



Accounting for cohort-specific variable growth in fisheries stock assessments: A case study from south-eastern Australia

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ARTICLE INFO

Article history:

Received 22 December 2011

Received in revised form 14 May 2012

Accepted 30 June 2012

Keywords:

Variable growth
Stock assessment
Integrated analysis
Stock Synthesis

ABSTRACT

Modern statistical fishery stock assessment models rarely account for temporal variability in mean length-at-age, and almost never describe cohort-specific effects. This study employs techniques for discerning temporal change to mean length-at-age from fisheries data and introduces recently developed stock assessment methods to account for this variability. Using Stock Synthesis, a statistical catch-at-age modelling framework, a stock assessment to account for cohort-specific variability in mean length-at-age was developed for blue grenadier, *Macruronus novaezelandiae*, an important commercial species in Australia's Southern and Eastern Scalefish and Shark Fishery. Key outputs of a standard stock assessment model that assumes static growth were compared to those of an alternative model that accounts for observed variability in length-at-age. Comparisons show that accounting for variable growth provides a better fit to time-series data and results in significant differences to key population estimates. These differences have implications for the estimation of quantities important to management and thus to scientific advice regarding recommended catch levels.

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1. Introduction

Variability in somatic growth is a widely acknowledged phenomenon for harvested fish species, with recent studies showing mean length-at-age can vary year-by-year (Arnekleiv et al., 2006), spatially (Gaertner et al., 2008), and between cohorts (Feltrim and Ernst, 2010). Such variability has been attributed to environmental change, intra- or inter-specific competition, and abiotic factors such as fishing induced changes to population size. Changes to growth are often accounted for using year-specific mean weight-at-age estimates in Virtual Population Analyses (VPA), but are rarely accounted for in contemporary statistical fisheries stock assessment models. Instead, these models generally assume growth is static through time, and use pooled age-length data to estimate a time-invariant length-at-age relationship (e.g. PFMC, 2009; Tuck, 2011). For many fisheries this assumption is necessary because the long-term data required to determine variation is unavailable. For others, the simplified approach is taken because a constant length-at-age relationship is thought to be adequate for stock assessment purposes.

Age-length data are collected routinely for many species as part of scientific monitoring programs for Australia's Southern and

Eastern Scalefish and Shark Fishery (SESSF), and are an important source of information for stock assessments (Smith et al., 2001). Age-length data and growth estimates enable the conversion of catch or abundance values in weight to catch or abundance in numbers, and are necessary for length composition predictions that are fit to observed length composition data when estimating model parameters. Availability of long time-series of age-length data for stocks such as the highly valued and abundant blue grenadier, *Macruronus novaezelandiae*, presents an opportunity to investigate if changes to mean length-at-age can affect the results of stock assessments.

Blue grenadier are found around the entire southern Australian coastline, including Tasmania. It is a moderately long-lived species with a maximum age of about 23 years (Russell and Smith, 2006). Maturity occurs around age four for males and age five for females, with length at 50 percent maturity being 57 cm for males and 64 cm for females (Russell and Smith, 2006). The species is characterized by highly variable recruitment, and the fishery has been largely sustained by a few very strong cohorts over the past 10–15 years. The fishery is divided into two sub-fisheries for assessment purposes: a 'spawning' sub-fishery operating on the spawning stock off the western coast of Tasmania in winter (June through August), and a 'non-spawning' sub-fishery operating in all other parts of the fishery at all other times (Punt et al., 2001; Tuck, 2009). Management of the fishery is implemented through catch limits specified via a harvest control rule. The harvest control rule requires estimates of current absolute and relative biomass from

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the assessment to calculate recommended catch limits (Smith et al., 2008).

The assessment method is based on the integrated analysis paradigm, (Maunder and Punt, 2013). Integrated analysis, in the form of statistical catch-at-age modelling, was first developed in the 1980s (Fournier and Archibald, 1982; Methot, 1989, 1990), and is used to assess many species in the SESSF and elsewhere around the world (e.g. ICES, 2006; PFMC, 2009; IATTC, 2011). Integrated analysis has become the preferred method for assessment in the SESSF because, among other reasons, it can combine multiple types of data, it does not require complete time-series of all data sources, and simulation testing reveals it to be a robust assessment method for a variety of SESSF species (Punt et al., 2002; Klaer and Wayte, 2011).

A key advantage of integrated analysis for fisheries stock assessment is that it can make full use of both age- and size-specific information. Factors important for describing population dynamics, such as maturity, fecundity, natural mortality, and gear selectivity, may variously be functions of age or size for the species in question, and integrated analysis models can specifically reflect this. As such, time-series data relating to both age and length, along with other data types, can be incorporated and accounted for in a single, combined objective function when using integrated analysis. The integration of age- and size-specific information requires a method to relate body size to age. This may be an age-length key which describes the distribution of age for each length, or a functional relationship between age and length, combined with an additional function relating length to mass. When using age-length relationships, it is common practice to account for individual variation in length-at-age by specifying or estimating a coefficient of variation around the mean relationship, but change over time in mean length-at-age, or indeed any form of temporal variability in growth, is rarely considered.

Assessments based on integrated analysis for the SESSF are now regularly implemented using Stock Synthesis (SS), a statistical-catch-at-age stock assessment modelling platform that can adapt to a wide range of assessment situations (Methot and Wetzel, 2013). The use of SS in implementing stock assessment models offers the advantage of allowing parameters that can vary through time, including annual and/or cohort specific variability in growth (Methot and Wetzel, 2013). This study shows that cohort-specific variability in mean length-at-age is a predominant form of temporal variability in growth for blue grenadier, and considers two alternative stock assessment models: one assuming static growth (generally the status quo for stock assessments in the SESSF and elsewhere), and an alternative model that estimates cohort-specific deviations from the mean growth function. Using SS, each model is independently applied to blue grenadier data, demonstrating key stock assessment results can depend on assumptions made about the nature of growth.

2. Methods

2.1. Data and initial analyses

Assessments for blue grenadier are based on catch data (by fleet, and including discarding rates), catch-rate data, length-based catch-composition data, age-length data (from otoliths sub-sampled from length-measured fish), and fishery-independent abundance indices from acoustic and egg-based surveys. Data from the years 1979 to 2007 were used in this study. Prior to the application of assessment models, observed age-length data were analysed to identify possible patterns of temporal variability in mean length-at-age.

As well as enabling the estimation of growth parameters, age-length data can be used to estimate mean lengths-at-age for

a population. Cohort related effects on growth can be discerned directly by grouping length-at-age observations by cohort, and making cohort-specific estimates of mean lengths-at-age. Year-by-year effects on growth are more difficult to detect. Year-specific effects on growth vary annual increases in the size of individuals in a single year, and are likely to affect all individuals, across all cohorts, in a population. These effects can be detected from repeated measures of individual fish, or inferred by tracking the 'growth increments' of individual cohorts, and comparing the average sizes of consecutive ages over consecutive years.

