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ARTICLE

Juvenile salmon and steelhead occupancy of stream pools treated and not treated with restoration structures, Entiat River, Washington

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Abstract: We observed habitat occupancy by juvenile Chinook salmon (*Oncorhynchus tschawytscha*) and steelhead trout (*Oncorhynchus mykiss*) at in-stream habitat restoration structures constructed in the Entiat River, Washington, USA. In 2009–2013, fish abundance measurements during rearing (July–October) showed high temporal variability in pools with restoration structures. Both species were more abundant at restored pools than at natural pools in early summer (July), but this difference was typically absent by September. Fish response to restoration structures also varied across years. When looking only at restored pools, there were strong seasonal fluxes in parameters describing the effects of temperature, water depth, and current velocity on fish abundance. Significant interaction terms such as current velocity × depth and temperature × current velocity were present for both species, suggesting that these may be important physical attributes improved by restoration. Through extensive sampling in untreated habitat, both within the treated segment and in nearby control segments, we found that when higher Chinook abundance was observed at restored pools, it was apparently attributable to an increase in habitat capacity and not due to depletion of fish from natural habitat in the same segment. Steelhead habitat selection was too inconsistent for conclusions about capacity, but we did not observe evidence that structures depleted untreated habitat.

Résumé : Nous avons examiné l'occupation de l'habitat par des saumons quinnat (*Oncorhynchus tschawytscha*) et des truites arc-en-ciel anadromes (*Oncorhynchus mykiss*) juvéniles dans des ouvrages de restauration d'habitat en cours d'eau construits dans la rivière Entiat (État de Washington, États-Unis). Les mesures d'abondance des poissons prises durant la période d'alevinage (de juillet à octobre) de 2009 à 2013 présentent une grande variabilité temporelle dans les fosses dotées d'ouvrages de restauration. Les deux espèces étaient plus abondantes dans les fosses restaurées que dans les fosses naturelles au début de l'été (juillet), mais une telle différence était typiquement absente en septembre. La réaction des poissons aux ouvrages de restauration variait également selon l'année. Les fosses restaurées présentaient de fortes variations des paramètres décrivant les effets de la température, de la profondeur de l'eau et de la vitesse du courant sur l'abondance des poissons. Des termes d'interaction significatifs comme vitesse du courant × profondeur et température × vitesse du courant étaient présents pour les deux espèces, donnant à penser que ces termes pourraient représenter d'importants attributs physiques améliorés par la restauration. Un vaste échantillonnage dans des habitats non traités, tant dans des tronçons traités que dans des tronçons témoins à proximité, a permis d'établir que, quand une plus grande abondance de saumons quinnat était observée dans des fosses restaurées, cela était apparemment le fait d'une augmentation de la capacité de l'habitat et non d'une diminution du nombre de poissons dans les habitats naturels du même tronçon. La sélection de l'habitat par les truites arc-en-ciel était trop irrégulière pour pouvoir en tirer des conclusions concernant la capacité; aucune observation n'indique toutefois que ces ouvrages réduiraient le nombre de poissons dans les habitats non traités. [Traduit par la Rédaction]

Introduction

Placement of in-stream habitat structures (reviewed in Whiteway et al. 2010) is one of the most common efforts to protect and recover salmon populations across the Pacific Northwest (USA). Other common techniques include riparian revegetation (e.g., Opperman and Merenlender 2004), floodplain reconnection (Morley et al. 2005), and consideration of nutrient additions (Bilby et al. 1998). In-stream structures are intended to increase pool availability, which is predicted to not only attract fish from lower quality habitat, but also to increase stream capacity and fish production to drive population recovery (Roni et al. 2010). The Upper Columbia River evolutionarily significant unit (ESU) of spring-run Chinook salmon (*Oncorhynchus tschawytscha*) and a distinct population segment (DPS) of anadromous steelhead trout (*Oncorhynchus mykiss*) have both been listed for protection under the Endangered Species Act. Since 1999, restoration programs have been established to apply some of the techniques listed above to recover these species to levels that ensure persistence (e.g., Ward et al. 2010). This study focuses on an in-stream habitat project designed primarily to benefit juvenile salmon and steelhead in a major sub-basin of the Upper Columbia River.

In-stream restoration consists of the addition of material, commonly large wood, to promote processes that restore channel morphology (Davidson and Eaton 2013), provide cover (Bond and Lake 2003*a*), and stimulate production of macroinvertebrate prey resources for fish (e.g., Hilderbrand et al. 1997; Kail et al. 2007). Subsequent to the implementation of restoration projects,

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monitoring and evaluation of their effectiveness is the only way to determine whether the intended objectives are met. Reviews of effectiveness monitoring studies (Roni et al. 2002, 2008; Smokorowski and Pratt 2007; Whiteway et al. 2010) show the challenges in evaluating the success of restoration and, in some cases, the lack of any effectiveness monitoring (Kail et al. 2007; Bernhardt et al. 2005, 2007).

An increase in fish abundance in treated areas is considered an indication of success (Roni et al. 2008). The challenge is that positive responses are not consistent (Smokorowski and Pratt 2007; Whiteway et al. 2010), implying that the likelihood of successful restoration is site- or species-specific (also see Pess et al. 2012). For example, successful creation of a more resilient stream channel can be difficult in highly dynamic rivers (Miller and Kochel 2010), and responses by macroinvertebrate communities to habitat modifications are occasionally ambiguous (e.g., Hilderbrand et al. 1997; Miller et al. 2010; Testa et al. 2011, but see Coe et al. 2006, 2009). The biological benefit of in-stream habitat enhancement to fish is often measured in terms of increased availability of habitat features that are sometimes correlated with increased fish abundance, growth, or survivorship. Changes to physical habitat are commonly reported (Whiteway et al. 2010), under the assumption that a response by fish will be correlated, but this full response is not always tested.

Ambiguity in observations of fish abundance relative to restoration structures may result from high spatial and temporal variability in fish distribution regardless of habitat condition, short-term movement among multiple habitat types, and (or) failure of the structures to sufficiently modify habitats. Detection of a response is likely to depend on whether the treatments appropriately match the habitat requirements of the species or life stage in question (Bond and Lake 2003*b*) and address processes that limit the densities of target organisms. Restoration effectiveness studies often fail to distinguish between simple redistribution of individuals among habitats (restored versus untreated) and actual increase in habitat capacity. Increase in habitat capacity can be defined as the number of individuals that can be supported by a habitat with a given set of physical attributes and (or) resources before life history traits such as mean individual growth and survival rate shift from positive to zero or negative (e.g., Scheuerell et al. 2006; Stewart et al. 2009). Detection of increased habitat capacity often requires mark–recapture studies that can address short-term growth, local immigration–emigration from habitat (Gowan and Fausch 1996), and short-term habitat affinity (Polivka 2010). In this report, we examine how extensive sampling of untreated habitat within a treated segment is a survey method that can be used to show apparent increases in capacity as opposed to redistribution of fish in response to habitat restoration.

