NOAA Technical Memorandum NMFS-NWFSC-63

Effects of the Federal Columbia River Power System on Salmonid Populations

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John G. Williams, Steven G. Smith, Richard W. Zabel,
William D. Muir, Mark D. Scheuerell, Benjamin P. Sandford,
Douglas M. Marsh, Regan A. McNatt, and Stephen Achord

Northwest Fisheries Science Center
Fish Ecology Division
2725 Montlake Boulevard East
Seattle, Washington 98112

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U.S. DEPARTMENT OF COMMERCE
Carlos M. Gutierrez, Secretary

National Oceanic and Atmospheric Administration
Vice Admiral Conrad C. Lautenbacher, Jr. USN (Ret), Administrator

National Marine Fisheries Service
William T. Hogarth, Assistant Administrator for Fisheries

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Abbreviations and Acronyms

BPA	Bonneville Power Administration
CJS	Cormack-Jolly-Seber
COE	[U.S. Army] Corps of Engineers
CSS	[Multi-State] Comparative Survival Study
CWT	coded-wire tag
DART	data access in real time
ESA	[U.S.] Endangered Species Act
ESU	evolutionarily significant unit
FCRPS	Federal Columbia River Power System
gam	generalized additive model
IDFG	Idaho Department of Fish and Game
kcfs	thousand cubic feet per second
LRT	likelihood ratio test
PATH	Plan for Analyzing and Testing Hypotheses
PIT	passive integrated transponder
RKm	river kilometer
SAR	smolt-to-adult return rate
SIMPAS	simulated passage model
SR	single-release [model]
SURPH	survival with proportional hazards
WTT	water travel time

Executive Summary

This technical memorandum summarizes past efforts to determine direct and indirect effects of the Federal Columbia River Power System (FCRPS) on Columbia River salmon stocks. We based analyses and derived results from juvenile and adult studies through the end of 2003 that address five major areas:

1) adult return rates,
2) transportation evaluations,
3) juvenile migrant survival,
4) links between juvenile survival, travel time, and the river environment, and
5) latent mortality associated with the FCRPS.

(For most past and present methods used to develop linkages between the FCRPS and salmon survival, this report refers readers to references containing the details.)

Our ability to discern FCRPS-related effects relates directly to the quality of available data, which is quite variable. We can precisely estimate survival of downstream migrants from release points to the uppermost dams and through the hydropower system, and we have begun to develop similar capabilities for upstream migrants. For several evolutionarily significant units (ESUs), we have developed a measure of the relative performance of transported fish compared to in-river migrants, but we have limited precision of sample sizes of adult returns. Unfortunately, we have limited ability to quantify the magnitude of hydropower system–related latent mortality. However, we believe a major component of latent mortality is the disruption of timing of transported fish and in-river migrants, and we are beginning to discern some migrational timing effects.

Areas of additional or continued study that would help resolve some uncertainties about effects of the FCRPS include:

- migrational timing and its effect on smolt-to-adult return rate (SAR) for both transported and in-river migrants,
- selectivity of bypass systems, for fish size as well as fish health, and
- mechanisms leading toward latent mortality.

Some of the data limitations noted above arise from the fact that adult return rates provide the best indicator of population performance, but this measure reflects the effects of several confounding factors, of which the FCRPS is but one. Clearly, ocean conditions have the dominant influence on adult return rates, overriding variability associated with the hydropower system. Return rates have increased by an order of magnitude since the upturn in ocean conditions that began in 1999, while survival through the hydropower system has remained relatively constant. Improvements in SAR, however, do not preclude the existence of hydropower system-related latent mortality or an interaction between latent mortality and ocean condition.

Transportation is not a panacea for negative effects of dams on fish stocks. When comparing annual indices of transported, wild, yearling Snake River spring-summer Chinook salmon (*Oncorhynchus tshawytscha*) and hatchery fall Chinook salmon versus in-river fish, in many cases transportation appeared to confer little benefit or harm. However, under certain times of the year and under low-flow conditions (particularly in 2001), transportation appeared to increase return rates of some segments of the yearling migrant populations. Further, the benefits of transportation decreased at transportation sites closer to Bonneville Dam. Thus future operations should focus on optimizing adult return rates, independent of the transportation process currently in operation. Strategies such as "spread the risk" and promotion of diversity suggest we should allow more fish to migrate in the river whenever it appears migration might lead to reasonable return rates compared to the alternatives. At times transportation may provide the best alternative. We note that transportation apparently has not provided any benefit to Snake River sockeye salmon.

Under most conditions, we have estimated relatively high direct (within the hydropower system) survival of yearling juvenile migrants, and substantial improvements in downstream survival appear unlikely, particularly improvements related to passage through dams. Summer subyearling migrants suffer greater mortality in reservoirs than do spring migrants, and improvements in river conditions may confer considerably improved survival. In 2001 the low survival experienced by spring migrants and generally lower survival of summer migrants likely resulted from conditions in the reservoirs, potentially low flow, and possibly a lack of spill. Therefore, we may face diminishing returns in terms of improving survival via technological fixes to dams. Efforts to reduce mortality in the reservoirs, understand how to reduce latent or indirect mortality (mortality expressed downstream of the hydropower system that results from hydropower system passage), and maintain diversity by improving habitat conditions in estuary and freshwater spawning and rearing habitats will likely have the strongest influence on overall stock viability.

For Snake River spring-summer Chinook salmon, we found that increased flow had a benefit to juvenile migrant survival, although the effect was small relative to the detriment that occurs when water temperatures become too high. For steelhead, the benefit of increased flow was apparently greater. However, in our multiple-regression model the benefit is offset somewhat by a countering trend of decreased steelhead survival as the season progresses, possibly related to their increased propensity to residualize as water temperature increased. For yearling Chinook salmon, temperatures above 13°C, typically reached in late May, appeared detrimental to survival. For both species, we consistently observed a strong relationship between flow and travel time. Thus increased flow may benefit spring migrants by moving them out of the lower Snake River before temperatures become too high.

Flow clearly can affect the timing of smolt migration to the estuary, which appears to greatly influence their SAR. Delayed migration, which reduces available energy reserves in smolts, could affect survival. Low-flow years exacerbate the problem, both within the hydro-power system and in freshwater areas upstream that fish negotiate before arriving at the first dam.

Introduction

The construction and operation of the 31 Federal Columbia River Power System (FCRPS) dams have contributed to the decline of anadromous salmon populations in the Columbia River basin and continue to affect them. (See Figure 1 for major dams in the Columbia River basin—not all are FCRPS dams.) While the dams provide about 60% of the Pacific Northwest region's hydroelectric generating capacity, supply irrigation water to more than a million acres of land, and store water to enhance flood control, they also block access to historical salmon spawning areas or alter their migratory corridor, increasing mortality both directly and indirectly. In addition to the FCRPS, human impacts from construction of hundreds of other dams, agriculture, commercial fishing, mining, and dredging all have affected various Columbia River basin anadromous salmon populations. Thus ascribing effects of the FCRPS is complicated.

Since completion of the FCRPS dams, many physical and operational changes occurred in an attempt to minimize impacts on anadromous salmon populations. Research shows that direct survival of salmonid migrants increased as the result of these changes. Thus the majority of deleterious effects to salmon from having passed through the FCRPS dams are expressed indirectly, but to an unknown degree, downstream of the hydropower system. Determining the extent to which direct and indirect effects of the hydropower system negatively affect salmon populations, in the context of all other factors, is critical to defining additional measures needed within the FCRPS to ensure salmon survival. Although we can measure annually direct survival and travel time of fish, inferences regarding delayed mortality often rely on long-term trends in adult fish return rates, data which are inherently variable. Thus estimating the extent to which the FCRPS and all other human activities affect salmon populations requires understanding direct and indirect effects in concert with natural variability in salmon populations. Our knowledge of natural salmon variability through time is lacking, but the historical record provides some indication of its magnitude.

Historical Background

The abundance of all animal populations fluctuates over time. For salmon, we most often tend to associate changes in populations to human activities; in many cases, rightly so. However, we generally lack knowledge of natural population fluctuations independent of human interactions. Despite a long Native American oral history in the Pacific Northwest, little hard information exists about the size and extent of historical salmon population fluctuations. Chapman (1986) estimated that peak adult salmon returns to the Columbia River basin in the 1800s ranged from 7.4 million to 8.8 million fish. Of these, Chapman estimated that spring and summer Chinook salmon (*Oncorhynchus tshawytscha*) numbered 500,000–590,000 and 2 million–2.5 million, respectively. However, at the end of the last ice age (approximately 15,000 years before present), glaciers covered most of the upper Columbia River basin and much

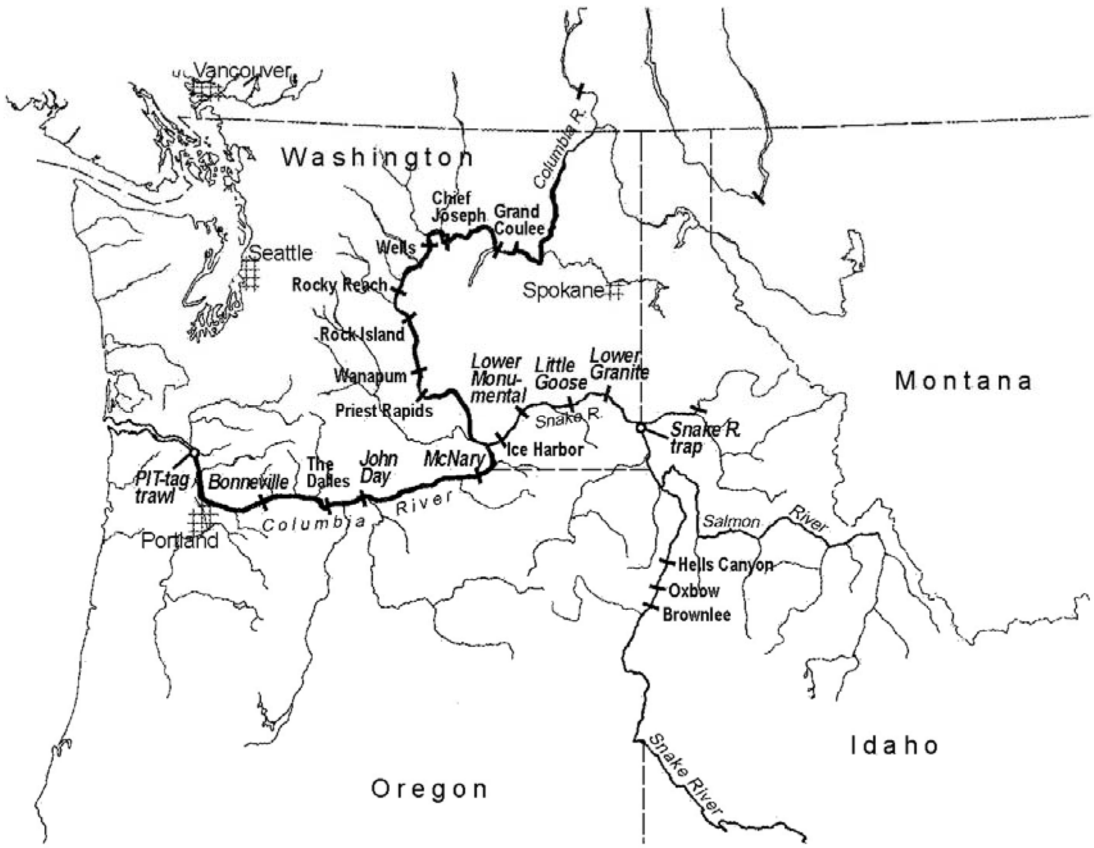

Figure 1. The Columbia River basin, with major hydroelectric generating dams and, in bold, PIT-tag detection sites at traps, dams, and the PIT-trawl.

of the Salmon River drainage (McPhail and Lindsey 1986). Thus these salmon populations are fairly recent in origin. Chatters et al. (1995) concluded that over the past 7,000 years, salmon production in the Columbia Basin varied tremendously with changes in climate. They speculated that average salmon populations were much lower approximately 3,500 years ago compared to recent centuries, but higher 1,200 years ago. These speculations comport with recent findings of Finney et al. (2002), which showed that Alaska sockeye salmon populations also varied greatly over the past 2,000 years.

Anecdotal evidence indicates that natural variations in Columbia River salmon abundance also occurred over shorter time spans. Chance (1973) quotes from a number of early diaries, which reported that in 1811 and again in the late 1820s salmon populations from the middle Columbia River (between the confluence of the Snake River and Kettle Falls) were so low that settlers and Native Americans relied on horse flesh for survival. Although Snake River basin salmon populations were probably also low at these times, based on catch records for the Columbia River basin as a whole, all stocks rebounded to high levels near the end of the century. At that time, Columbia River salmon populations began to decline dramatically as a result of overfishing. Beginning in the early twentieth century, the declines were exacerbated by environmental degradation due to mining, grazing, logging, water withdrawals for irrigation, and dams constructed on major tributaries for power production and water storage. Although stocks decreased, a sign of run size variability still existed. The upriver run (above Bonneville Dam) of spring Chinook salmon averaged 119,000 fish from 1940 to 1949, with an average harvest rate of 60%; increased to 208,000 fish from 1950 to 1959, with an average harvest rate of 60%; and decreased to 171,000 from 1960 to 1969, with an average harvest rate of 39% (WDFW and ODFW 2002).

Impacts from Dams

Concerns about the potential impacts of the FCRPS on anadromous fish were raised prior to the construction of Bonneville Dam (Griffin 1935). In fact, coincident with the dam's completion, studies began in 1939 to estimate survival of juvenile salmon passing through turbines and spill to determine the dam's effect on juvenile salmon (Holmes unpubl. report). Results from these studies and those by Schoeneman et al. (1961) at McNary Dam in the mid-1950s led to concern about the probable impact of dams on juveniles. As five additional dams were scheduled for construction on the mainstem Columbia and Snake rivers, a Fish Passage Program within the Bureau of Commercial Fisheries (now NOAA Fisheries Service) began to study the adaptability of salmon to new environments created by dams, effects of impoundments on fish migration, effects of dam passage on migrants, and ways to mitigate these effects.

Raymond (1979) provided the initial summary of changes in survival and travel time for yearling migrants that occurred during and after dam completion. In short, the 1966–1968 average annual survival of wild yearling Chinook salmon outmigrants from a trap on the Salmon River to Ice Harbor Dam averaged approximately 89% (Lower Monumental, Little Goose, and Lower Granite dams were not yet completed). Prior to the completion of John Day Dam, the 1966 and 1967 survival from Ice Harbor to The Dalles Dam averaged 64%. Combining these two estimates with an estimated survival between The Dalles and Bonneville dams provided overall juvenile Chinook salmon and steelhead survival estimates ranging between approxi-mately 40% and 55% through the stretch of river from the conjunction of the Clearwater and Snake rivers to below Bonneville Dam but with only four dams in place (Williams et al. 2001). After completion of the system (with eight dams in place), survival estimates for yearling Chinook salmon and steelhead decreased to mean values of approximately 16% and 11% (1975–1980), respectively (but near 0 for both in the very low-flow year of 1977) (Williams et al. 2001).

Reservoirs behind dams increased travel time for juvenile migrants. Annual travel time estimates for fish were 10 days (high flow) to 20 days (low flow) to migrate through the hydropower system with four mainstem dams in place (expansion of data from Raymond 1979), but after completion of all eight dams, annual travel time estimates ranged from 15 days (high flow) to 40 days (low flow).

Concurrent with research documenting direct effects of the dams on fish, other researchers worked on means to mitigate them. This research led the U.S. Army Corps of Engineers (COE) to construct juvenile bypass systems at dams, modify spillways, and implement a transportation program to collect fish at upstream dams and barge them to a release site below Bonneville Dam. Despite these efforts, by the early to mid-1990s, stocks had not recovered. As a consequence, 12 of 16 Columbia River basin evolutionarily significant units (ESU) (Waples 1991) were listed as threatened or endangered under the Endangered Species Act (ESA) (NMFS 1992).

The PATH Process

To provide information needed to write biological opinions (BiOp) associated with the stock listings and to develop estimates of FCRPS impacts, in 1995 the National Marine Fisheries Service (NMFS or NOAA Fisheries Service) created the Plan for Analyzing and Testing Hypotheses (PATH). A summary of the PATH process, based on a paper by Marmorek and Peters (2001), follows.

A group of approximately 30 scientists worked for nearly 5 years to develop analyses to explain the impact of the FCRPS on anadromous fish stocks above Bonneville Dam. PATH scientists identified two key uncertainties deemed to most strongly affect survival and recovery potentials of Snake River spring-summer and fall Chinook salmon: extra mortality of in-river migrants and the relative post–Bonneville Dam survival of transported fish compared to post–Bonneville Dam survival of in-river migrants (designated as *D*).

Extra mortality was a construct of the models used by PATH, a parameter used to account for any mortality occurring outside the juvenile migration corridor not accounted for by the other terms used in the PATH life cycle models such as productivity and carrying capacity, mortality in reservoirs and at dams, and estuarine and ocean mortality affecting all salmonid populations. The existence of extra mortality required the presumption that changes in ocean conditions had no systematic differences between impacts on upstream and downstream Columbia River stocks. No direct measurements of extra mortality were possible; it was only inferred from other measured quantities. Because the observed historical patterns in extra mortality were linked with several possible causes, PATH formulated three alternative hypotheses concerning extra mortality and the possibility of FCRPS actions to decrease it:

1. Dam removal—extra mortality resulted from adverse effects to smolts from migrating through the eight mainstem FCRPS dams. Removal of dams in the Snake River would eliminate extra mortality.

2. Ocean regime shift—extra mortality followed a 60-year cycle related to long-term cycles in ocean conditions. No FCRPS actions will directly reduce extra mortality, but extra mortality will eventually dissipate when ocean conditions improve.
3. Stock viability—extra mortality resulted from processes not affected by any FCRPS action or ocean regime shift. Stocks will remain low due to interactions with hatchery fish, the presence of diseases such as bacterial kidney disease (BKD), or reduction in nutrients associated with historical declines in spawning stock.

In the PATH models, *D* represents an annual value of the differential survival downstream of Bonneville Dam for transported fish compared to in-river migrants. Low values of *D* indicate that transported fish incurred greater mortality downstream of Bonneville Dam than in-river migrants. Further, a low enough *D* value would explain historical stock productivity patterns without requiring extra mortality to explain changes in productivity.

Many PATH participants believed that extra mortality existed; however, the group never reached consensus about whether it existed and, if so, what causes it. Schaller et al. (1999 and 2000), Deriso et al. (2001), Petrosky et al. (2001), and Budy et al. (2002) argued that extra mortality existed and is linked to the FCRPS. Zabel and Williams (2000) suggested that differences in productivity could have occurred as a result of differences in underlying stock responses to changing ocean conditions. Subsequent to PATH, Levin and Tolimieri (2001) and Levin (2003) found that Chinook salmon populations used in the PATH life cycle models for the Snake, upper Columbia, and middle Columbia rivers had different productivity and that productivity varied between different time periods but not consistently with changes in ocean conditions. The degree to which the hydropower system affects survival of fish that successfully migrated as far as below Bonneville Dam remains contentious. We provide more details about this mortality in the "Latent Mortality" section (page 106).

Stock Evaluations Subsequent to PATH

Due to the perceived complexity of PATH products by some Northwest Fisheries Science Center (NWFSC) scientists not involved with PATH, a matrix model was developed in 1999 to evaluate the status of listed Snake River spring-summer Chinook salmon stocks. The model results indicated that little room existed to increase stock productivity within the migration corridor of the FCRPS because of improvements made at dams between the mid-1970s and late 1980s. Results indicated that factors currently driving productivity occurred in the freshwater spawning and rearing areas and in estuary/early ocean residence (Kareiva et al. 2000). The matrix model set a value for *D* at 0.7 and used a range of values for delayed mortality.

Concurrent with matrix-modeling efforts, other NWFSC staff developed draft white papers to summarize knowledge about how the FCRPS affected stocks. After considering comments based on regional review, final versions of the white papers were posted on the NWFSC website (http://www.nwfsc.noaa.gov/publications/whitepapers/index.cfm). They covered the following:

- Passage of juvenile and adult salmonids past Columbia and Snake River dams.
- Predation on salmonids relative to the FCRPS.
- Salmonid travel time and survival related to flow in the Columbia River basin.
- Summary of research related to transportation of juvenile anadromous salmonids around Snake and Columbia River dams.

In developing the NMFS 2000 FCRPS BiOp (NMFS 2000), the Biological Effects Team reviewed and analyzed fish passage assumptions NMFS used in earlier fish passage modeling exercises, those developed in the PATH process, fish passage information contained in the four white papers, and the most recent empirical data to determine the fish passage parameters for input into the simulated passage (SIMPAS) model. To update the 2000 BiOp or develop a new one to replace it, NOAA Fisheries Service needs an update on effects of the FCRPS on ESA-listed salmonids in the Columbia River basin. In this technical memorandum we update information about hydropower system survival for listed juvenile and adult salmon through the mainstem Snake and Columbia River dams (to the extent data are available), results from transportation studies, flow effects on survival and travel time, and overall effects of FCRPS operations on adult returns. We focus primarily on Snake River spring-summer Chinook salmon, because they migrate through the entire FCRPS mainstem dam complex and they have the most empirical information. Fewer data exist for all other stocks, so we either provide incomplete information or make inferences where we deem reasonable.

Returns of many listed Columbia River salmon stocks in the last several years have far exceeded numbers seen in recent decades. Thus we also discuss associations between direct survival through the FCRPS and changes in adult returns. Again, we do this most effectively for Snake River spring-summer Chinook salmon, because we know the most about fluctuation over time. For other stocks, we mostly rely on changes in combined wild and hatchery adult returns to dams, because reliable estimates of wild adult returns and smolts do not exist.

The sections that follow provide summaries of methods and results from work described in recent annual reports to the COE and the Bonneville Power Administration (BPA) or in peer-reviewed literature. We direct readers who want additional information to those sources. In a few cases, some of this work is not readily available, because it is in press or in unpublished manuscripts under journal review. The authors will provide additional details of this information on request.

General Analytical Approach

The rapid decline of salmon stocks coincident with the completion of the Snake River dams in the early 1970s resulted in a singular paradigm that largely implicated the FCRPS as the primary reason for decreased salmon abundance. Although efforts have been under way since the early 1980s to mitigate FCRPS effects, the perspective and analytical framework to empirically define them—and solutions for them—concentrated on analyses and conclusions that implicate the FCRPS as the major influence on stocks. Scientific inquiry, however, relies on the acquisition of data from varied sources and from analyses and interpretation of data that explain relationships from an empirically based perspective. We cannot treat any one description as the most likely model or hypothesis a priori; instead, we must carefully weigh the available evidence against alternative hypotheses to explain probable FCRPS impacts on Columbia River basin salmon populations. Our analytical approach to assessing the effects of dams on salmon populations consisted of considering multiple working hypotheses. We used a variety of descriptions, models, and data sources to look for consistency in factors that could explain variable stock productivity over time. The results described in this report include smolt-to-adult returns (SAR) for untagged and passive integrated transponder (PIT)–tagged yearling and subyearling Chinook salmon populations, and SARs of transported and in-river migrating yearling and subyearling Chinook salmon from the upper Columbia River basin. We also used juvenile salmon migrant survival and migratory history studies that address the underlying mechanisms for reduced SARs such as reach survival, travel time, and latent mortality for yearling and subyearling Chinook salmon populations. Further, we discuss potential mechanistic causes for overall returns based on empirical data gathered from temporal timing of stocks moving through the FCRPS. These studies relied mainly on analyses of PIT-tagged fish. PIT tagging of juvenile salmonids began on a small scale in 1987 and has expanded tremendously since then, although not homogeneously throughout the Columbia River basin (Table 1).

This technical memorandum contains results from our widely varied analyses. We fully respect the approach of previous individual analyses, but we thought that we needed to consider all lines of evidence simultaneously, instead of relying on various studies in isolation. As detailed below, we believe our analyses indicate that the FCRPS has affected and still affects migrant fish. While we conclude that some level of hydropower system–related latent mortality exists, it does not override the strong returns resulting from good ocean conditions. We caution that ocean conditions will not remain favorable forever; therefore, we must continue to monitor FCRPS effects in concert with all other negative anthropogenic effects on salmon in order to avoid the losses incurred during the 1980s and 1990s.

Table 1. Annual numbers of fish PIT tagged and released in different areas of the Columbia River basin.

Outmigration year	Upper Columbia River[a]	Snake River	Middle lower Columbia River[b]	Columbia River[c]	Willamette River
1987	7,673	2,619	–	–	–
1988	–	19,728	25,088	–	–
1989	4,998	92,254	22,894	–	–
1990	7,857	66,804	22,099	1,700	–
1991	6,644	70,462	32,613	724	–
1992	11,021	66,144	30,645	1,002	–
1993	24,326	132,409	29,693	733	–
1994	33,916	335,845	1,853	721	1,775
1995	34,982	514,551	–	–	–
1996	46,213	373,356	3,044	2,980	–
1997	40,153	458,881	107,685	10,708	–
1998	147,133	589,815	200,595	12,666	–
1999	168,593	763,014	477,897	18,336	3,429
2001	214,688	561,453	178,734	33,025	7,791
2002	613,296	858,240	223,181	59,511	9,597
2003	1,023,730	907,460	121,805	124,748	3,927
Total	2,385,223	5,813,035	1,477,826	266,854	26,519

[a] Drainage above the confluence with the Yakima River (above RKm 539).

[b] Drainage between the confluence with the Wind and Yakima rivers (between RKm 252 and 539).

[c] Drainage from the Wind River to the ocean (below RKm 252).

Adult Return Rate

Rates Based on Nontagged Fish

Methods

SAR provides a measure of survival that encompasses smolt migration, estuary/ocean residence, and adult return stages. Where possible we calculated SAR by dividing returning adults from a single broodyear by the broodyear's smolts. Changes in SAR over a number of years provide an index of temporal variability in stock productivity. For Snake River spring-summer Chinook salmon, we estimated recent (1997 to 2001 outmigration) SAR from Lower Granite Dam, adjusted for annual downstream harvest, and compared them to earlier years' estimates of SAR (catch plus escapement) to the upper Snake River dam. In brief, from Petrosky et al. (2001) we used estimated wild adult (3-, 4-, and 5-year-old fish that spend 1, 2, or 3 years in the ocean) 1964–1999 returns (we adjusted 1993 to 1996 1-ocean fish for estimated additional returns to Oregon) and 1964–1999 harvest rates. We used Raymond (1988) for estimates of smolt abundance between 1964 and 1984. We derived estimates for wild smolts from 1993 to 2003 by expanding the daily collection of wild fish at Lower Granite Dam (FPC 2003a) by the daily estimates of detection efficiency (derived with methodology used in Sandford and Smith 2002) of wild smolts at the dam for each year. For smolt years 1995 to 2003, we adjusted smolt estimates by an estimated percentage of nonclipped hatchery fish arriving at the dam that were not identified as hatchery origin. This adjustment decreased numbers of wild smolts by 6%, 1%, 0%, 2%, 4%, 3%, 1%, 4%, and 4% for smolt years 1995 through 2003, respectively. We estimated smolt abundance from 1985 to 1993 based on a Beverton-Holt curve generated from estimated numbers of smolts from 1964 to 1984 and 1994 to 2003 ($R \cong 0.80$) and the estimated number of wild fish passing the upper Snake River dam[1] 2 years earlier. We estimated wild adult returns to Lower Granite Dam from 1997 through 2003 from annual fish counts of spring-summer Chinook salmon reported to have passed the dam. Fish counters at the dam enumerated fish as they passed through the counting window and assigned them to either a group with adipose fins (ostensibly wild fish) or a group without adipose fins (known hatchery fish with fins clipped as juveniles). We adjusted the clipped (missing adipose fin) hatchery fish returns by the estimated proportion of nonclipped (fish with an adipose fin, but possibly with other clipped fins) hatchery fish in the return. We used estimates of 89.6%, 87.7%, 86.5%, 96.0%, 92.3%, 89.6%, and 88.9% for identifiable adult (2- and 3-ocean fish) hatchery fish in return years from 1997 through 2003, respectively. We then subtracted the corrected hatchery count from the total adult return to derive the wild fish estimate.

To separate adult returns into the respective 2- and 3-ocean component, we used two methods. For the 1997 return year, we used PIT-tag data to estimate the percentage of 3-ocean fish

[1] Beginning in the late 1960s (Raymond 1988), the uppermost dam on the Snake River changed as follows: through 1968, Ice Harbor Dam; in 1969, Lower Monumental Dam; from 1970 to 1974, Little Goose Dam; and from 1975 to present, Lower Granite dam.

that returned from the 1994 outmigration. We expanded the estimated number of jacks (1-ocean fish) plus 2-ocean fish from the 1994 outmigration (data from Petrosky et al. 2001) to derive the number of 3-ocean fish to meet the estimated percentage in the return. We then subtracted this estimate from that of wild 1997 adults to derive the number of 2-ocean fish. For returns from 1998 through 2003, we used age-class data collected by Idaho Department of Fish and Game (IDFG) (1998–2001 data from Kiefer et al. [2002]; 2002–2003 data from IDFG[2]). We then estimated the total adult return for outmigration years from 1995 through 2001 (only through 2-ocean returns for the last year) by combining the estimated number of wild jacks with the 2- and 3-ocean returns for each year. To account for harvest rates in the Columbia River that varied between 0% and 40% over the time period, we expanded adult returns to the uppermost Snake River dam for the period between 1964 and 1999 based on estimated Columbia River harvest rates in Petrosky et al. (2001). We expanded adult returns for 2000 to 2003 based on unpublished harvest rates.[3]

For Snake River yearling Chinook salmon, in addition to SAR based on Petrosky et al. (2001), we plotted SAR for the period from 1964 to 1984 from Raymond (1988). For Snake River steelhead, we used Raymond's (1988) SAR estimates for the period from 1964 to 1984. We used Petrosky's (IDFG) updated steelhead SAR from 1985 to 1994, submitted as part of the PATH process (Marmorek et al. 1998). Petrosky[4] used the same methods used in the PATH report to develop preliminary 1995–2000 SAR estimates for subbasin planning. He cautioned that these estimates were preliminary, updated, wild adult and smolt numbers, which had not yet been reviewed by the Snake River Technical Recovery Team. Adult wild A-run and B-run estimates were also from the Technical Advisory Committee. Updated adult-age structure information was from Lower Granite Dam scale sampling for the 1995–2001 run years (cooperators were NMFS and IDFG, data collection and archiving; USFWS and Utah State University, scale reading).

For wild stocks where we lacked direct juvenile and adult information, we compared the median count of adult fish from the 2001–2003 return years to the median adult count from the 1992–2000 return years. We obtained counts of adult fish at dams for the composite wild and hatchery stocks from the Columbia River Data Access in Real Time (DART) website (CBR UW 2004) For natural-origin Snake River fall-run Chinook salmon, we used updated (unpublished) adult escapements for return years 2000–2002 over Lower Granite Dam developed by NOAA Fisheries Service (NMFS 2003) and adult returns from 1991 to 1999 from unpublished data submitted to the Biological Review Team for Chinook salmon.[5] We then compared the difference in median returns for adult fish between the two periods to the difference in median SARs for Snake River spring-summer Chinook salmon for the same periods.

[2] R. Kiefer, IDFG, Boise, ID 83707. Pers. commun., March 2004.

[3] P. Dygert, NOAA Fisheries Service, Seattle, WA. Pers. commun., December 2003.

[4] C. Petrosky, IDFG, Boise, ID. Pers. commun., March 2004.

[5] T. Cooney, NOAA Fisheries Service, Seattle, WA. Pers. commun., January 2003.

Results

Snake River spring-summer Chinook salmon

Estimated SAR (catch + escapement) of wild Snake River spring-summer Chinook salmon from the 1999 and 2000 outmigrations increased to levels only observed prior to construction of the final mainstem FCRPS dams (Figure 2). The median SAR of 3.0% (range 1.6–3.8%) from the 1998–2000 outmigrations was similar to the median SAR of 3.1% (range 1.9–4.6%) from the 1964–1970 outmigrations based on data from Petrosky et al. (2001), and 81% of the median 3.7% SAR (range 3.3–6.1%) for the same years based on Raymond's (1988) analyses. The median SAR of 3.0% from the 1998–2000 outmigrations was 5 times as high as the median SAR of 0.6% (range 0.20–1.9%) from the previous 10 years (1988–1997 out-migrations). From the low-flow 2001 outmigration, the SAR presently stands at approximately 1.6%, with 3-ocean fish still returning in spring and summer 2004. This return rate already exceeds total SARs for all wild Snake River spring-summer Chinook salmon outmigrations between 1976 and 1997. However, given the low number of smolts in the outmigrations because of earlier poorer returns, the absolute wild adult return did not reach the levels that occurred in the 1960s.

Snake River fall Chinook salmon

The median estimated SAR for natural-origin fall-run Chinook salmon between 2000 and 2002 was 3.4 times higher than the median adult return for the period 1991–1999 (Figure 3).

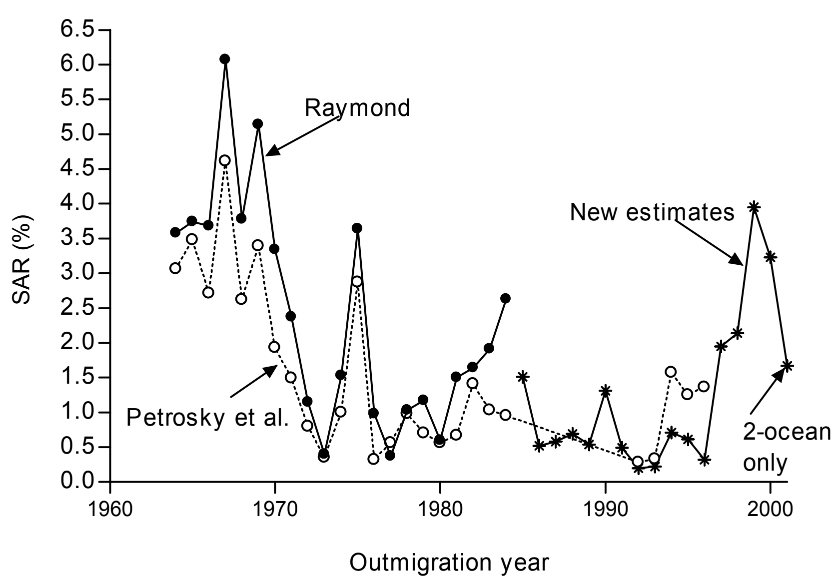

Figure 2. Estimated SAR for wild Snake River spring-summer Chinook salmon. Initial estimates from 1964 to 1984 are from Raymond (1988). Petrosky et al. (2001) used Raymond's smolt estimates, but they used a new algorithm to develop an alternative SAR for the 1964–1984 period. They also estimated SAR for outmigration years 1992–1996.

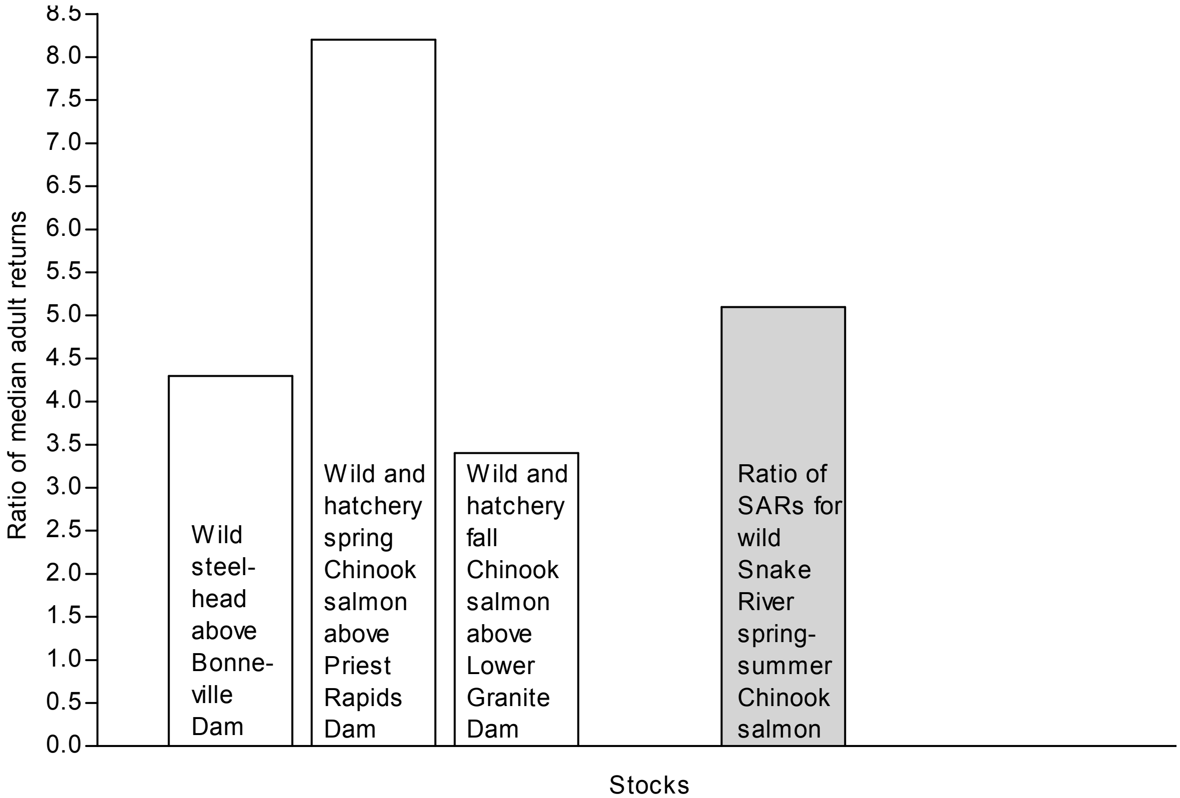

Figure 3. Ratio of the median adult fish count (2001–2003, from CBR UW 2004) for wild steelhead at Bonneville Dam and hatchery and wild spring Chinook salmon at Priest Rapids Dam divided by the median count at each respective dam for steelhead (1993–1000) and Chinook salmon (1991–2000). Data for fall Chinook salmon were derived from information supplied to the Chinook Salmon Biological Review Team and Technical Advisory Committee.

Upper Columbia River spring Chinook salmon

As with historical data, the response of spring Chinook salmon stocks in the upper Columbia River increased, but to a greater degree than wild Snake River spring-summer Chinook salmon. The median estimated adult return was nearly 8 times higher (Figure 3).

Wild steelhead above Bonneville Dam

Median counts of wild, upper-river summer steelhead at Bonneville Dam were 4.3 times higher, from 33,000 (range 24,000–58,000) to 143,000 (range 112,000–149,000) (Figure 3). We have no information on counts of wild steelhead into the upper Columbia River.

Wild Snake River steelhead

A plot of the trend over time indicates that SARs for Snake River steelhead increased considerably in 2002 and 2003 compared to the previous 10 years (Figure 4) and reached levels not observed since the early 1970s and middle 1980s.

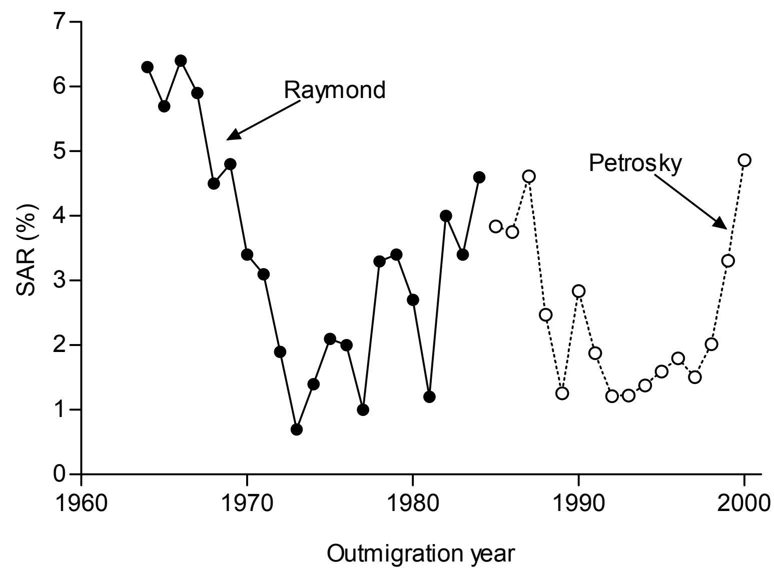

Figure 4. Estimated SAR of wild Snake River steelhead. Early data are from Raymond (1988). Data from 1985 to 2000 (1985–1994) are from Petrosky (submitted to PATH; see Marmorek and Peters 1998). Data from 1995 to 2000 are from C. Petrosky.[6]

Snake River sockeye salmon

We have little specific information about Snake River sockeye salmon. Between 1990 and 2001, 478 PIT-tagged sockeye salmon arriving at lower Snake River dams were transported, while 3,925 migrated in-river. Of these, two transported fish (0.4% SAR) and one in-river fish returned (0.03% SAR). Adult returns of sockeye salmon to Lower Granite Dam between 1990 and 2003 ranged from 3 to 282 fish (annual median was 13 fish). Snake River sockeye salmon have not demonstrated increased SARs in the last several years, similar to what occurred for Snake River Chinook salmon and steelhead.

Discussion

By any measure, Snake River spring-summer Chinook salmon abundance increased dramatically in the last few years. This increase apparently largely resulted from a shift in ocean conditions, and the changing ocean conditions, along with changes in climatic conditions that interacted with habitat, abundances of hatchery fish, and changes in flow within the hydropower system, led to the greater survival. However, the relative role of the hydropower system in overall stock performance is still uncertain. We do believe that improvements made to the hydropower system from the 1970s through the 1990s were crucial to preventing even more drastic declines during the recent period of poor ocean conditions and that possible negative effects of the hydropower system are more likely to influence stocks during periods of poor ocean conditions. Unfortunately, we cannot reliably predict future ocean conditions, and thus we

[6] C. Petrosky, IDFG, Boise, ID. Pers. commun., March 2004.

cannot rely on the persistence of good ocean conditions. With predictions of increased global warming in the near future, global climate change may actually lead to ocean conditions that are worse than any we have yet experienced. For these reasons, we must continue to assess the effects of the hydropower system in the context of all impacts, including those occurring in both seawater and freshwater habitats.

The high SAR estimates for the unmarked population do not surprise us. As outlined in the introduction, historically they varied (although for Snake River fish we only have empirical estimates since 1964). Williams and Matthews (1995) found that conditions in the hydropower system improved tremendously from those that initially caused large losses of juvenile migrants (Raymond 1979). Williams et al.(2001) also found that survival of yearling Snake River Chinook salmon through the present eight dams of the mainstem FCRPS recently matched or exceeded those estimated to have occurred when the mainstem FCRPS had only four dams. Without actual measures of survival, but under the presumption of success from transportation, Raymond (1988) and Williams (1989) predicted that large returns of Snake River spring-summer Chinook salmon could once again occur if ocean conditions improved. Using new modeling tools that predict adult returns based on ocean conditions that juveniles encounter during their first several months at sea, recent analyses by Scheuerell and Williams (in press) found that ocean conditions have a high correlation ($R^2 = 0.71$) with SARS of wild Snake River spring-summer Chinook salmon (see the "Large Scale Processes" subsection, page 123, for details). Recent research by Peterson and Schwing (2003) demonstrated that ocean conditions improved dramatically in 1999. We do not know how long these improved conditions will last, but at the time of these analyses we predicted good adult returns from juvenile outmigrations through 2003 (with adults returning through 2006) (Scheuerell and Williams in press). Based on 1990s returns, the comparative escapement to spawning when comparing one broodyear to the next one it produced [$\ln(\text{escapement}_{BY}/\text{escapement}_{BY-1})$] already exceeded 1.0 for 4 consecutive years, the longest stretch since such records began in the 1960s (Figure 5).

As with yearling Chinook salmon, estimated adult returns of natural-origin fall Chinook salmon to above Lower Granite Dam were nearly 3.5 times higher than outmigration levels in the early to mid-1990s. Total numbers of fall-run Chinook salmon over Lower Granite Dam also increased tremendously, but much of this increase resulted from large releases of Lyons Ferry Hatchery fish above the dam. Total numbers of natural-origin fish above Lower Granite Dam in recent years exceeded all levels observed since 1975, when the dam was completed. The two periods are not directly comparable, however, because harvest rates on fall Chinook salmon changed substantially after ESA listing of Snake River fall-run Chinook in 1992, and releases of unmarked hatchery fall Chinook salmon above Lower Granite Dam increased.

Steelhead SAR did not follow the same patterns as yearling Chinook salmon SAR. Ocean conditions appear to affect steelhead differently, although they do have an effect. British Columbia stocks also experienced a very steep decline in steelhead SAR in the early 1990s, which was attributed to changed ocean conditions (Welch et al. 2000). In the 1990s, low spawning populations (some the lowest in the last 35 years) produced comparatively low numbers of wild smolts compared to the 1960s. Thus even with recent large increases in adult returns, total adult returns of wild steelhead remain at nearly one-half the level of the 1960s.

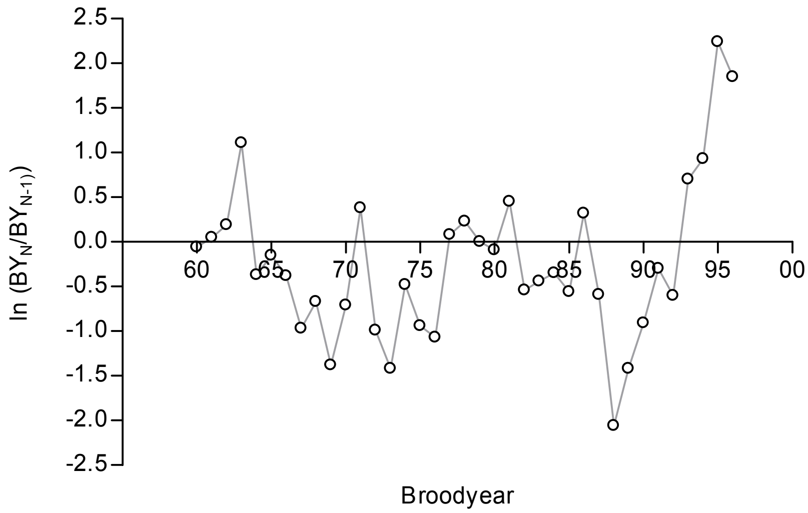

Figure 5. The $\ln(BY_N/BY_{N-1})$ for the composite wild spring-summer Chinook salmon population in the Snake River basin above the upper Snake River dams (Ice Harbor Dam in 1962, Lower Monumental Dam in 1969, Little Goose Dam in 1970, and Lower Granite Dam in 1975). BY_N = escapement over the upper Snake River dam for the current brood. BY_{N-1} = escapement over the upper Snake River Dam for the brood that produced offspring for the current brood.

Rates Based on PIT-Tagged Fish

Methods

We estimated annual SAR for PIT-tagged Snake River fish based on a Lower Granite Dam equivalent for smolts and adult returns to Lower Granite Dam by following the methods of Sandford and Smith (2002). We estimated how many fish passed the dam on each day of the migration season and totaled the daily estimates. To get each day's estimate, we used the following process:

1. For fish detected on a given day at Little Goose Dam that were previously detected at Lower Granite Dam, tabulate according to their detection (passage) day at Lower Granite Dam.
2. For fish detected on the same day at Little Goose Dam that were not previously detected at Lower Granite Dam, assign them an estimated "nondetection passage day" at Lower Granite Dam, assuming that their distribution over days at Lower Granite Dam was proportionate to that of fish detected at Lower Granite Dam.
3. Repeat this process for all days of detection at Little Goose Dam.
4. Sum all these detected and nondetected fish for a given day at Lower Granite Dam.

5. Estimate that day's detection probability by calculating the proportion of detected fish to the total of detected and nondetected fish (after making an adjustment for fish transported at Lower Granite Dam).
6. Divide the total detected number at Lower Granite Dam on that day (bypassed and transported) by the estimated detection probability to get an estimated daily total.

Formally, this process is referred to as the Schaefer method (Schaefer 1951). We modified the method slightly for estimates in the very early and late periods of the passage distribution where the above process was not applicable (i.e., for days when no detections occurred at Little Goose Dam of fish previously detected at Lower Granite Dam).

We then estimated SAR for various "detection-history categories," in particular for fish transported from Lower Granite, Little Goose, Lower Monumental, or McNary dams; for fish bypassed back to the river one or more times at these dams; and for fish never detected at these dams. (Results and discussion of SAR for multiply bypassed fish is contained in the "Latent Mortality" section, page 106.) To do this, we developed daily passage estimates at Lower Granite Dam using the following process:

1. For each daily Lower Granite passage group, we estimated detection probabilities at Little Goose, Lower Monumental, and McNary dams using the Cormack-Jolly-Seber survival model (Cormack 1964, Jolly 1965, Seber 1965).
2. We multiplied the estimated daily Lower Granite Dam total by the appropriate detection and transport probabilities. For example, the detection-history category "not detected at Little Goose Dam and then transported from Lower Monumental Dam" is equivalent to multiplying the Lower Granite Dam daily estimate by (1 – probability of Little Goose Dam detection) × (probability of Lower Monumental detection) × (probability of transportation from Lower Monumental Dam for fish detected there).
3. We summed the estimates for all daily groups to get total smolts in each detection-history category.

Next we calculated SAR. For a given detection-history category, this is the ratio of observed number of adults to estimated number of smolts. We also estimated the precision for the estimated SAR using bootstrap methods where the individual fish information (i.e., detection history, detection dates, and adult return record) and the entire estimation process were boot-strapped 1,000 times. Confidence limits were generated from the bootstrapped estimates. If no adult salmon returned, we used the "rule of 3," based on the estimated number of juveniles, to construct an approximate 95% confidence interval (Hanley and Lippman-Hand 1983).

Finally we weighted SAR of PIT-tagged fish by the estimated percentage for the detection history of the untagged population. Because the untagged fish population passing through the Lower Granite, Little Goose, and Lower Monumental dams bypass systems were transported, we used the estimated percentage of first-time detections of PIT-tagged fish at those dams to weight the SAR for transported fish at those dams. We combined these SAR with the estimated SAR for fish not detected at collector dams (including McNary Dam) plus the SAR of fish bypassed at McNary Dam to derive a weighted SAR for the total population based on SAR of PIT-tagged fish.

Results

Snake River spring-summer Chinook salmon

The overall estimated SAR for wild and hatchery spring-summer Chinook salmon (Lower Granite Dam to Lower Granite Dam, not adjusted for harvest) was based on weighting SAR of PIT-tagged fish by migration histories of the untagged population. It ranged from 0.1% to 2.3% (Figure 6).

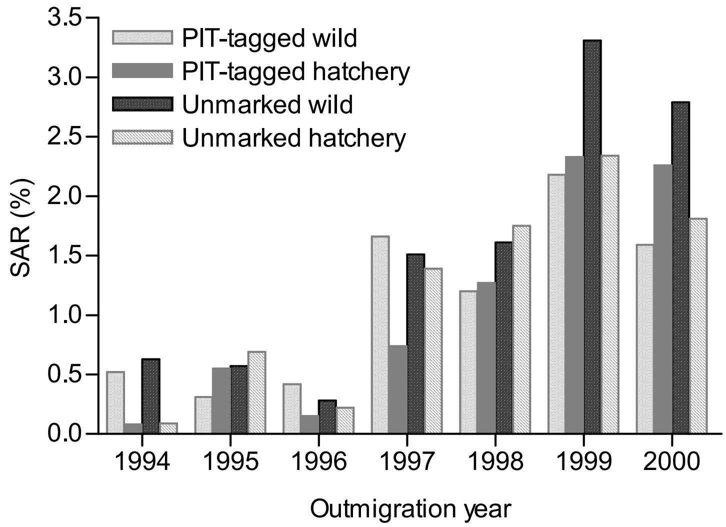

Figure 6. Estimated SAR for wild and hatchery Snake River spring-summer Chinook salmon, based on analyses of adult returns from the general untagged population and from SAR for PIT-tagged fish weighted by the estimated migration distribution of the untagged juvenile population. Total returns of PIT-tagged wild fish equaled 26, 60, 16, 40, 211, 720, and 594 from outmigration years 1994–2000, respectively. For the same years, total hatchery adult returns equaled 22, 14, 154, 87, 682, 1,690, 3,110, and 2,878, respectively.

Estimated annual SAR for PIT-tagged Chinook salmon marked above Lower Granite Dam with different detection histories as juveniles varied widely between years and dams for the 1993–2000 outmigrations (Table 2). Most estimates had wide 95% confidence bounds (Table 3). When confidence bounds between two different groups did not overlap, it indicated a significant difference in SAR between the two groups. Thus no significant differences existed for any comparison groups of wild spring-summer Chinook salmon. For hatchery spring-summer Chinook salmon, the annual SAR for fish transported from Lower Granite Dam was significantly higher than for in-river migrants (nondetected category) from migration years 1997–2000.

Snake River steelhead

The overall estimated SAR for wild and hatchery steelhead (Lower Granite Dam to Lower Granite Dam, not adjusted for harvest) based on weighting SAR of PIT-tagged fish by juvenile migration histories of the untagged population ranged from 0.3% to 3.1% (Figure 7).

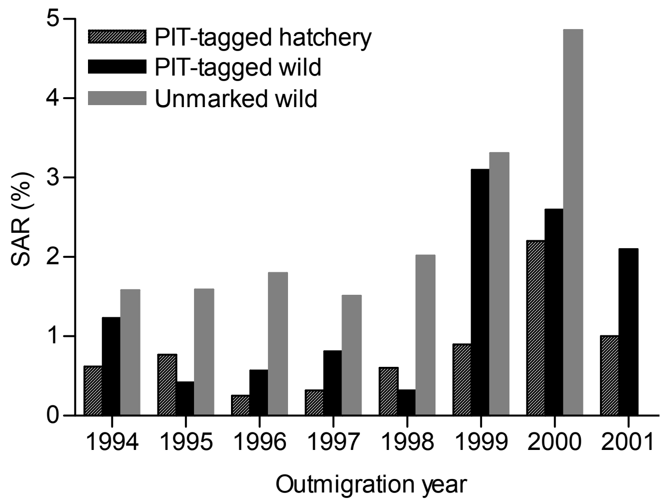

Figure 7. Estimated SAR for wild and hatchery Snake River steelhead based on analyses of fish PIT tagged as juveniles or the overall unmarked population (wild only). All analyses are based on juveniles and adults at Lower Granite Dam. Total returns of adult PIT-tagged wild fish from the 1994 through 2001 out-migrations equaled 21, 8, 15, 13, 25, 101, 283, 11, respectively. Total adult returns for hatchery fish from the same outmigration years equaled 51, 104, 69, 49, 76, 186, 267, and 9, respectively.

Table 2. Annual SAR (total adult returns/estimated juveniles) for spring-summer Chinook salmon PIT tagged above Lower Granite Dam with detection histories of groups that represented the unmarked population.

		Transported from (first time detected)				
Year	Rearing type[a]	Lower Granite Dam	Little Goose Dam	Lower Monumental Dam	McNary Dam	Nondetected
1993	W	0.10 (2/2088) 0.34 (1)	0.34 (1/295)	– (0/853)	– (0/605)	– (0/1056)
	H	0.09 (4/4643)	– (0/765)	– (0/2448)	– (0/1992)	0.06 (2/3161)
1994	W	0.71 (8/1128)	0.91 (4/441)	0.15 (1/648)	– (0/2670[c]	0.27 (6/2245)
	H	0.11 (2/1894)	0.12 (1/867)	0.11 (1/947)	0.02 (2/12368)[c]	0.09 (7/7707)
1995	W	0.39 (7/1781)	0.29 (1/345)	– (0/195)	NA	0.47 (9/1920)
	H	0.59 (14/2381)	0.79 (5/630)	0.39 (1/255)	NA	0.45 (27/6049)
1996	W	0.35 (1/284)	1.17 (1/86)	– (0/43)	NA	0.20 (4/2015)
	H	0.30 (6/2007)	– (0/510)	– (0/366)	NA	0.17 (29/17016)
1997	W	0.99 (2/202)	5.22 (2/38)	– (0/14)	NA	1.65 (14/847)
	H	0.89 (226/25523)[b]	0.70 (5/718)	0.69 (2/291)	NA	0.67 (162/24277)
1998	W	1.30 (11/848)	0.89 (3/336)	0.97 (1/104)	NA	1.43 (31/2169)
	H	1.74 (812/46772)[b]	0.84 (66/7853)[c]	0.57 (7/1238)[c]	NA	1.26 (260/20566)
1999	W	2.59 (32/1237)	2.15 (9/418)	1.75 (7/400)	NA	2.08 (73/3505)
	H	2.75 (698/25340)[b]	2.91 (481/16551)[b]	1.24 (25/2018)	NA	1.83 (567/30932)
2000	W	1.07 (4/374)	1.94 (6/309)	1.00 (2/201)	NA	2.17 (124/5718)
	H	3.08 (1029/33398)[b]	2.18 (310/14200)[b]	1.76 (86/4898)	NA	1.66 (755/45393)

[a] W = wild; H = hatchery.

[b] Groups significantly higher than nondetected fish.

[c] Groups significantly lower than nondetected groups.

Table 3. Bootstrapped confidence intervals (95%) around annual SAR (see Table 2) for Chinook salmon PIT tagged above Lower Granite Dam with detection histories of groups that represented the unmarked population.

