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Estuarine and early-marine survival of transported and in-river migrant Snake River spring Chinook salmon smolts

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Many juvenile Snake River Chinook salmon are transported downriver to avoid hydroelectric dams in the Columbia River basin. As mortality to the final dam is ~50%, transported fish should return as adults at roughly double the rate of nontransported fish; however, the benefit of transportation has not been realized consistently. "Delayed" mortality caused by transportation-induced stress is one hypothesis to explain reduced returns of transported fish. Differential timing of ocean entry is another. We used a large-scale acoustic telemetry array to test whether survival of transported juvenile spring Chinook is reduced relative to in-river migrant control groups after synchronizing ocean entry timing. During the initial 750 km, 1 month long migration after release, we found no evidence of decreased estuarine or ocean survival of transported groups; therefore, decreased survival to adulthood for transported Chinook is likely caused by factors other than delayed effects of transportation, such as earlier ocean entry.

Spring Chinook salmon, *Oncorhynchus tshawytscha*, declined dramatically in the Columbia River, USA, over the last century, initially due to over-harvesting[1,2] and, in later years, due to the impacts of hydroelectric dams[3–5]. Concurrent with the completion of the last four major dams within the Federal Columbia River Hydropower System (FCRPS or "hydrosystem"; Fig. 1) in the lower Snake River (a tributary of the Columbia River) in 1975, an unfavourable change in ocean climate also contributed to reduced survival of many salmon stocks in southern parts of their range, including spring Chinook salmon in Washington, Oregon, and California[6,7]. In 1992, following a precipitous decline in adult returns from the ocean, Snake River spring Chinook salmon were listed as threatened under the U.S. Endangered Species Act.

Since that time, billions of dollars have been spent on programs to reverse population decline and improve smolt (seaward migrating juvenile salmon) survival through dams and turbines, in tributary habitats and in the Columbia River estuary[8]. Direct mortality at the dams has been successfully reduced[9–11], and survival of Snake River spring Chinook smolts that migrate through the eight-dam, 460 km hydrosystem (a series of four dams in the lower Snake River, and four in the lower Columbia River) is now typically >50%[12], higher than Chinook populations that migrate a similar distance in the adjacent undammed Fraser River[13].

As another measure to mitigate juvenile salmon losses at the Snake River dams, transportation experiments were initiated in 1965, with migrating salmon smolts collected at dams and transported via truck to a location downstream of Bonneville Dam (the final dam that smolts must pass during their seaward migration). Initial adult return rates of transported spring Chinook smolts relative to smolts that migrated in the river were promising, and the amount of straying observed in returning adults was low, and so transportation was continued as a management strategy intended to rebuild salmon populations[14–18]. This program is still running today[17,19], although juvenile salmon are now transported in large, purpose-built barges[14,18].

Survival in the transportation barge during the ~36 hour trip from Lower Granite Dam (LGR) to below Bonneville Dam is currently near 100%[20], while survival of in-river migrants is approximately 50%[12]. For this reason, if there is no difference in survival in subsequent life stages, survival to adult return of transported fish should be approximately double that of in-river migrants[21,22]. Transported smolts do not, however, return at double the rate of the in-river migrant smolts that pass through the eight dams, and in some years transported smolts returned at lower rates than in-river migrants, indicating that the transportation program may have reduced adult return rates of spring Chinook[1,19].

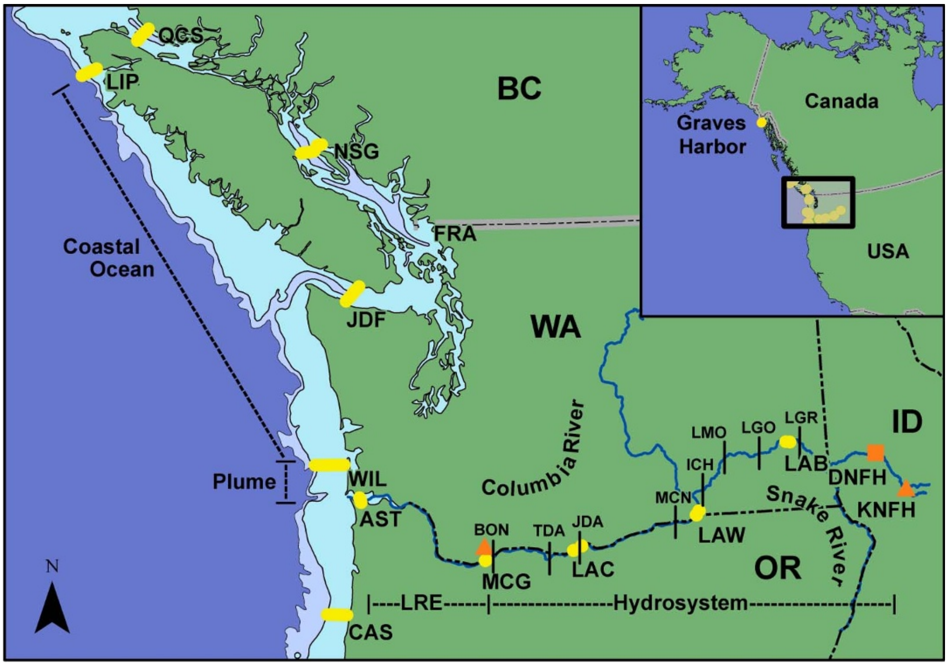

Figure 1 | Study area with acoustic tracking array (yellow dots and lines) and habitat designations (LRE=lower Columbia River and estuary). Spring Chinook smolts obtained at Dworshak National Fish Hatchery (DNFH; orange square) were either released at Kooskia NFH (KNFH) as in-river migrants, or transported and released into McGowans Channel (MCG), located just below Bonneville Dam (release sites are represented by orange triangles). Sub-arrays were deployed in Lake Bryan (LAB), Lake Wallula (LAW), Lake Celilo (LAC), MCG, Astoria (AST), Willapa Bay, WA (WIL), Lippy Point, BC (LIP), and Cascade Head, OR (CAS) and Graves Harbor, AK. No smolts were detected on POST sub-arrays in Juan de Fuca Strait (JDF), Northern Strait of Georgia (NSG), Queen Charlotte Strait (QCS), or on Fraser River (FRA) sub-arrays. The AST sub-array was not installed in 2006 and CAS was only deployed in 2009. Snake and Columbia River dams are indicated with vertical lines (LGR=Lower Granite, LGO=Little Goose, LMO=Lower Monumental, ICH=Ice Harbor, TDA=The Dalles, MCN=McNary, JDA=John Day, BON=Bonneville). Isobaths show the continental shelf edge at 200 m depth (offshore limit of the array during the study) and the 500 m depth interval.

