Use of a Net Rate of Energy Intake Model to Examine Differences in Juvenile Steelhead (Oncorhynchus mykiss) Densities and the Energetic Implications of Restoration

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Utah State University

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USE OF A NET RATE OF ENERGY INTAKE MODEL TO EXAMINE DIFFERENCES IN JUVENILE STEELHEAD (ONCORHYNCHUS MYKISS) DENSITIES AND THE ENERGETIC IMPLICATIONS OF RESTORATION

by

C. Eric Wall

A thesis submitted in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

in

Watershed Sciences

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2014
ABSTRACT

Use of a Net Rate of Energy Intake Model to Examine Differences in Juvenile Steelhead (Oncorhynchus mykiss) Densities and the Energetic Implications of Restoration

by

C. Eric Wall, Master of Science
Utah State University, 2014

Major Professor: Dr. Nicolaas W. Bouwes
Department: Watershed Sciences

Foraging models that weigh the energetic costs and benefits of habitat occupancy have been used to explain position choice among drift-feeding fishes, especially salmonids. In addition to position choice, recent research also suggests foraging model predictions indicate habitat quality. While foraging models have often been applied at spatial scales ranging from a single pool to a single stream reach, their broader simultaneous application across streams and basins remains rare. This thesis attempts to advance understanding of foraging modeling with the objectives i) to investigate a foraging model’s ability to predict fish density in the context of simultaneous, multi-reach model application, and ii) to investigate energetic implications of physical habitat change for the purposes of restoration design and monitoring.

To address objective i, we collected requisite data in 22 sites from the John Day River and Asotin Creek watersheds in Oregon and Washington, respectively. We modeled hydraulics, drift concentrations, foraging, swimming costs, carrying capacity, and fish density. We compared predicted and observed fish densities in our study sites to find that linear regression between observed and predicted density was significant ($R^2 = 0.61, p < 0.001$). We also found that the combination of assuming uniform drift density and simulating small
fish territories in the model exerted strong influence over predicted carrying capacities, with carrying capacity predictions increasing exponentially with increased spatial concentration of simulated foraging locations. Thus, the assumption of territory size is influential in estimating reach abundance.

To address objective ii, we collected data to support foraging modeling both before and after restoration in the South Fork of Asotin Creek in the Asotin Creek watershed. First, we compared foraging predictions based on the “before” data set with predictions based on simulated restoration in an attempt to evaluate and better understand the restoration design. Second, we compared foraging predictions based on the “before” and “after” data sets as part of an effort to monitor and understand restoration outcome. Results from the simulated and actual restorations showed similar patterns. While restoration structures provide energetic benefits to fish even though only six months had passed between our “before” and “after” data sets, the observed changes were not as large as the simulated changes. This study demonstrates one way foraging models might be used to help investigate restoration designs with respect to their intended outcomes. In addition, this work also identified mechanisms by which observed geomorphic changes might influence fish.
PUBLIC ABSTRACT

Use of a Net Rate of Energy Intake Model to Examine Differences in Juvenile Steelhead (Oncorhynchus mykiss) Densities and the Energetic Implications of Restoration

The Bonneville Power Administration (BPA) Fish and Wildlife Program mitigates for impacts of hydroelectric dams on ESA-listed salmon and steelhead populations in the Columbia River Basin (CRB). Considering the sizable investments in mitigation and the diversity of stream habitats within the CRB, there has been a pointed effort to develop and identify meaningful metrics relating to fish populations and trends in their habitat across the CRB. The Integrated Status and Effectiveness Monitoring Program (ISEMP) was developed in 2003 specifically for this purpose, and is tasked with developing and testing strategies for determining the status and trend of salmonid populations and their habitats in the CRB. This thesis was funded by the BPA, ISEM P, Eco Logical Research Inc., the Snake River Salmon Recovery Board, and the Intensively Monitored Watershed project in the Asotin Creek basin with the purpose of investigating the efficacy of foraging modeling as part of a large fish habitat monitoring program. The primary objectives were i) to assess a foraging model’s ability to predict fish density in study sites involved in long-term monitoring and ii) to evaluate energetic implications of restoration design and progress after implementation using a foraging model.

To assess the foraging model’s ability to predict fish density (objective i), we collected topography, drift, temperature, discharge, and fish population information to support foraging modeling, and we simulated flow patterns, drift, foraging, swimming costs, carrying capacity, and density. We then compared observed and predicted densities in 22 study sites from the John Day and Asotin Creek watersheds. The primary findings were:
• Linear regression between observed and predicted fish densities was significant ($R^2 = 0.61$, $p < 0.001$).

• When assuming spatially uniform drift densities and small fish territories, carrying capacity predictions were related to the number of foraging locations simulated, suggesting the model is highly sensitive to territory size assumptions.

To evaluate restoration design and monitor restoration progress (objective ii), we simulated foraging before restoration, after a virtual restoration (carried out using the restoration designs in a GIS environment), and again following restoration implementation. We used raster differencing to compare the “before” results to the virtual restoration results and then the “before” results to the “after” results. Hydraulic and foraging models suggested:

• Mean net energy intake increased following both simulated and actual restoration.

• Restoration structures generally slowed water’s progress through the study site or caused pooling, both resulting in an increase in energetically favorable areas.

• Generally, more areas shifted from another state to having an acceptable energy balance than to an unacceptable energy balance.

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Financial support for this work was provided by the Bonneville Power Administration, the Integrated Status and Effectiveness Monitoring Program, Eco Logical Research Inc., the Snake River Salmon Recovery Board, the Asotin Creek Intensively Monitored Watershed project, and the USU Quinney College of Natural Resources through a presidential fellowship. Without their support, this research certainly would not have been possible.

In addition to those that aided with funding, I would also like to extend a heart-felt thank you to those that supported me with ideas, discussion, encouragement, and guidance throughout this process. First and foremost, I would like to thank my advisor, Dr. Nick Bouwes, for taking a chance on a former math major who also happened to like streams and fish. I also owe special thanks to my committee members, Joe Wheaton and Mary Conner, for their insightful suggestions and advice. Steve Bennett and Reid Camp were invaluable resources and our late-night discussions regarding the day’s experiences in a remote Asotin bunk house remain some of my fondest memories from this project. Special thanks go to Andy Hill for collecting data in winter to support chapter 3 analyses. Thanks also to my ELR labmates Matt Archibald and Monica Blanchard for their support and friendships. I am also thankful for the numerous CHaMP technicians that collected data to support these analyses. Though there are too many to mention, Josh Reffner, Mackenzie Sullivan, Tara Reid, Mike Herr, and Joanie Kratzer played important roles in collecting data to support modeling in chapters 2 and 3. I cannot sufficiently thank Brian Bailey and Enid Kelley for all they do to help and support our wonderful graduate student community. Thank you, Brian and Enid. I am also thankful for all my wonderful graduate student peers, professors, and administrators. Lastly, I would like to thank friends and family, especially Dave and Dee Dee Wall, Tim and Lesley Donohue, and Devon Gershaneck for their tireless encouragement and support during this project.

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CHAPTER 1
INTRODUCTION

At an individual level, fitness is thought to be a measure of an organism's performance relative to conspecifics in a given environment. To achieve a relative fitness greater than zero, an organism must reach maturity and successfully reproduce. This typically entails finding adequate food resources to support metabolic processes, growth, and reproduction while simultaneously minimizing exposure to mortality risks such as predation or disease. To describe the performance of a group of individuals, ecologists have used production, typically measured as biomass per unit time per unit area, because it incorporates metrics related to fitness such as growth, reproduction, and survival (Kwak and Waters, 1997).

For stream fish, environmental characteristics such as temperature, food availability, predation risk, density of conspecifics, flow regime, and the presence of cover all influence habitat selection, foraging behavior, and ultimately, production of fish populations (Baker and Coon, 1997; Helfman, 1981; Hughes, 1998; Nislow et al., 1999). Habitat alteration is the leading cause of decline for many at-risk fish populations (Nehlsen et al., 1991). For these populations, gaining an improved understanding of how changes to habitat influence fish populations is vital to curbing declining population trends (Lawson, 1993). In efforts to better understand how habitat changes influence fish populations, stream ecologists have combined foraging, habitat use, and physiological models to provide a mechanistic perspective on the interactions between these behaviors and processes. It is hoped that this approach will increase the likelihood of successfully applying understanding to management problems and, ultimately, help improve long-term fish production in streams.

The foundation for mechanistic foraging models originates in foraging theory, which attempts to understand how long, when, and where organisms choose to forage. Early in the history of foraging theory, Holling (1959) documented the influence of food availability on feeding rates, describing three response types (Types I, II, and III) predators might exhibit in response to increased food availabilities. Concurrently, Holling also noted numerical
responses by which predator densities adjusted in response to changes in prey densities. Later, MacArthur and Pianka (1966) proposed that animals forage optimally, attempting to maximize a foraging-related currency such as net energy intake (NEI). An important assumption of optimal foraging theory is that the foraging-related currency, usually (NEI) or net rate of energy intake (NREI), correlates positively with fitness. Charnov (1976) extended the ideas of MacArthur and Pianka by describing a decision-making process by which optimally foraging animals could choose between food patches in an environment where resources are patchily distributed. His marginal value theorem suggested that foragers should leave a patch when that patch’s rate of yield equals the maximum average overall rate for the environment as a whole.

