

Original Article

Hierarchical model-based estimation of population growth curves for redfish (*Sebastes mentella* and *Sebastes fasciatus*) off the Eastern coast of Canada

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Northwest Atlantic (NWA) redfish (*Sebastes mentella* and *Sebastes fasciatus*) stocks are currently assessed using survey indicators and age-aggregated production models rather than age-based models because routine age readings are not available due to the difficulty in obtaining reliable measurements for these fish. However, recruitment is highly variable for redfish species so age-aggregated production models are not a good approach to provide short-term harvest advice. Recently a relatively large dataset of validated age readings was published that provide a good basis to model growth and its variability [i.e. population growth curve (PGC)]. In this article we propose a hierarchical random effects growth model that includes between-individual variation to estimate PGCs for 10 NWA redfish stocks and for males and females separately. These growth curves are required to develop age-based stock assessment models. External estimates of measurement error in length and age are included in our model to separate these sources of variation from the PGC variability. The hierarchical approach leads to more realistic growth curves than if each stock and sex are modelled separately. Model results indicated that *S. mentella* usually grow to larger sizes than *S. fasciatus* and that females of both these species grow to larger sizes than males. There was little evidence of a change in growth rates over time.

Keywords: ageing error, between-individual variation, covariate measurement error, mixed effects model, Von Bertalanffy growth curve.

Introduction

There are four redfish species of the genus *Sebastes* found in the North Atlantic (e.g. Planque *et al.*, 2013): Beaked redfish (*Sebastes mentella*), Acadian redfish (*Sebastes fasciatus*), Golden redfish (*Sebastes norvegicus*, previously referred to as *Sebastes marinus*), and Norway redfish (*Sebastes viviparus*). They occur in cool waters (3°–8°C) along the slopes of fishing banks and deep channels in depths of 100–700 m. In the Northwest Atlantic (NWA), redfish range from Baffin Island in the north to waters off New Jersey in the south; however, *S. norvegicus* is mostly found on the Flemish cap and *S. viviparus* is found in the Northeast Atlantic. There is a geographic distributional cline in the NWA with *S. mentella* in the north and *S. fasciatus* in the south, and in intermediate areas where both are found, *S. mentella* is generally

distributed deeper than *S. fasciatus*. However, in the Gulf of St Lawrence, *S. mentella* dominates (Gascon, 2003) and there is evidence of introgressive hybridization between *S. mentella* and *S. fasciatus* (Valentin *et al.*, 2014). These two species have very similar external morphological features which make their species differentiation difficult and nearly impossible by cursory examination (e.g. Gascon, 2003; Cadrin *et al.*, 2010). As a result, in the NWA *S. mentella* and *S. fasciatus* catches are usually reported as combined and these two species are managed together as beaked redfish.

There are currently nine redfish management areas in the NWA (Figure 1): (i) South Greenland in NWA Fisheries Organization (NAFO) Division 1F, (ii) Labrador Shelf (NAFO Divisions 2GHJ and 3K), (iii) Flemish Cap (Division 3M), (iv)

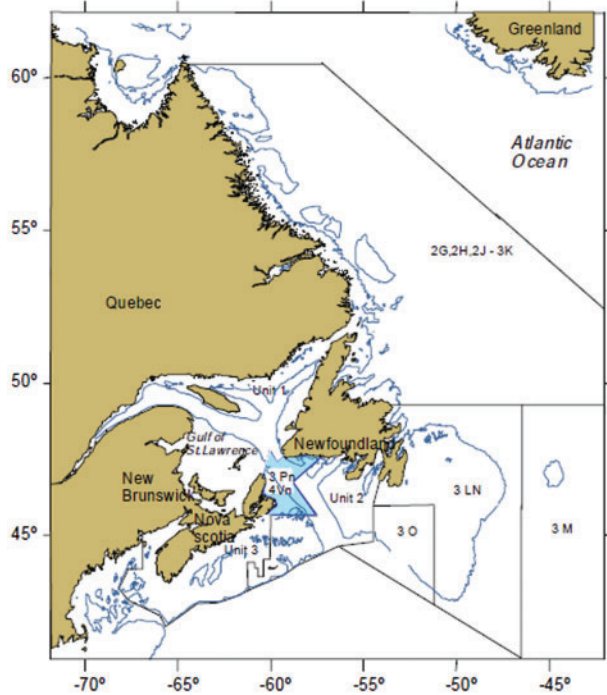


Figure 1. NWA redfish management units. The shaded zone is included in Unit 1 from January to May, and in Unit 2 from June to December. Grey lines indicate 200 m depth contours. Source: Modified from Gascon (2003).

Grand Banks (Divisions 3LN), (v) Southern Grand Banks (Division 3O), (vi) Gulf of St. Lawrence (Unit 1—Divisions 4RST and 3Pn4Vn during January to May), (vii) Laurentian Channel (Unit 2—Divisions 3Ps, 4Vs, 4Wfgi, and 3Pn4Vn during June to December), (viii) Scotian Shelf (Unit 3—Divisions 4WdegkX), and (ix) Gulf of Maine (NAFO Subarea 5). However, there is recent evidence of further sub-stock structure in the Northern Gulf of St. Lawrence (Valentin *et al.*, 2014). Except for the Flemish Cap and the Gulf of Maine stocks, redfish have been commercially fished by Canada since World War II. The most commonly fished areas were Subarea 2 + Division 3K, as well as Units 1–3 (Gascon, 2003). Catches peaked at 400 000 tons in 1959 (Lear, 1998) and ranged between 135 000 and 286 000 tonnes during 1960–1993. Since then catches have been much lower and were 23 000 tonnes in 2015 (source: NAFO STATLANT 21A database). Stock assessments began in the early 1970s. There has been almost no significant recruitment in the last 30 years and most stocks are depleted or collapsed (Valentin *et al.*, 2014). The directed fishery has been under a moratorium since 1995 in Unit 1, since 1998 in 2J3K, and from 1997 to 2009 in 3LN. Quotas have been generally declining in other areas. The Committee on the Status of Endangered Wildlife in Canada assessed the status of *S. fasciatus* and *S. mentella* in Canadian waters as endangered, threatened or special concern, depending on the area and species under consideration (see Valentin *et al.*, 2014).

Sebastes species in the North Atlantic can aggregate densely along the bottom of continental slopes but also form semi-pelagic schools at times which may lead to high variability in survey catches of redfish. In the NWA, recruitment tends to be episodic and significant year-classes have been observed from 5 to more than 12-year intervals (Gascon, 2003). Growth is usually faster in

southern areas than in northern areas, females grow faster than males, and *S. fasciatus* reaches a smaller size at age than *S. mentella* (Campana *et al.*, 2016). On average, redfish take ~8–10 years to reach commercial size (25 cm or 10 inches). Redfish are long-lived, slow-growing, and late-maturing. Devine and Haedrich (2011) summarized that the maximum age is 30–50 years for *S. fasciatus* and 60–75 years for *S. mentella* and *S. norvegicus* in the NWA. Average age at 50% maturity for most populations of *S. fasciatus* in the Canadian NWA is 5.5 years and 10–13 years for *S. mentella*.