In a 5-year study of postrestoration habitat occupancy by Chinook salmon and steelhead abundance at in-stream structures in a segment of a major river sub-basin in the Upper Columbia River, we observed fish numbers in restored and untreated (natural) stream pools to ask whether there was (*i*) greater occupancy by either species in restored habitat, (*ii*) within- and among-year variation in abundance of fish in each habitat type and association with physical variables in restored pools, and (*iii*) apparent increase in habitat capacity via restoration structures. Our comparisons of habitat occupancy in restored versus unrestored areas were at the habitat unit scale (pools). Our design is unique in its consideration of restoration effectiveness at this smaller spatial scale, combined with repeated and replicated sampling within the rearing season for our two study species. Many effectiveness monitoring programs only sample entire reaches, usually once per season, and posttreatment. To address whether restoration structures increased apparent capacity, we surveyed habitat occupancy in habitat units from multiple untreated segments for comparison with that in natural pools in the treated segment. If structures cause depletion of fish from untreated habitat units, we would expect mean fish density in natural pools in the treated segment to be lower than that in untreated segments. However, if we observe similar rates of occupancy by fish in all natural pools and relatively higher occupancy at restored pools, this is evidence that structures have increased habitat capacity in a treated segment.

Methods

Study system

The Entiat River, on the eastern side of the Cascade Mountains, Washington, is 69 km long, drains a watershed of approximately 1085 km² (Kirk et al, 1995), and flows into the Columbia River (Fig. 1) at river kilometre (rkm) 778.4. All study segments were located in the lower 12 km of the Entiat River, which is part of a geomorphic reach (lower 24 km) where bedrock constrains the channel to a somewhat narrower valley than in the middle or upper reaches (Godaire et al. 2009). Slope averages 1.04% (range: 0.68%–1.26%) and substratum is primarily composed of bedrock and small submerged boulders (diameter <40 cm) with some finer material (sand, gravel) mobilized by lateral erosion (Godaire et al. 2009). Wetted width averages 25.4 m (range 22.6–28.1 m) in the study segments.

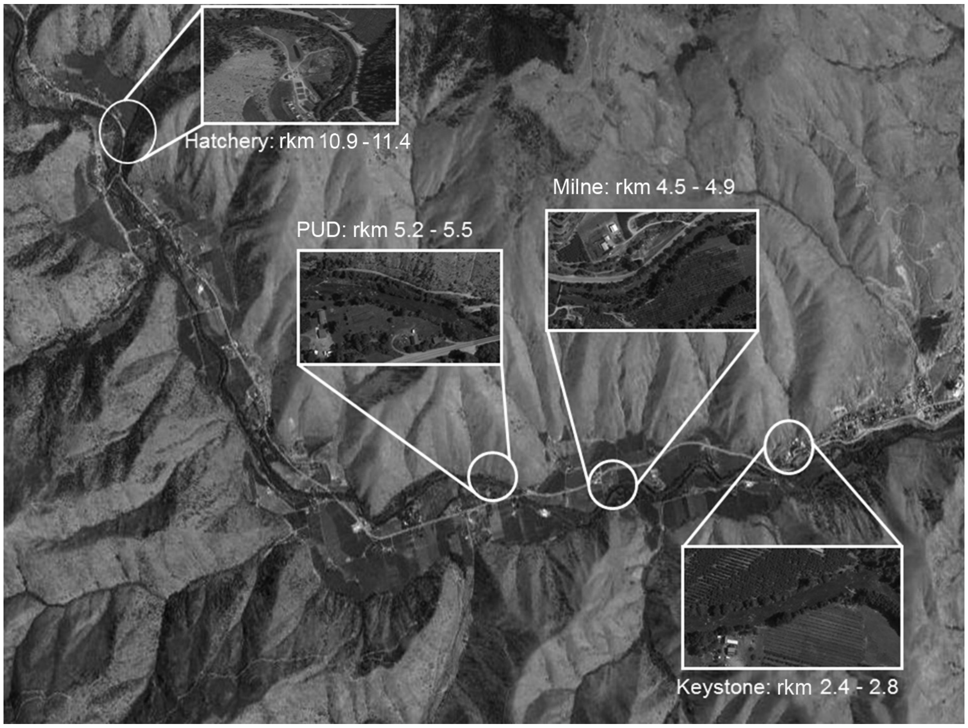
Salmonid populations in the Entiat River include Chinook salmon (*O. tschawytscha*), rainbow–steelhead trout (*O. mykiss*), migratory bull trout (*Salvelinus confluentus*), and a small population of coho salmon (*Oncorhynchus kisutch*). Study segments are primarily used as rearing and spawning habitat by steelhead trout and "stream-type" juvenile Chinook salmon. Both species rear in the mainstem river between June and late August; Chinook salmon begin moving downstream to overwintering habitats in early September prior to outmigration the following spring (Mullan 1987, 1989). Steelhead outmigration typically occurs at ages 2–3 with a small percentage of the smolt population including age 1 and age 4 individuals (Peven et al. 1994).

Study segments

In 2008, the "Milne" segment of the Entiat River (Fig. 1), spanning from rkm 4.5–4.8 upstream of the confluence with the Columbia River, was treated with restoration structures by collaborating state and federal natural resource management agencies. In this segment, both small engineered log jams (ELJs; $n = 5$) and rock barbs ($n = 5$) were installed to generate pools and increase habitat complexity. The ELJs are composed of one to three logs averaging 30–40 cm in diameter, embedded in the bank and bound together by steel cable. Rock barbs consist of a line of rocks averaging 25 cm in diameter, stacked vertically to emerge from the surface of the water, and extending from the bank for 3–4 m. Pools associated with ELJs and rock barbs range in surface area from 15–55 m². Engineering and implementation of these restoration structures preceded our involvement in the effectiveness monitoring research. Our knowledge of pretreatment conditions is limited to anecdotal information from the agencies involved and by sampling nearby untreated segments. Furthermore, in all sampling and analyses, we did not distinguish between structure types because of the low number of each type. At the beginning of this research, the Milne segment was the only treated segment in the Entiat River with sufficient total replication of in-stream structures for the study design we report here. Comparison of natural and restored pools within this segment enabled us to minimize the effects of any between-segment differences, such as terrestrial in-fall of prey, not accounted for by our sampling methods.

To assess fish habitat occupancy relative to artificial structures, we randomly selected (technique described below) natural pools (without structures) occurring in other locations in the Milne segment multiple times within each study year (2009–2013) for comparison with abundance at restored pools. Within each year, sampling occurred between ~15 July and 1 October. We also selected three untreated segments for comparison with the Milne

Fig. 1. Map of study area in the Entiat River (Washington, USA). The upstream and downstream end of each named study segment is located by river kilometre (rkm). Conducted sampling, frequency, and methods used at each segment are described in Table 1 and in Methods.



segment. These ranged from <1 to 7 km from Milne and were all within the lower geomorphic valley reach (Godaire et al. 2009); thus, it was reasonable to assume general similarity of habitat features among these segments, which are as follows: a segment ~400 m upstream of the Milne segment adjacent to a diversion canal maintained by the Chelan County Public Utility District ("PUD"; rkm 5.2–5.5), a segment downstream of the treated Milne segment ("Keystone"; rkm 2.4–2.8), and a segment on the property of the USFWS Entiat National Fish Hatchery ("Hatchery"; rkm 10.9–11.4). These segments enabled the comparison of fish density in untreated habitat in the restored segment with untreated habitat elsewhere and confirmation that multiple segments in a geomorphic reach had similar fish densities.

Fish sampling

Snorkel surveys

In the Milne segment, we conducted snorkel surveys in both restored pools and at randomly selected natural pools on the banks or stream margins. We selected the location of natural pools (n = 15) by using randomly generated distance measurements (range = 10–50 m) downstream from a fixed starting point at the upstream end of the segment (~rkm 4.7) combined with a coin toss to determine left or right river margin. At each natural pool, we visually surveyed the entire pool and measured the length and width of the pool to estimate surface area (m^2). When pool boundaries were not clear, we used a standardized area of 15 m^2. Restored pools were surveyed on the same day, and we measured the entire surface area. All fishes in natural and restored pools were identified and enumerated by species. Turbidity did not affect detection of fish during the study season; complete visibility for snorkeling was always >2–3 m, which permitted two snorkelers to completely see the survey area. A further measure to reduce visual errors was that the same two snorkelers completed the visual surveys while a third crew member recorded all data (see Pess et al. 2012). For all snorkel surveys, we quantified habitat attributes of study pools, including depth, current velocity, dissolved oxygen, and temperature.