Fretwell (1972) developed an important model of organism distribution in response to food resources: the ideal free distribution (IFD), a framework wherein individuals or groups of individuals distribute themselves as a function of resource availability. According to Fretwell’s IFD theory: in an environment where resources are patchily-distributed, where organisms have perfect knowledge of resource availability, and where they can move freely between patches without incurring costs of travel, they will distribute themselves proportionally to the resources available. This result may encourage the notion in ecology that patches with more individuals contain higher quality habitat. As a result, a fairly common assumption is that organism density is an indicator of habitat quality. While food is often the resource in focus with IFD theory, some stream ecologists have examined the influence of other environmental factors on IFD predictions. For example, Tyler and Gilliam (1995) incorporated the energetic costs of patch occupancy into IFD calculations to predict the distributions of drift-feeding fish in foraging locations with different water velocities. Giannico and Healey (1999) found that large differences in food density between patches or the presence of cover disrupted input-matching predictions of IFD theory. Hughes and Grand (2000) coupled IFD theory with a physiological model to predict the distribution of size-structured fish populations across temperature gradients.
Many studies investigating fish-habitat relationships have tried to correlate fish abundance or density with habitat characteristics such as depth, velocity, substrate characteristics, temperature, or water quality (Fausch et al., 1988). One of the most common methods for modeling habitat selection involves using habitat suitability indices (HSIs) in conjunction with a problem-solving framework such as the Instream Flow Incremental Methodology and its component model the Physical Habitat Simulation System (Milhous and Waddle, 2012). Though this approach has the advantage of explicitly describing characteristics of the physical stream environment (e.g. depth, velocity, substrate composition, or cover), there are limitations to employing HSIs. For example, HSIs may not apply outside the systems in which they were developed (Hayes et al., 2007; Nislow et al., 1999), biotic factors (e.g. food availability) that HSIs do not account for can alter habitat selection (Rosenfeld et al., 2005), and the assumption that areas with the most fish provide the highest quality habitat (made by many HSI models) may be invalid (Heggenes et al., 1991; Hobbs and Hanley, 1990; Rosenfeld et al., 2005; Van Horne, 1983).

Some stream ecologists have also used physiological or bioenergetics models to explain fish-habitat associations, in addition to foraging theory and HSI approaches (Rosenfeld, 2003). The foundation of these ideas is that a stream fish must balance the energetic costs of metabolism, growth, and reproduction against the energy available in the environment in the form of food. Accordingly, the total energy consumed by a fish must equal the sum of energies devoted to basal and active metabolic processes, growth, reproduction, and excreted wastes. For example, in a food-limited system, the majority of consumed energy may be devoted to metabolic processes with little remaining for growth or reproduction. By contrast, in a food-rich system, there may be sufficient energy to fuel metabolisms and achieve high growth rates and reproductive output.

By combining optimal foraging theory with a physiological description of energy expenditures, increasingly mechanistic models to describe fish foraging behavior have been developed. Fausch (1984) was the first to predict fish positions in an artificial stream based on the idea that fish feed optimally to maximize NEI. Fausch’s model used the fastest stream
velocity within two body-lengths of a fish’s feeding position to model prey drift rates. It also included a capture window located at the fish’s focal point (perpendicular to the direction of stream flow). Fish were modeled to ingest any prey item passing through the capture window. For each of 89 points in an artificial stream, Fausch determined the location of the capture window, approximated caloric density of drift passing through it, subtracted the energy required to maintain position there, and called the difference potential profit. Despite its simplicity, Fausch demonstrated success with this model at predicting position choice of coho salmon in an artificial stream.

Hughes and Dill (1990) later found Fausch’s model to be a poor predictor of Arctic grayling position choice in natural stream pools and improved the model. Hughes incorporated information about different size classes of prey, more accurate fish reaction distances, streambed topography and flow patterns. Over time, Hughes’ model became the model on which many others were based (see Guensch et al., 2001; Hughes, 1998; Jenkins and Keeley, 2010; Urabe et al., 2010), and recent studies have suggested that NREI predictions from the model are positively correlated with habitat quality (Jenkins and Keeley, 2010; Urabe et al., 2010). In 2003 and 2007, Hughes further developed his model, adding handling time for prey items, using assimilable energy rather than total energy content of prey, accounting for vertical velocity shear in the water column, and accounting for spatial variation in drift concentration (Hayes et al., 2007; Hughes et al., 2003).

Perhaps the most sophisticated of the Hughes and Dill (1990) variants, the Hayes et al. (2007) modeling approach incorporates components of foraging theory, physiology, distribution of individuals, and explicit spatial descriptions of streambeds. This approach begins with a spatially explicit, three-dimensional representation of the streambed. Hydraulic models use this streambed representation to generate spatially explicit depth and velocity estimates. A model of drifting food items uses hydraulic model output to predict spatially explicit food distribution, while a mechanistic foraging model predicts which drifting food items are ingested by foraging fish in the modeled stream area. Using energy consumed
(food ingested) and energy spent (metabolism and swimming costs), the approach calculates NREI as the difference of these two quantities. Assuming salmonids drift-feed in an optimal way, the model uses NREI as its foraging currency and assumes that this quantity correlates with fitness. Despite its potential to provide mechanistic context in understanding fish habitat selection and quality, the model has rarely been applied.

In this thesis, I apply the Hayes et al. (2007) model to investigate i) relationships between NREI predictions and juvenile steelhead (Oncorhynchus mykiss) densities and ii) energetic implications of restoration for juvenile steelhead. Specifically, I evaluate whether fish densities predicted by the NREI model are positively correlated with observed fish densities, and if instream restoration structures provide energetic benefits to fish. Results from this research will inform efforts to apply NREI models at spatial scales used by large monitoring programs, and they will also help assess the feasibility of implementing this complex modeling approach to help answer management questions at such large spatial scales.
CHAPTER 2

JUVENILE STEELHEAD TROUT (ONCORHYNCHUS MYKISS) DENSITIES IN
RELATION TO PREDICTIONS OF A NET ENERGY INTAKE MODEL

2.1 INTRODUCTION

Like many fish populations throughout the world, salmonids in the Pacific Northwest
are an extremely important cultural, recreational, and economic resource. Yet despite
the enormous costs society has invested in managing these populations (Bernhardt et al.,
2005), many are declining or endangered in response to habitat degradation caused by
anthropogenic activities (Moyle and Leidy, 1992; Nehlsen et al., 1991; Slaney et al., 1996),
and many more will likely be impacted by future environmental change (Sala et al., 2000;
Tilman et al., 2001). The disparity between investment in management efforts and current
population status is, in part, due to an incomplete understanding of the habitat requirements
of fish. Therefore, a clear mechanistic description of how fish use their environment is crucial
to the broader application of effective management and to restoration of fish populations
(Lawson, 1993).

While many past studies investigated patterns between fish and their habitats, most
were correlative or based on measures of preferential habitat use (Fausch et al., 1988). These studies helped identify habitat variables correlated with fish abundance, biomass, and
density at various points in time and space, but most lacked the experimental manipulation
necessary to identify causal mechanisms (Fausch et al., 1988). Another factor limiting
potential application of correlative and preferential use models is that they may have limited
explanatory power in systems where prevailing conditions are different than those used
for model development (Fausch et al., 1988; Nislow et al., 1999). For example, Binns
and Eiserman (1979) used multiple regression to develop a habitat quality index (HQC) to
predict trout biomass in Wyoming, but several tests of the HQI suggested it did not perform
well outside their geographic domain (Bowlby and Roff, 1986; Leiner, 1996). Despite the
ubiquitous use of correlative and preference-based models, these two limitations constrain
their utility in situations where managers need to identify differences in habitat quality or better understand the implications of alternative management scenarios.

In contrast to correlative models, approaches simulating biological mechanisms may provide a more definitive understanding of the cause-effect relationships underlying fish-habitat associations (Rosenfeld, 2003). Consequently, mechanistic models might be better suited to distinguishing areas of contrasting habitat quality or to understanding how alternative management options could influence fish populations. For example, after observing that drift-feeding fish appeared to forage optimally (by maximizing their exposure to food resources and simultaneously minimizing swimming costs (Fausch and White, 1981)), scientists proposed models simulating mechanisms governing prey capture success and energy intake in drift-feeding fish (Fausch, 1984; Hughes and Dill, 1990). By subtracting estimates of swimming costs (i.e. the energy needed to maintain position in a stream by swimming) from estimates of energy intake (i.e. energy gained from successful preycaptures as predicted by the prey capture success model), researchers estimated energetic tradeoffs associated with occupying different habitats. The quantified energetic profit or deficit is often referred to as net energy intake (NEI) or net rate of energy intake (NREI), and it can provide biological or ecological context that would be relatively more difficult to attain using correlative or preference-based methods alone (Nislow et al., 1999, 2000; Rosenfeld et al., 2013).

