Design and Analysis of Salmonid Tagging Studies in the Columbia Basin, Volume XXI

A Summary of Methods for Conducting Salmonid Fry Mark-Recapture Studies for Estimating Survival in Tributaries

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THE DESIGN AND ANALYSIS OF SALMONID TAGGING STUDIES IN THE COLUMBIA BASIN

VOLUME XXI

A Summary of Methods for Conducting Salmonid Fry Mark-Recapture Studies for Estimating Survival in Tributaries

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The Design and Analysis of Salmonid Tagging Studies in the Columbia Basin

Other Publications in this Series

Volume I: Skalski, J. R., J. A. Perez-Comas, R. L. Townsend, and J. Lady. 1998. Assessment of temporal trends in daily survival estimates of spring chinook, 1994-1996. Technical report submitted to BPA, Project 89-107-00, Contract DE-BI79-90BP02341.   24 pp. plus appendix.

Volume II: Newman, K. 1998. Estimating salmonid survival with combined PIT-CWT tagging. Technical report (DOE/BP-35885-11) to BPA, Project 91-051-00, Contract 87-BI-35885.

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Volume VI: Skalski, J. R., J. A. Perez-Comas, P. Westhagen, and S. G. Smith. 1998. Assessment of season-wild survival of Snake River yearling chinook salmon, 1994-1996. Technical report to BPA, Project 89-107-00, Contract DE-BI79-90BP02341. 23 pp. plus appendix.

Volume VII: Lowther, A. B., and J. R. Skalski. 1998. Monte-Carlo comparison of confidence interval procedures for estimating survival in a release-recapture study, with applications to Snake River salmonids. Technical report (DOE/BP-02341-5) to BPA, Project 89-107-00, Contract 90-BI-02341.

Volume VIII: Lowther, A. B., and J. R. Skalski. 1998. Improved survival and residualization estimates for fall chinook using release-recapture methods. Technical report (DOE/BP-02341-6) to BPA, Project 89-107-00, Contract 90-BI-02341.

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Volume X: Westhagen, P., and J. R. Skalski. 1998. Instructional guide to using program CaptHist to create SURPH files for survival analysis using PTAGIS data files. Technical report (DOE/BP-02341-4) to BPA, Project 89-107-00, Contract 90-BI-02341.

Volume XI: Skalski, J. R., R. L. Townsend, A. E. Giorgi, and J. R. Stevenson. Submitted. Recommendations on the design and analysis of radiotelemetry studies of salmonid smolts to estimate survival and passage efficiencies. Technical report to BPA, Project 89-107-00, Contract DE-BI79-90BP02341. 33 pp.

Volume XII: Ryding, K. E., and J. R. Skalski. 1999. A multinomial model for estimating ocean survival from salmonid coded wire-tag data. Technical report (DOE/BP-91572-3) to BPA, Project 91-051-00, Contract 96-BI-91572.

Volume XIII: Perez-Comas, J. A., and J. R. Skalski. 2000. Appraisal of system-wide survival estimation of Snake River yearling chinook salmon using PIT-tags recovered from Caspian tern and double-crested cormorant breeding colonies on Rice Island. Technical report to BPA, Project No. 8910700, Contract DE-BI79-90BP02341.

Volume XIV: Perez-Comas, J. A., and J. R. Skalski. 2000. Appraisal of the relationship between tag detection efficiency at Bonneville Dam and the precision in estuarine and marine survival estimates of returning pit-tagged chinook salmon. Technical report to BPA, Project No. 8910700, Contract DE-BI79-90BP02341.

Volume XV: Perez-Comas, J. A., and J. R. Skalski. 2000. Appraisal of the relationship between tag detection efficiency at Bonneville Dam and the precision in-river survival estimates of returning PIT-tagged chinook salmon. Technical report to BPA, Project No. 8910700, Contract DE-BI79-90BP02341.

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Volume XVIII: Burgess, C. A., T. J. Miller, and J. R. Skalski. 2003. Precision and accuracy of the transportation-to-inriver (T/I) ratio estimator of survival benefits to juvenile salmonids transported around the Columbia River Basin dams. Technical report to BPA, Project No. 19910500, Contract 00013690.

Volume XIX: Buchanan, R. A., and J. R. Skalski. 2006. Analysis of fall Chinook salmon PIT-tag data: Estimating transportation effects. Technical report to BPA, Project No. 198910700, Contract 00012494.

Volume XX: Skalski, J. R. 2006. Evaluation and recommendations on alternative hydroacoustic array deployments for the mouth of the Columbia River to provide estimates of salmonid smolt survival and movements. Technical report to BPA, Project No. 19910500, Contract 00013690.

Other Publications Related to this Series

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Buchanan, R. A., J. R. Skalski, and S. G. Smith. 2006. Estimating the effects of smolt transportation from different vantage points and management perspectives. North American Journal of Fisheries Management 26:460-472.

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Preface

Project 198910700 was initiated to develop the statistical theory, methods, and statistical software to design and analyze PIT-tag survival studies. This project developed the initial study designs for the NOAA Fisheries/University of Washington (UW) Snake River survival studies of 1993−present. This project continues to respond to the changing needs of the scientific community in the Pacific Northwest as they face new challenges to extract life-history data from an increasing variety of fish-tagging studies. The project's mission is to help assure tagging studies are designed and analyzed from the onset to extract the best available information using state-of-the-art statistical methods. In so doing, investigators can focus on the management implications of their findings without being distracted by concerns of whether the study's design and analyses are correct.

All studies in the current series, the Design and Analysis of Tagging Studies in the Columbia Basin, were conducted to help maximize the amount of information that can be obtained from fish tagging studies for the purposes of monitoring fish survival throughout its life cycle. Volume XXI of this series explores the ability to conduct release-recapture studies to estimate fry survival in tributary streams. A literature review of fish-marking techniques was conducted to identify feasible marking methods for fry, delineate them between individual-based and cohort-based marking methods, and whether reading the marks requires destructive or nondestructive sampling. Alternative statistical models were then examined, taking into account the physical traits of the marking methods, to determine valid methods of conducting release-recapture studies. The result is the identification of 9 valid statistical models and 11 release-recapture approaches out of a total of 16 possible study designs.

Abstract

Productivity and early fry survival can have a major influence on the dynamics of fish stocks. To investigate the early life history of fish, numerous methods have been developed or adapted to these much smaller fish. Some of the marking techniques provide individual identification; many others, only class identification. Some of the tagging techniques require destructive sampling to identify a mark; other methods permit benign examination and rerelease of captured fish. Sixteen alternative release-recapture designs for conducting fry survival investigations were examined. Eleven approaches were found capable of estimating survival parameters; five were not. Of those methods capable of estimating fry survival, five required unique marks, four required batch-specific marks, and two approaches required remarking and rereleasing captured fry. No approach based on a simple batch mark was capable of statistically estimating survival.

Executive Summary

Sixteen alternative approaches to conducting salmonid fry release-recapture studies for estimating survival were examined. The methods differ in whether individual-based or cohort-based marking techniques are used and whether destructive or nondestructive sampling is used to read the marks. Of the 16 release-recapture approaches examined, 11 methods have the potential to validly estimate survival using 9 different statistical models. The alternative release-recapture models are described, along with their assumptions, survival estimators, and associated variances. As a companion to this statistical review, 18 methods of fry marking are described, along with their ability to provide individual-based marks and nondestructive sampling. Investigators are encouraged to carefully coordinate their choice of marking techniques with the design of the release-recapture study and associated statistical model for analysis.

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Acknowledgements

1. Introduction

Tagging or marking of fish is an important fishery management tool for stock assessment, estimating survival and recruitment, evaluating movements, and habitat integration. The logistics of marking fish become more difficult and precarious the smaller the fish. This report summarizes some of the physical ways of marking salmon fry and using that tagging data to estimate fry survival.

This review will show that the statistical models for estimating fry survival will be dependent on two important tag considerations; (a) the ability to have individual-based identification or not and (b) whether the fish must be sacrificed or not to retrieve the tag information. The report begins with a review of available marking techniques for fry, followed by a review of potential release-recapture models for estimating fry survival.

In the Columbia Basin, vast amounts of information now exist on salmonid smolt survival during outmigration because of the use of PIT-tags, radio-tags, and acoustic-tags. These tag technologies are generally not applicable, however, for fry <80-100 mm. As a consequence, relatively little information exists during the early emergence in the natal streams and tributaries. The purpose here is to provide investigators with guidance on how to design and conduct fry survival studies during that important stage in salmon life history.

