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"Effect of Variability on Estimates of
Cohort Parameters Using Length-Cohort Analysis:
with a guide to its use and mis-use
by

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Effect of Variability on Estimates of Cohort Parameters Using Length-Cohort Analysis: with a guide to its use and mis-use

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Abstract

A mathematical derivation for length cohort analysis (LCA) is given. Equations are presented for evaluating the effects of variability in the input parameters and for changes in the size of the length interval. The LCA is applied to a harvested bivalve stock (Protothaca staminea). The variance of the estimate of L_∞ (in the von Bertalanffy growth model) has the greatest impact upon the variability of the estimated cohort parameters from LCA. Variability in the instantaneous natural mortality rate results in more error in the estimated cohort parameters than does variability in the terminal fishing mortality rate. A length interval of 3mm is the largest interval for grouping animals into a frequency histogram for our species. Any interval greater than 3mm introduces substantial error into the estimates of the cohort parameters. Equations and curves to predict the optimal size interval are presented.

Introduction

Cohort parameters such as age-specific fishing mortality and cohort strength are traditionally estimated by age-dependent methods such as "virtual population analysis (VPA)" (Gulland, 1965) and "cohort analysis" (Pope, 1972). These methods depend on accurate age determination, which is not always feasible, especially for tropical fish. Jones (1979,1984) proposed a method of length cohort analysis (LCA) to estimate the same parameters in a steady state population when the ages of the animals are not available. Jones (1979, 1984) adapted Pope's cohort analysis for LCA, but a theoretical background for LCA does need to be elaborated to better understand the method and to specify any assumptions that may be implicit. Reasoning by analogy simply does not provide an adequate scientific basis for the future development of LCA. The LCA method requires a growth model to transform ages into lengths, which in this case is the von Bertalanffy growth equation. As in cohort analysis, LCA requires that the rate of natural mortality and the rate of exploitation mortality of the terminal length group are known. The principle objectives of this contribution are a derivation of LCA and an appraisal of how variability in the essential input parameters contributes to errors in the estimates from a LCA.

The analytical expression derived for LCA is based on a negative exponential cohort model and on Baranov's catch equation, with length as the independent variable. The sensitivity of the LCA model is examined given variability in the: (i) sizes of the length interval in the histogram; (ii) von Bertalanffy growth parameters (L_∞ and K); (iii) estimate of the natural mortality rate over the length groups; (iv) estimate of the terminal (for the last length group) harvest mortality rate. The data in Jones (1979) for the Nephrops stock from the Firth

of Forth is used to indicate that the computer program of LCA is working as expected. The LCA is then applied to a bivalve population (Protothaca staminea) from Garrison Bay, San Juan Island, Washington. The advantage of using the bivalve stock is that it is well studied by the authors and unrealistic estimates would be detected.

Mathematical Analysis

Derivation of a Continuous Length Cohort Analysis (LCA)

1) Negative exponential length cohort model.

Assume a population composed of several discrete cohorts, each of which exponentially decreases in number as the age of each cohort increases and assume that the birthday of this cohort is the first day of each year. Cohort abundance thus decreases by

$$\frac{dN}{dt} = -ZN \tag{1}$$

with an initial condition of $N(0)=N_0$, where Z is an instantaneous total mortality rate. The solution of (1) is

$$N(t) = N_0 e^{-Zt} \tag{2}$$

Further, assume that the growth of an individual in any cohort follows a deterministic von Bertalanffy growth model, permitting the age of the cohort at any time instants to be exchanged with the length at age using the von Bertalanffy growth curve (Fig. 1). The rate of increase in the size of an average individual of length l in a cohort is

$$\frac{dl}{dt} = K(L_\infty - l) \tag{3}$$

with an initial condition of $l(t_0) = 0$. The solution of (3) is

$$l(t) = L_\infty \left(1 - e^{-K(t - t_0)} \right) \tag{4}$$

which can be solved in terms of t as

$$t = t_0 - (1/K) \ln \left(1 - l(t)/L_\infty \right). \tag{4a}$$

N(t) is a compound function N(l(t)) differentiable with respect to l and t,

$$\frac{dN}{dt} = \frac{dN}{dl} \times \frac{dl}{dt};$$

from which explicit dependence upon age t is removed using (1) and (3),

$$\frac{dN}{dl} [K(L_\infty - l)] = -ZN$$

or

$$\frac{dN}{N} = \frac{-Z dl}{K(L_\infty - l)} \tag{5}$$

Integration from N_0 to $N(l)$ and l_0 to l yields

$$N(l) = N_0 \left[\frac{(L_\infty - l)}{(L_\infty - l_0)} \right]^{Z/K} . \tag{6}$$

It follows that

$$N(l + \Delta l) = N_0 \left[\frac{L_\infty - (l + \Delta l)}{(L_\infty - l_0)} \right]^{Z/K} \tag{6a}$$

where, $N(l)$ is the number of individuals in the cohort that attain length l.

Assume that the population is in a steady state, such that a time independent length-frequency collection can represent all the cohorts (year classes) in the population and that the length-frequency distribution is grouped into intervals of length Δl. The number of individuals at the start of length interval $(l, l + \Delta l)$ can be expressed by dividing (6a) by (6).

$$N(l + \Delta l) = N(l) \left[\frac{L_\infty - (l + \Delta l)}{(L_\infty - l)} \right]^{Z/K} \tag{6b}$$

For convenience, define a function $A(l)$ that depends on l and Δl,

$$A(l) = \frac{L_\infty - l}{L_\infty - (l + \Delta l)} \tag{7}$$

so that (6b) becomes

$$N(l + \Delta l) = N(l)\, A(l)^{-Z/K} \tag{8}$$

Define that $\Delta t(l) = t(l + \Delta l) - t(l)$ and use (4a) to get

$$\Delta t(l) = -\frac{1}{K} \ln \frac{L_\infty - (l + \Delta l)}{L_\infty - l} = \frac{1}{K} \ln A(l) \tag{9}$$

Rearranging (9) yields

$$A(l)^{-Z/K} = e^{-Z\Delta t(l)} \tag{10}$$

which is the survival during the time interval $\Delta t(l)$ when fish grow from l to $l+\Delta l$. Parameters Z and K have the dimension of (1/time) and apply to all length groups.

2) Catch equation.

We have assumed that the annual instantaneous total mortality rate Z is constant over all length intervals Δl. Now, assume that there are length-specific instantaneous total, fishing, and natural mortality rates (each in 1/yr): $Z(l)$, $F(l)$ and $M(l)$, respectively, within each length interval $(l, l+\Delta l)$ and the time interval corresponding to this length interval is $(t(l), t+\Delta t(l))$. The catch at any time instant, given in terms of age of the cohort, of this interval (Gulland, 1969) is

$$\frac{dC}{dt} = F(l(t))\, N(l(t)) \tag{11}$$

Again, based on Figure 1, $C(t)$ is a compound function $C(l(t))$ and differentiable with respect to l and t, then the chain rule gives,

$$dC = F(l)\, N(l)\, dt = F(l)\, N(l)\, dl \frac{dt}{dl} = F(l)\, N(l) \frac{dl}{K[L_\infty - l]} \tag{11a}$$

The number of fish caught in any length interval $(l, l+\Delta l)$, denoted by $C(l)$, is found by integrating

the right-hand side of (11a) from l to $l+\Delta l$, when $F(l)$ is given as a constant over the interval Δl,

$$C(l) = \int_{l}^{l+\Delta l} F(l)\, N(x) \frac{dx}{K[L_\infty - x]} \tag{12}$$

where x is any point within the interval $(l, l+\Delta l)$. $N(x)$ can be found using (6b) with starting stock size $N(l)$ at length l:

$$N(x) = N(l) \left[\frac{L_\infty - x}{L_\infty - l} \right]^{Z/K}$$

Substitution into (12) and integrating yields

$$C(l) = \frac{F(l)\, N(l)}{K(L_\infty - l)^{Z(l)/K}} \times \frac{(L_\infty - x)^{Z(l)/K}}{Z(l)/K} \Bigg|_{l}^{l+\Delta l}$$

and, from (7),

$$C(l) = \frac{F(l)}{Z(l)} N(l)[1 - A(l)^{-Z(l)/K}] \tag{13}$$

3) Length cohort analysis

Using a method similar to that which Pope (1972) used to derive cohort analysis, LCA can be derived by first multiplying both sides of (8) by $A(l)^{M(l)/K}$:

$$N(l+\Delta l)\, A(l)^{M(l)/K} = N(l)\, A(l)^{-F(l)/K}$$

where, $Z(l) = M(l) + F(l)$, and adding and substracting $N(l)$ in the right-hand side of the previous equation,

$$N(l+\Delta l)\, A(l)^{M(l)/K} = N(l) - N(l)\,[1 - A(l)^{-F(l)/K}] \qquad (14)$$

Solving for $N(l)$ in (13),

$$N(l) = \frac{Z(l)C(l)}{F(l)\,[1 - A(l)^{-Z(l)/K}]} \,. \qquad (14a)$$

and substituting (14a) into equation (14) yields

$$N(l+\Delta l)\, A(l)^{M(l)/K} = N(l) - C(l)\,\frac{Z(l)\,[1 - A(l)^{-F(l)/K}]}{F(l)\,[1 - A(l)^{-Z(l)/K}]} \qquad (15)$$

Using the approximation $(1-e^{-x})/x \cong e^{-x/2}$ (Seber 1982), and substituting $A = A(\iota)$, $B = Z(\iota)/K$, and $x = B \ln A$, the approximation becaomes

$$\frac{(1 - A^{-B})}{B \ln A} \cong A^{-B/2}.$$

Rearranging and substituting again yields,

$$\frac{Z(\iota)}{[1 - A(\iota)^{-Z(\iota)/K}]} = A(\iota)^{Z(\iota)/2K} \frac{K}{\ln A(\iota)} \tag{15a}$$

Similarly, let $B = F(\iota)/K$ to obtain

$$\frac{F(\iota)}{[1 - A(\iota)^{-F(\iota)/K}]} = A(\iota)^{F(\iota)/2K} \frac{K}{\ln A(\iota)} \tag{15b}$$

Then simple substitution of the right-hand-sides of (15a) and (15b) into (15) yields

$$N(\iota+\Delta\iota)\, A(\iota)^{M(\iota)/K} = N(\iota) - C(\iota)\, A(\iota)^{M(\iota)/2K}.$$

The annual instantaneous natural mortality rate is usually assumed constant over all length intervals, i.e., $M(\iota)=M$ for all ι's, although it frequently is a poor assumption. Equation (16) thus becomes

$$N(l) = N(l+\Delta l)\, A(l)^{M/K} + C(l)\, A(l)^{M/2K} \tag{16}$$

This is essentially the same formula for length cohort analysis which is also given in Jones (1984), but which he reached by the replacement of the age unit in Pope's cohort analysis with a length unit, without mathematical verification. One difference between (16) and Jones' equation is that (16) is a continuous form. To make the transition from this continuous version of LCA to the discrete version (present by Jones), the following two assumptions are needed.

The equations (8) and (11) are based on the assumption that within any length interval (Δl), the decline in the number of fish in a cohort follows an exponential curve. The length cohort analysis, however, replaces this continuous exponential curve within any length interval by a "step" function, by assuming that: (i) the catch in that length interval is taken at the middle of the length interval and no natural mortality occurs at that exact point; and (ii) natural mortality occurs continuously according to an exponential curve while the cohort passes through the length interval (Fig. 2).

The population size $N(l)$ calculated from (16) is the number of fish at l, the beginning of the length interval (l, $l+\Delta l$). It is important to note that the middle point of the length interval is not generally at the center of the time period over which fish grow from l to $l+\Delta l$; it would be, if the growth model were linear instead of a von Bertalanffy growth equation.

Since (16) results from a Taylor series expansion, it is necessary to determine the range of values of M/K, F/K and A(ι) that must be satisfied to ensure a pre-specified error of approximation in (16). Using the same analysis as Pope (1972), it can be shown that when these parameters satisfy

$$0 < \frac{M(\iota)}{K} \ln A(\iota) < 0{\cdot}3 \quad \text{and} \quad 0 < \frac{F(\iota)}{K} \ln A(\iota) < 1{\cdot}2 \tag{17}$$

the error of the estimated N(ι) is less than 5% (Jones, 1984).

The estimation is a backward procedure, starting from the terminal length group. Let C(λ) denote the catch at terminal length group, λ, the population size in the group λ is

$$N(\lambda) = C(\lambda) / E(\lambda) \tag{18}$$

where, E(λ) = F(λ)/Z(λ) is the exploitation rate of the terminal length group λ. Thus, to start the estimation we need prior information about M and F(λ) In most of cases, a best guess of E(λ) is used instead of F(λ).

Derivation of Effects of Variability and Mis-estimation of Parameters

At this stage, it remains to determine the effects of variability in estimates of the parameters in the model (16). Since the different parameters enter non-linearly, it is possible for relatively small differences to be magnified and for large variability to have only a small

effect on the final result of LCA. Thus, the efforts that goes into estimating different parameters can be rationally allocated.

1) Effects of Changing the Size of Length Interval (Δl)

There is no objective way to group lengths. Length frequency data are frequently grouped into a histogram in intuitive accord with the purpose of the analysis and the properties of the data. The precision of the estimates from LCA will increase when smaller sized length intervals are used. The size of the length interval used for grouping lengths must, however, provide a number of individuals per Δl (length interval) that is not "too small". " Too small" means that the ideally smooth length curve is not made into a discrete series of small peaks with increased variability. Equation (17) states the requirement of precision for LCA. More specifically, the length interval Δl should be kept as small as possible to avoid a large value of $\Delta t(l) = (1/K)\ln A(l)$ because a large $\Delta t(l)$ always implies a large natural mortality within that length group, as shown in (17).

