Factors affecting sockeye salmon returns to the Columbia River in 2008

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Executive Summary

In 2008, more than 213,000 adult sockeye salmon *Oncorhynchus nerka* returned to the Columbia River Basin. This is the highest return since 1959. As in the previous 40 years, greater than 99% of these fish were destined for the Upper Columbia River. Nonetheless, the estimated 805 adults passing Lower Granite Dam marked the highest return there since 1968.

The high adult sockeye salmon returns in 2008 could have been due to increased freshwater production, favorable conditions for juvenile sockeye salmon during downstream migrations, favorable ocean conditions, or a combination of these factors. It is also possible these high returns resulted in part from reduced harvest or favorable conditions for adults during their upstream migration to spawning sites. Here we report analyses of each of these life cycle components to investigate their influence on the high observed return. This was to analyze the variation in adult return rates across recent years under contemporary conditions of the mainstem hydropower system. We made no attempt to relate these returns to those from early periods before or during dam construction.

Direct estimates of smolt-to-adult returns (SAR) for the total Columbia River population were possible, but for the Snake River population only an "Index SAR" could be calculated for juvenile outmigrations from 1998 to 2006. Most migrating Snake River sockeye juveniles were collected at Snake River dams and transported by barge to below Bonneville Dam, while nearly all Upper Columbia River sockeye juveniles migrated through the hydropower system and were not transported.

Snake River sockeye Index SARs were substantially lower than Columbia River sockeye SARs, in part simply because the migration distance incorporated into estimated SARs was longer for Snake River fish. Snake River Index SARs were estimated from arrivals of both juveniles and adults at Lower Granite Dam, while the Columbia River SARs were estimated from arrivals of juveniles at McNary Dam and adults at Bonneville Dam. A number of additional factors could have influenced the difference in SARs. For example, adults returning to the Snake River were largely of hatchery origin, while those from the Columbia River were mostly wild. Furthermore, these stocks are from different Evolutionarily Significant Units (ESUs). Therefore, we expect them to exhibit inherent differences that may influence stock productivity. These include genetic differences that control growth, size, and migration timing. Finally, the Snake River stock represents fish at the limit of their natural range, with the longest migrations and attaining the highest elevations to reach spawning sites.

There are several lines of evidence suggesting that changes in ocean productivity led to the high adult return observed in 2008. Estimated SARs for Upper Columbia and Snake River sockeye salmon stocks were highly significantly correlated ($R^2 = 0.87$, $P < 0.01$). In addition, there was no correlation between sockeye salmon SARs and indices of mainstem flow and percentage spill at hydropower projects in the Columbia River from McNary to Bonneville Dams. This suggests that the primary factors influencing the variation in annual adult returns acted downstream from Bonneville Dam and on both stocks in common. There was no evidence that adult escapements in 2008 were influenced by changes in ocean or river harvest.

In further support of this finding, we found some evidence that a common measure of ocean productivity, the Pacific Decadal Oscillation, influenced adult sockeye returns over a longer time period (1985-2006). Also, the large increase in Columbia River adult returns from the 2006 juvenile migration, and comparatively large number of 1-ocean fish from the 2007 outmigration, occurred coincident with an increase in ocean productivity as measured by a suite of indicators developed by the Northwest Fisheries Science Center for Chinook *O. tshawytscha* and coho *O. kisutch* salmon.

Surprisingly, we found a significant negative relationship between survival of juvenile sockeye salmon from the Upper Columbia River and an index of spill within the hydropower system between Rock Island and McNary Dams. This finding merits a more detailed review and analysis of specific project operations and passage conditions.

With respect to the Snake River, the Captive Broodstock Program has increased smolt production over the past decade, and the number of smolts estimated to have arrived at Lower Granite Dam correlated strongly ($R^2 = 0.653$, $P < 0.01$) with the number of adults returning to Lower Granite Dam two years later. Thus, the large return of adults to the Snake River in 2008 was in part a result of increased smolt production in 2006. Also, favorable environmental conditions above Lower Granite Dam in 2008 likely resulted in a relatively high proportion of adults reaching the spawning grounds that year.

We found no significant correlation between juvenile sockeye survival and indices of flow, percentage spill, and water temperature. Although an average of 75% of the juvenile sockeye arriving at Snake River dams from 1998 to 2006 were transported, we found no significant correlation between Index SARs for Snake River sockeye salmon and the percentage of fish transported, after adjusting for the SAR pattern common for both Upper Columbia River and Snake River basin stocks. Unfortunately, we could not directly compare return rates of PIT-tagged fish with different migration histories - transported, bypassed, or non-detected - because adult sockeye salmon returns of PIT-tagged fish were extremely low, and ranged from 0 to 3 fish per treatment group from juvenile migration years 2002-2007. Given the limited data, it is currently not clear whether transportation is beneficial, detrimental, or neutral for sockeye salmon.

The analyses conducted here were primarily correlative and limited by the type and amount of data currently available. Additional research will be required to develop more robust, definitive information on the factors affecting sockeye salmon in both river and ocean environments. This would include studies that directly measure the effects of transportation, evaluate the high variability in smolt survival from traps in the Snake River to Lower Granite Dam, provide measures of survival past dams and downstream of Bonneville Dam, and lead to development of ocean productivity indices to predict adult sockeye return rates.

In summary, the results discussed here provide a consistent pattern to explain the large return of adult sockeye to the Columbia River in 2008. Based on these results, we conclude that the factors responsible for the high return largely acted on fish downstream of Bonneville Dam and during the marine component of their life cycle, and not in the river upstream of Bonneville Dam.

Introduction

In 2008, adult returns of sockeye salmon *Oncorhynchus nerka* to the Columbia River were the highest since 1959 (Figure 1). As in each of the past 40 years, greater than 99% of this return was destined for spawning areas in the Upper Columbia River. Of the more than 213,000 adults passing Bonneville Dam, only an estimated 805 adults crossed Lower Granite Dam. However, this return to the Snake River was the highest observed since 1968.

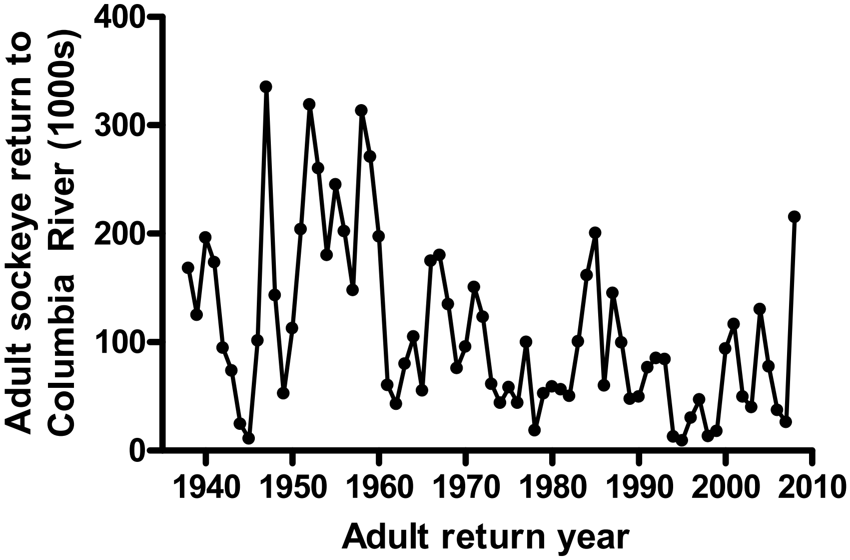

Figure 1. Yearly adult sockeye salmon return to the Columbia River (Bonneville Dam count plus Zone 1-5 harvest).

In this report we evaluate factors that likely contributed to the high adult sockeye salmon returns to the Columbia River in 2008. We examined elements from the entire life cycle and report on the following areas: freshwater production, conditions during the juvenile migration, and ocean conditions. We also evaluated the effects on adults of harvest and conditions experienced during the upstream migration. Because sockeye salmon that spawn in the Upper Columbia River have constituted nearly the entire return in recent years and the availability of more long-term data sets, we focused primarily on this stock. However, because the Snake River sockeye salmon ESU is listed as endangered under the U.S. Endangered Species Act (NMFS 1991) and operations at Snake River dams are often scrutinized in terms of their affect on fish survival, we also evaluated factors affecting this stock. In both rivers, to the extent that data were available, we evaluated smolt-to-adult return rates (SARs) to measure possible effects of different factors influencing adult returns.

General sockeye salmon life history

Three Evolutionarily Significant Units (ESU) (Waples 1991) of sockeye have been identified in the Columbia basin: 1) the Lake Wenatchee ESU; 2) the Okanagon River ESU that spawns in Osoyoos/Skaha Lakes along the US/Canada border; and 3) the Snake River ESU (Figure 2). Within these ESUs, three life history types occur: anadromous, resident and kokanee. The anadromous form spends up to 3 years in its nursery lake before migrating to sea as a smolt during spring. It may remain at sea up to 4 years before returning to the natal area to spawn (Bjornn et al. 1968; Foerster 1968; Groot and Margolis 1991). In the Columbia River, most anadromous sockeye spend 1 year in freshwater as juveniles and 2 years at sea as adults. The residual form are progeny of anadromous or residual fish that remain in fresh water to mature and reproduce; they produce mostly anadromous offspring (Foerster 1968; Groot and Margolis 1991; Ricker 1938). Residuals are part of the same ESU as the anadromous form. From an evolutionarily standpoint, this form may have evolved to act as a safety-net against failure of other year classes at sea. The third form, kokanee, is a resident, freshwater-adapted life-history type that evolved from anadromous fish, but is now genetically distinct from both the residual and anadromous sockeye salmon (Groot and Margolis 1991).

