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SURVEYS FOR BIOLOGICAL ANALYSIS

Estimation of Fishing and Natural Mortality When a Tagging Study is Combined with a Creel Survey or Port Sampling

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Abstract.—In a multiyear tagging study in which tag returns are obtained from a recreational or commercial fishery, it is possible to estimate total annual survival. Fishery biologists would also like to be able to estimate natural and fishing mortality rates from the tagging data, but this is not possible without the additional assumption that all tags are reported or that the reporting rate is known. In this paper we review the theory of the tagging models, and we show how to estimate the tag-reporting rate by either conducting a reward tagging study or an angler survey in conjunction with the tagging study. It is then possible to partition total mortality into fishing and natural mortality. We also show that for a 1-year tagging study, it is possible to estimate exploitation rate but not to estimate total or natural mortality.

In recent years there has been much analysis of results from multiyear banding studies of migratory birds. The methodology has been described in detail by Brownie et al. (1985). Although this methodology was developed for wildlife, it is just as applicable to fisheries tagging studies. In fact, it was partly a study on lake trout *Salvelinus namaycush* by Youngs and Robson (1975) that led to much of the recent work. Pollock and O'Connell (1989) have applied the Brownie models to Pacific halibut *Hippoglossus stenolepis* tagging studies.

In this paper we review the structure and assumptions of the models presented in Brownie et al. (1985). We then show how to generalize the formulation to allow for solicitation of tags. We discuss the use of reward tags in estimating the reporting rate for regular tags, which allows conversion of recovery rates to fishing exploitation rates. Following this, we proceed to the crux of our paper: the use of a creel survey or a port sampling program to estimate reporting rate as an alternative to reward tags. We then discuss in detail the important implications of these approaches, which allow separate estimation of fishing and natural mortality, and we conclude with an example followed by a brief discussion section.

Review of Tagging Models

Concepts

Using the notation for mortality rates in Ricker (1975), let us consider the possible fates of a fish tagged at the start of the year, based on diagrams in Brownie et al. (1985; Figure 1). We have

- S = the finite annual survival rate or the probability of surviving the year,
- u = the finite annual exploitation rate or the probability of being harvested during the year, and
- λ = the tag-reporting rate, or the probability that a tag will be found and reported to the fisheries biologist, given that the fish has been harvested.

If we can further assume that all fish killed are retrieved by the anglers, we have

$$v = 1 - S - u\,,$$

which is the finite natural mortality rate or the probability of dying from natural causes in the presence of fishing mortality. Note that the type of data we analyze supplies information directly only about harvested fish whose tags are reported.

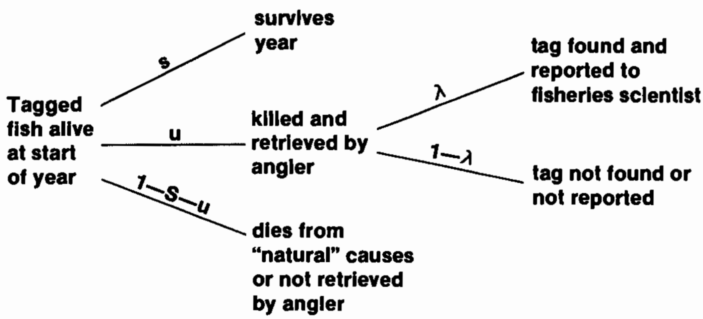

FIGURE 1.—Possible fates of a fish tagged at the start of the year, based on diagrams in Brownie et al. (1985).

Therefore, only the product $f = \lambda u$, which is called the tag-recovery rate, is estimable, and the component rates λ and u are not estimable without additional information, such as that generated by reward tags or creel surveys (or port samples), to be discussed later. A modified diagram that indicates which quantities are estimable is presented in Figure 2.

Model Structure

The data involve multiple-year taggings and recoveries. For data with this structure, provided the animals are not stratified by age-class, Brownie et al. (1985) devised a set of four models. The most general model is *Model 0*, which has the following matrix of expected recovery numbers if there are three tagging years and four recovery years:

Year, number tagged	Expected number of recoveries in year			
	1	2	3	4
1, N_1	$N_1f_1^*$	$N_1S_1f_2$	$N_1S_1S_2f_3$	$N_1S_1S_2S_3f_4$
2, N_2		$N_2f_2^*$	$N_2S_2f_3$	$N_2S_2S_3f_4$
3, N_3			$N_3f_3^*$	$N_3S_3f_4$

where S_i is the year-specific annual survival rate, f_i^* is the year-specific annual recovery rate for newly tagged fish, and f_i is the year-specific annual recovery rate for previously tagged fish. There may be a need to have separate recovery rates f_i and f_i^* for previously and newly tagged fish because fishing may begin before all tagging is completed, or the newly tagged fish may be more difficult to capture, or reporting rates may differ near and away from initial tagging sites.

Various restricted models can be specified by forcing certain parameters to remain constant over the years or over the cohorts.

Model 1 is a restriction of Model 0, where $f_i^* = f_i$ for all i. That is, all tagged fish have equal recovery rates in a given year irrespective of whether they are newly tagged or previously tagged.

Model 2 is a restriction of Model 1 where $S_i = S$ for all years. That is, all tagged fish have constant annual survival over all years in the study.

Model 3 is a restriction of Model 2 where $f_i = f$ for all years. That is, all tagged fish have constant annual survival and constant annual recovery rates over all years in the study.

