

## Estimating the Effects of Smolt Transportation from Different Vantage Points and Management Perspectives

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**Abstract.**—Smolt transportation is a major mitigation strategy in the Columbia River hydrosystem, yet measures of its effects on adult return rates are often unclear. Managers use a variety of transportation effect measures that need to be clearly defined and easy to understand. We develop eight alternative transportation effect measures based on a release–recapture model of juvenile and adult passive integrated transponder tag data and relate the measures to different management perspectives. The performance measures include site-specific transport–in-river ratios (*T/I*s) that view the effect of transportation operations at a site either separate from (“isolated”) or in the context of (“contextual”) the rest of the transportation system. Both relative and absolute systemwide measures of transportation effects are developed, as well as measures for fish in the release group had they been untagged. All performance measures are calculated by the program ROSTER. Transportation effect measures for summer Chinook salmon *Oncorhynchus tshawytscha* from the McCall and Pahsimeroi hatcheries released in the Snake River in 1999 range from the isolated site-specific relative value at Lower Granite Dam of 2.015 (SE = 0.152) to a systemwide relative value of 1.232 (SE = 0.036). This paper explains how these two estimates and the others are correct depending on perspective and management intent.

Transportation of salmonid smolts has been a major strategy to mitigate the effects of the Columbia and Snake river dams on salmonid migration and adult return rates since the 1970s. From 1985 to 2003, an average of 17 million smolts were transported annually. Migrating smolts are collected from the juvenile bypass system at transport dams, diverted to barges or trucks, transported downstream past the remaining dams, and released into the river downstream of Bonneville Dam (river kilometer [RKM] 234, measuring from the mouth of the Columbia River), the dam closest to the ocean (Figure 1). Currently, smolts are collected for transport at Lower Granite Dam (RKM 695), Little Goose Dam (RKM 635), and Lower Monumental Dam (RKM 589) on the Snake River and at McNary Dam (RKM 470) on the Columbia River. A number of parties have a stake in the smolt transportation program, including the Army Corps of Engineers, which operates the dams; the state, federal, and tribal agencies that manage fisheries and hatcheries; and NOAA Fisheries, which oversees the recovery of wild salmonid stocks. Hydropower managers are primarily interested in the effect of transportation operations at their dam, while fish managers are more interested in the effect of the entire transportation system on adult

returns to the fishery or hatchery. Because of its responsibility to promote the recovery of endangered salmonid populations imposed by the Endangered Species Act (1973), NOAA Fisheries has an interest in both viewpoints.

Different measures of transportation effects have evolved because of the different vantage points and management perspectives of various organizations. Alternative performance measures can differ greatly in both value and interpretation and can lead to unnecessary confusion. The purpose of this paper is to quantitatively define and compare some commonly employed estimators of transportation effects. We will show that there is not one but rather several useful measures of transportation effects—each valuable and helpful in evaluating a complex smolt transportation program from a different perspective.

Historically, the transportation effects from a particular dam have been evaluated using batch-marked fish and the relative recovery method (Ricker 1975). The relative recovery method compares smolt-to-adult return rates (SARs) from a paired release of treatment (transported) and control (nontransported, in-river) groups. The resulting measure that has typically been used to assess transportation effects is the transport–in-river ratio, *T/I*, defined as

$$\frac{T}{I} = \frac{r_T/N_T}{r_C/N_C}, \quad (1)$$

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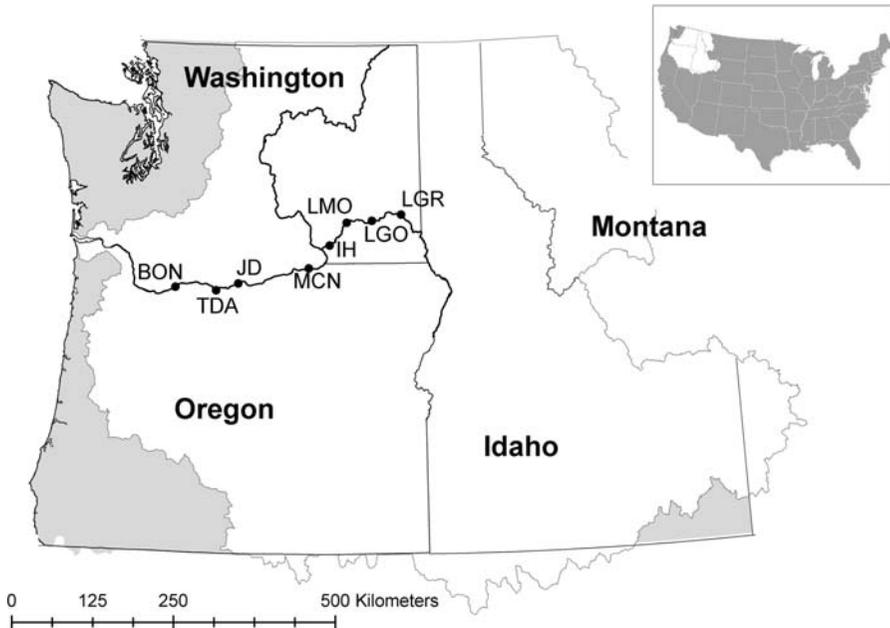


FIGURE 1.—Columbia and Snake river basins, with hydroelectric dams passed by summer Chinook salmon. Regions outside these two basins are shaded. Abbreviations of dam names are as follows: BON = Bonneville, TDA = the Dalles, JD = John Day, MCN = McNary, IH = Ice Harbor, LMO = Lower Monumental, LGO = Little Goose, and LGR = Lower Granite.

where  $N_T$  and  $N_C$  are the numbers of transported and control fish released at a dam and  $r_T$  and  $r_C$  are the corresponding numbers of subsequent adult recoveries. The relative recovery method is the basis of most of the measures of transportation effects currently used. Historically, fish in the control group have been at risk of subsequent transportation at downstream dams (Ward et al. 1997). Ward et al. suggested an ad hoc method of adjusting for the downstream transportation of the control group, assuming that any downstream transportation increases the return rate of that group.

Since the 1990s, it has been possible to estimate SARs and  $T/I$  values from equation (1) using data from passive integrated transponder (PIT) tags (Sandford and Smith 2002). Tagged smolts are detected in the juvenile bypass systems at dams. The resulting individual detection histories allow for more pointed comparisons of SARs to measure transportation effects without deliberate paired releases at each transport dam. Transported and in-river fish from a single release group may be identified from detection histories and SARs compared in terms of relative recoveries (Sandford and Smith 2002).

Two issues arise in using detection histories from PIT-tagged fish with equation (1). First, without a deliberate paired release at a dam, the size of the control group must be estimated because this group

now includes fish passing the dam undetected. Second, there is the issue of which detection histories should be used. Tagging studies estimate transportation effects for tagged fish, but often inference to an untagged population is sought. Typically, all untagged smolts entering the bypass system at a transport dam are transported, but some PIT-tagged smolts are intentionally diverted from the bypass system back to the river for study purposes. Thus, tagged and untagged smolts may experience dam passage differently, resulting in different  $T/I$  ratios for tagged and untagged fish. Sandford and Smith (2002) addressed these issues by comparing the SARs of transported fish with those of nondetected fish. The measures defined in both Sandford and Smith (2002) and Ward et al. (1997) are based on the relative recovery method and use ad hoc methods to handle the issues mentioned above. The result is a historical collection of metrics with varying properties, primarily designed to estimate dam-specific transportation effects.

In the late 1990s, detection of PIT-tagged adults became possible at several Columbia and Snake river dams. Reliable adult detections make feasible a different approach to measuring transportation effects. In particular, the combination of juvenile and adult PIT tag detections now makes it possible to incorporate transportation effects directly into a release–recapture model of the complete juvenile–adult migration

through the hydrosystem. The estimated parameters from this life cycle model can then be used to define and interpret a variety of alternative transportation effect measures.

