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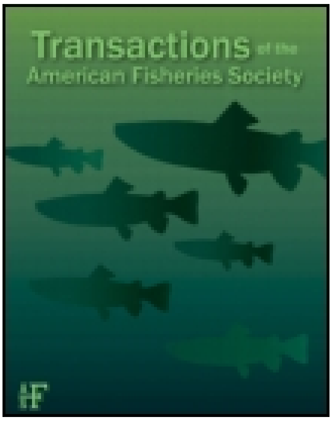

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Post-Hydropower System Delayed Mortality of Transported Snake River Stream-Type Chinook Salmon: Unraveling the Mystery

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Abstract.—Past research indicates that on an annual basis, smolts of stream-type Chinook salmon *Oncorhynchus tshawytscha* collected at Snake River dams and transported by barge to below Bonneville Dam have greater post-hydropower system mortality than smolts that migrate in-river. To date, this difference has most commonly been attributed to stress from collection and transportation, leading to decreased disease resistance or predator avoidance ability. Using both hatchery and wild passive integrated transponder (PIT) tagged Chinook salmon, we explored two mechanisms that either separately or jointly contributed to an alternative explanation: altered timing of ocean entry and lost growth opportunity leading to size-selective predation. Based on weekly estimates of in-river survival and adult return rates of smolts that were transported or that migrated in-river between Lower Granite and Bonneville dams, we found greater post-hydropower system mortality for smolts transported early in the season but greater mortality for in-river migrating smolts later in the season. Migrants took 2–4 weeks to travel between the two dams, while transported fish took less than 2 d. Thus, fish leaving Lower Granite Dam under the two transit modes encountered different conditions downstream from Bonneville Dam. Further, wild and hatchery migrants grew 6–8 and 5–6 mm, respectively, while transported fish had no apparent growth in the less than 2-d barge ride. Using length data and regression equations of size selectivity, we found that transported smolts were more vulnerable to predation by northern pikeminnow *Ptychocheilus oregonensis* (freshwater) and Pacific hake *Merluccius productus* (marine) than were migrants; this was particularly true for the smaller wild smolts transported early in the season. We concluded that the most parsimonious explanation for differential post-hydropower system mortality of transported Chinook salmon smolts related not to effects of stress but to differential size and timing of ocean entry.

After completion of the federal hydropower system on the Snake and Columbia rivers in 1975, the number of returning adult, stream-type, spring–summer Chinook salmon *Oncorhynchus tshawytscha* and steelhead *O. mykiss* declined, in large part as a result of reduced survival and delay of juvenile fish (smolts) during their downstream migration (Raymond 1979, 1988). For several decades, smolts have been collected at Snake River dams and trucked or barged downstream to below the last Columbia River dam for release to avoid mortality caused by dams (Ebel et al. 1973; Ebel 1980). During this period, dam mortality of in-river migrants has been reduced through structural and operational improvements at the dams, including improvements to or installation of juvenile bypass systems to keep smolts from entering turbines; predator removal and exclusion programs; flow augmentation; and the use of spill to pass smolts through nonturbine routes and reduce migrational delay. As a result of these efforts, the conditions encountered by in-river migrants at dams improved substantially (Williams and Matthews 1995), as did their survival (Muir et al. 2001; Williams et al. 2001, 2005).

Studies to evaluate the efficacy of smolt transportation (barging and trucking smolts) have generally shown a benefit, especially for steelhead. Yet, adult returns of transported smolts have generally fallen short of expectations, particularly for wild spring–summer Chinook salmon (Ward et al. 1997; Williams et al. 2005). In-river survival of spring–summer Chinook salmon (hereafter referred to as Chinook salmon) from the uppermost dam on the Snake River to below Bonneville Dam averaged about 40–50% in nondrought years (Williams et al. 2005), while survival of smolts transported to below Bonneville Dam is nearly 100% (Budy et al. 2002). Thus, if mortality were equal after the two groups arrived below Bonneville Dam, one would expect roughly twice the adult return rate from transported juveniles as from those that migrated in-river. However, in some years, migrants have had annual adult return rates nearly the same or slightly higher than transported fish. This indicates that

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transported smolts have suffered greater mortality than migrants from the time of their release below Bonneville Dam to their return as adults. The differential survival between transported fish and migrants suggests that events in the life history segment before arrival below Bonneville Dam differentially affect transported fish after their release. Differential post-hydrosystem survival between transported and migrant smolts has been referred to as D, after the term used to represent it in a mathematical model (Budy et al. 2002; Williams et al. 2005). Budy et al. (2002) posited that stress caused by collection and barging, or migration through the hydropower system, resulted in increased vulnerability to predators, impaired immune function, and metabolic disturbance, and that these effects resulted in delayed mortality.

The use of passive integrated transponder (PIT) tag technology in the Snake and Columbia rivers, where each fish has a unique tag code, has provided an unprecedented opportunity to evaluate survival over the entire life cycle of salmon. Passive integrated transponder tag detection systems are now installed in the juvenile bypass systems at most main-stem dams and in the adult fish ladders of half the dams that Snake River anadromous salmonids pass through, allowing evaluation of survival with much more precision than allowed by older technologies. Further, in recent years, substantially increased adult return rates of Snake River Chinook salmon (Scheuerell and Williams 2005) have led to considerably increased numbers of adult PIT-tagged fish. Consequently, managers are no longer limited to annual data, but can now analyze patterns on a weekly basis. The more refined recent data do not support the speculations of Budy et al. (2002).

