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The Importance of Juvenile Migration Tactics to Adult Recruitment in Stream-Type Chinook Salmon Populations

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Abstract
The existence of multiple migration tactics within a population has been observed for several fish species, and they may contribute differentially to adult recruitment. Relative contribution by juveniles using the same habitats on different schedules is variable; therefore, understanding and conserving this diversity should be important to fisheries managers. We investigated adult recruitment by two distinct juvenile migration tactics in several spawning populations of stream-type Chinook Salmon *Oncorhynchus tshawytscha* in Idaho: those leaving the spawning grounds as subyearlings during June through November (downstream rearing, or DSR, type) and those emigrating from natal areas 1 year after emergence (natal reach rearing, or NRR, type). The DSR type had greater juvenile abundance in all populations, although the NRR type exhibited better survival from the natal reach to the migratory corridor. The DSR type had greater survival from smoltification to adult return to freshwater compared with the NRR type. More DSR emigrants than NRR emigrants returned to freshwater as adults, although the difference was influenced by cohort and population. Adult recruits to stream-type Chinook Salmon populations in Idaho are comprised mostly of DSR emigrants, i.e., fish that dispersed from their natal habitats and reared in reaches downstream. This finding is ubiquitous, although the size of the effect depends on cohort and population. We demonstrated that juvenile Chinook Salmon in Idaho do indeed use downstream rearing habitats effectively, thereby increasing recruitment of adults back to the spawning gravels in these populations. This study illustrates how dispersive life histories are essential to achieve the full productive potential of migratory stream fish populations.

The return of spawning salmon to their natal areas is remarkable in its accuracy and in the consistency of its timing (Quinn 2005). Less is known about emigration, i.e., the downstream migration of juveniles. Recent work has led to a greater appreciation of the variation in the ways that juvenile salmon accomplish their journeys (e.g., Trudel et al. 2009), but the relative importance of how this life history diversity translates into adult recruitment is poorly understood.

The existence of multiple migratory life history types within a population has been observed for several fish species (Secor 1999). The life histories within a cohort of juvenile migratory fish often contribute differentially to recruitment into the adult population (Reimers 1973; Limburg 2001; Copeland and Venditti 2009). Given sufficient temporal variability, juveniles using the same habitats on different schedules may

have very different fates. Relative contribution by life history types is temporally variable; therefore, understanding and conserving this diversity should be important to fisheries managers (Hilborn et al. 2003; Kerr et al. 2010; Petitgas et al. 2010).

Many salmon populations in the Pacific Northwest are listed under the U.S. Endangered Species Act (Good et al. 2005). For effective conservation, population bottlenecks must be identified in order to be ameliorated. However, variations in life history, as identified above, may be affected differentially by proposed conservation measures. Habitat restoration has often been implemented with the goal of increasing returns of adult salmon (Katz et al. 2007). These are typically enhancements within spawning tributaries, which benefit most the portion of the population that resides there until smoltification. Characteristics of good spawning habitat are to some

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degree opposed to the characteristics of good rearing habitat, i.e., cold, well-oxygenated, sterile streams are ideal environments for incubating embryos, but juveniles need food and warmer temperatures for digestion (Mundie 1969; Quinn 2005). Therefore, rearing habitat limitations, rather than inadequate spawning gravels, are more likely to affect juvenile production in salmon populations (Quinn 2005).

Pacific salmon (genus *Oncorhynchus*) exhibit a continuum of life histories with respect to anadromy, which is one of the defining characteristics of the genus (Quinn and Myers 2004). Species, populations, and even individuals within populations may vary with respect to the time they spend in freshwater before emigrating to the sea as a smolt (Quinn 2005). For example, populations of Chinook Salmon *O. tshawytscha* are often classified (following Healey 1991) as stream-type (that is, they have an extended freshwater rearing phase and enter the ocean as yearlings) or ocean-type (they rear in freshwater for a shorter time and enter the ocean before their first winter as a subyearling). Within these broad categories there is considerable variation in how individual Chinook Salmon use the accessible freshwater habitat (e.g., Reimers 1973).

Dispersal of juvenile salmon for rearing and wintering is likely of demographic importance in populations with extended freshwater rearing. In some cases, juveniles disperse into small, nonnatal tributaries to rear or spend the winter (e.g., Murray and Rosenau 1989; Erkinaro et al. 1997; Bradford et al. 2001; Daum and Flannery 2011). On the Oregon coast, Coho Salmon *O. kisutch* use intermittent streams during the winter, even though these reaches are dry during the summer (Ebersole et al. 2006). Levings and Lauzier (1991) found that the main-stem reaches of the Fraser River basin, British Columbia, were used as winter habitat by juvenile Chinook Salmon. Large-scale dispersal by juvenile salmon should be important in large river basins where the habitats that can support downstream rearing are connected to natal reaches.

There are limitations to juvenile production by stream-type Chinook Salmon populations in relatively unaltered habitats in Idaho (Copeland and Venditti 2009; Walters et al. 2013). Here we present a more intensive investigation of the recruitment of natural-origin Chinook Salmon exhibiting two juvenile migration tactics. Juveniles of the first type (downstream rearing, or DSR) initially disperse downstream from natal habitat as parr, winter downstream in nonnatal reaches, and then enter the migration corridor as yearling smolts the following spring. Juveniles of the second type (natal-reach rearing, or NRR) rear in their natal habitat for roughly 1 year after emergence until the onset of smoltification and active seaward migration. Biologists have long known that DSR emigrants use downstream-rearing and wintering habitats in the lower stretches of the Salmon and Grande Ronde rivers or in the middle reaches of the Snake River (Chapman and Bjornn 1969; Raymond 1979; Figure 1), but explicit information on their early life history and fate through adulthood is lacking. Our goal was to elucidate the demographic importance of the two juvenile

migration tactics in 11 stream-type Chinook Salmon populations in Idaho by providing comparisons of (1) estimated emigrant abundance at exit from the natal reach, (2) estimated survival from natal reach to migration corridor entry, (3) estimated survival from migration corridor to adult return to freshwater, and (4) estimated total adult recruitment to freshwater as well as survival from natal reach to adult.

We made several predictions regarding survival among the stages defined above and number of adult recruits of each type. We knew that abundance of DSR emigrants would exceed abundance of NRR emigrants of the same cohort (Walters et al. 2013). A clear contrast in rate of survival from emigration from natal areas to migration corridor entry was anticipated because a portion of the DSR marked at emigration from natal areas die during the winter before the NRR from the same cohort were marked (hypothesis $[H]_1$: DSR < NRR). We hypothesized that the influence of initial emigration timing would become negligible after migration corridor entry because both DSR and NRR juveniles would be large, actively migrating smolts (H_2: DSR = NRR). Given H_1 and H_2, we hypothesized that survival from natal reach to adult would likely favor the NRR emigrants (H_3: DSR < NRR), but the DSR type would return more adults to freshwater because DSR emigrants were numerically dominant (H_4: DSR > NRR). We knew a priori that there would be differences among populations and among cohorts; therefore, these were included as factors in the analysis, but our focus was the comparison of the two types.

METHODS

Study populations.—We examined juvenile production for nine Chinook Salmon populations in Idaho (Figure 1) for 11 cohorts (fish spawned during 1997–2007). All populations are part of the Snake River spring–summer Chinook Salmon Evolutionarily Significant Unit, which is listed as threatened under the U.S. Endangered Species Act (NMFS 1992). All Snake River spring–summer Chinook Salmon are considered to have a stream-type life history (Good et al. 2005). Snake River spring–summer Chinook Salmon are genetically distinct from Chinook Salmon from other parts of the Columbia River basin and from the fall Chinook Salmon within the Snake River, which have an ocean-type life history (Waples et al. 2004; Narum et al. 2007). However, approximately one-third of the smolts from the Pahsimeroi River population emigrate to the ocean as subyearling smolts, which have very low adult return rates (Copeland and Venditti 2009; D. A. Venditti, unpublished data), so only the DSR and NRR emigrants from the Pahsimeroi River are used in this analysis.

