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Habitat affinity and density-dependent movement as indicators of fish habitat restoration efficacy

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Abstract. In mark-recapture assays from four different study years, the affinity of young-of-the-year Chinook Salmon (*Oncorhynchus tschawytscha*) and steelhead (*O. mykiss*) for stream pools restored with or created by engineered log structures was greater than that for pools without restoration, though with high interannual variability. From corresponding distribution and abundance data, it was clear that behavioral data are not always concordant with single observations of abundance. The same was true of the correlation between either behavior or abundance and physical characteristics of pools, although depth and current velocity had some explanatory power for both responses in Chinook. Density-dependent immigration into pools by Chinook indicated that restored pools have greater capacity for this species than unrestored pools; however no such pattern emerged for steelhead. Variation among individuals in body condition has implications for population-wide fitness and low variation was correlated with stronger affinity for pools. This suggests that pools mediate habitat-related trade-offs and that restoring them might have positive effects on fitness. Thus, behavioral data appear to provide stronger indications of restoration effectiveness than observational data alone.

Key words: habitat selection, density-dependence, salmonids, restoration, state-dependence.

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INTRODUCTION

Structures placed in streams to create or augment pools are a significant part of restoration efforts in the Pacific Northwest (Roni et al. 2002) because these habitats are important to the rearing phase of the life cycle of salmonids (Roni et al. 2008). For conservation agencies to evalute effectiveness of restoration efforts, appropriate metrics are required (Block et al. 2001). However, such studies usually rely upon comparisons of distribution of individuals among both restored and unrestored habitat (Bond and Lake 2003, Roni et al. 2008). This is an important basis for evaluation, but much of the literature shows small or no effects of restoration when only distribution and abundance are considered (Roni et al. 2008, Whiteway et al. 2010, Stranko et al. 2012). Furthermore, the inferential power of the results is limited by inadequate replication of structures or and observational scale mismatched with treatment scale (Roni et al. 2002, McMillan et al. 2013, Freedman et al. 2016, K. M. Polivka, R. A. Volking, S. M. Claeson, and R. D. Hosman *in press*), limiting the ability to detect and quantify the seasonal, annual, and among-species distribution patterns (Bradford and Higgins 2001). This does not necessarily indicate poorly placed or targeted restoration activities, but rather the need for consideration of more robust metrics of habitat selection, including those that more directly describe behavior (Kotler et al. 2016). These can include: 1) site fidelity, 2) density dependent movement, and 3) dependence of traits correlated with fitness, like body condition, on habitat selection related movement, all of which can be studied with relatively simple mark-recapture assays.

Site fidelity describes affinity to a habitat type, in which individuals maintain territories and/or to which they return after life-history-related movements or some other displacement (Greenwood 1980, Merkle et al. 2014). This behavior is presumably driven by habitat effects on fitness (e.g., growth, survival) that can vary at different spatial and temporal scales (Switzer 1993). Affinity of fish to relatively small activity centers, sometimes even as small as a single stream pool, can be identified by mark-recapture studies (Borkholder et al. 2002). Mark-recapture studies in stream salmonids have shown how movement and site fidelity of individuals can vary widely at the site or reach scales (Kahler et al. 2001, Sogard et al. 2009, Myrvold and Kennedy 2016). Movement at the scale of microhabitat types (e.g., stream pools), however, can be independent of reach-scale movement (Rodríguez 2002).

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Density dependence may determine the capacity of a habitat for further immigration and depends on the current occupancy of that habitat. In behavioral ecology, ideal free distribution theory (Fretwell and Lucas 1970, Kennedy and Gray 1993, Houston 2008) describes the density dependent settlement of unoccupied habitat. At low density, there is movement of individuals sampling the mosaic of habitat patches for the optimal one and immigration attraction to that habitat may be low. As settlement of habitats proceeds, under IFD assumptions, better habitat can support increasing levels of immigration and settlement until it reaches capacity at some optimal density. Then, at higher density, individuals are less likely to immigrate to or remain in the habitat due to crowding; thus immigration will decrease again and emigration will increase (Morris 1988). Observations of density-dependent immigration into a habitat patch (or emigration out) can therefore indicate differences in habitat capacity (Gundersen et al. 2002, Rémy et al. 2014). For a given density of individuals occupying the patch, better habitat will support more immigrants.

Resource-driven habitat affinity at the microhabitat scale for fish can involve habitat features such as food availability and cover from predation risk (Giannico and Healey 1999), both of which can be affected by in-stream habitat restoration. Foraging opportunities and cover are complementary resources that often contrast among habitat patches, among which individuals move according to the current levels of risk and food availability (Cresswell 1998, Brown and Kotler 2004). In streams, shallower, faster current velocity habitats offer rapid delivery of drifting aquatic macroinvertebrates as food, but higher risk of predation, particularly by avian predators. Deeper pools created by log structures, on the other hand, often offer cover from predators, but slower delivery of food. Individual based models have made predictions of movement between these complementary habitat types (Railsback et al. 1999, Railsback and Harvey 2002).

Use of complementary habitats among fish (Alofs and Polivka 2004, Polivka 2007, Ferrari et al. 2010) can depend on and affect an individual's physiological condition (McNamara and Houston 1990, Houston et al. 1993, Polivka 2011). The "asset protection principle" (Clark 1994) predicts that individuals in reduced condition take greater risks to obtain food, whereas individuals in good condition remain in safe patches, taking few foraging risks. This results in reduced variability in condition among individuals as poor-condition individuals succumb to predation and decreased foraging by individuals in good condition reduces energy reserves (Kotler et al. 2010, Polivka 2011) Selective predation on individuals in the best condition can also remove them from the

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population (Sinclair and Arcese 1995, Cresswell 1998). The end result is a high frequency of individual condition levels near the population average which can increase average survival at the population level (Polivka 2011). The complementary nature of pool habitat and shallower, faster-flowing habitat (Railsback et al. 1999, Railsback and Harvey 2002) would suggest that greater affinity for pools may be associated with reduced condition variability. Thus, augmenting pools with restoration structures and/or increasing pool frequency by adding structures may have positive fitness benefits to drive population growth.

In this multi-year study, I used mark-recapture assays over a short (24-hr) period to show that sub-yearling Chinook Salmon (*Oncorhynchus tschawytscha*) and steelhead trout (*O. mykiss*) have stronger affinity for restored habitat compared with unrestored habitat, at least across all years combined. Spatial, temporal, and among-species differences indicated by behavioral data showed that distribution and abundance data are not always indicative of habitat selection patterns. There was also evidence of density- and state-dependent movement. First, across the range of density of fish occupying the pool from Day 1 to Day 2, restored pools supported more immigrants than unrestored pools and thus restoration appears to increase capacity. Second, I calculated a condition index from size data on each individual and found a correlation between variation in body condition among individuals and affinity for pools. The key finding of this approach is that extending restoration effectiveness studies a step beyond distribution and abundance observations can uncover some of the mechanistic detail needed to better understand fish response to habitat restoration.

