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

Erin L. Rechisky[1], David W. Welch, Aswea D. Porter, Melinda C. Jacobs-Scott, and Paul M. Winchell

Kintama Research Services Ltd., Nanaimo, BC, Canada V9S 3B3

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

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.

Freely available online through the PNAS open access option.

[1]To whom correspondence should be addressed. E-mail: erin.rechisky@kintama.com.

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 hydro system 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 esti mating 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 aver age, 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 ad dress 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 in cluded 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 pop ulations. 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 be yond 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 comi gration are taken together, cumulative survival for both populations from Lake Wallula to Lippy Point covaried (Fig. 3). In 2006, cu mulative 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

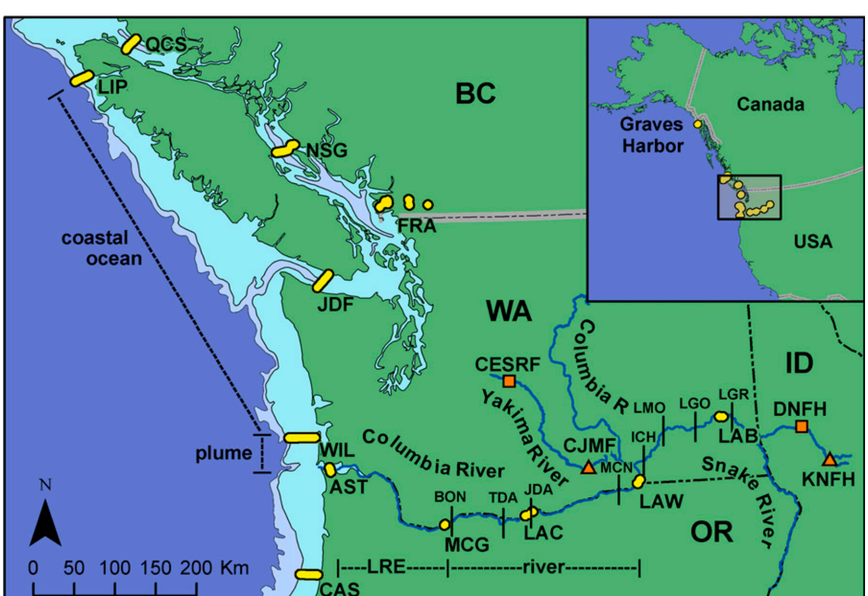

Fig. 1. Study area with acoustic tracking array (yel low dots and lines) and habitat designations. Hatch eries are represented by orange squares and release sites by orange triangles. Subarrays were deployed in Lake Bryan, Lake Wallula, Lake Celilo, McGowans Channel, Astoria, and Willapa Bay, WA; Lippy 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, North ern 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 Re search 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.

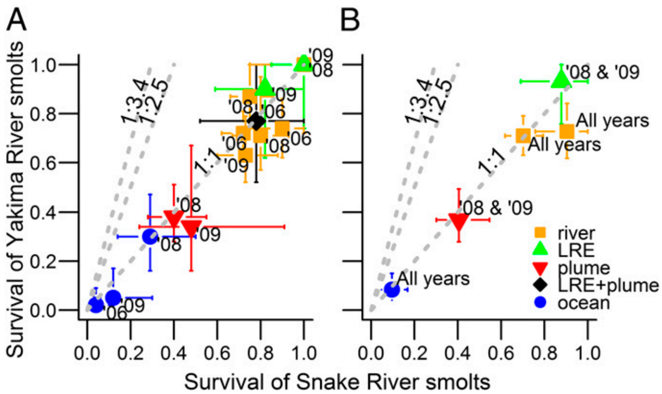

Fig. 2. Comparative survival of acoustic tagged Snake River and Yakima River spring Chinook salmon smolts in each migration segment (*A*) in 2006, 2008, and 2009 and (*B*) in all years combined. The dashed 1:1 line represents equal survival of both treatment types; data points above the line indicate 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.

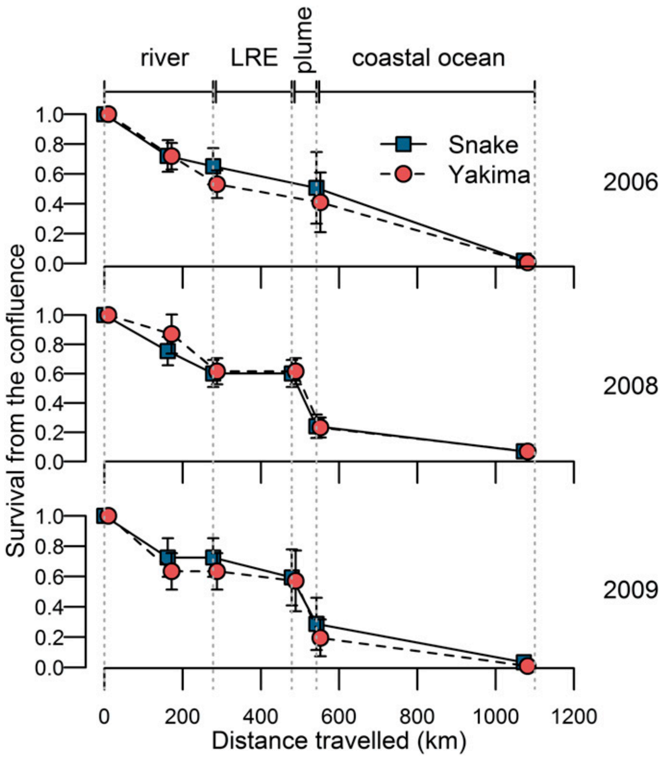

Fig. 3. Cumulative survival of Snake and Yakima River spring Chinook salmon smolts in the comigration pathway. Kilometer 0 is the location of the Lake Wallula subarray (below the confluence of the Snake, Yakima, and upper Columbia rivers). The Astoria subarray was not installed in 2006. Data points were 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 trans mitter 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 Co lumbia River, a period of more than 1.5 y. In a synthesis of ju venile Chinook salmon coded wire tagged recoveries from US and Canadian research surveys, Trudel et al. (42) provide dis tribution 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 pop ulations 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 $SAR_{Dworshak}$ 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 SAR_{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.

