A Catch-at-Length Analysis that Incorporates a Stochastic Model of Growth[1]

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A length-structured population model, which incorporates von Bertalanffy growth, is used to describe changes in population abundance over time. The model is incorporated into a catch-at-length algorithm that uses a non-linear least squares approach to estimate relative abundance, fishing mortality, selectivity, and the von Bertalanffy growth parameters L_∞ and k. The algorithm is applied to a simulated data set for Pacific cod (*Gadus macrocephalus*) and to catch data on *Pseudotolithus typus* and *Decapterus russellii*. The parameter estimates of Pacific cod obtained from this algorithm were comparable with the values that were originally used to simulate the data. Although the catch data of *P. typus* did not exhibit the full range of sizes present in the population due to differential vulnerability of the population to the fishery, the estimates of L_∞ and k reflect the growth over the entire size range of the population. Other population estimates for *P. typus* were in agreement with observed biological information. The estimated growth parameters L_∞ and k of *D. russellii* showed some discrepancy with the information available on mature individuals present in this fishery but appeared to adequately represent year 1 growth. The estimated population and exploitation parameters fit the observed catch-at-length. Estimates made with the catch-at-length approach can be improved by using auxiliary information that may be available on abundance, fishing effort, recruitment, and growth.

Nous avons utilisé un modèle de population fondé sur la répartition des tailles des poissons qui prend en compte les paramètres de croissance de von Bertalanffy pour décrire les variations de l'abondance d'une population dans le temps. Nous avons intégré ce modèle à un algorithme de prise par longueur qui utilise les moindres carrés de façon non linéaire pour estimer l'abondance, la mortalité due à la pêche et la sélectivité relatives de même que les paramètres de croissance L_∞ et k de von Bertalanffy. L'algorithme a été appliqué à un ensemble de données simulées relatives à la morue du Pacifique (*Gadus macrocephalus*) et à des données de capture relatives à *Pseudotolithus typus* et *Decapterus russellii*. Les valeurs estimées des paramètres pour la morue du Pacifique obtenues grâce à cet algorithme étaient comparables à celles qui ont été utilisées originalement pour simuler les données. Même si les données de capture de *P. typus* ne couvraient pas l'ensemble de la fourchette de taille de la population, à cause de la plus ou moins grande vulnérabilité des poissons à la pêche selon leur taille, les estimations de L_∞ et k étaient représentatives de la croissance pour l'ensemble des classes de taille de la population. D'autres estimations de population pour *P. typus* correspondaient à certaines données biologiques disponibles. Les paramètres de croissance estimée L_∞ et k pour *D. russellii* ont montré un écart par rapport aux informations disponibles sur les individus matures du stock de pêche, mais ils semblaient valables pour la première année de croissance des poissons. L'estimation de la population et les paramètres d'exploitation correspondaient avec les prises par longueur. Les estimations effectuées avec cette méthode des prises par longueur peuvent être améliorées si l'on utilise des informations supplémentaires éventuellement disponibles relatives à l'abondance, à l'effort de pêche, au recrutement et à la croissance.

The estimation of stock abundance, recruitment, fishing mortality, and gear selectivity is the principal objective of stock assessment. Many of the principal contemporary estimation procedures are based on the application of the Baranov catch equation (Ricker 1975) to catch data classified by age group. This has led to the development of several powerful stock assessment algorithms including virtual population analysis or VPA (Fry 1949; Gulland 1965; Murphy 1965), cohort analysis (Pope 1972); and catch-at-age analysis (Doubleday 1976; Fournier and Archibald 1982; Schnute 1985; Deriso et al. 1985). The classification of catch data into strata or groups that are homogeneous by age suggests that higher quality inferences (Quinn 1986) will result, but there are associated high costs. The determination of age may be hampered by inaccuracy, imprecision, or a lack of valid ageing methods (Lai 1985). These difficulties are partially resolved by the use of an estimation procedure based on the *length* composition of the catch.

Many length-based stock assessment methodologies depend on a von Bertalanffy growth model to translate length into age so that the exponential decay cohort model can be applied. Length–cohort analysis (Jones 1979, 1984; Lai and Gallucci 1987, 1988) and estimators of Z/k (e.g. Beverton and Holt 1956; Ssentongo and Larkin 1973) are among the most popular. How-

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ever, a number of assumptions fundamental to these length-based methods limit their applicability: (1) length distributions are in a steady state over time, (2) recruitment to the fishery is knife-edged and constant, and (3) growth is a deterministic process with length-at-age being well defined. The stock assessment estimation methodology developed in this paper makes no assumptions about the steady state of length distributions and the knife-edged constant recruitment; it computes gear selectivity as a function of fish length from the data, and it describes growth with a stochastic model based on the probability of individuals moving from one length category to another.

The input is catch data in the form of a time series of length distributions and a set of starting values to initiate the optimization algorithm. The output is a set of estimates of abundance and recruitment over length at specific times, fishing mortality over time, gear selectivity by fish length, as well as estimates of the growth parameters L_∞ and k from the von Bertalanffy model.

Model Development

The model that underlies this estimation procedure characterizes the dynamics of the population in terms of numbers at length over time. This length-structured mathematical model describes the exploitation and growth of individuals in the population explicitly in terms of length and is formulated in terms of two basic relationships. The first relates catch-at-length to abundance. The second characterizes changes in numbers at length from one time step to the next.

Catch $(C_{l,t})$ for a given length class l ($l = 1, \ldots, n$) and time t ($t = 0, \ldots, t_{\max}$) is related to the number of individuals in the population $(N_{l,t})$ in that length class at that time through a length-based exploitation rate $(\mu_{l,t})$. The general form of the Baranov catch equation (Ricker 1975) indexed in terms of length class rather than age, holds at time t for fish of length class l:

$$(1) \quad C_{l,t} = \mu_{l,t} N_{l,t}$$

where the exploitation rate $\mu_{l,t}$ represents the proportion of individuals that die due to fishing mortality, given they were in length class l at time t. The exploitation rate is therefore dependent on the fishing mortality rate $F_{l,t}$ and total mortality rate $Z_{l,t}$ of fish of length class l during time t in the following way:

$$(2) \quad \mu_{l,t} = \frac{F_{l,t}}{Z_{l,t}} (1 - e^{-Z_{l,t}})$$

where $F_{l,t}$ and $Z_{l,t}$ are in units of $1/\Delta t$. Combined, equations (1) and (2) reflect the standard form of the Baranov catch equation with individuals classified by length rather than age. The units of the time interval Δt may be expressed in years, as they are in most age-structured models, but they may also be expressed in terms of the time increment over which the observations were collected (e.g. months, weeks, etc.), which may also change from time step to time step.

Fishing mortality is a function of fishing effort and gear selectivity. We assume that fishing mortality is separable into a product of a length-specific selectivity coefficient s_l and a full-recruitment fishing mortality rate f_t at time t following Doubleday's (1976) approach for age-based groups and express it as

$$(3) \quad F_{l,t} = s_l f_t.$$

The length-specific selectivity coefficient s_l is interpreted as the fraction of fish in length class l subjected to the full effect of fishing mortality. It is represented by a gamma-type function:

$$(4a) \quad s_l = \frac{l^{\alpha_s} e^{-\beta_s l}}{\max_k (k^{\alpha_s} e^{-\beta_s k})}$$

or a logistic function:

$$(4b) \quad s_l = \frac{1}{1 + \alpha_s e^{-\beta_s l}}$$

where s_l is rescaled such that the largest s_l is set to 1 to ensure that fishing mortality rates are well defined. The first function is modified from an age-structured formulation suggested by Deriso et al. (1985) and is flexible enough to allow many realistic shapes for the selectivity curve, while the second function is more conventional and probably easier to use. In fact, these two relationships are very easy to apply and constrain. For example, in gamma-type functions, if the length class k where $s_k = 1$ is known, then $k = \alpha_s/\beta_s$ or $\alpha_s = \beta_s k$. The estimated parameters can further be reduced. Logistic curves also can be constrained in the length class l when $s_l = 0.5$ is known.

The total instantaneous mortality of individuals in length class l at time t is separable as the sum of the instantaneous fishing and natural mortality rates:

$$(5) \quad Z_{l,t} = F_{l,t} + M_{l,t}$$
$$= s_l f_t + M_{l,t}.$$

The relationship between the number of individuals $(N_{l,t})$ at time t and the number $(N_{l,t'})$ present at a later time t' is described in terms of the numbers of fish at length surviving and growing into the next time period. If growth is negligible for fish initially in length class l, at time t, then the total number of fish in length class l surviving to the start of time period t' is reduced only by mortality:

$$(6) \quad N_{l,t'} = N_{l,t} e^{-Z_{l,t}}$$

for each length class l ($l = 1, \ldots, n$).

