Comparative Survival Study (CSS)

2006 Design and Analysis Report:

Methodology for Obtaining Unbiased T/C Ratio Estimates

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Preface

A primary goal of the Comparative Survival Study (CSS) is to provide reliable (*i.e.*, unbiased, reasonably precise, and transparent) estimates of parameters describing the relative survival benefits due to various management strategies. In particular, the CSS estimates smolt-to-adult survival rates (SARs) for groups of fish (hatchery and wild spring/summer Chinook salmon, *Oncorhynchus tshawytscha*, and summer steelhead, *O. mykiss*) that out-migrate as juveniles via in-river and transportation passage routes, as well as the ratio of these SAR estimates (*i.e.*, transport:inriver ratio or *T*/*C*). Reviewers of the 2005 CSS Annual Report (see Appendix D in Berggren *et al.* 2005) suggested that the CSS estimators are inherently biased in their formulation and poorly documented. To address these concerns, the following document was prepared by Washington Department of Fish and Wildlife's Comparative Survival Oversight Committee member Kristen Ryding. While a description of the quantitative methods used to estimate CSS study parameters appears elsewhere (see Appendix A in Berggren *et al.* 2006), the purpose of this document is two fold: i) to provide a derivation of the main study parameters used by the CSS and ii) to describe their behavior, relative to a 'true' value, under various circumstances (*e.g.*, with and without actual transportation benefits).

The document is structured to build from a description of basic elements (*i.e.*, parameter definition and notation) to the theoretical expectation of key study parameters (*i.e.*, SARs and *T*/*C*) and their analogous estimators. Additionally, the main assumptions underlying the described estimators will be identified and discussed in brief. Finally, using a set of simple examples based on the derived estimators and a set of assumed inputs, this document illustrates that both SARs and *T*/*C*, as used in the CSS, are both accurate (*i.e.*, unbiased) and robust.

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Introduction

This section focuses on the derivation of the estimator used to assess the efficacy of transporting fish around dams on the Lower Snake and Columbia rivers versus migration using in-river routes. Fish are collected and put into the transport barges at one of three dams on the Lower Snake River. In order of occurrence, the three transport sites are Lower Granite Dam (LGR), Little Goose Dam (LGS), and Lower Monumental Dam (LMN). The transport system is considered to start at the first site, Lower Granite Dam and end at the barge release site below Bonneville Dam. Performance of the transportation system is assessed by comparing relative rate of adult returns back to Lower Granite Dam between juveniles that were transported and those that migrated in-river (control) through the hydro-system. Transport and control returns are compared by use of the transport-control or ${}^{T}\!/_{C}$ ratio, the focus of this study.

The CSS study does not divide a cohort into transport and in-river groups before release, but rather at the first transport site, LGR. Fish pass a dam through either detected through bypass system and then possibly transported, or through other routes undetected. Essential to understanding the derivation of the ${}^{T}\!/_{C}$ ratio are three elements of the study. First only fish not previously detected at a dam are barged. Second, probabilities of adult return back to LGR are based on the numbers of juveniles at LGR in each group. Third, fish passing undetected at LGR are considered to be in a transport or in-river migration route upon egress from the dam. This last condition owes to the fact that even in a river system where fish are subject to only transportation should they be detected, some mortality will occur in-river on the way to the barge site. Any loss associated with getting to the barge is part of the total mortality of transportation. Subsequently, fish are considered routed for either transportation at LGS or LMN prior to the onset of survival processes associated with downstream travel to these sites. All of these elements will be discussed further.

We outline the derivation of the T/C ratio from first principles. We begin by defining the notation and basic metrics used in the analysis. Derivation of the equations for calculating the numbers of juveniles and returning adults in each category follows. Next, we present the T/C ratio as a function of survival, detection, and transport probabilities and discuss its properties under the null condition analytically and through numerical examples. We conclude with a discussion of parameter estimation and associated assumptions of analytical methods.

Notation and Definitions

Unless otherwise indicated, the following subscripts are used to identify site-specific probabilities and observations following the convention of previous CSS reports;

1 = release site;

2 = Lower Granite Dam (LGR);

3 = Little Goose Dam (LGS);

4 = Lower Monumental Dam (LMN).

The following notation will be used in this section to show the derivation of the T/C estimator. Define the number of tagged fish released, survival, detection, and transport probabilities, and observations as follows,

N_0 = the number of tagged fish released;

S_1 = survival from release to Lower Granite Dam tailrace;

S_i^R = survival probability from the tailrace of site i to $i+1$ for fish passing in-river e.g.,

S_2^R = in-river survival from the tailrace of Lower Granite Dam to the tailrace of Little Goose Dam;

S_i^T = survival probability from the i to $i+1$ transport site for fish transported in the barge e.g., S_2^T = in-barge survival from the tailrace of Lower Granite Dam to the tailrace of Little Goose Dam;

S_L^x = the probability of surviving from the tailrace of LMN, the last transport site, through the Lower Snake and Columbia Rivers to the transport release site for group x, e.g., $S_L^{C_0}$ is the lower river survival probability for the in-river migration group;

S_O^x = the probability of surviving from the transport release site as juveniles back to Bonneville dam as adults for group x (includes estuary and marine survival);

S_A^x = the probability of surviving adult migration from Bonneville dam back to LGR;

p_i = detection probability (collection efficiency) at the ith site;

τ_i = the probability that a tagged, detected fish is transported at the *i*th site;

T_i = the number of juveniles in the transportation route (pathway) of the *i*th site;

T_0 = the total number of juveniles that entered the transport system, i.e., $\sum_i T_i$;

C_0 = the number of juveniles that migrated undetected at the transportation sites through the Lower Snake River hydro system, i.e., the in-river migration route;

$A_j^{T_i}$ = the number of age *j* adults returning to LGR out of T_i juveniles;

$A_j^{C_0}$ = the number of age j adults returning to LGR out of C_0 juveniles;

$SAR(T_0)$ = the proportion of fish that return as adults out of T_0 juveniles;

$SAR(T_i)$ = the proportion of fish that return as adults out of T_i juveniles, i.e., a site specific SAR;

$SAR(C_0)$ = the proportion of fish that return as adults out of C_0 juveniles.

Basic Metrics

Transportation effectiveness is measured against in-river migration by comparing smolt-to-adult return (SAR) proportion for the two groups as follows,

$$T/C = \frac{SAR(T_0)}{SAR(C_0)} \qquad (1)$$

where $SAR(T_0)$ and $SAR(C_0)$ are defined as above. Because the transportation system is regarded as starting at Lower Granite Dam (LGR), SARs are the proportion of fish in a cohort that survive from LGR as a juvenile back to LGR as an adult. The T/C ratio [Eq. (1)] is a measure of the relative rate of adult returns between the transportation group, (T_0), and in-river migrants, (C_0). Equation 1 will be greater than one when the number of adult returns relative to the number of juveniles in the transport group is greater than that of the in-river fish.

For the purposes of this study, *SAR*s are defined as the proportion of fish passing LGR as juveniles that return to LGR as adults and for control and transported fish are expressed in terms of adult returns and juveniles, as follows,

$$SAR(C_0) = \frac{A^{C_0}}{C_0} \qquad (2)$$

and

$$SAR(T_0) = \frac{A^{T_0}}{T_0} \qquad (3)$$

respectively. Numerators in Eq. (2) and (3) are the sums of adult returns from all age classes, e.g., $A^{T_0} = \sum_j A_j^{T_0}$. The *SAR* is a joint probability of surviving through several life stages that include migration from LGR through the Snake and Columbia Rivers (S_2, S_3, S_L), estuary migration and ocean residence (S_O), and adult return upstream back to LGR (S_A). Subsequently, an SAR can be expressed entirely as a function of independent survival probabilities.

Derivation of the smolt-to-adult return estimators: $SAR(C_0)$ ***and*** $SAR(T_0)$

Estimating the *SAR*s for in-river (control) and transported fish requires first calculating the numbers of juveniles (C_0 and T_0) and adults (A^{C_0} and A^{T_0}) comprising each group. Calculating the numbers of juveniles in each study group, C_0 and T_0, is the more complex part of the study and thus requires the most explanation. Central to understanding the methods used to arrive at $C_0, T_0, A^{C_0},$ and A^{T_0} are three elements of the study mentioned in the introduction,

1. Smolt-to-adult return ratios are measured as the proportion of juveniles in each group at LGR that return as adults to LGR.
2. Only fish not previously detected at a dam are transported.
3. Fish are considered routed to transport at a particular dam or in-river passage before mortality occurs.

Juveniles migrating downstream encounter the start of the hydro system at Lower Granite Dam, the first transport site. Comparing *SARs* between the two groups starting at LGR fully incorporates the experience of both groups. That only previously undetected fish are transported is meant to mimic the experience of the run-at-large, i.e., tagged and untagged fish. The last element of the study, that fish are considered as entering either one of four possible migration pathways at LGR, three transport and one control, is because we are interested in the survival of fish before and after the treatment is applied. Assigning routes before the survival process occurs gives an estimate of survival from beginning of the study at LGR to the end, also at LGR. Further, losses en route to a transport site are part of total transport mortality.

Conceptually, the “destined to be transported” part or third element of the CSS study can be difficult to convey. Consider a hypothetical river with two groups of fish, a treatment and control, and a dam, weir, or other obstacle in the middle (Figure 1). We are interested in studying the effect of the “treatment” (going through an obstacle), on survival from release to a point somewhere downstream of the treatment. In this study, logistics prevent assigning groups to the treatment ahead of time. A group of size N fish is released upstream at location A (Figure 1) and at location B, some fish go through the obstacle or treatment, at random, with probability p. Other fish do not encounter the obstacle, again at random, and pass freely down the river with probability $1-p$. The effect of the treatment on survival is measured by comparing total survival from release at location A to C, $S_A S_B$, for treatment fish and against that of the control group (**T** and **F** respectively).