1. Dynesius M, Nilsson C (1994) Fragmentation and flow regulation of river systems in the northern third of the world. *Science* 266(5186):753–762.
2. Chapman DW (1986) Salmon and steelhead abundance in the Columbia River in the 19th-century. *Trans Am Fish Soc* 115(5):662–670.
3. Ward DL, Boyce RR, Young FR, Olney FE (1997) A review and assessment of transportation studies for juvenile Chinook salmon in the Snake River. *N Am J Fish Manage* 17(3):652–662.
4. Mantua NJ, Hare SR, Zhang Y, Wallace JM, Francis RC (1997) A Pacific interdecadal climate oscillation with impacts on salmon production. *Bull Am Meteorol Soc* 78(6): 1069–1079.
5. Raymond HL (1979) Effects of dams and impoundments on migrations of juvenile Chinook salmon and steelhead from the Snake River, 1966 to 1975. *Trans Am Fish Soc* 108(6):505–529.
6. Schaller HA, Petrosky CE, Langness OP (1999) Contrasting patterns of productivity and survival rates for stream-type Chinook salmon (*Oncorhynchus tshawytscha*) populations of the Snake and Columbia rivers. *Can J Fish Aquat Sci* 56(6):1031–1045.
7. Raymond HL (1988) Effects of hydroelectric development and fisheries enhancement on spring and summer Chinook salmon and steelhead in the Columbia River basin. *N Am J Fish Manage* 8(1):1–24.
8. Hare SR, Mantua NJ, Francis RC (1999) Inverse production regimes: Alaska and West Coast Pacific salmon. *Fisheries (Bethesda, Md)* 24(1):6–14.
9. BPA (2010) *Bonneville Power Administration annual report, DOE/BP-4224* (Bonneville Power Administration, Portland, OR).
10. Ferguson JW, et al. (2007) Bypass system modification at Bonneville Dam on the Columbia River improved the survival of juvenile salmon. *Trans Am Fish Soc* 136(6): 1487–1510.
11. Muir WD, Smith SG, Williams JG, Hockersmith EE, Skalski JR (2001) Survival estimates for migrant yearling Chinook salmon and steelhead tagged with passive integrated transponders in the lower Snake and lower Columbia rivers, 1993-1998. *N Am J Fish Manage* 21(2):269–282.
12. Williams JG, Smith SG, Muir WD (2001) Survival estimates for downstream migrant yearling juvenile salmonids through the Snake and Columbia rivers hydropower system, 1966-1980 and 1993-1999. *N Am J Fish Manage* 21(2):310–317.
13. Faulkner JR, Smith SG, Muir WD, Marsh DM, Zabel RW (2011) *Survival estimates for the passage of spring-migrating juvenile salmonids through Snake and Columbia River dams and reservoirs, 2011* (Bonneville Power Administration, Portland, OR).
14. Welch DW, et al. (2008) Survival of migrating salmon smolts in large rivers with and without dams. *PLoS Biol* 6(10):e265.
15. Tuomikoski J, et al. (2012) *Comparative survival study (CSS) of PIT-tagged spring/summer Chinook and PIT-tagged summer steelhead, 2012 annual report* (Bonneville Power Administration, Portland, OR).
16. NPCC (2009) *Columbia River Basin Fish and Wildlife Program, Council Document 2009-09* (Northwest Power and Conservation Council, Portland, OR).
17. Deriso RB, Marmorek DR, Parnell IJ (2001) Retrospective patterns of differential mortality and common year-effects experienced by spring and summer Chinook salmon (*Oncorhynchus tshawytscha*) of the Columbia River. *Can J Fish Aquat Sci* 58(12):2419–2430.
18. Budy P, Thiede GP, Bouwes N, Petrosky CE, Schaller H (2002) Evidence linking delayed mortality of Snake River salmon to their earlier hydrosystem experience. *N Am J Fish Manage* 22(1):35–51.
19. Levin PS (2003) Regional differences in responses of Chinook salmon populations to large-scale climatic patterns. *J Biogeogr* 30(5):711–717.
20. Tucker S, et al. (2012) Annual coastal migration of juvenile Chinook salmon: Static stock-specific patterns in a highly dynamic ocean. *Mar Ecol Prog Ser* 449:245–262.
21. Weitkamp LA (2010) Marine Distributions of Chinook Salmon from the West Coast of North America Determined by Coded Wire Tag Recoveries. *Trans Am Fish Soc* 139(1): 147–170.
22. Schaller HA, Petrosky CE (2007) Assessing hydrosystem influence on delayed mortality of Snake River stream-type Chinook salmon. *N Am J Fish Manage* 27(3):810–824.
23. Petrosky C, Schaller H (2010) Influence of river conditions during seaward migration and ocean conditions on survival rates of Snake River Chinook salmon and steelhead. *Ecol Freshwat Fish* 19(4):520–536.
24. Haeseker SL, McCann JA, Tuomikoski J, Chockley B (2012) Assessing freshwater and marine environmental influences on life-stage-specific survival rates of Snake River spring-summer Chinook salmon and steelhead. *Trans Am Fish Soc* 141(1):121–138.
25. Clemens BJ, et al. (2009) Effects of transportation and other factors on survival estimates of juvenile salmonids in the unimpounded lower Columbia River. *Trans Am Fish Soc* 138(1):169–188.
26. McMichael GA, et al. (2010) The Juvenile Salmon Acoustic Telemetry System: A new tool. *Fisheries (Bethesda, Md)* 35(1):9–22.
27. Perry RW, et al. (2010) Estimating survival and migration route probabilities of juvenile Chinook salmon in the Sacramento-San Joaquin River Delta. *N Am J Fish Manage* 30(1):142–156.
28. Rechisky EL, Welch DW, Porter AD, Jacobs MC, Ladouceur A (2009) Experimental measurement of hydrosystem-induced delayed mortality in juvenile Columbia River spring Chinook salmon using a large-scale acoustic array. *Can J Fish Aquat Sci* 66: 1019–1024.
29. Melnychuk MC, Welch DW, Walters CJ, Christensen V (2007) Riverine and early ocean migration and mortality patterns of juvenile steelhead trout (*Oncorhynchus mykiss*) from the Cheakamus River, British Columbia. *Hydrobiologia* 582:55–65.
30. Chittenden CM, et al. (2008) Riverine, estuarine and marine migratory behaviour and physiology of wild and hatchery-reared coho salmon *Oncorhynchus kisutch* (Walbaum) smolts descending the Campbell River, BC, Canada. *J Fish Biol* 72(3): 614–628.
31. Welch DW, et al. (2011) In situ measurement of coastal ocean movements and survival of juvenile Pacific salmon. *Proc Natl Acad Sci USA* 108(21):8708–8713.
32. Rechisky EL, et al. (2012) Estuarine and early-marine survival of transported and in-river migrant Snake River spring Chinook salmon smolts. *Sci Rep* 2:448.
33. Burnham KP, Anderson DR (2002) *Model selection and multimodel inference: A practical information-theoretic approach* (Springer, New York, NY).
34. Peterson WT, et al. (2012) *Ocean Ecosystem Indicators of Salmon Marine Survival in the Northern California Current* 2012:79.
35. Tipping JM (2011) Effect of juvenile length on Chinook salmon survivals at four hatcheries in Washington State. *N Am J Aquaculture* 73(2):164–167.
36. Rechisky EL, Welch DW (2010) In *PNAMP Special Publication: Tagging, telemetry and marking measures for monitoring fish populations. A compendium of new and recent science for use in informing technique and decision modalities*, eds Wolf KS, O'Neal JS (Pacific Northwest Aquatic Monitoring Partnership Special Publication 2010-002. Available at www.pnamp.org/document/3635, Duvall, WA), pp 71–96.
37. Porter AP, et al. (2011) *Marine and freshwater measurement of delayed and differential-delayed mortality of Columbia and Snake River yearling Chinook smolts using a continental-scale acoustic telemetry array, 2010* (Bonneville Power Administration, Portland, OR).
38. DeHart KB, Tattam IA, Ruzycki JR, Carmichael RW (2012) *Productivity of spring Chinook Salmon and summer steelhead in the John Day River Basin* (Bonneville Power Administration, Portland, OR).
39. Scheuerell MD, Zabel RW, Sandford BP (2009) Relating juvenile migration timing and survival to adulthood in two species of threatened Pacific salmon (*Oncorhynchus* spp.). *J Appl Ecol* 46(5):983–990.
40. Fisher JP, Pearcy WG (1995) Distribution, migration, and growth of juvenile Chinook salmon, *Oncorhynchus tshawytscha*, off Oregon and Washington. *Fish Bull* 93(2): 274–289.
41. McMichael GA, et al. (2011) *Migratory behavior and survival of juvenile salmonids in the lower Columbia River, estuary, and plume in 2010, PNNL-20443* (Pacific Northwest National Laboratory, Richland, WA).
42. Trudel M, et al. (2009) Distribution and migration of juvenile Chinook salmon derived from coded wire tag recoveries along the continental shelf of Western North America. *Trans Am Fish Soc* 138(6):1369–1391.
43. Burke BJ, et al. (2013) Multivariate models of adult pacific salmon returns. *PLoS ONE* 8(1):e54134.
44. Kareiva P, Marvier M, McClure M (2000) Recovery and management options for spring/summer chinook salmon in the Columbia River basin. *Science* 290(5493):977–979.
45. Lindley ST, et al. (2009) *What caused the Sacramento River fall Chinook stock collapse? NOAA-TM-NMFS-SWFSC-447* (US Dept of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southwest Fisheries Science Center, Fisheries Ecology Division, Silver Spring, MD).
46. DFO (2012) *Assessment of west coast Vancouver Island Chinook and 2010 forecast, Can Sci Advis Sec Sci Advis Rep 2011/032* (Canada Dept of Fisheries and Oceans, Nanaimo, BC).
47. Rogers LA, et al. (2013) Centennial-scale fluctuations and regional complexity characterize Pacific salmon population dynamics over the past five centuries. *Proc Natl Acad Sci USA* 110(5):1750–1755.
48. Yakama Nation (2011) *Yakima/Klickitat Fisheries Project monitoring and evaluation for the performance period May 1, 2010 through April 30, 2011* (Bonneville Power Administration, Portland, OR).
49. White GC, Burnham KP (1999) Program MARK: Survival estimation from populations of marked animals. *Bird Study* 46:120–139.