NREI models were originally developed to provide a mechanistic framework in which habitat selection by drift-feeding salmonids could be investigated (Hughes and Dill, 1990). Early modeling efforts demonstrated that fish consistently chose foraging positions with high NREI values, supporting the hypothesis that energetic profitability influences fish habitat selection (Fausch, 1984; Hill and Grossman, 1993; Hughes and Dill, 1990). In the years since their original development, NREI models have demonstrated success predicting foraging locations for a variety of fish species (Guensch et al., 2001; Hughes et al., 2003; Jenkins and Keeley, 2010; Nislow et al., 1999; Urabe et al., 2010). Recently, by linking an NREI model with hydraulic and drift dispersion models, Hayes et al. (2007) predicted spatial
patterns of flow, drift density, fish foraging, and carrying capacity in a New Zealand pool. Hayes et al. (2007) used an iterative approach to estimate carrying capacity, by placing a representative virtual fish at the highest NREI location in their study site, simulating drift depletion downstream from that location, placing a second fish, simulating drift depletion downstream again, and so on, until no more locations were predicted to support fish. The number of fish predicted as being supported by the pool closely matched the number of fish observed (Hayes et al., 2007). Hayes et al. (2007), Jenkins and Keeley (2010), and Urabe et al. (2010) greatly expanded the spatial and temporal scales at which NREI models have previously been applied. While Hayes et al. (2007) found that their model closely predicted fish abundance, Jenkins and Keeley (2010) and Urabe et al. (2010) found positive correlations between predicted NREI values and fish biomass at their study sites, suggesting NREI could be an indicator of habitat quality.

The finding that NREI may be an indicator of habitat quality is consistent with concepts of ideal free distribution (IFD) theory (Fretwell and Lucas, 1969). Ideal free distribution theory posits that organisms with perfect knowledge of patchily distributed resources and the ability to move freely between patches will distribute themselves proportionally to available resources, so that the per capita gain is equal among foragers. If NREI is an indicator of habitat quality, then one might expect to see a positive correlation between NREI values (i.e. measures of patch quality) and observed fish abundances. The Hayes et al. (2007) modeling approach provides a mechanistic method for translating NREI values into predicted carrying capacity. Further, even if a potential relationship between predicted carrying capacity and observed abundance is not one-to-one, the presence of a positive correlation across a number of sites could still suggest predicted carrying capacity estimates are measures of relative habitat quality. In addition to energetic profitability, territoriality may also play a role in governing fish habitat selection, especially if dominant individuals exclude subdominants from profitable patches. Salmonids have been known to display territorial behavior (e.g. Keeley, 2000), possibly to the extent that absolute minimum territory sizes could act as regulatory mechanisms on maximum possible fish densities (Wood et al.,
Recent studies were able to apply NREI models at reach scales (Hayes et al., 2007; Urabe et al., 2010), while others found positive correlations between NREI values and fish biomass (Jenkins and Keeley, 2010; Urabe et al., 2010). Together, these advances suggest NREI modeling has potential as a tool for understanding differences in fish habitat at scales relevant to monitoring and recovery efforts for threatened fish populations. The Columbia Habitat Monitoring Program (CHaMP) is an effort to generate and implement a standard set of fish habitat monitoring methods across the Columbia River basin in watersheds chosen to represent a wide range of habitat conditions. The information CHaMP collects will be used to improve understanding of fish habitat requirements for salmonids listed under the Endangered Species Act (ESA). The CHaMP protocol was intentionally designed to support modeling efforts linking fish populations with habitat, including models like the Hayes et al. (2007) NREI model. Specifically, in addition to a suite of other habitat monitoring data, CHaMP collects high resolution topographic data, drift samples, temperature, discharge, and substrate composition information that can support two- or three-dimensional hydraulic models and other bioenergetic modeling efforts. In conjunction with fish sampling at CHaMP study sites, their dataset provided the information needed to evaluate the Hayes et al. (2007) NREI modeling approach.

In this paper, my first objective is to test the ability of the Hayes et al. (2007) NREI model to predict juvenile steelhead (Oncorhynchus mykiss) carrying capacity and density at 22 sites in the Columbia River basin encompassing a range of gradients, flow conditions, temperature regimes, and food availabilities. Under the assumptions of IFD theory, I hypothesize that NREI-predicted density estimates will be positively correlated with observed juvenile steelhead densities across sites. My second objective is to determine whether site-level NREI values are correlated with juvenile steelhead abundance, density, and biomass. I hypothesize that the number of suitable foraging locations will be positively correlated with fish abundance, and that the proportion of suitable foraging locations will be positively correlated with fish density. Lastly, I expect site-level NREI values to be positively correlated
with fish biomass based on Urabe et al.’s (2010) findings. Results from this study will help to further evaluate relationships between fish and NREI model predictions, and they will also help assess the feasibility of implementing this complex modeling process across sites from multiple watersheds as part of large scale monitoring programs such as CHaMP.

2.2 METHODS

2.2.1 Study sites

I measured physical habitat features and invertebrate drift, and I collected fish size and abundance data to support NREI modeling at 22 sites in two different watersheds, all involved in research and monitoring as part of the Columbia Habitat Monitoring Program (CHaMP). Data collection took place in thirteen sites in the John Day River watershed in northeastern Oregon and nine sites in the Asotin Creek watershed in southeastern Washington. The John Day River watershed drains a large portion of northeast Oregon (approximately 20700 km$^2$) before joining with the Columbia River, and the basin is characterized by coniferous forests at high elevations, perennial grasslands at middle elevations, and desert shrub-steppe at lower elevations. The Asotin Creek watershed drains approximately 518 km$^2$ of land in southeast Washington before meeting the Snake River, and typically encompasses coniferous forests in higher elevations and sagebrush steppe at lower elevations. Both watersheds support a number of ESA-listed fish species including steelhead trout, the focal species of this study. Data collection occurred between 21 June and 27 September, 2011. Selected site characteristics are summarized in Table 2.1.
Table 2.1: General characteristics of the 22 study sites.

<table>
<thead>
<tr>
<th>Site Number</th>
<th>Site</th>
<th>Site Area (m²)</th>
<th>Mean Wetted Width (m)</th>
<th>Mean Thalweg Depth (m)</th>
<th>Water Surface Gradient</th>
<th>Drift Density (Individuals/m³)</th>
<th>Measured Discharge (m³/s)</th>
<th>Mean STHD Modeled with NREI model</th>
<th>Measured Weight (g)</th>
<th>% Site Modeled</th>
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<td>1</td>
<td>Charley Creek F1H2</td>
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</table>
2.2.2 Data collection and processing

Physical habitat features

I used total stations to collect (x, y, z) coordinates describing the shape and structure of the stream channel and floodplain at each study site. I applied a topographically stratified sampling method (Brasington et al., 2000; Fuller et al., 2003) during surveys, whereby I collected higher point and breakline densities near breaks in slope or topographically complex areas and comparatively lower densities in areas with homogenous bedforms. I identified channel units during these surveys using a modification of the classification system described by Hawkins et al. (1993), and I included points mapping their boundaries in the topographic survey database. Finally, I processed the topographic data collection with GIS software to create digital elevation models (DEMs) of the stream channel and floodplain, water surface DEMs, water depth rasters, and polygon shapefiles delineating channel units.

I collected channel unit substrate size composition data at each site to help calculate an appropriate site-level roughness height estimate for subsequent hydraulic modeling. First, I estimated the percent of substrate in each of seven size categories: fines (<0.06mm), sand (0.06–2mm), fine gravel (2–16mm), coarse gravel (16–64mm), cobbles (64–250mm), boulders (250–4000mm), and bedrock (>4000mm). Next, I determined the area of each channel unit and the area of the whole site covered by each of the seven substrate size classes. Finally, I multiplied the coverage fractions for each substrate size class (excluding bedrock) by their corresponding size class midpoints and summed the results to yield a weighted average roughness height estimate for each site. This number served as a starting value for roughness height during hydraulic modeling.

I estimated site discharge during topography surveys using a velocity meter, tape measure, and depth rod. I divided wetted width into 15–20 equally spaced measurement stations and measured stream depth and velocity at 0.6 of the depth from the water surface at each station. For the first and last station, I calculated station discharge as 0.5 x station width x depth x velocity. For all other stations, I calculated station discharge as station width x depth x velocity. I calculated site discharge by summing the station discharges. Discharges
were collected at or near baseflow conditions and should be representative of stream flows for the summer and early fall.

I collected temperature data using in-stream temperature loggers (thirteen sites) or handheld thermometers (nine sites) to calculate the mean water temperature over the time period during which fish sampling occurred at each site. For sites with temperature loggers, I calculated the mean of many temperature readings throughout the day. At sites relying on handheld thermometers, I measured stream temperature at the start and end of fish sampling and averaged the two measurements.

**Invertebrate drift**

I deployed drift nets (1000µm mesh, 40cm tall x 20cm wide opening) at each study site to quantify the number, size distribution, and composition of invertebrates available to drift-feeding fish. I deployed two side-by-side nets approximately 25cm apart and within the thalweg at each site in a riffle near the upstream site boundary. I suspended them in the water column 2cm above the streambed to prevent benthic invertebrates crawling in, and I ensured that the net tops extended above the water surface to catch drifting terrestrial invertebrates. I collected all drift samples during the day (after dawn and before dusk) with durations ranging from three to five hours.

In addition to the one-per-site drift sample events intended to characterize the abundance and composition of drifting invertebrates at each site, I also sampled drift more intensively in Charley Creek F1H2 and North Fork Asotin Creek F1H2 to help us evaluate the Hayes et al. (2007) drift model. A series of cross sections located at the upstream and downstream site boundaries and at roughly one-quarter, one-half, and three-quarters of the total longitudinal site length were monumented and included in the topography surveys for these two sites. The monumented cross section start and end points allowed me to stretch measuring tapes across each cross section and position four nets (1000µm mesh, 12.7cm x 12.7cm mouth opening) to filter the majority of cross sectional discharge. Noting net positions on the measuring tapes allowed me to translate their locations to real-world coordinates because the geographic coordinates of cross section start and end points were
known. Net bottoms remained at least 2 cm above the stream bed during sampling while net tops remained above the water surface. Sampling duration for these smaller drift nets ranged from one to two hours.