Two metrics are typically used to evaluate the effectiveness of the transportation program: the "transport to in-river migrant ratio" (abbreviated in various ways, including "T/I" or "T:M"; we use T/I henceforth), and the "post-hydrosystem survival ratio" ("D"). Both ratios are currently estimated using fish that are tagged as juveniles with passive integrated transponder (PIT) tags, which are detected at selected dams when tagged fish return as adults. The T/I ratio is based on the proportion of tagged fish leaving LGR as juveniles that eventually return to be detected as adults at LGR after their ocean migration (smolt-to-adult return rate, or SAR). Thus, T/I is the ratio of the (LGR-to-LGR) SAR of transported fish ("T") to that of in-river migrants ("I"). When T/I >1, transportation provided a net benefit by producing higher return rates than leaving smolts to migrate downstream through the eight-dam hydrosystem. D is usually estimated as the component of the T/I ratio that represents relative estimated post-hydrosystem survival of transported and in-river migrant fish; however, D can be conceptualized as the ratio of return rates for transported and in-river fish, using Bonneville Dam (BON) as the starting point for smolts instead of LGR (BON-to-LGR SAR). When D<1, transported fish suffered more mortality after passing Bonneville Dam than their in-river counterparts. Thus, T/I includes survival downstream through the hydrosystem, during ocean migration, and during adult upstream migration through the hydrosystem, whereas D excludes mortality incurred by in-river smolts while migrating downstream. In principle, D is influenced by mortality that is caused by the transportation process but not expressed until after fish are released from the barge (i.e., "delayed" differential mortality), as well as by direct sources of mortality in the estuary and ocean that are not associated with delayed effects of transportation but have differential effect on transported and in-river migrant fish (see below).

Since the mid-1990s, transported spring Chinook smolts have had marginally better return rates than in-river migrants. The geometric mean $\widehat{T/I}$ for PIT-tagged wild Snake River spring Chinook was 1.19 (90% CI=0.89-1.58) for release years 1994 through 2009, indicating only a small benefit from transportation on average, while the geometric mean of $\hat{D}$ for these years was 0.61 (90% CI=0.49–0.75)[23], indicating that post-Bonneville Dam (or post-hydrosystem) survival of transported smolts was significantly lower than the in-river migrant smolts. Estimates of *T/I* and *D* were slightly higher for Dworshak National Fish Hatchery (NFH) spring Chinook (the population used in this study), but followed the same pattern. From 1997 to 2009, the geometric mean $\widehat{T/I}$ was 1.36 (90% CI=1.00–1.85), and the geometric mean of $\hat{D}$ was 0.75 (90% CI=0.60–0.94)[23], indicating that transported hatchery smolts also generally returned at a higher rate; however, when compared from Bonneville Dam to adult return, overall mortality was higher for transported smolts.

Vast resources have been allocated to investigate potential causes of differential post-hydrosystem mortality of transported and in-river migrating Chinook salmon smolts. Recent studies suggest that transportation-induced stress may lead to delayed mortality of transported smolts. These stressors include: i) physiological or behavioural stress associated with collection at juvenile fish bypass facilities through which transported fish must pass prior to entering the barge[22]; ii) stress associated with co-transportation with steelhead salmon, *O. mykiss*[24]; or iii) increased disease transmission in the transportation barge[25]. Transported smolts may also have reduced survival compared to in-river migrants as a result of direct rather than delayed effects of transportation. Muir et al.[26] hypothesized that smaller body size of transported smolts when released from the barges compared to smolts that migrated and fed for several weeks in the river may have lead to reduce survival. Confounded with this, earlier ocean entry of transported smolts may expose them to less favourable ocean conditions[26]. Upon adult return, impaired adult homing abilities for those that had been transported as smolts can lead to more straying into other river tributaries (leading to lower SAR) than for smolts that imprinted during in-river seaward migration[27].

Other studies failed to find a mechanism which may cause differential delayed mortality, variously reporting that transporting spring Chinook salmon smolts with increasing densities of juvenile steelhead did not result in lower smolt to adult return rates[28]; that transported smolts may be less susceptible to pathogens[29]; that susceptibility to pathogen transmission in the barge may be specifically related to the hatchery of origin[30]; and that transportation had little or no effects on auditory and olfactory systems of smolts[31].

Anderson et al.[32] provide a recent review of differential mortality studies in the Snake River Basin. Although there is no consensus on how differential mortality of transported spring Chinook salmon occurs, timing of transport is hypothesized to affect D[26] and the T/I ratio[33], with values for both being lowest early in the season. As a result, managers have delayed the start of the transportation program by several weeks in recent years[23].

If the early marine period is important for survival[34], then we would expect differential survival due to transportation to be manifested soon after ocean entry. It is therefore preferable to measure survival directly in the estuary and during the earliest period of the marine phase. This approach also allows us to avoid the potentially confounding effects of events occurring later in the marine life history. Additionally, by controlling for ocean-entry timing we are able to separate this direct effect on survival from the delayed effects of transportation.

The development of acoustic tags small enough to surgically implant into salmon smolts, and continental-scale telemetry arrays with which to track them, provides a technique for directly estimating freshwater and early marine survival after smolts migrate beyond the hydrosystem[13,35–37] and into the ocean[36,38–40]. Conceptually similar to the PIT tag system (a short range radio-frequency identification (RFID)-based system that can work at dams)[41], acoustic telemetry arrays can aid in determining when differential mortality occurs beyond the dams. Acoustic tags have three major advantages over PIT tags: 1) tag detections are not physically restricted to dams; 2) it is unnecessary to wait 2–3 years for the adult return of a cohort before making comparisons of the survival of transported and in-river groups; and 3) much smaller sample sizes can be used to achieve similar statistical precision because of the greater detection probability of acoustic tags. Although PIT tag studies have been essential for estimating SARs of transported and in-river migrating spring Chinook salmon, the marine survival of juvenile, immature, and maturing salmon over a 2–3 year period is confounded because SARs are estimated only upon adult return. The use of acoustic tags allows survival to be directly estimated during seaward migration in the lower river, estuary, and early marine life phase where transport-related effects on survival are most likely to be expressed.