Supporting Information

Rechisky et al. 10.1073/pnas.1219910110

SI Text

Smolt Distribution on Ocean Subarrays. Our survival models accurately accounted for any off shelf migration at Willapa Bay, WA, provided that the same proportion of both populations migrated around the subarray and that both populations subsequently returned to the shelf at Lippy Point, BC, Canada (i.e., smolts did not permanently emigrate from the shelf). To assess the extent to which off shelf migration may have occurred and the possible differences in migration behavior that might have affected our comparison of relative survival, we examined the distribution of tagged fish across the Willapa Bay subarray. In all years, both populations were widely distributed across the Willapa Bay subarray (Fig. S2), supporting the idea that smolts migrated primarily on the shelf. In 2006, however, the Yakima River population was uniformly distributed but the Snake River population peaked on the offshore end of the subarray (1). Although the distributions of these populations were different in 2006, it is unclear whether one of them may have differentially migrated off shelf, as individuals from both populations were detected on the farthest offshore receivers. The relatively large number of smolts from both populations detected on the Willapa Bay subarray in 2006 (Table S1) further supports the idea that smolts were mostly migrating on the shelf.

As very few fish were detected on the farthest offshore receivers at Lippy Point in all years, our assumption that smolts remain on the shelf is supported, and thus, our relative survival comparison is likely not affected. If individuals from one population routinely migrated around the Willapa Bay subarray or permanently emigrated from the shelf, then our relative survival comparison would be biased; however, we do not have evidence that this was occurring.

