This report was funded by the Bonneville Power Administration (BPA), U.S. Department of Energy, as part of BPA's program to protect, mitigate, and enhance fish and wildlife affected by the development and operation of hydroelectric facilities on the Columbia River and its tributaries. The views in this report are the author's and do not necessarily represent the views of BPA.

For additional copies of this report, write to:

Bonneville Power Administration
Public Information Office - ALP-22
P.O. Box 3621
Portland, OR 97208

Please include title, author, and DOE/BP number from back cover in the request.

ASSESSMENT OF THE FLOW-SURVIVAL RELATIONSHIP OBTAINED BY SIMS AND OSSIANDER (1981) FOR SNAKE RIVER SPRING/SUMMER CHINOOK SALMON SMOLTS

FINAL REPORT

Prepared by:
Cleveland R. Steward

under subcontract to

S.P. Cramer and Associate& Inc.

Prepared for:

U.S. Department of Energy
Bonneville Power Administration
Division of Fish and Wildlife
P.O. Box 3621
Portland, OR 97208-362 1

Project Number 93-013
Contract Number DE-AM79-93BP99654
Task Order Number DE-AT79-93BP00121

APRIL 1994

EXECUTIVE SUMMARY

This report critiques the methods, assumptions, and data which underpin the relationship between chinook smolt survival and river flow within the Snake and Columbia Rivers, as reported by Sims and Ossiander (198 1). Those authors obtained the linear relationship *log* Y = 2.488 + 0.395 log X, where Y is per-project survival, expressed as a percentage, and X is Snake River flow in thousands of cubic feet per second. Seven data pairs were used to derive the relationship; the pairs represented single season flow and survival values for the years 1973 through 1979. In each of these years, experiments were conducted to determine the percentage of chinook surviving between the forebay of the first dam encountered on the Snake River (Little Goose Dam in 1973-1974 and Lower Granite Dam thereafter) and either The Dalles Dam (1973- 1975) or John Day Dam (1976- 1979) on the Columbia River. Sims and Ossiander (198 1) calculated per-project survival -- the dependent variable – as the n^{th} root of the overall survival value, where n is the number of dams in place at the time. The independent variable was the mean daily flow at Ice Harbor Dam over the two week period centered on the date on which 50% of the annual smolt migration had passed that dam.

The basic experimental protocol used in smolt survival studies was to brand and release actively migrating chinook and steelhead at upstream locations (either trap sites or forebays of dams) and then to monitor the number of marked fish passing one or more dams downstream. Several "treatment" groups of chinook salmon were distinctively marked and released over the course of the outmigration. For each treatment group, survival was calculated as the fraction recovered at the downstream dam, adjusted for the collection (i.e., sampling) efficiency at that dam. Sampling efficiency was estimated by releasing marked groups of control fish immediately upstream of the dam and determining the fraction recovered. If sampling efficiency is designated e, and the fraction of treatment fish recovered is c, survival ($\hat{s}_i$) is calculated as

$$\hat{s} = \frac{c}{e} x \; 100$$

This formula was applied to mark-recovery data obtained for individual treatment-control groups and to data summed across all treatment and control groups.

Sampling efficiency at the dams varied with the sampling method used, with the biological characteristics of the chinook smolts and, in particular, with the relative amounts of water diverted through the powerhouse and over the spillway. In 1973-1975, a "flow-efficiency" curve was used to predict sampling efficiency at Ice Harbor Dam as a function of flow. Use of the curve was discontinued in 1975 after additional turbines were installed at the dam. In subsequent years, and at all other sampling locations, sampling efficiency was estimated by periodically releasing control fish above the recovery sites.

Although the original intent was to estimate survival for individual groups of chinook salmon, recovery rates were often too low or variable to enable group survival estimates. Even in years when sufficient data were collected, sample means and variances were not reported. Raymond (1979) calculated an "average" annual survival for 1973- 1975 by weighting group survival rates by the proportion of the unmarked fish present so that, for example, survival measured at the peak of the outmigration was weighted more heavily than survival measured at other times.

There is no evidence that proportional weighting was used in later years. Single season survival estimates were obtained by combining mark-recovery data across groups. These estimates may not have been representative of the run-at-large since there was no indication that experimental releases corresponded in frequency and timing to that of the unmarked population.

Overall survival in 1973-1976 was calculated as the product of survival rates determined independently for reaches above and below Ice Harbor Dam. Although sampling continued at Ice Harbor Dam in subsequent years, no experimental releases were made from that dam after 1976 that would have enabled lower river survival estimates. Raymond and Sims (1980) indicated that overall survival for 1977- 1979 was estimated by adjusting the observed recovery rate of treatment fish released into the forebay of Lower Granite Dam by their expected recovery rate at John Day Dam, as determined from measures of sampling efficiency. This appears to contradict earlier reports which implied that survival was calculated from the ratio of smolt population sizes at upper and lower dams, taking into account the number of fish collected and transported at Lower Granite and Little Goose Dams (Sims et al. 1976, 1977, 1978). For example, Sims et al. (1978) provided the formula

$$\bar{s} = [N_{lower} / (N_{upper} - T)] \times 100$$

where N_{upper} and N_{lower} are the estimates of the total number of smolts passing Lower Granite and John Day (or The Dalles) dams, respectively, and T is the number of smolts transported at intervening dams. Application of this formula to smolt abundance and transportation data found in Sims et al. (1976, 1977, 1978) and Raymond and Sims (1980) yielded survival estimates that agree precisely with those reported in the same documents.

After examining the original mark-recovery data files, it was determined that experimental releases necessary to estimate survival from Ice Harbor to either John Day or The Dalles were not made in 1977-1979. Therefore, the smolt population size at John Day could not be calculated by multiplying the lower river survival rate by the total number of smolts estimated to have passed Ice Harbor. However, it is also clear that the population size at John Day could not be directly ascertained since an unknown number of smolts from the upper Columbia River were mixed into the population. Population sizes at John Day may have been indexed to those estimated for Lower Granite, provided that the number of marked fish transported were known.

The magnitude of the chinook smolt outmigration at Ice Harbor in 1973-1979 and at Lower Granite in 1977-1979 was estimated from daily counts of smolts collected at those dams, corrected for sampling efficiency. Cumulative passage estimates for Ice Harbor Dam were used to determine the date when 50% of the total outmigration had passed that dam. Estimates of the mean daily flow during the 2 week period that bracketed this date were used in the flow-survival relationship of Sims and Ossiander (1981). There is no a ***priori*** reason to assume that two weeks was an appropriate time-scale to use in calculating mean daily flow.

Potential sources of error in the flow-survival relationship were evaluated with reference to key assumptions regarding the representativeness of experimental subjects and conditions, sampling procedures, tag effects, analytical methods, and the effects of extraneous environmental factors. Several assumptions judged critical to the validity of survival and flow estimates were identified and discussed in detail. It appears that experimental fish were not randomly drawn from the population but were nevertheless representative of unmarked fish. The methods used to brand, release, collect, and enumerate treatment and control fish were fairly well standardized. The number of marked fish released was reliably determined but was quite variable within and between years. Estimates of the number of marked fish recovered were subject to error due to brand illegibility, low recovery rates, and extrapolation methods.

Evidence for significant handling and tagging-related mortality was found, but was considered inconsequential since treatment and control fish were probably equally affected. However, the assumption that none of the control fish died from natural causes prior to recovery was unquestionably violated. Control fish were typically released several kilometers upstream from the recovery site to ensure that they were randomly mixed with treatment fish at the time of recovery. Recent studies suggest that predation on migrating chinook salmon may be significant over the distances traveled by the controls. Survival was underestimated to the extent that they died en route to the recovery site.

Researchers commented on the difficulty of timing the release of controls to coincide with the arrival of treatment fish (Raymond et al. 1974). Data from experiments conducted in the 1960s and early 1970s indicated that treatment and control fish from paired groups were often recovered at different times. The problem was partially circumvented at Ice Harbor through the use of a flow-efficiency curve, but was never fully solved at other recovery sites, or in later years when the curve could no longer be used.

For years when annual survival was calculated as the mean of several in-season estimates, it was assumed that measurements of group survival were independent. This assumption may not have held true if (1) flows over successive time intervals were autocorrelated, and (2) survival varied with flow. Survival estimates obtained for sections of river above and below Ice Harbor Dam were not independent since chinook released into the forebay of that dam served simultaneously as control and treatment fish.

As the independent variable in the flow-survival relationship, flow was indexed to the date of median passage of the entire smolt outmigration. Survival, however, was measured from sequential releases of treatment fish -- the number, timing, and size of which were not necessarily proportional to changes in the relative abundance of unmarked chinook in the river. So that annual survival estimates would be representative of the unmarked population, an "average" survival was determined by weighting individual treatment group survival estimates by the proportion of the total migration present. This computation may have introduced additional sources of error associated with sampling and estimating population size. For example, smolt abundance and time of peak migration may have been inaccurately estimated on more than one occasion due to late startup or premature termination of sampling at dams.

Spurious correlations may have been introduced into the regression analysis by the inclusion of survival values that had been computed from the same set of data as flow estimates. In 1973, 1974, and 1975, a flow-efficiency curve was used to predict sampling efficiency at Ice Harbor Dam. The resulting survival estimates, which were themselves a function of flow, were then regressed against flows that prevailed at the time that sampling efficiency was estimated.

Why were seasonal averages of survival and flow used in the regression analysis rather than individual treatment group survival and in-season flow estimates? From the standpoint of sample size and model validity, it would have made more sense to regress group survival rates against flows that occurred at the time of recovery. The reason appears to be that accurate measurements of survival of individual treatment groups were often hampered by small sample sizes and/or low recovery rates. The most dramatic example of this was 1977, when 5 marked groups of 28 to 15,987 chinook were released from Lower Granite Dam; of the total of 38,262 fish released, only 19 (0.06%) were subsequently recovered at Ice Harbor Dam (there is no record of recoveries at John Day or The Dalles dams). Paradoxically, recovery rates determined for forebay-released fish were frequently lower than those determined for chinook released further upstream. My analysis of unpublished mark-recovery data from 1966, 1967, 1968, and 1972 revealed that survival, calculated as the ratio of treatment and control group recovery rates, exceeded 100% on 8 out of 22 occasions for fish traveling from the lower Salmon River to Ice Harbor Dam. Group survival was not significantly correlated with flow. Similar results were obtained when the Ice Harbor flow-efficiency curve was used instead of control group recovery rates to estimate sampling efficiency.

Annual survival estimates used in the flow-survival relationship (Sims and Ossiander 1981) were compared with those reported in earlier documents. Several discrepancies were found:

1. Sims and Ossiander (198 1) specified a survival value of 5% for the 1973 outmigration. Raymond et al (1974) indicated that this value was the estimated survival to The Dalles

Dam of chinook released in the Salmon River. They reported 17% survival for chinook released at Little Goose Dam and subsequently recovered at The Dalles Dam.

2. Survival values reported by Raymond (1979) were lower than those used by Sims and Ossiander (1981) for 1974 (34% vs. 40%) and 1975 (23% vs. 25%).

3. Survival values reported by Sims et al. (1977, 1978) and Raymond and Sims (1980) were higher than those used by Sims and Ossiander (1981) in 1976 (30% vs. 24%), 1977 (3.3% vs. 2%), 1978 (44% vs. 37%), and 1979 (30% vs. 24%).

4. Although the 1975 survival value (25%) used by Sims and Ossiander (1981) was consistent with earlier reports, it represents a composite of survival estimates made separately for Rapid River Hatchery chinook (17%) and "native and other hatchery" chinook (38%).

Whereas survival was determined for chinook smolts migrating through segments of the Snake and Columbia Rivers, the flow used in the flow-survival relationship was measured at Ice Harbor Dam. Flow at Ice Harbor Dam may be a valid predictor of survival in the Snake River, but it is less appropriate for the Columbia River due to regional differences in hydrological conditions and water management. More to the point, separate flow-survival relationships should have been derived for the Snake and Columbia Rivers since flows, smolt population characteristics, and various mortality factors may have varied between reaches within the same years.

Evidence suggests that a disproportionate percentage of chinook smolts died at the first dam encountered on the Snake River, presumably due to the culling of unfit fish. Consequently, survival rates were generally lower in the Snake River than in the Columbia River. It should also be noted that the total and relative number of Snake and Columbia River projects upon which survival estimates were based changed over the 1973-1979 period. If survival differed between projects or depended in some way on the total number of projects, then the flow-survival relation may have been influenced by changes in the configuration and number of projects.

Sims and Ossiander (1981) incorrectly specified the total number of projects in 4 (possibly 5) of the 7 years for which overall survival was calculated. They indicated a total of 6 projects in 1974 when only 5 were present. The Dalles Dam was included in estimates of project totals for 1976-1979 when, in fact, survival had only been empirically determined for chinook migrating to John Day Dam. Recalculated per-project survival rates for these years averaged 3%-6% lower than those used in the flow-survival relationship.

In their derivation of a flow-survival model, Sims and Ossiander (1981) assumed that the basic relationship between independent and dependent variables did not change over the years that data were collected. One must make a similar assumption when using the model to predict survival for times or conditions other than those under which the data were collected. Several developments occurred both during and after the period of data collection which cast doubt on the validity of these assumptions. In particular,

1. The number of turbine units installed at Snake River Dams increased from 9 in 1973 to 24 in 1979; the relative amounts of water spilled and run through turbines has changed over time;

2. Average fish guidance efficiency increased from 0.12 in 1973 to 0.29 in 1979;

3. Mortalities attributed to lethal concentrations of dissolved nitrogen were significant in high flow years (e.g., 1974) prior to the installation of spill deflectors in 1976;

4. Variable amounts of debris accumulated in the forebays of mainstem dams depending on runoff conditions and efforts to effect its removal. Debris removal produced tangible benefits in terms of survivability of chinook migrants; and

5. Descaling and delayed mortality due to natural causes and sampling was extensive.

Annual per-project survival rates were negatively correlated with percent descaling and delayed mortality measured in transportation experiments during 1973 - 1979. Correlation analysis revealed that percent descaling and delayed mortality accounted for 86% and 49%, respectively, of the observed variation in percent survival. This compares to 76% of the variation explained by flow in the original flow-survival regression model. All three explanatory variables were strongly correlated. My attempt to include flow, percent descaling, and delayed mortality in a multiple regression model resulted in the inclusion of descaling rate alone as an independent variable; the addition of flow or delayed mortality did not significantly improve the predictive capability of the model.

There is concern over the potential effects that hatchery chinook may have had on wild fish survival, on survival estimates, and ultimately on the flow-survival relationship. The total number of hatchery-origin chinook passing the first dam on the Snake River between 1973 and 1979 ranged from 1.2 to 2.3 million fish. Hatchery chinook comprised between 53% and 75% of the total chinook smolt population passing the upper dam.

Hatchery chinook traveled more slowly, died at higher rates, and may have been more (or less) vulnerable to capture than were their wild counterparts. Survival estimates were therefore dependent on changes in the relative abundance and fitness of hatchery and wild fish over distance and through time.

Survival was estimated separately for hatchery and wild chinook up until 1975. Estimates of chinook survival from the Salmon River to the upper Snake River dam for the 1966-1972 period were for wild chinook smolts only. Estimates for the 1973-1979 period were combined estimates, even though separate estimates were obtained for hatchery and wild chinook in 1973-1975. When measured, survival rates for hatchery chinook were consistently lower than those observed for wild smolts, especially in the upper river. Higher mortality of hatchery fish may have been due to activation of bacterial kidney disease.

Hatchery fish may have lowered the survival of wild chinook smolts by competing for scarce resources, by attracting and supporting larger predator populations, by altering behaviors and activity levels, and by transmitting disease. However, there is no direct evidence that significant negative interactions actually occurred.

Impoundment of the Snake and Columbia rivers was accompanied by changes in the aquatic community. Predator species, both native and non-native, became more abundant and may have contributed to lower survival among chinook migrants over time.

From my assessment of the methods and data used by Sims and Ossiander (1981), I recommend that the flow-survival relationship ***not*** be generalized to existing populations and passage conditions. Fisheries managers, the public, and the fish themselves would be better served by data collected under present conditions using current technological and analytical techniques. At the same time, however, positive steps should be taken to increase ***inriver*** smolt survival rates to levels that permit the recovery and maintenance of upriver salmonid populations.

ACKNOWLEDGMENTS

This report was funded by the Bonneville Power Administration **(BPA),** U.S. Department of Energy, as part of **BPA's** program to protect, mitigate, and enhance fish and wildlife affected by the development and operation of hydroelectric facilities on the Columbia River and its tributaries. I am grateful to Laura Hamilton and Tim Fisher of BPA for their assistance in compiling portions of the historical database. Reviewers Michelle **DeHart,** Al Giorgi, Charlie Petroslq, and John Stevenson provided comments which were useful in revising an earlier **draft** of the report. The direction and **forebearance** provided by Debbie Watkins, BPA project leader, was much appreciated.

CONTENTS

FIGURES

TABLES

1 .0 INTRODUCTION

"The past is not what it used to be."
- Michael Bruton
*Alternative **Life-History** Styles of Fishes*

There has been much debate recently among fisheries professionals over the data and functional relationships used by Sims and Ossiander (1981) to describe the effects of flow in the Snake River on the survival and travel time of chinook salmon and steelhead smolts. The relationships were based on mark and recovery experiments conducted at various Snake and Columbia River sites between 1964 and 1979 (Figure 1) to evaluate the effects of dams and flow regulation on the migratory characteristics of chinook salmon and steelhead trout smolts. The reliability of this information is crucial because it forms the logical basis for many of the flow management options being considered today to protect upriver populations of chinook salmon and steelhead trout (Salmon River Recovery Team 1993).

Mainstem habitats in the Snake and Columbia rivers in the 1970s differed in many important respects from those that existed historically. New hydroelectric dams were being built and operated that not only impeded migration, they created lake-like environments through which smolts and adults were forced to pass (Table 1). By the mid-70s, mainstem survival had declined to less than half that observed during the previous decade (Raymond 1979). Most of the decline was attributed to increased turbine mortality at the dams, increased predation, lethal concentrations of dissolved gases that prevailed in high flow years, and increased residualism in low flow years.

Mainstem habitats continued to change in response to further hydrosystem developments, not all of which may be viewed as detrimental. Examples include improvements in fish bypass and transportation systems, installation of spillway deflectors, efforts to control predator populations, and an increased ability and commitment on the part of hydropower managers to "shape" mainstem flows and spill to facilitate migration. Although the survival of wild chinook salmon smolts has not been reliably measured in recent years, it has probably increased from levels observed in the 1970s. Nonetheless, further increases in smolt survival are needed if upriver stocks are to regain their former abundance.

In this paper I evaluate the primary data, assumptions, and calculations that underlie the flow-survival relationship derived by Sims and Ossiander (198 1) for chinook salmon smolts (Figure 2). Those authors used least squares regression analysis to fit a straight line to seven pairs of data corresponding to flow and survival estimates for the years 1973 through 1979 (Table 2). The line is described by the equation $\log Y = 2.488 + 0.395 \log X$, where Y is the average survival per dam and X is the mean daily flow at Ice Harbor Dam during the period of peak migration.

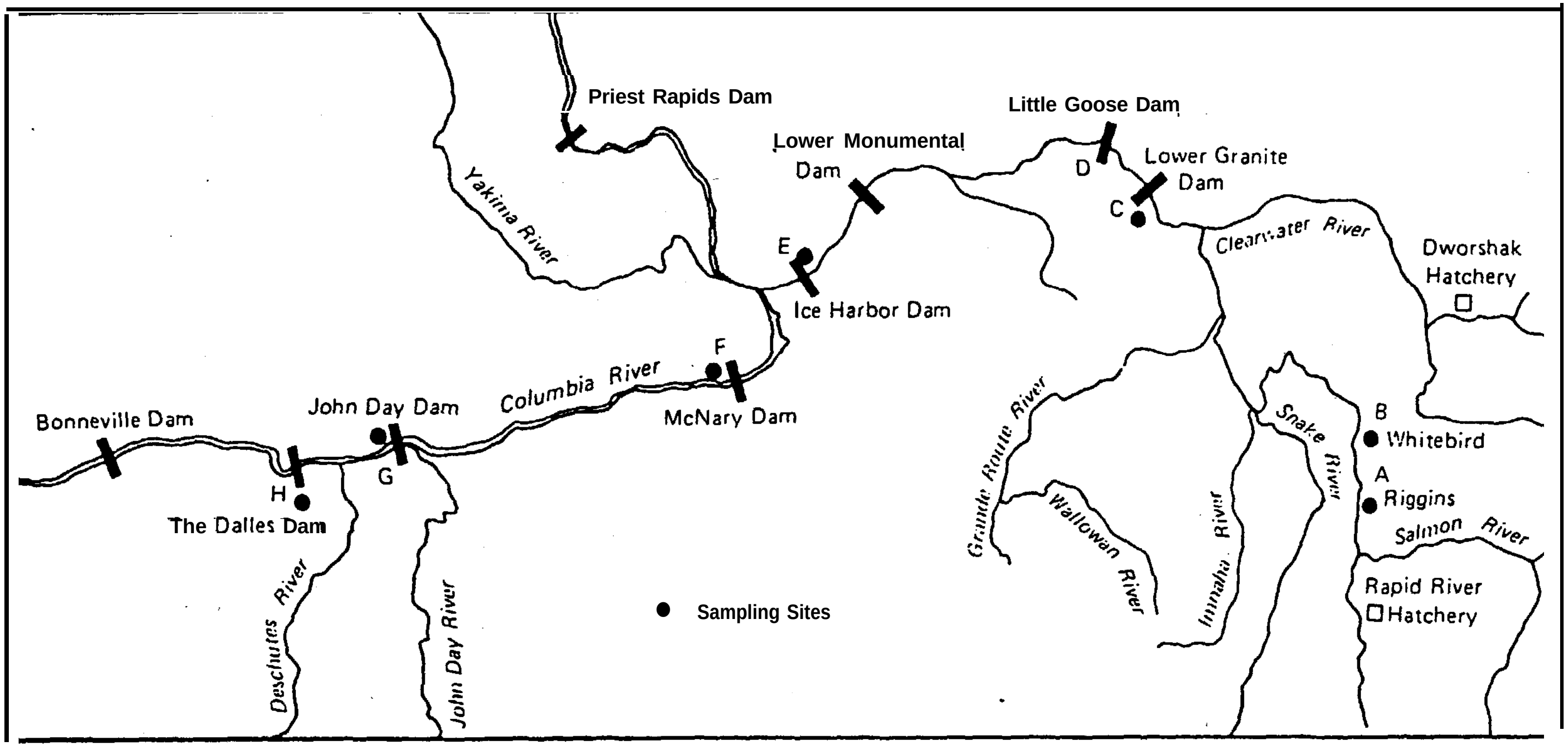

Figure 1. Major dams and smolt sampling sites on the lower Snake and Columbia Rivers.

Table 1. Characteristics of projects through which Snake River chinook salmon smolts must migrate en route to the ocean (Source: U.S. Army Corps of Engineers, 1992).