		Transported from (first time detected)				
Year	Rearing type[a]	Lower Granite Dam	Little Goose Dam	Lower Monumental Dam	McNary Dam	Nondetected
1993	W	0.00–0.19	0.00–1.01	0–0.35[b]	0.00–0.50[b]	0.00–0.28[b]
	H	0.02–0.17	0.00–0.39[b]	0–0.12[b]	0.00–0.15[b]	0.00–0.17
1994	W	0.19–1.16	0.18–2.35	0.00–0.35	0.00–0.11[b]	0.13–0.48
	H	0.00–0.27	0.00–0.34	0.00–0.23	0.00–0.03	0.04–0.18
1995	W	0.22–0.62	0.00–0.61	0–1.54[b]	NA	0.28–0.60
	H	0.30–0.83	0.33–1.38	0.00–0.86	NA	0.30–0.59
1996	W	0.00–1.43	0.00–3.72	0–6.98[b]	NA	0.00–0.46
	H	0.20–0.44	0.00–0.59[b]	0–0.82[b]	NA	0.12–0.21
1997	W	0.00–2.22	0.00–24.2	0–21.4[b]	NA	0.81–2.64
	H	0.80–0.96	0.31–1.12	0.00–1.35	NA	0.60–0.74
1998	W	0.72–2.31	0.28–1.58	0.00–3.13	NA	1.08–1.75
	H	1.66–1.81	0.70–0.97	0.32–0.81	NA	1.16–1.36
1999	W	1.66–3.27	0.71–3.38	0.93–2.80	NA	1.73–2.36
	H	2.58–2.97	2.62–3.09	0.91–1.83	NA	1.63–1.94
2000	W	0.25–1.91	0.81–3.41	0.00–1.81	NA	1.80–2.48
	H	2.93–3.27	1.86–2.42	1.32–2.34	NA	1.40–1.75

[a] W = wild; H = hatchery.

[b] Based on "rule of 3" where 0 adults returned.

Estimated annual SAR for PIT-tagged steelhead marked above Lower Granite Dam with detection histories as juveniles equivalent to the unmarked population varied widely between years and dams for the 1993–2000 outmigrations (Table 4). Most estimates had wide 95% confidence bounds (Table 5).

Discussion

For spring-summer Chinook salmon, few treatments of PIT-tagged fish from any year attained a SAR that met the 2% to 6% SAR range identified in PATH as a goal necessary for recovery of the listed stocks while allowing for historical harvest rates (Table 2). In contrast, our estimated SAR for the wild population based on total wild returns to Lower Granite Dam, divided by the estimated number of wild juveniles producing the adult returns for the same years, exceeded 2.5% in 1999 and 2000 (Figure 6). Estimated differences in SAR based on PIT-tagged versus untagged fish showed no clear trend in the early years, but this lack of trend may have resulted from estimating SAR from small numbers of adult returns. For wild fish, when total adult returns increased to over 200 fish, beginning in 1998, the estimated SAR based on PIT-tagged fish was clearly lower than the untagged estimate. We observed the same trends for wild steelhead. In all years, the estimated return rate for the untagged population exceeded the return rate of PIT-tagged fish (Figure 7).

Table 4. Annual SAR (total adult returns/estimated juveniles) for steelhead PIT tagged above Lower Granite Dam with detection histories of groups that represented the unmarked population.

		Transported from (first time detected)				
Year	Rearing type	Lower Granite Dam	Little Goose Dam	Lower Monumental Dam	McNary Dam	Nondetected
1993	W	0.24 (2/845)	– (0/76)	– (0/193)	1.85 (1/54)	– (0/358)
	H	0.05 (1/2036)	0.59 (1/170)	0.59 (2/340)	– (0/91)	0.35 (2/576)
1994	W	1.70 (6/352)	0.46 (1/218)	0.52 (1/194)	– (0/250)	0.93 (6/644)
	H	1.08 (21/1941)[b]	– (0/1007)	0.41 (2/489)	0.07 (1/1513)	0.10 (7/6910)
1995	W	– (0/287)	– (0/66)	4.17 (1/24)	NA	0.35 (1/285)
	H	0.70 (14/1993)	1.60 (5/312)	– (0/88)	NA	0.90 (11/1216)
1996	W	0.99 (1/101)	– (0/33)	– (0/11)	NA	0.52 (3/574)
	H	0.36 (4/1104)	– (0/353)	– (0/94)	NA	0.36 (14/3875)
1997	W	1.32 (3/227)	– (0/44)	– (0/23)	NA	0.43 (2/462)
	H	0.60 (10/676)	– (0/158)	– (0/119)	NA	0.17 (7/4129)
1998	W	0.33 (1/304)	– (0/93)	– (0/93)	NA	1.20 (9/747)
	H	0.63 (5/791)	0.24 (1/419)	0.52 (1/192)	NA	0.93 (24/2590)
1999	W	2.49 (6/241)	4.22 (4/95)	2.54 (2/79)	NA	2.79 (25/897)
	H	0.95 (8/838)	1.20 (4/333)	– (0/250)	NA	1.43 (37/2594)
2000	W	2.81 (7/249)	3.08 (4/130)	2.12 (3/141)	NA	1.82 (37/2017)
	H	3.04 (14/461)[b]	0.98 (1/102)	0.61 (1/163)	NA	0.97 (39/4040)

[a] W = wild; H = hatchery.

[b] Groups significantly higher than nondetected fish.

Table 5. Bootstrap confidence intervals (95%) around annual SAR (see Table 4) for steelhead PIT tagged above Lower Granite Dam with detection histories of groups that represented the unmarked population.

		Transported from (first time detected)				
Year	Rearing type	Lower Granite Dam	Little Goose Dam	Lower Monumental Dam	McNary Dam	Nondetected
1993	W	0.00–0.63	0.00–3.95[b]	0.00–1.55[b]	0.00–8.21	0–0.84[b] 0.34 (1) 0.42
	H	0.00–0.15	0.00–1.84	0.00–1.72	0.00–3.30[b]	0.00–0.99
1994	W	0.29–2.91	0.00–1.69	0.00–1.26	0.00–1.20[b]	0.28–1.95
	H	0.68–1.52	0.00–0.30[b]	0.00–0.89	0.00–0.14	0.04–0.15
1995	W	0.00–1.05[b]	0.00–4.55[b]	0.00–11.7	NA	0.00–1.05
	H	0.39–1.25	0.62–3.15	0.00–3.41[b]	NA	0.50–1.23
1996	W	0.00–3.96	0.00–9.09[b]	0.00–27.3[b]	NA	0.00–1.04
	H	0.17–0.57	0.00–0.85[b]	0.00–3.19[b]	NA	0.17–0.53
1997	W	0.00–2.59	0.00–6.82[b]	0.00–13.0[b]	NA	0.00–1.10
	H	0.23–1.08	0.00–1.90[b]	0.00–2.52[b]	NA	0.07–0.28
1998	W	0.00–1.02	0.00–3.23[b]	0.00–3.23[b]	NA	0.55–1.92
	H	0.14–1.25	0.00–0.70	0.00–1.64	NA	0.65–1.22
1999	W	0.80–4.46	1.07–9.09	0.00–8.10	NA	2.06–3.57
	H	0.49–1.64	0.59–2.00	0.00–1.20[b]	NA	1.08–1.86
2000	W	0.46–5.88	0.79–4.61	0.00–4.93	NA	1.30–2.31
	H	1.54–4.61	0.00–2.76	0.00–2.59	NA	0.60–1.34

[a] W = wild; H = hatchery.

[b] Based on “rule of 3” where 0 adults returned.

The results of our analyses suggest that SAR for PIT-tagged wild fish do not represent the total SAR for the unmarked population. Thus we conclude that although PIT-tagged wild Chinook salmon and steelhead provide useful data when assessing the difference in return rates of different treatment groups, they did not apparently represent SAR for the wild populations. On the other hand, we saw no evidence that estimating PIT-tagged hatchery Chinook salmon systematically resulted in underestimated SAR of untagged hatchery Chinook salmon. We have no SAR estimates for unmarked hatchery steelhead to compare to PIT-tagged steelhead. We urge caution, however, when using absolute return rates of hatchery PIT-tagged fish to make inferences about the total untagged population, because hatchery fish in the Snake River basin are not PIT tagged in proportion to the total hatchery population. Thus a bias will likely exist in PIT-tagged-derived SAR based on hatchery fish. We also note that these results came from data for studies conducted prior to the 2002 outmigration. Beginning in 2002, rather than return all detected wild PIT-tagged fish to the river at the upper Snake River dams, a proportion are now bypassed to the tailrace. Returns from these outmigrations should indicate whether lower rates of return from PIT-tagged fish, compared to estimates for the nontagged population, still exist.

Transportation Evaluations

Methods

We evaluated the efficacy of transportation two ways. First, we compared the return rate of transported fish to the return rate of control fish that migrated volitionally through the hydro-power system. This provided a ratio of return rates of transported (*T*) fish and in-river migrants (*I*), hereafter *T:I*. We also evaluated *D*, which is defined as the ratio of post-Bonneville Dam survival for transported fish to that of in-river migrants. Details of the methodology are provided below.

We based our evaluation of transportation on comparisons of SAR from fish PIT tagged as juveniles that migrated through the hydropower system (in-river fish) versus SAR of fish collected and transported (Figure 8). We based most of our evaluations on fish from two general sources: fish PIT tagged for the Multi-State Comparative Survival Study (CSS 2003) above Lower Granite Dam that passed through sort-by-code systems installed in bypass systems at collector dams (Lower Granite, Little Goose, and Lower Monumental dams on the Snake River and McNary Dam on the Columbia River), and those that were specifically released to evaluate transportation. Of the fish collected, some were automatically diverted to raceways for transportation, while others were returned to the river to allow estimation of survival for the downstream migrants. We also PIT-tagged juvenile fish collected at Lower Granite Dam, some of which we released into raceways for subsequent transportation and others we released to the dam's tailrace. Finally, because slide gates are not 100% effective at diverting PIT-tagged fish back to the river, some nondesignated fish PIT tagged above Lower Granite Dam get transported. We evaluated these fish where possible, but sample sizes were quite small, SAR for these groups have large confidence bounds.

Groups of fish PIT tagged above and at Lower Granite Dam each present advantages and disadvantages for evaluating transportation. For fish PIT tagged above the dam, those collected at Lower Granite Dam presumably represent the untagged population collected at the dam, while those not collected (therefore not detected) represent the unmarked population of fish that passed the dam through turbines and spill. However, for fish tagged above the dam, we do not have a direct measure of how many nondetected fish pass the dam, but we can estimate this number. Moreover, when an adult that was not detected as a juvenile returns, we do not know when it passed the dam as a juvenile. For these fish groups, we can only estimate annual transport to in-river ratios (*T:I*) and annual values of *D*. For fish PIT tagged at Lower Granite Dam, no "true" controls exist because all fish for studies are first collected from the dam's juvenile bypass facilities. Thus no sample exists that represents untagged, uncollected fish. However, tagging at dams has some advantages. After release, we know the number of downstream migrants that subsequently represent the untagged population. Further we can estimate temporal SAR trends for transported and in-river migrants. From this we can estimate temporal *D* trends.

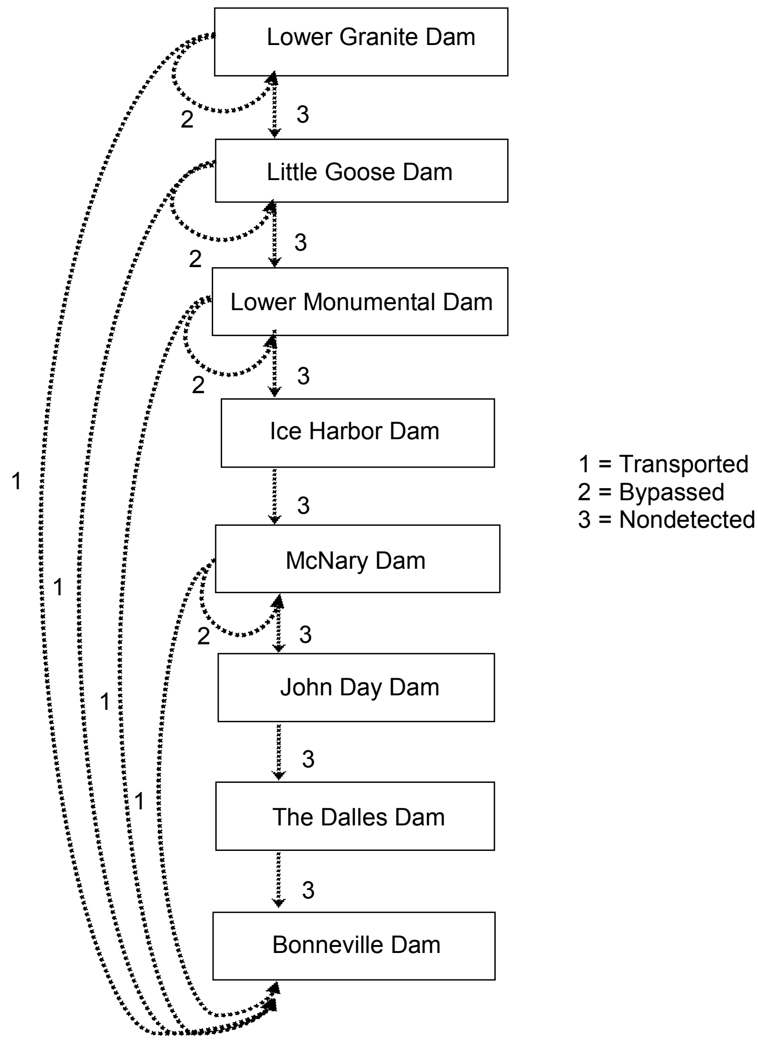

Figure 8. Three pathways that juvenile salmon travel on their way downstream through the mainstem Snake and Columbia rivers.

Studies specifically designed to evaluate transportation of Snake River fall Chinook salmon began only in 2001. However, since PIT-tag systems do not effectively bypass 100% of PIT-tagged fish back to the river, each year a relatively small number of PIT-tagged fish arriving at Lower Granite, Little Goose, Lower Monumental, and McNary dams are transported. In 1995, we began PIT tagging and releasing Lyons Ferry Hatchery fall Chinook salmon in the Clearwater and free-flowing Snake River above Lewiston to evaluate survival. We estimated SAR for the combined fish group transported from any collector dam and compared them to SAR of the combined fish bypassed only once at each dam. We also conducted separate analyses for fish detected prior to 1 September and fish detected on 1 September or later. We further developed ratios of combined transported fish:combined bypassed fish for each year, and we developed 95% confidence bounds for the ratios.

We used two data sets to evaluate transportation for upper Columbia River subyearling Chinook salmon at McNary Dam. For the first set, we used data from studies in 1995 and 1996 to evaluate the efficacy of transportation at McNary Dam (after construction of the new juvenile bypass/collection facilities in 1994). In those 2 years, approximately 110,000 and 120,000 juvenile subyearling Chinook salmon, respectively, were collected in the juvenile bypass facility at the dam and coded-wire tagged (CWT). Fish were tagged 5 days per week in proportion to the daily collection. Each day approximately 60% of the fish were released to the dam's tailrace through the bypass facility pipe; the other 40% were transferred into barges and released downstream of Bonneville Dam. Evaluations of transported fish returns, compared to those released to the McNary Dam tailrace, were based on CWT recoveries from commercial and recreational fisheries and hatcheries. For the second data set, we used subyearling Chinook salmon PIT tagged at McNary Dam in 2001 and 2002 to provide additional transportation evaluations to determine whether results from the 1995 and 1996 studies applied under the apparently improved ocean conditions that began in 1999.

Estimating *D* (PATH Method)

The PATH definition of *D* (see Figure 4.2-1 caption in Marmorek and Peters 1998) involves terms for "direct survival" of in-river migrants and "direct survival" of transported juvenile fish. This requires estimating the number of fish in each group (transported or in-river migrants) that were alive in the river below Bonneville Dam. To estimate post–Bonneville Dam survival, the number of adult returns to Lower Granite Dam counted in each group is divided by the estimated number of juveniles counted below Bonneville Dam. The estimate of *D* is calculated as the ratio of transported group post-Bonneville Dam survival to in-river migrant group post-Bonneville Dam survival.

For a given dam, the expected return rates (SAR) for transported and in-river migrants each have two components: the expected survival probability from the dam to below Bonneville Dam and the expected survival probability from below Bonneville Dam to adult return. The SAR can be described by the following equations:

$$SAR_T = S_T \cdot \lambda_T \tag{1}$$

and

$$SAR_I = S_I \cdot \lambda_I \tag{2}$$

where the subscripts *T* and *I* refer to transported and in-river migrants, respectively; *S* is the downstream survival component; and λ is the post-Bonneville Dam component. The ratio of the SAR is the familiar *T:I* ratio:

$$T:I = \frac{SAR_T}{SAR_I} = \frac{S_T}{S_I} \cdot \frac{\lambda_T}{\lambda_I} = \frac{S_T}{S_I} \cdot D \tag{3}$$

This equation decomposes the *T:I* ratio into downstream and post-Bonneville Dam components and introduces the parameter *D*, which is the ratio of post-Bonneville Dam survival for transported fish to that for in-river migrants. If transported fish and in-river migrants have the same survival probability from the transport release site to return as adults, then $D = 1.0$. If transported fish incur greater mortality after release from the barge, then $D < 1.0$.

Transportation benefits fish stocks from a particular location only if the expected SAR for transported fish exceeds that for in-river migrants (i.e., if $T{:}I > 1.0$). Because S_T (survival in the barge from the collection dam to below Bonneville Dam) is near 1.0, the decision reduces to comparing survival to below Bonneville for fish left in the river versus differential post-Bonneville Dam survival. In terms of the equations, transportation benefits fish only if $D > S_I$.

One consequence of this relationship is that if D is the same for each transportation site, then the benefit of transportation is greater for collection sites farther upstream. This is because S_I increases for sites farther downstream. In other words, fish transported from Lower Granite Dam avoid the higher direct mortality incurred by fish prior to their collection and transportation from McNary Dam. The value of D may depend on the collection site; thus we apply a separate value for each collection site. We did not estimate survival from above Lower Granite Dam to the tailrace, because both in-river migrants and transported juveniles transited the same area in common; thus any value cancels calculations, with no effect on estimated D.

The estimated number of in-river migrants (control group) alive below Bonneville Dam is derived by multiplying the annual estimate of the number of “control” fish arriving at Lower Granite Dam by the estimated annual average survival between Lower Granite and Bonneville Dam tailrace. With the PATH definition, it is impossible to calculate date-specific differential survival between transported fish and the “true” control group within a single migration season. While we can estimate the number of juveniles in the “never-detected” category that passed Lower Granite Dam on any particular day, we have no way of knowing what day a returning adult in that category passed Lower Granite Dam as a juvenile. Thus we cannot calculate the SAR for the never-detected group for a specific date.

Estimating *D* (Non-PATH Method)

We also determined how differential post-Bonneville survival between transported and in-river migrants might change within a single migration season. As identified above, we used fish marked at Lower Granite Dam and compared transported fish to those released into the tailrace that subsequently had the same detection history as the untagged fish population. We used 6-day blocks for fish marked and released at Lower Granite Dam and compared SAR for those transported within each block to those released to the dam tailrace that subsequently had the same detection history as unmarked fish in the population. For studies in 2000, the transport groups were developed from fish collected at Little Goose Dam. We used the same methods to determine temporal D values that we used to determine average D over the season.

Results

Snake River Spring-Summer Chinook Salmon

Annual estimates of SAR for transported and in-river migrants

Based on Sandford and Smith's (2002) methodologies, which were applied to fish PIT tagged above Lower Granite Dam from 1993 through 2003, we estimated that the combined annual percentage of the nontagged Chinook salmon population transported from Lower Granite, Little Goose, Lower Monumental, and McNary dams ranged from approximately 62% to nearly 100% (Table 6). Clearly, the status of the yearling Chinook salmon in the Snake River basin depends to a large degree on the efficacy of transportation.

Estimated annual SAR for PIT-tagged and transported Chinook salmon marked above Lower Granite Dam during outmigration years 1993–2000 varied widely between years and dams (Table 2), as did the 95% confidence bounds (Table 3). For hatchery spring-summer Chinook salmon, the annual SAR for fish transported from Lower Granite Dam was significantly higher than for in-river migrants (nondetected category) from migration years 1997–2000 and from Little Goose Dam in 1999 and 2000. On the other hand, nondetected fish returned at higher rates than hatchery and wild fish transported from McNary Dam in 1994 and hatchery fish transported from Little Goose and Lower Monumental dams in 1998.

Annual SAR for PIT-tagged, juvenile spring-summer Chinook salmon marked at Lower Granite Dam during outmigration years 1995–2000 varied widely between years and at sites (Table 7). The fish included in these results were first-time detections at the respective dam. For fish marked at Lower Granite Dam, first-time detection was defined as after release from Lower Granite Dam (nondetected fish represented the route of passage of the nontagged population downstream of Lower Granite Dam). Annual adult returns for wild spring-summer Chinook salmon collected and marked at Lower Granite Dam indicated significantly higher annual SAR for transported fish in 1995 and 1999, but not in 1996, 1998, and 2000 (Table 8). Nondetected hatchery (1999) and wild (2000) fish returned at significantly higher rates than fish transported from Lower Monumental Dam.

Table 6. Estimated combined annual percentage of the nontagged yearling Chinook salmon population transported from Lower Granite, Little Goose, Lower Monumental, and McNary dams.

Year	Wild	Hatchery
1993	88.5	88.1
1994	87.7	84.0
1995	86.4	79.6
1996	71.0	68.7
1997	71.1	71.5
1998	82.5	81.4
1999	85.9	77.3
2000	70.4	61.9
2001	99.0	97.3
2002	72.1	64.2
2003	70.4	61.5

Table 7. Annual SAR (total adult returns/estimated number of juveniles) for spring-summer Chinook salmon PIT tagged at Lower Granite Dam for transportation studies between 1995 and 2000, compared to annual SAR of fish not detected downstream after release at Lower Granite Dam (fish that represented the migration history for the nontagged population).

Year	Rearing type[a]	Transported from: Lower Granite Dam	Little Goose Dam[b]	Lower Monumental Dam[b]	McNary Dam	Nondetected
1995	W	0.38 (91/24066)[c]	0.39 (9/2318)	0.31 (3/968)	NA	0.23 (26/11495)
	H	0.54 (448/83063)[c]	0.37 (17/4562)	0.37 (4/1086)	NA	0.32 (123/38543)
1996	W	0.11 (9/7949)	– (0/350)	–(0/140)	NA	0.08 (4/5223)
	H	0.13 (47/35632)	0.10 (1/1001)	–(0/523)	NA	0.11 (27/25060)
1997			– No studies –			
1998	W	0.60 (34/5689)	– (0/2350)	–(0/70)	NA	0.95 (28/2932)
	H	0.62 (245/39596)	0.32 (6/1864)	0.16 (1/610)	NA	0.57 (134/23552)
1999	W	2.10 (176/8384)[c]	0.70 (1/143)	0.86 (2/234)[d]	NA	1.35 (26/1920)
	H	1.97 (833/42273)[c]	2.09 (12/574)	0.87 (13/1486)[d]	NA	1.45 (242/16664)
2000[e]	W	NA	1.47 (255/17371)	0.81 (7/869)	NA	1.46 (384/26329)
	H	NA	NA	NA	NA	NA

[a] W = wild; H = hatchery.

[b] Fish transported from Little Goose and Lower Monumental dams include only first-time detections downstream of Lower Granite Dam.

[c] Groups significantly higher than nondetected fish.

[d] Groups significantly lower than nondetected groups.

[e] Fish were tagged at Lower Granite Dam, released into the tailrace, and collected and transported from Little Goose Dam.

Table 8. Confidence intervals (95%) around annual SAR (see Table 7) for spring-summer Chinook salmon PIT tagged at Lower Granite Dam for transportation studies between 1995 and 2000, compared to intervals around annual SAR of nondetected fish (fish that represent the migration history for the nontagged population).

Year	Rearing type[a]	Transported from: Lower Granite Dam	Little Goose Dam	Lower Monumental Dam	McNary Dam	Nondetected
1995	W	0.29–0.45	0.17–0.59	0.10–0.54	NA	0.17–0.27
	H	0.51–0.57	0.26–0.48	0.18–0.57	NA	0.28–0.36
1996	W	0.05–0.18	0.00–0.86[b]	0.00–2.14[b]	NA	0.02–0.15
	H	0.10–0.17	0.00–0.21	0.00–0.57[b]	NA	0.07–0.14
1997			No studies			
1998	W	0.46–0.76	0.00–1.28[b]	0.00–4.29[b]	NA	0.61–1.28
	H	0.58–0.67	0.16–0.54	0.00–0.50	NA	0.48–0.65
1999	W	1.82–2.45	0.00–2.92	0.00–1.82	NA	0.94–1.79
	H	1.90–2.06	1.04–3.31	0.53–1.27	NA	1.32–1.59
2000[c]	W	NA	1.36–1.61	0.55–1.17	NA	1.36–1.55
	H	NA	NA	NA	NA	NA

[a] W = wild; H = hatchery.

[b] Used "rule of 3" where 0 adults returned.

[c] Fish were tagged at Lower Granite Dam, released into the tailrace, and collected and transported from Little Goose Dam.

Transport location-specific and overall annual estimates of differential post-Bonneville Dam survival (*D*)

Annual estimates provide a general illustration of differences in return rates between transported and in-river migrants and differences between transport locations.

Large adult returns in recent years generally improved our ability to estimate the ratio of post-Bonneville Dam survival for transported fish to that of in-river migrants separately for each transportation dam and greatly improved precision of the overall estimate. In all comparisons of hatchery and wild Snake River spring-summer Chinook salmon, the greatest number of returning PIT-tagged adults came from the 1999 and 2000 outmigrations (Tables 9 and 10).

Results were not consistent. To summarize them, we offer the following observations:

1. For wild and hatchery fish, the geometric mean annual *D* from migration years 1994 through 2000 ranged between 0.55 and 0.61. That is, averaged over years and across migration seasons, survival for fish transported from below Bonneville Dam as a juvenile to return as an adult has averaged less than two-thirds that of in-river migrants that arrived below Bonneville Dam.
2. Wild and hatchery spring-run Chinook salmon transported from Lower Monumental Dam have had the lowest average post-Bonneville Dam survival. Average in-river survival from Lower Monumental Dam to Bonneville Dam has exceeded this average *D*, indicating that fish not transported from Lower Monumental Dam had higher average annual SAR than fish transported from the site.
3. For wild spring-summer Chinook salmon, average differential post-Bonneville Dam survival for fish transported from Lower Granite Dam roughly equaled the average survival of in-river migrants that migrated between Lower Granite and Bonneville dams. Wild Chinook salmon transported from Lower Granite Dam in 2000 had particularly low annual post-Bonneville Dam survival. Thus on an average annual basis, transportation provided no benefit. In some years transported fish had higher average annual returns than in-river fish, but in some years it was lower.
4. For hatchery spring-summer Chinook salmon, average differential post-Bonneville Dam survival for fish transported from Lower Granite Dam has considerably exceeded the average estimated survival for the in-river migrants between Lower Granite and Bonneville dams. Thus on an average annual basis, transportation led to increased returns when compared to in-river fish.
5. Small sample sizes resulted in imprecise annual *D* estimates. For example, even with more than 2,000 returns of hatchery Chinook salmon in 2000, the 95% confidence interval was still wide (Table 10). The number of juvenile fish from the outmigration, however, provided the ability to make a relatively precise estimate for survival of in-river migrants between Lower Granite and Bonneville dams.

Table 9. Annual estimates of differential post-Bonneville Dam survival (*D*) for wild Snake River spring-summer Chinook salmon transported from various dams and for weighted average from all sites. Total adult returns are provided in parentheses (when adults in a category = 0, the number of juveniles is given as well). All fish were tagged upstream from Lower Granite Dam. Approximate 95% confidence intervals for weighted averages are in brackets.

Year	Nontrans-ported*	Transported from: All sites	Lower Granite Dam	Little Goose Dam	Lower Monumental Dam
1994	6	0.683 (13) [0.254, 1.844]	0.770 (8)	1.187 (4)	0.239 (1)
1995	10	0.457 (8) [0.177, 1.184]	0.559 (7)	0.467 (1)	(0/195)
1996	5	1.081 (2) [0.202, 5.783]	0.688 (1)	2.453 (1)	(0/43)
1997	17	0.498 (4) [0.162, 1.539]	0.224 (2)	1.262 (2)	(0/14)
1998	48	0.430 (15) [0.238, 0.783]	0.480 (11)	0.334 (3)	0.421 (1)
1999	104	0.656 (48) [0.460, 0.934]	0.730 (32)	0.641 (9)	0.563 (7)
2000	174	0.336 (12) [0.184, 0.613]	0.245 (4)	0.474 (6)	0.274 (2)
		Geometric mean: 0.553	**0.478**	**0.779**	**0.353**

* Nontransported fish are PIT-tagged fish with passage histories most representative of nontagged fish that migrated to Bonneville Dam in-river.

Table 10. Annual estimates of differential post-Bonneville Dam survival (*D*) for hatchery Snake River spring-summer Chinook salmon transported from various dams and for weighted average from all sites. Total adult returns are in parentheses (when adults in category = 0, the number of juveniles is given as well). All fish were tagged upstream from Lower Granite Dam. Approximate 95% confidence intervals for weighted averages are given in brackets.

Year	Nontrans-ported[a]	Transported from: All sites	Lower Granite Dam	Little Goose Dam	Lower Monumental Dam
1994[b]	7	0.316 (6) [0.104, 0.963]	0.314 (2)	0.445 (1)	0.468 (1)
1995	32	0.886 (20) [0.501, 1.572]	0.808 (14)	1.238 (5)	0.661 (1)
1996	32	0.409 (6) [0.168, 0.995]	0.780 (6)	(0/510)	(0/366)
1997	185	0.523 (233) [0.430, 0.639]	0.561 (226)	0.469 (5)	0.517 (2)
1998	336	0.638 (885) [0.561, 0.727]	0.829 (812)	0.405 (66)	0.319 (7)
1999	736	0.903 (1203) [0.821, 0.993]	0.930 (697)	1.036 (481)	0.477 (25)
2000	915	0.870 (1426) [0.798, 0.948]	0.961 (1030)	0.726 (310)	0.658 (86)
		Geometric mean: 0.606	**0.700**	**0.654**	**0.502**

[a] Nontransported fish are PIT-tagged fish with passage histories most representative of nontagged fish that migrated to Bonneville Dam in-river.

[b] Two fish transported from McNary Dam returned as adults. Estimated differential post-Bonneville Dam survival for McNary transport = 0.098.

Within-season variability in transportation and *D*

For fish PIT tagged at Lower Granite Dam, we have known timing for transported and subsequently nondetected fish. From these fish we determined that not only did SAR vary over the course of the outmigration, but the variation in timing changed between years. Transported Chinook salmon had greater temporal changes in SAR than in-river migrants (Figures 9, 10, 11, and 12). For wild fish, due to higher variability about SAR estimates, we detected only one

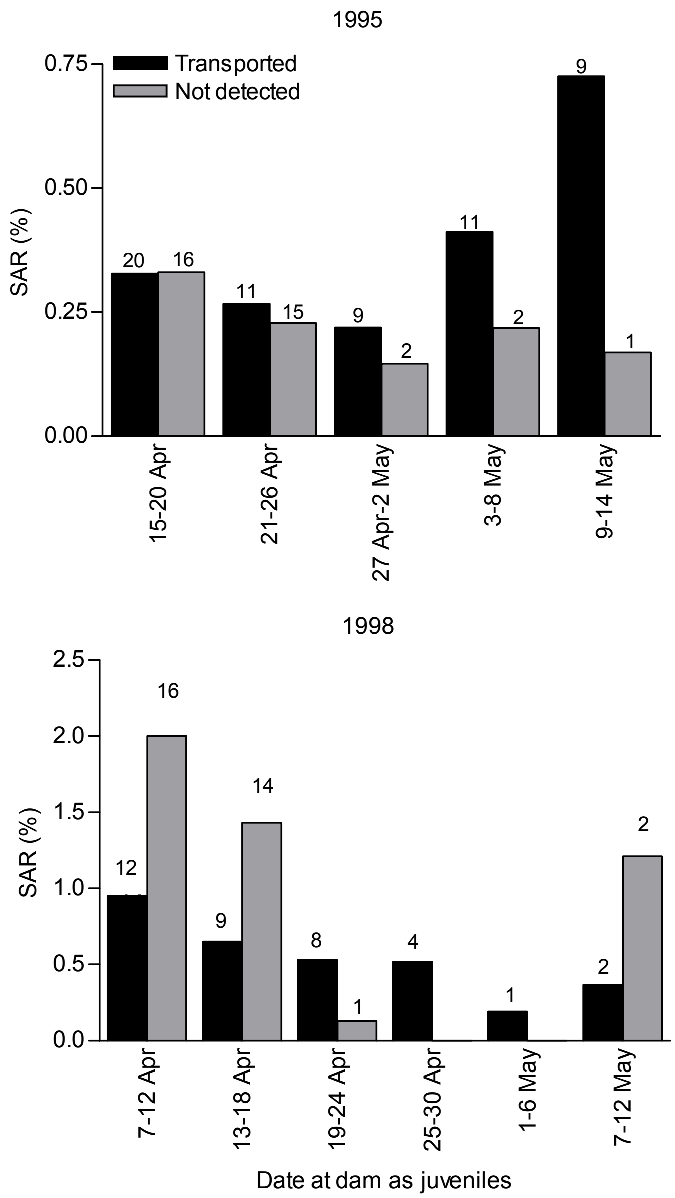

Figure 9. Temporal change in SAR of wild Snake River spring-summer Chinook salmon PIT tagged at Lower Granite Dam, 1995 and 1998. No significant differences in return rates were detected between treatment group pairs. Numbers above the bars indicate total SAR for each group.

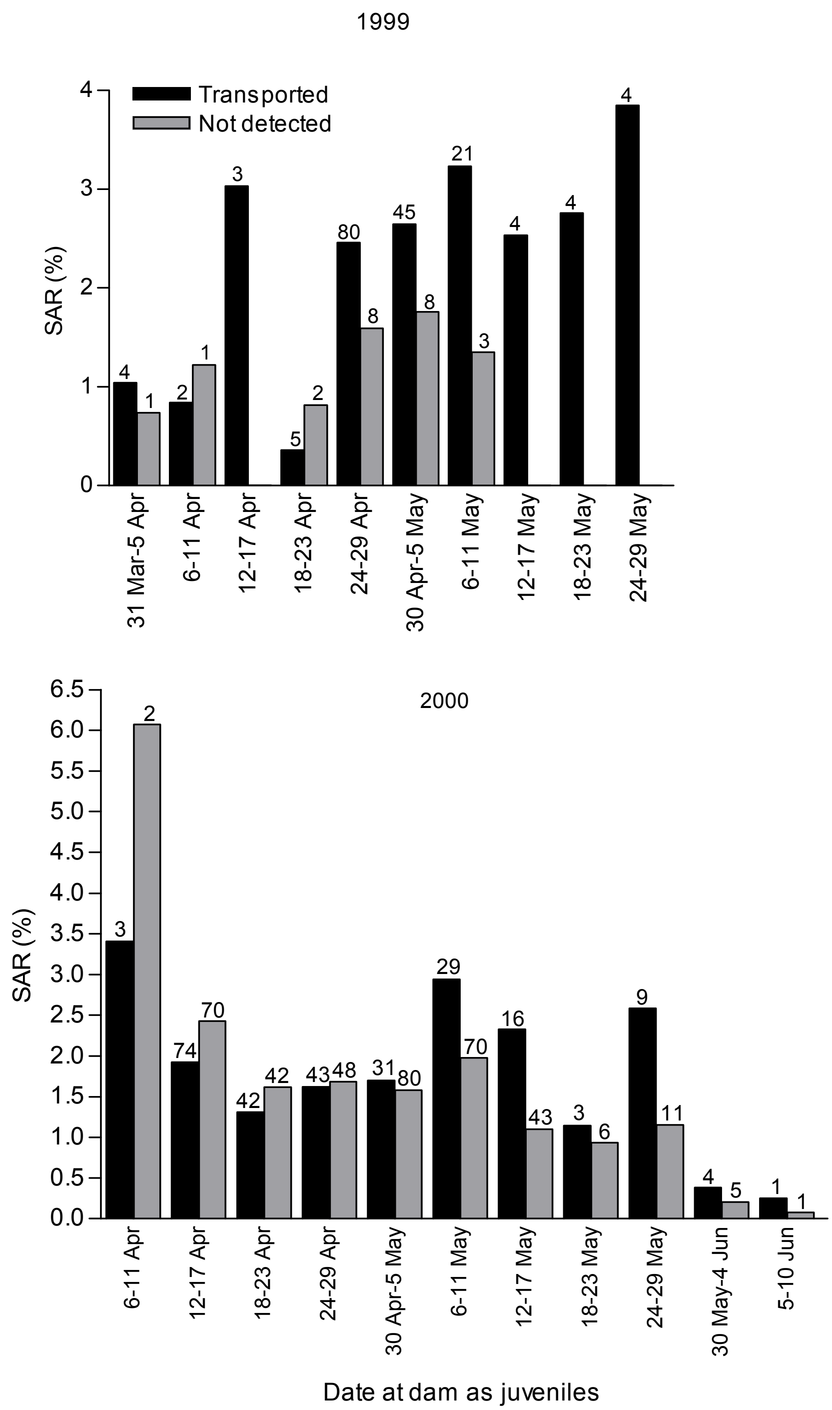

Figure 10. Temporal change in SAR of wild Snake River spring-summer Chinook salmon PIT tagged at Lower Granite Dam, 1999 and 2000. In 2000, in one treatment pair, transported fish returned at significantly higher rates. Numbers above the bars indicate the total adult returns for each group.

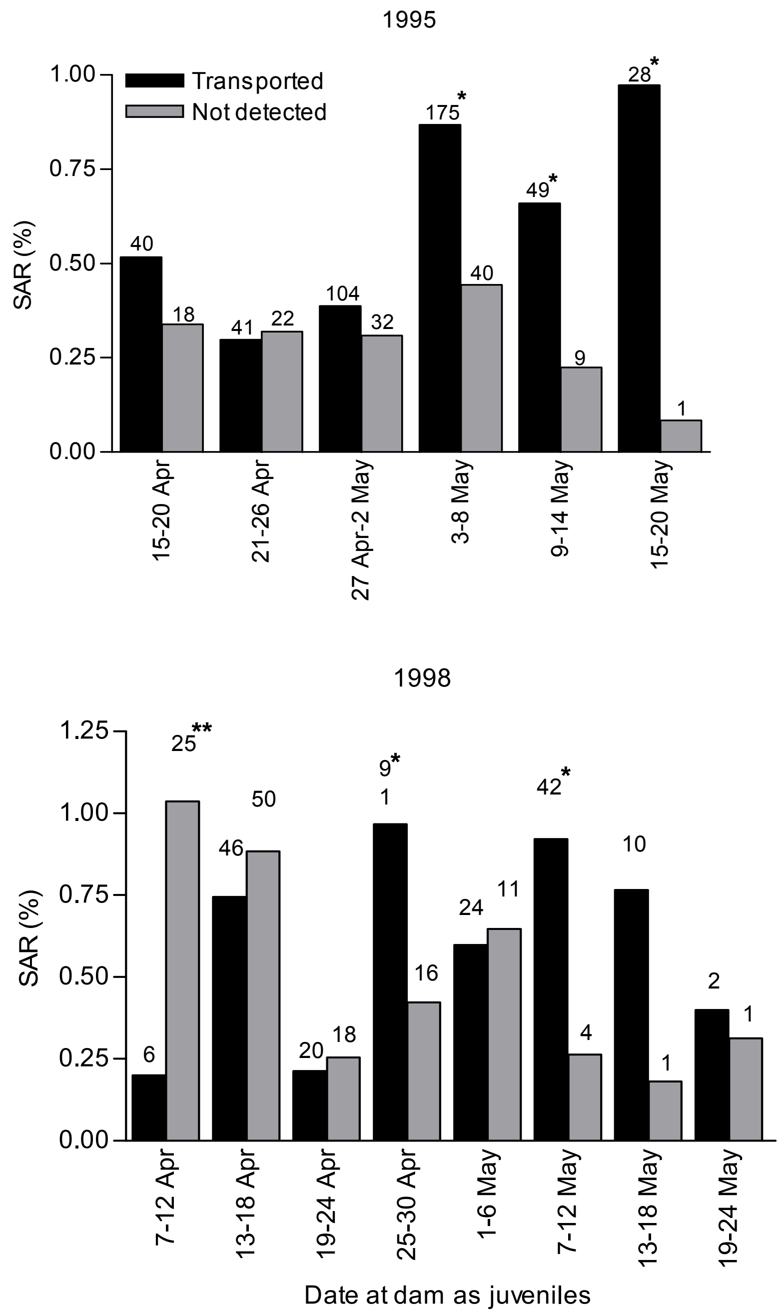

Figure 11. Temporal change in SAR of hatchery Snake River spring-summer Chinook salmon PIT tagged at Lower Granite Dam, 1995 and 1998. * = significantly higher return rates of transported fish occurred for several treatment pairs in both years; ** = a significantly higher return rate of nondetected fish occurred for one treatment pair in 1998. Numbers above the bars indicate total adult returns for each group.

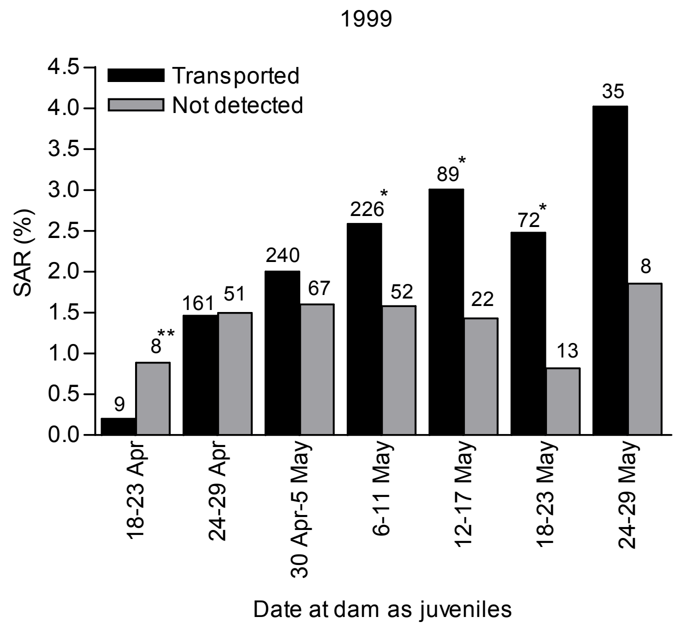

Figure 12. Temporal change in SAR of hatchery Snake River spring-summer Chinook salmon PIT tagged at Lower Granite Dam, 1999. * = significantly higher return rates occurred for transported fish in several treatment pairs. A significantly higher rate for nondetected fish occurred in one treatment pair. Numbers above the bars indicate total adult returns for each group.

significantly higher SAR in one treatment pair (the transported fish in the 12–18 May 2000 period returned at higher rates). The SAR of hatchery fish had tighter confidence bounds, and thus we detected more significant differences in treatment pairs. In 1998 and 1999, the earliest nondetected in-river fish migrating below Bonneville Dam returned at significantly higher rates than transported fish, whereas in all years transported fish returned at significantly higher rates for several group pairs during the mid to late outmigration.

Adult upstream conversion rates

In 2002 and 2003, based on PIT-tag detections at Bonneville and Lower Granite dams of wild 2- and 3-ocean spring-summer Chinook salmon adults returning from the 2000 and 2001 outmigrations, transported and in-river fish had nearly the same high adult conversion rates (Table 11). These conversion rates (the percentage of adult fish at Bonneville Dam estimated to

Table 11. Conversion rates (number of adult fish detected at Lower Granite Dam/number of adult fish detected at Bonneville Dam) for adult wild spring-summer Chinook salmon PIT tagged as juveniles at Lower Granite Dam in 2000 and 2001 and either returned to the river or transported.

Year of outmigration	Year of adult return	In-river	Transported
2000	2002	0.86 (196/228)	0.87 (97/111)
	2003	0.82 (324/394)	0.84 (117/140)
2001	2003	NA	0.92 (91/99)

have migrated successfully to the upper dam) were not adjusted for harvest between Bonneville and McNary dams (zone 6). They far exceed the average values ascribed to the hydropower system used in recent PATH analyses (Marmorek et al. 1998). As adult fish passage facilities and upstream conditions have changed comparatively little in the past several decades, analyses based on old conversation rates likely contain considerable error.

Snake River Fall Chinook Salmon

For juvenile fish detected prior to 1 September, in 4 out of 6 years the SAR of the combined bypassed group exceeded the SAR of the combined transported group (Figure 13). For juvenile fish detected in the late period, transported and bypassed fish each had 2 years when they returned at higher rates than the other (Figure 14). However, the confidence bounds about the ratios for groups extended from 0 (or nearly so) to higher than 1 (and mostly considerably higher than 1). Thus no empirical evidence exists to suggest that transportation either harms or helps fall Chinook salmon. This does not, however, constitute evidence that T:I = 1. Based on variability in results, we suggest that the average T:I likely falls somewhere between 0.67:1 and 1:50:1. (This range is symmetric around 1.0 on the multiplicative scale [1:3 to 3:2], not on the additive scale.) Given the relationships among in-river survival, T:I, and D, this implies that D lies in the range determined by multiplying an estimate of in-river survival by the likely range in T:I; i.e., (0.67)*(in-river survival) to (1.50)*(in-river survival). No evidence exists to suggest that changes in juvenile in-river survival between Lower Granite and Bonneville dams would have any effect on the survival of either transported or in-river migrants after they pass Bonneville Dam. Thus because D pertains only to post-Bonneville Dam survival of transported fish relative to that of in-river fish, without further information we expect the range of likely values for D suggested above will hold even under changes in juvenile survival.

Upper Columbia River Subyearling Migrants

In 1995 and 1996, subyearling Chinook salmon transported from McNary Dam generally had higher return rates than in-river migrants when flows at the dam exceeded approximately 6,500 m^3/second (approximately 225,000 cubic feet per second) and water temperatures remained below 18°C (Figures 15 and 16). Counter to studies in the early 1980s conducted at the old juvenile facility at McNary Dam, where transported fish returned at 2 to 4 times the rate of fish released to the dam tailrace, these results suggested that transporting subyearling Chinook salmon under conditions of higher water temperatures and lower flows decreased adult return rates compared to returning fish to the river. The preliminary returns from fish PIT tagged in 2001 and 2002 (a total of 62 1-ocean and 2-ocean returns from marking in 2001 and 143 1-ocean returns from marking in 2002) did not apparently decrease as the season progressed, as had occurred in the earlier years (Figures 17 and 18, compared to Figures 15 and 16).

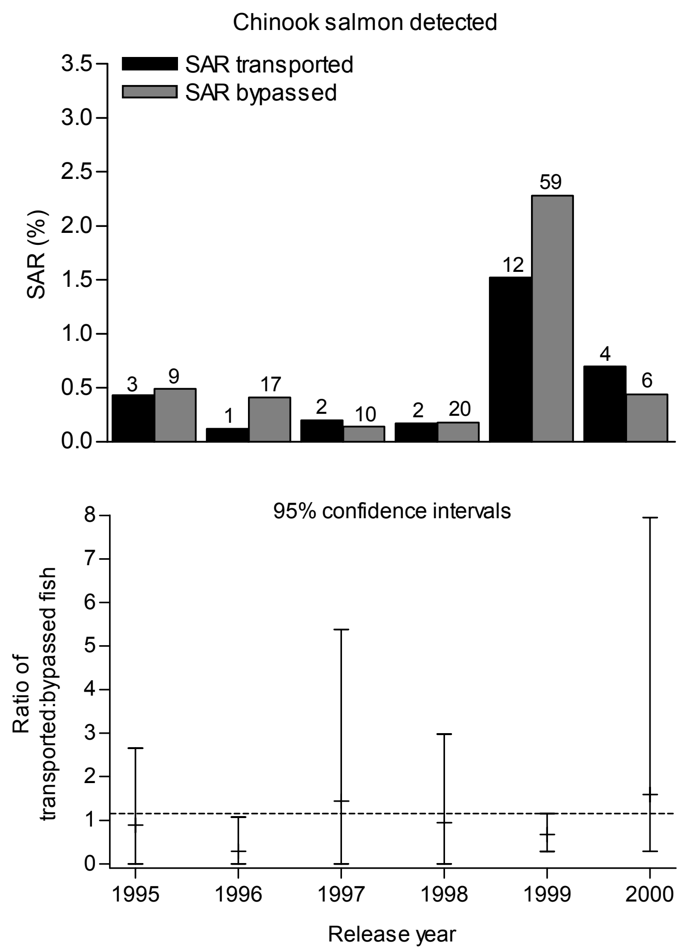

Figure 13. SAR of PIT-tagged, hatchery Snake River fall Chinook salmon released above Lower Granite Dam and bypassed or transported from Lower Granite, Little Goose, Lower Monumental, or McNary dams (not adjusted to Lower Granite Dam equivalents) prior to 1 September 1995–2000, with ratios of transported:bypassed fish and 95% confidence bounds. Numbers above the bars indicate total adult returns for each group.

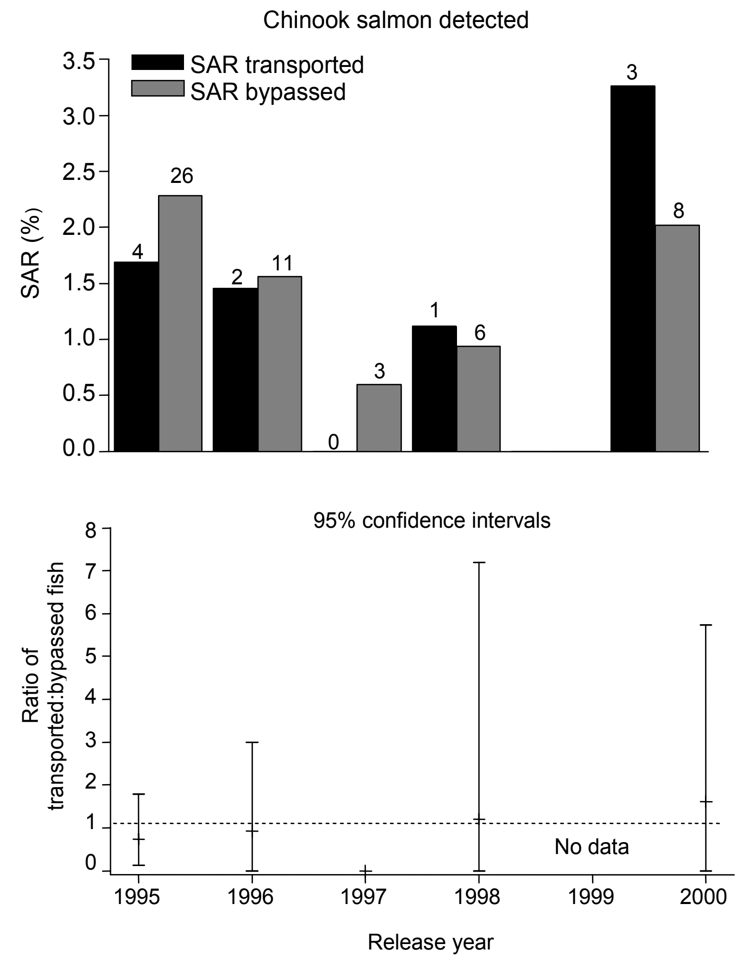

Figure 14. SAR of PIT-tagged, hatchery Snake River fall Chinook salmon released above Lower Granite Dam and bypassed or transported from Lower Granite, Little Goose, Lower Monumental, or McNary dams (not adjusted to Lower Granite Dam equivalents) on 1 September or later, 1995–2000, with ratios of transported:bypassed fish and 95% confidence bounds. Numbers above the bars indicate total adult returns for each group.

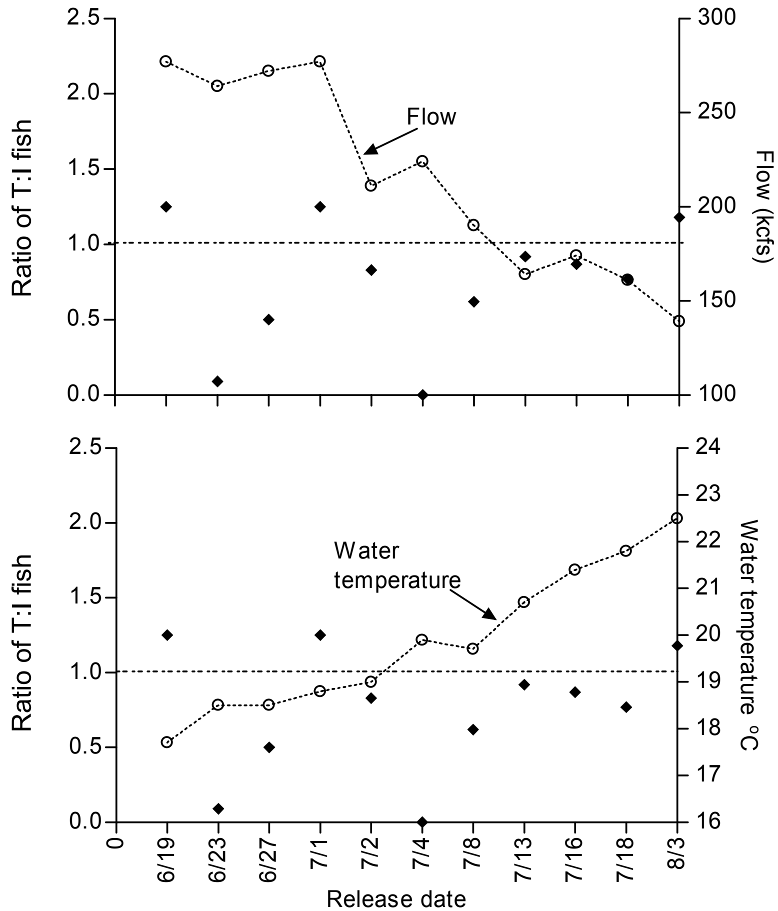

Figure 15. Relative recovery rates of coded-wire-tagged adult summer-fall Chinook salmon recovered from fisheries or at hatcheries from subyearling fish tagged as juveniles in 1995 at McNary Dam and either transported (T) to below Bonneville Dam or released into the tailrace of McNary Dam (I = in-river).

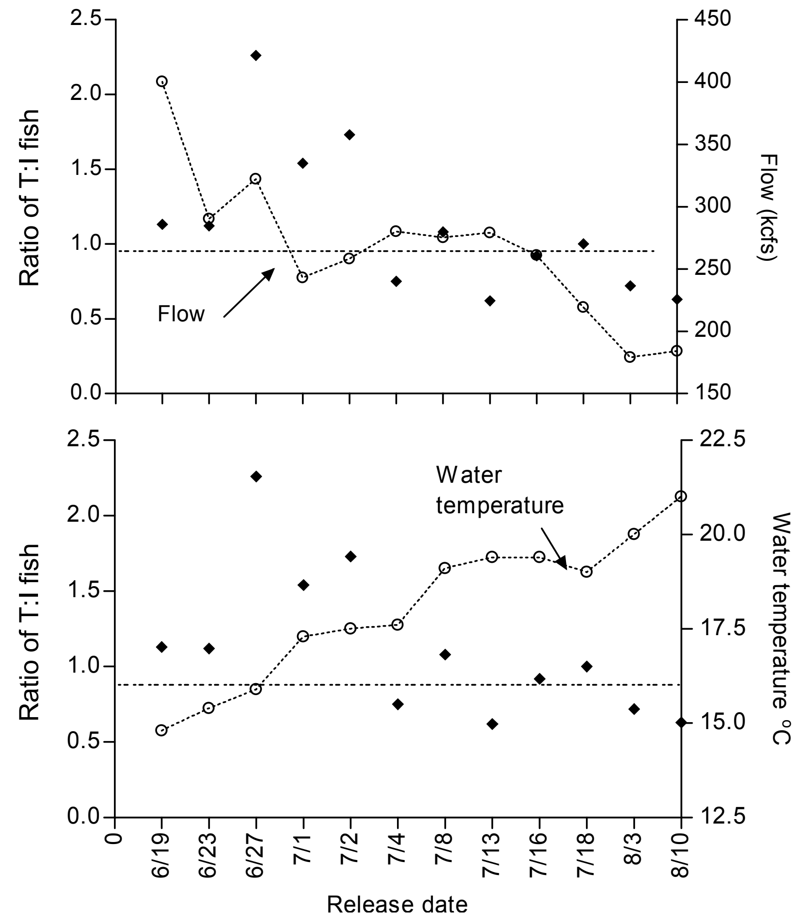

Figure 16. Relative recovery rates of coded-wire-tagged adult summer-fall Chinook salmon recovered in fisheries or at hatcheries from subyearling fish tagged as juveniles at McNary Dam in 1996 and either transported (T) to below Bonneville Dam or released into the tailrace of McNary Dam (I = in-river).

