

Review of Marking Methods and Release-Recapture Designs for Estimating the Survival of Very Small Fish: Examples from the Assessment of Salmonid Fry Survival

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The survival of very small fish can have a major impact on the dynamics of fisheries stocks. Numerous marking techniques have been developed or adapted to small fish in order to investigate either early life histories or small-sized species. Some techniques provide batch marks, while others provide individually unique identification with or without the need for destructive sampling. We review 20 marking techniques in the context of conducting survival studies for small fish, with examples focused on salmonid fry survival. Sixteen alternative release-recapture designs for conducting survival investigations are also examined. Eleven approaches are found capable of estimating survival parameters, while five are not. Of those methods capable of estimating fish survival, five require unique marks, and six permit batch-specific marks. No approach based on a single release of batch-marked fish is capable of statistically estimating survival. Investigators are encouraged to carefully coordinate their choice of marking technique with the design and analysis of the release-recapture model used.

Keywords external marks, internal marks, mark-recapture, survival estimation, tagging

INTRODUCTION

Small fish represent both the early life stages of many species and the adults of other species. Measuring the survival of small fish is important for effective management of many protected populations (e.g., Pacific salmonids, *Oncorhynchus* spp.). Legal, ethical, and economic considerations make it imperative that survival studies be carefully designed and conducted. Electronic tags (e.g., acoustic, radio, satellite) are commonly used on larger fish for estimating survival and recruitment, stock assessment, evaluating movements, and assessing alternative management practices. For smaller fish (<65-mm fork length), the logistics of marking and conducting release-recapture studies is more difficult and precarious. Fewer tagging options are available,

and tagging and handling effects are often intensified relative to larger fish. Furthermore, survival estimation methods are more dependent on tag choice than for larger fish. The result is a relative lack of precise survival information through early life stages or for small fish, in general.

For example, vast amounts of information now exist on the survival of anadromous Pacific salmonids between smolt out-migration and adult upriver returns arising from Passive Integrated Transponder (PIT) tags (e.g., Prentice et al., 1990; Skalski et al., 1998; Smith et al., 2002; Buchanan and Skalski, 2007), radio tags (Skalski et al., 2001), and acoustic tags (Ploskey et al., 2007). However, these tag technologies are typically not applicable for small juvenile salmonids between emergence from the gravel and seaward migration, a life stage referred to as fry by some salmon biologists. Fry may be relatively stationary, or may migrate upstream or downstream to feed. At some point, the anadromous species will engage in directed seaward migration. The inability to tag very small fish with existing electronic

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tags such as PIT tags or acoustic tags has resulted in relatively little detailed survival information on salmonids during their early life history prior to seaward migration.

However, some investigators have reported survival estimates for early salmonid life stages. For example, survival from the fry to smolt life stage was estimated to range from 3–34% for Chinook salmon (*O. tshawytscha*) in the Sacramento River (Kjelson et al., 1982). Hunter (1959) reported fry mortality for chum (*O. keta*) and pink (*O. gorbuscha*) salmon to range from 22.6–85.5% in as short as a 2.6-km journey to the sea. Bax (1983) estimated average daily mortality of juvenile coho (*O. kisutch*, mean fork length 50 mm) of 31–46% immediately after entry into saltwater. The wide ranges in these survival estimates are exemplary of the lack of information available on the early life stages of salmonid populations.

Nevertheless, many marking methods do exist for small fish. Marking methods may be classified using two basic considerations: whether or not individual-based identification is possible, and whether or not the fish must be sacrificed to retrieve tag information. Similarly, numerous release-recapture study designs are available to estimate fish survival, varying in the number of release groups used and the locations of the individual releases. However, not all marking methods are compatible with all release-recapture designs. Consequently, selecting an appropriate combination of marking method and release-recapture design is crucial.

In this article, we review 20 marking methods for small fish, ranging from visual tags to genetic markers. In conjunction with the range of marking methods, we also review 16 alternative release-recapture designs, including single release-recapture designs (e.g., Skalski et al., 1998), staggered entry designs (e.g., Pollock et al., 1989), paired-release recapture designs (e.g., Burnham et al., 1987, pp. 64–173), and single release-remark-rerelease designs (e.g., Burnham et al., 1987, pp. 198–200). This review will illustrate the interdependency between tag choice and release-recapture design and analysis. The examples and vocabulary used will focus on survival estimates for salmonid fry, but conclusions about the marking methods and release-recapture designs are also applicable to other small migratory fish.

This article will begin with a review of available marking techniques for small fish. Considerations regarding fish size limitations, numbers of unique marks possible, and the ability to read the mark nondestructively will be summarized. The feasibility of alternative release-recapture study designs will then be reviewed, taking into account characteristics of the marking techniques. The goal of this review is to help investigators identify key aspects of marking and release-recapture techniques that will provide the needed information on critical early life history stages. A more technical review of this same material that includes details of the statistical estimation procedures can be found in Skalski and Griswold (2006). Readers are also encouraged to read about fish marking techniques in Nielsen (1992) and release-recapture methods in Seber (1982) and Burnham et al. (1987).

