

Estimating mortality rates from tag recoveries: incorporating over-dispersion, correlation, and change points

Shuichi Kitada, Kazuhiko Hiramatsu, and Hirohisa Kishino

Kitada, S., Hiramatsu, K., and Kishino, H. 1994. Estimating mortality rates from tag recoveries: incorporating over-dispersion, correlation, and change points. – ICES J. mar. Sci., 51: 241–251.

In this article we studied the maximum-likelihood estimation of fishing and natural mortality rates with a change point from time series of tag recovery data. Our statistical models consider the change in the mortality rates and take account of over-dispersion and correlation involved in the recovery data. First, we considered a partial-likelihood approach for the multinomial model. Explicit estimators and variances of the fishing mortality rates were derived. However, the recovery data are usually over-dispersed, mainly because of aggregation in the population. For this problem, we considered the normal distribution model as an approximation of the Dirichlet compound multinomial distribution. When we compare the viability of different reared groups, it is important to note that the estimated parameters are correlated, even if they were obtained separately. This is because those groups were exposed to the same environments and therefore the resultant recovery data have correlations. We constructed a joint-likelihood function, taking account of the correlations among the time series of recoveries. Two groups of hatchery-reared red seabream were analyzed to demonstrate the methodology.

Key words: tag recoveries, maximum-likelihood estimation, fishing and natural mortality rates, over-dispersion, correlation change points.

Received 12 June 1992; accepted 9 December 1993.

Shuichi Kitada: Japan Sea-Farming Association, 2-1-5 Arakawa, Arakawa-ku, Tokyo 116, Japan. Present address: Department of Aquatic Biosciences, Tokyo University of Fisheries, 4-5-7 Konan, Minato-ku, Tokyo 108, Japan. Kazuhiko Hiramatsu: National Research Institute of Far Seas Fisheries, 5-7-1 Orido, Shimizu 424, Japan. Hirohisa Kishino: Ocean Research Institute, University of Tokyo, 1-15-1 Minamidai, Nakano-ku, Tokyo 164, Japan. Present address: Department of Social and International Relations, University of Tokyo, 3-8-1 Komaba, Meguro-ku, Tokyo 153, Japan.

Introduction

Coastal fishery stock enhancement programs by means of hatchery releases have been actively conducted in Japan. Evaluating the effectiveness of the enhancement programs is important. We can evaluate the impact of stocking by three measures: recovery rate, the mark ratio (ratio of marked fish stocked to the total number of landings), and survival rate. The recovery rate is the only measure for direct evaluation of the effectiveness. The method for direct estimation of the recovery rate by two-stage sampling survey of commercial landings in fish markets was proposed (Kitada *et al.*, 1992). The mark ratio estimated in Kitada *et al.* (1992) is a relative measure to evaluate the ratio of released fish in the wild population. On the other hand, it is particularly important for the improvement of the quality of the hatchery to monitor the mortality rates of fingerlings for the

period soon after release. These mortality rates depend on stocking variables such as quality, size, number, time or site of stocking, and the type of tags.

In fisheries, mortality can be attributed to either fishing or natural causes. These are usually called fishing and natural mortality rates. We are able to know the capture likelihood of fingerlings from the fishing mortality rate, and the viability from the natural mortality rate. The natural mortality rate of released fingerlings is expected to be quite high in the short period soon after release, but settle down after a few days. If we know the length of this critical period, we can develop effective methods of conservation for the released fingerlings. In this study we consider the estimation of fish mortality rates with some change-point alternatives against constant mortality rates.

The statistical model for estimating the fishing and natural mortality rates has been based on the

multinomial distribution (Gulland, 1955). First, we considered a partial-likelihood approach for the multinomial model. Explicit estimators and variances of the fishing mortality rates are derived here. However, the multinomial model is invalid when the recovery data are over-dispersed, which is common in field experiments mainly because of clustering in the population. Taking the over-dispersion into account, we considered the normal distribution model as an approximation of the Dirichlet compound multinomial distribution, and studied the effect of the over-dispersion on the estimates.

It is often also important to compare the mortality rates between the different release groups. We can get a high detection power of the difference in the mortality rates by releasing the different groups of fingerlings into the same area at the same time. However, the estimated mortality rates are correlated because the recovery data between different groups are correlated. Taking their correlation into account, we proposed simultaneous estimation of the mortality rates from tag recoveries of two groups. As an example, we applied our methods to the case of red seabream, *Pagrus major*, in the Seto Inland Sea. The change-point mortality rates and the quality difference of fingerlings between two hatcheries were investigated. The χ^2 test under a 2×2 contingency table for the hypothesis of the same recovery rates of two groups is also discussed.

Multinomial model and a change-point alternative

Suppose that N tagged fish are released at time $t=0$, total n fish recaptured at known times t_1, t_2, \dots, t_k , P_i is the probability that an individual tagged fish surviving until t_{i-1} will be recaptured at i th time interval (t_{i-1}, t_i), and the number of tagged fish actually captured at this time interval is n_i . It is assumed that all tagged fish that are recovered are reported. If the wild and tagged fish are randomly distributed, the likelihood of the recoveries is given by (Seber, 1982):

$$\begin{aligned} L(F, Z | n_1, \dots, n_{k+1}) &= \prod_{i=1}^k \binom{N - \sum_{j=1}^{i-1} n_j}{n_i} p_i^{n_i} q_i^{N - \sum_{j=1}^i n_j} \\ &= \frac{N!}{(N-n)! \prod_{i=1}^k n_i!} \prod_{i=1}^k p_i^{n_i} \left(1 - \sum_{i=1}^k P_i\right)^{N-n}, \end{aligned} \quad (1)$$

where $p_i (= 1 - q_i)$ is the probability of an individual being caught in the i th interval, and is given by:

$$p_i = P_i / \exp\left\{-\int_0^{t_i} Z(u) du\right\}. \quad (2)$$

The general form for P_i is given by:

$$P_i = \int_{t_{i-1}}^{t_i} p(t) dt, \quad (3)$$

where $p(t)$ is the instantaneous rate of recapture; that is:

$$p(t) = F(t) \exp\left\{-\int_0^t Z(u) du\right\}. \quad (4)$$

$F(t)$ is the fishing mortality rate and $Z(t) = F(t) + M(t)$, where $Z(t)$ and $M(t)$ are the total and natural mortality rates. These rates are all instantaneous. Many methods for estimating the fishing and natural mortality rates have been developed by using this full-likelihood function as follows. Gulland (1955) derived the explicit estimators of the constant mortality rates for exact-time and uncensored recovery data. Paulik (1963) also considered estimation of constant mortality rates for censored data which was ungrouped or grouped by time intervals. Kitahara *et al.* (1986) discussed the estimation of the constant fishing mortality rate with a few closed fishing seasons. Hearn *et al.*'s method (1987) is for exact-time data and has no restriction on the fishing mortality rate when the complete tagging experiment is assumed. Leigh (1988) derived the variance of Hearn *et al.*'s natural mortality estimator. Farebrother (1988) considered estimation when the fishing and natural mortality rates are some function of time.

