Ministry for Primary Industries
Manatū Ahu Matua

Development of natural mortality priors for ling (*Geypterus blacodes*) stock assessments in New Zealand

New Zealand Fisheries Assessment Report 2017/55

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ISSN 1179-5352 (online)
ISBN 978-1-77665-698-1 (online)

October 2017

New Zealand Government

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EXECUTIVE SUMMARY

Edwards, C. T. T. (2017) Development of natural mortality priors for ling (*Geypterus blacodes*) stock assessments in New Zealand.

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The natural mortality parameter is an important determinant of productivity within age and length-structured stock assessment models. However it is often difficult to estimate and is instead usually assumed to be a fixed value, or provided with a strongly informative prior. For ling stock assessments in New Zealand, estimates of natural mortality (M) often depend on the data-weighting assumptions within the model, indicating that the structural assumptions of the model are probably incorrect.

Building on earlier work, the purpose of this study is to provide updated informative prior values for M for each of the currently recognised ling stocks. These recommendations are based on life-history theory, although other approaches were also considered. To provide the necessary growth and maturity parameter estimates, all available life-history data were re-analysed. The estimated M values were sex-specific and notably different from previous recommendations.

Project code: DEE201002LINC

1. Introduction

A review by Horn (2005) of the available life-history data for ling (*Geypterus blacodes*) in New Zealand waters revealed marked spatial differences, which led to the classification of four primary stocks: the Chatham Rise (LIN 3&4-CR); Sub-Antarctic (LIN 5&6-SA); West Coast South Island (LIN 7-WC); and, Cook Strait (LIN 7-CK). These support the majority of fishing, with lesser fisheries also present off the East Coast North Island (LIN 2) and on the Bounty Plateau (LIN 6B). The stock structure then proposed has persisted in subsequent assessments (e.g. Horn et al., 2013).

The underlying biological differences between stocks have prompted investigation into whether the natural mortality rates may also be different. Natural mortality is an important parameter within cohort-based stock assessment models of the type routinely used for ling. It is a measure of both population productivity and individual longevity, and can be estimated within the assessment model if the correct data are available, and our statistical assumptions are met (Lee et al., 2011; Francis, 2012). These data consist of reliable catch and abundance data, from which productivity can be estimated, and an age frequency distribution. However, it is often the case that stock assessment data give conflicting signals, and in this case the age-frequency profile can suggest a different natural mortality than the abundance trend (e.g. Dunn et al., 2013). Preference is usually given to fitting the abundance data, according to recommendations by Francis (2011). However, it would still be preferable to re-design the model so that it is better able to match the data, directly solving this vexatious issue.

One possible reason for conflicting signals in the data is a structural difference between the fishery processes that generate the observations and the model being used to represent them. In the context of ling, a major structural uncertainty is the definition of stock boundaries. If attempts to model the data fail, then this would be an obvious feature of the modelling that could be re-examined.

The problem of stock definition provides context for the primary purpose of the work presented here, which attempts to propose or estimate the natural mortality directly for each stock. This estimate could be used as an informative prior in the stock assessment. Ling assessments have been found to be highly sensitive to the choice of prior, and therefore renewed investigation of appropriate prior values is warranted. There is a large amount of theoretical literature which predicts that natural mortality will be correlated with other life-history characteristics (e.g. Charnov, 1993), and this was the justification for a study by Horn (2008), who used differences in the maximum age to suggest that natural mortality may differ between stocks. Since then, a great deal more data have been collected, and the work presented here will address this problem using new data and methods.

1.1. Previous recommendations

Horn (2008) used a variety of age-based methods to predict M for the primary ling stocks. The best justified is based on a simple model of exponential death: $N_a/N_0 = p = \exp(-Ma)$, where p is the proportion of recruits that survive to age a. This gives the relationship in Equation 1. Typically p is taken to be a small value between 0.01 and 0.05 (Hewitt & Hoenig, 2005), and a is then the maximum observed age.

$$M = \frac{-\ln(p)}{a_{max}} \tag{1}$$

This simple relationship has been popularised by Quinn & Deriso (1999) and Hewitt & Hoenig (2005), but appeared much earlier (often being credited to Tanaka, 1960). Although a useful guide, it is really an estimate of the total mortality Z unless the population is unexploited. This is rarely the case, particularly since the large age sample sizes required to estimate a_{max} would generally only be available in well developed fisheries. Attempting to take this into account by using observed values of a_{max} and estimates of the fishing mortality F from recent stock assessments (with $Z = M + F$), Horn (2008) used Equation 1 to propose the recommendations in Table 1. Notably M is thought to be higher in the Cook Strait and on the West Coast South Island, due to the absence of older age classes in these areas.

Table 1: Prior natural mortality estimates recommended by Horn (2008).

Stock	Notation	Recommended M
West Coast South Island	LIN 7-WC	0.23
Cook Strait	LIN 7-CK	0.25
Chatham Rise	LIN 3&4-CR	0.13
Sub-Antarctic	LIN 5&6-SA	0.19
East Coast North Island	LIN 2-EC	-
Bounty Plateau	LIN 6B-BY	-

1.2. Review of life-history correlates

Correlations between M and other life-history characteristics can be broadly defined as theoretical and empirical, with some overlap since empirical relationships across species have often been used to refine or support theoretical propositions. Numerous relationships exist, and have been described and reviewed exhaustively by Kenchington (2014). The scope of the current work to a large extent conforms to the recommendations made therein. The required notation is listed in Table 2.

1.2.1. Maximum age

The relationship between M and a_{max} described in Equation 1, when used with $p = 0.01$, gives $M \approx 4.6/a_{max}$ (a formula first applied by Sekharan, 1975). Bayliff (1967) investigated the same relationship, but estimated the regression coefficient from empirical data. This idea was further developed empirically by Hoenig (1983) who proposed that $M \approx 4.3/a_{max}$. There is therefore some consistency between theoretical and empirically based relationships between M and a_{max}, which may have furthered their widespread use.

The use of empirical relationships to derive M from a_{max} still receives popular attention, being most recently advocated by Then et al. (2015), who introduced a two parameter model:

$$M = \frac{\mu}{(a_{max})^{\beta}}$$

with both μ and β estimated from empirical data collected across a range of species.

However this empirical approach suffers from a number of drawbacks. Most obviously, as a regression-based estimator, it cannot be any more accurate than the prior values of M and a_{max} used in deriving the expressions. Given the difficulty of ageing fish accurately and extreme sampling error associated with collecting rare data (the oldest individual) from any resource with fluctuating year class strengths, these data are of doubtful quality. Gear selectivity can also bias observed a_{max} in either direction,

Table 2: Table of notational terms used to describe life-history relationships.

Notation	Description	Units
M	natural mortality	year^{-1}
a_{max}	maximum age	year
α	age at maturity	year
l	length	cm
l_α	length at maturity	cm
l_∞	asymptotic length	cm
k	growth coefficient	year^{-1}
t_0	age at length $l = 0$	year
p	survival to age a_{max}	proportion of recruits

further affecting the estimation procedure. When applying the estimated relationship to a given resource, these criticisms are still relevant, since the resource in question will have its own particular set of errors associated with the estimation of a_{max}, which will differ from those that underlie the generic relationship. Kenchington (2014) summarised this problem by stating that the effective sample size used to estimate a_{max} in the target stock, that is the sample size expected to yield a_{max} given a truly random sample across age classes and assuming the exponential death model to be correct, should match the sample size in prior studies underlying the regression. If this is not the case, which is almost certainly true, then the estimator will be biased.

1.2.2. Life-history theory

Life-history theoretic approaches to the estimation of M begin with a description of female fecundity as a function of age, growth and death. The age at maturity is then obtained as the age at which fecundity is maximised. From that point it is possible to derive a number of relationships between female M and other life history traits.

We begin with assumptions that length at age (l_a) follows the von Bertalanffy growth formula, that weight (w_a) is allometrically related to length, and that fecundity (F_a) is proportional to the weight:

$$l_a = l_\infty(1 - \exp(-k(a - t_0))) \tag{2}$$

$$w_a = c l_a^b \tag{3}$$

$$F_a = e^{-Ma} c[l_\infty(1 - \exp(-k(a - t_0)))]^b \tag{4}$$

The fecundity is equivalent to reproductive fitness of the individual. Taking the derivative of F_a with respect to age and setting it equal to zero we obtain the age at which fecundity is maximised. Assuming that evolution by natural selection has produced a life-history strategy that maximises individual fitness, this age is taken to be the age at maturity α (Roff, 1984; Mangel, 1996):

$$\alpha = \frac{1}{k} \ln\left(\frac{(bk + M)\exp(kt_0)}{M}\right) \tag{5}$$

If α occurred before maximum fecundity, then energy for growth would be diverted to egg production before reproductive capacity peaked, and if α occurred after the maximum, mortality would claim individuals at their reproductive peak before they reproduced. Substitution of α back into Equation 2 then gives the relationship (Beverton, 1992):

$$l_\alpha = l_\infty \left(\frac{b}{b + M/k} \right) \tag{6}$$

This model leads directly to two estimators of female natural mortality. First, Equation 5 can be solved for M to give the estimator (Rikhter & Efanov, 1976):

$$M = \frac{bk}{\exp(k(\alpha - t_0)) - 1} \tag{7}$$

Alternatively, Equation 6 can be solved to give the estimator (Roff, 1984):

$$M = bk \left(\frac{l_\infty}{l_\alpha} - 1 \right) \tag{8}$$

Jensen (1996) made the additional assumption that the age at maturity is equal to the age at which growth starts to slow (i.e. the point of maximum curvature or *inflexion* of the growth curve describing weight at age; Equation 3), because resources will be diverted towards egg production at that point in the life cycle. The inflexion point is obtained by taking the second derivative with respect to age, setting it equal to zero, and solving for age. This gives the relation (Jensen, 1985):

$$\alpha = \frac{\ln(b)}{k} + t_0 \tag{9}$$

Assuming that $t_0 = 0$ allows derivation of the dimensionless relationships in Equation 10, first by substituting Equation 9 into Equation 5 to give Equation 10a, and then substituting this result back into Equation 9 to give Equation 10b. Finally substitution of Equation 9 into Equation 2 gives the relationship in Equation 10c.