Age-length data, available for years between 1984 and 2007, were examined for temporal changes to mean length-at-age. Year-specific growth increments were created by calculating differences between average length-at-age values among consecutive years and consecutive age classes. The resulting values were converted to residuals by dividing each one by the average value of its specific age-increment. Cohort-specific length-at-age residuals were created by dividing each length-at-age observation by the average of the length observations for that age. Subsequent Q-Q plots of both sets of residuals indicated they were positively skewed, and close to log-normally distributed. As such, residuals were plotted against their corresponding year or cohort in the form of boxplots to show the distribution of points around the $y=1$ reference line and thus any year- or cohort-specific effects on growth.

2.2. Overview of the assessment method

The first step in the development of a stock assessment using SS is the specification of a population dynamics model appropriate for the species being assessed. This involves assumptions about the nature of the stock dynamics. Where possible, these assumptions are based upon relevant studies of the biology of the species in question, or failing that, upon studies of similar species. For example, the blue grenadier assessment includes an assumption that the relationship between spawning biomass and recruitment can be described by a Beverton-Holt stock-recruitment function with a 'steepness' parameter value of 0.9, based on studies of similar species in New Zealand (Punt et al., 1994). The next step is to specify details for the implementation of an observation model, based on the type and quantity of data available for the stock. Key structural specifications for the blue grenadier assessment models examined here are outlined in Table 1. Full details of the most recent stock assessment are given in Tuck et al. (2012) and are not reproduced here as the focus of this work is on the implications of assumptions regarding growth. For a user manual and technical description of the full range of model options available as part of the SS package, see the NOAA Fisheries Toolbox website (<http://nft.nfsc.noaa.gov>) and (Methot and Wetzel, 2013). All models presented here were implemented in SS Version 3.2.

2.3. Model estimation of growth

Length composition data are randomly sampled from the fishery catch. A random sample of these length data are selected for ageing, and the observed age-length composition is converted to a 'conditional age-at-length' composition matrix, giving the proportion of catch during year y in length-class l that is of age a . These data enable the estimation of growth parameters within the assessment model and form part of an estimation procedure that accounts for the effects of size-selective fishing gears. Using the estimated growth parameters, expected mean length-at-age vectors are determined and combined with a known mass-length relationship to calculate expected mass-at-age. Incorporation of ageing error is made by specifying the expected standard deviation of age estimates for each age (based on estimates of multiple readers for a sub-sample of aged fish). Formal details on the specification

Table 1

Key structural specifications for blue grenadier assessment models (SG and CDG). Additional growth related specifications are outlined in Section 2.

| Structural component | Specification | Estimated/fixed |
|---|---|------------------------|
| Fishery structure | Spawning and non-spawning sub-fisheries | – |
| Natural mortality | Age-independent, sex-specific | Fixed |
| Maturity | Logistic function of length | Fixed |
| Sex structure | Two sex (male and female) | – |
| Selectivity | Spawning: logistic function of length Non-spawning: dome-shaped function of length | Estimated Estimated |
| Initial state | Survey: logistic function of length | Estimated |
| Stock–recruitment relationship | Unfished equilibrium age-structure (1960) | Estimated |
| Functional form | Beverton–Holt (steepness = 0.9) | Fixed |
| Variation in recruitment | Log-normal (recruitment variation, $\sigma_R = 1$) | – |
| Years recruitment deviations estimated | 1961–2004 | – |
| Growth | | |
| Years cohort deviations estimated | 1977–2004 | – |
| Target standard deviation of growth deviation estimates | 0.2 | Fixed |

of errors associated with mean length-at-age observations, and the contributions to the objective function related to fitting to the age–length and length data components can be found in Methot and Wetzel (2013).

Two alternative assumptions are considered about the nature of growth through time for blue grenadier: first, that the length-at-age relationship remains static, and second, that the length-at-age relationship is cohort-specific, such that it can change depending on cohort year. Each of these alternative assumptions requires a structurally different stock assessment model with regard to the estimation of growth parameters.

2.4. Static growth

The ‘static growth’ (SG) model incorporates the assumption that mean length-at-age is always equal to the value predicted by a time-invariant age–length relationship. Parameters for a gender specific age–length relationship are estimated within the assessment model using a special parameterization of the von Bertalanffy growth equation. Mean length-at-age is calculated from growth parameters at the beginning of the model start year, and then progressed forward through time according to constant growth parameters. As such, mean length-at-age in the initial population is calculated from:

$$L_{0,\gamma,a} = L_{\infty,\gamma} + (L_{1,\gamma} - L_{\infty,\gamma})e^{-k_\gamma(a-a_3)}, \quad (1)$$

where $L_{0,\gamma,a}$ is the mean length in the beginning of the model start year at age a for gender γ , L_1 is the mean length for gender γ at age a_3 (a specified reference age near the youngest age well-represented in the data), k is the von Bertalanffy growth coefficient, and $L_{\infty,\gamma}$ is the mean asymptotic length for gender γ . The notation presented here is intended to be consistent with the full SS model description (see Methot and Wetzel, 2013). As such, the notation for parameters a_3 and a_4 is retained despite no reference to parameters a_1 and a_2 (used for specification of age specific natural mortality) in this paper.

When the oldest age well-represented in the data is close or equal to the maximum age, L_{∞} is estimated directly. Otherwise, L_{∞} is calculated from:

$$L_{\infty,\gamma} = L_{1,\gamma} + \frac{L_{2,\gamma} - L_{1,\gamma}}{1 - e^{-k_\gamma(a_4-a_3)}}, \quad (2)$$

where $L_{2,\gamma}$ is the mean length at age a_4 , a specified reference age near the oldest age well-represented in the data. Mean length is incremented across model time-steps (years) as:

$$L_{y+1,\gamma,a+1} = L_{y,\gamma,a} + (L_{y,\gamma,a} - L_{\infty,\gamma})(e^{-k_\gamma} - 1), \quad (3)$$

where $L_{y,\gamma,a}$ is the mean length at the beginning of year y at age a for gender γ . The coefficient of variation in length changes linearly

with length at age between parameters specified for ages a_3 and a_4 for gender γ . The standard deviation of length-at-age for each gender γ is given by:

$$\sigma_{\gamma,a} = \begin{cases} \tilde{L}_{\gamma,a} CV_{1,\gamma} & \text{for } a \leq a_3, \\ \tilde{L}_{\gamma,a} \left(CV_{1,\gamma} + \frac{(L_{\gamma,a} - L_{1,\gamma})}{(L_{2,\gamma} - L_{1,\gamma})} (CV_{2,\gamma} - CV_{1,\gamma}) \right) & \text{for } a_3 < a < a_4, \\ \tilde{L}_{\gamma,a} CV_{2,\gamma} & \text{for } a \geq a_4, \end{cases} \quad (4)$$

where $\sigma_{\gamma,a}$ is the standard deviation of length at age a for gender γ , $CV_{1,\gamma}$ is the coefficient of variation for length at age a_3 for each gender γ , $CV_{2,\gamma}$ is the coefficient of variation for length at age a_4 for gender γ and $CV_2 \geq CV_1$. The standard deviation of length at age, σ_a controls the variation around predicted length-at-age which is fit to the observed age–length and length composition data.