The problem of a change-point hazard rate has been studied in the framework of life testing (Anderson and Senthilselvan, 1982; Matthews and Farewell, 1982; Nguyen *et al.*, 1984). The hazard function is defined as:

$$Z(t) = \begin{cases} Z_1 & (0 \leq t \leq t_r) \\ Z_2 & (t > t_r) \end{cases}, \quad (5)$$

where t_r indicates a change point and Z_1, Z_2 are hazard rates. This is called a change-point hazard rate model and is often applied to cancer mortality studies. The hazard rates are supposed to be time-varying but it is difficult to specify the functional forms. In the fishery context, the step function model can be a good first approximation of the time-varying hazard function, considering the variability of data. In our case, there are two mortality rates; the natural mortality rate, M , and the fishing mortality rate, F . We define the following three models.

Model 1: $Z = F + M (0 \leq t \leq t_k)$.

For Model 1, $p(t)$ and P_i is given by:

$$p(t) = F e^{-Zt}, \quad (6)$$

$$P_i = \frac{F}{Z} (e^{-Zt_{i-1}} - e^{-Zt_i}). \quad (7)$$

Model 2: $Z_1 = F_1 + M_1 (0 \leq t \leq t_r)$, $Z_2 = F_2 + M_2 (t_r < t \leq t_k)$.

For Model 2, $p(t)$ and P_i is given by:

$$p(t) = \begin{cases} F_1 e^{-Z_1 t} & (0 \leq t \leq t_r) \\ F_2 e^{-Z_1 t_r - Z_2 (t - t_r)} & (t_r < t \leq t_k) \end{cases}, \quad (8)$$

$$P_i = \begin{cases} \frac{F_1}{Z_1} (e^{-Z_1 t_{i-1}} - e^{-Z_1 t_i}) & (1 \leq i \leq \tau) \\ \frac{F_2}{Z_2} e^{-Z_2 t_i} (e^{-Z_2(t_{i-1}-t_i)} - e^{-Z_2(t_i-t_{i+1})}) & (\tau+1 \leq i \leq k) \end{cases} \quad (9)$$

Model 3: $Z_1 = F + M_1 (0 \leq t \leq t_\tau)$, $Z_2 = F + M_2 (t_\tau < t \leq t_k)$.

For Model 3, $p(t)$ and P_i are given by expressions similar to Equations (8) and (9).

Partial likelihood for multinomial model

First, we consider the approach for estimating Z by the partial likelihood (Cox, 1975). The merit of using this approach is its short computation time in our context. When there are many models to compare, such as the change-point alternatives, the CPU time becomes critical. The likelihood is decomposed into two factors as:

$$L(Z, F | n_1, \dots, n_{k+1}) = L_1(Z | n_1, \dots, n_k, n) \cdot L_2(Z, F | n), \quad (10)$$

where $L_1(Z | n_1, \dots, n_k, n)$ is the conditional likelihood of n_1, \dots, n_k given the total recovery n , and L_2 is the residual.

The information on the total mortality rate is included mainly in the conditional likelihood L_1 , whereas the residual likelihood L_2 has the most information on the fishing mortality. Hence, we have the following two-step procedure: (1) to estimate Z maximizing L_1 ; and (2) to obtain estimates of F maximizing L_2 substituting the estimates of Z . We can estimate Z only from recapture times where N is not required. The most important reason for using methods that estimate Z only is that they are not sensitive to constant rates of non-reporting, death on release, and the like.

For Model 1, we have:

$$L_1 = \frac{n!}{\prod_{i=1}^k n_i!} \prod_{i=1}^k Q_i^{n_i}, \quad (11)$$

$$L_2 = \frac{N!}{(N-n)!n!} \left\{ \int_0^{t_k} p(t) dt \right\}^n \left\{ 1 - \int_0^{t_k} p(t) dt \right\}^{N-n}, \quad (12)$$

where $Q_i = P_i / \int_0^{t_k} p(t) dt$. As the integral of the instantaneous mortality rate is given by:

$$\int_0^{t_k} p(t) dt = \frac{F}{Z} (1 - e^{-Z t_k}), \quad (13)$$

we have the conditional probability recaptured at the i th interval as:

$$Q_i = \frac{e^{-Z t_{i-1}} - e^{-Z t_i}}{1 - e^{-Z t_k}} \quad (1 \leq i \leq k). \quad (14)$$

The MLE of Z exists if and only if $n_1 < n$ and $\sum_{i=1}^k n_i(t_{i-1} + t_i) < n t_k$ and is obtained as the unique positive root of the equation (Kulldorff, 1961):

$$\sum_{i=1}^k \frac{n_i(t_i - t_{i-1})}{e^{(t_i - t_{i-1})Z} - 1} - \frac{n t_k}{e^{Z t_k} - 1} - \sum_{i=2}^k n_i t_{i-1} = 0. \quad (15)$$

F is estimated from $\partial \log L_2 / \partial F = 0$, where:

$$L_2 = \frac{N!}{(N-n)!n!} \left\{ \frac{F}{Z} (1 - e^{-Z t_k}) \right\}^n \quad (16)$$

$$\times \left\{ 1 - \frac{F}{Z} (1 - e^{-Z t_k}) \right\}^{N-n}.$$

Hence, we have:

$$\hat{F} = \frac{n \hat{Z}}{N(1 - e^{-Z t_k})} \quad (17)$$

(Kitada and Hirano, 1987).

For the change-point alternatives, we can use the partial-likelihood approach only in the case where the fishing mortality rate and the natural mortality rate have the same change point. Estimation for Model 2 and asymptotic variances are given in the Appendix.