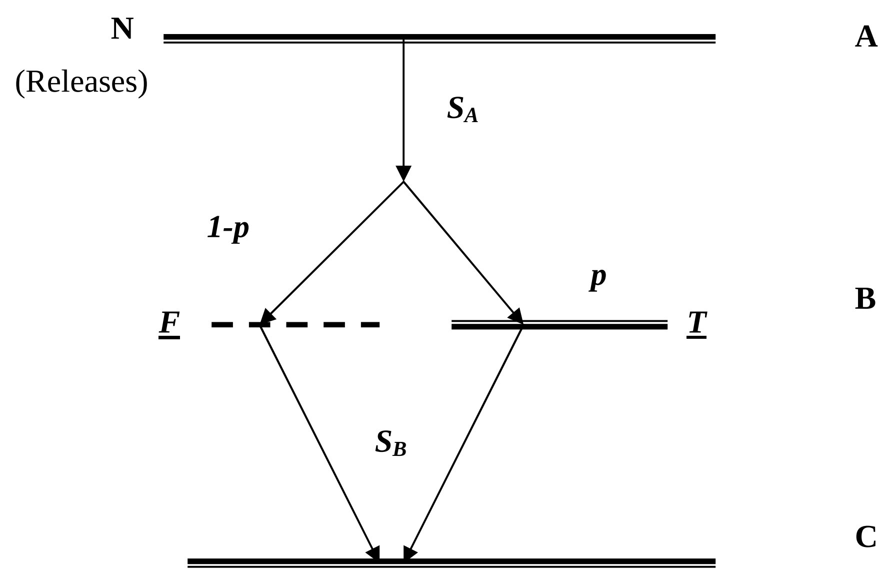

Figure 1. Diagram of a hypothetical river to illustrate the concept of "destined to be in a route of passage" in the CSS study.

Based on the branch diagram in Figure 1, one can estimate of the number of group **T** fish by considering survival *then* passage route. The number in group **T** is comprised of those that first survived with probability S_A *then* passed through the treatment with probability p and is expressed mathematically as follows,

$$T = NS_A p .$$

The number of treatment fish surviving from treatment application (passing the obstacle) to the end of the study at point **C** is as follows,

$$T_C = NS_A pS_B .$$

By use of the expression for the number of treatment fish above, the estimate of the proportion of fish surviving to the last point, is as follows,

$$\frac{T_C}{T} = \frac{NS_A pS_B}{NS_A p} = S_B ,$$

This is not the original metric of interest, $S_A S_B$.

Now consider assigning a route of passage prior to the onset of survival processes between **A** and **B**. Any released fish can pass through the treatment with probability p (because they have not died yet). The expected number of released fish passing through the treatment is Np . Some of these fish will die along the way with probability $\left(1 - S_A\right)$, and the remainders survive with probability S_A. After the survivors pass through the treatment at **B**, some mortality will occur on the way to point **C** with probability $1 - S_B$, and the rest of the fish will survive to **C** with probability S_B. The total number in the treatment group is then comprised of those that died between **A** and **B**, and between **B** and **C**, plus the survivors from **A** to **C**, expressed mathematically as follows,

$$\begin{aligned} T &= \underbrace{Np\left(1 - S_A\right)}_{\text{Died between } \mathbf{A} \text{ and } \mathbf{B}} + \underbrace{NpS_A\left(1 - S_B\right)}_{\text{Died between } \mathbf{B} \text{ and } \mathbf{C}} + \underbrace{NpS_A S_B}_{\text{Survived to } \mathbf{C}} \\ T &= Np. \end{aligned}$$

The proportion of fish surviving to site **C** out of T fish is now estimated as follows,

$$\frac{T_C}{T} = \frac{NS_A pS_B}{Np} = S_A S_B .$$

This is the original metric of interest. Hence, the idea of a destined route of passage is perhaps more accurately considered as the expected number of fish taking a particular route prior to mortality, where expectation is defined statistically as the number of trials (fish released) times the probability of being in a particular passage category.

Alternatively, one could partition site-to-site mortality between the two groups. The number of fish dying between points **A** and **B** is $N\left(1-S_B\right)$ (Figure 1). The expected number of treatment (**T**) and control (**F**) mortalities is $N\left(1-S_A\right)p$ and $N\left(1-S_A\right)\left(1-p\right)$, respectively. The expected number of fish surviving to site **B** but not to site **C** is $NS_A\left(1-S_B\right)$. The expected number of mortalities between sites **B** and **C** in the treatment and control groups is $NS_A\left(1-S_B\right)p$ and $NS_A\left(1-S_B\right)\left(1-p\right)$, respectively. The total number of fish in each group is the sum of the mortalities in each river section, plus the number surviving to site **C**. The total number of fish in control group **F** is calculated as follows,

$$
\begin{aligned}
F &= N\left(1-S_A\right)\left(1-p\right)+NS_A\left(1-S_B\right)\left(1-p\right)+NS_AS_B\left(1-p\right) \\
F &= N\left(1-p\right),
\end{aligned}
$$

and the total number of fish in the treatment group (**T**) calculated as above.

This simple example is analogous to the process encountered in the CSS study where the treatment for some groups is applied after the start of the experiment. Whether we pre-assign a route of passage, divide mortalities proportionally among the different groups, or divide by survival, e.g., $T = {NS_Ap}/{S_A}$, the results are the same. In all cases, we would arrive at an estimate of the number in each group that will allow us to estimate survival from the beginning to the end of the experiment. We will continue with the idea of taking into account particular “fates” and apportioning mortality among groups to further motivate the derivation of the T/C ratio as the system becomes more complex.

The fish release site, the three transportation sites in the Lower Snake River, and possible passage routes under consideration in this study are as in Figure 2. We present passage routes for the three transport dams, LGR, LGS, and LMN in detail because this is where juvenile fish are routed to transport or in-river passage. The river system can be considered as two separate sections. Below LNM, fish are in transport around the remaining dams or migrate in-river through the hydro system. Above Lower Monumental Dam fish are classified between the two main study groups, transport and control. It is here that mortality associated with potential passage routes is taken into account as described above.

At the start of a migration season a cohort of tagged fish is released into the Snake River above LGR (Figure 2). The expected number of tagged fish arriving at LGR regardless of eventual passage route is the number of tagged releases, N_0, multiplied by the probability of surviving to LGR, expressed as follows,

$$N_0 S_1^R .$$

At LGR, fish pass through the juvenile bypass system with probability p_2 (also called “collected”) or through other routes with probability $1 - p_2$. Fish entering the bypass system can be transported with probability τ_2 (Figure 2). Fish exiting LGR via non-detect routes can be transported at LGS or LMN, or migrate in-river undetected. Post LGR passage and the associated fates within the routes under consideration in the CSS are shown using a branch diagram (Figure 2).

The derivation of each of the metrics used to compare in-river migration to transportation performance will refer back to Figure 2. We derive mathematical expressions for the basic metrics T/C, $SAR(T_0)$, and $SAR(C_0)$, and present numerical examples from a deterministic perspective, i.e., no variance. Estimation of survival, detection, and transport parameters is discussed briefly. Estimators for $SARs$ and the T/C ratio are then expressed as functions of estimable parameters. We conclude by listing the assumptions of the methods and their importance in making inferences to the population.

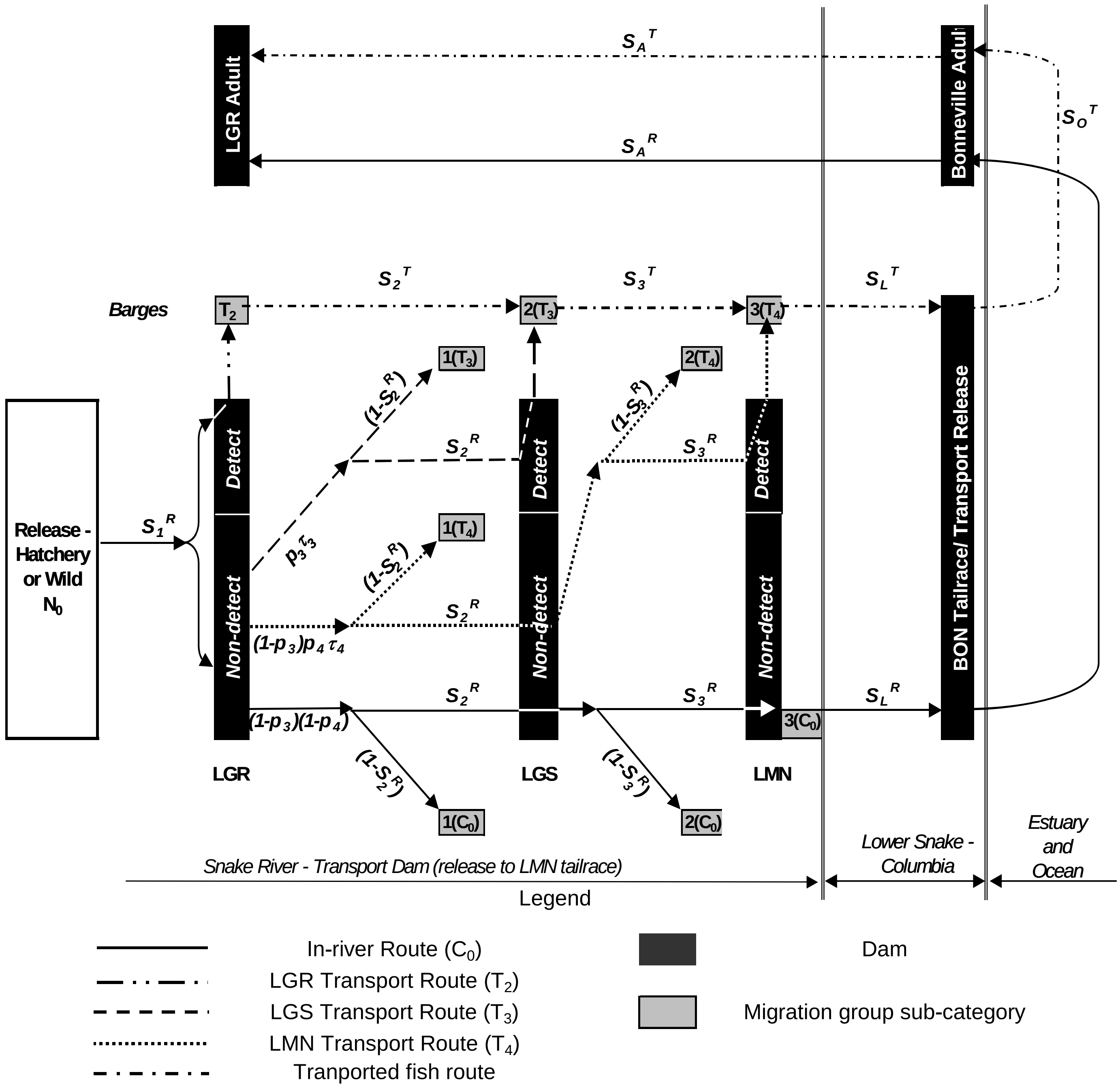

Figure 2. Schematic of the Lower Snake and Columbia River system with focus on the three transport sites, the migration routes, and the sub-categories or possible fates within each group.