For analytical convenience, let the length frequency data be grouped into equal intervals of size Δl. Let $C(l)$ be the catch with lengths between length l and $l+\Delta l$. We examine the consequence of combining the $C(l)$ over $n\Delta l$'s into a larger group, i.e., with a length range from l to $l+n\Delta l$. The catch with length between length l to $l+n\Delta l$ is

$$C'(l) = \sum_{i=0}^{n-1} C(l+i\Delta l) \tag{19}$$

From length cohort analysis and equation (16), the estimated stock size using the combined length group of l to $l+n\Delta l$ is

$$N'(l) = N'(l+n\Delta l)\,\alpha(l)^{M/K} + C'(l)\alpha(l)^{M/2k} \tag{20}$$

From equation (7) and for Δl all equal,

$$\alpha(l) = \frac{L_\infty - l}{L_\infty - (l+n\Delta l)}$$

$$= \frac{L_\infty - l}{L_\infty - (l+\Delta l)} \times \frac{L_\infty - (l+\Delta l)}{L_\infty - (l+2\Delta l)} \times \ldots\ldots \times \frac{L_\infty - [l+(n-l)\Delta l]}{L_\infty - (l+n\Delta l)}$$

$$= \prod_{i=0}^{n-1} A(l+i\Delta l) \tag{21}$$

Using a length interval of size Δl, $N(l)$ was calculated by equation (16). Applying this equation n times to obtain the relationship between $N(l)$ and $N(l+n\Delta l)$:

$$N(l)=N(l+\Delta l)\,A(l)^{M/K}+C(l)\,A(l)^{M/2K}$$

$$=[N(l+2\Delta l)\,A(l+\Delta l)^{M/K}+C(l+\Delta l)\,A(l+\Delta l)^{M/2K}]\,A(l)^{M/K}+C(l)\,A(l)^{M/2K}$$

$$=N(l+n\Delta l)\alpha(l)^{M/K}+\sum_{i=0}^{n-1} C(l+i\Delta l)\,A(l+i\Delta l)^{M/2K}\left\{(L_\infty-l)/[L_\infty-(l+i\Delta l)]\right\}^{M/K} \tag{22a}$$

$$=N(l+n\Delta l)\alpha(l)^{M/K}+\sum_{i=0}^{n-1} C(l+i\Delta l)\,\beta(l)^{M/2K} \tag{22}$$

where,

$$\beta(l+i\Delta l)=\frac{(L_\infty-l)^2}{\{L_\infty-(l+i\Delta l)\}\,\{L_\infty-[l+(i+1)\Delta l]\}}$$

Then, defining $\Delta N(l)$ as the difference between (20) and (22):

$$\Delta N(l)=[N'(l+n\Delta l)-N(l+n\Delta l)]\,\alpha(l)^{M/K}+C'(l)\,\alpha(l)^{M/2K}$$

$$-\sum_{i=0}^{n-1} C(l+i\Delta l)\,\beta(l+i\Delta l)^{M/2K} \tag{23}$$

The $\Delta N(l)$ in equation (23) is the difference between the areas A and B in Fig. 3. This is because the catches in several smaller intervals were combined into a larger interval and then it

is assumed that the combined catch is taken at the middle of this larger length interval. $\Delta N(l)$ is composed of two components: (i) the difference between $N'(l+n\Delta l)$ and $N(l+n\Delta l)$ projected to length l; and (ii) the difference between the projections of combined catch $C'(l)$ and individual $C(l+n\Delta l)$'s, to length l.

Dividing both sides of (23) by $N(l)=N(l+n\Delta l)\prod_{i=0}^{n-1} A(l+i\Delta l)^{-Z(l+i\Delta l)/K}$, and using (21) the relative error ratio is

$$\rho[N(l)] = \Delta N(l)/N(l)$$

$$= \rho[N(l+n\Delta l)]\prod_{i=0}^{n-1} A(l+i\Delta l)^{-F(l+i\Delta l)/K}$$

$$+\frac{1}{N(l)}\sum_{i=0}^{n-1} C(l+i\Delta l)\left\{\alpha(l)^{M/2K} - \beta(l+i\Delta l)^{M/2K}\right\} \tag{24}$$

Let

$$\rho[N(l)] = \rho[N(l+n\Delta l)]\prod[a] + \frac{1}{N(l)}\sum C(l+i\Delta l)\{[b]-[c]\} \tag{24a}$$

where $\Pi[a] = \Pi\, A(l+i\Delta l)^{-F(l+i\Delta l)/K} = e^{-\Sigma[F(l+i\Delta l)\Delta t(l+i\Delta l)]}$, for $i=0,1,\ldots,n-1$.

$$[b] = \alpha(l)^{M/2K}$$

$$[c] = \beta(l+i\Delta l)^{M/2K}$$

The first term in (24a) indicates that $\rho[N(l+n\Delta l)]$ over the length interval $(l+n\Delta l,\ l+2n\Delta l)$, which is adjacent to the interval $(l,\ l+n\Delta l)$, is decreased by $\Pi[a]$ because of the negative $F(l+i\Delta l)$ in the power of [a]. The sign and magnitude of the second term in (24a) depend upon the relative values of [b] and [c]: $[b]<[c]$ for those length groups with $l > (l+n\Delta l/2)$ and $[b]>[c]$, otherwise. It is easy to show that $[b]-[c]$ for the length groups close to L_∞ is larger than that for the length groups far from L_∞. For length groups where $l << L_\infty$, $[b]-[c]\rightarrow 0$ and $\rho[N(l+n\Delta l)]\Pi[a]$ dominates $\rho[N(l)]$.

To calculate the relative error of the estimated fishing mortality rate, integrated over the length interval $(l,\ l+n\Delta l)$, $F\Delta t'(l)$, where $\Delta t'(l) = \Sigma\Delta t(l+i\Delta l)$, we expressed $\Delta F\Delta t'(l)$ as

$$\Delta F\Delta t'(l) = F'\Delta t'(l) - \sum_{i=0}^{n-1} F(l+i\Delta l)\Delta t(l+i\Delta l)\ .$$

From which it follows that (Appendix A):

$$\rho[F\Delta t'(l)] = \Delta F(l)\Delta t(l) \Big/ \sum_{i=0}^{n-1} F(l+i\Delta l)\Delta t(l+i\Delta l)$$

$$= \ln \frac{1+\rho[N(l+\Delta l)]}{1+\rho[N(l)]} \Big/ \sum_{i=0}^{n-1} F(l+i\Delta l)\Delta t(l+i\Delta l) \qquad (25)$$

The relative error in differnet choices of Δl and this is $\Delta t'(l)$ are utilzed in the computation section.

2) Errors Due to Variation in L_∞ and K

Length cohort analysis assumes that the growth of individuals follows the deterministic von Bertalanffy growth model, therefore, to each length there corresponds only one age (Fig. 1); in other words, the time period required for a fish to grow from length l to $l+\Delta l$ is $\Delta t(l)$ as presented in equation (9) must be unique as a consequence. The t_0 in the von Bertalanffy equation will be ignored without loss of generality. The statistical estimation of L_∞ and K are possible sources of error in the application of the model. These errors can result from:
(i) measurement error in estimating age and length; (ii) individual variation in growth; and (iii) the values of L_∞ and K are wrongly guessed.

A covariance matrix can be obtained when age-length data is fit by a von Bertalanffy growth equation using non-linear regression (Gallucci and Quinn, 1979). Let $V(L_\infty)$, V(K)

and $COV(L_\infty,K)$ denote the variance and covariance of L_∞ and K. These statistics represent the uncertainty in the estimates of the von Bertalanffy parameters. Error source (ii) is associated with growth variability as each individual grows according to the von Bertalanffy model with its own (L_∞,K) (Sainsbury, 1980). That is L_∞ and K become random variables which are distributed with a joint distribution with the population mean of $E(L_\infty)$ and E(K), and covariance of $V(L_\infty)$, V(K), and $COV(L_\infty,K)$. The other source of error may be due to the wrongly guessed L_∞ and K.

Let $N(t) = f(L_\infty,K)$ and be analytical in the domain D defining the random variables L_∞ and K with means of $E(L_\infty)$ and E(K). Then, from Taylor's Theorem (Kreyszig, 1972), there exists precisely one power series with center (mean) at $[E(L_\infty),E(K)]$, which represents $f(L_\infty,K)$. This first-oder Taylor's series approximation is also known as the Delta method (Seber, 1982), that is,

$$f(L_\infty,K) = f[E(L_\infty),E(K)] + (\partial f/\partial L_\infty)\,|_{L_\infty}\,[L_\infty - E(L_\infty)] + (\partial f/\partial K)\,|_K\,[K - E(K)] + R \qquad (26)$$

$$\text{where } R = \frac{\partial^2 f}{2\,\partial L_\infty \partial K}[L_\infty - E(L_\infty)][K - E(K)] + \frac{\partial^2 f}{2\,\partial L_\infty^2}[L_\infty - E(L_\infty)]^2$$

$$+ \frac{\partial^2 f}{2\,\partial K^2}[K - E(K)]^2 + \ldots\ldots$$

Define that $f[E(L_\infty), E(K)] = E[N(\iota)]$, $L_\infty - E(L_\infty) = \Delta L_\infty$, $K - E(K) = \Delta K$; and ignore R which contains the second and higher order terms.

$$N(\iota) \cong E[N(\iota)] + \frac{\partial N(\iota)}{\partial L_\infty}\Big|_{L_\infty} \Delta L_\infty + \frac{\partial N(\iota)}{\partial K}\Big|_{K} \Delta K$$

Let

$$\Delta N(\iota) = N(\iota) - E[N(\iota)] = \frac{\partial N(\iota)}{\partial L_\infty}\Big|_{L_\infty} \Delta L_\infty + \frac{\partial N(\iota)}{\partial K}\Big|_{K} \Delta K$$

Then the error ratio can be calculated, if $E(L_\infty)$ and $E(K)$ are known, as

$$\rho[N(\iota)] = \frac{\Delta N(\iota)}{E[N(\iota)]}$$

$$= \frac{1}{E[N(\iota)]} \left(\frac{\partial N(\iota)}{\partial L_\infty}\Big|_{L_\infty} \Delta L_\infty + \frac{\partial N(\iota)}{\partial K}\Big|_{K} \Delta K \right) \qquad (27)$$

Further, the variance of $N(\iota)$ can be found by

$$\mathrm{Var}[N(\iota)] = E\{N(\iota) - E[N(\iota)]\}^2$$

$$= E[\Delta N(\iota)]^2$$

$$= E[\frac{\partial N(\iota)}{\partial L_\infty}\Delta L_\infty + \frac{\partial N(\iota)}{\partial K}\Delta K]^2$$

$$= E[\frac{\partial N(\iota)}{\partial L_\infty}(\Delta L_\infty)^2 + \frac{\partial N(\iota)}{\partial K}(\Delta K)^2 + \frac{\partial^2 N(\iota)}{\partial L_\infty \partial K}(\Delta L_\infty)(\Delta K)]$$

$$=[\frac{\partial N(\iota)}{\partial L_\infty}]^2 V(L_\infty) + [\frac{\partial N(\iota)}{\partial K}]^2 V(K) + 2[\frac{\partial^2 N(\iota)}{\partial L_\infty \partial K}]\,\mathrm{cov}(L_\infty, K) \qquad (28)$$

Working backward from the abundance in the terminal length category λ, $N(\lambda)$ is estimated first.

$$N(\lambda) = C(\lambda)\,Z(\lambda)/F(\lambda)$$

which does not involve L_∞ and K. Therefore, the variance of $N(\lambda)$ can be assumed to be zero. Since by definition, $\lambda = \iota + n\Delta\iota$, the variance of $N(\lambda - \Delta\iota)$ follows (27):

$$V[N(\lambda - \Delta\iota)] = (\frac{\partial N(\lambda - \Delta\iota)}{\partial L_\infty}|_{L_\infty})^2 V(L_\infty) + (\frac{\partial N(\lambda - \Delta\iota)}{\partial K}|_K)^2 V(K)$$

$$+ 2(\frac{\partial 2N(\lambda - \Delta\iota)}{\partial L_\infty \partial K}|_{L_\infty, K})\mathrm{COV}(L_\infty, K) \qquad (29)$$

and so on for $V[N(\lambda-2\Delta\iota)]$,...., $V[N(\iota)]$. To calculate $N(\iota)$ from $N(\lambda)$, (22) can be applied by letting $\lambda = \iota+n\Delta\iota$:

$$N(\iota) = N(\lambda)\alpha(\iota)^{M/K} + \sum_{i=0}^{n-1} C(\iota+i\Delta\iota)\,\beta(\iota+i\Delta\iota)^{M/2k} \tag{30}$$

where,

$$\beta(\iota+i\Delta\iota) = \frac{(L_\infty - \iota)^2}{\{L_\infty-(\iota+i\Delta\iota)\}\{L_\infty-[\iota+(i+1)\Delta\iota]\}} .$$

The derivatives of $N(\iota)$ respect to L_∞ and K are derived in Appendix B. Equation (28) becomes

$$V[N(\iota)] = \left\{N(\lambda)\emptyset_{L\infty} + \sum_{i=0}^{n-1} C(\iota+i\Delta\iota)\theta_{L\infty}\right\}^2 V(L_\infty)$$

$$+\left\{N(\lambda)\emptyset_K + \sum_{i=0}^{n-1} C(\iota+i\Delta\iota)\theta_K\right\}^2 V(K) + 2\left\{N(\lambda)\emptyset_{L\infty K} + \sum_{i=0}^{n-1} C(\iota+i\Delta\iota)\theta_{L\infty K}\right\} COV(L_\infty,K) \tag{31}$$

The instantaneous fishing mortality rate summed over length interval $(l, l+\Delta l)$, $F(l)\Delta t(l)$, can be written as

$$F(l)\Delta t(l) = [Z(l) - M]\Delta t(l) = Z(l)\Delta t(l) - M\Delta t(l)$$

$$= \ln N(l) - \ln N(l+\Delta l) - (M/K) \ln A(l)$$

Let $H(l) = (M/K) \ln A(l)$. By the Delta method, the variance of $F(l)\Delta t(l)$ is found as

$$V[F(l)\Delta t(l)] = V[\ln N(l)] + V[\ln N(l+\Delta l)] + (\partial H(l)/\partial L_\infty|_{L_\infty})^2 V(L_\infty)$$

$$+ (\partial H(l)/\partial K|_K)^2 V(K) + 2(\partial^2 H(l)/\partial L_\infty \partial K|_{L_\infty,K}) COV(L_\infty,K) \qquad (32)$$

where

$$V[\ln N(l)] = V[N(l)]/N(l)^2$$

$$V[\ln N(l+\Delta l)] = V[N(l+\Delta l)]/N(l+\Delta l)^2 \qquad (33)$$

The derivatives of $H(l)$ respect to L_∞ and K are given in Appendix C. The relative error $\rho[N(l)]$ and the variances of $N(l)$ and $F(l)$ are utilized in the computation section.