To account for growth, a model is incorporated that combines the inherent variability seen in individual growth with the general nonlinear trend frequently observed for the population as a whole. Growth is represented by the proportion $P_{l,l'}$ of surviving individuals in length class l during a fixed time interval. The proportion $P_{l,l'}$ of individuals that grow from a length class l to all length classes l' ($l' = l, \ldots, n$) is assumed to be represented by a probability distribution function that can be parameterized by its mean and its variance. The mean represents the average growth increment which then can be described by any standard deterministic growth model. The variance represents the individual variability in growth, which in many circumstances is proportional to the mean (Schnute and Fournier 1980; Fournier and Breen 1983); together, under such a formulation, the mean and variance uniquely determine the proportion of individuals going from one length class to another.

For example, to represent the mean of the distribution, consider growth following the von Bertalanffy model:

$$(7) \quad L_t = L_\infty (1 - e^{-k(t - t_0)})$$

where L_t is the length of an individual at age t, t_0 is the time correction factor for the size at birth or recruitment, L_∞ is the theoretical asymptotic length of an individual, and k is the Brody growth constant. Based on this model, the growth increment Δ_l

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over a unit time interval $(t, t+1)$ for a fish starting at length class l at time t with length of L_t can be described as (Chapman 1960)

(8) $\quad \Delta_l = L_{t+1} - L_t$

that may vary from individual to individual. By fixing L_t at the midlength (l_*) of the length class l, Δ_l represents the change in length of an individual initially in length class l. The mean growth increment $\bar{\Delta}_l$ for the individuals in length class l is then the average change in length of individuals initially in length class l:

(9) $\quad \bar{\Delta}_l = (L_\infty - l_*)(1 - e^{-k})$,

an expression that is independent of t_0.

By differencing, as in equation (8), the need for interpretation of time as age in equation (9) is eliminated. Other growth models could be used but the von Bertalanffy growth model offers the most in terms of comparative opportunities in the literature.

For this work, a gamma distribution was used to represent the variation in growth described as above. The gamma distribution was chosen for its versatility and flexibility in approximating several functional forms. It is also definable entirely in terms of its first and second moments, thus reducing the number of parameters to be estimated. Flexibility is required to describe the different patterns of growth for small and large fish. Smaller fish grow faster and the distribution of the change in length Δ_l may be slightly skewed positively. Larger fish grow more slowly, which tends to restrict the growth to adjoining length categories, and the distribution of Δ_l is more concentrated about the mean.

The gamma distribution expressed in terms of the parameters α_l and β (Hogg and Craig 1970) is

(10) $\quad g(x|\alpha_l,\beta) = \dfrac{1}{\beta^{\alpha_l}\Gamma(\alpha_l)} x^{\alpha_l - 1} e^{-x/\beta}$

where x represents Δ_l (the growth increment, given a fish was originally in lengthclass l). The mean change in length is given by $\bar{\Delta}_l = \alpha_l\beta$ and the variance is given by $\sigma_l^2 = \alpha_l\beta^2 = \beta\bar{\Delta}_l$ which is proportional to the mean, as required. In this expression, β is also the coefficient of variation which is used to incorporate the growth variability of individuals in the population. Given l_* and β, the parameters α_l, and consequently $\bar{\Delta}_l$ and σ_l^2, are functions of the two von Bertalanffy parameters L_∞ and k.

The catch observations are classified into length classes, and the growth of individuals in a length class, say class l, where the length of these individuals may range in length from l_1 to l_2 is approximated by the growth of a midlength individual $(l_* = (l_1 + l_2)/2)$ of the class. The expected proportion of individuals growing from length class l to length class l' can then be found by integrating over the length range (l'_1,l'_2) of the receiving length class l' at the beginning of the next time period t':

(11) $\quad P_{l,l'} = \displaystyle\int_{l'_1}^{l'_2} g(x|\alpha_l,\beta)dx$.

Any fish that enters into a length class with the midlength greater than L_∞ is assumed to remain in the class subject to survivorship (i.e. $P_{l',l'} = 1$ for $l' \geq L_\infty$).

A similar model for growth was developed by Gutreuter and Anderson (1985) in describing the effect of body size on recruitment in largemouth bass (*Micropterus salmoides*) populations.

They noted that a gamma distribution function usefully incorporates a variance in the change in length that increases as a function of the change in length. DeAngelis and Coutant (1979) used a partial differential equation growth model and showed that the variance about mean length increases, perhaps quadratically, as a function of time. The von Bertalanffy model, used as above, constrains the number of parameters needed to describe growth to three parameters, L_∞, k, and β, while allowing a stochastic description of growth.

Equations (6) through (11) are now used to calculate the total number of fish $N_{l',t'}$ of lengthclass l' at the start of the next time step t' as

(12) $\quad N_{l',t'} = \displaystyle\sum_l P_{l,l'}N_{l,t}e^{-Z_{l,t}}$.

In this formulation, growth is time (age) invariant. The model can be modified to allow for functional dependence to represent more complex growth patterns.

To complete the description of the dynamics, a renewal function which includes recruitment to the fishery is added to equation (12):

(13) $\quad N_{l',t'} = \displaystyle\sum_l P_{l,l'}N_{l,t}e^{-Z_{l,t}} + R_{l',t'}$

where recruitment to the fishery may occur over a range of length classes. Recruitment specified in this way more generally represents the type of recruitment observed in nature where variation in growth, behavior, or food supply can result in individuals entering the main body of the population at various sizes. Length-specific selectivity (s_l) is then combined with recruitment to the population to reflect the effective entry of individuals to the catch (Gulland 1969). There are several ways of representing recruitment to length class categories beyond the first length class. For example, recruitment to each length class might be represented by a series of constant values $\{R_{l,t}: l = 1,\ldots,n\}$ for each time step t. In the estimation procedure outlined below, however, recruitment is separated into a time-dependent variable R_t and a length-dependent variable p_l, representing the proportion of recruits going to each length class:

(14) $\quad R_{l,t} = R_t p_l$.

One advantage of separating variables is that R_t can be compared with recruitment estimates from standard procedures, such as recruitment to the first age class, while the proportion of recruits going into length classes $\{l: l = 1,\ldots,n\}$ may be represented by another two-parameter gamma distribution, such as the one shown in equation (10), with recruitment parameters α_r and β_r.

The model (13) describes a linear transition of the number of individuals in length class l at time t to the numbers in length class l' at time t'. This model may also be written in matrix notation:

(15) $\quad \begin{bmatrix} N_{1,t'} \\ N_{2,t'} \\ \vdots \\ N_{l',t'} \\ \vdots \\ N_{n,t'} \end{bmatrix} = \begin{bmatrix} P_{1,2} & 0 & & & & 0 \\ P_{1,2} & P_{2,2} & & & & \\ & & * & & & \\ & & & P_{l,l} & & \\ & & & & * & 0 \\ P_{1,n} & P_{2,n} & & & P_{n-1,n} & P_{nn} \end{bmatrix}$

$$\times \begin{bmatrix} S_{1,t} & 0 & & & & 0 \\ 0 & S_{2,t} & & & & \\ & & * & & & \\ & & & S_{l,t} & & \\ & & & & * & 0 \\ 0 & & & & 0 & S_{n,t} \end{bmatrix} \begin{bmatrix} N_{n,t} \\ N_{2,t} \\ \cdot \\ \cdot \\ \cdot \\ N_{n,t} \end{bmatrix} + \begin{bmatrix} R_{1,t} \\ R_{2,t} \\ \cdot \\ \cdot \\ \cdot \\ R_{n,t} \end{bmatrix} + \begin{bmatrix} w_{1,t} \\ w_{2,t} \\ \cdot \\ \cdot \\ \cdot \\ w_{a,t} \end{bmatrix}$$

with $S_{l,t}$ now representing the exponential survivorship, $e^{-Z_{l,t}}$, term in equation (6). Note that Sainsbury (1982) used a length-based transition matrix similar in form to equation (15) to study the pattern of recruitment in a yield-per-recruit analysis and addressed the implications minimum size limits have on yield and yield-per-recruit.

Equation (1) can also be expressed in matrix form:

$$(16) \quad \begin{bmatrix} C_{1,t} \\ C_{2,t} \\ \cdot \\ \cdot \\ \cdot \\ C_{n,t} \end{bmatrix} = \begin{bmatrix} \mu_{1,t} & 0 & & & & 0 \\ 0 & \mu_{2,t} & & & & \\ & & * & & & \\ & & & \mu_{l,t} & & \\ & & & & * & 0 \\ 0 & & & & 0 & \mu_{n,t} \end{bmatrix} \begin{bmatrix} N_{n,t} \\ N_{2,t} \\ \cdot \\ \cdot \\ \cdot \\ N_{n,t} \end{bmatrix} + \begin{bmatrix} v_{1,t} \\ v_{2,t} \\ \cdot \\ \cdot \\ \cdot \\ v_{n,t} \end{bmatrix}.$$

Time-dependent error vectors w_t and v_t are included in equations (15) and (16), respectively, to make the derivation complete and to reflect the stochastic nature of the real population.

Note that the standard age-structured model is a special case of the above, with the subdiagonal probabilities of the length transition matrix P in equation (15) equal to 1 and all other elements 0.

