On the growth parameters of Atlantic cod as a function of body size

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Abstract

The coefficient H of the growth equation $dw/dt = Hw^m - kw^n$ is interpreted as indicating the satiation level achieved. H tended to be highest in medium-sized cod of several stocks. Relating H to food concentration in the North Sea indicated that most cod stocks are almost satiated when H is maximum. This occurs at body weights to which fish food is most plentiful. Closest to satiation are Faroe Bank cod. Calculations were performed with two sets of values of m, n and k, one estimated from growth rates, another from respiration rates of fed and fasting cod. Although markedly different the two sets of values led to almost the same conclusions except when daily rations were calculated.

Introduction

In most cases when using growth equations of the type

$$\frac{dw}{dt} = Hw^m - kw^n \tag{1}$$

it is tacitly assumed that the four parameters remain constant through the lifetime of the fish. When the first term is interpreted as a function of ingestion it is obvious that changes in food concentration would be reflected in at least the coefficient H. Majkowski & Waiwood (1981) investigated this in cod collected in 1977 in the Southern Gulf of St. Lawrence. Calculating H for each age group they found an increase with body size. The parameter values used were $m = 0.56$, $n = 0.83$ and $k = 2.94 \, g^{1-n} y^{-1}$. The quantity actually calculated is the ingestion coefficient $H' = H/0.48$. Fig. 1 is a plot of $\ln H'$ against $\ln w$. The slope is $b = 0.129$ with 95 % confidence limits of ± 0.085. The intercept with the ordinate axis is 3.092 whose antilog is 22.0 which shall be used disregarding problems of back transformation from log values. Multiplying by 0.48 gives the quantity $H_0 = 10.6$ belonging in the growth equation. Eq (1) is replaced by

$$\frac{dw}{dt} = (H_0 w^b) w^m - kw^n = H_0 w^{b+m} - kw^n = 10.6 w^{0.69} - 2.94 w^{0.83} \tag{2}$$

Unfortunately, this result has two obvious interpretations. Either, m was erroneously estimated in the first place and b is a correction term for m or else the satiation, or feeding, level (i.e., the fraction of maximum feeding rate actually achieved) in-
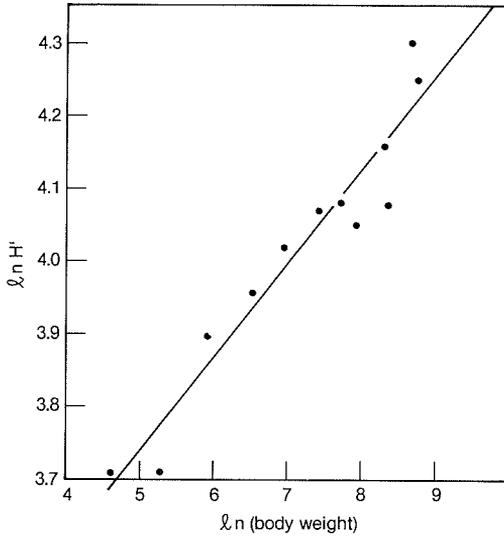
Fig. 1. Gulf of St. Lawrence cod. The ingestion parameter *H'* as a function of body size, log scale. *H'* as calculated by Majkowski & Waiwood (1981).

creases with body size. The interpretation does not affect the work of Majkowski & Waiwood (1981) because their purpose was to calculate the food consumption by age group which is independent of whether w^b belongs with w^m or with H'.

The distinction between the two hypotheses becomes important in considerations of density dependent mortality. It is often not clear how the final adjustment of recruit numbers take place when the difference between strong and weak year-classes is small in spite of an enormous juvenile mortality with survival of one in a million or so. North Sea cod is a good example (Ursin 1982). If it turns out that satiation level and hence, growth rate do in many cases increase with body size far into the adult stage, then competition with older fish might cause growth rates to depend on the biomass of these. The mortality suffered until a certain size is reached would be higher when the adult stock is large.

Because of the ambiguity of the results of Majkowski & Waiwood it is advisable to discuss the choice of growth parameters for cod before venturing upon an analysis of the indications that feeding level is an increasing function of body size in the cod of the Gulf of St. Lawrence and elsewhere.

Cod growth parameters

General

Spawning losses are not explicit in eq 1. Consider instead the formulation

$$\frac{dw}{dt} = Hw^m - kw^n - P(t)w^p \tag{3}$$

where the last term describes spawning losses in grams body weight with a coefficient *P* varying in time, being zero in juveniles and undergoing a seasonal cycle in adults. Disregarding the spawning term tends to bias estimates of kw^n. An

upwards bias of n may be expected because p often takes on values of one or more, and n values less than one. When H and m are estimated from the same data set as k and n the bias may affect these too because of correlations introduced with the estimation procedure. If p takes on values near m (which is usually smaller than n) the effect of disregarding the spawning term might be an underestimate of the positive term as assumed by Majkowski & Waiwood (1981), but available estimates of cod spawning losses give p values of 1.09 and 1.38 which are more likely to bias the kw^n term.

Input values of m, n and k

A wide range of pairs of values of m and n produce a fish growth curve when used in eq 1 or eq 3. The correct values of m and n are those making H and k independent of body size at constant satiation level, i.e., when the same fraction of full satiation is achieved at all sizes. Throughout the animal kingdom (excepting insects) n very often takes on values within a range of 0.70–0.85, as appears from the extensive material of respiration data presented by Hemmingsen (1960). Ursin (1979) used an intermediate value of $n = 0.78$ for cod, plaice (*Pleuronectes platessa*) and herring (*Clupea harengus*) in the North Sea and found $m = 0.58$ to match it in growth curves of the eq 3 type with explicit spawning losses. For cod was found $k = 2.0$ on a per year basis. The disadvantage of this approach is that m and k were estimated assuming constant H (constant satiation level), an assumption whose realism is being tested in this paper. A trend of H with body size in North Sea cod would therefore not be detected with the parameter values $(m, n, k) = (0.58, 0.78, 2.0)$.

It is therefore desirable to investigate as an alternative a parameter set estimated without the use of growth data. This is possible using mainly respiration data for fed and starving cod as presented by Saunders (1963) from which Ursin (1967) estimated $(m, n, k) = (0.69, 0.84, 5.11)$ at 10 °C. The k value is remarkably high. Comparing the routine metabolism kw^n with the North Sea estimate we find the Saunders one about four times higher for medium to large cod. The latter estimate makes cod an extremely active fish, like herring or trout. Surprising as this may be there is supporting evidence from Kohler (1964) who measured maintenance ration. Majkowski & Waiwood (1981) calculated their k value from this making necessary assumptions on transfer efficiences. Calculated this way the routine metabolism becomes two to four times higher than with the North Sea estimate, depending on which assumptions on other parameters are made. Jones & Hislop (1978) measured transfer efficiences and fasting metabolism for small cod and found n to be about 0.7–0.8. Their data permit estimating k for 10 °C as 3.4 ($n = 0.78$) or 2.6 ($n = 0.84$). This is intermediate between the North Sea estimate and the Saunders estimate.

We are facing a discrepancy between growth parameter values estimated mainly from field observations of growth rates and from laboratory experiments on cod. As shown below, both sets give a fair description of field data on size at age at 10 °C. When estimating H, essentially an ingestion parameter, from growth rates it is found, however, that much more food is required to satisfy the Saunders parameter set in order to make up for the high routine metabolism.

