Estimating stock abundance from size data

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Abstract.–The projection of resource production and the effect of removals on fisheries populations are based on abundance estimates, particularly estimates of the most current abundance. Monte Carlo methods were used to investigate a size-based method of estimating abundance for instances where the age of caught fish cannot be established, but where size samples and a growth schedule exist. Neither process variability (recruitment dates, growth rates, and unobserved change rates) nor sampling error (catch estimation, growth rate estimation, and relative abundance sampling) adversely affected estimation, although low sampling intensities often decreased precision. Abundances of recently recruited fish too small to occur in relative abundance samples more than once were estimated with large uncertainty. Inappropriately wide size-class widths caused uncertain abundance estimates of larger size-classes. However, if size-classes were of suitable width, the abundance of fish large enough to occur in abundance samples more than once were accurately and precisely estimated even in cases of high process variability and small sample sizes. Sampling gear efficiency (catchability) coefficients were often estimated without large bias but imprecisely. The exponent of the unobserved change rate (including natural mortality) was estimated precisely, but estimates were often biased. High correlations between estimates of the unobserved change rate and sampling gear efficiencies were not often observed. Estimation characteristics were unlike those based on virtual population analysis calculations. Maximum-likelihood estimates of the most recent abundances were accurate and precise, yet calculations of historical abundances were biased and extremely imprecise.

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Most often, the objective of fisheries regulations is to insure that stock abundance does not decrease or, if abundance is low, to increase it. The welfare of the entire stock may be of concern, or only a part of it such as the adult portion (spawning stock). These objectives are obtained by limiting yields (weight caught) to stock growth or, in instances were abundance is low, to less than stock growth. Abundance estimates are the bases for this regulation strategy. An opinion as to whether stock abundance is currently depressed or not is based on a comparison of an estimate of current abundance with estimates of previous abundances. Stock production (growth) in the immediate future is projected from the estimate of current abundance. Since the production projection is the basis for the yield limit, the estimate of current abundance determines the yield limit. Because it is a critical element of regulatory responsibility, abundance estimation methodology is of major interest.

Most estimation methods are based on age data. These methods specify that the population is entirely composed of unique groups of fish of equal age (cohorts) and that all members of a cohort grow into the first exploitable size (recruit) instantaneously before fishing begins once each year. These two requirements rarely, if ever, occur. Most populations spawn during several months, or sometimes throughout the entire year, so that annual or even monthly cohorts do not really exist. The growth of the young fish to sizes large enough to be caught is a continuous process so that recruitment is typically an ongoing phenomena. These biological realities are often ignored, and age-based analysis methods are used anyway.

Since the primary data element of age-based methods is the number of caught fish of each age, the ages of caught fish must be determined. Sometimes this requirement is difficult to satisfy. Major circuli from differing bone densities or the chemical composition of skeletal structures (scales, fin spines, or otoliths) have been validated as age marks in only 3.4% of age determination studies (Beamish and McFarlane 1983). Even in cases where indirect evidence of validation seems ample (Kreuz et al. 1982), direct measurement of growth from mark and recapture data can document a very different reality (Pikitch and Demory 1988). Collecting and processing samples can be so difficult and time consuming that large data voids occur. Frequent molting and the absence of bony tissue preclude the possibility of using hardpart ageing methods for many invertebrates, and the technology to determine age from somatic tissue does not currently exist.

These problems can be avoided by methods that model populations in terms of size and time rather than age and years (or months). Size-based methods need not require that the population be composed of age-specific cohorts nor that recruitment be an instantaneous, one-time event. The first size-based methods, however, are not so constructed.

The original technique to assess fish stocks from size instead of age data is a stepwise double-estimation procedure (see Pauly et al. 1987 for an example). Size-specific catches are first transformed to age-specific catches by using an inverted growth equation (Ricker 1975:221) or statistical estimators based on growth data (Clark 1981, Bartoo and Parker 1982, Shepherd 1985, Hoenig and Heisey 1987, Kimura and Chikuni 1987) so that the stock is assumed to be composed of age-specific cohorts. Size-to-age transformation methods that require size-frequencies only (i.e., growth data are not required) are available (Macdonald and Pitcher 1979, Pauly 1982, Fournier et al. 1990), but Monte Carlo tests have shown pronounced weaknesses in these methods (Hampton and Majkowski 1987, Rosenberg and Beddington 1987, Basson et al. 1988). Virtual population analysis (Ricker 1948, Fry 1949, Jones 1961, Gulland 1965, Murphy 1965) is then applied to the transformed catch, but the system of cohort-specific catch equations is underdetermined (Agger et al. 1971, Doubleday 1975, Ulltang 1977, Pope and Shepherd 1982). The inclusion of auxiliary data (total fishing effort, catch effort, or other relative abundance samples) using any of several statistical procedures (Laurec and Bard 1980; Paloheimo 1980; Anon. 1981b, 1983, 1984, 1986; Parrack 1981, 1986; Collie and Sissenwine 1983; Deriso 1985; Pope and Shepherd 1985; Mendelssohn 1988) eliminates that problem, so abundances can be estimated. If based on actual age data, virtual population analysis using auxiliary information does estimate stock abundances and fishing mortality rates reasonably well if the natural mortality rate is known (Deriso 1985, Pope and Shepherd 1985), but if the method is used without actual age data, its statistical characteristics are unknown. If the population is not composed of true age-specific cohorts or if the ageing of caught fish is problematic, the method is not appropriate. Spawning often is too protracted to establish cohorts and fish cannot be aged with reasonable certainty; yet because it is simple and tractable, this method is used anyway.

Several size-based abundance estimation methods do not employ data auxiliary to catches (Jones 1974 and 1981, Brethes and Desrosiers 1981, Lai and Gallucci 1988). Instead of using fishing effort or relative abundance samples to overcome the determination problem, they assume that the size-frequency of the catch, and thus of the stock (and recruitment magnitudes), is constant (in steady state). That assumption greatly restricts the usefulness of these methods.

Three items seem important when considering stock-abundance estimators. First, the data an estimator requires often may preclude its use if such data is not usually available. Next, since the likelihood procedure requires one, often a sampling distribution for an observed statistic is assumed even though support for the assumption cannot be offered. The resulting estimator thus might be entirely based on an inappropriate probability expression. Last, the statistical properties of an estimator are of concern. An estimator may be too imprecise to be useful unless sample sizes are unrealistically large, or its bias may be too large to ignore during estimation.

Since the method of least squares is not based on probability theory, statistical characteristics of such estimators are very uncertain. The likelihood procedure tends to generate estimators with superior statistical characteristics, but success is not guaranteed. Commonly, estimators of parameters of nonlinear models are problematic. They cannot be written in closed form so their expectations, which lead to bias and variance expressions, cannot be derived analytically. Since the estimator's performance characteristics cannot be predicted, they must be established from Monte Carlo studies. If such studies do not exist, the estimator's usefulness is unknown.

The first size-based procedure, a least-squares estimator, was developed (Beddington and Cooke 1981) and applied to sperm whales (Anon. 1981a, Cooke and Beddington 1982, Cooke et al. 1983b, Shirakihara and Tanaka 1983, de la Mare and Cooke 1984) to assess the northwestern Pacific stock (Beddington et al. 1983, Cooke and de la Mare 1983b, Shirakihara and Tanaka 1983). It is based entirely on size-specific catches and assumes a known adult-progeny ratio instead of using fishing effort or other auxiliary data. The statistical characteristics of the estimator were established with extensive Monte Carlo studies (Cooke et al. 1983a, Cooke and de la Mare 1983a, Shirakihara and Tanaka 1984, de la Mare and Cooke 1985 and 1987, Shirakihara et al. 1985, de la Mare 1988).

The method of Fournier and Doonan (1987) was derived by the likelihood method by assuming that catch and effort are each lognormal random variables and that the first four moments of length-frequencies are normal random variables. Monte Carlo tests established the estimator's ability to predict optimal long-term fishing effort, but the errors of the stock-abundance estimates are not described. The maximum-likelihood method of Schnute et al. (1989) assumes that the annual ratio of total yield to total effort is a normal random variable. The statistical characteristics of the estimator are not described.

The method of Sullivan et al. (1990) is a least-squares estimator based on catches, but Kalman filter methodology also may be used to obtain estimates (Sullivan 1989). The method does not require data other than catches even though it is well known that, in the case of age-based (VPA) methods, the system of catch equations without auxiliary data is not determined (Agger et al. 1971, Doubleday 1975, Ulltang 1977, Pope and Shepherd 1982). Sullivan et al. (1990) suggest expanding the number of terms in the sum of squares to include effort and abundance indices if meaningful weights for these auxiliary data can be found (guidance for finding such weights is not provided). The statistical characteristics of the estimator are not yet described.

The lack of Monte Carlo tests of the performance of these estimators is a particular concern because, without knowledge of their statistical behavior, little certainty can be placed on the resulting estimates. Some of the estimators were developed by the likelihood method, but the justification for assuming the chosen sampling distributions often seems weak or lacking. The usefulness of those estimators that require total fishing effort seem limited, since that statistic is often estimated from catch and effort samples rather than enumerated. Most of the methods estimate the parameters of individual growth as part of the solution vector. This seems questionable in view of findings in a study of the separation of central moments of individual distributions from distribution mixtures (Hasselbald 1966), studies of the magnitude of correlation between estimates of growth-equation parameters (Gallucci and Quinn 1979), and of the performance of methods that estimate growth parameters from size distributions (Hampton and Majkowski 1987, Rosenberg and Beddington 1987, Basson et al. 1988). Also, most of the methods are based on elaborate population models, a characteristic that leads to two problems. First, such models often include deterministic stock-recruitment functions, and such functions are regarded as unrealistic representations of the dynamics of fish stocks. Second, since the population model is extensive, it includes a large number of parameters that must be estimated. It is well known that an exact representation of a real-world system is not possible; hence, a suitably parsimonious model that is a useful approximation with an informative structure is superior (Box 1979). The most germane variables are the current size-specific abundances since they will determine stock production in the immediate future.

The object of this study was to develop an abundance estimator that would be appropriate in almost all cases, whether or not the population is composed of cohorts, or whether or not age data is available. Effort was taken to write the estimation model as parsimonious as possible, to base estimation on data commonly collected from most fisheries, and to insure that the correct sampling distribution was used in the likelihood procedure. The bulk of the study was directed at describing the statistical characteristics of the estimator over a broad range of conditions from Monte Carlo simulations.

Methods

Abundance estimator

An abundance estimator was developed that uses a model of individual growth, size-specific catches and catch dates, and size-specific abundance observations (sighting data, research cruise catch-per-tow, etc.). The estimator makes three assumptions:

(1) Unobserved phenomena that change stock abundance (immigration, emigration, unrecorded catch, predation, and disease) are a (continuous) Poisson process with combined rate z,
(2) the size of an individual on a date is a known deterministic function of size on another date, and
(3) the sample average of relative abundance observations is a normally-distributed random variable with an expectation equal to a portion of absolute abundance.

The estimator uses a growth model to relate sizes and dates and an abundance model to project abundance from observed catches scaled to relative abundance observations.

Consider T time-periods, not necessarily of equal duration, so that $0<t<T$. Within period t, relative abundance was observed on date y_t, then a catch occurred on date c_t. The number of fish caught on date c_t was C_t. Abundance on the date of the relative abundance observation (date y_t) is of interest; let this abundance (numbers of fish) be N_t. From assumption (1),

$$N_{t+1} = [N_t\, e^{-z_t(c_t-y_t)} - C_t]\, e^{-z_t(y_{t+1}-c_t)}.$$

Abundance on the date of the final abundance sample (i.e., N_T) is of most interest because stock production in the immediate future depends on it. Writing the above equation in terms of N_T as a time-series gives a simple forward projection of abundance on each relative abundance sampling date:

$$N_t = N_T\, e^{\sum_{k=t}^{T-1} z_k(y_{k+1}-y_k)} + \sum_{k=t}^{T-1} C_k\, e^{z_k(c_k-y_k)+\sum_{i=t}^{k-1} z_i(y_{i+1}-y_i)}.$$

If the unobserved change rate is assumed temporally invariant, this simplifies to

$$N_t = N_T\, e^{z(y_T-y_t)} + \sum_{k=t}^{T-1} C_k\, e^{z(c_k-y_t)}.$$

Each catch is subtracted separately; catching is not assumed to occur continuously at a constant rate. Abundance changes due to unobserved events are, however, assumed to occur continuously at a constant rate.

The model suggested by Chapman (1961) and Richards (1959) may be used to include growth. Letting A, m, b, and k be parameters, s the size, and t the time from birth, the general model

$$s_t = (A^{1-m} - b\,e^{-k \cdot t})^{\frac{1}{1-m}}$$

is the "logistic" function of Verhulst if $m=2$, the Brody (monomolecular, von Bertalanffy) model if $m=0$, and it approaches the Gompertz function as m approaches unity. Using the rationale of Fabens (1965) where s_1 is the size at time t_1 and s_2 is the size at time t_2, the above growth model leads to

$$s_2 = (A^{1-m} - (A^{1-m} - s_1{}^{1-m})\,e^{-k(t_2-t_1)})^{\frac{1}{1-m}}. \qquad (1)$$

This satisfies assumption (3), without reference to the actual age of individuals, by expressing size as a continuous function of time, but if growth is intermittent or has changed, a specialized model is most appropriate. From (1), or a more suitable model, let

l' = the size of a fish on date y_T that was size s on date y_t,
u' = the size of a fish on date y_T that was size $s+1$ on date y_t,
a' = the size of a fish on date c_k that was size s on date y_t, and
b' = the size of a fish on date c_k that was size $s+1$ on date y_t,

where l', u', a', and b' fall in size-classes l, u, a, and b. Including size in the abundance equation gives

$$N_{t,s} = \qquad (2)$$

$$\int_{l'}^{u'} N_{T,w}\,dw\,e^{z(y_T-y_t)} + \sum_{k=t}^{T-1} \int_{a'}^{b'} C_{k,w}\,dw\,e^{z(c_k-y_t)}.$$

If size-classes are suitably narrow, the frequency of size within size-classes tends to be proportional to size. The frequency of size within a class is therefore approximated by a trapezoid (i.e., trapezoidal integral approximation). The number of fish within the size class is

$$F_s = \int_s^{s+1} f_w\,dw = ½(s+1-s)\,(f_s+f_{s+1})$$

$$= ½(f_s - f_{s+1}),$$

where s is a size class, f_s is the frequency at size s, and F_s is the number within size-class s. Let the largest fish fall in class S:

$$f_S = ½F_S \text{ because } f_{S+1} = 0.$$

Rewriting gives $f_S = 2\,F_S$.

Proceeding to smaller sizes,

$$F_{S-1} = ½(f_{S-1}+f_S) \quad = ½(f_{S-1}+2F_S)$$
$$\text{so } f_{S-1} = 2(F_{S-1}-F_S).$$

$$F_{S-2} = ½(f_{S-2}+f_{S-1}) = ½(f_{S-2}+2F_{S-1}+2F_S)$$
$$\text{so } f_{S-2} = 2(F_{S-2}-F_{S-1}+F_S).$$

$$\vdots \qquad \vdots$$

$$F_s = ½(f_s+f_{s+1})$$
$$= ½(f_s+2F_{s+1}-2F_{s+2}+\ldots \pm 2F_S).$$

Rearrangement gives the general expression for the frequency at size-class bounds:

$$f_s = 2(F_s - F_{s+1} + F_{s+2} - F_{s+3} + \ldots \pm F_S).$$

The frequency of any size, s, within class s is also required:

$$f_{s'} = f_s + \frac{f_{s+1}-f_s}{s+1-s}(s'-s) = f_s + (s'-s)\,(f_{s+1}-f_s).$$

The approximate integrals for equation (2) are thus:

$$\text{If } u = l\text{:} \int_{l'}^{u'} N_{t,w}\,dw =$$

$$½(u'-l)\,(\eta_l + (l'-l)(\eta_{l+1}-\eta_l) + (u'-l)(\eta_{l+1}-\eta_l),$$

or

$$\text{if } u > l\text{:} \int_{l}^{u'} N_{t,w}\,dw =$$

$$½(l+1-l')(\eta_l + (l'-l)(\eta_{l+1}-\eta_l) + \eta_{l+1}) + \ldots$$

$$\ldots ½(u'-u)(2\eta_u + (u'-u)(\eta_{u+1}-\eta_u))$$

$$+ \sum_{i=l+1}^{u-1} N_{T,i},$$

and

$$\text{if } b = a: \int_{a'}^{b'} C_{k,w}\, dw =$$

$$\tfrac{1}{2}(b'-a')(\varsigma_a + (a'-a)(\varsigma_{a+1}-\varsigma_a) + \varsigma_b$$

$$+ (b'-b)(\varsigma_{b+1}-\varsigma_b)),$$

or

$$\text{if } b < a: \int_{a'}^{b'} C_{k,w}\, dw =$$

$$\tfrac{1}{2}(a+1-a')(\varsigma_a + (a'-a)(\varsigma_{a+1}-\varsigma_a) + \varsigma_{a+1}) + \ldots$$

$$\ldots \tfrac{1}{2}(b'-b)(2\varsigma_b + (b'-b)(\varsigma_{b+1}-\varsigma_b)),$$

where $\eta_s = 2(N_{T,s} - N_{T,s+1} + N_{T,s+2} - N_{T,s+3} + \ldots \pm N_{T,S}$,

and $\varsigma_s = 2(C_{k,s} - C_{k,s+1} + C_{k,s+2} - C_{k,s+3} + \ldots \pm C_{k,S}$.

