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A COMPREHENSIVE REVIEW OF THE YUKON RIVER SALMON TAGGING PROGRAM CONDUCTED BY THE CANADIAN DEPARTMENT OF FISHERIES AND OCEANS

By

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INTRODUCTION

The Canadian Department of Fisheries and Oceans (DFO) has conducted a salmon tagging program on the Yukon River annually since 1982, with the exception of 1984. Chinook salmon (*Oncorhynchus tshawytscha*) and chum salmon (*Oncorhynchus keta*) are captured in fish wheels near the international border between the United States and Canada and are marked with spaghetti tags. All captured fish are sexed, aged, and returned alive to the river. The recovery of tags, as well as the date and location of recoveries, provides valuable information concerning the movements of migrating chinook and chum salmon within the Canadian portion of the Yukon River (Cronkite and Johnston, 1989a; Cronkite and Johnston, 1989b). The specific objectives of the program are many and varied. However, the objectives can be summarized and stated as the goal of providing fishery managers and biologists with annual estimates of population size, exploitation rates, and other parameters critical in managing the complex Yukon River fisheries.

The information provided by the DFO Yukon River tagging program is essential to biologists of both the United States and Canada responsible for the management of Yukon River salmon stocks. However, additional importance is attached to the program in light of the treaty negotiations being held between the United States and Canada concerning joint management and harvest sharing of trans-boundary Yukon River chinook and chum salmon stocks. At the time when an agreement is reached, the DFO tagging program will also be invaluable to both sides in evaluating their compliance with treaty obligations.

The purpose of this document is to provide a thorough review of the methodology currently employed in the DFO tagging program. Although Brannian (1986) conducted a similar review of the program, changes in the methodology employed by the DFO, the increased level of agreement between the treaty negotiating teams, and recent advancements in the analysis of capture-recapture data warrants an additional review.

We begin the review with a summary of two methods of analyzing capture-recapture data. One of the methods is currently employed by the DFO while the other has only been developed relatively recently. The assumptions underlying the two methods are discussed in detail. This discussion is followed by an analysis of the 1987 and 1988 tagging data using the recently developed method. These analyses serve primarily as an illustration of the new estimation procedures and the results obtained are not intended to supersede the results published by the DFO (Cronkite and Johnston, 1989a; Cronkite and Johnston, 1989b). We close the review with an evaluation of the methods and results presented and a list of specific recommendations for future implementations of the DFO Yukon River tagging program.

PARAMETER ESTIMATION

The objectives of the DFO tagging program include the estimation of the population sizes and the exploitation rates, defined here as the number of individuals entering the Canadian portion of the Yukon River and the proportion of the populations harvested in the various Canadian fisheries, respectively, for chinook and fall chum salmon. As these estimates are important to the US/Canada treaty negotiations and the annual management of the Yukon River chinook and fall chum fisheries, the techniques used to obtain the estimates are reviewed in detail. We first present two procedures for obtaining maximum likelihood estimates of the population size. The first of these procedures is currently employed by the DFO (Cronkite and Johnston, 1989a; Cronkite and Johnston, 1989b), while the second procedure is an alternative whose use should be considered. Although the details of the estimation procedures are presented elsewhere, they are included here for completeness and to facilitate the discussion of the procedures that follows their presentation.

Before presenting the procedures, we first introduce notation common to both procedures. Let

N = the number of individuals in the population,

N_i = the number of individuals in the ith stratum, and

S = the number of strata.

The details of the estimation procedures are now presented.

Population Size: Chapman's Single Recapture Model

The DFO is currently using Chapman's estimation procedure, which is also known as the modified Petersen procedure (Ricker, 1987; Seber, 1982). Studies for which the Chapman procedure is appropriate involve two capture events; individuals captured during the first capture event are marked and returned to the population while individuals captured in the second capture event are examined for the presence or absence of marks. The random variables observed during the course of a study are defined as

n_{i1} = the number of individuals belonging to the ith stratum captured and marked in the first capture event,

n_{i2} = the number of individuals belonging to the ith stratum captured in the second capture event, and

m_{i2} = the number of marked individuals belonging to the ith stratum observed during the second capture event.

The Chapman estimation procedure requires a number of assumptions to hold;

1. The population is closed,
2. All individuals within a stratum have an equal probability of capture in the first capture event,
3. Marking does not affect the probability of capture in the second capture event,
4. The individuals belonging to the ith stratum captured in the second capture event constitute a simple random sample from the ith stratum,
5. All recoveries are known, and
6. The strata are independent.

Under the above assumptions, the probability distribution of m_{i2}, given n_1 and n_2, is a hypergeometric distribution (Hogg and Craig, 1978) with parameters N_i, n_1, and n_2. Therefore, given the conditional distribution of m_2, a maximum likelihood estimator of the population size, N, is given by

$$\hat{N} = \sum_{i=1}^{s}\left[\frac{(n_{i1} + 1)(n_{i2} + 1)}{(m_{i2} + 1)} - 1\right]. \tag{1}$$

This estimator is unbiased if $n_{i1} + n_{i2} \geq N_i$ for all i (Seber, 1982). Note that the ith term of equation (1) is an estimator of the ith stratum's sub-population size N_i.

An estimator of the variance of $\hat{N}$, denoted $v(\hat{N})$, is given by

$$v(\hat{N}) = \sum_{i=1}^{s}\left[\frac{(n_{i1} + 1)(n_{i2} + 1)(n_{i1} - m_{i2})(n_{i2} - m_{i2})}{(m_{i2} + 1)^2(m_{i2} + 2)}\right]. \tag{2}$$

Equation (2) is an unbiased estimator under the same conditions in which equation (1) is unbiased (Seber, 1982).

Approximate $(1 - \alpha)100\%$ confidence intervals can be constructed about $\hat{N}$ using two methods. The first method is the usual asymptotic normal approximation (Rao, 1973);

$$\hat{N} \pm z_{(1-\frac{\alpha}{2})}\sqrt{v(\hat{N})}. \tag{3}$$

The second method involves basing confidence intervals upon the conditional distribution of the random variable m_2, for which a number of exact tables and approximations are available (Ricker, 1987). The DFO employs an approximation based upon a poisson approximation to the hypergeometric distribution (Ricker, 1987). A 95% confidence interval is constructed about $\hat{N}_i$ by first obtaining the

95% confidence limits for m_{i2} according to

$$m_{i2} + 1.92 \pm 1.96\sqrt{m_{i2} + 1}. \tag{4}$$

The confidence limits of m_{i2} are then substituted into the ith term of equation (1) to obtain the confidence limits for $\hat{N}_i$. There is no procedure for combining the confidence intervals about the $\hat{N}_i$ into a confidence interval for $\hat{N}$.

General hypotheses concerning the population and sub-population sizes can be conducted using the asymptotic normality of maximum likelihood estimates (Rao, 1973). Such hypotheses tests would be conducted using the procedures found in any introductory statistics text (e.g., Sokal and Rohlf, 1987).

Population Size: A Log-Linear Model

Although log-linear models have been employed in population size estimation for a number of years (e.g., Bishop, Fienberg, and Holland, 1975), a number of recent advancements in their application to population size estimation have been made (Evans, 1989). These advancements have permitted log-linear models and procedures for population size estimation to be expressed in general terms, using compact notation, for the first time.

The applicability of log-linear models to population size estimation is based on the recognition that the expectations of frequencies observed in capture-recapture studies can be expressed as products of the parameters of interest (Bishop et. al., 1975). Let

f_{i10} = the number of individuals belonging to the ith stratum that were captured in the first capture event but were not captured in the second capture event,

f_{i01} = the number of individuals belonging to the ith stratum that were captured in the second capture event but were not captured in the first capture event,

f_{i11} = the number of individuals belonging to the ith stratum that were captured in both capture events,

f_{i00} = the number of individuals belonging to the ith stratum that were not captured in either capture event,

p_{i1} = the probability a member of the ith stratum is captured in the first capture event,

$p_{i2|0}$ = the probability a member of the ith stratum is captured in the second capture event, given it was not captured in the first capture event, and

$p_{i2|1}$ = the probability a member of the ith stratum is captured in the second capture event, given it was captured in the first capture event.

Under the above parameterization, the expectations of the observed frequencies can be expressed as

$$E[f_{i10}] = N_i p_{i1}(1 - p_{i2|1}),$$
$$E[f_{i01}] = N_i(1 - p_{i1})p_{i2|0},$$
$$E[f_{i11}] = N_i p_{i1} p_{i2|1}, \text{ and}$$
$$E[f_{i00}] = N_i(1 - p_{i1})(1 - p_{i2|0}).$$

Note that the expectations are products of the parameters of interest, i.e., probabilities of capture and strata population sizes. As products, the logarithms of the expectations are linear functions of the logarithms of the parameters; i.e.,

$$\ln(E[f_{i10}]) = \ln(N_i) + \ln(p_{i1}) + \ln(1 - p_{i2|1}),$$
$$\ln(E[f_{i01}]) = \ln(N_i) + \ln(1 - p_{i1}) + \ln(p_{i2|0}),$$
$$\ln(E[f_{i11}]) = \ln(N_i) + \ln(p_{i1}) + \ln(p_{i2|1}), \text{ and}$$
$$\ln(E[f_{i00}]) = \ln(N_i) + \ln(1 - p_{i1}) + \ln(1 - p_{i2|0}).$$

These observations form the basis of expressing the above relationship in the form of a log-linear model. Since much of the more recent work is not yet widely available in the literature , and for the sake of completeness, many details available elsewhere are repeated here. The details of the estimation procedure and the form of the estimators are largely adopted from Evans (1989). However, the discussions of Bishop et. al. (1975) are also valuable. In specifying the estimation procedures, it is convenient to use matrix notation, with which we assume the reader is familiar. We also assume the reader is familiar with basic statistical operations performed on random matrices. Seber (1977) provides a good general reference to such operations.

Some additional notation is required to present the log-linear model and the associated estimation procedures. The notation presented is specific to a single recapture study, though the extensions to multiple recapture studies are completely transparent. Let

$f = (f_{111}, f_{110}, f_{101}, f_{211}, \ldots, f_{S10}, f_{S01})'$,

$\beta = (\ln(N_1), \ln(p_{11}), \ln(1-p_{11}), \ln(p_{12|0}), \ln(1-p_{12|0}), \ln(p_{12|1}), \ln(1-p_{12|1}), \ln(N_2), \ldots, \ln(p_{S2|1}), \ln(1-p_{S2|1}))'$,

$$X_i = \begin{matrix} 1 & 1 & 0 & 0 & 0 & 1 & 0 \\ 1 & 1 & 0 & 0 & 0 & 0 & 1 \\ 1 & 0 & 1 & 1 & 0 & 0 & 0, \end{matrix}$$

I_S = an S by S identity matrix,

X = I_S .*. X_i, where .*. denotes the Kronecker product,

θ = $\exp(\beta)$, where exp denotes element-wise exponentiation,

μ = $\exp(X\beta)$,

D_v = a diagonal matrix with the elements of the vector v along the diagonal, and

Σ_v = the covariance matrix of the vector v.

As with the Chapman model, our presentation of the log-linear model requires a number of assumptions to hold;

1. The population is finite,
2. The frequencies f_{i10}, f_{i01}, f_{i11}, and f_{i00} have a multinomial probability distribution,
3. All recoveries are known, and
4. The strata are independent.

Using the above notation, the log-linear relationship presented above can be expressed as

$$\ln(f) = X\beta + \epsilon, \tag{5}$$

where ϵ is an unobservable random (error) vector. Within each stratum, there are seven parameters but only three observations (f_{i10}, f_{i01}, and f_{i11}); that is, the model is over-parameterized. Therefore, in order to obtain unique maximum likelihood estimates, some constraints must be placed on the elements of β. Three constraints within each stratum are obviously desirable; one would wish to constrain $p_{i1} + (1 - p_{i1})$, $p_{i2|0} + (1 - p_{i2|0})$, and $p_{i2|1} + (1 - p_{i2|1})$ to equal 1. As the model parameters are the logarithms of the probabilities, these are nonlinear constraints. Additional constraints are needed. Unfortunately, the most logical constraint is to equate $p_{i2|0}$ and $p_{i2|1}$; this is equivalent to introducing assumption 3 of the Chapman procedure. These constraints can be expressed as

$$R\theta = r, \tag{6}$$

and

$$A\beta = a, \tag{7}$$

where

$$R_i = \begin{matrix} 0 & 1 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 & 1, \end{matrix}$$

$R = I_S \;.\!*\!.\; R_i$,

$r =$ a 3*S by 1 vector of ones,

$A_i = (0\ 0\ 0\ 1\ 0\ 1\ 0)$,

$A = I_S \;.\!*\!.\; A_i$, and

a = an S by 1 vector of zeros.