Using a large-scale acoustic telemetry array, we tracked the movements of size-matched groups of acoustic tagged, one-year-old Chinook salmon smolts reared at Dworshak NFH (see Methods). Smolts were released directly into the river (IR) or transported (TR) by truck from the hatchery to the barges at LGR and then by barge 650 km to a release point approximately 10 km downstream of Bonneville Dam in 2006 ($n_{IR}=380$, $n_{TR}=203$), 2008 ($n_{IR}=395$, $n_{TR}=199$), and 2009 ($n_{IR}=389$, $n_{TR}=392$; Table 1). We then used the telemetry data to estimate and compare post-hydrosystem survival. In conventional transport operations, smolts are collected from dams in the Snake River and immediately barged downstream; therefore, transported smolts typically enter the ocean about three weeks earlier than their counterparts migrating in-river. For our experiment, we held transported groups at the hatchery until the in-river migrant groups were projected to arrive below Bonneville Dam, and timed their transport so release from the barge would roughly match the arrival of the in-river migrants at the release point below Bonneville Dam (McGowans Channel). This coordinated the migration timing of smolts from both treatment groups so that they experienced similar ocean conditions, and reduced the confounding of potential transportation effects such as stress[24], reduced growth opportunity[26], or increased disease transmission[25], with temporal variation in ocean survival[42,43]. We then calculated post-hydrosystem transport to in-river survival ratios in the three sequential post-hydrosystem habitats through which smolts co-migrate (lower Columbia River estuary, plume, and coastal ocean). We hypothesized that transported smolt survival is the same as in-river migrant survival in the co-migration pathway downstream of Bonneville Dam after controlling for body size and time of ocean entry; the alternative hypothesis is that survival of transported smolts is lower than in-river migrant survival. The results presented here report the first direct test of the hypothesized effect of transportation on subsequent survival of transported spring Chinook salmon smolts relative to in-river migrating smolts in the estuary and coastal ocean.

Table 1 | Summary of Dworshak NFH spring Chinook salmon smolts that were implanted with an acoustic tag and a passive integrated transponder (PIT) tag. All fish were transferred and tagged at Kooskia NFH. In 2006, fish were tagged with V9-6L acoustic transmitters. In 2008 and 2009, smolts were tagged with V7-2L acoustic transmitters. In-river (IR) migrating groups were released at Kooskia NFH; transported (TR) fish were released below Bonneville Dam. FL= fork length, g=grams

Year	Release Group	Release Date	# Tagged	Mean length at tagging (mm FL; range)	Mean mass at tagging (g; range)	Tag burden (% mass)
2006	IR 1	1-May	190	146.9 (140–208)	35.2 (26.9–117.5)	9.2 (2.6–11.5)
	IR 2	8-May	190	145.6 (140–192)	34.0 (27.4–83.7)	9.4 (3.7–11.3)
	TR 1	6-Jun	102	154.5 (141–168)	42.5 (30.8–55.3)	7.4 (5.6–10.1)
	TR 2	14-Jun	101	154.6 (140–168)	41.9 (28.5–55.5)	7.5 (5.6–10.9)
2008	IR 1	25-Apr	197	146.2 (130–159)	37.5 (23.3–55.5)	4.4 (2.9–6.9)
	IR 2	2-May	198	146.3 (131–159)	37.3 (23.9–52.7)	4.5 (3.0–6.7)
	TR 1	17-May	100	149.4 (135–159)	39.9 (26.5–52.3)	4.1 (3.1–6.0)
	TR 2	23-May	99	148.3 (131–158)	39.3 (26.2–51.8)	4.2 (3.1–6.1)
2009	IR 1	4-May	195	142.3 (130–162)	33.1 (21.9–54.7)	5.0 (2.9–7.3)
	IR 2	11-May	194	142.4 (130–164)	33.6 (23.7–54.1)	4.9 (3.0–6.8)
	TR 1	27-May	191	142.5 (130–164)	34.2 (22.3–59.1)	5.0 (2.5–7.7)
	TR 2	3-Jun	201	142.7 (130–164)	32.4 (22.4–54.8)	4.9 (2.7–7.2)

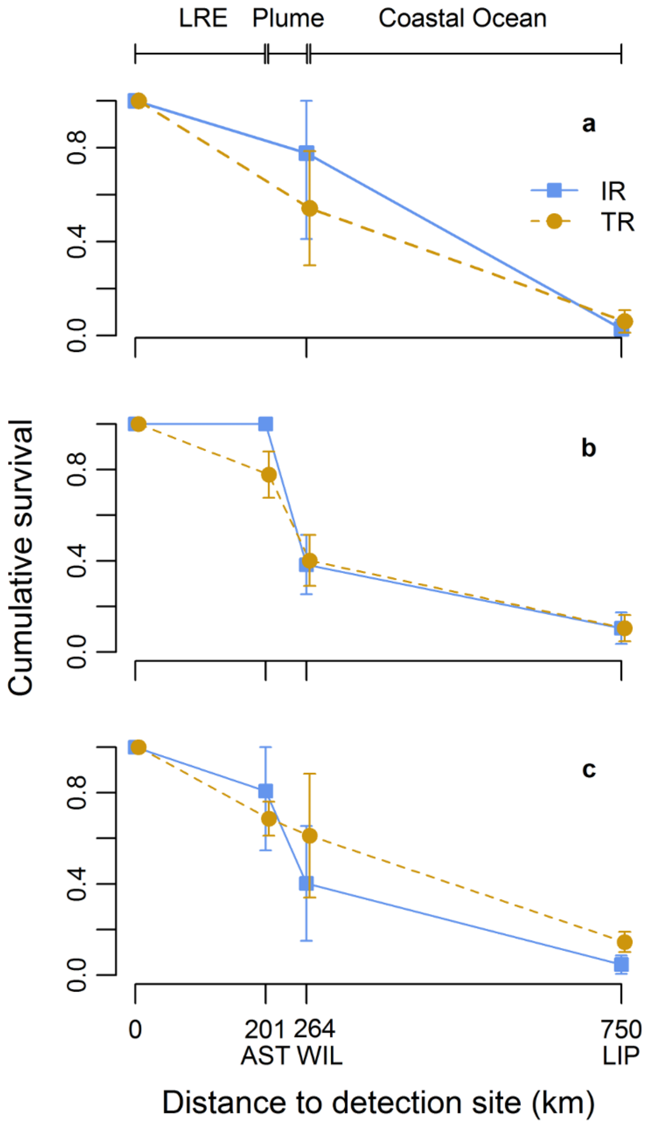

Figure 2 | Post-hydrosystem cumulative survival of in-river (IR) and transported (TR) Dworshak hatchery spring Chinook salmon smolts to Astoria (AST), Willapa Bay, WA (WIL), and Lippy Point, BC (LIP; error bars show 95% confidence intervals) in 2006 (a), 2008 (b), and 2009 (c). Kilometre 0 is the location of the McGowans Channel sub-array downstream of Bonneville Dam where IR smolts were detected, and where TR smolts were released from the barge. The Astoria sub-array was not installed in 2006. Data points were adjusted to prevent overlap of confidence intervals.

