Influence of multiple dam passage on survival of juvenile Chinook salmon in the Columbia River estuary and coastal ocean

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Edited by Peter M. Kareiva, The Nature Conservancy, Seattle, WA, and approved February 11, 2013 (received for review November 29, 2012)

Multiple dam passage during seaward migration is thought to reduce the subsequent survival of Snake River Chinook salmon. This hypothesis developed because juvenile Chinook salmon from the Snake River, the Columbia River's largest tributary, migrate >700 km through eight hydropower dams and have lower adult return rates than downstream populations that migrate through only 3 or 4 dams. Using a large-scale telemetry array, we tested whether survival of hatchery-reared juvenile Snake River spring Chinook salmon is reduced in the estuary and coastal ocean relative to a downstream, hatchery-reared population from the Yakima River. During the initial 750-km, 1-mo-long migration through the estuary and coastal ocean, we found no evidence of differential survival; therefore, poorer adult returns of Snake River Chinook may develop far from the Columbia River. Thus, hydrosystem mitigation efforts may be ineffective if differential mortality rates develop in the North Pacific Ocean for reasons unrelated to dam passage.

delayed mortality | marine survival | acoustic telemetry

The Columbia River basin has the fourth largest virgin mean annual discharge in North America and has been classified as "strongly affected" by high fragmentation of the river resulting from the construction of many large dams and from major irrigation consumption (1). Flooding, fish habitat loss, proliferation of nonindigenous aquatic species, and extensive modification of the riparian zone resulted from the river fragmentation; however, this altered river system provides electricity, irrigation, flood control, transportation, and recreation to people in the region. For salmon, dams alter migration routes and speeds and act as large obstacles that adults must navigate around during their migration to upstream spawning grounds (via fish ladders) and that juveniles must pass through (via spill over the dam, fish bypasses, or turbines) during their seaward migration.

Before dam construction, Columbia River basin spring Chinook salmon, *Oncorhynchus tshawytscha,* abundance declined dramatically because of overharvesting (2). Several decades later, populations began to rebound, likely as a result of strict harvest regulations (3) and improved ocean conditions (4). However, salmon populations were further affected by the construction of hydroelectric dams on both the Columbia River and its largest tributary, the Snake River (5–7). Just as construction of the last of four major dams in the lower Snake River was being completed in the late 1970s, an unfavorable change in ocean climate also contributed to the reduced survival of many salmon stocks in southern parts of their range (4, 8). In 1992, Snake River spring Chinook salmon were listed as threatened under the US Endangered Species Act.

Since that time, billions of dollars have been spent on programs to improve smolt (seaward-migrating juvenile salmon) survival through dams and turbines, in tributary habitats, and in the Columbia River estuary (9). As a result, direct smolt mortality at the dams has been successfully reduced (10–12), and survival of Snake River spring Chinook salmon smolts that migrate through the eight-dam, 460-km hydrosystem (a series of four dams in the lower Snake River and four dams in the lower Columbia River) is now typically 50% (13), which is higher than that observed for Chinook salmon populations that migrate a similar distance in the adjacent undammed Fraser River (14). However, despite increases in freshwater smolt survival, smolt-to-adult return rates (SARs) of the aggregate wild Snake River spring Chinook salmon run averaged only 1.1% over the last decade (15), which is well below the recovery target of 4% and the minimum target of 2% (16). Therefore, approximately one in two smolts survive the hydrosystem, but only one in 50 of these survivors then survives the Columbia River estuary and North Pacific Ocean to return as adults 2–3 y later.

In contrast, the SAR of wild spring Chinook salmon from two mid–Columbia River tributaries (the John Day and Yakima rivers) was 4.3% and 3.1%, respectively, during the same period (15). These smolts only migrate through the lower Columbia River dams and are not exposed to Snake River dam passage. Thus, the lower productivity of the Snake River population was attributed to their combined exposure to the four lower Snake River dams and the four lower Columbia River dams during seaward migration (6, 17). Budy et al. (18) reviewed the possible stressors that Snake River spring Chinook salmon may encounter during their downstream migration and concluded that the accumulation of multiple stressors results in hydrosystem-induced delayed mortality (henceforth, "delayed mortality") that occurs in the estuary and coastal ocean.

The marine phase, however, may also differentially affect the survival of spring Chinook salmon stocks. Populations may migrate at different speeds or times or to different parts of the ocean, where they are exposed to different conditions, or they may migrate concurrently but respond differentially to ocean conditions (19). Catches of salmonids on the continental shelf during research surveys indicate that Columbia River basin spring Chinook salmon (including the Snake River populations) are widely distributed between Vancouver Island and southeast Alaska during their first summer at sea (20). Recoveries of mature Columbia River spring Chinook salmon from the commercial fishery also indicate that ocean distributions vary considerably (21). Coastal migration patterns appear to be consistent between years, regardless of changes in ocean conditions, and this lack of plasticity suggests a genetic control that may prevent populations from migrating away from poor-quality marine areas (20).

