A Likelihood-Based Model of Fish Growth With Multiple Length Frequency Data

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A model for individual growth is an important component in the analysis of fishery resources. Time series of body-length frequency data (LFD) contain information on average individual growth, but age is a latent variable and this makes it difficult to extract growth information objectively. A new method is described here that relaxes some of the assumptions of currently available approaches and that can be used even with large gaps in the time series of LFD. The new method is based on a non-Bayesian hierarchical model where the growth model contains hyper-parameters that depend on parameters of normal mixture models underlying the LFD. Growth hyper-parameters are estimated using a multivariate normal marginal-estimated likelihood function. The method is applied to the squat lobster *Pleuroncodes monodon* with LFD from six surveys, leading to a precise model of individual growth due to the large sample size in the original LFD sets. ADMB computer code and datasets used in this article are supplied as supplemental material.

Key Words: Marginal likelihood; Mixture models; Multivariate normal; Squat lobster.

1. INTRODUCTION

Individual body growth is a fundamental biological process and a model for this process can be applied in many contexts. To estimate a growth model averaged across individuals in a population it is best to have cross-sectional paired observations of age and body size from many individuals of different age, or longitudinal observations of body size and age from many individuals that started at different ages. However, age data can be difficult to obtain, whereas body size data usually are easily available, especially from fish and invertebrates subject to fishing and regular monitoring. In many fish and invertebrate populations young individuals enter the population through pulses of recruitment, forming cohorts that exist contemporaneously. Thus, in fisheries it has been common practice to turn a vector of body length data into a matrix of counts at length categories, to try to ascertain the presence of

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pulses of recruitment as modes in the histogram of length frequency data (LFD). In the histogram, age is an unobserved, latent variable and so is the mean length at age.

The current standard in growth modeling with LFD is the MULTIFAN algorithm of Fournier et al. (1990) and the extension MULTIFAN-CL by Fournier, Hampton, and Sibert (1998). MULTIFAN-CL models both growth and population dynamics using time series of LFD. In MULTIFAN the model of each LFD is a scaled mixture of normal distributions, with each component distribution representing a cohort of fish, the means laying on a von Bertalanffy growth model, and the standard deviations linearly related to the means. This is essentially the model introduced by Macdonald and Pitcher (1979), but generalized to time series of LFD. The method developed here can be considered a generalization of the MULTIFAN algorithm in the sense that (1) no relation between the means and the standard deviations is assumed, (2) the mixture of cohorts can be modeled by a mixture of distributions other than normal, and (3) the growth model can be any suitable model, not necessarily von Bertalanffy's. The first generalization is important because in some marine populations the variability in length at age is more determined by presettlement processes, such as the duration of the hatching season, than by postsettlement processes, such as the history of environments experienced by specific cohorts. Therefore, variability of length at age is mostly fixed in early life for each cohort, so it is a characteristic of the cohort that does not change much with time. This happens, for example, in the squat lobster (Roa 1993), the example application in this article. The second generalization is also important because the distribution of length-at-age can be skewed by process such as differential observability of individuals at the tails of the distribution. This happens, for example, when a fishing net selects only the largest fish of young cohorts as a result of mesh size. The third generalization accounts for the fact that many fish and invertebrates do not conform to the strictly constant negative acceleration of growth rate in length underlying the von Bertalanffy formulation (for example, see Arkhipkin and Roa-Ureta 2005). From a more pragmatical point of view, our method is a viable alternative to MULTIFAN when the time series of LFD have large gaps, for in those cases cohorts could not be followed through time. The method presented here only uses the time serial information for model checking, not for estimation.

2. DATA, METHODS, AND STATISTICAL MODELS

2.1. DATA AND BACKGROUND KNOWLEDGE

Twelve LFD sets from six surveys (1982, 1983, 1984, 1986, 1991, and 1996) carried out on the northern branch of the squat lobster (*Pleuroncodes monodon*) population off central Chile (details in Roa and Tapia 1998, 2000), plus three more LFD sets from surveys (1993, 1994, and 1996) of the nursery grounds (Roa et al. 1995; Roa and Tapia 1998) are used in this work. Growth models were estimated separately for males and females. Previous results (Gallardo et al. 1994) showed that recruitment onto this population occurs as a pulse once per year. In addition, the distribution of body length for each cohort at recruitment is well approximated by a normal density (Roa et al. 1995). So the mixture

models for each LFD were normal mixture models where each age component is an annual cohort.

