

Stomach evacuation rates of Atlantic cod (*Gadus morhua*) estimated from stomach contents and growth rates

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Abstract

The weights of stomach contents differ by a factor of at least two between cod stocks with similar patterns of growth. If we assume that food consumption is in proportion to the weight of the stomach contents the estimated evacuation rates must also differ by the same factor. In most, but not in all, stocks the differences can be described as an effect of the size of food items. An alternative assumption is that food consumption is proportional to the square root of the weight of stomach contents. This also brings the estimates of stomach evacuation rates of some stocks into accordance with published estimates based on feeding experiments.

Introduction

At an international gathering in Woods Hole in 1981 Dr Keith Brander, Lowestoft, U.K., pointed out marked differences in the weight of stomach contents of cod in different localities. We have pursued the subject by looking at differences in food particle size and in the percentage of fish in the diet. Our aim was to interpret the differences in terms of growth, food consumption and digestion in order to elucidate the reasons for the differences. Although some progress was made it seems as if our main achievement is to specify some outstanding problems and indicate certain inadequacies of most previous stomach sampling programs.

Theory

Stomach evacuation

Let us express the rate of stomach evacuation as

$$\frac{dS}{dt} = \frac{dR}{dt} - \alpha S^\beta \quad (1)$$

where S is the weight of stomach contents, R is food consumed, β is a constant and α may be expanded as a function of prey type, predator size or other factors.

After a discrete meal the rate of stomach evacuation becomes

$$\frac{dS}{dt} = -\alpha S^\beta. \quad (2)$$

Considering food consumption over a long time or dealing with mean values of stomach contents we put the rate of change of stomach contents to zero and get

$$\frac{dR}{dt} = \alpha S^\beta. \quad (3)$$

Eq. 2 indicates how to estimate α and β from observations on digestion. Eq. 3 suggests how to estimate α and β from field data on mean stomach contents when food consumption is otherwise known (see below) or, alternatively, how to calculate food consumption once α and β are known.

Pennington (1985) showed that the unbiased estimator of food consumption is the mean of the values of S^β (weight of total stomach contents raised to a power) for each individual fish, rather than raising the mean stomach contents to this power. The latter procedure would bias the result except for $\beta = 1$. The importance of this point is illustrated by a simple example. Assume, that we have sampled 2 data sets of 4 fish each, with the following quantities (grams) in the stomachs:

	S_1	S_2	S_3	S_4	\bar{S}	$\bar{S}^{0.5}$	$(\bar{S})^{0.5}$
(1)	16	16	0	0	8	2	2.83
(2)	4	4	4	4	4	2	2

The mean values 8 and 4 indicated by a bar, are the true estimators of food consumption if $\beta = 1$ and we find that fish of group (1) eat twice as much as the others. If $\beta = 0.5$, however, we conclude that they eat the same amount. The estimator is 2 in either case. Taking the square root of the mean we find, erroneously, that (1) eat 41% more than (2). The correct form of eq. 3 therefore is

$$\frac{dR}{dt} = \alpha \bar{S}^\beta. \quad (3a)$$

Growth and food consumption

Growth can be described as a function of food consumption by the expression (Ursin 1979):

$$\frac{dW}{dt} = B \frac{dR}{dt} - AB \frac{dR}{dt} - kW^n \quad (4)$$

where W is body weight, B the fraction assimilated of food consumed and A the fraction of this lost in the processes of feeding and sometimes called 'apparent specific dynamic action'. The last term is the routine metabolism of a fasting fish. We can rewrite eq. 4 as

$$\frac{dW}{dt} = v \frac{dR}{dt} - kW^n; \quad v = (1-A)B. \quad (4a)$$

Food consumption is described as a function of body weight:

$$\frac{dR}{dt} = fhW^m \quad (5)$$

where h is a temperature dependent coefficient and f the satiation, or feeding, level, ranging from 0 (starvation) to 1 (satiation).

The quantity

$$H_m = \nu h \quad (6)$$

and the satiation level by size class for several stocks of cod were estimated by Ursin (1984). Estimates were obtained for two sets of values of the m of eq. 5 and n and k of eq. 4:

	m	n	$k(d^{-1})$	$H_m(d^{-1}g^{1-m})$
(1)	0.58	0.78	0.00548	0.1077
(2)	0.69	0.84	0.01400	0.0803

The first group of values was estimated mainly from growth rates in the sea. The values in the second row were estimated from respiration experiments and indicate an extremely high metabolic rate. Both sets satisfactorily describe the growth of cod, but with different results for f and H_m . Either, or both, may be in error, but it seems impossible at present to discriminate between them. In this paper we use the first group primarily on the suspicion that the cod used in the experiments were excited and therefore had increased metabolic rates.

An estimate of ν (eq. 4a) is required to estimate h from eq. 6. It is assumed that 90% of the energy in the food is assimilated and that 20% of the assimilated food energy is lost in feeding, digestion, etc. This leads to $\nu = (1 - 0.2) 0.9 = 0.72$ and to the estimates of $h = 0.150$ and $h = 0.112$ from parameter set no. 1 and no. 2 respectively. Estimates of satiation levels are given below.

The interpretation of plots of stomach contents against body size

Eliminating the rate of food consumption from eqs 3a and 5 and rearranging gives:

$$\bar{S}^\beta = f \frac{h}{\alpha} W^m \quad (7)$$

A plot of $\ln \bar{S}^\beta$ against $\ln W$ gives a straight line with slope m if f and α are independent of body size. If they are both power functions of W we can write

$$f = f_0 W^{f_1}; \quad \alpha = \alpha_0 W^{\alpha_1}; \quad \bar{S}^\beta = f_0 \frac{h}{\alpha_0} W^{m+f_1-\alpha_1} \quad (8)$$

which lends a different interpretation to the slope. Because values of f by size class of cod are supposed to be known, an alternative procedure is to rearrange the terms in eq. 8 to represent the stomach contents at satiation:

$$\frac{\bar{S}^\beta}{f} = \frac{h}{\alpha_0} W^{m-\alpha_1} \quad (9)$$

This simplifies the interpretation of the log transformed parameters. The intercept is $\ln(h/\alpha_0)$ and the slope is $m - \alpha_1$.