$$M\alpha = \ln(b) \frac{b}{b-1} \tag{10a}$$

$$\frac{M}{k} = \frac{b}{b-1} \tag{10b}$$

$$\frac{l_\alpha}{l_\infty} = 1 - \exp(-\ln(b)) \tag{10c}$$

The three relationships in Equation 10 are considered to be reasonably consistent across species (i.e. invariant; Charnov, 1993), or at least much less variable than their constituent parameters. As a result they have received a great deal of attention as potential estimators of M (e.g. Beverton, 1963; Roff, 1984; Ralston, 1987; Charnov & Berrigan, 1990; Hewitt et al., 2007), although it is notable that the justification is often based on empirical observation rather than the theoretical derivation given above.

Assuming isometric growth (i.e. $b = 3$), Jensen (1996) concluded that $M\alpha = 1.65$ and $M/k = 1.5$. Empirical data have generally validated this latter assertion (Charnov, 1993; Jensen, 1996; Charnov et al., 2013; Hamel, 2015) but a recent review by Prince et al. (2015) proposed the M/k ratio to have a much broader range than previously thought, of between 0.5 to 3.0, dependent on the life-history strategy of the species. Prince et al. (2015) examined the relationship between M/k and the life-history invariant l_α/l_∞; defined by the relationship in Equation 6. They showed that although based on theoretical considerations of growth and age at maturity, this relationship can nevertheless explain much of the observed empirical variation in M/k.

An inevitable property of these theoretical estimators of M (equations 7 and 8) concerns their dependency on estimated growth parameters. Most fish length-at-age data sets drawn from exploited populations contain insufficient data on large, old fish to provide confident estimates of asymptotic size. Such data allow reasonably precise estimation of the product of k and l_∞ but not of the value of either parameter alone. It is therefore particularly important to translate the accuracy of growth parameter estimates into valid uncertainty estimates for the derived M estimate.

1.2.3. Empirical correlation

Gislason et al. (2008) proposed that M should scale with the length of an individual l and the von Bertalanffy parameter l_∞, and subsequently explored this relationship with empirical data (Gislason et al., 2010). It was found to have good predictive abilities and was further validated in collaboration with Charnov et al. (2013), who proposed a simplified one-parameter form:

$$M = k\left(\frac{l}{l_\infty}\right)^{-1.5} \tag{11}$$

Furthermore, they suggested that the relationship would hold across species: by replacing l with l_α (the length at maturity) to give M_α. However the application of l_α data to predict M using this relationship has not been studied directly.

1.3. Relationships applied to ling

Both age- and length-based estimators were applied in this study. Due to the statistical inconsistencies associated with the age-based empirical estimators of Hoenig (1983) and Then et al. (2015), the theoretical relationship described in Equation 1 will be given preference here. This does not negate the need to seek a reliable estimate of a_{max} for ling, and given the dependency of this estimate on the sampling regime and exploitation history of ling stocks, these age-based estimates of M should be interpreted as an approximate guide only.

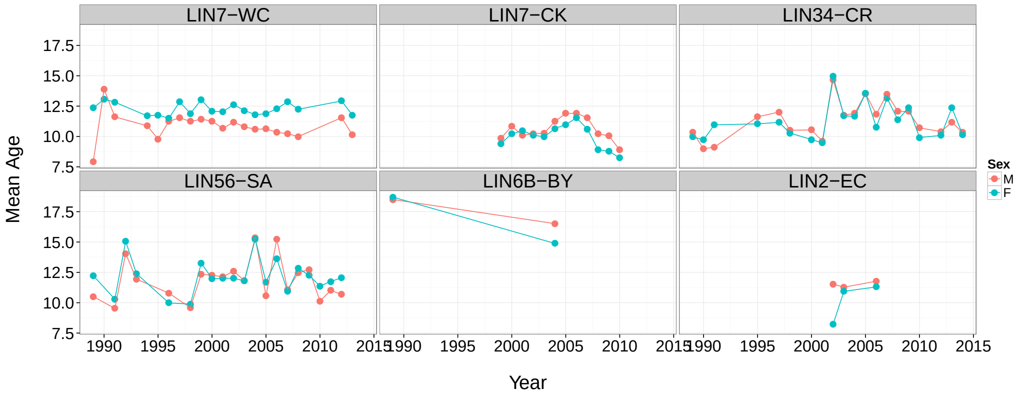
Two length-based approaches will also be used, namely the theoretical relationship specified in Equation 8 and the empirical relationship:

$$M = k\left(\frac{l_\alpha}{l_\infty}\right)^{-\beta} \tag{12}$$

which is derived from Equation 11. This latter estimator will need to be calibrated by fitting it as a regression to published estimates of the life-history parameters. This will allow estimation of β, which can in turn be used to generate M values for ling.

Both length-based approaches will require estimates of k, l_α and l_∞ for the ling stock in question. Equation 8 will additionally require an estimate of b, whereas Equation 12 will require an estimate of β from regression across multiple species. These formulations can be equated to the relationship $M = k\mu = kb/(b-1)$ proposed by Charnov (1993) and derived above as the invariant ratio in Equation 10b. Assuming $b = 3$, $\beta = 1$ and $l_\alpha/l_\infty = 2/3$, we obtain $\mu = 1.5$ for both length-based estimators, which is the expected value reported by Jensen (1996). However the observations of Prince et al. (2015) that μ might vary by species group, and the fact that Equation 12 has not yet been calibrated using data on the length at maturity, require us to depart from this proposal by using the estimated values $\hat{b}$ and $\hat{\beta}$.

(a) Mean age



(b) Maximum age

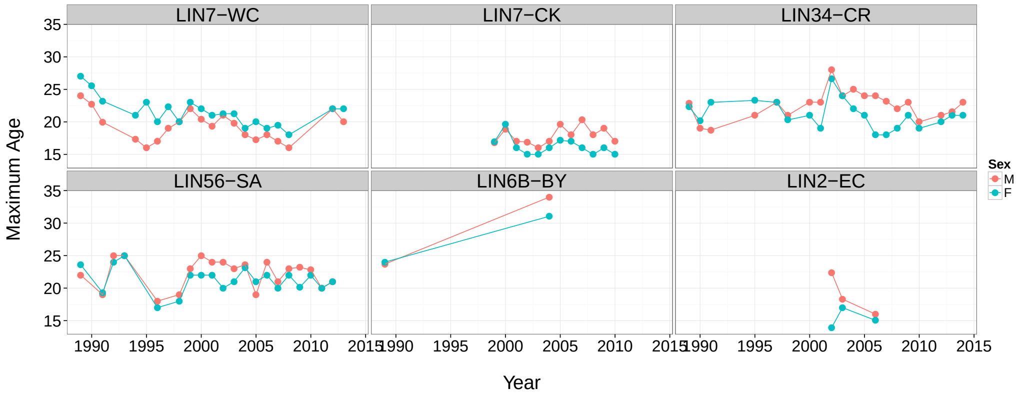
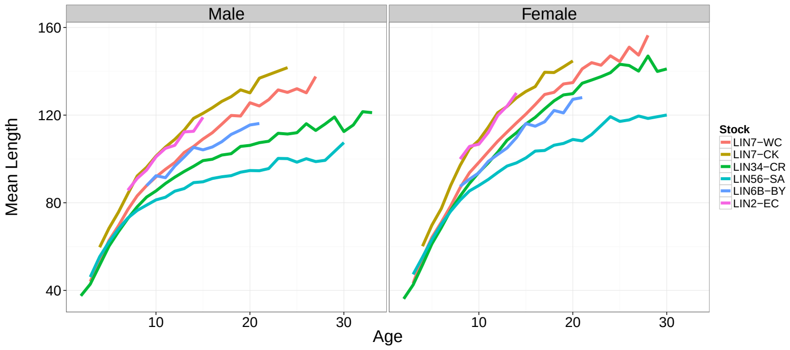


Figure 1: Mean age and maximum age over time for each stock and sex. Only estimates made from more than twenty data-records are shown.

