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"Effects of Parameter Variability
on Length-Cohort Analysis"
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Effects of parameter variability on length-cohort analysis

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The equations of length-cohort analysis are used to derive analytical expressions for the errors in stock abundance (N_i) and fishing mortality ($F_i\Delta t_i$) that would result from: (i) the use of different-sized length intervals (Δl) in length-frequency histograms of catch. (ii) the use of incorrectly guessed natural mortality rates (M). and (iii) the use of incorrectly guessed terminal fishing (F_i) mortality rates. Further, the variances of N_i and $F_i\Delta t_i$ are derived as a function of the estimated variances of the von Bertalanffy growth parameters. L_∞ and K. Together. these analytical results allow the prediction. in terms of the estimates from a length-cohort analysis. of the consequences of incorrectly guessed and/or noisy values of M. F_λ, L_∞, K. and different Δl. The results are applied to a bivalve fishery on *Protothaca staminea* in Garrison Bay. Washington. The results show that the estimated N_i and $F_i\Delta t_i$ are extremely sensitive to variation in M. For example. a difference of ±0.1 in the estimate of M leads to a 40 % to 50 % error in the estimates. Relatively low variances in the von Bertalanffy parameters result in coefficients of variation that range from 80 % to 140 % for N_i and from 270 % to 7160 % for $F_i\Delta t_i$.

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Introduction

Virtual Population Analysis (Gulland. 1965) and its approximation. Cohort Analysis (Pope. 1972). are standard techniques for stock assessment when historical catch-at-age data are available. Jones (1979, 1984) proposed a length-cohort analysis (LCA) in which length-frequency data are used to construct a synthetic cohort when information about growth and mortality is available but age data are not. It is assumed that the length-frequency distribution of a catch (made up of many year classes) at any time is representative of the catch from one cohort over the years in the fishery. i.e.. that a steady state prevails. It is also assumed that individuals grow according to a von Bertalanffy curve. Just as in Pope's Cohort Analysis. the computation in LCA proceeds inversely starting with the largest animals in a length-frequency histogram. i.e.. the terminal length interval (λ. L_∞). and proceeding stepwise over all length intervals (l. l+Δl) to the smallest fully recruited size in the catch. l_c. An LCA (see Jones. 1979. 1984; Lai and Gallucci. 1987a) estimates the stock sizes attaining terminal length λ and lengths l using

$$N_\lambda = C_\lambda Z_\lambda / F_\lambda \qquad (1)$$

and

$$N_l = N_{l+\Delta l} A_l^{M/K} + C_l A_l^{M/2K} \qquad (2)$$

and the corresponding fishing mortality over each length interval (l. l+Δl)

$$F_l\Delta t_l = \ln(N_l/N_{l+\Delta l}) - M\Delta t_l \qquad (3)$$

where

C_l = the catch in number assumed to occur at the middle of the length interval (l. l+Δl).

C_λ = the catch in number in the terminal length interval (λ. L_∞).

N_l = the stock size at the beginning of the length interval (l. l+Δl).

N_λ = the stock size attaining length λ.

A_l = $(L_\infty - l)/[L_\infty - (l+\Delta l)]$.

Δt_l = the time required for a fish to grow from length l to l+Δl. and

$$= \frac{1}{K} \ln A_l \quad \text{(See Gulland. 1969).}$$

L_∞ and K = von Bertalanffy growth parameters.

F_λ = the instantaneous fishing mortality rate in the terminal length interval (λ. L_∞).

M = the instantaneous natural mortality rate assumed constant over all lengths.

$F_l \Delta t_l$ = the fishing mortality in length interval $(l, l+\Delta l)$, and

$Z_l \Delta t_l$ = the total mortality in length interval $(l, l+\Delta l)$.

Lai and Gallucci (1987a) derive a catch equation in length

$$C_l = N_l \frac{F_l}{Z_l} (1 - A_l^{-Z/K})$$

of which (1) is a special case when $l = \lambda$ and all of the larger lengths are compressed into the interval (λ, L_x) and where, as a consequence, $A_\lambda^{-Z/K} = 0$. Pope (1972) uses a similar expression based on the Baranov catch equation to cover the case where older ages are compressed into the last age group. Equation (2) is the canonical equation of LCA and can be derived by analogy with Pope's Cohort Analysis (Jones, 1979, 1984) or analytically (Lai and Gallucci, 1987a). Equation (3) is a restatement of $Z_l = F_l + M$ for $l_c \leq l \leq \lambda$.

The input parameters are: (i) M, (ii) F_λ, (iii) the size of the length interval Δl (not necessarily equal) which is used to group catch data in a length-frequency histogram, and (iv) L_x and K which are used to transform age into length. Since input parameters are frequently difficult to estimate and may be no more than guesses, it is important to know how the estimated N_l and $F_l \Delta t_l$ respond to errors. The principal contributions of this paper are the mathematical derivation of the relative error estimators $\varrho[N_l]$ and $\varrho[F_l \Delta t_l]$ for each type of error and the derivation of theoretical variance estimators for N_l and $F \Delta t_l$. It is shown that the estimates of N_l in any LCA may have an unexpectedly large coefficient of variation. The use of the estimators is demonstrated with a bivalve population. *Protothaca staminea*, found in Garrison Bay in northern Puget Sound in the Pacific Northwest of the USA.

Methods

The sensitivity of a model to parameter error or variation can be investigated analytically or with a simulation study. In a simulation the parameters of interest are assigned an allowable range of values, the model is run for suitable combinations of values, and patterns are sought in the output. In this paper, the sensitivity of the model is evaluated analytically using expressions derived for the relative error ratios and the variances of the model's output, N_l and $F_l \Delta t_l$.

1. Derivation of expressions to investigate the effects of changing the size of the length interval

The current guideline for the choice of the size of interval Δl for the length-frequency histogram is that it must provide a number of individuals in each Δl that is

not too small (Jones, 1984). Simultaneously, it is also true that the precision of an LCA increases with smaller Δl. Thus, the optimal choice of Δl is a balance between two guidelines.

Let the length-frequency data be grouped into a histogram with equal intervals of size Δl, and let C_l be the catch in number within length interval $(l, l+\Delta l)$. We examine the consequence of combining the C_l from n individual units of Δl into a new larger length interval $(l, l+n\Delta l)$. Catch in the old and the new (denoted with a prime) length interval is related by

$$C_l' = \sum_{i=0}^{n-1} C_{l+i\Delta l}. \tag{4}$$

The corresponding estimate of abundance follows from (2),

$$N_l' = N_{l+n\Delta l}' \alpha_l^{M/K} + C_l' \alpha_l^{M/2K} \tag{5}$$

where:

$$\alpha_l = \prod_{i=0}^{n-1} A_{l+i\Delta l}.$$

The input parameters M, F_λ, L_x, and K are constant for the old and new length-frequency distributions. Constant F_λ implies that the new and old terminal length interval (λ, L_x) is not changed, so $N_\lambda' = N_\lambda$.

