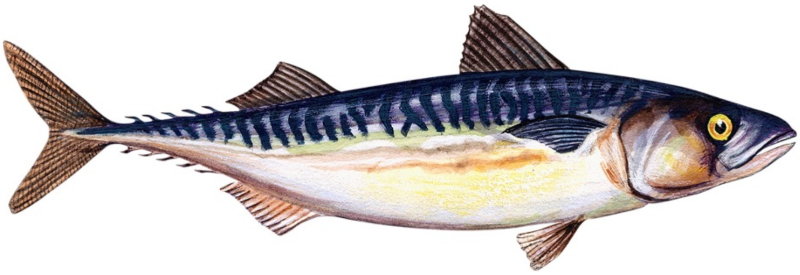
Investigation of a growth model incorporating density dependence for the mackerel management plan simulations.

Thomas Brunel

Report number C134/15



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Summary

This report presents a framework to model density dependent growth for the North East Atlantic mackerel. The model used is the classical von Bertalanffy equation, but modified so that growth is reduced when stock size increases. The model developed was able to reproduce quite closely the trends in the observed historical weight-at-age data. This framework can therefore be incorporated in the simulation tool used for the mackerel management plan evaluation. But since the actual mechanisms through which stock size affects growth are not identified, density dependent growth should not be used as the base case scenario in simulations. However 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.

1. Assignment

This research was carried out to answer a "kennis voor beleid vraag" from the Ministerie of Economic Affairs (DGAN-ELVV-Europees Visserijbeleid). The question was formulated as follows :

"Het makreelbestand is momenteel erg groot, maar de makrelen groeien steeds trager. Het lijkt er op dat een (te) groot bestand slecht is voor de vangbare hoeveelheid. De wetenschappelijke discussie is stilgevallen door gebrek aan goede gegevens hierover. Dat maakt het voor de wetenschap moeilijk om advies uit te brengen aan de kuststaten (EU/NOR/FRO/IJS) over het optimale beheer van makreel in de NO Atlantische Oceaan. EU en NL hebben groot belang bij een goed advies. Het antwoord op de gestelde vraag is nodig voor een goed advies van ICES over het beheer en het vangstniveau voor 2016 en later."

The underlying questions in this assignment are :

- What is the current scientific knowledge on mackerel growth, and how can we provide more definitive answers regarding the drivers of the changes?
- How can we deliver management advice which takes better into account the changes in growth and their drivers?

2. Introduction

Fish mean weight-at-age of North East Atlantic Mackerel has been sharply declining over the last decade. Simulations run for the recent management plan evaluations (WKMACLTMP , ICES 2014a) however were based on the assumption, among others, that the mean weight-at-age of the fish in the future would be similar to the recently observed values (last three years). Owing to the sharp decline in weight-at-age, the average weight-at-age calculated over the recent years is therefore markedly lower than the average over the historical period (1980-2013). Simulations run during WKMACLTMP have shown that reference points are sensitive to the assumptions on future weights, even if the effect is small (e.g. Fmsy =0.22 when using the average over the last 3 years vs. Fmsy=0.24 when using the average over the historical period).
The hypothesis that the large size of the stock causes increased competition for food has been proposed to explain the slowing in growth in the recent years. Recent scientific work provides some support for this hypothesis. Jansen and Burns (2015) have found a negative relation between juvenile size and both the biomass of the adults and the abundance of juveniles. A manuscript under revision (Olafsdottir et al. submitted) investigated mackerel growth between age 3 and age 8 and described a marked reduction in growth. They provide indication that the trend towards a slowing of adult growth is concomitant with trends in the size of both the mackerel and the Norwegian spring spawning herring stocks. The authors also included temperature as an explanatory factor for the changes in growth and concluded that its effect was not significant.
Both studies highlight correlations between mackerel growth and stock size variables, which are consistent with the density dependent hypothesis.

Despite the relatively limited evidence for density dependence (and the lack of investigation of any other potential cause for the changes in growth) the Coastal States for mackerel are preparing a request to ICES to re-estimate the reference points for mackerel using a simulation tool in which density dependent growth should be incorporated.

