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Fast growth inferred for northern Benguela shallow-water hake *Merluccius capensis* using annual survey- and monthly commercial length-frequency distributions

M.R. Wilhelm[a,b,*], C.L. Moloney[b], S. Paulus[c], J-P. Roux[d]

[a] Department of Fisheries and Aquatic Science, University of Namibia, PO Box 462, Henties Bay, Namibia
[b] Marine Research Institute and Department of Biological Sciences, University of Cape Town, Private Bag X3, Rondebosch 7701, South Africa
[c] National Marine Information and Research Centre, Ministry of Fisheries and Marine Resources, Swakopmund, Namibia
[d] Lüderitz Marine Research, Ministry of Fisheries and Marine Resources, Lüderitz, Namibia

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ABSTRACT

The hypothesis that fast growth rates demonstrated for 3–21-month-old *Merluccius capensis* continue for older fish is tested. Cohort-specific growth rates of *M. capensis* between 6 and 65 cm total length were described using a von Bertalanffy growth function (VBGF) fitted to annual/bi-annual research survey length-frequency distributions (LFDs) from 1995 to 2011 and monthly commercial LFDs from 1998 to 2011. These data were combined with cohort analysis of younger fish from seal scat data to provide cohort-specific growth rates for cohorts hatched from 1994 to 2008. The fitted VBGF gave L_t (cm) = 108.6*{1-exp[−0.199*(t(y) + 0.025)]}. *M. capensis* grow between 1.4 and 0.8 cm month^{-1} from ages 1 to 5 years, varying by 0.2 cm month^{-1} among cohorts. This is about twice as fast as growth rates previously estimated from otolith methods, which therefore need to be re-evaluated. It follows that *M. capensis* should have higher natural mortality rates and a greater stock productivity than previously believed, emphasizing the need to review this in the current stock assessment approaches.

1. Introduction

Growth rates described from otoliths depend on reader interpretations of translucent and opaque zonation (Morales and Payne, 1985). These can vary widely and influence stock assessment results and management advice (e.g., Bertignac and de Pontual, 2007; Wilhelm et al., 2008). Length-frequency analyses can be used to provide independent corroboration of growth rates estimated from otolith analyses since known-age fish for the validation of otolith age determination procedures are difficult to obtain. This has been done for shallow-water hake *Merluccius capensis* Castelnau 1861 in the northern Benguela, mainly using data collected from the International Commission for Southeast Atlantic Fisheries (ICSEAF, e.g. Preñski, 1978; Morales-Nin, 1991). Length-frequency methods rely on adequate data at sufficient sampling (monthly or bi-monthly) intervals to be useful (Kimura et al., 2006). Monthly changes in length are needed to accurately calculate the t_0 parameter in the von Bertalanffy growth function (VBGF) and to describe early growth rates of young fish. This is important to correctly assign ages 0–2 years using otolith age determination methods.

Recently, cohort analysis of Namibian *M. capensis* using length-frequencies of otoliths collected from fur seal scats on at least monthly intervals revealed rapid growth rates of about 1 cm month^{-1} up to ages of about 1.5 years (Wilhelm et al., 2013). Four cohorts selected from these data were used to show that *M. capensis* otoliths form three translucent zones (a summer translucent zone followed by a winter and a summer translucent zone) during the first 1.5 years of their life (Wilhelm et al., 2015a), resulting in a previous under-estimation of their otolith-based ages.

Northern Benguela hake stocks comprise both *M. capensis* and the deep-water hake *Merluccius paradoxus* Franca 1960. The fisheries sector is an important economic resource in Namibia, making up a large part of Namibia's exports (NPC, 2015), and *M. capensis* forms the majority of the total hake biomass (Kirchner et al., 2012; Wilhelm et al., 2015b). It is therefore important that research is undertaken to fully understand growth rates and otolith zonation of >1.5-year old *M. capensis*.

Cohort analysis of young hake (Wilhelm et al., 2013) has given a good indication of the approximate hatch date and early slope

* Corresponding author.
E-mail addresses: mwilhelm@unam.na (M.R. Wilhelm), coleen.moloney@uct.ac.za (C.L. Moloney), sarah.paulus@mfmr.gov.na (S. Paulus), jprouxnamibia@gmail.com (J.-P. Roux).

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of the growth curve needed to calculate growth rates from length-frequency analysis for older fish. If fast growth rates and biannual translucent zone formation, observed in young *M. capensis*, continue in older fish, *M. capensis* could have shorter life spans and faster mortality rates than previously believed. This would alter hake age determination criteria and also affect stock assessment results, assessments of the status of the stock and subsequent management advice (e.g., Bertignac and de Pontual, 2007). It is therefore important to test the fast-growth hypothesis for all sizes and ages of *M. capensis*.

The overall aims of this paper were: (1) to describe growth rates of *M. capensis* independent of otoliths, using length-frequency distribution (LFD) data by combining data from fur seal scats (up to 25 cm TL fish, Wilhelm et al., 2013) with data from research surveys (up to 60 cm TL fish) and commercial fisheries samples (up to 80 cm TL fish) and (2) to test if there are significant fluctuations in growth rates between cohorts and between areas (North and South) by using random effects of (a) cohort and (b) area in a non-linear mixed effects model.

2. Material and methods

2.1. Length-frequency analysis and growth rate analysis

Length-frequency analysis was performed on 36 LFDs from research surveys between May 1995 and February 2011 and 295 monthly LFDs from commercial catches between January 1998 and December 2011. The LFDs were assigned to two main areas (North and South) along the Namibian coast.