On a sampling date, r measures are recorded and sample mean calculated for each size class:

$$Y_{t,s} = \sum_{k=1}^{r} \frac{Y_{t,s,k}}{r}.$$

According to assumption (3), the expectation of relative abundance is

$$E[Y_{t,s}] = f[\beta|Y,C] = q_s\, N_{t,s},$$

where β contains the sampling-gear efficiency coefficients (the q_s), the unobserved change rate (z), and the abundance of each size-class on date y_T (the $N_{T,s}$). $N_{t,s}$ is as defined by (2), Y indicates a matrix of relative abundance observations and C catches. Since it is a mean, clearly

$$Y_{t,s} \sim N\left(f[\beta|Y,C],\ \frac{\sigma^2[Y_{t,s}]}{r}\right)$$

(assumption 3). This implies the likelihood,

$$L(\beta) = \prod_{t,s}^{n} (2\pi)^{-1/2}\, \sigma[Y_{t,s}]^{-1}\, e^{-1/2(Y_{t,s}-f[\beta|Y,C])^2 + \sigma^2[Y_{t,s}]},$$

where n is the product of the number of size-classes and sampling dates. Maximizing its logarithm (constant terms ignored),

$$-\sum_{t}^{T}\sum_{s}^{S} (Y_{t,s} - f[\beta|Y,C])^2 \div \sigma^{||}[Y_{t,s}] \qquad (4)$$

with respect to β yields maximum-likelihood estimates of the q_s, the $N_{T,s}$, and z. Maximization was achieved by minimizing the negative of (4) by the "Marquardt" method (Morrison 1960, Marquardt 1963, Conway et al. 1970, Gallant 1975, Press et al. 1986).

This estimator is equivalent to common least-squares if size and date variances are equal, but that restriction seems unlikely. Since

$$\sigma^2[Y_{t,s}] = N_{t,s}^{2}\ \mathrm{Var}[q_s], \qquad (5)$$

abundance is the dominant term. Abundance is dependent on reproductive success and a mortality history. Both are time-variant, so an assumption of equal variances is inappropriate.

This abundance estimator possesses few restrictions. Relative-abundance measures and catches can occur on any date. Any number of catches, or none at all, can occur between relative abundance samples or visa versa. The period of data collection may be short; the time-series may be brief. Individual growth can follow any form. Most important, recruitment to the exploited stock can occur continuously so that breeding (spawning) and birth (hatching) need not happen just once during each period. Reproduction may be continuous so age-specific cohorts need not exist. This estimator is not a cohort analysis, but it uses similar data.

Monte Carlo tests

Each test was designed to collect a history of estimator performance over many applications of the method in similar circumstances. Each test was composed of several trials. On each trial, a new exploited population was simulated, followed by relative abundance sampling, growth rate estimation, and catch estimation. Next, β was estimated by (4) from the data collected in the second step. Last, estimation error for each element of $\hat{\beta}$ was calculated. The familiar measure of error, $e = (\hat{\beta}-\beta)$, where β is the vector of population parameters estimated by $\hat{\beta}$, was not appropriate because β changed from one simulation to the next. Error was measured by the sufficient statistic $\in = \hat{\beta} \div \beta$. The bias of each element of β was estimated as the average $\in$ over the n trials (Monte Carlo samples). If a particular estimate was unbiased, then $\mu[\in] = 1$ for that parameter. The estimated error variance of each parameter, $s^2[\in]$, was also calculated.

A significance level for bias larger than 10% was found by computing the probability of the standard normal random variable as follows:

$$\text{significance level}\begin{pmatrix}\text{HO: }\mu[\in]\geqslant 0.9\\ \text{HA: }\mu[\in]<0.9\end{pmatrix} =$$

$$\int_{-\infty}^{Z} f_p\,dp,\ Z = (\bar{\in}-0.9)\div[s(\in)/\sqrt{n}].$$

$$\text{significance level}\begin{pmatrix}\text{HO: }\mu[\in]\leqslant 1.1\\ \text{HA: }\mu[\in]>1.1\end{pmatrix} =$$

$$\int_{Z}^{\infty} f_p\,dp = 1.0 - \int_{-\infty}^{Z} f_p\,dp, =$$

$$(\bar{\in}-1.1)\div[S(\in)/\sqrt{n}].$$

The results between tests were statistically compared by placing confidence intervals on the difference between the biases (Law and Kelton 1982:319) and using the variance ratio test (*F* test) to compare error variances.

In each Monte Carlo test, the intent was to complete trials until the estimate of bias was within a given bound with a prescribed probability (Law and Kelton 1982). Several parameters were estimated, so several biases were involved. It was too costly to confirm that all bias estimates were trustworthy and many parameters were not of primary interest, so the error of last-period total stock size (∈[N(T.)]) was used as the reference statistic. Trials were completed until

$$1.96^2 \cdot s^2(\in[N(T.)]) \div n \leqslant \Phi^2,$$

where Φ was usually small. The 95% confidence bound half-lengths for all parameters were computed to indicate how well bias was estimated for each parameter.

The method of Schrage (1979) was used to generate uniform random variables because it is portable and known to perform well (Law and Kelton 1982:227–228). Normal random variables were generated by the polar method (Law and Kelton 1982:259). The method of Scheuer and Stoller (1962) was used to generate correlated bivariate normal random numbers.

In most trials, the lives of 20,000 fish were individually simulated over 20 time-periods. A history of abundance and catch was created, then abundance sampling, catch estimation, and growth parameter estimation was simulated. Each fish possessed a unique growth pattern and recruitment date and independently encountered unobserved events and fishing death. The result of these encounters, growth rates, and recruitment dates were tabulated into size-class and date-specific matrices of numerical abundance and catch. The sequence of events of the population simulation is diagrammed in Appendix 1. A detailed description of the simulation and justification of control variable levels is given by Parrack (1990).

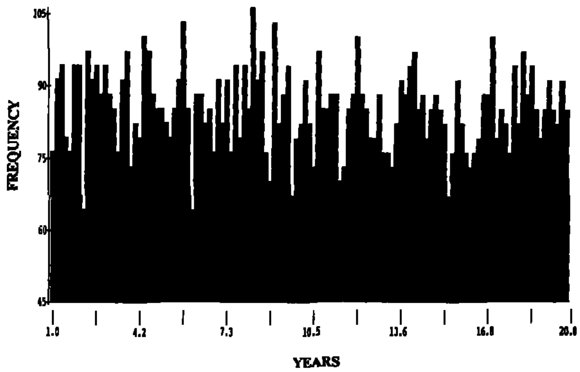

Figure 1
Frequency of recruitment dates from one trial of uniform recruitment simulations.

Von Bertalanffy growth was simulated by fixing m of equation (1) null: For each fish, A and k of (1) were drawn as normal random variables. The expectations were set near those estimated for many stocks, including Pacific cod (N.J.C. Parrack 1986), and their coefficients of variation (cv) were set as high or higher than common in other studies (≤0.4).

Two kinds of recruitment were considered, uniform and seasonal. The uniform pattern (Fig. 1) simulated continuous recruitment of constant magnitude. The date each fish recruited to the minimum size category was drawn as a U(1,20) random variable. Seasonal recruitment dates were drawn from normal distributions so that recruitment magnitudes varied U(1,20) between periods and so that a typical "pulse" of young fish recruited once each period, with some recruitment occurring continuously. The recruitment peak was simulated to occur randomly during April, May, and June by drawing the expected recruitment date for each period U(0.25,0.50). Protracted and contracted seasonal recruitment patterns were considered. Seasonal protracted recruitment was simulated by drawing the standard deviation of recruitment dates U(0.20,0.33) so that 80% of recruitment occurred randomly within ±3–5 months of the peak (Fig. 2). Seasonal contracted recruitment was simulated by drawing the standard deviation U(0.13,0.26) so that 80%

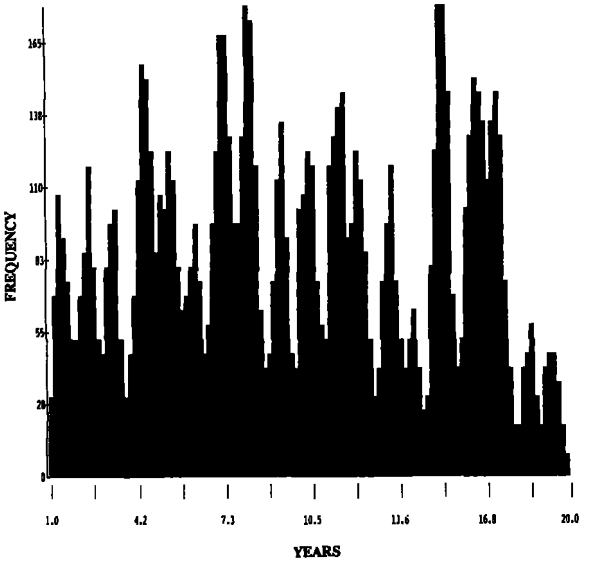

Figure 2
Frequency of seasonal, protracted recruitment dates from one trial. Peak recruitment occurs 1 April–1 June, 80% occurs within 3–5 months of the peak, and recruitment levels vary.

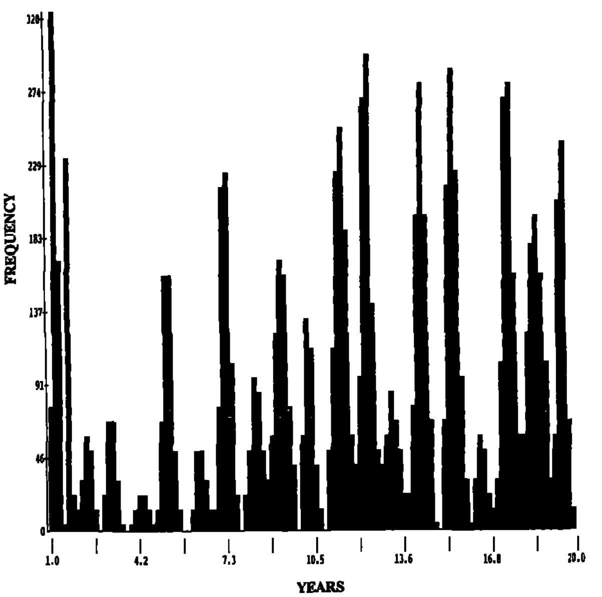

Figure 3
Frequency of seasonal, contracted recruitment dates from one trial. Peak recruitment occurs 1 April–1 July, 80% occurs within 2–4 months of the peak, and recruitment levels vary 20-fold between time periods.

of recruitment occurred randomly within ±2–4 months of the peak (Fig. 3).

The unobserved change rate was simulated both temporally invariant and variant. If variant, then $z_t \sim U(z_1, z_2)$ on each new trial; z_1 and z_2 were simulation control variables. Catching was simulated either as a single event that occurred once each midperiod or as a continuous event in each period. Fishing mortality was not imposed until period 6 so that the stock would accumulate as soon as possible after simulation initialization. In most tests the fishing mortality rate was drawn $U(F_1, F_2)$ on each new trial; F_1 and F_2 were control variables. Period-specific rates were set constant over all trials in two tests to guarantee a stock depletion caused by a rapid increase in fishing levels.

Sampling simulation included the generation of catch estimates, growth parameter estimates, and relative abundance measures. Populations and catches were generated over 20 time-periods. Relative abundance samples and catch estimates were simulated in the last four periods only, but catches were considered to be removed after the date of abundance samples so catch in the last period was irrelevant to estimation (and thus was not computed).

Size-class and date-specific catch estimates were drawn from a Gaussian distribution with catches from the simulator as the expectations and with variances specified by a cv. The estimator of catches was thus unbiased, and estimation errors (estimator variances) were proportional to catches.

A complete simulation of growth sampling and estimation was deemed too costly, so a reasonable proxy of unbiased estimation was used. Let A_i be a growth parameter of fish i such that $A_i \sim N(A, \sigma^2[A]$. Defining the uniqueness in growth of fish i as $\tau_i = A_i - A$, $\sigma^2[A] = \Sigma \tau_i^2/N$. Let A_i be unbiasedly measured by a_i with normal error so that $a_i = A_i + e_i$, $e_i \sim N(0, \sigma^2[e])$. Since $e_i = a_i - A_i$, $\sigma^2[e] = \Sigma e_i^2/N$, $\sigma^2[a_i] = E\{a_i - E[a_i]\}^2 = \sigma^2[A] + \sigma^2[e] + 2\sigma[\tau, e]$ where the last term is null because τ and e are independent. Using the sample mean of g fish to estimate A, $\sigma^2[\dot{A}] = (\sigma^2[A] + \sigma^2[e])/g$, so that growth-parameter estimation variance is separated into two parts, that of inherent variability from fish to fish and that of growth measurement error. CV's were used as simulation control input instead of variances, so growth parameter estimates were $N(A, A^2 (cv[A]^2 + cv[e]^2)/g)$ random variables. In reality, all growth parameters are estimated simultaneously. As a rule, growth parameter estimates are highly negatively correlated (Gallucci and Quinn 1979, Knight 1968, Burr 1988) with correlation coefficients often −0.90 or less. Estimates of k and A of (1) were drawn as normal random correlated variables (Rubinstein 1981:86) with a correlation coefficient of −0.95. The number of fish sampled for growth (g) was specified in the simulation indirectly as a probability level and limit of a confidence bound. For a $1-\alpha$ level confidence interval on A of bound length $2\Phi A$,

$$\Phi A = Z(1-\alpha/2)\,\sigma[\hat{A}] = Z(1-\alpha/2)\sqrt{A^2(cv[\hat{A}]^2+cv[e]^2)/g},$$

so

$$g = Z^2\left(1-\frac{\alpha}{2}\right)(cv[\hat{A}]^2 + cv[e]^2) \div \Phi^2.$$

On each sampling date r, relative abundance samples, $1 \leqslant k \leqslant r$, were simulated as

$$Y_{t,s} = \sum_{k=1}^{r} Y_{t,s,k} \div r = \sum_{k=1}^{r} q_{s,k}\, N_{t,s} \div r,$$

$$q_{s,k} \sim N\,(q_s,\ cv[q]^2\, q_s^2),$$

where cv[q] and the q_s were simulation constants. The q_s were 0.025, 0.05, 0.175, 0.225, 0.2425, and 0.25 (smallest to largest size-class) in most simulations. Several other variations were tried, and it was found that these constants did not affect results at all. Cv's of q were 0.4 or less. The observation and its variance were calculated as the maximum likelihood estimates,

$$Y_{t,s} = \sum_{k}^{r} Y_{t,s,k}/r$$

$$s^2[Y_{t,s}] = \sum_{k}^{r} (Y_{t,s,k}-Y_{t,s})^2/(r^2-r).$$

The sample size (r) was fixed indirectly by two control variables, the probability level and confidence-bound width for $Y_{t,s}$ where $\sigma^2[Y_{t,s}]$ is as (5). If a $1-\alpha$ level confidence interval on $Y_{t,s}$ was to be of bound length $2 \bullet \Phi \bullet N_{t,s} \bullet q_s$ then:

$$\Phi\, N_{t,s}\, q_s = \left(1-\frac{\alpha}{2}\right)\sigma[Y_{t,s}],$$

$$r = Z^2(1-\alpha/2)\, cv[q]^2 \div \Phi^2.$$

Sampling error entered the simulation as variation in q_s, not as variation in the $Y_{t,s}$; the variance of the abundance index was not an input.

These simulations encompassed many possibilities, but not all. Random variation was simulated in all process variables (z, growth parameters and recruitment magnitude, duration, and timing), but time trends were not. A different unobserved change rate was drawn for each time-period ($z_t \sim N(\mu_z,\ \sigma^2[z])$), but the expectation and variance were constant over time and size. Different growth parameters were drawn for each fish, but the expectations and variances were the same for all fish. Recruitment magnitudes for each time-period were drawn from a uniform distribution so time trends were not simulated. A different recruitment peak (i.e., the expectation of recruitment date) was drawn for each time-period from a common expectation and variance. A duration of recruitment (i.e., variance of recruitment date) was drawn for each time-period, but with the same expectation and variance. Random variation was simulated in sampling variables (catch estimates, growth parameter estimates, and the q_s), but biased estimates were not simulated. Although a different vector of sampling efficiencies (the q_s) were drawn for each sampling date, the expectation and variance for each size was temporally constant.

Results

The Monte Carlo tests fall into two categories: those that investigate the influence of population process variability on estimation errors, and those that test the effects of sampling and data estimation. Process variability includes recruitment phenomena, growth rates, and unobserved change due to emigration, immigration, natural death, and unrecorded catch. Sampling variation and data estimation includes four topics: catch estimation error, unrecorded dates of catch, growth parameter estimation error, and variability in sampling-gear efficiency coefficients, and thus in the abundance indices. Each of these items were studied separately in 14 tests.

Population process variability

For these tests, catches, dates of catch, and population growth parameters were considered to be known, and sampling gear efficiencies (the q's) invariant so that all sampling variation was absent. Catches were taken at midperiod. The probability of death due to catching in each period was an U(0.05, 0.2) random variable, and asymptotic size was 11.95 units (i.e., 119.5 cm, with 10 cm intervals).