2.2. STAGE 1—MIXTURE MODEL IDENTIFICATION AND ESTIMATION

The number of year classes composing each mixture of normal distributions, as a model of the raw LFD, is unknown because age is a latent variable. Here this is treated as a model identification problem (sensu Akaike 1974), not as a problem of estimation (as in Roa and Ernst 1996 and Laslett, Eveson, and Polachek 2004) or hypothesis testing (Fournier, Hampton, and Sibert 1990). Consider the following normal mixture problem for observations of length y grouped in classes of width δ

$$H(y, \delta) = n \sum_{j=1}^{J} \int_{y-\delta}^{y+\delta} f(u|\mu_j, \sigma_j^2) \, du \, \omega_j, \qquad \sum_{j=1}^{J} \omega_j = 1, \ 0 \le \omega_j \le 1, \qquad (2.1)$$

where H is the expected number of observations lying in the interval defined by $[y - \delta, y + \delta]$, for some small δ, n is the total number of observations, f is a normal probability density function depending on parameters μ_j and σ_j^2, ω_j is proportion of f in the mixture, and J is the number of component distributions. Our application concerns individual squat lobsters whose carapace length lies in an interval of 1 mm ($\delta = 0.5$) and J is the unknown number of cohorts. As pointed out above, selectivity of the fishing gear may affect the shape of the length distribution at early ages when using commercial fishing LFD, making these distributions less prone to be modeled by normal distributions. In the case of our applications this is considered a minor problem since the LFD was collected during scientific surveys, whereby effort was made to catch all sizes of squat lobster available in the study area.

In selecting among the prospective mixture models, several objective criteria are available. The first criterion is the quality of convergence results after careful exploration of initial values for parameters. Convergence failure here includes any of the following cases: divergence, nonpositive definite Hessian matrix, or unreliable parameter estimates. Covergence failure may occur for several reasons, including inability of the algorithm to handle complex multidimensional optimization problems. The software used in this work, ADMB (*otter-rsch.com*) uses automatic differentiation, an extension to C++ that allows optimization of a differentiable function over hundreds of dimensions. Thus, I attributed cases of convergence failure as evidence that the mixture model that failed to converge was misspecified, either because of too many or too few mixture components. In the cases when convergence was achieved and the Hessian was positive definite, I considered that convergence failed if it resulted in very low mixture proportions and/or very high standard deviations. Specifically, proportion mixtures close to 1% and/or standard deviation higher than 4 mm were deemed unreliable. The second criterion, the Akaike information criterion (*AIC*), applies to models that converged to a positive-definite Hessian and whose parameters are reliable. The total number of parameters in the mixture models is $3J - 1$ so the *AIC* is

$$AIC_J = -2 \Big(\max_{\theta} \log L_J - (3J - 1) \Big). \qquad (2.2)$$

$AIC_{\min}$ is the *AIC* of the model with the smallest distance to the true unknown model. It is considered that a difference of 2 in *AIC* represents a "significant difference" between two models (Sakamoto, Ishiguro, and Kitagawa 1986, ch. 4, remark 2). Here a different procedure, based on the likelihood concept of the "strength of evidence" (Royall 1997), is adopted. The *AIC* weights (Burnham and Anderson 2002)

$$AW(M_J|\{M\}) = \frac{e^{-(1/2)(AIC_J - AIC_{\min})}}{\sum_J e^{-(1/2)(AIC_J - AIC_{\min})}} \tag{2.3}$$

are computed, where M_J is the model of order J and $\{M\}$ is the set of models being compared. Then Akaike ratios are computed, defined as

$$AR(M_J, M_{J'}) = \frac{AW(M_J)}{AW(M_{J'})}, \tag{2.4}$$

and interpreted in analogy with the Law of Likelihood (Hacking 1965; Tsou and Royall 1995; Royall 1997), i.e., Akaike ratios measure the strength of the evidence in favor of model J vis-à-vis J' given the set $\{M\}$. Specifically, the following benchmark is set: if one specific model vis-à-vis another has an *AIC* ratio of 8 or higher, then there is enough evidence in favor of the former model (see Royall's (1997, p. 11–12) canonical experiment). Otherwise the *AIC* is inconclusive. If the *AIC* is inconclusive for both female and male models of the LFD for a given year, but points in the same direction in both datasets, then the model order with the lowest *AIC* in both sexes is selected. A final check of model selection can be completed in Stage 2. This is a check of serial consistency. For consecutive years the model identification stage must yield year classes that, when connected to form cohorts, will show increasing mean individual size with increasing year index. Specifically, let $[t, a, \hat{\mu}_{t,a}]$, be a year class with t the year index, a the age class, and $\hat{\mu}_{t,a}$ the estimated mean length. Then for year classes $[t, a, \hat{\mu}_{t,a}]$ and $[t+1, a+1, \hat{\mu}_{t+1,a+1}]$, $\hat{\mu}_{t+1,a+1} > \hat{\mu}_{t,a}$ because animals tend to grow with time (see Premise I below).

