ESTIMATING KRILL RECRUITMENT AND ITS VARIABILITY

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Abstract

A maximum likelihood method is developed for the decomposition of krill density-at-length data into the proportion of recruits in a population sampled by a net haul survey. Preliminary results from a series of five net haul surveys in the South Atlantic and the Indian Ocean sectors of the Southern Ocean give a mean recruitment rate for 1+ krill (the ratio of the number of krill aged one year to the number of krill aged one year and above) of 0.339 with a standard deviation (SD) of 0.100. The corresponding result for recruitment for 2+ krill (the ratio of the number of two-year-old krill to the number aged two and above) from nine surveys is 0.552 with a standard deviation of 0.074. A number of the assumptions needed for reliable results is discussed.

Résumé

Développement d'une méthode de maximum de vraisemblance décomposant les données de densité par longueur de krill et en dérivant la proportion de recrues dans une population échantillonnée par une campagne d'évaluation par chalutages. Les premiers résultats d'une série de cinq campagnes d'évaluation par chalutages menées dans les secteurs atlantique et indien de l'océan Austral donnent un taux de recrutement moyen, pour le krill âgé de 1+ (rapport entre le nombre d'individus de krill âgés de un an et celui de un an et plus) de 0,339, avec un écart-type (SD) de 0,100. Le résultat correspondant pour le recrutement du krill de 2+ (rapport entre le nombre d'individus de krill âgés de deux ans et celui de deux ans et plus), obtenu à partir de neuf campagnes d'évaluation, est de 0,552, avec un écart-type de 0,074. Un certain nombre d'hypothèses requises pour l'obtention de résultats fiables sont ici discutées.

Резюме

Для преобразования данных по плотности-при-длине криля в пропорцию особей, вступающих в популяцию, обследованную траловой съемкой, был разработан метод максимальной вероятности. Предварительные результаты по серии пяти траловых съемок в южно-атлантическом и индоокеанском секторах Южного океана дают средний коэффициент пополнения для криля 1+ (соотношение количества криля возрастом один год к количеству криля возрастом один год и более) равный 0,339 при стандартном отклонении (SD) в 0,100. Соответствующая величина пополнения для криля 2+ (соотношение количества криля возрастом два года к количеству криля возрастом два года и более), полученный в результате девяти съемок, равна 0,552 при стандартном отклонении в 0,074. Обсуждается ряд предположений, необходимых для получения надежных результатов.

Resumen

Se ha desarrollado un método de máxima verosimilitud para la reagrupación de los datos de densidad por talla del kril en base a la proporción de reclutas de una población muestreada por una prospección de arrastre. Los resultados preliminares de una serie de prospecciones de arrastre realizadas en los sectores del Atlántico sur y del océano Indico del océano Austral dan una tasa de reclutamiento medio de kril de edad 1+ (la proporción de kril de más de un año (en unidades) con respecto al kril de un año y más) de 0.339, con una desviación típica (SD) de 0.100. El resultado correspondiente al reclutamiento de kril de edad 2+ (la proporción de kril de 2 años con respecto al número total de dos años y más) de nueve prospecciones es 0.552, con una desviación típica de 0.074. Se discuten varias hipótesis necesarias para obtener resultados fiables.

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

INTRODUCTION

At least year's meeting of the Working Group on Krill (WG-Krill), a procedure was outlined for estimating krill recruitment variability (SC-CAMLR, 1992). Appendix E suggested that an analysis of length frequency data, possibly using the method of MacDonald and Pitcher (1979), should be carried out in order to determine the proportion of recruits in krill samples collected in net surveys. This paper describes a method which has been developed along these lines. A companion paper (de la Mare, 1994) describes how the results of the method can be used to model krill recruitment.

The aim of the method is to estimate the proportion of recruits in samples from krill populations. The proportion of recruits, also known as the gross recruitment rate, $R(t)$, is the ratio of the numbers in age class t to the numbers in that age class and above, that is:

$$R(t) = \frac{A_0}{\sum_{i=t}^{n} A_i} \qquad (1)$$

where A_i is the number of animals in age class i, and n is the age of the oldest animals in the population present in non-eligible numbers. Thus, we need only to be able to separate one young age class from all the others; it is not necessary to be able to distinguish between the older age classes.

The problem with krill is that there is no reliable method of direct age determination. One indirect method for determining numbers-at-age is based on the decomposition of length frequency distributions into separate distributions of length for each age class (MacDonald and Pitcher, 1979). Figure 1 shows the length frequency distribution which would be roughly applicable to Antarctic krill, along with the length frequency distributions of each age class. It is clear that there is little prospect of accurately decomposing the mixture for age classes 3 and above. However, this is not necessary for calculating $R(t)$.

