CCAMLR Science, Vol. 14 (2007): 43–66

A VON BERTALANFFY GROWTH MODEL FOR TOOTHFISH AT HEARD ISLAND FITTED TO LENGTH-AT-AGE DATA AND COMPARED TO OBSERVED GROWTH FROM MARK–RECAPTURE STUDIES

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Abstract

Length-at-age data for Patagonian toothfish (*Dissostichus eleginoides*) at Heard Island (Division 58.5.2) were fitted using a von Bertalanffy (VB) growth model taking into account response-biased sampling of fish that were aged. Subsampling of random length-frequency (LF) data used to obtain the samples of fish for ageing used length-bin sampling involving a fixed sample size per bin. Estimation of the VB parameters used a definition of the likelihood function based on variable probability (VP) sampling due to the pre-specified length-dependent selectivity function for trawl fishing and the additional effect of length-bin sampling on sampling probabilities. The VB curve fitted to the length-at-age data, ignoring VP sampling and assuming normal errors with constant coefficient of variation using iteratively weighted least squares (IWLS), predicted substantially lower mean length-at-age for older ages compared to the VB curve fitted using VP maximum likelihood (MLP) with length-bin relative probabilities defined using fishing selectivity alone. This was due to the feature of the selectivity function of a sharp decline from 'full' selection at 1 000 mm length down to 1% selection for a length of 1 600 mm. When length-bin sampling frequencies were also included in defining relative probabilities, the VP maximum likelihood (MLPLB) and IWLS-estimated curves were more similar.

Predicted and observed values of annual growth rate (AGR) for lengths measured at release and first recapture in mark–recapture studies were compared where predictions used the VB parameter estimates obtained from the length-at-age data and the Fabens (1965) form of the VB growth model. Formulae for adjusting predictions for bias imparted by the use of the Fabens model were developed and showed that the bias is relatively small for the range of release lengths in the data. Predictions of AGR using the MLPLB-estimated VB parameters were closer to, but still substantially higher than, the mean trend in observed AGR values with release length compared with those obtained using IWLS-estimated parameters. A young-age adjustment (less than 5 years old) to the VB model is also given in order to give more realistic predictions of mean length-at-age for young fish.

Résumé

Un modèle de croissance de von Bertalanffy (VB) est ajusté aux données de longueur selon l'âge de la légine australe (*Dissostichus eleginoides*) de l'île Heard (division 58.5.2), compte tenu du biais d'échantillonnage des poissons dont l'âge est déterminé, attribué à la variable expliquée. Le sous-échantillonnage aléatoire des données de fréquence des longueurs (LF) qui permet d'obtenir les échantillons pour la détermination de l'âge se fait par intervalles de longueurs, en prenant un échantillon de taille prédéterminé pour chaque intervalle. L'estimation des paramètres de VB utilise une définition de la fonction de vraisemblance basée sur un échantillonnage de probabilité variable (VP) en raison de la fonction de sélectivité prédéterminée dépendante de la longueur applicable à la pêche au chalut et de l'effet additionnel de l'échantillonnage par intervalles de longueurs sur les probabilités de l'échantillonnage. La courbe de VB adaptée aux données de longueurs selon l'âge, qui ne tient pas compte de l'échantillonnage de VP, mais qui reconnaît les erreurs normales associées au coefficient de variation constant obtenu par les moindres carrés pondérés itérés (IWLS), prévoit une moyenne de longueur selon l'âge nettement moins élevée pour les poissons les plus âgés par rapport à la courbe de VB ajustée par le maximum de vraisemblance (MLP) pour l'échantillonnage de VP et dont les probabilités relatives des intervalles de longueurs sont définies au seul moyen de la sélectivité de la pêche. Ceci est dû à la caractéristique de la fonction de sélectivité consistant en un déclin abrupt, d'une sélection «totale» à 1 000 mm de longueur à une sélection de 1% pour la longueur de 1 600 mm. Lorsque les fréquences de l'échantillonnage par intervalles de longueurs sont incluses dans les probabilités relatives, la courbe estimée par le maximum de vraisemblance basé sur la VP (MLPLB) et la courbe estimée par les IWLS sont plus proches.

Les valeurs prévues et les valeurs observées du taux de croissance annuel (AGR) des poissons mesurés à la remise à l'eau et à la première recapture dans les études de marquage sont comparées. Les valeurs prévues reposent sur les estimations des paramètres de VB obtenues des données de longueurs selon l'âge et de la version de Fabens (1965) du modèle de croissance de VB. Les formules mises au point pour corriger, dans les prévisions, le biais introduit par l'utilisation du modèle de Fabens, montrent que le biais est relativement faible pour l'intervalle de longueurs des données sur les poissons relâchés. Les valeurs d'AGR prévues à l'aide des paramètres estimés par la méthode MLPLB sont proches, tout en restant nettement supérieures, de la tendance moyenne des valeurs observées sur les poissons remis à l'eau par rapport à celles obtenues avec les paramètres estimés par les IWLS. En outre, le modèle de VB est ajusté pour tenir compte des jeunes poissons (moins de 5 ans d'âge), afin de donner des prédictions plus réalistes de la longueur selon l'âge des jeunes poissons.

Резюме

К данным о распределении длин по возрастам для патагонского клыкача (*Dissostichus eleginoides*) у о-ва Херд (Участок 58.5.2) была подобрана модель роста по Берталанфи (VB) с учетом зависящего от смещения отклика выборки рыбы, возраст которой был определен. При подвыборке случайных данных по частоте длин (LF), использовавшихся для получения образцов рыбы в целях определения возраста, применялась выборка по интервалам длин с фиксированным размером выборки в интервале. При оценке параметров VB использовалось определение функции правдоподобия, основанное на случайной выборке с переменной вероятностью (VP), обусловленной заранее определенной и зависящей от длины функцией селективности для тралового промысла и дополнительным влиянием отбора по диапазонам длин на выборочные вероятности. Кривая VB, подобранная к данным о распределении длин по возрастам, без учета выборки VP и при допущении о нормальных ошибках с постоянным коэффициентом изменчивости, использующем итерационно взвешенные оценки по методу наименьших квадратов (IWLS), дала существенно более низкие значения средней длины по возрастам для более старших возрастных групп по сравнению с кривой VB, построенной по максимальному правдоподобию VP (MLP) с относительными вероятностями диапазонов длин, определенными на основании только промысловой селективности. Это было вызвано особенностью функции селективности, т.е. резким сокращением от "полного" отбора для 1000 мм длины до 1% отбора для длины 1600 мм. Когда в определение относительных вероятностей были также включены выборочные частоты интервалов длин, кривые, рассчитанные по максимальному правдоподобию VP (MLPLB) и IWLS, были более сходными.

Проведено сравнение расчетных и наблюдавшихся значений ежегодных темпов роста (AGR) для длин, измеренных при освобождении и первой повторной поимке в исследованиях по мечению–повторной поимке, где в расчетах использовались оценки параметров VB, полученные по данным о распределении длин по возрастам и форме модели роста VB по Фабенсу (Fabens, 1965). Были разработаны формулы корректировки в расчетах систематической ошибки, появляющейся при использовании модели Фабенса, которые показали, что систематическая ошибка относительно мала для полученного по данным диапазона длин при освобождении. Оценки AGR, в которых использовались параметры VB, рассчитанные по MLPLB, были ближе, но по-прежнему значительно выше средней тенденции в наблюдавшихся значениях AGR по длине при освобождении по сравнению с теми, что были получены по параметрам, рассчитанным в IWLS. Также сделана поправка для младших возрастов (менее 5 лет) в модели VB, с тем чтобы получить более реалистичные расчеты средней длины по возрастам для молоди рыбы.

Resumen

Se aplicó un modelo de crecimiento de von Bertalanffy (VB) a los datos de la talla por edad de la austromerluza negra (*Dissostichus eleginoides*) en Isla Heard (División 58.5.2), tomando en cuenta el sesgo de la muestra utilizada para la determinación de la edad atribuido a la respuesta de los peces. El submuestreo aleatorio de los datos de frecuencias de tallas (LF) utilizado para obtener muestras para la determinación de la edad se hizo por intervalos de tallas, tomando una muestra de tamaño predeterminado para cada intervalo. La estimación de los parámetros de VB utilizó una definición de la función de verosimilitud para el muestreo de probabilidad variable (VP), para tomar en cuenta la selectividad predeterminada por la talla aplicable a la pesca de arrastre y el efecto adicional del muestreo por intervalo de tallas en la probabilidad del muestreo. La curva de VB ajustada a los datos de talla por edad sin tomar en cuenta el muestreo VP, suponiendo que los errores son normales con un coeficiente de variación constante aplicando una ponderación iterativa con el método de mínimos cuadrados (IWLS) da como resultado un promedio de la talla por edad bastante menor para los peces de mayor edad, en comparación con la curva de VB ajustada con una función de probabilidad de máxima verosimilitud (MLP) para el muestreo VP y definiendo las probabilidades relativas de los intervalos de tallas solamente mediante la selectividad de la pesca. Esto se debió a que la selectividad disminuyó bruscamente, de la selección "total" para peces de 1 000 mm de largo a una selección de 1% para peces de 1 600 mm de largo. Cuando se incluyen las frecuencias del muestreo por intervalo de tallas en la definición de las probabilidades relativas, las curvas de la probabilidad de máxima verosimilitud para el muestreo VP (MLPLB) y las curvas de VB estimadas con el método de mínimos cuadrados ponderados (IWLS) se asemejan más.

Se compararon los valores pronosticados con los valores observados de la tasa de crecimiento anual (AGR) correspondientes a las tallas medidas al liberar el pez y al volver a capturarlo en los estudios de marcado y recaptura. Los valores pronosticados utilizaron estimaciones de los parámetros de VB obtenidas de los datos de talla por edad y la versión de Fabens (1965) del modelo de crecimiento de VB. Las fórmulas desarrolladas para ajustar el sesgo de los valores pronosticados por el modelo Fabens demostraron que éste es relativamente pequeño para el rango de tallas de los datos sobre peces liberados. Los valores de AGR pronosticados con los parámetros de VB estimados con el método MLPLB fueron más parecidos (pero siempre bastante mayores) a la tendencia promedio de los valores de AGR correspondientes a las tallas observadas al liberar el pez marcado que los obtenidos con los parámetros estimados con el método IWLS. Asimismo, se proporciona un ajuste para los peces de menor edad (menores de 5 años de edad) en el modelo de VB a fin de obtener pronósticos más realistas del promedio de la talla por edad para los peces juveniles.

