is between 1.0 and 2.0. In the majority of cases, however, the values cluster around 2.0.

Figure 5 shows the ratio of consumption calculated using mean stomach content to the consumption calculated using individual stomachs, for an initial stomach content ratio of 2.0.

Figure 4 Estimated initial stomach content ratio

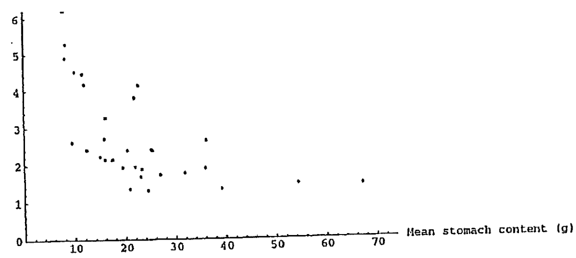
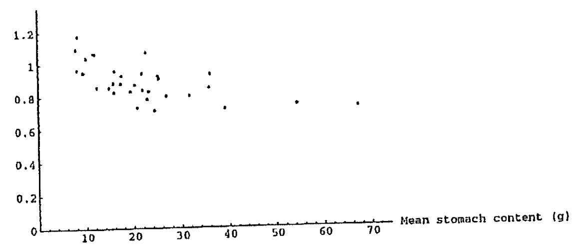


Figure 5 Ratio of consumption calculated using mean stomach content and consumption calculated using individual stomachs



The dependence of the initial stomach content ratio on the mean stomach content will lead to an overestimation of the consumption rate in case of low stomach content and an underestimation in the case of high stomach content. It is tempting to try find a more robust "rule of the thumb" by calculating the consumption rate directly from measured variables by regressing and where this bias is removed.

In a series of regressions, the true consumption was used as response variable with various combinations of independent variables. Three different regression formulas were tried:

Relation 1 $$Consumption\ rate = A \times var1^{B \times var2}$$

Relation 2 $$Consumption\ rate = A \times var1^{B} e^{C \times var2}$$

Relation 3 $$Consumption\ rate = A \times var1^{B} \times var2^{C}$$

The independent variables used are:

Mean content	Mean content calculated over all stomach content groups
Time	Average feeding interval used in the model (not observable)
Median	Median content calculated over all stomach content groups
First	The relative amount of stomachs in the first (0-10g) stomach content group, including empty stomachs
Variance	Variance of the stomach content

All independent variables are taken from the model results. With the exception of time, which is not directly observable, the modeled values should not deviate much from the measured values if the fit to the data is good.

Only the cases where the total number of stomachs in the distribution exceeds 30 are used. The results are shown in table 1. By "variance reduction" is meant the variance of the residuals divided by the variance in the data.

Table 1 Consumpion regressions

Var1	Var2	Formula type	Variance reduction standard model	Variance reduction uniform feeding interval model	Variance reduction meal size independent on body size
Mean content	Time	1	0.754	0.760	0.822
		2	0.026	0.021	0.012
		3	0.022	0.021	0.012
	First	1	0.119	0.141	0.143
		2	0.035	0.042	0.014
		3	0.086	0.105	0.096
	Variance	1	0.579	0.534	0.708
First	Time	1	0.837	0.936	0.709
		2	0.062	0.064	0.084
		3	0.084	0.100	0.119
	Mean content	1	0.496	0.470	0.584
		2	0.101	0.130	0.140
		3	0.086	0.122	0.096
Median	Time	1	0.921	0.957	0.782
		2	0.050	0.050	0.010
		3	0.049	0.050	0.010
	First	1	1.000	1.062	0.968
		2	0.052	0.053	0.013
		3	0.048	0.056	0.020
	Variance	1	0.625	0.563	0.744
Mean	Mean-median	1	0.528	0.534	0.497
		2	0.057	0.069	0.037
		3	0.074	0.097	0.058
Mean		1	0.122	0.150	0.108
Median		1	0.055	0.055	0.019
Variance		1	0.399	0.464	0.343
First		1	0.105	0.134	0.143

The best fit is obtained using mean stomach content and the estimated average feeding interval as independent variables. However, the latter is not a directly observable entity. From the regressions using only observable quantities, regressions using formula 2 with mean stomach content and the relative number of stomachs in the first group as independent variables gives the best fit for all three models. A further analysis of this regression is shown in table 2.

On the diagonal is the standard deviation of the residuals. Off-diagonal are the standard deviations of the difference between the modeled results using the estimated parameters (assumed model) and the modeled results using the parameters estimated by each of the other two models (true model). The diagonal elements reflects the data error for each model, while the off-diagonal elements reflect the model error.