Such behavior could also explain why, despite improved ocean conditions since 1998–1999 and correlating higher adult return rates, Snake River spring Chinook salmon SARs covary with, but remain lower than, mid-Columbia populations (22). In contrast, river conditions (such as faster river velocity during smolt migration) were associated with improved adult returns, in addition to cold sea temperatures and increased coastal upwelling (23). Freshwater smolt survival during seaward migration and subsequent SARs were also positively correlated, supporting the

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Author contributions: D.W.W. designed research; E.L.R., M.C.J.-S., and P.M.W. performed research; E.L.R. and A.D.P. analyzed data; and E.L.R., D.W.W., and A.D.P. wrote the paper.

Conflict of interest statement: D.W.W. is president and owner of Kintama Research Services, an environmental consultancy that designed and operates the main elements of the acoustic telemetry array described in this article.

This article is a PNAS Direct Submission.

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This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1219910110/-/DCSupplemental.

hypothesis that difficult or slow migration through the hydrosystem results in delayed mortality in the estuary and ocean (24).

These analyses, however, are based on mark-recapture data from fish that were tagged as juveniles and were then captured or detected as returning adults, rather than direct measurements of survival during the critical weeks in the estuary and coastal ocean immediately after dam passage. Stressful freshwater passage subsequently manifesting itself as mortality in the ocean, and the direct effects of the ocean on survival (both soon after ocean entry and for the rest of the marine phase), are confounded when using adult return rates. The only way to discriminate between these sources of mortality is to directly estimate survival downstream of the final dam during estuarine and early marine migration.

The development of acoustic tags small enough to surgically implant into salmon smolts, and the large-scale telemetry arrays with which to track them, provides a technique for directly estimating survival in the lower reaches of large rivers (14, 25–27) and into the coastal ocean (28–32), making it unnecessary to wait 2–3 y for the adults to return before evaluating delayed mortality. Using a continental-scale acoustic telemetry array (Fig. 1), we tracked the movements and estimated survival of size-matched groups of acoustic-tagged, 1-y-old hatchery spring Chinook salmon smolts from the Snake River and from a downstream population from the Yakima River to northern Vancouver Island, a distance of 750 km beyond the final dam. SARs for the Yakima River population, which migrates through half the number of dams, were, on average, 3.4 times higher than for the Snake River population (15) during this study. We then used an information theoretic approach (33) to investigate whether survival of Snake River smolts was lower than that of Yakima River smolts. Our results substantially extend the period of life history during which is it possible to address whether delayed mortality occurs in juvenile salmon from the Columbia River basin and expand and further support the findings of our first-year pilot study in 2006 (28).

Results

Estimated survival in each of the migration segments in the area of comigration was similar for Snake and Yakima River spring Chinook salmon (Fig. 2). From Lake Wallula to Lake Celilo, survival ranged between 0.72–0.75 for Snake River smolts and 0.63–0.87 for Yakima River smolts (Table 1; see Table S1 for the number of fish detected on each subarray). From Lake Celilo to McGowans Channel, survival ranged between 0.8–1.0 for Snake River smolts and 0.71–1.0 for Yakima River smolts. In 2006, survival from below Bonneville Dam to Willapa Bay (which included the lower Columbia River, estuary, and plume) was 0.78 (SE = 0.19) for Snake River smolts and 0.77 (SE = 0.18) for Yakima River smolts.

In 2008, following the installation of the Astoria subarray, we were able to partition survival between the lower Columbia River and estuary (LRE) and the plume. We found that survival in the LRE was consistently very high and ranged between 0.82 and 1.0 for both populations in 2008 and 2009. Survival in the plume during those years ranged between 0.34 and 0.48 for both populations. This was surprisingly low, given the short migration distance of only 63 km between subarrays and given that joint survival in the LRE and plume was substantially higher in 2006, at 0.77 and 0.78 for the two populations, indicating that plume survival must have been much higher in 2006. Thus, we observed substantial interannual variability in plume survival and strong covariation between populations.

We also observed interannual variability and covariation in estimated survival during the 485-km, 1-mo-long migration beyond the plume in the coastal ocean to Lippy Point, BC, Canada. In 2006, a year of poor to intermediate ocean conditions (34), coastal ocean survival was lowest for both populations (only 0.04 for Snake River smolts and 0.02 for Yakima River smolts). In 2008, a year of much improved ocean conditions, coastal survival was an order of magnitude higher for both populations (0.29 and 0.30). In 2009, when ocean conditions were intermediate, coastal survival estimates were intermediate as well (0.12 and 0.04).

