PERSPECTIVE

"If You Build It…": Methodological Approaches to Detect Postrestoration Responses in Stream Fishes

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Habitat restoration to recover fish populations takes place worldwide, yet studies of its efficacy are fraught with challenges. One difficulty comes from studies of fish responses that are too focused on whether abundance has increased in the restored habitat, limiting the methodology to observational data of fish density. However, many other tools are available for evaluation of restoration. I review a set of conceptually based methods that colleagues and I used to assess restoration efficacy in a model river system to show the strength of considering alternative approaches. Although it was relatively easy to determine that fish are attracted to instream restoration structures (engineered log jams), spatial and temporal variability in the results requires approaches that more closely examine the distinction between increases in density and increases in habitat capacity. Furthermore, I show that efficacy research should be augmented with consideration of behavior, the spatial scale of the postrestoration studies, the response of life history traits (e.g., growth), and the applicability of habitat selection theory. These detailed studies often, but not always, identify benefits of restoration that go beyond simple observations of fish abundance. They are therefore methods that are worth considering by researchers involved in postrestoration fish monitoring.

INTRODUCTION

River habitat restoration directed at impacted or threatened native fishes occurs on a global scale and encompasses a wide range of approaches (Roni et al. 2018). These conservation actions usually fall into one of the following categories: restoring flow via floodplain reconnection and side channel enhancement (Morley et al. 2005), riparian revegetation (Opperman and Merenlender 2004), barrier removal (Gardner et al. 2013), nutrient additions (Benjamin et al. 2020), and structural enhancement in important riverine habitat units—often pools when the target species favors slower streamflow (Roni 2005; Roni et al. 2018). Engineered log jams (ELJs) are one of the most common techniques to augment pools (Bond and Lake 2003). The effectiveness of these at changing stream hydrodynamics and quality of fish habitat is the topic of much discussion (Roni et al. 2015a). Methodology is usually part of that discussion and below I focus on a few specific methods that may be employed to add mechanistic detail to habitat restoration studies that is lacking in some approaches.

Multiple reviews of studies report the fish response to various restoration efforts, summarizing those that evaluate the biological response to restoration in quantitative terms (Roni et al. 2018; Krall et al. 2019; Foote et al. 2020). Restoration studies reviewed in that literature focus on detection and quantification of changes in physical habitat conditions and/or direct measurements of change in mean density of the target species. In cases when postrestoration monitoring focuses on physical habitat characteristics, it relies upon the assumption that measured changes in habitat will lead to associated changes in fish abundance (Lichatowich et al. 1995). Correlations may be weak despite statistical significance and may not be consistent across space and/or time (Meffe and Sheldon 1988; Hale et al. 2019), thus limiting their applicability. Subsequent measurement of change in mean fish density therefore becomes dependent on its specific physical context and possibly limits the scope of inferences to the case study being reported.

As indicated previously, the available inferences frequently must be couched in caveats invoking interannual variability in fish density, different responses among species, or some restoration sites with no response at all (Roni et al. 2015a; Krall et al. 2019; Foote et al. 2020). This is often because the data collected are "snapshots in time" of density differences between habitats or reaches about which the inferences are made. Although distributional patterns thus identified are important steps in evaluation, they do not incorporate temporal variability or mechanistic details. The resulting variability in results highlights the need for study approaches that address those details of fish–habitat relationships to identify a positive fish response to restoration. Finally, observations of differences in mean density are not always indicators of differences in fitness (Van Horne 1983) without additional theoretical basis that addresses underlying ecological issues such as density dependence (e.g., Morris 1988).

One persistent question is whether studies at smaller scales (e.g., stream reaches) can be scaled up to make whole river basin inferences (Roni et al. 2015b). Inappropriately scaled studies can lead to some of the ambiguity and variability in results discussed above (Polivka et al. 2019; Foote et al. 2020). Modeling efforts to understand salmonid population dynamics, including large-scale lifecycle models, seek to understand the influence of, for example, habitat capacity on those dynamics (Scheuerell et al. 2006; Honea et al. 2009). Capacity is the number of individuals the habitat unit or reach can support before density dependence becomes strong enough to limit further occupancy. However, the scaling issues inherent in effectiveness studies (Polivka et al. 2019) may make it difficult to empirically show changes in capacity beyond small, habitat-scale (e.g., average density in pools) responses. Alternatively, mark–recapture studies enable analysis of density-dependent movement and fidelity

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to different habitat types in mobile species such as salmonids (Rodríguez 2002) with implications for capacity (Polivka 2020). At the reach scale, incorporation of both restored and unrestored habitat in effectiveness studies can widen the inference of capacity increase (Polivka and Claeson 2020), which may make larger-scale population models more informative.

Here, I discuss a set of studies in a single study system in which I began with distribution and density, showing that, through the variability identified, more mechanistic studies are needed. This is because such studies lead to the testing of ecological concepts, in addition to answering the questions of restoration effectiveness, thus giving the methods general applicability to fish species outside this study system. My intent here is not to conduct another metanalysis of restoration projects (e.g., Roni et al. 2015b, 2018), but to present a set of focused studies that address specific questions and that have robust inferences. I describe below the specific methods that collaborators and I employed in postrestoration research to add one or more mechanistic details rooted in broader ecological concepts. After starting with comparisons of relative density in pools, I next show methods that distinguish increases in capacity from density differences brought about by movement among habitats of varying quality. I then focus on performance metrics (growth), and behavioral ecology to tie habitat selection to fitness. Each study built upon the data from the previous. In turn, the results provided explanatory paradigms that circumvented some of the uncertainty mentioned above and provided important information to the furthering of restoration ecology. Their demonstrated inferential power and applicability in a wide range of study systems make these methodological approaches applicable to stream fish habitat restoration studies worldwide.

