ANALYSIS OF DOUBLE-TAGGING EXPERIMENTS

JERRY A. WETHERALL[1]

ABSTRACT

Statistics arising from double-tagging experiments may be applied to estimate tag-shedding probabilities directly, to estimate parameters of underlying theoretical shedding models, or to estimate mortality rates free of tag-shedding bias.

Simple maximum likelihood estimators of tag retention rates, along with their asymptotic variances, may be derived assuming conditional multinomial sampling models. If specific models of shedding are of interest, limitations of existing theory may be reduced by assuming the Type II shedding rate is time-dependent. In the more realistic models and their simpler precursors, parameters may be estimated by least squares or by maximum likelihood methods. Complications arising in the direct maximization of the conditional likelihood may be circumvented by use of iteratively reweighted Gauss-Newton algorithms available in standard statistical software packages. Simple diagnostic plots may be helpful in model selection.

When a sequence of double-tagged cohorts is released, recapture statistics may be treated separately or combined to estimate common shedding rates, but a more general linear model may be used to fully exploit the structure of the experiment and to estimate both common parameters and those unique to each cohort.

When recapture times are unknown but the experiment spans a sufficiently long period, the ratio of constant Type II tag-shedding rate to constant Type II total mortality rate may be estimated. Under similar circumstances, but with exact recapture times known for each fish, maximum likelihood estimates of both parameters may be computed.

If only the Type II mortality rate is of interest, it may be estimated free of tag-shedding bias by simple linear regression of appropriate double-tagging statistics, if Type II shedding and Type II mortality are constant during the experiment.

The estimation of fishing mortality rate, exploitation rate, and population size through mark and recapture experiments is often complicated by the incidental shedding or loss of marks. Failure to account for tag shedding may lead to biased parameter estimates. Thus a well-designed tagging experiment will incorporate some provision for estimating shedding rates and computing correction factors.

The approach usually taken is to release a group, or perhaps several groups of double-tagged fish, and then to estimate shedding rates using information on the number of fish returned in a sequence of recapture samples still bearing both tags and on the number of returns with only one tag remaining. A variety of statistical methods and estimation procedures have been developed. Papers by Beverton and Holt (1957), Gulland (1963), Chapman et al. (1965), Robson and Regier (1966), Chapman (1969), Bayliff and Mobrand (1972), Seber (1973), Laurs et al. (1976),

Arnason and Mills (1981), Kirkwood (1981), and Seber and Felton (1981) are particularly noteworthy. In recent years attention has focused primarily on the regression methods developed by Chapman et al. (1965) and extended first by Bayliff and Mobrand (1972) and most recently by Kirkwood (1981).

Despite the extensive literature on double-tagging there is need for an integration of existing thought and for development of new ideas and statistical methods. Accordingly, this paper surveys basic tag-shedding theory and the most widely used analytical techniques, and describes a variety of new models and estimation procedures. Left unaddressed are several important aspects of planning double-tagging experiments. These are the subject of a companion paper by Wetherall and Yong (1981).

TAG LOSS IN SINGLE-TAGGING EXPERIMENTS

To establish a context for later derivations we begin by reviewing the process of tag loss in a population of single-tagged fish. In such a popu-

lation, losses may be caused by fishing mortality or recapture, natural mortality, tagging mortality (mortality induced by the application or presence of the tag), permanent emigration, or by tag shedding. In addition, recaptured tags are considered "lost" if not detected in the catch and recovered, or, when recovered, if not returned or reported.

bined effects of fishing mortality, $F(x)$, natural mortality, $M(x)$, instantaneous tag shedding, $L(x)$, and remaining losses, $G(x)$. The usual assumptions are that the Type II losses operate in the manner of independent Poisson processes with constant rates and that the recovery and reporting rates also are constant. Under these conditions the model takes the familiar form

$$E(r_i) = \eta N_s(0)\left(\frac{F}{F + X}\right)\left(1 - \exp(-(F + X)\Delta_i)\right)\left(\exp(-(F + X)t_i)\right) \quad (1)$$

Beverton and Holt (1957) recognized two kinds of losses, which they designated Type I and Type II (these are called Type A and Type B by Ricker 1975). Type I losses are those which, in effect, reduce the number of tags initially put out. They result from the pulse of tagging mortality and tag shedding occurring immediately after release (or in a relatively brief period following release) and from the nonrecovery and nonreporting of tag recaptures. Type II losses are those happening steadily and gradually over an extended period following release of the tagged fish.

These relations may be stated more succinctly in a simple mathematical model. Let $E(r_i)$ denote the expected number of returns of tags recaptured in the ith time interval following the release of $N_s(0)$ single-tagged fish. Then

where $\eta = \pi \rho \zeta$
$X = M + L + G.$

A variety of estimation schemes based on this equation have been developed, notably by Paulik (1963). These have been reviewed along with other mark-and-recapture approaches by Cormack (1968) and Seber (1973). The importance of assumptions on Type I and Type II losses in these procedures depends on which parameters are of central concern in the experiment. In fisheries applications the parameter most often focused on is the fishing mortality rate, F. Paulik's single-release regression model with constant Δ, for estimating F and the exploitation rate, $\mu = (F/(F + M))[1 - \exp(-(F + M)\Delta)]$ stems directly from Equation (1). In this situation, if Type I losses are present the model will estimate ηF rather than

$$E(r_i) = \pi \rho N_s(0) \int_{t_i}^{t_i+\Delta_i} F(u)\,\zeta(u)\,\exp\left(-\int_0^u H(x)\,dx\right)du$$

where t_i = time at the beginning of interval i

Δ_i = length of time interval i

$1 - \pi$ = probability that a tag is lost due to immediate tagging mortality

$1 - \rho$ = probability that a tag is shed immediately following release

$F(u)$ = instantaneous fishing mortality rate at time u

$1 - \zeta(u)$ = probability that a tag recaptured at time u is not recovered and reported (a Type I loss)

$H(x)$ = total instantaneous rate of Type II tag loss at time x.

Here $H(x)$ represents the unspecified com-

F. Subsequent estimates of X will be too large. Further, estimates of the exploitation rate will be negatively biased, and if these are used along with $N_s(0)$ to estimate total population sizes, such estimates will be inflated. Of course, this is the general effect of Type I losses on Petersen estimates.

If Type II tagging mortality or Type II tag shedding occur, the estimate of F from this single-release model will not be affected, but the estimate of μ will be less than the true exploitation rate of the unmarked population.

Sometimes all recaptures are made during subintervals of equal length imbedded and irregularly spaced within the total recapture period (e.g., in a salmon fishery with a complex pattern of open and closed periods). In this case, Paulik shows that the single-release model based on Equation (1) will give estimates of F and X

which are unaffected by Type I losses, and in fact will yield an estimate of η as well as the usual estimates of F and X. Since the conditions required for this scheme will not often be encountered, it will usually be necessary to conduct a multiple-release experiment, with at least one preseason release, in order to obtain separate estimates of F, X, and η. Models appropriate to this situation have also been extensively developed by Paulik (1963).