Keywords: response-biased sampling, variable-probability sampling, maximum likelihood, Fabens model, young-age adjustment, CCAMLR

Introduction

Unbiased and precise estimation of population-average length-at-age is important for the assessment of fish stocks. Fisheries assessments for Patagonian toothfish (*Dissostichus eleginoides*) for each of the South Georgia and Heard Island plateau (HIMI) regions carried out under the auspices of CCAMLR using either the generalised yield model (Constable and de la Mare, 1996, 2002) or the integrated assessment framework, as implemented in CASAL (Bull et al., 2005; Hillary et al., 2006), require estimates of mean length-at-age and the coefficient of population variation about the mean. Therefore, prediction of population-average length-at-age, where the population is defined as the wild population in the area in which the population can effectively be considered to be closed (i.e. minimal emigration or immigration), is an important component of the assessment approach for the HIMI fisheries (Division 58.5.2) (SC-CAMLR, 2004).

Growth models for fish length, required for fisheries management, are often fitted to length–age data obtained by sampling fish from hauls, measuring their length and then removing an otolith or other hard part in order to determine age by counting the number of annual growth 'rings'. Commonly, the von Bertalanffy (VB) growth curve is used to describe the growth trajectory of population-average length-at-age and is fitted through the cloud of length–age points, given length as the response variable. This approach assumes that, conditional on age, the probability of sample unit selection due to fishing (i.e. selectivity) does not depend on length. However, if, for a particular length range, fish are less vulnerable to capture, then this assumption will be violated when this (unconditional) length-based selectivity does not operate indirectly through age-dependent selectivity. This response-biased sample selection will result in bias in the VB parameter estimates, apart from any bias due to parameter-effects nonlinearity or intrinsic nonlinearity of the VB model

(Ratkowsky, 1983; Bates and Watts, 1988). In contrast, age-dependent selectivity, where the unconditional probability of selecting an individual is not constant across age, does not introduce any (additional) bias into the estimation of the VB parameters, since the VB model is conditioned on age. For random subsampling from the haul, Goodyear (1995) demonstrated empirically, using simulated age–length data, that age-dependent selectivity of fishing does not introduce bias into estimates of mean length-at-age, and Candy (2005) proved this result analytically; however, length-dependent selectivity does introduce bias. The effect of length-dependent selectivity on VB parameter estimation has been studied by Troynikov (1999), Lucena and O'Brien (2001), Taylor et al. (2005) and Candy (2005). Troynikov (1999) used Bayes theorem to define a maximum likelihood estimation procedure for the VB model parameters incorporating pre-specified length-dependent fishing selectivity, which is appropriate if fish are sampled with equal probability for ageing from the on-deck length-frequency (LF) sample. Lucena and O'Brien (2001) incorporated gear selectivity in their estimation of the VB parameters by simply fitting separate VB models to length-at-age data obtained from purse-seine fisheries to that from the gill-net fishery for bluefish (*Pomatomus saltatrix*) in southern Brazil. More recently, Taylor et al. (2005) estimated the VB parameters in the presence of size-selective fishing, assuming that the length-bin frequencies of catch-at-age are multinomially distributed, with expected values dependent on growth parameters and growth variation as well as simultaneously estimated size selectivity, abundance-at-age, natural mortality and historical fishing mortality. This approach considers the estimation of VB parameters as part of an integrated approach to modelling length–age frequency data in the complete catch rather than just the aged random subsample. The difficulty with this approach is that freedom from bias in the estimated VB parameters is dependent on the other model components also being correctly specified. The level of precision at which these other model components are estimated would also undoubtedly affect the precision of the VB parameter estimates. Also, individual fish lengths are not employed in the estimation but are grouped into length classes. The advantage of this method for estimating growth parameters is that it simultaneously estimates the size-selectivity function along with the VB model and other model parameters. However, the model of Taylor et al. (2005) assumes that the on-deck sampling scheme used to obtain the age–length data is an equi-probability scheme, which makes this model invalid for the response-stratified sampling scheme described below.

For most hauls there are far more fish than can be measured in practice, even for the relatively simple measure of total length, so the haul is sampled for lengths with a sample size of, say, N_h for haul h from which a further subsample of n_h fish is taken for age determination. If a haul is considered to be a sample itself, then the N_h fish represents a subsample and the n_h otoliths a sub-subsample. This final sub-subsample, accumulated across all hauls, provides the set of length-at-age data used to fit the growth model. The first subsample for length measurement is typically a simple random sample giving equal probability of selecting any particular fish in the haul with fish tallied into length bins; this sample is denoted the length-frequency (LF) sample. Although the sub-subsample of length- and age-measured fish is also obtained randomly, length-dependent probabilities may be involved in selecting fish from the LF sample. One sampling scheme that could be used is length-bin (LB) sampling (Goodyear, 1995), whereby length bins of, say, 10 mm are used and a maximum number of fish specified for a complete fishing season are retained in each bin for age determination. In the statistical literature this is called response-stratified (RS) sampling (Jewell, 1985). This is an unequal probability selection scheme and has different properties from the scheme known as variable probability (VP) sampling, whereby fish are selected by on-deck sub-subsampling after all fish in the LF sample are first allocated to length bins and a bin is then randomly selected with probability given by a function of length, and a fish is drawn at random from the selected bin. This process is repeated until the required total sample size across bins is achieved. Note that this sampling scheme could only feasibly be carried out separately for each haul, however, operating such a VP sampling protocol at the haul level would be impractical, requiring fishery observers to keep the LF samples in sorted bins during commercial fishing operations while sampling was carried out. On the other hand LB sampling of LF samples is easy to apply operationally, since LF sampled fish subsampled for ageing are accumulated into length bins progressively over the fishing season as they are encountered and sampling is discontinued for a particular bin when the maximum predetermined sample size for that bin is achieved.

Considering fishing as a sampling process, and length-dependent fishing selectivity as the property of this 'sampling' process that gives rise to fishing being a variable probability (VP) sampling scheme, is therefore distinguished from response stratified (RS) subsampling of the on-deck LF sample with the particular implementation of general RS sampling that is described, denoted as LB sampling.

Length-bin sampling has been used to select fish for age determination in the HIMI trawl fishery as described later.

The maximum likelihood theory for estimating the VB parameters that is presented here is an extension of that described in Jewell (1985) for RS sampling which additionally incorporates VP sampling due to fishing and length-dependent fishing selectivity. Also, because for length-bin sampling the bin sample sizes are fixed and not random as in VP sampling, there is a distinction in theory between VP and RS sampling. However, it is shown that if a conditional maximum likelihood (ML) estimator is used, this ML estimator turns out to be the same irrespective of which of these two sampling protocols is explicitly modelled. Estimation of the trawl selectivity curve is described elsewhere and assumed to be known for this study, with its most important feature being a sharp decline in selectivity from 100% at 1 000 mm to 1% at 1 600 mm.

Predicted and observed values of annual growth rate (AGR) for lengths measured at release and first recapture in mark–recapture studies were compared where predictions used the VB parameter estimates obtained from the length-at-age data and the Fabens (1965) form of the VB growth model. Formulae for adjusting predictions for bias imparted by the use of the Fabens model were developed. These formulae used various assumptions about both the distributions of the unknown age-at-release and random fish-level effects for asymptotic length (Francis, 1988; Wang and Thomas, 1995).

Methods

Age–length data

For the HIMI Patagonian toothfish trawl fishery, the sampling protocol for age determination specifies that a maximum sample size of 10 fish for each 10 mm length bin be sampled for the range of lengths between 400 and 1 000 mm for a given fishing season. For length bins outside this range, the same restriction on sample size is made, but due to the rarity of fish caught in these length bins, the maximum sample size is usually not achieved.

Age–length data were obtained for three research cruises carried out prior to 1997 and commercial cruises from 1999/2000 to 2002/03, giving a total set of 3 196 age–length pairs obtained from otolith readings. Otoliths were prepared, read and validated using the methods described in Krusic-Golub and Williams (2005) and Krusic-Golub et al. (2005). The corresponding random length-frequency samples for these research cruises were also obtained and combined with the data from commercial cruises to give total length-bin frequencies for both the age–length data and random length-frequency data. The nominal date assumed for ring formation was 1 December, and otoliths for which there was an unacceptable degree of uncertainty in the read age were removed from the dataset. Ages were adjusted to account for time from ring formation to capture date.

Mark–recapture data

For the mark–recapture program for the HIMI trawl fishery, the total number of released fish that were recaptured and measured for length at both tagging and recapture was 1 874 with releases and recaptures taking place between April 1998 and May 2006. Lengths at release ranged from 431 to 1 200 mm, with a maximum length of recapture was 1 317 mm. Days-at-liberty ranged from 1 to 2 529, with 898 recaptures occurring after 175 days and 270 before 20 days at liberty. The median value of days-at-liberty was 163. Only mark–recapture length increments for which the value of days-at-liberty was at least 175 were employed, because this period gave a 0.9 probability of a positive increment in length as determined by Candy et al. (2005). Candy fitted a binomial/logistic model to the binary data defined by (1 = positive increment, 0 = zero or negative increment) with predictor variable days-at-liberty.

Length-dependent selectivity function

The trawl fishing selectivity function used here is described by the 4-segment function

$$\begin{aligned} P(L) &= \exp\left\{0.0051L - 0.0494\left(\frac{L}{100}\right)^2\right\}; \quad L \geq 1030 \\ &= 1 - \frac{400-L}{200}; \quad 200 < L < 400 \\ &= 1; \quad 400 \leq L < 1030 \\ &= 0; \quad L \leq 200 \end{aligned} \tag{1}$$

where $P(L)$ is the probability of selecting, by fishing, a fish of length L (mm) relative to the probability of observing, independent of fishing (if that were possible), a fish of length L in the population. The upper arm of the selectivity function (1) (i.e. selectivity for lengths greater than 1 030 mm) was estimated by Candy (2006) using random length-frequency data from concurrent trawl and longline fishing for this fishery for the 2002/03 to 2004/05 fishing seasons. The lower arm of the selectivity function (1) (i.e. selectivity for lengths less than 400 mm) was not formally estimated but is based on general observation of the length-frequency data. The selectivity function (1) is given in Figure 1. The most important feature of this selectivity function for this study is the sharp decline in selectivity from 100% at near 1 000 mm to 1% at 1 600 mm.

Growth model

Denote the expected value of length, L, given age, A, assuming that $L^{(Pop)}$ is a random length from a theoretical random sample from the wild population of fish, by $\mu(A, \theta)$ so that

$$E(L^{(Pop)} \mid A) = \mu(A, \theta) = L_\infty (1 - \exp\{-\kappa(A - t_0)\}) \quad (2)$$

and

$$L^{(Pop)} = \mu(A, \theta) + \varepsilon$$

where L is length (mm), A is age (years), $\theta = (L_\infty, \kappa, t_0)$ are the VB parameters corresponding to the population-average asymptotic length, growth rate, and age when length is expected to be zero respectively, and ε is an error term assumed to be normally distributed with zero expectation and constant coefficient of variation (CV) where

$$Var\{\varepsilon \mid \mu(A, \theta)\} = \sigma^2\mu^2(A, \theta)$$

so that CV is given by σ. Assuming that the sample of length–age data has sample selection probabilities that are independent of length, then the above model can be optimally estimated using an iteratively weighted least squares (IWLS) fitting algorithm, where the statistical weights are the inverse of the variances estimated at the previous iteration's estimate of θ.