The multinomial log-likelihood (i.e., support function) was the same as that presented by MacDonald and Pitcher (1979)

$$-\ln L(\boldsymbol{\theta}|\tilde{H}(y, \delta)) = -n \sum_{y=1}^{Y} \tilde{\lambda}_y(\tilde{H}) \ln_y(\boldsymbol{\theta}), \tag{2.5}$$

where $\boldsymbol{\theta}$ is the vector of parameters in the mixture, $\tilde{H}$ is the observed frequency in length category $[y - \delta, y + \delta]$, and the λ_y and $\tilde{\lambda}_y$ are estimated and observed relative frequencies at length category, with Y the number of length categories.

The same restrictions set by MacDonald and Pitcher (1979) were introduced into ADMB 6.0.2 (Otter Research Ltd.) code: (1) the sum of proportions of the component distributions adds up to 1, (2) the means of the component distributions are distinct, and (3) the component standard deviations are all higher than 0. These conditions were set by establishing bounds for parameter estimates. Models whose parameter estimates consistently hit the bounds were dropped from consideration and designated as convergence failure. The resulting estimated parameters for the mixtures are maximum likelihood estimates. ADMB code and data files are available on *JABES* repository.

2.3. STAGE 2—AGE ASSIGNMENT

The relevant output of Stage 1 is a matrix with as many rows as there were components in the mixtures of all LFD sets pooled together, and two columns, one for the mean body length estimate and another for the year index of each component. In Stage 2 it is necessary to classify each mean body length estimate into a specific age class, i.e., a new column of ages has to be added to the Stage 1 output matrix. To accomplish this two biological premises are introduced. Premise I is a weak assumption stating that individuals tend to grow as they age. This premise means that when sorting all year-indexed mean lengths, and the corresponding year index, into ascending mean length, those further down the list are imprecisely older. Premise II is the strong assumption that each year no more than one cohort and no less than one cohort enter the population. The "no more than one cohort" part means that it is not possible that two mean lengths with the same year index will belong to the same age class. The "no less than one cohort" part means that it is not possible that two consecutive mean lengths with the same year index will belong to two non-consecutive age classes.

The practical consequence of Premise I and the "no more than one cohort" part of Premise II is that, in the list of mean lengths in ascending order and their year index, it is necessary to introduce an age transition whenever a year index repeats itself. For example, in females the sorted list yielded the following order in the first seven year-class indices: the three juvenile year classes, 96, 82, 84, 96, ... Thus an age transition must be included between the sixth and seventh year classes because the 96 year index repeats and there cannot be two years classes with the same year index in the same age class. This procedure would yield a unique age assignment if all years were represented by the same number of components. In the present application this is not the case so there are still ambiguities, in particular regarding the age class of the first year class from each year. The check of serial consistency helps resolve these ambiguities, as will be shown below.

Up to this point the age classes are relative. However, if the absolute age of one age class were known then the absolute age of each age class would be known, to a certain degree of accuracy (years, or year and months). In the application in this article the age of the first year class is known to be 0 years from survey observations in the nursery grounds in 1993, 1994, and 1996. Thus, consecutive age classes were assigned an absolute age value consisting of an integer number of years.

2.4. STAGE 3—GROWTH MODEL ESTIMATION

The relevant output resulting from Stages 1 and 2 are the pairs of mean body length estimates and absolute age for the several year classes thought to be present in the whole set of LFD, plus the estimated covariance matrices from each mixture fit. These pairs and the covariance matrices are the observations to be used in fitting the growth model, namely Schnute's growth model, as reparameterized by Arkhipin and Roa-Ureta (2005),

$$y(a; \boldsymbol{\theta}) = y_0 \big[(\nu^b/(1-b) - y_0^b)(1 - e^{-K(a-a_0)}) \big]^{1/b} \tag{2.6}$$

where y_0, ν, K, b, and a_0 are parameters. In this five-parameters model, two are known for the squat lobster, namely $a_0 = 0$ and $y_0 = 5.45$ mm. Moreover, in Arkhipkin and Roa-Ureta's reparameterization the ν parameter is the inflection point of the growth curve in body length units, the length separating a juvenile growth regime with positive acceleration of growth and an adult growth regime with negative acceleration of growth. Previous research showed that the squat lobster grows asymptotically, i.e., with negative acceleration of growth, over most of its lifespan (Roa 1993; Roa and Tapia 1998). So a further simplification can be introduced by making the inflection point ν equal to the initial length y_0. This yields

$$y(a; \boldsymbol{\theta}) = y_0 \left[1 + (b/(1-b))\left(1 - e^{-K(a-a_0)}\right) \right]^{1/b}, \tag{2.7}$$

where $\boldsymbol{\theta} = [b \ K]$ is the parameter vector. This is a two-parameter growth model whose acceleration of growth in length units is not constant.

The exact likelihood function for the matrices of age and mean length at age for each year of data as a function of growth parameters is, in general, not expressible in closed form because the polytomous age variable is not observed, it is a latent variable, as is mean length at age. Instead, a marginal likelihood function as an approximation to the exact likelihood function is developed here. This allows fitting the growth model to mean length and age including the uncertainty on estimated mean lengths as evaluated in the estimated covariance matrices, and carrying over the relevant part of the original statistical information in the raw length frequency data.