2. Review of Fry Marking Techniques

This section provides a brief review of methods for marking salmonid fry (<100 mm in fork length [FL]). Fry here is defined as the stage of development between alevin and parr. When marking very small fish, consideration must be given to affecting growth and survival. Recent innovations have attempted to address these concerns.

Studies which use marking techniques are widely varied, and the type of mark is dependent on study objectives, the period of time over which the mark is required to be detectable, and sample size required (Nielson 1992). Marking technologies are classified into three categories of detection (Pacific Salmon Commission 2006):

1. Immediate visual: Marks that can be immediately seen by the unaided eye.
2. Immediate Specialized Detection: Marks that can be immediately detected with the proper sampling equipment. Every fish must be analyzed, because these marks do not have a visual identifier
3. Delayed Detection: Marks that require sacrificing the fish or sampling harvested fish to obtain the tag or tissue for specialized laboratory analysis.

Each category of detection is further subdivided at the level to which the mark can be distinguished: individuals, groups, or batch, and whether the method is suitable for mass marking (MM) and mass selective fisheries (MSF). Also we must consider each of the following styles of marking for the type of investigation to which it is best suited: externally visible, internal marks, external marks, internal tags, natural marks, biotelemetric tags, genetic identifiers and chemical marking (Table 2.1).

2.1 External Marks

Externally visible tags suitable for marking salmonid fry include visible implant elastomer (VIE) and visible implant filament (VIF) tags.

2.1.1. VIE Tags

The VIE tag consists of a biocompatible, two-part, fluorescent, silicone, elastomer material that is mixed and injected into tissue as a liquid with a hypodermic syringe. After 24 h at room temperature, it cures into a pliable solid, providing an externally visible internal mark that fluoresces under ultraviolet light. The fluorescent elastomer is available in four colors, and recognition of individuals is possible through the use of different body locations and colors (Bonneau et al. 1995, Choe and Yamazaki 1998). VIE -tagged wild Age 0 brown trout (*Salmon trutta*) (26 – 70 mm) experienced negligible mortality, and all marks were recognizable upon recapture 39 – 83 day after marking (Olsen and Vollestad 2001). Green and yellow VIE post-ocular tagged rainbow trout became undetectable when a blue-filtered flashlight and amber glasses were used to aid in mark detection and rates of detection were found to be related to marking skill (Close 2000). Advantages of this type of tag are low tag mortality, the ability to mark very small fish in the field with little training needed to recognize marks, and not requiring sacrificing the fish. Disadvantages are the inability to distinguish more than about 240 individuals, the possibility of tissue growth occluding visibility of marks, and the reliance on highly trained techs in order to avoid excessive tag losses. VIE tags may be appropriate for short-term survival and movement studies.

2.1.2. VIF Tags

VIF tags are made of plastic and coded with a three-digit alphanumeric code. Tag placement by syringe in transparent periocular eye tissue exhibited excessive stress whereas tag placement in the tissue between fin rays improved the ability to successfully tag fish smaller than 150-mm fork length (Shepard et al. 1996, Wenburg and George 1995). Shepard et al. (1996) found a retention rate of 58% for VIF tags in wild westslope rainbow trout

Table 2.1. Summary of marking techniques for fry <100 mm and the ability for unique codes for ease of identifiability and permanency of the mark and minimum fish size requirements.

Mark technique	Unique codes possible	Suitable for mass mark	Category of detection*	Stability	Minimum size
External Marks					
Fluourescent elastomer (VIE)	240	No	IV or ISD	Variable	26 mm
Fluourescent filament (VIF)	3-character alpha-num	No	IV or ISD	Variable	50 mm
Pigments	Limited to few	Yes	IV NS	Temporary	Fry
Immersion dyes	4 or 5	Yes	IV NS	Low	25 mm
Flourescent	Limited	Yes	ISD	Low	25 mm
Adipose clip	None	Yes	IV	0-4% Regen.	50 mm
Ventral clip	None	Yes	IV	0-44% Regen.	50 mm
Adipose clip & CWT	Unlimited	Yes	DD	Variable	<2.1 g HLCWT >2.1 g FLCWT
Ventral clip & CWT	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	Poor	100 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
Natural Marks					
Strontium isotope ratios	None	Yes	DD NS	Permanent	None
Chemical Marks					
Oxytetracycline	Limited	Yes	DD S	High	None
Strontium chloride	Limited	Yes	DD S	12-16 mos.	None
Calcein immersion	Limited	Yes	ISD S or NS	12-16 mos.	None
Tetracycline	Limited	Yes	DD S	High	None

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.

*FLCWT – full-length, coded-wire tag
  HLCWT – half-length, coded-wire tag

Table 2.1 (Continued)

Mark technique	Unique codes possible	Suitable for mass mark	Category of detection*	Stability	Minimum size
Otolith Marks					
Otolith thermal	Unlimited	Yes	DD S	Permanent	Emergent fry – advanced yearling
Dry mark otolith (eggs)	Unlimited	Yes	DD S	Permanent	Only for eggs
Genetic	Unlimited	Yes	DD NS	100%	N/A
Molecular/laser	Limited to few	Yes	ISD NS	30 mos.	8 days post-yolk absorption
Biotelemetric					
PIT	Unlimited	Yes	ISD	98-100%	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
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*FLCWT – full-length, coded-wire tag
  HLCWT – half-length, coded-wire tag

(*Oncorhynchus* sp.) as small as 100 mm; tag loss rate was inversely related to FL. Bailey et al. (1998) reported retention rates of 73% after 2 years in coho marked at a mean length of 108 mm. Recognition of tags may not be a significant problem as inexperienced technicians successfully detected the body locations of VI tags 91% and 98% of the time after only 1 h of training though tag retention is thought to be closely related to technician skill (Hale and Gray 1998). Advantages of the system are little or no effects of the tag on survival or growth, the ability to mark large numbers of fish in the field with unique codes, immediate detection of marks with minimal training, and the ability to release recaptured fish after recording the tag. Disadvantages are special training and experience needed to successfully mark fish and the possibility of tissue growth occluding marks. Types of studies suited for VIF tags are short-term mortality and growth as well as movement studies and abundance estimation.

2.1.3. Dye Marking

Dye marking may be suitable for mass marking for short-duration studies where it is necessary to distinguish only a few experimental lots. Dussault and Rodriguez (1997) found that Alcian Blue dye mark retention was low for individuals recaptured 10-14 months after injection and that dye applied to pelvic or pectoral fin locations induced high mortality in smaller fish ~55 mm. Bismark brown dye has been used successfully applied in short term (<3 mos) abundance estimates of migrating sockeye salmon (*Oncorhynchus nerka)* smolt populations (Carlson et al. 1998). Gaines and Martin (2004) dual-marked chinook salmon (*Oncorhynchus tshawytscha)* fry (mean fork length = 57.7 mm) with spray-dye fluorescent pigments and Bismarck brown stain, and applied single marks of each type. Daily mortality was less than 0.15% for all marked fish for 3 d after marking. The authors concluded that the dual-marking technique provides a feasible method to differentially mass-mark fish with minimal mortality for short-term studies. It was found that dual-marking improved mark recognition. This technique is efficient, inexpensive, produces an immediately recognizable mark, and can be applied to large numbers of fish in the field with little training. Disadvantages include lack of unique codes and short lifespan of the mark.

2.1.4. Fin Excision

One of the oldest and simplest of methods of marking fish is fin-clipping. Johnson (2004) used a pelvic fin clip on Atlantic salmon fry to provide a means of distinguishing first summer survival and growth in salmon planted as eggs versus those planted as fry. The adipose fin clip is the external mark of choice used to recognize CWT marked salmon (*Oncorhynchus* spp.) in commercial fishery sampling and was sequestered for that purpose until 1996. Delayed mortality of clipped fish is a function of size. Coble (1967) suggested that salmonids smaller

than 90 mm FL are especially vulnerable. Mortality is lower for adipose and pelvic fin clips (McNeil and Crossman 1979). In order to avoid biased estimates, studies involving adipose fin clips should be accompanied by an assessment of the rate of naturally missing fins (Blankenship 1990). Advantages are low cost, efficiency of application, and immediate visibility of mark. Disadvantages include lack of unique codes, fin regeneration, and delayed mortality due to the fin clip. Fin clipping may be appropriate for flagging interior marks and movement, abundance estimation, growth studies in situations where groups and individuals need not be identifiable, and where there are no other uses of the same mark to which it could be confused.