Accordingly, when all migration segments in the area of comigration are taken together, cumulative survival for both populations from Lake Wallula to Lippy Point covaried (Fig. 3). In 2006, cumulative survival ranged between 0.01 and 0.02. With improved ocean conditions, cumulative survival increased to 0.07 for both populations in 2008 and then declined in 2009, to 0.01–0.03.

After approximately 2 mo in the ocean, several smolts were detected on the acoustic subarray in Alaska; however the low numbers detected on this subarray (>1,000 km north of Lippy Point) prevented us from estimating survival to this location (*Materials and Methods*). The estimated detection probabilities, *p*, of other subarrays are presented in Table S2.

Model selection results indicated that in individual years, there was little to no support for the delayed mortality (DM) model in which survival was parameterized separately in each of the post–Bonneville Dam migration segments (Table 2). The common model, which estimated survival in each migration segment for both populations combined, was the highest-ranked model and had higher Akaike's Information Criteria (AIC) weights in all years. The ΔAICc scores of the DM model ranged between 0.8 and 3.9, and ΔAICc scores of the base model ranged between 2.2

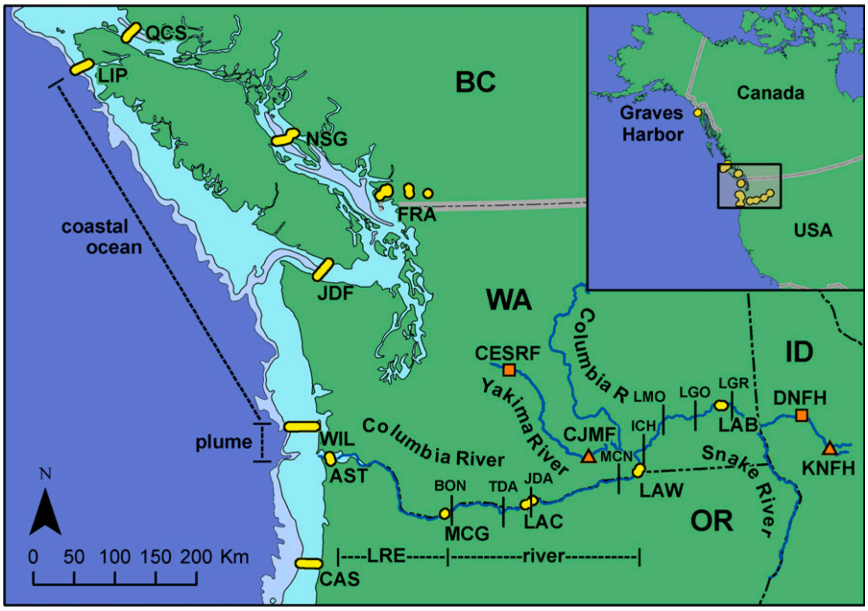

Fig. 1. Study area with acoustic tracking array (yellow dots and lines) and habitat designations. Hatcheries are represented by orange squares and release sites by orange triangles. Subarrays were deployed in Lake Bryan, Lake Wallula, Lake Celilo, McGowans Channel, Astoria, and Willapa Bay, WA; Lippy Point, BC, Canada; Cascade Head, OR; and Graves Harbor, AK. No smolts were detected on Pacific Ocean Shelf Tracking subarrays in the Juan de Fuca Strait, Northern Strait of Georgia, or Queen Charlotte Strait or on the Fraser River subarrays. Snake and lower Columbia River dams are indicated with vertical lines. Isobaths show the continental shelf edge at 200 and 500 m depth. AST, Astoria; BON, Bonneville; CAS, Cascade Head; CESRF, Cle Elum Supplementation and Research Facility; CJMF, Chandler Juvenile Monitoring Facility; DNFH, Dworshak National Fish Hatchery; FRA, Fraser River; ICH, Ice Harbor; JDA, John Day; JDF, Juan de Fuca Strait; KNFH, Kooskia NFH; LAB, Lake Bryan; LAC, Lake Celilo; LAW, Lake Wallula; LGO, Little Goose; LGR, Lower Granite; LIP, Lippy Point; LMO, Lower Monumental; MCG, McGowans Channel; MCN, McNary; NSG, Northern Strait of Georgia; QCS, Queen Charlotte Strait; TDA, The Dalles; WIL, Willapa Bay.

