**Beyond redistribution: In-stream habitat restoration increases capacity for young-**

**of-the-year Chinook salmon and steelhead in the Entiat River, WA**

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Suggested running head – Fish habitat restoration and capacity

**Abstract**:

We conducted snorkel surveys for juvenile salmonids in reaches of the Entiat River

(Washington, USA) treated with engineered log jams (ELJs), and in reaches without

treatments, to determine if habitat-unit-scale observations can identify whether

restoration has increased the habitat capacity of a reach. The conceptual basis and field

methodology emphasize fish density data (fish/habitat area in $m^2$) from unrestored habitat

within a reach treated with ELJs compared to surveys in 1) unrestored habitat in untreated

reaches and 2) restored habitat in treated reaches. A Bayesian generalized linear model

enabled us to quantify density differences among habitat types using advanced

computational statistics. Modal density of young-of-the-year Chinook salmon

(*Oncorhynchus tschawytscha*) and steelhead (*O. mykiss*) was at least 3.1-fold and 2.7-fold

greater, respectively, in restored habitat compared with unrestored habitat for all treated

reaches examined. To distinguish the density differences in those reaches as capacity

increases rather than redistribution from poor habitat to good habitat, we compared

density in unrestored habitat in both treated and untreated reaches. Here we found no

differences for either species, confirming that the increased density in restored habitat

units did not come from depletion of unrestored habitat in the same reach. We thus

concluded that restoration increased the habitat capacity of the reach at the scale of pools

created by ELJs.

In the United States, public agencies, academic researchers, and private

consultants are engaged in activities related to the management and restoration of aquatic

habitat to recover valuable fisheries (Katz et al. 2007; Roni et al. 2008), involving

millions of dollars of public and other funds annually (Bernhardt et al. 2005; O'Neal et

al. 2016). In the Pacific Northwest region, for example, managers have thus far

implemented restoration projects in several hundred kilometers of stream habitat to

improve rearing conditions for salmonid fishes. Use of large wood or other material to

build in-stream habitat structures is one of the most common techniques to protect and

recover salmon populations across the region (Roni et al. 2015; Hillman et al. 2016).

Large wood structures (engineered log jams; ELJs) are intended to promote processes

that restore channel morphology (Davidson and Eaton 2013), increase pool availability

(Roni et al. 2010), provide cover (Bond and Lake 2003a), and stimulate production of

macroinvertebrate prey resources for fish (e.g., Hilderbrand et al. 1997; Kail et al. 2007).

An important component of this restoration is the evaluation of its efficacy by

demonstrating a biological response using the most robust metrics available (Block et al.

2001).

Habitat modeling tools such as Ecosystem Diagnosis and Treatment (EDT;

Lichatowich et al. 1995; Lestelle and Mobrand 1996) and Physical Habitat Simulation

System (PHABSIM; Bovee 1982) use fish-habitat correlations to guide restoration

actions based on the assumption that specific habitat improvements will increase fish

abundance and effectively increase fish populations. However, correlative analyses (e.g.,

multiple regression, ordination methods) may lead to overestimation of the effect that

manipulation of habitat variables will have on fish abundance due to weak correlation

coefficients, despite statistical significance (Shirvell 1989; Lammert and Allan 1999),

complex interactions between habitat variables (Beechie and Sibley 1997), variable

scales of inference (Feist et al. 2010), and model uncertainty (McElhaney et al. 2010).

Furthermore, field surveys can show underutilization of "good" habitat, possibly due to

responses to biological factors (e.g., escapement/seeding, food availability, predation

risk, or competition) not measured as part of physical habitat surveys (Polivka 2005).

Thus, fish restoration effectiveness studies that rely upon the comparison of mean fish

density in restored vs. unrestored habitats (e.g., Bond and Lake 2003b; Roni et al. 2008),

often show small or no effects of restoration (Roni et al. 2008; Whiteway et al. 2010,

Stranko et al. 2012; Hillman et al. 2016). When positive numerical responses are

observed, the distributional patterns can vary greatly by species, year, and time period

within a rearing season (Pess et al. 2012; Polivka et al. 2015).

Increased capacity to support fishes is one hypothesized outcome of restoration

given the relatively consistent association between total habitat area and fish abundance

(Hankin and Reeves 1988; Solazzi et al. 2000; Connor et al. 2001). Habitat capacity

increases can be demonstrated by increases in total fish density (fish/m$^2$ surface area,

e.g.), relative to pre-restoration conditions, measurable at the scale of the restoration

effort. Many post-restoration monitoring programs thus try to identify capacity increases

via measurements of density increases in restored habitat. However, such observations

may simply indicate that individuals have redistributed themselves within a reach from

poorer habitat to restored habitat (Roni 2019).  This may be attributable to the possibility

of missing important spatial or temporal patterns in fish distribution among habitats with

an observation design that is strongly linked to one scale or another (Fausch et al. 2002).