Over-dispersion and correlation

Use of the multinomial distribution assumes that data are taken by simple random sampling. However, many fish species are distributed in patches which are differentially harvested. The recoveries of these species therefore may be over-dispersed. The multinomial distribution model is expected to be robust against over-dispersion, but the standard errors are negatively biased. When we test the null hypotheses or when we compare some statistical models, we tend to select too-complicated models. The Dirichlet compound multinomial distribution (Johnson and Kotz, 1969) is considered as a generalization of the multinomial distribution which takes account of over-dispersion. The means, variances, and covariances of $n_i (i=1, \dots, k)$ of this distribution are $E[n_i] = NP_i$, $V[n_i] = \sigma^2 NP_i(1 - P_i)$ and $Cov[n_i, n_j] = -\sigma^2 NP_i P_j$, where σ^2 is the dispersion parameter. Here, we consider a normal approximation of the model.

From the first expression of Equation (1), we get the following normal distribution model.

$$L(n_1, \dots, n_{k+1}) = \frac{1}{(2\pi \sigma^2)^{k/2} \left(\prod_{i=1}^k m_i p_i q_i \right)^{1/2}} \quad (18)$$

$$\times \exp \left\{ -\frac{1}{2} \sum_{i=1}^k \frac{(n_i - m_i p_i)^2}{m_i p_i q_i \sigma^2} \right\},$$

where $m_i = N - \sum_{j=1}^i n_j$. From the second expression of Equation (1), we get:

$$L(n_1, \dots, n_{k+1}) = \frac{1}{(2\pi N \sigma^2)^{k/2} \left(\prod_{i=1}^{k+1} P_i\right)^{1/2}} \quad (19)$$

$$\times \exp \left\{ -\frac{1}{2} \sum_{i=1}^{k+1} \frac{(n_i - N P_i)^2}{N P_i \sigma^2} \right\},$$

where $n_{k+1} = N - n$, $P_{k+1} = 1 - \sum_{i=1}^k P_i$. These likelihoods are asymptotically equivalent. Here, we use the later model. We treat σ^2 as an active parameter. By substituting P_i of Models 1, 2, and 3 to Equation (19), we obtain the likelihood function for the change-point alternatives against the constant mortality model. We can estimate parameters under various given change points, and select the best-fit model by using the Akaike information criterion (AIC; Akaike, 1973); $AIC = -2 \log \hat{L} + 2s$, where s is the number of free parameters. We take the change point of the best-fit model as our final estimate.

Taking account of the correlation between the recoveries of the two groups, the conditional likelihood of $n_i \equiv (n^{(1)}, n^{(2)})$ given n_1, \dots, n_{i-1} is expressed by:

$$L(n_i | n_1, \dots, n_{i-1}) = \frac{1}{2\pi \{m_i^{(1)} m_i^{(2)} p_i^{(1)} p_i^{(2)} q_i^{(1)} q_i^{(2)} (1 - \rho^2)\}^{1/2} \sigma_{(1)} \sigma_{(2)}} \quad (20)$$

$$\times \exp \left[-\frac{1}{2(1 - \rho^2)} \left\{ \sum_{j=1}^2 \frac{(n_i^{(j)} - m_i^{(j)} p_i^{(j)})^2}{m_i^{(j)} p_i^{(j)} q_i^{(j)} \sigma_{(j)}^2} - 2\rho \frac{(n_i^{(1)} - m_i^{(1)} p_i^{(1)}) (n_i^{(2)} - m_i^{(2)} p_i^{(2)})}{\sqrt{m_i^{(1)} p_i^{(1)} q_i^{(1)} m_i^{(2)} p_i^{(2)} q_i^{(2)}} \sigma_{(1)} \sigma_{(2)}} \right\} \right],$$

where suffix (1), (2), and j refer to the release group, and ρ is the correlation coefficient. From this conditional likelihood, we obtain the joint-likelihood function:

$$L(n_1, \dots, n_{k+1}) = \frac{1}{(2\pi)^k \left(\prod_{i=1}^k m_i^{(1)} m_i^{(2)} p_i^{(1)} p_i^{(2)} q_i^{(1)} q_i^{(2)}\right)^{1/2} (1 - \rho^2)^{k/2} (\sigma_{(1)} \sigma_{(2)})^k} \quad (21)$$

$$\times \exp \left[-\frac{1}{2(1 - \rho^2)} \sum_{i=1}^k \left\{ \sum_{j=1}^2 \frac{(n_i^{(j)} - m_i^{(j)} p_i^{(j)})^2}{m_i^{(j)} p_i^{(j)} q_i^{(j)} \sigma_{(j)}^2} - 2\rho \frac{(n_i^{(1)} - m_i^{(1)} p_i^{(1)}) (n_i^{(2)} - m_i^{(2)} p_i^{(2)})}{\sqrt{m_i^{(1)} p_i^{(1)} q_i^{(1)} m_i^{(2)} p_i^{(2)} q_i^{(2)}} \sigma_{(1)} \sigma_{(2)}} \right\} \right],$$

or equivalently:

$$L(n_1, \dots, n_{k+1}) = \frac{1}{(2\pi)^k (N^{(1)} N^{(2)})^{k/2} \left(\prod_{i=1}^{k+1} P_i^{(1)} P_i^{(2)}\right)^{1/2} (1 - \rho^2)^{k/2} (\sigma_{(1)} \sigma_{(2)})^k} \quad (22)$$

$$\times \exp \left[-\frac{1}{2(1 - \rho^2)} \sum_{i=1}^{k+1} \left\{ \sum_{j=1}^2 \frac{(n_i^{(j)} - N^{(j)} P_i^{(j)})^2}{N^{(j)} P_i^{(j)} \sigma_{(j)}^2} - 2\rho \frac{(n_i^{(1)} - N^{(1)} P_i^{(1)}) (n_i^{(2)} - N^{(2)} P_i^{(2)})}{\sqrt{N^{(1)} P_i^{(1)} N^{(2)} P_i^{(2)}} \sigma_{(1)} \sigma_{(2)}} \right\} \right],$$

where $n_{k+1}^{(j)} = N^{(j)} - n^{(j)}$, $P_{k+1}^{(j)} = 1 - \sum_{i=1}^k P_i^{(j)}$.

Maximizing the full-likelihood function numerically, we can obtain estimates of mortality rates, ρ , and σ^2 , simultaneously. Standard errors of these parameters

It is important to compare the viability of several groups of fingerlings. Besides experimental studies in laboratories, the comparison in the field is indispensable. A possible statistical procedure of detecting the difference from the recoveries would be to see whether estimated mortality rates are significantly different or not. However, the different groups of fingerlings were released simultaneously, at the same place and the same time, to compare the survival rates under the same environment. They would make patches, and it is expected that those patches of different groups are spatially correlated. Hence, the recovery data of these groups may be correlated.