We sampled fish in all of the study segments in July and September 2009 (Table 1) to compare natural pools at Milne with those in completely untreated segments. We conducted snorkel surveys (n = 15) at randomly selected (see procedure above) natural pools in the three untreated segments in July but only at "PUD" and "Hatchery" in September owing to access restrictions. On the same day, we conducted snorkel surveys in the treated Milne segment in both the restored pools and at randomly selected natural pools. These assays would show whether structures added fish capacity to a segment or whether they simply drew fish away from untreated habitat within that segment. In all unrestored habitat units, we standardized the surface area sampled to 15 m^2 and used the estimated area of restored pools to calculate fish density ($\text{fish}\cdot m^{-2}$).

Seine samples

Seine capture sampling was conducted every 2–3 weeks each year at the treated and natural pools in the Milne segment. We captured fish using a 3 m × 1.5 m × 3 mm seine net. Two crew members blocked the downstream end of the pools with the seine while two other crew members snorkeling in the water directed fish into the seine using large hand nets. Captured fish were counted and identified. Individual fish that were not captured in the seine were caught individually using the hand nets. Fish visually identified, but observed to have escaped capture ($n \leq 3$–4 fish in <5% of samples), were added to the respective species total for each sampling unit. After recording, we released fish at the capture site. We also recorded habitat attributes as before (pool area, depth, current velocity, dissolved oxygen, and temperature).

Owing to high river discharge in 2010 and 2011, all sampling was delayed until early August, leading to time constraints such that snorkel surveys were omitted in 2010 and seine samples were omitted in 2011. Table 1 clarifies the sampling techniques used in each study year. For analysis of among-year variation, 2010 seine

Table 1. Data collection dates (2009–2013) and techniques used for survey (snorkeling) or sampling (seine capture) all study segments (Fig. 1), including both restored and natural pools in the treated (Milne) segment.

	Segment	Pool	Snorkel survey	Seine sample
Milne	Treated	Restored ($n = 10$)	2009: July–September 2011–2013: every 2 weeks, August–October	2009: every 2 weeks July–September 2010, 2012–2013: every 2 weeks, August–October
		Natural ($n = 15$)	2009: July–September 2011–2013: every 2 weeks, August–October	— —
PUD	Control	Natural ($n = 11$)	2009: July and September	2009: every 2 weeks, July–September; 2010, 2012–2013: every 2 weeks, August–October
Keystone	Control	Natural ($n = 15$)	2009: July	—
Hatchery	Control	Natural ($n = 15$)	2009: July–September	—

Note: Because of changes in budget, addition of sampling segments in separate valley segments of the Entiat River, and flow conditions, not all survey techniques could be completed in all seasons and in all years.

samples were added to snorkel survey data. Within a year, we partitioned the study season to distinguish samples from earlier in the summer sampling season (late July – early August; "early season"), midsummer samples (middle–late August; "midseason"), and late summer samples (September; "late season"). We used the first sample from each time period described above to represent each season in analyses of abundance differences among sampling seasons. Although there were more sampling data available for each time period, we avoided, except where necessary for analysis, the combination of seine and snorkel data.

Data analysis

From the measurements of temperature, depth, and current velocity, we compiled descriptive data related to the physical habitat attributes of restored pools. We used generalized linear models (GLMs) assuming a Poisson error distribution to address questions about patterns of habitat occupancy by fish in restored pools and in natural pools. We fit models separately for the abundance of Chinook salmon and of steelhead trout, with pool size, year, within-year season timing (early, mid-, or late season), and whether the pool was natural or restored as predictors. Within-season variability observed during preliminary work in this study system (Polivka 2010) justified the use of a season × structure interaction term, and we also considered a year × structure interaction term for annual differences in effects of structures. Significant categorical terms in the GLM were identified using ANOVA. To identify any effect of combining data from seine and snorkel samples as a result of the sampling limitations described above, we fit models based only on one sampling technique for comparison of results with the analysis of the full data set. Analyses based only on snorkel survey data excluded data from 2010, and samples based only on seine capture data excluded 2011 data. Furthermore, we excluded year as a term in these analyses.

We explored within- and among-year patterns in detail to isolate and understand temporal variability in fish habitat occupancy relative to restored structures. We first divided the full data set into the three periods of each season and fit separate GLMs for each period. Next, we fit separate GLMs for each year of the study. Partitioning data by each year enabled consideration of only one sampling technique per annual data set. We examined temporal differences in whether the GLM coefficient describing the association of abundance with structures differed from zero within or among years.

Next, we asked which attributes are correlated with fish abundance in restored pools. Using data from treated pools in all years, we fit GLMs for each species. Pool size, year, and measured habitat variables (depth, current speed, dissolved O_2, and temperature) were the potential predictors. Based on exploratory analysis after the first 3 years of data had been collected, depth and current velocity emerged as consistent correlates of fish abundance (Polivka 2010; K. Polivka, unpublished data). Thus we selected depth × current velocity interactions plus changes in each among early, mid-, and late season samples (depth × season, current velocity × season). We included year × depth and year × velocity terms as possible indicators of annual differences in larger-scale hydrologic processes. Finally, we included a current velocity × temperature term to explore possible bioenergetics implications of habitat selection relative to restored pools (e.g., Hughes 1998). We fit the full a priori model and eliminated any nonsignificant predictors using χ^2 tests on deviance explained.

The next question was whether pools with restoration structures showed higher fish density relative to natural pools because they increased the apparent capacity of a treated river segment or whether any increase in fish density came simply from depletion of fish from natural pools within that segment. We compared mean fish density estimated from randomized snorkel surveys in natural pools at Milne with that in pools from the other three untreated segments sampled and with restored pools at Milne using a one-way ANOVA, with segment as the factor and Tukey's HSD pairwise comparisons for each pair of segments. We conducted separate analyses for each species and each study period (July or September 2009). Because the key question was whether untreated habitat in the Milne segment had been depleted relative to other segments in this major geomorphic reach (Godaire et al. 2009), we conducted the same analysis but excluded structures and examined the results with pairwise comparisons among segments.

Results

Mean (±SD) river discharge across the five study years in the study segments ranged from 370.8 ± 71.4 cubic feet per second (cfs; 1 cfs = 28.316 $\text{L}^3\cdot\text{s}^{-1}$) at the beginning of early season to 161.6 ± 35.7 cfs by the end of late season. As expected with this characteristic decline in discharge, mean current velocity in restored pools declined from 0.19 ± 0.11 $\text{m}\cdot\text{s}^{-2}$ in early season to 0.14 ± 0.11 $\text{m}\cdot\text{s}^{-2}$ by late season. Mean pool depth declined from 54.7 ± 10.7 to 41.8 ± 8.8 cm. Mean temperature across the 5 years was 17.6 ± 2.53 °C in early season and cooled to 13.7 ± 3.5 °C by late season.

Are there more fish at restored pools compared with natural pools?

Models built from data collected in the Milne study segment indicated a strong response to structures across the five study years for both species ($p \ll 0.0001$; Table 2). Pool size was a significant positive correlate of abundance for both species ($p \ll 0.0001$), and both species showed significant structure × season time and year × season time interaction terms (Table 2), suggesting differences within and among years in the response to structures.