Data collection.—Emigrating Chinook Salmon juveniles were collected by a rotary screw trap, typically located near the lower extent of major spawning areas. The traps were deployed as early as possible in the spring (usually early March) and operated until the formation of ice prevented trap
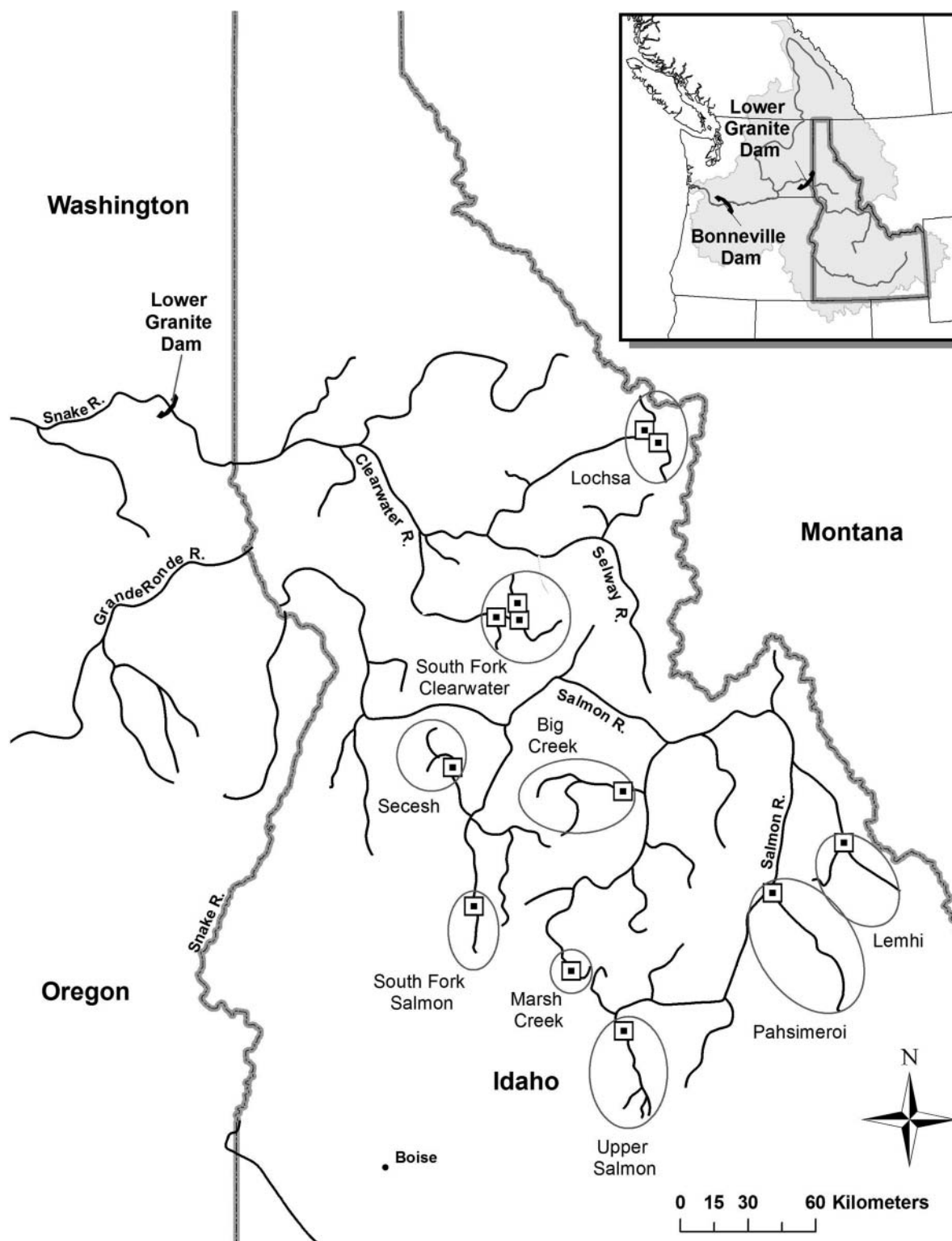
FIGURE 1.   Location of study reaches and Chinook Salmon populations in Idaho. Squares indicate locations of rotary screw traps. Inset shows the study area in relation to the Columbia River basin and Bonneville Dam.

operation (usually the middle of November). Before they were processed, all fish were anesthetized with a buffered solution of tricaine methanesulfonate (MS-222). Trap tenders processed fish at least once daily. Fish were counted and measured, and a subsample was tagged with a PIT tag. The transponder in these tags emits a unique code that can be read by a detector when the tag passes through a magnetic field (Prentice et al. 1990). All fish were measured to the nearest 1 mm from the tip of the snout to the fork of the caudal fin (FL) and scanned for the presence of a PIT tag. Size and visual characteristics (e.g., silver color and parr marks) were used to distinguish NRR (which emigrate directly to the ocean) and DSR (which winter downstream from the trap and emigrate the following spring) for 2–4-week period when both migratory types were captured concurrently (Figure 2). After processing, all PIT-tagged fish were released approximately 0.5 km upstream from the trap. Efficiency of the trap was calculated from recaptures of these fish. Recaptured fish and any individuals not tagged were released below the trap.

Tagging procedures followed recommendations of the PIT Tag Steering Committee (1999). Natural-origin fish (as evidenced by an intact adipose fin) ≥60 mm FL were eligible for tagging (see procedures below). We assumed there was no size-related effect from tagging on growth or survival within the size range tagged (see Ombredane et al. 1998). Tags were injected into the body cavity using a hypodermic needle. Needles and tags were sterilized in ethanol for 10 min prior to and between uses. Essentially all NRR emigrants trapped were tagged. We tagged DSR emigrants at a rate determined by the expected number of emigrants and the number of tags available for the year, which spread tagging effort over the entire migratory period. Tagging data were recorded into a computer file each day and were uploaded to the central repository for all PIT-tagging activities in the Columbia Basin (PIT Tag Information System [PTAGIS], www.ptagis.org) within 48 h.
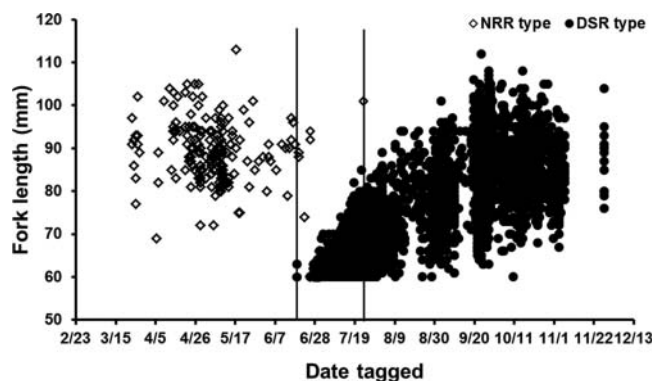

FIGURE 2. An example of the separation between natal-reach-rearing (NRR) and downstream-rearing (DSR) types of Chinook Salmon based on length and time of capture. Data are from individuals tagged from the Marsh Creek population in 2008. The NRR are from the 2006 cohort, and the DSR are from the 2007 cohort. Vertical lines indicate the period of time when the two types were collected concurrently. Dates are given as month/day.