Note that the concept of "marginal likelihood" that is being used here differs from the Bayesian concept of marginal likelihood. The latter is an "integrated likelihood," whereas the former is the likelihood function of a function of the data (Royall 1997). Formally, the marginal likelihood is similar to an empirical likelihood, except that it is parametric. A formal definition can be found in Pawitan (2001, p. 278). Let the data $\tilde{H}$ be transformed into (y, w), where y are the maximum likelihood estimates of the mean lengths at age and w are any other estimates from the data resulting from all other processes unaccounted for in the model of Equation (2.7). Let the parameter controlling y be θ, the parameter of interest, and let η be the nuisance parameter controlling w. The exact likelihood of data $\tilde{H}$ can be decomposed in the following manner, $L(\theta, \eta \mid \tilde{H}) = p_{\theta,\eta}(y, w) = p_\theta(y) p_{\theta,\eta}(w|y)$. $p_\theta(y)$ is the marginal likelihood of θ. It is based on part of the data, but the part that seems most relevant to the model being estimated.

In the mixture distribution models, the maximum likelihood estimates of the mean length at age in each mixture form a multidimensional random vector with dimension equal to the number of year classes in the mixture models identified in Stage 1. These multivariate random vectors are the unitary observations to fit the growth model. Given some weak regularity conditions, it is well known that maximum likelihood estimates are random variables that asymptotically converge in distribution to a normal distribution (Manoukian 1986, p. 89). Thus, it is reasonable to assume a multivariate normal distribution for the vectors of mean length at age. Because the different LFD are independent in producing the maximum likelihood estimates of the mean lengths at age for each year of data, the joint marginal likelihood for each sex is the product of the year-specific marginal

likelihoods. However, this marginal likelihood contains the covariance matrix parameters as nuisance parameters. To eliminate these nuisance parameters from the inference on the parameter of interest, K and b, they are replaced with the numerical estimates obtained when fitting the mixture models, turning the marginal likelihood into a marginal-estimated likelihood function,

$$L_{M-E}(\{K, b\}|\{\hat{\boldsymbol{\mu}}_{82}, \ldots, \hat{\boldsymbol{\mu}}_{96}\})$$

$$\propto |\hat{\Sigma}_{82}|^{-1/2} \exp\left[-\frac{1}{2}(\hat{\boldsymbol{\mu}}_{82} - \hat{\boldsymbol{\mu}}(K, b))^T \hat{\boldsymbol{\Sigma}}_{82}^{-1} (\hat{\boldsymbol{\mu}}_{82} - \hat{\boldsymbol{\mu}}(K, b))\right] \times \cdots$$

$$\times |\hat{\Sigma}_{96}|^{-1/2} \exp\left[-\frac{1}{2}(\hat{\boldsymbol{\mu}}_{96} - \hat{\boldsymbol{\mu}}(K, b))^T \hat{\boldsymbol{\Sigma}}_{96}^{-1} (\hat{\boldsymbol{\mu}}_{96} - \hat{\boldsymbol{\mu}}(K, b))\right] \tag{2.8}$$

where $\hat{\boldsymbol{\mu}}_{82} = \left[\hat{\mu}(a_1)_{82} \quad \cdots \quad \hat{\mu}(a_J)_{82}\right], \ldots, \hat{\boldsymbol{\mu}}_{96} = \left[\hat{\mu}(a_1)_{96} \quad \cdots \quad \hat{\mu}(a_J)_{96}\right]$ are the vectors of mean lengths at age estimated for years 82, 83, 84, 86, 91, and 96 in the mixture models, $\hat{\boldsymbol{\Sigma}}$ are the corresponding numerical covariance matrices, and $\hat{\boldsymbol{\mu}}(K, b)$ is the vector of mean length at age predicted by the growth model. This estimation method follows the general strategy outlined by Royall (1997, p. 155). ADMB 6.0.2 code was written to carry out the maximization of the marginal-estimated likelihood of hyper-parameters K and b. Codes and data files are available on *JABES* repository.

3. RESULTS

3.1. STAGE 1

In 10 out of 12 model identification problems, one of the candidate models was clearly superior because of convergence failure of some prospective models or because the *AIC* ratio clearly identified the order of the best working model (Table 1). In both sexes 1991 models of order 3 and 4 were tied. However, in both sexes the 4-order model had the fourth component with a proportion parameter near to 1%. This, and the fact that in both sexes there was a slight superiority of model order 3, allowed the identification of the latter. Visually, the working models gave a reasonably good fit for all 12 cases (Figure 1). Twenty-four components were identified in females, 25 in males.