Note that the above constraints are placed on the parameters within strata, i.e., the constraints preserve the independence of the strata. Additional constraints, within or between strata, are formed by modifying the elements of R, r, A, and a. The constraints are placed upon the model by adding a negative term to the likelihood function;

$$- c(R\theta - r) - c(A\beta - a), \tag{8}$$

where c is a large positive constant (Evans, 1989).

Maximum likelihood estimates of β are obtained using the Newton-Raphson algorithm

$$\beta_i = \beta_{i-1} + P_{i-1}^{-1} G_{i-1} \tag{9}$$

(McCormick, 1983). The matrix G_{i-1} is the gradient, i.e., the matrix of the first partial derivatives of the modified likelihood function with respect to β, evaluated at β_{i-1} and P is the hessian, i.e., the matrix of the second partial derivatives of the modified likelihood function with respect to β, evaluated at β_{i-1};

$$\begin{aligned} G_{i-1} &= X'(f - \mu_{i-1}) - cD_\theta R'(R\theta_{i-1} - r) - cA'(A\beta_{i-1} - a). \\ P_{i-1} &= X'D_\mu X + cD_\theta R'RD_\theta + cA'A , \end{aligned} \tag{10}$$

where $\theta_{i-1} = \exp(\beta_{i-1})$ and $\mu_{i-1} = \exp(X\beta_{i-1})$ (Evans, 1989).

The iterative process of equation (10) is started with an initial guess, β_0, and is repeated until the difference between successive updates β_i and β_{i-1} is minimal. Upon termination of the iteration, the vector β_i is taken to be the maximum likelihood estimate and is denoted $\hat{\beta}$. The parameter vector of interest, θ, is estimated as

$$\theta = \exp(\beta). \tag{11}$$

A vector of the estimated strata sub-population sizes, denoted $\tilde{N}$, can be extracted from $\hat{\theta}$ as

$$\tilde{N} = (I_S .*. W_1)\theta, \tag{12}$$

where W_1 is a 1 by 7 vector with a 1 in the first position and zeros elsewhere. The estimate of the population size is then

$$\hat{N} = 1'_S \tilde{N}, \tag{13}$$

where 1_S is an S by 1 vector of ones.

The within stratum frequencies (f_{i10}, f_{i01}, f_{i11}, and f_{i00}) are assumed to be multinomial random variables. This assumption permits specification of the variance of f. The estimated covariance matrix of f, $\hat{\Sigma}_f$, is a block diagonal matrix with each block consisting of the covariance matrix of a multinomial vector, i.e., the ith block is given by $\hat{\Sigma}_{fi}$, where

$$\Sigma_{fi} = D_{\mu_i} - \left(\frac{1}{\hat{N}_i}\right)\mu_i \mu'_i \tag{14}$$

and $\hat{\mu}_i$ is the ith sub-vector of $\hat{\mu} = \exp(X\hat{\beta})$ pertaining to the ith stratum (Agresti, 1990).

The estimated covariance matrices of $\hat{\beta}$, $\hat{\theta}$, $\tilde{N}$, and the variance of $\hat{N}$ are derived from $\hat{\Sigma}_f$;

$$\hat{\Sigma}_\beta = P^{-1}X'\hat{\Sigma}_f XP^{-1}, \tag{15}$$

$$\hat{\Sigma}_\theta = D_\theta \hat{\Sigma}_\beta D_\theta, \tag{16}$$

$$\hat{\Sigma}_{\tilde{N}} = (I_S \;.*.\; W_1)\hat{\Sigma}_\theta(I_S \;.*.\; W_1)', \tag{17}$$

and

$$v(\hat{N}) = 1'_S\hat{\Sigma}_{\tilde{N}}1_S. \tag{18}$$

(Evans, 1989).

Hypothesis tests, concerning both β (linear hypotheses) and θ (non-linear hypotheses), can be conducted. Linear hypotheses of the form

$$H\beta = h \tag{19}$$

and non-linear hypotheses of the form

$$H\theta = h \tag{20}$$

can be tested using a Wald test statistic, denoted W. In the linear case, the Wald test statistic is given by

$$W = (H\hat{\beta} - h)'(H\hat{\Sigma}_{\beta}H')^{-1}(H\hat{\beta} - h), \tag{21}$$

while in the non-linear case the Wald test statistic is given by

$$W = (H\hat{\theta} - h)'(H\hat{\Sigma}_{\theta}H')^{-1}(H\hat{\theta} - h). \tag{22}$$

In both the linear and non-linear case, the Wald test statistic is asymptotically distributed as a chi-squared random variable with degrees of freedom equal to the rank of the hypothesis matrix H (Agresti, 1990). If hypotheses concerning β and θ are non-significant, parameter estimates under the "reduced" model can be obtained by vertically concatenating the constraint matrices (R and/or A) with the hypothesis matrices (H) and the constraint vectors (r and/or a) with the hypothesis vectors (h).

Exploitation Rates

Although a primary objective of the DFO tagging program is the estimation of population size, other parameters characterizing the population are also of interest. Examples include sex and age composition, migration rates, and exploitation rates. Currently, estimates of these parameters are computed by treating the observed data as a single sample from the population (Cronkite and Johnston, 1989a; Cronkite and Johnston, 1989b). However, estimates of these parameters are most properly computed by first obtaining estimates within strata and combining the strata estimates to obtain estimates which relate to the population. For the sake of economy, the estimation procedure for exploitation rates is presented as an example. However, the procedures for estimating other parameters involve the same general approach.

Estimates of exploitation rates can be obtained in two ways. Under the Chapman model, within stratum exploitation rates, denoted δ_i, can be estimated as

$$\hat{\delta}_i = \frac{m_{i2}}{n_{i2}}. \tag{23}$$

Under the log-linear model, within stratum exploitation rates are estimated as

$$\hat{\delta}_i = \hat{p}_{i2|0} = \hat{p}_{i2|1}. \tag{24}$$

Analytical estimators of the variances of the $\hat{\delta}_i$ can be derived in a straight forward manner under the assumption that the number of individuals captured in the second capture event is fixed. For this reason, the variance estimators should be viewed as conditional estimators that are likely to be negatively biased estimates of the unconditional variances. Under the Chapman model

$$v(\hat{\delta}_i) = \left(1 - \frac{n_{i2}}{\hat{N}_i}\right)\left(\frac{\hat{\delta}_i(1 - \hat{\delta}_i)}{n_{i2} - 1}\right), \tag{25}$$

(Seber, 1982). Under the log-linear model,

$$\hat{\delta} = (I_S \mathbin{.*.} W_2)\theta, \tag{26}$$

and

$$\hat{\Sigma}_{\hat{\delta}} = (I_S \;.\!*.\; W_2)\hat{\Sigma}_{\hat{\delta}}(I_S \;.\!*.\; W_2)', \tag{27}$$

where $\hat{\delta} = (\hat{\delta}_1, \hat{\delta}_2, \ldots, \hat{\delta}_S)'$ and W_2 is a 1 by 7 vector with a 1 in the 6th position and zeros elsewhere.

In some cases, an estimate of the population exploitation rate, δ_P, may be required. An estimator of δ_P is more difficult to obtain. The estimator must be obtained as a weighted average of the stratum exploitation rate estimators, where the weights are the stratum sub-population size estimators. This estimator of δ_P, under both the Chapman and log-linear models, is most easily expressed in scalar notation as

$$\hat{\delta}_P = \left(\frac{1}{\hat{N}}\right)\sum_{i=1}^{S} \hat{N}_i \hat{\delta}_i, \tag{28}$$

Note that the estimators involved in equation (28) might correspond to the estimators derived under either of the models. The use of random weights, i.e., sub-population size estimators, complicates the estimation of the variance of $\hat{\delta}_P$. However, an asymptotic estimator of the variance of $\hat{\delta}_P$ can be derived using the delta method (Seber, 1982). In scalar notation the estimator is given by

$$v(\hat{\delta}_P) = \left(\frac{1}{\hat{N}^2}\right)\left(\sum_{i=1}^{S}\left[v(\hat{N}_i)\,(\hat{\delta}_i-\hat{\delta}_P)^2 + v(\hat{\delta}_i)\,\hat{N}_i^2\right] + \right.$$

$$2\left[\sum_{i=1}^{S}\sum_{j=i+1}^{S} cov(\hat{N}_i,\hat{N}_j)\,(\hat{\delta}_i-\hat{\delta}_P)\,(\hat{\delta}_j-\hat{\delta}_P) + cov(\hat{\delta}_i,\hat{\delta}_j)\,\hat{N}_i\hat{N}_j \quad (29)\right.$$

$$\left.\left.\sum_{i=1}^{S}\sum_{j=1}^{S} cov(\hat{\delta}_i,\hat{\delta}_j)\,(\hat{\delta}_i-\hat{\delta}_P)\,\hat{N}_j\right]\right).$$

The estimator $v(\hat{\delta}_p)$ can be expressed in matrix notation, though some additional notation is required. Letting τ be the vertical concatenation of the vectors $\hat{\delta}$ and $\hat{N}$, i.e.,

$$\tau = W_{12}\theta, \; where$$
$$W_{12} = \begin{pmatrix} W_1 \\ -- \\ W_2 \end{pmatrix}, \tag{30}$$

an estimator of the covariance matrix of τ is given by

$$\hat{\Sigma}_\tau = W_{12}\hat{\Sigma}_\theta W_{12}'. \tag{31}$$

Now, let the vector d be the derivative of the estimator $\hat{\delta}_p$ with respect to the vector τ, i.e.,

$$d = \left(\frac{1}{\hat{N}}\right)(\hat{N}_1,\ \hat{N}_2,\ \ldots,\ \hat{N}_S,\ \hat{\delta}_1-\hat{\delta}_P,\ \hat{\delta}_2-\hat{\delta}_P,\ \ldots,\ \hat{\delta}_S-\hat{\delta}_P). \tag{32}$$

Then, the estimator of the variance of $\hat{\delta}_p$ can be expressed in matrix notation as

$$v(\hat{\delta}_P) = d\hat{\Sigma}_{\tau}d' \tag{33}$$

(Bishop et. al., 1975).

Note that when using the Chapman model the between strata covariance terms (e.g., $\text{cov}(\hat{\delta}_i,\hat{\delta}_j)$, i not equal j) are zero. This is also true for the log-linear model when no between strata constraints are imposed on the model. In these cases, equation (29) is considerably simplified.

MODEL ASSUMPTIONS

The assumptions forming the basis of the models discussed in section 2 are now reviewed in detail. The discussion attempts to focus on the validity of the assumptions specifically in relation to the DFO Yukon River tagging program, rather than in general terms. As was previously mentioned, many of the assumptions can be relaxed without seriously jeopardizing the statistical properties of the population size estimators. The conditions under which the assumptions can be relaxed are also discussed. As the assumptions of the log-linear model are quite similar to those of the Chapman model, the discussion focuses on the assumptions of the Chapman model. However, differences between the assumptions of the two models and the robustness of the models to violations of the assumptions are noted. We now proceed to review the assumptions of the Chapman model, in the order in which they were presented. The discussion draws heavily upon Seber (1982) and a similar review conducted by Brannian (1986).

Assumption 1

The Chapman model assumes that the population of interest is closed. This assumption is seriously violated in the DFO tagging program. Violations of this assumption result from (1) new individuals continually entering the system, i.e., from the US/Canada border to the confluence of the Stewart and Yukon rivers (Cronkite and Johnston, 1989a; Cronkite and Johnston, 1989b), (2) both tagged and non-tagged individuals continually leaving the system, and (3) tag-induced mortality of tagged individuals. Assume, momentarily, that the capture events are conducted over relatively short, temporally separated, spans of time relative to the rate at which individuals enter or leave the system. If marked and unmarked individuals leave the system at equal rates, and no individuals enter the system, the estimator produces a valid estimate of the population size at the time of the first capture event. If no individuals leave the system, but new individuals enter the system, the Chapman estimator produces a valid estimate of the population size at the time of the second capture event. If marked and unmarked individuals leave the system, even at the same rate, and new individuals enter the system, the estimator over-estimates the population size at the time of both capture events, i.e., the estimator is positively biased (Seber, 1982).