However, even in the multiple-release models the Type II tagging mortality and Type II shedding will generate an underestimate of the true exploitation rate. Thus while the problems imposed by Type I losses may be circumvented by more elaborate experimental designs, the undesired effects of Type II losses remain. Two remedies are possible: 1) The single-tagging may be supplemented with a double-tagging experiment and other special studies to estimate Type II components and determine correction factors, or 2) double-tagging may be used exclusively to estimate mortality rates unaffected by Type I and Type II shedding. Both strategies are treated below. We note here that even when tag shedding and mortality are not the chief concerns of a tagging experiment, double-tagging is often employed simply to increase expected recovery rates (e.g., Hynd 1969; Bayliff 1973).

MODELS OF DOUBLE-TAGGING

We restrict our attention to the case where members of the population are marked with two tags differing in position of attachment and possibly type (call these Type A and Type B). We assume the burden of carrying both tags is equal to the stress of carrying either one alone. Further, we assume that the probabilities of loss are the same for each tag of a specified type and independent of the status of the other tag. Suppose a cohort of fish is double-tagged at time 0. For any fish still alive at time t, the probability that the Type A tag has been shed can be stated as

$$\Omega_A(t) = 1 - \rho_A g_A(t)$$

where $g_A(t) = \exp\left(- \int_0^t L_A(u)\ du\right).$

An analogous expression exists with respect to tag B. Where shedding rates are assumed to be the same for tag Types A and B the subscripts

can be dropped, i.e., the common probability of shedding by time t is

$$\Omega(t) = 1 - \rho g(t). \tag{2}$$

If we set $L(u) = L$(constant), Equation (2) embodies the assumptions of Bayliff and Mobrand (1972)—Type II shedding is a simple Poisson process with an identical constant rate for each tag, so that each tag has the same probability of shedding by time t. Moreover, in due course all surviving fish will have shed both tags as long as $L > 0$, i.e., $\Omega(\infty) \rightarrow 1$.

The validity of this particular set of assumptions has recently been challenged by results of tag-shedding studies with northwest Atlantic bluefin tuna, *Thunnus thynnus*, (Baglin et al. 1980) and with southern bluefin tuna, *T. maccoyii*, (Kirkwood 1981). In the former case, it was found that the Type II shedding rate increased with time. In Kirkwood's analysis it was apparent that the Type II rate decreased markedly over time. Therefore, it clearly would be advantageous to construct a model permitting time-dependent Type II shedding rates. Kirkwood approached this problem by attacking the common assumption of uniform shedding probabilities among all fish in the cohort. Instead, he considered the Type II shedding rate for each tag applied to be constant over time, but further assumed that the rate for each tag was a random variable with specified probability density. In this light, the deterministic model at Equation (2) is replaced by the expectation $J(t) = E[\Omega(t)] = 1 - \rho E[g(t)]$. The average time-varying shedding rate at time t may now be defined as

$$\Psi(t) = \frac{E\{g(t) \cdot L\}}{E\{g(t)\}}$$

where the expectations are taken with respect to the probability density of L. Following standard principles of reliability theory, this may be reduced to

$$\Psi(t) = - \frac{\partial \ln E\{g(t)\}}{\partial t}.$$

Under Kirkwood's assumptions $\Psi(t)$ will decrease with time as long as there is variation in shedding rate among tags, i.e., there will be a continuous culling of tags with relatively high shedding probabilities. This concept is clearly an

attractive alternative to the Bayliff-Mobrand model.

Problems in which the instantaneous loss rate is treated as a random variable arise in a variety of contexts ranging from bioassay to analysis of labor turnover in corporations. Because of its unimodality and mathematical tractability, the distribution often selected to describe this variation is the gamma distribution with mean λ and variance λ^2/b (e.g., see Bartholomew 1973:186 or McNolty et al. 1980). As Kirkwood (1981) showed, for the tag-shedding problem, this choice leads to

$$J(t) = 1 - \rho\left(\frac{b}{b + \lambda t}\right)^b \qquad (3)$$

so that

$$\Psi(t) = \frac{b\lambda}{b + \lambda t} \, .$$

The Bayliff-Mobrand model is now seen as a special deterministic case; when $b \to \infty$, $J(t) \to 1 - \rho \exp(-\lambda t)$ and $\Psi(t) \to \lambda$. Kirkwood considered a further elaboration of Equation (3) by assuming only a fraction of the tags, δ, will have a nonzero probability of shedding; the remainder are regarded as permanently attached. In this event the expected probability of shedding by time t is

$$J(t) = \delta\left[1 - \rho\left(\frac{b}{b + \lambda t}\right)^b\right]. \qquad (4)$$

While this approach significantly advances the realism and flexibility of tag-shedding theory, it fails to account for the apparent increase in average shedding rate as observed in the Atlantic bluefin tuna. Thus, although permitting variation in shedding rate among tags, it still considers the rate for each tag to be constant over time.

This condition is not apt to hold. As Kirkwood (1981) himself pointed out, plastic dart tags may become so firmly imbedded and overgrown by tissue as time passes that the probability of shedding approaches zero. This is most apt to occur in species which grow slowly, such as the southern bluefin tuna. On the other hand, it is well known that various metallic tags may corrode with time and their shedding probabilities increase. Plastic tags also deteriorate.

Accordingly, consider the Type II shedding rate to be a function of time, $L(t)$. A relatively

simple model for this situation is $L(t) = \alpha + \beta t^{(\gamma-1)}$, permitting a wide variety of forms for the instantaneous shedding process. In general, all three parameters of this model could be specified as random variables. Thus with $\alpha > 0$, $\beta > 0$, and $-\infty < \gamma < \infty$ the probability of shedding might increase over time for some fish in a cohort, decrease for others, and be constant for the remainder. However, to simplify the analysis assume here that γ is fixed and identical for all members of the cohort. Now if α and β are independently distributed as gamma random variables we have

$$J(t) = \delta\left[1 - \rho\left(\frac{b}{b + \lambda t}\right)^b \left(\frac{\gamma c}{\gamma c + \xi t^\gamma}\right)^c\right] \qquad (5)$$

and

$$\Psi(t) = \left(\frac{b\lambda}{b + \lambda t}\right) + \left(\frac{\gamma c \, \xi t^{\gamma-1}}{\gamma c + \xi t^\gamma}\right)$$

where the new symbols are ξ, the expected value of β, and c, the reciprocal of the squared coefficient of variation of β. Hence, if between-tag variability in α and β approaches zero,

$$J(t) \to \delta\left\{1 - \rho \exp\left[-\left(\frac{\lambda t + \xi t^\gamma}{\gamma}\right)\right]\right\}$$

and $\Psi(t) \to \lambda + \xi t^{(\gamma-1)}$. In the basic model at Equation (4), for tags still in place at time t the conditional probability of shedding in the interval $(t, t + dt)$ is independent of t. In the extended model at Equation (5), this conditional probability may also increase or decrease with t depending on γ.

While elaboration of the tag-shedding equations in this manner is straightforward, it is doubtful whether a very clear discrimination between such parameter-laden models is possible given the usual recapture statistics. Distinctions between the extended models are reduced by the integration of the shedding processes over several recapture periods and are further obscured by sampling variation.