Estimation

The model depicted in equations (15) and (16) is a linear dynamic system and falls into a family of state space models frequently used by engineers, economists, and statisticians (Akaike 1974a, 1974b; Harvey 1981; Priestley 1981; Aoki 1987). If the error vectors w_t and v_t can be assumed to be multivariate Gaussian, then the analysis follows directly from the state space Kalman filter methodology (Kalman 1960; Kalman and Bucy 1961).

Under the assumption of no system error ($w_t = 0$) in equation (15), which means that (i) an exact proportion of individuals go from one length category to the successive ones and (ii) survivorship and recruitment operate deterministically, and with the additional assumption that error (v_t) in the catch equation (16) is independently and identically distributed, the model parameters may be estimated using a nonlinear least squares approach to minimize the resdiual sum of squares:

$$(17) \quad RSS_{catch} = \sum_{l,t} (C'_{l,t} - C_{l,t})^2$$

where $C'_{l,t}$ is the predicted catch-at-length and $C_{l,t}$ is the observed catch-at-length at time t.

The observed data are catch in number over a set of specified length classes, taken over equally spaced time intervals. The observations of catch $C_{l,t}$ in number in length classes $l = 1$, . . .,n at times $t = 0$, . . ., t_{max} are used to estimate the population parameters defined above. The parameters to be estimated are the parameters α_s and β_s for selectivity functions, full recruitment fishing mortality f_t, initial population numbers at length $N_{l,0}$ ($l = 1$, . . ., n), recruitment to the fishery R_t over time $t = 1$, . . ., t_{max}, the recruitment distribution parameters α_r and β_r, and the growth parameters L_∞ k, and β.

In practice, if any parameters happen to be known, these known parameters can be fixed in estimation. However, if some

parameters can be obtained from additional observation (e.g. when the fishing efforts are known), then they can be used as auxiliary data. In this example, a functional relationship

$$f_t = qE_t$$

is used, where q is catchability to be estimated and assumed constant over time and E_t is observed fishing effort at time t. Then the residual sum of squares to be minimized becomes

$$RSS = \sum_{l,t} (C'_{l,t} - C_{l,t})^2 + \lambda \sum_t (f'_t - f_t)^2$$

where λ is the weight that describes the degree of confidence in the effort estimates. Other auxiliary data, such as hydroacoustic estimation of population size at any time, mean length-at-age from age determination, and survey data on recruitment, can also be included in the same manner without difficulty.

When it is valid to assume that the elements of the observation error vector v_t are independent identically distributed Gaussian random variables, that is, when

$$v_t \sim N(0, \sigma^2 I)$$

where 0 is a vector of zeros, σ^2 is a constant variance, and I is the identity matrix (a diagonal matrix of ones), then the solution to the least squares fit is also the maximum likelihood solution (Seber 1977). Other assumptions about the system equation and the catch equation error structure may be made that can result in more complicated and sometimes more reasonable forms of the least squares formulation (e.g. a weighted least squares formulation).

A Marquardt–Levenberg optimization algorithm is used to find the least squares estimates of the model parameters. The optimization routines require that initial estimates of the unknown parameters be supplied. There is some sensitivity to those initial parameter estimates due to local minima in the sum of squares function. Initial value sensitivity can be investigated by using an array of initial estimates (Sullivan 1988; Lai and Gallucci 1989). In the analyses to follow, the initial estimates are arrived at from the available literature. In some instances, certain parameters are assumed to be fixed and known in order for the parameter space to be well defined.

In the estimation procedure, only the values of $N_{l,0}$ need be estimated. The values of $N_{l,t}$ for $t = 1$, . . ., t_{max} can be computed recursively from $N_{l,t-1}$, the abundance at the preceding time steps using equation (15). To simplify the parameter space even further, $N_{l,0}$ is calculated from the total initial population abundance N_0 (where $N_0 = \sum_l N_{l,0}$) using the frequency distribution of the initial catch-at-length ($C_{l,0}$) and length-specific fishing mortalities estimated by the algorithm. This procedure is presented further in Appendix 1.

Model Application and Analysis

The model was applied to one simulated data set and two commercial fishery data sets. The simulated data set was generated to describe the dynamics of Pacific cod (*Gadus macrocephalus*) in the eastern Bering Sea. One set of data was collected from commercial catch of *Pseudotolithus typus* from the Cameroon coast (Djama 1988) and the other is based on market survey data from the commercial catch of *Decapterus russellii* from the Java Sea, Indonesia (Widodo 1988). The simulated data set is presented to highlight certain features of the estimation procedure as it applies to a set of observations for which

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TABLE 1. Parameter values used in the simulation.

Parameter	Value
Number of age classes	12
Abundance at:	
Age 1	1.10×10^9
Age 2	2.14×10^8
Age 3	1.20×10^7
Age 4	1.10×10^7
Age 5	6.00×10^6
Age 6	6.00×10^6
Age 7	2.10×10^6
Age 8	1.00×10^6
Age 9	1.00×10^6
Age 10	1.00×10^6
Age 11	1.00×10^6
Age 12	1.00×10^6
N_0	1.36×10^9
Number of time steps (years)	10
Number of length classes	45
α_r	37.00
β_r	0.50
R_1	4.42×10^8
R_2	1.32×10^8
R_3	1.39×10^8
R_4	8.60×10^7
R_5	9.00×10^7
R_6	1.65×10^8
R_7	1.05×10^8
R_8	1.28×10^8
R_9	9.70×10^7
M	0.30
α_s	0.10
β_s	30.00
f_0	0.42
f_1	0.44
f_2	0.46
f_3	0.48
f_4	0.47
f_5	0.48
f_6	0.45
f_7	0.48
f_8	0.40
f_9	0.43
L_∞	83.00
κ	0.24
β	1.0

the underlying system structure and the underlying process parameters are known a priori. The second two analyses demonstrate the applicability of this approach in the context of actual fishery data.

Gadus macrocephalus Simulation

For initial validation of the estimation procedure, a hypothetical data set was created using a computer-simulated model based on equations (1) and (13). Parameter values representing the initial population size, growth, recruitment, natural and fishing mortality, and selectivity were chosen to reflect the dynamics exhibited by Pacific cod in the eastern Bering Sea. The parameter values were set equal to actual estimates arrived at by Bakkala and Low (1985), so that the model dynamics would be representative of observations from the natural system. The initial population was based on the survey estimates

of population number at ages (Bakkala and Low 1985) and transformed into forty-five 2-cm-wide length classes using an age–length key (Lai 1985). The simulation depicts population numbers and catch numbers in terms of forty-five 2-cm-wide length classes and 10 time intervals, each a year in duration. Fishing mortality was allowed to differ from one year to the next, while selectivity was assumed to be a logistic function (4b). The growth increment Δ_l was calculated for each length class l by using the values of L_∞ and k given in Lai (1985), while β was set equal to 1, indicating a variance in growth that is equal to the mean. The recruitment distribution was set equal to the observed length distribution of age 1 individuals given for the first year (1978) of the time series in Bakkala and Low (1985). Independently distributed Gaussian error, with variance equal to 10^5 times the average number of individuals observed in a catch–length class, was added to the observations to simulate the observation error v_t. In this example, the constant of proportionality reflects a coefficient of variation of approximately 0.2. A summary of the parameters used in the simulation is given in Table 1.

The simulated data set is characterized by an influx of the strong 1977 year class in the first year (1978) that grows and declines, giving way in influence in subsequent years to the stronger influence of recruitment (see Fig. 1). For the first estimation with the simulated data, the initial values of all parameters were set to true values (Table 2). In the second estimation, the initial values of all parameters were randomly set to $\pm 30\%$ of the true values (Table 2). All parameters except natural mortality (M) were subject to estimation in these two cases.

Figure 1 compares the estimated catch values with the catch values from a simulation where the input values were varied $\pm 30\%$ from the (known) true values. In both estimations, the parameters estimated (Table 2) show good correspondence within known values, although some difference in the recruitment estimates can be seen over later time periods. Here, as in catch-at-age analysis (Deriso et al. 1985; Kimura 1989), auxiliary information may prove useful in obtaining better estimates. Note, however, that even with deviations of $\pm 30\%$, the estimation algorithm appeared to be robust.

Pseudotolithus typus

In order to ascertain the applicability of this approach under more realistic circumstances, two fisheries data sets were selected from existing literature. The first set of data is the 1984 monthly length–frequency distributions (February – November) of longneck croaker (Pseudotolithus typus: Sciaenidae) collected from commercial fisheries in Cameroon (Djama 1988). This species is one of two major finfish species caught by industrial trawl fisheries at depths between 10 and 50 m off the Cameroon coast. Five companies conducted industrial fishing during that period, and data were collected from two of these companies. The data are considered to be representative of the length–frequency distribution of all landings. The procedures used to estimate the catch-at-length for each month were described by Djama (1988).