Medium-Term Tag Loss. 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 (2). In 2006, 95% of V9 tagged Snake River smolts and 83% of Yakima River smolts retained their tags for nearly 3 mo. Retention of the smaller V7 transmitter was excellent for Snake River smolts (>96%) for the duration of the studies in 2008 and 2009 (5 6 mo). However, we were unable to quantify medium term tag effects for Yakima River smolts in 2008 and 2009, as the captive studies were ended after approximately 1 mo because of disease outbreak or unknown mass mortality (tag retention to this point was 95 100%). Presumably, medium term retention of the smaller V7 tag would be greater than the V9 tag, but given the 18% long term tag loss of very small passive integrated transponder (PIT) tags reported by Knudsen et al. (3) for the Yakima River hatchery population, tag loss could be problematic for long term tagging studies for this particular population. Nevertheless, acoustic tag retention at sea was likely high. For example, in 2006, by the time Snake River V9 acoustic tagged smolts reached the Lippy Point subarray (median arrival time, 58 d), 98% of captive Snake River fish still retained their tags. By the time the V9 tagged Yakima population reached the Lippy Point subarray (median arrival time, 46 d), 91% of captive smolts still had tags intact. If we correct for tag loss observed in our holding study, our cumulative survival estimates from Lake Wallula to Lippy Point for Snake River smolts only change from 1.86% to 1.89% in 2006, and Yakima smolt survival increases only from 0.75% to 0.79%. Thus, although some acoustic tag loss likely occurred in free swimming smolts, 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 Materials and Methods

Populations Studied. Spring Chinook salmon originating from the Clearwater River subbasin are not part of the Snake River evolutionarily significant unit (ESU), but survival to adult return is routinely estimated for Dworshak spring Chinook salmon and is lower than listed populations in other Snake River subbasins, as well as the downstream Columbia River populations (4). Because of space limitations at Dworshak Hatchery, each year ~1,500 spring Chinook smolts were transferred to Kooskia National Fish Hatchery (NFH) (60 km upstream of Dworshak NFH) 1 3 mo before tagging. In addition to ample working space, springtime water temperatures at Kooskia NFH (12 13 °C) were warmer than water temperatures at Dworshak NFH (4 10 °C). The warmer temperatures facilitated the more rapid growth necessary to attain minimum body size requirements for tagging; however, it was still necessary to retain the fish for several weeks beyond the typical hatchery release date (~April 1) to ensure that a sufficient number of smolts exceeded the minimum size requirement. As a result, tagged smolts migrated an additional 60 km in the Clearwater River 3 6 wk later than conventionally released Dworshak spring Chinook smolts. Nevertheless, in all years, median date of passing Lower Granite Dam (the first dam the smolts encountered in the Snake River) lay within the 55th to 85th passage index date percentiles for yearling hatchery Snake River spring Chinook, according to data from the Fish Passage Center.

Tag Specification and Surgical Protocol. All acoustic tags transmitted a unique identification code and were programmed to provide operational life spans long enough to cover the observed duration of the migration to the Lippy Point subarray (up to 3 mo). In 2006, we surgically implanted V9 6L coded acoustic transmitters (9 × 21 mm, 3.1 g in air, 2 g in water), and in 2008 2009 we used smaller V7 2L transmitters (7 × 20 mm, 1.6 g in air, 0.75 g in water). A 0.1 g PIT tag was also placed in the body cavity (through the incision) of all acoustic tagged smolts. We did this to ensure that tagged smolts were diverted back into the river at the dam bypass facilities and not collected for transport to below Bonneville Dam. Acoustic tag burdens were generally within the maximum recommended for salmon smolts (5, 6).

The larger, more powerful V9 6L transmitter used in 2006 had a greater detection radius than the smaller V7 tag used in 2008 2009. This provided higher detection probabilities by the telemetry array but imposed a greater tag burden on the animals; however, assessment of size at release of tagged animals relative to size at release of survivors reaching Willapa Bay showed no distortions in the distributions (7). In addition, models that included fork length as a covariate did not perform as well as models excluding fork length, suggesting that the tags did not substantially affect survival (2, 7).

At each hatchery, we tagged two release groups of ~200 fish. The same surgical protocol was used in all years for both treatment types; a detailed description of the protocol is provided in Rechisky and Welch (2). In brief, portable surgical units were assembled on site, and fish surgery was carried out by experienced, veterinarian trained staff. Fish were anesthetized individually in 70 ppm tricaine methane sulphonate (Western Chemical) buffered with 140 ppm $NaHCO_3$. Fork length was measured to the nearest millimeter, and weight was measured to the nearest tenth of a gram. A maintenance dose of buffered anesthetic (50 ppm) was pumped through the fish's mouth and over the gills while an incision was made at the ventral midline, midway between the pelvic and pectoral fins. Each smolt was double tagged by placing a PIT and an acoustic tag through the incision into the peritoneal cavity. Depending on tag type, 1 2 absorbable sutures were used to close the incision. Immediately after surgery, fish were placed into a recovery bath and monitored. Fish generally regained equilibrium and reactivity within minutes. After release, we uploaded the PIT tag data into the Columbia River Basin PIT Tag Information System database, which is maintained by the Pacific States Marine Fisheries Commission. Acoustic tagging metadata was provided to the Pacific Ocean Shelf Tracking (POST) project, which is currently managed by the Ocean Tracking Network (OTN).

Acoustic Array Elements and Location. The marine elements of the acoustic telemetry array were composed of individual VEMCO receivers positioned above the seabed of the continental shelf to form a series of listening lines or acoustic subarrays extending from near shore out to ~200 m depths. Individual receivers recorded the date and time that acoustic transmitters (tags) were detected, and these detections were used to estimate survival of each population to each subarray. During the study, marine components of the array extended from coastal Washington (Willapa Bay) through southern British Columbia (Lippy Point) and up to southeast Alaska (Graves Harbor; Fig. 1). Subarrays were also deployed in the lower Columbia River in McGowans Channel below Bonneville Dam (the final dam) and in several reservoirs or "lakes" created by the dams: Lake Celilo, downstream of John Day Dam; Lake Wallula, below the confluence of the Columbia and Snake rivers; and Lake Bryan, below Lower Granite Dam in the Snake River.