However, on the basis of these conceptual models of the tag-shedding process we can now write the well-known equations describing the expected number of tags of a specified type still attached at time t. For $N_d(0)$ fish initially double-tagged with Types A and B tags, let

$$S(t) = \pi \cdot \exp\left(-\int_0^t Z(u)du\right)$$

be the probability of survival to time t, where $1 - \pi$ = probability of immediate mortality and $Z(u) = H(u) - L(u)$ is the time dependent instantaneous death rate. Then the expected number of fish bearing a single tag of Type A at time t is $N_A(t) = N_d(0) \, S(t) \, J_B(t)(1 - J_A(t))$. An analogous expression may be written for $N_B(t)$, and if the two tags are considered identical, the subscripts A and B may be dropped to yield

$$N_s(t) = N_A(t) + N_B(t)$$

$$= 2N_d(0) \, S(t) \, J(t) \, (1 - J(t)),$$

the expected number of fish still bearing a single tag at time t.

The expected number of double-tagged fish at time t when A and B types are differentiated is $N_d(t) = N_d(0) \, S(t)(1 - J_A(t))(1 - J_B(t))$ or when no distinction is made between A and B types, $N_d(t) = N_d(0) \, S(t)(1 - J(t))^2$. In any event, the total number of fish expected at time t with one or two tags remaining is $N_.(t) = N_s(t) + N_d(t)$.

The processes described above are not directly observable, so inferences about the shedding rates must be made on the basis of catch statistics. When recapture effort is exerted during a time interval we assume it is applied continuously. During a period of length Δ_i beginning at time t_i the expected number of recaptures of tagged fish in category j is therefore

$$E(r_{ji}) = \int_{t_i}^{t_i + \Delta_i} F(u) \, N_j(u) \, du \qquad (6)$$

where $j = A, B, s, d, \cdot$.

To complete the integral at Equation (6) it has been customary to make two key assumptions at this juncture (Chapman et al. 1965). First, we assume the fishing mortality rate, $F(u)$, is a step function constant within each recapture interval, i.e., $F(u) = F_i$ for $t_i < u < t_i + \Delta_i$. Second, we assume the average value of $N_j(u)$ during the interval is approximately equal to $N_j(t_i + \Delta_i/2)$. [This approximation is generally quite good for Δ_i of 1 yr or less. If $N_j(u)$ is linear over the interval the relation is exact regardless of Δ_i.] Under these conditions the set of recapture equations becomes

$$E(r_{ji}) = F_i \, \Delta_i \, N_j(\tau_i) \qquad (7)$$

where $\tau_i = t_i + \Delta_i /2$.

The standard procedures for estimating shedding rate parameters, and many of those to be described shortly, rely on a sequence of ratios of the estimated or observed number of recaptures from the various categories during successive fishing periods. It is clear from the equations above that such ratios will be functions of τ_i and the shedding parameters only, and independent of F_i, $N_d(0)$ and any parameters of the survival function $S(\tau_i)$.

Further, the ratios will be unaffected by nonrecovery or nonreturn as long as these processes operate at constant levels with respect to recaptures during a given time interval and at the same rates for each tagged fish category. Throughout this paper we assume this is so. However, this latter condition is one which could be violated easily, particularly if catches are not inspected carefully for tag recaptures. Where fish are handled individually there may be no difference in recovery rates between single- and double-tagged fish. Otherwise, recovery rates may be greater in double-tagged individuals. Once tagged fish are recovered, there may be further problems with respect to return rates. Laurs et al. (1976) in a study of shedding rates in North Pacific albacore, *T. alalunga*, and Myhre (1966) in experiments with Pacific halibut, *Hippoglossus stenolepis*, allowed for the possibility that a certain proportion of double-tagged recoveries would be misreported as having only a single tag. [For example, a fisherman might pocket one of the tags as a souvenir, or one tag might be simply lost after recapture.]

ESTIMATION OF SHEDDING RATES AND PARAMETERS

In the analysis of tag-shedding data a broad range of objectives may be pursued, and these give rise to a variety of estimation problems and approaches. Fundamentally, of course, the analyst wishes to correct systematic bias in estimates of basic population parameters caused by tag loss. There are several ways to do this. Where concurrent single-tagging and double-tagging experiments are conducted, information on shedding rates from the double-tagging may be used to compute adjustment factors, which in turn are applied to recoveries from the primary single-tagging study. Thus in single-tag estimation procedures based on Equation (1), for example, r_i would simply be replaced by

$$r'_i = r_i \, \kappa_i^{-1}, \tag{8}$$

where κ_i, estimated from double-tagging, is the probability that a tag will still be attached at time τ_i. If returns from the double-tagging experiment are too few to provide an estimate of κ_i for each recapture interval, interpolation is necessary. In any event, in this approach only minimal assumptions need be made about the manner in which shedding occurs.

In most treatments of tag shedding, however, a specific model is postulated for the shedding process. Once the parameters of such a model are estimated, appropriate adjustments for tag shedding are made either to the single-tag recovery data, as above, or directly to estimated population parameters. A third strategy is to conduct the experiment entirely with double-tagged fish, and to estimate mortality rates and other population parameters directly, in such a way that no corrections are necessary.

These various approaches are discussed now in greater detail, assuming a continuous recapture process. For situations in which tagged fish are recaptured once at most, but only in point samples, some estimation procedures are given by Seber (1973) and Seber and Felton (1981). For multiple-recapture models of the Jolly-Seber type, again with point sampling, the reader should consult Arnason and Mills (1981).

Estimating Adjustment Factors for Single-Tag Recoveries

Here we estimate κ_i, the probability of tag retention at time τ_i, the midpoint of the ith recapture period. We assume the shedding probabilities for each tag are identical and independent of the status of the other tag, and that recovery and reporting rates are the same for recaptured fish bearing either one tag or two. Under these conditions the number of double-tag recoveries, r_{di}, is proportional to κ_i^2 and the number recovered with only a single tag remaining, r_{si}, is proportional by the same factor to $2\kappa_i(1 - \kappa_i)$. Of the total number of recoveries from the double-tagging experiment in the ith period, the proportion bearing two tags is therefore

$$P_{di} = \frac{\kappa_i}{2 - \kappa_i} .$$

Maximum likelihood (ML) estimates of the κ_i are

now easily derived. We assume the conditional distribution of r_{di}, given $(r_{di} + r_{si})$, is binomial with parameter P_{di}. The likelihood of the ith recapture sample is thus

$$\mathcal{L}_i = \left(\frac{r_i!}{r_{di}! \; r_{si}!} \right) \left(\frac{\kappa_i}{2 - \kappa_i} \right)^{r_{di}} \left(1 - \frac{\kappa_i}{2 - \kappa_i} \right)^{r_{si}} .$$

The ML estimator of κ_i is easily found:

$$\hat{\kappa}_i = \frac{2r_{di}}{r_{si} + 2r_{di}} . \tag{9}$$

This result is also given by Seber (1973) under somewhat different assumptions. The asymptotic variance of $\hat{\kappa}_i$ is

$$\sigma^2_{\hat{\kappa}_i} = \frac{\kappa_i(1 - \kappa_i) \, (2 - \kappa_i)^2}{2r_{.i}} . \tag{10}$$

As usual, numerical estimates are computed by inserting $\hat{\kappa}_i$ in place of κ_i.

Note that $\hat{\kappa}_i$ has a small negative statistical bias. In fact, using a Taylor series expansion it may be shown that

$$E(\hat{\kappa}_i) \simeq \kappa_i \left[1 - \frac{(1 - \kappa_i) \, (2 - \kappa_i)}{2r_{.i}} \right] .$$

Bias increases with time out, i.e., as κ_i decreases, and is inversely related to the total number of recaptures. When $\kappa_i = 0.5$ and $r_{.i} = 10$, the negative bias in $\hat{\kappa}_i$ is <4%.