If we assume that the length distributions have normal distributions with a constant coefficient of variation k, the expected density in length class j is the sum of n distributions in the length interval of the j^{th} class, given by:

$$d_j = \sum_{i=t}^{n} D_i \left[\Phi\left(\frac{\mu_i - \ell_{j+1}}{k\mu_i} \right) - \Phi\left(\frac{\mu - \ell_j}{k\mu_i} \right) \right] \qquad (2)$$

where ℓ_j and ℓ_{j+1} are the length bounds of the j^{th} length interval, D_i is the total density of animals aged i in the population, $\Phi(.)$ denotes the cumulative standard normal function, μ_i is the mean of the length distribution for animals of age i. The values of D_i, μ_i and k are estimated by finding the values for them which result in d_j having a good fit to the distribution of observed densities-at-length from surveys. The assumption of a constant coefficient of variation is reasonable since it implies that older animals exhibit a greater range of lengths. This assumption has the advantage of reducing the number of parameters to be estimated in fitting the model, and ensures an orderly relationship between the variance estimated for each mixture component. The estimated value of $R(t)$ for the survey is given by:

$$R(t) = \frac{D_t}{\sum_{i=t}^{n} D_i} \qquad (3)$$

Only D_t and the sum of D_i need to be estimated accurately. The values of μ_i, k and the individual $D_i \mid_{i>0}$ are 'nuisance' parameters. We need be only concerned that their values provide a good fit to the data; we are not particularly interested in their values, except that they should be consistent with what is known about krill biology.

A MAXIMUM LIKELIHOOD METHOD FOR ANALYSING MIXTURE DISTRIBUTIONS

The major problem encountered during this analysis is that the existing methods are not applicable to densities estimated from net haul surveys. MacDonald and Pitchers' (1979) method assumes that length frequency data have no unusual statistical properties. The usual method assumes that length frequency data are representative of a population, with the frequencies in each length class having Poisson distributions. This would be valid in the case where the animals in question are randomly and independently distributed, and the frequencies consist of a complete enumeration of all the samples.

Unfortunately most net haul survey densities do not have these statistical properties. The statistical distribution of net haul densities has to allow for an often substantial probability that a given haul will produce a zero density estimate (i.e., the net was empty). The statistics of such distributions have been examined by Aitchison (1955), and Pennington (1983) has recommended using Aitchison's delta distribution as the underlying statistical model when analysing net haul survey data. This recommendation is followed in the method developed here. The delta distribution consists of a discrete probability at the origin, and a lognormal distribution for the non-zero observations.

Simulation studies show that the sampling distribution of the mean for delta distributions can be skewed, given the numbers of observations typical in trawl surveys. Simple transformations of the data or their mean do not lead to summary statistics which capture all the features of the sampling distribution. The likelihood for the sampling distribution of the mean cannot be expressed in terms of summary statistics, and so the full data set has to be used in calculating the likelihood of given parameter values. The delta distribution has the following probability function:

$$f\left(x;p,\lambda,\sigma^2\right)=(1-p)\mathrm{I}_0(x)+p\frac{1}{x\sqrt{2\pi\sigma}}e^{-\frac{1}{2}(\ln x-\lambda)}\mathrm{I}_{(0,\infty)} \tag{4}$$

where p is the proportion of observations of x which are > 0, λ and σ^2 are the parameters of the lognormal distribution of the non-zero observations, $\mathrm{I}_0[.]$ is an indicator function which takes the value 1 when $x = 0$ and 0 otherwise, and $\mathrm{I}_{(0,\infty)}[.]$ takes the value 0 when $x = 0$ and 1 when $x > 0$. The first term represents a discrete probability mass at the origin and the second, a probability density. The log-likelihood of a vector of observations $\mathbf{x} = x_1 \ldots x_N$ from a delta distribution is given by:

$$\ln\left[\mathscr{L}\left(x_1 \ldots x_N;p,\lambda,\sigma^2\right)=(N-m)\ \ln(1-p)+m\ln p\right.$$
$$-\frac{m}{2}\ln\sigma^2-\frac{1}{2\sigma^2}\sum_{x>0}(\ln x_i-\lambda)-\sum_{x>0}\ln x_i-\frac{m}{2}\ln 2\pi \tag{5}$$

where N is the total number of observations and m is the number of non-zero observations. The last two terms are additive constants which can be ignored when maximising the likelihood function to calculate estimates. In the method described here, it is the densities for a given length class in each haul which constitute the x_i. Using Aitchison's (1955) formulae, the maximum likelihood estimate of the mean value of density in the j^{th} length class is calculated as follows:

$$\begin{aligned}
\bar{d}_j &= \frac{m}{N}e^{\bar{y}}G_m\left(\frac{1}{2}s^2\right), && m>1\\
\bar{d}_j &= \frac{x_1}{N}, && m=1\\
\bar{d}_j &= 0, && m=0
\end{aligned} \tag{6}$$

where $\bar{y}$ and s^2 are the sample mean and sample variance of the log of the non-zero observations and:

$$G_m(t)=1+\frac{m-1}{m}t+\sum_{j=2}^{\infty}\frac{(m-1)^{2j-1}}{m^j(m+1)(m+3)\ldots(m+2j-3)}\cdot\frac{t^j}{j!} \tag{7}$$

Using a likelihood ratio approach (Cox and Hinkley, 1974), asymptotic confidence intervals on the mean density can be found as the roots of the following function:

$$\mathrm{q}(d)=\left[\ln\mathscr{L}\left(\mathbf{x};p,\lambda,\sigma^2\right)\middle|\begin{array}{l}p=\frac{m}{N},\\ \lambda=\frac{1}{m}\sum_{x_i>0}\ln x_i\ ,\\ \sigma^2=\frac{1}{m}\sum_{x_i>0}(\ln x_i-\lambda)^2\end{array}\right]$$
$$-\mathrm{Sup}\left[\ln\mathscr{L}\left(\mathbf{x};p,\lambda,\sigma^2\right)\middle|\begin{array}{l}0<p\le 1,\\ \lambda=\ln\left(\dfrac{d}{p\mathrm{G}_m\left(\frac{1}{2}\sigma^2\right)}\right),\\ 0<\sigma^2<\infty\end{array}\right]-\frac{1}{2}\chi_{1,\alpha}{}^2 \tag{8}$$

where $\chi_{1,\alpha}{}^2$ is the critical value of the χ^2 distribution with one degree of freedom, at the α probability level.