Let $n^{(1)}$, $n^{(2)}$ be the recovery data of two release groups, and θ_1 , θ_2 be the vectors representing their mortality rates. Even if θ_1 , θ_2 are estimated separately from each of the recovery data, the estimates $\hat{\theta}_1 = \theta_1(n^{(1)})$ and $\hat{\theta}_2 = \theta_2(n^{(2)})$ are correlated, since the data $n^{(1)}$ and $n^{(2)}$ are not independent.

except the change point are also obtained from the Hessian matrix numerically. The precision of the change-point estimate could be a topic for further

Table 1. Tag recoveries from two groups of red seabreams tagged with Red and White tags. The number released for each group is 20 000.

Days after release	Number of recoveries		Days after release	Number of recoveries	
	Red	White		Red	White
1	338	266	17	74	64
2	274	194	18	39	62
3	193	205	19	8	14
4	296	308	20	82	78
5	169	183	21	4	3
6	176	170	22	26	19
7	67	45	23	25	17
8	98	102	24	36	38
9	14	14	25	9	7
10	71	71	26	8	14
11	28	26	27	15	21
12	76	74	28	17	19
13	83	77	29	4	2
14	5	4	30	19	25
15	124	125			
16	44	47	Total	2422	2294

discussion. Studies on confidence limits of these kind of models have started in phylogenetic analyses using bootstrap methods (Felsenstein, 1985).

The case of red seabream

Red seabream is an important coastal fishery resource and its annual catch in Japan was 13 734 tons in 1990. The demand for red seabream is high, whereas the annual catch of red seabream has been gradually decreasing. Aquaculture of red seabream has made rapid progress and the annual production reached 51 568 tons in 1992. However, few suitable sites for aquaculture remain around the coast of Japan. Red seabream is therefore one of the main species of the Japanese stock enhancement programs for coastal marine resources.

Our case study deals with the two releases of red seabream conducted in the same field at the same time. The objective of this experiment was to compare the mortality rates of the two groups reared by different methods. We prepared two groups of fingerlings. They had been born from the same adult fish but reared in different hatcheries. We attached red tags to one group and white ones to the other group (henceforth we call them Red and White). The mean size was 10 cm in total length for each group, respectively. We kept tagged fish in net cages over two nights before release, and dead or weakened fingerlings were removed. We released 20 000 tagged fish of Red and White, respectively, in the fishing ground of commercial trawlers in the Seto Inland Sea on 30 September 1989. We conducted the release while sailing our boat to scatter the fingerlings throughout the area. The Red and White tagged fish were mixed on release. Before the release we asked fishermen's

co-operatives who fished around the release site for their co-operation in reporting recoveries.

The number of recoveries gradually decreased as the water temperature dropped, hence we censored the recovery data at the 30th day. The total recovery of Red was 2422 and that of White was 2294 (Table 1). The recovery rates were 0.121 and 0.115, respectively. The declining trends in recoveries with time were very similar for Red and White tags. Fitting the negative exponential curves to the recovery data, the variation of the recovery was large (Fig. 1). We can see that the recovery declines rapidly soon after release, but after some time it becomes stable. Hence, we analyze the model with a change-point alternative.

First, we analyzed the recovery data of Red using the multinomial model. The estimates and their standard errors from the full likelihood and the conditional likelihood took the same values, although the standard errors of F_2 were slightly different (Table 2). Comparing the AIC values for model 1, model 2, and model 3 under various change points, the model 2 under the change point of 14 days was selected (Fig. 2). On the other hand, the partial log-likelihood values ($-\text{Log } L_1$) generated a pattern similar to the AIC values of the full likelihood for model 2 (Figs 2, 3). The CPU time of calculation of the partial-likelihood model is much shorter than that of the full-likelihood model, although we have to evaluate the covariance between \hat{Z} estimated from the partial likelihood L_1 and \hat{F} estimated from the residual likelihood L_2 to obtain the variance of \hat{M} . Under the multinomial distribution, the χ^2 test for goodness-of-fit rejected the hypothesis even on the best-fit model. This is because the variability of the recovery data was larger than expected assuming simple random

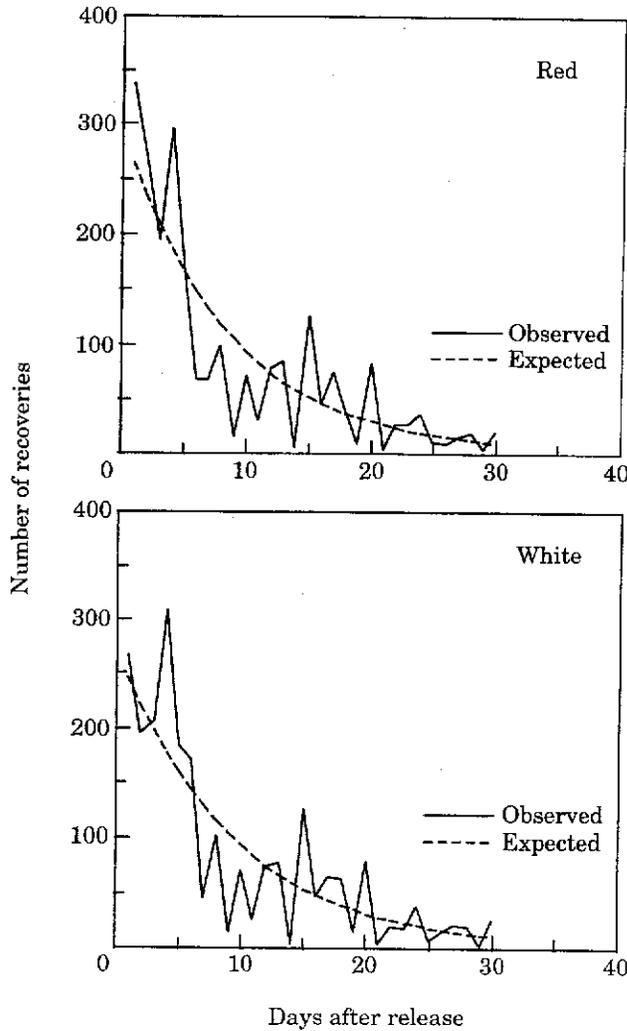


Figure 1. Observed and expected recoveries of Red seabream tagged with Red and White tags for 30 days after release.

Table 2. Estimates and standard errors of parameters of Red tags based on the full likelihood and the partial likelihood of the multinomial model.