We queried the PTAGIS database for detections of tagged fish as they entered the migratory corridor as smolts at Lower Granite Dam and as returning adults ascending Bonneville Dam (Figure 1). Lower Granite Dam (695 km from the ocean) is the first dam encountered by smolts during seaward migration. Smolts pass the dam primarily through turbine intakes or over the spillway when water is spilled. A portion of the PIT-tagged smolts entered the turbine intakes and was routed away from the powerhouse by submersible bar screens into a bypass fitted with PIT tag monitors that detected PIT-tagged fish with nearly 100% efficiency (Prentice et al. 1990). Bonneville Dam (234 km from the ocean) is the first dam encountered by adults returning to freshwater, and above this point other potentially confounding factors come into play (e.g., nonselective harvest and spill management); therefore, this is a logical endpoint for our study. The ladders that provide adult passage are also equipped with highly efficient PIT tag monitors (i.e., probability of detection ≈1.0: Fryer et al. 2012). We downloaded the detection data for both juveniles and adults from the central database. Detection information was linked to the tagging information.

Data analyses.—Abundance of each emigrant type as they exited the natal reach (natural-origin fish only) was estimated with mark–recapture software designed specifically for time-stratified rotary screw trap data developed by Steinhorst et al. (2004). Periods during which the DSR and NRR passed the traps were further stratified based on changes in flow, temperature, or other variables that affect trap efficiency. Abundance of all emigrants from a cohort by type was estimated using a summation of Bailey's modified estimator (Ricker 1975),

$$N_j = \sum_{i=1}^{k} c_i(m_i + 1)/(r_i + 1),$$

where N_j is number of emigrants of type j, k is the number of periods designated, c_i is the number of all fish captured, m_i is the number of tagged fish released in period i, and r_i is number of recaptures in period i. The estimator was computed using an iterative maximization of the log likelihood, assuming fish are captured independently with probability p_i (equivalent to trap efficiency) and tagged fish mix thoroughly with untagged fish. To get population abundance in populations with more than one trap, abundances were summed because the traps were sampling different tributaries (e.g., in the South Fork Clearwater River population; Figure 1). The point estimates of abundance from each population are used for determining tagging rates. There was no spawning observed in Marsh Creek in 1999; therefore, we excluded that cohort from the analysis. The Big Creek rotary screw trap was first run in 2007, so there are only data from the 2006 and 2007 cohorts for that population.

We estimated survival of each migratory type based on the number of tags placed and then detected at Lower Granite and

Bonneville dams. Survival from trap to Lower Granite Dam (S_{t-l}) and the probability of detection at the dam were computed using a Cormack–Jolly–Seber model implemented by SURPH software (Lady et al. 2010). Survival from smolt emigration at Lower Granite Dam to adult return to Bonneville Dam, commonly referred to as smolt-to-adult return (SAR) rate, was computed as the number of PIT tags detected on adult return at Bonneville Dam divided by the number of tags passing Lower Granite Dam (tags detected in juveniles adjusted for detection probability). Survival rate of fish passing the traps to adulthood (S_a) was estimated by dividing the number of adult detections by the number of PIT tags placed in each cohort because detection probability of adults ascending the Bonneville Dam fish ladders is essentially 1.0 (Fryer et al. 2012) and therefore equivalent between migratory types.

Our goal was to understand the importance of the migratory types to population dynamics, which requires an estimate of adult abundance. Total adult recruitment back to freshwater was the number of tags detected expanded by the tagging rate for each combination of migration tactic, cohort, and population. The tagging rate was estimated by dividing the number of tags placed by the abundance of each emigrant type as they exited the natal reach.

We used a model selection approach to inference. Models were compared and a final model selected for inference based on Akaike's information criterion (AIC) corrected for small sample sizes (AIC_c), which is a quantitative metric that measures a tradeoff of model fit versus parsimony (Burnham and Anderson 2002). We report the ANOVA statistics for each selected model. Acceptable risk of type 1 error was set at 0.05. All models were implemented as general linear models using Systat version 13. Performance of each selected model was assessed by inspection of the residuals.

Each survival metric (S_{t-l}, SAR, S_a) was compared between types by taking the natural logarithm of partitioned survival by DSR emigrants over that of NRR emigrants for each population by cohort. Therefore, we tested the ratio of survival, i.e., $\log_e$ (DSR S/NRR S), which is interpreted as the number of DSR surviving for each surviving NRR emigrant. Thus, the global model was

$$\mathrm{Log}_e(\mathrm{DSR}\,S/\mathrm{NRR}\,S) = \beta_o + \beta_{yr} + \beta_{pop} + \varepsilon,$$

where β_o is the overall mean, β_{yr} is the cohort effect, β_{pop} is the population effect, and ε is residual error. We tested for an interaction between population and cohort with Tukey's test of additivity (Steel et al. 1997). Briefly, predicted values from the main effects model are output and the analysis is rerun using the squared predicted values as a regressor. In this analysis, each cohort by population combination is considered a replicate. We excluded year-class failures from the SAR and S_a analyses (i.e., no adults detected from either type). There were several instances in which adults were detected from one type

but not from the other, so we added a small constant to each SAR and S_a estimate. The minimum observed SAR (0.001101) and S_a (0.000174) were used, which approximate the lowest survival that was detectable. Given that there were more zeros in NRR returns, these additions provided conservative metrics with which to test hypotheses. The value of β_o was used to evaluate hypotheses H_1, H_2, and H_3.

Total adult recruitment was modeled using a square-root transformation before analysis ($y' = \sqrt{y + 0.5}$) to address parametric model assumptions (Zar 1999). There may be differences among cohorts and populations, so these were included to account for their effects and potential interactions. The global model used was then

$$\begin{aligned} N = \beta_o &+ \beta_{type} + \beta_{yr} + \beta_{pop} + (\beta_{type} \times yr) \\ &+ (\beta_{type} \times \beta_{pop}) + (\beta_{pop} \times \beta_{yr}) + \varepsilon, \end{aligned}$$

where β_{type} is the effect of emigrant type and the other parameters are as defined above. Because we were specifically interested in the effects of emigrant type, only models with that effect were evaluated. Models considered included the global model, main effects only, and all possible combinations of two-way interactions. The primary interest is in the difference between adult recruitment by type, so the value of β_{type} was used to evaluate hypothesis H_4.

RESULTS

There were 330,336 juvenile Chinook Salmon PIT-tagged among the 11 cohorts represented in this study, and of these 0.3% were detected as adults returning to Bonneville Dam. We PIT-tagged 2.2% of the DSR emigrants and 10.4% of the NRR emigrants. There were 906 DSR tags and 226 NRR tags detected as adults at Bonneville Dam. The abundance of DSR emigrants exiting the natal reaches was much greater than that of the NRR emigrants, averaging 85.8% of the juvenile production over all populations and cohorts. The average proportion of DSR emigrants ranged from 98.9% in the Secesh population to 70.8% in the South Fork Clearwater population. Selected details of trapping results and estimates used in the analyses are presented in Table A.1 in the Appendix.

Differential Life Stage Survival

Survival from trap to Lower Granite Dam was almost always higher for NRR emigrants than for DSR emigrants (Figure 3). The average $\log_e$ ratio of S_{t-l} was −0.89, i.e., survival of NRR emigrants was 2.4 times higher on average. The only positive $\log_e$ ratio was in the 2007 cohort from the Secesh River, in which S_{t-l} was higher for DSR emigrants. All other $\log_e$ S_{t-l} ratios were negative and ranged from −0.01 to −2.52.

