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MODELLING KRILL RECRUITMENT

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Abstract

A method is developed for using observed values of the mean proportion of recruits and its variance to model recruitment in a krill population in terms of numbers of recruits. The method includes the calculation of natural mortality and other parameters consistent with the observed proportional recruitment parameters. A procedure is given for generating families of recruitment functions which are consistent with the statistical uncertainty in the observed recruitment parameters.

Résumé

L'auteur développe une méthode d'utilisation des valeurs observées de la proportion moyenne de recrues et de sa variance pour modéliser le recrutement, exprimé en nombre de recrues, dans une population de krill. Cette méthode comporte un calcul de la mortalité naturelle et d'autres paramètres en rapport avec les paramètres de recrutement proportionnel observés. Dans ce document est exposée une procédure permettant de constituer des familles de fonctions de recrutement qui soient en accord avec l'incertitude statistique dans les paramètres du recrutement observés.

Резюме

Разработан метод использования наблюдаемых величин средней пропорции вступающих в популяцию особей и ее изменчивости с целью моделирования пополнения в популяцию криля, выраженного в единицах численности. Этот метод предусматривает вычисление естественной смертности и других параметров, соответствующих наблюдаемым параметрам пропорционального пополнения. Дается процедура получения семейств функций пополнения, которые соответствуют статистической неопределенности в наблюдаемых параметрах пополнения.

Resumen

Se elabora un modelo que utiliza los valores observados de la proporción promedio de los reclutas y su varianza con el objeto de modelar el reclutamiento de una población de kril en función del número de reclutas. El método incluye el cálculo de la mortalidad natural y otros parámetros coherentes con los parámetros observados de reclutamiento proporcional. Se presenta un procedimiento para generar grupos de funciones de reclutamiento que son coherentes con la incertidumbre estadística de los parámetros observados de reclutamiento.

Keywords: krill, population, modelling, recruitment, mortality, CCAMLR

INTRODUCTION

In a paper published in this volume, de la Mare (1994) presents a method for estimating the proportions of recruits in krill populations based on the analyses of length data from a number of net hauls. The available data have been used to obtain preliminary estimates for the population distribution of proportional krill recruitment, in terms of a mean and variance. The aim of this paper is to present a method of using these data to model krill recruitment and its variability in a way which is consistent with the data and which takes into account uncertainty in the parameter estimates. This methodology can then be incorporated into the krill simulation model used in calculating precautionary catch limits. This will allow the somewhat arbitrary method of modelling recruitment and its variability currently used to be replaced by a method which is based on parameters which can be estimated.

MODEL DEVELOPMENT

In modelling a krill population we need, in each year of a simulation, a random recruitment in terms of number of krill. If we assume that recruitment is independent of stock size over the range of interest, the recruitment is a random variable with constant mean and variance, that is the recruitments over a series of years are independent, identically distributed random variables. However, what we can estimate in practice is not the numbers of recruits over time, but rather the proportion of recruits. Thus we need a method of converting the parameters we can estimate, the mean and variance in the proportion of recruits, into random numbers of recruits, which in simulations will reproduce the observed mean and variance in the proportion of recruits.

The proportion of recruits, known as the $R(t)$ rate, is the ratio of numbers in age class t to the numbers in that age class and above, that is:

$$R(t) = \frac{A_t}{\sum_{i=t}^{n} A_i} \tag{1}$$

where A_i is the number of animals in age class i, and n is the age of the oldest age class present in non-negligible numbers in the population. This can also be written:

$$R(t) = \frac{A_t}{A_t + \sum_{i=t+1}^{n} A_i} \tag{2}$$

where A_t is the number of recruits in the population.