Calculation of in-river (Control) SAR

Calculation of the number of juveniles for the undetected in-river passage group is the simplest among the three possible post LGR routes to describe (solid line, Figure 2). A fish passing undetected through the three transport sites is first undetected through LGR with probability $1-p_2$. Of the number of fish in the tailrace in LGR, an expected proportion of $(1-p_3)(1-p_4)$ will be in the in-river migration route or C_0 group.

Fish in this undetected pathway are comprised of three groups each representing a possible fate. First, a fish could die in-river between LGR and LGS with probability $\left(1-S_2^R\right)$ (C_0^1, Figure 2). Expressed as a function of cohort release size N_0, detection, and survival probabilities the number of C_0^1 juveniles is written as follows,

$$C_0^1 = N_0 S_1^R (1-p_2)(1-p_3)(1-p_4)\left(1-S_2^R\right).$$

The two other possible fates are represented by juveniles that survive to LGS but die between LGS and LMN with probability $S_2^R\left(1-S_3^R\right)$ (C_0^2, Figure 2) and fish that survive to the tailrace of LMN with probability $S_2^R S_3^R$ (C_0^3, Figure 2). The total number of fish in the undetected category, C_0, is the sum of the three groups and is expressed mathematically as follows,

$$C_0 = \left[\underbrace{N_0 S_1^R (1-p_2)(1-p_3)(1-p_4)(1-S_2^R)}_{C_0^1} \right] + \left[\underbrace{N_0 S_1^R (1-p_2)(1-p_3)(1-p_4) S_2^R (1-S_3^R)}_{C_0^2} \right]$$
$$+ \left[\underbrace{N_0 S_1^R (1-p_2)(1-p_3)(1-p_4) S_2^R S_3^R}_{C_0^3} \right],$$

or more simply,

$$C_0 = N_0 S_1^R (1-p_2)(1-p_3)(1-p_4). \tag{4}$$

A returning adult that migrated undetected through the Lower Snake River as a juvenile would have had to survive undetected from the LGR tailrace to the LMN tailrace with probability $(1-p_3)(1-p_4) S_2^R S_3^R$ and survive in-river to the Bonneville tailrace with probability S_L^R. Subsequent to in-river migration as a juvenile, a fish would then need to survive migration through estuary, then ocean residence back to Bonneville with probability S_O^R, and finally survive adult migration back to LGR with probability S_A^R (solid line, Figure 2). Under the assumption of independent probabilities, the number of fish in the C_0 group that return as adults, A^{C_0}, is expressed as a function of release numbers, detection, and survival as follows,

$$A_{C_0} = N_0 S_1^R (1-p_2)(1-p_3)(1-p_4) S_2^R S_3^R S_L^R S_O^R S_A^R. \tag{5}$$

By the definition of Eq. (2) and use of the juvenile and adult numbers (Eq. (4) and (5), respectively), the SAR for fish migrating in-river is as follows,

$$SAR\left(C_0\right) = \frac{A_{C_0}}{C_0},$$

or,

$$SAR\left(C_0\right) = \frac{N_0 S_1^R \left(1-p_2\right)\left(1-p_3\right)\left(1-p_4\right) S_2^R S_3^R S_L^R S_O^R S_A^R}{N_1 S_1^R \left(1-p_2\right)\left(1-p_3\right)\left(1-p_4\right)}.$$

Simplifying the above equation leads to an expression for $SAR\left(C_0\right)$ that is a function exclusively of survival probabilities through each life stage from LGR as a juvenile to LGR as an adult

$$SAR\left(C_0\right) = S_2^R S_3^R S_L^R S_O^R S_A^R. \tag{6}$$

Calculation of the transport *SAR*

Although conceptually similar, determining the number of fish in the transport system is more complex than calculating juvenile numbers passing in-river. The total number of T_0 juveniles is the sum of the number transported from each of the three barge sites, LGR, LGS, and LNM or T_2, T_3, and T_4, respectively. The derivation for the numbers of juveniles in each transport group is similar to that of the C_0 group where the possible fates of fish en route to the barge site are considered. Expressions for adult returns are more easily calculated than juvenile numbers. We derive the smolt-to-adult return rate for transported fish by considering site-specific transport route and adult return numbers.

Calculation of transported juveniles, returning adults, and SAR: Lower Granite Dam

The number of fish transported from LGR is the most easily calculated of all the transport groups (Figure 2). Fish survive from release to LGR with probability, S_1^R, are detected with probability p_2, and are transported with probability τ_2. The total number of fish transported from LGR, T_2, is expressed mathematically as follows,

$$T_2 = N_0 S_1^R p_2 \tau_2 . \qquad (7)$$

A fish transported as a juvenile at LGR returning as an adult to LGR has to first survive past LGS and LMN in the barge with joint probability $S_2^T S_3^T$, then survive transport through the lower Snake and Columbia rivers to the transport release site with probability S_L^T (Figure 2). Upon release, the same fish would have to survive estuary migration and ocean residence back to Bonneville with probability S_O^T and finally survive upstream migration to LGR with probability S_A^T (Figure 2). The total number of adults returning to LGR that were transported as juveniles, A_{T_2}, is expressed in terms of release numbers, detection, transport, and survival probabilities as follows,

$$A_{T_2} = N_0 S_1^R p_2 \tau_2 S_2^T S_3^T S_L^T S_O^T S_A^T . \qquad (8)$$

By the definition of Eq. (3), the site-specific return probability for fish transported from LGR, $SAR(T_2)$, is written as,

$$SAR(T_2) = \frac{A_{T_2}}{T_2} = \frac{N_0 S_1^R p_2 \tau_2 S_2^T S_3^T S_L^T S_O^T S_A^T}{N_0 S_1^R p_2 \tau_2}$$

or, more simply,

$$SAR\left(T_2\right) = S_2^{T_2} S_3^{T_2} S_L^{T_2} S_O^{T_2} S_A^{T_2} . \quad (9)$$

Hence, the SAR for fish transported from LGR can be expressed solely as a joint survival probability through several life stages.

Calculation of transported juveniles, returning adults, and SAR: Little Goose Dam

The expected number of fish not detected at LGR is expressed as follows, $N_0 S_1^R \left(1 - p_2\right)$. Juveniles in this group are routed to one of three pathways, transport at LGS, transport at LMN, or in-river passage (Figure 2). The probability of being in the LGS transport group is $p_3 \tau_3$. Of these fish, some will die in-river on the way to LGS with probability $\left(1 - S_3^R\right)$ (T_3^1), and the rest survive with probability S_2^R (T_3^2). The expected number of fish in this route, T_3, can therefore be expressed as

$$T_3 = \underbrace{N_0 S_1^R \left(1 - p_1\right) p_3 \tau_3 \left(1 - S_2^R\right)}_{T_3^1} + \underbrace{N_0 S_1^R \left(1 - p_1\right) p_3 \tau_3 S_2^R}_{T_3^2} ,$$

or

$$T_3 = N_0 S_1^R \left(1 - p_1\right) p_3 \tau_3 . \quad (10)$$

Fish returning to LGR as adults that were in the LGS transport pathway as juveniles in the tailrace of LGR (dotted line, Figure 2) would have had to survive in-river to the transport site with probability S_2^R. Subsequent to entering the barge at LGS, a fish would have had to survive in the barge past LMN to the transport release site with joint probability, $S_3^T S_L^T$, survive in the estuary migration, ocean residence and back to BON with probability S_O^T, and finally survive in-river migration as an adult back to LGR with probability S_A^T (dotted-dashed line, Figure 2). Hence, the number of fish in the LGS pathway surviving from LGR as a juvenile back to LGR as an adult can be written as,

$$A_{T_3} = N_0 S_1^R \left(1 - p_2\right) p_3 \tau_3 S_2^R S_3^T S_L^T S_O^T S_A^T, \tag{11}$$

Following the definition of Eq. (3), the site specific smolt-to-adult return proportion for fish in the LGS transport route, $SAR\left(T_3\right)$, is as follows,

$$SAR\left(T_3\right) = \frac{N_0 S_1^R \left(1 - p_2\right) p_3 \tau_3 S_2^R S_3^T S_L^T S_O^T S_A^T}{N_0 S_1^R \left(1 - p_2\right) p_3 \tau_3}$$

or more simply,

$$SAR\left(T_3\right) = S_2^R S_3^T S_L^T S_O^T S_A^T. \tag{12}$$

Again, the *SAR* for fish transported at LGS is a function of the probability of surviving from LGR as a juvenile back to LGR as an adult through all associated life stages. The $SAR\left(T_3\right)$ also includes S_2^R, the survival through that portion of the river traveled by juveniles to the transport site.