Candy et al. (2005) described a young-age adjustment to the VB model in order to obtain more realistic predictions of length-at-age for fish below age λ. This adjusted VB model (VBA) is given by

$$E(L^{(Pop)} \mid A) = L_\infty (1 - \exp\{-\kappa(A - t_0)\})\exp\{\delta(A, \lambda)\, \alpha_0\, (A - \lambda)\} \quad (3)$$

where

$$\delta(A, \lambda) = 1;\ A \le \lambda$$
$$= 0;\ A > \lambda$$

and α_0 and λ are parameters to be estimated.

Maximum likelihood estimation under VP sampling of lengths

The likelihood is specified for the length-at-age data under VP sampling using length bins determined by the length-bin sampling procedure and sampling probabilities are determined by combining equation (1) and length bin relative sampling frequencies.

The length bin (or strata as defined by Jewell, 1985) lower limits for subsampling the random LF data for ageing are given by $K_1 < .. < K_j < \ldots < K_{r-1}$ so that a fish of length L is allocated to bin j (i.e. $L \in B_j$) if $K_{j-1} \le L < K_j$ with endpoints defined as $K_0 = 0$, $K_r = +\infty$. Next, define the ratio of the probability of a fish that is in length bin j being in the LF sample to that for the wild population, using a step function approximation to equation (1) and the above length bins as

$$p_j^{(LF)} \equiv Prob\left(L^{(LF)} \in B_j\right) / Prob\left(L^{(Pop)} \in B_j\right) = P\left(K_j'\right)$$

where $K_j' = \left(K_{j-1} + K_j\right)/2$ for $j = 2,\ldots,r-1$ and as convenient endpoints set $K_r' = K_{r-1} + \left(K_{r-1} - K_{r-2}\right)/2$ and $K_1' = K_1 - \left(K_2 - K_1\right)/2$.

In the absence of length-dependent fishing selectivity, then $p_j^{(LF)} \equiv 1$. Let the realised sample size in length bin j for the total LF sample for a given fishing season or the aggregate of a number of fishing seasons be N_j and let $N = \sum_{j=1}^{r} N_j$. Let the subsample of the LF sample of fish selected for ageing be denoted as n_j and $n = \sum_{j=1}^{r} n_j$. Length-bin sampling specifies that some or all of the bins have a fixed sample size of, say, m, so that unlike simple random subsampling (i.e. equal probability selection) of the LF sample, the expectation of n_j/n conditional on n is not equal to N_j/N for length bins with a pre-sampling fixed sample size.

Combining length bin relative sampling frequencies with the selectivity function relative probabilities gives empirical relative probabilities of sample selection of $p_j^* = p_j^{(LF)} n_j N / \left(n N_j\right)$, $j = 1,\ldots,r$. Since these probabilities are relative they can be scaled, for example, so that $p_j' = p_j^* / p_1^*$ for $j = 2,\ldots,r$ and $p_1' \equiv 1$ and define $p^* = \left(p_1^*,\ldots,p_r^*\right)$ and $p' = \left(p_1',\ldots,p_r'\right)$ so that the term N/n no longer appears in p'. Note that for the LF data the N_j are observed totals for the season(s) and not weighted totals using statistical weights of the ratio of the total weight of fish in the LF sample as a proportion of the total weight of fish in the haul, as is common practice in presenting a stratum-size weighted total of LF data where each haul is considered a sampling stratum. Following standard statistical theory for binomial proportions, the unweighted total of LF numbers in length bin j across hauls, N_j, conditional on N, is a sufficient statistic for γ_j where $\gamma_j = Prob(L^{(LF)} \in B_j)$.

Therefore, if fish from the finite wild population could be selected independently for age determination without replacement (but assuming the available population is very large compared to N) with probability, relative to that of the wild population, proportional to p_j^* (i.e. if γ_j is replaced by N_j/N while noting that $Prob(L^{(LB)} \in B_j) = n_j/n$), then under this variable probability (VP) sampling scheme, and assuming that the VB model (equation 2) is correct, the probability density of the LB sample given age is given by (Jewell, 1985)

$$f_{VP}\left(L^{(LB)} = l \mid A^{(LB)} = a\right) = \frac{p_j^*\phi\left[\varepsilon/\left\{\sigma\mu(a,\theta)\right\}\right]}{\sum_{j=1}^{r} p_j^*\left[\Phi\left[G_j/\left\{\sigma\mu(a,\theta)\right\}\right]-\Phi\left[G_{j-1}/\left\{\sigma\mu(a,\theta)\right\}\right]\right]}$$
$$;\left(l \in B_j \mid a; \quad j = 1,\ldots,r\right) \qquad (4)$$

where $\phi(\ )$ is that standard normal density function, $\Phi(\ )$ is the corresponding cumulative density function and $G_j = K_j - L_\infty(1 - \exp\{-\kappa(a - t_0)\})$.

It can be seen from equation (4) that replacing p^* by p' does not change the probability density function (4).

If it is assumed that p' is known, then maximum likelihood estimation requires minimising the following negative log-likelihood with respect to (θ, σ) after extending the notation in an obvious way,

$$-\ln\left\{\ell\left(\theta,\sigma \mid L = l, A = a, p'\right)\right\} =$$
$$0.5\left[\begin{array}{l}\sum_{i=1}^{n}\varepsilon_i^2(\theta)/\left\{\sigma\mu\left(a_i,\theta\right)\right\}^2 + \\ \sum_{i=1}^{n}\ln\left(\left\{\sigma\mu\left(a_i,\theta\right)\right\}^2\right) + n\ln(\pi)\end{array}\right]$$
$$+\sum_{i=1}^{n}\ln\left\{\sum_{j=1}^{r}p_j'\left[\begin{array}{l}\Phi\left(G_{i,j}\left(\theta,a_i\right)/\left\{\sigma\mu\left(a_i,\theta\right)\right\}\right) - \\ \Phi\left(G_{i,j-1}\left(\theta,a_i\right)/\left\{\sigma\mu\left(a_i,\theta\right)\right\}\right)\end{array}\right]\right\}$$
$$-\sum_{j=1}^{r}n_j\ln\left(p_j'\right). \qquad (5)$$

The VP sampling scheme assumes that, although n is fixed, the n_j are random so that equation (4) does not correctly describe the density of lengths obtained by subsampling the LF sample using LB sampling with the n_j fixed. However, Appendix 1 shows that if the LB sampling process is modelled directly and the parameters γ_j are replaced by their sufficient statistics, then the conditional likelihood (McCullagh and Nelder, 1989, p. 248) (i.e. conditional on these sufficient statistics) is the same as that give by equation (5).

Note that the last term in equation (5) does not involve the VB parameters, but is included to allow for the possibility that parameters defining $p_j^{(LF)}$ could be estimated simultaneously with the other parameters. Although this is feasible for linear models as outlined by Hausman and Wise (1981), Candy (2005) noted, based on simulation studies, that in practice for the VB model such simultaneous estimation is not reliable, even under a known simulation model. VB parameter estimates obtained using the VP likelihood were calculated using the 'nlminb' function in S-plus (Insightful, 2001) and the 'fitnonlinear' directive in GenStat (Lawes Agricultural Trust, 2002) was used to corroborate the 'nlminb' estimates and provide standard errors for parameter estimates which are not available from 'nlminb'.

Comparison of VB-predicted growth to mark–recapture data

Growth predicted from the fitted VB model was compared to observed growth increments from mark–recapture samples. Since age is not measured for the majority of recaptured fish, empirical annual growth rates (AGRs), R, given by

$$R = (L_c - L_r)/D$$

were used to carry out this comparison where D is days-at-liberty divided by 365 and L_r and L_c are the lengths measured at release and recapture respectively. These observed values of R were compared to predicted values from the VB model and corresponding parameter estimates obtained from the fit to the length-at-age data. The predicted value of R can be obtained from a state-space or Fabens (1965) formulation of equation (2) by predicting L_c conditional on L_r and D so that

$$L_c = L_\infty\left[1-\left(1-\frac{L_r}{L_\infty}\right)\exp\{-\kappa D\}\right]+e_c$$

where e_c is a random error term. If the expected value of L_c conditional on L_r and D is expressed, suppressing the obvious dependence on VB parameters, as

$$E(L_c \mid L_r, D) = L_\infty \left[1 - \left(1 - \frac{L_r}{L_\infty}\right)\exp\{-\kappa D\}\right] + E(e_c \mid L_r) \quad (6)$$

then

$$E(R \mid L_r, D) = \frac{L_\infty - L_r}{D}\left[1 - \exp\{-\kappa D\}\right] + \frac{E(e_c \mid L_r)}{D}. \quad (7)$$

Note that the expected value of R given by equation (7) does not depend on the age of the fish at tagging and recapture, but only on the difference in time between these events and, further, equation (7) does not incorporate the VB parameter t_0. Note also that if $E(e_c \mid L_r)$ is not zero, then applying the Fabens form of the VB growth mode using VB parameters estimated from length-at-age data will give biased predictions of L_c conditional on L_r and D. The theoretical problem Francis (1988) noted with the Fabens model in the extreme case is that if L_r is greater than L_∞ then growth predicted from equations (6) and (7), assuming $E(e_c \mid L_r) \equiv 0$, will be negative whereas, in the absence of measurement error, actual growth in length cannot be negative, so that in this case $E(e_c \mid L_r, L_r > L_\infty)$ must be greater than zero. The difficulty with evaluating $E(e_c \mid L_r)$ over the range of L_r is that it requires assumptions about the distribution of the unknown age-at-first-capture. Appendix 2 gives a model-based investigation of $E(e_c \mid L_r)$ using (i) a random-asymptote version of the VB model that assumes that random individual departures from an asymptote of L_∞ have zero expected value and (a) a uniform distribution or (b) an unspecified distribution with zero skew, and (ii) an exponential distribution for age-at-first-capture that has a mortality rate parameter, κ_m, which is related to the VB parameter, κ, for each of the two cases $\kappa_m = 2\kappa$ and $\kappa_m = \kappa$ (Francis, 1988). Assumption (i)(a) combined with (ii) allows an analytical solution to $E(e_c \mid L_r)$, while replacing (i)(a) with (i)(b) is used to provide a second-order approximation to this expected value, as described in Appendix 2. From the results in Appendix 2 (equation A11), it can be seen that this approximation assuming $\kappa_m = 2\kappa$ is given by

$$E(e_c \mid L_r) \cong -2\sigma^2\left(1 - 2\frac{L_r}{L_\infty}\right)\left(\frac{L_\infty - L_r}{L_\infty^2} + \sigma^2\frac{L_\infty - 3L_r}{L_\infty^2}\right)^{-1}\left(1 - \exp\{-\kappa D\}\right). \quad (8)$$

Equation (8) shows that $E(e_c \mid L_r)$ is only zero when $L_r = 0.5L_\infty$ and is increasingly negative as L_r decreases below this value and increasingly positive as L_r increases above this value. Appendix 2 gives the corresponding second-order approximation when $\kappa_m = \kappa$ (equation A12) and the exact formulae for assumption (i)(a) for values of κ_m of 2κ (equation A9) and κ (equation A10). Jensen (1996) derived a value of κ_m of 1.5κ based on Beverton and Holt invariants. Note that the mark–recapture data do not contribute to the estimation of L_∞ and κ but these data are only used to compare predictions with observations using estimates of these parameters obtained from the length-at-age data.

