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PRIMARY RESEARCH PAPER

Contrasting life-cycle impacts of stream flow on two Chinook salmon populations

David L. Arthaud · Correigh M. Greene · Kimberly Guilbault · James V. Morrow Jr.

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Abstract Stream flow affects many aspects of freshwater fish biology, but the extent to which variation in stream flow influences productivity of anadromous salmonid populations across their entire life cycle is not well known. We compared relationships of stream flow and productivity for Chinook salmon (*Oncorhynchus tshawytscha*) from two systems in the Salmon River basin in Idaho: the Lemhi River, a watershed subjected to intensive water use for irrigation, and Marsh Creek, a drainage with a natural hydrograph. We estimated rates of productivity based on monitoring at four life stages: the number of eggs initiating each cohort, juveniles migrating from the natal tributary past an outmigrant trap, smolts surviving to the Snake River, and adults returning to spawn. Using model selection techniques, we examined whether river flow experienced during these life stages explained variation above and beyond predictors of climate associated with each stage. In the Lemhi River, tributary stream flow during early residence exhibited strong correlations with egg–trap, egg–smolt, and egg–adult return rates, and was consistently a better predictor of productivity than stream flow occurring during late summer. Model selection indicated that early rearing flow was the single best predictor of both egg–trap and trap–smolt transition rates in the Lemhi River, and path analysis revealed a strong set of pathways linking rearing flow to adult return rate primarily through egg–trap productivity. These patterns were much less strongly exhibited or nonexistent in Marsh Creek. However, for both populations, migration flow in the Columbia River was the best predictor of smolt–adult return rates. Potentially confounding climatic variables exhibited relatively weak effects upon both early life histories and tributary flow, but were included in the best models of migration flows and smolt–adult return rate. These results suggest that effects of stream flow on juvenile salmonids in flow-altered systems can have substantial impacts on returning adults.

Keywords Stream flow · Snake River · Chinook salmon · Survival

Introduction

Stream flow is a primary habitat component and driver of processes which form and maintain freshwater

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D. L. Arthaud · J. V. Morrow Jr. (✉)
National Marine Fisheries Service, 10095 W Emerald Street, Room: 180, Boise, ID 83704, USA
e-mail: Jim.morrow@noaa.gov

C. M. Greene · K. Guilbault
Division of Environmental Conservation, Northwest Fisheries Science Center, 2725 Montlake Blvd East, Seattle, WA 98112, USA

habitat necessary to meet the biological needs of aquatic organisms (Poff et al., 1997; Bunn & Arthington, 2002). However, flow characteristics can affect fish populations and their habitat in a variety of ways. Variations in stream flow can affect water quality (Ebersole et al., 2001; Poole & Berman, 2001; Dahm et al., 2003; Ebersole et al., 2003; May & Lee, 2004; Miller et al., 2008), amount of drifting invertebrates (Townsend & Hildrew, 1976; Elliott, 2002; Boulton, 2003; Lake, 2003; Nislow et al., 2004; Harvey et al., 2006; Miller et al., 2007), and refugia available for rearing salmonids (Hardy et al., 2006). Studies have identified positive relationships between stream flow volume and a variety of fish population parameters including feeding and condition factor (Weisberg & Burton, 1993), population biomass (Nislow et al., 2004; Harvey et al., 2006), growth of individuals (Nislow et al., 2004; Harvey et al., 2006; Alonso-González et al., 2008), migration survival (McCormick et al., 1998; Connor et al., 2003), and year class strength (Ricker, 1975; Scarnecchia, 1981; Elliott et al., 1997; Mitro et al., 2003). Studies have also identified negative relationships between stream flow volume and year class strength (Cattanéo et al., 2002; Smith, 2000; Jensen & Johnsen, 1999; Lobón-Cerviá, 2003) and Alonso-González et al. (2008) demonstrated negative impacts of both floods and drought on juvenile salmonids. However, impacts of flow across the life cycle have been difficult to quantify, particularly for species capable of large-scale movements.

Pacific salmon (*Oncorhynchus* spp.) are highly migratory fishes that are often affected by human caused reductions in stream flow. Many salmon populations spawn and rear in semi-arid basins in the Pacific Northwest, which have a long history of natural variation in water supply (Dettinger & Diaz, 2000). However, the predictable seasonal patterns of stream flow to which salmon have evolved have been altered by reservoir construction for hydropower and by diversions for irrigated agriculture, mining, municipal, and other uses. Quantifying the overall biological impacts of changes to stream flow upon populations is necessary to describe flow regimes that will maintain self-sustaining salmon populations, yet the potential effects of altered stream flows might be expected to be muted by variation in survival at other life stages, or by regional climatic variation (Lawson et al., 2004).

In this study, we examined the influence of natal tributary stream flow (tributary flow) on two well-monitored independent spawning populations of the Snake River spring/summer Chinook salmon (*Oncorhynchus tshawytscha*) in Idaho's Salmon River drainage. Many tributaries of the Salmon River have been diverted for irrigated agriculture, mining, municipal, and other uses to the extent that stream flows during the growing season are a fraction of what they were historically (Lichatowich & Mobrand, 1995; Brannon et al., 2004). However, the Salmon River drainage also contains vast undeveloped areas with whole river systems that still have natural hydrographs. The two systems we examined, the Lemhi River and Marsh Creek, represent endpoints in the spectrum of flow management from heavily utilized to nearly pristine. The Lemhi River watershed has numerous water diversions for irrigated agriculture, while the Marsh Creek watershed is essentially undeveloped with a natural hydrograph. Extensive monitoring of juvenile and adult Chinook salmon since 1994 within these two systems enabled us to evaluate whether stream flow predicted survival at early life stages, and whether impacts to survival at these stages had detectable effects on adult returns. This study therefore provides an assessment of the potential effects of stream flow alterations across the entire life cycle.

Methods

Study sites

The Lemhi River and Marsh Creek drainages are located within the Salmon River drainage in central Idaho (Fig. 1). The study sites are within 130 km of each other, are influenced by snowmelt runoff, and are characterized by low-gradient channels meandering through meadows with undercut banks and willow thickets. Both systems have healthy riparian habitat due to general lack of development in Marsh Creek and extensive riparian fencing in the Lemhi watershed, but Marsh Creek has more extensive floodplain habitat and likely has more high-quality off-channel habitat during high stream flow. The sites differ in that the Lemhi River is warmer and consequently has higher primary production (Bjornn, 1978), its hydrography is more dominated by