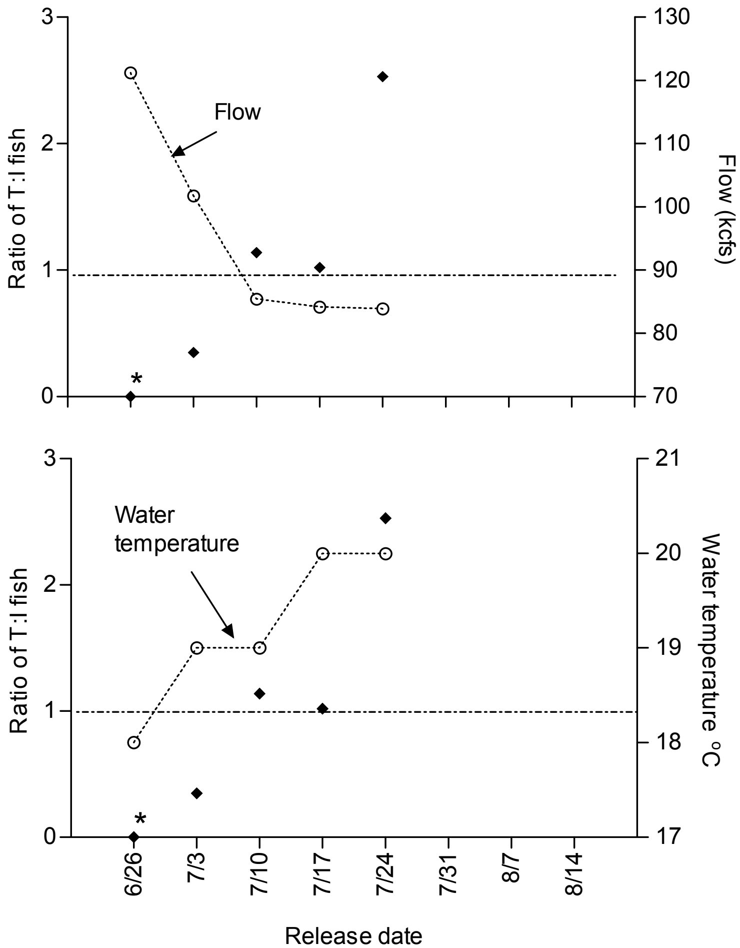

Figure 17. Relative recovery rates based on SAR for combined weekly releases of transported (T) and in-river (I) subyearling Chinook salmon PIT tagged and released at McNary Dam in 2001, plotted with weekly average water temperature and flow. Data include only 62 total 1-ocean and 2-ocean fish that returned: * indicates no transported fish returned.

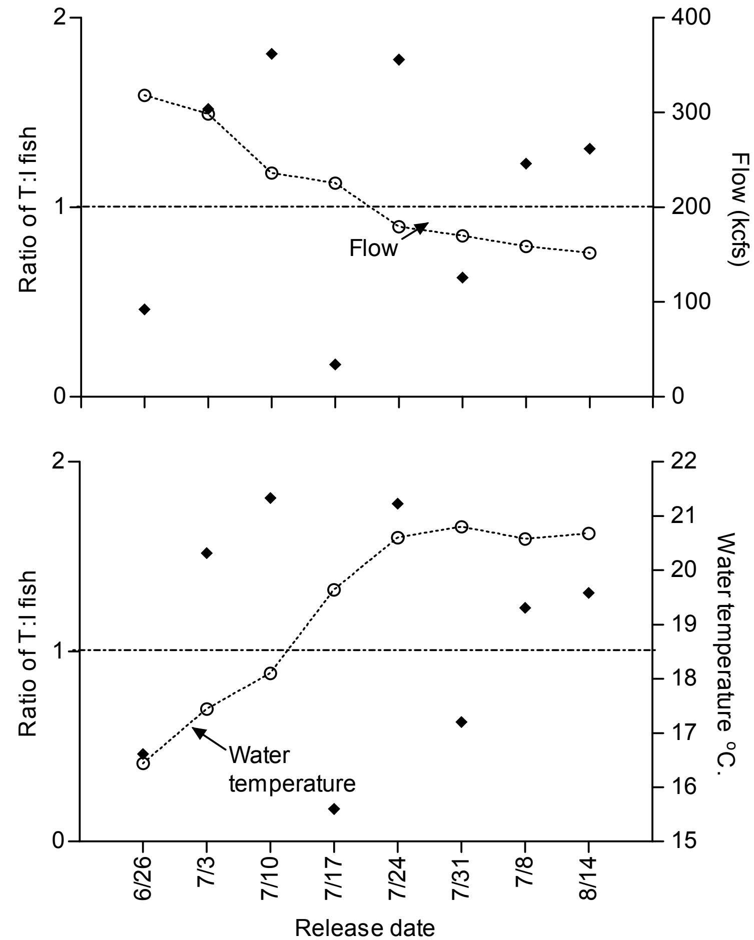

Figure 18. Relative recovery rates based on SAR for combined weekly releases of transported (T) and in-river (I) subyearling Chinook salmon PIT tagged and released at McNary Dam in 2002, plotted with the weekly average water temperature and flow. Only 143 total 1-ocean fish have returned to date.

Snake River Steelhead

Annual estimates of SAR for transported and in-river migrants

Based on Sandford and Smith (2002) methodologies applied to fish PIT tagged above Lower Granite Dam from 1993 through 2003, we estimated that the combined annual percentage of the nontagged steelhead (*Oncorhynchus mykiss*) population transported from Lower Granite, Little Goose, Lower Monumental, and McNary dams ranged from approximately 68% to nearly 100% (Table 12). As with yearling Chinook salmon, because of the high proportion of steelhead transported, the status of Snake River basin steelhead depends to a large degree on the efficacy of transportation.

Table 12. Estimated combined annual percentage of the nontagged steelhead population transported from Lower Granite, Little Goose, Lower Monumental, and McNary dams.

Year	Wild	Hatchery
1993	93.2	94.7
1994	91.3	82.2
1995	91.8	94.3
1996	79.8	82.9
1997	87.5	84.5
1998	88.2	87.3
1999	87.6	88.5
2000	83.9	81.5
2001	99.3	96.7
2002	75.2	70.4
2003	72.9	68.4

Estimated annual SAR for steelhead PIT tagged above Lower Granite Dam and transported during outmigration years 1993 to 2000 varied widely between years and dams (Table 4), as did the 95% confidence bounds (Table 5). At any one dam the number of wild steelhead juveniles generally was 300 fish or less, and adult returns of wild steelhead in most years at any one dam rarely exceeded five fish. For hatchery steelhead in migration years 1994 and 2000, the annual SAR for fish transported from Lower Granite Dam was significantly higher than for in-river migrants (nondetected category).

Annual SAR for PIT-tagged juvenile steelhead marked at Lower Granite Dam during outmigration years 1998 to 2000 varied widely between years, treatments, and sites (Table 13). The fish included in these results were first-time detections at the respective dam. For fish marked at Lower Granite Dam, first-time detection was defined as after release from Lower Granite Dam (nondetected fish represented the route of passage of the nontagged population downstream of dam). The annual SAR of transported wild and hatchery steelhead were significantly higher for transported fish than in-river migrants from both the 1999 and 2000 outmigrations (Table 14). Too few fish returned from the 1998 marking to determine differences in return rates.

Table 13. Annual SAR (total adult returns/estimated number of juveniles) for steelhead PIT tagged at Lower Granite Dam for transportation studies between 1998 and 2000, compared to annual SAR of fish not detected downstream after release at Lower Granite Dam (fish that represented the migration history for the nontagged population). Fish transported from Little Goose Dam and Lower Monumental Dam include only first-time detections downstream of Lower Granite Dam.

		Transported from				
Year	**Rearing type[a]**	**Lower Granite Dam**	**Little Goose Dam**	**Lower Monumental Dam**	**McNary Dam**	**Nondetected**
1998	W	NA	0.35 (1/287)	– (0/231)	NA	0.37 (7/1878)
	H	NA	0.71 (7/990)	0.43 (2/462)	NA	0.41 (24/5835)
1999	W	1.42 (86/6052)[c]	0.80 (1/125)	3.14 (5/159)	NA	0.54 (8/1471)
	H	1.07 (441/41057)[c]	1.43 (15/1048)[c]	0.46 (4/870)	NA	0.79 (82/10442)
2000[b]	W	NA	3.96 (979/24738)[c]	4.75 (88/1854)[c]	NA	1.85 (435/23506)
	H	NA	1.99 (11/553)	1.39 (5/360)	NA	0.85 (79/9276)

[a] W = wild; H = hatchery.

[b] Fish were tagged at Lower Granite Dam, released into the tailrace, collected, and transported from Little Goose Dam.

[c] Returns are significantly higher than nondetected fish.

Table 14. Confidence intervals (95%) around annual SAR (see Table 13) for steelhead PIT tagged at Lower Granite Dam for transportation studies between 1998 and 2000, compared to intervals around annual SAR of nondetected fish (fish that represent the migration history for the nontagged population).

		Transported from				
Year	**Rearing type[a]**	**Lower Granite Dam**	**Little Goose Dam**	**Lower Monumental Dam**	**McNary Dam**	**Nondetected**
1998	W	NA	0.00–1.05	0.00–1.30[c]	NA	0.16–0.62
	H	NA	0.10–1.39	0.00–1.25	NA	0.27–0.56
1999	W	1.18–1.69	0.00–2.48	0.60–6.84	NA	0.27–0.90
	H	1.02–1.14	1.01–1.81	0.23–0.70	NA	0.63–0.92
2000[b]	W	NA	3.78–4.13	3.87–5.79	NA	1.71–1.99
	H	NA	0.98–3.39	0.27–2.79	NA	0.70–1.07

[a] W = wild; H = hatchery.

[b] Fish were tagged at Lower Granite Dam, released into tailrace, collected, and transported from Little Goose Dam.

[c] "Rule of 3" was used.

Transport location-specific and overall annual estimates of differential post-Bonneville Dam survival

In this section we summarize data on annual estimates of *D* for steelhead. Large adult returns in recent years generally improved our ability to estimate differential post-Bonneville Dam survival separately for each transportation dam and greatly increased the precision of the overall estimate. For hatchery and wild Snake River steelhead, the greatest number of returning PIT-tagged adults occurred in 1999 and 2000 (Tables 15 and 16).

Table 15. Annual estimates of differential post-Bonneville Dam survival (D) for Snake River wild steelhead transported from various dams and for weighted average from all sites. Total adult returns are provided in parentheses (when adults in a category = 0, the number of juveniles is given as well). All fish were tagged upstream from Lower Granite Dam. Approximate 95% confidence intervals for weighted average are in brackets.

		Transported from			
Year	**Nontrans-ported***	**All sites**	**Lower Granite Dam**	**Little Goose Dam**	**Lower Monumental Dam**
1994	6	0.531 (8) [0.178, 1.581]	0.663 (6)	0.211 (1)	0.266 (1)
1995	1	0.981 (1) [0.058, 16.710]	(0/287)	(0/66)	10.023 (1)
1996	5	0.978 (2) [0.181, 5.279]	0.678 (1)	2.214 (1)	(0/11)
1997	4	0.536 (3) [0.115, 2.492]	0.844 (3)	(0/44)	(0/23)
1998	9	0.118 (1) [0.014, 0.976]	0.165 (1)	(0/93)	(0/93)
1999	18	1.013 (12) [0.475, 2.163]	0.735 (6)	1.343 (4)	0.882 (2)
2000	41	0.691 (14) [0.368, 1.296]	0.660 (7)	0.801 (4)	0.613 (3
	Geometric mean:	**0.582**	**0.550**	**0.842**	**1.757**

* Nontransported fish are PIT-tagged fish with passage histories most representative of nontagged fish that migrated to Bonneville Dam in-river.

Table 16. Annual estimates of differential post-Bonneville survival (*D*) for Snake River hatchery steelhead transported from various dams and for weighted average from all sites. Total adult returns are provided in parentheses (when adults in a category = 0, the number of juveniles is given as well). All fish were tagged upstream from Lower Granite Dam. Approximate 95% confidence interval for weighted average given in brackets.

		Transported from			
Year	**Nontrans-ported**[a]	**All sites**[b]	**Lower Granite Dam**	**Little Goose Dam**	**Lower Monumental Dam**
1994	7	2.707 (23) [1.140, 6.429]	3.684 (20)	(0/1007)	1.943 (2)
1995	14	0.435 (19) [0.214, 0.884]	0.392 (14)	0.996 (5)	(0/88)
1996	17	0.294 (4) [0.097, 0.896]	0.446 (4)	(0/353)	(0/94)
1997	8	0.968 (10) [0.374, 2.505]	1.615 (10)	(0/158)	(0/119)
1998	26	0.326 (7) [0.139, 0.767]	0.374 (5)	0.152 (1)	0.373 (1)
1999	41	0.332 (12) [0.171, 0.642]	0.336 (8)	0.457 (4)	(0/250)
2000	41	1.051 (14) [0.562, 1.967]	1.291 (13)	(0/102)	0.345 (1)
	Geometric mean:	**0.627**	**0.776**	**0.411**	**0.630**

[a] Nontransported fish are PIT-tagged fish with passage histories most representative of nontagged fish that migrated to Bonneville Dam in-river.

[b] In 1994, one fish transported from McNary Dam returned as an adult. Estimated differential post-Bonneville Dam survival for McNary Dam transport = 0.417.

Nonetheless, as with yearling Chinook salmon, results were not consistent. To summarize results, we offer the following observations:

- For hatchery and wild steelhead, the geometric mean annual estimated *D* from migration years 1994 through 2000 ranges widely (Tables 15 and 16). Sometimes survival for transported fish from below Bonneville Dam as a juvenile to return as an adult is lower than the in-river migrants; other times it is higher.

- For hatchery steelhead, average differential post-Bonneville Dam survival for fish transported from Lower Granite Dam considerably exceeded the average estimated survival for the in-river migrants that migrated between Lower Granite and Bonneville dams. (Data are not sufficient to judge for wild steelhead.)
- It is very difficult to estimate annual *D* values precisely. The number of juvenile fish from the outmigration, however, provided the ability to make a relatively precise estimate of survival for in-river migrants between Lower Granite and Bonneville dams.

Within-season variability in transportation and *D*

For steelhead PIT tagged at Lower Granite Dam, we have known timing for transported and, subsequently, nondetected fish. From these fish we determined that not only did SAR vary over the course of the outmigration, but the variation in timing changed between years (Figures 19 and 20). No consistent pattern appeared. The majority of treatment pairs did not have significant differences in adult returns. As with wild spring-summer Chinook salmon, it appeared that SAR were generally slightly higher for the first fish groups in a season. Likewise, transported fish tended to have higher SAR during the middle of the migration.

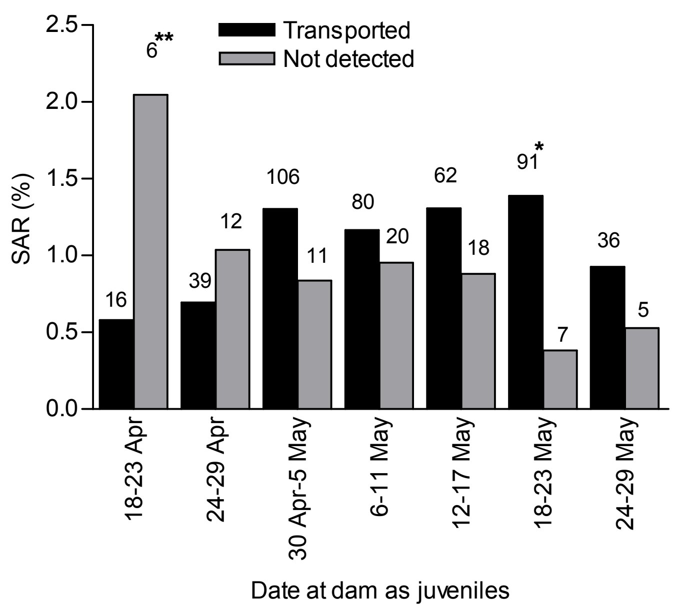

Figure 19. Temporal change in SAR of hatchery Snake River steelhead PIT tagged at Lower Granite Dam. In one treatment pair, significantly more nondetected fish returned.(**) In another pair, significantly more transported fish returned.(*) Numbers above bars indicate total adult returns for each group.

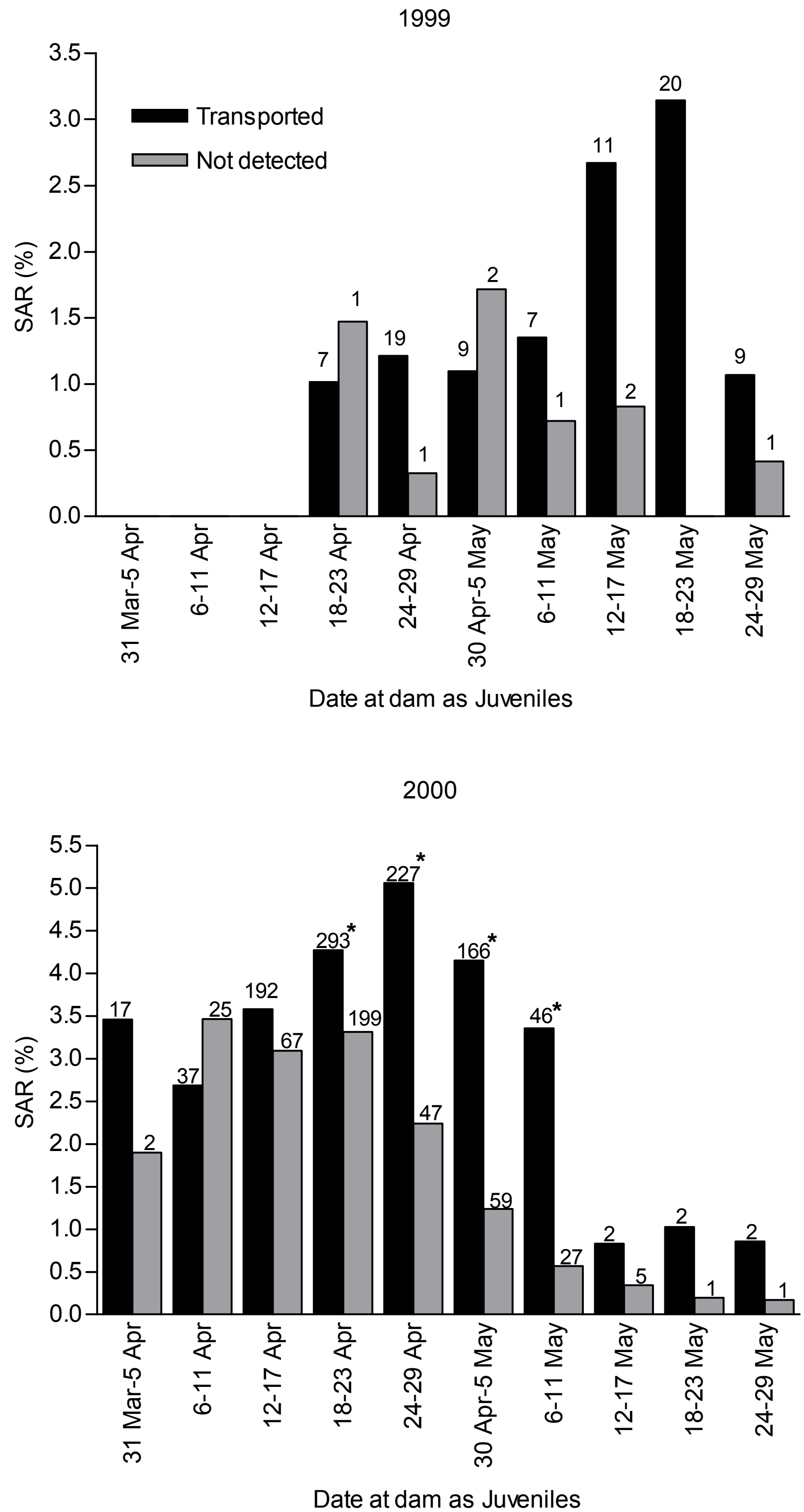

Figure 20. Temporal change in SAR of wild Snake River steelhead PIT tagged at Lower Granite Dam, 1999 and 2000. For four treatment pairs, significantly more transported fish returned (*) than nondetected fish. Numbers above bars indicate total adult returns for each group.

Adult upstream conversion rates

Between 2001 and 2003, based on PIT-tag detections at Bonneville and Lower Granite dams of wild 1- and 2-ocean steelhead adults returning from the 2000 outmigrations, transported fish had lower conversion rates to Lower Granite Dam than in-river fish (Table 17). We know that steelhead transported as juveniles return to the river generally later than in-river migrant juveniles, thus some conversion rate differences may relate to differences in harvest directed at steelhead or incidental to fall Chinook salmon harvest. We have not yet had the opportunity to evaluate this possibility. Another possibility for the difference could relate to higher stray rates for transported fish compared to in-river fish. Again we have no data at this time to determine the reason for this difference.

Table 17. Conversion rates (number of adult fish detected at Lower Granite dam/number of adult fish detected at Bonneville Dam) for wild adult steelhead PIT tagged as juveniles at Lower Granite Dam in 2000 and 2001 and either returned to the river or transported.

Year of outmigration	Year of adult return	In-river	Transported
2000	2001	0.83 (347/418)	0.70 (316/451)
	2002	0.78 (286/366)	0.71 (320/450)
2001	2002	NA	0.65 (194/298)
	2003	NA	0.96 (136/142)

Discussion

Results of all transportation studies clearly indicate that transported fish survive at lower rates downstream of Bonneville Dam than fish that migrate through the hydropower system. Nonetheless, for wild yearling Chinook salmon and steelhead, in almost all cases fish transported after 1 May returned at similar or higher rates than fish that migrated through the FCRPS reservoirs and dams. In some years, fish transported as early as 15–20 April returned at higher rates than in-river fish, but not consistently. For subyearling migrants, it did not appear that transportation consistently provided higher returns. In fact, in many comparisons, the fish that migrated through reservoirs and dams had higher return rates than those transported (because of very low sample sizes, differences were not statistically significant). The higher returns occurred even though the presumed—but not directly measured—survival of in-river migrants was generally quite low.

Yearling Chinook salmon transported by barge from Snake River dams arrived to their release point below Bonneville Dam typically in about 1.5 days, while those that migrated through the seven remaining dams took from 3 to 4 weeks early in the migration season, to less than 2 weeks by the end of May (Smith et al. 2000a and 2000b, Zabel et al. 2001). Thus smolts marked on the same day, but either transported or returned to the river, most likely encountered different physical and biological conditions within the estuary and nearshore ocean upon their arrival. The Columbia River estuary and nearby ocean are very dynamic environments. Coastal winds, upwelling, sea surface temperatures, and other physical conditions can change very quickly (Garcia Berdeal et al. 2002). Large changes in biological conditions (such as forage fish abundance and predatory fish abundance) in the Columbia River plume (Emmet and Brodeur 2000, Emmett et al. 2001) and the estuary[7] have been observed between and within years. Growth and survival of salmonids in their first months at sea appear critical to determining overall salmonid year-class strength. This is based on the relationship between returns of jack salmon with numbers of adults returning from the same broodyear class in later years, and between ocean purse seine catches of juvenile salmonids in June and subsequent jack and adult returns (Pearcy 1992).

Much of the observed seasonal, average delayed mortality for transported fish could simply result from varying ocean conditions at the time they enter the ocean. This comports with estimates of *D* observed in fish we marked at dams and results reported in the CSS, where *D* was lowest for the earliest migrating stocks (Lookingglass and Dworshak Hatcheries) and highest for the later migrants from McCall and Imnaha River acclimation ponds (CSS 2003).

Our analyses of seasonal trends in post-Bonneville Dam survival suggests that within-season variation could have important implications for management decisions that a single seasonal estimate of *D* would mask. If the efficacy of transportation is largely determined by time of ocean entry, then for early migrating stocks delay of arrival below Bonneville Dam should increase survival. Alternatively, for early migrating hatchery stocks, later hatchery release dates might lead toward a later arrival date at transport dams. Unfortunately, at this time we have no way to predict conditions that will exist when smolts first arrive in the estuary or ocean.

The smoltification process in salmonids causes morphological, behavioral, and physiological changes that affect downstream migration as well as the ability to survive in the marine environment. This process is regulated by developmental stage, photoperiod, and water temperature cues that enable salmonids to migrate when environmental conditions are most favorable for downstream passage and survival in the sea (Folmar and Dickhoff 1980, Wedemeyer et al. 1980). The act of migration further stimulates smolt development (Zaugg et al. 1985, Muir et al. 1994). Spring-summer Chinook salmon and steelhead migrations in the Snake and Columbia rivers show similar seasonal patterns each year, beginning in early April and tailing off near the end of May. Zaugg and Wagner (1973) found that gill Na + –K + ATPase (an indicator of migratory readiness) and migratory urge declined at water temperatures of 13°C and higher. Steelhead that migrate too late in the season, when water temperatures are above this threshold, may have a tendency to residualize. Although this same behavior has not been demonstrated in spring-summer Chinook salmon, exposure to water temperatures above 13°C has been shown to retard gill Na + –K + ATPase activity (Muir et al. 1994). Furthermore, Congleton et al. (2004) found that hatchery spring-summer Chinook salmon arriving at the collector dams had depleted the majority of their energy reserves; for those fish left in-river to migrate (not transported), energy reserves became depleted as they progressed downstream. Energy depletion was greater for smolts arriving at the dams later in the migration season and during the prolonged migration, as observed during the 2001 low-flow year. Construction of the FCRPS altered smolt migration timing. Regardless of when fish arrive at Lower Granite Dam, the nontransported fish certainly take longer to migrate through the entire FCRPS, and they arrive later at the ocean and likely in different condition than they did historically. Further, transported fish cover the distance more quickly and arrive at the ocean sooner than they would have in an unregulated system.

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[7] R. Emmett, NOAA Fisheries Service, Newport, OR. Pers. commun., December 2003.

The hypotheses that transportation-induced stress or disease transmission (Budy et al. 2002) cause lower adult returns are not supported by the temporal variability in measured values of *D* and SAR. If these hypotheses held true, we would not expect to see the much higher SAR and *D* values later in the season. It appears more likely that early transported fish arrive too soon to the estuary.

Although *D* values below 1.0 indicate a differential mortality between transported and in-river migrants, we expect that some transported fish would die due to natural selection if they continued their downstream migration through the hydropower system. Very low values of *D*, however, indicated a substantial differential mortality after release from transportation barges compared to the fish that survived to below Bonneville Dam after migrating through the FCRPS reservoirs and dams. Aside from a differential mortality between fish transported from upper Snake River dams (2% mortality in barges assumed) and fish that migrated in-river to below Bonneville Dam (approximately 50% mortality), the two groups marked on the same day have substantially different timing to the ocean (20–25 days for the earliest fish, and 15 days or less for the latest fish). We presume that the late migrants leaving Lower Granite Dam may miss the window of opportunity for best survival conditions by arriving too late below Bonneville Dam. The declining lipid reserves for late migrants observed by Congleton et al. (2004) may also decrease their survival.

Nonetheless, on average when the annual weighted *D* is combined with the average survival through the hydropower system, it yielded for wild spring-summer Chinook salmon and steelhead an overall survival estimate for the entire stock of approximately 50%. This value is as high or higher than the estimated survival of juvenile fish migrating through the FCRPS when only four dams and reservoirs existed during the 1960s (Williams et al. 2001).

With the low number of adult returns of PIT-tagged fish to date, especially for wild fish, definitive conclusions are not possible. We tentatively conclude that *D* values for fish transported from Lower Monumental and McNary dams are lower than for dams farther upstream. Combined with the higher survival to Bonneville Dam for fish left in the river at McNary Dam, a spring transportation program at McNary Dam likely provides only marginal benefits at best to Snake River stocks. There is no evidence that *D* values for Chinook salmon transported from Little Goose Dam are lower than for fish transported from Lower Granite Dam.

Although annual SAR for fish PIT tagged above Lower Granite Dam generally exceeded those of fish PIT tagged at the dam, ratios of return rates of transported to nondetected fish (which migrate past dams through turbines and spill) were similar. Thus results from studies with fish PIT tagged at Lower Granite Dam provide information on the relative differences in return rates of transported and in-river migrant fish in the population. The numbers of wild fish tagged above Lower Granite Dam estimated to have arrived at the dam were very small. The vast majority of these fish were bypassed back to the river; therefore, the SAR of transported and nondetected wild fish tagged above Lower Granite Dam had large errors. This made statistical power very low to show differences in return rates among fish with different juvenile migration histories.

If *D* varies from location to location, a combination of strategies at different locations might maximize survival of in-river migrants. For instance, if *D* is high for fish transported from Lower Granite Dam, but low for fish transported from dams farther downstream, it might make sense to choose configurations and operations to maximize collection and transportation of smolts at Lower Granite Dam, but not to collect and transport fish at downstream dams. This strategy would involve eliminating or reducing spill at Lower Granite Dam and spilling to the gas cap (a maximum level of supersaturated atmospheric gases set for the forebays and tailraces of dams) and full bypass operations at all other dams. Options to change collection strategies at dams to potentially benefit spring Chinook salmon, of course, may have no effect or negative effect for other species.

For subyearling Chinook salmon, a severe lack of data on transported fish hindered our ability to provide good comparisons between transported and in-river fish. Solving this problem will require directing more collected and detected PIT-tagged fish toward transportation (and that will require sufficient PIT-tagged fish for evaluation purposes). Preliminarily, our analyses suggest that transportation appeared to neither greatly harm nor help the fish. Thus a combination of transportation and good conditions for fish not collected and transported is consistent with a "spread the risk" strategy until more is known.

Juvenile Migrant Survival

Methods

Reach Survival Estimates

All mainstem dams on the lower Snake and Columbia rivers except The Dalles Dam have juvenile fish bypass facilities (Figure 1) (Matthews et al. 1977). These systems use screens to divert migrant smolts away from turbine intakes and into gatewells. Fish pass out of gatewells through orifices into a collection channel, where they pass directly to a pipe that discharges them to the tailrace, or they pass through a dewatering section leading to sampling or collection facilities. Except for Ice Harbor Dam, all bypassed fish pass through detectors that identify nearly 100% of PIT-tagged fish. PIT-tagged fish detected in facilities at Lower Granite, Little Goose, Lower Monumental, and McNary dams (collector dams, also called transport dams) are routed to raceways for loading into trucks or barges for subsequent transportation to below Bonneville Dam or routed back to the river via a slide gate (Marsh et al. 1999). The most downstream site for detecting PIT-tagged juvenile fish is in the Columbia River estuary between RKm 65 and 84, where a two-boat trawl tows a PIT-tag detector (Ledgerwood et al. 2000).

We estimated survival probabilities for juvenile migrant fish from PIT-tag detection histories. The estimated survival probability for a particular segment of the migration corridor provided a group-level statistic, interpreted as an estimate of the proportion of the group that survived the segment. PIT-tagged fish were defined as a "group" for survival estimation in three primary ways:

1. Fish tagged at the same time and released as a batch at a single point (typical for studies that address a specific research question and for daily samples of fish collected at a smolt trap).
2. Tagged fish held together in a holding facility for a period of time and then released from the same point over a short period of time (typical for volitional releases from hatcheries).
3. Tagged fish released at various sites upstream from a particular dam, then grouped according to the date when they were detected at the dam and returned to the tailrace (typical for attempts to gather a time series of survival estimates throughout the migration season).

For estimates and analyses in this report, groups sometimes contain both hatchery and wild fish, or we treat the two rearing types separately. In all cases, a fish group includes only one species.

No matter how the group was defined, survival probabilities were estimated using the detection records (detection histories) for every individual fish in the group. Because each PIT tag is uniquely coded, and because returning a portion of detected fish to the river allows detection at multiple dams, we analyzed the detection history data using a multiple-recapture model for single-release groups. We used a model originally presented and investigated by Cormack (1964), Jolly (1965), and Seber, known as the Cormack-Jolly-Seber (CJS) model or single-release (SR) model. Use of this model for survival estimation using PIT-tagged fish was first described in detail by Skalski (1998).

For survival estimation using the SR model, we needed at a minimum the release of a PIT-tagged fish group at the beginning of the river segment of interest, one detection site where at least some of the detected fish were returned to the river for subsequent detection opportunities, and at least one detection site farther downstream. If there were only one detection site downstream from the release site, or if all detected fish at the first site were removed from the river, then we could not distinguish failure to detect a passing (surviving) fish from mortality before arrival at the detection site (i.e., we could not estimate survival probabilities separately from detection probabilities). Fish detected downstream from the first detection site constitute a sample of the fish that were alive at the first site; they were used to estimate the proportion of fish passing the first site that were detected (detection probability). Having obtained the estimate of the detection probability, we then estimated the survival probability. When there was a series of detection sites with return-to-river capabilities, we estimated survival from release to the first site, then between each pair of consecutive sites, except that the inability to distinguish mortality from the failure to detect a surviving fish always precluded estimation between the last two sites.

In 1993 when a study specifically designed to estimate migrant smolt survival began, PIT-tag detectors were operational only at Lower Granite, Little Goose, Lower Monumental, and McNary dams. Only Lower Granite and Little Goose dams were equipped with slide gates to divert PIT-tagged fish from the bypass system back to the river. Under this configuration, we could only estimate survival for groups of fish from the point of release above Lower Granite Dam to the Lower Granite Dam tailrace and from Lower Granite Dam tailrace to Little Goose Dam tailrace. PIT-tag detectors and slide gates were added gradually to other dams after 1993 (in a downstream direction). Under present conditions, provided the estuarine trawl detected sufficient fish from the group, we could estimate survival for any group of PIT-tagged fish from any release point upstream from Bonneville Dam to its tailrace.

In this section, we present all survival estimates from point of release (or the tailrace of a dam) to the tailrace of a dam downstream. All survival and detection probability estimates were computed using a statistical computer program for analyzing release-recapture data called survival with proportional hazards (SURPH), developed at the University of Washington (Skalski et al. 1993, Smith et al. 1994).

Assumptions of single-release model

Using the SR model, the passage of a single PIT-tagged salmonid through the hydropower system is modeled as a sequence of events. Examples of such events are survival from the Lower Granite Dam tailrace to Little Goose Dam tailrace and detection at Little Goose Dam. Each event has an associated probability of occurrence. The detection history is the record of the event outcomes. (As previously noted, the detection history is an imperfect record of outcomes. If the history ends with one or more zeroes, we cannot distinguish mortality from survival without detection). The SR model represents detection history data for a group of tagged fish as a multinomial distribution: each multinomial cell probability (detection history probability) is a function of the underlying survival and detection event probabilities. Estimates of survival probabilities under the SR model are random variables, subject to sampling variability. When true survival probabilities are close to 1.0 or when sampling variability is high, it is possible for estimates of survival probabilities to exceed 1.0. For practical purposes, estimates should be considered equal to 1.0 in these cases.

Three key assumptions led to the multinomial cell probabilities used in the SR model:

1. Fish in a single group of tagged fish have common event probabilities (each conditional detection or survival probability is common to all fish in the group).
2. Event probabilities for each individual fish are independent from those for all other fish.
3. Each event probability is conditionally independent from all other probabilities.

For a broader description of these assumptions and how they may be tested, see Burnham et al. (1987) and Zabel et al. (2002).

To varying degrees, the three assumptions were inevitably violated for any particular group of migrating salmonids. Reasons why the assumptions might not have strictly held related to variation in fitness among fish in a group; for example, variation in migration rate means that individuals from the same group may have passed a dam under different conditions, and inherent traits or behavioral preferences might make detection of some fish more likely at all dams.

Violations of model assumptions can cause bias in resulting parameter estimates. However, known causes and degrees of SR model violations for migrating juvenile salmonids have been investigated and shown to cause minimal bias (Skalski 1998). Studies were planned and analyses designed to minimize the potential of significant bias due to violation of model assumptions.

Data sources and limitations

Information for juvenile salmonids PIT tagged and released in the Columbia River basin was obtained from the regional Pacific States Marine Fisheries Commission PIT-tag information system (PTAGIS) database (PSMFC 2004). We grouped fish by migration year, species, run, rearing type, release site, and in some cases by date or time period.

Sometimes, due to small or zero sample sizes at the most downstream observation sites, caused by very poor survival to those sites or low detection rates at those sites, survival for some cohorts for the McNary to John Day Dam or John Day to Bonneville Dam reaches was not estimated or alternative survival estimates were calculated using the pooled estimate for a particular species, run, or rearing type. In particular, estimates to Bonneville Dam were not calculated for mid-Columbia and Yakima River groups until 2001 and 2002, respectively.

Our estimates were calculated using only information available from PTAGIS (PSMFC 2004). We were not aware of all experimental caveats and details involved in the studies for which many of the fish were tagged. Thus although we used available PIT-tagged fish for survival estimates, we recognize that not all fish were released for the sole purpose of estimating downstream reach survival. Therefore some survival estimates, even if mathematically correct, may not reflect or represent true survival among the untagged population.

Annual average survival estimates from Lower Granite and McNary dams

Between 1993 and 2003, hatchery and wild yearling Chinook salmon and steelhead were tagged in varying numbers at various locations upstream from Lower Granite Dam. Studies were conducted involving fish collected and tagged at Lower Granite Dam and then released into the tailrace. To estimate survival for each year, we created daily release groups from Lower Granite Dam by combining fish tagged at the dam and released into the tailrace with previously tagged fish that were detected at the dam and returned to the tailrace the same day. For each daily group, detection data downstream from Lower Granite Dam were usually sufficient to calculate SR model survival estimates between Lower Granite and Little Goose dams, between Little Goose and Lower Monumental dams, and between Lower Monumental and McNary dams. If data for a daily group were not sufficient, we pooled adjacent days until estimates to McNary Dam were possible.

To obtain survival estimates downstream of McNary Dam, we regrouped fish into daily groups at McNary Dam, using the same methods described above for Lower Granite Dam. Detection data downstream from McNary Dam were usually not sufficient for each daily group. Therefore, we pooled the daily groups into weekly groups. For weekly groups leaving McNary Dam, we estimated survival between McNary and John Day dams and between John Day and Bonneville dams.

Using these methods, we obtained estimates for particular river sections from multiple groups of PIT-tagged fish throughout each migration season. Annual average estimates for these river sections were obtained using a mean weighted by relative variability of the estimate. This method resulted in survival estimates with little or no bias (Muir et al. 2001).

Annual average survival estimates through the entire hydropower system

For Snake River yearling Chinook salmon and steelhead, we estimated the annual mean survival probability from the head of Lower Granite Dam reservoir to Bonneville Dam tailrace. We calculated this estimate by multiplying three components: 1) the estimate of survival from the Snake River trap (near the head of the reservoir) to Lower Granite Dam (hatchery and wild fish pooled), 2) the weighted mean survival estimate for daily groups from Lower Granite Dam tailrace to McNary Dam tailrace, and 3) the weighted mean estimate for weekly groups from McNary Dam tailrace to Bonneville Dam tailrace.

Probability of Detecting PIT-Tagged Fish Versus Length at Tagging

Zabel et al. (2004) estimated the relationship between detection probability (at Little Goose, Lower Monumental, and McNary dams) versus length at tagging for spring-summer Chinook salmon and steelhead (hatchery and wild) PIT tagged and released at Lower Granite Dam during the years 1998 through 2002. We present the methods and results of this analysis in the subsections that follow.

Data

Study fish were yearling Chinook salmon and steelhead of both wild and hatchery origin. The fish were captured, PIT tagged, and released at Lower Granite Dam as part of transportation studies (Harmon et al. 2000, Marsh et al. 2001). We analyzed control fish that were released to the tailrace. Our analysis comprised all release groups by species and origin from 1998 to 2002 that contained at least 10,000 fish released in a year. Because survival and detection probabilities may vary over a season, we divided each yearly release group into six weekly release groups over the period 10 April to 21 May. The tagged fish were potentially detected in the bypass systems at Little Goose, Lower Monumental, McNary, John Day, and Bonneville dams (Figure 1). We combined detections at the last two sites to increase the sample size so that an individual fish had four opportunities for detection.

Survival and detection probability estimation

First, we introduce three terms (based on terminology from Lebreton et al. 1992) for the site-specific survival and detection probabilities:

1. φ_{nw} is the probability of fish released in week w (w = 1,2,…,6) surviving through the nth river segment (n = 1,2,3).
2. p_{nw} is the probability of detecting an individual from the wth release group at the nth detection site, given the individual was alive at that site.
3. β_w is the combined probability for fish released in week w of surviving the last river segment and being detected at the last site, since the data cannot distinguish between these two probabilities.

To incorporate length of fish into the analysis, we modified the CJS model (for details see Zabel and Achord 2004) by expressing survival and detection probabilities as functions of fish length. We used a logit link to ensure that survival and detection probabilities ranged from 0 to 1. For example, the relationship for fish released in week w between detection probability at site n and length was

$$p_{nw}(l) = \frac{\exp(\alpha_{0,nw} + \alpha_{l,n} \cdot l)}{1 + \exp(\alpha_{0,nw} + \alpha_{l,n} \cdot l)} \tag{4}$$

where l is fish length (standardized to have 0 mean) and a is the coefficient. Note that we allowed overall survival and detection probabilities (i.e., the intercept terms) to vary by weekly release group, but we kept site-specific length effects constant across a season to keep the analysis tractable. If length was not included in the probability, the above equation reduced to

$$p_{nw} = \exp(\alpha_{0,nw}) / 1 + \exp(\alpha_{0,nw}) \tag{5}$$

which is a constant. When all survival and detection probabilities were related to length, we referred to the model as $\phi_1(l)\ \phi_2(l)\ \phi_3(l)p_1(l)p_2(l)p_3(l)$. As an aside, if fish residualize, it is considered a mortality in the modeling. Thus size-selective residualism (or male precocity) is incorporated in the survival term and does not bias the estimation of size-selective detection probabilities.

Model parameters were estimated using maximum likelihood (Mood et al. 1974). The likelihood function was numerically optimized with respect to the parameters. Standard errors were estimated based on numerical approximations of the Hessian matrix (Burnham et al. 1987). We used the readily available software MARK (White and Burnham 1999) and SURPH (Lady et al. 2001) to conduct all analyses.

We constructed alternative models by either including or not including length relationships in each survival and detection probability. To compare alternative models, we used likelihood ratio tests (LRTs) (Mood et al. 1974). The LRTs were designed so that they compared a null model to a more complex alternative model. We implemented a top-down approach to the model selection process. In other words, we began with a full model,

$$\varphi_1(l)\varphi_2(l)\varphi_3(l)p_1(l)p_2(l)p_3(l), \tag{6}$$

where all survival and detection probabilities were related to length. Then we determined if we could remove individual length relationships (in either a survival or detection probability) based on an LRT. At each step we chose the candidate length relationship for testing whose length coefficient (α_l) had the lowest coefficient of variation (CV, mean/standard error). If the null hypothesis of the LRT was not rejected (there was no support for including the length term in the model), then the length term was removed. We then designated this simpler model as the alternative model and attempted to remove an additional length term. We repeated the process until we rejected a null hypothesis and thus accepted the more complex alternative model.

Once we completed our model selection analyses, we focused on an additional question: How does the existence of length-related recapture probabilities affect our ability to estimate population-wide survival? In particular, does the commonly used CJS model, which ignores variability in recapture probabilities among individuals, produce biased results? To address this question, we estimated population survival using two methods:

- Method 1: Ignore length relations in detection and survival probabilities and use the CJS model, $\phi_1\phi_2\phi_3p_1p_2p_3$. The weekly survival estimates were combined into a seasonal mean, with each weekly estimate weighted by the number of fish released per week.
- Method 2: Include length-related detection probabilities where appropriate, but ignore length effects on survival. In other words, use model $\phi_1\phi_2\phi_3p_1(*)p_2(*)p_3(*)$, where * means include the length relationship or not depending on results from the model selection process. Again, weekly survival estimates were combined into a weighted mean for the season.

Results

Snake River Yearling Chinook Salmon Survival

Hatchery release groups

Seven hatcheries in the Snake River basin released PIT-tagged yearling spring and summer Chinook salmon each year between 1993 and 2003: Dworshak, Kooskia, Lookingglass, Rapid River, McCall, Pahsimeroi, and Sawtooth. For each hatchery each year we identified the

PIT-tagged fish group that was most representative of the hatchery's production release. For these groups of yearling Chinook salmon, we calculated estimates of survival from release to the Lower Granite Dam tailrace. Many of the groups were released as a batch on a single occasion; others were released volitionally over a period of days from hatchery ponds or raceways.

Mean estimated survival from Snake River basin hatcheries to the tailrace of Lower Granite Dam (average for hatcheries combined) has ranged from a low of 0.494 in 1997 to 0.697 in 2000. For all hatcheries, average survival has been higher since 1998 than it was in 1993 through 1997 (Table 18).

A strong inverse relationship exists between survival and migration distance ($r^2 = 0.941$, $p < 0.001$) (Figure 21), with mean survival highest (0.765) from Dworshak National Fish Hatchery (116 km from Lower Granite Dam), and lowest (0.403) from Sawtooth National Fish Hatchery (747 km from Lower Granite Dam). However, survival from Sawtooth and Pahsimeroi hatcheries improved in recent years, likely due to better control of BKD, weakening the relationship between distance and survival to Lower Granite Dam.

Table 18. Estimated survival for yearling Chinook salmon from Snake River basin hatcheries to the tailrace of Lower Granite Dam, 1993–2003. Distance (km) from each hatchery to Lower Granite Dam in parentheses in header. Standard errors are in parentheses following each survival estimate.

Year	**Dworshak (116)**	**Kooskia (176)**	**Imnaha River weir (209)**	**Rapid River (283)**	**McCall (457)**	**Pahsimeroi (630)**	**Sawtooth (747)**	**Mean**
1993	0.647	0.689	0.660	0.670	0.498	0.456	0.255	0.554
	(0.028)	(0.047)	(0.025)	(0.017)	(0.017)	(0.032)	(0.023)	(0.060)
1994	0.778	0.752	0.685	0.526	0.554	0.324	0.209	0.547
	(0.020)	(0.053)	(0.021)	(0.024)	(0.022)	(0.028)	(0.014)	(0.081)
1995	0.838	0.786	0.617	0.726	0.522	0.316	0.230	0.576
	(0.034)	(0.024)	(0.015)	(0.017)	(0.011)	(0.033)	(0.015)	(0.088)
1996	0.776	0.744	0.567	0.588	0.531	—	0.121	0.555
	(0.017)	(0.010)	(0.014)	(0.007)	(0.007)		(0.017)	(0.096)
1997	0.576	0.449	0.616	0.382	0.424	0.500	0.508	0.494
	(0.017)	(0.034)	(0.017)	(0.008)	(0.008)	(0.008)	(0.037)	(0.031)
1998	0.836	0.652	0.682	0.660	0.585	0.428	0.601	0.635
	(0.006)	(0.024)	(0.006)	(0.004)	(0.004)	(0.021)	(0.033)	(0.046)
1999	0.834	0.653	0.668	0.746	0.649	0.584	0.452	0.655
	(0.011)	(0.031)	(0.009)	(0.006)	(0.008)	(0.035)	(0.019)	(0.045)
2000	0.841	0.734	0.688	0.748	0.689	0.631	0.546	0.697
	(0.009)	(0.027)	(0.011)	(0.007)	(0.010)	(0.062)	(0.030)	(0.035)
2001	0.747	0.577	0.747	0.689	0.666	0.621	0.524	0.653
	(0.002)	(0.019)	(0.003)	(0.002)	(0.002)	(0.016)	(0.023)	(0.032)
2002	0.819	0.787	0.667	0.755	0.592	0.678	0.387	0.669
	(0.011)	(0.036)	(0.012)	(0.003)	(0.006)	(0.053)	(0.025)	(0.055)
2003	0.720	0.560	0.715	0.691	0.573	0.721	0.595	0.654
	(0.008)	(0.043)	(0.012)	(0.007)	(0.006)	(0.230)	(0.149)	(0.028)
Mean	0.765	0.671	0.665	0.653	0.571	0.526	0.403	—
	(0.026)	(0.032)	(0.015)	(0.034)	(0.024)	(0.045)	(0.052)	

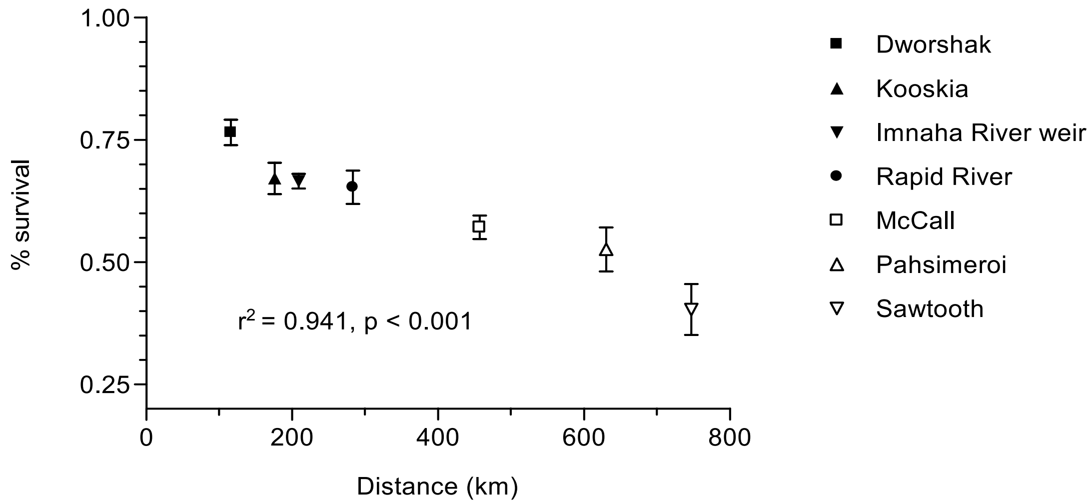


Figure 21. Estimated survival, with standard errors, from release at Snake River basin hatcheries to Lower Granite Dam tailrace, 1993–2003, versus distance (km) to Lower Granite Dam. The correlation between survival and migration distance is also shown.

Salmon and Snake River trap release groups

We estimated survival from release to Lower Granite Dam for wild and hatchery PIT-tagged yearling Chinook salmon and steelhead from the Salmon River (White Bird) and Snake River smolt traps. While fish were tagged and released nearly daily from these traps, daily groups rarely had sufficient data to calculate reliable survival estimates. For traps, we pooled all fish tagged and released between the beginning of operations in the spring and 31 May. Estimated survival between 1993 and 2003 to the tailrace of Lower Granite Dam for yearling Chinook salmon PIT-tagged at the Salmon River trap (233 km upstream from Lower Granite Dam) averaged 0.777 for hatchery fish and 0.862 for wild fish (Table 19).

Estimated survival from the Snake River trap, at the head of Lower Granite Reservoir (52 km upstream from Lower Granite Dam), to the tailrace of Lower Granite Dam averaged 0.929 for hatchery yearling Chinook salmon and 0.935 for wild yearling Chinook salmon between 1993 and 2003 (Table 20).

Annual average survival estimates from Lower Granite and McNary dams

Except for the low-flow year, 2001, mean estimated survival from Lower Granite Dam tailrace to McNary Dam tailrace between 1998 and 2003 was consistent from year to year, ranging from a low of 0.729 for wild Chinook salmon in 2003 to a high of 0.791 for both hatchery and wild fish in 1999 (Table 21). In 2001, mean estimated survival was only about 55%. Over the 5 years (excluding the low-flow year, 2001), average estimated survival was nearly identical for hatchery (0.766) and wild (0.767) Chinook salmon.

Table 19. Estimated survival for yearling Chinook salmon from the Salmon River (Whitebird) trap to Lower Granite Dam tailrace (233 km), 1993–2003. Standard errors are in parentheses. Simple arithmetic means across all years are given.

Year	Hatchery	Wild
1993	0.782 (0.019)	0.832 (0.014)
1994	0.761 (0.024)	0.817 (0.017)
1995	0.802 (0.012)	0.863 (0.011)
1996	0.735 (0.026)	0.822 (0.029)
1997	NA	NA
1998	0.740 (0.012)	0.926 (0.016)
1999	0.800 (0.013)	0.909 (0.012)
2000	0.806 (0.015)	0.920 (0.021)
2001	0.819 (0.007)	0.878 (0.009)
2002	0.792 (0.016)	0.844 (0.016)
2003	0.728 (0.016)	0.807 (0.011)
Mean	0.777 (0.010)	0.862 (0.014)

Table 20. Estimated survival for yearling Chinook salmon from the Snake River trap (near head of Lower Granite Reservoir) to Lower Granite Dam tailrace (52 km), 1995–2003. Standard errors are in parentheses. Simple arithmetic means across all years are given.

Year	Hatchery	Wild
1993	0.823 (0.016)	0.847 (0.024)
1994	0.951 (0.029)	0.913 (0.036)
1995	0.886 (0.013)	0.944 (0.015)
1996	0.974 (0.032)	0.984 (0.039)
1997	NA	NA
1998	0.928 (0.013)	0.915 (0.019)
1999	0.930 (0.013)	0.950 (0.011)
2000	0.911 (0.018)	0.951 (0.023)
2001	0.956 (0.015)	0.921 (0.058)
2002	0.925 (0.027)	0.985 (0.038)
2003	1.001 (0.030)	0.943 (0.033)
Mean	0.929 (0.016)	0.935 (0.013)

Data were not sufficient to estimate survival from McNary Dam tailrace to Bonneville Dam tailrace for any Snake River yearling Chinook salmon until 1999. From 1999 to 2003, data were sufficient to estimate survival for pooled hatchery and wild groups, but not for the rearing types separately. Annual average estimates ranged from 0.501 in 2001 to 0.763 in 2002, and averaged 0.667 for the 5 years 1999–2003 (Table 21).

Annual average survival estimates through the FCRPS

For yearling Chinook salmon (hatchery and wild combined), estimated survival through the hydropower system, from the Snake River trap at the head of Lower Granite Reservoir to the

Bonneville Dam tailrace, through eight mainstem dams and reservoirs, ranged from 0.266 in the low-flow year of 2001 to 0.551 in 2002 (Table 22).

Comparison of wild and hatchery yearling Chinook salmon

Wild yearling Chinook salmon had nearly equal to slightly higher survival than hatchery-reared fish between the Salmon and Snake River traps and Lower Granite Dam tailrace (Tables 19 and 20). Hatchery and wild yearling Chinook salmon had similar average estimated survival from the Lower Granite Dam tailrace to the McNary Dam tailrace, through four dams and reservoirs (Table 21). Annually, estimated survival has been similar for hatchery and wild yearling Chinook salmon, with neither stock having consistently higher survival. In estimating juvenile downstream migrant survival for these stocks the similarity in survival between

Table 21. Estimated survival from Lower Granite Dam tailrace to McNary Dam tailrace and from McNary Dam tailrace to Bonneville Dam tailrace for hatchery and wild yearling Chinook salmon, 1998–2003. Standard errors are in parentheses. Simple arithmetic means across all years are given.

	Lower Granite to McNary Dam		**McNary to Bonneville Dam**
Year	**Hatchery**	**Wild**	**Hatchery + wild**
1998	0.773 (0.012)	0.771 (0.015)	NA
1999	0.791 (0.007)	0.791 (0.014)	0.704 (0.058)
2000	0.763 (0.026)	0.775 (0.014)	0.640 (0.122)
2001	0.556 (0.019)	0.541 (0.027)	0.501 (0.027)
2002	0.759 (0.008)	0.768 (0.026)	0.763 (0.079
2003	0.746 (0.019)	0.729 (0.020)	0.728 (0.030)
Mean			
All years	0.731 (0.036)	0.729 (0.039)	0.667 (0.046)
Excluding 2001	0.766 (0.008)	0.767 (0.010)	0.709 (0.026)

Table 22. Hydropower system survival estimates derived by combining empirical survival estimates from various reaches for Snake River yearling Chinook salmon (hatchery and wild combined), 1997–2003. Standard errors are in parentheses.

Year	**Snake River trap to Lower Granite Dam**	**Lower Granite Dam to Bonneville Dam**	**Snake River trap to Bonneville Dam**
1997	NA	NA	NA
1998	0.925 (0.009)	NA	NA
1999	0.940 (0.009)	0.557 (0.046)	0.524 (0.043)
2000	0.929 (0.014)	0.486 (0.093)	0.452 (0.087)
2001	0.954 (0.015)	0.279 (0.016)	0.266 (0.015)
2002	0.953 (0.022)	0.578 (0.060)	0.551 (0.057)
2003	0.993 (0.023)	0.532 (0.023)	0.528 (0.023)
Mean			
All years	0.949 (0.010)	0.486 (0.054)	0.464 (0.052)
Excluding 2001	0.948 (0.012)	0.538 (0.020)	0.514 (0.021)

PIT-tagged hatchery and wild fish through this reach and from the Snake River trap to the Lower Granite Dam tailrace (about 50% of the hydropower system) supports the use of hatchery fish as surrogates for wild fish.

Upper Columbia River Yearling Migrant Survival

Fewer years of PIT-tag data exist for fish stocks from the upper Columbia River basin compared to those in the Snake River basin. Nonetheless, the data indicate that juveniles migrating from the two basins under normal flow conditions had similar survival (Tables 23 and 24 compared to Table 22). This was not the case in the 2001 low-flow year. Fish from the upper Columbia River had higher estimated survival to the McNary Dam tailrace (hatchery releases), and sometimes from the Bonneville Dam tailrace (dam releases), than fish from the Snake River. A spill program existed at upper Columbia River dams in 2001, but not at Snake River dams, thus possibly explaining some of the difference in survival. For fish released at dams, a stock effect may also have played a part. Yearling summer-fall Chinook salmon released at upper Columbia River dams also had higher survival from McNary Dam to Bonneville Dam, whereas spring Chinook salmon from the Yakima River did not. Yakima River spring Chinook salmon had survival similar to Snake River spring Chinook in the lower river.