Project	First Year of Operation	Dam Location (River Mile)	Reservoir Name	Reservoir Capacity (acre feet)	Reservoir Elevation Normal Operating Range (msl)	Reservoir Length (mi)
Lower Granite Dam	1975	107.5	Lower Granite Lake	49,000	733-738	43.9
Little Goose Dam	1970	70.3	Lake Bryan	49,000	633638	37.2
Lower Monumental	1969	41.6	Lake Herbert G. West	20,000	537-540	28.7
Ice Harbor Dam	1962	9.7	Lake Sacajawea	25,000	437-440	31.9
McNary Dam	1953	292	Lake Wallula	185,000	335-340	61.6
John Day Dam	1968	215.6	Lake Umatilla	500,000	265-268 (7/1-10/1) 260-265 (11/1-6/1)	76.4
The Dalles Dam	1957	191.5	Lake Celilo	53,000	155-160	24
Bonneville Dam	1937	146.1	Lake Bonneville	100,000	71.5-76.5	45

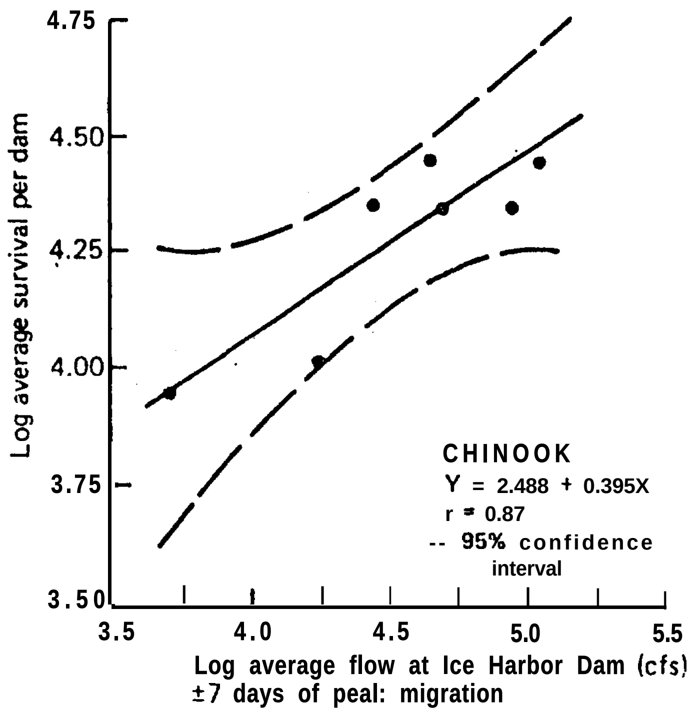

Figure 2. Flow-survival relationship derived by Sims and Ossiander **(198 1,** Figure 6) for yearling chinook salmon, 1973- 1979.

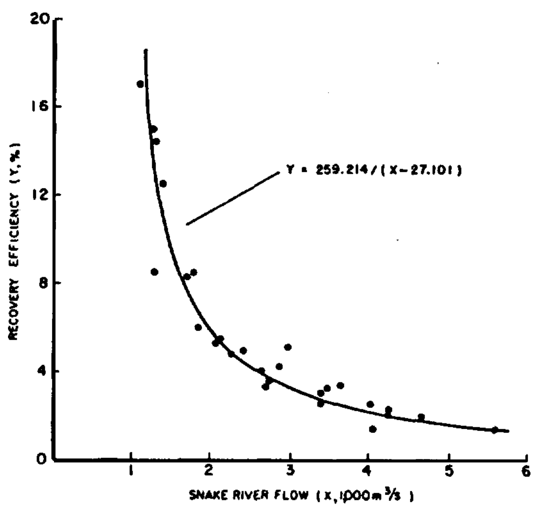

Figure 3. Chinook smolt flow-efficiency curve developed for Ice Harbor Dam (Source: Raymond 1979, Figure 2).

Table 2. Overall survival of Snake River chinook salmon smolts and prevailing flow and spill, 1973-1979. Data are from Sims and Ossiander (1981, Table 5).

Year	Survival to The Dalles Dam (%)	Survival per project (%)	Flow at Ice Harbor Dam (kcfs)[1]	Mean spill (kcfs)
1973	5	55	71	8.6
1974	40	86	158	102.8
1975	25	79	140	102.8
1976	24	79	110	67.0
1977	2	52	40	2.0
1978	37	85	106	34.7
1979	24	79	85	8.3

A major objective was to determine how survival and flow were estimated for each of the years 1973 through 1979. Techniques used to sample chinook migrants and to estimate survival and flow are evaluated in Section 3.0. Calculations of survival and flow required reference to chinook smolt timing and abundance, so I have also reviewed the methods used to estimate these parameters.

The validity of the flow-survival data and the regression model by which they are expressed rests on several key assumptions concerned with sampling and statistical procedures. These assumptions and evidence for and against their having been met are discussed in Section 4.1. Several numerical discrepancies were noted in flow and survival values reported by Sims and Ossiander (198 1) and those found in other documents and unpublished records. The discrepancies and their potential causes are discussed in Section 4.2.

Year-to-year variability in natural and anthropogenic factors affecting the migratory environment and their potential effects on survival and flow estimates are discussed in Section 4.3. Changes in the hydrographic regime, hydrosystem structure, the biological community, and the chinook population itself may have altered the basic relationship between flow and survival. I have attempted to show that the survival of outmigrating chinook salmon may have been influenced by factors which were to some extent independent of flow, such as physical injury and interactions with hatchery fish. By pointing out alternative explanations for the Sims and Ossiander (198 1) flow-survival relationship and by highlighting some of the limitations of the data upon which it was based, it is hoped that an appropriate conclusion is reached. Namely, that decision makers today would be better served by data collected under existing conditions using current technological and analytical techniques.

2.0 SOURCES OF INFORMATION

As a first step, I assembled and reviewed published and unpublished material retrieved from National Marine Fisheries Service (NMFS) archives. Sims and Ossiander (198 1) refer to Raymond et al. (1975) and Raymond (1979) as sources of information on the data and methods which were used to calculate survival. Raymond and his colleagues initiated studies of chinook and steelhead smolt survival, timing, travel time and relative magnitude of the runs in 1964. Carl Sims became principle investigator on the smolt survival studies in 1975. Both he and Frank Ossiander, a statistician at NMFS, remained involved until Al Giorgi assumed control of the smolt survival studies in 1985.

Although not specifically mentioned in Sims and Ossiander (198 1), data collected in the late 1970s under the direction of another NMFS researcher -- Don Park -- also figured in survival estimation. Park headed the agency's smolt transportation studies -- a long-term (and still ongoing) investigation of the feasibility of collecting chinook and steelhead smolts at Snake River dams and transporting them by barge and truck to release sites in the lower Columbia River below Bonneville Dam.

Raymond left copious handwritten notes and calculations of smolt survival and abundance on file when he retired from NMFS. This material was carefully reviewed and referenced against similar information compiled in published reports. I was unable to locate supplemental notes or calculations that may have been left on file at NMFS by Sims, Ossiander, or Park. Most of the information discussed with reference to these individuals was obtained either from published reports or from a partial record of release and recovery data. Original data sheets from the late 1970's were located at NMFS. With the assistance of Laura Hamilton[1], I reanalyzed mark/recapture and transportation data from 1978 and 1979 in an attempt to validate run timing and survival estimates for those years. We were unsuccessful for several reasons, as discussed below, so made no further effort to reproduce survival estimates from data recorded for earlier years,

3.0 THE HISTORICAL DATABASE AND GENERAL ANALYTICAL APPROACH

Under the direction of Howard Raymond, researchers from the Bureau of Commercial Fisheries (now NMFS) began monitoring chinook and steelhead smolts in 1964 in the Salmon River and at Ice Harbor Dam (Table 3). At the time, only Bonneville, The Dalles, McNary, and Ice Harbor dams existed on the lower Columbia and Snake Rivers (Figure 1). NMFS' smolt monitoring program was expanded to include The Dalles Dam and McNary Dam in 1966, and John Day Dam following its construction in 1968. Sampling for smolts at Little Goose Dam on the Snake River began upon completion of the dam in 1970. Lower Granite Dam was built in 1975, and thereafter became the uppermost hydroelectric project to be monitored for smolts.

At each monitoring site, smolts were collected, enumerated, and examined for marks more-or-less continuously during the outmigration season. Subsamples of fish were marked with thermal brands and released into the river to continue their downstream journey. Up to thirty individual groups of fish could be distinctively marked each year by changing the brand orientation and/or location every 3 to 7 days (Raymond 1979). Smolt monitoring based on recoveries of externally marked fish continued until the development of the passive integrated transponder (PIT) tag in the mid-1980s (Prentice et al. 1990). Smolts are now implanted with PIT tags and passively monitored as they pass through specially designed detection facilities at Lower Granite, Little Goose, Lower Monumental, and McNary Dams.

Before the advent of PIT tags, NMFS biologists relied on external mark-recapture data collected at various monitoring sites to quantify, for both chinook salmon and steelhead, (1) the rate of travel between release and recovery sites under a variety of flow conditions, (2) the proportion of fish surviving between these points, and (3) the abundance and timing of smolts migrating past various Snake and Columbia River dams. NMFS researchers attempted to obtain separate estimates for sequentially released groups of uniquely marked fish, but were

[1] A graduate student at the University of Washington at the time.

Table **3.** **Mark** and release sites for treatment and control groups of chinook salmon (M_t and M_c, respectively), and sites at which both groups were recovered (R_t and R_c, respectively) during **1973-1979.**

	First Year of Operation	1973	1974	1975	1976	1977	1978	1979
Rapid River Hatchery	1966	M_t	M_t	M_t				
Riggins Smolt Trap	1964	M_t	M_t	M_t	M_t	M_t		
Whitebird Smolt Trap	1964	M_t	M_t	M_t	M_t	M_t		
Lower Granite Dam	1975			M_t	M_t	M_t	M_t	M_t
Little Goose Dam	1970	M_t	M_t					
Lower Monumental Dam	1969							
Ice Harbor Dam	1962	M_t, M_c R_t, R_c	M_t, M_c R_t, R_c	M_t, M_c R_t, R_c	M_t, M_c R_t, R_c			
McNary Dam	1953							
John Day Dam	1968				M_c R_t, R_c	M_c R_t, R_c	M_c R_t, R_c	M_c R_t, R_c
The Dalles Dam	1957	M_c R_t, R_c	M_c R_t, R_c	M_c R_t, R_c				
Bonneville Dam	1937							

unsuccessful. Virtually all estimates of timing, travel time, survival, and run size were reported as seasonal averages.

3.1 Smolt Survival

Survival of yearling chinook between the uppermost dam on the Snake River and The Dalles or John Day Dam on the Columbia River was determined for each of the years 1966-1979, with the exception of 1971, when there was no sampling at either of the lower dams. The flow-survival relationship derived by Sims and Ossiander (1981) was based on data from the years 1973-1979. The authors did not explain why they excluded years prior to 1973 from their analysis.

As originally conceived, the calculation of survival was relatively straightforward; it was the fraction of marked fish released from an upstream site that were subsequently recovered at a downstream site, adjusted for the sampling (collection) efficiency of the downstream site. If M_i fish are marked and released at an upstream site, where the subscript i denotes a paired treatment-control group $(i = 1, 2, \ldots, n)$ released within a season, and R_i fish are subsequently recovered at a downstream site, then $c_i = R_i/M_i$ is the fraction of treatment fish in group i recovered

Sampling or collection efficiency, e_i, at the downstream site can be estimated as the fraction of control fish released immediately upstream of the site that are subsequently recaptured, $e_i = r_i/m_i$, where m_i is the number of fish in treatment-control group i released, and r_i is the number of control fish eventually recovered.

The percentage, $\hat{s}_i$, of treatment fish in group i that survive to the downstream site is estimated as:

$$\hat{s}_i = \frac{c_i}{e_i} \times 100 \qquad \text{Eq. 1}$$

Paulik and Robson (1969) provide equations for deriving confidence limits. For $\hat{s}_i$ to be a valid estimate of the survival of treatment fish in group i, the following assumptions must hold true:

1. treatment and control fish are randomly mixed,
2. the probability of recovery is the same for all fish,
3. the probability of mortality due to handling and marking is the same for all fish, and
4. control fish suffer no additional mortality prior to recapture.

Since most treatment fish arrived at downstream dams over time periods of variable flow and, hence, sampling efficiency, an average sampling efficiency was calculated based on proportional recoveries at different flows. To use Raymond's (1979, p. 5 11) example, if 30%

of the treatment fish in a particular group were recovered at an efficiency of 8%, 50% at 4%, and 20% at 2%, then the average sampling efficiency for that group was 8%(0.3) + 4%(0.5) + 2%(0.2)= 4.8%. If the percentage of treatment fish recovered over the same time interval was 2.6%, $\hat{s}_i$ would be 2.6 / 4.8 = 54%.

In most years, brand recoveries were enumerated in subsamples from the sampled (dipnetted gatewells or bypass) population and expanded to estimate r_i and m_i. Thus, it was assumed that subsampled fish were representative of (randomly selected from) the unsampled population, and that the proportion of fish subsampled was accurately determined.

If n paired groups of treatment and control fish are sequentially released, then average survival can be calculated:

$$\bar{s} = \frac{\sum_{i=1}^{n} \hat{s}_i}{n} \times 100 \qquad \text{Eq. 2}$$

Sample variance for the n independent estimates:

$$s^2 = \frac{\sum_{i=1}^{n} \left(\bar{s} - \hat{s}_i\right)^2}{n-1} \qquad \text{Eq. 2a}$$

For $\bar{s}$ to be representative of the population at large, it must be assumed that either survival does not vary over time (i.e., each group is a true replicate), or marked fish are exposed to the same kind and degree of mortality, with the exception of marking and handling effects, as are unmarked fish. Clearly, the former assumption is untenable under a variable flow regime. The assumption of equal probability of mortality would only be achieved through frequent and random sampling.

Raymond (1979) elected to weight treatment-control group survival estimates by the proportion of the total annual migration (indexed to the release site[2]) represented by each group to determine average annual survival. If the proportion of the total migration at time of release is denoted p_i, then

---

[2] To be representative, individual $\hat{s}_i$'s should be weighted by the proportion of the run ***passing the release site*** at the time test fish were released. As Raymond (1979, p 5 11) noted, however, the number of smolts passing Lower Granite and Little Goose Dams was not empirically measured; it was estimated as the product of $\hat{s}_i$ and the number of fish passing Ice Harbor Darn.

$$\bar{s} = \sum_{i=1}^{n} \left(\hat{s}_i p_i \right) \qquad \text{Eq. 3}$$

Thus, if $\hat{s}_i$'s of 50%, 30%, 25%, 50%, and 30% were obtained for five treatment groups over the course of a season, and 10%, 20%, 40%, 20%, and 10% of the total run was represented, respectively, by each of the groups, then the average annual survival was (50%)(0.1) + (30%)(0.2) + (25%)(0.4) + (50%)(0.2) + (30%)(0.1) = 34%. This example is taken from page 5 12 of Raymond (1979). All of the previously stated assumptions apply.

The number of smolts passing Ice Harbor Dam during a sampling interval was determined by dipnetting gatewells (nine in all) at the dam, and then dividing by the sampling efficiency determined for that time interval.

Sampling efficiency was observed to decline predictably with increasing flow at all dams for both chinook salmon and steelhead trout, especially after water began to be spilled. The desirability of developing a mathematical relationship from multiple observations in order to be able to predict sampling efficiency as a function of river flow at a recovery site was recognized as early as 1967 (Raymond et al. 1974). If a flow-efficiency curve specific to a recovery site could be developed, it was reasoned, it would be unnecessary to continually release control fish above the site to estimate its sampling efficiency at different flows. Moreover, estimates of $\bar{s}$ would be more precise since the $\hat{s}_i$'s were based on sampling efficiencies determined for comparatively short time intervals (and constant flows) at the time of recovery. One potential drawback to using a flow-efficiency curve is that it requires the assumption that the relation between sampling efficiency and flow does not change (because of changes in the environment, the fish, or both) after the development of the flow-efficiency curve.

Data were collected in 1964-69 and 1972 for the purpose of establishing flow-efficiency curves for The Dalles and Ice Harbor dams. A chinook salmon flow-efficiency curve was never produced for The Dalles Dam. The curve developed for Ice Harbor Dam (Figure 3) underwent considerable refinement after 1972 (without benefit of new data) before emerging in final form in Raymond (1979). More is said later of the versatility Raymond displayed in developing and applying the Ice Harbor flow-efficiency curve to estimate chinook smolt survival and abundance.

Summary data (total number of fish marked and recovered) relating to sampling efficiencies at lower river dams, and to recoveries at Little Goose Dam, were reported for 1973 and 1974 (Raymond et al. 1974 - Table 6; 1975 - Appendices), but not for later years. According to Raymond (1979, p. 5 10), sampling efficiencies were not determined at Little Goose or Lower Granite dams during 1973-1975 because of potential conflict with ongoing fish transportation experiments. Sampling efficiency was determined for Lower Granite Dam from 1976- 1979 by releasing smolts in the forebay of the dam and determining the proportion recovered in the fingerling collection system at the dam. Sampling efficiency was used in conjunction with counts of fish collected in the fingerling collection system to estimate the total number of smolts passing Lower Granite Dam. As will be shown later, the ratio of population sizes at

John Day and Lower Granite dams was used to estimate survival in the Snake River and Columbia River during **1976- 1979.**

Sampling efficiency data from **1973-** 1975 specific to individual treatment and control fish releases during could not be located in NMFS reports or files. Summary data for 1973 and 1974 were reported by Raymond et al. (1974 **-** Table 6; 1975 **-** Appendices). I discuss elsewhere mark-recovery data for 1976-1979 that was found in **NMFS** files (see Section 4.23 **Sampling Efficiency)**.

The Ice Harbor flow-efficiency curve (Figure 3) was used by Raymond (1979) to estimate population size and p_i at that dam during sampling intervals of relatively constant flow during 1973-1975. With the installation of three additional turbine units at Ice Harbor Dam in the summer of 1975, the relation between flow and sampling efficiency at the dam changed. As a consequence, the flow-efficiency curve was not used to estimate survival following the 1975 season. Sampling efficiency was measured directly from recovery rates of fish released in the **forebay** of Ice Harbor Dam during 1976-1979.

Raymond et al. (1975) used the chinook flow-efficiency curve developed for Ice Harbor Dam to predict sampling efficiency at that dam in 1974 for sampling intervals ranging from 2 to 20 days. Sampling intervals corresponded to periods of comparatively stable flow during the chinook outmigration. Claiming that too few chinook were marked and recovered in 1974 to estimate survival for individual treatment-control groups, Raymond et al. (1975; see their Appendix Table A2) devised two other approaches to estimating $\bar{s}$: one to estimate survival to Ice Harbor Dam, the other to estimate survival in the lower river.[3] To accomplish the former, Raymond et al. (1975) first calculated an average recovery rate, F, for treatment fish by combining mark-recovery data across all groups:

$$\bar{c} = \frac{\sum_{i=1}^{n}(R_i)}{\sum_{i=1}^{n}(M_i)} \qquad \text{Eq. 4}$$

He then estimated an average seasonal efficiency:

$$\bar{e} = \sum_{i=1}^{n}(e_i q_i) \qquad \text{Eq. 5}$$

---

3 Raymond et al. (1975 Report, App A2) noted that "There were not enough fish recovered on a weekly basis in 1974 to provide estimates of week to week differences in survival. Therefore, in 1974, weekly releases were combined for the entire outmigration to provide a seasonal survival estimate through each stretch of river."

where sampling efficiency, e_i, is determined for each flow interval j using the chinook flow-efficiency curve and q_i is the proportion of the total number of marks recovered in the same time interval. Note that the average sampling efficiency was weighted by fraction of marks recovered and ***not*** by the proportion of the total run passing the dam, as claimed by Raymond (1979). The reader should consult Appendix Table A2 in Raymond et al. (1975) for sample calculations of $\bar{e}$.

Survival, $\bar{s}$, from Little Goose Dam to Ice Harbor Dam was calculated as:

$$\bar{s} = \frac{\bar{c}}{\bar{e}} \times 100 \qquad \text{Eq. 6}$$

Implicit to Eq. 6 is the assumption that the number of marks recovered in any time interval is proportional to the total number of fish present in the same time interval. For $\bar{s}$ to be representative, recoveries of treatment fish over the outmigration period should correspond in frequency and timing to that of the unmarked population.

Equation 6, where $\bar{e}$ is determined by Eq. 5, could not be used to estimate survival below Ice Harbor Dam in 1974 (or in later years) because flow-efficiency curves were never completed for downstream dams. To complicate matters further, Raymond et al. (1975; Appendix A2) concluded that "insufficient numbers were recovered from forebay releases at The Dalles Dam for accurate measure of our sampling efficiency there in 1974." An average sampling efficiency, $(\bar{e})$, was therefore calculated by summing across control groups.

$$\bar{e} = \frac{\sum_{i=1}^{n}(r_i)}{\sum_{i=1}^{n}(m_i)} \qquad \text{Eq. 7}$$

Because the number of recoveries in 1974 precluded estimates of group survival, Raymond et al. (1975) calculated the average survival of chinook migrating from Ice Harbor to The Dalles Dam by combining treatment and control fish recoveries over the entire season:

$$\bar{s} = \frac{\bar{c}}{\bar{e}} \times 100$$

$$= \frac{\sum_{i=1}^{n}(R_i)\sum_{i=1}^{n}(m_i)}{\sum_{i=1}^{n}(r_i)\sum_{i=1}^{n}(M_i)} \times 100 \qquad \text{Eq. 8}$$

In 1974, only 15 (Σr_i) control fish were recovered out of a total of 6,372 (Σm_i) released over the season. Average sampling efficiency, $\bar{e}$, at The Dalles Dam was therefore 15 / 6372 = 0.24% (Raymond et al. 1975; Appendix A2 [NB: Although the authors used Σm_i = 6,372 in their calculations, they indicated elsewhere (Appendix Table B5) that 6,500 fish were actually released]). For the same time period, the average recovery rate, $\bar{c}$, was 13 / 6,500 = 0.20%. Thus, 83% (= 0.20 / 0.24) of the spring chinook passing Ice Harbor Dam in 1974 were estimated to have survived to The Dalles Dam.

A different survival estimate was obtained using Eq. 8 than would have been had $\hat{s}_i$ been calculated for each treatment-control group, and then averaged to give a single season value (Eq. 3), or had an average weighted sampling efficiency been used in the denominator (Eq. 6). A major drawback to the "sum-across-groups" approach is that it does not permit measures of statistical variance to be derived from group survival estimates. Sampling variance and its square root, called the standard error of the estimate, are measures of the precision among the survival estimates. Eq. 8 also incorrectly assumes that the probability of mortality does not vary over time among marked and unmarked fish.

Average annual survivals were typically estimated by one of the preceding methods (Eqs. 3, 6, or 8) for two reaches: (1) the Snake River extending between the upper dam and Ice Harbor Dam, and (2) the Columbia River between Ice Harbor Dam and the lower dam. However, if the number of treatment fish passing the upper and lower dams were known, overall survival could have been estimated without reference to Ice Harbor Dam mark-recovery data. Rewriting Equation 8, a smolt abundance estimator is obtained that is equally applidable to groups of treatment fish or to the entire smolt population:

$$\bar{s} = (N_{lower} / N_{upper}) \times 100 \qquad \text{Eq. 9}$$

When based on observations of treatment fish, N_{upper} is the known release (either M_i or ΣM_i) of treatment fish at the upstream site. N_{lower} is the abundance of treatment fish at the downriver site [either R_i / e_i or ($\Sigma R_i / \bar{e}$)], after adjusting for sampling efficiency.

When based on estimates of total smolt abundance, N_{upper} and N_{lower} are independent estimates of the total number of unmarked migrants passing each site. Mark-recapture data are typically required to estimate sampling efficiencies at both sites.

In point of fact, Sims et al. (1978, Table 2, p. 13) provided a formula for calculating overall survival that was similar to Eq. 9, except that N_{upper} and N_{lower} referred to total numbers of migrants rather than numbers of marked fish, and N_{upper} is reduced by T, the number of fish collected and transported before reaching the downstream dam:

$$\bar{s} = [N_{lower} / (N_{upper} - T)] \times 100 \qquad \text{Eq. 10}$$

If N_{upper} and N_{lower} are estimates of total smolt abundance at the two dams, application of Eq. 10 requires only that the total number of fish removed from the population be known, and does not require knowledge of the number of ***marked fish*** transported. However, Eq. 10 can be used to estimate $\bar{s}$ for individual groups of marked fish if the numbers of those fish that were transported can be estimated. This was actually done in later years (Sims et al. 1983, Appendix Table 12).

Application of Eq. 10 to smolt abundance data found in Sims et al. (Tables 3 & 4 - 1976; Table 2 - 1977; Table 2 - 1978) and Raymond and Sims (Table 6 - 1980) yields survival estimates that agree precisely with those reported in the same documents. This would appear to explain the footnote to Table 4 in Sims et al. (1977, p. 12), which refers to "800,000 chinook salmon ... transported below Bonneville Dam subtracted from total smolts passing Lower Granite Dam for calculations of survival."

There is additional evidence to suggest that Eq. 10 might have been used to calculate survival during 1976-1979, at least for the section of river between Lower Granite and Ice Harbor Dams. Sims and Ossiander (1981, p. 5) reported that population estimates at Lower Granite Dam during 1976- 1979 were independently estimated by applying efficiency releases to samples from the fingerling collection system. With independent estimates of N at Lower Granite and Ice Harbor dams, a ratio-based estimate of survival is possible.