MODEL STUDY SYSTEM: CHINOOK SALMON AND STEELHEAD TROUT IN THE ENTIAT RIVER, WASHINGTON, USA

Watersheds of the interior northwestern USA and eastern British Columbia, Canada, form the interior Columbia River basin (ICRB). Throughout the region, anadromous salmon have historically been of strong ecological, economic, and cultural significance (Bottom et al. 2009). Large-scale declines in the populations of Chinook Salmon *Oncorhynchus tschawytscha* and Coho Salmon *O. kisutch*, as well as steelhead *O. mykiss* have resulted from extensive harvest of adults, habitat degradation in streams, a network of hydropower facilities that are obstacles to escapement of spawning adults, and introgression or competition with hatchery-produced individuals. Stream habitat degradation primarily affects the juvenile stage, because the first year of these species' life history is spent there prior to outmigration.

Conservation strategies for salmonids in the ICRB are targeted toward genetically distinct population groupings key to the overall genetic diversity of the species in the ICRB and as a whole (evolutionarily significant units [ESUs]; Waples 1995). Threatened and endangered ESUs occur in various sections of the ICRB, usually in groupings of subbasins where spawning streams occur. Several subbasins were selected as intensively monitored watersheds (IMWs), in which intensive restoration was planned. A critical stipulation of IMW programs was that this restoration must be coupled with rigorous monitoring programs to evaluate restoration effectiveness (Bennett et al. 2016). The work summarized here includes data obtained both within and outside IMW-related research, as the Entiat IMW was discontinued after 2017.

The Entiat River in the north-central region of the state of Washington (Figure 1) is part of the upper Columbia River ESU for Chinook Salmon and steelhead. Chinook

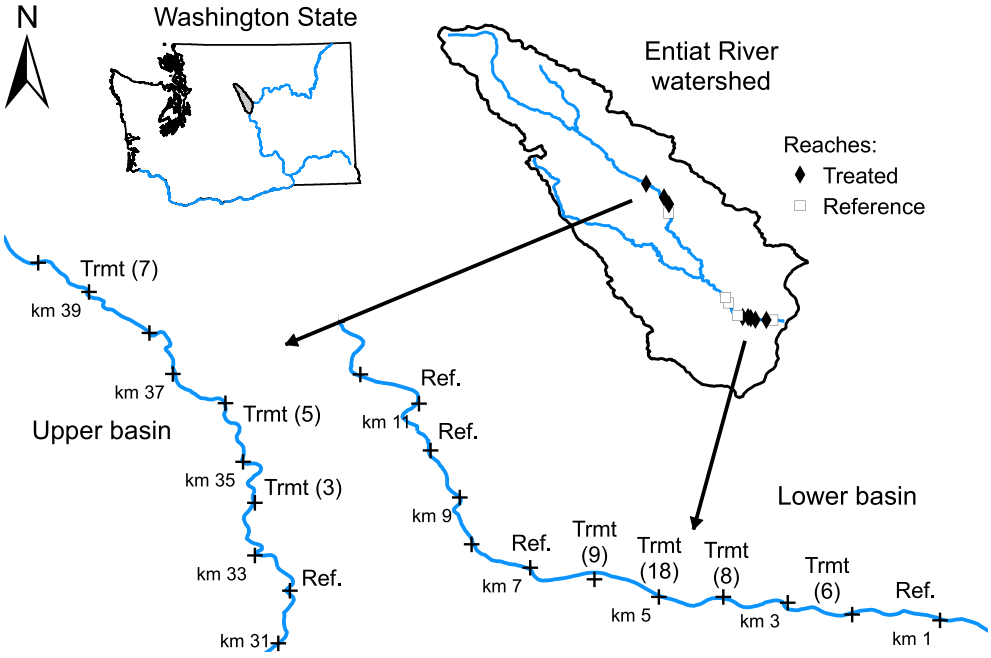

Figure 1. Restoration in the Entiat River, Washington. The segment of the interior Columbia River basin in the state of Washington with the location of the Entiat River subbasin (49.657°,-120.224°). Map of the upper and lower valley segments where reaches with habitat enhanced with engineered log jams (ELJs) occur. Locations of study reaches with ELJs are indicated with black diamonds on the whole basin inset and denoted Trmt with the number of ELJs in parentheses on the detailed map. Untreated reference reaches are denoted with open squares and specified as Ref. River kilometers of all reaches, relative to the confluence with the Columbia River of each study reach are noted for scale.

Salmon of this ESU are listed as endangered and steelhead are listed as threatened under the Endangered Species Act in the United States. The river drains an area of 1,085 km^2 on the east slope of the Cascade Mountains. Postglacial geology and other geomorphic properties divide the river into three major basin segments (Godaire et al. 2009): an upper valley segment (river km 34–41 from confluence with the Columbia River), a middle segment (river km 26–34), and a lower segment (river km 0–26). Restoration in the Entiat River was motivated by the reduction in habitat quality brought about by land use practices such as projects that constrain the river channel, road and residential development, agriculture, timber harvest, and recreation (Sixta 2010). The Entiat IMW began in 2008 with planned phases of restoration projects scheduled in 2008, 2011, 2014, i.e., every 3 years, though the program was terminated early. Restoration sites consisted of reaches ~400–800 m long (Figure 1), hereafter called "reaches," where a variety of restoration projects took place. Restoration projects included protection of high-quality reaches, riparian restoration, and instream habitat enhancements (typically ELJs) to create rearing/growing habitat in pools. The research summarized here involved reaches treated only with ELJs.