Snake River Subyearling Fall Chinook Salmon Survival

Summer-migrating subyearling fall Chinook salmon have a much more complex migration pattern than spring-migrating salmonids. Thus results from PIT-tag studies did not fall into neat, discrete parts. Most data on fall Chinook salmon survival came from studies using fish released upstream from Lower Granite Dam. Since 1992, Connor et al. (2003a) have beach seined, PIT tagged, and released wild fall Chinook salmon in their rearing areas. Since 1995, NOAA Fisheries Service has also PIT-tagged subyearling fall Chinook at Lyons Ferry Hatchery, trucked them upstream above Lower Granite Dam, and released them at a time and size to match wild subyearling fall Chinook salmon in their rearing areas (Smith et al. 2003). Since travel time to the Lower Granite Dam typically averaged 1 month or more from time of release after tagging, survival estimates to Lower Granite Dam represented survival during both rearing and migration (Connor et al. 2003a, 2003b, Smith et al. 2003). Subyearling fall Chinook salmon rear and develop physiologically as they migrate, and their migration rate increased with migration distance and increased size. Unlike yearling smolts, which generally all migrated quickly to Lower Granite Dam, some fall Chinook salmon did not begin migrating for months. Thus for yearling smolts, standard techniques to measure travel times or survival did not work as well. From 1995 to 2000, we released nearly 200,000 PIT-tagged smolts above Lower Granite Dam. Subsequently we detected only about 68,700. Of these, approximately 13% were not detected at a Snake River dam until after 1 September of the year, some not until the following spring. The early fish had SAR of about 0.32%, while the late fish had SAR of about 1.55%. For the "active" migrants (early fish), those that passed the Snake River dams in June, July, and August in the year of release for the hatchery fish, the median pooled travel time for all years from release to detection at Lower Granite Dam averaged 43.5 days (Smith et al. 2003). Within each

Table 23. Survival estimates for upper Columbia River yearling Chinook salmon. Standard errors are in parentheses.

Year	Release site[a]	No. of fish	Release site to Rocky Reach Dam		Rocky Reach to McNary Dam		Release site to McNary Dam		McNary to John Day Dam		John Day to Bonneville Dam		Release site to Bonneville Dam	
Hatchery spring Chinook salmon														
1999	Above RIS	14,894	0.782	(0.030)	0.727[b]	(0.053)	0.570[c]	(0.015)	0.890[c]	(0.018)	–	–	–	–
2000	Above RIS	14,877	0.705	(0.028)	0.692[b]	(0.088)	0.543[c]	(0.051)	0.892[c]	(0.064)	–	–	–	–
2001	Above RIS	15,014	0.756	(0.014)	0.565	(0.015)	0.461	(0.036)	0.812	(0.051)	0.788	(0.264)	0.312	(0.024)
2002	Above RIS	404,138	0.799	(0.074)	0.642	(0.032)	0.522	(0.017)	0.856	(0.012)	0.867	(0.079)	0.400	(0.015)
2003	Above RIS	355,321	–	–	–	–	0.559	(0.025)	0.892	(0.006)	0.796	(0.044)	0.416	(0.040)
Hatchery summer Chinook salmon														
1999	Wells Hatchery	5,998	–	–	–	–	0.390[c]	(0.050)	1.258[c]	(0.520)	0.995	(0.319)	0.374	(0.110)
2000	Wells Hatchery	5,997	–	–	–	–	0.208[c]	(0.020)	0.582	(0.081)	0.695	(0.036)	0.146	(0.017)
	Above RIS	45,981	–	–	–	–	0.962	(0.011)	0.738	(0.012)	0.695	(0.036)	0.568	(0.208)
2001	Wells Hatchery	6,000	0.443	(0.031)	0.483	(0.061)	0.214[c]	(0.020)	0.407[c]	(0.100)	–	–	–	–
	Above RIS	90,118	–	–	–	–	0.723	(0.026)	0.863	(0.018)	0.787	(0.067)	0.506	(0.020)
	Below RIS	113,333	–	–	–	–	0.817	(0.031)	0.922	(0.009)	0.788	(0.050)	0.601	(0.060)
2002	Wells Hatchery	5,992	0.591	(0.034)	0.759	(0.063)	0.450[c]	(0.030)	0.792[c]	(0.160)	1.202	(0.217)	0.304	(0.286)
	Above RIS	90,125	–	–	–	–	0.771	(0.024)	0.866	(0.013)	1.202	(0.217)	0.876	(0.060)
2003	Wells Hatchery	5,996	–	–	–	–	0.449	(0.025)	1.158	(0.456)	–	–	–	–
	Above RIS	103,907	–	–	–	–	0.787	(0.034)	0.856	(0.035)	0.846	(0.024)	0.582	(0.030)
	Below RIS	117,149	–	–	–	–	0.767	(0.024)	0.942	(0.022)	0.667	(0.126)	0.492	(0.090)
Wild spring Chinook salmon														
2003	Above RIS	6,402	–	–	–	–	0.324	(0.021)	1.072	(0.033)	0.740	(0.053)	0.233	(0.066)

[a] Above RIS = hatchery and wild fish released upstream of Rock Island Dam. Below RIS = hatchery fish released downstream of Rock Island Dam. Summer Chinook salmon released from Wells Hatchery are a separate category.

[b] Includes data from Bickford et al. 2001.

[c] Includes data from Columbia Basin Research, online at www.cbr.washington.edu/pitSurv/ [accessed March 2004].

Table 24. Survival estimates for PIT-tagged yearling Yakima River Chinook salmon. Standard errors are in parentheses.

Year	Release site	No. of fish	Release site to Prosser Dam		Prosser to McNary Dam		Release site to McNary Dam		McNary to John Day Dam		John Day to Bonneville Dam		Release site to Bonneville Dam	
Hatchery spring Chinook salmon														
1999	Above Roza Dam	39,702	0.517	(0.025)	0.909	–	0.472	(0.023)	0.929	(0.024)	–	–	–	–
2000	Above Roza Dam	40,417	0.474	(0.016)	0.712	(0.027)	0.339	(0.019)	0.683	(0.041)	–	–	–	–
	Below Roza Dam	7,929	–	–	–	–	0.749	(0.025)	0.683	(0.041)	–	–	–	–
2001	Above Roza Dam	41,234	0.313	(0.037)	0.638	(0.006)	0.201	(0.021)	0.757	(0.040)	–	–	–	–
	Below Roza Dam	895	–	–	–	–	0.496	(0.022)	0.812	(0.105)	–	–	–	–
2002	Above Roza Dam	40,701	0.395	(0.021)	0.732	(0.009)	0.289	(0.016)	0.938	(0.036)	1.150	(0.146)	0.348	(0.047)
	Below Roza Dam	1,261	–	–	–	–	0.520	(0.030)	0.938	(0.036)	0.356	(0.186)	0.214	(0.104)
2003	Above Roza Dam	41,671	0.378	(0.029)	0.660	(0.035)	0.253	(0.030)	1.041	(0.071)	0.914	(0.139)	0.227	(0.043)
	Below Roza Dam	4,308	–	–	–	–	0.510	(0.022)	0.877	(0.079)	0.914	(0.139)	0.288	(0.079)
Wild spring Chinook salmon														
1999	Above Roza Dam	312	0.581	(0.089)	0.923	(0.192)	0.538	(0.084)	0.866	(0.056)	–	–	–	–
	Below Roza Dam	3,040	–	–	–	–	0.774	(0.022)	0.866	(0.056)	–	–	–	–
2000	Above Roza Dam	6,209	0.678	(0.065)	0.600	(0.027)	0.414	(0.044)	0.814	(0.055)	–	–	–	–
	Below Roza Dam	5,727	–	–	–	–	0.819	(0.036)	0.795	(0.048)	–	–	–	–
2001	Above Roza Dam	2,179	0.312	(0.010)	0.759	(0.027)	0.237	(0.011)	0.631	(0.070)	–	–	–	–
	Below Roza Dam	1,606	–	–	–	–	0.688	(0.019)	0.658	(0.055)	–	–	–	–
2002	Above Roza Dam	8,717	0.397	(0.021)	0.658	(0.044)	0.254	(0.026)	0.870	(0.054)	0.921	(0.424)	0.187	(0.085)
	Below Roza Dam	3,022	–	–	–	–	0.643	(0.010)	0.870	(0.054)	0.626	(0.247)	0.267	(0.006)
2003	Above Roza Dam	7,803	0.377	(0.016)	0.728	(0.024)	0.274	(0.015)	0.883	(0.113)	0.782	(0.288)	0.198	(0.071)
	Below Roza Dam	9,333	–	–	–	–	0.637	(0.008)	0.768	(0.045)	1.156	(0.054)	0.549	(0.016)

migration year, the median migration rate between each pair of dams was substantially greater between Lower Monumental and McNary dams and between McNary and Bonneville dams than between pairs of dams upstream from Lower Monumental Dam (Figure 22).

Survival of both wild and hatchery fish to Lower Granite Dam varied widely among years and within years, with survival declining as the migration season progressed, flows decreased, and water clarity and temperature increased (Connor et al. 2003a, Smith et al. 2003). Certainly a need exists for an estimated average survival through the Lower Granite Dam reservoir. However, with data collected to date we could not partition the mortality that occurred within

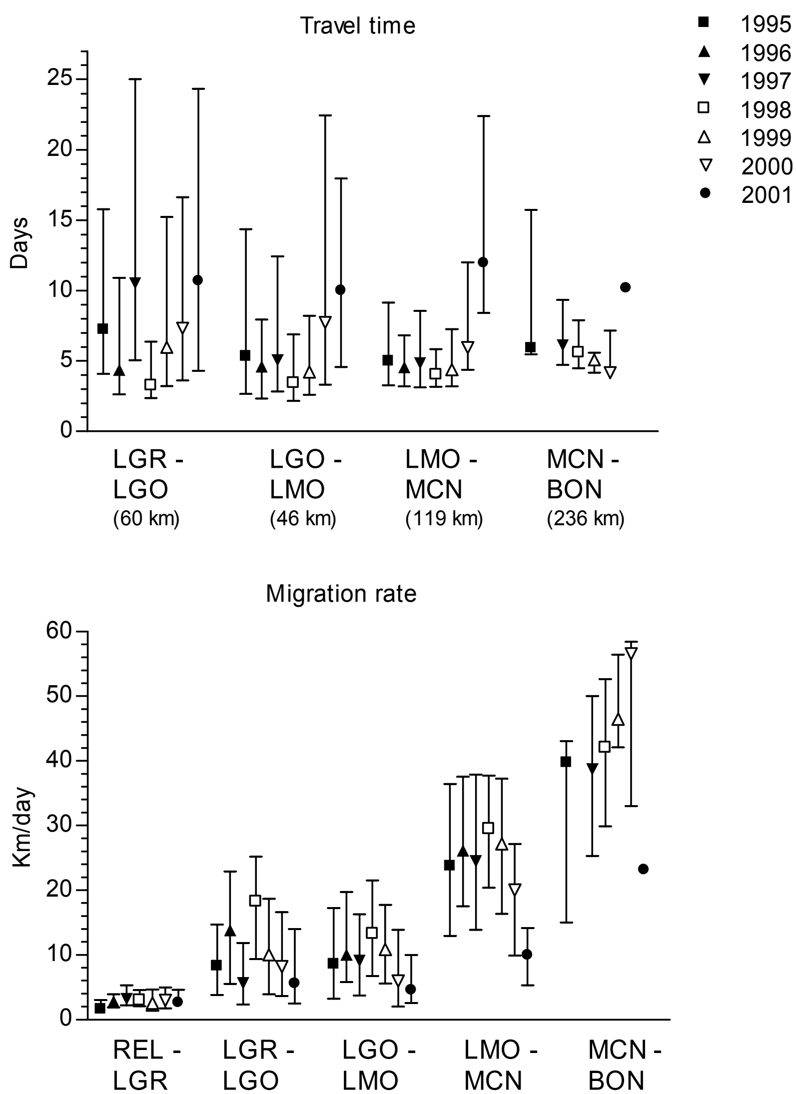


Figure 22. Median travel times and migration rates (with 20th and 80th percentiles) for PIT-tagged hatchery fall Chinook salmon, 1995–2001. Rel = release site in the Snake River, LGR = Lower Granite Dam, LGO = Little Goose Dam; LMO = Lower Monumental Dam, MCN = McNary Dam, and BON = Bonneville Dam. The lengths of the reaches are in parentheses in the upper panel.

the hydropower system, because measures of survival (and travel time) represented both rearing and migration.

Connor et al. (2003a) divided wild subyearling fall Chinook salmon into four equally sized cohorts for each year (1998–2000). They estimated 57% to 88% survival to Lower Granite Dam tailrace for the earliest migrating cohort, PIT tagged in early to mid-May, to 36% for fish tagged in mid-June. For hatchery subyearling Chinook salmon, estimated survival was 35% to 55% for early June releases, 16% to 49% for mid-June releases, and 2% to 24% for the last releases in early July for fish released at Billy Creek near Asotin, Washington, during those years (Figure 23) (Smith et al. 2002b, 2003).

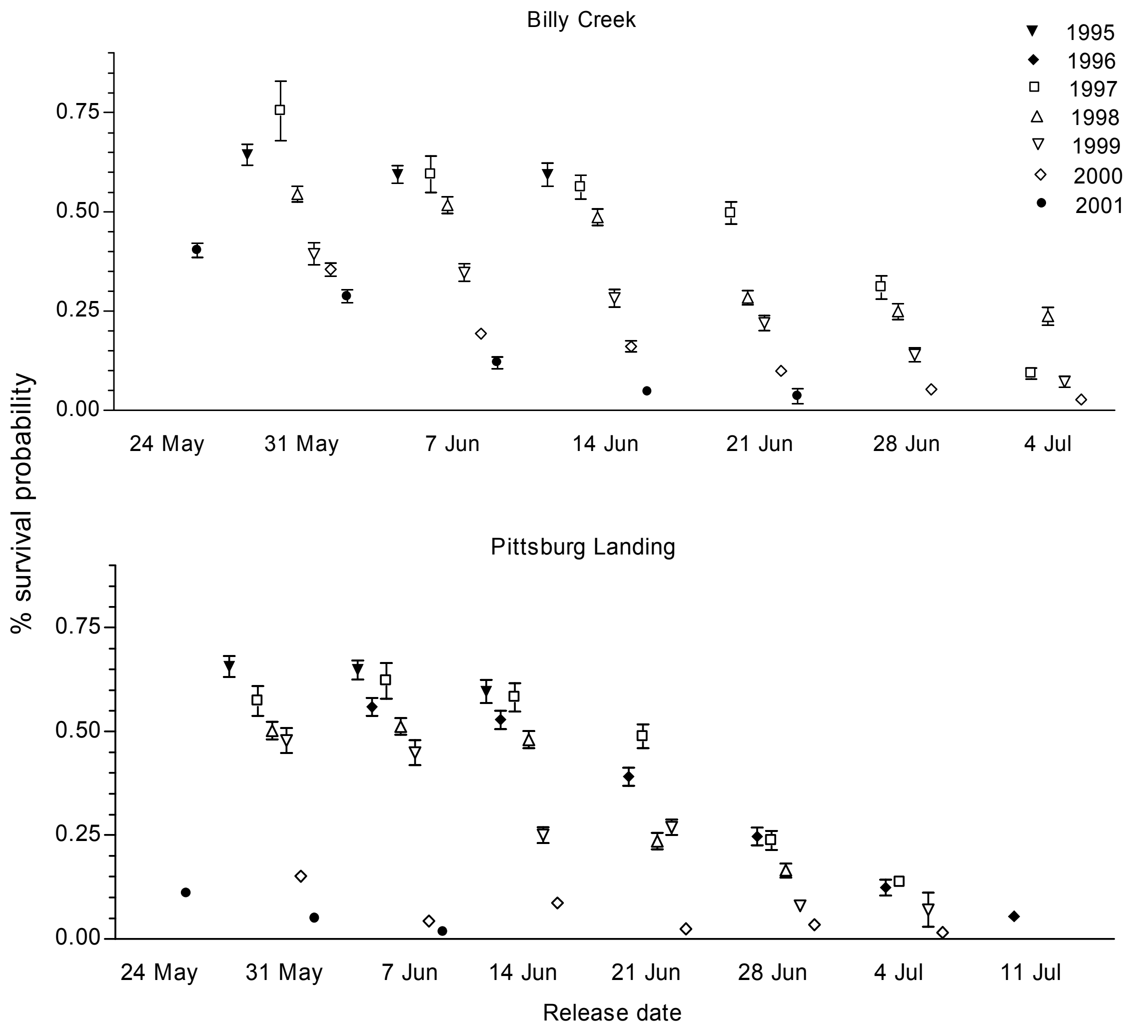


Figure 23. Estimated survival probabilities (with standard errors) from point of release in the Snake River (Billy Creek or Pittsburg Landing) to the tailrace of Lower Granite Dam for PIT-tagged hatchery subyearling fall Chinook salmon, 1995–2001.

Estimating survival for subyearling Chinook salmon below Lower Granite Dam was also difficult. Because of lower detection efficiencies (due to lower fish guidance efficiencies for fall Chinook), fewer PIT-tagged fish, poor survival to Lower Granite Dam, and fish dispersed over a wide time period, survival for Snake River fall Chinook was only estimated as far as the Lower Monumental Dam tailrace through 2001, and only for hatchery-origin fish (Smith et al. 2002a, 2003). Survival between the Lower Granite and Lower Monumental Dam tailraces has been highly variable, with a general decline in mid to late August, and has been much lower overall than for migrating yearling spring Chinook salmon (Figure 24). We did not estimate survival over this reach for 2002. Due to larger releases of fish in 2003, we estimated survival between the Lower Granite and McNary Dam tailraces. Survival ranged from 75% for fish leaving Lower Granite Dam the second week in June to 22% for fish leaving the second week in July.

We have no survival estimates for juvenile fish that migrated in September and October, nor for undetected fish. But, based on adult returns of PIT-tagged fish, these groups accounted for 14% and 36% of the total adult return of the in-river PIT-tagged fish released from 1995 through 2000. Nonetheless, the PIT-tagged fish did not represent the untagged population because all untagged fish collected at dams were transported. Thus we had expected that nearly all adult returns to Lower Granite Dam would come from untagged fish transported from collector dams as juveniles. Recently however, results from reading scales of adult fall Chinook salmon passing Lower Granite Dam indicated that 40% to 50% of the adult return came from fish that entered the ocean as yearlings (Connor et al. in press). This suggests that many transported fish overwintered in the estuary, juveniles migrated during the winter (outside of the juvenile bypass system operation window) and were not collected or transported, or juveniles collected and transported in the fall decreased growth sufficiently to show an apparent overwinter, freshwater check on the scale. In any case, this indicates a substantial change from hypothesized historical migration patterns for the fish.

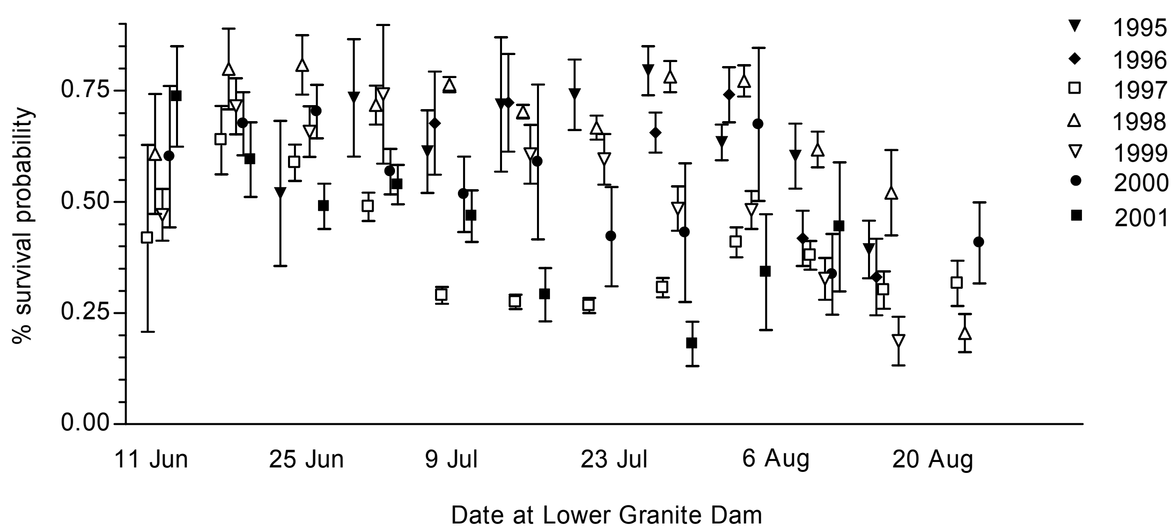


Figure 24. Estimated survival probabilities (with standard errors) to the tailrace of Lower Monumental Dam for PIT-tagged hatchery subyearling fall Chinook salmon leaving Lower Granite Dam, by week, 1995–2001.

Juvenile fall Chinook salmon historically moved out of the upper Snake River spawning and rearing areas in late March and early April. The peak of the run passed Ice Harbor Dam by mid-June. The construction of the Hells Canyon dams substantially altered conditions for migrant fish. Thus little in the migration of juvenile fall Chinook salmon under present conditions matches historical run timing.

Upper Columbia River Subyearling Migrant Survival

Fewer years of PIT-tag data exist for fish stocks from the upper Columbia River basin compared to the Snake River basin. Depending on year and release site, survival values ranged widely (Tables 25 and 26).

Snake River Steelhead Survival

Hatchery release groups

Two hatcheries in the Snake River basin, Dworshak and Clearwater, released PIT-tagged fish most years between 1993 and 2003. Although we estimated survival for release groups, because the hatcheries released fish at numerous sites within the Clearwater basin, we did not tabulate survival from the hatcheries to Lower Granite Dam, as we did for yearling Chinook salmon.

Salmon and Snake River trap release groups

From 1993 to 2003, estimated survival to the Lower Granite Dam tailrace for steelhead PIT tagged at the Salmon River trap (223 km above Lower Granite Dam) averaged 0.854 for hatchery fish and 0.869 for wild fish (Table 27).

From 1993 to 2003, estimated survival from the Snake River trap, at the head of Lower Granite Reservoir (52 km above Lower Granite Dam), to the Lower Granite Dam tailrace averaged 0.927 for hatchery steelhead and 0.935 for wild steelhead (Table 28).

Annual average survival estimates from Lower Granite and McNary dams

Except for the low-flow year (2001), mean estimated survival from Lower Granite Dam tailrace to McNary Dam tailrace from 1997 to 2003 ranged from a low of 0.533 for hatchery steelhead in 2002 to a high of 0.746 for wild fish in 1999 (Table 29). In 2001, mean estimated survival was very low: 0.170 for hatchery steelhead and 0.168 for wild. Over the 5 years (excluding 2001), average estimated survival was 0.606 for hatchery and 0.670 for wild steelhead.

Data were not sufficient to estimate survival from McNary Dam to Bonneville Dam for any Snake River steelhead until 1997. From 1997 to 2003, data were sufficient to estimate survival from McNary Dam tailrace to Bonneville Dam tailrace for pooled hatchery and wild groups, but not for the rearing types separately. Annual average estimates ranged from 0.250 in

Table 25. Survival estimates for PIT-tagged upper Columbia River subyearling Chinook salmon and percentage recovery of PIT-tagged fish on bird islands. Standard errors are in parentheses.

Year	Release site[a]	No. of fish	PIT-tag recovery on bird islands	Release site to McNary Dam		McNary Dam to John Day Dam		John Day Dam to Bonneville Dam		Release site to Bonneville Dam	
Hatchery fall Chinook											
1999	Below RIS	6,778	0.0081	0.800[b]	(0.037)	0.720[b]	(0.017)	–	–	–	–
2000	Below RIS	6,091	0.0144	0.624[b]	(0.068)	0.483[b]	(0.069)	–	–	–	–
2001	Below RIS	35,762	0.0063	0.667[b]	(0.050)	0.683[b]	(0.062)	–	–	–	–
2002	Below RIS	66,554	0.0051	0.716[b]	(0.019)	0.778[b]	(0.030)	0.788	(0.116)	0.390	(0.040)
2003	Below RIS	81,253	0.0028	0.558	(0.034)	0.820	(0.042)	–	–	–	–
Wild fall Chinook											
1999	Above Yakima	5,042	0.0113	0.398	(0.024)	0.833	(0.119)	–	–	–	–
2000	Above Yakima	10,967	0.0098	0.432	(0.035)	–	–	–	–	–	–
2001	Above Yakima	9,481	0.0127	0.366	(0.025)	0.563	(0.029)	–	–	–	–
2002	Above Yakima	414	0.0048	0.402	(0.058)	0.696	(0.290)	–	–	–	–
2003	Above Yakima	2,975	0.0084	0.315	(0.020)	0.600	(0.122)	–	–	–	–

[a] Below RIS = hatchery and wild fish released downstream of Rock Island Dam. Above Yakima = wild fish released above confluence of Columbia and Yakima rivers.

[b] Includes data from Columbia Basin Research, online at www.cbr.washington.edu/pitSurv/.

Table 26. Survival estimates for PIT-tagged Yakima River fall Chinook salmon and percentage recovery of PIT-tagged fish on bird islands. Standard errors are in parentheses.

Year	Release site	No. of fish	PIT-tag recovery on bird islands	Release site to McNary Dam		McNary Dam to John Day Dam		John Day Dam to Bonneville Dam		Release site to Bonneville Dam	
Hatchery fall Chinook											
1999	Below Roza Dam*	7,324	0.0104	0.588	(0.108)	0.669	(0.053)	–	–	–	–
2000	Below Roza Dam*	4,051	0.0222	0.645	(0.119)	0.573	(0.137)	–	–	–	–
2001	Below Roza Dam*	3,979	0.0206	0.330	(0.037)	0.696	(0.113)	–	–	–	–
2002	Below Roza Dam*	4,001	0.0165	0.223	(0.011)	0.867	(0.132)	0.723	(0.239)	0.149	(0.047)
2003	Below Roza Dam*	3,987	0.0025	0.183	(0.083)	0.783	(0.071)	0.716	(0.000)	0.147	(0.055)
Wild fall Chinook											
1999	Below Roza Dam*	876	0.0011	0.790	(0.021)	0.720	(0.188)	–	–	–	–
2000	Below Roza Dam*	1,979	0.0344	0.272	(0.025)	–	–	–	–	–	–

* Fish released downstream of Roza Dam.

Table 27. Estimated survival for hatchery and wild steelhead from the Salmon River (Whitebird) trap to Lower Granite Dam tailrace (233 km), 1993–2003. Standard errors are in parentheses. Simple arithmetic means across all years are given.

Year	Hatchery	Wild
1993	0.875 (0.011)	0.832 (0.019)
1994	NA	NA
1995	0.882 (0.013)	0.892 (0.025)
1996	0.851 (0.022)	0.956 (0.060)
1997	0.872 (0.017)	0.876 (0.062)
1998	0.879 (0.016)	0.892 (0.070)
1999	0.825 (0.014)	0.816 (0.039)
2000	0.870 (0.019)	0.815 (0.041)
2001	0.786 (0.009)	0.878 (0.019)
2002	0.814 (0.041)	0.780 (0.050)
2003	0.885 (0.028)	0.952 (0.092)
Mean	0.854 (0.011)	0.869 (0.018)

Table 28. Estimated survival for hatchery and wild steelhead from the Snake River trap (near head of Lower Granite Reservoir) to Lower Granite Dam tailrace (52 km), 1995–2003. Standard errors are in parentheses. Simple arithmetic means across all years are given.

Year	Hatchery	Wild
1993	0.917 (0.008)	0.898 (0.009)
1994	NA	NA
1995	0.936 (0.011)	0.955 (0.013)
1996	0.941 (0.020)	0.973 (0.022)
1997	0.963 (0.016)	0.968 (0.051)
1998	0.926 (0.010)	0.919 (0.017)
1999	0.908 (0.012)	0.910 (0.024)
2000	0.947 (0.014)	0.977 (0.027)
2001	0.893 (0.008)	0.958 (0.010)
2002	0.893 (0.019)	0.899 (0.023)
2003	0.946 (0.018)	0.893 (0.026)
Mean	0.927 (0.008)	0.935 (0.011)

2001 to 0.770 in 1998, and averaged 0.540 for the 7 years (Table 29). Estimated survival between McNary Dam tailrace and Bonneville Dam tailrace was lower in all 3 years from 2001 to 2003 than in any year between 1997 and 2000.

Annual average survival estimates from Lower Granite and McNary dams

Except for the low-flow year 2001, from 1997 to 2003 mean estimated survival from Lower Granite Dam tailrace to McNary Dam tailrace ranged from a low of 0.533 for hatchery steelhead in 2002 to a high of 0.746 for wild fish in 1999 (Table 29). In 2001, mean estimated survival was very low: 0.170 for hatchery steelhead and 0.168 for wild. Over the 5 years (excluding 2001), average estimated survival was 0.606 for hatchery and 0.670 for wild steelhead.

Table 29. Estimated survival from Lower Granite Dam tailrace to McNary Dam tailrace and from McNary Dam tailrace to Bonneville Dam tailrace for hatchery and wild steelhead, 1998–2003. Standard errors are in parentheses. Simple arithmetic means across all years are given.

	Lower Granite to McNary		McNary to Bonneville
Year	**Hatchery**	**Wild**	**Hatchery + wild pooled**
1997	0.728 (0.053)*		0.651 (0.082)
1998	0.644 (0.015)	0.698 (0.030)	0.770 (0.081)
1999	0.673 (0.019)	0.746 (0.019)	0.640 (0.024)
2000	0.574 (0.038)	0.714 (0.028)	0.580 (0.047)
2001	0.170 (0.013)	0.168 (0.010)	0.250 (0.016)
2002	0.533 (0.045)	0.593 (0.039)	0.488 (0.090)
2003	0.606 (0.028)	0.597 (0.022)	0.510 (0.015)
Mean			
All years	0.533 (0.075)	0.586 (0.087)	0.540 (0.071)
Excluding 1997 and 2001	0.606 (0.025)	0.670 (0.031)	0.598 (0.051)

* Hatchery and wild pooled; data insufficient to estimate separately.

Data were not sufficient to estimate survival from McNary Dam to Bonneville Dam for any Snake River steelhead until 1997. From 1997 to 2003 data were sufficient to estimate survival from McNary Dam tailrace to Bonneville Dam tailrace for pooled hatchery and wild groups, but not for the rearing types separately. Annual average estimates ranged from 0.250 in 2001 to 0.770 in 1998 and averaged 0.540 for the 7 years (Table 29). Estimated survival between McNary Dam tailrace and Bonneville Dam tailrace was lower in all 3 years from 2001 to 2003 than in any year from 1997 to 2000.

Annual average survival estimates

For steelhead (hatchery and wild combined), estimated survival through the hydropower system, from the Snake River trap at the head of Lower Granite Reservoir to the Bonneville Dam tailrace through eight mainstem dams and reservoirs, ranged from a low of 0.038 in the 2001 low-flow conditions of to 0.462 in 1998 (Table 30).

Comparison of wild and hatchery steelhead

Wild steelhead had slightly higher survival than hatchery-reared fish between the Lower Granite Dam tailrace and the McNary Dam tailrace, through four dams and reservoirs (Table 29). For steelhead, estimated survival through this reach averaged about 5% higher for wild fish compared to hatchery origin, with wild steelhead survival higher in 4 of the 6 years (Table 29).

Upper Columbia River steelhead survival

Fewer years of PIT-tag data exist for fish stocks from the upper Columbia River basin than for those in the Snake River basin. Nonetheless, the data indicate that juveniles migrating from the two basins under normal flow conditions have similar survival (Table 31 compared to Tables 29 and 30). This was not the case in the 2001 low-flow year. Fish from the upper Columbia River had higher estimated survival to the McNary Dam tailrace (hatchery releases) and sometimes

Bonneville Dam tailrace (dam releases) than did fish from the Snake River. A spill program existed at upper Columbia River dams in 2001, but not at Snake River dams, possibly explaining some of the difference in survival. For fish released at dams, a stock effect may also have played a part.

Table 30. Hydropower system survival estimates derived by combining empirical survival estimates from various reaches for Snake River steelhead (hatchery and wild combined), 1997–2003. Standard errors are in parentheses.

Year	Snake River trap to Lower Granite Dam	Lower Granite Dam to Bonneville Dam	Snake River trap to Bonneville Dam
1997	0.964 (0.015)	0.474 (0.069)	0.457 (0.067)
1998	0.924 (0.009)	0.500 (0.054)	0.462 (0.050)
1999	0.908 (0.011)	0.440 (0.018)	0.400 (0.016)
2000	0.964 (0.013)	0.393 (0.034)	0.379 (0.032)
2001	0.911 (0.007)	0.042 (0.003)	0.038 (0.003)
2002	0.895 (0.015)	0.262 (0.050)	0.234 (0.045)
2003	0.932 (0.015)	0.309 (0.011)	0.288 (0.011)
Mean			
All years	0.928 (0.010)	0.346 (0.060)	0.323 (0.057)
Excluding 2001	0.931 (0.012)	0.396 (0.038)	0.370 (0.038)

Table 31. Survival estimates for upper Columbia and Yakima rivers steelhead.

Year	Release site[a]	No. of fish	Release site to McNary Dam		McNary Dam to John Day Dam		McNary Dam to Bonneville Dam	
Hatchery summer steelhead								
1999	Above Rock Island Dam	134,251	0.616	(0.013)	1.016	(0.013)	–	–
2000	Above Rock Island Dam	63,227	0.607	(0.009)	0.861[b]	(0.059)	–	–
2001	Above Rock Island Dam	4,029	0.203	(0.029)	0.535	(0.146)	0.178	(0.078)
2002	Above Rock Island Dam	3,623	0.529	(0.107)	1.119	(0.168)	0.856	(0.349)
2003	Above Rock Island Dam	39,1203	0.447	(0.014)	1.027	(0.025)	0.800	(0.042)
Wild summer steelhead								
1999	Rock Island Dam	1,156	0.635	(0.055)	1.103	(0.148)	–	–
2000	Rock Island Dam	1,200	0.679	(0.102)	0.873	(0.224)	–	–
2001	Rock Island Dam	1,174	0.211	(0.022)	0.304	(0.082)	–	–
2002	Rock Island Dam	1,200	0.623	(0.063)	0.680	(0.125)	–	–
Wild spring-summer steelhead (Yakima)								
1999	Lower Yakima	1,241	0.798	(0.033)	0.967	(0.099)	–	–
2002	Lower Yakima	1,335	0.314	(0.054)	0.924	(0.302)	0.560	(0.585)
2003	Lower Yakima	575	0.394	(0.099)	0.860	(0.359)	–	–

[a] In the upper Columbia River, hatchery fish were released upstream of Rock Island Dam (designated "Above Rock Island Dam"), and wild fish were released at Rock Island Dam. In the Yakima River, fish released downstream of Roza Dam are designated "Lower Yakima."

[b] Includes data from Bickford et al. (2001).

Snake River sockeye salmon survival

We have much less information about Snake River sockeye salmon (*Oncorhynchus nerka*) than for Snake River Chinook salmon and steelhead. Although the sample sizes were small, and consequently survival estimates were imprecise, by pooling all PIT-tagged sockeye salmon smolts detected and returned to the Lower Granite Dam tailrace each year, we could estimate survival between Lower Granite and McNary dams from 2000 to 2003 (Table 32). In 2003, estimated survival for sockeye smolts was similar to that for yearling Chinook salmon, but in the other 3 years estimated sockeye salmon survival was considerably lower (see Table 21).

The experience of PIT-tagged fish does not represent that of the untagged population, however. As with Chinook salmon, most untagged sockeye salmon smolts were collected and transported to below Bonneville Dam. Nonetheless, few adult sockeye salmon returned to Lower Granite Dam from 1990 to 2003. The median annual return was 13 (range 3 to 282). Low numbers of returning adults suggest that transportation provides little if any benefit to Snake River sockeye salmon. Moreover, based on PIT-tag data, the alternative of in-river migration looks poor.

Table 32. Survival estimates for sockeye salmon smolts PIT tagged and released upstream from Lower Granite Dam. All smolts detected and returned to the Lower Granite Dam tailrace in each year were pooled into one group. Standard errors are in parentheses.

Year	No. of smolts	Lower Granite Dam to Little Goose Dam	Lower Granite Dam to Lower Monumental Dam	Lower Monumental Dam to McNary Dam	Lower Granite Dam to McNary Dam
2000	496	0.902 (0.131)	0.703 (0.138)	0.884 (0.251)	0.560 (0.142)
2001	610	0.760 (0.053)	0.504 (0.087)	0.623 (0.275)	0.239 (0.099)
2002	262	0.819 (0.100)	0.832 (0.144)	0.584 (0.142)	0.397 (0.085)
2003	679	0.838 (0.039)	1.044 (0.116)	0.829 (0.164)	0.725 (0.122)

Probability of Detecting PIT-Tagged Fish Versus Length at Tagging

We analyzed data from over 340,000 PIT-tagged fish in nine release groups. Detection probability was clearly related to fish length for all release groups. The model selection process chose length relationships in 21 out of 24 year/site combinations (Figures 25 and 26). In 20 out of 21 cases where a length relationship was selected, the length coefficient α_l was negative, indicating that smaller fish had a higher probability of detection.

When we compared the two methods for estimating population survival, we found a high level of correlation and little evidence for bias (Figure 27). Comparing method 1 to method 2, the survival estimates produced by the two methods were very highly correlated (r = 0.999) and method 1 produced survival estimates that averaged 0.02% lower than method 2.

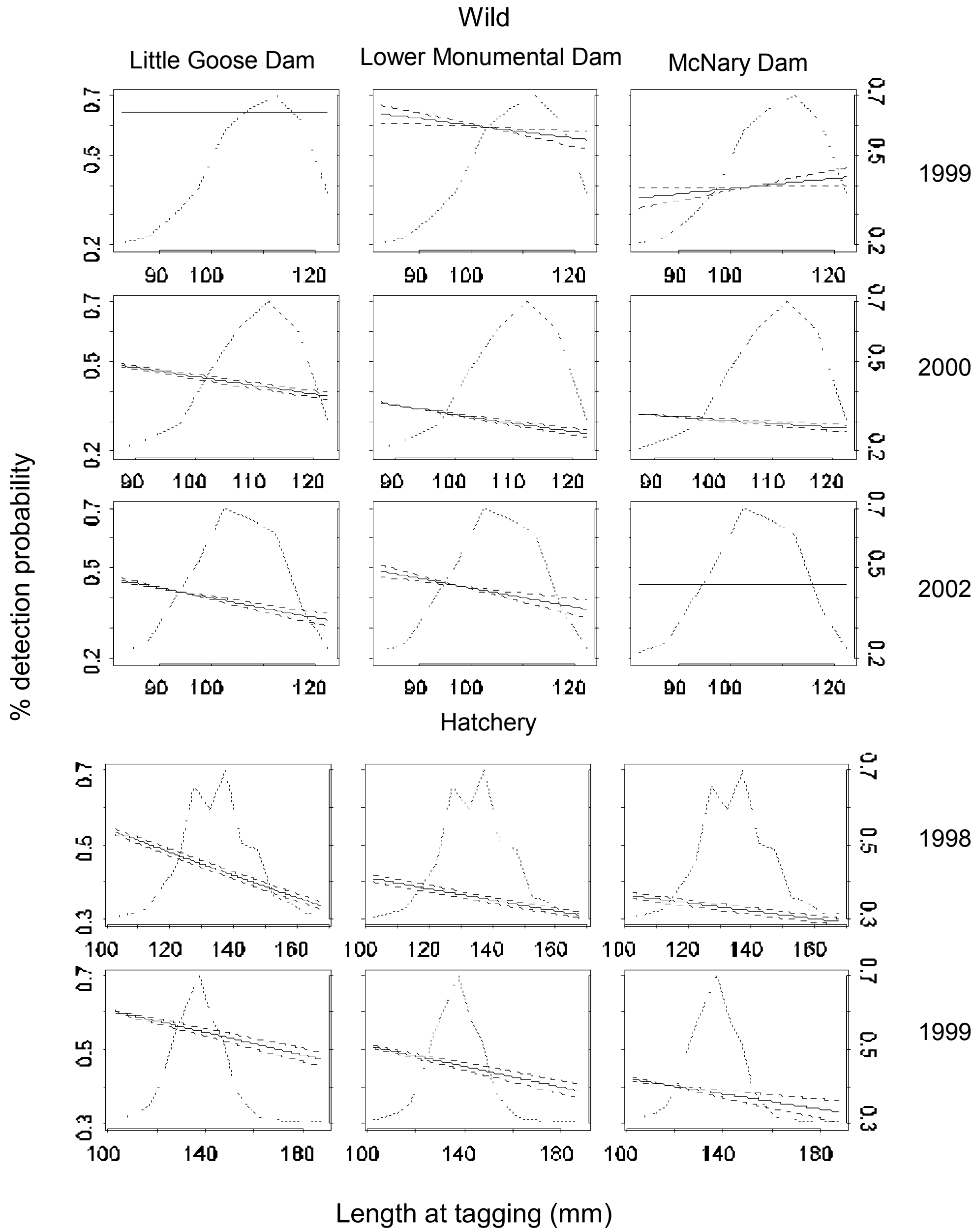


Figure 25. Relationships between detection probability (solid line) and fish length (mm) for Snake River spring-summer Chinook salmon released at Lower Granite Dam. Dashed lines represent approximate 95% confidence intervals. Nonsignificant relationships do not have confidence intervals plotted. Dotted lines are the scaled distribution of lengths in 5-mm increments.

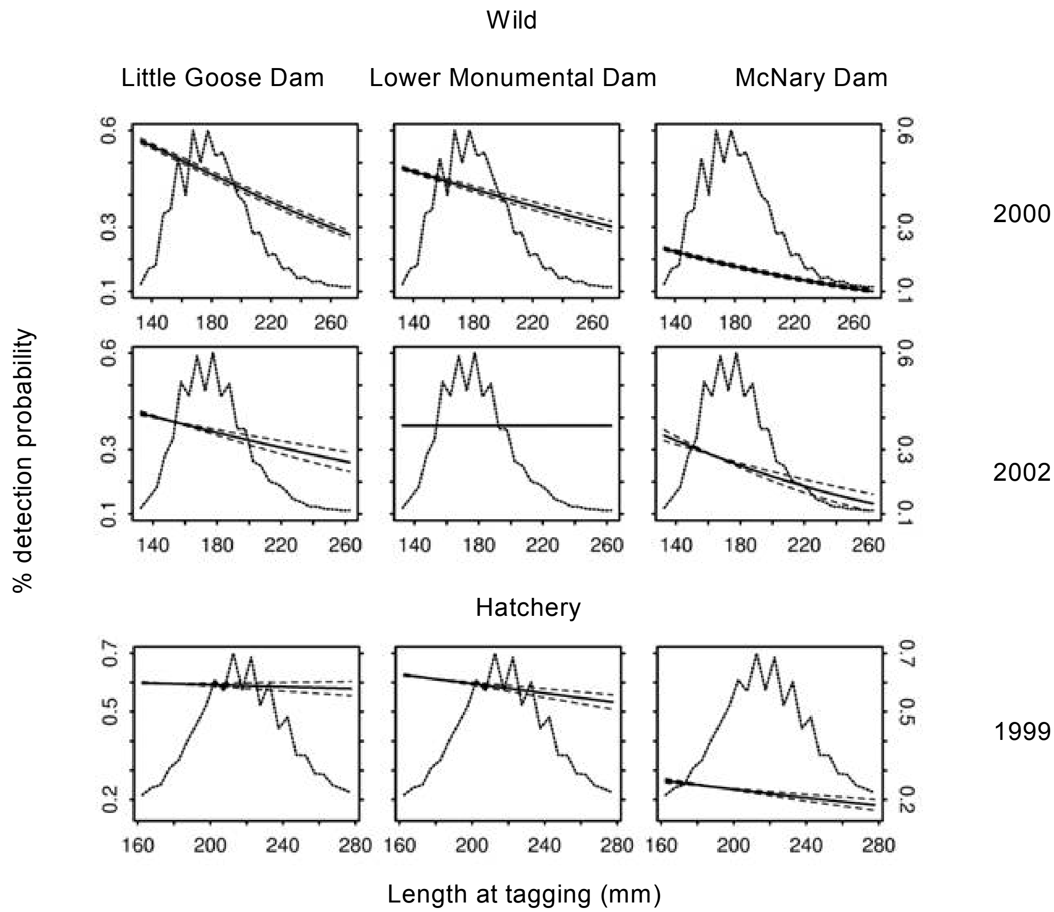


Figure 26. Relationships between detection (solid line) probability and fish length (mm) for Snake River steelhead released at Lower Granite Dam. Dashed lines represent approximate 95% confidence intervals. Nonsignificant relationships do not have confidence intervals plotted. Dotted lines are the scaled distribution of lengths in 5-mm increments.

Discussion

Probability of Detecting PIT-Tagged Fish Versus Length at Tagging

This analysis clearly demonstrated a negative relationship between detection probability and fish length for juvenile Snake River spring-summer Chinook salmon and Snake River steelhead. Thus bypassed fish did not represent a random sample of the migrant population. Fortunately, this relationship did not appear to bias CJS model survival estimates. However, the results do call into question the conclusion of Budy et al. (2002) that passage through bypass systems results in delayed mortality (this is discussed in greater detail in the "Latent Mortality" subsection, page 106). Also, the results have implications for transportation studies. Transported and in-river control fish (nondetected fish) may represent different population segments, which might partially explain the relatively poor performance of transported fish. Detailed analyses of detection probability by tagging length is needed in the future.

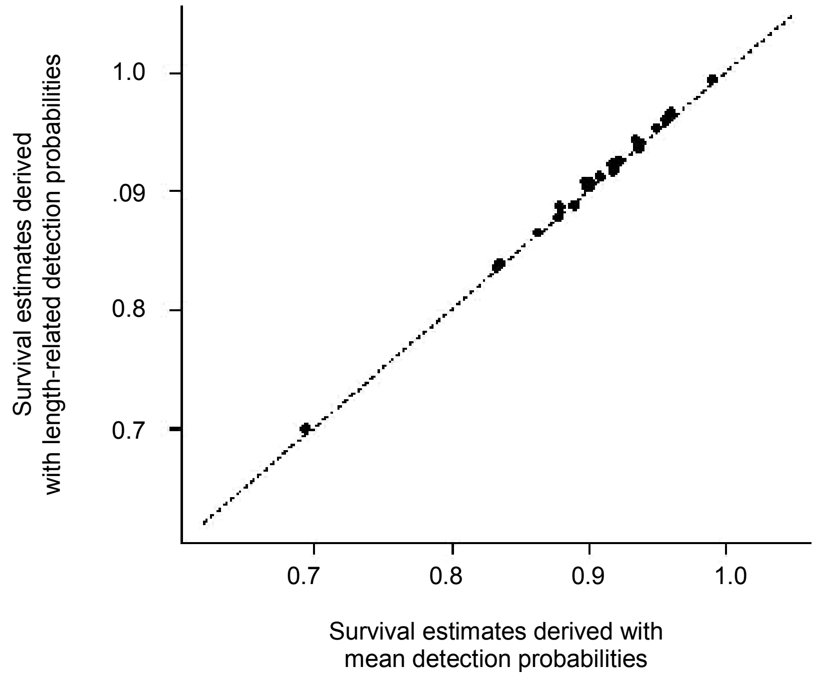


Figure 27. Comparison of survival estimates derived assuming mean detection probabilities (Cormack-Jolly-Seber method) and those using length-related detection probabilities. Wild and hatchery spring-summer Chinook salmon and steelhead were tagged and released at Lower Granite Dam (1998–2002), and survival was estimated from Lower Granite to Little Goose Dam, Little Goose to Lower Monumental Dam, and Lower Monumental to McNary Dam. The dashed line is the one-to-one line.

Avian Predation

All PIT-tagged fish from the Snake River that survived to the McNary pool were subject to predation by piscivorous birds residing on various islands, including Caspian terns, double-crested cormorants, gulls, and pelicans. The bird colony locations included but were not limited to Richland Island, Island 18, Foundation Island, Badger Island, and Crescent Island. All of these islands are located in the McNary Dam reservoir, mostly above the confluence with the Snake River. Predation also occurred from birds residing in various locations below McNary Dam to the mouth of the Columbia River and much of this information is contained in Fresh et al. (in press).

Beginning in 1998, NOAA Fisheries Service researchers began visiting bird colonies after the end of the nesting season and scanning for PIT tags. The recovery data are available from the PTAGIS database (PSMFC 2004). To investigate avian predation from bird colonies in the McNary Dam pool, the most valuable information is an estimate of the proportion of fish entering the pool that were taken by piscivorous birds. However, we have no PIT-tag estimates of survival to the head of McNary Dam pool. Instead, for Snake River fish we calculated the proportion of PIT-tagged fish that were detected as they passed Lower Monumental Dam whose tags were later detected on a bird colony. For fish from the upper Columbia River, we calculated the proportion of entire hatchery releases recovered on bird colonies. We also obtained records from PIT-tagged smolts if the tag was deposited on a colony and in such a way that it was detectable. Thus these proportions constitute minimum estimates of mortality from bird predation. When compared across fish cohorts or years, the proportions represent a relative impact index.

Between 1998 and 2003, the greatest avian predation apparently occurred in the low-flow year 2001 (Table 33), a year in which over 10% of PIT-tagged steelhead released in the upper Columbia River and more than 20% of PIT-tagged steelhead detected at Lower Monumental Dam were later recovered on bird colonies. However, PIT-tagged fish made up a much larger portion of all Snake River fish that remained in the river below Lower Monumental Dam; without spill, a higher percentage of nontagged fish were transported. Thus the total number of salmonid smolts taken by avian predators in 2001 was probably not as elevated as suggested by these proportions. Nonetheless, as the survival estimates presented in the "Results" subsection (page 51) are based on these PIT-tagged fish, increased avian predation on PIT-tagged fish is a partial explanation of the low estimates we obtained in 2001.

Snake River steelhead were taken by birds in much larger proportions than Snake River yearling Chinook salmon. Recovery proportions for upper Columbia River stocks were lower than for Snake River stocks, but this is partly because the release group numbers do not take into account mortality from the release site to the head of the McNary Dam reservoir (wide range in values of survival from release site to McNary Dam). If mortality averaged 50% to McNary Dam, doubling these recovery proportions, then avian predators had similar effects on upper Columbia River fish.

Table 33. Recovery percentages of PIT-tagged steelhead recovered from McNary pool bird colonies. Percentages are based on the number of fish detected at Lower Monumental Dam for Snake River fish and numbers released for upper Columbia River fish.

Year	Snake River yearling Chinook salmon	Snake River steelhead	Upper Columbia River steelhead
1998	0.49	4.20	NA
1999	0.84	4.51	1.92
2000	0.98	3.66	2.36
2001	5.59	21.06	11.49
2002	1.19	10.09	3.81
2003*	1.06	3.71	1.34

* Crescent Island Caspian tern colony was the only site sampled.

Juvenile Survival, Travel Time, and River Environment

Methods

Snake River Spring Migrants

Smith et al. (2002b) investigated relationships among survival, travel time, and river conditions for migrant yearling Chinook salmon and steelhead in the lower Snake River. They analyzed data from PIT-tagged juveniles migrating through the river segment between the Lower Granite and McNary Dam tailraces in the 1995 through 1999 migration seasons. Other researchers have conducted similar analyses to evaluate effects of these variables on salmonid survival and commented on the approaches (see NPPC 2003 and USFWS 2003).

The following is not intended as a comprehensive update of the findings of Smith et al. (2002b), nor as a comprehensive response to the documents noted above, which were submitted to the Northwest Power Planning Council, Portland, Oregon. Instead, we address selected issues concerning the relations of survival and travel time with river conditions that arose after the 1999 migration season. In particular, incorporating observations from the low-flow year 2001 sheds light on how salmonids respond to conditions not observed before PIT-tag data became available. In the discussion that follows, we note when additional years of data did not alter previous conclusions and we describe instances when new information suggests new hypotheses to explain patterns.

As described in earlier sections, we used fish PIT tagged above and at Lower Granite Dam for migration years 1999 to 2003. We developed survival estimates as described in the "Juvenile Migrant Survival" section (page 46).

Median travel time

Travel times were calculated for yearling Chinook salmon and steelhead for the following reaches:

1) Lower Granite Dam to Little Goose Dam (60 km),
2) Little Goose Dam to Lower Monumental Dam (46 km),
3) Lower Monumental Dam to McNary Dam (199 km),
4) Lower Granite Dam to McNary Dam (225 km),
5) Lower Granite Dam to Bonneville Dam (461 km),
6) McNary Dam to John Day Dam (123 km),
7) John Day Dam to Bonneville Dam (113 km), and
8) McNary Dam to Bonneville Dam (236 km).

Travel time between any two dams was calculated for each fish detected at both dams as the number of days between last detection at the upstream dam (generally at a PIT-tag detector close enough to the outfall site that fish arrived in the tailrace within minutes after detection) and first detection at the downstream dam. Travel time included the time required to move through the reservoir to the forebay of the downstream dam and any delay associated with residence in the forebay, gatewells, or collection channel prior to detection in the juvenile bypass system.

Migration rate through a river section was calculated as the length of the section (km) divided by the travel time (days), which included any delay at dams as noted above.

For each group, we determined the 20th percentile, median, and 80th percentile travel times and migration rates. The true, complete set of travel times for a release group includes travel times of both detected and nondetected fish. However, using PIT tags, travel times cannot be determined for a fish that traverses a river section but is not detected at both ends of the section. Travel time statistics are computed only from travel times for detected fish, which represent a sample of the complete set. Nondetected fish pass dams via turbines and spill; thus their time to pass a dam is typically minutes to hours shorter than fish detected passing to the tailrace via the juvenile bypass system.

River environment variables

We used the methods of Smith et al. (2002b) to calculate indices of exposure to various river conditions, including river discharge (flow in thousands of cubic feet per second [kcfs]), percentage of flow that passes over spillways, and water temperature (°C). Indices were calculated at Little Goose, Lower Monumental, and McNary dams for each release group, based on its detection distribution at each dam.

In analyses of relations between survival and travel time and indices of exposure for data from 1995 through 1999, Smith et al. (2002b) used only the indices calculated for Lower Monumental Dam, after confirming that spill, temperature, and flow levels were very similar between Little Goose and Lower Monumental dams. Levels of these variables remained similar for data collected from 2000 through 2003, with the exception of spill percentage in 2002. The analyses reported here continue the use of Lower Monumental Dam indices for temperature and flow (but see next paragraph). In all years from 1995 through 2003 except 2002, spill percentages at Lower Monumental and Little Goose dams were sufficiently similar that the index for one dam served to represent conditions at both. This was not true in 2002 because spill continued at customary levels at Little Goose Dam, but there was little spill at Lower Monumental Dam in April and May. For spill percentage in the analyses reported here, we used the mean of the indices calculated for the two dams. Though a more refined index is possible, we felt that the mean, which tended to be about half the spill percentage index in most other years, was a reasonable representation of migration through the system, which provided spill at only one of the two dams in 2002.

The Fish Passage Center analyzed flow travel time for juvenile migrants and concluded that exposure to water velocity was likely more important to an individual migrant's response than exposure to flow volume (DeHart et al. 2003). Accordingly, in addition to the indices used in Smith et al. (2002b), the analyses in this section include a variable to reflect water travel time

(WTT). We derived our approximate WTT variable from the flow exposure indices at Lower Monumental and McNary dams and from Figures 1 and 2 of the Fish Passage Center's 2002 annual report (FPC 2003b, DeHart et al. 2003). For each daily release group from Lower Granite Dam, we calculated WTT days from Lower Granite Dam to Ice Harbor Dam using the exponential decay equation (Figure 1 from DeHart et al. 2003)

$$28.97e^{-0.02148 f_1} + 3.160 \tag{7}$$

where f_1 is the flow exposure index (kcfs) at Lower Monumental Dam, and from Ice Harbor Dam to McNary Dam using the equation (Figure 2 from DeHart et al. 2003)

$$12.12e^{-0.008776 f_2} + 1.232 \tag{8}$$

where f_2 is the flow exposure index (kcfs) at McNary Dam. The total WTT for each group was the sum of these two components.

Mortality per day versus water travel time

To investigate interactions among the relations of travel time, survival, and WTT, we calculated the following quantity for each release group from Lower Granite Dam:

$$\text{Mort. per Day} = 1 - \hat{S}^{(1/TT)} \tag{9}$$

and examined its relationship to WTT ($\hat{S}$ and TT are the group's estimated survival probability and median travel time from Lower Granite Dam to McNary Dam, respectively). For example, if fish travel time was positively related to WTT, but reach survival was not, then the mortality per day must decrease as WTT and fish travel time increase. Conversely, if mortality per day is constant, then a positive relationship between WTT and fish travel time would result in a positive relationship between reach survival and WTT, independent of any other flow-related effects on survival.

Threshold models for survival versus flow

As Smith et al. (2002b) observed, survival estimates varied little within seasons when the flow level was moderate to high. After accounting for differences in annual means, Smith et al. (2002b) found no relation between 1995–1999 survival estimates and flow exposure for yearling Chinook salmon, and only a weak relation for steelhead.