Restoration programs often aim to make effects detectable at a whole-reach scale (Roni et

al. 2013; Roni et al. 2018a; Bennett et al. 2016); thus, many effectiveness studies are

designed to compare fish density among restored and unrestored reaches. Although the

reach scale is seen as a meaningful one for the measurement of many physical and

biological processes (Frissell et al. 1986), it can be problematic because the effects of in-

stream structures can sometimes be very localized (Polivka et al. 2019).

Tools such as the BACI (before-after-control-impact) design (Bernstein and

Zalinski 1983) make it relatively straightforward to assess the effects of habitat

restoration. The design offers the advantage that these effects can be distinguished from

background variation common to all observations and from differences among

reaches/sites (Popescu 2012). Challenges to using such a design include finding suitable

reference sites and collecting comparable data between reference and treatment sites

(Conner et al. 2016). Moreover, although BACI studies enable detection of effects at

spatial scales from habitat units to whole reaches (Roni et al. 2018b), they are only

possible when there are adequate pre-treatment data, which is difficult to ensure unless

restoration projects are planned well in advance. At larger scales, such as comparing

whole reaches, most effectiveness study designs, including BACI, are subject to

replication issues (Stewart-Oaten et al. 1986; Conner et al. 2016), which can exacerbate

difficulties in observing a density increase in restored habitat given high variability

inherent in the study system (Underwood 1994). What is needed is a method that is

scaled appropriately to detect effects at the scale of restoration, is robust to the variability

in fish density that often confounds effectiveness study results, and that can identify real

or apparent capacity increases, even when pre-treatment data are not available.

Studies at the patch scale address the replication of habitat units (e.g., pools,

riffles, glides; Cramer and Ackerman 2009) in restoration treatments and can identify the

extent to which the effects of restoration are localized (Polivka et al. 2019). Comparison

of unrestored habitat patches in a treated reach against restored habitat patches (usually

ELJ pools) in the same reach, and then against unrestored habitat patches in untreated

reaches can indicate apparent capacity increases (Polivka et al. 2015). Furthermore, such

a comparison can be made without pre-treatment data, but requires that other assumptions

be met. Prior to treatment, stream reaches in which restoration is planned should have the

same average fish density per habitat as the nearby, untreated reaches (Figure 1a),

assuming that treatment and control reaches have similar geomorphic, hydrological and

ecological characteristics. This assumption could be affected by seeding levels from

spawning in the previous year (i.e., different numbers of juveniles resulting from year-to-

year fluctuations in escapement), but can still be verified for untreated reaches

sufficiently near the reach to be treated (Gowan and Fausch 1996; Kennedy et al. 2014).

To identify a capacity increase when pre-treatment data are not available, post-treatment

fish density in restored habitats is examined for one of these hypothetical patterns:

1) *Redistribution of fish within the treated reach*. Fish density is higher in restored

habitats relative to unrestored habitats in a treated reach, but density is lower in

unrestored habitats in the treated reach relative to all habitats in untreated reaches (which

are, of course, also unrestored). This is due to the movement of fish to the restored

habitats from unrestored habitats within the reach, such that total average reach density

has not changed (Figure 1b).

2) *Type 1 capacity increase*. Fish density is higher in restored habitats relative to

unrestored habitats in a treated reach, and remains equal across unrestored habitats in

both treated and untreated reaches. In this case, the fish that occur in restored habitat add

to the density observed in unrestored habitat and therefore represent an apparent capacity

increase. (Figure 1c; Polivka et al. 2015).

3) *Type 2 capacity increase*. Fish density is higher in restored habitats relative to

unrestored habitats in the treated reach, and higher in unrestored habitats in treated

reaches relative to those in untreated reaches. In this case, restoration has increased

capacity of *all* habitats in the treated reach (Figure 1d) and a density increase at the reach

scale might be observed.

Here, we apply the hypotheses in Figure 1 to post-treatment patterns of fish

density from snorkel observations in eight reaches of the Entiat River, over multiple post-

treatment years. We used a Bayesian analytical approach to deal with non-normally

distributed density data – also a common issue in effectiveness studies. From this field

methodology and analysis we were able to address whether restoration increases juvenile

rearing capacity at both the habitat unit and reach scales in a manner distinguishable from

redistribution of fish from poorer habitat to good habitat in a restored reach. Verification

of this distinction can potentially aid study designs in systems where restoration effects

are difficult to detect.