Ageing redfish is difficult and time-consuming. Growth parameters reported in different studies have varied widely, in part because of the difficulty of distinguishing among the redfish species (Campana *et al.*, 2016), but also because the annual increments in immature fish are poorly defined while those in old individuals are often narrow and difficult to interpret (Nedreås 1990; Stransky *et al.*, 2005). In addition, a substantial portion of the published studies on *Sebastes* spp age and growth used either whole otoliths or scales, both of which are now known to produce significant age underestimation bias in adult fish (Campana, 2001). As a result, most laboratories investigating stock dynamics of redfish have not implemented routine age readings because of the difficulty in obtaining reliable measurements (e.g. Stransky *et al.*, 2005). Hence, survey indicators and age-aggregated production models have been used for stock assessment rather than age-based models (e.g. DFO, 2012). These age-aggregated approaches are certainly not best practice for stocks like redfish and there are several research initiatives under-way to improve their stock assessment by better utilizing the available size, age, morphological, and genetic measurements.

Campana *et al.* (2016) recently provided a relatively large dataset of validated age readings, based on image-enhanced burnt thin sections, that provide a good basis to model growth and its variability [i.e. population growth curves (PGCs)]. In this article we estimate PGC's for 10 NWA redfish stocks with Canadian fisheries, and for males and females separately. This is an ambitious objective and important to improve the assessment of these stocks. The data in Campana *et al.* (2016), and more specifically the range of ages, were not always extensive enough at the stock and sex level to support reliable PGC estimation and extrapolations for stock assessment. We use a hierarchical model-based approach with main effects for species and sex, and random stock specific interactions, to address this data deficiency. Essentially with this approach we use growth information from other species and stocks where data are deficient, and account for the uncertainty due to insufficient data. This is similar to meta-analysis approaches to improve the assessment of data-poor stocks (e.g. Punt *et al.*, 2011; Thorson *et al.*, 2015).

Some of the ongoing research initiatives for NWA redfish include age-based assessment models fitted to survey indices and estimates of fishery catches, including length composition information. PGC's are used to transform age-based model quantities to length-based ones to fit to data. Hence, the variation of fish size at age is also a focus of this paper. The distribution of size at age in growth samples includes individual variation but also variability due to measurement errors (MEs) in lengths and ages. The ME sources of variation should be removed from a PGC. We use a hierarchical PGC model to account for stock and sex variation in growth rates, and also include a random effect to account for other between-individual variability in growth rates. Hierarchical random-effect PGC models have been proposed by

others in Bayesian (e.g. Helser and Lai 2004, He and Bence 2007) and non-Bayesian settings (e.g. Schaalje *et al.*, 2002, Morrongiello and Thresher, 2015) and we extend the latter approaches to include ME in age and between-individual variability.

We use a covariate ME modelling approach for observations of ages and lengths based on external estimates of their ME variances to separate these sources of nuisance (i.e. not a population characteristic of interest) variability from stock, sex and between-individual variability. Including ME in the length response variable is standard but including ME in the age covariate is not. Proper accounting of covariate ME is important for more reliable statistical inferences and to avoid the “bias attenuation” problem in which regression parameter estimates are biased towards zero when covariate ME is present (e.g. Carroll *et al.*, 2006). Covariate ME is also referred to as “errors in variables” and this problem has been long recognized in fisheries science when fitting linear regression models (e.g. Schnute *et al.*, 1990), stock-recruit models (e.g. Walters and Ludwig 1981), simple biomass production models (e.g. Uhler, 1980), and growth models. Kitakado (2000) investigated methods to account for ME’s in release lengths in growth models based on length increment data obtained in tag-recapture studies. Suh and Schafer (2002) investigated fitting the Von Bertalanffy (VonB) model to fish growth data with ME’s in ages but for which there was a small validation sample of fish with accurate age measurements. Cope and Punt (2007) investigated including ageing error from reader comparisons when fitting VonB growth curves. However, in practise covariate ME is often not accounted for in regression analyses of fisheries or other ecological data (Denham *et al.*, 2011), although there are many published exceptions in addition to those listed earlier (e.g. Hwang *et al.*, 2007). Part of the problem is that some of the methods proposed to adjust for covariate ME are too complicated to be routinely implemented and do not easily extend to hierarchical models like we use. We propose a practical approach to include ME in age. Our PGC model is novel in that we include ageing error in a hierarchical generalized VonB growth model for many redfish stocks that also includes between-individual variation in growth.

Material and methods

Samples of redfish were collected with otter trawls aboard research vessels in 2001, 2002, 2011, and 2013, mostly during routine annual groundfish surveys. Fish species was determined based on the genotype at 13 microsatellite loci (Valentin *et al.*, 2014). Lengths were usually measured to the nearest millimeter although some samples from 2J3K and Unit 3 redfish were measured to the nearest centimetre. Age determinations were based on a combination of the “crack and burn” and section methods, whereby the sagittal otolith was cut transversely through the core with an Isomet saw and subsequently charred over the flame of an alcohol lamp. Ages (i.e. years since birth) were determined from high resolution images after digital enhancement with Adobe Photoshop CS2 using grey level expansion and an unsharp mask filter (Campana *et al.*, 2016). The final product was 933 length and age measurements representing six *S. fasciatus* stocks and four *S. mentella* stocks (Table 1). A small number of juvenile Unit 3 *S. fasciatus* were aged which gives important information about size at young ages (i.e. 2-5). For the other stocks much of the growth data were for ages ≥ 8 . The number of length and age measurements for each stock and sex ranged from 10 to 91 which

Table 1. Redfish growth data summary.

Stock	Species	Length		Age			Length		Age			
		n	med	med	L	U	n	med	med	L	U	
		Juveniles										
Unit3	fas	12	9.0	3	2	5						
		Males			Females							
2J3K	fas	13	22.0	7	4	22	24	25.0	8	4	11	
3LN	fas	32	24.5	11	5	19	27	27.4	10	5	18	
3O	fas	18	23.0	10	7	18	14	22.9	9	6	13	
Unit1	fas	37	28.2	17	8	27	54	32.3	14	7	36	
Unit2	fas	40	27.5	13	7	24	81	30.3	13	8	21	
Unit3	fas	31	24.0	12	4	30	83	33.0	14	4	38	
2J3K	men	65	29.0	8	4	13	61	30.0	9	5	14	
3LN	men	10	28.0	8	5	11	20	27.6	8	6	14	
Unit1	men	69	32.3	21	14	40	66	35.0	21	9	38	
Unit2	men	91	33.0	21	18	35	85	35.0	21	13	33	

fas, *S. fasciatus*, men, *S. mentella*; n, sample size; med, median; L, 2.5th percentile; U, 97.5th percentile. Total n is 933.

is often insufficient to estimate PGC’s separately. To address this problem we use a hierarchical random effects modelling approach.