This set of four nested models goes from the most general, Model 0, to the most restrictive, Model 3. Note that it is possible to have more recovery than tagging years, and that for some models not all survival and recovery rates are estimable. Brownie et al. (1985) provided a computer program, ESTIMATE, that determines the best model and estimates its survival and recovery rates. Most fisheries tagging studies require Model 0 or Model 1. Model 2 and Model 3 tend to be too restrictive. Pollock and O'Connell (1989)

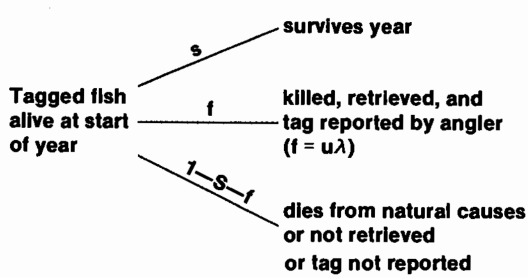

FIGURE 2.—Modified diagram of possible fates of a fish tagged at the start of the year, based on the diagrams in Brownie et al. (1985). This diagram shows only the estimable quantities S, f, and $1 - S - f$.

found Pacific halibut to require Model 0. Note that the models can be applied to any time periods of equal length, not just to years.

Brownie et al. (1985) also considered more-general models for situations where age-classes have differential survival and recovery rates. However, these models require that the animals be of known age. Our approach to estimating the reporting rate and then converting the recovery rate to an exploitation rate can be modified to handle age-structured tagging data.

Model Assumptions

There are six assumptions behind the multiyear tagging models reviewed earlier (Nichols et al. 1982; Pollock and Raveling 1982; Brownie et al. 1985, page 6). Below, we list these assumptions and discuss them as they relate to fish-tagging studies. The discussion is based on Pollock and Raveling (1982).

(1) The tagged sample is representative of the target population.—This assumption is obvious but very important, especially if heterogeneity of survival and recovery rates (violation of assumption 6) occurs. If, for example, tagging tended to take place in areas with very heavy fishing pressure, it could give the appearance of high recovery rates and low survival rates for the entire region. To avoid this, tagging studies should be designed so that the tagging is dispersed over a wide area of each region under study and is in proportion to the population density in the area. Alternatively, one is implicitly assuming that the tagged fish mix thoroughly throughout the whole area, which is usually unrealistic.

(2) There is no tag loss.—Nelson et al. (1980) used simulations to examine this assumption and found that, when tag loss occurs, it produces a negative bias on survival estimates that is relatively worse for species with high survival rates. The recovery rate estimates will also be negatively biased. Often, a double-tagging study is needed to obtain estimates of tag loss so that estimates of survival and recovery rates can be adjusted (Seber 1982, page 94).

(3) Survival rates are not influenced by tagging.—The importance of this assumption is obvious: if tagging substantially increases mortality, the survival estimates will not apply to untagged fish. Sometimes it may be practical to hold fish in enclosures to evaluate short-term tagging mortality.

(4) The year (fishing season) of tag recovery is correctly tabulated.—Sometimes anglers report tags from fish caught in previous years. We do not know the incidence of delayed reporting for many fisheries, but it does act to produce a positive bias on survival estimates.

(5) The fate of each tagged fish is independent of the fate of other tagged fish.—This assumption is probably violated in almost all practical applications of tag return models. Fish are not independent entities in terms of survival or other characteristics. This will not cause model bias in any estimators, but it will mean that true sampling variances are larger than those given by the statistical models. Thus, any calculated confidence intervals will be narrower than they should be.

A simplistic example for illustration is to consider a population composed of independent pairs of fish that behave as though each pair is a single individual. A sample of n individuals from this population is effectively only one-half of n and, hence, any sampling variances will be twice those for the models that assume the sample is n independent individuals. The actual situation in real populations is much more complex, with many partially dependent members, but the effective sample size may still be much less than the actual sample size.

(6) All tagged fish within an identifiable class have the same annual survival and recovery probabilities.—We believe heterogeneity of survival and recovery rates is likely to occur in practice (a violation of this assumption), but we do not know how serious it will be in fish-tagging studies. Nichols et al. (1982) and Pollock and Raveling (1982) examined this assumption using analytical methods and simulation. They found that if only recovery rates are heterogeneous, there is no bias in survival estimates and the recovery rate estimates can be viewed as averages for the population (assuming that the tagging sample is random). If survival probabilities are heterogeneous over the population, there is likely to be a strong positive relationship between the survival probabilities of an individual from year to year. There is also likely to be a negative relationship between survival and recovery probabilities for an individual. In this situation, survival rate estimators will generally have a negative bias. The negative bias will be more serious when the average survival rate is high and the study is short. It is theoretically possible for the survival rate estimators to have a positive bias. This could occur if there

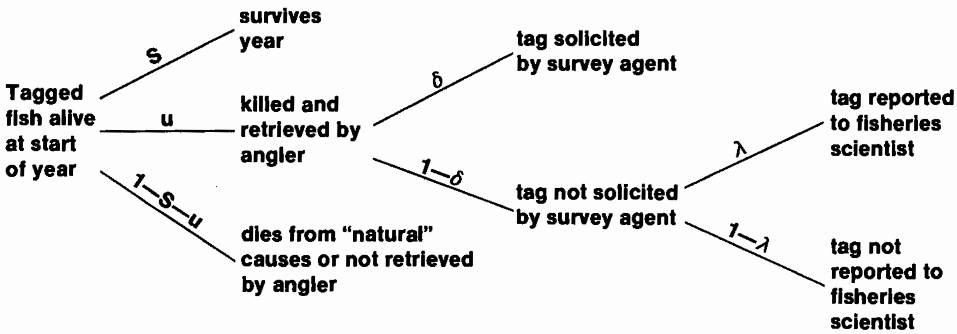

FIGURE 3.—Possible fates of a fish tagged at the start of the year, extended from the diagrams in Brownie et al. (1985) to allow formally for solicitation.

were segments of the population with markedly different survival rates but similar recovery rates, which implies that the differences in survival among population segments would have to be mostly due to differences in natural mortality. This might occur if different environmental conditions (e.g., disease level, food supply, pollution, water temperature) were encountered by the segments or if there were genetic variability in the population. Some of these factors may vary on a local or a regional scale.