In 2008 and 2009, an additional subarray was deployed in the Columbia River estuary at Astoria, WA, allowing lower Columbia River and estuary (LRE) and plume survival to be separately measured. For this study, the LRE is defined as the tidal area ranging from Bonneville Dam to Astoria, and the plume is defined as the area from Astoria to the Willapa Bay subarray. Although the plume technically begins at the river mouth (not Astoria), the distance between the subarrays sited at Astoria and Willapa Bay was only 63 km and encompassed the plume. In 2009, an additional subarray was deployed in the coastal ocean 131 km south of the Columbia River mouth near Cascade Head, OR; no smolts from this study were detected on that array.

Survival Estimation. All acoustic detection data from the array were first screened for potential false positive detections, which were rare: Excluded data typically formed less than 0.1% of the total recorded detections. All acoustic tagged fish migrating in the river were included in our study, regardless of their specific route through the dams (e.g., spill, bypass, or turbine), except for a few Snake River smolts that were inadvertently collected and transported from lower Snake River dams (16 in 2006, 0 in 2008, and 3 in 2009). Court ordered spill was occurring at the four lower Snake River dams and the four lower Columbia River dams, which reduced the chance that smolts migrated through the turbine and the bypass.

In each year of the study, we assessed the goodness of fit of our data with the bootstrap goodness of fit test within Program MARK (8). To do so, we fit the most general Cormack Jolly Seber (CJS) (9 11) model (survival, ϕ, and detection probability, p, were estimated for each treatment type at each subarray). If there was overdispersion resulting from a lack of fit of the data to the model, it was corrected by dividing the model deviance by the mean expected deviance (from 1,000 bootstrapped simulations) to yield an overdispersion factor, $\hat{c}$ (12). If $\hat{c}$ was greater than 1, the resulting SEs on the estimates were inflated (multiplied) by the estimated $\hat{c}$ value. In 2006, the $\hat{c}$ overdispersion factor was 1.9. In 2008, there was no overdispersion ($\hat{c}$ = 0.94), and in 2009, $\hat{c}$ was 1.12. There was no overdispersion ($\hat{c}$ = 1) for the model in which common survival parameters were estimated for each of the treatment types across 2008 and 2009 (survival was estimated in the hydrosystem, in the LRE and plume separately, and the coastal ocean). Finally, $\hat{c}$ was 1.7 for the model in which common survival parameters were estimated for each of the treatment types across all 3 y (survival was estimated for the hydrosystem, the LRE and plume combined, and the coastal ocean).

Survival was estimated in each migration segment for each treatment type for each year, and we made no additional assumptions about the cause of variability in $\hat{\varphi}$ (e.g., fish body size, travel time, etc.). Assessments of tag loss, tagging induced mortality, tag operational life span, and survival differences between taggers (surgical skill) indicated that these factors did not have significant influence on the survival estimates during the time required for the freely migrating tagged smolts to pass Lippy Point (13). We allowed p to vary for each treatment type and subarray in freshwater, but p only varied by subarray in the ocean where sample size was low (i.e., we used the full data set to estimate a common p parameter for both populations at Willapa Bay). We also included in our models two additional groups (each N ≅ 200) of Snake River spring Chinook salmon smolts that were tagged with the same acoustic tag type and then transported (as part of a different comparison) to better quantify p of the Willapa Bay detection line (14). Confidence intervals for ϕ and p were estimated using the profile likelihood method. This model served as the base model from which we extracted survival and detection estimates.

For each population, we then estimated both cumulative survival in the comigration corridor between the Lake Wallula and Lippy Point subarrays as the product of the segment specific survival estimates and the variances with the delta method.

We also estimated survival across all years. We used a reduced CJS model in which a common survival probability was estimated for each treatment type for all years between each detection subarray, and the detection probabilities were parameterized as for the year separate models but were allowed to vary by year (i.e., a separate parameter was estimated for each treatment type in each year). Because the Astoria subarray was not deployed in 2006, it was necessary to run two separate models to obtain average survival estimates to all detection sites: one to estimate average survival across all years (2006, 2008, and 2009) in the river, the LRE and plume combined, and the coastal ocean, and another to estimate average survival across 2008 and 2009 in the LRE and in the plume as separate migration segments.

The detection probability of the Lippy Point subarray was fixed in all years. We did this for several reasons: (1) too few fish were detected on the Alaska subarray to estimate p at Lippy Point, (2) CJS analyses of p for other fully intact marine subarrays with similar receiver geometry, bounded by landmasses on either side, and with ample detections beyond the subarray in question (which renders them directly estimable) showed that marine detection rates are very consistent across multiple sites and multiple years (~0.90% for V9 transmitters and ~0.67% for V7 transmitters at three sites in 4 y) (15); (3) all marine receivers were deployed at approximately equal spacing; (4) the smolt distribution on the Lippy Point line was centered on the inner to middle continental shelf in all years, indicating that fish were confined to the shelf; and (5) if estimates at Lippy Point are biased, they should be equally biased for both treatment types, as identical acoustic tags were used in each year. Because the key scientific test involves whether Snake River smolts have lower post Bonneville Dam survival than the Yakima River smolts, some inaccuracy in this final p assumption is acceptable; however, we required the assumption that the two tagged groups behaved similarly (i.e., that travel rate and potential offshore emigration beyond the shelf arrays were equal).

Strength of Evidence for Delayed Mortality. We used Akaike's Information Criteria (AIC) to evaluate the strength of evidence for delayed mortality of the Snake River spring Chinook salmon population relative to the Yakima River population by comparing the performance of a model in which the effect of treatment (population) was removed in segments in which both groups migrated in common (i.e., downstream of the tributaries the groups were pooled, and only a single common survival parameter was estimated for each migration segment between Lake Wallula and Lippy Point), both to the base model described in *SI Materials and Methods*, *Survival Estimation* and to a model that more specifically represented delayed mortality downstream of Bonneville Dam. The base model included separate survival parameters for the Snake and Yakima River groups between all detection sites (from release to Lippy Point). The delayed mortality (DM) model included common survival parameters for the two populations in each of the common migration segments upstream of Bonneville Dam (from Lake Wallula to McGowans Channel); downstream of Bonneville Dam, survival parameters were estimated for each group in each migration segment to Lippy Point. Under the delayed mortality hypothesis, the differential effects of hydrosystem passage are limited to the estuary and coastal ocean. Detection probability was parameterized identically for all models. We conducted this analysis for each year of data, as well as for all years combined (with LRE and plume combined).