We shall consider the two types of plots:

$$\ln \bar{S}^\beta = \ln f_0 \frac{h}{\alpha_0} + (m + f_1 - \alpha_1) \ln W \quad (8a)$$

and

$$\ln(\bar{S}^\beta/f) = \ln \frac{h}{\alpha_0} + (m - \alpha_1) \ln W. \quad (9a)$$

Comparing data from a wide distribution of Atlantic cod it is necessary to consider h and α_0 as functions of temperature. Assuming an exponential relationship of α_0 to temperature we have

$$\alpha_0 = \alpha_{00} e^{pT} \quad (10)$$

where T is temperature in degrees Celsius. The following estimates of the coefficient p are available:

Tyler 1970 (cod, 2-10°C)	0.132
Bagge 1981, quoting Hodal 1977 (cod, 5-15°C)	0.073
Jones 1974 (cod, whiting, haddock, 6-12°C)	0.081
Kjørboe 1978 (flounder, 10-15°C)	0.081
Elliott 1972 (brown trout, 5-15°C)	0.111
Mean	0.096

The mean is close to the estimate by Elliott whose experiments produced remarkably consistent results.

Ursin (1984) used two sets of data on the temperature dependence of the ingestion coefficient h in cod. Exponential approximation over the interval from 2°C to 10°C gives estimates of p equal to 0.13 and 0.08. These are about the same size as the exponents for α_0 quoted above and therefore tend to cancel for h/α_0 which is the quantity appearing in the equations. Accordingly, stomach contents were plotted against body size without correction for temperature differences. The values of h given above refer to 10°C. Estimated values of α_0 automatically refer to the same temperature – and to the same time unit.

As an example of the application of eq. 8a consider the estimate by Daan (1973) of a slope of 1.01 for $\beta = 1$. Daan further assumed $\alpha_1 = -0.33$ and $m = 0.67$. Thus, $m + f_1 - \alpha_1 = 1.01$ from which $f_1 = 0.01$.

Material

Fourteen sets of data on stomach contents as a function of body weight in cod are available. Satiation levels by size class of cod have been estimated for eleven of these. The percentage of fish in the diet, by size class of cod, is known in eleven cases and the mean weight of food items in the stomach in nine, see Table 1. The

Table 1. Cod stomach data. The aberrant first observation for W. Scotian waters was omitted throughout.

Cod weight W(g)	Stomach content S(g)	Mean prey weight w(g)	Fish %	Satiation level f	Cod weight W(g)	Stomach content S(g)	Mean prey weight w(g)	Fish %	Satiation level f
1. N. Gulf of St. Lawrence					7. S. North Sea				
298	18.8		97		7.3	0.168	0.055	28	0.48
689	23.4		97		45.7	0.539	0.233	18	0.63
1327	42.4		95		142	1.90	0.722	27	0.76
2270	44.6		82		407	5.92	1.81	43	0.84
3579	64.7		81		840	15.1	4.02	53	0.86
5314	110		95		1628	27.9	5.97	57	0.88
8849	225		96		2671	52.3	7.41	58	0.89
2. E. Newfoundland and Labrador					4390	82.5	9.79	57	0.79
298	16.4		76		5991	99.5	10.8	65	0.72
699	18.2		83		8847	130	16.2	86	0.70
1327	45.5		72		8. SE. North Sea				
2270	40.0		80		6.4	0.13	0.03	13	0.48
3579	178		73		21.5	0.29	0.09	24	0.56
3. W. Scotian waters					59.3	0.65	0.21	13	0.67
(15.9	0.687	0.0151	0	0.58)	125	1.23	0.35	15	0.75
136	0.545	0.0227	0	0.75	195	2.10	0.50	15	0.80
611	3.22	0.249	15	0.85	383	6.42	1.44	18	0.84
1529	7.18	0.700	16	0.80	858	13.2	2.57	30	0.86
3152	10.7	1.20	25	0.72	1664	27.7	4.40	40	0.89
5574	33.2	6.43	66	0.81	5139	140	13.7	80	0.72
10755	155	22.0	83	0.84	9. North Sea, ICES				
4. Gulf of Maine					22.0	0.33	0.16	29	0.49
14.6	0.056	0.0336	0	0.49	54.5	0.75	0.27	33	0.55
158	1.47	0.830	4	0.58	122	1.30	0.40	32	0.60
557	3.38	0.255	36	0.82	187	2.54	0.57	39	0.65
1501	8.52	0.782	55	0.97	429	6.33	0.88	46	0.70
3201	26.3	2.38	83	0.80	852	14.7	2.19	48	0.74
5501	32.6	4.54	63	0.74	1951	36.4	3.69	58	0.84
10493	139	61.6	56	0.78	5718	111	12.1	71	0.80
5. Georges Bank					12250	220	36.1	84	0.74
14.2	0.065	0.0094	0	0.68	10. Baltic				
172	0.802	0.0213	2	0.81	17.2	0.243	0.0185	6	0.56
556	2.71	0.141	8	0.82	33.4	0.452	0.0227	6	0.57
1517	15.7	1.18	14	0.72	54.0	0.660	0.0343	29	0.58
3071	33.7	2.32	20	0.70	123	1.40	0.0415	19	0.59
5556	63.6	7.08	56	0.75	233	2.83	0.0649	22	0.60
11149	194	38.0	57	0.76	366	4.82	0.1025	24	0.59
6. N. North Sea					11. Sound				
4.6	0.13	0.053	5	0.44	351	3.05	0.126	35	0.52
28.0	0.28	0.111	19	0.51	529	4.61	0.167	47	0.52
147	1.99	0.305	51	0.62	780	6.02	0.247	56	0.51
386	5.22	1.20	70	0.69	1126	10.8	0.337	59	0.60
829	10.1	3.33	69	0.74	1423	20.3	0.584	77	0.68
1575	25.0	7.04	85	0.81	1915	26.8	0.987	83	0.74
2797	35.5	10.6	90	0.85	2379	24.7	1.66	90	0.80
4530	98.9	26.9	94	0.83	3084	29.8	8.85	98	0.83
6228	94.4	16.9	88	0.78	4631	42.1	40.6	99	0.86
9383	107	25.5	94	0.67					

