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Abstract: Data from mark-recapture studies are used to estimate population rates such as exploitation, survival, and growth. Many of these applications assume negligible tag loss, so tag shedding can be a significant problem. Various tag shedding models have been developed for use with data from double-tagging experiments, including models to estimate constant instantaneous rates, time-dependent rates, and type I and II shedding rates. In this study, we used conditional (on recaptures) multinomial models implemented using the program SURVIV (G.C. White. 1983. *J. Wildl. Manage.* 47: 716-728) to estimate tag shedding rates of lake trout (*Salvelinus namaycush*) and explore various potential sources of variation in these rates. We applied the models to data from several long-term double-tagging experiments with Lake Superior lake trout and estimated shedding rates for anchor tags in hatchery-reared and wild fish and for various tag types applied in these experiments. Estimates of annual tag retention rates for lake trout were fairly high (80-90%), but we found evidence (among wild fish only) that retention rates may be significantly lower in the first year due to type I losses. Annual retention rates for some tag types varied between male and female fish, but there was no consistent pattern across years. Our estimates of annual tag retention rates will be used in future studies of survival rates for these fish.

Résumé : Les données tirées d'études de marquage-recapture sont utilisées pour évaluer différents taux relatifs aux populations, notamment les taux d'exploitation, de survie et de croissance. Bon nombre de ces applications supposent une perte négligeable de marques, de sorte que la perte d'étiquettes peut être un problème important. Nous avons développé différents modèles de perte de marques qui seront utilisés avec des données provenant d'expériences de double marquage, notamment des modèles pour évaluer des taux instantanés constants, des taux chronologiques et des taux de pertes de marque de type I et II. Dans le cadre de la présente étude, nous avons utilisé des modèles multinominaux conditionnels (aux recaptures) mis en oeuvre à l'aide du programme SURVIV (G.C. White. 1983. *J. Wildl. Manage.* 47 : 716-728) pour estimer le taux de perte de marques chez le touladi (*Salvelinus namaycush*) et explorer différentes sources potentielles de variation de ces taux. Nous avons appliqué les modèles aux données de plusieurs expériences de double marquage à long terme du touladi du lac Supérieur et estimé le taux de perte de marques à ancrage chez des poissons d'élevage et des poissons sauvages et pour différents types de marques utilisées dans ces expériences. Les estimations du taux annuel de conservation des marques pour le touladi étaient assez élevées (80-90%), mais nous avons des indications (chez les poissons sauvages seulement) que le taux de conservation peut être significativement plus faible au cours de la première année en raison des pertes de type I. Pour certains types de marques, les taux annuels de conservation étaient variables chez les mâles et les femelles, mais nous n'avons observé aucun profil régulier au cours des années. Nos estimations du taux annuel de conservation des marques serviront dans des études futures du taux de survie de ces poissons.

[Traduit par la Rédaction]

Introduction

Tag retention can be a significant problem in fisheries applications that use marked or tagged fish to study exploitation, survival, growth, migration and movement, stock composition, stock size, or spawning escapement. For example,

in the presence of tag loss, survival rates estimated from mark-recapture studies are negatively biased (Arnason and Mills 1981; Pollock 1981; Nichols and Hines 1993). Data for estimating tag shedding rates are provided typically by double-tagging experiments (Beverton and Holt 1957; Seber 1982).

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Beverton and Holt (1957) described two types of tag losses in fish: type I losses, which occur immediately after tagging, and type II losses occurring subsequently. In short-term experiments and assuming constant shedding rates, type II rates can be estimated from the Chapman et al. (1965) model, whereas the Bayliff and Moberg (1972) model is used when both type I and II shedding occurs. Under these models, probabilities of tag loss are modeled as a (linear) function of time. The slope provides an estimate of the constant type II loss rate.

In some cases, constant shedding rates are not tenable. For example, type II shedding rates have been observed to both increase with time (Baglin et al. 1980) as tags deteriorate or fail with age and decrease with time (Kirkwood 1981) as tags with higher failure rates are shed earlier in the experiment. Kirkwood (1981) proposed that for some species, particularly long-lived ones such as southern bluefin tuna (*Thunnus maccoyii*), tag shedding rates vary among tags, thus appearing time dependent. His time-dependent model of tag shedding uses exact times at liberty and requires rather large sample sizes (i.e., many recaptures). Estimates of tag shedding rates from the Kirkwood (1981) model often have low precision (Hampton and Kirkwood 1990; Lai and Culver 1991; Fabrizio et al. 1996). In general, models that use exact time at liberty for recaptures (as opposed to pooled recaptures) are not as useful for sparse data (Wetherall 1982). Additionally, inference in time-dependent models may be more difficult. In one study, for example, recapture data were fit equally well by two different models: one had a constant type II rate and included type I shedding and the other model included a decreasing type II rate with no type I shedding (Hampton and Kirkwood 1990). Model selection in this and similar situations can be problematic.

In addition to type I shedding and time dependency, tag shedding models have been parameterized to account for other sources of variation in shedding rates, such as tag age (Nichols et al. 1992), tag type (Wetherall 1982; Barrowman and Myers 1996), tagging operator (Xiao 1996), and permanence of some tags (Kirkwood 1981; Fabrizio et al. 1996). Additional complexities of double-tagging experiments have been modeled including the flexibility to use either pooled or exact times at liberty and possible tag interactions (Xiao 1996). We note, however, that among a group of similarly marked fish, tags may be retained at rates that vary with characteristics of the marked individuals such as size (Waldman et al. 1990), sex (Brewin et al. 1995), and possibly other factors.

The purpose of this study was to develop models for estimating tag retention rates of lake trout (*Salvelinus namaycush*) and investigating multiple sources of variation in these rates. The sources of variation that we considered included measurable features of the fish and aspects of the double-tagging experiment. We used a widely available program, SURVIV (White 1983), to fit various models and to compute test statistics and statistics useful in model selection. We applied the modeling approach to data from double-tagging experiments with lake trout in the Gull Island Shoal area of southwestern Lake Superior. We were able to accommodate complex experimental design features and investigate the effect of sex, tag age, and origin of fish (hatchery or wild) on tag retention rates.

Methods

Double-tagging experiments

Since the 1960's, mark-recapture experiments have been conducted with lake trout in the Gull Island Shoal area, primarily for estimation of population size and survival rates. This population is a mixture of wild and hatchery-reared fish that were stocked annually near Gull Island Shoal as part of an effort to rehabilitate this species in Lake Superior (Swanson and Swedberg 1980; Hansen et al. 1995). Lake trout were captured in gill nets set in the Gull Island Shoal area during the October spawning season from 1973 to 1992 (Fig. 1). For each fish, we determined sex by expression of milt or eggs and noted the presence of fin clips, which denoted hatchery fish. Double-tagging experiments in fisheries applications typically use fin mutilation as a permanent mark (e.g., Robson and Regier 1966; Tranquilli and Childers 1982), but we could not use fin mutilation because lake trout stocked in Lake Superior are systematically fin clipped with a variety of fin clip combinations that indicate year-class. Instead, fin clips served as a distinguishing feature of hatchery-reared fish.