These ELJs were expected to benefit subyearling Chinook Salmon and steelhead abundance, growth, and survival. Post restoration monitoring consisted of large-scale monitoring throughout the subbasin and focused habitat use research (Polivka et al. 2015). This study system enabled research into the questions of capacity, scale of study, fitness benefits, and application of habitat selection theory. The staggering of the implementation schedule led to fewer restored reaches available for study earlier in the research program. This affected the breadth of the possible inferences but was ameliorated when ELJs were implemented in more reaches.

APPROACH 1 – "IF YOU BUILT IT, DID THEY COME?"

It was straightforward to show that fish occur at higher density in habitat restored with ELJs. However, with ELJs only in one reach starting in 2008, multiple observations within and among years were required to document how the temporal and among-species variability affected inferences about the fish response. Significant positive coefficients from generalized linear models (GLMs; modeled with a Poisson distribution) showed that there was higher abundance of both Chinook Salmon (GLM coefficient ~1.6) and steelhead (GLM coefficient ~1.0) in the pools created by restoration structures compared with untreated pools in the same reach (Polivka et al. 2015). This increase, particularly for Chinook Salmon, was correlated with the deeper and slower flowing water, characteristic of restored pools. In both species, increased abundance in restored habitat did not occur in some years, and there was no difference in fish abundance among habitats by late in the rearing season (early September) of any year (Polivka et al. 2015).

With only one or a few restoration reaches available, there are constraints on statistical power, limiting the ability to extend inferences to larger scales. Moreover, many of the correlations between fish abundance and physical habitat are not as consistent as assumed; fish sometimes underutilize seemingly high quality or productive habitat and overutilize relatively poor habitat (Polivka 2005; Jeffres and Moyle 2012). The estimated correlation strength is sometimes subsequently used to parameterize complex models that predict fish distribution among habitats at larger scales (Lichatowich et al. 1995; Scheuerell et al. 2006). If these correlations are not always reliable or consistent, then studies that address more detailed mechanisms of habitat selection are needed, such as those described below.

APPROACH 2 – "IF YOU BUILT IT, AND THEY CAME, DID HABITAT CAPACITY INCREASE?"

When greater fish density in restored habitat units relative to unrestored habitat units is observed, it is possible that this simply represents redistribution of individuals from poorer habitat to the enhanced habitat, with no overall increase in the fish population (Roni 2019). Although enhanced habitat may still benefit individuals that use it, an increase in habitat capacity is necessary for long-term salmonid population growth as predicted by lifecycle models addressing these species (Scheuerell et al. 2006; Honea et al. 2009, 2016). One way to define a capacity increase is to observe higher densities in restored habitat with no density decreases in unrestored habitat in the same reach (Polivka and Claeson 2020).

A quantitatively robust way to do this empirically is with a before-after-control-impact (BACI) design, which has been extensively described elsewhere (Stewart-Oaten 1986; Conner et al. 2016; Roni et al. 2018). However, BACI monitoring requires adequate pretreatment data and appropriate control reaches. Rigorous quantification of fish density prior to restoration treatments was not done as part of the Entiat IMW (Roni et al. 2015b). Polivka et al. (2015) and Polivka and Claeson (2020) showed that comparison of unrestored pools in a reach with ELJ treatments, combined with sampling of pools in untreated reaches, enables detection of apparent capacity increases, even in the absence of pretreatment data. This makes assessment of the density difference between restored and unrestored habitat in the treated reach more robust.

The conceptual framework is illustrated in Figure 2 and is based on three categories of fish density data: (1) in pools restored with ELJs found in treated reaches, (2) in untreated pools in those same treated reaches, and (3) in untreated pools in untreated reference reaches. The key comparison is 2 versus 3 because if density in 2 is the same as in 3, i.e., no concomitant decrease in untreated pools in treated reaches, then increases in density due to restoration, 1, are not simply due to redistribution (Roni 2019; Polivka and Claeson 2020). If density in 2 is greater than in 3, then increases due to restoration have resulted in a whole-reach capacity increase, i.e., density in all pools in the treated reach is greater than in all pools in untreated reaches (Figure 2; Polivka and Claeson 2020). In both of those cases, increases in habitat capacity result in the reach as a whole gaining fish. However, this effect may be isolated to the treated pools (Polivka et al. 2019), as opposed to increasing density in all habitats in the treated reach (Figure 2).

In the Entiat River, data from reaches in both the upper and lower basins showed increased habitat capacity. Chinook density was 3–13 times greater in ELJ pools compared with unrestored habitat in the same reach and steelhead density was 1.7–6.0 times greater (Polivka and Claeson 2020). It is important to note that all density measurements will have errors about the mean not shown in Figure 2. In this case, the statistical validity of density differences was determined with the use of Bayesian GLMs. The model structure involved comparisons of fish counts by habitat unit and included both fixed and random effects. Density was back-calculated from the GLM coefficients produced by iterative analysis and shown by a form of bootstrapping to be meaningfully different with 100%