The maximum likelihood estimates of the parameters of the mixture distribution are obtained by maximising the sums of the log-likelihoods for each length class. It is useful to designate the parameters of the mixture distribution as:

$R(t)$: the parameter of primary interest, and
θ: a vector of the nuisance parameters consisting of $D_{t+1} .. D_n$, k and $\mu_{t+1} .. \mu_n$

The value of D_t used in calculating the mixture is derived from $R(t)$ and the $D_{i>t}$ as:

$$D_t = \frac{R(t)}{1-R(t)} \sum_{i=t+1}^{n} D_i \tag{9}$$

The likelihood function for fitting the mixture distribution can be written as:

$$h(R_1;\theta) = \sum_{j=1}^{n} \text{Sup} \left(\ln \mathcal{L}\left(\mathbf{x}_j; p_j, \lambda_j, \sigma_j^2\right) \middle| \begin{array}{l} 0 < p_j \le 1, \\ \lambda_j = \ln\left(\dfrac{d_j}{p_j G_m\left(\frac{1}{2}\sigma_j^2\right)} \right) \\ 0 < \sigma_j^2 < \infty \end{array} \right) \tag{10}$$

where d_j is the expected value of the density in length class j derived from equation (2), with the mixture distribution with parameters $R(t)$ and θ. Note that estimating $R(t)$ and θ requires maximising $h(R(t),\theta)$, which in turn requires maximising the likelihood for the delta distribution in each length class. All these maximisations have to be carried out numerically. The parameters p_j and σ_j^2 are also nuisance parameters. The maximisations are carried out subject to the following constraints:

$0 \le R(t) < 1$

$\mu_t^- \le \mu_t \le \mu_t^+ < \mu_{t+1}^- \le \mu_{t+1} \le \mu_{t+1}^+$
$< \ldots < \mu_n^- \le \mu_n \le \mu_n^+$

$k^- \le k \le k^+$

where a superscript + or - represents a numerically specified constraint. Apart from the well known advantages of statistical efficiency, working with log-likelihood allows asymptotic confidence intervals and variances to be calculated for the parameters. In particular we are interested in a variance estimate for $R(t)$. This is estimated from the second derivative of a quadratic function (Cox and Hinkley, 1974) passing through the points:

$$\left\{\hat{R}(t)-\delta,\ h\left(R(t)=\hat{R}(t)-\delta\right)\right\},\ \left\{\hat{R}(t),\ h\left(R(t)=\hat{R}(t)\right)\right\},$$
$$\left\{\hat{R}(t)+\delta,\ h\left(R(t)=\hat{R}(t)+\delta\right)\right\}$$

where δ is small. In determining these points, $R(t)$ is fixed as specified, but the vector of nuisance parameters is re-estimated by re-maximising the likelihood function. Thus the estimate obtained is for the marginal variance of $R(t)$. Although asymptotic variance estimates are not always accurate for non-normal sampling distributions, they should be adequate for providing relative weights for the subsequent estimation of the distribution statistics of $R(t)$ estimates.

This procedure has been implemented in a computer program (NMIX) which has been submitted to the CCAMLR Secretariat. Calculating the estimates is computer intensive, taking up to two hours on a very fast personal computer.

Figure 2 gives an example of the results which were obtained by fitting a mixture distribution to the net haul survey conducted by the *Nella Dan* during SIBEX II. The salient feature to note in this figure is the very wide and highly asymmetric confidence intervals around each observed density. Figure 3 shows the marginal values of -(log-likelihood) for values of $R(1)$ over the range 0 to 0.99. The best estimate of $R(1)$ corresponds to the minimum on the curve, which occurs at $R(1) = 0.528$. The figure also shows the asymptotic 95% confidence interval for the $R(1)$ estimate of 0.27 to 0.77. A quadratic fitted in the region of the minimum gives an asymptotic variance estimate of 0.002256 for the estimate of $R(1)$. This corresponds to a standard error for the estimate of 0.0475. The encouraging feature is that the confidence interval on the $R(1)$ estimate is well behaved, even though the data from the surveys lead to extremely skewed sampling distributions of mean densities at each length with very long upper tails.

RESULTS

Data from a number of krill trawl surveys were available in a form suitable for the method. The required data are the haul-by-haul densities by length class. Table 1 lists the sources of the available data. Only densities estimated using RMT8 nets have been considered in these analyses. Table 2 gives the values used for the various constraints in deriving the estimates. Table 3 gives preliminary results from these surveys, with $R(t)$ estimated for both putative one-year-old and two-year-old age classes. Five putative age classes (components) are used in fitting the distribution to the one-year-old and

Table 1: Krill surveys from which net haul data were analysed for proportions of recruits.