Results

Estimated survival from Bonneville Dam to the northwestern end of Vancouver Island ranged between 0.03–0.14 for both treatment types during our three year study (Fig. 2; Table 2), with highest survival in the lower Columbia River and estuary (LRE) in 2008 and 2009 (0.69–1.0), and in the LRE and plume combined in 2006 (0.54–0.78; Fig. 3, Table 3). In all years, survival was lowest in the coastal ocean between Willapa Bay, WA, and Lippy Point, BC (0.04–0.29; Fig. 3; Table 3). Estimated survival in the plume was intermediate despite the short migration distance (0.40–0.51), except in 2009, when transported smolts had the highest survival through that migration segment (0.87). Estimated detection probabilities of the acoustic receiver sub-arrays are presented in Supplementary Table S1.

Our finding that most mortality occurs in the coastal ocean hinges on our assumption that the detection probability of the Lippy Point sub-array, p_{LIP}, was similar to other Pacific Ocean Shelf Tracking (POST) marine sub-arrays that could be directly assessed (too few smolts reached the final sub-array in Alaska, 1000 km distant, to allow direct estimation of p_{LIP}; see Methods and Supplementary Table S2). If our assumption is incorrect, then survival estimates in the coastal ocean (Willapa Bay to Lippy Point) will be under or overestimated. We looked more closely at the sensitivity of survival estimates in the coastal ocean relative to p_{LIP} (Supplementary Fig. S1), and found that coastal ocean survival remains low for both TR and IR groups over a range of assumed values, and our conclusions do not change. In any event, because both TR and IR smolts were implanted with the same tag type, the relative survival of the two groups should be invariant because p_{LIP} should be the same for both groups.

Transported smolts did not survive as well as the IR migrants after release in the LRE and plume combined in 2006, and in the LRE in 2008 and 2009 (Table 3; Fig. 3), and the resulting ratios (TR/IR) for individual years were significantly <1 in 2006 ($R=0.70$, $SE=0.12$, $z=-2.55$, $p=0.02$) and 2008 ($R=0.78$, $SE=0.05$, $z=-4.3$, $p<0.01$; Table 2), indicating that TR smolts had lower relative survival. The estimated survival ratios in the LRE for 2008 and 2009 combined ($R=0.86$, $SE=0.10$, $z=-1.31$, $p=0.10$), and LRE and plume combined in all years ($R=0.86$, $SE=0.11$, $z=-1.16$, $p=0.12$) were also <1, but this effect was not significant (Table 2).

Once in the plume and coastal ocean, transported smolts survived either better than or the same as the IR groups. In the plume (2008, 2009, and 2008 and 2009 combined) all ratios were >1. In the coastal ocean, survival ratios were >2 in 2006, 2009, and all years combined, indicating that TR smolts had twice the survival of IR smolts from Willapa Bay to Lippy Point. In 2008, the survival ratio in the coastal ocean was 0.87 ($SE=0.35$), although this ratio was not significantly less than 1 ($z=-0.35$, $p=0.36$).

Despite depressed survival of TR smolts in the LRE, the overall TR/IR post-hydrosystem survival ratio across all three habitats from McGowans Channel to Lippy Point was >2 in 2006 and >3 in 2009, i.e., 2–3 times greater survival for TR smolts. In 2008 the ratio was 0.85, but again this was not significantly less than 1 ($z=-0.40$, $p=0.35$). The total ratio averaged across all three years was 1.84 ($SE=0.65$), indicating that TR smolts generally had higher post-hydrosystem survival compared to IR smolts. If differential mortality caused by transportation occurred in TR smolts soon after release and the differential persisted for one month, the MCG-LIP ratios would have been less than 1.0. Therefore, our results demonstrate that when IR and TR smolts of approximately the same size enter the ocean concurrently, survival of TR smolts is comparable or better than IR smolts, which is inconsistent with hypotheses that decreased post-hydrosystem survival to adult return of transported fish is due to stress caused by transportation.

Discussion

Transported spring Chinook smolts typically survive to return as adults at rates only slightly better than in-river migrants, despite avoiding the approximately 50% mortality experienced during the 460 km migration down the eight-dam FCRPS[23]. If differential delayed mortality caused by stressful transportation is expressed after release within the first month of life in the coastal ocean, we would expect to see reduced post-hydrosystem survival for transported smolts compared to smolts that migrated in-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 one month after ocean entry, we did not observe lower survival for TR smolts. Thus, our results do not support the hypothesis that transportation-induced stress leads to higher mortality of smolts in the early marine period. It is likely that it is the accelerated timing of ocean entry which occurs during conventional transport practice that leads to differences in post-hydrosystem SARs

Table 2 | Post-hydrosystem survival estimates (S), survival ratios ($R=S_{TR}/S_{IR}$), and z-test results for in-river (IR) and transported (TR) Dworshak spring Chinook salmon smolts. In-river fish were released at Kooskia NFH; transported fish were released below Bonneville Dam. LRE= lower Columbia River and Estuary. See Figure 1 for migration segment abbreviations. We could not estimate estuary and plume survival independently in 2006 because the Astoria sub-array was not deployed that year. Bold p-values indicate z statistics significantly less than 1