The AIC scores were adjusted for small sample size, which is denoted by AICc. When overdispersion occurred and $\hat{c}$ was applied to the model set, a quasi AICc was computed (16). To evaluate the strength of evidence for the competing models, we assessed the difference in the AICc scores (ΔAICc) and AICc weights (or quasi AICc where applicable).

Model Assumptions. For all subarrays, we recognized standard CJS model assumptions: (*i*) every tagged individual has equal survival probability and equal probability of detection following release, (*ii*) sampling periods are instantaneous, (*iii*) emigration is permanent, and (*iv*) tags are not lost.

For coastal ocean subarrays that were unbounded on the offshore end, we required three additional assumptions: (*v*) fish departing the Columbia River swam north, (*vi*) their migration was confined to the coastal zone spanned by the subarrays, and (*vii*) detection probability of the Lippy Point subarray was equivalent to that of other coastal subarrays with similar geometry (14). Assumptions (*v*) and (*vi*) are supported by evidence from ocean sampling programs that demonstrate that juvenile spring Chinook salmon remain almost entirely on the continental shelf and primarily migrate north on leaving the river (17–20). In addition, we deployed a subarray 131 km south of the Columbia River mouth at Cascade Head, OR (Fig. 1), in 2009 to validate assumption (*v*), but no smolts from this study were detected. See Fig. S3 for more information on assumption (*vii*).

1. Rechisky EL, Welch DW, Porter AD, Jacobs MC, Ladouceur A (2009) Experimental measurement of hydrosystem-induced delayed mortality in juvenile Columbia River spring Chinook salmon using a large-scale acoustic array. *Can J Fish Aquat Sci* 66: 1019–1024.
2. Rechisky EL, Welch DW (2010) In *PNAMP Special Publication: Tagging, telemetry and marking measures for monitoring fish populations. A compendium of new and recent science for use in informing technique and decision modalities*, eds Wolf KS, O'Neal JS (Pacific Northwest Aquatic Monitoring Partnership Special Publication 2010-002, (Duvall, WA), pp 71–96. Available at www.pnamp.org/document/3635.
3. Knudsen CM, et al. (2009) Effects of passive integrated transponder tags on smolt-to-adult recruit survival, growth, and behavior of hatchery spring Chinook salmon. *N Am J Fish Manage* 29(3):658–669.
4. Tuomikoski J, et al. (2012) *Comparative Survival Study (CSS) of PIT-tagged spring/summer Chinook and PIT-tagged summer steelhead, 2012 annual report* (Bonneville Power Administration, Portland, OR).
5. Brown RS, Geist DR, Deters KA, Grassell A (2006) Effects of surgically implanted acoustic transmitters >2% of body mass on the swimming performance, survival and growth of juvenile sockeye and Chinook salmon. *J Fish Biol* 69(6):1626–1638.
6. Brown RS, et al. (2010) An evaluation of the maximum tag burden for implantation of acoustic transmitters in juvenile Chinook salmon. *N Am J Fish Manage* 30(2):499–505.
7. Porter AP, et al. (2011) *Marine and freshwater measurement of delayed and differential-delayed mortality of Columbia and Snake River yearling Chinook smolts using a continental-scale acoustic telemetry array, 2010* (Bonneville Power Administration, Portland, OR).
8. White GC, Burnham KP (1999) Program MARK: Survival estimation from populations of marked animals. *Bird Study* 46:120–139.
9. Cormack RM (1964) Estimates of survival from the sighting of marked animals. *Biometrika* 51:429–438.
10. Jolly GM (1965) Explicit estimates from capture-recapture data with both death and immigration- Stochastic model. *Biometrika* 52:225–247.
11. Seber GAF (1965) A note on the multiple recapture census. *Biometrika* 52:249–259.
12. Cox DR, Snell EJ (1989) *Analysis of binary data* (Chapman and Hall, New York, NY).
13. Porter AP, et al. (2010) *Marine and freshwater measurement of delayed and differential-delayed mortality of Snake River spring Chinook smolts using a continental-scale acoustic telemetry array, 2009* (Bonneville Power Administration, Portland, OR).
14. Rechisky EL, et al. (2012) Estuarine and early-marine survival of transported and in-river migrant Snake River spring Chinook salmon smolts. *Sci Rep* 2:448.
15. Welch DW, et al. (2011) In situ measurement of coastal ocean movements and survival of juvenile Pacific salmon. *Proc Natl Acad Sci USA* 108(21):8708–8713.
16. Burnham KP, Anderson DR (2002) *Model selection and multimodel inference: A practical information-theoretic approach* (Springer, New York, NY).
17. Peterson WT, Morgan CA, Fisher JP, Casillas E (2010) Ocean distribution and habitat associations of yearling coho (*Oncorhynchus kisutch*) and Chinook (*O. tshawytscha*) salmon in the northern California Current. *Fish Oceanogr* 19(6):508–525.
18. Bi HS, Ruppel RE, Peterson WT (2007) Modeling the pelagic habitat of salmon off the Pacific Northwest (USA) coast using logistic regression. *Mar Ecol Prog Ser* 336: 249–265.
19. Fisher JP, Pearcy WG (1995) Distribution, migration, and growth of juvenile Chinook salmon, *Oncorhynchus tshawytscha*, off Oregon and Washington. *Fish Bull* 93(2): 274–289.
20. Trudel M, et al. (2009) Distribution and migration of juvenile Chinook salmon derived from coded wire tag recoveries along the continental shelf of Western North America. *Trans Am Fish Soc* 138(6):1369–1391.