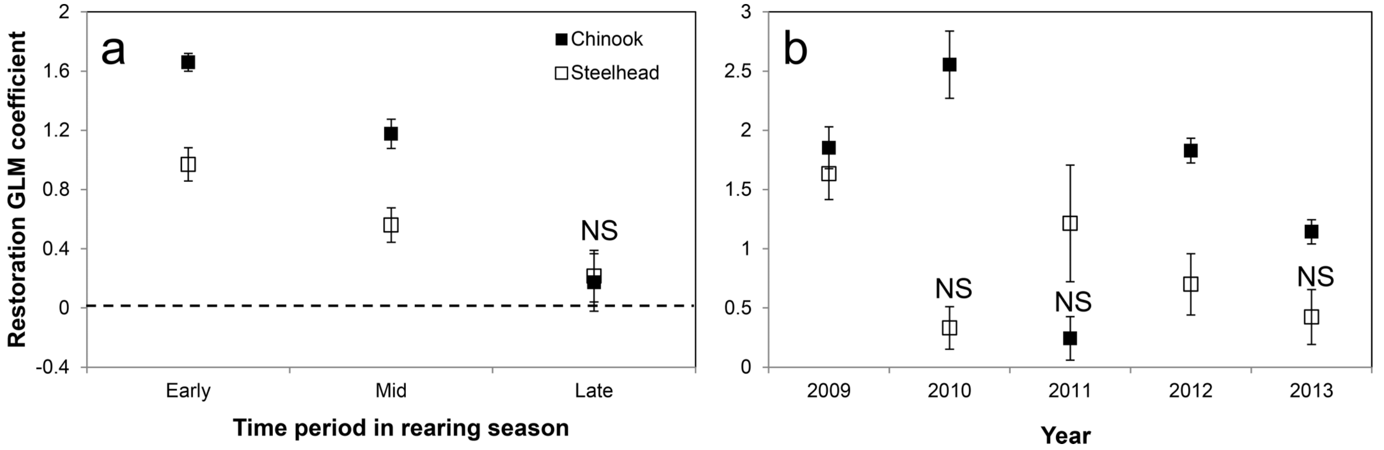
The positive response to structure was evident in early and mid-season surveys as indicated by significant positive coefficients in GLMs separated by time period for both species, whereas late season coefficients were not significantly different from zero for either species (Fig. 2*a*). Models built on data from individual years showed positive coefficients for structure that were significant in each year except 2011 for Chinook salmon and significant

Table 2. Results of generalized linear models (GLMs) analyzing abundance of (*a*) Chinook salmon and (*b*) steelhead trout in microhabitat restored with Structures (engineered log jams and rock barbs) versus natural microhabitat in all samples taken in 2009–2013, but categorized by within-year season timing (Season).

	Coefficient	df	Deviance	Residual df	Residual deviance	*p*
(*a*) Chinook salmon						
Pool size	+	1	1795.59	308	7168.2	<0.0001
Year	+	4	872.69	304	6295.5	<0.0001
Structures	+	1	1217.15	303	5078.4	<0.0001
Season timing	–	2	2018.27	301	3060.1	<0.0001
Season × structures	+/–	2	23.18	299	3036.9	<0.0001
Year × structures	–	4	124.95	295	2912.0	<0.0001
(*b*) Steelhead						
Pool size	+	1	252.83	308	1689.57	<0.0001
Year	+/–	4	485.40	304	1204.17	<0.0001
Structures	+	1	108.11	303	1096.05	<0.0001
Season timing	–	2	115.88	301	980.17	<0.0001
Season × structures	–	2	31.13	299	949.05	<0.0001
Year × structures	–	4	69.79	295	879.25	<0.0001

Note: All coefficients from the GLM are listed plus an ANOVA against a χ^2 distribution showing significance of individual terms and time-varying interaction terms. Coefficients values were derived from GLMs and are represented as positive (+), negative (–), or mixed (+/–) where different levels of categorical variables (i.e., year, season timing) had either positive or negative coefficients.

Fig. 2. (*a*) Estimated coefficients (±SE) of the association of Chinook salmon and steelhead abundance with structures in separate GLM analyses for early (mid-July – early August), mid- (middle to late August), and late (September) season samples. Coefficients illustrate the structure × season interaction found in the GLM fit to the entire data set (see Table 2). (*b*) Estimated coefficients (±SE) of the association of Chinook salmon and steelhead abundance with structures in separate GLM analyses for each year (year × structure interaction; Table 2) of the study, 2009–2013. NS, not significant ($p > 0.05$).



for steelhead in all years except 2010 and 2013 (Fig. 2*b*). Comparison of models generated using only identical methods showed no differences in the response to structure with the exception that the season × structure term became nonsignificant for steelhead observed in snorkel surveys ($p = 0.104$).

Do habitat features explain fish density within restored pools?

Models linking Chinook salmon abundance with physical features of restored pools included significant positive associations with pool size, depth, and current velocity, but a negative correlation with temperature (Table 3*a*). Dissolved oxygen was the one term eliminated for lack of a significant effect. All interaction terms included in the a priori model were significant, and many of them indicated within- and among-year variation in temperature, depth, and current velocity. Outside of temporal variation, the current velocity × depth and current velocity × temperature interactions were significant ($p < 0.0001$; Table 3*a*).

The stepwise selection procedure in the model of steelhead data eliminated dissolved oxygen and depth along with the interaction term current velocity × year. Pool depth was, however, present in interaction terms with current velocity and seasonal timing. Steelhead and Chinook salmon had similar significant associations of terms such as temperature, current velocity, pool size, year, and season, but the correlation with temperature was positive for steelhead. The remaining interaction terms involving temporal differences were significant as well as current velocity × depth and current velocity × temperature (Table 3*b*). No results changed as a result of using only snorkel samples or only seine samples.

Do natural pools in treated segments differ in fish density from those in untreated segments?

In the 2009 comparison of both restored and natural pools in the Milne segment with natural pools in the untreated study segments, early season (July) density of both Chinook salmon (Fig. 3*a*; $F_{[4,58]} = 7.90$, $p < 0.0001$) and steelhead (Fig. 3*b*; $F_{[4,58]} = 6.76$, $p = 0.0002$) differed among segments, but specific patterns differed by species. In the July 2009 assay, Chinook salmon density at Milne was significantly higher in pools with structures than in natural pools in any of the control segments (Fig. 3*a*; $p = 0.00002–0.0004$,

Table 3. Deviance values and significance from ANOVA (tested against a χ^2 distribution) on generalized linear models (GLMs) of physical variables associated with abundance of (*a*) Chinook samon and (*b*) steelhead trout in restored pools only.