The above statements can be verified for a study in which the capture events are distinct in time and are conducted over periods of time that are short relative to the rate at which individuals enter and leave the system. In the DFO tagging program, individuals are entering and leaving the system continually during both capture events, suggesting the Chapman estimator may be positively biased. In addition, the capture events are conducted simultaneously through time. The effect that this has on the properties of the Chapman estimator is not clear. Individuals entering the system are captured and tagged with a certain probability and tagged and non-tagged individuals are leaving the system at rates that are probably equal. If the probabilities of capture in the fish wheel and in the commercial fishery are constant over time, the degree to which the Chapman estimator is effected may be reduced.

It seems clear that the statements usually made concerning violations of this assumption (e.g., Seber, 1982) are not directly and fully applicable to riverine fish tagging studies in which population size estimation, using the Chapman model, is a primary objective. The statistical properties of the estimator may or may not be compromised. Although a model based upon a time stratification might partially alleviate the problem, the underlying theory of such models has not been completely developed. Similarly, use of an open population model, with multiple capture events being defined by time, would eliminate the problem. However, existing open population models are only capable of estimating the population at specific points in time, corresponding to the capture events, not the total population size of interest here.

The log-linear model does not require the population to be closed, which is an obvious advantage in this study. The log-linear model assumes only that the observed frequencies have a multinomial distribution. That is, individuals may enter and leave the system if each individual is subject to the probabilities of capture in both capture events.

Assumption 2

The Chapman model assumes that all individuals belonging to a stratum have an equal probability of capture in the first capture event. If this assumption does not hold, the Chapman estimator is biased. However, relatively little is known concerning the robustness of the estimator to violations of this assumption. Seber (1982) states that the bias is reduced if different methods of capturing individuals are used in the two capture events. This statement hinges upon the relationship between the probabilities of capture in the two capture events. If the probability of capture in the first capture event is independent of the probability of capture in the second capture event, the quality of the estimator is not seriously affected (Seber, 1982); otherwise, the estimator is biased and the magnitude of the bias may be substantial.

In the DFO tagging program, the degree to which the probabilities of capture in the fish wheel and the commercial fishery are dependent is unknown. While the question is difficult to address directly, the log-linear model permits the covariance of the probabilities of capture in the capture events to be estimated (equation 16). An examination of these covariance terms would provide some indication of whether or not this assumption is violated.

Assumption 3

The Chapman model assumes that marking does not affect the probabilities of capture in the second capture event. This assumption was also incorporated into the log-linear model to obtain unique estimators. A violation of this assumption has a direct effect on the bias of the estimators under both models. If the probability of recapture of marked individuals is greater than that for unmarked individuals, the population size estimator is negatively biased; if the converse relationship exists, the estimator is positively biased.

The loss of tags from tagging mortality is almost certainly a problem in the DFO tagging study. The DFO currently assumes that 10% of all tagged individuals suffer tag-induced mortality and the observed frequencies are "adjusted" correspondingly (Cronkite and Johnston, 1989a; Cronkite and Johnston, 1989b). Unfortunately, this parameter may be difficult to estimate without conducting a separate study. In addition, tagging may invoke behavior responses or the tags may physically influence the probability of capture in the commercial fishery. Although these factors are also difficult to investigate, their effect might be assessed within the framework of the existing study by deploying more than one type of tag.

Assumption 4

The Chapman model assumes that the individuals belonging to a stratum captured in the second capture event constitute a simple random sample of individuals from that stratum. Similarly, the log-linear model assumes that the observed frequencies are multinomial random variables, i.e., a simple random sample from a multinomial distribution. Although a simple random sample is difficult or impossible to collect in practice, this assumption can be relaxed if the individuals belonging to a stratum have equal probabilities of capture in the second capture event (Seber, 1982). The validity of this assumption is difficult to test in the framework provided by the Chapman model. If additional stratification is possible, chi-squared tests can be conducted to investigate the validity of this assumption within strata (Seber, 1982; Brannian, 1986). However, if probabilities of recapture are not related to the values of the additional stratification variable, the problem will not be detected. In other words, a significant test indicates the problem exists, but a non-significant test does not prove that the problem does not exist. However, the use of this testing approach is discouraged. Such tests serve only to indicate that a more efficient stratification system is warranted. The preferred approach is to start with a fully stratified model and conduct hypothesis tests to determine constraints that may be appropriately placed upon the model parameters. Therefore, the best means of satisfying this assumption is through the use of an efficient stratification system.

Assumption 5

Both models assume that all recoveries are known. This assumption can be violated in three ways; by a loss of tags before recapture occurs, non-reporting of observed tags, and failure to observe the tags of recaptured individuals. If tags are lost before recapture occurs or observed tags are not reported, the effect is a failure to recognize tagged individuals captured in the commercial fishery, resulting in a positively biased estimator. Non-reporting of observed tags produces a negatively biased estimator if the individuals are not counted in the commercial harvest.

In the DFO tagging program, it seems highly probable that some number of recaptures are not reported. Commercial fishermen may not report observed recaptures for a number of reasons. Similarly, due to the large number of individuals handled, some tags may be unobserved by the commercial fishermen. The extent to which these problems exist is unknown and extremely difficult to quantify. The only efficient method of dealing with tag loss is to adopt a double tagging strategy. Increased monitoring of the commercial harvest would be necessary to assess whether or not all recaptures are being observed. The problem of non-reporting observed recaptures is more difficult and no solution is immediately apparent without some knowledge of why it might be occurring and who may be actively non-reporting recaptures.

Assumption 6

Both models require the strata to be independent. No method of testing the validity of this assumption is obvious, but it is probably not seriously violated.

An Additional Assumption

Although it is not explicitly stated in the list of assumptions for either model, both models assume that all random variables (frequencies) are known without error. This is not currently the case. Although the stratum to which each individual captured in the fish wheels is known without error, the individuals captured in the commercial fishery are currently classified into the strata based on samples from the total commercial harvest (Cronkite and Johnston, 1989a; Cronkite and Johnston, 1989b). The current level at which the commercial harvest is sampled, approximately 400 individuals, is insufficient to perform the classification with the required accuracy. The sampling error associated with estimating the strata composition of the commercial harvest introduces a potentially large source of variability that is not accounted for in the variance estimators. For that reason, the variance estimators should be viewed as conditional estimators that are negatively biased estimators of the true variance. The only means of alleviating this problem is to increase the level at which the commercial harvest is sampled.

EXAMPLES

As examples, chinook and chum data, collected during the 1987 and 1988 DFO Yukon River tagging studies, were analyzed using the log-linear estimation procedures. The results obtained by the DFO using the Chapman estimator (Cronkite and Johnston, 1989a; Cronkite and Johnston, 1989b) are summarized and compared to the estimates produced by the log-linear approach. In the cases when DFO analyzed data using more than one model, the results from the more highly stratified model are presented. However, the results are not completely comparable because, in general, the log-linear models used here are more highly stratified than were the Chapman models employed by DFO. Since the primary purpose of these analyses is to illustrate the log-linear estimation techniques, the data are not re-analyzed using fully stratified Chapman models.

A number of analyses of the four sets of data, denoted 1987 chinook, 1988 chinook, 1987 chum, and 1988 chum, were conducted. Each set of data was analyzed using a log-linear model with a sex and age stratification. In the analyses of chum data, four age categories were defined; (1) age 3 salmon, (2) age 4 salmon, (3) age 5 and age 6 salmon, and (4) salmon of unknown age. Four age categories were also used in the analyses of chinook data; (1) age 4 and age 5 salmon, (2) age 6 salmon, (3) age 7 and age 8 salmon, and (4) salmon of unknown age. Although DFO excluded individuals of unknown age from their analyses (Cronkite and Johnston, 1989a; Cronkite and Johnston, 1989b), they were included here since they are valid observations as long as the factors affecting ageability of salmon did not change between capture in the fish wheels and capture in the commercial fishery.

Probabilities of capture in both fish wheels and gill nets are commonly believed to be a function of the size of fish. Although the interaction of many morphological characteristics may determine an individuals's "size" with respect to probabilities of capture, length is likely to be one of the more important characteristics (Petersen, 1964). For that reason, the data were also analyzed using a sex and length stratification. In the analyses of chum data, four length categories were defined; (1) LC1 denotes fish of less than 600 millimeters (mm) in length, (2) LC2 denotes fish of between 600 and 649 mm in length, (3) LC3 denotes fish of between 650 and 699 mm in length, and (4) LC4 denotes fish of at least 700 mm in length. Four length categories were also defined in the analyses of the chinook data; (1) LC1 denotes fish of less than 800 mm in length, (2) LC2 denotes fish of between 800 and 899 mm in length, (3) LC3 denotes fish of between 900 and 999 mm in length, and (4) LC4 denotes fish of at least 1000 mm in length. These length categories were selected after a brief investigation of the lengths of captured fish, but were in no way selected to influence the parameter estimates.

For the purpose of these examples, each of the above stratification systems was considered to be a factorial design (e.g., Montgomery, 1976) . That is, the stratification was considered to be composed of the interaction of two independent factors, sex and age or sex and length (length category). Under this framework, the "interaction" of the two factors and the "main effects" are of primary interest. In each case, the hypothesis that the interaction of the factors was non-existent was tested. If the test was non-significant, the interaction was constrained to equal zero and a reduced model was fit to the data. Under the reduced model, the hypotheses that the main effects are non-existent were tested. Although it did not happen, if all three of the above hypothesis tests were non-significant, a completely pooled model would have resulted. The factorial approach serves to illustrate the log-linear hypothesis testing procedure and the advantage of beginning with a full stratified model under situations familiar to persons with some knowledge of experimental design and analysis of variance techniques. However, a more general approach would permit more flexibility in hypothesis testing.

The eight analyses were performed using the general approach described above. In each case, the population size and the population exploitation rate were estimated. The hypothesis that the sex-age interaction was zero was accepted in the analysis of the 1987 chum data under the sex and age stratification ($W = 9.635840$, $df = 6$, $p = 0.1408$). Therefore, the interaction was constrained to be zero and parameter estimates were obtained under the reduced model. The hypothesis that the main effect of sex was non-zero was accepted ($W = 837.5330$, $df = 2$, $p < 0.0001$) as was the hypothesis that the main effect of age was non-zero ($W = 255.4504$, $df = 6$, $p < 0.0001$), so no further constraints were placed upon the model. Only the results of the reduced model are presented. In all other cases, the hypothesis that the factor interaction was non-zero was accepted (i.e., $p > 0.05$). Therefore, no constraints were placed upon the models and estimates were obtained under fully stratified models. The estimated population sizes are presented in Table 1. The estimated probabilities of capture are presented in graphical form in Figures 1 through Figures 8. The estimated population exploitation rates are presented in Table 2.

The DFO currently applies a tag loss correction factor of 10% in their analyses (Cronkite and Johnston, 1989a; Cronkite and Johnston, 1989b). The sensitivity of the population size estimator to the magnitude of this correction factor was briefly examined. The 1987 chinook data was analyzed using tag loss correction factors of 0%, 5%, 10%, 15%, and 20% under the sex and length stratification. The estimates of population size obtained using these tag loss correction factors are graphed in Figure 9.

All analyses were performed using version 2.0 of the Gauss 386 programming language (Aptech Systems, 1989), which is a matrix-based language. As examples of the language and the construction of hypothesis matrices, the programs used to obtain the 1987 chum full and reduced parameter estimates, under the sex and age stratification, are presented in Appendix A and Appendix B, respectively.

DISCUSSION

Although the population size estimation procedures appear quite different, this perceived difference is largely a result of the different notation used by the models. In fact, a number of similarities exist. The assumptions under which the estimation procedures are derived are similar, both estimation procedures are maximum likelihood procedures, and both procedures estimate many of the same types of parameters. However, the estimation procedures are different in a number of important ways, most of which involve the model assumptions and the hypothesis testing procedures.

The assumptions of the log-linear model are slightly less rigid than the assumptions of the Chapman model. The log-linear model does not assume the population under consideration is closed. Also, the log-linear model permits the covariance of the estimated probabilities of capture to be estimated, which is useful in assessing violation of assumption 2 of the Chapman model. These features of the log-linear model provide clear advantages in the DFO tagging program.