The relationship between N_l and $N_{l-n\Delta l}$ is found by using (2) n times to calculate

$$N_{l+\Delta l} = N_{l+2\Delta l} A_l^{M/K} + C_{l+\Delta l} A_{l+\Delta l}^{M/2K}$$

which is substituted into (2) again and then $N_{l+2\Delta l}$ is written in terms of $N_{l+3\Delta l}$, etc., until

$$N_l = N_{l+n\Delta l} \alpha_l^{M/K} + \sum_{i=0}^{n-1} C_{l+i\Delta l} A_{l+i\Delta l}^{M/2K} \left[\frac{L_x - l}{L_x - (l+i\Delta l)} \right]^{M/K}$$

$$= N_{l+n\Delta l} \alpha_l^{M/K} + \sum_{i=0}^{n-1} C_{l+i\Delta l} \beta_{l+i\Delta l}^{M/2K} \tag{6}$$

where,

$$\beta_{l+i\Delta l} = \frac{(L_x - l)^2}{[L_x - (l+i\Delta l)]\{L_x - [l+(i+1)\Delta l]\}}.$$

After some algebraic manipulation, the relative error of N_l is defined by $\varrho[N_l] = \Delta N_l/N_l$, where $\Delta N_l = N_l' - N_l =$ (5) − (6), becomes

$$\Delta N_l = (N_{l+n\Delta l}' - N_{l+n\Delta l}) \alpha_l^{M/K} + \sum_{i=0}^{n-1} C_{l+i\Delta l} (\alpha_l^{M/2K} - \beta_{l+i\Delta l}^{M/2K}). \tag{7}$$

Division of both sides of (7) by

$$N_l = N_{l+n\Delta l} \prod_{i=0}^{n-1} A_{l+i\Delta l}^{Z_{l+i\Delta l}/K}$$

yields the relative error

$$\varrho[N_l] = \varrho[N_{l+n\Delta l}] \prod_{i=0}^{n-1} A_{l+i\Delta l}^{-F_{l+i\Delta l}/K} +$$

$$+ \frac{1}{N_l} \sum_{i=0}^{n-1} C_{l+i\Delta l} (\alpha_l^{M/2K} - \beta_{l+i\Delta l}^{M/2K}) \qquad (8)$$

in which the second term dominates since the magnitude of the first term decreases as the number of intervals n increases.

The relative error of fishing mortality $\varrho[F_l \Delta t_l]$ in length interval (l, l+nΔl) is defined by

$$\varrho[F_l \Delta t_l] = \frac{\Delta F_l \Delta t_l}{\sum_{i=0}^{n-1} F_{l+i\Delta l} \Delta t_{l+i\Delta l}}.$$

Since $\Delta t_l' = \Sigma \Delta t_{l+i\Delta l}$ and M is a constant,

$$\Delta F_l \Delta t_l = F_l' \Delta t_l' - \sum_{i=0}^{n-1} F_{l+i\Delta l} \Delta t_{l+i\Delta l}$$

$$= (F_l' \Delta t_l' + M \Delta t_l') - \Sigma(F_{l+i\Delta l} + M) \Delta t_{l+i\Delta l}$$

$$= \Delta Z_l \Delta t_l$$

$$= \ln\left(\frac{N_{l+n\Delta l}'}{N_l'}\right) - \ln\left(\frac{N_{l+n\Delta l}}{N_l}\right)$$

$$= \ln\left[\frac{1 + \varrho[N_{l+n\Delta l}]}{1 + \varrho[N_l]}\right].$$

Therefore, the relative error of $F_l \Delta t_l$ is a function of $\varrho[N_l]$ and $\varrho[N_{l+n\Delta l}]$,

$$\varrho[F_l \Delta t_l] = \ln\left(\frac{1 + \varrho[N_{l+n\Delta l}]}{1 + \varrho[N_l]}\right) \Big/ \sum_{i=0}^{n-1} F_{l+i\Delta l} \Delta t_{l+i\Delta l}. \qquad (9)$$

2. Derivation of expressions to investigate the effects of errors in natural and terminal fishing mortalities

If the "correct" natural mortality rate is M and the terminal fishing mortality rate is F_λ, N_l is calculated using (2). Unfortunately, M and F_λ are usually based on only vague impressions of the resource's dynamics, but both parameters are necessary inputs into any LCA model.

When a value different from the "correct" M, say M', is chosen, N_l' is calculated with (2)

$$N_l' = N_{l+\Delta l}' A_l^{M'/K} + C_l A_l^{M'/2K}. \qquad (10)$$

To find ΔN_l, let $\Delta M = M' - M$ and subtract (2) from (10),

$$\Delta N_l = (N_{l+\Delta l}' A_l^{M'/K} - N_{l+\Delta l} A_l^{M/K}) + C_l A_l^{M/2K} (A_l^{\Delta M/2K} - 1).$$

The addition and subtraction of $N_{l+\Delta l} A_l^{M'/K}$ and rearrangement yields

$$\Delta N_l = A_l^{M/K}[\Delta N_{l+\Delta l} A_l^{\Delta M/K} + N_{l+\Delta l}(A_l^{\Delta M/K} - 1)] +$$

$$+ C_l A_l^{M/2K}(A_l^{\Delta M/2K} - 1).$$

The relative error $\varrho[N_l] = \Delta N_l/N_l$ follows from dividing the RHS by $N_l = N_{l+\Delta l} A_l^{Z/K}$;

$$\varrho[N_l] = A_l^{-F_l/K} \varrho[N_{l+\Delta l}] A_l^{\Delta M/K} + A_l^{-F_l/K}(A_l^{\Delta M/K} - 1) +$$

$$+ \frac{C_l}{N_l} A_l^{M/2K}(A_l^{\Delta M/2K} - 1).$$

Substitution of

$$\frac{C_l}{N_l} A_l^{M/2K} = 1 - A_l^{-F_l/K}$$

and simplification yields,

$$\varrho[N_l] = \varrho[N_{l+\Delta l}](A_l^{-F_l/K})(A_l^{\Delta M/K}) +$$

$$+ (A_l^{-F_l/K})(A_l^{\Delta M/K} - 1) + (A_l^{\Delta M/2K} - 1)(1 - A_l^{-F_l/K}),$$

which is further simplified by expanding and rearranging the second and the third terms:

$$\varrho[N_l] = \varrho[N_{l+\Delta l}](A_l^{-F_l/K})(A_l^{\Delta M/K}) +$$

$$+ (A_l^{\Delta M/2K} - 1)(1 - A_l^{F_l/K} A_l^{\Delta M/2K}). \qquad (11)$$

When a value different from the "correct" F_λ, say F_λ', is chosen in addition to the incorrectly chosen M', the error is introduced directly into $\Delta N_\lambda = N_\lambda' - N_\lambda$, where $N_\lambda' = C_\lambda Z_\lambda'/F_\lambda'$ and $Z_\lambda' = M' + F_\lambda'$. The relative error of N_λ, $\varrho(N_\lambda)$, is obtained by dividing ΔN_λ by (1):

$$\varrho[N_\lambda] = \frac{Z_\lambda' F_\lambda}{Z_\lambda F_\lambda'} - 1 = \frac{1 + \varrho[Z_\lambda]}{1 + \varrho[F_\lambda]} - 1 \qquad (12)$$

where $\varrho[Z_\lambda] = Z_\lambda'/Z_\lambda - 1$ and $\varrho[F_\lambda] = F_\lambda'/F_\lambda - 1$.

Substitution of (12) into (11) and proceeding backward, step by step, from length λ to an arbitrary l (over a total of n length groups), yields the equation for $\varrho[N_l]$:

$$\varrho[N_i] = \varrho[N_\lambda](\alpha_i^{\Delta M/K})\left(\prod_{i=0}^{n-1} A_{i+i\Delta i}^{-F_{i+i\Delta i}/K}\right) +$$

$$+ \sum_{i=0}^{n-1}\left[(A_{i+i\Delta i}^{\Delta M/2K} - 1)(1 + A_{i+i\Delta i}^{-2F_{i+i\Delta i}+\Delta M/2K}) \times\right.$$

$$\left. \times \left(\prod_{j=0}^{i} A_{i+j\Delta i}^{-F_{i+j\Delta i}/\Delta M/K}\right)\right] \tag{13}$$

where $A_{i+j\Delta i}^{-F_{i+j\Delta i}/K} = 1$ when $j = i = 0$. This equation has the following implications:

(i) When the "correct" M is input with F', it follows that $\Delta M = 0$, $\alpha_i^{\Delta M/K} = 1$, $A_{i+i\Delta i}^{\Delta M/2K} - 1 = 0$, and the second term vanishes.

(ii) Then, the relative error $\varrho[N_i]$ depends on the sign of ΔF, in $\varrho[N_i]$; $\varrho[N_i]$ will decrease as LCA proceeds from λ to l_c and converges to an asymptotic value.

(iii) When the "correct" F, is input with M', it follows that $\varrho[N_i] = \varrho[Z_i]$ from (12). The signs of $\varrho[N_i]$ and $\varrho[N_i]$ depend on the sign of ΔM. If $\Delta M < 0$, two terms of the RHS of (13) are also negative and decrease in absolute value as i and j increase. If $\Delta M > 0$, $\alpha_i^{\Delta M/K} > 1$, the decrease due to the second component in the first term will not be as effective as in the case of $\Delta M < 0$. When $\Delta M > 0$, $\varrho[N_i]$ grows exponentially, mainly owing to the first term, as I decreases.

The relative error ratio of $F_i\Delta t_i$ is computed as

$$\varrho[F_i\Delta t_i] = (F_i'\Delta t_i - F_i\Delta t_i)/F_i\Delta t_i$$

$$= [(Z_i'\Delta t_i - Z_i\Delta t_i) - \Delta M\Delta t_i]/F_i\Delta t_i$$

$$= \left[-\ln\left(\frac{N_i'}{N_{i+\Delta i}'}\right) + \ln\left(\frac{N_i}{N_{i+\Delta i}}\right)\right]/F_i\Delta t_i - \frac{\Delta M}{F_i}$$

$$= \frac{1}{F_i\Delta t_i}\ln\left(\frac{N_i N_{i+\Delta i}'}{N_i' N_{i+\Delta i}}\right) - \frac{\Delta M}{F_i}$$

$$= \frac{1}{F_i\Delta t_i}\ln\left(\frac{1 + \varrho[N_{i+\Delta i}]}{1 + \varrho[N_i]}\right) - \frac{\Delta M}{F_i}. \tag{14}$$

3. Derivation of expressions to investigate errors due to variation of L_x and K

Length-cohort analysis assumes that the growth of all individuals follows the deterministic von Bertalanffy growth model in which there is a unique theoretical one-to-one relationship between length and age. In reality, variation in individual growth can be viewed as a stochastic process expressed in terms of probability density functions of the growth parameters L_x and K (Sainsbury, 1980). When age or tag data are available, one can estimate the variation of L_x and K with the

estimated covariance matrix (Gallucci and Quinn, 1979). When these data are not available, the LCA still requires values of L_x and K, except that now they must be chosen based on experience. In either case, L_x and K can be viewed as random variables with means $E(\dot{L}_x)$ and $E(\dot{K})$ and variances $V(\dot{L}_x)$, $V(\dot{K})$, and $Cov(\dot{L}_x,\dot{K})$. Since the estimated $\dot{N}_i$ is an analytic function of $\dot{L}_x$ and $\dot{K}$, it can be expanded in the neighborhood of the point $[E(\dot{L}_x),E(\dot{K})]$ using the Delta method (Seber, 1973) to find the variance of $\dot{N}_i$,

$$Var(\dot{N}_i) = \left(\frac{\partial N_i}{\partial L_x}\right)^2 V(\dot{L}_x) + \left(\frac{\partial N_i}{\partial K}\right)^2 V(\dot{K}) +$$

$$+ 2\left(\frac{\partial^2 N_i}{\partial L_x \partial K}\right) Cov(\dot{L}_x,\dot{K}). \tag{15}$$

Note that the $Var(\dot{N}_\lambda)$ is zero since (1) contains neither $\dot{L}_x$ nor $\dot{K}$.