Finding definitive evidence that density dependent factors are affecting mackerel 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, increased feeding migration distances due to the increased competition for space). 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. In addition, such a model can directly be incorporated in the simulation tool used to estimate reference points and to evaluate the performance of management strategies, thereby facilitating the incorporation of these effects in the management advice.

3. Method

Based on theoretical expectations[1], 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 :

$$L_{t,a} = L_{infB} - \left(L_{infB} - L_{t-1,a-1}\right) exp(-K)$$

Where

$$L_{infB} = L_{inf} - g\ B_{t-1}$$

Here, the annual growth is modelled as a function of the length of the same cohort one year earlier $L_{t-1,a-1}$, and the parameters K (growth coefficient) and L_{infB} (asymptotic length), where L_{infB} is a linear function of stock size B_{t-1} with a slope g describing the strength of the density dependence.

This model was fitted on the historical mean weight-at-age in the stock (WGWIDE, ICES 2014b), transformed into length.

After estimating the parameters L_{inf}, K and g, the model was used to predict past growth, using the historical SSB values. The Jansen and Burns (2015) model was used to produce predictions for the initial length at age (age 1), and the von Bertalanffy model was used to predict the growth afterwards.

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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) of mackerel (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.

4. Results

The estimated parameter values (maximum likelihood) are given in the table below. All parameters in the model are significant.

Parameter	Meaning	Value	
K	Growth coefficient	0.25	($year^{-1}$)
Linf	Intercept for the asymptotic length model	43.43	(cm)
g	Intensity of the density dependence effect on the asymptotic length model	7.33×10^{-07}	(cm per tonne o SSB)
Sigma	Standard deviation of the model	0.0215	

The figure 1 bellow gives an illustration of the two extreme growth curves resulting of growing at high or at low SSB (figure 1)

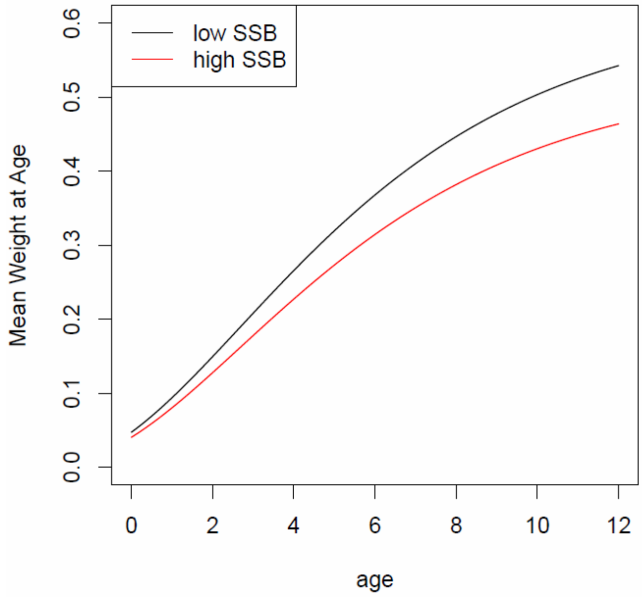

Figure 1: life-time growth curves predicted from the modified von Bertalanffy model with an asymptotic weight corresponding to a low SSB (black curve) and to a high SSB (red curve).

The predicted weight-at-age time series show trends very similar to the trends observed in the historical data (figure 2). The only exception was for age 1 for which the historical data do not show any trend. The historical data (weights at age 1 in the stock) however are based on mature fish only, which represents a very small proportion of the age 1 individuals. The age 1 data should therefore not be considered representative of the whole population and the comparison between the model predictions and the observed should not be considered relevant.