FRY MARKING TECHNIQUES

Investigators have at their disposal a variety of fish marking techniques ranging from external to internal marks, genetic identification, and chemical markers. The appropriate technique depends on logistics, costs, fish size, number of fish available for marking, and the requirements of the release-recapture model ultimately used to estimate survival. There are multiple ways of classifying the large number of marking techniques. We classify marking technologies here as either external or internal, the aggregation level to which the mark can be distinguished (individual or batch), and whether the method is suitable for mass marking. We also classify each method based on its type of detection, as categorized by the Pacific Salmon Commission (2006):

1. Immediate visual (IV)—marks that can be seen immediately by the unaided eye;
2. Immediate specialized detection (ISD)—marks that can be detected immediately with the proper sampling equipment (every fish must be analyzed because these marks lack a visual identifier); and
3. Delayed detection (DD)—marks that require sacrificing the fish or sampling harvested fish to obtain the tag or tissue for specialized laboratory analysis.

External Marks

External marks involve modifying the appearance of the marked fish, using techniques ranging from pigments, dyes, and tattoos to fin clips and the attachment or insertion of physical tags whose detection is either IV or ISD (Table 1). Fin excision or fin clipping is among the oldest and simplest methods of marking fish, where a fin (e.g., pelvic or adipose) is wholly or partially removed for subsequent identification with a group or batch of fish. Freeze branding using straight-line letters (e.g., T, V, X, I) and various combinations of letter orientation and body placement provides up to 30 possible distinct marks. Dye marking uses a colored dye of one or more stains or pigments applied via immersion or injection. High-pressured sprays are sometimes used to mark fish with pigments that fluoresce under black light. Dye marking may be suitable for mass marking for short-term studies where it is necessary to distinguish only a few experimental lots. The Visible Implant Fluorescent (VIF) tag is a small plastic strip coded with a three-digit alphanumeric code and attached at one of a number of body locations (e.g., between fin rays or in periocular eye tissue). The Visible Implant Elastomer (VIE) tag consists of a biocompatible two-part silicone-based material that is mixed and injected into tissue as a liquid, which then cures into a pliable solid after 24 hours at room temperature. This is actually an internal mark but is externally visible under either ambient or ultraviolet light. The elastomer used in the VIE tag is available in various fluorescent and non-fluorescent colors, and recognition of individuals

Table 1 Summary of marking techniques for small fish, the availability of unique codes for ease of identifiability, permanency (stability) of the mark, and minimum fish size or life stage requirements

Mark technique	Unique codes possible	Suitable for mass mark	Category of detection*	Stability	Minimum fish size or life stage
External marks					
Fluorescent elastomer (VIE)	240	No	IV or ISD	Variable	26 mm
Fluorescent filament (VIF)	3-character alpha-num	No	IV or ISD	Variable	50 mm
Dye marking	Limited (i.e., ≤ 30)	Yes	IV or ISD, NS	Variable	25–50 mm
Adipose clip	None	Yes	IV	0–4% regeneration	50 mm
Ventral clip	None	Yes	IV	0–47% regeneration	50 mm
Adipose or ventral clip and CWT (coded wire tag)	Unlimited	Yes	DD	Variable	<2.1 g HLCWT >2.1 g FLCWT
Tattoos	Limited	No	IV, NS	Low	100 mm
Freeze branding	Limited	No	IV, NS	Low	50 mm
Internal marks					
Half-length CWT (HLCWT)	Unlimited	Yes	DD, S	Variable	<2.1 g
Full-length CWT (FLCWT)	Unlimited	Yes	DD	Variable	>2.1 g
Genetic	Unlimited	Yes	DD, NS	Permanent	None
Molecular/laser	Limited	Yes	ISD, NS	30 months	8 days post-yolk absorption
Strontium isotope ratios	None	Yes	DD, NS	Permanent	None
Oxytetracycline	Limited	Yes	DD, S	High	None
Strontium chloride	Limited	Yes	DD, S	High	None
Calcein immersion	Limited	Yes	ISD, S or NS	4–12 months	None
Tetracycline	Limited	Yes	DD, S	High	None
Otolith thermal	Unlimited	Yes	DD, S	Permanent	Emergent fry–advanced yearling
Dry mark otolith (eggs)	Unlimited	Yes	DD, S	Permanent	Only for eggs
PIT	Unlimited	Yes	ISD, NS	85–100%	50 mm

*Detection categories.

IV: Immediate Visual—marks that can be easily and immediately seen by the unaided eye.

ISD: Immediate Specialized Detection—marks that can be immediately detected with the proper equipment. Every fish must be analyzed because these fish do not have a visual identifier.

DD: Delayed Detection—marks that require sacrificing the fish or sampling harvested fish to obtain the tag or tissue for specialized laboratory analysis.

S: Sacrificing the fish is required.

NS: No sacrifice of the fish is required.

is possible by using different combinations of colors and body locations (Bonneau et al., 1995; Choe and Yamazaki, 1998).