The results section shows that accounting for $E(e_c \mid L_r)$ in equation (7) using equation (8) makes only a slight difference to predictions of annual growth for the range of L_r in the data, compared to predictions that assume $E(e_c \mid L_r)$ is zero.

Results

Length-at-age data

Figure 2 shows the sample sizes of aged fish and total length-frequency sample size aggregated into 100 mm length bins from 200 to 1 800 mm. Frequencies are plotted at the length bin midpoint. These frequencies are totals over all fishing seasons. Note that although the length-bin sampling rule actually specified 10 mm wide length bins and was applied with a fixed sample size of 10 fish separately for each fishing season, the data were aggregated both across fishing seasons and into 100 mm bins. This was done to avoid the large number of bins that had a zero sample size of aged fish when the data were not aggregated in this way. The VP maximum likelihood estimation used these 100 mm length bins and sampling frequencies aggregated across seasons. If aggregation across fishing seasons had been unnecessary, then the log-likelihood (equation 5) would simply be the sum of the log-likelihood contributions for each season calculated using season-specific values of p_j^* (Candy, 2005).

Figure 3 shows length-at-age data and the IWLS-fitted VB curve. Maximum likelihood estimates of the VB parameters and the CV parameter, σ, were obtained using log-likelihood (equation 5) with length bin relative probabilities determined either from fishing selectivity alone (i.e. $p_j^* = P(K_j')$) (MLP estimation) or by combining both fishing selectivity and length-bin sampling relative frequencies (i.e. $p_j^* = P(K_j')n_j / N_j$) (MLPLB estimation). The parameter estimates for the VB model (equation 2) fitted using IWLS, MLP and MLPLB estimation methods are given in Table 1, which also gives the parameter estimates for the additional parameters α_0 and λ in the VBA model (equation 3). These last estimates were obtained by MLPLB while fixing

Table 1: Growth model parameter estimates obtained for HIMI trawl fishery length-at-age data.

Fitting method	Model parameters (SE)					
	L_∞	κ	t_0	α_0	λ	σ
IWLS	1975.5 (74.8)	0.03947 (0.0023)	–2.3041 (0.1173)			0.1069 (0.0169)
MLPLB	2870.8 (286.6)	0.02056 (0.0027)	–4.2897 (0.2056)			0.1034 (0.0141)
MLP	3129.8 (286.2)	0.02188 (0.0025)	–2.7700 (0.1352)			0.1095 (0.0152)
MLPLB (VBA)	2870.8	0.02056	–4.2897	0.0400 (0.0034)	5.1085 (0.0602)	0.1012 (0.0148)

the estimates of $\theta = (L_\infty, \kappa, t_0)$ to those obtained from the fit of the VB model (equation 2) using MLPLB. Figure 4 shows the fitted VB curves using the above three estimation methods along with the fit of the VBA model.

Mark–recapture data

Figure 5 shows the annual growth rates, R, from the mark–recapture model versus length-at-release for days-at-liberty greater than 175. Note that some increments can be negative due to measurement error. The predicted VB relationships using equation (7) and the IWLS and MLPLB parameter estimates, assuming $E(e_c \mid L_r)$ is zero, are also shown in Figure 5, along with the fitted loess smoother (Insightful, 2001, p. 435) with 99% confidence bars shown at seven different release lengths. The predicted curves are not completely smooth due to variation in predicted R caused by variation in days-at-liberty. So although the observed annual growth rates, R, shown in Figure 5 do not depend on days-at-liberty, each observed value has an associated value of D and the corresponding predictions from equation (7) can be seen to depend on D. Some smoothing of the predictions in an attempt to remove this variation, has been carried out by averaging predictions across values of D for each unique value of length-at-release and fitting a spline smoother through these averaged predictions.

The effect of adjusting predictions of annual growth from equation (7) for non-zero $E(e_c \mid L_r)$ using equation (8) is shown in Figure 6. Alternatively, when equation (7) was adjusted using $E(e_c \mid L_r)$ calculated assuming a uniform distribution, $U(-c, c)$, for random deviations from L_∞ using equation (A9) in Appendix 2, and calculating $c = \sqrt{3\sigma L_\infty}$ (i.e. equating variances since the variance of V given $V \sim U(-c, c)$ is $\frac{1}{3}c^2$), gave very similar results to those obtained using equation (8) (graphs not shown). Figure 7 shows that the bias in L_∞, given by $E(e_c \mid L_r)\ (1 - \exp\{-\kappa D\})^{-1}$ (see Appendix 2), expressed as a percentage of L_∞ calculated for each of the equations (A9) to (A12) given in Appendix 2, was no greater than –2% for the observed range of release lengths.

Discussion

The effect of the fixed sample size rule used for the length-bin sampling on sampling frequencies can be clearly seen in Figure 2 where, for the 400 to 1 000 mm length range, sample sizes are constant at near 500 (corresponding to approximately 100 fish per season for each 100 mm bin, since the equivalent of almost five seasons were combined), whereas the random length-frequency sample shows a very peaked distribution for this length range.

Figure 3 shows the good fit of the IWLS-estimated VB curve to the observed length–age data, but due to the combined effect of (i) the length-bin sampling method and (ii) the length-dependent fishing selectivity, these data do not fairly represent the distributions of length-at-age for the wild population, assuming in the case of (ii) that the selectivity function (equation 1) is valid. Note the relatively small number of fish either greater than 1 000 mm in length or greater than 20 years in age. This is due to the combined effect of natural and fishing mortality and the effect of trawl selectivity as quantified by equation (1). Figure 4 shows that if only the effect of fishing selectivity is considered on length bin relative probabilities, then the IWLS-fitted curve underestimates mean length-at-age for ages above 15 years. When length bin relative sampling frequencies were also included in defining relative probabilities, the maximum likelihood- (MLPLB) and IWLS-estimated curves were more similar but the former was ‘flatter’ and gave slightly lower predictions of mean length-at-age for ages in the 8–20 year range. This translated to larger predictions for the MLPLB-fitted curve for ages below 5 years and above 25 years. The predicted length-at-age-zero is 242 mm (SE = 5 mm), which is unrealistically large for post-larval fish compared to the value obtained from the IWLS-estimated VB parameters of 172 mm (SE = 5 mm). This could be interpreted as a failure of the MLPLB-fitted curve to give realistic predictions for these young ages, especially since the assumed selectivity curve for the 200 to 400 mm length range suggests that larger fish of a given age in the wild population are over-selected relative to their smaller cohorts for this young age range. This apparent failure could also throw doubt on predictions for ages above 5 years; however, it is not the estimation method that is at fault, since Figure 5 shows that for the 400 to 1 000 mm length range, the MLPLB-estimated VB parameters give better predictions (i.e. closer to the curve obtained from the loess smoother) of observed values of R from the independent mark–recapture data than those obtained from the IWLS-estimated VB parameters. The problem lies in the inflexibility of the VB model, given that it has only three free parameters. If there is an early-age (i.e. below age 5) phase of growth which is different from a later-age growth phase, then extra model terms and parameters to adjust the VB model are required. The VBA model (equation 3) went some way towards rectifying this problem (see Figure 4b) with a predicted mean length-at-age-zero of 197 mm (SE = 5 mm).

Figure 5 shows that growth rates from mark–recapture studies are lower, on average, than expected from the fitted VB curves, and although only data for days-at-liberty greater than 175 were used, some component of D for the observed values in Figure 5 could be made up of a period of zero growth after tagging (Xiao, 1994). Another possible cause of this apparent bias could be that measurement errors may not, on average, cancel out. Therefore, if the error in recapture length minus the error in release length is, on average, negative and actual growth is close to zero, then this could result in what appears to be 'negative' growth. Candy et al. (2005) presented a method for adjusting for these 'nuisance' effects on observed growth based, in part, on the binomial/logistic model mentioned earlier. Figure 6 shows that the bias in applying the Fabens form of the VB model with VB parameters estimated from length-at-age data is relatively small. When the different adjustments for this bias given in Appendix 2 were applied, it was found that the absolute value of expected bias was small as long as length-at-release did not approach the estimate of the VB parameter representing asymptotic length.

In work not described above, the length-at-recapture data were combined with the length-at-age data to provide a maximum likelihood estimation procedure which simultaneously obtained MLPLB estimates from the length-at-age data and maximum likelihood estimates from the length-at-recapture data conditional on the lengths-at-release using the Fabens model. Separate error variance parameters were estimated for each dataset. Since the Fabens model conditions on length-at-release, the corresponding error variance would be expected to be much smaller than that for the length-at-age data, which proved to be the case. Neither the effect of fishing selectivity on the VB estimates for the Fabens model, nor the different theoretical values of the L_∞ parameter between the two models that condition on either age or length-at-release were considered. This is reasonable, since very few lengths-at-recapture were greater than 1 030 mm, which is the length at which fishing selectivity starts to decline from 1, and for the restricted range of lengths-at-release, given earlier results, any discrepancy between expected values of L_∞ is likely to be small. If bias correction of the Fabens-based estimate of L_∞ is required, given the results in Figure 7, then the linear distribution-free bias adjustment of Wang (1998) would be a good approach to take (see Appendix 2). The results of this maximum likelihood estimation were not reported here, both for brevity and because the estimation gave a close to linear relationship between length and age, due to an extremely large estimate of L_∞ resulting from the strong influence of the mark–recapture data. This mean length-at-age relationship was not considered realistic, and reflects the limited range of both length-at-release and days-at-liberty in the data and the lack of a strong trend in growth rate with release length (Figure 5). This lack of trend is possibly due to the variable magnitude of tagging 'shock' on growth, so the above approach was not pursued further here. More detail can be made available on request (S. Candy).