Recruitment patterns Uniform recruitment test results (Table 1) show little bias and high precision in estimates of abundance and q's. Significance levels for the hypothesis of bias = 1.0 (unbiased) versus bias≠1.0 (biased) were <0.00005 in almost every case, but bias

Table 1

Monte Carlo tests of populations processes. Catches, dates of catch, and population growth parameters were assumed known. Sampling gear efficiencies (q) were invariant. The probability of death due to catching in each period was a U(0.05, 0.2) random variable. Catches occurred at midperiod. Asymptotic size (i.e., μ[A]) was 11.95.

	Recruitment patterns						
	Uniform	Protracted	Contracted	z variable	Variable growth Test 1	Variable, rapid growth - Test 2	Variable, slow growth - Test 3
μ[k]	0.17	0.17	0.17	0.17	0.17	0.34	0.085
cv[A & k]	0.00	0.00	0.00	0.00	0.40	0.40	0.40
Loss rate z	0.10	0.10	0.10	U(0.1,0.4)	0.10	0.10	0.10
Recruit levels	constant	U(1, 20)	U(1, 20)	U(1, 20)	U(1, 20)	U(1, 20)	U(1, 20)
Recruit dates	U(1, 20)	$N(\mu,\sigma^2)$	$N(\mu,\sigma^2)$	$N(\mu,\sigma^2)$	$N(\mu,\sigma^2)$	$N(\mu,\sigma^2)$	$N(\mu,\sigma^2)$
$\mu(t)$		U(0.25, 0.5)	U(0.25, 0.5)	U(0.25,0.5)	U(0.247, 0.5)	U(0.247, 0.5)	U(0.247, 0.5)
$\sigma(t)$		U(0.2, 0.33)	U(.13, 0.26)	U(0.2, 0.33)	U(0.2, 0.33)	U(0.2, 0.33)	U(0.2, 0.33)
95% CI of bias of N(T.)							
½ width achieved	0.0024	0.0114	0.0160	0.0139	0.0434	0.0457	0.0498
Number of trials	1010	210	775	105	109	327	32

Variable	Bias	s^2[∈]	Bias	s^2[∈]	Bias	s^2[∈]	Bias	s^2[∈]	Bias	s^2[∈]	Bias	s^2[∈]	Bias	s^2[∈]
N(T, 3)	0.9711	0.0032	1.1319	0.0333	1.3138	0.2460	1.1569	1.0508	0.7575	0.0204	0.8594	0.0319	0.8542	0.0456
N(T, 4)	0.9923	0.0152	0.9140	0.2824	0.9780	1.5205	0.9833	0.0955	1.0697	0.0588	0.7410	0.0152	0.8815	0.0379
N(T, 5)	0.9986	0.0055	0.9710	0.0527	0.9802	0.1454	1.0191	0.0364	0.9596	0.0134	0.9087	0.0168	0.9745	0.0044
N(T, 6)	0.9941	0.0010	1.0271	0.0078	1.0632	0.0165	1.0511	0.0341	0.9964	0.0010	1.0168	0.0101	1.0051	0.0036
N(T, 7)	0.9989	0.0016	0.9651	0.0072	0.9383	0.0133	0.9742	0.0046	0.9850	0.0010	0.9892	0.0041	0.9989	0.0036
N(T, 8)	1.0049	0.0005	1.0044	0.0012	1.0018	0.0041	0.9925	0.0017	1.0041	0.0003	0.9899	0.0013	1.0364	0.0043
N(T, 9)	0.9912	0.0008	0.9933	0.0024	0.9940	0.0036	1.0003	0.0024	0.9924	0.0004	0.9911	0.0004	1.0219	0.0100
N(T,10)	1.0084	0.0009	0.9916	0.0036	0.9905	0.0087	0.9735	0.0122	1.0200	0.0007	0.9991	0.0004	1.0836	0.0241
N(T,11)	0.9752	0.2291	0.6789	1.5190	0.4585	2.1818	0.2999	5.7229	1.0590	0.4399	1.2595	0.1852	1.9661	1.5290
N(T,12)									2.3825	2.7796	3.2020	1.3185	3.7363	5.9230
N(T,13)									2.9063	5.4646	3.8776	2.0041	5.5877	13.3879
N(T,14)									3.3177	8.3135	4.8876	1.9756	9.0415	77.7329
N(T,15)									3.9400	19.2576	6.3783	2.9742	11.3780	166.9735
N(T,16)									4.4074	45.0368	8.3752	6.7119	14.2365	403.7108
N(T,17)									5.5771	120.2284	11.3020	27.2042	14.9405	905.7713
N(T,18)									5.1845	203.8775	15.4323	50.7470	18.1915	903.7181
N(T,19)									9.6012	870.1467	23.3307	358.9141	26.6017	1253.4483
N(T,20)									1.3244	222.7073	26.9926	486.5381	11.0799	640.3803
N(T,21)									4.1712	169.5628	38.8813	2180.3053	24.4425	2117.6233
N(T,22)									−1.5598	53.1271	40.2471	3481.6977	2.3077	9.6225
N(T,23)									1.9878	41.6990	48.5059	4438.4966		
N(T,24)									−8.5990	2.7742	33.4447	6841.2892		
N(T,25)											32.0736	4537.5995		
N(T,26)											1.6141	5790.4488		
N(T.)	0.9908	0.0015	1.0064	0.0071	1.0491	0.0516	1.0245	0.0053	1.0988	0.0535	1.8714	0.1781	1.1147	0.0206
q(3)	1.0331	0.0039	0.9010	0.0209	0.8103	0.0410	0.8891	0.0268	1.3544	0.0543	1.2201	0.0676	1.4094	0.1195
q(4)	1.0178	0.0036	0.8844	0.0085	0.7299	0.0185	0.8728	0.0091	1.1304	0.0161	1.3772	0.0487	1.1669	0.0297
q(5)	0.9977	0.0030	0.9787	0.0067	0.9292	0.0181	0.9581	0.0058	1.0987	0.0118	1.2252	0.0325	1.0611	0.0064
q(6)	1.0090	0.0012	1.0212	0.0033	1.0177	0.0091	1.0161	0.0043	1.0478	0.0031	1.1014	0.0104	1.0094	0.0043
q(7)	0.9870	0.0011	1.0758	0.0062	1.1436	0.0137	1.0855	0.0073	1.0110	0.0023	1.0738	0.0063	0.9641	0.0025
q(8)	1.0133	0.0015	0.9290	0.0046	0.8422	0.0100	0.8780	0.0157	0.9706	0.0056	1.0444	0.0033	0.9198	0.0114
q(9)	1.0311	0.0039	1.0462	0.0199	1.0381	0.0275	0.9848	0.0437	0.9363	0.0100	1.0057	0.0044	0.9531	0.0258
q(10)	0.9717	0.0190	0.9655	0.1925	0.9282	0.2356	0.7786	0.3357	0.8790	0.0230	0.9282	0.0058	0.8257	0.0304
q(11)	0.7365	0.1902	0.6016	1.5307	0.8387	1.7031	0.1939	2.5069	0.5449	0.3805	0.4157	0.0087	0.4976	0.0643
q(12)									0.4371	0.0403	0.3132	0.0056	0.3373	0.0272
q(13)									0.3349	0.0263	0.2554	0.0047	0.2187	0.0129
q(14)									0.2587	0.0174	0.1940	0.0588	0.1427	0.0084
q(15)									0.1777	0.0124	0.1510	0.0221	0.0983	0.0038
q(16)									0.1242	0.0051	0.1171	0.0049	0.0654	0.0019
q(17)									0.0887	0.0036	0.0822	0.0029	0.0437	0.0015
q(18)									0.0589	0.0020	0.0580	0.0012	−0.2827	2.9493
q(19)									0.0394	0.0022	0.0365	0.0009	0.7259	13.8313
q(20)									−0.0925	1.0754	0.0247	0.0003	−0.1340	0.1934
q(21)									0.2614	2.9476	0.0165	0.0001	−0.0174	0.0165
q(22)									−0.1324	0.5450	0.0200	0.0473	−9.6131	278.5656
q(23)									−0.3803	3.0233	0.5313	53.3122		
q(24)									0.0163	0.0000	0.0122	0.2028		
q(25)									0.0177	0.0001	−0.0096	0.0421		
q(26)											−2.1688	167.9745		
z	1.5847	0.0715	1.6436	0.1442	1.8264	0.2772			1.9012	0.3023	2.7344	0.5514	0.9394	0.1280
exp(z)	1.0608	0.0008	1.0676	0.0017	1.0877	0.0034			1.0959	0.0036	1.1926	0.0075	0.9946	0.0013

was not large; the significance levels for the hypotheses of bias $\leq 10\%$ were >0.99995 for all estimates. Precision was not a problem, although error variances were not zero.

Since sampling variation was zero and the estimation model encompassed all of the population characteristics simulated, the estimation bias and imprecision were unexpected. The only possible source of that error are the integral approximations required in estimation.

The estimate of the unobserved change rate (z) was biased high by about 60% and its error variance was large. It entered estimation in an exponent, so the term in the model was the exponent of z (the reciprocal of "survival" from unobserved change), not z. The error term was again computed on the exponent of the estimate of z instead of z. The estimated bias was ten times lower and the error variance was several orders of magnitude less. This result proved consistent in all tests of population processes.

Partial correlation coefficients between parameter estimates did not exhibit meaningful trends. Although some adjoining abundance estimates were correlated (probably because the abundances were), evidence of other correlations were absent. Estimates of z were not correlated with the estimates of the q's or abundances; estimates of the q's were not correlated with abundance estimates. This result proved consistent. The correlation matrices for this and following tests are not shown for the sake of brevity but are presented in Parrack (1990).

The two seasonal recruitment tests (protracted and contracted patterns) show increased bias and imprecision. As the recruitment frequency contracted, bias and error variance-of-abundance estimates of the smallest and largest size-classes increased. This problem was worst for the largest size-class. Estimates of the q's also degraded.

Unobserved change rate The estimator assumes that the rate of change due to phenomena that cannot be observed (natural death, migration, unrecorded catch) is constant over periods. Since the assumption is undoubtedly false, estimation errors resulting from assigning a U(0.1, 0.4) random variable to z for each period were investigated. Other simulation characteristics were as in the seasonal protracted recruitment test. The 95% confidence intervals on the difference of abundance estimation bias between this test and the protracted recruitment test included zero for size-classes 3 and 4, most others, and total abundance. Error variances were likely equal for size-classes 3, 4, and total abundance (SL 0.005, SL<0.000, SL<0.000). Correlations between estimates were low. A fourfold random variability in z did not affect estimation at all.

Growth Three tests consider highly variable growth. The cv's of asymptotic size and k were 0.4. Test 1 simulated the same growth parameters as the protracted recruitment test (k 0.17), test 2 considered growth twice as rapid (k 0.34), and test 3 growth twice as slow (k 0.085). All other simulation control variables are the same as the protracted recruitment test, so the results are comparable.

The results of all three tests were very similar. All reflected the high variation of asymptotic size: the parameter vector included size-classes larger than the asymptote. Abundance and q estimates of these classes (12 and larger) were worthless; huge bias and imprecision occurred. Abundances of smaller size-classes in all three tests were more precise than in the protracted recruitment test where growth was not variable. Biases and error variances of abundance and q estimates for size-class 11 and smaller were very similar in the three tests; performance seemed unaffected by growth rates. The exponent of z was again estimated much better than z in all three tests; estimates were precise although significant bias was present in the case of rapid, variable growth. Evidence of correlated estimates was absent. The introduction of an extremely high level of variation on individual growth parameters did not negatively affect estimates.

Data estimation and sampling

Errors attributable to sampling and the compilation of various input statistics were studied in seven tests. Catches are rarely censused as assumed by the estimator; estimates are usually the available statistics. The estimator models the dates of each catch, yet catch statistics are usually summed over an interval of dates. Growth rates are assumed to be known, but that is never possible; growth parameters must be estimated. Last, the variability in sampling-gear efficiency coefficients, and thus in the abundance indices, is also a source of uncertainty.

Most of the simulation control variables in these seven tests were the same as in the protracted recruitment test. Asymptotic size was 11.95, growth k was 0.17, the unobserved loss rate (z) was fixed at 0.1, and the seasonal, protracted recruitment pattern was employed; thus recruitment levels varied 20-fold between periods. Catching was simulated differently than in the protracted recruitment test. Catching was continuous (see Appendix 1, step 4) instead of a single subtraction at midperiod, and the fishing mortality rate (F) was a U(0.1, 0.4) random variable.

Catch dates A single scenario was used to investigate the importance of recording each catch date and modeling each catch separately. The summed catch over each period was assumed to be known, but not

Table 2

Monte Carlo tests for the effects of sampling variation. $\mu[A]=11.95$, $\mu[k]=0.17$, $z=0.1$, and seasonal, protracted recruitment was simulated. Catching was simulated as a continuously occurring event. The instantaneous rate of fishing mortality was a U(0.1, 0.4) random variable.

			Growth parameter measurement error			Relative abundance	
	Unknown catch date	Catch estimation error	40% Error	15% Error	with process variance	cv[q] 0.4, *r*3	cv[q] 0.2, *r*16
cv[A & k]	0.00	0.00	0.00	0.00	0.20	0.00	0.00
Catch estimation							
catch dates	absent	absent	absent	absent	absent	absent	absent
cv[C(t,s)]	0.00	0.40	0.00	0.00	0.00	0.00	0.00
Growth estimation							
cv[error]	0.00	0.00	0.40	0.15	0.15	0.00	0.00
precision level	—	—	—	—	0.02	—	—
probability level	—	—	—	—	0.95	—	—
fish sampled, g	1	1	1	1	601	1	1
Sampling efficiency							
cv[q(s)]	0.00	0.00	0.00	0.00	0.00	0.40	0.10
precision level	—	—	—	—	—	0.50	0.05
probability level	—	—	—	—	—	0.95	0.95
sample size, r	1	1	1	1	1	3	16
95% CI of bias of N(T.)							
½width achieved	0.0155	0.0197	0.4789	0.0210	0.0198	0.0354	0.0198
Number of trials	101	84	192	198	79	200	52

Variable	$\bar{\in}$	$s^2[\in]$	$\bar{\in}$	$s^2[\in]$	$\bar{\in}$	$s^2[\in]$	$\bar{\in}$	$s^2[\in]$	$\bar{\in}$	$s^2[\in]$	$\bar{\in}$	$s^2[\in]$	$\bar{\in}$	$s^2[\in]$
N(T, 3)	1.1081	0.0295	1.1817	0.0646	1.8710	217.1297	1.1439	0.1424	0.9947	0.0355	1.3381	5.2758	1.0972	0.0768
N(T, 4)	0.9710	0.3532	1.0314	0.2057	1.0034	3.4342	0.9228	1.0249	1.0184	0.0767	0.9247	3.0564	0.9288	0.0823
N(T, 5)	1.0009	0.0253	0.9350	0.0398	1.1353	3.4290	1.0028	0.1066	1.0026	0.0108	0.8733	0.2110	0.9128	0.0471
N(T, 6)	1.0162	0.0052	1.0197	0.0034	1.3096	6.9835	1.0375	0.0511	0.9902	0.0011	1.0156	0.0289	1.0092	0.0056
N(T, 7)	0.9740	0.0051	0.9660	0.0055	1.3544	12.7702	0.9675	0.0170	0.9953	0.0009	0.9530	0.0430	0.9191	0.0119
N(T, 8)	1.0000	0.0010	0.9956	0.0079	1.6209	17.9277	1.0437	0.0598	1.0019	0.0010	1.0243	0.0194	1.0239	0.0045
N(T, 9)	1.0003	0.0007	0.9939	0.0061	1.5861	11.9433	1.0458	0.0952	0.9959	0.0008	0.9703	0.0079	0.9688	0.0024
N(T,10)	0.9914	0.0045	0.9973	0.0012	2.6909	26.6738	1.3480	1.1729	1.0096	0.0019	1.0077	0.0112	1.0021	0.0004
N(T,11)	0.8191	3.9963	0.7914	1.2824	3.4334	111.2210	1.2774	5.3882	1.1619	0.3091	1.1734	1.1168	0.9568	0.1516
N(T,12)									2.3955	1.6866				
N(T,13)									3.4498	5.9767				
N(T,14)									3.2299	16.5785				
N(T,15)									3.6964	41.8706				
N(T,16)									0.4291	92.2468				
N(T,17)									6.5117	174.0005				
N(T,18)									1.5430	10.9191				
N(T,19)									18.1902	768.6451				
N(T.)	1.0242	0.0063	1.0259	0.0086	1.4105	11.4628	1.0416	0.0226	1.0542	0.0081	1.0345	0.0653	0.9799	0.0053
q(3)	0.9180	0.0200	0.8754	0.0291	1.3725	9.3538	0.9143	0.0715	1.0346	0.0290	0.9655	0.1063	0.9661	0.0460
q(4)	0.8578	0.0062	0.8729	0.0126	1.5114	25.7585	0.8825	0.0451	1.0391	0.0157	0.8933	0.0776	0.9397	0.0124
q(5)	0.9715	0.0051	0.9725	0.0103	2.0644	87.9064	1.0305	0.3386	1.0472	0.0098	1.0162	0.0709	1.0402	0.0091
q(6)	1.0046	0.0043	1.0141	0.0065	1.9815	47.7841	1.0593	0.1689	1.0315	0.0021	1.0467	0.0553	1.0629	0.0045
q(7)	1.0783	0.0059	1.0679	0.0065	2.0977	54.6183	1.0887	0.0294	1.0112	0.0022	1.1524	0.0767	1.1242	0.0159
q(8)	0.9093	0.0058	0.9342	0.0061	1.5326	20.5395	0.9387	0.0249	0.9900	0.0058	0.9596	0.0590	0.9590	0.0075
q(9)	1.0159	0.0190	1.0447	0.0239	1.7836	46.8489	1.0023	0.0620	0.9735	0.0082	1.1949	0.1016	1.1582	0.0194
q(10)	1.0151	0.1572	1.0147	0.0816	1.4402	25.2990	0.8819	0.1195	0.9388	0.0293	1.0083	0.1004	0.9874	0.0182
q(11)	0.5695	0.8583	0.8320	1.4223	1.4677	34.9181	0.9667	0.5829	0.6416	0.0701	0.9200	0.6084	0.8700	0.1365
q(12)									0.3774	0.0303				
q(13)									0.2138	0.0091				
q(14)									0.1017	0.0042				
q(15)									0.0488	0.0012				
q(16)									−3.1478	425.1308				
q(17)									0.0866	0.0670				
q(18)									−0.0707	0.0967				
q(19)									1.2251	4.4242				
z	0.8137	0.1022	1.6881	0.2587	0.2301	25.5499	1.0396	0.0219	0.1835	0.0000	0.8525	1.0626	0.8542	0.2896
exp(z)	0.9820	0.0010	1.0736	0.0031	0.9828	0.0416	1.0527	0.0067	1.0898	0.0022	0.9913	0.0104	0.9869	0.0029

the dates of the catches. The accumulated catch each period was assigned to the midpoint of each period for estimation. The results (Table 2) were almost identical with those of the protracted recruitment test (Table 1). The 95% confidence interval (Welch 1938) on the difference between total-abundance estimation bias of the protracted recruitment test and this test included zero (−0.0014 to 0.0372). The error variances were very similar (0.0072 and 0.0063). Estimates were not correlated. The absence of exact catch dates did not affect estimation.