2.1.5. Freeze Branding

Freeze branding may provide a useful mark for short-term (less than a year), fry-marking studies not requiring individual capture histories. Advantages include ease of application, low cost, and ability to mass mark as many as 1000 fish per hour. A disadvantage of the technique is that marks fade and become unrecognizable with time (Bryant et al 1990). The authors used a brand 1 mm x 5 mm for young coho salmon (*Oncorhynchus kisutch)* less than 50 mm total length. Straight-line letters—T, V, X, U or I—were used and found to provide the best level of correct recognition upon recapture. By altering the orientation of these letters and changing the side of the fish marked, 30 distinct marks can be made. The freeze brand may work well for short-term studies requiring identification of only a few groups.

2.2 Internal Marks

2.2.1. Coded Wire Tags (CWT),

Peltz and Miller (1990) concluded that half-length coded wire tags (HLCWT) can be used to estimate return proportions from pink salmon (*Oncorhynchus gorbuscha)* hatchery releases numbering in the hundreds of millions. The authors emphasized the importance of the maintenance of a constant proportion of marked fish among all release groups. Possible sources of error using CWT tagging are differential mortality between tagged and untagged fish, tag loss, regeneration of clipped adipose fins, straying due to olfactory damage caused by the tagging procedure, nonrandom distribution of marks in the population (Seber 1982), occurrence in the population of naturally missing adipose fins, the presence of wild fish in the returning broodstock, and error in determination of the proportion of marked fish among the original hatchery releases.(Peltz and Miller 1990, Habicht et al. 1998). Evidence that CWT placement in pink salmon fry is related to straying was found to be inconclusive, giving mixed results for the two-year study carried out by Habicht et al. (1998). Blankenship (1990) found

that by holding CWT-tagged pink salmon fry for 29 d after tagging a final level of tag loss can be ascertained. The same study recommended that in order to avoid excessive and prolonged tag loss fish smaller than 2.1 g be tagged with HLCWT while fish larger than 2.1 g receive full-length coded wire tags (FLCWT). Blankenship (1990) reported production size releases averaged less than 5% tag loss 30 d after tagging and no significant tag loss 200-300 d after tagging. Kaill et al. (1990) evaluated the use of HLCWT on newly emergent pink salmon fry (mean weight, 0.26 g) and found that estimates of short-term retention rates ranged from 93 to 100% using experienced taggers. Estimated long-term retention rates were 75, 50, 65 and 84% for the years 1983-1986. However, the estimates did not take into consideration human error in recognizing the adipose fin clip nor was there an adjustment for the rate of naturally occurring missing adipose fins. Advantages of CWTs are low cost (8-9 cents/tag), availability of unique codes, and the apparent minimal effect on growth and survival. Disadvantages are the possibility of lost tags and expensive delayed laboratory detection requiring sacrificing the fish.

2.2.2. Natural Marks

Natural geochemical signatures have been found to be useful as a population marking technique (Campana and Thorrold 2001, Barnett-Johnson et al. 2005, Bacon et al. 2004). In a study of Atlantic salmon populations in tributaries of the Connecticut River, Kennedy et al. (2000) found stream-specific Sr isotopic ratios ($^{87}Sr/^{86}SR$) in calcified tissues of salmon parr within 3 months of stocking and were able to differentiate fish from different geographical areas. The authors point out that the site-specific uptake and incorporation of isotopic signatures makes this technique useful for distinguishing fish populations in both wild and managed settings. Kennedy et al. (2002) used micromilling techniques to extract strontium (Sr) isotopic signatures from the otoliths of four returning Atlantic salmon and detected distinct signatures from four lifecycle stages, including prefeeding hatchery development, rearing stream growth, smolt outmigration, and ocean residence.

2.2.3. Chemical Marks

Oxytetracycline (OTC), calcein, and strontium are routinely used in fisheries programs to mark otoliths and other calcified tissue in fish as a way to evaluate fish management strategies. Calcein (2,4-bis[N,N-di(carbomethyl)-amino-methyl]fluorescein; molecular weight, 622) marking can be accomplished by immersing very young fish in a bath containing either (1) 125-250 mg/L calcein for 1 – 6 hr; or (2) 2.5-5.0 g/L for 1-7 min. A pre-treatment immersion of fish in a 1-5% solution of non-iodized salt for ~3.5 min facilitates the osmotic transfer of calcein into calcified tissues (Johnson 2003). The study found that marks faded on exposure to direct sunlight. Frenkel et al. (2002) and Bart et al. (2001) noted that when immersion was

preceded by a 30-s ultrasound exposure mark endurance in caudal fin rays was increased in small rainbow trout (*Oncorhynchus mykiss*) (~.2-.3 g). A general positive relationship was found between mark endurance and fish size. Differences were not found in growth rates between control fish and the different treatments within any of the size groups (.2, .3 and 1.0 g). Brook trout (*Salvelinus fontinalis)* (~1 g) and Atlantic salmon (0.8 g) fed calcein for 5 d showed calcein scale marks 7-10 d postmarking (Honeyfield et al. 2006). Brook trout were marked twice with distinct bands when fed calcein 5 months apart. Increased concentration of calcein in food produced increased mean pixel luminosity in brook trout scales. Longer-term retention of calcein marks has been reported in fish injected or immersed in calcein. Rainbow trout retained their external marks for at least 12 months in young fish (Negus and Tureson 2004, Frenkel et al. 2002). Calcein-marked Atlantic salmon have been recovered from the wild after 16 months (Mohler 2004). Strontium and calcein otolith marking has an advantage over thermal marking in that wild fish can be marked by holding fish in large immersion vats or raceways (Alaska Department of Fish &Game 2005).

Tetracycline exposure appears to be an inferior otolith-marking technique compared to temperature manipulation. Marks can be faint and difficult to distinguish, and the number of patterns is more limited; incident-light fluorescence microscopy is also required (Brothers 1990).

2.2.4. Otolith Marks

Otolith banding as an identification mark can be produced by exposing fish to cycles of high and low temperatures or alternating 5-day periods of feeding and starvation (Buckley and Blankenship 1990). The method produces a permanent mark. The most practical use of this system is to identify large groups of fish from artificial production, which is especially useful in the management of terminal-area salmonid fisheries that harvest mixed stocks and where identification of groups can be effective in controlling exploitation rates (Volk et al. 1987). Advantages to otolith marking when it is necessary to assess early life stages where it is required to discriminate between experimental lots include: (1) It is applicable to the very youngest and smallest stages of all species, including embryos. (2) It produces a permanent mark. (3) It is accomplished in batches with minimal or no manipulation or handling of the fish. (4) Groups or lots can be uniquely marked (Brothers 1990). Disadvantages or limitations of otolith marking include: (1) Fish must be sacrificed to remove and examine otoliths or even to detect the presence of the mark unless there is an external marker such as an adipose clip. (2) Otolith marking does not allow recognition or coding of individuals. (3) The production of marks and the preparation of otoliths for viewing those marks requires the development of

special techniques and skills which go well beyond that required by most marking systems. (4) Otolith marking is not easily applied to the marking of wild fish in the field.

The dry method of otolith marking is based on periodic changes of the water regime during incubation of the eggs. The eggs are dried in incubators, usually at 24-hour intervals. One dark and one light ring are formed for each marking cycle during which the eggs are kept dry for 24 hours and washed with water during the next 24 hours. A disadvantage of the dry marking method is that it cannot be used for marking salmon larvae and fry. However, the method is simple, convenient, and requires no special equipment (2005, Alaska Department of Fish and Game 2005). The technique was developed in Russia where it is used extensively (Akinicheva and Rogatnykh 2000).

2.2.5. Genetic Marking

Genetic marking uses selective breeding to alter frequencies of alleles in the marked population so it can be distinguished from unmarked populations. Gharret and Seeb (1990) list the following factors necessary for consideration of marker alleles: (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) Select a relatively large brood stock so that genetic variability will be sustained. (4) Adequate resources to mark the population and subsequently to detect the mark in mixtures. (5) Selection for single allele markers can produce optimum genetic marks.