Calculation of transported juveniles, returning adults, and SAR: Lower Monumental Dam

The number of juveniles on the transport route to LMN, T_4, can meet three possible fates; not survive between LGR and LGS with probability $\left(1-S_2^R\right)$(T_4^1), survive to LGS tailrace and die on the way to LMN with probability $S_2^R\left(1-S_3^R\right)$ (T_4^2), or survive to the transport site with probability $S_2^R S_3^R$ (T_4^3). The total number of fish in the LMN transport route is the sum of the number of fish in these groups and is expressed mathematically as,

$$T_4 = \left[\underbrace{N_0 S_1^R\left(1-p_2\right)\left(1-p_3\right)p_4\tau_4\left(1-S_2^R\right)}_{T_4^1}\right] + \left[\underbrace{N_0 S_1^R\left(1-p_2\right)\left(1-p_3\right)p_4\tau_4 S_2^R\left(1-S_3^R\right)}_{T_4^2}\right] + \left[\underbrace{N_0 S_1^R\left(1-p_2\right)\left(1-p_3\right)p_4\tau_4 S_2^R S_3^R}_{T_4^3}\right].$$

Simplifying the above equation gives the number of fish in the LMN transport route as a function of tag release numbers, survival, detection, and transport probabilities as follows,

$$T_4 = N_0 S_1^R\left(1-p_2\right)\left(1-p_3\right)p_4\tau_4 . \tag{13}$$

The number of fish surviving the LMN transport route and returning to LGR as adults is expressed mathematically as

$$A_{T_4} = N_0 S_1^R\left(1-p_2\right)\left(1-p_3\right)p_4\tau_4 S_2^R S_3^R S_L^T S_O^T S_A^T . \tag{14}$$

By use of the definition in Eq. 3, the site-specific SAR for fish in the LMN transport route, $SAR(T_4)$, is expressed as,

$$SAR(T_4) = \frac{N_0 S_1^R (1-p_2)(1-p_3) p_4 \tau_4 S_2^R S_3^R S_L^T S_O^T S_A^T}{N_0 S_1^R (1-p_2)(1-p_3) p_4 \tau_4},$$

or more simply,

$$SAR(T_4) = S_2^R S_3^R S_L^T S_O^T S_A^T \quad (15)$$

Again, the SAR for fish in this passage route is a function of survival probabilities only, including some in-river survival associated with traveling to the transport site, i.e., $S_2^R S_3^R$.

Transport smolt-to-adult return rate, $SAR(T_0)$

The SAR for transported fish is, by definition [Eq. (3)], the number of returning adults divided by the number of juveniles in the transport system. Total juveniles in the transport system, T_0, are calculated from the numbers each transport sub-group [Eqs. (7), (10), and (13)] as follows,

$$T_0 = N_0 S_1^R \left(p_2 \tau_2 + (1-p_2) p_3 \tau_3 + (1-p_2)(1-p_3) p_4 \tau_4 \right). \quad (16)$$

The expected number of returning adults, A_{T_0}, out of T_0 transported juveniles is calculated by the sum of Eqs. (8), (11), and (14) as follows,

$$A_{T_0} = N_0 S_1^R \left(p_2 \tau_2 S_2^T S_3^T S_L^T S_O^T S_A^T + (1-p_2) p_3 \tau_3 S_2^R S_3^T S_L^T S_O^T S_A^T + (1-p_2)(1-p_3) p_4 \tau_4 S_2^R S_3^R S_L^T S_O^T S_A^T \right).$$

The smolt-to-adult return proportion for fish in the transport system [Eq. 3] is expressed as follows,

$$SAR(T_0) = \frac{A_{T_0}}{T_0},$$

or

$$SAR(T_0) = \frac{p_2\tau_2 S_2^T S_3^T S_L^T S_O^T S_A^T + (1-p_2)\, p_3\tau_3 S_2^R S_3^T S_L^T S_O^T S_A^T + (1-p_2)(1-p_3)\, p_4\tau_4 S_2^R S_3^R S_L^T S_O^T S_A^T}{p_2\tau_2 + (1-p_2)\, p_3\tau_3 + (1-p_2)(1-p_3)\, p_4\tau_4} \quad (17)$$

Alternatively, the transport *SAR* can be expressed as a weighted average across all transport groups, with weights equal to the proportion of fish transported from each site. The transport *SAR* as a weighted average is written as follows,

$$SAR(T_0) = \sum_{i=2}^{4} w_i SAR(T_i), \quad (18)$$

where $w_i = \frac{T_i}{T_0}$, the proportion of fish in each of the *i* transport routes [Eqs. (7), (10), and (13) for $T_2, T_3,$ and T_4, respectively] and $SAR(T_i)$, the site specific *SARs* defined in Eqs. (9), (12), and (15).

T/C Ratio, behavior under the null hypothesis [$H_O:(T/C)=1$] and numerical examples

The transport to in-river survival ratio can be written in terms of site-specific adult return probabilities [Eq. (1)] as follows,

$$T/C = \frac{\dfrac{p_2\tau_2 S_2^{T_2} S_3^{T_2} S_L^{T_2} S_O^{T_2} S_A^{T_2} + (1-p_2)\,p_3\tau_3 S_2^R S_3^{T_3} S_L^{T_3} S_O^{T_3} S_A^{T_3} + (1-p_2)(1-p_3)\,p_4\tau_4 S_2^R S_3^R S_L^{T_4} S_O^{T_4} S_A^{T_4}}{p_2\tau_2 + (1-p_2)\,p_3\tau_3 + (1-p_2)(1-p_3)\,p_4\tau_4}}{S_2^R S_3^R S_L^R S_O^R S_A^R}$$

or,

$$T/C = \frac{p_2\tau_2 S_2^{T_2} S_3^{T_2} S_L^{T_2} S_O^{T_2} S_A^{T_2} + (1-p_2)\,p_3\tau_3 S_2^R S_3^{T_3} S_L^{T_3} S_O^{T_3} S_A^{T_3} + (1-p_2)(1-p_3)\,p_4\tau_4 S_2^R S_3^R S_L^{T_4} S_O^{T_4} S_A^{T_4}}{S_2^R S_3^R S_L^R S_O^R S_A^R\left[p_2\tau_2 + (1-p_2)\,p_3\tau_3 + (1-p_2)(1-p_3)\,p_4\tau_4\right]} \qquad (19)$$

Using the convention of Sanford and Smith (1991) and Buchanan (2005), the site-specific T/C ratios can be expressed as $R_i = \dfrac{SAR(T_i)}{SAR(C_0)}$ and Eq. (19) re-expressed as,

$$T/C = \frac{R_2 \cdot p_2\tau_2 + R_3 \cdot (1-p_2)\,p_3\tau_3 + R_4 \cdot (1-p_2)(1-p_3)\,p_4\tau_4}{\left[p_2\tau_2 + (1-p_2)\,p_3\tau_3 + (1-p_2)(1-p_3)\,p_4\tau_4\right]},$$

or

$$T/C = \sum_{i=2}^{4} w_i R_i \qquad (20)$$

where w_i is defined as in Eq. (18). The overall ${}^{T}\!/\!{}_{C}$ ratio can be written as an average of site specific ratios, R_i weighted by the probability of being transported from each site. However, Eqs. (19) and (20) are specific to the design elements of the CSS study and not a general ${}^{T}\!/\!{}_{C}$ ratio for all possible situations.

Behavior of ${}^{T}\!/\!{}_{C}$ *under the null*

One of the ways to check the properties of an equation is to observe the behavior under the null hypothesis, the only condition under which the outcome is known. For the ${}^{T}\!/\!{}_{C}$ ratio, the null hypothesis means that there is no difference in the rate of relative adult returns between transported and in-river migrating juveniles. No difference in relative survival between transported and control fish could be satisfied under the following set conditions,

$$S_2^{T_i} = S_2^R;\ S_3^{T_i} = S_3^R;\ S_4^{T_i} = S_4^R;\ S_L^{T_i} = S_L^R;\ S_O^{T_i} = S_O^R;\ \text{and } S_A^{T_i} = S_A^R, \forall i\ .$$

If true, then $R_i = 1$ for all *i* and Eq. (20), the ${}^{T}\!/\!{}_{C}$ ratio is equal to one. Note that the result does not depend on detection and transport probabilities but only on survival.

Numerical example 1a: Equal return rates between transport and control groups (Null model), 100% transport

To further illustrate the calculations to arrive the T/C ratio for a cohort of fish, we consider a year in which the rates of return are the same for both groups, i.e., the null condition of no difference between the transport and control group with regard to smolt-to-adult return ratios. Illustrating the properties of the T/C ratio is easiest under this scenario. Moreover, examining conditions under the null hypothesis is one way to verify that a particular estimator behaves as expected. In this example, probabilities of survival are the same for fish in the transport group and control groups (Table 1). For simplicity, detection probabilities are equal among the three sites and all detected fish are transported, i.e., $\tau_2 = \tau_3 = \tau_4 = 1$. We relax these last conditions in the next example. Numbers of fish comprising transport and control groups are presented in Table 2, given a fixed cohort release size and the stated probabilities. Starting from the release site to eventual return as an adult, we follow a cohort of fish through a simplified life history to illustrate the calculation of the T/C ratio (Eq. (19)).

Table 1. Hypotheical survival, detection, and transport probabilities for a cohort of 50,000 tagged fish.

Segment	Segment designation (i)	In River Survival S_i^R	Transport Route Survival S_i^T	Location (i)	Capture Probability p_i	Transport Probability τ_i
Rel to LGR	1	0.8		LGR (2)	0.3	1.00
LGR to LGS	2	0.8	0.8	LGS (3)	0.3	1.00
LGS to LMN	3	0.8	0.8	LMN (4)	0.3	1.00
LMN-BON (L)	L	0.5	0.5			
BON-BON (Ocean)	O	0.05	0.05			
BON-LGR	A	0.8	0.8			

Table 2. Numbers of fish comprising each migration category sub-categories, e.g., C_0^1, for a hypothetical release of 50,000 fish and the probabilities given in Table 1. Shaded boxes correspond to the shaded sub-categories in Figure 2.