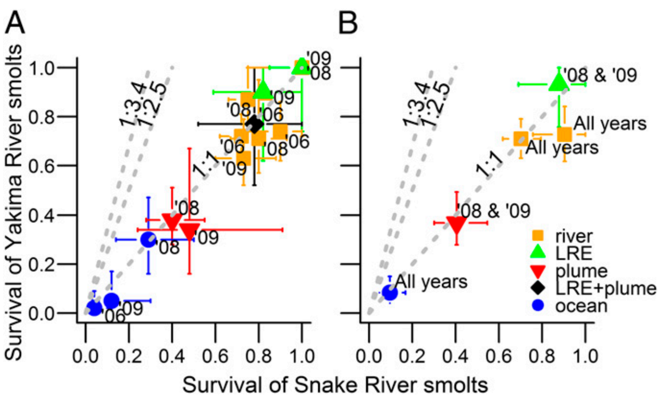

Fig. 2. Comparative survival of acoustic-tagged Snake River and Yakima River spring Chinook salmon smolts in each migration segment (*A*) in 2006, 2008, and 2009 and (*B*) in all years combined. The dashed 1:1 line represents equal survival of both treatment types; data points above the line indicate lower survival of Snake River fish. The 1:2.5 line indicates the survival disparity predicted by the delayed mortality hypothesis, using the ratio of Snake:Yakima adult return rates averaged over 2000–2009. The 1:3.4 line indicates the average survival disparity predicted over the years of our study. "River" estimates are from Lake Wallula to Lake Celilo and from Lake Celilo to McGowans Channel. The Astoria subarray was not deployed in 2006; therefore, LRE survival was combined with plume survival in that year. Error bars, 95% confidence intervals.

and 6.0. With all years combined, the weights of the three competing models were very similar; however, the common model still performed best. Thus, our data do not provide evidence that delayed mortality occurred in the estuary or coastal ocean in the first 5–6 wk after migrating out of the hydropower system, let alone the 3.4-fold increase in relative survival of the Yakima River population (Fig. 2).

Discussion

Before the initiation of this proof-of-concept acoustic telemetry project, the survival of Columbia River salmon smolts in estuarine and coastal ocean environments was the subject of intense speculation, but virtually no direct information was available. Hatchery-reared Yakima spring Chinook salmon smolts typically survive to return as adults at 2.5 times the rate of Dworshak National Fish Hatchery (NFH) smolts, and during the years of our study, they returned at 3.4 times the rate (15). If delayed mortality of Snake River smolts caused by stressful dam passage is expressed in the estuary or within the first month of life in the coastal ocean, we would expect to see reduced posthydrosystem survival of the Snake River population compared with smolts migrating from the Yakima River. Despite tracking size-matched groups with similar ocean entry timing as far as northern Vancouver Island, 750 km beyond the last dam, and for approximately 1 mo after ocean entry, we did not observe lower survival for Snake River smolts. Thus, our results do not support the hypothesis that hydrosystem-induced stress leads to higher mortality of hatchery-reared Snake River spring Chinook salmon in the estuary and early marine period. If our results are accurate, the survival difference to adult return likely occurs sometime beyond the first month at sea and may not be hydrosystem-related. This is an important finding because mitigation efforts in the Columbia River basin, which are partially based on the assumption that "latent" effects of the dams in the ocean are large, may be ineffective if differential mortality occurs in the North Pacific Ocean for reasons unrelated to dam passage.

Several limitations remain on our finding that Snake River fish did not experience reduced mortality relative to the Yakima controls. All smolts in the study were grown to a larger size to accommodate the acoustic transmitters, and as a result, size at release was in the upper fraction of the untagged population (however, see Fig. S1, which illustrates how the smaller transmitter used in 2008 and 2009 enabled us to tag ~70% of the size distribution). Although there is evidence that larger smolt size may lead to higher SARs for hatchery Chinook (35), within the size range we tagged, survival was not a function of fork length in any year (36, 37). Furthermore, John Day River wild spring Chinook are among the smallest smolts at the onset of seaward migration, yet their return rates are among the highest (15, 38). Thus, it is unclear whether larger body size compensated for hydrosystem-induced stress.

The extra holding time also meant that timing of release was later than what is typical for both populations. Because migration timing may also play a role in determining SARs (39), later ocean entry timing might have either reduced survival prospects for both populations or differentially affected survival.

In all years, we attempted to match ocean entry timing and mean body size of the two populations. We did this successfully in 2008 and 2009; however, in 2006 there was some difference in ocean entry timing, with Snake River smolts arriving at Bonneville Dam 2–3 wk earlier than the Yakima River smolts (owing to high river flows). In addition, Yakima River smolts were larger on average than Snake River smolts in that year. Nevertheless, survival was similar for both populations in 2006 and was not a function of body size (36, 37).