The log-linear approach encourages the estimation of parameters under a fully stratified model. Constraints, derived from non-significant hypothesis tests, are then placed upon the model to obtain refined estimates with smaller estimated variances. This process continues until all hypotheses of interest have been tested and all appropriate constraints have been placed upon the parameters. This approach has the advantage of permitting higher order hypotheses, such as complex interactions between strata or "factors", to be tested before more simple hypotheses. As a result, researchers are less likely to "pool" strata inappropriately. For this reason, beginning with a fully stratified model is more desirable than beginning with a completely reduced model and stratifying the model based upon the results of chi-square tests as is currently done (Cronkite and Johnston, 1989a; Cronkite and Johnston, 1989b).

Although a fully stratified Chapman model might also be employed, complex hypothesis tests are more difficult to conduct. Currently, between strata hypothesis tests are generally limited to tests designed to indicate that a finer stratification system is needed in order to meet the model assumptions (Cronkite and Johnston, 1989a; Cronkite and Johnston, 1989b). Such hypothesis tests can also be performed in the log-linear framework, however, a broader range of tests that more completely examine the validity of the assumptions can be conducted. Such tests can be very useful in evaluating the validity of model assumptions but are difficult to perform in the framework provided by the Chapman model.

Because of the similarities between the models, the estimates obtained under the models might be expected to have similar statistical properties. In fact, the estimates of population size presented in Table 1 are not extremely different. Unfortunately, very little information indicating which method performs better is available. Evans (1989) conducted a small number of simulations which suggest that the log-linear estimator of population size generally performs as well as or better than the Chapman estimator. However, when the probabilities of capture in both capture events were fairly large (greater than 0.3), the Chapman estimator had slightly superior properties. These simulation results are not extremely revealing since they were conducted with very small population sizes under conditions exactly satisfying the model assumptions. A great deal of work comparing the statistical properties and performance of the estimators in more complex situations needs to be done.

For the reasons given above, the log-linear model appears to be the model of choice. This choice is based upon the extreme flexibility and generality of the model, the estimation procedure, and, in particular, the hypothesis testing procedure. This generality permits capture-recapture data to be more fully and completely analyzed than is the case under the Chapman model. Although the log-linear estimation procedure is more complex than the Chapman estimation procedure, computational complexity is not as limiting as it was only a few years ago. The computations are easily performed by a computer, particularly with the aid of matrix-based computer software.

A number of important aspects of the DFO tagging program, that are relatively independent of the model under which estimates are computed, need to be addressed. Perhaps most importantly, it is likely that the sex and age stratification system currently employed by the DFO could be improved. If the probabilities of capture are a function of the "size" of individuals, as is commonly believed, it is highly desirable to stratify on a variable which is highly correlated with size or directly on size itself. In this way the advantages of stratification can be fully realized. As is apparent in the examples, age is not such a variable. The estimated coefficients of variation of the population size estimates, which provide the most reliable means of comparing estimates, decreased substantially under a sex and length stratification in three of the four sets of data. The fact that the estimated coefficient of variation was larger under the sex and length stratification than under the sex and age stratification for the 1987 chum data is more likely to indicate an abnormality in those particular data than weaken the argument for using a length stratification.

The stratification system used has a great influence on the statistical quality of the estimators. For that reason, the most efficient possible stratification system must be used. While length may not provide the best possible stratification, it is likely to be a more efficient discriminator than is age. Although the establishment of length categories might be viewed as being somewhat arbitrary, there is no statistical reason they might not be employed. If the categories can be established based on suspected relationships with probabilities of capture, the quality of parameter estimates could improve markedly. An investigation of the literature might provide clues as to what categories might be most useful. In addition, exploratory analyses of existing data might prove beneficial and might even suggest additional measures of size that might be more discriminating than length, such as "condition index" measures (Bailey, 1968).

Parameters other than population sizes, such as exploitation rates, should be estimated within strata. If a population estimate is desired, the strata estimates should be combined using the methods presented. This is especially important in the estimation of exploitation rates. Both models assume the probability of capture in the second capture event, the exploitation rate, is equal for all members of a stratum, and potentially different between strata. For that reason, estimates of exploitation rates obtained using "pooled" data are as suspect as estimates of population size obtained from pooled data when strata differences in the probabilities of capture are known, or assumed, to exist. Although the estimator given in equation (28) is mathematically biased, the magnitude of the bias is likely to be much smaller than that of a pooled estimate, particularly if the probability of capture differs substantially among the strata.

The tag loss correction factor applied by DFO is one important component of these analyses that is completely under the control of the analysts. For that reason, it is important to determine appropriate correction factors as accurately as possible. As was previously mentioned, the DFO currently assumes 10% of all tagged individuals suffer tag loss and this correction factor was applied to both 1987 and 1988 chinook and chum data (Cronkite and Johnston, 1989a; Cronkite and Johnston, 1989b). However, the proportion of individuals suffering tag loss is likely to vary annually, between species, and perhaps within a season. Since the estimators are sensitive to the value of the correction factor used (Figure 9), methods of estimating the correction factor should be developed and estimates should be made on a regular, if not annual, basis as long as these estimation techniques are employed.

In general, the estimation procedures discussed in this manuscript were developed for the study of small mammal populations, although some of the early applications involved populations of fish in lakes and big game. Much of the subsequent work in this area has focused on ways of forcing the techniques into situations for which they were not designed. This is apparent in the large body of literature devoted to special cases in which the model assumptions are violated but the quality of the estimators is maintained (e.g., Seber, 1982). In that respect, the application of the techniques to such non-standard situations will always be characterized by substantial efforts to ensure the data are appropriate for the analysis methods. Such an approach is highly undesirable and severely hampers the credibility of scientific work. A greatly preferred approach would be to focus effort on developing methodology which is appropriate for the data. Although the development of new methodology is often difficult and protracted, it is the only way to both substantially improve the quality of the estimates and have reasonable confidence in the quality of the estimates.

RECOMMENDATIONS

We now make a number of specific recommendations concerning the continuation of the DFO Yukon River tagging program. The recommendations are derived from discussions throughout the preceding text and no further justifications are presented here. An attempt has been made to list the recommendations in the order of their priority. We recognize that the DFO is under no obligation to adopt these recommendations and, in fact, some of the recommendations may be difficult, or impossible, to implement in the near term. However, we view all of the following recommendations to be important in maintaining the quality of the DFO tagging program:

1. Devote funding and personnel to develop methodology specific to riverine fish tagging programs.
2. Abandon the use of an age stratification in preference to a length, or size, stratification.
3. Increase monitoring of the commercial fishery and sampling of the commercial harvest.
4. Adopt the log-linear estimation procedure.
5. Investigate the statistical properties of the Chapman and log-linear estimators using simulation techniques.
6. Compute estimates of exploitation rates, and similar parameters,

within strata.

7. Investigate tag loss more fully on a regular basis.
8. Examine the possibility of employing a double-tagging strategy.
9. Use exploratory analyses of existing data to investigate the relationship between length and probability of capture and search for other potentially useful measures of size.
10. If the Chapman estimator continues to be used, either estimate the within strata variances and use the estimates to construct a confidence interval for the total population size or determine how the same objective might be accomplished using the conditional distributions of the m_i frequencies.

ACKNOWLEDGEMENTS

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Table 1. Estimates of population size and standard errors, coefficients of variation, and upper and lower 95% confidence limits of the estimates obtained under the various models and stratification systems.

Data	Quantity	Chapman DFO	Log-linear Sex, Age	Log-linear Sex, Length
	$\hat{N}$	30,622	31,439	28,686
	se($\hat{N}$)	*	2,862	1,429
1987	cv($\hat{N}$)	*	9.10%	4.98%
Chinook	Lower Limit	27,408	25,830	25,885
	Upper Limit	34,186	37,049	31,487
	$\hat{N}$	44,373	42,226	39,937
	se($\hat{N}$)	*	2,605	2,194
1988	cv($\hat{N}$)	*	6.17%	5.49%
Chinook	Lower Limit	*	37,119	35,635
	Upper Limit	*	47,436	44,239
	$\hat{N}$	118,061	115,425	121,654
	se($\hat{N}$)	*	3,653	5,149
1987	cv($\hat{N}$)	*	3.16%	4.23%
Chum	Lower Limit	130,379	108,264	111,561
	Upper Limit	106,896	122,731	131,746
	$\hat{N}$	73,419	73,650	73,981
	se($\hat{N}$)	*	3,080	2,887
1988	cv($\hat{N}$)	*	4.18%	3.90%
Chum	Lower Limit	*	67,613	68,321
	Upper Limit	*	79,687	79,641

* Estimates not computed by DFO.

Table 2. Estimates of population exploitation rates and the standard errors and coefficients of variation of the estimates obtained under the various models and stratification systems.

Data	Quantity	Chapman DFO	Log-linear Sex, Age	Log-linear Sex, Length
1987 Chinook	$\hat{\delta}_p$	35.5%	31.4%	34.4%
	$se(\hat{\delta}_p)$	*	0.028	0.017
	$cv(\hat{\delta}_p)$	*	9.14%	5.04%
1988 Chinook	$\hat{\delta}_p$	29.7%	30.6%	32.3%
	$se(\hat{\delta}_p)$	*	0.019	0.018
	$cv(\hat{\delta}_p)$	*	6.21%	5.54%
1987 Chum	$\hat{\delta}_p$	34.4%	33.7%	32.0%
	$se(\hat{\delta}_p)$	*	0.011	0.014
	$cv(\hat{\delta}_p)$	*	3.20%	4.25%
1988 Chum	$\hat{\delta}_p$	43.7%	39.7%	39.6%
	$se(\hat{\delta}_p)$	*	0.017	0.016
	$cv(\hat{\delta}_p)$	*	4.20%	3.92%

* Estimates not computed by DFO.

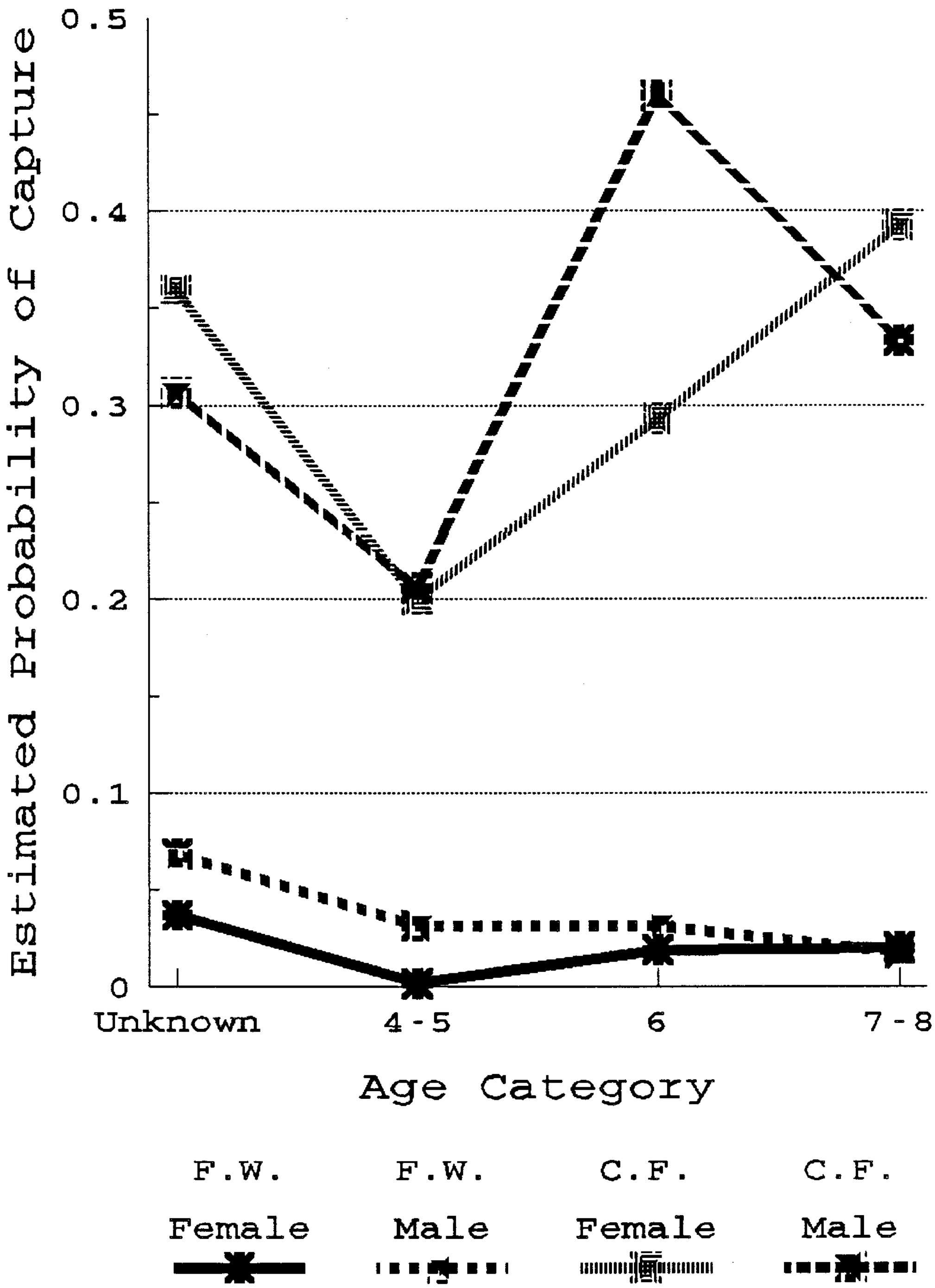

Figure 1. Estimated probabilities of capture for chinook in 1987 obtained under the sex and age stratification system.