If fishing selectivity is assumed to be age-dependent rather than length-dependent, due for example to ontogenetic movement of older fish to deeper water beyond the depth range of the trawl gear, then only the length-bin sampling relative frequencies need to be considered for estimation, since in this case $p_j^* = n_j N / \left(n N_j \right)$. Here, it has been assumed that any such movement is length-dependent and this, when combined with possible gear avoidance by larger fish due to their increased ability to swim faster than the tow speed, results in the under-selection of larger fish as quantified by equation (1). The estimation method has been formulated in a way that easily accommodates other forms of selectivity function to equation (1) since selectivity enters the VP log-likelihood (equation 5) via the length bin midpoint values given by $p_j^{(LF)}$. Also, to some degree, the uncertainty in the selectivity-at-length is taken into account since the p_j^*, incorporating $p_j^{(LF)}$, are expected values so that the marginal length-bin frequencies for the length-at-age sample are realisations from a multinomial distribution about this expected value, as seen from the last term in equation (5). This can be seen in practice in Table 1 where the standard errors for the MLPLB and MLP parameter estimates are substantially larger than those for the IWLS estimates. However, uncertainty in the VB parameter estimates due to any inaccuracy in the selectivity function parameter values, or due to mis-specification of its functional form, are not accounted for. If it were possible to estimate the $p_j^{(LF)}$ simultaneously with the VB parameters either non-parametrically or parametrically (i.e. via a selectivity function) using the length-at-age data alone, then the uncertainty in selectivity could be fully accounted for. However, Candy (2005), using simulation, found that only if the correct VB parameters were pre-specified and not estimated, could the $p_j^{(LF)}$ be reliably estimated from the length-at-age sample. Also, ageing errors, in terms of their precision and bias, have not been accounted for in the estimation procedures and further research is planned on quantifying the with- and between-reader ageing error (D. Welsford, pers. comm.) in order to incorporate the precision of these errors into estimation. To do this, methods developed for fitting non-linear models with measurement error (Carroll et al., 1995) could be incorporated into the VP likelihood.

Simulation studies carried out by Candy (2005) using lognormal errors (i.e. which have the same variance-to-mean relationship as the constant CV normal error model used here) showed that the maximum VP likelihood estimator of the VB parameters was reliable given correctly specified values of $p_j^{(LF)}$, and was superior to the other estimators considered, including that obtained using inverse-probability weighted least squares (Pfeffermann, 1993). Also, considering length-bin sampling alone, these simulation studies showed that length-bin sampling of 100 fish per 100 mm length bin gave considerably more efficient (i.e. lower variance) estimates of mean length-at-age predicted from VB parameter estimates when the VP likelihood was used compared to ordinary least squares estimates obtained using simple random subsampling of the LF sample for age determination with the same total sample size.

In the general statistical literature, estimation of regression model parameters under response-biased sampling, where sample units are selected with a probability that is a function of the response, has been studied in the case of linear (DeMets and Halperin, 1977; Hausman and Wise, 1981; Jewell, 1985; Vardi, 1985; Pfeffermann, 1993), generalised linear (Chen, 2001) and multilevel linear (Pfeffermann et al., 1998) regression. This study and that of Candy (2005) are the first studies to consider response-stratified sampling in the context of fitting a non-linear model, and also the first studies to consider the combined effects of two separate response-biased sampling processes on estimation.

Conclusions

A von Bertalanffy growth model with a young-age adjustment was fitted to length-at-age data for Patagonian toothfish caught by the Heard Island trawl fishery, taking into account the length-bin sub-sampling process used to select fish for ageing from the random length-frequency samples, and also taking into account an assumed length-dependent fishing selectivity function. When predictions from the Fabens form of the VB model were compared to growth rates obtained from mark–recapture studies, although in general growth was over-predicted, the model fitted using the definition of maximum likelihood that incorporated variable probability sample selection gave a greater correspondence to the mark–recapture growth than that obtained when sampling probabilities were ignored.

Acknowledgements

We are grateful to Prof. André Punt, Dr Dirk Welsford, and an anonymous referee for helpful comments on this manuscript. WG-FSA documents cited in this paper are available from the authors.

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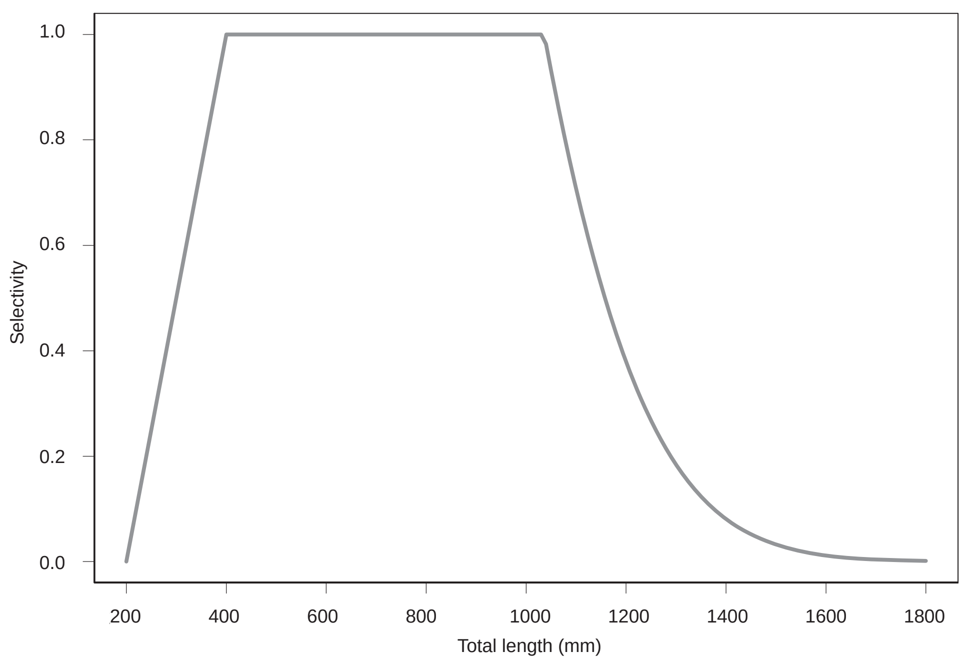

Figure 1: Relative selection probability, $P(L)$, versus length, L, with upper arm estimated by Candy (2006) and with assumed lower breakpoint and lower limb.

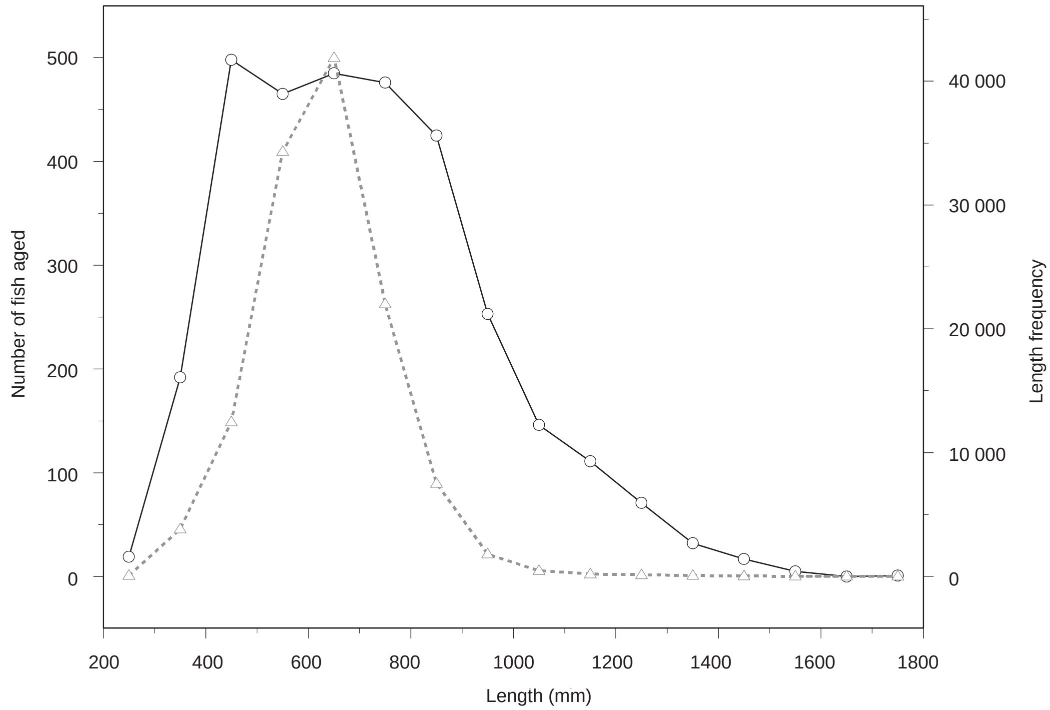

Figure 2: Number of fish sampled by 100 mm length bin for each of the length-frequency sample (dashed line, triangles) and the subsample of aged fish (solid line, circles) aggregated across five fishing seasons. Points shown at length bin midpoint.

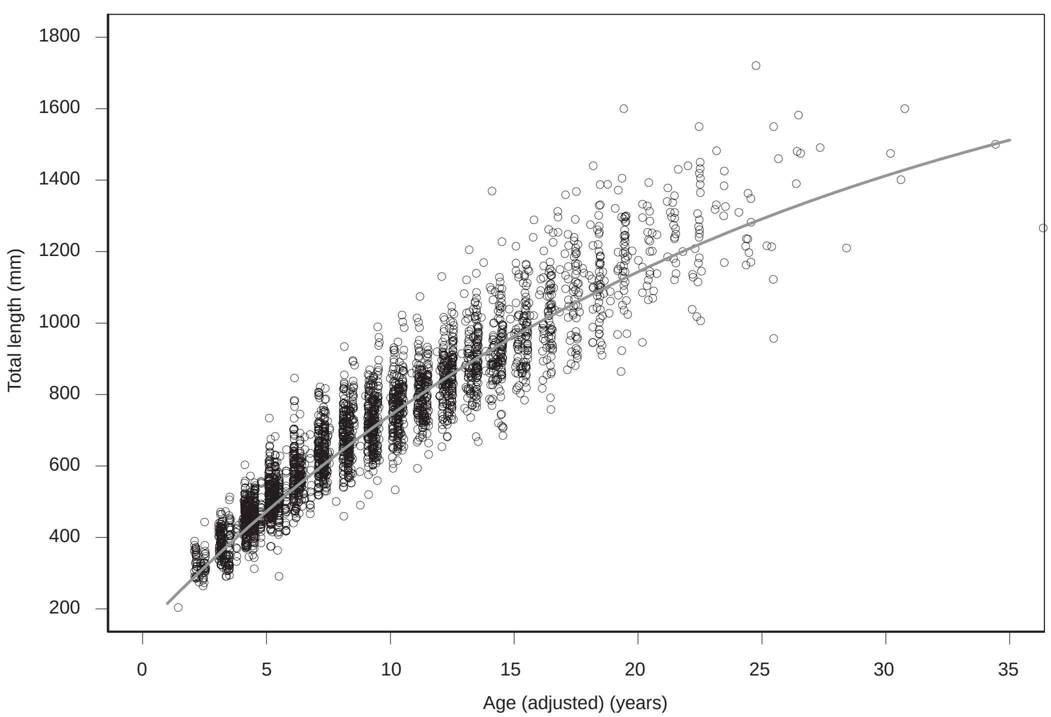

Figure 3: Length-at-age data for HIMI trawl fishery and IWLS-fitted VB curve.