Mean mass-at-age is determined by converting mean length-at-age from the age–length relationship to mean mass based on the length–mass relationship:

$$w_{\gamma,a} = \alpha L_{\gamma,a}^\beta, \quad (5)$$

where $w_{\gamma,a}$ is the mean mass for gender γ at age a , and α and β are estimated parameters, obtained by regressing the mass of individual sampled fish on their measured lengths. For SESSF species, the length–mass relationship is assumed to be constant through time, because the data required to estimate it are not collected annually.

2.5. Cohort-specific time-varying growth

The ‘cohort dynamic growth’ (CDG) model describes a population in which fish of particular cohorts may be smaller or larger at age (have slower or faster growth) than would be expected from a static mean length-at-age relationship. The CDG model differs from the SG model by the addition of an extra set of parameters to the von Bertalanffy growth equation described above. A cohort specific growth deviation parameter, v , is estimated within the model for each cohort in a specified range. The exponential of this parameter, e^v , is applied as a scalar multiplier to the calculated increments in mean length across time steps (between ages). Thus, for cohort c , mean length is incremented across model time steps (years) as:

$$L_{\gamma,a+1,c} = L_{\gamma,a,c} + (L_{\gamma,a,c} - L_{\infty,\gamma})(e^{-k_\gamma} - 1)(e^{v_c}), \quad (6)$$

where $L_{\gamma,a,c}$ is the mean length for gender γ at age a for cohort c , and e^v is the scalar multiplier applied to cohort c .

2.6. Application of the models

The SG and CDG assessment models were used to assess blue grenadier stocks based on the data available up until 2007. These models were identical except that (a) $v_c = 0$ for all c for model SG

while some of the ν_c are estimated for the CDG model, and (b) the CDG model also includes a normal penalty on the fluctuations of the ν_c , i.e., $(1/2\sigma_\nu^2)\sum \nu_c^2$ where the value for σ_ν was set semi-arbitrarily to 0.5. Age-length data were available for a wide range of ages, including age-1, so the parameter a_3 was set to 1. Ideally, the ν_c parameters should be treated as random effects. However, within the errors-in-variables estimation framework that underlies SS, it is necessary to select a set of cohorts for which to estimate ν_c (with the remaining ν_c values set to 0). This is similar to how deviations about the stock-recruitment relationship are treated for most stock assessments that use SS. Selection of the set of cohorts for which to estimate ν_c was achieved by first estimating ν_c for all cohorts between 1961 and 2007 and identifying those cohorts for which the standard error of the parameter estimate was low relative to the prior standard deviation of 0.5. A rough rule of thumb was that cohorts for which the standard error of ν_c was <0.2 would be estimated in the final model runs, with the remaining ν_c set to 0. Consequently, values for ν_c were estimated for the 1977 to 2004 cohorts (inclusive).

3. Results and discussion

3.1. Initial analyses

Both cohort- and year-specific effects were evident from plots to examine temporal variability in growth (Fig. 1). Year-to-year variability in annual growth increments appear random with respect to time (Fig. 1a), with little evidence of long term increases or declines in yearly average growth. There are however several individual years in which substantial proportions of calculated growth increment residuals sit to one side of the $y = 1$ reference line. Many of these 'strong effects', however, correspond to years with small numbers of calculated residuals. Variability in mean lengths-at-age between cohorts (Fig. 1b) appears prominent, with boxplot median markers falling in many cases above or below the $y = 1$ reference line. In particular, data from the 1991–92 and 2003–04 cohorts indicate they are fast growing cohorts, each with very large numbers of observations, and the majority of those observations, sitting above the reference line. Following the same reasoning, but in reverse, data from the 1993–94 cohorts indicate they are slow growing cohorts. Unlike year-specific effects, cohort-specific effects show a distinct pattern of auto-correlation. For the 1984–92 cohorts, growth appears to steadily increase, before dropping to a slow growth rate for the 1993 cohort, and then steadily increasing, on average, through until the 2004 cohort. Such a pattern could indicate the effects of density-dependent processes acting on growth, especially given the variable nature of cohort-strength for blue grenadier, but could also arise as a consequence of ageing error. Additionally, the calculated residuals provide far greater information about cohort-specific growth effects than they do for year-specific effects. This is because cohort effects can be determined directly from mean length-at-age observations, whereas year-specific effects require data pertaining to 'growth increments'. In this analysis, yearly growth increments were inferred from the differences between average length-at-age values among consecutive years and consecutive age classes. These calculations are indicative of year-to-year changes in growth rates but due to the requirement for data from consecutive years and age classes, there are very few observations on which to base confident assertions regarding year-by-year variation.

The degree to which variability in growth will affect the results of a stock assessment cannot be determined *a priori*, and will depend on the specific details and formulation of the assessment models. We can infer from these plot diagnostics that cohort-specific growth is a predominant feature of the blue grenadier