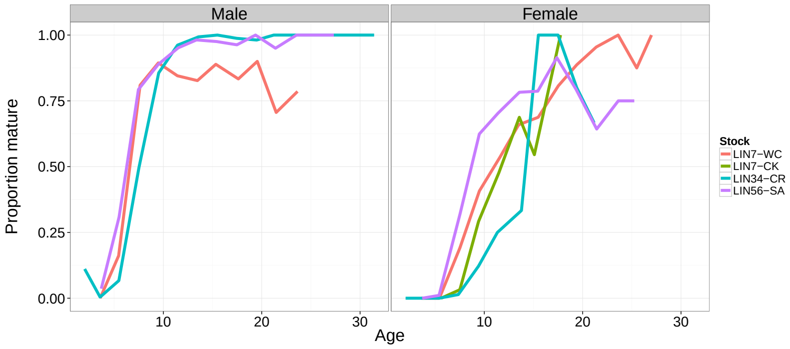
The estimator in Equation 8 has been given preference to that in Equation 7, despite their common origin. This is because age-based maturity data is typically more sparse than length-based maturity data. Nevertheless, estimating female M from Equation 8 allows us to predict the age at maturity (from Equation 5), which can be checked against independent empirical estimates. In this way the assumptions that underpin the derivation can be validated.

1.4. Study outline and objectives

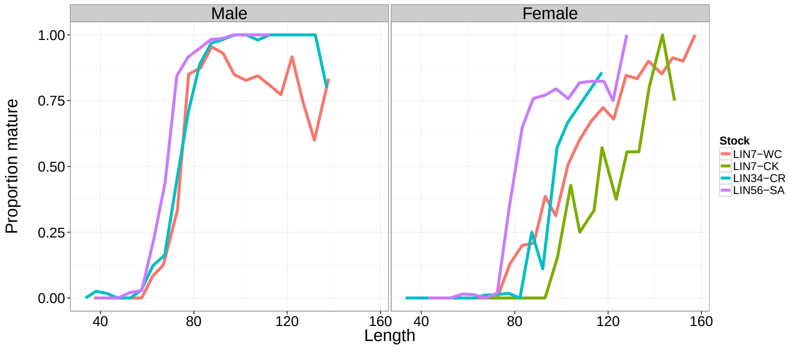
The objective of this study is to provide updated estimates of the natural mortality using known correlations between M and other life-history characteristics, specifically age, growth and maturity. This requires that two preliminary analyses be conducted before priors for M can be obtained. First, it is necessary to provide an updated analysis of all the life-history data collected from the various ling stocks in New Zealand. This is addressed in Section 2. Second, the empirical relationship proposed by Charnov et al. (2013) requires estimation of the additional β parameter (Equation 12) from data collected across a variety of species. This will be addressed in Section 3. Finally, the results from these two preceding analyses will be applied in Section 4 to generate priors for M for each ling sex and stock.



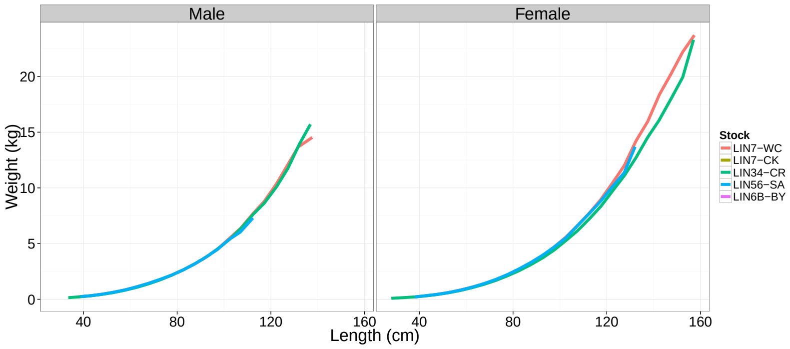
(a) Mean length at age



(b) Proportion mature at age



(c) Proportion mature at length



(d) Weight at length

Figure 2: Life-history relationships for each stock and sex, estimated as average values directly from the empirical data. Minimum samples sizes for each estimated value were $n > 9$ for parts (a) and (d); and $n > 3$ for parts (b) and (c).

2. Stock specific life-history data

Stock definitions currently applied to ling assessments were based on apparent spatial differences in life-history characteristics (Horn, 2005). These stock definitions are retained here, and life-history parameters are re-estimated for each stock and sex using the most recently available data.

2.1. Maximum age

The maximum age was estimated as the upper 95th percentile of the age distribution, referred to as a_{95}. This is a more robust estimate of the maximum age than the maximum age actually observed, since the quantile is less sensitive to sampling or ageing error, and arguably more representative of overall survival rates in the population. Estimation of the quantile is still sensitive to the sampling selectivity, and therefore a_{95} was estimated using only data from the fully selected age classes. A value for the threshold age at selectivity a_{sel} was obtained from the mode of the age frequency distribution. Modal values were estimated from data combined across years, and only age classes greater than the mode were included in the estimation of a_{max}.

Figure 1 shows the mean and maximum ages by stock, sex and year. Temporal changes in either the mean age or a_{95} would be expected in an exploited stock. However the data are very variable and there appear to be no clear trends, with the exception of the maximum age in LIN 7-WC, which decreases over time. The existence of a trend in this stock but not in LIN 3&4-CR or LIN 5&6-SA is consistent with the west coast population being demographically isolated from the Chatham Rise and sub-Antarctic regions. Notably also, the maximum age in LIN 7-CK is consistently lower than the other stocks. This could indicate the demographic isolation of the Cook Strait population, although an hypothesis of age-dependent migration could also provide an explanation. The exploitation of ling dates back to at least 1975, fourteen years before the earliest age data examined here, exemplifying the problems associated with this type of approach.

To identify an appropriate a_{max} for estimation of M, the maximum age (a_{95}) was estimated by stock and sex using data pooled across years (Figure 1). The same procedure was repeated with data combined across stocks and across sexes. Results are listed in Table 3. Values of a_{max} ranged from 17 to 35. The youngest ages were observed in LIN 7-CK and LIN 2-EC, although in the latter case the sample size was very small. The oldest ages were observed in LIN6-BY. The heavily sampled LIN 7-WC, LIN 3&4-CR and LIN 5&6-SA stocks had values of $a_{max} \approx 24$. Sex specific differences were obvious for observed maximum ages, but not for estimates of a_{max}, with the maximum estimated age for males being only 1–2 years older than females. Because of the way the a_{max} was calculated for the combined stocks, i.e. by first combining the data and then recalculating the quantile, the estimate is dominated by those stocks with the largest sample sizes. Thus $a_{max} \approx 24$ for all stocks combined, which is approximately equal to estimates from LIN 7-WC, LIN 3&4-CR and LIN 5&6-SA.

2.2. Growth and Maturity

Differences in the mean length at age between stocks are clearly apparent from the empirical data (Figure 2a). Growth in the Cook Strait is apparently fastest (LIN 7-CK), and similar to the West Coast South Island (LIN 7-WC). Growth in the sub-Antarctic is slowest (LIN56-SA), with the Chatham Rise intermediate between these two extremes (LIN 3&4-CR). Data from LIN 2-EC and LIN6-BY

Table 3: Observed maximum age and a_{max} from empirical age data, disaggregated by stock and sex. Observations are also made from the data combined by sex and stock. The value of M is an estimate based on Equation 1, given as a range assuming $p = (0.05, 0.15)$. The sample size refers to the number of samples used to estimate a_{max} (i.e. greater than a_{sel}).

Stock	Sex	Sample size	Observed max.	a_{max}	a_{sel}	M
LIN 7-WC	M	1353	36	26.0	10	0.12 – 0.19
	F	2358	38	24.0	12	0.16 – 0.25
	M+F	3711	38	25.0	12	0.15 – 0.23
LIN 7-CK	M	1998	42	19.1	10	0.21 – 0.33
	F	1713	29	18.0	8	0.19 – 0.30
	M+F	3711	42	19.0	8	0.17 – 0.27
LIN 3&4-CR	M	4758	45	25.0	8	0.11 – 0.18
	F	4841	46	24.0	8	0.12 – 0.19
	M+F	9599	46	24.0	8	0.12 – 0.19
LIN 5&6-SA	M	4144	41	24.0	7	0.11 – 0.18
	F	7007	39	23.0	8	0.13 – 0.20
	M+F	11151	41	23.0	8	0.13 – 0.20
LIN 6B-BY	M	187	40	34.7	13	0.09 – 0.14
	F	212	37	35.0	12	0.08 – 0.13
	M+F	399	40	35.0	12	0.08 – 0.13
LIN 2-EC	M	151	33	19.5	8	0.16 – 0.26
	F	126	19	16.8	8	0.22 – 0.34
	M+F	277	33	18.0	8	0.19 – 0.30
All stocks	M	12591	45	24.0	8	0.12 – 0.19
	F	16257	46	23.0	8	0.13 – 0.20
	M+F	28848	46	24.0	8	0.12 – 0.19

were few, but from what are available: growth in LIN 2-EC tracks that for LIN 7-CK, and growth in LIN 6B-BY appears closest to LIN 3&4-CR.