We fit VonB PGC models by stock (*s*) and sex ($x = F, M$). We assume a 50:50 sex ratio for unsexed juveniles. For convenience we indicate each species/management unit/sex category as *g*, and there are a total of 21 categories which we denote by the set *G*. We also include a model component to account for between individual variations in growth. We assume growth rates are constant over time but examine the appropriateness of this assumption. Campana *et al.* (2016) found little evidence of long-term (20-year) changes in growth rates within Unit 2 redfish, despite marked changes in age composition. The VonB PGC model formulation we use gives length as a function of age (*a*),

$$L_g(a) = \{L_{\infty g} 1 - (1 - r_g) \exp(-k_g a)\} \exp(\varepsilon_{I_g}), \quad (1)$$

where $L_{\infty g}$ is the asymptotic length (as $a \rightarrow \infty$), k_g is a growth rate parameter, $r_g = L_g(0)/L_{\infty g}$ is the size at birth relative to the maximum size, and ε_{I_g} accounts for individual variation. We assume $\varepsilon_{I_g} \sim N(0, \sigma_I^2)$ are independent and identically distributed (iid) for all individuals and across all levels of $g \in G$. This is considered further in the Discussion. The VonB model is derived from the differential equation (ignoring ε_{I_g}) $\partial l(a)/\partial a = k\{L_{\infty} - l(a)\}$ and the initial size, $L(0)$. The growth rate at birth (i.e. slope at the origin) is $kL_{\infty}(1 - r)$ and $\partial l(a)/\partial a$ declines to zero as age increases.

The VonB assumption of a linear decline in growth rates as size increases may not be completely appropriate over a broad range of redfish ages for a variety of reasons, including changes in growth rates due to maturation or prey composition. We address this by using a more general PGC model that can accommodate a greater variety of growth dynamics. The generalized VonB model (i.e. VonBg) is

$$L_g(a) = L_{\infty g} \{1 - (1 - r_g) \exp(-k_g a^{\gamma_g})\} \exp(\varepsilon_{I_g}). \quad (2)$$

This is a simplified version of the Schnute-Richards growth model (Schnute and Richards 1990; Quinn and Deriso, 1999).

Campana *et al.* (2016) found that *S. fasciatus* and *S. mentella* had similar growth patterns and that growth was usually fairly similar across stocks, but *S. mentella* tended to grow to a slightly larger asymptotic size. We account for these similarities using mixed-effects multiplicative models for the VonB parameters. We assume

$$L_{\infty g} = L_{\infty} L_{\infty sp} L_{\infty x} \delta_{\infty g}, \tag{3a}$$

where L_{∞} is a common parameter for all stocks, $L_{\infty sp}$ is an *S. mentella* species (*sp*) effect (the effect for *S. fasciatus* is one), $L_{\infty x}$ is a sex effect for males, and $\delta_{\infty g}$ are random stock/sex effects that are iid $\log(\delta_{\infty g}) \sim N(0, \sigma_{\infty}^2)$. Similarly,

$$k_g = k k_{sp} k_x \delta_{kg}, \log(\delta_{kg}) \sim N(0, \sigma_k^2), \tag{3b}$$

$$L_g(0) = \lambda_o \delta_{og}, \log(\delta_{og}) \sim N(0, \sigma_o^2), \tag{3c}$$

$$\gamma_g = \gamma \delta_{\gamma g}, \log(\delta_{\gamma g}) \sim N(0, \sigma_{\gamma}^2). \tag{3d}$$

Note that we do not assume species or sex fixed-effects for $L_g(0)$ or the VonB parameter γ_g in Equation (2). We assume that these random effects are independent across levels of G but we assume that $\rho = \text{Corr}(\delta_{\infty g}, \delta_{kg})$ is nonzero and is an estimated parameter. The L_{∞} and k parameters have an intrinsic inverse relationship (e.g. Quinn and Deriso, 1999) and are usually negatively correlated which is why we include correlation in the $\delta_{\infty g}$ and δ_{kg} random effects.

The data available to estimate model parameters (θ , see next Section) are $n = 933$ measurements of age and length for randomly sampled redbfish. Let L_{oi} denote the observed length (including ME) for the i th fish with actual or true length L_i and let A_{oi} and A_i be the observed and true ages. For simplicity we assume that measurements of both length and age are continuous, similar to Cope and Punt (2007). We assume a multiplicative ME model for length,

$$L_{oi} = L_{gi}(A_i) \exp(\varepsilon_{Lgi}), \tag{4}$$

where $L_{gi}(A_i)$ is obtained from either Equation (1) or (2), and the ε_{Lgi} are iid $N(0, \sigma_L^2)$ for all $i \in g$ and $g \in G$. This assumption reflects our belief that ME will be smaller for very small fish (i.e. < 20 cm) compared with larger sizes (i.e. > 20 cm). Errors in age will also usually increase with age because it is more difficult to count annual otolith growth increments in older fish. Hence, we assume multiplicative ME in ages,

$$A_{oi} = A_i \exp(\varepsilon_{Ag}), \tag{5}$$

where the ε_{Ag} are iid $N(0, \sigma_A^2)$ for all $i \in g$ and $g \in G$. These assumptions are considered further in the ‘‘Discussion’’ section. It is difficult to separate the age and length ME’s and the individual variation in fish growth (i.e. ε_{Lg}) based only on samples of ages and lengths. For example, it is clear from Equations (4) and (2) that ε_{Lgi} and ε_{Lg} are completely confounded. Hence, we simply assume values for σ_L^2 and σ_A^2 . Based on our expert judgement we feel length measurements are accurate within ± 1 cm at larger sizes (~ 30 cm). Assuming this accuracy is achieved 95% of the

time suggests that $\sigma_L = 0.5/30 \approx 0.017$ which is the value we use for σ_L . The age reader comparisons of Campana *et al.* (2016) indicated that the ME coefficient of variation (CV) was about 6%, which suggests $\sigma_A = 0.06$ is a reasonable choice.

Note that values for σ_L^2 and σ_A^2 are not completely confounded like σ_L^2 and σ_L^2 . We can find a value for σ_A^2 that maximizes the data likelihood (see below). However, in preliminary simulation testing we found that estimates of σ_A^2 were highly variable and biased, which we feel introduced bias into estimates of σ_L^2 and directly affected the variability in PGC’s. This bias issue is analogous to more simple ME models where it is well known that response and covariate ME variances are confounded in normal linear regressions models but not necessarily in some nonlinear models, although variance parameter estimates are often not stable and useful (see Section 8.1.2 in Carroll *et al.*, 2006). Hence, we decided to simply fix σ_A at the value indicated by age reader comparisons.