Survey No.	Vessel	Experiment	BIOMASS	Region	Period
1	*Marion Dufresne*	FIBEX	DUFX	Indian Ocean	Jan-Feb 81
2	*Walther Herwig*	FIBEX	HEFX	Atlantic	Jan-Mar 81
3	*Nella Dan*	FIBEX	-	Indian Ocean	Jan-Mar 81
4	*Professor Siedlecki*	SIBEX I	SIS1	Atlantic	Dec 83-Jan
5	*Nella Dan*	SIBEX II	NDS2	Indian Ocean	Jan-Feb 85
6	*Nella Dan*	ADBEX I	-	Indian Ocean	Feb-Apr 82
7	*Nella Dan*	ADBEX II	-	Indian Ocean	Jan-Feb 84
8	*Nella Dan*	AAMBER	-	Indian Ocean	Feb-Apr 87
9	*Aurora Australis*	AA2	-	Indian Ocean	Jan-Feb 91
10	*Aurora Australis*	CROCK	-	Indian Ocean	Jan-Feb 93

Table 2: Constraints used in calculating the estimates.

Constraint on $R(t)$ = 0 - 0.9999999999 Constraints on mixture component means	
Component Number	Range Allowed for Mean (mm)
1	16-28
2	30-40
3	41-48
4	49-52
5	53-56
Constraint on coefficient of variation of components = 0.01 - 0.20 (unless otherwise noted).	

Table 3: Preliminary results from the surveys with $R(t)$ estimated for both putative one- and two-year-old age classes.

One-year-old Recruitment			
Survey No.	$R(1)$	Std Error	CV of Length-at-age
1	-	-	-
2	**0.706**	**0.0463**	**0.139**
3	**0.167**	**0.0468**	**0.096**
4	**0.370**	**0.0422**	**0.153**
5	**0.528**	**0.0475**	**0.117**
6	0.001	0.0010	0.117
7	0.016	0.0273	0.087
8	0.025	0.0174	0.085
9	**0.314**	**0.0113**	**0.150**
10	0.064	0.0269	0.103
Two-year-old Recruitment			
Survey No.	$R(2)$	Std Error	CV of Length-at-age
1	**0.286**	**0.0645**	**0.071**
2	**0.360**	**0.1183**	**0.096**
3	**0.096**	**0.0592**	**0.091**
4	**0.968**	**0.0540**	**0.169**
5	0.320	0.0560	0.157
5	**0.431**	**0.0877**	**0.119***
6	**0.561**	**0.0851**	**0.110**
7	**0.557**	**0.2715**	**0.084**
8	**0.231**	**0.1300**	**0.084**
9	**0.556**	**0.0063**	**0.083***
10	0.020	0.1307	0.095

* CV of length-at-age constrained above at 0.12. Bounding the CV at 0.2 allowed for a fit which hit the constraint, which seems unlikely in light of the general run of the results.

above data, and four age classes in fitting to two-year-old and above.

The observed and expected fits of the length density distributions are shown in Figures 4 to 8. The observed points on these figures are the mean densities for each length calculated using equation (6). The error bars represent the asymptotic 95% confidence intervals on the mean densities calculated according to equation (8). As shown in the single example, the results have standard errors for the $R(t)$ estimates which are reasonably small, even though in many cases the confidence intervals on the individual densities-at-length are very wide. Thus, despite the poor precision of density estimates from net haul surveys, the method developed here is able to extract useful information on recruitment rates.

Assuming that the biological characteristics of krill are the same in the entire Southern Ocean, it is valid to combine samples from different regions to estimate distributional statistics for the $R(t)$ rate. The estimates in Table 3 shown in boldface are used in calculating the mean and variance of $R(t)$. The estimates of the inverse variance weighted mean and variance of the $R(1)$ estimates, taking the group with mean length in the range 18 to 28 mm as age class 1, are:

Number of surveys	5
Mean $R(1)$ estimate	0.339
Standard error	0.050
Standard deviation	0.100
CV of $R(1)$ distribution	0.295

The corresponding results for $R(2)$, taking the second group with mean length in the range 30 to 38 mm as age class 2, are:

Number of surveys	9
Mean $R(2)$ estimate	0.552
Standard error	0.026
Standard deviation	0.074
CV of $R(2)$ distribution	0.135

Pooling all the estimates gives:

Number of surveys	14
Mean $R(t)$ estimate	0.495
Standard error	0.035
Standard deviation	0.125
CV of $R(t)$ distribution	0.253

The information above is sufficient to calculate estimates of natural mortality (M) (assuming fishing mortality has been small) and variability in the annual number of recruits. The methods for these calculations are presented in de la Mare (1994, this volume).

DISCUSSION

The analyses above make the following assumptions about the length density data:

1. The net samples are representative of the length structure of a self-sustaining krill population for the range of age classes considered.