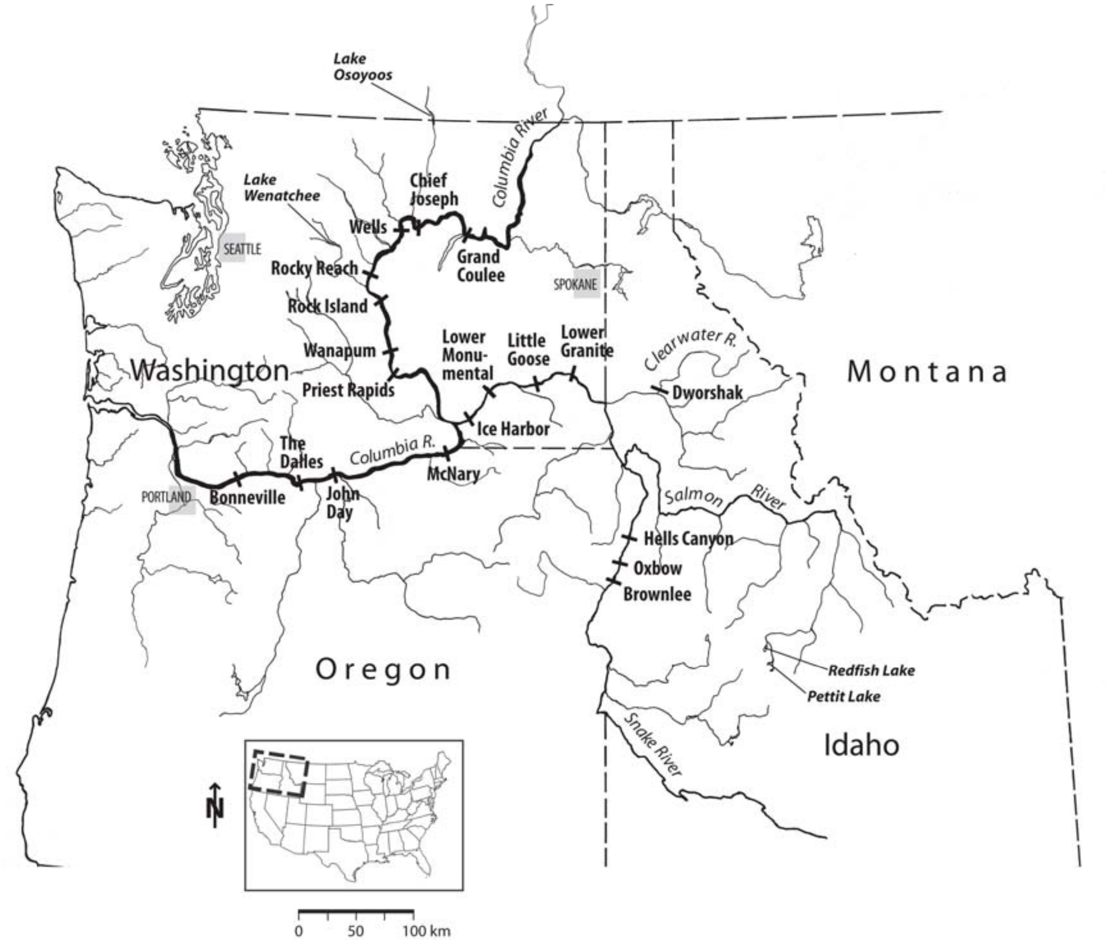

Figure 2. Map of the Columbia River Basin noting the location of major sockeye salmon spawning lakes (Osoyoos, Wenatchee, and Redfish Lakes) and mainstem dams.

Historically, several populations of Snake River sockeye salmon spawned in Oregon and Idaho lakes. In the late 19th and early 20th centuries, construction of dams on headwater reaches of rivers and at lake outlets eliminated access to spawning grounds for many populations. In Idaho, the anadromous life form was nearly extirpated by construction in 1910 of Sunbeam Dam on the Salmon River. Currently, Redfish, Pettit, and Alturas Lakes and the Captive Broodstock Program contain the remnants of the Snake River sockeye salmon ESU. This population is unique in that it is the southernmost spawning population in existence. Returning adults from the population travel the farthest inland (> 1,400 km) and attain the highest elevation spawning grounds (> 1,980 m) of any sockeye salmon population in the world. Although the population appeared quite healthy in the 1950s, with hundreds or thousands of fish returning to

Redfish Lake most years, it declined precipitously to the point where a total of 3 fish returned to Redfish Lake during 1988-1990, and the ESU was listed as endangered under the Endangered Species Act in 1991 (NMFS 1991).

For Redfish Lake sockeye salmon, both the anadromous and residual forms are beach spawners. These forms reproduce in the lake during October, whereas kokanee spawn in a tributary to the lake during August and early September. Both the residual and anadromous forms of sockeye salmon in Redfish Lake are included in the ESA listing, whereas kokanee in the lake is not. A large population of kokanee also resides in Dworshak Reservoir, and when spill from the reservoir occurs during spring, large numbers of juvenile kokanee are often flushed from the reservoir and arrive at Lower Granite Dam. This complicates estimates of the number of anadromous juvenile sockeye salmon (smolts) arriving at Lower Granite Dam in a given year.

Adult abundance

For the period 1938-2002, we used estimates of sockeye salmon adult returns to the Columbia River developed by Washington Department of Fish and Wildlife/Oregon Department of Fish and Wildlife (WDFW/ODFW 2002). For the period 2003-2008 we obtained adult counts at Bonneville Dam from University of Washington's DART web site (http://www.cbr.washington.edu/dart). We increased these counts by estimated harvest in the river reach below Bonneville Dam (Columbia River Compact Zones 1-5) based on unpublished data from Compact reports. Although exhibiting interannual variability, the number of adults returning to the Columbia River has not displayed any significant trend over the past 40 years (Figure 1).

Columbia River sockeye

Our analyses of Columbia River sockeye included all adult returns to the Columbia River and estimates of smolt arrivals at McNary Dam. We recognize that this mixed the two Upper Columbia River basin ESUs with the Snake River basin ESU, but because the Snake River ESU produced a very small proportion of these smolts and adults, we assumed that the results essentially reflected factors associated with the Upper Columbia River stocks. For adult returns, we thus used the data graphed in Figure 1.

Freshwater production

The Osoyoos/Skaha Lakes system is more productive and is about 5 times larger than Lake Wenatchee (Mullan 1986). Consequently, natural smolt production is higher in Lake Osoyoos than in Lake Wenatchee (12.4 compared to 6.3 lbs fish/acre; Mullan, J., pers. comm. as cited in Peven 1987). Smolts leaving Lake Osoyoos are also larger on average than those leaving Lake Wenatchee (>100 mm and 9.2 g vs. 86 mm and 6.2 g; Hyatt and Rankin 1999; Peven 1987). Lake Wenatchee fish typically migrate as juveniles through the mid-Columbia in early May, while Osoyoos/Skaha Lakes fish migrate in late May or early June (Peven 1987). However, because the Lake Wenatchee and Okanagon River ESUs share a common migratory pathway and dam counts of smolts and adults are not distinguished by ESU, we treated all fish from the Upper Columbia as a single unit in the analyses that follow.

Hatchery enhancement programs have released fry or pre-smolts sockeye into Lake Wenatchee and Osoyoos/Skaha Lakes the year before they migrate to the ocean since 1993. The smolts that subsequently migrate from these releases, with exception of a couple of years (see section below), represent a small fraction of the total sockeye juvenile migration.

Downstream juvenile migration

We estimated survival of juvenile sockeye from the tailrace of Rock Island Dam to the tailrace of McNary Dam using standard methods (Skalski 1998; Williams et al. 2001). Release groups were comprised of individual PIT-tagged fish that were tagged or detected at Rock Island Dam and subsequently detected at or below McNary Dam (i.e., John Day Dam, Bonneville Dam, or in the PIT trawl detection system operated at river kilometer 75). Because of limited sample sizes, survival estimates were not possible for Upper Columbia River fish in 2003 or prior to 1997. Survival estimates in the remaining years from 1997 to 2008 ranged from 0.40 to 0.79 (Table 1).

Table 1. Survival estimates (with standard errors in parentheses) and environmental exposure indices for juvenile sockeye salmon migrating from Rock Island Dam to McNary Dam.

	Rock Island to McNary				
	Survival		**Exposure Indices**		
	S	**(s.e.)**	**Flow (kcfs)**	**Spill (%)**	**Temp (^oC)**
1996	--	--	332.0	32.9	10.7
1997	0.397	(0.119)	478.0	51.8	12.3
1998	0.624	(0.058)	319.8	43.1	12.6
1999	0.559	(0.029)	258.3	46.7	11.1
2000	0.487	(0.114)	242.5	44.3	13.7
2001	0.657	(0.117)	137.0	36.5	15.5
2002	0.531	(0.044)	202.8	35.7	11.6
2003	--	--	--	--	--
2004	0.648	(0.114)	238.1	38.1	14.0
2005	0.720	(0.140)	264.9	40.9	12.7
2006	0.793	(0.062)	321.8	28.7	12.8
2007	0.625	(0.046)	266.0	22.9	13.0
2008	0.644	(0.094)	353.6	26.4	12.3

We evaluated the relationship between juvenile migrant survival and river conditions within the hydropower system between Rock Island and McNary Dams by regressing annual estimated survival for the overall Columbia River sockeye salmon population against indices of the population's exposure to river flow, percentage spill at dams, and water temperature. Flow and temperature were measured at McNary Dam. Indices were the average daily flow and temperature between dates of the 25th and 75th passage percentiles of PIT-tagged fish detected at the dam. For percentage spill we calculated the average daily percentage spill between the dates of the 25th and 75th percentiles of PIT-tag detection at McNary Dam, the average daily percentage spill at Priest Rapids Dam for the period 5 days prior to the McNary passage dates, and the average daily percentage spill at Wanapum Dam for the period 6 days prior to the McNary dates. The 5-6 d offset periods were derived from distance between dams and typical travel time for sockeye between Rock Island and McNary Dams. Survival was significantly negatively correlated with percentage spill, but was not correlated with flow or water temperature (Figure 3).