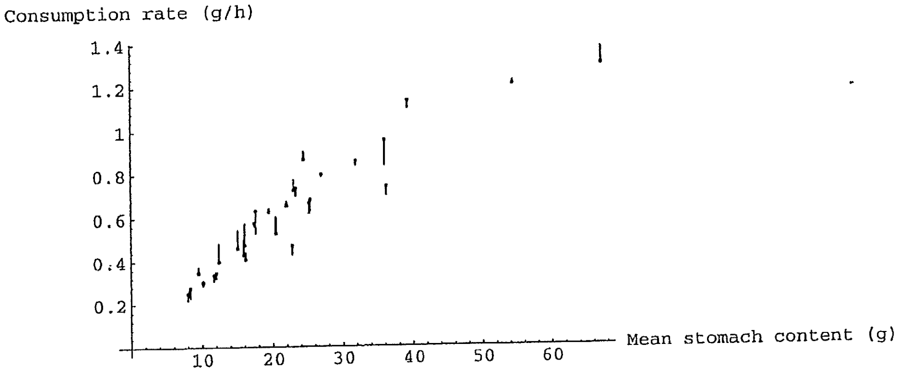
Table 2 Inter-model standard deviations

		True model		
Assumed model		Main	Uniform feeding interval	Size independent meal
	Main	0.053	0.013	0.095
	Uniform feeding interval	0.015	0.062	0.115
	Size independent meal	0.103	0.118	0.023

The model using size independent meal size yields the lowest variance of residuals. However, assuming this model to be true yields standard deviations higher than 0.1 if either of the two other models are true. If the main model is assumed true, the standard error of the model deviations is lower than 0.1 for either of the two other models. If the highly unrealistic size independent meal model is ruled out, we see that model error is smaller than the data error.

Figure 6 shows the consumption rate estimated using the main model together with the values calculated from the above regression. The points are the model results, the bars show the distance to the estimated consumption rate.

Figure 6 Consumption rates from the main model



The maximum deviation is about 0.1 g/h, which is considerably lower than the uncertainty connected to using a fixed value of the initial stomach content ratio.

Discussion

In the calculation of consumption rates from field data there is a fundamental uncertainty connected to the appropriate value to use for the initial stomach content in models that assumes that the digestion rate is dependent on this variable. The present paper seeks to overcome this difficulty by fitting a stochastic simulation model to a histogram of the stomach content distribution of field data and take the consumption rate from the model. This procedure would yield good estimates of the consumption rate provided all reasonable models when fitted to the data would give more or less the same consumption rate estimate. The paper shows that this is the case for two different models for the average feeding interval. Thus, the suggested method looks promising and a wider variety of models should be tried.

The consumption rate estimates calculated from a given model that is fit to a data set is shown to have a different dependence on mean stomach content than one gets by using a fixed initial stomach content ratio. When regressing the model consumption rates to a simple regression model where the mean stomach content and the relative number of stomachs of very small (or zero) stomach content are independent variables, a very good predictor is found.

Thus, there might be some hope that extensive simulation and testing would yield a stochastic feeding model and a formula where the consumption rate could be calculated from easily observable quantities.

When using this approach in assessing consumption rates, the model should also be augmented to allow for feeding on different food objects. Also, a new model for the evacuation rate will appear shortly, in which the dependence of the evacuation rate on the initial stomach content and on the body weight will be decoupled from each other (dos Santos and Jobling, pers. comm.).