Note further that since the likelihood function is conditioned on $r_{.i}$, inferences based on Equations (9) and (10) apply strictly only to the particular experimental outcome being studied, and not to the broader class of results which might be obtained in replications of the experiment. Providing that the approximation in Equation (7) is valid, a more complicated unconditional model would yield the same estimate of κ_i, but the variance of $\hat{\kappa}_i$ would be greater, reflecting the stochastic nature of the mortality and recapture processes which lead to the $r_{.i}$. Since our interest is in estimating shedding rates and not mortality rates, as a rule we consider only the simpler conditional likelihoods.

Above we have assumed the two tags are identical insofar as shedding rates are concerned. When they are subject to different shedding rates another set of estimators is required. Where A and B tags are identified, the number of A-

type recaptures, r_{Ai}, is proportional to $\kappa_{Ai}(1 - \kappa_{Bi})$ while r_{Bi} is proportional to $\kappa_{Bi}(1 - \kappa_{Ai})$. The number of double-tagged recaptures is proportional to $\kappa_{Ai} \kappa_{Bi}$. We assume the number of recaptures in the three classes are trinomial given $r_{Ai} + r_{Bi} + r_{di}$, with conditional probabilities

$$P_{Ai} = \frac{\kappa_{Ai}(1 - \kappa_{Bi})}{1 - (1 - \kappa_{Ai})(1 - \kappa_{Bi})}$$

$$P_{Bi} = \frac{\kappa_{Bi}(1 - \kappa_{Ai})}{1 - (1 - \kappa_{Ai})(1 - \kappa_{Bi})}$$

$$P_{di} = \frac{\kappa_{Ai} \kappa_{Bi}}{1 - (1 - \kappa_{Ai})(1 - \kappa_{Bi})} .$$

These assumptions lead to the *ML* estimates

$$\hat{\kappa}_{Ai} = \frac{r_{di}}{r_{Bi} + r_{di}} \quad \text{and} \quad \hat{\kappa}_{Bi} = \frac{r_{di}}{r_{Ai} + r_{di}} .$$

Estimating Parameters of Specific Models

Regression Methods

Despite the directness and simplicity of the general adjustment procedure outlined above, most double-tag analyses have aimed at unraveling specific underlying mechanisms of the tag-shedding process. The probability of tag retention, κ_i, is then seen as a continuous function of time and a vector of model parameters, θ, to be estimated from the recapture data. In the terminology established above, $\kappa_i = 1 - J(\tau_i)$. Thus if $\hat{\kappa}_i$ or some transformation of $\hat{\kappa}_i$ is plotted against τ_i the form of an appropriate shedding model may be revealed. In fact, this is the approach adopted in much of the recent tag-shedding literature, and various weighted regression procedures have been developed to handle the parameter estimation. The general formulation of these is: find θ such that

$$S(\theta) = \sum_{i=1}^{n} w_i (y_i - f_i(\theta))^2$$

is minimum. In the two-parameter Bayliff-Mobrand model $y_i = \ln \hat{\kappa}_i$, where $\hat{\kappa}_i$ is given in Equation (9), and $f_i(\theta) = \ln \rho - L\tau_i$. In the four-parameter Kirkwood model

$$y_i = 1 - \hat{\kappa}_i$$

and

$$f_i(\theta) = \delta \left\{ 1 - \rho \left(\frac{b}{b + \lambda \tau_i} \right)^b \right\}.$$

In both cases the authors suggest setting $w_i = r_i$. This is not optimal in a statistical sense, but is clearly preferable to equal weighting. It should be noted further that neither the Bayliff-Mobrand model nor the Kirkwood model is based on an explicit consideration of error structure for the observations. For example, there is considerable support in the literature for a multiplicative error in the recapture process, i.e., $r_{si} = E(r_{si}) \exp(\epsilon_{si})$ and $r_{di} = E(r_{di}) \exp(\epsilon_{di})$ and in this case the algebra leads one to the nonlinear model

$$\ln \left\{ \frac{r_{si}}{2 r_{di}} \right\} = \ln \left\{ \frac{J(\tau_i)}{1 - J(\tau_i)} \right\} + \epsilon_i$$

where ϵ_i has mean 0 and variance $\sigma_{\epsilon_i}^2$. Appropriate weights for this model are

$$w_i = \sigma_{\epsilon_i}^{-2} \simeq \frac{r_{si} \, r_{di}}{r_i} .$$

The regression models discussed here have assumed that recaptures are obtained from a single cohort of tagged fish. However, it is often the case that several lots of tagged fish are released at different times, so the recaptures in a particular interval may come from different cohorts. In this event the analysis may be applied to each of the m cohorts separately, provided these are fairly large. When multiple releases are made but the individual cohorts are small, so that relatively few recaptures are expected from each cohort, the usual procedure is to assume mortality rates and shedding rates are constant and identical for each group and to simply aggregate the recapture statistics from the several releases. Let the recapture intervals be of equal length, Δ, and let r_{sij} and r_{dij} denote the number of single-tagged and double-tagged fish from the jth cohort recaptured during the ith interval following that cohort's liberation. Employing the Bayliff-Mobrand linear regression model, one can estimate $\ln \rho$ and L in the usual manner as

$$\hat{\beta} = (X^T W X)^{-1} X^T W Y \qquad (11)$$

where $\beta = [\ln \rho \ L]^T$

$X = \{x_{ij}\}$ is the augmented data matrix

693

such that $x_{i1} = 1$ for all i and
$$x_{i2} = -(i - 1/2) \Delta$$
$Y = \{y_i\}$ is the vector of dependent variables with elements

$$y_i = \ln\left\{ \frac{2 \sum\limits_{j=1}^{m_i} r_{dij}}{\sum\limits_{j=1}^{m_i} r_{sij} + 2 \sum\limits_{j=1}^{m_i} r_{dij}} \right\} . \qquad (12)$$

Here W is a matrix of statistical weights, and m_i is the number of cohorts for which recapture statistics are available in the ith postrelease interval. The symbol T denotes the matrix transpose.

If sufficient recaptures are obtained to analyze each cohort separately (say $r_{ij} \geq 10$) but a common shedding rate is assumed, several alternative approaches are available. First we can treat the separate releases as partial replicates of the same experiment and construct the dependent variables as the logarithms of the geometric means of individual statistics for each cohort. Thus to estimate $\ln\rho$ and L we use Equation (11) as before but now set

$$y_i = \sum_{j=1}^{m_i} \ln\left(\frac{2r_{dij}}{r_{sij} + 2r_{dij}}\right) \Big/ m_i. \qquad (13)$$

Although as an estimator of $\ln\hat{x}_i$ Equation (13) usually has slightly greater negative bias than Equation (12), such bias is negligible and the approach taken in Equation (13) has the advantage that statistical weights may be calculated empirically for cases where $m_i \geq 2$. In particular, define the ith diagonal element of W as

$$w_{ii} = m_i(m_i - 1)\left[\sum_{j=1}^{m_i}\left(\ln\left(\frac{2r_{dij}}{r_{sij} + 2r_{dij}}\right) - y_i \right)^2 \right]^{-1}$$

where y_i is given by Equation (13), and let $w_{ij} = 0$ for $i \neq j$. When some of the m_i are equal to 1, then the w_{ii} may be computed using the delta method as

$$w_{ii} = m_i^2\left[\sum_{j=1}^{m_i}\left(\frac{r_{sij}(r_{sij} + r_{dij})}{r_{dij}(r_{sij} + 2r_{dij})^2} \right) \right]^{-1}$$

on the assumption that the r_{dij} and r_{sij} are complementary binomial variables.