Returning to the ambiguity of the Majkowski & Waiwood (1981) estimates of H as a function of body weight (cf. eq 2) it is interesting to note that considering b of the expression $H = H_0 w^b$ as a correction term for m brings the Majkowski-Waiwood parameter values closer to the Saunders set: –

	b	m	$b+m$	n	k
Saunders	0	0.69	0.69	0.84	5.11
M. & W.	0.13	0.56	0.69	0.83	2.94

However, this interpretation of b is not borne out by size at age data on other cod stocks, as discussed below.

Estimating H as a function of body size

The two sets of parameter values used below are: –

m	n	k	
0.58	0.78	2.0	'NS parameters'
0.69	0.84	5.11	'Sa parameters'

They are both supposed to describe growth at 10 °C which is the approximate annual mean bottom temperature in the Southern and Central North Sea from which data was used to estimate the 'NS parameters'.

Dividing the value of k (2.0 or 5.11) in each of the two parameter sets by 365 provides two equations for daily growth: –

$$\Delta w = Hw^{0.58} - 0.00548 w^{0.78} \quad \text{(NS param.)}$$
$$\Delta w = Hw^{0.69} - 0.01400 w^{0.84} \quad \text{(Sa param.)}$$

$\left.\right\} \quad (4)$

H is estimated from annual increments. The procedure was to guess an initial value of H (per day) and sum the daily increments. If more than 366 days were required to accomplish the observed annual increment the computation was repeated with a higher value of H. If less than 365 days were needed, H was reduced. The new H value was calculated as

$$H_n = H_{n-1} \cdot (\text{number of days divided by } 365)^{0.125} \qquad (5)$$

Such series always converged. After each year the fraction of body weight spawned was subtracted (see below) before resuming the H estimation for the next age group. A temperature correction of k was carried out (see below) when the temperature to which the stock is exposed was not 10 °C.

Spawning losses

The fraction π of body weight spawned per year was determined from fecundity data for the Southern Gulf of St. Lawrence (Ware 1980, from Powles 1958) and the North Sea (Oosthuizen & Daan 1974). Using egg weights from the latter (0.075 mg dry weight, multiplied by 5 to convert to wet weight) we have the following parameter estimates to fill in the expression $\pi = Pw^{p-1}$ (eq 3): –

	P	p
Gulf of St. Lawrence	0.0042	1.38
North Sea	0.0735	1.09
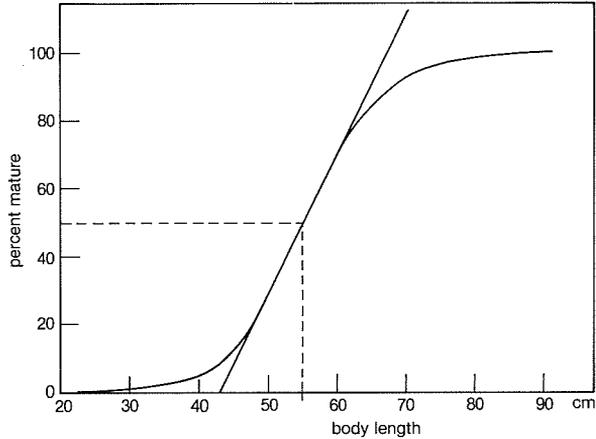
Fig. 2. Maturation ogive for cod as used in this paper.

The main difference is that the fecundity of small cod is lower in the Gulf of St. Lawrence. For $w = 20000$ g we find $\pi = 0.18$ in either case. The Gulf of St. Lawrence estimate was used only for the area where it is calculated. Other stocks are from more temperate waters for which the North Sea estimate was adopted.

Estimates of spawning losses for males are not available. They may be lower but, on the other hand, males often have higher k than females (Ursin 1967). Using the same π and k values for both sexes seems the better solution at the moment.

Powles (1958, Gulf of St. Lawrence) and Oosthuizen & Daan (1974, North Sea) plot percentage mature against body length for males and females and for age groups or years. The curves are similar and a crude mean was calculated, see Fig. 2. Readings from Fig. 2 were multiplied by the π values to give fraction spawned on a population basis. The linear approximation in Fig. 2 was adopted when constructing growth curves.

Growth as a function of temperature

H and k are assumed temperature dependent. Taylor's (1958) data on growth in cod stocks in relation to temperature was analysed by Ursin (1963) on the assumption that $1/H$ and $1/k$ can both be described as catenary functions of temperature. The results are not quite satisfactory. Taylor used surface temperatures when bottom temperatures would have been more relevant and Ursin assumed that H and k reached maximum at the same low temperature (12.8 °C) whereas the k maximum is likely to be reached at higher temperatures. We are, however, particularly interested in the low temperature parts of the curves which are probably the more reliable. Fig. 3A depicts the reciprocals of the catenary functions

$$\left.\begin{array}{l} 1/\hat{k}(T) = \cosh\,(0.267(T-12.8)) \\ 1/\hat{H}(T) = \cosh\,(0.168(T-12.8)) \end{array}\right\} \quad (6)$$

where $\hat{k}$ and $\hat{H}$ are on an arbitrary scale which is adjusted to NS parameter values $k(10)$ and $H(10)$ by putting

$$\left.\begin{array}{l} k(T) = k(10)\hat{k}(T)/\hat{k}(10) \\ H(T) = H(10)\hat{H}(T)/\hat{H}(10) \end{array}\right\} \quad (7)$$
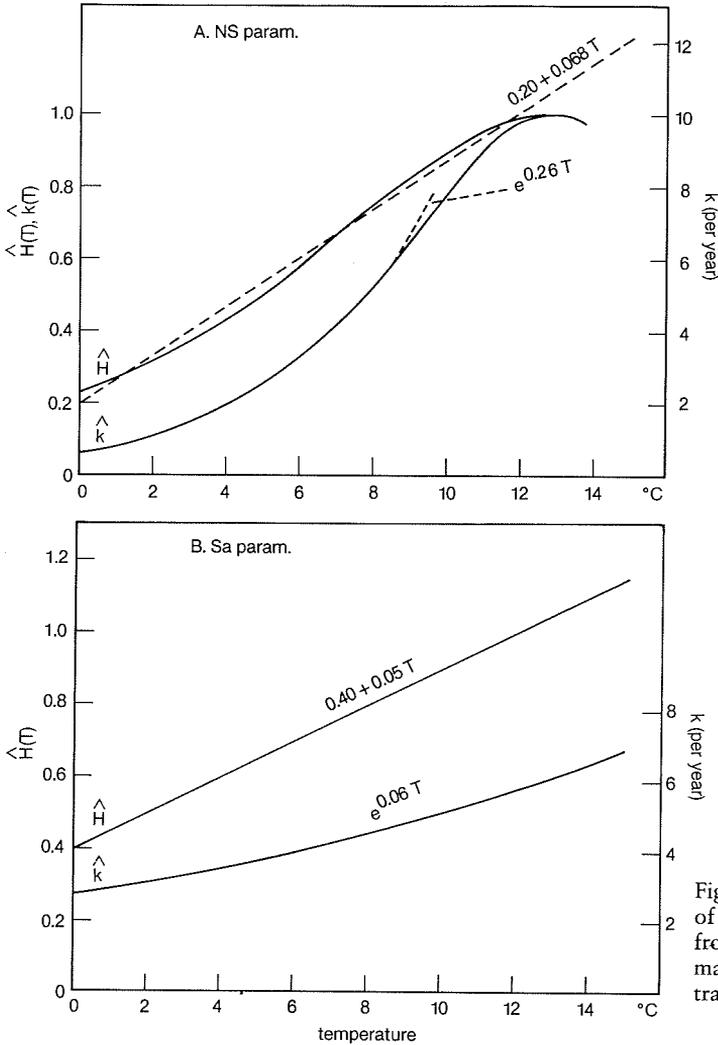
Fig. 3. H and k as functions of temperature as estimated from two sources of information. $\hat{H}$ and $\hat{k}$ are on arbitrary scales.