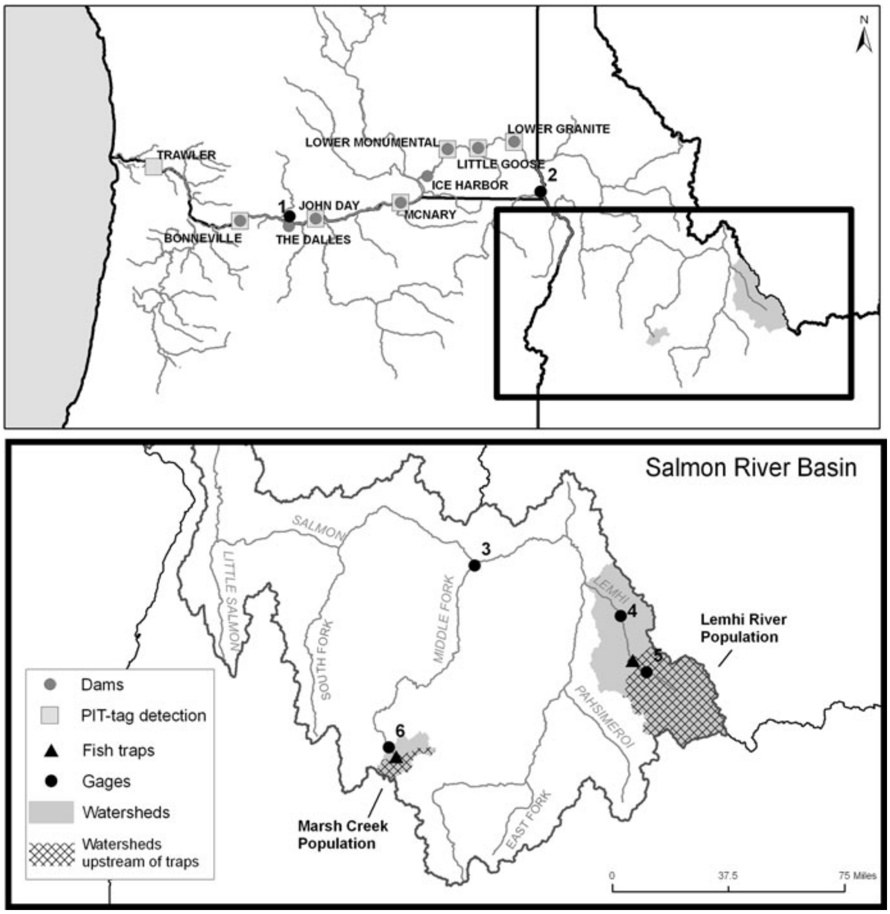

Fig. 1 Map of the Salmon River and Columbia River drainage, showing Lemhi River and Marsh Creek, outmigrant traps and gages in these tributaries, the PIT-tag detection array within the Columbia hydropower system, and stream flow gages used in the analysis. Numbered flow gages are: (1) Columbia River at The Dalles, (2) Snake River at Anatone, (3) Middle Fork Salmon River at Shoup, (4) Lemhi River at Lemhi, (5) Lemhi River at MacFarland, (6) Marsh Creek at Cape Horn Creek

Table 1 Drainage characteristics (±standard deviation, sample size indicated where applicable) of the upper watersheds of the Lemhi River and Marsh Creek

Characteristics	Lemhi	Marsh
Drainage area (km^2)	1,901	127
Percent forested	23	69
Percent irrigated agriculture	11	0[a]
Mean elevation (m)	2,268	2,210
Mean annual precipitation (cm)	20.5 ± 0.51, 27 years	31.3 ± 0.51, 38 years
Mean annual discharge (m^3/s)	6.1 ± 0.51, 10 years	1.9 ± 0.67, 10 years
Average stream width (m)	9.5 ± 1.5, 8 transects	5.9 ± 0.6, 4 transects

[a] Irrigation rights totaling <0.1% of study area were not exercised throughout the period of this study

groundwater fed springs, its drainage is almost an order of magnitude larger, its floodplains occur at lower elevations, it has lower annual precipitation than Marsh Creek, and its stream channel is slightly wider (Table 1). Another key difference between these drainages is that water is diverted from the Lemhi River and its tributaries to irrigate approximately 24,000 ha of agricultural lands, which greatly reduces stream flow in the mainstem and dries most of the tributaries during the irrigation season (BLM, 1998). In contrast, there were no active water diversions in the Marsh Creek drainage during the time data were collected for this study.

Biological data

Spring/summer Chinook salmon spawn in Marsh Creek and the upper reaches of the Lemhi River in August and September, and eggs incubate in gravel nests (redds) through the winter. Young of the year hatch from January to February and typically rear in freshwater for 1 year before migrating down the Salmon, Snake and Columbia Rivers to the ocean as smolts (Copeland & Venditti, 2009). They spend 1–3 years in the ocean before migrating back to their natal stream to spawn. Before smolting, some juveniles rear in the natal stream reach for the entire year, but many move downstream during the first growing season and overwinter between the natal reach and the Snake River (Bjornn, 1971, 1978). A small proportion of juveniles actually migrate to the ocean as subyearlings (Connor, 2001; Copeland & Venditti, 2009), although returns of subyearling migrants are very low or nonexistent. All Snake River spring/summer Chinook salmon must migrate past mainstem dams on the Snake and Columbia Rivers that are equipped with passive integrated transponder (PIT) tag scanning arrays. Detections of Lemhi River and Marsh Creek Chinook salmon at these arrays have shown that the bulk of downstream migration occurs between April and June and is rapid enough that fish normally reach the ocean within one to two months after passing Lower Granite Dam on the Snake River.

Counts of spawning adults provided two demographic endpoints for our analysis. First, we used adult returns to estimate the overall production from each cohort. The Idaho Department of Fish and Game (IDFG) counts redds in all available habitat upstream from juvenile fish traps on the Lemhi River and Marsh Creek, and estimates adult population size by multiplying redds by a constant representing the number of adults per redd (Walters et al., 1999). Adult returns were tracked back to particular brood years based on returns of PIT tagged fish in each population. We assumed the proportions of redds made by age-4 and age-5 fish were the same as the proportion of age-4 and age-5 returning PIT tagged adults (Scheuerell & Williams, 2005).

Adult counts also were used to estimate the total number of eggs initiating each cohort. In order to calculate the number of eggs produced by each brood, we multiplied the count of redds that were spawned upstream of the traps by a constant of 4,000 eggs per redd (Healey, 1991). The total number of eggs was used to estimate juvenile density dependence in regression models, to estimate starting population size of each cohort, and to estimate return rates across the entire life cycle (i.e., adult returns per egg). Adult return rate was expressed as the ratio between cohort-specific adults counted in returns and the number of eggs in that cohort's brood year.

The second stage at which fish could be enumerated was at tributary traps downstream of spawning areas. Idaho Department of Fish and Game personnel have sampled out-migrating juvenile Chinook salmon at the Lemhi River screw trap (river km 49) and the Marsh Creek screw trap (river km 11) since spring of 1997 (Fig. 1). A total of 239,000 juvenile Chinook salmon were captured over the 10 year study period. Traps were generally operated from mid-March to mid-November in Marsh Creek and from mid-March to early December in the Lemhi River. Trapping was not conducted in Marsh Creek in 2000, because no redds were counted in 1999, so the Marsh Creek 1999 brood was not included in the analysis. The Lemhi River trap was not fished during May 30 to August 29 of 1997 for unknown reasons. In this case only, we estimated cohorts by assuming that number of fish missed during this period comprised the same proportion of the cohort that was caught during the same period in other years. In other years, fish captured in the Lemhi River trap from May 30 to August 29 averaged only 4% of the total, so error due to estimating capture during summer 1997 was likely small.

We delineated life history variants of out-migrating juveniles into groups, generally following Bjornn (1978) and Copeland & Venditti (2009). These were: yearling smolts, fall parr, summer parr, subyearling smolts, and fry. Year classes were distinguished based on length and trapping date. Yearling smolts were captured from March to June, and exhibited silver scaling typical during smolting. Fall parr were captured as subyearlings from September to December, while summer parr were captured as subyearlings in March–August. Subyearlings exhibiting silver scaling typical during smolting were captured in May–June, but only in the Lemhi River. These apparent subyearling smolts were combined with the summer parr group for our analyses at the trap. Fry were subyearlings of <60 mm fork length (FL) that were also combined with the summer parr group.