METHODS

Study System

The Entiat River is a major tributary sub-basin of the Interior Columbia River Basin in north central Washington State, USA. Its confluence with the Columbia River is at $49.657°$ N, $120.224°$ W. In this sub-basin, a common habitat restoration action is construction of in-stream structures to create rearing pools for young-of-the-year Chinook salmon (listed as endangered) and steelhead (listed as threatened). Restoration is linked with multi-agency monitoring to evaluate its effectiveness (Bennett et al. 2016). Chinook juveniles rear in stream pools and emigrate out of the sub-basin to

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the mainstem Columbia River if suitable overwintering habitat is not available in the river (Hillman et al. 1987), with smolt outmigration after one year of freshwater residency. Steelhead can rear in the streams for 1-3 years before outmigration. Predation risk primarily comes from birds (belted kingfisher, *Ceryle alcyon*; great blue heron, *Ardea herodias*) and semi-aquatic mammals (e.g., river otter, *Lontra canadensis*. Larger, predatory fish such as resident and fluvial bull trout (*Salvelinus confluentus* have been observed in deeper pools created by larger in-stream structures such as channel-spanning weirs, but not in the smaller pools created by the engineered log jams (ELJs) that comprised restoration projects in the river.

For this study, I used two closely situated reaches in the lower geomorphic valley segment (Godaire et al. 2009) of the river $\sim$ 5 km upstream of the Columbia (Figure 1). The restored reach (river km 4.5-4.9) has N = 11 ELJ and rock structures installed in 2008. The unrestored reach (river km 5.2-5.5) has N = 11 natural pools usually formed between small boulders, lacking wood cover, and smaller than the ones created by the structures in the restored reach. Polivka et al. (2015) showed that this reach is an appropriate control reach.

Fish Capture and Marking

All fish handling was conducted under US Dept. of Commerce, NOAA-Fisheries, Permit No. 1422 and is consistent with guidelines published by the American Fisheries Society (Nickum et al. 2004). Field crews conducted behavioral assays during early in the rearing season (July) of 2009, 2012, 2013, and 2016; gaps in study years occurred when high river flows affected the schedule of this and concurrent studies (Polivka 2010, Polivka et al. 2015, 2019, Polivka and Claeson in review), and, in 2014, owing to a large sediment deposition following a fire in the upper basin.

Because electrofishing can be invasive for behavioral studies (Mesa and Schreck 1989), crews captured fish using a 3 m $\times$ 1.5 m seine with 3 mm mesh. Because pulling a seine along the cobble and rock substrate is ineffective, two field-crew members stood at the downstream end of the pool and held the seine open as two other members snorkeling in the water used large hand nets to coerce fish into the seine and sometimes to capture fish individually. Underwater visibility in the Entiat River is 4-5 m such that two snorkelers can see the entire sampled area and account for any fish, by species, that escaped capture, yielding relatively accurate fish counts. Comparison of five years of seine capture data and snorkel-only fish counts in this study system showed no difference

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in abundance patterns (Polivka et al. 2015), indicating that concealment of fish by ELJ structure, for example, does not substantially affect the ability to capture or recapture fish in restored pools. Polivka (2010) obtained preliminary data on individual growth by mark and recapture periods ranging from 15-60 d suggesting reliable capture ability for fish that reside in pools over long periods of time, relative to the time frame of this study. Relative lack of structure in unrestored pools increased confidence that all fish were captured; no escaped fish in unrestored pools were reported in Polivka (2010) or Polivka et al. (2015). At each pool, depth, temperature, current velocity, pool area and dissolved oxygen were measured.

Captured fish were placed in insulated, aerated buckets and mildly anaesthetized with MS-222 (< 0.1 g $\cdot$ l^{-1}) for 2-3 minutes. Sub-yearling fish in this study system range from 50-75 mm (Chinook) and 35-70 mm (steelhead), depending on growth rates. Following identification and recording of size data (standard length, SL, in mm and mass in g), fish were marked with a subcutaneous injection of visual implant elastomer (VIE; Northwest Marine Inc.). Following marking, fish were transferred to another insulated, aerated bucket where they were allowed to fully recover from anaesthetization. The recovery period was at least 10 min, or after a full righting response with fish appearing alert and responsive, before they were released to the capture pool. After 24 hours, the pool was re-sampled and the number of both recaptured individuals and newly captured unmarked fish were noted.

Data Analysis

Affinity patterns over time

Pools in this study system vary widely in fish abundance both within and among restored and unrestored reaches (Polivka et al. 2015). This has made comparison of mean recapture proportions statistically intractable (Polivka 2010). Across the range of values of fish marked on Day 1 (N_{marked}), the number of recaptures on Day 2 ($N_{recaptured}$) should increase linearly. The slope (β) of the line fit through the data is an estimate of the average recapture probability for that set of pools. Differences between the slopes (e.g., $\beta_{restored} > \beta_{unrestored}$), evaluated by using a $N_{marked} \cdot$ habitat type term in a linear model would indicate differences in affinity for restored and unrestored habitat.

I specified the models for each species as generalized linear mixed-effects models (GLMMs),

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assuming a Poisson error distribution. I assumed *a priori* that the relationship between $N_{recaptured}$ on Day 2 and N_{marked} on Day 1 passed through the origin because pools with no fish captured (or marked) on Day 1 were excluded. Habitat type and number of fish marked were designated as fixed effects and year as the random effect. Because pool area is a strong positive correlate of fish abundance (Polivka et al. 2015), and thus affected the number of fish marked to begin with, it was entered into each model as an offset parameter to prevent fitting a negative value (Zuur et al. 2009). This offset also enables some indication that observed habitat selection and affinity for restored pools is not simply an artifact of restoration creating larger pools. I compared four candidate GLMMs for each species to determine the importance of habitat and annual effects: 1) equal slopes of the regression lines for the two habitat types (i.e., no $N_{marked} \cdot$ habitat interaction term) with the random effect (year) included, 2) equal slopes and no random effect, 3) unique slopes (including interaction term) plus the random effect, 4) unique slopes and no random effect. I selected the best model using the Akaike Information Criterion (AIC; Burnham and Anderson 2002). If the best model was one of the models that included a $N_{marked} \cdot$ habitat type interaction term, I concluded that fish differed in their affinity for restored vs. unrestored habitat and calculated habitat-specific βs. Given the multi-year nature of the study, I expected the best model to include year as a random factor, justifying within-year analyses. To ensure that the offset parameter did not cause some systematic lack of model fit, I re-ran the analyses with pool area designated as a simple predictor.