The von Bertalanffy growth curve (Equation 2) was fitted to the available length at age data. To obtain estimates of k and l_∞, the Francis (1988) parameterisation was used, which estimates three lengths $\{L_1, L_2, L_3\}$ at the corresponding ages $\{T_1, T_2, T_3\}$. This parameterisation was proposed to improve estimation performance by reducing the correlation between parameters. Input ages T_1 and T_3 were obtained from the 10% and 90% quantiles of the observed ages, with T_2 taken as the mean of the two. Values for $\{\hat{k}, \hat{l_\infty}, \hat{t_0}\}$ can be back-calculated from the parameter estimates (Francis, 1988). The estimation was conducted within a Bayesian hierarchical framework using the R-package **rstan** (Code Listing A1), which implemented an MCMC algorithm to yield posterior distributions of the von Bertalanffy growth parameters. For this, and all other Bayesian analyses, the default **rstan** MCMC sampling regime was used, resulting in four independent chains of 2000 samples, with the first half of each chain discarded. Parameter estimates are listed in Table A1.

The weight at length relationship (Equation 3) was also estimated within a Bayesian framework (Code Listing A2). The exponent term b is of primary interest for estimating natural mortality. Finally it was necessary to estimate the length at maturity l_α, which was taken to be the length at 50% maturity l_{50} (Jennings et al., 2001), and can be estimated as such from the fit of a logistic curve to the data

(Chen & Paloheimo, 1994). Visual inspection suggested that this ogive would not fit the maturity data well at larger sizes, particularly for LIN 7-WC, which appeared to have bi-phasic increase in the maturity at age (Figure 2b) and length (Figure 2c). Exploratory fits suggested that a bi-logistic function (Meyer, 1994) could provide a better description of the data, however, for this study we retained the more commonly applied logistic model (Code Listing A3):

$$m_l = \frac{1}{1+\exp(-(l-l_{50})/\delta))} \tag{13}$$

where δ determines the rate of increase in the ascending limb of the curve (more specifically, $1/\delta$ is the instantaneous rate of maturation).

Estimates for δ and l_{50} are given in Table A2. For all stocks the length at maturity is noticeably larger for females. Of the stocks with the most data, fish in LIN 5&6-SA appear to mature at the shortest length, and fish in LIN 7-WC mature at the longest length. The length at maturity in LIN 3&4-CR is very close to that for LIN 7-WC. There are relatively fewer data from LIN 7-CK, and from females only. However it appears that females in this stock have the largest length at maturity of all the stocks for which data have been collected.

Estimates of b for the weight-length relationship are given in Table A3. Females tended to have higher estimated b values, meaning that at any given length females are typically heavier.

3. Estimation of empirical correlation

Empirical relationships between M and other life-history correlates are usually based on large databases of this information, collated from global studies, the most well known being FISHBASE (www.fishbase.org). However many of the estimates of M contained in FISHBASE are themselves derived from life-history correlations. To circumvent this problem, Gislason et al. (2010) screened the literature for reliable estimates of M and specifically excluded those derived from invariant relationships of the type already described. The GISLASON database is consequently much smaller than FISHBASE (168 records compared to 7943), but of greater utility for estimating correlations between M and growth.

The GISLASON database was used by Charnov et al. (2013), but unfortunately does not contain estimates of l_α. The length at maturity was therefore imputed using the `TaxonomicImputer()` function from the R-package **fishnets**. This function first calculated a mean l_α per species or species group using the FISHBASE data, and then applied these mean values to the GISLASON database. The procedure worked well, and most of the predicted l_α values lay close to the value expected from the invariant in Equation 10c: $l_\alpha \approx l_\infty(2/3)$. However, because of missing data it reduced the size of the database to 138 records.

To parameterise the relationship proposed by Charnov et al. (2013), the log-linear relationship:

$$\ln(M) = \ln(k) + \beta \ln(l_\alpha/l_\infty) \tag{14}$$

was fitted using Bayesian methods. Standard regression approaches would treat k, l_α and l_∞ as measured without error. However, this is clearly not the case, and ignoring this uncertainty could bias the estimate of β. An alternative procedure, which better accommodates uncertainty in the explanatory variables, is an Error in Variables (EiV) model (Fuller, 1987). An EiV model explicitly accounts for estimation error associated with the predictors, in this case database values of k, l_α and

l_∞. This is achieved by including the estimated parameters k', l'_α and l'_∞, which are assumed to have prior log-normal (LN) distributions that are centred on the database values:

$$\begin{gathered}k' \sim LN(\ln(k), \sigma_k^2)\\ l'_\alpha \sim LN(\ln(l_\alpha), \sigma_{l_\alpha}^2)\\ l'_\infty \sim LN(\ln(l_\infty), \sigma_{l_\infty}^2)\end{gathered}$$

These are then used within the regression model:

$$\eta = \ln(k') + \beta \ln\left(l'_\alpha / l'_\infty\right)$$

where η is the expected value of $\ln(M)$. Assuming a log-normal error:

$$M \sim LN(\eta, \sigma^2)$$

We are primarily concerned with estimation of the parameter β, which relates M to the growth parameters, and σ^2, which describes the error around this predictive relationship. For these parameters uninformative uniform (U) and inverse-Gamma (IG) prior distributions were assumed:

$$\begin{gathered}\beta \sim U(-10, 10)\\ \sigma^2 \sim IG(0.0001, 0.0001)\end{gathered}$$

For implementation of the model it was necessary to supply input values for the estimation error variances. For the sake of parsimony, when fitting the EiV model it was assumed that the explanatory variables had all been measured with the same coefficient of variation, which for a log-normal distribution is equivalent to the assumption that $\sigma_k = \sigma_{l_\alpha} = \sigma_{l_\infty}$. A 20% coefficient of variation was assumed, giving $\sigma_{k,l_\alpha,l_\infty} = 0.2$. This choice of measurement error was arbitrary, but seemed reasonable. Exploratory model fits with alternative measurement error assumptions returned a consistent posterior median estimate of $\hat{\beta}$. However there was an inverse relationship with the residual error described by $\hat{\sigma}$, with higher measurement error being associated with lower residual error. This is how the model would be expected to behave, since it is designed to partition the uncertainty between these two error components. With a coefficient of variation greater than 30% the model did not converge, indicating that an assumed measurement error of this magnitude would have been too high to identify the proposed relationship.

The regression was conducted using the R-package **rstan** (Code Listing A4), yielding posterior distributions from which median and 95% credibility intervals were obtained, giving $\hat{\beta} = -0.98\ [-1.23, -0.74]$ and $\hat{\sigma} = 0.78\ [0.68, 0.90]$. Fit of the regression to observed values of $\ln(M)$ is illustrated in Figure 3.

4. Derivation of natural mortality priors

4.1. Maximum age

Assuming an age of selectivity a_{sel}, Equation 1 can be re-written with the denominator equal to the number of age classes that have elapsed between a_{sel} and a_{max} (i.e. $a_{max} - a_{sel}$). Furthermore, by using a_{95} as an estimate of a_{max} we are assuming that at least 5% of the selected population has survived to an older age, i.e. $p \geq 0.05$ (Equation 1). Estimates of M based on these assumptions are listed in Table 3 as a range, assuming $p = (0.05, 0.15)$.

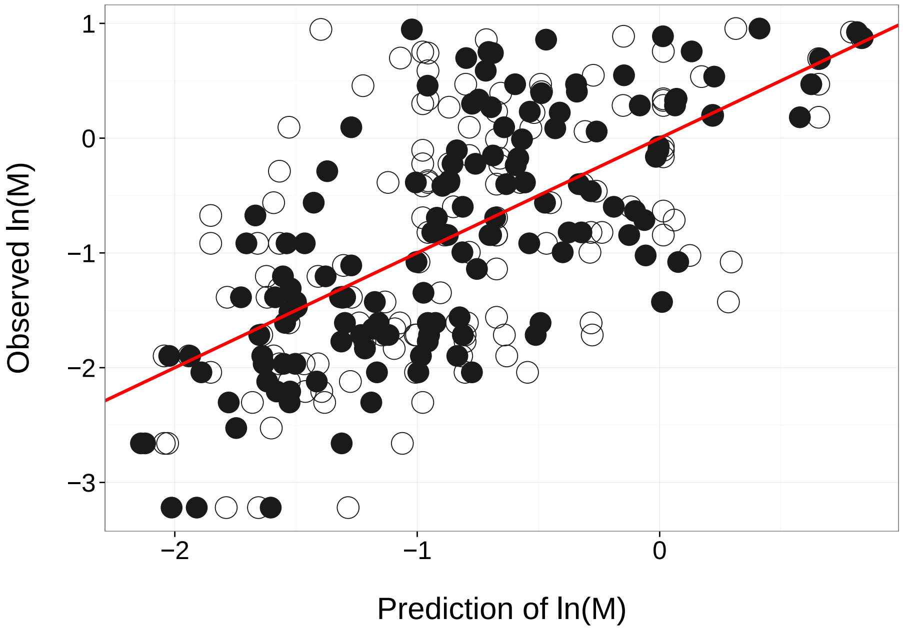


Figure 3: Observed values of $\ln(M)$ plotted against values predicted by the regression model in Equation 14. Values along the red line are equivalent. Two regressions are shown, assuming no measurement error (open circles) and with a coefficient of variation of 20% (filled circles). The difference demonstrates how uncertainty in the prediction is reduced when measurement error is assumed, since the difference between observed and predicted values is reduced.

