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Modelling environmentally induced change in size at age for Atlantic Canada cod stocks

by

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ABSTRACT

Length at age data was used to fit a growth curve in which the predicted yearly increment in length is a function of the environmental factors prevelant during that year. The analysis was performed on seven NAFO regional cod stocks, with inclusion of the environmental factors population density and bottom temperature. These environmental factors were highly significant and explained as much as two thirds of the variability in the data.

RESUME

On s'est servi des données sur la longueur selon l'âge pour établir une courbe de croissance dans laquelle les augmentations annuelles de longueur prévues sont fonctions des facteurs environnementaux présents durant l'année considérée. L'analyse a porté sur sept stocks régionaux de morue de l'OPANO et a pris en compte comme facteurs environnementaux la densité de population et la température du fond. Ces facteurs se sont avérés très importants et ont permis d'expliquer la variabilité des données, dans une proportion allant jusqu' à deux tiers.

INTRODUCTION

We developed an equation for growth that utilizes environmental information to predict incremental yearly growth. Our model is a modification of the conventional three parameter (L_∞, k, a) von Bertalanffy growth curve (for length). We can test whether the environmental factors are statistically significant from the difference in residual sum of squares between our model and the conventional von Bertalanffy.

Although the von Bertalanffy growth curve is deduced on physiological grounds (von Bertalanffy 1938; Gulland 1983), this study is empirical. The conventional von Bertalanffy growth curve was chosen as a suitable base model because it models expected length as a monotone increasing function of age with an asymptotic limit L_∞. We seek the modification to the von Bertalanffy growth curve that best models observed length at age data. There are several ways in which the modification can be performed, we have considered three:

1. Environment dependent growth parameter k. L_∞ fixed.
2. Environment dependent asymptotic length L_∞. k fixed.
3. As for 2, but where loss in growth is unrecoverable. k fixed.

There are other possible modifications, for example, one could formulate both k and L_∞ to be environment dependent. This possibility has not been pursued since we felt that modelling environmental dependence in both k and L_∞ would be an overparametrization. As our analyses subsequently show, the three modifications above are flexible enough to model environmental dependence of growth.

A notable feature of our model is that it is derived by modelling predicted (expected) growth *increments* to be environmentally dependent. For each yearclass we sum the environmentally dependent predicted growth increments to get an environmentally dependent predicted growth trajectory for that yearclass. (We use the term "growth trajectory" rather than "growth curve" because the fitted growth model is no longer a smooth curve since it reacts to changing environmental conditions. Also, every yearclass has a different growth trajectory.) The parameters of our model are estimated by minimizing the (weighted) squared difference between the predicted growth trajectory and the observed length at age data.

THE DATA

Length at age data from research cruises were used. We had cod data available for NAFO regions 2J,3K,3L,3N,3O,3Ps and 4TVn. The environmental information used was stock biomass and water temperature anomoly. The temperature anomoly data was derived from Station 27 (Lat. 47°32.8′N, Long. 52°35.2′W) bottom depth (176m) measurements from 1946 to 1989. Petrie et al. (1988) showed the temperature data at Station 27 to be correlated to the temperature at Hamilton Bank (Lat. 54°N, Long.55°W). Thus, we felt that Station 27 temperature anomolies should be reasonable indices of temperature anomoly for the NAFO regions we analyzed.

THE MODELS

The environmentally dependent growth models are modifications of the three parameter (L_∞, k, a) von Bertalanffy, given by

$$L_t = L_\infty(1 - ae^{-kt}) \tag{1}$$

where L_t is the expected length of a fish at age t.

The environmental conditions experienced by a fish in a given year will affect the growth increment in that year more than it will affect the fishes overall length (since that is a composite of the life history of the fish). So, we modified growth increments to be environmentally dependent. This required rewriting equation (1) in a form that gives the expected increase in length between ages $t-1$ and t (Gulland 1983, pg 91),

$$\begin{aligned} L_1 &= L_\infty(1 - ae^{-k}) \quad \text{and} \\ L_t - L_{t-1} &= (L_\infty - L_{t-1})(1 - e^{-k}) \quad t = 2, \ldots. \end{aligned} \tag{2}$$

The environmental effects are modelled by allowing k or L_∞ in equation (2) to be functions of the environmental conditions.