Model		Full likelihood		Partial likelihood	
		Estimate	S.E.	Estimate	S.E.
1	Z	0.1196	0.0031	0.1196	0.0031
	F	0.0149	0.0004	0.0149	0.0004
	M	0.1047	0.0028	0.1047	
2	t_r	14		14	
	Z_1	0.1862	0.0067	0.1862	0.0067
	Z_2	0.1554	0.0108	0.1554	0.0108
	F_1	0.0190	0.0007	0.0190	0.0007
	F_2	0.0613	0.0071	0.0613	0.0065
	M_1	0.1672	0.0061	0.1672	
	M_2	0.0940	0.0098	0.0940	

sampling rather than because the fitted models were all too incomplete to explain the data. We obtained the

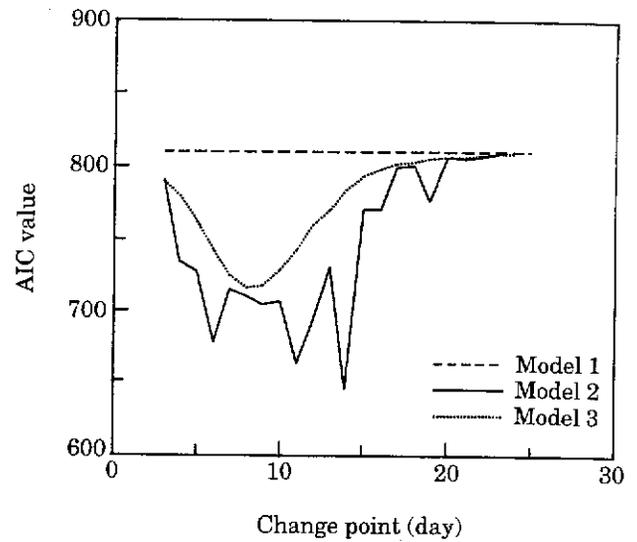


Figure 2. The behavior of the Akaike information criterion (AIC) for Red tag recoveries for model 1, model 2, and model 3 of the multinomial model.

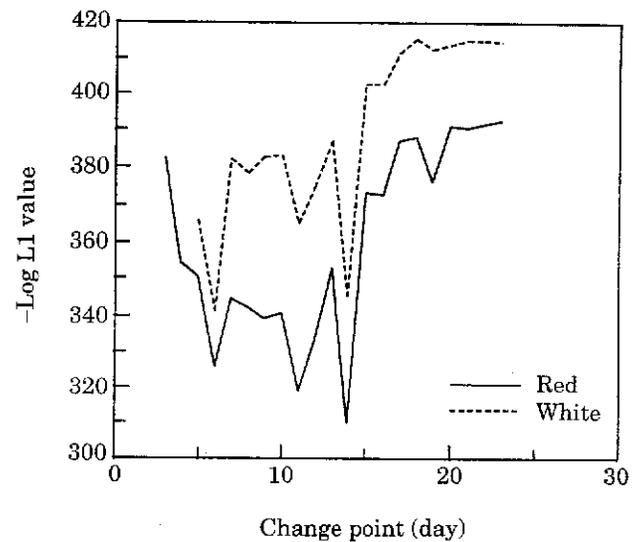


Figure 3. The behavior of the partial log likelihood of Red and White for model 2 of the multinomial model.

change-point estimate for Red as 14, but some other local minimums of the AIC value existed (Fig. 2). We could not clearly detect the minimum that shows the change point because the variability of the recovery data was underestimated.

Hence, we analyzed the data using the normal approximation model to take over-dispersion into account. Before using this model, we tested the goodness of the approximation for the multinomial model. Under $N=20\ 000$, $Z=0.01$, $F=0.02$, $k=30$, we generated the recovery data of multinomial random variables. We estimated Z and F by Equations (1) and (19) and calculated means and standard errors of the parameters through 100 simulations. The means and standard errors

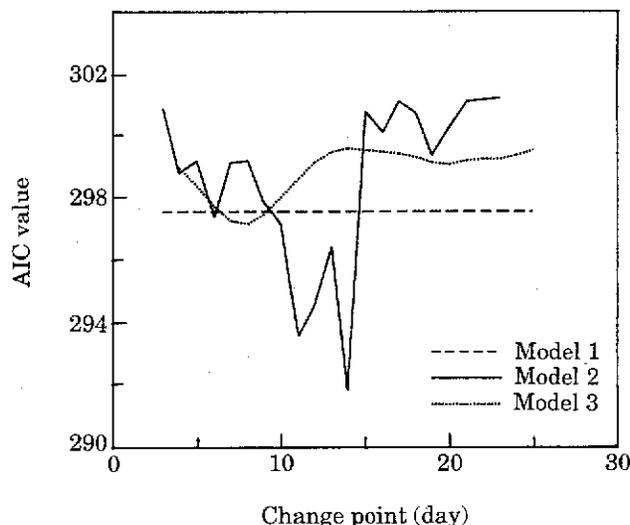


Figure 4. The behavior of the akaile information criterion (AIC) for Red tag recoveries for model 1, model 2, and model 3 of the normal approximation model of $\sigma^2 > 1$.

Table 3. Estimates and standard errors for fish with Red tags for model 2 of $\sigma^2 = 1$ and $\sigma^2 > 1$.

Model	$\sigma^2 = 1$		$\sigma^2 > 1$	
	Estimate	S.E.	Estimate	S.E.
t_r	14		14	
Z_1	0.1666	0.0062	0.1757	0.0238
Z_2	0.1489	0.0094	0.1754	0.0355
F_1	0.0183	0.0006	0.0183	0.0025
F_2	0.0511	0.0054	0.0563	0.0230
M_1	0.1484	0.0057	0.1574	0.0219
M_2	0.0978	0.0085	0.1191	0.0324
σ^2			14.73	4.16
AIC	589.09		291.80	

for Z and F for the multinomial and its approximation were equivalent.

Using the normal distribution model with σ^2 , the curve of the AIC value became smoother, and the clear minimum of the AIC value was observed at the 14th day (Fig. 4). The AIC value of the best-fit model with $\sigma^2 > 1$ was very small compared with the model with $\sigma^2 = 1$ (Table 3). Point estimates of parameters took almost the same values for both models, but standard errors were quite large taking into account the over-dispersion (Table 3). This indicates that the fluctuation of the recovery data was $\sqrt{14.73}$ times larger than the multinomial distribution. Model 2 was selected with a change point on the 14th day, but this model assumes that F and M change on the same day, which may not be reasonable. Hence, we considered a fourth model in which M is constant but F changes on the 14th day. The AIC value for this model was smaller than that of model 2 (Table 4), suggesting a constant natural mortality rate.