4.2. Growth

Estimates of female M based on Equation 8 made use of the posterior distributions of b, k, l_α and l_∞ generated as described in Section 2.2. This gives the M estimates in Table 4 and Figure 5a. Typically, M is between 0.23 and 0.30 for males, but between 0.12 and 0.16 for females. There is therefore a noticeable difference between the sexes, with the LIN 7-WC stock appearing to have the greatest discrepancy. According to the life history theory described above, the estimated sex-based differences in M are due to the their different growth curves: females grow slower (to bigger sizes) and mature later (Figure 2 and Tables A1 and A2), and on this basis alone we would expect them to have lower natural mortality rates – because only if they do have lower natural mortality will their reproductive fitness be maximised. Caution should be exercised however, because of the uncertainty associated with estimating growth, particularly for an exploited population in which the larger individuals will be missing.

For LIN 7-CK, an estimate of M could only be obtained for females, because maturity data were only available for this sex. Taking the confidence intervals into account, estimates of M for females in LIN 7-WC, LIN 7-CK and LIN 3&4-CR are almost indistinguishable. Female M for LIN 5&6-SA appears to be slightly higher. For males, M in LIN 5&6-SA and LIN 3&4-CR are essentially the same, whereas the M in LIN 7-WC is significantly higher.

The life-history theory used to derive the estimator of M applied here also predicts the age at maturity as a function of growth and M (Equation 5). Estimates of the age at maturity $\alpha = a_{50}$ were therefore obtained from independent data, by fitting a logistic curve analogous to that in Equation 13 (Code Listing A3). Results are given in Table A4. This maturity estimate can be used to validate the assumptions that underlie the implemented relationship between M, growth and length at maturity

Table 4: Estimates of the natural mortality M based on either a theoretical relationship with growth and maturity (as described by Equation 8) or the empirical relationship described by Equation 12.

Stock	Sex	Estimate and 95% CI			
		Theoretical		Empirical	
LIN 7-WC	M	0.30	[0.26,0.35]	0.19	[0.05,0.64]
	F	0.15	[0.14,0.17]	0.13	[0.04,0.46]
	M+F	0.19	[0.18,0.21]	0.14	[0.04,0.41]
LIN 7-CK	M	-		-	
	F	0.12	[0.09,0.15]	0.14	[0.04,0.45]
	M+F	-		-	
LIN 3&4-CR	M	0.23	[0.22,0.24]	0.19	[0.06,0.60]
	F	0.13	[0.11,0.15]	0.12	[0.03,0.39]
	M+F	0.24	[0.23,0.25]	0.17	[0.05,0.57]
LIN 5&6-SA	M	0.23	[0.21,0.24]	0.23	[0.07,0.83]
	F	0.16	[0.14,0.17]	0.17	[0.05,0.55]
	M+F	0.22	[0.21,0.23]	0.21	[0.06,0.67]
All stocks	M	0.29	[0.28,0.30]	0.24	[0.08,0.73]
	F	0.14	[0.13,0.15]	0.15	[0.05,0.50]
	M+F	0.23	[0.22,0.24]	0.19	[0.07,0.64]

(Equation 8), because it is possible to predict the age at maturity using M and the growth parameters. These are compared to the empirical estimates of α in Figure 4. There is a reassuringly close match. Using a similar logic we can also plot the invariant relationships in Equation 10. Assuming $t_0 = 0$, it is possible to plot the relationship between our estimate of M and that predicted by each life history invariant (Figure 6). Of these, the relationship depicted in Figure 6a is most convincing, since it makes use of α, which is obtained from independent data. This result is again reassuring, since it provides further validation of the underlying theoretical model.

4.3. Empirical correlation

Application of an empirical correlation for predictive purposes is achieved using posterior prediction, whereby parameter values are sampled from their posterior distributions. This procedure generates posterior distributions for M, from which estimates can be extracted as median values. The error associated with these predictions reflects uncertainty in both the estimated parameters, via their posterior distributions, and the predictive relationship, via the σ parameter. The log-normal error described by σ reflects the empirically observed residual distribution of M values around the regression line (Figure 3). By including this error in the prediction we are assuming that the predictive model is not accurate. An alternative assumption would be that the model is accurate, and that the residual distribution is a result of poorly estimated M values in the GISLASON database. It is impossible to distinguish between these two hypotheses. Instead, a measurement error assumption can be applied to M, in the same way that it was applied to the explanatory variables. Assuming $\sigma_M = 0.5$, natural mortality values were therefore generated assuming:

$$\eta_p = \ln(k_p) + \beta_p \ln\left(l_{\alpha,p}/l_{\infty,p}\right)$$

$$M_p \sim LN(\eta_p, \sigma_p^2 - \sigma_M^2)$$

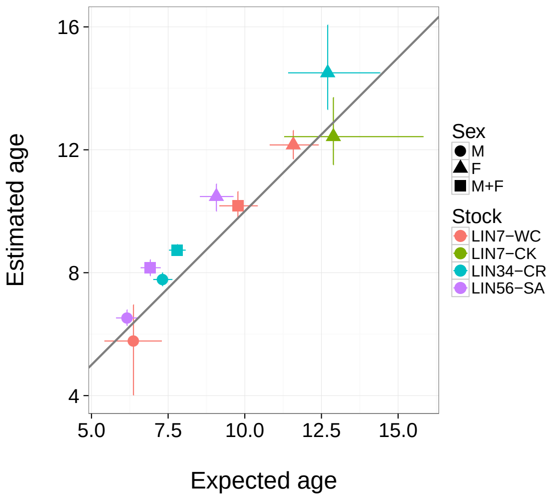


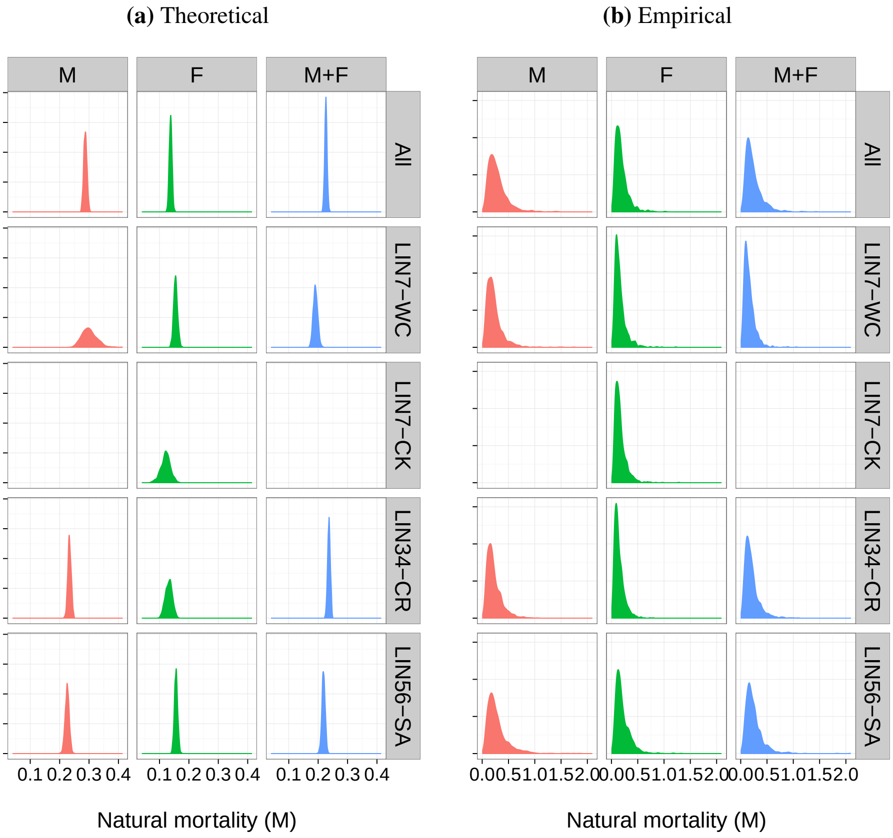
Figure 4: Expected age at maturity predicted by life-history theory (Equation 5) compared to independent estimates from the empirical data. The diagonal solid line represents equivalence.

where the p subscript refers to a sample from the posterior distribution of that parameter. The posterior distributions for k, l_α and l_∞ were obtained for each ling sex and stock as described in Section 2.2, whereas the distributions for β and σ were obtained from the regression in Section 3.

These results are listed in Table 4 and plotted in Figure 5b. The uncertainty associated with these estimates is noticeably much wider than for the estimates derived using a theoretical approach, as reflected in the wider credibility intervals. Again, the structure of the model and estimated growth and maturity parameters lead to a prediction that M is higher in males. This is most noticeable for LIN 5&6-SA, which has a predicted male M of 0.23. For both LIN 7-WC and LIN 3&4-CR male M is around 0.19 (there were no male maturity data collected from LIN 7-CK, meaning that a value of M could not be estimated for this stock). It is noticeable however, that whereas for females there is a close correpsondence between values of M generated by the theoretical and empirical approaches, this is not true for males. With the exception of LIN 5&6-SA, the male estimates of M are smaller using the empirical approach. Indeed, even the relative rates are different, with LIN 5&6-SA now having the highest value. For females, there is a clear correspondence between values produced using life-history theory and the empirical estimates. Consistent with the theoretical estimates, LIN 5&6-SA has the highest female M, of around 0.17. For the other stocks female M is around 0.14, with no clear distinction between them.