[A]Methods

[C]*Study system*.—The Entiat River is a tributary of the Upper Columbia River in

Washington State, USA (Figure 2). Its headwaters are in the Cascade Mountains and the

river flows ~ 69 river kilometers to its confluence with the Columbia River (49.6567 N,

120.2244 W; river km 778). Species targeted by restoration efforts include anadromous

Chinook salmon *Oncorhynchus tschawytscha* and steelhead trout *O. mykiss*. The

freshwater phase is an important component of the life cycle of these two species and in-

stream habitat restoration is designed to enhance sub-yearling growth and survival.

Although some non-salmonid species and age 1+ steelhead are present in each of our

study reaches, we focused our sampling and analysis on sub-yearling Chinook salmon

and steelhead. The Chinook sub-yearlings in the Entiat are a mix of spring-run and

summer-run and overlap during the study season. Genetic testing gives moderate to good

probabilities of being able to distinguish runs (Degroseillier et al. 2018), but with some

hybridization and spatial overlap, run type cannot be assumed. During the study years,

total estimated spawning escapement of spring and summer runs (mean ± sd) in the

previous season was 338 ± 142 and 258 ± 85 adults, respectively (Fraser et al. 2018).

There were two years in which Spring Chinook escapement and one year in which

Summer Chinook escapement were slightly below 1 SD of the respective means. Thus

our analysis did not consider annual differences in total seeding (e.g., density differences

among habitats resulting from an unusually large Spring or Summer run) as a mechanism

for habitat distribution of sub-yearlings reported below. Other salmonids are present in

low abundance; cutthroat trout (*O. clarki*) and resident rainbow trout occur above the

barrier to anadromy, which is upstream of our uppermost study reach. Bull trout

(*Salvelinus confluentus*) move between the Entiat and mainstem Columbia and, although

they can occur at our study sites, as can other resident freshwater fishes, none were

observed during the study.

The restoration projects studied here were implemented in the Entiat watershed as

part of a systematic program of restoration combined with post-treatment monitoring

(Bennett et al. 2016). Treatment reaches (N =5) occurred in the lower part of the Entiat

River basin, located between river km 2.7 and 6.4 (Table 1). Four untreated study reaches

occurred among them with the most upstream reach at river km 11.4. The mean wetted

width of lower basin reaches during the study was 23 m. Treated reaches in the upper

basin (N = 3) occur between river km 34.6-39.9 with only one available control reach

("Upper Control," UC; Table 1). The UC reach had naturally occurring log structures as

well as untreated habitat and thus offered the opportunity to compare the effects on fish

density of man-made ELJs with that of natural ELJs. The mean wetted width of upper

basin reaches during the study was 21 m. Although the upper and lower basins are

considered geomorphically distinct, (Godaire et al. 2009), both have similar substrate and

gradient, and are used here only to identify the study reaches longitudinally.

[C]*Study reaches*—In the Entiat River, reaches were selected for treatment with ELJs by

conservation agencies based on a combination of landowner willingness and

recommendations following the completion of reach assessments for hydrologic

conditions that were best suited for favorable outcomes of restoration (e.g., Sixta 2010).

All reaches with ELJs were included in this study as treated reaches (Figure 2, Table 1).

Untreated reaches were the nearest available reaches with public or private permissible

access in which no habitat restoration structures were installed. We refer to treated and

untreated reaches as such, and to restored and unrestored habitats as pools that were

created/restored with ELJs versus river habitat units (not necessarily pools) that had no

restoration structures.

The five lower basin reaches were treated with ELJs in July and August 2014,

whereas the three upper basin reaches were treated in September 2012 (Table 1). ELJs in

lower basin reaches created pools with a mean area of 38.0 m$^2$ (range = 2.9-310 m$^2$) and

in the upper basin with mean area 79.1 m$^2$ (range = 20.4 – 232.2 m$^2$). Because fish

activity and density in the Entiat River tend to be highest in July compared to other

summer months (Polivka et al. 2015), post-treatment surveys in both upper and lower

basins took place in July (lower basin 2015-2016; upper basin 2013-2016). The upper-

basin reach "Tyee" not surveyed in 2016 due to a change in accessibility.

[C]*Sampling design*—Fish density data came from snorkel observations in reaches of the

upper and lower basins designed after those in Polivka et al. (2015) where unrestored

habitat units were selected in a spatially randomized manner in both treated and untreated

reaches. Restored units (ELJ pools) are sampled in treated reaches as they were

encountered during the sampling of unrestored units.  The general approach was to

establish a starting point at the upstream end of each reach regardless if treated or

untreated. We selected 15 unrestored habitat patches (standardized to 15m$^2$: 3 x 5 m) by

first using randomly generated distance measurements following the method of Polivka et

al. (2015). Random distances had a minimum of 10 m and a maximum distance of total

reach length divided by 15 (e.g., "Kiosk" reach length of 805 m/15 = 54 m maximum