Fish captured in good condition were double-tagged with anchor tags, of which at least one was imprinted with a unique identification number. We used three types of numbered anchor tags (FD-67, FD-67C, or FD-68BC) as well as an unnumbered anchor tag (FD-67F) that we refer to as a plain tag (see Fabrizio et al. (1996) for a complete description of tag types). Plain tags are actually anchor flag tags (Wydoski and Emery 1983) that we modified by removing the flattened pendant. We double-tagged 10 236 lake trout.

Different tag types used during this study represent design improvements introduced by the manufacturer (Floy Tag & Manufacturing, Inc.). The FD-67C tag was shorter than the FD-67 tag, and the plastic bead on the FD-68BC tag was introduced to prevent separation of the colored tube from the nylon anchor. In 1973 and 1974, we double-tagged lake trout with identically numbered tags (FD-67) (Table 1). Fish double-tagged in 1978, 1979, 1980, and 1982 received a numbered FD-67C tag and a plain tag; those double-tagged in 1984 and 1985 carried an FD-68BC tag and a plain tag (Table 2). Because plain tags were color-coded by year, we could determine the year of tagging for fish that retained only a plain tag.

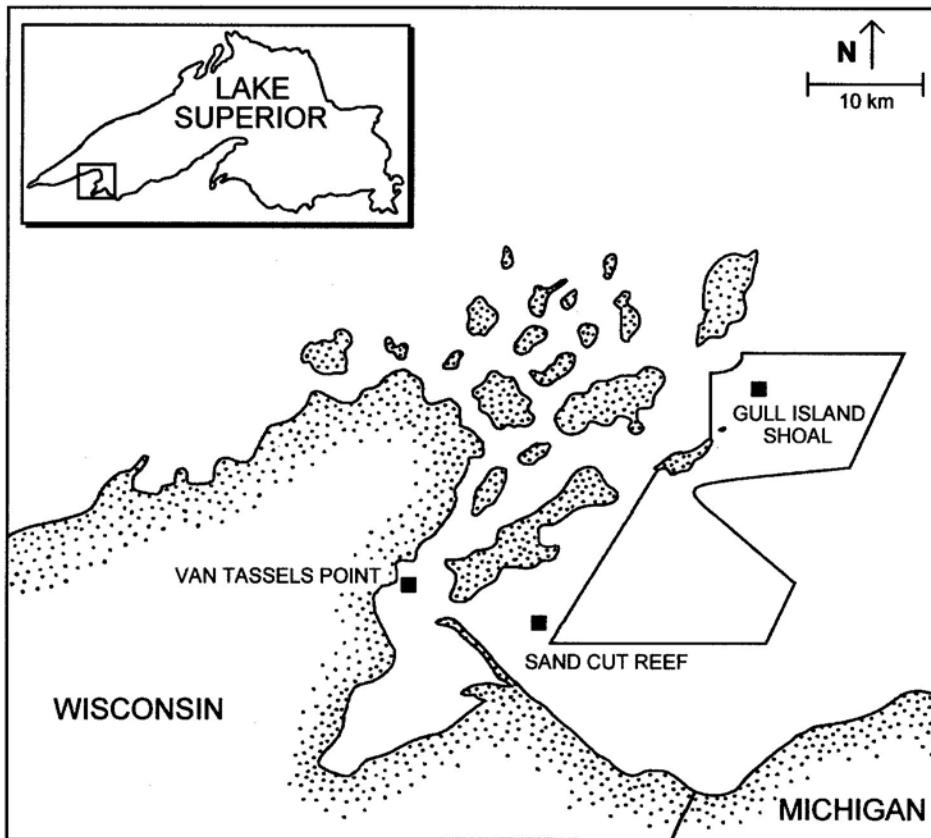
All fish were double-tagged by B.L.S., except for the 1985 cohort of 42 fish double-tagged by S.T.S. We tested all tags for disintegration failure before insertion and used only intact tags as had been done in other studies (e.g., Mourning et al. 1994). Tags were inserted on either side of the fish, just below the dorsal fin. This placement, followed by gentle tugging and rotation of the tag, ensured that the T-bar was firmly locked between adjacent pterygiophores. Interpterygiophore distances of adult lake trout were significantly less than one half the width of the T-bar (Fabrizio et al. 1996), so variation in retention rates was not associated with fish size in this study.

Fish were recaptured annually (1974–1992) in the Gull Island Shoal area during subsequent tagging operations. We did not consider recapture information from Lake Superior commercial or tribal fishers because we could not be sure that tags would be detected and reported accurately. If fishers reported only one tag when in fact both numbered tags were actually present, tag shedding rates would be overestimated. Note also that fishers' reporting of plain-tagged fish that had shed the numbered tag was not possible because plain tags carried no reporting instructions.

Models for two numbered tags

We developed models to estimate tag retention rates by conditioning on fish that were recaptured with at least one tag. This conditioning on recaptured fish required the assumption that capture probability did not depend on whether the fish had one or two tags.

Fig. 1. Study area in Lake Superior showing three sampling sites in the Gull Island Shoal area. The solid line demarcates the Gull Island refuge, a 70 000-ha area in which commercial and sport fishing have been prohibited since 1976.



We first estimated annual tag retention rates for lake trout from double-tagging experiments conducted in 1973 and 1974 (Table 1). In both years, fish received two identical anchor tags prior to release in the Gull Island shoal area of southwestern Lake Superior.

We defined π_{ij} as the probability that a tag applied in year i is retained until year j given the fish was alive in year j . If a fish received two tags (i.e., it was not recaptured between i and j and given an additional tag), then we can observe two types of recaptures in year j : $r_{ij}^{(1)}$ is the number of fish tagged in year i and recaptured in year j with a single tag and $r_{ij}^{(2)}$ is the number of fish tagged in year i and recaptured in year j with both tags. Note that $r_{ij}^{(*)} = r_{ij}^{(1)} + r_{ij}^{(2)}$ is the number of fish tagged in year i and recaptured in year j with at least one tag. Double-tagged fish that lost both tags were unobservable. We now write the expectation for the number of double-tagged fish released in year i and recaptured with both tags in year j conditional on the total number of fish double-tagged in year i and recaptured in year j as

$$(1) \quad E(r_{ij}^{(2)} | r_{ij}^{(*)}) = \frac{r_{ij}^{(*)} P(r_{ij}^{(2)})}{P(r_{ij}^{(*)})} = \frac{\pi_{ij} r_{ij}^{(*)}}{2 - \pi_{ij}}$$

where $P(r_{ij}^{(2)})$ and $P(r_{ij}^{(*)})$ are the respective probabilities that a fish double-tagged in year i and captured in year j has exactly two tags remaining in year j and at least one tag remaining in year j . The ratio $P(r_{ij}^{(2)})/P(r_{ij}^{(*)})$ can be viewed as the expected fraction of recaptured fish with one or two tags, $r_{ij}^{(*)}$, that still retains both tags.