3) Effects of Variability in Natural and Terminal Fishing Mortalities

If the true natural mortality rate is M and terminal fishing mortality rate is $F(\lambda)$, the number of individuals of length l can be calculated using (16):

$$N(l) = N(l+\Delta l)A(l)^{M/K} + C(l)A(l)^{M/2K} \tag{34}$$

In many studies, M and $F(\lambda)$ are given numerical values based only on rather vague impressions of the resource dynamics. If we pick some values different from the true M and $F(\lambda)$, say M' and $F'(\lambda)$, the number of individuals at length l becomes

$$N'(l) = N'(l+\Delta l)A(l)^{M'/K} + C(l)A(l)^{M'/2K} \tag{35}$$

Substracting (35) from (34) leads to $\Delta N(l)$,

$$\Delta N(l) = [N'(l+\Delta l)A(l)^{M'/K} - N(l+\Delta l)A(l)^{M/K}] + C(l)A(l)^{M/2K}[A(l)^{\Delta M/2k} - 1]$$

$$= [N'(l+\Delta l)A(l)^{M'/K} - N(l+\Delta l)A(l)^{M'/K} + N(l+\Delta l)A(l)^{M'/K} - N(l+\Delta l)A(l)^{M/K}]$$

$$+ C(l)A(l)^{M/2K}[A(l)^{\Delta M/2K} - 1]$$

$$= \{\Delta N(l+\Delta l)A(l)^{M'/K} + N(l+\Delta l)A(l)^{M/K}[A(l)^{\Delta M/K} - 1]\}$$

$$+ C(l)A(l)^{M/2K}[A(l)^{\Delta M/2K} - 1]$$

$$= A(\iota)^{M/K} \{\Delta N(\iota+\Delta\iota)A(\iota)^{\Delta M/K} + N(\iota+\Delta\iota)\,[A(\iota)^{\Delta M/K} - 1]\}$$

$$+ C(\iota)A(\iota)^{M/2K}\,[A(\iota)^{\Delta M/2K} - 1] \tag{36}$$

Dividing both sides of (20) by $N(\iota) = N(\iota+\Delta\iota)A(\iota)^{Z(\iota)/K}$, the relative error ratio, $\rho[N(\iota)]$, is

$$\rho[N(\iota)] = A(\iota)^{M/K}\left\{\frac{\Delta N(\iota+\Delta\iota)}{N(\iota+\Delta\iota)} A(\iota)^{-Z(\iota)/K} A(\iota)^{\Delta M/K} + A(\iota)^{-Z(\iota)/K}\,[A(\iota)^{\Delta M/K} - 1]\right\}$$

$$+ \frac{C(\iota)}{N(\iota)} A(\iota)^{M/2K}\,[A(\iota)^{\Delta M/2K} - 1] \tag{37}$$

Substitute (8) into (34),

$$N(\iota) = N(\iota)\,A(\iota)^{-Z(\iota)/K}\,A(\iota)^{M/K} + C(\iota)A(\iota)^{M/2K}$$

$$= N(\iota)\,A(\iota)^{-F(\iota)/K} + C(\iota)A(\iota)^{M/2K}$$

Rearranging this equation,

$$\frac{C(\iota)A(\iota)^{M/2K}}{N(\iota)} = 1 - A(\iota)^{-F(\iota)/K}$$

Substituting this into (36),

$$\rho[N(l)] = A(l)^{M/K}\{\ \rho[N(l+\Delta l)]\ A(l)^{-Z(l)/K}\ A(l)^{\Delta M/K} + A(l)^{-Z(l)/K}\ [A(l)^{\Delta M/K} - 1]\}$$

$$+\ [\ 1 - A(l)^{-F(l)/K}\ ][A(l)^{\Delta M/2K} - 1]$$

$$= \rho[N(l+\Delta l)]\ A(l)^{-F(l)/K}\ A(l)^{\Delta M/K}\ +\ A(l)^{-F(l)/K}\ [A(l)^{\Delta M/K} - 1]$$

$$+\ [\ 1 - A(l)^{-F(l)/K}\ ][A(l)^{\Delta M/2K} - 1] \qquad (38a)$$

Expanding the second and third terms on the right-hand side of (38a) and rearranging,

$$\rho[N(l)] = \{\rho[N(l+\Delta l)]\ A(l)^{-F(l)/K}\ A(l)^{\Delta M/K}\} + \{[A(l)^{\Delta M/2K} - 1][1 - A(l)^{-F(l)/K}\ A(l)^{\Delta M/2K}] \qquad (38)$$

Starting from the last length group, λ, the number of individuals calculated by using $F(\lambda)$, M, $F'(\lambda)$, and M' are

$$N(\lambda) = C(\lambda)\frac{Z(\lambda)}{F(\lambda)}$$

and

$$N'(\lambda) = C(\lambda)\frac{Z'(\lambda)}{F'(\lambda)}$$

Then

$$\rho[N(\lambda)] = \frac{C(\lambda)\dfrac{Z'(\lambda)}{F'(\lambda)} - C(\lambda)\dfrac{Z(\lambda)}{F(\lambda)}}{C(\lambda)\dfrac{Z(\lambda)}{F(\lambda)}}$$

$$= \frac{Z'(\lambda)\,F(\lambda)}{Z(\lambda)\,F'(\lambda)} - 1 = \frac{1 + [Z'(\lambda)/Z(\lambda) - 1]}{1 + [F'(\lambda)/F(\lambda) - 1]} - 1$$

$$= \frac{1 + \rho[Z(\lambda)]}{1 + \rho[F(\lambda)]} - 1 \qquad (39)$$

Substituting (39) into (38) and proceeding backward to the length group ι, the generalized equation of $\rho[N(\iota)]$ is

$$\rho[N(\iota)] = \rho[N(\lambda)]\,\alpha(\iota)^{\Delta M/K}\{A(\lambda-\Delta\iota)^{-F(\lambda-\Delta\iota)/K}\,A(\lambda-2\Delta\iota)^{-F(\lambda-2\Delta\iota)/K}\ldots A(\iota)^{-F(\iota)/K}\}$$

$$+\ [A(\lambda-\Delta\iota)^{-\Delta M/2K}-1][1+A(\lambda-\Delta\iota)^{(-2F(\lambda-\Delta\iota)+\Delta M)/2K}]\times$$

$$[A(\lambda-2\Delta\iota)^{(-F(\lambda-2\Delta\iota)+\Delta M)/K}\ldots A(\iota)^{(-F(\iota)+\Delta M)/K}]$$

$$+\ \ldots\ldots$$

$$+\ [A(\iota)^{-\Delta M/2K}-1][1+A(\iota)^{(-2F(\iota)+\Delta M)/2K}]$$

$$= \rho[N(\lambda)]\,\alpha(\iota)^{\Delta M/K}\prod_{i=1}^{n}\{A(\iota+i\Delta\iota)^{-F(\iota+i\Delta\iota)/K}\}$$

$$+\ \sum_{i=0}^{n-1}\Big\{[A(\iota+i\Delta\iota)^{\Delta M)/2K}-1]\,[1+A(\iota+(i-1)\Delta\iota)^{(-2F(\iota+(i-1)\Delta\iota)+\Delta M)/2K}]\times$$

$$[\prod_{j=0}^{i}A(\iota+j\Delta\iota)^{(-F(\iota+j\Delta\iota)+\Delta M)/K}]\Big\}$$

$$= \rho[N(\lambda)]\,\alpha(\iota)^{\Delta M/K}\prod_{i=1}^{n}\{[a]\}+\sum_{j=0}^{i}\{[b][c][d]\} \qquad (40)$$

where, $n = (\lambda - \iota)/\Delta\iota$ is the number of length groups between length ι to λ,

$$[a] = A(\iota+i\Delta\iota)^{-F(\iota+i\Delta\iota)/K}$$

$$[b] = A(\iota+i\Delta\iota)^{\Delta M)/2K}{}_{-1}$$

$$[c] = 1+A(\iota+(i-1)\Delta\iota)^{(-2F(\iota+(i-1)\Delta\iota)+\Delta M)/2K}$$

$$[d] = [\prod_{j=0}^{i} A(\iota+j\Delta\iota)^{(-F(\iota+j\Delta\iota)+\Delta M)/K}]$$

and when j=i=0, let $A(\iota+j\Delta\iota)^{(-F(\iota+j\Delta\iota)+\Delta M)/K} = 1$.

It is more convenient to examine (40) in the following ways: (i) Fix M and change $F(\lambda)$, ie., $\Delta M/K=0$, $\alpha(\iota)^{\Delta M/K}=1$ and [b]=0. π[a] is a positive value and decreases as i increases because a<1. The second term in (40) vanishes. Thus, the relative error ratio is dependent upon $\rho[N(\lambda)]$ and the sign of $\Delta F(\lambda)$ and will be decreased by π[a] as i increases.

(ii) Fix $F(\lambda)$ and change M, ie., $\rho[N(\lambda)]= \rho[Z(\lambda)]$ whose sign is dependent upon ΔM. The sign of [b] is dependent upon ΔM and [c] and [d] are positive values, thus, the sign of the second term is dependent upon ΔM. If $\Delta M<0$, then $0<\alpha(\iota)^{\Delta M/K}<1$. The values of π[a] and [d] decline as i and j increase. Thus, the relative error ratio will be reduced from a quite large

$\rho[N(\lambda)]$ to an asymptotic level as the LCA processes backward starting from λ. However, if $\Delta M>0$, $\alpha(\iota)^{\Delta M/K}>1$, and the attenuation of $\pi[a]$ will be not so effective as in the case of $\Delta M<0$. If $\Delta M>F>0$, the relative error ratio will accumulate exponentially from λ to ι. The second term in (40) accumulates to a positive value, but its effect is not as strong as the first term.

The relative error ratio of $F(\iota)\Delta t(\iota)$ can be computed as

$$\rho[F(\iota)\Delta t(\iota)] = [F'(\iota)\Delta t(\iota) - F(\iota)\Delta t(\iota)] / F(\iota)\Delta t(\iota)$$

$$= \{[Z'(\iota)\Delta t(\iota) - Z(\iota)\Delta t(\iota)] - \Delta M\Delta t(\iota)\}/ F(\iota)\Delta t(\iota)$$

$$= \left[-\ln \frac{N'(\iota)}{N'(\iota+\Delta\iota)} + \ln \frac{N(\iota)}{N(\iota+\Delta\iota)} \right] \Big/ F(\iota)\Delta t(\iota) - \Delta M \Big/ F(\iota)$$

$$= \frac{1}{F(\iota)\Delta t(\iota)} \ln \left[\frac{N(\iota)\, N'(\iota+\Delta\iota)}{N'(\iota)\, N(\iota+\Delta\iota)} \right] - \Delta M/F(\iota)$$

$$= \frac{1}{F(\iota)\Delta t(\iota)} \ln \left[\frac{1+\rho[N(\iota+\Delta\iota)]}{1+\rho[N(\iota)]} \right] - \Delta M/F(\iota) \qquad (41)$$

The relative error $\rho[N(\iota)]$ and $\rho[F(\iota)\Delta t(\iota)]$ are utikized in the computation section.

Mathematical Computation and Data Analysis

Example for Jones' data

Confidence in a numerical result from a complex computer algorithm based on a long analytical derivation is often like accepting an article of faith. Since we re-derived the equations for LCA and since we want to check our computer program, the data given in Jones (1979, Appendix 1) for male Nephrops was repeated. The estimates of the von Bertalanffy growth parameters of the hake are L_∞= 70cm and K = 0·5/yr. The annual instantaneous natural mortality rate, M=0·2/yr, provides M/K= 0·4. Assume that the

$E(\lambda) = F(\lambda)/Z(\lambda) = 0{\cdot}7$, where λ=65cm corresponds to the terminal length group (65-70cm), the population size at the start of the length group λ is calculated with (17) to be

$$N(\lambda) = 3 \times 10^3 / 0{\cdot}7 = 4{\cdot}29 \times 10^3$$

and that of 60-65cm group from (16a) is

$$N(\lambda-\Delta\iota) = 4{\cdot}29 \times 10^3 \, [(70 - 60)/(70-65)]^{0{\cdot}4} + 10 \times 10^3 \, [(70 - 60)/(70-65)]^{0{\cdot}4/2}$$

$$= 17{\cdot}14 \times 10^3$$

The survival calculated in Table 1 is the ratio of the number surviving to each successive length group. For example, for the 55-60cm group ,

$$S = 17{\cdot}14 / 122{\cdot}10 = 0{\cdot}14$$

where, $122{\cdot}10 \times 10^3$ is the number of survivors in the 50-55cm group. This estimate is the

proportion of fish surviving during the time required to grow from 55cm to 60cm. Therefore, S is **not an annual** survival rate. The corresponding instantaneous total mortality is

$$Z\Delta t = -\ln(S) = 1{\cdot}963$$

The exploitation rate, $E = F/Z = C(l)/[N(l)-N(l+\Delta l)]$, for the 55-60cm group is calculated by

$$E = F/Z = 94 / [122{\cdot}10 - 17{\cdot}10] = 0{\cdot}896$$

Then, the corresponding fishing mortality in 55-60cm group is

$$F\Delta t = E\,(Z\Delta t) = 1{\cdot}758$$

Because L_∞ and K are known, we can compute Δt for each length group (the second column in Table 1). The annual instantaneous total and fishing mortality rates, $Z(l)$ and $F(l)$ are calculated from $Z(l) = Z\Delta t/\Delta t$ and $F(l) = F\Delta t/\Delta t$. For 55-60cm group,

$$F(l) = 1{\cdot}758/0{\cdot}811 = 2{\cdot}167 \quad \text{and} \quad Z(l) = 1{\cdot}963/0{\cdot}811 = 2{\cdot}421.$$

A comparion of the results in Table 1 with those in Jones (1979, Appendix 1) show the results to be exactly the same.

LCA on <u>Protothaca staminea</u>

We demonstrate now the impacts of variability in the input estimates by using the equations derived. To minimize the faith aspect, a case is chosen where we have a great deal of auxiliary data from field experiments where variances of estimates are ususally available. Further, the system is well-known to us and some sense of intuition about what is reasonable has developed.

The family of bivalves in Garrison Bay, Washington has been under investigation for about a decade. Papers by Scherba and Gallucci (1976), Gallucci and Rawson (1979), Gallucci and Gallucci (1982), Gallucci (1985) and Gallucci, Lai and Orensanz (in prep.) describe the environment, the bivalves and the data management scheme. Protothaca staminea is a Venerid, hardshell clam harvested commerically over most of the Pacific coast of North America, and is thus important to non-federal, regional, management agencies. In Garrison Bay it is harvested recreationally. Tagging experiments and an analysis of growth based on the Von Bertalanffy model yielded the following estimates:

$L_\infty = 61{\cdot}0$mm, $V(L\infty) = 7{\cdot}053$

$K = 0{\cdot}346$, $V(K) = 0{\cdot}00017$

An estimate of natural mortality, M, was computed by using two sets of data: data from creel census experiments where the size distributions of harvested clams were sampled to get a length frequency distribution of harvest, C(l), and data from a stratified random sampling design where all clams present in each sample unit were identified and measured. A length-frequency distribution of the stratified random sampling data was converted into an observed population abundance (Gallucci and Rawson, 1979) for each length group, N(l). The LCA algorithm was applied to the C(l) distribution to compute a predicted abundance, N(l)^, by iterating over natural mortality M until the sum of squares between N(l) and N(l)^ was minimized for all l-values. The validity of this approach rests upon the generally high reliability that can be placed upon estimates from benthic surveys. Recruitment in the benthos is an active area of research. While definitive processes are only partially understood, it is clear that the operating factors for a bivalve stock are

more accessible to study than is common for marine fisheries in general. Further, our study have shown that, for this population, there are sequences of years with approximately constant recruitment (Orensanz, unpubl. dissertation).

A value of M must be selected to initiate the analysis. Although it could be guessed at, and frequently is, we have choosen a somewhat unorthodox way to "compute" M. The estimated M is 0.47 and results from minimizing $\Sigma((N(\iota)-N(\iota)^{\wedge})^2$, where, $N(\iota)$ is the estimated population size from stratified random sampling data (Gallucci and Rawson 1979) and $N(\iota)^{\wedge}$ is the predicted population size from (16) for a given M. An independent study has come up with an M which is about 50% lower. The key issue in this case is what is the smallest sized bivalve that will be included in the mortality estimation. This is vague and subject to interpretation but we feel that M=0.47 is a realistic estimate for this analysis.