These functions are being used with NS parameters only, because H and k can be estimated as functions of temperature from Saunder's respiration data, although with a minimum of observations. $H(T)$ can be estimated only as a straight line and $k(T)$ as a simple exponential. The functions (Fig. 3B) are as follows (cf. Ursin 1967):

$$k(T) = k(10)\exp(0.06(T-10))$$
$$\hat{H}(T) = 0.40 + 0.05T;\ H(T) = H(10)\hat{H}(T)/\hat{H}(10) \tag{8}$$

The H function, although somewhat flatter, does not differ too much from a linear approximation to the catenary function (Fig. 3A), but the k function is markedly flatter. The first part of the catenary of Fig. 3A is nicely approximated by an exponential with a rate constant of 0.26 whereas we here find one of 0.06. Never-
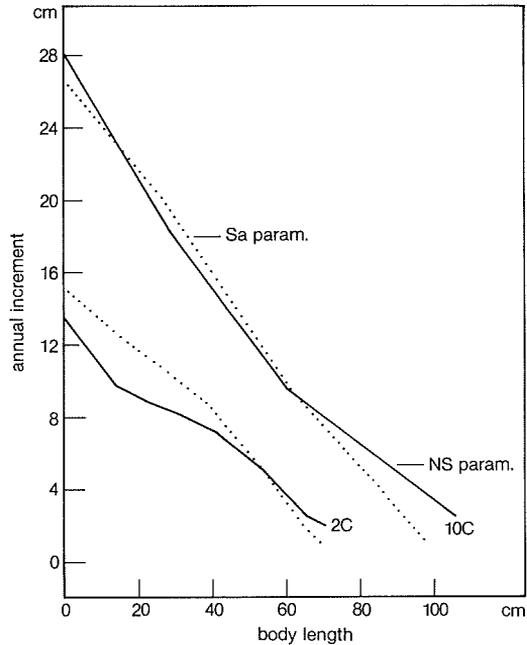
Fig. 4. Effects of temperature corrections using the two methods of Fig. 3.

theless, the combined effect of the pair of curves is similar in the two cases as illustrated in Fig. 4 which shows annual length increments as calculated with NS parameters and with Sa parameters for 2 °C and 10 °C. $H(T)$ is independent of body size in both cases (NS: $H(10) = 27.7$; Sa: $H(10) = 24.5$).

Table 1. Lengths (cm) at age in the cod stocks used in the analysis. Figures in brackets represent graphical extrapolations to the date of birth. The bottom row states the temperatures at which the cod have been assumed to live.

Age	Southern Gulf of St. Lawrence	Gulf of Maine	Georges Bank	Southern North Sea	Northern North Sea	Faroe Bank	Faroe Plateau
0	(0.5)	(0.5)	(0.5)	(0.5)	(0.5)	(0.5)	(0.5)
1	(14)	14.9	22.4	15.6	15.0	(28)	(30)
2	(24)	26.9	44.1	41.2	35.6	50.8	46.8
3	31.9	39.6	58.0	60.4	52.4	68.5	59.2
4	39.6	57.9	65.6	76.2	68.4	83.9	69.4
5	47.0	68.0	74.9	84.5	80.9	93.5	76.6
6	54.4	76.1	83.2	92.2	91.0	97.9	82.3
7	60.8	78.2	90.6	95.9	95.6	103.2	87.1
8	66.3	86.8	97.1			102.4	93.5
9	71.8	94.2	102.9			106.5	96.8
10	74.9	98.0	104.6				
11	80.5	102.5					
12		107.5					
$T(°C)$	3	6	8	10	10	8	8

Size at age data

Table 1 shows the sets of length at age data used in the analysis. Conversions between weights and lengths were performed assuming $w = 0.01L^3$. In some cases (Fig. 9 illustrates one) this convention could have been refined, but trials showed the effect to be minute. Annual increments are plotted against lengths at the beginning of the year in Fig. 5. Some data sets contain no young cod of less than two or three years, but the size when first observed is an important information on the growth in the first years of life. Partitioning into annual increments was performed by graphical interpolation between the first observation and the date of birth at which a length of 0.5 cm is assumed. The method is illustrated in Fig. 6 for Gulf of St. Lawrence cod.

The bottom temperatures at which the various cod stocks are supposed to live are more or less guessed. Dr. Marvin Grosslein, NMFS, Woods Hole, most kindly put together some data pertaining to the Northwest Atlantic stocks. The temperatures used – which may easily be wrong by one degree – are found in the bottom row of Table 1.

Each data set of Table 1 requires a few comments: –

1. Southern Gulf of St. Lawrence. Data from Majkowski & Waiwood (1981) and Majkowski (in press). Data refer to January 1977, 1978 and 1979 and June 1978. There seems to be little growth in the first half of the year.
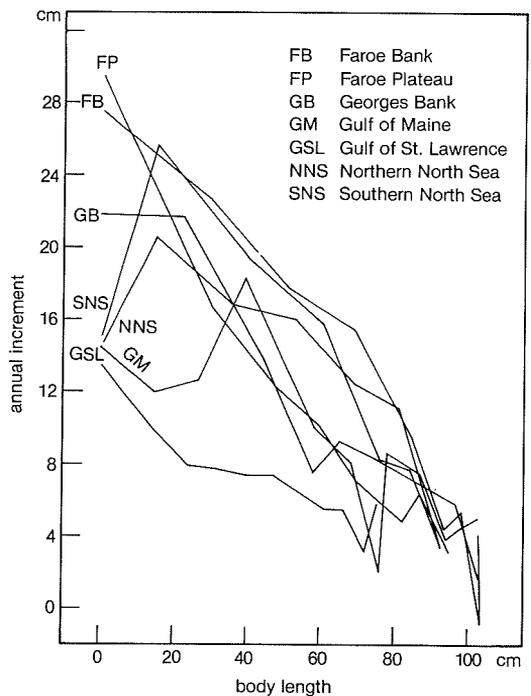
Fig. 5. All cod stocks. Annual increments, not corrected for temperature differences.
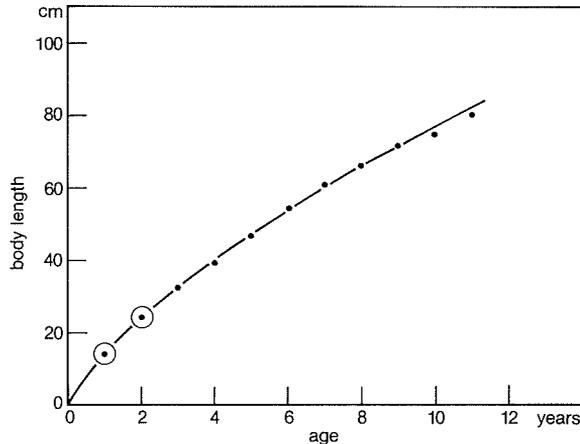
Fig. 6. Gulf of St. Lawrence cod. An example of how annual increments of young cod were obtained by extrapolation to the birth data on eye-fitted growth curves.