Habitat	Migration Segment	Years used in survival estimation	S_{TR}	SE (S_{TR})	S_{IR}	SE (S_{IR})	R	SE (R)	Z-stat	p-value
LRE & plume	MCG-WIL	2006	0.54	0.12	0.78	0.19	0.70	0.12	−2.11	**0.02**
Coastal ocean	WIL-LIP	2006	0.11	0.05	0.04	0.03	2.96	2.35	1.37	0.91
Total post-hydrosystem	MCG-LIP	2006	0.06	0.02	0.03	0.02	2.07	1.64	0.92	0.82
LRE	MCG-AST	2008	0.77	0.05	1.00	0.00	0.77	0.05	−3.93	**<0.01**
Plume	AST-WIL	2008	0.51	0.07	0.40	0.07	1.27	0.24	1.27	0.90
Coastal ocean	WIL-LIP	2008	0.25	0.07	0.29	0.09	0.87	0.35	−0.35	0.36
Total post-hydrosystem	MCG-LIP	2008	0.10	0.03	0.12	0.04	0.85	0.36	−0.40	0.35
LRE	MCG-AST	2009	0.69	0.04	0.82	0.15	0.84	0.16	−0.92	0.18
Plume	AST-WIL	2009	0.87	0.21	0.48	0.17	1.81	0.53	2.01	0.98
Coastal ocean	WIL-LIP	2009	0.24	0.07	0.12	0.06	2.06	1.09	1.36	0.91
Total post-hydrosystem	MCG-LIP	2009	0.14	0.02	0.05	0.02	3.12	1.56	2.28	0.99
LRE	MCG-AST	2008 & 2009	0.75	0.03	0.88	0.10	0.86	0.10	−1.31	0.10
Plume	AST-WIL	2008 & 2009	0.60	0.07	0.41	0.06	1.48	0.21	2.83	1.00
LRE & plume	MCG-WIL	All years	0.52	0.05	0.61	0.08	0.86	0.11	−1.16	0.12
Coastal ocean	WIL-LIP	All years	0.21	0.04	0.10	0.03	2.15	0.75	2.20	0.99
Total post-hydrosystem	MCG-LIP	All years	0.11	0.02	0.06	0.02	1.84	0.65	1.73	0.96

typically observed between transported and in-river migrating spring Chinook smolts. As Muir et al.[26] hypothesized, altered timing of ocean entry for transported smolts, which arrive 2–4 weeks earlier than in-river migrants, may place them into less favourable ocean conditions.

To further test this hypothesis, we transported a single group of acoustic tagged smolts (n=196) on April 17, 2009, approximately five weeks earlier than the other two groups transported that year. Smolts were transported several days after tagging, to allow recovery, (but were not delayed at the hatchery) in order to simulate

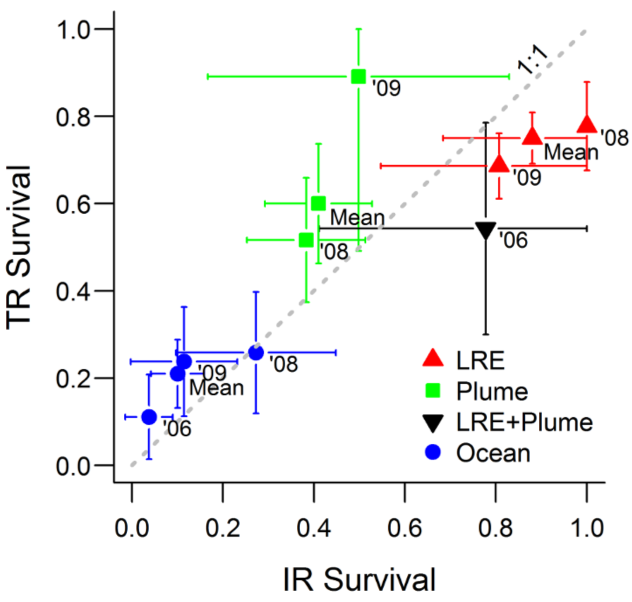

Figure 3 | Comparative survival of in-river (IR) and transported (TR) Dworshak hatchery spring Chinook smolts (error bars are 95% confidence intervals). The dashed 1 : 1 line represents equal survival of both treatment types; data points falling below the line indicate lower survival of TR fish. The Astoria sub-array was not deployed in 2006; therefore, we could not separate Lower Columbia River and estuary (LRE) survival from Plume survival in 2006.

conventional transportation practice early in the migration season. These early transport (T_0) smolts had noticeably different migration behaviours compared to the TR groups held for several weeks and then transported[44]. Overall survival from release to Lippy Point was 0.08 (SE=0.02) for the early transport group, and 0.14 (SE=0.02) for the later released TR groups. Thus, survival of transported smolts that were released earlier, and therefore entered the ocean earlier, was only 58% of the delayed-entry transport groups. As estuarine survival was nearly identical (T_0=0.70, SE=0.05; TR=0.69, SE=0.04), this survival difference occurred in the plume and coastal ocean.

Our results lend support to the altered ocean entry timing hypothesis. Although transportation apparently caused negligible harm to these smolts, altered ocean arrival timing will continue to be a consequence of conventional transport practice unless transportation is only initiated when ocean conditions are more favourable for survival.

Several factors may have influenced our finding that transported fish did not experience reduced mortality relative to in-river migrants in the first month of ocean life. First, all smolts in the study were grown to a larger size (≥140 mm FL in 2006, ≥130 mm FL in 2008 and 2009) to accommodate the acoustic transmitters and, as a result, size at release was larger (but see Supplementary Fig. S2) and timing of release of both IR and TR groups was later than for typical Dworshak spring Chinook. There is some evidence that larger smolt size may lead to increased SARs for hatchery Chinook salmon[45]. Juvenile migration timing may also play a significant role in determining subsequent SARs. Wild Snake River spring Chinook migrating seaward early in the season (until mid-May) had high and relatively stable SARs, which then decreased substantially for smolts that migrated later in the season[42]. Adult return rates of transported smolts declined later in the season as well; however, relative to in-river migrants, transported smolt SAR was higher (i.e., T/I ratios increased)[26,33]. Thus, it is possible that larger body size or later migration timing may have ameliorated stress caused by transportation.