Only fish with FL > 60 mm (non-fry) were tagged with PIT tags. Non-fry captured for the first time were counted and released downstream from the trap or tagged and released upstream from the trap. Between 830 and 6,200 fish were tagged annually from each cohort and location, and over 48,000 fish were tagged for the entire study (Table 2). Fry were not tagged, but were counted and released downstream from the trap.

Recaptures of fish tagged and released upstream from the trap were used to estimate trap efficiency using the Lincoln–Peterson estimator as modified by Bailey (1951; see Ricker, 1975), and tested in Steinhorst et al. (2004). Total catch of yearling smolts, fall parr, summer parr, and subyearling smolts were divided by group-specific trap efficiencies to get group-specific population estimates. Aggregate estimates of trap efficiency (10–29%, Table 2) indicated that juveniles were fully recruited to the sampling gear. Fry catch was expanded using the summer parr trap efficiency. Cohort population size was the sum of the group population sizes. Standard errors of cohort size varied from 1 to 9% of the mean for all years (Table 2).

We calculated group-specific and cohort egg–trap productivity by dividing trap population estimates by the total number of eggs laid by adults the previous summer. Because the time period used to estimate juvenile abundance extended over most of a year, egg–trap productivity is a combination of survival and emigration, so we refer to it as egg–trap transition rate. Both the group-specific and cohort egg–trap transition rates likely exhibit biases. The transition rate estimate for the entire cohort is almost certainly influenced by migration rates of subyearling groups, which do not experience overwinter mortality above the traps. Also, transition rates for each group lack an estimate of survival of residents to each period when life history types migrate. However, both group-specific and cohort egg-to-trap transition rates

Table 2 Tributary stream flow, trap statistics, and transition rate estimates of juvenile Chinook salmon originating from the Lemhi River and Marsh Creek

Population	Brood year	Mean May flow (m^3/s)	Mean August flow (m^3/s)	Tagged fish	Trap efficiency	Population estimate (SE)	Egg–trap transition rate (SE)
Lemhi	1996	126	135	836	0.15	7,793 (678)	0.065 (0.006)
	1997	195	166	3,592	0.15	50,122 (2,111)	0.251 (0.011)
	1998	130	69	1,667	0.15	12,897 (813)	0.079 (0.005)
	1999	81	79	1,589	0.15	13,620 (974)	0.071 (0.005)
	2000	85	88	1,565	0.13	13,488 (976)	0.036 (0.003)
	2001	67	77	3,281	0.11	33,186 (1,765)	0.024 (0.001)
	2002	72	71	4,145	0.22	20,404 (640)	0.042 (0.001)
	2003	65	72	1,364	0.18	9,805 (621)	0.035 (0.002)
	2004	98	68	1,396	0.16	12,111 (780)	0.101 (0.006)
	2005	59	85	1,357	0.19	7,512 (459)	0.038 (0.002)
Marsh	1996	743	93	1,032	0.28	3,808 (203)	0.159 (0.008)
	1997	403	82	2,398	0.17	32,214 (1,551)	0.216 (0.010)
	1998	415	82	2,389	0.10	75,824 (4,810)	0.558 (0.035)
	1999	349	50	0	–	0	–
	2000	213	38	1,664	0.19	17,448 (925)	0.145 (0.008)
	2001	303	54	3,748	0.41	125,579 (2,515)	0.285 (0.006)
	2002	372	57	6,181	0.29	189,152 (3,761)	0.498 (0.010)
	2003	295	58	3,098	0.28	332,585 (9,730)	0.381 (0.011)
	2004	323	52	2,347	0.20	16,291 (753)	0.127 (0.006)
	2005	627	63	4,567	0.18	41,845 (1,455)	0.498 (0.017)

Standard errors for egg–trap transition rate depend directly upon standard errors of the population estimate measure the population at the most appropriate spatial scale for detecting relationships with tributary flow.

The final stage at which fish could be enumerated is during migration out of the Snake and Columbia Rivers. Tagged fish migrating through the Columbia River hydropower system can be detected at arrays located at several dams (Fig. 1), and detections of these fish are kept in the public database PTAGIS (http://www.pitagis.org). Tag detection data were obtained from PTAGIS for subyearling smolts, summer parr, fall parr, and yearling smolts. In order to calculate an unbiased estimate of survival, we tracked each group to the yearling smolt stage at Lower Granite Dam (Fig. 1) and estimated an egg–smolt survival rate. Survival probabilities for the trap to Lower Granite Dam migration were estimated using Cormack–Jolly–Seber methods (Burnham et al., 1987; Skalski et al., 1998) employed by the MARK program software (White & Burnham, 1999). We used a naive full heterogeneity model wherein detection histories from six downstream dams and the estuary trawler (Fig. 1) were used to estimate survival probabilities of life history types to Lower Granite Dam. Some fish were removed from in-river migration and subsequently barged downstream as part of a hydropower mitigation effort. We treated these fish as removals in MARK. We calculated the egg–smolt survival rate by summing the products of the group-specific egg–trap transition rates and the group-specific trap-Lower Granite Dam survival rates.

We then calculated a cohort trap–smolt productivity estimate by dividing the egg–smolt survival rate by the cohort egg–trap transition rate. This resulted in a weighted average of the group-specific trap-Lower Granite Dam productivity. Like egg–trap rates, trap–smolt productivity is influenced by migration rates of younger groups, so we refer to this metric as trap–smolt transition rate.

We estimated smolt–adult return (SAR) rate by dividing the number of adults returning to the natal tributary by the estimated number of smolts reaching Lower Granite Dam. This metric is a combination of survival of juveniles migrating from Lower Granite Dam to the Pacific Ocean, survival in the Pacific Ocean, and survival of adults migrating from the Pacific Ocean to the natal tributaries. SAR is therefore affected by both freshwater and ocean conditions.

Measures of stream flow

We characterized seasonal differences in the hydrographs of these two systems to examine the effects of stream flow upon demographic attributes of Chinook salmon. Gage data from several sources were used to derive estimates of stream flow in Marsh Creek and the Lemhi River. There were no permanent streamflow gages in Marsh Creek. However, the correspondence between temporary gage records from 1994 to 1995 (Marsh Creek at Cape Horn, river km 14), and a downstream gage on the Middle Fork Salmon River (Middle Fork Salmon at Shoup), indicated that the Middle Fork gage would serve as a good proxy with synchronous flows ($r(8\ \mathrm{df}) = 0.938$, $P < 0.01$) when adjusted by the size of Marsh Creek relative to the Middle Fork. The Lemhi River has multiple gaging stations, but the one closest to spawning areas and most reflective of local rearing conditions is the McFarland gage (river km 58). The McFarland gage started operating in 1997 and is generally operated from mid-April through mid-October. The best indicator of the historical hydrograph within the Lemhi drainage is the gage at Lemhi (river km 46.3), which occurs just below Hayden Creek, a relatively unregulated tributary.