We assumed from the harvest data that fishing mortality for the terminal length group is about $F(\lambda) = 0{\cdot}1$. The LCA program was used with the input data on growth and mortality to obtain the estimates in Table 2. These estimates show reasonable magnitudes of abundance in the size classes and they show that a relatively major jump occurs in the estimate of fishing mortality (and thus in annual total mortality) in the low 40mm range. This result coincides nicely with the harvest data.

Effects due to changing size of length interval

The results in Table 2 are carried out based on the histogram of Protothaca staminea with a 1mm size interval. We now group the histogram into 3mm, 5mm, 7mm and 9mm size intervals respectively. In order to avoid the effects of changing M and $F(\lambda)$, we set the final length interval to be 1mm. In general, the estimates of stock size ($N'(\lambda)$) for data grouped with Δl >1mm is progressively overestimated as Δl increases from 1mm to 9mm (Fig. 4). The relative error ratio, $\rho[N(l)] = [N'(l) - N(l)]/N(l)$ where $N(l)$ is the estimate for data grouped at 1mm, is quite large at length group $\lambda - \Delta l$. $\rho[N(l)]$ declines to different, apparently asymptotic levels each corresponding to Δl being used. The point where $\rho[N(l)]$ is approximately constant is where $M\Delta t(l)$ becomes less than 0·3 regardless of Δl.

The instantaneous fishing mortality rate, $F'\Delta t'(l)$, of grouped histograms is underestimated as Δl increases (Fig.5). Further, $\rho[F\Delta t'(l)]$ oscillates with a trend such that its absolute value increases for larger Δl. In contrast to $\rho[N(l)]$, $\rho[F\Delta t'(l)]$is in the negative direction. For both estimates, the absolute relative errors are larger than 5% when Δl >5mm.

This example shows that Δl =3mm is probably the largest Δl that could be used for grouping the length frequency distribution of Protothaca staminea because $\rho[N'(l)]$ and $\rho[F'(l)\Delta t'(l)]$ are greater than 5% when a larger Δl is used. The leasson here is to keep as many length intervals in the fully recruited stock (about 40mm) as possible. The factor of $M\Delta t(l) > 0{\cdot}3$ may also play an important role if the majority of fully recruited bivalve length groups (eg., l>40mm) are combined such that $M\Delta t(l) > 0{\cdot}3$. This follows from the fact that $\rho[N(\lambda-\Delta l)]$ increases drastically and then declines as the backward computation of LCA proceeds.

Errors due to variation of L_∞ and K

The variances of L_∞ and K were estimated from the tagging data. $Cov(L_\infty,K)$ is not available from the estimation so we assume that $Cov(L_\infty,K)=0$, e.g., see Sainsbury (1980). Using $V(L_\infty)=7{\cdot}053$ and $V(K)=0{\cdot}00017$ and (31), the 95% confidence intervals for $N(l)$ and $F(l)\Delta t(l)$ are shown in Figures 6 and 7.

Figure 6 shows that the 95% confidence interval (95% c.i.) of $N(l)$ increases almost exponentially as LCA progresses backward. In contrast, the 95% c.i. of $F(l)$ decreases to an

apparent asymptotic level when $l<44$mm (Fig.7).

It is of interest to examine which component in (28) or (31) dominates the variance of $N(l)$. Figure 8 shows how the derivative of $N(l)$ varies with respect to L_∞ and K. It is obvious that

$$|\partial N/\partial K| \cong |\partial^2 N/\partial L_\infty \partial K| >> |\partial N/\partial L_\infty|. \quad (42)$$

However, Figure 9 shows that $|\partial N/\partial L_\infty|^2 V(L_\infty) \cong V[N(l)]$. This implies that $V(L_\infty)$, which is much larger than V(K), is the main factor that determines the values of $V[N(l)]$. It can also be shown that the evidence that the selection of the value of L_∞ is less critical, as long as the value is approximately right, but the value of $V(L_\infty)$ is important. Thus, if a population has a large $V(L_\infty)$, LCA must be used with caution.

In addition to the question of how $N(l)$ affected by the variance of estimated L_∞ and K, there is also the question of how does $N(l)$ change if the input L_∞ and K are guessed incorrectly. Equation (27) addresses this question. It is possible to plot a sensitivity, $\rho(N(l)$, to evaluate the question, but the inequality (42) clearly indicates that estimates of $N(l)$ are more sensitive to deviation from the true values of K than L_∞.

Effects due to variability of M and F(λ)

According to Table 2, the true M and F(λ) are assumed to be 0·47 and 0·1 respectively. We will examine the effects of changing M and F(λ) separately. First, fix F(λ) and change M by 0·2, 0·3, 0·7, 0·8, 0·9 and 1·0. When M=0·2 and 0·3, $\Delta M<0$ and $\rho[N(\iota)]<0$. The absolute value of $\rho[N(\lambda)]$ is reduced by $0<\alpha(\iota)^{\Delta M/K}<1$ and $0<\pi[a]<1$ graduately from the last length group backward to the preceeding groups. Also, $[b]<0$, $[c]>1$, which makes the second term in (40) negative. However, $0<[d]<1$, the value of [d] declines as j increases, and thus decreases the magnititude of the second term. As shown in Fig. 10, $\rho[N(\iota)] \cong -1{\cdot}0$ when $\Delta M<0$, and remains quite constant over all length groups.

As expected, $\rho[N(\iota)]>0$ and accumulates geometrically as $\Delta M>0$ (Fig. 10). Although $\rho[N(\iota)]$ is attenuated by $\pi[a]$, $\alpha(\iota)^{\Delta M/K}>1$ will decrease the effect due to $\pi[a]$. Also, the second termin (40) accumulates ΔM over all length groups in LCA. The effects increase rapidly as ΔM becomes larger because ΔM is accumulated as a power in (40). Evidently, increase of M' from M=0·47 causes more error in $\rho[N(\iota)]$.

Effect of ΔM on $\rho[F(\iota)]$ is opposite to the direction of $\rho[N(\iota)]$. $\rho[F(\iota)\Delta t(\iota)]<0$ when $\Delta M>0$ and $\rho[F(\iota)\Delta t(\iota)]>0$, otherwise (Fig. 11). The values of $\rho[F(\iota)\Delta t(\iota)]$ increase as the LCA proceeds backward through the length groups, but its magnitude is not as large as that of $\rho[N(\iota)]$.

It should be noted that when M increases and becomes greater than $M\Delta t(\iota) >0{\cdot}3$, $\rho[N(\iota)]$ is under-estimated because $N(\iota)$ is expanded with a Taylor series expansion where the remainder is omitted. Further, $\rho[F(\iota)\Delta t(\iota)]$ appears to be over-estimated as seen in Fig. 13.

When we fix M and change $F(\lambda)$ from 0·1 to 0·01, 0·05, 0·2, 0·3, 0·5 and 1·0, $\rho[N(\lambda)]$ is quite large at the beginning and then becomes approximately asymptotic at the 44mm length group (Fig.12). This should be expected because the second term vanishes ([b]=0) and $\rho[N(\lambda)]$ is attenuated by $\pi[a]$. Figure 12 also shows that $\Delta F(\lambda)<0$ (i.e., $F(\lambda)=0{\cdot}01$ and 0·05) causes greater error in $\rho[N(\iota)]$ than $\Delta F(\lambda)>0$ ($F(\lambda)= 0{\cdot}2, 0{\cdot}3, 0{\cdot}5$, and 1·0).

Figure 13 shows that the dirction of $\rho[F(\iota)\Delta t(\iota)]$ corresponding to $\Delta F(\lambda)$ opposites that of $\rho[N(\iota)]$. When $\Delta F(\lambda)>0$, $\rho[N(\iota)]>0$ and decreases rapidly from a large positive value to an apparent asymptotic close to zero. However, when $\Delta F(\lambda)<0$, $\rho[N(\iota)]<0$ and appears to be asymptotic from the negative direction.

Discussion

The results of a length-based cohort analysis are not the end-product in the management of a fishery. Usually the results will be used to estimate a potential yield and perhaps guide decisions about how that yield may be extracted, e.g., with respect the pressure that may be put on size or age groups. Upon these decisions there usually rest an array of important socio-economic consequences. One concern, therefore, of cohort analysis should be the extent that variability in the data and the variances of the estimates combine to introduce uncertainty in the results. Another concern is the peculiarity of any model itself, viz., are the effects of biased or highly variable estimates magnified or minimized in the generation of the output from the model.

These types of concerns were not obvious in the literature until the 1985 conference at Mazara del Vallo on length-based fish stock assessment. Prior to the meeting, only Laurec and Mesnil (1985) had raised the issue of the sensitivity of the results the manager gets to the variability in the input data for LCA. Our analysis provides a prescription for predicting the error that will result from poor estimates of input parameters and for predicting the effects of different grouping of length intervals. The next step is the filtering of such results to the level of making specific recommendations for specific stocks.

In our example, the results of the LCA on Protothaca staminea show a trend that is similar to the species harvesting history, but this must be carefully interpreted. The confidence intervals around the estimated values of $N(l)$ and $F(l)$ are quite large and the c.v. of $N(l)$ is greater than 500%. We recommend that the estimates of $N(l)$ be viewed as indicators of the

characteristics of a cohort subject to harvesting pressure, rather than used as the exact estimates of the population size. The standard deviation of L_∞ is 2·67cm with a coefficient of variation (c.v.) less than 5%. Nevertheless, even this low variance of L_∞ contributes substantially to the overall variance of $N(l)$ via (28).

The parameters L_∞ and K are treated as deterministic rather than stochastic (i.e., $E(L_\infty)=L_\infty$ in (27)). The relative error ratios $\rho[N(l)]$ and $\rho[F(l)]$ accumulate to a high level because of the large values in $\partial N/\partial K$ and $\partial N/\partial L_\infty$ around the true L_∞ and K (Fig. 6). This illustrates how difficulties may result via the choice of L_∞, e.g., by choosing the largest size fish (Jones, 1985) or the largest size plus 5% (Pauly, 1983). Instead, being aware of how L_∞ contributes to the variability of $N(l)$, implies that L_∞ should be very carefully estimated.

When LCA is carried out on a length frequency histogram with a length grouping of Δl, it is based on the supposition that catches are evenly distributed over smaller intervals within Δl. In our bivalve example, using Δl=3mm instead of 1mm introduces a $\rho[N(l)]$=2.5% for lower l-values and a $\rho[N(l)]$>5% for higher l-values. Working with Pope's age cohort analysis, Sims (1982) varied the time intervals between catch samples (analogous to varying the age interval, if steady state is assumed) and found that $\rho[N(t)]$ was minor unless M and F are both high. Since length and age are linked by the von Bertalanffy growth model in LCA, a

similar pattern should also occur. In fact, $\rho[N(l)]$ did increase when Δl changed from 1mm to 3mm, 5mm, 7mm, and 9mm, as did $F(l)$. Figure 4 shows that $\rho[N(l)]$ increases rapidly when $M\Delta t(l)>0{\cdot}3$. It appears to us that $M\Delta t(l)>0{\cdot}3$ is more important than the assumption that catches be evenly distributed over the smaller intervals within Δl. Thus, Δl should be selected such that the condition of equation (17) is true for all length groups.

The results in Fig. 4 provide a useful criterion by which to judge whether LCA is an appropriate method to analyze a given length frequency data set. LCA should not be employed when too many length groups do not satisfy the condition in (17).

In our bivalve example, an over-estimate of the natural mortality rate may cause more error in both $N(l)$ and $F(l)$ than an under-estimate would. Sims (1984) found a similar result for Pope's age cohort analysis. Variability in the natural mortality rate (M) results in more error than variabilty in the terminal fishing mortality rate, which can usually only be guessed at, whereas one might expect M to be somewhat known from independent experiments. Thus, if M cannot be estimated confidently, the estimated cohort parameters should be used only as population indicators.

The derivation of the theory of length cohort analysis is similar to that of Pope's age cohort analysis, and thus the assumptions made in age cohort analysis can be found in length cohort analysis. The most notable assumption is that a relatively large part of the total loss from the population be due to fishing. This guarantees that the catch at length sample represents a major part of the information about the total loss from the population. In other

words, $F >> M$ and thus, the estimation of stock size $N(l)$ is a good replication of the population even if M is poorly known.

There are, however, some differences between age cohort analysis and length cohort analysis which include:

(i) The steady state assumption for length cohort analysis is essential because the length cohort analysis is done on only one collection of length frequency samples at a particular instant. Therefore, the length freq ·ency data collected must be able to replicate the progress of the cohort; thus, significant effort needs to go into obtaining a representative sample. Jones (1984) suggested that length frequencies over several years be summed together to smooth the variability due to the effects of year-class and mortality rate fluctuation, but the consequences of this prescription are not known.

(ii) Length cohort analysis estimates the average numbers attaining each length l during a year, as well as the average number in a length interval at "any" particular moment under the assumption of steady state. Thus, the birthday of the cohort need not be assumed to be the first day of the birth year, but, the growth parameters for all individuals must be essentially

the same. Therefore, $N(l)$ indicates the number of individuals who attain the length l irrespective of the time at which this happens during the course of a year. In contrast, age cohort analysis does not involve the growth of fish and the assumption of steady state, but it does assume that the birthday is the first day of the year, so that $N(t)$ is the average number in a cohort attaining age t at the beginning of the year and no further additions occur until the next year.

(iii) Equation (5) implies that $l < L_\infty$. This condition requires that the upper bound of the terminal length group (λ) be smaller than L_∞. Therefore, length groups of $l > L_\infty$ should be combined into the terminal group. This is the reason that the average number in the terminal length group is estimated by (18). Another reason to combine data for $l > L_\infty$ is that the length frequency for extremely large fish cannot always be collected precisely and there may be many empty length intervals in the histogram.

(iv) The length cohort analysis also assumes that age and length are in a one-to-one correspondence and thus are deterministically convertible. This may be the critical point that deviates from reality.

(v) Since the middle of the length interval is not equal to the middle of the age interval, length cohort analysis is restricted to the use of the average length composition over a given time period (Jones, 1984). Cohort analysis, however, permits the use of either an estimate of the average age composition in any year (ie., synthetic cohort), or an estimate of the numbers from a year-class as its abundance decays over its life time.

Of course, LCA is not the only approach for a length based analysis of a cohort. If the two assumptions made for LCA hold (steady state and convertibility of age and length by the von Bertalanffy growth model), a length-based virtual population analysis (here called LVPA) analogous to that of Gulland (1965) can be developed. To see this, divide (8) by (13)

$$\frac{N(l+\Delta l)}{C(l)} = \frac{Z(l)\ A(l)^{-Z(l)/K}}{F(l)\ \{1 - A(l)^{-Z(l)/K}\}} . \qquad (42)$$

Assuming that the instantaneous natural mortality rate (M) and the terminal instantaneous fishing mortality rate ($F(\lambda)$) are known, the stock size in the terminal length group (λ), can be calculated by rearranging (13) as

$$N(\lambda) = \frac{C(\lambda)\, Z(\lambda)}{F(\lambda)\left[1 - A(\lambda)^{-Z(\lambda)/K}\right]} . \tag{43}$$

$F(\lambda-\Delta t)$ is estimated by substituting $N(\lambda)$ and $C(\lambda-\Delta t)$ into (42) and solving by numerical iteration (Johnson and Riess, 1982). $N(\lambda-\Delta t)$ is estimated by substituting $F(\lambda-\Delta t)$ and $N(\lambda)$ into (8). Applying this procedure in reverse, the sequence of parameters $F(\lambda-2\Delta t)$, $N(\lambda-2\Delta t)$, $F(\lambda-3\Delta t)$, $C(\lambda-3\Delta t)$ can be estimated until the first length group is reached.