In this paper, we briefly describe a life cycle release–recapture model that uses both juvenile and adult PIT tag detections, then define and discuss several alternative definitions and estimators of transportation effects. We compare the different measures theoretically and through an example. Finally, we compare their application in evaluating and managing a complex hydrosystem for the benefit of both fisheries and hydropower production.

### Methods

#### *Expository Example: 1999 Summer Chinook Salmon Released from the Snake River*

To compare the different transportation effect measures defined in this paper, PIT tag release and detection data from summer Chinook salmon *Oncorhynchus tshawytscha* released in the Snake River upstream of Lower Granite Dam in 1999 will be used. Release and detection data for 51,318 McCall and Pahsimeroi hatchery-raised summer Chinook salmon were obtained from the PTAGIS database maintained by the Pacific States Marine Fisheries Commission. Juvenile detections were available from Lower Granite (LGR), Little Goose (LGO), Lower Monumental (LMO), McNary (MCN), John Day (JD), and Bonneville (BON) dams, and adult detections in the years 1999, 2000, 2001, and 2002 were available from the adult fish ladders at Bonneville and Lower Granite dams. Fish were transported from LGR, LGO, LMO, and MCN (only five summer Chinook salmon were transported from MCN).

The singular purpose of this example is to demonstrate the potential differences among the various transportation effect measures presented in this paper. The example is not intended to provide definitive results for summer Chinook salmon of any other stock, hatchery or wild. Inference can be made only to the McCall and Pahsimeroi hatchery summer Chinook salmon stocks in 1999. The instructional value of this example is in the relative change in estimated values from one measure of transportation effects to another.

#### *Life Cycle Release–Recapture Model*

Buchanan (2005) developed a release–recapture model that follows PIT-tagged salmonid smolts from their release point through their juvenile out-migration, ocean stage, and adult return migration. A modification of a Cormack–Jolly–Seber model (Cormack 1964; Jolly 1965; Seber 1965), it uses both juvenile

detections during out-migration and adult detections by year of return. Because all fish in a release group are from the same juvenile cohort, the year of adult detection corresponds to age at maturity. The model uses the single release–recapture method of Skalski et al. (1998) but incorporates transportation effect parameters and adult upriver detections. It also adjusts for known removals at the dams by right-censoring the records of fish entering the sampling rooms. Estimable parameters are in-river survival for both juveniles and adults ( $S_i$  and  $S_{ij}$ , respectively, where  $i$  indicates the dam or reach and  $j$  indicates the adult age-class), joint ocean survival and age-class- $j$  maturation ( $S_{v+1,j}$ ), and site- and age-specific transportation effects ( $R_{ij}$ ) (Figure 2). The  $S_{v+1,j}$  parameters represent the joint probability of surviving in the estuary and ocean and returning to freshwater as an adult in age-class  $j$ , as well as the life stage linking smolts and adults (e.g., Bonneville-to-Bonneville survival). Dam-specific detection probabilities ( $p_i$  and  $p_{ij}$ ), censoring rates ( $c_i$  and  $c_{ij}$ ), and juvenile transportation rates ( $t_i$ ) are also estimable. Only the joint probability of survival and detection ( $\lambda_j$ ) can be estimated in the last adult reach. The likelihood is a product multinomial and can be solved numerically using the program ROSTER (River–Ocean Survival and Transportation Effects Routine) to find maximum likelihood estimates (MLEs; Table 1) and associated standard errors. In addition to estimating the model parameters, the program calculates the transportation effect measures (which are functions of the model parameters) defined in this paper. The statistical software is publicly available at <http://www.cbr.washington.edu/paramest/roster>.

#### *Estimators of Transportation Effects*

Several issues arise in defining measures of transportation effects. The first pertains to estimating the effects on untagged fish. As with any tagging study, statistical inference is limited to the fish that were tagged. From a management perspective, the desire is to project transportation effects from the tagged release group to those same fish if they had not been tagged. However, because the bypass systems at juvenile detection dams treat tagged and untagged fish differently, whether a fish is tagged or not can have an effect on its chances of transportation and subsequent return as an adult. The difference in transportation practices for tagged and untagged smolts therefore prevents direct inference of  $T/I$  ratios developed for tagged smolts to untagged smolts. Nevertheless, as long as the survival parameters ( $S_i$  and  $S_{ij}$ ) and site- and age-specific model  $T/I$  parameters ( $R_{ij}$ ) are assumed to be valid whether a smolt is tagged or not, we can derive transportation effect measures for the smolts in the

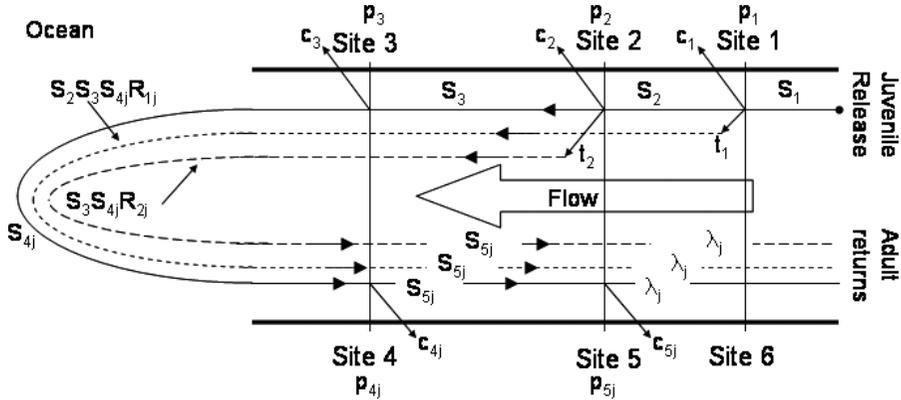


FIGURE 2.—Schematic of parameters estimated by the release–recapture PIT tag model for the study design with three juvenile detection sites (sites 1, 2, and 3), three adult detection sites (sites 4, 5, and 6), and juvenile transportation possible at sites 1 and 2. Arrows indicate migration paths. Vertical bars indicate detection sites. The parameters used in the transportation effect measures are defined in Table 1. Other parameters are the juvenile censoring rate ( $c_j$ ), age- $j$  adult detection probabilities at sites 4 and 5 ( $p_{4j}$  and  $p_{5j}$ ), age- $j$  adult censoring rates at sites 4 and 5 ( $c_{4j}$  and  $c_{5j}$ ), and age- $j$  adult “last-reach” parameters ( $\lambda_j$ ).

release group if they had not been tagged. We refer to these estimates as performance measures for untagged fish.

Assuming the detection rate of tagged smolts within the bypass system is 100% (Muir et al. 2001; Sandford and Smith 2002), the detection probability in the release–recapture model ( $p_i$ ) is simply the rate at which both tagged and untagged smolts enter the bypass system, conditional on reaching the dam (spillway and turbines combined). Prentice et al. (1990a, 1990b) found no difference in the rate at which tagged and untagged smolts enter the bypass systems. Let  $t_i''$  represent the conditional probability that an untagged smolt in the bypass system at site  $i$  is transported. Then the product  $p_i t_i''$  is the joint probability that an untagged smolt will enter the bypass system and be transported at dam  $i$ . Tagging data cannot be used to obtain an estimate of  $t_i''$ . Instead, it must be estimated from transport operations and treated as a known parameter in the transportation effect calculations.