2. Increasing age leads to a monotonic increase in mean length-at-age, which gives rise to a mixture distribution.

3. Krill do not naturally shrink to the extent that the smallest component considered in the mixture can become polluted with animals of greater ages, but which have shrunk into the length range of the young animals.

Substantial violation of these assumptions will lead to biased estimates. WG-Krill should bear these points in mind when examining the results presented here.

The results suggest that many (all) of the existing surveys may not satisfy assumption 1. WG-Krill should review the survey results in order to eliminate those which can be identified as unreliable on the basis of survey design or execution. This process should also be used to identify criteria needed for the development of improved methods for the design and execution of future net haul surveys.

With regard to assumptions 2 and 3, there must be some doubt at this stage whether they strictly hold true, given the possibility that krill may shrink (Ikeda and Dixon, 1982). However, shrinking alone is not necessarily a problem. If shrinkage occurs in a way which preserves the order of lengths between age classes across the population, the method is not invalidated. A weaker assumption is sufficient; the method is valid so long as growth prior to the period of the surveys increases the sizes of older animals, even if they have become scrambled by shrinkage, to above the length distribution of the incoming recruits. This is because the analysis treats the parameters of the older components as nuisance parameters. The clear peaks for putative one-year-old krill suggest that this weaker assumption is more likely to hold in the case where this is the youngest age class considered. However, a number of surveys show very low densities of putative one-year-olds. Either these animals were indeed largely absent from the population in those years, or the survey results are not representative for this age class. If the former is true then the results should be included in the estimates of mean recruitment rate and its variability. If the latter, then these particular results should not be used. The analyses of recruitment of two-year-old krill require the stronger assumption of preservation of the length ordering of the population. Therefore these results should be regarded with greater caution.

Since the results of the method appear promising from a purely statistical point of view, it should be worth putting further effort into designing and carrying out more net haul surveys, particularly if the surveys can be improved to ensure that the one-year-old animals are correctly represented.

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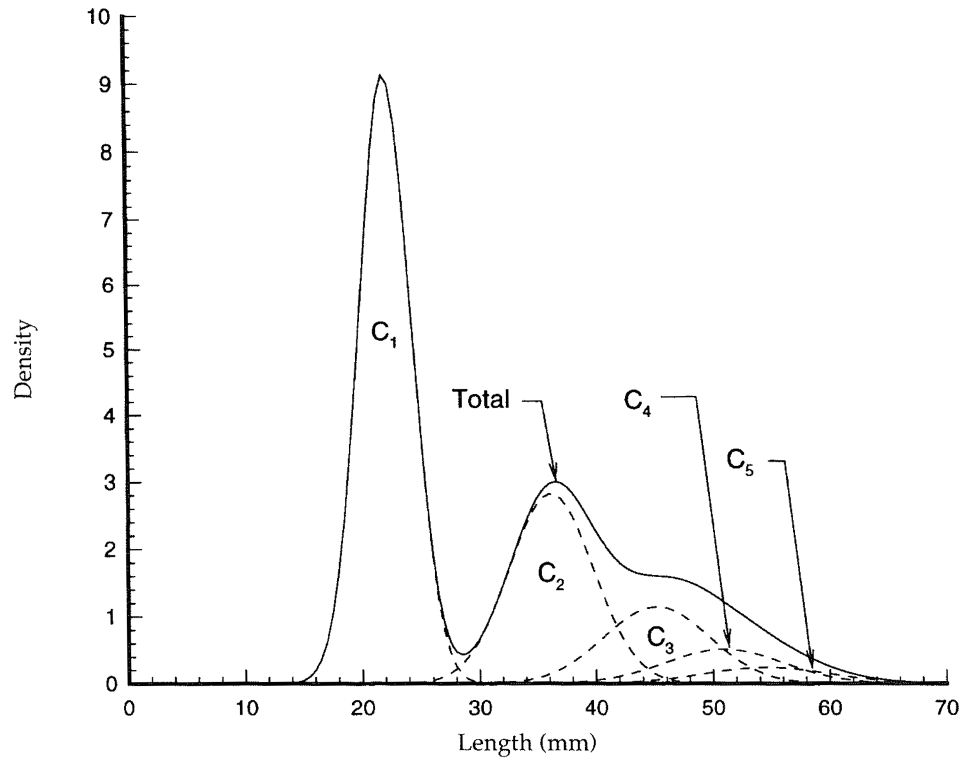


Figure 1: Schematic mixture distribution generated from five nominal age classes with length-at-age distributions C_1 to C_5, and growth and mortality within the range expected for Antarctic krill.