Appendix

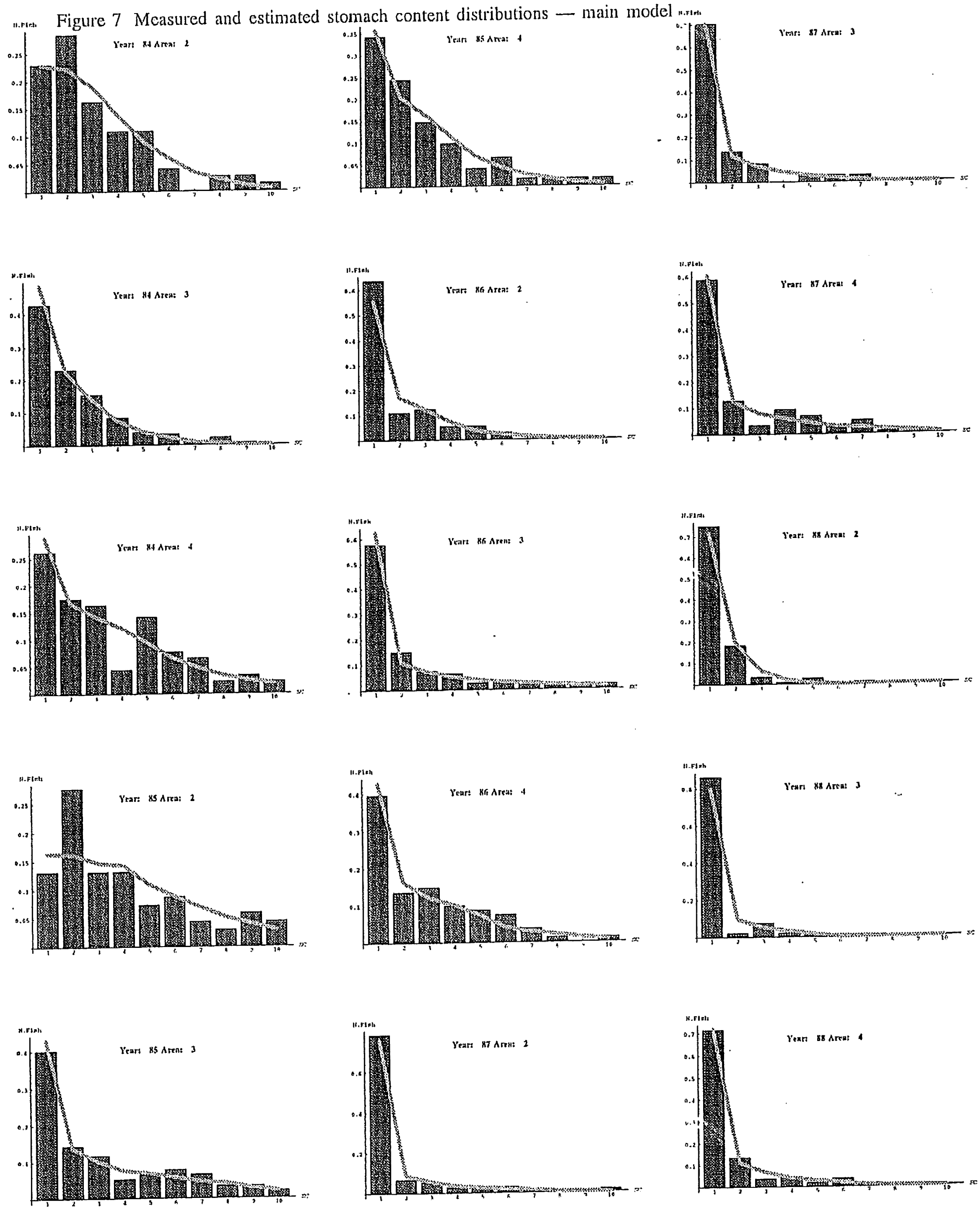
Table 3 Parameter estimates

			Main model			Uniform feeding interval			Meal size independent of body size			
Year	Area	Exp. no	c	m1	t	c	m1	t	c	m1	t	N
84	2	1	0.90	6	27	1.01	7	30	0.62	3	24	74
	3	2	0.56	13	52	0.64	1	29	0.47	10	49	183
	4	3	0.84	30	62	0.78	41	62	0.62	30	73	92
85	2	4	1.10	6	33	1.18	5	31	0.77	5	33	69
	3	5	0.70	42	129	0.64	51	125	0.57	9	107	155
	4	6	0.70	29	54	0.71	3	75	0.50	15	50	123
86	2	7	0.48	24	84	0.48	7	75	0.29	29	102	74
	3	8	0.43	13	184	0.45	29	225	0.34	15	180	382
	4	9	0.63	39	85	0.67	5	62	0.48	14	67	81
87	2	10	0.27	11	219	0.35	2	143	0.19	4	236	77
	3	11	0.32	9	140	0.32	12	145	0.24	10	121	37
	4	12	0.44	5	128	0.48	3	93	0.32	40	139	119
88	2	13	0.37	8	49	0.65	5	18	0.26	16	67	159
	3	14	0.23	7	156	0.19	22	226	0.18	4	162	149
	4	15	0.31	11	154	0.32	3	133	0.26	0	107	164
	6	16	0.48	14	218	0.51	57	199	0.52	5	396	17
89	2	17	0.22	0	243	0.20	0	283	0.16	2	258	127
	3	18	0.62	21	81	0.61	9	74	0.48	11	78	311
	4	19	0.29	5	155	0.29	5	194	0.23	2	125	372
	6	20	0.53	8	38	0.54	7	30	0.51	18	36	48
90	2	21	0.60	26	104	0.60	9	72	0.38	28	118	231
	3	22	0.84	6	51	0.81	11	60	0.62	10	62	329
	4	23	0.50	8	103	0.48	11	159	0.33	0	106	130
	6	24	0.77	26	52	0.80	1	34	0.50	12	52	83
91	2	25	1.22	15	54	1.32	13	56	0.84	2	46	610
	3	26	1.37	5	55	1.45	5	54	0.93	8	65	218
	4	27	0.54	14	73	0.60	2	41	0.37	8	57	91
	6	28	0.57	9	70	0.60	3	50	0.38	3	49	57