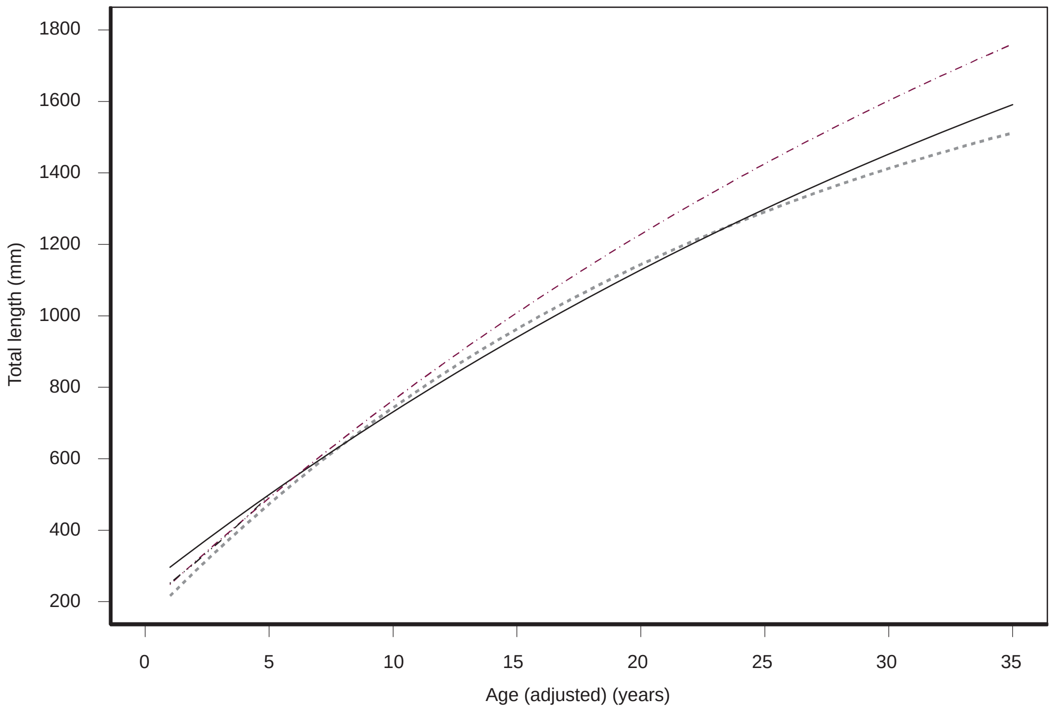

Figure 4(a): VB curves for a range of parameter values. These were for IWLS fit (dashed line), MLPLB fit (solid line), and MLP fit (dash-dot line), MLPLB fit of the VBA model (dash-dot-dot-dot line) (see Figure 4b).

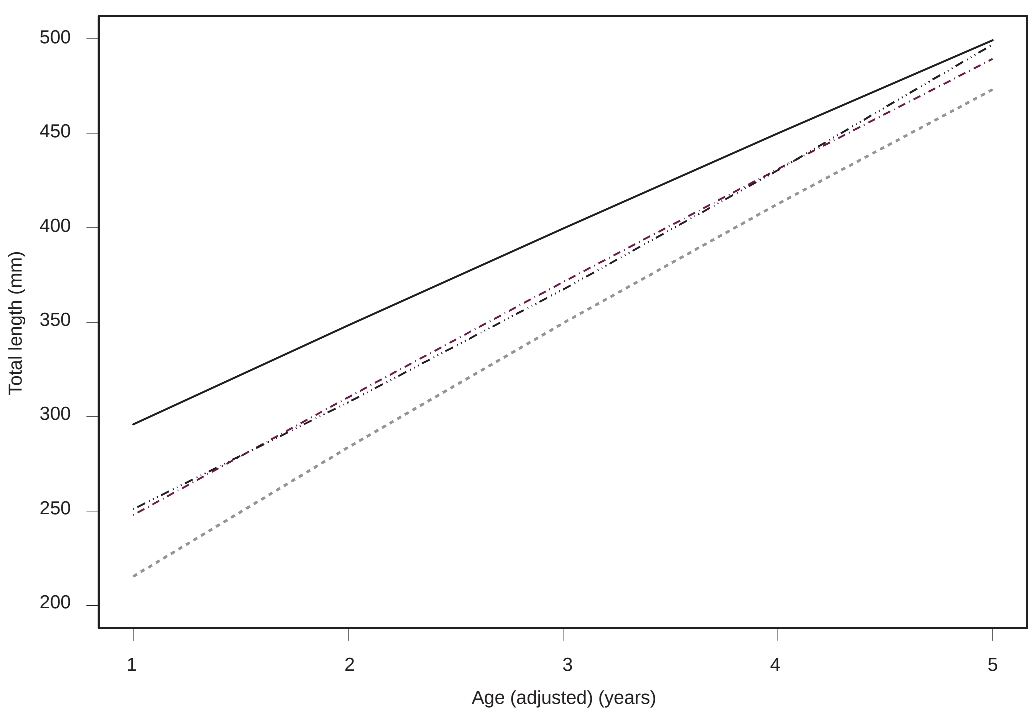

Figure 4(b): VB curves for a range of parameter values for reduced length and age ranges. IWLS fit (dashed line), MLPLB fit (solid line), and MLP fit (dash-dot line), MLPLB fit of the VBA model (dash-dot-dot-dot line).

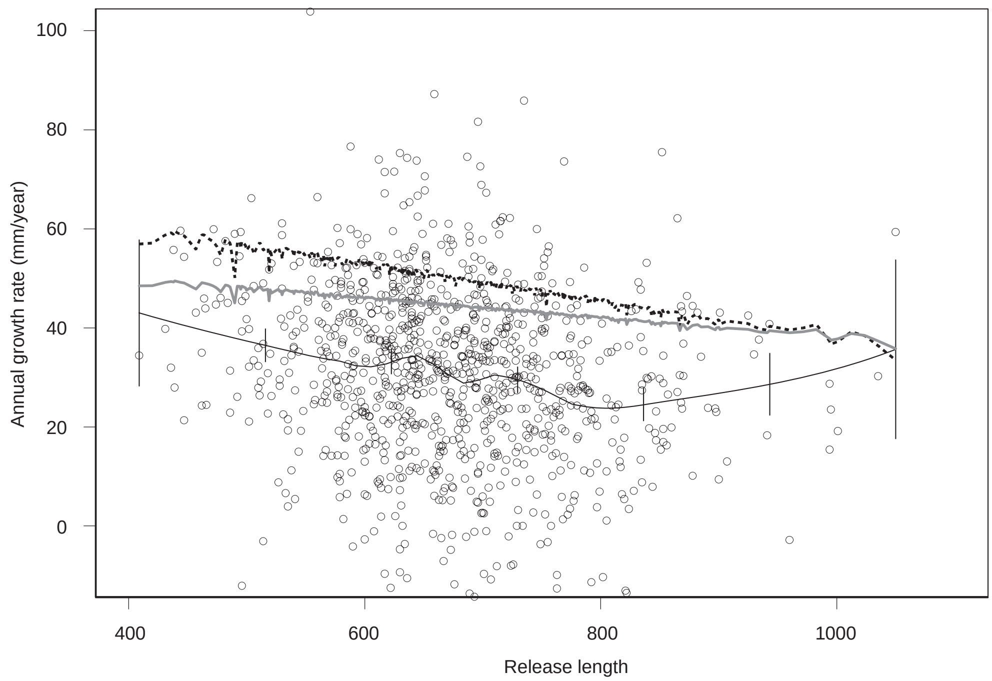

Figure 5: Annual growth rates, R, versus length-at-release showing smoothed predictions obtained from equation (7) and VB parameters estimated using length-at-age data combined with IWLS (dashed black line) and MLPLB (solid grey line) and loess curve (solid black line) fitted to the observed values of R. Bars on the loess curve represent 99% confidence limits.

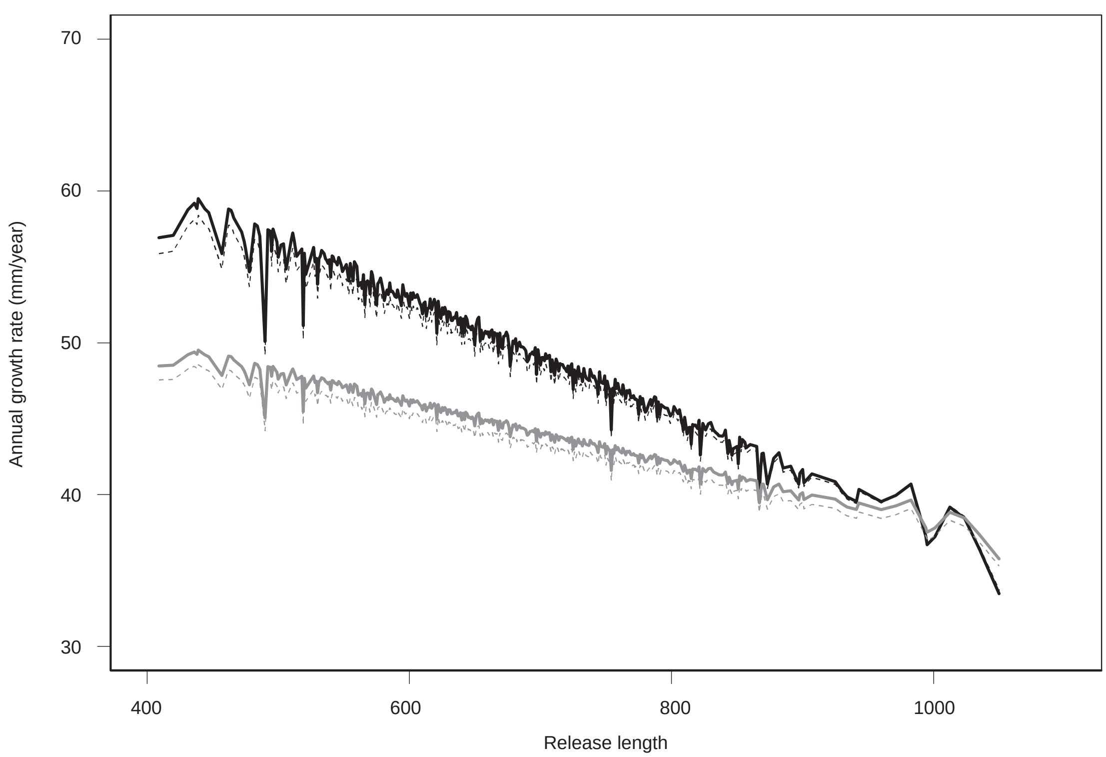

Figure 6: Annual growth rates, R, versus length-at-release showing smoothed predictions obtained from equation (7) with VB parameters estimated using length-at-age data combined with IWLS (solid black line) and MLPLB (solid grey line) and corresponding bias-corrected predictions (dashed lines) obtained by combining equations (7) and (8).