Environmental conditions experienced by fish will vary from year to year and from habitat to habitat. Thus we need to consider the possibility that different age fish will experience different environmental conditions in the same year. To allow for this, we denote by $k(i,t)$ the value of the growth parameter k determined by environmental conditions for an age t fish in year

i. Similarly for $L_\infty(i,t)$. For example, $L_\infty(1985,7)$ denotes the value of the asymptotic length that is applicable in 1985 for a 7 year old fish. Specification of possible functional forms of $k(i,t)$ and $L_\infty(i,t)$ is left to the next section.

Our modification fits the same growth model to all yearclasses, yet every yearclass has a different expected growth trajectory since no two yearclasses experience the same environmental conditions. For ease of notation the models are presented for the yearclass of fish spawned in 1970. Then (if L_∞ is environment dependent), $L_\infty(1970+t,t)$ denotes the applicable asympotic length to be used in equation (2) for the 1970 yearclass at age t.

Model 1. Environment dependent k.

Since k is now a function of environmental variables we write (2) as

$$\begin{aligned} L_1 &= L_\infty(1-ae^{-k(1971,1)}) \quad \text{and} \\ L_t - L_{t-1} &= (L_\infty - L_{t-1})(1-e^{-k(1970+t,t)}) \quad t=2,\ldots. \end{aligned} \tag{3}$$

Summing these growth increments gives the expected length at age (the growth trajectory). The expected length of an age t fish in the 1970 yearclass is

$$L_t = L_\infty\left(1 - a\exp(-\sum_{i=1}^{t} k(1970+i,i))\right) \tag{4}$$

Note that (4) reduces to (1) when environmental conditions are "steady", because then $k(1970+i,i)=k,\ i=1,\ldots,t$.

Model 2. Environment dependent L_∞.

For the 1970 yearclass this model is specified by

$$\begin{aligned} L_1 &= L_\infty(1971,1)(1-ae^{-k}) \quad \text{and} \\ L_t - L_{t-1} &= (L_\infty(1970+t,t) - L_{t-1})(1-e^{-k}) \quad t=2,\ldots. \end{aligned} \tag{5}$$

As before, summing these growth increments gives the growth trajectory.

For older fish it is possible that $(L_\infty(1970+t,t)-L_{t-1})$ may be negative (this could occur in "bad" years in which the temperature is extremely cold), implying that the fish lost length in that year. In using this model we decided not to allow the possibility of fish loosing length by setting $L_t = L_{t-1}$ when $L_\infty(i,t) < L_{t-1}$.

REMARK. In models 1 and 2 the change in growth due to environmental factors is, in a sense, temporary. For example, if environmental conditions are very unfavourable for age t fish in year i then the expected size increase in that year will be reduced. This will be modelled by a relatively small value of $k(i,t)$ or $L_\infty(i,t)$. Upon return to more normal environmental conditions the fish will gradually recover the lost growth, bit by bit each year. The next model is a modification of Model 2 whereby the environmental effects on growth are permanent. The growth lost in a bad year is not recoverable (though it may be offset by favourable conditions in subsequent years).

Model 3. Environment dependent L_∞ (permanent effect).

For the three parameter von Bertalanffy an alternative way to represent the expected increase in length between ages $t-1$ and t is

$$L_t - L_{t-1} = L_\infty a e^{-k(t-1)}(1-e^{-k}) \quad t = 2,\ldots. \tag{6}$$

The value L_∞ can be regarded as the asymptotic length of a fish under stable environmental conditions. To include environmental effects, we write (for the 1970 yearclass)

$$L_t - L_{t-1} = L_\infty(1970+t,t) a e^{-k(t-1)}(1-e^{-k}) \quad t = 2,\ldots. \tag{7}$$

The difference in growth between equations (6) and (7) is

$$(L_\infty - L_\infty(1970+t,t)) a e^{-k(t-1)}(1-e^{-k}),$$

which will be denoted by $d(1970+t,t)$. Model 3 is the growth trajectory given by retaining the values $d()$ throughout the life of the fish, i.e., the expected length at age t of a fish in the 1970 yearclass is

$$L_t = L_\infty(1 - a e^{-kt}) - \sum_{i=1}^{t} d(1970+i,i) \tag{8}$$

One could also modify model 1 (environment dependent k) in a similar fashion.