I measured water depth in each net and water velocity at each net’s mouth (centered laterally, at 60% of the depth from the water surface to the bottom of the net mouth) at the time of deployment. At the conclusion of sampling, I recorded net mouth velocity again and transferred each net’s contents to jars containing 95% EtOH. The larger, paired drift nets for each site were processed by pooling the site’s jars, sorting to family level, separating invertebrates into 3mm size classes, and counting abundances in each family by size class. I divided the total number of invertebrates for the pooled sample by the total volume of water filtered by both drift nets to calculate the drifting invertebrate concentration for that site. The smaller drift nets intended to be used for drift model evaluation were processed in an identical manner except pooling was not necessary (i.e. each net was processed individually).

**Fish size and abundance**

We used two-pass mark-recapture fish sampling on two consecutive days at each site, and I estimated juvenile steelhead abundance using the bias-adjusted Lincoln-Petersen mark-recapture model. Depending on site conditions, we herded fish into fyke-netted seines or handheld dip nets with an electroshocker. We weighed, measured, and marked individuals if appropriate. Steelhead greater than 70mm received a passive integrated transponder tag or had a fin clipped to facilitate identifying recaptured individuals in subsequent sampling. I divided abundance estimates by site areas to estimate steelhead densities, and I multiplied densities by mean fish weights to calculate site biomass values.
2.2.3 Modeling

Modeling overview

I used an adaptation of the procedure described in Hayes et al. (2007) to simulate flow patterns, spatial patterns of invertebrate drift, steelhead foraging, carrying capacities, fish densities, and the resulting reach-scale NREI patterns (Figure 2.1). Like Hayes et al. (2007), I simulated hydraulics using River2D, a two-dimensional, depth-averaged hydraulic modeling software package (Steffler and Blackburn, 2002). Converged River2D solutions were converted to 2.5D with the stream tubes model, which divides River2D solutions into tubes of equal discharge separated by cross sections. This step allows the simulation of vertical velocity gradient and also discretizes the stream space into cells needed for operation of the drift, foraging, and NREI models. Next, the drift model simulated drifting invertebrates passing between cells and cross sections while the foraging model predicted foraging success and energy intake throughout the modeled site. Finally, the NREI model estimated the energetic tradeoffs of foraging successes and swimming costs, and a fish placement algorithm estimated carrying capacity. The modeling procedure was identical to Hayes et al. (2007) with the exception that I used an automated fish placement algorithm to speed the process of estimating carrying capacity (see Hayes et al., 2012).

Fig. 2.1: Overview of the NREI modeling process.
Hydraulic modeling

I used River 2D to simulate steady-state flow patterns at all study sites. Raster cell coordinates from DEM cells, roughness height estimates, discharge measurements, and information from the processed topographic surveys served as inputs to River 2D. River 2D has breakline creation capabilities, but because topography surveys implemented breaklines and the resulting DEMs had relatively small cell sizes (10cm x 10cm), I did not recreate breaklines in the River2D environment. After creating River 2D Bed files for each site, I used the River2D Mesh program to create computational meshes. I concentrated computational nodes at an approximate spacing of 0.1m in the immediate vicinity of the upper and lower flow boundaries, and I distributed nodes uniformly at 0.25m spacing elsewhere. Discharge estimates served as the upstream boundary condition for each site, and downstream water surface elevation estimates from topography surveys were used for the downstream boundary condition. Modeling assumed no losses or gains from groundwater or tributaries for all reaches, and I varied roughness until differences between inflow and outflow and predicted versus observed water levels were minimized at each site. Simulations continued until the solution change between subsequent model steps was sufficiently small to be considered converged.

I recorded spatially explicit depth and velocity measures at Charley Creek F1H2 and North Fork Asotin Creek F1H2 for hydraulic model calibration and validation. I collected depths and velocities at monumented cross sections for two different discharges at each site using a Marsh-McBirney velocity meter. Cross sections were spaced roughly every 10–15 longitudinal meters throughout the two study sites. Again, monumented cross sections at these two sites were included in topography surveys, so I stretched measuring tapes, measured depths and velocities, and recorded their locations along the tapes. Depth-velocity pairs and their tape locations were then translated to real-world coordinates using GIS software. Calibration data for Charley Creek F1H2 were collected at 0.263 m$^3$/s, while validation data were collected at 0.209 m$^3$/s. Calibration data for North Fork Asotin Creek F1H2 were collected at 1.654 m$^3$/s, while validation data were collected at 0.718 m$^3$/s.
Collecting calibration and validation at all 22 modeled sites was, unfortunately, time and cost prohibitive. Therefore, I necessarily assume that acceptable hydraulic modeling results for these two sites suggest the possibility of reasonable modeling results at others.

**Stream tubes modeling**

The stream tubes model converted converged River 2D hydraulic solutions to tubes of equal discharge separated by cross sections. I assigned the number of horizontal and vertical stream tubes at a site based on stream size. Streams with a mean wetted width less than or equal to six meters were assigned four lateral stream tube divisions for each meter of wetted width while all other streams were assigned three divisions per meter of wetted width. Streams with mean thalweg depths greater than 0.25m were assigned one vertical stream tube for every 0.05m of mean thalweg depth, while all other streams were assigned 5 vertical stream tubes. Choosing stream tube density has tradeoffs: while modelers might achieve higher spatial resolution (and, possibly, increased realism) with relatively high numbers of stream tubes, they could also inflate processing time and reduce overall modeling efficiency. Similarly, cross section spacing plays a role in spatial resolution as well. I used cross section spacing of 0.2m for all sites because this value offered acceptable spatial resolution and it was also in the recommended range (Kelly et al., 2005). I chose these stream tube density and cross section spacing rules because I believed they offered a balance of spatial resolution and computational efficiency, and because they provided multiple NREI predictions inside typically reported steelhead territories (e.g. Keeley and McPhail, 1998). Thus, NREI point density would not limit predicted fish density in my simulations.

**Drift modeling**

I assessed the abilities of two drift models to predict drifting invertebrate concentration in Charley Creek F1H2 and North Fork Asotin Creek F1H2, with the intention that these efforts would inform drift modeling in the remaining study sites. First, I tested the original Hayes et al. (2007) drift model, which uses an entry rate parameter to continually resupply the water column with invertebrates and counteract the effects of settling. Second, I tested
a drift model based on the hypothesis that invertebrate entrainment is related to flow conditions. This model sets water column drift concentrations to a reach average value at any (x, y) location satisfying a set of hydraulic requirements, while invertebrates settle at a constant rate elsewhere in the model. Because this model used a velocity threshold as the hydraulic prerequisite for entraining drift into the water column, I will hereafter refer to it as the “velocity threshold drift model.” To parameterize the drift models, I determined invertebrate settling rates using live specimens removed from drift nets, a microscope, a stop watch, and a one liter glass beaker. I identified individual specimens to family level and 3mm size class, timed their descents through 10cm of water.

At the conclusion of drift sampling, I produced observed vs. predicted drift density (individuals/m$^3$) plots to evaluate the performance of both drift models. Low observed invertebrate numbers in some nets complicated modeling drift at the scale of individual family-size class combinations. For this reason, I chose to model drifting invertebrates using generic data from the most abundant size class. All drifting invertebrate prey items were modeled as a single class of 4mm invertebrates weighing 0.0003g when dry, settling at a rate of 0.0101 m/s based on the settling rate time trials.

Foraging and NREI modeling

I used mean fish length and weight and mean daily water temperature from each site’s electro-fishing survey as inputs to the foraging model. Because the foraging model’s predictions have only been evaluated relative to the foraging performance of brown trout (Salmo trutta)(Hughes et al., 2003), I assumed a 55% foraging success rate also applied for steelhead. Fish were assumed to hold foraging positions 5cm from the streambed in the model, and I used steelhead-specific bioenergetics parameters (Hayes et al., 2007) in NREI calculations. The fish placement algorithm judged virtual foraging locations as being capable of supporting fish if their NREI predictions were greater than or equal to zero. By definition, this is the value at which inputs and expenditures are equal, and it implies fish should be able to attain a maintenance ration (Hayes et al., 2007). Examples of the resulting hydraulic model, NREI, and fish placement predictions are shown in Figure 2.2.
Fig. 2.2: Predicted depths and velocities for North Fork Asotin Creek F1H2 at the validation discharge (left), corresponding NREI predictions (middle), and NREI with predicted fish locations (right).
Predicted densities, summarized NREI metrics, and fish observations

After simulating flow patterns, drifting invertebrates, steelhead foraging, fish placement, and site-level carrying capacity using the NREI model, I calculated predicted densities by dividing predicted carrying capacities by site areas, and I calculated predicted biomass by multiplying predicted densities by mean fish weights. I evaluated the NREI model’s predictive ability by comparing observed and predicted fish densities. I also tested the hypothesis that summarized NREI information is relevant to fish populations by plotting observed fish abundance on the number of suitable foraging locations at each site, observed fish density (fish/m²) on the proportion of suitable foraging locations, and observed fish biomass on mean site NREI values (treating negative NREI values as zero, as per Urabe et al. (2010)).