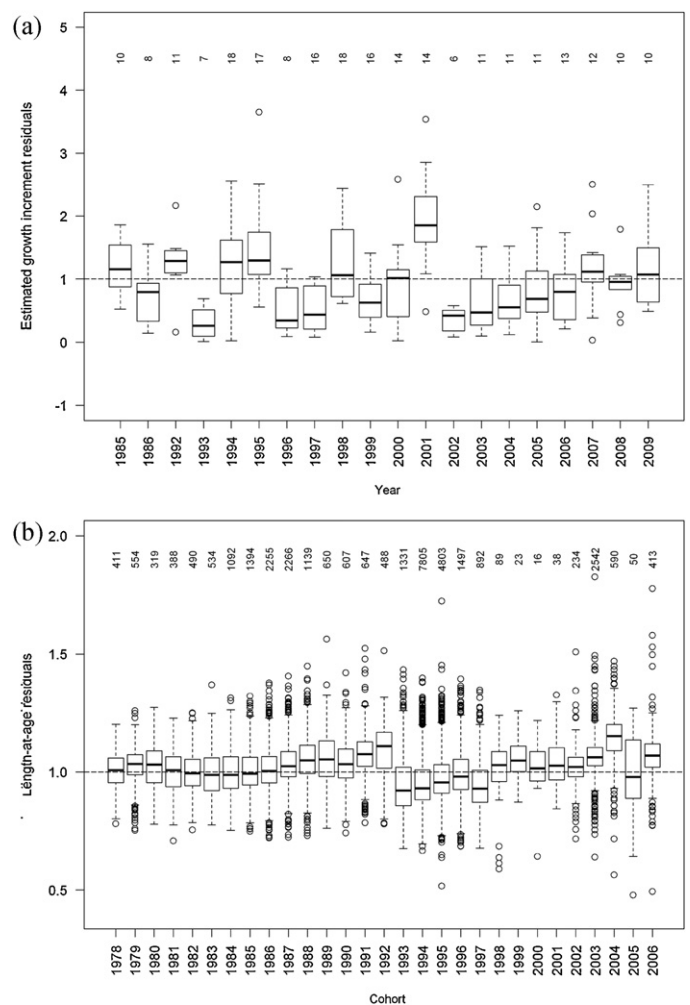


Fig. 1. (a) Year-specific annual growth increment residuals for blue grenadier. Boxplots show distributions of ratios of yearly observed growth increments compared to their group means. (b) Cohort-specific length-at-age residuals for blue grenadier. Boxplots show distributions of ratios of individual length-at-age observations compared to their group means. Numbers inside the plots represent the number of residual calculations per individual boxplot.

stock, as indicated by the age-length observations. As such, for the purposes of this study, we investigated the effects of modelling cohort-specific variability in growth, with the knowledge and intention of excluding specific year-by-year effects that could be explored in further analyses.

3.2. Outputs of the alternative models

Both the SG and CDG assessment models were able to converge to a solution when applied to the data available for blue grenadier. Though the models produced qualitatively similar results, there were marked differences between estimates of population level quantities in some years.

The CDG model mimics the observed data well by estimating the 1992 and 2004 cohorts to be the fastest growing cohorts (with multipliers of 1.37 and 1.42 respectively) and by estimating the 1994 cohort to be a markedly slow growing cohort, with a multiplier of 0.58 (Fig. 2). The 1991, 1993 and 1999 cohorts were estimated to be growing at least 10 percent faster than average and the 1984, 1987 and 1995–1997 cohorts were estimated to be growing at least 10 percent slower.

Variability in observed mean length-at-age through time is ignored by the SG model (Fig. 3a) but is reflected in the CDG model

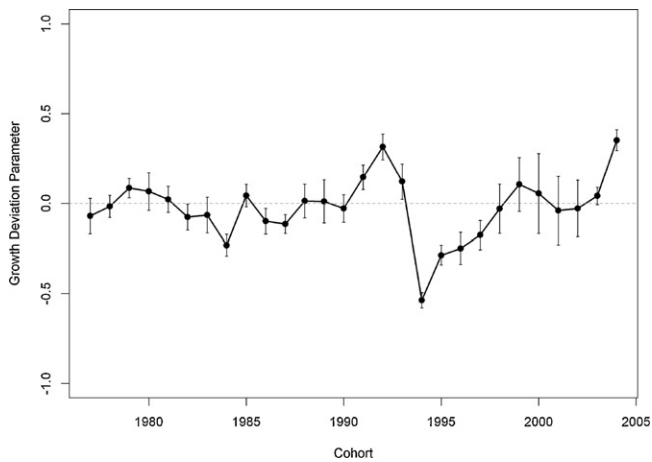


Fig. 2. Series of cohort growth deviation parameter estimates with standard deviations, as estimated by the Cohort Dynamic Growth model for blue grenadier.

by year-specific expected length-at-age vectors. The length-at-age vector for the model end-year (2007) (Fig. 3b) shows the increase in expected size of 3 year old fish (from the fast growing 2004 cohort) and the striking decrease in expected size of 13 year old fish (from the slow growing 1994 cohort). The effect of accounting for faster or slower growing cohorts is clearly visible when yearly expected length-at-age vectors are viewed in series (Fig. 4). Here, cohort growth deviations are seen to propagate through time and produce characteristic dips and ridges in the surface plot. The effect of the estimated slow growing 1994 cohort for example is visible as a large dip, first seen with the estimated size of 1 year old fish in 1995 and continuing through until the model end-year.

The better fit of the CDG model to age-length observations for cohorts 1990–98 is shown in Fig. 5. The CDG model fits the observed data well, being particularly good at describing the expected mean length-at-age of the 1990, 1991 and 1995–1998 cohorts. However, the 1992 cohort appears to have fast growing young individuals that reach a reduced average maximum length compared to other cohorts, an effect that cannot be accounted for by the growth parameters estimated in the CDG model, and the observed age-length data of the 1993 and 1994 cohorts are not fit particularly well.

The integrated analysis model takes the effects of selectivity and ageing error into account when estimating expected mean

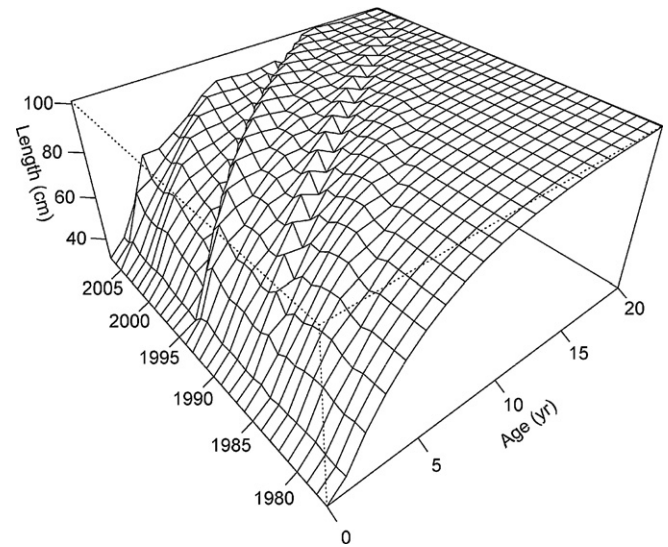


Fig. 4. Surface showing time series of expected mean length-at-age by year for female blue grenadier, estimated by the Cohort Dynamic Growth model.

lengths-at-age. As such, the large amount of ageing error associated with the age-length data of the 1993 cohort results in a cohort-specific growth deviation estimate that could be close to the true growth trajectory, even though it does not match with observations. This is one advantage of estimating growth parameters as part of an integrated analysis. In contrast, the growth deviation estimate for the 1994 cohort should be made with high precision, and match the observations, as there is ample accurate data associated with this cohort. However, the CDG model appears to overestimate the decrease in growth of the 1994 cohort, possibly due to correlation of the growth estimates with fixed values for natural mortality and steepness, or with the associated strong recruitment estimate for the 1994 cohort.