With additional years of data, the lowest survival estimates were observed in the lowest flow year, 2001. Along with the recognition that zero survival would likely result if flow were zero, and with the observation of little or no relation between flow and survival at moderate to high flow levels, the 2001 data suggest that a "threshold effect" may exist. That is, there may be a flow level above which survival has little variability, but below which survival decreases with decreasing flow.

We have no hypothesized mechanism to suggest a theoretical basis for the exact "shape" of such a threshold relation (although we recognize that WTT might relate to such a mechanism).

However, we explored two mathematical forms that might describe the relationship: a sigmoid curve and a piecewise linear regression line.

The sigmoid curve had the following equation form (Boltzmann sigmoid):

$$Y = Bottom + \frac{(Top - Bottom)}{1 + e^{(V50 - X)/Slope}} \tag{10}$$

where X and Y were the independent (flow exposure index) and dependent (estimated survival) variables, respectively, and Top, Bottom, V50, and Slope were parameters we estimated. A sigmoid curve is S shaped: assuming positive Slope, the curve rises from low to high values of X and Y, with relatively shallow slope at low and high ends of the range of X values, and steeper slope in the intermediate range. The Bottom and Top parameters are the minimum and maximum Y values on the curve, respectively. The V50 parameter is the X value for which Y is halfway between Bottom and Top, and Slope describes the steepness of the curve, with larger values denoting a shallower curve. We used this form for estimated survival only. In these models, the Bottom parameter was always set equal to 0.0.

The selected piecewise linear regression model was the one that minimized sum of squared error among models with the following properties: linear relationship between flow exposure and estimated survival when the exposure was below the threshold and no relationship when the exposure was above the threshold (survival constant, equal to the fitted value of the linear regression line at the threshold flow value). Selection of the threshold, or break point, was part of the least-squares optimization.

Both the sigmoid curve and the piecewise linear-regression model were fitted using unweighted least squares. For the piecewise linear fit, we used bootstrap methods to characterize uncertainty in estimation of maximum survival, slope below the threshold, and most importantly, the threshold.

Generalized additive and multiple-regression models

We explored multiple-regression (analysis of covariance) models that included year-effects variables and two or more quantitative environmental variables. Because the independent variables were correlated with each other, and because some relations had notable nonlinearity, we checked multiple-regression models using the generalized additive model (gam) function of S-Plus (MathSoft 2000), a nonparametric multiple-regression technique. The nonparametric splines calculated in the gam function were used to suggest parametric curve functions (polynomials) to use in parametric multiple-regression models. Resulting multiple-regression models were rejected if graphic inspection of residuals revealed remaining nonlinearity or notable lack of normality. Partial fits of predictor variables from the generalized additive models were plotted without vertical axis labels. All variables in a gam model, and therefore the vertical axis in partial fit plots, are transformed and scaled, making direct interpretation of units impossible. Relative influence of individual predictor variables can be gauged by the relative range of the partial fit functions, and the shape of the nonlinear relation between predictor and dependent variable can be seen.

All gam and multiple-regression models for survival estimates were weighted by respective inverse relative variances (inverse of coefficient of variation squared) of the survival estimates. Multiple-regression models for travel time were unweighted.

Run-of-River Subyearling Chinook Salmon from McNary Dam

Study groups of PIT-tagged migrants

In 1999 through 2002, we collected run-of-river subyearling Chinook salmon (mostly wild fish from the Hanford Reach) at McNary Dam, PIT tagged them, and released them. Study designs and release sites varied from year to year, but we included a series of releases into the McNary Dam tailrace each year. For this analysis, we combined individual (daily) release groups of subyearling Chinook salmon into McNary Dam tailrace into weekly groups for 1999 to 2002 (Table 34).

Table 34. Numbers of run-of-river subyearling Chinook salmon (mostly wild fish from the Hanford Reach) collected and tagged at McNary Dam and released in the McNary Dam tailrace, 1999–2002.

Release dates	1999	2000	2001	2002
19–25 June	3,704	5,102	6,089	4,156
26 June–02 July	8,146	5,045	7,511	5,468
03–09 July	6,267	5,138	3,814	5,655
10–16 July	9,195	5,038	6,935	3,703
17–23 July	5,692	3,100	5,703	9,710
24–30 July	–	–	8,494	10,675
31 July–06 August	–	–	–	5,328
07–13 August	–	–	–	8,001
14–20 August	–	–	–	3,664

Travel time and survival estimates

For all fish detected at John Day Dam, we calculated the time (days) from release at McNary Dam to first detection at John Day Dam. Then for each weekly group we calculated the median travel time (days). We constructed detection histories for each weekly pooled group and used the SR model to calculate survival estimates from release to John Day Dam. Detection histories were only two digits long, indicating detection at and below John Day Dam (Bonneville Dam in all years and estuary trawl in 2002).

River environment variables

We calculated indices of exposure to the following river condition variables: river discharge (flow in kcfs); amount of flow over spillways (kcfs); percentage of flow that passed over spillways; water temperature (°C); and water clarity (Secchi disk reading). We obtained daily values for each of these variables from the DART web site (CBR UW 2004). In a few cases, we interpolated data for days when it was missing or obviously incorrect (e.g., Secchi disk reading of 0 between 2 days that each had readings of 5 m). We calculated indices of exposure at McNary Dam for each weekly group as the averages of the respective daily values at McNary Dam during the week of release. For John Day Dam, exposure indices were based on the group's distribution of detections at the dam. For each weekly release group we tabulated John Day detections by day, then determined the days on which the 25th and 75th percentiles of passage occurred. The John Day Dam exposure indices were the averages of the respective daily values at John Day Dam between the dates of the 25th and 75th percentiles (inclusive).

We used various graphical methods, pairwise product-moment correlations, and simple and multiple linear regression modeling to explore relations among indices of exposure to selected environmental factors and survival and travel time. Because of concomitant temporal trends in river conditions, exposure indices for release groups of PIT-tagged fish were generally highly correlated with each other and with release dates. Correlation of such magnitude among predictor variables generally makes it very difficult for multivariate statistical methods to distinguish the relative importance of the predictors' influence on the response variable. Nonetheless, we explored bivariate patterns and used multivariate methods to shed light on relations. Samples were of sufficient size that correlations with relatively little explanatory power (e.g., $r^2 = 0.16$) were statistically significant ($P < 0.05$). One response to this is to lower the level required to declare a correlation significant. Our approach, however, was simply to focus on the amount of variability in the response variable that is "explained" by variability in the predictor (i.e., the r^2 value).

In some regression models of data from multiple years, we used variables for "year effects" to account for differences in annual mean survival and travel time potentially not captured by the environmental variables. We also calculated "adjusted" predictor and response variables by subtracting the respective overall means from each unadjusted variable. Correlation between adjusted predictor and adjusted response would indicate a within-season relationship between the variables beyond differences in annual means. However, lack of correlation between adjusted variables could occur if there was no within-season relationship, or if differences in annual means of travel time or survival (annual effects) were due to year-to-year differences in the predictor variable and the within-year ranges of the predictor variable did not overlap sufficiently.

Results

Snake River Yearling Chinook Salmon

Travel time versus flow and water travel time

Except for the low flow year of 2001, the annual median travel time (days) for all PIT-tagged Snake River spring-summer Chinook salmon passing between Lower Granite and Bonneville dams from 1 April to 31 May each year varied by only a few days (Table 35). Based on earlier data derived from Raymond (1979), these times were approximately 40–50% longer than when no dams existed in the mainstem Snake and Columbia rivers (Figure 28).

Table 35. Median travel time (days) of PIT-tagged yearling Chinook salmon between Lower Granite Dam and Bonneville Dam, 1995–2003.

Year	Median travel time (days)
1995	18.4
1996	16.2
1997	14.1
1998	19.0
1999	16.1
2000	16.4
2001	31.0
2002	16.9
2003	14.4

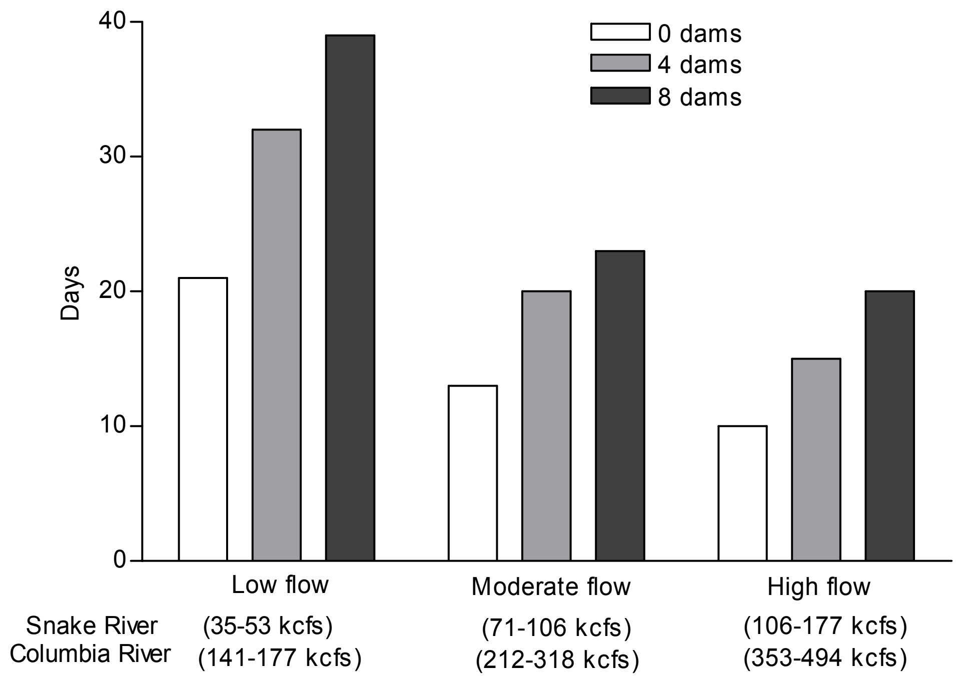


Figure 28. Estimated annual average travel times for yearling Chinook salmon through the section of the lower Snake and Columbia rivers now inundated by mainstem hydropower dams (approximately from Lewiston, Idaho, to Bonneville Dam tailrace). Estimates for the 0- and 4-dam scenarios are derived after data in Raymond (1979). Data for 8 dams were derived from PIT-tagged fish between 1997 and 2003.

Within individual years, median travel time for groups of PIT-tagged yearling Chinook salmon has generally decreased throughout the migration season as flows have generally increased (Figure 29) and as WTT has decreased (Figure 30). However, water velocity is clearly not the only driver of travel time in all years: in 1998, and especially in 2002 and 2003, the early part of the migration season featured relatively long periods of nearly constant flow. In these years, nonetheless, median travel times for yearling Chinook salmon decreased throughout the period, even without change in flow. This result suggests that physiological characteristics of juvenile fish (possibly degree of smoltification) or physiological responses to day length or moon phase might have influenced migration rates more than flow.

As in Smith et al. (2002b), this observation is supported by the partial fits for a generalized additive model of travel time that included year effects and nonparametric splines for date and flow (Figure 31). This model indicated that flow had a nearly linear effect on travel time throughout the range of observed flow exposures, but that release date had more influence early in the season, until about the end of April. A generalized additive model using the WTT index gave essentially the same information.

Survival and mortality versus water travel time

Smith et al. (2002b) found that the relationship between flow exposure and survival of yearling Chinook salmon within seasons was generally weak and inconsistent. Translating the flow exposure measures into a WTT index resulted in qualitatively similar results (Figure 32). Significant ($\alpha = 0.05$) negative slopes (increased WTT related to decreased survival) occurred for data within the 1998, 2000, and 2003 seasons; the R^2 was 35% in 2003 and 11% in the other 2 years. Results in 2001 depended on whether the analysis was weighted according the relative precision of the estimates.

Including all years in an unweighted analysis resulted in a significant regression (Figure 33). Data from 2001 were highly influential in this result; excluding 2001 data resulted in a slightly negative but not significant slope and no predictive value (see subsections below on threshold models, multiple regression, and discussion of 2001, pages 84–88).

For years other than 2001, estimated mortality per day tended to decrease with increasing WTT (bottom panel, Figure 34). Data from 2001 stood apart from data from other years (top panel, Figure 34) and appeared to indicate two distinct sets of release groups. See the “Snake River Spring Migrants” subsection (page 101), for discussion of this pattern.

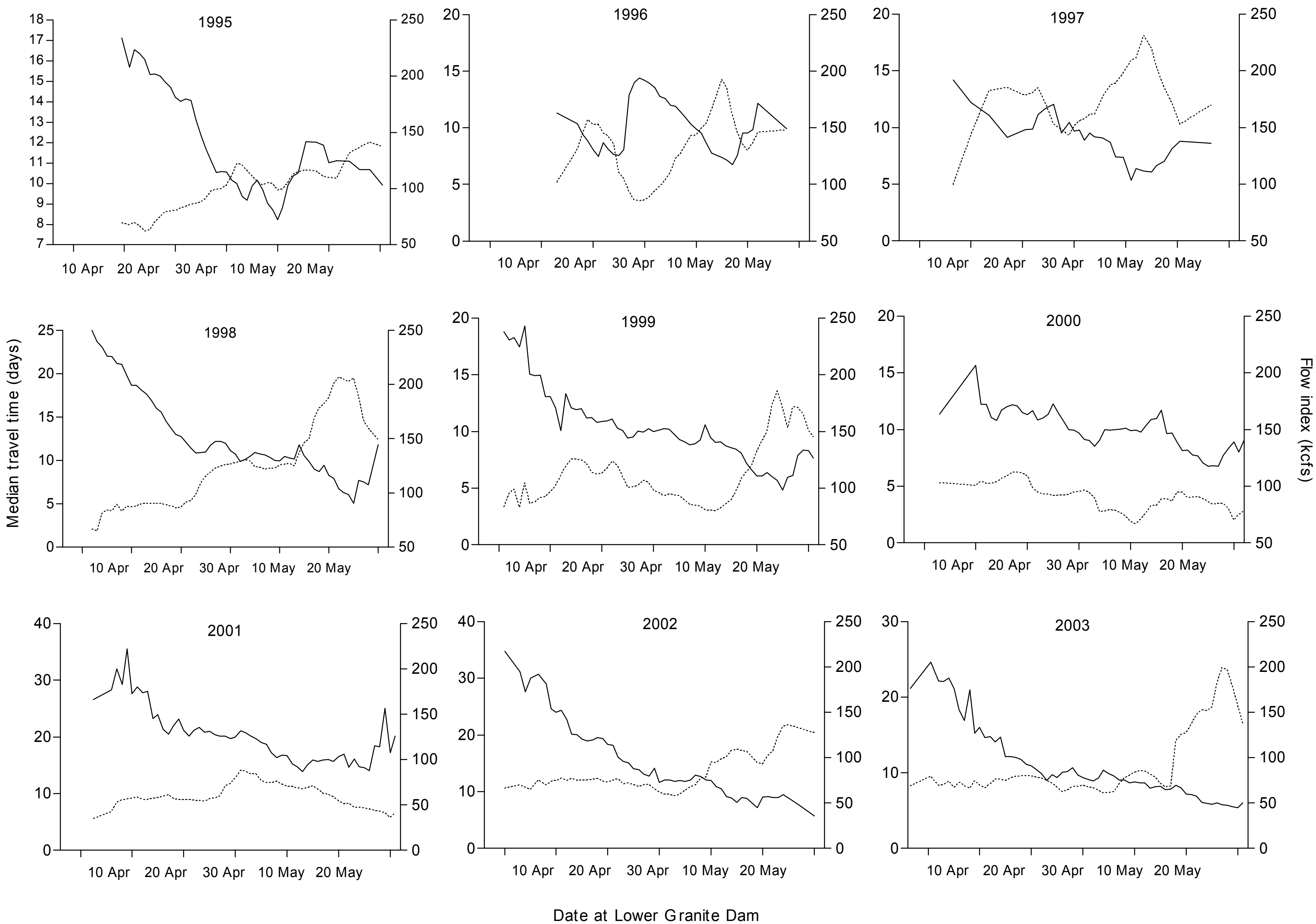


Figure 29. Median travel time (solid line) and flow exposure index (dotted line) for PIT-tagged Snake River yearling Chinook salmon groups, 1995–2003.

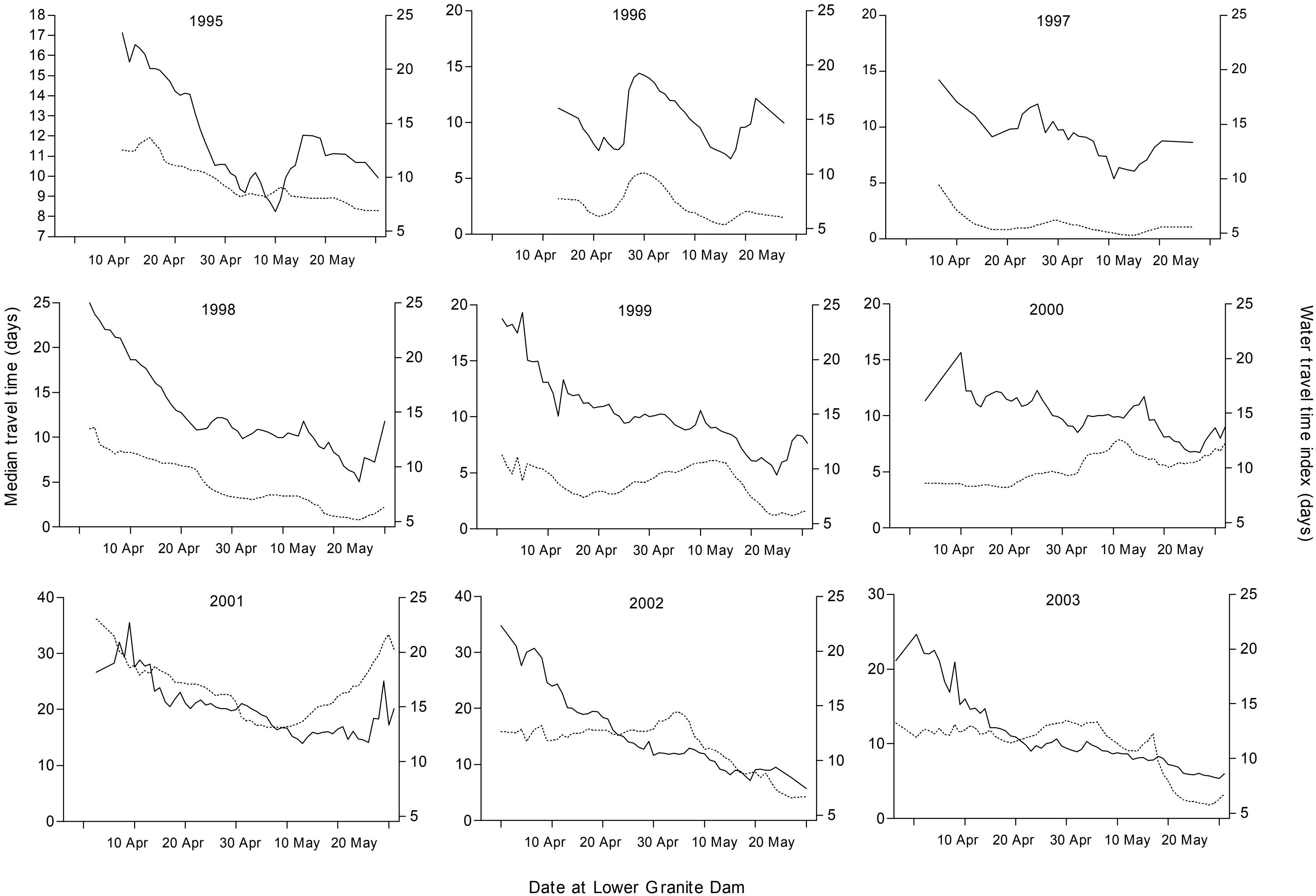


Figure 30. Median travel time (solid line) and water travel time (dotted line) for PIT-tagged Snake River yearling Chinook salmon groups, 1995–2003.

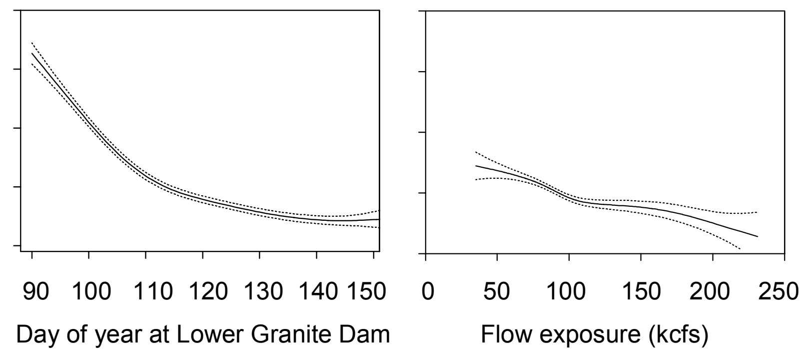


Figure 31. Partial fits for generalized additive model of median travel time from Lower Granite Dam to McNary Dam (days), with pointwise 95% confidence intervals, yearling Chinook salmon, 1995–2003. Predictor variables were release dates from Lower Granite Dam, flow exposure index (kcfs), and year effects. Because all variables were transformed, Y-axis units are not meaningful. Relative influence on travel time is judged by relative ranges of transformed predictor variables, which are all plotted with the same Y-axis scale. Shape of the relationship is judged by the spline.

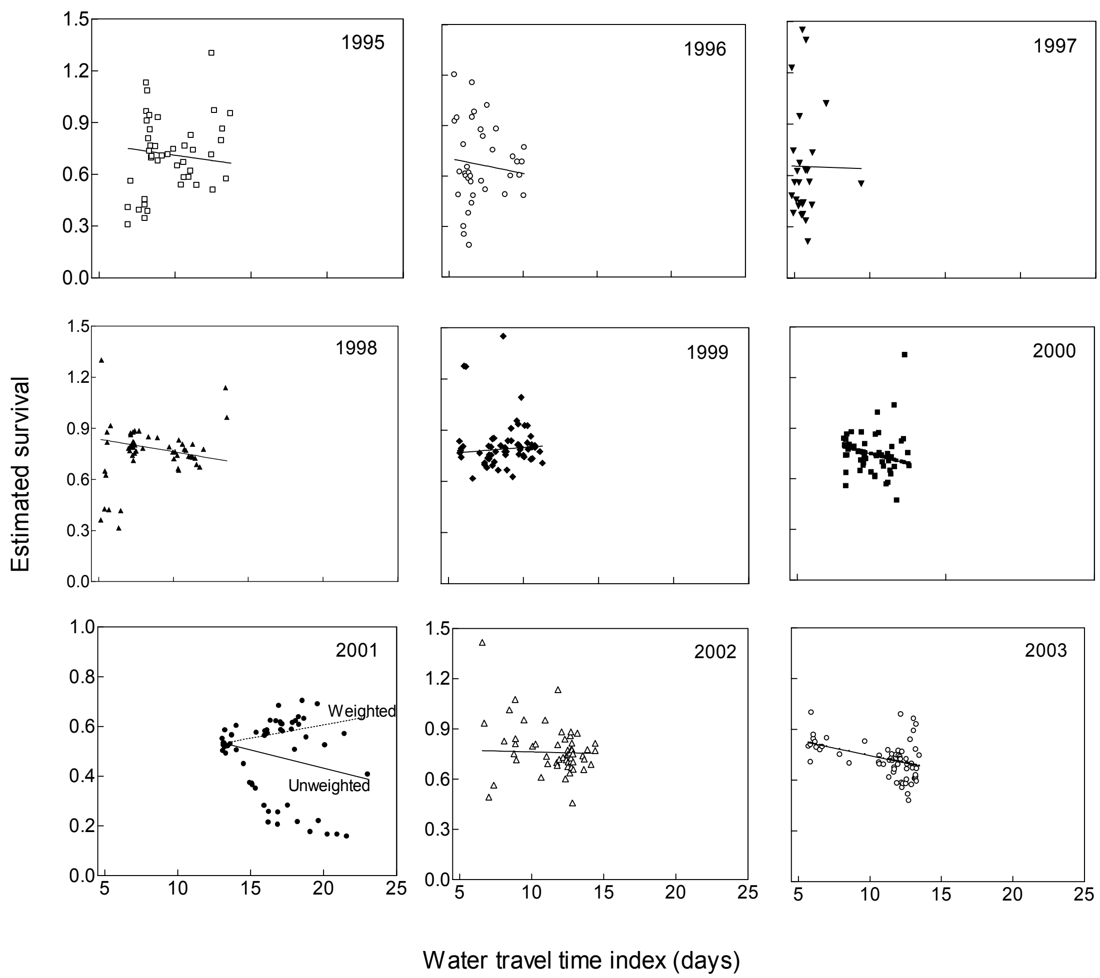


Figure 32. Estimated survival from Lower Granite Dam to McNary Dam for PIT-tagged Snake River yearling Chinook salmon, plotted against water travel time index, 1995–2003.

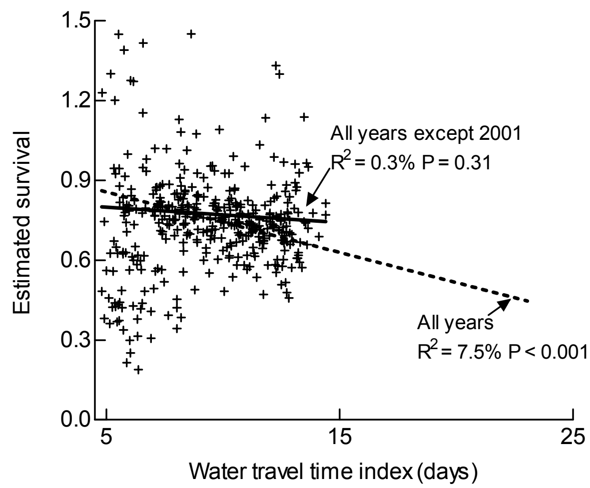


Figure 33. Estimated survival from Lower Granite Dam to McNary Dam versus water travel time for PIT-tagged yearling Snake River Chinook salmon, 1995–2003. ○ = data from 2003: + = data from all other years.

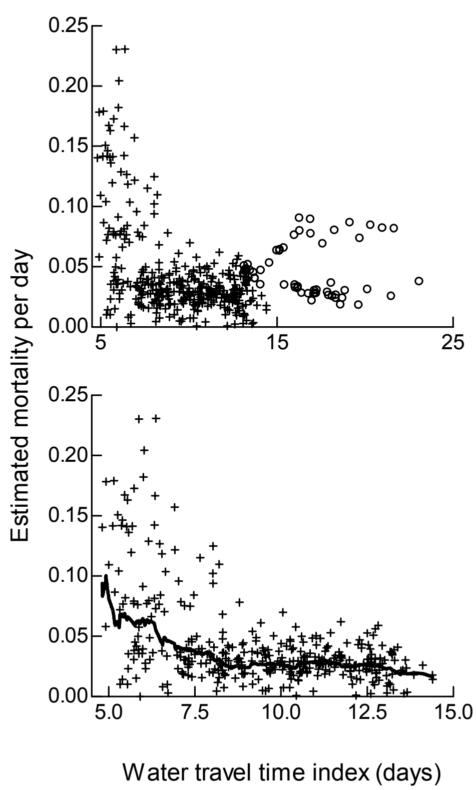


Figure 34. Estimated mortality per day versus water travel time index for PIT-tagged yearling Snake River Chinook salmon, 1995–2003. Top panel includes 2001 data (○); bottom panel excludes 2001. Lowess smooth (black line) in bottom panel indicates that mortality per day tended to increase with decreased water travel time.

Threshold models for survival versus flow

The equation for the best-fit Boltzmann curve (Figure 35) was

$$SURV = \frac{0.7854}{1 + e^{(48.13 - F)/9.72}} \tag{11}$$

with R^2 = 10.5%. The best-fit piecewise linear regression model was almost identical to the Boltzmann curve (Figure 35). The threshold flow exposure value was 73.0 kcfs; maximum survival was 0.777, and the linear equation for survival below the threshold was

Bootstrap 95% confidence intervals on the estimated parameters are as follows: maximum survival (0.752,0.835); slope (0.0053,0.0181); and threshold (70.1, 99.4).

$$SURV = -0.2954 + 0.0147F. \tag{12}$$

Importantly, we note that without the low-flow, low-survival points from 2001, we could not fit the threshold models. The 2001 points "pulled down" the curve or line in the low-flow range. Further, the individual points from 2001 do not fit the curves very well. Taken as a whole, the points from 2001 effectively acted as a single "center of gravity" or almost as a single point that obscured the within-season dynamics.

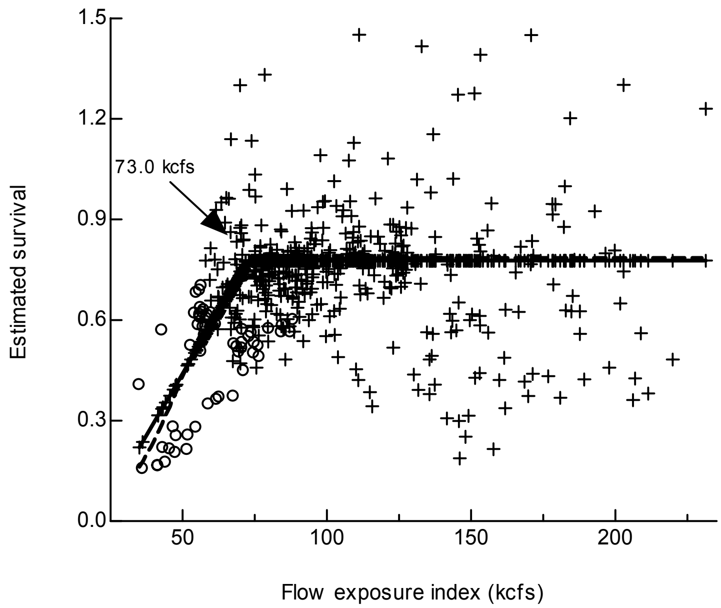


Figure 35. Best-fit sigmoid curve (dashed line) and piecewise linear regression model (solid line) for estimated survival from Lower Granite Dam to McNary Dam for PIT-tagged, yearling Snake River Chinook salmon versus flow exposure index, 1995–2003. ○ = data from 2001; + = all other years. Point of "break," or threshold, is not precisely estimated.

Generalized additive and multiple-regression models for survival

Exploratory analysis using generalized additive models (gam) suggested a regression model for survival that used functions of the indices of WTT, percent spill, and water temperature exposure. Partial fits from the gam indicated temperature had little effect on survival when water temperature was low to moderate, but that the strongest relationship to survival estimates was that of temperature when it was high (Figure 36). The influence of WTT and percentage spill was small relative to the dramatic decrease in survival that occurred at high temperatures. The spline indicated that a small decline in survival began at a temperature exposure of 11.85°C, decline became steeper between 12.0 and 13.0°C, and above 13.0°C the decline was sharp and nearly linear. Of the 458 release groups in the data set, 159 (35%) had temperature exposure indices greater than 11.85°C, and 70 (15%) were greater than 13.0°C (27 groups in 2001 had a temperature index greater than 13.0°C). Indices of 11.85°C or above were reached for at least a few groups in every year of the study; 13.0°C was reached in all years but 1996 and 2002 (for only one group in 2003).

At temperature exposures below 11.85°C, differences in temperature exposure had little influence on survival (spline for temperature in Figures 36 and 37 is nearly flat in that range). When temperatures were in this lower range, as they were for 65% of the release groups, the WTT index had the strongest association with estimated survival (Figure 37). From the smallest WTT (4.8 days) to about 14.0 days, the decline in survival was nearly linear. Beyond 14.0 days, there was little association. For the spill percentage index (spill %), there was a peak in survival at about 20.6% spill; survival was lower on either side of 20.6%.

Data were sparse at WTT greater than 14.0 days (10% of groups) or spill % less than 10% (57 groups with 0% spill, all from 2001; only 9 groups with spill percentage exposure between 0% and 10%). The highest survival values for the spill percentage spline were at 0% spill. All these points were from 2001, and the peak survival at 0% spill in the partial fit from the multiple regression was due to confounding with the year effect for 2001.

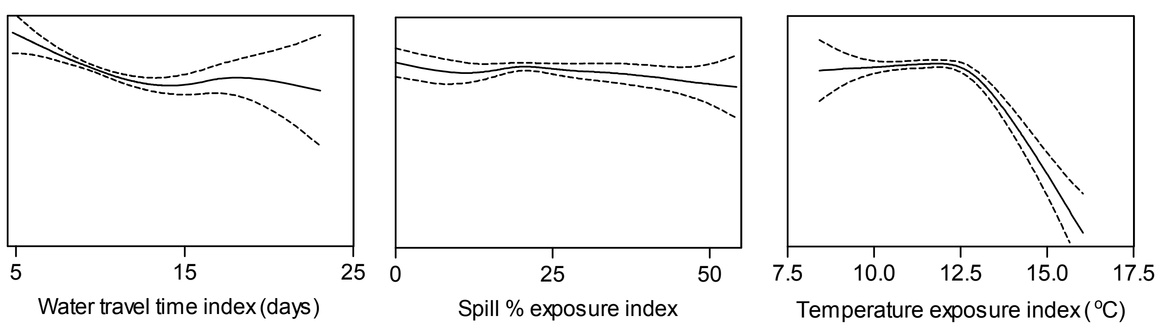


Figure 36. Partial fits (transformed nonparametric splines) for generalized additive model for estimated survival from Lower Granite Dam to McNary Dam, with pointwise 95% confidence limits, yearling Chinook salmon, 1995–2003. Predictor variables were year effects, water travel time index (days), spill percentage index, and temperature index (°C). Because all variables were transformed, Y-axis units are not meaningful. Relative influence on survival is judged by relative ranges of transformed predictor variables, which are all plotted on the same Y-axis scale. Shape of the relationship is judged by the spline itself. All data are illustrated; that is, full range of temperature exposures.

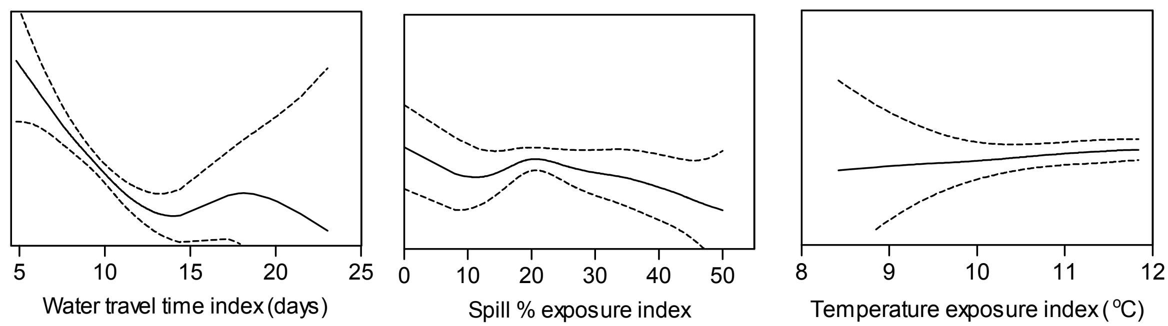


Figure 37. Partial fits (transformed nonparametric splines) for generalized additive model for estimated survival from Lower Granite Dam to McNary Dam, with pointwise 95% confidence intervals, yearling Chinook salmon, 1995–2003. Predictor variables were year effects, water travel time index (days), spill percentage index, and temperature index (°C). Because all variables were transformed, Y-axis units are not meaningful. Relative influence on survival is judged by relative ranges of transformed predictor variables, which are all plotted on the same Y-axis scale. Shape of the relationship is judged by the spline itself. Fits were based on all data; only release groups with temperature exposure less than 11.85°C are illustrated (i.e., a subset of Figure 36; range of Y axes is about 35% of those in Figure 36).

Based on the generalized additive model results, we fit a multiple-regression model (Table 36) that included year effects, a function of WTT that was linear between the minimum 4.8-day WTT and 14.0 days and flat above 14.0 days, a function of temperature that was flat up to 13.0°C and linear above it, a function of spill percentage that was flat below 10% and a second-order polynomial above that level.

Data from 2001 clearly did not fit a model of survival as strictly a function of flow or WTT (e.g., Figures 32 through 34). The multiple-regression model that included strong effects at high temperatures provided a much better fit for 2001 data (Figure 38).

Snake River Steelhead

Travel time versus flow and water travel time

With the exception of the low-flow year of 2001, the annual median travel time (days) for all Snake River steelhead passing between Lower Granite and Bonneville dams from 1 April to 31 May each year varied by only a few days (Table 37).

Within seasons, median travel time for groups of PIT-tagged steelhead has consistently tracked the WTT index (Figure 39). Results from a generalized additive model (including year effects and nonparametric splines for date and flow exposure index) indicated that date also influenced travel time for steelhead (Figure 40), but not as much as flow. Unlike the result for yearling Chinook salmon, flow appeared to have more influence than date on steelhead travel time throughout the migration season. A generalized additive model using the WTT index gave essentially the same information.

Table 36. Summary of multiple-regression model for estimated survival of yearling Chinook salmon between tailraces of Lower Granite and McNary dams, 1995–2003. R^2 for this model is 78.1%.

Parameter	Estimate	Standard error	t statistic	P value
Intercept	0.6610	0.0376	17.58	0.000
Year effects				
1996	–0.0891	0.0464	–1.92	0.056
1997	–0.1039	0.1142	–0.91	0.364
1998	0.0469	0.0337	1.39	0.164
1999	0.0644	0.0330	1.95	0.052
2000	0.0466	0.0358	1.30	0.194
2001	–0.0875	0.0377	–2.32	0.021
2002	0.0678	0.0349	1.94	0.053
2003	0.0448	0.0359	1.25	0.213
Slope for WTT < 14 days[a]	0.0104	0.0026	–3.99	<0.001
Slope for TEMP > 13°C[b]	–0.1378	0.0112	–12.29	<0.001
% spill[c] < 10: linear	0.00283	0.00179	1.58	0.115
% spill < 10: quadratic	–0.0000942	0.0000416	–2.26	0.024
F statistic for % spill < 10 polynomial			$F_{2,445} = 3.25$	0.040

[a] WTT = water travel time index. To calculate fitted value: if WTT > 14 contribution is 0; if WTT < 14 use 0.0104*(14 – WTT).

[b] TEMP = temperature exposure index. To calculate fitted value: if TEMP < 13 contribution is 0; if TEMP > 13 use –0.1378*(TEMP – 13).

[c] % spill = percentage spill index. To calculate fitted value, if % spill < 10 contribution is 0; if % spill > 10 use 0.00283*(% spill – 10) – 0.0000942*(% spill – 10)2.

Table 37. Median travel time (days) of PIT-tagged steelhead between Lower Granite Dam and Bonneville Dam, 1995–2003.

Year	Median Lower Granite Dam–Bonneville Dam travel time (days)
1995	20.2
1996	15.3
1997	12.2
1998	14.4
1999	15.4
2000	13.6
2001	29.8
2002	18.4
2003	15.4

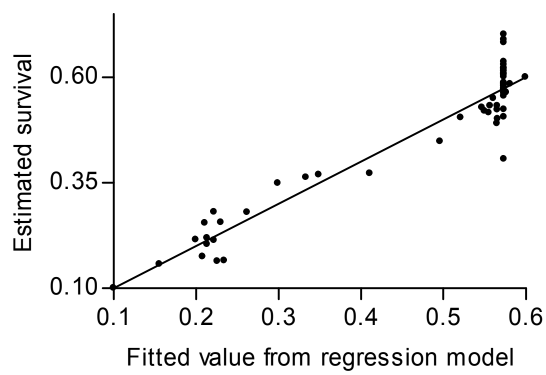


Figure 38. Observed survival estimates for Snake River yearling Chinook salmon between Lower Granite Dam and McNary Dam in 2001 plotted against fitted values from selected multiple-regression model including functions for water travel time and temperature (and spill percentage, which was 9 for all 2001 groups). Multiple fitted values of 0.574 were for early season groups migrating in low flows and low water temperatures.

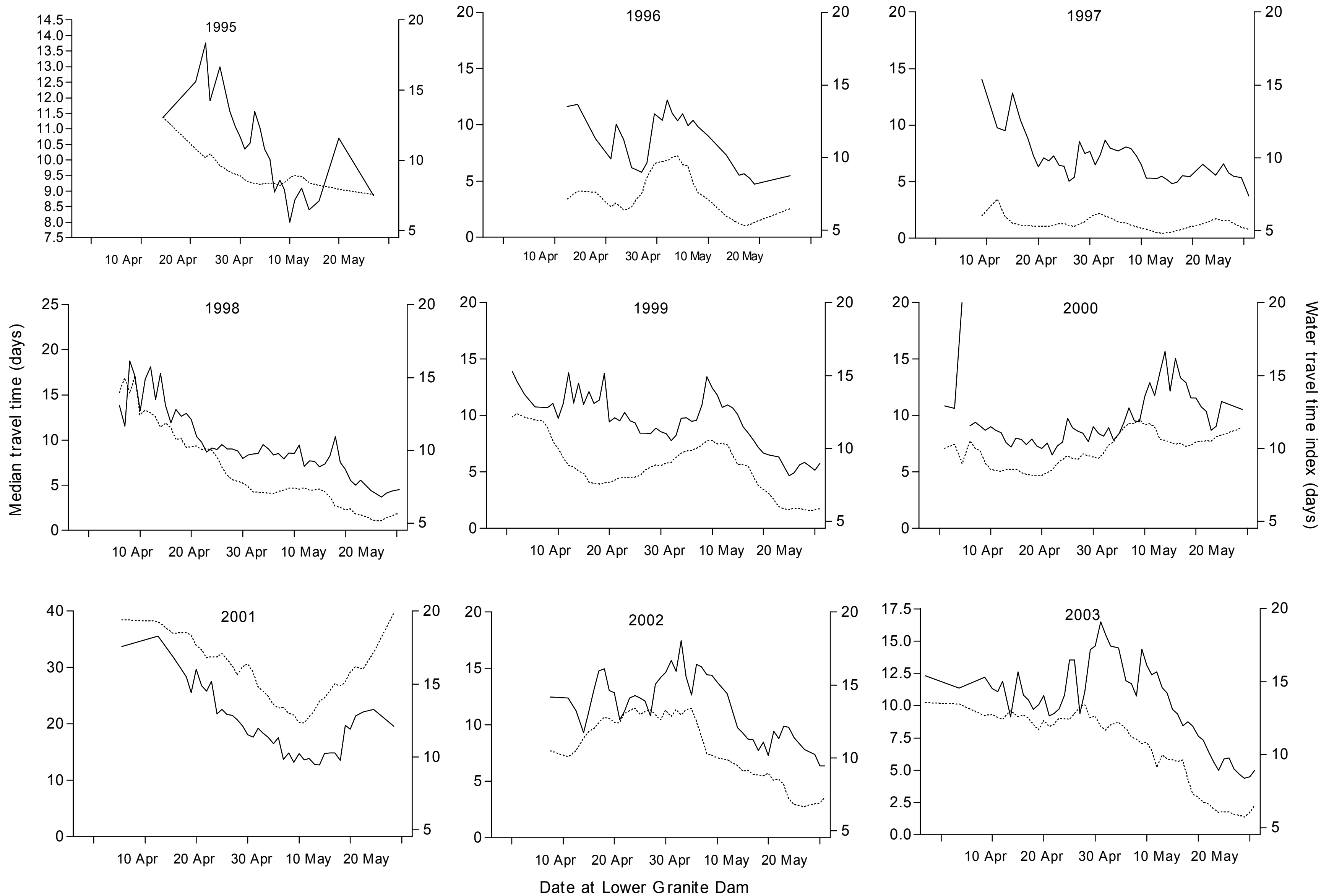


Figure 39. Median travel time (solid line) and water travel time index (dotted line) for groups of PIT-tagged Snake River steelhead, 1995–2003.

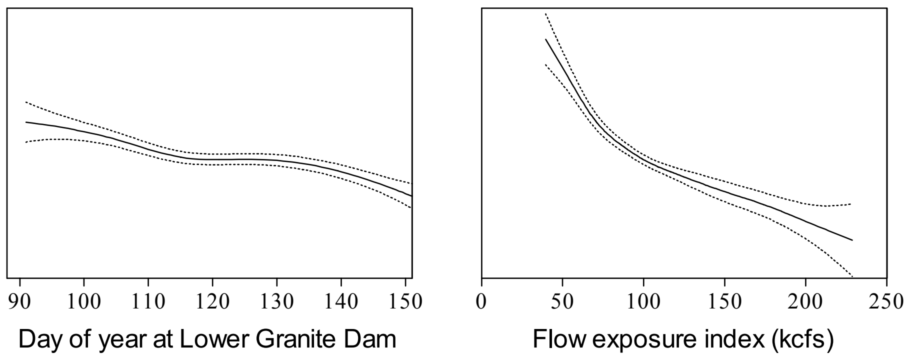


Figure 40. Partial fits for generalized additive model of steelhead median travel time from Lower Granite to McNary dams (days), with pointwise 95% confidence intervals, 1995–2003. Predictor variables were release date from Lower Granite Dam, flow exposure index (kcfs), and year effects. Because all variables were transformed, Y-axis units are not meaningful. Relative influence on travel time is judged by relative ranges of transformed predictor variables, which are all plotted with the same Y-axis scale. Shape of the relationship is judged by the spine itself.

Survival and mortality versus water travel time

Smith et al. (2002b) found that the relationship between flow exposure and survival of steelhead within seasons was generally weak and inconsistent. Translating the flow exposure measures into a WTT index resulted in qualitatively similar results (Figure 41). Significant (α = 0.05) negative slopes (increased WTT related to decreased survival) occurred for data within the 1995, 1999, and 2000 seasons. The R^2 values were 16%, 21%, and 51%, respectively. Only 2000 had an R^2 value that appeared mildly predictive.

Including all years in an unweighted analysis resulted in a significant simple linear regression (Figure 42). As with yearling Chinook salmon, data from 2001 were highly influential in this result, and the 2001 data do not fit the line well at all (there are substantial problems with residuals). Excluding 2001 data there is a slight and significant negative slope, but little predictive value (see following subsections on “Threshold models for survival versus flow,” page 91, and “Snake River Spring Migrants,” page 101). For years other than 2001, estimated mortality per day was fairly constant, regardless of WTT (bottom panel, Figure 43). This indicates that the observed relationship between WTT and steelhead travel time induces a relationship between WTT and steelhead survival. Data from 2001 clearly stand apart from data from other years (top panel, Figure 43). The “baseline” mortality per day appeared to be higher, and, contrary to the more constant pattern for other years, the estimated mortality per day decreased with increasing WTT.

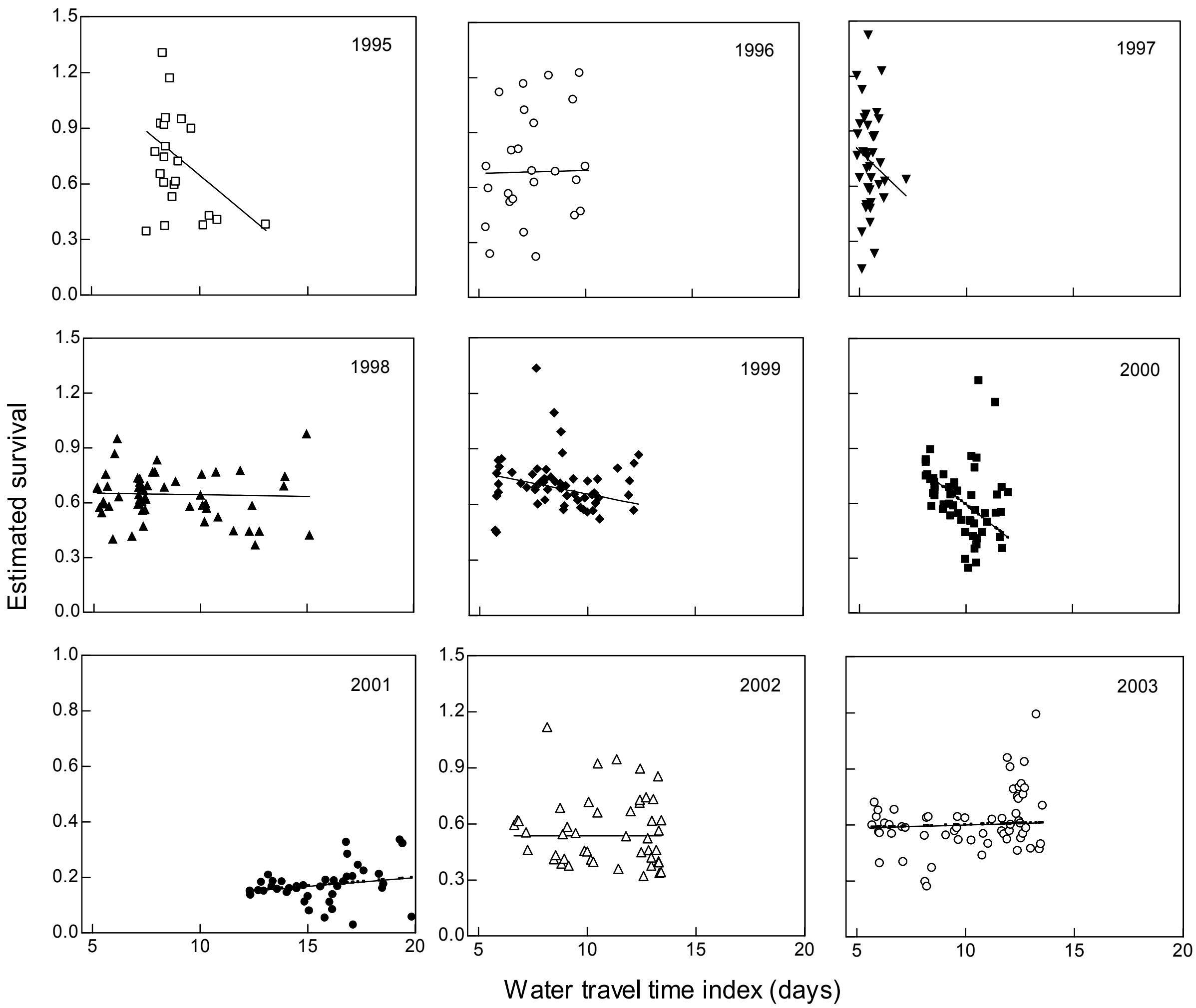


Figure 41. Estimated survival from Lower Granite Dam to McNary Dam for PIT-tagged Snake River steelhead, plotted against water travel time index, 1995–2003.

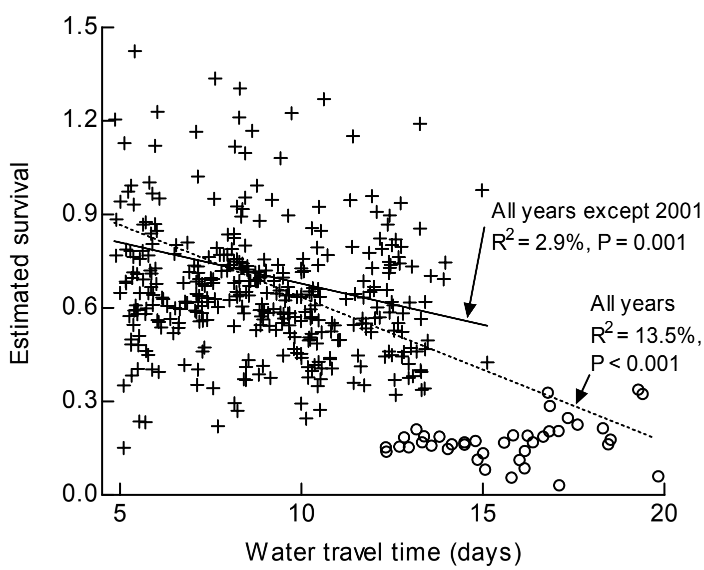


Figure 42. Estimated survival from Lower Granite Dam to McNary Dam versus water travel time for PIT-tagged Snake River steelhead, 1995–2003. ○ = data from 2001; + denotes data from all other years.

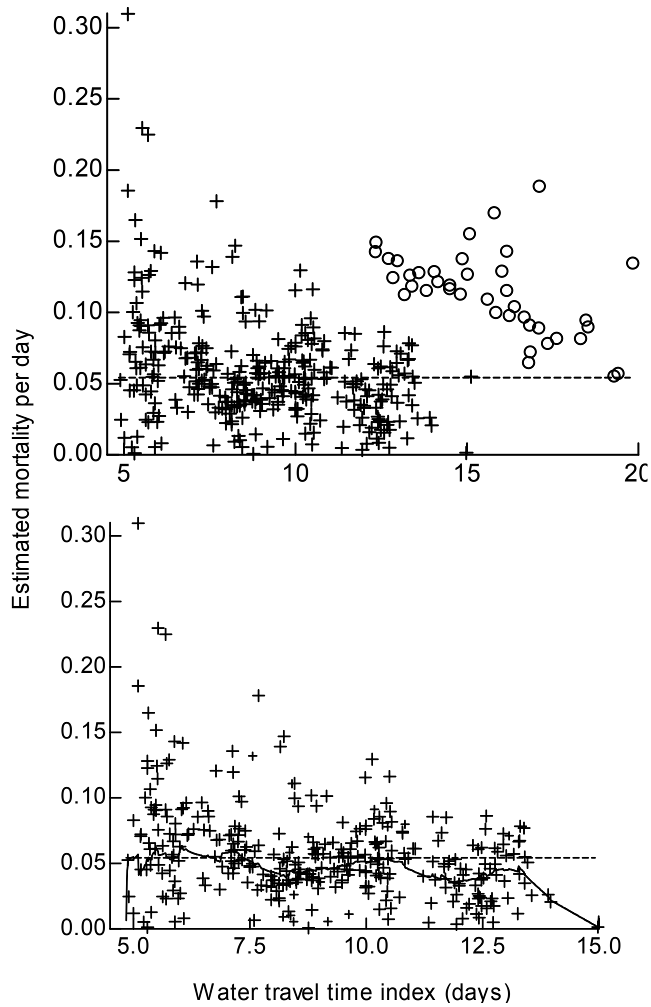


Figure 43. Estimated mortality per day versus water travel time for PIT-tagged Snake River steelhead, 1995–2003. Top panel includes 2001 data (○); bottom panel excludes 2001. Lowess smooth (black line) in bottom panel indicates that mortality per day was fairly constant at different water travel times, consistent with existence of both fish travel time/water travel time and survival/water travel time relationship.

Threshold models for survival versus flow

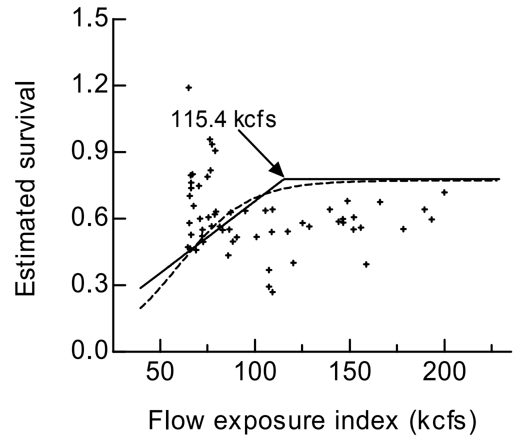
The equation for the best-fit Boltzmann curve (Figure 44) was as follows:

$$SURV = \frac{0.7728}{1 + e^{(59.48 - F)/18.64}} \tag{13}$$

with R^2 = 10.2%. In the best-fit piecewise linear regression model (Figure 44), the threshold flow exposure value was 115.4 kcfs, maximum survival was 0.779, and the linear equation for survival below the threshold was

$$SURV = 0.0316 + 0.0065F. \tag{14}$$

Figure 44. Best-fit sigmoid curve (dashed line) and piecewise linear regression model (solid line) for estimated survival from Lower Granite Dam to McNary Dam for PIT-tagged Snake river yearling Chinook salmon versus flow exposure index, 1995–2003. ○ = data from 2001; + = data from all other years. Point of "break" or threshold is estimated extremely imprecisely.



Bootstrap 95% confidence intervals on the estimated parameters are maximum survival (0.693, 0.849), slope (0.0046, 0.0202), and threshold (78.9, 132.6).

As with yearling Chinook salmon without the low-flow, low-survival points from 2001, we could not fit the threshold models. The 2001 points "pulled down" the curve or line in the low-flow range. Further, the individual points from 2001 do not fit the curves very well. Taken as a whole, the points from 2001 effectively acted as a single "center of gravity," or almost as a single point that obscured the true within-season dynamics.

Generalized additive and multiple-regression models for survival

Two different multiple-regression models were suggested by exploratory analysis using gams. Both models included functions of indices of WTT and % spill. Each model had a third variable: temperature index in one case and release date in the other. Although the R^2 value for the regression model with date was slightly higher (70.9%) than with temperature (68.3%), we illustrate the model that includes water temperature (Figure 45).