	Coefficient	df	Deviance	Residual df	Residual deviance	*p*
(*a*) Chinook salmon						
Current velocity	+	1	59.63	126	5365.0	<0.0001
Pool size	+	1	283.21	125	5081.7	<0.0001
Year	+/–	4	1162.03	121	3919.7	<0.0001
Depth	+	1	588.06	120	3331.7	<0.0001
Temperature	–	1	275.74	119	055.9	<0.0001
Season	+/–	2	1102.60	117	1953.3	<0.0001
Current velocity × depth	–	1	68.15	116	1885.2	<0.0001
Current velocity × season	–	2	65.90	114	1819.3	<0.0001
Depth × season	+/–	2	262.35	112	1556.9	<0.0001
Year × temperature	+/–	4	80.49	108	1476.4	<0.0001
Current velocity × year	+/–	4	118.92	104	1357.5	<0.0001
Current velocity × temperature	+	1	8.46	103	349.1	0.0036
(*b*) Steelhead						
Current velocity	+	1	28.67	126	1045.60	<0.0001
Pool size	+	1	10.06	125	1035.55	0.0015
Year	+/–	4	346.34	121	689.21	<0.0001
Temperature	+	1	32.74	120	656.46	<0.0001
Season	–	2	114.80	117	539.95	<0.0001
Depth × season	+/–	3	12.18	114	527.77	0.0068
Current velocity × temperature	–	1	15.65	113	512.12	<0.0001
Current velocity × season	–	2	6.76	111	505.36	0.0340
Year × temperature	–	4	17.43	107	487.94	0.0016
Current velocity × depth	–	1	6.54	106	481.39	0.0105

Note: Coefficients are derived from GLMs and are represented as positive (+), negative (–), or mixed (+/–) where different levels of categorical variables (i.e., year, season timing) had either positive or negative coefficients.

Tukey's HSD), including natural pools within the Milne segment itself (p = 0.0021). There was no evidence that Chinook density in untreated pools in the Milne segment differed from that in untreated pools in any other segment (p = 0.800–0.999), nor was there evidence that Chinook density differed across untreated segments. In contrast, late season Chinook salmon density was not significantly different in pools at any segment or for restored pools in the Milne segment ($F_{[3,50]}$ = 0.739, p = 0.534; Fig. 3*c*).

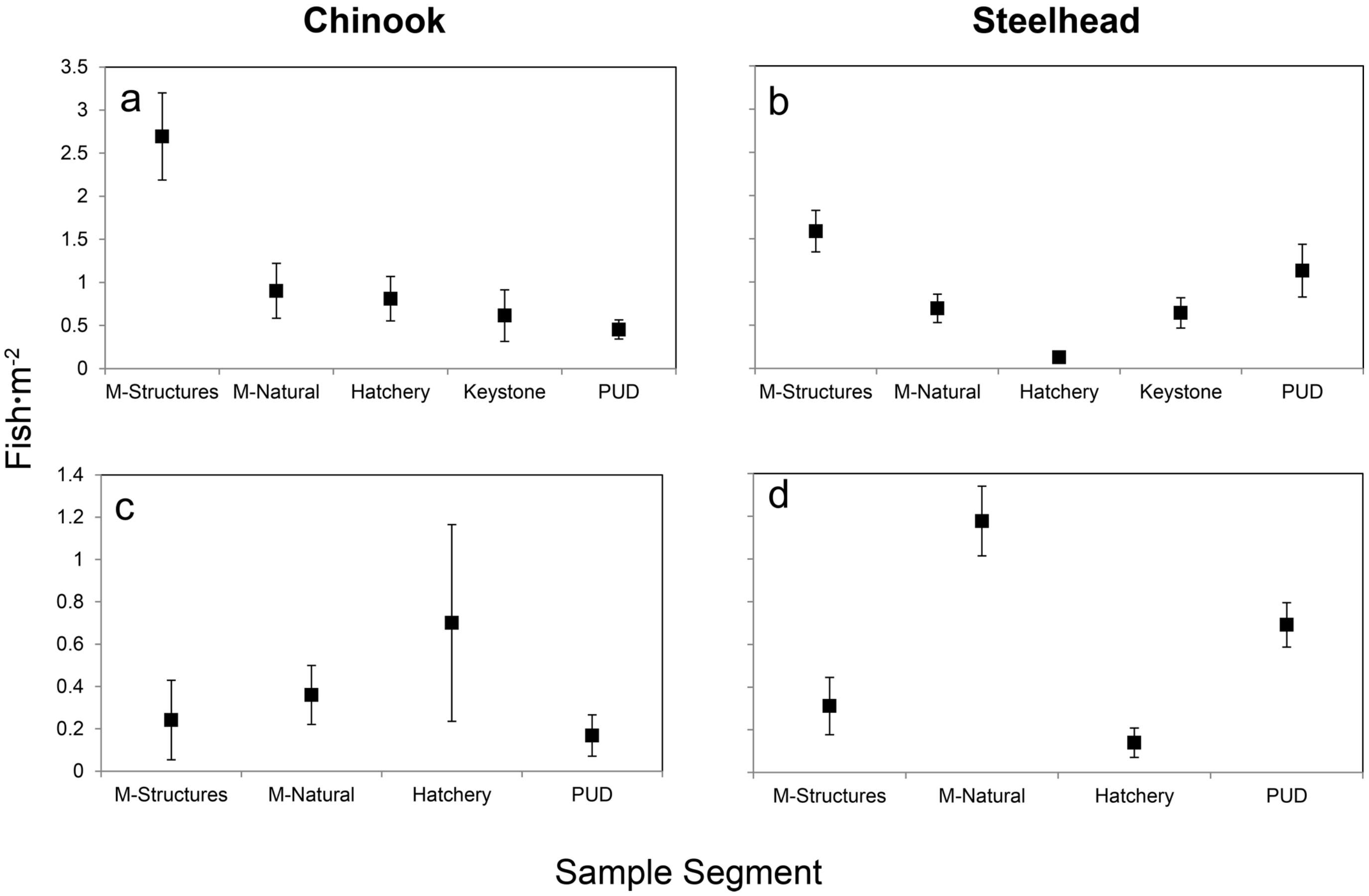
In the July 2009 survey, heterogeneity in steelhead density was explained by higher density at structures at Milne than at all natural pools except at the PUD segment (p = 0.592; Fig. 3*b*). All untreated segments had statistically equivalent mean density (Tukey's HSD pairwise comparisons; p = 0.300–0.999) with the exception that the PUD segment had higher mean density than the Hatchery segment (p = 0.003). In the mid-September survey, steelhead density showed a highly unpredictable pattern and some differences among segments, but no evidence of depletion of fish from untreated habitat by structures. The observed heterogeneity among segments in mean steelhead density per pool ($F_{[3,50]}$ = 14.92, $p \ll 0.0001$; Fig. 3*d*) was the result of unusually high density at natural pools in the Milne segment. Natural pools at Milne had higher steelhead density than the restored pools (p = 0.0002), the PUD segment (p = 0.024), and the Hatchery ($p < 0.0001$). Mean steelhead density in the Hatchery segment was also lower than that in the PUD segment (p = 0.008). Mean density at restoration structures was reduced to the same level as natural pools in the Hatchery (p = 0.800) and PUD segments (p = 0.201). In no case did exclusion of the restored pools from this analysis, for either species, change these results.

Discussion

In-stream structures have been shown to be associated with increased abundance of target fish species (Rosenfeld et al. 2000; Pess et al. 2012). Although some effectiveness monitoring studies have reported interannual variation (Pess et al. 2012), within-year variation was not identified in those earlier studies. Indeed, only some studies identify any measurable effect of restoration (Roni et al. 2002; Whiteway et al. 2010), which may be at least partially attributed to a failure of study designs to account for within-year variation in fish habitat occupancy. In our study, this variation resulted in the restoration status of a pool being a poor predictor of fish abundance later in the summer for either of our study species. The importance of restored habitat for rearing and growth diminished over the season. Within- and among-year variability in the association of fish abundance with structures suggests that effectiveness monitoring results can depend on (*i*) when monitoring studies take place with respect to the phenology of life history transitions in habitat use or (*ii*) inconsistent habitat selection by target species. Interannual variation in use of sites with ELJs compared with untreated sites and differences in the response to these treatments among species or size classes within a species has characterized fish habitat occupancy patterns in restoration projects similar in size to our study site (Pess et al. 2012).