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Table 1 continued

Cod weight W(g)	Stomach content S(g)	Mean prey weight w(g)	Fish %	Satiation level f	Cod weight W(g)	Stomach content S(g)	Mean prey weight w(g)	Fish %	Satiation level f
12. Faroes					2441	27.8			0.79
180	2.4			0.77	3075	30.4			0.81
330	3.5			0.75	3810	38.5			0.79
950	7			0.72	4655	57.7			0.78
1300	11			0.72	6141	54.7			0.72
1700	27			0.72	8574	80.6			0.59
2100	49			0.71	14. Iceland				
2800	35			0.68	5.6	0.10		35	
3300	44			0.67	20	0.15		44	
4000	34			0.65	54	0.28		12	
5000	88			0.68	114	0.75		52	
6000	113			0.72	208	1.8		60	
13. Irish Sea					429	3.7		45	
34	0.38			0.95	911	10		64	
156	1.33			0.87	1664	12		58	
343	6.18			0.82	2746	18		64	
527	7.28			0.78	4219	32		81	
768	11.4			0.74	6141	67		81	
1072	15.3			0.91	8574	109		92	
1447	15.8			0.72	11576	408		90	
1901	22.4			0.76	16882	537		100	

sources are listed below. Unless otherwise stated the estimates of satiation level are from Ursin (1984).

West Atlantic

1. Northern Gulf of St. Lawrence. Minet & Perodou 1978.
2. East of Newfoundland and Labrador. Minet & Perodou 1978.
3. West Scotian waters. Satiation estimates from unpublished data on size-at-age. National Marine Fisheries Service, Woods Hole. Not previously published in this form:
4. Gulf of Maine. Same source.
5. Georges Bank. Same source.

North Sea

6. Northern North Sea (mostly Central North Sea in ICES terminology). Daan 1973.
7. Southern North Sea. Daan 1973.
8. Roundfish area 6 (Southeastern North Sea). Daan 1981. Satiation levels as in 7., above.
9. Entire North Sea. ICES fish stomach investigation. Daan 1983. Satiation levels as in 6, above.

Other areas

10. Western Baltic (Kiel Bay). Not previously published in the present form. Courtesy Dr W. Arntz. Satiation levels from size-at-age data in Arntz 1980.
11. The Sound between Denmark and Sweden. Not previously published in the present form. Courtesy Dr O. Bagge. Satiation levels from unpublished data on size-at-age. Courtesy Dr O. Bagge.
12. Faroe waters. Jones 1966. Satiation levels for Faroe Plateau.
13. Irish Sea. Unpublished. Courtesy Dr Keith Brander.
14. Iceland waters, mostly north and east. Pálsson 1981, 1983.

All or most investigators have tried to distinguish between regurgitated and truly empty stomachs and have tried to exclude fish suspected of feeding in the trawl. For this investigation empty stomachs, but not regurgitated ones, were included when specified in the source. Minet & Perodou (1978) excluded empty stomachs, but these were extremely rare, about 1%.

Stomach contents as a function of cod weight

Fig. 1 shows log-log plots of stomach contents against cod weight in an application of eq. 8 for $\beta = 1$. The differences between the Woods Hole and the North Sea data are striking. Growth rates are almost the same in the two regions (Ursin 1984), but there is about twice as much in the stomachs of North Sea cod as in those from Georges Bank, Gulf of Maine and West Scotian waters. As might be expected under these circumstances, a correction for satiation level by applying eq. 9 to simulate full satiation, does not appreciably change the results. This is shown in Fig. 2 although satiation levels are not available for all data sets. Estimates of the intercepts and slopes relating to Fig. 1 & 2 are in Table 2 which also gives the ensuing estimates of α_0 and α_1 of eq. 9. Fig. 3 shows the estimated values of the coefficient α of stomach evacuation as calculated for cod weights from 10 g to 10 kg.

The differences appearing in Figs 1-3 are not merely between west and east because the highest stomach content weights are observed in the two data sets from Canadian waters (Fig. 1) in localities just north of the range of the Woods Hole data. We have tried to find a cause for the observed differences of stomach contents in the treatment of regurgitated or truly empty stomachs, or in differences in the treatment of unidentifiable material. However, there seems little doubt that the observed differences in stomach contents, and hence in evacuation rates, are real.

Differences in sampling design as to months of the year, hours of the day or water depths do not seem responsible either. Temperature differences can be ruled out because of the similarity of temperatures on Georges Bank and in the North Sea.

The causes of the differences in stomach contents weight must be sought in the food composition or in the frequency distribution of weight of food in the stomachs (p. 64).