longitudinal distance between unrestored habitat surveys). This ensured that all

randomly-selected unrestored habitat patches occurred within and likely throughout the

entire length of the designated reach. Surveys proceeded from the upstream end of the

reach and each randomly generated distance was used to determine the distance

downstream to the next survey patch from the previous. The survey took place on either

the left or right river margin, selected via coin toss. Only habitat patches occurring on the

stream margin were surveyed because mid-channel surveys have been found to provide

little additional information in other salmonid streams (Beechie et al. 2005) and the river

margin is where ELJs were placed. The standardized area of 15 m$^2$ for unrestored habitat

patches was often smaller than the pool area of ELJ-restored pools, but we account for

the effect of area in the analysis (see below).

Patches typically consisted of pools or slower-flowing glides, but generally not

riffles because riffles are not a substantial component of stream margin habitat in the

Entiat River. Unrestored habitat units were surveyed by one snorkeler working in an

upstream to downstream direction, visually identifying and enumerating all fishes

present.  Chinook and steelhead in the study reaches were typically age-0, but any age 1+

or larger steelhead were noted, when observed. In treated reaches, ELJ-restored pools

were encountered during the movement downstream between unrestored habitat surveys.

As ELJs were encountered, restored habitat surveys were conducted in the entire pool and

total pool area was measured. For these, two snorkelers would survey the pool starting

from opposite ends, because these pools tended to be larger and this would decrease the

chance of fish being missed due to the increased habitat complexity of the ELJ. The

survey crew would then continue downstream following the random distances to the next

unrestored habitat survey. In the upper basin, the survey protocol was identical, with the

exception that, in the control reach (UC), unrestored habitat surveys were conducted

along with surveys at the naturally occurring log structures.

Turbidity does not affect detection of fish in this river as visibility for snorkeling

is always >2–3 m at all but the highest flows, which permitted snorkelers to completely

see the survey area. In unrestored habitats, lack of physical structure ensured accurate

fish counts because the entire $15m^2$ area was completely visible (Polivka et al. 2015).

However, the ELJ structures varied in their complexity and it is possible that fish could

be obstructed from view, resulting in underestimation of density at restored habitats. This

would make the estimate of any effect of restoration on density more conservative.

[C]*Data analysis*—Data consisted of fish density (fish/$m^2$) observations in pools created

by or restored with ELJs, in randomly selected unrestored habitat in treated reaches, in

randomly selected unrestored habitat in untreated reaches, and at natural structures in the

UC reach in the upper basin. In each case, these were fish counts with accompanying

measures of pool area. The key comparisons in our design (Figure 1) are 1) between

restored and unrestored habitat in treated reaches 2) between unrestored habitat in both

treated and untreated reaches and 3) in the upper basin between restored habitat in treated

reaches and natural structures in the UC reach. To consider each species and upper and

lower valley segments, this required a total of ten analyses: Comparisons 1 and 2 for two

basin segments and for two species (8 analyses); plus comparison 3 for two species but

for one basin segment (2 analyses). Because comparison 1 in the upper basin included

pools created by natural structures and untreated habitat in the UC reach, comparison 3

identified whether there was a disproportionately stronger density response to natural

structures vs. ELJs. We excluded age 1+ steelhead from the analysis as they were only ~

10% of total steelhead observed.

For each comparison, we fit a Bayesian generalized linear hierarchical model

using the R software package BRMS (Bürkner 2017; R Core Team 2019; Stan

Development Team 2019). Models all consisted of the same basic structure. Because we

used count data by habitat unit and exploratory analysis indicated overdispersion of the

data, due partly to the frequent observation of zero fish in unrestored habitat units, we

assumed a negative binomial distribution and verified the modeled distribution using

posterior predictive checks. Presence or absence of restoration structures ("Treatment")

was a fixed effect, but with an additional level in the upper Entiat accounting for the

presence of natural structures in the "UC" reach. The interaction term year x stream reach

was a random effect because each one is a grouping variable (2 years x 5 reaches, Lower

Entiat; 4 years x 4 reaches, Upper Entiat). Pool area (log-transformed) was included in all

models as an offset term given its positive relationship to fish abundance (Polivka et al.

2015) and to enable back transformation of model output values to density (fish/m$^2$). We

did not include a fixed effect term to look for differences among the treated reaches

because pairwise comparisons involve reductions in the data that possibly lead to

systematic lack of fit or, alternatively, over-report effect sizes (Head et al. 2015). During

model specification, we found that the coefficients for year were close to zero. We did a

Leave One Out (LOO) cross-validation without year and the model with year x reach

term was more parsimonious with the data. This specification was also supported by

$\hat{R}$ values and the convergence time for the different models.