Table 4. Estimates and standard errors for fish with Red tags for model 4 under $\sigma^2 > 1$.

Z_1	0.1604 (0.0138)
Z_2	0.1916 (0.0282)
F_1	0.0171 (0.0018)
F_2	0.0483 (0.0168)
M	0.1433 (0.0128)
σ^2	15.34 (4.32)
AIC	290.45

Table 5. Estimates and standard errors for the best-fit model (model D) obtained by simultaneous estimation under model 4.

	Red Tags	White Tags
Z_1	0.1700 (0.0152)	0.1593 (0.0166)
Z_2	0.1982 (0.0289)	0.1813 (0.0287)
F_1	0.0178 (0.0018)	0.0158 (0.0017)
F_2	0.0460 (0.0161)	0.0377 (0.0143)
M	0.1522 (0.0141)	0.1436 (0.0155)
σ^2	21.39 (6.46)	23.68 (7.19)
ρ	0.95 (0.014)	

We also obtained the same change-point estimate for White, and the estimates of other parameters were similar. To compare the mortality rates of Red and White, we considered the likelihood [Equation (22)] taking the correlation between the recovery data of the two groups into account. We considered four models with regard to P_i and ρ :

- Model A: $P_i^{(1)} = P_i^{(2)}$ and $\rho = 0$,
- Model B: $P_i^{(1)} = P_i^{(2)}$ and $\rho \neq 0$,
- Model C: $P_i^{(1)} \neq P_i^{(2)}$ and $\rho = 0$,
- Model D: $P_i^{(1)} \neq P_i^{(2)}$ and $\rho \neq 0$.

The maximum log-likelihood values for models A, B, C, and D were -284.55 , -254.27 , -286.16 , and -250.00 , respectively. The correlation, ρ , was estimated to be over 0.9, and the models assuming no correlation (models A, C) were rejected. It was suggested that two groups were mixed and distributed in the same area, hence we compared model B with model D. The likelihood ratio was $-2 \times (-254.27 + 250.00) = 8.54$ ($p = 0.074$ with d.f. of 4). We could not reject the hypothesis of no difference between the two groups (Table 5). We concluded that the rearing way of different two hatcheries did not influence the quality of the fingerlings.

Discussion and concluding remarks

By means of the χ^2 test under a 2×2 contingency table, it was possible to test the hypothesis that the recovery rates of the two groups are the same. The numbers recaptured and not recaptured were 2422 (2294) and

17 578 (17 706) for Red and (White), respectively. For this data we calculate the χ^2 statistic to be 3.94, and therefore reject the null hypothesis (d.f. of 1, $p=0.047$). This corresponds to analyzing only by the residual likelihood L_2 [Equation (16)] in the partial-likelihood approach. Denoting the recovery rates for each group by $P^{(1)}$ and $P^{(2)}$, the null hypothesis (H_0) is $P^{(1)}=P^{(2)}=P$. The joint residual likelihood function for group 1 and group 2 is given by:

$$L_r = L_2^{(1)} L_2^{(2)}, \quad (23)$$

if the recoveries of the two groups are independent. The maximum-likelihood estimates of P , $P^{(1)}$, and $P^{(2)}$ are obtained from $\log L_r$ as $(n^{(1)}+n^{(2)})/(N^{(1)}+N^{(2)})$, $n^{(1)}/N^{(1)}$, $n^{(2)}/N^{(2)}$, respectively. We obtained the maximum value for $\log L_r$ of $-14\,508.80$ (H_0) and $-14\,506.83$ (H_1). The likelihood ratio statistic was equal to 3.93 and we rejected the null hypothesis (d.f. of 1, $p=0.047$). This result was consistent with the χ^2 test for the recovery rate, and led to different conclusions from former analysis. However, it is invalid because the over-dispersion and correlation are ignored.

When the recovery period is long enough, this hypothesis means the same value of F/M for the two groups. In evaluating the quality of fingerlings, it is better to investigate both of F and M , because it is supposed that weaker fingerlings have higher natural mortality rates and are easily caught. In addition, the essential parameters for field experiments such as σ^2 and ρ can only be estimated when we deal with serial recoveries.

The problem of over-dispersion has been overcome by quasi-likelihood approach. The quasi-likelihood estimating equation for the mortality rates of the group j , θ_j is given by:

$$U(\theta_j) = \sum_{i=1}^{k+1} \nabla_{\theta_j} (N P_i^{(j)}) \frac{n_i^{(j)} - N P_i^{(j)}}{N P_i^{(j)}} = 0. \quad (24)$$

The dispersion parameter can also be estimated from:

$$\hat{\sigma}_{(j)}^2 = \frac{1}{k-s} \sum_{i=1}^{k+1} \frac{(n_i^{(j)} - N \hat{P}_i^{(j)})^2}{N \hat{P}_i^{(j)}}. \quad (25)$$

The variance-covariance matrix of $\hat{\theta}_j$ is given by:

$$V(\hat{\theta}_j) = \hat{\sigma}_{(j)}^2 \left(\sum_{i=1}^{k+1} \frac{1}{N P_i^{(j)}} \nabla_{\theta_j} (N P_i^{(j)}) \nabla_{\theta_j}^T (N P_i^{(j)}) \right)^{-1} \quad (26)$$

where T refers to the transposed matrix (McCullagh and Nelder, 1989). However, the quasi-likelihood framework does not include the estimation when paired data have the correlation treated in this paper. This problem is left for further studies.

Maximum-likelihood procedures are powerful statistical tools for many applications, but proper modeling is important. We have observed that, when we apply the multinomial model to field survey data, the standard

errors of the estimates are often negatively biased. To solve this problem, Dirichlet compound multinomial and negative binomial distributions have been considered. In this paper we applied the normal distribution models as approximations of these models to the data in the framework of maximum-likelihood procedure. We expect that this approach will prove useful and practical to field survey experiments in general.

Acknowledgments

We thank Drs William S. Hearn, CSIRO Division of Fisheries, Jeffrey L. Thorne, Department of Statistics, North Carolina State University, and Makoto Shimizu, Department of Agriculture, University of Tokyo, for their useful comments on the earlier version of this paper. We also thank the anonymous referees for their comments which greatly improved the original manuscript.