We will derive the transportation effect measures for untagged smolts simply by replacing  $t_p$ , the conditional transportation rate for tagged smolts, with  $t_i''$ . The direct inference for these measures is to the fish in the release group had they been treated as untagged smolts. Some measures (i.e.,  $R_{ij}$  and  $R_j$ ) do not depend on  $t_i$  and so are valid for both tagged and untagged fish. The remaining measures are presented first for tagged fish and then for untagged fish.

The second issue is whether to treat a transport dam in isolation from the rest of the transportation system or in the context of that system. The Columbia River basin includes multiple transport dams, so a fish that is

not transported at one site (say, LGR) may be transported at a downriver site (say, LGO). If transportation from LGO affects adult returns, then the effect of transportation at LGR will be confounded with the effect of transportation at LGO unless the effect of transportation at LGR can be isolated from the rest of the transportation system. This “isolated” viewpoint is useful for assessing the effect of transportation from site  $i$  (e.g., LGR) relative to no transportation system whatsoever. The “contextual” viewpoint, on the other hand, treats transport site  $i$  in the context of the entire transportation system, including possible transportation from downriver dams. This viewpoint is useful for dam managers who must decide whether or not to transport smolts that are in their bypass system. The isolated and contextual viewpoints are the same for the final transport site, but differ for upriver sites. We present both isolated and contextual site-specific measures of transportation effects.

The third issue in defining measures of transportation effects is whether to measure the effects of transportation at individual sites or the overall effects of the entire transportation system. The site-specific viewpoint is useful for hydropower managers at the individual dams and is the basis of the performance measures in Ward et al. (1997) and Sandford and Smith (2002). However, that viewpoint largely ignores the importance of the proportion of smolts that are transported at the various transport dams. It might be suspected that the overall efficacy of the entire transportation system depends on the proportion of smolts entering the transportation system and the

TABLE 1.—Model parameters estimated from release–recapture data that are used to define alternative measures of transportation effects. The number of juvenile detection sites =  $v$  and the number of adult age-classes =  $w$ . Sites are numbered consecutively, so that site  $v + 1$  is the first adult detection site.

Parameter	Definition
$S_1$	Probability of survival from release point to first detection site.
$S_i$	Conditional probability of survival from detection site $i - 1$ to detection site $i$ ( $i = 2, \dots, v$ ) for in-river fish.
$S_{v+1,j}$	Conditional joint probability of surviving from site $v$ to site $v + 1$ and returning to site $v + 1$ in adult age-class $j$ ( $j = 1, \dots, w$ ).
$p_i$	Conditional probability of detection at detection site $i$ ( $i = 1, \dots, v$ ) given survival to site $i$ in-river.
$t_i$	Conditional probability of being transported from site $i$ ( $i = 1, \dots, v$ ) given detection at that site and no censoring.
$R_{ij}$	Transport–in-river ratio ( $T/I$ ) for fish transported from site $i$ ( $i = 1, \dots, v$ ) and returning in adult age-class $j$ ( $j = 1, \dots, w$ ); defines survival of transported fish relative to survival of nontransported fish.

relative effect when it occurs. Therefore, a systemwide expression of  $T/I$  is needed to convey the overall effects of transportation on smolt-to-adult returns. We present both a relative measure of the overall effect of the transportation system and an absolute measure of that effect. Taken together, these two systemwide measures give a complete picture of the effect of the entire transportation system on adult returns.

In summary, we present eight alternative measures of transportation effects: (1) isolated site- and age-specific  $T/I$  values for tagged and untagged fish ( $R_{ij}$ ), (2) isolated site-specific  $T/I$  values for tagged and untagged fish ( $R_i$ ), (3) contextual site-specific  $T/I$  values for tagged fish ( $RC_i$ ), (4) contextual site-specific  $T/I$  values for untagged fish ( $RC_i^U$ ), (5) a systemwide  $T/I$  value for tagged fish ( $R_{SYS}$ ), (6) a systemwide  $T/I$  value for untagged fish ( $R_{SYS}^U$ ), (7) an absolute systemwide transportation effect for tagged fish ( $R_{ABS}$ ), and (8) an absolute systemwide transportation effect for untagged fish ( $R_{ABS}^U$ ). The measures for untagged fish are valid for fish in the release group had they been treated as untagged. Maximum likelihood estimates of these eight measures are found by substituting maximum likelihood estimates for the parameters. Variance estimates can be found using the delta method (Seber 1982:7–9) and the estimated variance–covariance matrix from the maximum likelihood fitting routine.

*Isolated site- and age-specific T/I values for tagged and untagged fish ( $R_{ij}$ ).*—The effects of smolt transportation on adult returns are incorporated into the release–recapture model (Buchanan 2005) in terms of the site- and age-specific parameters,  $R_{ij}$ . The  $R_{ij}$  measures are the building blocks of the remaining measures of transportation effects. The  $R_{ij}$  parameter is the ratio of the age-class- $j$  adult return rates for two groups: those transported from site  $i$  (treatment group) and those not transported from site  $i$  or any other downriver transport site (control group). Thus,  $R_{ij}$  defines the survival of transported smolts relative to that of nontransported smolts. In particular, the year- $j$

adult return probability of smolts transported from site  $i$  uses the in-river survival probabilities

$$\Pr(\text{adult return in year } j \mid \text{transported from site } i) = S_{i+1} \cdots S_v S_{v+1,j} R_{ij} \tag{2}$$

Parameter  $R_{ij}$  in the release–recapture likelihood model measures the effect of smolt transportation on a returning adult age-class in isolation from the rest of the transportation system. By construction,  $R_{ij}$  eliminates the effects of any downriver transportation activities in order to examine the site- $i$ -specific effects of the transportation program. The  $R_{ij}$  parameters consider the effects of transportation only for those smolts actually transported at site  $i$ .

*Isolated site-specific T/I values for tagged and untagged fish ( $R_i$ ).*—The parameter  $R_{ij}$  is specific to age-class- $j$  adults. The age-specific  $T/I$  ratios for site  $i$  may be combined to give a site-specific  $T/I$  pooled over all adult age-classes. This site-specific transportation effect is denoted  $R_i$  and is defined as

$$R_i = \Pr(\text{adult return} \mid \text{transported from site } i) \div \Pr(\text{adult return} \mid \text{in-river from site } i; \text{no other transportation}) = \frac{\sum_{j=1}^w S_{v+1,j} R_{ij}}{\sum_{j=1}^w S_{v+1,j}} \tag{3}$$

where  $w$  is the number of adult age-classes. The control group for  $R_i$  is composed of all fish reaching site  $i$  that are not transported there or at any downriver dam. Examination of equation (3) indicates that  $R_i$  is a weighted average of the age-specific  $R_{ij}$  with weights equal to the age-specific ocean return probabilities,  $S_{v+1,j}$ . The parameter  $R_i$  is analogous to the site-specific  $T/I$  measure derived in Sandford and Smith (2002) and estimates the relative transportation effect at dam  $i$  isolated from the rest of the transportation system. Like  $R_{ij}$ ,  $R_i$  measures the effect of dam- $i$  transportation

operations unconfounded by any downriver transportation activities.

*Contextual site-specific T/I values for tagged fish (RC<sub>i</sub>).*—We define RC<sub>i</sub> as the site-specific T/I ratio for site *i*, where the denominator represents a control group that may be transported downriver, that is,

$$RC_i = \frac{\Pr(\text{adult return} \mid \text{transported from site } i)}{\Pr(\text{adult return} \mid \text{not transported from site } i)}.$$

The control group for RC<sub>i</sub> is composed of all tagged fish that survive to and pass site *i* but that are not transported there. These control fish may be transported at a downriver site, or they may migrate wholly in-river. The expression for RC<sub>i</sub> is as follows (see Appendix 1):

$$RC_i = \frac{R_i}{\sum_{k=i+1}^v \left[ p_k t_k R_k \prod_{s=i+1}^{k-1} (1 - p_s t_s) \right] + \prod_{s=i+1}^v (1 - p_s t_s)}. \tag{4}$$

The parameter  $1 - p_s t_s$  is the probability of passing site *s* without being transported there, conditional on reaching it. We interpret any product whose initial index is greater than its final index as being equal to 1. For example,  $\prod_{s=i+1}^i (1 - p_s t_s) = 1$ . The parameter RC<sub>i</sub> is equivalent to *R<sub>i</sub>* divided by the overall effect of the downriver transportation system on return rates for fish passing site *i* in-river.