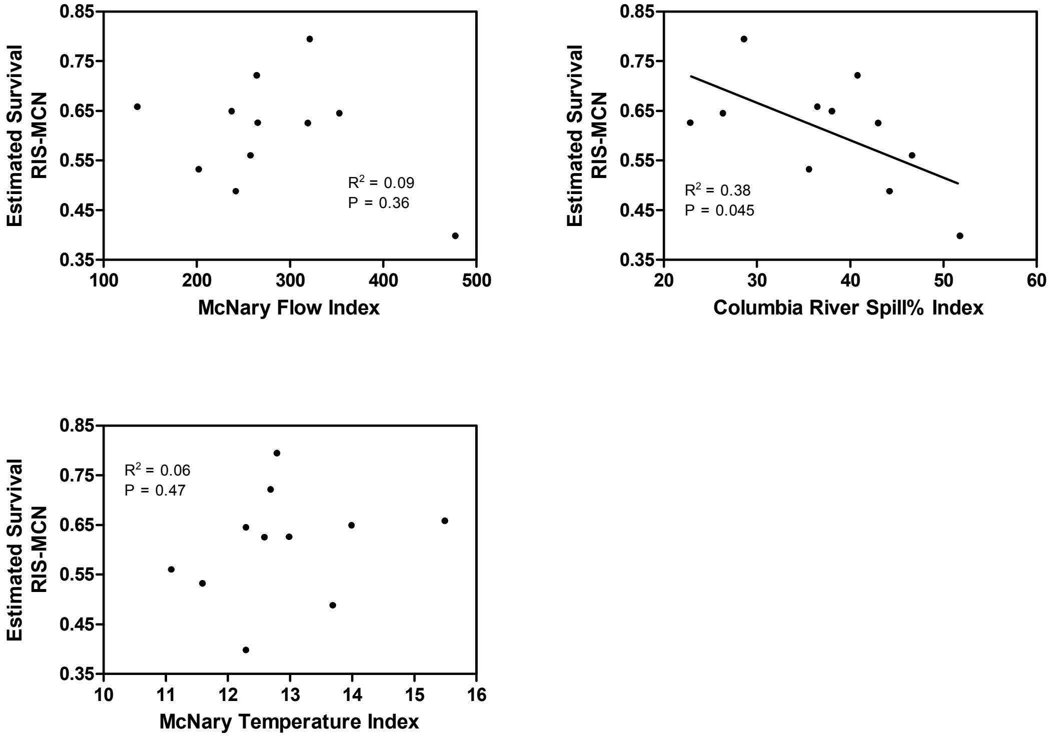

Figure 3. Survival of Upper Columbia River sockeye salmon (estimated from Rock Island Dam to McNary Dam) versus exposure indices for flow (kcfs, top left), spill% (top right), and temperature (^{o} C, bottom left), juvenile outmigration years 1997-2008.

We estimated smolt abundance at McNary Dam - the farthest possible upstream PIT-tag detection site on the Columbia River. For this estimate, we combined the Smolt Monitoring Program estimated yearly collection of hatchery and wild smolts at the McNary Dam juvenile bypass system (JBS) from 1995 to 2007 (http://www.fpc.org). We divided that total by the estimated annual mean detection efficiency estimates for PIT-tagged sockeye salmon smolts at the dam. We then expanded this estimate for the recent years to account for the change in sampling schedule at the JBS from every day to every other day. We then estimated detection efficiency using CJS (Cormack 1964; Jolly 1965;

Seber 1965) maximum-likelihood procedures on data from PIT-tagged sockeye salmon released from upstream sites in the Columbia River and subsequently detected at McNary, John Day, or Bonneville Dams. We estimated that since 1995, between 0.43 and 4.76 million smolts arrived at McNary Dam each year (Table 2). The estimated percentage of wild smolts passing the dam was greater than 95% for all migration years, except 1996 (81%) and 2005 (89%).

Table 2. Estimated annual number of sockeye salmon smolts from the Upper Columbia River and Snake River Basins combined arriving at McNary Dam, subsequent adult return (totaled for each outmigration year) to Bonneville Dam, and annual SAR.

Outmigration Year	Smolts passing McNary Dam[a]	Adults passing Bonneville[b]	SAR (%)
1995	2,879,662	51,839	1.80
1996	502,153	3,373	0.67
1997	429,543	18,713	4.36
1998	2,856,110	103,178	3.61
1999	3,319,327	112,457	3.39
2000	523,331	49,325	9.43
2001	1,093,809	15,056	1.38
2002	3,118,111	145,741	4.67
2003	4,757,209	73,930	1.55
2004	2,486,746	33,881	1.36
2005	601,769	12,549	2.09
2006	2,849,102	230,665	8.10
2007	2,633,346		

[a] The number of smolts arriving at McNary Dam is comprised of nearly 100% Columbia River stocks due to low production and transportation operations in the Snake River.

[b] Estimated total adults returning to Bonneville Dam from individual juvenile migration years, except for 2006, which was estimated based on returns to date of 1- and 2-ocean fish (203,538) expanded by the long-term proportion of 3-ocean fish (~12%).

There is no information on survival of migrating juvenile sockeye salmon below Bonneville Dam. However, survival of juvenile Chinook salmon migrating through the lower Columbia River below Bonneville Dam during spring has been studied since 2005. Estimated survival for acoustic-tagged yearling Chinook salmon subsampled from the composite population passing Bonneville Dam and pooled across all releases each year was 0.691 (s.e.= 0.030) in 2005 and 0.671 (s.e.= 0.021) in 2006 (Lynn McComas, NOAA, NW Fisheries Science Center, pers. communication). While extremely limited, the available data for yearling Chinook salmon suggest that conditions juvenile sockeye experienced below Bonneville Dam in 2006 were likely not substantially different from 2005, or responsible for the nearly four-fold difference in estimated adult return rate between these years (Table 2).

Smolt to adult returns

To estimate smolt-to-adult return rates (SARs) for Columbia River sockeye, we began with smolt abundance estimates (Table 2) and adult returns to the Columbia River (Figure 1). Next, we obtained adult age-class composition from Columbia River Intertribal Fish Commission (CRITFC). Each year, CRITFC staff read scales from a sample of adult sockeye collected at Bonneville Dam and determine their age at ocean entry and at adult return to freshwater. Together, the freshwater and ocean ages identify the age class of a returning adult. For scale analyses from 1998-2008, we accessed the CRITFC web site (http://www.critfc.org/). J. Fryer (CRITFC, pers. communication) provided data on adults returning to Bonneville Dam in 1996 and 1997. From these data, we estimated the proportion of the return each year that came from each juvenile year class. For each adult return year, we multiplied the estimated proportion of fish in each age class by the total adults that returned that year (from Figure 1). The resulting adult return numbers were assigned to the appropriate juvenile year class, and summed to estimate the total adult return for each juvenile migration year from 1995 to 2006 (Table 2). Not all adults from the 2006 juvenile migration year have returned to date. To estimate the number of adults returning from this migration year, we expanded the 1- and 2-ocean fish observed to date from 2006 by the mean percentage of 3-ocean fish that returned to Bonneville Dam over the preceding 10 years (approximately 12%). The estimated and projected annual SAR of the unmarked Columbia River sockeye salmon population for migration years 1995 through 2007 ranged from 0.7 to 9.4% (Table 2).

We then evaluated the relationship between Upper Columbia River smolt abundance and adult abundance from 1995 to 2006 and found a significant ($P < 0.05$)

although relatively weak relationship ($R^2 = 0.34$), suggesting that smolt production did not explain much of the high return observed in the Columbia River in 2008.

We also evaluated the relationship between SARs and juvenile migration conditions within the hydropower system downstream from McNary Dam by regressing annual Columbia River sockeye SAR estimates against two hydropower system operational indices: 1) an index of flow in the lower Columbia River based on flow at McNary Dam during the smolt migration season; and 2) an index based on total percentage spill at McNary, John Day, The Dalles, and Bonneville Dams during the smolt migration period. The flow index was the weighted average of daily flow values at McNary Dam, with daily weights equal to the combined number of Snake River and Upper Columbia River PIT-tagged smolts detected. Weighted average percentage spill values were calculated for McNary, John Day, and Bonneville Dams using the same method. The spill index for comparison with SAR was the (unweighted) average of the weighted averages for the three dams. The annual estimated SAR for the combined population of fish at McNary Dam had very low correlation and no significant linear relationship with either flow in the lower Columbia River ($R^2 = 0.04$, $P = 0.52$) (Figure 4), or the index of spill at McNary, John Day, The Dalles, and Bonneville Dams ($R^2 = 0.12$, $P = 0.28$) (Figure 5).

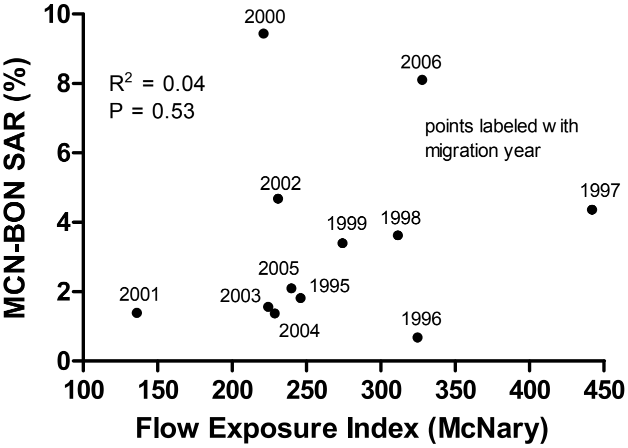

Figure 4. SAR of the combined Columbia River basin sockeye salmon population (smolts at McNary Dam to adults at Bonneville Dam) plotted against an index of lower Columbia River flow (kcfs) (based on outflow at McNary Dam) during the juvenile outmigration, 1995-2006.

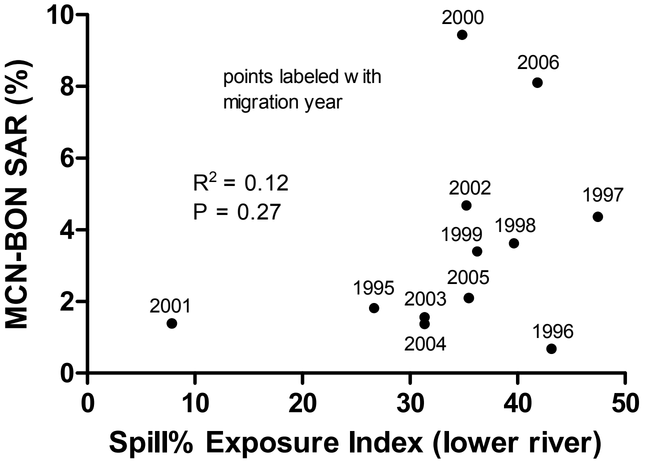

Figure 5. SAR of the combined Columbia River basin sockeye salmon population (smolts at McNary Dam to adults at Bonneville Dam) plotted against an index of spill exposure (based on spill percentages at McNary, John Day, The Dalles, and Bonneville Dams) during the juvenile outmigration, 1995-2006.