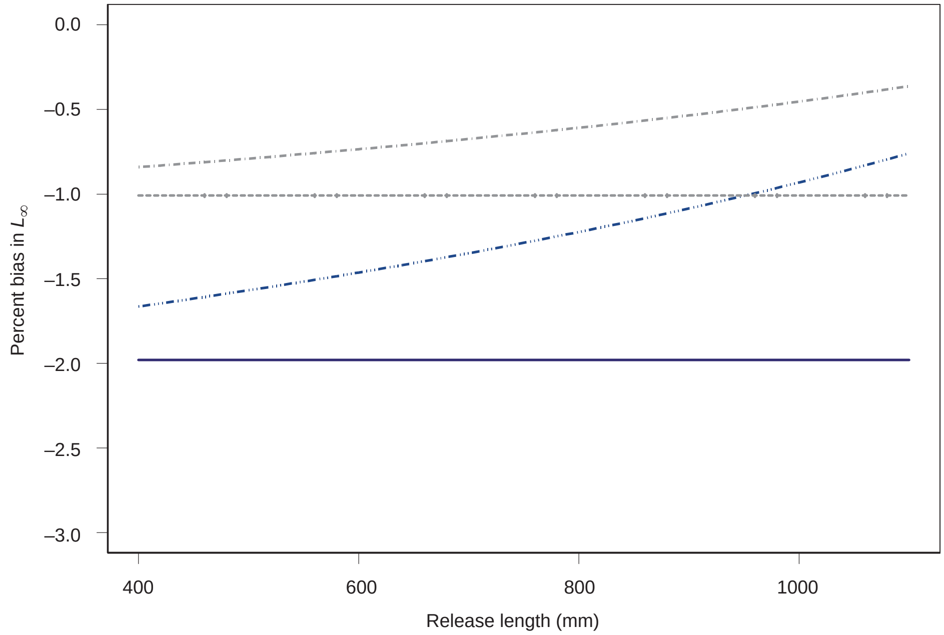

Figure 7: Bias in L_∞ due to non-zero expected error expressed as a percentage of the asymptote parameter versus length-at-release assuming: (i) a uniform distribution for random individual-fish deviations from the population average asymptote and mortality rate twice the VB rate parameter (dash-dot line), (ii) as for (i) except mortality rate equal to the VB rate parameter (dashed line), (iii) distribution-free random individual-fish deviations with skew of zero and with mortality rate twice the VB rate parameter (dash-dot-dot-dot line), and (iv) as for (iii), except mortality rate equal to the VB rate parameter (solid line).

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о: (i) равномерном распределении присущих особям случайных отклонений от средней асимптоты популяции и коэффициенте смертности, в два раза превышающем этот параметр VB (штрихпунктирная линия), (ii) как для (i), за исключением того, что коэффициент смертности равен коэффициенту в параметрах VB (пунктирная линия), (iii) непараметрических случайных отклонениях, присущих особям, с нулевым смещением и с коэффициентом смертности, в два раза превышающим этот параметр VB (линия из пунктира с тремя точками), и (iv) как для (iii), за исключением того, что коэффициент смертности равен коэффициенту в параметрах VB (сплошная линия).

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APPENDIX 1

SPECIFICATION OF THE LIKELIHOOD FOR THE AGE–LENGTH SAMPLE UNDER RESPONSE-STRATIFIED SAMPLING ACCOUNTING FOR LENGTH-DEPENDENT FISHING SELECTIVITY

The following theory is an expansion of that given by Jewell (1985) for response-stratified sampling for regression modelling to account for length-dependent fishing selectivity.

The probability density function (PDF) of length conditional on age, considering the length-bin sample as a response-stratified (RS) sample obtained by r independent sampling processes (i.e. one for each bin) in contrast to the VP sampling protocol, described in the introduction, which has one sampling process only, is given by

$$\begin{aligned} f_{RS}\left(L^{(LB)}=l \,\middle|\, A^{(LB)}=a\right) &= \sum_{j=1}^{r} Prob\left(L^{(LB)}=l,\ l \in B_j \,\middle|\, A^{(LB)}=a\right) \\ &= \sum_{j=1}^{r} s_j b_j \end{aligned} \quad \text{(A1)}$$

where

$(L^{(LB)}, A^{(LB)})$ is the set of random variables from the LB sample for length and age respectively (for the remainder for probabilities $A^{()} = a$ will be abbreviated to $A^{()}$ and $L^{()} = l$ abbreviated to $L^{()}$), $s_j = Prob(L^{(LB)} \mid L^{(LB)} \in B_j, A^{(LB)})$, and $b_j = Prob(L^{(LB)} \in B_j \mid A^{(LB)})$. Specifying the density of length conditional on age for the wild population as $f(L^{(Pop)} = l \mid A^{(Pop)})$, then

$$s_j = \frac{f\left(L^{(Pop)}=l \,\middle|\, A^{(Pop)}\right) I_{\left[K_{j-1},K_j\right)}\left(L^{(Pop)}=l\right)}{\int_{K_{j-1}}^{K_j} f\left(L^{(Pop)}=l \,\middle|\, A^{(Pop)}\right) dl} \quad \text{(A2)}$$

where $I_{\left[K_{j-1},K_j\right)}(L=l)$ is an indicator function given by

$$\begin{aligned} I_{\left[K_{j-1},K_j\right)}(L=l) &= 1\ ;\ K_{j-1} < l \le K_j \\ &= 0\ ;\ otherwise \end{aligned}$$

and

$$b_j = \frac{Prob\left(A^{(LB)} \,\middle|\, L^{(LB)} \in B_j\right) Prob\left(L^{(LB)} \in B_j\right)}{Prob\left(A^{(LB)}\right)}. \quad \text{(A3)}$$

Component s_j, given by equation (A2), is easily determined from the theoretical distribution of length given age in the wild population as specified by equation (2). Component b_j is more difficult to specify, so each term in equation (A3) is now specified in terms of known quantities and quantities to be estimated. First note that

$$Prob\left(L^{(LB)} \in B_j\right) = \frac{n_j}{n},\ \sum_{j=1}^{r} n_j = n,$$

where the n_j are assumed to be fixed and therefore the proportions n_j/n are also fixed.

The other term in the numerator of equation (A3), in the absence of age-dependent fishing selectivity, is given by

$$Prob(A^{(LB)} \mid L^{(LB)} \in B_j) = Prob(A^{(Pop)} \mid L^{(Pop)} \in B_j)$$

and further

$$Prob\left(A^{(Pop)} \,\middle|\, L^{(Pop)} \in B_j\right) = \frac{Prob\left(L^{(Pop)} \in B_j \,\middle|\, A^{(Pop)}\right) Prob\left(A^{(Pop)}\right)}{Prob\left(L^{(Pop)} \in B_j\right)}. \quad \text{(A4)}$$

The denominator of equation (A4) is given by

$$Prob\left(L^{(Pop)} \in B_j\right) = \frac{1}{C'} \frac{Prob\left(L^{(LF)} \in B_j\right)}{P\left(K'_j\right)} = \frac{1}{C'} \frac{\gamma_j}{P\left(K'_j\right)}$$

where $\gamma_j = Prob\left(L^{(LF)} \in B_j\right) = \frac{E\left(N_j|N\right)}{N}$ and $C' = \sum_{j=1}^{r} \frac{\gamma_j}{P\left(K'_j\right)}$ (i.e. scaling the expected value of the LF sample probability by the selectivity function). The first term in the numerator of equation (A4) is given by

$$Prob\left(L^{(Pop)} \in B_j \middle| A^{(Pop)}\right) = \int_{K_{j-1}}^{K_j} f\left(L^{(Pop)} = l \middle| A^{(Pop)}\right) dl$$

so combining terms gives

$$b_j = \frac{1}{C} \frac{n_j}{n} \frac{P\left(K'_j\right)}{\gamma_j} \int_{K_{j-1}}^{K_j} f\left(L^{(Pop)} = l \middle| A^{(Pop)}\right) dl \qquad \text{(A5)}$$

where $C = \sum_{j=1}^{r} \frac{n_j}{n} \frac{P\left(K'_j\right)}{\gamma_j} \int_{K_{j-1}}^{K_j} f\left(L^{(Pop)} = l \middle| A^{(Pop)}\right) dl$

after noting that both the terms C' and $Prob(A^{(Pop)})/Prob(A^{(LB)})$ drop out of equation (A5) due to the scaling by C (this is also the case for n which is removed below).

Therefore, after replacing the parameters γ_j by their sufficient statistics, N_j/N; $j = 1,\dots,r$, in equation (A5) gives

$$b_j = \frac{n_j P\left(K'_j\right)}{N_j} \frac{\int_{K_{j-1}}^{K_j} f\left(L^{(Pop)} = l \middle| A^{(Pop)}\right) dl}{\sum_{j=1}^{r} \frac{n_j P\left(K'_j\right)}{N_j} \int_{K_{j-1}}^{K_j} f\left(L^{(Pop)} = l \middle| A^{(Pop)}\right) dl}.$$

Earlier, the definition $f_{RS}\left(L^{(LB)} = l|A\right) = \sum_{j=1}^{r} s_j b_j$ was given so that combining the s and b terms and carrying out the summation gives

$$f_{RS}\left(L^{(LB)} = l|A\right) = \sum_{j=1}^{r} \frac{n_j P\left(K'_j\right)}{N_j} f\left(L^{(Pop)} = l|A\right) I_{\left[K_{j-1}, K_j\right)}(l) \left[\sum_{j=1}^{r} \frac{n_j P\left(K'_j\right)}{N_j} \int_{K_{j-1}}^{K_j} f\left(L^{(Pop)} = l|A\right) dl\right]^{-1}. \qquad \text{(A6)}$$

Since it was specified earlier that $p_j^* = n_j P\left(K'_j\right)/N_j$, then assuming $f(L^{(Pop)} = l \mid A)$ is the normal/constant CV density function and conditioning on the N_j, the negative log-likelihood obtained from equation (A6) for length and age sampled under length-dependent fishing selectivity and length-bin subsampling is exactly the same as that for VP sampling derived from $f_{VP}(L^{(LB)} = l \mid A)$ and given by equation (5). Note that since likelihoods condition on both L and A, the indicator function $I_{\left[K_{j-1}, K_j\right)}(l)$ is known *a posteria*, so that the first summation in equation (A6) combined with the indicator function values corresponds in terms of the log-likelihood to the log of the individual bin-specific probabilities (without summation) in equation (4). It was assumed above that the n_j are fixed before sampling takes place and are achieved in the sampling process for all length bins, but in the description of the sampling protocol used for the HIMI fisheries, the nominal fixed sample size was not achieved in bins located in the tails of the length distribution (i.e. less than 400 mm or greater than 1 000 mm). For these length bins where n_j is variable, the same conditioning argument can be used for the likelihood as was done for the length-frequency sample proportions by conditioning on the sufficient statistics for the proportions for these bins given by their realised sample values n_j/n.