The abundance N_i can be written as a function of L_x, K, and N_λ by rewriting (6) as

$$\dot{N}_i = \dot{N}_\lambda \alpha_i^{M/K} + \sum_{i=0}^{n-1} C_{i+i\Delta i}\beta_{i+i\Delta i}^{M/2K} \tag{16}$$

where $\lambda = l+n\Delta l$. The derivatives of N_i in (15) with respect to L_x and K are derived in Appendix A. Using the notation of Φ's and θ's in Appendix A, (15) is rewritten as

$$V(\dot{N}_i) = \left(\dot{N}_\lambda \Phi_{L_x} + \sum_{i=0}^{n-1} C_{i+i\Delta i}\theta_{L_x}\right)^2 V(\dot{L}_x) +$$

$$+ \left(\dot{N}_\lambda \Phi_K + \sum_{i=0}^{n-1} C_{i+i\Delta i}\theta_K\right)^2 V(\dot{K}) +$$

$$+ 2\left(\dot{N}_\lambda \Phi_{L_x,K} + \sum_{i=0}^{n-1} C_{i+i\Delta i}\theta_{L_x,K}\right) Cov(\dot{L}_x,\dot{K}). \tag{17}$$

To obtain a corresponding variance for the estimates of F_i from LCA, the instantaneous fishing mortality rate is summed over each length interval (l, l+Δl), and $F_i\Delta t_i$ is written as

$$F_i\Delta t_i = Z_i\Delta t_i - M\Delta t_i = \ln\dot{N}_i - \ln\dot{N}_{i+\Delta i} - (M/K)\ln A_i.$$

The variance is found by expanding with the Delta method.

$$V(F_i\Delta t_i) = V(\ln\dot{N}_i) + V(\ln\dot{N}_{i+\Delta i}) + \left(\frac{\partial H_i}{\partial L_x}\right)^2 V(\dot{L}_x) +$$

$$+ \left(\frac{\partial H_i}{\partial K}\right)^2 V(\dot{K}) + 2\left(\frac{\partial^2 H_i}{\partial L_x \partial K}\right) Cov(\dot{L}_x,\dot{K}) \tag{18}$$

where: $H_i = (M/\hat{K})\ln A_i$, $V(\ln \hat{N}_i) = V(\hat{N}_i)/\hat{N}_i^2$, and $V(\ln \hat{N}_{i+\Delta i}) = V(\hat{N}_{i+\Delta i})/\hat{N}_{i+\Delta i}^2$. The derivatives of H_i with respect to $\hat{L}_\infty$ and $\hat{K}$ are given in Appendix A. Note that the coefficients of the covariance term in (17) and (18) are negative and are also found in Appendix A.

$$\hat{L}_\infty = 61.0 \text{ mm}, \quad V(\hat{L}_\infty) = 7.053,$$
$$\hat{K} = 0.346, \quad V(\hat{K}) = 0.00017,$$
$$M = 0.2, \text{ and } F_\lambda = 0.1.$$

Results

The dynamics and management of the bivalves in Garrison Bay have been under investigation for about a decade. The environment, the bivalves, and the management scheme are described in Scherba and Gallucci (1976), Gallucci and Rawson (1979), Gallucci and Gallucci (1982), Gallucci (1985), Orensanz and Gallucci (1988), and Gallucci and Lai (in prep.). One of the bivalves, *Protothaca staminea*, is a venerid hard-shell clam harvested commercially and recreationally along most of the Pacific coast of North America. The bivalve is found in the shallow subtidal and intertidal regions and is thus subject to heterogeneous environments.

Tagging experiments and other analysis in Garrison Bay provided the following estimates:

Parameters estimated from this long-term experiment are considered the "correct" values and are used with 1979 catch data in an LCA to generate the N_i and $F_i\Delta t_i$ estimates in Table 1. The analysis was done with $\Delta l = 1$ mm using the program "LCAN" (Lai and Gallucci, 1987b). The program is for an IBM-PC and compatibles and is available from the authors. These N_i and $F_i\Delta t_i$ are the basis for computing the relative errors from different choices of M and F_λ and from the use of Δl-values greater than 1 mm. The variances of N_i and $F_i\Delta t_i$ are computed using the above-noted variances of L_∞ and $\hat{K}$.

Table 1 contains the estimates of N_i and $F_i\Delta t_i$ using "LCAN" on the catch data with $\Delta l = 1$ mm. These estimates show expected abundances in all the size classes, and they show a relatively major increase in $F_i\Delta t_i$ (and thus $Z_i\Delta t_i$) around 48 mm, which is in fact the dominant harvested size. The estimates of N_i and $F_i\Delta t_i$ are considered the "correct" values against which estimates de-

Table 1. The results of a length-cohort analysis on *Protothaca staminea* using 1979 catch data.

Length (l) (mm)	Δt_i (yr)	Catch (C_i)	Abundance (N_i)	$F_i\Delta t_i$	$Z_i\Delta t_i$	F_i/Z_i	Z_i (yr^{-1})
29–30	0.0918	8	47688				
30–31	0.0948	8	46813	0.00017	0.01852	0.00914	0.20184
31–32	0.0980	5	45926	0.00017	0.01913	0.00902	0.20182
32–33	0.1014	25	45030	0.00011	0.01971	0.00558	0.20112
33–34	0.1051	50	44101	0.00056	0.02084	0.02691	0.20553
34–35	0.1091	49	43134	0.00115	0.02217	0.05171	0.21091
35–36	0.1134	17	42155	0.00115	0.02296	0.05004	0.21054
36–37	0.1180	66	41193	0.00041	0.02308	0.01768	0.20360
37–38	0.1230	85	40167	0.00162	0.02522	0.06434	0.21375
38–39	0.1285	170	39107	0.00214	0.02675	0.08019	0.21744
39–40	0.1345	170	37947	0.00441	0.03011	0.14657	0.23435
40–41	0.1410	95	36772	0.00455	0.03144	0.14474	0.23385
41–42	0.1482	126	35656	0.00262	0.03083	0.08511	0.21860
42–43	0.1563	221	34490	0.00359	0.03324	0.10808	0.22424
43–44	0.1652	348	33212	0.00653	0.03778	0.17281	0.24179
44–45	0.1752	997	31790	0.01071	0.04375	0.24478	0.26483
45–46	0.1865	998	29716	0.03243	0.06748	0.48062	0.38513
46–47	0.1994	1796	27648	0.03481	0.07212	0.48267	0.38666
47–48	0.2142	2188	24806	0.06855	0.10845	0.63207	0.54386
48–49	0.2313	2861	21625	0.09440	0.13727	0.68766	0.64090
49–50	0.2515	2411	17851	0.14539	0.19176	0.75822	0.82890
50–51	0.2755	2058	14624	0.14897	0.19938	0.74719	0.79282
51–52	0.3045	1620	11839	0.15612	0.21134	0.73870	0.76722
52–53	0.3404	1420	9568	0.15193	0.21297	0.71338	0.69940
53–54	0.3859	905	7565	0.16652	0.23479	0.70923	0.68973
54–55	0.4455	705	6133	0.13262	0.20995	0.63167	0.54402
55–56	0.5269	854	4936	0.12789	0.21716	0.58893	0.48743
56–57	0.6449	442	3632	0.20092	0.30676	0.65498	0.58215
57–58	0.8315	295	2778	0.13874	0.26803	0.51763	0.41560
58–59	1.1719	171	2081	0.12227	0.28891	0.42322	0.34748
59–L$_\infty$[a]	–	498	1494	0.09654	0.33132	0.29139	0.28273
				0.10000	0.30000	0.33333	–

[a]$L_\infty = 61$ mm.

rived from incorrect, inappropriate, or noisy input parameters Δl, M, F_λ, L_∞, and K are compared.