In the past, RC<sub>i</sub> has been estimated by the simple relative recovery fraction in equation (1) (Ward et al. 1997). When two groups of fish are released at a dam (one transported and the other returned to the river), RC<sub>i</sub> is the ratio of SARs from the paired-release investigation. Should downriver transportation activities benefit adult returns (i.e., increase the control SAR), then the value of RC<sub>i</sub> will be smaller than that of *R<sub>i</sub>*. Conversely, should transportation activities below site *i* prove detrimental, then the value of RC<sub>i</sub> will be greater than that of *R<sub>i</sub>*. Hence, the site-specific estimates RC<sub>i</sub> are not immune to the effects of downriver transportation activities but may help a dam manager decide whether it is worthwhile to transport smolts at site *i*, given downriver transport operations. Note that by definition RC<sub>i</sub> = *R<sub>i</sub>* at the last transport site.

*Contextual site-specific T/I values for untagged fish (RC<sub>i</sub><sup>U</sup>).*—The contextual site-specific T/I ratios RC<sub>i</sub> defined above are developed for tagged fish. We denote the T/I ratios for untagged fish using the same basic notation as for tagged fish but with the superscript *U*. The untagged version of the contextual site-specific T/I ratio is

$$RC_i^U = \frac{R_i}{\sum_{k=i+1}^v \left[ p_k t_k^U R_k \prod_{s=i+1}^{k-1} (1 - p_s t_s^U) \right] + \prod_{s=i+1}^v (1 - p_s t_s^U)}. \tag{5}$$

The parameter  $1 - p_s t_s^U$  is the probability of an untagged smolt passing site *s* without being transported, conditional on reaching it. Like RC<sub>*i*</sub>, RC<sub>*i*</sub><sup>U</sup> is a site-specific T/I ratio that assesses dam-*i* transportation operations in the context of the entire downriver transportation system but for untagged rather than tagged fish. The fish described by this untagged estimator are the fish in the release group had they been handled as untagged fish in the bypass systems.

*Systemwide T/I value for tagged fish (R<sub>SYS</sub>).*—One way to define a systemwide transportation effect is to compare the return rates of smolts under the transportation system with the return rate of smolts without the transportation system. This approach compares the return rate of *all* smolts, transported or not, under an existing transportation system with the return rate estimated as if no transportation had occurred, that is, as if there had been complete in-river migration. Define *R<sub>SYS</sub>* as the systemwide T/I ratio for tagged fish, namely (see Appendix 2),

$$R_{SYS} = \frac{\Pr(\text{adult return} \mid \text{transportation system})}{\Pr(\text{adult return} \mid \text{no transportation system})} = \sum_{i=1}^v \left[ p_i t_i R_i \prod_{k=1}^{i-1} (1 - p_k t_k) \right] + \prod_{i=1}^v (1 - p_i t_i). \tag{6}$$

The measure *R<sub>SYS</sub>* is the weighted average of the isolated site-specific *R<sub>i</sub>* measures with weights equal to the migration path probabilities and using *R<sub>i</sub>* = 1 for the nontransportation path. The parameter *R<sub>SYS</sub>* represents the overall effect of the transportation system on return rates, integrating across all transport sites. It considers the return rate of the entire release group, not only that of the transported smolts. Because salmonid recovery in the Columbia River basin depends on the overall adult return rate, *R<sub>SYS</sub>* is fundamental to management of the hydrosystem. The measure *R<sub>SYS</sub>* is a function of the site-specific *R<sub>i</sub>* values and the fraction of tagged smolts arriving at a dam that are transported (*p<sub>i</sub>t<sub>i</sub>*). If the *p<sub>i</sub>t<sub>i</sub>* values are low, *R<sub>SYS</sub>* will be low even if the site-specific ratios *R<sub>i</sub>* are high. In other words, even if transportation were highly effective, the overall benefit of the transportation system would be low if only a small proportion of smolts were transported. Using equation (6), managers of the transportation system may explore the potential effects of changing bypass rates (*p<sub>i</sub>*) or conditional transportation rates (*t<sub>i</sub>*) on the expected value of *R<sub>SYS</sub>*.

Systemwide *T/I* value for untagged fish ( $R_{SYS}^U$ ).—The systemwide *T/I* for untagged fish,  $R_{SYS}^U$ , is

$$R_{SYS}^U = \sum_{i=1}^v \left[ p_i t_i^U R_i \prod_{k=1}^{i-1} (1 - p_k t_k^U) \right] + \prod_{i=1}^v (1 - p_i t_i^U). \tag{7}$$

Like  $R_{SYS}$ ,  $R_{SYS}^U$  is a weighted average of the isolated site-specific *T/I* ratios  $R_i$  but with weights equal to the migration path probabilities for untagged fish. It is a measure of the overall effect of the transportation system had the release group been treated as untagged fish passing through the hydrosystem.

*Absolute systemwide transportation effect for tagged fish ( $R_{ABS}$ ).*—The systemwide parameter  $R_{SYS}$  is useful as a relative measure, but alone it is inadequate in characterizing the effects of a smolt transportation system on adult returns. It is possible to have a large relative effect on return rates yet a small absolute change. This is especially a concern if the return rates of adult salmon are very low. Thus, an absolute measure of transportation effects is complementary to the relative measure. Define  $R_{ABS}$  as an absolute systemwide measure of the overall effect of the transportation system on adult return rates, namely,

$$R_{ABS} = \frac{\text{Pr}(\text{adult return} \mid \text{transportation system})}{\text{Pr}(\text{adult return} \mid \text{no transportation system})}. \tag{8}$$

The measure  $R_{ABS}$  is the difference in SARs between strategies (transportation system versus complete in-river migration) and hence is the absolute change in return rates due to transportation. Each term in equation (8) was derived in defining  $R_{SYS}$ , giving

$$R_{ABS} = \left( S_1 \cdots S_v \sum_{j=1}^w S_{v+1,j} \right) (R_{SYS} - 1), \tag{9}$$

where  $S_1 \cdots S_v \sum_{j=1}^w S_{v+1,j}$  is the survival rate from the juvenile release site to the first adult detection site for nontransported fish. The parameter  $R_{ABS}$  is the product of this in-river return rate and the relative increase in return rates due to the transportation system ( $R_{SYS} - 1$ ). We can also express the in-river return rate as the product of survival from release to the first transport site,  $S_{RT}$ , and in-river survival from the first transport site to the first adult site,  $S_{TA}$ , that is,

$$S_1 \cdots S_v \sum_{j=1}^w S_{v+1,j} = S_{RT} S_{TA};$$

thus,

$$R_{ABS} = S_{RT} S_{TA} (R_{SYS} - 1). \tag{10}$$

It is apparent from equation (10) that the absolute

systemwide transportation effect is proportional to  $S_{RT}$ . In other words, the potential benefit or detriment of a transportation system depends on the proportion of smolts that survive to the first transport site. None of the ratio estimators ( $R_{ij}$ ,  $R_i$ ,  $RC_i$ ,  $RC_i^U$ ,  $R_{SYS}$ , and  $R_{SYS}^U$ ) reflects survival to the transport site. From equation (10), it is obvious that if  $R_{SYS} > 1$ , then increasing natural survival to the first transport site increases  $R_{ABS}$ . The effect of changes to in-river survival downstream of the first transport site is less obvious. Because  $R_{SYS}$  is ultimately a function of the site- and age-specific *T/I* ratios  $R_{ij}$ , the value of  $R_{ABS}$  depends on downriver juvenile survival and ocean return rates for both transported and in-river fish. As a result, an increase in  $R_{ABS}$  may be due to improved returns of transported fish relative to nontransported fish ( $R_i > 1$ ), improved survival to the transport site ( $S_{RT}$ ) together with  $R_{SYS} > 1$ , higher transportation rates of bypassed fish ( $t_i$ ) together with  $R_i > 1$ , or some combination of these factors. Like  $R_{SYS}$ , the value  $R_{ABS}$  is an integrated measure of the overall effects of the transportation system compared with an in-river migration strategy. Both  $R_{SYS}$  and  $R_{ABS}$  are necessary to provide a complete picture of the overall effect of the transportation system on the return rates of tagged smolts.