Catch estimation error The effects of estimating catches rather than enumerating them were investigated by drawing size-class-specific catch estimates as normal random variables with expectation $C(t,s)$ and variance $(cv[C] \cdot C(t,s))^2$. This simulated unbiased catch estimation and estimation error proportional to catches. A large degree of catch estimation uncertainty was imposed ($cv[C] = 0.40$). Simulation control variables were the same as in the catch date test and the protracted recruitment test. Results were also similar. The bias of total abundance estimates was about the same for all three tests and the error variances were nearly so. Correlated estimates were not evident. Confidence intervals (95%) on the difference in bias between this test and the protracted recruitment test included zero for all size-classes and total abundance. The error variance for size-class 3 was different ($SL < 0.0005$) and might have been different for size-class 4 (SL 0.052), but probably not for total abundance (SL 0.142) and all others. Imprecise catch estimates did not impact bias or error variance.

Growth parameter estimation error The effect of imprecise growth parameter estimates was also considered. Estimates of growth parameters were simulated as normal correlated random variables with expectations equal to those of the population. As explained in the Monte Carlo methods section, the variance of a growth parameter estimate is composed of two parts: process variation due to variant individual growth, and growth measurement error. Simulation control constants were therefore the cv of A and of k, the growth measurement error cv, the two constants required to compute the sample size used to estimate the growth parameters, and the correlation coefficient between estimates (−0.95). Simulation constants were as in the catch date test except those related to growth parameter estimation.

Three tests were carried out, two without process variation. First, the effect of two measurement error cv's was studied in the absence of growth variability. The sample size was set at one fish in these two tests so affects due to measurement error would be magnified. Then, the combined effect of process variation and estimation error was considered.

In the first test with extremely imprecise growth parameter estimates (cv 0.4), Monte Carlo trials were carried out until it became obvious that little more information would be gained with further computations. Error variances were huge (Table 2). Only the exponent of z was reasonably estimated. Many estimates were correlated, particularly those of z with those of sampling-gear efficiency coefficients. Even without individually variant growth rates (an unlikely prospect), large growth-parameter measurement error created significant uncertainty.

The second test simulated 15% measurement error. A 95% confidence interval on the difference between the bias of total abundance estimates between this and the protracted recruitment test included zero, but the error variances were probably different ($SL < 0.0001$); most error variances were higher. Bias was unaffected although error variance approximately doubled. The estimates did not seem correlated. The introduction of a 15% growth measurement error increased error variances but did not affect bias.

The third test simulated both process error (cv 0.2) and 15% growth measurement error, but with a sample size such that 95% confidence intervals on the estimate of the expectation of growth parameters were with precision ±2% ($g = 601$ fish). The 95% confidence interval on the difference in bias of total abundance estimates between this test and the protracted recruitment test included zero (−0.0220 to 0.0238) although error variances perhaps differed ($SL \approx 0.05$). Estimates were not correlated. Apparently 15% (or less) measurement error, even with natural growth variation, minimally affects estimation.

Gear efficiency variability The estimator is derived from the density function of relative abundance observations (Y), but the effect of Y variability on estimation error was not of large interest. The variance of Y is $\sigma^2[Y_{t,s}] = N_{t,s}{}^2 cv[q]^2$. The dominant term is the square of abundance, so as abundance increases, $\sigma^2 [Y_{t,s}]$ increases. This may be dampened a bit by an increase in q with size, but the dominant factor in the variance expression for the observations is abundance. Abundance levels cannot be controlled or anticipated beforehand, so knowledge of the effect of Y variability is of little value. Knowledge of the effect of q variability is useful, however, since care may be taken in the selection and design of sampling gear.

Studies that document the statistics necessary to calculate the variability of relative abundance sampling-gear efficiencies are not common. Studies of commerical fishery statistics offer different but useful information. Yield is a portion of biomass; the proportion is the product of fishing effort and q for the fishing method. Since yield is the product of q, effort, and biomass, then yield-per-effort equals the product of q and biomass and q is yield-per-effort divided by biomass. It then follows that the cv's of q and yield-per-effort are equal. The cv of yield-per-effort of the Pacific halibut longline fishery is estimated to be 0.02 (Quinn et al. 1982), and that of Newfoundland flounder trawlers on the Grand Bank (Smith 1980) is estimated to be about the same. The levels used in these simulations (0.4 and 0.2) are about an order of magnitude higher than those.

Effects of the variability in q on estimation errors were investigated in three tests. All simulation constants were as in the protracted recruitment test except those related to abundance sampling. Simulation control constants were cv[q] and the two constants required to compute the sample size. Although they were probably unrealistically large, a cv[q] of 0.4 was used in the first test and 0.2 was used in the second.

First, the impact of extreme variability (cv 0.4) and extremely light sampling was tested. The sample size (*r* 3) was such that a 95% confidence interval on relative abundance was within ±50% of the expectation. The extremely high cv[q] and low relative-abundance sample size were not reflected in error variances as much as expected (Table 2), but error variances were higher than those of the protracted recruitment test. Most abundance estimates were biased by less than 10%. Estimates were not correlated.

Next, the cv[q] was reduced to 0.1 and the sample size was increased so that a 95% confidence interval on relative abundance was within ±5% of the expectation (*r* 16). The result was very similar to those of the first test except error variances were much lower. Biases of abundance estimates were ±10% or less and estimates were not correlated.

There was no evidence that high variation in the q_s biased abundance estimates even if sample sizes were insufficient, but error variances were affected. Error variance was considerably reduced with reasonable sample sizes.

Bias

The results of these experiments (Tables 1 and 2) show that abundances and gear efficiencies (q's) of the smallest and largest size-classes were often biased. Bias did not occur with uniform, constant recruitment and no sampling variation, but as process and sampling variation increased, bias in estimates of the smallest and largest sizes became pronounced.

Each expected value is a proportion of calculated abundance. The abundance calculation sums future catches (data), last-period abundance (estimates), and an amount for unobserved changes (estimate). Future catches and terminal abundance are thus the major components of each projection. Both catch and final abundance must be integrated over size. The integration of catch over size at each catch date following the date of the expected value is required. The integration of abundance over size on the date of the final relative abundance sample is also necessary. All integrals are approximated, so these calculations are the source of the bias. The amount of error incurred at each integration depends on how well the trapezoidal rule approximates the size distribution. Since the size frequency within a size-class is never smooth, the approximation will be in error with the amount depending on the degree of smoothness within the size-class. If growth is variable or the number of fish is small, clumps in size frequencies can result from chance alone, but the major factor is the growth and recruitment pattern combination.

Narrowing the size-classes eliminates this problem. If they are narrowed enough to eliminate clumping caused by the particular recruitment frequency contraction, the size frequency within size-classes will be smooth and the trapezoidal approximation will be accurate. The seasonal contracted pattern of recruitment test 3 was again used to demonstrate this. An asymptotic size of 120 cm was simulated with recruitment occurring at 20 cm. First, it was assumed that the data were collected in 20 cm intervals so that the asymptotic size was 6 and the recruitment size was class 1. In the second case, it was assumed that data were collected in 2 cm groups so that the asymptotic size was 60 and the recruitment size was class 10. The unobserved change rate was set at 0.2 in both tests, and all other simulation control variables were as in the contracted recruitment test.

Ninety-two trials were required to obtain a 95% confidence interval half-length of 0.05 on the bias of total abundance in bias test 1 with 20 cm interval data. Estimates of the smallest and largest size-class abundances were biased and the error variances were very large (Table 3), particularly for the largest size-class. The estimate of the survival from unobserved change (z) was, however, reasonably accurate and precise.

Only 16 trials were required to obtain a 95% confidence interval half-length of 0.03 on the bias of total abundance in bias test 2 with two-unit size-interval data because the error variances were very low. Estimates of the first three size groups were probably biased by 10% or more, but the rest were not. Only six of the 47 estimates were probably biased at all (0.95 level). The estimate of the exponent of z was also not biased. Although the matrix was too large to be included (194 rows and columns), there was no evidence that estimates were correlated.

Table 3

Biases for 20 cm size-class width data (bias test 1, 92 trials) versus biases for 2 cm size-class width data (bias test 2, 16 trials).

Bias test	Variable	Estimates		Bias 95% CI ½-width	Significance levels	
		Bias	$s^2[\in]$		HO:Bias≥0.9 HA:Bias<0.9	HO:Bias≤1.1 HA:Bias>1.1
1	N(20–39)	1.2941	0.1332	0.0746	1.0000	0.0000
2	N(20–21)	1.8093	0.5273	0.3558	1.0000	0.0000
2	N(22–23)	1.5883	0.2529	0.2464	1.0000	0.0001
2	N(24–25)	1.5190	0.3576	0.2930	1.0000	0.0025
2	N(26–27)	1.1204	0.0790	0.1377	0.9991	0.3856
2	N(28–29)	0.9746	0.0578	0.1178	0.8927	0.9815
2	N(30–31)	0.8908	0.0124	0.0545	0.3699	1.0000
2	N(32–33)	1.0826	0.0440	0.1028	0.9997	0.6303
2	N(34–35)	0.9963	0.0002	0.0073	1.0000	1.0000
2	N(36–37)	1.0142	0.0032	0.0276	1.0000	1.0000
2	N(38–39)	0.9924	0.0005	0.0109	1.0000	1.0000
1	N(40–59)	1.0071	0.0234	0.0313	1.0000	1.0000
2	N(40–41)	1.0052	0.0003	0.0089	1.0000	1.0000
2	N(42–43)	1.0009	0.0000	0.0032	1.0000	1.0000
2	N(44–45)	1.0013	0.0001	0.0041	1.0000	1.0000
2	N(46–47)	0.9977	0.0001	0.0042	1.0000	1.0000
2	N(48–49)	1.0060	0.0008	0.0136	1.0000	1.0000
2	N(50–51)	0.9966	0.0004	0.0097	1.0000	1.0000
2	N(52–53)	1.0022	0.0000	0.0030	1.0000	1.0000
2	N(54–55)	0.9985	0.0001	0.0046	1.0000	1.0000
2	N(56–57)	0.9998	0.0000	0.0013	1.0000	1.0000
2	N(58–59)	0.9969	0.0001	0.0047	1.0000	1.0000
1	N(60–79)	0.9741	0.0288	0.0347	1.0000	1.0000
2	N(60–61)	1.0046	0.0001	0.0045	1.0000	1.0000
2	N(62–63)	0.9975	0.0002	0.0077	1.0000	1.0000
2	N(64–65)	0.9998	0.0000	0.0018	1.0000	1.0000
2	N(66–67)	0.9998	0.0001	0.0059	1.0000	1.0000
2	N(68–69)	1.0026	0.0002	0.0062	1.0000	1.0000
2	N(70–71)	0.9959	0.0002	0.0071	1.0000	1.0000
2	N(72–73)	1.0034	0.0001	0.0060	1.0000	1.0000
2	N(74–75)	1.0025	0.0001	0.0050	1.0000	1.0000
2	N(76–77)	1.0039	0.0003	0.0081	1.0000	1.0000
2	N(78–79)	1.0004	0.0001	0.0049	1.0000	1.0000
1	N(80–99)	1.0517	0.0745	0.0558	1.0000	0.9553
2	N(80–81)	0.9982	0.0003	0.0080	1.0000	1.0000
2	N(82–83)	1.0009	0.0001	0.0045	1.0000	1.0000
2	N(84–85)	1.0037	0.0002	0.0067	1.0000	1.0000
2	N(86–87)	1.0013	0.0000	0.0010	1.0000	1.0000
2	N(88–89)	0.9995	0.0000	0.0016	1.0000	1.0000
2	N(90–91)	0.9992	0.0001	0.0054	1.0000	1.0000
2	N(92–93)	0.9994	0.0000	0.0009	1.0000	1.0000
2	N(94–95)	0.9963	0.0001	0.0041	1.0000	1.0000
2	N(96–97)	0.9989	0.0000	0.0017	1.0000	1.0000
2	N(98–99)	0.9974	0.0000	0.0022	1.0000	1.0000
1	N(100–119)	6.4942	254.5641	3.2603	0.9996	0.0006
2	N(100–101)	1.0003	0.0000	0.0007	1.0000	1.0000
2	N(102–103)	0.9997	0.0003	0.0091	1.0000	1.0000
2	N(104–105)	0.9979	0.0003	0.0105	1.0000	1.0000
2	N(106–107)	0.9997	0.0000	0.0005	1.0000	1.0000
2	N(108–109)	1.0009	0.0000	0.0005	1.0000	1.0000
2	N(110–111)	0.9981	0.0000	0.0035	1.0000	1.0000
2	N(112–113)	1.0000	0.0000	0.0005	1.0000	1.0000
1	N(T.)	1.1808	0.0592	0.0497	1.0000	0.0007
2	N(T.)	1.0388	0.0049	0.0342	1.0000	0.9998