Model selection for S_{t-l} was not straightforward. The AIC_c for the full model was 58.95 but the main effects were not significant, making their interaction hard to interpret. The next
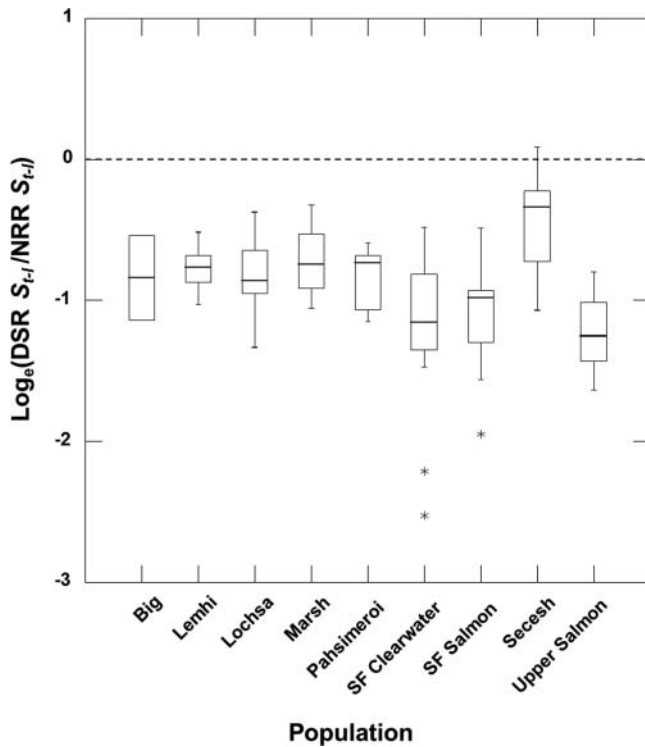
FIGURE 3. Log_e ratios of survival of Chinook Salmon from the trap to Lower Granite Dam (S_{t-l}). Points above zero (dashed line) indicate better survival by downstream-rearing emigrants; points below zero indicate better survival by natal-reach-rearing emigrants. Boxes represent the middle 50% of the observations and the median is shown by the bisecting line. Whiskers show range of values within 1.5 times the interquartile range. Outliers are represented by asterisks (*).

best model had an AIC_c of 60.21 (a difference of <2), indicating an equivalent amount of support (Burnham and Anderson 2002), so we selected that model for inference. The selected model of relative juvenile survival included both population and cohort effects (Table 1). The estimate of β_o (–0.90) was significantly less than zero ($F = 628.3$, $P < 0.001$); therefore, survival to Lower Granite Dam was significantly greater for NRR emigrants. The predicted difference between DSR S_{t-l} and NRR S_{t-l} was least in the Secesh population and greatest in the South Fork Clearwater population. Similarly by cohort, the predicted difference between DSR S_{t-l} and NRR S_{t-l} was greatest in the 2001 cohort and least in the 1998 cohort. However, note that S_{t-l} estimates for DSR emigrants included winter mortality whereas S_{t-l} for NRR emigrants did not because the latter were not tagged until exiting the natal reach after winter.

Relative SAR was more variable but tended to favor DSR emigrants (Figure 4). The average log_e SAR ratio was 0.50, which means that DSR SAR was 1.6 times higher on average. However, values ranged from −3.1 to 3.7. The extremes occurred when adults of one emigrant type but not the other were detected in a cohort. Of the 78 cohorts that produced an adult recruit, there were 26 instances of zero returns by one type when the other produced adults. In 18 of these 26 instances, the NRR type produced no adults.

The best model of relative SAR included a population effect (Table 1). This model had an AIC_c weight > 0.99, indicating it essentially was the only supportable model. The estimate of β_o (0.43) was significantly greater than zero ($F = 8.64$, $P < 0.004$); therefore, predicted survival from Lower Granite Dam to adult return was significantly greater for DSR

TABLE 1. Results of ANOVA of the selected models for survival from natal reach to Lower Granite Dam (S_{t-l}), smolt-to-adult survival (SAR), survival to adulthood (S_a), and number of adult returns (number) for Chinook Salmon.

| Source	Sums of squares	df	Mean squares	F-ratio	P-value
Log_e ratio S_{t-l}					
Population	5.48	8	0.69	8.43	<0.001
Cohort	4.75	10	0.48	5.85	<0.001
Error	5.69	70	0.08		
Log_e ratio SAR					
Population	33.48	8	4.19	2.69	0.01
Error	107.22	69	1.55		
Log_e ratio S_a					
Population	74.67	8	9.33	4.22	<0.001
Error	152.62	69	2.21		
Number					
Population	2,635.91	8	329.49	15.17	<0.001
Cohort	1,669.74	10	166.97	7.69	<0.001
Type	1,665.05	1	1,665.05	76.66	<0.001
Population × Type	2,389.61	8	298.70	13.75	<0.001
Cohort × Type	720.06	10	72.01	3.32	<0.001
Error	3,040.65	140	21.72		
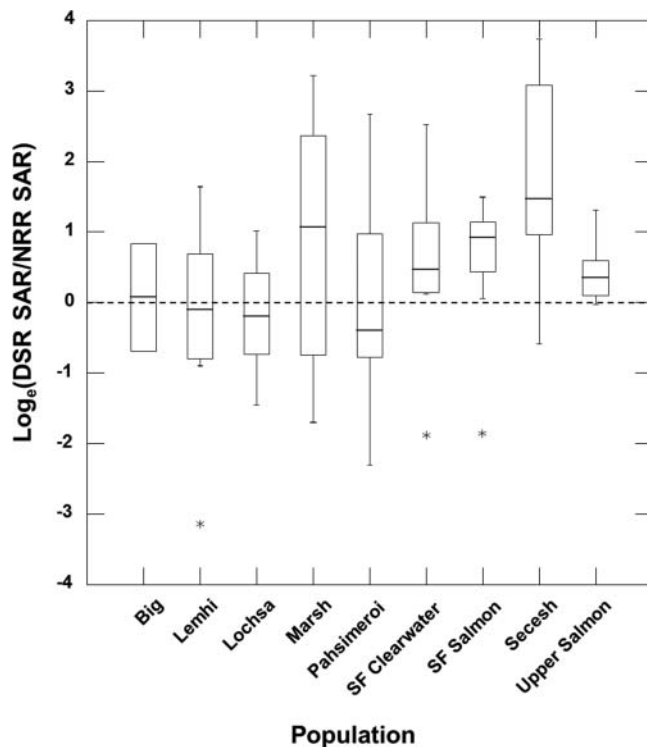
FIGURE 4. Log_e ratios of smolt-to-adult return (SAR) rate for Chinook Salmon. Points above zero (dashed line) indicate better survival by downstream-rearing emigrants; points below zero indicate better survival by natal-reach-rearing emigrants. Boxes represent the middle 50% of the observations and the median is shown by the bisecting line. Whiskers show range of values within 1.5 times the interquartile range. Outliers are represented by asterisks (*).

FIGURE 5. Log_e ratios of survival of Chinook Salmon from the trap to adult recruitment (S_a). Points above zero (dashed line) indicate better survival by downstream-rearing emigrants; points below zero indicate better survival by natal-reach-rearing emigrants. Boxes represent the middle 50% of the observations and the median is shown by the bisecting line. Whiskers show range of values within 1.5 times the interquartile range. Outliers are represented by asterisks (*).

emigrants. The predicted log_e SAR ratio favored DSR emigrants in six populations and NRR emigrants in three populations. The ratio of DSR SAR to NRR SAR was highest in the Secesh and lowest in the Lemhi populations.

Survival rate to adulthood (S_a) was extremely variable (Figure 5), averaging 0.38% over type, populations, and years. Note that the average includes cohort failures, which are omitted from the models reported below. Survival among cohorts that returned adults varied from 0.11% in the 1999 cohort to 1.13% in the 2006 cohort. Among populations, S_a was greatest for Big Creek (1.56%), but this was based only on two cohorts when there were better-than-average returns in all populations. For the other populations, S_a varied from 0.11% (South Fork Clearwater) to 0.50% (Lemhi River). Averaging over all population and cohort combinations, mean S_a was 0.32% and 0.43% for DSR emigrants and NRR emigrants, respectively.