The observed catch-at-length data are grouped into 1-cm 48 length classes with midlengths ranging from 10.5 to 57.5 cm. No information was available for April, so a single time step of twice Δt was used between March and May. Although information on natural mortality (M) was not available, Djama (1988) was able to obtain estimates of $L_\infty = 83$ cm, $k = 0.025 \cdot \text{yr}^{-1}$, and $Z/k = 8.53$ by using Wetherall's method
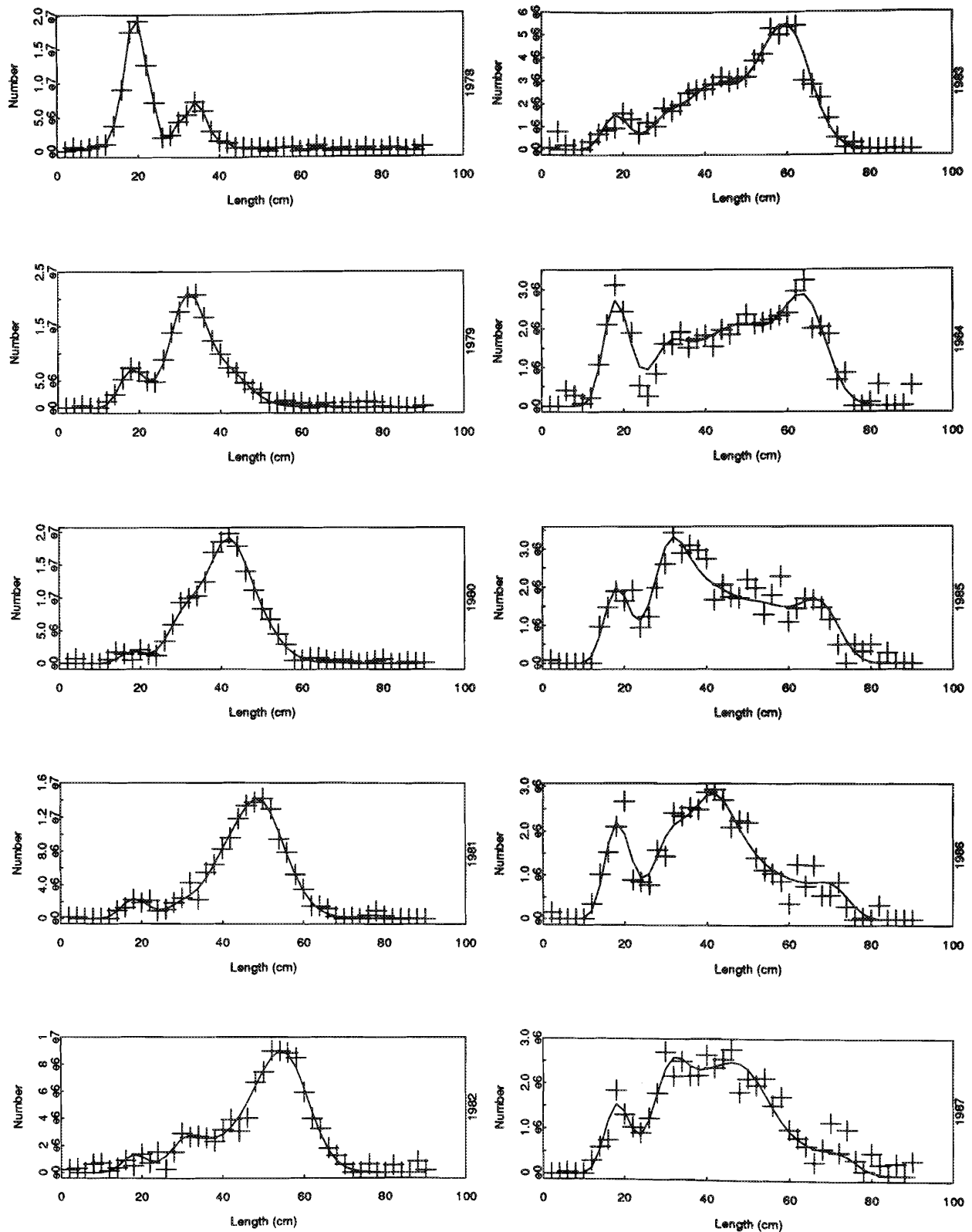
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FIG. 1. Simulated (+) and estimated (solid line) catch-at-length data of Pacific cod over 10 consecutive time periods. Simulated catches were generated for a Pacific cod population during 1978–87. Catch estimates were obtained from the catch-at-length least squares algorithm, using initial parameter values which varied ± 30% from the true value.

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TABLE 2. Simulated and estimated parameter values for Pacific cod.

		Estimate 1		Estimate 2	
	True	Initial (set equal to true values)	Estimated	Initial (set to ±30% of true values)	Estimated
N_0	1.36×10^9	1.36×10^9	1.39×10^9	1.00×10^9	1.39×10^9
α_r	37.0	37.0	30.4	25.0	30.4
β_r	0.5	0.5	0.56	0.7	0.56
R_1	4.42×10^8	4.42×10^8	4.13×10^8	5.75×10^8	4.12×10^8
R_2	1.32×10^8	1.32×10^8	1.16×10^8	9.30×10^7	1.16×10^8
R_3	1.39×10^8	1.39×10^8	1.50×10^8	1.81×10^8	1.50×10^8
R_4	8.60×10^7	8.60×10^7	8.76×10^7	1.06×10^8	8.75×10^7
R_5	9.00×10^7	9.00×10^7	9.85×10^7	6.30×10^7	9.81×10^7
R_6	1.65×10^8	1.65×10^8	1.94×10^8	1.15×10^8	1.93×10^8
R_7	1.05×10^8	1.05×10^8	1.40×10^8	1.50×10^8	1.39×10^8
R_8	1.28×10^8	1.28×10^8	1.89×10^8	9.00×10^7	1.87×10^8
R_9	9.70×10^7	9.70×10^7	1.42×10^8	1.06×10^8	1.41×10^8
α_s	0.1	0.1	0.1	0.3	0.1
β_s	30.0	30.0	32.5	20.0	32.5
f_0	0.42	0.42	0.51	0.3	0.51
f_1	0.44	0.44	0.52	0.6	0.52
f_2	0.46	0.46	0.52	0.3	0.52
f_3	0.48	0.48	0.51	0.65	0.51
f_4	0.47	0.47	0.50	0.25	0.50
f_5	0.48	0.48	0.51	0.60	0.51
f_6	0.45	0.45	0.46	0.70	0.46
f_7	0.48	0.48	0.46	0.30	0.46
f_8	0.40	0.40	0.38	0.60	0.38
f_9	0.43	0.43	0.35	0.30	0.35
L_∞	83.0	83.0	86.1	95.0	86.1
κ	0.24	0.24	0.23	0.30	0.23
β	1.0	1.0	1.04	1.40	1.04

(Wetherall 1986) and $L_\infty = 60$ cm and $k = 0.1 \cdot \mathrm{yr}^{-1}$ by using ELEFAN (Pauly and David 1981). According to the estimates by Wetherall's method, the resulting estimate of total mortality is $Z = 2.14 \cdot \mathrm{yr}^{-1}$, suggesting a natural mortality of around $1.0 \cdot \mathrm{yr}^{-1}$. However, initial runs of the algorithm indicated that the value for M might be too high (i.e. the resulting total instantaneous fishing mortalities were too low, less than $0.0001 \cdot \mathrm{yr}^{-1}$). As a result, the value of M was set equal to $0.6 \cdot \mathrm{yr}^{-1}$ (or $0.05 \cdot \mathrm{mo}^{-1}$), and selectivity was assumed to be a logistic function. The proportionality constant β in the growth equation was evaluated for its influence on predicted growth. The larger the value of β, the wider the distribution of the growth increment Δ_l. To demonstrate the effect of alternative choices of β on the resulting estimates, results are presented for three applications of the algorithm: (i) β fixed at 0.5, (ii) β fixed at 1.0, and (iii) β variable and its value determined by application of the algorithm.

Table 3 lists the results from the three applications of the algorithm. The results show that α_r, β_r, α_s, and β_s did not change substantially from one application to the next. All three runs indicated that all sizes of fish were fully vulnerable to the gear. Djama (1988) reported that the industrial fishery used trawl net gear with stretch mesh sizes ranging from 30 to 40 mm in the cod end, which is capable of retaining all fish larger than 10 cm. The third application of the algorithm estimated β to be 2.14, which is considered too large and results in too wide a spread of the growth increment Δ_l as shown in Fig. 2. Figure 2 indicates that more than 40% of the fish in the 10-cm length class can grow more than 4 cm in a 1-mo period when $\beta = 2.14$, while $\beta = 0.5$ and 1.0 give more reasonable results. This

conclusion is also supported by examination of the other estimated parameters (see Table 3). Values of L_∞ were 100.17, 102.46, and 50.18 cm, corresponding to β's of 0.5, 1.0, and 2.14, respectively, and were obtained by the three applications of the estimation procedure. These estimates can be compared with the maximum length of 118 cm observed in the 1984 catch as reported by Djama (1988). Since there were 242 fish with lengths greater than 60 cm in the 1984 catch, which were omitted from the reported catch-at-length data by Djama (1988), the third estimate of $L_\infty = 50.18$ cm seems unrealistic. Also, Bayagbona (1969), using age determination data, obtained an estimate of $L_\infty = 103$ cm and $k = 0.29 \cdot \mathrm{yr}^{-1}$ for the same species in Nigeria. Figure 3 shows the fit of the growth curve, with $L_\infty = 100.17$ cm and $k = 0.029 \cdot \mathrm{mo}^{-1}$, resulting from an estimation with $\beta = 0.5$, to the observations.