We initiated the models with weakly informative priors (e.g., half student-$t$ prior

with 3 degrees of freedom and a scale parameter that depends on the standard deviation

of the response after applying the link function, i.e., the defaults provided by BRMS) and

for each we ran four chains for 2000 iterations, using the first 1000 iterations as a warm

up and thinning by 1 iteration, giving a total of 4000 samples (1000 per chain). We

plotted chains and parameter pairs for all models to make sure the chains converged and

parameters were identifiable. We also examined model statistics to ensure that $\hat{R}$ was less

than 1.1.

To determine whether there were differences in fish density (D) across habitat

types, we extracted the 4000 posterior estimates for the fixed effects (i.e., $D_{restored}$,

$D_{unrestored}$, $D_{natural}$), back-transformed the draws, and took the difference ($D_{restored}$ -

$D_{unrestored}$). Using this vector of differences, we calculated a 95% highest (Posterior)

density interval (HDI) using an algorithm described in Kruschke (2015). We considered

fish density to be different among habitats if the 95% credible interval for that difference

did not overlap zero. We used these same procedures to compare unrestored habitat in

treated reaches with unrestored habitat in untreated reaches for each species and for the

upper and lower basin segments separately.

[A]Results

The two years of post-treatment sampling in the lower basin yielded a total of 328

surveys, 58 of which were at the ELJ-restored pools distributed among the five treated

reaches, and 270 of which were in randomly-selected unrestored habitat units in treated

and untreated reaches, combined. The four years of post-treatment surveys in the upper

basin yielded 294 surveys, consisting of 52 at the ELJ-restored pools and 17 at the

naturally occurring log structures in the UC reach. The number of structures in that reach

varied for each year of the study due to wood aggregation and wash-out (N = 3 (2013), 5

(2014, 2015), and 4 (2016)). Across all study reaches and habitat units, we observed 1504

sub-yearling Chinook and 887 steelhead in the lower basin and 1189 sub-yearling

Chinook and 273 steelhead in the upper basin. Overdispersion of the data was

exacerbated by surveys with zero fish (no Chinook in 145 and 221 surveys, and no

steelhead in 148 and 236 surveys, in the lower and upper basins, respectively) and by

positive counts varying across orders of magnitude.

307            Pools created by restoration with ELJs showed higher fish density than unrestored

habitat patches. In the lower basin segment, restored habitat in the five treated reaches

had, on average, 2.9-fold greater density of sub-yearling Chinook salmon and 1.7-fold

greater density of steelhead than unrestored habitat in those same reaches (Figure 3A).

Draws from the posterior distributions of density in each habitat ($D_{restored}$, $D_{unrestored}$) led to

a distribution of density differences between habitat types ($D_{restored}$ - $D_{unrestored}$) with a

95% credible interval > 0 in 100% of the draws for both species (Table 2). In treated

reaches of the upper basin, restored habitat had a 13-fold higher density of Chinook and a

6.8-fold higher density of steelhead than unrestored habitat in the same reaches (Figure

3B). Despite the magnitude of those differences in overall means, the draws from

posterior distributions led to a 95% credible interval that nearly overlapped zero in both

species (Table 2). There were no density differences for either species between restored

habitats in treated reaches and habitats with natural structures in the UC reach (Figure

3B), indicating that ELJ structures are good analogs for natural structures, at least in this

study system. This also indicates that natural structures did not meaningfully contribute

to the observed overall difference between restored and unrestored habitat in the upper

basin.

324            For the second key comparison in detection of a capacity increase, unrestored

habitat in treated reaches did not differ in density (of either species) from unrestored

habitat in untreated reaches in the lower basin (Figure 4A), nor were there density

differences between unrestored habitat in treated reaches in the upper basin segment and

unrestored habitat in the UC reach that only had natural structures (Figure 4B). In both

the upper and lower basins, the lack of a difference between unrestored habitats in treated

reaches and in untreated reaches indicates a Type 1 capacity increase (Figure 1). In the

lower basin, however, Chinook density was higher in unrestored habitats of treated

reaches than in unrestored habitats of untreated reaches in nearly 93% of the draws from

the posterior distribution. Thus lower basin restoration could be approaching a Type 2

capacity increase that may become evident in later post-restoration years. From both pairs

of figures it is clear that the lower basin has a higher density of both species than the

upper basin.