For analyses related to juveniles in rearing tributaries, we used average May and average August stream flow during the year of emergence (i.e., brood year +1). We used average May tributary stream flow for the following reasons: (1) it is near the beginning of the irrigation season in the Lemhi River when diversions first cause base-level flows to contrast with naturally rising flow levels, (2) it is near the onset of peak snowmelt when river discharge indicates the volumetric magnitude and seasonal duration of runoff for the remainder of the water year, (3) most of each cohort is still resident in the Lemhi River and Marsh Creek at this time of year, and (4) habitat conditions soon after emergence are important determiners of salmonid cohort survival (Lobón-Cerviá, 2007). We used average August tributary stream flow because: (1) it is the only time in which base flow conditions in Marsh Creek occur while a substantial portion of the cohort is still resident and (2) stream flow during the dry season has been considered as more unfavorable for salmonid populations than spring stream flow (Crozier & Zabel, 2006). We also expressed average monthly stream flow as a percentage of mean annual discharge to compare habitat quality as described by Tennant (1976).

Most juveniles from Snake River spring/summer Chinook salmon migrate downstream through the Snake and Columbia rivers during late spring and early summer of their second year (Muir et al., 2001). We used mean stream flow for April–June of the second year measured at the Snake River gage at Anatone, Washington (Snake migration flow) and in the Columbia River at The Dalles, Oregon (Columbia migration flow) to characterize migration flow. The Anatone gage is between the Salmon River and Lower Granite Dam and provides a good representation of stream flow in the lower Snake River portion of the migration corridor, and The Dalles gage is between the Dalles Dam and Bonneville Dam and provides a good representation of stream flow in the lower Columbia River.

Climate data

A number of studies of Chinook salmon in the Columbia River have documented correlations between climate indices and survival rates (Scheuerell & Williams, 2005; Crozier et al., 2008). Because stream flow could covary with climate indices, thereby confounding predicted effects of stream flow on survival, we examined whether climatic variation at particular life stages covaried with stream flow and survival. We examined four different time periods: (1) the period during snowpack accumulation (October–March) at the beginning of a brood year (BY), (2) the period during early rearing when flows decrease from spring peak to base flow (April–September in BY + 1), (3) the overwinter period for yearlings (October–March in BY + 1), and (4) downstream migration (April–June in BY + 2) or early ocean rearing (May–July in BY + 2). Within each time period, we calculated averages of the Pacific Decadal Oscillation (PDO, http://jisao.washington.edu/pdo/) and El Nino/Southern Oscillation (ENSO, http://www.cdc.noaa.gov/enso/enso.mei_index.html). These values were used in multiple regressions of productivity measures.

Statistical analysis

If reduced stream flow in the Lemhi River constrained life-cycle productivity, tributary stream flow should be closely correlated with egg–adult return rates as well as juvenile productivity. Juvenile productivity should also be lower in the Lemhi River than in Marsh Creek. We tested these predictions using Pearson correlation coefficients and paired *t* tests. Additionally, egg–adult return rate in the Lemhi River should be more strongly influenced by egg–smolt survival than SAR, and egg–smolt survival in turn should be more strongly influenced by egg–trap transition rate than trap–smolt rate. We tested these predictions using multiple linear regression.

To better understand the possible interdependencies of stream flow and climate across the life cycle, we used path analysis (Wright, 1934; Mitchell, 1993; Wootton, 1994) incorporating climate measures, stream flow variables, egg number, and productivity metrics for each watershed (Fig. 2). Our approach assumed that: (1) any effects of environmental parameters on egg–adult return rate must primarily influence egg–trap transition rate, trap–smolt transition rate, and SAR; (2) climate metrics could affect stream flow but could also have other possible effects on productivity rates; and (3) environmental variables would primarily influence temporally concurrent life stages. The exception to this last assumption was that climate from October to March could influence stream

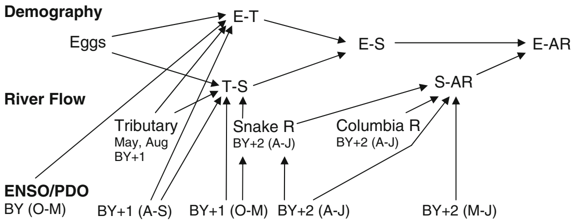

Fig. 2 Demographic, flow, and climate variables considered in path analyses linking juvenile and adult return rates in the Lemhi River and Marsh Creek. Demographic data explaining egg–adult return rates (E–AR) are either egg–smolt survival (E–S) or smolt–adult return rate (S–AR). Egg–smolt survival can be further subdivided into egg–trap (E–T) and trap–smolt (T–S) transition rates. Eggs can explain density dependence during rearing stages. Tributary flow data can explain variation in E–T and T–S rates, while migration flow data (Snake and Columbia Rivers) can explain variation in T–S and S–AR rates. Climate data (El Nino/Southern Oscillation, ENSO; Pacific Decadal Oscillation, PDO) can explain variation in either flow or demographic variables. All environmental data are temporally linked to life stage specific time periods by reference to brood year (BY), and specifying winter snowpack accumulation (October–March, O–M), tributary rearing (April–September, A–S), downstream migration (April–June, A–J), or ocean entry (May–July, M–J)

flow in the following spring and summer through changes in snowpack.

Our path analysis started with the multiple linear regressions connecting egg–trap and trap–smolt transition rates to egg–smolt survival, and egg–smolt survival and SAR to egg–adult return rate. These regressions provided three productivity endpoints to relate with environmental variables: egg–trap and trap–smolt transition rates and SAR. Using AIC (Akaike's information criterion) model selection (Burnham & Anderson, 2002), we examined possible multiple regression models of each productivity metric and for each metric of stream flow. Because of the relatively few number of years available for analysis relative to the number of possible variables for some models, we used a backwards parameter selection method in which we identified the best three-parameter model and the best two-parameter model, and compared these to all single parameter models and the null model (constant only). We selected the best models using AIC_c, the AIC score with small sample size adjustment (Burnham & Anderson, 2002). We considered particular models as having good support when competing models resulted in $\Delta\mathrm{AIC}_c$ (the difference between a given model and the best model) ≥ 3. We used standardized regression coefficients from the best models in the path analysis, although we noted when alternatives existed ($\Delta\mathrm{AIC}_c < 3$).

Results

Patterns of stream flow

We found strong differences in absolute levels of stream flow during juvenile rearing within and among the years encompassed in this study and between river systems. The seasonal pattern of Marsh Creek stream flow indicated a strong snowmelt-dominated hydrograph with peak flow occurring from May to July and a steady decline through late summer (Fig. 3). Two river gages indicated that the Lemhi River hydrographs exhibited a different pattern (Fig. 3). The gage at McFarland is most closely associated with spawning grounds and showed little snowmelt-dominated signal. In fact, in two of the 10 years in this study, stream flow at the McFarland gage dropped to its lowest annual levels in May. The gage at Lemhi is located just downstream of a largely unregulated tributary (Hayden Creek) and exhibits a snowmelt-dominated hydrograph despite water diversions that cause a pronounced drop in stream flow during the summer. These hydrographs indicate that a large portion of the spring snowmelt associated with spawning and rearing grounds is removed from the Lemhi River for irrigation.