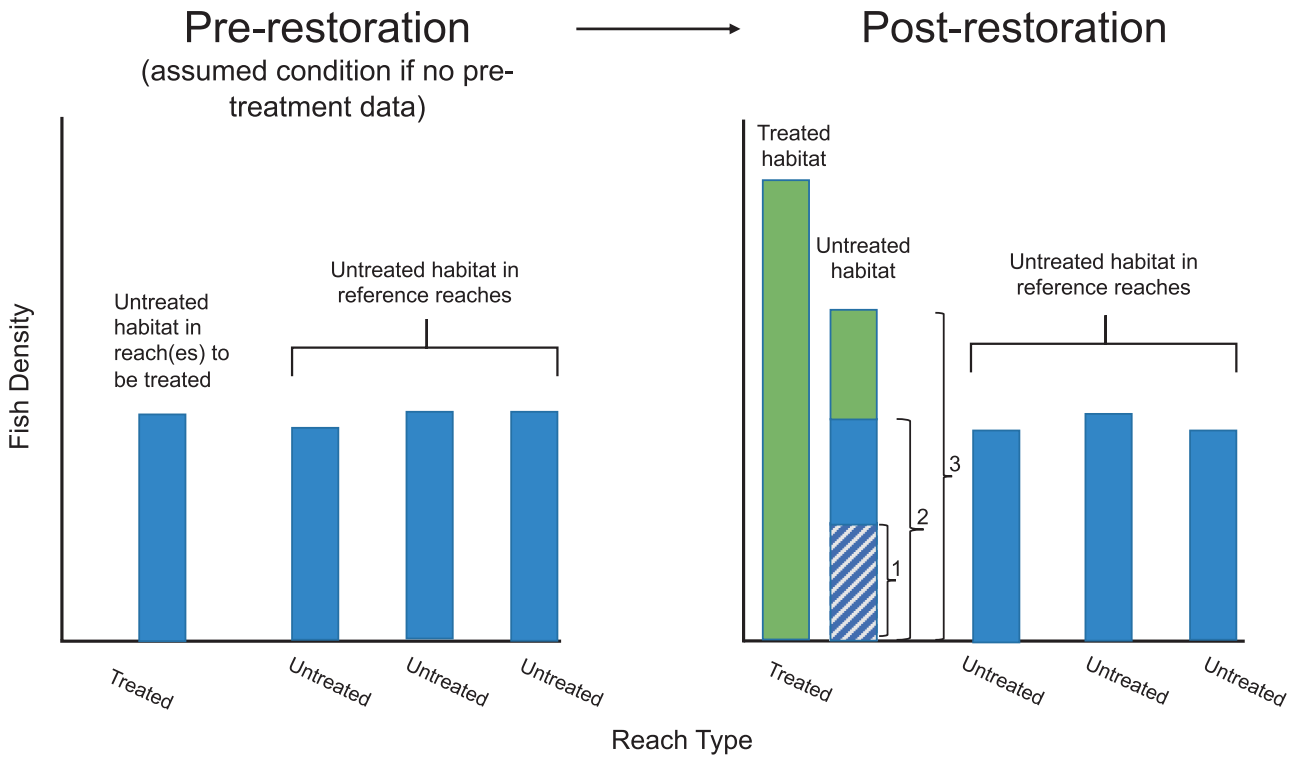

Figure 2. Conceptual paradigm for determination of a capacity increase. Prior to the restoration action, mean fish density in the reach scheduled for treatment is assumed to be similar to that of appropriately chosen reference reaches not scheduled for treatment. Postrestoration, untreated habitat in the treated reach indicates whether restoration has added capacity as numbered: (1) a blue/white hatched segment shows density in the case where it is lower than mean density in untreated reaches, indicating that the increase seen in treated habitat results from redistribution of fish from poorer habitat. (2) A blue segment (including hatched region) shows total mean density unchanged in untreated habitat in the treated reach relative to untreated reaches, indicating that fish added by restoration represent a true capacity increase. (3) A green region shows density added to untreated habitat along with fish occurring in treated habitat, indicating that capacity of all habitat in the reach has increased. Demonstrating this last condition is challenging due to the scale of the effects of restoration (see Polivka et al. 2019).

credibility. By the same method, untreated habitat in treated reaches was not quantitatively different from that in untreated reaches (comparison 2 versus 3 above). Thus, there was an overall capacity increase, but fish density did not increase in untreated habitats in treated reaches with ELJs present.

This approach still requires suitable reference reaches (Kennedy et al. 2014), and enough reaches were available in the lower basin (Figure 1). In the upper basin, there was only one suitable and accessible untreated reach within a reasonable distance of the treated reaches, so conclusions about capacity were more tenuous, but comparison between natural and engineered log jams was possible (Polivka and Claeson 2020). The presence of naturally occurring log jams in the upper basin reference reach demonstrated that ELJs were good analogs for natural structures (Polivka and Claeson 2020), an important inference that has been lacking.

Larger-scale monitoring in the Entiat IMW is designed to detect a watershed scale effect of restoration in keeping with the scale of the design of the restoration (Roni et al. 2015b). Whole-reach surveys and reach-scale mark–recapture to estimate abundance and survival found density differences for both species in off-channel habitats compared with the main channel and some survivorship enhancement due to restoration (Hillman et al. 2019). However, these were "fine-scale" effects and whole-watershed effects on habitat or fish metrics have not been detected with reach-to-watershed scale monitoring (Hillman et al. 2019). Because reach and watershed scale studies can have such highly variable results, Polivka et al. (2019) suggested that it may be more effective to work from the patch or habitat unit scale in restored reaches to make determinations about the spatial scale of restoration efficacy. We asked how widely the observed (Polivka et al. 2015) positive effects of restoration were observable into the rest of a treated reach. There were two key results: (1) ELJs tend to have very localized effects—fish density declined to low values as little as 5–10 m away from the pool created by the ELJ. (2) When the survey area around an ELJ (and including the fish in the ELJ pool) was increased to only two times the area of the ELJ pool, and including that pool, fish density became indistinguishable from that found in surveys of unrestored habitat in a treated reach (Polivka et al. 2019).