The question is unresolved as to whether survival from Lower Granite to Ice Harbor Dam (or, less likely, from Lower Granite to John Day Dam) in the late 1970's was determined from ratio estimates (Eq. 10) of total smolt abundance or numbers of marked fish. I believe that survival was estimated from a comparison of marked fish recoveries that had been adjusted to reflect collection efficiencies and losses due to transportation. Raymond and Sims (1980) appear to confirm this view, as evidenced by their statement: "survival is estimated by comparing the actual recovery rate of marked fish released at a given dam with the expected recovery rate at that dam as determined from measures of sampling efficiency." As pointed out above, to estimate survival from the ratio of number of marked fish passing upper and lower dams, one needs to know the number of marked fish collected and transported at intervening dams. How this number was actually determined is unknown.

There is strong evidence to suggest that Eq. 10 was used to calculate survival from Lower Granite to Ice Harbor Dam and from Ice Harbor to John Day Dam in 1976. Eq. 10 was also used to estimate survival from Lower Granite to John Day Dam in 1977-1979. It was *not* used to estimate survival in the Snake River in years prior to 1976 since, as Raymond (1979, p. 5 11) remarked, the "magnitude of populations at Lower Granite and Little Goose dams was determined from the percentage of fish marked at Lower Granite or Little Goose dams that survived to Ice Harbor Dam and applying that proportion to the numbers of fish estimated at Ice Harbor Dam." To use his example: "If 2 million chinook salmon were estimated at Ice Harbor Dam and survival was 50% between Little Goose and Ice Harbor dams, then 4 million fish must have passed Little Goose Dam." If survival from Ice Harbor to The Dalles or John Day dams remained at 50%, then 1 million fish must have passed the lower dam. In other words, survival was estimated first, and then applied to the smolt abundance determined for Ice Harbor Dam to estimate populations at other dams.

Sims et al. (1982) did not estimate survival from Lower Granite to John Day dam in 1981 because sampling efficiencies and the number of marked fish transported at McNary Dam were not measured. Although smolt monitoring was conducted at McNary Dam in the following year, researchers confronted a similar problem when Little Goose Dam sampling was discontinued. However, by making certain assumptions about survival between Lower Granite and Little Goose Dam, and collection efficiency at Little Goose Dam, Sims et al. (1983, Appendix 12) were able to estimate the survival of individually marked groups of chinook in 1982. Group survival ($\hat{s}_i$) was estimated by:

1. dividing observed recovery rates at Lower Granite and John Day dams by prevailing sampling efficiencies to estimate the total number of marked fish in each group that arrived at the two dams,

2. estimating N_{upper} – the number of fish in a group that passed Lower Granite Dam – by subtracting the estimated number of marked fish that were collected and transported from the dam,

3. estimating N_{lower} – the number of fish in a group that would have arrived at John Day Dam had none been transported at intervening dams – by subtracting the estimated number of marked fish, that were collected and transported from Little Goose and McNary dams, and then

4. calculating $\hat{s}_i = (N_{lower} / N_{upper}) \times 100$ (Eq. 10).

An average survival, $\bar{s}$, was calculated as the mean of the four group survival estimates.

3.2 Smolt Abundance

Mention is made briefly here of the method used to calculate instantaneous and cumulative numbers of chinook migrants passing Ice Harbor Dam and Lower Granite Dam. Population estimates for Ice Harbor Dam, in particular, were important since the flow associated with the date of median passage at that dam was the independent variable in the flow-survival relationship of Sims and Ossiander (198 1). Lower Granite Dam is considered because empirical estimates of smolt abundance obtained there in 1976-1979 may have been used in survival calculations. Population sizes at The Dalles and John Day dams were indexed to Ice Harbor Dam estimates in 1973-1978, and to the Lower Granite Dam estimate in 1979, and so are of little interest. Little Goose populations in 1973 and 1974 were similarly indexed to Ice Harbor Dam.

Details on the methods used to sample smolts and estimate their abundance at Ice Harbor Dam prior to 1976 are provided by Bentley and Raymond (1968), Raymond et al. (1975), and Raymond (1979). Raymond's unpublished notes yielded valuable information. The magnitude of the chinook smolt population in years 1964 through 1975, excluding 1969, was determined by summing for a year time-specific gatewell catches divided by the prevailing sampling efficiency. To estimate the total number of smolts passing the dam over a given time interval, the number of fish collected in each gatewell was divided by the sampling efficiency for that time interval. It was occasionally necessary to expand catches to unsampled gatewells and time periods (mainly weekend days; Raymond, unpublished notes). A flow-efficiency curve similar to the one portrayed in Figure 3 was used to estimate sampling efficiency over short time intervals of comparatively stable flow. Flow-efficiency curves were not applied after 1975 due to an increase in the number of turbines operating at the Ice Harbor Dam.

It is assumed that direct measures of sampling efficiency were used to expand chinook smolt counts in later years, but few details could be gleaned from Sims et al. (1976, 1977, 1978) or Raymond and Sims (1980). The authors tabulated weekly smolt catches at Ice Harbor Dam and other sampling locations; they also indicated the week in which 50% of the total sample had been collected. But the dates indicated were based on the unexpanded counts and did not take sampling efficiency into account. I was unable to locate sampling efficiency data (i.e., control group mark-recovery data) specific to Ice Harbor Dam for 1977-1979. Without this information, it remains unclear exactly how population sizes and, more importantly, dates of median passage were estimated.

Sims and Ossiander (198 1) and Sims et al. (198 1, p. 2) clearly indicated that population estimates for Lower Granite Dam in 1976-1979 were obtained by dividing the number of fish collected from the fingerling collection system by the efficiency of collection, as empirically determined from releases of control fish into the forebay above the dam. However, this contradicts information provided by Sims et al. (1976, 1977) and Raymond and Sims (1980), who stated that smolt numbers at Lower Granite Dam were estimated by first determining the fraction of marked fish surviving from that dam to Ice Harbor Dam and, after adjusting for transportation losses, multiplying that fraction by the Ice Harbor population estimate. The fact that sampling efficiency may not have been estimated and survival to Ice Harbor Dam went reported' after 1976 begs the question of how the median date of passage (and, hence, mean flow) at the dam was actually determined for later years.

3.3 Transportation

Beginning in 1968, an attempt was made to improve the survival of chinook and steelhead smolts by collecting them at strategic locations in the Columbia basin during their downstream migration, and then transporting them downstream of Bonneville Dam for release. Smolts were collected and transported from 1973 to 1979, except 1974, from Lower Granite Dam and/or Little Goose Dam (Table 4). Sims and Ossiander (198 1, Table 1, p. 7) indicated that chinook salmon smolts were not transported in 1973, but Park and Ebel (1975) and Raymond (1979) provided data which suggested otherwise. The number of chinook smolts transported from the two Snake River dams increased from 247,000 fish in 1973 to 2.1 million in 1979 (Smith et al. 1980). Mass transportation at McNary Dam began in 1979 with the transportation of 0.3 million yearling chinook salmon.

Although the total number of fish collected and transported from Snake River dams was routinely estimated, the lack of published estimates of the number or percentage of *treatment* fish transported suggests that no special effort was made in this regard. Clearly, marked fish, once collected, were not returned to the river. In most years, therefore, an unknown fraction of the treatment fish were "lost" to transportation before they arrived at Ice Harbor Dam. If no compensatory adjustments were made to account for these losses, survival estimates based on mark recoveries would be biased downwards. The effect would be especially notable in low-survival years such as 1977 when a high percentage (70%) of the run-at-large was transported (Table 4).

I found no mention in NMFS reports of specific computational steps taken to account for transportation of marked fish.[4] The record clearly shows that removal effects were not considered in the calculation of transportation benefits (Park 1985), so it seems unlikely that NMFS researchers attempted to do so when calculating survival. Interestingly, Sims et al. (1984, p. 10) declined to estimate survival for 1983 migrants because they "did not sample at Little Goose Dam and have no way of determining how many marks were collected and transported." Raymond and Sims (1980, p. 17) claimed that survival estimates for 1979 migrants were adjusted for fish transported from McNary Dam, but did not explain how they estimated the number of marked fish transported or how the corrections were made. Without evidence to the contrary, I conclude that transportation data on marked fish were not collected in any of the years 1973-1979, but that survival was estimated nonetheless. From consideration of the information at hand, I question the validity of the methods used by Raymond, Sims, et *alia* to estimate smolt survival as well as the accuracy of the resulting estimates.

3.4 Timing of Peak Migration

By Raymond's (1979, p. 5 10) definition, the peak of the chinook smolt migration at a particular dam coincided with the date when the cumulative daily total of yearling chinook salmon collected at the dam reached 50%. The numbers of fish collected were related to prevailing sampling efficiency to determine when 50% of the outmigration has passed. The peak migration date is relevant to the present discussion because each flow datum in the flow-survival curve of Sims and Ossiander (198 1) was calculated as the mean daily river discharge at Ice Harbor Dam over a fifteen day period that centered on the date of peak migration of smolts past that dam in a given year.

---

[4] However, unpublished notes by Raymond imply that survival estimates were adjusted for transportation in 1973 and 1975 (and possibly other years). I found no information on how this was actually done, so cannot verify the results.

Table 4. Estimated population size at upper Snake River dam, and total number of yearling chinook salmon smolts transported at Little Goose (197 1-1973 and 1976-1978), Lower Granite (1975-1979), and McNary (1979) dams for the period 1971-1979. Values are from (1) Sims and Ossiander (1981), (2) Raymond (1979), and (3) Raymond (1988), and (4) Smith et al. (1980). Percent transported (5) is estimated from (3) and (4).

Year	Population Size (x 1,000,000) (1)	(2)	(3)	Number Transported (x 1,000) (4)	Percent Transported (%) (5)
1971	-	4.0	3.4	109	3.2
1972		5.0	3.9	360	9.2
1973	5.0	5.0	4.0	247	6.2
1974	3.5	3.5	3.0	0	0
1975	4.0	4.0	3.9	414	10.6
1976	5.1	-	4.3	751	17.5
1977	2.0		1.8	1365	75.8
1978	3.18		2.7	1623	60.1
1979	4.27		3.6	2409 [1]	66.9

[1] Includes 300,000 spring chinook transported from McNary Dam in 1979.

Dates of peak migration past Ice Harbor Dam for the years of interest ranged from 28 April in 1975 to 26 May in the following year (Figure 4). The average number of days separating the dates of peak migration at the upper dam and Ice Harbor Dam during 1973- 1979 was 7.5 days, compared to 11 days difference between peak migration dates determined for Ice Harbor Dam and the lower dam. Thus, chinook smolts spent 1.5 times as long in the lower reach as in the upper reach.

In most years, approximately 40% to 60% of the total run passed Ice Harbor Dam during the fifteen day window used in mean daily flow calculations. The frequency distribution of fish passing Ice Harbor Dam, as reflected by weekly smolt counts at that dam, was typically skewed to the right [see Appendix Tables in Sims et al. (1976, 1977, 1978) and Raymond and Sims (1980)].

3.5 Flow Estimates

Each data pair used by Sims and Ossiander (198 1) to construct the flow-survival relationship (Figure 2) consisted of a single season "per-project" survival and the mean daily flow that occurred at Ice Harbor Dam during the peak of migration. Whereas survival was determined for both Snake and Columbia River segments, mean daily flow estimates were based solely on measurements of Snake River discharge. Mean daily flow was determined for the fifteen day period centered on the date of peak migration. Flows varied considerably over the period of interest, including record high and low flows in 1974 and 1977, respectively (Table 5).

Chinook salmon typically migrate as smolts during the ascending limb of the Snake River hydrograph, with the peak of migration occurring approximately one month prior to peak runoff. Although higher flows occurring near the end of the outmigration period might be expected to result in a frequency distribution that is somewhat skewed to the left, plots of weekly smolt count data at Ice Harbor Dam typically indicate a pronounced tail in the last few weeks of the season.

4.0 POTENTIAL SOURCES OF ERROR

NMFS researchers faced formidable logistical problems in devising and carrying out a smolt sampling program on the Snake and Columbia rivers. The relationship between smolt survival and flow that is the subject of this paper was the product of a remarkable effort on the part of many individuals. However, acceptance of the relationship should be contingent on the validity of several assumptions regarding the representativeness of the fish and experimental conditions, sampling protocols, tagging effects, methods of analysis, and the effects of extraneous variables. If the more important of these assumptions were not met, inferences concerning the effect of flow on smolt survival may be incorrect. In the next section, I identify key assumptions and discuss the likelihood that they were met.

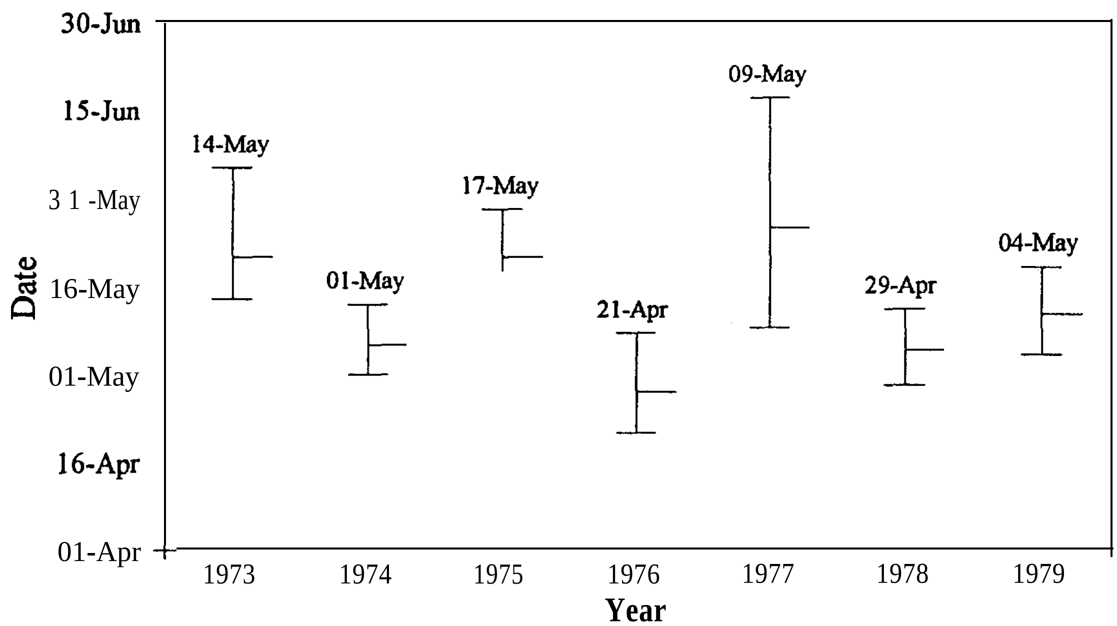

Figure 4. Dates of peak passage of chinook salmon migrants at upper dam (high bar), Ice Harbor Dam (mid bar), and lower dam (low bar). Upper dam passage dates are labeled. (Source: Sims and Ossiander [1981], Table 3).

Table 5. Snake River monthly flow (kcfs) at Ice Harbor Dam during periods of chinook salmon smolt migration.

Year	April		May	
	Mean	Range	Mean	Range
1964	65	53-77	120	75-197
1965	115	51-222	152	126-211
1966	63	34-81	77	44-113
1967	44	36-53	108	37-202
1968	47	34-80	75	38-110
1969	120	101-153	140	84-179
1970	47	35-60	118	46-196
1971	112	82-139	188	129-243
1972	99	67-129	143	85-199
1973	33	214-43	60	35-89
1974	131	111-163	131	82-176
1975	75	44-109	121	79-179
1976	111	71-153	153	95-191
1977	30	9-53	40	12-60
1978	78	59-124	100	79-122
1979	57	28-75	100	78-143

I then consider the validity of methods used to compute recovery rates, sampling efficiency, and other parameters required for survival and flow estimation. The reliability of the flow-survival curve depends upon the appropriateness of methods used to reduce and analyze the data.

The final section is concerned with environmental factors that may have acted independently or in concert with flow to effect changes in survival over the period of interest. Particular attention is given to the effects of transportation, hatchery fish, and modifications to dams.

4.1 Sampling and Statistical Assumptions

This section describes assumptions that were relevant to the estimation of survival, flow, and their statistical relation to one another. Some of the more important experimental assumptions were explicitly acknowledged and evaluated (Raymond 1979); others, as will be shown went untested. I begin by listing key assumptions. Survival estimates determined from recovery rates of treatment and control fish are essentially paired release-recapture estimates, so most of the assumptions listed by Burnham et al. (1987, pp. 5 l-52) are apropos. Drawing on Raymond (1979), Ricker (1975), Burnham et al. (1987), and Dauble et al. (1993), the fifteen assumptions judged most critical to the validity of survival estimates are:

1. ***Treatment and control fish are randomly drawn from the same population andpossess biological characteristics that are similar to unmarked smolts,***

2. ***Numbers of marks (M_i and m_i) and recoveries (R_i and r_i) are exactly known or can be measured with negligible error,***

3. ***Brands remain legible and are accurately read,***

4. ***The probability of survival and recovery of individual fish is unaffected by the presence or fate of other fish,***

5. ***All fish within an experimental replicate have the same probability of survival and recovery,***

6. ***Probability of mortality due to handling, marking, and transporting to the release site is the same for treatment and control fish and is known,***

7. ***Control fish suffer no additional mortality prior to recovery (or alternatively, the number of control fish that die is known),***

8. ***Treatment, control, and unmarked&h are complete& mixed and, where coincident, have the same probability of survival and recovery,***

9. ***The number of treatment&h collected and transported downriver is either negligible or is exactly known,***

10. ***If replicate observations ($\hat{s}_i$'s) are averaged to estimate mean survival ($\bar{s}$), the data must be statistically independent over replicates,***

11. ***For $\bar{s}$ to accurately reflect a seasonal average, sampling effort must be proportional to the relative abundance of unmarked fish in the river over time.***

The validity of flow estimates and the relationship between smolt survival and flow requires three additional assumptions:

12. ***The flow metric used was appropriate and was reliably measured,***

13. ***Statistical analyses of the flow-survival data are based on the correct models,***

14. ***The basic relationship between survival and flow did not change during 1973-1979.***

Finally, for the flow-survival relationship to be applicable today, it must be assumed that:

15. ***Conditions that existed in 1973-1979 are representative of conditions to which the flow-survival model is to be applied.***

Assumption I. Random and Representative Samples

Results may have been biased and/or estimates of error variance inflated if samples were not randomly drawn for marking or recovery purposes, or if treatment or control fish possessed characteristics that were atypical of the population-at-large. This particular assumption is difficult to evaluate since it requires comparison of the biological characteristics and probabilities of capture of marked and unmarked fish. Due to the practical constraints of sampling a large river, random samples could not be obtained, so the possibility cannot be ruled out that fish collected at the dams may not have been representative of the unsampled population. Captured fish may have been more (or less) susceptible to mortality than were fish which eluded capture.

Treatment fish were drawn from samples collected at an upper dam and controls were collected at a downstream site. Migratory characteristics of smolt populations are expected to change as weaker fish are culled and smoltification progresses (Giorgi et al. 1988). As long as these changes are consistent across treatment, control, and unmarked groups of fish, experimental subjects may be considered representative of the population-at-large. There is no reason to believe that this assumption did not hold true.

Assumptions of random sampling and representativeness should not be confused with Assumption 8 below, which requires complete mixing of treatment, control, and unmarked fish at time of recovery.

Assumption 2. Enumeration of M_i, R_i, m_i, and r_i

Several issues are germane to the assumption of reliable mark-recovery data. One concerns possible variability in sampling and reporting methods, and is discussed here. A second issue – brand legibility – is addressed under Assumption 3. A final issue concerns "corrections" made to the data to account for transportation, variations or gaps in sampling effort, etc., and the potential effects of these adjustments on sampling efficiency and survival estimates. The subject of data corrections is covered in later sections of this report (see Section 4.2 Analytical Methods).

One would presume that NMFS researchers used standardized methods for marking, releasing, collecting, and enumerating fish since failure to do so would threaten the validity of the experiments. It is assumed that these methods were equally efficient during all years, and that errors in estimating marks and recoveries were negligible. However, there is considerable evidence that procedures used to collect and examine fish varied between years and, as 'a consequence, may have affected survival statistics. At Ice Harbor Dam, migrants were dip-netted from gatewell units until 1970, when the U.S. Army Corps of Engineers drilled orifices in each gatewell to permit passage via the ice and trash sluiceway. As Raymond (1979, p. 508) pointed out, it was necessary to assume that "numbers ofjuveniles collected in the sluice trap from 1970 to 1975 were comparable to those taken by dip-netting gatewells in 1964 to 1969." Raymond claimed that there was no difference in the two methods but does not provide data. It is implausible that dipnetting of several (3 to 9) large gatewells (the dipnets measured 18.5 long x 11.5 wide x 6.0 ft deep) sampled smolts as effectively as a trap located in the ice and trash sluiceway of the dam. The gatewells were not dipnetted every day of the week, and in some years only three gatewells were sampled, so although adjustments were made to, extrapolate the data to other times and units, sampling efficiency probably declined.[5] On the other hand, there is some question whether all fish that enter a gatewell actually exit via an orifice, and not through the turbine units. If this occurred to any significant degree, then dipnetting may have recovered a greater proportion of fish arriving at the dam than did passive trapping. Regardless of the direction of change, if changes in sampling efficiency did in fact occur, then the flow-efficiency curve which had been developed in part from 1960's data was incorrectly used to estimate survival in 1973-1975.

As a general rule, the precision of survival estimates is positively related to the fraction of marks recovered (m_i/M_i and r_i/R_i). The extremely low recovery rates recorded for treatment

---

[5] Bentley and Raymond (1968, p 126) stated: " The proportion of the population sampled each year was based on catches in unit two, which was available for continuous sampling during all three years except for one week in 1964...All three units were fished continuously only in 1966."

and control chinook salmon in **1973-1979** (see Section **4.2.1** Sample Sizes) cast considerable doubt on the accuracy of associated survival estimates. It should also be noted that when the measurement of a variable such as survival is not perfectly reliable, there is a tendency for extreme scores to regress or move toward the mean (Kirk 1982). The concern here is that empirical estimates of low and high recovery rates may be higher and lower, respectively, than their true values.

Further evaluation of potential biases that may have been introduced by sampling variability is precluded by the lack of information on the methods used to collect smolts and examine them for marks after 1975.

Assumption 3. Brand losses

In keeping with Assumption 2, this assumption deals with the specific case of brand retention. Raymond's unpublished notes revealed that a variety of brands (both hot and cold), fin clips, and tattoos were tried in the 1960's. The marks were not all equally effective due to illegibility, fin regeneration, and tag-induced mortality, so by 1973 all fish released in survival and transportation experiments were marked with a cold brand (Sims et al. 1978, Raymond and Sims 1980, Park 1985). Raymond (unpublished notes, ca. 1964) reported that cold brands remained legible for up to 45 days, easily exceeding the length of time required by chinook smolts to migrate from the upper dam to The Dalles dam in 1973-1979 (Sims and Ossiander 1981). However, Sims et al. (1981, p. 2) specifically cited problems with "brand recognition" as a factor preventing direct measurement of collection efficiencies at Lower Granite Dam in 1980.

Any unaccounted for losses of tags due to brand illegibility, errors in reading, etc. would reduce the number of marked fish recovered and, therefore, cause a downward bias in survival estimates. Brand recognition is influenced by the method of marking, the symbols to mark the fish, the length of time the brand remains legible, and the conditions under which the brand is read **(Wydoski** and Emery 1983). It is unlikely that a control fish could be branded, released, and subsequently recovered either before the brand had time to develop into a telltale colorless scar or after growth and healing had rendered the mark illegible. Brand loss would probably have been more common among treatment fish since they spent a longer time in the river before recovery. However, it would be presumptive to conclude that brand loss among treatment fish significantly affected survival estimates.

Neither Raymond (1979) nor Sims and Ossiander (1981) mentioned adjustments to release data to account for tag "loss." However, Park (1985) claimed that numerical adjustments were made in transportation experiments, so it is possible that corrected numbers were used in survival studies as well. I do not believe so.