Relating SARs to ocean conditions

Several large-scale ocean and atmospheric indicators influence the coastal ocean environment, and they in turn affect local physical conditions and the productivity of coastal waters for juvenile salmon. Large-scale indicators include the Pacific Decadal Oscillation (PDO) (Mantua et al. 1997) and the Multivariate El Nino Southern Oscillation (MEI). For the past 12 years, the Northwest Fisheries Science Center has been observing how these indicators, as well as local and regional physical and biological indicators, relate to juvenile salmon abundance and subsequent adult returns. We developed an index of 11 physical and biological ocean ecosystem indicators to monitor the productivity of the coastal waters, the survival of juvenile salmon, and ultimately adult returns (http://www.nwfsc.noaa.gov/research/divisions/fed/oeip/a-ecinhome.cfm). To date, our indices have focused on relating ocean productivity factors with Chinook *O. tshawytscha* and coho *O. kisutch* salmon adult returns.

To address whether SARs for Upper Columbia River sockeye salmon were related to ocean conditions, we first evaluated whether the available smolt index data at McNary Dam for migration years 1985-1994 could be used to develop a longer SAR time series. If SARs based on uncorrected smolt counts (i.e., raw passage index counts) were highly correlated with those based on corrected counts (i.e., passage index counts corrected with PIT-tag detection probabilities as calculated above), then we could use the correlation to adjust the early period SARs. In fact, SARs using corrected and uncorrected smolt counts were highly correlated ($R^2 = 0.914$, $P < 0.001$), and we estimated the early period SARs accordingly to expand the time series.

Using the longer SAR time series (1985-2006), we evaluated whether Columbia River SARs were related to monthly indices of the Pacific Decadal Oscillation (PDO). The PDO is an index of sea surface temperature anomalies in the North Pacific Ocean that is commonly used in analysis of how salmon respond to ocean conditions. We performed a multiple regression of SARs versus monthly PDO indices for each juvenile migration year. Similar to the approached developed by Zabel et al. (2006) we compared SARs to monthly PDO indices for a full year beginning in May of the outmigration year. The combination of months that provided the best fitting model based on Akaike information criterion (AIC) values contained monthly indices for August and October in the first year in the ocean and March and April in the second year in the ocean ($R^2 = 0.61$, $P = 0.002$). The regression coefficients associated with August (first year) and April (second year) were negative, meaning cooler ocean temperatures and stronger upwelling were positively associated with SAR. The coefficients associated with October (first year) and March (second year) were positive, meaning warmer temperatures and weaker upwelling were positively associated with SAR. The moderately strong relationship we obtained indicates that ocean conditions likely play a role in determining SAR, but the particular months we found important were different from previous analyses (ICTRT and Zabel, 2007) of Chinook and coho salmon and steelhead, indicating that sockeye are likely utilizing different ocean productivity factors.

To further explore the recent adult sockeye returns, we compared Columbia River sockeye SARs to Snake River spring/summer Chinook SARs from 1985 to 2006 to determine whether common factors were driving the pattern of variability in both spring-migrating Columbia River basin salmonids. The weak correlation ($R^2 = 0.16$, $P = 0.076$) provided additional evidence that Columbia River sockeye were not responding to the same ocean factors as Snake River spring/summer Chinook salmon. Not surprisingly, when we compared Columbia River sockeye SARs for migration years 1998-2006 to the suite of factors reported in our ocean index, we found a weak correlation between the rank order of ocean indicators (a high rank is associated with poor ocean conditions whereas a low rank is associated with good ocean conditions) and the rank order of sockeye SARs ($R^2 = 0.13$, $P = 0.33$). However, we also observed that either higher sockeye SARs or larger numbers of returning adults were associated with either intermediate or good ocean conditions, whereas lower SARs or low numbers of returning adults were associated with poor ocean conditions.

Harvest

Sockeye, pink, and chum salmon rear in the Gulf of Alaska and central North Pacific Ocean. At one time substantial harvest of all three species occurred in a high seas driftnet fishery directed at squid. However, based on genetic analysis of fish caught in this fishery, very few of the sockeye were from southern British Columbia or Washington (Orlay Johnson, NOAA, NW Fisheries Science Center, pers. communication). Furthermore, in 1993 the United Nations Convention for the Conservation of Anadromous Stocks in the North Pacific Ocean prohibited directed fishing for salmonids in international waters north of 33°N latitude. Today, all regulated harvest occurs within the Exclusive Economic Zone (EEZ), and most of this is in terminal areas such as approaches to the Fraser River and Bristol Bay. Thus, we found no evidence that changes in ocean harvest levels could have resulted in the increased adult return in 2008. Harvest during the upstream migration, but below Bonneville Dam (management Zones 1-5 under the Columbia River Compact; http://wdfw.wa.gov/fish/crc/crcindex.htm), made up approximately 0.5% of the total adult return in 2008 and had little influence on the size of the return.

Upstream adult migration

We found an extremely strong relationship between adult escapement above Bonneville Dam and adult counts at Rock Island Dam over a broad range of returns over the past 20 years (Figure 6). Taking into account harvest in the Management Zone 6 fishery between Bonneville and McNary Dams, the average yearly proportion of fish that successfully migrated between Bonneville and Rock Island Dams since 1978 was approximately 89%, or roughly 98% survival per dam. The year 2008 was no exception, where 91% of the fish counted at Bonneville Dam were counted at Rock Island Dam.

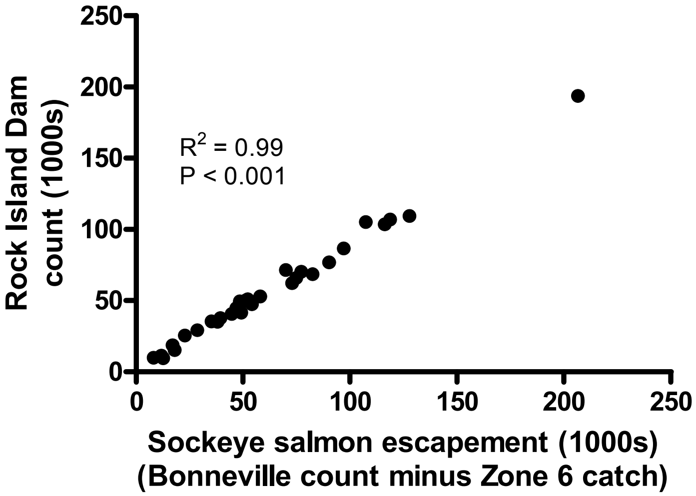

Figure 6. Relationship between upstream escapement (Bonneville Dam count minus the estimated Zone 6 harvest) and subsequent Rock Island Dam adult count, adult return years 1978-2008.

Snake River sockeye

As discussed above, due to the importance of this ESU and its listing under ESA we evaluated factors that affected adult returns of Snake River sockeye in 2008 and over the last decade. For these analyses, we used separate smolt and adult abundance estimates from those used for the Columbia River as a whole. For adult abundance, we used escapement to upper Snake River dams: Ice Harbor from 1962-1968, Lower Monumental in 1969, Little Goose from 1970-1974, and Lower Granite from 1975-2008. These data were obtained from University of Washington's DART web site (http://www.cbr.washington.edu/dart). We adjusted counts from 2005 to 2008 when a removable spillway weir was operated during the summer. Based on PIT-tag detections in 2008, the weir increased adult counts by approximately 11% due to adults falling back through the weir and being counted twice. From 1962 to 2008, estimated total adult returns to the Snake River varied between 1 and 1,300 fish (Figure 7). Patterns of variation in return numbers were dissimilar from those of Columbia River sockeye as a whole, and displayed a significant decline until the most recent decade when efforts to recover the ESU appear to have increased returns compared to the 1985-1998 period (Figure 1).

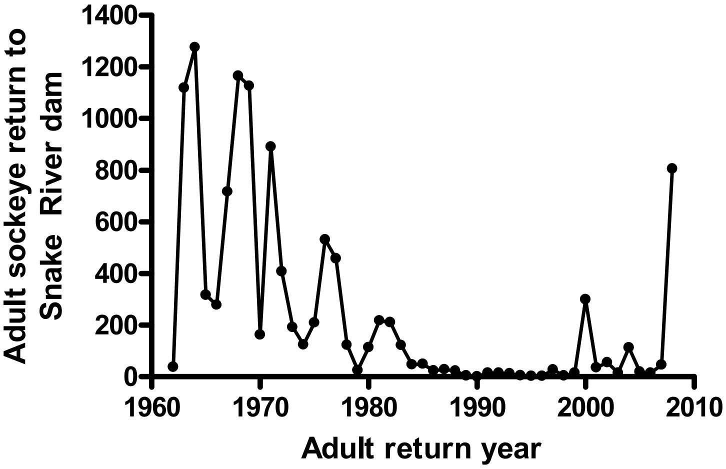

Figure 7. Yearly adult sockeye salmon counts at upper Snake River Dam (Ice Harbor Dam (1962-68), Lower Monumental Dam (1969), Little Goose Dam (1970-1974), and Lower Granite Dam (1975-2008). (2006-2008 counts decreased by ca. 11% to adjust for estimated fallback due to operation of the removable spillway weir.)

Freshwater production

A Captive Broodstock Program (Program) was initiated in 1991 to avoid extinction of Snake River sockeye salmon (Flagg et al. 1995; Flagg et al. 2004). Both NOAA Fisheries and Idaho Department of Fish and Game (IDFG) maintain Redfish Lake sockeye salmon captive broodstocks. Groups of fish are reared at two or more facilities to protect these important genetic lineages from catastrophic loss. IDFG rears captive broodstock groups until they reach full-term maturity in fresh well water at the Eagle Fish Hatchery near Boise, ID. NOAA Fisheries rears captive broodstock groups using two methods, with one group reared to maturity in fresh well water, and a second group reared from the smolt to adult stages in seawater at its Manchester Research Station near Port Orchard, WA. All 16 wild anadromous adults that returned to Redfish Lake between 1991 and 1998 were captured and spawned for the Program, and an additional 900 smolts and 25 residual sockeye salmon were captured for Program rearing in 1991-1993.