Bias test	Variable	Estimates		Bias 95% CI ½-width	Significance levels	
		Bias	$s^2[\in]$		HO:Bias≥0.9 HA:Bias<0.9	HO:Bias≤1.1 HA:Bias>1.1
1	q(20–39)	0.8296	0.0207	0.0294	0.0000	1.0000
2	q(20–21)	0.6373	0.0560	0.1160	0.0000	1.0000
2	q(22–23)	0.6924	0.0504	0.1101	0.0001	1.0000
2	q(24–25)	0.7464	0.0621	0.1221	0.0068	1.0000
2	q(26–27)	0.9410	0.0465	0.1057	0.7766	0.9984
2	q(28–29)	1.0818	0.0616	0.1216	0.9983	0.6151
2	q(30–31)	1.1408	0.0234	0.0749	1.0000	0.1431
2	q(32–33)	0.9545	0.0300	0.0849	0.8959	0.9996
2	q(34–35)	0.7751	0.0463	0.1055	0.0101	1.0000
2	q(36–37)	0.6608	0.0531	0.1129	0.0000	1.0000
2	q(38–39)	0.7494	0.0379	0.0954	0.0010	1.0000
1	q(40–59)	1.0050	0.0125	0.0228	1.0000	1.0000
2	q(40–41)	0.9352	0.0099	0.0487	0.9216	1.0000
2	q(42–43)	1.0218	0.0205	0.0701	0.9997	0.9856
2	q(44–45)	1.0357	0.0093	0.0473	1.0000	0.9961
2	q(46–47)	0.8792	0.0154	0.0608	0.2513	1.0000
2	q(48–49)	0.7148	0.0542	0.1141	0.0007	1.0000
2	q(50–51)	0.7373	0.0333	0.0894	0.0002	1.0000
2	q(52–53)	0.8691	0.0090	0.0464	0.0960	1.0000
2	q(54–55)	1.0389	0.0438	0.1025	0.9961	0.8786
2	q(56–57)	1.0358	0.0056	0.0365	1.0000	0.9997
2	q(58–59)	0.8082	0.0187	0.0670	0.0036	1.0000
1	q(60–79)	0.9049	0.0193	0.0284	0.6333	1.0000
2	q(60–61)	0.6377	0.0760	0.1351	0.0001	1.0000
2	q(62–63)	0.8143	0.0401	0.0982	0.0434	1.0000
2	q(64–65)	0.9890	0.0204	0.0700	0.9936	0.9991
2	q(66–67)	1.0381	0.0257	0.0785	0.9997	0.9388
2	q(68–69)	0.8908	0.0447	0.1036	0.4306	1.0000
2	q(70–71)	0.7287	0.0583	0.1183	0.0023	1.0000
2	q(72–73)	1.0168	0.0152	0.0604	0.9999	0.9965
2	q(74–75)	1.0449	0.0163	0.0626	1.0000	0.9577
2	q(76–77)	0.8313	0.0415	0.0998	0.0886	1.0000
2	q(78–79)	0.7050	0.0727	0.1321	0.0019	1.0000
1	q(80–99)	0.7632	0.2257	0.0971	0.0029	1.0000
2	q(80–81)	0.9684	0.0392	0.0970	0.9167	0.9961
2	q(82–83)	1.0334	0.0214	0.0717	0.9999	0.9657
2	q(84–85)	0.6644	0.0478	0.1071	0.0000	1.0000
2	q(86–87)	0.9742	0.0679	0.1277	0.8727	0.9732
2	q(88–89)	0.7991	0.0914	0.1481	0.0909	1.0000
2	q(90–91)	0.7715	0.0667	0.1266	0.0233	1.0000
2	q(92–93)	0.9841	0.0515	0.1148	0.9244	0.9761
2	q(94–95)	0.7314	0.1194	0.1749	0.0294	1.0000
2	q(96–97)	0.8420	0.0390	0.1000	0.1279	1.0000
2	q(98–99)	0.9202	0.1227	0.1835	0.5856	0.9726
1	q(100–119)	0.1117	0.5453	0.1509	0.0000	1.0000
2	q(100–101)	0.7954	0.1388	0.1952	0.1467	0.9989
2	q(102–103)	0.9848	1.5099	0.6680	0.5983	0.6323
2	q(104–105)	1.0579	0.0507	0.1224	0.9943	0.7497
2	q(106–107)	0.8840	0.0867	0.1923	0.4350	0.9862
2	q(108–109)	0.8992	0.0936	0.2682	0.4976	0.9289
2	q(110–111)	1.0052	0.1531	0.3835	0.7047	0.6860
2	q(112–113)	1.0121	0.0004	0.0238	1.0000	1.0000
1	exp(z)	0.9716	0.0135	0.0237	1.0000	1.0000
2	exp(z)	0.9783	0.0169	0.0637	0.9920	0.9999

Estimates of the first three size-classes were both biased and imprecise. Poor estimates of the smallest few size-classes were expected. These classes lacked a catch history at the time of the last sample, so these estimates of abundance (at the time of the last relative abundance sample) were a function of the last-period relative abundance sample only.

Examples

Two tests were used to discover what might be expected when assessing populations with no periodicity in recruitment at all; recruitment dates were completely protracted uniformly through time (Fig. 1). Most control variables were the same in the two tests. Data were assumed to be available in two-unit size intervals. A 120-unit asymptotic size fell in size-class 60, and a 30-unit recruitment size in class 15. The growth parameter k was left at 0.17. Continuous fishing was simulated; the fishing mortality rate (F) for each period was drawn from a U(0.3, 0.8) distribution. The expectations of sampling efficiencies (q_s) were arbitrarily chosen so that their regression on size was sigmoid, reaching an asymptote at size-class 30 (0.028, 0.031, 0.033, 0.038, 0.044, 0.053, 0.069, 0.101, 0.153, 0.190, 0.218, 0.234, 0.242, 0.247, 0.249, and 0.250). Catch estimates were simulated to be imprecise (cv 0.4). A 10% growth measurement error was simulated. Sampling intensities were the same in both tests; sample sizes for growth parameter estimates and for relative abundance observations were such that a 95% CI was of width ±5%.

Although the levels of population processes were the same in both tests, the amount of process variability was much higher in test 2. Normal growth variability was simulated in test 1 and extreme variability in test 2. The rate of unobserved change in test 1 was constant, but varied three-fold in test 2. The variance of sampling efficiencies was set one order of magnitude larger than that observed for commercial fishing gear in test 1 and twice that in test 2.

Error variances-of-abundance estimates were very low in the case of normal process variability (Table 4). Estimates of all but the smallest six size-classes were biased by 10% or less, if at all, and were precise. Bias (more than 10%) and imprecision of the smallest six size-class estimates was expected because the smaller fish were barely represented in the catch and appeared in the relative abundance samples just once. Estimates of the sampling efficiencies (the q_s) tended to be imprecise. Some were biased from 20% to 30% and a few even more. The estimate of survival from unobserved change was biased low (about 15%), yet precise. Estimates did not tend to be correlated. The correlations between the estimate of the unobserved change rate (z) and other estimates (Table 5), particularly of the q_s, were of interest because other studies found corre-

Table 4

Monte Carlo test results for two examples of constant, uniform recruitment.

	Example 1, Normal process variability	Example 2, High process variability
Loss rate z	0.20	U(0.2, 0.6)
Growth cv[A & k]	0.20	0.40
Growth estimation		
cv[error]	0.10	0.10
precision level	0.05	0.05
probability level	0.95	0.95
fish sampled, g	77	262
Sampling efficiency		
cv[q(s)]	0.20	0.40
precision level	0.05	0.05
probability level	0.95	0.95
sample size, r	62	246
95% CI of bias of N(T.)		
½ width achieved	0.0149	0.024
Number of trials	97	64

	Estimates		Bias 95% CI ½ width	Significance levels		Estimates		Bias 95% CI ½ width	Significance levels	
	Bias	Variance		HO:Bias⩾0.9 HA:Bias<0.9	HO:Bias⩽1.1 HA:Bias>1.1	Bias	Variance		HO:Bias⩾0.9 HA:Bias<0.9	HO:Bias⩽1.1 HA:Bias>1.1
N(T,15)	0.7669	0.0368	0.0382	0.0000	1.0000	0.5605	0.0273	0.0405	0.0000	1.0000
N(T,16)	0.7556	0.0520	0.0454	0.0000	1.0000	0.6660	0.0633	0.0616	0.0000	1.0000
N(T,17)	0.8022	0.0718	0.0533	0.0002	1.0000	0.7294	0.0567	0.0583	0.0000	1.0000
N(T,18)	0.9012	0.0960	0.0617	0.5157	1.0000	0.7382	0.0765	0.0678	0.0000	1.0000
N(T,19)	0.8423	0.0689	0.0522	0.0152	1.0000	0.7538	0.0754	0.0673	0.0000	1.0000

Table 4 (continued)

	Estimates		Bias 95% CI ½ width	Significance levels		Estimates		Bias 95% CI ½ width	Significance levels	
	Bias	Variance		HO:Bias≥0.9 HA:Bias<0.9	HO:Bias≤1.1 HA:Bias>1.1	Bias	Variance		HO:Bias≥0.9 HA:Bias<0.9	HO:Bias≤1.1 HA:Bias>1.1
N(T,20)	0.8227	0.0662	0.0512	0.0015	1.0000	0.7826	0.0722	0.0658	0.0002	1.0000
N(T,21)	0.9475	0.0440	0.0418	0.9871	1.0000	0.8975	0.0738	0.0666	0.4702	1.0000
N(T,22)	1.0006	0.0001	0.0019	1.0000	1.0000	0.9982	0.0003	0.0042	1.0000	1.0000
N(T,23)	1.0007	0.0001	0.0020	1.0000	1.0000	1.0012	0.0004	0.0051	1.0000	1.0000
N(T,24)	0.9973	0.0001	0.0024	1.0000	1.0000	0.9993	0.0005	0.0053	1.0000	1.0000
N(T,25)	0.9992	0.0001	0.0019	1.0000	1.0000	0.9979	0.0002	0.0037	1.0000	1.0000
N(T,26)	0.9995	0.0001	0.0020	1.0000	1.0000	0.9946	0.0003	0.0040	1.0000	1.0000
N(T,27)	0.9979	0.0000	0.0012	1.0000	1.0000	0.9938	0.0002	0.0038	1.0000	1.0000
N(T,28)	0.9984	0.0000	0.0013	1.0000	1.0000	0.9970	0.0001	0.0022	1.0000	1.0000
N(T,29)	0.9992	0.0000	0.0012	1.0000	1.0000	0.9944	0.0004	0.0050	1.0000	1.0000
N(T,30)	0.9973	0.0000	0.0013	1.0000	1.0000	0.9944	0.0002	0.0032	1.0000	1.0000
N(T,31)	1.0008	0.0001	0.0016	1.0000	1.0000	0.9948	0.0002	0.0038	1.0000	1.0000
N(T,32)	0.9965	0.0001	0.0016	1.0000	1.0000	0.9956	0.0001	0.0028	1.0000	1.0000
N(T,33)	0.9984	0.0000	0.0010	1.0000	1.0000	0.9954	0.0001	0.0030	1.0000	1.0000
N(T,34)	0.9973	0.0000	0.0014	1.0000	1.0000	0.9951	0.0005	0.0055	1.0000	1.0000
N(T,35)	0.9987	0.0001	0.0015	1.0000	1.0000	0.9948	0.0002	0.0034	1.0000	1.0000
N(T,36)	0.9950	0.0002	0.0026	1.0000	1.0000	0.9944	0.0004	0.0051	1.0000	1.0000
N(T,37)	0.9974	0.0001	0.0017	1.0000	1.0000	0.9960	0.0001	0.0029	1.0000	1.0000
N(T,38)	0.9977	0.0001	0.0020	1.0000	1.0000	0.9980	0.0002	0.0034	1.0000	1.0000
N(T,39)	0.9984	0.0000	0.0011	1.0000	1.0000	0.9989	0.0001	0.0029	1.0000	1.0000
N(T,40)	0.9984	0.0001	0.0014	1.0000	1.0000	0.9946	0.0002	0.0035	1.0000	1.0000
N(T,41)	0.9980	0.0001	0.0016	1.0000	1.0000	0.9964	0.0001	0.0029	1.0000	1.0000
N(T,42)	0.9975	0.0001	0.0016	1.0000	1.0000	0.9983	0.0001	0.0019	1.0000	1.0000
N(T,43)	0.9988	0.0001	0.0015	1.0000	1.0000	0.9991	0.0000	0.0017	1.0000	1.0000
N(T,44)	0.9985	0.0001	0.0016	1.0000	1.0000	0.9971	0.0001	0.0026	1.0000	1.0000
N(T,45)	0.9996	0.0000	0.0006	1.0000	1.0000	0.9977	0.0001	0.0026	1.0000	1.0000
N(T,46)	0.9997	0.0000	0.0006	1.0000	1.0000	0.9995	0.0000	0.0009	1.0000	1.0000
N(T,47)	0.9997	0.0000	0.0014	1.0000	1.0000	1.0041	0.0016	0.0113	1.0000	1.0000
N(T,48)	1.0000	0.0000	0.0000	1.0000	1.0000	1.0475	0.0902	0.0931	0.9990	0.8655
N(T,49)	0.9984	0.0001	0.0022	1.0000	1.0000	0.9992	0.0000	0.0016	1.0000	1.0000
N(T,50)	1.0245	0.0480	0.0579	1.0000	0.9947	1.2121	1.1789	0.3952	0.9392	0.2892
N(T,51)	0.9994	0.0000	0.0011	1.0000	1.0000	1.0000	0.0000	0.0000	1.0000	1.0000
N(T,52)	0.9744	0.0256	0.0503	0.9981	1.0000	1.0000	0.0000	0.0000	1.0000	1.0000
N(T,53)	0.9152	0.2376	0.1663	0.5709	0.9853	1.2839	0.9669	0.5151	0.9280	0.2420
N(T,54)	1.0519	0.0840	0.1093	0.9968	0.8060	0.9500	0.0250	0.0980	0.8413	0.9987
N(T,55)	1.0000	0.0000	0.0000	1.0000	1.0000	0.8944	0.1003	0.2069	0.4790	0.9743
N(T,56)	1.0000	0.0000	0.0000	1.0000	1.0000	0.8500	0.1350	0.2940	0.3694	0.9522
N(T,57)	1.0000	0.0000	0.0000	1.0000	1.0000	1.2500	0.2500	0.4900	0.9192	0.2743
N(T,58)	0.9000	0.0400	0.1960	0.5000	0.9772	2.0500	2.2050	2.0580	0.8633	0.1828
N(T,59)	0.6500	0.3675	0.6860	0.2375	0.9007	1.4500	0.0050	0.0980	1.0000	0.0000
N(T,60)	0.1000	0.6050	1.0780	0.0729	0.9655					
N(T.)	0.9023	0.0056	0.0149	0.6165	1.0000	0.7959	0.0096	0.0240	0.0000	1.000
q(15)	1.3860	0.1273	0.0710	1.0000	0.0000	1.9296	0.3080	0.1360	1.0000	0.0000
q(16)	1.4553	0.2337	0.0962	1.0000	0.0000	1.7558	0.6789	0.2019	1.0000	0.0000
q(17)	1.4210	0.3804	0.1227	1.0000	0.0000	1.4925	0.1753	0.1026	1.0000	0.0000
q(18)	1.2625	0.2663	0.1027	1.0000	0.0010	1.6064	0.6341	0.1951	1.0000	0.0000
q(19)	1.3163	0.2459	0.0987	1.0000	0.0000	1.5429	0.4501	0.1644	1.0000	0.0000
q(20)	1.3521	0.2433	0.0982	1.0000	0.0000	1.4564	0.4088	0.1566	1.0000	0.0000
q(21)	1.1274	0.0701	0.0527	1.0000	0.1544	1.2697	0.1354	0.0901	1.0000	0.0001
q(22)	1.0136	0.0295	0.0342	1.0000	1.0000	1.0701	0.0400	0.0490	1.0000	0.8842
q(23)	1.0494	0.0236	0.0306	1.0000	0.9994	1.0805	0.0313	0.0434	1.0000	0.8113
q(24)	1.0770	0.0349	0.0372	1.0000	0.8875	1.0460	0.0401	0.0491	1.0000	0.9846
q(25)	1.0515	0.0266	0.0324	1.0000	0.9983	1.0328	0.0437	0.0512	1.0000	0.9949
q(26)	1.0264	0.0288	0.0338	1.0000	1.0000	0.9658	0.0560	0.0580	0.9870	1.0000
q(27)	0.9990	0.0386	0.0391	1.0000	1.0000	1.0400	0.0476	0.0534	1.0000	0.9861
q(28)	1.0209	0.0333	0.0363	1.0000	1.0000	0.9478	0.0739	0.0666	0.9202	1.0000
q(29)	0.9869	0.0450	0.0422	1.0000	1.0000	0.9101	0.0623	0.0611	0.6264	1.0000
q(30)	0.9408	0.0390	0.0393	0.9790	1.0000	0.9330	0.0487	0.0540	0.8843	1.0000
q(31)	0.9596	0.0434	0.0415	0.9976	1.0000	0.8261	0.0839	0.0710	0.0206	1.0000
q(32)	0.9150	0.0425	0.0410	0.7631	1.0000	0.9050	0.0622	0.0611	0.5634	1.0000
q(33)	0.9620	0.0444	0.0419	0.9981	1.0000	0.8922	0.0814	0.0699	0.4138	1.0000
q(34)	0.9051	0.0598	0.0486	0.5808	1.0000	0.8964	0.0935	0.0749	0.4623	1.0000
q(35)	0.9179	0.0619	0.0495	0.7603	1.0000	0.8245	0.0933	0.0748	0.0240	1.0000
q(36)	0.8685	0.0924	0.0605	0.1537	1.0000	0.7950	0.1000	0.0775	0.0039	1.0000
q(37)	0.8611	0.0802	0.0563	0.0883	1.0000	0.7620	0.0863	0.0720	0.0001	1.0000
q(38)	0.8240	0.0971	0.0620	0.0082	1.0000	0.7804	0.1357	0.0903	0.0047	1.0000
q(39)	0.7925	0.0791	0.0560	0.0001	1.0000	0.7502	0.1244	0.0871	0.0004	1.0000

Table 4 (continued)

	Estimates		Bias	Significance levels		Estimates		Bias	Significance levels	
	Bias	Variance	95% CI ½ width	HO:Bias≥0.9 HA:Bias<0.9	HO:Bias≤1.1 HA:Bias>1.1	Bias	Variance	95% CI ½ width	HO:Bias≥0.9 HA:Bias<0.9	HO:Bias≤1.1 HA:Bias>1.1
q(40)	0.8476	0.1304	0.0722	0.0775	1.0000	0.7426	0.0887	0.0747	0.0000	1.0000
q(41)	0.7956	0.0730	0.0546	0.0001	1.0000	0.7352	0.4793	0.1737	0.0315	1.0000
q(42)	0.6863	1.5698	0.2546	0.0500	0.9993	0.7424	0.1202	0.0885	0.0002	1.0000
q(43)	0.8525	0.1842	0.0882	0.1455	1.0000	0.8617	0.1037	0.0829	0.1827	1.0000
q(44)	0.8133	0.0973	0.0648	0.0044	1.0000	0.8777	0.1561	0.1044	0.3375	1.0000
q(45)	1.0254	2.2033	0.3119	0.7846	0.6804	0.8420	0.0913	0.0799	0.0774	1.0000
q(46)	0.8358	0.1309	0.0774	0.0519	1.0000	1.0564	0.9370	0.2606	0.8803	0.6284
q(47)	0.3470	25.6967	1.1397	0.1708	0.9023	63.2003	<99999.99	121.9043	0.8417	0.1590
q(48)	0.8576	0.6898	0.1974	0.3370	0.9919	1.0744	0.3067	0.1716	0.9768	0.6152
q(49)	0.7220	0.4331	0.1638	0.0166	1.0000	0.0008	75.0753	3.0502	0.2817	0.7600
q(50)	0.9710	3.3934	0.4868	0.6124	0.6983	2.7969	115.6154	3.9135	0.8290	0.1977
q(51)	−0.3572	73.2005	2.4998	0.1621	0.8734	0.7113	2.1593	0.6141	0.2735	0.8926
q(52)	−3.7106	632.0744	12.6793	0.2380	0.7715	0.8225	0.6106	0.3610	0.3370	0.9340
q(53)	1.0422	0.3956	0.2146	0.9031	0.7011	1.7977	6.0280	1.2861	0.9144	0.1438
q(54)	1.0498	0.3516	0.2237	0.9054	0.6700	2.2403	8.9080	1.8499	0.9222	0.1135
q(55)	0.0243	7.1499	1.2023	0.0767	0.9602	3.6459	67.4526	5.3658	0.8421	0.1762
q(56)	4.1165	89.6428	6.1858	0.8459	0.1696	3.2914	12.9452	2.8790	0.9482	0.0679
q(57)	0.8978	0.0700	0.2116	0.4919	0.9694	0.9321	0.0669	0.2536	0.5980	0.9028
q(58)	−3.1313	74.4663	8.4568	0.1751	0.8366	0.6640	0.2346	0.6713	0.2454	0.8985
q(59)	−5.6513	172.1638	14.8479	0.1936	0.8136	0.7438	0.0005	0.0294	0.0000	1.0000
q(60)	−0.3459	7.3840	3.7661	0.2584	0.7741					
exp(z)	0.6422	0.0084	0.0182	0.0000	1.0000					

lations (Paloheimo 1980, Collie and Sissenwine 1983). These estimates do not seem highly correlated.