Similarly, we can focus on double-tagged fish from release group i that are recaptured with only one tag in year j . The conditional expectation for this group of fish can be written as

$$(2) \quad E(r_{ij}^{(1)} | r_{ij}^{(*)}) = \frac{r_{ij}^{(*)} P(r_{ij}^{(1)})}{P(r_{ij}^{(*)})} = r_{ij}^{(*)} \left[1 - \frac{\pi_{ij}}{(2 - \pi_{ij})} \right]$$

The ratio $P(r_{ij}^{(1)})/P(r_{ij}^{(*)})$ can be viewed as the expected fraction of recaptured fish with one or two tags, $r_{ij}^{(*)}$, that retains only one tag. This ratio is simply the complement of the expected fraction retaining both tags (see eq. 1). The conditional expectations 1 and 2 lead to the following conditional binomial probability model:

$$(3) \quad P(r_{ij}^{(1)}, r_{ij}^{(2)} | r_{ij}^{(*)}) = \frac{(r_{ij}^{(*)})!}{(r_{ij}^{(1)})!(r_{ij}^{(2)})!} \times \left[\frac{\pi_{ij}}{(2 - \pi_{ij})} \right]^{r_{ij}^{(2)}} \left[1 - \frac{\pi_{ij}}{2 - \pi_{ij}} \right]^{r_{ij}^{(1)}}$$

Some of the fish double-tagged in 1974 and subsequently recaptured with at least one tag were given a third numbered tag and rereleased following the initial and subsequent recaptures (Table 1, multiple recaptures). Some of these rereleases had both of the original 1974 tags and some had only one of the 1974 tags. When these fish marked with a year j tag (a non-1974 tag applied in the year of initial recapture) were recaptured with the year j tag intact, the number of remaining 1974 tags was also recorded.

Let $r_{j(2)k}^{(*)}$ denote the number of rereleases in year j with two 1974 tags remaining at the time of release that were subsequently recaptured in year k with the year j tag intact. Let $r_{j(2)k}^{(0)}$, $r_{j(2)k}^{(1)}$, and $r_{j(2)k}^{(2)}$ denote the number of these recaptures (members of $r_{j(2)k}^{(*)}$) that had zero, one, and two 1974 tags remaining, respectively. The con-

Table 1. Number of lake trout tagged with two numbered tags (FD-67) for the double-tagging experiments in 1973 ($N = 77$) and 1974 ($N = 583$).

Years at liberty	Hatchery		Wild		Total
	Male	Female	Male	Female	
1973 releases					
Not seen again	44	24	3	1	73 ^a
1	2				2
2		1			1
6		1			1
1974 releases					
Not seen again	87	25	289	99	501 ^b
1	5	1	17	3	26
2	4		5	4	13
3	3		8		11
4			4	1	5
5	1		1		2
6			1		1
7			1	2	3
8			1		1
9			1		1
10			1		1
12			1		1
18			1		1
Multiple	2		13	1	16

Note: "Multiple" refers to fish recaptured more than once, e.g., fish recaptured after 2 years at liberty, released, and recaptured 3 years later.

^aIncludes one hatchery fish of unknown sex.

^bIncludes one wild fish of unknown sex.

ditional expectations for these three classes of recaptures can be written as

$$(4) \quad E(r_{j(2)k}^{(0)} | r_{j(2)k}^{(c)}) = r_{j(2)k}^{(c)}(1 - \pi_{jk})^2$$

$$E(r_{j(2)k}^{(1)} | r_{j(2)k}^{(c)}) = r_{j(2)k}^{(c)}(2\pi_{jk}(1 - \pi_{jk}))$$

$$E(r_{j(2)k}^{(2)} | r_{j(2)k}^{(c)}) = r_{j(2)k}^{(c)}\pi_{jk}^2$$

These expectations lead to the following conditional multinomial model:

$$(5) \quad P(r_{j(2)k}^{(0)}, r_{j(2)k}^{(1)}, r_{j(2)k}^{(2)} | r_{j(2)k}^{(c)}) = \frac{(r_{j(2)k}^{(c)})!}{(r_{j(2)k}^{(0)})!(r_{j(2)k}^{(1)})!(r_{j(2)k}^{(2)})!} \times [(1 - \pi_{jk})^2]^{r_{j(2)k}^{(0)}} [2\pi_{jk}(1 - \pi_{jk})]^{r_{j(2)k}^{(1)}} [\pi_{jk}^2]^{r_{j(2)k}^{(2)}}$$

Some of the rereleases in year j had already lost one of the 1974 tags and were released in year j with one new tag from year j and one 1974 tag. Denote the number of fish from this group recaptured in year k with the year j tag intact as $r_{j(1)k}^{(c)}$. Let $r_{j(1)k}^{(0)}$ and $r_{j(1)k}^{(1)}$ denote the respective number of these recaptures that had zero and one 1974 tag remaining at the time of recapture in year k . The conditional expectations for these classes of recaptures are

$$(6) \quad E(r_{j(1)k}^{(0)} | r_{j(1)k}^{(c)}) = r_{j(1)k}^{(c)}(1 - \pi_{jk})$$

$$E(r_{j(1)k}^{(1)} | r_{j(1)k}^{(c)}) = r_{j(1)k}^{(c)}\pi_{jk}$$

These expectations lead to the following binomial model:

$$(7) \quad P(r_{j(1)k}^{(0)}, r_{j(1)k}^{(1)} | r_{j(1)k}^{(c)}) = \frac{(r_{j(1)k}^{(c)})!}{(r_{j(1)k}^{(0)})!(r_{j(1)k}^{(1)})!} \times (\pi_{jk})^{r_{j(1)k}^{(1)}} (1 - \pi_{jk})^{r_{j(1)k}^{(0)}}$$

Note that models 5 and 7, which are based on rereleases, focus on tag loss parameters and statistics associated with the 1974 tags and not the tags applied at the first recapture. (None of the 1973-tagged fish were recaptured following initial capture and rerelease.) The above models were not developed for estimating tag loss of year j tags. Also note that the use of conditional binomial and multinomial distributions requires the assumption that the loss of one tag is independent of the loss of the other.