Djama (1988) reported that this stock exhibits continuous recruitment; however, with $\beta = 1.0$, recruitment was estimated to occur only in June, August, October, and November, while with $\beta = 0.5$, recruitment was estimated to occur in May and July as well. Figure 4 compares the observed and estimated catch-at-length data. The first modes of all distributions were consistently matched up between the observed and the estimated catches. Recruitment in March and September was expected to be minimal due to the high levels of recruitment taking place in the previous months. The mean length of recruitment is at 19.5 cm which corresponds to length class 10. Figure 4 shows that the peaks of the first component in March and September are at length class 12 (with $l_* = 21.5$ cm) and with a small number of individuals in length classes 0–11. This indicates that the two peaks of the first component in these two

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TABLE 3. Parameter estimates of *Pseudotolithus typus* (f, M, and k are in mo^{-1}).

Parameter	Estimate 1	Estimate 2	Estimate 3
N_0	1.98×10^8	3.66×10^8	1.26×10^8
α_r	48.7	48.7	43.8
β_r	0.40	0.40	0.45
R_1	0	0	0
R_2	4.90×10^7	0	0
R_3	9.81×10^7	0	4.90×10^6
R_4	2.50×10^7	0	0
R_5	2.76×10^7	3.06×10^8	1.19×10^7
R_6	0	0	0
R_7	3.45×10^8	2.08×10^8	1.35×10^7
R_8	4.80×10^9	4.07×10^8	3.27×10^8
α_s	1.0	1.0	1.0
β_s	0.001	0.001	0.001
f_0	0.060	0.032	0.098
f_1	0.028	0.030	0.105
f_2^a	0.066	0.038	0.161
f_3	0.042	0.037	0.107
f_4	0.034	0.034	0.107
f_5	0.026	0.026	0.074
f_6	0.012	0.012	0.037
f_7	0.020	0.023	0.058
f_8	0.003	0.004	0.005
L_∞	100.17	102.46	50.18
k	0.029	0.020	0.093
β	0.5^b	1.0^b	2.144
M	0.05^b	0.05^b	0.05^b
RSS	5.1×10^6	7.4×10^6	5.3×10^6

$^a f_2$ in 2-mo intervals.
^{b} Parameters fixed during the estimation procedure.

months are mainly the results of growth rather than the influx of recruitment. The recruitment in November was particularly strong, as was also reported by Djama (1988). This estimation of recruitment pattern is also similar to the fluctuation of proportion of the first components in each month reported in Djama (1988). Fishing mortality estimates ranged from a high of $0.066 \cdot \text{mo}^{-1}$ ($0.792 \cdot \text{yr}^{-1}$) in May to a low of $0.003 \cdot \text{mo}^{-1}$ ($0.036 \cdot \text{yr}^{-1}$) in November. This corresponds to total mortality rate estimates that range from $1.392 \cdot \text{yr}^{-1}$ in May to $0.636 \cdot \text{yr}^{-1}$ in November during a 1-mo period. The low fishing mortality rate estimated for November is likely due to a reduced number of large fish in the catch coupled with the strong recruitment.

Decapterus russellii

The second of the two fisheries data sets to be examined is based on length composition data collected in 1986 from commercial market landing of the species *Decapterus russellii* from the Karimun, one of the five fishing grounds in the Java Sea, over monthly intervals from May to December, a subset of the data analyzed by Widodo (1988). The catch-at-length observations are classified into twenty-eight 0.5-cm-wide length categories with midlengths ranging from 7.0 to 20.5 cm.

This species has been the major target of purse seine fisheries operating in the Java Sea, Indonesia (Widodo 1988). The annual catch of this species represents roughly 30–40% of the total combined landings in biomass for all commercial fish species caught in the Java Sea. The total monthly commercial catch was known and assumed to have the same length distribution observed in the length–frequency samples. A length–weight relationshp was used to determine the average weight of fish in each of the monthly samples. This average weight was divided into the total biomass of the catch for each month to obtain the total number of fish caught per month. The fish catch in number was then distributed among length classes according to the length–frequency distribution observed for each month in the market sample. Fishing mortality was allowed to vary with time, while selectivity was constrained to be equal to 1 for length classes 14–20 (corresponding to fish lengths ranging from 13.5 to 16.5 cm). Natural mortality was set equal to $0.08 \cdot \text{mo}^{-1}$ ($0.92 \cdot \text{yr}^{-1}$), the middle of the range of estimates of natural mortality ($0.65 - 1.19 \text{ yr}^{-1}$) obtained by Widodo (1988).

In the May observations, two distinct length–frequency distributions were evident. We chose to include only the first distribution, over the 10 length classes ranging from 7.0 to 11.5 cm, because those individuals greater than 11.5 cm, which made up the second distribution, appeared to contribute little to the subsequent catch. The data are therefore interpreted to represent the dynamics of the incoming recruits to this fishery.

For this example, a range of discrete values for β was used in the estimation and the best set of estimates were chosen based on a sum of squares criterion. The results of three of these estimations (with $\beta = 0.25, 0.35$, and 0.45) are shown in Table 4. Over the range of values chosen, $\beta = 0.35$ resulted in the minimum sum of squares. Figure 5 shows the catch observations in comparison with the catch estimates obtained from the catch-at-length estimation procedure under this set of parameter estimates. The initial length–frequency distribution of individuals shown in the first time period (May) depicts a population of smaller individuals entering the fishery. The drop-off in the number of individuals occurring over smaller length classes in July is interpreted by the algorithm to reflect an influx of new recruits into the population in July, followed by growth into the main body of the population in the ensuing months, and its magnitude is reflected in the recruitment estimate. The recruitment distribution parameters, estimated by the algorithm and shown in Table 4 for $\beta = 0.35$, reflect a mean length of recruitment (4.4 cm), occurring around the eighth length class with a variance of 2.2 cm^2 corresponding to a standard deviation across about 1.5 length classes. The recruitment to the fishery in other months is negligible. The parameters estimated by the algorithm create a model fit that reflects the recruitment and growth of recruits as well as the survival and growth of the body of larger individuals. Again, the fishing mortality parameters appear to be fairly consistent in magnitude over time with the exception of the first time period, suggesting again that a trade-off may exist between the estimates of population numbers and fishing mortality. The model does not fit as well for August and October, presumably because of a shift in gear selectivity or a change in the sampling mechanism. As with the other data sets, selectivity is assumed to be constant throughout the time period of the sample, with estimates $\hat{\alpha}_s = 4.51$ and β_s essentially zero. The growth parameters L_∞ and k are estimated to be 17.53 cm and $0.47 \cdot \text{mo}^{-1}$. A length of 17.5 cm is contained in the 20th length class, indicated in Fig. 5. Figure 6 shows two growth curve trajectories through the relative length–frequencies exhibited by the catch.