Raymond and Sims (1980) indicated that up to 75 hatchery smolts (identified by adipose clips) were collected daily to provide "information relative to survival from the various upstream hatcheries," but gave no further details. Hatchery fish were marked with coded wire tags prior to release. Coded wire tag recovery data are typically used to calculate smolt-to-adult survival rates. Sims et al. (198 1, p. **2),** however, noted that estimates of smolt survival, timing, etc. were obtained by expanding coded wire tag samples to the total ad-clips collected each day at a particular site. Results were variable for hatchery chinook smolts recovered at Lower Granite Dam due, in part, to low recovery rates; it was estimated that only 1 out of every 26 tagged chinook passing the dam was sampled.

Assumptions 4 and 5. Equal and independent probabilities of survival and recovery

Of the Assumptions considered, 4 and 5 are two of the more critical and difficult to satisfy. These assumptions state that each fish within a treatment or control group has, on average, the same probability of dying or being captured, and that this probability is not conditioned by the presence of other fish. There are very few data by which to evaluate these assumptions.

Unequal probabilities of survival may have been caused by local, short-term variations in smolt densities, especially those caused by transportation, by the presence of hatchery fish, and by differences in migratory behavior, especially in routes taken in passing dams. The removal of large numbers of smolts at transportation collection facilities in the 1970's caused smolt densities to vary rapidly over short distances. Changes in local densities alter the frequency and intensity of interactions among migrating chinook salmon. Local spatial distributions may also be affected if aggregative or dispersal tendencies are density-dependent. It has been suggested, for example, that solitary Atlantic salmon smolts are attracted to schools of actively migrating smolts and will conform their behaviors to those of the school (Hansen and Jonsson 1985). Although the consequences of varying densities and rates of encounter among chinook smolts are not well-understood, energy expenditures, feeding rates, social interactions, risk of predation, and other factors affecting individual survival might be expected to change.

Hatchery fish comprised 50% to 75% of the total number of smolts passing the first dam they encountered on the Snake River in 1973-1979 (Raymond 1988). Based on more recent data, it seems reasonable to suspect that hatchery and wild chinook smolts differed in terms of survivability or catchability (Muir et al. 1990, Achord et al. 1992; see general review by Steward and Bjornn 1990). Differences in smoltification and disease status among hatchery and wild chinook salmon may also have affected the relative probabilities of survival and recovery at dams (Giorgi et al. 1988, Elliott and Pascho 1991, 1992).

Past studies do not provide conclusive evidence that hatchery-reared chinook salmon affect the survival of individual wild chinook smolts, or vice versa (Steward and Bjornn 1990). However, mean survival, when estimated for a mixed population, would appear to depend on differences in the relative abundance and rates of recovery and survival of hatchery and wild smolts. The ratio of hatchery to wild fish probably changed between Lower Granite and Ice Harbor dams, even though no additional hatchery fish were released between the two dams, for the simple reason that wild fish survived at significantly higher rates than hatchery fish at the outset of their migration (they also traveled more rapidly; see below) (Raymond 1979). Any decrease in the ratio of hatchery to wild fish in the run-at-large would have resulted in correspondingly fewer hatchery fish in control groups than in treatment groups. Changes in the composition of experimental groups may have introduced bias into survival estimates and increased the variance associated with those estimates.

Hoffman and Skalski (1993) concluded that a single-release, multiple-recapture approach to estimating survival is robust to violations of the assumption of homogeneous survival probabilities. Their simulation studies indicated that differential mortality in the various passage routes through hydroelectric dams does not bias survival estimates unless there is mortality in the bypass route below the point of detection. It is unclear whether the survival estimation methods employed by Raymond, Sims, et al. exhibited similar properties.

Assumption 6. Mortality related to handling, etc.

In this category can be placed experimental fish whose death prior to recovery can be directly or indirectly attributed to marking. Effects of this sort will generally be hard to detect. For the purpose of estimating survival, it is not necessary that mortality due to handling, marking, and transporting to the release site be negligible or even of consistent magnitude; it is only necessary that the number of treatment and control fish that die from these causes can be estimated. Mortalities can be subtracted from the original numbers of fish marked and released in each experimental group. However, there is no record of measurements or computational adjustments being made by NMFS researchers to account for tagging and handling mortality incurred during 1973-1979 survival experiments. .

Raymond (unpublished notes, ca. 1966) referred to limitations in body size when applying a thermal brand to salmonid smolts. He noted that in 1964 "only larger fish (>90 mm) could be marked; the smaller fish (10% or so of the run) may have survived at different rates or have been collected at different efficiencies." A similar sampling bias may have prevailed in later years. If larger smolts were more likely than smaller smolts to receive marks, and if probability of survival was positively correlated with fish size, then the survival of marked fish may have been higher than that of the unmarked population.

Raymond (1979) raised the issue of sampling-related mortality but suggested that differences were "minimal between sites and between years" during 1964-1975. In support of this claim, Raymond (1979) pointed to the positive relationship between sampling efficiency and flow and the positive correlation between juvenile survival and subsequent adult returns. Aside from the fact that these observations do not prove the point, I found ample circumstantial evidence to suggest that sampling-related mortality was a recurrent problem and that it varied across sites and over time.

For example, after 1975 treatment fish were transported by truck to the head of Lower Granite reservoir for release. During 1973-l 974, however, treatment fish were introduced directly into the tailrace of Little Goose Dam via a flexible hose (Gene Matthews, NMFS, personal communication). Mortalities associated with the two methods of release – transport vs. direct release – very likely were different.

Park (1985) summarized results of 48 h delayed mortality tests conducted with juvenile chinook salmon and steelhead under the transportation program during 1975-1980 (Table 6). Delayed mortality of smolts was measured after transportation by truck to release sites downstream of Bonneville Dam. Highest mortalities occurred in 1977, when approximately 30% of the transported fish died. The data provided by Park (1985), while not pertaining to fish used in survival experiments, nevertheless give some indication of the variability and magnitude of losses that may have occurred between projects and years. With improved passage conditions and handling techniques, mortality of chinook salmon smolts due to the effects of collection and marking at Snake River dams has declined in recent years to 0.5-l .2% (Matthews et al. 1988).

In 1979, delayed mortality was determined for both transported and non-transported chinook salmon migrants at Lower Granite Dam (Smith et al. 1980) and McNary Dam (Park et al. 1980, p. 4). Mortality of branded controls (non-transported) at Lower Granite Dam averaged 5 .0%, compared to 3.1% for fish that were branded and transported by barge. At McNary Dam, delayed mortality averaged 5.7% for controls, compared to 7.2% and 20.4% for fish transported by barge and truck, respectively. Although the results were not subjected to statistical analysis, it seems reasonable that similar levels of handling and marking mortality prevailed among fish used in survival experiments in 1979. Delayed mortalities may actually have been higher among treatment and control fish since, unlike the transportation controls, they were trucked to release sites after marking.

In later years, NMFS researchers adjusted mark releases to account for marking and reservoir mortality, which they assumed to range from 10% to 20% among experimental groups of fish at Lower Granite and McNary dams (Sims et al. 1982, App. Table F1, Sims et al. 1984, p. 8). These values were based on delayed mortality data for non-transported spring chinook obtained by Park et al. (1981, 1983).

Assumption 7. In-river mortality of control fish

Another critical assumption of the methods used by NMFS researchers to estimate survival is that none of the control fish released in the forebay of a recovery dam died before they arrived back at the dam. This assumption may have been violated since control releases were typically made several miles upstream of recovery dams to ensure interspersion, and recoveries of controls were often prolonged over several days. For example, “forebay” releases were made at various times approximately 33 miles upstream from Lower Granite Dam, 13 miles above Little Goose Dam, and 8 and 13 miles above Ice Harbor Darn. Recent studies have suggested that predation on migrating chinook salmon may be significant over reaches of comparable length within Columbia River reservoirs (Vigg et al. 1991).

Downstream migrations of marked fish were presumably slowed until the fish recovered from the stress of handling, etc. High stress levels and significant migrational delays may have predisposed experimental fish to increased mortality. The time it took to recover 50% of the

Table 6. Delayed mortality (48 h) of chinook salmon migrants that were marked and transported from Lower Granite, Little Goose, and McNary dams to release sites downstream from Bonneville Dam, 1973-1980. Data are from Park (1985) unless otherwise noted.

Year	Average (%)	Range (%)
	Lower Granite Dam	
1975	**11.5**	**0.5-34.0**
1976	**4.7**	**0.0-31.6**
1977	**30.0**	**2.3-62.8**
1978	**17.1**	**6.5-43.7**
1979	**3.1**	
1980	**1.9**	
	Little Goose Dam	
1973	**17.2[a]**	
1974	**10.2[b]**	**-**
1977	**42.5**	**16.7-73.8**
1978	**13.1**	**0.0-52.0**
1979	**19.8[c]**	
	McNary Dam	
1978	**19.1**	**0.0-60.0**
1979	**20.4**	
1980	**6.8**	**-**

[a] **Ebel et al. (1973)**
[b] **Ebel et al. (1974)**
[c] **Smith et al. (1980)**

total number of fish recovered from each of 21 groups released into the forebay of Ice Harbor Dam during 1966-1972 ranged from less than 1 day to over 13 days (mean 6.4 days; Table 7). Survival estimates will be inflated to the extent that control releases failed to survive up to the time that they passed the dams.

Assumption 8. Random mixing

This assumption states that treatment and control fish within an experimental group are randomly mixed with each other and with the unmarked population. Also, marked fish suffer the same mortality and are as vulnerable to recovery as the unmarked.

Dauble et al. (1993) underscored the importance of random mixing (i.e., complete overlap at the time of recovery) of treatment and control fish to assure equal sampling probabilities. This assumption is more likely to be violated if control and treatment fish are released at different times, at distant locations, or under different environmental conditions. If treatment and control fish arrive at the recovery site at different times, survival estimates can still be obtained as long as sampling efficiencies did not change over the period of recovery. The assumption of random mixing becomes less tenable as sample sizes (either marks or recoveries) decrease.

Raymond et al. (1974) remarked on the difficulty of timing a forebay release to coincide with the arrival of upstream releases so that both groups were recovered at identical efficiencies: "When seasonal flows vary, it is often difficult to match recoveries of various marked fish releases." Given that flow regimes in most years were unstable, random mixing was probably the exception rather than the rule.

The hypothesis of random mixing of marked and unmarked fish was "tested" in 1972 by releasing marked fish on both sides of the river above trap and dam sampling sites (Raymond et al. 1975, Raymond 1979). According to Raymond (1979), "the assumption is satisfied if recovery rates from both release points are comparable." In fact, no significant difference in recovery rates was found (see his Table 1), but this misses the point. Unmarked fish were not involved in the comparison so the conclusion that they were randomly interspersed with marked fish was unwarranted.

Raymond et al. (1975) and Raymond (1979) also reasoned that the assumption of random mixing held true if the ratio of marked-to-unmarked fish collected in gatewells was similar to ratios obtained in samples collected with fyke nets, beach seines, and purse seines. They indicated that the catch composition of all samples was similar, but neglected to provide data and statistical analyses to support their claim.

As Dauble et al. (1993) pointed out, efforts to release control fish far enough upstream so that random mixing is ensured may reduce the likelihood that all control fish will survive until they arrive back at the dam. The potentially conflicting logistical demands imposed by various assumptions are a primary reason that Dauble et al. (1993) chose not to endorse survival estimation methods based on sampling efficiencies.

Table 7. Release and recovery dates, and elapsed time to recover (at Ice Harbor Dam) 10%, 50%, and 90% of the chinook salmon released into the Salmon River and the forebay of Ice Harbor Dam, 1966- 1972. Data were provided by H. Raymond to R.H. Lander (1972).

Year	Replicate	Median Release Date	Median Recovery Date	Number of Days to 10%, 50%, and 90% Cumulative Recovery
Fish Released into Forebay of Ice Harbor Dam				
1966	1	April 7	April 14	4 : 7 : 16
	2	April 8	April 15	-1 : 7 : 11
	3	April 22	April 30	3 : 8 : 14
	4	April 23	April 27	1 : 4 : 13
1967	1	April 13	April 26	5 : 13 : 19
	2	April 20	April 27	4 : 7 : 12
	3	April 27	May 3	1 : 6 : 12
	4	May 3	May11	5 : 8 : 20
	5	May 10	May 23	6 : 13: 15
	6	May 17	May 24	2 : 7 : 9
1968	1	April 10	April 15	1 : 15: 14
	2	April 17	April 24	1 : 7 : 19
	3	April 24	April 30	2 : 6 : 22
	4	May 1	May 7	2 : 6 : 19
	5	May 8	May 14	1 : 6 : 13
	6	May 15	May 20	1 : 5 : 8
1972	1	April 11	April 11	-1 : 0 : 17
	2	April 20	April 26	4 : 6 : 18
	3	April 26	May 1	2 : 5 : 16
	4	May 3	May 9	0 : 6 : 15
	5	May 10	May 13	1 : 3 : 7

Table 7 (continued).

Year	Replicate	Median Release Date	Median Recovery Date	Number of Days to 10%, 50%, and 90% Cumulative Recovery
	Fish Released into Salmon River near Whitebird			
1966	1	March 29	April 15	10 : 17 : 30
	2	April 4	April 19	11 : 15 : 28
	3	April 15	April 29	8 : 14 : 22
	4	April 27	May 9	8: 11 : 13
	5[a]			
1967	1	March 24	April 21	20 : 28 : 47
	2	April 7	April 25	11 : 18 : 36
	3	April 13	May3	13 : 20 : 33
	4	April 28	May 9	2 : 11 : 24
	5	May 4	May15	6: 11 : 20
	6	May 15	May 24	8 : 9 : 16
1968	1	March 27	April 23	19 : 27 : 41
	2	April 6	April 30	16 : 24 : 42
	3	April 16	May 4	13 : 18 : 34
	4	April 25	May 9	11: 14 : 20
	5	May 2	May 14	7 : 12 : 16
	6	May 6	May 17	8: 11: 15
1970	1	April 6	May 7	23 : 31 : 38
	2	April 15	May 11	22 : 26 : 30
	3	April 20	May 13	20 : 23 : 26
	4	May 6	May 19	7 : 13 : 18
	5	May 15	May 26	8: 11: 13
1971	1	March 29	April 21	17 : 23 : 33
	2	April 3	April 30	18 : 27 : 32
	3	April 15	May 2	12 : 17 : 20
	4	April 21	May 5	12 : 14 : 19
	5	April 30	May 11	9 : 12 : 18
1972	1	March 17	April 24	24 : 38 : 55
	2	April 6	April 26	16 : 20 : 36
	3	April 2 1	May 10	12 : 19 : 29
	4	May 1	May 13	10: 12: 21
	5	May 6	May 20	11 : 14 : 19

[a] Release and recovery dates were not provided in original table.

Assumption 9. Transportation losses are known

Prior to 1980, significant numbers of yearling chinook salmon were collected and transported from Ice Harbor Dam in 1968-1970, Little Goose Dam in 1971-1973 and 1976- 1978, Lower Granite Dam during 19751979, and McNary Dam in 1979 (Table 5). With the exception of 1974, when no fish were transported, the number of fish transported steadily increased from 109,000 fish in 1971 to over 2.4 million fish in 1979. The percentage of fish transported ranged from 0% in 1974 to 76% in 1977 (Park 1985).

In 1977, approximately 750,000 to 800,000 chinook salmon smolts were collected at Little Goose and Lower Granite dams and transported downstream by truck (Smith et al. 1980, Sims et al. 1977, p. 10). In a footnote to their Table 4, Sims et al. (1977, p. 12) noted that transported smolts were "subtracted from total smolts passing Lower Granite Dam for calculations of survival." Raymond and Sims (1980, p. 17) indicated that survival estimates for 1979 were adjusted for fish transported from McNary Dam, but do not explain how they arrived at that number. Aside from these two references, I found no further discussion of computational adjustments made. to account for losses to transportation. If adjustments were in fact made, the question remains as to whether calculations of survival were based on estimates of the number of ***marked fish*** transported, in which case mark-recovery data could be used, or were based simply on the *total number **of fish*** transported, which would imply that population size ratios were used to estimate survival.

Assumption IO. Statistical independence

Here, it is assumed that replicate observations were independent, so that, for example, they were unaffected by the order in which they were obtained. However, departures from independence would be expected *a priori* because (1) flows over successive time intervals are autocorrelated, and (2) survival varied with flow.

In the spring of each of the years 1973-1979, several treatment and control groups, each bearing unique brands, were experimentally released into the Snake and Columbia rivers. Why were they not treated as independent samples? The reason, I believe, is that the fraction of marked fish recovered from individual groups and the timing of their recovery was too variable for them to serve as replicate observations (see earlier discussion). When survival rate is calculated from recovery of only a few marked fish, it must be used with caution (Ricker 1975).

Estimates of survival between the upper dam and Ice Harbor, and between Ice Harbor and the lower dam were not independent and should therefore not be multiplied together to estimate survival between upper and lower dams. Fish released and subsequently recovered at of Ice Harbor Dam were used to estimate the sampling efficiency of that dam as a prelude to calculating survival between the upper dam and Ice Harbor Dam. Rates of recovery of the same fish at downriver dams were used to calculate survival from Ice Harbor Dam to the lower dam. Survival estimates for Snake River and Columbia River reaches were thus not independently derived. It should also be noted that the number of marked fish intercepted at the dam immediately downstream of their release were probably not subtracted from the total number of fish marked prior to computing recovery rates dowmiver dams. Using an example taken from Raymond's unpublished notes, 86,43 1 fish were marked and released into the forebay of Ice Harbor Dam in 1968. Of these fish, 7,238 were subsequently recovered at Ice Harbor Dam, and 1,390 were recovered at The Dalles. In calculating the proportion recovered at The Dalles, Raymond neglected to subtract 7,238 from 86,43 1 to account for the reduction in size of the marked population. By not doing so, he underestimated recovery rates by 0.15%. Survival estimates would have been underestimated by a greater amount.

Assumption I I. Proportional sampling effort

If an average survival is to be estimated from replicate observations, the frequency and timing of individual estimates should be indexed to the relative abundance of unmarked fish in the river at the same time. There are two important reasons why this assumption should hold true:

1. "Flow" in the flow-survival relationship was based upon the date of peak passage of the entire run, and not simply on the timing of experimental fish.

2. Smolt survival is not constant over the outmigration period, but varies with time-dependent variables such as river flow and water temperature.

Raymond (1979) estimated average annual survival in 1973-1975 by weighting individual group survival estimates by the proportion of the total migration passing the release site. It is not clear whether Sims followed Raymond's example, even though in all years daily estimates of the number of smolts passing the upper dam were required to determine the date of peak passage.

Indexing interval-specific survival estimates to smolt population sizes presumes that sampling of marked and unmarked fish at the release site spanned the entire outmigration period. On at least two occasions, estimates of total smolt abundance and time of peak migration (which is sensitive to population estimates) may have been inaccurate due to late startup or premature termination of sampling at dams. In 1975, smolt monitoring at The Dalles Dam was conducted from 1 May to 3 1 May. Outmigration from the Salmon River (Riggins) peaked on 7 May. Travel time from the Salmon River trap to The Dalles Dam averaged 21 days (the same as in 1974), putting the peak of the outmigration there at approximately 28 May (Sims et al. 1976). It is improbable that the latter half of the smolt outmigration would have passed The Dalles Dam before sampling there was terminated.[6]

---

[6] Survival estimates for the lower river in 1975 may have been based, at least in part, on data collected at John Day Dam, where sampling began on 11 May and continued until 28 December.

An unusually late startup date at Lower Granite Dam in 1977 – 29 April (Sims et al. (1978, p. 3) – may have resulted in a significant portion of that year's smolt run being missed, thereby invalidating the "average" survival estimate obtained for that year. If substantial numbers of fish migrated past Lower Granite Dam before smolt monitoring began, then the peak passage mean flow in 1977 was probably lower than the 40 kcfs calculated by Sims and Ossiander (198 1). Dates of peak passage of chinook smolts were earlier in the preceding and following years – 2 1 April in 1976 and 29 April in 1978 (Sims and Ossiander 198 1, Table 3). In 1973 and 1979, however, later dates of peak passage (14 and 17 May) were recorded. Smolt trap data indicate that migration from the Salmon River was later than usual in 1977, and since river flows were exceptionally low that year, a 9 May peak migration date is not altogether unreasonable. The only way to reliably determine whether sampling at Lower Granite Dam in 1977 might have missed the first part of that year's run is to examine trends in the daily smolt count data for the dam. These data, unfortunately, could not be found.

Assumption 12. Flow measurements

For each of the survival-flow data pairs used in the least squares regression analysis conducted by Sims and Ossiander (1981), "flow" was determined as the mean daily flow past Ice Harbor over a two week period, centered on the date that 50% of the entire smolt outmigration had passed the dam. If the date of peak passage was incorrectly determined, then the'mean flow for that year would be in error.

There is a question as to whether flows averaged over the two week peak migration period were representative of the conditions under which smolts actually migrated. Although it makes sense to weight flows according to the number of fish present, there is no *apriori* reason to assume that two weeks is an appropriate time-scale on which to base flows. It is much more plausible that migrating smolts respond to trends and changes in flow on smaller time-scales (Smith et al. 1993).

Flow was calculated at Ice Harbor Dam on the Snake, yet overall survival was determined for both Snake and Columbia River segments. If flows in the Snake and Columbia River are strongly correlated, then discharge at Ice Harbor Dam may be satisfactory as an independent variable. However, I see little point in using flow measured at a single dam in an analysis purporting to relate flow and survival in both the Snake River *and* the Columbia River. Flows at Ice Harbor Dam may be a valid predictor of survival in the Snake River, but they are less appropriate for the Columbia River. This is particularly true for years such as 1977, when special releases of water ("Operation Fish-Flow") resulted in higher flows in the Columbia River, but not in the Snake River (Sims et al. 1978, p. 7). Raymond and Sims (1980) noted that similar levels of spill were provided at Columbia River mainstem dams in 1977, 1978, and 1979, but that survival was much lower in 1977 than in 1978-79.

The bottom line is this: separate flow-survival relationships should have been derived for the Snake and Columbia rivers since flows, smolt population characteristics, and various mortality factors may have varied between reaches within the same years.

I made no special attempt to assess the reliability of the stage-discharge relationship used to estimate flow at Ice Harbor Dam during 1973-1979. I recalculated mean daily flow values associated with dates of peak outmigration (± 7 days) for the years of interest and found that they corresponded closely with those used by Sims and Ossiander (1981). However, there were minor inconsistencies in reporting of mean flow values in the various NMFS reports. For example, Sims et al. (1977, p. 7) indicated that the mean daily flow at peak migration in 1975 was 160 kcfs, whereas Sims and Ossiander (198 1) reported 140 kcfs (this appears to be the correct value). The reason for this discrepancy is not known.

Assumption 13. Statistical models

One of the problems with applying correlation-regression analysis to the flow-survival database is that survival estimates, as Raymond (1979) calculated them, are themselves a function of flow-based sampling efficiencies. If we have a set of flows, $y_i, \ldots, y_n$, measured at the same time that survivals are measured as $\hat{s}_i = c_i / e_i$, where $e_i = f(1/y_i)$, and then look at the relation of y to s, we would expect to find a strong, positive correlation between the two parameters. Spurious relations – that is, relations that may have little to do with the true flow-survival relationship – may be introduced because flow and survival estimates are computed from the same set of data. This is an important limitation of the use of flow-efficiency curves in survival estimation.

I did not attempt to fit a different curve to the Sims and Ossiander (198 1) flow-survival data, but note that Sims et al. (1983) replaced the original log-linear model with one based on an inverted polynomial function to describe the relation between flow and survival using data from 1973-1979, plus 1980 and 1982 (Figure 5). There is no compelling biological basis for believing that the relation between survival and flow is linear rather than curvilinear. To the naked eye, the 1980 and 1982 data would not appear to have much effect on the shape of the curve since they are tightly clustered with several other data points. Differences in the models selected by Sims and Ossiander (198 1) and Sims et al. (1983) reveal doubt in the mind of the authors as to the true relationship between flow and survival, especially at higher flows.

One final point is that virtually all regression models require assumptions of homoscedasticity (i.e., common variance) and normality of mean survival values for any given flow. These assumptions are given ample treatment in basic statistics texts, and so will not be discussed further here. Sample sizes used to construct the flow-survival relationship were too small to determine whether or not these assumptions were satisfied.