We have some evidence that smolts may have migrated past the ocean subarrays undetected. Several of the tagged smolts that returned to the Columbia River as adults 2 y later (which were detected by passive integrated transponder tag detectors at the dams) were not detected as smolts on all of the ocean subarrays. Therefore, a few individuals may have migrated around the coastal ocean subarrays or swum undetected over subarrays or in locations where receivers were lost, or tag acoustic power may have degraded with time. Provided these factors affected both populations equally, the comparison of relative survival would remain unchanged. In addition, smolts from both populations were widely distributed across the Willapa Bay subarray (Fig. S2); however, because smolts appeared to be confined to the shelf at Lippy Point, our survival models account for any undetected or off-shelf migrant smolts at Willapa Bay, and thus

Table 1. Estimated survival (standard error) of acoustic-tagged Snake and Yakima River spring Chinook salmon smolts by habitat

		Snake River				Yakima River			
Habitat	Migration segment	2006	2008	2009	All years	2006	2008	2009	All years
Tributary	Release–LAW*	0.62 (0.04)	0.49 (0.03)	0.57 (0.03)	0.54 (0.02)	0.68 (0.03)	0.75 (0.02)	0.84 (0.02)	0.75 (0.02)
Mainstem	LAW–LAC	0.72 (0.05)	0.75 (0.05)	0.73 (0.07)	0.70 (0.04)	0.72 (0.05)	0.87 (0.07)	0.63 (0.06)	0.71 (0.04)
Mainstem	LAC–MCG	0.90 (0.08)	0.80 (0.07)	1 (0)	0.90 (0.08)	0.74 (0.06)	0.71 (0.07)	1 (0)	0.73 (0.06)
LRE + plume†	MCG–WIL	0.78 (0.19)	NA	NA	NA	0.77 (0.18)	NA	NA	NA
LRE	MCG–AST	NA	1 (0)	0.82 (0.15)	0.88 (0.1)	NA	1 (0.01)	0.90 (0.19)	0.93 (0.09)
Plume	AST–WIL	NA	0.40 (0.07)	0.48 (0.17)	0.41 (0.06)	NA	0.38 (0.06)	0.34 (0.13)	0.37 (0.05)
Coastal ocean	WIL–LIP	0.04 (0.03)	0.29 (0.09)	0.12 (0.06)	0.10 (0.03)	0.02 (0.02)	0.30 (0.08)	0.05 (0.04)	0.08 (0.03)

Counts of fish detected on each subarray are reported in Table S2. AST, Astoria, WA; LAC, Lake Celilo, WA; LAW, Lake Wallula, WA; LIP, Lippy Point, BC, Canada; MCG, McGowans Channel, WA; WIL, Willapa Bay, WA.

*Note that distance to Lake Wallula was ~3 times longer for Snake River smolts.

†We could not separate estuary and plume survival in 2006 because the Astoria subarray was not deployed that year.

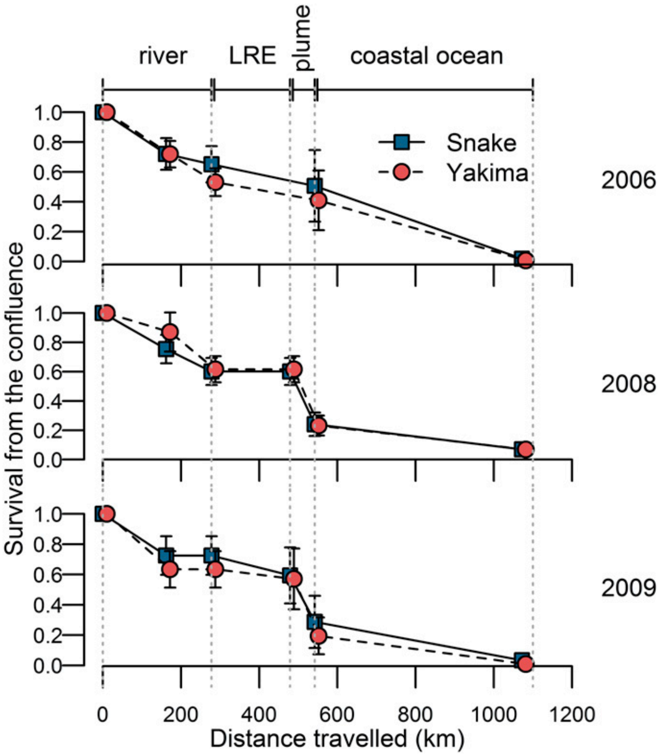

Fig. 3. Cumulative survival of Snake and Yakima River spring Chinook salmon smolts in the comigration pathway. Kilometer 0 is the location of the Lake Wallula subarray (below the confluence of the Snake, Yakima, and upper Columbia rivers). The Astoria subarray was not installed in 2006. Data points were adjusted to prevent overlap of 95% confidence intervals.

the survival estimates would not be affected. This statement holds true as long as the same proportion of both populations migrated around the Willapa Bay subarray (*SI Text*).

We have some concern that medium-term (>30 d) tag loss may be greater for the Yakima River population. Our studies of tagged smolts retained and held in freshwater tanks for up to several months at the release sites found that Yakima smolts had greater rates of transmitter expulsion (36). We also found, however, that the effect of tag loss during the first 5–6 wk after release relative to natural mortality in the coastal ocean is likely negligible (*SI Text*).