3.2. STAGE 2

To the 24 components in females and 25 in males resulting from Stage 1, three juveniles (0-yr) age classes from Roa and Tapia (2000) were added. The application of Premise I and the "no more than one cohort" part of Premise II yielded a good age classification and ambiguities were resolved by recourse to the serial consistency model check. For example, in females, if the first year class of 96, 82, and 84 belong in the same age class, the age class 2, it would imply that the third year class of 1982 actually decreased in mean size in one year, $[t = 82, a = 3, \hat{\mu}_{t,a} = 29.6] \rightarrow [t + 1 = 83, a + 1 = 4, \hat{\mu}_{t+1,a+1} = 28.5]$. Putting the first year class of 1982 in the third year class yielded serial consistency. The full check after this correction in females shows: $[82, 2, 16.8] \rightarrow [83, 3, 25.7] \rightarrow [84, 4, 32.3], [82, 3, 24.5] \rightarrow$ $[83, 4, 28.5] \rightarrow [84, 5, 35.4], [83, 2, 21.2] \rightarrow [84, 3, 27.6], [84, 1, 18.6] \rightarrow [86, 3, 25.7], [84, 2, 22.3] \rightarrow [86, 4, 32.5]$; all increasing in mean length. In males the result was [82, 2,

Table 1. Strength of evidence about the order of mixture models for the length distribution of squat lobsters using Akaike's theorem. The *AIC* ratio is the ratio between the model with the lowest *AIC* and the model under which the ratio is shown. Empty cells indicate that the model was not attempted for that particular year-sex combination. CF (convergence failure) indicates that the estimation was attempted, but there was no convergence or that the Hessian was not positive definite or that the mean and/or standard deviation of some component distributions consistently hit the bounds.

Year	Quantity	Females				Males			
1982	Model order	3	**4**	5	6	3	**4**	5	6
	−LogLikelihood	CF	**16,006**	CF	CF	20,242	**20,232**	CF	CF
	N° parameters		**11**			8	**11**		
	AIC		**32,034**			40,500	**40,487**		
	AIC ratio					898			
1983	Model order	**3**	4	5	6	**3**	4	5	6
	−LogLikelihood	**15,046**	CF	CF	CF	**23,756**	CF	CF	
	N° parameters	**8**				**8**			
	AIC	**30,109**				**47,528**			
1984	Model order	3	4	**5**	6	3	4	**5**	6
	−LogLikelihood	9,772	9,770	**9,760**	CF	19,156	19,152	**19,142**	CF
	N° parameters	8	11	**14**		8	11	**14**	
	AIC	19,560	19,561.7	**19,549**		38,329	38,326	**38,312**	
	AIC ratio	299	713			4,915	1212		
1986	Model order	**3**	4	5	6	3	**4**	5	6
	−LogLikelihood	**8,030**	8,030	CF		13,767	**13,755**	CF	
	N° parameters	**8**	11			8	**11**		
	AIC	**16,077**	16,083			27,551	**27,532**		
	AIC ratio		17			12,088			
1991	Model order	**3**	4	5	6	**3**	4	5	6
	−LogLikelihood	**13,357**	13,356	CF		**18,151**	18,148	CF	
	N° parameters	**8**	11			**8**	11		
	AIC	**26,731**	26,734			**36,318**	36,319		
	AIC ratio		4				3		
1996	Model order	5	**6**	7		5	**6**	7	8
	−LogLikelihood	22,735	**22,715**	CF		36,225	**36,211**	CF	CF
	N° parameters	14	**17**			14	**17**		
	AIC	45,498	**45,464**			72,478	**72,456**		
	AIC ratio	$>1 \times 10^6$				44,356			

16.9] → [83, 3, 28.0] → [84, 4, 32.1], [82, 3, 25.5] → [83, 4, 34.8] → [84, 5, 36.6], [83, 2, 21.7] → [84, 3, 28.0] → [86, 5, 38.1], and [84, 1, 18.1] → [86, 3, 28.5], all increasing in mean length. The confirmed age assignment is shown in Figure 2.

