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Investigation of a growth model incorporating density-dependence for the Cod 3M management plan simulations.

by

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Abstract

This document presents a framework to model density dependent growth for the Flemish Cap Cod. The model used is the classical von Bertalanffy equation, but modified so that growth is reduced when stock size increases. The effect correlation between growth and temperature was also analyzed. This empirical model was able to reproduce closely the trends in the observed historical weight-at-age data. This framework can therefore be incorporated in the simulation tool used for the management plan evaluation. However, since the actual mechanisms through which stock size affects growth are not identified, we advise not to use this density dependent growth as the base case scenario in simulations. It can be used in sensitivity tests which can be conducted to assess the potential impact of density dependent growth on simulation output, such as Fmsy.

Introduction

Fish mean weight-at-age of 3M cod stock have varied markedly over time, with an increase in mean weight at age across ages from the early 1990s to the mid-2000s, and a sharp decrease since then (Figure 1). These variations, indicating changes in the growth pattern, have happened whilst the stock went through a collapse in the mid-2000 and a quick recovery afterwards. Such a concomitant pattern of increasing growth while stock size declines (followed by the opposite) suggests a density dependent effect on growth.

Finding definitive evidence that density dependent factors are affecting growth would require the identification of the underlying mechanisms (e.g. reduction of the food available per capita due to the increased number of conspecific individuals). Such studies require the analysis of large amounts for field data, and/or, the development of complex modelling tools (individual based, energy based model).

Investigating the question of density dependent growth using a growth model represents an intermediary step between simple correlation analyses and complex data intensive research projects. Unlike simple correlations which look at correspondence in temporal variations, the growth model used here provides a theoretical framework to represent how life time growth patterns are changed in relation to changing stock size.

Similarly, changes in temperature, affecting individuals metabolism, are also expected to affect growth. These effects can be incorporated together with density dependence in a growth model.

Here, a density-dependent growth model incorporating both density dependence and temperature effects is developed based on the stock mean weight at age matrix used in the assessment. The aim is to be able to reproduce the past variations in mean weights, based on past metrics of stock size (assessment model output) potentially representing the intensity of density-dependent growth limitation and temperature. This model can then be directly incorporated in the simulation tool used to estimate reference points and to evaluate the performance of management strategies, in order for instance, to investigate the sensitivity of reference points such as Fmsy to the assumption made on future growth.

Material and Methods

1. Data exploration

Growth changes

Patterns can be observed in the stock mean weights matrix (Figure 1). The most remarkable feature in is the increasing trend followed by a decreasing trend in age 2 to 7. The start of a decreasing part seems to be postponed for older ages, suggesting that the change in growth mostly affected cohorts at younger ages and were not compensated for changes in growth in the later part of their life. Other less pronounced changes in weight at age can be followed along the cohorts life, such as small increase followed by a small decrease occurring in the earlier 1990s.

One possible explanation for these different patterns is that long term cohort effects could reflect slow changes in growth (for instance linked to changes in stock size) while year-effects could be related to anomalies in factors affecting growth (e.g. extreme environmental conditions). In addition to these patterns, there is noise in the data, as illustrated occasional decrease in mean weight in a cohort between successive years.

Finally, variations in weight at age 8 were not included in the analyses, since they represent a plus group, combining individuals of different cohorts.

Analysis of the correlations in weight at age between the successive ages of a cohort show that the mean weight at age 2 is not linked to the weight of the cohort at age 1 (Figure 2), but that the weight at ages older than 2 is highly correlated to the weight one year before (except for the plus group). This shows that most of the variation observed in weight at age occur during the second year of life.

Link between length at age 1 and potential descriptors of density dependence

Correlations between length at age 1 and a series of variables potentially representing the intensity of density dependence mechanisms affecting growth during the first year were investigated. Those variables were the size of the cohort (log of the recruitment of the same cohort), size of previous cohort, the total abundance of juveniles (ages 1-3), all possibly representing the amount of individuals with which young individuals may compete for food during their first year of life. None of the correlations tested was found significant, the highest correlation being observed with log (rec) (Figure 3), with a tendency to have fish of smaller length at age 1 for larger cohorts.