PARAMETRIZATION OF ENVIRONMENTAL EFFECTS

Recall that the growth parameter k that is applicable for the age t yearclass of fish in year i (i.e., the $i-t$ yearclass) was denoted $k(i,t)$. Since we used population density and temperature as evironmental variables, we can write $k(i,t) = k(\text{density}(i,t), \text{temp}(i,t))$ where $\text{density}(i,t)$ and $\text{temp}(i,t)$ are the density and temperature applicable to age t fish in year i.

It is not clear what the appropriate measure of the population "density" experienced by an age t fish should be. One possibility is to use numbers of fish or biomass of fish in the yearclass or in a grouping of neighbouring yearclasses (e.g., ages $t-1, t$ and $t+1$). At this stage of the analysis, population density is simply measured by total (3+) biomass, regardless of fish age. (Preliminary analysis showed that total biomass fits better than yearclass biomass.) Similarly, the temperature anomoly in any year was assumed to be the appropriate measure for all fish of all ages. Thus, for now, we can write $k(i) = k(\text{biomass}(i), \text{temp}(i))$ and $L_\infty(i) = L_\infty(\text{biomass}(i), \text{temp}(i))$ instead of $k(i,t)$ and $L_\infty(i,t)$.

In the fits presented below the environmental factors were modelled beginning at age 3 because we felt that the 3+ biomass would not be a good indicator of the population density experienced by 1 and 2 year old fish. (Using cohort size for these younger fish is an avenue we shall explore.)

The analyses performed to date have used the linear parametrization

$$k(i) = k(\text{biomass}(i), \text{temp}(i)) = k_0 - d\ \text{biomass}(i) - t\ \text{temp}(i) \qquad (9)$$

and

$$k(i) = k(\text{biomass}(i), \text{temp}(i)) = k_0 - \frac{d}{\text{biomass}(i)} - t\ \text{temp}(i). \qquad (10)$$

Similarly for $L_\infty(i)$. In fitting Model 1 using the parametrizations of (9) or (10) there are five parameters to estimate, (L_∞, k_0, a, d, t). In (9), the value k_0 can be interpretted as the growth parameter for a fish experiencing no population density pressure in a normal temperature year. Analyses were also performed using biomass alone or temperature alone.

The linear parametrization (9) is invariant (unaffected) by location and scale changes in the variables biomass and temp. (The $\frac{d}{\text{biomass}(i)}$ term in (10) is not location invariant.) In practice this is a very convenient property since, for example, the growth curve fitted by either (9) or (10) will be the same regardless of whether biomass is in pounds or kilograms (change in scale) and whether temperature is degrees Celsius or Fahrenheit (change in location and scale).

FITTING THE MODELS

The growth curve models were fitted in SAS using the nonlinear regression procedure NLIN. We used length at age data on all yearclasses for which environmental measurements were available. Each observation consisted of the mean observed length at age. The observations were therefore weighted by the sample size (the number of fish aged). To fit the model parametrized by (9), five parameters are estimated.

Procedure NLIN does estimate a covariance matrix for the estimated parameters. However, with nonlinear regression the parameters can be biased and the estimated covariances may be very approximate. Thus, when performing hypothesis tests it is preferable to use the form of the F-statistic where the numerator is expressed in terms of a difference in residual sum of squares (RSS) rather than use the estimated covariance matrix (Ratkowsky 1983; Seber and Wild 1989, pg 199).

SUMMARY OF RESULTS

For the Northern cod stocks (2J, 3K and 3L) models 1 - 3 were fitted using biomass alone, temperature alone, and biomass and temperature together (Tables 1.1-3.3) using the linear parametrization given by (9). The 4TVn stock was modelled with just biomass alone (Table 4.1). For Northern cod, with only one exception, model 2 fitted better than model 1 which in turn fitted better than model 3. The exception is the biomass fit to 3L (Table 3.1). It is interesting to note that this is also the *only* fit in which the environmental variables were *not* statistically significant. The model under the null hypothesis ($d = 0$) is the 3 parameter von Bertalanffy which had a residual sum of squares (RSS) of 170990. Model 1 fitted biomass best but the reduction in RSS was slight, to 169731. Furthermore, though biomass was not significant by itself, it was significant in the presence of temperature. Using temperature, Model 2 gave the best fit (RSS=122327) and the additional inclusion of biomass resulted in a significant reduction to 116748.