2.3 RESULTS

2.3.1 Hydraulic modeling

Results from hydraulic modeling indicate models at Charley Creek F1H2 and North Fork Asotin Creek F1H2 performed well enough to preserve major patterns of depths and velocities, despite the shallow, turbulent nature and coarse bed materials at these sites (Figures 2.3, 2.4). For the calibration flows, mean absolute depth errors were 0.05m and 0.05m and mean absolute velocity errors were 0.18m/s and 0.20m/s for Charley Creek F1H2 and North Fork Asotin Creek F1H2, respectively. For validation flows, mean absolute depth errors were 0.07m and 0.04m while mean absolute velocity errors were 0.16m/s and 0.19m/s. Though mean errors for North Fork Asotin Creek F1H2 are equal to or greater than those for Charley Creek F1H2 in three of four cases, the North Fork Asotin Creek F1H2 model did a better job preserving the overall pattern of depths and velocities. While I was not able to collect validation data for all 22 sites in this study, all sites were processed identically up to the stage of validation. Due to the lack of validation data at other sites, I necessarily assume reasonable results at these two sites suggest the possibility of reasonable results at others.
Fig. 2.3: Hydraulic model calibration (top) and validation (bottom) results for Charley Creek F1H2.
Fig. 2.4: Hydraulic model calibration (top) and validation (bottom) results for North Fork Asotin Creek F1H2.
2.3.2 Drift modeling

Calibration of the Hayes et al. (2007) drift model using a randomly selected subset of observed drift data and the entryRate model parameter produced mixed results in Charley Creek F1H2 and North Fork Asotin Creek F1H2. Linear regression between observed and predicted drift densities was significant at North Fork Asotin Creek F1H2 (\(p = 0.01\), \(R^2 = 0.39\); Figure 2.5A), but observed and predicted densities were not well correlated at Charley Creek F1H2 (Figure 2.5B). Additionally, tuning model predictions with the reEntry model parameter resulted in unnaturally high predicted concentrations of invertebrates in the stream margins and I was unable to correct this result using the timeNearBed model parameter. Tests of the velocity threshold drift model produced high drifting invertebrate concentrations in the thalweg and in riffles, which is consistent with the paradigm of riffles as drift sources, but observed and predicted drift densities were not well correlated for either North Fork Asotin Creek F1H2 (Figure 2.5C) or Charley Creek F1H2. Because neither model performed well at both sites predicting spatially-variable drift densities, I elected to assume spatially uniform drift densities, a common assumption in NREI modeling applications (Hughes et al., 2003; Jenkins and Keeley, 2010; Railsback et al., 2009; Rosenfeld and Ptolemy, 2012; Urabe et al., 2010). All further analyses, including efforts to estimate carrying capacity, were conducted under the assumption of spatially uniform drift densities.
Fig. 2.5: Attempted calibration of the Hayes et al. (2007) drift model using the reentry rate parameter at North Fork Asotin Creek F1H2 (A) and at Charley Creek F1H2 (B); Attempted calibration of the velocity threshold drift model at North Fork Asotin Creek F1H2 (C). Attempted calibration of the velocity threshold drift model in Charley Creek F1H2 produced similar results.
2.3.3 Predicted densities, summarized NREI metrics, and fish observations

Linear regression between observed and predicted fish density was significant ($R^2 = 0.61$, $p < 0.001$, Figure 2.6A). Three John Day sites, however, were dominated by presumably young-of-year steelhead with mean site fish lengths of 69mm, 66mm, and 61mm. For comparison, the rest of the site means ranged from 86mm to 134mm. Hayes et al. (2007) cautioned that increased stream tube densities may be necessary for appropriate foraging predictions when modeling fish smaller than their 0.5m brown trout, and I attempted to account for this by increasing stream tube density relative to the densities used by Hayes et al. (2007) (see discussion). Nevertheless, one of these sites appeared to be highly influential, so I withheld these three sites and repeated the analysis to find that the regression was still significant ($R^2 = 0.39$, $p = 0.004$, Figure 2.6B). Although model fit decreased, the slope of the relationship remained somewhat similar. Basin-specific regression was significant for sites in the John Day watershed ($R^2 = 0.66$, $p = 0.0007$ for all sites, Figure 2.6C; $R^2 = 0.52$, $p = 0.019$ for sites with mean fish lengths at least 70mm, Figure 2.6D), but observed and predicted fish densities were not well correlated for study sites in the Asotin Creek watershed (Figures 2.6C and D). The total number of suitable foraging positions at each site was not well correlated with fish abundance, whether all sites were analyzed together or if basins were analyzed separately (Figure 2.7). The proportion of suitable foraging positions was weakly significant as a predictor of fish density ($R^2 = 0.18$, $p = 0.051$, Figure 2.8A) when all 22 sites were included in analysis, but it was not well correlated when sites with very small fish were excluded from analysis or in individual basins with or without (Figure 2.8B) very small fish. Finally, mean site NREI was not a significant predictor of fish biomass in the study sites, whether I considered all sites together or the basins individually (Figure 2.9).

It became apparent during the course of modeling that cross section spacing plays a role in determining carrying capacity as predicted by the model. In fact, fish placement in the model can only occur on cross sections (because this is where NREI calculations are made) by design, so the maximum possible prediction for a site is limited by the number of cross sections used during simulation. This is less apparent when simulating spatially
Fig. 2.6: Observed and predicted juvenile steelhead densities for all sites (A; black line), sites with mean fish length at least 70mm (A; dashed gray line), all John Day sites (B; red line), John Day sites with mean fish length at least 70mm (B; dashed red line), and Asotin sites (B; blue line).
Fig. 2.7: Observed abundance vs. suitable foraging locations for John Day sites (red line), John Day sites with mean fish length at least 70mm (B; dashed red line), and Asotin sites (blue line).
Fig. 2.8: Observed steelhead density vs. predicted proportion of suitable foraging locations for all sites (A), John Day sites with mean fish length at least 70mm (B; dashed red line), and Asotin sites (B; blue line).
Fig. 2.9: Observed biomass vs. mean NREI prediction for John Day sites (red line), John Day sites with mean fish length at least 70mm (dashed red line), and Asotin sites (blue line).
variable drift because fish consumption of drift eventually exceeds drift supply as the model simulates placement of additional fish. Under this set of conditions, modelers eventually encounter a residual drift amount that can no longer support additional fish. This is how the model predicts carrying capacity. Our assumption of spatially uniform drift eliminates the drift depletion calculation, resulting in a comparatively high predicted carrying capacity. To illustrate this result, I predicted carrying capacity for a single site, North Fork Asotin Creek F1H2, at a variety of cross section spacing values (Figure 2.10). Predicted carrying capacity and processing times both increased markedly as I decreased the space between cross sections, and I found that predicted carrying capacity never reached an asymptote.

Fig. 2.10: Predicted carrying capacity (number of fish) at North Fork Asotin Creek F1H2 as a function of cross section spacing.
2.4 DISCUSSION

2.4.1 Predicted densities, summarized NREI metrics, and fish observations

The primary objective of this study was to assess the ability of the Hayes et al. (2007) NREI model to predict fish density in reach-scale study sites. Previous attempts to predict abundance or biomass with NREI models have been made for a large New Zealand pool (80m x 20m; Hayes et al., 2007), riffle and pool habitat units over four months of a year (Jenkins and Keeley, 2010), and multiple streams in different watersheds (Urabe et al., 2010). While these studies suggested the validity of NREI model applications at spatial or temporal scales larger than what had been previously attempted, two of the three (Jenkins and Keeley, 2010; Urabe et al., 2010) used measured depths and velocities at fixed points in time to calculate NREI, and the third simulated NREI in a single (but large) habitat unit with homogenous flow characteristics. Measuring individual depth and velocity values is a perfectly valid method for collecting inputs to NREI models, but it places practical limits on the spatial density of NREI predictions that can be achieved, and it requires that modelers collect depth and velocity data for every set of flow conditions to be modeled. In addition, this approach to NREI modeling cannot be extended to predict the energetic consequences of future changes to stream channel structure (i.e. as in restoration) because it requires the ability to measure existing depths and velocities. The large New Zealand pool described by Hayes et al. (2007) was an ideal test site for evaluation of their NREI model, but research suggesting NREI models predict differences in habitat quality between habitat types (e.g. Jenkins and Keeley, 2010) emphasized the need for evaluation of NREI models in continuous, reach-scale study sites characterized by a variety of habitat types and flow patterns. By modeling depths and velocities with hydraulic models rather than measuring each depth and velocity individually, I was able to achieve NREI prediction density of approximately 50 NREI predictions per square meter of stream. For comparison, Urabe et al. (2010) and Jenkins and Keeley (2010) most likely achieved NREI prediction densities of two and four NREI predictions per square meter, respectively. The increased density achieved through the use of hydraulic models in this study provides spatial resolution that
equals or exceeds juvenile steelhead territory requirements. This is important for studies attempting to estimate carrying capacity (or density) because relatively coarse spacing of NREI predictions could leave some stream areas unoccupied simply because they were not evaluated by the NREI model or fish placement algorithm.

My finding that NREI-predicted fish density was significant as a predictor of observed fish density is novel and demonstrates that reach-scale NREI predictions have relevance to fish populations. This finding might be important to researchers or managers involved in monitoring efforts because it suggests NREI models can help understand the energetic consequences of differential habitat use at reach scales. The importance of energetics to fish habitat selection is well documented (Rosenfeld and Boss, 2001; Rosenfeld et al., 2005; Tyler and Gilliam, 1995), but this study is the first to demonstrate the utility of high density NREI predictions at reach scales and in multiple streams.