The unobserved change rate was a random variable in the second test, so its estimation error was not computed. Error characteristics-of-abundance estimates were extremely similar to those of example one; apparently high process variability does not adversely affect estimation even in the presence of sampling variance.

Table 5

Correlation coefficients between estimates of the unobserved change rate (z) and all other estimates.

Estimate	Rho	Estimate	Rho	Estimate	Rho	Estimate	Rho
N(T,15)	0.46	N(T,38)	0.08	q(15)	−0.53	q(38)	−0.18
N(T,16)	0.34	N(T,39)	0.11	q(16)	−0.30	q(39)	0.09
N(T,17)	0.45	N(T,40)	0.21	q(17)	−0.36	q(40)	−0.03
N(T,18)	0.20	N(T,41)	0.22	q(18)	−0.24	q(41)	0.02
N(T,19)	0.27	N(T,42)	0.22	q(19)	−0.18	q(42)	−0.09
N(T,20)	0.23	N(T,43)	0.15	q(20)	−0.18	q(43)	−0.14
N(T,21)	0.23	N(T,44)	0.08	q(21)	−0.22	q(44)	−0.01
N(T,22)	0.11	N(T,45)	0.31	q(22)	−0.22	q(45)	−0.07
N(T,23)	0.27	N(T,46)	0.20	q(23)	−0.16	q(46)	0.03
N(T,24)	0.22	N(T,47)	0.04	q(24)	−0.15	q(47)	0.11
N(T,25)	0.21	N(T,48)	0.19	q(25)	−0.27	q(48)	0.11
N(T,26)	0.10	N(T,49)	0.13	q(26)	−0.31	q(49)	0.08
N(T,27)	0.19	N(T,50)	0.26	q(27)	−0.26	q(50)	0.12
N(T,28)	0.22	N(T,51)	0.22	q(28)	−0.10	q(51)	0.02
N(T,29)	0.29	N(T,52)	0.11	q(29)	−0.35	q(52)	−0.11
N(T,30)	0.09	N(T,53)	0.16	q(30)	−0.10	q(53)	0.15
N(T,31)	0.17	N(T,54)	0.12	q(31)	−0.43	q(54)	0.15
N(T,32)	0.19	N(T,55)	0.21	q(32)	0.09	q(55)	0.02
N(T,33)	0.21	N(T,56)	0.16	q(33)	−0.17	q(56)	−0.05
N(T,34)	0.25	N(T,57)	0.06	q(34)	−0.19	q(57)	0.15
N(T,35)	0.18	N(T,58)	0.03	q(35)	−0.02	q(58)	−0.11
N(T,36)	0.08	N(T,59)	0.06	q(36)	0.04	q(59)	−0.11
N(T,37)	0.23	N(T,60)	−0.03	q(37)	−0.01	q(60)	−0.06

The contracted seasonal recruitment pattern (Fig. 3), conventionally interpreted as age-specific cohorts, was used in the last two examples. Growth parameters were the same as the two previous examples and growth variation was moderate (cv 0.1). Sampling efficiencies were also unchanged and their variability set at that of example 1 ($cv[q] = 0.2$). The unobserved change rate randomly varied five-fold ($z_t \sim U(0.05, 0.25)$). Catching was continuous so each period's catch was assigned to midperiod for estimation. Overfishing was simulated by rapidly increasing exploitation enough to decrease stock abundance 36% during the four periods of sampling (last four). The fishing mortality rates for periods 6–19 were: 0.05, 0.1, 0.15, 0.2, 0.25, 0.3, 0.6, 0.4, 0.5, 0.8, 0.6, 0.8, 1.0, and 1.2. Example 3 simulated very low sampling levels and example 4, high levels. It was of interest to find if abundance would be correctly estimated during overfishing under either sampling condition.

Example 3 was the limited-data case. The growth measurement error was large (cv 0.20) and the sample size for growth parameter estimation was moderate (95% CI of width ±5%, 77 fish). The precision of catch estimates was low (cv[C] = 0.4) and relative abundance sampling was meager (95% CI of width ±30%, two samples each period).

Error variances of the smallest seven size class abundance estimates were very large (Table 6), but error variances were low for size-classes 25 and larger. Usefully narrow confidence intervals on the bias of these estimates were obtained with few trials. Significance levels suggested that abundance estimates of size-classes 17–21 might not have been biased and unbiased estimation seemed likely for size-classes 22 and larger. Estimates of sampling gear efficiencies (q(s)) also seemed accurate although error variances were high.

Example four simulated sufficient sampling. A growth parameter measurement error (cv 0.05) and sample size (99% CI of width ±1%, 829 fish) more characteristic of databases for heavily sampled fisheries were used. Catches were precisely estimated (cv[C] = 0.2) and relative abundance sampling was at a very sufficient level (99% CI of width ±3%, 295 samples each period).

Biases (Table 6) were very similar to those of example 3. Abundance estimates for the smaller size-classes that appeared in relative abundance samples just once were probably biased by more than 10%, but the rest were not. Estimates of q for the smallest 10 size-classes were biased by more than 10% and the rest were probably not. Most error variances for stocksize estimates were several times smaller than those of example 3, and some were an order of magnitude smaller. Likewise, the error variance of q estimates was also smaller. As may be expected, sufficient sampling levels increased precision but did not affect bias. Abundance estimates of sizes that appeared in abundance samples more than once were estimated accurately when overfishing occurred, whether or not sampling levels were sufficient or not.

Estimates of historical stock sizes are usually used to find out if stock abundance is increasing or decreasing. Errors of virtual population analysis back-calculations of cohort- specific abundances converge as dates decrease (Agger et al. 1971, Pope 1972, Jones 1981). Conventional wisdom is thus that abundance estimates for the last period are extremely uncertain, but due to the convergence, estimated abundance trends are reliable. For this size-based estimator, (2) provides abundance calculations before date y(T) from the estimates available at the solution of (4).

Error characteristics of historical abundance estimates (Table 7) were unexpected. Bias and error variance increased as dates decreased. Last-period

Table 6

Examples for seasonal, contracted recruitment and overfishing.

	Example 3, Limited sampling	Example 4, Sufficient sampling
Catch estimation		
catch dates	absent	absent
cv[C(t, s)]	0.40	0.20
Growth estimation		
cv[error]	0.20	0.05
precision level	0.05	0.01
probability level	0.95	0.99
fish sampled, g	77	829
Sampling efficiency		
cv[q(s)]	0.20	0.20
precision level	0.30	0.03
probability level	0.95	0.99
sample size, r	2	295
Number of trials	83	128

	Estimates		Bias	Significance levels		Estimates		Bias	Significance levels	
			95% CI	HO:Bias≥0.9	HO:Bias≤1.1			95% CI	HO:Bias≥0.9	HO:Bias≤1.1
	Bias	Variance	½ width	HA:Bias<0.9	HA:Bias>1.1	Bias	Variance	½ width	HA:Bias<0.9	HA:Bias>1.1
N(T,15)	9.3261	759.7793	5.9301	0.9973	0.0033	12.8103	1297.3179	6.2399	0.9999	0.0001
N(T,16)	8.3623	546.7384	5.0304	0.9982	0.0023	8.3910	128.6375	1.9649	1.0000	0.0000
N(T,17)	2.0437	320.3240	3.8505	0.7198	0.3155	3.4678	49.7123	1.2215	1.0000	0.0001
N(T,18)	1.8321	42.6741	1.4054	0.9032	0.1536	1.2202	1.3293	0.1997	0.9992	0.1191
N(T,19)	0.9011	1.3723	0.2520	0.5033	0.9391	0.7992	0.3075	0.0961	0.0199	1.0000
N(T,20)	1.1948	1.6789	0.2788	0.9809	0.2525	0.8677	0.3403	0.1011	0.2657	1.0000

Table 6 (continued)

	Estimates		Bias	Significance levels		Estimates		Bias	Significance levels	
	Bias	Variance	95% CI ½ width	HO:Bias≥0.9 HA:Bias<0.9	HO:Bias≤1.1 HA:Bias>1.1	Bias	Variance	95% CI ½ width	HO:Bias≥0.9 HA:Bias<0.9	HO:Bias≤1.1 HA:Bias>1.1
N(T,21)	1.3401	5.0248	0.4823	0.9632	0.1646	1.7942	1.3107	0.1983	1.0000	0.0000
N(T,22)	0.9265	0.1610	0.0863	0.7262	1.0000	0.8043	1.2599	0.1945	0.1673	0.9986
N(T,23)	0.9335	0.4053	0.1370	0.6840	0.9914	0.8082	0.7830	0.1533	0.1203	0.9999
N(T,24)	0.9017	0.7664	0.1895	0.5072	0.9799	0.9673	0.1843	0.0744	0.9619	0.9998
N(T,25)	0.9988	0.0606	0.0533	0.9999	0.9999	1.0007	0.0106	0.0179	1.0000	1.0000
N(T,26)	0.9540	0.0476	0.0472	0.9875	1.0000	1.0021	0.0032	0.0098	1.0000	1.0000
N(T,27)	0.9890	0.0186	0.0295	1.0000	1.0000	0.9898	0.0055	0.0129	1.0000	1.0000
N(T,28)	0.9865	0.0129	0.0246	1.0000	1.0000	0.9855	0.0109	0.0181	1.0000	1.0000
N(T,29)	0.9596	0.0341	0.0400	0.9983	1.0000	0.9795	0.0174	0.0230	1.0000	1.0000
N(T,30)	1.0184	0.0600	0.0530	1.0000	0.9987	0.9979	0.0235	0.0269	1.0000	1.0000
N(T,31)	0.9606	0.0254	0.0349	0.9997	1.0000	0.9916	0.0084	0.0161	1.0000	1.0000
N(T,32)	0.9922	0.0073	0.0188	1.0000	1.0000	0.9945	0.0029	0.0094	1.0000	1.0000
N(T,33)	1.0158	0.0266	0.0359	1.0000	1.0000	0.9861	0.0022	0.0082	1.0000	1.0000
N(T,34)	0.9851	0.0117	0.0240	1.0000	1.0000	0.9824	0.0040	0.0112	1.0000	1.0000
N(T,35)	0.9700	0.0138	0.0260	1.0000	1.0000	0.9846	0.0025	0.0090	1.0000	1.0000
N(T,36)	0.9908	0.0339	0.0411	1.0000	1.0000	0.9921	0.0008	0.0052	1.0000	1.0000
N(T,37)	0.9852	0.0071	0.0195	1.0000	1.0000	0.9988	0.0004	0.0038	1.0000	1.0000
N(T,38)	0.9807	0.0027	0.0126	1.0000	1.0000	0.9992	0.0006	0.0048	1.0000	1.0000
N(T,39)	0.9874	0.0116	0.0278	1.0000	1.0000	0.9957	0.0003	0.0037	1.0000	1.0000
N(T,40)	0.9841	0.0024	0.0132	1.0000	1.0000	0.9986	0.0004	0.0042	1.0000	1.0000
N(T,41)	0.9992	0.0010	0.0090	1.0000	1.0000	1.0001	0.0001	0.0028	1.0000	1.0000
N(T,42)	1.0102	0.0314	0.0549	1.0000	0.9993	1.0002	0.0000	0.0013	1.0000	1.0000
N(T,43)	0.9924	0.0012	0.0115	1.0000	1.0000	0.9987	0.0001	0.0025	1.0000	1.0000
N(T,44)	0.9798	0.0101	0.0452	0.9997	1.0000	0.9986	0.0001	0.0027	1.0000	1.0000
N(T,45)	0.9833	0.0012	0.0158	1.0000	1.0000	1.0000	0.0000	0.0000	1.0000	1.0000
N(T,46)	0.9854	0.0006	0.0141	1.0000	1.0000	1.0000	0.0000	0.0000	1.0000	1.0000
N(T,47)	1.0000	0.0010	0.0253	1.0000	1.0000	1.0000	0.0000	0.0000	1.0000	1.0000
N(T,48)	0.8000	0.0200	0.1960	0.1587	0.9987	1.0000	0.0000	0.0000	1.0000	1.0000
N(T,49)						1.0000	0.0000	0.0000	1.0000	1.0000
N(T.)	1.1369	32.0777	1.2185	0.6484	0.4763	1.1493	29.8091	0.9459	0.6973	0.4593
q(15)	0.3282	0.1186	0.0741	0.0000	1.0000	0.2474	0.0501	0.0388	0.0000	1.0000
q(16)	0.3998	0.2084	0.0982	0.0000	1.0000	0.2984	0.0519	0.0395	0.0000	1.0000
q(17)	0.7850	0.7019	0.1802	0.1055	0.9997	0.6889	0.2424	0.0853	0.0000	1.0000
q(18)	1.3854	0.9594	0.2107	1.0000	0.0040	1.2926	0.6908	0.1440	1.0000	0.0044
q(19)	1.9397	2.7953	0.3597	1.0000	0.0000	1.6785	0.6126	0.1356	1.0000	0.0000
q(20)	1.3499	0.6184	0.1692	1.0000	0.0019	1.4341	0.3226	0.0984	1.0000	0.0000
q(21)	0.9199	0.4187	0.1392	0.6104	0.9944	0.6845	0.0844	0.0503	0.0000	1.0000
q(22)	0.6958	0.2367	0.1047	0.0001	1.0000	0.5667	0.0730	0.0468	0.0000	1.0000
q(23)	0.7353	0.2491	0.1074	0.0013	1.0000	0.6515	0.0753	0.0475	0.0000	1.0000
q(24)	0.9467	0.5200	0.1561	0.7213	0.9729	0.7885	0.0992	0.0546	0.0000	1.0000
q(25)	1.0306	0.3424	0.1266	0.9784	0.8584	0.9317	0.0882	0.0515	0.8861	1.0000
q(26)	1.0431	0.2997	0.1185	0.9910	0.8266	1.0073	0.0575	0.0415	1.0000	1.0000
q(27)	1.0743	0.3260	0.1236	0.9971	0.6583	0.9851	0.0475	0.0377	1.0000	1.0000
q(28)	1.0729	0.4116	0.1389	0.9927	0.6489	0.9155	0.0586	0.0419	0.7658	1.0000
q(29)	1.0112	0.3553	0.1290	0.9545	0.9113	0.9105	0.0767	0.0482	0.6652	1.0000
q(30)	0.9345	0.4927	0.1519	0.6719	0.9836	0.9002	0.0721	0.0471	0.5027	1.0000
q(31)	1.0777	0.5119	0.1568	0.9869	0.6096	0.8955	0.0796	0.0495	0.4297	1.0000
q(32)	1.0668	0.3685	0.1339	0.9927	0.6864	0.9643	0.1123	0.0587	0.9841	1.0000
q(33)	1.0548	0.2669	0.1139	0.9961	0.7818	1.0293	0.1086	0.0578	1.0000	0.9918
q(34)	1.0891	0.4220	0.1442	0.9949	0.5588	0.9230	0.1037	0.0569	0.7862	1.0000
q(35)	1.2517	1.4470	0.2670	0.9951	0.1327	0.9907	0.1106	0.0597	0.9985	0.9998
q(36)	1.0885	0.5550	0.1664	0.9868	0.5537	1.0126	0.1046	0.0591	0.9999	0.9981
q(37)	1.0643	0.3099	0.1286	0.9939	0.7066	1.0658	0.1899	0.0814	1.0000	0.7950
q(38)	1.2725	1.2458	0.2713	0.9964	0.1064	0.9944	0.0895	0.0589	0.9992	0.9998
q(39)	0.9949	0.7569	0.2239	0.7970	0.8211	1.0445	0.2018	0.0923	0.9989	0.8806
q(40)	1.1630	0.5160	0.1934	0.9962	0.2617	0.9748	0.1302	0.0806	0.9656	0.9988
q(41)	1.3898	1.4057	0.3320	0.9981	0.0435	0.9666	0.2227	0.1130	0.8761	0.9896
q(42)	1.4005	2.9713	0.5342	0.9668	0.1351	1.0596	0.2525	0.1316	0.9913	0.7265
q(43)	1.0215	0.2530	0.1643	0.9263	0.8256	−0.7903	123.8881	3.4933	0.1715	0.8556
q(44)	0.9185	0.2248	0.2132	0.5674	0.9524	1.1289	0.8725	0.3051	0.9293	0.4263
q(45)	4.0163	137.2726	5.4127	0.8704	0.1455	1.4194	2.0954	0.5674	0.9636	0.1350
q(46)	1.2540	0.3985	0.3572	0.9740	0.1990	1.0488	0.0964	0.1396	0.9816	0.7639
q(47)	1.2032	0.2502	0.4002	0.9312	0.3067	1.9698	5.6933	1.4101	0.9315	0.1133
q(48)	1.1792	0.2007	0.6210	0.8109	0.4013	1.0484	0.0029	0.0473	1.0000	0.9839
q(49)						0.9818	0.0718	0.2626	0.7291	0.8113

Table 7

Error statistics of historical abundance estimates from example 4.