With the 4TVn stock the reduction in RSS arising from fitting biomass is radical. Here model 3 fits a little better than the other two.

We then explored the parametrization of (10) (using $\frac{1}{\text{biomass}}$) using model 2 on 2J3KL cod. This choice performed far better than parametrization (9) and so we continued these analyses on all remaining NAFO stocks for which data was available. Table 5 gives the percentage of the residual sum of squares from the conventional three parameter von Bertalanffy growth curve that is explained by inclusion of the environmental parameters. In the presence of temperature, $\frac{1}{\text{biomass}}$ was significant in every case. The only nonsignificant fits were when fitting $\frac{1}{\text{biomass}}$ alone to 3N and 3O and when fitting temperature anomoly alone to 3Ps.

DISCUSSION

These results show that there is a strong correspondence between length at age and the environmental factors biomass and temperature. Moreover, the models provide a quantitative estimate of the environmental effects. For example, model 1 in Table 1.3 (biomass and temperature fitted to 2J cod) estimates that the effect of a reduction in temperature of one half of a degree Celcius is a change in k of -0.011 (half of estimated parameter t, -0.022). Model 2 estimates the effect to be a reduction in L_∞ of 17.1 cm.

There are still many other parametrizations to try and other environmental factors to consider. For example, we have used our model to examine the effect of capelin biomass on cod growth (Millar et al. 1990).

We finish with a word of caution. Although we have established (and quantified) a statistical relationship between the environmental factors and length at age, this does not prove a causal relationship. Also, the effect on recruitment and fecundity of the environmental factors, and the interactions between growth, recruitment and fecundity are not well known. It would therefore be premature to study, for example, the effect on yield curves of incorporating these results.

Some conclusions can be made from these studies. For example, when rebuilding a stock from a state of decline it may be the case that fish growth will slow as the biomass increases.

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Table 1.1

Biomass fitted to 2J cod. (Year≤1988), 202 obs

Model	L_∞	k	a	d	RSS	d.o.f.
2 parm VB	100.	0.141	(1.00)	(0.0	180787.	200
3 parm VB	167.	0.049	0.90	(0.0)	148338.	199
k (rec)	155.	0.066	0.91	9.4E-9	125772.	198
L_∞ (rec)	158.	0.068	0.92	1.8E-5	120978.	198
L_∞ (unrec)	214.	0.040	0.92	2.5E-5	131050.	198

Table 1.2

Temperature fitted to 2J cod. (Year≤1987), 188 obs

Model	L_∞	k	a	t	RSS	d.o.f.
2 parm VB	102.	0.137	(1.00)	(0.0	155962.	186
3 parm VB	164.	0.052	0.90	(0.0)	128592.	185
k (rec)	161.	0.054	0.90	-0.013	122550.	184
L_∞ (rec)	152.	0.060	0.90	-29.4	119959.	184
L_∞ (unrec)	171.	0.049	0.90	-27.0	124920.	184

Table 1.3

Biomass and temperature fitted to 2J cod. (Year≤1987), 188 obs

Model	L_∞	k	a	d	t	RSS	d.o.f.
2 parm VB	102.	0.137	(1.00)	(0.0	(0.0)	155962.	186
3 parm VB	164.	0.052	0.90	(0.0)	(0.0)	128592.	185
k (rec)	148.	0.075	0.92	1.2E-8	-0.022	96421.	183
L_∞ (rec)	150.	0.078	0.94	1.8E-5	-34.2	88905.	183
L_∞ (unrec)	234.	0.037	0.93	3.0E-5	-58.6	105031.	183

Table 2.1

Biomass fitted to 3K cod. (Year$\leq$1988), 187 obs

Model	L_∞	k	a	d	RSS	d.o.f.
2 parm VB	107.	0.137	(1.00)	(0.0	121896.	185
3 parm VB	158.	0.059	0.90	(0.0)	97022.	184
k (rec)	169.	0.063	0.91	9.9E-9	78797.	183
L_∞ (rec)	184.	0.058	0.92	2.3E-5	75243.	183
L_∞ (unrec)	211.	0.045	0.92	2.9E-5	81402.	183