In this paper, we explore two lines of evidence that we feel provide the most parsimonious explanation of differential post-hydropower system mortality of transported and migrant Chinook salmon: altered timing of ocean entry and lost growth opportunity leading to size-selective predation. We also explore why benefits of transportation appear greater for hatchery Chinook salmon than for wild Chinook salmon.

Methods

Study area.—Juvenile Chinook salmon were collected at Lower Granite Dam (river km 695) on the Snake River and either transported to below Bonneville Dam (river km 234) on the Columbia River or returned to the river to resume their migration (Marsh et al. 1999) (Figure 1). Smolts were also collected and transported from Little Goose Dam (river km 635), Lower Monumental Dam (river km 589), and in some years, McNary Dam (river km 470). We used only the transportation data from Lower Granite Dam in our analysis. Returning PIT-tagged adults were later detected in the ladder as they migrated past Lower Granite Dam (Harmon 2003).

Migration timing.—To evaluate the relationship between arrival timing and the efficacy of transportation for juvenile smolts to below Bonneville Dam, the smolt-to-adult-return rates (SARs) of hatchery (juvenile migration years 1997–2002) and wild (juvenile migration years 1998, 1999, and 2002) Chinook salmon that were PIT tagged at or above Lower Granite Dam and either collected and transported from (SAR_T) or returned to the river to continue their migration (SAR_M) from Lower Granite Dam were calculated. The number of PIT-tagged juveniles arriving at Lower Granite Dam each day in each of these two categories and the subsequent number of returning adults detected at Lower Granite Dam were counted for each week (for weeks with >200 juveniles) and the SAR calculated. For hatchery fish, we focused our analysis exclusively on smolts tagged upstream from and detected at Lower Granite Dam because this allowed us to determine precisely when they passed the dam, and there were sufficient numbers of juveniles and returning adults. However, insufficient numbers of wild Chinook salmon were tagged upstream from Lower Granite Dam, so we relied on fish tagged at Lower Granite Dam.

Estimates of Chinook salmon (hatchery and wild combined) travel time (days) between Lower Granite and Bonneville dams were available for each week from research we conducted (unpublished NMFS data available in annual contract reports to the Bonneville Power Administration). We calculated weekly hydropower system survival estimates (S_M) by multiplying the wild or hatchery Chinook salmon weekly estimate from Lower Granite Dam tailrace to McNary Dam tailrace by the yearly average (wild and hatchery combined) between McNary Dam tailrace and Bonneville Dam tailrace (data in the lower river were not sufficient to make weekly estimates) using data from these studies. Survival estimates from McNary Dam tailrace to Bonneville Dam tailrace were not possible for 1997 and 1998, so we used per-kilometer expansions of survival estimates from upper reaches.

To evaluate the efficacy of transportation, we calculated the ratio of the SARs of weekly transported (SAR_T) and migrant (SAR_M) groups, calculated as

$$T:M = SAR_T/SAR_M.$$

If transportation fully mitigated for losses that otherwise would occur from migration through the hydropower system, we would expect no difference between the rate of adult return between transported and migrant fish that survived to downstream from

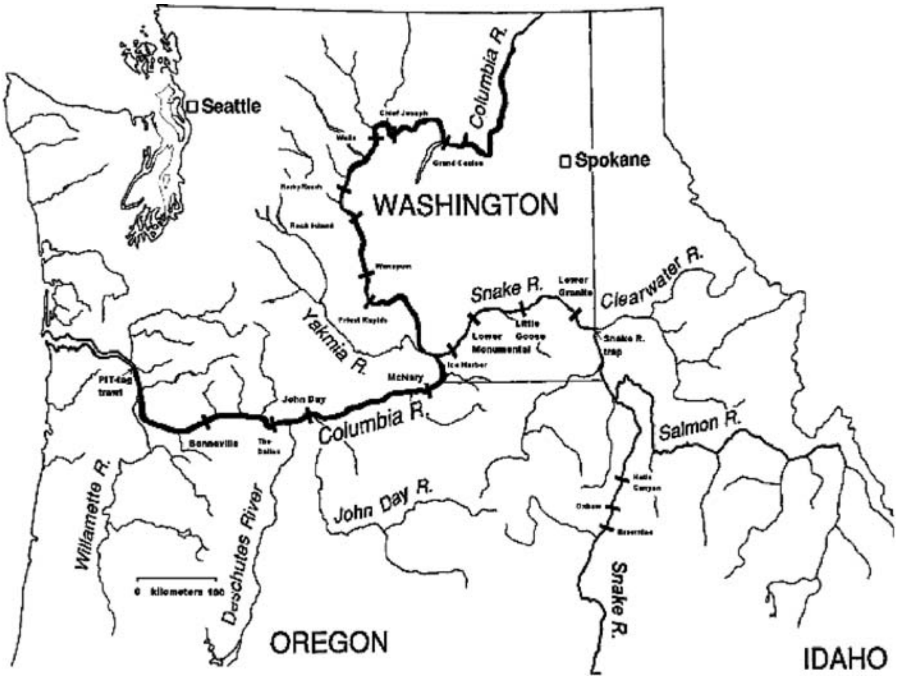

FIGURE 1.—Map of the study area, showing locations of dams (shown as bars across river) on the main-stem Snake and Columbia rivers in the Pacific Northwest.