We modeled the π_{ij} cell probabilities as functions of an initial tag retention probability, γ , and annual tag retention probabilities, θ_k . In this model, γ is the complement of the probability of type I shedding. Because all initial releases were in 1973 and 1974 (most in 1974), we defined i and j in terms of "tag age" rather than calendar year. So, θ_1 corresponds to the probability that a tag "surviving" the initial tag loss event is retained from the year of tagging ($i = 0$) to the time of recapture in year 1 ($j = 1$). We now have

$$\pi_{0j} = \gamma \prod_{k=1}^j \theta_k$$

= $P(\text{tag is present } j \text{ years after initial application})$

for $j = 1, \dots, K$

where K is the maximum observed tag age. Only two fish from these double-tagging experiments were recaptured with times at liberty greater than 10 years (12 and 18 years) (Table 1), so we simplified the model by assuming that the age-specific θ_k were equal after 10 years at liberty (i.e., $\theta_{10} = \theta_{11} = \theta_{12} = \dots = \theta_{10+}$). We

Table 2. Number of double-tagged lake trout released with a plain tag (FD-67F) and a numbered anchor tag (either type FD-67C or FD-68BC) and recaptured 1 year after tagging.

Numbered tag type	Release year	Number of tagged fish released						Number of recaptures that shed the numbered tag						Number of recaptures that retained the numbered tag							
		Hatchery			Wild			Hatchery			Wild			Hatchery			Wild				
		M	F	U	M	F	U	M	F	Total	M	F	Total	M	F	Total	M	F	Total		
FD-67C	1978	219	121	17	1225	730	30	2342	4	1	10	62	12	2	155	47	10	57	112	29	141
	1979	336	151	1	940	433	1	1862	1	1	1	24	11	1	98	22	1	23	77	10	87
	1980	148	47	1	1421	300	8	1925	2	1	1	21	3	1	110	18	8	26	102	4	106
FD-68BC	1982	288	76	7	1367	518	15	2271	3	1	8	82	9	1	156	71	8	79	128	19	147
	1984	132	48	2	717	231	4	1134	3	1	1	3	5	1	50	3	1	4	41	4	45
	1985				42			42													

Note: M, male; F, female; U, unknown sex.

modeled tag retention rates separately for males and females and for hatchery and wild fish.

Cell probabilities for captures of rereleased fish, π_{jk} , were modeled slightly differently than recaptures of initial releases. As noted in the probability models for captures of rereleased fish (eqs. 4-7), the cell probabilities correspond to the interval between rerelease (time j) and subsequent recapture (time k). If we retain the above notation of denoting the year of initial tagging as $i = 0$ and that of initial recapture as j , then j corresponds to the age of the tag, in years. Statistics for rereleases that are eventually recaptured are subscripted by j and k , denoting the ages at rerelease and subsequent recapture, respectively. The cell probabilities for recaptures of rereleases thus differ from those of new releases in not including either a θ_0 or a γ parameter. For example, consider the following two cell probabilities for recaptures of rereleases:

$$\pi_{23} = \theta_2$$

$$= P(\text{tag is present 1 year after rerelease at tag age 2})$$

$$\pi_{35} = \theta_3\theta_4$$

$$= P(\text{tag is present 2 years after rerelease at tag age 3}).$$

The annual tag retention probabilities (θ_k) are subscripted by the appropriate tag ages, and the π_{jk} do not include γ parameters because the modeling corresponds to time periods that do not include the year following initial release.

We combined the conditional probability models 3, 5, and 7 for all recaptures of all three kinds of releases ($r_{ij}^{(c)}$, $r_{j(2)k}^{(c)}$, and $r_{j(1)k}^{(c)}$) into a product-multinomial model parameterized by the γ and θ_k tag retention parameters. We used program SURVIV (White 1983) to compute maximum likelihood estimates under this multinomial model. SURVIV also computed goodness-of-fit tests and Akaike's information criterion (AIC) to aid in model selection (e.g., see Lebreton et al. 1992; Burnham and Anderson 1998).

Models for one numbered tag

For the study with numbered and plain tags, the modeling differed, as we restricted recapture information to the year following tagging with a plain tag (Table 2). We did not extend the modeling of plain tag recapture data to years following the first because of the ambiguity associated with later recaptures. For example, recapture status the first year following tagging will not be known for a fish recaptured (with a tag) 2 years following tagging. If the fish captured in year 2 was not captured previously in year 1, then we would like to model the tag survival probability associated with the recapture event as $\theta_1\theta_2$. However, if the fish was captured in year 1, then this event will have already been modeled as θ_1 , and we would model the recapture in year 2, conditional on year 1 rerelease, with just θ_2 . Only recaptures occurring in the first year after tagging can be modeled with no ambiguity about previous history, and we restricted our modeling to this group for this reason. Because of this restriction, each fish contributed at most one recapture to the data set. We could not test for type I shedding, as plain tags permit estimation of tag retention probability for only the first year after release. Estimation is based on the first-year recaptures of fish retaining a plain tag in year $i + 1$. Denote these recaptures as $r_{i,i+1}^{(c)}$. Some of these recaptures still had the numbered tag in year $i + 1$ (denote these as $r_{i,i+1}^{(0)}$) and some had lost the numbered tag (denote these as $r_{i,i+1}^{(1)}$). If $\pi_{i,i+1}$ is the probability that a new numbered tag in year i is retained until year $i + 1$, then we write the conditional (on $r_{i,i+1}^{(c)}$) expectations as

$$(8) \quad E(r_{i,i+1}^{(1)} | r_{i,i+1}^{(c)}) = r_{i,i+1}^{(c)}(\pi_{i,i+1})$$

$$E(r_{i,i+1}^{(0)} | r_{i,i+1}^{(c)}) = r_{i,i+1}^{(c)}(1 - \pi_{i,i+1}).$$

These expectations lead to the conditional binomial model:

$$(9) \quad P(r_{i,i+1}^{(0)}, r_{i,i+1}^{(1)} | r_{i,i+1}^{(c)}) = \frac{(r_{i,i+1}^{(c)})!}{(r_{i,i+1}^{(0)})!(r_{i,i+1}^{(1)})!} \times [\pi_{i,i+1}]^{r_{i,i+1}^{(1)}} [1 - \pi_{i,i+1}]^{r_{i,i+1}^{(0)}}$$

Releases of fish with plain tags occurred during six different years and involved both sexes of hatchery-reared and wild fish (Table 2). Each release group for which at least one recapture occurred led to a model of the type in eq. 9, and these were combined into a product-binomial for all release groups. The $\pi_{i,i+1}$ represented the probability that a tag would be retained from the time of initial release in year i until the time of recapture in year $i + 1$. We used a single parameter, θ , for this probability, which included both type I and type II tag loss. These two types of loss could not be estimated separately under this design. As before, we used SURVIV (White 1983) to compute maximum likelihood estimates of tag retention rates, goodness-of-fit tests, likelihood ratio tests, and AIC values.