[A]Discussion

Although it is relatively easy to show that fish are attracted to in-stream habitat

restoration structures, there are challenges to demonstrating that increased fish density

represents an increase in habitat capacity. The empirical basis of the method presented

here serves effectively when pre-treatment data are lacking on fish density in the area to

be restored, thus making BACI designs intractable. Like BACI, however, we relied upon

an assumption that is difficult to demonstrate conclusively. Nevertheless, in this case we

had a sufficient number of treated and untreated reaches to distinguish between a capacity

increase and simple redistribution of fish. Moreover, we provided an analytical

framework that addresses the issue of overdispersion in data that occurs, for example,

when there is a considerable amount of unused habitat resulting in observations of zero

fish. The field methodology involves sampling at the habitat unit ("patch") scale (Frissell

et al. 1986), which may be difficult to extrapolate to larger scales as may be desired by

restoration planners (Roni et al. 2008). Our method is robust to many of these concerns

and even showed a trend toward a larger scale effect in one group of treated reaches in

our study system. Finally this study design is broadly applicable to myriad restoration

projects that lack rigorous pre-treatment data, and combined with pre-treatment data

would be even more powerful.

Our approach rests upon the assumption that unrestored habitat in treated and

untreated reaches show the same value of the response variable (fish density or

presence/absence). A BACI design does not depend on this assumption and only requires

that a treated area show a greater positive change, relative to an untreated area, following

the treatment (Roni et al. 2013; Conner et al. 2016; Roni et al. 2018ab). However, stream

restoration is often opportunistic as it is dependent upon the convergence of habitat in

need of improvement with feasibility of implementing restoration treatments; thus, pre-

treatment data are not always available.  However, our key assumption could be affected

by differences among reaches prior to treatment.  For example, if the treated reach had

lower density than other reference reaches prior to treatment, then a density difference

between restored and unrestored habitat within that reach could be interpreted as

redistribution, thus underestimating the positive response to restoration. Given that we

surveyed multiple untreated reaches in the lower basin and found that unrestored habitat

there did not differ from unrestored habitat in treated reaches, it is unlikely that the extent

to which we observed a density increase in restored habitat was affected by unobserved

variation.

We show that what happens in unrestored habitat gives information about how to

interpret observed density increases in restored habitat. However it also depends on the

availability of multiple suitable control reaches, which may not be available under some

restoration programs or in some watersheds. In our case, land ownership and local

physical conditions resulted in only a single reference reach being available in the upper

basin, further complicated by the presence of natural log structures. Thus we couldn't be

certain of a Type 1 vs. Type 2 capacity increase in the treated reaches in the upper basin

because we were not able to sample reaches without structures, man-made or natural.

This reference reach did, however, provide the advantage of showing that the ELJs are, at

least, good analogs for natural structures.

The mobility of salmonids and the dependence of spatial scale on their

relationships with habitat characteristics (Feist et al. 2003, 2010), mean that movement

and habitat settlement patterns may affect comparisons of unrestored habitat among

treated and untreated reaches. Ideal free distribution theory (Fretwell and Lucas 1969;

Morris 1988) describes how habitat quality affects settlement of habitats at varying

densities. Depending on whether the difference among habitats is qualitative or

quantitative, the density difference in individuals between higher quality habitats and

lower quality habitats may be larger at low total population density than when population

density is higher (Morris 1988). In this study system, years with low total fish density

could therefore result in large density differences between restored and unrestored habitat

in treated reaches if restored habitat is settled preferentially (quantitative difference;

Morris 1988). Moreover, all unrestored habitats in untreated reaches would be settled at

about the same rate, and comparison of treated and untreated reaches might thus show

that unrestored habitat in treated reaches had lower density than in untreated reaches.

This would give the appearance that the density difference between restored and

unrestored habitat in a treated reach was simply due to redistribution, leading to

underestimation of the habitat improvement by restoration. Variation in the total number

of sub-yearling Chinook seeking habitat can result from year-to-year differences in

escapement. These differences were not substantial in this system during the study years,

but may need to be considered elsewhere.

Statistical issues in both this and with BACI designs may result from low

replication (Conner et al. 2016). This was particularly an issue at the Dillwater reach in

the upper basin where few structures were installed to begin with, some of which were

above the water line during low late-summer flows. This supports the need for analytical

techniques, such as ours, capable of combining multiple treated reaches and years to

determine restoration efficacy. We frequently observed zero fish at the habitat scale;

however, the Bayesian GLM fitting routine precluded the need for zero-inflated

frequentist models (e.g., Zuur et al. 2009). Moreover, it afforded a robust method of

back-calculating fish density and examining the entire posterior distribution of the

density estimate for meaningful differences in density among habitat types. Bayesian

approaches can also improve the interpretability of results from BACI designs while

dealing with replication issues (Conner et al. 2016).