We estimate the fixed-effect parameters

$$\theta = (L_{\infty}, L_{\infty sp}, L_{\infty x}, k, k_{sp}, k_x, \lambda_o, \gamma, \rho, \sigma_L^2, \sigma_{\infty}^2, \sigma_k^2, \sigma_o^2, \sigma_{\gamma}^2)$$

based on the marginal maximum likelihood method which we describe later. However, we first need to specify joint log-likelihoods for θ and the random effects which require probability density functions for the data and random effects. Let $f_X(x)$ be the density function for a random variable X , and let $f_{Y,X}(x,y)$ denote the bivariate density function for the random variables X and Y . Let $f_{Y|X}(y)$ be the conditional density of Y given $X = x$ is fixed. The marginal density for age and length measurements of the i th fish is

$$f_{A_{oi}, L_{oi}}(a_o, l_o | \theta) = \int \int f_{A_{oi}, L_{oi} | A_i, L_i}(a_o, l_o | \theta) f_{A_i, L_i}(a, l | \theta) \partial a \partial l. \tag{6}$$

Equation (6) is based on the ME models for length and age, and the PGC model, integrated over true but unknown length and age. To simplify equations we hide the dependence of probability densities on the θ parameters. If age and length ME’s are independent then

$$f_{A_{oi}, L_{oi} | A_i, L_i}(a_o, l_o) = f_{A_{oi} | A_i}(a_o) f_{L_{oi} | L_i}(l_o), \tag{7}$$

and Equations (4) and (5) specify $f_{L_{oi} | L_i}(l_o)$ and $f_{A_{oi} | A_i}(a_o)$. The joint density of the true age and length can be partitioned as $f_{A_i, L_i}(a, l) = f_{L_i | A_i = a}(l) f_{A_i}(a)$. Between-individual and between-stock variations in growth rates affect $f_{L_i | A_i}(l)$. Assume $i \in g$ and let $\underline{U} = (\varepsilon_{Lg}, \delta_{\infty g}, \delta_{kg}, \delta_{og}, \delta_{\gamma g})$ be a vector of all the random effects in Equations (2) and (3a–3d). Note that $\underline{U} \in \mathbb{R}_5 = (-\infty, \infty) \times \dots (-\infty, \infty)$.

$$f_{L_i | A_i}(l) = \int_{\underline{u} \in \mathbb{R}_5} f_{l_i | A_i, \underline{U} = \underline{u}}(l) f_{\underline{U}}(\underline{u}) \partial \underline{u}, \tag{8}$$

where $f_{\underline{U}}(\underline{u}) = f_{\varepsilon_{Lg}}(u_1) f_{\delta_{\infty g}, \delta_{kg}}(u_2, u_3) f_{\delta_{og}}(u_4) f_{\delta_{\gamma g}}(u_5)$. Except for $\delta_{\infty g}$ and δ_{kg} , we have assumed that the random effects are independent. We also assume that, conditional on \underline{u} , the size of the i th fish in the sample is given exactly by Equation (2). This implicitly involves the assumption that the survey gears used to sample fish were not length selective, and this is considered further in the Discussion. Hence,

$$\begin{aligned}
 & f_{A_i, L_{oi}}(a_o, l_o) \\
 &= \int_{a \in \mathbb{R}^+} \int_{\underline{u} \in \mathbb{R}_s} f_{A_i|A_i}(a_o) f_{L_{oi}|L_i=L_g(A_i), \underline{U}=\underline{u}}(l_o) f_{\underline{U}}(\underline{u}) f_{A_i}(a) \partial a \partial \underline{u}.
 \end{aligned} \tag{9}$$

A somewhat controversial issue (e.g. Huang *et al.*, 2006) is how to treat the distribution of true ages, $f_{A_i}(a)$. Flexible models may be more robust (e.g. Carroll *et al.*, 1999) but are more difficult to implement. Suh and Schafer (2002) used a nonparametric estimator of $f_{A_i}(a)$ to estimate the VonB model via an EM algorithm. Cope and Punt (2007) favored the gamma distribution for A_i over the simpler one-parameter exponential distribution. Note that our model is an extension of Suh and Schafer (2002) and Cope and Punt (2007) who only considered fitting a single growth model without between-individual variation. Mohammed (2015) found that estimation of the VonB model with between-individual variation in growth and assuming a simple gamma distribution for $Pr(A_i)$ was robust to substantial deviations in the true age distribution. Hence, we use the same approach as Cope and Punt (2007) and assume

$$f_{A_i}(a) = \frac{a^{\alpha-1} \exp(-a/\beta)}{\beta^\alpha \Gamma(\alpha)}. \tag{10}$$

The α and β parameters also have to be estimated and are included in the parameter vector θ . We investigate the sensitivity of results to an alternate and more flexible model for the true age distribution in which we use different Gamma parameters for each of the ten stocks.

Let D be the set of all data, $D = \{(a_1, l_1, g_1), \dots, (a_n, l_n, g_n)\}$. We assume fish were randomly selected from the survey catches for age measurements. This assumption is also considered further in the Discussion. The log-likelihood function for θ is

$$l(\theta) = \sum_{g \in G} \sum_{i \in g} \log \{f_{A_i, L_{oi}}(a_i, l_i | \theta)\}, \tag{11}$$

and is based on Equations (6)–(9).

The template model builder (TMB; Kristensen *et al.*, 2016) package within R (R Core Team, 2016) was used to implement the model. The MLE's of θ maximize $l(\theta)$. The user has to provide C++ computer code to calculate $f_{L_{oi}|L_i=L_g(A_i), \underline{U}=\underline{u}}(l_o)$, $f_{A_i|A_i}(a_o)$, $f_{A_i}(a)$ and $f_{\underline{U}}(\underline{u})$, but the integration in Equation (9) required for Equation (11) is numerically evaluated in TMB using the Laplace approximation. The random effects \underline{U} and A_i can be predicted by maximizing the joint likelihood, which is the integrand of Equation (9). Additional information on these procedures is provided by Skaug and Fournier (2006). TMB uses automatic differentiation to evaluate the gradient function of Equation (11) and in the Laplace approximation. The gradient function is produced automatically. This greatly improves parameter estimation using a derivative-based optimizer. We use the *nlm* function within R (R Core Team, 2016) to find the MLE for θ . Source code (R and TMB) is provided as Supplementary Materials. The file *maked.R* creates the inputs to TMB which is run via *fit.R*.