5. Conclusions and recommendations

From Table 4 it appears that estimates of female M from the theoretical and empirical models are consistent. Not only that, they are reasonably consistent across stocks, with LIN 5&6-SA being the highest and LIN 7-CK being the lowest. For LIN 3&4-CR, LIN 5&6-SA and "All stocks", these estimates also match those derived from the maximum age in Table 3. This is not true for LIN 7-WC and LIN 7-CK, in which the age based estimates are higher than both the theoretical and empirical length-based estimates, indicating that older females are not being observed in these areas. One reason for this may be the migration of larger females to other areas. In LIN 3&4-CR



(a) Theoretical

(b) Empirical

Figure 5: Posterior distributions of natural mortality from theoretical and empirical estimators.

and LIN 5&6-SA there is a close correpondence between theoretical, growth based estimates of M and those based on a_{max}, indicating that the natural mortality rates predicted by the rates of growth and maturation in these areas yields the anticipated maximum age. If those older individuals are not being observed (as in LIN 7-WC and LIN -7-CK) they might be moving elsewhere. The converse argument, that growth and maturity rates in LIN 7-WC and LIN 7-CK have been poorly estimated, may be true for LIN 7-CK (particularly for l_α – which is larger than for the other stocks), but is unlikely to explain the discrepancy for the heavily sampled LIN 7-WC.

In contrast, there appears to be very little correspondence between the estimators of male M. One of the most striking features of the length-based analyses is that male M is higher than female M, but to what extent is unclear. In contrast, this pattern is not observed in the age-based estimates (Table 3), which predict that male and female M are similar. In choosing an estimator for the prior, the age-based estimates are the least reliable, being susceptible to the sampling and assumed exploitation pattern, and unacknowledged patterns of migration (as discussed above). However the theoretical estimates do not appear to be justified either. Despite the model on which they are based being able to accurately predict the age at maturity (Figure 4), estimates of male M are simply too high, since they would not allow individuals to reach observed ages of 40+ years (Table 3). With regard to the empirical estimator, it was parameterised using estimates of M from both sexes in the GISLASON database (almost all the listed life-history data was for both sexes combined) and it is therefore impossible to determine the exact validity of this approach for predicting sex-specific natural moratlity rates. Indeed, this may explain why the empirical estimates exhibit a lower degree of sexual dichotomy.

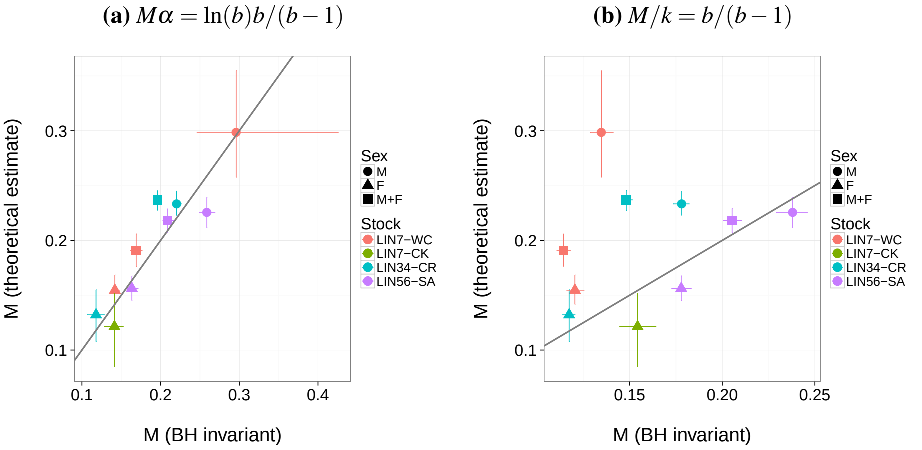


Figure 6: Relationship between theoretical estimates of M (Equation 8) and estimates of M obtained directly from the life-history invariant relationships proposed by Jensen (1996). Values of α, k and b where estimated for each ling sex and stock as described in the main text.

Because of the above reservations concerning realism of the predicted male M, these have been discarded. However the theoretical derivation of female M appears sound, and based on this justification they have been used to construct the recommended values for M listed in Table 5.

Table 5: Prior female natural mortality estimates recommended by the analyses presented in this report. There were insufficient data to provide a recommendation for LIN 2-EC or LIN 6B-BY. The approach failed to provide realistic values for males.

Stock	Notation	Recommended Female M
West Coast South Island	LIN 7-WC	0.15
Cook Strait	LIN 7-CK	0.12
Chatham Rise	LIN 3&4-CR	0.13
Sub-Antarctic	LIN 5&6-SA	0.16

Compared to those in Horn (2008) (Table 1), the values listed in Table 5 are notably similar for LIN 3&4-CR and LIN 5&6-SA, but different for LIN 7-WC and LIN 7-CK. In the current analysis, the relative differences between stocks is much less clear. The female M values suggest a LIN 7-WC/LIN 5&6-SA grouping with $M \approx 0.16$ and a LIN 7-CK/LIN 3&4-CR grouping with $M \approx 0.13$. However because the credibility intervals overlap, this discrepancy could be justifiably ignored, instead assuming a value of female $M \approx 0.14$ for all stocks.

Further work will be required to produce a natural moratlity estimates for males. This could include a more involved modelling approach, that shares data between stocks in order to better define the life history parameters on which M is based. Until then, it is recommended that stock assessments place a prior on female M only. To inform estimation of male M, it could be estimated relative to the female value, with an additional prior on this difference.

It is interesting to speculate how these updated recommendations, based on revised life-history parameter estimates, could be used to update the stock structure assumptions for ling. However further work would be needed to investigate whether these alternative structural changes would improve stability of the stocks assessments.

6. Acknowledgements

This work was funded by the Ministry for Primary Industries (Wellington, New Zealand), under project code DEE201002LINC. The author is grateful for analytical suggestions made by the working group, to Jim Roberts for discussion, and to Ian Doonan and Peter Horn (NIWA, Wellington, New Zealand) for thorough reviews of this report.

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Appendix: Results tables

Table A1: Estimated parameters for the von Bertalanffy growth curve (Equation 2 and Code Listing A1).

Stock	Sex	Parameter	Estimate and 95% CI	
LIN 7-WC	M	l_∞	141	[138.69,143.55]
		k	0.09	[0.09,0.1]
		t_0	-1.18	[-1.34,-1.03]
	F	l_∞	164.15	[161.71,166.7]
		k	0.08	[0.08,0.09]
		t_0	-0.75	[-0.87,-0.63]
	M+F	l_∞	160.24	[158.06,162.61]
		k	0.08	[0.08,0.08]
		t_0	-1.16	[-1.28,-1.06]
LIN 7-CK	M	l_∞	148.17	[145.18,151.44]
		k	0.1	[0.1,0.11]
		t_0	-0.93	[-1.17,-0.71]
	F	l_∞	162.1	[158.39,166.42]
		k	0.11	[0.1,0.12]
		t_0	-0.08	[-0.29,0.11]
	M+F	l_∞	151.55	[149.3,154]
		k	0.11	[0.11,0.12]
		t_0	-0.38	[-0.54,-0.23]
LIN 3&4-CR	M	l_∞	115.16	[114.3,116.02]
		k	0.12	[0.12,0.13]
		t_0	-0.86	[-0.95,-0.77]
	F	l_∞	158.68	[156.59,160.81]
		k	0.08	[0.08,0.08]
		t_0	-0.89	[-0.97,-0.81]
	M+F	l_∞	132.8	[131.7,133.89]
		k	0.1	[0.1,0.11]
		t_0	-0.83	[-0.9,-0.76]

Table A1: Estimated parameters for the von Bertalanffy growth curve (continued).

Stock	Sex	Parameter	Estimate and 95% CI	
LIN 5&6-SA	M	l_∞	97.33	[96.73,97.99]
		k	0.16	[0.16,0.17]
		t_0	-1.16	[-1.34,-1]
	F	l_∞	116.61	[115.69,117.6]
		k	0.12	[0.12,0.13]
		t_0	-1.3	[-1.45,-1.17]
	M+F	l_∞	107.7	[107.1,108.32]
		k	0.14	[0.14,0.15]
		t_0	-1.1	[-1.22,-0.99]
LIN 6B-BY	M	l_∞	126.32	[122.37,131.37]
		k	0.11	[0.09,0.13]
		t_0	-1.71	[-3.33,-0.48]
	F	l_∞	145.11	[139.98,151.5]
		k	0.09	[0.08,0.11]
		t_0	-1.43	[-2.58,-0.53]
	M+F	l_∞	133.99	[130.7,137.96]
		k	0.1	[0.09,0.12]
		t_0	-1.36	[-2.38,-0.51]
LIN 2-EC	M	l_∞	147.92	[137.33,163.87]
		k	0.1	[0.07,0.13]
		t_0	-1.01	[-2.63,0.14]
	F	l_∞	151.2	[140.3,168.43]
		k	0.14	[0.1,0.18]
		t_0	0.7	[-0.12,1.29]
	M+F	l_∞	144.45	[137.15,154.04]
		k	0.13	[0.11,0.16]
		t_0	0.29	[-0.4,0.85]
All stocks	M	l_∞	112.06	[111.49,112.6]
		k	0.15	[0.15,0.15]
		t_0	-0.41	[-0.49,-0.34]
	F	l_∞	135.88	[134.96,136.79]
		k	0.11	[0.11,0.11]
		t_0	-0.56	[-0.63,-0.5]
	M+F	l_∞	124.2	[123.66,124.75]
		k	0.13	[0.13,0.13]
		t_0	-0.5	[-0.55,-0.44]

Table A2: Estimated parameters for the logistic maturity at length ogive (Equation 13 and Code Listing A3). Model fits are illustrated in Figure A1.