The differential rate at which migrants returned as adults was not influenced by cohort but there were differences among populations (Table 1). This model also had an AIC_c weight > 0.99, indicating it essentially was the only supportable model. The ratio of DSR S_a to NRR S_a was highest in the Secesh and lowest in the Lemhi populations. The estimate of β_o (-0.11) was not significantly different from zero ($F = 0.35$, $P = 0.56$);

therefore, survival from the natal reach to adult return to freshwater was equivalent between types after population and cohort effects were accounted for.

Total Adult Recruitment

We estimated that 23,449 adults returned to freshwater from our study populations from the 11 cohorts. Of these, 89.5% were returning DSR emigrants. The highest overall recruitment was by the 2006 cohort with 4,601 adult recruits. The lowest overall recruitment was by the 1999 cohort with only 45 recruits. There were 12 instances of recruitment failure among the study populations, of which half were in the 1999 cohort. The South Fork Clearwater and Lochsa populations each had three failures: the 1999, 2001, and 2005 cohorts. In most cases the majority of the returning adults were DSR emigrants (Figure 6). Conversely, adult spawning cohorts composed mostly of returning NRR emigrants only occurred when adult recruitment was very low. The cohorts dominated by NRR adults (14 out of 78) had an average estimated return of only 36 fish.

For inferences about total adult recruitment, we selected the model including all main effects plus two interactions:

FIGURE 6. Proportion of the adult Chinook Salmon recruits that exhibited the downstream-rearing tactic (DSR) in relation to total adult recruitment for each population and cohort.
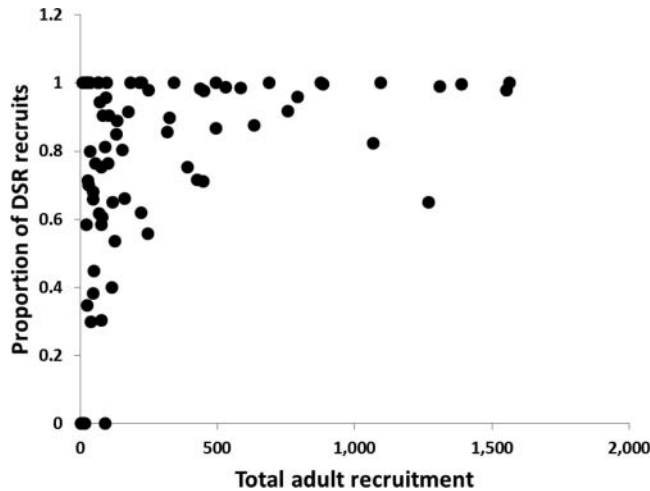

FIGURE 7. Comparison of total adult recruitment by emigrant type and population for Chinook Salmon. For each population, data for downstream-rearing emigrants are on the left (open boxes) and natal-reach-rearing emigrants are on the right (shaded boxes). Boxes represent the middle 50% of the observations and the median is shown by the bisecting line. Whiskers show range of values within 1.5 times the interquartile range. Outliers are represented by asterisks (*).

between emigrant type and population, and between emigrant type and cohort (Table 1). The selected model was 32.8 times (AIC$_c$ weight, 0.97) more likely than the next best model (AIC$_c$ weight, 0.03), which had the main effects and one interaction term (emigrant type and population).The selected model always predicted more DSR emigrants than NRR emigrants to return, which was supported by PIT tag observations. Migrant type had a significant effect on the number of returning adults ($\beta_{type} = 3.64$; Table 1). The predicted difference between types was lowest in Pahsimeroi, followed by Lochsa, South Fork Clearwater, and Lemhi populations, respectively (Figure 7).

DISCUSSION

Our goal was to compare the demographic performance of the DSR and NRR types in order to increase understanding of the dynamics of the Chinook Salmon study populations. We confirmed that NRR emigrants survive from natal reach to the migration corridor at a greater rate (H_1: DSR < NRR). However, the second prediction (H_2: DSR = NRR) was refuted because we found that SARs were not equivalent; therefore, the influence of type was not negligible after entering the migratory corridor (DSR > NRR). Consequently, the third prediction (H_3: DSR < NRR) was refuted because survival from natal reach to adult was equivalent between types (DSR = NRR). Total adult recruitment to stream-type Chinook Salmon populations in Idaho is comprised mostly of fish that dispersed from their natal habitats and reared in reaches downstream prior to smoltification (DSR type), although the size of the effect depended on cohort and population. This result corroborated our last prediction (H_4: DSR > NRR).

We conclude that DSR emigrants are the more productive juvenile type in stream-type Chinook Salmon populations in

Idaho. The relative survival advantage between the two types ($\log_e S_a$) varies around zero among populations. However, the numerical advantage of the DSR type carries through to adult recruitment back to freshwater, although ratios of survival rates were much more variable than the numerical effect. The numerical advantage of adults produced from DSR emigrants arises from a greater abundance at exit from natal reaches but was not constant in time. For example, in cohorts returning fewer than 100 fish, NRR emigrants dominated numerically (Figure 6). Logically, relative fitness was greater for the NRR type for those populations at those times. We discuss the implications of our results for fitness and population dynamics below.

Demographic Effects of Diversity in Juvenile Migration Tactics

Our study demonstrates the importance of different migratory tactics to population recruitment and resilience. Diversity in migratory life histories spreads demographic risk (Kerr et al. 2010) and some life histories may tend to produce most of the spawning population. The more dispersive type is often the more productive component of the population (e.g., Kraus and Secor 2005), as we also found. In effect, the dispersive

type expands the niche of the population to take advantage of a greater expanse of the accessible habitat, resulting in greater adult recruitment to the spawning population (e.g., Neville et al. 2006; Morita et al. 2009; Anderson et al. 2013).

The fitness of a migratory life history is sensitive to the costs of movement (Gross 1987; Hendry et al. 2004); therefore, migratory fishes need connected stream reaches with rearing habitats of good quality to use (Northcote 1997). Connectivity to high-quality rearing habitats is important, even if these areas are not used for spawning and are distant from natal reaches (Anderson et al. 2013). Nonnatal habitats can provide significant survival and growth advantages for juvenile salmon, especially through winter (Ebersole et al. 2006). There may be indirect synergistic benefits to individual fitness from the ability to use a suite of habitats because juveniles that rear well tend to have good life performance (Lindström 1999; Metcalfe and Monaghan 2001; Taborsky 2006).The populations in this study have several hundred kilometers of river between their natal reaches and Lower Granite Dam (266 to 747 km), below which there is no record of them rearing. Much of this area above the dam is within statutory wilderness and therefore is affected minimally by anthropogenic factors, and also offers the riverscape connectivity necessary for dispersive life histories to be successful (Baguette et al. 2013). Population dynamics of stream fishes are greatly affected by the ability to move among habitats and exploit food resources (Schlosser 1995; Northcote 1997; Wipfli and Baxter 2010). Watersheds with a high degree of habitat complementation and connectivity support more robust salmon runs than watersheds with lower habitat complementation and connectivity (Kim and Lapointe 2011).