Bonneville Dam. We estimated the relative return rates by computing a value D:

$$D = (S_M)(T : M)/S_T,$$

where S_T (survival during barge transportation) was set at 0.98 (Budy et al. 2002). If transported and migrant fish survive at equal rates from release below Bonneville Dam to adult return, then D is equal to 1, whereas a value of D less than 1 indicates that transported fish died at a higher rate after release below Bonneville Dam to adult return.

Growth opportunity.—We determined the growth of migrant wild Chinook salmon by comparing the mean difference between fork lengths of fish that were PIT tagged and measured at Lower Granite Dam and the lengths of the same individuals when later recaptured using the sort-by-code system (Marsh et al. 1999) at Bonneville Dam (Congleton et al. 2005). Because we did not tag hatchery Chinook salmon at Lower Granite Dam, we estimated growth of migrant fish by comparing the average length of fish collected in the sort-by-code systems at Lower Granite and Bonneville dams of previously PIT-tagged fish (not necessarily the same individuals at each dam, but the same population). We assumed negligible growth for transported fish in the less than 2-d ride to below Bonneville Dam. We compared growth of wild migrant fish with cohorts transported from Lower Granite Dam during the early, middle, and late portions of the migration. For hatchery fish, we could make only a single seasonal comparison, as we did not directly measure the same individuals at the two dams.

Size selectivity of predator.—We estimated vulnerability of smolts to predation by northern pikeminnow *Ptychocheilus oregonensis*, the most abundant smolt predator in the Columbia River, using a regression equation ($r^2 = 0.96$, $P < 0.001$) developed by Poe et al. (1991) relating maximum smolt fork length (Y) with predator length (X), calculated as

$$Y = 0.716(X) - 84.435.$$

We used the derived mean smolt fork lengths of transported and migrant fish at Bonneville Dam calculated for the early, middle, and late portions of the migration for wild fish, and over the entire migration for both wild and hatchery fish to estimate the minimum-sized northern pikeminnow that could prey on them. We then calculated the percentage of the northern pikeminnow population large enough to prey on Chinook salmon from each group based on length-frequency data for northern pikeminnow captured by electrofishing downstream of Bonneville Dam in 2002 and 2003 (T. Friesen, Oregon Department of Fish and Wildlife, unpublished data).

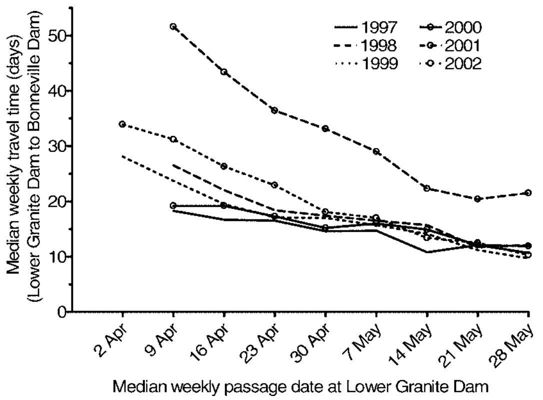

FIGURE 2.—Travel time (d) for stream-type Chinook salmon migrating from Lower Granite Dam to Bonneville Dam during 1997–2002.

This analysis was repeated for Pacific hake *Merluccius productus,* a highly abundant predator in the Columbia River plume, which sometimes preys on salmon smolts (Beacham 1991; Emmett 2006). We used a regression equation ($r^2 = 0.23$, $P < 0.001$) developed by Emmett (2006) relating maximum prey total length (Y) with predator length (X), calculated as

$$Y = 0.350838(X) - 33.3482.$$

Because insufficient numbers of salmonids were recovered from Pacific hake stomachs, the equation was based on lengths of northern anchovy *Engraulis mordax*, Pacific herring *Clupea pallasii*, and whitebait smelt *Allosmerus elongatus*, all of which are similar in size and shape to juvenile salmonids (Emmett 2006). The mean fork lengths for transported and migrant Chinook salmon arriving downstream from Bonneville Dam were converted to total length using the equation of Vigg et al. (1991) and then used in our equation to estimate the minimum-sized Pacific hake that could prey on smolts. We used the length frequency distribution for Pacific hake captured in the Columbia River plume in May and June of 2002 and 2003 (R. Emmett, National Marine Fisheries Service, unpublished data) to calculate the percentage of the Pacific hake population large enough to prey on Chinook salmon from each group.

Results

Migration Timing

The annual migration of Snake River Chinook salmon smolts through the hydropower system has a consistent trend (Figure 2). In most years, fish took more than 4 weeks to travel from Lower Granite Dam to Bonneville Dam at the beginning of the season, but less than 2 weeks near the end. Very low river flow in 2001 resulted in substantially increased migration time. Despite the wide within-year ranges in travel time, estimated juvenile Chinook salmon survival varied little within or between years except in 2001 (Tables 1, 2). As noted earlier, transported Chinook salmon always covered the distance in less than 2 d with consistently high survival.