Timing of sampling is important in effectiveness monitoring studies. Our observations of within-year decrease in total abundance of both species (Table 2) and no observable effect of restoration in late season samples (Fig. 2*a*) are likely influenced by both seasonal timing of life history transitions and inconsistent habitat use. In Upper Columbia River sub-basins, such as the Entiat River, Chinook salmon (particularly "summer-run" individuals) move downstream in late summer (Hillman et al. 1987; Bjornn and Reiser 1991). Emigration of summer-run individuals can explain low habitat occupancy and reduced detectability of differences between restored and unrestored habitat. In our study, Chinook density in all habitat units in all study segments declined from early season to late season (Figs. 2*a*, 3*a*, 3*c*), indicating emigration from both restored and natural pools. However, immigration of spring-run Chinook salmon into our study segments from headwater streams in the upper geomorphic valley reach of the river

Fig. 3. Mean (±SE) natural pool density in all control segments (PUD = rkm 5.2–5.5; Hatchery = rkm 10.9–11.4; Keystone = rkm 2.4–2.8) and in the Milne treated segment both in restored (M-Structures) and natural (M-Natural) pools for both Chinook salmon and steelhead in early season (*a*, *b*) and late season (*c*, *d*) snorkel surveys, 2009 only.



might also be expected by these life history patterns (Bradford and Higgins 2001). Lack of evidence of this by late September (Polivka 2010; K. Polivka, unpublished data) makes effectiveness monitoring research directed specifically at spring Chinook in restored rivers challenging.

Both Chinook salmon and steelhead increase their use of interstitial spaces as temperatures cool (Hillman et al. 1989), so the reduced abundance observed in later sampling periods may simply be due to thermally induced behavioral changes. Our results may reflect lower fish detectability via either snorkeling or seine samples; however, late season temperatures (mid-September and early October) still exceeded the typical minimum for daytime activity in both species (8–10 °C; Bradford and Higgins 2001). Our late season sampling involved the same methods as early season sampling and was not designed to detect increased use of interstitial spaces. This would likely require electrofishing, which, owing to permit restrictions and inconsistency with early season sampling methods, was not warranted in this study. Regardless, overall Chinook abundance declined and restored pools were no longer more occupied than untreated pools. So, any emigration by summer-run individuals does not change the conclusion that temporal changes occurred in the difference in habitat occupancy relative to restoration. Steelhead density in natural pools in the Milne segment did not decrease later in the season (Figs. 3*b*, 3*d*), so neither interstitial space use nor emigration accounts for all changes in the observed abundance at restored versus natural pools.

Inconsistency in habitat selection by both species was evident from nonsignificant associations with structure in some years (steelhead in 2010 and Chinook in 2011; Fig. 2*b*). However, these may have been the result of delays (~2 weeks) in the start of sampling due to high river discharge. Delays in sampling make it more likely for results to be affected by declines in observed abundance during the sampling season. In 2013, however, the lack of a significant positive association with structures for steelhead occurred despite a normal start time for sampling, so additional factors must influence habitat selection behavior in this species.

Additional explanatory challenges for the habitat selection patterns in steelhead, similar to those in other study systems (Beechie et al. 2005; Sogard et al. 2009), came from the observed shift to higher density at untreated pools within the treated Milne segment relative to structures in the 2009 comparison of multiple untreated segments (Figs. 3*b*, 3*d*). Resident life history forms of *O. mykiss* (rainbow trout) could possibly co-occur with anadromous steelhead and may influence the seasonal pattern of occupancy in restored versus natural pools. Our study population was likely dominated by anadromous steelhead, because resident rainbow trout are more common further upstream in a watershed (e.g., Narum et al. 2008; Mills et al. 2012), and our study segments are 40–45 km downstream of the nearest barrier to anadromy. Also, juvenile rainbow trout select similar habitat to anadromous steelhead (Bjornn and Reiser 1991) and are not likely to add variation to the data.

Behavior, competition, growth, and bioenergetics analysis are likely better indicators of a positive response to structure than simple observations or estimates of abundance. Measurement of these indicators can facilitate the examination of other hypotheses for abundance differences among habitats, such as prey availability. Interaction terms from the models, such as current velocity × temperature, indicate that energetic trade-offs may be important in describing habitat occupancy by both species (e.g., Hughes 1998). Measurement of fish growth rates under varying prey availability (from both drift and terrestrial in-fall), temperature, and current velocity conditions (e.g., Hill and Grossman 1993; Hughes 1998; Rosenfeld and Boss 2001; Rosenfeld et al. 2005) would facilitate further evaluation of the benefit of structures. In preliminary mark–recapture studies, growth of individuals of each species was greater in pools with restoration structures than in untreated habitat (Polivka 2010).

Study of competitive interactions between Chinook salmon and steelhead might indicate other information about the biological effects of structures. We observed both substantial overlap in occupancy of restored pools and similar associations of each species' abundance with most measured habitat attributes and interaction terms. Our findings contrast with early studies of stream habitat partitioning in these species (Everest and Chapman 1972), indicating that Chinook salmon occupy deeper, slower velocity areas and that steelhead trout occupy shallower, faster velocity areas. Habitat overlap among salmonids occurs in study systems where high-quality pools are readily available (e.g., Roper et al. 1994). Observed habitat overlap in our study system suggests that experimental testing of whether competitive interactions are alleviated by restoration is warranted. Steelhead are often generalists, occupying all microhabitat types in streams, but favor pools when competitive interactions are released (e.g., Young 2001, 2004; Spina et al. 2005) or when pool availability is increased (Hearn 1987). Our time series of species abundance data will allow the use of regression-based approaches (e.g., Pfister 1995) to explore competition relative to habitat restoration.

Association of species abundance with pool depth and current velocity, either directly or through interaction terms (Table 3), has implications for restoration under projected climate change scenarios. River discharge declines through the course of the sampling season and is clearly associated with decreased mean pool depth and current velocity. For snowmelt-dominated sub-basins like the Entiat River, climate warming is predicted to increase winter precipitation. Combined with warmer temperatures, winter flows are expected to increase with earlier peak discharge and decreased mean late-summer discharge (e.g., Hamlet 2011). In the Entiat River, reduced summer discharge and the consequent shallower pools and slower current velocity may affect restoration effectiveness for both of our study species.

Demonstration that restoration has increased stream capacity, rather than simply redistributing individual fish, is an important indicator of overall restoration effectiveness (Gowan and Fausch 1996). We have not yet isolated the mechanism resulting in more fish at restored pools, but we showed that restoration approximately doubled the density of both species in the early part of the rearing season. For Chinook salmon, this is very likely an increase in capacity for the restored segment, whereas the high occupancy of untreated pools in the late season by steelhead makes conclusions about habitat capacity difficult for this species. Understanding how restoration affects capacity, and of spatial and temporal variability in rearing habitat selection, can inform spatially explicit salmon life cycle models that can be used to predict whole sub-basin population response to restoration (e.g., Honea et al. 2009).

Our finding that mean abundance of both species was greater in restored pools coupled with observations of within- and among-year variation has implications for monitoring programs in the region as a whole. In sub-basins of the Upper Columbia River, effectiveness monitoring of restoration is usually done at a larger scale (whole sub-basin), and some studies only involve sampling treated and control reaches one to four times per year (Roni et al. 2002; Whiteway et al. 2010). Temporal trends identified in this study may explain some of the ambiguity in results of previous studies; yet, a repeated within-year sampling design might not be practical for multiple, geographically disparate restored sites. Nevertheless, extensive, repeated sampling that includes untreated habitat units within a treated river segment, and comparing it with occupancy at restored habitat, can identify increases in fish abundance and inform conclusions about habitat capacity.