External marks have been used with a variety of wild and hatchery salmonid species. Freeze branding has been used with young coho salmon smaller than 50 mm in total length (Bryant et al., 1990). Johnson (2004) used a pelvic fin clip on Atlantic salmon (*Salmo salar*) fry, and many species of Pacific salmon (*Oncorhynchus* spp.) have been marked with adipose fin clips to indicate the presence of a coded wire tag (CWT) in commercial fisheries. Currently, hatchery salmon smolts are commonly marked with an adipose fin clip to distinguish them from wild fish in mark-selective fishing. Coble (1967) and McNeil and Crossman (1979) have addressed the techniques of fin excision and clipping, while Armstrong (1949), Shetter (1951), Johnson and Ugedal (1988), and Coombs et al. (1990) have all addressed fin regeneration among salmonids. Several types of dye marking techniques have been used with varying degrees of success with brook trout (*Salvelinus fontinalis*) and Atlantic salmon (Moffett et al., 1977; Dussault and Rodriguez, 1997), migrating sockeye salmon (*O. nerka*; Carlson et al., 1998), and Chinook salmon (*O. tshawytscha*) fry (mean fork length = 57.5 mm; Gaines and Martin, 2004). Wild, age 0 brown trout (*Salmo trutta*, fork

length = 26–70 mm) have been successfully marked with VIE tags and experienced negligible tagging mortality (Olsen and Vollestad, 2001). Both wild rainbow trout (*O. mykiss*; Shepard et al., 1996) and coho salmon (mean fork length = 108 mm; Bailey et al., 1998) have been tagged with VIF tags, as well as wild coastal cutthroat trout (*O. clarki*; Wenburg and George, 1995).

In general, fin excision and dye marking may be suitable for mass marking of small fish (e.g., 50-mm fork length), but used alone are of no or limited use in identifying unique individuals or treatment groups. Tattoos and freeze branding are unsuitable for mass marking, but provide identification of a limited number (e.g., ≤ 30) of unique individuals or groups. The VIE and VIF tags allow for identification of unique individuals or groups numbering in the hundreds (VIE) and thousands (VIF), but are unsuitable for mass marking. Tag retention of external marks is low or variable, in general, as marks fade or are occluded by tissue growth or regeneration. In some cases, tag retention or detection depends strongly on the skill of the tagger (e.g., VIE and VIF tags; Hale and Gray, 1998; Close, 2000), but in general, tag detection requires little or no training. Because of low tag retention and variable mortality effects of tagging (e.g., marked

fish may be more vulnerable to predation than unmarked fish), most external marks are suitable only for short-term studies of fry survival, movement, or abundance. The exception is fin excision, which may be used for long-term studies if rates of fin regeneration and naturally missing fins are taken into account (Blankenship, 1990).

Internal Marks

Internal marks require specialized detection equipment that either may be used to sample nondestructively in the field (ISD), or else require sacrificing the fish and detection in the laboratory (DD). Internal marks range from injectable tags such as the CWT or PIT (Passive Integrated Transponder) tags, to tissue marking using chemical marks or laser tags, and genetic manipulation. The CWT tag is available as half-length (HLCWT) or full-length (FLCWT) tags, and in the past have been used with an adipose fin clip to indicate their presence. Blankenship (1990) recommended that fish smaller than 2.1 g be tagged with HLCWT, and larger fish be tagged with FLCWT. The CWT tag is available in both batch form and sequential form, with the latter providing identification of individual fish. PIT tags are biotelemetric tags that may be injected into juvenile salmon as small as 55 mm, but may not be applicable to very small fry. They may be read with portable PIT readers at short range (≤ 36 cm, Cucherousset et al., 2005), or with fixed-site detectors placed across rivers and streams, with detection ranges up to 76 cm (Sandy Downing, NMFS, personal communication). Marks on calcified tissue such as the otoliths or caudal fin rays generally require destructive and specialized laboratory detection techniques. Tissue marks may be naturally occurring, such as stream-specific strontium (Sr) isotope ratios or temperature-induced otolith marks specific to incubation sites (Quinn et al., 1999), or purposely applied via temperature or feeding regime manipulation or water-bath immersion using solutions of oxytetracycline (OTC), calcein, or strontium. New tissue or serum-marking techniques that use molecular or laser tags are being developed with nondestructive, in-field detection using handheld devices (John Sternick, Mansfield University, and Bill Krise, U.S. Fish and Wildlife Service; U.S. Patents 7189366, 20070148709). Genetic marking uses selective breeding to alter frequencies of alleles in the marked population to distinguish it from the unmarked population.

Much of the work using chemical marks has been done with Atlantic salmon and non-migratory salmonid species. For example, stream-specific strontium isotopic ratios have been used to study Atlantic salmon in tributaries of the Connecticut River (Kennedy et al., 2002). Calcein marks have been studied in both Atlantic salmon (Mohler et al., 2002; Honeyfield et al., 2006) and rainbow trout (Bart et al., 2001; Frenkel et al., 2002; Negus and Tureson, 2004), as well as in brook trout (~ 1 g; Honeyfield et al., 2006).