Link between annual growth and density dependence

The Von Bertalanffy model was used to predict the annual growth based on the size observed at the start of the year:

$$\hat{L}_{t+1,a+1} = L_{inf} - (L_{inf} - L_{t,a})\, exp(-(K).$$

The difference between the observed length at age $L_{t,a}$ and the modelled ones $\hat{L}_{t,a}$ represent annual growth anomalies by year and age. In order to investigate the potential density dependent effect, correlation between these growth anomalies and a series of variables were investigated (recruitment of the cohort, total stock biomass, and adult stock biomass).

The highest correlations were observed with the total stock biomass (Figure 4), but correlations are significant only for growth during age 1, 2 and 5, whilst being negative for all ages.

Links with bottom temperature

The relationship between growth at temperature was investigated with similar analysis as for the relationships with metrics chosen to quantify density dependence.

There was a small positive, though non-significant, correlation between the length at age 1 and the bottom temperature the previous year. Likewise, the correlation between growth anomalies in the subsequent ages and the corresponding temperature were weak and non-significant.

2. Modelling approach

Based on theoretical expectations1, Lorentzen and Enberg (2001) proposed a modification of the von Bertalanffy growth model which accounts for density-dependent effects. In this model, the asymptotic length (model parameter corresponding to the theoretical length of a fish of an infinite age) decreases when the biomass of the stock increases. Here the model was extended to incorporate an effect of temperature on the growth coefficient K:

$$L_{t+1,a+1} = L_{infB,a} - (L_{infB,a} - L_{t,a})\, exp\big(-(K_y)$$

Where

[1] The von Bertalanffy equation is a popular model for growth in fisheries science. It was originally derived from an energy allocation theory of growth, in which instantaneous growth rate is the difference between energy acquisition and energy consumption for maintenance. This can be formalized as follows :

$${}^{dw}/_{dt} = \eta w^{2/3} - \lambda w$$

Where w is individual weight, t is the age of the fish, η is the coefficient for the energy intake rate and λ is the coefficient for the energy consumption rate for maintenance.

The integration of this differential equation gives the following function for weight as a function of time

$$w(t) = \left({}^{\eta}/_{\lambda}\right)^3 \left[1 - e^{-\lambda(t-t_0)/3}\right]^3$$

One can recognize the von Bertalanffy growth equation, in which the coefficients are expressed in terms of energy allocation parameters

$$k = {}^{\lambda}/_{3}$$

$$w_{inf} = \left({}^{\eta}/_{\lambda}\right)^3$$

We can expect that competition for food (which is how density dependence would affect growth) would result in a lower energy acquisition rate (smaller η), but is not likely to modify the basal metabolism (maintenance, same λ). The equations above then imply that the growth coefficient k should be insensitive to density while the asymptotic weight should be negatively affected by density dependence. Both the growth coefficient k and the asymptotic weight w_{inf} , are proportional to λ (inversely for w_{inf}), the rate of energy use for maintenance. Since maintenance is increases with temperature, it is therefore expected that growth coefficient would increase with temperature, while the asymptotic weight would decrease.

$L_{infB,a} = L_{inf} - g_a B_t$, and

$K_y = K + \tau\ Temp_y$

The annual growth is modelled as a function of the length of the same cohort at the start of the year $L_{t,a}$, and the parameters K_y (growth coefficient) and L_{infB} (asymptotic length), where L_{infB} is a linear function of total stock biomass B_t with a slope g_a describing the strength of the density dependence for a given age-class and the growth coefficient K_y is influenced by the annual bottom temperature $Temp_y$.

