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A Note on the Growth of the Arctic Cod and Haddock.

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I. Basic data.

When examining some growth data for Arctic cod and haddock attempts were made to apply the Bertalanffy growth function. The empirical basis for the use of this function is that the rate of growth in length of the fish declines in linear relation to the length. To test this one can plot l_{t+1} against l_t (the "Walford transformation") or $l_{t+1} - l_t$ against l_t. Figures 1 and 2 show the last type of plot for available data for cod and haddock. (The USSR data are used with the kind permission of dr. Ju. Ju. Marty, VNIRO). Most of these plots do not coincide with the Bertalanffy type of growth pattern. On the contrary it is indicated that the growth rate at first increases to a maximum value for intermediate fish sizes, and then decreases for larger sizes. This means that the growth curve for length has an inflection.

It is necessary to discuss whether this unusual growth pattern could be the effect of biased sampling. The cod data and part of the haddock data are mean length of age groups of fish caught by trawl (and for Norway partly by long-line). The trawl mesh size used is probably around 80 mm. The selection range for cod of this mesh size is approximately 21 - 37 cm, for haddock 19 - 35 cm. When an age group is growing through the selection range, the mean length as evaluated from samples taken by trawl will be biased. In the present case it is probable that the data are not significantly biased by gear selectivity for mean lengths from approximately 45 cm and upwards. No bias from gear selectivity can appear in the growth data from scales shown for haddock.

Peculiar to the stocks of Arctic cod and haddock is the comparatively long interval between the juvenile stage and maturity. It is in this adolescent stage that the increase of rate of growth occurs. This adolescent growth pattern may not be a particular phenomenon for the Arctic stocks of cod and haddock. The often low age of first maturity of many of our best known fish species would usually make it difficult to observe such a growth stage. In the Arctic halibut which matures at the age of 8 - 10 years, a similar increase of rate of growth in the adolescent stage has been found. (Tjemsland, Bergen, in manuscript).

As a next step plots of $\lg l_{t+1} - \lg l_t$ against $\lg l_t$ were tried. These plots are shown in figures 1 and 2.

II. Discussion of the Gompertz equation.

The plots of $\lg l_{t+1} - \lg l_t$ against $\lg l_t$ suggest a linear relationship which means that the data would fit the Gompertz equation:

(1) $$l_t = b \cdot e^{-\frac{1}{k} \cdot e^{a-kt}}$$ (See Beverton & Holt (1957) p. 97 eq. (9.1))

because this equation can be modified to

$$\lg l_{t+1} - \lg l_t = (1 - e^{-k}) \lg b - \lg l_t (1 - e^{-k})$$

The constants of integration, a and b, of the Gompertz equation (1) can be defined by the conditions:

$$l_t = L_\infty \text{ for } t = \infty$$

$$l_t = l_{t_o} \text{ for } t = t_o$$

In this way we find that $b = L_\infty$ and $k \cdot \lg \frac{L_\infty}{l_{t_o}} = e^{a-kt_o}$

Equation (1) can therefore be written on the following form

(2) $$\lg \frac{l_t}{l_{t_o}} = \lg \frac{L_\infty}{l_{t_o}} \left[1 - e^{-k(t-t_o)} \right]$$

For $\lg l_{t_o} = o$ i.e. $l_{t_o} = 1$

(3) $$\lg l_t = \lg L_\infty \left[1 - e^{-k(t-t_o)} \right]$$

If in (3) we substitute $\lg l_t$ by l_t we obtain the Bertalanffy equation

(4) $$l_t = L_\infty \left[1 - e^{-k(t-t_o)} \right]$$

The biological significance of the difference between equations (3) and (4) is that the Bertalanffy relationship is concerned with absolute rate of growth, that of Gompertz concerns relative growth rate since $\frac{d}{dt}\left[\lg l\right] = \frac{1}{l}\frac{dl}{dt}$. The significance of the parameters t_o and k of the two equations differs accordingly. Thus in (4) t_o is the value of t for $l = o$, but in (3) the value of t for $\lg l = o$. For k the difference can be appreciated from the following mathematical expressions of the relative change of growth rates:

$$\frac{d}{dt}\left(\frac{dl}{dt}\right) = -k\frac{dl}{dt}$$ (Bertalanffy)

$$\frac{d}{dt}\left(\frac{1}{l}\frac{dl}{dt}\right) = -k\left(\frac{1}{l}\frac{dl}{dt}\right)$$ (Gompertz)

The Gompertz curve has an inflection at $l_t = \frac{L_\infty}{e}$ (e = basis of Naperian logarithm).