Most internal marks have the advantage of being both long-lasting (or permanent) and applicable to fish of any size. Nat-

ural, chemical, and genetic marks have no minimum fish size, and molecular and laser marks may be applied to very young fish (Table 1). Half-length CWTs have been successfully used on newly emergent pink salmon (*O. gorbuscha*) fry (mean weight = 0.26 g; Kaill et al., 1990). PIT tags have been used on salmon as small as 55 mm (Prentice et al., 1990), although conflicting reports exist on the effect of PIT tags on growth and survival (e.g., Prentice et al., 1990, vs. Brakensiek and Hankin, 2007). Peterson et al. (1994) found no difference in overwinter growth and survival between juvenile coho salmon as small as 2.8 g (65-mm fork length) that were tagged with either PIT tags or sequential CWT tags. Other studies suggest that the effect of PIT tags on survival may be both size- and species-dependent (Acolas et al., 2007) or dependent on tagger experience. Retention of internal marks ranges from 4–16 months for chemical markers using calcein immersion (Frenkel et al., 2002; Mohler, 2003; Negus and Tureson, 2004), to over 21 months using a strontium chloride marker (Schroder et al., 1995), to permanent retention for strontium isotopic ratios (Kennedy et al., 2002) and thermal otolith marking (Brothers, 1990; Buckley and Blankenship, 1990). Some chemical markers fade on exposure to direct sunlight (e.g., calcein immersion; Johnson, 2003), and a general positive relationship was found between mark endurance and fish size for chemical marking of small rainbow trout (~ 0.2 – 0.3 g; Bart et al., 2001; Frenkel et al., 2002). Retention of CWTs depends on fish size and skill of the taggers (Blankenship, 1990; Kaill et al., 1990; Peltz and Miller, 1990). Early studies of PIT tags showed high tag retention (Prentice et al., 1990), but recent work documents tag losses of up to 15% in returning adults (Knudsen et al., 2009) and up to 30% in juvenile brown trout smaller than 57 mm at tagging (Acolas et al., 2007). PIT tag retention may depend partly on the skill of the taggers.

All the internal marks considered here are suitable for mass marking. Some (i.e., sequential CWT, PIT tags) allow for identification of an unlimited number of unique individuals. Other techniques similarly have an unlimited number of unique codes available but are more practically applied as batch marks (e.g., otolith marking, genetic marking). Purposely applied chemical marks may be used for unique identification of a limited number of groups or batches, while natural marks such as strontium isotopic ratios cannot be used to differentiate among groups from the same stream.

Detection of internal marks often requires a high level of skill, involving laboratory work and sacrifice of the fish. In particular, detection of chemical and otolith marks requires destructive sampling, and detection and interpretation of otolith marks depend on the skill of the technician. Coded wire tags also require destructive, laboratory-based detection. On the other hand, portable, handheld detectors have been developed for PIT tags (Destron Fearing Corporation) and the experimental molecular and laser tags. Fixed-site PIT tag detectors may be located at dams, traps, and across streams or small rivers, providing automatic detection of PIT-tagged fish. Genetic marking requires a high degree of knowledge both to design a marking study and to detect the marks. Gharrett and Seeb (1990) list several

factors necessary for consideration of using genetic marking: (1) information on the range and time of spawning and the sizes of the target population and the populations from which it is to be discriminated are needed to determine the utility of a mark; (2) life-history information is needed to determine the extent of follow-up marking necessary; (3) selection of a relatively large brood stock is required so that genetic variability will be sustained; (4) adequate resources are necessary to mark the population and subsequently detect the mark in mixtures; (5) selection for single allele markers can produce optimum genetic marks.

MARKING AND RELEASE-RECAPTURE DESIGNS

Four general types of release-recapture designs are typically used with tagging or marking studies to estimate fry survival through either time or space. The four classes of release-recapture methods considered here are: (1) single release-recapture models, (2) staggered-entry release-recapture models, (3) paired release-recapture models, and (4) single release-remark-rerelease models. In the following descriptions of release-recapture models, R represents the release group, S represents survival, and p represents the conditional detection probability. The release-recapture methods are described using spatial imagery (e.g., river reaches, detection sites), but may be interpreted using temporal imagery instead (e.g., sampling periods, detection occasions) if survival through time rather than space is of interest. The estimation goal is an unbiased point estimate of the probability of survival in the initial river reach or time period (e.g., S_1), unconfounded with the probability of detection at the first sampling occasion (e.g., p_1).

The basis for the most powerful and flexible designs is the single release-recapture model with uniquely marked fish. In this scenario, each fish produces a complete capture history, which can be used to estimate survival and detection probabilities in all reaches except the last. Staggered-entry designs allow new fish to enter the study at downstream detection sites for improved estimation processes and/or estimable survival in additional cases. Similar in appearance to the staggered-entry designs are the paired release-recapture designs. In these designs, fish are released above and below the river reach of interest, with subsequent recaptures downstream. This design allows estimation of survival in the river reach between the upstream and downstream release sites. Estimation of survival in downriver reaches may also be possible, depending on the marking and recapture approach used in the study. Finally, the single release-remark-rerelease design uses batch-marked fish released at the top of the river reach of interest. First-time recaptured fish are given a second mark for subsequent identification. Should these fish be recaptured a second time, they are removed from the study. Two alternative protocols for the single release-remark-rerelease design using the resulting partial capture history data are reviewed: Scheme A, in which a fish is given a second

site-specific mark upon first recapture, with mark-releases occurring at all site locations except the last, and Scheme B, in which a fish is given a second mark only if recaptured at the first downstream recapture site (Burnham et al., 1987).