To address annual differences and to compare behavior with observations of distribution and abundance, I used two sets of GLMs for each year: one for behavior (including the interaction term as above) and one to describe fish abundance on Day 1. I also compared whether physical habitat characteristics (depth, current velocity, temperature, pool area) are consistent predictors of either $N_{recaptured}$ or of Day 1 abundance (N_{marked}). A similar analysis appears in Polivka et al. (2015), but that study uses repeated data within each year, whereas this analysis uses only data specific to Day 1 of the mark-recapture trials. As such, it is consistent with most restoration effectiveness monitoring efforts in the region (i.e., single observations of fish abundance; Roni et al. 2015, Hillman et al. 2016).

Selection of the best affinity and abundance GLMs proceeded stepwise with the removal of non-significant ($p > 0.05$) predictors, until the resultant model contained only significant terms.

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Model output for GLM in R (R Core Team 2018) provides AIC scores and I used these to confirm that the model with only significant predictors also had the lowest AIC score. These models identified 1) the years in which $\beta_{restored}$ and $\beta_{unrestored}$ indicated different levels of habitat affinity if the best model had a significant interaction term, 2) whether any differences in affinity corresponded to differences among habitats in abundance, and 3) whether affinity and abundance were associated with the same physical attributes of pools.

In all models describing affinity, both for individual years and years combined, I considered potential issues with capture success. On Day 2, captures consisted of $N_{recaptured}$ + unmarked individuals. Unmarked individuals were generally assumed to be immigrants into the pool between Day 1 and Day 2; however, they could also be individuals not captured on Day 1 that remained in the pool. To determine whether this affected model outcome, I re-analyzed all data by assuming that Day 1 individuals observed to have escaped capture remained in the pool as recaptures. Assumptions about any Day 2 individuals that were not captured were too weak to justify further adjustment of the models.

Density-dependent immigration, emigration, and capacity

Total immigration likely depends on pool size, so I first examined the linear relationship between pool area and total immigrants with linear regression. To determine whether restored pools allowed for greater density dependent immigration relative to unrestored pools, I took the number of immigrants (i.e., unmarked fish captured on Day 2) and examined how it was affected by the density of fish maintaining occupancy of the pool (i.e., recaptured) over the 24 hour period. For this relationship, I tested the fit of the data to a Ricker-style function (Ricker 1954). Such functions are of the form xe^{1-x} and are widely used in fisheries to describe density dependent processes (e.g., Sharma et al. 2005). The specific modification used here is:

$$I = Rae^{-bR} + \lambda, \tag{1}$$

where I = number of immigrants, R = density of recaptured fish and a and b describe the shape of the response curve. The peak level of immigration is $I = \frac{a}{be}$ at recapture density $R = \frac{1}{b}$ and λ is a term added to represent a constant level of density-independent immigration, particularly given that immigration may be observed at zero density of recaptures. With three parameters in need

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of estimation (a, b and λ), data from all years were combined to avoid over-fitting of the model (Anderson 2008). I used total number of immigrants rather than immigrant *density* because pools vary in size and density and two pools of a different size can have the same total density. The larger pool will possibly have the capacity for a greater number of immigrants, but this may translate to low immigrant density for the relative amount of available habitat. Because the total number of pools per year sampled on Day 1 was, at most, 11 and was first reduced by the number of fish in which there were zero captures on Day 1 in any given year, I had insufficient replication to evaluate random effects of individual years and individual pools. However, those same limitations resulted in different combinations of pools used each year. Also, different cohorts of fish were sampled each year; thus, each year's data had a reasonable level of independence and thus were combined as a whole for analysis.

Parameters from Equation (1) for each habitat type (restored or unrestored pools) were estimated by non-linear least squares, which is generally equivalent to maximum likelihood estimation, especially for small sample size when the assumption of normality may not hold (Amemiya 1977, Anh 1988). The output included the 95% confidence interval for each parameter. If the results showed a large difference in the parameter value, but wide confidence intervals, I used a randomization procedure to compare the values. I made a random draw from the values in the 95% confidence interval around the parameter estimate and generated a uniformly distributed set of 10,000 values for each parameter in each habitat. From the set of 10,000 values for that parameter, I drew, with replacement, 1000 values, and calculated the difference (e.g., $a_{restored} - a_{unrestored}$) for each pair. I then examined the 95% Highest Density Interval (HDI) for the 1000 values of that difference. A parameter was considered different between habitats if the 95% HDIs for the difference did not overlap zero.

Examination of density dependent emigration is a simpler process as emigration is expected to increase linearly with density. However it may also be an artifact of the total number of fish marked in a pool, total pool area or there may be differences in total emigration by habitat type. Therefore, I constructed another linear model using each of these parameters. To determine whether habitat type affected density dependence, I included a habitat $\times$ density interaction term. I performed analysis of variance on these models to identify significant predictors of total emigrants.

To examine whether condition variability among individuals was correlated with habitat affin-

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ity as predicted by habitat selection trade-offs, I tested the correlation between the coefficient of variation in the Fulton Condition Index for fish (K; Anderson and Neumann 1996) and habitat affinity β. The Fulton Index relates length (L) and mass (m) as:

$$K = (\frac{m}{L^3}) \times 10^6 \tag{2}$$

Although the scaling exponent for L can vary among species, I used a log(mass) vs. log(length) regression to determine that the exact value was 2.997 ± 0.013 and thus not meaningfully different from 3. The key question is whether among-individual variability in condition affects affinity for a habitat type. Here, I considered pools, whether restored or unrestored and used the β values obtained from the linear models which already showed relative differences in affinity. I calculated the coefficient of variation in the condition index (CVCI) among individuals recaptured in each pool. If a lower CVCI occurs where a habitat trade-off is predicted to be available (i.e., pools; Railsback and Harvey 2002), then there should be a negative correlation between β and CVCI and thus stronger affinity indicating state-dependent use of pools. I used the Pearson correlation r to evaluate this correlation for both species. If pools offer a trade-off in resources relative to shallower, faster-flowing habitats (Railsback et al. 1999, Railsback and Harvey 2002), then CVCI and β should be negatively correlated. Specifically, a lower CVCI should be associated with stronger affinity for pools.