Stock	Sex	Parameter	Estimate and 95% CI	
LIN 7-WC	M	l_{50}	71.43	[65.81,75.93]
		δ	18.2	[14.84,22.72]
	F	l_{50}	106.16	[103.98,108.32]
		δ	14	[12.38,15.99]
	M+F	l_{50}	93.42	[90.96,95.73]
		δ	19.42	[17.36,21.71]
LIN 7-CK	M	l_{50}	-	
		δ	-	
	F	l_{50}	123.57	[117.64,131.82]
		δ	12.7	[9.11,19.12]
	M+F	l_{50}	-	
		δ	-	
LIN 3&4-CR	M	l_{50}	73.37	[72.41,74.31]
		δ	4.85	[4.39,5.38]
	F	l_{50}	106.4	[101.23,112.67]
		δ	8.42	[6.62,10.64]
	M+F	l_{50}	78.26	[77.47,79.05]
		δ	5.79	[5.35,6.29]
LIN 5&6-SA	M	l_{50}	67.89	[66.94,68.75]
		δ	4.18	[3.69,4.75]
	F	l_{50}	84.38	[82.99,85.75]
		δ	8.49	[7.56,9.61]
	M+F	l_{50}	73.35	[72.4,74.3]
		δ	8.75	[8.04,9.54]
All stocks	M	l_{50}	70.49	[69.73,71.24]
		δ	7.15	[6.67,7.67]
	F	l_{50}	99.02	[97.5,100.69]
		δ	14.37	[13.37,15.51]
	M+F	l_{50}	80.67	[79.76,81.5]
		δ	13.87	[13.16,14.67]

Table A3: Estimated parameters for the weight-length relationship (Equation 3 and Code Listing A2).

Stock	Sex	Parameter	Estimate and 95% CI	
LIN 7-WC	M	c	0.00135	[0.00127,0.00143]
		b	3.28	[3.27,3.3]
	F	c	0.00101	[0.000948,0.00107]
		b	3.36	[3.34,3.37]
	M+F	c	0.0011	[0.00106,0.00115]
		b	3.33	[3.32,3.34]
LIN 7-CK	M	c	0.00187	[0.00114,0.00318]
		b	3.23	[3.12,3.34]
	F	c	0.000536	[0.000337,0.000901]
		b	3.51	[3.4,3.61]
	M+F	c	0.00102	[0.000693,0.00147]
		b	3.37	[3.29,3.45]
LIN 3&4-CR	M	c	0.00122	[0.00119,0.00124]
		b	3.3	[3.3,3.31]
	F	c	0.00128	[0.00125,0.0013]
		b	3.29	[3.28,3.29]
	M+F	c	0.00127	[0.00125,0.00129]
		b	3.29	[3.29,3.3]
LIN 5&6-SA	M	c	0.00206	[0.00197,0.00215]
		b	3.19	[3.18,3.2]
	F	c	0.00128	[0.00123,0.00132]
		b	3.3	[3.29,3.31]
	M+F	c	0.00146	[0.00142,0.0015]
		b	3.27	[3.26,3.27]
LIN 6B-BY	M	c	0.0022	[0.00123,0.00389]
		b	3.19	[3.06,3.31]
	F	c	0.00136	[0.000652,0.00321]
		b	3.3	[3.12,3.45]
	M+F	c	0.00146	[0.000907,0.00248]
		b	3.28	[3.17,3.38]
LIN 2-EC	M	c	0.00124	[0.00042,0.00452]
		b	3.32	[3.03,3.56]
	F	c	0.000312	[9.77e-05,0.00111]
		b	3.61	[3.33,3.86]
	M+F	c	0.000577	[0.000233,0.00136]
		b	3.48	[3.29,3.68]
All stocks	M	c	0.00137	[0.00134,0.00139]
		b	3.28	[3.28,3.28]
	F	c	0.00118	[0.00116,0.00121]
		b	3.31	[3.31,3.32]
	M+F	c	0.00125	[0.00124,0.00127]
		b	3.3	[3.3,3.3]

Table A4: Estimated parameters for the logistic maturity at age ogive (Equation 13 and Code Listing A3). Model fits are illustrated in Figure A2.

Stock	Sex	Parameter	Estimate and 95% CI	
LIN 7-WC	M	a_{50}	5.77	[3.96,6.91]
		δ	4.55	[3.58,6.24]
	F	a_{50}	12.14	[11.63,12.62]
		δ	3.02	[2.67,3.44]
	M+F	a_{50}	10.19	[9.73,10.66]
		δ	3.81	[3.42,4.27]
LIN 7-CK	M	a_{50}	-	
		δ	-	
	F	a_{50}	12.46	[11.47,13.72]
		δ	2.06	[1.49,3.02]
	M+F	a_{50}	-	
		δ	-	
LIN 3&4-CR	M	a_{50}	7.79	[7.59,7.99]
		δ	1.04	[1,1.15]
	F	a_{50}	14.54	[13.33,16.05]
		δ	1.8	[1.43,2.3]
	M+F	a_{50}	8.73	[8.56,8.91]
		δ	1.16	[1.07,1.26]
LIN 5&6-SA	M	a_{50}	6.53	[6.28,6.79]
		δ	1.43	[1.27,1.64]
	F	a_{50}	10.46	[10.01,10.9]
		δ	2.77	[2.44,3.16]
	M+F	a_{50}	8.16	[7.89,8.42]
		δ	2.47	[2.28,2.7]
All stocks	M	a_{50}	7.31	[7.14,7.48]
		δ	1.62	[1.51,1.73]
	F	a_{50}	11.86	[11.58,12.16]
		δ	2.53	[2.36,2.73]
	M+F	a_{50}	9.25	[9.09,9.41]
		δ	2.37	[2.26,2.49]

Appendix: Results figures

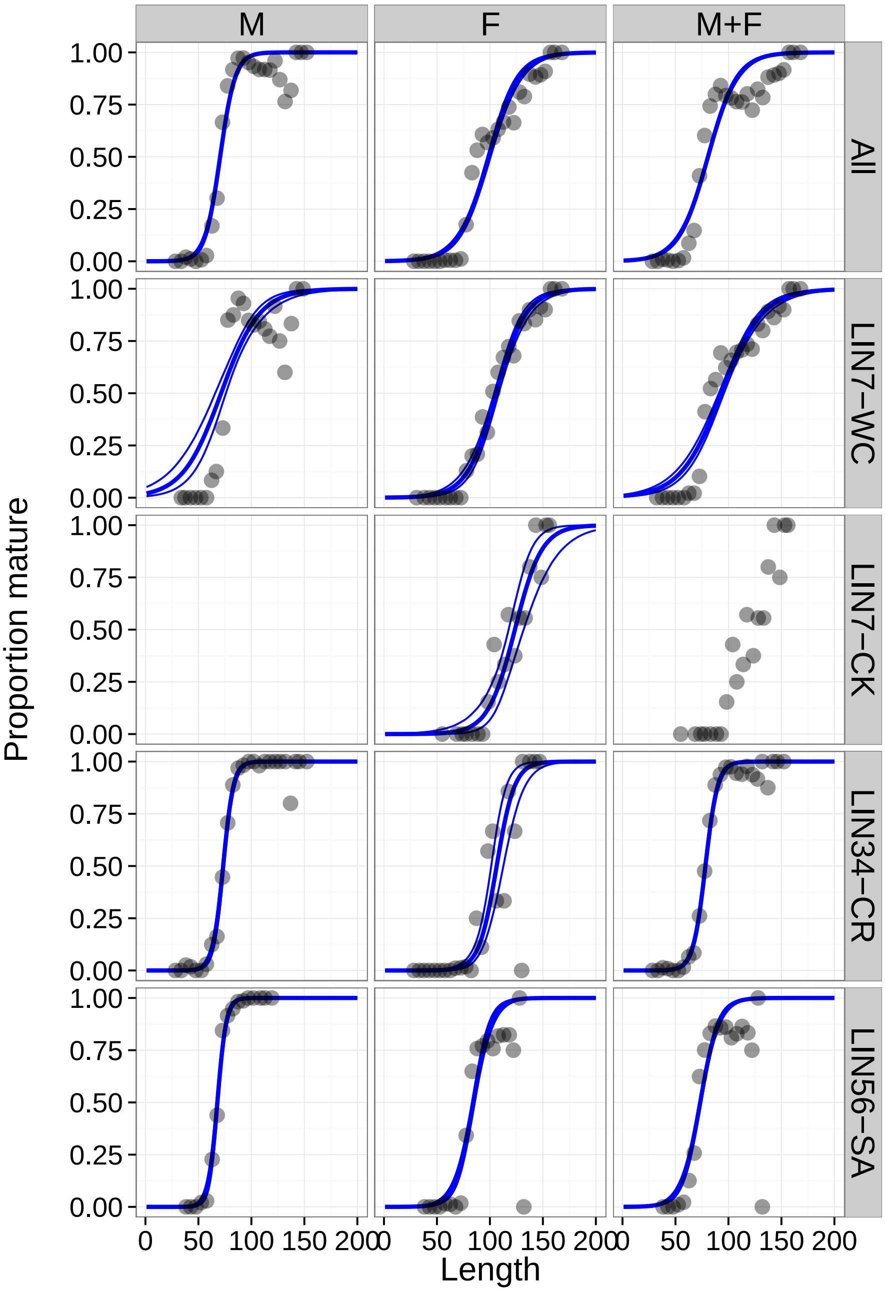

Figure A1: Logistic ogive fit to maturity at length data.