Spawning occurs mostly in June (Powles 1958). Age group 3 was therefore assumed to be three years old in both January and June and the four data sets averaged accordingly. The partitioning of the first three years' growth (Fig. 5) may be unrealistic, but indicates (Fig. 6) that the sum of increments in those three years was high enough to account for a growth following the same pattern as for older cod.

2. Gulf of Maine and Georges Bank. Penttila & Gifford (1976) gives five data sets each referred to a date. Those with ages stated as 1.30, 2.30, etc., for the Gulf of Maine and as 1.25, 2.25, etc., for Georges Bank were used because these seem to correspond to actual ages of full years.

3. North Sea. Daan (1974) gives data for each quarter of the year. Those for the first quarter were used because they match data for special sampling of young cod. Data are separate for the Southern North Sea and the Northern North Sea, the latter corresponding approximately to area 4B (Central North Sea) in ICES terminology.

4. Faroe Bank and Faroe Plateau. Data was read off Fig. 1 of Jones (1966) who kindly informs me that the spawning date was two years before the first observation which is at 2.25 years on the abscissa scale.

The general impression when inspecting Fig. 5 is that the growth rates of young cod vary considerably, but seem to converge towards an increment of about 4 cm per year for cod of about 100 cm long.

Estimates of H for North Sea cod

Fig. 7 shows the two data sets for North Sea cod represented as in Fig. 5, but enveloped by curves calculated with constant values of H. The impression is that growth conditions are best for medium-sized cod, but except for the low incre-
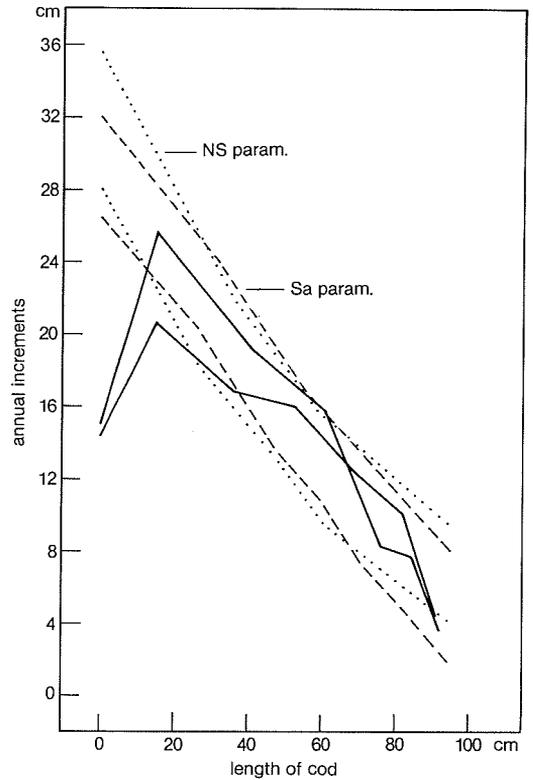
Fig. 7. Annual increments of cod from the North Sea (Table 1), enveloped by calculated increments using Saunders parameters and North Sea parameters, all with constant H throughout. H values were 24.5, 28.3 (Sa) and 27.7, 36.5 (NS).

ments observed in the first year of life the variation is small. Fig. 8 (data in Table 2) shows values of H estimated for each age-group plotted in two ways as a function of body size. The plots of $\ln H$ against $\ln w$ do not encourage estimation of corrections to the exponent m as described page 1. Sa parameters result in more stable H values than NS parameters. This nourishes a suspicion that a parameter set (m, n, k) might be found which makes H independent of body size. The observed varia-

Table 2. Estimates of H (per year) for age groups of North Sea cod.

Age	Southern North Sea			Northern North Sea		
	Mean length (cm)	H		Mean length (cm)	H	
		NS param.	Sa Param.		NS param.	Sa param.
0-1	2.7	13.9	16.2	2.6	13.3	15.7
1-2	25.4	32.4	26.2	23.1	26.2	22.8
2-3	49.9	34.2	26.8	43.2	28.4	24.0
3-4	67.8	35.7	27.8	59.9	33.5	26.7
4-5	80.2	28.4	25.3	74.4	33.0	26.8
5-6	88.3	29.4	26.1	85.8	32.4	27.0
6-7	94.0	24.8	24.6	93.3	26.0	25.0
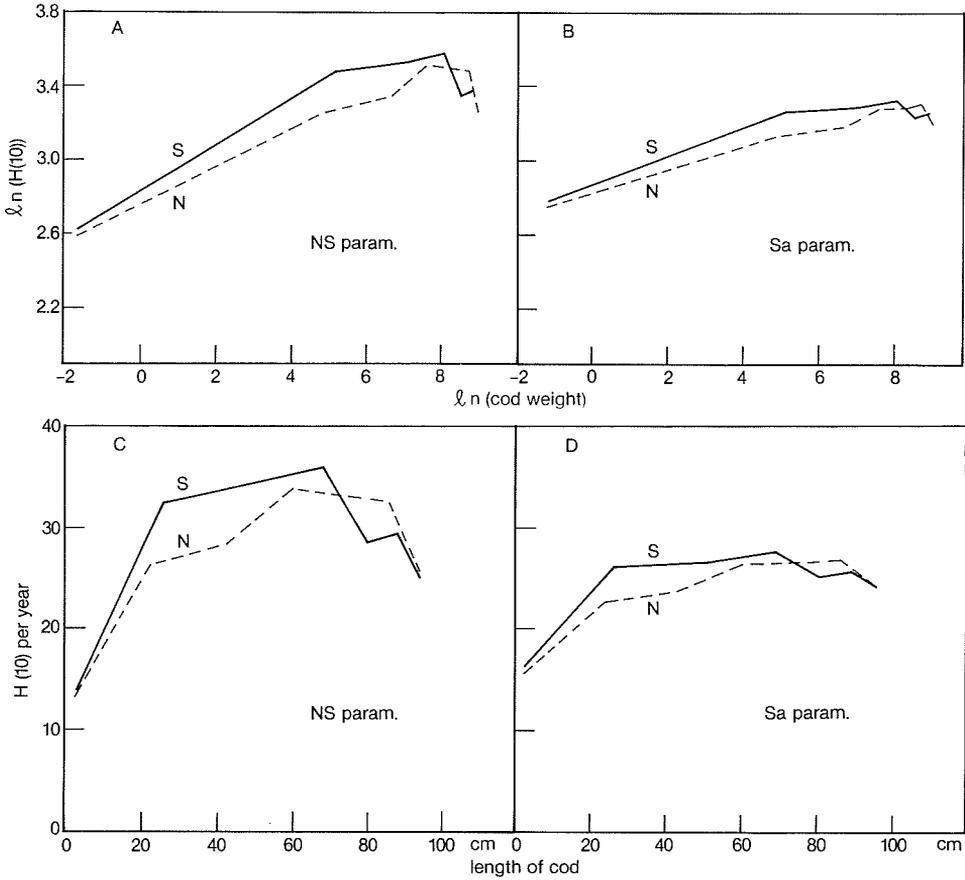
Fig. 8. North Sea cod. H as a function of body size.

tion of H is, however, supported by two independent sources of information namely, on the condition of the cod and on food concentrations.