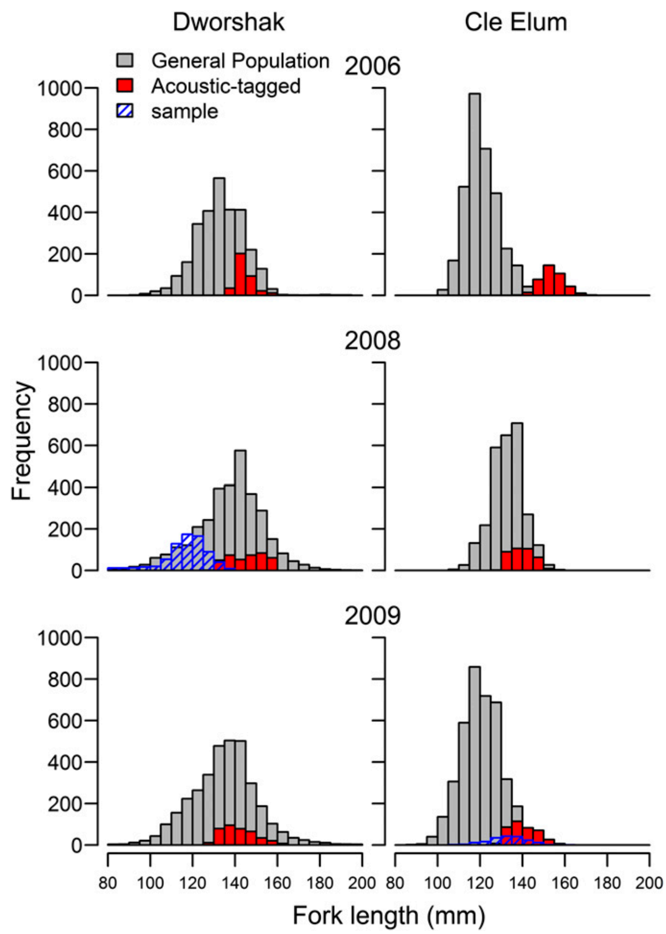

Fig. S1. Size frequency distributions for Snake and Yakima River hatchery yearling Chinook smolts in 2006, 2008, and 2009. Red bars represent fork length at the time of tagging for acoustic tagged smolts. Gray bars represent the general population. The general population of Snake River hatchery smolts was sampled at Lower Granite Dam, according to data provided by the Pacific States Marine Fisheries Commission. The general population of Yakima (Cle Elum hatchery only) smolts, according to data provided by the Yakama Nation Fisheries, was sampled at the Chandler Juvenile Monitoring Facility (CJMF) in 2006 and 2008 and at Roza Dam in 2009. Blue bars in 2008 represent the size distribution of untagged Dworshak spring Chinook sampled at the hatchery just before release and several weeks before acoustic tagged fish were released. Note that these prerelease measurements were only available in 2008, according to data provided by US Fish and Wildlife Service. Blue bars in 2009 for the Yakima smolts represent Cle Elum smolts sampled at CJMF. Few smolts were sampled at CJMF that year, so we reported sizes for a larger sample of fish measured upstream at Roza Dam as the general population. Note, however, that the Roza Dam fish were smaller on average than those sampled at CJMF.

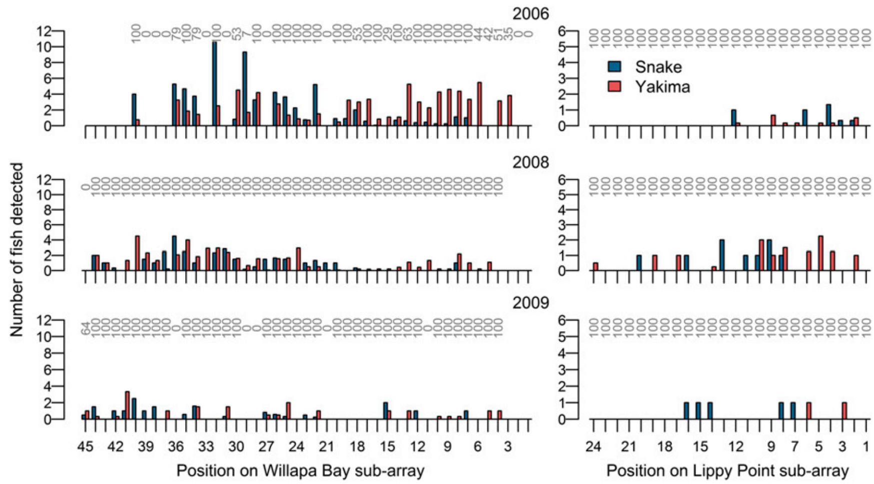

Fig. S2. Distribution of acoustic tagged Yakima and Snake River spring Chinook salmon smolts on the Willapa Bay and Lippy Point subarrays. Position 1 on the *x* axis represents the eastern most acoustic receiver nearest shore, and the final position represents the shelf break (~200 m depth). If a fish was detected at more than one receiver, an equal proportion was allocated to all receivers detecting that fish; for example, if an identification code was detected on two receivers, each receiver was assigned a value of 0.5. A total of 40 receivers were deployed at Willapa Bay in 2006 (to 32 km offshore), and 45 were deployed in 2008 and 2009 (to 36 km offshore). In 2008, receiver 45 was not operational; therefore, the subarray was effectively 44 receivers in length. Positions 1, 2, and 3 of the Willapa Bay subarray were not redeployed in 2008 and 2009 because shallow depths resulted in acoustic nodes washing ashore within weeks of de ployment in 2006. A total of 24 receivers were deployed at Lippy Point in all years (to 19 km offshore). The values above the bars indicate the proportion of time each receiver was operational during the migration period. Note that in 2008, the smolt detected on the most offshore receiver was also detected on another receiver several kilometers inshore.