1. The effects due to changing the size of the length interval, Δl

The data in Table 1 are the result of an LCA with $\Delta l = 1$ mm. The histogram is reconstructed into 3-mm, 5-mm, 7-mm, and 9-mm size intervals and the results from an LCA compared to when $\Delta l = 1$ mm. The grouping of Δl values proceeds in reverse from the group $(\lambda - \Delta l, \lambda)$ to the smallest size group. The error contours in Figure 1 (upper) show that $\varrho[N_i]$ increases rapidly as Δl is increased from 1 mm to 9 mm. The RHS of each curve shows a region of rapidly increasing error to the right of the dashed line which is roughly the locus of points or the left boundary where $M\Delta t_i > 0.3$. This is empirical confirmation of the constraint noted by Pope (1972) that $M\Delta t < 0.3$ when $\Delta t = 1$ yr. On the LHS of the dashed line, the error contours are stable and de-

crease asymptotically to a constant error $\varrho[N_i]$ for any Δl.

Figure 1 (lower) shows that the fishing mortality $F_i'\Delta t_i'$ from the pooled histograms is underestimated as Δl increases except in the length interval $(\lambda - \Delta l, \lambda)$ which precedes (λ, L_∞). The large positive values for $\varrho[F_{\lambda - \Delta l} \Delta t_{\lambda - \Delta l}]$ in all new Δl's are due to the overestimation of $N_{\lambda - \Delta l}$ when large Δl's are used (Fig. 1 (upper)). Note that $N_i' = N_\lambda$ for the terminal length intervals (λ, L_∞). The value of $\varrho[F_i\Delta t_i]$ is seen to oscillate and increase in absolute value for larger Δl.

For the bivalve example, $\Delta l = 3$ mm is probably the largest Δl that could be used for grouping the length-frequency distribution of *Protothaca staminea* because $\varrho[N_i]$ and $\varrho[F_i\Delta t_i]$ are greater than 5 % when a larger Δl is used. It is clear from the contours that the objective should be to retain as many length intervals (Δl) as possible, especially for the sizes on the RHS of the dotted line.
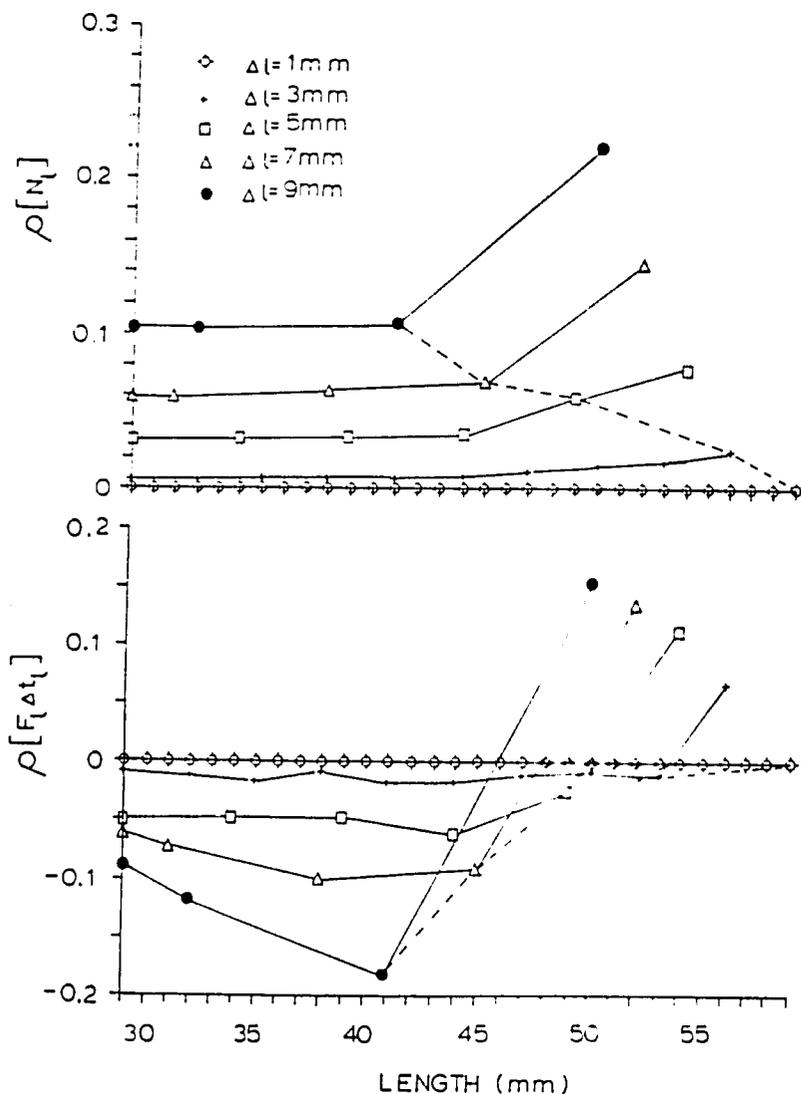

Figure 1. Relative error of N_i and $F_i\Delta t_i$ corresponding to the use of different-sized Δl in the length-frequency histograms. The dashed lines correspond to the region of the plane where $M\Delta t_i > 0.3$, a theoretical upper bound (see results) and thus where relative errors show a large increase. $M = 0.2$ and $F_\lambda = 0.1$.

2. The effects due to errors in the choices of M and F_λ

For this analysis the data in Table 1, based on $M = 0.2$ and $F_\lambda = 0.1$, are considered the "correct" values. We next examine the effects of separately changing M and F_λ. First, fix F_λ and change M to 0.05, 0.1, 0.3, 0.5, and 0.7. When $M = 0.05$ and 0.10, $\Delta M < 0$ and $\varrho[N_i] < 0$. Figure 2 (upper) shows that when $\Delta M < 0$, $\varrho[N_i] \cong -0.5$ (or N_i' is underestimated by about 50% of N_i) and remains constant over all length groups. When $\Delta M > 0$, $\varrho[N_i] > 0$ and increases rapidly as M increases from 0.3 to 0.7. This is due to $\alpha_i^{\Delta M/K}$ being greater than unity and the fact that (12) accumulates the error due to ΔM over all length groups in the LCA.