Table 3 (Continued) Parameter estimates

92	2	29	0.79	11	49	0.89	8	43	0.55	17	60	96
	3	30	0.67	11	56	0.68	0	60	0.47	11	59	168
	4	31	0.64	18	54	0.63	6	46	0.44	1	43	77
	5	32	1.58	17	82	7.60	182	436	5.42	76	371	15
	6	33	0.81	11	24	0.79	6	20	0.52	11	31	17

Figure 7 Measured and estimated stomach content distributions — main model



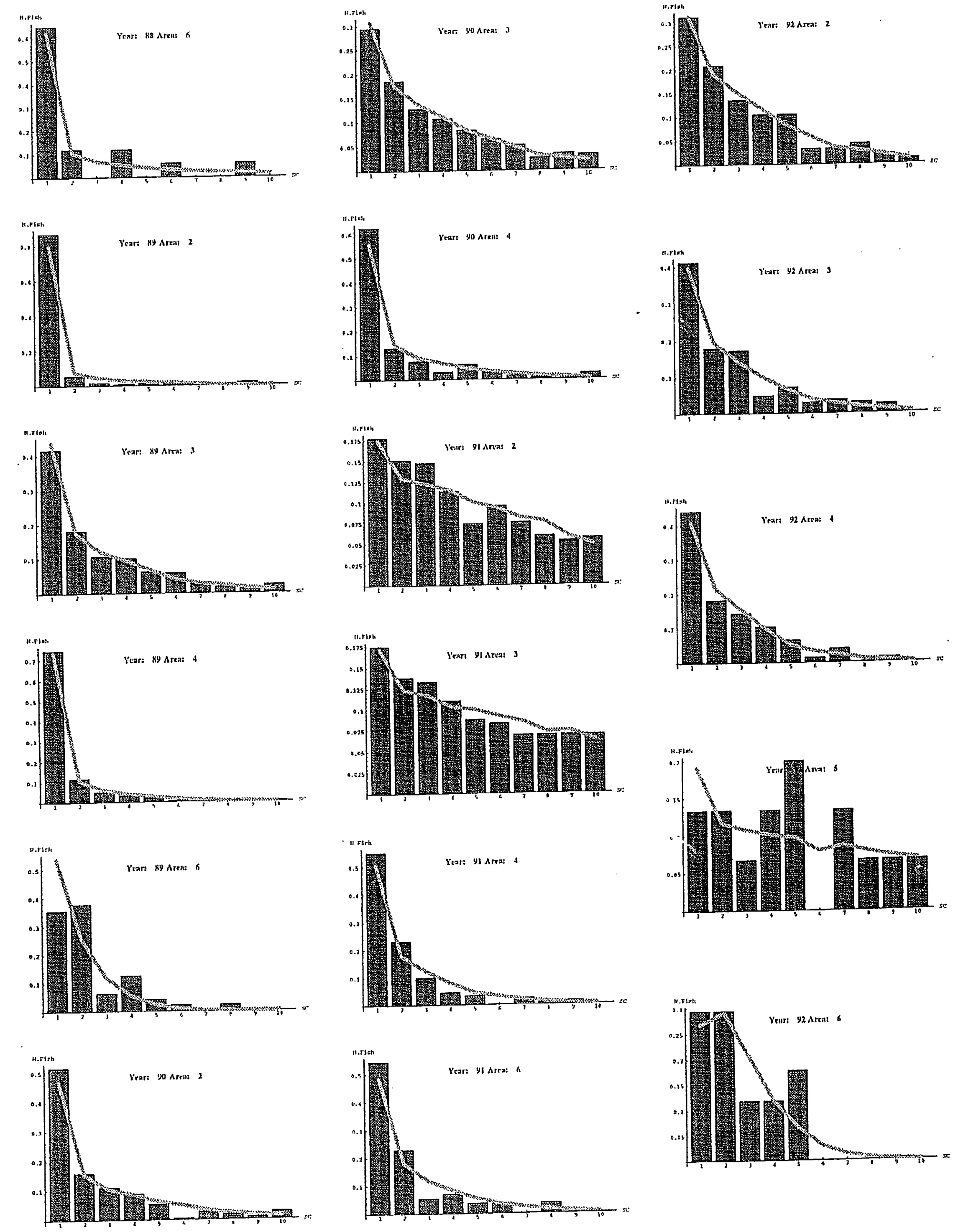

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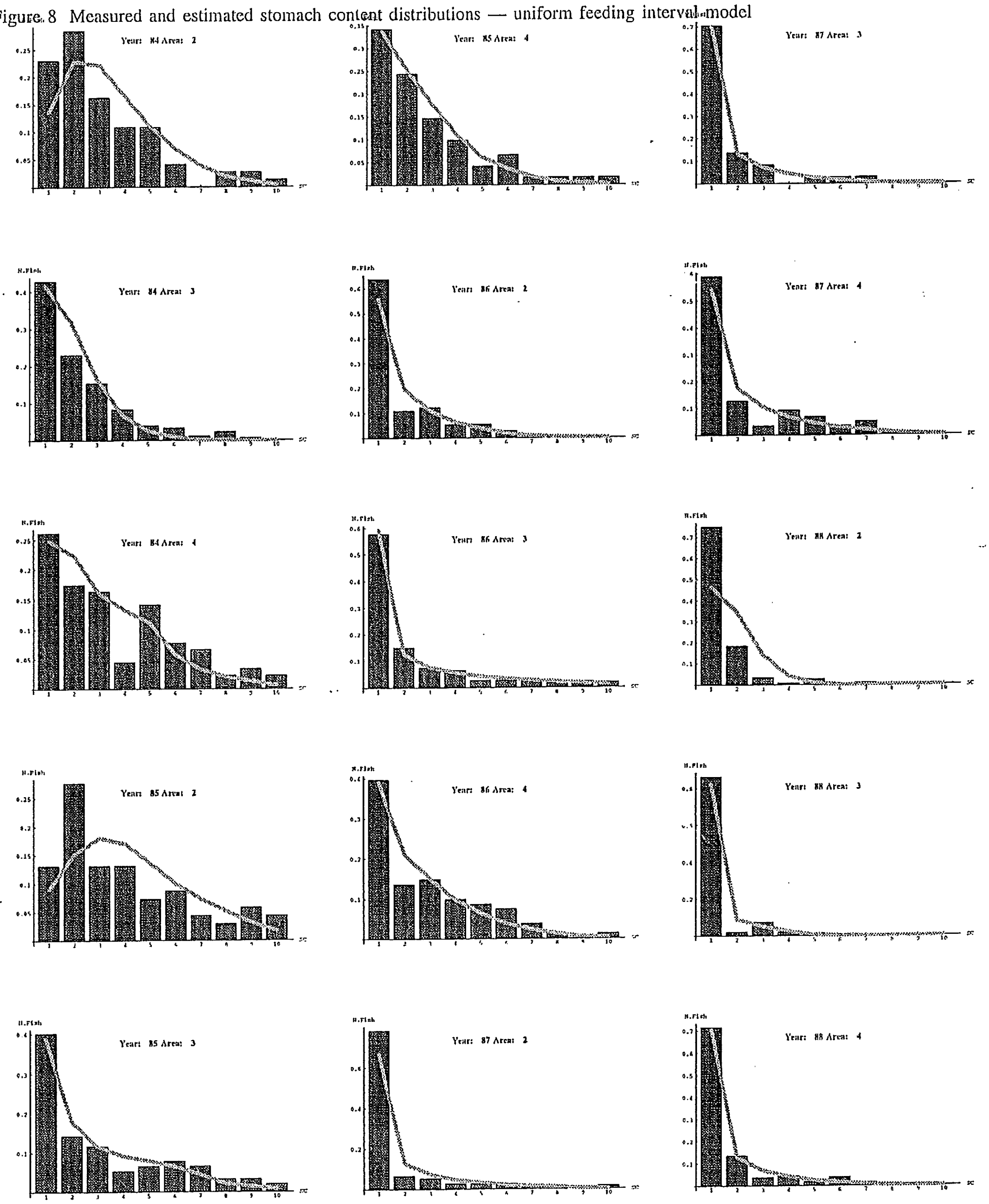
Figure 8 Measured and estimated stomach content distributions — uniform feeding interval model