These findings appear to exacerbate the problem, suggesting that even reach-scale effects may not be detectable, given the variability in the data. Because the method described in Polivka and Claeson (2020) can detect one type of capacity increase within reaches if it exists (Figure 2, case 2), it is at least possible to make inferences about restoration efficacy at that scale. However, it remains difficult to speculate on whether these positive results may apply at the whole

watershed/basin scale, which is the scale at which restoration is designed (Roni et al. 2015b, 2018). The methodological approaches presented here describe (Polivka et al. 2019) and solve (Polivka and Claeson 2020) the problem of making inferences at the reach scale, but the lesson of this approach is that watershed-scale conclusions may be intractable given the variability at smaller scales.

APPROACH 3 – "IF YOU BUILT IT AND THEY CAME, DID THEY DEMONSTRATE HIGHER PERFORMANCE?"

Differences in density do not necessarily indicate habitat superiority, unless fitness differences can also be identified (Van Horne 1983). The most powerful evidence that a particular habitat type is most favorable to an organism is that selection of that habitat results in advantages to the individual in terms of its ability to survive, grow, or reproduce. Fitness benefits of a putatively superior habitat may be difficult to demonstrate without the sometimes-tenuous assumption that distribution indeed reflects the relative benefits of each habitat to individuals occupying it (see Approach 4 below). Individual growth data are commonly used to assess habitat quality (Davies et al. 2016), but this is not often done in evaluation of habitat restoration, especially with fishes. In some IMWs, including the Entiat, larger-scale survivorship data, strongly indicative of fitness, have been collected, or at least attempted (Hillman et al. 2019).

Early life history growth in streams is a measurable trait that can at least indicate habitat quality, even if inferring lifetime fitness differences is only weakly justified. More importantly, examination of data for concordance between growth and density differences between restored and unrestored habitat can increase confidence in the efficacy of restoration by showing that occupancy of restored habitat translates into a positive response in the fish. In salmonids, individuals that grow larger prior to overwintering and/or downstream migration to the ocean often have higher survival rates than smaller individuals (Zabel and Achord 2004). Therefore, if growth in natal streams during the juvenile stage can be enhanced by restoration actions, the potential to increase fitness might be achieved via increased survival in the early life history. The drawback to this approach is that salmonids only spend one phase of their lifecycle growing in streams; therefore, inferences about fitness may still be tenuous. For other species, however, growth may be a very robust metric of restoration efficacy. Furthermore, growth data may be combined with density data in order to estimate total fish production, another metric that can lead to robust inferences about restoration success (Zu Ermagessen et al. 2016).

Growth is typically measured using mark–recapture studies, which can be challenging when performing these studies on relatively mobile species or large populations. This can lead to low recapture rates, which is particularly the case for Chinook Salmon in unrestored habitat, except in the short term (Polivka 2020). To address this issue, we developed a mathematical model that could simultaneously describe the change in size of recaptured individuals and include the "snapshots" through time of the size of individuals only captured once, but at different points during the growing season. Separate parameters in the model accounted for two ways in which a growth benefit might be manifested: the first described how timing of the growth curve could show larger size earlier in one habitat versus the other (Figure 3A) and the second described a steeper incline in the curve indicating a more rapid growth rate (Figure 3B), or both could occur (details in Polivka et al. 2020).

In studies that use growth to evaluate restoration efficacy, it is important to consider concordance between the growth data and observations of density differences between restored and unrestored habitat. In all of the study years for which growth data were available, and for the years combined, Chinook Salmon juveniles were more abundant in restored than in unrestored habitat. Use of restored habitat resulted in higher growth, as indicated by the model parameter that showed that individuals that remained in

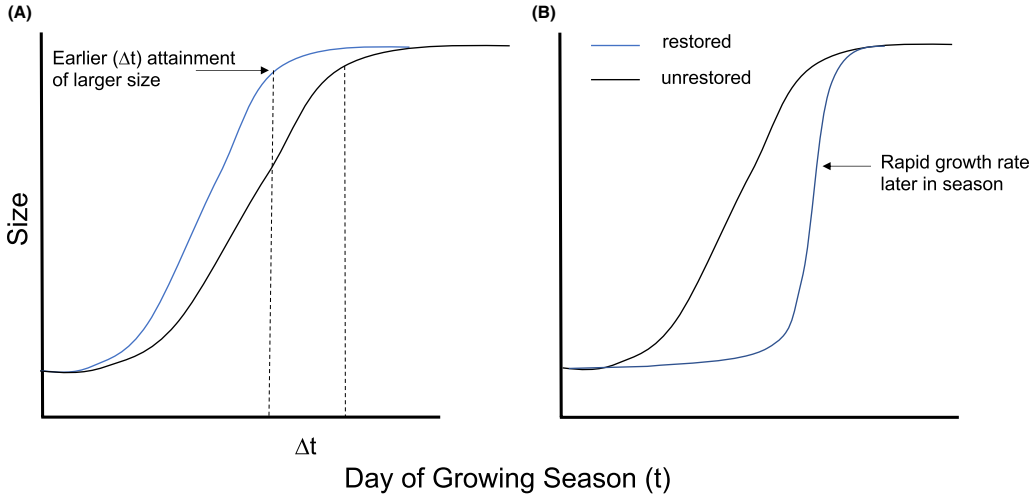

Figure 3. Growth curves from a mechanistic model of size over time (t). The model fit to both Chinook Salmon and steelhead in the Entiat River showed differences in model parameters (Polivka et al. 2020). The model describes size over time of both recaptured individuals and individuals captured once but not recaptured. Model parameter differences between restored (blue lines) and unrestored habitat (black lines) can result in attainment of larger size earlier in the growing season, but with the same rate of growth in the steepness of the curve, as was observed in Chinook Salmon (**A**), or rapid growth (steeper curve) at some point in the season that can result in attainment of maximum size at the same time as individuals in the other habitat, as was observed in steelhead (**B**).