The direction of $\varrho[F_i\Delta t_i]$ due to changes in M is opposite to that of $\varrho[N_i]$, viz., $\varrho[F_i\Delta t_i] < 0$ when $\Delta M > 0$ and $\varrho[F_i\Delta t_i] > 0$ otherwise (Fig. 2 (lower)). For any M, the value of $\varrho[F_i\Delta t_i]$ increases as length decreases, but the effect is less than that in $\varrho[N_i]$. Poor choices of M are clearly more detrimental to N_i than to $F_i\Delta t_i$.

In Figure 3 (upper), M is fixed and F_λ changed from

0.1 ("correct" value) to 0.01, 0.05, 0.2, 0.3, 0.5, and 1.0; $\varrho[N_i]$ is large at the beginning and then decreases and becomes approximately constant in the 29- to 40-mm range. This is expected because when $\Delta M = 0$, the second term in (13) vanishes and the first term is dominated by its second half. Figure 3 (upper) also shows that $\Delta F_\lambda < 0$ (i.e., $F_\lambda = 0.01$ and 0.05) causes a larger error $\varrho[N_i]$ than does $\Delta F_\lambda > 0$ ($F_\lambda = 0.2, 0.3, 0.5$, and 1.0).

Figure 3 (lower) shows that the direction of $\varrho[F_i\Delta t_i]$ corresponding to ΔF_λ is opposite to the direction of $\varrho[N_i]$. When $\Delta F_\lambda > 0$, $\varrho[N_i] > 0$ and decreases rapidly from a large positive value (at $l = \lambda = 59$ mm) to a value less than 10% (at $l = 29$ mm) and when $\Delta F_\lambda < 0$, $\varrho[N_i] < 0$ and approximately constant.

3. Errors due to the variance of $\hat{L}_\infty$ and $\hat{K}$

The variances of $\hat{L}_\infty$ and $\hat{K}$ of *Protothaca staminea* were estimated from tagging experiments. $Cov(\hat{L}_\infty, \hat{K})$ is not available from the estimation so we assume that Cov
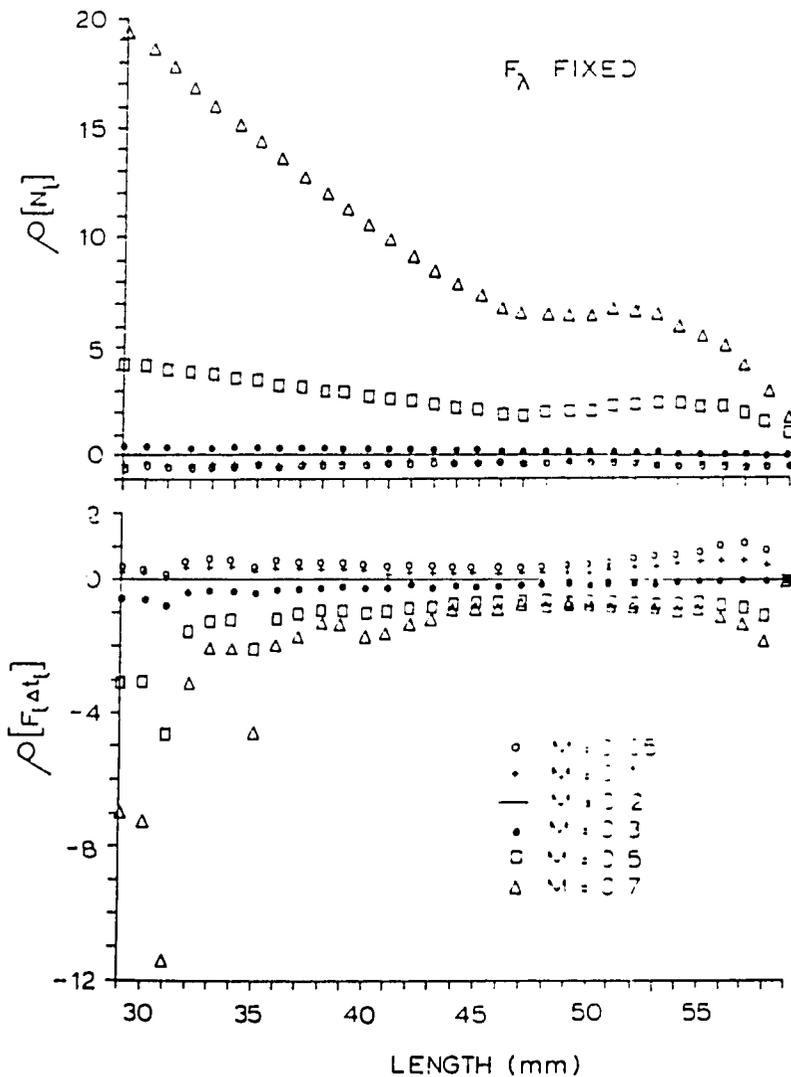

Figure 2. Relative error of N_i and $F_i\Delta t_i$ as M changes from 0.2 (the "correct" value) to 0.05, 0.1, 0.3, 0.5, and 0.7, while F_λ is fixed.
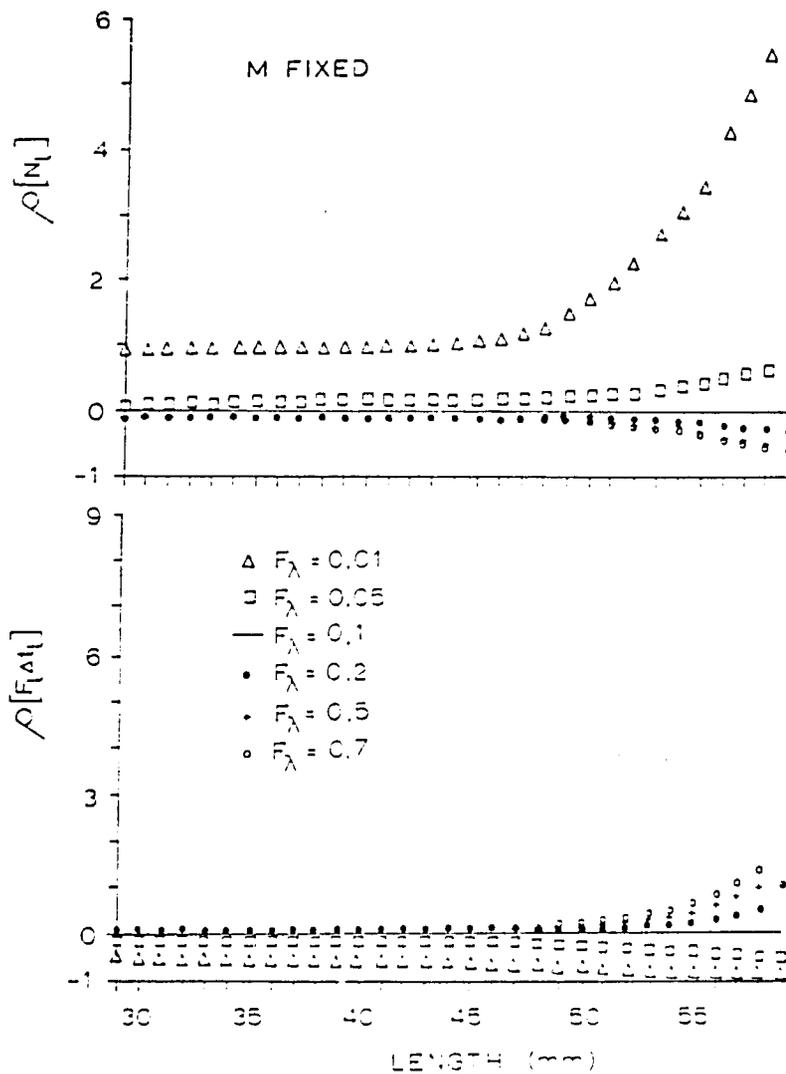
Figure 3. Relative error of N_i and $F_i\Delta t_i$ as F_λ changes from 0.1 (the "correct" value) to 0.01, 0.05, 0.2, 0.5, and 1.0, while M is fixed.