A second approach when the shedding rates are constant and the r_{ij} are sufficiently large is to treat returns from each of the m releases separately and then average the individual estimates. Thus the overall estimate of L, for example, would be

$$\hat{L} = \sum_{j=1}^{m} w_j' \hat{L}_j$$

where $\hat{L}_j$ is the estimated slope from the linear regression of

$$y_{ij} = \ln\left(\frac{2r_{dij}}{r_{sij} + 2r_{dij}} \right)$$

on τ_i. Here the individual estimate of L from the jth cohort is given a weight w_j' inversely proportional to its relative variance. In practice we substitute the statistic

$$\hat{w}_j' = \frac{\hat{\sigma}_{\hat{L}_j}^{-2}}{\sum\limits_{j=1}^{m} \hat{\sigma}_{\hat{L}_j}^{-2}} ,$$

$\hat{\sigma}_{\hat{L}_j}^{-2}$ being the estimated variance of L_j computed in the jth regression. For the regression analysis itself, appropriate statistical weights for the y_{ij} would be proportional to

$$\hat{\sigma}_{y_{ij}}^{-2} = \frac{r_{dij}(r_{sij} + 2r_{dij})^2}{r_{sij}(r_{sij} + r_{dij})} .$$

Finally, the variance of $\hat{L}$ may be estimated as

$$\hat{\sigma}_{\hat{L}}^2 = \sum_{j=1}^{m} \hat{w}_j'^2 \hat{\sigma}_{\hat{L}_j}^2 = \left[\sum_{j=1}^{m} \hat{\sigma}_{\hat{L}_j}^{-2} \right]^{-1} .$$

A third approach is to assume that the set of regression estimates from the m cohorts are sampled from an underlying but unspecified stochastic process which, with respect to the estimation of Type II shedding rate, has mean L and variance σ_L^2. The regressions of y_{ij} on τ_i are unweighted, and empirical estimates of L and σ_L^2 are given very simply by

$$\hat{L} = \sum_{j=1}^{m} \hat{L}_j \Big/ m$$

and

$$\hat{\sigma}_L^2 = \sum_{j=1}^{m} (\hat{L}_j - \hat{L})^2 \Big/ m(m - 1),$$

694

where $\hat{L}_j$ is the regression estimate corresponding to the jth cohort.

A shortcoming of many double-tag analyses is that attention has been focused on estimating constant ρ and L despite the existence of multiple-release statistics. In fact the multiple-release experiment permits a more elaborate assessment of shedding processes, with the level of detail determined by specific characteristics of the experimental design. To illustrate this, consider an experiment with six recapture periods of equal length, Δ. Two cohorts of double-tagged fish are released, at the beginning of the first and fourth periods. We assume there is a unique Type I shedding rate associated with each cohort, and that the Type II shedding rate is the same for each group but is a function of time following release. Specifically, we assume the latter rate is constant for two recapture intervals following the release of any cohort, may then change to another constant level for two more periods, and so on.

The recapture statistics from the experiment may be arrayed as follows:

Recapture interval:

Release group	*1*	*2*	*3*	*4*	*5*	*6*
1	r_{s11}	r_{s12}	r_{s13}	r_{s14}	r_{s15}	r_{s16}
	r_{d11}	r_{d12}	r_{d13}	r_{d14}	r_{d15}	r_{d16}
2				r_{s21}	r_{s22}	r_{s23}
				r_{d21}	r_{d22}	r_{d23}

Note that $m_1 = m_2 = m_3 = 2$ and $m_4 = m_5 = m_6 = 1$.

The parameter vector $\beta = [\ln\rho_1 \ \ln\rho_2 \ L_1 \ L_2 \ L_3]^T$ may now be estimated from Equation (11) with Y as given in Equation (13) and the data matrix defined as

$$X = \begin{bmatrix} 1/2 & 1/2 & -\Delta/2 & 0 & 0 \\ 1/2 & 1/2 & -3\Delta/2 & 0 & 0 \\ 1/2 & 1/2 & -2\Delta & -\Delta/2 & 0 \\ 1 & 0 & -2\Delta & -3\Delta/2 & 0 \\ 1 & 0 & -2\Delta & -2\Delta & -\Delta/2 \\ 1 & 0 & -2\Delta & -2\Delta & -3\Delta/2 \end{bmatrix}.$$

As usual, the covariance matrix of $\hat{\beta}$ is estimated by $\hat{V} = (X^T W X)^{-1}$.

With a little imagination this general linear model can easily be adapted to accommodate a wide variety of multiple-release experimental designs. Standard analysis of covariance techniques may be applied to test the associated hypotheses concerning β.

Maximum Likelihood Methods

As an alternative to the least squares methods we now describe some *ML* procedures for estimating the model parameters in the single-release case. Given the total number of recaptures in the ith period we again assume the numbers falling in the various classes are multinomially distributed. Thus when the A and B tags are identical there are just two classes, and the numbers in each are binomial variables with conditional expectations

$$E(r_{di}) = r_{\cdot i} \ P_{di}$$

$$= r_{\cdot i} \left\{ \frac{1 - J(\tau_i)}{1 + J(\tau_i)} \right\}$$

$$= r_{\cdot i} \left\{ \frac{[1 - J(\tau_i)]^2}{1 - J(\tau_i)^2} \right\}$$

and $E(r_{si}) = r_{\cdot i} (1 - P_{di})$. Assuming further that the statistics for successive periods are mutually independent, the joint likelihood function for the double-tag recovery data $\{r_{d1} \ r_{d2}, \ldots, r_{dn}\}$ given $\{r_{\cdot 1}, r_{\cdot 2}, \ldots, r_{\cdot n}\}$ is

$$\mathcal{L} = \prod_{i=1}^{n} \left(\frac{r_{\cdot i}!}{r_{di}! \ r_{si}!} \right) P_{di}^{r_{di}} (1 - P_{di})^{r_{si}} \quad (14)$$

where P_{di} is a function of τ_i and the vector of parameters to be estimated, θ.