2.2.6. Molecular/Laser Mark

These tags are in the experimental stage and consist of biotinylated bovine serum albumin taken up by fish in five-minute water baths and included tags added to the serum albumin taken up by fish in five-minute water baths. Tags added to the serum albumin and attached to the serum protein molecules were laser tags or other fluorescent tags. In laboratory tests on Atlantic salmon fry, it was possible to read tags 30 months after tagging without sacrificing fish. A handheld, portable, electro-optical tag detection system reads light emissions at the excitable wavelength of the tag, or fluorescent dye on the protein providing identification of the tag group (U.S. Fish and Wildlife Service, National Fish Hatchery, http://www.fws.gov/fisheries/nfhs/ftc/FTCwhatsnew.htm).

2.3 Biometric Tags

2.3.1. PIT Tags

Passive integrated transponder (PIT) tags can be injected into juvenile salmon as small as 55 mm without jeopardizing growth or survival (Prentice et al. 1990). PIT-tag releases were successfully used to estimate survival and to estimate sampling variability of survival estimates for comparison with model-based variance estimates and to assess mixing of detected and nondetected chinook salmon smolts (Skalski et al. 1998). Portable PIT readers have been developed (Destron Fearing Corporation) and field tested for use with 2.1 mm X 11.5 mm PIT tags on brown trout (*Salmo trutta*) in shallow streams (Cucherousset et al. 2005). The detection range was 36 cm and $73.3 \pm 5.8\%$ to $93.3 \pm 11.5\%$ of age-0 trout were detected depending on the stream section. Advantages of PIT tags are the ability to tag large numbers of fish in the field, identify individual fish, expect high tag retention, experience tag longevity of around ten years, and have minimal impact on growth. A disadvantage of the system is the requirement that a tagged fish be within a distance of less than one meter of a tag interrogation system for successful detection of the signal.

3. Methods

Sixteen different marking and release-recapture designs were examined to determine their utility in estimating fry survival. The objective of all the study designs was to estimate fry survival in the initial river reach or sampling period (i.e., S_1) of interest. These designs were examined in conjunction with either unique fry marking methods or batch-marking techniques. Consideration included whether fry were either rereleased or not rereleased after capture. In other words, whether examination for marks required destructive (i.e., without rerelease) or nondestructive (i.e., with rerelease) sampling techniques to identify marked fish.

The most powerful and flexible design 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 probabilities and detection probabilities in all reaches but the last.

Staggered-entry designs allow new fish to enter the study at downstream detection sites. The infusion of new fish into the design can improve estimation processes and/or allow survival to be estimable in case where it otherwise may not.

Similar in appearance to the staggered-entry designs are the paired release-recapture designs. In these approaches, fish are released above and below the river reach of interest with subsequent recaptures downstream. Emphasis of this design is estimation of survival in the first

reach. However, estimation of survival downriver is also possible, depending on the marking and recapture approach used in the study.

The final release-recapture designs considered are the release-remark-rerelease designs. In this study approach, batch-marked fish are released at the top of the river reach of interest. First-time recaptured fish are given a second mark for subsequent identification. Should this fish be recaptured a second time, it is removed from the study. Two alternative protocols using the partial capture history data are reviewed.

For each of the 16 protocols reviewed , the ability to estimate survival in the first one or few reaches was examined based on the properties of minimum sufficiency and separability of parameters. In other words, the protocols were examined to determine whether there was sufficient information permitting survival estimation or not. For those models that provided a valid means of estimation, details are presented.

4. Results

Of the 16 different combinations of marking and release-recapture designs evaluated for fry survival studies, 11 approaches provided estimates of survival for one or more reaches (Table 4.1). Five of the feasible approaches required uniquely marked individuals. Four of the other feasible approaches used multiple batch marks. The last two feasible approaches require applying an additional batch mark to fry recaptured and rereleased. None of the methods which relied on a single common batch mark to identify study fish provided a valid means of estimating fry survival. Subsequent discussion describes in greater detail the statistical and logical approaches of the methods capable of estimating fry survival.

4.1 Model M_1: Single release – individual marks – nondestructive sampling (Scenario 2)

This study design with uniquely marked fry and nondestructive sampling provides maximum estimation capability. The single release with subsequent downriver recapture and rereleases permits survival and capture probabilities to be uniquely estimated in all reaches but the last (Fig. 4.1). Only the joint probability of surviving and being detected (i.e., $\lambda = Sp$) can be estimated for the last reach. The model is a special case of the full capture history model of Burnham et al. (1987:112-116) when only one of release in a paired-release is considered. Skalski et al. (2001) has applied the model to estimate salmonid smolt survival using PIT tags in the Columbia River. The summary detections are the number of fry in each of the 2^k possible capture histories in a k-reach investigation.

Table 4.1. Alternative approaches to conducting fry survival studies and their ability to provide valid estimates of reach survival. Marking and release-recapture scenarios identified in parentheses.

Scenario	Survival estimable	Model
I. Single release-recapture		
A. Unique individual marks		
1. Destructive sampling (1)	No	--
2. Nondestructive sampling (2)	Yes	M_1
B. Common batch mark		
1. Destructive sampling (3)	No	--
2. Nondestructive sampling (4)	No	--
II. Staggered entry		
A. Unique individual marks		
1. Destructive sampling (5)	Yes	M_2
2. Nondestructive sampling (6)	Yes	M_3
B. Common batch mark		
1. Destructive sampling (7)	No	--
2. Nondestructive sampling (8)	No	--
C. Unique batch marks		
1. Destructive sampling (9)	Yes	M_2
2. Nondestructive sampling (10)	Yes	M_4
III. Paired release		
A. Unique individual marks		
1. Destructive sampling (11)	Yes	M_5
2. Nondestructive sampling (12)	Yes	M_6
B. Unique batch marks		
1. Destructive sampling (13)	Yes	M_5
2. Nondestructive sampling (14)	Yes	M_7
IV. Single release – remark – rerelease		
A. Two batch marks (15)	Yes	M_8
B. Multiple batch marks (16)	Yes	M_9

Figure 4.1. Schematic of Model M_1 using a single release of uniquely marked individuals and nondestructive sampling. Using this method, survival (S) can be estimated in all but the last reach (Burnham et al. 1987, Skalski 1998). ● denotes rerelease/nondestructive sampling.
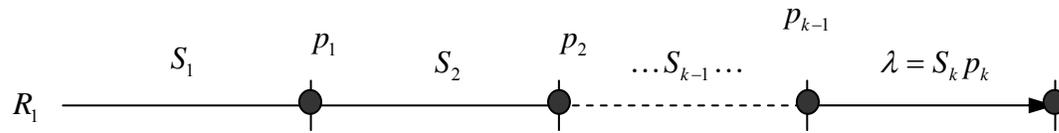
The statistical model (Burnham et al. 1987, Skalski et al. 1998) provides closed-form estimators for the survival and capture probabilities. Burnham et al. (1987) provides two goodness-of-fit statistics called T_2 and T_3 that can be used to assess whether upstream detection history has an affect on subsequent downstream survival. The release-recapture design has also received considerable attention where survivals are subsequently regressed against environmental covariates to study the survival relationships (Lebreton et al. 1992, Skalski et al. 1993). Two statistical software packages, SURPH http://www.cbr.washington.edu/paramEst/SURPH/) and SURGE (http://www.phidot.org/software/surge/surge.html) can be used to provide survival estimates, standard errors, and subsequent survival analyses. Hoffmann and Skalski (1995) extended the model to examine the relationship between individual covariates and survival and detection processes. Program SURPH allows regression analyses using both group covariates and individual-based covariates.
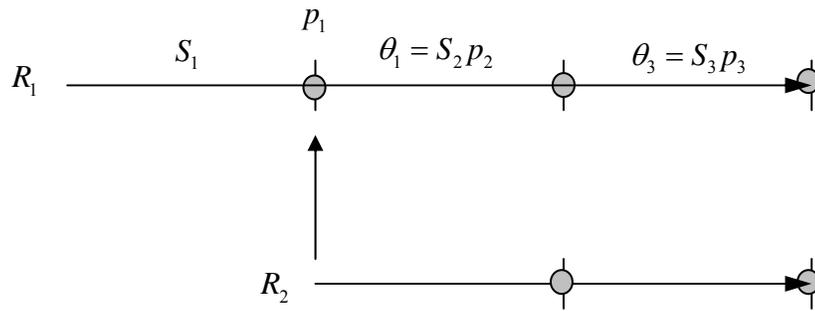
4.2 Model M_2: Staggered entry – individual or unique batch marks – destructive sampling (Scenarios 5, 9)

Destructive sampling to examine individual fry for marks results in no individual being recaptured more than once during the course of the study. For this reason, there is no effective advantage of unique marks over that of batch-specific marks. It is adequate to simply be able to identify a fry to a specific release group in this staggered-entry design. Hence, whether individual or batch marks are used, the statistical model is the same.