Second, there were some differences in ocean entry timing and mean body size at tagging for TR and IR smolts (in 2006 only). In all years, we attempted to release TR fish below Bonneville Dam at approximately the time IR fish passed Bonneville Dam so that smolts could co-migrate and experience common estuarine and ocean conditions, minimizing the potential confounding of variable ocean survival conditions with transportation. We also attempted to size

Table 3 | Estimated survival ($\hat{\phi}$) of transported and in-river migrant Dworshak spring Chinook smolts by habitat. Confidence intervals (95%) were estimated using the profile likelihood method. All fish were transferred and tagged at Kooskia NFH. In-river (IR) migrating groups were released at Kooskia NFH; transported (TR) fish were released below Bonneville Dam. See Figure 1 for habitat designations. Counts of fish detected on each sub-array are reported in Supplementary Table S2. LRE=lower Columbia River and estuary. (a) Smolts were transported via barge around the hydrosystem, therefore survival was set to 1. (b) We could not estimate estuary and plume survival independently in 2006 because the Astoria sub-array was not deployed that year

	Transported			In-river		
	$\hat{\phi}$	SE ($\hat{\phi}$)	95% CI	$\hat{\phi}$	SE ($\hat{\phi}$)	95% CI
Hydrosystem (646 km)						
2006	1 [(a)]			0.40	0.04	0.32–0.49
2008	1 [(a)]			0.30	0.03	0.24–0.35
2009	1 [(a)]			0.41	0.04	0.33–0.49
LRE+Plume (264 km) [(b)]						
2006	0.54	0.12	0.37–0.86	0.78	0.19	0.52–1.0
LRE (201 km)						
2008	0.77	0.05	0.68–0.88	1.0	0	0.85–1.0
2009	0.69	0.04	0.61–0.78	0.82	0.15	0.59–1.0
Plume (63 km)						
2008	0.51	0.07	0.38–0.67	0.40	0.07	0.28–0.55
2009	0.87	0.21	0.58–1	0.48	0.17	0.24–0.91
Ocean (485 km)						
2006	0.11	0.05	0.04–0.23	0.04	0.03	0.01–0.12
2008	0.25	0.07	0.14–0.40	0.29	0.09	0.14–0.50
2009	0.24	0.07	0.15–0.39	0.12	0.06	0.03–0.30

match the IR and TR treatment groups. Nevertheless, IR smolts arrived at Bonneville Dam two to three weeks earlier than the TR groups in 2006, owing to high river flows, and TR smolts were 8–9 mm larger on average at tagging then the IR smolts. As plume conditions can change rapidly[46] (potentially within two to three weeks), the increased survival of TR smolts in the coastal ocean in that year may be confounded with mismatched timing of ocean entry[42]; TR smolts may have encountered different, or more favourable, ocean conditions when they reached the ocean several weeks after the IR smolts. Transported smolts may have also had a slight size advantage over the IR smolts in 2006, but we found that within the size range of smolts that we tagged, survival was not a function of body size[47,48]. In 2008 and 2009, the time of ocean entry and mean body size was similar for both groups.

Third, there is some uncertainty as to whether smolts may have migrated around the coastal ocean sub-arrays, as individuals were detected on the farthest offshore receiver nodes at Willapa Bay, and several tagged fish that returned to the Columbia River as adults (which were detected by PIT tag detectors at the dams) were not detected as smolts on the ocean sub-arrays. In all years, however, the majority of the fish that were detected from both treatment types migrated between 20–30 km offshore and within the boundaries of the Willapa Bay sub-array (Supplementary Fig. S3). At the Lippy Point sub-array further along the migration pathway, detections of acoustic-tagged smolts were almost completely confined to the inner half of the continental shelf in all years, although some returning adults were not detected as smolts on this sub-array. The movement of some individuals off the shelf, or non-detection of individuals that migrated over the sub-arrays on the shelf, would bias survival estimates low. As the Dworshak spring Chinook population generally has a very low SAR, very few of our acoustic tagged adults or jacks were detected upon return (juvenile migration year 2006=0, 2008_{IR}=2, 2008_{TR}=3, 2009_{IR}=1, 2009_{TR}=5) which precluded us from quantifying this potential bias; however, unless a different proportion of smolts from each treatment type was detected, the relative survival comparison between TR and IR smolts remains unaffected.

Lastly, there is a possibility that yearling Chinook smolts may migrate south upon ocean entry. McMichael et al.[49], found that acoustic tagged and tracked yearling Chinook smolts were detected within the Columbia River plume up to ~15 km to the west and south of the river mouth when surface ocean currents were more southerly in 2010. To address this concern, we deployed a sub-array south of the Columbia River mouth near Cascade Head, OR, in 2009; none of the smolts tagged in this study were detected on this sub-array (131 km distant), except for two smolts (1%) from the 2009 early transport (T_0) group, demonstrating that few yearling Chinook smolts migrate south upon ocean entry.

Estimated survival of IR migrants in the LRE was high in all years, ranging between 0.82–1.0, consistent with other telemetry studies[37,49,50]. Transported smolt survival was slightly depressed relative to the IR group immediately following release into the LRE, but subsequent survival in the plume and coastal ocean was comparable or better. With all habitats (i.e., segments of the migration pathway) combined, the three year mean post-hydrosystem survival estimate to Lippy Point was substantially higher for TR smolts.

Reduced survival of TR smolts following release into the LRE prompted us to look more closely at post-release mortality, i.e., mortality that occurs in the first migration segment following release, as this could be confounded with transportation-induced delayed mortality. TR smolts were transferred directly from the hatchery to the barge and then to the lower river downstream of Bonneville Dam; therefore, we hypothesized that transported smolts experienced initially elevated and similar levels of mortality after release into the LRE compared to IR smolts because they had never encountered predators[51]. In-river smolts, which would also be similarly naïve after release from the hatchery, would have experienced this additional elevated mortality in the Clearwater River, not in the LRE, thus explaining the reduced survival of the TR smolts relative to the IR smolts between Bonneville Dam and Willapa Bay in 2006, and between Bonneville Dam and Astoria in 2008 an 2009. To statistically compare post-release mortality for IR and TR smolts, we used a Monte Carlo procedure to assess the mortality rate in the first migration segment following release (Supplementary Fig. S4). In all three years, there was no statistical difference in post-release mortality rate per km of travel for TR smolts from below Bonneville Dam to their first detection site compared to IR smolts from the hatchery in the Clearwater River to their first detection site below LGR (Lake Bryan). Thus, both treatment types suffered similar loss rates following release. We interpret this period of initially high post-release mortality as likely due to culling of less fit or less wary smolts by predators.

