Relative magnitude of cohort, age, and year effects on size at age of exploited marine fishes

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ABSTRACT

Variation in individual growth rates contributes to changes over time in compensatory population growth and surplus production for marine fishes. However, there is little evidence regarding the prevalence and magnitude of time-varying growth for exploited marine fishes in general, whether it is best approximated using changes in length-at-age or weight-at-length parameters, or how it can be represented parsimoniously. We therefore use a database of average weight in each year and age for 91 marine fish stocks from 25 species, and fit models with random variation in length and weight parameters by year, age, or cohort (birth-year). Results show that year effects are more parsimonious than age or cohort effects and that variation in length and weight parameters provide roughly similar fit to average weight-at-age data, although length parameters show a greater magnitude of variability than weight parameters. Finally, the saturated model can explain nearly 2/3 of total variability, while a single time-varying factor can explain nearly 1/2 of variability in weight-at-age data. We conclude that time-varying growth can often be estimated parsimoniously using a single time-varying factor, either internally or prior to including 'empirical' weight at age in population dynamics models.

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1. Introduction

Growth in size of individual animals (i.e., somatic growth) is one of the primary demographic mechanisms contributing to population growth, and hence to sustainable harvest of exploited fishes. Growth rates are implicit in many biomass dynamics models, and must be explicitly approximated in age-structured population models (Quinn and Deriso, 1999). These latter models therefore require detailed information regarding somatic growth, and failure to accurately approximate growth can cause population models to perform poorly when used to provide management advice (Helser and Brodziak, 1998).

Changes over time in somatic growth rates have been documented for many fish taxa, including salmon (Ruggerone et al., 2005) and groundfishes (Clark and Hare, 2002; Daan et al., 1990; Mehl and Sunnana, 1991). Average individual growth rates may vary over time due to environmental, biological, and anthropogenic factors, including changes in environmental temperature, inter- or intra-species competition, and selective fishing mortality (Sinclair et al., 2002). Time-varying growth can have important implications for management targets and outcomes because it can accompany or even cause changes in spawning potential (Brander, 2007). Variable growth can also contribute to observed variability in 'surplus production' for exploited fishes (Helser and Brodziak, 1998; Rijnsdorp, 1994; Ruggerone et al., 2007), and to population regulation via changes in spawning output (Marshall and Frank, 1999).

There are many ways to model time-varying growth. Besides deterministic models of density-dependent growth (Helser and Brodziak, 1998), weight-at-age data may be analyzed using smoothed or blocked averages (Clark and Hare, 2002), using cohort-specific growth rates (Whitten et al., 2013), or using year-specific growth increments (Minte-Vera, 2004). Alternatively, researchers may input weight-at-age data directly into population dynamics models as "empirical weight-at-age" data (as is commonly done with virtual population assessment models), and hence avoid any parametric model for fish growth in age-structured models (Ianelli et al., 2012; Stewart et al., 2012). Empirical weight-at-age data may

or may not be smoothed prior to inclusion in population models, and this smoothing process may again include different year, age, and cohort effects.

Despite this diversity of methods to approximate average growth rates and account for variability in growth around the average, we know of no previous meta-analysis regarding the form or magnitude of variation in growth over time for exploited marine fishes. We therefore develop a single-species model for time-varying weight-at-age data, which includes age, year, and cohort effects representing variability in parameters for the length-at-age or weight-at-length relationship, and apply this model to data from 91 stocks worldwide. We specifically seek to answer the following three questions: (1) Which specification of age, year and/or cohort effects, either individually or in combination, is most parsimonious for explaining the variation in weight at age? (2) What is the relative magnitude of age, year, and cohort effects? and (3) What proportion of variability is explained by a model that has only a single time-varying factor (which either explains the most variability or is most parsimonious)? We then conclude by discussing the implications for population dynamics and stock assessment models that seek to approximate time-varying growth, and the broader implications for marine ecology.

2. Methods

2.1. Theory and models

Individual growth is approximated in many fisheries models using the von Bertalanffy growth function (VBGF, Von Bertalanffy, 1957). Given the assumption that body mass scales as the cube of body length (which is approximately met for many fish groups; Froese et al., 2014), this growth model can be expressed as the following growth rate in body length L (all symbols are defined in Table 1):

$$\frac{dL}{dt} = A - B \times L \tag{1}$$

where dL/dt is the growth rate (in units length per time), A is an anabolic rate representing the increase in length as a function of body size, and B is a catabolism rate representing the maintenance costs of each unit of body length (Mangel, 2006). This differential equation represents a linear decrease in growth rates with increasing length and its solution shows that body length asymptotically approaches an asymptotic maximum length L_∞ at a rate governed by growth coefficient k:

$$L_t = L_\infty (1 - e^{-k(t-t_0)}) \tag{2}$$

where t_0 is the age at which L_t would intersect $t = 0$. In converting Eq. (2) to (1), the Brody growth coefficient $k = B$ and maximum length $L_\infty = A/B$ (Charnov et al., 2013; Mangel, 2006). We then convert this length to a body mass, again assuming the isometric (cubic) scaling of body mass to length:

$$W_t = \alpha L_\infty^3 (1 - e^{-k(t-t_0)})^3 \tag{3}$$

where αL_∞^3 can also be expressed as asymptotic maximum weight W_∞. Exploratory analysis confirms that there is little information to estimate different or species-specific values for the allometric scaling of weight at length, given that most species in this analysis have few samples near the asymptote of the growth schedule. We use this expression (Eq. (3)) to emphasize the three main parameters under consideration: the VBGF coefficient k (governing individual growth rates in relative terms) and L_∞ (representing maximum length) are derived from metabolism and catabolism rates (A and B), while the coefficient scaling length to weight α (representing tissue density, body shape, and other factors affecting individual

Table 1
List and definition of symbols used in the text and equations.

Parameter name	Symbol
Length	L
Growth rate (in length)	dL/dt
Anabolic rate	A
Catabolic rate	B
Asymptotic maximum length	L_∞
Length at age t	L_t
Brody growth coefficient	k
"Age" at birth	t_0
Weight at age t	W_t
Asymptotic maximum weight	W_∞
Weight per unit volume	α
Brody growth coefficient for age a and year t	$k_{a,t}$
Average value for brody growth coefficient	k_0
Deviation (in log-space) of $k_{a,t}$ due to cohort effects	$\varepsilon^{(k)}_{t-a}$
Deviation (in log-space) of $k_{a,t}$ due to year effects	$\tau^{(k)}_t$
Deviation (in log-space) of $k_{a,t}$ due to age effects	$\omega^{(k)}_a$
Variance (in log-space) of deviations of $k_{a,t}$ due to cohort effects	$\sigma^{(k)}_{\varepsilon2}$
Variance (in log-space) of deviations of $k_{a,t}$ due to year effects	$\sigma^{(k)}_{\tau2}$
Variance (in log-space) of deviations of $k_{a,t}$ due to age effects	$\sigma^{(k)}_{\omega2}$
Average value for weight per unit volume	α_0
Deviation (in log-space) of $\alpha_{a,t}$ due to cohort effects	$\varepsilon^{(\alpha)}_{t-a}$
Deviation (in log-space) of $\alpha_{a,t}$ due to year effects	$\tau^{(\alpha)}_t$
Deviation (in log-space) of $\alpha_{a,t}$ due to age effects	$\omega^{(\alpha)}_a$
Variance (in log-space) of deviations of $\alpha_{a,t}$ due to cohort effects	$\sigma^{(\alpha)}_{\varepsilon2}$
Variance (in log-space) of deviations of $\alpha_{a,t}$ due to year effects	$\sigma^{(\alpha)}_{\tau2}$
Variance (in log-space) of deviations of $\alpha_{a,t}$ due to age effects	$\sigma^{(\alpha)}_{\omega2}$
Coefficient of variation of observation errors in observed weight at age data	σ_W^2
Observed average weight at age a in year t	$w_{a,t}$
Minimum observed age	a_{min}
Maximum observed age	a_{max}
Estimated expected length at a_{min}	L_{min}
Estimated expected length at a_{max}	L_{max}
Age	a
Year	t
Reference age (used in summations)	a'
Reference year (used in summations)	t'

weight at a given length) is derived from energy storage relationships. Differences in α among individuals and/or relative to some standardized value can be interpreted as Fulton's condition factor given our assumption of isometric weight at age (Nash et al., 2006), so we interpret changes in α over time as changes in average condition factor. We separate the more conventional W_∞ into L_∞ and α because the length-at-age relationship (i.e., L_∞) may be influenced by different biological processes than the weight-at-length relationship (α).

We are specifically interested in variability over time in growth rates. We therefore investigate two modifications to the VBGF. The first postulates that anabolism A and catabolism B both increase (or decrease) by the same proportion, but weight scaling α is unchanged, such that k varies and W_∞ is constant over time:

$$k_{a,t} = k_0 \times \exp\left[\varepsilon^{(k)}_{t-a} + \tau^{(k)}_t + \omega^{(k)}_a\right] \tag{4}$$

where $k_{a,t}$ is the growth coefficient for age a in year t, k_0 is the average value for $k_{a,t}$, $\varepsilon^{(k)}_{t-a}$ is the 'cohort-effect' of being born in calendar year $T - A$ on parameter k, $\tau^{(k)}_t$ is the 'year-effect' of year t on parameter k, and $\omega^{(k)}_a$ is the 'age-effect' of age a on parameter k. The hypothesis of variation in individual growth rate k is pragmatic, given that it allows for a closed-form computation of predicted weight-at-age (see Eq. (5)). However, variation in individual growth rate k is also biologically plausible whenever different years/ages/cohorts have increased activity rates (catabolism), and increased activity leads to a proportional increase in feeding success (anabolism; see Shelton et al., 2012). Density and year effects would therefore be predicted a priori when individual cohorts or