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References

Beechie, T.J., Liermann, M., Beamer, E.M., and Henderson, R. 2005. A classification of habitat types in a large river and their use by juvenile salmonids. Trans. Am. Fish. Soc. **134**: 717–729. doi:10.1577/T04-062.1.

Bernhardt, E.S., Palmer, M.A., Allan, J.D., Alexander, G., Barnas, K., Brooks, S., Carr, J., et al. 2005. Synthesizing U.S. river restoration efforts. Science, **308**: 636–637. doi:10.1126/science.1109769.

Bernhardt, E.S., Sudduth, E.B., Palmer, M.A., Allan, J.D., Meyer, J.L., Alexander, G., Follastad-Shah, J., Hassett, B., Jenkinson, R., Lave, R., Rumps, J., and Pagano, L. 2007. Restoring rivers one reach at a time: results from a survey of U.S. river restoration practitioners. Restor. Ecol. **15**: 482–493. doi:10.1111/j.1526-100X.2007.00244.x.

Bilby, R.E., Fransen, B.R., Bisson, P.A., and Walter, J.K. 1998. Response of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (*Oncorhynchus mykiss*) to the addition of salmon carcasses to two streams in southwestern Washington, U.S.A. Can. J. Fish. Aquat. Sci. **55**(8): 1909–1918. doi:10.1139/f98-094.

Bjornn, T.C., and Reiser, D.W. 1991. Habitat requirements of salmonids in streams. *In* Influences of forest and rangeland management on salmonid fishes in their habitats. *Edited by* W.R. Meehan. American Fisheries Society Special Publication 19, Bethesda, Md. pp. 83–138.

Bond, N.R., and Lake, P.S. 2003*a*. Characterizing fish–habitat associations in streams as the first step in ecological restoration. Aust. Ecol. **28**: 611–621. doi:10.1046/j.1442-9993.2003.t01-1-01317.x.

Bond, N.R., and Lake, P.S. 2003*b*. Local habitat restoration in streams: Constraints on the effectiveness of restoration for stream biota. Ecol. Manage. Restor. **4**: 193–198. doi:10.1046/j.1442-8903.2003.00156.x.

Bradford, M.J., and Higgins, P.S. 2001. Habitat-, season-, and size-specific variation in diel activity patterns of juvenile chinook salmon (*Oncorhynchus tshawytscha*) and steelhead trout (*Oncorhynchus mykiss*). Can. J. Fish. Aquat. Sci. **58**(2): 365–374. doi:10.1139/f00-253.

Coe, H., Kiffney, P.M., and Pess, G.R. 2006. A comparison of methods to evaluate the response of periphyton and invertebrates to wood placement in large Pacific coastal rivers. Northw. Sci. **80**: 298–307.

Coe, H., Kiffney, P., Pess, G.R., Kloehn, K., and McHenry, M. 2009. Periphyton and invertebrate response to wood placement in large Pacific coastal rivers. River Res. Appl. **25**: 1025–1035. doi:10.1002/rra.1201.

Davidson, S.L., and Eaton, B.C. 2013. Modeling channel morphodynamic response to variations in large wood: implications for stream rehabilitation in degraded watersheds. Geomorphology, **202**: 59–73. doi:10.1016/j.geomorph.2012.10.005.

Everest, F.H., and Chapman, D.W. 1972. Habitat selection and spatial interaction by juvenile chinook salmon and steelhead trout in two Idaho streams. J. Fish. Res. Board Can. **29**(1): 91–100. doi:10.1139/f72-012.

Godaire, J., Russell, K., and Bountry, J. 2009. Entiat tributary assessment, Chelan County, Washington. US Bureau of Reclamation, Technical Service Center, Denver, Colo.

Gowan, C., and Fausch, K.D. 1996. Long-term demographic responses of trout populations to habitat manipulation in six Colorado streams. Ecol. Appl. **6**: 931–946. doi:10.2307/2269496.

Hamlet, A.F. 2011. Assessing water resources adaptive capacity to climate change impacts in the Pacific Northwest Region of North America. Hydrol. Earth Syst. Sci. **15**: 1427–1443. doi:10.5194/hess-15-1427-2011.

Hearn, W.E. 1987. Interspecific competition and habitat segregation among stream-dwelling trout and salmon: a review. Fisheries, **12**: 24–31. doi:10.1577/1548-8446(1987)012<0024:ICAHSA>2.0.CO;2.

Hilderbrand, R.H., Lemly, A.D., Dolloff, C.A., and Harpster, K.L. 1997. Effects of large woody debris placement on stream channels and benthic macroinvertebrates. Can. J. Fish. Aquat. Sci. **54**(4): 931–939. doi:10.1139/f96-334.

Hill, J., and Grossman, G. 1993. An energetic model of microhabitat use by rainbow trout and rosyside dace. Ecology, **74**: 685–698. doi:10.2307/1940796.

Hillman, T.W., Griffith, J.S., and Platts, W.S. 1987. Summer and winter habitat selection by juvenile Chinook salmon in a highly sedimented Idaho stream. Trans. Am. Fish. Soc. **116**: 185–195. doi:10.1577/1548-8659(1987)116<185:SAWHSB>2.0.CO;2.

Hillman, T.W., Chapman, D.W., Spaulding, J., and Griffith, J.S. 1989. Summer and winter ecology of juvenile Chinook salmon and steelhead trout in the Wenatchee River, Washington. Don Chapman Consultants, Inc. Report to Chelan County Public Utility District, Wenatchee, Wash.

Honea, J.M., Jorgensen, J.C., McClure, M.M., Cooney, T.D., Engie, K., Holzer, D.M., and Hilborn, R. 2009. Evaluating habitat effects on population status: influence of habitat restoration on spring-run Chinook salmon. Freshw. Biol. **54**: 1576–1592. doi:10.1111/j.1365-2427.2009.02208.x.

Hughes, N. 1998. A model of habitat selection by drift-feeding stream salmonids at different scales. Ecology, **79**: 281–294. doi:10.1890/0012-9658(1998)079[0281:AMOHSB]2.0.CO;2.

Kail, J., Hering, D., Muhar, S., Gerhard, M., and Preis, S. 2007. The use of large wood in stream restoration: experiences from 50 projects in Germany and Austria. J. Appl. Ecol. **44**: 1145–1155. doi:10.1111/j.1365-2664.2007.01401.x.

Kirk, T., Kerr, P., and Riddle, H. 1995. Draft initial watershed assessment, water resources inventory area 46, Entiat River watershed. Washington Department of Ecology Open File Report 95-02, Olympia.

Scheuerell, M.D., Hilborn, R., Ruckelshaus, M.H., Bartz, K.K., Lagueux, K.M., Haas, A.D., and Rawson, K. 2006. The Shiraz model: a tool for incorporating anthropogenic effects and fish–habitat relationships in conservation planning. Can. J. Fish. Aquat. Sci. **63**(7): 1596–1607. doi:10.1139/f06-056.

Miller, J.R., and Kochel, R.C. 2010. Assessment of channel dynamics, in-stream structures and post-project channel adjustments in North Carolina and its implications to effective stream restoration. Environ. Earth Sci. **59**: 1681–1692. doi:10.1007/s12665-009-0150-1.

Miller, S.W., Budy, P., and Schmidt, J.C. 2010. Quantifying macroinvertebrate responses to in-stream habitat restoration: applications of meta-analysis to river restoration. Restor. Ecol. **18**: 8–19. doi:10.1111/j.1526-100X.2009.00605.x.