References

- Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. *In* 2nd International Symposium on Information Theory, pp. 267–281. Ed. by B. N. Petrov and F. Csáki. Akadémiai Kiadó, Budapest.
- Anderson, J. A., and Senthilselvan, A. 1982. A two step regression model for hazard function. *Applied Statistics*, 31: 44–51.
- Cox, D. R. 1975. Partial likelihood. *Biometrika*, 62: 269–276.
- Felsenstein, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution*, 39: 783–791.
- Farebrother, R. W. 1988. Maximum likelihood estimates of mortality rates from single-release tagging studies. *Journal du Conseil International pour l'Exploration de la Mer*, 44: 229–234.
- Gulland, J. A. 1955. On the estimation of population parameters from marked members. *Biometrika*, 42: 269–270.
- Hearn, W. S., Sandland, R. L., and Hampton, J. 1987. Robust estimation of the natural mortality rate in a completed tagging experiment with variable fishing intensity. *Journal du Conseil International pour l'Exploration de la Mer*, 43: 107–117.
- Hiramatsu, K., and Kishino, H. 1989. Stock identification by maximum likelihood method. Derivation of variance estimator. Document submitted to the Annual Meeting of the International North Pacific Fisheries Commission, Seattle, USA, November 1989. 14 pp.
- Johnson, N. L., and Kotz, S. 1969. *Discrete distributions*. J. Wiley & Sons, New York. 328 pp.
- Kitada, S., and Hirano, K. 1987. Estimation of mortality coefficients from grouped tag recoveries (in Japanese). *Nippon Suisan Gakkaishi*, 53: 1765–1770.
- Kitada, S., Taga, Y., and Kishino, H. 1992. Effectiveness of a stock enhancement program evaluated by a two-stage sampling survey of commercial landings. *Canadian Journal of Fisheries and Aquatic Sciences*, 49: 1573–1582.
- Kitahara, T., Takahashi, K., Hujikawa, Y., Ishida, K., and Yoshio, J. 1986. Estimation of fishing mortality coefficient from tag recoveries in a finite period with a few closed seasons. *Nippon Suisan Gakkaishi*, 52: 579–584.
- Kulldorff, G. 1961. Contributions to the theory of estimation from grouped and partially grouped samples. *J. Wiley & Sons*, New York. 144 pp.

Leigh, G. M. 1988. A comparison of estimates of natural mortality from tagging experiments. *Biometrika*, 75: 347-353.

McCullagh, P., and Nelder, J. A. 1989. *Generalized linear models*, 2nd edn. Chapman and Hall, London. 511 pp.

Matthews, D. E., and Farewell, V. T. 1982. On testing for a constant hazard against a change-point alternative. *Biometrics*, 38: 463-468.

Nguyen, H. T., Rogers, G. S., and Walker, E. A. 1984. Estimation in change-point hazard rate models. *Biometrika*, 71: 299-304.

Paulik, G. J. 1963. Estimates of mortality rates from tag recoveries. *Biometrics*, 49: 28-57.

Seber, G. A. F. 1982. *The estimation of animal abundance and related parameters*, 2nd edn., Griffin, London. 654 pp.

Appendix

Estimates and asymptotic variances by conditional likelihood

For model 2, conditional rate of recapture at i th interval is given by:

$$Q_i = \begin{cases} \frac{e^{-Z_1 t_{i-1}} - e^{-Z_1 t_i}}{1 - e^{-Z_1 t_i}} & (1 \leq i \leq \tau) \\ \frac{e^{-Z_2 t_{i-1}} - e^{-Z_2 t_i}}{1 - e^{-Z_2(t_k - t_i)}} & (\tau < i \leq k) \end{cases} \quad (A.1)$$

The likelihood functions are given by:

$$L_1 = \frac{m_1!}{\prod_{i=1}^{\tau} n_i!} \prod_{i=1}^{\tau} Q_i^{n_i} \frac{m_2!}{\prod_{i=\tau+1}^k n_i!} \prod_{i=\tau+1}^k Q_i^{n_i}, \quad (A.2)$$

$$L_2 = \frac{N!}{(N-n)!m_1!m_2!} \left\{ \int_0^{t_{\tau}} p(t) dt \right\}^{m_1} \left\{ \int_{t_{\tau}}^{t_k} p(t) dt \right\}^{m_2} \left\{ 1 - \int_0^{t_k} p(t) dt \right\}^{N-n}, \quad (A.3)$$

where $m_1 = \sum_{i=1}^{\tau} n_i$, $m_2 = \sum_{i=\tau+1}^k n_i$. We estimate the total mortality rates, Z_1 and Z_2 , by dividing the recoveries for two parts under a given t_{τ} between time $0 < t_{\tau} < t_k$ by Equation (15). The estimation procedure of t_{τ} is as follows. The partial likelihood L_1 is divided into two parts:

$$\log L_1(Z_1) = \log m_1! - \sum_{i=1}^{\tau} \log n_i! + \sum_{i=1}^{\tau} n_i \log (e^{-Z_1 t_{i-1}} - e^{-Z_1 t_i}) - n_1 \log (1 - e^{-Z_1 t_{\tau}}) \quad (1 \leq i \leq \tau) \quad (A.4)$$

and:

$$\log L_1(Z_2) = \log m_2! - \sum_{i=\tau+1}^k \log n_i! + \sum_{i=\tau+1}^k n_i \log (e^{-Z_2 t_{i-1}} - e^{-Z_2 t_i}) - n_2 \log \{1 - e^{-Z_2(t_k - t_{\tau})}\} \quad (\tau+1 \leq i \leq k). \quad (A.5)$$

The log likelihood for L_1 is given by:

$$\log L_1 = \log L_1(Z_1) + \log L_1(Z_2). \quad (A.6)$$

The t_{τ} which maximizes this log likelihood is accepted as the estimate of t_{τ} .