Segment	Fish Surviving to Site, In-river **(Bold)** (Undetected in Snake R.)			Total Mortalities Between Sites	In River Mortalities to C_0 category	In River Mortalities to T_0 category	Fish Added to Barge At Site **(Bold)**	Fish in Barge At Site (**Bold**)	Mortalities in Barge Between Sites
	Total	Control Group C_0	Transport Group T_0						
Rel to **LGR**	28000						12000 (T_2)	12000	
LGR to **LGS**	15680	10976 $(C_0^2 + C_0^3)$	4704 $(T_4^2 + T_4^3)$	5600	2744 (C_0^1)	1680 (T_3^1) 1176 (T_4^1)	6720 (T_3^2)	16320	2400
LGS to **LMN**	8781	8781 (C_0^3)		3136	2195 (C_0^2)	941 (T_4^2)	3763 (T_4^3)	16819	3264
LMN-**BON**	4390							8410	
BON-**BON** (Ocean residence)	220							420	
BON-**LGR**	176							336	

We begin by calculating the numbers of juveniles in each passage group, i.e., C_0 and T_0. At a hatchery above Lower Granite Dam, 50,000-tagged fish are released ($N_1 = 50,000$). Of this tag release group, 12,000 juveniles are put to the barge at LGR T_2, (Figure 2) calculated by Eq. (7) as follows,

$$\begin{aligned} T_2 &= N_0 S_1^R p_2 \tau_2 \\ &= 50000(0.8)(0.3)(1) \\ T_2 &= 12,000 \end{aligned}$$

Fish surviving to LGR pass undetected are comprised of the C_0, T_3, and T_4 groups, calculated as,

$$\begin{aligned} C_0 + T_3 + T_4 &= N_0 S_1^R (1 - p_2) \\ C_0 + T_3 + T_4 &= 50000(0.8)(1 - 0.3). \\ C_0 + T_3 + T_4 &= 28,000 \end{aligned}$$

Of the number of fish in the tailrace of LGR, $(1 - S_2^R)$% of each group will not make it to the next site (Figure 2). Because getting to an eventual passage route will have associated mortality, we apportion number of mortalities within the reach (segment of the river) according to the probability a fish will be in a particular route of passage among three groups. The total number of mortalities, $28000 \cdot (1 - S_2^R)$, between LGR and LGS are comprised of the C_0^1, T_3^1, and T_4^1 groups (Figure 2), each calculated as follows,

$$\begin{aligned} C_0^1 &= N_0 S_1^R (1 - p_2)(1 - p_3)(1 - p_4)(1 - S_2^R) \\ &= 50000(0.8)(0.7)(0.7)(0.7)(0.2) \\ C_0^1 &= 2744, \end{aligned}$$

$$
\begin{aligned}
T_3^1 &= N_0 S_1^R (1-p_2)\, p_3 \tau_3 \left(1-S_2^R\right) \\
&= 50000(0.8)(0.7)(0.3)(1)(0.2) \\
T_3^1 &= 1680,
\end{aligned}
$$

and

$$
\begin{aligned}
T_4^1 &= N_0 S_1^R (1-p_2)(1-p_3)\, p_4 \tau_4 \left(1-S_2^R\right) \\
&= 50000(0.8)(0.7)(0.7)(0.3)(1)(0.2) \\
T_4^1 &= 1176.
\end{aligned}
$$

The second fate for fish in the LGS transport path is survival to the barge. The number of fish in the T_3^2 group that is eventually added to the T_2 surviving fish already in the barge is calculated by,

$$
\begin{aligned}
T_3^2 &= N_0 S_1^R (1-p_2)\, p_3 \tau_3 S_2^R \\
&= 50,000(0.8)(0.7)(0.3)(1)(0.8) \\
T_3^2 &= 6720.
\end{aligned}
$$

All of the T_3 transport group, those on the LGS transport pathway (route) are accounted for at this site. The total number of T_3 fish is $T_3^1 + T_3^2 = 1,680 + 6,720 = 8,400$.

Arriving at the tailrace of LGS are the remainder of the fish in the C_0 and T_4 groups. Juveniles that will eventually migrate in-river (C_0 group) and have survived the second river segment (LGR to LGS) plus those that will be transported at LMN (T_4) and survived through this reach comprise the 15,680-tagged fish in the tailrace of LGS. Of these fish, $\left(1-S_3^R\right)$ percent, or 3,136 juveniles, will meet the second fate of not surviving to LMN, groups C_0^2 and T_4^2 (Figure 2). The numbers in each group are calculated as follows, respectively,

$$\begin{aligned} C_0^2 &= N_0 S_1^R \left(1-p_2\right)\left(1-p_3\right)\left(1-p_4\right) S_2^R \left(1-S_3^R\right) \\ &= 50000(0.8)(0.7)(0.7)(0.7)(0.8)(0.2) \\ &= 2195 \end{aligned}$$

and

$$\begin{aligned} T_4^2 &= N_0 S_1^R \left(1-p_2\right)\left(1-p_3\right) p_4 \tau_4 S_2^R \left(1-S_3^R\right) \\ &= 50{,}000(0.8)(0.7)(0.7)(0.3)(1)(0.8)(0.2) \\ T_4^2 &= 941. \end{aligned}$$

The third fate for the C_0 fish is survival to the tailrace of LMN and eventual passage through the hydro system. The number in the group is calculated as

$$\begin{aligned} C_0^3 &= N_0 S_1^R \left(1-p_2\right)\left(1-p_3\right)\left(1-p_4\right) S_2^R S_3^R \\ &= 50{,}000(0.8)(0.7)(0.7)(0.7)(0.8)(0.8) \\ C_0^3 &= 8781 \end{aligned}$$

The third fate for the fish in the LGS transport group, T_4^3, is eventual survival to the barge for downstream passage. The number of fish in this group is calculated as follows,

$$\begin{aligned} T_4^3 &= N_0 S_1^R \left(1-p_2\right)\left(1-p_3\right) p_4 \tau_4 S_2^R S_3^R \\ &= 50{,}000(0.8)(0.7)(0.7)(0.3)(1)(0.8)(0.8) \\ T_4^3 &= 3763 \end{aligned}$$

The total number of fish in the control group is the sum of the C_0 mortalities between LGR and LMN plus the number of fish surviving to LNM tailrace is computed as,

$$
\begin{aligned}
C_0 &= C_0^1 + C_0^2 + C_0^3 \\
C_0 &= 2744 + 2195 + 8781 \\
C_0 &= 13720
\end{aligned}
$$

This is equivalent to calculating the expected number of C_0 fish by Eq. (4) as follows,

$$
\begin{aligned}
C_0 &= N_1 S_1^R (1 - p_2)(1 - p_3)(1 - p_4) \\
&= 50,000(0.8)(0.7)(0.7)(0.7) \\
C_0 &= 13720.
\end{aligned}
$$

The total number of fish in the T_0 group is the sum of all possible fates between LGR and LMN for fish in the transport routes, calculated as follows,

$$
\begin{aligned}
T_0 &= T_2 + \left(T_3^1 + T_4^1\right) + T_3^2 + T_4^2 + T_4^3 \\
&= 12000 + (2856) + 6720 + 941 + 3763 \\
T_0 &= 26280
\end{aligned}
$$

Of the 8781 fish in the C_0 group that survived to LMN, 4,390 juveniles survived migration through the rest of the system to the tailrace of Bonneville with $8781 \cdot S_L^R$, and 220 eventually returned as adults to Bonneville Dam (BON). Of these adult returns, 176 fish were eventually observed at LGR. The expected number of adults in the control group returning to LGR is calculated by Eq. (5) as follows,

$$
\begin{aligned}
A_{C_0} &= N_1 S_1^R (1 - p_2)(1 - p_3)(1 - p_4) S_2^R S_3^R S_L^R S_O^R S_A^R \\
&= 50,000(0.8)(0.7)(0.7)(0.7)(0.8)(0.8)(0.5)(0.05)(0.8) \\
A_{C_0} &= 176
\end{aligned}
$$

The smolt-to-adult return proportion for control fish in calculated by the definition in Eq. (2) as follows,

$$\begin{aligned} SAR(C_0) &= \frac{A_{C_0}}{C_0} \\ &= \frac{176}{13720} \\ SAR(C_0) &= 0.0128 \end{aligned}$$

Alternatively, the SAR can be calculated as the product of survival probabilities [Eq. (6)] as follows,

$$\begin{aligned} SAR(C_0) &= S_2^R S_3^R S_L^R S_O^R S_A^R \\ &= (0.8)(0.8)(0.5)(0.05)(0.8) \\ SAR(C_0) &= 0.0128. \end{aligned}$$

The number of adults returning to LGR of the transported fish is again slightly more complex. Of the 12,000 T_2 juveniles put in the barge, 9600 survived to LGS and 2400 died on the way, i.e., $S_2^T = 0.8$. At the second transport site, LGS, 6,720 of the T_3 fish were added. A total of 16,320 juveniles were alive in the barge upon leaving LGS. Between LGS and LMN, 3,264 juveniles died, i.e., $S_3^T = 0.8$ and 3,763 T_4 surviving juveniles were added at LMN. Subsequently, there were 16,819 live fish in the barge upon entering the lower hydro system. Survival in the barge through the lower river, S_L^T was 50% , hence only 8,410 were released alive below BON. Of these, 420 survived to adult return (sum of all age classes; $S_O^T = 0.05$) at BON, and 336 were observed at LGR. From these data, the smolt-to-adult return proportion for fish in the T_0 group is calculated according to the definition of an SAR [Eq. (3)] as follows,

$$
\begin{aligned}
SAR(T_0) &= \frac{A_{T_0}}{T_0} \\
&= \frac{336}{26208} \\
SAR(T_0) &= 0.0128.
\end{aligned}
$$

The $SAR(T_0)$ can also be computed using site specific $SARs$ Eq (18) as follows,

$$
\begin{aligned}
SAR(T_2) &= S_2^{T_2} S_3^{T_2} S_L^{T_2} S_O^{T_2} S_A^{T_2} \\
&= (0.8)(0.8)(0.5)(0.05)(0.8) \\
SAR(T_2) &= 0.0128
\end{aligned}
$$

and for T_3 and T_4, $SAR(T_3) = 0.0128$ and $SAR(T_4) = 0.0128$, respectively. The proportions of T_0 fish transported from each site, $w_2, w_3,$ and w_4, are calculated as follows,

$$
w_2 = \frac{12000}{26280} = 0.456, w_3 = \frac{8400}{26280} = 0.320, \text{ and } w_4 = \frac{5880}{26280} = 0.224,
$$

respectively. Then, using Eq. (18) $SAR(T_0)$ is,

$$
SAR(T_0) = w_2 SAR(T_2) + w_3 SAR(T_3) + w_4 SAR(T_4)
$$

$$
\begin{aligned}
SAR(T_0) &= 0.456(0.0128) + 0.320(0.0128) + 0.224(0.0128) \\
SAR(T_0) &= 0.0128.
\end{aligned}
$$

By use of the definition in Eq. 1, the T/C ratio is calculated as follows,

$$\begin{aligned} T/C &= \frac{SAR(T_0)}{SAR(C_0)} \\ &= \frac{0.0128}{0.0128} \quad , \\ T/C &= 1 \end{aligned}$$

or by Eq. (20) where $R_i = \frac{SAR(T_i)}{SAR(C_0)}$, as

$$\begin{aligned} T/C &= w_2 R_2 + w_3 R_3 + w_3 R_4 \\ &= 0.456(1) + 0.320(1) + 0.224(1) \\ T/C &= 1. \end{aligned}$$

In the next example, not all collected (detected) fish are transported.