When the A and B tags are not identical, the recaptures are partitioned into three disjoint classes, and the numbers in each are trinomial with expectations

$$E(r_{Ai}) = \frac{J_B(\tau_i) \ (1 - J_A(\tau_i))}{1 - J_B(\tau_i) \ J_A(\tau_i)} \ r_{\cdot i} = r_{\cdot i} \ P_{Ai}$$

$$E(r_{Bi}) = \frac{J_A(\tau_i) \ (1 - J_B(\tau_i))}{1 - J_B(\tau_i) \ J_A(\tau_i)} \ r_{\cdot i} = r_{\cdot i} \ P_{Bi}$$

and

$$E(r_{di}) = \frac{(1 - J_A(\tau_i)) \ (1 - J_B(\tau_i))}{1 - J_B(\tau_i) \ J_A(\tau_i)} \ r_{\cdot i}$$

$$= r_{\cdot i} \ (1 - P_{Ai} - P_{Bi}).$$

Now the joint conditional likelihood of the recapture sample is

$$\mathcal{L} = \prod_{i=1}^{n} \left(\frac{r_i!}{r_{Ai}!\ r_{Bi}!\ r_{di}!} \right) P_{Ai}{}^{r_{Ai}}\ P_{Bi}{}^{r_{Bi}}$$
$$\times\ (1 - P_{Ai} - P_{Bi})^{r_{di}}.$$

In either case, once the underlying model and the corresponding elements of θ are identified, the ML estimates of θ may be computed by maximizing $\mathcal{L}$ directly using a variety of iterative search procedures. In some situations the derivatives of $\mathcal{L}$ with respect to θ are easily derived, but even then only numerical solutions are possible.

For example, when A and B tags are identical and $J(\tau_i) = 1 - \rho(\exp(-L\tau_i))$, the ML estimates of ρ and L are found by solving the system of equations

$$0 = \sum_{i=1}^{n} \tau_i\ C_i \quad \text{and} \quad 0 = \sum_{i=1}^{n} C_i$$

where $C_i = \dfrac{(1 + P_{di})\ (r_{di} - P_{di}\ r_i)}{1 - P_{di}}$

$$= J(\tau_i)^{-1}\left\{ r_{di} - r_i\ \left(\frac{1 - J(\tau_i)}{1 + J(\tau_i)} \right) \right\}$$

$$= J(\tau_i)^{-1}\{r_{di} - E(r_{di})\}.$$

The asymptotic covariance matrix of $\hat{L}$ and $\hat{\rho}$ may then be derived in the usual manner by inverting the corresponding negative information matrix

$$I = \begin{bmatrix} \sum_{i=1}^{n} \tau_i^2\ D_i & -\dfrac{1}{\rho} \sum_{i=1}^{n} \tau_i\ D_i \\[2em] -\dfrac{1}{\rho} \sum_{i=1}^{n} \tau_i\ D_i & \dfrac{1}{\rho^2} \sum_{i=1}^{n} D_i \end{bmatrix}$$

where $D_i = \dfrac{r_i\ P_{di}\ (1 + P_{di})^2}{1 - P_{di}}$.

Explicit analytical solutions are possible when there is only a single recapture period centered at τ and the model is reduced to a one-parameter function of either the Type I or Type II shedding rate, i.e., either $J(\tau) = 1 - \exp(-L\tau)$ or $J(\tau) = 1 - \rho$. In this event the ML estimate of L (with $\rho = 1$) is

$$\hat{L} = -\frac{1}{\tau}\ \ln\left\{ \frac{2r_d}{r_s + 2r_d} \right\} \tag{15}$$

with asymptotic variance estimated by

$$\hat{\sigma}_{\hat{L}}^2 = \frac{r_s\ (r_s + r_d)}{\tau^2 r_d\ (r_s + 2r_d)^2}\ ,$$

or when shedding is a function of ρ only (with $L = 0$)

$$\hat{\rho} = \frac{2r_d}{r_s + 2r_d} \tag{16}$$

and

$$\hat{\sigma}_{\hat{\rho}}^2 = \frac{r_s\ 2r_d}{(r_s + 2r_d)^3}\ .$$

In the case of identical A and B tags a convenient alternative to direct maximization of the likelihood function is to fit the recapture data to their expectations using an iteratively reweighted Gauss-Newton algorithm. To accomplish this one may use routines available in certain standard statistical software packages, e.g., BMDP[2]. Specifically, we find an admissible value of θ which minimizes the sum of squares

$$S' = \sum_{i=1}^{n} w_i[r_{di} - E(r_{di})]^2.$$

Since the r_{di} are assumed to be binomial (i.e., of "regular exponential" form), minimizing S' with a Gauss-Newton routine is equivalent to maximizing the likelihood of Equation (14) provided the weights used are the reciprocals of the variances of the r_{di} and are recomputed at each iteration based on the current parameter values (Wedderburn 1974; Jennrich and Moore 1975; Jennrich and Ralston 1978). In this case the weights must be $\tilde{w}_i = [r_i\ \tilde{P}_{di}\ (1 - \tilde{P}_{di})]^{-1}$, where $\tilde{P}_{di}$ is the function P_{di} evaluated at the current parameter estimates. Asymptotic standard errors for the parameter estimates are also computed by the BMDP routine.

A similar device may be used when a distinction is made between A and B tags. Given $r_{Ai} + r_{di}$ we assume r_{di} is binomial with expectation $E_B(r_{di}) = (r_{Ai} + r_{di})\ (1 - J_B(\tau_i))$. Analogously,

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[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

$E_A(r_{di}) = (r_{Bi} + r_{di}) (1 - J_A(\tau_i))$. Thus an iteratively reweighted Gauss-Newton algorithm minimizing

$$S'_B = \sum_{i=1}^{n} w_{Bi} (r_{di} - E_B(r_{di}))^2$$

with $w_{Bi} = \tilde{w}_{Bi} = [(r_{Ai} + r_{di}) \tilde{J}_B(\tau_i)(1 - \tilde{J}_B(\tau_i))]^{-1}$ is used to compute ML estimates of shedding parameters for the B class of tags. A parallel procedure gives ML estimates of parameters for the A class. Note that the two sets of parameter estimates are not independent.

Unknown Recapture Times

A tacit assumption in the foregoing procedures is that the time between release and recapture for each returned fish is known to "interval accuracy," and that exact recapture time information is available for only a fraction of the recoveries, so that all recoveries are grouped into the n time intervals to permit estimation. This will often be the case. However, in some fisheries it is conceivable that only the crudest sort of information is available on recapture times. For estimation purposes, all that is known is r_d and r_s, the total number of recaptures in each class over the experimental period $(0, T)$. When T is relatively small, say 1 yr or less, then estimation of a single Type I or Type II shedding parameter is possible, as in Equation (15) or (16). In an experiment of longer duration this is not feasible. However, it is possible under certain circumstances to estimate the ratio of the Type II shedding rate to other Type II losses. Let fishing be constant, continuous, and uniform at an instantaneous rate F. Assume further that the total instantaneous mortality rate is a constant, Z, and that shedding of tags occurs at an instantaneous rate L. If there are no Type I losses, the ratio of $E(r_s)$ to $E(r_d)$ in a double-tagging experiment approaches

$$x = \frac{2L}{Z + L}$$

as $T \to \infty$. Thus if $L = aZ$, a moment estimator of a is provided by

$$\hat{a} = \frac{\hat{x}}{2 - \hat{x}}$$

$$= \frac{r_s}{2r_d - r_s}, \quad 0 \le \frac{r_s}{r_d} < 2 \qquad (17)$$

and if one has an estimate of Z which has a systematic bias due to Type II shedding, say Z^*, then a corrected estimate may be obtained, i.e., $Z^* = Z^*(1 + \hat{a})^{-1}$.