Assuming that the relation between weight and length of the fish is $w = q \cdot l^n$, the Gompertz equation for growth in weight will be

(5) $$\lg \frac{w_t}{w_{t_o}} = \lg \frac{w_\infty}{w_{t_o}} \left[1 - e^{-k(t-t_o)} \right]$$

For $\lg l_{t_o} = o$ $w_{t_o} = q$ and equation (5) becomes

$$\lg \frac{w_t}{q} = \lg \frac{w_\infty}{q} \left[1 - e^{-k(t-t_o)} \right]$$

The inflection point is at $w_t = \frac{w_\infty}{e} \approx .368\, w_\infty$. For the Bertalanffy relation the inflection is at $w_t = \left(\frac{n-1}{n}\right)^n \cdot w_\infty$ which gives the value $.296 w_\infty$ for $n = 3$.

III. Fit of data to Gompertz equation.

The methods of estimating the parameters of the Gompertz equation are analogous to those for the Bertalanffy equation. Tables 1 and 2 show the observed lengths, and the estimated parameters and lengths from groups of data of Arctic cod and haddock and also for North Sea cod and haddock (data from Beverton and Holt, 1957). Figure 3 shows the fit of the estimated growth curves to the observations.

IV. Growth and population density.

Two sets of growth data for Arctic cod and one set for Arctic haddock were used to compare growth and population density. The most extensive data are Rollefsen's observations of the growth of the "skrei" which comprise the year-classes 1926-47. These were grouped in slow -, medium -, and fast growing fish (B, A and C of tables 1 and 3). The catch in numbers per gill net vessel per week, of each yearclass over the age range 8 - 11 years were used as an index of its abundance. When estimating the population density to relate to the growth of a yearclass the abundance of the nearest preceding and succeeding yearclasses were added to that of the yearclass itself. The mean population density indices for each group of yearclasses estimated in this way are compared with the values of L_∞ and K in table 3.

The other set of cod data compares immature cod from Region I in a prewar and a postwar period (groups D and E of table 1). Use has been made of both English and Norwegian catch data to estimate stock density. For the postwar period the catch per unit effort of English trawlers of age groups 5 - 7 in Region I is taken as an index of abundance of each yearclass. The ratio of this abundance index to that obtained in Lofoten on higher age groups of the same yearclass shows little variation for the yearclasses 1942-48. The mean value of these ratios has therefore been used to estimate the abundance of the age groups 5 - 7 of the prewar yearclasses 1927-34 from the Lofoten data (which give their abundance over the age range 8 - 11 years). Finally, the mean values of the abundance of age groups 5 - 7 are taken as the population density index with which to relate the growth data from each year of sampling.

For haddock the data compares the growth of the yearclasses 1943 and 1948 in Region I (groups D and E of table 2). The index of stock density is the catch per unit effort of English trawlers in Region I in the years 1946/48 and 1951/53 respectively.

Figure 4 shows plots of the relative variations of L_∞ and stock density index and K and stock density index. There is a clear indication in the data of a decrease of L_∞ with increasing population density. The bottom graph suggests that this change in L_∞ is mainly an effect of a change of K. (This K is not equivalent to the Bertalanffy K, see section II).

An example of a difference in growth where the value of K is the same is offered by groups B and C of Arctic haddock (see table 2). These are fast- and slow growing groups of fish of the same yearclass. Their external growth environment has probably been largely the same, and the difference in the growth of the two groups should therefore be ascribed to differences in the internal environment.

Table 1. Fit of data to Gompertz's equation. Observed lengths and estimated parameters and lengths for groups of data of Arctic cod and for North Sea cod.