To estimate survival in the first reach, marked fry must be released upstream and sampled at a minimum of two downstream locations. Fry captured at the first downstream sampling location are examined for marks and the number enumerated. At this site, a new and distinctive batch of fry are released. Both the initial (R_1) and secondary (R_2) releases are then susceptible to destructive sampling at a second downstream site (Fig. 4.2). To estimate survival in additional reaches, new and distinctive batches of marked fry must also be released at subsequent detection sites. At least one detection site must exist below the last river reach of interest. Survival cannot be estimated in that last reach.

The likelihood model for a three-reach design with staggered entry only at the first downstream recapture location can be expressed as a product of two multinomial distributions, where

Figure 4.2. Schematic of Model M_2 using staggered entry with uniquely marked individuals or batch marks and destructive sampling. Using this method, survival (S) can be estimated only between staggered entry locations R_1 and R_2. ◯ denotes removal/destructive sampling.

$$L\left(S_1, p_1, \theta_1, \theta_2 \mid \underset{\sim}{x}, \underset{\sim}{y}\right) =$$

$$\binom{R_1}{\underset{\sim}{x}} \left(S_1 p_1\right)^{x_1} \left(S_1\left(1-p_1\right)\theta_1\right)^{x_2} \left(S_1\left(1-p_1\right)\theta_2\right)^{x_3}$$

$$\cdot \left(1 - S_1 p_1 - S_1\left(1-p_1\right)\left(\theta_1 + \theta_2\right)\right)^{R-x.}$$

$$\cdot \binom{R_2}{\underset{\sim}{y}} \theta_1^{y_1} \theta_2^{y_2} \left(1-\theta_1-\theta_2\right)^{R_2-y.}$$

(1)

where

S_i = probability of fry recovery in the ith reach $(i=1,\ldots,3)$;

p_i = probability a fry is recovered at the ith recovery site $(i=1,\ldots,3)$;

$\theta_1 = S_2 p_2$;

$\theta_2 = S_2\left(1-p_2\right)S_3 p_3$;

x_i = number of fry recovered at the ith recapture site $(i=1,\ldots,3)$ for the first release of size R_1;

y_i = number of fry recovered at the ith recapture site $(i=1,\ldots,3)$ for the second release of size R_2.

The likelihood model has four parameters and four minimum sufficient statistics, permitting closed-form estimators. Because there are only two staggered entries, only survival in the first reach between the two release locations can be estimated, where

$$\hat{S}_1 = \frac{R_2\left(x_2 + x_3\right) + x_1\left(y_2 + y_3\right)}{R_1\left(y_2 + y_3\right)}$$

(2)

$$\hat{p}_1 = \frac{x_1\left(y_2 + y_3\right)}{R_2\left(x_2 + x_3\right) + x_1\left(y_2 + y_3\right)}$$

(3)

$$\hat{\theta}_1 = \frac{x_2 + y_2}{R_1\hat{S}_1\left(1-\hat{p}_1\right) + R_2}$$

(4)

$$\hat{\theta}_2 = \frac{x_3 + y_3}{R_1 \hat{S}_1 (1 - \hat{p}_1) + R_2} \tag{5}$$

The variance of $\hat{S}_1$ can be estimated using the delta method, where

$$\begin{aligned} \text{Var}(\hat{S}_1) &\doteq \frac{S_1}{R_1(\theta_1 + \theta_2)} \\ &\cdot \left[1 - S_1(\theta_1 + \theta_2) - p_1(1 - \theta_1 - \theta_2) + R_2(\theta_1 + \theta_2)^2 (1 - \theta_1 - \theta_2) S_1 (1 - p_1)^2 \right] \end{aligned} \tag{6}$$

and the variance estimated by substituting in the parameter estimates.

Assumptions of Model M_2 include the following:

1. All fry have equal and independent fates.

2. Marked fry are correctly identified and designated to the correct release group.

3. Release groups have equal downstream survival probabilities.

4. Release groups have equal downstream detection probabilities.

Goodness-of-fit to model M_1 can be tested using an R x C contingency table test (Zar 1999) of the form:

		Release group	
		R_1	R_2
Recovery Site	2nd	x_2	y_2
	3rd	x_3	y_3

$$\tag{7}$$

with one degree of freedom. Program USER (http://www.cbr.washington.edu/paramEst/USER/) cam be programmed to numerically analyze likelihood model (1) and other special cases of the staggered-entry design.

4.3 Model M₃: Staggered entry – individual marks – nondestructive sampling (Scenario 6)

This staggered-entry design using uniquely marked individuals and rerelease of captured individuals is the release-recapture model of Cormack (1964). This model is also a special case of the Jolly (1965) - Seber (1965) model where only numbers of marked animals recaptured and released are recorded, and mark-to-unmark ratios ignored.

Unique survival and capture probabilities can be estimated for all but the last reach. In the last reach, only the joint probability of surviving and being capture (i.e., $\lambda = S_k p_k$) at the last location can be estimated (Fig. 4.3). Although closed-form estimation for the survival and capture probabilities exist, statistical software such as SURPH, SURGE, or SURVIVE can be used to numerically estimate the parameters and standard errors. Program SURPH will provide profile likelihood confidence intervals.

4.4 Model M₄: Staggered entry – unique batch marks – nondestructive sampling (Scenario 10)

In this variation of the staggered-entry design, survival can be estimated between release sites for all but the last reach. In Fig. 4.4, only the uppermost reach is available for survival estimation. The nondistributive sampling, combined with batch-level marking, results in capture data that is no longer mutually exhaustive and exclusive. For example, fry first detected at recapture location 2 cannot be distinguished from fry first recaptured at location 3.

The likelihood model describing the staggered-entry release-recapture design of Fig. 4 can be parsimoniously written as follows:

$$L\left(S_1, p_1, \gamma_1, \gamma_2 \middle| \underset{\sim}{x}, \underset{\sim}{y}\right) =$$

$$\binom{R_1}{x_1}\left(S_1 p_1\right)^{x_1}\left(1 - S_1 p_1\right)^{R_1 - x_1}\binom{R_1}{x_2}\left(S_1 \gamma_1\right)^{x_2}\left(1 - S_1 \gamma_1\right)^{R_1 - x_2}$$

$$\cdot\binom{R_1}{x_3}\left(S_1 \gamma_2\right)^{x_3}\left(1 - S_1 \gamma_2\right)^{R_1 - x_3}\binom{R_2}{y_2}\gamma_1^{y_2}\left(1 - \gamma_1\right)^{R_2 - y_2} \tag{8}$$

$$\cdot\binom{R_2}{y_3}\gamma_2^{y_3}\left(1 - \gamma_2\right)^{R_2 - y_3},$$

where

Figure 4.3. Schematic of Model M_3 using a staggered entry with uniquely marked individuals and nondestructive/rerelease sampling. Using this method, survival (S) can be estimated for all reaches by the last. ● denotes rerelease/nondestructive sampling.
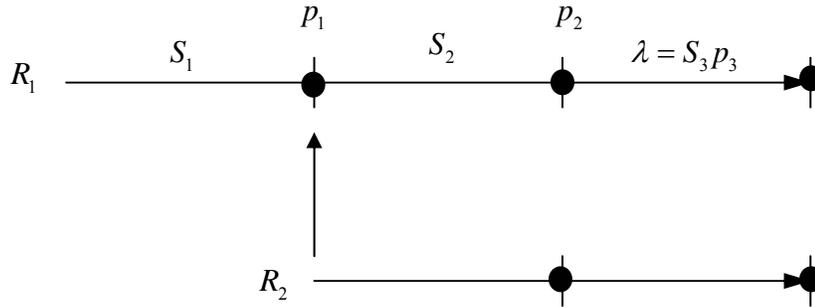
Figure 4.4. Schematic of Model M_4 using staggered entry with unique batch marks and nondestructive sampling. Using this method, survival (S) can be estimated only for the reaches between batch releases. ● denotes rerelease/nondestructive sampling.
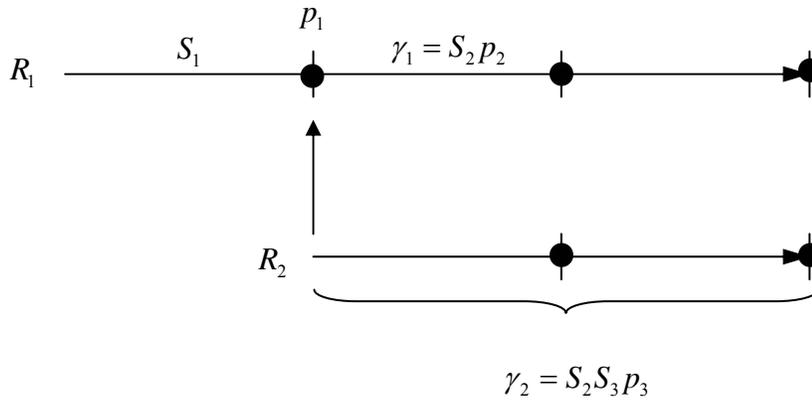
$$\gamma_1 = S_2 p_2,$$

$$\gamma_2 = S_2 S_3 p_3.$$

The likelihood has four parameters $(S_1, p_1, \gamma_1, \gamma_2)$ and five minimum sufficient statistics, requiring numerical estimation. Program USER can be readily programmed to estimate the model parameters, standard errors, and profile likelihood confidence intervals.