Assumptions 14 and 15. Representativeness of experimental conditions

By this assumption it is meant that the relation between survival and flow did not vary between years while the data were being collected, and that the relation remains a valid predictor for times (e.g., years) or conditions other than those under which the data were collected. It should be stressed that the flow-survival regression is strictly valid only for flows falling within

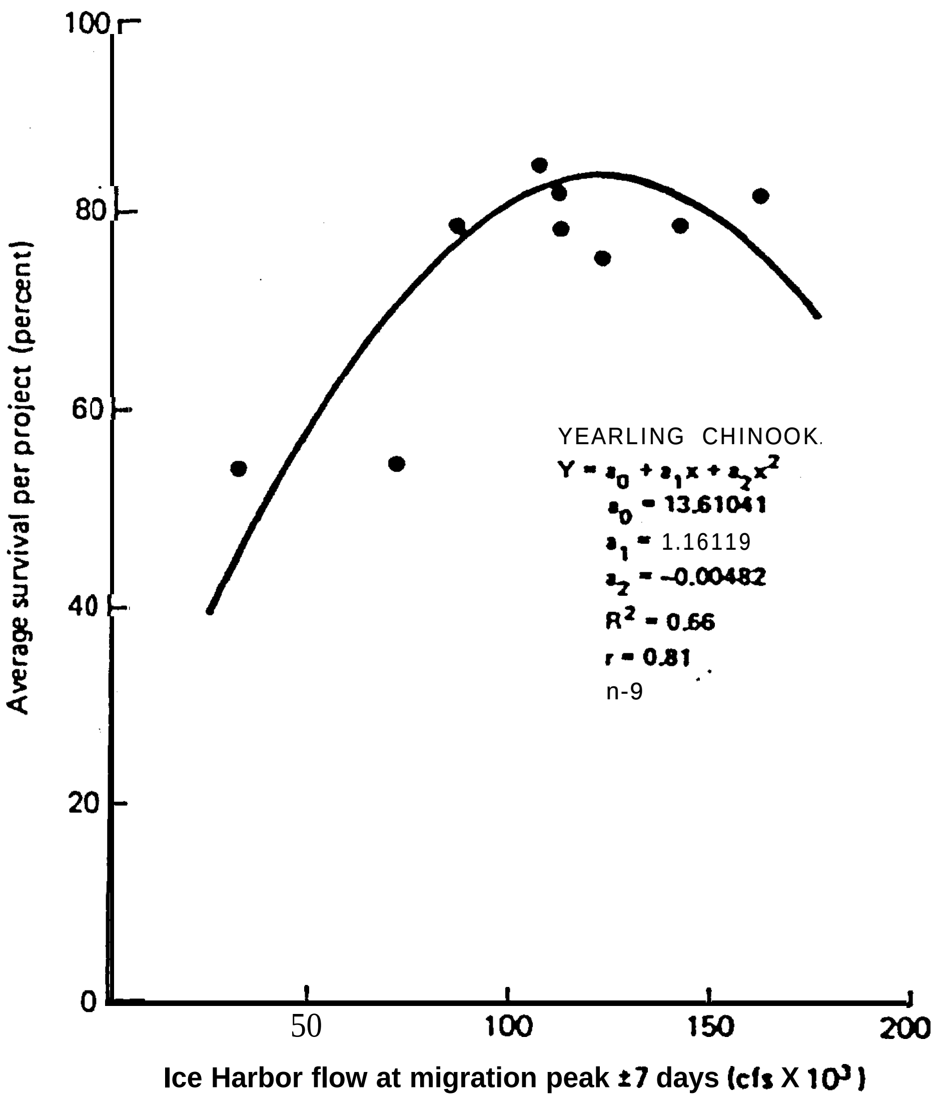

Figure 5. Non-linear relationship between flow and survival obtained by Sims et **al.** (1983) using data from 1973-1979, 1980, and 1982.

the range of observed values, i.e., 40 to 160 kcfs. One should extrapolate with caution outside these limits.

Application of the flow-survival relationship requires the assumption that the dependency relation between flow and survival has not changed because of changes in the environment, the fish, or both. As discussed in later sections, several developments occurred both before and after 1979 that may prevent extrapolation of the flow-survival relationship to contemporary settings.

4.2 Analytical Methods

To the extent that information was available, the primary mark-recovery data, the numerical and statistical methods used to analyze them, and the results of the analyses are discussed in detail in this section.

4.2.1 Sample sizes

Although many of the assumptions discussed above are theoretically independent of sample size, those relating to random and representative sampling of the smolt population are not. Both the number of groups and the number of fish marked and recovered per group have important effects on the precision of annual survival estimates and, ultimately, on the kinds of statistical analyses and inferences that can be derived from those estimates.

Information on the number of experimental groups and the number of fish marked and recovered within each group was not routinely included in NMFS reports. However, data sheets which tabulated marks and recoveries for 1976-1979 were located in NMFS archived files. These data sheets were used to reconstruct the information provided in Table 8. Some of the data sought from this period were missing and therefore could not be summarized; the absence of such data merely indicates that we were unable to locate it, and is not meant to give the impression that it was not collected. To the best of my knowledge, the data used to calculate the statistics presented in Table 8 were accurate and complete. With these qualifications in mind, we make the following observations:

1. The total number of fish marked and released was variable across dams and years.

2. The number of replicate groups marked and released each year was variable across dams and years.

3. The number of fish marked per group was variable within and across years; the number of fish per group was inversely related to the total number of groups released. Thus, more experimental fish were released at Lower Granite Dam but they were divided among fewer replicate groups than at downriver dams.

Table 8. Reported number of chinook salmon smolts marked and recovered at various dams during 19761979. This information was abstracted from the original NMFS data sheets; the data could not be verified for accuracy and should therefore be considered unreliable.

Year	Release Site / Recovery Site	Number of Fish Recovered: Range	Total	Percent Recovery: Range	Mean
1976	***Lower Granite Dam: 3 markedgroups numbering 56 to 18,312 fish (total: 28,688)***				
	Ice Harbor Dam	0 - 240	248	0.0% - 1.1%	0.9%
	McNary Dam	0 - 286	312	0.0% - 1.6%	1.1%
	John Day Dam	1 - 80	121	0.0% - 1.1%	0.9%
1976	***Ice Harbor Dam: 8 markedgroups numbering 291 to 2,033 fish (total: 14,800)***				
	Ice Harbor Darn	o- 91	203	0.0% - 2.4%	1.4%
	McNary Dam	1 - 129	239	0.1% - 3.0%	1.6%
	John Day Dam	1 - 31	62	0.2% - 1.1%	0.4%
1976	***John Day Dam: 8 markedgroups numbering 212 to1,319 fish (total: 5,940)***				
	John Day Dam	1 - 13	40	0.1% - 1.4%	0.7%
1977	***Lower Granite Dam: 5 markedgroups numbering 28 to 15,987 fish (total: 38,262)***				
	Ice Harbor Dam	o- 11	19	0.0% - 3.6%	0.06%
1978	***Lower Granite Dam: 4 marked groups numbering 2,144 to 15,232 fish (total: 46,094)***				
	Ice Harbor Dam [a]	3 - 63	127	0.1% - 0.4%	0.4%
	John Day Dam	0- 69	191	0.0% - 0.5%	0.4%
	The Dalles Dam	0- 27	40	0.0% - 0.1%	0.1%
1978	***John Day Dam: 30 marked groups numbering 26 to 636 fish (total: 7,281)***				
	John Day Dam	0- 16	113	0.0% - 7.7%	1.6%
	The Dalles Dam	o- 3	15	0.0% - 1.8%	0.2%
1979	***Lower Granite Dam: 4 marked groups numbering 5,772 to 19,760 fish (total: 50,629)***				
	Ice Harbor Dam	27 - 154	357	0.0% - 2.7%	0.7%
	McNary Dam	78 - 788	1367	1.1% - 4.0%	2.7%
	John Day Dam	12 - 117	161	0.0% - 0.6%	0.3%
	The Dalles Dam	0- 27	40	0.01% - 0.1%	0.1%
1979	***John Day Dam: 20 markedgroups numbering 92 to 425 fish (total: 4,536)***				
	John Day Dam	92 - 425	32	0.0% - 4.2%	0.7%
	The Dalles Dam	o- 3	8	0.0% - 1.2%	0.2%

[a] Recovery data for one of the release groups (brand LAP1/5) could not be found and so were excluded from range and mean calculations.

4. The proportion of fish recovered from each marked group was extremely variable and generally low.

Raymond's notes indicated that he deleted from the database data for experimental groups which he considered unreliable. In 1972, for example, the last group of fish released into the forebay at Ice Harbor Dam (actually 2 groups released simultaneously on both sides of the river) was recovered at a much lower rate (0.34% and 0.45%) than were the preceding 5 groups (range 2.46 - 5.75). Raymond did not use the last group in survival calculations for that year.

4.2.2 Recover-v Data

NMFS studies were designed to measure within-season survival over a range of environmental conditions. Survival was estimated by subsampling the chinook smolt population rather than by marking and resampling the entire population and computing the parameter exactly. If multiple subsamples (i.e., individual release groups) were taken, then it should have been possible to analyze survival data by individual release groups to get empirical variance estimates. Sampling variance among $\hat{s}_i$'s would give some indication of within-season variability and precision of the annual survival estimates.

Estimates of sampling variance or standard error normally accompany point estimates of a parameter. Why NMFS researchers chose not to report variance estimates is unclear, since individual $\hat{s}_i$'s were computed and averaged in early survival studies. In some years, the number of fish recovered might have been too variable to reliably calculate $\hat{s}_i$. With regard to sampling variability, Sims et al. (1984, p. 24) remarked that in 1982 and 1983, "the variance around our survival estimates was too great to permit adequate definition of between-year flow/survival relationships. We will make no further efforts in this area until the precision of our existing collection efficiency curves are (sic) substantially upgraded."

Another reason that Raymond, Sims, *et alia* may have opted to forego estimates of group survival was the extremely small fraction of marked fish recovered in some years, especially from upstream releases. Raymond and Sims noted (on p. 10 of their 1975 proposal) that during "the high runoff of 1974, efficiency [at The Dalles Dam] dropped below 0.5% and recoveries from Little Goose Dam were insufficient to assess survival from there to the John Day-Dalles area with any degree of statistical confidence." Data provided by Raymond et al. (1975; Appendix AZ) indicated recovery rates of 0.2% for treatment *and* control fish at The Dalles Dam in 1974.

As low as these rates may seem, recovery rates were an entire order of magnitude lower in 1977. Sims et al. (1978; p. 17) cite data from an experiment to measure differences in survival of fish released in frontroll and backroll areas at Little Goose Dam: out of a total of 75,751 chinook salmon smolts marked and released at the dam, only 14 (0.02%) were recovered later at The Dalles. The authors concluded that "recoveries at downstream dams were too low to measure statistical differences between frontroll and backroll releases." Sims et al. (1978) chose to apply "past collection efficiencies" to estimate population sizes at the upper dam (Lower Granite) in 1977 due to extremely low recoveries of control fish.

Problems associated with low recovery rates were not limited to the 1973-1979 period. Raymond (unpublished notes) provided examples from earlier years, and Smith et al. (1993; see their Table 27) provided examples from the 1980s which point to widespread problems. The long-term record also contains numerous examples in which a higher proportion of treatment fish than control fish were recovered, with the result that survival estimates exceeded 100% (Raymond, unpublished data; Sims et al. 1982, p. 22). Compare, for example, the total proportion of treatment fish (Salmon River release) and control fish (forebay release) recovered at Ice Harbor Dam in 1966, 1967, 1968, 1972 (Table 9). In all years except 1972, recovery rates were higher for treatment fish. Control fish either died en route to the dam or were less susceptible to recapture than were treatment fish. This unexpected result obviously makes survival estimation based on data summation impossible.

There appears to have been sampling problems in other years as well. Noting that Little Goose Dam forebay recoveries in 1971 were approximately 40% less than those calculated for fish released into the Salmon River near Riggins, Idaho, Raymond opined, "the fish must have been under stress." In 1974, recoveries at Ice Harbor Dam of Lower Granite Dam releases were less than 60% of those recorded for fish released into the Salmon River near Riggins, Idaho (Raymond, unpublished notes). Fish released in the forebay of Ice Harbor Dam in the same year were recovered at McNary Dam in higher proportions than were fish released in the Ice Harbor tailrace.

Sims et al. (1982, p. 22) provided examples from later years in which within-year flow-survival estimates exceeded 100%. Referring to their Table 2, survival rates of 120% and 102% were estimated for two of the four experimental groups of fish that traversed the Columbia River between Ice Harbor and John Day dams.

Since estimates of survival for individual release groups were on occasion unreliable, annual survival was often computed by summing the total number of treatment fish marked over the season, dividing this by the total number of treatment fish recovered at the downstream dam, and then dividing again by the average sampling efficiency of that dam. Sampling efficiency itself was determined by summation of marks and recoveries over the entire season. Sampling variance could not be determined by this technique since all mark and recovery data had been combined to obtain a single season survival estimate.

4.2.3 Samulinn Efficiency

Sampling efficiencies at Columbia River dams were observed to vary as a function of flow. The amount of water spilled, in particular, was important since it affected the movement and distribution of smolts, and fish passing over the spillway were not sampled. Efficiencies were quite variable. At Ice Harbor dam, for example, as recovery rates as high as 17% were

Table 9. Recovery and survival rates for chinook salmon migrants released into the Salmon River (treatment fish) and the **forebay** (controls) of Ice Harbor Dam, and then recovered at that dam. Survival calculations assume that treatment and control fish were paired by group within years. Data were provided by H. Raymond to RH. Lander (1972).

		Treatment Fish			Control Fish			
Year	Group	Number Released	Number Recovered	Percent Recovered	Number Released	Number Recovered	Percent Recovered	Percent survival
1966	1	4798	329	6.9	2143	117	5.5	125.6
	2	5582	338	6.1	1771	105	5.9	102.1
	3	3929	96	2.4	3341	119	3.6	68.6
	4	4379	95	2.2	2980	56	1.9	115.4
	5	1033	18	1.7				
	Total	**19721**	876	**19.3**	**10235**	**397**	**16.8**	**114.5**
1967	1	1501	89	5.9	2107	150	7.1	83.3
	2	6690	547	8.2	5100	433	8.5	96.3
	3	7430	618	8.3	7236	616	8.5	97.7,
	4	2365	119	5.0	4594	192	4.2	120.4
	5	5255	153	2.9	4594	192	4.2	69.7
	6	896	11	1.2	2124	26	1.2	100.3
	Total	22636	1448	25.7	23648	**1459**	26.6	96.5
1968	1	3358	363	10.8	7843	1334	17.0	63.6
	2	647 1	944	14.6	17499	2180	12.5	117.1
	3	2952	374	12.7	15711	1292	8.2	154.1
	4	2120	119	5.6	15711	1292	8.2	68.3
	5	2129	113	5.3	21964	1159	5.3	100.6
	6	2078	63	3.0	11371	542	4.8	63.6
	Total	**15750**	**1613**	41.2	82256	6465	38.9	105.8
1972	1	17780	226	1.3	4097	231	5.6	22.5
	2	16682	234	1.4	4097	231	5.6	24.9
	3	9725	86	0.9	5023	172	3.4	25.8
	4	28865	123	0.4	5543	121	2.2	19.5
	5	7615	19	0.2	5543	121	2.2	11.4
	Total	80667	688	4.2	24303	876	**19.1**	22.2

recorded for control releases at low flows (1968 tests), when little water (and few fish) were passed over the spillway, and as low as 1% at high flows, when increasing amounts of water were spilled over the face of the dam (Table 9). At other projects – John Day Dam, for example – sampling efficiencies of less than 1% were commonplace (Table 8).

A flow-efficiency curve was developed for Ice Harbor Dam by Raymond and applied in 1973-1975 to estimate smolt survival and run size. At Ice Harbor during 19751979, and at John Day and The Dalles dams during 1973-1979, sampling efficiency was determined from recovery rates of control fish released immediately upstream of the dams at more-or-less the same time that treatment fish were in transit.

Sampling efficiency data for 1973- 1979 were not routinely reported. Sims et al. (1976, 1977, 1978) and Sims and Ossiander (1981) declined to provide data. Raymond et al. (1974, 1975) tabulated the total number of chinook and steelhead released in forebays of Little Goose and Ice Harbor dams and subsequently recovered at downstream dams in 1973 and 1974. Efficiencies were not provided for individual control groups, nor were they specifically related to river flows or treatment groups.

Raymond (1979, p. 509) noted that a flow-efficiency curve was not developed for The Dalles, even though his unpublished and published writings clearly indicated his intent to do so. That Raymond (1979) neither explained his failed attempt, nor discussed the problems this might have posed was rather odd considering his touting of the Ice Harbor Dam efficiency curve as "a major breakthrough." The Ice Harbor curve, the reader is informed, permitted estimates in years "when fish were too stressed from gas bubble disease to be marked and released for efficiency measurements." These same constraints presumably prevailed at other dams in years of high levels of dissolved atmospheric gases (1969-1972 and 1974). Another advantage of a flow-efficiency curve, says Raymond (1979), was that it permits greater temporal resolution – "daily if necessary" – of the number of smolts passing a dam. These benefits were not realized at The Dalles Dam or, following 1975, at Ice Harbor Dam.

Even though a relation between sampling efficiency and river flow was not established for The Dalles Dam, Raymond (1979) claimed that "recoveries of upstream releases have been sufficient to provide meaningful estimates of survival" at the dam in years of low and average flow. Efficiencies at The Dalles under these conditions ranged between 2 and 6%, considerably lower than those calculated under similar flow conditions at Ice Harbor. In high flow years, efficiency was less than 1% which, Raymond (1979) remarked, "greatly reduces confidence in estimates of survival."

Raymond et al. (1975) refer the reader to Raymond, Bentley, and Ossiander (1975) for computational details on efficiency curves for chinook and steelhead. The reference as cited was never published and a draft could not be located. The only published information relating to the derivation of sampling efficiencies is found in Raymond et al. (1974, 1975) and Raymond (1979). The information provided in these documents lacks detail and is somewhat contradictory. For example, the graph of chinook sampling efficiency versus flow for Ice Harbor, first published in Raymond (1975), underwent considerable refinement without benefit of new data before emerging in final form in Raymond (1979). Figure 6 plots the same flow-efficiency curve as it appears in two published and one unpublished documents.

Raymond's notes and published writings did not describe how the flow parameter used in the flow-efficiency regression was calculated. Each group of control fish was typically released over a period of several days; they were recovered over an even greater time interval. No effort was made to calculate a weighted mean flow to account for flow fluctuations which might have occurred while fish in a group were in transit.

Far more problematic than curve fitting techniques are computational errors that may have occurred in Raymond's treatment of the sampling efficiency data. The errors relate to numerical expansions of numbers based on the number of gatewells sampled and the number of days when sampling was not conducted. To give some idea of the complexity of the problem, consider the following statement made by Raymond (unpublished notes, letter to "Bob"):

> "What I need is average % catch by gatewell with respect to flow and turnover or exit rate in general when a gatewell has not been fished daily. I have catch and mark release records so we can later adjust the measured to an expected efficiency based on fishing effort."

The Ice Harbor flow-efficiency curve was based on the proportion of marks recovered in Unit 2 gatewells (3 in all) that were expanded to the remaining units of the dam. Twenty seven independent observations of flow and sampling efficiency were made during 1964 - 1969 (with the exception of 1966), and 1972. Actual recoveries were expanded on the basis of the proportion of fish collected from Unit 2 gatewells compared to Unit 1 and 3 gatewells in 1966, when all three units were sampled concurrently. The proportion collected from Unit 2 averaged 40%, but the original (unpublished) data reveal that Unit 2 catches comprised anywhere from 15 to 70% of the total recoveries of forebay-released fish (the cause for this variability is unknown). Raymond's notes suggested that individual gatewells displayed different sampling efficiencies. Bentley and Raymond (1968, p. 126) recovered 1.5% of previously marked control fish from gatewells A, B, and C of Unit 2 at Ice Harbor Dam in 1966. Another 2.5% fish were recovered from Units 1 and 3 gatewells, with the total proportion caught varying between 2% and 6% during high and low flows, respectively. In any event, Raymond used a factor of 2.5 to expand his Unit 2 recovery proportions to those used in his efficiency curve.

If recoveries of marked fish at Ice Harbor Dam in subsequent years were based on samples taken from Unit 2 alone, then expanded sampling efficiency estimates would have been unnecessary. However, in an effort to provide an alternate route through the dam, the U.S. Army Corps of Engineers drilled orifices in all gatewells in 1970. From then on, smolt counts were based on sluice trap catches of fish from all gatewells. A "whole dam" sampling efficiency was therefore needed.

The accuracy of the Ice Harbor Dam flow-efficiency curve is difficult to assess but what few data exist suggest that sampling efficiency may have been overestimated. From data and

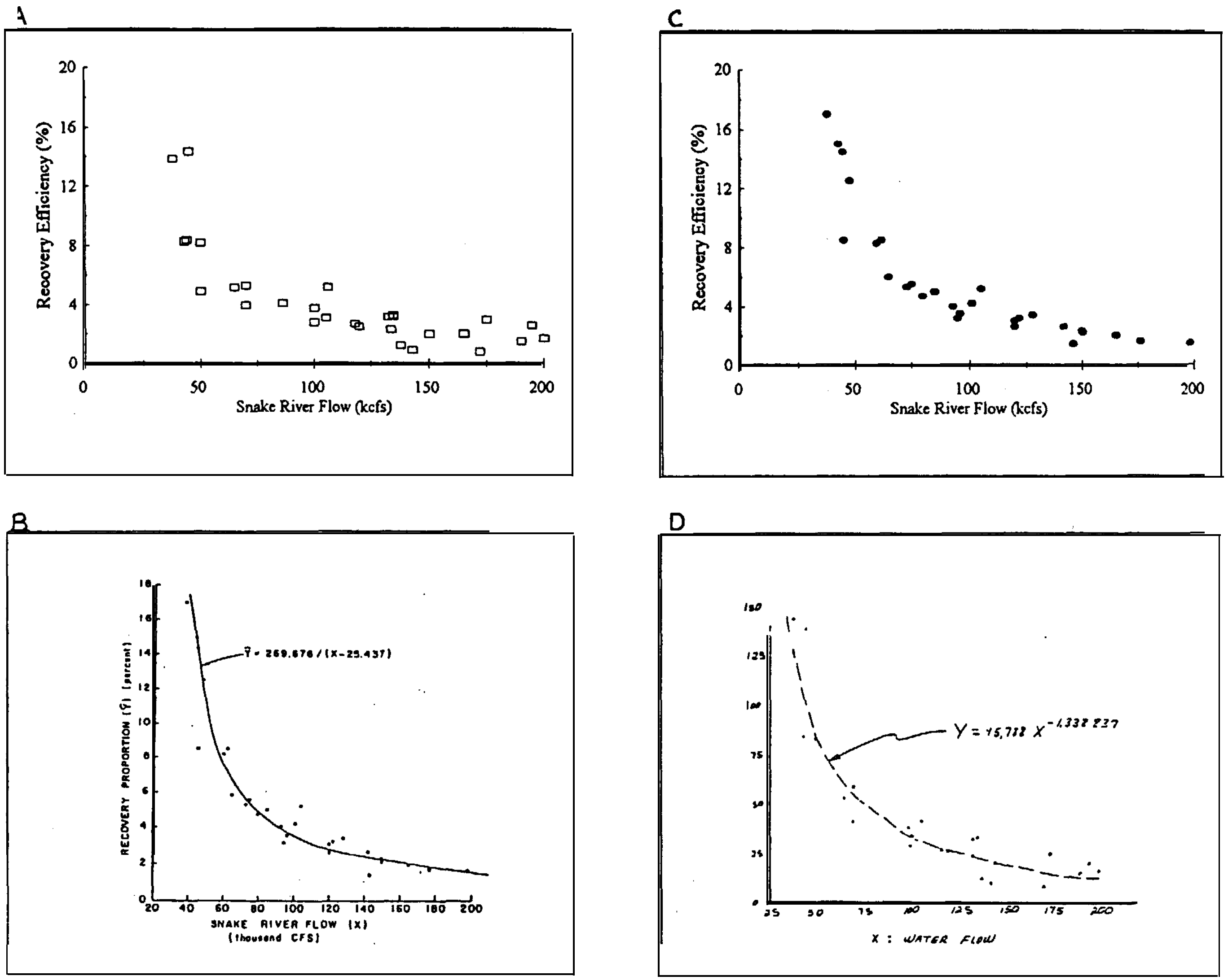

Figure 6. Variations of Ice Harbor flow-efficiency curve for chinook salmon smolts: Figures A and B display data from 1964, 1965, 1967-69; Figures C and D display data from the same years plus 1972. Figures A and C are drawn from data in unpublished tables compiled by Raymond; Figure B is a reproduction of Figure Al from Raymond et al. (1975); Figure D is a reproduction of an unpublished graph from NMFS files.

calculations performed by Raymond et al. (1975, see his Appendix A2 and Appendix Table B2), for example, it can be seen that the 2.4% "average" sampling efficiency at Ice Harbor Dam in 1974 was conspicuously higher than efficiencies reported that year for McNary and The Dalles dams (1.3% and 0.2%, respectively). The observed sampling efficiency, based on control fish recoveries, was 0.9%, or 58 fish recovered out of 6,500 marked and released. The observed efficiency was considerably less than that predicted by the flow-efficiency curve. It was also less than the proportion of Little Goose-released fish recovered at Ice Harbor Dam (1.12 %). Had 0.9% been used instead of 2.4% as an average efficiency value, a survival rate of greater than 100% would have resulted.