Generalization to Allow for Tag Solicitation

When we began work on this article, we realized that the structure (Figure 1) of the Brownie et al. (1985) models does not allow for tags to be solicited by survey agents or other biologists. A more realistic structure for fisheries studies (and, in fact, for many wildlife studies) is Figure 3. There is a certain unknown probability (δ) that a tag will be solicited. Of course if a tag is solicited, then we assume that it is reported with certainty. Not all the quantities presented in Figure 3 are estimable without further information. If we define the recovery rate of solicited tags as $f_s = u\delta$ and the recovery rate of unsolicited tags as $f_r = u(1 - \delta)\lambda$, it is possible to transform Figure 3 to Figure 4, which presents only the estimable quantities S, f_s, and f_r. Estimation is now more complex because we have to consider two types of tags. Let us consider the generalization of Model 0 for this situation (Table 1).

We can obtain estimates for this Model 0 and the generalizations of the other models in Brownie et al. (1985) by using a general program SURVIV (White 1983). From estimates of $\hat{S}, \hat{f}_s, \hat{f}_r$, we can then obtain estimates of the exploitation rate u if we know or can estimate the reporting rate (λ):

$$\hat{u} = \hat{f}_s + \hat{f}_r/\hat{\lambda} .$$

The expected (E) or average value of $\hat{u}$ is

$$\begin{aligned} E(\hat{u}) &\approx u\delta + \frac{u(1-\delta)\lambda}{\lambda} \\ &= u\delta + u(1-\delta) \\ &= u , \end{aligned}$$

so that $\hat{u}$ will be unbiased in large samples. Notice that it is not necessary to estimate δ, because it drops out when we use the equation above.

Estimation of Tag-Reporting Rate (λ)

Reward Tags

One approach to estimating the tag-reporting rate (λ) is to use two types of tags in a special study. One type (control) is the standard-type tag, whereas the other type offers a high reward for its

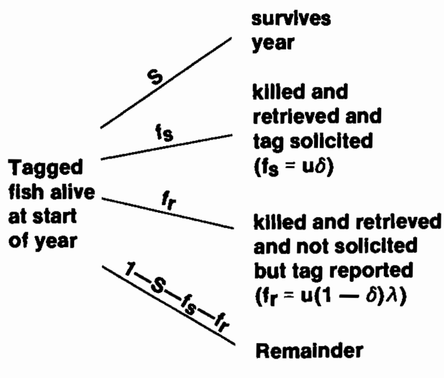

FIGURE 4.—Modified diagram for possible fates of a fish tagged at the start of the year, based on Brownie et al. (1985) and extended to allow formally for solicitation.

TABLE 1.—Generalization of Model 0.

Year of tagging	Number tagged	Expected number of recoveries in year for solicited and unsolicited tags: 1	2	3	4	Mode of recovery
1	N_1	$N_1 f^*_{1s}$	$N_1 S_1 f_{2s}$	$N_1 S_1 S_2 f_{3s}$	$N_1 S_1 S_2 S_3 f_{4s}$	Solicited
		$N_1 f^*_{1r}$	$N_1 S_1 f_{2r}$	$N_1 S_1 S_2 f_{3r}$	$N_1 S_1 S_2 S_3 f_{4r}$	Reported
2	N_2		$N_2 f^*_{2s}$	$N_2 S_2 f_{3s}$	$N_2 S_2 S_3 f_{4s}$	Solicited
			$N_2 f^*_{2r}$	$N_2 S_2 f_{3r}$	$N_2 S_2 S_3 f_{4r}$	Reported
3	N_3			$N_3 f^*_{3s}$	$N_3 S_3 f_{4s}$	Solicited
				$N_3 f^*_{3r}$	$N_3 S_3 f_{4r}$	Reported

return. The data consist of recoveries of tags of both the control and reward types. The basic estimate of reporting rate (λ) was developed by Henny and Burnham (1976) and applied to mallard ducks *Anas platyrhynchos*. It was also discussed by Conroy and Blandin (1984) and applied to black ducks *Anas rubripes*. The estimates are given by

$$\hat{\lambda} = \frac{R_h/N}{R^1/N^1 - R_s/N}, \qquad (1)$$

with

$$\widehat{\text{var}}(\hat{\lambda}) = (\hat{\lambda})^2 \left\{ \frac{1}{R_h} + \left(\frac{\hat{\lambda}}{R_h}\right)^2 \left[\left(\frac{N}{N^1}\right)^2 R^1 + R_s \right] \right\}; \qquad (2)$$

$\hat{\lambda}$ = the estimated reporting rate of control tags,
R_h = the number of first-year recoveries of control tags from anglers,
R_s = the number of first-year recoveries of control tags solicited by the fisheries scientist,
R^1 = the total number of first-year recoveries of reward tags,
N = the number of control tags applied, and
N^1 = the number of reward tags applied.

The above situation corresponds to the simplest reward tag experiment, which consists of one tagged sample (N, N^1) and one recovered sample (R_h, R_s, R^1). The estimate depends critically on the assumption that all of the recaptured special reward tags are reported. If this assumption is violated, then it causes a potentially serious positive bias on the reporting-rate estimator (Conroy and Williams 1981). The estimator allows for some tags to be solicited from anglers by the fisheries scientist conducting the study, and it assumes all these tags are reported.

Another assumption is that angler behavior does not change in response to the study. For example, if the reward study is advertised, anglers may become more likely to report regular tags. Also, anglers may begin to fish specifically for reward tags. Ideally, the reward notice should be displayed prominently on the tag so that it is not likely to be overlooked. Obviously, this can present operational difficulties.