*Absolute systemwide transportation effect for untagged fish ( $R_{ABS}^U$ ).*—The absolute systemwide transportation effect for untagged fish,  $R_{ABS}^U$ , is found by replacing the relative measure for tagged fish,  $R_{SYS}$ , with the relative measure for untagged fish,  $R_{SYS}^U$ , giving

$$R_{ABS}^U = (S_1 \cdots S_v \sum_{j=1}^w S_{v+1,j}) (R_{SYS}^U - 1). \tag{11}$$

Together,  $R_{ABS}^U$  and  $R_{SYS}^U$  can be used to make inferences about the effects of the transportation system on the return rates of the release group had it been treated as untagged fish throughout the hydrosystem.

*Scenario: Multiple Transport Sites*

We have derived alternative measures of transportation effects, depending on the reference group or fish of inference and the level of specificity desired (site or systemwide). The site-specific measures ( $R_i$ ,  $RC_i$ , and  $RC_i^U$ ) will be equal at some locations but not at others. Additionally, it is not always obvious whether transportation measures will be greater for tagged or untagged smolts. To clarify both these issues, we examine a theoretical transportation scenario consisting of three juvenile detection sites (dams) with transportation possible at sites 1 and 2 but not at site 3. Site 4 is the first adult detection site. The eight

transportation effects measures are compared for this scenario.

**Results**

*Scenario: Multiple Transport Sites*

With two transport sites, there are six site-specific *T/I* ratios ( $R_1, RC_1, RC_1^U, R_2, RC_2,$  and  $RC_2^U$ ) and four systemwide transportation effect measures ( $R_{SYS}, R_{SYS}^U, R_{ABS},$  and  $R_{ABS}^U$ ). Because there is no transportation site downstream of site 2 (i.e.,  $t_3 = t_3^U = 0$ ), we expect the site-specific isolated and contextual *T/I* ratios to be equal for site 2 (i.e.,  $R_2 = RC_2 = RC_2^U$ ). However, because of the transportation at site 2, (i.e.,  $t_2, t_2^U > 0$ ), we expect the site-specific isolated and contextual *T/I* ratios for site 1 (i.e.,  $R_1, RC_1,$  and  $RC_1^U$ ) to differ. The site-specific *T/I* ratios for tagged and untagged fish are

$$R_1 = \frac{\sum_{j=1}^w S_{4j}R_{1j}}{\sum_{j=1}^w S_{4j}} \quad R_2 = \frac{\sum_{j=1}^w S_{4j}R_{2j}}{\sum_{j=1}^w S_{4j}}$$

$$RC_1 = \frac{R_1}{1 - p_2t_2(1 - R_2)} \quad RC_2 = \frac{R_2}{1 - p_3t_3} = R_2$$

$$RC_1^U = \frac{R_1}{1 - p_2t_2^U(1 - R_2)} \quad RC_2^U = \frac{R_2}{1 - p_3t_3^U} = R_2.$$

As expected, the isolated and contextual *T/I* ratios are equal for both tagged and untagged smolts at site 2 owing to the absence of subsequent downstream transportation. However, the contextual *T/I* ratios ( $RC_1$  and  $RC_1^U$ ) differ from the isolated value ( $R_1$ ) at site 1 because of transportation at site 2. If site-2 transportation increases adult return rates (i.e.,  $R_2 > 1$ ), then both  $RC_1 < R_1$  and  $RC_1^U < R_1$  because the return rates of site-1 control fish are augmented by transportation from site 2. In general, the site-specific *T/I* ratios (i.e.,  $R_i, RC_i,$  and  $RC_i^U$ ) will be equal for the final transport site but not for upriver transport sites.

Typically, a larger proportion of untagged smolts than tagged smolts are transported (i.e.,  $t_i^U > t_i$ ). If this is true for site 2, and if site-2 transportation increases adult return rates (i.e.,  $R_2 > 1$ ), then  $RC_1^U < RC_1$  because a larger proportion of the untagged control fish from site 1 are transported at site 2 than the tagged control fish. On the other hand, if  $t_2^U > t_2$  but site-2 transportation decreases adult return rates (i.e.,  $R_2 < 1$ ), then  $RC_1^U > RC_1$ . This is because the untagged control fish from site 1 are at greater risk of the detrimental transportation at site 2 than are the tagged control fish from site 1. Obviously, the relative sizes of the tagged and untagged site-specific *T/I* ratios depend on both

conditional transportation rates ( $t_i, t_i^U$ ) and isolated *T/I* ratios ( $R_i$ ) for downstream sites.

The systemwide transportation effect measures for tagged and untagged smolts are as follows:

$$R_{SYS} = p_1t_1R_1 + (1 - p_1t_1)[1 - p_2t_2(1 - R_2)]$$

$$R_{SYS}^U = p_1t_1^UR_1 + (1 - p_1t_1^U)[1 - p_2t_2^U(1 - R_2)]$$

$$R_{ABS} = S_1S_2S_3 \sum_{j=1}^w S_{4j} \{ p_1t_1R_1 + (1 - p_1t_1) \times [1 - p_2t_2(1 - R_2)] - 1 \}$$

$$R_{ABS}^U = S_1S_2S_3 \sum_{j=1}^w S_{4j} \{ p_1t_1^UR_1 + (1 - p_1t_1^U) \times [1 - p_2t_2^U(1 - R_2)] - 1 \}.$$

With the addition of more transport sites, the expressions for the systemwide transportation effect measures become more complex and it becomes increasingly difficult to make general observations from these expressions. However, we see that either both the systemwide measures for untagged smolts will be greater than those for tagged smolts (i.e.,  $R_{SYS}^U > R_{SYS}$  and  $R_{ABS}^U > R_{ABS}$ ) or they will both be smaller (i.e.,  $R_{SYS}^U < R_{SYS}$  and  $R_{ABS}^U < R_{ABS}$ ). How the transport measures for untagged smolts will compare with those for tagged smolts depends on the isolated  $R_i$  values and the transportation fractions for both tagged and untagged smolts (i.e.,  $p_i t_i$  and  $p_i t_i^U$ , respectively). In general, we cannot assume that the transportation effect measures for untagged smolts will necessarily be greater than those for tagged smolts.

*The Summer Chinook Salmon Example Revisited*

From the release of 51,318 PIT-tagged, hatchery-raised summer Chinook salmon smolts, a total of 26,274 were detected during out-migration at one or more of the six juvenile detection sites (Table 2). Of these detected smolts, 10,538 were ultimately transported, 14,526 were returned to the river after juvenile detection, and 1,210 were censored because they were rehandled at the dams. A total of 1,007 unique adults were detected during upstream migration at either Bonneville or Lower Granite dam. Of these detected adults, 472 were transported as juveniles and 535 were not transported (Table 2).