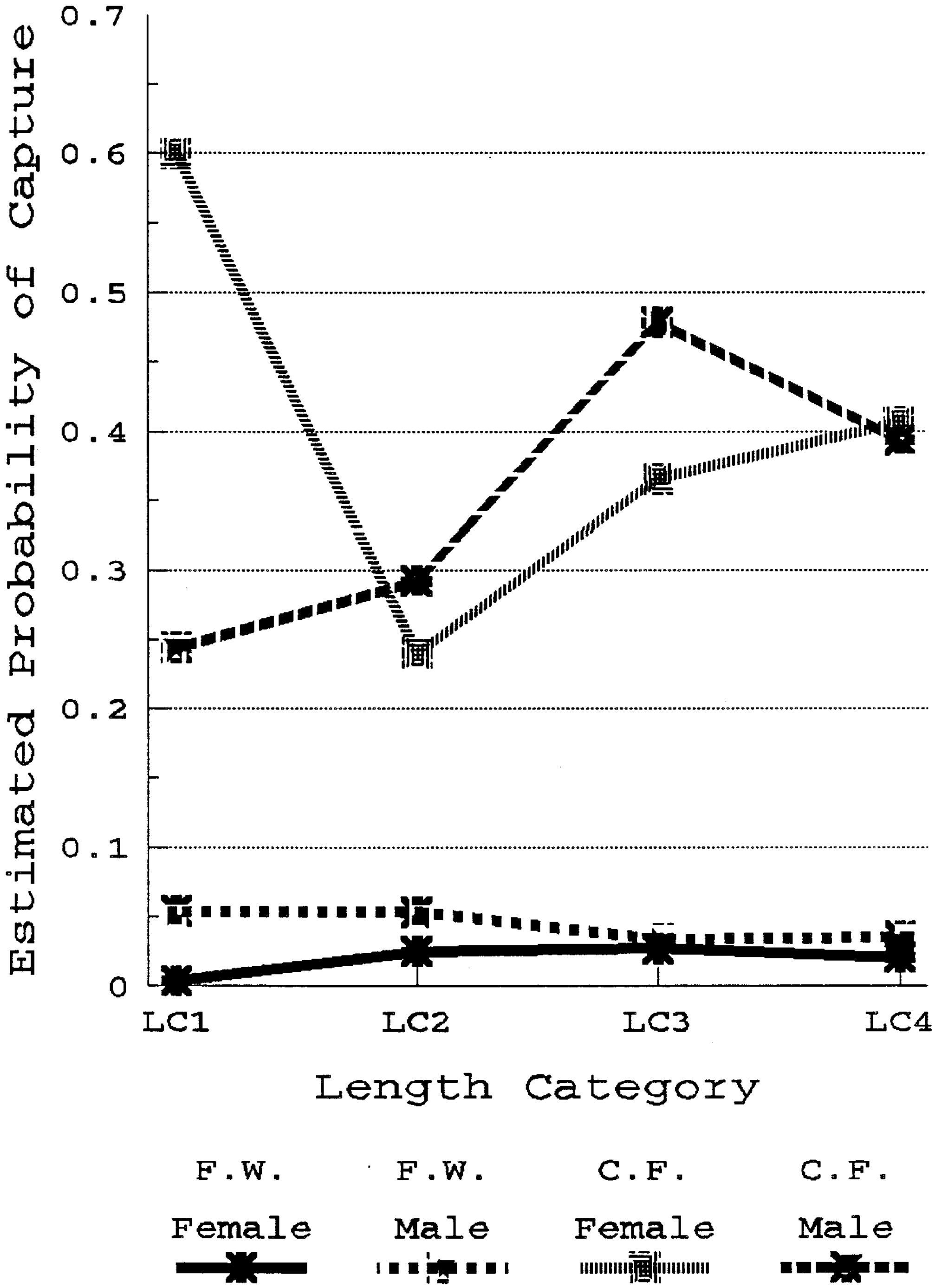

Figure 2. Estimated probabilities of capture for chinook in 1987 obtained under the sex and length stratification system.

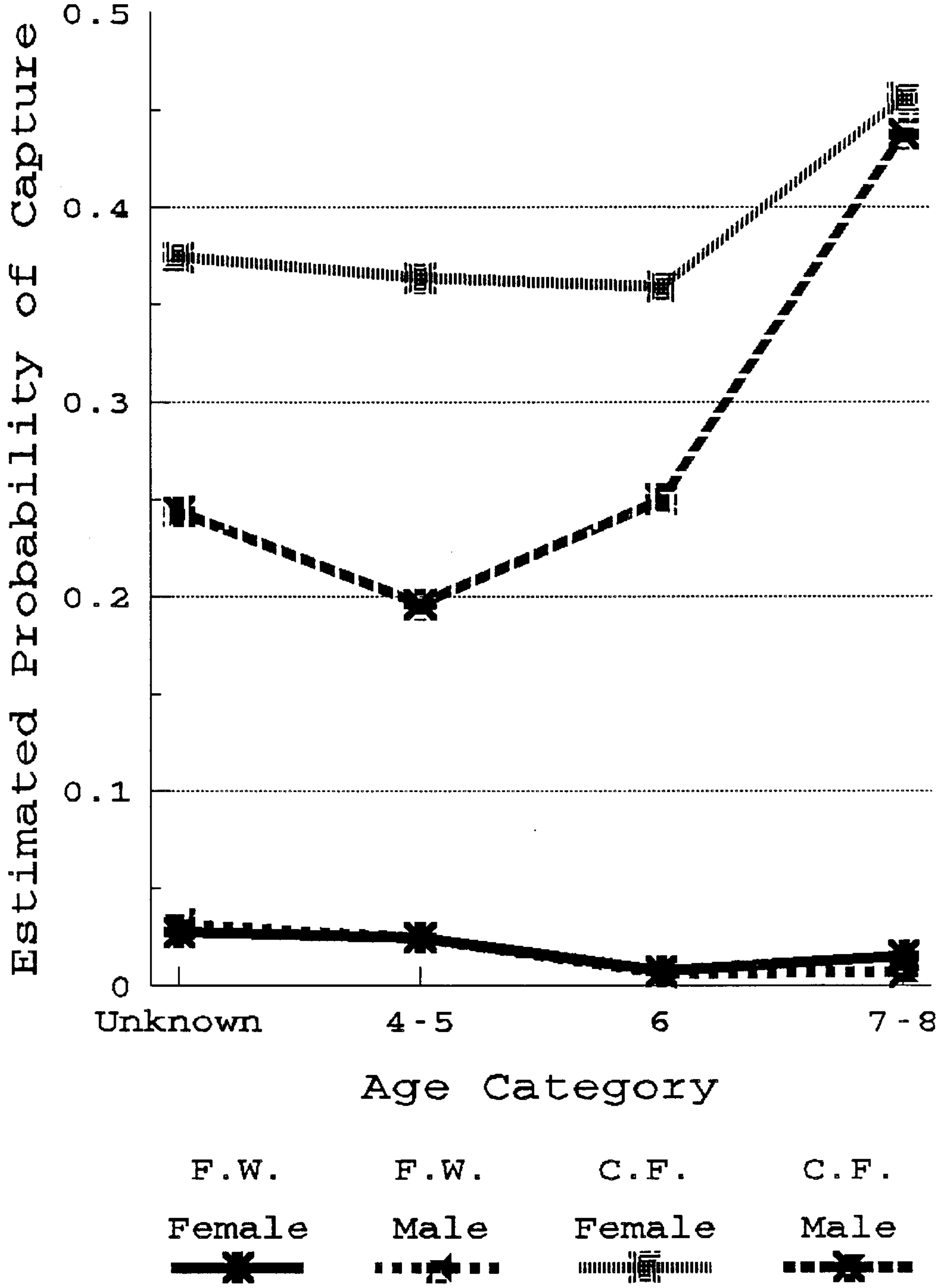

Figure 3. Estimated probabilities of capture for chinook in 1988 obtained under the sex and age stratification system.

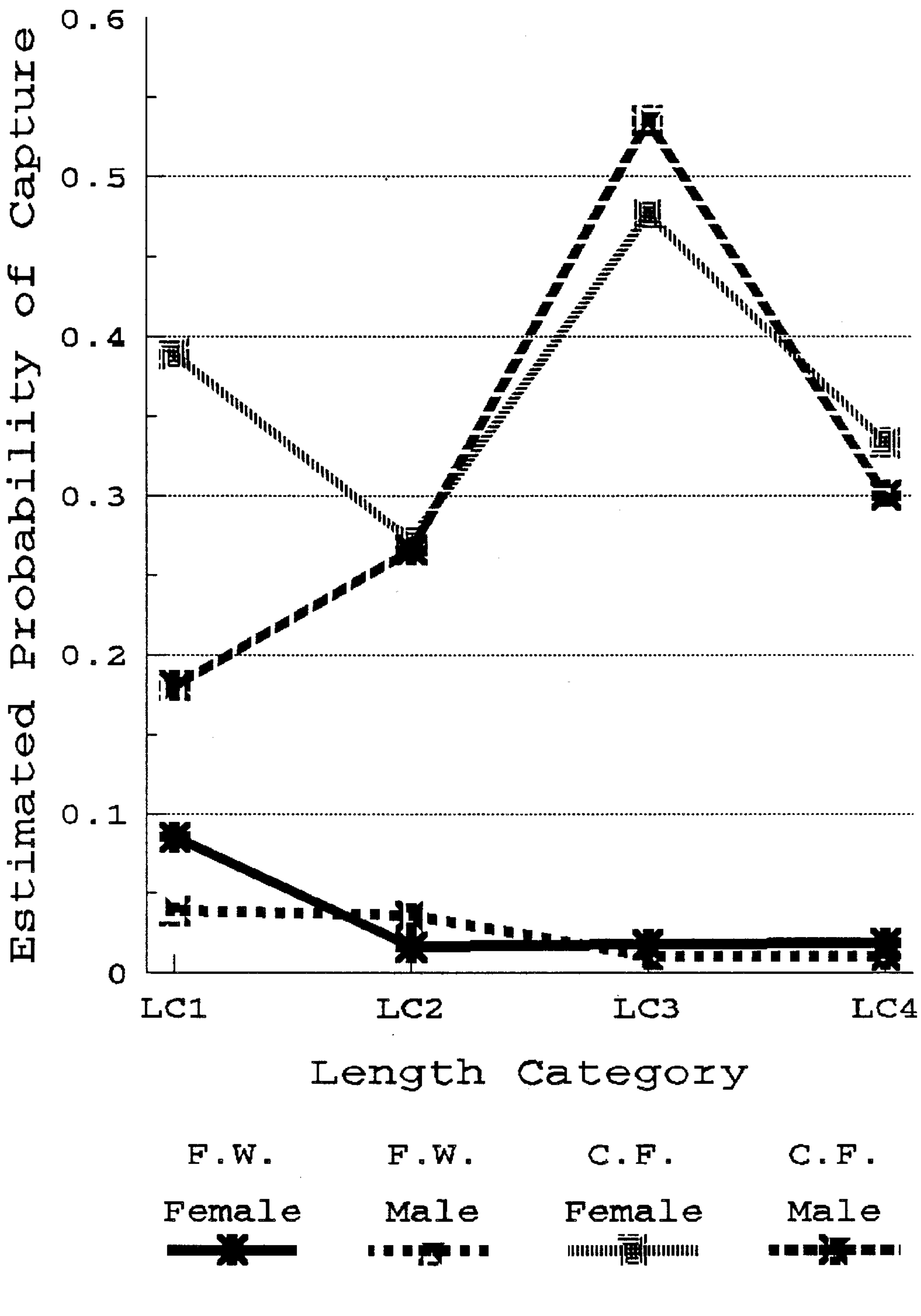

Figure 4. Estimated probabilities of capture for chinook in 1988 obtained under the sex and length stratification system.