These effects are shown further in a summary of the fit of the CDG model to the age-length data (Fig. 6). Median lines of cohort-specific boxplots sit close to the $y=1$ reference line, indicating that all cohorts are fit reasonably well, but notably, most of the median lines sit above the reference line. This further demonstrates the effect of accounting for gear selectivity on data collection and growth estimates. As there is unavoidable

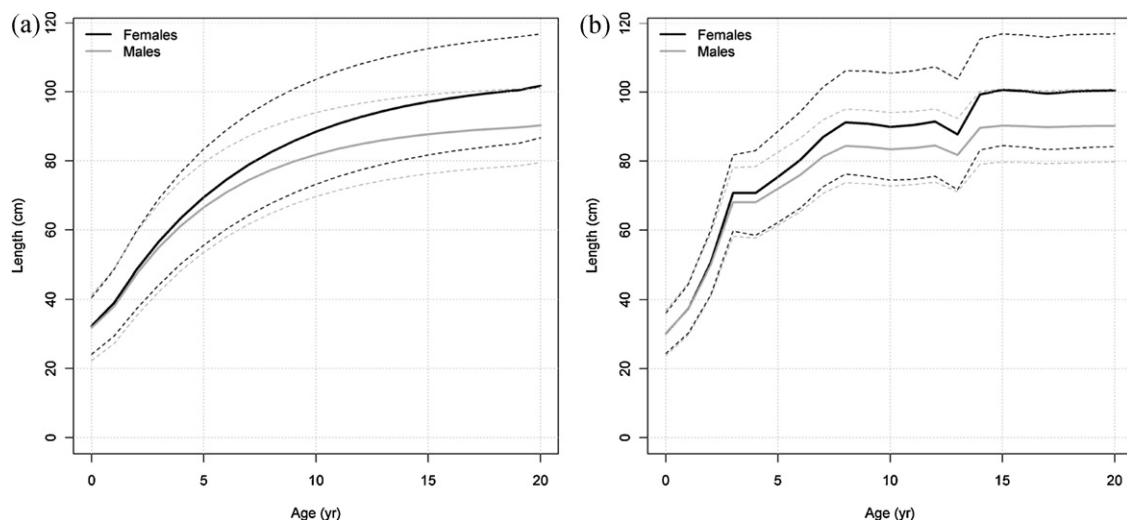


Fig. 3. Expected mean length-at-age of blue grenadier (solid lines) with 95 percent credibility intervals (dashed lines) estimated by (a) the Static Growth model and (b) the Cohort Dynamic Growth model (for 2007, the model end-year). Females are shown in black, males are shown in gray.

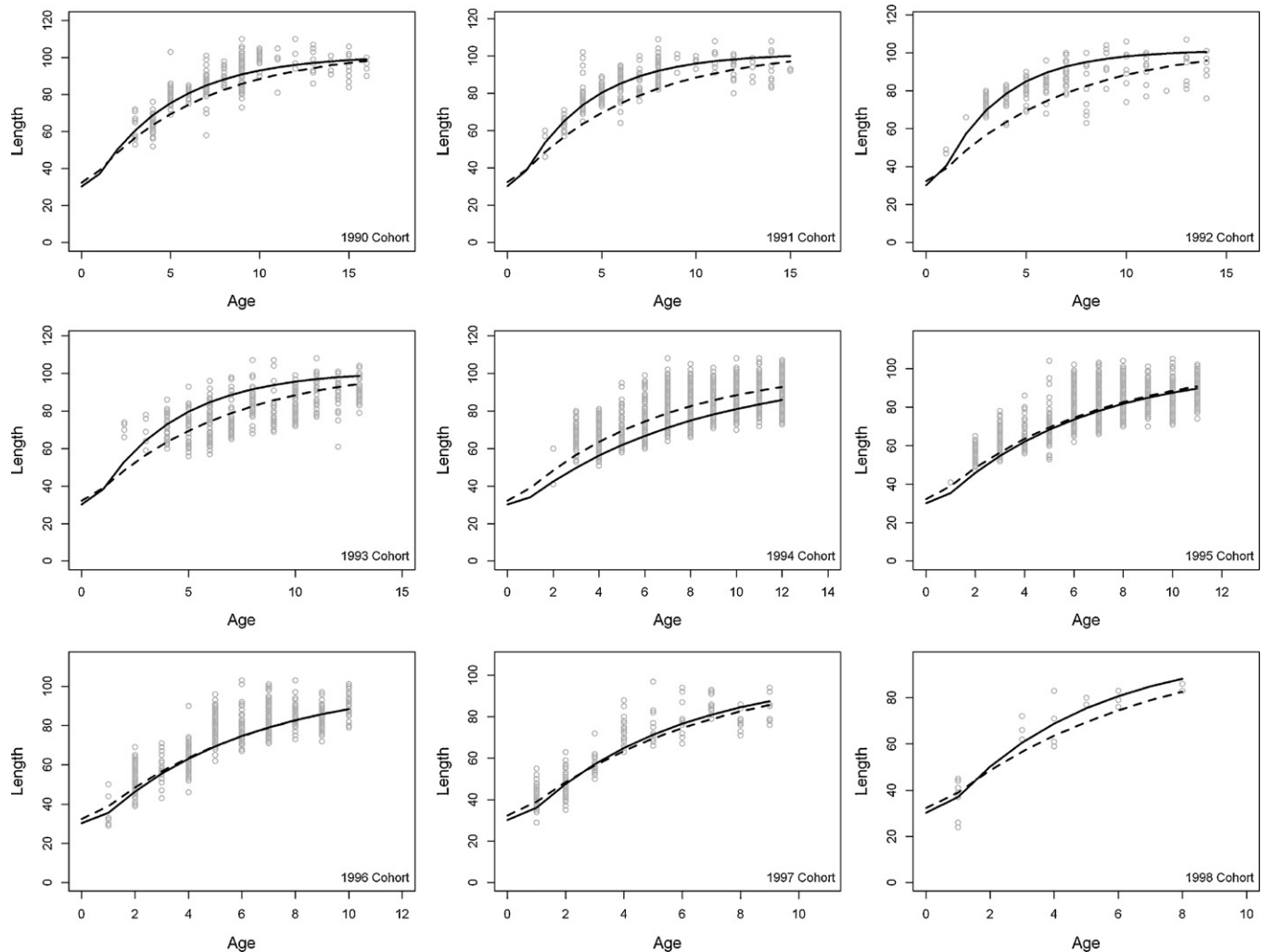


Fig. 5. Cohort specific age-length observations with expected mean length-at-age lines estimated by the Cohort Dynamic Growth (solid lines) and Static Growth (dashed lines) models for female blue grenadier. Estimates of length-at-age from the Static Growth model are the same for all cohorts.

selection of fast growing young fish during size-selective fishing, the observed age-length data is expected to sit above the true population growth trajectory, especially for young fish (Ricker, 1969).