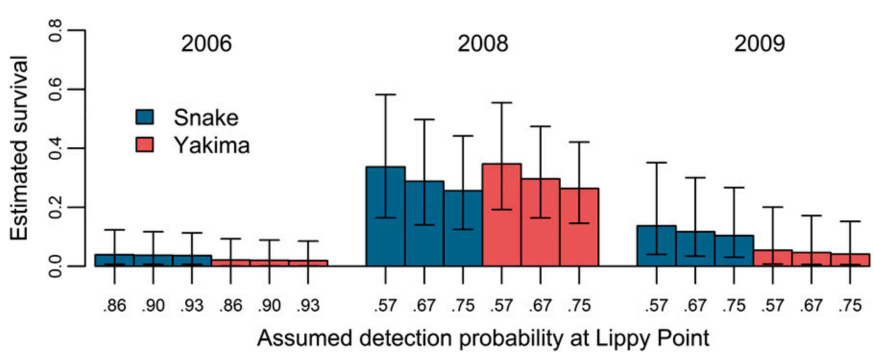

Fig. S3. Sensitivity of survival estimates to assumptions of detection probability at Lippy Point. The baseline assumption used in our analysis is that $P = 0.90$ in 2006 (V9 transmitter) and $P = 0.67$ in 2008 and 2009 (V7 transmitter). To examine how coastal ocean survival estimates (from Willapa Bay to Lippy Point) of acoustic tagged spring Chinook smolts might change with variation in detection probability (p) at Lippy Point, we reran our survival models using the upper and lower 95% confidence bounds on the baseline estimates. The baseline estimate and confidence intervals were estimated for the same tag types used in migrating juvenile salmon at other coastal subarrays with similar geometry in a previous study (1). Because all fish received identical tags within each year, we assumed that the detection efficiency of the Lippy Point subarray should be equal for the two groups. Plausible assumptions about the p of the Lippy Point subarray resulted in relatively small changes in estimated coastal ocean survival. Importantly, our conclusion that Snake River smolt survival was not reduced relative to Yakima River smolts should not be affected by the detection probability of the subarray.

1. Welch DW, et al. (2011) In situ measurement of coastal ocean movements and survival of juvenile Pacific salmon. *Proc Natl Acad Sci USA* 108(21):8708–8713.

Table S1. Summary of detections of Snake and Yakima River hatchery spring Chinook salmon smolts detected on the acoustic array

			No. fish detected						
Year	Release group	No. fish released	Lake Wallula	Lake Celilo	McGowans Channel	Astoria	Willapa Bay	Lippy Point	Graves Harbor
2006	Snake 1	190	102	55	58		41	1	1
	Snake 2	190	114	46	48		42	3	1
	Yakima 1	199	127	74	49		18	2	0
	Yakima 2	199	144	79	75		61	0	0
2008	Snake 1	197	96	44	8	54	21	7	1
	Snake 2	198	95	32	9	41	13	2	0
	Yakima 1	189	123	29	8	63	24	7	0
	Yakima 2	189	147	53	10	68	25	6	0
2009	Snake 1	195	96	26	11	43	10	1	0
	Snake 2	194	106	30	12	39	8	4	0
	Yakima 1	199	171	46	15	58	10	1	0
	Yakima 2	194	150	13	7	55	8	1	0

Table S2. Estimated detection probability ($\hat{p}$) of acoustic subarrays

Year	Population	Subarray*	$\hat{p}$	SE ($\hat{p}$)	95% CI
2006	Snake	LAB	0.97	0.01	0.93 0.99
		LAW	0.92	0.03	0.85 0.97
		LAC	0.60	0.06	0.48 0.71
		MCG	0.69	0.07	0.55 0.82
	Yakima	LAW	1.00	0.00	0.98 1
		LAC	0.79	0.05	0.68 0.87
		MCG	0.86	0.05	0.74 0.94
	Both	WIL	0.71[†]	0.15	0.48 0.93
	Both	LIP	0.90	fixed	NA
2008	Snake	LAB	0.96	0.01	0.92 0.98
		LAW	0.98	0.01	0.95 1.00
		LAC	0.52	0.05	0.42 0.61
		MCG	0.15	0.03	0.09 0.22
		AST	0.81	0.06	0.69 0.91
	Yakima	LAW	0.96	0.02	0.92 0.98
		LAC	0.33	0.04	0.26 0.41
		MCG	0.10	0.02	0.06 0.16
		AST	0.75	0.05	0.64 0.85
	Both	WIL	0.74[‡]	0.07	0.58 0.87
	Both	LIP	0.67	Fixed	NA
2009	Snake	LAB	0.95	0.02	0.92 0.98
		LAW	0.91	0.03	0.85 0.95
		LAC	0.32	0.05	0.24 0.42
		MCG	0.14	0.03	0.09 0.21
		AST	0.64	0.11	0.44 0.82
	Yakima	LAW	0.97	0.01	0.94 0.99
		LAC	0.22	0.04	0.16 0.30
		MCG	0.11	0.02	0.06 0.16
		AST	0.60	0.12	0.44 0.80
	Both	WIL	0.29	0.07	0.20 0.44
	Both	LIP	0.67	Fixed	NA

*Subarrays were deployed in the Snake River in Lake Bryan (LAB), below the confluence of the Columbia and Snake rivers in Lake Wallula (WAL), in Lake Celilo near John Day Dam (LAC), below Bonneville Dam in McGowans Chan nel (MCG), in the Columbia River estuary (Astoria, AST), north of the plume (Willapa Bay, WIL), and the coastal ocean (Lippy Point, LIP). A subarray was deployed south of the Columbia River mouth at Cascade Head, OR, but no fish from this study were detected. Data from both populations were used to estimate one detection parameter at WIL. Detection probability was fixed at LIP in all years. The AST subarray was not deployed in 2006.

[†]The $\hat{p}$ at WIL in 2006 was consistent with the 25% loss of the equipment at this site (largely to commercial fishing activities; i.e., if the assumed p for V9 tags was 0.90 (1), and gear loss was 25%, then the expected $\hat{p}$ is 0.68 (0.90*0.75), similar to our estimated value.

[‡]The $\hat{p}$ at WIL in 2008, when we had zero equipment loss during the fish migration season, was 0.74, consistent with the average $\hat{p}$ of V7 transmitters on bounded subarrays of 0.67 (1). In 2009, however, $\hat{p}$ at WIL declined to 0.29, possibly because of gear loss resulting from fishing (12% loss), changes in acoustic transmitter programming, and/or biological fouling of some receivers.

NA, not applicable.

1. Welch DW, et al. (2011) In situ measurement of coastal ocean movements and survival of juvenile Pacific salmon. *Proc Natl Acad Sci USA* 108(21):8708–8713.