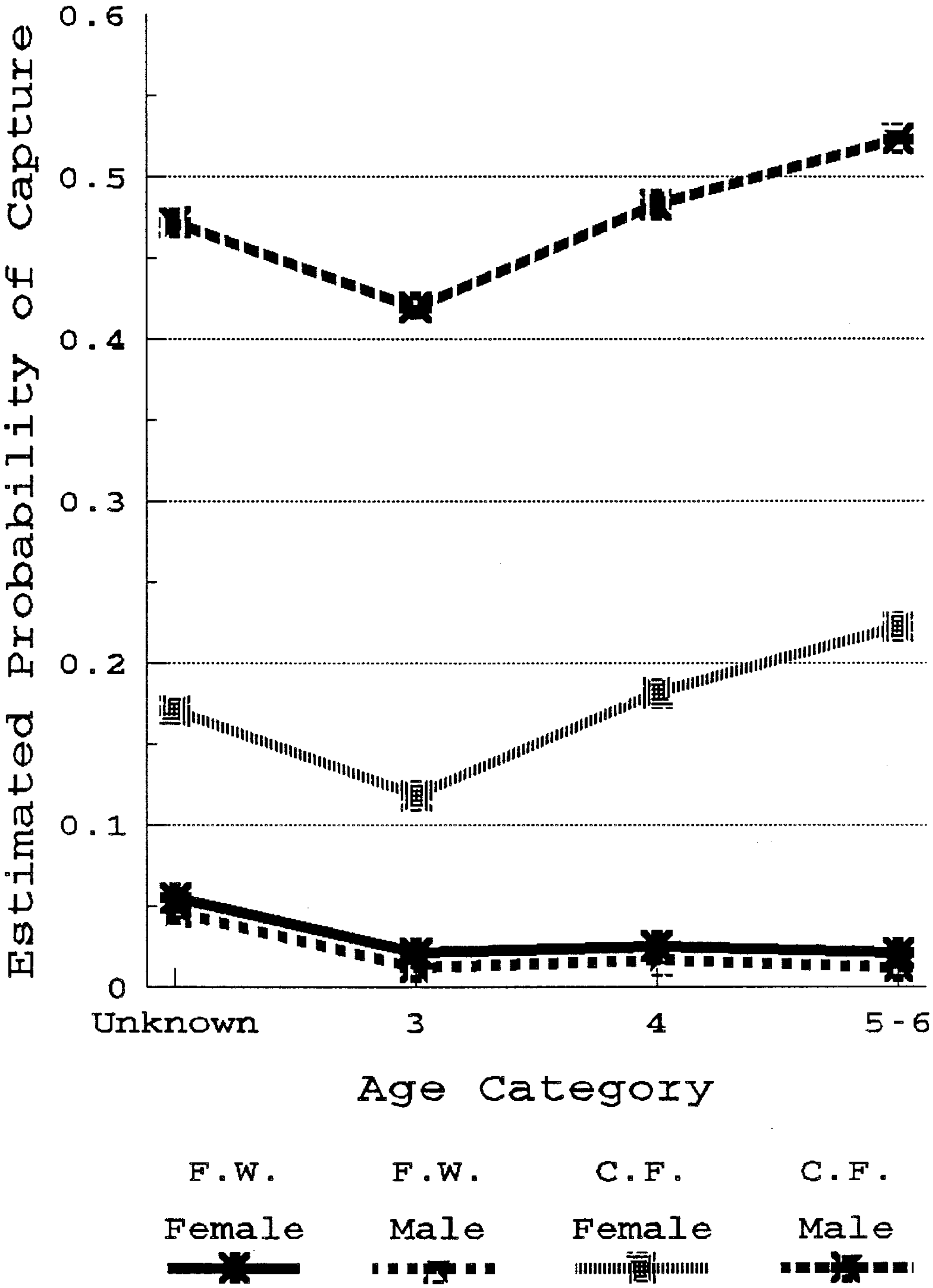

Figure 5. Estimated probabilities of capture for chum in 1987 obtained under the sex and age stratification system.

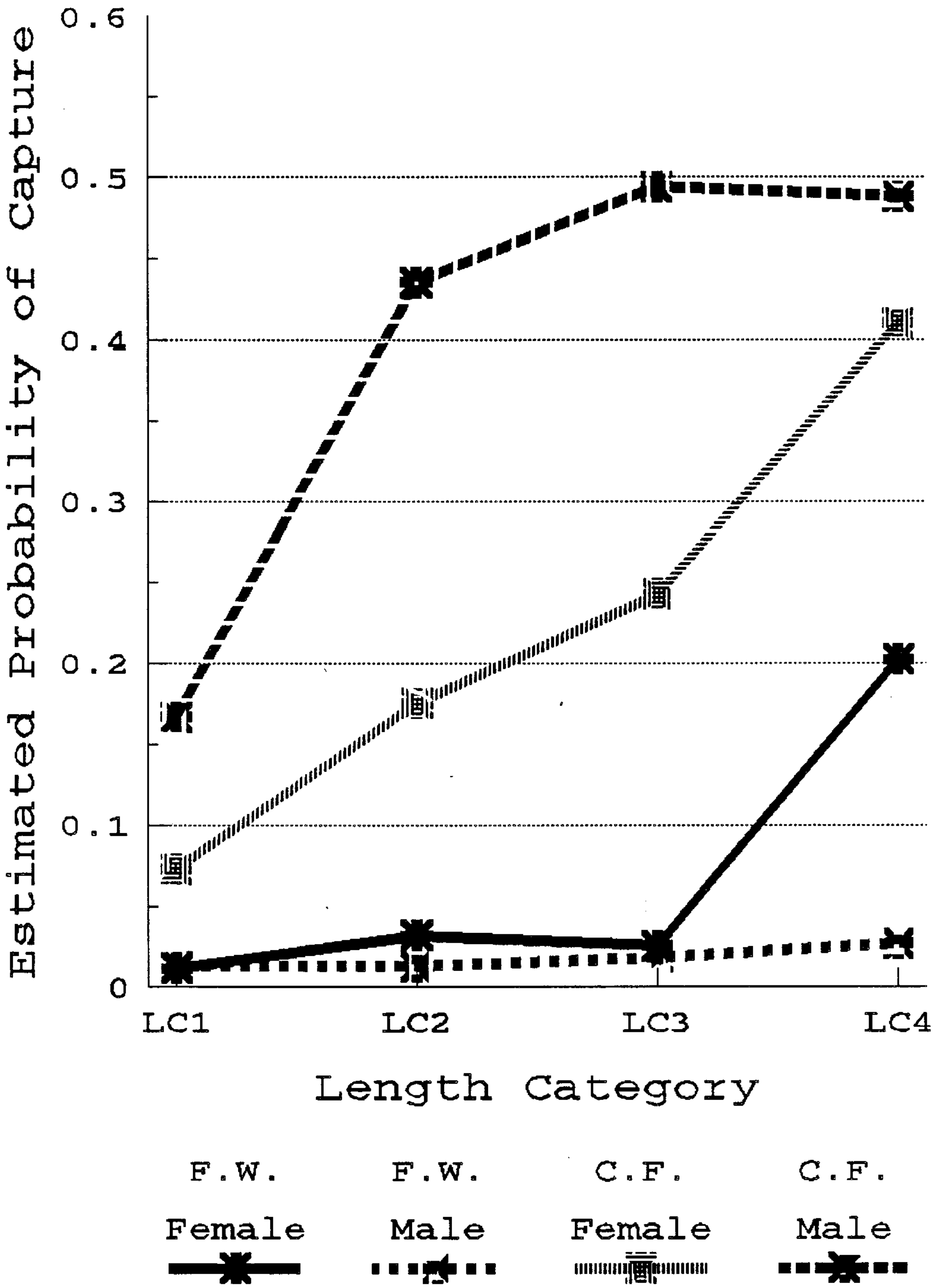

Figure 6. Estimated probabilities of capture for chum in 1987 obtained under the sex and length stratification system.

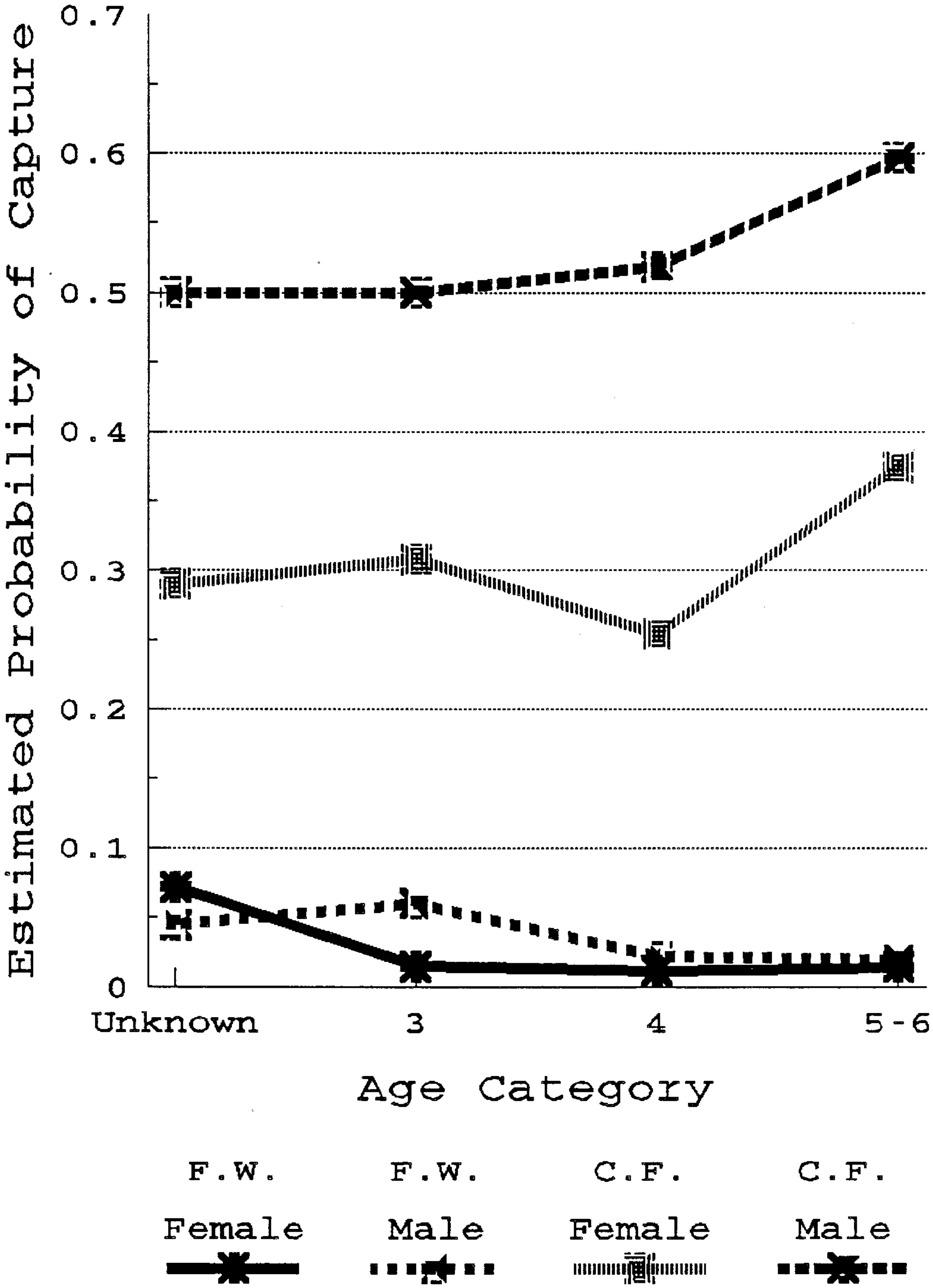

Figure 7. Estimated probabilities of capture for chum in 1988 obtained under the sex and age stratification system.