APPENDIX 2

INVESTIGATION OF BIAS IN PREDICTIONS OF MARK–RECAPTURE GROWTH USING THE FABENS MODEL AND A RANDOM-ASYMPTOTE VB LENGTH-AT-AGE MODEL

In order to investigate more explicitly the expectation $E(e_c \mid L_r)$ in equations (6) and (7), consider a random-effect version of the VB model (equation 2) whereby the asymptote parameter L_∞ varies across fish according to a uniform distribution between lower and upper limits of $L_\infty - c$ and $L_\infty + c$ respectively, as in Francis (1988). Therefore a random fish has a VB asymptote of $L_\infty + V$ where V is distributed as $U(-c, c)$ and the expected value and skew of the distribution for V are both zero. Note that with only one observation per fish, it is not possible to estimate the random effect $V = v$ simultaneously with the error term ε in equation (2) in the following random effects model of length-at-release

$$L_r = (L_\infty + v)\,(1 - \exp\{-\kappa(A - t_0)\}). \qquad \text{(A7)}$$

Using equation (A7) to redefine equation (6) gives

$$L_c = (L_\infty + v)\left[1 - \left(1 - \frac{L_r}{(L_\infty + v)}\right)\exp\{-\kappa D\}\right] + e'_c$$

which can be re-expressed as

$$L_c = L_\infty\left[1 - \left(1 - \frac{L_r}{L_\infty}\right)\exp\{-\kappa D\}\right] + v\left(1 - \exp\{-\kappa D\}\right) + e'_c\,. \qquad \text{(A8)}$$

It can reasonably be assumed that $E(e'_c \mid L_r) \equiv 0$ for all values of L_r. The expected value of L_c conditional on L_r and D is now given, after re-expressing equation (A8), by

$$E(L_c \mid L_r, D) = [L_\infty + E(v \mid L_r)](1 - \exp\{-\kappa D\}) + L_r \exp\{-\kappa D\}.$$

From the above, and from equation (6), then $E(e_c \mid L_r) = E(v \mid L_r)(1 - \exp\{-\kappa D\})$. The distribution of $V = v$ conditional on L_r can be expressed using Bayes theorem as

$$f(v \mid L_r) = \frac{f_L(L_r \mid v)\, f_v(v)}{f_L(L_r)}\,.$$

The distribution of L_r conditional on v, given (equation A7), depends on the unobserved distribution of age-at-first-capture, A. If it is assumed that A has an exponential distribution given by

$$f_A(A) = \kappa_m \exp\{-\kappa_m A\}$$

then the distribution of $f_L(L_r \mid v)$ is proportional to

$$\frac{1}{L_\infty + v - L_r}\left(\frac{L_\infty + v - L_r}{L_\infty + v}\right)^{\frac{\kappa_m}{\kappa}}.$$

Given that the unconditional distribution of v is expressed by $f_V(v) = (2c)^{-1}$, then combining these density functions and ignoring constants gives

$$f(v \mid L_r) = C^{-1}\frac{1}{L_\infty + v}\left(\frac{L_\infty + v - L_r}{L_\infty + v}\right)^{\frac{\kappa_m}{\kappa} - 1}$$

where

$$C = \int_{c'}^{c} \frac{1}{L_\infty + v}\left(\frac{L_\infty + v - L_r}{L_\infty + v}\right)^{\frac{\kappa_m}{\kappa} - 1} dv$$

and where

$$c' = -c \quad ; L_r < L_\infty - c$$
$$= L_r - L_\infty \; ; L_r \geq L_\infty - c.$$

If it is assumed that $\kappa_m \equiv 2\kappa$ then

$$E(v|L_r, L_r < L_\infty - c) = \int_{-c}^{c} vf(v|L_r)\,dv$$
$$= \left[1 - \frac{L_\infty + L_r}{2c}\ln\left(\frac{L_\infty + c}{L_\infty - c}\right) + \frac{L_\infty L_r}{(L_\infty + c)(L_\infty - c)}\right]\left[\frac{1}{2c}\ln\left(\frac{L_\infty + c}{L_\infty - c}\right) - \frac{L_r}{(L_\infty + c)(L_\infty - c)}\right]^{-1} \quad \text{(A9)}$$

and

$$E(v|L_r, L_r \geq L_\infty - c) = \int_{L_r - L_\infty}^{c} vf(v|L_r)\,dv$$
$$= -\left[(L_r + L_\infty)\ln\left(\frac{L_\infty + c}{L_r}\right) + \{L_r - (L_\infty + c)\}\left(1 + \frac{L_\infty}{L_\infty + c}\right)\right]\left[\ln\left(\frac{L_\infty + c}{L_r}\right) - \frac{L_r - (L_\infty + c)}{L_\infty + c}\right]^{-1}.$$

Note that the lower limit in the above integral for the case where $L_r \geq L_\infty - c$ is $L_r - L_\infty$, because for this range of L_r the value of v cannot be below $L_r - L_\infty$. Note also that, given $L_r \leq L_\infty$, as c approaches zero then $E(v \mid L_r)$ also approaches zero. This is as expected, since when c ≡ 0 then equation (A7) is entirely deterministic and the Fabens model is simply an algebraic re-expression of the VB model. If it is assumed, as in Francis (1988), that $\kappa_m \equiv \kappa$, then

$$E(v|L_r, L_r < L_\infty - c) = \int_{-c}^{c} vf(v|L_r)\,dv$$
$$= \left[\frac{1}{2c}\ln\left(\frac{L_\infty + c}{L_\infty - c}\right)\right]^{-1} - L_\infty \quad \text{(A10)}$$

and

$$E(v|L_r, L_r \geq L_\infty - c) = \int_{L_r - L_\infty}^{c} vf(v|L_r)\,dv$$
$$= -(L_r - L_\infty - c)\left[\ln\left(\frac{L_\infty + c}{L_r}\right)\right]^{-1} - L_\infty.$$

Note that the above formulae derived assuming $\kappa_m \equiv \kappa$ are different from those obtained by Francis (1988) using the same assumptions.

It is unrealistic to assume a uniform distribution for V, so if it is assumed less stringently that V has an expected value of zero, variance σ_v^2, and 3rd (central) moment of zero, then V could be distributed as a normal. In that case, relating equations (2) and (A7) shows that $\varepsilon = v/L_\infty$ so that $\sigma_v^2 = L_\infty^2\sigma^2$. Assuming that V is normally distributed does not allow an explicit formula for $E(v \mid L_r)$ to be specified as in the case above of a uniform distribution; however, for values of L_r that allow integration over the complete, or close to complete (i.e. $L_r \leq L_\infty - 3\sigma_v$) range of V, then $E(v \mid L_r)$ can be expressed as the ratio of two expected values, so that

$$E(v|L_r, L_r < L_\infty - 3\sigma_v) = \frac{\int_{L_\infty - 3\sigma_v}^{\infty} vf(v|L_r)f(v)\,dv}{\int_{L_\infty - 3\sigma_v}^{\infty} f(v|L_r)f(v)\,dv}$$
$$\cong \frac{E\{vf(v|L_r)\}}{E\{f(v|L_r)\}}$$

and approximating $f(v|L_r) = \dfrac{L_\infty + v - L_r}{(L_\infty + v)^2}$ (i.e. assuming that $\kappa_m \equiv 2\kappa$ and noting that any constant terms cancel in the above ratio) by a second-order Taylor series approximation about $v \equiv 0$ gives

$$E\left(v \middle| L_r, L_r < L_\infty - 3\sigma_v\right) \cong \frac{2\sigma_v^2 f'_{v=0}\left(L_r \middle| v\right)}{f'_{v=0}\left(L_r \middle| v\right) + \frac{1}{2}\sigma_v^2 f''_{v=0}\left(L_r \middle| v\right)}$$

$$= -2\sigma^2\left(1 - 2\frac{L_r}{L_\infty}\right)\left(\frac{L_\infty - L_r}{L_\infty^2} + \sigma^2 \frac{L_\infty - 3L_r}{L_\infty^2}\right)^{-1} \quad \text{(A11)}$$

where $f'_{v=0}\left(L_r|v\right)$ and $f''_{v=0}\left(L_r|v\right)$ represent first and second derivatives respectively, with respect to v evaluated at $v = 0$. If alternatively it is assumed that $\kappa_m \equiv \kappa$, then the corresponding expression to equation (A11) is independent of L_r, since $f(v \mid L_r) = (L_\infty + v)^{-1}$ so that

$$E\left(v \middle| L_r, L_r < L_\infty - 3\sigma_v\right) \cong \frac{-2\sigma^2 L_\infty}{1+\sigma^2}. \quad \text{(A12)}$$

Wang and Thomas (1995) calculate the equivalent expression to $E(L_\infty + v \mid L_r)$ in their equation (7), but in applying the general expression for this expectation they use the assumption that age-at-capture has a uniform distribution, which is unrealistic for our case of a long-lived species (see also Wang, 1998). Also, they do not account, as has been done above, for the fact that the integration range over which this expectation is evaluated depends on the value of length-at-release. Wang's (1998) estimated bias adjustment for the Fabens model is distribution-free and only assumes a linear relationship between $E(v \mid L_r) + L_\infty$ and L_r, but this relationship is not exactly linear for the entire range of L_r in any of the relevant formulae given above. However, the results section shows (see Figure 7) that for a range in L_r that does not approach L_∞, Wang's linear relationship is a qood approximation. Even so, Wang's bias adjustment must be estimated simultaneously with the VB parameters (L_∞, κ) from the mark–recapture data, so its use is not appropriate when simply comparing the observed AGRs to those predicted using the length-at-age based estimates of the VB parameters.