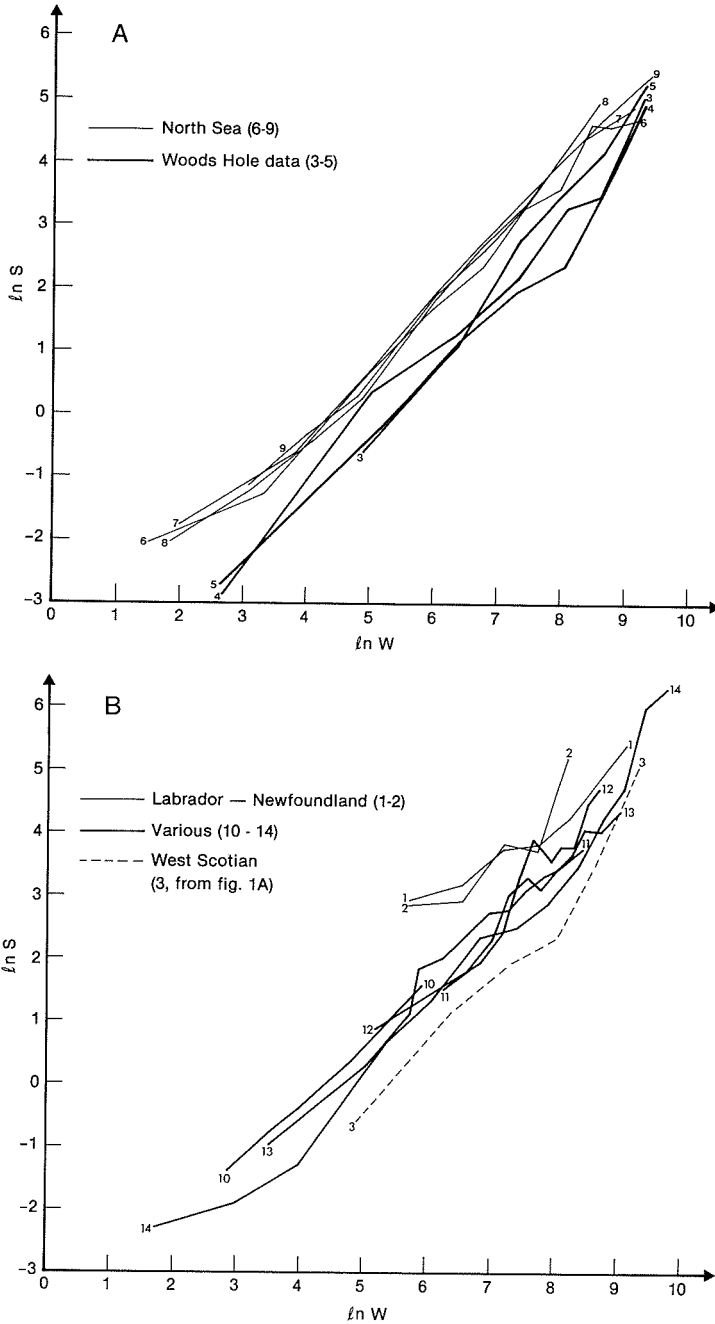


Fig. 1. Log-log plots of stomach contents against cod weight. A, North Sea data compared to Woods Hole data. B, other data, with West Scotian waters (Woods Hole) inserted for comparison. Numbers refer to the list p. 68.

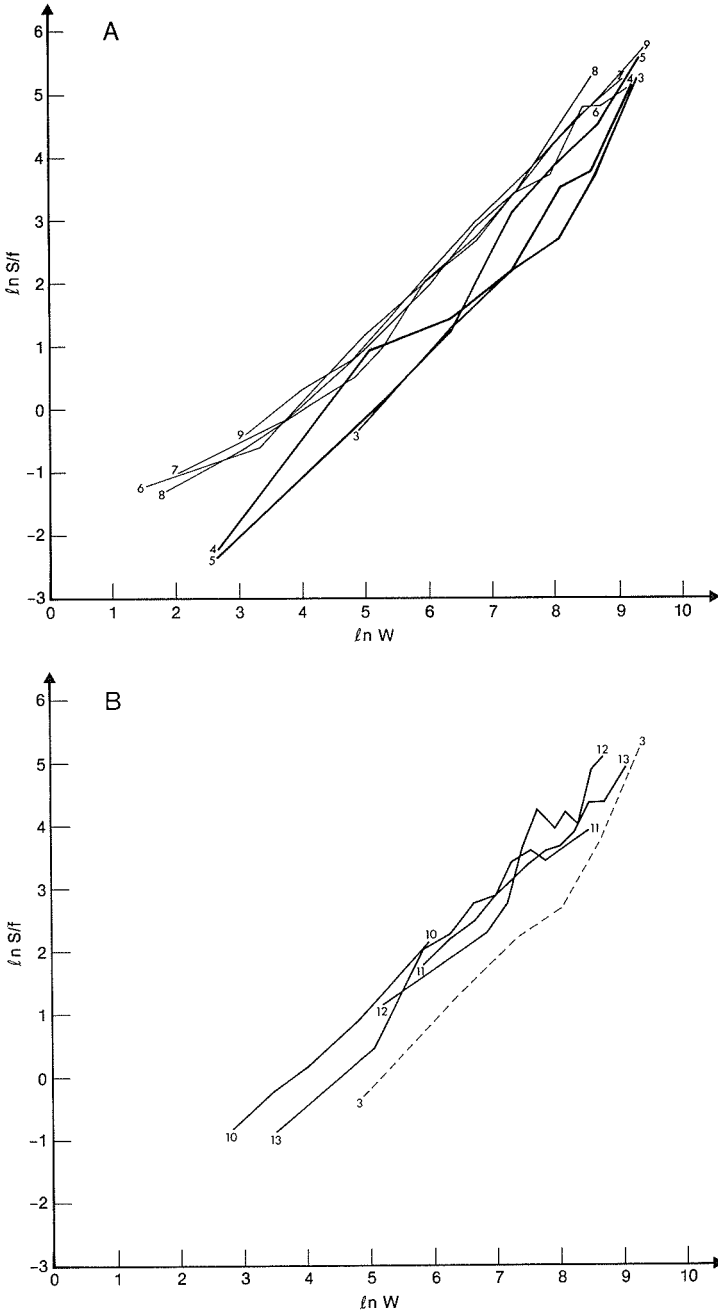


Fig. 2. As Fig. 1, but stomach contents divided by the satiation level f , simulating full satiation.

Table 2. Parameter estimations from various linear regressions. Data in Table 1. See also Figs 1, 2, 5 and 6. There was not corrected for bias due to back transformation from logarithmic values.