Daan (1974) plotted the condition coefficient ($K = w/L^3$) against body length for the material of North Sea cod used in this paper (Fig. 9). Condition varies in
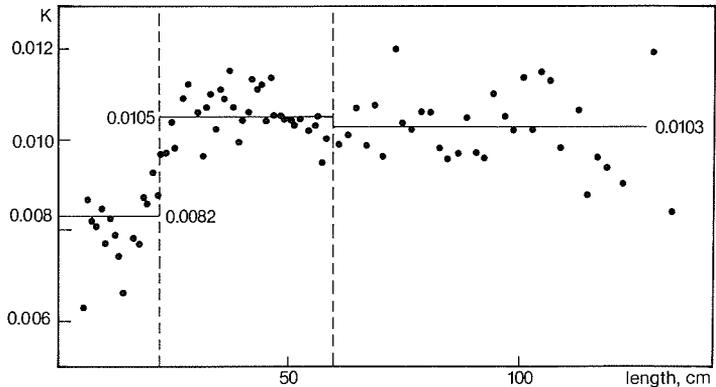
Fig. 9. Condition coef-
ficient in relation to
length in North Sea cod.
Horizontal lines repres-
ent mean values for dif-
ferent length ranges.
Points represent means
per cm-group.
From Daan (1974).

much the same way as the *H* values of Figs 8C and 8D, perhaps because of differences in food supply.

The available food as a function of body size can be estimated if only in a somewhat oblique way. Ursin (1982) has an estimate of the size frequency distribution of fish per square metre in the North Sea in 1971-72. The figures are
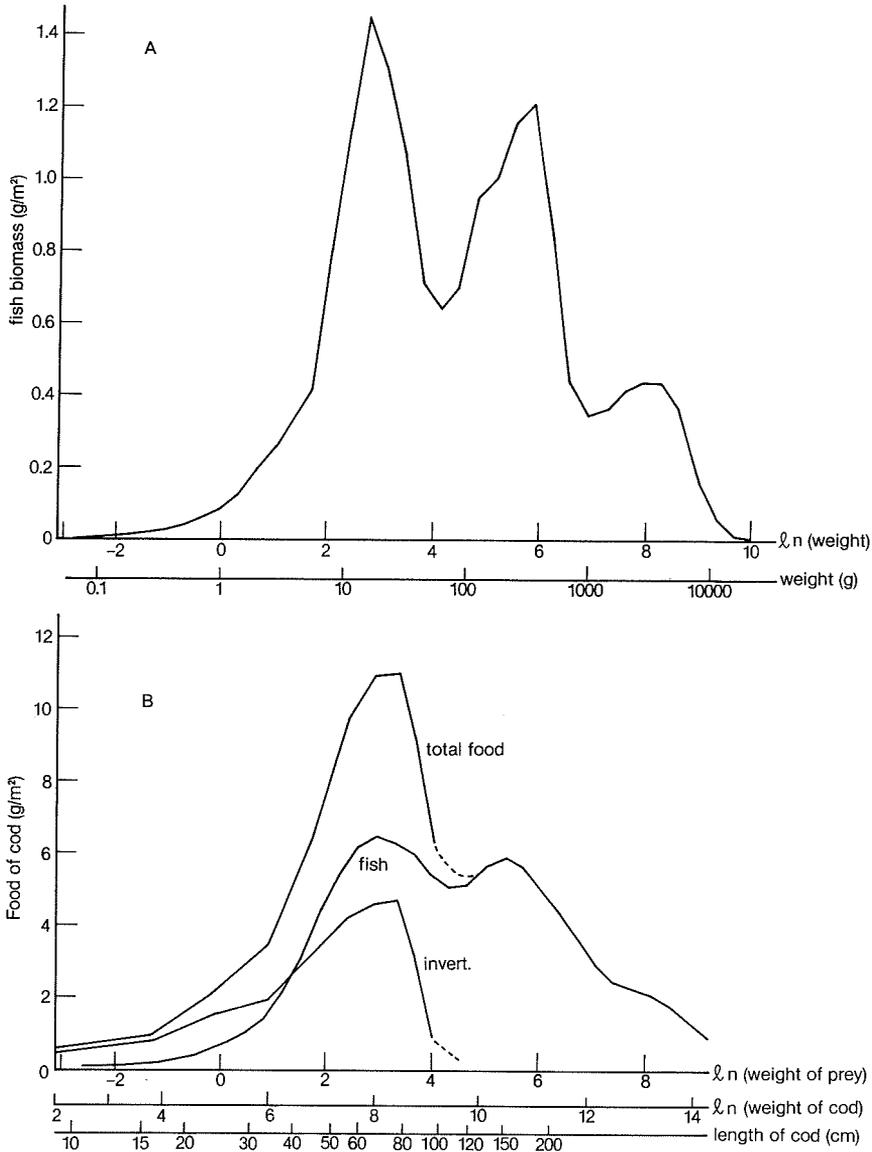
Fig. 10. North Sea. A, total fish biomass by logarithmic size classes of body weight. B, available food for cod by size classes of prey and of cod, assuming that the preferred predator: prey size ratio is independent of cod size.

numbers per logarithmic size class interval, the interval being $0.5 \ln 2 = 0.3466$. From this was calculated the biomass (g/m²) for the same size classes (Fig. 10A). The curve has three modes. The first is dominated by sprat (*Sprattus sprattus*), Norway pout (*Trisopterus esmarki*) and sandeels (*Ammodytes*). The second mode is dominated by old herring (*Clupea harengus*) and mackerel (*Scomber scombrus*) and the third by old saithe *(Gadus virens)* and cod. In order to estimate the amount of fish available for cod of different sizes we make the assumption that all fish species are equally good food, i.e., are equally accessible, equally appreciated. The sizes of prey consumed by cod were estimated by Ursin (1973) in terms of a log-normal distribution of predator : prey size ratios. The mean of the distribution was 5.11 with a standard deviation of 1.04. As an approximation it is assumed that everything within a range of 5.11 ± 1.04 is equally good and nothing else accepted. The antilogs give the median size ratio as 166:1 and the range as between 59:1 and 469:1. On the log scale the range is 2.08 or 6 size classes of Fig. 10A. Calculating moving sums of 6 therefore gives the biomass of fish available as food for each size class of cod, see Fig. 10B, the curve marked 'Fish'. Total available food is obtained from fish food and percentage fish in the stomachs as given by Daan (1973) for the Southern and the Northern North Sea separately (Table 3). Unfortunately, it is necessary to use the same data for fish food in both cases. Invertebrate food is found by subtraction. It is assumed that invertebrate food is as good (accessible, appreciated) as fish of the same size. If this is not the case it means that invertebrate biomasses were weighted by an unknown factor different from the factor of one allotted to fish biomasses. The factor is ρ in the notation of Andersen & Ursin (1977).