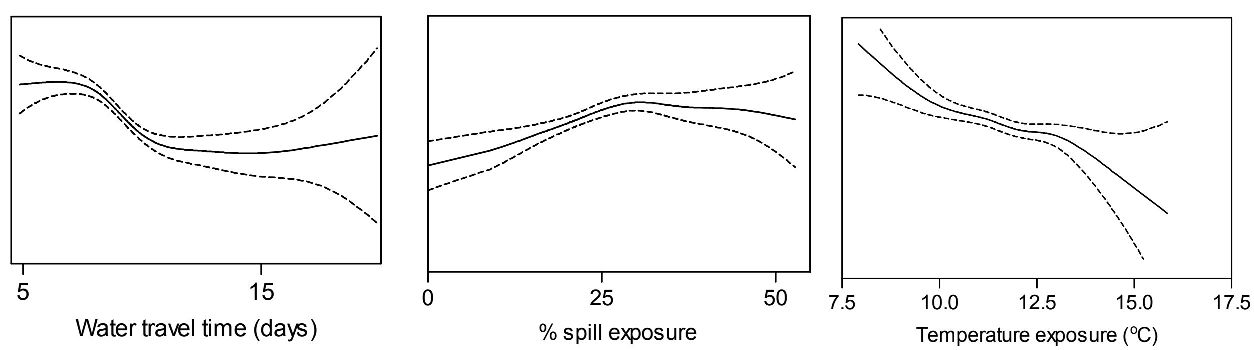


Figure 45. Partial fits (transformed nonparametric splines) for generalized additive model for estimated steelhead survival from Lower Granite Dam to McNary Dam, with pointwise 95% confidence limits, 1995–2003l. Predictor variables were year effects, water travel time index (days), spill percentage index, and temperature index (°C). Because all variables were transformed, Y-axis units are not meaningful. Relative influence on survival is judged by relative ranges of transformed predictor variables, which are all plotted on the same Y-axis scale. Shape of the relationship is judged by the spline itself.

Based on the gam results (Figure 45), we fit a multiple-regression model (Table 38) that included year effects, a function of WTT that was linear for WTT less than 11.3 days and flat for longer travel times, a function of % spill that was linear for the 0%–30.4% range and flat above it, and a function of water temperature that was linear throughout the observed range.

Table 38. Summary of multiple-regression model for estimated survival of steelhead between tailraces of Lower Granite and McNary dams, 1995–2003. R^2 for this model is 68.3%.

Parameter	**Estimate**	**Standard error**	**t statistic**	**P value**
Intercept	0.9905	0.0915	10.83	<0.001
Year effects				
1996	–0.1127	0.0804	–1.40	0.162
1997	–0.1465	0.0809	–1.81	0.071
1998	–0.0873	0.0661	–1.32	0.188
1999	–0.0433	0.0642	–0.67	0.501
2000	–0.0725	0.0657	–1.10	0.271
2001	–0.3668	0.0754	–4.86	<0.001
2002	–0.1253	0.0687	–1.82	0.069
2003	–0.1297	0.0662	–1.96	0.051
Slope for WTT index < 11.34[a]	0.0310	0.0044	7.05	<0.001
Slope for % spill < 30.4[b]	–0.0036	0.0013	–2.72	0.007
Slope for temp.[c]	–0.0276	0.0062	–4.42	<0.001

[a] WTT = water travel time index. To calculate fitted value: if WTT > 11.34, contribution is 0; if WTT < 11.34, use 0.0310*(11.34 – WTT).

[b] % spill = percentage spill index. To calculate fitted value: if % spill > 30.4, contribution is 0; if % spill < 30.4, use –0.0036*(30.4 – % spill).

[c] Temp. = temperature exposure index.

Run-of-River Subyearling Chinook Salmon from McNary Dam

River conditions for 1999–2002

The study period included 1 year with relatively high flow, especially in late summer (1999), 1 year with very low flow (2001), and 2 intermediate years (2000 and 2002) (Figures 46 and 47). Water temperature was strongly correlated with flow: water was warmest in 2001, coolest in 1999, and intermediate the other 2 years. Flow and water temperature at McNary and John Day dams were very highly correlated (Figures 46 and 47), but spill and water clarity differed between the two dams. At McNary Dam there were large differences from year to year in percentage of flow that was spilled (Figure 46). Spill usually did not occur when flow was below 175 kcfs (no spill occurred at all in 2001 after 19 June and at McNary Dam on 44 days between 19 June and 31 August 2000 and on 29 days in 2002, mostly in August). When flow was above 175 kcfs, the rate and percentage of spill were highly correlated with flow. Because the study fish were collected in the bypass system at McNary Dam and released in the tailrace, it is very unlikely that spill at McNary Dam influenced their travel time or survival to John Day Dam. Therefore, beyond the description above, we made no further use of the variable.

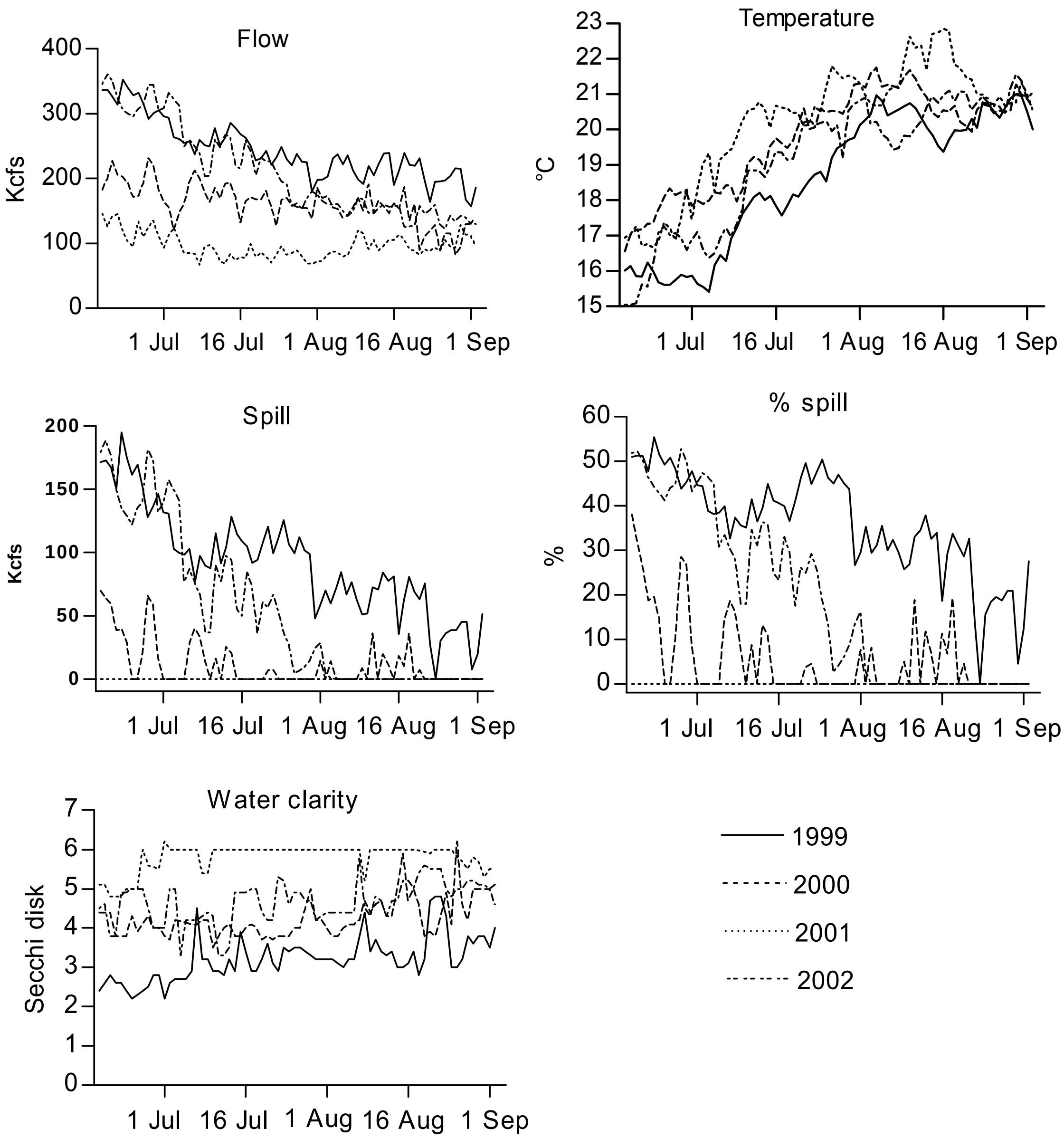


Figure 46. River conditions at McNary Dam, 19 June–31 August, 1999–2002.

Spill occurred at John Day Dam on all days between 19 June and 31 August 1999, 2000, and 2002 and on no days in 2001 (Figure 47). The percentage of total flow spilled was fairly constant in 1999, and averaged 26.6% between 19 June and 31 August. In 2000 spill alternated between blocks of days with average of a little less than 30% and blocks a little more than 40%. The average for 2000 was 34.7%. The average percentage spilled in 2002 was 29.2%. The relatively constant spill percentage in years at John Day Dam (in 2001 spill was constant at 0%) resulted in a lack of correlation between flow and percentage of flow spilled, but also resulted in a lack of contrast in spill percentage among the years 1999, 2000, and 2002.

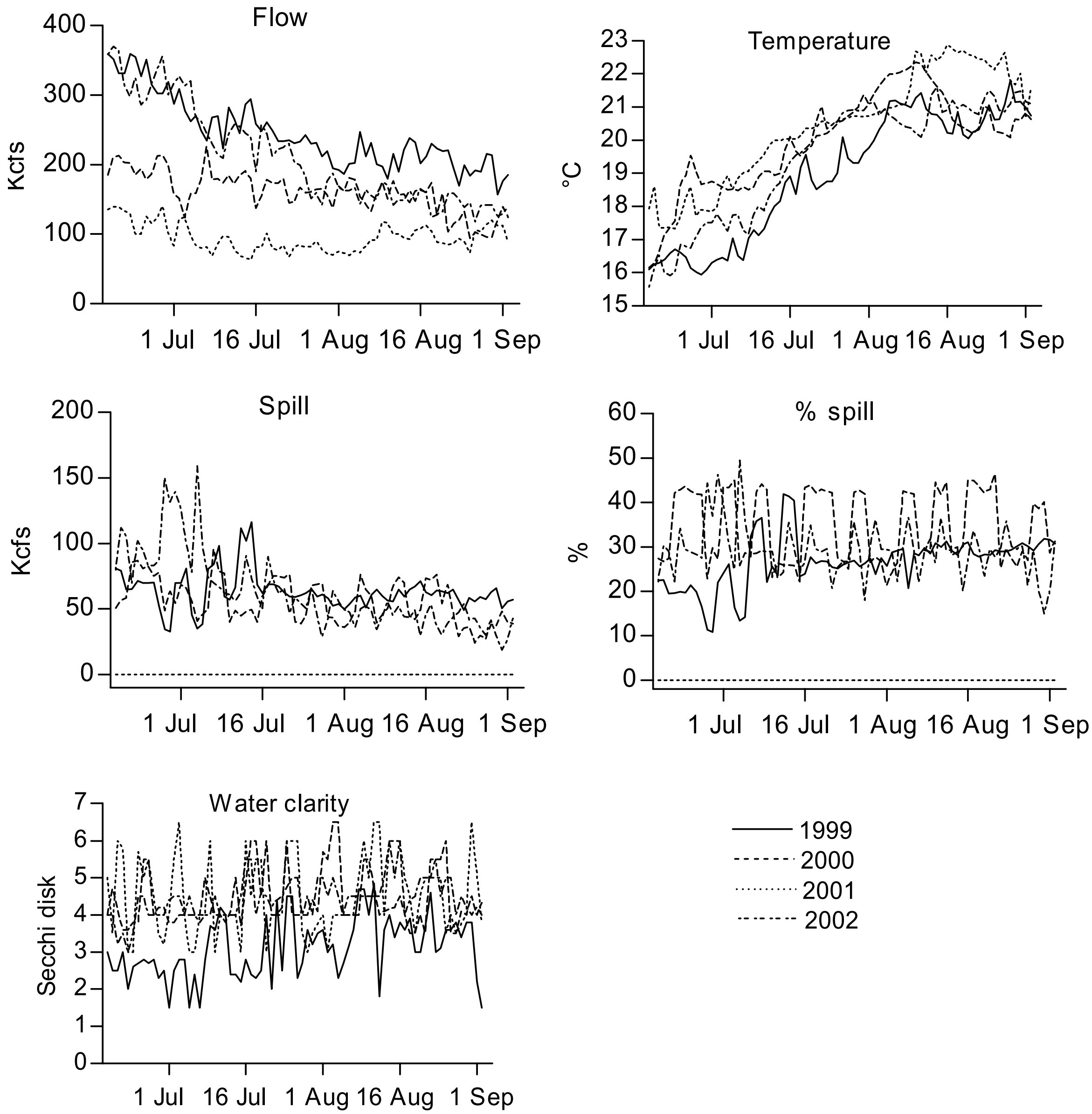


Figure 47. River conditions at John Day Dam, 19 June–31 August 1999–2002.

At McNary Dam, water clarity was correlated with flow and temperature on an annual basis: water was clearest in 2001, most turbid in 1999, and intermediate in 2000 and 2002 (Figure 46). A similar pattern in annual average clarity occurred at John Day Dam (Figure 47), though with less difference among years (2001 was not nearly as different from 2000 and 2002 as it was at McNary Dam), and with more variability in the reported data within years.

Travel time, survival estimates, and river environment indices

We calculated survival estimates, median travel times, and river condition indices for groups for 5 weeks in the years 1999–2000, 6 weeks in 2001, and 9 weeks in 2002 (Table 39). Exposure indices were generally highly correlated with each other (Table 40). For example, the

Table 39. Survival estimates and median travel times from McNary Dam to John Day Dam, and river condition indices for weekly groups of run-of-river subyearling Chinook salmon released in the tailrace of McNary Dam.

Year	Dates at McNary Dam	Estimated survival to John Day Dam (standard error)		Median travel time (days)	McNary Dam indices			John Day Dam indices				
					Flow (kcfs)	Temp. (C°)	Clarity (Secchi)	Flow (kcfs)	Spill (kcfs)	Spill (%)	Temp. (C°)	Clarity (Secchi)
1999	6/19–25	0.788	(0.042)	4.3	333.4	16.0	2.5	302.8	33.5	11.1	16.0	2.6
1999	6/26–7/02	0.746	(0.032)	3.8	305.1	15.7	2.5	287.7	56.6	19.4	16.4	2.3
1999	7/03–09	0.765	(0.059)	5.5	255.3	16.3	3.1	265.4	83.4	31.5	18.0	3.1
1999	7/10–16	0.770	(0.053)	5.2	267.6	18.0	3.1	242.8	63.5	26.2	18.9	3.2
1999	7/17–23	1.026	(0.162)	6.4	238.6	18.2	3.2	230.4	61.0	26.5	19.2	3.4
2000	6/19–25	0.593	(0.195)	4.4	197.6	17.2	4.1	198.0	66.3	34.1	19.1	4.8
2000	7/26–7/02	0.547	(0.228)	5.3	188.8	18.1	4.0	170.7	61.0	35.6	18.5	4.2
2000	7/03–09	0.675	(0.256)	6.5	173.6	18.2	4.2	173.1	56.5	33.2	19.4	4.7
2000	7/10–16	1.974	(1.108)	11.2	172.5	19.1	3.9	162.3	56.0	34.3	20.4	4.8
2000	7/17–23	0.616	(0.233)	8.8	162.6	19.9	3.8	160.4	49.9	31.1	20.9	4.6
2001	6/19–25	0.572	(0.026)	13.8	125.0	16.9	4.9	89.0	0.0	0.0	19.3	4.2
2001	6/26–7/02	0.560	(0.036)	27.6	117.3	17.6	5.7	79.7	0.0	0.0	20.6	4.3
2001	7/03–09	0.520	(0.077)	26.9	92.1	19.2	5.8	84.9	0.0	0.0	21.1	4.4
2001	7/10–16	0.655	(0.054)	16.6	80.8	20.5	6.0	79.1	0.0	0.0	20.7	4.2
2001	7/17–23	0.586	(0.048)	13.7	82.2	20.4	6.0	84.1	0.0	0.0	21.0	4.1
2001	7/24–30	0.597	(0.049)	13.3	81.5	21.4	6.0	90.5	0.0	0.0	21.5	4.7
2002	6/19–25	0.888	(0.079)	3.8	325.9	15.7	4.5	308.7	100.7	32.3	16.9	4.3
2002	6/26–7/02	0.964	(0.086)	4.6	322.1	17.0	4.5	271.2	90.9	32.9	17.6	4.2
2002	7/03–09	0.679	(0.033)	5.2	262.4	16.8	4.2	252.3	69.8	27.6	18.2	4.0
2002	7/10–16	0.814	(0.078)	5.0	239.8	18.7	4.2	225.5	60.9	26.9	19.0	4.7
2002	7/17–23	0.598	(0.069)	4.8	228.7	19.7	4.8	185.6	50.5	27.5	20.7	4.5
2002	7/24–30	0.655	(0.076)	7.7	173.0	20.1	4.6	160.5	46.9	29.3	20.7	4.6
2002	7/31–8/06	0.811	(0.231)	8.7	159.3	20.2	4.6	152.9	40.6	26.4	21.3	5.3
2002	8/07–13	0.448	(0.078)	5.6	156.5	20.1	4.6	145.8	40.5	27.7	21.1	5.0
2002	8/14–20	0.571	(0.131)	4.9	144.3	20.9	5.3	149.9	43.4	29.0	20.9	5.0

Table 40. Product-moment correlation coefficients (r) among independent variables for groups of subyearling Chinook salmon released in McNary Dam tailrace, 1999–2002. Each variable was adjusted by subtracting respective annual mean.

		McNary Dam indices			John Day Dam indices			
		Flow	**Temp. (C°)**	**Clarity**	**Flow**	**Spill**	**% spill**	**Temp. (C°)**
McNary Dam indices	Flow							
	Temp. (C°)	–0.84[a]						
	Clarity	–0.53	0.61					
John Day Dam indices	Flow	0.94[a]	–0.79[b]	–0.43				
	Spill	0.64[b]	–0.60	–0.04	0.72[b]			
	% spill	–0.05	–0.06	0.39	0.01	0.70[b]		
	Temp. (C°)	–0.90[a]	0.88[a]	0.56	–0.90[a]	–0.55	0.10	
	Clarity	–0.73[b]	0.63[b]	0.48	–0.69[b]	–0.35	0.19	0.78[b]

[a] $r^2 > 0.65$

[b] $0.40 < r^2 < 0.65$

product-moment correlation coefficients (r) between flow and temperature exposure were –0.84 and –0.90 for McNary Dam and John Day Dam indices, respectively. Flow indices at the two dams were very highly correlated (r = 0.94), as were the two temperature indices (r = 0.88). For analyses of relationships with survival and travel time, it was clearly not necessary to use indices of flow and temperature for both dams; they gave essentially the same information. We chose to use the flow and temperature indices from John Day Dam. Similarly, the spill volume index was too highly correlated with either the flow index or the spill percentage index (or both), to provide unique information, so we did not use the spill volume index. Correlations between indices of water clarity at the two dams were not as strong. It is possible that the two separate indices could give independent information as predictor variables in travel time and survival models.

Unadjusted for annual means, pairwise correlations were highly significant (P < 0.01) between median travel time and all variables except the John Day clarity index (Figure 48 and Table 41). Adjusted for annual means, none of the adjusted variables was significantly correlated with adjusted median travel time (P > 0.05) (Table 41).

The difference between results for adjusted and unadjusted data for travel time is caused almost exclusively by the "separation" of 2001 data from that of other years and by the narrow range of indices within 2001. Particularly for the John Day flow index, it is not possible to determine from the data whether the points from 2001 belong on the same line as those from other years, or whether there are generalized year effects that affect both the flow index and travel time, but without a causal link. Assuming that the points are appropriately fit to a single flow/travel time function, it appears the relationship is curved (Figure 48); for a fixed difference (kcfs) in flow volume, the reduction in travel time (slope of the curve) was greater at lower flow levels than at higher flow. Because water velocity is related to flow volume, a plausible explanation for the shape of the curve is a direct link between water velocity and migration rate for subyearling Chinook salmon.

Table 41. Product-moment correlations between river environment exposure indices and median travel time and estimated survival between McNary Dam tailrace and John Day Dam tailrace for run-of-river subyearling Chinook salmon, 1999–2002. Correlations (r) and corresponding P values are given for unadjusted variables and for variables adjusted for annual means. P values are for two-sided test of null hypothesis of zero correlation.

	Median travel time (1999–2002)				Estimated survival (excludes 2000)			
	Unadjusted		Adjusted		Unadjusted		Adjusted	
Index	r	P value	r	P value	r	P value	r	P value
Flow at John Day Dam	–0.747	<0.001	–0.256	0.250	0.714	<0.001	0.506	0.032
Temp. (C°) at John Day Dam	0.518	0.008	0.297	0.179	–0.610	0.004	–0.384	0.116
% spill at John Day Dam	–0.756	<0.001	0.011	0.962	0.501	0.024	0.260	0.297
Clarity at McNary Dam	0.651	<0.001	0.040	0.861	–0.584	0.007	–0.118	0.641
Clarity at John Day Dam	0.188	0.367	0.225	0.314	–0.381	0.097	–0.107	0.674

For analyses of relations between river indices and estimated survival, we omitted data from 2000 because the estimates were not sufficiently precise (i.e., standard errors were too large, see Table 39). Unadjusted for annual means, pairwise correlations were highly significant ($P < 0.01$) between estimated survival and all variables except the John Day clarity index (Figure 49 and Table 41). Adjusted for annual means, the correlations between estimated survival and the temperature index, the clarity indices, and the % spill index at John Day Dam were not significant. However, there was a significant correlation between adjusted estimated survival and adjusted John Day flow index (Table 41).

In 1999 and 2001, the within season (i.e., using data from 1 year at a time) correlation between John Day flow index and estimated survival was negative (greater flow related to lower survival) but not significant. In 2000 when the range of the flow index was greater, the correlation was positive and significant. There is no indication of a curved relationship between flow and survival over the range of observed flow index (Figure 49). In the multiyear analysis, the regression line slopes for adjusted and unadjusted flow were nearly the same and indicated that, on average, each 10 kcfs increase in the flow index was associated with a 1.3%–1.5% increase in survival.

The temperature index at John Day Dam was also sufficiently correlated with the flow index to make independent assessment of these two variables impossible. Certainly the two predictors are too correlated for multiple-regression methods to separate effects of the two variables (when both are included, the flow variable is statistically significant and the temperature variable is not). However, the pairwise relationship of estimated survival with temperature deserves a closer look, because a causal mechanism is plausible.

Careful examination of the observed temperature index data indicates there was a gap in the range of temperature data: while points are fairly evenly distributed over the rest of the range, there were no data between 19.3°C and 20.6°C (Figure 49). It is noteworthy that for the data with a temperature index less than 19.3°C (10 data points from 1999 and 2002) the slope

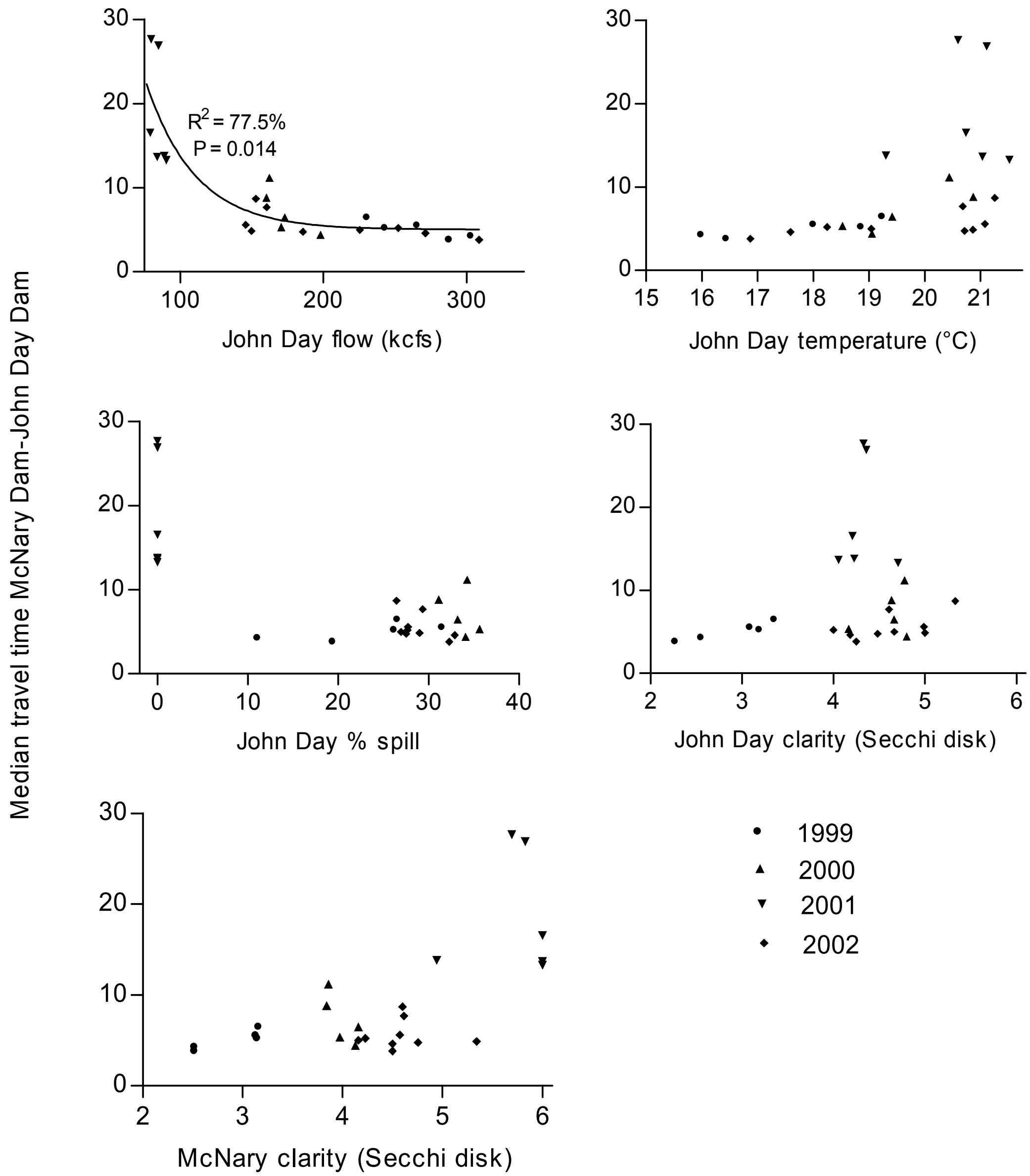


Figure 48. Median travel time between McNary and John Day dams plotted against various river condition indices for run-of-river subyearling Chinook salmon released in the McNary Dam tailrace, 1999–2002. Flow index panel illustrates exponential-decay curve fit to data.

between survival and temperature was nearly zero. Similarly, for data with an index greater than 20.6°C (10 points from 2001 and 2002) the slope was nearly zero (Figure 49). The mean estimated survival was 0.801 for groups that migrated in cooler water and 0.600 for groups that migrated in warmer water, suggesting there may be a threshold temperature around 20°C, above which survival decreases markedly.

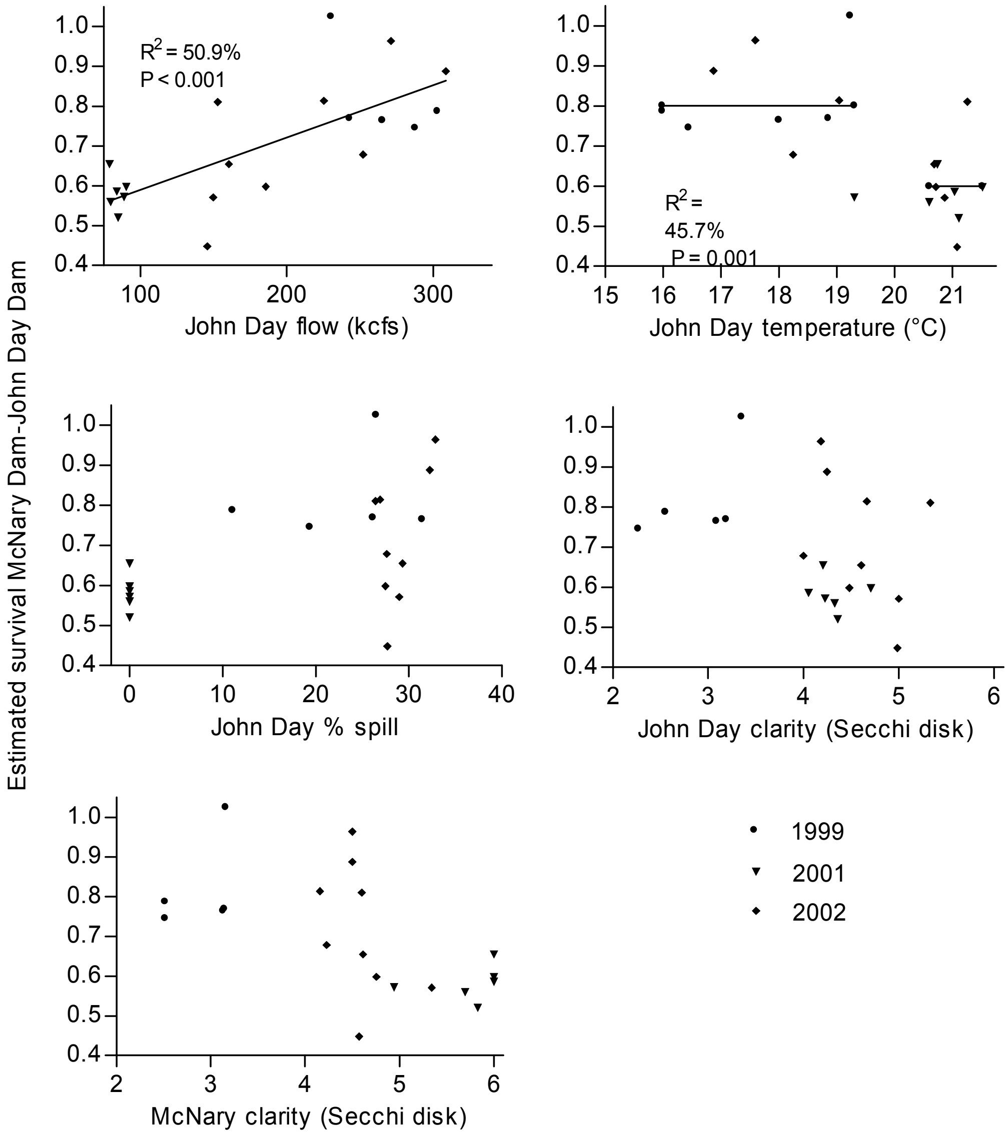


Figure 49. Estimated survival between McNary Dam tailrace and John Day Dam tailrace plotted against various river condition indices for run-of-river subyearling Chinook salmon released in tailrace of McNary Dam, 1999, 2001, and 2002. Flow index panel illustrates simple linear regression line without year effects. Temperature index panel illustrates constant mean survival above and below 20°C.

Discussion

As a consequence of FCRPS dam construction on the main stem of the lower Snake and Columbia rivers, the average travel time of yearling Chinook salmon and steelhead migrating between the confluence of the Clearwater and Snake rivers to the lower river below Bonneville Dam has increased substantially. As a result, for smolts left in-river to migrate, timing of arrival to the estuary and nearshore ocean is delayed on average by several weeks. As discussed in the "Transportation Evaluations" section (page 21), timing of ocean entry can greatly affect SAR. Coupled with the declining lipid reserves in migrating yearling Chinook salmon observed by

Congleton et al. (2004), fish arrived to the estuary later and likely with lower energy reserves than they did prior to completion of the FCRPS, and even more so in low-flow years. It seems reasonable that flow can affect survival below the hydropower system. The data also suggest the possibility of an ocean × FCRPS interaction that causes fish in poor condition to do even worse in years with poor ocean conditions. We have no direct measurements to confirm this speculation. Furthermore, as a consequence of the FCRPS construction, springtime flows and turbidity have been greatly reduced, which likely has led to increased vulnerability of smolts to predators on ocean entry.

Snake River Spring Migrants

For spring migrants from the Snake River (steelhead and yearling Chinook salmon), conclusions regarding the influence of the river environment on travel time and survival depended in very large part on the interpretation of information from the low-flow year 2001. Data from that year were highly influential (or outliers) in univariate analyses of the influence of flow (cf., Figures 33–35 and 42–44). Threshold models for survival versus flow exposure cannot even be estimated without including the low-flow data along with the more moderate- to high-flow data from other years. The 2001 data are crucial to fitting models of flow and survival to data points from 1995 through 2003. This is especially true for the specific threshold models included here, but would be equally true, for example, in data sets that use different groupings (say weekly) at Lower Granite Dam. The 2001 data tends to function much like a single point in such multiyear analyses, particularly the "anchor points" of low survival late in 2001.

Because it is tempting to interpret the threshold models as a prescription for a certain amount of flow, it is crucial to note the extreme imprecision in the breakpoint estimates. The estimated breakpoint for yearling Snake River Chinook salmon was 73.0 kcfs, but bootstrap methods were used to calculate a 95% confidence interval of 70.1 to 99.4. For Snake River steelhead, the situation was even worse: the breakpoint estimate was 115.4 kcfs, but we reach 95% confidence in our interval only if it is as wide as somewhere between 78.9 and 132.6 kcfs. We know that salmonid survival will approach zero if flow is zero, and we know that survival was lower in low-flow 2001 than the more constant survival levels we have seen with moderate to high flow. But the current data give almost no information for establishing an exact threshold above which survival is as high as it can get and below which survival drops off more or less steeply.

The cases where within-year data from 2001 do not fit the multiyear trends (e.g., positive slope between WTT and estimated survival for steelhead within 2001; apparent occurrence of two distinct sets of release groups of yearling Chinook salmon) should lead to closer examination of mortality patterns in 2001. The greatest WTTs (lowest flow volumes) in the entire data set occurred at the beginning and end of 2001 (middle and bottom panels, Figure 50). Both the highest and lowest yearling Chinook salmon survival of 2001 occurred during these periods, which caused the two distinct sets of points (Figure 50). Survival during the peak flows of 2001 was no higher than in the low flows at the beginning of the season. The "missing variable" is water temperature (top panel, Figure 50). In the entire data set of 458 yearling Chinook salmon release groups, only 13 experienced temperature exposures greater than 15°C. Of these, 12

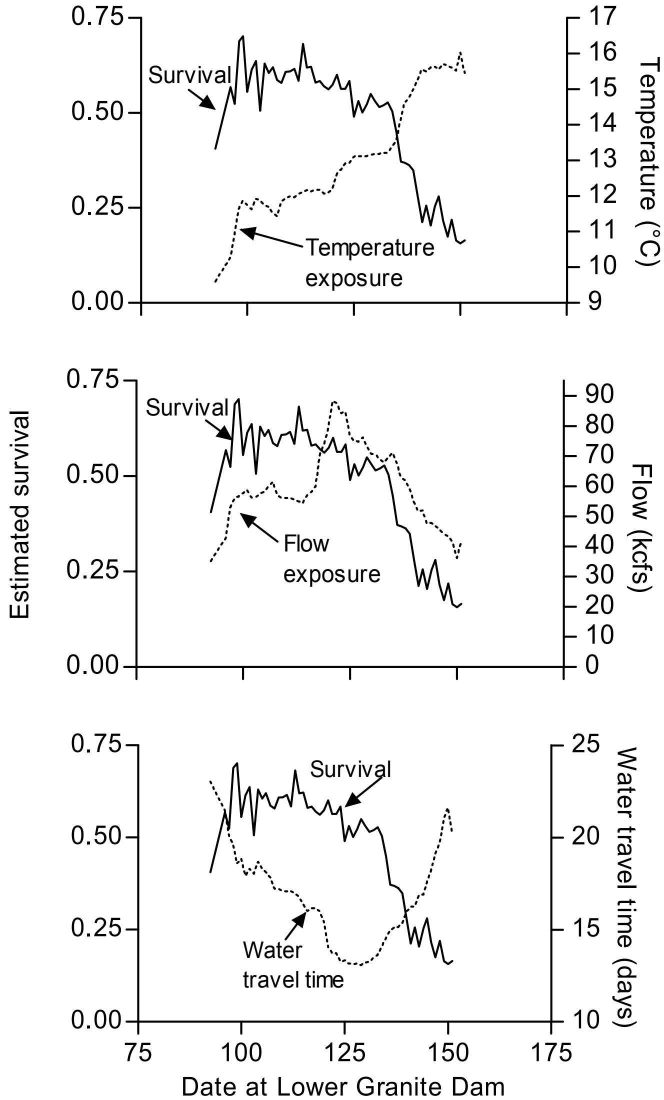


Figure 50. Estimated survival from Lower Granite Dam to McNary Dam for PIT-tagged Snake River yearling Chinook salmon, 2001, plotted with flow exposure, water travel time index, and temperature exposure against data at Lower Granite Dam.

occurred at the end of the 2001 season. The low flows in 2001 extremely influenced past modeled relationships between WTT and survival, particularly because they generally did not consider the unique water temperature pattern that year. Some recent analyses showed that the within-season data from 2001 were better modeled using temperature rather than flow, and Anderson and Van Holmes (2004) concluded that "the relationship [between WTT and survival] is spurious... temperature, not flow, produced the correlation."

The new multivariate analyses in this technical memorandum corroborate the conclusion that exposure to very warm water was likely the most influential environmental condition affecting juvenile salmonid survival in the mainstem Snake River in 2001. However, though the effects are small relative to that of elevated temperature, our results also suggest that at lower temperatures WTT and spill levels also influence survival. Other researchers have also included temperature, WTT, and % spill in multiple linear models to analyze the impact of these factors on juvenile survival (State Managers et al. 2003). The generalized additive and nonlinear multiple-regression models used here advance understanding by providing a more refined model of the nature of the relationships between these variables and juvenile salmonid survival.

For yearling Chinook salmon, when temperatures were below 13°C, our generalized additive and multiple-regression models indicated that variation in survival is relatively small, but that variation was related to WTT and spill. The multiple-regression model for yearling Chinook salmon featured a WTT threshold at 14 days, which was consistent with flow at Lower Monumental Dam of about 70 kcfs. However, having adjusted for temperature, the "flat" part of the fitted model occurred when WTT is greater than 14 days, in which range flows are low, while in the univariate threshold flow model there was a slope in this range. This occurred because of the other variables in the model and because WTT is essentially the inverse of flow. Inversion is a strong transformation, and the resulting models emphasized different parts of the range. In the multivariate model, there was relatively little change in survival over large changes in flow: WTT of 5 days was consistent with 196 kcfs flow at Lower Monumental Dam, and WTT of 10 days occurred with average Lower Monumental Dam flow exposure of 93 kcfs. Predicted survival for these two WTT values differed by only 0.05, equal to the difference in predicted survival for only a 0.4°C difference in temperature when temperature was above 13°C. These results should serve as a further caveat against simple application of the univariate flow threshold model. For steelhead, the multiple-regression model for survival had a linear decrease throughout the entire WTT range, perhaps consistent with the extremely imprecise estimate of a threshold in the univariate flow model.

Multivariate models of survival for both species included functions for % spill. For steelhead, survival increased linearly as % spill increased from 0% to 29.4%, at which predicted survival reached a maximum. Above 29.4%, survival did not increase further (but did not decrease). For models of yearling Chinook salmon, predicted survival reached its maximum at about 20.6% (generalized additive model) or 25.0% (multiple-regression model). In all cases, the point of maximum survival is not precisely estimated; these estimates may be a rough guideline. In the case of yearling Chinook salmon, there was some suggestion that % spill above the maximum could result in decreased survival, particularly when water temperatures were high.

Multivariate models indicated that the condition that had strongest effect on survival of yearling Chinook salmon was high water temperatures. The date on which temperature at Lower Monumental Dam reached 13°C varied from year to year, ranging from 7 May in 1998 to 11 June in 1997. The average date on which this apparent threshold temperature was reached was 25 May. In addition, as noted in the section on juvenile reach survival, Zaugg and Wagner (1973) found that gill Na + –K + ATPase (an indicator of migratory readiness) and migratory urge declined at water temperatures of 13°C and higher. Steelhead that migrate too late in the season, when water temperatures are above this threshold, may have a tendency to residualize. Residualization leads to lower estimates of survival, because mortality and cessation of migration cannot be distinguished using PIT-tag data.

For both species, we observed a strong and consistent relationship between flow and travel time. This suggests that one effect of springtime flow in the Snake River is to help juvenile salmonid migrants move out of the river before temperatures get too high. This might be especially important in low-flow years such as 2001. In this sense, it may be justifiable to interpret the temperature effects on survival we observed, at least to some degree, as indirect flow effects, mediated through smolt travel time.

The strong effects on survival of elevated temperatures, the average late-May date of occurrence of such temperatures, and the relatively minor effects of % spill and WTT are all consistent with previous informal observations that survival for Snake River spring migrants tends to be fairly constant for the first several weeks of the season, beginning in early April and extending to mid to late May, when survival decreases in many years.

However, as reflected in the year-effect coefficients in the multiple-regression models, the level of the nearly constant early to mid-season survival can vary considerably from year to year. This suggests that large-scale processes, most probably related to climate, affect the average quality (vitality) of fish arriving in the FCRPS each year. The magnitude of the estimated year effects, relative to those for the FCRPS-related variables of WTT, water temperature, and % spill suggests that events that occur in the juvenile fish life cyle above the FCRPS partially determine survival through it.

Our results indicate that survival of juvenile migrants through the highly modified FCRPS migration corridor is relatively good at moderate- to high-flow levels, but poor at low-flow levels, particularly for steelhead. At low-flow levels, the FCRPS causes the river to function more like a series of impoundments and less like a river. Prior to dam construction, variations in migration conditions likely had less effect on juvenile survival because the slope of the natural channel gradient provided a lower limit for juvenile migration travel times. With the dams in place and reservoir elevations held constant, at low-flow levels WTT is reduced more than it would be in a free-flowing river with fluctuating levels. At some threshold level, migrants likely lose the cues necessary to migrate successfully.

Run-of-River Subyearling Chinook Salmon from McNary Dam

Based on the data available from run-of-river subyearling Chinook salmon from 1999 through 2002, we have insufficient information to make definitive statements regarding potentially complex dynamics among travel time, survival, and environmental (river) conditions between McNary Dam and John Day Dam. For example, strong correlations among river conditions (flow, spill, temperature) made it impossible to determine which variable had the strongest influence on response variables. Further, because within most years there was a relatively narrow range in river condition values, and with little overlap between years in some cases, it was not possible to separate processes and relations that occur within migration seasons from potential annual differences due to generalized "year effects."

We provide the following conclusions for run-of-river subyearling Chinook salmon from McNary Dam (tempered with the above caveats):

1. Travel time (migration rate) between McNary and John Day dams likely depended on water velocity. Increasing flow had more effect on reducing travel time when flow was low than when it was high.
2. Before adjusting for differences in annual means, estimated survival was significantly correlated with flow, temperature, and % spill at John Day Dam. After adjusting for annual means, only the correlation with flow remained significant. This result apparently occurred because there was not sufficient within-year variation in temperature or % spill indices to distinguish between generalized year effects and direct influence of temperature or % spill. (For example, lower mean survival in 2001 may have been due to the lack of spill at John Day Dam or due to some other difference between years. Lacking periods of 0% spill in the other years, we cannot determine which is the case).
3. Travel time may have affected survival, because faster travel meant less exposure to predators in John Day reservoir.
4. Average survival was nearly constant for water temperature below 19.3°C, and nearly constant, but considerably lower for water temperature above 20.6°C. There may be a threshold temperature, above which increased mortality occurs in this reach.

The relationships identified among flow, temperature, travel time, and survival of subyearling fall Chinook salmon between McNary and John Day dams are consistent with those found for subyearling Chinook salmon in the Snake River (Connor et al. 2003a and 2003b, Smith et al. 2003). In both locations, the effects of flow and temperature were confounded, making it difficult to confidently predict the effect of either variable independently. In laboratory studies, Marine et al. (2004) found that exposure of Sacramento River fall Chinook salmon fry to water temperatures above 20°C resulted in decreased growth, increased osmoregulatory impairment, and increased vulnerability to predation. That temperature value was near the same temperature threshold found to affect survival for fall Chinook salmon migrants in the McNary to John Day Dam reach.

Latent Mortality Associated with the FCRPS

Comparing SAR with estimates of survival through the FCRPS (for both juveniles migrating downstream and adults migrating upstream) clearly indicates that the majority of mortality suffered by both transported and in-river migrants during the smolt-to-adult life stage occurs outside the hydropower system. Current survival within the hydropower system is typically as high or higher than it was during the 1960s, when the FCRPS consisted of only four mainstem dams, and survival for transported fish is even higher. Yet overall adult return rates of Snake River spring migrants have rarely approached estimated return rates from the 1950s and 1960s. Thus considerable effort has gone into studies and analyses to determine why the adult return rates were depressed, particularly for outmigration years 1977–1996. Explanations for the differences in adult return rates range from changes in ocean conditions to "delayed" effects on juveniles as a result of their passage through the hydropower system. Other factors, such as the number of hatchery fish released into the system, may also play a role. We believe all these factors may have contributed to decreased adult returns during at least some part of the last 25 years. While we can identify a number of possible mechanisms to account for differences in stock productivity over time, the debate is fueled by a lack of quantifiable empirical evidence to support or refute competing hypotheses. In the sections that follow, we first define "latent mortality" and attempt to eliminate some of the confusion associated with this definition. Then we discuss efforts to quantify latent mortality, including the use of downstream stocks as controls for upstream stocks.

Definitions

We define latent mortality associated with the FCRPS (for Snake River fish) as any mortality that occurs after fish pass Bonneville Dam as juveniles that would not occur if the FCRPS dams did not exist. Latent mortality associated with the FCRPS might result from changes in migration timing; injuries or stress incurred during migration through juvenile bypass systems, turbines, or spill at dams that does not cause direct mortality; disease transmission or stress resulting from the artificial concentration of fish in bypass systems or barges (Williams 2001, Budy et al. 2002); depletion of energy reserves from prolonged migration (Congleton et al. 2004); altered conditions in the estuary and plume as a result of FCRPS construction or operation; or disrupted homing mechanisms.

To standardize the discussion, we introduce the following notation (Figure 51). First, we designate survival terms using S and mortality terms using $\mu = 1 - S$. Terms for in-river migrants are denoted by the subscript I and terms for transported fish by the subscript T. We partition survival and mortality into the following life stages: downstream migration through the hydropower system (subscript ds), estuary/ocean (subscript e/o), and upstream migration through the hydropower system (subscript us). We further partition the estuary/ocean stage to reflect

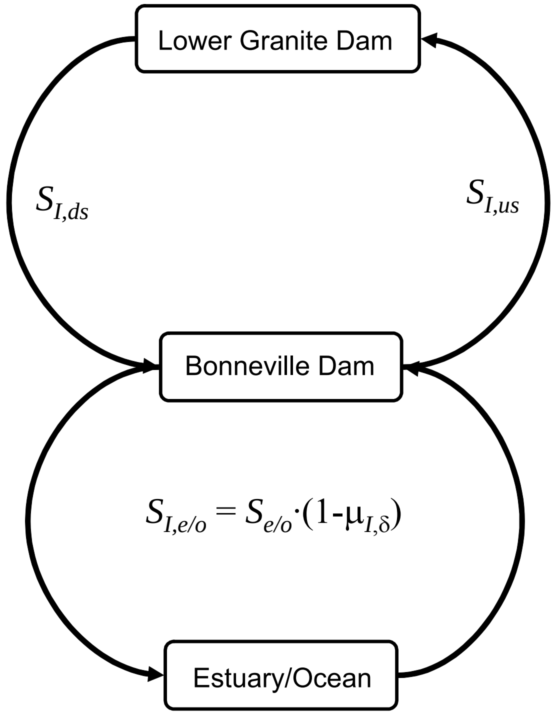


Figure 51. Survival (S) and mortality (μ) affecting Snake River anadromous salmonids migrating in-river (denoted by subscript I) at various life stages. The life stages are: downstream migration through the hydropower system (ds), estuary/ocean (e/o), and upstream migration through the hydropower system (I). The estuary/ocean survival is partitioned into survival that would occur in the absence of the hydropower system ($s_{e/o}$) and latent mortality associated with the passage through the hydropower system ($\mu_{I,\alpha}$). Transported fish (denoted by subscript T) are affected by the same survival and mortality processes and are represented by changing the subscript I to T.

mortality that would occur in the absence of the hydropower system ($S_{e/o}$) and hydropower system-related latent mortality (subscript δ), which applies to both transported fish and in-river migrants. This partitioning of estuary/ocean survival reflects an assumption that for in-river fish, latent mortality is essentially entirely expressed in the estuary/ocean stage. Thus SAR of in-river and transported fish are expressed as

$$SAR_I = S_{I,ds} \cdot S_{e/o} \cdot (1 - \mu_{I,\delta}) \cdot S_{I,us} \tag{15}$$

$$SAR_T = S_{T,ds} \cdot S_{e/o} \cdot (1 - \mu_{T,\delta}) \cdot S_{T,us} \tag{16}$$

Note that we use the same natural seawater survival ($S_{e/o}$) for both in-river and transported fish. This is the survival that fish would experience in the absence of dams. Also, we use different upstream survival terms for in-river and transported fish. Differential upstream survival for the two groups could result from latent mortality for transported fish related to impaired homing, for example. Based on the equations above, we express D as:

$$D = \frac{(1 - \mu_{T,\delta}) \cdot S_{T,us}}{(1 - \mu_{I,\delta}) \cdot S_{I,us}} \tag{17}$$

Note that any difference in upstream survival between transported and in-river juvenile migrants is also expressed in *D*.

The term "latent mortality associated with the FCRPS" encompasses several definitions used in the past: delayed mortality, extra mortality, and *D,* all of which have specific definitions but have often been used loosely and almost interchangeably. Extra mortality is a term that arose in the PATH process. Marmorek and Peters (2001) defined extra mortality as

> . . . any mortality occurring outside of the juvenile migration corridor that is not accounted for by either: 1) productivity parameters in spawner-recruit relationships; 2) estimates of direct mortality within the migratory corridor (from passage models); or 3) for the delta model only, common year effects affecting both Snake River and Columbia River stocks. Extra mortality can in theory occur either before or after the hydropower migration corridor.

Thus extra mortality is purely a modeling construct. Further, hydropower effects were just one of several hypotheses that were proposed in PATH to explain extra mortality. Thus "extra mortality" is not synonymous with "latent mortality related to the hydropower system." For this reason, we do not use the term extra mortality (a modeling construct) to describe hydropower system-related latent mortality.

Another source of confusion arises from the relationship between *D* and "delayed" mortality associated with in-river migrants. *D* refers to the ratio of smolt:adult survival (measured from below Bonneville Dam to Lower Granite Dam) of transported fish relative to that of in-river migrants. Because *D* is typically below 1.0 for Snake River spring-summer Chinook salmon and steelhead, it provides one measure of latent mortality for transported fish, but not an absolute measure; it is only relative to in-river fish. This latent mortality may result from stress experienced on the barge, disruption of timing to the estuary, or increased straying or fallback of adult migrants. While we cannot identify specific mechanisms that lead to $D < 1.0$, we can directly estimate *D*, because it relates to the juvenile survival and SAR for in-river migrants. Of course, the SAR for in-river migrants includes any hydropower-related latent mortality, so the magnitude of *D* depends on the magnitude of latent mortality of in-river migrants. Thus *D* is not an absolute measure of the latent mortality of transported fish, because the amount of latent mortality expressed in *D* varies with hypothesized (not measured) levels of hydropower-related latent mortality of in-river migrants.

Efforts to Quantify the Magnitude of FCRPS Latent Mortality

Quantifying the magnitude of latent mortality (for either transported or in-river migrants) is extremely difficult. This is primarily because no suitable control exists. Several methods have been explored to overcome this shortcoming, and in this section we discuss several of them.

Upstream/Downstream Comparisons

In attempting to evaluate FCRPS impacts on upper Columbia and Snake River basin stocks, several groups of people (Marmorek et al. 1998 and 2004, Schaller et al. 1999, Deriso et al. 2001) have conducted analyses using downstream stocks (e.g., spring Chinook salmon from the John Day River basin) as controls for upstream stocks (e.g., spring-summer Chinook salmon from the Snake River basin), while Zabel and Williams (2000) pointed out potential problems with these analyses.[8] Schaller et al. (1999) observed differential temporal responses in productivity between upstream and downstream stocks after completion of the final four hydropower dams on the lower Snake and Columbia rivers. They attributed these changes to the hydropower system, but they did not estimate latent mortality per se. Deriso et al. (2001) estimated differential mortality between upstream and downstream stocks. When considering a variety of assumptions about potential direct mortality incurred passing through the mainstem dams on the Snake and Columbia rivers, they observed that upstream stocks consistently suffered more mortality than could be attributed to changes from historical productivity patterns. Certainly the initial completion of dams in the Snake River caused drastic changes in Snake River stock productivity, and thus their initial decreased productivity compared to downstream stocks was not surprising. However, given the large changes in FCRPS dams and operations that juvenile migrants presently encounter compared to the initial years following completion of the dams (Williams and Matthews 1995) and the substantial increase in juvenile migrant survival compared to earlier years (Williams et al. 2001), latent mortality mechanisms would likely need to have changed over the last 25 years to explain continued differences in productivity patterns between upstream and downstream stocks. So while analyses of the covariability of populations are inherently interesting, we also think it is extremely difficult to ascribe differences in variability among stocks to particular factors, particularly those that represent a relatively small proportion of the entire life cycle (such as migration through the hydropower system). Below we provide several lines of reasoning.

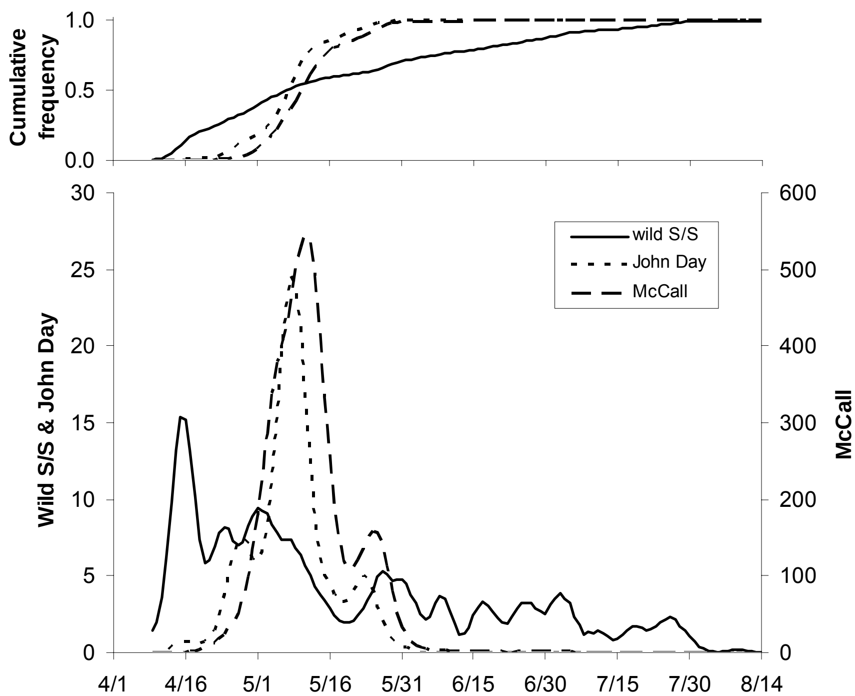
Salmon biology

Salmon populations are notorious for their local adaptation (Richer 1972, Taylor 1991, Unwin and Glova 1997, Hendry et al. 2000), which has led to extreme biodiversity among populations (Hilborn et al. 2003). Even within salmon populations, a diversity of life history strategies are supported, and differential growth opportunities between freshwater and seawater habitats, along with cost of migration, are presumed factors that contribute to the selection of life history traits (Gross 1987, Randall et al. 1987, Gross et al. 1988, Taylor 1990a). Further, upstream/downstream comparisons of past modeling efforts assumed that the major source of environmentally induced variability in salmon productivity arose from ocean conditions, and that the two stock groupings would show high levels of covariability under the assumption that they shared a common ocean habitat. However, Bradford (1995) concluded that, across all of the salmon species he analyzed, the freshwater environment contributed considerably to the variability in egg-to-adult survival. Further, Myers et al. (1997) found no correlation between freshwater survival rates among salmon populations more than a few hundred kilometers apart. As just one example of differences between John Day River spring Chinook salmon stocks and the wild stocks from the Snake River basin, the former have a relatively narrow migration window,

[8] For further discussion of analyses using downstream stocks, see Appendix A.

based on PIT-tag detections at Bonneville Dam, while the latter, representing the untagged population, have a very extended migration (Figure 52) based on estimated timing of transported PIT-tagged fish to below Bonneville Dam. Furthermore, hatchery fish from McCall, which have demonstrated the highest SAR for hatchery fish in the Snake River, also showed a narrow migration window similar to those wild fish from the John Day River. As noted earlier, migratory timing can have a large influence on adult returns. Thus we believe it is likely that poor correlation in freshwater survival could exist between upstream and downstream stocks. Not surprisingly then, salmon populations from distinct Columbia River basin regions responded differently to large-scale climate patterns (Levin 2003), and poor correlation existed between productivity patterns of upstream and downstream Columbia River stocks (Botsford and Paulsen 2000).