ELJ-enhanced pools reached larger size earlier in the season (Figure 3A; Polivka et al. 2020). The growth benefit was concordant with density for three of the five individual study years and for all years combined. However, the lack of concordance in the two years mentioned above implies that observation of density differences alone can be misleading as to the extent of the restoration benefit. Steelhead only showed a growth benefit in two of the five study years, likely owing to seasonal differences in recruitment to the stream habitat and to their high variability in habitat use (Polivka and Claeson 2020). In those two years, steelhead showed smaller size in restored habitat early in the season, as indicated by the first model parameter (Figure 3A), but then the second model parameter indicated steeper growth in restored habitat (Figure 3B). There was no overall effect on steelhead growth with all five study years combined. Interestingly, in one of the years in which steelhead showed higher growth among individuals in restored habitat (2010), there was not a quantitatively meaningful difference in steelhead density between restored and unrestored habitats (Polivka et al. 2015). Thus, the growth studies identified a case in which the benefit of restoration would have been missed by measurement of density alone. These cases point to the importance of growth data in restoration efficacy studies for fishes.

Another fitness advantage could potentially come from the antipredator vigilance that is enabled by safe habitats such as those with ELJ cover. The habitat tradeoff between foraging in shallower, faster flowing habitats with high food delivery, but high predation risk and relatively safe habitats, such as those created by ELJs, often leads to predation risk management behaviors that stabilize among-individual variation in body condition, another correlate of fitness (Clark 1994; Conrad et al. 2011). Convergence on a stable mean body condition can potentially increase fitness (Luttbeg and Sih 2010), and Polivka (2020) found correlative evidence of convergence associated with ELJ habitat enhancement. It is important to note, however, that increased juvenile survival from improved growth and condition may only partially augment fitness or may not at all if other life stages are also impacted. Thus, the importance of growth and condition data will likely be species-specific when applied across study systems in fish restoration ecology.

APPROACH 4 - INCORPORATING HABITAT SELECTION THEORY INTO HABITAT RESTORATION STUDIES

Habitat selection theory offers the opportunity to contextualize fish distribution data and generate predictions about fitness differences identified in density data collected in most postrestoration monitoring studies. The analyses assume the presence of ecological tradeoffs among costs and benefits of habitat selection, and that the intensity of these tradeoffs across habitat types is often density dependent. Density dependence in habitat selection relative to habitat or resource availability is described by the ideal free distribution (IFD; Fretwell and Lucas 1970). Assuming that individuals are free to move among habitat patches in heterogeneous environments with few to no costs, habitats should be settled and reach equilibrium densities in each proportional to their quality, and fitness should be equal at those relative densities. Differences in total population size may affect the density of individuals in each habitat type, but the proportional distribution of individuals among habitats should be indifferent to population size. Although this conceptual framework was developed >50 years ago, and its assumptions do not always hold, its ability to address density dependence is still robust (Avgar et al. 2020) and therefore applicable to restoration studies.

The IFD is the basis for isodar theory ("iso" = equal, "dar" = Darwinian fitness), an analytical tool that assumes that at the equilibrium (the IFD), fitness is equal in each habitat. The isodar is the linear relationship between density in one habitat (e.g., restored habitat) and another habitat (e.g., unrestored) across a range of total population densities (Morris 1988, 2003). It is thus generated by fitting a line to points representing the density in each habitat (Figure 4). The slope and intercept of the isodar quantify the difference in productivity between habitats. A slope >1 indicates preference for the habitat on the *y*-axis (Figure 4, red line, slope = 1). An intercept >0 indicates that the habitat on that axis is more productive and begins to be occupied first, with settlement of the other habitat beginning later. An intercept = 0 indicates that habitats are sampled by individuals and settled at the same time, but in proportion to their relative quality as indicated by the slope (Morris 1988).

Figure 4 is the calculated isodar for density over time for habitats in the reach restored in 2008 (see Approach 1 above), using average density in restored habitats versus unrestored habitats for each species in each year of the study (2009–2016). I used Bayesian regression to fit the isodar to

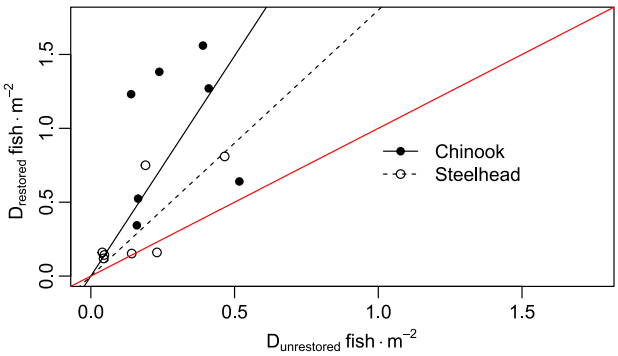

Figure 4. Density-dependent habitat selection by Chinook Salmon and steelhead in the Entiat River. The isodar (solid line, filled circles, Chinook Salmon; dashed line, open circles, steelhead) relates fish density (D) in restored habitat to corresponding fish density in unrestored habitat and assumes equilibrium densities in each habitat with respect to fitness. Red line (slope = 1) shows equal density in each habitat type at equilibrium. Data points for each species represent mean annual density for individual years (2009–2016) in treated versus untreated habitat in a reach of the lower Entiat River basin ("Trmt (18)"; Figure 1). Isodars were fit by Bayesian regression using stan and R ("brms" package; R Core Team 2019; Stan Development Team 2019). Models were initiated with weakly informative priors (i.e., the defaults provided by "brms"), and for each four chains for 2,000 iterations were run, using the first 1,000 iterations as a warmup and thinning by one iteration, giving a total of 4,000 samples (1,000 per chain). Model statistics were examined to ensure that the model had converged with $\hat{R} < 1.1$. Chinook Salmon showed preference for restored habitats (slope = 2.98; 95% credible interval 1.22–4.82), whereas steelhead appeared to show equal preference for restored and unrestored habitat, despite a trend toward a preference for restored habitat (slope = 1.80; 95% credible interval 0.84–2.86).