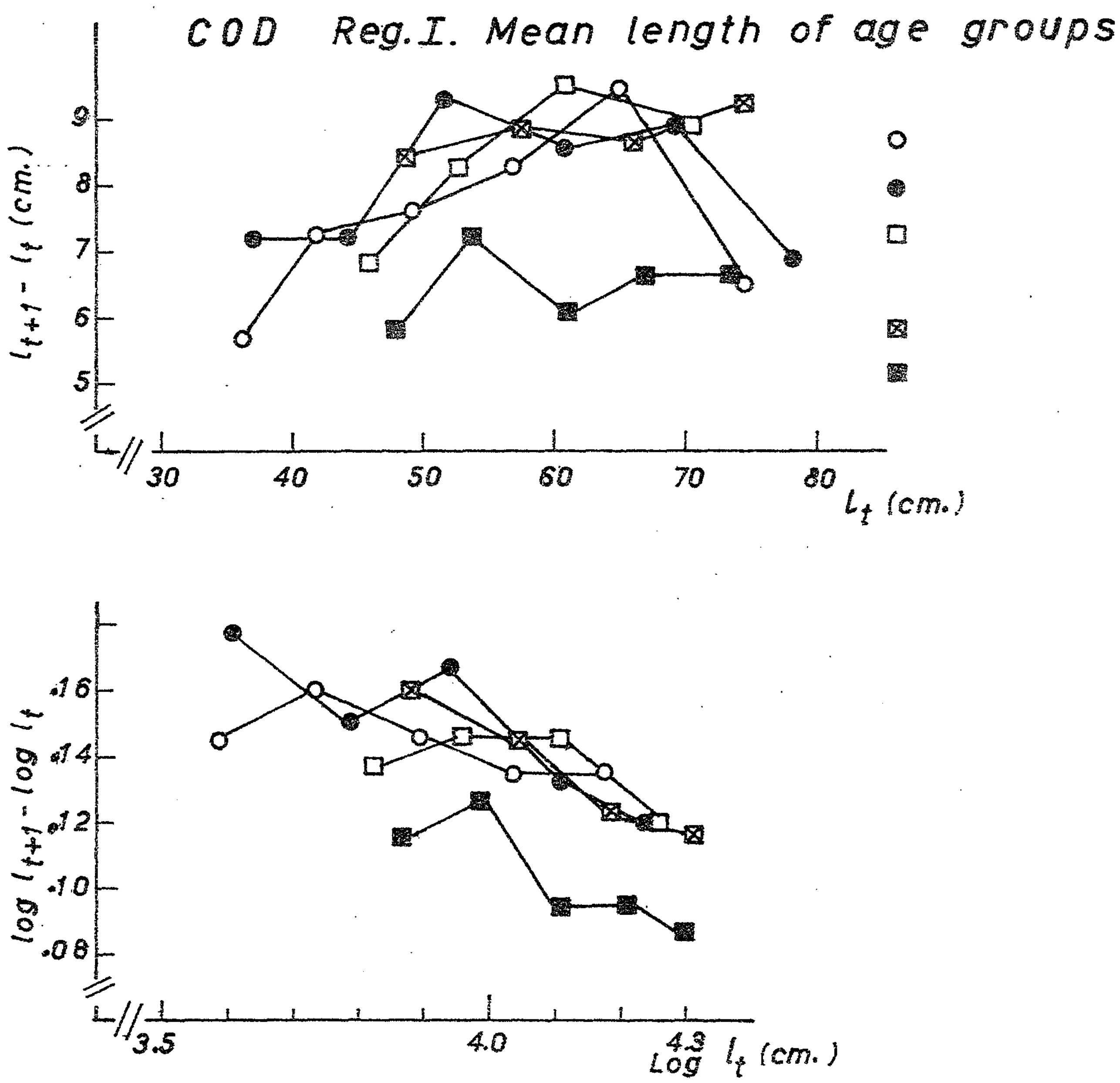
	ARCTIC COD										NORTH SEA COD		
	Reg. I, Norway 1934, -35, -37, -38, -39.		Reg. I, USSR and Norway, 1949-58		Reg. IIa, Norway Yearclasses 1925, -28, -29, -30, -38, -39		Reg. IIa, Norway Yearclasses 1931 - 37.		Reg. IIa, Norway Yearclasses 1926, -27, 1940-47.		Beverton & Holt (1957) table 16.6		
	D		E		A		B		C		F		
t	l_t obs.	l_t estim.	l_t obs.	l_t estim.	l_t obs.	l_t estim.	l_t obs.	l_t estim.	l_t obs.	l_t estim.	t	l_t obs.	l_t estim.
4	47.8	47.0	46.1	45.6							1	18	18.3
5	53.7	53.8	53.5	53.8							2	36	35.4
6	60.9	60.9	62.2	62.4							3	55	53.3
7	67.0	67.0	71.0	71.2							4	68	68.7
8	73.6	74.0	80.1	80.0							5	78	80.2
9	80.2	80.1			84.9	84.8	80.2	80.3	87.6	87.5	6	89	88.5
10					88.0	88.2	84.4	84.4	91.1	91.3			
11					91.2	91.2	88.1	88.1	94.9	94.9			
12					94.1	94.0	91.4	91.2	98.5	98.3			
	L_∞ = 133.6 cm		L_∞ = 205.3 cm		L_∞ = 117.4 cm		L_∞ = 109.6 cm		L_∞ = 134.2 cm			L_∞ = 103.5 cm	
	K = .143		K = .117		K = .126		K = .176		K = .106			K = .48	
	t_o = -6.8		t_o = -6.8		t_o = -12.3		t_o = -6.4		t_o = -14.0			t_o = -1.05	