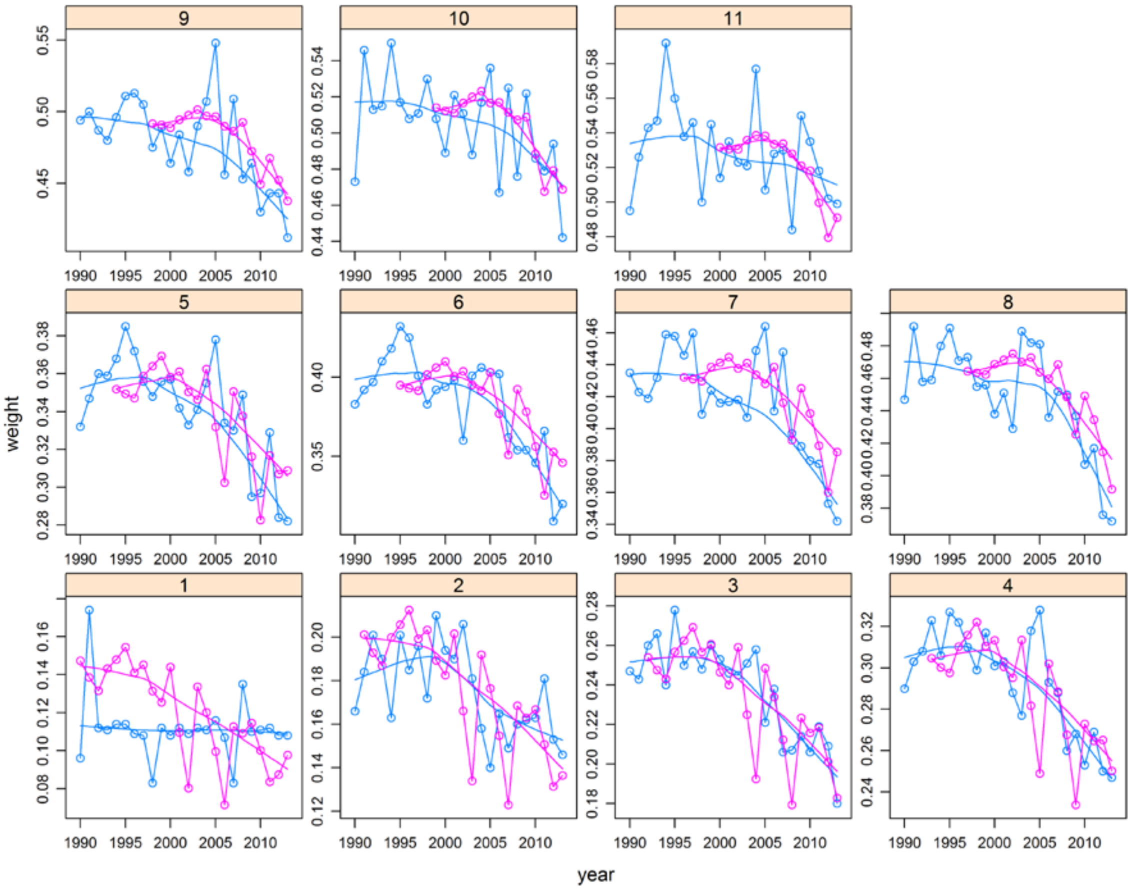

Figure 2 : historical performance of the density dependent growth model : observed (blue dotted line) vs. predicted (pink dotted line) weight-at-age (age 1 bottom left to 11 top right). The blue and pink solid lines show the temporal trend in the observed and modelled weights.

5. Discussion

The results of the present work were presented during an ad hoc meeting organized by the pelagic industry (Bergen, Norway,13-14 August 2015) and also attended by Norwegian scientists. The conclusion of the group was that, should density dependence be incorporated, the model would provide a good framework to represent density dependent growth in a management strategy evaluation work. Alternative methods were also presented, based on a simple linear prediction of weight-at-age as a function of stock size. This option however does not represent growth as a cumulative process throughout the life of individuals (i.e. weight-at-age 12 is predicted from stock size only, independent on the weight of the same cohort at age 11). Therefore, if stock size changes in time, unrealistic lifetime growth curves can result from such an approach (for instance very slow growth in the early life and very high growth in the late life when the stock size declines). This is not the case with the von Bertalanffy model used here, as it is the growth increment which is modelled (as a function of length at the start of the year and stock size) and not the weight.