To advance our knowledge of the dynamics of these populations, it is necessary to understand the fitness values of the emigrant types that comprise them and when each type is likely to be successful. It is unclear from the data in hand at what point DSR emigrants may achieve a true survival advantage over NRR emigrants. In this study, winter survival is accounted for in DSR emigrants, whereas it is not in NRR emigrants. Winter can be a stressful season for young salmonids (Cunjak et al. 1998; Huusko et al. 2007; Brown et al. 2011). If winter survival is accounted for in the NRR type, DSR fitness may be higher than NRR fitness, but we do not have reliable survival estimates in the natal reaches of the study populations. Smith and Griffith (1994) reviewed studies of winter survival in 24 populations of juvenile salmonids exposed to prolonged periods of 0°C temperatures and estimated mean survival was 0.50 (SD = 0.18). Mitro and Zale (2002) estimated winter survival was 0.20 in good habitat for young Rainbow Trout *O. mykiss* in Henrys Fork in Idaho near our study area (we use this as a benchmark for severe winter conditions). Clearly, there should be some amount of winter mortality on fish remaining in their natal reaches until emigration.

We conducted a thought experiment to examine the likely consequences of winter mortality on relative fitness between the emigrant types. Consider S_w^*, the NRR winter survival threshold at which S_a is equivalent between types. This threshold is related to S_a by $\log_e(1) = \log_e[\text{DSR } S_a/(\text{NRR } S_a \times S_w^*)]$, which simplifies to $S_w^* = \text{DSR } S_a/\text{NRR } S_a$. For the 1998 cohort in the upper Salmon River, the closest data point to the model intercept β_o (–0.11), S_w^* is 0.92. On average across the data set, likely winter survival will be such that the DSR type should have higher relative fitness. The S_w^* will vary among populations and is lowest for the Lochsa population (0.32). Severe winter conditions imply that the DSR migrant type has the higher relative fitness in all populations. Winter severity will vary, which may explain why there was a significant cohort effect on total adult recruitment but not on S_a. Certainly, the presence of significant population and cohort effects on total adult recruitment imply that relative fitness is not constant. This thought experiment underscores the importance to salmon conservation of dispersive life histories and the rearing and wintering habitats that support them; however, no studies have yet demonstrated that alternative migratory tactics have equal or unequal average fitness in salmonid fishes (Dodson et al. 2013).

Juvenile Chinook Salmon exhibiting the DSR migration tactic achieved a survival advantage over the NRR emigrants in SAR. Theoretically, dispersing individuals may accrue benefits by avoiding conspecific competition or deteriorating environmental conditions but incur costs by expenditures of limited time and energy as well as the risk of failure, i.e., mortality (Bowler and Benton 2005; Baguette et al. 2013). In this case, we hypothesize that the proximate advantages of downstream rearing are (1) earlier and easier final emigration the following spring and (2) increased overwinter survival and additional growth opportunity. These two hypotheses are not mutually exclusive.

In terms of demography, dispersive life history types increase population productivity and resilience, but resident life histories enhance stability, and thus both contribute to population persistence (Kerr et al. 2010). In the stream-type Chinook Salmon populations of Idaho, the capacity of the habitat to produce NRR emigrants is limited, whereas production of DSR emigrants is less constrained (Walters et al. 2013). In most of Idaho, the salmon spawning reaches are infertile (Sanderson et al. 2009) and have a short growing season. Salmon spawning is concentrated by philopatry, but rearing space and food usually limit smolt production rather than spawning habitat (Quinn 2005). This tension impels movement by juveniles to prepare for successful emigration to, and survival in, the ocean. The tradeoff between freshwater foraging opportunities versus winter mortality encourages diversity in migratory life histories (Dodson et al. 2013). Given limitations in spawning reaches, the DSR type should be more important in recovery as abundance is increasing, while the

NRR emigrants should buffer the population during periods of low abundance (Figure 6).

Implications for the Snake River Basin

For population-specific assessment and management of Chinook Salmon in the Snake River basin, a better understanding of rearing and winter habitats is needed. Migrating salmonids often show fidelity to feeding and refuge habitats (Northcote 1997); therefore, specific reaches may be important to a population. In interior Oregon, Tattam (2006) found that most individuals of a steelhead (anadromous Rainbow Trout) population spent the winter in a relatively short reach in the main stem of the South Fork John Day River. Confined use of habitat increases population vulnerability to catastrophe. In this study, we demonstrated recruitment of fish from downstream rearing habitats into the adult population, but we do not know the extent of these habitats. However, DSR emigrants typically arrive at Lower Granite Dam approximately a month earlier than the NRR emigrants (Venditti et al. 2005), suggesting that habitats occupied by DSR emigrants during winter are a significant distance downstream from the natal reaches. Our results suggest a broad focus is needed in restoration plans and that rearing reaches downstream from spawning grounds should also be addressed. In general, this study has interesting demographic implications for how migratory populations of stream fish use accessible habitats and how managers may use this understanding to increase adult recruitment.

Similarly, management of the migration corridor is focused on the aggregate rather than specific populations of concern. If there are weak stocks, the aggregate approach may inhibit effectiveness of recovery actions. Early ocean entrance seems to be important to survival to adulthood (Scheuerell et al. 2009). Several studies have demonstrated that delayed emigration to the ocean results in lower survival (Petrosky and Schaller 2010; Haeseker et al. 2012). Because DSR emigrants have a different timing into the migration corridor (Venditti et al. 2005), management actions in the migratory corridor may affect populations differently.

In summary, juvenile salmon migrate to the ocean where they can maximize growth and therefore eventual fecundity. Stream-type Chinook Salmon in Idaho spawn in some of the highest, most remote locations accessible. Here they potentially overseed the rearing capacity of natal habitats with eggs but maximize early survival and therefore production of fry, even though current adult escapements are well below historical abundance. However, these streams are infertile with short growing seasons and harsh winters. It is logical that salmon populations constrained by rearing and wintering habitat in natal reaches would exhibit some amount of juvenile movement to avoid these constraints. We demonstrated that juvenile Chinook Salmon in Idaho do indeed use downstream rearing habitats effectively, thereby increasing recruitment of adults back to the spawning gravels in these populations. This study illustrates how dispersive life histories are essential to achieve the full productive potential of migratory stream fish populations.

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Appendix: Trap and Population Statistics

TABLE A.1. Summary of trap operations and values used in the analyses of Chinook Salmon by population, cohort, and tactic. These include number of tags placed and estimates of trap efficiency, juvenile abundance (juvenile $\widehat{N}$), survival from trap to Lower Granite Dam (S_{t-l}), smolt-to-adult return rate (SAR), survival from trap to adult (S_a), and total adult recruitment (adult $\widehat{N}$). Tactics are downstream rearing (DSR) or natal-reach rearing (NRR).

Cohort	Tactic	Tags	Trap efficiency	Juvenile $\widehat{N}$	S_{t-l}	SAR	S_a	Adult $\widehat{N}$
— **Big Creek**								
2007	DSR	3,185	0.0923	46,555	0.3970	0.0301	0.0119	555
	NRR	829	0.1000	9,331	0.6810	0.0124	0.0084	79
2006	DSR	5,454	0.2372	44,461	0.2580	0.0718	0.0185	823
	NRR	725	0.0400	18,981	0.5140	0.0456	0.0234	445
— **Lemhi**								
2007	DSR	3,223	0.0991	28,928	0.3335	0.0093	0.0031	90
	NRR	340	0.1997	1,190	0.7172	0.0041	0.0029	4
2006	DSR	3,327	0.3440	12,909	0.3175	0.0293	0.0093	120
	NRR	258	0.2610	644	0.7539	0.0308	0.0233	15
2005	DSR	2,452	0.2743	11,052	0.3281	0.0394	0.0061	68
	NRR	310	0.3162	1,206	0.7200	0.0086	0.0032	4
2004	DSR	2,063	0.1584	9,951	0.2658	0.0055	0.0015	14
	NRR	409	0.3374	1,312	0.6800	0.0108	0.0073	10
2003	DSR	1,613	0.1491	6,375	0.1961	0.0000	0.0000	0
	NRR	383	0.2559	1,590	0.4700	0.0000	0.0000	0
2002	DSR	4,147	0.2167	17,981	0.2646	0.0046	0.0012	22
	NRR	586	0.2872	2,000	0.5300	0.0000	0.0000	0
2001	DSR	2,580	0.0792	40,429	0.1712	0.0045	0.0008	31
	NRR	370	0.1005	2,898	0.4800	0.0113	0.0054	16
2000	DSR	1,908	0.1283	10,836	0.3109	0.0084	0.0026	28
	NRR	199	0.1313	1,489	0.5200	0.0097	0.0050	7
1999	DSR	1,918	0.1434	12,246	0.2743	0.0000	0.0000	0
	NRR	142	0.1631	852	0.5800	0.0243	0.0141	12
1998	DSR	1,847	0.1486	10,739	0.3693	0.0147	0.0054	58
	NRR	283	0.1555	1,818	0.6700	0.0158	0.0106	19
1997	DSR	3,586	0.1597	40,425	0.3788	0.0029	0.0011	45
	NRR	623	0.1293	4,930	0.7400	0.0087	0.0064	32