The reliability of the model was assessed through detailed examination of model estimates and residuals. Sensitivity analyses to some model assumptions were also performed. A simulation self-test (i.e. Deroba *et al.*, 2014) was conducted in which the

model was fit to simulated data generated by the model. This does not address the reliability of the assumptions of the model but rather it simply addresses how reliable are model estimates assuming the model is correct. We conducted self-test simulations by conditioning on the predicted ε_{I_g} individual variability random effects when generating simulation data. However, these effects were not fixed when estimating the model with the simulated data. We generated 1000 simulated data sets.

PGC's were computed based on model predictions of size at ages 0–40 that also included the between-individual variation term ε_{I_g} (i.e. Equations 1 or 2). We assumed that fish are binned in one cm lengths classes for the PGC's. The probability that an age a fish with estimated length \hat{L}_a is in length class C was computed using a Normal distribution approximation,

$$Pr(L \in C) = \phi \left\{ \frac{\log(C + \frac{1}{2}) - \log(\hat{L}_a)}{se\{\log(\hat{L}_a)\}} \right\} - \phi \left\{ \frac{\log(C - \frac{1}{2}) - \log(\hat{L}_a)}{se\{\log(\hat{L}_a)\}} \right\}, \tag{12}$$

where ϕ is the cumulative probability distribution function for a standard normal random variable. The ADREPORT() feature of TMB was used to provide standard errors of estimates of log-length at age, $se\{\log(\hat{L}_a)\}$, in Equation (12).

Results

In preliminary analyses we found that estimates of $L_g(0)$ were essentially zero for both the VonB and VonBg models so we simplified the model by assuming $L_g(0)$ and r_g were zero, and removed the λ_o parameter in θ . The VonBg model resulted in a significantly better fit to our data (Table 2, M1) compared with the VonB model (M2) as evidenced by the lower AIC statistic. Model M3 is provided to examine the sensitivity to assumptions about ME variation in length (σ_L). As expected this model fit exactly the same as M1 and all parameter estimates were identical except for σ_L which was lower in M3 because of the higher values of σ_L compared with M1. This resulted in more narrow distributions of length at age (results not shown). Model M4 is provided to examine the sensitivity to assumptions about ME variation in age (σ_A). Parameter estimates were fairly similar and σ_L was lower as expected. Although this model had a lower AIC we do not conclude this is a better fitting model for reasons outlined in the Methods section. Model M5 had different parameters for the Gamma distribution of true ages for each stock. However, parameter estimates and CV's (Table 2) were similar to M1 indicating a lack of sensitivity of the VonBg and VonB parameters to the choice of distribution for true ages. Hence, we prefer model M1 for estimating PGC's.

The species and sex effects for L_∞ (i.e. $L_{\infty,sp}$, $L_{\infty,sex}$) from model M1 (Table 2) indicate that this parameter was about 12% higher for *S. mentella* and 9% higher for females. This is consistent with the redfish literature. However, k was about 7% higher for *S. mentella* and 15% lower for females. The VonBg γ parameter was significantly lower than one. There was also additional between-stock variation in these parameters. The stock-specific predicted values of these parameters follow the same patterns overall (Figures 2–4). Female L_∞ was always higher than male L_∞ , and *S. mentella* L_∞ was usually higher than for *S. fasciatus*. The exception to this latter trend is in NAFO Divisions 3LN. In NAFO Division 3O, *S. fasciatus* had a substantially lower L_∞ for

Table 2. Estimates (Est) of model parameters with percent CV (CV \times 100), for five model formulations (see below).

	M1		M2		M3		M4		M5	
AIC:	-304.5		-255.0		-304.5		-332.6		-1242.4	
Quantity	Est	CV	Est	CV	Est	CV	Est	CV	Est	CV
L_{∞}	30.837	5.7	29.801	4.9	30.837	5.7	30.930	5.7	30.796	5.6
k	0.306	19.6	0.209	16.4	0.306	19.6	0.282	19.3	0.299	18.9
γ	0.787	6.1	-	-	0.787	6.1	0.817	5.8	0.794	6.0
$L_{\infty sp}$	1.115	8.6	1.101	7.7	1.115	8.6	1.097	8.5	1.121	8.4
k_{sp}	1.065	28.6	0.956	25.8	1.065	28.6	1.096	27.7	1.039	27.4
$L_{\infty x}$	1.093	2.2	1.082	1.1	1.093	2.2	1.090	2.0	1.100	2.2
k_x	0.845	8.4	0.996	4.2	0.845	8.4	0.874	8.4	0.840	8.3
σ_{∞}	0.127	25.9	0.116	23.9	0.127	25.9	0.128	24.8	0.123	26.7
σ_k	0.413	28.4	0.375	27.3	0.413	28.4	0.404	27.3	0.393	28.1
ρ	-0.974	4.1	-0.920	6.1	-0.974	4.1	-0.978	3.4	-0.967	4.5
σ_{γ}	0.089	26.6	-	-	0.089	26.6	0.075	27.8	0.087	26.8
σ_I	0.083	2.6	0.087	2.6	0.060	5.1	0.077	2.9	0.083	2.6

M1, VonBg (base):	$\sigma_L = 0.016$	$\sigma_A = 0.06$	Gamma age distribution (GAD)
M2, VonB ($\gamma = 1$):	$\sigma_L = 0.016$	$\sigma_A = 0.06$	GAD
M3, VonBg (test σ_L):	$\sigma_L = 0.06$	$\sigma_A = 0.06$	GAD
M4, VonBg (test σ_A):	$\sigma_L = 0.016$	$\sigma_A = 0.1$	GAD
M5, VonBg (test age):	$\sigma_L = 0.016$	$\sigma_A = 0.06$	stock specific GAD

AIC is the Akaike information criterion.

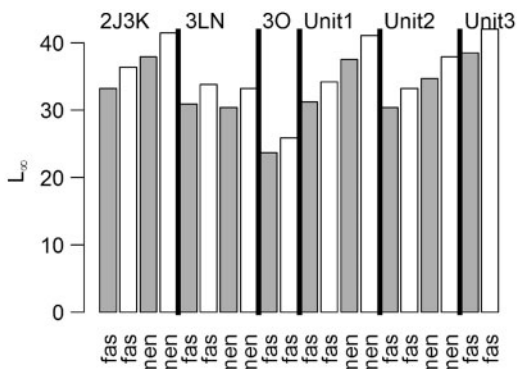


Figure 2. Estimates of L_{∞} for six *S. fasciatus* (fas) and four *S. mentella* (men) stocks. Males are indicated with shaded bars and females with white bars. Management units are listed at the top.

both sexes (Figure 2) than other stocks but higher k 's (Figure 3). *Sebastes mentella* in NAFO Divisions 2J3K and Units 1 and 2 had higher L_{∞} 's for both sexes. The between-stock CV for k (i.e. σ_k) was much larger than for L_{∞} (Table 2) indicating more between-stock variation in growth rates than in asymptotic sizes. There were some large correlations in parameter estimates for model M1, as is typical when fitting VonB growth models. The estimators of L_{∞} and k were negatively correlated (-0.78). Similarly the species effects for L_{∞} and k were negatively correlated (-0.92). However, the sex effect correlation was much lower (-0.39). The estimators of σ_{∞} and σ_k were positively correlated (0.90). The Gamma age distribution (GAD) parameters (α and β) were negatively correlated (-0.94). Otherwise correlations in parameter estimates were much lower and often close to zero. These correlations are considered further in the Discussion.