Figure 52. Five-day running average of the number of smolts arriving at Bonneville Dam in 2000 for fish



from the John Day River migrating in-river, and for two fish groups transported from Lower Granite Dam (wild fish from the Snake River and McCall Hatchery fish). The relatively early and protracted arrival timing of the wild Snake River fish is evident in the cumulative frequency plot.

Potential problems with models

All the analyses listed above relied on models, yet using models with potentially mis-specified parameters has added another element of uncertainty. All the analyses assumed without testing that the Ricker model appropriately described the population dynamics of the analyzed populations. In fact, the Ricker model is often rejected when compared to simpler models of Snake River stocks (Zabel and Levin 2002). Further, the use of spawner and reconstructed recruit data constitutes a model that requires several assumptions. The potential multiplication of errors associated with the stock reconstructions could have potentially led to unidentified bias. One assumption in particular might have accounted for many temporal differences between upstream and downstream stocks identified in the analyses. In the run reconstructions for PATH, values used for adult survival generally ranged from 40% to 60% through eight dams (Marmorek et al. 1998). Recent data from PIT tags suggest that adult upstream survival exceeds 85% for yearling Chinook salmon (see Table 11). Thus, when models used conditions with eight dams in place and compared them to what might occur with four dams removed, the high upstream adult mortality used in the models resulted in an inflation of the upstream/downstream differences attributed to latent mortality. Further, the models used in the analyses generally ignored differential environmental effects that occurred in several distinct life stages, particularly those associated with freshwater spawning and rearing.

Potential problems with data used

Data quality problems exacerbated the problems with models. Past spawner counts were notoriously noisy because of the high degree of sampling error (Holmes 2001), which led to limited power to detect effects with these data (Hinrichsen 2001). Thus using these data to measure the magnitude of latent mortality is problematic. Further, data quality was unequal among populations. The John Day populations in particular lacked age composition data in early years. Zabel and Levin (2002) demonstrated that the practice of applying mean-age com-positions to returning adults in run reconstruction led to severe biases in estimated stock-recruit model parameters. When we considered all these sources of uncertainty, we concluded that the uncertainty of any estimate of FCRPS-related latent mortality using upstream/downstream comparisons was large enough to render the estimates misleading and essentially useless.

Multiply Bypassed Fish

The comparison of SAR from in-river migrants with different juvenile migration histories showed that, for some stocks in some years, multiply bypassed fish returned at significantly (one-sided tests) lower rates than fish that were never detected in a bypass system (Sandford and Smith 2002). Most data from the 1995 through 1998 outmigrations indicated that multiply bypassed spring-summer Chinook salmon and hatchery steelhead had lower SAR than those not detected at collector dams (Figures 53 and 54). Budy et al. (2002) interpreted this as direct evidence that fish passing through bypass systems suffered “delayed” mortality. However, in more recent data, SAR did not differ for wild steelhead (2000 outmigration) or wild Chinook salmon (1999 and 2000 outmigrations) (Figures 53 and 54).

In this subsection we present an alternative hypothesis for the observation that multiply detected fish sometimes returned at lower rates than nondetected fish. We hypothesize that because bypass systems select for smaller fish (see discussions related to Figures 25 and 26) and that smaller fish typically have returned at lower rates (see the “Selective Mortality” section, page 119), multiply bypassed fish would also return at comparatively lower rates.

To test this hypothesis, we examined whether the combination of observed patterns in size-selective guidance and size-selective mortality could lead to lower return rates of multiply

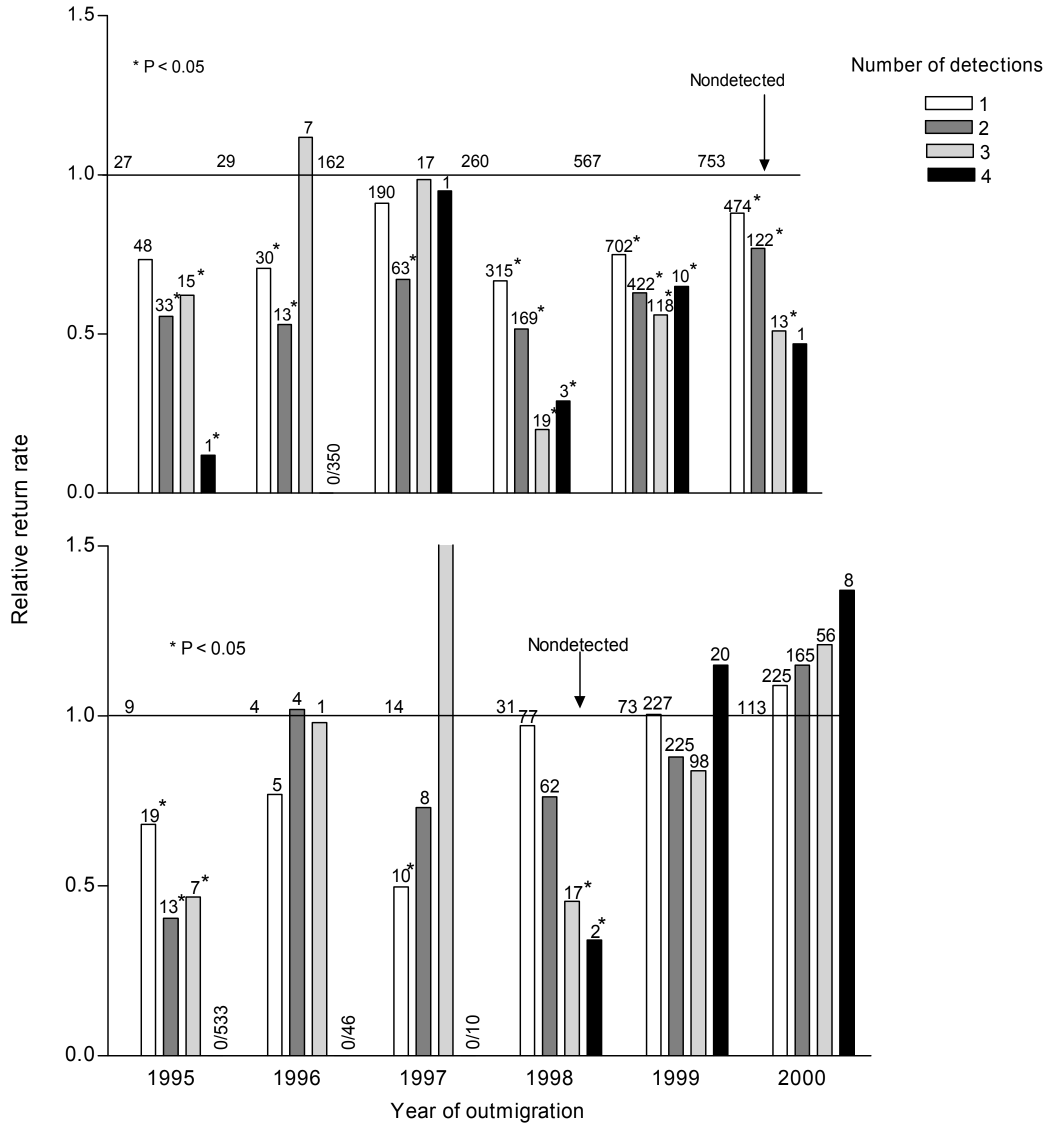


Figure 53. Relative adult return rates of hatchery (top chart) and wild (bottom chart) spring-summer Chinook salmon marked above Lower Granite Dam and detected between 0 and 4 times during their migration through Lower Granite, Little Goose, Lower Monumental, and McNary dams. Nondetected fish had a relative return rate of 1.0. Numbers above the line and bars indicate total adult returns. Lack of a bar indicates no adults returned (0 adults/estimated number of juveniles).

bypassed fish. We did not attempt to predict return rates for specific years and stocks, rather we examined general behavior based on data from wild spring Chinook salmon and steelhead. First we allowed the slope parameter of the size-selective guidance relationship to vary across observed values. We then used these relationships to estimate size distributions of nondetected fish and fish detected three times (out of four opportunities). We then assumed that size-selective mortality varied linearly with fish length, and we estimated the slope of this relationship for various values in the range of observed selection coefficients. Based on this estimate, we

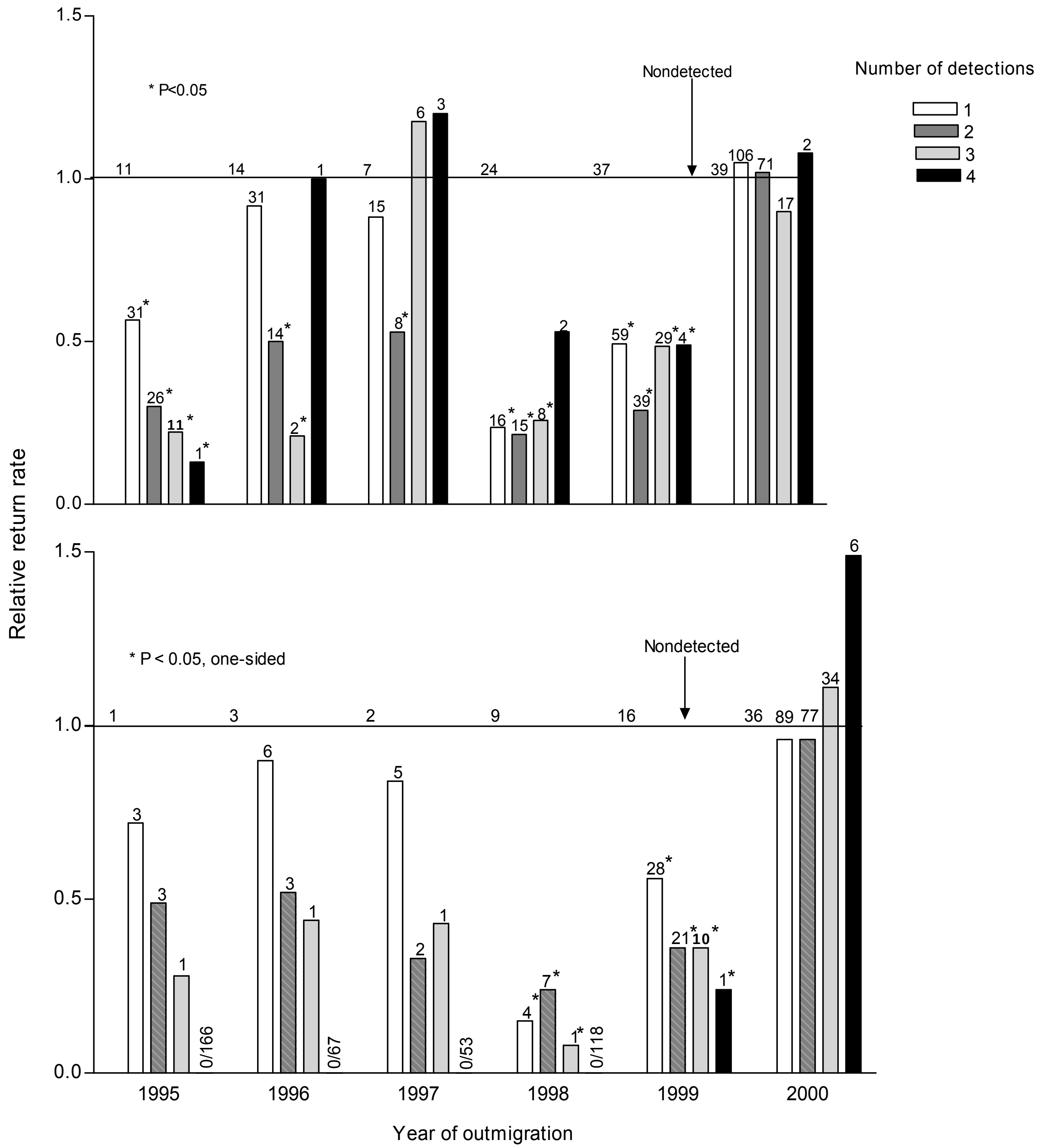


Figure 54. Relative return rates of hatchery (top chart) and wild (bottom chart) steelhead marked above Lower Granite Dam and detected between 0 and 4 times during their migration through Lower Granite, Little Goose, Lower Monumental, and McNary dams. Nondetected fish had a relative return rate of 1.0. Numbers above the line and bars indicate total adult returns. Lack of a bar indicated no adults returned (0 adults/estimated numbers of juveniles).

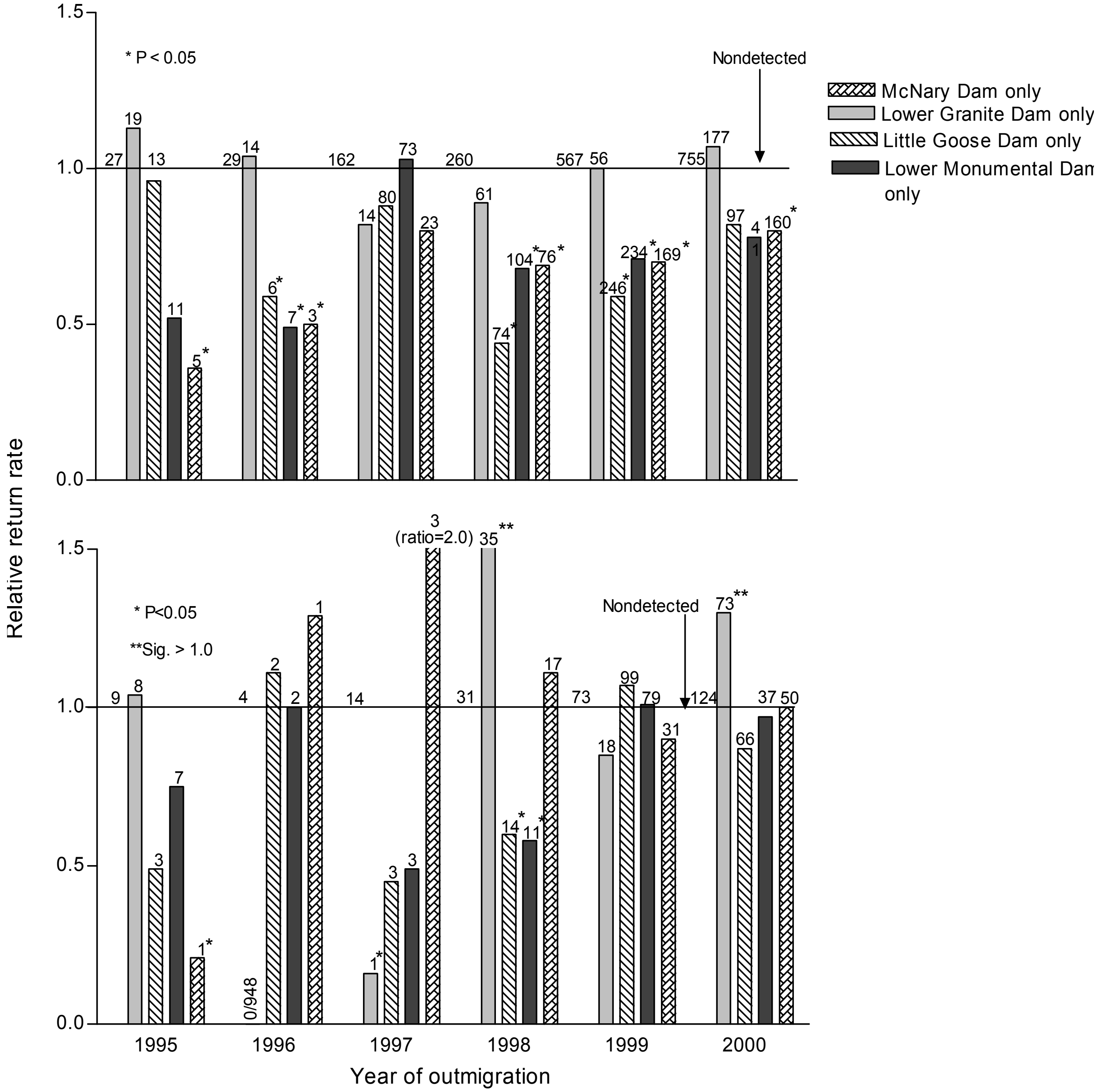


Figure 55. Relative adult return rates of hatchery (top chart) and wild (bottom chart) spring-summer Chinook salmon marked above Lower Granite Dam and detected only at Lower Granite, Little Goose, Lower Monumental, or McNary dams. Nondetected fish had a relative return rate of 1.0. Numbers above the lines indicated total adult returns. Lack of a bar indicated no adults returned (0 adults/estimated number of juveniles).

then compared return rates of multiply detected to nondetected fish (Figure 55). From this analysis, we concluded that the combination of size-selective guidance and size-selective mortality can lead to substantially depressed return rates of multiply detected fish. Further, and potentially independent of size, differential collection may occur because of the physiological condition of fish. In 1987 and 1989 at Lower Granite Dam, Elliot and Pascho (1991) found consistently higher levels of BKD in fish guided into gatewells (equivalent to detected PIT-tagged fish) than for fish collected in fyke nets (equivalent to undetected PIT-tagged fish passing through turbines). Thus multiply bypassed fish could presumably die at higher rates than nondetected fish. Differential guidance of less fit fish may also explain why transported fish returned at lower rates than nondetected fish.

A further complication is that return rates vary by specific detection sites (Figures 56 and 57). In particular, fish only detected at Lower Granite Dam tend to return at higher rates than nondetected fish, while fish detected at the lower dams tend to return at lower rates. This could result either from different selection regimes (for size or other traits such as disease level) exist-ing at the bypass systems, or from different bypass configurations, or some combination of both. For example, the Lower Granite Dam bypass system does not contain fish separation by size capability; therefore fish do not encounter the same amount of dewatering structures and flumes as do fish at the lower three dams. The complexity of the issue certainly merits continued study.

Given the propensity for bypassed fish to return at lower rates, we emphasize that it is important to take care when identifying control fish. We note that in all our evaluations, transportation effectiveness and estimates of *D* relied on nondetected fish to represent in-river migrants, yet these fish that did not enter bypass systems at collector dams represented less than 30% of the population. Thus in the future, if we consider alternative operational scenarios that include less transportation than presently occurs, we will need to reconsider the population of control fish to accurately represent potential in-river migrants.

Disrupted Timing

The construction of the FCRPS has resulted in the extension of travel times of downstream migrants. Zabel and Williams (2002) observed that for 1 out of 2 years they analyzed, in-river migrants that migrated earlier in the season returned at higher rates than later migrants. This pattern also occurred in 2 of the 3 years analyzed since then (see “Selective Mortality” section, page 119). Thus, delayed entry into the estuary may have led to lower return rates, which is a form of latent mortality associated with passage through the hydropower system. More detailed analyses with more years of data hold promise to estimate the magnitude of this effect. Similarly, fish transported as juveniles, particularly early in the season, arrived below Bonneville Dam earlier than they would have had they migrated through a free-flowing river. We believe this has also contributed to poorer than expected return rates, which again is a form of latent mortality.

Latent Mortality of Transported Fish

We believe the strongest evidence for some form of latent mortality is that estimates of *D* are consistently well below 1.0 for all Snake River ESUs. Since transported fish return from below Bonneville Dam at substantially lower rates than in-river migrants, they must suffer from some form of latent mortality. Regardless of the cause—timing issues, greater susceptibility to predation, disease or stress due to crowding, or problems with homing—transported fish incurred mortality as a result of transportation that was not expressed until after the fish were released from the barges.

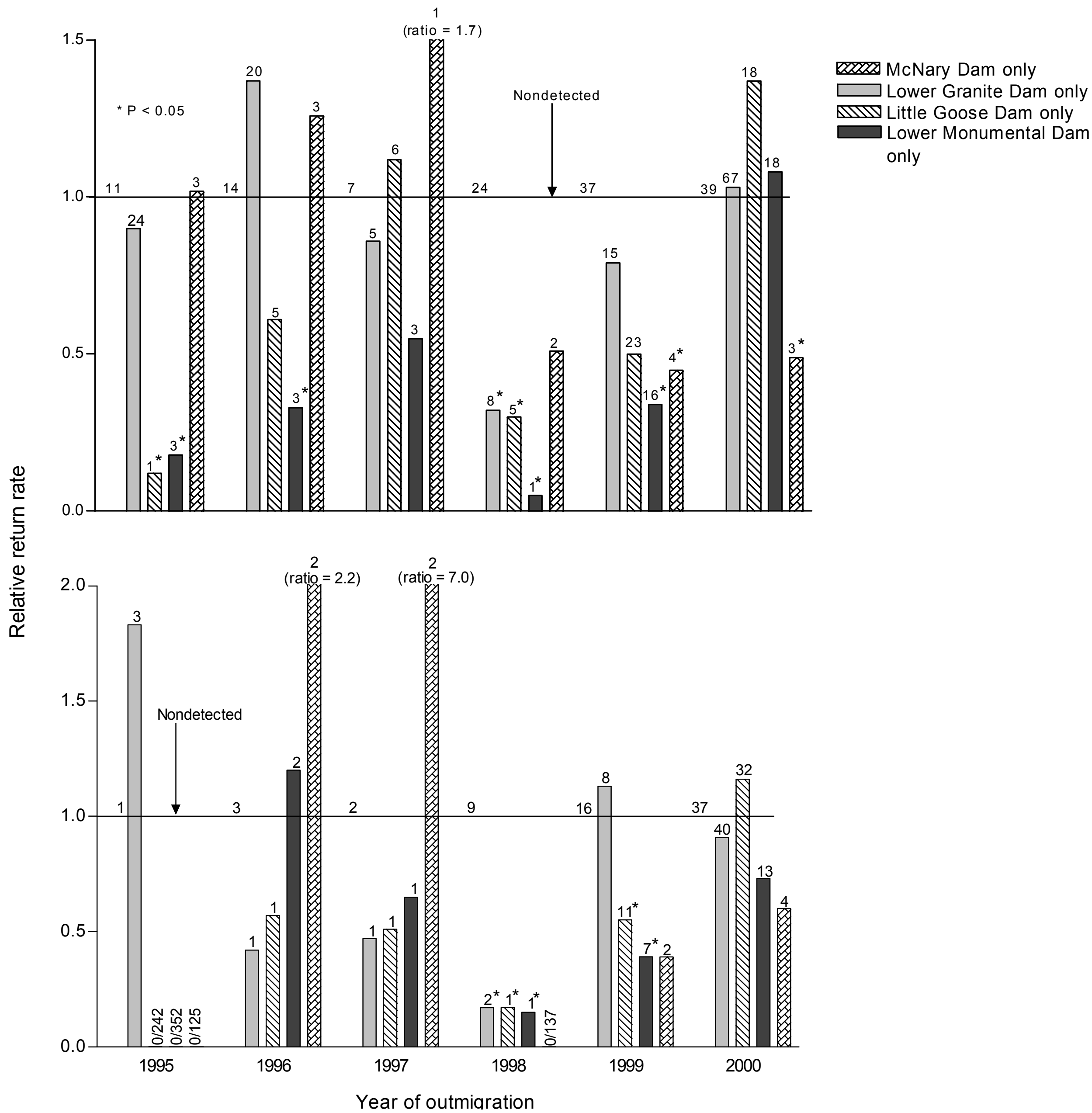


Figure 56. Relative adult return rates of hatchery (top chart) and wild (bottom chart) steelhead marked above Lower Granite Dam and detected only at Lower Granite, Little Goose, Lower Monumental, or McNary dams. Nondetected fish had a relative return rate of 1.0. Numbers above the lines indicated total adult returns. Lack of a bar indicated no adults returned (0 adults/estimated number of juveniles).

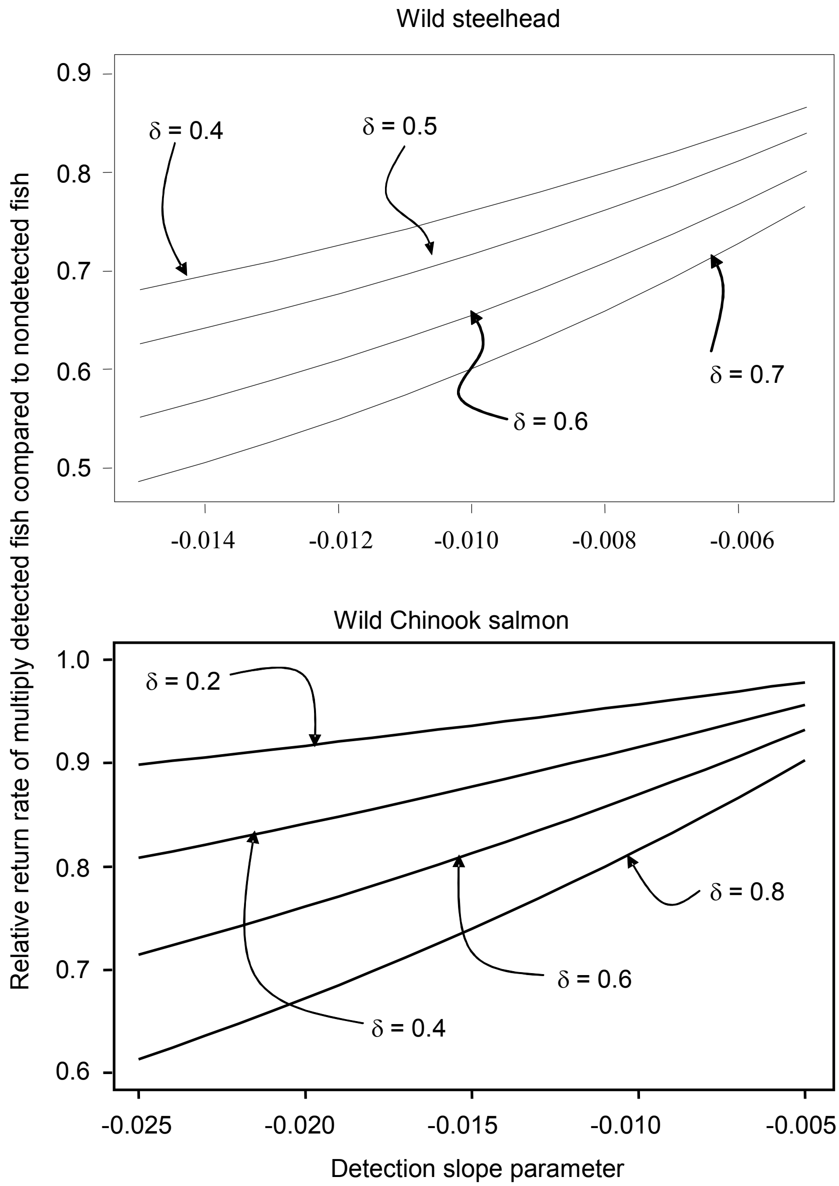


Figure 57. Relative return rates of multiply bypassed fish compared to nondetected fish under a range of values for the slope parameter of the length-selective guidance relationship and the length-based selection coefficient.

Discussion

Based on the evidence presented above, clearly some level of latent mortality exists. However, we have very limited capability to precisely estimate the overall magnitude of hydropower system-related latent mortality for either transported fish or nondetected in-river migrants. Certainly we have much stronger evidence for substantial latent mortality of transported fish (see values of *D* in the "Transportation Evaluations" section, page 21). For in-river migrants, and based on the likely disruption of historical migration-timing patterns, an assumption that some level of latent mortality exists appeared reasonable. However, recent return rates of wild fish, and modeling efforts that suggest the ability to predict them (see the "Large-Scale Processes" subsection, page 123), imply that hydropower system-related latent mortality under the ocean conditions that juveniles encountered in 1999 and 2000, in and of itself, would not prevent stocks from returning to abundances observed before the hydropower system was completed. We do not argue that recent return rates could not have been even higher—we have no evidence for this one way or another. We also recognize the possibility that much higher latent mortality may have existed when smolts experienced poor ocean conditions. Our observation that length-related, selective mortality appeared related to ocean conditions does support a hypothesis that latent mortality might increase under poor ocean conditions. However, little other evidence supports or refutes this hypothesis. So we are left with the rather unsatisfying conclusion that for in-river migrants, hydropower system-related latent mortality ranges somewhere from very weak to potentially strong. Further, we have little data at present to discern among this broad range of alternatives.

Selective Mortality

As indicated in the previous section, numerous factors affect SAR. Some recent efforts by Zabel and Williams (2002) determined that size and migration timing of fish within popula-tions influenced SAR. In this section we expand on results from Zabel and Williams (2002).

The first step in the analysis involved calculating the directional selection coefficient (Endler 1986), which for trait *x* is defined as

$$\delta = \frac{\bar{x}_R - \bar{x}_T}{\sqrt{\mathrm{var}_T}} \tag{18}$$

where $\bar{x}$ is the mean value of the trait in the entire tagged population (*T*) and in returning adults (*R*). Note that the returning adults represented a subpopulation of the entire tagged population, and we refer to their traits at the time of tagging. If the trait is length, for instance, then a positive value of δ means that larger fish returned at a higher rate than smaller ones. We performed a Monte Carlo test to determine whether the selection coefficient was significantly different from zero (for details, see Zabel and Williams 2002).

In the top plot of Figure 58, points above the horizontal dashed line (i.e., greater than 0) indicate that larger fish returned at greater rates than smaller ones. In the bottom plot, points below the line (i.e., less than 0) indicate that earlier migrants returned at greater rates than later migrants, and the opposite held true for points above the line.

When we updated the results from Zabel and Williams (2002) by adding more years (1998 through 2000 for Snake River spring-summer Chinook salmon and Snake River steelhead for 1999 and 2000), the main conclusions still held: the size of individuals and the timing of their outmigration strongly influenced return rates. Selective mortality based on fish length was generally not as strong in 1998 through 2000 as it was in 1995 and 1996 for spring-summer Chinook salmon (perhaps due to better ocean conditions), although the level of length-based selective mortality was similar across years for transported wild fish (Figure 58 and Table 42). For the 2 years of data on steelhead return rates, we observed strong length-based selective mortality, with steelhead in all groups incurring greater selective mortality than Chinook salmon (Figure 58 and Table 42). In-river spring-summer Chinook salmon migrants early in the season typically returned at higher rates, as demonstrated by negative selection coefficients ($P < 0.05$ for 4 out of 5 years for wild fish and 3 out of 5 years for hatchery fish) (Table 43). While the magnitude of timing-based selection varied yearly for in-river migrants, the pattern of variability was consistent among hatchery and wild Chinook salmon and steelhead, with strong selection in 1995, 1998, and 2000 and weaker selection in 1995 and 1999 (Figure 58, bottom plot). Timing-based selection was variable for transported fish, with fish transported early in the season returning at higher rates in some years, and fish transported later returning at higher rates in other years. Also, there was little consistency between wild and hatchery Chinook salmon.

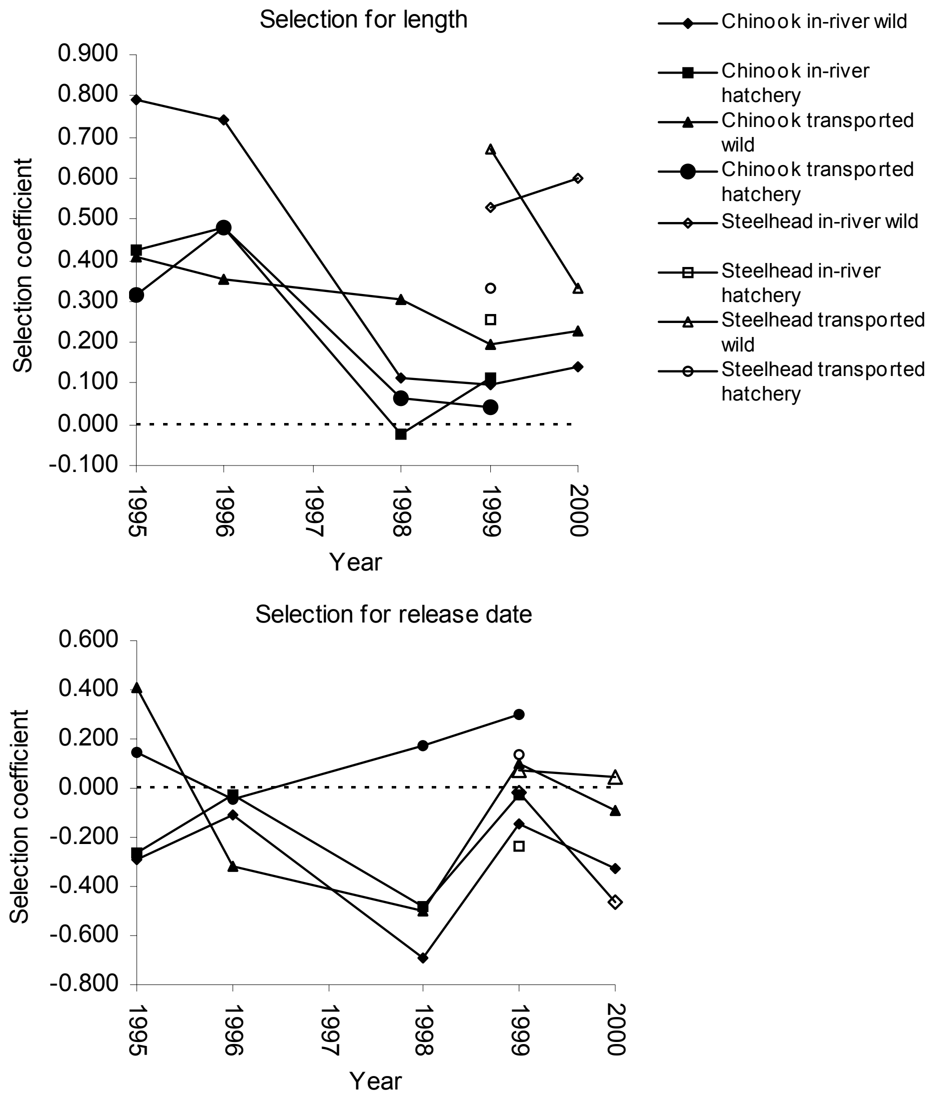


Figure 58. Selection coefficients by year for length at release (top) and release date (bottom).

Table 42. Sample size (*N*) and mean length (mm) at tagging (standard errors are in parentheses) for the total tagged population and returning adults of Snake River spring-summer Chinook salmon and steelhead PIT tagged at Lower Granite Dam, 1995–2000.

	Total population		Returning adults		%		
Release group	***N***	**Mean length**	***N***	**Mean length**	**return**	δ[a]	**P value**[b]
Snake River spring-summer Chinook salmon							
1995							
In-river wild	5,331	107.37 (0.11)	5	113.80 (3.44)	0.094	0.790	0.039
In-river hatchery	21,596	136.55 (0.12)	62	143.95 (2.20)	0.287	0.422	0.001
Transport wild	3,369	106.84 (0.14)	12	110.17 (2.87)	0.356	0.409	0.079
Transport hatchery	15,583	136.17 (0.14)	93	141.62 (1.30)	0.597	0.315	0.002
1996							
In-river wild	1,392	109.31 (0.07)	7	115.00 (1.83)	0.050	0.741	0.023
In-river hatchery	53,420	139.45 (0.06)	53	146.59 (2.31)	0.099	0.479	0.001
Transport wild	8,656	110.49 (0.08)	10	113.00 (1.50)	0.116	0.351	0.139
Transport hatchery	36,867	139.62 (0.07)	53	146.30 (2.14)	0.144	0.477	0.001
1998							
In-river wild	8,676	113.01 (0.07)	53	113.75 (0.82)	0.611	0.115	0.208
In-river hatchery	61,541	135.72 (0.05)	229	135.43 (0.75)	0.372	-0.025	0.643
Transport wild	5476	111.97 (0.09)	33	114.09 (1.13)	0.603	0.306	0.036
Transport hatchery	38,773	135.95 (0.06)	243	136.73 (0.67)	0.627	0.062	0.169
1999							
In-river wild	11,827	109.38 (0.08)	152	110.20 (0.58)	1.285	0.099	0.106
In-river hatchery	61,491	137.82 (0.05)	891	139.29 (0.43)	1.449	0.114	0.001
Transport wild	8,113	109.43 (0.09)	172	111.05 (0.56)	2.120	0.196	0.004
Transport hatchery	43,169	138.16 (0.06)	866	138.71 (0.37)	2.006	0.042	0.110
2000							
In-river wild	42,899	110.38 (0.03)	605	111.37 (0.27)	1.410	0.139	0.000
Transport wild	15,414	109.77 (0.06)	261	111.41 (0.43)	1.693	0.228	0.000
Snake River steelhead							
1999							
In-river wild	8,338	186.36 (0.30)	64	200.80 (3.68)	0.768	0.528	< 0.001
In-river hatchery	59,487	218.78 (0.10)	380	224.81 (1.25)	0.639	0.253	< 0.001
Transport wild	5853	186.56 (0.35)	82	204.66 (3.06)	1.401	0.672	< 0.001
Transport hatchery	40,525	219.61 (0.12)	439	227.60 (1.11)	1.083	0.333	< 0.001
2000							
In-river wild	47,998	184.69 (0.13)	936	201.72 (1.11)	1.950	0.602	< 0.001
Transport wild	22,212	183.77 (0.18)	959	192.70 (0.95)	4.317	0.331	< 0.001

[a] δ is the selection coefficient (see eq. 17).

[b] P value is based on a Monte Carlo test to determine if it is greater than 0. If $P < 0.05$, then δ is significantly greater than 0 at the $\alpha = 0.05$ level.

Table 43. Sample size (*N*), mean release day of the year (standard error is in parentheses) for the total tagged population and returning adults of Snake River spring-summer Chinook salmon and steelhead PIT tagged at Lower Granite Dam.

	Total population		Returning adults				
Release group	***N***	**Mean rls date**	***N***	**Mean rls date**	**% return**	**δ[a]**	**P value[b] (2 tailed)**
Snake River spring-summer Chinook salmon							
1995							
In-river wild	31,766	119.81 (0.10)	63	114.81 (1.94)	0.198	–0.290	0.007
In-river hatchery	104,279	121.06 (0.03)	321	118.42 (0.43)	0.308	–0.268	0.000
Transport wild	21,359	119.84 (0.10)	78	125.77 (2.07)	0.365	0.410	0.000
Transport hatchery	81,780	120.95 (0.03)	455	122.29 (0.40)	0.556	0.143	0.001
1996							
In-river wild	14,078	117.62 (0.09)	7	116.43 (4.27)	0.050	–0.112	0.427
In-river hatchery	53,976	126.52 (0.04)	53	126.23 (1.97)	0.098	–0.030	0.416
Transport wild	8699	117.80 (0.11)	10	114.5 (2.62)	0.115	–0.314	0.167
Transport hatchery	37,027	126.09 (0.05)	53	125.68 (1.41)	0.143	–0.042	0.382
1998							
In-river wild	8,714	111.93 (0.13)	53	103.79 (1.14)	0.608	–0.687	< 0.001
In-river hatchery	61,853	114.55 (0.04)	230	109.17 (0.61)	0.372	–0.481	< 0.001
Transport wild	5,496	111.83 (0.16)	34	106.09 (1.44)	0.619	–0.499	< 0.001
Transport hatchery	39,032	114.96 (0.06)	245	116.86 (0.68)	0.628	0.174	0.004
1999							
In-river wild	11,853	118.79 (0.13)	152	116.65 (0.73)	1.282	–0.148	0.029
In-river hatchery	61,742	121.88 (0.04)	892	121.67 (0.29)	1.445	–0.023	0.242
Transport wild	8128	119.88 (0.14)	172	121.11 (0.75)	2.116	0.098	0.101
Transport hatchery	43,305	122.74 (0.04)	867	125.37 (0.27)	2.002	0.296	< 0.001
2000							
In-river wild	43,241	124.55 (0.08)	610	119.29 (0.51)	1.411	–0.331	< 0.001
Transport wild	15,535	120.37 (0.13)	261	118.97 (0.89)	1.680	–0.087	0.078
Snake River steelhead							
1999							
In-river wild	8361	124.41 (0.16)	64	124.08 (1.73)	0.765	–0.022	0.431
In-river hatchery	59,759	128.26 (0.05)	381	125.16 (0.56)	0.638	–0.234	< 0.001
Transport wild	5872	126.40 (0.19)	83	127.40 (1.31)	1.413	0.069	0.263
Transport hatchery	40,771	128.29 (0.06)	442	130.00 (0.53)	1.084	0.134	0.003
2000							
In-river wild	48,357	117.22 (0.05)	941	112.02 (0.24)	1.946	–0.467	< 0.001
Transport wild	22,360	113.00 (0.06)	964	113.45 (0.26)	4.311	0.049	0.059

[a] δ is the selection coefficient (see eq. 17).

[b] P value is based on a Monte Carlo test to determine if it is greater than or less than 0. If $P < 0.05$, then δ is significantly greater or less than 0 at the $\alpha = 0.05$ level.

Discussion

In this section, we consider important issues that do not fit into the major topics presented in the preceding sections. We also discuss issues that tie together conclusions from several sections.

Large-Scale Processes

Increasing evidence points to dramatic changes in the marine ecosystem of the North Pacific Ocean over the past 2000 years resulting from shifts in climate (Finney et al. 2002, Moore et al. 2002). Throughout this region, variations in zooplankton, benthic invertebrates, seabirds, and fish all have been connected to changes in ocean-climate conditions (McGowan et al. 1998). In particular, analyses of data from the last 100 years demonstrated a strong influence of ocean conditions on catches and the production of Pacific salmon (*Oncorhynchus* spp.) across a range of spatial and temporal scales (Mantua et al. 1997, Beamish et al. 1999). The varied response of salmon to past environmental changes likely reflects their complex life history strategies and the wide diversity of freshwater and marine habitats that they occupy (Hilborn et al. 2003).

Recent analyses suggest that Chinook salmon from the Columbia River basin also respond to cyclic changes in ocean-climate conditions. Modeling exercises directed at explaining the negative effects of various anthropogenic activities on the productivity of Snake River spring-summer Chinook salmon identified the estuary and ocean environments as important sources of unexplained variation in stock performance (Kareiva et al. 2000, Wilson 2003). Using catch records from commercial fisheries, Botsford and Lawrence (2002) found reasonable correlations between the inferred survival of Columbia River Chinook salmon and physical attributes of the ocean, such as sea-surface temperature and coastal upwelling. Building upon these previous studies, Scheuerell and Williams (in press) (see Appendix B) found that by beginning with the first SAR estimate in 1964, they could actually forecast the subsequent observed changes in the smolt-to-adult survival of Snake River spring-summer Chinook salmon through 2000 from variation in coastal ocean upwelling, including the rapid decline between the 1960s and 1970s and the increase in the late 1990s (Figure 59). Furthermore, their model predicts a SAR of 2.5, 2.9, and 3.0 for 2001–2003 outmigrations, respectively. All these analyses highlight the important effects of the ocean in determining smolt-to-adult survival, and they support Pearcy's (1992) assertion that the primary influence of the ocean on salmon survival occurs early within the first year that juveniles occupy coastal waters.

The climate processes that affect the ocean's physical environment, and thereby influence salmon growth and survival, also affect climate patterns in rainfall and temperature on the continental land masses (Rodionov and Assel 2003, Coulibaly and Burn 2004). For instance, during time periods of relatively poor ocean conditions for Columbia River salmon, such as those indicated by a positive phase of the Pacific Decadal Oscillation (PDO) (Mantua et al. 1997), we

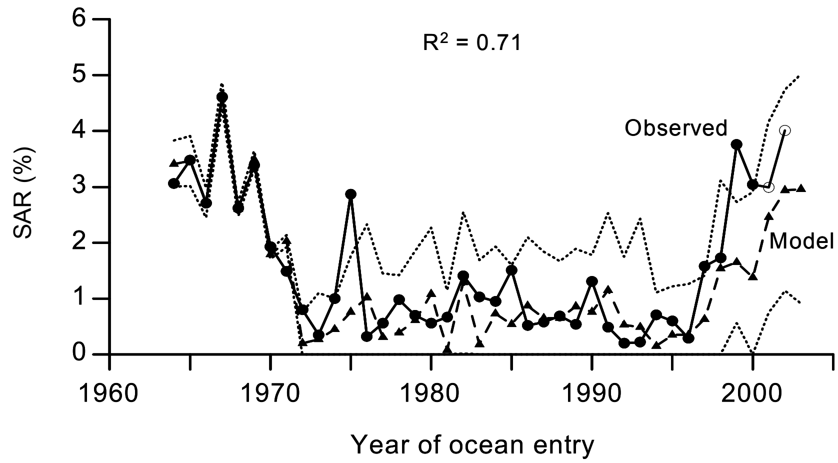


Figure 59. Time series of the observed SAR survival for wild Snake River spring-summer Chinook salmon (●) from 1965–2002 compared to the forecasts (▲) from a time series model based on the coastal ocean upwelling index at 45°N 125°W. Dotted lines represent the 90% credible limits around the forecasts. Note that the SAR estimates for the 2001 and 2002 outmigrations (○) are preliminary in that they are based on age-3 (jack) returns in 2002 and age-3 plus age-4 returns in 2003. The forecast for the SAR for the 2003 outmigration is also shown.

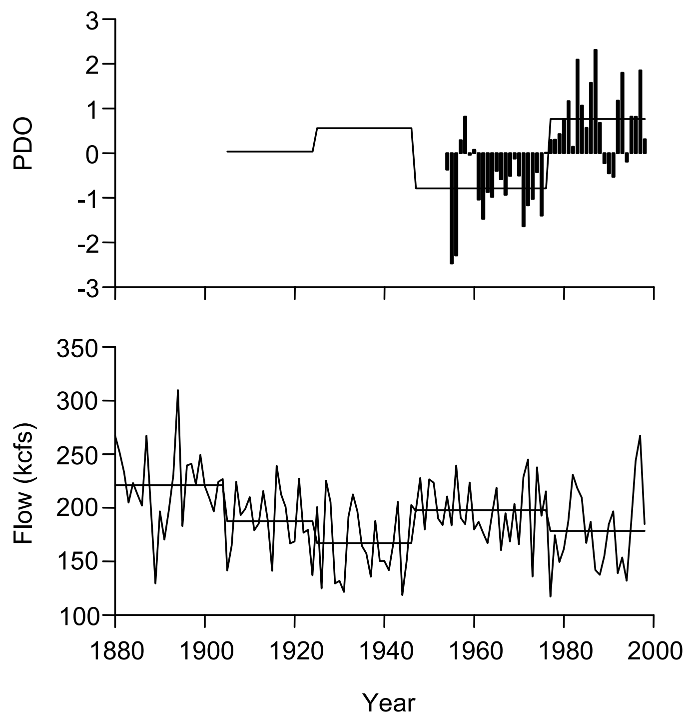


Figure 60. Normalized time series of the Pacific Decadal Oscillation (PDO, top) and Columbia River flow at The Dalles Dam (bottom). The mean of each series over the various regime intervals as defined by Mantua et al. (1997) is superimposed to illustrate the ocean-land teleconnections evident in many climate processes. Note that when the PDO index is predominantly positive (e.g., 1977–1998), ocean conditions are deemed poor for Columbia River salmon. During these same time periods, river flows are also below the long-term mean.

also observe below-average river flows in the Columbia River basin (Figure 60), suggesting additional negative effects on salmon populations (reviewed by Budy et al. 2002). We note also that the highest salmon catches in the Columbia River occurred during the 1880s, coinciding with the period of the highest normalized Columbia River flows in the last 120 years. Several lines of evidence suggest the Northeast Pacific underwent another ocean regime shift in 1998 (Peterson and Schwing 2003). Already we have witnessed improved smolt-to-adult survival and subsequent adult returns in recent years, suggesting a positive switch in the environmental conditions that favor salmon growth and survival. Assuming these patterns in ocean and continental climate hold, salmon populations in the Pacific Northwest should continue to respond favorably until conditions switch again. Concentrating more effort on forecasting changes in salmon responses to future climate change and negative anthropogenic activities should help us to better manage Columbia River salmon and avoid the massive losses incurred during the last period of poor climate conditions.

Diversity

Dams have become major selective forces on migratory salmonid populations. They dramatically change environmental conditions in the migratory corridor, including reducing river velocities, blocking spawning areas, and fostering altered biotic communities. The history of Snake River fall Chinook salmon provides an extreme example of this. Historically, most Snake River fall Chinook spawned above the Hells Canyon Dam complex; now the entire ESU spawns below Hells Canyon in a much altered temperature regime (Ebel 1968, Connor et al. 2003a). Further, it is likely that in the pre-impoundment era, most ocean-type Chinook salmon fry in the Columbia River basin were swept by spring flows to the estuary (Mains and Smith 1964, Park 1969) where most of their juvenile rearing occurred. In the current river configuration, ocean-type Chinook salmon originating from the Snake River, Hanford Reach, or upper Columbia River encounter slack water in impounded reservoirs and hold up to rear to a larger size before continuing to migrate volitionally.

The fact that salmon populations have the capability to evolve rapidly (Hendry et al. 2000) and that we have demonstrated strong selective forces on some stocks (see "Selective Mortality" section, page 119) suggests Columbia River salmonids will evolve in response to selective pressures created by dams. We do not know the long-term consequences of these selective pressures because they have only acted on populations for 10–15 generations. Thus while almost all management is focused on actions that will take effect within a generation, we believe it is important to also consider the impacts of management actions on evolutionary time scales. In particular, how will dams and their associated mitigation actions affect the diversity of salmonid populations?

NOAA Fisheries Service defines a viable salmonid population as "an independent population of any Pacific salmonid (genus *Oncorhynchus*) that has a negligible risk of extinction due to threats from demographic variation, local environmental variation, and genetic diversity changes over a 100-year time frame" (McElhany et al. 2000). Genetic diversity is important because it protects a species by allowing a wider use of environments, protects against short-term spatial and temporal environmental changes, and provides the raw material for surviving long-term environmental change (McElhany et al. 2000). Indeed, Hilborn et al. (2003) concluded that the entire Bristol Bay sockeye salmon population has remained at a high level specifically due to diversity of populations. Thus efforts to ensure diversity in listed Columbia River stocks is warranted. To this end, NOAA Fisheries Service suggests it is necessary to "limit or remove human-caused selection or straying that weakens the adaptive fit between a salmonid population and its environment or limits a population's ability to respond to natural selection" (McElhany et al. 2000).

Similarly, the Independent Scientific Group recommended that "because the full assemblage of salmonids in the Columbia River basin probably used many migration strategies, a diversity of management schemes should be used to assist migration. Without diversity of management, there is likely to be further stock selection" (ISG 1996). Fish bypass systems, spill-ways, the use of transportation, flow augmentation, and other management strategies may select for particular stocks or life histories and could therefore reduce diversity if used exclusively. Therefore, in their review of transportation, the Independent Scientific Advisory Board con-cluded that "spreading the risk of negative outcomes among alternative routes of hydroelectric passage is advisable to prevent a recovery action designed for one listed species from becoming a factor in the decline of another species," and "in the face of uncertainties associated with potential negative effects of transportation on genetic and life history diversity" (ISAB 1998).

We concur. In light of these conclusions and the material presented in this report, we believe particular attention needs to focus on:

- exploration of alternative transportation strategies, including allowing more fish to migrate volitionally, adopting seasonally varying transportation schemes, and considering ways to delay the delivery of early transported migrants to the estuary;
- the ability of augmentation and spill to speed downstream migration;
- consideration of population structure in mitigation actions to determine whether actions equally benefit all segments within and between populations; and
- how anthropogenic changes potentially create selection pressures on fish stocks, e.g., whether the unprecedentedly large avian predator populations select against larger fish.

Hydropower System and Harvest

The estimated SAR of spring-summer Chinook salmon to the upper dam on the Snake River provides an index of escapement over time. The estimated SAR to Lower Granite Dam for the last several broodyears actually exceeded most of those in the 1960s (Figure 61). As depicted in Figure 52, to some degree this return rate resulted from reduced mainstem harvest on the upstream stocks. The data suggest that if the ocean conditions that produced the present higher rates of return continue for a few years into the future, and if harvest rates continue at the current levels, absolute adult escapement over Lower Granite Dam could possibly exceed levels observed in the 1960s. We infer from these data that a decreased harvest rate on adult salmon has potentially offset the loss of juveniles that results from mortalities caused by passage through the hydropower system, and that under good ocean conditions, this change might allow for the maintenance of stock viability.

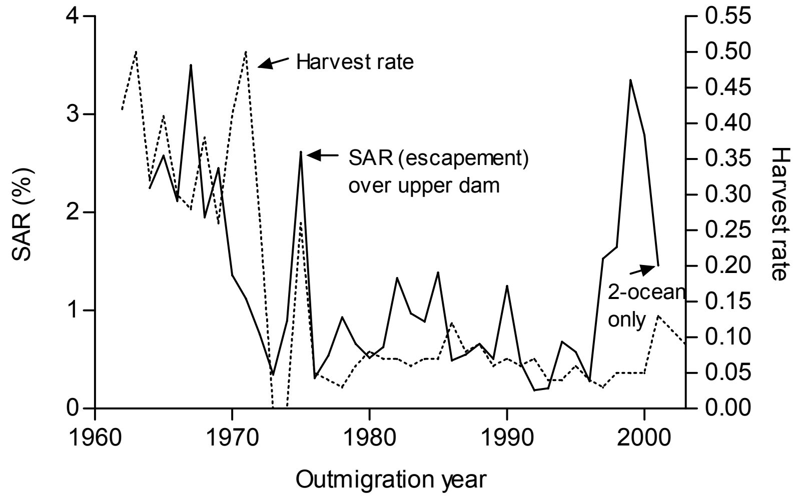


Figure 61. Estimated (escapement-based) SAR of spring-summer Chinook salmon to the upper dam on the Snake River (solid line) and estimated annual harvest rate (dashed line).

Summary and Conclusions

Our ability to discern FCRPS-related effects is directly related to the quality of available data, which is quite variable. We can precisely estimate survival of downstream migrants from release points to the uppermost dams and through the hydropower system, and we are developing similar capabilities for upstream migrants. For several ESUs, we are developing a general sense of the relative performance of transported fish compared to in-river migrants, but we are somewhat limited by sample sizes of adult returns. Unfortunately, we have limited ability to quantify the magnitude of hydropower system-related, latent mortality. However, we believe a major component of latent mortality is the disruption of migration timing of transported fish and in-river migrants, and we are beginning to discern some migrational timing effects.

Areas where additional or continued study would help resolve some uncertainties about effects of the FCRPS include

- migrational timing and its effect on SAR for both transported and in-river migrants,
- selectivity of bypass systems, for fish size as well as fish health, and
- mechanisms leading toward latent mortality.

Some of the data limitations discussed above arise from the fact that probably the best indicator of population performance is adult return rate, but this measure reflects the effects of several confounding factors, of which the FCRPS is but one. Given the existence of the hydropower system, it is clear, though, that ocean conditions are the dominating factor in determining return rates, overriding variability associated with the hydropower system. Return rates have increased by an order of magnitude since the recent upturn in ocean conditions, while survival through the hydropower system has remained relatively constant. Improvements in SAR, however, do not preclude the existence of FCRPS-related latent mortality or a latent mortality/ocean condition interaction.

Transportation is not a panacea. When comparing annual indices of transported wild yearling Snake River spring-summer Chinook salmon and hatchery fall Chinook salmon versus in-river fish, in many cases, transportation appeared to confer little benefit or harm. However, under certain times of the year and low-flow conditions (particularly in 2001), transportation appeared to increase return rates of some segments of the yearling migrant populations. Further, the benefits of transportation decreased at sites closer to Bonneville Dam. Thus future operations should focus on optimizing adult return rates independent of the transportation process currently in operation. Strategies such as “spread the risk” and promotion of diversity suggest we should allow more fish to migrate in the river whenever it appears in-river migration might lead to reasonable rates of return compared to alternatives. At times, transportation may provide the best alternative. We do note that transportation apparently has not provided any benefit to Snake River sockeye salmon.

Direct juvenile survival under most conditions for yearling migrants is relatively high, and substantial improvements in downstream survival appear unlikely, particularly improve-ments related to passage through dams. Summer migrants suffer greater mortality in reservoirs than do spring migrants, and improvements in river conditions may confer considerable survival improvements. The low survival experienced by spring migrants in 2001 and generally lower survival of summer migrants likely resulted from conditions in the reservoirs, potentially low flow, and possibly a lack of spill. Therefore, we believe that we may face diminishing returns in terms of improving survival via technological fixes to dams. Efforts to reduce mortality in the reservoirs, obtaining an understanding about to how to reduce latent mortality, and maintaining diversity by improving habitat conditions in the estuary and in freshwater spawning and rearing habitats will likely have the most influence on overall stock viability.

For spring-summer Chinook salmon from the Snake River, we found that increased flow had a benefit to juvenile migrant survival, though the effect was small relative to the detriment that occurs when water temperatures become too high. For steelhead, the benefit of increased flow was apparently greater. However, in our multiple-regression model the benefit is offset somewhat by a countering trend of decreased steelhead survival as the season progresses, possibly related to increased propensity to residualize as water temperature increases. For yearling Chinook salmon, temperatures above 13°C appeared detrimental to survival; these temperatures are typically reached in late May. For both species, we have consistently observed a strong relationship between flow and travel time. Thus one benefit of flow may be to move spring migrants out of the lower Snake River before temperatures become detrimental.

Flow clearly can affect smolt migration timing to the estuary, and arrival timing appeared to greatly influence their SAR. Delayed migration reduces available energy reserves in smolts, and it could have affected survival, a condition exacerbated in low-flow years, both within the hydropower system and in the freshwater areas upstream that fish negotiate prior to arriving at the first dam.

References

Adkison, M. D., and B. P. Finney. 2003. The long-term outlook for salmon returns to Alaska. Alaska Fish. Res. Bull. 10:83–94.