Today, the Program has first, second, and third generation lineages of these fish in culture, and efforts are underway to re-introduce populations in nearby Alturus and Pettit Lakes. The Program reintroduction plan follows a "spread-the-risk" philosophy incorporating multiple release strategies and sites (Redfish, Alturas, and Pettit Lakes). Progeny from the Program have been reintroduced to Sawtooth Valley waters at different life stages using a variety of release methods. Since releases began in the mid 1990s, more than 860,000 eyed eggs have been planted to in-lake incubator boxes. In addition, 2,500 mature adults were released to spawn naturally, 1.3 million parr were released to overwinter and migrate the following spring, and 575,000 smolts were released to migrate immediately. However, releases of different life-history stages during early years of the Program did not lead to many adult returns. An evaluation in the early 2000s (Hebdon et al. 2004) determined that returning adults had mostly come from the smolt releases. Thus, more emphasis in recent years has been placed on smolt production and release, but production remained low through 2004 due to limited rearing space.

Downstream juvenile migration

We did not use our standard CJS methods to estimate the number of sockeye smolts arriving at Lower Granite Dam because for several migration years the estimates based on using CJS methods far exceeded the total number of sockeye smolts estimated to have left the Stanley Basin. The overestimate of smolts at Lower Granite Dam likely resulted from kokanee arriving at the dam from Dworshak Reservoir being counted as sockeye smolts.

Instead, for the 2001-2007 migration years we used estimates of smolts arriving at Lower Granite Dam made by IDFG and submitted to the Program technical review team (unpublished data). For 1998-2000, we estimated the number of smolts arriving at the dam by using estimates of PIT-tagged sockeye salmon leaving Sawtooth Basin traps in 1998 and 1999. We used the average of 1998 and 1999 to represent survival in 2000. These estimates were then applied to the estimated total number of smolts leaving the Sawtooth Basin (also made by IDFG and submitted to the Program technical review team). Since 1998, the estimated number of smolts arriving at Lower Granite Dam has ranged from approximately 5,300 to 110,000 (Table 3). This wide range reflects the number of smolts departing Stanley Basin and the wide range in estimates of survival to

Lower Granite Dam for smolts caught in traps in the Stanley Basin. From 1994 to 2008, these estimates ranged from 0.120 (s.e.= 0.013) in 2007 to 0.799 (s.e.= 0.277) in 2005.

We also estimated survival from Lower Granite Dam to McNary Dam for Snake River juveniles migrating from 1996 to 2008. Because of limited sample sizes survival estimates were not possible before 1996, or in 1997 and 2004. Estimated survival ranged from 0.21 (s.e.= 0.063) to 0.76 (s.e.= 0.103) (Table 4). Using PIT-tagged fish released upstream from Lower Granite Dam, there are several options for estimation of survival from the tailrace of Lower Granite Dam (LGR) to the tailrace of McNary Dam (MCN). Particularly for 2006, the choice of estimation method influenced the resulting survival estimate. A discussion of these options appears in the Appendix. For the analyses that follow, we used the full data set of all PIT-tagged sockeye released upstream from LGR, estimating survival from the upstream release point to MCN, then removing the estimate of survival from release to LGR to obtain the LGR-to-MCN estimate. The Appendix explains this choice.

Table 3. Production estimates for ESA-listed endangered Redfish Lake sockeye salmon from Stanley Basin Lakes (combined Redfish, Alturas, Pettit lakes) adjusted to outmigration year for juveniles (all estimates made by IDFG, except as footnoted).

Migration year	Release of pre-smolts	Number of pre-smolts outmigrating	Number of smolts released	Release of pre-spawning adults	Number of eyed eggs planted	Estimated sockeye juveniles passing LGR
1998	141,871	61,877	81,615	0	0	96,669[a]
1999	40,271	38,750	9,718	21	20,311	24,664[a]
2000	72,114	12,971	148	271	65,200	5,298[a]
2001	106,166	16,595	13,915	79	0	7,356
2002	140,410	25,716	38,672	190	30,924	16,958
2003	76,788	26,116	0	315	199,666	9,603
2004	130,716	22,244	96	241	49,134	9,749
2005	72,108	61,474	78,330	173	51,239	68,855
2006	107,292	33,401	86,052	464	184,601	109,779
2007	82,105	25,848	101,676	494	51,008	88,398

[a] Estimated by multiplying survival estimates for Sawtooth trap PIT-tagged sockeye to Lower Granite Dam in 1998 and 1999 (derived using DART) [for 2000, the average of survival estimates from 1998 and 1999] times the IDFG estimate of "Total estimated outmigration".

Table 4. Survival estimates (with standard errors in parentheses) and environmental exposure indices for juvenile sockeye salmon migrating from Lower Granite Dam to McNary Dam.

	Survival		**Exposure Indices**		
	S	**(s.e.)**	**Flow (kcfs)**	**Spill (%)**	**Temp(^{o}C)**
1996	0.283	(0.184)	158.8	42.5	11.8
1997	--	--	164.6	39.5	11.4
1998	0.689	(0.157)	130.4	27.4	12.5
1999	0.655	(0.083)	161.2	30.5	11.8
2000	0.679	(0.110)	87.4	28.2	13.8
2001	0.205	(0.063)	61.0	0.0	14.3
2002	0.524	(0.062)	111.7	20.2	11.7
2003	0.669	(0.054)	173.3	37.7	12.3
2004	--	--	101.3	5.7	12.4
2005	0.388	(0.078)	97.4	8.7	12.7
2006	0.630	(0.083)	168.6	39.5	12.4
2007	0.679	(0.066)	88.1	25.3	12.8
2008	0.763	(0.103)	144.2	40.0	10.6

We evaluated the relationship between juvenile survival and migration conditions within the hydropower system between Lower Granite and McNary Dams by regressing annual estimated survival of the Snake River sockeye salmon population against indices of exposure to river flow, percentage spill at downstream dams, and water temperature. For each variable, we calculated a average daily value for all dates between the 25th and 75th passage percentiles of PIT-tagged fish detected at each of three dams: Lower Granite, Little Goose, and Lower Monumental. The Snake River exposure index was then the average of the three dam-specific indices. No significant correlations ($P > 0.05$) were found between survival and any of the conditions evaluated (Figure 8).

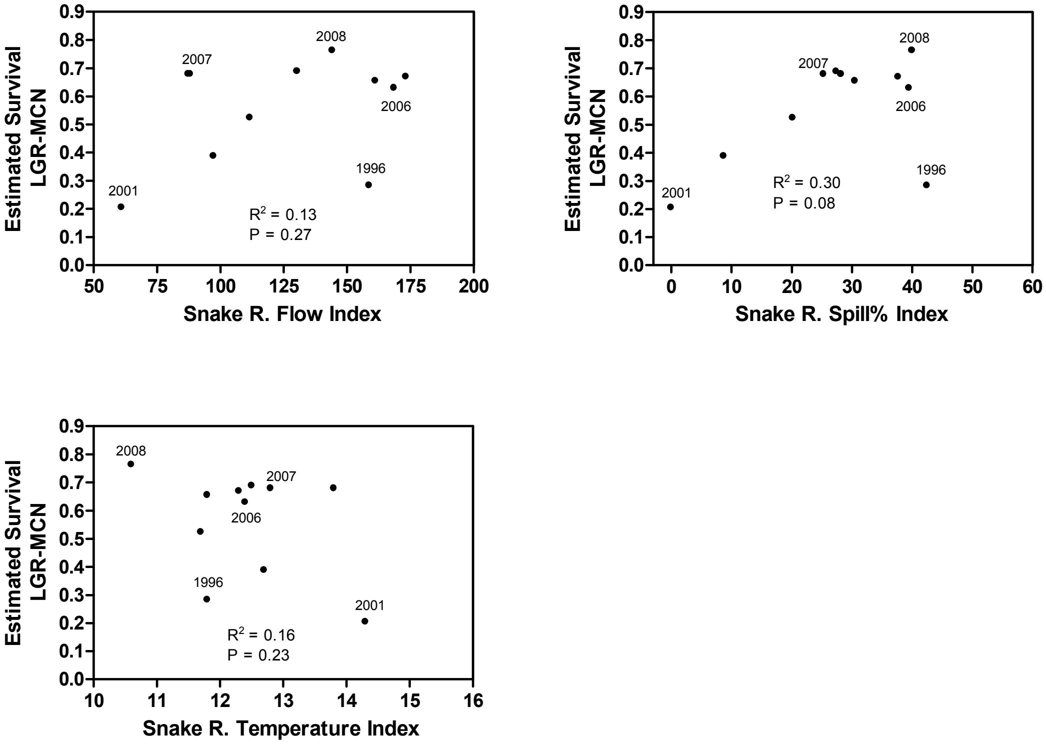

Figure 8. Survival of juvenile Snake River sockeye salmon (estimated from Lower Granite Dam to McNary Dam) versus exposure indices for flow (kcfs, top left), spill% (top right), and temperature (^{o}C, bottom left), outmigration years 1996-2008. Data points for key years are noted (high flow-1996; low flow-2001; years the 2008 return outmigrated-2006, 2007).

Smolt to adult returns

For analyses of Snake River SARs, we could not use the same methodology that we used for Columbia River sockeye, as age-class determinations were not available from the relatively few adults that returned each year to Lower Granite Dam. Therefore, we compared all adult returns to Lower Granite Dam with juveniles that migrated from the dam 2 years earlier for each return year. We assumed ocean-age 2 was the dominant age class, as it averaged 84% (range 71-97%) of adults sampled at Bonneville between 1987 and 2005. This allowed us to develop a SAR index for migration years 1998 to 2006. This "Index SAR" for the 1998-2006 juvenile migrations ranged from 0.08 to 1.04% (Table 5).