RESULTS

Affinity patterns by year

For both species, the GLMMs selected by AIC included year as a random factor, and the best model for each contained a significant interaction term ($N_{marked} \times$ habitat, $P < 0.0001$), indicating unique slopes for restored and unrestored pools (Table 1). With all years combined, the affinity of each species was greater for restored habitat; however, for Chinook, the difference was very small (Chinook, $\beta_{restored}$ = 0.258 $\pm$ se = 0.02, $\beta_{unrestored}$ = 0.226 $\pm$ 0.02; steelhead, $\beta_{restored} = 0.573 \pm 0.04$, $\beta_{unrestored} = 0.388 \pm 0.02$). There was no indication of a systematic lack of fit with these models, whereas removal of the offset parameter led to problems with convergence in Model 1 (same slope, no random effect). Thus, the original model specification, with offset parameter, is

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justified.

In analyses of individual years, Chinook showed higher affinity for restored pools in 2009 and 2013, but did not differ in habitat affinity in 2012 and marginally favored unrestored habitat in 2016 ($N_{marked} \cdot$ habitat, p = 0.058; Table 2; Figure 2a). Early season habitat affinity and abundance were concordant in 2009 and 2013 and affinity was typically correlated with similar pool characteristics as abundance, including deeper, slower flowing water (Table 2). Mean depth in each habitat type was 56.5 $\pm$ 20.1 cm (restored) and 44.8 $\pm$ 9.6 cm (unrestored). Mean current velocity was 18.0 $\pm$ 10.0 cm $\cdot$ s^{-1} (restored) and 32.8 $\pm$ 15.1 cm $\cdot$ s^{-1} (unrestored). Temperature was indicated as a significant correlate in some models, but the correlation often was opposite in direction for affinity vs. abundance (Table 2).

Steelhead affinity was also variable from year to year (Table 2; Figure 2b) and the strong difference in β with years combined (above) appeared to be primarily influenced by the strong difference favoring restored habitat in 2013 (Table 2). Affinity for unrestored habitat was indicated in 2012; no other year showed a difference in β. Affinity in 2016 could not be determined by GLM because only three unrestored pools had any marked fish (N = 1-2) and, in each case, zero recaptures. Steelhead abundance favored restored habitats in 2009 and 2013, but not in 2012 or 2016. Physical correlates did not have much explanatory power for either abundance or affinity in steelhead (Table 2). In both species and both response variables (affinity vs. abundance), the model resulting from stepwise selection of terms also had the lowest AIC score, thereby validating stepwise selection.

Density-dependent immigration/emigration

Regression analysis showed a significant linear increase in the number of immigrants with pool area for Chinook ($F_{1,71}$ = 20.48, $p < 0.0001$) but not for steelhead ($F_{1,61}$ = 0.634, p = 0.424). The fitted Ricker-style functions for each habitat type (Figure 3) indicated a higher peak immigration level in restored habitat ($a_{restored}$ = 115.2, $a_{unrestored}$ = 27.76) The 95% HDI of this difference among habitats was $>$ zero (range = 3.33-225.74, Figure 4). The confidence intervals for b and λ from each habitat overlapped substantially, so they were not analyzed further. The lack of difference in the shape parameter b indicates that peak immigration occurs at the same recapture density regardless of habitat type and the lack of a difference in λ indicates that habitats have equal levels

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of density independent immigration, particularly for pools in which all fish emigrated (zero recapture density). Inspection of a plot of immigrants vs. recaptures revealed no pattern that warranted fitting the immigration model to steelhead data.

The analyses for both Chinook and steelhead emigration indicated some effects of density on emigration from restored and unrestored pools 3, consistent with movement according to habitat settlement rules. However, total number of fish marked was the strongest predictor of total number of emigrants for both species. Density was positively correlated with total emigrants for both species but there was only a significant habitat $\times$ density interaction term for steelhead, indicating a difference in the slopes of the emigrants vs. total density relationship for each habitat. These were (with 95% credible interval), restored: 9.70 (7.98-11.42) and unrestored: 4.93 (2.78-7.08).

Condition dependent movement

A lower coefficient of variation in condition index (CVCI) among individual Chinook salmon was negatively correlated with affinity (β) for pools with β values combined for all years and both restoration types (Pearson r = -0.874, P = 0.010; Figure 5. This implies that pools offer the ability to optimize habitat selection trade-offs resulting in reduced variability in condition among individuals and that these individuals have, on average, stronger affinity for pools. The regression β for restored habitat in 2016 was not significant (Table 2) and was therefore omitted from this analysis. For steelhead, there was a slight negative, but non-significant correlation between the coefficient of variation in condition and the slope of the habitat affinity relationship (Pearson r = -0.097, P = 0.855) and, thus, no indication that selection of pools was related to condition variability.

DISCUSSION

Habitat selection patterns indicated by mark-recapture data and additional inferences about capacity and behavior indicated a positive overall response to restoration. This result is not surprising in the context of previous work in this study system (Polivka et al. 2015), and highlights the benefit of including mark-recapture studies in a multi-year program of restoration effectiveness research. This is an important extension of that previous work because it not only confirms the dependence of observations on year and species (Pess et al. 2012, Polivka et al. 2015), but it also provides

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some mechanistic details, such as density- and state-dependence to extend inferences beyond the high variability of single annual surveys of distribution and abundance (Roni et al. 2008, Whiteway et al. 2010). These details usually bolstered the results of abundance surveys for Chinook, but sometimes contradicted them for steelhead, and exacerbated the difficulty of making conclusions about steelhead response to restoration.

It is unclear why, with years combined, there was a relatively small affinity difference ($\beta_{restored} - \beta_{unrestored}$) between the two habitat types for Chinook. Assuming this is not a case where a quantitative difference is not biologically meaningful, one issue might be that the assumption of a linear recapture function, above some number of individuals initially marked in a given habitat, may not hold. At high population levels, density dependence may cause the number of recaptured individuals to decelerate as the number marked grows. This did not appear to be the case over the range of Day 1 capture numbers observed here, but could become evident with more frequent mark-recapture observations with high initial fish density. Regardless, density-dependent immigration suggests that the habitats in this system might already be fairly well saturated, and linear models may still be appropriate to estimate basic site fidelity.

The linear approach to habitat selection behavior here is analogous to the use of isodars (Morris 1988) and suggests that isodars could potentially extend the understanding of behavioral mechanisms associated with the response to habitat restoration. Isodars help identify the extent to which individuals perceive a difference in habitat quality, and how density dependence resulting from the presence of conspecifics or heterospecifics affects settlement of (Muller et al. 1997), and switching between habitats (Greene and Stamps 2001). Consequences of spatial and temporal overlap in habitat and potential interspecific competition between Chinook and steelhead, in the context of restoration, is outside the scope of this work, but is under separate analysis (unpublished data).