Recently, wildlife scientists have attempted to establish the level of reward necessary to achieve near-perfect reporting of reward tags (Nichols et al., in press). If reward tags of three or more values are used, recovery rate can be modeled as a function of the reward level. As the reward increases, the recovery rate approaches an asymptote corresponding to 100% reporting (Nichols et al., in press). Unfortunately, necessary reward levels vary by species and location.

We strongly urge that fisheries scientists abandon the practice of using lotteries. Lotteries may increase the reporting rate but they do not allow its estimation because there is no subset of tags presumed to be reported with certainty.

Use of Creel Surveys or Port Samples

Another approach to estimating the tag-reporting rate (λ) is to use a creel survey or port sampling scheme. When the survey agent is interviewing anglers or commercial fishermen and checking their catch, we assume the probability of a tag being reported is one; whereas when the survey agent is not interviewing, the angler or commercial fisherman reports the tag with probability λ (for $0 \le \lambda \le 1$).

The estimate is given by

$$\hat{\lambda} = \frac{R_h}{\hat{R} - R_s}, \qquad (3)$$

with

$$\widehat{\text{var}}(\hat{\lambda}) \simeq \frac{\hat{\lambda}(1-\hat{\lambda})}{\hat{R} - R_s} + \frac{\hat{\lambda}(1-\hat{\lambda})\,\widehat{\text{var}}(\hat{R})}{(\hat{R} - R_s)^3}; \qquad (4)$$

R_h = the number of tags recovered by anglers or commercial fishermen that are reported to the fisheries scientist in the absence of solicitation,

$\hat{R}$ = an estimate of the total number of tags recovered by anglers or commercial fishermen, and

R_s = the number of tags recovered by anglers or commercial fishermen that were solicited by the survey agent; therefore

$\hat{R} - R_s$ = the estimated number of tags recovered by anglers or commercial fishermen that are available to be reported with probability λ.

Notice that R, the total number of tags recovered by anglers or commercial fishermen, has to be estimated from a creel survey or port sample that runs concurrently with the tagging study. The method of estimation of R and its variance depends on the nature of the sampling scheme used. The fisheries scientist expands the number of tags found by the agent to the number that would have been found if the agent were present all the time (i.e., to the case where the agent or agents carry out a census of the fishery). The variance of $\hat{\lambda}$ given in equation (4) is found with a Taylor's series method (Seber 1982, page 7), and the derivation is given in Appendix 1. It should be a reasonable approximation unless $(\hat{R} - R_s)$ is small, which is unlikely.

It is important to realize that this method depends on three important assumptions: (1) the agent and the angler or commercial fisherman do not miss any tags on fish that are examined; (2) the angler or commercial fisherman does not conceal solicited tags so that they are all reported; and (3) the survey design is based on probability sampling (i.e., a proper sampling survey design) so that the estimate of R does not suffer from model bias.

Separation of Fishing and Natural Mortality Estimates

Earlier, we emphasized that it is possible to estimate survival rate (S) and the two recovery rates (f_s, f_r) from a multiyear study. We also showed how to estimate the reporting rate of tags (λ) by using reward tags or a creel survey. Now, we use these earlier results to estimate the exploitation rate ($\hat{u}$) by the relationship

$$\hat{u} = \hat{f}_s + \hat{f}_r/\hat{\lambda}\ . \tag{5}$$

It is also possible to estimate the natural mortality that occurs in the presence of fishing mortality (i.e., expectation of natural death; Ricker 1975) by subtraction from the total mortality $(1 - \hat{S})$ so that

$$\hat{v} = 1 - \hat{S} - \hat{u}\ . \tag{6}$$

Given that $\widehat{\text{var}}(\hat{S})$, $\widehat{\text{var}}(\hat{f}_s)$, $\widehat{\text{var}}(\hat{f}_r)$, $\widehat{\text{cov}}(\hat{S}, \hat{f}_s)$, $\widehat{\text{cov}}(\hat{S}, \hat{f}_r)$, and $\widehat{\text{cov}}(\hat{f}_s, \hat{f}_r)$ are available (e.g., from program SURVIV) and $\widehat{\text{var}}(\hat{\lambda})$ is available from an independent study of tag-reporting rate, we have by the Taylor's series method (Seber 1982, page 7):

$$\widehat{\text{var}}(\hat{u}) = \widehat{\text{var}}(\hat{f}_s) + \left(\frac{\hat{f}_r}{\hat{\lambda}}\right)^2 \left[\frac{\widehat{\text{var}}(\hat{f}_r)}{\hat{f}_r^2} + \frac{\widehat{\text{var}}(\hat{\lambda})}{\hat{\lambda}^2}\right] + \frac{2}{\hat{\lambda}}\,\widehat{\text{cov}}(\hat{f}_s, \hat{f}_r)\ ; \tag{7}$$

$$\widehat{\text{var}}(\hat{v}) = \widehat{\text{var}}(\hat{S}) + \widehat{\text{var}}(\hat{u}) + 2\,\widehat{\text{cov}}(\hat{S}, \hat{u})\ ; \tag{8}$$

$$\widehat{\text{cov}}(\hat{u}, \hat{v}) = -[\widehat{\text{cov}}(\hat{S}, \hat{u}) + \widehat{\text{var}}(\hat{u})]\ ; \tag{9}$$

$$\widehat{\text{cov}}(\hat{u}, \hat{S}) = \widehat{\text{cov}}(\hat{S}, \hat{f}_s) + \frac{1}{\hat{\lambda}}\,\widehat{\text{cov}}(\hat{S}, \hat{f}_r)\ ; \tag{10}$$

$$\widehat{\text{cov}}(\hat{v}, \hat{S}) = -[\widehat{\text{cov}}(\hat{S}, \hat{u}) + \widehat{\text{var}}(\hat{S})]\ . \tag{11}$$

Note that we assume $\hat{\lambda}$ is independent of $\hat{f}_s$, $\hat{f}_r$, and $\hat{S}$ because it is based on a separate study.