Curiously, in 1973 the sampling efficiency observed at Ice Harbor Dam was also 0.9% (102 control fish recovered out of 12,000 released), even though flows were much lower in 1973 than in 1974 (Table 5). Sampling efficiency would be expected to be higher at lower flows.

Based on the foregoing assessment I conclude that the Ice Harbor Dam flow-efficiency curve does not provide adequate estimates of reach survival because of inaccuracies in the methods used in its computation.

4.2.4 In-season Survival Estimates

Given reliable mark-recovery data, a logical approach to establishing a flow-survival relationship would be to use survival ($\hat{s}_i$) and mean daily flows calculated for individual experimental groups. The major advantages of this approach are obvious: one obtains a larger sample size and a relation based on short-interval estimates rather than seasonal averages of survival and flow. Unfortunately, the number of fish recovered from individual groups was often too low or variable to be of much use in this regard. I was unable to assemble a reliable set of data from the 1973-1979 period that would enable a comparison of flow and survival for individually released groups.

However, a dataset from the 1966-1972 period was located. In 1972, Raymond provided detailed mark and recovery data to the statistician R.H. Lander for his review and comment. The data, which are reproduced in Table 9, pertained to the number and timing of chinook salmon released in individually marked groups in the lower Salmon River, and subsequently recovered at Ice Harbor Dam in 1966-1972, except 1969, when funding shortfalls curtailed field studies. Recovery rates were reported for 3 1 treatment groups and 21 control groups (no data were provided for control groups that may have been released in 1970 and 1971). I analyzed these data to see if a correlation exists between survival values calculated for individual groups and flows that prevailed at the time that the groups were recovered. Two approaches were taken to estimating survival.

Method I. Survival was estimated as the ratio of treatment and control group recovery rates, where each treatment group was paired with the control group from the same year having the most similar median date of recovery. This was the approach originally envisioned by Raymond. Dividing the recovery rate of the treatment group by the recovery rate of its matching control group provided an estimate of survival. Because no data were available for control groups that might have been released in 1970 and 1971, survival was determined by Method 1 for a total of 21 treatment groups from 1966, 1967, 1968, and 1972.

Method 2. There were three steps to calculating survival by the second method:

1. For each treatment group, a mean daily flow was estimated for (a) the median recovery date, (b) the fifteen day period centered on the median recovery date (i.e., ± 7 days), and (c) the period beginning and ending on the dates when 10% and 90% of the fish in the group had been recovered.

2. Sampling efficiency associated with each flow statistic was determined using Raymond's (1979) flow-efficiency curve (Figure 3); note that forebay-released (i.e., control) fish and not treatment fish were used to construct the flow-efficiency curve, and

3. Treatment group survival was estimated by dividing the proportion recovered by sampling efficiency.

Survival values obtained by Methods 1 and 2 were then regressed against flow statistics associated with the 50% recovery date, the 50% recovery date ± 7 days, and the 10% to 90% recovery dates (see Step 1 of Method 2). The strength of association between flow and survival variables was not noticeably improved by scalar transformation of the data.

The proportion of treatment 'fish recovered at Ice Harbor Dam that had been released in the Salmon River in 1966, 1967, 1968 and 1972 (Figure 7) shows the same pattern that Raymond (1979) observed for forebay-released fish (Figure 3). At low flows, such as occurred in the early part of the 1968 outmigration, double-digit recovery rates were recorded. A parabolic decline in the proportion of fish recovered was observed at higher flows.

When the proportion of fish recovered from each treatment group is adjusted by its control group recovery rate, a survival estimate results. Survival rates determined in this fashion were regressed against mean daily flow (Figure 8). Regardless of the flow statistic used, the correlation between flow and survival is weak. This is particularly true when 1972 data are excluded from the analysis (recall that Lower Monumental and Little Goose dams were built in 1969 and 1970, so the comparatively low survival rates from 1972 reflect the effects of those dams). The resulting straight-line regression equations and correlation coefficients evidence a downward trend in survival with increasing flow, but the correlation between the two variables was not found to be significant. Another obvious point to be considered is that survival rates frequently exceeded 100% – an unrealistic outcome that signals potential violations of underlying methodological assumptions.

Survival rates determined by Method 2 also exceeded 100% for several treatment groups (Figure 9). Since a flow-efficiency relationship was used to estimate survival, data from 1970 and 1971 were retained in the correlation analysis. Survival rates did not appear to vary predictably with flow when the independent variable was the l-day mean flow associated with

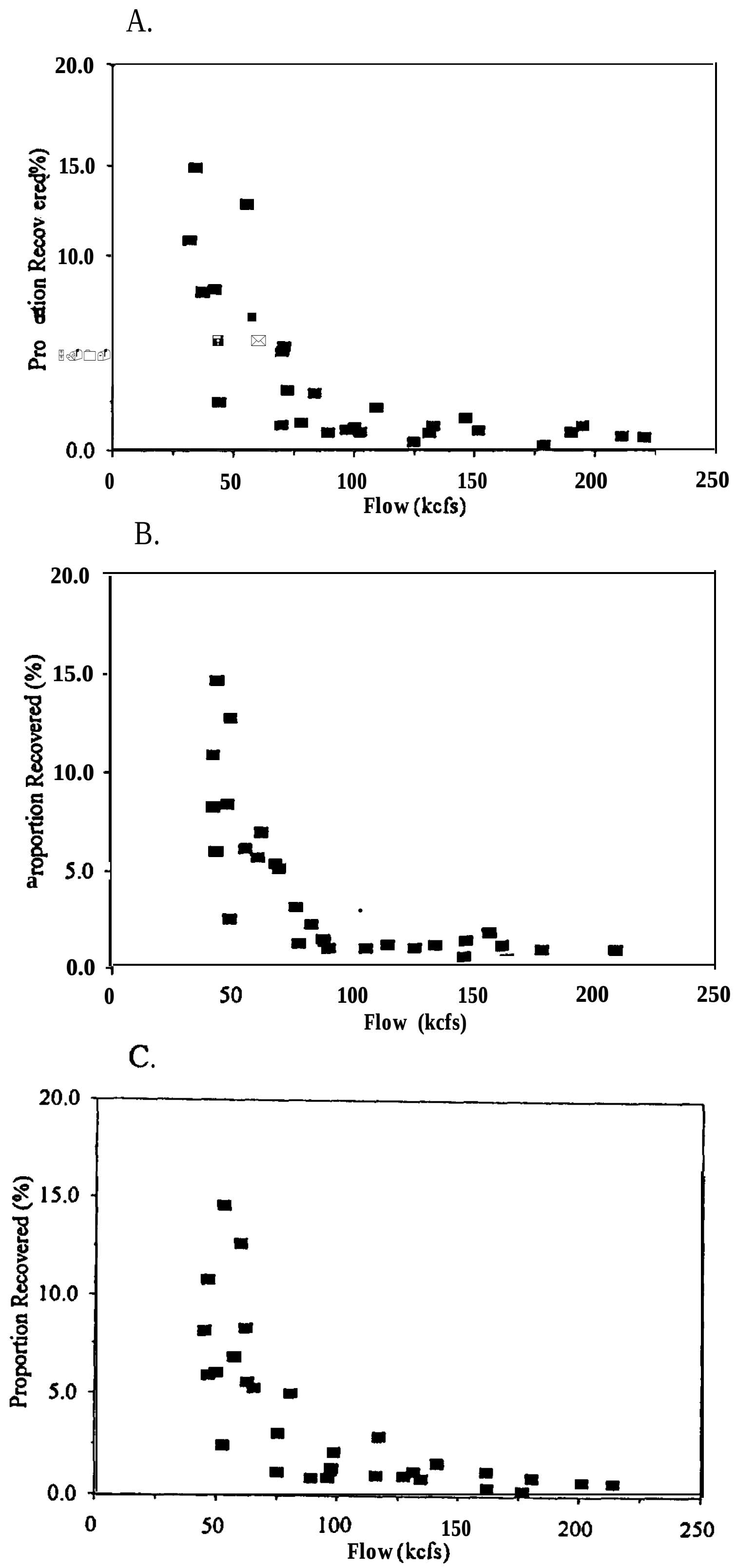

Figure 7. Proportion of fish released into the Salmon River in 1966, 1967, 1968 and 1972 subsequently recovered at Ice Harbor Dam, expressed as a function of flow.

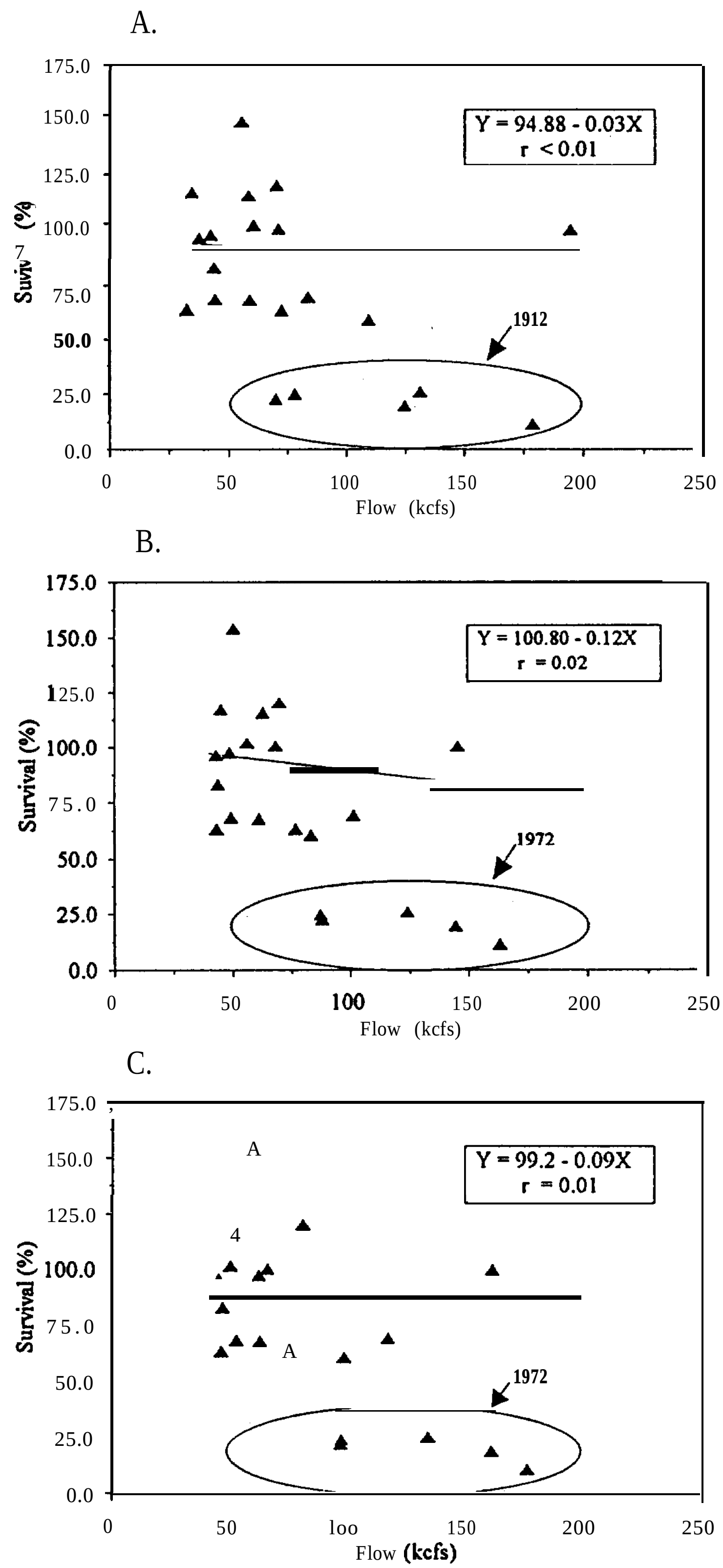

Figure 8. Survival to Ice Harbor Dam of fish released into the Salmon River, determined by Method 1 (see text for details), plotted against river flow associated with (A) the 50% recovery date (B) the 50% recovery date ± 7 days, and (C) the 10% to 90% recovery dates.

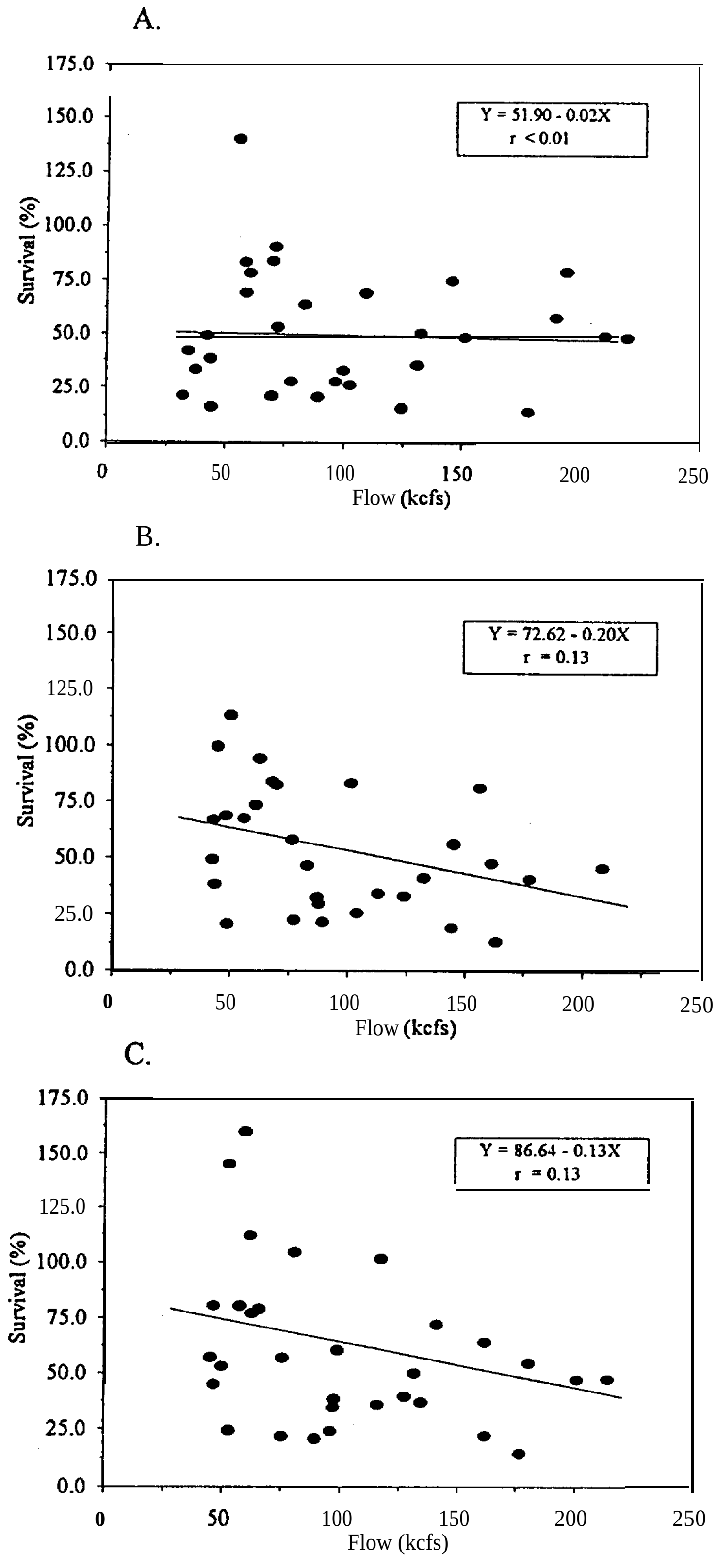

Figure 9. Survival to Ice Harbor Dam of fish released into the Salmon River, determined by Method 2 (see text for details), plotted against river flow associated with (A) the 50% recovery date (B) the 50% recovery date ± 7 days, and (C) the 10% to 90% recovery dates.

the median date of recovery. When plotted against the other flow statistics, however, survival decreased with increasing flows. The slopes of both regression lines were significantly different from zero **($p < 0.05$),** indicating that flow was a useful predictor of survival under the conditions that prevailed at the time. That the relation between the two variables was a negative one was unexpected, since a positive flow-survival relationship was obtained by Sims and Ossiander (198 1) using annual average survival estimates.

4.2.5 Annual Survival Estimates

In this section I compare annual survival estimates gleaned from Sims and Ossiander (198 1) and other published sources and highlight major discrepancies in reported values on a year-by-year basis (Table 10). I have tried to identify underlying causes for the discrepancies where practical, but emphasize that my analysis was constrained by incomplete information. One only needs to peruse Raymond's handwritten notes to appreciate the flexibility of his treatment of mark-recovery data from the 1960's and 1970's. I found numerous instances where Raymond had changed numbers, deleted data, and applied different analytical approaches to the same data. I do not suggest, however, that scientific objectivity was sacrificed in the process. To some extent, exploratory analysis and consideration of alternative treatments of the data are acceptable and necessary actions.

It should be noted that inconsistencies in reported values were not limited to chinook salmon survival estimates, but extended to other parameters as well. Compare (see Table 4 above), for example, estimates of annual smolt population size found in Sims and Ossiander (198 1; Table 1), Raymond (1979; Table 8) and Raymond (1988; Table 2). They differ by as much as 1.1 million smolts for any given year. Population estimates found in Raymond's earlier works (e.g., Raymond et al. 1975, Table 5) tended to be larger, but not consistently so, than values found in his 1988 paper.

1973

Major discrepancies were noted in survival values reported for the 1973 outmigration (Table 10). Sims and Ossiander (198 1), Raymond (1979), and Raymond et al. (1975) give 5% as the survival rate of chinook salmon between Little Goose Dam to The Dalles Dam. However, mark-recovery data and survival estimates provided by Raymond et al. (1974; see his Tables 6, 10, and 11) clearly indicate that this value (5%) was the estimated survival to the Dalles Dam of fish released in the Salmon River near Whitebird, Idaho. For the stretch of river between Little Goose and The Dalles dams, Raymond et al. (1974) pegged annual survival at 17%. Raymond et al. (1974) noted (p. 9) that "sampling problems precluded survival estimates at Ice Harbor in 1973," and therefore declined to estimate survival in the Snake River and Columbia River sub-reaches (note, however, that reach estimates were provided in a later publication (Raymond 1979; his Table 11).

Raymond et al. (1975) reported a 50% loss of yearling chinook at Little Goose Dam in 1973. If treatment-control recovery data from Table 6 of Raymond et al. (1974) are used to calculate survival to Ice Harbor Dam from Little Goose Dam, survival was 29% if Little Goose forebay controls are used in the calculation, or 55% if Little Goose tailrace controls are used. Approximately 9% of fish released in the forebay of Ice Harbor Dam survived to The Dalles Dam.

Table 10. Annual survival values (%) for yearling chinook migrants, as reported by various authors for the period 1973-1979. Reach '1 = Little Goose Dam (1973-1974) or Lower Granite Dam (1975-1979) to Ice Harbor Dam; Reach 2 = Ice Harbor Dam to The Dalles Dam (1973-1975) or John Day Dam (1976-1979); Reach 3 = overall survival from upper to lower dam.

	1973			1974			1975			1976			1977			1978			1979		
Source	1	2	3	1	2	3	1	2'	3	1	2	3	1	2	3	1	2	3	1	2	3
Raymond et al. (1974)		-	17	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Raymond et al. (1975)	-	-	5	47	82	40	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sims et al. (1976)	-	-	-	-	-	40	36	69	25	-	-	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	**[24**	69	**17]**[1]	-	-	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	**[50**	69	**38]**[2]	-	-	-	-	-	-	-	-	-	-	-	-
Sims et al. (1977)	-	-	-	-	-	-	-	-	25	63	48	30	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	**[63**	48	**30]**[1]	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	**[63**	48	**30]**[2]	-	-	-	-	-	-	-	-	-
Sims et al. (1978)	-	-	5	-	-	-	-	-	25	-	-	30	-	-	3	-	-	-	-	-	-
Raymond and Sims (1980)	-	-	-	-	-	-	-	-	-	-	-	-		—	-	-	-	**44**	-	-	**30**
Raymond (1979)	12	42	5	50	71	34	36	69	23	-	-	-	-	-	-	-	-	-	-	-	-
Sims and Ossiander (1981)	-	-	5	-	-	40	-	-	25	-	-	24	-	-	2	-	-	**37**	-	-	**24**

[1] Survival estimates are for Rapid River Hatchery chinook salmon.

[2] Survival estimates are for "native and other hatchery" chinook salmon.

1974

Raymond et al. (1975) combined recovery data over the entire 1974 outmigration to estimate survival through each stretch of river. They estimated survival rates of 47% and 82% in the upper and lower river, respectively, or 40% overall. The latter value jibes with Sims and Ossiander (1981). However, Sims et al. (1983, p. 23) listed a per project survival value for the entire river of 0.82. When this value is raised to the sixth power (chinook smolts had to migrate past six projects at the time), an overall survival value of 30% is obtained. This was the only discrepancy found in published values.

Survival calculations for the 1974 chinook outmigration were detailed in Appendix A of Raymond et al. (1975). Sampling efficiencies at McNary and The Dalles dams were based on recoveries of control fish released at those dams. Raymond et al. (1975) used The Dalles data to calculate survival below Ice Harbor Dam, even though "insufficient numbers were recovered from forebay releases at The Dalles Dam for accurate measure of (our) sampling efficiency there in 1974."

Although control groups of chinook salmon were released and recovered at Ice Harbor Dam, Raymond et al. (1975) opted to use a flow-efficiency curve to estimate an "average" sampling efficiency (2.4%) rather than use the observed efficiency (0.9% of the control fish were recovered). Had Raymond used the observed rate, a survival estimate of 126% would have been obtained for chinook salmon migrating through the upper river.

1975

Sims and Ossiander (198 1) reported that overall survival of chinook salmon migrating to The Dalles Dam in 1975 averaged 25%. Although this value is consistent with those found in earlier and later reports, it warrants further discussion because it represents a composite value for hatchery and wild fish. Sims et al. (1976; see his Table 4, p. 13) provided the following details:

Stretch of River	Rapid River Hatchery	Natives and Other Hatchery	Overall Survival
From:			
Salmon R. and hatcheries to Ice Harbor Dam	65%	85%	
Lower Granite Dam to Ice Harbor Dam	24%	50%	36%
Ice Harbor Dam to The Dalles Dam	69%	69%	69%
Lower Granite Dam to The Dalles Dam	17%	38%	25%

No information was given regarding the source and relative number of "other hatchery" fish included in survival estimates. However, chinook salmon released from Rapid River Hatchery obviously fared poorly in the upper ‘reaches of the river. Sims et al. (1976, p. 12) ascribed the higher mortality rate to the culling of weaker hatchery fish at dams. If Rapid River fish are excluded, overall survival would increase from 36% to 50% in the Snake River, and 25% to 3 8% overall.