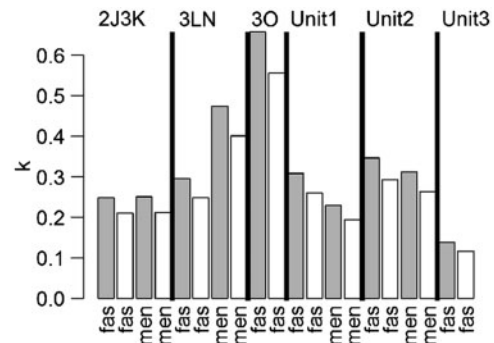


Figure 3. Estimates of k for six *S. fasciatus* (fas) and four *S. mentella* (men) stocks. Males are indicated with shaded bars and females with white bars. Management units are listed at the top.

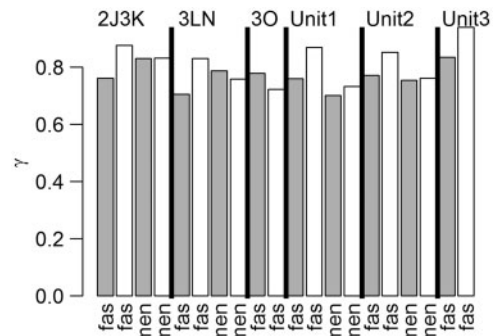


Figure 4. Estimates of γ for six *S. fasciatus* (fas) and four *S. mentella* (men) stocks. Males are indicated with shaded bars and females with white bars. Management units are listed at the top.

Comparisons of predicted PGC's (Figure 5) show that there is broad similarity in PGC's across these two species and the various NWA stocks, particularly among Unit 1 stocks and sexes. Also, for all stocks, growth rates reduced substantially for ages greater than 10 and by age 30 most fish were very close to their model maximum size. The biggest difference in this general pattern was for Division 3O *S. fasciatus*; this stock had a higher growth rate ($k = 0.56$ for females and 0.66 for males) but a lower asymptotic size ($L_{\infty} = 26$ cm for females and 24 cm for males) than the other stocks where L_{∞} was usually between 30 and 40 cm and growth rates were much lower ($k \sim 0.25$). *Sebastes mentella* in NAFO Divisions 3LN also reached a much smaller size relative to the other *S. mentella* stocks. The lower L_{∞} 's for Unit 2 are somewhat unusual but the residuals for this stock (Supplementary Figure S1) suggest potential model mis-specification and a slight under-estimation of L_{∞} . Otherwise the residuals for other stocks do not indicate mis-specification. A residual pattern vs. year would indicate a change in growth rates over time but we did not find any evidence of this for any of the stocks (results not shown).

PGC's and 95% CIs (Figure 6) provide a good description of the overall variability in the growth data. The resulting PGC's are illustrated for *S. mentella* in NAFO Divisions 2J3K (Figure 7a—males; Figure 7b—females). The distribution of size at age for females is wider than for males. PGC's for all stocks are shown in the Supplement Materials (Supplementary Figures S2-S7).

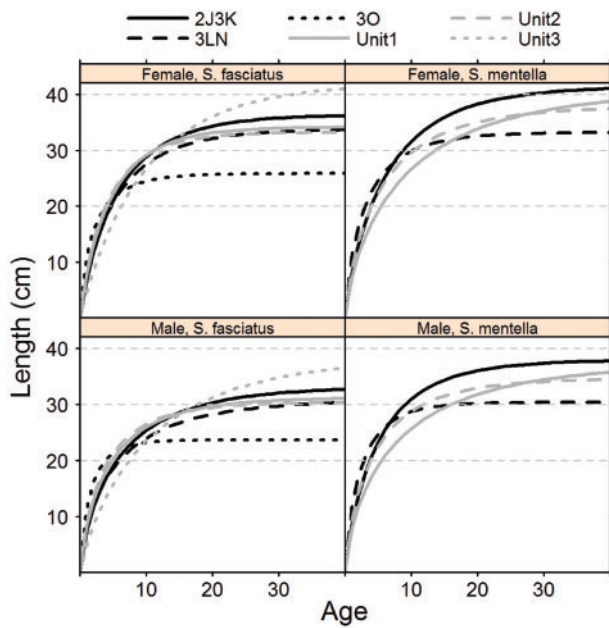


Figure 5. Comparisons of growth curves for NWA redfish stocks. Panels are for sex and species. Grey horizontal references lines are shown at 20, 30, and 40 cm.

The self-test simulations showed that L_∞ and the associated sex and species effects were estimated with high precision and accuracy (Figure 8). This is not surprising because much of the growth data are for larger sized redfish that mostly provide information on L_∞ . Between-individual variation (σ_I) was also estimated with high precision which is also not surprising because the other related variance parameters for ME in length and age were fixed. Hence, the remaining variance in the within-stock/sex distribution of size at age can only be accounted for by σ_I . However, the estimates of σ_I were slightly negatively biased because the standard deviation of the predicted values for the ε_{I_g} 's (0.078) used to generated simulation data was less than the estimate of σ_I (0.083; see Table 2). The between-stock variability in L_∞ (i.e. σ_∞^2) was estimated accurately but with much less precision which is consistent with the higher CV's for this parameter in Table 2. There are only 21 stock/sex combinations to base this variance parameter on, and consequently it is not estimated with as high of precision as σ_I . The k and γ parameters and their between-stock variance parameters (i.e. σ_k^2 and σ_γ^2) were estimated less accurately but the results still seemed reliable. The simulation performance of stock-specific predictions of the VonBg parameters followed similar patterns (Supplementary Figures S8a-c). The L_∞ 's were usually estimated accurately (Supplementary Figure S8a). The K 's were well estimated except for Division 3O *S. fasciatus*. The stock-specific γ parameters were slightly over-estimated (Supplementary Figure S8c) and closer to one (i.e. a VonB model) which suggests that the model is somewhat biased in detecting this type of a departure from the standard VonB model.