Most habitat restoration is implemented under the assumption that amelioration of some limiting physical characteristic is the key to species recovery (Roni et al. 2002, 2008, Hillman et al. 2016). Although there was generally a consistent influence of depth and current velocity as correlates of Chinook abundance and habitat affinity, the models did not consistently identify a given factor in each year. Furthermore, there was almost no correlation between physical characteristics and either steelhead abundance or behavior and these only showed modest effects given multiple sampling occasions within and among years (Polivka et al. 2015). Thus, focus of restoration

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primarily on manipulation of physical habitat characteristics may neglect to address other mechanisms important to population recovery and measurement of changes in physical habitat parameters may not be suitable metrics of a realized benefit to fish.

It was through multi-year data in both past (Polivka et al. 2015), and this present work that benefits to restoration in this study system could be inferred. The four study years, taken individually, highlighted the variability that leads to the frequent observation that positive response to restoration can be inconsistent (Smokorowski and Pratt 2007, Roni et al. 2008, Whiteway et al. 2010). Although strengthened by multi-year data, the comparison here was between individual restored pools within a single reach and individual restored pools in an unrestored reach. Data from multiple reaches would likely also increase the robustness of all biological inferences. New reaches have been restored with ELJs in this sub-basin since 2012; however, three of those reaches occur in the upper valley segment of the river (Godaire et al. 2009), and those that are in the lower valley segment have fewer structures (N = 4-8) than the restored reach studied here. This has made it difficult, both practically and statistically, to combine reaches (K. M. Polivka and S. M. Claeson, *submitted manuscript*), which also lack data from earlier years due to the timing of restoration.

Because the design of these mark-recapture studies also made it possible to make inferences about density- and state-dependent habitat movements, they provide additional mechanistic detail regarding fish response to restoration. Showing that restored pools had higher capacity for immigration by Chinook across the observed density of fish occupying pools of either habitat type is an example of a result that goes beyond observations of distribution and abundance. Density dependent emigration did not inform conclusions about capacity increases due to habitat restoration. Even the habitat difference in steelhead was most likely attributable primarily to association with more total marked fish contributing to the number of fish moving out of the two habitats, particularly given no density-dependent immigration in this species. Life cycle models make predictions about whole-population responses to restoration based, in part, on hypothetical capacity increases (Scheuerell et al. 2006, Honea et al. 2009). Until there is understanding of the wide variability in the response of fish to restoration, such as the capacity increases shown here, across additional reaches, or in other sub-basins, however, whole-life-cycle inferences may be difficult.

Nevertheless, short-term evidence that body condition (correlated with survival) is affected by restoration in a beneficial way was supported by the negative correlation between variation and

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condition and habitat affinity for Chinook. A strong trade-off between foraging and predation risk, such as that indicated for stream pools (Railsback et al. 1999, Railsback and Harvey 2002, Railsback et al. 2005), is predicted to reduce variation among individuals in body condition (Clark 1994, Cresswell 1998, Kotler et al. 2010, Polivka 2011). Limited prior evidence has been found in study systems similar to this one (Bradford and Higgins 2001) and here, detection of the pattern required examination of fish selection for pools regardless of restoration status. Nevertheless, there is a strong correlation between Chinook abundance and pool area in this study system (Polivka et al. 2015). Because condition variation among individuals has implications for longer-term fitness (Kotler et al. 2010), creation of larger pools through restoration with ELJs may help to optimize fitness for a greater number of individuals based on state-dependent habitat selection (Nonacs 2001).

Site fidelity studies of this kind are applied across many taxonomic groups (Webb and Shine 1997, Sommerfeld et al. 2015) and the behavioral patterns observed can indicate the animal's perception of habitat quality (Heap et al. 2014). Although behavioral assays are not usually part of fish habitat restoration effectiveness studies (but see Freedman et al. 2016), I show here that they may yield more robust ways of inferring benefits of restoration at the individual and, to a lesser extent, population levels. Such an approach can prevent overconfidence in single observations of distribution and abundance and even indicate a benefit of restoration when there is no observed difference in abundance between restored and unrestored habitat.

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TABLE 1: Generalized linear mixed effects model (GLMM) fits of number of recaptures to number initially marked in 24hr site fidelity assays in restored vs. unrestored pools (2009, 2012, 2013, 2016). Models considered were: 1) fit lines with equal slopes for both habitats (no $N_{marked} \times$ habitat interaction term included) and including study year as a random factor, 2) equal slopes and no random effect, 3) unique slopes (with interaction term) and the random effect, 4) unique slopes and no random effect. Model selection by AIC (best fit model in boldface).

Model	Slopes	Year effect	Affinity	ΔAIC
a) Chinook Salmon				
3	**unique**	**yes**	**restored**	**0**
1	same	yes	NA	17.2
4	unique	no	restored	86.0
2	same	no	NA	99.6
b) Steelhead				
3	**unique**	**yes**	**restored**	**0**
1	same	yes	NA	8.2
4	unique	no	restored	9.0
2	same	no	NA	18.6

TABLE 2: GLM analysis indicating year by year affinity differences for restored or unrestored habitat identified by $N_{marked} \times$ habitat (significant differences among habitats in slope (β) shown in bold). From separate GLMs, significant abundance differences among restored and unrestored habitats. For both affinity and abundance, models were selected by stepwise removal of non-significant terms. Significant positive (+) and negative (-) correlations of physical habitat parameters shown for each group of models. *Non-significant slopes; NA: Zero recaptures in N=3 pools, only 1-2 fish marked per pool

Year	$\beta_{restored}$	$\beta_{unrestored}$	Affinity correlates	Abundance	Abundance correlates
a) Chinook					
2009	**0.259**	0.105	pool area (+), depth(+), current (-)	restored	depth (+), temperature (+)
2012	0.186	0.270	depth (+), current (-), temperature (-)	restored	depth (+), current (-), temperature (-)
2013	**0.307**	0.248	pool area (+), temperature (+)	restored	pool area (+), depth (+), current (-), temperature (+)
2016	0.019*	**0.219**	temperature (-)	NS	depth (-)
b) Steelhead					
2009	0.592	0.586	current (-), temperature (-)	restored	current (-), temperature (+)
2012	0.250	**0.603**	NS	NS	NS
2013	**0.542**	0.081*	NS	restored	NS
2016	0.206	NA	NS	NS	NS

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TABLE 3: Analysis of variance on a linear model showing the effects on total number of Chinook (a) and steelhead (b) emigrants from restored (N = 11) and unrestored (N = 10) pools during the first 24 h after capture and marking. Significant density dependence indicated by *; total emigration was correlated with total density for both species, but density dependence via a significant habitat × density interaction term was indicated only for steelhead.