The model assumptions include the following:

1. All fry have equal and independent fates.

2. Marked fry are correctly identified and designated to the correct release group.

3. Release groups have equal downstream survival probabilities.

4. Release groups have equal downstream detection probabilities.

Goodness-of-fit to Model M_4 can be tested using the 2 x 2 contingency table test (7).

4.5 Model M_5: Paired-release – individual marks or unique batch marks – destructive sampling (Scenarios 11, 13)

The destructive sampling to identify fry and designate the fry to specific batches eliminates the possibility of capturing a fish more than once. Hence, whether a fry is individually marked or simply batch marked does not change the nature of the recorded data (Fig. 4.5). This model was first recommended by Ricker (1958) and is sometimes referred to as the relative recovery method. Burnham et al. (1987:78-84) designated the approach as the "first capture history" method.

The general likelihood model for this paired design, regardless of the number of downstream recovery sites, can be written as:

$$L\left(S_1, \varphi \mid x_., y_.\right) = \binom{R_1}{x_.} \left(S_1 \varphi\right)^{x_.} \left(1 - S_1 \varphi\right)^{R_1 - x_.} \binom{R_2}{y_.} \varphi^{y_.} \left(1 - \varphi\right)^{R_2 - y_.}, \tag{9}$$

where

Figure 4.5. Schematic of Model M$_5$ using a paired release with unique individual marks or unique batch marks and destructive sampling. Using this method, survival (S) can only be estimated between release locations of R_1 and R_2. ◌ denotes removal/destructive sampling.
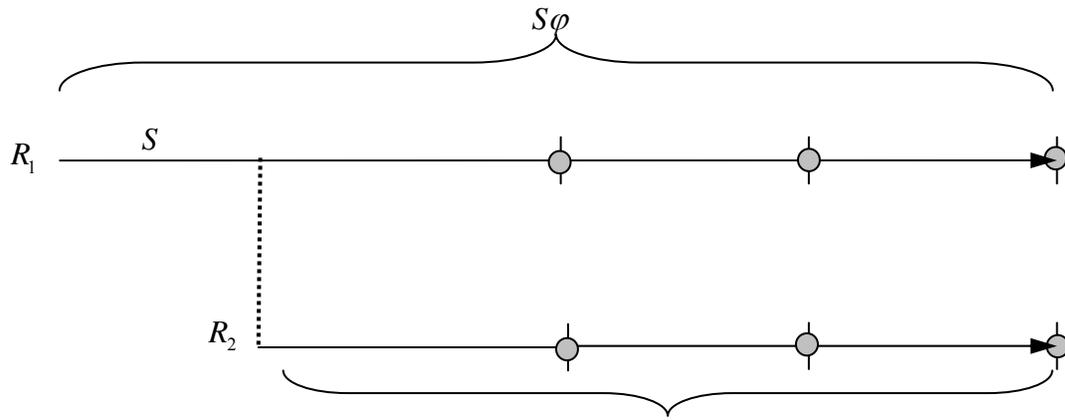
$$\varphi = S_1 p_1 + S_1 (1 - p_1) S_2 p_2 + S_1 (1 - p_1) S_2 (1 - p_2) S_3 p_3$$

φ = probability of a fry surviving from release location R_2 and being recaptured downstream,

$$x_. = \sum_{i=1}^{k} x_i = \text{total number of } R_1 \text{ fry recovered downstream,}$$

$$y_. = \sum_{i=1}^{k} y_i = \text{total number of } R_2 \text{ fry recovered downstream.}$$

The model has two parameters (S_1, φ) and two minimum sufficient statistics, permitting closed-from estimators.

Survival in the first reach can be estimated by the quotient

$$\hat{S}_1 = \frac{R_2 x_.}{y_. R_1}, \tag{10}$$

$$\varphi = \frac{y_.}{R_2}. \tag{11}$$

The survival estimator has the sampling variance of

$$\text{Var}\left(\hat{S}_1\right) = \frac{S_1}{\varphi} \left[\frac{(1 - S_1 \varphi)}{R_1} + \frac{S_1 (1 - \varphi)}{R_2} \right], \tag{12}$$

which can be estimated by

$$\widehat{\text{Var}}\left(\hat{S}_1\right) = \hat{S}_1^2 \left[\frac{1}{x_.} - \frac{1}{R_1} + \frac{1}{y_.} - \frac{1}{R_2} \right]. \tag{13}$$

The assumption of Model M_5 are essentially the same as those previously stated for Models M_2 and M_4. However, the dimensionality of the model does not permit an independent test of model assumptions based on the summaries $x_.$ and $y_.$. Instead, the assumption of shared probability φ can be tested on the basis of the `arrival patterns of the release groups to the downstream detection sites.

Either a chi-squared test of homogeneity (Zar 1999:488-491) or a Kolmogorov-Smirnov test of homogeneous distribution (Conover 1980:368-377) can be used to assess whether arrival timing

was the same for both release groups. The inference from the tests is that if the release groups arrived downstream at the same time(s), they experienced the same recapture environment and capture probabilities. These tests of homogeneity cannot, however, discern differential survival probabilities among release groups.

4.6 Model M_6: Paired release – individual marks – nondestructive sampling (Scenario 12)

This model is an extension of Scenario 2 described by Burnham et al. (1987:112-129) as the "complete capture history" model. In essence, each release group functions as an independent, single release-recapture model with uniquely marked individuals that are nondestructively sampled (Fig. 4.6). Release R_1 estimates survival S_{11} and release R_2 estimates survival S_{21} (Fig. 4.6). Then the survival in the reach between release locations is estimated by the quotient

$$\hat{S} = \frac{\hat{S}_{11}}{\hat{S}_{21}} \tag{14}$$

with associated variance estimator

$$\widehat{\operatorname{Var}}\left(\hat{S}\right) = \hat{S}^2 \left[\frac{\operatorname{Var}\left(\hat{S}_{11}\right)}{\hat{S}_{11}^2} + \frac{\operatorname{Var}\left(\hat{S}_{21}\right)}{\hat{S}_{21}^2} - \frac{2\operatorname{Cov}\left(\hat{S}_{11},\hat{S}_{21}\right)}{\hat{S}_{11}\hat{S}_{21}} \right]. \tag{15}$$

With multiple downstream detection sites, sequential model testing and Akaike information criterion (AIC) (Burnham and Anderson 1998) can be used to identify the most parsimonious statistical model to describe the joint releases. The preferred model would share common downstream detection and survival rates where the values are equal, thereby improving the precision of the remaining model parameters.

4.7 Model M_7: Paired release – batch marks – nondestructive sampling (Scenario 14)

In this approach, each release group receives a different batch mark that does not distinguish between individuals. Fry are recaptured downstream at one or more downstream locations are rereleased without further marking (Fig. 4.7). Hence, a fish may be caught multiple times without the investigator's knowledge. Burnham et al. (1987:100-105) designated this approach as 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.