In performing the release–recapture analysis (Table 3), adult returns in 1999 and 2000 (i.e., “jacks” and “1-oceans”) were pooled (age-class 1), with the adults returning in 2001 and 2002 forming age-classes 2 and 3, respectively. No fish transported at LMO returned as age-class-1 adults (i.e., 1999 or 2000 returns). The

MLE of  $R_{31}$  (see Table 3) is therefore 0, but because of the very small number of smolts transported from LMO,  $R_{31}$  would need to be greater than 1.5 for the expected number of transported smolts detected as age-class-1 adults to be greater than 1. With too few smolts transported at LMO to detect any moderate effect on adult returns to age-class 1, we assumed that transportation at LMO had no effect on returns to this age-class and set  $R_{31}$  to 1 for the purpose of estimating the remaining transportation effect values. Only five summer Chinook salmon were transported from MCN, so no transportation effect could reasonably be estimated for that site; therefore, for the purposes of this example, the five smolts were considered censored. In estimating  $T/I$  values for untagged fish, we assumed that all bypassed untagged smolts were transported at LGR, LGO, and LMO (i.e.,  $t_1^U = t_2^U = t_3^U = 1$ ). We tested for homogeneity of adult detections with respect to treatment (transported or in-river) and found no evidence of a transportation effect on adult detections or survival upriver of BON ( $\chi^2 = 5.337$ ,  $df = 6$ ,  $P = 0.5014$ ). This suggested that any transportation effects ended at BON, the first adult detection site. We therefore pooled all adult detections across transport treatment groups above BON (Table 2) and estimated common adult parameters by site and age-class (i.e.,  $p_{7j}$ ,  $\lambda_j$ ). All transportation effects were estimated to BON; because of the homogeneity of adult detections upriver, the estimated  $T/I$  ratios also apply to returns to LGR.

Site-specific values of the isolated  $T/I$  ratio  $R_i$  were highest at LGR ( $\hat{R}_1 = 2.015$ ,  $\widehat{SE} = 0.152$ ), intermediate at LGO ( $\hat{R}_2 = 1.396$ ,  $\widehat{SE} = 0.112$ ), and lowest at LMO ( $\hat{R}_3 = 1.098$ ,  $\widehat{SE} = 0.403$ ) (Table 4). If transportation is beneficial, we would expect the isolated  $R_i$  ratios to be higher for upriver transport sites because groups transported from upriver sites avoid more dams than groups transported from downriver sites. Thus,  $R_i$  reflects the relative location of site  $i$  in the hydrosystem as well as the effectiveness of the transportation operations at site  $i$ . The difference between the isolated and contextual site-specific  $T/I$  ratios was greatest at LGR:  $\hat{R}_1 = 2.105$  versus  $\widehat{RC}_1 = 1.857$  (Table 4). The difference in the isolated and contextual values of the  $T/I$  ratio at LGR is because substantial smolt transportation occurred downriver at LGO with a  $T/I$  ratio greater than 1 (i.e.,  $\hat{R}_2 = 1.396$ ,  $\widehat{SE} = 0.112$ ). The isolated and contextual site-specific  $T/I$  ratios at LGO were nearly identical ( $\hat{R}_2 = 1.396$ ,  $\widehat{SE} = 0.112$ ;  $\widehat{RC}_2^U = 1.395$ ,  $\widehat{SE} = 0.112$ ) because downriver transportation at LMO was inconsequential, with a  $T/I$  ratio of approximately 1 (i.e.,  $\hat{R}_3 = 1.098$ ,  $\widehat{SE} = 0.403$ ) (Tables 3, 4).

The contextual  $T/I$  ratios for tagged and untagged fish were slightly different at both LGR ( $\widehat{RC}_1 = 1.857$ ,

$\widehat{SE} = 0.134$ ;  $\widehat{RC}_1^U = 1.665$ ,  $\widehat{SE} = 0.200$ ) and LGO ( $\widehat{RC}_2^U = 1.395$ ,  $\widehat{SE} = 0.112$ ;  $\widehat{RC}_2^U = 1.348$ ,  $\widehat{SE} = 0.215$ ). For both LGR and LGO,  $\widehat{RC}_i^U < \widehat{RC}_i$  because a larger proportion of the untagged control fish benefited from downriver transportation than tagged control fish. The difference between the tagged and untagged ratios was greater at LGR than LGO because transportation at LGO appeared more beneficial for LGR control fish than transportation at LMO for LGO control fish.

For this release of tagged summer Chinook salmon smolts in 1999, the estimated systemwide  $T/I$  ratio ( $\hat{R}_{SYS}$ ) was 1.232 ( $\widehat{SE} = 0.036$ ) with an asymptotic 95% confidence interval of 1.164–1.303. This means that the smolt-to-adult return rate of this release group was estimated to be 23% higher than it would have been with no transportation. Had these smolts been untagged, the estimated systemwide  $T/I$  ratio ( $\hat{R}_{SYS}^U$ ) would have been 1.386 ( $\widehat{SE} = 0.088$ ) (Table 4). The benefit of transportation would be greater for untagged than for tagged smolts because of the assumption that all untagged fish entering the bypass system were transported. The estimated absolute systemwide transportation effect ( $\hat{R}_{ABS}$ ) was an increase of 0.0045 (i.e., 0.45%;  $\widehat{SE} = 0.0006$ ) in the SAR for tagged fish. For reference, the overall return rate to BON for the 1999 release was 0.0236 (2.36%;  $\widehat{SE} = 0.0009$ ). The estimated absolute improvement in SAR for these fish if untagged ( $\hat{R}_{ABS}^U$ ) was 0.0074 (0.74%;  $\widehat{SE} = 0.0015$ ).

### Discussion

Different management perspectives require different measures of the transportation effect. It is important to clearly specify which performance measures are being used in a given situation. As illustrated by the Snake River summer Chinook salmon example, the different transportation effect measures can vary from a relative systemwide measure of  $\hat{R}_{SYS} = 1.232$  to the isolated site-specific measure of  $\hat{R}_1 = 2.015$  to the site- and age-specific value of  $\hat{R}_{33} = 3.003$  (Table 4). Thus, confusion may arise unless the type of measure being used is clearly identified.

The appropriate choice of transportation effect measure depends on the context of the application. However, some general observations apply. First, managers and scientists are primarily interested in the effects of transportation on an untagged population rather than the experimental tagged population. Also, the site- and age-specific  $T/I$  ratios  $R_{ij}$  are useful primarily for model parameterization and defining the site-specific and systemwide  $T/I$  ratios. Unless the focus is the interaction between transportation and age of return, attention should be directed to either the site-specific values ( $R_i$  or  $RC_i^U$ ) or the systemwide values ( $R_{SYS}^U$  and  $R_{ABS}^U$ ).

TABLE 2.—Modified *M*-array (Burnham et al. 1987) for summer Chinook salmon from the McCall and Pahsimeroi hatcheries released in the Snake River above Lower Granite Dam (LGR) in 1999. Other dam abbreviations are as follows: LGO = Little Goose, LMO = Lower Monumental, MCN = McNary, JD = John Day, and BON = Bonneville. Adult age-classes are as follows: 1 = 1999 and 2000 adults; 2 = 2001 adults, and 3 = 2002 adults. The first column identifies the release site for the row. Transport sites have two release rows; the first is for the nontransported group, the second for the transported group (Tr).