The SG model estimates a large recruitment in 1994 followed by a peak in recruitment in 1995, but the CDG model estimates a peak in recruitment in 1994 followed by a second large recruitment in 1995 (Fig. 7). This effect is largely due to the differences in length-at-age expectations of the different models. For example, the large number of fish sampled in the 80 cm length-class in 2002 is expected to represent the seven year-old age class by the SG model and contributes to the estimate of a large recruitment in the year 1995. In the CDG model, the same fish are expected to be part of the 8 year old age-class, and instead contribute to the estimate of a large recruitment in the year 1994. There are further marked differences between the two models towards the end of the time series, when the SG model estimates much higher and lower numbers of recruits than the CDG model in 2003 and 2004 respectively.

Another cause of differences in estimated recruitment strength relates to the specification of selectivity. Selectivity is assumed to be a time-invariant function of length for blue grenadier, and selectivity-at-age is calculated from the expected mean lengths-at-age, together with the standard deviations of length-at-age, in any given year. Therefore, in the SG model, selectivity is a time-invariant function of age, but in the CDG model, selectivity is a function of both age and time. The SG model calculates the mean length-at-age of the 2003 and 2004 cohorts based on the constant mean length-at-age relationship, and because they are small, expects they are only partially selected. The high abundance of

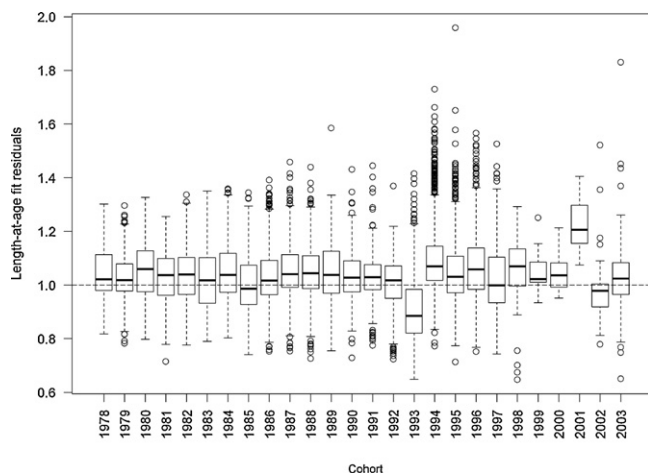


Fig. 6. Cohort-specific length-at-age fit residuals for blue grenadier. Boxplots show the distribution of differences between individual age-length observations and corresponding expected mean lengths-at-age by cohort, as estimated by the Cohort Dynamic Growth model.

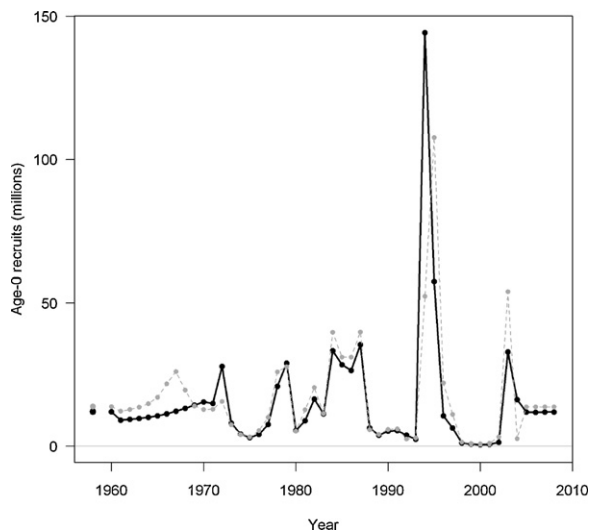


Fig. 7. Time-series of age-0 recruits for blue grenadier, estimated by the Cohort Dynamic Growth model (solid black line) and the Static Growth model (dashed gray line).

small fish caught in 2007 (the model end-year) is therefore almost entirely ascribed to a large recruitment of the more highly selected 2003 cohort. In contrast, the CDG model estimates that the 2003 and 2004 cohorts are fast growing, thus larger than expected by the SG model, and more fully selected in 2007. Accordingly, the CDG model ascribes the high abundance of small fish caught in 2007 to relatively high recruitment distributed across years 2003 and 2004. The CDG model is also better able to account for large numbers of discarded fish in 1997 and 1998. The SG model expects fish from the highly abundant 1994 cohort to be large and thus retained by the fishery in those years. The CDG model however calculates that fish from the 1994 cohort are slow growing and therefore more correctly expects those fish to be undersized and discarded in 1997 and 1998.

For most of the 1980s the SG model estimates many thousands of tonnes less spawning biomass than the CDG model (e.g. 40k tonnes c.f. 47k tonnes in 1984), but this pattern is reversed between 1998 and the mid-2000s, when the SG model estimates many thousands of tonnes more spawning biomass than the CDG model

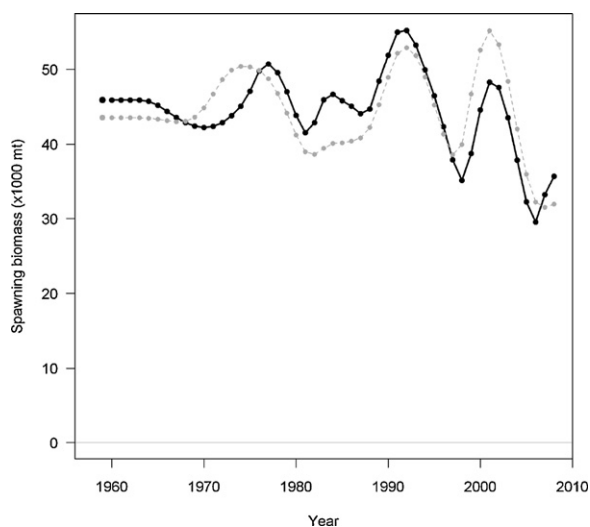


Fig. 8. Female spawning biomass trajectory for blue grenadier, estimated by the Cohort Dynamic Growth model (solid black line) and the Static Growth model (dashed gray line).

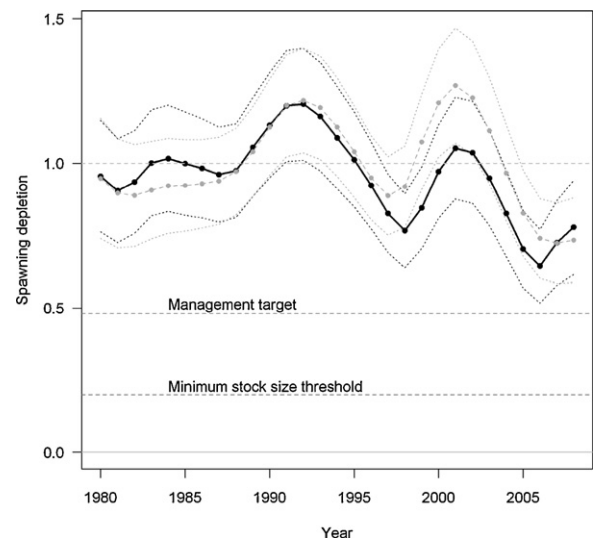


Fig. 9. Female spawning depletion (ratio of current spawning biomass to unfished equilibrium spawning biomass) trajectory for blue grenadier with 95 percent credible intervals, estimated by the Cohort Dynamic Growth model (solid and dashed black lines) and the Static Growth model (dashed gray lines) in relation to relevant management targets.