Results for the Southern North Sea are plotted in Fig. 10B. Food reaches a maximum for medium-sized cod. The relationship of H to food concentration (total available food) is shown in Fig. 11 (data from Table 3) with hyperbolas
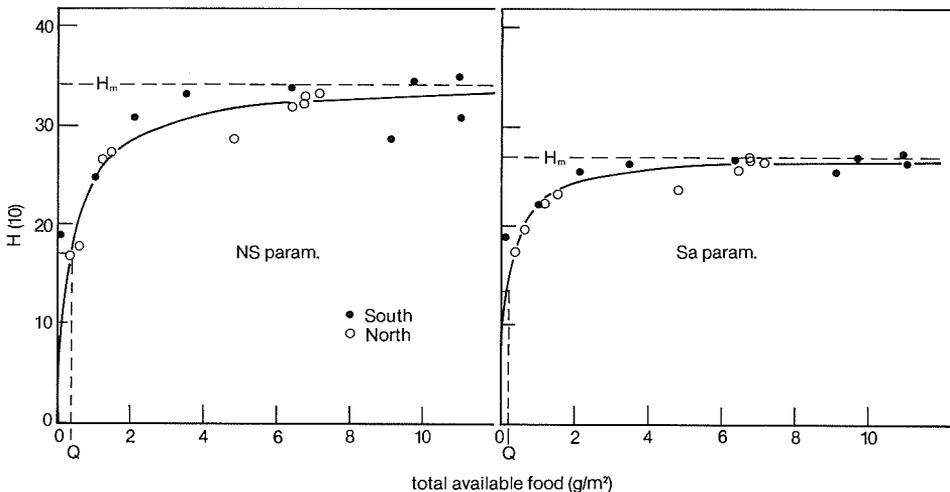
Fig. 11. North Sea cod. Satiation as indicated by H, as a function of food concentration.

Table 3. North Sea cod. Calculation of total available food from available fish and percentage of fish in stomach contents.

Length of cod (cm)	% fish in stomach	Food, g/m²			H	
		Fish	Invert.	Total	NS param.	Sa param.
Southern North Sea:						
9.0	27.6	0.027	0.071	0.098	19.0	19.0
16.6	17.8	0.174	0.804	0.978	24.8	22.3
24.2	27.0	0.570	1.542	2.112	31.0	25.6
34.4	43.1	1.488	1.962	3.450	33.2	26.2
43.8	52.9	3.360	2.994	6.354	33.9	26.6
54.6	56.7	5.514	4.212	9.726	34.7	27.0
64.4	57.9	6.336	4.602	10.938	35.0	27.4
76.0	57.3	6.324	4.710	11.034	31.0	26.3
84.3	65.3	5.958	3.168	9.126	28.8	25.6
96.0	85.5	5.400	0.918	6.318	–	–
Northern North Sea:						
7.7	5.0	0.017	0.323	0.340	16.8	17.5
14.1	18.7	0.106	0.460	0.566	17.9	19.7
24.5	50.9	0.590	0.569	1.159	26.6	22.6
33.8	70.4	1.046	0.439	1.485	27.4	23.4
43.6	68.6	3.310	1.516	4.826	28.8	23.7
54.0	85.1	5.446	1.954	6.400	32.1	25.6
65.4	89.5	6.372	0.748	7.120	33.2	26.6
76.8	93.9	6.301	0.409	6.710	32.9	27.0
85.4	88.2	5.908	0.790	6.698	32.5	27.0
97.9	94.3	5.350	0.324	5.674	–	–

fitted to the points. Designating by H_m the asymptotic value of H, by f the fraction of satiation achieved and by ϕ the total available food per m² we have: —

$$H = fH_m; \qquad f = \frac{\phi}{\phi + Q}$$

where Q is the half saturation constant. Omitting the aberrant value for the smallest size group in the Southern North Sea the estimates become: —

	H_m	$Q(g/m^2)$
NS parameters	34.2	0.378
Sa parameters	27.0	0.196

The cod is found to be almost satiated at the highest food concentrations. As shown below, there is reason to believe that H_m is underestimated and hence, satiation overestimated. The highest values of food concentration may be unrealistic because of overestimating the stocks of small fish (sprat, Norway pout, sandeels; Ursin 1977).

Estimates of H for other stocks

Fig. 12 and Table 4 contain data similar to those for the North Sea in Fig. 8B and Table 2, adjusted to North Sea temperature, 10°C. Mean values of ln$H$ calculated with Sa parameters suggest a trend with body size whereas NS parameters produce
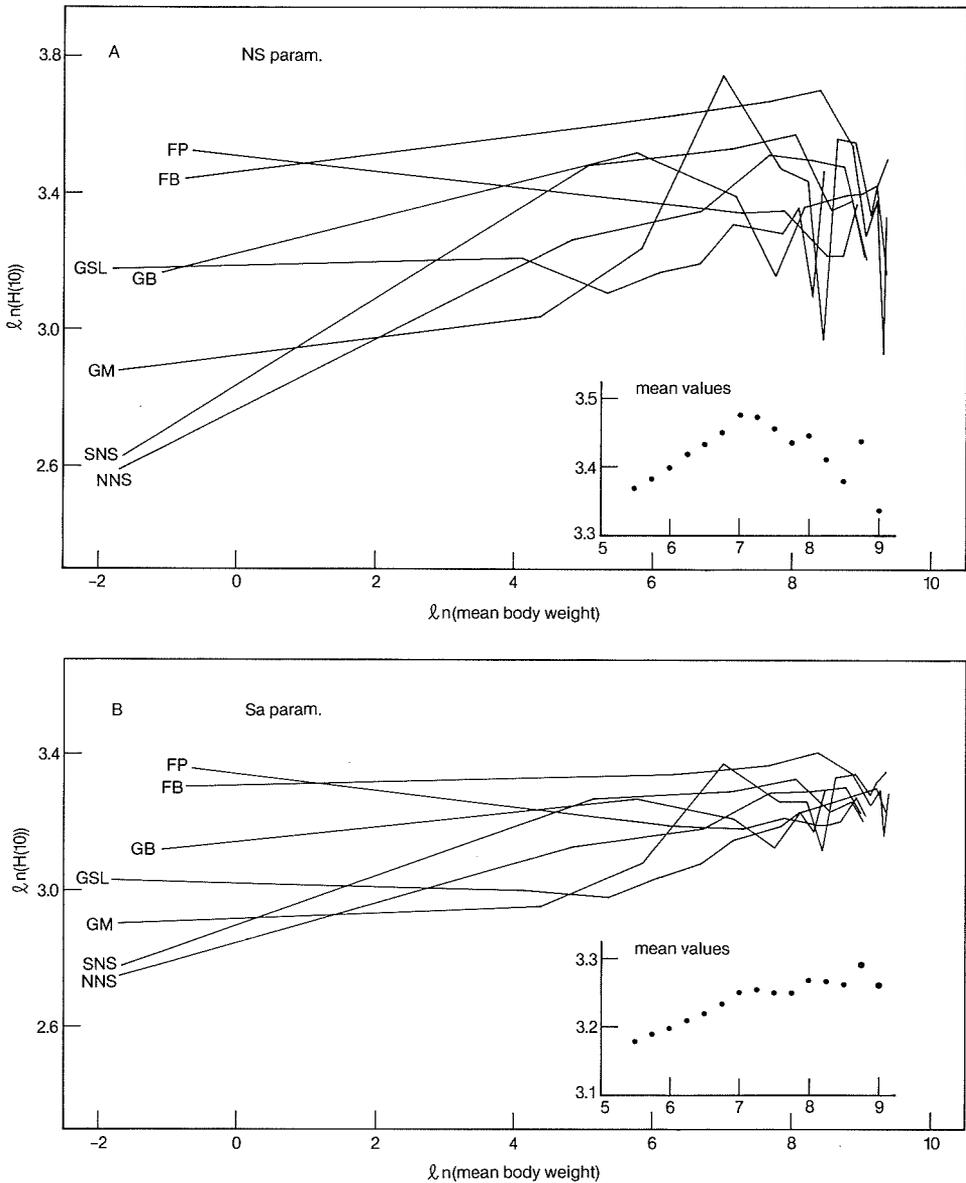
Fig. 12. All cod stocks. Variation of H, adjusted to 10°C with body weight on a log scale.