LVPA may provide more accurate estimates than LCA since it does not use a Taylor series approximation. In fact, LVPA may be recommended if the condition in (17) is not adequately fulfilled.

It can be argued that there are also other growth models which can be used to replace the von Bertalanffy model in either LCA or LVPA. The mathematical derivations would follow along lines similar to those given in this paper.

The FORTRAN programs and documentation used in this paper for LCA are available through the authors via the Management Assistance for Artisanal Fisheries (MAAF) project at the authors' address in the School of Fisheries, University of Washington.

Acknowledgments

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Appendix A. Derivation of $\Delta F \Delta t'(l)$ in Equation (25)

$$\Delta F \Delta t'(l) = F' \Delta t'(l) - \sum_{i=0}^{n-1} F(l+i\Delta l)\Delta t(l+i\Delta l) .$$

$$= [Z'(l) - M]\Delta t'(l) - [\sum_{i=0}^{n-1} Z(l+i\Delta l)\Delta t(l+i\Delta l) - \sum_{i=0}^{n-1} M\Delta t(l+i\Delta l)]$$

$$= [Z'(l)\Delta t'(l) - \sum_{i=0}^{n-1} Z(l+i\Delta l)\Delta t(l+i\Delta l)] - [M\Delta t'(l) - \sum_{i=0}^{n-1} M\Delta t(l+i\Delta l)]$$

Because M is constant over the length and $\Delta t'(l)$ can be partitioned into the sum of $\Delta t(l+i\Delta l)$, the term $[M\Delta t'(l) - \sum_{i=0}^{n-1} M\Delta t(l+i\Delta l)]$ vanishes.

$$\Delta F \Delta t'(l) = \ln \frac{N'(l+n\Delta l)}{N'(l)} - \sum_{i=0}^{n-1} \ln \frac{N[l+(i+1)\Delta l]}{N(l+i\Delta l)}$$

$$= \ln \frac{N'(l+n\Delta l)}{N'(l)} - \ln \left\{ \frac{N(l+\Delta l)}{N(l)} \times \frac{N(l+2\Delta l)}{N(l+\Delta l)} \times \ldots\ldots \times \frac{N(l+n\Delta l)}{N(l+(n-1)\Delta l)} \right\}$$

$$= \ln \frac{N'(\iota+n\Delta\iota)}{N'(\iota)} - \ln \frac{N(\iota+n\Delta\iota)}{N(\iota)}$$

$$= \ln \frac{N'(\iota+n\Delta\iota)}{N(\iota+n\Delta\iota)} - \ln \frac{N'(l)}{N(\iota)}$$

$$= \ln \frac{1+\rho[N(\iota+n\Delta\iota)]}{1+\rho[N(\iota)]}$$

Appendix B. Derivatives of $N(l)$ with Respect to L_∞ and K

From equation (30),

$$N(l) = N(\lambda)\alpha(l)^{M/K} + \sum_{i=0}^{n-1} C(l+i\Delta l)\,\beta(l)^{M/2k}$$

where,

$$\alpha(l) = \frac{L_\infty - l}{L_\infty - (l+n\Delta l)}$$

and

$$\beta(l) = \frac{(L_\infty - l)^2}{\{L_\infty-(l+i\Delta l)\}\{L_\infty-[l+(i+1)\Delta l]\}}$$

It is obvious that $\partial N/\partial L_\infty$, $\partial N/\partial K$ and $\partial^2 N/\partial L_\infty \partial K$ are dependent on $\alpha(l)$ and $\beta(l)$. Define the following terms:

$$\emptyset_{L_\infty}=\partial\alpha(l)/\partial L_\infty; \qquad \emptyset_K=\partial\alpha(l)/\partial K; \qquad \emptyset_{L_\infty K}=\partial^2\alpha(l)/\partial L_\infty\partial K$$

and

$$\theta_{L_\infty}=\partial\beta(l)/\partial L_\infty; \qquad \theta_K=\partial\beta(l)/\partial K; \qquad \theta_{L_\infty K}=\partial^2\beta(l)/\partial L_\infty\partial K.$$

The explicit forms of these variables are

$$\emptyset_{L\infty} = (M/K)\ \alpha(\iota)^{M/K}\left[\frac{1}{L_\infty - \iota} - \frac{1}{L_\infty - (\iota + n\Delta\iota)}\right]$$

$$\emptyset_K = -(M/K2)\ \alpha(\iota)^{M/K}\ \ln \alpha(\iota)$$

$$\emptyset_{L\infty K} = -(1/K)\ \emptyset_{L\infty}[(M/K)\ \ln \alpha(\iota) + 1] = \emptyset_{L\infty}\{[\emptyset K/\alpha(\iota)] - (1/K)]\}$$

$$\theta_{L\infty K} = (M/2K)\ \beta(\iota)^{M/2K}\left\{\frac{1}{L_\infty - \iota} - \frac{2\,[L_\infty - (\iota + i\Delta\iota)] + \Delta\iota}{[L_\infty - (\iota + i\Delta\iota)][L_\infty - (\iota + (i+1)\Delta\iota)]}\right\}$$

$$\theta_K = -(M/2K^2)\ \beta(\iota)^{M/2K}\ \ln \beta(\iota)$$

$$\theta_{L\infty K} = \theta_{L\infty}\ \beta(\iota)^{-M/2K}[\theta_K - (M/2K^2)/\beta(\iota)]$$

Appendix C. Derivation of $H(\iota)$ with Respect to L_∞ and K

$$\frac{\partial H(\iota)}{\partial L_\infty} = \frac{\partial}{\partial L_\infty} \ln A(\iota)^{M/K} = \frac{M}{K}\left(\frac{1}{L_\infty - \iota} - \frac{1}{L_\infty - (\iota+\Delta\iota)}\right)$$

$$\frac{\partial H(\iota)}{\partial K} = \frac{\partial}{\partial K} \ln A(\iota)^{M/K} = -\frac{M}{K^2} \ln A(\iota)$$

$$\frac{\partial H(\iota)}{\partial L_\infty \partial K} = \frac{\partial^2}{\partial L_\infty \partial K} \ln A(\iota)^{M/K}$$

$$= -\frac{\partial}{\partial L_\infty}\left(\frac{M}{K^2} \ln A(\iota)^{M/K}\right)$$

$$= -\frac{M}{K^2}\left(\frac{1}{L_\infty - \iota} - \frac{1}{L_\infty - (\iota+\Delta\iota)}\right)$$

Table 1. LCA on Jones' data (Jones, 1979, Appendix 1).

Length (mm) (l)	$\Delta t(l)$	Catch (10^3)	Stock Size (10^3)	$F\Delta t(l)$	$Z\Delta t(l)$	$F(l)/Z(l)$	$Z(l)$
10.0-15.0	.1740	1	20246.46	.00005	.03485	.00144	.20029
15.0-20.0	.1906	163	19552.93	.00853	.04666	.18287	.24476
20.0-25.0	.2107	1390	18661.60	.07909	.12126	.65223	.57547
25.0-30.0	.2356	4120	16530.45	.29424	.34172	.86106	1.45065
30.0-35.0	.2671	4730	11745.63	.53243	.58717	.90678	2.19862
35.0-40.0	.3083	3040	6529.37	.65196	.71591	.91068	2.32210
40.0-45.0	.3646	1650	3191.22	.76469	.84133	.90891	2.30726
45.0-50.0	.4463	827	1375.86	.98278	1.07950	.91040	2.41884
50.0-55.0	.5754	312	467.47	1.21278	1.34249	.90338	2.33328
55.0-60.0	.8109	94	122.10	1.75832	1.96331	.89559	2.42106
60.0-65.0	1.3863	10	17.14	1.07826	1.38625	.77783	.99996
65.0-70.0	--	3	4.29	--	--	.70	--

L_∞=70.0mm, K=0.5, M=0.2, M/K=0.4, $F(\lambda)/Z(\lambda)$=0.7, where λ=65mm.

$F\Delta t(l)$ and $Z\Delta t(l)$ are the integrated instantaneous fishing and total mortality rates over the corresponding length group l.

$\Delta t(l)$ is the time required for an individual to grow from l to $l+\Delta l$, where Δl=5mm.

Table 2. LCA on Protothaca staminea in 1975.

Length (mm) (ℓ)	$\Delta t(\ell)$	Catch $C(\ell)$	Stock Size $N(\ell)$	$F\Delta t(\ell)$	$Z\Delta t(\ell)$	$F(\ell)/Z(\ell)$	$Z(\ell)$
10.0- 11.0	.0572	7.0	4641.64	.00153	.02843	.05380	.49673
11.0- 12.0	.0584	2.0	4511.54	.00045	.02789	.01612	.47770
12.0- 13.0	.0596	.0	4387.44	.00000	.02801	.00000	.47000
13.0- 14.0	.0608	1.0	4266.25	.00024	.02884	.00825	.47391
14.0- 15.0	.0622	.0	4144.99	.00000	.02921	.00000	.47000
15.0- 16.0	.0635	1.0	4025.65	.00025	.03011	.00838	.47397
16.0- 17.0	.0650	1.0	3906.25	.00026	.03079	.00844	.47400
17.0- 18.0	.0664	1.0	3787.82	.00027	.03150	.00851	.47404
18.0- 19.0	.0680	1.0	3670.38	.00028	.03224	.00859	.47407
19.0- 20.0	.0696	2.0	3553.93	.00057	.03331	.01718	.47822
20.0- 21.0	.0714	1.0	3437.52	.00030	.03384	.00874	.47415
21.0- 22.0	.0732	3.0	3323.14	.00092	.03531	.02602	.48256
22.0- 23.0	.0751	5.0	3207.85	.00159	.03687	.04306	.49115
23.0- 24.0	.0771	2.0	3091.72	.00066	.03688	.01786	.47855
24.0- 25.0	.0792	6.0	2979.76	.00205	.03927	.05229	.49593
25.0- 26.0	.0814	9.0	2865.01	.00321	.04147	.07732	.50939
26.0- 27.0	.0838	10.0	2748.62	.00372	.04309	.08626	.51437
27.0- 28.0	.0863	9.0	2632.69	.00349	.04405	.07933	.51050
28.0- 29.0	.0889	6.0	2519.24	.00243	.04423	.05504	.49738
29.0- 30.0	.0918	3.0	2410.23	.00127	.04440	.02866	.48387
30.0- 31.0	.0948	15.0	2305.56	.00667	.05122	.13031	.54043
31.0- 32.0	.0980	7.0	2190.45	.00328	.04933	.06640	.50343
32.0- 33.0	.1014	2.0	2085.03	.00098	.04865	.02020	.47969
33.0- 34.0	.1051	9.0	1986.02	.00466	.05406	.08612	.51430
34.0- 35.0	.1091	7.0	1881.51	.00382	.05509	.06941	.50506
35.0- 36.0	.1134	14.0	1780.66	.00811	.06138	.13205	.54152
36.0- 37.0	.1180	11.0	1674.64	.00678	.06223	.10887	.52743
37.0- 38.0	.1230	14.0	1573.61	.00920	.06701	.13726	.54479
38.0- 39.0	.1285	12.0	1471.61	.00844	.06882	.12261	.53569
39.0- 40.0	.1345	17.0	1373.74	.01285	.07605	.16899	.56561
40.0- 41.0	.1410	22.0	1273.15	.01802	.08430	.21375	.59782
41.0- 42.0	.1482	19.0	1170.22	.01695	.08663	.19565	.58437
42.0- 43.0	.1563	37.0	1073.11	.03641	.10987	.33138	.70309
43.0- 44.0	.1652	36.0	961.46	.03968	.11735	.33817	.71034
44.0- 45.0	.1752	36.0	855.00	.04484	.12722	.35247	.72607
45.0- 46.0	.1865	50.0	752.86	.07185	.15958	.45026	.85554
46.0- 47.0	.1994	62.0	641.82	.10661	.20045	.53183	1.00527
47.0- 48.0	.2142	55.0	525.24	.11651	.21734	.53606	1.01471
48.0- 49.0	.2313	47.0	422.64	.12470	.23363	.53375	1.00993
49.0- 50.0	.2515	43.0	334.58	.14628	.26477	.55248	1.05287
50.0- 51.0	.2755	26.0	256.75	.11411	.24380	.46805	.88505
51.0- 52.0	.3045	26.0	201.20	.14905	.29256	.50946	.96075
52.0- 53.0	.3404	12.0	150.17	.09034	.25054	.36058	.73598
53.0- 54.0	.3859	10.0	116.89	.09808	.27974	.35059	.72486
54.0- 55.0	.4455	15.0	88.36	.20772	.41825	.49664	.93879
55.0- 56.0	.5269	6.0	58.16	.12353	.37182	.33222	.70562
56.0- 57.0	.6449	5.0	40.10	.15555	.45987	.33824	.71307
57.0- 58.0	.8315	4.0	25.32	.21048	.60408	.34844	.72653
58.0- 59.0	1.1719	3.0	13.84	.32696	.88698	.36863	.75689
59.0- 60.0	--	1.0	5.70	.10000	.57000	.17544	--

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Fig. 2 A demonstration of the concept of length cohort analysis. Catch is assumed to be taken at the middle of a length interval (solid lines). Dashed line indicates catch is taken continuously over the length interval.

Fig. 3 A demonstration of the consequence of using smaller (solid lines) and larger (dashed lines) sized length intervals in LCA.

Fig. 4 Relative error ratio of $N(l)$ corresponding to the use of different sized Δl. From upper to lower curves: Δl= 9mm, 7mm, 5mm, and 3mm. Right-hand side of dashed lines indicates the length intervals where $M\Delta t(l)>0{\cdot}3$.

Fig. 5 Relative error ratio of $F\Delta t(l)$ corresponding to the use of different sized Δl. From upper to lower curves: Δl=3mm, 5mm, 7mm, and 9mm.

Fig. 6 The 95% confidence interval for $N(l)$ with $V(L_\infty)=7{\cdot}053$ and $V(K)=0{\cdot}00017$. The solid line is the estimated $N(l)$ and dashed lines are the 95% confidence interval.

Fig. 7 The 95% confidence interval of $F\Delta t(l)$ with $V(L_\infty)=7{\cdot}053$ and $V(K)=0{\cdot}00017$. The solid line is the estimated $N(l)$ and dashed lines are the 95% confidence interval.

Fig. 8 The values of the derivatives of $N(\iota)$ with respect to L_∞, K, and $L_\infty K$. The solid line is $|\partial N/\partial L_\infty|$, the dashed line is $|\partial N/\partial K|$, and the dotted line is $|\partial^2 N/\partial L_\infty \partial K|$.

Fig. 9 The values of $(\partial N/\partial L_\infty)^2 V(L_\infty)$ (dashed line) and $V[N(\iota)]$ (solid line).