In this work, we found a negative effect of the mackerel stock size on the theoretical maximum length for mackerel. Using the growth model developed, it was possible to reproduce the recent trend (but not interannual variations) observed in the mean weights-at-age. This work therefore provides an additional indication that density dependent effects may be influencing the growth in NEA mackerel.

Density dependent growth implies that the energy available for growing is reduced due to increasing intraspecific competition. Hence, the intensity of density dependence should not depend only on stock size, but rather on ratio between stock size and the ecosystem's carrying capacity for mackerel. The carrying capacity is not constant, and may vary due to the effect of environmental changes (changes in prey abundance, in competing species abundance, changes in the geographical extension of the suitable habitat for mackerel). In addition, growth, as all physiological processes, is directly influenced by the local physical conditions (e.g. temperature) experienced by the fish.

Therefore, this growing body of evidence for a density dependence effect has to be supported by studies aiming at identifying the actual underlying mechanisms. Such studies should focus on the quantification of how the amount of food available per capita has varied and under the influence of which factors (may it be changes in the size of the stock, of competing species, of the production of food by the ecosystem or of the spatial distribution of the food). This would require the analysis and modelling of spatio-temporal data on mackerel distribution, stomach contents, plankton abundances. It is also necessary to understand with which efficiency the energy resulting from this food intake is channeled into somatic growth. The energy available for growing will be depending on other energetic costs such as basic metabolism, cost for migration, investment in reproduction, which all may be influenced by external (environmental) factors. This could be studied using energy allocation models such as DEBs (Dynamic Energy Allocation Budget models).

Until we have a good understanding of the density dependent and density independent factors that govern the changes in mackerel dynamics, it seems difficult to incorporate adequately any of those factors in the simulations carried out to give advice on the appropriate levels of exploitation. Indeed if the actual mechanisms through which stock size has affected growth are not identified, we cannot be certain of the reversibility of the changes observed in the recent past.

For the time being, density dependent growth should not be used as the base case scenario in simulations. However 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.

6. Additional Remark

The model presented here has not been incorporated in the mackerel management plan simulations yet. This would require a significant amount of time both to modify the program and to run new simulations. But there are two simulation studies available that shed some light on what to expect.

During the Bergen ad-hoc meeting group in which this model was presented, another simulation platform implementing density dependent growth as an option (HCS, Skagen 2015) was parameterized using mackerel data to give a first approximation of the difference in Fmsy arising from a density dependent v.s. independent growth formulation. The resulting difference in FMSY estimates between these two calculations was of about 0.03.

In addition, the WKMACLTMP (ICES, 2014a) report presented results from a simulation for a so called “reversible biology” scenario, in which the weights at age increase in the future back to the long term mean, which is, qualitatively, what is expected to happen if growth is density dependent. In this simulation, the difference in Fmsy arising from a density dependent v.s. independent growth formulation was of 0.02.

Consequently, for the time being, it is considered that the results from the WKMACLTMP corresponding to the “reversible” scenario give a fair approximation of the dynamics of the stock with density dependent growth.

7. Quality Assurance

IMARES utilises an ISO 9001:2008 certified quality management system (certificate number: 124296-2012-AQ-NLD-RvA). This certificate is valid until 15 December 2015. The organisation has been certified since 27 February 2001. The certification was issued by DNV Certification B.V. Furthermore, the chemical laboratory of the Fish Division has NEN-EN-ISO/IEC 17025:2005 accreditation for test laboratories with number L097. This accreditation is valid until 1th of April 2017 and was first issued on 27 March 1997. Accreditation was granted by the Council for Accreditation.

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Justification

Rapport C134/15
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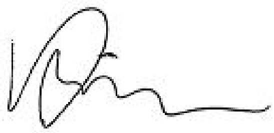
The scientific quality of this report has been peer reviewed by the a colleague scientist and the head of the department of IMARES.

Approved: N. Hintzen
Researcher

Signature: 

Date: 23 of September 2015

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Date: 23 of September 2015