Model building and selection

For both types of double-tagging experiments (two numbered tags, numbered tag plus plain tag), we built several models by considering the effects of fish origin (hatchery versus wild), sex (male versus female), tag age (for 1973 and 1974 tags), and year of release (for plain-tagged fish). We used model building approaches described in Lebreton et al. (1992) and constrained model parameters to search for more parsimonious models. For example, with the plain tag data, we might assume no temporal variation in first-year tag retention rates and use a four-parameter model to estimate rates for hatchery male, hatchery female, wild male, and wild female fish. The four θ parameters corresponding to these four groups can be constrained to a three-parameter model by setting retention rates equal for female fish (regardless of origin). All models that we explored were nested within the general model of origin, sex, and time or tag age effects.

Our approach to estimation of retention rates and selection of models parallels that typically used for survival rates. Model selection was accomplished using AIC as described in Burnham and Anderson (1992), Lebreton et al. (1992), and Burnham et al. (1995). Models with too many parameters, while providing good fit, are characterized by estimates with low precision. Models with too few parameters may not fit the data adequately and can produce biased estimates. Model selection can be viewed as an optimization problem, where AIC is the objective function indicating which model achieves the optimal balance between fit and number of parameters (Burnham and Anderson 1992, 1998). SURVIV computes the AIC for each model; models with lower AIC's are considered better models. When the most general model did not fit the data adequately, we used a quasiliikelihood approach to testing (Burnham et al. 1987) and computed QAIC following methods in Anderson et al. (1994). We also used the small-sample corrections suggested by Anderson et al. (1994) to compute AIC_c and QAIC_c. However, these small-sample corrections modified AIC and QAIC by small amounts and made no difference in model selection. We therefore considered AIC and QAIC values in the remainder of the study. Rather than presenting the QAIC values, we present Δ QAIC, which is the difference between the model's QAIC and the lowest QAIC among all models considered. Burnham and Anderson (1998) recommended using this approach. In some cases, we used an analysis of deviance F test to determine the significance of a particular test between tag retention models (Lebreton et al. 1992). We used the analysis of deviance approach to test specific hypotheses, not in model selection.

Results

Two numbered tags

We constructed and evaluated several models to estimate retention rates for FD-67 tags (Table 3). The model with full origin, sex, and age specificity of retention rates (model Origin-Sex-Type I_{origin-sex-tag age}) was the most general model that could be fit to the data. This model exhibited a significant lack of fit (goodness-of-fit test: $G = 48.28$, $df = 21$, $P < 0.05$), indicating structural inadequacy of the model, overdispersion in the data, or both. If the data are overdispersed, AIC cannot be used in model selection (Anderson et al. 1994). We suspected overdispersion in our data because some of the fish tagged on the same day were later recaptured together. This type of "pairing" or schooling behavior leads to a lack of independence among observations (overdispersion) and results in extrabinomial variation (Anderson et al. 1994). Although model parameter estimates are not affected by extrabinomial variation, variance estimates and related likelihood statistics (such as AIC) are biased (Anderson et al. 1994). Using a quasiliikelihood approach, we adjusted for overdispersed data by estimating the variance inflation factor ($\hat{c} = G/df = 48.28/21 = 2.299$) from the general model and then using \hat{c} to estimate variances and calculate QAIC values for each model (Anderson et al. 1994).

The model we selected to best describe tag retention rates in lake trout tagged with FD-67 tags was a three-parameter model that included type I retention rates for wild fish only and otherwise constant (over tag age and sex) annual retention rates for wild and hatchery fish (model Origin-Type I_w) (Table 3). Annual retention rates of FD-67 tags were somewhat higher for hatchery fish ($\theta_H = 0.94$, 95% CI = 0.85–1.0) than for wild fish (year 1, $\gamma_w\theta_w = 0.64$, 95% CI = 0.41–0.86; years 2, 3, etc., $\theta_w = 0.88$, 95% CI = 0.78–0.99) (Fig. 2). The data supported the notion that type I shedding may be occurring in wild fish, but there was insufficient evidence for type I shedding in hatchery fish. We could not reject the hypothesis that the type I retention rate for hatchery fish was 1.0 using an analysis of deviance F test of model Origin-Type I_w versus Origin-Type I_{H,w} ($F = 0.483$, $df = 1$, 21 , $P = 0.989$). Under the model Origin-Type I_{H,w}, the estimated type I retention rate for hatchery fish was 0.86 (95% CI = 0.66–1.0). Although we recovered about equal proportions of hatchery (4.0%) and wild fish (4.4%) 1 year after release, our inability to detect type I shedding in hatchery fish may be due to the smaller numbers of releases, and hence recaptures, of hatchery fish 1 year after tagging (eight compared with 20 wild fish recaptured) (Table 1). We also tested the null hypothesis of no difference in tag retention rates for hatchery and wild fish. We found little evidence for differences between hatchery and wild fish ($F = 3.827$, $df = 1, 21$, $P = 0.128$).

One numbered tag

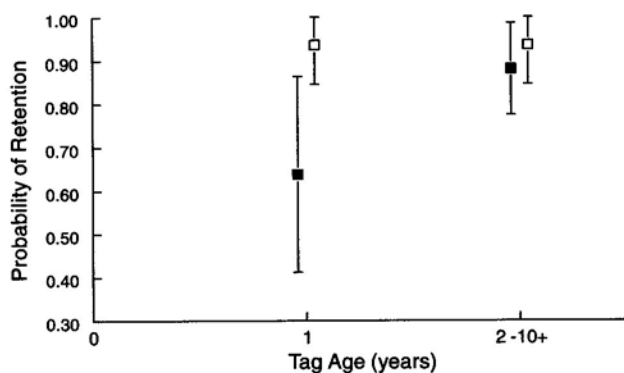
As with data from the double-tagging experiment using FD-67 tags, we constructed several models to account for variation in tag retention rates due to origin and sex. We also considered year of release and tag type as possible sources of variation, but note that these two factors are related (see Table 2). All retention rates estimated from the double-

Table 3. Tag retention models fit to the lake trout double-tagging experiments from 1973 and 1974.