Finally, other studies have demonstrated that some Columbia River yearling Chinook salmon smolts may migrate south on ocean entry. Coded wire–tagged and acoustic-tagged yearling spring Chinook salmon were recaptured (40) or detected (41) south of the river mouth when surface ocean currents were southerly; however, in the case of the coded wire–tagged fish, nearly all recaptures occurred to the north of the river mouth 1 mo later, indicating that northward migration soon occurs (acoustic-tagged fish could not be detected beyond the plume). This was further demonstrated by Trudel et al. (42): only 1.6% (1/64) of mid–Columbia River spring run smolts, 2.3% (3/132) of upper–Columbia River springs, and 0% (0/116) of Snake River spring–summer smolts were captured south of the Columbia River mouth along the Oregon shelf. In the present study, we deployed an additional subarray to test the assumption that smolts did not migrate south; none were detected.

If these factors differentially affect survival, the effect would have to be large enough to mask a 3.4-fold difference in apparent survival to Lippy Point (assuming that all delayed mortality caused by prior hydrosystem experience is expressed by the end of the first month at sea). As we found no survival difference within the comigration corridor, the difference likely develops farther north. This suggests either that hydrosystem-induced mortality of hatchery-origin Snake River spring Chinook is greatly delayed or that differences in the subsequent ocean life histories influence survival of these genetically distinct population groupings. It remains unclear whether smaller, wild smolts have similar survival as the smolts reported here, although recent advances in transmitter miniaturization mean that it is now feasible to repeat these experimental tests using wild smolts.

Very little stock-specific distribution information is available for Columbia River spring Chinook from the time they migrate north of British Columbia to the time they return to the Columbia River, a period of more than 1.5 y. In a synthesis of juvenile Chinook salmon coded wire–tagged recoveries from US and Canadian research surveys, Trudel et al. (42) provide distribution information for Dworshak NFH and Yakima River hatchery spring Chinook recaptured over a 12-y sampling period. Although few tagged fish were recovered (Dworshak, $n = 11$; Yakima, $n = 8$), their capture locations provide some insight into stock-specific differences in survival. Juveniles from both populations were captured between the Columbia River and central British Columbia; a Dworshak fish was captured as far north as central Alaska, but no Yakima River fish were captured in

Table 2. Model selection results for survival models investigating whether survival of Snake River spring Chinook salmon is lower than Yakima River spring Chinook salmon

Year	Name	Model*	QAICc†	ΔQAICc	QAICc weights	Model likelihood	Number of parameters	QDeviance
2006	Common	ϕ (gr:seg:trib + seg:WAL–LIP) *p*	1,914.5	0	0.54	1	15	1,884.3
	DM	ϕ (seg:river + gr:seg:LREO) *p*	1,915.8	1.3	0.28	0.53	16	1,883.6
	Base	ϕ (gr:seg) *p*	1,916.7	2.2	0.18	0.34	18	1,880.4
2008	Common	ϕ (gr:seg:trib + seg:WAL–LIP) *p*	4,036.6	0.0	0.84	1.00	20	3,996.2
	DM	ϕ (seg:river + gr:seg:LREO) *p*	4,040.5	3.9	0.12	0.14	22	3,996.1
	Base	ϕ (gr:seg) *p*	4,042.5	6.0	0.04	0.05	24	3,994.0
2009	Common	ϕ (gr:seg:trib + seg:WAL–LIP) *p*	3,853.4	0.0	0.55	1.00	20	3,813.0
	DM	ϕ (seg:river + gr:seg:LREO) *p*	3,854.1	0.8	0.37	0.68	22	3,809.8
	Base	ϕ (gr:seg) *p*	3,857.3	3.9	0.08	0.14	24	3,808.8
All	Common	ϕ (gr:seg:trib + seg:WAL–LIP) *p*	5,620.6	0.0	0.39	1.00	31	149.8
	DM	ϕ (seg:river + gr:seg:LREO) *p*	5,621.0	0.4	0.32	0.81	32	148.2
	Base	ϕ (gr:seg) *p*	5,621.2	0.6	0.28	0.73	34	144.4

ϕ, survival probability; AICc, Akaike's Information Criteria with low sample size; DM, delayed mortality model; gr, treatment group (population); LREO, lower river, estuary, and ocean; *p*, detection probability; Q, correction for overdispersion was made; river, river upstream of Bonneville Dam; seg, migration segment; trib, tributary; WAL–LIP, Lake Wallula, WA to Lippy Point, BC, Canada; All, all years combined. See *SI Materials and Methods* for model name descriptions.

*In all models, detection probability (*p*) was estimated identically (*Methods*).

†AICc is presented for 2008.

southeast or central Alaskan waters. This is consistent with our telemetry data, which show that only Dworshak fish were detected in southeast Alaska. Although both studies are based on few Alaskan observations, life history differences may lead to different ocean distributions, and thus potentially large differential survival rates.