Anderson, J. J., and C. Van Holmes. 2004. An analysis of smolt survival with implications to flow management. Unpubl. manuscr. Online at www.cbr.washington.edu/papers/jim/FlowSurvivalAnalysisNRC.html [accessed September 2004].

Beamer, E. M., and G. R. Pess. 1999. Effects of peak flows on Chinook (*Oncorhynchus tshawytscha*) spawning success in two Puget Sound river basins. *In* R. Sakrison and P. Sturtevant (eds.), Pro-ceedings, American Water Resources Association Annual Water Resources Conference, p. 67–70.

Beamish, R. J., D. J. Noakes, G. A. McFarlane, L. Klyashtorin, V. V. Ivanov, and V. Kurashov. 1999. The regime concept and natural trends in the production of Pacific salmon. Can. J. Fish. Aquat. Sci. 56(3):516–526.

Beamish, R. J., C. E. M. Neville, and A. J. Cass. 1997. Production of Fraser River sockeye salmon (*Oncorhynchus nerka*) in relation to decadal-scale changes in the climate and the ocean. Can. J. Fish. Aquat. Sci. 54:543–554.

Beckman, B. R., D. A. Larsen, and W. W. Dickhoff. 2003. Life history plasticity in Chinook salmon: Relation of size and growth rate to autumnal smolting. Aquaculture 222:149–165.

Bickford, S. A., J. Skalski, R. Townsend, S. McCutcheon, R. Richmond, R. Frith, and R. Fechhelm. 2001. Project survival estimates for yearling summer steelhead migrating through the Wells Hydroelectric Facility, 2000. Public Utility District (PUD) No. 1 of Douglas County. (Available from Douglas County PUD, 1151 Valley Mall Parkway, East Wenatchee, WA 98802.)

Bosch, Bill. 2004. Unpublished smolt-to-adult return data. (Available from Yakama Nation, Fisheries Program, P.O. Box 151, Toppenish, WA 98948.)

Botsford, L. W., and C. A. Lawrence. 2002. Patterns of co-variability among California Current Chinook salmon, coho salmon, Dungeness crab, and physical oceanographic conditions. Progr. Oceanogr. 53(2-4):283–305.

Botsford, L. W., and C. M. Paulsen. 2000. Assessing covariability among populations in the presence of intraspecies correlation: Columbia River spring-summer Chinook salmon (*Oncorhynchus tshawytscha*) stocks. Can. J. Fish. Aquat. Sci. 57:616–627.

Bradford, M. J. 1995. Comparative review of Pacific salmon survival rates. Can. J. Fish. Aquat. Sci. 52:1327–1338.

Budy, P., G. P. Thiede, N. Bouwes, C. E. Petrosky, and H. Schaller. 2002. Evidence linking delayed mortality of Snake River salmon to their earlier hydrosystem experience. N. Am. J. Fish. Manag. 22(1):35–51.

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-recap. Am. Fish. Soc. Monogr. 5:1–437.

CBR UW (Columbia Basin Research, University of Washington). 2004. Data from Columbia River Data Access in Real Time (DART), Adult Passage Composite Report web site. Online at http://www.cqs.washington.edu/dart/adult.html [accessed September 2004].

Chance, D. H. 1973. Influence of the Hudson's Bay Company on the native cultures of the Colville District. NW Anthropol. Res. Notes 7, Part 1.

Chapman, D. W. 1986. Salmon and steelhead abundance in the Columbia River in the nineteenth century. Trans. Am. Fish. Soc. 115:662–670.

Chatters, J. C., V. L. Butler, M. J. Scott, D. M. Anderson, and D. A. Neitzel. 1995. A paleoscience approach to estimating the effects of climatic warming on salmonid fisheries of the Columbia River basin. Can. Spec. Publ. Fish. Aquat. Sci. 121:489–496.

Congleton, J. L., T. Wagner, J. Evavold, J. Hafner, D. Fryer, and B. Sun. 2004. Evaluation of physiological differences in transported, in-river migrating, and multiple-bypassed juvenile salmon. (Available from Idaho Cooperative Fish and Wildlife Research Unit, University of Idaho, Moscow, ID 83844.)

Connor, W. P., H. L. Burge, J. R. Yearsley, and T. C. Bjornn. 2003a. Influence of flow and temperature on survival of wild subyearling fall Chinook salmon in the Snake River. N. Am. J. Fish. Manag. 23(2):362–375.

Connor, W. P., J. G. Sneva, K. F. Tiffan, R. K. Steinhorst, and D. Ross. In press. Two alternative juvenile life histories for fall Chinook salmon in the Snake River basin. Trans. Am. Fish. Soc.

Connor, W. P., R. K. Steinhorst, and H. L. Burge. 2003b. Migrational behavior and seaward movement of wild subyearling fall Chinook salmon in the Snake River. N. Am. J. Fish. Manag. 23(2):414–430.

Cormack, R. M. 1964. Estimates of survival from the sightings of marked animals. Biometrika 51:429–438.

Coronado, C., and R. Hilborn. 1998. Spatial and temporal factors affecting survival in coho salmon (*Oncorhynchus kisutch*) in the Pacific Northwest. Can. J. Fish. Aquat. Sci. 55:2067–2077.

Cottingham, K. L., and S. R. Carpenter. 1998. Population, community, and ecosystem variates as ecological indicators: Phytoplankton responses to whole-lake experiments. Ecol. Appl. 8:508–530.

Coulibaly, P., and D. H. Burn. 2004. Wavelet analysis of variability in annual Canadian streamflows. Water Resour. Res. 40(3):W03105.

CSS (Comparative Survival Study). 2003. Comparative Survival Study (CSS) of PIT tagged spring/summer Chinook—Mark/recapture activities and bootstrap analysis. Draft annual report to BPA, migration years 1997–2000. (Available from Fish Passage Center, 2501 SW First Ave., Suite 230, Portland, OR 97201.)

DeHart, M., T. Berggren, M. Filardo, L. Basham, D. Benner, H. Fanzoni, S. Rassk, J. McCann, D. Wood, C. McCarty, and D. Watson. 2003. Fish Passage Center. Project No. 1994-03300. BPA Report DOE/BP-00004288-1. Online at http://www.efw.bpa.gov/cgi-bin/FW/publications.cgi [accessed September 2004].

Deriso, R. B., D. R. Marmorek, and I. J. Parnell. 2001. Retrospective patterns of differential mortality and common year-effects experienced by spring and summer Chinook salmon (*Oncorhynchus tshawytscha*) of the Columbia River. Can. J. Fish. Aquat. Sci. 58(12):2419–2430.

Ebel, W. J., and C. H. Koski. 1968. Physical and chemical limnology of Brownlee Reservoir, 1962–1964. Fish. Bull. 67:295–335.

Elliott, D. G., and R. J. Pascho. 1991. Juvenile fish transportation: Impact of bacterial kidney disease on survival of spring/summer Chinook salmon stocks. Annual report to U.S. Army Corps of Engineers, Walla Walla District, Contract E86880047, Walla Walla, WA.

Emmett, R. L., and R. D. Brodeur. 2000. Recent changes in the pelagic nekton community off Oregon and Washington in relation to some physical oceanographic conditions. N. Pac. Anadr. Fish. Comm. Bull. 2:11–20.

Emmett, R. L., P. J. Bentley, and G. K. Krutzikowsky. 2001. Ecology of marine predatory and prey fishes off the Columbia River, 1998 and 1999. U.S. Dept. Commer. NOAA Tech Memo. NMFS-NWFSC-51.

Endler, J. A. 1986. Natural selection in the wild. Princeton University Press, Princeton, NJ.

Finney, B. P., I. Gregory-Eaves, M. S. V. Douglas, and J. P. Smol. 2002. Fisheries productivity in the northeastern Pacific Ocean over the past 2,200 years. Nature 416(6882):729–733.

Folmar, L. C., and W. W. Dickhoff. 1980. The parr-smolt transformation (smoltification) and seawater adaptation in salmonids. Aquaculture 21:1–37.

FPC (Fish Passage Center). 2003a. Data from the Fish Passage Center. Online at http://www.fpc.org [accessed September 2004].

FPC (Fish Passage Center). 2003b. Fish Passage Center annual report 2002. FPC of the Columbia Basin Fish and Wildlife Authority, Portland, OR. Online at http://www.fpc.org/fpc_docs/Annual_FPC_Report/FPC2002_Annual_Report.pdf [accessed September 2004].

Fresh, K. L., E. Casillas, L. L. Johnson, and D. L. Bottom. In press. Role of the estuary in the recovery of Columbia River basin salmon and steelhead: An evaluation of the effects of selected factors on salmonid population viability. U.S. Dept. Commer. NOAA Tech. Memo. NMFS-NWFSC.

Garcia Berdeal, I., B. M. Hickey, and M. Kawase. 2002. Influence of wind stress and ambient flow on a high discharge river plume. J. Geophys. Res. 107(C9):3130. doi:10,1029/2001JC000932.

Gargett, A. E. 1997. The optimal stability “window:” A mechanism underlying decadal fluctuations in North Pacific salmon stocks? Fish. Oceanogr. 6:109–117.

Greene, C. M., and T. J. Beechie. 2004. Consequences of potential density-dependent mechanisms on recovery of ocean-type Chinook salmon (*Oncorhynchus tshawytscha*). Can. J. Fish. Aquat. Sci. 61:590–602.

Griffin, L. E. 1935. Certainties and risks affecting fisheries connected with damming the Columbia River. Northwest Sci. 9:25–30.

Groot, C., and L. Margolis. 1991. Pacific salmon life histories. University of British Columbia Press, Vancouver, BC, Canada.

Gross, M. R. 1985. Disruptive selection for alternative life histories in salmon. Nature 313:47–48.

Gross, M. R. 1987. Evolution of diadromy in fishes. Am. Fish. Soc. Symp. 1:14–25.

Gross, M. R. 1991. Salmon breeding behavior and life-history evolution in changing environments. Ecology 72:1180–1186.

Gross, M. R., R. M. Coleman, and R. M. McDowall. 1988. Aquatic productivity and the evolution of diadromous fish migration. Science 239:1291–1293.

Hanley, J. A., and A. Lippman-Hand. 1983. If nothing goes wrong is everything right? J. Am. Med. Assoc. 249:1743–1745.

Harmon, J. R., D. M. Marsh, N. N. Paasch, K. L. Thomas, K. W. McIntyre, B. P. Sandford, and G. M. Matthews. 2000. Research related to transportation of juvenile salmonids on the Columbia and Snake rivers, 1999. (Available from Northwest Fisheries Science Center, Fish Ecology Division, 2725 Montlake Blvd. E., Seattle, WA 98112.)

Hendry, A. P., J. K. Wenburg, P. Bentzen, E. C. Volk, and T. P. Quinn. 2000. Rapid evolution of reproductive isolation in the wild: Evidence from introduced salmon. Science 290:516–518.

Hilborn, R., and C. Coronado. 1997. Changes in ocean survival of coho and Chinook salmon in the Pacific Northwest. *In* R. L. Emmett and M. H. Schiewe (eds.), Estuarine and ocean survival of northeastern Pacific salmon: Proceedings of the workshop, March 20–22, 1996, Newport, OR. U.S. Dept. Commerce, NOAA Tech. Memo. NMFS-NWFSC-29.

Hilborn, R., T. P. Quinn, D. E. Schindler, and D. E. Rogers. 2003. Biocomplexity and fisheries sustainability. Proc. Natl. Acad. Sci. USA 100(11):6564–6568.

Hill, M. F., L. W. Botsford, and A. Hastings. 2003. The effects of spawning age distribution on salmon persistence in fluctuating environments. J. Anim. Ecol. 72:736–744.

Hinrichsen, R. A. 2001. High variability in spawner-recruit data hampers learning. Can. J. Fish. Aquat. Sci. 58(4):769–776.

Holmes, E. E. 2001. Estimating risks in declining populations with poor data. Proc. Natl. Acad. Sci. 98:5072–5077.

Holmes, H. B. Unpubl. report. U.S. Bureau of Commercial Fisheries.

Hutchings, J. A., and M. E. B. Jones. 1998. Life history variation in growth rate thresholds for maturity in Atlantic salmon. Can. J. Fish. Aquat. Sci. 55 (Suppl. 1):22–47.

ISAB (Independent Scientific Advisory Board). 1998. Response to the questions of the Implementation Team regarding juvenile salmon transportation in the 1998 season. Northwest Power and Conservation Council. Online at http://www.nwppc.org/fw/isab/isab98-2letter.htm [accessed September 2004].

ISG (Independent Scientific Group). 1996. Return to the river: Restoration of salmonid fishes in the Columbia River ecosystem. Northwest Power and Conservation Council. Online at http://www.nwppc.org/library/1996/96-6/default.htm [accessed September 2004].

Jolly, G. M. 1965. Explicit estimates from capture-recapture data with both death and immigration—Stochastic model. Biometrika 52:225–247.

Kareiva, P., M. Marvier, and M. McClure. 2000. Recovery and management options for spring/summer Chinook salmon in the Columbia River basin. Science 290(5493):977–979.

Kiefer, R. B., P. R. Bunn, and J. Johnson. 2002. Natural production monitoring and evaluation, July 1, 2001–June 30, 2002. Idaho Department of Fish and Game report number 02-24. (Available from IDFG, P.O. Box 25, Boise, ID 83707.)

Lady, J., P. Westhagen, and J. R. Skalski. 2001. Survival under proportional hazards (SURPH 2.1), Columbia Basin research, University of Washington, Seattle. Online at http://www.cbr.washington.edu/paramEst/SURPH/Manual/index.html [accessed September 2004].

Lamon, E. C., III, S. R. Carpenter, and C. A. Stow. 1998. Forecasting PCB concentrations in Lake Michigan salmonids: A dynamic linear model approach. Ecol. Appl. 8:659–668.

Lebreton, J.-D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: A unified approach with case studies. Ecol. Monogr. 62:67–118.

Ledgerwood, R. D., B. A. Ryan, E. P. Nunnallee, and J. W. Ferguson. 2000. Estuarine recovery of PIT-tagged salmonids from the Lower Granite Dam transportation study, 1998. (Available from Northwest Fisheries Science Center, Fish Ecology Division, 2725 Montlake Blvd. E., Seattle, WA 98112.)

Levin, P. S. 2003. Regional differences in responses of Chinook salmon populations to large-scale climatic patterns. J. Biogeogr. 30(5):711–717.

Levin, P. S., S. Achord, B. E. Feist, and R. W. Zabel. 2002. Nonindigenous brook trout and the demise of Pacific salmon: A forgotten threat. Proc. Royal Soc. London B 269:1663–1670.

Levin, P. S., and N. Tolimieri. 2001. Differences in the impacts of dams on the dynamics of salmon populations. Anim. Conserv. 4:291–299.

Lichatowich, J. A., L. E. Mobrand, L. C. Lestelle, and T. S. Vogel. 1995. An approach to the diagnosis and treatment of depleted Pacific salmon populations in Pacific Northwest watersheds. Fisheries 20:10–18.

Mains, E. M., and J. M. Smith. 1964. The distribution, size, time, and current preferences of seaward migrant Chinook salmon in the Columbia and Snake rivers. Washington Dept. Fisheries Fish. Res. Papers 2(3):5–43.

Mantua, N. J., S. R. Hare, Y. Zhang, J. M. Wallace, and R. C. Francis. 1997. A Pacific interdecadal cli-mate oscillation with impacts on salmon production. Bull. Am. Meteorol. Soc. 78(6):1069–1079.

Marine, K. R., and J. J. Cech, Jr. 2004. Effects of high water temperature on growth, smoltification, and predator avoidance in juvenile Sacramento River Chinook salmon. N. Am. J. Fish. Manag. 24:198–210.

Marmorek, D. R., and C. Peters (eds.). 1998. Plan for analyzing and testing hypotheses (PATH): Preliminary decision analysis report on Snake River spring/summer Chinook. ESSA Technologies, Vancouver, Canada. Online at http://www.efw.bpa.gov/Environment/PATH/reports/pdar/index.htm [accessed September 2004].

Marmorek, D. R., and C. Peters. 2001. Finding a PATH toward scientific collaboration: Insights from the Columbia River basin. Conserv. Ecol. 5(2):8.

Marmorek, D. R., C. N. Peters, and I. Parnell (eds.). 1998. PATH final report for fiscal year 1998. Prepared by ESSA Technologies, Ltd., Vancouver, Canada. Online at http://www.efw.bpa.gov/PATH/index.html [accessed December 2003].

Marmorek, D. R., M. K. Porter, I. J. Parnell, and C. Peters (eds.). 2004. Comparative Survival Study workshop, 11-13 February 2004, Bonneville Hot Springs Resort. ESSA Tech. Ltd., Vancouver, B.C., Canada.

Marsh, M. M., J. R. Harmon, N. N. Paasch, K. L. Thomas, K. W. McIntyre, B. P. Sandford, and G. M. Matthews. 2001. Research related to transportation of juvenile salmonids on the Columbia and Snake rivers, 2000. (Available from Northwest Fisheries Science Center, Fish Ecology Division, 2725 Montlake Blvd. E., Seattle, WA 98112.)

Marsh, D. M., G. M. Matthews, S. Achord, T. E. Ruehle, and B. P. Sandford. 1999. Diversion of salmonid smolts tagged with passive integrated transponders from an untagged population passing through a juvenile collection system. N. Am. J. Fish. Manag. 19:1142–1146.

MathSoft. 2000. S-Plus 6.0 guide to statistics, vol. 1. MathSoft, Seattle, WA.

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 Dam. Mar. Fish. Rev. 39(7):10–14.

McElhany, P., M. H. Ruckelshaus, M. J. Ford, T. C. Wainwright, and E. P. Bjorkstedt. 2000. Viable salmonid populations and the recovery of evolutionarily significant units. U.S. Dept. Commerce, NOAA Tech. Memo. NMFS-NWFSC-42.

McGowan, J. A., D. R. Cayan, and L. M. Dorman. 1998. Climate-ocean variability and ecosystem response in the northeast Pacific. Science 281(5374):210–217.

McPhail, J. D., and C. C. Lindsey. 1986. Zoogeography of the freshwater fishes of Cascadia (the Columbia system and rivers north to the Stikine). *In* C. H. Hocutt and E. O. Wiley (eds.), The zoogeography of North American freshwater fishes, p. 615–637. Wiley, New York.

Miller, D. R., J. G. Williams, and C. W. Sims. 1983. Abundance and distribution of juvenile salmonids off the Washington and Oregon coasts in 1980. Fish. Res. 2:1–17.

Mobrand, L. E., J. A. Lichatowich, L. C. Lestelle, and T. S. Vogel. 1997. An approach to describing ecosystem performance “through the eyes of salmon.” Can. J. Fish. Aquat. Sci. 54:2964–2973.

Mood, A. M., F. A. Graybill, and D. C. Boes. 1974. Introduction to the theory of statistics. Third edition. McGraw-Hill Book Company, New York.

Moore, G. W. K., G. Holdsworth, and K. Alverson. 2002. Climate change in the North Pacific region over the past three centuries. Nature 420(6914):401–403.

Muir, W. D., A. E. Giorgi, and T. C. Coley. 1994. Behavioral and physiological changes in yearling Chinook salmon during hatchery residence and downstream migration. Aquaculture 127:69–82.

Muir, W. D., S. G. Smith, J. G. Williams, E. E. Hockersmith, and J. R. Skalski. 2001. Survival estimates for migrant yearling Chinook salmon and steelhead tagged with passive integrated transponders in the lower Snake and lower Columbia rivers, 1993–1998. N. Am. J. Fish. Manag. 21(2):269–282.

Myers, R. A., G. Mertz, and J. Bridson. 1997. Spatial scales of interannual recruitment variations of marine, anadromous, and freshwater fish. Can. J. Fish. Aquat. Sci. 54:1400–1407.

Nickelson, T. E. 1986. Influences of upwelling, ocean temperature, and smolt abundance on marine survival of coho salmon (*Oncorhynchus kisutch*) in the Oregon production area. Can. J. Fish. Aquat. Sci. 43:527–535.

NMFS (National Marine Fisheries Service). 1992. Endangered and threatened species; Threatened status for Snake River spring/summer Chinook salmon; threatened status for Snake River fall Chinook salmon. Federal Register [Docket #910947-2043. 50 CFR Part 227] 57:14653.

NMFS (National Marine Fisheries Service). 2000. Endangered Species Act Section 7 biological opinion on the reinitiation of consultation on operation of the Federal Columbia River Power System, including the juvenile fish transportation program, and 19 Bureau of Reclamation projects in the Columbia Basin. 21 December 2002. (Available from NMFS, Northwest Region, 7600 Sand Point Way NE, Seattle, WA 98115.)

NMFS (National Marine Fisheries Service). 2003. Unpubl. data developed for the Technical Advisory Committee. Provided in a memo dated 1 December 2003 from Norma Jean Sands to Peter Dygert and Cindy Lefleur. (Available from Northwest Fisheries Science Center, Conservation Biology, 2725 Montlake Blvd. E., Seattle, WA 98112.)

NPPC (Northwest Power Planning Council). 2003. State, federal, and tribal anadromous fish managers comments on the draft document "Mainstem amendments as they relate to flow/survival relationships for salmon and steelhead." Online at http://www.fpc.org/fpc_docs/240-02final.pdf [accessed January 2003].

Park, D. L. 1969. Seasonal changes in downstream migration of age-group 0 Chinook salmon in the upper Columbia River. Trans. Am. Fish. Soc. 98:315–317.

Pearcy, W. G. 1992. Ocean ecology of North Pacific salmonids. University of Washington Press, Seattle.

Peterman, R. M., M. J. Bradford, and J. L. Anderson. 1986. Environmental and parental influences on age at maturity in sockeye salmon (*Oncorhynchus nerka*) from the Fraser River, British Columbia. Can. J. Fish. Aquat. Sci. 43:269–274.

Peterman, R. M., B. J. Pyper, M. F. Lapointe, M. D. Adkison, and C. J. Walters. 1998. Patterns of covariation in survival rates of British Columbian and Alaskan sockeye salmon (*Oncorhynchus nerka*) stocks. Can. J. Fish. Aquat. Sci. 55:2503–2517.

Peterson, W. T., and F. B. Schwing. 2003. A new climate regime in northeast Pacific ecosystems. Geophys. Res. Ltrs. 30(17):1896.

Petrosky, C. E., H. A. Schaller, and P. Budy. 2001. Productivity and survival rate trends in the freshwater spawning and rearing stage of Snake River Chinook salmon (*Oncorhynchus tshawytscha*). Can. J. Fish. Aquat. Sci. 58(6):1196–1207.

Pole, A., M. West, and J. Harrison. 1994. Applied Bayesian forecasting and time series analysis. Chapman & Hall, New York.

PSMFC (Pacific States Marine Fisheries Commission). 2004. Data on juvenile salmonids PIT tagged and released in the Columbia River basin from PIT-tag information system (PTAGIS) database. Online at www.psmfc.org [accessed July 2004].

Quinn, T. P., and M. J. Unwin. 1993. Variation in life-history patterns among New Zealand Chinook salmon (*Oncorhynchus tshawytscha*) populations. Can. J. Fish. Aquat. Sci. 50:1414–1421.

Randall, R. G., M. C. Healy, and J. B. Dempson. 1987. Variability in length of freshwater residence of salmon, trout, and char. Am. Fish. Soc. Symp. 1:27–41.

Raymond, H. L. 1979. Effects of dams and impoundments on migrations of juvenile Chinook salmon and steelhead from the Snake River, 1966 to 1975. Trans. Am. Fish. Soc. 108:505–529.

Raymond, H. L. 1988. Effects of hydroelectric development and fisheries enhancement on spring and sum-mer Chinook salmon and steelhead in the Columbia River basin. N. Am. J. Fish. Manage. 8:1–24.

Regetz, J. 2003. Landscape-level constraints on recruitment of Chinook salmon (*Oncorhynchus tshawytscha*) in the Columbia River basin, USA. Aquat. Conserv.: Mar. Freshw. Ecosyst. 13:35–49.

Ricker, W. E. 1972. Hereditary and environmental factors affecting certain salmonid populations. *In* R. C. Simon, and R. A. Larkin, (eds.), The stock concept of Pacific salmon. H.R. MacMillan Lectures in Fisheries, University of British Columbia, Vancouver, Canada, p. 19–160.

Rodionov, S., and R. A. Assel. 2003. Winter severity in the Great Lakes region: A tale of two oscillations. Climate Res. 24(1):19–31.

Roni, P., and T. P. Quinn. 1995. Geographic variation in size and age of North American Chinook salmon. N. Am. J. Fish. Manag. 15:325–345.

Sandford, B. P., and S. G. Smith. 2002. Estimation of smolt-to-adult return percentages for Snake River basin anadromous salmonids, 1990–1997. J. Agric. Biol. Environ. Stat. 7(2):243–263.

Schaefer, M. B. 1951. Estimation of the size of animal populations by marking experiments. Fish. Bull. 52:191–203.

Schaller, H. A., C. E. Petrosky, and O. P. Langness. 1999. Contrasting patterns of productivity and survival rates for stream-type Chinook salmon (*Oncorhynchus tshawytscha*) populations of the Snake and Columbia rivers. Can. J. Fish. Aquat. Sci. 56(6):1031–1045.

Schaller, H. A., C. E. Petrosky, and O. P. Langness. 2000. Reply to Zabel and Williams' comments on "Contrasting patterns of productivity and survival rates for stream-type Chinook salmon (*Oncorhynchus tshawytscha*) populations of the Snake and Columbia rivers" by Schaller et al. (1999). Can. J. Fish. Aquat. Sci. 57(8):1742–1746.

Scheuerell, M. D., D. E. Schindler, A. H. Litt, and W. T. Edmondson. 2002. Environmental and algal forcing of *Daphnia* production dynamics. Limnol. Oceanogr. 47:1477–1485.

Scheuerell, M. D. and J. G. Williams. In press. Forecasting climate-induced changes in the survival of Snake River spring/summer Chinook salmon. Fish. Oceanogr.

Schoeneman, D. E., R. T. Pressey, and C. O. Junge. 1961. Mortalities of downstream migrant salmon at McNary Dam. Trans. Am. Fish. Soc. 90:58–72.

Seber, G. A. F. 1965. A note on the multiple recapture census. Biometrika 52:249–259.

Skalski, J. R. 1998. Estimating season-wide survival rates of outmigrating salmon smolts in the Snake River, Washington. Can. J. Fish. Aquat. Sci. 55:761–769.

Skalski, J. R., A. Hoffman, and S. G. Smith. 1993. Testing significance of individual and cohort-level covariates in animal survival studies. *In* J. D. Lebreton and P. M. North (eds.), The use of marked individuals in the study of bird population dynamics, p. 9–28. Birkhauser Verlag, Basel, Switzerland.

Smith, S. G., J. R. Skalski, W. Schlechte, A. Hoffman, and V. Cassen. 1994. Statistical survival analysis of fish and wildlife tagging studies. SURPH-1 manual. (Available from University of Washington, Center for Quantitative Science, HR-20, Seattle 98195.)

Smith, S. G., W. D. Muir, S. Achord, E. E. Hockersmith, B. P. Sandford, J. G. Williams, and J. R. Skalski. 2000a. Survival estimates for the passage of juvenile salmonids through Snake and Columbia River dams and reservoirs, 1998. (Available from Northwest Fisheries Science Center, Fish Ecology Division, 2725 Montlake Blvd. E., Seattle, WA 98112.)

Smith, S. G., W. D. Muir, G. A. Axel, R. W. Zabel, J. G. Williams, and J. R. Skalski. 2000b. Survival estimates for the passage of juvenile salmonids through Snake and Columbia River dams and reservoirs, 1999. (Available from Northwest Fisheries Science Center, Fish Ecology Division, 2725 Montlake Blvd. E., Seattle, WA 98112.)

Smith, S. G., W. D. Muir, E. E. Hockersmith, G. A. Axel, W. P. Connor, and B. D. Arnsberg. 2002a. Survival of hatchery subyearling fall Chinook salmon in the Snake River and lower Snake River reservoirs, 1998–2001. (Available from Fish Ecology Division, Northwest Fisheries Science Center, 2725 Montlake Blvd. E., Seattle, WA 98112.)

Smith, S. G., W. D. Muir, J. G. Williams, and J. R. Skalski. 2002b. Factors associated with travel time and survival of migrant yearling Chinook salmon and steelhead in the lower Snake River. N. Am. J. Fish. Manag. 22(2):385–405.

Smith, S. G., W. D. Muir, E. E. Hockersmith, R. W. Zabel, R. J. Graves, C. V. Ross, W. P. Connor, and B. D. Arnsberg. 2003. Influence of river conditions on survival and travel time of Snake River subyearling fall Chinook salmon. N. Am. J. Fish. Manag. 23:939–961.

State, Federal, and Tribal Anadromous Fish Managers. 2003. State, federal, and tribal anadromous fish managers comments on the Northwest Power Planning Council draft mainstem amendments as they relate to flow/survival relationships for salmon and steelhead. January 2003. Online at http://www.fpc.org/fpc_docs/240-02final.pdf [accessed August 2004].

Taylor, E. B. 1990a. Environmental correlates of life-history variations in juvenile Chinook salmon, *Oncorhynchus tshawytscha* (Walbaum). J. Fish. Biol. 37:1–17.

Taylor, E. B. 1990b. Phenotypic correlates of life-history variation in juvenile Chinook salmon, *Oncorhynchus tshawytscha*. J. Anim. Ecol. 59:455–468.

Taylor, E. B. 1991. A review of local adaptation in Salmonidae, with particular reference to Pacific and Atlantic salmon. Aquaculture 98:185–207.

Unwin, M. J., and G. J. Glova. 1997. Changes in life history parameters in a naturally spawning population of Chinook salmon (*Oncorhynchus tshawytscha*) associated with releases of hatchery-reared fish. Can. J. Fish. Aquat. Sci. 54:1235–1245.

USFWS (U.S. Fish and Wildlife Service). 2003. Appendix A: U.S. Fish and Wildlife Service review of the Northwest Power and Conservation Council's approach to the flow-survival relationships for spring migrant juvenile salmon and steelhead contained in the draft "Mainstem amendments to the Columbia River Basin Fish and Wildlife Program." 4 February 2003. Online at http://www.nwppc.org/fw/program/mainstem/2002-16comments/USFWS.pdf [accessed August 2004].

Vollestad, L. A., J. Peterson, and T. P. Quinn. 2004. Effects of freshwater and marine growth rates on early maturation in male coho and Chinook salmon. Trans. Am. Fish. Soc. 133:495–503.

Waples, R. S. 1991. Definition of "species" under the Endangered Species Act: Application to Pacific salmon. U.S. Dept. Commer. NOAA Tech. Memo. NMFS F/NWC-194.

Ward, B. R., and P. A. Slaney. 1988. Life-history and smolt-to-adult survival of Keogh River steelhead trout (*Salmo gairdneri*) and the relationship to smolt size. Can. J. Fish. Aquat. Sci. 45:1110–1122.

WDFW and ODFW (Washington Department of Fish and Wildlife and Oregon Department of Fish and Wildlife). 2002. Status report, Columbia River fish runs and fisheries, 1938–2000 (tables only). Online at http://www.dfw.state.or.us/ODFWhtml/InfoCntrFish/InterFish/crm.html#annual [accessed November 2003].

Wedemeyer, G. A., R. L. Saunders, and W. C. Clarke. 1980. Environmental factors affecting smoltification and early marine survival of anadromous salmonids. Mar. Fish. Rev. 42:1–14.

Weitkamp, L., P. Busby, and K. Neely. 1997. Geographical variation in life histories of salmonids. *In* R. L. Emmett and M. H. Schiewe (eds.), Estuarine and ocean survival of northeastern Pacific salmon: Proceedings of the workshop. U.S. Dept. Commerce, NOAA Tech. Memo. NMFS-NWFSC-29.

Welch, D. W., B. R. Ward, B. D. Smith, and J. P. Eveson. 2000. Temporal and spatial responses of British Columbia steelhead (*Oncorhynchus mykiss*) populations to ocean climate shifts. Fish. Oceanogr. 9(1):17–32.

White, G. C., and K. P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. Bird Study Suppl. 46:120–138.

Williams, J. G. 1989. Snake River spring and summer Chinook salmon: Can they be saved? Regul. Rivers: Res. Manag. 4:17–26.

Williams, J. G. 2001. Potential impacts of *Renibacterium salmoninarum* on adult returns of Snake River spring-summer Chinook salmon. Bull. Natl. Res. Inst. Aquacul. Suppl. 5:55–59.

Williams, J. G., and G. M. Matthews. 1995. A review of flow and survival relationships for spring and summer Chinook salmon, *Oncorhynchus tshawytscha*, from the Snake River basin. Fish. Bull. 93(4):732–740.

Williams, J. G., S. G. Smith, and W. D. Muir. 2001. Survival estimates for downstream migrant yearling juvenile salmonids through the Snake and Columbia rivers hydropower system, 1966–1980 and 1993–1999. N. Am. J. Fish. Manag. 21(2):310–317.

Wilson, P. H. 2003. Using population projection matrices to evaluate recovery strategies for Snake River spring and summer Chinook. Conserv. Biol. 17(3):782–794.

Yamamoto, S., K. Morita, and A. Goto. 1999. Geographic variations in life-history characteristics of white-spotted charr (*Salvelinus leucomaenis*). Can. J. Zool. 77:871–878.

Zabel, R. W., and S. Achord. 2004. Relating size of juveniles to survival with and among populations of Chinook salmon. Ecology 85(3):795–806.

Zabel, R. W., and P. S. Levin. 2002. Simple assumptions on age composition lead to erroneous conclusions on the nature of density dependence in age-structured populations. Oecologia 133(3):349–355.

Zabel, R. W., S. G. Smith, W. D. Muir, D. M. Marsh, J. G. Williams, and J. R. Skalski. 2001. Survival estimates for the passage of spring-migrating juvenile salmonids through Snake and Columbia River dams and reservoirs, 2000. (Available from R. W. Zabel, Northwest Fisheries Science Center, 2725 Montlake Blvd. E., Seattle, WA 98112.)

Zabel, R. W., S. G. Smith, W. D. Muir, D. M. Marsh, J. G. Williams, and J. R. Skalski. 2002. Survival estimates for the passage of spring-migrating juvenile salmonids through Snake and Columbia River dams and reservoirs, 2001. (Available from R. W. Zabel, Northwest Fisheries Science Center, 2725 Montlake Blvd. E., Seattle, WA 98112.)

Zabel, R. W., T. Wagner, J. L. Congleton, S. G. Smith, and J. G. Williams. 2004. Estimating population survival and selection for phenotypic traits despite confounding behavioral variability. Unpubl. manusc. (Available from R. W. Zabel, Northwest Fisheries Science Center, 2725 Montlake Blvd. E., Seattle, WA 98112.)

Zabel, R. W., and J. G. Williams. 2000. Comments on “Contrasting patterns of productivity and survival rates for stream-type Chinook salmon (*Oncorhynchus tshawytscha*) populations of the Snake and Columbia rivers” by Schaller et al. (1999). Can. J. Fish. and Aquat. Sci. 57(8):1739–1741.

Zabel, R. W., and J. G. Williams. 2002. Selective mortality in Chinook salmon: What is the role of human disturbance? Ecol. Appl. 12(1):173–183.

Zaugg, W. S., E. F. Prentice, and F. W. Waknitz. 1985. Importance of river migration to the development of seawater tolerance in Columbia River anadromous salmonids. Aquaculture 51:33–47.

Zaugg, W. S., and H. H. Wagner. 1973. Gill ATPase activity related to parr-smolt transformation and migration in steelhead trout (*Salmo gairdneri*): Influence of photoperiod and temperature. Comp. Biochem. Physiol. 45B:955–965.

Appendix A

Submission by Idaho Department of Fish and Game on Upstream/Downstream Comparisons[9]

Upstream/downstream differences in smolt-to-adult return rates (SARs) should be used as one method to empirically estimate hydrosystem caused latent mortality of upstream stocks. The best available scientific information indicates that similar stocks of anadromous fish (e.g., stream type chinook salmon), that enter the ocean through the same (or nearby) estuary at similar times, have similar SARs (Adkison and Finney 2003, Beamish et al. 1997, Coronado and Hilborn 1998, Hilborn and Coronado 1997, Peterman et al. 1998, and Weitkamp et al. 1997). The best available scientific data indicate that stream type Chinook salmon from the Yakima and Snake rivers have the same general pattern of SARs during recent periods of both poor and good ocean productivity, but the Yakima River fish consistently return at a higher rate (Figure A-1). Considerable evidence suggests that the consistently lower SARs for Snake River chinook salmon is a result of hydrosystem induced delayed (latent) mortality (e.g., Budy et al. 2002). Therefore, the difference in these SARs would be an empirical estimate of the differential mortality between Snake River and downriver chinook salmon. An alternative hypothesis proposed by NOAAF is that the differences in SARs are a result of the genetic differences in intrinsic productivity between these two populations.

Researchers in the region are currently generating information that could be used to evaluate the question whether upstream/downstream SAR differences should be used to estimate latent mortality empirically. The number of streams and anadromous populations in the Columbia Basin that are being PIT-tagged in sufficient numbers to estimate SARs has been increasing recently, and will likely continue to increase. As increasing numbers of SAR estimates become available for wild/natural populations, they should fit into one of two basic patterns depending on which of the two competing hypothesis is correct. If latent hydrosystem mortality is largely responsible for the SAR differences, the downstream populations should have consistently higher SARs. If the NOAAF hypothesis is correct, the result will be more variable; with some of the downstream wild/natural populations having lower and other downstream populations having higher SARs.

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[9] This submission subsection of Appendix A is reprinted verbatim from an attachment (titled "Technical Comments on BiOp Remand collaboration process") to a memo to Robert Lohn, NOAA Fisheries Service Regional Administrator, from Sharon W. Kiefer, Anadromous Fish Manager, IDF&G, dated 16 June 2004. (Available from NOAA Fisheries Service, Northwest Regional Office, 7600 Sand Point Way NE, Seattle, WA 98115.)

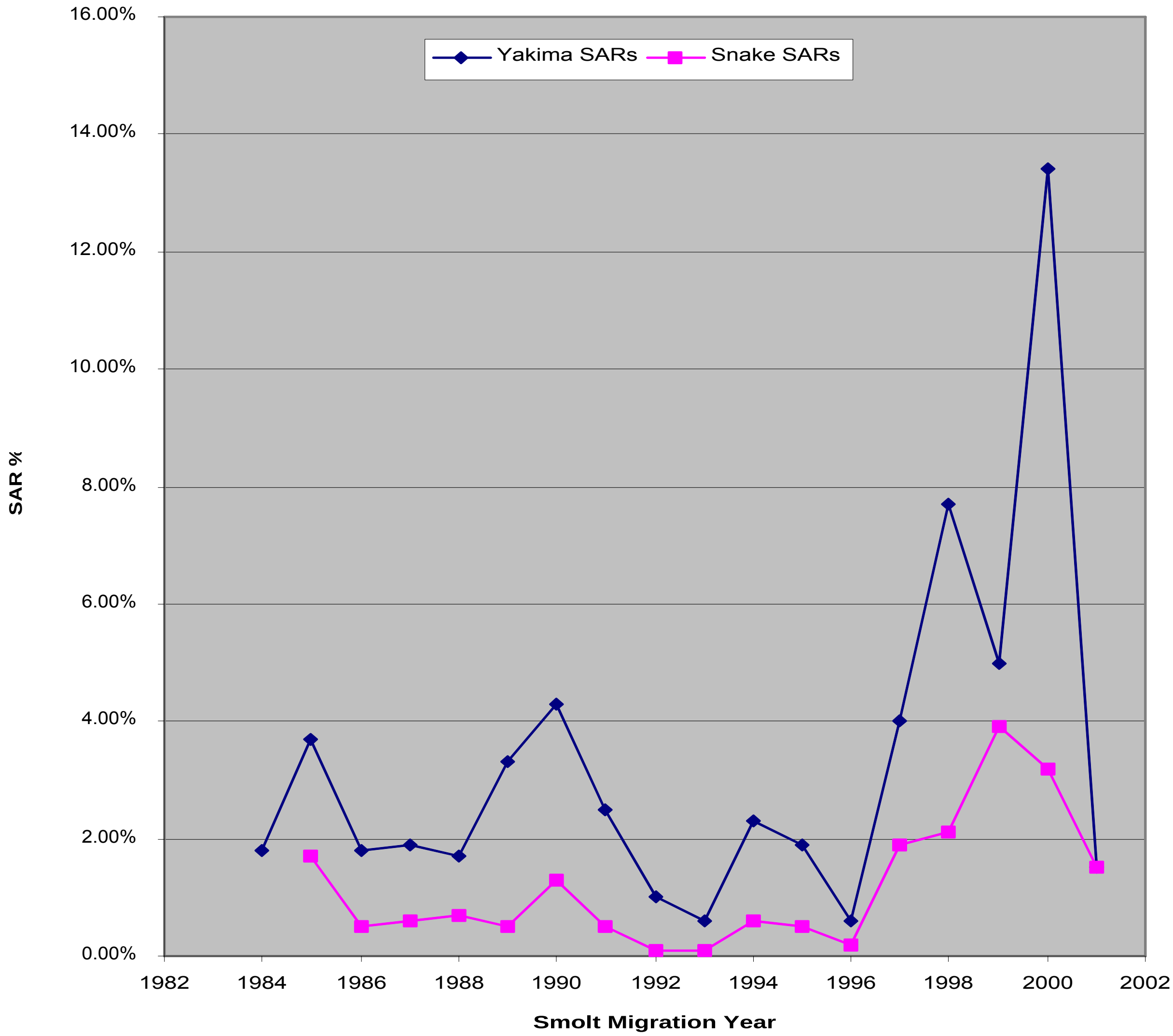

Figure A-1. Comparison of Snake and Yakima rivers wild/natural stream type chinook salmon smolt-to-adult return rates (SARs). Yakima River SARs from Bill Bosch, Yakima Nation fisheries (personnel communication), and Snake River SARs from NOAAF May 6, 2004 draft technical memorandum "Effects of the Federal Columbia River Power System on Salmon Populations."

Potential exists to evaluate this question as a result of tribal efforts to re-establish coho salmon into the Yakima and Snake rivers. The Nez Perce Tribe has been releasing lower Columbia River origin coho smolts into the Clearwater River since 1998 for reintroduction. Lower Columbia River coho have also been used by the Yakama Nation to re-establish coho in the Yakima River. Because similar hatchery stock was used for both of these reintroduction efforts, intrinsic productivity differences should be minimized and SAR comparison should be possible.

There may be the opportunity to consider concepts for actual directed research to evaluate these two competing hypotheses, such as exchanging yearling hatchery releases of stream type chinook between upriver and downriver areas. Clearly, releases would have to be into locations where returning adults would be intercepted prior to spawning in order to eliminate or greatly minimize effects of undesirable stock interactions or straying. Comparisons of SARs between the test releases and normal inbasin releases could provide additional insights into whether the observed differences observed between Snake and Yakima rivers SARs are primarily a result of intrinsic productivity differences between stocks or latent mortality.

Literature Cited

Adkison, Milo D. and Bruce P. Finney. 2003. The Long-Term Outlook for Salmon Returns to Alaska. Alaska Fishery Research Bulletin 10(2):83–94.

Beamish, Richard J., Chrys-Ellen M. Neville, and Alan J. Cass. 1997. Production of Fraser River sockeye salmon (*Oncorhynchus nerka*) in relation to decadal-scale changes in the climate and the ocean. Can. J. Fish. Aquat. Sci. Vol. 54:543–554.

Budy, P., G. P. Thiede, N. Bouwes, C. E. Petrosky, and H. Schaller. 2002. Evidence linking delayed mortality of Snake River salmon to their earlier hydrosystem experience. NAJFM 22(1):35–51.

Coronado, Claribel and Ray Hilborn. 1998. Spatial and temporal factors affecting survival in coho salmon (Oncorhynchus kisutch) in the Pacific Northwest. Can. J. Fish. Aquat. Sci. Vol. 55:2067–2077.

Hilborn, Ray and Claribel Coronado. 1997. Changes in ocean survival of coho and Chinook salmon in the Pacific Northwest. In, Emmett, R.L., and M.H. Schiewe (editors). 1997. Estuarine and ocean survival of Northeastern Pacific salmon: Proceedings of the workshop. U.S. Dep. Commerce, NOAA Tech. Memo. NMFS-NWFSC-29, 313 p.

Peterman, Randall M., Brian J. Pyper, Michael F. Lapointe, Milo D. Adkison, and Carl J. Walters. 1998. Patterns of covariation in survival rates of British Columbian and Alaskan sockeye salmon (*Oncorhynchus nerka*) stocks. Can. J. Fish. Aquat. Sci. Vol. 55:2503–2517.

Weitkamp, Laurie, Peggy Busby, and Kathleen Neely. 1997. Geographical variation in life histories of salmonids. In, Emmett, R.L., and M.H. Schiewe (editors). 1997. Estuarine and ocean survival of Northeastern Pacific salmon: Proceedings of the workshop. U.S. Dep. Commerce, NOAA Tech. Memo. NMFS-NWFSC-29, 313 p.

NOAA Fisheries Service's Comment on IDFG's Upstream/Downstream Comparison

The IDFG submission suggests that one approach for approximating the magnitude of latent (delayed) mortality caused by the hydropower system would involve comparing the SARs of populations that vary in the number of dams that they must pass during their migrations to and from the ocean. Unfortunately, testing for this so-called "upstream/downstream comparison" relies on a statistical model that simply includes one term to account for the number of dams without any specific allowance for other intrinsic and extrinsic factors. We know that a suite of endogenous and exogenous factors affect the survival of salmon throughout their life. Genetic diversity among populations leads to differences in their sex ratio, size and age at maturity, fecundity, egg size, and spawning behavior, all of which contribute to variation in the intrinsic productivity of salmon populations (Gross 1985, Peterman et al. 1986, Ward and Slaney 1988, Taylor 1990b, Gross 1991, Quinn and Unwin 1993, Roni and Quinn 1995, Unwin and Glova 1997, Hutchings and Jones 1998, Beckman et al. 2003, Hill et al. 2003). Similarly, spatial and temporal disparities in survival arise from variation in the amount of spawning and rearing habitat, the density of predators, the density of conspecific and other competitors, prey availability, the presence of exotic species, pathogens, temperature, flow, and water quality (Groot and Margolis 1991, Lichatowich et al. 1995, Mobrand et al. 1997, Beamer and Pess 1999, Yamomoto et al. 1999, Levin et al. 2002, Regetz 2003, Greene and Beechie 2004, Vollestad et al. 2004, Zabel and Achord 2004). Even with no dams in place, we would expect that all these important features would vary for populations across the Columbia River basin. Thus, although freshwater productivity of some stocks might appear similar during some time periods, we would not expect to observe similar patterns in the time series of freshwater productivity for the various stocks over a long time.

The accompanying text by IDFG claims that the "best available scientific information indicates that similar stocks of anadromous fish (e.g., stream type chinook salmon), that enter the ocean through the same (or nearby) estuary at similar times, have similar SARs (Beamish et al. 1997, Hilborn and Coronado 1997, Weitkamp et al. 1997, Coronado and Hilborn 1998, Peterman et al. 1998, Adkison and Finney 2003)." However, none of the cited references actually supports this argument. Adkison and Finney (2003) never mention SARs per se; instead they argue that the overall stock productivity tends to follow cyclic changes in the ocean environment and that regional differences exist in the response of salmon stocks to climate. Beamish et al. (1997) only presented SAR data for one population (Chilko Lake sockeye salmon) and indicated that overall patterns in the combined spawner-recruit data from a variety of Fraser River stocks may mask important stock-specific freshwater and marine effects. Similarly, Peterman et al. (1998) demonstrated that high mortality in the ocean synchronized the otherwise highly variable freshwater survival indices among Bristol Bay sockeye salmon, but none of their data indicated similar marine survival rates for neighboring stocks over time—only that they tended to rise and fall together. Hilborn and Coronado (1997) and Coronado and Hilborn (1998) tested whether the marine survival rates of hatchery coho salmon would co-vary by geographic region. They found that fish from the lower Columbia River clustered with those from the Oregon coast, but this was not surprising due to the similarities in freshwater life stages among hatchery fish that are spawned, fed, and reared independent of environmental variability. Again relying on hatchery coho salmon, Weitkamp et al. (1997) found that the recovery of CWTs could be grouped only by very broad regions, such that the Washington coast differed from the Oregon and California coasts.

As an example of the potential for upstream/downstream comparisons, IDFG presents SAR data for Chinook from the Snake River (data from NOAA Fisheries Service) and Yakima River (data from Yakama Nation Fisheries based on estimates from the Chandler Facility) (Figure A-1). Not presented is the caveat Bill Bosch[10] provided to NOAA Fisheries Service in early 2004 regarding the data from Chandler, which stated "Smolt accounting at Prosser is based on statistical expansion of Chandler smolt trap sampling data using available flow data and estimated Chandler entrainment rates. Chandler smolt passage estimates are prepared primarily for the purpose of comparing relative wild versus Cle Elum Supplementation and Research Facility passage estimates and not for making survival comparisons. While these Chandler smolt passage estimates represent the best available data, there is likely a relatively high degree of error associated with these estimates due to inherent complexities, assumptions, and uncertainties in the statistical expansion process. Therefore, these estimates are subject to revision." Data from PIT-tagged wild fish suggest a high bias in SARs based on estimates of fish at the Chandler facility. Wild Yakima River fish PIT tagged in 2000 and released below Roza Dam had a juvenile survival to McNary Dam of 81.9% (Table 24 of this technical memorandum). The preliminary SAR based on adult returns back to Bonneville Dam is 3.2% (Bosch 2004), which suggests that the SARs for wild Yakima River spring Chinook salmon from the 2000 outmigration were much lower than estim-ates based on the Chandler facility and closer to the estimated SARs for wild Snake River fish.

We agree that testing for FCRPS-induced latent mortality is worthwhile, but at present we see no effective reference system for comparing such mortality with that of Snake River spring-summer Chinook salmon. As suggested by IDFG, increased PIT tagging across populations within the Columbia River basin should allow for more comparisons of population-specific SARs in the future. If SARs across populations show no identifiable patterns coincident with the number of dams, the cause of the variation among populations would remain a mystery. If, however, we consistently find that SARs are lower for populations that pass more dams during their migrations, the cause would still remain unclear due to the enormous number of uncontrolled variables and inherent differences in stock productivity owing to genetic and environmental drivers.

[10] W. Bosch, Yakama Nation Fisheries, Toppenish, WA 98948, pers. commun.. March 2004.

Appendix B

Time-Series Model for Forecasting SARs from Coastal Ocean Upwelling

We modeled the effect of ocean-climate conditions on salmon survival using a class of Bayesian time series models known as dynamic linear models (DLMs), a form of the more general Kalman filter (Pole et al. 1994). This technique has been applied effectively to ecological data, and the methodology has been described in detail elsewhere (Cottingham and Carpenter 1998, Lamon et al. 1998, Scheuerell et al. 2002), so we describe it briefly here. At each time step *t* the observed response variable (Y_t, a scalar) is sequentially fitted to the $1 \times m$ vector of predictor variables (X_t) with the $m \times 1$ regression parameter vector (θ_t) plus an error term (t, a scalar) according to the observation equation

$$Y_t = X_t\theta_t + \upsilon_t \qquad \upsilon_t \sim N[0,V_t] \tag{19}$$

The observation errors υ_t have a variance V_t that is time-dependent and is usually not known well enough to approximate it with a fixed value. Therefore, as the analysis proceeds through time, V_t is estimated from all of the prior data. The discounting scheme described below also applies to V_t.

The DLM makes use of changes in the parameter set over time through a system equation. Using prior information from Bayesian learning, the $m \times 1$ vector of regression parameters (t) evolves through time according to the first-order Markov process

$$\theta_t = G\theta_{t-1} + \omega_t \qquad \omega_t \sim N[0,W_t] \tag{20}$$

The $m \times m$ system evolution matrix G dictates how the parameters change systematically through time while the $m \times 1$variance vector ω_t describes the stochastic change in each of the parameter estimates (θ_t) over time. The system variance matrix (W_t) has the variance in ω_t along the diagonal and zeros elsewhere. W_t is determined by the component discount factors applied to the posterior covariance matrix of the previous time step (Pole et al. 1994). In our case, there are no within-season effects, and therefore the evolution matrix G collapses to the identity matrix I, and therefore the change in the parameter set θ_t is governed entirely by the variance vector ω_t.

One-year forecasts are generated at each time step, and the parameters are updated as new information is incorporated into the model. Through the use of discounting, prior data are given weights that determine how influential the prior data are when updating the parameter estimates. These discounts represent the rate of exponential decay of useful information, such that when the discount is 1 (its maximum value), all of the prior information is retained. A discount value approaching 0, on the other hand, means no prior information is used at all. In general, the lower the discount value, the faster a parameter can change through time, but at the cost of decreased precision of the estimate. Therefore, in ecological applications, we typically select discounts greater than 0.8 because we wish to maximize the precision of our model forecasts. In this case, we selected the discounts by varying them systematically and then minimizing the negative log-likelihood of the overall model. Our final discounts were 0.9, 0.95, and 0.9 for the trend, regression, and variance blocks, respectively.

Ocean-Climate Data

We chose the Pacific Coastal Upwelling Index (CUI), otherwise known as the Bakun Index, as our measure of ocean-climate conditions. Coastal upwelling is thought to influence salmon during their ocean residence through bottom-up forcing of the marine food web (Nickelson 1986, Gargett 1997). Other researchers have used coastal upwelling as an ocean environment factor in comparing catches of Pacific salmon and Dungeness crab in this region (Botsford and Lawrence 2002). We obtained the CUI from the National Marine Fisheries Service Pacific Fisheries Environmental Laboratory (PFEL, online at http://www.pfeg.noaa.gov). PFEL generates monthly indices of intensity of large-scale, wind-induced coastal upwelling at 15 standard locations along the west coast of North America (each 3 degrees of latitude from 21°N to 60°N). Following Botsford and Lawrence (2002), we chose the CUI for 45°N lat. 125°W long. to compare with ocean survival of Chinook salmon from the Columbia River basin. This area of the North Pacific represents a region that salmon from the Columbia River move into after reaching the ocean (Miller et al. 1983). Previous studies suggest that the primary influence of the ocean on salmon survival occurs within the first year that juveniles occupy coastal waters (Pearcy 1992). Through the use of Bayes Factors, we identified the April, September, and October upwelling indices as the best predictor variables; therefore the model results presented in this technical memorandum are based on those metrics.

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61 **Berejikian, B.A., and M.J. Ford. 2004.** Review of relative fitness of hatchery and natural salmon. U.S. Dept. Commer., NOAA Tech. Memo. NMFS-NWFSC-61, 28 p. NTIS number pending.

60 **Ford, M.J., T.A. Lundrigan, and P.C. Moran. 2004.** Population genetics of Entiat River spring Chinook salmon. U.S. Dept. Commer., NOAA Tech. Memo. NMFS-NWFSC-60, 45 p. NTIS PB2004-107039.

59 **Sloan, C.A., D.W. Brown, R.W. Pearce, R.H. Boyer, J.L. Bolton, D.G. Burrows, D.P. Herman, and M.M. Krahn. 2004.** Extraction, cleanup, and gas chromatography/mass spectrometry analysis of sediments and tissues for organic contaminants. U.S. Dept. Commer., NOAA Tech. Memo. NMFS-NWFSC-59, 47 p. NTIS PB2004-105739.

58 **Beechie, T.J., E.A. Steel, P. Roni, and E. Quimby (editors). 2003.** Ecosystem recovery planning for listed salmon: an integrated assessment approach for salmon habitat. U.S. Dept. Commer., NOAA Tech. Memo. NMFS-NWFSC-58, 183 p. NTIS PB2004-105734.

57 **Rogers, J.B. 2003.** Species allocation of *Sebastes* and *Sebastolobus* sp. caught by foreign countries from 1965 through 1976 off Washington, Oregon, and California, USA. U.S. Dept. Commer., NOAA Tech. Memo. NMFS-NWFSC-57, 117 p. NTIS PB2004-105737.

56 **MacCall, A.D., and T.C. Wainwright (editors). 2003.** Assessing extinction risk for West Coast salmon. U.S. Dept. Commer., NOAA Tech. Memo. NMFS-NWFSC-56, 198 p. NTIS PB2003-104642.

55 **Builder Ramsey, T., et al. 2002**. The 1999 Northwest Fisheries Science Center Pacific West Coast upper continental slope trawl survey of groundfish resources off Washington, Oregon, and California. U.S. Dept. Commer., NOAA Tech. Memo. NMFS-NWFSC-55, 143 p. NTIS PB2003-104641.

54 **Krahn, M.M., et al. 2002.** Status review of Southern Resident killer whales *(Orcinus orca)* under the Endangered Species Act. U.S. Dept. Commer., NOAA Tech. Memo. NMFS-NWFSC-54, 133 p. NTIS PB2003-104520.

53 **Waknitz, F.W., T.J. Tynan, C.E. Nash, R.N. Iwamoto, and L.G. Rutter. 2002**. Review of potential impacts of Atlantic salmon culture on Puget Sound chinook salmon and Hood Canal summer-run chum salmon evolutionarily significant units. U.S. Dept. Commer., NOAA Tech. Memo. NMFS-NWFSC-53, 83 p. NTIS PB2002-108143.

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