This method may also be used where single-tagging and double-tagging experiments are run concurrently. Then if $N_d(0)$ fish are released double-tagged and $N_s(0)$ with single tags, let r'_d and r'_s be recaptures from each group still bearing the initial complement of tags. Under the same assumptions as above this leads to

$$\hat{a} = \frac{r'_s N_d(0) - r'_d N_s(0)}{2r'_d N_s(0) - r'_s N_d(0)}, \quad 1 \le \frac{r'_s N_d(0)}{r'_d N_s(0)} < 2.$$

Exact Recapture Times

Turning now to the other end of the spectrum, under ideal conditions it is possible that the exact time out will be known for each fish returned. When exact recapture times are available for all fish the returns from a single-tagging experiment may be analyzed using ML procedures first developed by Gulland (1955) and later elaborated by Chapman (1961) and Paulik (1963). These rest on the assumption of binomial recapture probabilities based on constant Type II loss rates and on a resulting conditional recapture time distribution which is truncated negative exponential. Chapman et al. (1965) extended the same concepts to returns of fish initially double-tagged and still retaining both tags upon recapture, and showed that the difference between the estimated total Type II loss rate in a double-tagging experiment and the corresponding total Type II loss rate in a single-tagging study yielded an estimate of L. They noted that this is the best estimate of L possible using only the recapture information from a single-tagging experiment and from fish put out and returned with two tags. Left open was the possibility of combining this information with recapture times for fish initially double-tagged but returned with only one tag still attached. For this class of fish the distribution of recapture times is more complicated.

We now consider an exact recapture time model for an experiment based exclusively on fish initially double-tagged. Suppose $N_d(0)$ double-tagged fish are released at time 0. Over the course of the experiment, terminating at time T, a total of r_d fish are recaptured and returned with both tags intact, and r_s with only a single tag remaining. In addition, for each tagged fish returned

697

we assume the exact recapture time is known, i.e., we know $\{t_{s1}, t_{s2}, ..., t_{sr_s}\}$ and $\{t_{d1}, t_{d2}, ..., t_{dr_d}\}$.

Let $\Phi_d = Pr$ {fish is returned with both tags intact in $(0, T)$} and $\Phi_s = Pr$ {fish is returned with one tag remaining in $(0, T)$}. Then, assuming independence between fish and between the two tags initially applied, the numbers of returns in the various classes are trinomial random variables, i.e.,

$$Pr\{r_d, r_s\} = \frac{N_d(0)!}{r_d!\, r_s!\, (N_d(0) - r_d - r_s)!}$$
$$\times \Phi_s^{r_s}\, \Phi_d^{r_d}(1 - \Phi_s\, \Phi_d)^{N_d(0)-r_s-r_d}.$$

Following principles set out previously we write the recapture probabilities as

$$\Phi_s = 2 \int_0^T F(u)\, S(u)\, J(u)\, (1 - J(u))\, du$$

and

$$\Phi_d = \int_0^T F(u)\, S(u)\, (1 - J(u))^2\, du.$$

Further, the conditional probability densities for recapture times are

$$f_s(t) = \begin{cases} 2F(t)\, S(t)\, J(t)(1 - J(t))/\Phi_s & 0 < t < T \\ 0 & \text{otherwise} \end{cases}$$

$$f_d(t) = \begin{cases} F(t)\, S(t)(1 - J(t))^2/\Phi_d & 0 < t < T \\ 0 & \text{otherwise.} \end{cases}$$

The joint likelihood function for the observed numbers of single- and double-tag recoveries and the respective sets of recapture times may now be written as

$$\mathcal{L} = Pr\{r_d, r_s\} \prod_{i=1}^{r_s} f_s(t_{si}) \prod_{i=1}^{r_d} f_d(t_{di}).$$

For specified forms of $F(u)$, $S(u)$, and $J(u)$ computation of ML estimates may now be contemplated, although the form of $\mathcal{L}$ is apt to be exceedingly complex in most situations. For example, taking the most elementary case, assume that $J(u) = 1 - \exp(-Lu)$, $S(u) = \exp[-(M + F)u]$ and $F(u) = F$ for $0 < u < T$. Also let $T \to \infty$. Under these conditions the log-likelihood becomes

698

$$\ln \mathcal{L} = K + r_. \ln F + (N_d(0) - r_.)$$
$$\times \ln\left(1 - \frac{2LF^2}{(F + M + L)(F + M + 2L)^2}\right)$$
$$- (F + M)\, T_. - L(T_s + 2T_d)$$
$$+ \sum_{i=1}^{r_s} \ln(1 - \exp(-Lt_{si}))$$

where K is a function of the observations only,

$$T_s = \sum_{i=1}^{r_s} t_{si}, \qquad T_d = \sum_{i=1}^{r_d} t_{di},$$

$$T_. = T_s + T_d, \quad \text{and} \quad r_. = r_s + r_d.$$

Using numerical methods this may now be maximized as a function of F, M, and L in the usual manner to yield ML estimates of these parameters, as well as asymptotic variance estimates.

A simpler approach which yields information on $Z = F + M$ and L is to condition the likelihood of r_d and r_s on the total number of recaptures, $r_.$, i.e.,

$$Pr\{r_d, r_s\} = \left(\frac{r_.!}{r_s!\, r_d!}\right)\left(\frac{\Phi_s}{\Phi_s + \Phi_d}\right)^{r_s}\left(\frac{\Phi_d}{\Phi_s + \Phi_d}\right)^{r_d}.$$

This gives the log-likelihood

$$\ln \mathcal{L} = K' + r_.\, \{\ln(Z + L) + \ln(Z + 2L)$$
$$- \ln(Z + 3L)\} - ZT_. - L(T_. + T_d)$$
$$+ \sum_{i=1}^{r_s} \ln(1 - \exp(-Lt_{si})) \qquad (18)$$

where K' is independent of Z and L.

Differentiating Equation (18) with respect to Z and L and setting the derivatives to zero one finds that the ML estimates of Z and L satisfy, among other relations, the equation

$$\frac{T_.}{r_.} = \frac{1}{Z + L} + \frac{1}{Z + 2L} - \frac{1}{Z + 3L}.$$

Combining this with the result at Equation (17) leads immediately to a solution for $\hat{Z}$, i.e.,

$$\hat{Z} = \frac{r.}{T.}\left[\frac{1}{1 + \hat{a}} + \frac{1}{1 + 2\hat{a}} - \frac{1}{1 + 3\hat{a}}\right]$$

whence $\hat{L} = \hat{a}\,\hat{Z}$.

Estimating Mortality Rates by Double-Tagging All Fish

In most of the preceding sections we assumed the basic purpose in double-tagging was to provide auxilliary information on shedding rates which could then be applied to correct recapture statistics or mortality rate estimates obtained in a primary single-tagging experiment. An attractive alternative is to use double-tagged fish entirely and to estimate the mortality rates and other vital parameters in such a way that no bias corrections are necessary. If exact recapture times are recorded, the ML model just discussed is appropriate. When recapture data are grouped into n time intervals of length Δ_i centered at times τ_i, a convenient context for developing this approach is the single-tagging regression model suggested by Chapman (1961) and discussed further by Cormack (1968) and Seber (1973). This takes the form

$$\ln\left(\frac{r_i}{f_i\,\Delta_i}\right) = \ln[qpN_s(0)] - qf_i' - X\tau_i + e_i \quad (19)$$

where f_i = the nominal fishing effort during period i

$f_i' = \sum\limits_{j=1}^{i-1} f_j\,\Delta_j + \dfrac{f_i\,\Delta_i}{2}$ = the estimated nominal effort up to time τ_i

q = the catchability coefficient

e_i = a random error term.