Calculating Natural Mortality

The first parameter we need to fix for the krill model is the rate of natural mortality (M). In an unexploited population which is on average in equilibrium, the proportion of recruits is a function of S, the survival rate from one age class to the next, which is given by:

$$S = e^{-M} \tag{3}$$

If M is assumed to be independent of age up to age n, and infinite thereafter, then in an equilibrium population the $R(t)$ rate is:

$$\tilde{R}(t) = \frac{1}{\sum_{i=t}^{n} S^{i-t}} \tag{4}$$

S can be found as the root of the function:

$$f\left(S, \tilde{R}(t)\right) = \frac{1 - S^{n+1}}{1 - S} - \frac{1}{\tilde{R}(t)} \tag{5}$$

This is easily solved using Newton's method, using:

$$f'\left(S, \tilde{R}(t)\right) = \frac{1 - S^{n+1}}{(1 - S)^2} - \frac{(n+1)S^n}{1 - S} \tag{6}$$

A starting guess for the iteration should be $S \rightarrow 1$. Simulation tests show that the value of S calculated using the average value $\bar{R}(t)$ from the net haul surveys as the value for $\tilde{R}(t)$ is slightly too high (because $\bar{R}(t)$ is a random variable). A less biased average value for the simulated $R(t)$ is obtained when the value for S is calculated with $\tilde{R}(t)$ used in equations (5) and (6) set to $\bar{R}(t) + V\left[\bar{R}(t)\right]$.

Correcting the Variance in $R(t)$ for the Effects of Variability in the Population Size

Although we can use the average value of the $R(t)$ rate for generating random values of recruitment, we are not able to use directly the observed variance estimate of $R(t)$ from independent samples to generate the random values. This is because the variance of $R(t)$ includes a component of variation due to the cumulative effects of variability in recruitment in every age class. If we put:

$$T = \sum_{i=t+1}^{n} S^{i-t} \tag{7}$$

then (4) can be written as:

$$\tilde{R}(t) = \frac{1}{1+T} \quad (8)$$

from which it follows that:

$$\left(\frac{\tilde{R}(t)}{1-\tilde{R}(t)}\right)\overline{A}_t T = \overline{A}_t \quad (9)$$

where $\overline{A}_t$ is the average number of recruits to be produced by the model. If $\tilde{R}(t)$ is replaced by a random observation with the appropriate properties, it follows that the random recruitment A is given by:

$$A_t = \left(\frac{R(t)}{1-R(t)}\right)\overline{A}_t T \quad (10)$$

Clearly, even though $R(t)$ can only take values in the range 0 - 1, A_t can have a large positive value as $R(t) \rightarrow 1$.

The variance needed in generating random $R(t)$ values, by means of equation (10), is that which would apply when there is no variation in the total population older than the recruiting age class. This variance can be found by using the delta method approximation for the variance of a function of random variables. Equation (2) is the quotient of two random variables, and hence the delta method expansion for the variance of (2) is given by:

$$\mathrm{V}[R_I] \approx \left[\frac{\mathrm{E}[A_t]}{\mathrm{E}\left[A_t + \sum_{i=t+1}^{n} A_i\right]}\right]^2 \times \left[\frac{\mathrm{V}[A_t]}{\mathrm{E}[A_t]^2} + \frac{\mathrm{V}\left[A_t + \sum_{i=t+1}^{n} A_i\right]}{\mathrm{E}\left[A_t + \sum_{i=t+1}^{n} A_i\right]^2} - \frac{2 \cdot \mathrm{Cov}\left[A_t, A_t + \sum_{i=t+1}^{n} A_i\right]}{\mathrm{E}[A_t]\mathrm{E}\left[A_t + \sum_{i=t+1}^{n} A_i\right]}\right] \quad (11)$$

where E[.] denotes the expected value, V[.] the variance and Cov[.,.] the covariance. It can be shown that:

$$\frac{\mathrm{E}[A_t]}{\mathrm{E}\left[A_t + \sum_{i=t+1}^{n} A_i\right]} = \frac{1}{1+T} \quad (12)$$