We estimate F_1 and F_2 , from $\partial \log L_2 / \partial F_1 = 0$ and $\partial \log L_2 / \partial F_2 = 0$, where:

$$L_2 = \frac{N!}{(N-n)!m_1!m_2!} \left\{ \frac{F}{Z_1} (1 - e^{-Z_1 t_{\tau}}) \right\}^{m_1} \left\{ \frac{e^{-Z_1 t_{\tau}} F}{Z_2} (1 - e^{-Z_2(t_k - t_{\tau})}) \right\}^{m_2} \\ \times \left\{ 1 - \frac{F}{Z_1} (1 - e^{-Z_1 t_{\tau}}) - \frac{e^{-Z_1 t_{\tau}} F}{Z_2} (1 - e^{-Z_2(t_k - t_{\tau})}) \right\}^{N-n}. \quad (A.7)$$

The estimator of F_1 and F_2 is given by:

$$\hat{F}_1 = \frac{m_1 \hat{Z}_1}{N (1 - e^{-\hat{Z}_1 t_{\tau}})}. \quad (A.8)$$

$$\hat{F}_2 = \frac{m_2 \hat{Z}_2}{N e^{-\hat{Z}_2 t_k} \{1 - e^{-\hat{Z}_2(t_k - t_0)}\}} \quad (\text{A.9})$$

The asymptotic variance of \hat{Z} are given by:

$$V(\hat{Z}) = \left(- \frac{\partial^2 \log L_1}{\partial Z^2} \right)^{-1} \quad (\text{A.10})$$

For the case of equal unit length of each time interval α , the variance for model 1 is given by (Kulldorff, 1961):

$$V(\hat{Z}) = \left\{ \frac{\alpha^2 e^{Z\alpha}}{(e^{Z\alpha} - 1)^2} - \frac{t_k^2 e^{Zt_k}}{(e^{Zt_k} - 1)^2} \right\}^{-1} \quad (\text{A.11})$$

For model 2, we can obtain variances from Equation (A.11) by substituting t_k for $(t_k - t_0)$.

The asymptotic variances of \hat{F} are given by (Hiramatsu and Kishino, 1989)

$$V(\hat{F}) = \left(- \frac{\partial^2 \log L_2}{\partial F^2} \right)^{-1} \left\{ \left(- \frac{\partial^2 \log L_2}{\partial F^2} \right) + \frac{\partial^2 \log L_2}{\partial F \partial Z} V(\hat{Z}) \frac{\partial^2 \log L_2}{\partial Z \partial F} \right\} \left(- \frac{\partial^2 \log L_2}{\partial F^2} \right)^{-1} \quad (\text{A.12})$$

Concrete forms of the asymptotic variance of \hat{F} for the conditional multinomial model are given by the following equations.

Model 1:

$$V(\hat{F}) = \left(- \frac{\partial^2 \log L_2}{\partial F^2} \right)^{-1} \left\{ - \frac{\partial^2 \log L_2}{\partial F^2} + \frac{\partial^2 \log L_2}{\partial F \partial Z} V(\hat{Z}) \frac{\partial^2 \log L_2}{\partial Z \partial F} \right\} \left(- \frac{\partial^2 \log L_2}{\partial F^2} \right)^{-1} \quad (\text{A.13})$$

where:

$$\frac{\partial^2 \log L_2}{\partial F^2} = - \frac{1}{F^2} \frac{nN}{N-n} \quad (\text{A.14})$$

$$\frac{\partial^2 \log L_2}{\partial F \partial Z} = - \frac{N^2}{Z^2} \frac{1}{N-n} (Z t_k e^{-Z t_k} + e^{-Z t_k} - 1) \quad (\text{A.15})$$

Model 2:

$$V(\hat{F}) = \begin{pmatrix} V(\hat{F}_1) & \text{Cov}(\hat{F}_1, \hat{F}_2) \\ \text{Cov}(\hat{F}_2, \hat{F}_1) & V(\hat{F}_2) \end{pmatrix} = \begin{pmatrix} - \frac{\partial^2 \log L_2}{\partial F_1^2} & - \frac{\partial^2 \log L_2}{\partial F_1 \partial F_2} \\ - \frac{\partial^2 \log L_2}{\partial F_2 \partial F_1} & - \frac{\partial^2 \log L_2}{\partial F_2^2} \end{pmatrix}^{-1} \quad (\text{A.16})$$

$$\times \left\{ \begin{pmatrix} - \frac{\partial^2 \log L_2}{\partial F_1^2} & - \frac{\partial^2 \log L_2}{\partial F_1 \partial F_2} \\ - \frac{\partial^2 \log L_2}{\partial F_2 \partial F_1} & - \frac{\partial^2 \log L_2}{\partial F_2^2} \end{pmatrix} + \begin{pmatrix} \frac{\partial^2 \log L_2}{\partial F_1 \partial Z_1} & \frac{\partial^2 \log L_2}{\partial F_1 \partial F_2} \\ \frac{\partial^2 \log L_2}{\partial F_2 \partial Z_1} & \frac{\partial^2 \log L_2}{\partial F_2 \partial Z_2} \end{pmatrix} \begin{pmatrix} V(\hat{Z}_1) & 0 \\ 0 & V(\hat{Z}_2) \end{pmatrix} \right.$$

$$\left. \times \begin{pmatrix} \frac{\partial^2 \log L_2}{\partial Z_1 \partial F_1} & \frac{\partial^2 \log L_2}{\partial Z_1 \partial F_2} \\ \frac{\partial^2 \log L_2}{\partial Z_2 \partial F_1} & \frac{\partial^2 \log L_2}{\partial Z_2 \partial F_2} \end{pmatrix} \right\} \times \begin{pmatrix} - \frac{\partial^2 \log L_2}{\partial F_1^2} & - \frac{\partial^2 \log L_2}{\partial F_1 \partial F_2} \\ - \frac{\partial^2 \log L_2}{\partial F_2 \partial F_1} & - \frac{\partial^2 \log L_2}{\partial F_2^2} \end{pmatrix}$$

where:

$$\frac{\partial^2 \log L_2}{\partial F_1^2} = - \frac{m_1}{F_1^2} \frac{N - m_2}{N - n}, \quad (\text{A.17})$$

$$\frac{\partial^2 \log L_2}{\partial F_2^2} = - \frac{m_2}{F_2^2} \frac{N - m_1}{N - n}, \quad (\text{A.18})$$

$$\frac{\partial^2 \log L_2}{\partial F_1 \partial Z_1} = - \frac{N}{Z_1^2} \frac{N - m_2}{N - n} (Z_1 t_r e^{-Z_1 t_r} + e^{-Z_1 t_r} - 1), \quad (\text{A.19})$$

$$\frac{\partial^2 \log L_2}{\partial F_2 \partial Z_2} = - \frac{N}{Z_2^2} \frac{N - m_1}{N - n} e^{-Z_1 t_r} \{ Z_2 (t_k - t_r) e^{-Z_2 (t_k - t_r)} + e^{-Z_2 (t_k - t_r)} - 1 \}. \quad (\text{A.20})$$

A.9)
A.10)
A.11)
A.12)
wing
A.13)
A.14)
A.15)
16)