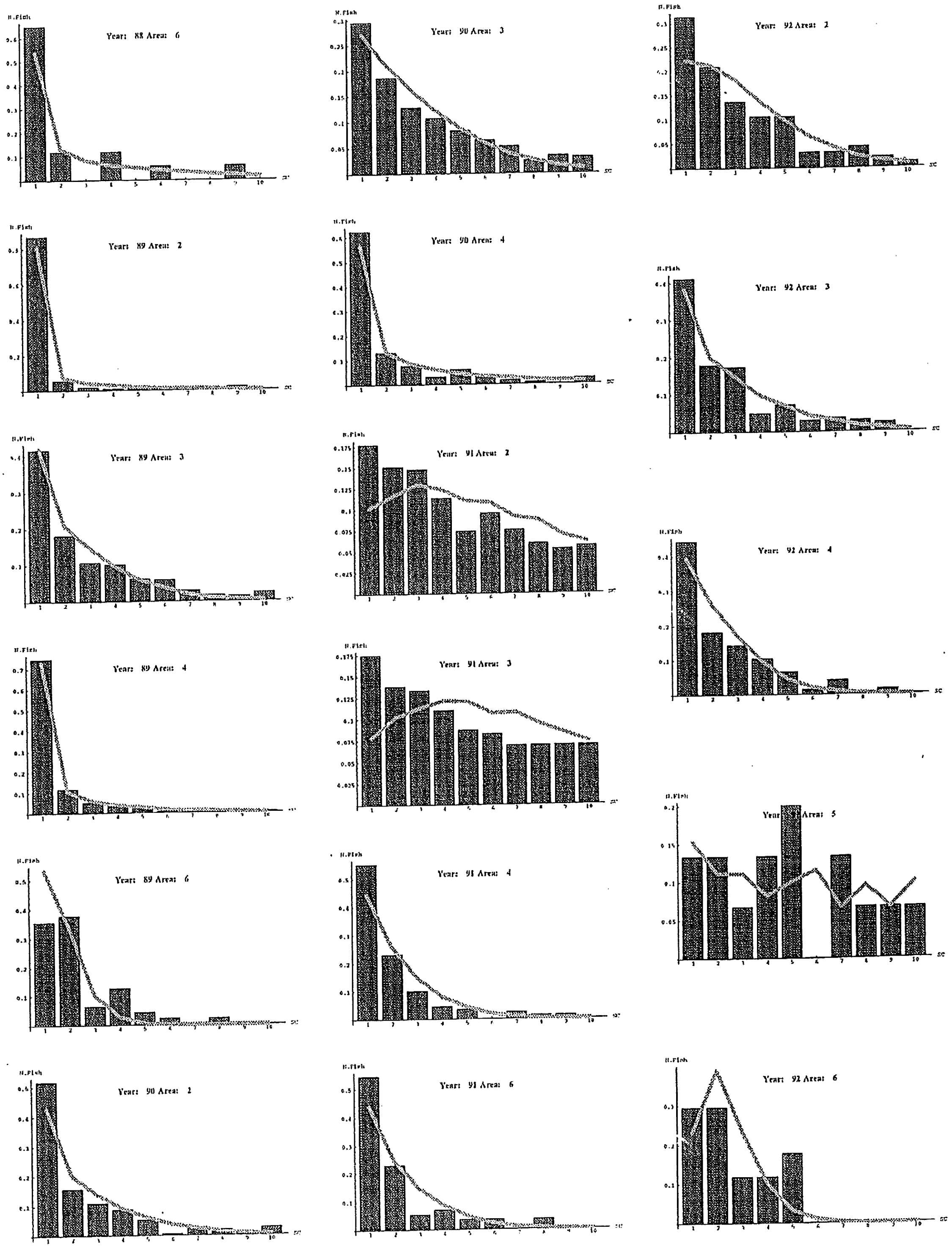

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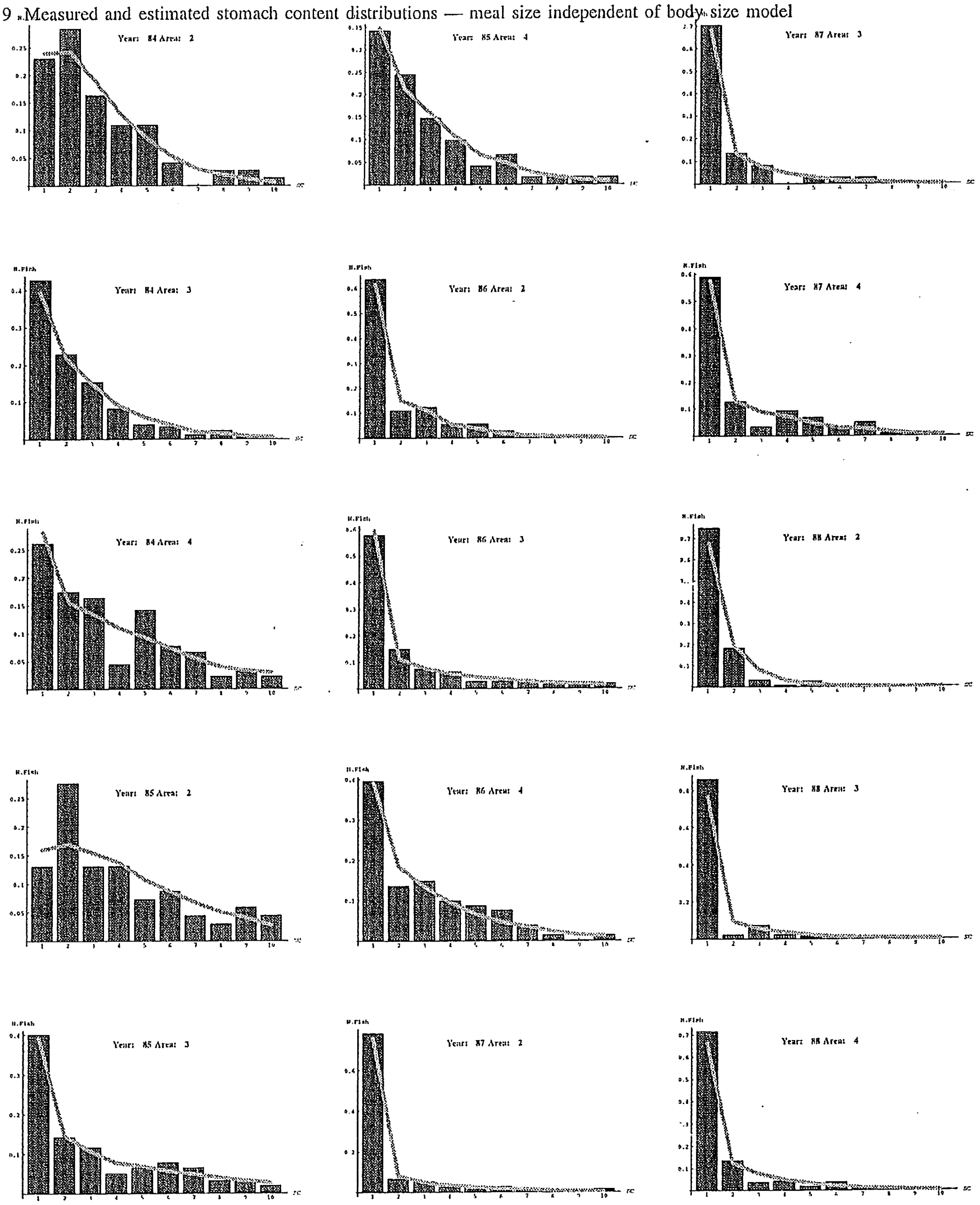