Model	Notation	<i>p</i>	ΔQAIC
Origin–Sex–Type I _{HM,HF,WM,WF} –Tag Age	($\gamma_{HM}\theta_{HM1}$) $\theta_{HM2}\theta_{HM3}\theta_{HM4.5}\theta_{HM6.9}$ ($\gamma_{HF}\theta_{HF1}$) $\theta_{HF2}\theta_{HF3.6}$ ($\gamma_{WM}\theta_{WM1}$) $\theta_{WM2}\theta_{WM3}\theta_{WM4}\theta_{WM5}\theta_{WM6}\theta_{WM7}\theta_{WM8}\theta_{WM9}\theta_{WM10}$ ($\gamma_{WF}\theta_{WF1}$) $\theta_{WF2}\theta_{WF3.4}\theta_{WF5}\theta_{WF6.7}$	23*	34.08
Origin–Sex–Type I _{HM,HF,WM,WF} –Tag Age _{restricted}	($\gamma_{HM}\theta_{HM1}$) $\theta_{HM2}\theta_{HM3}\theta_{HM4.9}$ ($\gamma_{HF}\theta_{HF1}$) $\theta_{HF2.6}$ ($\gamma_{WM}\theta_{WM1}$) $\theta_{WM2}\theta_{WM3}\theta_{WM4}\theta_{WM5}\theta_{WM6}\theta_{WM7}\theta_{WM8}\theta_{WM9}\theta_{WM10}$ ($\gamma_{WF}\theta_{WF1}$) $\theta_{WF2}\theta_{WF3.7}$	19*	26.73
Origin–Sex–Type I _{HM,HF,WM,WF}	$\gamma_{HM}\theta_{HM}$ $\gamma_{HF}\theta_{HF}$ $\gamma_{WM}\theta_{WM}$ $\gamma_{WF}\theta_{WF}$	8	8.32
Origin–Sex–Type I _{HF,WM,WF}	θ_{HM} $\gamma_{HF}\theta_{HF}$ $\gamma_{WM}\theta_{WM}$ $\gamma_{WF}\theta_{WF}$	7	6.55
Origin–Sex–Type I _{WM,WF}	$\theta_{HM}\theta_{HF}$ $\gamma_{WM}\theta_{WM}$ $\gamma_{WF}\theta_{WF}$	6	4.90
Origin–Sex–Type I _{H,W}	$\gamma_H\theta_{HM}\theta_{HF}$ $\gamma_W\theta_{WM}\theta_{WF}$	6	4.56
Origin–Sex	$\theta_{HM}\theta_{HF}$ $\theta_{WM}\theta_{WF}$	4	5.97
Origin–Type I _{H,W}	$\gamma_H\theta_H$ $\gamma_W\theta_W$	4	1.52
Origin–Type I _W	θ_H $\gamma_W\theta_W$	3	0
Origin–Type I	$\gamma_H\theta_H\theta_W$	3	0.12
Sex	$\theta_M\theta_F$	2	4.96
Origin	$\theta_H\theta_W$	2	2.22
Simple–Type I	$\gamma\theta$	2	1.83
Simple	θ	1	3.19

Note: All lake trout were tagged with two numbered tags (type FD-67). Type I retention rates are denoted γ and type II rates are denoted θ . Subscripts refer to male (M), female (F), hatchery (H), and wild (W) fish. Other subscripts refer to tag age (1, 2, etc., in years) or to a range of tag ages (4.5, 6.9). An asterisk after the number of parameters (*p*) indicates that type I retention and first-year tag retention rates were not separately estimable; these rates are denoted in parentheses, e.g., ($\gamma_{HM}\theta_{HM1}$).

Fig. 2. Estimated retention rates of FD-67 tags in wild (■) and hatchery (□) lake trout from Gull Island Shoal, Lake Superior. The bars around the point estimates represent 95% CI. Tag age 10+ includes observations from fish at liberty 10 or more years.



tagging experiment with plain tags are first-year retention rates, combining type I and II rates.

The most general model we fit had tag retention parameters that varied by sex, source, and year of application (model Origin–Sex–Year) (Table 4). The model was fully saturated, permitting use of AIC (rather than QAIC) in model selection.

The model with the lowest AIC (Origin–Sex–Year_{WM}) had nine parameters: one tag retention rate for hatchery males, one for hatchery females, six for wild males, and one for wild females (Table 4). In general, estimated tag retention rates were about 0.80 (Fig. 3) except for hatchery females, which exhibited lower retention rates ($\theta_{HF} = 0.50$, 95% CI = 0.10–0.90). Year-specific parameters were necessary to account for variation in retention rates among wild males, and this variation did not appear to be associated with tag type for wild males (likelihood ratio test between models Origin–Sex–Year_{WM} and Origin–Sex–Tag Type_{WM}: $\chi^2 = 23.825$, *df* = 4, *P* < 0.05). The retention rate for the 1985 releases could not be estimated reliably with model Origin–Sex–

Table 4. Tag retention models fit to the lake trout double-tagging experiments from 1978, 1979, 1980, 1982, 1984, and 1985.