Table 2. Fit of data to Gompertz's equation. Observed lengths and estimated parameters and lengths for groups of data of Arctic haddock and for North Sea haddock.

	ARCTIC HADDOCK Reg. I, USSR 1950-58; Norway 1949-53. Mean length of age groups. A		1948-yearclass from scales. Fish mature at 5 years. B		1948-yearclass from scales. Fish not mature at 6 years. C		1943-yearclass from scales sampled spring 1949. D		1948-yearclass from scales sampled autumn 1953. E		NORTH SEA HADDOCK Beverton & Holt (1957) Table 16.5 F	
t	l_t obs.	l_t estim.	l_t obs.	l_t estim.	l_t obs.	l_t estim.	l_t obs.	l_t estim.	l_t obs.	l_t estim.	l_t obs.	l_t estim.
1			17.8	17.6	16.2	16.1	17.0	17.1	17.4	17.2	17.0	18.2
2	25.8	25.7	25.3	25.3	22.7	22.9	24.6	24.0	23.9	24.2	24.5	24.1
3	32.9	33.1	33.5	33.9	30.3	30.3	30.7	30.9	31.9	32.0	29.5	29.3
4	40.2	40.2	43.1	42.9	38.0	38.1	36.6	37.4	40.2	40.1	33.5	33.6
5	46.9	46.9	51.7	51.9	46.1	45.8	43.4	43.2	48.0	48.1	37.0	37.1
6	52.8	52.8									40.0	39.8
7	58.0	57.9										
	L_∞ = 80.2 cm		L_∞ = 113.3 cm		L_∞ = 97.5 cm		L_∞ = 67.7 cm		L_∞ = 105.0 cm		L_∞ = 47.0 cm	
	K = .25		K = .217		K = .217		K = .28		K = .21		K = .35	
	t_o = -3.4		t_o = -3.3		t_o = -3.3		t_o = -3.0		t_o = -3.5		t_o = -3.0	

Table 3. L_∞, K and population density index for two sets of data for Arctic cod and one set of data for Arctic haddock. For definition of groups see tables 1 and 2.

	L_∞	Rel. variation L_∞	K	Rel. variation K	Population Density index	Rel. variation Density
ARCTIC COD						
Skrei						
Group A	117.4	.98	.126	.93	2282	1.01
" B	109.6	.91	.176	1.29	2985	1.32
" C	134.2	1.11	.106	.78	1494	.67
Young cod						
Group D	133.6	.79	.143	1.10	70.0	1.26
" E	205.3	1.21	.117	.90	40.7	.74
ARCTIC HADDOCK						
Group D	67.7	.78	.28	1.14	210	1.33
" E	105.0	1.22	.21	.86	106	.67



○ USSR Reg. I 1946-51

● USSR Reg. I 1952-58

□ Norway March-June 1949-58

⊠ Norway October 1949-58

■ Norway 1934-39

Fig. 1. Growth data from mean length of age groups of Arctic cod. Plots of $l_{t+1} - l_t$ against l_t and $\lg l_{t+1} - \lg l_t$ against $\lg l_t$ for same data.