Variable	n	Error variance	Bias estimate	Variable	n	Error variance	Bias estimate	Variable	n	Error variance	Bias estimate
N(1,15)	128	115.5114	5.9596	N(1,27)	128	0.1871	0.9173	N(1,39)	91	0.4743	0.7745
N(2,15)	128	86.8395	6.0680	N(2,27)	128	0.1899	0.8982	N(2,39)	91	0.5662	0.9049
N(3,15)	128	119.8275	5.3517	N(3,27)	128	0.4459	1.0290	N(3,39)	91	0.4302	1.0320
N(4,15)	128	1296.6914	12.8388	N(4,27)	128	0.0056	0.9896	N(4,39)	91	0.0003	0.9957
N(1,16)	128	30.4340	4.2588	N(1,28)	128	0.4354	0.9534	N(1,40)	77	1.1408	0.9088
N(2,16)	128	184.7422	7.4660	N(2,28)	128	0.2830	1.0502	N(2,40)	77	0.7205	1.0607
N(3,16)	128	68.0011	6.3408	N(3,28)	128	0.4060	1.1279	N(3,40)	77	0.4176	0.9065
N(4,16)	128	128.6176	8.3893	N(4,28)	128	0.0109	0.9854	N(4,40)	77	0.0004	0.9986
N(1,17)	128	10.8289	1.7620	N(1,29)	127	0.3800	0.9685	N(1,41)	67	0.8746	1.0508
N(2,17)	128	50.7792	2.9860	N(2,29)	127	0.6222	1.2014	N(2,41)	67	0.7359	0.9693
N(3,17)	128	6.3308	2.2878	N(3,29)	127	0.6897	1.1322	N(3,41)	67	0.6803	1.1584
N(4,17)	128	49.7113	3.4675	N(4,29)	127	0.0174	0.9794	N(4,41)	67	0.0001	1.0001
N(1,18)	128	0.5225	0.8387	N(1,30)	125	1.3161	1.1217	N(1,42)	56	0.2236	0.5534
N(2,18)	128	1.8065	1.0217	N(2,30)	125	0.6497	1.1361	N(2,42)	56	0.9773	0.8919
N(3,18)	128	1.3119	1.1786	N(3,30)	125	0.6635	1.1661	N(3,42)	56	0.8370	1.0048
N(4,18)	128	1.3292	1.2202	N(4,30)	125	0.0234	0.9971	N(4,42)	56	0.0000	1.0002
N(1,19)	128	0.2076	0.5674	N(1,31)	125	0.4402	0.9570	N(1,43)	39	0.3770	0.7205
N(2,19)	128	0.6367	0.7745	N(2,31)	125	0.7042	1.1035	N(2,43)	39	0.7222	1.0594
N(3,19)	128	0.2891	0.8107	N(3,31)	125	1.2571	1.1914	N(3,43)	39	0.5246	0.9171
N(4,19)	128	0.3074	0.7989	N(4,31)	125	0.0084	0.9916	N(4,43)	39	0.0001	0.9987
N(1,20)	128	0.3131	0.6707	N(1,32)	125	0.4139	0.8962	N(1,44)	36	0.3870	0.8145
N(2,20)	128	0.7200	0.8515	N(2,32)	125	0.4712	1.0943	N(2,44)	36	0.3686	0.8018
N(3,20)	128	0.4237	0.9559	N(3,32)	125	0.6876	1.1207	N(3,44)	36	0.2355	0.8025
N(4,20)	128	0.3411	0.8679	N(4,32)	125	0.0029	0.9944	N(4,44)	36	0.0001	0.9986
N(1,21)	128	1.3938	1.2717	N(1,33)	125	0.2451	0.7301	N(1,45)	25	0.4571	0.8148
N(2,21)	128	0.9207	1.3560	N(2,33)	125	0.4089	1.0021	N(2,45)	25	0.3210	0.8143
N(3,21)	128	1.5664	1.6328	N(3,33)	125	0.6057	1.1316	N(3,45)	25	0.1735	0.7110
N(4,21)	128	1.3111	1.7941	N(4,33)	125	0.0022	0.9864	N(4,45)	25	0.0000	1.0000
N(1,22)	128	3.4192	1.7054	N(1,34)	123	0.7671	0.8896	N(1,46)	19	0.3338	0.6204
N(2,22)	128	6.9873	2.0668	N(2,34)	123	0.5906	0.9968	N(2,46)	19	0.3380	0.5746
N(3,22)	128	7.5242	2.6186	N(3,34)	123	0.9354	1.1637	N(3,46)	19	0.1914	0.8296
N(4,22)	128	1.2599	0.8042	N(4,34)	123	0.0040	0.9824	N(4,46)	19	0.0000	1.0000
N(1,23)	128	1.1626	1.6450	N(1,35)	119	0.2867	0.8088	N(1,47)	11	0.1290	0.4227
N(2,23)	128	1.6512	1.5052	N(2,35)	119	0.6020	1.0950	N(2,47)	11	0.2434	0.4377
N(3,23)	128	8.1272	2.3806	N(3,35)	119	0.7955	1.1538	N(3,47)	11	0.0694	0.9398
N(4,23)	128	0.7830	0.8082	N(4,35)	119	0.0025	0.9846	N(4,47)	11	0.0000	1.0000
N(1,24)	128	1.2296	1.3307	N(1,36)	115	0.2635	0.6926	N(1,48)	5	0.1338	0.4633
N(2,24)	128	2.6137	1.3469	N(2,36)	115	0.4223	0.9411	N(2,48)	5	0.0132	1.0800
N(3,24)	128	23.1672	1.9363	N(3,36)	115	0.7491	1.0997	N(3,48)	5	0.1087	0.7000
N(4,24)	128	0.1842	0.9673	N(4,36)	115	0.0008	0.9921	N(4,48)	5	0.0000	1.0000
N(1,25)	128	0.5672	0.9923	N(1,37)	110	0.2637	0.6720	N(1,49)	4	0.1558	0.3750
N(2,25)	128	0.7867	0.9758	N(2,37)	110	0.5350	0.8555	N(2,49)	4	0.4950	1.1000
N(3,25)	128	5.6842	1.4490	N(3,37)	110	0.6735	1.0410	N(3,49)	4	0.0050	0.9500
N(4,25)	128	0.0106	1.0005	N(4,37)	110	0.0004	0.9986	N(4,49)	4	0.0000	1.0000
N(1,26)	128	0.2515	0.8747	N(1,38)	99	0.8277	0.8260				
N(2,26)	128	0.8233	0.9564	N(2,38)	99	0.2681	0.7480				
N(3,26)	128	3.1000	1.2203	N(3,38)	99	0.8225	1.2851				
N(4,26)	128	0.0032	1.0024	N(4,38)	99	0.0006	0.9989				

abundance estimates were accurate, but those of preceding periods were not. Error variances of estimates before the last period tended to be one to two orders of magnitude higher than those of the last period. This implies that abundance trends estimated in this manner probably will be wrong. In this example, the problem is large enough to mask much of the 36% decrease in abundance; the downward abundance trend would not be clear in calculations of historical stock sizes.

Discussion

These Monte Carlo tests show that size-based methods can be accurate and precise estimators of stock abundance. Population characteristics need not conform to the restrictive assumptions of traditional VPA methods. Any sort of fish stock can be successfully addressed with size-based techniques, an important aspect when assessing populations where ageing is impossible or where recruitment is not periodic.

These results imply that little will be gained from the extensive age sampling programs that are the foundation of VPA-based methods. They are not needed if size-based methods are used; only size samples and the rate of growth are required. Light, periodic growth sampling is sufficient to monitor possible growth rate changes through time. Also, since growth rates are required instead of ages, mark-recapture methods can be used to obtain growth measures if hardpart interpretations (age is not observed on hardparts; instead, characteristic marks are interpreted as annular occurrences) are difficult or expensive to obtain.

The method of abundance estimation developed in this study, a meticulous bookkeeper of size data as is the method of Beddington and Cook (1981), is primitive compared with other size-based methods (Fournier and Doonan 1987, Schnute et al. 1989, Sullivan 1989, Sullivan et al. 1990). Its degree of success in estimating abundance suggests that complete population-model structures are unnecessary. Estimates were usefully accurate and precise even with very high process variability. Very pronounced individual growth variation did not cause estimation problems. These results show that precise, accurate abundance estimates are possible with any recruitment pattern imaginable. It was a particular surprise to find that temporally variant (fourfold) unobserved change rates ("natural mortality" of Ricker (1948) but including migration and unrecorded catch) did not affect estimation at all. That result is reassuring, since the rate is probably extremely variable in nature.

Sampling problems did not seem to degrade estimation either. The level of catch estimation error proved unimportant and there was no indication that exact catch dates need to be recorded. Highly variable sampling efficiencies (q_s) did not cause estimation problems, particularly when sample sizes were adequate. Highly variable individual growth rates (20%) and significant growth measurement error (15%) did not adversely affect abundance estimation when sampling was sufficient. Very large growth-parameter measurement error (40%) and small sample size destroyed performance; although bias was not a problem, extreme error variances and correlated estimates were.

It is of particular interest that this was the only test where estimates of the unobserved change rate (z) and sampling efficiencies (q) were highly correlated. The lack of a pronounced correlation between sampling gear efficiencies and the unobserved change rate in all other tests except this one was unexpected; similar studies of VPA-based methods (Paloheimo 1980, Collie and Sissenwine 1983) found such correlation a major characteristic. It thus seems possible that ageing errors, or the violation of a connected VPA assumption, contributed to correlation in those studies.

Abundances of most size-classes were estimated precisely with little or no bias, but biased and imprecise abundance estimates occurred in three circumstances. First, abundances of very small fish that were recruited between the next-to-last and last relative abundance sample were estimated poorly. A recruitment group had to be present in the relative abundance samples twice to be estimated with a useful degree of certainty. In practice, this problem is easily fixed if obtaining certain estimates of recent recruitment of small fish is important enough to justify the cost of additional samples during the last period. Since the estimator is not based on equal time units, only dates, additional sample(s) will monitor the size-classes of interest several times instead of just once. Second, wide size-classes caused bias and imprecision, particularly for larger sizes. This bias was easily eliminated by narrowing size-classes. Last, calculations of historical abundances were in large error. It is well known that VPA calculations are poor for the most recent period of data and improve as dates decrease. Though they are not germane to current production levels, estimates of the oldest stock sizes are the most certain ones in VPA. The exact opposite is true for this size-based method. Estimates of historical abundances obtained in the solution calculation should not be used; error variances of these computations are very large. Since the estimates of the final-period abundances are accurate and precise, this is probably not a problem even if historical stock-size estimates are needed. Although the procedure was not tested, these estimates might be obtained by starting with the initial four periods of data, estimating the fourth period abundance vector, and then progressing forward one period at a time. Abundance in the first three periods cannot be estimated but subsequent abundances can. The relation between the number of periods in the data and estimation errors was not investigated, but the authors- experience with VPA-based methods indicates little, if any, would be gained with a longer time-series.

This study shows that *a priori* knowledge of the unobserved change rate (z) is not required to accurately and precisely estimate abundance with this size-based method, yet it is well known (Paloheimo 1980, Collie and Sissenwine 1983, Deriso 1985, Pope and Shepherd 1985) that such knowledge is necessary when applying VPA-based procedures.

This study suggests that the unobserved change rate (z) will often be estimated with bias, yet z should be included in the vector of estimates anyway. Monte Carlo tests of the Beddington and Cook model established that simultaneous estimation of a natural mortality schedule (analogous to the unobserved change rate in this study) is necessary to avoid biased abundance estimates (de la Mare 1988). If z is fixed instead of estimated, abundance estimation bias is assured because stock size is a function of that rate. It thus seems prudent to include the rate in the vector of estimates to avoid abundance estimation bias even if it is not useful. When necessary, Monte Carlo methods can be used to establish interval estimates on e^{-z}. This study indicates that estimates of e^{-z} are often biased, yet precise. The estimate of error variance over the 97 trials of example 1 was 0.0084, so the 95% CI width is $\pm 1.96\sqrt{(0.0084 \div 97)}$ or ± 0.0182, and the bias adjustment is 0.6422.

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Citations

Agger, P., I. Boetius, and H. Lassen
1971 On errors in virtual population analysis. Int. Counc. Explor. Sea Doc. CM 1971/H:16, 10 p.
Anonymous
1981a Report of the sub-committee on sperm whales (Appendix II). Rep. Int. Whaling Comm. 31:100–101.
1981b Report of the ad hoc working group on the use of effort data in assessments. Int. Counc. Explor. Sea Doc. CM 1981/G:5, 65 p.
1983 Report of the working group on methods of fish stock assessment. Int. Counc. Explor. Sea Doc. CM 1983/Assess:17, 73 p.
1984 Report of the working group on methods of fish stock assessments. Int. Counc. Explor. Sea Doc. CM 1984/Assess: 19, 56 p.
1986 Report of the ad hoc multispecies assessment working group. Int. Counc. Explor. Sea Doc. CM 1986, 10 p.
Bartoo, N.W., and K.R. Parker
1982 Stochastic age-frequency estimation using the von Bertalanffy growth equation. Fish. Bull., U.S. 81:91–96.
Basson, M., A.A. Rosenberg, and J.R. Beddington
1988 The accuracy and reliability of two new methods for estimating growth parameters from length-frequency data. J. Cons. Cons. Int. Explor. Mer 44:277–285.
Beamish, R.J., and G.A. McFarlane
1983 The forgotten requirement for age validation in fisheries biology. Trans. Am. Fish. Soc. 112:735–743.
Beddington, J.R., and J.G. Cooke
1981 Development of an assessment technique for male sperm whales based on the use of length data from the catches, with special reference to the North-west Pacific stock. Rep. Int. Whaling Comm. 31:747–760.
Beddington, J.R., J.G. Cooke, and W.K. de la Mare
1983 Estimations of the western North Pacific sperm whale population using the length distribution of catches. Rep. Int. Whaling Comm. 33:747–749.
Box, G.E.P.
1979 Robustness in the strategy of scientific model building. *In* Launer, R.L., and G.N. Wilkinson (eds.), Robustness in statistics, p. 201–236. Academic Press, NY.
Brethes, J.F., and G. Desrosiers
1981 Estimation of potential catches of an unexploited stock of soft-shell clam (*Mya arenaria*) from length composition data. Can. J. Fish. Aquat. Sci. 38:371–374.
Burr, R.L.
1988 Inferring the distribution of the parameters of the von Bertalanffy growth model from length moments. Can. J. Fish. Aquat. Sci. 45:1779–1788.
Chapman, D.G.
1961 Statistical problems in dynamics of exploited fisheries populations. *In* Proc., 4th Berkeley symp. math. stat. and probability. Contrib. Biol. and Probl. Med. 4:153–168. Univ. Calif. Press.
Clark, W.G.
1981 Restricted least-squares estimates of age composition from length composition. Can J. Fish. Aquat. Sci. 38:297–307.
Collie, J.S., and M.P. Sissenwine
1983 Estimating population size from relative abundance data measured with error. Can. J. Fish. Aquat. Sci. 40:1871–1879.
Conway, G.R., N.R. Glass, and J. C. Wilcox
1970 Fitting nonlinear models to biological data by Marquardt's algorithm. Ecology 51(3):503–507.
Cooke, J.G., and J.R. Beddington
1982 Further development of an assessment technique for male sperm whales based on length data from the catches. Rep. Int. Whaling Comm. 32:239–241.
Cooke, J.G., and W.K. de la Mare
1983a Description of and simulation studies on the length-specific sperm whale assessment technique. Rep. Int. Whaling Comm. 33:741–745.
1983b Further analyses for the location of the possible stock boundary for the North-West Pacific sperm whale based on length distributions of males. Rep. Int. Whaling Comm. 33: 275–277.
Cooke, J.G., W.K. de la Mare, and J.R. Beddington
1983a Some aspects of the reliability of the length data for the western North Pacific stock of sperm whales. Rep. Int. Whaling Comm. 33:265–267.
1983b An extension of the sperm whale model for the simulation of the male population by length and age. Rep. Int. Whaling Comm. 33:731–733.
de la Mare, W.K.
1988 Extended sensitivity trials on the length-specific method for estimating the size of exploited sperm whale populations. Rep. Int. Whaling Comm. 38:243–248.
de la Mare, W.K., and J.G. Cooke
1984 A new model for the female sperm whale incorporating aspects of the reproductive cycle. Rep. Int. Whaling Comm. 34:251–254.
1985 Analyses of the sensitivity of the length-specific estimation procedure to some departures from underlying assumptions. Rep. Int. Whaling Comm. 35:193–197.