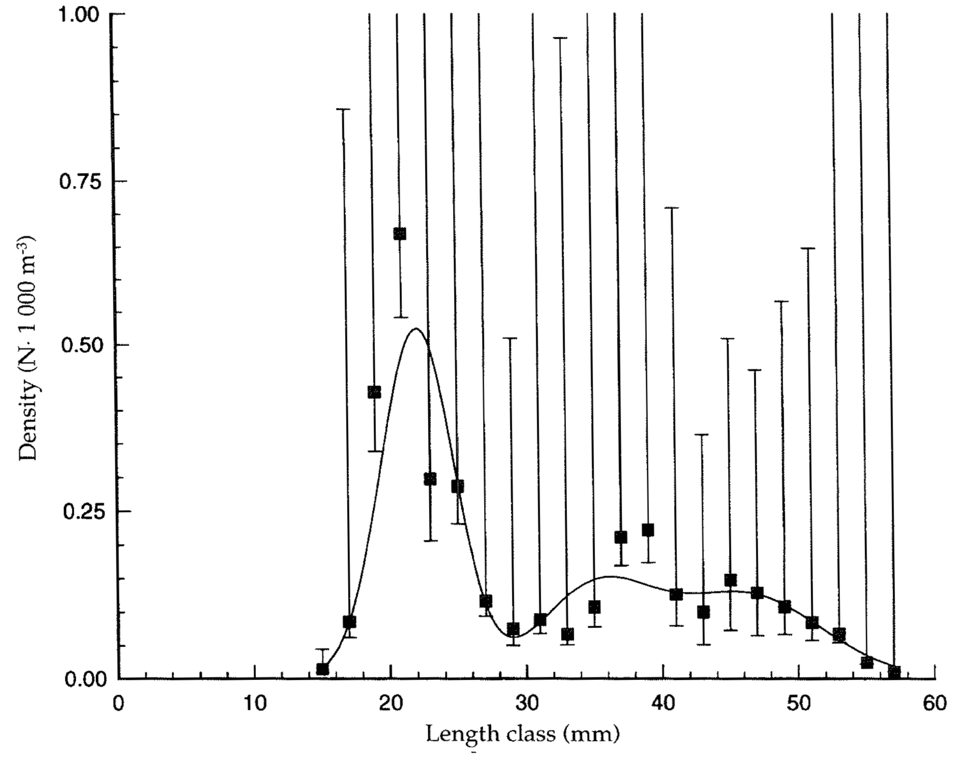


Figure 2: Fit of a mixture distribution to the density-at-length distribution obtained from a net survey by the *Nella Dan* during SIBEX II.

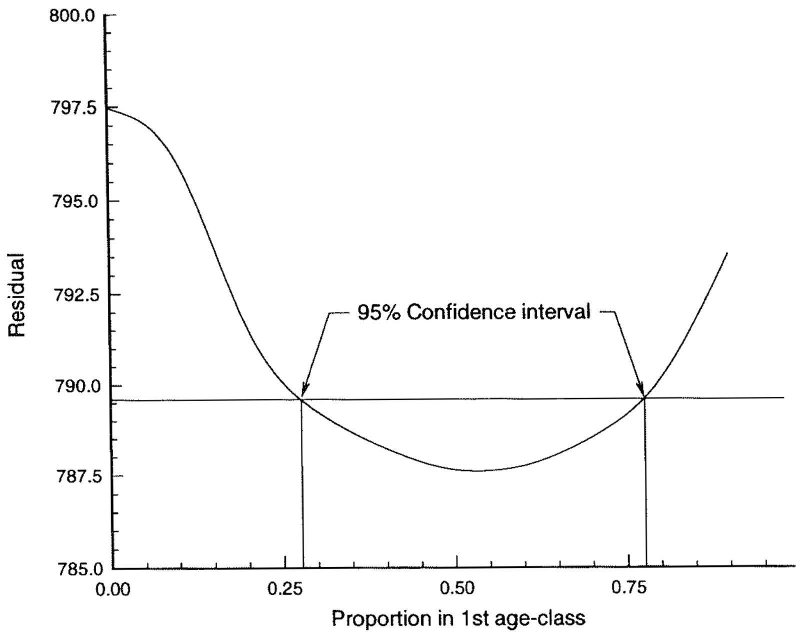


Figure 3: Residual function values versus $R(1)$ rate for the SIBEX II net survey data of the *Nella Dan*, showing the asymptotic 95% confidence interval. The maximum likelihood estimate of the $R(1)$ rate is at the minimum of the curve.