M FIXED

$\Delta \quad F_\lambda = 0.01$
$\square \quad F_\lambda = 0.05$
$— \quad F_\lambda = 0.1$
$\bullet \quad F_\lambda = 0.2$
$\bullet \quad F_\lambda = 0.5$
$\circ \quad F_\lambda = 0.7$

LENGTH (mm)

$(\dot{L}_x, \dot{K}) = 0$ although it is well known that $\dot{L}_x$ and $\dot{K}$ are negatively correlated. Because the coefficients associated with $Cov(\dot{L}_x, \dot{K})$ in (17) and (18) are negative values, our estimates of variances and 95% confidence intervals (95% c.i.) for N_i and $F_i\Delta t_i$ are larger than when $Cov(\dot{L}_x, \dot{K}) \neq 0$ is included. Using $\dot{L}_x = 61.0$ mm, $\dot{K} = 0.346$, $V(\dot{L}_x) = 7.053$, and $V(\dot{K}) = 0.00017$ as the standards from the bivalve example and (17), the 95% c.i. for N_i and $F_i\Delta t_i$ are shown in Figure 4. Figure 4 (upper) shows that the 95% c.i. of N_i increases rapidly as length decreases. In contrast, Figure 4 (lower) shows that the 95% c.i. of $F_i\Delta t_i$ decreases rapidly at first and then becomes approximately constant for $1 < 44$ mm.

The coefficient of variation (c.v.) of N_i decreases from 140% at $1 = 58$ mm to 78% at $1 = 29$ mm; while the c.v. of $F_i\Delta t_i$ decreases from 460% at $1 = 58$ mm to 270% at $1 = 48$ mm and then increases to 7160% at $1 = 29$ mm. These extraordinarily large c.v.'s are a serious concern for the user of an LCA.

In the bivalve case, we find that $|\partial N_i/\partial K|$ is 15 times larger than $|\partial N_i/\partial L_x|^2$ at $1 = 58$ mm but is 210 times larger at $1 = 29$ mm. This indicates that the estimate of $Var(N_i)$ is more sensitive to a unit of change in K than a unit of change in L_x. This can be anticipated because K appears as a power in (2).

Discussion

The results of a length-based cohort analysis are not the end-product in the assessment of a fishery for management purposes. The results are usually used to estimate a potential yield and perhaps to guide decisions about how that yield may be extracted, e.g., with respect to the allowable exploitation pressure that may be put on length or age groups. One of the contributions of this paper is to help clarify the complex question of how variability in the catch data and the variance of the

estimates of the growth parameters combine in the results.

The very high coefficients of variation in these parameters are not unique to the bivalve example but are also found in other organisms, such as the *Nephrops* example in Jones (1979). One of the advantages of the analytical type of investigation over an investigation by simulation is that the cause of the high variance of the estimates of N_l and $F_l\Delta t_l$ can be traced to variation in K, suggesting where to focus attention in the estimation of growth parameters. This sensitivity of the estimates of any LCA to variance in the input parameters is disconcerting and must be of concern whenever an LCA is used to generate estimates of abundance. Perhaps LCA results should be used only as indices to reflect relative changes in abundance.

The sensitivity to L_x and K is of special concern when a specific growth study has not been done and estimates of L_x and K are not available. In such situations, Jones

(1984) suggested choosing the largest fish and Pauly (1983) suggested choosing the largest plus 5%. Whatever is done must be done with the understanding that a unit change in L_x leads to a big change in N_l (i.e., $\partial N_l/\partial L_x$ is very steep). The choice of K is more complicated because K and L_x are inextricably related (Gallucci and Quinn, 1979) and because K cannot be guessed by observation. Since the ratio M/K arises naturally in the formulation of LCA, it is fortunate that M/K is more easily estimated than either M or K alone. It has been suggested that M/K is in the range of 0.8 to 2.2 for most of the fish species in the world (Beverton and Holt, 1959). In the bivalve case, M = 0.2, K = 0.38 and M/K = 0.53, which is out of the suggested range. This implies that guesses of M/K extrapolated from fish to other organisms could be risky.