In this particular model one obtains estimates of q and X, and, since $N_s(0)$ is known, an estimate of p as well. However, in the presence of Type II shedding the exploitation rate for any period will be underestimated, i.e., hidden in $\hat{X}$ will be the term L. The usual procedure would be to correct $\hat{X}$ by subtracting $\hat{L}$, where $\hat{L}$ is obtained in an independent double-tagging experiment. Instead, if we apply the model directly to recapture statistics from a double-tagging experiment ($N_d(0)$ fish initially double-tagged) we will obtain an estimate of X unaffected by Type II losses and in

need of no corrections. This is accomplished by substituting the dependent variable

$$\ln\left\{\left(\frac{r_{si} + 2r_{di}}{2\Delta_i\,f_i}\right)\Big/\left(\frac{2r_{di}}{r_{si} + 2r_{di}}\right)\right\}. \quad (20)$$

Further, it now transpires that the estimate of the regression intercept term is free of Type I shedding effects, i.e., one will estimate $\ln[qN_d(0)]$ rather than $\ln[qpN_d(0)]$.

If we assume r_{si} and r_{di} are complementary binomial variables given r_i, and that r_i is Poisson, then approximately correct weights for the regression employing Equation (20) are

$$w_i = \left[\frac{1}{r_i}\left(1 + \frac{r_{si}^3}{(r_{si} + 2r_{di})^2\,r_{di}}\right)\right]^{-1}.$$

When effort statistics are not available so that a constant fishing mortality rate must be assumed, or when there is a linear dependence between the two independent variables f_i' and τ_i, then separate estimates of q and X are not possible using the single-tag model of Equation (19) unless Type I errors are absent. Nor is p estimable. Instead, one may only regress $\ln(r_i/\Delta_i)$ on τ_i to yield estimates of $\ln[pFN_s(0)]$ and $(F+X)$. But when the model is applied to a double-tagging experiment under the same restrictions, it is still possible to estimate both q and X unaffected by shedding.

Note that the dependent variable of Equation (20) from the double-tagging experiment is analogous to the one of Equation (19) appropriately corrected for tag shedding, as in Equation (8). In both cases the recaptures r_{di} and r_{si} are assumed to be point samples taken exactly at τ_i. Thus while in the example above $\kappa_i = p\exp(-L\tau_i)$, the correction procedure of Equation (8) and the method outlined here are independent of assumptions on the manner of tag shedding (cf. Seber 1973:281), provided the recapture intervals are reasonably small (say 1 yr or less).

SUMMARY AND CONCLUSIONS

The aim of this paper has been to extend the theory and methodology of estimating tag-shedding rates through double-tagging. Attention was focused on the situation most commonly encountered in fishery applications, wherein two identical tags are placed on each member of an

experimental cohort, tagged fish are recaptured at most once in a fishery which is essentially continuous, and the time at liberty is known exactly for only a fraction of the recapture sample.

The regression models studied by Chapman et al. (1965), Bayliff and Mobrand (1972), and Kirkwood (1981) were extended to permit the Type II shedding rate for each tagged fish to be a function of time. Both deterministic and stochastic versions were presented and previously published models were shown to be special cases.

If all tags are subject to the risk of shedding, i.e., if $\delta = 1$, and if data are available from several recapture periods, a simple plot of $\ln\hat{\kappa}_i$ against τ_i will reveal whether the average Type II shedding rate, $\Psi(t)$, is constant; if it is, the relationship will be linear. In this event the most parsimonious model consistent with the data will be the deterministic model based on a constant Type II shedding rate, L. In addition, if the points suggest a negative intercept on the ordinate the Type I retention rate, ρ, may be added to the parameter set. One may then carry out the parameter estimation using either the Bayliff-Mobrand linear regression model, or the nonlinear regression of $\ln(r_{si}/2r_{di})$ on τ_i, depending on which error structure is assumed. However, since the plot of $\ln\hat{\kappa}_i$ versus τ_i is approximately linear even with multiplicative error in the recapture process, it probably makes little difference which estimation method is used as long as proper statistical weights are incorporated.

If $\delta = 1$ and the plot of $\ln\hat{\kappa}_i$ versus τ_i is nonlinear, one of the more complicated tag-shedding models is called for. A trend which is concave downward suggests that $\Psi(t)$ is increasing with time and points to the stochastic model of Equation (5) or its deterministic counterpart. On the other hand, upward concavity could be explained either by a model in which the Type II shedding rate decreased with time or by Kirkwood's (1981) hypothesis, or by a combination of the two as in Equation (5).

Another useful diagnostic plot is $1 - \kappa_i$ against τ_i. These are the variables considered in Kirkwood's nonlinear model. When L is constant the plotted points will be traced by a line analogous to a von Bertalanffy growth curve with asymptote δ and location parameter ρ, and they should indicate which of these two parameters to include in the model and how much precision to expect in the resulting estimates. (In passing, it is worth mentioning that if δ is to be estimated jointly with L, a longer experiment is required to

ensure high precision in the parameter estimates than if L alone is being estimated.)

The treatment of recaptures from double-tagging experiments with multiple cohorts was discussed in the context of the Bayliff-Mobrand model. Alternative methods of combining information from several cohorts to estimate common shedding parameters were proposed, and a general linear model approach was suggested for situations where more elaborate structural assumptions are made. A full numerical evaluation of these procedures remains to be done.

As an alternative to the least squares regression methods usually employed, some new ML procedures were presented. These are more difficult to use than the regression techniques, but offer advantages in some situations. For example, when only two recapture periods are possible one cannot compute the precision of regression estimates in the Bayliff-Mobrand model, but standard errors in the equivalent ML model are still estimable. The most promising method for deriving ML estimates in the general case may be the iteratively reweighted Gauss-Newton algorithm. Indeed, if one has access to the right computer software (such as the BMDPAR and BMDP3R programs supplied by BMDP) this approach is nearly as easy to use as the simple Bayliff-Mobrand linear regression method. A sensible procedure would be to first study the diagnostic plots suggested above for the regression analysis, and then fit the selected model using an iteratively reweighted least squares algorithm.

The estimation procedures discussed above are applicable when data are grouped by recapture interval. For situations in which the exact time at liberty is known for each recapture an unconditional ML model was developed. This may be applied not only to estimate shedding rates but also to estimate mortality rates unaffected by shedding. However, in its general form the likelihood function is rather complicated and only numerical solutions would be possible in most situations. Analytical estimators for L and Z were derived for a simplified conditional likelihood. Besides the more stringent data requirements this model requires the extra assumption of constant mortality rates during the experiment.

In the final section it was shown that through double-tagging it is possible to estimate mortality rates free of tag-shedding biases even when the recapture data are available only to interval-

700

accuracy, and without resort to the usual concurrent single-tagging experiment. The model was developed in the simple context of a fixed Type II shedding rate, but the principle applies to more complicated shedding processes as well. If the burden imposed by the second tag can be neglected, it therefore seems advantageous to double-tag all fish. In any case, when shedding is appreciable the greater overall recovery rates from double-tagging make the exclusive use of double-tagged fish a proposition well worth considering.

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