Table 2.2

Temperature fitted to 3K cod. (Year$\leq$1987), 176 obs

Model	L_∞	k	a	t	RSS	d.o.f.
2 parm VB	108.	0.137	(1.00)	(0.0	120304.	174
3 parm VB	158.	0.059	0.90	(0.0)	95899.	173
k (rec)	162.	0.058	0.90	-0.021	86295.	172
L_∞ (rec)	154.	0.063	0.90	-44.4	82149.	172
L_∞ (unrec)	172.	0.052	0.90	-41.0	90475.	172

Table 2.3

Biomass and temperature fitted to 3K cod. (Year$\leq$1987), 176 obs

Model	L_∞	k	a	d	t	RSS	d.o.f.
2 parm VB	108.	0.137	(1.00)	(0.0	(0.0)	120304.	174
3 parm VB	158.	0.059	0.90	(0.0)	(0.0)	95899.	173
k (rec)	179.	0.059	0.91	9.7E-9	-0.019	66806.	171
L_∞ (rec)	186.	0.058	0.92	2.3E-5	-46.3	61598.	171
L_∞ (unrec)	265.	0.034	0.93	4.0E-5	-73.9	71480.	171

Table 3.1

Biomass fitted to 3L cod. (Year≤1988), 303 obs

Model	L_∞	k	a	d	RSS	d.o.f.
2 parm VB	171.	0.068	(1.00)	(0.0	171348.	301
3 parm VB	166.	0.072	1.01	(0.0)	170990.	300
k (rec)	167.	0.071	1.00	1.1E-9	169731.	299
L_∞ (rec)	165.	0.072	1.00	1.5E-6	170185.	299
L_∞ (unrec)	164.	0.072	1.01	1.9E-6	169899.	299

Table 3.2

Temperature fitted to 3L cod. (Year≤1987), 286 obs

Model	L_∞	k	a	t	RSS	d.o.f.
2 parm VB	172.	0.068	(1.00)	(0.0	150308.	284
3 parm VB	162.	0.076	1.01	(0.0)	148953.	283
k (rec)	161.	0.077	1.01	-0.015	123524.	282
L_∞ (rec)	164.	0.076	1.01	-23.4	122327.	282
L_∞ (unrec)	162.	0.076	1.01	-23.8	128574.	282

Table 3.3

Biomass and temperature fitted to 3L cod. (Year≤1987), 286 obs

Model	L_∞	k	a	d	t	RSS	d.o.f.
2 parm VB	172.	0.068	(1.00)	(0.0	(0.0)	150308.	284
3 parm VB	162.	0.076	1.01	(0.0)	(0.0)	148953.	283
k (rec)	161.	0.080	1.02	2.5E-9	-0.019	119605.	281
L_∞ (rec)	169.	0.076	1.02	4.5E-6	-30.3	116748.	281
L_∞ (unrec)	167.	0.076	1.01	3.9E-6	-30.8	125121.	281

Table 4.1

Biomass fitted to 4TVn cod. (Year$\leq$1987), 290 obs

Model	L_∞	k	a	d	RSS	d.o.f.
2 parm VB	85.	0.160	(1.00)	(0.0	531907.	288
3 parm VB	117.	0.079	0.90	(0.0)	506681.	287
k (rec)	130.	0.105	0.98	1.2E-7	168928.	286
L_∞ (rec)	172.	0.071	0.97	1.4E-4	172779.	286
L_∞ (unrec)	150.	0.091	0.99	1.5E-4	156817.	286

NAFO region	$\frac{1}{\text{biomass}}$	temp	$\frac{1}{\text{biomass}}$ and temp
2J	43	13	51
3K	43	18	48
3L	4	22	33
3N	2	15	23
3O	2	18	20
3Ps	12	1	12
4TVn	61	14	66

Table 5. The percentage of the residual sum of squares from a conventional three parameter von Bertalanffy fit that is explained by the environmental factor(s) using model 2 (L_∞, recoverable growth).