The natural mortality rate, v, depends on the amount of fishing mortality. Similarly, the exploitation rate, u, depends on the amount of natural mortality. It is usually of interest to isolate the components of mortality. This can be accomplished if one makes assumptions about the timing of the different types of mortality, as we do below.

Following Ricker (1975, page 11), we define the following:

F = instantaneous fishing mortality rate (in units of year^{-1});

M = instantaneous natural mortality rate (in units of year^{-1}); and

Z = instantaneous total mortality rate = $F + M$.

Then the following relationships also hold:

$S = e^{-Z}$ = annual survival rate or probability of surviving a year;

$m = 1 - e^{-F}$ = conditional fishing rate or probability of dying in a year from fishing mortality if there is no natural mortality; and

$n = 1 - e^{-M}$ = conditional natural mortality rate or probability of dying in a year from natural mortality if there is no fishing mortality.

Thus we can estimate the instantaneous rate of total mortality as follows:

$$\hat{Z} = -\log_e \hat{S}\,, \tag{12}$$

with

$$\widehat{\text{var}}(\hat{Z}) \simeq \frac{1}{\hat{S}^2}\,\widehat{\text{var}}(\hat{S})\,. \tag{13}$$

Ricker (1975) describes two types of fisheries. In a type I fishery, fishing activity is restricted to a small part of the year such that fishing and natural mortality occur sequentially rather than concurrently. For convenience, we set the beginning of the year at the beginning of the fishing season so that natural mortality occurs after fishing. Then

$$u = m_{\text{I}} = 1 - e^{-F_{\text{I}}}$$

so that estimates are obtained by

$$\hat{m}_{\text{I}} = \hat{u}\,, \tag{14}$$

and

$$\hat{F}_{\text{I}} = -\log_e(1 - \hat{u})\,, \tag{15}$$

where the subscript I indicates estimates are for a type I fishery. Also, because $Z = F + M$,

$$\hat{M}_{\text{I}} = -\log_e \hat{S} - \hat{F}_{\text{I}} = -\log_e \hat{S} + \log_e(1 - \hat{u})\,. \tag{16}$$

Finally, n_{I} can be estimated by

$$\hat{n}_{\text{I}} = 1 - e^{-\hat{M}_{\text{I}}} = \hat{v}/(1 - \hat{u})\,. \tag{17}$$

Variances for these quantities can be derived by the Taylor's series method:

$$\widehat{\text{var}}(\hat{m}_{\text{I}}) = \widehat{\text{var}}(\hat{u})\,; \tag{18}$$

$$\widehat{\text{var}}(\hat{F}_{\text{I}}) \simeq (1 - \hat{u})^{-2}\,\widehat{\text{var}}(\hat{u})\,; \tag{19}$$

$$\widehat{\text{var}}(\hat{M}_{\text{I}}) \simeq \hat{S}^{-2}\,\widehat{\text{var}}(\hat{S}) + (1 - \hat{u})^{-2}\,\widehat{\text{var}}(\hat{u}) + 2\,\hat{S}^{-1}(1 - \hat{u})^{-1}\,\widehat{\text{cov}}(\hat{S}, \hat{u})\,; \tag{20}$$

$$\widehat{\text{var}}(\hat{n}_{\text{I}}) \simeq (1 - \hat{u})^{-2}\,\widehat{\text{var}}(\hat{v}) + \hat{v}^2(1 - \hat{u})^{-4}\,\widehat{\text{var}}(\hat{u}) + 2\,\hat{v}(1 - \hat{u})^{-3}\,\widehat{\text{cov}}(\hat{u}, \hat{v})\,. \tag{21}$$

In a type II fishery, fishing and natural mortality occur concurrently. Letting the subscript II indicate a type II fishery, we have

$$u = \frac{-F_{\text{II}}(1 - S)}{\log_e S}\,,$$

so

$$\hat{F}_{\text{II}} = \frac{-\hat{u}\,\log_e \hat{S}}{1 - \hat{S}}\,; \tag{22}$$

and

$$v = \frac{-M_{\text{II}}\,(1 - S)}{\log_e S}\,,$$

so

$$\hat{M}_{\text{II}} = \frac{-\hat{v}\,\log_e \hat{S}}{1 - \hat{S}}\,. \tag{23}$$

Also,

$$\hat{m}_{\text{II}} = 1 - e^{-\hat{F}_{\text{II}}}\,, \tag{24}$$

and

$$\hat{n}_{\text{II}} = 1 - e^{-\hat{M}_{\text{II}}}\,. \tag{25}$$

Variances of these estimates also are obtained by the Taylor's series method:

$$\widehat{\text{var}}(\hat{F}_{\text{II}}) \simeq \left(\frac{\log_e \hat{S}}{1 - \hat{S}}\right)^2 \widehat{\text{var}}(\hat{u}) + \left[\frac{\hat{u}\,\log_e \hat{S} + \hat{u}\left(\frac{1}{\hat{S}} - 1\right)}{(1 - \hat{S})^2}\right]^2 \widehat{\text{var}}(\hat{S}) + \frac{2\,\log_e \hat{S}}{1 - \hat{S}}\left[\frac{\hat{u}\,\log_e \hat{S} + \hat{u}\left(\frac{1}{\hat{S}} - 1\right)}{(1 - \hat{S})^2}\right] \cdot \widehat{\text{cov}}(\hat{S}, \hat{u})\,; \tag{26}$$