This model was fitted on the historical mean weight-at-age in the stock transformed into length. Since the model predicts $L_{t+1,a+1}$ as a function of $L_{t,a}$, it cannot be fitted for the first age in the weight at age matrix (age 1). A separate model was therefore developed for length at age 1, based on linear regression between annual length at age 1, the strength of the corresponding cohort (log(Rec)) and the bottom temperature.

After estimating the parameters L_{inf}, K , g_a and τ, the model was used to predict past growth, using the historical TSB values and recruitment values and the temperature time series. Reconstructed weight-at-age time series were visually compared to the observed ones to determine whether the model managed to reproduce the past changes in growth, and could therefore be used to simulate future weights in an MSE.

Results

Model for age 1 length.

The linear regression model for length at age 1 indicated that the effect of log(recruitment) and of bottom temperature (of the previous year) were significant. The coefficient of the regression are given in the Table 1. As expected, the size of the cohort has a negative effect on the length at age 1, while the bottom temperature has a positive effect. Figure 5 shows both regressions.

Growth from age 1 onwards

Parameter estimation was carried out using maximum likelihood. For the modified Von Bertalanffy model, three configurations were tested:

- DD2pars : One with only 2 age specific parameters for the density dependence effect, one for juveniles, g1-2 and one for adults g3-7
- DD7pars : One with one parameter per age class, g1, ..., g7,
- DD7pars and temp : One with one parameter per age class, g1, ..., g7 and a age independent parameter for the effect of temperature on K

The estimated parameter values for each model are given in the Table 2. For the most simple model, model DD2pars, the inclusion of the 2 additional parameters representing the effect of density-dependence on the juveniles and on the adults, significantly improved model fit compared to a simple von Bertalanffy model (p = 0.008). Further decoupling density dependence parameters into age specific estimates (model DD7 pars) improved model fit again (p<0.001). Finally, incorporating an age-invariant effect of temperature on K further improved model fit (p<0.001).

The predicted weight-at-age time series broadly reproduces the trends observed in the historical data (Figure 6). The model manages to recreate the increase in growth in the early 2000s and the following decrease. There is however a substantial temporal lag after age 3 where the model's weight increase earlier than the observed ones, resulting in a period with modelled weights higher than observed ones. For the decreasing part, the model is close to observations. There is little difference between the predicted values from the 3 models, except for model DD 2par which results in a little less dynamic variations of weights at age.

Conclusions

Exploratory analyses indicate that most of the changes in growth operate on individuals during the first 2 years of their lives, and that less variability occurs during the growth of the subsequent year. Growth during the first years (length at age 1) was inversely related to the size of the cohort (log(recruitment)). Growth during second year (but also later ages also less significantly) correlated best with total stock biomass.

Using these observations, a framework was proposed to simulate future weights at age for 3M cod in which changes in growth are driven by changes in stock size, thereby reproducing a density-dependent growth mechanism. On a goodness of fit point of view, the most complex models (with age specific density dependence parameters, effect of temperature) did perform better than simpler ones. However, when it comes to use the model to simulate weights at age, the different versions of the model managed to recreate trends in stock weights which are reasonably comparable to those observed in the data.

Based on the results obtained and taking into account the difficulty of simulating future temperatures, the most advisable OM to implement in the case of 3M cod would be based on a growth model with a DD7pars configuration.

The OM to be designed would use this model to estimate the mean weights at age in the future catches and stock but it would be necessary to decide how the values at age of the other necessary parameters such as PR, maturity, M, etc are obtained.

References

Lorentzen K. and Enberg, K. 2001. Density-dependent growth as a key mechanism in the regulation of fish populations: evidence from among-population comparisons. Proc. R. Soc. Lond. B (2002) 269, 49–54.