Fig. 10 Relative error ratio of $N(\iota)$ as M takes the values 0·1, 0·2, 0·7, 0·8, 0·9, and 1·0 (from lower to upper curves), while $F(\lambda)$ is fixed.

Fig. 11 Relative error ratio of $F\Delta t(\iota)$ as M takes the values 0·1, 0·2, 0·7, 0·8, 0·9, and 1·0 (from upper to lower curves), while $F(\lambda)$ is fixed.

Fig. 12 Relative error ratio of $N(\iota)$ as $F(\lambda)$ takes the values 0·01, 0·05, 0·2, 0·3, 0·5, and 1·0 (from upper to lower curves), while M is fixed.

Fig. 13 Relative error ratio of $F\Delta t(\iota)$ as $F(\lambda)$ takes the values 0·01, 0·05, 0·2, 0·3, 0·5, and 1·0 (from lower to upper curves), while M is fixed.

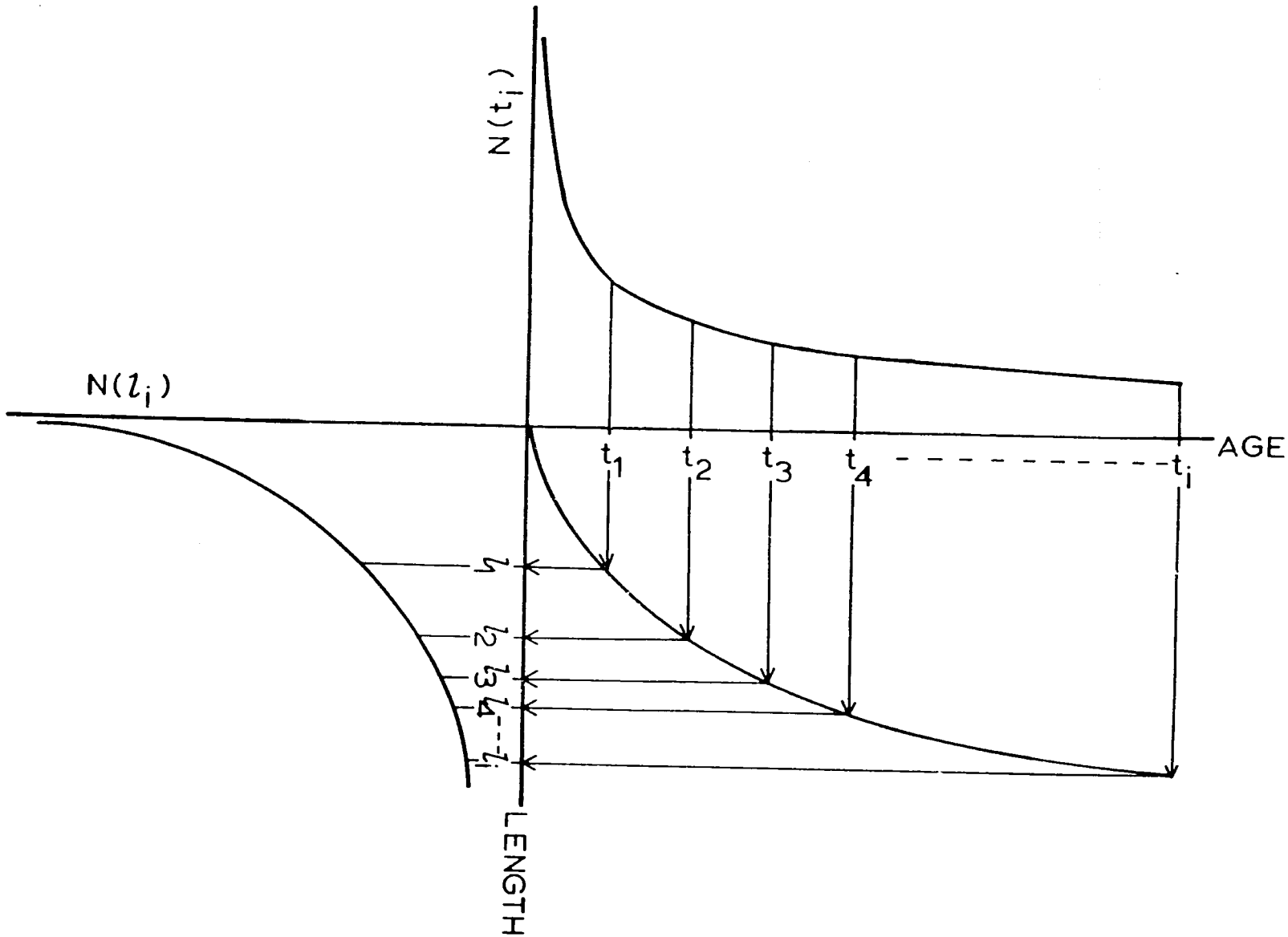

Fig. 1 A demonstration of how age and length of a cohort are related.

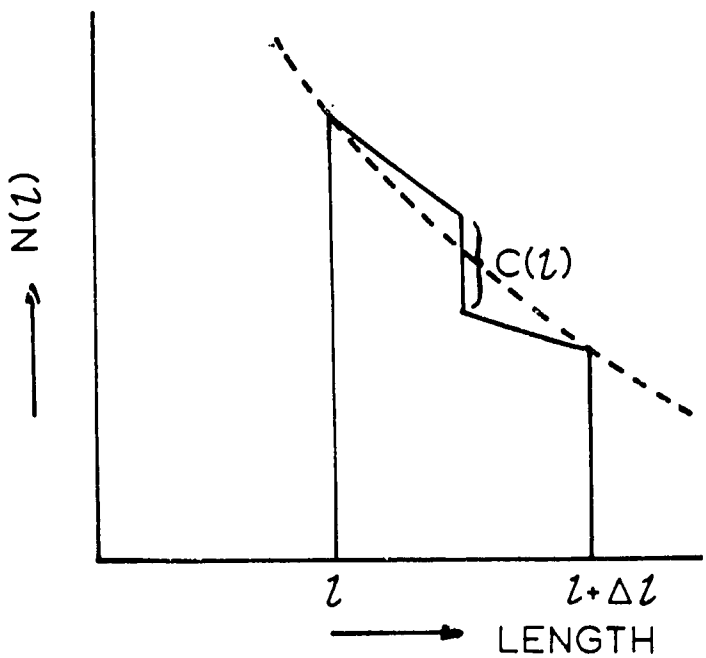

Fig. 2 A demonstration of the concept of length cohort analysis. Catch is assumed to be taken at the middle of a length interval (solid lines). Dashed line indicates catch is taken continuously over the length interval.

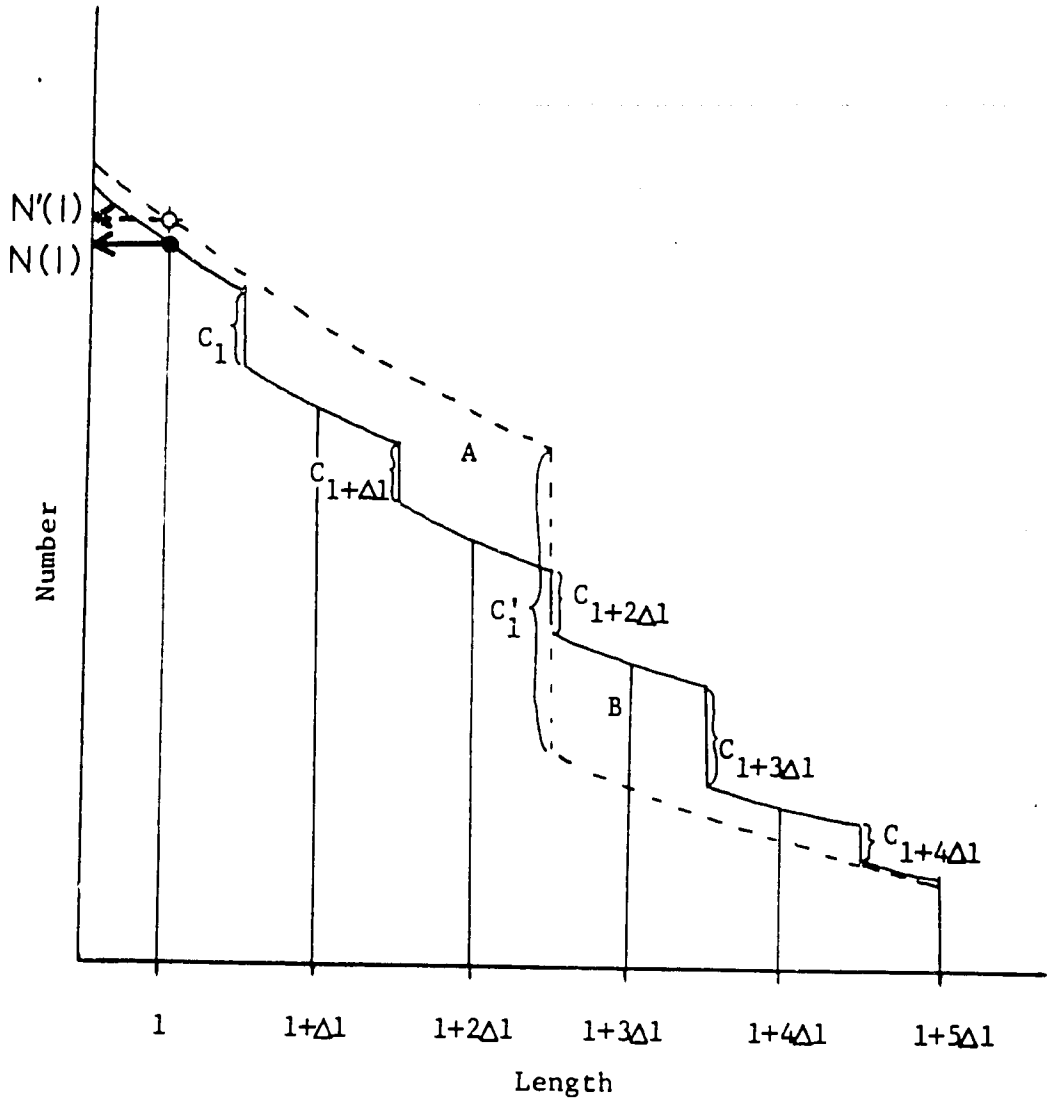

Fig. 3 A demonstration of the consequence of using smaller (solid lines) and larger (dashed lines) sized length intervals in LCA.

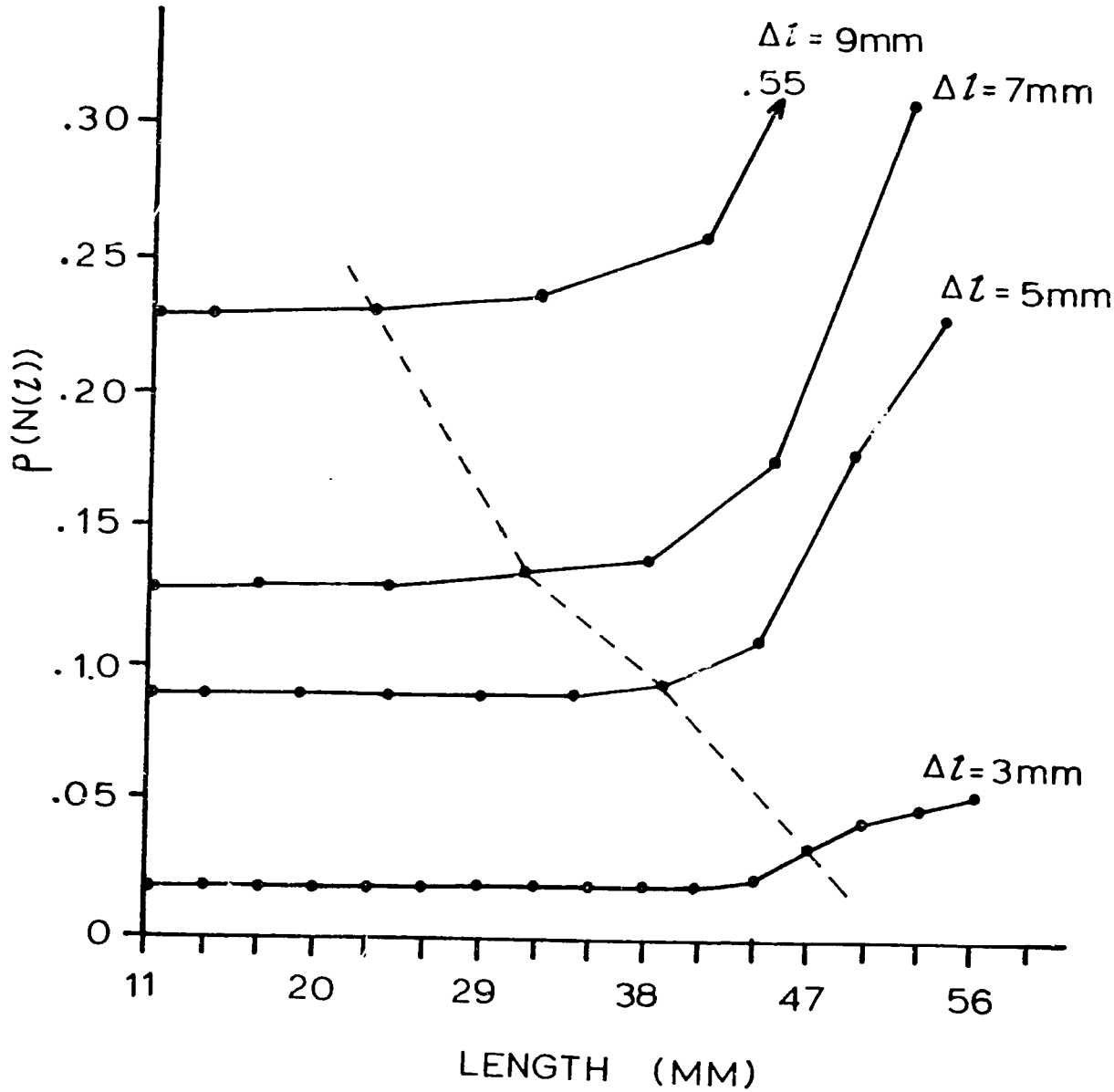

Fig. 4 Relative error ratio of N(l) corresponding to the use of different sized Δl. From upper to lower curves: Δl= 9mm, 7mm, 5mm, and 3mm. Right-hand side of dashed lines indicates the length intervals where $M\Delta r(l)>0.3$.