Yearly average SARs for hatchery Chinook salmon that were transported from Lower Granite Dam were higher than SARs for those left in the river to migrate each year from 1997 through 2002, resulting in annual T:M ratios ranging from 1.27 in 1997 to 25.09 in 2001 (Figure 3; Table 1). Annual estimates of D were also mostly near 1, with the clear exception in the 2001 low-flow year. However, SARs for transported fish and migrants varied greatly within each season, as did T:M ratios and D. Transported fish generally returned at lower rates than migrant fish early in each season (T:M < 1) as a result of much greater mortality downstream from Bonneville Dam (i.e., much lower values of D early in the season).

Yearly average SARs for wild Chinook salmon that were transported from Lower Granite Dam were lower than for those left in the river in 1998, but higher in 1999 and 2002, resulting in T:M values less than 1 in 1998 and greater than 1 in 1999 and 2002. However, similar to hatchery Chinook salmon, SARs for transported fish and migrants varied greatly within each season. Estimated T:M was less than 1 early in April in all years and usually greater than 1 thereafter; D was also generally lower early in the season.

Growth Opportunity

In 2002, migrant wild Chinook salmon grew an average of 8 mm between Lower Granite and Bonneville dams (Table 3). The amount of growth varied over the season, with the greatest growth occurring for early migrants, which had the longest travel times. Hatchery smolts had lower apparent average growth rates (5 mm) than wild smolts. Wild smolts averaged 106 mm in length (28 mm shorter than the average hatchery smolt) at the beginning of their migration through the hydropower system at Lower Granite Dam. Length and growth data were similar in 2003.

Size Selectivity of Predators

The size differential in smolts arriving below Bonneville Dam influenced their estimated vulnerability to predation by northern pikeminnow. Most significantly, wild smolts were vulnerable to a higher percentage of the northern pikeminnow population than were hatchery smolts. Further, a higher percentage of the northern pikeminnow population had the ability to

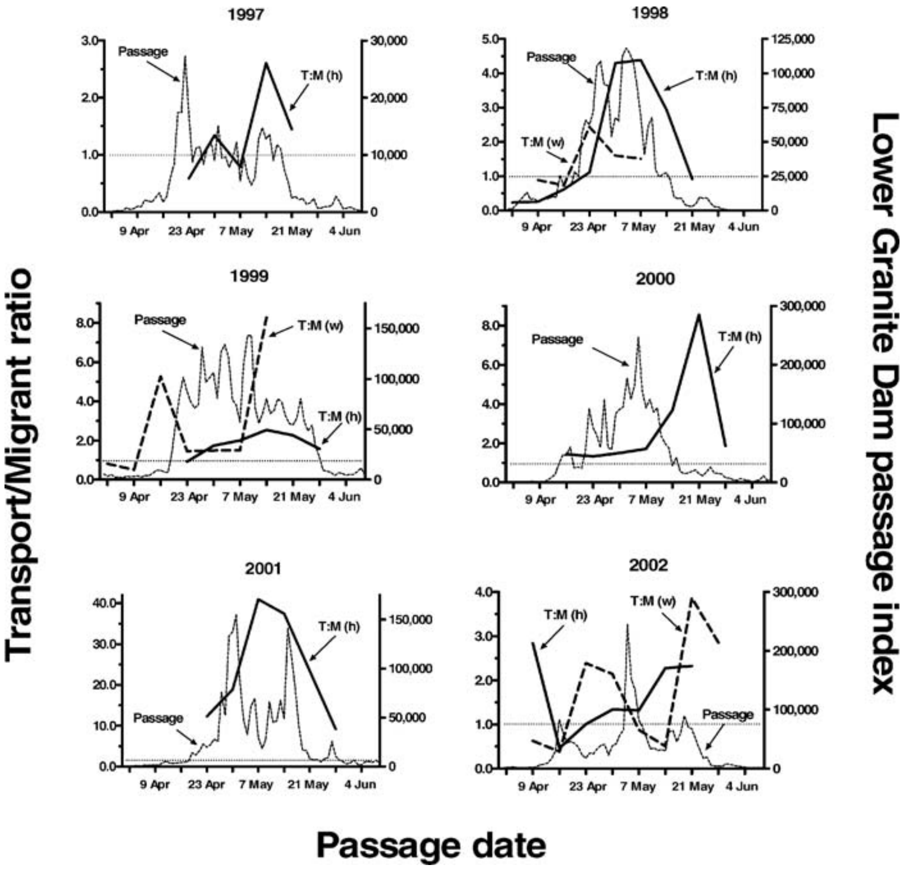

FIGURE 3.—Weekly transport–migrant ratios (*T*:*M*) of smolt-to-adult returns for hatchery (h) and wild (w) spring–summer Chinook salmon transported from or returned to the Snake River at Lower Granite Dam, 1997–2002. The daily passage index of spring–summer Chinook salmon at Lower Granite Dam is also shown. Note differences in scale on *y*-axes.

consume transported fish than migrants because transported fish were smaller (Figure 4). Results were similar for Pacific hake predation in the Columbia River plume, but to an even greater degree. In 2002, more than 50% of the Pacific hake population was large enough to consume wild smolts, while few were large enough to consume hatchery smolts. Further, early in the season about twice as many transported wild Chinook salmon were susceptible to consumption by Pacific hake than those in the migrant group (Figure 5). Fewer smolts from all categories were vulnerable to Pacific hake predation in the plume in 2003 because of the smaller size of Pacific hake present that year.