Site and category	Release	Adult detection sites (age-class)												Number detected
		Juvenile detection sites						BON			LGR			
		LGR	LGO	LMO	MCN	JD	BON	1	2	3	1	2	3	
Initial release	51,318	7,311	11,495	4,142	1,964	552	810	2	30	8	19	65	16	26,414
LGR	1,896		835	285	156	46	57	0	3	0	0	5	2	1,389
LGR-Tr	5,007							5	75	7	26	126	19	258
LGO	6,772			2,415	1,087	295	348	0	9	3	3	28	3	4,191
LGO-Tr	5,350							6	58	8	20	98	19	209
LMO	6,317				1,718	574	546	1	22	4	8	40	6	2,919
LMO-Tr	176							0	1	1	0	2	1	5
MCN	4,739					712	628	2	21	2	15	37	7	1,424
MCN-Tr	5							0	0	0	0	0	0	0
JD	2,115						320	1	11	2	5	23	2	364
BON														
Juvenile	2,709							2	36	2	10	69	11	130
Age-class 1	19										17			17
Age-class 2	266											217		217
Age-class 3	37												28	28
Number detected		7,311	12,330	6,842	4,925	2,179	2,709	19	266	37	123	710	114	
Number censored		408	208	349	181	64	0	0	0	0				

Each of the measures  $R_i$ ,  $RC_i^U$ ,  $R_{SYS}^U$ , and  $R_{ABS}^U$  is useful for management from a particular perspective. Fish managers are concerned with the overall effect of the transportation program, so they may use the systemwide measures. They may also consider the isolated site-specific ratios together with the bypass rates ( $p_i$ ) and conditional transportation rates ( $t_i^U$ ) to identify which dams drive the systemwide estimates. For example, the systemwide  $T/I$  ratio for the 1999 summer Chinook salmon data was 1.386 based on the assumption of 100% transportation of untagged smolts in the bypass system ( $t_i^U = 1$ ). The isolated  $T/I$  ratio at LGR was considerably higher, at  $\hat{R}_1 = 2.015$ , but the bypass (i.e., detection) rate at LGR was low ( $\hat{p}_1 = 0.2190$ ). Both LGO and LMO had higher bypass rates ( $\hat{p}_2 = 0.4832$ ,  $\hat{p}_3 = 0.3646$ ) but lower site-specific  $T/I$  ratios ( $\hat{R}_2 = 1.396$ ,  $\hat{R}_3 = 1.098$ ). Thus, the relatively low bypass rate and high  $T/I$  ratio at LGR are balanced by the relatively high bypass rates and low  $T/I$  estimates at LGO and LMO, giving the systemwide measure ( $R_{SYS}^U = 1.386$ ).

Managers of specific dams have a more localized viewpoint and are interested primarily in the effects of their dam operations on survival and return rates. The values  $p_i$ ,  $t_i^U$ , and  $RC_i^U$  give that information. For example, the contextual  $T/I$  ratio for untagged fish at LGR ( $RC_1^U$ ) was estimated as 1.665 ( $\widehat{SE} = 0.200$ ), while the contextual  $T/I$  ratio for untagged fish at LMO ( $RC_3^U$ ) was estimated as 1.098 ( $\widehat{SE} = 0.403$ ). Thus, it appears that LGR transportation in 1999 positively affected

adult returns, but it is less obvious that LMO transportation affected adult returns. While dam managers are interested in site-specific measures, fishery and hatchery managers are generally more interested in survival through the entire hydrosystem and adult return rates. The transportation effect measures reflecting these viewpoints are  $R_{SYS}^U$  and  $R_{ABS}^U$ .

In the 1999 summer Chinook salmon example, the effects of transportation were discernible only as far as Bonneville Dam. However, juvenile transportation may increase adult straying rates, thus decreasing perceived upriver adult survival. Extending the transportation effect measures to include adult effects upstream of Bonneville requires additional upriver adult survival parameters distinguished by treatment group, reach, and age-class. Program ROSTER can be used to estimate these adult parameters and test for transportation effects upriver. The result is an even more complex set of transportation effect measures from which to choose.

Although our approach is not the first to use PIT tag data to estimate transportation effects, it is the first to define transportation effect measures in terms of probability parameters estimated from a life cycle model. Sandford and Smith (2002) used PIT tag data to estimate SARs for fish following different migration routes (e.g., transported, detected but not transported, and never detected), which enabled them to estimate transportation effect measures by comparing SARs for transported and nontransported fish.

TABLE 3.—Maximum likelihood estimates for summer Chinook salmon from the McCall and Pahsimeroi hatcheries released in the Snake River upstream of Lower Granite Dam in 1999. The first (or only) subscript indicates the detection site: 1 = Lower Granite (juvenile), 2 = Little Goose, 3 = Lower Monumental, 4 = McNary, 5 = John Day, 6 = Bonneville (juvenile), 7 = Bonneville (adult), 8 = Lower Granite (adult). Where present, the second subscript indicates the adult age-class: 1 = 1999 and 2000 adults, 2 = 2001 adults, and 3 = 2002 adults.

Category	Parameter	Estimate	Standard error
Juvenile survival	$S_1$	0.6506	0.0076
	$S_2$	0.9123	0.0135
	$S_3$	0.9403	0.0125
	$S_4$	0.9093	0.0197
	$S_5$	1.1069	0.0535
	$S_6$	0.6162	0.0536
Juvenile detection	$p_1$	0.2190	0.0033
	$p_2$	0.4832	0.0043
	$p_3$	0.3646	0.0052
	$p_4$	0.2969	0.0065
	$p_5$	0.1200	0.0059
	$p_6$	0.2430	0.0185
Conditional transportation rate	$t_1$	0.7253	0.0054
	$t_2$	0.4413	0.0045
	$t_3$	0.0271	0.0020
	$t_4$	0.0011	0.0005
Age-specific joint ocean survival and maturation	$S_{71}$	0.0067	0.0011
	$S_{72}$	0.0410	0.0038
	$S_{73}$	0.0075	0.0012
Adult detection	$p_{71}$	0.1382	0.0312
	$p_{72}$	0.3056	0.0173
	$p_{73}$	0.2456	0.0404
Final reach	$\lambda_1$	0.8947	0.0704
	$\lambda_2$	0.8158	0.0238
	$\lambda_3$	0.7567	0.0706
Site- and age-specific $T/I^a$	$R_{11}$	1.9079	0.4131
	$R_{12}$	2.1083	0.1816
	$R_{13}$	1.6000	0.3709
	$R_{21}$	1.3663	0.3115
	$R_{22}$	1.3971	0.1306
	$R_{23}$	1.4187	0.3229
	$R_{32}$	0.7678	0.4125
	$R_{33}$	3.0031	1.9928

<sup>a</sup> Transport-in-river ratio.

This relative recovery approach is appropriate for a site-specific focus, but it is not appropriate for a systemwide focus unless assumptions are made about in-river and barge survival. Our model-based approach provides greater flexibility in focus (site-specific or systemwide) and perspective (isolated or contextual) when estimating transportation effects. It also provides an easy and flexible way of generating estimates for untagged fish that are represented by the release group, but, unlike Sandford and Smith (2002), it does not require that all untagged fish be transported at the first transport dam they bypass. Additionally, the model-based approach provides easily computed standard errors and is more transparent than the semiparametric approaches used by Ward et al. (1997) or Sandford and Smith (2002). It should be noted that the modeling approach was not possible before reliable adult PIT tag detection became available.

The release-recapture modeling approach taken here may be used to address additional research concerns. For example, it is possible to define measures of delayed differential mortality ( $D$ ) using model parameters, where  $D$  is the ratio of the post-Bonneville survival rate for transported fish to the analogous rate for nontransported fish (Budy et al. 2002). Just as there are multiple perspectives and definitions of transportation effect measures, so there are multiple definitions of  $D$ . There are limits to what can be learned from this type of modeling, however. While the model allows for comparison of return rates with and without the transportation system (e.g.,  $R_{SYS}$ ), it is unable to compare return rates with and without the hydrosystem. Dam removal would affect in-river and ocean survival in ways not estimable by the model presented here.