Discussion

We developed a hierarchical mixed-effects model to describe growth curves and variation in NWA *S. mentella* and *S. fasciatus* redfish stocks. This included modelling between-stock and

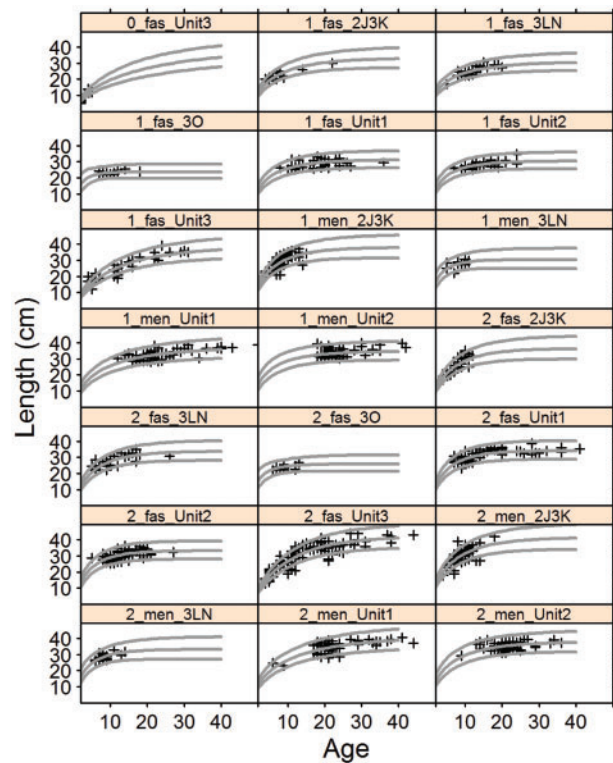


Figure 6. Sex specific growth curves (grey lines, predictions and 95% CIs) for six *S. fasciatus* (fas) and four *S. mentella* (men) stocks. Juveniles = 0, males = 1, females = 2. Points are observations.

between-individual variability in size at age. Our main purpose for developing this model is to estimate stock- and sex-specific PGC's to use in stock assessment models. The distribution of size at age in a PGC is caused by between-individual variability in growth rates. We also accounted for externally derived estimates of ME variability in age and length. We do not want to include ME sources of variability in PGC's which is why it is important to model these sources separately and remove their influence on estimates of between-individual variation. We used the VonB growth model which is commonly applied to redfish growth data (e.g. Gascon, 2003; Stransky et al, 2005; Campana et al., 2016); however, we found evidence of VonB lack-of-fit that was fairly consistent for males and females and all of the stocks. The VonB model resulted in mostly positive residuals at younger ages (i.e. age < 10; results not shown) and this problem was substantially reduced with the VonBg model. However, the growth model we used is somewhat complicated and additional investigation of model goodness of fit may be useful.

It seems we are the first to consider ageing error in hierarchical mixed effects PGC models, but covariate ME in mixed effect models has been studied by others (see examples in Carroll et al., 2006). The literature usually reports similar biases in mixed effects regression parameter estimates compared with ordinary generalized linear models but the biases in variance parameter estimators varies from case to case (Wang et al., 1998), depending on the nature of the covariate MEs. Wang and Davidian (1996) and Tosteson et al. (1998) found that not accounting for covariate ME results in substantial positive biases in variance parameters reflecting differences amongst individuals. This is

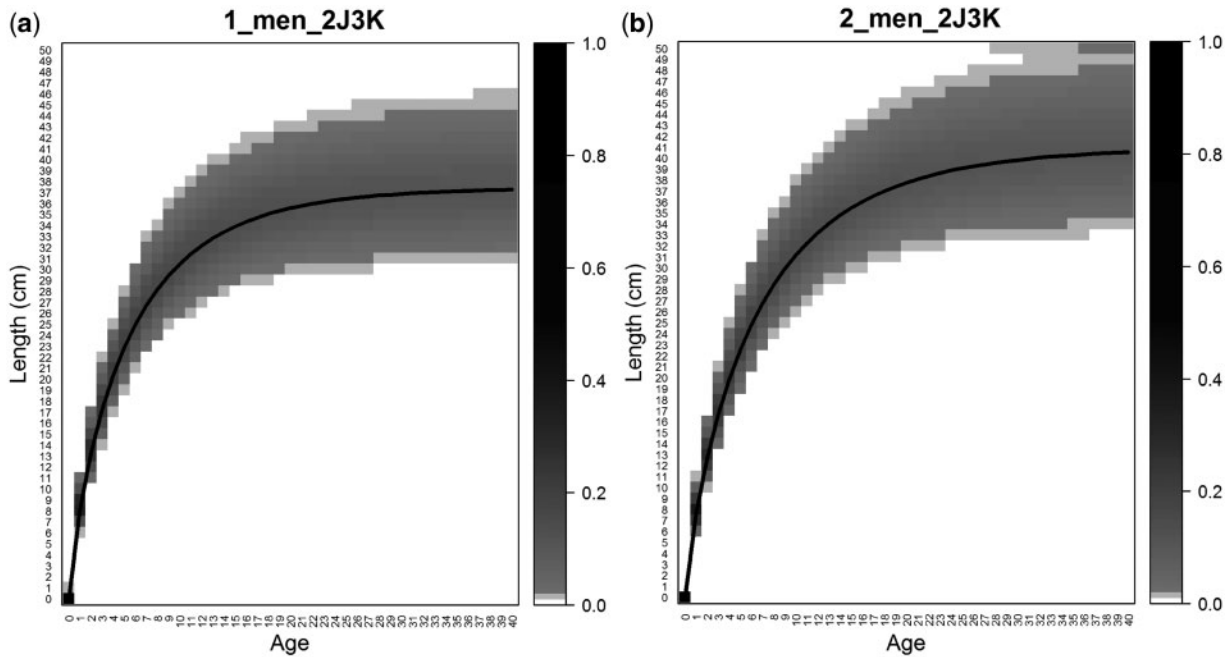


Figure 7. (a) PGC for *S. mentella* males in NAFO Divisions 2J3K. Each column indicates the conditional (on age) probability of being in 1 cm length classes. The shading indicates the probability level. The black curve is the model predicted mean length at age. (b) PGC for *S. mentella* females in NAFO Divisions 2J3K.

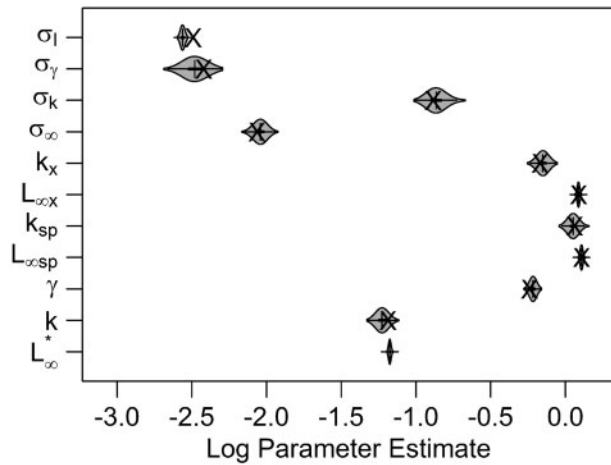


Figure 8. Model M1 self-test simulation results for some model parameters. Simulations results are plotted as kernel densities using the vioplot R package (Adler, 2005). Values used to generate simulation data are indicated by X's. * L_{∞} is divided by 100 (i.e. in metres).

particularly relevant for us because it indicates that not accounting for length and age ME's will result in inaccurate PGC's in which the distribution of length at age is too variable.