Discussion

The two lines of evidence presented—altered timing of ocean entry, and lost growth opportunity leading to size-selective predation—provide the most parsimonious explanation for differential post-hydropower system mortality between transported and migrant Snake River Chinook salmon, and demonstrate the difficulty in developing mitigation strategies to improve survival of salmon migrating through dammed rivers. In the Snake and Columbia rivers, collection and transportation of juvenile Chinook salmon eliminates nearly half or more of the direct mortality the juvenile fish would otherwise suffer were they left in the river to migrate through the hydropower system. Yet, because transportation reduces travel time to less than 2 d, their timing of ocean entry is altered, their growth opportunity is limited, and their vulnerability to predators is increased.

Transported smolts now arrive below Bonneville Dam, and hence the Pacific Ocean, from 2 to 4 weeks earlier than migrants (or as much as 7 weeks earlier in a drought year). Because they enter the ocean weeks apart, they encounter considerably different ocean conditions affecting growth, predation, and survival.

TABLE 1.—Hatchery Chinook salmon weekly and yearly estimates of percent migrant survival (S_M) from Lower Granite Dam (Snake River) to Bonneville Dam (Columbia River), percent smolt-to-adult return for fish transported (SAR_T) or returned to the river (SAR_M) at Lower Granite Dam, transport migrant ratio ($T{:}M$), and post-hydropower system differential survival (D) for fish that were PIT tagged upstream of Lower Granite Dam, 1997–2002. A constant value of 0.98 was used for survival during transport (S_T).

	April					May				
Variable	2	9	16	23	30	7	14	21	28	Year
1997										
S_M		48.7	42.1	63.0	40.3	31.4	43.1			42.5
SAR_T			0.10	0.81	1.09	0.86	1.09	0.30	0.76	0.89
SAR_M			0.00	1.36	0.81	1.10	0.42	0.21		0.69
$T{:}M$				0.59	1.34	0.79	2.61	1.45		1.27
D				0.37	0.54	0.25	1.13			0.54
1998										
S_M		46.5	47.7	51.0	50.0	52.1	52.9	56.4	42.4	49.4
SAR_T	0.43	0.59	0.77	0.98	2.22	2.37	2.39	1.74		1.73
SAR_M	1.84	2.27	1.25	0.88	0.52	0.54	0.82	1.88		0.73
$T{:}M$	0.23	0.26	0.62	1.11	4.30	4.39	2.93	0.92		2.36
D		0.12	0.30	0.57	2.15	2.29	1.55	0.52		1.17
1999										
S_M	51.5	54.1	45.4	54.7	56.0	56.5	57.5	56.7	49.5	55.7
SAR_T			0.00	0.76	2.32	3.20	4.01	3.86	4.61	2.75
SAR_M			0.80	0.82	1.33	1.60	1.57	1.70	2.93	1.47
$T{:}M$				0.93	1.74	2.00	2.55	2.27	1.57	1.87
D				0.52	0.99	1.15	1.50	1.31	0.79	1.06
2000										
S_M			58.2	45.6	48.6	46.8	45.5	45.6	52.0	48.8
SAR_T			1.61	1.97	2.71	3.34	3.99	4.27	1.71	3.07
SAR_M			1.12	1.48	1.80	1.95	1.08	0.50	0.91	1.56
$T{:}M$			1.44	1.33	1.51	1.71	3.69	8.55	1.87	1.97
D			0.85	0.62	0.75	0.82	1.71	3.98	0.99	0.98
2001										
S_M		15.4	28.8	29.5	29.6	25.9	22.8	17.5	8.3	27.8
SAR_T	0.00	0.68	0.91	0.66	1.02	1.64	1.17	1.02	1.02	1.09
SAR_M	0.00	0.00	0.00	0.05	0.05	0.04	0.03	0.00	0.11	0.04
$T{:}M$				12.26	18.84	40.94	37.43		9.16	25.09
D				3.69	5.69	10.82	8.71		0.78	7.12
2002										
S_M	44.9	55.0	56.5	58.4	59.1	58.0	59.3	60.0		57.9
SAR_T	0.98	1.08	0.35	0.67	0.85	1.00	1.96	2.08		1.20
SAR_M		0.38	0.75	0.66	0.63	0.76	0.86	0.89	0.41	0.76
$T{:}M$		2.84	0.47	1.01	1.34	1.32	2.28	2.33		1.59
D		1.59	0.27	0.60	0.81	0.78	1.38	1.43		0.94

A spring transition typically occurs at the mouth of the Columbia River in late March through early April, when winds shift to the northwest, initiating seasonal upwelling and a switch in currents toward the south (Bilbao 1999; Logerwell et al. 2003). Environmental conditions in the Columbia River plume also change dramatically during this time, as flow volumes and turbidity increase from the spring runoff (Hickey 1989). These changes affect the seasonal abundance of potential smolt predators including Pacific hake, jack mackerel *Trachurus symmetricus*, spiny dogfish *Squalus acanthias*, and alternative prey (e.g., northern anchovy and Pacific herring) and affect predator dynamics in the Columbia River plume (Emmett 2006). Further, the abundance of smolts in the estuary and plume also changes (Dawley et al. 1986). Arriving too early probably decreases survivability, as was found for early migrating coho salmon *O. kisutch*, including those from the lower Columbia River (Ryding and Skalski 1999). Lum (2003) found that coho salmon leaving Auke Creek, Alaska, during the peak of the migration returned at the highest rate.