Numerical example 1b: Equal return rates between transport and control groups (Null model), differential detection and survival probabilities among transport sites.

In this example, all survival probabilities are as in example 1a, however, each transport site has a different detection (collection) probability (Table 3). Furthermore, transport probabilities are less than one and differ among the three sites (Table 3). Again, we follow a cohort of 50,000 tagged fish from release to eventual return as an adult to LGR and compute the number of fish in each category and at each stage of migration through the three transport dams (Table 4), the SARs for each group and T/C ratio.

As in Example 1a, 40,000 fish survive to LGR, 24,000 of which are undetected (Table 4). However, this time only 10,560 of 16,000 collected (detected) juveniles are transported, i.e., $T_2 = 10,560$, Eq. (7). The remaining 5,440 juveniles that were detected (collected) are returned to the river for the purposes of estimating survival and detection probabilities. Because these fish have a prior detection history, they are not subject to transport, nor can they be included in the C_0 category. Thus, they are no longer part of the study except for purposes of parameter estimation.

Table 3. Hypothetical reach survival and site-specific detection and transport probabilities for Example 1b.

Segment	Segment designation (i)	In-river Survival S_i^R	Transport Route Survival S_i^T	Location (i)	Capture Probability p_i	Transport Probability τ_i
Rel to LGR	1	0.8		LGR (2)	0.4	0.66
LGR to LGS	2	0.8	0.8	LGS (3)	0.35	0.5
LGS to LMN	3	0.8	0.8	LMN (4)	0.5	0.6
LMN-BON (L)	L	0.5	0.5			
BON-BON (Ocean)	O	0.05	0.05			
BON-LGR	A	0.8	0.8			

Table 4. Hypothetical numbers of fish in each category and sub-category (intermediate calculations) for Example 1b. Shaded cells correspond to sub-categories in Figure 2. Release size is 50,000 tagged fish.

Segment	Fish Surviving to Site **(Bold)**, In-river (Undetected in Snake R.)			Total Mortalities In-river Between Sites	In-river Mortalities to C_0 category	In-river Mortalities to T_0 category	Fish Added to Barge At Site **(Bold)**	Fish in Barge At Site (**Bold**)	Mortalities in Barge Between Sites
	Total	Control Group C_0	Transport Group T_0						
Rel to **LGR**	24000						10560 (T_2)	10560	
LGR to **LGS**	12480	6240 $(C_0^2 + C_0^3)$	3744 $(T_4^2 + T_4^3)$	4800	1560 (C_0^1)	840 (T_3^1) 936 (T_4^1)	3360 (T_3^2)	11808	2112
LGS to **LMN**	4992	4992 (C_0^3)		2496	1248 (C_0^2)	749 (T_4^2)	2995 (T_4^3)	12442	2362
LMN-**BON**		2496						6221	
BON-**BON**		125						311	
BON-**LGR**		100						249	

Of the 24,000 undetected fish in the tailrace of LGR, 4,800 die within the next river reach and include 1,560 C_0 fish (C_0^1, Figure 2; Table 1), 840 T_3 fish (T_3^1, Figure 2 and Table 4), and 936 T_4 fish (T_4^1, Figure 2; Table 4). The numbers in each of these sub-categories are calculated as follows, respectively,

$$\begin{aligned} C_0^1 &= N_0 S_1^R (1-p_2)(1-p_3)(1-p_4)(1-S_2^R) \\ &= 50000(0.8)(0.6)(0.65)(0.5)(0.2) \\ C_0^1 &= 1{,}560, \end{aligned}$$

$$\begin{aligned} T_3^1 &= N_0 S_1^R (1-p_2)\, p_3 \tau_3 (1-S_2^R) \\ &= 50000(0.8)(0.6)(0.35)(0.5)(0.2) \\ T_3^1 &= 840, \end{aligned}$$

and

$$\begin{aligned} T_4^1 &= N_0 S_1^R (1-p_2)(1-p_3)\, p_4 \tau_4 (1-S_2^R) \\ &= 50{,}000(0.8)(0.6)(0.65)(0.5)(0.6)(0.2) \\ T_4^1 &= 936. \end{aligned}$$

The 1,464 unaccounted for mortalities in the LGR-LGS reach ($4{,}800 - C_0^1 - T_3^1 - T_4^1 = 1{,}464$) are part of the group of juveniles that are detected in the Snake River at least once but are not transported and thus are no longer part of the study.

Surviving to transport at LGS are 3,360 juveniles ($T_3^2 = 3{,}360$). The number of juveniles placed in transport at LGS is calculated as follows,

$$
\begin{aligned}
T_3^1 &= N_0 S_1^R \left(1 - p_2\right) p_3 \tau_3 S_2^R \\
&= 50000(0.8)(0.6)(0.35)(0.5)(0.8) \\
T_3^1 &= 3,360.
\end{aligned}
$$

The total number of fish in the LGS transport group is the sum of the two T_3 sub-groups, those dying in the second river reach (LGR to LGS) and those that survive to actual transport, or $T_3 = T_3^1 + T_3^2 = 4,200$. This is equivalent to the result obtained by computing the expected number fish in the LGS transport group by use of Eq. (10).

Entering the river reach below LGS are 6,240 and 3,744 fish remaining in the C_0, and T_4 migration routes, respectively. Of the control fish, 1,248 do not survive to the next dam (C_0^2), and 4,992 arrive at the tailrace of LMN (C_0^3). The numbers in each sub-category are calculated as,

$$
\begin{aligned}
C_0^2 &= N_1 S_1^R \left(1 - p_2\right)\left(1 - p_3\right)\left(1 - p_4\right) S_2^R \left(1 - S_3^R\right) \\
&= 50,000(0.8)(0.6)(0.65)(0.5)(0.8)(0.2) \\
C_0^2 &= 1,248
\end{aligned}
$$

and

$$
\begin{aligned}
C_0^3 &= N_1 S_1^R \left(1 - p_2\right)\left(1 - p_3\right)\left(1 - p_4\right) S_2^R S_3^R \\
&= 50,000(0.8)(0.6)(0.65)(0.5)(0.8)(0.8) \\
C_0^3 &= 4,992.
\end{aligned}
$$

Of the 3,744 remaining fish in the LMN transport pathway, 749 die in the reach below LGS ($T_4^2 = 749$; Figure 2; Table 4), and 2,995 survive to actual transport ($T_4^3 = 2,995$). The numbers of fish in each of the T_4 sub-categories, T_4^2 and T_4^3, are estimated as follows,

$$\begin{aligned} T_4^2 &= N_1 S_1^R (1-p_2)(1-p_3) p_4 \tau_4 S_2^R (1-S_3^R) \\ &= 50,000(0.8)(0.6)(0.65)(0.5)(0.6)(0.8)(0.2) \\ T_4^2 &= 749 \end{aligned}$$

and

$$\begin{aligned} T_4^3 &= N_1 S_1^R (1-p_2)(1-p_3) p_4 \tau_4 S_2^R S_3^R \\ &= 50,000(0.8)(0.6)(0.65)(0.5)(0.6)(0.8)(0.8) \\ T_4^3 &= 2,995. \end{aligned}$$

The total number of fish in the LNM transport group (pathway) is the sum of fish experiencing one of three possible fates on the way to the barge: dying in the 2nd river reach (the T_4^1 group); surviving to the tailrace of LGS but not to LMN (the T_4^2 group); and arriving to actual transport at LMN (the T_4^3 fish). The total number of T_4 fish is,

$$\begin{aligned} T_4 &= T_4^1 + T_4^2 + T_4^3 \\ &= 936 + 749 + 2995 \\ T_4 &= 4,680. \end{aligned}$$

The total number of fish in the transport group, T_0, can be calculated by either summing the totals of the individual pathways as follows,

$$T_0 = T_2 + T_3 + T_4$$
$$= 10,590 + 4200 + 4680$$
$$T_0 = 19,440,$$

or by use of Eq.(16),

$$T_0 = N_1 S_1^R \left[p_2 \tau_2 + (1 - p_2) p_3 \tau_3 + (1 - p_2)(1 - p_3) p_4 \tau_4 \right]$$
$$= 50,000(0.8)\left[(0.4)(0.66) + (0.6)(0.35)(0.5) + (0.6)(0.65)(0.5)(0.6)\right]$$
$$T_0 = 19,440$$

The total number of juveniles in the control groups is calculated by use of subgroups as follows,

$$C_0 = C_0^1 + C_0^2 + C_0^3$$
$$= 1560 + 1248 + 4992$$
$$C_0 = 7800$$

or by use of Eq. (4)

$$C_0 = N_1 S_1^R (1 - p_2)(1 - p_3)(1 - p_4)$$
$$= 50,000(0.8)(0.6)(0.65)(0.5)$$
$$C_0 = 7,800.$$

The adults that return out of the T_0 juveniles in the transport routes are calculated by considering the 10,560 fish that were transported at LGR (Table 4). Of these fish, 80% survive to LGS where 3,360 fish are added (Table 3 and Table 4). Upon leaving LGS, 11,808 juveniles are in transport, i.e., $10,560(0.8) + 3,360 = 11,808$, with 80% surviving to LMN ($S_3^T = 0.8$; Table 3). At the final transport site, 2995 T_4^3 fish are added. Twelve-thousand four hundred forty-two (12,442) juveniles are then barged downstream past the dams on the Columbia River. Survival in the barge through the lower river reaches to the release site below Bonneville Dam is 50%. Hence, only 6,221 live fish are released from the barge. Survival from transport release back to Bonneville as an adult for the T_0 fish is 5%, and 311 adults are observed at BON. Adult in-river survival is 80% and 249 adult fish return out of the 19,440 in the T_0 group leaving LGR as juveniles. The SAR for the transport category is calculated by Eq. (3) as follows,

$$
\begin{aligned}
SAR(T_0) &= \frac{A_{T_0}}{T_0} \\
&= \frac{249}{19440} \\
SAR(T_0) &= 0.0128.
\end{aligned}
$$

Alternatively, $SAR(T_0)$ can be calculated use of Eq. (18). The SARs for each transport group are the same as in Example 1a , $SAR(T_2) = 0.0128$, $SAR(T_3) = 0.0128$ and $SAR(T_4) = 0.0128$. The proportion of T_0 fish in each of the three transport groups, $w_2, w_3,$ and w_4, are calculated as,

$$w_2 = \frac{10590}{19440} = 0.5448, w_3 = \frac{4200}{19440} = 0.2160, \text{ and } w_4 = \frac{4680}{19440} = 0.2407,$$

respectively, and $SAR(T_0)$ estimated as,

$$SAR(T_0) = \sum_{i=2}^{4} w_i SAR(T_i)$$

$$SAR(T_0) = 0.5448(0.0128) + 0.2160(0.0128) + 0.2407(0.0128)$$
$$SAR(T_0) = 0.0128.$$

Although not all detected fish were transported and detection probabilities differed among sites, $SAR(T_0)$ is the same as in Example 1a, indicating that the calculation for the smolt-to-adult return proportion depends only on survival probabilities.