Table 1. Coefficient of the linear regression of length at age 1 against log recruitment and bottom temperature

coefficient	Estimate	Std. Error	t value	Pr(>|t|)
Intercept	13.1401	3.9749	3.306	0.00286**
log(rec)	-0.3546	0.1594	-2.224	0.03539*
btemp	2.5398	0.9976	2.546	0.01744*
residual standard deviation	1.785			

Table 2. Parameter estimates (and confidence intervals) for the 3 growth models for 3M cod

Model DD2pars			Model DD7pars			Model DD7pars and temp		
AIC = 1226			AIC = 1194			AIC = 1151		
parameter	estimate	CI	parameter	estimate	CI	parameter	Estimate	CI
L_{inf}	215	157-465	L_{inf}	190	+	L_{inf}	148	+
K	7.39e-01	2.94e-02 1.16e-01	K	8.94e-02	+	K	8.22e-02	+
g_{12}	4.19e-04	1.36e-04 8.52e-04	g_1	4.74e-04	+	g_1	4.37e-04	+
g_{37}	2.80e-04	7.07e-05 9.97e-04	g_2	3.58e-04	+	g_2	3.20e-04	+
			g_3	4.01e-04	+	g_3	3.17e-04	+
			g_4	5.35e-04	+	g_4	3.76e-04	+
			g_5	4.42e-04	+	g_5	2.83e-04	+
			g_6	3.25e-04	+	g_6	1.85e-05	+
			g_7	-7.90e-04	+	g_7	-3.82e-04	+
						τ	1.35e-02	+
residual standard deviation	4.84	4.41-5.36	residual standard deviation	4.56	+	residual standard deviation	4.35	+

+ : model fit has not converged

Fig. 1. Variation of stock mean weight at age at age, cod 3M, use in the assessment.