The site with the highest observed and predicted densities appeared to exert heavy influence on the relationship between observed and predicted fish densities. Because I am not developing a predictive relationship that can be dramatically altered by influential points, but rather validating a simulation model with observation data, I believe inclusion of this influential point is important to test a broader range of conditions. However, if this and other points represent site conditions that are potentially inappropriate for this application of the model then their influence deserves further inspection. This site and two others had average fish sizes much smaller than the rest of the study sites. These three sites had mean fish lengths between 61mm and 69mm while all other sites ranged from 86mm to 134mm, and their mean fish weights spanned from 3.5g to 6.9g while all other sites ranged from 11.74g to 42.7g. Hayes et al. (2007) cautioned that increased stream tube density would be needed to adequately model foraging dynamics for fish smaller than the 0.5m brown trout in their study, and they also suggested increases in the lateral direction might be more important than increases in the vertical direction. The stream tube density rules I applied increased lateral tube density by an approximate factor of five and vertical tube density by an approximate factor of three when compared to the tube densities used
by Hayes et al. (2007). Removal of the sites with smaller fish from analysis reduced data
range and also slightly decreased the fit of the model. However, removing these sites had
minimal effect on the slope of the observed versus predicted relationship, suggesting that
the model may still be appropriate for smaller fish.

The result that predicted carrying capacity is strongly linked to cross section spacing
is important and demands that modelers use caution when applying this model to predict
carrying capacity or fish density. In the North Fork Asotin Creek F1H2 simulations, fish
predictions never leveled off at any cross section spacing value. In fact, the opposite actually
happened, because the rate at which predicted carrying capacity increased accelerated as
cross sections were placed closer together. This behavior was undoubtedly caused, at least
in part, by my assumption that drift is spatially uniform, because this assumption implies
no drift depletion calculations will be made in the model. This cross section-carrying ca-
pacity pattern is an artifact of model algorithms and cannot be changed outright without
changing the model itself. However, it can be controlled so as to elicit reasonable patterns
of fish predictions, as I have done here. I controlled for the effects of cross section spacing on
predicted carrying capacity by modeling all study sites with a constant cross section spacing
value. As an added control, modelers could also enforce territoriality rules on the fish place-
ment algorithm, though I did not choose to do that for this study. These findings suggest
that cross section spacing or territoriality rules could be used to calibrate model output.
This is an area for future research, but I would suggest using territoriality rules instead of
cross section spacing because this allows the highest NREI prediction resolution. Though
we evaluated 22 study sites in two different watersheds, further model tests with more sites
across a range of environmental gradients would further improve our understanding of the
model’s ability to predict fish density.

My secondary objectives in this study were to determine if site-level NREI summary
metrics were correlated with fish population measures. Results indicated the predicted
number and proportion of energetically suitable foraging locations were generally not well
correlated with observed fish abundance and density, suggesting that fish habitat selection
is influenced by more than the quantity of energetically suitable habitat alone. Cover, for instance, is not included in the NREI model and Grand and Dill (1997) demonstrated that cover and energetic profitability jointly influenced habitat selection for fish under predation pressure. As a second explanation, perhaps the spatial configuration of suitable foraging habitat is important in addition to the quantities or proportions of suitable locations. For instance, two streams could have the same number and proportion of suitable foraging locations, but support different numbers of fish if the fish display territorial behaviors (Figure 2.11). Though I did not explicitly impose territory rules when predicting carrying capacity with the NREI model, the 0.2m cross section spacing implied that fish could be no closer to one another than 0.2m because the fish placement algorithm only allows one fish per cross section. Steelhead are known to exhibit territorial behavior (Imre et al., 2004; Keeley, 2000) and it has been suggested that territory size has the potential to regulate salmonid populations (Grant and Kramer, 1990; Wood et al., 2012). Further NREI model simulations using empirically derived territories could be a fruitful area of future research.

![Fig. 2.11: An example of how the spatial configuration of suitable foraging locations could influence predicted carrying capacity. Streams A and B have the same number (3) and proportion (3/10) of suitable foraging locations, but should support a different number of territorial fish because of the spatial configuration of suitable positions.](image)

In contrast to Urabe et al.’s (2010) findings, my results indicated mean NREI and site biomass were not well correlated. One possible explanation is that fish in the two studies have highly contrasting disturbance histories. The masu salmon (Oncorhynchus masou) in
Urabe et al.’s study experienced minimal natural and anthropogenic disturbances, including the absence of recreational fishing pressure or severe flood events for at least three years prior to their study. In contrast, steelhead in the Asotin Creek and John Day River watersheds are listed as threatened under the ESA, at least in part due to anthropogenic disturbance including the series of dams (eight and three, respectively) Asotin Creek and John Day River steelhead must pass as they return to their natal streams to spawn. Considering their disturbance histories and the ESA listings for Asotin Creek and John Day River steelhead populations, it is conceivable that fish in Urabe et al.’s study might be closer to carrying capacity than those in the Asotin Creek or John Day River watersheds, and that factors other than quantified energetic profitability (e.g. mean NREI value) are limiting to the Asotin Creek and John Day River populations. If energetic profitability is not limiting for Asotin Creek and John Day River fish (i.e. they are not food limited), then one might not expect a strong relationship between mean NREI (a measure of energetic profitability) and fish biomass. An alternative explanation is that, again, spatial configuration of NREI could play a role in determining habitat selection. For example, two different sets of NREI predictions could have the same mean value but entirely different distributions, both in range (i.e. in the range of NREI values themselves) and in space. If territoriality is important in determining the distribution of organisms, it is conceivable that these two NREI prediction sets could support different numbers of identical fish.

2.4.2 Drift modeling

This study was designed to evaluate relationships between NREI values predicted by the Hayes et al. (2007) NREI model and fish populations in reach-scale study sites with diverse physical and environmental characteristics. Because the quantity of drifting invertebrates is an important input to NREI models, I began by investigating the performance of two drift models. The Hayes et al. (2007) drift model has successfully predicted drift concentration patterns in a large New Zealand pool, but settling and entrainment patterns in large pools are surely less complex than in entire stream reaches containing a variety of habitat types. While I was unable to achieve acceptable results for both sites in our model test, differences
between test sites may offer insight into drift model performance and future attempts to model drift. Relevant works by Ciborowski (1983a,b, 1987), upon which the Hayes et al. (2007) drift model are based, investigated a 65m-wide, shallow stream in which velocity and depth “increase[d] linearly with increasing distance from the river margin” (Ciborowski, 1987). This description more closely resembles flow patterns in North Fork Asotin Creek F1H2, where results from my test of the Hayes et al. (2007) drift model were significant. In contrast to North Fork Asotin Creek F1H2, Charley Creek F1H2 is narrower with more rapid turnover between habitat units, and comparatively more complex and turbulent flow patterns. Leung et al. (2009) suggested turbulence and the short length of habitat units in this type of stream may homogenize drift concentrations. The narrower range of observed drift values in Charley Creek F1H2 drift samples would seem to support this hypothesis.

The velocity threshold drift model performed poorly at predicting invertebrate concentrations for both test sites. While links between velocity, shear stress, and drift have been suggested Brittain and Eikeland (1988); Gibbins et al. (2010), my attempt to relate drift concentrations to velocity alone was probably an oversimplification. Flow conditions certainly have the capacity to influence drift patterns (e.g. catastrophic drift), but drift propensity can be influenced by a suite of factors unrelated to hydraulic conditions including behavioral mechanisms of several invertebrate taxa Brittain and Eikeland (1988).

The drift model test results highlight common challenges associated with drift modeling. Drift samples are known to display substantial spatial and temporal variation (Shearer et al., 2002), even between replicate drift nets sampling the same cross section (Weber, 2009). Although previous studies that suggested reasonable repeatability of drift values for a site (Weber, 2009) were used in the development of the CHaMP protocol, recent assessment of two years of CHaMP monitoring data suggests the site-level drift biomass was highly variable (CHaMP, 2013b). However, some of this can be attributed to poor techniques in sampling drift such as allowing nets to clog, imprecise measures of water velocity at the net, and collection during times of high flow (spring) or debris (fall). The drift nets used in this study were relatively small and highly sensitive to these errors because of the small
volume of water sampled and low number of invertebrates collected. This brings doubt into whether these samples represent appropriate observations for model validation. The time, money, and effort required to collect and process drift samples, combined with their high variability, are all serious challenges to modelers attempting to develop or test models that predict spatial drift concentrations.

2.4.3 Implications for widespread implementation

Part of the motivation for this study was to assess the feasibility of implementing this complex, multi-step modeling process at CHaMP sites as part of ongoing monitoring and recovery efforts. I was able to apply the NREI model at 22 sites, but each of those required considerable time and effort, despite the fact that topography, temperature, and drift data were already being collected by CHaMP. The combination of hydraulic, stream tubes, drift, foraging, and NREI modeling usually required between one and four days once the inputs had been collected, with the majority of that time being spent in River 2D and working with the stream tubes model. I found that River 2D produced acceptable depth and velocity predictions in the study sites, but other hydraulic modeling platforms (e.g. Delft 3D) might offer improved automation and efficiency to help speed modeling efforts. The stream tubes model successfully divided cross sections into tubes of equal discharge at most sites, but it did exhibit some problems in areas with complex flow patterns or around sharp bends, and finer cross section spacing such as the values used in this study seemed to increase the occurrence of these problems. In two streams, I was not able to create stream tubes for portions of the wetted channel at all using the stream tubes program, and consequently, model fish could not be placed in those areas because they can only be placed on cross sections. The drift, foraging, and NREI models required between 35 minutes and 13 hours (mean processing time was roughly 3 hours) depending on the size of the site being modeled, but any single change to model inputs (e.g. a change in temperature) required re-simulation and the same time investment over again. Unfortunately, the net effect of these complications makes calibration, validation, and sensitivity analysis (though I did not attempt this) extremely difficult, especially if hundreds of sites are to be simulated, as is
the case for CHaMP.