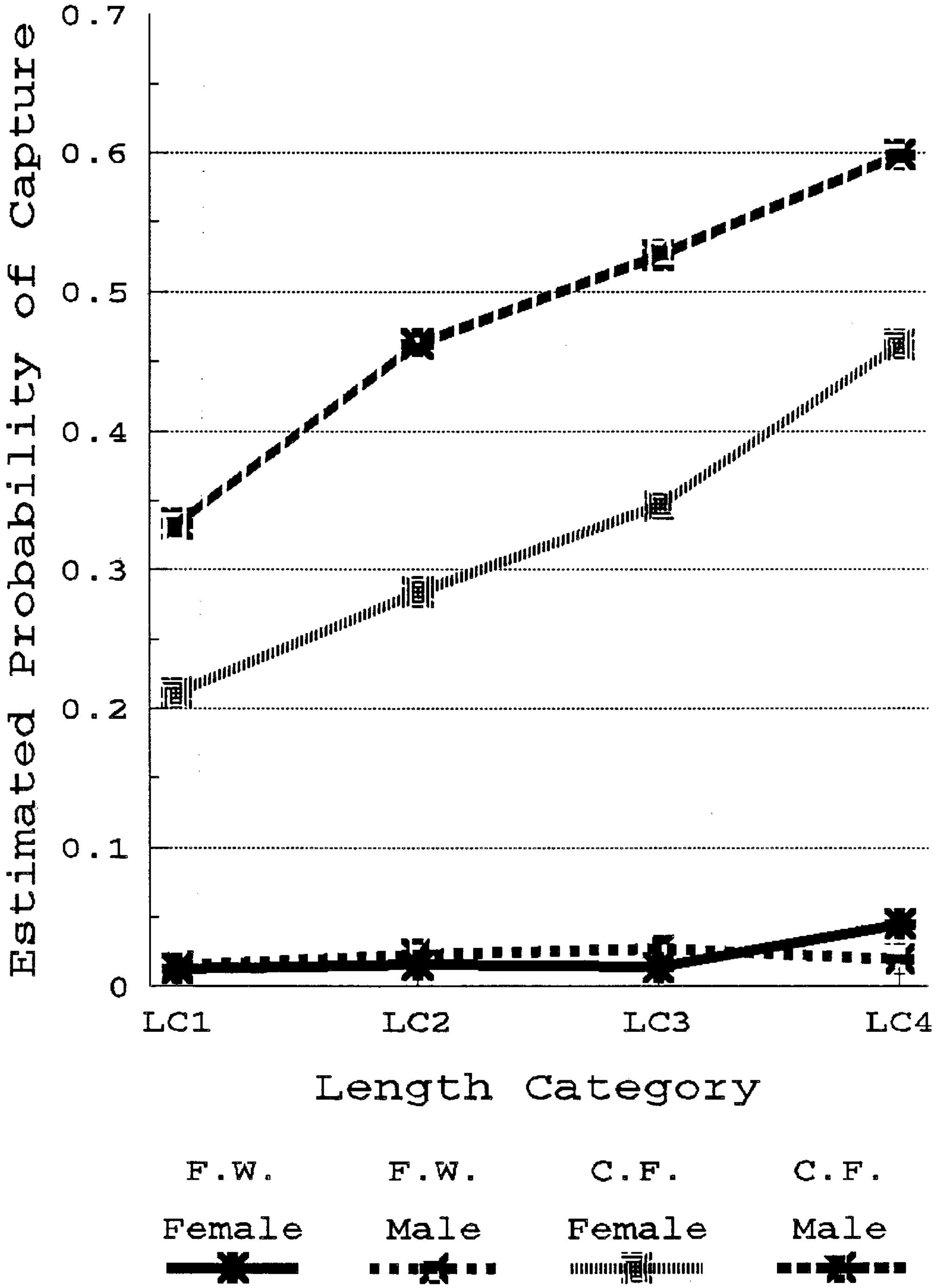

Figure 8. Estimated probabilities of capture for chum in 1988 obtained under the sex and length stratification system.

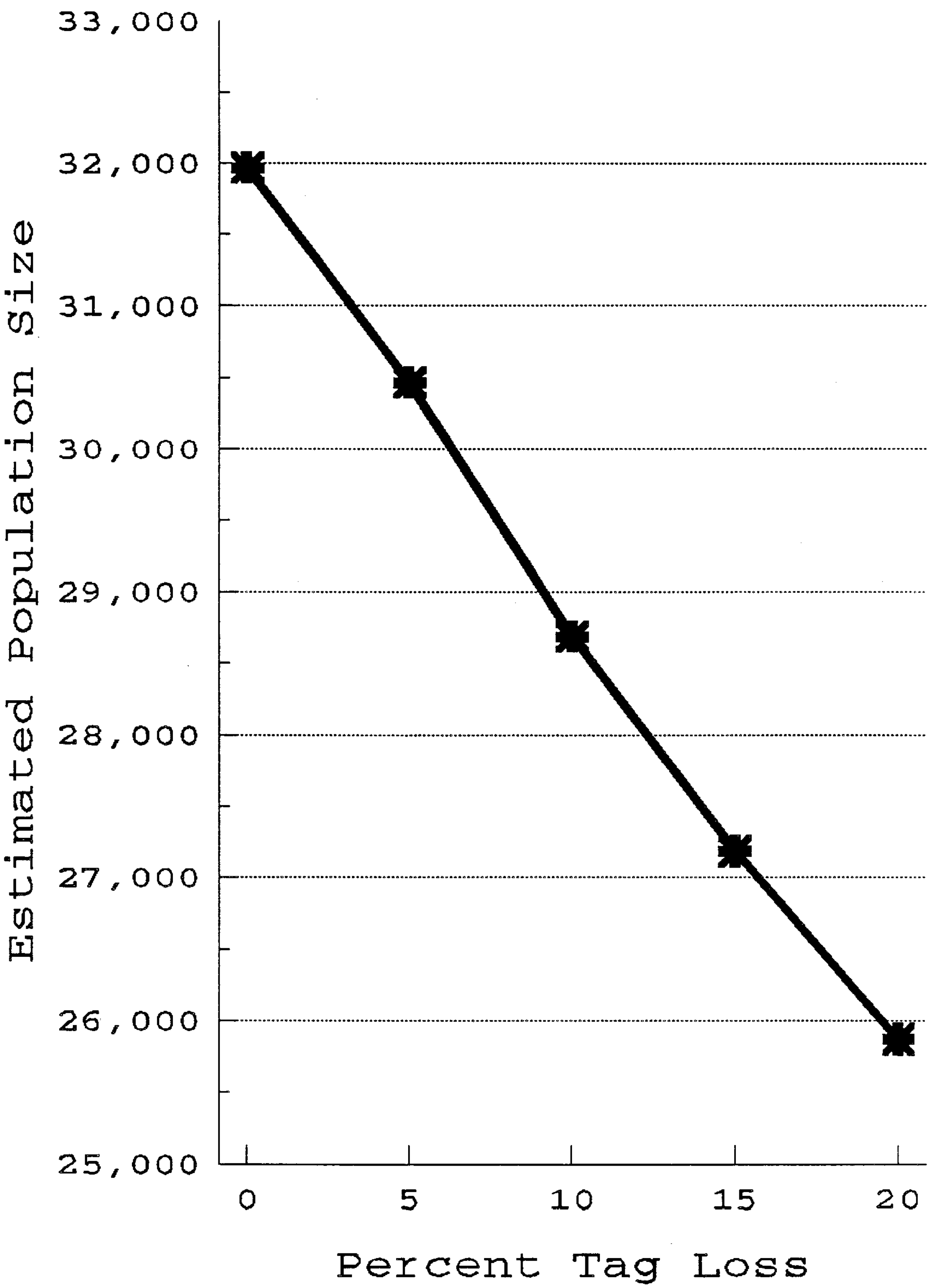

Figure 9. Estimated population sizes of chinook in 1987 obtained by applying various tag loss correction factors under the sex and length stratification system.

Appendix A

```
/**********************************************************************/
/*                                                                    */
/* program capturel                                                   */
/*                                                                    */
/**********************************************************************/
/*                                                                    */
/* JEFF BROMAGHIN                                                     */
/* AUGUST, 1990                                                       */
/*                                                                    */
/**********************************************************************/
/*                                                                    */
/* THIS PROGRAM COMPUTES MAXIMUM LIKELIHOOD ESTIMATES OF THE          */
/* PARAMETERS OF A LOG-LINEAR MODEL OF CAPTURE-RECAPTURE DATA.   THE  */
/* OBSERVED FREQUENCIES ARE ASSUMED TO FOLLOW A MULTINOMIAL           */
/* DISTRIBUTION.   LINEAR AND NON-LINEAR HYPOTHESIS TESTS ARE         */
/* CONDUCTED USING THE WALD TEST STATISTIC, WHICH IS ASYMPTOTICALLY   */
/* DISTRIBUTED AS A CHI-SQUARE RANDOM VARIABLE.                       */
/*                                                                    */
/**********************************************************************/

/*  DATA INPUT  */
LET F[24,1] =  69 278  955  7 38 229 181 841  7222 39 118 1694
              167 185 3613 11 13 855 312 326 18195 58  75 5297;

LET X[3,7] = 1 1 0 0 0 1 0
             1 1 0 0 0 0 1
             1 0 1 1 0 0 0;

LET RR[3,7] = 0 1 1 0 0 0 0
              0 0 0 1 1 0 0
              0 0 0 0 0 1 1;

LET HH[1,7] = 0 0 0 1 0 -1 0;

STRATA = 8;
IS = EYE(STRATA);
X = IS .*. X;
RR = IS .*. RR;
HH = IS .*. HH;
R = ONES(ROWS(RR),1);
H = ZEROS(ROWS(HH),1);


/*  INITIALIZE VARIABLES FOR ESTIMATION  */
TRAP 1;
COUNT = 1;
C = 10000000;
B1 = (ONES(1,STRATA) .*. ((LN(SUMC(F)/STRATA))~
     ((ONES(1,((COLS(X) - STRATA)/(2*STRATA)))) .*.
```

```
    (-1.20- -.3584))))';
IX = EYE(ROWS(X));
IB = EYE(ROWS(B1));

/*  ITERATE TO SOLUTION  */
DO WHILE COUNT <= 50;
  PRINT "ITERATION  " COUNT;
  MU = EXP(X*B1);
  THETA = EXP(B1);
  DTHETA = DIAGRV(IB,THETA);
  DMU = DIAGRV(IX,MU);
  P = INV(X'*DMU*X + C*DTHETA*RR'*RR*DTHETA + C*HH'*HH);
  IF SCALERR(P);
    ERR1 = 1;
    GOTO EXIT;
  ENDIF;
  G = X'*(F - MU) - C*DTHETA*RR'*(RR*THETA - R) - C*HH'*(HH*B1 - H);
  B2 = B1 + P*G;
  DIFF = B2 - B1;
  ERR = DIFF'*DIFF;
  IF ERR <= 0.0000001;
    ERR1 = 0;
    GOTO EXIT;
  ENDIF;
  COUNT = COUNT + 1;
  B1 = B2;
ENDO;


/*  EXIT AND PRINT RESULTS IF NO ERROR OCCURRED  */
EXIT:;
IF ERR1 == 1;
  PRINT "The second derivative matrix is singular";
  PRINT "Abnormal program termination...";
ELSEIF COUNT > 50;
  PRINT "The maximum allowable number of iterations was exceeded";
  PRINT "Abnormal program termination...";
ELSE;
  FORMAT /RD 14,6;
  LPRINT "******************* PROGRAM CAPTURE *******************";
  LPRINT " ";
  LPRINT " ";
  LPRINT "ITERATIONS TO CONVERGENCE CRITERION  =  " COUNT;
  LPRINT " ";
  LPRINT " ";
  MU = EXP(X*B2);
  THETA = EXP(B2);
  DMU = DIAGRV(IX,MU);
  DTHETA = DIAGRV(IB,THETA);

  /*  ESTIMATE THE VARIANCE OF THE OBSERVED FREQUENCIES  */
  LET W1[1,7] = 1 0 0 0 0 0 0;
```

```
W1 = IS .*. W1;
NHATVEC = W1*THETA;
BLOCKI = IS .*. ONES(3,3);
S = (BLOCKI .* (MU*MU')) ./ (NHATVEC .*. ONES(3,ROWS(MU)));
VF = DMU - S;

/*  COMPUTE OTHER ESTIMATES  */
VB = P*X'*VF*X*P;
VTHETA = DTHETA*VB*DTHETA;
NHAT = SUMC(NHATVEC);
VNHAT = ONES(1,STRATA)*W1*VTHETA*W1'*ONES(STRATA,1);

/*  ESTIMATE EXPLOITATION RATES  */
LET W2[1,7] = 0 0 0 0 0 1 0;
W2 = IS .*. W2;
DELTA = W2*THETA;
TAU = DELTA|NHATVEC;
W12 = W2|W1;
VTAU = W12*VTHETA*W12';
DELTAP = SUMC(DELTA .* NHATVEC)/NHAT;
TAUD = NHATVEC|(DELTA - DELTAP);
VDELTAP = (TAUD'*VTAU*TAUD)/(NHAT*NHAT);


/*  OUTPUT ESTIMATES OF INTEREST  */
LPRINT "MAXIMUM LIKELIHOOD PARAMETER ESTIMATES:" THETA;
LPRINT " ";
LPRINT " ";
LPRINT "PARAMETER VARIANCE ESTIMATES:" DIAG(VTHETA);
LPRINT " ";
LPRINT " ";
LPRINT "N-HAT   =   " NHAT;
LPRINT "var(N-HAT)  =   " VNHAT;
LPRINT " ";
LPRINT " ";
LPRINT "ESTIMATED POPULATION EXPLOITATION RATE (DELTAP):" DELTAP;
LPRINT "v(DELTAP):" VDELTAP;


/*  TEST HYPOTHESES  */
LET HH1[6,56] = 0 1 0 0 0 0 0 0 -1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
                0 -1 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
                0 0 0 1 0 0 0 0 0 0 -1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
                0 0 0 -1 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
                0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 -1 0 0 0 0 0 0 0 0 0 0 0 0
                0 -1 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0
                0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 -1 0 0 0 0 0 0 0 0 0 0
                0 0 0 -1 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0
                0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 -1 0 0 0 0 0
                0 -1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0
                0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 -1 0 0 0
                0 0 0 -1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0;
```

```
  WALD = (HH1*THETA)'*INV(HH1*VTHETA*HH1')*HH1*THETA;
  LPRINT " ";
  LPRINT " ";
  LPRINT "TEST OF THE SEX*AGE INTERACTION";
  LPRINT " ";
  LPRINT "WALD TEST STATISTIC  =  " WALD;
  DF = RANK(HH1);
  LPRINT "DEGREES OF FREEDOM  =  " DF;
  LPRINT "p-VALUE  =  " CDFCHIC(WALD,DF);
ENDIF;
```