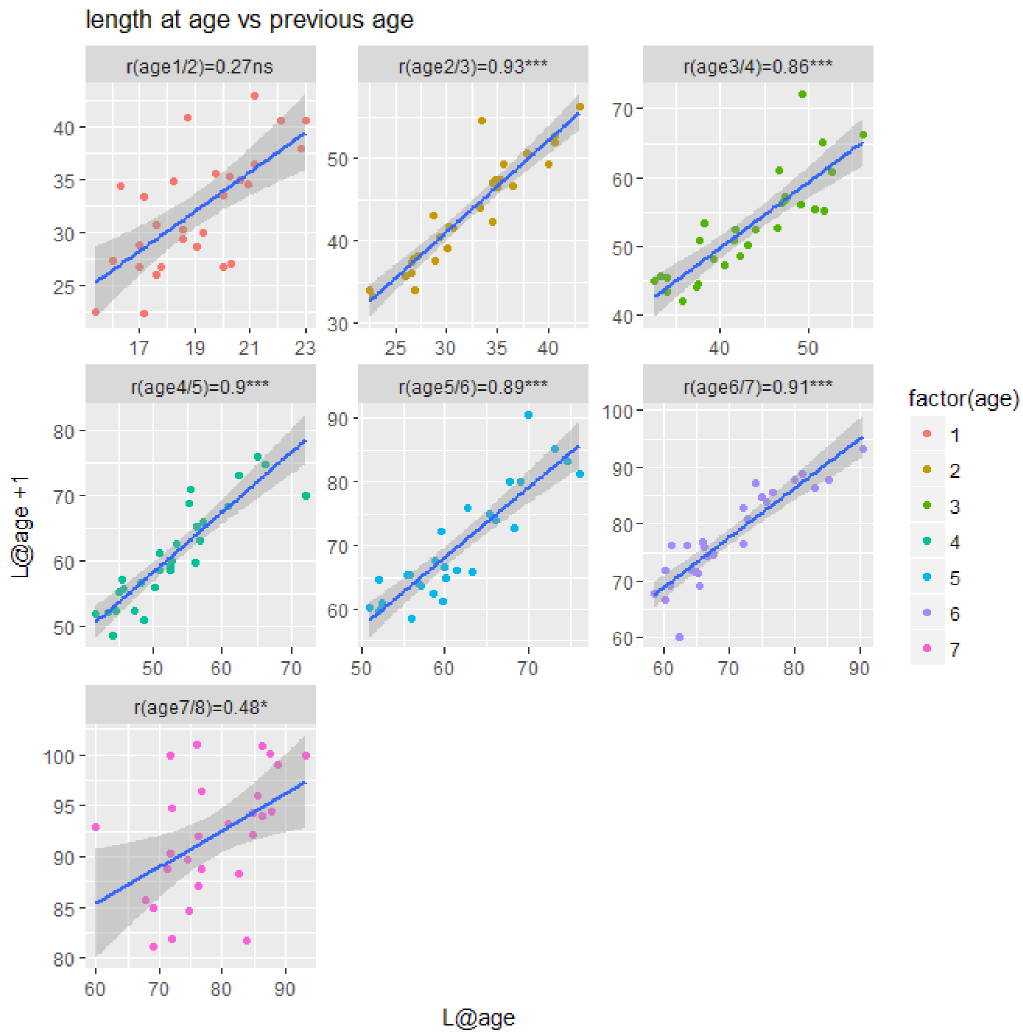

Fig. 2. Relationship between mean length of a cohort a successive ages (correlation coefficient indicated on top of each panel) , excluding the extreme value of 2004 for age 1.

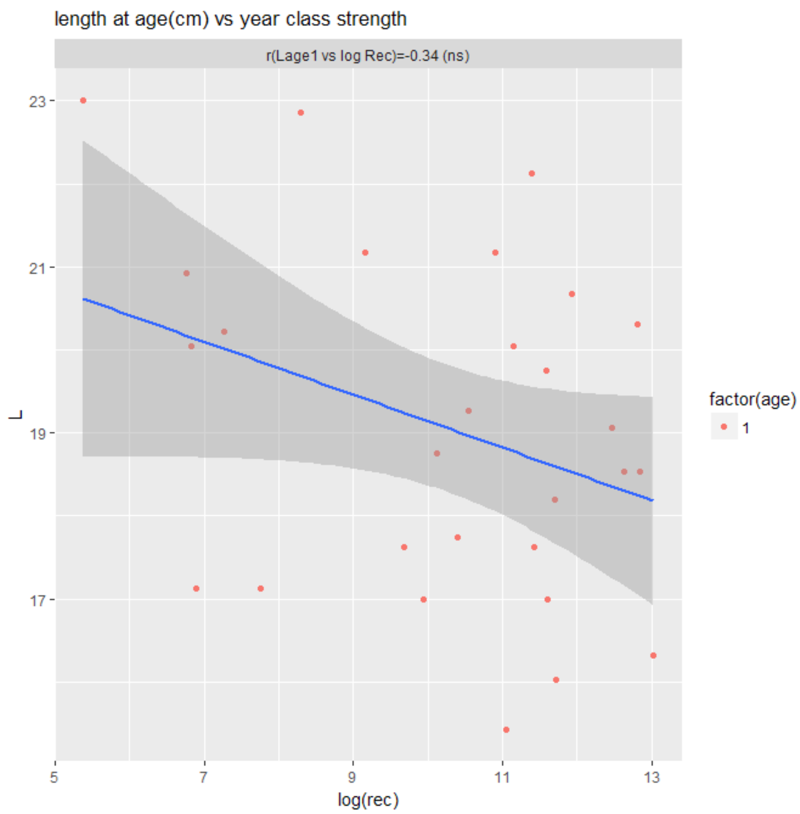

Fig. 3. Relationship between fish mean length at age 1 and the size of the cohort (in log) , excluding the extreme value of 2004.