Ordinate Abscissa	$\ln S$ $\ln W$		$\ln(S/f)$ $\ln W$					$\ln w$ $\ln W$		$\ln \alpha$, eq. 7 $\ln w$	
	-inter- cept	slope	$\ln \alpha_0$		$h = 0.15; m = 0.58$			-inter- cept	slope	$-\ln a_0$ $-a_1$	
			$-\ln h$	$m - \alpha_1$	$\ln \alpha_0$	α_0	$-\alpha_1$				
E. Newf. Id & Labrador	2.41	0.86									
N. Gulf of St. Lawrence	1.30	0.70									
These pooled	1.60	0.74									
W. Scotian waters	6.63	1.19	6.31	1.18	4.42	83.1	0.60	11.28	1.51	0.08	0.41
Gulf of Maine	5.70	1.11	4.86	1.03	2.96	19.3	0.45	7.19	1.04	0.15	0.40
Georges Bank	6.22	1.21	5.90	1.20	4.00	54.6	0.62	9.21	1.28	0.48	0.47
These pooled	6.02	1.15	5.47	1.11	3.57	35.5	0.53	8.62	1.20	0.24	0.43
N. North Sea	4.00	0.97	3.12	0.89	1.22	3.39	0.31	4.94	0.91	0.46	0.35
S. North Sea	4.11	1.00	3.46	0.95	1.56	4.76	0.37	4.38	0.81	0.44	0.44
SE. North Sea	4.50	1.06	3.76	0.98	1.86	6.42	0.40	5.30	0.92	0.44	0.44
North Sea, ICES	4.59	1.07	3.72	0.99	1.88	6.23	0.41	4.85	0.85	0.53	0.48
These pooled	4.27	1.02	3.51	0.95	1.61	5.00	0.37	4.94	0.88	0.46	0.42
Baltic	4.21	0.96	3.58	0.94	1.68	5.37	0.36	5.59	0.54	2.09	0.67
Sound	5.21	1.08	3.06	0.84	1.16	3.19	0.26	15.37	2.12	0.74	0.08
These pooled	4.18	0.95	3.30	0.88	1.40	4.06	0.30	8.46	1.17	0.67	0.19
Iceland	5.16	1.09									
Faroes	5.12	1.10	5.04	1.14	3.15	23.3	0.56				
Irish Sea	4.19	0.96	4.32	1.02	2.43	11.4	0.44				
These pooled	4.65	1.06	4.56	1.06	2.66	14.3	0.48				
All data pooled	4.61	1.04	3.87	0.96	1.97	7.17	0.38	6.20	0.96	0.50	0.36

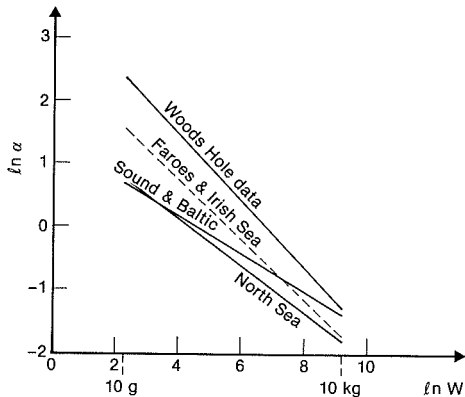


Fig. 3. The coefficient α of stomach evacuation plotted against cod weight (log scales) assuming food consumption proportional to stomach contents (i.e., $\beta = 1$, eq. 3).

The influence of food composition

Species effects

High stomach contents weights might be caused by large amounts of indigestible material (molluscs with heavy shells, ophiuroids). Yet, there are few molluscs in the North Sea material where high stomach contents were found, and ophiuroids are plentiful only in stomachs from the Sound. Invertebrates are often found to have less caloric value than fish and might be consumed in larger quantities to make up for this. However, it is the North Sea and Canadian materials with their high stomach contents weights that also have a high percentage of fish (Table 1, Fig. 4). The alternative for cod to fish prey is usually crustaceans. If the latter produce a different stomach evacuation rate the tendency of small cod to eat crustaceans would influence the regression of stomach contents upon body size. However, Bagge (1981, quoting Hodal 1977) and ICES (1982, experiments by H. Heessen, unpubl.) found little if any difference in evacuation times of fish and crustaceans when these were fed whole to cod. Even the time lag from ingestion until the skin is penetrated and digestion actually begins seems to be approximately the same in Heessen's experiments.

Prey size effects

Using a linear model of stomach evacuation Daan (1973) assumed digestion time proportional to the diameter of food items. He concluded, that digestion time is also proportional to the cube root of predator weight. Swenson & Smith (1973), data recalculated by Jobling (1981), found meals of smaller prey evacuated more rapidly in walleye whereas Elliott (1972) found no effect when feeding different sizes of food items to brown trout. The food items in both cases did not differ by more than a factor of 4 in weight, whereas in this investigation the factor is 1000. Fig. 5 shows the relationship of the mean size of food items to body size to the extent this information is available from Table 1. Cod in the North Sea appear to be quite different than those in the Woods Hole data, the Baltic and the Sound. In the North Sea there is a linear and almost proportional relationship of prey size to cod size. In the other areas the relation seems curvilinear and the prey size except in very large cod is much smaller (Figs 1, 2, 4, 5). The prey of medium-sized cod is ten times bigger in the North Sea while there is little or no quantitative or qualitative difference in the prey of large cod. High stomach contents, large prey and high percentages of fish tend to go together although data from the Baltic and the Sound are exceptions.

The hypothesis proposed by Daan (1973, see above) can be formalized as

$$\alpha = a_0 w^{-0.33} \text{ or, generalizing, } \alpha = a_0 w^{a_1} \quad (11)$$

where w is the prey size. Rearranging eq. 7 we can put

$$\alpha = fhW^m/S$$

and calculate individual values of α from the data of Table 1 and previously adopted values of h and m . Thus, a_0 and a_1 can be estimated from