Survey LFDs were obtained from routine annual demersal surveys by the Ministry of Fisheries and Marine Resources (MFMR) Namibia. There were 15 surveys in January–February (austral summer) from 1996 to 2011 and two additional surveys in May 1995 and September 1996 (Burmeister, 2001). The survey vessels use a Gisund Super two-panel bottom trawl with 20 mm outer-codend mesh, lined with 10 mm inner-net, with a vertical net opening of 4.2–4.5 m. From each trawl haul, a sub-sample of *M. capensis* was measured for fish total length (TL) and the number of fish was raised to the total mass of the haul (by multiplying by a raising factor, RF1) and then raised to the trawl time (by multiplying by a second factor, RF2) to obtain the total number of fish per 30 min trawled in each length class (cm). Raising factors were obtained as follows: RF1 = total mass of the haul/mass of the sample and RF2 = 30 min/total trawl time for that haul. This was totalled for each of the two areas for each survey: North (17–23.99°S) and South (24–29°S) (see Fig. 1 for an example of a survey track).

Commercial samples were collected since January 1998 by the on-board fisheries observer programme of MFMR. A sample taken from a trawl (individual fish were measured to the nearest cm TL, rounded down in all cases) was raised to the vessel's catch (using RF1). The vessel catch was then raised to the fleet's catch by day (RF3 = total catch for that day/vessel's catch) and then by month (RF4 = total catch for the month/catch for the day) in each of four areas the catch was taken from: North shallow (<24°S, <350m), North deep (<24°S, ≥350m), South shallow (≥24°S, <350m) and South deep (≥24°S, ≥350m). For the purposes of this analysis, shallow and deep were combined in each area to obtain one LFD respectively for North and South for each month. The commercial vessels use a minimum codend mesh size of 110 mm and most of them use a vertical net opening of 4–8 m.

Otolith samples were obtained from fur seal scats collected at least once a month from 1994 to 2009. Measurements of otolith lengths (OL) were converted to fish lengths (TL), where $TL = 0.6997(OL_{undigested} + 2.170)\hat{1}.362$ (Wilhelm et al., 2013). Fish length frequency distributions from the fur seal scat samples, and their assumed cohorts, were used to define early growth rates and t_0 in the current analysis. This method has been described in detail by Wilhelm et al. (2013).

The robust approach of Laslett et al. (2004) was used for length frequency analysis. This approach involves a first step of estimating mean lengths of modes in an LFD sample, and then calculating growth rates in a second step. The estimation method suggested by MacDonald and Pitcher (1979), Fournier et al. (1990) and Laslett et al. (2004) was used for the first step. It was assumed that (1) lengths of the fish in each age group a are normally distributed around their mean length L_a, and (2) the standard deviations (σ_a) of lengths around the mean L_a are a linear function of L_a ($\sigma_a = cv * L_a$, where cv is the coefficient of variation, which was estimated).

For each sample for each 1-cm TL-class, the proportion of fish (p_i) expected in length class i in age group a was calculated by drawing from a normal distribution with mean length L_a and standard deviation $\sigma_a = cv * L_a$, with the probability density component p_{ia} (L_a, σ_a), where

$$p_{i,a}(L_a, \sigma_a) = \frac{1}{2\pi\sigma_a} \exp\left(\frac{-(L_i - L_a)^2}{2\sigma_a{}^2}\right) \quad (1)$$

To get a new expected proportion at length (Ep_i), p_i is multiplied by the relative abundance expected in each age group (q_a),

$$Ep_i = \sum_{i=1}^{A} q_a p_i \quad (2)$$

where A is the maximum number of age groups (or discernible modes), determined visually (usually initially three), and $q_{a>}$ 0 was obtained by setting an initial proportion (depending on the number of discernible modes, such that $\sum_{i=1}^{A} q_a = 1$) for each age group. The initial mean length was set at e.g. $L_j = 10$ cm (when visible, only for survey samples), 25 cm (when visible, most often only for survey samples), 35 cm, 45 cm and 55 cm (most often only for commercial samples) respectively for age groups 0.5 y, 1.5 y, 2.5 y, 3.5 y and 4.5 y. Fish TLs measured during the surveys and commercial observer sampling were rounded down to the nearest cm (integer measurements) so the mean of each length class was the midpoint (e.g., the mean of the 1 cm length class is 1.5 cm), and assigned to L_i in Eq. (1).

The parameters $\hat{L_a}$ and $\hat{q_a}$ were estimated iteratively for each age group and $\hat{cv}$ was estimated for all age groups in each LFD sample by minimizing the binomial log-likelihood function (Fournier et al., 1990):

$$-LL = -\sum_{i=1}^{A} Op_i \ln(Ep_i) \quad (3)$$

where Op_i is the observed proportion in each length class i. Since the log-likelihood function was fitted for each LFD sample independently, the sample size n was not necessary in the function. After the first fit to each LFD, if the relative abundance of an age group (q_a) was estimated as <0.001, or if the cv was ≪0.1 or if visual inspection indicated over-fitting, the number of age groups was reduced to $A - 1$ and the model was re-fitted until all criteria were met and the best fit obtained.

In the second step of the length frequency analysis, ages were assigned to the mean lengths obtained from the first step, using the following assumptions:

1) The mid-date of each survey and the mid-date of each month in which commercial LFDs were collected was used as the date of collection for each LFD sample.