There is evidence that increasing conservation actions and technological fixes within the Columbia River basin may not increase salmon population growth rates to sustainable levels. First, there is a significant correlation between ocean conditions that juvenile spring Chinook salmon encounter after ocean entry and the number of adults subsequently returning to the Columbia River (34, 43). For example, in 2005, ocean conditions were ranked lowest in a 14-y time series and the wild Snake River spring Chinook SAR from that outmigration year was also lowest, whereas in 2008, ocean conditions were ranked highest and subsequent adult returns reached the conservation goal of 4% for the first time. Second, our early marine survival estimates also correlate with ocean conditions: In 2008, smolt survival was an order of magnitude greater than in 2006, and 2009 was intermediate, consistent with mean rank scores of ocean conditions. Finally, modeling exercises demonstrated that even if hydrosystem survival were 100%, population growth rates would continue to decline unless reductions in first-year mortality, particularly early ocean and estuarine mortality, occurred (44).

Recent fluctuations and collapses of Chinook populations are not unique to the Columbia River basin. The collapse of the Sacramento River fall Chinook salmon run prompted complete closure of the California Chinook fishery in 2008 (45). Poor returns persisted for several years, but 2012 return rates are predicted to be some of the largest in decades, according to the Pacific Fishery Management Council. In British Columbia, west coast Vancouver Island Chinook populations are a stock of concern, and despite relatively pristine freshwater habitat and harvest reductions, the stock shows no sign of rebuilding (46). In 2012, the governor of Alaska requested disaster relief funds after severe restrictions or closures of Chinook salmon fisheries in the Yukon, Kuskokwim, and Kenai rivers, according to a State of Alaska news release. In all cases, marine survival was considered one of the most important factors leading to these declines. As our results indicate that the large difference in survival of hatchery-reared Snake and mid–Columbia River spring Chinook appears not to be caused by hydrosystem-induced delayed mortality, Columbia River salmon managers will need to recognize that the survival problem may be on a scale far larger than that of the Columbia River basin. Similar findings have also been reported for sockeye salmon, with large and persistent differences in long-term productivity of populations from even nearby river systems (47). Given the possibility of persistent differences in salmon production, managers may need to adopt a more pragmatic view of what level of technical "fix" to compensate for poor ocean conditions is both appropriate and possible within the Columbia River basin.

Materials and Methods

Populations Studied. The Snake River population of spring Chinook salmon used in this study was reared at the Dworshak NFH on the Clearwater River (a tributary of the Snake River); however, for logistical purposes we transferred smolts to Kooskia NFH for tagging (*SI Materials and Methods*). For the juvenile migration years used in this study, the geometric mean $\mathrm{SAR}_{\mathrm{Dworshak}}$ was 0.78 (2006, 0.68; 2008, 1.33; and 2009, 0.52), which is slightly higher than the average over the last decade (from 2000 to 2010, the geometric mean SAR was 0.66%) (15). This population migrates through eight dams before reaching the Columbia River estuary, and distance from release to the Columbia River mouth was 870 km (Fig. 1).

The Yakima River population was reared at the Cle Elum Supplementation and Research Facility on the upper Yakima River and is part of the mid-Columbia evolutionarily significant unit (ESU). Smolts were released from Cle Elum Supplementation and Research Facility acclimation sites and then collected from the lower Yakima River at the Chandler Juvenile Monitoring Facility in Prosser, WA, 194–249 km downstream of the acclimation sites, and held for tagging. We collected fish at the Chandler Juvenile Monitoring Facility to maximize our sample size, as mortality in the Yakima River has been as high as 80% in recent years (48). For the juvenile migration years used in this study, the geometric mean $\mathrm{SAR}_{\mathrm{Yakima}}$ was 2.62 (2006, 1.65; 2008, 4.98; and 2009, 2.23; 3.4 times the Dworshak SAR), which is considerably higher than the average over the last decade (from 2000 to 2010, the geometric mean SAR was 1.6%). This population migrates through four dams, and the distance to the Columbia River mouth from release was 615 km.

Tagged Dworshak smolts were released from the Kooskia NFH 2–4 wk earlier than Yakima smolts to allow time for them to migrate the additional 350 km and through the four Snake River dams so that timing of ocean entry (and presumably ocean conditions) would be similar. The comigration corridor extended from the confluence of the Columbia and Snake rivers to northwestern Vancouver Island, a distance of nearly 1,100 km.

Tag Specifications and Surgical Protocol. All work involving live fish met the standards laid out by the Canadian Council on Animal Care and was annually reviewed and approved by the Animal Care Committee of Vancouver Island University, Nanaimo, BC, Canada (applications 2006–08R, 2006–08R-2, and 2009–11R).