Despite apparent improvement of habitat capacity observed here and in Polivka et

al. (2015), a given density increase associated with ELJ restoration can be difficult to

observe at the reach scale. In a focused study at three of the five lower basin reaches

studied here, Polivka et al. (2019) demonstrated that observed density increases at ELJ-

restored pools are very localized, sometimes indistinguishable only 5-10 m away, or by

increasing the sampling area around a restored pool to only 2X the area of the pool. This

does not necessarily negate the apparent capacity increases observed here; it merely

demonstrates that there can be a large difference between restored and unrestored habitat

in a treated reach. Monitoring programs often emphasize a reach-scale perspective based

on earlier recommendations (Bennett et al. 2016; Roni et al. 2013). From extensive

surveys here and in Polivka et al. (2015), it is clear that detection of reach-scale capacity

increase vs. basic density increase requires: 1) separate surveys of restored and

unrestored habitat *within* a treated reach and 2) availability of and access to physically

and biologically similar untreated reaches. The first stipulation suggests that reach scale

surveys might not be effective at detecting Type 1 capacity increases if unrestored habitat

within the treated reach obfuscates the effect of restoration, or when the effect of ELJs is

very localized (Polivka et al. 2019). The second stipulation means that the characteristics

of control reaches should thus be a consideration both for restoration site selection and

for post-restoration effectiveness monitoring designs.

The inability to distinguish between redistribution and capacity increase following

restoration due do study design or scale issues is a possible explanation for inconsistent

responses (Smokorowski and Pratt 2007; Whiteway et al. 2010), small or no observed

effects of restoration (Roni et al. 2008; Stranko et al. 2012; Hillman et al. 2016), or

positive responses that vary by species, year, and time period within a rearing season

(Pess et al. 2012; Polivka et al. 2015). We have shown that juvenile salmonid habitat

capacity increased via the Type 1 outcome (Figure 1), distinguishable from simple

redistribution.  Studies that are more mechanistic in nature are required to support

observations of capacity increases here and in related studies (Beechie et al. 2015), such

as linking capacity increases to improvements in traits correlated with fitness, such as

sub-yearling growth or survival through any subsequent life stage (Achord et al. 2007;

Polivka et al. *in review*). Restoration in spawning streams is implemented to augment

habitat for sub-yearling, an important stage of the "stream-type" life history when

considerable growth and development take place in streams (Groot and Margolis 1991).

The apparent capacity increase described here for the upper and lower geomorphic basin

segments of the Entiat River indicate that restoration is benefitting Chinook salmon and,

to a less definite extent, steelhead early in their life history.

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Table 1. Lower and upper basin study reaches, their upstream reach location along the

river, reach length, treatment type, and the number of wood structures (ELJ or natural)

surveyed per reach. Unrestored habitat (N=15/reach) was also surveyed at each untreated

and treated reach. Reach names were designated by restoration project sponsors and

usually refer to a landmark or sponsoring entity.

| Basin segment | River (km) | Reach length (m) | Reach name | Treatment (year) | Structures (#) |
|---|---|---|---|---|---|
| Lower Entiat R. | | | | | |
| | 2.1 | 805 | Kiosk | Untreated | |
| | 2.7 | 322 | Keystone | Treated (ELJ 2014) | 6 |
| | 4.3 | 322 | Yakama | Treated (ELJ 2014) | 8 |
| | 5.1 | 644 | Asher/Milne | Treated (ELJ 2014) | 7 |
| | 5.6 | 483 | PUD | Treated (ELJ 2014) | 3 |
| | 6.4 | 322 | Harrison S.C. | Treated (ELJ 2014) | 6 |
| | 7.2 | 644 | Harrison ref. | Untreated | |
| | 10.3 | 644 | Roaring Crk. | Untreated | |
| | 11.4 | 644 | Hatchery | Untreated | |
| Upper Entiat R. | | | | | |
| | 32.8 | 483 | Upper Control (UC) | Untreated (natural) | 5 |
| | 34.6 | 483 | Dillwater | Treated (ELJ 2012) | 3 |
| | 36.2 | 805 | Tyee | Treated (ELJ 2012) | 5 |
| | 39.9 | 1287 | 3D | Treated (ELJ 2012) | 7 |

666  Table 2. Mean and modal differences in fish density (D) drawn from the posterior

667  distribution of generalized linear models fit to survey data in each indicated habitat type

668  from treated and untreated reaches in the Entiat River. The 95% highest density interval

669  (HDI) of each comparison is given. HDIs that do not overlap zero (*) indicate meaningful

670  differences in density ($\Delta$D).