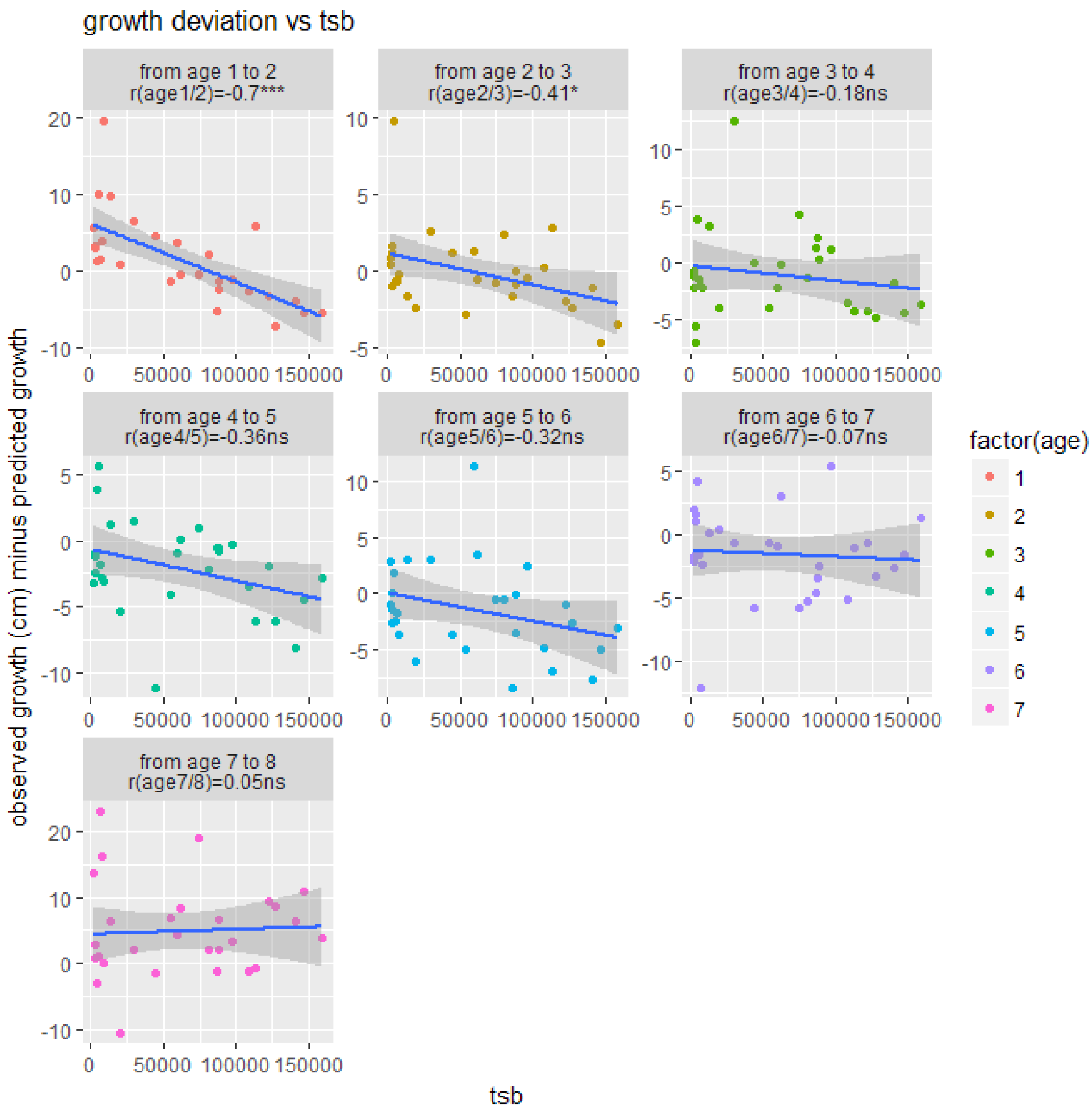

Fig. 4. Relationship between growth anomalies (observed length minus length predicted from a Von Bertalanffy model) and the total stock biomass.