Figure 4.6. Schematic of Model M_6 using a paired release with unique individual marks and nondestructive sampling. Survival (S) can be estimated for each reach and detection location except the last. Survival between release locations is estimated as the quotient, $\hat{S}_{11}/\hat{S}_{21}$. ● denotes rerelease/nondestructive sampling.
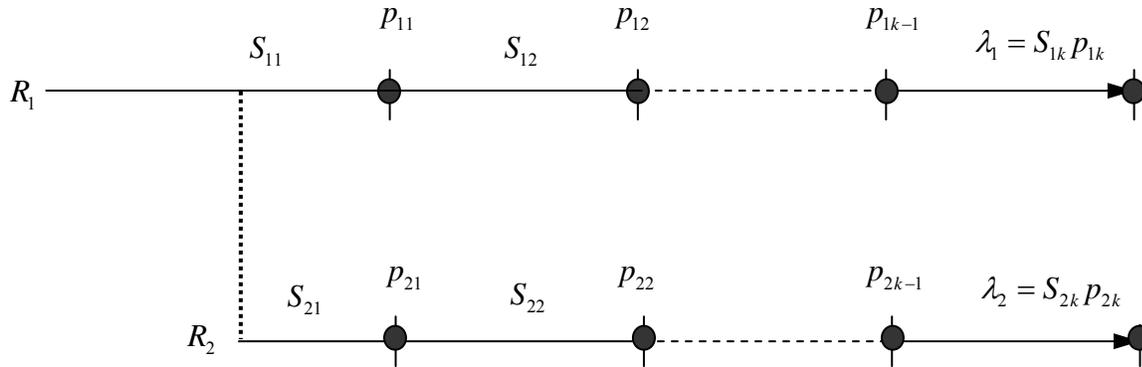
Figure 4.7. Schematic of Model M_7 using a paired release with batch-specific marks and nondestructive sampling. This method can only estimate survival (S) between release locations based on quotient of relative detections between release groups. ● denotes rerelease/nondestructive sampling.
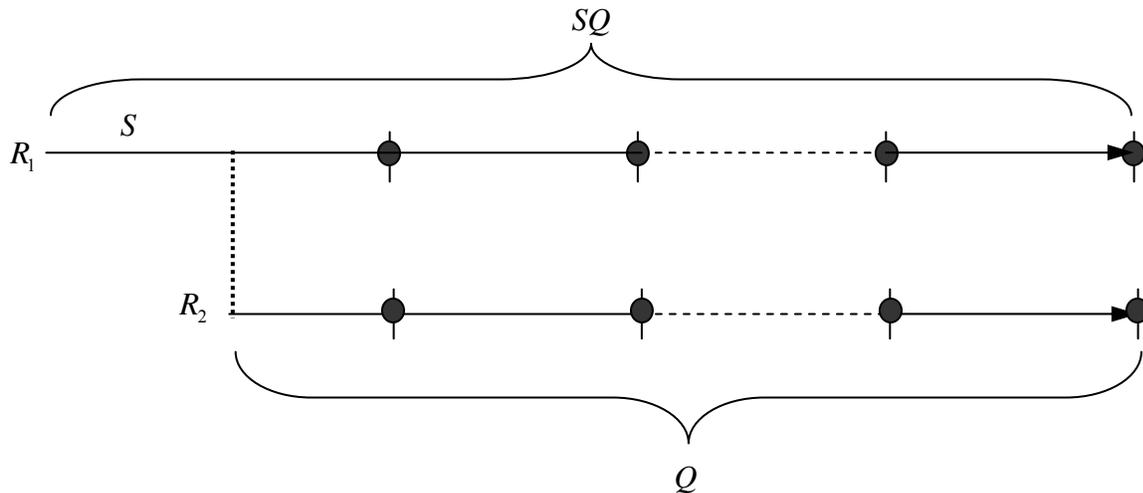
The joint likelihood model for the paired releases can be written as

$$L = \prod_{i=1}^{k}\binom{R_1}{x_i}\left(S_1\theta_i\right)^{x_i}\left(1-S_1\theta_i\right)^{R_1-x_i}\cdot\prod_{i=2}^{k}\binom{R_2}{y_i}\theta_i^{y_i}\left(1-\theta_i\right)^{R_2-y_i} \tag{16}$$

where

x_i = number of R_1 fish recaptured and re-released at the ith recapture location

$(i = 1,\ldots,k)$;

y_2 = number of R_2 fish recaptured and re-released at the ith recapture location

$(i = 1,\ldots,k)$;

θ_i = joint probability of surviving to and being captured at the ith recapture location

$(i = 1,\ldots,k)$ for R_2 fish.

Model (16) is appropriate as long as all recaptured fish are re-released alive (i.e., no handling mortality) or handling mortality is independent of release group (Burnham et al. 1987:106). Burnham et al. (1987) suggest using an R × C contingency table to determine whether loss rates are homogeneous between release groups. The method of moments estimator for S is Eq. (10) with variance estimator (12). However, Burnham et al. (1987:105) suggest the slightly "better" variance formula

$$\widehat{\mathrm{Var}}\left(\hat{S}\right) = \hat{S}^2\left\{\frac{1}{x_{\bullet}}-\frac{1}{R_1}\left[\sum_{j=2}^{k}\left(\frac{x_j}{x_{\bullet}}\right)^2\right]+\frac{1}{y_{\bullet}}-\frac{1}{R_2}\left[\sum_{j=2}^{k}\left(\frac{y_j}{y_{\bullet}}\right)^2\right]\right\}, \tag{17}$$

where

x_j = number of fish in release R_1 detected at recapture site j ($j = 2, \ldots, k$);

y_j = number of fish in release R_2 detected at recapture site j ($j = 2, \ldots, k$).

Burnham et al. (1987:104) generally do not recommend this study approach because of the model nonspecificity problems and recommend instead the use of the first capture history protocols (i.e., Model M_5) if feasible. However, if survival of the study fish is important as in the case of listed (endangered) species, then this method is performed.

4.8 Model M_8: Single release-remark-rerelease – two batch marks

This scenario falls under the general category of "partial capture history" methods of Burnham et al. (1987:146-172). There are numerous ways of implementing this general procedure. Each variation has its own likelihood model and associated survival estimators. The general process beings with 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, a fish is given a second mark that is site-specific with mark-releases occurring at all site locations but the last. In Scheme B, a fish is given a second mark if recaptured at the first downstream recapture site. At all other locations, the fish is simply examined for the marking code(s) and removed (Fig. 4.8).

Scheme B is the simplest to implement, requiring just two distinguishing markers and, consequently, will be discussed first. Define the following terms:

R_1 = number of fish initially released,

S_1 = probability of survival in the reach between release R_1 and the first downstream recovery site,

p_1 = probability of capture at the first recovery site,

λ = probability a fish survives below the first recovery site and is recaptured somewhere downstream,

x_1 = number of fish recaptured at the first recovery site,

x_{23} = number of fish recovered for the first time at the second or subsequent recovery sites,

R_2 = number of fish among x_1 that are given a second mark and rereleased,

y_{23} = number of double-marked fish from R_2 that are subsequently recovered.

Figure 4.8. Schematic of Model M_8 using a release-remark-rerelease method. An initial release of batch-marked fish (R_1) with remark-release capabilities at the first recovery site and removal sampling only. Fish caught at the initial site are given a second mark and rereleased (R_2). ● denotes rerelease/nondestructive sampling; ○ denotes removal/destructive sampling.
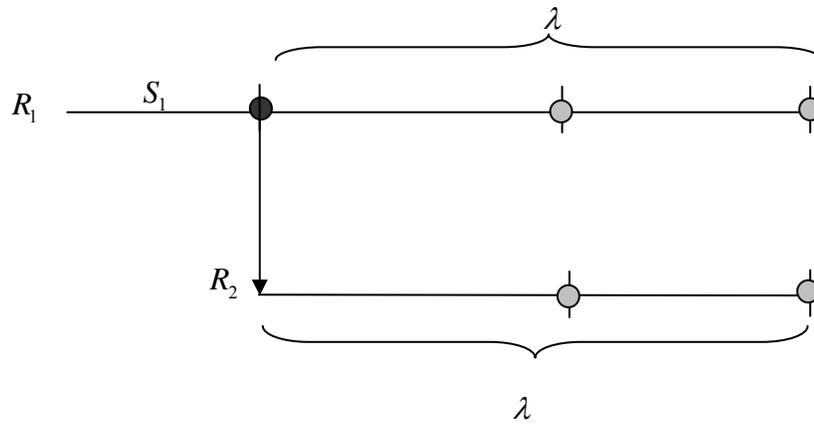
The likelihood model for the release-remark-rerelease method can then be written as follows:

$$L = \binom{R_1}{x_1, x_{23}} \left(S_1 p_1\right)^{x_1} \left(S_1 \left(1-p_1\right)\lambda\right)^{x_{23}} \left(1-S_1 p_1 - S_1\left(1-p_1\right)\lambda\right)^{R_1 - x_1 - x_{23}} \cdot \binom{R_2}{y_{23}} \lambda^{y_{23}} \left(1-\lambda\right)^{R_2 - y_{23}}. \tag{18}$$