TABLE A.1.   Continued.

Cohort	Tactic	Tags	Trap efficiency	Juvenile $\widehat{N}$	S_{t-l}	SAR	S_a	Adult $\widehat{N}$
				Lochsa				
2007	DSR	1,020	0.2635	4,604	0.3763	0.0182	0.0069	32
	NRR	175	0.1372	1,287	0.8906	0.0128	0.0114	15
2006	DSR	2,187	0.4207	6,137	0.2522	0.0272	0.0069	42
	NRR	163	0.0902	2,128	0.6773	0.0091	0.0061	13
2005	DSR	1,508	0.2059	9,861	0.1655	0.0000	0.0000	0
	NRR	116	0.0442	2,166	0.5531	0.0000	0.0000	0
2004	DSR	3,398	0.2250	27,780	0.2769	0.0064	0.0018	49
	NRR	358	0.0750	5,707	0.6543	0.0085	0.0056	32
2003	DSR	2,130	0.1631	81,849	0.2145	0.0000	0.0000	0
	NRR	515	0.0998	4,998	0.5347	0.0036	0.0019	10
2002	DSR	2,964	0.1672	41,443	0.1768	0.0057	0.0010	42
	NRR	351	0.0706	4,624	0.3325	0.0171	0.0057	26
2001	DSR	3,259	0.2046	38,426	0.1012	0.0000	0.0000	0
	NRR	426	0.0815	5,014	0.3834	0.0000	0.0000	0
2000	DSR	2,288	0.2027	53,563	0.2025	0.0086	0.0017	94
	NRR	168	0.1014	1,705	0.4052	0.0147	0.0060	10
1999	DSR	623	0.2113	4,735	0.3814	0.0000	0.0000	0
	NRR	284	0.0654	4,025	0.5538	0.0000	0.0000	0
1998	DSR	1,226	0.0890	13,794	0.3418	0.0143	0.0049	68
	NRR	360	0.0640	7,045	0.4983	0.0167	0.0083	59
1997	DSR	2,764	0.1607	50,400	0.3054	0.0047	0.0014	73
	NRR	704	0.0782	12,234	0.5901	0.0024	0.0014	17
				Marsh Creek				
2007	DSR	6,324	0.2216	39,412	0.3272	0.0174	0.0057	224
	NRR	265	0.3596	1,053	0.4514	0.0000	0.0000	0
2006	DSR	7,051	0.2708	31,834	0.3714	0.0363	0.0135	429
	NRR	190	0.2895	691	0.6300	0.0167	0.0105	7
2005	DSR	4,489	0.1663	36,077	0.2527	0.0106	0.0027	96
	NRR	79	0.3333	228	0.5900	0.0000	0.0000	0
2004	DSR	2,118	0.1395	18,700	0.2088	0.0023	0.0005	9
	NRR	211	0.3684	854	0.5200	0.0000	0.0000	0
2003	DSR	2,520	0.2715	207,358	0.1000	0.0000	0.0000	0
	NRR	729	0.3478	2,142	0.2800	0.0049	0.0014	3
2002	DSR	3,920	0.2520	139,993	0.1554	0.0000	0.0000	0
	NRR	2,174	0.4423	6,226	0.3300	0.0014	0.0005	3
2001	DSR	3,127	0.4334	112,584	0.1672	0.0019	0.0003	36
	NRR	650	0.3812	2,084	0.4800	0.0000	0.0000	0
2000	DSR	1,566	0.1642	14,823	0.3602	0.0142	0.0051	76
	NRR	119	0.2542	465	0.5400	0.0311	0.0168	8
1998	DSR	2,124	0.1024	61,880	0.3020	0.0265	0.0080	495
	NRR	263	0.1686	1,694	0.6300	0.0000	0.0000	0
1997	DSR	2,180	0.1892	29,396	0.3321	0.0069	0.0023	67
	NRR	157	0.0921	1,881	0.6900	0.0000	0.0000	0
				Pahsimeroi				
2007	DSR	856	0.0928	10,610	0.2841	0.0041	0.0012	12
	NRR	77	0.0548	1,080	0.5124	0.0507	0.0260	28
2006	DSR	860	0.1730	6,407	0.2200	0.0793	0.0174	112
	NRR	276	0.1451	1,853	0.6700	0.0162	0.0109	20

TABLE A.1. Continued.

Cohort	Tactic	Tags	Trap efficiency	Juvenile $\widehat{N}$	S_{t-l}	SAR	S_a	Adult $\widehat{N}$
2005	DSR	2,374	0.0624	46,065	0.2300	0.0073	0.0017	78
	NRR	817	0.1243	6,595	0.5500	0.0067	0.0037	24
2004	DSR	1,995	0.1276	14,029	0.2027	0.0074	0.0015	21
	NRR	1,461	0.2244	6,731	0.6400	0.0021	0.0014	9
2003	DSR	1,920	0.0935	37,977	0.2200	0.0000	0.0000	0
	NRR	1,422	0.2392	6,187	0.4300	0.0065	0.0028	17
2002	DSR	2,639	0.1063	26,394	0.2300	0.0033	0.0008	20
	NRR	810	0.2518	3,433	0.4800	0.0051	0.0025	8
2001	DSR	2,721	0.0794	36,176	0.1992	0.0000	0.0000	0
	NRR	1,304	0.2452	6,189	0.5800	0.0013	0.0008	5
2000	DSR	320	0.0614	5,610	0.2100	0.0149	0.0031	18
	NRR	127	0.0439	4,083	0.6100	0.0000	0.0000	0
1999	DSR	1,434	0.1622	10,316	0.2700	0.0000	0.0000	0
	NRR	120	0.1391	1,924	0.5300	0.0000	0.0000	0
1998	DSR	825	0.1109	15,751	0.3700	0.0131	0.0048	76
	NRR	320	0.1234	2,646	0.7400	0.0211	0.0156	41
1997	DSR	878	0.1408	7,855	0.3602	0.0063	0.0023	18
	NRR	478	0.1261	3,485	0.7300	0.0115	0.0084	29
Secesh								
2007	DSR	4,265	0.0546	128,935	0.2521	0.0270	0.0068	877
	NRR	409	0.1659	1,685	0.2310	0.0000	0.0000	0
2006	DSR	4,971	0.2475	55,098	0.2772	0.0450	0.0125	687
	NRR	176	0.0000	0	0.4945	0.0000	0.0000	0
2005	DSR	3,325	0.1896	227,198	0.1943	0.0294	0.0057	1,298
	NRR	616	0.1070	2,422	0.2681	0.0182	0.0049	12
2004	DSR	3,516	0.1433	392,659	0.1318	0.0302	0.0040	1,563
	NRR	514	0.0636	3,739	0.1853	0.0000	0.0000	0
2003	DSR	4,764	0.1039	876,489	0.1436	0.0015	0.0002	184
	NRR	1,108	0.1786	4,613	0.2367	0.0000	0.0000	0
2002	DSR	3,327	0.1412	568,760	0.0951	0.0063	0.0006	342
	NRR	1,026	0.0982	6,619	0.2770	0.0000	0.0000	0
2001	DSR	6,967	0.1886	747,244	0.0990	0.0029	0.0003	215
	NRR	1,067	0.1231	5,471	0.2369	0.0000	0.0000	0
2000	DSR	5,232	0.2402	357,372	0.1596	0.0192	0.0031	1,093
	NRR	436	0.2180	1,355	0.4279	0.0000	0.0000	0
1999	DSR	5,390	0.2888	45,092	0.3463	0.0021	0.0007	33
	NRR	716	0.2877	2,025	0.4182	0.0000	0.0000	0
1998	DSR	3,604	0.1477	103,977	0.3181	0.0419	0.0133	1,385
	NRR	351	0.1381	1,441	0.3223	0.0088	0.0028	4
1997	DSR	6,601	0.1231	177,971	0.2640	0.0052	0.0014	243
	NRR	287	0.2438	1,378	0.3429	0.0102	0.0035	5
South Fork Clearwater								
2007	DSR	3,371	0.3538	27,404	0.1876	0.0127	0.0024	65
	NRR	818	0.1673	6,761	0.3035	0.0000	0.0000	0
2006	DSR	1,592	0.3198	7,171	0.1965	0.0064	0.0013	9
	NRR	1,103	0.1579	9,643	0.3405	0.0053	0.0018	17
2005	DSR	683	0.0846	7,444	0.0818	0.0000	0.0000	0
	NRR	2,329	0.2726	10,192	0.3565	0.0000	0.0000	0