In fact no generality is lost if we put $\mathrm{E}[A_t] = 1$ everywhere, and so:

$$\mathrm{E}\left[A_t + \sum_{i=t+1}^{n} A_i\right] = 1+T \quad (13)$$

If the recruitment in each year is randomly and independently distributed, then it can be shown that:

$$\mathrm{V}\left[A_t + \sum_{i=t+1}^{n} A_i\right] = \mathrm{V}[A_t]\left(\sum_{i=t}^{n} S^{2(i-t)}\right) \quad (14)$$

and

$$\mathrm{Cov}\left[A_t, A_t + \sum_{i=t+1}^{n} A_i\right] = \mathrm{V}[A_t] \quad (15)$$

Substituting equations (12) to (15) into (11) and expressing the result for the unknown variance of A_t (for $\mathrm{E}[A_t] = 1$) gives:

$$\mathrm{V}[A_t] = \frac{\mathrm{V}[R(t)](1+T)^2}{1 + \frac{\sum_{i=t}^{n} S^{2(i-t)}}{(1+T)^2} - \frac{2}{1+T}} \quad (16)$$

We require the intrinsic variability in $R(t)$ for the case where the population above the age at recruitment is constant at its expected value. This new random variable, denoted $R(t)^*$, given by:

$$R(t)^* = \frac{A_t}{A_t + \mathrm{E}[A_t]T} \quad (17)$$

has the expected value:

$$\mathrm{E}[R(t)^*] = \frac{1}{1+T} \quad (18)$$

as required, and variance from the delta method given by:

$$\mathrm{V}[R(t)^*] = \left(\frac{1}{1+T}\right)^2 \mathrm{V}[A_t]\left(1 + \frac{1}{(1+T)^2} - \frac{2}{1+T}\right) \quad (19)$$

Substituting (16) and simplifying gives:

$$V[R(t)^*] = \frac{V[R(t)]T^2}{T^2 + \sum_{i=t+1}^{n} S^{2(i-t)}} \qquad (20)$$

Thus, random proportions of recruits can be drawn from a distribution with mean equal to the observed mean, and variance calculated according to equation (20) above. Since the proportion of recruits is bounded 0 - 1, a beta distribution would be appropriate for generating the random values.

Bias Correction for the Mean Number of Recruits

Because the number of recruits given by equation (10) has a random variable in the denominator, the mean of the distribution of recruitments will be biased. The delta method can be used to calculate a bias correction factor. The expected value of the random part of equation (10), expressed in terms of the random variable $R(t)^*$, is given by:

$$E\left[\frac{R(t)^*}{1-R(t)^*}\right] \approx \frac{\overline{R}(t)^*}{1-\overline{R}(t)^*} - \frac{\mathrm{Cov}[R(t)^*, 1-R(t)^*]}{(1-\overline{R}(t)^*)^2} + \frac{\overline{R}(t)^* V[1-R(t)^*]}{(1-R(t)^*)^3} \qquad (21)$$

where $\overline{R}(t)^*$ is estimated by $\overline{R}(t)$. It is easily shown that:

$$\mathrm{Cov}[R(t)^*, 1-R(t)^*] = -V[R(t)^*] \qquad (22)$$

and

$$V[1-R(t)^*] = V[R(t)^*] \qquad (23)$$

Thus it follows that:

$$A_t = \left(\frac{R(t)}{1-R(t)} - B\right)\overline{A}_t T \qquad (24)$$

where

$$B = V[R(t)^*]\left(\frac{1}{(1-\overline{R}(t))^3}\right) \qquad (25)$$

Equation (24) should generate random recruitments which have approximately the correct mean. However, simulation tests show that the correction factor in equation (24) slightly overcorrects for the bias, and a better result is obtained with:

$$B = V[R(t)^*]\left(\frac{1}{(1-\overline{R}(t))^3}\right)\overline{R}(t) \qquad (26)$$

This still appears to be slightly biased, and additional modifications could reduce the bias further. However, bias correction is not necessary if the population model is used in a way which involves scaling results to the mean unexploited population size, and the model is exercised for n years without exploitation prior to calculating the mean unexploited population size. By that time the slight bias in recruitment will have worked its way through all the age classes.