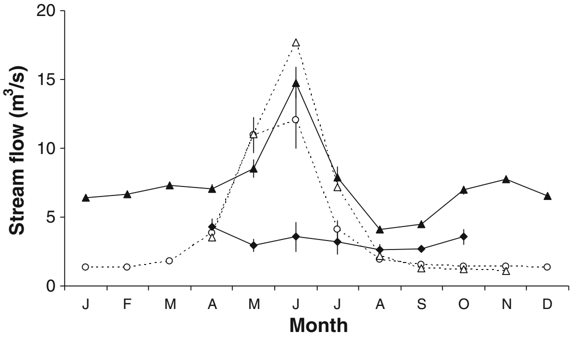

Fig. 3 Stream flow of Marsh Creek and the upper Lemhi River between 1996 and 2006, represented as the average across months. *Open triangles* represent Marsh Creek data in 1995, *open circles* represent data from the Middle Fork Salmon River gage adjusted by the watershed area of Marsh Creek, *closed diamonds* represent the Lemhi River at McFarland, and *closed triangles* represent the Lemhi River at Lemhi. *Error bars* denote standard errors. Missing months for particular gages denote time periods for which flow was never measured

Across years, May stream flow in the Lemhi River and Marsh Creek was not significantly correlated ($r(8\ \mathrm{df}) = 0.203$, $P > 0.5$), and was two to ten times less in the Lemhi River than in Marsh Creek (paired $t(9) = -7.048$, $P < 0.001$; Lemhi mean = 2.8 m^3/s, Marsh mean = 12.2 m^3/s). August stream flow was weakly correlated ($r(8\ \mathrm{df}) = 0.622$, $P = 0.055$) and magnitude of flow was similar (Lemhi mean = 2.6 m^3/s, Marsh mean = 2.3 m^3/s). A comparison of stream flow expressed as percentage of mean annual discharge (MAD) revealed sharp differences between the two streams. In Marsh Creek, May stream flow averaged 329% of MAD (range 173–605%) whereas in the Lemhi River at the McFarland gage it averaged 42% (range 26–84%). Differences in August flows, expressed as a percentage of MAD, were not as pronounced but were still higher in Marsh Creek (mean 51%, range 31–76%) than the Lemhi River (mean = 39%, range 29–72%) (paired $t(9) = -2.36$, $P < 0.02$). Based on Tennant's (1976) classification of river flow conditions, stream flow in Marsh Creek was always above "optimum" (60–100% MAD) for the first part of the growing season and declined to "optimum," "excellent" (50–59% MAD), "good" (40–49% MAD), or "fair to degrading" (30–39% MAD) during late summer. In contrast, stream flow in the Lemhi River was never above "optimum" during the growing season and was "fair to degrading" or worse for the entire growing season in 6 of the 10 years.

During downstream migration, fish from both populations encounter altered flow conditions in both the Snake River and Columbia River. Snake River migration flow varied between 823 and 2,540 m^3/s (annual mean = 1,579 m^3/s) during the years of this study, which is 44–119% of the historical average going back to 1959. As flow depletions of the Snake River commenced in the early 1860s, these contemporary flows are a smaller proportion of long-term historical flows. Columbia migration flow varied between 3,707 and 9,236 m^3/s (annual mean = 6,880 m^3/s), which is 44–99% of the historical average going back to 1879. Flow in the Snake River has shown substantial variation over the last 50 years, with a trend indistinguishable from 0 (-4 m^3/s per year, $r(48\ \mathrm{df}) = 0.084$, $P > 0.1$). In the Columbia River, flow has exhibited a much more systematic decline over time (-324 m^3/s per year, $r(128\ \mathrm{df}) = 0.526$, $P < 0.001$). Nevertheless, flows were still relatively high in spring and during the period of our study, and flow from April to June expressed as a percentage of unimpaired MAD varied between 62–190% and 56–139% in the Snake and Columbia Rivers, respectively. This puts the Snake and Columbia rivers intermediate to the Lemhi River and Marsh Creek with respect to flow conditions.

Our examination of effects of climate patterns on stream flow revealed relatively few strong climate correlates with flow during tributary rearing, and much stronger effects of climate on migration flows. Model comparison using AIC supported an effect of neither PDO nor ENSO on stream flow in the Lemhi River (see Electronic supplementary material—appendix), as the best model was a constant. The best model of stream flow in Marsh Creek included PDO during spring–summer, but had marginal support compared to the null (constant only) model ($\Delta AIC_c = 2.0$). In the Snake River, we detected a weak effect of ENSO during fall and winter, but this model was little different from the null model ($\Delta AIC_c = 0.5$). In contrast, the best model of Columbia River flow included effects of Snake River flow, as well as ENSO and PDO during both winter and spring. This model was slightly better than an alternative model that included only effects of Snake River flow and fall–winter PDO ($\Delta AIC_c = 1.4$).

Effects of flow on return rates of adults

Egg–adult return rates did not significantly differ between populations (paired $t(7) = 0.591$, $P > 0.1$), and both populations exhibited positive correlations with stream flow (Table 2) experienced during rearing. In the Lemhi River, return rate was highly correlated with rearing stream flow in May, and slightly less so with stream flow in August. In Marsh Creek, return rate was strongly correlated with rearing stream flow in August. Notably, adult returns in the Lemhi River never surpassed the per capita replacement rate when natal stream flow in May was less than the average over the time period examined, whereas adult returns in Marsh Creek surpassed replacement in 2 of the 5 years in which May stream flow was below average. In comparison to relationships with tributary flow, correlations of return rate with migration flows in the Snake and Columbia Rivers were relatively weak for both populations.

Due to the relatively small number of years in the dataset, we examined whether these correlations were sensitive to data from particular years. For tributary flow, the only datum with strong sensitivity was the highest flow year, and removal of this datapoint eliminated only the strong correlation between Lemhi adult return rate and August tributary flow. Relationships between adult return rate and migration flows were relatively insensitive to removal of particular data points. Removal of the highest migration flow year improved this correlation for the Lemhi River, and removal of brood year 1998 data (a moderate migration flow year) improved the correlation for Marsh Creek.

If low rearing flows were the primary source of variation in mortality for these populations, adult return rates should correlate much more strongly with early juvenile survival than survival at later stages. We tested this prediction by dividing the life cycle at the smolt stage (at Lower Granite Dam), and using egg–smolt survival and SAR as two predictors in a multiple linear regression on adult return rate (egg to

Table 3 Regression output of egg–smolt survival and smolt–adult return rate on egg–adult return rates in the Lemhi River and Marsh Creek, including unstandardized slopes ($B \pm$ standard error, SE), standardized slope coefficients, and *t* tests and their *P* values

Population	Survival parameter	Unstandardized coefficients		Standardized coefficients	*t*	*P*
		B	SE			
Lemhi	Egg–smolt	0.016	0.001	0.791	12.939	<0.001
	Smolt–adult	0.010	0.002	0.311	5.086	0.002
Marsh	Egg–smolt	0.012	0.001	0.756	12.413	<0.001
	Smolt–adult	0.020	0.003	0.447	7.332	0.001

adult return). This regression explained 98 and 96% of the variation in adult return rate for Lemhi River and Marsh Creek, respectively. In the Lemhi River population, the influence of egg–smolt survival on adult return rate was over twice the effect of SAR as judged from standardized beta values (Table 3). The Marsh Creek population showed a similar pattern, although the difference in standardized beta values was less extreme. These patterns existed despite higher variation in egg–smolt survival than SAR in both the Lemhi River (SD = 0.03 vs. 0.02, respectively) and Marsh Creek (SD = 0.04 vs. 0.01, respectively).