One might argue that survival estimates (and a flow-survival relationship) should be solely based on wild fish, especially if the quality and relative abundance of hatchery fish in the outmigration varied **from** year-to-year. Raymond (unpublished notes), in fact, made a concerted effort to exclude hatchery fish from his calculations in earlier years. Arguments for including hatchery fish **are based** on the fact that then, as now, hatchery fish were numerically dominant in the outmigration. It also happened that in most years survival rates were not estimated separately for hatchery and wild fish. I will return to the subject of hatchery fish in a later section.

1976

In contrast to **1975,** survival rates reported for hatchery and wild fish did not differ in 1976. Sims et al. (1977) provided the following data (see their Table 2):

		Millions of Fish			
Source	Passing Lower Granite **Dam**	Number **Transported**	Number Remaining	Passing Ice Harbor Dam	Passing John Day **Dam**
Rapid River Hatchery	**3.36**	**0.55**	**2.81**	**1.77**	**0.85**
Native and Other Hatchery	**1.74**	**0.25**	**1.49**	**0.93**	**0.45**
Total	**5.10**	**0.80**	**4.30**	**2.70**	**1.30**

Using these data, survival can be estimated for Rapid River and Native/Other Hatchery **groups** of salmon as follows:

Stretch of River	Rapid River Hatchery	Natives and Other Hatchery	Overall **Survival**
From:			
Lower Granite Dam to **Ice Harbor Dam**	**1.77/2.81 = 63%**	**0.93/1.49 = 63%**	**2.70/4.30 = 63%**
Ice Harbor Dam to The **Dalles** Dam	**0.85/1.77** = 48%	**0.45/0.93** = 48%	**1.30/2.70** = 48%
Lower Granite Dam to **The Dalles Dam**	**0.85/2.81** = 30%	**0.45/1.49** = 30%	**1.30/4.30** = 30%

It would be incorrect to conclude from this evidence that hatchery and wild fish survived at the same rates during their downstream passage in 1976. A more likely explanation is that survival was calculated for the entire outmigration without regard to fish origin. Estimates of the number of hatchery and wild fish passing various dams and being transported at Lower Granite and Little Goose dams reflect the assumption that hatchery fish made up a constant proportion of the outmigration.

1977

1977 was conspicuous for the extremely low survival of chinook and steelhead migrating that year. Sims et al. (1978, pp. 12-13) reported 3.3% (20,000 out of 600,000 migrants) survival from Lower Granite to The Dalles Dam; Sims and Ossiander (1981) use 2% as the 1977 survival value. In spite of this discrepancy, there is little question that survival was abysmally low that year; both the exceptionally low spring runoff and the poor adult return (1977 remains the lowest adult return on record) lend credence to this view. However, it seems reasonable to question the accuracy of the 2-3% survival value given that (1) as many as 70% of the treatment fish were transported, yet no computational adjustment was made to account for these losses (see Section 3.3 Transportation), and, (2) "all survival estimates (we)re based on very small numbers of mark recaptures" (Sims et al. 1978, p. 5). The 1977 mark-recovery data certainly appear to bear this statement out (Table 10 above); only 0.06% – 19 out of 38,262 – of the fish released at Lower Granite Dam were recovered at Ice Harbor Dam. As no mark-recovery data could be found for other dams, survival could not be estimated, and further speculation regarding the accuracy of the 1977 survival estimates is inappropriate.

1978

Raymond and Sims (1980, their Table 6) summarized chinook smolt survival data for 1978 and 1979. For 1978, they reported 69% survival between Lower Granite and Ice Harbor dams, 64% for Ice Harbor to John Day dams, and 44% survival overall. Sims and Ossiander (1981) gave 37% as the survival rate between Lower Granite Dam and John Day Dam. No explanation was given for the disparity in the two estimates. All subsequent reports of 1978 survival are consistent with the value given in Sims and Ossiander **(1981).**

The 1978 mark-recovery database retrieved from NMFS files indicated that approximately 0.4% of the fish (19 1 out of 46,094) released at Lower Granite Dam were recovered at John **Day** Dam (Table 12). Fish released into the forebay of John Day Dam were recovered at a rate of 1.6% (113 out of 7,281 released). If these two values are taken to be accurate, 1978 survival would have been closer to 27%. This estimate should not be used since the accuracy and completeness of the data could not be verified.

1979

Again, survival values reported by Raymond and Sims (1980) and Sims and Ossiander (198 1) do not agree (Table 10). Whereas Raymond and Sims (1980) reported 30% survival for 1979, Sims and Ossiander (198 I) used a value of 24% in their flow-survival analysis. No explanation was given for the difference in reported values. Survival could not reliably be determined from the mark-recapture data obtained from NMFS files.

4.2.6 Per-Proiect Survival Estimates

Sims and Ossiander (198 1) calculated "per project" survival rates for chinook salmon migrating from the upper dam on the Snake River to either John Day Dam or The Dalles Dam on the Columbia River as a function of flow at Ice Harbor Dam. Per-project survival was calculated as $\hat{s}_{pp} = \bar{s}^{1/d}$, where d was the total number of projects, which included the uppermost Snake River dam, since treatment fish were released in the forebay of that dam, but did not include the lowermost Columbia River dam, where treatment fish were enumerated. Although Sims and Ossiander (198 1) do not list the number of projects used in their calculations, a number can be calculated from the $\hat{s}_{pp}$ and $\bar{s}$ values they provided in their Table 5. There are several discrepancies between the number of projects determined from these values and the number of projects calculated from known release and recovery sites (Table 11).

A "project", as used by Sims and Ossiander (198 1), consisted of a dam and the reach of river extending to the next dam downstream. This definition, however, was not consistently applied. To cite one example, fish that served as controls in 1977 were released at the head of the Lower Granite reservoir near Clarkston, WA (River Mile 742); there were no near-dam forebay releases (Park et al. 1979, Appendix Table 1, p. 5). In 1978, however, all of the Lower Granite Dam releases were made just upstream (RM 696) of the dam. Thus, control fish had to swim through 6 reservoirs in 1977, but only 5 reservoirs in 1978 (survival was estimated to John Day Dam). Nevertheless, Sims and Ossiander (1981) used 6 projects to estimate per-project survival for both years.

According to Sims and Ossiander (198 1), Little Goose Dam was the upper dam and The Dalles Dam the lower dam used to calculate per-project survival for both 1973 and 1974. From their Table 5, however, the number of projects used to estimate per-project survival for these years was 5 and 6, respectively. The number should have been 5 for both years. This was the number of projects used by Sims and Ossiander (1981) to calculate per-project travel time estimates for both years. Based on an overall survival of 40%, the 1974 per-project survival rate was 83%, and not 86% as indicated.

In 1975, experimental fish were released in the forebays of Lower Granite Dam, Ice Harbor Dam, and The Dalles Dam (Sims et al. 1976). As Sims and Ossiander (1981) correctly indicated, 6 projects were passed from Lower Granite to The Dalles Dam.

Controlled releases of smolts into The Dalles Dam forebay to estimate sampling efficiency were discontinued in 1976. Although smolt monitoring continued at The Dalles Dam, survival through the lower Columbia River between 1976 and 1979 was

Table 11. Number of Snake and Columbia River projects used by Sims and Ossiander (1981) to calculate "per project" survival, compared to the number of projects ascertained from original literature sources.

			Number of Projects			
Year	Upper Dam	Lower Dam	Snake River	Columbia River	Total	Sims and Ossiander (1981)
1973	Little Goose Dam	The Dalles Dam	3	2	5	5
1974	" " "	" " "	3	2	5	6
1975	Lower Granite Dam	John Day Dam	4	2	6	6
1976	" " "	" " "	4	1	5	6
1977[1]	" " "	" " "	4	1	5	6
1978	" " "	" II "	4	1	5	6
1979	" " "	" " "	4	1	5	6

[1] Sampling was conducted in 1977 at both John Day and The Dalles dams. Overall survival was determined for the reach extending from Lower Granite to "John Day-The Dalles Dams" (Sims et al. 1978).

estimated from samples collected at John Day Dam (Sims et al. 1977, 1978; Raymond and Sims 1980). The heading ("Survival to The Dalles Dam") of the second column in Table 5 of Sims and Ossiander (1981) is therefore incorrectly labeled. From 1976-1979, survival was estimated for chinook salmon that passed 4 dams – Lower Granite, Little Goose, Lower Monumental, and Ice Harbor – on the Snake River, but only 1 dam – McNary – on the Columbia River. Thus, the number of projects upon which per-project survival was estimated should have been 5, and not 6, as indicated by Sims and Ossiander (198 1). Per-project survival rates for 1976-1979 ranged 3%-6% lower than those indicated in Table 5 of Sims and Ossiander (198 1).

The relative number of Snake River and Columbia River projects upon which overall survival estimates were based ranged from 3:2 in 1973 to 4:2 in 1975 to 4:1 from 1976 onwards (Table 11). If survival differed among projects or was in some way dependent on the number of projects present, then the flow-survival relation reported by Sims and Ossiander (198 1) may have been influenced by changes in the composition and relative number of Snake River and Columbia River projects over the 1973-1979 period.

Historically, fingerling chinook migrant survival rates were lower in the Snake River than in the Columbia River. From 1969 to 1975, survival from the upper Snake River dam to Ice Harbor Dam averaged 36%. Over the same time period, approximately 58% of the fish passing Ice Harbor Dam survived to The Dalles (Raymond 1979). This difference may have been due to "first dam" effects, by which disproportionately high mortalities were sustained by chinook populations at the uppermost dam, relative to other dams downstream. In 1968, according to Raymond's notes, "most (60-75%) of the total mortality occurred at Ice Harbor Dam" (the uppermost dam at the time). Raymond (1979) noted that passage through Little Goose Dam resulted in 50% survival in 1973, compared to an average survival of 57-58% at the remaining dams. Variability in per-project survival may have been due to unusually stressful conditions at the upper dams, such as those caused by large accumulations of debris through which migrating smolts were forced to pass (see Section 4.3.2.3 Debris Removal). Raymond (1979, p. 524) suggested that weaker fish were being culled out by stress at the first few darns, and that mortality due to predation decreased in the downstream direction ("the largest populations of migrants at upper dams would draw predator fish and birds to these areas"). Raymond and Sims (1980, p. 18) noted that in 1979 "the major problem was at Lower Granite Dam where chinook salmon mortality was measured at 27%." [i.e., survival = 73%] If this mortality is excluded, survival from the tailrace of Lower Granite Dam to John Day Dam is much higher (41% rather than 30% (value from Raymond and Sims 1980) or 33% rather than 24% (value from Sims and Ossiander 1981). This equates to a per-dam survival of 86% (vs. 82%) or 83% (vs. 79%).

Because Raymond, Sims, *et alia* included hatchery fish in their survival estimates, survival probably increased with distance downstream as large numbers of hatchery fish succumbed early on to the rigors of migration. Data are presented below to support the claim that hatchery chinook salmon smolts survived at much lower rates in upper reaches of the Snake River.

Projects on the Columbia River may have been less hazardous in general than those the Snake River if a greater fraction of water was spilled at lower river dams, and if the risk of injury or death decreased as spill increased. Raymond (1979) attributed differences in reach survivals to prevailing levels of dissolved atmospheric gas; conditions during the early 1970's were much worse in the Snake River than in the Columbia River. However, survival was also lower in the Snake River during low flow years such as 1973 and 1977, when gas supersaturation was not a problem, and during years after fliplips (spillway deflectors) had been installed at dams to reduce dissolved gas supersaturation in the river.

4.2.7 Timing Of Peak Migration

Recall that population estimates for Ice Harbor Dam were determined from the sampled number of unmarked smolts weighted by prevailing sampling efficiencies. Because sampling efficiency varied with flow, and flow fluctuated over time, estimates of the timing of peak migration were influenced by the accuracy of sampling efficiency estimates. Timing was also affected by (1) the proportion of hatchery fish in the population, since releases of hatchery fish did not always coincide with the date of peak migration of wild migrants, and (2) the dates on which smolt monitoring at Ice Harbor Dam began and ended, since truncation of either tail of the frequency distribution might skew the estimated date of peak migration.

The survival values in the flow-survival relationship were single season estimates based on recoveries of marked chinook salmon which, more often than not, did not correspond in frequency or timing to the passage of unmarked smolts. It was inappropriate to index the survival of experimental fish to the date of peak migration of the unmarked population. It would have been better to index survival to the dates of passage of marked fish and, hence, to the flow conditions under which survival was estimated.

4.3 Additional Sources Of Variation

The 1970's were characterized by natural and human-caused variations in environmental conditions unlike any seen previously on the Snake and Columbia River. Year-to-year variability and cumulative changes in factors affecting the migratory environment may have altered the basic relationship between flow and survival. They may also have affected the accuracy and precision of survival estimates, especially if measurement error was correlated with environmental variability.

Raymond (1979) provided a good overview of major climatalogical, hydrological, and other factors which may have affected chinook smolt survival in the years 1966 to 1975. He suggested that the major causes of mortality during this period were passage through turbines at the dams, predation, migrational delays, and prolonged exposure to lethal concentrations of dissolved gases. The effects of these factors on chinook salmon survival varied considerably between years, and since they tended to covary with each other and with flow, it was difficult to assess their relative importance on survival for any given year.

Flows varied considerably over the period of interest, including record high and low flows in 1974 and 1977, respectively (Table 5). Higher flows were spilled at Snake River dams during the smolt outmigrations in 1974-76 and 1978 (Sims and Ossiander 198 1). Survival was high **during these** years but was less variable than in non-spill years.[7] Survival increased with flow even when no spill occurred (i.e., all water was run through the powerhouses); from this it might be inferred that turbine and/or reservoir passage survival may also have increased with increases in **flow**.

In the following sections I review some of the natural and anthropogenic factors that may have **affected** survival or its measurement among marked groups of chinook salmon smolts during the 1973-1979 period. I focus on the natural variability in the timing of outmigration and the physical condition of smolts at the outset of migration, structural and operational changes in the hydrosystem, and biological interactions between hatchery chinook, wild chinook, and resident fish. The relative importance of sources of mortality other than flow is indicated whenever available information permitted an assessment.

4.3.1 Timing and Magnitude of Migration

The physiological, morphological, and behavioral changes in juvenile salmon that convey the ability to migrate downstream are synchronized by environmental factors, including photoperiod, streamflow, water temperature, and perhaps lunar periodicity (Groot 1981; Muir et al. 1992). Annual variability in environmental cues, along with population-specific differences in endogenous rhythms and migratory fitness, may offer partial explanation for the large interannual variation in chinook smolt survival observed in the 1970's.

Dates of peak migration past Ice Harbor Dam in **1973-** 1979 ranged from 28 April in 1975 to 26 May in the following year.

Raymond (1979 and unpublished notes) gives the impression that he considered water temperature a greater influence on migration timing than stream discharge. He commented on migrational delays occasioned by unseasonably cold weather; e.g., "The outmigration of native chinook smolts was delayed by cold spring weather in 1975. Significant numbers of smolts never did show at the **Riggins** trap on the Salmon River. Those that did were delayed until warm weather began about May 5."

All else being equal, delays in the start of migration may have worked to the **advantage** of chinook migrants. Several authors have noted that chinook salmon migrating later in the spring tend to travel faster than early spring migrants (Muir et al. 1992; Smith et al. 1993); travel rate appears to be related to stage of smoltification **(Beeman** et al. 1991). On the other

---

[7] Sims and Ossiander (198 1) indicated that up to 8 kcfs per dam was spilled during "non-spill" years. This needs to be checked out **further.**

hand, smolts that get a late jump on migration may have fewer lipid reserves to see them through their journey. Overwinter conditions are important in this regard: if chinook salmon smolts began their migrations in a debilitated state following a particularly severe winter, lower than normal survival would be expected.

4.3.2 Changes in the Hydro-System and Mainstem Environment

4.3.2.1 Power Generation Capacity and Bypass Changes

Smolt survival during the 1973-1979 period was no doubt influenced by the increase in the total number of turbine units installed or operating at dams on the mainstem Columbia and Snake Rivers. The total number of units installed at Snake River dams increased from 9 in 1973 to 24 in 1979 (Table 12) (Park 1980, 1993). The number of installed units that were actually operated also varied between years. Reduced power loading at Lower Granite and Lower Monumental dam during the 1975 outmigration was one of factors responsible for the high survival of chinook salmon and steelhead that year.[8] Noting that only one turbine unit was operating at Lower Granite Dam, and that most of the river flow passed over the spillway, Sims et al. (1976, p. 1) concluded that "fingerling mortality under these conditions would not be representative of the mortality that would normally be occurring when all turbines were on line."

Other system modifications that affected chinook smolt survival in the 1970's included the installation of traveling screens to divert migrating smolts away from turbines and into bypass and collection systems at dams (Park 1980). Installation and testing of screens began in 1971. Lower Granite Dam was the first dam on the Columbia River to have fully screened operating turbines (Matthews 1977). Not only were the number of diversion screens increased, but they were made more efficient so that fewer injuries and mortalities resulted. Average fish guidance efficiency of mainstem dams increased from 0.12 in 1970 to 0.32 by 1980 (McConnaha 1990) (Table 13).

At least one other change in bypass conditions occurred – this one unexpected – to undermine confidence in the flow-survival relationship. In 1975, higher than normal mortalities occurred at Ice Harbor Dam (Sims et al. 1976, p. 17). Stoplogs, normally emplaced in the lower sluice at the dam to create a plunge pool to cushion the fall of migrants passing from the upper to the lower sluice, were either washed out or inadvertently removed between 1974 and 1975. Without a plunge pool, fewer than 50% of the fingerlings passing down the sluice in 1975 were believed to have survived (Sims et al. 1976, p. 18). Since dam-related mortality would have been much lower had the stoplogs been installed, the overall survival value (25%) used for that year as input in the flow-survival regression analysis was probably too low.

8 Raymond (unpublished notes) indicated that in 1975 only one turbine unit was operated at Lower Granite Dam as well.

Table 12. Number of turbine units at hydroelectric dams on the Snake River, 1968-1979.[1]

Dam	Cumulative number of turbine units in place											
	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979
Lower Granite Dam	0	0	0	0	0	0	0	3	3	3	6	6
Little Goose Dam	0	0	0	3	3	3	3	3	3	3	6	6
Lower Monumental Dam	0	0	3	3	3	3	3	3	3	3	3	6
Ice Harbor Dam	3	3	3	3	3	3	3	6	6	6	6	6
Total	3	3	6	9	9	9	9	15	15	15	21	24

[1] **Data source: Bell et al. (1976), Park (1993)**

Table 13. Adjusted fish guiding efficiencies, spring chinook, 1970-1980.[1]

Dam	1970	1972	1973	1974	1975	1976	1977	1978	1979	1980
Lower Granite Dam				-	0.69	0.69	0.69	0.69	0.69	0.69
Little Goose Dam	0.00	0.00	0.00	0.00	0.46	0.46	0.69	0.69	0.69	0.69
Lower Monumental Dam	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03
Ice Harbor Dam	0.40	0.40	0.40	0.40	0.40	0.40	0.40	0.40	0.40	0.40
McNary Dam	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.11	0.32
John Day Dam	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
The Dalles Dam	0.40	0.40	0.40	0.40	0.40	0.40	0.40	0.40	0.40	0.40
Bonneville Dam	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Average	0.12	0.12	0.12	0.12	0.25	0.25	0.28	0.28	0.29	0.32

[1] Data source: McConnaha (1990)

4.3.2.2 Spill and Problems with Gas Supersaturation

As new turbine units were installed and water and hydropower managers gained greater control over river flows, less spilling occurred at mainstem Columbia River Dams, except in years of above average runoff. Spill, through its effects on the movement and distribution of smolts, directly affected survival. During periods of spill, at least a portion of the smolt population are able to pass over the spillway and avoid the dam's turbines. Changes in the relationship between river flow and the proportion of water spilled during the 1970's may have altered the basic relation between survival and flow. Levels of spill that approach those of the early 1970's are uncommon today.

Sims and Ossiander (1981) identified spill as a key factor affecting chinook survival, noting that: "The relationship between survival and spill has a much faster rate of change than the relationship between survival and flow. A proportionate increase in spill at low magnitudes will yield a greater increase in survival than the same proportionate increase in flow...A moderate increase in spill, for spill in the lower range of value, will yield substantial improvements in survival." The authors observed that spill, like flow, was strongly correlated with survival during the period of interest.

Spill was actually deleterious to migrating smolts in high flow years prior to 1977. Migration conditions during years when large quantities of water were being spilled were notable for high concentrations of dissolved gases. Prolonged exposure of migrants to supersaturated nitrogen gas (greater than 130%) was implicated as a major cause of smolt losses, ranging from zero in the low flow year of 1973 to 80% in high flow years such as 197 1 (Ebel and Raymond 1976). Nearly two-thirds of the 66% loss of chinook salmon in 1974 was caused by nitrogen supersaturation (Ebel et al. 1975, p. 24). The authors concluded that survival would have been much higher, on the order of 70-80%, had spill deflectors been in place. Mortalities attributable to gas bubble disease began to decline with the installation of fliplips at Little Goose and McNary Dams in 1976 (Ebel and Raymond 1976).

Petrosky (1991) suggested "backing out" mortality attributable to gas supersaturation if estimates could be obtained. Unfortunately, no data are available which would permit modification of annual survival estimates.

4.3.2.3 Debris Removal

During 1981, the U.S. Army Corps of Engineers undertook a major effort to remove debris that accumulated in the forebay of Lower Granite and other dams (Park 1993, p. 7). Problems associated with debris buildup were prevalent throughout the 1970's, in particular at upper dams during high flow years. Although effective debris control was not initiated at the upper Snake River dams until 1981, earlier attempts to remove debris produced tangible benefits in terms of survivability of chinook migrants and transported fish. Debris removal and control efforts reduced descaling and injury in collection systems. In 1979, for example, the average percent descaling before and after debris was removed from trash racks was 12 and 6%, respectively (Smith et al. 1980, p. 6).

4.3.3 Scale Loss and Delayed Mortality

One commonly used index of mainstem passage conditions and their effects on migrating chinook salmon smolts is the percentage of fish observed with significant (>10%) scale loss; data collected in the 1970's as part of the transportation studies were summarized by Park (1985). Descaling rates measured during this period were variable between dams and years, ranging from 4.0 to 23% (Table 14). The percentage of chinook migrants that were descaled or injured declined over time. In 1972, over 50% of the chinook sampled from McNary Dam gatewells were descaled (Raymond, unpublished data). By 1978-80, the percentage of descaled fish had dropped to 10-20%. The progressive decline in descaling was attributed to debris removal, *decreasing* amounts of spill, and improved bypass conditions at the dams (Park 1985).

Descaling rates varied both within a season and between years at a given dam; they also varied among chinook smolts recovered at different dams in the same year. In 1972, for example, the annual average descaling rate was 16.6% at Little Goose Dam (Park 1985, p. 2-14) and over 50% Ice Harbor Dam (Raymond, unpublished notes). In both 1978 and 1979, annual descaling rates were 2 to 13% higher at Little Goose Dam than at Lower Granite Dam. This evidence suggests that, in terms of descaling, the effects of dams on the fitness and composition of the smolt population may have been accumulative and detrimental.[9]

Evidence was provided in Section 4.1 (Sampling and Statistical Assumptions) of significant sampling-related mortality in most years (Table 6). Delayed mortality was determined from tests conducted with chinook salmon and steelhead controls under the transportation program, 1975-1980. The values reflect handling effects, but if handling procedures were similar from one year to the next, then the values also give some indication of the interannual variability in smolt condition and bypass conditions at the dams.

To see whether any of the variation in the per-project survival rates reported by Sims and Ossiander (198 1) could be explained by delayed mortality and percent descaling, simple and multiple regression analyses were performed for the years for which data were available (Tables 7 and 8). These are very crude analyses because of the small sample sizes and assumptions involved, but they nevertheless give insight into mechanisms responsible for observed rates of survival. Bivariate correlation coefficients were calculated for the following variables: per-project survival, Snake River flow (log-transformed), percent delayed mortality, and percent descaling rates (Table 15). The number of yearling chinook that died in 48h delayed mortality tests and the percentage of migrants exhibiting a significant loss of scales

---

[9] It also suggests that treatment fish captured and released at upper dams on the Snake River may have experienced different, possibly less, handling and tagging stress-related mortalities than did control fish released at John Day and The Dalles dams. If this occurred, the resulting survival estimates would be in error.

Table 14. Percentage of descaled (> 10%) spring chinook salmon migrants sampled from the marking facility at Lower Granite, Little Goose, and McNary dams, 1972-1980. Data are from Park (1985) unless otherwise noted.