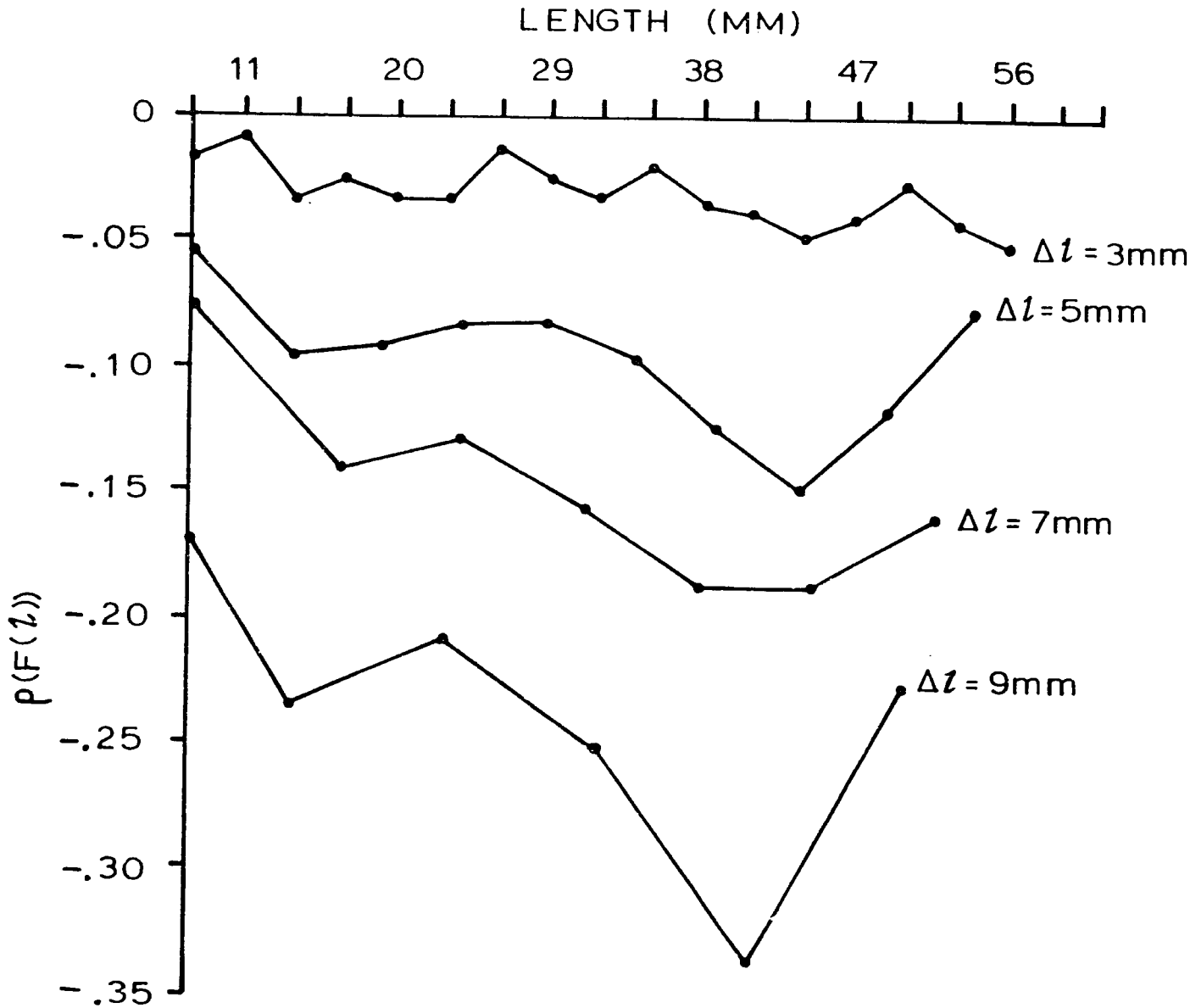

Fig. 5 Relative error ratio of $F\Delta l(l)$ corresponding to the use of different sized Δl. (From upper to lower, Δl=3mm, 5mm, 7mm, and 9mm)

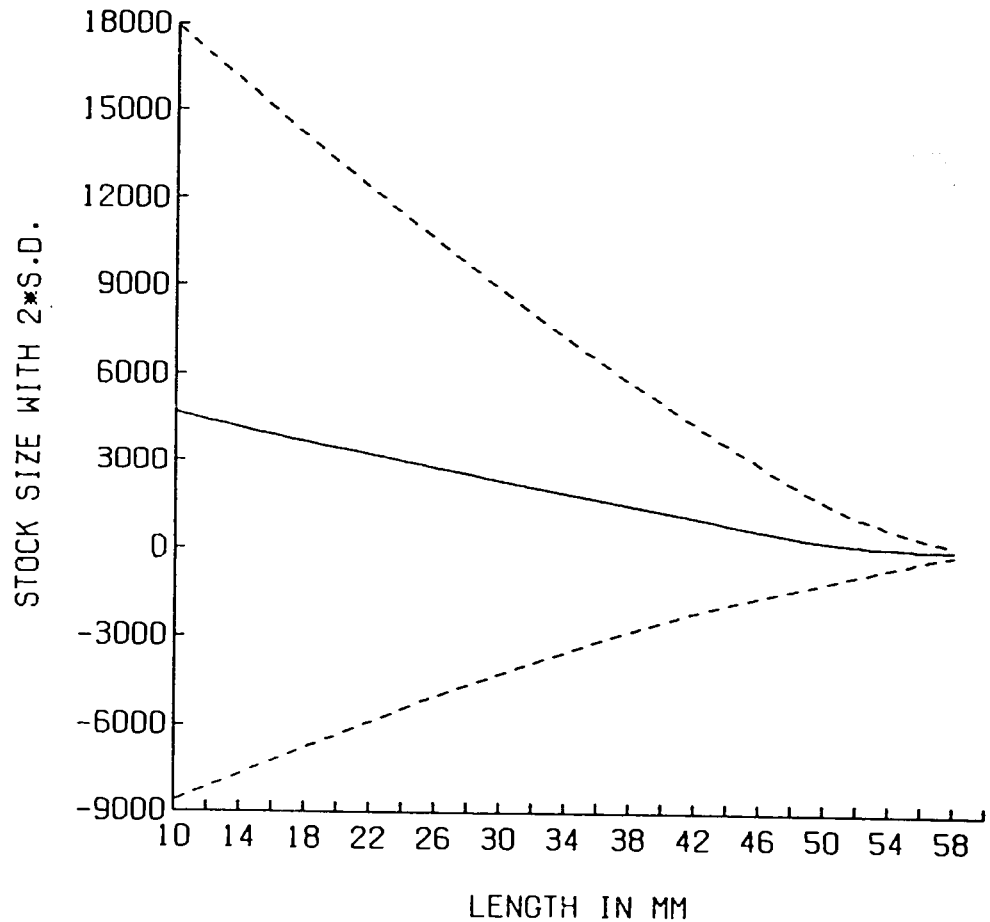

Fig. 6 The 95% confidence interval for N(l) with $V(L_\infty)=7{\cdot}053$ and $V(K)=0{\cdot}00017$.

The solid line is the estimated N(l) and dashed lines are the 95% confidence interval.

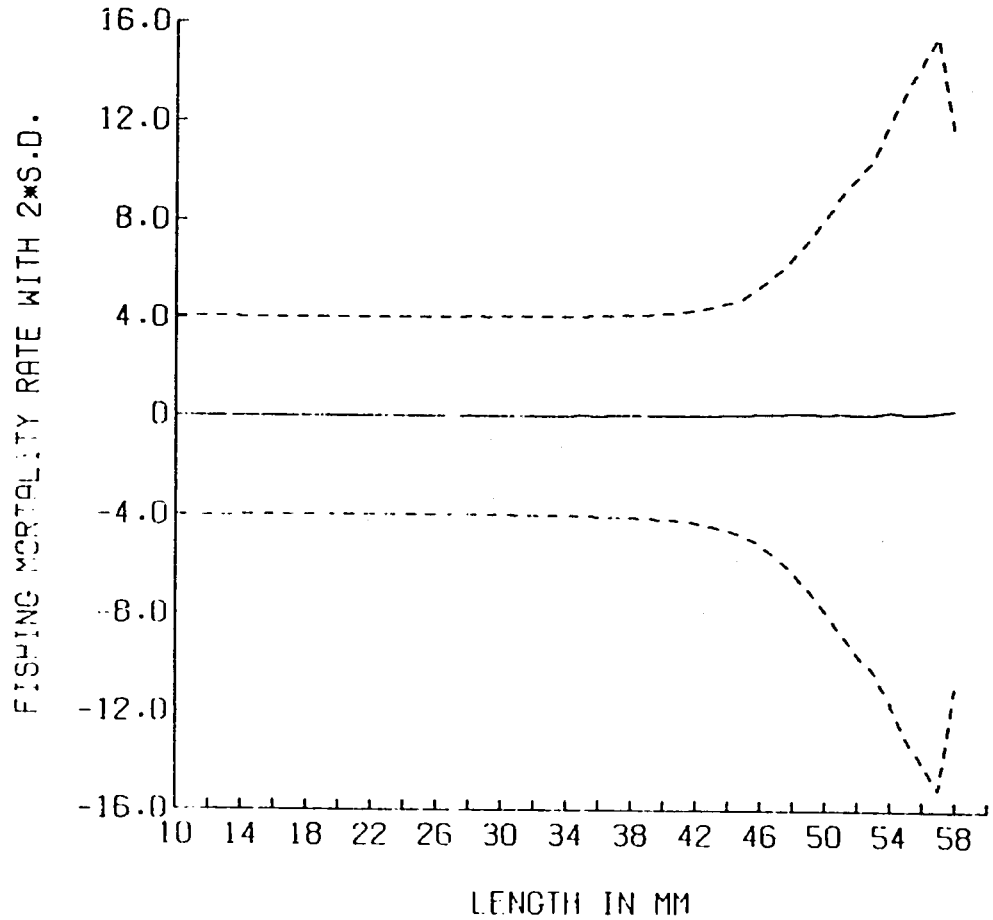

Fig. 7 The 95% confidence interval of $F\Delta t(l)$ with $V(L_\infty)=7{\cdot}053$ and $V(K)=0{\cdot}00017$.

The solid line is the estimated $N(l)$ and dashed lines are the 95% confidence interval.

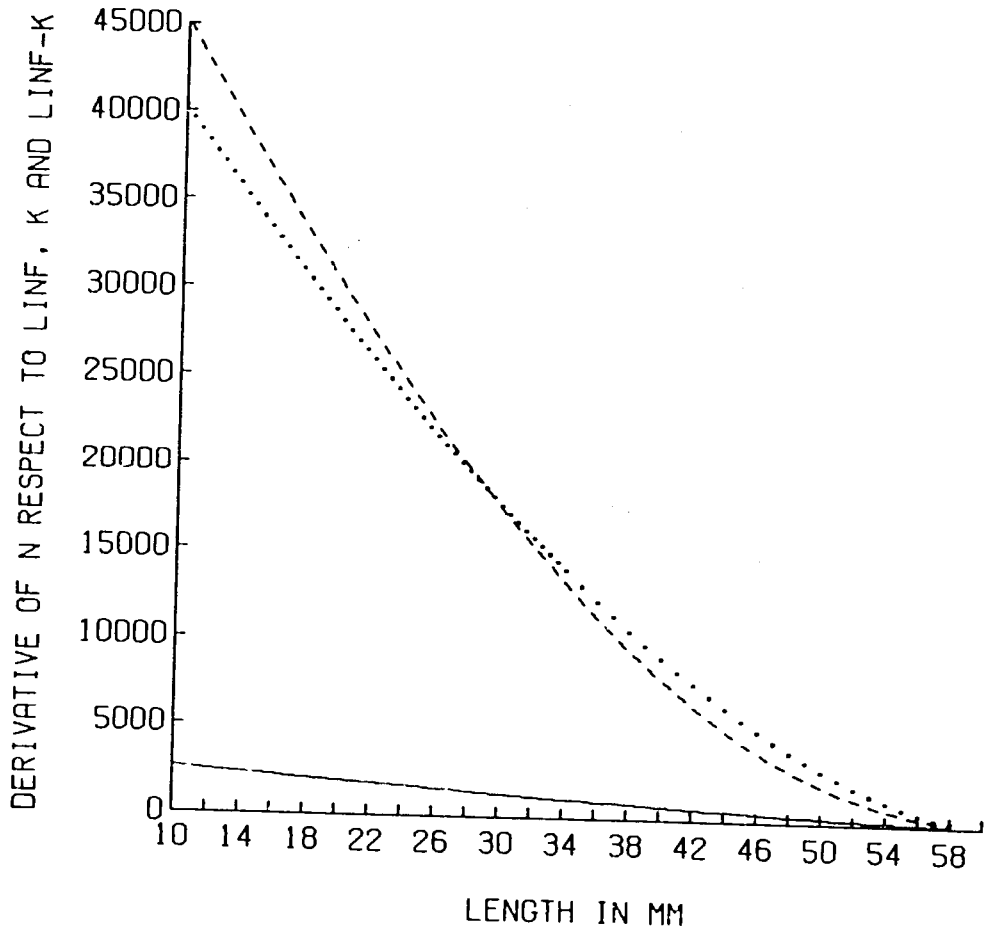

Fig. 8 The values of the derivatives of N(t) with respect to L_∞, K, and $L_\infty K$. The solid line is $|\partial N/\partial L_\infty|$, the dashed line is $|\partial N/\partial K|$, and the dotted line is $|\partial^2 N/\partial L_\infty \partial K|$.

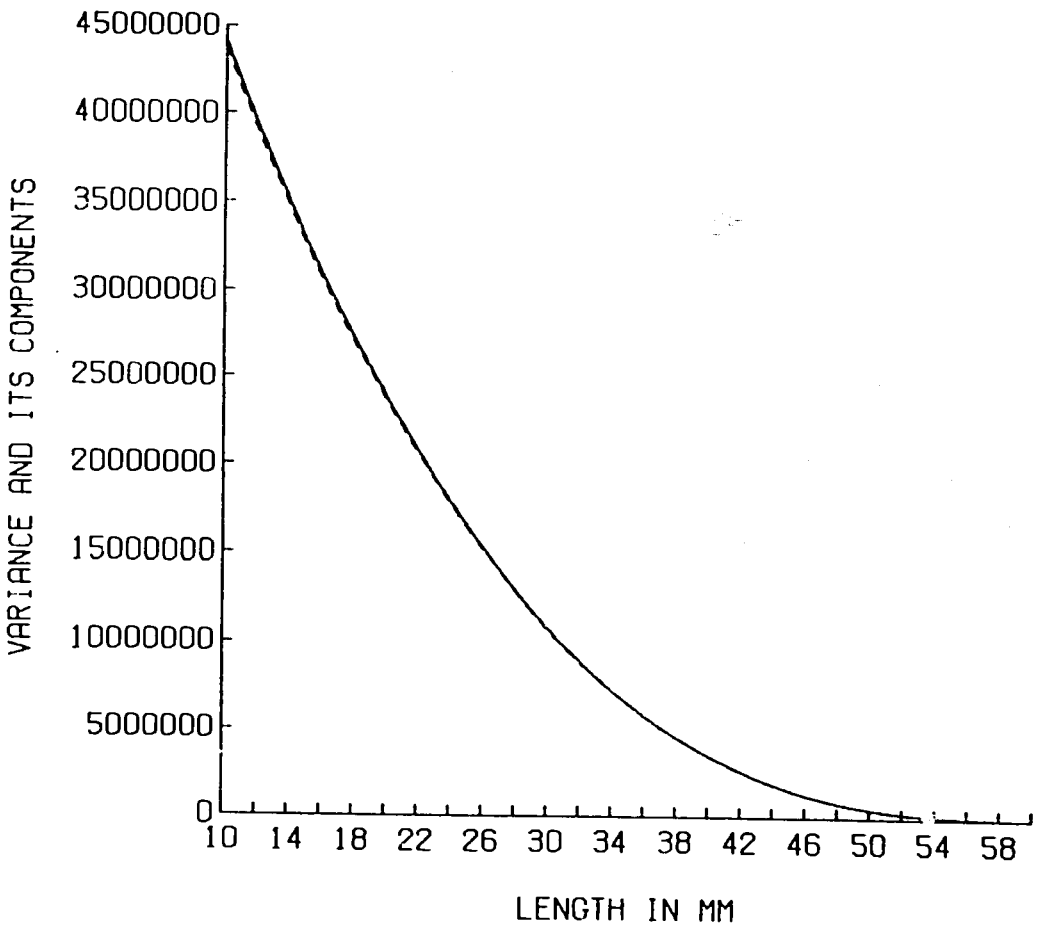

Fig. 9 The values of $(\partial N/\partial L_\infty)^2 V(L_\infty)$ (dashed line) and $V[N(t)]$ (solid line).