Survival estimation depends on separating the probability of survival from the probability of detection, both of which influence the number of marked fish that are recovered or recaptured at a given sampling occasion. In most studies, an independent estimate of the detection probability will be unavailable, so the detection data themselves will be used to separate the survival and detection probabilities. This is done either by comparing the numbers of fish with different detection histories, or else by comparing the relative recoveries of different release groups, under the assumption that all groups have common detection probabilities. The former approach requires individually marked fish with nondestructive sampling, so that detection histories are identifiable. The latter approach requires at least two distinguishable groups of fish. Thus, the ability of each release-recapture design to estimate survival depends on the fish-marking technique used. In particular, the crucial features are whether marked unique individuals can be identified, or only groups of fish are identifiable (i.e., batch marks), and whether or not sampling is destructive. We reviewed 16 marking and release-recapture scenarios for the ability to estimate survival through the first reach or sampling period. For each of the 16 protocols reviewed, the ability to estimate survival was characterized based on the properties of minimum sufficiency and separability of parameters, i.e., was there enough information to permit survival estimation. All scenarios are described in Table 2. Those that allow estimation of survival are described in more detail below.

We found that 11 of the 16 marking and release-recapture scenarios provide estimates of survival for one or more reaches

Table 2 Alternative scenarios for conducting fry survival studies and their ability to provide valid estimates of reach survival. Study designs are SRR = single release-recapture; SE = staggered entry; PR = paired-release; and SRRR = single release-remark-rerelease. Marks are UI = unique individual mark and B = batch mark (with number of unique marks used). Sampling codes are DS = destructive sampling and NDS = nondestructive sampling

Study design	Marks	Sampling	Survival estimable?	Figure
SRR	UI	DS	No	—
SRR	UI	NDS	Yes	1
SRR	B (1 mark)	DS	No	—
SRR	B (1 mark)	NDS	No	—
SE	UI	DS	Yes	2
SE	UI	NDS	Yes	2
SE	B (1 mark)	DS	No	—
SE	B (1 mark)	NDS	No	—
SE	B (>1 mark)	DS	Yes	2
SE	B (>1 mark)	NDS	Yes	2
PR	UI	DS	Yes	3a
PR	UI	NDS	Yes	3b
PR	B (>1 mark)	DS	Yes	3a
PR	B (>1 mark)	NDS	Yes	3a
SRRR	B (2 marks)	Mix	Yes	4
SRRR	B (>2 marks)	Mix	Yes	5

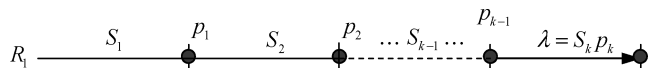


Figure 1 Schematic of scenario using a single release of uniquely marked individuals and nondestructive sampling with k sampling sites. Using this method, survival (S) can be estimated in all but the last reach (Burnham et al., 1987; Skalski et al., 1998). Nondestructive sampling is denoted by ●.

(Table 2). No scenario that used a single group of commonly batch-marked fish (i.e., a single mark was used) provided sufficient information to estimate survival, regardless of sampling method or study design. In addition, the single-release design combined with destructive sampling cannot yield survival estimates. Investigators should be aware of these limitations as they design fry survival studies.

Only one scenario using the single-release design provided survival estimates. This scenario requires uniquely marked individuals and nondestructive sampling and permits estimation of survival and capture probabilities in all reaches except the last (Figure 1). This model is a special case of the full capture history model of Burnham et al. (1987, pp. 112–116) when only one release in a paired release is used. Skalski et al. (2001) used the model to estimate salmonid smolt survival using PIT tags in the Columbia River. The summary data are the number of fry in each of the 2^k possible capture histories in a k -reach investigation. The statistical model (Burnham et al., 1987; Skalski et al., 1998) provides closed-form estimators for the survival and capture probabilities. Burnham et al. (1987) provides two goodness-of-fit statistics called T_2 and T_3 that can be used to assess whether upstream detection history has an effect on subsequent downstream survival. This release-recapture design has also received considerable attention where survival probabilities are regressed against environmental and/or individual covariates to study survival relationships (Lebreton et al., 1992; Skalski et al., 1993).

Several staggered-entry design scenarios may provide survival estimates, as long as either unique individual marks or unique sets of batch marks (e.g., a separate batch for each release) are used (Table 2). For all cases with staggered entry, survival can be estimated for the river reach between the release sites, as long as there is at least one sampling location downstream of the last release location (Figure 2). Fry captured at the first downstream sampling site are examined for marks and the number enumerated. If nondestructive sampling is used, marked fry are returned to the river. In all cases, at the first sampling site, a new and distinctive group of fry is released. Both the initial (R_1) and secondary (R_2) releases are then susceptible to sampling (destructive or not) at later downstream sites (Figure 2). To estimate survival in additional reaches using batch marks, new and distinctive batches of marked fry must also be released at subsequent detection sites (Figure 2). Destructive sampling results in each fish being recaptured at most once, so the same statistical model is used whether unique individual marks or batch marks are used. With unique individual marks and nondestructive sampling, the statistical model is the release-recapture model of Cormack (1964) and a special case