Table 5. Estimated outmigration of sockeye salmon smolts from the Sawtooth Basin in Idaho and adult returns passing Lower Granite Dam.

Out-migration Year	Total estimated sockeye juveniles	Adult return year	Number of adults passing LGR	Index SAR (%)
1998	96,669	2000	299	0.31
1999	24,664	2001	36	0.15
2000	5,298	2002	55	1.04
2001	7,356	2003	14	0.19
2002	16,958	2004	113	0.67
2003	9,603	2005	18[a]	0.19
2004	9,749	2006	15[a]	0.15
2005	68,855	2007	46[a]	0.07
2006	109,779	2008	805[a]	0.73
2007	88,398	2009		

[a] adjusted for fallback rate of 11% at Lower Granite Dam estimated from PIT-tag data from adults in 2008. Of 16 PIT-tagged adults passing the dam, 2 passed through the ladders twice, thus 16/18 = 0.89.

We then evaluated the relationship between the Index SARs for Snake River sockeye salmon and survival estimates for juveniles that migrated from Lower Granite to McNary Dam and found none (Figure 9). In part, the lack of a relationship likely resulted from very small sample sizes of juveniles (the starting juvenile population and population arriving at McNary Dam), as well as small numbers of adults. In addition, the majority of juveniles were transported and did not experience conditions within the Snake River.

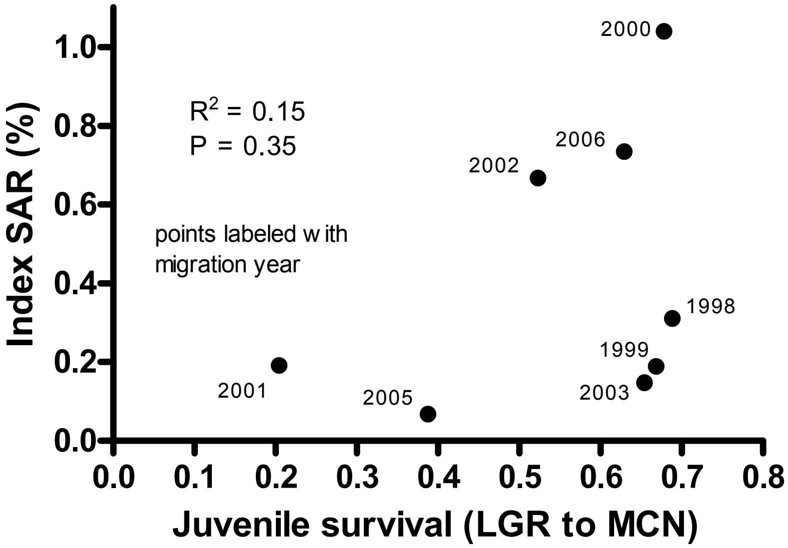

Figure 9. Comparison of annual Snake River sockeye salmon Index SAR estimates with annual survival estimates of smolts from Lower Granite Dam to McNary Dam, juvenile outmigration years 1998-2006.

We also examined a number of factors possibly related to high returns to the Snake River in 2008. We correlated annual adult returns from 2000 to 2008 to smolt abundance in the proceeding two years and found a relatively strong correlation ($R^2 = 0.66$, $P < 0.01$). Thus, the increased smolt production in 2006 was a likely contributor to the high return to the Snake River in 2008.

The Index SAR for Snake River sockeye at Lower Granite Dam (Table 6) is a combined measure for transported and non-transported juvenile fish. During migration years 1998 to 2006, the estimated percentages of juvenile sockeye arriving at Lower Granite Dam that were subsequently transported from a dam on the Snake River were 69, 76, 51, 94, 65, 73, 96, 88, and 64%, respectively. To analyze the effects of transportation on sockeye, we first determined whether data from PIT-tagged sockeye salmon could provide any reliable information regarding the influence of transportation on adult returns to the Snake River. For the 2002 through 2007 migration years, fewer than 45,000 PIT-tagged sockeye salmon were released into the Snake River Basin. Unfortunately, there was no single year where we could directly compare return rates of PIT-tagged fish with different migration histories - transported, bypassed, or non-detected - because adult sockeye salmon returns of PIT-tagged fish were extremely low, and ranged from 0 to 3 fish per migration-history group in these years.

Lacking data for direct comparison, we simply correlated the percentage transported with estimated Index SARs (Table 5) and found a significant negative correlation ($R^2 = 0.71$, $P < 0.01$). However, the percentage of Snake River sockeye salmon transported was also negatively correlated with SARs of Columbia River sockeye salmon (Table 2) ($R^2 = 0.73$, $P < 0.01$). Moreover, the three migration years with lowest percentage of Snake River smolts transported and the three years with greatest Index SAR were the same (2000, 2002, and 2006), and also coincided with high SARs for the combined Columbia River population from McNary Dam. In sum, the SAR of sockeye salmon from the Snake River, which included large proportions of transported fish, seemed to follow a very similar pattern to the SAR of another group of sockeye salmon that were not transported at all (Table 2).

The next analysis of transportation effects on Snake River sockeye salmon used Columbia River SAR as an index of factors the two stocks experienced in common. That is, we assumed that the effects of common factors were reflected in the Columbia River SARs. To adjust for common factors, we first regressed Snake River Index SAR on Columbia River SAR. The linear trend of this relationship was assumed to represent the effect of common factors. Thus, the residuals from this regression represent an index of the variation in Snake River SAR that was not explained by common factors, but was potentially explained by factors unique to the experience of juveniles in the Snake River. This index of SAR variation had virtually zero correlation with the percentage of fish transported ($R^2 = 0.01$, $P = 0.77$) (Figure 10).

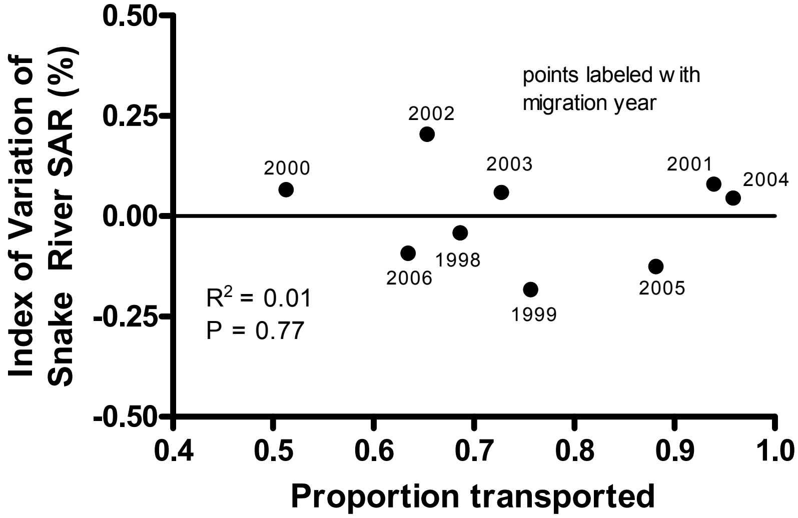

Figure 10. Relationship between the proportion of Snake River sockeye salmon juveniles transported and an index of Snake River-specific variation of subsequent Index SARs (residuals of regression of Snake River Index SARs on Columbia River SARs), juvenile outmigration years 1998-2006.

Relating SARs to ocean conditions and harvest

See discussion of Columbia River sockeye, above.

Conditions adults experienced migrating upstream

Conditions experienced by Snake River adults were similar to those experienced by Columbia River adults up to the mouth of the Snake River, and these conditions were discussed above in the previous section on Columbia River fish. Since 1984, the annual number of adults counted at Ice Harbor Dam has not exceeded 100 fish with the exception of 2000 (216 adults) and 2008 (539 adults). These counts were not consistently the same, higher, or lower than counts at Lower Granite Dam. Therefore, we did not attempt to relate adult passage success to environmental conditions in the lower Snake River. Since 2000, the proportion of fish that have successfully migrated from Lower Granite Dam to the Sawtooth Basin has varied from 9 to 86% (Table 6). Keefer et al. (2008) observed that of 31 adult Snake River sockeye salmon radio tagged at Lower Granite Dam in 2000, all had similar migration rates initially. However, individuals tagged later in the season eventually slowed their migration and were less successful in reaching spawning areas when water temperatures exceeded 21°C. In 2008, conditions in the Snake River were generally cooler than in recent years, and the majority of fish passed Lower Granite Dam when water temperature was ≤ 18°C. Water temperature at the Anatone gauge on the Snake River near Asotin, WA did not exceed 21°C until 26 July 2008. The majority of fish had likely passed this location by this date, assuming migration rates were similar to the average 36.8-61.3 $km \cdot d^{-1}$ reported by Naughton et al. (2005). Thus, the high variability in successful adult migration since 2000 has likely been related to environmental conditions, with the high proportion observed in 2008 resulting from favorable conditions that year. However, these conditions did not have any effect on the number of adults counted at Columbia or Snake River dams in 2008.

Table 6. Proportion of adult sockeye salmon counted at Lower Granite Dam that successfully migrated to the Sawtooth Basin, 2000-2008.

Year	Number of adults passing LGR (data from DART)	Number of adults returning to Sawtooth Basin (data from IDFG)	Proportion
2000	299	257	0.86
2001	36	26	0.72
2002	55	22	0.40
2003	14	3	0.21
2004	113	27	0.24
2005	18[a]	6	0.32
2006	15[a]	3	0.19
2007	46[a]	4	0.09
2008	805[a]	636	0.79

[a] adjusted for fallback rate of 11% at Lower Granite Dam based on PIT-tag data from adults in 2008. [Of 16 PIT-tagged adults passing the dam, 2 passed through the ladders twice, thus 16/18 = 0.889]

Comparisons between Columbia and Snake stocks

Of the analyses conducted, perhaps the most important is the highly significant correlation between Columbia River sockeye salmon SARs and the Snake River sockeye Index SARs ($R^2 = 0.87$, $P < 0.001$) (Figure 11). This provided strong evidence of common patterns in adult variability, and that factors influencing the variability acted similarly on both groups of fish. The common factors were evidently not experienced in the juvenile migration phase of the life cycle, as there was essentially no correlation in estimated juvenile passage survival measured within the hydropower system between the two groups of fish ($R^2 = 0.068$, $P = 0.47$). Moreover, there were differences in correlations of juvenile survival and percentage spill between the two groups. In the Columbia River, estimated juvenile survival between Rock Island and McNary Dams was significantly negatively correlated with percentage spill (Figure 3). However, estimated survival of juvenile Snake River sockeye salmon from Lower Granite to McNary Dams was positively correlated with percentage spill, but the correlation was not significant ($P = 0.08$; Figure 8).