Effects of flow on juvenile productivity

If rearing stream flows constrain adult return rates, measures of juvenile productivity should be higher in Marsh Creek than the Lemhi River, and rearing flow should be strongly correlated with survival or movements of juvenile fish above outmigrant traps. Indeed, we found significant differences between Lemhi River and Marsh Creek populations in egg–trap transition rates (paired $t(8) = 3.644$, $P < 0.01$) and egg–smolt survival (paired $t(8) = 2.709$, $P < 0.05$). Both egg–trap transition rate and egg–smolt survival (Fig. 4) for the Lemhi population exhibited strong correlations ($r(8\ \text{df}) = 0.90$ and 0.95, respectively; $P < 0.001$) with May rearing flow, and slightly lower correlations with August flow ($r(8\ \text{df}) = 0.74$ and 0.82, respectively; $P < 0.05$). In contrast, egg–trap transition rate in Marsh Creek exhibited weak relationships with both May and August flow ($r(7\ \text{df}) = 0.01$ and 0.13, respectively; $P > 0.1$), even as egg–trap rates appeared to be an extension of Lemhi rates with one outlier (Fig. 4). Egg–smolt

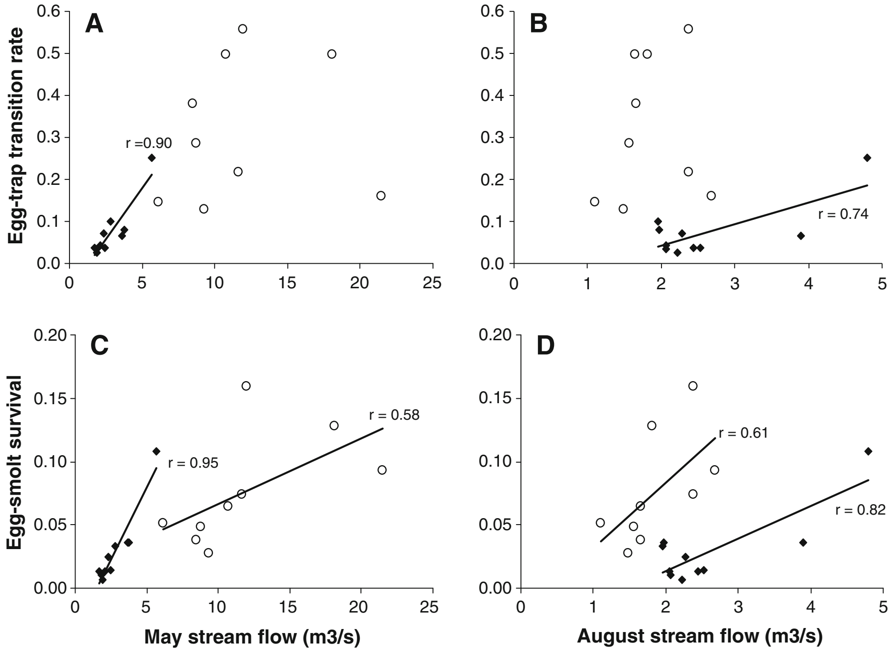

Fig. 4 Transition rates from eggs to outmigrant trap (**A**, **B**) and egg–smolt survival rate (**C**, **D**) as functions of tributary stream flow in May (**A**, **C**) and August (**B**, **D**) in the Lemhi River (*black diamonds*) and Marsh Creek (*open circles*). *Lines* represent significant correlations

Table 4 Regression output of egg–trap and trap–smolt transition rates on egg–smolt survival in the Lemhi River and Marsh Creek, including unstandardized slopes (*B* ± standard error, SE), standardized slope coefficients, and *t* tests and their *P* values

Population	Survival parameter	Unstandardized coefficients		Standardized coefficients	*t*	*P*
		B	SE			
Lemhi	Egg–trap	0.418	0.014	0.933	30.436	<0.001
	Trap–smolt	0.056	0.011	0.156	5.077	0.001
Marsh	Egg–trap	0.256	0.040	0.991	6.380	0.001
	Trap–smolt	0.236	0.046	0.799	5.149	0.002

survival in Marsh Creek exhibited stronger correlations with May and August flows ($r(7\text{ df}) = 0.58$ and 0.61, respectively; $P < 0.05$) compared to egg–trap values.

Our sensitivity analysis of tributary productivity metrics to particular data points revealed that most correlations were robust to data point removal. The only noteworthy exception was that in the Lemhi River, removal of the highest flow year eliminated the strong correlation of rearing flow in August with both egg–trap transition rate and egg–smolt survival.

We also examined the relative importance of tributary rearing by subdividing egg–smolt survival into egg–trap and trap–smolt transition rates and examining the strength of each rate on variation in egg–smolt survival (Table 4). In both river systems, the primary influence was egg–trap transition rate. However, in the Lemhi River the standardized beta for egg–trap transition was nearly six times that of the trap–smolt transition, while in Marsh Creek the difference was much less extreme.

Path analysis of flow and climate relationships

We used AIC model selection and path analysis to evaluate the potential influence of multiple flow and climate signals and density dependence upon three segments of the life cycle: egg–trap and trap–smolt transition rates and SAR (Table 5). For egg–trap transition rate, the best model for the Lemhi River included only a strong effect of tributary flow in May, but the best model for Marsh Creek was the null model. For trap–smolt transition rate, the best model for the Lemhi River was also tributary flow in May, although this model was marginally better than the null model ($\Delta\text{AIC}_c = 1.5$). Similarly, the best model at this stage for Marsh Creek was eggs, which also was slightly better than the null model ($\Delta\text{AIC}_c = 1.6$). The best model of SAR for the Lemhi population included Columbia River flow during migration and ENSO during ocean entry, and for Marsh Creek included Columbia River flow during migration. Both of these models had competing alternatives (Table 5) that included subsets of flow in the Columbia River or the Snake River, or ENSO.

Path analysis linking demographic, stream flow, and climate predictors showed strong evidence for cascading effects of tributary flow in the Lemhi River but not in Marsh Creek (Fig. 5). The total effect of rearing flow on adult return rates (the product of standardized betas along a path, summed for egg–trap and trap–smolt pathways) equaled 0.74, while the combined effects of migration flow and ENSO at ocean entry were 0.17 and 0.19, respectively. In contrast, the product of standardized betas on adult return rates derived from rearing flow for Marsh Creek was effectively 0, since models that included tributary flow were not supported. Even if the best relationship for tributary rearing flow (i.e., as measured in August) had been used to connect egg–trap and trap–smolt pathways, the combined effect of rearing flow would have been 0.32, less than the total path magnitudes for eggs or migration flow. Because the best regression models lacked strong climate linkages to either stream flow or productivity in both tributary rearing and migration stages, climate-driven pathways upon life-cycle productivity through links in both tributary and migration stages were absent for both populations (Fig. 5).