In the bivalve example, $\Delta l = 3$ mm (instead of 1 mm) introduces about a 1% $\varrho[N_l]$ and a 1% $\varrho[F_l\Delta t_l]$ for $l \le 53$ mm. For $l \ge 56$ mm, there is a 2% $\varrho[N_l]$ and
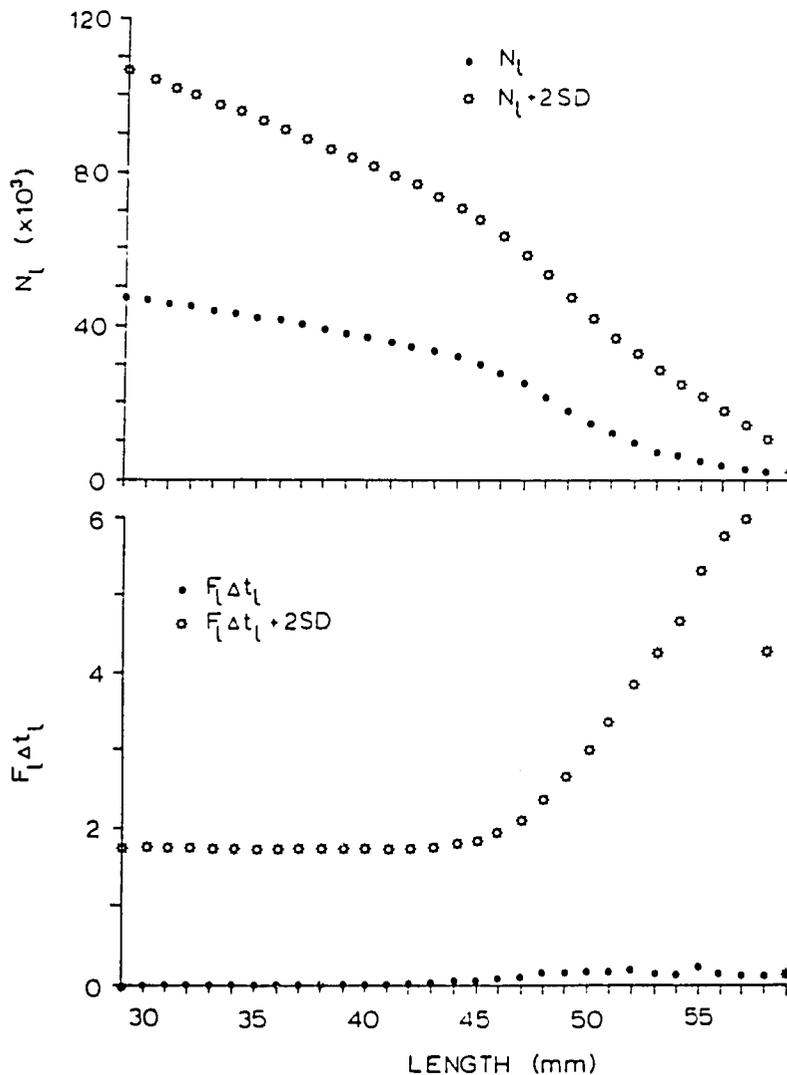

Figure 4. The 95% confidence interval (the lower bound is negative) for N_l and $F_l\Delta t_l$ with $V(L_x) = 7.053$ and $V(K) = 0.00017$.

$\varrho[F_i \Delta t_i]$. The relative errors obviously increase for larger Δl values. The size of Δl is associated with the condition that $M\Delta t_i > 0.3$ (Jones, 1984; Lai and Gallucci, 1987a). This inequality is not satisfied on the RHS of the dashed line in Figure 1 (upper), which may explain the extreme jumps in Figure 1 (lower). Further, to assist in the selection of the size of Δl, the conditions

$$M\Delta t_i \text{ or } \left(\frac{M}{K}\right) \ln A_i < 0.3 \text{ and } F_i \Delta t_i < 1.2$$

should be satisfied (Lai and Gallucci, 1987a).

The relationship between M and F_k is seen in Figures 3 and 4. The relative error in N_i is many times larger when M varies than when F varies, and is in the opposite direction. Thus, the accuracy of an LCA is more sensitive to poorly chosen M- than F_k-values. Sims (1984) found a similar result for Pope's Cohort Analysis.

This work shows that there are consistent patterns in the relative errors of abundance and fishing mortality in Pope's Cohort Analysis and in LCA as a consequence of incorrectly chosen input parameters, except that the relative errors are usually much higher in LCA. Since length-frequency distributions are easily assembled over many years they can be used to evaluate the steady-state assumption by looking for trends or shifts in the modes of either newly recruited or fully recruited animals. Nevertheless, the greater dependence of LCA on a steady state and on the von Bertalanffy growth model suggests that much less faith may be put in the results of LCA than in Pope's Cohort Analysis.

Acknowledgments

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Appendix A

Derivatives of N_i with respect to L_z and K

From Equation (20),

$$N_i = N_i \alpha_i^{M/K} + \sum_{i=0}^{n-1} C_{i+i\Delta i} \beta_{i+i\Delta i}^{M/2K}$$

where $\alpha_i = \prod_{i=0}^{n-1} A_{i+i\Delta i}$, and

$$\beta_{i+i\Delta I} = \frac{(L_x - I)^2}{[L_x - (I + i\Delta I)]\{L_x - [I + (i+1)\Delta I]\}} \cdot$$

It is obvious that $\partial N_i / \partial L_x$, $\partial N_i / \partial K$ and $\partial^2 N_i / \partial L_x \partial K$ are dependent on α_i and β_i. Define the following terms:

$$\Phi_{L_x} = \partial \alpha_i / \partial L_x; \quad \Phi_K = \partial \alpha_i / \partial K; \quad \Phi_{L_x K} = \partial^2 \alpha_i / \partial L_x \partial K;$$

$$\theta_{L_x} = \partial \beta_i / \partial L_x; \quad \theta_K = \partial \beta_i / \partial K; \quad \theta_{L_x K} = \partial^2 \beta_i / \partial L_x \partial K;$$

and $H_i = \left(\dfrac{M}{K} \right) \ln A_i.$

The explicit forms of these variables are

$$\Phi_{L_x} = \left(\frac{M}{K} \right) \alpha_i^{M/K} \left[\frac{1}{L_x - I} - \frac{1}{L_x - (I + n\Delta I)} \right]$$

$$\Phi_K = - \left(\frac{M}{K^2} \right) \alpha_i^{M/K} \ln \alpha_i$$

$$\Phi_{L_x K} = - \left(\frac{1}{K} \right) \Phi_{L_x} \left[1 + \left(\frac{M}{K} \right) \ln \alpha_i \right]$$

$$\theta_{L_x} = \left(\frac{M}{2K} \right) \beta_i^{M/2K} \left(\frac{1}{L_x - I} - \frac{2[L_x - (I + i\Delta I)] + \Delta I}{[L_x - (I + i\Delta I)]\{L_x - [I + (i+1)\Delta I]\}} \right)$$

$$\theta_K = - \left(\frac{M}{2K^2} \right) \beta_i^{M/2K} \ln \beta_i$$

$$\theta_{L_x K} = \theta_{L_x} \beta_i^{-M/2K} \left[\theta_K - \left(\frac{M}{2K^2} \right) \Big/ \beta_i \right]$$

$$\frac{\partial H_i}{\partial L_x} = \frac{\partial \ln(A_i^{M/K})}{\partial L_x} = \left(\frac{M}{K} \right) \left[\frac{1}{L_x - I} - \frac{1}{L_x - (I + \Delta I)} \right]$$

$$\frac{\partial H_i}{\partial K} = \frac{\partial \ln(A_i^{M/K})}{\partial K} = - \left(\frac{M}{K^2} \right) \ln A_i$$

$$\frac{\partial^2 H_i}{\partial L_x \partial K} = \frac{\partial^2 \ln(A_i^{M/K})}{\partial L_x \partial K} = - \left(\frac{M}{K^2} \right) \left[\frac{1}{L_x - I} - \frac{1}{L_x - (I + \Delta I)} \right]$$