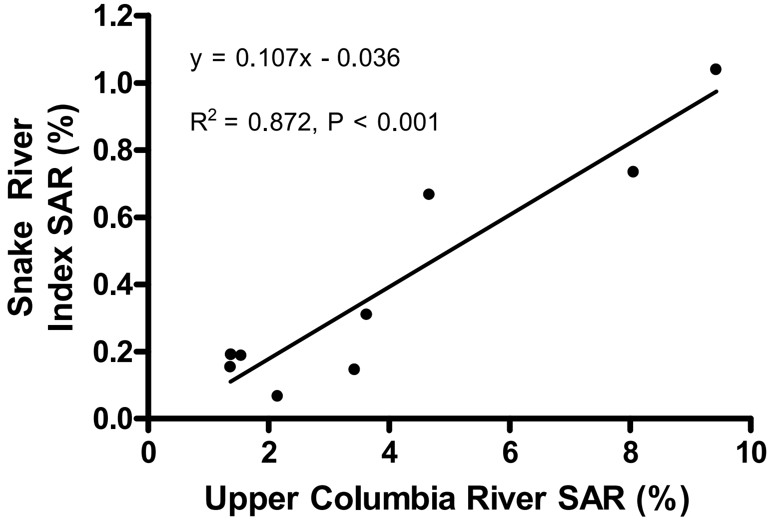

Figure 11. Comparison of estimated SAR for combined Columbia River sockeye salmon population (smolts at McNary Dam and adults at Bonneville Dam) with Index SAR for Snake River sockeye salmon (smolts and adults at Lower Granite Dam), juvenile outmigration years 1998-2006.

Discussion

Adult returns of the composite population of sockeye salmon in the Columbia River Basin have shown wide fluctuations since 1940. Sockeye SARs also display a high level of inter-annual variability (Table 2), but fall within the range of SARs for other sockeye populations from southern British Columbia, Canada, and Lake Washington in

Washington State (Koenings et al. 1993). However, in certain years the SARs of Columbia River Basin sockeye (e.g., 9.4% for migration year 2000; Table 2) were substantially higher than those of Chinook salmon and steelhead (3.3 and 5% for wild Snake River spring Chinook salmon and steelhead respectively for migration year 2000; Williams et al. 2005). This suggests that favorable environmental conditions can result in a substantial year-to-year increase in sockeye SARs, and the response can differ from other species. It appears this was the case for juvenile sockeye salmon migrating from the Columbia River Basin in 2006, when the conditions they experienced that year were favorable and resulted in an estimated SAR of 8.10 % (Table 2).

The significant correlation between sockeye SARs in both rivers is evidence that returns in 2008 were most likely influenced by factors downstream of Bonneville Dam. This result was similar to Peterman et al. (1998), who found that covariation in the survival characteristics of sockeye salmon was highest amongst stocks that resided in close proximity to each other. We found no significant evidence that the large returns in 2008 arose from substantial changes in conditions experienced while migrating inriver as juveniles or adults or from a change in harvest rates in the ocean or river.

Development of ocean ecosystem productivity indicators to date has focused on the influence of ocean conditions on Chinook and coho salmon returns. The rank order of indicators developed for other species had a weak correlation ($R^2 = 0.13$) with the rank order of adult sockeye returns from 1996 to 2008, likely because the indicators did not incorporate food resources important to juvenile sockeye salmon upon first entering the ocean. However, on a broader scale, changes in ocean conditions have been shown to influence Pacific salmon production trends (Mantua et al. 1997; Beamish et al. 1999; Mueter et al. 2005).

Peterman et al. (1998) also concluded that the early ocean environment affected the survival of juvenile sockeye salmon and drove observed variation in adult return rates. Similarly, we observed that for juvenile migration years 1998 to 2006, 4 of 4 years with either intermediate or good ocean conditions (as predicted by our suite of indicators) were associated with higher sockeye SARs (greater than 3%) or more than 100,000 returning adult sockeye salmon. In contrast, 4 of 5 years with poor ocean conditions were associated with SARs lower than 3% or adult returns less than 100,000. We also found evidence that ocean productivity as indexed by the PDO influenced adult sockeye returns from 1985 to 2006.

Snake River Index SARs were much lower than Columbia River SARs, and a number of factors might have influenced the disparity in return rates. First, the distances incorporated into the techniques used to estimate the SARs were different between the two stocks. Snake River Index SARs were calculated from Lower Granite to Lower Granite Dam, whereas Columbia River SARs were calculated between McNary and Bonneville Dams. Second, adults returning to the Snake River came largely from the Captive Broodstock Program while those from the Columbia River were mostly wild. Wild salmonids typically have higher survival from the smolt to the adult life stage (e.g., Williams et al. 2005). Finally, fish from the two areas come from three different ESUs. Differences in overall SARs between the ESUs were likely affected by differences in environmental conditions experienced by the ESUs, as well as fundamental genetic differences, which control growth, size, and migration timing.

Surprisingly, we found a significant negative relationship between survival of juvenile sockeye salmon from the Upper Columbia River and an index of spill within the hydropower system between Rock Island and McNary Dams. This finding is in opposition to a large body of information indicating that increased spill at dams, within limits, improves the survival of juvenile steelhead and Chinook salmon migrating during spring (e.g. Muir et al. 2001; Ferguson et al. 2005). It merits a more detailed review and analysis of specific project operations and passage conditions.

Regarding the transportation of juvenile sockeye from Snake River dams, the low abundance of juveniles to date has limited the ability to conduct studies that directly measure the efficacy of transportation. After adjusting for common factors in the patterns of the Snake River Index SARs and Columbia River SARs, we found no significant correlation between Snake River sockeye salmon Index SARs and the percentages of fish transported. Given the limited data, it is currently not clear whether transportation is beneficial, detrimental, or neutral for sockeye salmon.

The analyses conducted here were primarily correlative and limited by the type and amount of data currently available. Additional research will be required to develop more robust, definitive information on the factors affecting sockeye salmon in both river and ocean environments. This would include studies that directly measure the effects of transportation on sockeye salmon; ascertain whether the high variability in smolt survival from traps in the Snake River to Lower Granite Dam is the result of natural variability or other factors; provide measures of survival past dams and downstream of Bonneville Dam; and lead to development of ocean productivity indices to predict adult sockeye return rates.

In summary, the results discussed here provide a consistent pattern to explain the large return of adult sockeye to the Columbia River in 2008. Based on these results, we conclude that the factors responsible for the high return largely acted on fish downstream of Bonneville Dam and during the marine component of their life cycle, and not in the river upstream of Bonneville Dam.

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Appendix
Notes on Estimation of Survival Between Lower Granite and McNary Dams

For studies using PIT-tagged fish released upstream from Lower Granite Dam, there are several options for estimation of survival from the tailrace of Lower Granite Dam (LGR) to the tailrace of McNary Dam (MCN). All options use versions of the Cormack-Jolly-Seber (CJS) Model of mark-recapture data, but they differ in the particular set of recapture data used. In this paper's analyses involving juvenile survival between LGR and MCN dams, we used the full data set of all PIT-tagged sockeye released upstream from LGR, estimating survival from the upstream release point to MCN, then removing the estimate of survival from release to LGR to obtain the LGR-to-MCN estimate. In this appendix, we discuss the reasons for our choice.

One method that is very familiar from our work with spring migrants in the survival study program is to select only fish that were detected at LGR and known to have been returned to the tailrace there. Here we will refer to these fish as "11s," which refers to their detection history; the first "1" indicates release upstream from LGR and the second indicates detection and return to river at LGR. Lower Granite Dam is then used as the "release site" in a single-release/multiple-recapture (SR/MR) analysis, using downstream detector dams as recapture sites. The result of this analysis is survival probability estimates and corresponding standard errors for consecutive river reaches: LGR to Little Goose Dam (LGO), LGO to Lower Monumental Dam (LMN), and LMN to McNary Dam (MCN). The product of these estimates is the survival probability estimate from Lower Granite Dam tailrace to McNary Dam tailrace. The standard error of this product is calculated from the standard errors and covariances between estimates for individual reaches. When large numbers of PIT-tagged spring migrants are available, we group fish detected at Lower Granite Dam into weekly or even daily groups, according to the date of LGR detection. Each group is then analyzed independently using the SR/MR model. If fewer PIT-tagged fish are detected and returned to the tailrace at LGR, the date groupings are sometimes wider, such as biweekly, monthly, or even a single group for the entire season.

A second method uses the same LGR-detected “11” fish as in the method above, but augments the sample with fish not detected at LGR but detected at Little Goose Dam (LGO) and returned to the tailrace there. Here we will refer to these fish as “101s,” referring to their detection history as described above. This strategy is analogous to a multiple-release/multiple-recapture (MR/MR) design, similar to an avian or mammalian recapture study where previously untagged animals are trapped, tagged, and added to the sample on occasions throughout a study. If a date restriction is used, for example weekly groups of fish in LGR tailrace, this MR/MR approach requires an assumption regarding travel time from LGR to LGO: if a fish is not detected at LGR and then detected at LGO, we obviously cannot know for certain which weekly LGR group it belongs to. Only by assuming a travel time can such a fish be assigned to an LGR weekly group. However, if only a single group is used for the entire season, then no travel time assumption is required – all “101s” are combined with all “11s” in the MR/MR analysis. In its summer 2008 memo on sockeye survival, the FPC reported using the MR/MR approach, and employed a LGR passage date restriction and a travel time assumption for “101s” to build their sample.

The MR/MR approach can be extended to further “first release sites” at Lower Monumental Dam (LMN) (“1001” fish released upstream from LGR, first detected at LMN and then returned to the tailrace) and McNary Dam (MCN) (“10001”s). Further travel time assumptions are required if a date restriction is applied at LGR.