It should be noted that Model (18) is a compressed version of Model (1), yielding essentially the same survival estimator. The maximum likelihood estimates are

$$\hat{S}_1 = \frac{R_2 x_{23} + x_1 y_{23}}{R_1 y_{23}}$$

$$\hat{p}_1 = \frac{x_1 y_{23}}{R_2 x_{23} + x_1 y_{23}} \tag{19}$$

$$\hat{\lambda} = \frac{y_{23}}{R_2}.$$

The variance of $\hat{S}_1$ is approximated by the delta method to be

$$\mathrm{Var}\left(\hat{S}_1\right) \doteq \frac{S_1}{R_1 \lambda}\left[1 - S_1 \lambda - p_1\left(1-\lambda\right) + R_2 \lambda^2\left(1-\lambda\right)S_1\left(1-p_1\right)^2\right], \tag{20}$$

with variance estimated by substituting the MLEs into Eq. (20).

The key assumptions of this release-remark-rerelease method are the following:

1. All fish have equal and independent probabilities of survival and capture.

2. Marking and remarking have no effect on survival and recapture.

For these assumptions to be true, the recapture and remarking techniques at the first downstream recovery site must be benign. For this protocol, only survival in the first reach can be estimated. A goodness-of-fit test can be constructed, using an R × C contingency-table test of homogeneity of the recovery counts at the removal sites for single- and double-marked fish of the form:

| Recovery	Single mark	Double mark
Site 2	x_2	y_2
Site 3	x_3	y_3
$\vdots$	$\vdots$	$\vdots$

analogous to (7).

4.9 Model M_9: Single release-remark-rerelease – multiple batch marks

In the previous method (i.e., Model M_8), recaptured fish were remarked at only the first downstream recovery site. This allows estimation of survival only between the initial release location and the first detection site. However, if first-time recaptured fish are given a site-specific second mark, then survival can be estimated in all reaches but the last. This method is designated as Scheme A in Burnham et al. (1987:149-349). In this approach, any fish recaptured a second time (i.e., with two marks) is removed form the population (Fig. 4.9). In the case of k reaches, there needs to be k uniquely identified batch marks that can be applied two at a time. Consequently, the logistics of multiple batch marks and multiple remarking locations add complexity beyond the simple Scheme B described earlier.

In the case of three reaches, the joint likelihood model for the release-remark-rerelease scheme can be written as follows:

$$
\begin{aligned}
L = & \binom{R_1}{\underset{\sim}{x}} (S_1 p_1)^{x_1} \left(S_1 (1-p_1) S_2 p_2 \right)^{x_2} \left(S_1 (1-p_1) S_2 (1-p_2) \lambda \right)^{x_3} \\
& \cdot \left(1 - S_1 + S_1 (1-p_1) \left[(1-S_2) + S_2 (1-p_2)(1-\lambda) \right] \right)^{R_1 - x.} \\
& \cdot \binom{R_2}{\underset{\sim}{y}} (S_2 p_2)^{y_2} \left(S_2 (1-p_2) \lambda \right)^{y_3} \left(1 - S_2 + S_2 (1-p_2)(1-\lambda) \right)^{R_2 - y.} \\
& \cdot \binom{R_3}{\underset{\sim}{z}} \lambda^{z_3} (1-\lambda)^{R_3 - z_3} ,
\end{aligned}
\tag{21}
$$

29

Figure 4.9. Schematic of Model M$_9$ using a release-remark-rerelease method with multiple-batch marks. 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. ● denotes rerelease/nondestructive sampling; ○ denotes removal/destructive sampling.
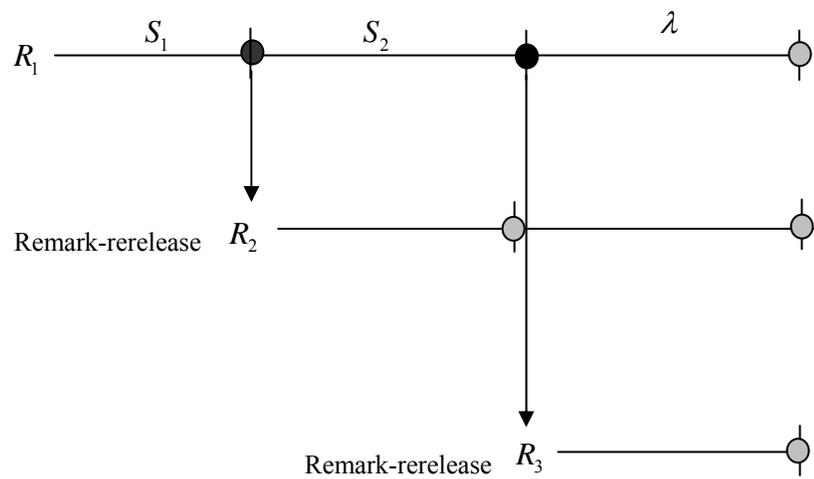
where

R_i = number of fish released at the *i*th release location;

x_i = number of R_1 fish caught for the first time at the ith recovery location $(i = 1, \ldots, 3)$;

$$\sum_{i=1}^{3} x_i = x_{\cdot};$$

y_i = number of R_2 fish caught for the first time at the *i*th recovery location $(i = 2, 3)$;

$$\sum_{i=1}^{3} y_i = y_{\cdot};$$

z_i = number of R_3 fish caught for the first time at the *i*th recovery location $(i = 3)$;

S_i = probability of survival in the *i*th reach $(i = 1, 2)$;

p_i = probability of recapture at the *i*th recovery site $(i = 1, 2)$;

$\lambda = S_3 p_3$ = joint probability of surviving the last reach and being detected.

The maximum likelihood estimators are as follows:

$$\hat{\lambda} = \frac{z_3}{R_3}$$

$$\hat{p}_2 = \frac{(x_2 + y_2) z_3}{(x_2 + y_2) z_3 + (x_3 + z_3) R_3}$$

$$\hat{p}_1 = \frac{x_1}{x_1 + \dfrac{(x_2 + x_3)}{\hat{S}_2 \left(\hat{p}_2 + (1 - \hat{p}_2) \hat{\lambda} \right)}}$$

$$\hat{S}_2 = \frac{y_2 + y_3}{R_2 \left(\hat{p}_2 + (1 - \hat{p}_2) \hat{\lambda} \right)}$$

$$\hat{S}_1 = \frac{x_1}{R_1} = \frac{x_2 + x_3}{R_1 \hat{S}_2 \left(\hat{p}_2 + (1 - \hat{p}_2) \hat{\lambda} \right)}.$$

The model assumptions are essentially the same of those of Model M_8. Again, $R \times C$ contingency-table tests of homogeneity of downstream recovery patterns can be used as a test of goodness of fit.

5. Discussion and Conclusions

The choice of design for the fry survival study will depend on a number of considerations, including:

1. Marking capability and ability to read mark(s).

2. Recovery methods.

3. Desired precision.

4. Model assumptions.

The art of implementing a successful fry survival study will be in the integration of these interrelated demands and constraints.

Typically, estimation precision will be improved the more detailed the release-recapture data. This means using unique fish identification methods will be preferable to batch marks, all else being equal. No release-recapture method is feasible with a single batch mark. The necessity to use multiple release groups or the ability to obtain partial capture history data from double marking fish is required at a minimum. However, double marking fish (i.e., M_8 and M_9) can result in undue stress on the rereleased individuals, biasing estimation techniques.

The more detailed release-recapture data permits tests of model assumptions often unavailable in simpler procedures and also allows more model parameters to be estimated, including capture rates and multiple reach survival estimates.

The choice between a single-release and a paired-release approach depends on more than logistical convenience. In a single-release, 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.

All of the model options presented in this report can be readily programmed to provide survival estimates using Program USER (http://www.cbr.washington.edu/paramest/user/)./ The software provides a flexible model-building capability to determine the estimability of the approach and also provides estimates of survival and associated standard errors. Determining the estimability of the model should be a necessary first step in any well-designed, release-recapture investigation.

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