$$\ln \alpha = \ln a_0 + a_1 \ln w, \quad (11a)$$

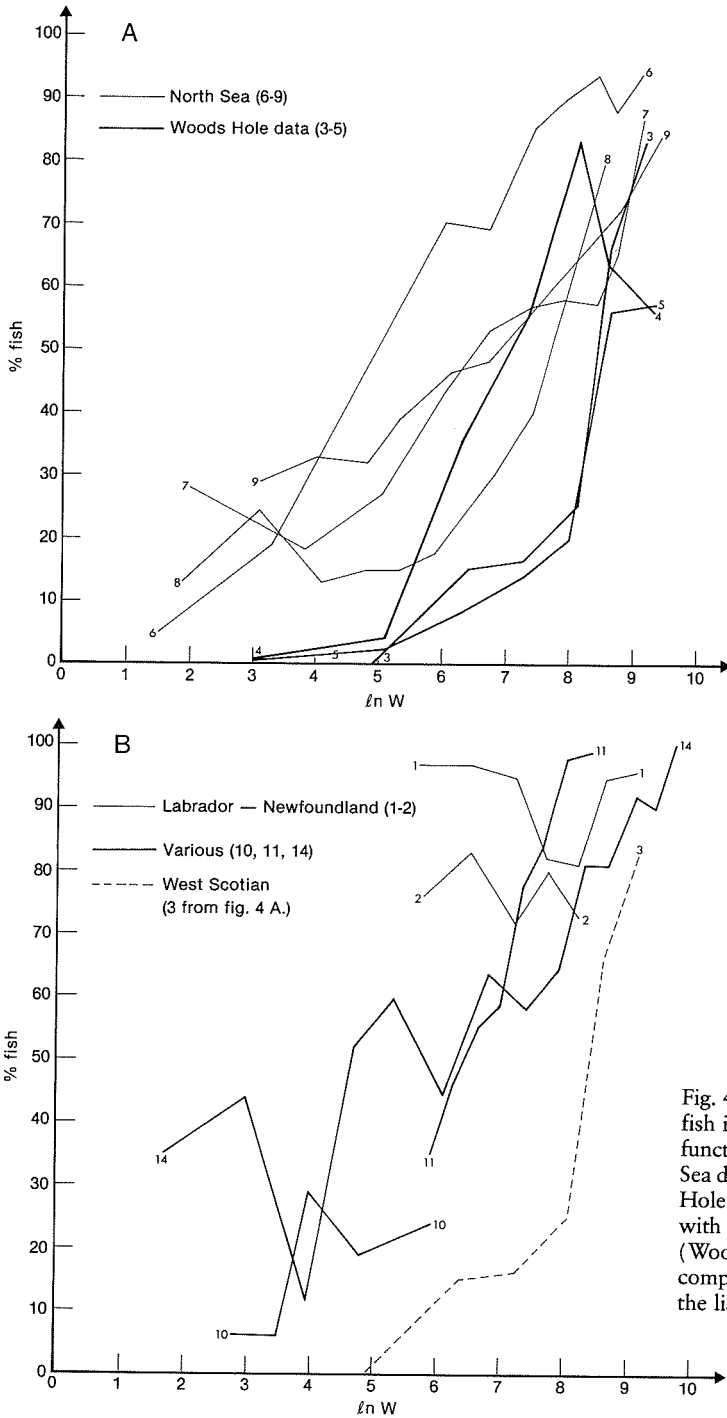


Fig. 4. Percent by weight of fish in cod stomachs, as a function of cod size. A, North Sea data compared to Woods Hole data. B, other data, with West Scotian waters (Woods Hole) inserted for comparison. Numbers refer to the list p. 68.

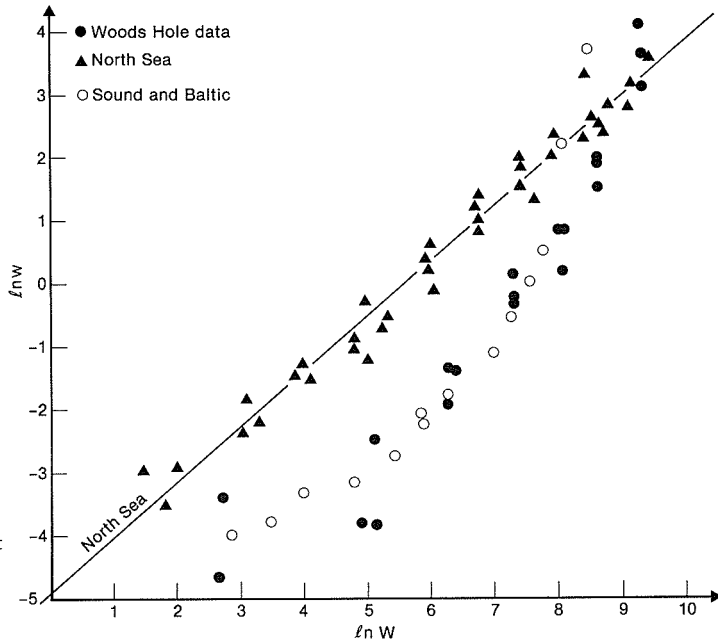


Fig. 5. Log-log scale plot of prey size w as a function of cod size W .

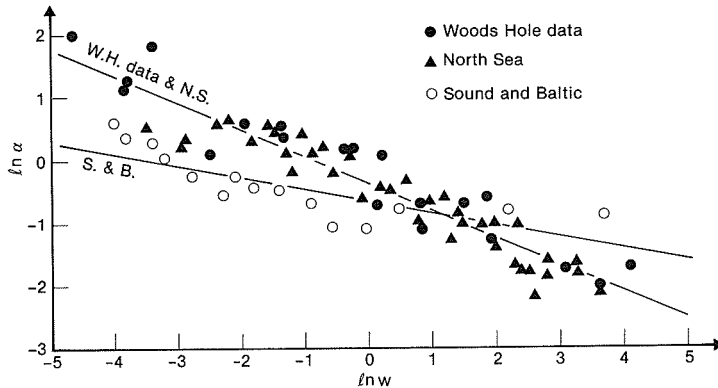


Fig. 6. Stomach evacuation rates calculated as $\alpha = fbW^m/S$ and plotted as a logarithmic function of prey weight.

see Fig. 6 and Table 2. The necessary information is available for the Woods Hole data, the North Sea, the Sound and the Baltic. The two former data sets present α as a convincingly linear function of prey size with almost identical parameter values. The two latter data sets differ and the linearity is poor. Pooling data we obtain

	$\ln a_0$	a_0	a_1
Woods Hole & North Sea	-0.38	0.68	-0.43
Sound & Baltic	-0.67	0.51	-0.19
All data pooled	-0.50	0.61	-0.36

The final estimate of $a_1 = -0.36$ is so close to the expected -0.33 that Daan's hypothesis cannot be rejected. Yet, the aberrant values of α calculated for the Sound and the Baltic, for which no explanation is offered, leave a suspicion that the correlation of stomach evacuation rates with prey sizes is spurious even though it explains the difference between amounts of stomach contents in the North Sea and in the Woods Hole material.