the data points for each species. The slope of each species' isodar was >1 (Figure 4; statistical details given in caption), but the 95% confidence interval for the steelhead isodar overlapped 1, suggesting no meaningful difference in habitat preference for steelhead. This is consistent with other findings of variable habitat selection in this species that suggest more generalist habitat selection behavior (Whiteway et al. 2010; Polivka et al. 2015). Notably, the overlap of the two species' isodars with each other further suggests that these species have similar habitat selection patterns that warrant further examination.

In fish ecology, isodars have also been used to compare different habitat units, such as riffles versus pools (Rodríguez 1995), which may be desirable, particularly in identifying habitat preferences prior to restoration. Comparison of isodars among species, as I have presented here, may be useful in considering habitat overlap and potential for competition between native and nonnative species when restoration questions involve the effects of nonnatives (Morita et al. 2004). Because isodars are determined through consideration of density dependence, they can be used to identify and evaluate density-dependent mechanisms operating at additional stages in the life history of species such as salmonids (Falcy 2015; Huntsman et al. 2017).

Restoration targeted at more than one ecologically similar species might increase the potential for competition between them if they both preferentially select the enhanced habitat. Indeed, that potential is further indicated for this study system by partially overlapping isodars (Figure 4). Habitat selection theory provides tools for discerning how species with similar habitat requirements partition heterogeneous landscapes. Isoleg analysis describes density dependent habitat selection ("iso" = equal, "legos" = choice) by delineating densities at which species use habitat more selectively, more opportunistically, or with equal frequency (Rosenzweig 1981). Habitats are sampled and density of each species is plotted in state space to generate hypotheses about preferred habitat types and how the presence or absence of a heterospecific influences habitat selection (Figure 5). The isolegs may then be estimated from the data sometimes using selectivity metrics derived from field experiments (Abramsky et al. 1990).

Isolegs thus identify optimal habitat selection strategies for each species, preferred habitats for each, and circumstances under which species may overlap in a given habitat type (Pimm and Rosenzweig 1981). To identify the interspecific competitive effects between Coho Salmon and steelhead, Young (2004) used this approach in an artificial stream experiment. Polivka et al. (in review) used a combination of isoleg analysis, linear habitat selection functions, and a field experiment to analyze habitat partitioning in the Entiat River system. From this, there is preliminary indication that ELJ-enhanced pools facilitate coexistence of species because steelhead select shallower ELJ pools and Chinook Salmon select deeper ones. In unrestored pools, steelhead limited immigration by Chinook Salmon, whereas this competitive effect was absent in restored pools, likely facilitated by the partitioning of shallow and deep microhabitat. These approaches (isodars, isolegs) to habitat selection in fishes are infrequently used in fish ecology (but see Rodríguez 1995; Young 2004; Falcy 2015; Hunstman et al. 2017) and this study system suggests their applicability to fish restoration studies where such approaches are lacking.

IMPLICATIONS AND CONCLUSIONS

This review summarizes methods from specific studies that can be applied to postrestoration research in a wide range of study systems involving fish (Table 1). These include survey techniques that reveal capacity increases, measurement of growth, behavioral metrics, and density-dependent habitat selection theory (e.g., isodars), all of which may be applied to species other than the summarized salmonid studies (Shepherd and Litvak 2004; Kristiansen et al. 2009). These methods are intended to answer some of the common questions posed by such research programs, which include the following: At what spatial scale are the effects of restoration detectable through monitoring? Are comparisons of mean density adequate to determine the biological response to restoration? How can ecological theory be applied to stream fish habitat restoration studies? The methods described above are either new (Approach 2) or infrequently used (others) approaches to quantify and/or evaluate restoration success. The stream system with juvenile salmonids provided a rich case study for the validation of those methods.

The approach most commonly taken is to sample distribution and abundance in restored habitat relative to unrestored habitat (Bond and Lake 2003). Because the results can be affected by the timing or intensity of sampling (Whiteway et al. 2010; Polivka et al. 2015), the lesson from Approach 1 is to at least increase the frequency of sampling, particularly within a study year (Condal et al. 2020). Interannual variability in total population size and, therefore, density across all habitat types may also affect the results. Approach 4 discusses analytical tools from habitat selection theory that help contextualize density dependence across space and time to provide fisheries managers with broader ways of interpreting the results of postrestoration studies, even when primary data collected are observations of distribution and abundance.