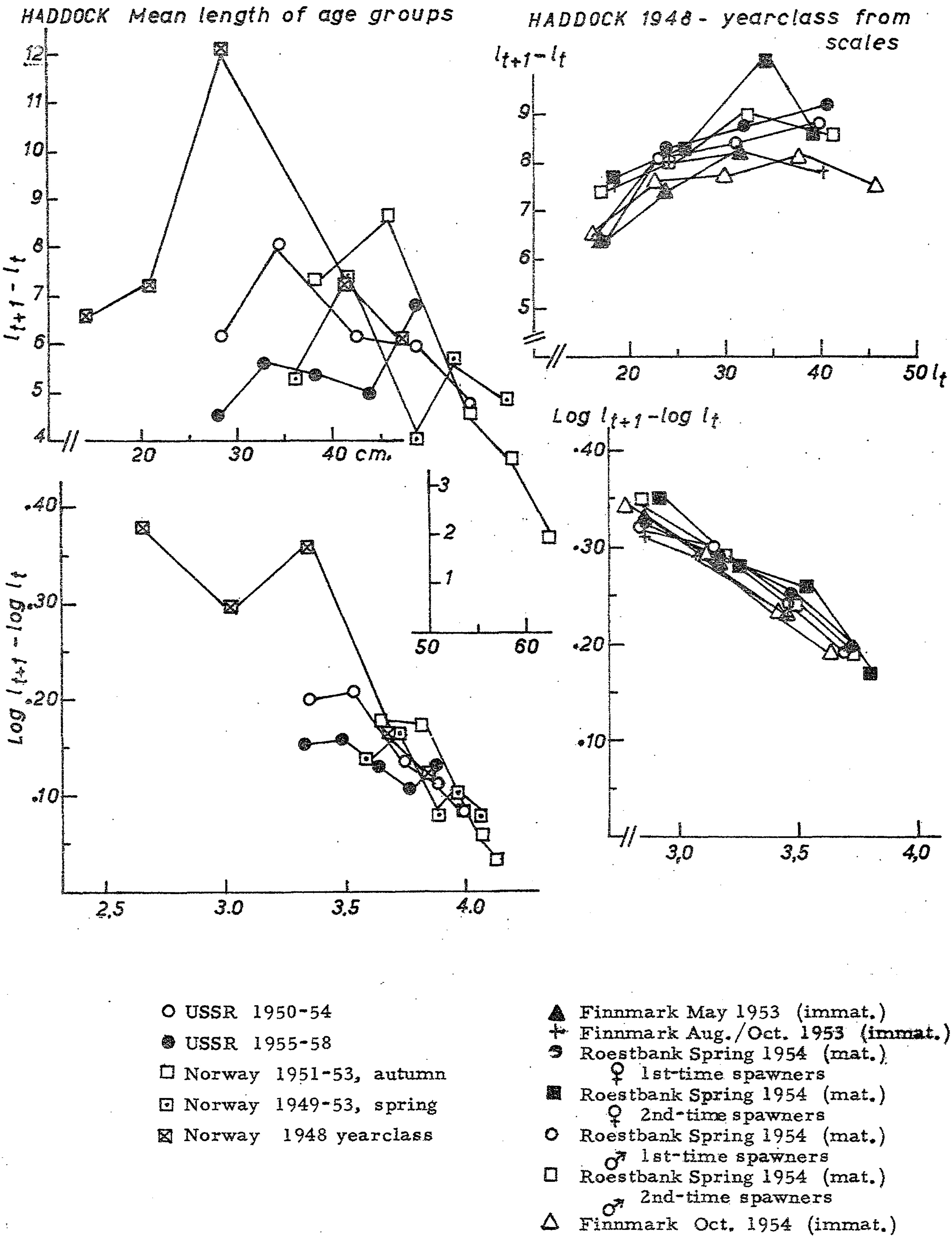


Fig. 2. Growth data from mean length of age groups and from scales of Arctic haddock. Plots of $l_{t+1} - l_t$ against l_t and $\lg l_{t+1} - \lg l_t$ against $\lg l_t$ for same data.