$$\widehat{\text{var}}(\hat{M}_{\text{II}}) \simeq \left(\frac{\log_e \hat{S}}{1 - \hat{S}}\right)^2 \widehat{\text{var}}(\hat{v}) + \left[\frac{\hat{v}\,\log_e \hat{S} + \hat{v}\left(\frac{1}{\hat{S}} - 1\right)}{(1 - \hat{S})^2}\right]^2 \widehat{\text{var}}(\hat{S}) + \frac{2\,\log_e \hat{S}}{1 - \hat{S}}\left[\frac{\hat{v}\,\log_e \hat{S} + \hat{v}\left(\frac{1}{\hat{S}} - 1\right)}{(1 - \hat{S})^2}\right] \cdot \widehat{\text{cov}}(\hat{S}, \hat{v})\,; \tag{27}$$

$$\widehat{\text{var}}(\hat{m}_{\text{II}}) \simeq e^{-2\hat{F}_{\text{II}}}\,\widehat{\text{var}}(\hat{F}_{\text{II}})\,; \tag{28}$$

$$\widehat{\text{var}}(\hat{n}_{\text{II}}) \simeq e^{-2\hat{M}_{\text{II}}}\,\widehat{\text{var}}(\hat{M}_{\text{II}})\,; \tag{29}$$

$\widehat{\text{cov}}(\hat{S}, \hat{u})$ and $\widehat{\text{cov}}(\hat{S}, \hat{v})$ are given by (10) and (11), respectively.

TABLE 2.—Array of anglers' tag recoveries for a hypothetical example based roughly on a lake trout study of Youngs and Robson (1975).

Year of tagging	Number tagged	Recovery year 1	2	3	Mode of recovery
1	1,000	58	31	16	Solicited
		48	24	12	Reported
2	1,000		60	29	Solicited
			49	23	Reported
3	1,000			61	Solicited
				49	Reported

We also note that sometimes only a single-year tagging study is possible. Then, $\hat{f}_s$ and $\hat{f}_r$ will be the observed proportion of tags recovered of each type, and the exploitation rate (u) can still be estimated from equation (5), and the $\widehat{\text{var}}(\hat{u})$ from equation (7). In this case the two $\widehat{\text{var}}(\hat{f})$ used in equation (7) will be the binomial variance, $\widehat{\text{var}}(\hat{f}) = \hat{f}(1 - \hat{f})/N$, where N is the number of fish tagged in that 1 year. With 1 year of data, however, it is not possible to estimate the total survival ($\hat{S}$) or the natural mortality ($\hat{v}$) or any quantities that depend on them.

Example

This small artificial example is based approximately on a tagging study of lake trout reported by Youngs and Robson (1975). In Table 2 we present the tag-return data for solicited and reported tags for the first 3 years of tagging and the first 3 years of recovery. In Table 3 we present the expected values of the cells for the model fitted, which is a generalization of Model 1. In Table 4 we present the survival and recovery rate estimates ($\hat{S}_i$, $\hat{f}_{is}$, $\hat{f}_{ir}$, respectively, for $i = 1, 2, 3$) and their standard errors obtained with the program SURVIV.

Suppose that during the second year a creel survey on the lake in this example produced the following results:

$$R_h = 73,\ R_s = 91,\ \hat{R} = 441, \text{ and } \widehat{\text{SE}}(\hat{R}) = 39.4\,.$$

The estimate of reporting rate ($\hat{\lambda}$) and its variance, based on equations (3) and (4), would be

$$\hat{\lambda} = \frac{R_h}{\hat{R} - \hat{R}_s} = \frac{73}{441 - 91} = 0.2086,$$

and

$$\widehat{\text{var}}(\hat{\lambda}) \simeq \frac{\hat{\lambda}(1-\hat{\lambda})}{(\hat{R} - R_s)} + \frac{\hat{\lambda}(1-\hat{\lambda})\,\widehat{\text{var}}(\hat{R})}{(\hat{R} - R_s)^3}$$

$$= \frac{0.2086 \times 0.7914}{441 - 91} + \frac{0.2086 \times 0.7914 \times 39.4^2}{(441 - 91)^3}$$

$$= 0.000472 + 0.000006$$

$$= 0.000478.$$

Therefore,

$$\widehat{\text{SE}}(\hat{\lambda}) \simeq \sqrt{\widehat{\text{var}}(\hat{\lambda})} = 0.022\,.$$

Notice that in this example the second term of the variance expression is negligible.

If we assume the estimate of reporting rate in this example applies to all years, we can obtain estimates of $\hat{u}_i$ and $\hat{v}_i$ with equations (5) and (6). These estimates are presented in Table 4. For example,

$$\hat{u}_1 = \hat{f}_{1s} + \hat{f}_{1r}/\hat{\lambda} = 0.0580 + 0.0480/0.2086$$

$$= 0.2881\,,$$

and

$$\hat{v}_1 = 1 - \hat{S}_1 - \hat{u}_1 = 1 - 0.5155 - 0.2881$$

$$= 0.1964\,.$$

We can also obtain standard errors of the estimates, based on equations (7) and (8). These are also presented in Table 4. Estimates of still other quantities are possible, depending on our assumptions about the timing of the fishery.

TABLE 3.—Array of expected cell values for the data presented in Table 2. The model is a generalization of Model 1. We have to consider cells for solicited and recovered tags.