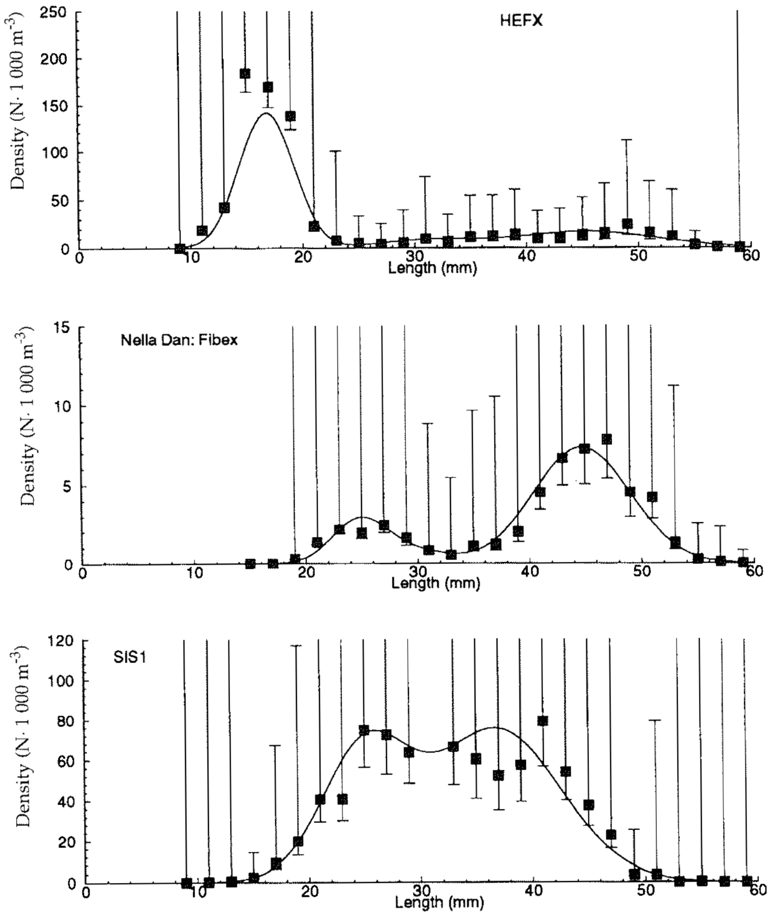


Figure 4: The fit of mixture distributions to density-at-length data from various surveys, with a youngest putative age of one year. Top - *Walther Herwig* during FIBEX, centre - *Nella Dan* during FIBEX and bottom - *Professor Siedlecki* during SIBEX I.

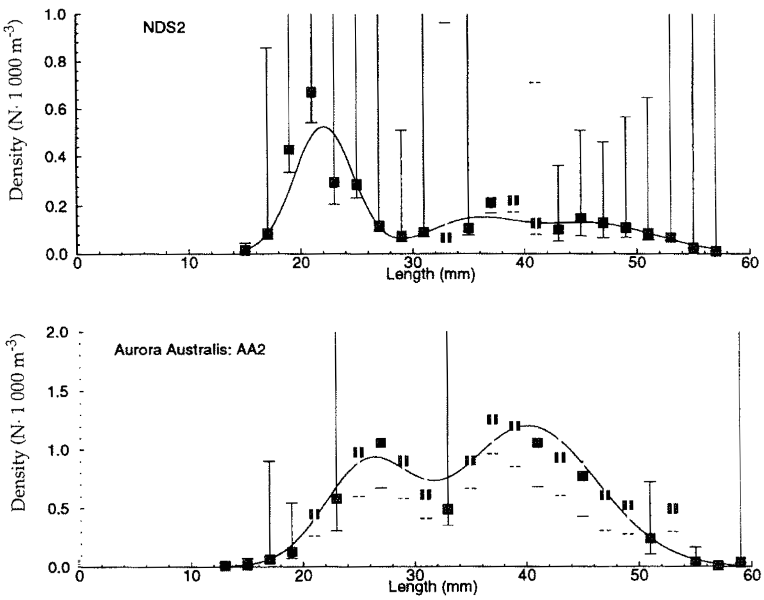


Figure 5: The fit of mixture distributions to density-at-length data from various surveys, with a youngest putative age of one year. Top - *Nella Dan* during SIBEX II, bottom - *Aurora Australis* during AA2.

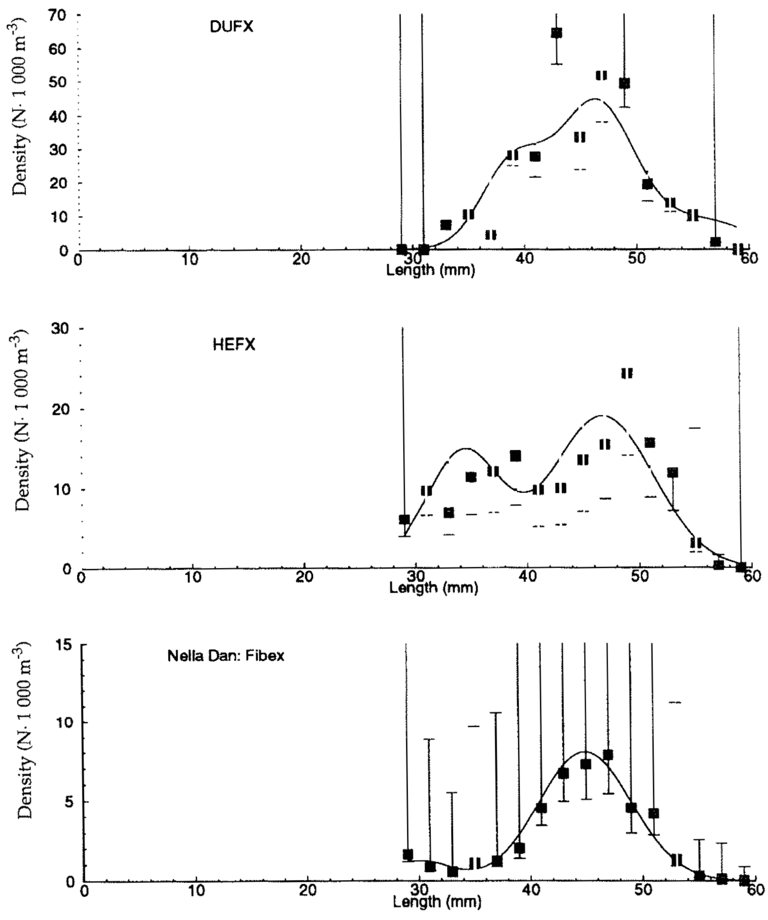


Figure 6: The fit of mixture distributions to density-at-length data from various surveys, with a youngest putative age of two years. Top - *Marion Dufresne* during FIBEX, centre - *Walther Herwig* during FIBEX and bottom - *Nella Dan* during FIBEX.