Our directly estimated early marine survival probabilities are consistent with interannual predictions of juvenile salmon survival based on coastal ocean indicators[52], supporting the hypothesis that transported smolts may experience increased mortality upon early entry into the coastal ocean, particularly in years when early marine survival rates are lower than hydrosystem survival. Post-hydrosystem survival rates to adult return of PIT tagged only, transported Dworshak spring Chinook smolts[23] was substantially lower than in-river migrant PIT tagged smolts for outmigration years 2006 ($\hat{D}$= 0.60, CI=0.43–0.83) and 2009 ($\hat{D}$=0.61, CI=0.37–0.95), but less so in 2008 ($\hat{D}$=0.84, CI=0.63–1.12), when ocean conditions were particularly favourable for juvenile salmon survival[52]. Our estimates of coastal marine survival from Willapa Bay to Lippy Point for acoustic tagged smolts were relatively low in 2006 and 2009 and highest in 2008 (for both treatment types), and in 2008 only, survival estimates of IR smolts in the hydrosystem and coastal ocean were comparable (0.30 from release to Bonneville Dam, ~650 km; 0.29 from Willapa Bay to Lippy Point, ~530 km). In contrast, coastal ocean survival was only 1/3rd–1/10th hydrosystem survival in 2006 and 2009. Thus, the increased *D* estimate for PIT tagged smolts in 2008 could simply be the result of transferring transported smolts between two habitats with similar survival rates. In 2006 and 2009, transported PIT tagged Dworshak smolts may have spent several additional weeks exposed to higher ocean mortality rates than the in-river migrants experienced in the hydrosystem, potentially providing a simple explanation for why $\hat{D}$ ratios were <1 in 2006 and 2009. This is an important finding, in that efforts to reduce stress and disease transfer during barging are likely to fail if the true cause of reduced adult returns is increased exposure to poor ocean conditions.

A better understanding of the mechanisms causing differential mortality should lead to improved management decisions. The results of our study suggest that differential ocean entry timing is the most likely cause of D ratios less than 1, not transportation-induced stress. Strategies such as delaying the start of transportation, or using ocean indicators, direct early marine survival estimates, and climate-based predictive models[53] to potentially make real-time decisions as to when to start or end transportation may therefore be effective measures that could increase SARs for some Chinook populations.

Methods

Smolt acquisition and acoustic tagging. We used spring Chinook salmon smolts reared at the Dworshak NFH, on the Clearwater River (a tributary of the Snake River) as the source population; however, for logistical purposes we transferred smolts to a nearby hatchery (Kooskia NFH) for tagging (See Supplementary Methods). All work involving live fish was annually reviewed and pre-approved as meeting or exceeding the standards laid out by the Canadian Council on Animal Care. Annual reviews of submitted protocols and approvals were made by the Animal Care Committee of Vancouver Island University, Nanaimo, BC, Canada (application # 2006-08R, 2006-08R-2, 2009-11R).

In 2006, we used individually identifiable VEMCO V9-6L coded acoustic transmitters (9×21 mm, 3.1 g in air, 2 g in water) and in 2008-09 we used smaller V7-2L transmitters (7 mm×20 mm, 1.6 g in air, 0.75 g in water). The same surgical protocol was used in all years for both treatment types. A brief description is given in the Supplementary Methods with more details provided in Rechisky and Welch[47].

In each year, approximately 600–800 smolts were surgically implanted with acoustic transmitters (Table 1). We attempted to size-match tagged fish within and between treatment groups in each year while randomly assigning fish to treatment groups. In 2008 and 2009, mean FL, mass, and tag burden (tag mass as a percent of body mass) were similar both between release groups and across treatment types; however, in 2006 the TR groups were 8–9 mm larger than IR groups on average and thus tag burden was less for the transported groups (Table 1). These tag burdens generally lie within maximum recommended tag burdens for salmon smolts[54,55] and assessment of size at release of tagged animals relative to size at release of survivors reaching Willapa Bay showed no distortions in the distributions[48]. Further, 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[47,48]. In 2006 and 2008, we released twice as many IR as TR smolts to compensate for mortality in the Clearwater River and during hydrosystem migration and to obtain roughly balanced sample sizes upon arrival below Bonneville Dam; however, in 2009 additional tags were available to increase the number of transported smolts. The IR groups were released from Kooskia NFH into Clear Creek which flows successively into the Clearwater, Snake, and Columbia rivers (Fig. 1). Distance to Bonneville Dam was 637 km. Transported fish were held for up to several weeks at Kooskia NFH until in-river migrant groups were estimated to be nearing Bonneville Dam, and were then transferred by truck to a barge at Lower Granite Dam. Barge transport time to below Bonneville Dam (a distance of 470 km) was approximately 36 hours. Smolts were released from the barge ~7–12 km downstream of Bonneville Dam in the evening between 19:10–22:50. Distance to the Columbia River mouth at Cascade Head , OR was 222–227 km, depending on the release site. Observers on the barges reported no mortalities of acoustic tagged fish in any year of the study and we assumed survival during transport was 100%. Release dates, fish size, and tag burdens are reported in Table 1; sex was not determined.

Acoustic array elements and location. The marine elements of 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 receiver sub-arrays (referred to as "sub-arrays") extending from near-shore out to ~200 m depths. The receivers recorded the date and time that acoustic transmitters (tags) were detected, and these detections were used to estimate survival to each sub-array. During the study, the array extended from coastal Washington through southern British Columbia and up to southeast Alaska (Fig. 1). Sub-arrays were also deployed within the Snake and Columbia rivers (see Welch et al.[56], Porter et al.[57], Porter et al.[44] for site-specific details on sub-array performance). This design allowed us to track the smolts for 2,500 km from the release site in the Snake River through the hydrosystem, lower Columbia River and estuary (LRE), plume, and coastal ocean to Graves Harbor, Alaska. We report hydrosystem survival of IR smolts to the sub-array located in the lower Columbia River at McGowans Channel (MCG) at river kilometre (rkm) 224 (10 km below Bonneville Dam). For both treatment types, we report survival in the LRE and plume from MCG to Willapa Bay, WA (WIL; 264 km beyond Bonneville Dam) and in the coastal ocean from WIL to Lippy Point, BC (LIP; 749 km beyond Bonneville Dam). In 2008 and 2009, an additional sub-array was deployed in the Columbia River estuary at Astoria, WA (AST; 201 km below Bonneville Dam), allowing 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 sub-array. Although the plume technically begins at the river mouth (not Astoria), the distance between the sub-arrays sited at Astoria and Willapa Bay was only 63 km and encompassed the plume. In 2009, an additional sub-array was deployed in the coastal ocean south of the Columbia River mouth at Cascade Head, OR; no smolts from our treatment groups were detected on this array.