Table 4. Other than North Sea stocks. Body size and H values, original and adjusted to 10 °C. Lengths are in brackets when extrapolation was done.

Age	Mean length (cm)	NS param. H(T)	H(10)	Sa param. H(T)	H(10)	Mean length (cm)	NS param. H(T)	H(10)	Sa param. H(T)	H(10)	Mean length (cm)	NS param. H(T)	H(10)	Sa param. H(T)	H(10)
	Gulf of St. Lawrence ($T=3$°C)					Gulf of Maine ($T=6$°C)					Georges Bank ($T=8$°C)				
0-1	(2.5)	10.0	24.1	12.7	20.7	(2.6)	11.5	17.8	14.2	18.3	(3.2)	19.7	23.8	20.3	22.9
1-2	(18.3)	10.2	24.7	12.3	20.0	20.0	13.5	21.0	14.9	19.2	31.4	28.0	33.8	23.4	26.3
2-3	(27.6)	9.2	22.3	12.0	19.7	32.6	16.4	25.5	17.0	21.8	50.6	24.6	29.7	22.0	24.7
3-4	35.5	9.8	23.8	12.8	21.0	47.9	27.3	42.3	22.6	29.1	61.7	19.6	23.6	20.3	22.8
4-5	43.1	10.1	24.4	13.3	21.8	62.7	20.8	32.2	20.2	26.0	70.1	23.8	28.8	22.4	25.3
5-6	50.5	11.3	27.3	14.3	23.4	71.9	20.0	31.0	20.2	26.0	78.9	24.4	29.4	23.0	25.9
6-7	57.5	11.2	27.0	14.6	23.8	77.1	12.5	19.4	17.6	22.6	86.8	24.7	29.8	23.5	26.5
7-8	63.5	11.0	26.6	14.8	24.3	82.4	22.6	35.1	21.8	28.0	93.8	24.7	29.9	23.8	26.8
8-9	69.0	11.8	28.6	15.4	25.3	90.4	22.4	34.7	22.0	28.3	100.0	24.9	30.1	24.2	27.2
9-10	73.4	9.2	22.2	14.6	23.9	96.1	18.1	28.0	20.6	26.5					
10-11	77.6	13.2	32.0	16.4	26.9	100.2	19.7	30.6	21.4	27.6					
11-12						105.0	21.3	33.0	22.2	28.5					
	Faroe Bank ($T=8$°C)					Faroe Plateau ($T=8$°C)									
0-1	(3.6)	25.8	31.1	24.3	27.3	(3.7)	28.0	33.8	25.7	28.8					
1-2	(37.7)	31.4	37.9	25.0	28.2	(37.5)	24.0	29.0	21.4	24.1					
2-3	59.0	32.4	39.2	25.7	28.9	52.6	23.3	28.1	21.5	24.1					
3-4	75.8	33.6	40.5	26.5	29.9	64.1	23.6	28.5	22.1	24.9					
4-5	88.6	28.4	34.3	25.0	28.1	72.9	21.7	26.2	21.7	24.4					
5-6	95.7	22.0	26.6	22.9	25.8	79.4	20.8	25.1	21.6	24.3					
6-7	100.5	24.3	29.3	24.0	27.0	84.6	20.7	24.9	21.8	24.6					
7-8	102.8	15.5	18.7	20.9	23.5	90.3	24.0	28.9	23.4	26.3					
8-9	104.4	23.1	27.8	23.7	26.7	95.1	20.2	24.4	22.2	25.0					
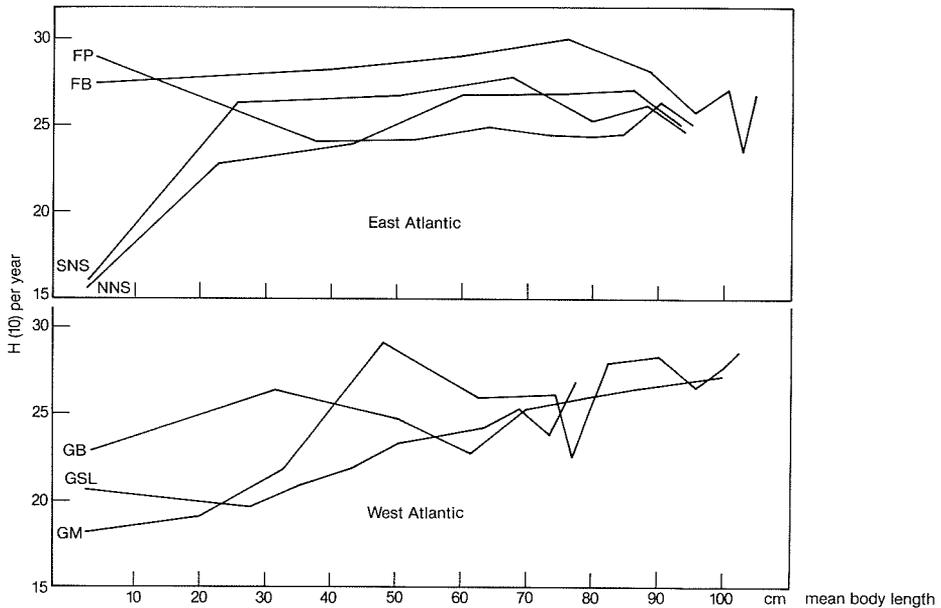
Fig. 13. Sa parameters only. Variation of H, adjusted to 10 °C, with length of cod.