I found the Hayes et al. (2007) NREI modeling approach to be an impressive contribution to the NREI modeling literature during the course of this study. Unfortunately, however, the time and energy involved in using such a complex and high-resolution model still precludes its usability when faced with simulating hundreds of sites. A number of options exist, however, that have potential to greatly improve chances of implementation at this scale. For example, hydraulic models that allow raster inputs as topography data sets are available, which is convenient and efficient because many topography data sets are in raster formats to begin with. Using hydraulic models that support raster inputs, such as Delft 3D, can alleviate modelers of the need to convert existing topography data sets to other formats so as to be compatible with the particular input requirements of different hydraulic modeling packages. While stream tubes are currently needed to take advantage of the Hayes et al. (2007) drift dispersion model, the assumption of uniform drift density could simplify drift modeling considerably, alleviating the requirement that stream space be discretized into tubes of equal discharge. Further, assuming spatially uniform drift densities and treating the set of NREI predictions as a point cloud could allow fish placement via a territoriality algorithm and the elimination of the one-fish-per-cross-section rule. Ultimately, modelers must choose a modeling strategy carefully so that modeling efforts are appropriate for the question or problem at hand. Though I believe these suggestions have the potential to increase efficiency and simplify NREI model calculations, whether or not to implement them must be considered on a case-by-case basis as to which of these suggestions, if any, might be appropriate for a specific modeling scenario.
CHAPTER 3
DESIGN EVALUATION AND MONITORING OF RESTORATION WITH A NET RATE OF ENERGY INTAKE MODEL SUGGESTS POST-ASSISTED LOG STRUCTURES ARE ENERGETICALLY BENEFICIAL FOR JUVENILE STEELHEAD TROUT (ONCORHYNCHUS MYKISS)

3.1 INTRODUCTION

Efforts to restore or rehabilitate aquatic habitats in response to degradation caused by anthropogenic activities have become commonplace throughout the world (Roni et al. 2008). The number of restoration projects has grown exponentially in recent years, and it has been estimated that annual spending on restoration exceeds $1 billion in the United States alone (Bernhardt et al., 2005). Despite the prevalence of stream restoration, few projects evaluate mechanistic linkages between target fish populations and restoration design or effectiveness (Katz et al., 2007; Lake et al., 2007). Unfortunately, many completed projects have not been monitored adequately to evaluate effectiveness (Bernhardt et al., 2005; Roni et al., 2008), or monitoring was not properly designed to identify the mechanistic linkages between restoration actions and the target populations (Katz et al., 2007; Roni et al., 2008), ultimately leaving the success of many projects in question and limiting our ability to learn from them (Roni et al., 2008). These findings and observations highlight a current need to examine restoration design and effectiveness in a mechanistic context.

The physical habitat simulation system (PHABSIM) (Milhous and Waddle, 2012) and its variants are the most widely applied models for predicting effects of restoration on fish populations (Reiser et al., 1989; Tharme, 2003). These models typically combine habitat suitability curves representing abiotic factors into a habitat suitability index indicating the overall suitability of specific stream areas for a particular species or age class of fish. In general, habitat suitability curves can be based on expert opinion or values sourced from the literature, habitat utilization curves, or habitat preference curves (Bovee et al., 1998). Though originally developed to evaluate alternative flow scenarios (Stalnaker et al., 1995),
PHABSIM-type models have since been applied in a wider variety of settings including the evaluation of alternative channel designs for stream restoration ((e.g. de Jalon and Gortazar, 2007)). Despite their prevalence, these models have been criticized for lacking biological realism (Orth, 1987) and because the empirically derived habitat suitability curves central to their predictions may not be transferrable between rivers with different flow, temperature, or food resource regimes (Thomas and Bovee, 1993). These shortcomings stem from the models’ implicit assumption that physical variables alone (i.e. depth, velocity, substrate, and cover) determine fish habitat selection. For example, Rosenfeld et al. (2005) found fish changed patterns of habitat selection in response to altered food availabilities, demonstrating that physical variables alone cannot always describe or predict complex dynamics evident in biological systems. This lack of a functional understanding of fish foraging behavior and its role in habitat selection is a major weakness for PHABSIM-type models (Hayes et al., 2007).

Net energy intake (NEI) or net rate of energy intake (NREI) models for drift-feeding fish combine descriptions of physical habitat (usually depths, velocities, and drift density estimates) with foraging and bioenergetics models to quantify the energetic tradeoffs of occupying different habitats. Typically, NREI estimates are calculated by predicting the energetic profits and metabolic costs of foraging in one or more locations and subtracting costs from profits. They were originally developed to explain position choice by drift-feeding fish in dominance hierarchies (Fausch, 1984; Hughes and Dill, 1990), but NREI models have since been applied in a variety of settings. For example, NREI models have been used to explain size-based differences in habitat selection and profitability (Rosenfeld and Boss, 2001), to estimate carrying capacity (Hayes et al., 2007), to examine habitat segregation by species (Piccolo et al., 2008), and as an indicator of habitat quality (Jenkins and Keeley, 2010; Urabe et al., 2010). Because they incorporate an understanding of foraging behavior and metabolism, NREI models can potentially provide information that could not be attained by considering physical habitat variables alone. For example, NREI modeling suggested early season habitat as a limiting factor of juvenile abundance by predicting that
half of all early season juveniles were occupying energetically deficient habitat compared to only 8% for late season fish (Nislow et al., 1999, 2000). Jenkins and Keeley (2010) used an NREI model to demonstrate potential size-based differences in cutthroat response to climate-related temperature changes. These studies emphasize the importance of incorporating foraging behavior, energy inputs, and metabolic costs, along with physical characteristics in understanding fish habitat requirements. Despite their demonstrated value, NREI model application to investigate consequences of habitat change for fish remains rare. In the context of restoration design and monitoring, NREI modeling could be a valuable tool for stream restoration practitioners because it would allow them to mechanistically link channel design considerations with ecological principles affecting fish performance. A mechanistic understanding of these relationships should increase the likelihood of successfully extrapolating these approaches to novel locations.

Several NREI approaches were empirical in nature, using depth and velocity values measured on cross sections to characterize the hydraulic environment (e.g. Jenkins and Keeley, 2010; Urabe et al., 2010). However, collecting individual depth and velocity measures by hand may place practical limits on the number of NREI predictions that can be made because of the time involved in collection. Additionally, this method lacks the ability to provide depth and velocity measures under contrasting topography scenarios without actually modifying the channel and collecting measurements with the new topography. Alternatively, hydraulic models can be used to provide reasonable depth and velocity predictions (e.g. Jowett and Duncan, 2012) at a much finer spatial resolution than can be attained by field measurements, as well as depth and velocity predictions for manipulated virtual topographies.

Hayes et al. (2007) linked hydraulic and NREI models for detailed examination of likely foraging locations to help understand carrying capacity and growth potential of stream habitat for salmonids. The Hayes et al. (2007) NREI model links hydraulic and drift dispersion models with foraging and bioenergetics models to estimate spatially explicit NREI values. Their model also estimates carrying capacity using an iterative approach.
that places a representative virtual fish on the most upstream cross section with a suitable NREI value and then simulates drift depletion downstream. A second fish is placed at the next downstream cross section with a suitable NREI value, and the process is repeated until no more fish can be supported. Their model closely predicted fish abundance in a large New Zealand pool (Hayes et al., 2007), but has not otherwise been evaluated.

In this study, I use an adaptation (Hayes et al., 2012) of the Hayes et al. (2007) NREI model to link restoration design hypotheses and fish energetics in the context of an ongoing stream restoration project in Asotin, Washington. First, I use the NREI model with data from pilot restoration experiments and restoration designs to investigate the hypothesis that in-stream structures will increase NREI and carrying capacity at treatment sites relative to their original state. This step is intended to mechanistically evaluate the restoration design prior to implementation. Second, after structure installation at a study site, I use pre- and post-installation topographic surveys of in-stream structures to document predicted changes in NREI. This step is intended to monitor restoration progress after structure installation. This work demonstrates one way NREI models might be used help understand and evaluate alternative physical habitat scenarios and their implications for fish.