Assumptions

We assumed that growth samples were selected at random from the research survey catches. In fact the redfish growth data were collected using a length-stratified sampling design in NAFO

Divisions 3O, 3LN, and 2J3K. This can potentially result in over-estimation of L_{∞} and under-estimation of k (e.g. Goodyear, 1995; Bettoli and Miranda, 2001) if the stratification is not accounted for, and the biases can be large (Mohammed, 2015). A sampling-design adjusted approach (e.g. Echave *et al.*, 2012) is often used to adjust mean length at age to account for length-stratified sampling. Candy *et al.* (2007) proposed a similar adjustment for individual growth data but also included adjustments to deal with gear selectivity which is not an important issue for us (see below). However, such adjustments may not perform well in removing design bias with individual length-age data (Mohammed, 2015). Those results suggested over-estimation of L_{∞} and under-estimation of k if the stratification was not taken into account (a result similar to Echave *et al.*, 2012), but the sampling-design adjusted approach led to over-estimation of k and under-estimation of L_{∞} by similar magnitudes compared with the unadjusted estimators. Mohammed (2015) showed that the VonB growth model that included between-individual variability gave much better estimates whether length-stratification was accounted for or not. Hence we have not made any adjustments for length stratified sampling because the model we use also included between-individual variability. This type of sampling design is also known as response-biased or two-phased sampling and it is well known that not accounting for this type of sampling can lead to severely biased regression model estimation (e.g Jewell, 1985; Breslow *et al.*, 2009; Scott and Wild, 2011). A variety of approaches have been proposed to deal with this problem and examining this for the redfish growth data may be a useful area for additional research.

We implicitly assumed that the survey gears used to sample fish were not length selective. Most of our data are for fish sizes

that are fully selected by the research survey gear and we expect that selectivity is not an important issue. However, there will be some size selectivity at smaller sizes so that our samples of young ages may represent fast growers. We also assumed that age and length ME's are independent which will be true if the length of a fish is not known or not somehow used by age readers when estimating fish age.

We assumed no bias in the length and age measurements. Campana *et al.* (2016) confirmed the accuracy of their age interpretations across a range of ages using both bomb radiocarbon and cohort tracking, which would have detected any significant ageing bias. Nor do we have reason to expect bias in the length measurements. We also assumed fixed values for the ME variance in length and age and we assumed these ME's had a lognormal distribution. In practice these measurements only take discrete values and it is straightforward to extend our methods to use more realistic discrete ME models such as the ageing error models in Punt *et al.* (2008) or Hanselman *et al.* (2012). Additional research should be conducted to determine if better approaches to modelling length and age ME's for redfish produce improved PGC's. In addition, a better approach is to include likelihood components for length and age reader comparison data which would then include uncertainty about ME variance parameters in the calculation of PGC's. However, we do not anticipate that this would have much effect on PGC's.

To estimate PGC's we assumed that the true distribution of age for the various sampled fish could all be described by a simple gamma distribution. However, the data come from multiple stocks and several years and it is likely that the distribution of true ages is considerably different than our assumption. It seems that this assumption is not very important because a sensitivity analysis using a much more flexible distribution for true ages produced very similar PGC estimates for all stocks and sexes.

We accounted for individual variation in growth using a multiplicative effect (ε_{lg}) to the growth models that we assumed had a lognormal distribution. How this is done can directly affect the PGC's. It is common to include individual variability in the VonB L_∞ and k parameters (e.g. Alós *et al.*, 2010) and our approach is identical to including multiplicative variability in L_∞ but not k . If there is between-individual variability in k then not accounting for this can lead to biased estimates of k if the variability is large (e.g. Sainsbury, 1980). Shelton and Mangel (2012) advocated an alternative formulation of the VonB function based on the differential generating equation, $\partial l(a)/\partial a = q - kl(a)$. They suggested that q and k were independent parameters. They included individual variation in both q and k (i.e. q_i and k_i) but with a parametric relationship, $q_i = \gamma k_i^\nu$; that is, $\log(q_i)$ is a linear function of $\log(k_i)$. D'Arcy and Thorson (2016) used the same formulation in an application of growth increments from tagging. We investigated this approach in preliminary analyses and did not find that q and k were less statistically dependent than L_∞ and k nor did we find that $\log(q_i)$ was approximately a linear function of $\log(k_i)$. However, individual variation may exist in both growth rates and asymptotic sizes and the growth rates may influence the asymptotic sizes such that individual $L_{\infty i}$ may be positively correlated with k_i (e.g. Vincenzi *et al.*, 2014) or negatively correlated. Although it was difficult for us to separate the effects of individual variation in L_∞ and k based on the redfish growth data, different approaches may fit the data similarly but produce different PGC's. This requires further research.

Conclusions

Model results indicated that, overall, *S. mentella* grow to larger sizes than *S. fasciatus* and that females of both these species grow to larger sizes than males. This is consistent with other literature results (e.g. Gascon, 2003). The only discrepancy was Division 3LN redfish, where both *S. mentella* and *S. fasciatus* had similar growth rates although females still grew larger than males. However, there were some large correlations in the estimates of some of the model parameters which is commonly found when fitting VonB models. This reduces the reliability of parameter estimates and makes it more difficult to compare growth for different populations using these parameter estimates. Alternative model formulations exist that can have lower correlations (e.g. Francis, 1988). However, these correlations should have little impact on the reliability of the estimated PGC's. Model results indicated broad similarity in the PGC's across these two species and the various NWA stocks. The biggest difference was for Division 3O *S. fasciatus* which had a higher growth rate but a lower asymptotic size. There was little evidence of a change in growth rates over time which is a similar finding to Campana *et al.* (2016).

The hierarchical mixed effect model we used for redfish growth is a practical approach to address data limitations for each individual stock and sex. We included additional information on age and length MEs to separate these sources of variability from between-individual variation in growth and to estimate PGC's that represent the distribution of length at age in the stock and not just the samples. These PGC's are an important contribution to improving the assessment of redfish stocks by facilitating the use of age-based models for data poor stocks that do not have annual and extensive age sampling programs. This approach may have applications to other stocks with insufficient growth information such as Pacific rockfish species.

Supplementary data

Supplementary material is available at the ICESJMS online version of the article.

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