Table 5. All cod stocks. Percentage satiation (by 10 cm length groups, interpolated) based on H_m estimates obtained by averaging the three highest H values for Faroe Bank cod.

| Length (cm) | NS parameters ($H_m = 39.3$) | | | | | | | Average |
	Gulf of St.Lawrence	Gulf of Maine	Georges Bank	S. North Sea	N. North Sea	Faroe Bank	Faroe Plateau	
10	62	49	67	50	46	82	84	63
20	62	53	76	71	57	90	80	70
30	58	63	85	83	68	93	76	75
40	61	85	81	85	71	97	74	79
50	69	104	76	87	78	98	72	83
60	68	86	63	89	85	100	72	80
70	70	79	73.	88	84	102	68	81
80		71	75	72	83	98	64	77
90		88	76	71	74	89	73	78
100		78	76			76		77
Aver.	64	76	75	77	72	92	74	

| Length (cm) | Sa parameters ($H_m = 29.3$) | | | | | | | Average |
	Gulf of St.Lawrence	Gulf of Maine	Georges Bank	S. North Sea	N. North Sea	Faroe Bank	Faroe Plateau	
10	70	64	81	66	63	94	96	76
20	68	66	85	81	75	95	91	80
30	69	73	89	90	79	96	86	83
40	74	86	88	91	81	96	82	85
50	80	98	85	92	86	98	82	89
60	82	91	80	93	91	99	84	89
70	86	89	86	93	92	101	84	90
80		87	89	86	92	100	83	90
90		96	91	88	95	94	89	92
100		94	93			92		93
Aver.	76	84	87	87	84	96	86	

a maximum for medium-sized cod. A similar maximum is discernible in the East Atlantic stocks even with SA parameters (Fig. 13). Changes in H with body weight therefore cannot be interpreted as a means of estimating a correction to any of the two estimates of m. They must be due to variation of the feeding level (satiation), with a tendency to food scarcity for small cod except in the Faroe area.

The degree of satiation (or feeding level, f) achieved by cod of different stocks and sizes can be calculated using North Sea results. However, Faroe Bank cod achieve H values above the estimated H_m values. The feeding levels in Table 5 were calculated on the assumption that an average of the three highest consecutive values of H for Faroe Bank cod (Table 4) is the asymptotic value. This makes the North Sea asymptotes correspond to 87% (NS) or 92% (Sa) satiation. The main difference between the two sets of estimates is that Sa parameters lead to the conclusion that all stocks are nearer satiation, 86% on an average, against 76%

with NS parameters. The two agree that Faroe Bank cod are nearest satiation and
Gulf of St. Lawrence cod farthest from it.

These results depend critically on the temperature corrections. Assuming 2 °C
instead of 3 °C would bring Gulf of St. Lawrence cod on level with other stocks.
Yet, if 3 °C is a wrong choice, then 4 °C, rather than 2, seems more realistic.
Another problem is whether the temperature functions adopted are realistic. Fig.
14 illustrates their effects. Again, more drastic corrections might have brought the
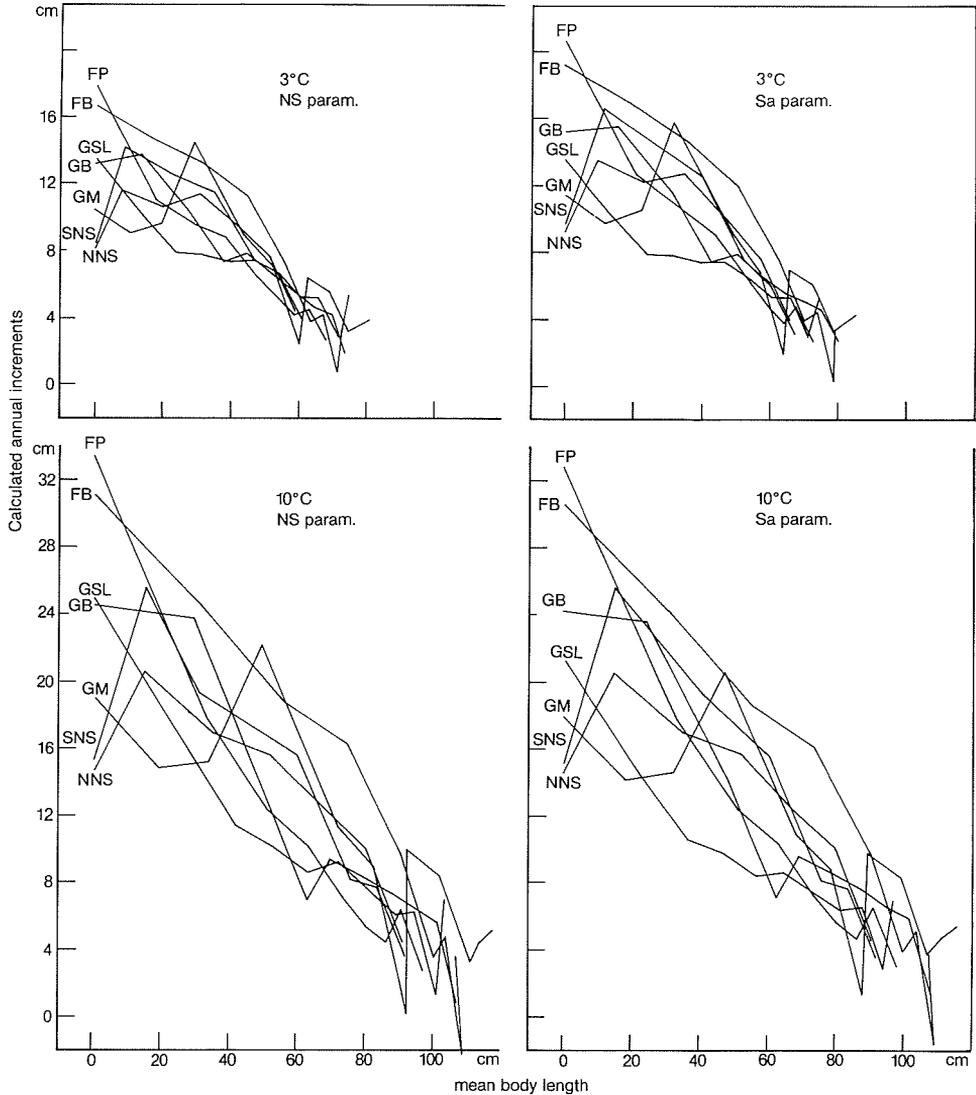
Fig. 14. All cod stocks. Calculated annual increments after adjustment to 3 °C and 10 °C. Compare with
the unadjusted increments of Fig. 5.

Table 6. $H_m w^m$ (proportional to daily ration) as a function of body size.

Weight (g)	NS parameters $m = 0.58$; $H_m = 39.3$	Sa parameters $m = 0.69$; $H_m = 29.3$	Ratio Sa/NS
1	0.11	0.08	0.74
10	0.41	0.39	0.96
100	1.56	1.92	1.23
1000	5.92	9.42	1.59
10000	22.52	46.15	2.05

Gulf of St. Lawrence cod on level with others, but there is at the moment not much reason to believe that temperature dependence of growth is underestimated in this paper.

The often minute differences between results obtained with the two sets of parameter values in spite of considerable differences between these should not lead to the conclusion, that it does not matter which of them (if any) is correct. The difference between them is spelled out when food consumption is calculated. Making the same assumptions on the efficiency of assimilation and on apparent specific dynamic action in the two cases, the daily ration becomes proportional to Hw^m. Table 6 shows for $H = H_m$ as estimated from Faroe Bank data, that in large cod the daily ration depends by a factor 2 upon the choice of parameter set. With the values of conversion efficiency parameters adopted by Majkowski & Waiwood (1981) the actual daily rations would be about twice the values in Table 6.

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