Discussion

A length-structured stochastic model is presented as a tool for stock assessment, which differs from existing length-based stock assessment methods (e.g. Jones 1984; Lai and Gallucci
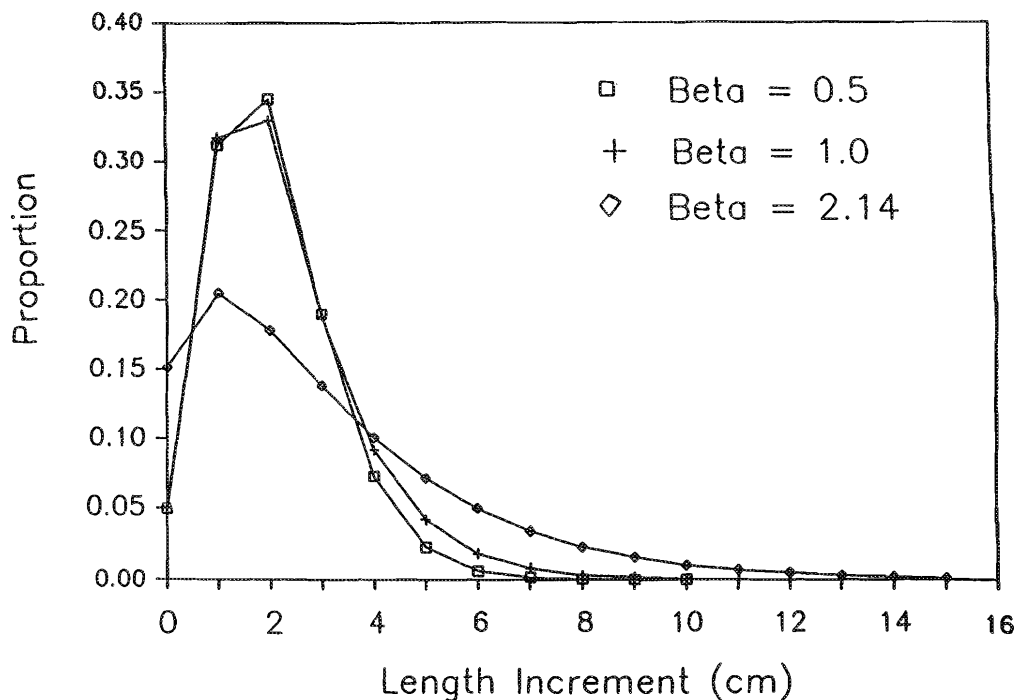
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FIG. 2. Distributions of growth increment of fish in the 10-cm length class during a 1-mo period for β = 0.5, 1.0, and 2.14.
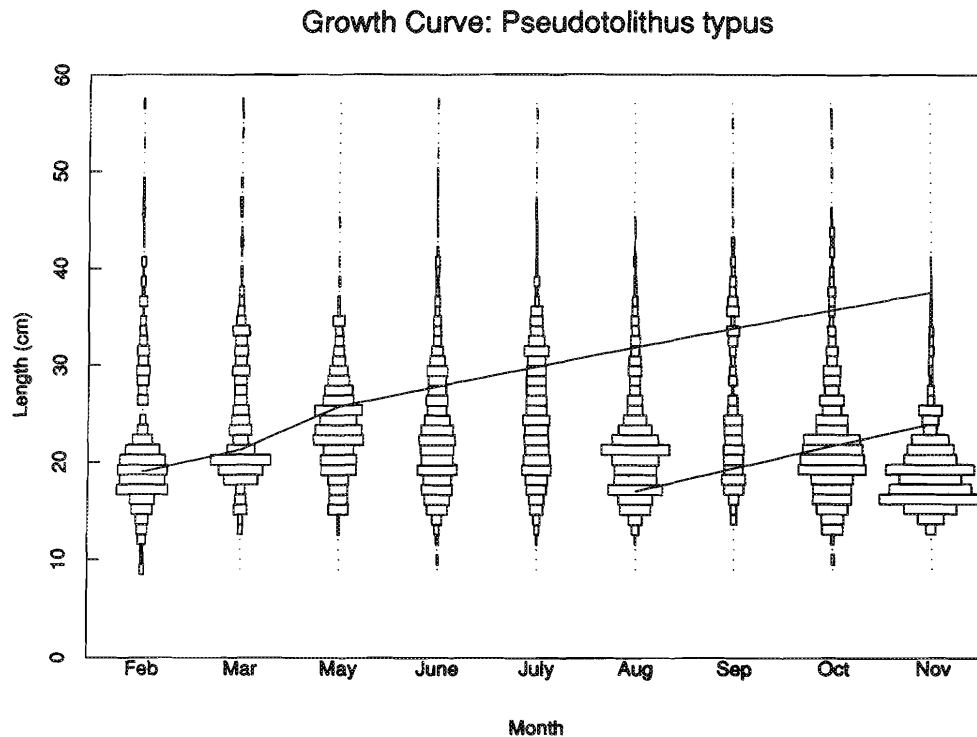
Growth Curve: Pseudotolithus typus

FIG. 3. Growth curve trajectories through catch length–frequencies for *Pseudotolithus typus* based on estimates of $\hat{L}_\infty = 100.17$ cm and $\hat{k} = 0.287 \cdot mo^{-1}$. Each bar indicates the relative catch-at-length.

1988) in many ways. One difference is that growth is included in the model dynamics through a length-based transition matrix whose elements represent growth as the proportion of individuals moving from one length class to another. In this manner, we do not require the assumption of deterministic growth of fish (i.e. growth is identical for all individuals in the population such that all fish of the same age have the same length). The elements of the transition matrix are parameterized in terms of the von Bertalanffy growth parameters, although other parameterizations with alternative growth models are possible.
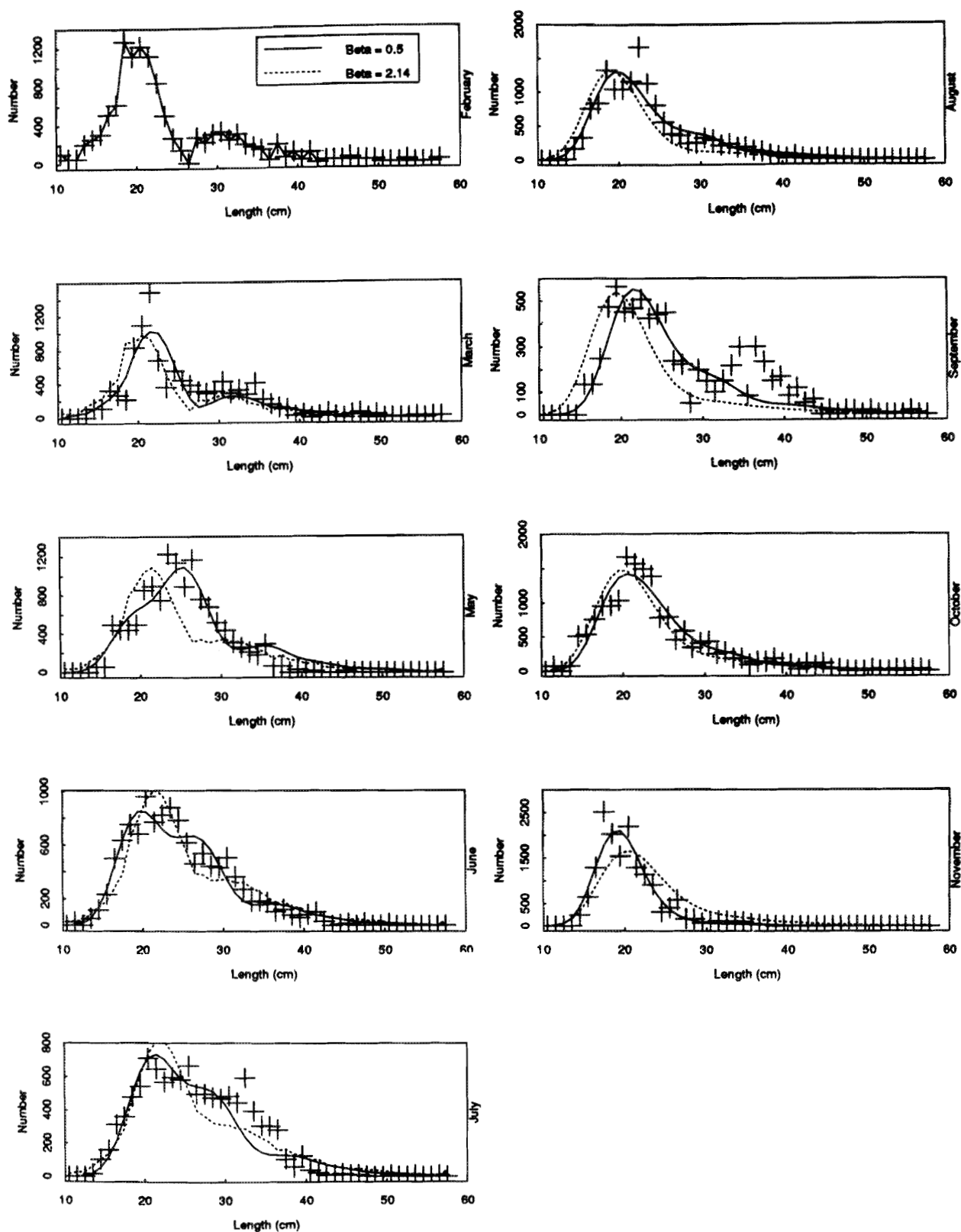
Pseudotolithus typus

FIG. 4. Observed (+) and estimated (solid and broken lines) catch-at-length of *Pseudotolithus typus* in units of 100 fish for each length class over nine time periods ($\beta = 0.5$, $\beta = 2.14$).

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TABLE 4. Parameter estimates of *Decapterus russellii* for three different fixed values of the growth parameter β.

Parameter	Estimate 1 ($\beta = 0.25$)	Estimate 2 ($\beta = 0.35$)	Estimate 3 ($\beta = 0.45$)
N_0	3.4×10^9	5.4×10^9	6.3×10^9
α_r	3.49	8.44	12.26
β_r	1.09	0.52	0.38
R_1	0	0	0
R_2	1.9×10^{10}	3.7×10^{10}	5.0×10^{10}
R_3	0	0	0
R_4	0	0	0
R_5	0	0	0
R_6	0	0	0
R_7	0	0	0
α_s	3.83	4.51	4.81
β_s	0	0	0
f_0	0.0949	0.1575	0.2047
f_1	0.0800	0.0069	0.0063
f_2	0.1114	0.0084	0.0076
f_3	0.0019	0.0011	0.0008
f_4	0.0027	0.0015	0.0011
f_5	0.0016	0.0009	0.0007
f_6	0.0015	0.0008	0.0007
f_7	0.0011	0.0006	0.0005
L_∞	17.59	17.53	17.10
κ	0.47	0.47	0.513
β	0.25[a]	0.35[a]	0.45[a]
M	0.08[a]	0.08[a]	0.08[a]
RSS	8.2×10^{13}	7.7×10^{13}	7.8×10^{13}

[a]Parameters fixed during the estimation procedure.