Because of the large sample sizes likely to be

TABLE 4.—Observed transportation effect measures for summer Chinook salmon from the McCall and Pahsimeroi hatcheries released in the Snake River upriver of Lower Granite Dam in 1999. Values given are ratios or differences of probabilities rather than percentages. Where present, the second subscript indicates the adult age-class: 1 = 1999 and 2000 adults, 2 = 2001 adults, and 3 = 2002 adults. Standard errors are in parentheses.

Site	Transportation effect measures									
	$R_{i1}$	$R_{i2}$	$R_{i3}$	$R_i$	$RC_i$	$RC_i^U$	$R_{SYS}$	$R_{SYS}^U$	$R_{ABS}$	$R_{ABS}^U$
Lower Granite	1.908 (0.413)	2.108 (0.182)	1.600 (0.371)	2.015 (0.152)	1.857 (0.134)	1.665 (0.200)				
Little Goose	1.366 (0.312)	1.397 (0.131)	1.419 (0.323)	1.396 (0.112)	1.395 (0.112)	1.348 (0.215)				
Lower Monumental	1 <sup>a</sup>	0.768 (0.412)	3.003 (1.993)	1.098 (0.403)	1.098 (0.403)	1.098 (0.403)				
Systemwide							1.232 (0.036)	1.386 (0.088)	0.0045 (0.0006)	0.0074 (0.0015)

<sup>a</sup> Parameter set to 1; no standard error estimated.

needed for this model, it is tempting to combine fish from multiple sources to form a large release group. However, maturity and survival rates in the estuary and ocean vary with origin as well as with migration timing, species, run, and rearing type. Additionally, bypass and transportation rates and effects may depend on smolt size. Pooling release groups over these factors will result in estimates that are weighted averages of the actual estimates for the different release groups. The natural heterogeneity in migration parameters across factors such as stock, rearing type, and migration timing indicates that researchers should avoid combining release groups across such factors.

The complexity of a multilocation smolt transportation system requires an array of performance measures to adequately characterize both site-specific and systemwide effects. A life cycle, release–recapture model was used to describe basic survival, detection, diversion, and transportation processes for PIT-tagged fish. We have demonstrated how this basic sampling model can subsequently be used to carefully formulate and compare measures of transportation effects. This quantitative approach defines exactly what is being estimated and helps avoid unnecessary duplication or confusion. By the invariant property of maximum likelihood estimation and the desirable asymptotic properties of minimum variance, unbiasedness, and normality, this model-based strategy provides fishery managers with a convenient yet powerful approach to describing complex resource management problems and communicating results in a statistically defensible manner.

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**Appendix 1: Derivation of the Contextual Site-Specific  $T/I$  Ratio for Tagged Fish ( $RC_i$ )**

The transportation effect measure  $RC_i$  is defined as

$$RC_i = \frac{\Pr(\text{adult return} \mid \text{transported from site } i)}{\Pr(\text{adult return} \mid \text{not transported from site } i)}.$$

The numerator can be expressed using the isolated  $T/I$  ratio,  $R_i$ , namely,

$$\begin{aligned} &\Pr(\text{adult return} \mid \text{transported from site } i) \\ &= S_{i+1} \cdots S_v R_i \sum_{j=1}^w S_{v+1,j}. \end{aligned} \tag{A.1.1}$$

The denominator is

$$\begin{aligned} &\sum_{j=1}^w \Pr(\text{adult return in year } j \mid \text{not transported at site } i) \\ &= \sum_{j=1}^w \left[ \Pr(\text{transported downstream, return in year } j \mid \text{not transported at site } i) \right. \\ &+ \left. \Pr(\text{not transported downstream; return in year } j \mid \text{not transported at site } i) \right] \\ &= \sum_{j=1}^w \left[ S_{i+1} \cdots S_v S_{v+1,j} \left\{ \sum_{k=i+1}^v \left[ p_k t_k R_{kj} \prod_{s=i+1}^{k-1} (1 - p_s t_s) \right] \right. \right. \\ &\quad \left. \left. + \prod_{s=i+1}^v (1 - p_s t_s) \right\} \right], \end{aligned}$$

where  $1 - p_s t_s$  is the probability of passing site  $s$  without being transported, conditional upon reaching it. We interpret any product whose initial index is greater than its final index as being equal to 1. For example,

$$\prod_{s=i+1}^i (1 - p_s t_s) = 1.$$

Then,

$$\begin{aligned} RC_i &= \left( S_{i+1} \cdots S_v R_i \sum_{j=1}^w S_{v+1,j} \right) \\ &\div \left[ \sum_{j=1}^w \left[ S_{i+1} \cdots S_v S_{v+1,j} \left\{ \sum_{k=i+1}^v \left[ p_k t_k R_{kj} \prod_{s=i+1}^{k-1} (1 - p_s t_s) \right] \right. \right. \right. \\ &\quad \left. \left. + \prod_{s=i+1}^v (1 - p_s t_s) \right\} \right] \right] \\ &= \frac{R_i}{\sum_{k=i+1}^v \left[ p_k t_k R_k \prod_{s=i+1}^{k-1} (1 - p_s t_s) \right] + \prod_{s=i+1}^v (1 - p_s t_s)}. \end{aligned} \tag{A.1.2}$$

**Appendix 2: Derivation of the Systemwide  $T/I$  Ratio ( $R_{SYS}$ )**

The systemwide  $T/I$ ,  $R_{SYS}$ , is defined as

$$R_{SYS} = \frac{\Pr(\text{adult return} \mid \text{transportation system})}{\Pr(\text{adult return} \mid \text{no transportation system})}. \tag{A.2.1}$$

There is only one juvenile migration path that smolts can follow if they are to return as adults in a system without transportation: they must survive in-river from the initial juvenile release point and return to the first adult detection site. This gives the probability of returning in the denominator as simply

$$S_1 \cdots S_v \sum_{j=1}^w S_{v+1,j}.$$

Smolts that migrate in a system with transportation, on the other hand, have multiple migration routes depending on the transport sites. They may migrate wholly in-river, or they may be transported from any one of the transport sites. The numerator of equation (A.2.1) can be expressed as follows:

$\Pr(\text{adult return} \mid \text{transportation system})$

$$\begin{aligned} &= \sum_{i=1}^v \left[ S_i p_i t_i S_{i+1} \cdots S_v \left( \sum_{j=1}^w S_{v+1,j} R_{ij} \right) \right. \\ &\quad \left. \times \prod_{k=1}^{i-1} S_k (1 - p_k t_k) \right] \\ &+ \left( \sum_{j=1}^w S_{v+1,j} \right) \prod_{i=1}^v S_i (1 - p_i t_i) \\ &= S_1 \cdots S_v \sum_{j=1}^w S_{v+1,j} \left\{ \sum_{i=1}^v \left[ p_i t_i R_i \prod_{k=1}^{i-1} (1 - p_k t_k) \right] \right. \\ &\quad \left. + \prod_{i=1}^v (1 - p_i t_i) \right\}. \end{aligned} \tag{A.2.2}$$

Dividing the adult return probability under the transportation system in expression (A.2.2) by the probability of adult return without the transportation system gives

$$R_{SYS} = \sum_{i=1}^v \left[ p_i t_i R_i \prod_{k=1}^{i-1} (1 - p_k t_k) \right] + \prod_{i=1}^v (1 - p_i t_i). \tag{A.2.3}$$