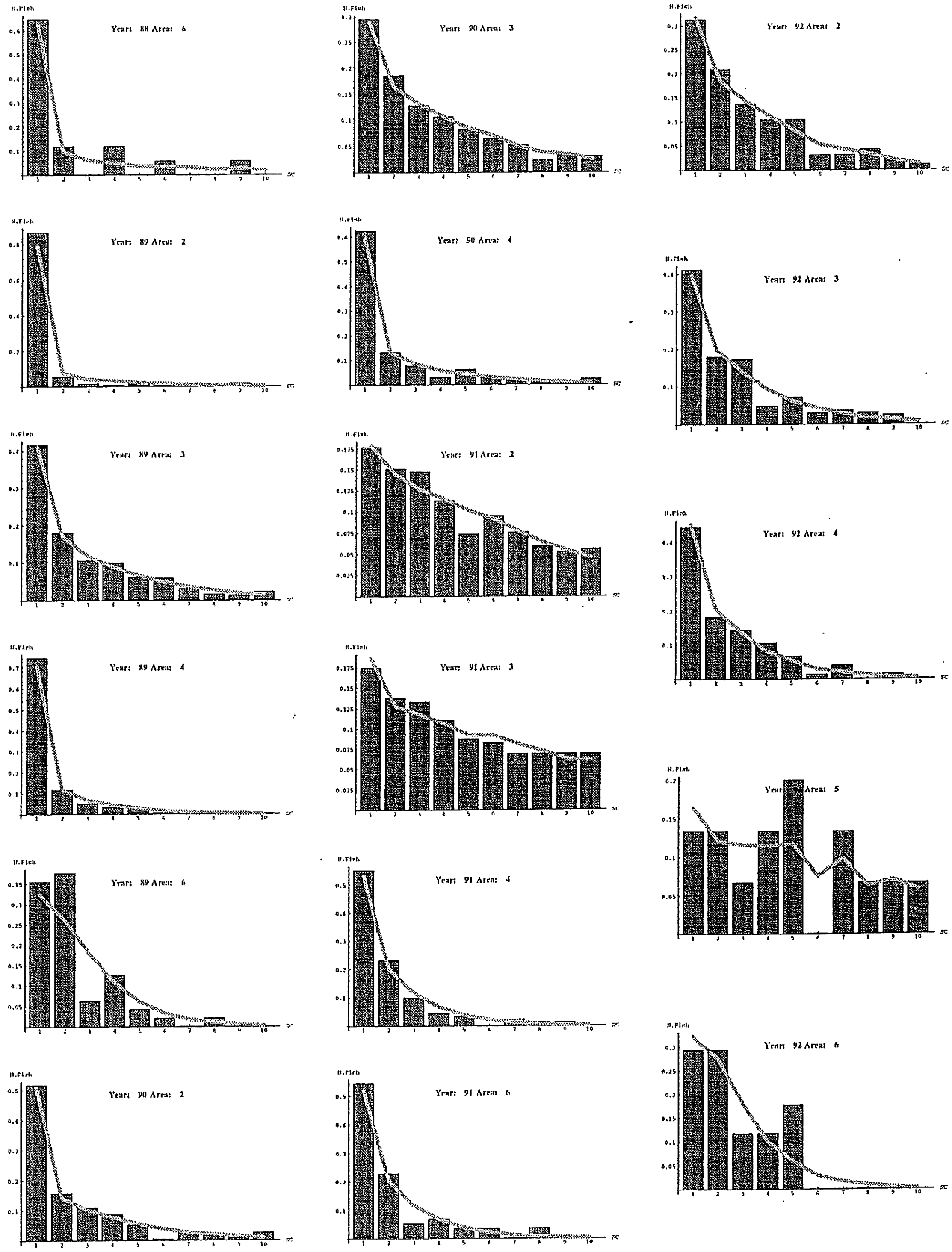
Figure 9. Measured and estimated stomach content distributions — meal size independent of body size model