Year of tagging	Number tagged	Recovery year 1	2	3	Mode of recovery
1	N_1	N_1f_{1s}	$N_1S_1f_{2s}$	$N_1S_1S_2f_{3s}$	Solicited
		N_1f_{1r}	$N_1S_1f_{2r}$	$N_1S_1S_2f_{3r}$	Reported
2	N_2		N_2f_{2s}	$N_2S_2f_{3s}$	Solicited
			N_2f_{2r}	$N_2S_2f_{3r}$	Reported
3	N_3			N_3f_{3s}	Solicited
				N_3f_{3r}	Reported

Discussion

In this paper we have shown that a multiyear tagging study, combined with reward tagging or with a creel or port sample survey, enables fishery biologists to estimate both exploitation and natural mortality rates. This is important for fisheries

TABLE 4.—Parameter estimates and SEs (in parentheses), based on tagging data and a creel survey. The survival and recovery-rate estimates were obtained with program SURVIV and the hypothetical tagging data. The creel survey, also hypothetical, is used to illustrate the methodology of the article. The exploitation and natural mortality rates are based on an estimated reporting rate of $\hat{\lambda}$ = 0.2086 ($\widehat{SE}(\hat{\lambda})$ = 0.022).

Year	Survival rate ($\hat{S}_i$)	Solicited recovery rate ($\hat{f}_{is}$)	Reported recovery rate ($\hat{f}_{ir}$)	Exploitation rate ($\hat{u}_i$)	Natural mortality rate ($\hat{v}_i$)
1	0.5155 (0.0657)	0.0580 (0.0074)	0.0480 (0.0068)	0.2881 (0.0409)	0.1964 (0.0758)
2	0.4799 (0.0707)	0.0600 (0.0066)	0.0482 (0.0059)	0.2911 (0.0374)	0.2990 (0.0780)
3		0.0614 (0.0068)	0.0486 (0.0059)	0.2944 (0.0369)	

management, because it is difficult to obtain reasonable natural mortality estimates of exploited populations by other methods (Vetter 1988).

Two other methods of estimating reporting rate were not considered in this paper. Youngs (1974) showed that it is possible to estimate reporting rate directly from multiyear tagging data without any additional information. His method, however, requires strong assumptions of constant natural mortality rates and constant reporting rates over years. Green et al. (1983) suggested that reporting rates could be estimated if survey agents surreptitiously planted tags in creeled fish. We suspect this approach might drastically alter angler behavior. Also, the doctored catch would have been inspected already, so anglers might overlook or disregard the plants.

In this paper we have proposed reward tags as one approach to the separation of fishing and natural mortality. This approach depends critically on the assumption that reward tags are returned with certainty. This assumption needs to be investigated for important fisheries through studies of the effect of reward size on recovery rate, as has been done in wildlife studies (Nichols et al., in press). We emphasize that the use of a lottery to boost the recovery rate of tags is logically faulty. The money would be better spent on high reward tags, which allow reporting rates to be estimated.

There is a need for future work on the utility of reward tagging, compared with that of creel or port surveys, to estimate reporting rate. Creel or port sampling surveys may be more expensive, but they provide important additional information on the recreational or commercial fishery. In addition to estimates of mortality and its components, a tagging study combined with a creel or port sampling program can provide estimates of the catchability coefficient q. Assuming fishing mortality F is proportional to fishing effort E (E is estimated by sampling the fishery), we have

$$\hat{q} = \hat{F}/\hat{E}.$$

We also can estimate population size as catch divided by exploitation rate. Finally, if the age composition of the catch is also estimated, then a sequential population analysis (e.g., virtual population analysis, cohort analysis) can also be computed. In this time of scarce resources, attempts should be made to design multimethod studies that give a better return on the dollars spent.

Many fisheries are exploited by both commercial fishing and sportfishing groups. It is often of interest to estimate the exploitation rate experienced by the stock and to apportion the rate to the two user groups. This can be accomplished by modifying the table of expected tag returns to account for three types of tag returns: solicited tags, tags voluntarily reported by user group 1, and tags voluntarily reported by user group 2. White's (1983) program SURVIV can be used to obtain estimates of the probability of a tag being recovered by solicitation (f_s), the probability of a tag being reported by user group i ($f_r^{(i)}$ for i = 1, 2), and the survival rate S. (See Appendix 2 for details.)

In the wildlife area, banding data have been used to study the question of whether natural and hunting mortality are additive or compensatory or a combination of the two. The first important paper on this question was by Anderson and Burnham (1976), who relied on the extensive banding data for mallards. Since then, many papers on mallards have been published (Anderson et al. 1982; Nichols and Hines 1983; Burnham and Anderson 1984; Burnham et al. 1984; Nichols et al. 1984). The evidence suggests some degree of sex-related compensation, at least for some age-classes. Pollock et al. (1989) studied northern bobwhite *Colinus virginianus* and found evidence for additivity in a population with a late hunt. It would be interesting to attempt to apply similar analyses to fisheries tagging data. Virtually all models of fisheries population dynamics assume that natural mortality and fishing mortality are additive.

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Appendix 1: Derivation of the Variance of the Reporting-Rate Estimate

The derivation of the variance of the reporting-rate estimate (equation 4) is as follows. First we use a result presented by Seber (1982, page 9) for conditional random variables:

$$\text{var}(\hat{\lambda}) = \text{E}_{\hat{R}}[\text{var}(\hat{\lambda}|\hat{R})] + \text{var}_{\hat{R}}[\text{E}(\hat{\lambda}|\hat{R})]$$

and

$$\text{var}(\hat{\lambda}) = \text{E}_{\hat{R}}[\text{var}(\hat{\lambda}|\hat{R})]$$

because the second term equals zero since the expectation of $\hat{\lambda}$ does not depend on $\hat{R}$. Therefore,

$$\text{var}(\hat{\lambda}) = \text{E}\left[\frac{\lambda(1-\lambda)}{\hat{R} - R_s}\right],$$

because the conditional distribution of $\hat{\lambda}$ is binomial.