Response	df	MS	F	*p*
a) Chinook Salmon				
N_{marked}	1	59852	2980.6	<0.0001
Pool area	1	161.0	8.02	0.006
Total density	1	99.0	4.92	0.030*
Habitat	2	17.0	0.87	0.424
Habitat × density	1	17.0	0.88	0.355
Resid.	67	20.0		
b) Steelhead				
N_{marked}	1	880	256.7	<0.0001
Pool area	1	11.29	3.29	0.075
Total density	1	46.85	13.66	0.0005*
Habitat	2	1.15	0.334	0.7517
Habitat × density	1	42.90	12.51	0.0008*
Resid.	58	4.11		

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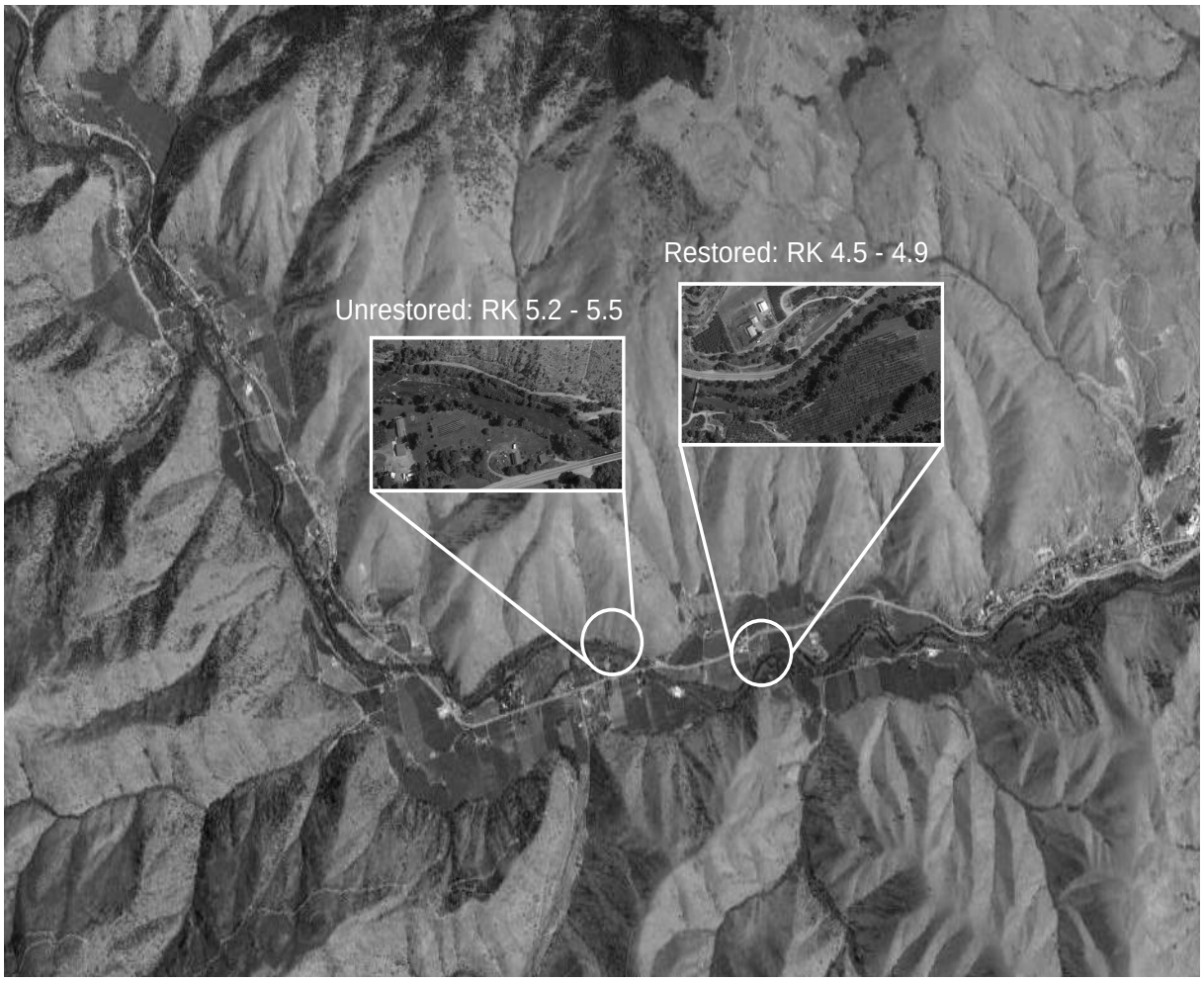

FIG. 1: Map of the segment of the Entiat River where study reaches containing restored and unrestored pools were located (RK = river kilometer, measured upstream from confluence with Columbia River).

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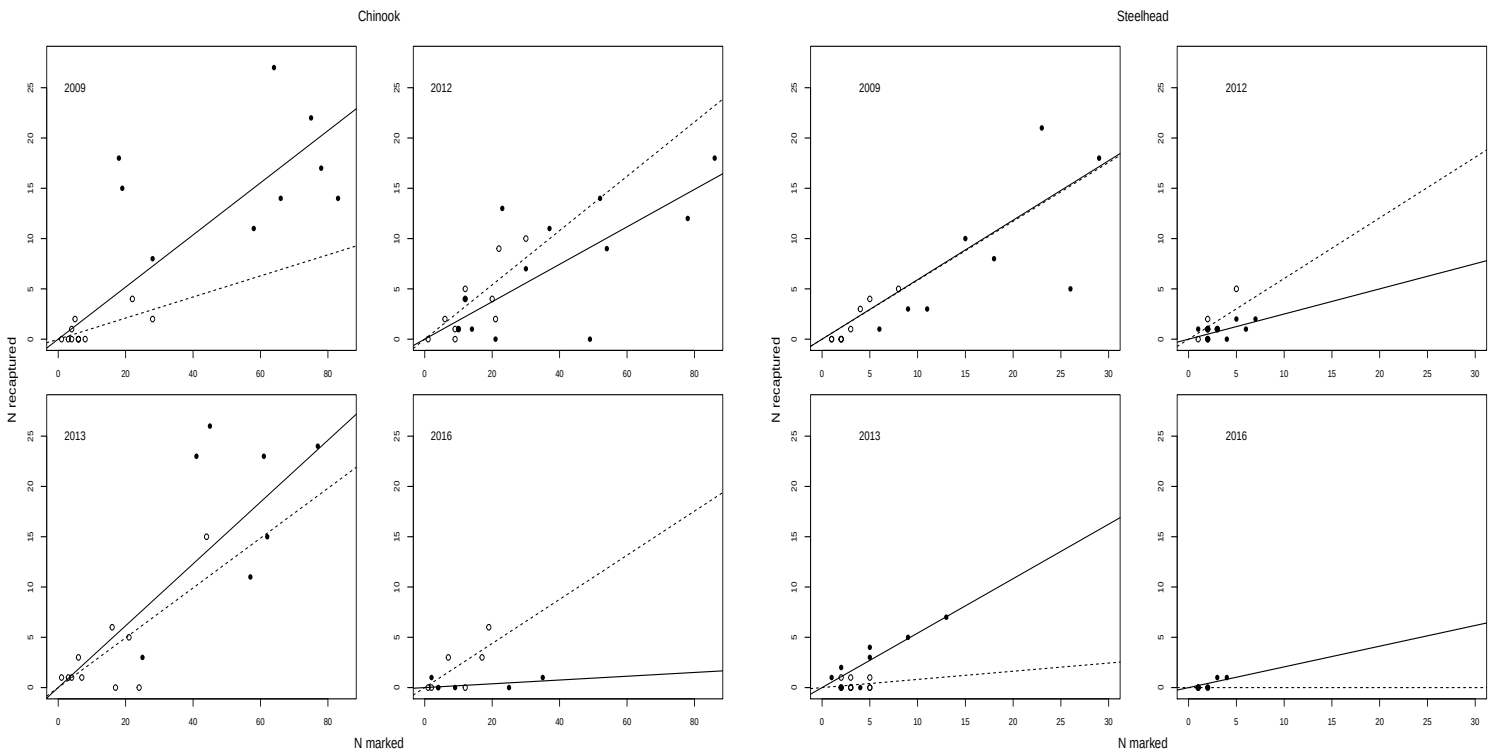