All told, this results in four SR/MR or MR/MR options that use a “start-at-LGR” strategy:

(1) Use “11” fish only.

(2) Use “11” and “101” fish.

(3) Use “11”, “101”, and “1001” fish.

(4) Use “11”, “101”, “1001” and “10001” fish.

From a group of tagged fish released upstream at Lower Granite Dam, there are two detection histories that give no information regarding survival between LGR and MCN: fish detected and transported from LGR, and fish migrating inriver but never detected after release. All other detection histories give information. All “start-at-LGR” options use subsets of the entire set of fish that provide information on LGR-to-MCN survival. Option (1) obviously ignores all fish that are not detected and returned to the river at LGR. Option (2) adds “101s”, but ignores “1001s” and “10001s”. None of the options uses fish that are transported after first detection at LGO, LMN, and MCN.

Appendix Table 1 shows the numbers of PIT-tagged fish in various detection history categories, and the percentages of possible information-giving tagged fish used in various options using the “start-at-LGR” strategy. On average, only a little over one-third of tagged sockeye released upstream from LGR were detected and returned to the river at LGR (i.e., annual average of percentage of “11s” from 1994-2008 was 36.3%). Moreover, in only one year were there more than 1,000 “11s.” Adding “101s” brings the annual average up to about 60% of the fish that provide LGR-MCN survival information.

There is a method—call it option (5)—that always uses 100% of the fish that carry the relevant information. Option (5) is a SR/MR analysis using the group released upstream from LGR as the single release and estimating survival in four reaches: Release-to-LGR, LGR-to-LGO, LGO-to-LMN, and LMN-to-MCN. As before, the product of the estimates (except for release-to-LGR) is the survival probability estimate from Lower Granite Dam tailrace to McNary Dam tailrace, and the standard error of the product is calculated from the standard errors and covariances between the estimates for the individual reaches. This option is attractive when the number of tagged fish is relatively small, so that the proportion of fish that provide data for the analysis is maximized. The downside is that it is not possible use these fish and also group the samples by date of passage at LGR. However, if an annual survival estimate is of most interest, then the need to maximize sample size may outweigh the inability to restrict by date.

Given the assumptions of the Cormack-Jolly-Seber model, which underlies both the SR/MR and MR/MR analyses, all of the methods outlined above give estimates of the same parameter. That is, expected survival from Lower Granite to McNary Dam is assumed to be the same for all fish that traverse that section of the river. Thus, the expected values of estimates arising from all five methods are the same. Of course, there will be differences in precision of the estimates (i.e., standard errors) related to sample size, and random variation will result in variations among the estimates given by the different methods. However, there is no *a priori* reason to suspect that one method will give estimates that are consistently higher or lower than any other method.

To investigate how much the estimates might vary, we applied each of the five methods to the annual data from PIT-tagged sockeye released upstream from Lower Granite Dam. We derived estimates of survival probability between Lower Granite and McNary Dam using each method (Appendix Table 2). The results showed the expected trends in precision—using more data usually results in a smaller standard error. With one or two notably exceptional years, estimates from the various methods were relatively stable—for any particular year, the range of estimates tended to be similar to the standard errors of individual estimates. The greatest variability among methods occurred with 2006 and 2008 data. In 2008, all methods except that using only "11" fish gave similar estimates, but "11" fish amounted to only 18.6% of available data (Appendix Table 1).

In 2006, using only "11" fish (22.3% of available) resulted in an estimate greater than 1.0, and methods (2) through (5) also resulted in a wide range of estimates. The observed pattern in the 2006 estimates occurred because fish that were detected for the first time at McNary Dam were highly significantly more likely detected again downstream than were fish detected at McNary Dam which had already been detected at least once at an upstream dam. This violated an assumption of the CJS Model and made the 2006 estimate problematic. Methods 1, 2, and 3 omit fish detected for the first time at McNary Dam, and the assumption violation does not occur. However, in all three of those methods, there were estimates for individual reaches that were greater than 1.0. Using method (1) LGO-LMN survival was estimated at 1.674 and LGR-MCN survival was 1.296, as seen in Appendix Table 1. Using method (2) estimated survival was 1.019 for LGO-LMN and 1.036 for LMN-MCN, and using method (3) estimated survival was 1.213 for LMN-MCN. Only methods (4) and (5) give admissible estimates for all individual reaches, but these methods incur the assumption violation.

For PIT-tagged steelhead and yearling Chinook salmon, we almost always use option (1) for survival estimates in reaches that begin at Lower Granite Dam. This option gives maximum flexibility for LGR date restrictions without travel time assumptions, and the abundant PIT-tag data on these spring migrants sufficiently supports the approach. The option is clearly less suitable when data are as sparse as for PIT-tagged sockeye.

Without *a priori* reasons to include data from “101” fish but to exclude data from “1001” and “10001” fish, we see no support for choosing option (2) over option (4). Given the objective of augmenting data that is otherwise too sparse, we do not see justification for “going halfway” – if the MR/MR approach with data starting at LGR is to be used at all, it should use all possible data, including fish detected for the first time at LMN and MCN. However, we further see no advantage of option (4) over option (5), as (5) uses the additional data with no additional cost. Thus, in the case of data too sparse for date restrictions at LGR, our strong general recommendation for estimating LGR-to-MCN survival is to use option (5).

In the case of the sockeye data analyzed here, the Snake River data for option (5) (and for option (4)) lead to a violation of an assumption of the CJS model for the 2006 data. In light of this, and on the basis of the reasoning set forth above, we believe that the decision is not whether to choose between the option (5) estimate of 0.630 (s.e. 0.083) and the option (2) estimate of 0.850 (0.189), but rather whether to use the option (5) estimate or to omit the 2006 data point from the analysis entirely. Omission of the 2006 data point makes almost no difference in the nature of the statistical relationships depicted in Figures 7 and 8 (in particular, R^2 values are changed minimally). Therefore, we opted to leave the 2006 survival estimate of 0.630 in the analyses.

Appendix Table 1. Annual numbers of PIT-tagged sockeye released upstream from Lower Granite Dam, numbers with various detection histories, numbers giving information on Lower Granite-to-McNary survival, and percentage of those providing information used in various analysis options using “start-at-LGR” strategy.

Counts									**Percentage of all fish giving information on LGR-MCN survival**		
	Released upstream	Never detected	Trans. LGR	Giving LGR-MCN surv. info	Det. Hist ”11”	Det. Hist. “101”	Det. Hist. “1001”	Det. Hist. “10001”	Det. Hist. “11”	Det. Hist. “11” + “101”	Det. Hist. “11” + “101” + “1001” + “10001”
2008	6651	5195	8	1448	269	578	369	60	18.6	58.5	88.1
2007	7078	5811	27	1240	471	259	125	152	38.0	58.9	81.2
2006	6431	4690	9	1732	386	720	392	73	22.3	63.9	90.7
2005	8051	5999	501	1551	311	108	30	30	20.1	27.0	30.9
2004	6651	5228	915	508	55	14	12	15	10.8	13.6	18.9
2003	11305	9260	132	1913	707	739	194	102	37.0	75.6	91.1
2002	4603	3629	18	956	255	303	238	81	26.7	58.4	91.7
2001	3296	2556	23	717	603	92	13	3	84.1	96.9	99.2
2000	6359	5107	34	1218	496	277	182	143	40.7	63.5	90.1
1999	8395	6890	177	1328	334	538	283	56	25.2	65.7	91.2
1998	16522	13474	760	2288	1112	458	399	52	48.6	68.6	88.3
1997	1997	1850	4	143	60	26	49	2	42.0	60.1	95.8
1996	8966	7966	143	857	512	150	133	16	59.7	77.2	94.6
1995	4217	4042	36	139	70	21	30	2	50.4	65.5	88.5
1994	767	611	10	146	30	30	21	2	20.5	41.1	56.8
average 1994-2008									36.3	59.6	79.8
average 1998-2008									33.8	59.1	78.3
average 1998-2008, exc. 2004									36.1	63.7	84.3

Appendix Table 2. Estimated annual probability of survival between Lower Granite Dam and McNary Dam using five different subsets of available data.

	Det. Hist. “11”	Det. Hist. “11” + “101”	Det. Hist. “11” + “101” + “1001”	Det. Hist. “11” + “101” + “1001” + “10001”	All fish released upstream	Range of survival estimates (max-min)	Std. Dev. of survival estimates
2008	0.512 (0.138)	0.723 (0.143)	0.761 (0.129)	0.724 (0.101)	0.763 (0.103)	0.251	0.105
2007	0.657 (0.118)	0.613 (0.084)	0.595 (0.074)	0.645 (0.067)	0.679 (0.066)	0.084	0.034
2006	1.296 (0.686)	0.850 (0.189)	0.944 (0.187)	0.668 (0.091)	0.630 (0.083)	0.666	0.267
2005	0.359 (0.104)	0.387 (0.105)	0.423 (0.122)	0.364 (0.077)	0.388 (0.078)	0.064	0.025
2004	NA	NA	0.606 (0.228)	0.757 (0.288)	0.741 (0.254)	0.151	0.083
2003	0.715 (0.114)	0.700 (0.075)	0.701 (0.070)	0.653 (0.055)	0.669 (0.054)	0.062	0.026
2002	0.393 (0.075)	0.428 (0.059)	0.468 (0.063)	0.512 (0.065)	0.524 (0.062)	0.131	0.055
2001	0.248 (0.104)	0.205 (0.068)	0.212 (0.071)	0.200 (0.062)	0.205 (0.063)	0.048	0.019
2000	0.560 (0.142)	0.594 (0.126)	0.584 (0.113)	0.645 (0.114)	0.679 (0.110)	0.119	0.048
1999	NA	0.518 (0.090)	0.606 (0.092)	0.629 (0.083)	0.655 (0.083)	0.137	0.059
1998	NA	0.847 (0.345)	0.721 (0.227)	0.674 (0.157)	0.689 (0.157)	0.173	0.079
Average Std. Err.	0.185	0.128	0.125	0.105	0.101		