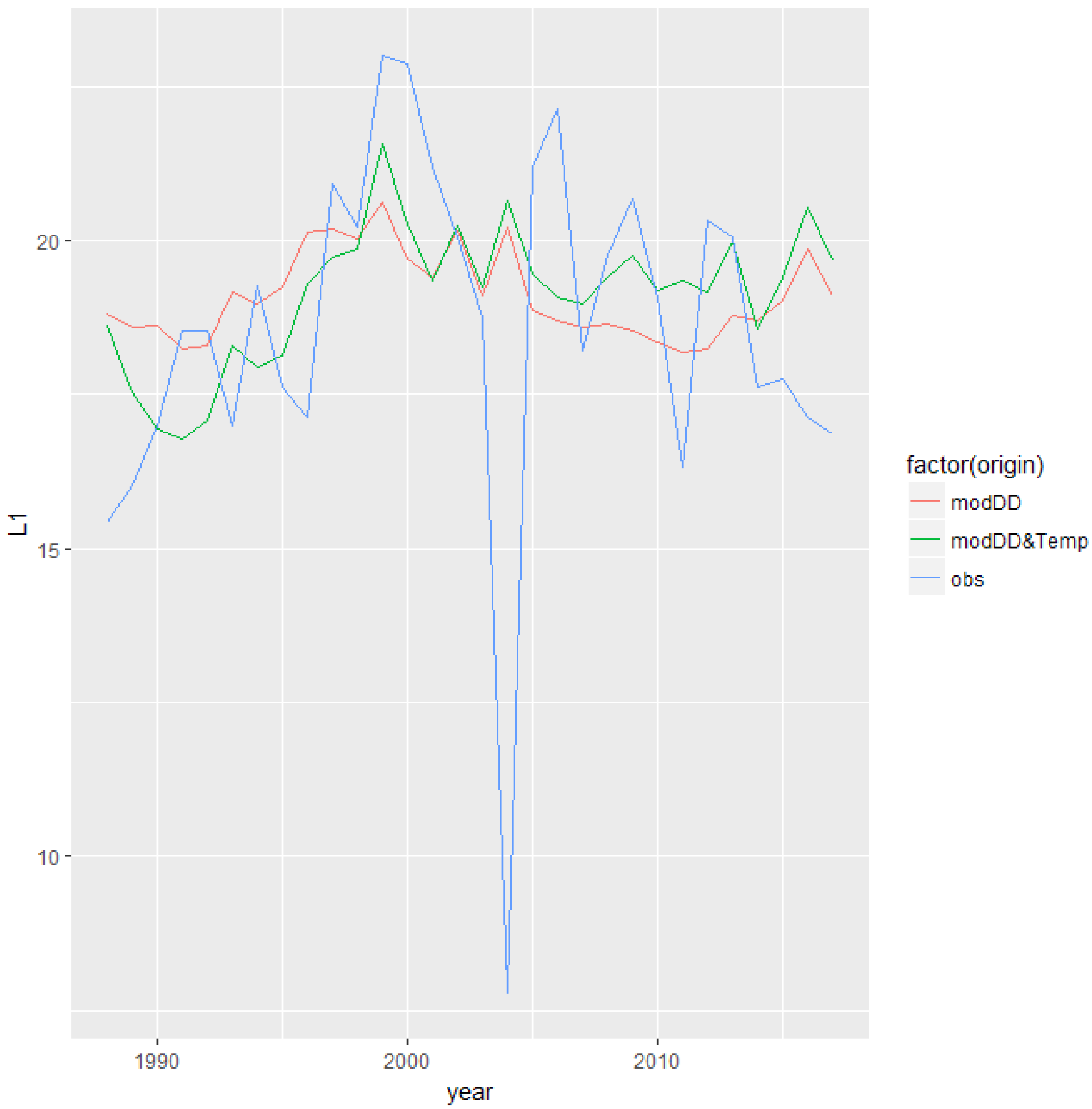

Fig. 5. Comparison of the predicted length at age 1 with the observed data. modDD: linear regression with effect of log recruitment only, modDD&temp, linear regression with effect of log recruitment and bottom temperature. Note that there is no data for length at age 1 prior to 1988, and that predictions from modDD&Temp cannot be made before 1989 because no temperature data is available before this date.