TABLE A.1. Continued.

Cohort	Tactic	Tags	Trap efficiency	Juvenile $\widehat{N}$	S_{t-l}	SAR	S_a	Adult $\widehat{N}$
2004	DSR	2,725	0.1671	72,679	0.1453	0.0101	0.0015	107
	NRR	570	0.1222	15,795	0.4689	0.0075	0.0035	55
2003	DSR	5,736	0.1684	139,993	0.1584	0.0011	0.0002	24
	NRR	3,881	0.1792	26,053	0.5027	0.0000	0.0000	0
2002	DSR	3,141	0.1445	192,887	0.0519	0.0123	0.0006	123
	NRR	2,434	0.1212	36,072	0.4739	0.0017	0.0008	30
2001	DSR	1,028	0.1000	94,471	0.0341	0.0000	0.0000	0
	NRR	2,800	0.1200	27,228	0.4257	0.0000	0.0000	0
2000	DSR	902	0.1300	19,463	0.1615	0.0069	0.0011	22
	NRR	1,832	0.2400	16,298	0.5510	0.0030	0.0016	27
1999	DSR	411	0.2595	1,802	0.2201	0.0000	0.0000	0
	NRR	324	0.1869	1,739	0.4898	0.0000	0.0000	0
1998	DSR	2,372	0.1993	116,223	0.2055	0.0123	0.0025	294
	NRR	1,767	0.1923	19,047	0.4716	0.0108	0.0051	97
1997	DSR	1,825	0.0399	528,900	0.1706	0.0000	0.0000	0
	NRR	1,444	0.1836	32,445	0.4569	0.0061	0.0028	90
South Fork Salmon								
2007	DSR	5,975	0.1996	52,946	0.2401	0.0230	0.0055	292
	NRR	1,491	0.3116	4,866	0.6100	0.0110	0.0067	33
2006	DSR	2,203	0.1762	69,770	0.2287	0.0476	0.0109	760
	NRR	944	0.4034	3,004	0.5800	0.0183	0.0106	32
2005	DSR	5,533	0.2878	63,248	0.2333	0.0108	0.0025	160
	NRR	2,008	0.4648	5,977	0.3800	0.0066	0.0025	15
2004	DSR	4,351	0.2889	313,995	0.1350	0.0136	0.0018	577
	NRR	1,561	0.4358	6,443	0.3600	0.0036	0.0013	8
2003	DSR	2,566	0.2020	546,670	0.1305	0.0000	0.0000	0
	NRR	2,583	0.3666	7,562	0.3800	0.0000	0.0000	0
2002	DSR	3,449	0.1290	761,350	0.0948	0.0061	0.0006	441
	NRR	1,375	0.2656	5,121	0.3800	0.0057	0.0022	11
2001	DSR	2,246	0.1588	659,711	0.0656	0.0204	0.0013	881
	NRR	587	0.3325	2,354	0.4600	0.0037	0.0017	4
2000	DSR	1,312	0.1721	132,065	0.1071	0.0000	0.0000	0
	NRR	650	0.3167	3,813	0.5100	0.0060	0.0031	12
1999	DSR	1,394	0.0979	194,042	0.1900	0.0000	0.0000	0
	NRR	480	0.2312	6,888	0.4800	0.0000	0.0000	0
1998	DSR	4,478	0.0932	242,991	0.2008	0.0311	0.0063	1,519
	NRR	1,582	0.1575	9,055	0.3800	0.0100	0.0038	34
1997	DSR	2,811	0.0668	366,613	0.1559	0.0091	0.0014	522
	NRR	949	0.1916	6,932	0.5200	0.0020	0.0011	7
Upper Salmon								
2007	DSR	1,579	0.0196	74,983	0.2070	0.0275	0.0057	427
	NRR	1,210	0.2264	5,728	0.6300	0.0184	0.0116	66
2006	DSR	3,331	0.0349	112,624	0.1938	0.0403	0.0078	879
	NRR	369	0.0351	9,964	0.6600	0.0287	0.0190	189
2005	DSR	4,094	0.0167	257,673	0.1576	0.0171	0.0027	692
	NRR	575	0.0464	12,010	0.5800	0.0090	0.0052	63
2004	DSR	4,456	0.0555	177,721	0.1313	0.0137	0.0018	319
	NRR	1,634	0.0919	17,682	0.5700	0.0129	0.0073	130

TABLE A.1. Continued.

Cohort	Tactic	Tags	Trap efficiency	Juvenile $\widehat{N}$	S_{t-l}	SAR	S_a	Adult $\widehat{N}$
2003	DSR	2,982	0.1261	137,286	0.1034	0.0032	0.0003	46
	NRR	4,126	0.1232	47,435	0.5300	0.0027	0.0015	69
2002	DSR	4,194	0.0955	193,337	0.1086	0.0066	0.0007	138
	NRR	2,507	0.1965	34,049	0.4700	0.0068	0.0032	109
2001	DSR	3,587	0.1224	164,990	0.1283	0.0065	0.0008	138
	NRR	2,649	0.1771	28,182	0.5200	0.0058	0.0030	85
2000	DSR	2,557	0.1448	59,827	0.1687	0.0301	0.0051	304
	NRR	695	0.0409	28,096	0.5900	0.0073	0.0043	121
1999	DSR	908	0.0864	14,691	0.2487	0.0000	0.0000	0
	NRR	384	0.1882	1,991	0.6200	0.0000	0.0000	0
1998	DSR	1,019	0.0402	30,750	0.2617	0.0337	0.0088	272
	NRR	527	0.1061	4,868	0.5800	0.0164	0.0095	46
1997	DSR	353	0.0523	8,020	0.2922	0.0097	0.0028	23
	NRR	279	0.0291	14,683	0.6600	0.0054	0.0036	53