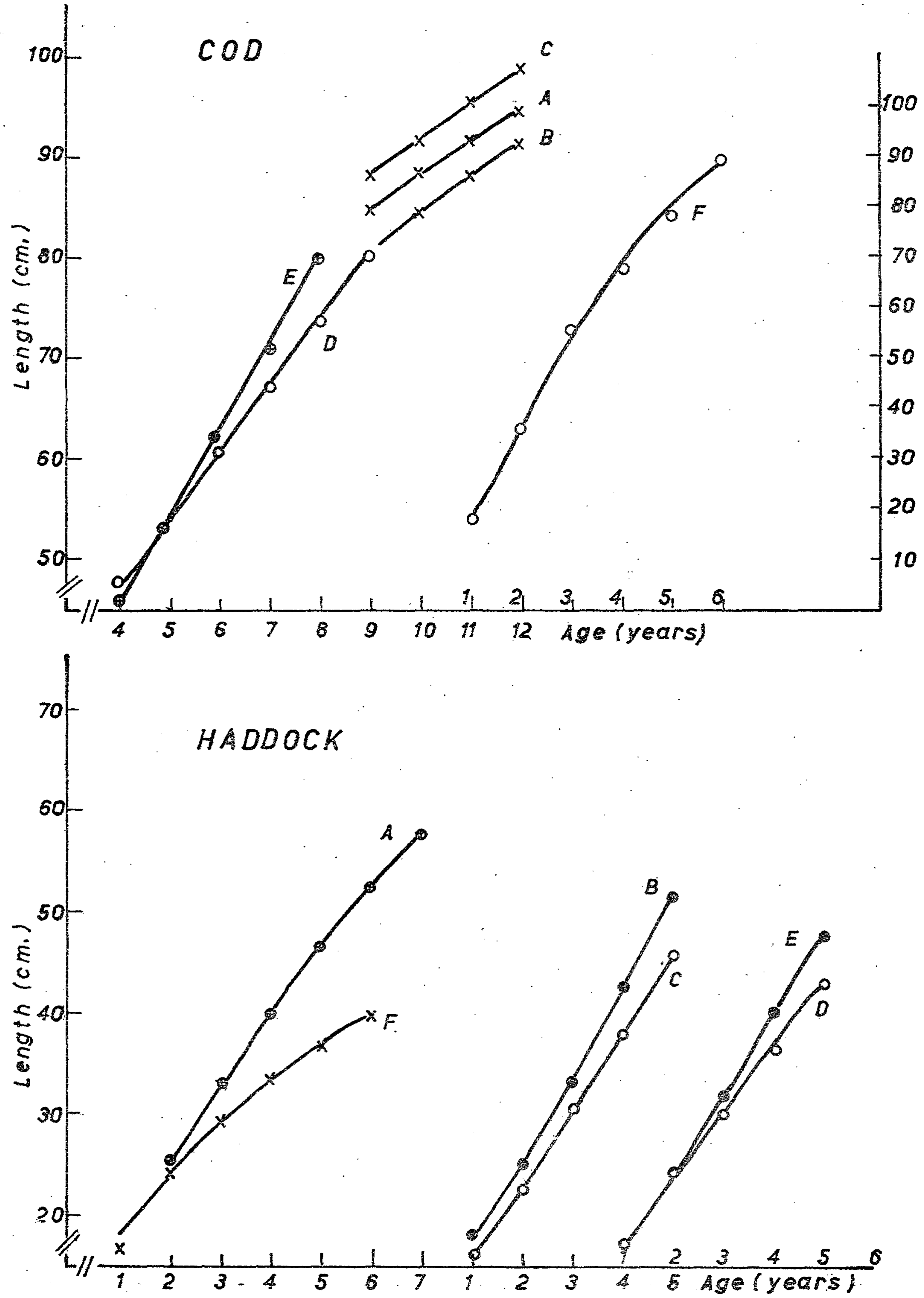


Fig. 3. Fit of data to Gompertz' equation. A - E Arctic stocks, F North Sea stocks. For further explanation see tables 1 and 2.