FIG. 2: Habitat affinity, shown as the linear fit of $N_{recaptured}$ vs. N_{marked}) for restored (solid lines, filled symbols) and unrestored (dashed lines, open symbols) in 24-hr mark-recapture assays in each year for sub-yearling Chinoook salmon and steelhead. Overall habitat differences in affinity for all years combined indicated by GLMM fits described in Table 1; slopes of lines and significant within-year differences given in Table 2.

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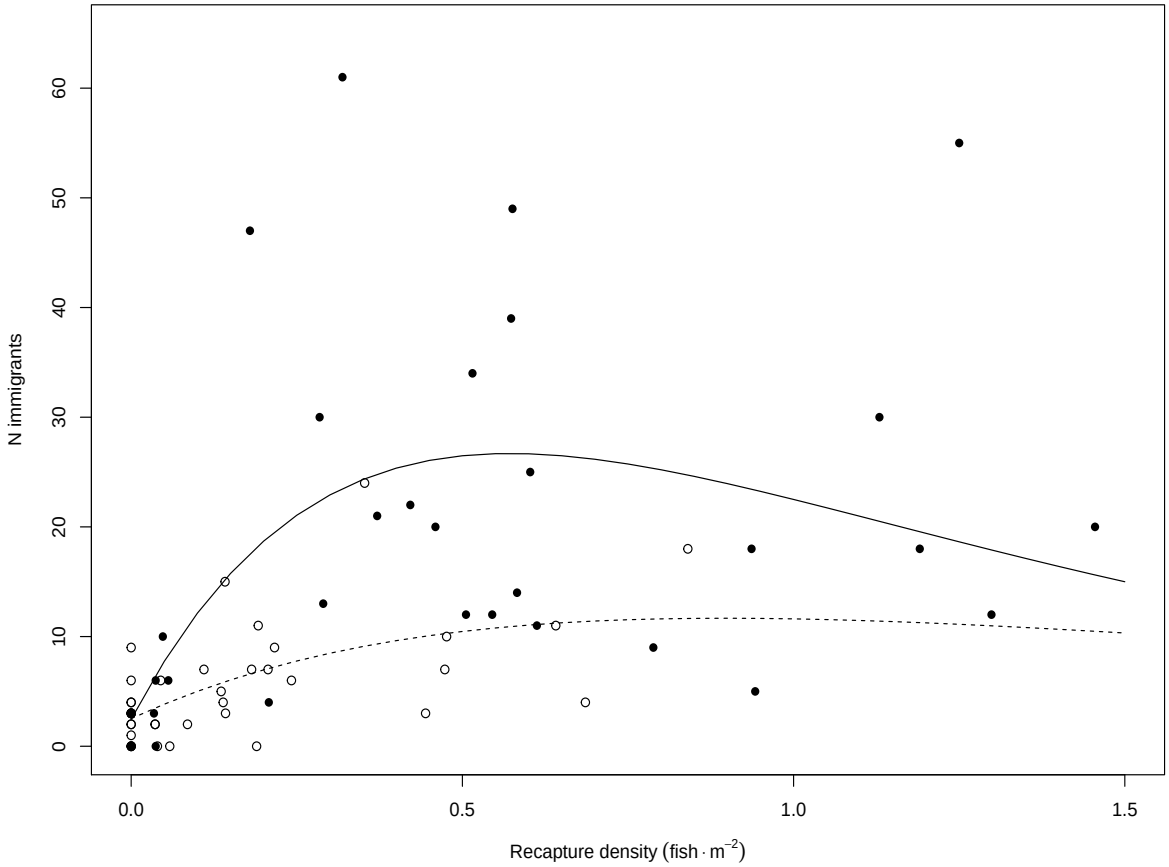

FIG. 3: Immigration of young of the year Chinook Salmon into restored (solid line, filled circles) and unrestored (dashed line, open circles) pools over a 24-h period as a function of the density of fish maintaining affinity for those pools over that period (recaptures). Density dependence is described by the fit of the Ricker model curve (see Eq. 1) and non-linear least squares estimation of parameters indicates higher total immigration (significantly different a term in Eq. 1) in restored pools (see Fig. 4