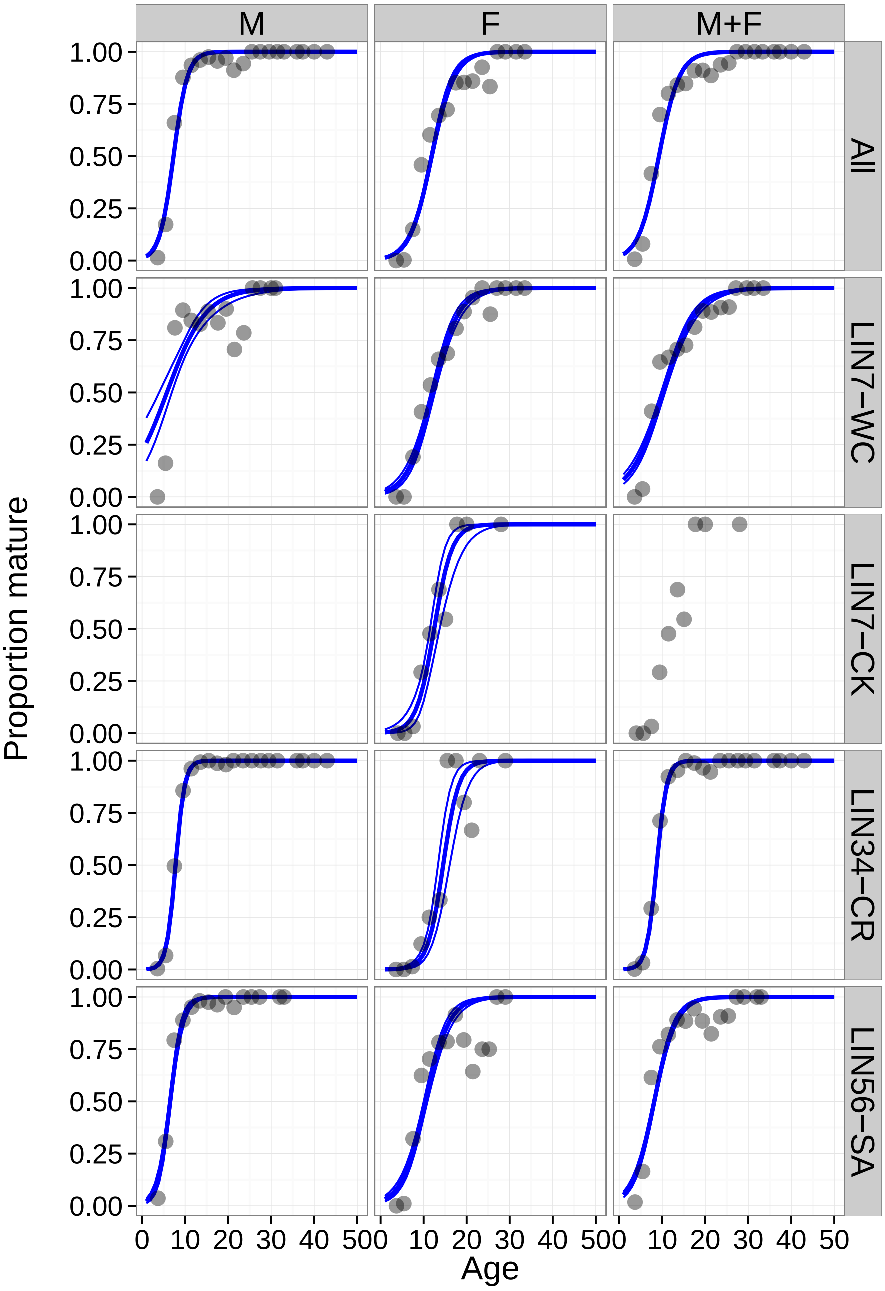

Figure A2: Logistic ogive fit to maturity at age data.

Appendix: Code listings

Code listing A1: rstan code for fitting a Francis (1988) parameterisation of the von Bertalanffy growth curve to data on length `y`, at age `x`, with reference ages `t`.

```
data {
      int N;
      vector[2] t;
      vector[N] x;
      vector[N] y;
}
transformed data {
      vector[3] T;
      T[1] <- t[1];
      T[3] <- t[2];
      T[2] <- mean(t);
}
parameters {
      vector<lower=0>[3] L;
      real<lower=0.01> sigma;
}
transformed parameters {
      real r;
      real r2;

      r <- (L[3] - L[2])/(L[2] - L[1]);
      r2 <- pow(r,2);
}
model {
      sigma ~ uniform(0.01,10);
      L ~ uniform(20,200);
      for (n in 1:N) {
            real mu;
            mu <- fmax(L[1] + (L[3]-L[1]) * (1 -
               pow(r,2*(x[n]-T[1])/(T[3]-T[1])))/ (1 - r2),1e-6);
            y[n] ~ lognormal(log(mu),sigma);
      }
      if(r<0) increment_log_prob(-1000);
}
generated quantities {

      real linf;
      real k;
      real t0;

      real lgth[200];

      vector[N] mu;
      vector[N] resid;

      # residuals
      for (n in 1:N)
            mu[n] <- L[1] + (L[3]-L[1]) * (1 -
               pow(r,2*(x[n]-T[1])/(T[3]-T[1])))/ (1 - r2);
```

```
      resid <- log(y ./ mu);

      # VB growth parameters
      linf <- L[1] + (L[3] - L[1]) ./ (1 - r2);
      k    <- -2 * log(r) / (T[3] - T[1]);
      t0   <- T[1] + 1/k * log((linf - L[1]) / linf);

      # Length at age
      for(a in 1:200) {
            lgth[a] <- L[1] + (L[3]-L[1]) * (1 -
               pow(r,2*(a-T[1])/(T[3]-T[1]))))/ (1 - r2);
      }
}
```

Code listing A2: rstan code for fitting of weight-length relationship to data on weigth y, at length x

```
data {
      int N;
      vector[N] x;
      vector[N] y;
}
parameters {
      real<lower=0.0,upper=1.0> c;
      real<lower=1, upper=10> b;
      real<lower=0.01> sigma;
}
transformed parameters {
      # expected proportion mature
      vector[N] mu_log;
      mu_log <- log(c) + b * log(x);
}
model {
      sigma ~ uniform(0.01,10);
      y ~ lognormal(mu_log,sigma);
}
generated quantities {
      # weight at length
      real wgt[200];
      for(l in 1:200) {
            wgt[l] <- c * pow(l,b);
      }
}
```

Code listing A3: rstan code for fitting of maturity ogive to data on binary maturity y, at length or age x

```
data {
      int N;
      vector[N] x;
      int y[N];
}
parameters {
      real<lower=1,upper=200> delta;
      real<lower=1,upper=200> x50;
```

```
}
transformed parameters {
      # expected proportion mature
      vector[N] pi;
      for(n in 1:N) {
            pi[n] <- 1 / (1 + exp(-(x[n] - x50) / delta));
      }
}
model {
      y ~ bernoulli(pi);
}
generated quantities {
      # maturity at age or length
      real mat[200];
      for(l in 1:200) {
            mat[l] <- 1 / (1 + exp(-(l - 150) / delta));
      }
}
```

Code listing A4: rstan code for fitting of an errors in variables regression to observed nautral mortality values `m`

```
data {
      int N;
      vector[N] m;
      vector[N] k;
      vector[N] lmat;
      vector[N] linf;
      real cv;
}
parameters {
      vector<lower=0.001>[N] k_prime;
      vector<lower=0.001>[N] lmat_prime;
      vector<lower=0.001>[N] linf_prime;

      real<lower=0,upper=10> sigma2;
      real<lower=-10,upper=10> beta;
}
transformed parameters {
      vector[N] eta;

      real sigma;
      real sigma_bullet;

      eta <- log(k_prime) + beta * log(lmat_prime ./ linf_prime);

      sigma     <- sqrt(sigma2);
      sigma_bullet <- sqrt(log(pow(cv,2)+1));
}
model {
      sigma2 ~ inv_gamma(0.0001,0.0001);
      beta ~ uniform(-10,10);

      k_prime ~ lognormal(log(k) ,sigma_bullet);
      lmat_prime ~ lognormal(log(lmat),sigma_bullet);
```

```
      linf_prime ~ lognormal(log(linf),sigma_bullet);

      m ~ lognormal(eta,sigma);
}
```