Fänge & Grove (1979) presented circumstantial support of Daan's hypothesis. Using published data they partitioned the fish species into micro- meso- and macrophags according to particle sizes in their natural diet, and plotted digestion time against temperature for each category. Microphags were found to digest 2-3 times faster than mesophags and these again 2-3 times faster than macrophags. The predator : prey size ratios for the three categories are difficult to quantify, but may be crudely assessed as 10000 : 1, 1000 : 1 and 100 : 1. Reading the digestion times at 15°C from Fig. 4 in the Fänge & Grove paper we find approximately 7.1, 22 and 54 hours. A linear regression of \ln (hours) on \ln (relative particle size) gives $a_1 = -0.44$ which, considering the crudeness of the approach is not too far from the expected value of -0.33 .

The square root assumption

So far we have assumed that food consumption is proportional to the weight of the stomach contents. It has been argued (Jobling 1981) that assuming proportionality with the square root of stomach contents weight may be more realistic. This means putting $\beta = 0.5$ instead of $\beta = 1$ in eqs 1-3. As already mentioned, an unfortunate consequence of this is that mean stomach contents are replaced in the various expressions by the mean of individual values of the square root of stomach contents. This limits the material to data sets in which each stomach was worked up separately namely, the Woods Hole data and data from the Baltic and the Sound. North

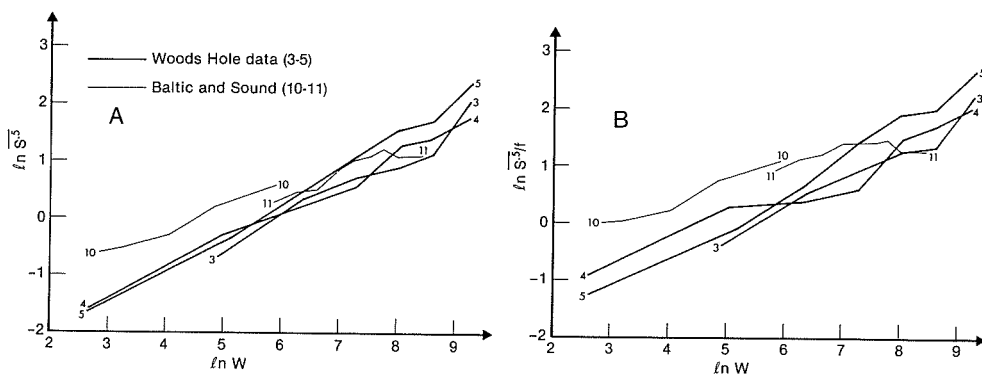


Fig. 7. Plots of stomach contents as a function of cod size on the assumption that food consumption is proportional to the square root of stomach contents (i.e., $\beta = 0.5$, eq. 3). For comparison with Figs 1 & 2 in which food consumption is assumed proportional to stomach contents ($\beta = 1$).

Table 3. Data for parameter estimation. *A* on the assumption that food consumption is proportional to the square root of stomach contents. *B* for comparison with the results of Jones (1974).

A $m=0.58; h=0.15$			B $m=0.69; h=0.1115$		A $m=0.58; h=0.15$			B $m=0.69; h=0.1115$	
W	$\bar{S}^{0.5}$	<i>f</i>	$\bar{S}^{0.46}$	<i>f</i>	W	$\bar{S}^{0.5}$	<i>f</i>	$\bar{S}^{0.46}$	<i>f</i>
W. Scotian waters					Baltic				
136	0.512	0.75	0.519	0.78	17.3	0.555	0.56	0.577	0.71
611	1.447	0.85	1.376	0.86	25.4	0.585	0.57	0.607	0.71
1529	2.036	0.80	1.866	0.86	57.0	0.732	0.58	0.743	0.71
3152	2.503	0.72	2.255	0.86	128	1.245	0.59	1.210	0.71
5574	3.094	0.81	2.712	0.92	223	1.514	0.60	1.443	0.72
10755	7.776	0.84	6.332	0.95	374	1.733	0.59	1.636	0.72
Gulf of Maine					Sound				
14.6	0.199	0.49	0.221	0.64	351	1.331	0.52	1.269	0.67
158	0.765	0.58	0.744	0.69	529	1.618	0.52	1.518	0.68
557	1.209	0.82	1.133	0.83	780	1.698	0.51	1.568	0.69
1501	1.788	0.97	1.637	0.96	1126	2.441	0.60	2.201	0.75
3201	3.597	0.80	3.107	0.89	1423	2.776	0.68	2.445	0.80
5501	4.065	0.74	3.516	0.89	1915	3.034	0.74	2.639	0.84
10493	5.981	0.78	4.939	0.94	2379	3.384	0.80	2.907	0.88
Georges Bank					3084				
14.2	0.192	0.68	0.213	0.81	4631	3.116	0.86	2.633	0.94
172	0.726	0.81	0.731	0.87					
556	1.543	0.82	1.455	0.88					
1517	3.058	0.72	2.746	0.86					
3071	4.687	0.70	4.043	0.84					
5556	5.526	0.75	4.680	0.89					
11149	10.888	0.76	8.811	0.93					

Sea data was, in all four cases, worked up by batches of stomachs belonging to the same size class of cod. This makes it impossible to consider the important differences between the weights of stomach contents in the Woods Hole and the North Sea material. These might be due to differences in the frequency distribution of weight of food in the stomachs as indicated in the example on p. 64. Prey size differences may enter the picture in an oblique way because fish feeding on many small items are likely to have a different weight frequency distribution in the stomachs than others feeding on big lumps which are consumed at long intervals. These problems cannot be analysed at present.

Fig. 7, based on data in Table 3, shows plots of square-root-means of stomach contents against cod weight for comparison with Figs 1 & 2. Taking square roots does not even out the differences. Data from the Baltic remain inexplicably high. Parameter estimates (Table 4) reveal that under the square root assumption the stomach evacuation rate α is positively correlated with body weight whereas these are negatively correlated under the assumption of $\beta = 1$. Obviously, there exists a value β ($0.5 < \beta < 1$) from which it can be concluded that α is independent of cod size. But this does not have to be the true value of β . Table 4 does not encourage conclusions. We can only note that pooling the entire material leads to

Table 4. Estimates of stomach evacuation parameters (α_0 and α_1) on the assumption that food consumption is proportional to the square root of stomach contents.