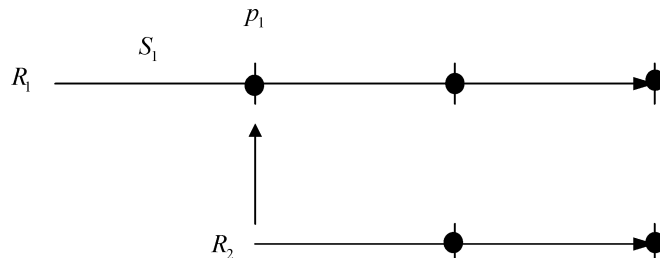


Figure 2 Schematic of scenario using staggered-entry design. If destructive sampling is used with either uniquely marked individuals or multiple batch marks, then survival (S) can be estimated only between staggered-entry locations. Nondestructive sampling used with uniquely marked individuals allows estimation of survival for all reaches except the last. Nondestructive sampling with multiple batch marks allows estimation of survival only between staggered-entry locations. Sampling (either destructive or nondestructive, as appropriate) is denoted by ●.

of the Jolly (1965)–Seber (1965) model where only numbers of marked animals recaptured and released are recorded, and mark-to-unmark ratios are ignored. Unique survival and capture probabilities can be estimated for all but the last reach. Batch marks combined with nondestructive sampling provide an estimate of survival for only the first reach, using a different statistical model than for the unique individual marks. With batch marks, the survival parameter and its associated variance must be estimated numerically (Skalski and Griswold, 2006).

The paired release design can be used with either batch marks or individual marks and either destructive or nondestructive sampling to estimate survival (Figure 3). Destructive sampling with a paired release can yield a survival estimate only for the reach between release locations, regardless of how many downstream recovery sites exist (Figure 3a). This protocol is referred to as the “relative recovery” method by Ricker (1958) and the “first capture history” method by Burnham et al. (1987), who provide a closed-form estimator of S (survival) and a variance estimator (pp. 78–84). The paired release design used with uniquely marked individuals and nondestructive sampling (Figure 3b) is an extension of the single-release design with the same marks. It falls under the “complete capture history” method of Burnham et al. (1987, pp. 112–129), who provide a closed-form estimator of S and a variance estimator. In essence, each release group functions as an independent single release-recapture model with uniquely marked individuals and nondestructive sampling (Figure 3b). The paired release may be used to account for post-release handling mortality, which cannot be detected with a single release.

In a paired release with batch marks and nondestructive sampling, each release group receives a different mark, and fry that are recaptured at one or more downstream locations are rereleased without further marking (Figure 3a). Hence, a fish may be caught multiple times without the investigator’s knowledge. Burnham et al. (1987, pp. 100–105) called this approach the “unknown capture history” method. The method is complicated by the fact that individual fish cannot be categorized into mutually exclusive and exhaustive capture histories. This method

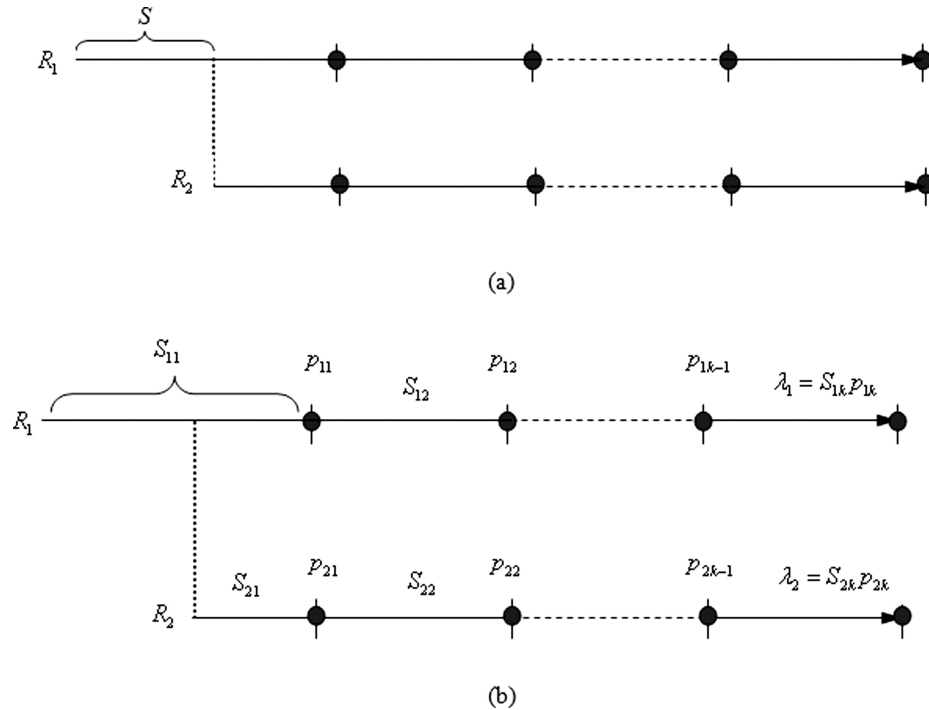


Figure 3 Schematic of scenario using a paired-release design. Destructive sampling used with either unique individual marks or multiple batch marks, or nondestructive sampling using multiple batch marks, allows for estimation of survival (S) only between release locations (a). Nondestructive sampling with unique individual marks allows estimation of survival for each reach except the last (b). Sampling (either destructive or nondestructive, as appropriate) is denoted by ●.