Discussion

Several lines of evidence support the hypothesis that low rearing flows in the Lemhi River impacted adult return rates. First, we documented large differences in

Table 5 AIC analysis of regression models for egg–trap, trap–smolt, and smolt–adult return (SAR) rates

Survival metric	Lemhi				Marsh			
	Model	R^2	K	$\Delta\mathrm{AIC}_c$	Model	R^2	K	$\Delta\mathrm{AIC}_c$
Egg–trap	Constant	0	2	12.2	**Constant**	**0**	**2**	**0**
	Tributary flow May	**0.810**	**3**	**0**	Tributary flow May	0.015	3	4.7
	Tributary flow Aug	0.549	3	8.5	Tributary flow Aug	0.017	3	4.6
	Eggs	0.122	3	15.2	Eggs	0.064	3	4.2
	ENSO BY + 1 (A–S)	0.276	3	13.3	ENSO BY + 1 (A–S)	0.092	3	3.9
	PDO BY + 1 (A–S)	0	3	16.5	PDO BY + 1 (A–S)	0.101	3	3.8
	Tributary flow May, ENSO BY + 1 (A–S)	0.856	4	17.8	Tributary flow May, PDO BY + 1 (A–S)	0.245	4	9.5
	Tributary flow May, ENSO BY + 1 (A–S), Eggs	0.856	5	26.7	Tributary flow May, PDO BY + 1 (A–S), Eggs	0.594	5	15.9
Trap–smolt	*Constant*	*0*	*2*	*1.5*	*Constant*	*0*	*2*	*1.6*
	Tributary flow May	**0.436**	**3**	**0**	*Tributary flow May*	*0.403*	*3*	*1.8*
	Tributary flow Aug	*0.408*	*3*	*0.6*	*Tributary flow Aug*	*0.352*	*3*	*2.5*
	Snake R. flow BY + 2 (A–J)	*0.212*	*3*	*3.4*	Snake R. flow BY + 2 (A–J)	0.268	3	3.6
	Eggs	0.250	3	2.9	**Eggs**	**0.511**	**3**	**0**
	ENSO BY + 1 (A–S)	0.023	3	5.6	ENSO BY + 1 (A–S)	0.102	3	5.6
	ENSO BY + 2 (A–J)	0.201	3	3.3	ENSO BY + 2 (A–J)	0.066	3	5.7
	PDO BY + 1 (A–S)	0.091	3	4.9	PDO BY + 1 (A–S)	0.122	3	5.3
	PDO BY + 2 (A–J)	0.048	3	3.4	PDO BY + 2 (A–J)	0.262	3	3.7
	Tributary flow May, ENSO BY + 1 (A–S)	*0.613*	*4*	*2.4*	Eggs, Tributary flow Aug	0.660	4	3.9
	Tributary flow May, ENSO BY + 1 (A–S), Eggs	0.732	5	7.9	Eggs, Tributary flow Aug, ENSO BY + 2 (A–J)	0.818	5	10.3
SAR	Constant	0	2	3.6	Constant	0	2	8.2
	Snake R. flow BY + 2 (A–J)	*0.467*	*3*	*2.7*	Snake R. flow BY + 2 (A–J)	0.650	3	5.4
	Columbia R. flow BY + 2 (A–J)	0.438	3	3.2	**Columbia R. flow BY + 2 (A–J)**	**0.821**	**3**	**0**
	ENSO BY + 2 (A–J)	0.286	3	4.9	ENSO BY + 2 (A–J)	0.601	3	5.9
	ENSO BY + 2 (M–J)	*0.511*	*3*	*1.9*	ENSO BY + 2 (M–J)	0.062	3	13.3
	PDO BY + 2 (A–J)	0.269	3	5.5	PDO BY + 2 (A–J)	0.431	3	9.2
	PDO BY + 2 (M–J)	0.374	3	4.1	PDO BY + 2 (M–J)	0.414	3	9.5
	Columbia R. flow BY + 2 (A–J), ENSO BY + 2 (M–J)	**0.812**	**4**	**0**	*Columbia R. flow BY + 2 (A–J), ENSO BY + 2 (A–J)*	*0.927*	*4*	*1.5*
	Columbia R. flow BY + 2 (A–J), ENSO BY + 2 (M–J), Snake R. flow BY + 2 (A–J)	0.894	5	6.9	Columbia R. flow BY + 2 (A–J), ENSO BY + 2 (A–J), ENSO BY + 2 (M–J)	0.927	5	20.2

Models shown are a single constant, all single parameter models, and the two- and three-parameter models with the lowest AIC_c (corrected for small sample size). All models include a constant. The best models are shown in bold and competing models in italics

PDO Pacific Decadal Oscillation, *ENSO* El Nino/Southern Oscillation, *BY* brood year, *A–S* April–September, *A–J* April–June, *M–J* May–July, R^2 coefficient of determination, *K* parameters estimated (including constant and variance), ΔAIC_c difference of AIC_c from best model

seasonal hydrographs between the Lemhi River and a reference site (Marsh Creek). Second, raw correlations between rearing flow and adult return rate were extremely strong for the Lemhi population. Third, the sole predictor in the best model of both egg–trap and trap–smolt transition rates in the Lemhi River was

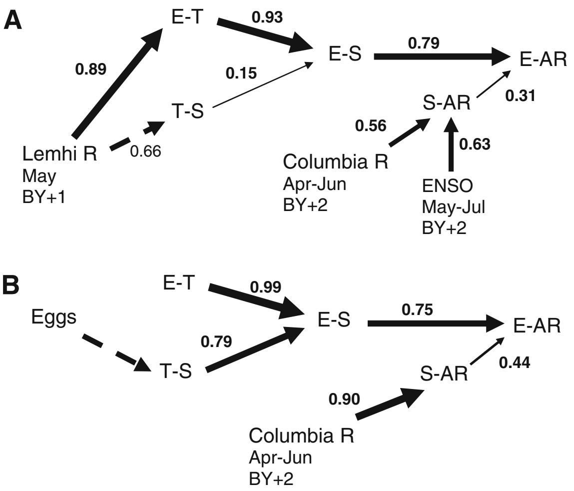

Fig. 5 Path analysis of effects of eggs, flow, and climate on adult return rates in the Lemhi River (**A**), and Marsh Creek (**B**) (see Fig. 2). Values represent standardized regression coefficients supported by AIC analysis. *Arrow* thickness is proportional to coefficients. *Dashed arrows* represent relationships that are weakly supported by AIC analysis (see Table 5). No links are included when the null (constant only) regression model had greatest support

Table 6 Pearson correlations (with number of years) between egg–adult return rate and stream flow at rearing and migration life stages

Flow variable	Lemhi	Marsh
Tributary flow	**0.983 (9)**	0.473 (8)
May	***P* < 0.001**	*P* = 0.237
Tributary flow	**0.881 (9)**	**0.746 (8)**
Aug	***P* = 0.002**	***P* = 0.034**
Snake R. flow	0.658 (9)	0.320 (8)
Apr–Jun BY + 2	*P* = 0.054	*P* = 0.440
Columbia R. flow	0.583 (9)	0.400 (8)
Apr–Jun BY + 2	*P* = 0.100	*P* = 0.326

Tributary flows are flows in May or August calculated for the Lemhi River and Marsh Creek for young-of-the-year fish in brood year (BY + 1). Flows during migration (BY + 2) are for Snake River at Anatone and Columbia River at The Dalles. Strong correlations are marked in bold

rearing flow. Fourth, path analysis revealed a strong set of pathways linking rearing flow to egg–adult return rate primarily through egg–trap transition rate. These patterns were much less strongly exhibited or nonexistent in Marsh Creek.