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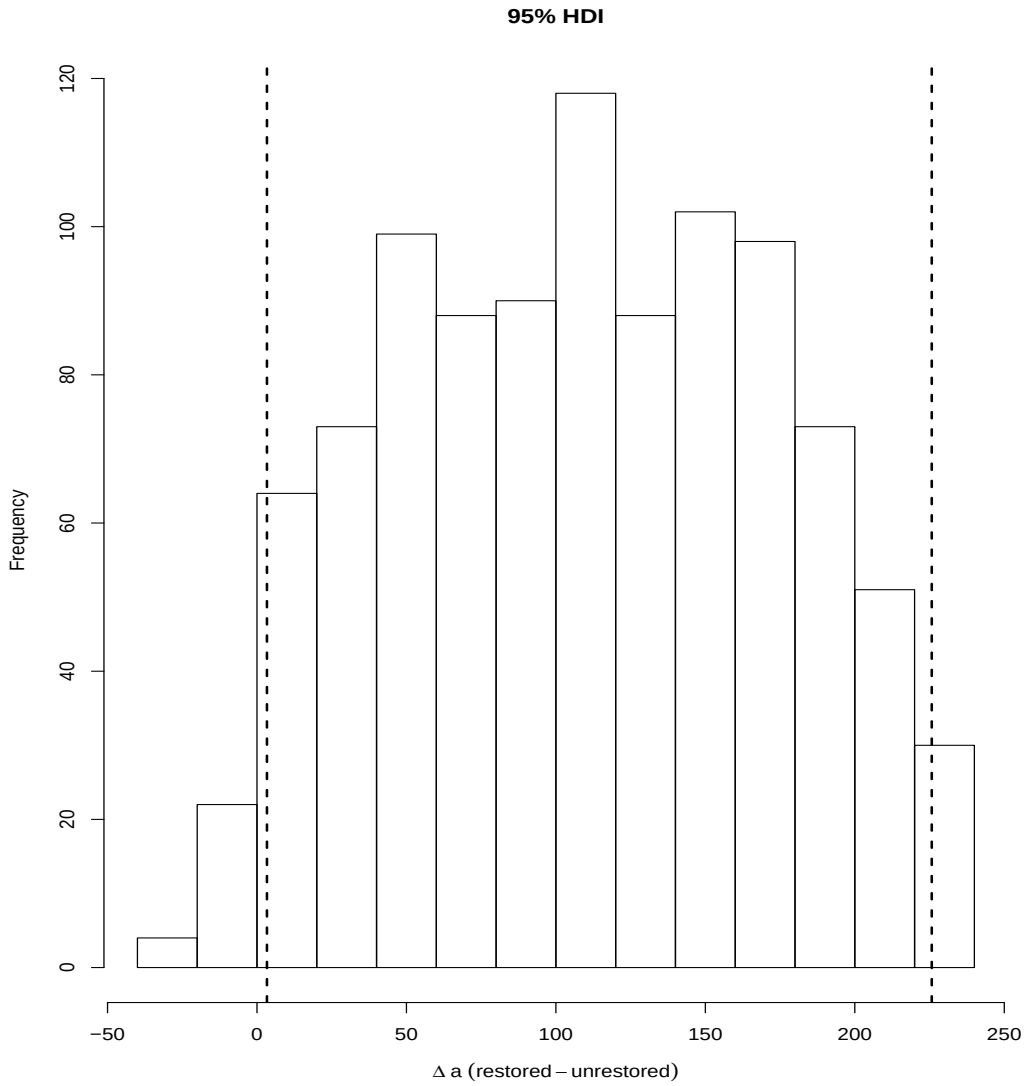

FIG. 4: Histogram with 95% Highest Density Interval (HDI) for the habitat difference in the a parameter of the Equation 1 describing density-dependent immigration into restored or unrestored pools (see Fig. 3). See text for description of the derivation of the HDI. The 95% bounds (dashed lines) show $a_{restored} - a_{unrestored} > 0$, indicating restored pools have a higher immigration capacity for a given density of individuals remaining in the pool (i.e., $a_{restored} > a_{unrestored}$

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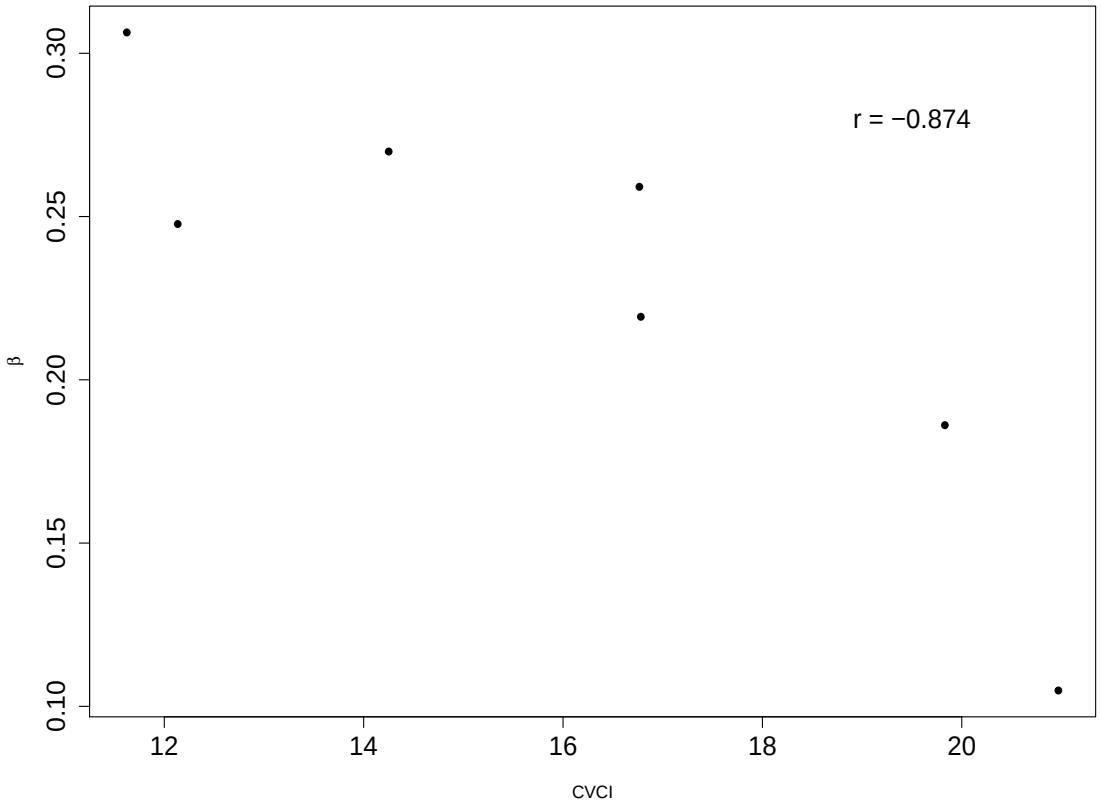

FIG. 5: Correlation between the strength of juvenile Chinook habitat affinity, indicated by the slopes (β) in each habitat type (taken from Table 2) and the coefficient of variation in condition index (K; CVCI) of recaptured individuals in each habitat type and year. When considering all years and habitats, stronger affinity for pools (regardless of restoration) was correlated with a lower CVCI (p = 0.010). Data from restored habitat in 2016 were omitted because β was not significantly different from zero.