The results of simulation tests of the model, given in Table 1, show that a satisfactory method has been obtained for converting the observed parameters on proportional recruitment into numerical recruitments with the required properties. It is interesting to note that the coefficient of variation (CV) in the numerical recruitment is considerably greater than the CV in the proportional recruitment.

Accounting for Uncertainty in the Estimates of the Proportional Recruitment Distribution

Equations (19) and (25) enable the generation of random annual recruitments for given values of mean proportional recruitment and its variance. In practice there is uncertainty in these two quantities, which can be taken into account in Monte Carlo simulations used in calculating precautionary catch by drawing the values used in each simulation from appropriate sampling distribution limits (for details on the method of calculating the precautionary catch limits see Butterworth, Punt and Basson, 1991). In the case of $V[R(t)]$, a suitable distribution is a χ^2 distribution with N - 1 degrees of freedom, where N is the number of observations used in estimating the proportional recruitment distribution parameters. Thus, prior to starting each simulation, a new $V[R(t)]$ is generated by:

Table 1: Results achieved by the krill recruitment model for 10 000 trials.

Average $R(1)$		CV	Average Recruits	Recruits CV
True	0.3	0.333	100	
Simulated	0.299964	0.333	101.469	0.466
True	0.5	0.200	100	
Simulated	0.499196	0.202	99.034	0.373
True	0.5	0.283	100	
Simulated	0.496260	0.296	99.675	0.596
True	0.7	0.143	100	
Simulated	0.690438	0.159	99.818	0.483

$$V[R(t)] = \frac{\Gamma(N-1, 2(N-1)) V_{obs}[R(t)]}{N-1} \quad (27)$$

where $\Gamma(x,y)$ denotes a random deviate from a gamma distribution with mean x and variance y. If this is chosen first, the value for the average of $R(t)$ for that simulation can be drawn from a normal distribution:

$$\overline{R}(t) = N\left[\overline{R}(t)_{(obs)}, V[R(t)]\right] \quad (28)$$

where $N[\mu,\sigma^2]$ denotes a random deviate from a normal distribution with mean μ and variance σ^2. Given that the distribution of $R(t)$ is bounded 0 - 1 and reasonably bell-shaped, the sampling distribution of $\overline{R}(t)$ should approach a normal distribution for a relatively small sample size. It is unlikely that random values of $\overline{R}(t)$ will fall outside the range 0 - 1, and if these are rare, and the normal distribution truncated at the feasible range, very little bias should be introduced. The value of $\overline{R}(t)$ is used to calculate the natural mortality for this particular realisation using equations (5) and (6). The variance is adjusted according to equation (20) and then used to calculate the parameters for a beta distribution which in turn is used to generate random observations on the recruitment proportion for equation (24). A beta random variable has the probability density function:

$$f(x;a,b) = \frac{1}{B(a,b)} x^{a-1}(1-x)^{b-1} \quad , \qquad x \geq 0 \quad (29)$$

with mean:

$$\mu = \frac{a}{a+b} \quad (30)$$

and variance:

$$\sigma^2 = \frac{ab}{(a+b)^2(a+b+1)} \quad (31)$$

It is easily shown that:

$$a = \frac{1-\mu}{k^2} - \mu \quad (32)$$

where k is the CV, and:

$$b = a\left(\frac{1}{\mu} - 1\right) \quad (33)$$

Thus, the parameters a and b are determined for a particular realisation of the recruitment function by substituting the random values for the mean and CV derived from expressions (27) and (28) into equations (32) and (33).

This process will result in a family of recruitment distributions which is consistent with the data used in estimating the observed mean and variance in proportional recruitment. However, the family of distributions is also statistically consistent in the sense that it will converge on the true recruitment function as $N \rightarrow \infty$, provided, of course, the assumption holds that $R(t)$ has a beta distribution.

A computer program which tests the recruitment modelling method presented here has been submitted to the CCAMLR Secretariat.

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Légendes des tableaux

Список таблиц

Lista de las tablas