is appropriate as long as all recaptured fish are rereleased alive (i.e., no handling mortality) or handling mortality is independent of release groups (Burnham et al., 1987, p. 106). Burnham et al. (1987) suggest using an $R \times C$ (row-by-column) contingency table to determine whether loss rates are homogeneous between release groups. This method has a closed-form estimator of reach survival and associated variance estimator (Burnham et al., 1987, p. 105).

The final release-recapture design is the single release-remark-rerelease design using batch marks and a combination of destructive and nondestructive sampling (Figures 4 and 5). This scenario falls under the general category of “partial capture

history” methods of Burnham et al. (1987, pp. 146–172). There are numerous ways of implementing this general procedure, and each variation has its own likelihood model and associated survival estimators. The general process begins with a single release of a common batch-marked group of fish. Upon first recapture, the fish acquire an additional mark and are subsequently re-released. Upon second recapture, the fish are removed from the population. Burnham et al. (1987) describe two alternative schemes, A and B. In Scheme A, recaptured fish are given a second, site-specific mark at the time of their first recapture, regardless of which recovery site it occurs at (except the last) (Figure 4). This allows survival to be estimated in all reaches but

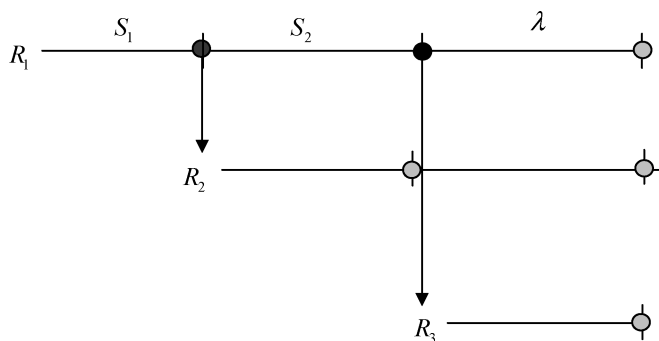


Figure 4 Schematic of scenario using a release-remark-recapture method with multiple batch marks and three sampling occasions, Scheme A. First-time recaptured fish from release R_1 receive a second site-specific mark. All fish recaptured for the third time are removed from the population. Nondestructive sampling is denoted by ●; destructive sampling (removal) is denoted by ○.

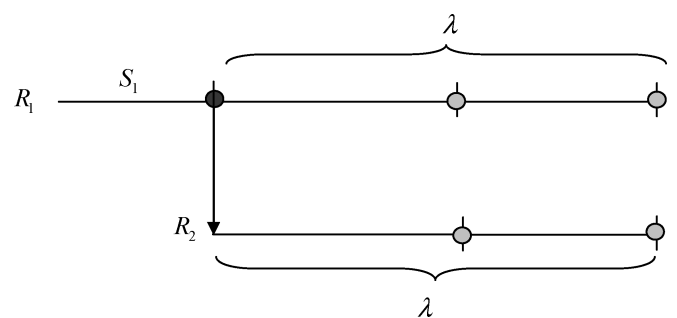


Figure 5 Schematic of scenario using a release-remark-rerelease method with multiple batch marks and three sampling occasions, Scheme B. Marked fish from the initial release (R_1) that are caught at the first sampling site are given a second mark and rereleased (R_2). Marked fish that are caught at any other sites are removed from the population. Nondestructive sampling is denoted by ●; destructive sampling (removal) is denoted by ○.

the last. In this approach, only fish recaptured a second time (i.e., with two marks) are removed from the population (Figure 4). In the case of k reaches, Scheme A requires k uniquely identified batch marks that can be applied two at a time. In Scheme B, a fish is given a second mark only upon recapture at the first downstream recapture site. At all other locations, the fish is simply examined for the marks and removed (Figure 5). Thus, Scheme B requires just two distinguishing batch marks and is considerably simpler than Scheme A. However, survival can be estimated only in the first reach using Scheme B.

Modeling assumptions are essentially the same for Schemes A and B. In particular, the recapture and remarking techniques at the first downstream recovery site must be benign. For both schemes, a goodness-of-fit test can be constructed, using an $R \times C$ contingency table test of homogeneity of the recovery counts at the removal sites for fish with different marking patterns. Burnham et al. (1987) provide closed-form estimators and variances for survival for Scheme A, and Skalski and Griswold (2006) provide them for Scheme B.

DISCUSSION

In this article, we have briefly reviewed both fish-marking techniques and release-recapture designs for survival investigations for small fish, with direct application to small, migrating juvenile salmonids (fry). Further information on fish-marking techniques is available in Nielsen (1992). The special challenges of investigating the life history of small fish limit the feasible combinations of marking technique and statistical design. However, both the marking methods and the release-recapture designs described here may be used in investigations of large or small fish of other species or salmonids in later life stages. Application of the release-recapture designs to non-migratory organisms requires recasting the designs in a temporal, rather than spatial, framework.