Ordinate Abscissa	$\ln S^{0.5}$ $\ln W$		$\ln(\overline{S^{0.5}/f})$ $\ln W$				
			$h = 0.15; m = 0.58$				
	–interc.	slope	$\ln \alpha_0$ $-\ln h$	$m - \alpha_1$	$\ln \alpha_0$	α_0	α_1
W. Scotian waters	3.33	0.55	3.01	0.54	1.12	3.06	0.04
Gulf of Maine	2.97	0.51	2.12	0.43	0.22	1.25	0.15
Georges Bank	3.31	0.60	2.98	0.59	1.09	2.97	-0.01
These pooled	3.14	0.55	2.59	0.51	0.70	2.01	0.07
Baltic	1.81	0.40	1.18	0.38	-0.71	0.49	0.20
Sound	1.85	0.38	-0.20	0.14	-2.20	0.11	0.44
These pooled	1.59	0.34	0.71	0.28	-1.18	0.31	0.30
All data pooled	2.43	0.46	1.70	0.40	-0.20	0.82	0.18

the estimate (eqs 3 & 8):

$$\frac{dR}{dt} = \alpha \overline{S^{0.5}} = \alpha_0 W^{\alpha_1} \overline{S^{0.5}} = 0.82 W^{0.18} \overline{S^{0.5}}. \quad (12)$$

There is, however, experimental support for the square root proportionality. Jones (1974) fed meals of various sizes to haddock (*Melanogrammus aeglefinus*) whiting (*Merlangius merlangus*) and cod, also of various sizes, and found the relationship

$$\frac{dR}{dt} = Q(L/40)^{1.4} S^{0.46} \quad (13)$$

where L is the length of the fish. Q was estimated for various kinds of food and was 0.15 per hour on an average at 6°C, corresponding to 0.207 at 10°C, applying the temperature adjustment determined by Jones. Converting from length to weight (= 1% of length cubed) and from hours to days gives

$$\frac{dR}{dt} = \alpha_0 W^{\alpha_1} S^{\beta} = 0.24 W^{0.467} S^{0.46} \quad (13a)$$

Jones (l.c.) also performed the calculations using the actual weights of the fish and found $\alpha_1 = 0.44$, but the corresponding value of α_0 is not stated. The resemblance to the result in eq. 12 is notable although eq. 12 and eq. 13a are not strictly comparable. To achieve comparability eq. 12 can be recalculated for $\beta = 0.46$ as estimated by Jones. Moreover, it seems appropriate to use the alternative set of growth parameters (p. 65) which refers to cod in aquarium experiments. This implies the replacement of $m = 0.58$ by $m = 0.69$ and of $h = 0.15$ by $h = 0.1115$ which leads to a different set of estimates of satiation levels, Table 3. The results (Table 5) are more in agreement with Jones's experiments than the former ones, but great differences between sets persist. The pooled data for the Baltic and the Sound provide a particularly close fit to the results of experiments (eq. 13a):

Table 5. Estimates of stomach evacuation parameters (α_0 and α_1), comparable through choice of values of other parameters to experimental results by Jones (1974).

Ordinate Abscissa	$\ln S^{0.46}$ $\ln W$		$\ln(S^{0.46}/f)$ $\ln W$				
	-interc.	slope	$\ln \alpha_0$ $-\ln b$		$m = 0.69; h = 0.1115$		
$m - \alpha_1$			$\ln \alpha_0$	α_0	α_1		
W. Scotian waters	2.88	0.45	2.43	0.41	0.24	1.27	0.28
Gulf of Maine	2.76	0.47	2.14	0.40	-0.05	0.94	0.29
Georges Bank	3.07	0.55	2.83	0.54	0.64	1.89	0.15
These pooled	2.81	0.48	2.39	0.44	0.20	1.22	0.25
Baltic	1.67	0.37	1.31	0.36	-0.88	0.41	0.33
Sound	1.62	0.32	0.29	0.18	-1.90	0.15	0.51
These pooled	1.42	0.30	0.87	0.26	-1.32	0.27	0.43
All pooled	2.15	0.40	1.64	0.35	-0.55	0.57	0.34

$$\frac{dR}{dt} = 0.27 W^{0.43} S^{0.46}.$$

In the previous analyses we were led to consider precisely these data influenced by some factor not appreciated in the analysis. Now, one realizes that instead, it may be the rest of the material that is thus influenced. Alternatively of course, the experiments may have been biased by some uncontrolled factor.

Conclusions

In spite of the extensive literature on cod food consumption and digestion it must be realized that we still have only the vaguest of ideas of how food consumption depends on body size and of what determines the stomach evacuation rate.

After the first part of this paper the reader may find himself half convinced that the rate of stomach evacuation in cod can be described by the expression

$$\frac{dS}{dt} = 0.61 w^{-0.36} S$$

(where w is prey weight, S the weight of stomach contents) or possibly by

$$\frac{dS}{dt} = 7.2 W^{-0.38} S$$

(where W is cod weight).

After the second part of the paper he may be inclined to agree with Jones (1974) that

$$\frac{dS}{dt} = 0.24 W^{0.47} S^{0.46}.$$

Support of either of these hypotheses is found in the data presented here and in the literature, and none of them can be convincingly rejected at our present level of knowledge.

Hopes for deciding between the hypotheses in the future are not bad. It has only recently been realized that stomach contents investigations must be based on an appreciation of predator and prey sizes as well as type of prey.

Experimental work on digestion was for a long time hampered by a lack of the realization that natural foods should be used to simulate natural conditions. Many of the most quoted papers on fish digestion (including Jones 1974) are based on meals of fish fillets or shrimp relieved of their shells. One consequence of this is that little attention has been paid to the possible influence of prey size upon the rate of digestion.

There are few fish species on which a paper like this could be written at present, but with the increasing understanding of which information is relevant, there is likely to be far better data for a fair number of species after another ten years.

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