It may not always be possible to infer effects of restoration at spatial scales above those at which the restoration was

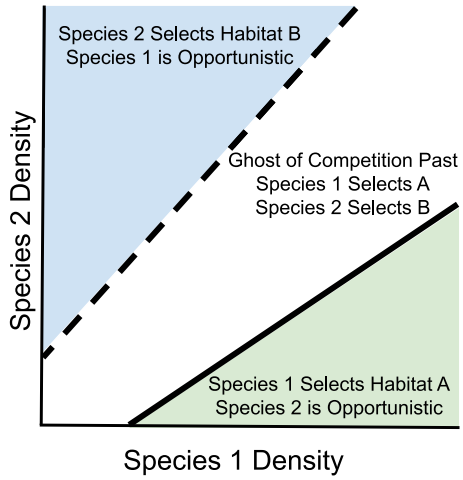

Figure 5. Isolegs, habitat selection, and partitioning. Isolegs are state space plots of the relative density of each species across habitats and indicate ranges of density where each species strongly selects its preferred habitat type or can opportunistically use all habitat types. The estimated lines separate regions and show the set of species densities in which each species is a specialist on its preferred habitat. This region is known as the "ghost of competition past" (Morris et al. 2000) and could describe habitat partitioning between Chinook Salmon and steelhead in the Entiat River, Washington.

Table 1. Summary of methodological approaches in postrestoration research discussed in this review.

Method	Advantages	Limitations	References
(1) Observations of density, restored versus unrestored habitat	Direct comparison of mean density	High spatial, temporal, and among-species variability. Not always accompanied by (e.g.,) increased growth or other performance metric	Whiteway et. al. (2010); Polivka et al. (2015)
(2) Comparison of untreated habitat in both treated and untreated reaches	Distinction between habitat capacity increase and redistribution of individuals. Good substitute when pretreatment data (e.g., for before-after-control-impact design) are not available	Requires geomorphically comparable reference reaches	Polivka and Claeson (2020)
(3) Mechanistic model to analyze short term growth	Growth differences between restored and unrestored habitat indicate fitness-correlated benefit of restoration. Mark–recapture data used to measure growth may also be used to estimate movement behavior (i.e., habitat selection versus distribution)	Depends on sufficient recapture rate to provide robust estimate of growth. Model uses size-over-time to compensate for this, but model validation still requires direct measurement of growth	Anderson et al. (2019); Polivka (2020); Polivka et al. (2020)
(4) Habitat selection Theory – isodars	Density dependent estimate of habitat productivity. Can be applied to time series of density observations commonly collected in post-restoration monitoring studies	Requires many paired habitat comparisons across a range of density	Figure 4; Rodríguez (1995); Falcy (2015); Huntsman et al. (2017)
(5) Habitat selection Theory – isolegs	Density dependent habitat partitioning between species; advantageous when more than one ecologically similar species is the target of restoration	Unclear when there is considerable habitat overlap between species	Young (2004); Polivka et al. (in review)

implemented. Habitat scale studies may show that the effects of addition of large woody debris are localized (Polivka et al. 2019), dependent on differences in habitat, species, or river size (e.g., Marttila et al. 2019) or nonexistent for some species (e.g., Nicol et al. 2004). Roni (2019) further reviewed the extent to which fish densities observed in restored habitats may simply be the result of movements by fish in which individuals are redistributed from poorer habitats to the enhanced ones. Some of the studies reviewed showed that this was the case. The lesson from Approach 2 is that it is possible to show that restoration increases total habitat capacity for fish, and whether this inference is applicable to the whole reach in which restoration occurs (Polivka and Claeson 2020). In salmonid study systems, managers often wish to infer that any observations of apparent restoration success apply at the whole basin or whole fish population scale based on detection of reach-scale effects (Roni et al. 2015b). However, the requirements for a whole-reach capacity increase (see Figure 2, case 3) may be difficult to observe. Thus, inferences regarding even broader basin or population scale effects may not be appropriate or possible even if they may be occurring. This methodological challenge is therefore a persistent one, requiring further development.

Growth and behavioral studies can both highlight and address some of the variability that leads to ambiguity in the inferred response to restoration seen in some study systems, particularly in salmonids (e.g., Whiteway et al. 2010; Polivka et al. 2015; Roni 2019). Approach 3 shows that examination of fitness-correlated traits such as growth can indicate benefits of restoration not apparent from density data (Polivka et al. 2020). Indeed, growth is a common indicator of (1) habitat quality for fish in different study systems (Meng et al. 2000; Polivka 2005; Searcy et al. 2007), and (2) the overall conservation status of a species (Tarkan et al. 2016). Studies that focus on direct measurement of fish growth can complement predictive models such as bioenergetics models (e.g., Hafs et al. 2014) because it can be used to approach restoration ecology mechanistically (e.g., Able et al. 1999; Anderson et al. 2019; Huntsman et al. 2021; Marsh et al. 2022). As a correlate of fitness, growth can be used to complement studies of survivorship, or as a substitute when survivorship studies are inconclusive or intractable. Fish species in other study systems vary in their behavioral response to restoration, especially addition of pool-forming wood such as ELJs, sometimes because they are generalists, using habitat types that are not the focus of restoration (Marttila et al. 2019). Basic mark–recapture studies can show selectivity is not always apparent in distributional data (Polivka 2020) and habitat selection theory can distinguish generalist species that use multiple habitats from selective species that may specialize more on the habitat type being enhanced through restoration.

Fish habitat restoration ecology is a complex field, particularly when applied in the dynamic environment of rivers and streams. Nevertheless, there are many available ecological approaches that can be taken depending on what is best suited to the species and study system at hand. Here I described several approaches taken in a case study involving juvenile salmonids in a single river basin (Table 1). This set of approaches is not exhaustive; bioenergetics and physiology are other subdisciplines with the potential to provide mechanistic details that describe the response of fish to restoration. If data are available, I urge restoration ecologists to go beyond comparisons of fish density when assessing restoration effectiveness by considering focused, detailed, and theory-driven methods.

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