Year	Mean (%)	Range (%)
	Lower Granite Dam	
1975	13.0	-
1976	7.0	4.0-13.0
1977	27.0[a]	14.0-33.0
1978	7.0	
1979	5.3	1.0-12.0
1980	4.0	1.0-11.0
	Little Goose Dam	
1972	16.6[b]	-
1973	19.6[b]	-
1977	23.9	6.0-49.2
1978	20.0	6.0-44.0
1979	8.1[c]	
	McNary Dam	
1978	10.0	-
1979		-
1980	20.0	-

[a] Ebel et al. (1977)

[b] Park et al. (1980)

[c] Smith et al. (1980)

Table 15. Bivariate correlation coefficients and significance levels (in parentheses) for selected variables relating to chinook salmon smolt migrations, 1973-1979. Values are based on a sample size (*n*) of 7 except for correlations involving the descaled variable, in which case *n* = 6 (no data for 1974). Flow values were transformed to their logarithms; all other values are untransformed.

	Survival (%)	Logarithm of Flow (kcfs)	Delayed Mortality (%)	Descaled (%)
Survival (%)	1.00 (0.00)			
Logarithm of Flow (kcfs)	0.87 (0.01)	1.00 (0.00)		
Delayed Mortality (%)	-0.70 (0.08)	-0.69 (0.08)	1.00 (0.00)	
Descaled (%)	-0.93 (0.01)	-0.77 (0.07)	0.86 (0.03)	1.00 (0.00)

were negatively correlated with per-project survival rates (Figure 10). The percentage of descaled smolts was more highly correlated with survival than was Snake River flow, even with one less data point (i.e., 1974) used in the regression analysis. Interpretation of these results is complicated by the strong covariation among flow, delayed mortality, and descaling rate. An attempt to include all three variables into a multiple regression model using a liberal F-to-enter criterion (0.1) resulted in the inclusion of only descaling rate as an independent variable; the addition of flow or delayed mortality did not significantly improve the predictive capability of the model.

4.3.4 Biological Interactions

4.3.4.1 Hatchery Fish

A major uncertainty surrounding the flow-survival relationship is the effect that hatchery fish may have had on survival estimates. The number of chinook salmon released from hatcheries above Snake River dams increased steadily once Rapid River Hatchery began production in 1966. Hatchery steelhead releases also increased. The total number of hatchery-origin chinook passing the first dam on the Snake River between 1973 and 1979 ranged from 1.2 to 2.3 million fish. Hatchery chinook smolts comprised anywhere from 53% (in 1973) to 75% (in 1978) of the total smolt population passing the upper dam.

Concern over potential effects of hatchery chinook on the flow-survival relation are justified on several grounds. Hatchery chinook traveled more slowly, died at higher rates, and may have been more (or less) vulnerable to capture than were their wild counterparts. Overall survival estimates were therefore dependent on changes in the relative abundance and fitness of hatchery and wild fish over distance and through time. Raymond and Sims were acutely aware of the potential for problems of this type. Raymond went so far as to estimate survival separately for hatchery and wild chinook up until 1975. His estimates of survival from the Salmon River to the upper Snake River dam for the 1966-1972 period were for wild chinook smolts only (Lander 1972; Raymond, unpublished notes).

Raymond (unpublished notes) compiled release data along with estimates of the number of chinook smolts passing the first and last dam they encountered on the Snake and Columbia rivers (Table 16). He also estimated the survival of hatchery chinook from Rapid River Hatchery to the first dam, and from there to The Dalles Dam. These values can be compared to survival rates reported for wild chinook in Table 10 (1966-1968: Salmon River to Ice Harbor Dam) and for wild and hatchery fish combined (1973-1975: upper to lower dam) in Table 11 of Raymond (1979). In all years except 1973, survival was lower among hatchery fish (the rate of adult return of hatchery fish was also consistently lower than that of wild fish over the same period [Raymond 19881). The greatest disparity was observed in 1966-1968 when survival to the first dam from the Salmon River averaged 16% for hatchery fish, compared to 89% for wild fish over the same distance. Recent studies suggest that survival rates for hatchery chinook remain well-below those for wild chinook, presumably due to a higher incidence of bacterial kidney disease among hatchery fish (causative agent: *Renibacterium salmoninarum*) (Achord et al. 1991, Matthews 1992).

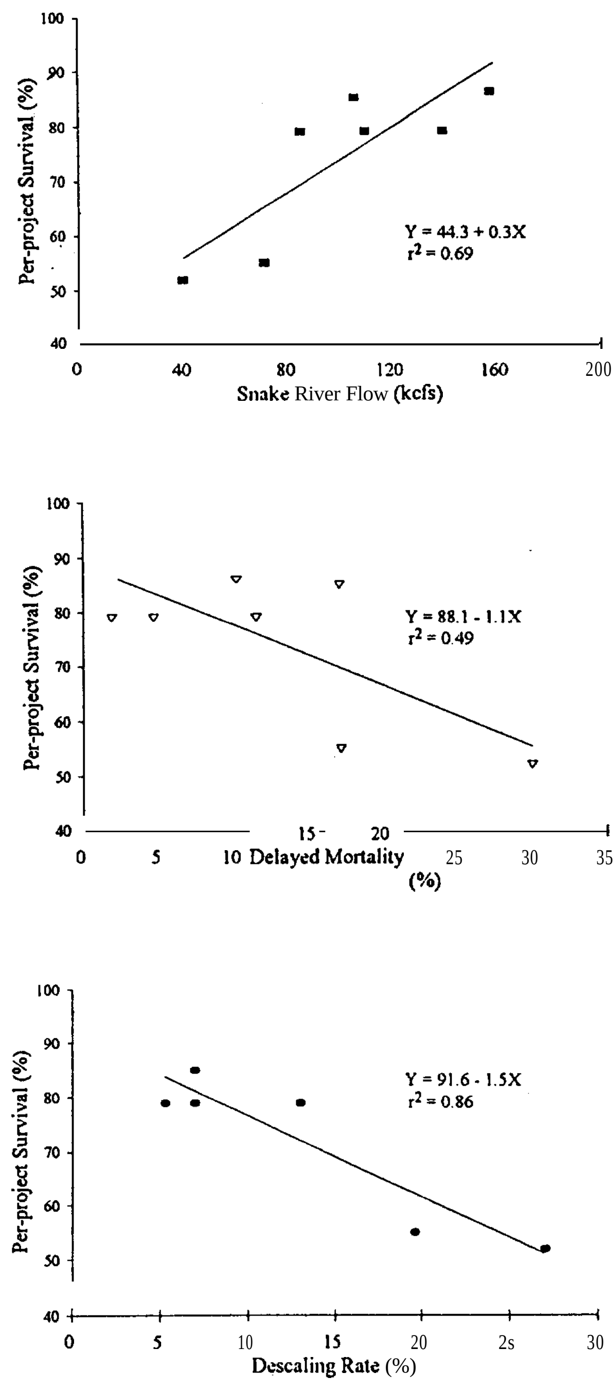

Figure 10. Per-project survival as a function of Snake River flow, delayed mortality, and percent descaling. Data and sources are identified in Tables 4, 6, and 14.

Table 16. Numbers of juvenile chinook salmon released from Rapid River Hatchery and survival estimates, 1966-1975. S_1 = survival from hatchery to upper dam; S_2 = survival from upper to lower dam; S_3 = survival from hatchery to lower dam. These data were compiled by H.L. Raymond, but were not published.

Year	Number of Chinook Smolts (thousands) Hatchery releases	Passing upper dam	Passing upper dam	Survival S_1	S_2	S_3
1966	580	75	45	13%	60%	8%
1967	450	60	36	13%	60%	8%
1968	1470	340	204	21%	60%	13%
1969	960	300	175	31%	58%	18%
1970	3400	1500	400	44%	27%	12%
1971	3000	1300		45%		
1972	2800	1400	112	50%	4%	8%
1973	2900	1450	75	50%	2-3%	5%
1974	2700	1200	270	44%	10%	23%
1975	3400	2200	340	65%	11%	13%

Interestingly, survival of hatchery fish from Rapid River to the upper Snake River dam increased from 13 to 65% between 1966 and 1975. Raymond claimed that increased survival during this period resulted from an improvement in hatchery operations and the production of higher quality hatchery smolts. One such improvement was the switch from raceway to pond-rearing at Rapid River Hatchery in the late 1960s. The survival of pond-reared fish was significantly higher than that of raceway-reared fish (Raymond, unpublished data). Disease control may also have improved over time (Ebel et al. 1973).[10] It is unknown whether the quality of hatchery fish continued to improve during the 1975-1979 period.

Hatchery fish may have lowered the survival of co-migrating wild chinook smolts. While little is known of hatchery and wild fish interactions, hatchery chinook and steelhead smolts could conceivably affect the survival of wild smolts through competition for scarce resources, by attracting and supporting larger predator populations, by altering behaviors and activity levels, and by transmitting disease. The outcome of these kinds of interactions depends on the relative abundance of hatchery and wild fish and the degree to which they overlap in time and space. Density-dependent mortality may have been an important if somewhat unknown factor affecting hatchery and wild chinook survival. With the exception of 1977, the total number of chinook and steelhead smolts migrating down the Snake River in the 1970s exceeded the number estimated to have migrated in 1964-1969 (Raymond 1988).

Survival rates used in the flow-survival relationship were combined estimates, even though separate estimates were obtained for hatchery and wild chinook in 1973-1975. The magnitude of the combined estimates depended on changes in the composition of the smolt population and changes in the relative fitness of hatchery and wild fish over time. In 1975, for example, an estimated 17% of the hatchery fish survived from Lower Granite Dam to The Dalles Dam, compared to 38% of the wild chinook. An "average" smolt survival value of 25% was reported by Raymond (1979) and used in the flow-survival regression analysis. Sims et al. (1976, p 12) attributed the lower survival observed in 1975 to the dominance of hatchery fish in the outmigration.

Raymond (unpublished data) determined that hatchery fish took 23 days to travel from Whitebird to Ice Harbor in 1974 compared to 14-15 days for wild fish. Sims et al. (1983) also observed that hatchery chinook traveled much more slowly than did "river run" chinook smolts. Their conclusion: "Based on this finding, we question the validity of using releases of marked hatchery fish to estimate survival and behavior of river run fish."

---

10 A letter from E. Parrish, superintendent of Rapid River Hatchery, to H. Raymond in 1970 stated that the year "started on a rather sour note... Kidney disease took a heavy toll of the (chinook) smolts that were being held here for transplanting...We had on hand 1,857,927 fish, and either lost them to the disease, or killed and buried to prevent the disease from spreading." In contrast, Raymond noted in 197 1 that the Rapid River release in 1970 included "two million fish released with kidney disease that were to have been buried." The final disposition of the diseased fish remains unclear.

4.3.4.2 *Changes In The Biological Community*

With the physical and limnological changes that attended the impoundment of the Snake and Columbia rivers came changes in the aquatic community. The abundance of certain native species of fishes declined as free-flowing stretches of river were inundated and transformed into slow water habitats. Other organisms, non-native species in particular, became more abundant with the result that biomass and production increased over historical levels (Li et al. 1987). Predation mortality on chinook smolts probably increased as populations of squaw-fish ***(Ptychocheilus oregonensis),*** walleye ***(Stizostedion vitreum),*** smallmouth bass ***(Micropterus dolomieu),*** and channel catfish *(Ictalurus punctatus)* grew. Recent studies estimated that **14%** of the juvenile salmon that migrated through John Day reservoir were consumed by these predators (Rieman et al. 1991). A high level of predation by squawfish, in particular, is common throughout the mainstem Snake and Columbia rivers, enough so that a large-scale program to reduce the abundance of this species was initiated by Bonneville Power Administration in 1990 (Shively et al. 1991). From this evidence it may be inferred that survival of yearling chinook in 1973- 1979 probably varied with fluctuations in predator populations. However, the extent to which smolt survival may have been affected by increased rates of predation and other changes in the biological community is unknown.

5.0 SUMMARY AND CONCLUSIONS

Few would contest the statement that chinook salmon smolts are more likely to survive a journey of several hundred kilometers if they cover the distance in less time, or that their survival and rate of travel will be positively related to flow. However, the exact relationship between flow, rate of travel, and survival can only be determined through careful observation over a broad range of flows. Virtually all scientists who have tried to estimate smolt survival have encountered formidable experimental problems. The flow-travel time and flow-survival relationships obtained by Sims and Ossiander (1981) and the survival studies upon which they are based represent the best efforts made to date in this regard. The general relationships depicted may appear intuitive, but are they valid?

This report has provided a critical analysis that attempts to answer the question "How valid is the flow-survival relationship?" Validity is assessed with respect to experimental design, sampling and analytical methods, and interpretability and applicability of the results. The primary assumptions underpinning the relationship are discussed along with potential causes of and explanations for discrepancies in reported flow and survival estimates. The major points to be made in this regard are:

- There were significant year-to-year differences in the number and operation of projects, locations of release, and sampling activities;

- Recoveries of marked fish were variable and low - too low in most cases to permit calculation of mean survival and variance from individual group estimates;

- An unknown fraction of control fish died prior to recovery, possibly causing negative and positive biases, respectively, in sampling efficiencies and survivals;

- Control fish were often recovered at lower rates, at different times, and under different conditions than were treatment fish;

- Reductions in the number of treatment fish due to transportation were not directly incorporated into survival calculations;

- Survival estimates were determined for treatment fish released on schedules that did not necessarily correspond to the timing or relative abundance of the run-at-large. The flow metric used in the flow-survival relationship was improperly indexed to the date of peak passage (± 7 days) of the unmarked population at Ice Harbor Dam.

- A flow-efficiency curve was used to calculate a weighted mean annual survival to Ice Harbor Dam for the years 1973- 1975. Spurious correlations exist in the flow-survival relationship since the flow-efficiency curve and the flow variable used in the relationship were computed from the same set of data;

- Changes in the hydrosystem, logistical constraints, and unanticipated results forced investigators to sum mark-recovery data across replicates after 1975; this approach to estimating "average" annual survival rates resulted in the loss of information (e.g., within-season variability in survival) and lower accuracy;

- Since multiple treatment-control releases were made in all years, within-season estimates of precision (standard error) of the observed survival rates were possible; however, only single-season survival estimates were routinely reported;

- A disproportionate share of chinook smolts died at the first dam encountered on the Snake River. Survival was estimated for a section of river that comprised variable and unbalanced numbers of Snake River and Columbia River dams. The flow-survival relation may have been influenced by changes in the configuration and number of projects; and

- Separate flow-survival relationships should have been derived for the Snake and Columbia Rivers since runoff conditions, hydrosystem operations, smolt population characteristics, and various sources of mortality may have varied between reaches within the same years;

- Survival values used in the flow-survival relationship did not agree in many instances with values reported elsewhere.

Evidence was provided to demonstrate that chinook smolt survival in 1973-1979 may have varied in response to factors other than flow. Survival and flow were strongly correlated with post-sampling (i.e., delayed) mortality and descaling rates measured in transportation studies being conducted at the same time. Factors affecting mainstem passage, including factors responsible for the observed variability in delayed mortality and descaling, varied annually and may have exerted a strong influence on the migratory behavior and survival of chinook salmon smolts.

Sampling conditions were too variable, the methods employed to collect and analyze the data were too unreliable, and the statistical model used to describe the relationship was too simplistic to justify its use as a predictive tool. Concerns over the validity of the data and the mathematical model under which they are subsumed must be addressed before any thought is given to applying them. My assessment led me to conclude that the flow-survival relationship should ***not*** be generalized to existing populations and settings. Further analysis of the historical **dataset** to extract additional information is unwarranted. New field studies and analytical approaches are needed to clarify the relation between survival and flow within the context of current management needs.

Although I question the validity and usefulness of the Sims and Ossiander (1981) **flow-survival** relationship, I have made no attempt to define the "true" flow-survival relationship based on my interpretation of the data. To do so would require that I superimpose my own assumptions on data of questionable quality, and would in all certainty provoke further controversy. Nevertheless, my own opinion is that, *ceterisparibus,* a positive relationship exists between river flow and smolt survival, and that it can be satisfactorily **quantified** by applying improved statistical methodologies to mass marking and recovery data. It is up to today's researchers and managers to commit the resources necessary to identify the causes, magnitude, and locations of smolt mortality under present conditions. At the same time, positive steps should be taken to increase *in-river* smolt survival to levels that permit the recovery and maintenance of upriver **salmonid** populations. Shaping flows to better approximate the conditions under which these populations evolved would be an appropriate first step.

6.0 LITERATURE CITED

Achord, S., G.M. Matthews, O.W. Johnson, and D.M. Marsh. 1992. Use of PIT tags to monitor the smolt migrations of spring and summer chinook salmon stocks in the Snake River basin. 1989-199 1. Pages l-13 *in* Bolinger, C. and J. Congleton, editors. Passage and survival of juvenile chinook salmon migrating from the Snake River basin. Proceedings of a technical workshop held at the University of Idaho, February 26-28, 1992.

Beeman, J., D. Rondorf, J. Faler, P. Haner, S. Sauter, and D. Venditti. 1991. Assessment of smolt condition for travel time analysis. U.S. Fish and Wildlife Service 1990 Annual Report to Bonneville Power Administration (Contract DE-AI79-87-BP35245).

Bentley, W.W., and H.L. Raymond. 1968. Collection ofjuvenile salmonids from turbine intake gatewells of major dams in the Columbia River system. Transactions of the American Fisheries Society 97: 124- 126.

Bentley, W.W., and H.L. Raymond. 1976. Delayed migrations of yearling chinook salmon since completion of Lower Monumental and Little Goose dams on the Snake River. Transactions of the American Fisheries Society 105: 422-424.

Berggren, T.J., and M.J. Filardo. 1993. An analysis of variables influencing the migration of juvenile salmonids in the Columbia River basin. North American Journal of Fisheries Management 13 : 48-63.

Bruton, M.H. 1990. Alternative Life History Styles of Fishes. Kluwer Academic Publishers. Dordrecht, Netherlands.

Burnham, K.P., D.R. Anderson, G.C. White, C. Brownie, and K.H. Pollock. 1987. Design and analysis methods for fish survival experiments based on release-recapture. American Fisheries Society Monograph 5.

Dauble, D. D., J.R. Skalski, and A.E. Giorgi. 1993. Evaluation and application of statistical methods for estimating smolt survival. Report to Bonneville Power Administration (Contract DE-AI79-90-BP626 11).

Ebel, E.J., D.L. Park and R.C. Johnsen. 1973. Effects of transportation on survival and homing of Snake River chinook salmon and steelhead trout. U.S. Fish and Wildlife Service. Fisheries Bulletin 7 1: 549-563.

Ebel, E.J., R.F. Krcma, D.L. Park., H.L. Raymond, E. Slatick, E.M. Dawley, and G.A. Swan. 1974. Evaluation of fish protective facilities at Little Goose Dam and review of other studies relating to protection of juvenile salmonids in the Columbia and Snake Rivers, 1974. National Marine Fisheries Service, Seattle, Washington.

Ebel, E. J., H.L. Raymond, G.E. Monan, W.E. Farr, and G.K. Tononaka. 1975. Effect of atmospheric gas supersaturation caused by dams on salrnon and steelhead trout of the Snake and Columbia rivers. National Marine Fisheries Service, Seattle, Washington.

Ebel, E.J., and H.L. Raymond. 1976. Effect of atmospheric gas saturation on salmon and steelhead trout of the Snake and Columbia rivers. United States National Marine Fisheries Service Marine Fisheries Review 38: 1-14.

Elliott, D.G., and R.J. Pascho. 199 1. Juvenile fish transportation: Impact of bacterial kidney disease on survival of spring/summer chinook salmon stocks. U.S. Fish and Wildlife Service, Seattle, Annual Report 1989 to the U.S. Army Corps of Engineers, **Walla Walla,** Washington (Contract E86880047).

Elliott, D.G., and R.J. Pascho. 1992. Juvenile fish transportation: Impact of bacterial kidney disease on survival of spring/summer chinook salmon stocks, 1990. U.S. Fish and Wildlife Service, Seattle, Annual Report 1989 to the U.S. Army Corps of Engineers, **Walla Walla,** Washington (Contract E86890043).

Giorgi, A.E., G.A. Swan W.S. Zaugg, T.C. Coley, and T.Y. Barila. 1988. Susceptibility of chinook salmon smolts to bypass systems at hydroelectric dams. North American Journal of Fisheries Management 8: 25-29.

Groot, C. 1981. Modification of a theme – a perspective on migration behaviro of Pacific salmon. Pp. 1-21 *in* E.L. **Brannon** and E.O. Salo, editors. Salmon And Trout Migratory Behavior Symposium. University of Washington, Seattle.

Hansen, L.P., and B. Jonsson. 1985. Downstream migration of hatchery-reared smolts of Atlantic salmon ***(Salmo salar*** L.) in the River Imsa, Norway. Aquaculture 45: 237-248.

Hoffman, A., and J.R. Skalski. 1993. Evaluation of release-recapture models for Snake river survival studies. Appendix A *in* Dauble, D. D., J. Skalski, and A.E. Giorgi. 1993. Evaluation and application of statistical methods for estimating smolt survival. Report to Bonneville Power Administration (Contract **DE-AI79-90-BP62611)**.

Kindley, R. 199 1. The flow/survival/time travel relationship: review and analysis of supporting information and rationale for flows for juvenile spring and summer chinook migrations. Report to Pacific Northwest Utilities Conference Committee, Portland, Oregon.

Kirk, R.E. 1982. Experimental Design: Procedures for the Behavioral Sciences. Brooks/Cole Publishing Company, Monterey, California.

Lander, R.H. 1972. Review of pre- and post-impoundment estimates for survival and abundance of Snake River chinook salmon. Report to the National Marine Fisheries Service, Seattle, Washington.

Li, H.W., C.B. Schreck, C.E. Bond, and E. Rextad. 1987. Factors influencing changes in fish assemblages of Pacific Northwest streams. Pages 193-202 *in* W.J. Matthews and D.C. Hein, editors. Community and Evolutionary Ecology of North American Stream Fishes. University of Oklahoma Press, Norman.

Matthews, G.M., G.A. Swan, and J.R. Smith. 1977. Improved bypass and collection system for protection of juvenile salmon and steelhead trout at Lower Granite Darn. Marine Fisheries Review 47: 28-34.

Matthews, G.M., D.L. Park, J.R. Harmon, and T.E. Ruehle. 1988. Evaluation of transportation of juvenile salmonids and related research on the Columbia and Snake Rivers, 1987. National Marine Fisheries Service Research Report to the U.S. Army Corps of Engineers (Contract DAW68-84-H0034).

Matthews, G.M., S. Achord, J.R. Harmon, O.W. Johnson, D.M. Marsh, B.P. Sandford, N.N. Paasch, K.W. McIntyre, and K.L. Thomas. 1992. Evaluation of transportation of juvenile salmonids and related research on the Columbia and Snake Rivers, 1990. National Marine Fisheries Service Research Report to the U.S. Army Corps of Engineers (Contract DAW68-84-H0034).

McConnaha, C. 1990. Analytical Methods Work Group: Flow/survival relationship. Memorandum to the Monitoring and Evaluation Group of the Northwest Power Planning Council.

Muir, W. D., C.S. McCutcheon, A.E. Giorgi, W.S. Zaugg, W.W. Dickhoff, and B.R. Beckman. 1988. Behavior and physiology studies in relation to yearling chinook guidance at Lower Granite and Little Goose Dams, 1987. National Marine Fisheries Service Research Report to the U.S. Army Corps of Engineers (Contract DAW68-84-HO034).

Muir, W.D., A.E. Giorgi, W.S. Zaugg, W.R. Hirtzel, and B.R. Beckman. 1990. An assessment of the relationship between smolt development and fish guiding efficiency at Lower Granite Dam. National Marine Fisheries Service Research Report to the U.S. Army Corps of Engineers (Contract DAW68-84-H0034).

Muir, W.D., W.S. Zaugg, C.S. McCutcheon, and J.G. Williams. 1992. Biological manipulation of migration rate: The use of advanced photoperiod to accelerate smoltification in yearling chinook salmon, 1990. National Marine Fisheries Service Report to Bonneville Power Administration (Contract DE-AI79-87-BP35245).

DOE/BP-99654-13
April 1994
725