Chinook salmon presumably evolved to enter the ocean when they are physiologically prepared for transition to the marine environment and with their migration timed to arrive when physical and environmental conditions in the ocean are at optimal levels (Folmar and Dickhoff 1980; Wedemeyer et al. 1980). Because of decreased water velocity in reservoirs upstream of dams, Snake River Chinook salmon now

TABLE 2.—Wild Chinook salmon weekly and yearly estimates of percent migrant survival (S_M) from Lower Granite Dam (Snake River) to Bonneville Dam (Columbia River), percent smolt-to-adult return for fish transported (SAR_T) or returned to the river (SAR_M) at Lower Granite Dam, transport migrant ratio (T:M), and post-hydropower system differential survival (D) for fish that were PIT tagged at Lower Granite Dam in 1998, 1999, and 2002. A constant value of 0.98 was used for survival during transport (S_T).

	April					May				
	2	9	16	23	30	7	14	21	28	Year
					1998					
S_M		51.9	53.8	52.2	61.6	53.8	54.9	45.9	42.7	53.2
SAR_T		1.41	0.65	0.31	0.60	0.41	0.00			0.60
SAR_M		1.58	0.90	0.13	0.37	0.27	0.31			0.63
T:M		0.89	0.73	2.44	1.60	1.51				0.94
D		0.47	0.40	1.30	1.01	0.83				0.51
					1999					
S_M	52.7	57.7	57.6	55.9	56.5	53.0	50.4	53.5		55.7
SAR_T	1.04	0.78	1.26	1.33	2.72	2.30	4.53			2.11
SAR_M	1.27	1.53	0.24	0.91	1.82	1.53	0.55			1.22
T:M	0.82	0.51	5.26	1.46	1.49	1.50	8.27			1.73
D	0.44	0.30	3.09	0.83	0.86	0.81	4.25			0.98
					2002					
S_M		56.5	56.3	67.8	53.7	58.0	48.8	65.9	83.9	58.6
SAR_T		0.89	0.38	1.31	1.02	0.57	0.47	2.42	1.69	1.25
SAR_M		1.41	0.97	0.55	0.48	0.65	0.92	0.62	0.59	0.69
T:M		0.63	0.39	2.39	2.14	0.88	0.51	3.87	2.86	1.81
D		0.36	0.22	1.65	1.17	0.52	0.25	2.60	2.45	1.08

require about twice the time to migrate through the lower Snake and Columbia rivers as they did before dam construction (Williams et al. 2005). Altering ocean entry timing by accelerating arrival (by transporting) or delaying it (extended migration for in-river migrants) can result in smolts entering the ocean under less than optimum conditions with an impaired physiological condition. Congleton et al. (2005) found that Chinook salmon migrating in-river had exhausted their lipid reserves well before passing Bonneville Dam, particularly in low-flow years when migration was extended. The poorer performance of late season migrants is probably due to ocean entry beyond the optimum migration window and declining physiological condition.

On the other hand, transported smolts arriving to the estuary early in the season do not appear to lack the physiological development for seawater entry. Chinook salmon smolts can survive direct transfer from freshwater to seawater (e.g., see Hoar 1976). Zaugg et al. (1985) and Muir et al. (1994) showed that gill Na^+-K^+ ATPase activity increased in hatchery spring Chinook salmon when sampled at downstream locations after release, demonstrating the importance of

TABLE 3.—Average fork lengths (mm; SEs in parentheses) of wild and hatchery Chinook salmon measured at Lower Granite (LGR) and Bonneville (BON) dams, changes in length, and median travel time (d) between dams in 2002 and 2003. Wild fish are divided into early (Apr 10–30), middle (May 2–17), and late (May 19–Jun 5) migrants.

	Wild migrants				
Variable	Early	Middle	Late	All	Hatchery all
			2002		
N	24	30	34	88	620
Length at LGR	102 (1.6)	106 (1.4)	108 (1.3)	106 (0.8)	134 (0.4)
Length at BON	114 (1.1)	111 (1.1)	115 (1.1)	113 (0.7)	138 (0.4)
Δ length	13 (1.4)	5 (0.6)	7 (0.7)	8 (0.6)	5
Travel time	31 (1.6)	18 (0.6)	15 (0.4)	20 (0.9)	
			2003		
N	34	21	30	85	368
Length at LGR	106 (0.9)	104 (1.5)	111 (1.2)	107 (0.7)	132 (0.6)
Length at BON	115 (1.1)	110 (1.5)	116 (1.1)	114 (0.7)	138 (0.7)
Δ length	9 (1.0)	5 (1.0)	5 (0.5)	6 (0.5)	6
Travel time	25 (1.0)	20 (0.7)	14 (0.5)	20 (0.7)	

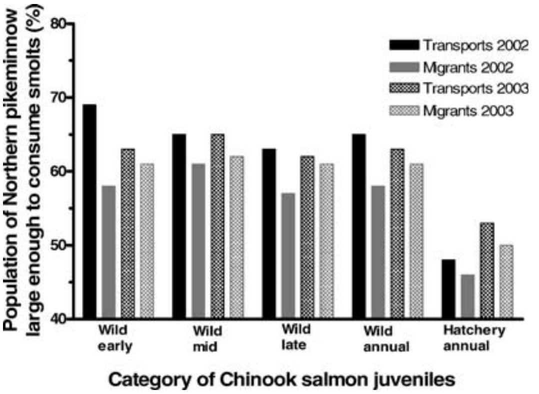

FIGURE 4.—Percentage of the northern pikeminnow population in the Columbia River below Bonneville Dam that was large enough to consume the average stream-type Chinook salmon (wild or hatchery; transported or migrant) from the Snake River in 2002 and 2003.