Mills, J.S., Dunham, J.B., Reeves, G.H., McMillan, J.R., Zimmerman, C.E., and Jordan, C.E. 2012. Variability in expression of anadromy by female *Oncorhynchus mykiss* within a river network. Environ. Biol. Fish. **93**: 505–517. doi:10.1007/s10641-011-9946-4.

Morley, S.A., Garcia, P.S., Bennett, T.R., and Roni, P. 2005. Juvenile salmonid (*Oncorhynchus* spp.) use of constructed and natural side channels in Pacific Northwest rivers. Can. J. Fish. Aquat. Sci. **62**(12): 2811–2821. doi:10.1139/f05-185.

Mullan, J.W. 1987. Status and propagation of chinook salmon in the mid-Columbia River through 1985. US Fish and Wildlife Service Biol. Rep. **89**(3): 1–111.

Mullan, J.W. 1989. Growth, survival, and production of salmon and steelhead in a controlled section of Icicle Creek, Washington. US Fish and Wildlife Service, Leavenworth, Wash.

Narum, S.R., Hatch, D., Talbot, A.J., Moran, P., and Powell, M.S. 2008. Iteroparity in complex mating systems of steelhead *Oncorhynchus mykiss* (Walbaum). J. Fish Biol. **72**: 45–60. doi:10.1111/j.1095-8649.2007.01649.x.

Opperman, J.J., and Merenlender, A.M. 2004. The effectiveness of riparian restoration for improving instream fish habitat in four hardwood-dominated California streams. N. Am. J. Fish. Manage. **24**: 822–834. doi:10.1577/M03-147.1.

Pess, G.R., Liermann, M., McHenry, M.L., Peters, R.J., and Bennett, T.R. 2012. Juvenile salmonid response to the replacement of engineered logjams (ELJs) in the Elwha River. River Res. Appl. **28**: 872–881. doi:10.1002/rra.1481.

Peven, C.M., Whitney, R.R., and Williams, K.R. 1994. Age and length of steelhead smolts from the mid-Columbia River Basin, Washington. N. Am. J. Fish. Manage. **14**: 77–86. doi:10.1577/1548-8675(1994)014<0077:AALOSS>2.3.CO;2.

Pfister, C.A. 1995. Estimating competition coefficients from census data: a test with field manipulations of tidepool fishes. Am. Nat. **146**: 271–291. doi:10.1086/285798.

Polivka, K.M. 2010. Population ecology and effectiveness monitoring of small-scale instream habitat restoration structures in the Entiat River. *In* Upper Columbia Regional Technical Team 2010 Analysis Workshop Synthesis Report. *Edited by* M.B. Ward, J. Morgan, and C. Baldwin. Prepared for the Upper Columbia Salmon Recovery Board by the Upper Columbia Regional Technical Team and Terraqua, Inc., Wenatchee, Wash., UCSRB.

Roni, P., Beechie, T.J., Bilby, R.E., Leonetti, F.E., Pollock, M.M., and Pess, G.R. 2002. A review of stream restoration techniques and a hierarchical strategy for prioritizing restoration in Pacific Northwest Watersheds. N. Am. J. Fish. Manage. **22**: 1–20. doi:10.1577/1548-8675(2002)022<0001:AROSRT>2.0.CO;2.

Roni, P., Hanson, K., and Beechie, T. 2008. Global review of the physical and biological effectiveness of stream habitat rehabilitation techniques. N. Am. J. Fish. Manage. **28**: 856–890. doi:10.1577/M06-169.1.

Roni, P., Pess, G., Beechie, T., and Morley, S. 2010. Estimating changes in coho salmon and steelhead abundance from watershed restoration: How much restoration is needed to measurably increase smolt production? N. Am. J. Fish. Manage. **30**: 1469–1484. doi:10.1577/M09-162.1.

Roper, B.B., Scarnecchia, D.L., and La Marr, T.J. 1994. Summer distribution of and habitat use by chinook salmon and steelhead within a major basin of the South Umpqua River, Oregon. Trans. Am. Fish. Soc. **123**: 298–308. doi:10.1577/1548-8659(1994)123<0298:SDOAHU>2.3.CO;2.

Rosenfeld, J.S., and Boss, S. 2001. Fitness consequences of habitat use for juvenile cutthroat trout: energetic costs and benefits in pools and riffles. Can. J. Fish. Aquat. Sci. **58**(3): 585–593. doi:10.1139/f01-019.

Rosenfeld, J.S., Porter, M., and Parkinson, E. 2000. Habitat factors affecting the abundance and distribution of juvenile cutthroat trout (*Oncorhynchus clarki*) and coho salmon (*Oncorhynchus kisutch*). Can. J. Fish. Aquat. Sci. **57**(4): 766–774. doi:10.1139/f00-010.

Rosenfeld, J.S., Leiter, T., Lindner, G., and Rothman, L. 2005. Food abundance and fish density alters habitat selection, growth, and habitat suitability curves for juvenile coho salmon (*Oncorhynchus kisutch*). Can. J. Fish. Aquat. Sci. **62**(8): 1691–1701. doi:10.1139/f05-072.

Smokorowski, K.E., and Pratt, T.C. 2007. Effect of a change in physical structure and cover on fish and fish habitat in freshwater ecosystems — a review and meta-analysis. Environ. Rev. **15**: 15–41. doi:10.1139/a06-007.

Sogard, S.M., Williams, T.H., and Fish, H. 2009. Seasonal patterns of abundance, growth and site fidelity in juvenile steelhead in a small coastal California stream. Trans. Am. Fish. Soc. **138**: 549–563. doi:10.1577/T08-172.1.

Spina, A.P., Allen, M.A., and Clarke, M. 2005. Downstream migration, rearing abundance, and pool habitat associations of juvenile steelhead in the lower main stem of a south-central California stream. N. Am. J. Fish. Manage. **25**: 919–930. doi:10.1577/M04-105.1.

Stewart, G.B., Bayliss, H.R., Showler, D.A., Sutherland, W.J., and Pullin, A.S. 2009. Effectiveness of engineered in-stream structure mitigation measures to increase salmonid abundance: a systematic review. Ecol. Appl. **19**: 931–941. doi:10.1890/07-1311.1. PMID:19544735.

Testa, S., III, Shields, F.D., Jr., and Cooper, C.M. 2011. Macroinvertebrate response to stream restoration by large wood addition. Ecohydrology, **4**: 631–643. doi:10.1002/eco.146.

Ward, M.B., Morgan, J., and Baldwin, C. 2010. Upper Columbia Regional Technical Team 2010 Analysis Workshop Synthesis Report. Prepared for the Upper Columbia Salmon Recovery Board by the Upper Columbia Regional Technical Team and Terraqua, Inc., Wenatchee, Wash.

Whiteway, S.L., Biron, P.M., Zimmermann, A., Venter, O., and Grant, J.W.A. 2010. Do in-stream restoration structures enhance salmonid abundance? A meta-analysis. Can. J. Fish. Aquat. Sci. **67**(5): 831–841. doi:10.1139/F10-021.

Young, K.A. 2001. Habitat diversity and species diversity: testing the competition hypothesis with juvenile salmonids. Oikos, **95**: 87–93. doi:10.1034/j.1600-0706.2001.950110.x.

Young, K.A. 2004. Asymmetric competition, habitat selection and niche overlap in juvenile salmonids. Ecology, **85**: 134–149. doi:10.1890/02-0402.