In each year of the study, we surgically implanted nearly 800 yearling Chinook salmon smolts with individually identifiable 69-kHz acoustic transmitters (VEMCO, Amirix System Inc.; Table 3). We attempted to size-match tagged fish within and between treatment groups in each year, although there was some variation in 2006 (Table 3). More details are provided in *SI Materials and Methods* and ref. 36.

Acoustic Array Elements and Location. The array design allowed us to track the smolts for 2,500 km from the release site in the Snake River through the hydrosystem, LRE, plume, and coastal ocean to Graves Harbor, Alaska, although our study focuses on the comigration area between Lake Wallula and Lippy Point. See Fig. 1 and *SI Materials and Methods* for array details.

Survival Estimation. For each year of the study, detection histories for each tagged individual were formed and estimates of survival and detection probability and their associated SEs were calculated for each population, using a model that was a special case of the Cormack-Jolly-Seber model for live-recaptured animals implemented with Program MARK (49). We then estimated survival across all 3 y of the study where possible (see *SI Materials and Methods* for model details).

The detection probability, p, of the Lippy Point (northwest Vancouver Island) subarray was not estimable using standard Cormack-Jolly-Seber methods because too few tagged smolts were detected in Alaska each year ($n_{2006} = 2$ Snake; $n_{2008} = 1$ Snake; $n_{2009} = 0$) to provide adequate information regarding the performance of the Lippy Point subarray; therefore, we assumed the p of the Lippy Point subarray was 0.90 for the V9 (VEMCO) tag used in 2006 and 0.67 in 2008 and 2009, when the less-

Table 3. Tagging summary for Snake and Yakima River spring Chinook salmon smolts

Population	Release date	n*	Mean length (FL; range), mm	Tag burden (% mass)†
2006				
Snake	May 1	190	146.9 (140–208)	9.2 (2.6–11.5)
	May 8	190	145.6 (140–192)	9.4 (3.7–11.3)
Yakima	May 30	199	154.5 (140–173)	7.3 (4.8–10.3)
	June 6	199	154.5 (140–168)	7.5 (5.2–10.8)
2008				
Snake	April 25	197	146.2 (130–159)	4.4 (2.9–6.9)
	May 2	198	146.3 (131–159)	4.5 (3.0-6.7)
Yakima	May 15	189	140.3 (129–158)	5.8 (3.9–7.3)
	May 21	189	140.4 (131–157)	5.8 (4.3–7.2)
2009				
Snake	May 4	196	142.3 (130–162)	5.0 (2.9–7.3)
	May 11	196	142.4 (130–164)	4.9 (3.0-6.8)
Yakima	May 18	199	141.3 (130–159)	5.7 (4.1–7.5)
	May 25	194	140.6 (130–159)	5.7 (4.2–6.9)

FL, fork length.

*All smolts were implanted with both acoustic and passive integrated transponder tags. In 2006, fish were tagged with V9-6L acoustic transmitters (9 × 21 mm, 3.1 g in air, 2 g in water). In 2008 and 2009, smolts were tagged with V7-2L acoustic transmitters (7 × 20 mm, 1.6 g in air, 0.75 g in water).

†Percentage tag burden was calculated as tag mass in air divided by fish mass in air.

powerful V7 (VEMCO) tag was used. We evaluated whether relative survival of the two populations was sensitive to assumptions of p at Lippy Point. We found that under several detection scenarios, the relative survival comparison was not affected (Fig. S3; see *SI Materials and Methods* for additional model assumptions).

Strength of Evidence for Delayed Mortality. To evaluate the strength of evidence for delayed mortality of the Snake River spring Chinook salmon population relative to the Yakima River population, we used Akaike's Information Criteria to compare the performance of three competing survival models (Table 2; *SI Materials and Methods*).

ACKNOWLEDGMENTS. We thank Adrian Ladouceur, Phillip Pawlik, Michael Pawlik, Andrea Osborn, and Dusty Cummings for fish tagging assistance; the many vessel captains who worked with us to maintain the acoustic array; the staff at Kooskia and Dworshak NFHs (Adam Izbicki, Kenny Simpson, Gerald Fogleman, James Niles, and Ray Jones) and Yakama Fisheries (Joe Blodgett, Michael Fiander, Mark Johnston, Dave Fast, Bill Bosch, and David Lind); and Dave Marvin for assistance with the Passive Integrated Transponder Tag Information System. Funding for this work was provided by the US Department of Energy, Bonneville Power Administration (Project 2003-114-00). Additional subarrays (Juan de Fuca, Northern Strait of Georgia, and Queen Charlotte Strait) in Fig. 1 were owned by the Pacific Ocean Shelf Tracking project and funded by the Gordon and Betty Moore Foundation and the Alfred P. Sloan Foundation. This work is a contribution to the Census of Marine Life.

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