3.3. STAGE 3

The estimated model for each sex is shown in Figure 3 with parameter estimates in Table 2. In the figure, the size of points is proportional to the reciprocal of the asymptotic standard errors to appreciate which component distributions have stronger effects on the estimated model. In the case of females, the second component of 1982 and the second component of 1983 carry more weight in estimating the model, whereas in males the second and third components of 1982 are more influential.
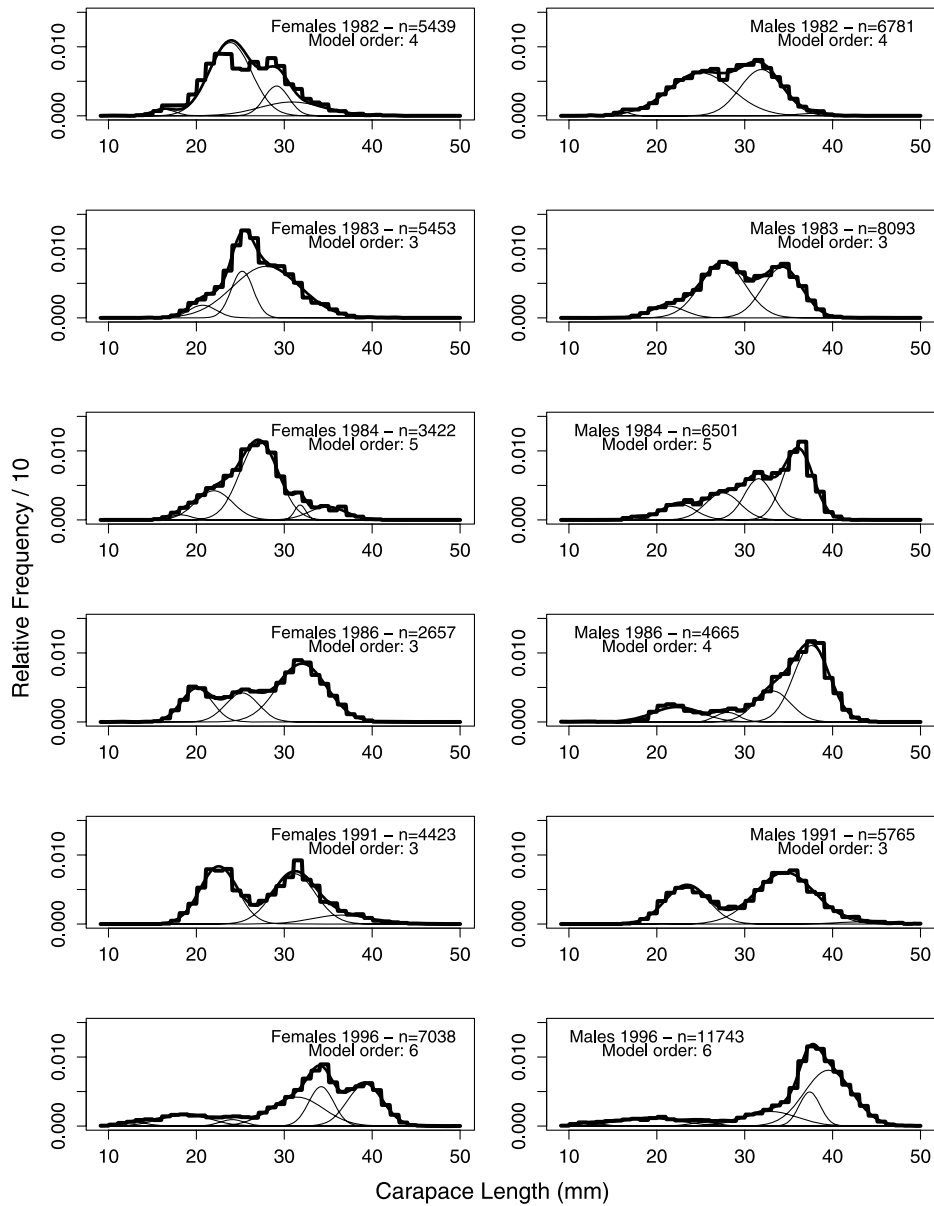
Figure 1.   Length frequency data (step curve) and fitted mixture models (envelope line) for six surveys and two sexes of the squat lobster. Each normal distribution (inner lines) represents an annual cohort.