Model	Notation	<i>p</i>	Δ AIC
Origin–Sex–Year	$\theta_{HM78}\theta_{HM79}\theta_{HM80}\theta_{HM82}\theta_{HM84}$ $\theta_{HF78}\theta_{HF79}\theta_{HF80}$ $\theta_{WM78}\theta_{WM79}\theta_{WM80}\theta_{WM82}\theta_{WM84}\theta_{WM85}$ $\theta_{WF78}\theta_{WF79}\theta_{WF80}\theta_{WF82}\theta_{WF84}$	19	3.34
Origin–Sex–Year _{WM,WF}	$\theta_{HM}\theta_{HF}$ $\theta_{WM78}\theta_{WM79}\theta_{WM80}\theta_{WM82}\theta_{WM84}\theta_{WM85}$ $\theta_{WF78}\theta_{WF79}\theta_{WF80}\theta_{WF82}\theta_{WF84}$	13	1.59
Origin–Sex–Year _{WM}	$\theta_{HM}\theta_{HF}$ $\theta_{WM78}\theta_{WM79}\theta_{WM80}\theta_{WM82}\theta_{WM84}\theta_{WM85}$	9	0
Origin–Sex–Year _{WM} –Tag Type _{WM}	θ_{WF} $\theta_{HM}\theta_{HF}$ $\theta_{WM78}\theta_{WM79}\theta_{WM80}\theta_{WM82}\theta_{WM(BC)}$ θ_{WF}	8	3.09
Origin–Sex–Tag Type _{HM,WM,WF}	$\theta_{HM(C)}\theta_{HM(BC)}\theta_{HF}$ $\theta_{WM(C)}\theta_{WM(BC)}\theta_{WF(C)}\theta_{WF(BC)}$	7	15.59
Origin–Sex–Tag Type _{WM,WF}	$\theta_{HM}\theta_{HF}$ $\theta_{WM(C)}\theta_{WM(BC)}\theta_{WF(C)}\theta_{WF(BC)}$	6	15.74
Origin–Sex–Year _{WM} –Tag Type _{WM}	$\theta_{HM}\theta_{HF}$ $\theta_{WM(C)}\theta_{WM(BC)}\theta_{WM80}\theta_{WF}$	6	5.00
Origin–Sex–Tag Type _{WM}	$\theta_{HM}\theta_{HF}$ $\theta_{WM(C)}\theta_{WM(BC)}$ θ_{WF}	5	15.82
Origin–Sex _W –Tag Type _{WM}	θ_H $\theta_{WM(C)}\theta_{WM(BC)}\theta_{WF}$	4	16.47
Origin–Sex _H –Tag Type _w	$\theta_{HM}\theta_{HF}$ $\theta_{W(C)}\theta_{W(BC)}$	4	13.03
Origin–Sex	$\theta_{HM}\theta_{HF}$ $\theta_{WM}\theta_{WF}$	4	22.86
Origin–Tag Type	$\theta_{H(C)}\theta_{W(C)}$ $\theta_{H(BC)}\theta_{W(BC)}$	4	13.08
Sex–Tag Type	$\theta_{M(C)}\theta_{F(C)}$ $\theta_{M(BC)}\theta_{F(BC)}$	4	13.35
Origin–Tag Type _w	θ_H $\theta_{W(C)}\theta_{W(BC)}$	3	13.68
Tag Type _{origin}	$\theta_{H(C)}\theta_{W(C)}$ $\theta_{(BC)}$	3	11.88
Tag Type	$\theta_{(C)}\theta_{(BC)}$	2	10.09
Origin	$\theta_H\theta_W$	2	22.06
Sex	$\theta_M\theta_F$	2	22.38
Simple	θ	1	20.46

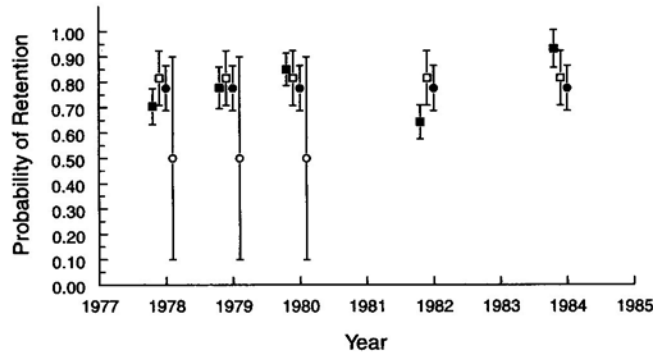
Note: All lake trout were tagged with a plain tag and one numbered tag (either type FD-67C (denoted C in subscripts) or FD-68BC used in 1984 and 1985 (denoted BC in subscripts)). Tag retention rates, θ , apply to numbered tags only; subscripts refer to male (M), female (F), hatchery (H), and wild (W) fish; years are denoted by the last two digits; *p* is the number of parameters in the model.

Year_{WM} because sample size for this group of releases was very small. Both Δ AIC values and the likelihood ratio test between models Origin – Sex – Year_{WM} and Origin – Sex – Year_{WM} – Tag Type_{WM} ($\chi^2 = 5.092$, *df* = 1, *P* < 0.05) provided support for the model in which retention rates for FD-68BC tags in 1984 and 1985 were different. Unlike the estimated retention rate for the 1985 releases, the estimated retention rate for the 1984 releases was high ($\hat{\theta}_{1984} = 0.93$, 95% CI = 0.86–1.0).

We noted that the retention rate for wild males tagged with FD-67C tags in 1980 was higher ($\hat{\theta}_{1980} = 0.85$) than

those for the three other groups of wild males tagged with FD-67C tags ($\hat{\theta}$ varied between 0.64 for 1982 releases and 0.78 for 1979 releases). We hypothesized that the higher retention rate for the 1980 release was associated with the use of different-colored FD-67C tags in that year (the only year for which numbered tags varied in color). Two sets of FD-67C tags were used in 1980: one set with grey tubing (53.6% of the tags) and another with orange (46.4%). A χ^2 test of differences in proportion of fish recaptured in 1981 with grey and orange tags provided no evidence of a difference ($\chi^2 = 0.003$, *P* > 0.05). Thus, the higher retention rate

Fig. 3. Estimated retention rates of FD-67C and FD-68BC tags in wild male (■), hatchery male (□), wild female (●), and hatchery female (○) lake trout from Gull Island Shoal, Lake Superior. These rates, shown as point estimates with 95% CI, represent tag retention after 1 year at liberty and apply to releases from 1978, 1979, 1980, 1982, and 1984. Results for the 1985 releases are not plotted because only wild males were tagged in 1985 and the resulting estimate was unreliable, being based on a single recapture.



for the 1980 releases does not appear to be associated with differences in performance quality or durability of the different colors used that year. Similarly, retention rates for the 1984 releases were significantly greater than those for the 1978 and 1982 releases (Fig. 3). The greater sample sizes used to model retention rates of FD-67C tags in wild males permitted estimation of retention rates for each year. Annual fluctuations in these rates represented a source of significant variation in the data (likelihood ratio test between models Origin-Sex-Year_{WM} and Origin-Sex: $\chi^2 = 32.863$, $df = 5$, $P < 0.05$).

Discussion

In this paper, we demonstrated that SURVIV, originally developed to model survival rates (White 1983), can be used to estimate tag retention rates for fish. This application requires specifying the conditional binomial or multinomial probabilities for each recaptured fish in the double-tagging experiment. Under the SURVIV framework, conditional binomial (and multinomial) probability models are functions of the number of fish recaptured with at least one tag and the probability of a tag being retained from year i to year j . This probability was defined as a product of the type I retention rate and the annual tag retention rate.

Data from lake trout double-tagged with two numbered tags were used to examine differences in retention rates with tag age and estimate the additional type I losses. The flexibility of our modeling approach allowed us to accommodate a unique aspect of the double-tagging experiments. Unlike most double-tagging studies, we could "observe" double-tagged fish that were recaptured with no tags. These observations were possible because some of the fish from the 1974 experiment were tagged multiple times.