The number of adults returning to LGR out of the 7,800 juveniles in the C_0 first must survive to the LMN tailrace. Out of the 4992 C_0 juveniles in the tailrace of LMN (Table 4), only half survive through the hydro system from below LNM to the tailrace of BON, or 2,496 fish. Survival back to BON as an adult is 5%. Hence, 125 C_0 fish are observed at BON as a returning adult, and 100 survive upstream migration to LGR. The $SAR(C_0)$ is calculated by Eq. (2) as follows,

$$\begin{aligned} SAR(C_0) &= \frac{A_{C_0}}{C_0} \\ &= \frac{100}{7800} \\ SAR(C_0) &= 0.0128, \end{aligned}$$

or by Eq. (6) as in Example 1a. The $SARs$ for both groups are the same as in the previous example and the T/C ratio is also the same, i.e., $T/C = 1.$ The only change between the two examples is the detection and transport probabilities. Because the transport SAR does not depend on detection and transport probabilities when site-specific $SARs$ are the same, the

$^{T}\!/_{C}$ ratio as calculated by Eq. (19) (or Eq. (20)) is independent of these parameters under the null hypothesis, as expected.

Numerical example 2: Estimating the $^{T}\!/_{C}$ *ratio using survival, detection and transport probabilities under Eq. (19)*

The last two examples focused on the behavior of the $^{T}\!/_{C}$ ratio under the null hypothesis. In addition, the examples demonstrated how mortality between the groups can be partitioned by apportioning survival among possible routes of passage. The numerical examples further motivate the derivation of the $^{T}\!/_{C}$ ratio from first principles. In this next example, we examine a cohort release for which there was a clear benefit of transportation. However, we calculate the $^{T}\!/_{C}$ ratio entirely from survival, detection, and transport probabilities by use of Eq. (19).

Consider a cohort with survival, detection, and transport probabilities listed in Table 5. From these data $SAR(T_0)$ is estimated by use of Eq. (17) written as follows,

$$SAR(T_0) = \frac{p_2\tau_2 S_2^T S_3^T S_L^T S_O^T S_A^T + (1-p_2)\, p_3\tau_3 S_2^R S_3^T S_L^T S_O^T S_A^T + (1-p_2)(1-p_3)\, p_4\tau_4 S_2^R S_3^R S_L^T S_O^T S_A^T}{p_2\tau_2 + (1-p_2)\, p_3\tau_3 + (1-p_2)(1-p_3)\, p_4\tau_4}.$$

The numerator is calculated by the probabilities in Table 5 as,

$$\begin{aligned}Num. = {} & p_2\tau_2 S_2^T S_3^T S_L^T S_O^T S_A^T \\ & +\left(1-p_2\right) p_3\tau_3 S_2^R S_3^T S_L^T S_O^T S_A^T \\ & +\left(1-p_2\right)\left(1-p_3\right) p_4\tau_4 S_2^R S_3^R S_L^T S_O^T S_A^T\end{aligned}$$

$$\begin{aligned}Num. = {} & (0.4)(0.5)(0.9)(0.8)(0.6)(0.075)(0.8) \\ & +(0.6)(0.6)(0.66)(0.8)(0.8)(0.6)(0.075)(0.8) \\ & +(0.6)(0.4)(0.5)(0.6)(0.8)(0.9)(0.6)(0.075)(0.8) \\ Num. = {} & 0.0125,\end{aligned}$$

the denominator calculated as,

$$\begin{aligned}Denom. &= p_2\tau_2 + \left(1-p_2\right) p_3\tau_3 + \left(1-p_2\right)\left(1-p_3\right) p_4\tau_4 \\ &= (0.4)(0.5)+(0.6)(0.6)(0.66)+(0.6)(0.4)(0.5)(0.6) \\ Denom. &= 0.5096,\end{aligned}$$

and the $SAR\left(T_0\right)$ calculated as,

$$\begin{aligned}SAR\left(T_0\right) &= \frac{Num.}{Denom.} \\ &= \frac{0.0125}{0.5096} = 0.0246\end{aligned}.$$

The SAR for the control group is calculated by Eq. (6) as follows,

$$\begin{aligned}SAR\left(C_0\right) &= S_2^R S_3^R S_L^R S_O^R S_A^R \\ &= (0.8)(0.9)(0.3)(0.075)(0.9)\end{aligned}$$

$$SAR\left(C_0\right) = 0.0146$$

By the definition of Eq. (1), the T/C ratio is,

$$T/C = \frac{SAR(T_0)}{SAR(C_0)}$$

$$= \frac{0.0246}{0.0146}$$

$$T/C = 1.69$$

Calculating the T/C ratio from the numbers of fish in each of the C_0 and T_0 sub-categories (Table 6) is presented as a check of the above equation as follows,

$$T/C = \frac{\left(\frac{A_{T_0}}{T_0}\right)}{\left(\frac{A_{C_0}}{C_0}\right)} = \left(\frac{\frac{501}{(8000+1901+7603+576+230+2074)}}{\frac{70}{(960+384+3456)}}\right)$$

$$T/C = 1.69\,.$$

Table 5. Hypothetical reach survival and site-specific detection and transport probabilities:used in Example 2.

Segment	Subscript (i)	In River Survival S_i^R	Transport Route Survival S_i^T	Location (*i*)	Capture Probability p_i	Transport Probability τ_i
Rel to LGR	1	0.8		LGR (2)	0.4	0.5
LGR to LGS	2	0.8	0.9	LGS (3)	0.6	0.66
LGS to LMN	3	0.9	0.8	LMN (4)	0.5	0.6
LMN-BON (L)	L	0.3	0.6			
BON-BON	O	0.08	0.07			
BON-LGR	A	0.9	0.8			

Table 6. Number of fish in each category and sub-group calculated from the probabilities in Table 5 and a release size of 50,000 tagged fish. Shaded cells correspond to sub-categories in Figure 2.

Segment	Fish Surviving to Site, In-river **(Bold)** (Undetected in Snake R.)			Total Mortalities Between Sites	In River Mortalities to C_0 category	In River Mortalities to T_0 category	Fish Added to Barge At Site **(Bold)**	Fish in Barge At Site (**Bold**)	Mortalities in Barge Between Sites
	Total	Control Group C_0	Transport Group T_0						
Rel to **LGR**	28000						8000 (T_2)	8000	
LGR to **LGS**	7680	3840 $(C_0^2+C_0^3)$	2304 $(T_4^2+T_4^3)$	4800	960 (C_0^1)	1901 (T_3^1) 576 (T_4^1)	7603 (T_3^2)	14803	800
LGS to **LMN**	3456	3456 (C_0^3)		768	384 (C_0^2)	230 (T_4^2)	2074 (T_4^3)	13916	2961
LMN-**BON**		1037						8350	
BON-**BON**		78						626	
BON-**LGR**		70						501	

Estimation

We derived expressions for calculating $SAR(T_0)$, $SAR(C_0)$ and T/C from first principles. We started by defining each metric then applied the definitions to arrive at a mathematical expression for them. An unbiased estimator of any of the above metrics should result in an appropriate expressions presented earlier, i.e., Eq 1, 2 or 3 for T/C, $SAR(C_0)$, and $SAR(T_0)$, respectively. An unbiased estimator of T/C should reduce Eqs. (1), (19), or (20) given that only fish with no previous detection are transported, that survival is measured from LGR as juveniles to LGR as adults, that comparisons are made to a control group as defined earlier, and that no T_0 returning adults were un-transported (migrated in-river). To explain the derivation and concepts of the CSS study we used sub-categories that are not directly observable. In this section, we re-write the equations as functions of parameters that are estimable from detections of tagged fish.

Estimates of reach survival, and site-specific detection and transport probabilities are obtained by use of maximum likelihood methods described earlier. The numbers of juveniles in the transport and control groups are estimated by use of the maximum likelihood estimators (MLEs) of the survival parameters. The estimators for T_0 and C_0 are written as follows, respectively,

$$\hat{T}_0 = N_1\hat{S}_1^R\left(\hat{p}_2\hat{\tau}_2 + (1-\hat{p}_2)\hat{p}_3\hat{\tau}_3 + (1-\hat{p}_2)(1-\hat{p}_3)\hat{p}_4\hat{\tau}_4\right)$$

and

$$\hat{C}_0 = N\hat{S}_1^R(1-\hat{p}_2)(1-\hat{p}_3)(1-\hat{p}_4),$$

where the symbol ^ denotes an MLE of a parameter. The estimators for T_0 and C_0 will be unbiased if the MLEs are unbiased.

Once juveniles enter a transport barge they are not observed again until they return to Bonneville as adults. Hence, the survival probabilities S_2^T, S_3^T, S_L^T and S_O^T are not separately estimable for any of the T_i transport groups. Rather, we use the joint probability of surviving in the transport barge (from detection to release in the estuary) and subsequent marine residence to return at BON. By use of the joint probability, the expected number of adults observed at BON that were transported from LGR as juveniles is expressed as follows,

$$A_{T_2} = N_0 S_1^R p_2 \tau_2 \left(S_2^T S_3^T S_L^T S_O^T \right) S_A^T$$
$$A_{T_2} = N_0 S_1^R p_2 \tau_2 S_{BON}^{T_2} S_A^T$$

The SAR for fish in the LGR transport route is expressed as a function of estimable parameters as follows,

$$SAR\left(T_2\right) = S_{BON}^{T_2} S_A^T$$

and estimated by,

$$\widehat{SAR}\left(\hat{T}_2\right) = \hat{S}_{BON}^{T_2} \hat{S}_A^T \qquad (21)$$

where $\hat{S}_{BON}^{T_2}$ is the estimator for the joint probability $\left(S_2^T S_3^T S_L^T S_O^T \right)$.