4. DISCUSSION

4.1. INFERENCE FRAMEWORK

Age (a) and mean length at age (μ_a) are not directly observed. The distribution of these latent variables is controlled by the growth parameters $\boldsymbol{\theta}$. In a hierarchical Bayesian inference framework, the prior distribution of growth parameters would be
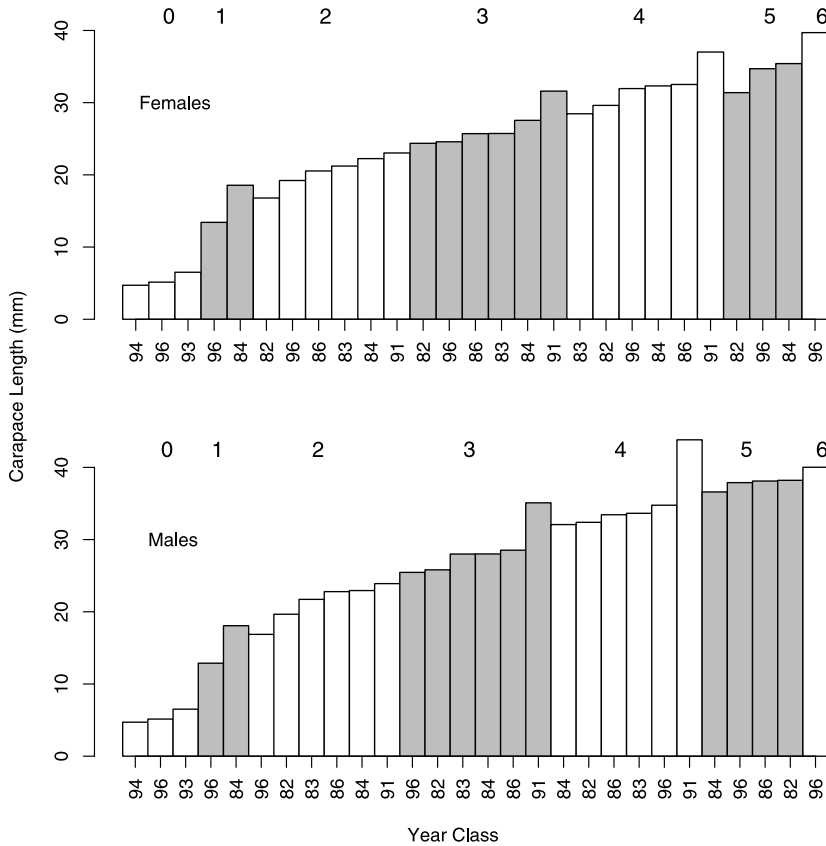
Figure 2. Assignment of age class to the year classes in Figure 1 using Premises I and II from Stage 1. Consecutive age classes are shown with contrasting shading. Also shown are the integer parts of the age of each age class.

$\Pr(\theta \mid \{\mu_a, a\}) \Pr(\{\mu_a, a\} \mid \gamma) \Pr(\gamma) = \pi(\theta, \{\mu_a, a\}, \gamma)$, whereas the joint posterior distribution would be $\Pr(\theta, \gamma, \{\mu_a, a\} \mid \tilde{H}) = \pi(\theta, \{\mu_a, a\}, \gamma) \Pr(\tilde{H} \mid \gamma)$, where γ are the parameters of the mixtures, and $\tilde{H}$ are the LFD. Here we show a non-Bayesian hierarchical model of estimation of growth parameters θ based on an approximate marginal likelihood function for the hyperparameters θ. This inferential approach is close to the direct-likelihood school of inference (Edwards 1972; Royall 1997; Lindsay 1999a).

A critical stage of the analysis is the model selection of scaled mixtures for the several sets of LFD. Inspection of Figure 1 may suggest that some selected models were suspicious. For example, (1) females 1983 has a very wide component implying a cohort spread over most of the length range, (2) females 1984 has the opposite situation with a small cohort very precisely located along the length range, and (3) males 1996 has a cohort that is completely covered by another cohort. The first case is not open to discussion because it was the only model that yielded proper convergence. However, the other two models were selected because the Akaike weights strongly supported those models. This author shares the view of Akaike (1974), Lindsey (1999b), and Bunrham and Anderson (2002), that hypothesis testing is not a proper framework for model selection. In the case of the ap-
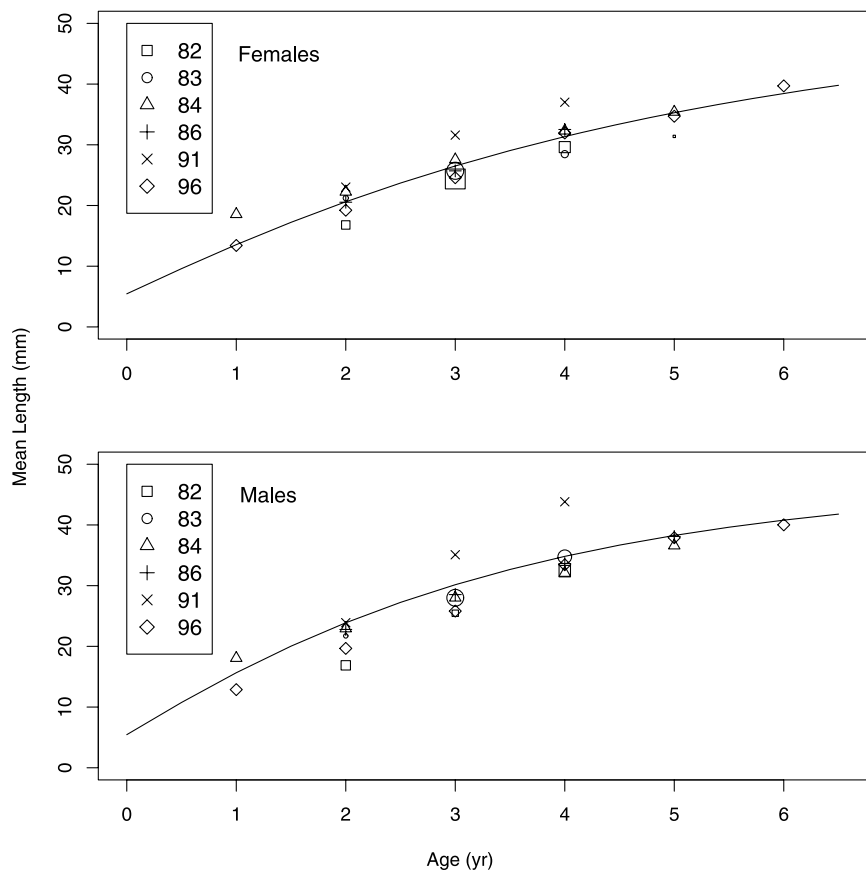
Figure 3.   Estimated mean length at age in mixture distribution models of length frequency data and estimated growth model using a marginal-estimated likelihood function. The size of symbols is proportional to the reciprocal of the span of each men length-at-age maximum likelihood estimate.