Now, using a Taylor series method (Seber 1982, page 7) and taking expectations of the first two terms, we obtain the following approximation, which is used in equation (4):

$$\text{var}(\hat{\lambda}) \simeq \frac{\lambda(1-\lambda)}{\text{E}(\hat{R}) - R_s} + \text{var}(\hat{R})\left[\frac{\lambda(1-\lambda)}{(\text{E}(\hat{R}) - R_s)^3}\right].$$

To obtain the estimate, we replace $\text{E}(\hat{R})$ by $\hat{R}$, $\text{var}(\hat{R})$ by $\widehat{\text{var}}(\hat{R})$, and λ by $\hat{\lambda}$.

Appendix 2: Estimation When Two User Groups Exploit a Stock

Many fisheries are exploited by both commercial fishing and sportfishing groups. It is often of interest to estimate the exploitation rate experienced by the stock and to apportion the rate to the two user groups. This can be accomplished by modifying the table of expected tag returns to account for three types of tag returns: solicited tags, tags voluntarily reported by user group 1, and tags voluntarily reported by user group 2. White's (1983) program SURVIV can be used to obtain estimates of the probability of a tag being recovered by solicitation (f_s), the probability of a tag being reported by user group i ($f_r^{(i)}$ for i = 1, 2), and the survival rate S.

We assume that independent estimates of the reporting rates $\hat{\lambda}^{(i)}$ are obtained by conducting separate creel surveys or port sampling surveys for each user group. Then equation (5) in the text is generalized to

$$\hat{u} = \hat{f}_s + \frac{\hat{f}_r^{(1)}}{\hat{\lambda}^{(1)}} + \frac{\hat{f}_r^{(2)}}{\hat{\lambda}^{(2)}}. \quad \text{(A2.1)}$$

The estimator for the probability of dying of natural causes remains as in text equation (6):

$$\hat{v} = 1 - \hat{S} - \hat{u}; \quad \text{(A2.2)}$$

$\hat{u}$ now comes from (A2.1).

The variance of (A2.1) is estimated by

$$\widehat{\text{var}}(\hat{u}) = \widehat{\text{var}}(\hat{f}_s) + \left(\frac{\hat{f}_r^{(1)}}{\hat{\lambda}^{(1)}}\right)^2 \left[\frac{\widehat{\text{var}}(\hat{f}_r^{(1)})}{(\hat{f}_r^{(1)})^2} + \frac{\widehat{\text{var}}(\hat{\lambda}^{(1)})}{(\hat{\lambda}^{(1)})^2}\right] + \left(\frac{\hat{f}_r^{(2)}}{\hat{\lambda}^{(2)}}\right)^2 \left[\frac{\widehat{\text{var}}(\hat{f}_r^{(2)})}{(\hat{f}_r^{(2)})^2} + \frac{\widehat{\text{var}}(\hat{\lambda}^{(2)})}{(\hat{\lambda}^{(2)})^2}\right]$$
$$+ \frac{2}{\hat{\lambda}^{(1)}}\widehat{\text{cov}}(\hat{f}_s, \hat{f}_r^{(1)}) + \frac{2}{\hat{\lambda}^{(2)}}\widehat{\text{cov}}(\hat{f}_s, \hat{f}_r^{(2)}) + \frac{2}{\hat{\lambda}^{(1)}\hat{\lambda}^{(2)}}\widehat{\text{cov}}(\hat{f}_r^{(1)}, \hat{f}_r^{(2)}). \quad \text{(A2.3)}$$

The variance of equation (A2.2) is the same as text equation (8):

$$\widehat{\text{var}}(\hat{v}) = \widehat{\text{var}}(\hat{S}) + \widehat{\text{var}}(\hat{u}) + 2\,\widehat{\text{cov}}(\hat{S}, \hat{u}) ,$$

but note that $\widehat{\text{cov}}(\hat{S}, \hat{u})$ is now

$$\widehat{\text{cov}}(\hat{S}, \hat{u}) = \widehat{\text{cov}}(\hat{S}, \hat{f}_s) + \frac{1}{\hat{\lambda}^{(1)}}\,\widehat{\text{cov}}(\hat{S}, \hat{f}_r^{(1)}) + \frac{1}{\hat{\lambda}^{(2)}}\,\widehat{\text{cov}}(\hat{S}, \hat{f}_r^{(2)}) .$$

Also, $\widehat{\text{cov}}(\hat{u}, \hat{v})$ is as in text equation (9):

$$\widehat{\text{cov}}(\hat{u}, \hat{v}) = -[\widehat{\text{cov}}(\hat{S}, \hat{u}) + \widehat{\text{var}}(\hat{u})] ,$$

and $\widehat{\text{cov}}(\hat{v}, \hat{S})$ is as in text equation (11):

$$\widehat{\text{cov}}(\hat{v}, \hat{S}) = -[\widehat{\text{cov}}(\hat{S}, \hat{u}) + \widehat{\text{var}}(\hat{S})] .$$

Note that we assume that $\hat{\lambda}^{(1)}$ is independent of $\hat{\lambda}^{(2)}$ and that both are independent of $\hat{f}_s$, $\hat{f}_r^{(1)}$, $\hat{f}_r^{(2)}$, and $\hat{S}$ since the reporting rates are estimated from separate studies.

The proportion of the exploitation rate attributable to a given user group is equal to the proportion of the total catch taken by that user group. Let $\hat{C}_i$ be the estimated catch from user group i. Then the rate of exploitation by user group i, u_i, is estimated by

$$\hat{u}_i = \frac{\hat{C}_i}{\hat{C}_1 + \hat{C}_2}\,\hat{u} .$$

Note that $\hat{u} = \hat{u}_1 + \hat{u}_2$.