(e.g. 47k tonnes c.f. 39k tonnes in 1999) (see Fig. 8). This is another effect of the different ways the SG and CDG models determine length-at-age of the highly abundant 1994 and 1995 cohorts. Beginning in approximately 1998, these highly abundant cohorts began to dominate the spawning component of the population. The SG model calculates mean length- and thus mean mass-at-age for these cohorts to be much larger than does the CDG model, which estimates them to be slow growing cohorts. As such, and because maturity is modelled as a function of expected length, the estimated spawning biomass is much greater for the SG model than the CDG model for all years in which the highly abundant slow growing cohorts dominate the population biomass.

The two models also differ in the estimated time-trajectories of female spawning depletion, B_{Curr}/B_0 (ratio of estimated current to unfished equilibrium spawning biomass). For years 1998–2001, the estimates of female spawning depletion from either model lie outside the 95 percent confidence limits of the alternative model (Fig. 9). As scientific advice regarding recommended catch levels depends on estimates of current and future spawning depletion, advice based on these alternative models could differ greatly. Based on the results of the SG model and the relevant SESSF harvest control rule (Smith et al., 2008), the recommended annual catch limit for blue grenadier would average 6200 tonnes for the 5 year period following the model end-year. The same limit from the CDG model would be more than 10 percent higher at 7010 tonnes. Such differences between recommended catch limits arising from alternative models would be even greater in years when median spawning depletion estimates were outside 95 percent confidence limits. In this study, those years correspond to periods when the population is dominated by abundant and slow growing year classes.

The relative fit of the models to the data can be assessed by comparing values of the negative of the logarithm of the likelihood function. As this value is minimized in the fitting process, a smaller value implies a better fit. The CDG model has greatly reduced negative log-likelihood values compared to the SG model for the discard, length composition, and conditional age-at-length data components, indicating a vastly improved ability to fit to those data (Table 2). A great improvement in overall model fit is evident from a comparison of the total negative log-likelihood values: the fit of the CDG model betters the SG model by over 400 points. Though an improvement in fit is expected given the addition of

Table 2

Comparison of the total value of, and contribution from each of the data sources to, the negative log-likelihood for each model. Lower values indicate a better fit to data. “EP” denotes the number of estimated parameters.

| Data type | SG model (EP = 67) | CDG model (EP = 95) |
|----------------------|-----------------------|------------------------|
| Survey | 23.99 | 22.44 |
| Discard | 132.36 | 73.96 |
| Length composition | 915.29 | 668.47 |
| Age-at-length | 632.36 | 520.10 |
| Recruitment | 26.90 | 29.35 |
| Parameter priors | 1.71 | 1.47 |
| Parameter deviations | 0.00 | 10.64 |
| Total | 1732.62 | 1326.43 |

extra parameters, the very large improvement in total likelihood combined with a relatively small increase in the number of estimated parameters (28 extra parameters for growth deviations in the CDG model) indicates the CDG model is the better of the two at describing the observed data and stock dynamics for blue grenadier. Model selection can however be problematic for models of this type as total likelihood calculations are made without methods to properly account for the true effect of parameter deviations. As such, hypothesis testing and model choice must be approached with caution.

3.3. General discussion

These results demonstrate important outputs of stock assessment models can be sensitive to structural assumptions made about growth. For the blue grenadier assessment, accounting for cohort-specific variability in growth results in estimates of spawning biomass, recruitment, and relative spawning depletion that differ markedly from those of a ‘standard’ assessment that assumes a static growth function.

Variability in mean length-at-age of blue grenadier has been observed for some time (Punt and Smith, 2001). To deal with this issue previously, mean length- and mean mass-at-age matrices have been estimated from year-specific age-length keys, length frequency data and a mass-length relationship and specified directly in integrated analysis style assessment models (Method 2 of Punt and Smith, 2001). Direct specification of empirical mass-at-age matrices to capture variability in growth has also recently been used, for example, in North America for assessments of Pacific hake (Stewart and Forrest, 2011). Although such methods explicitly account for variability in mean size-at-age through time, they are not conceptually consistent with an integrated analysis estimation procedure. This is because data used to construct mean length- and mean mass-at-age matrices are subject to sampling error, whereas integrated analysis methods assume such matrices are free from associated errors (Punt and Smith, 2001). Stock assessments implemented in SS overcome this issue by allowing length-at-age information to be treated as data, so year-specific length-at-age vectors, and associated errors, can be estimated directly within the assessment model. This method offers several advantages: it automates the process for interpolating values of length- and mass-at-age for years in which data are not available while taking the population dynamics into consideration; it allows for estimation of between-individual variation in length-at-age; and it accounts for interactions between selectivity and estimation of growth parameters; all of which are common problems rarely accounted for by empirical based procedures.

One advantage of empirical based methods is the ability to account for multiple patterns of variation in mean size-at-age. For example, in the North American Pacific hake fishery (Stewart and Forrest, 2011), there have been dramatic declines in maximum size,

increases in growth rate, and both seasonal and cohort-specific variation in mean length-at-age. In aggregate, these patterns can be captured by the use of empirical mass-at-age matrices, but are extremely difficult to account for with the use of parametric growth models. Methods like those employed in this study might therefore be most suitable when the observed variability in size-at-age is restricted to one particular form.

The cohort-specific variability in observed mean length-at-age for blue grenadier, together with the improved fit to data provided by the CDG model, indicates growth rates (especially those of young fish) depend on cohort-specific factors. Such factors might include food availability or water temperature during the first years of growth, or density-dependent factors such as within- and between-cohort competition for resources. The latter possibility is supported by estimates of growth deviations and recruitment from the CDG model. The fast growing cohorts of 1991–1993 and 1999 correspond to years of very low recruitment and were each preceded by several consecutive years of low recruitment. The slow growing cohorts of 1984, 1987, and 1994–1995 correspond to years of high or very high recruitment, and the slow growing 1996 and 1997 cohorts were preceded by the highest levels of recruitment recorded for the fishery. Growth rates of juvenile blue grenadier therefore appear to be affected by the number and/or density of fish in the same cohort and in cohorts that precede them, a form of density-dependent growth. This suggests stock assessments of other species that are likely to be affected by density-dependent growth, such as those exhibiting highly variable recruitment, might also benefit from these methods to estimate variation in mean length-at-age. Density-dependence in growth can greatly affect the predicted outcomes of stock responses to fishing (Rose et al., 2001; Bardos et al., 2006), so a more thorough modelling approach would relate growth to an indicator of density, such as recruitment strength. This would be particularly useful for improving the accuracy of projections and thus the predictive capability of models. For blue grenadier however, and likely for other species where growth is affected by fluctuations in recruitment, the ability to predict changes in growth will be limited by the ability to predict future levels of recruitment.