plications here, the suspicious models selected within the Akaike framework are actually consistent with the view that variability of length at age is a characteristic of each cohort, fixed in early life due to presettlement processes of the marine environment (Roa 1993).

Table 2.   Estimates of individual growth parameters for the Schnute model for females and males of the squat lobster.

| | | | Coformation or covariance matrix | |
		Value or estimate	K (yr^{-1})	b
Females	Max. support	−6,253.7		
	K (yr^{-1})	0.229	5.7×10^{-6}	
	b	0.851	-2.8×10^{-6}	1.4×10^{-6}
Males	Max. support, AIC	−7,773.0		
	K (yr^{-1})	0.324	4.2×10^{-6}	
	b	0.837	-1.2×10^{-6}	3.6×10^{-7}

Thus, some cohorts will be widely spread over the length distribution and others will be confined within narrow bounds, depending on processes such as the duration of the spawning season and the duration of larval life.

4.2. COMPARISON WITH PREVIOUS METHODS

The problem treated in this article can be described as a latent-variable nonlinear regression model where the predictor variable (age) is polytomous and latent, the response variable (length) is continuous and manifest, and the data are clustered. This description highlights the complexity of the problem. Thus, all methods proposed to extract the growth information from series of LFD, including the method proposed here, assume that the latent variable has been revealed; made manifest, in this case, by the population ecology concepts of Stage 2.

There are at least two other methods to extract the growth information modeling the LFD as mixtures of scaled normal distributions. The first method, MULTIFAN, is the current standard. In the first version the number of normal components in each LFD was fixed by results of the frequentist test of hypothesis based on the likelihood ratio test (MULTIFAN, Fournier, Hampton, and Sibert 1990), in spite of the fact that, for the case of the number of components in mixtures, the likelihood ratio test does not apply because the necessary regularity conditions are not met (Lo, Mendel, and Rubin 2001). The hypothesis test was later changed to posterior Bayes factors (MULTIFAN-CL, Fournier, Hampton, and Sibert 1998). Still, because MULTIFAN-CL is a model of population dynamics, it is affected by large gaps in the time series of LFD. The method presented here, being more modest in purpose, is not affected by these gaps, as shown in the example application with the squat lobster. Also, the additional flexibility of selecting any suitable growth model may prove useful in applications. For example, with the likelihood function as defined in Equation (2.8) and the squat lobster data, the von Bertalanffy model was attempted, but it converged to impossibly high estimates of the asymptotic length.

Laslett, Eveson, and Polachek (2004) described a stage-based method to analyze multiple LFD sets in order to extract individual growth information. The major shortcoming in their two-stage procedure is that they ignored the problem of model identification in the selection of the order of the mixture model. Instead they eliminated inconvenient data (body length > 130 cm) and fitted 5-order mixture models to all LFD sets. If they observed visual evidence of overfitting in any particular LFD then they reduced the model to 4-order, and so on until the visual overlapping of model and histogram was deemed satisfactory. They also ignored some potentially important sources of information and uncertainty in the original LFD. This is because from the first stage of mixture modeling they only retain the mean length estimates and their asymptotic standard errors. Thus, the error term in their random effects model has a variance equal to the asymptotic standard errors of the mean length estimates. To account for all the variability in their original LFD sets, this error term should have had a multivariate normal distribution with matrices of different size, depending on the number of components selected for each LFD. They recognized this problem, though for their particular case the multivariate structure was weak (p. 222). In general however, their procedure is tantamount to assuming that the mean length parameter estimates from

the several mixture models from several LFD sets are independent random variables. However, this is not true by construction because some mean length estimates came from the same LFD set and in each LFD set the mean length estimates were constrained to be different. This latter constrain may cause some high correlations. Our own estimated covariance matrices show an important number of high correlations. Our method takes into account the complete multivariate structure by considering each vector of mean length estimates from each LFD set as the unitary observation value in the fit of the growth model.

SUPPLEMENTAL MATERIALS

Computer code and data: Computer code and data for the mixture model fit and growth model fit. (13253_2009_9_MOESM1_ESM.pdf)

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