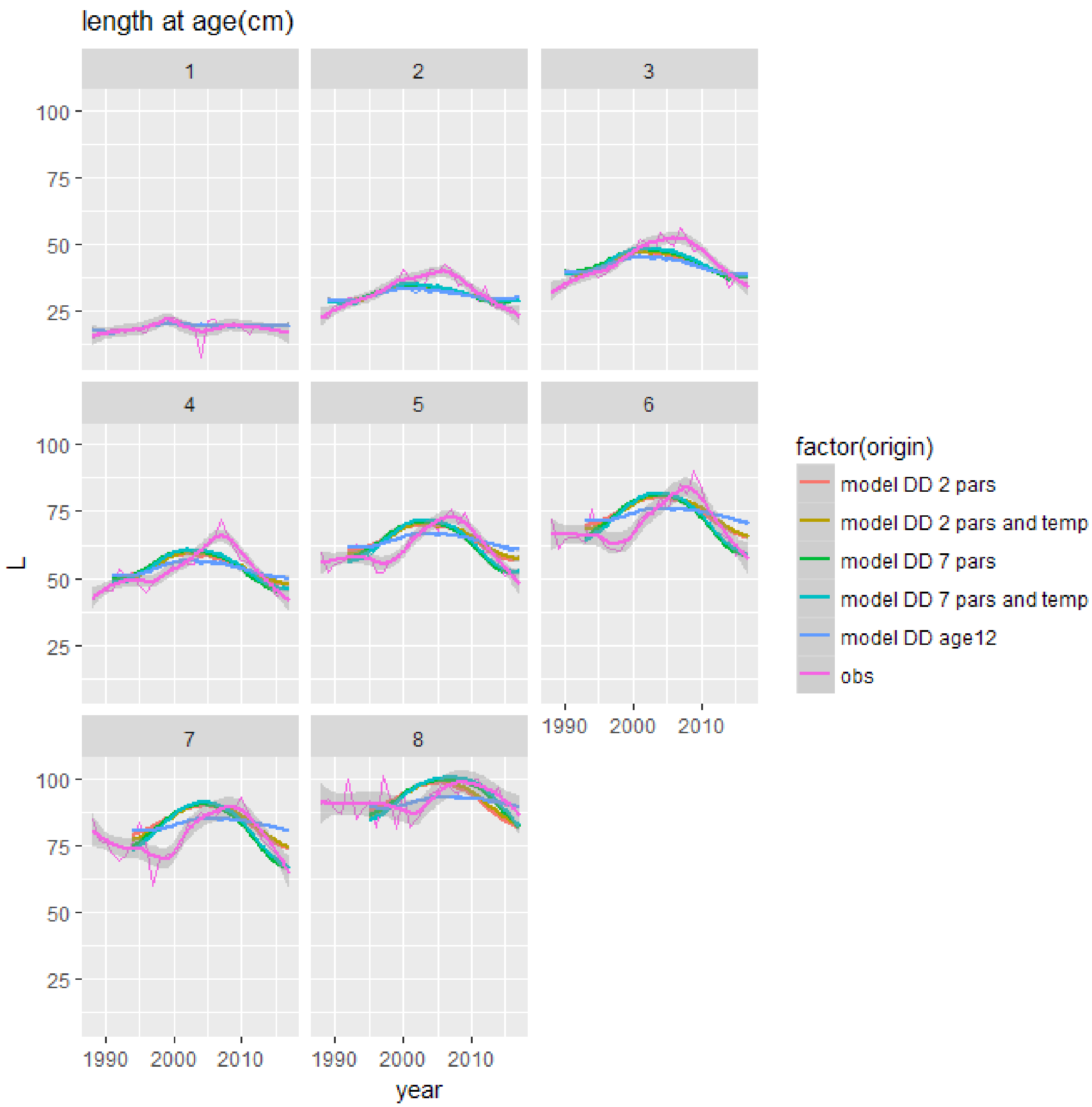

Fig. 6. Historical performance of the density dependent growth model: observed (obs) vs. predicted (3 different models) weight-at-age