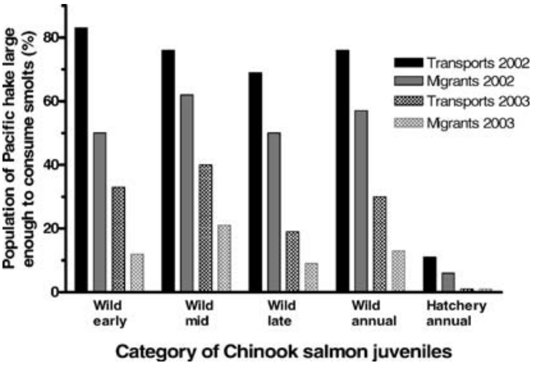

FIGURE 5.—Percentage of the Pacific hake population in the Columbia River plume that was large enough to consume the average stream-type Chinook salmon (wild or hatchery; transported or migrant) from the Snake River in 2002 and 2003.

river migration for full development. However, Congleton et al. (2000) found that wild spring Chinook salmon smolts in the Snake River did not show this pattern. Snake River wild fish already had high levels of smoltification, perhaps because they had already migrated a sufficient distance for parr–smolt transformation to occur before arrival at Lower Granite Dam.

Migrants actively feed and grow during their downstream migration through the Snake and Columbia rivers (Muir and Coley 1996), but this opportunity is limited for transported smolts. Consequently, migrant wild smolts were about 6–8 mm longer and hatchery smolts were 5–6 mm longer than transported smolts on arrival downstream of Bonneville Dam. Length differences between transported and migrant wild smolts were greatest early in the season, when migrants had the longest travel times. The same was probably true for hatchery smolts, although we had no data to explore seasonal trends. Because we were unable to measure individual PIT-tagged hatchery fish at Lower Granite and Bonneville dams as we did for wild fish, their reported growth is affected to an unknown degree by size-selective predation between Lower Granite and Bonneville dams, or potential size selectivity of the Bonneville Dam bypass system. This could account for the slightly lower estimated growth found for hatchery smolts.

Transportation probably increases predation vulnerability of smolts through two mechanisms. First, fish transported early arrive outside the normal migratory window and in comparatively small numbers with respect to the overall fish migration. Thus, they may face increased predation risk if their numbers are insufficient for effective schooling or swamping behavior needed to escape predator concentrations. A lack of effective schooling can decrease the smolts' vigilance, improve predator recognition and assessment, and decrease predator confusion (Magurran 1990; Pitcher and Parrish 1993). Second, the smaller size of transported fish contributes to size-selective predation downstream from Bonneville Dam and in the ocean. In freshwater, northern pikeminnow predation occurs in all Snake and Columbia River reservoirs, but the highest rate occurs in the lower Columbia River, particularly directly downstream from Bonneville Dam (Ward et al. 1995) near the transportation release site. Piscivorous fish generally consume smaller prey (Sogard 1997) as a result of size-influenced differences in burst swimming speeds of both predator and prey (Webb 1986) and because of predator gape limitations (Hart and Hamrin 1988). Shively et al. (1996) found the average size of Chinook salmon smolts in stomachs of northern pikeminnow ranged from 4 to 9 mm shorter than fish collected from a nearby trap; their observations were similar to findings reported by Poe et al. (1991).

In the marine environment, size-selective predation occurs for sockeye salmon *O. nerka* (Koenings et al. 1993), pink salmon *O. gorbuscha* (Moss et al. 2005), and coho salmon (Holtby et al. 1990). Holtby et al. (1990) found that large coho salmon smolts had a survival advantage when marine survival was relatively poor but had little advantage in good ocean years. They attributed this difference to size-selective predation, probably by Pacific hake, which commonly prey on fish similar in size and shape to salmon smolts (Outram and Haegele 1972; Livingston and Alton 1982; Tanasichuk et al. 1991). Pacific hake abundance along the Pacific coast, estimated at 2.6–4.0 million metric tons (Helser et al. 2004), makes them a potentially important smolt predator. Emmett (2006) found five Chinook salmon in slightly more than 3,000 Pacific hake stomachs containing food he examined from the Columbia River plume. Given the much lower abundance of Chinook salmon smolts relative to similar-sized prey in this environment (e.g., northern anchovy), and a Pacific hake population probably numbering in the millions of fish (greater than 1.5×10^9 fish along the Pacific coast), considerable predation by Pacific hake probably occurs on size-vulnerable salmon smolts.