Data analysis. All acoustic detection data from the array were first screened for potential false positive detections, which were rare; excluded data typically formed <0.1% of the total recorded detections. In-river fish were defined as any acoustic tagged fish migrating in the river, regardless of their specific route through the dams (e.g. spill, bypass or turbine). We excluded from the analysis a few IR smolts inadvertently collected and transported from lower Snake River dams (2006: 16; 2008: 0; 2009: 3).

Survival estimation. For each year of the study, capture (detection) histories for each tagged individual were formed and estimates of survival and detection probability and their associated standard errors were calculated using a suite of models that were special cases of the Cormack-Jolly-Seber (CJS) model for live-recaptured animals implemented with Program MARK[58]. Confidence intervals were estimated using the profile likelihood method. We estimated goodness of fit (see Supplementary Methods) and then estimated apparent survival (ϕ) for each treatment type between each sub-array. We allowed detection probability (p) to vary for each treatment type and sub-array in freshwater, but only by sub-array in the ocean (i.e., a common p parameter was estimated for TR and IR groups for coastal ocean sub-arrays using the full data set). We then estimated cumulative post-hydrosystem survival to Lippy Point as the product of the segment-specific survival estimates for each treatment type, and estimated the variance with the Delta Method.

As a final step, we estimated survival for each treatment type across all three years of the study. We used a reduced CJS model where a common survival probability was estimated for each treatment type for all years, 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. We refer to the estimate of the common parameter as the 'average' survival across years. Because the Astoria sub-array 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 for all years (2006, 2008, 2009) in the LRE and plume combined, and another to estimate average survival for 2008 and 2009 combined in the LRE and in the plume as separate migration segments. We used the former model to estimate average survival across all three years in the coastal ocean. We then used these average survival estimates, as well as the survival estimates produced for individual years, to statistically compare post-hydrosystem survival of the TR and IR smolts as described below.

For all sub-arrays, we recognized CJS model assumptions: every tagged individual has equal survival probability and equal probability of detection following release, sampling periods are instantaneous, emigration is permanent, and tags are not lost. Assessments of tag loss, tagging induced mortality, tag operational lifespan, 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[44].

For coastal ocean sub-arrays that were unbounded offshore, we required three additional assumptions: i) fish departing the Columbia River swam north; ii) their migration was confined to the coastal zone spanned by the sub-arrays; and iii) detection probability of the Lippy Point sub-array was 0.90 for the V9 tag used in 2006 and was 0.67 in 2008 and 2009 when the less powerful V7 tag was used. Assumptions (i) and (ii) 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 upon leaving the river[59–63]. As well, we deployed a sub-array 131 km south of the Columbia River mouth at Cascade Head, OR (Fig. 1) in 2009 to validate assumption (i); only two acoustic tagged smolts, both from the early transported (T_0) group, were detected on this southern sub-array.

The detection probability of the Lippy Point (NW Vancouver Island) sub-array was not estimable using standard CJS methods because too few tagged smolts were detected in Alaska each year to provide adequate information ($N_{2006}=2$ IR; $N_{2008}=1$ IR; $N_{2009}=1$ TR). In order to estimate survival to Lippy Point, we assumed the specific values listed in assumption (iii) given the performance of similar sub-arrays for which it was possible to use CJS to estimate detection probability. The basis for this assumption and the implications of its violation are discussed in the Supplementary Methods. We conclude that as long as the real detection probability is similar for the TR smolts and the IR controls, our key scientific test of whether TR smolts have lower post-hydrosystem survival than IR controls is not affected.

Post-hydrosystem survival ratios. To compare post-hydrosystem survival of TR and IR smolts, we calculated survival ratios of TR smolts that were released near the McGowans Channel sub-array, to the post-hydrosystem survival of IR smolts from McGowans Channel onwards. This approach excluded upstream mortality for IR smolts and allowed a survival comparison within common migration segments for the two groups. To assess the evidence for lower TR survival, we tested whether the survival ratios were significantly less than 1 (i.e., whether TR smolts had lower survival than IR smolts) on the anti-log scale or less than 0 on the log scale. On the log scale, the z-statistic can be formed as:

$$\hat{z}=\frac{ln(\hat{R}_i)-0}{\widehat{SE}(ln(\hat{R}_i))}=\frac{ln(\hat{R}_i)}{\widehat{SE}(\hat{R}_i)/\hat{R}_i} \quad (1)$$

Where $\hat{R}_i$ is the estimated survival ratio (TR smolts to IR smolts) for the common migration segments below Bonneville Dam, and $\widehat{SE}(\hat{R}_i)$ is the standard error of the ratio as determined by the Delta Method. We tested the z-statistic at the 5% significance level.

We used the z-test to compare the survival of TR smolts to IR smolts in each of the common migration segments: i) LRE and plume ($S^{TR}_{MCG-WIL}/S^{IR}_{MCG-WIL}$) in 2006 and for all years combined; ii) coastal ocean ($S^{TR}_{WIL-LIP}/S^{IR}_{WIL-LIP}$) for individual years and for all years combined; iii) LRE alone ($S^{TR}_{MCG-AST}/S^{IR}_{MCG-AST}$) for 2008 and 2009 and for 2008 and 2009 combined; and iv) plume ($S^{TR}_{AST-WIL}/S^{IR}_{AST-WIL}$) for 2008 and 2009 and for 2008 and 2009 combined, when the Astoria sub-array was in place (see Fig. 1 for sub-array abbreviations). We also calculated a post-hydrosystem survival ratio which included all migration segments (v) LRE, plume, and coastal ocean, ($S^{TR}_{MCG-LIP}/S^{IR}_{MCG-LIP}$), for all individual years and for all years combined.

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Author contributions

DWW conceived the experiments. ELR, MJS, PMW, and JLM conducted the fieldwork. ELR, ADP and DWW analyzed the data. ELR wrote the manuscript. All authors reviewed and edited the manuscript.

Additional information

Supplementary information accompanies this paper at http://www.nature.com/scientificreports

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