Appendix B

```
/************************************************************************/
/*                                                                      */
/* program capturel                                                     */
/*                                                                      */
/************************************************************************/
/*                                                                      */
/* JEFF BROMAGHIN                                                       */
/* AUGUST, 1990                                                         */
/*                                                                      */
/************************************************************************/
/*                                                                      */
/* THIS PROGRAM COMPUTES MAXIMUM LIKELIHOOD ESTIMATES OF THE            */
/* PARAMETERS OF A LOG-LINEAR MODEL OF CAPTURE-RECAPTURE DATA.   THE    */
/* OBSERVED FREQUENCIES ARE ASSUMED TO FOLLOW A MULTINOMIAL             */
/* DISTRIBUTION.   LINEAR AND NON-LINEAR HYPOTHESIS TESTS ARE           */
/* CONDUCTED USING THE WALD TEST STATISTIC, WHICH IS ASYMPTOTICALLY     */
/* DISTRIBUTED AS A CHI-SQUARE RANDOM VARIABLE.                         */
/*                                                                      */
/************************************************************************/

/*  DATA INPUT  */
LET F[24,1] =  69 278  955  7 38 229 181 841  7222 39 118 1694
              167 185 3613 11 13 855 312 326 18195 58  75 5297;

LET X[3,7] = 1 1 0 0 0 1 0
             1 1 0 0 0 0 1
             1 0 1 1 0 0 0;

LET RR[3,7] = 0 1 1 0 0 0 0
              0 0 0 1 1 0 0
              0 0 0 0 0 1 1;

LET HH[1,7] = 0 0 0 1 0 -1 0;

STRATA = 8;
IS = EYE(STRATA);
X = IS .*. X;
RR = IS .*. RR;
HH = IS .*. HH;
R = ONES(ROWS(RR),1);
H = ZEROS(ROWS(HH),1);


/*  CONSTRAIN SEX*AGE INTERACTION TO ZERO  */
LET HH1[6,56] = 0 1 0 0 0 0 0 0 -1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
                0 -1 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
                0 0 0 1 0 0 0 0 0 0 -1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
                0 0 0 -1 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
                0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 -1 0 0 0 0 0 0 0 0 0 0 0 0
```

```
                0 -1 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0
                0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 -1 0 0 0 0 0 0 0 0 0 0
                0 0 0 -1 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0
                0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 -1 0 0 0 0 0
                0 -1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0
                0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 -1 0 0 0
                0 0 0 -1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0;
RR = RR|HH1;
R = R|ZEROS(ROWS(HH1),1);


/*  INITIALIZE VARIABLES FOR ESTIMATION  */
TRAP 1;
COUNT = 1;
C = 10000000;
B1 = (ONES(1,STRATA) .*. ((LN(SUMC(F)/STRATA))~
     ((ONES(1,((COLS(X) - STRATA)/(2*STRATA)))) .*.
     (-1.20~ -.3584))))';
IX = EYE(ROWS(X));
IB = EYE(ROWS(B1));

/*  ITERATE TO SOLUTION  */
DO WHILE COUNT <= 50;
  PRINT "ITERATION  " COUNT;
  MU = EXP(X*B1);
  THETA = EXP(B1);
  DTHETA = DIAGRV(IB,THETA);
  DMU = DIAGRV(IX,MU);
  P = INV(X'*DMU*X + C*DTHETA*RR'*RR*DTHETA + C*HH'*HH);
  IF SCALERR(P);
    ERR1 = 1;
    GOTO EXIT;
  ENDIF;
  G = X'*(F - MU) - C*DTHETA*RR'*(RR*THETA - R) - C*HH'*(HH*B1 - H);
  B2 = B1 + P*G;
  DIFF = B2 - B1;
  ERR = DIFF'*DIFF;
  IF ERR <= 0.0000001;
    ERR1 = 0;
    GOTO EXIT;
  ENDIF;
  COUNT = COUNT + 1;
  B1 = B2;
ENDO;


/*  EXIT AND PRINT RESULTS IF NO ERROR OCCURRED  */
EXIT:;
IF ERR1 == 1;
  PRINT "The second derivative matrix is singular";
  PRINT "Abnormal program termination...";
ELSEIF COUNT > 50;
```

```
    PRINT "The maximum allowable number of iterations was exceeded";
    PRINT "Abnormal program termination...";
  ELSE;
    FORMAT /RD 14,6;
    LPRINT "******************** PROGRAM CAPTURE ********************";
    LPRINT " ";
    LPRINT " ";
    LPRINT "ITERATIONS TO CONVERGENCE CRITERION  =  " COUNT;
    LPRINT " ";
    LPRINT " ";
    MU = EXP(X*B2);
    THETA = EXP(B2);
    DMU = DIAGRV(IX,MU);
    DTHETA = DIAGRV(IB,THETA);

    /*  ESTIMATE THE VARIANCE OF THE OBSERVED FREQUENCIES  */
    LET W1[1,7] = 1 0 0 0 0 0 0;
    W1 = IS .*. W1;
    NHATVEC = W1*THETA;
    BLOCKI = IS .*. ONES(3,3);
    S = (BLOCKI .* (MU*MU')) ./ (NHATVEC .*. ONES(3,ROWS(MU)));
    VF = DMU - S;

    /*  COMPUTE OTHER ESTIMATES  */
    VB = P*X'*VF*X*P;
    VTHETA = DTHETA*VB*DTHETA;
    NHAT = SUMC(NHATVEC);
    VNHAT = ONES(1,STRATA)*W1*VTHETA*W1'*ONES(STRATA,1);

    /*  ESTIMATE EXPLOITATION RATES  */
    LET W2[1,7] = 0 0 0 0 0 1 0;
    W2 = IS .*. W2;
    DELTA = W2*THETA;
    TAU = DELTA|NHATVEC;
    W12 = W2|W1;
    VTAU = W12*VTHETA*W12';
    DELTAP = SUMC(DELTA .* NHATVEC)/NHAT;
    TAUD = NHATVEC|(DELTA - DELTAP);
    VDELTAP = (TAUD'*VTAU*TAUD)/(NHAT*NHAT);


    /*  OUTPUT ESTIMATES OF INTEREST  */
    LPRINT "MAXIMUM LIKELIHOOD PARAMETER ESTIMATES:" THETA;
    LPRINT " ";
    LPRINT " ";
    LPRINT "PARAMETER VARIANCE ESTIMATES:" DIAG(VTHETA);
    LPRINT " ";
    LPRINT " ";
    LPRINT "N-HAT  =  " NHAT;
    LPRINT "var(N-HAT)  =  " VNHAT;
    LPRINT " ";
    LPRINT " ";
```

```
   LPRINT "ESTIMATED POPULATION EXPLOITATION RATE (DELTAP):" DELTAP;
   LPRINT "v(DELTAP):" VDELTAP;


   /*  TEST HYPOTHESES  */
   LET HH2[2,56] = 0  1 0 0 0 0 0 0  1 0 0 0 0 0 0  1 0 0 0 0 0 0  1 0 0 0 0 0
                   0 -1 0 0 0 0 0 0 -1 0 0 0 0 0 0 -1 0 0 0 0 0 0 -1 0 0 0 0 0
                   0 0 0  1 0 0 0 0 0 0  1 0 0 0 0 0 0  1 0 0 0 0 0 0  1 0 0 0
                   0 0 0 -1 0 0 0 0 0 0 -1 0 0 0 0 0 0 -1 0 0 0 0 0 0 -1 0 0 0;

   WALD = (HH2*THETA)'*INV(HH2*VTHETA*HH2')*HH2*THETA;
   LPRINT " ";
   LPRINT " ";
   LPRINT "TEST OF THE SEX EFFECT";
   LPRINT " ";
   LPRINT "WALD TEST STATISTIC  =  " WALD;
   DF = RANK(HH2);
   LPRINT "DEGREES OF FREEDOM  =  " DF;
   LPRINT "p-VALUE  =  " CDFCHIC(WALD,DF);

   LET HH2[6,56] = 0 1 0 0 0 0 0 0 -1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
                   0 1 0 0 0 0 0 0 -1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
                   0 0 0 1 0 0 0 0 0 0 -1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
                   0 0 0 1 0 0 0 0 0 0 -1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
                   0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 -1 0 0 0 0 0 0 0 0 0 0 0 0
                   0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 -1 0 0 0 0 0 0 0 0 0 0 0 0
                   0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 -1 0 0 0 0 0 0 0 0 0 0
                   0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 -1 0 0 0 0 0 0 0 0 0 0
                   0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 -1 0 0 0 0 0
                   0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 -1 0 0 0 0 0
                   0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 -1 0 0 0
                   0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 -1 0 0 0;

   WALD = (HH2*THETA)'*INV(HH2*VTHETA*HH2')*HH2*THETA;
   LPRINT " ";
   LPRINT " ";
   LPRINT "TEST OF THE AGE EFFECT";
   LPRINT " ";
   LPRINT "WALD TEST STATISTIC  =  " WALD;
   DF = RANK(HH2);
   LPRINT "DEGREES OF FREEDOM  =  " DF;
   LPRINT "p-VALUE  =  " CDFCHIC(WALD,DF);

ENDIF;
```