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Bibliography

Anon . 1993. Report of the Atlanto-Scandian Herring and Capelin Working Group. *ICES C.M.1993/Assess:6.*

Anon . 1994. Report of the Atlanto-Scandian Herring and Capelin Working Group. *ICES C.M.1994/Assess:8.*

Bogstad B. and Mehl S. 1992. The North-East arctic cod stock's consumption of various prey species 1984-1989. *Pp. 59-72 in Bogstad, B. and Tjelmeland, S. (eds.). Interrelations between fish species in the Barents Sea. Proceedings of the fifth PINRO-IMR symposium, Murmansk 12 - 16 August 1991.*

Santos dos J. and Jobling M. 1992. A model to describe gastric evacuation in cod, Gadus morhua, fed natural prey. *ICES Journal. mar. Sci. 49, 145-154.*

Eadie W.T. James F.E. Roos M., Drijard D. and Sadoulet B. *Statistical methods in experimental physics.* North-Holland Publishing Company, Amsterdam, first edition, 1971.

Magnusson K. 1992. A model of predation. *Science Institute, University of Iceland,RH-16-92.*

Mehl S. 1989. The North-East Arctic cod stock's consumption of commercially exploited prey species in 1984-1986. *Rapp. P-v. Reun. Cons. int. Explor. Mer, 188: 185-205.*

Stefansson G. and Palsson O.K. 1993. Statistical analyses of stomach content data. *ICES 1993/CCC Symposium/No.46.*

Tjelmeland S. and Bogstad B. 1993. The Barents Sea capelin stock collapse: A lesson to learn. *Pp. 127-139 in S.J. Smith, J.J.Hunt and D.Rivard (ed.): Risk Evaluation and Biological Reference Points for Fisheries Management, Halifax 19-22 November 1991. Can. Spec. Publ. Fish. Aquat. Sci. 120.*

Ulltang O. 1994. Multispecies models for the Barents Sea. Basic philosophy and modelling approach. *Unpublished manuscript.*