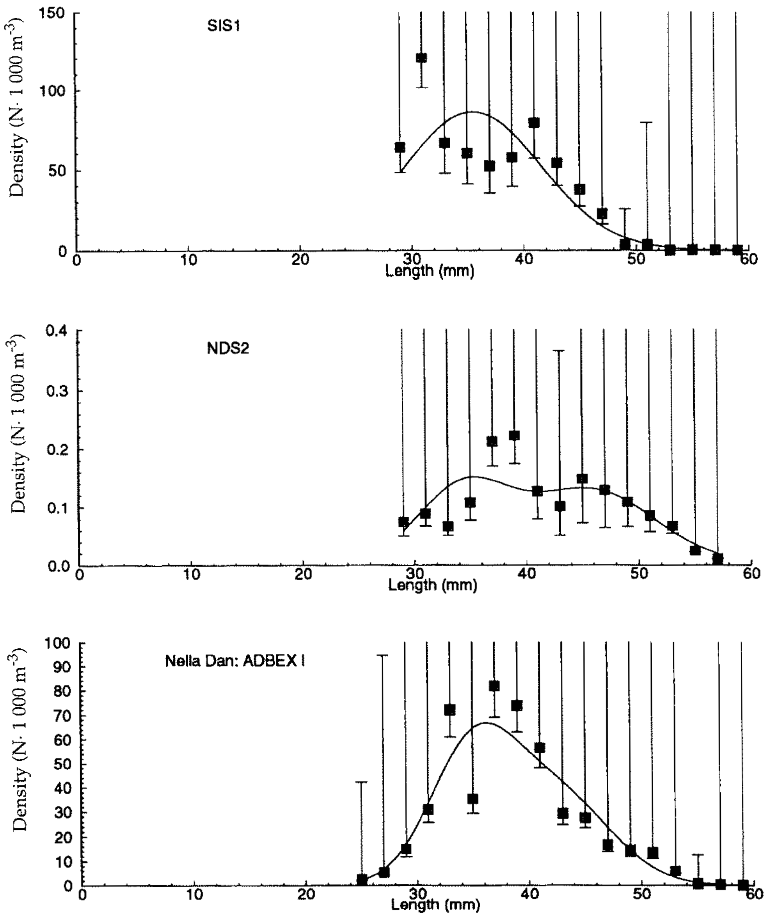
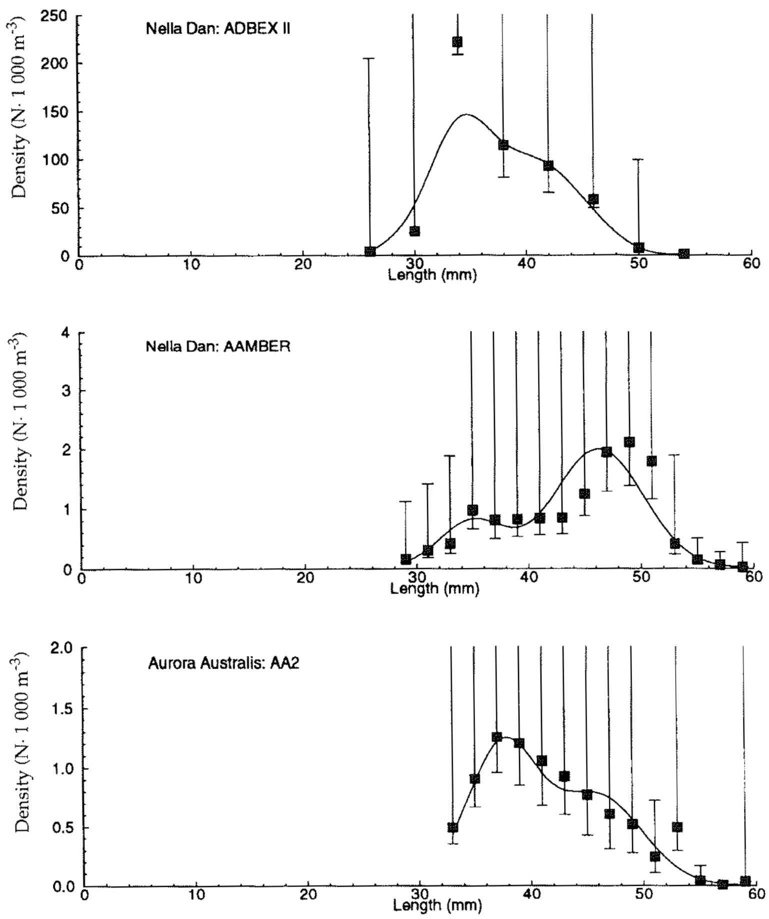


Figure 7: The fit of mixture distributions to density-at-length data from various surveys, with a youngest putative age of two years. Top - *Professor Siedlecki* during SIBEX I, centre - *Nella Dan* during SIBEX II and bottom - *Nella Dan* during ADBEX I.



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