The appropriate combination of marking technique and release-recapture design depends on the size of the fish in the population of interest, the geographical distribution of the population, the logistical and financial considerations of marking and sampling, and the overall goal of the investigation. The successful implementation of a fry survival study will depend on the proper integration of fish marking and release-recapture techniques. The small size of salmonid fry limits the types of marking methods available and, consequently, limits and influences the design of the release-recapture study.

For example, chemical marks are useful in studying the smallest fish. However, most chemical markers require sacrificing the fish to detect the mark, and most are available with only a limited number of unique codes possible. These limitations mean that either a paired release or staggered-entry model must be used, with each release group uniquely marked. No single-release model is possible using only destructive sampling. Natural marks such as strontium isotopic ratios have the

advantage of being detected without sacrificing the fish, but they have the severe disadvantage of having only one unique mark per stream. Such isotopic signatures cannot be used to estimate absolute survival, unless they are used with a staggered-entry or paired-release model and the assumption that fish from different streams (i.e., with different isotopic signatures) have the same survival. The VIE tags are also suitable for small fish and can be detected with nondestructive sampling and offer up to 240 unique codes. Thus, VIE tags could be used with a single release-recapture design. However, with only 240 unique codes possible, VIE tags are not suitable for estimation of long-term survival using the single-release design. It would be more practical to use VIE tags with a staggered-entry, paired-release, or single release-remark-rerelease design in which a second mark is used, such as a fin clip.

Marking techniques that offer an unlimited number of unique codes include the CWT and the PIT tag. The CWT requires destructive sampling, so it cannot be used with the single release-recapture design to estimate survival. Instead, a staggered-entry or paired-release design must be used. PIT tags have often been used with the single release-recapture design to estimate survival of larger salmonids (e.g., smolts as in Skalski et al., 1998) and have been successfully used with salmonids as small as 65 mm (e.g., Peterson et al., 1994). However, PIT tags may not be suitable for very small fish (e.g., <50 mm) because of possible tag effects (Acolas et al., 2007).

Aside from marking considerations, there are statistical reasons for choosing one release-recapture design over another. In general, designs that use more detailed data yield more precise estimators and allow for more complete testing of assumptions. The "full capture history" method of Burnham et al. (1987), with uniquely marked individuals and nondestructive sampling, will provide the greatest precision and flexibility. However, as we have seen, marking techniques that may be most reasonably applied to the smallest fish often give less detailed data because of destructive sampling, batch marks, or both. In such cases, it is necessary to use either multiple releases, each with its own unique batch mark, or else double-marking in a version of the single release-remark-rerelease design. In double-marking studies, the second mark need not be the same type as the first mark. For example, an immersion dye and a fin clip may be used as the two marks. Care must be taken when devising double-marking studies because the fish stress caused by the double mark may bias the resulting survival estimates. Also, it should be expected that precision of survival estimators will degrade if sampling without rerelease is required due to destructive sampling.

The choice between a single-release and a paired-release approach depends on the degree of any anticipated marking and handling effects. In a single-release approach, any post-release handling mortality will be incorporated in the survival estimates for the first one or few reaches. Paired-release models potentially eliminate this source of bias, assuming both upstream and downstream release groups experience similar handling effects. It should be noted that all of the single-release methods

presented here can be arranged as a paired release to estimate survival in the intervening reach between initial release locations (Burnham et al., 1987). The presence and degree of post-release handling mortality should therefore be taken into account when selecting between single and paired releases.

A variety of statistical software is available for analyzing the release-recapture data from a survival investigation. Data from uniquely marked individuals and nondestructive sampling using either a single release-recapture, staggered-entry, or paired-release design can be analyzed by the software packages SURPH (<http://www.cbr.washington.edu/paramest/surph/>), SURGE (<http://www.phidot.org/software/surge/surge.html>), and MARK (<http://welcome.warnercnr.colostate.edu/~gwhite/mark/mark.htm>), among others. These packages each provide survival estimates, standard errors, and subsequent survival analyses against available covariates. In addition, all of the model options presented in this report can be readily programmed to provide survival estimates in Program USER (<http://www.cbr.washington.edu/paramest/user/>). This software has a flexible model-building capability to determine the estimability of the approach and also provides estimates of survival, associated standard errors, and profile likelihood confidence intervals. We strongly urge investigators to determine the estimability of their statistical model as a first step in any well-designed, release-recapture investigation.

The development of marking techniques for small fish continues to be an active and important area of investigation. This review suggests that development be coordinated from the start with the anticipated estimation goals and study designs in mind. In so doing, efficient and successful investigations can be planned to gain information about this important group of fish.

ACKNOWLEDGMENTS

Funding for this work came from the Pacific Northwest region's electrical ratepayers through the Columbia River Fish and Wildlife Program administered by the Bonneville Power Administration through Project No. 1989110700. We are indebted to Dr. Al Giorgi, Earl Prentice, and an anonymous reviewer for their helpful suggestions on improvements to earlier drafts of this manuscript.

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