Estimates of growth parameters and growth parameter deviations can be confounded by assumptions regarding other parameters associated with productivity, such as steepness of the stock recruitment curve and natural mortality. Values for both steepness and natural mortality were assumed and fixed in the models presented in this study, and could correlate strongly with key growth parameters such as k and L_{∞} . Although model outputs did not indicate any strong dependence of growth parameters upon other model parameters, simulation analyses like those performed recently by Lee et al. (2011) to determine the reliability of estimates for natural mortality in stock assessments could help to determine whether estimates of temporal growth deviations are reliable and robust. Additionally, these methods could be used to determine if the CDG model can accurately differentiate between cohort- and year-specific effects.

The ability of the CDG model to accurately estimate cohort growth deviations is also limited by the quantity of age-length data available for each cohort, and thus on the relative numbers of fish available to the fishery from each cohort. Cohort growth deviations are poorly estimated for years of low recruitment and for recent cohorts yet to enter the fishery. Because weak year-classes have little bearing on the calculation of population level quantities, precise estimation of their growth is not critical. However, the estimation of growth parameters of recent cohorts is critical for accurate estimation of population level quantities, and especially for forecasting population responses to fishing. The accuracy and efficacy of the CDG model could therefore be improved by additional fishery-independent sampling of young fish or, in the

case of the blue grenadier fishery, by length and age sampling of undersized discarded fish.

The need to determine a timeframe over which to estimate deviations to growth parameters, and to pre-specify the standard deviation of the distributional assumption, presents an interesting case for further study. There have been recent efforts to develop and scrutinize methods for estimating year-specific recruitment variability (Methot and Taylor, 2011) and the methods applied in this study to estimate growth variability are similar in principle. We recommend similar research and development of methods for estimating year- or cohort-specific growth deviations. Methods that fully integrate over the penalized deviates or random effects in the calculation of likelihood values would also be beneficial, and could improve model selection and hypothesis testing. Ultimately, models that allow for inter-annual or cohort-specific variability in growth could become standard assessment techniques, as has modelling variability in recruitment.

Another approach to dealing with variability in growth in stock assessments (or with variability in length-based fishing gear selectivity) involves converting the observed length composition for each given year to the corresponding age composition (or *vice versa*), and estimating growth parameters outside of the model. If growth (or selectivity) varies from one year to the next, then annual age-length keys can account for the variability (e.g. Punt et al., 2001). We chose to estimate changes to growth inside the assessment model to more fully align with an integrated analysis procedure, but the criticisms levelled here at the estimation of growth outside the stock assessment model, could also be made for the estimation of maturity-at-length and other factors. In the models studied here, maturity-at-length was necessarily pre-specified and fixed with respect to time, because the data required to estimate the relationship, or temporal changes to it, are not available for species from the SSSF. Because there could be temporal changes to this relationship, and to other important measures such as mass-at-length, improved stock assessment models for blue grenadier could include the raw data used to determine these relationships, and thus allow for relevant parameters to be estimated inside the models. Given the central hypothesis of, and evidence for temporal variability to growth, data relating to mass-at-length for blue grenadier should be collected more regularly in the future.

The aim of this study was to make comparisons between the CDG model and a more 'standard approach'; we achieved that by implementing a model that follows the usual assumption of static growth, and comparing it to another model that accounts for cohort-specific variation in mean length-at-age. By implementing both alternatives with an integrated analysis procedure, and by using a standard stock assessment framework (SS), we can be sure that changes in model fit and subsequent model outputs are due to the single change relating to estimation of variability in mean lengths-at-age. Further study should focus on comparing alternative methods for dealing with temporal variability in growth in stock assessment models. This could include comparing the efficacy of models employing growth deviation parameters to those that use fixed estimates of annual mass-at-age. Simulation analyses could help to determine which methods work best and whether cohort- or year-specific growth is occurring in a 'real' population.

3.4. Conclusion

We recommend that sensitivity to alternative assumptions about growth be routinely examined for fisheries stock assessments. Mean length-at-age might vary primarily between years, rather than between cohorts, or gradual changes to mean length-at-age or asymptotic size might occur over long periods. Patterns in observed age-length data should be examined and used to decide which methods are likely to suit the stock assessment at hand. The

use of SS for stock assessments facilitates this by providing many options for modelling variation in expected size-at-age. SS permits growth parameters to vary by year with year-specific deviations, for series of years though the specification of time-blocks, by a random walk process for a specified period, to trend from one set of specified parameters to another over a defined period, through functional linkage to environmental time-series data, and by the direct input of annual mass-at-age data. Any combination of these methods could be implemented for a stock if observed trends in age-length data indicated it to be appropriate. In many cases however, mean length-at-age will be sufficiently uniform to satisfy the assumptions of static growth, in which case simpler SG style models (with fewer parameters) would be preferable.

This study demonstrates the benefits of testing stock assessment models with alternative structural assumptions and of accounting for variation in mean length-at-age where observations indicate significant change through time. In this case, we identified that the SSSF blue grenadier stock could be better modelled by the inclusion of model parameters to describe cohort-specific variability in growth. The explorations of alternative models showed how changes to stock assessment model structure can result in significant differences to key outputs, and at the same time, provide useful insights into the nature and possible causes of variability in growth.

Acknowledgements

The authors are grateful to Andre Punt for initial development of the blue grenadier stock assessment models, and to Rick Methot and Gavin Fay for guidance and feedback relating to the use of Stock Synthesis and interpretation of its outputs. Additional members of the NOAA Stock Assessment team are thanked for useful discussions and input, particularly Ian Stewart and Ian Taylor. Members of the SSSF stock assessment team at CSIRO: M. Haddon, R. Little, R. Thomson, J. Upston, and J. Day, are also thanked for helpful comments and suggestions in the early stages of the study. Special thanks to Sally Wayte for providing a helpful review of the manuscript. The authors would also like to thank R.I.C.C. Francis and an additional anonymous reviewer for providing insightful and constructive reviews that improved the manuscript. Funding for AW was provided by an Australian Postgraduate Award and a CSIRO Postgraduate Studentship under the Wealth from Oceans National Research Flagship.

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