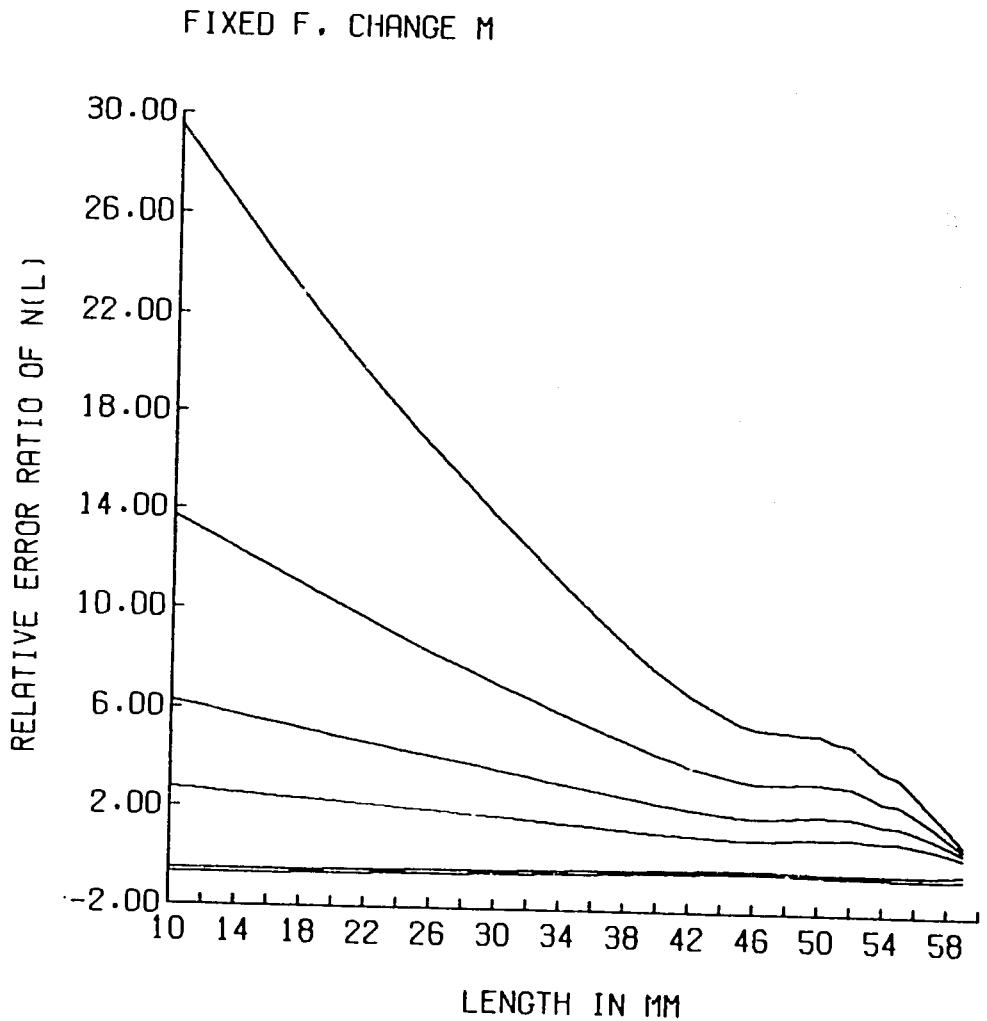

Fig. 10 **Relative error ratio of N(l) as M takes the values 0·1, 0·2, 0·7, 0·8, 0·9, and 1·0 (from lower to upper curves), while F(λ) is fixed.**

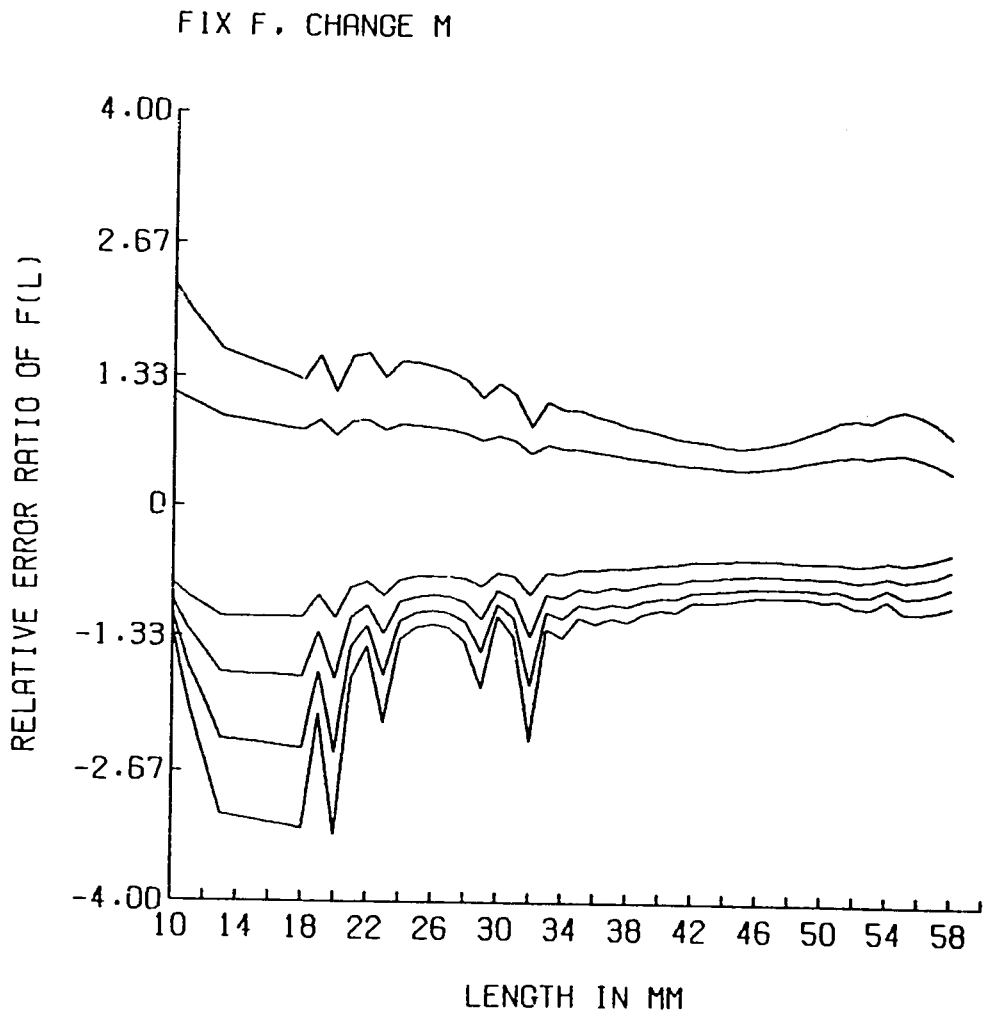

Fig. 11 Relative error ratio of $F\Delta t(t)$ as M takes the values 0·1, 0·2, 0·7, 0·8, 0·9, and 1·0 (from upper to lower curves), while $F(\lambda)$ is fixed.

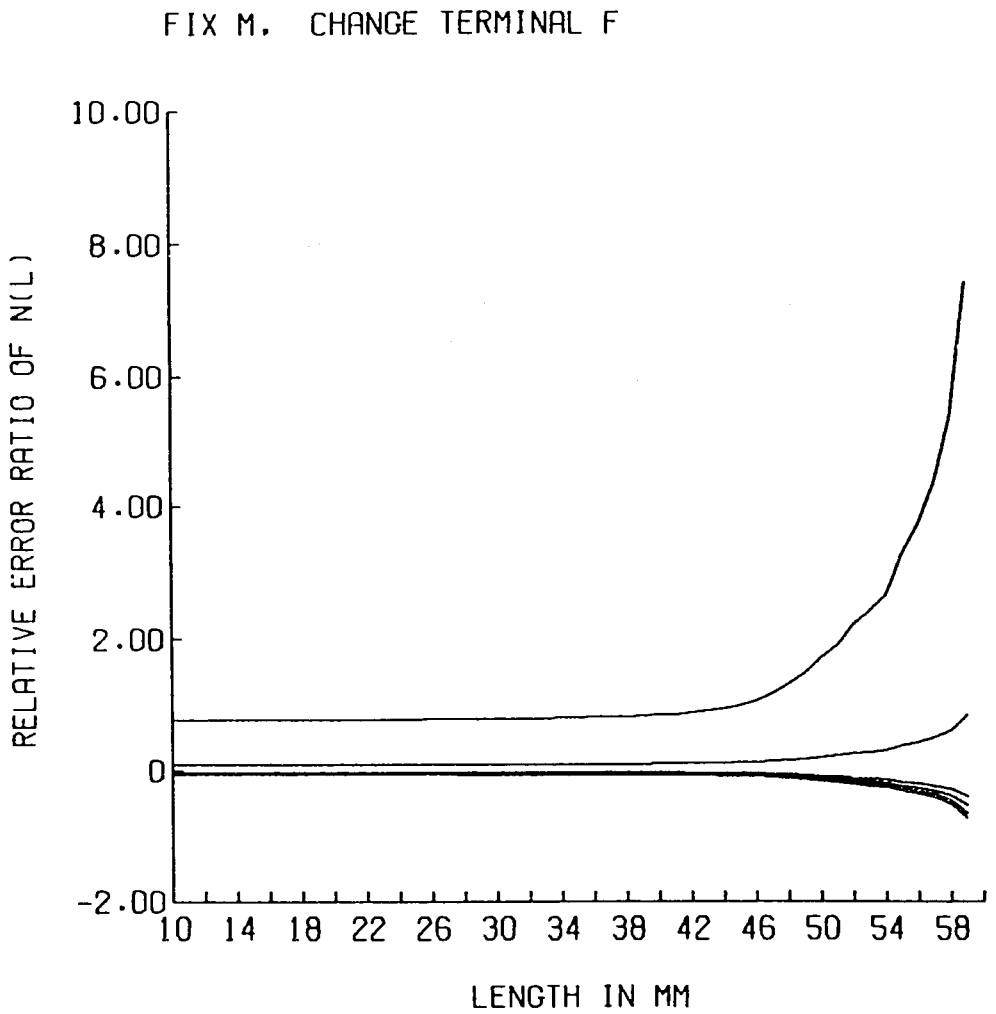

Fig. 12 **Relative error ratio of N(l) as F(λ) takes the values 0·01, 0·05, 0·2, 0·3, 0·5, and 1·0 (from upper to lower curves), while M is fixed.**

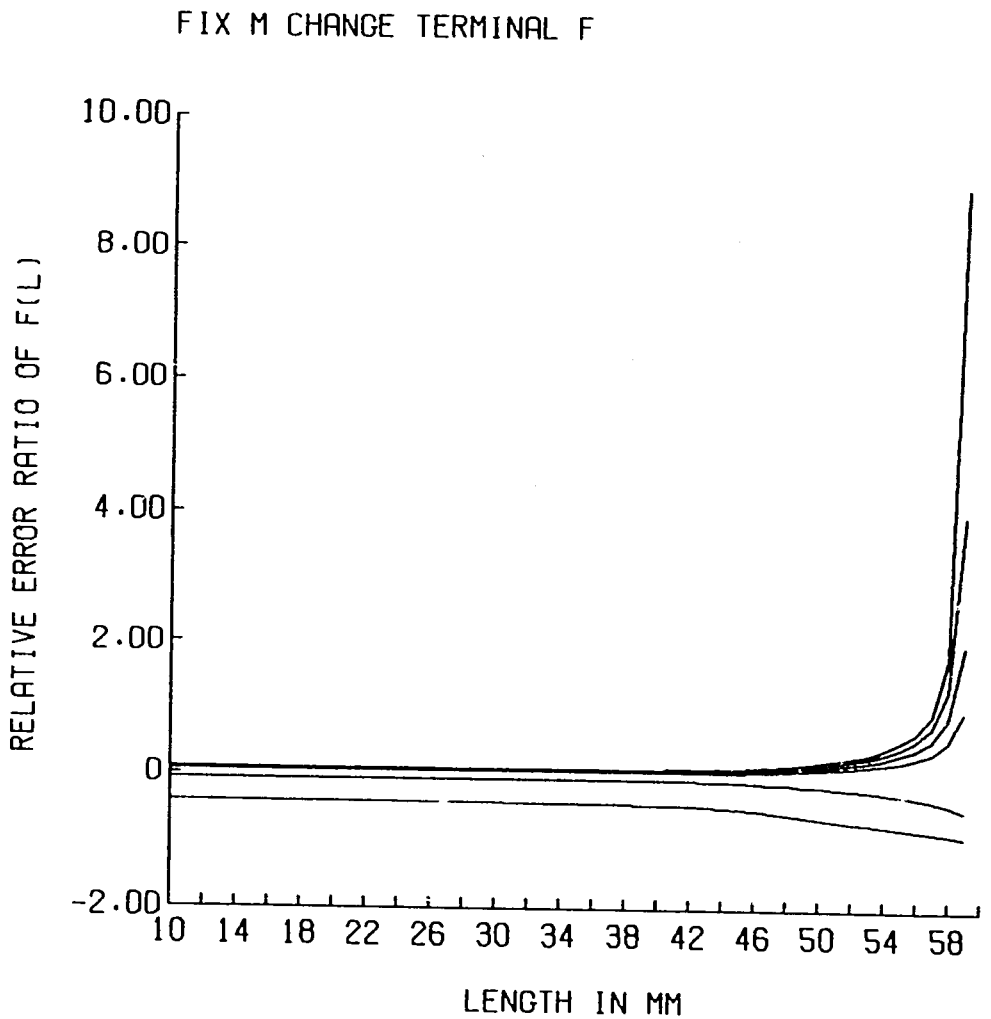

Fig. 13 **Relative error ratio of $F\Delta t(l)$ as $F(\lambda)$ takes the values 0·01, 0·05, 0·2, 0·3, 0·5, and 1·0 (from lower to upper curves), while M is fixed.**