We found that fish in the Lemhi River appeared most sensitive to flow in their first spring, when regional tributary flows are normally at their peak. In the upper reaches of the Lemhi, this time period can actually represent the annual low flow because of water diversions. In contrast, fish in Marsh Creek appeared more sensitive to flows in August, which has traditionally been considered the period of flow limitations in snowmelt-dominated systems (Crozier & Zabel, 2006). This difference suggests that the pattern of water withdrawals in the Lemhi has altered the temporal context for which Chinook salmon are adapted, and could be one reason why average egg–trap transition rate and egg–smolt survival are over four and two and a half times lower, respectively, than in Marsh Creek.

We also detected potential effects of migration flows on adult return rates in both populations via variation in smolt–adult return rate (Table 5), although overall influence of migration flow on life cycle of either population appeared much less pronounced than tributary flows on the Lemhi River population (Table 6; Fig. 5). This was likely due to several factors: (1) year class strength was set before smolting in the Lemhi River, (2) migration flow levels, while clearly reduced from historical levels, were nevertheless at peak stages during migration, and (3) smolt–adult return rate is more predictable by ocean conditions than freshwater variation. Other researchers have detected flow-dependent survival relationships for migrating salmonids in the Columbia River Basin (Muir et al., 2001; Connor et al., 2003; Smith et al., 2003; Zabel et al., 2008) and elsewhere (Kocik & Taylor, 1987; McCormick et al., 1998), although relatively few efforts have put the effects of migration flows in the context of the life cycle.

In comparison to rearing and migration flows, the influence of climate variables appeared relatively weak. Within the rearing life stage, we found a statistically significant effect of PDO upon flow in Marsh Creek, but this model was not well supported over the null hypothesis of no climate influences. During the migration life stage, both ENSO and PDO were supported in the best model of flow in the Columbia River, and we also found a strong influence of ENSO during ocean entry in the Lemhi population. However, the influence of climate variables on adult returns in the context of rearing flow variation was relatively small. This is not an entirely surprising finding, given that climate rarely affects fish directly, but influences demography through its effects on causal variables like food availability, water temperature, and flow (Petersen & Kitchell, 2001). Moreover, our relatively small sample size of demographic data precluded all but the strongest environmental correlates from being included in models. We discovered that AIC scores strongly depended upon the small sample size adjustment, and that some poorly supported models that included climate could explain a substantial proportion of the variation in demographic rates (Table 5). These patterns suggest that climate patterns should be more detectable in longer time series of demographic data. Where long time series were available (e.g., >50 years of data on climate and flow in the Columbia River), climate was a strong predictor in some but not all cases (e.g., relationships of climate and flow in the Columbia vs. the Snake River, see Electronic supplementary material—appendix). Previous studies focusing on longer time series of smolt–adult return rate and adult returns have found support for climate teleconnections (Beamish & Bouillon, 1993; Mantua et al., 1997; Lawson et al., 2004; Scheuerell & Williams, 2005). Nevertheless, our results consistently showed that in the Lemhi River, flow variables had stronger explanatory power than climate predictors, corroborating some studies that have detected higher covariation in life-cycle production at subbasin rather than basinwide scales (Schaller et al., 1999; Botsford & Paulsen, 2000; Deriso et al., 2001). Studies that have included flow as well as climate signals in the context of the life cycle have also shown strong effects of flow (e.g., Greene et al. 2005). Models of single spawning populations with long time series that can disentangle effects of flow from other environmental variables are clearly needed to evaluate the influence of hydromodification against the backdrop of climate variation at multiple life stages.

The influence of climate upon productivity has often been put in the context of the dominance of ocean conditions in predicting population fluctuations of anadromous salmonids (Beamish & Mahnken, 2001; Scheuerell & Williams, 2005). As our intent in this article was to focus on relationships of survival with flow, a systematic effort predicting the influence of marine conditions on SAR or adult return rates is beyond the scope of this paper. However, the pattern of survival for the Lemhi population (Fig. 5) provides strong evidence that year class strength was set at an early life stage. Egg–smolt mortality for the Lemhi population averaged 97%, and was as high as 99% across the time period of our study. The pattern for the Marsh Creek population was similar in some respects (e.g., egg–trap transition rate had the strongest standardized regression coefficient). Variation in egg–smolt survival was larger than variation in smolt–adult return rate for both populations, suggesting that the early rearing period may be a critical life stage even in relatively pristine systems. This idea is supported by studies of environmental predictors across the life cycle (Friedland et al., 2003; Greene et al., 2005), life-cycle modeling demonstrating high sensitivity of productivity to survival at early life stages for migratory and resident populations of salmonids (Elliott, 1987; Elliott et al., 1997; Honea et al., 2009), and studies of negative size-dependent mortality in salmonids (McGurk, 1996; Einum & Fleming, 2004; Lobón-Cerviá, 2007). More studies that partition survival across the life cycle and characterize early freshwater survival are needed to determine whether the patterns in the relatively short time series for these two populations typify a general property of stream-rearing anadromous fish.

While our findings suggest that reductions in stream flow can influence a population's productivity, several uncertainties exist. Other differences aside from hydromodification exist between the Lemhi River and Marsh Creek (Table 1), so it is difficult to determine the extent to which differences in survival between these populations can be attributed solely to variation in stream flow. In this respect, monitoring over multiple years within the Lemhi River provides the strongest support for flow-related reductions in productivity. While the number of years of monitoring within the Lemhi River is still relatively small and therefore potentially vulnerable to spurious patterns, our sensitivity analyses indicate that correlations between stream flow and productivity are statistically robust to outliers. Our results justify continued population monitoring and predictive modeling of future returns to verify effects of stream flow. Experimental studies (e.g., Suttle et al. 2004) and studies of the fates of fish in the context of daily variation in flow (e.g., Sykes et al., 2009) will further strengthen support for causal linkages between stream flow and population productivity.

In sum, our results suggest that water use has dramatic effects for freshwater-rearing fish, even those with extensive anadromous life histories. Water use has increased dramatically during the last century (Gleick, 1998), and pressure on water availability is especially high in dry climates (Benejam et al., 2009) such as the Mediterranean basin and the western United States. In the western United States, 10 of the 12 native species of *Oncorhynchus* and *Salvelinus* are listed under the Endangered Species Act throughout all or part of their range and all are potentially affected by water use. Constraints of rearing flows in areas with strongly modified hydrographs may become stronger as entire systems shift in response to global climate change (Crozier et al., 2008), which is predicted to lower snow pack and increase summer temperature (Mote et al., 2003). Our findings suggest that management strategies for improving stream flow in arid and semi-arid systems with highly modified hydrographs deserve further consideration.

These findings also provide important perspectives on monitoring fish populations. Our findings depended upon long-term monitoring data of multiple life stages, using a variety of methods (spawner surveys, outmigrant trapping, PIT tagging). We found that a large component of mortality was explained during the early rearing stages. Thus, mark-recapture designs that focus solely upon later stages of migration may provide misleading indices of flow-mediated impacts on survival because they could miss most of the mortality within a cohort. By the same token, monitoring designs of mixed stocks may underestimate the effects of water withdrawals on single stocks. For example, our assessment of the impacts of low flows would be less severe if our sample focused only on the areas downstream from where Lemhi and Marsh populations merged. Future monitoring efforts of salmonids in semi-arid environments would benefit by improved resolution of both hydrographic and population data at early life stages. If the Lemhi River is any indication of the water use challenges in these environments, our ability to predict population dynamics and recover populations despite a changing climate will depend upon accurate assessments of status at these early stages.

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