| Basin segment | Species | $\Delta$D mean | $\Delta$D mode | 95% HDI |
|---|---|---|---|---|
| Lower Entiat R. | | | | |
| $D_{restored}$ - $D_{unrestored}$ habitats in treated reaches | | | | |
| | Chinook | 0.41 | 0.34 | 0.18 – 0.68* |
| | Steelhead | 0.14 | 0.08 | 0.05 – 0.26* |
| $D_{unrestored}$ - $D_{unrestored}$ habitats in treated versus untreated reaches | | | | |
| | Chinook | 0.09 | 0.002 | -0.05 – 0.27 |
| | Steelhead | 0.03 | -0.07 | -0.09 – 0.14 |
| | | | | |
| Upper Entiat R. | | | | |
| $D_{restored}$ - $D_{unrestored}$ habitats in treated reaches | | | | |
| | Chinook | 0.25 | 0.38 | 0.03 – 0.59* |
| | Steelhead | 0.04 | 0.04 | 0.001 – 0.12* |
| $D_{restored}$ – $D_{natural}$ habitats in treated and control (UC) reaches | | | | |
| | Chinook | 0.12 | 0.10 | -0.29 – 0.65 |
| | Steelhead | 0.02 | 0.03 | -0.06 – 0.13 |
| $D_{unrestored}$ - $D_{unrestored}$ habitats in treated versus untreated reaches | | | | |

672  Basin segment      Species      $\Delta$D mean      $\Delta$D mode      95% HDI

673  Lower Entiat R.

674  $D_{restored}$ - $D_{unrestored}$ habitats in treated reaches

675               Chinook      0.41      0.34      0.18 – 0.68*

676               Steelhead      0.14      0.08      0.05 – 0.26*

677  $D_{unrestored}$ - $D_{unrestored}$ habitats in treated versus untreated reaches

678               Chinook      0.09      0.002      -0.05 – 0.27

679               Steelhead      0.03      -0.07      -0.09 – 0.14

681  Upper Entiat R.

682  $D_{restored}$ - $D_{unrestored}$ habitats in treated reaches

683               Chinook      0.25      0.38      0.03 – 0.59*

684               Steelhead      0.04      0.04      0.001 – 0.12*

685  $D_{restored}$ – $D_{natural}$ habitats in treated and control (UC) reaches

686               Chinook      0.12      0.10      -0.29 – 0.65

687               Steelhead      0.02      0.03      -0.06 – 0.13

688  $D_{unrestored}$ - $D_{unrestored}$ habitats in treated versus untreated reaches

| 689 | Chinook | -0.09 | -0.21 | -0.33 – 0.06 |
| 690 | Steelhead | -0.15 | -0.14 | -0.25 – 0.02 |

Figure captions

Figure 1. Theoretical fish densities at restored habitats ("Structures") and unrestored

habitats ("Untreated") within a treated reach, relative to unrestored habitats within

untreated reaches. A) Pre-treatment fish density at unrestored habitats in treated reaches

and in untreated reaches. Post-treatment observations can involve: B) re-distribution of

fish in the treated reach from unrestored habitat to restored habitat, C) additional fish in

restored habitat, but no decrease in density in unrestored habitat relative to unrestored

habitat in all untreated reaches, or D) increased density in restored habitat, and unrestored

habitat in the treated reach is also increased relative to unrestored habitat in all untreated

reaches.

Figure 2. Locations of the treated reaches (with ELJs indicated by black diamonds) and

untreated (control) reaches [natural log jams (Upper Control) or no wood at all (Hatchery,

Roaring C., Harrison Ref., Kiosk)] in the upper and lower basin segment of the Entiat

River. The upstream end of each control reach is indicated (white square). Additional

details on reaches and treatments are given in Table 1.

Figure 3. Estimate of modal Chinook and steelhead density (± 95% confidence interval)

from a generalized linear model of fish counts from A) five reaches treated with

restoration structures in the lower basin of the Entiat River and B) three treated reaches in

the upper basin. Comparisons are between habitats restored with ELJs and unrestored

habitats in the same reach. In the upper basin, an additional comparison was made

between modal density in habitats restored with ELJs and habitats created by natural

wood structures. Displayed are the percentages of draws from the posterior distribution in

each habitat type in which the difference in fish density between habitats ($\Delta$D) was $> 0$

(see Table 2 for details).

Figure 4. Estimate of modal Chinook and steelhead density ($\pm$ 95% confidence interval)

from a generalized linear model of fish counts comparing unrestored habitat in A) five

each of treated and untreated reaches in the lower basin of the Entiat River and B) three

treated reaches and one untreated reach (UC) in the upper basin where habitats with

natural log structures occurred. Displayed are the percentages of draws from the posterior

distribution in each habitat type in which the difference in fish density between habitats

($\Delta$D) was $> 0$ (see Table 2 for details).

a) Prediction: Equal density, untreated habitat in planned treatment + control reaches.

Alternative hypotheses:

b) Depletion of poorer habitat within reach ("redistribution")

c) Higher density in restored habitats of treated reach: TYPE 1 capacity increase

d) Higher density in all habitats of treated reach: TYPE 2 capacity increase