The expected number of adult returns for juveniles that were in the LGS transport pathway is expressed as,

$$A_{T_3} = N_0 S_1^R \left(1 - p_3\right) p_3 \tau_3 S_2^R \left(S_3^T S_L^T S_O^T\right) S_A^T$$
$$A_{T_3} = N_0 S_1^R \left(1 - p_3\right) p_3 \tau_3 S_2^R S_{BON}^{T_3} S_A^T,$$

and the SAR for T_3 written as,

$$SAR\left(T_3\right) = S_2^R S_{BON}^{T_3} S_A^T,$$

and estimated by

$$\widehat{SAR}\left(\hat{T}_3\right) = \hat{S}_2^R \hat{S}_{BON}^{T_3} \hat{S}_A^T \qquad (22)$$

where $\hat{S}_{BON}^{T_3}$ is the estimator for the joint the probability that a T_3 fish returns to BON as an adult. The number of adults and the SAR for T_4 fish, the LMN transport route are expressed as follows, respectively

$$A_{T_4} = N_0 S_1^R \left(1 - p_2\right)\left(1 - p_3\right) p_4 \tau_4 S_2^R S_3^R S_{BON}^{T_4} S_A^T$$

and

$$SAR\left(T_4\right) = S_2^R S_3^R S_{BON}^{T_4} S_A^T$$

with an associated estimator for the SAR,

$$\widehat{SAR}\left(\hat{T}_4\right) = \hat{S}_2^R \hat{S}_3^R \hat{S}_{BON}^{T_4} \hat{S}_A^T \qquad (23)$$

where $\hat{S}_{BON}^{T_4}$ is the estimator for the joint probability $S_L^T S_O^T$. Hence, all of the site-specific transport $SARs$ are probabilities of making a round trip from LGR as a juvenile back to LGR as an adult.

The fish in the control group are never observed at any of the Snake River transport dams. Unlike the T_0 group, there are no direct observations of fish in the C_0 group and the number must be calculated from the estimated survival and detection probabilities. These fish may be detected in the Columbia River and will be observed upon adult return. Reach specific survival probabilities between transport sites, S_2^R and S_3^R, are estimable from detections of transported fish and non-transported fish passing through detection routes. However, for simplicity we will express the number of adult returns as follows,

$$A_{C_0} = N_0 S_1^R (1-p_2)(1-p_3)(1-p_4)\left(S_2^R S_3^R S_L^R S_O^R\right) S_A^R$$
$$A_{C_0} = N_0 S_1^R (1-p_2)(1-p_3)(1-p_4) S_{BON}^{C_0} S_A^R$$

where $S_{BON}^{C_0}$ is the joint probability $\left(S_2^R S_3^R S_L^R S_O^R\right)$. The $SAR(C_0)$ is then written as,

$$SAR(C_0) = S_{BON}^{C_0} S_A^R$$

and estimated by,

$$\widehat{SAR}\left(\hat{C}_0\right) = \hat{S}_{BON}^{C_0} \hat{S}_A^R, \qquad (24)$$

where $\hat{S}_{BON}^{C_0}$ could be calculated from the number of control group observations at Bonneville Dam and $\hat{C}_0$.

Using the above joint probabilities, the T/C ratio is expressed as follows,

$$T/C = \frac{p_2\tau_2 S_{BON}^{T_2} S_A^{T_2} + (1-p_2) p_3\tau_3 S_2^R S_{BON}^{T_3} S_A^{T_3} + (1-p_2)(1-p_3) p_4\tau_4 S_2^R S_3^R S_{BON}^{T_3} S_A^{T_4}}{S_{BON}^R S_A^R \left[p_2\tau_2 + (1-p_2) p_3\tau_3 + (1-p_2)(1-p_3) p_4\tau_4 \right]}$$

and estimated by,

$$\widehat{T/C} = \frac{\hat{p}_2\hat{\tau}_2 \hat{S}_{BON}^{T_2} \hat{S}_A^{T_2} + (1-\hat{p}_2) \hat{p}_3\hat{\tau}_3 S_2^R \hat{S}_{BON}^{T_3} \hat{S}_A^{T_3} + (1-\hat{p}_2)(1-\hat{p}_3) \hat{p}_4\hat{\tau}_4 \hat{S}_2^R \hat{S}_3^R \hat{S}_{BON}^{T_3} \hat{S}_A^{T_4}}{\hat{S}_{BON}^R \hat{S}_A^R \left[\hat{p}_2\hat{\tau}_2 + (1-\hat{p}_2) \hat{p}_3\hat{\tau}_3 + (1-\hat{p}_2)(1-\hat{p}_3) \hat{p}_4\hat{\tau}_4 \right]}. \qquad (25)$$

Example 3: Estimation of T/C ratio using estimable survival, detection, and transport probabilities.

Consider a cohort release with estimated survival, detection, and transport probabilities listed in Table 7. The $SARs$ and T/C ratio can be calculated from probabilities only using Eq. (25) . The numerator of Eq. (25) is calculated as follows,

$$\begin{aligned}\widehat{Eq(25)}_{NUM} &= \hat{p}_2\hat{\tau}_2\hat{S}_{BON}^{T_2}\hat{S}_A^{T_2} + (1-\hat{p}_2)\,\hat{p}_3\hat{\tau}_3\hat{S}_2^R\hat{S}_{BON}^{T_3}\hat{S}_A^{T_3} + (1-\hat{p}_2)(1-\hat{p}_3)\,\hat{p}_4\hat{\tau}_4\hat{S}_2^R\hat{S}_3^R\hat{S}_{BON}^{T_3}\hat{S}_A^{T_4} \\ &= (0.3)(0.5)(0.0292)(0.75) \\ &\quad +(0.7)(0.4)(0.66)(0.9)(0.0324)(0.75) \\ &\quad +(0.7)(0.6)(0.3)(0.6)(0.9)(0.8)(0.0405)(0.75)\end{aligned}$$

$$\widehat{Eq(25)}_{NUM} = 0.0033 + 0.004 + 0.0017 = 0.0090$$

the denominator calculated as,

$$\begin{aligned}\widehat{Eq.(25)}_{DENOM} &= \hat{S}_{BON}^R\hat{S}_A^R\left[\hat{p}_2\hat{\tau}_2 + (1-\hat{p}_2)\,\hat{p}_3\hat{\tau}_3 + (1-\hat{p}_2)(1-\hat{p}_3)\,\hat{p}_4\hat{\tau}_4\right] \\ &= (0.8)(0.8)(0.0638)(0.85)\left[(0.3)(0.5)+(0.7)(0.4)(0.66)+(0.7)(0.6)(0.3)(0.6)\right] \\ &= 0.03468\left[0.15+0.1848+0.0756\right] \\ \widehat{Eq.(25)}_{DENOM} &= 0.0143\end{aligned}$$

and the T/C ratio estimated by use of Eq. (25) as,

$$\widehat{T/C} = \frac{0.0090}{0.0143} = 0.631\,.$$

Table 7: Hypothetical survival, detection, and transport probabilities for Example 3.

Segment	Subscript (i)	In River Survival S_i^R	C_0 In-river route Survival	Transport Route Survival S_i^T	LGR (T_2) Transport Route Survival	LGS (T_3) Transport Route Survival	LMN (T_4) Transport Route Survival	Location (i)	Capture Probability p_i	Transport Probability τ_i
Rel to LGR	1	0.8						LGR (2)	0.3	0.5
LGR to LGS	2	0.8		0.9		0.9	0.9	LGS (3)	0.4	0.66
LGS to LMN	3	0.8		0.8			0.8	LMN (4)	0.3	0.6
LMN-BON (L)	L	0.85	0.0408	0.9	0.0292	0.0324	0.0405			
BON-BON (Ocean)	O	0.075		0.045						
BON-LGR	A	0.85	0.85	0.75	0.75	0.75	0.75			

Assumptions

Empirical results can only be inferred to a population in the context of the assumptions under which a study was conducted. Estimation of survival, detection and transport probabilities, *SARs* and *T/C* ratios require the following set of assumptions.

1. Tagged fish in the study are representative of the population.
2. All fish in a release group have equal detection and survival probabilities.
3. All fish in a release group have equal probabilities of a particular capture history.
4. Fates of individual fish are independent.
5. Previous detections have no influence on subsequent survival or detection probabilities.
6. Release numbers, capture histories, and PIT tag codes are accurately recorded and known.
7. Only detected fish are subject to transport.
8. Tagged fish removed for use in other studies are known and accurately recorded.
9. All tagged fish in a cohort release migrate through the Snake and Columbia Rivers within the same season and while the bypass facility and transport systems are operational, i.e., there is no delayed migration of tagged fish.
10. Harvest survival is the same for transported and in-river categories.

11. River conditions for same-age returns of a cohort are the same for the T_0 and C categories.

The first five assumptions are regarded as statistical in that they dictate the choice of statistical model used in parameter estimation. Assumption 1 is required when making inferences to untagged fish. If tagged fish are not representative of the run-at-large, then inferences are limited to the segment of the population most represented by tagged fish or restricted only to tagged fish. Assumptions 2 through 5 are necessary to obtain unbiased estimates of detection, survival, and transport probabilities and associated variance estimates.

Assumptions 7 through 12 are associated with elements of the CSS study and the life history characteristics fish in the study. Assumption 7 is an element of the study and was discussed earlier. Unobserved tagged fish are regarded as either mortalities or non-detects. Hence, if fish are removed for use in other studies or for monitoring, tag codes should be accurately recorded and noted so that survival and or detection probabilities are not biased. Assumption 9 is required to meet the assumption that all fish have equal detection and transport probabilities. Equations for the metrics of the CSS study were derived under this assumption and severe departures from assumption 9 will require a different set of equations. The last two assumptions are meant to assure that transport and control fish differ only with regard to the treatment, i.e., juvenile migration through transport or in-river passage. Part of the treatment includes timing of estuary and ocean entrance. However, if fish in either group are subject to different harvest probabilities or river conditions as an adult, then differences in *SARs* will not be wholly attributable to the treatment.