1987 Further sensitivity trials in the length specific method for estimating the size of exploited sperm whale populations. Rep. Int. Whaling Comm. 37:219–222.

Deriso, R.B.

1985 Catch-age analysis with auxiliary information. Can. J. Fish. Aquat. Sci. 42:815–824.

Doubleday, W.G.

1975 A least squares approach to analyzing catch at age data. Int. Comm. Northwest Atl. Fish. Res. Doc. 75/35, 22 p.

Fabens, A.J.

1965 Properties and fitting the von Bertalanffy growth curve. Growth 29:265–289.

Fournier, D.A., and I.J. Doonan

1987 A length-based assessment method utilizing a generalized delay-difference model. Can. J. Fish. Aquat. Sci. 44:422–437.

Fournier, D.A., J.R. Sibert, J. Majkowski, and J. Hampton

1990 MULTIFAN: A likelihood-based method for estimating growth parameters and age composition from multiple length-frequency data sets illustrated using data for southern bluefin tuna. Can. J. Fish. Aquat. Sci. 47:301–317.

Fry, F.E.J.

1949 Statistics of a lake trout fishery. Biometrics 5:27–67.

Gallant, A.R.

1975 Nonlinear regression. Am. Stat. 29(2):73–81.

Gallucci, V.F., and T.J. Quinn II

1979 Reparameterization, fitting, and testing a simple growth model. Trans. Am. Fish. Soc. 108:14–25.

Gulland, J.A.

1965 Estimation of mortality rates. Annex to Rep. Arctic Fish. Working Group, Int. Counc. Explor. Sea Doc. CM 1965(3), 9 p.

Hampton, J., and J. Majkowski

1987 An examination of the accuracy of the Elefan computer programs for length based stock assessment. *In* Pauly, D., and G.P. Morgan (eds.), Length-based methods in fisheries research, p. 203–216. ICLARM (Int. Cent. Living Aquat. Resour. Manage.) Conf. Proc. 13, Manila.

Hasselblad, V.

1966 Estimation of parameters for a mixture of normal distributions. Technometrics 8:431–444.

Hoenig, J.M., and D.M. Heisey

1987 Use of a log-linear model with the EM algorithm to correct estimates of stock composition and to convert length to age. Trans. Am. Fish. Soc. 116:232–243.

Jones, R.

1961 The assessment of long-term effects of changes in gear selectivity and fishing effort. Mar. Res. (Scotl.) 1961(2):1–19.

1974 Assessing the long term effects of changes in fishing effort and mesh size from length composition data. Int. Counc. Explor. Sea Doc. CM 1974/F:33, 13 p.

1981 The use of length composition data in fish stock assessments (with notes on VPA and cohort analysis). FAO Fish. Circ. 734, 60 p.

Kimura, K.K., and S. Chikuni

1987 Mixtures of empirical distributions: An iterative application of the age-length key. Biometrics 43:23–35.

Knight, W.

1968 Asymptotic growth: An example of nonsense disguised as mathematics. J. Fish. Res. Board Can. 25:1303–1307.

Kreuz, K.F., A.V. Tyler, and G.H. Kruse

1982 Variation in growth of Dover soles and English soles as related to upwelling. Trans. Am. Fish. Soc. 111:180–192.

Lai, H.L., and V.F. Gallucci

1988 Effects of parameter variability on length-cohort analysis. J. Cons. Cons. Int. Explor. Mer 45:82–92.

Laurec, A., and F.X. Bard

1980 Analyse multicohorte sur deux classes d'age. Int. Com. Cons. Atl. Tunas Collect. Vol. Sci. Pap XV (SCRS-1979):1–20.

Law, A.M., and W.D. Kelton

1982 Simulation modeling and analysis. McGraw-Hill, NY, 400 p.

Macdonald, P.D.M., and T.J. Pitcher

1979 Age groups from size frequency data: A versatile and efficient method of analyzing distributing mixtures. J. Fish. Res. Board Can. 36:987–1001.

Marquardt, D.W.

1963 An algorithm for least-squares estimation of non-linear parameters. J. Soc. Ind. Appl. Math 11(2):431–441.

Mendelssohn, R.

1988 Some problems in estimating population sizes from catch-at-age data. Fish. Bull., U.S. 86:617–630.

Morrison, D.D.

1960 Methods for nonlinear least squares problems and convergence proofs, tracking programs, and orbit determination. Proc. Jet Propul. Lab. Sem. (1960):1–9.

Murphy, G.I.

1965 A solution of the catch equation. J. Fish. Res. Board Can. 9:450–491.

Paloheimo, J.E.

1980 Estimation of mortality rates in fish populations. Trans. Am. Fish. Soc. 109:378–386.

Parrack, M.L.

1981 An assessment of the Atlantic bluefin tuna resource. Int. Com. Cons. Atl. Tunas Collect. Vol. Sci. Pap. XV:259–272.

1986 A method of analyzing catches and abundance indices from a fishery. Int. Com. Cons. Atl. Tunas Collect. Vol. Sci. Pap. XXIV:209–221.

1990 Estimating stock abundance from size data. Ph.D. diss., School Fish., Univ. Wash., Seattle, 116 p.

Parrack, N.J.C.

1986 Aspects of Pacific cod biology and population dynamics in the North Pacific. M.S. thesis, Univ. Wash., Seattle, 157 p.

Pauly, D.

1982 Studying single species dynamics in a tropical multispecies context. *In* Pauly, D., and G.I. Murphy (eds.), Theory and management of tropical fisheries, p. 33–70. ICLARM (Int. Cent. Living Aquat. Resour. Manage.) Conf. Proc. 9, Manila.

Pauly, D., M.L. Palomares, and F.C. Gayanilo

1987 VPA estimates of monthly population length composition, recruitment, mortality, biomass and related statistics of Peruvian anchoveta, 1953 to 1981. *In* Pauly, D., and I. Tsukayama (eds.), The Peruvian anchoveta and its upwelling ecosystem: Three decades of change, p. 142–166. ICLARM (Int. Cent. Living Aquat. Resour. Manage.) Stud. Rev. 15, Manila.

Pikitch, E.K., and R.L. Demory

1988 Assessment of scales as a means of aging Dover sole. Trans. Am. Fish. Soc. 117:345–349.

Pope, J.G.

1972 An investigation of the accuracy of virtual population analysis using cohort analysis. Int. Comm. Northwest Atl. Fish. Res. Bull. 9:65–74.

Pope, J.G., and J.G. Shepherd

1982 A simple method for the consistent interpretation of catch-at-age data. J. Cons. Cons. Int. Explor. Mer 40:176–184.

1985 A comparison of the performance of various methods for tuning VPAs using effort data. J. Cons. Cons. Int. Explor. Mer 42:129–151.

Press, W.H., B.P. Flannery, S.A. Teukolsky, and W.T. Vetterling

1986 Numerical recipes, the art of scientific computing. Cambridge Univ. Press, Cambridge, 818 p.

Quinn, T.J., S.H. Hoag, and G.M. Southward

1982 Comparison of two methods of combining catch-per-unit-effort data from geographic regions. Can. J. Fish. Aquat. Sci. 39:837–846.

Richards, F.J.

1959 A flexible growth function for empirical use. J. Exp. Botany 10(29) 290–300.

Ricker, W.E.

1948 Methods of estimating vital statistics of fish populations. Indiana Univ. Publ. Sci. Ser. 15, 101 p.

1975 Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191, 382 p.

Rosenberg, A.A., and J.R. Beddington

1987 Monte Carlo testing of two methods for estimating growth from length frequency data, with general conditions for their applicability. *In* Pauly, D., and G.P. Morgan (eds.), Length-based methods in fisheries research, p. 283–289. ICLARM (Int. Cent. Living Aquat. Resour. Manage.) Conf. Proc. 13, Manila.

Rubinstein, R.Y.

1981 Simulation and the Monte Carlo method. John Wiley, NY, 278 p.

Scheuer, E.M., and D.S. Stoller

1962 On the generation of normal random vectors. Technometrics 4:278–281.

Schnute, J.T., L.J. Richards, and A.J. Cass

1989 Fish survival and recruitment: Investigations based on a size-structured model. Can. J. Fish. Aquat. Sci. 46:743–769.

Schrage, L.

1979 A more portable Fortran random number generator. ACM (Assoc. Comput. Machines) Trans. Math. Software 5: 132–138.

Shepherd, J.G.

1985 Deconvolution of length compositions. Int. Counc. Explor. Sea Methods Working Group, Working paper, 7 p.

Shirakihara, K., and S. Tanaka

1983 An alternative length-specific model and population assessment for the western North Pacific sperm whales. Rep. Int. Whaling Comm. 33:287–294.

1984 Simulation studies on length-specific population assessment techniques for western North Pacific sperm whales. Rep. Int. Whaling Comm. 34:259–264.

Shirakihara, K., S. Tanaka, and T. Nakano

1985 Further simulation studies on length-specific population assessment techniques for western North Pacific sperm whales. Rep. Int. Whaling Comm. 35:199–203.

Smith, S.J.

1980 Comparison of two methods of estimating the variance of the estimate of catch per unit effort. Can. Fish. Aquat. Sci. 37:2346–2351.

Sullivan, P.J.

1989 Kalman filter approach to catch at length analysis. Ph.D. diss., Univ. Wash., Seattle, 160 p.

Sullivan, P.J., H.L. Lai, and V.F. Gallucci

1990 A catch-at-length analysis that incorporates a stochastic model of growth. Can. J. Fish. Aquat. Sci. 47:184–198.

Ulltang, O.

1977 Sources of errors in and limitations of virtual population analysis (cohort analysis). J. Cons. Cons. Int. Explor. Mer 37:249–260.

Welch, B.L.

1938 The significance of the difference between two means when the population variances are unequal. Biometrika 25:350–362.

Appendix: Simulation steps of Monte Carlo tests
Control variables are F_1, F_2, z_1, p_t, μ_1, μ_2, σ_1, σ_2, μ_k, cv[k], μ_A, cv[A], cv[q], cv[C]

Compute the following once each trial for $1 \leqslant t \leqslant\leqslant T$:

```
1 If the $F_t$ are variable, $F_t \sim U(F_1, F_2)$
2 If the $z_t$ are variable, $z_t \sim U(z_1, z_2)$
3 If a single catch occurs once each period, then
  A probability of unobserved events (z) during $y_t$ to $c_t$ is $Pr[z']_t = 1 - e^{-z_t(c_t - y_t)}$,
  B probability of being caught (on date $c_t$) is $Pr[C]_t = F_t$,
  C probability of unobserved events (z) during $c_t$ to $y_{t+1}$ is $Pr[z']_t = 1 - e^{-z_t(y_{t+1} - c_t)}$, or
4 If catching is continuous, then
  A probability of death during $y_t$ to $y_{t+1}$ is $Pr[D]_t = 1 - e^{-(z_t + F_t)(y_{t+1} - y_t)}$, and
  B $Pr[z]_t = Pr[D]_t \, z_t \div (z_t + F_t)$.
5 If recruitment is seasonal, then
  A $p_t \sim U(1, 20)$ where $p_t$ is the proportion recruited during period t,
  B $\delta_t = \sum_{i=1}^{t} p_i \sum_{j=1}^{T-1} p_j$ = the accumulative frequency,
  C $\mu_t \sim U(\mu_1, \mu_2)$, and
  D $\sigma_t \sim U(\sigma_1, \sigma_2)$.
```

Compute the following once for each fish:

```
6 Draw growth parameters k and A such that
  A $k \sim N(\mu_k, (\mu_k \, cv[k]^2)$,
  B $A \sim N(\mu_A, (\mu_A \, cv[A]^2)$.
7 Draw a recruitment data, $t_1$, such that
  A if recruitment is uniform, then $t_1 \sim U(1, 20)$, or
  B if recruitment is seasonal,
    (1) draw t with probability specified by $\delta$,
    (2) draw $t_1 \sim N(\mu_t, \sigma^2{}_t)$.
8 If fishing is continuous, then
  A for the time period of recruitment draw u where $u \sim U(0, 1)$.
    (1) If $u \leqslant z_{t1}(1 - e^{-(z_{t1} + F_{t1})(y_{t1+1} - t_1)} \div (z_{t1} + F_{t1})$, the fish exited of unobserved causes; STOP.
    (2) If not, but if $u \leqslant 1 - e^{-(z_{t1} + F_{t1})(y_{t1+1} - t_1)}$, the fish was caught; go to step 8C(2)(a).
    (3) If neither occurred, the fish lived through the time period of recruitment; continue.
  B Add a fish to the abundance matrix.
    (1) $t = t + 1$.
    (2) $t_1 = y_t$.
    (3) $s_1$ = the lower bound of the minimum size-class.
    (4) Compute the size-class from equation (1).
    (5) $N_{t,s2} = N_{t,s2} + 1$.
    (6) If $t = T$, STOP.
  C Draw u where $u \sim U(0, 1)$.
    (1) If $u \leqslant Pr[z]_t$, the fish exited dur to unobserved events; STOP.
    (2) If not, but if $u \leqslant Pr[D]_t$, the fish was caught.
      (a) Draw u where $u \sim U(0, 1)$.
      (b) $t_2 = t + u$.
      (c) Compute the size-class equation (1).
      (d) Add to the catch matrix: $C_{t,s} = C_{t,s} + 1$; STOP.
```

```
    (3) If neither occurred, the fish survived; go to step 8B.
9 If fishing occurs just once each period, then
  A If $t_1 < c_{t1}$, the fish recruited before the catch.
    (1) Draw u where $u \sim U(0,1)$.
    (2) If $u \leq 1 - e^{-z_{t1}(c_{t1} - t_1)}$, the fish exited unobserved events before date $c_t$; STOP.
    (3) If not, the fish survived to the catch date; go to step 9F.
  B If $t_1 = c_{t1}$, the fish recruited on the catch date; go to step 9F.
  C If $t_1 > c_{t1}$, the fish recruited after the catch.
    (1) Draw u where $u \sim U(0,1)$.
    (2) If $u \leq 1 - e^{-z_{t1}(y_{t1+1} - t_1)}$, the fish exited due to unobserved events before the next abundance sample (date $y_{t+1}$); STOP.
    (3) If not, the fish survived fishing and so was alive on the next sampling date: $t = t+1$.
  D Add a fish to the abundance matrix.
    (1) $t_2 = y_t$.
    (2) $s_1$ = lower bound of the minimum size-class.
    (3) Compute the size-class from equation (1).
    (4) $N_{t,s2} = N_{t,s2} + 1$.
    (5) If $t = T$, STOP.
  E Draw u where $u \sim U(0,1)$. If $u \leq Pr[z']_t$, the fish exited due to unobserved events before the date of catch; STOP.
  F Draw u where $u \sim U(0,1)$. If $u \leq Pr[C]_t$, the fish was caught on date $c_t$.
    (1) $t_2 = c_t$.
    (2) $s_1$ = lower bound of the minimum size-class.
    (3) Compute the size-class when caught from equation (1).
    (4) $C_{t,s2} = C_{t,s2} + 1$.
    (5) STOP.
  G Draw u where $u \sim U(0,1)$.
    (1) If $u \leq Pr[z']_t$, the fish exited due to unobserved events before the next abundance sampling date; STOP.
    (2) If not, the fish survived to the next relative abundance sample date.
      (a) $t = t+1$.
      (b) Go to step 9D.
```

Collect samples once each trial:

```
10 Draw an extimate of the growth parameters such that
   $\rho[\hat{A}, \hat{k}] = -0.95$,
   $\hat{k} \sim N(\mu_k, \mu_k^2(cv[k]^2 + cv[e_k]^2) div g$, and
   $\hat{A} \sim N(\mu_A, \mu_A^2(cv[A]^2 + cv[e_A]^2) \pm g$.
11 Draw an extimate of catch for all t and s where $\hat{C}_{t,s} \sim N(C_{t,s}, C_{t,s}\, cv[C]^2)$.
12 For each t and s draw $q_{t,s,k} \sim N(q_s, (q_s\, cv[q]^2)$ for $1 \leq k \leq r$.
13 Calculate $Y_{t,s}$ and $s^2[Y_{t,s}]$.
14 Determine the largest sampled size-class.
```