Previously described methods for estimating tag retention rates have generally focused on estimation of constant rates (e.g., Chapman et al. 1965; Bayliff and Mobrand 1972; Fabrizio et al. 1996). A few models of time-dependent variation in retention rates have been described (e.g., Kirkwood

1981; Hampton and Kirkwood 1990). Our approach can be tailored to the study design and permits subsetting of the data (e.g., males versus females or by tag type), inclusion of type I rates, and variation of retention rates according to features of the tagged fish (e.g., sex, size, or origin) or aspects of the experiment. Decisions concerning the importance of factors in accounting for variation in tag retention rates are made during the model selection process using AIC or QAIC, although other objective functions could be used. In the case of nested models, the significance of factors can be tested with likelihood ratio tests or analyses of deviance (Lebreton et al. 1992).

Our estimates of annual tag retention rates for lake trout were fairly high (80–90%), but we found evidence (among wild fish only) that retention rates may be significantly lower in the first year due to type I losses. Are type I losses real? Although we were unable to detect type I losses, we suspect that they may have indeed occurred among hatchery fish. Our inability to detect lower first-year retention rates in hatchery fish may have been due to small sample sizes (too few recaptures) rather than to any biological or behavioral differences between wild and hatchery fish. One possible mechanism that may contribute to lower tag retention rates in the first year is tag disintegration. We noted that on average, 11% of the recaptured fish carried defective tags (Fabrizio et al. 1996). These fish retained the T-bar (the anchor) but not the nylon tube (the portion of the tag inscribed with a number). Although we tested for this type of tag failure before inserting the anchor tags, it remained a problem with some of the tags. However, it is not possible to unequivocally ascribe these losses to the first year because we could not determine the year of tagging for fish recaptured with defective tags.

According to our data from double-tagging experiments with FD-67C and FD-68BC tags, tag retention rates may vary between male and female lake trout. Brewin et al. (1995) found differences in shedding rates for male and female brown trout (*Salmo trutta*) tagged with Floy anchor tags. We found no evidence for annual differences in tag retention rates for wild female lake trout, although one explanation for this is that sample sizes were small. In some years, retention rates for wild males were slightly higher than for wild females, and in other years the opposite was true. Variations in tag retention rates between sexes may reflect behavioral differences of lake trout. However, if tag shedding was associated with persistent behavioral differences between male and female fish, we should have observed a consistent pattern in retention rates through time (see Fig. 3). We recommend additional double-tagging experiments with larger sample sizes, particularly for female lake trout, so that this source of variation in retention rates can be reexamined. In addition, these experiments should be conducted with two numbered tags so that type I shedding rates can be estimated as well.

Some of the data from this study were also analyzed by Fabrizio et al. (1996), who estimated constant tag shedding rates for three types of tags using nonlinear models. In general, the results presented here compare favorably with those in Fabrizio et al. (1996), although the nonlinear models describe constant tag shedding rates for all lake trout (no subsets were investigated). The results of the two studies are not

directly comparable because we examined tag shedding rates from subsets of data (e.g., male and female fish) and were also able to include data that could not be used with the non-linear modeling approach.

Although not demonstrated here, another possible source of variation in tag retention rates is the tag operator. Hearn et al. (1991) warned against pooling recapture data from different taggers because they often display different skill levels or follow slightly different procedures. Using the approach developed in our study, tagger effects can be tested with likelihood ratio tests of nested models. Other modeling approaches permit likelihood ratio testing as well (e.g., see Barrowman and Myers 1996; Hampton 1997). It may also be desirable to determine if the skill of an individual tagger improved or deteriorated over time (years); the probability of tag retention is expected to increase as skill increases over time. Except for the lower retention of tags from the 1982 experiment, this expectation appears to be supported by results for wild males tagged with FD-67C tags (Fig. 3). (Retention rates were modeled as constants for wild females, hatchery females, and hatchery males and thus were not useful in examining this issue.) However, improvement in the tagger's skill may be offset by factors associated with the tagging operation. For example, tag placement and insertion are more accurate and effective on a stable platform, but tagging becomes difficult in rough seas.

All of our modeling and results are based on the assumption that tags on a fish are lost independently. This may not always be the case (e.g., see Diefenbach and Alt 1998). One approach to such dependence is to model the initial tag retention probability (conditional on no previous tag loss) with one parameter and the probability of loss of the second tag (conditional on loss of the first tag) with a different parameter. Such modeling would appear to require three tags, at least two individually numbered tags and a third tag (or some other mark) identifying the fish as part of the study. The modeling would then be conditional on fish captured with the third tag or mark and would model events associated with the loss of zero, one, or two numbered tags.

Considered in isolation, tag loss is fairly uninteresting from both management and ecological perspectives. One of the primary motivating factors for our study of tag retention rates was the desire to estimate survival rates for this population of lake trout in Lake Superior. In the presence of tag loss, survival rates must be adjusted to "correct" for the loss of tags, and this is typically performed using a posteriori methods. For example, $\hat{\phi} = \hat{\phi}/\hat{\theta}$, where $\hat{\phi}$ is the adjusted (for tag loss) survival rate for fish, $\hat{\phi}$ is the estimated survival rate for tagged fish (complement includes fish death and tag loss), and $\hat{\theta}$ is the estimated tag retention rate, assumed to be constant over time (Pollock 1981). However, when tag retention rates are less than survival rates, post hoc adjusted estimates of annual survival rates are greater than 100% (e.g., see Fabrizio et al. 1997). When survival rates are high, adjustments such as these should be avoided. In addition, variation in tag retention over time and with tag age render a posteriori "corrections" for tag loss more difficult. In cases where tag retention rates are not constant over time or for a release cohort, we believe that the most reasonable approach to survival rate estimation involves development of joint likelihoods that incorporate models of both tag retention and

fish survival (e.g., Nichols et al. 1992; Nichols and Hines 1993). These models will include parameters for fish survival, tag retention, and recapture or recovery probabilities. Such models can be used in studies where all fish are double-tagged or in situations where some releases are double-tagged and others are tagged singly. These models can be tailored to reflect virtually any kind of study, as long as samples of double-tagged fish are released for the estimation of tag retention probability. A major strength of such an approach is the ability to provide not only unbiased estimates of survival rates in the face of tag loss, but also associated estimates of sampling variance that properly incorporate the sampling variance-covariance structure imposed by the double-tagging and tag loss sampling.

In summary, we estimated annual tag shedding rates for lake trout from Gull Island Shoal, Lake Superior, with software originally designed to estimate annual survival rates. The modeling approach we described affords several benefits including (i) availability of software, (ii) availability of well-established model selection procedures, (iii) modeling flexibility, (iv) ability to draw inferences about the relevance of factors associated with subsets of the data such as sex and origin, and (v) ability to directly incorporate tag shedding rates in survival models.

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