Pacific hake size and abundance along the Pacific coast varies annually (Smith et al. 1990; Emmett 2006) and seasonally (Emmett 2006), with abundance typically increasing in late spring or early summer as they migrate northward (Smith et al. 1990). Because wild Chinook salmon were much smaller than their hatchery counterparts (average difference of 28 mm in 2002 and 25 mm in 2003), they were more vulnerable to a larger proportion of the two predator populations we examined. This provides an explanation for the higher post-hydropower system mortality observed for wild smolts.

Focusing our analysis exclusively on fish transported or returned to the river to migrate from Lower Granite Dam resulted in higher *T*:*M* ratios and *D* values than if we had included fish transported from dams downstream from Lower Granite Dam, or if we had defined our migrant group as only smolts that were never detected at a Snake River dam (Berggren et al. 2005; Williams et al. 2005). However, our intent was not to evaluate the efficacy of smolt transportation from the Snake River per se, but rather to identify mechanisms to explain observed differential post-hydropower system mortality between transported and in-river migrants. Using smolts transported from a downstream dam would have complicated travel time and survival estimation for each group, while using fish not detected within the hydropower system would have precluded weekly SAR, *T*:*M*, and *D* estimation, as it is not possible to determine when a nondetected smolt migrated through the system.

Based on average annual estimates of *D*, Budy et al. (2002) argued, with little empirical data, that collection and transportation of fish causes stress and disease, and that this is the probable causative mechanism for increased differential mortality downstream of Bonneville Dam. We have shown that *D* can vary widely within migration seasons and from year to year. Transported smolts survive worse than in-river migrants from below Bonneville Dam to return as adults at some times and survive better at other times. This empirical observation is more compatible with our proposed mechanisms of altered timing of ocean entry, lost growth opportunity, and size-selective predation than with a stress- or disease-related hypothesis.

Congleton et al. (2000) examined the stress response of Chinook salmon and steelhead transported from Lower Granite Dam and reported that Chinook salmon were more stressed by barge transportation than were steelhead, and that Chinook salmon circulating cortisol concentrations were positively correlated with steelhead densities in the barge. In laboratory studies, Kelsey et al. (2002) found that the presence of hatchery steelhead altered the behavior of Chinook salmon and increased their blood cortisol level significantly. Nonetheless, Wagner et al. (2004) examined the relationship between barge loading densities of steelhead and Chinook salmon SARs transported from Lower Granite Dam and found no relationship. Further, slope coefficients were positive rather than negative (Chinook salmon SAR tended to increase with increased steelhead density in the barge) in all years evaluated. The results of Wagner et al. (2004) are consistent with our results, showing that transport usually provided the least benefit and resulted in the highest delayed mortality (lowest *D*) for Chinook salmon early in the migration season when steelhead densities were low.

Although elevated stress (measured by circulating cortisol levels) has been attributed to passage through dam bypass or collection systems and from barging, cortisol levels usually return to pre-stress levels in a relatively short time (Matthews et al. 1986; Maule et al. 1988; Mesa 1994; Congleton et al. 2000). Furthermore, a stress response is a healthy, normal reaction for an animal facing adversity (Pickering 1993; Schreck 2000). Olla and Davis (1992) found that juvenile coho salmon quickly recovered the ability to avoid predatory lingcod *Ophiodon elongatus* after experiencing mild stress, even though cortisol levels in circulation remained elevated. Similarly, Mesa (1994) showed that stressed juvenile Chinook salmon were preferentially eaten by northern pikeminnow but only within a short period after the stress event; there was no difference in predation after 1 h of recovery.

With greater understanding of the mechanisms causing post-hydropower system mortality, operational changes could be made that might improve survival. Chinook salmon that are transported early in the migration season typically have the highest differential mortality. Thus, a strategy to delay transportation of early arriving fish should increase their SAR. They would enter the ocean later in the migration season when more smolts are present and ocean conditions are probably more favorable. Furthermore, keeping early migrants in-river would allow additional growth opportunity and should reduce their vulnerability to size-selective predators. They would, however, face mortality rates of 50–60% as they migrate through the eight main-stem hydropower dams (Williams et al. 2001). Such a strategy for Chinook salmon might, on the other hand, negatively affect juvenile steelhead, which generally show a benefit from transportation throughout the migration season (Williams et al. 2005). Currently, it is not possible to collect and transport steelhead separately from Chinook salmon at Snake River dams. Conversely, transporting a higher percentage of Chinook salmon smolts later in the season would optimize their ocean entry timing and should lead to improved survival.

We attribute the less-than-envisioned benefits of transportation of Chinook salmon (particularly wild fish) to alteration of timing of the smolt migration, which has also led to differential size-selective freshwater and seawater predation. These results demonstrate the difficulty in mitigating for the reduced survival that has resulted from dam construction. Nonetheless, without initiation of transportation in the late 1970s, a period before dam passage and other system improvements for migrants, Chinook salmon stocks may have gone extinct (Kareiva et al. 2000). Barring removal of Snake and Columbia River dams—a very contentious and controversial proposition presently debated in the Pacific Northwest—restoration of historical migration conditions will not occur. Thus, whether transported or left in-river to migrate, juvenile salmonids will continue to encounter migratory conditions unlike those under which they evolved. Clearly, there are no easy solutions to problems in the Snake and Columbia rivers, but further modifications and actions may help some.

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