Another major difference is that we do not require the assumption of steady state. In this manner, we are able to estimate recruitment, abundance, and fishing mortality across time and reflect the dynamics of exploitation over time.

A nonlinear least squares algorithm is used to estimate initial population abundance, recruitment, fishing mortality, selectivity, and the growth parameters simultaneously. As with traditional age-structured analyses (Fournier and Archibald 1982; Deriso et al. 1985), the uniqueness of the parameters is dependent on the structure of the information in the catch and the presence or absence of auxiliary information (e.g. independent sample surveys for the determination of absolute abundance).

The error structure of the observation process was assumed to be additive and independent and identically distributed. In the case of a length-based analysis, and specifically for the examples presented here, additive *iid* error was preferable to multiplicative *iid* error, since the log-transformations that are used for analysis of the latter error tend to obscure the salient features in the dynamics, particularly those representing growth. A more accurate approach perhaps would be to use a length-class specific weighting factor with the weights proportional to the variance associated with each class. Estimating these weights simultaneously with the other parameters is possible, but the estimates computed in this way are often unstable. More sophisticated approaches toward modeling both process and observation error are currently being explored (Mendelssohn 1988; Sullivan 1988).

Because no age information on the population is necessary, this approach can be applied to populations for which ageing is impractical (e.g. no validated ageing methods, substantial ageing errors, etc.). Another possible application is to a fishery targeted on individuals younger than 1 yr old as exemplified by

the application to *D. russellii*. However, caution must be exercised in that some estimates of population parameters may not be representative of all life history stages of the species.

The number of parameters to be estimated may seem large but the number is comparable with that estimated by many catch-at-age procedures and is comparable with applications of optimization techniques in the physical sciences. The correlation between various parameter estimates can be made explicit and a sensitivity analysis of the estimates to different assumptions can be made. An examination of the residuals, that is, the difference between observed and expected catch values, along with the associated sum of squares statistic, is one way of determining the appropriateness of the estimates. Other assumptions, such as the approximation of growth by a gamma distribution growth model, can be tested by comparing the estimation results with those obtained under alternative growth models or by comparison with laboratory to field experiments. The sensitivity of the estimates of fixed parameters, which are assumed known, can also be explored.

In all three of the examples discussed above, some parameters were fixed prior to the application of the estimation procedure. In principle, any parameter may be fixed if its value is known. In some instances, it may be necessary to fix a parameter that is not precisely known. The natural mortality parameter M is one such parameter. The estimates of fishing mortality f_t are confounded with M, so M must be fixed to obtain a unique set of estimates. Thus, the best estimates of the f_t's result when M is the best possible; it is important to have a good estimate of M to obtain a good estimate of the f_t's. This issue exists in many stock assessment models, no matter if age or length based (Sims 1984; Lai and Gallucci 1988).

Another set of parameters that may have to be fixed prior to application of the algorithm is that governing the recruitment distribution (i.e. α_r and β_r). It is sometimes necessary to constrain the parameters to a series of likely length categories to prevent confounding of the recruitment distribution with the overall population distribution. Since in some situations recruitment occurs at every time step, it can happen that the recruit population and the adult population become virtually indistinguishable. One way that this may occur is in the steady-state case, where recruitment comes in to replace in each length class the losses due to growth and death. In this case, the length–frequency distribution of the population is the same year after year. Based on length–frequency data alone, it is impossible to distinguish this case from the one where a population exists with no growth, uniform mortality, and no recruitment, or the case where the adult population dies off at the end of the year only to be fully replaced by the new recruits at the beginning of the next year. Constraints are needed to define the estimation surface (e.g. see Hay et al. 1988). In the two examples presented in this paper, it is not necessary to fix these parameters. This is because the samples were obtained at a reasonable temporal resolution and there were periods over which recruitment clearly took place and others where it clearly did not. The recruits entered the fishery as a subpopulation that gradually grew into the main population. Because it was clear when recruitment took place, the recruitment distribution was clearly defined over the appropriate time periods, allowing the estimation surface to be fitted. In other situations, auxiliary information may be available such as independent estimates of recruitment, levels of maturity, or growth, which then can be used to better define the estimation surface.
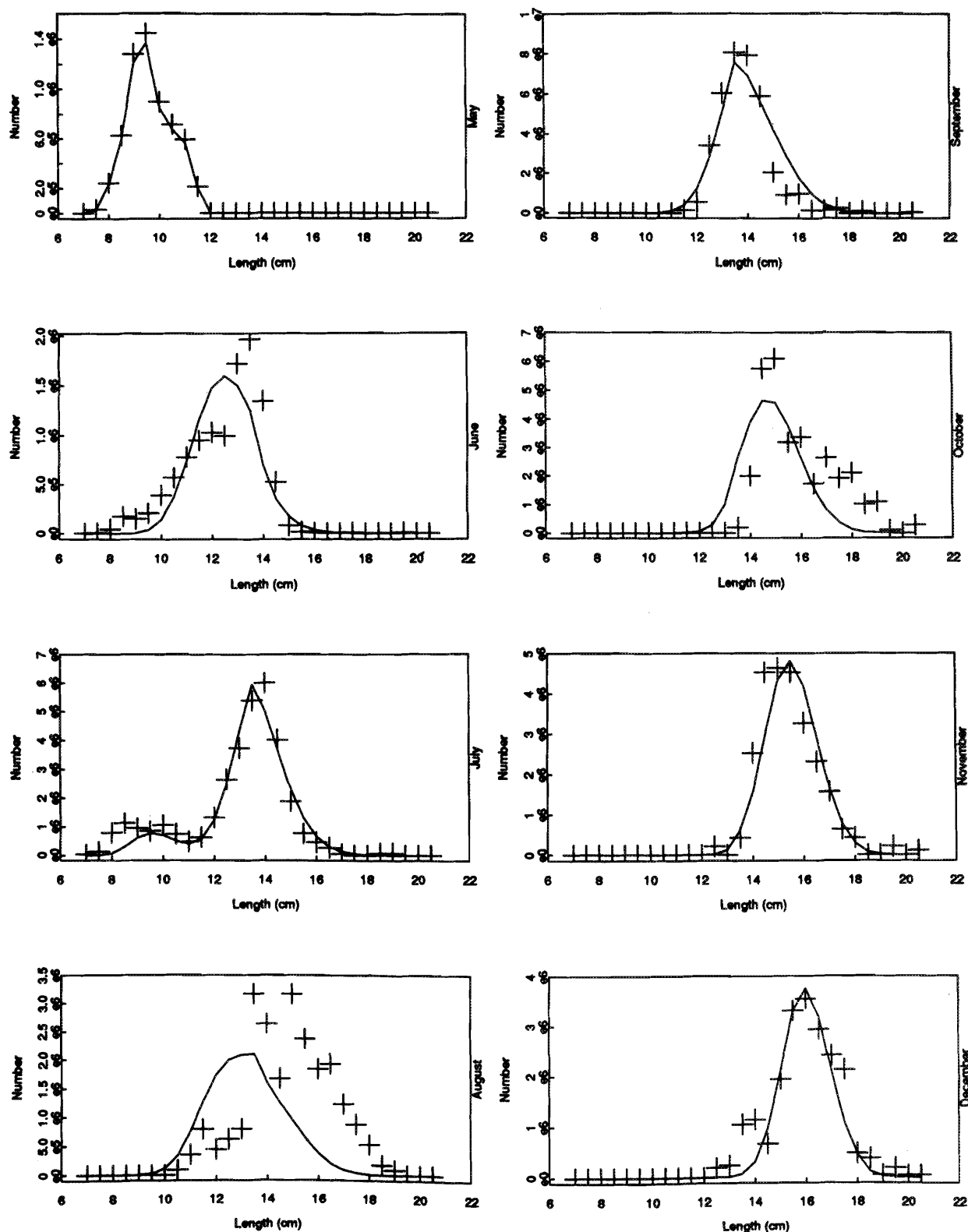
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Fig. 5. Observed (+) and estimated (solid line) catch-at-length of *Decapterus russellii* over eight consecutive time periods (β = 0.35).

Another parameter that sometimes requires greater attention is the growth distribution parameter β. The estimation of this parameter did not always prove feasible under the nonlinear optimization algorithm that we used. In these situations, a rea-sonable choice for β can be made by systematically fixing β at different values, running the estimation procedure, and choos-ing a value for β which minimizes the sum of squares obtained over the set of β's. While this approach may not be the best

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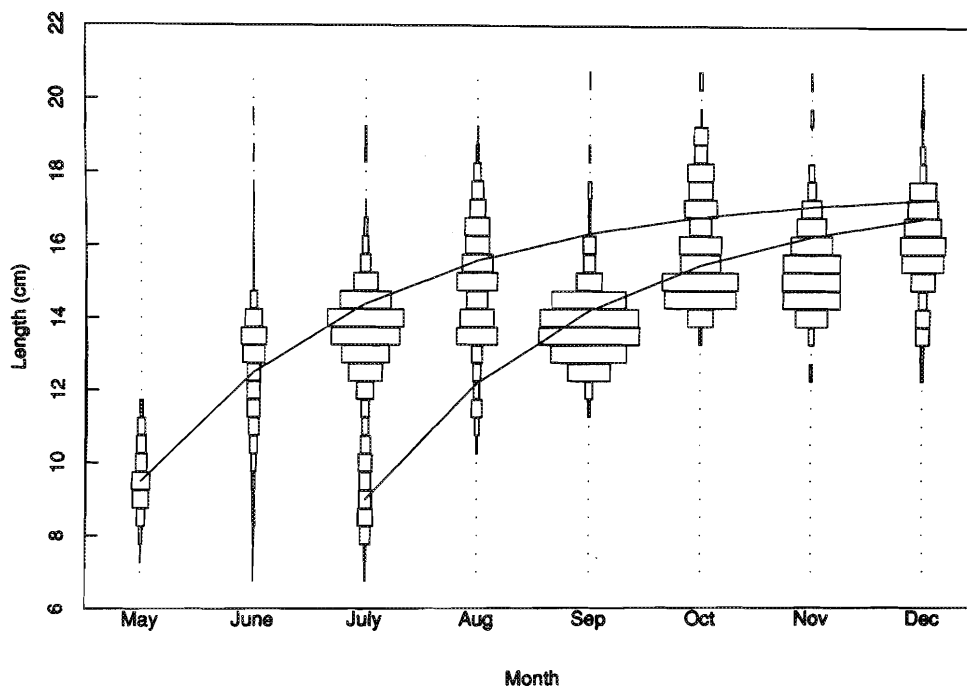
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Growth Curve: Decapterus russellii

FIG. 6. Growth curve trajectories through catch length–frequencies for *Decapterus russellii* based on estimates of $\hat{L}_\infty = 17.53$ cm and $\hat{k} = 0.47 \cdot mo^{-1}$. Each bar indicates the relative catch-at-length.

method for estimating β, it worked reasonably well for the case of *D. russellii*. Furthermore, changes in β resulted in relatively minor changes in the other parameter estimates (see Table 4) indicating that the other parameter estimates were fairly robust to the chosen value of β. In the case of *P. typus*, the sum of squares was fairly constant throughout the range of β. In this case, the presence or absence of pattern in the catch residuals was used to indicate which fit was better. Other information, which was not incorporated directly into the model, such as the relative magnitude of recruitment in different months and independent estimates of the growth parameters, was also used to judge the quality of the estimate.

As discussed above in the Model Application and Analysis section, estimates of certain parameters, specifically the growth parameters L_∞ and k for the two commercial fisheries examples, can differ from those obtained by other procedures. In the example of *P. typus*, the growth parameter L_∞ ranges from as low as 61.1 cm to as high as 105 cm, while the corresponding estimates of k range from 0.346 to $0.217 \cdot yr^{-1}$ (Djama 1988). The catch-at-length analysis presented here estimates $L_\infty = 100.17$ cm and $k = 0.344 \cdot yr^{-1}$. These estimates are on the extreme end of their ranges, but they do appear to accurately reflect the nature of the stock dynamics as discussed earlier.

In the example of *D. russellii*, Widodo (1988) estimated L_∞ in the range of 24.7 – 28.3 cm and k in the range of 0.39 – $0.50 \cdot yr^{-1}$ whereas the catch-at-length analysis determined L_∞ to be 17.5 cm and k to be $0.47 \cdot mo^{-1}$ or $5.6 \cdot yr^{-1}$. These differences reflect the seasonal growth pattern of incoming 0-yr-old recruits and is consistent with that observed in the year 1 growth of this and related species (Sreenivasan 1982; Widodo 1988). However, it cannot be used to extrapolate the growth of older age fish.

In both examples discussed above, the estimated L_∞ and k adequately describe the growth of individuals represented in the

catch. The values of L_∞ and k may differ from those obtained by other means, but together they do provide a good description of the observed growth, and as a consequence, the other simultaneously obtained estimates of abundance, recruitment, and survivorship are reliable relative to this description of growth. One method for examining the range of growth parameter values that provide a similar fit to the set of observations is to examine the two-dimensional projection of the log-likelihood contour surface (Sullivan 1988). For the examples discussed here, this is equivalent to examining the residual sum of squares surface under the optimal parameter estimates while varying the values of two parameters of interest. This can be done for any pairwise comparisons between parameters and, in particular, for the set of growth parameters L_∞ and k.

Given the good fit of the estimates to the simulation data, which represented several years of growth, a series of observations covering several years, taken at monthly or quarterly increments, should provide growth parameter estimates that better reflect the growth of older fish for this species. However, one should avoid tacking the time series onto itself repeatedly to extend the time series sequence for analysis, as the assumption of a recurrent state that this step implicitly makes can severely bias the estimates obtained by any length-based procedure when the assumption is incorrect. If a time series over several years is available, and seasonal variations in growth are expected, then it is interesting to note that the catch-in-length analysis presented here can incorporate the seasonal von Bertalanffy growth model developed by Pauly and Gaschutz (1979), with the power factor $D = 1$, in the form

$$\bar{\Delta}_t = (L_\infty - l)(1 - e^{-k\Delta s})$$

where

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and where Δs is the time since the last period (i.e. $t - t_s$) and n represents the number of time increments in a year (e.g. $n = 12$ for monthly increments of length $\Delta t = 1$). It could also incorporate other growth models such as the Gompertz and Richardson models.

It should also be noted that in the catch-at-length analysis presented here, fishing selectivity and growth are estimated simultaneously; thus, length–frequency maxima that occur in the population, but are not fully reflected in the catch due to selectivity, are accounted for.

In summary, the catch-at-length procedure outlined above provides a general estimation structure through which estimates may be obtained on population size, survivorship, recruitment, and growth. The procedure can be easily modified to account for alternative forms of growth and alternative representations of stochastic variation. However, as with all estimation procedures, care should be given to the quality of the information that is fed into the procedure. The quality of the estimates can only be as good as the quality of the data used by the procedure. For catch data in particular, one fundamental point of concern is that the sample data be representative of the length–frequency distribution observed in the commercial landings. Often, there is not enough information from a single set of samples to provide an adequate picture of what is going on in the population, so data are combined across fishing trips, gear types, management areas, or time periods. Pooling the data must be done only when trends or inconsistencies in the data do not exist. A thoroughly thought-out sampling design followed by a detailed statistical analysis of the data, prior to the application of the catch-at-length algorithm, are necessary to insure high-quality data and to insure that the data are representative of the population of interest.

The program CASA (Catch-At-Size Analysis) used in this analysis is written in FORTRAN 77. The computations presented here were run on a DEC MicroVax II. A user's guide and program on an MS-DOS formatted 5 1/4-inch disc may be obtained from V. F. Gallucci, Management Assistance for Artisanal Fisheries, Center for Quantitative Science, University of Washington, HR-20, Seattle, WA 98195.

Acknowledgments

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Appendix 1

Instead of estimating all $N_{l,0}$ for $l = 1, \ldots, n$, these variables can be reparameterized into one variable,

$$N_0 = \sum_l N_{l,0},$$

by the following relationshps. Using equation (6) to obtain

$$\text{(A.1)} \quad N_{l,0} = \frac{C_{l,0}(Z_{l,0}}{F_{l,0}(1 - e^{-Z_{l,0}})},$$

let P_l be the proportion at length class l in the population. From (A.1):

$$\text{(A.2)} \quad P_t = \frac{N_{l,0}}{N_0} = \frac{C_{l,0}Z_{l,0}/F_{l,0}(1 - e^{-Z_{l,0}})}{\sum C_{l,0}Z_{l,0}/F_{l,0}(1 - e^{-Z_{l,0}})}.$$

By dividing the numerator and denominator on the right-hand side by $\Sigma C_{l,0} = C_0$, P_l is rewritten as

$$\text{(A.3)} \quad P_l = \frac{q_{l,0}Z_{l,0}/F_{l,0}(1 - e^{-Z_{l,0}})}{\sum q_{l,0}Z_{l,0}/F_{l,0}(1 - e^{-Z_{l,0}})}$$

where

$$q_{l,0} = \frac{C_{l,0}}{\sum_l C_{l,0}} = \frac{C_{l,0}}{C_0}$$

is the length composition of the catch at $t = 0$. An estimate of the length composition $\hat{q}_{l,0}$ follows from the use of the length distribution of the catch data at $t = 0$, which can be used in equation (A.3) to estimate $\hat{P}_l$.

The length distribution of abundance $N_{l,0}$ can now be estimated from

$$\hat{N}_{l,0} = \hat{P}_l N_0$$

if an initial estimate of N_0 is known. This procedure reduces n estimates of $N_{l,0}$ to one estimate of N_0.

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