3.2 METHODS

3.2.1 Study area and restoration design

South Fork Asotin Creek, near Asotin, Washington, is one of three streams involved in an experimental watershed restoration evaluating effectiveness of high density large woody debris (HDLWD) structures as tools to increase salmonid production. Following three years of pre-treatment monitoring (summer 2009, summer through fall 2010 and 2011), HDLWD installation began in summer 2012. Though HDLWD structures associated with the larger watershed restoration experiment can take many forms, those in our 40m-long study are post-assisted log structures (PALS), each consisting of a cluster of 10cm-diameter wooden posts driven vertically into the substrate in a staggered pattern (Figure 3.1). Structures are angled relative to the banks and have layers of logs and branches woven between them. The
posts forming each structure extend from the right or left bank to span between 40% and 70% of the total channel width, and posts in the structures have been trimmed in height to match an estimate of local annual peak flow elevation. According to the restoration design, PALS will be strategically placed to promote scour and deposition resulting in a more complex array of habitat in the treatment areas through a network of PALS acting in concert to effect geomorphic change. The hypothesized response to PALS includes a flow constriction fostering the creation of undercut banks and scour pools near the instream ends of installed structures and eddy bar formation directly downstream (Figure 3.2).

Fig. 3.1: Plan view post-assisted log structure illustration from the Asotin Creek restoration project design report (Wheaton et al., 2012).
Existing boulder or bank irregularity

Post-assisted log structure constricts 40-70% of flow width

Undercut bank forms; may promote recruitment of new woody debris

Eddy bar deposit forms in shadow of structure

Central bar forms where flow diverges again; may promote channel widening downstream and further recruitment of new woody debris

Legend
- Velocity vectors
- Wooden posts
- Woody debris of various sizes, shapes, and complexity
- 12” to 18” diameter logs (variable length of 4’ to 6’; can be handled by two people)

Fig. 3.2: Example of hypothesized response to post-assisted log structure installation in a relatively simple, plane bed channel. The flow constriction created by PALS fosters scour both on the opposite bank and from the stream bed near the constriction point. Eddy bars form directly downstream of installed structure and again at the second flow diversion (Wheaton et al., 2012).
3.2.2 Data collection

I collected field data during the summers of 2011 and 2012 and in February 2013 to support NREI modeling in the study site. I used the restoration plan along with findings from pilot studies in the treatment basin and with site-level information to model steelhead energetics. I modeled NREI using an adaptation (Hayes et al., 2012) of the NREI modeling process described by Hayes et al. (2007). Briefly, I collected topography information, discharge estimates, temperature measures, and drift samples to support the NREI modeling process, but more detailed descriptions of the model’s data requirements can be found in Chapter 2 of this thesis and in Hayes et al. (2007).

Physical habitat features

I used total stations and a topographically stratified sampling method (Brasington et al., 2000; Fuller et al., 2003) in the study area to collect a network of (x, y, z) points describing the stream channel, its major features (pools, grade breaks, bars, etc.), and the floodplain. I conducted the first survey on 23 July, 2012, prior to PALS installation, and I repeated the survey on 13 February, 2013, after PALS had been in place for six months. I converted the surveyed point features and breaklines to triangular irregular networks (TINs) and created digital elevation models (DEMs) of the stream channel and the water surface using GIS software. Post-assisted log structure post locations were noted during their installation in summer 2012 after the 2012 topography survey. During the 2013 topography survey, I recorded the center-most (x, y, z) point on the top of each PALS post, and I also surveyed (x, y, z) points on the bank-side and stream-side endpoints of the top layer of woody debris in each structure. These points were withheld from the point cloud used to create the 2013 digital elevation model (DEM), and instead used later in a GIS environment to help model PALS explicitly in the stream channel. I estimated site discharge using velocity meters, tape measures, and depth rods as described in CHaMP (2013a) at the time of each topography survey. Topography surveys at pilot structures during the summers of 2011 and 2012 were conducted and processed using the same methods to describe stream channel response to structures at the PALS pilot experiment sites. In-stream temperature
loggers recorded all temperatures.

As part of the 2012 topography survey, I identified channel units in the study area and estimated their substrate size compositions to help calculate an appropriate site-level roughness height for hydraulic modeling. I used a modification of the hierarchical classification system described in Hawkins et al. (1993) to identify channel units, and I included (x, y, z) points delineating their boundaries in the 2012 survey database. For each channel unit, I estimated and recorded the percent of substrate present in each of seven size categories (fines: <0.06mm; sand: 0.06–2mm; fine gravel: 2–16mm; coarse gravel: 16–64mm; cobbles: 64–250mm; boulders: 250–4000mm; bedrock: >4000mm). I digitized and connected the channel unit boundary points using GIS software to form channel unit polygons, and I used the polygon areas and substrate size information to determine the fraction of the whole site covered by each substrate size class. I multiplied the site coverage fractions (excluding bedrock) by their corresponding size class midpoints and summed the results to yield a weighted average roughness height estimate for the study area.

**Invertebrate drift**

I collected drift samples on 11 August 2011 by deploying a pair of drift nets (1000µm mesh, 40cm tall x 20cm wide mouth opening) in a riffle upstream of the study site to quantify the number, size distribution, and composition of drifting invertebrates available to drift-feeding fish. Nets were placed approximately 25cm apart within the thalweg and were suspended in the water column 2cm above the streambed to prevent benthic invertebrates from crawling in. I suspended the tops of net mouths above the water surface to capture drifting terrestrial invertebrates. Nets filtered the water column for approximately four hours during the middle of the day. I measured water depth and net mouth velocity (centered laterally, at 60% of the depth from the water surface to the bottom of the net mouth) for each net at the start of sampling, and I measured velocity again before removing the nets and transferring their contents to separate jars containing 95% EtOH. For processing, I pooled the nets’ contents, sorted invertebrates to family level, and counted abundances in
3mm size classes within each family. The total number of invertebrates for the pooled sample was divided by the total volume of water filtered by both drift nets to calculate drifting invertebrate concentration as number of individuals per cubic meter of water. Inputs for NREI modeling are summarized in Table 3.1.

Table 3.1: Summary of NREI model inputs. Water temperature and representative fish lengths and weights taken from 2011 electro-fishing surveys.

<table>
<thead>
<tr>
<th>Year</th>
<th>Discharge (m$^3$/s)</th>
<th>Temperature ($^\circ$C)</th>
<th>Drift Concentration (No./m$^3$)</th>
<th>Representative Fish Length (m)</th>
<th>Representative Fish Weight (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2012</td>
<td>0.13</td>
<td>15.0</td>
<td>1.9</td>
<td>0.109</td>
<td>18.03</td>
</tr>
<tr>
<td>2013</td>
<td>0.24</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

3.2.3 Analysis

Evaluating design hypotheses

I simulated topographic changes consistent with the restoration’s design hypotheses and results from pilot PALS experiments to create hydraulic model input files that could be used to simulate NREI in the study site. My goal was to create a simulated restoration topography prior to actual structure installation in treatment sites that could be used to investigate whether PALS provide an energetic benefit to juvenile steelhead. I began this process by quantifying the typical topographic change at PALS in the treatment basin. Researchers installed pilot PALS in each of three streams involved in the experimental watershed restoration during the summer of 2011 and surveyed topography in their vicinities. After high spring runoff in 2012, they returned, surveyed topography again, and quantified topographic changes by comparing data from the two years. I summarized the spatially explicit change results by measuring simple characteristics of change features such as length, width, and feature depth or height (Table 3.2).

I used the summarized topographic change information along with the restoration’s design and geomorphic change hypotheses to help simulate restoration at the study site using the 2012 DEM as a starting point. I created 10cm elevation contours on the 2012
Table 3.2: Summary of topographic change characteristics associated with post-assisted log structures in pilot experiments.

<table>
<thead>
<tr>
<th>Change Characteristic</th>
<th>Observed Range (m)</th>
<th>Mean Value (m)</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Erosion Length</td>
<td>3.0–19.0</td>
<td>10.4</td>
<td>10</td>
</tr>
<tr>
<td>Erosion Width</td>
<td>0.5–3.7</td>
<td>2.3</td>
<td>10</td>
</tr>
<tr>
<td>Erosion Depth</td>
<td>0.05–0.7</td>
<td>0.3</td>
<td>10</td>
</tr>
<tr>
<td>Deposition Length</td>
<td>2.0–8.0</td>
<td>3.9</td>
<td>11</td>
</tr>
<tr>
<td>Deposition Width</td>
<td>1.0–3.5</td>
<td>1.9</td>
<td>11</td>
</tr>
<tr>
<td>Deposition Height</td>
<td>0.1–0.8</td>
<td>0.2</td>
<td>11</td>
</tr>
</tbody>
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DEM using GIS software, and I created new 3D polyline features to strategically expand or condense areas delineated by the 2012 contours, simulating erosion and deposition in areas adjacent to PALS. The restoration plan’s design hypotheses and the summarized results of the PALS pilot experiments guided both the location and magnitude of the simulated topographic change. I converted the 3D polylines to 3D point features, and I replaced any changed areas of the underlying topography (values from the 2012 DEM) with the simulated erosional and depositional features. I TINned and rasterized the results and converted the raster cell centers to 3D point features to facilitate the remaining tasks in hydraulic model input file creation.

I used the restoration design and information from the pilot PALS experiments to simulate the presence of PALS in the study site for the simulated restoration hydraulic model input files. I identified the single 3D point feature closest to each PALS post and added 0.4m to its z-value because 0.4m was a typical post height in the PALS pilot experiments. Once I had simulated PALS posts, I connected them to form a polygon at each structure, and I added 0.3m to the z-value of any non-PALS-post topography points within the polygon because 0.3m of debris accumulation at PALS bases was typical in the pilot PALS experiments as of 2013 (two years after PALS installation).

To finalize the hydraulic model input files simulating restoration, I assigned a spatially explicit roughness height for each of the 3D topography point features. Woody debris woven through PALS likely increases flow resistance, so I simulated increased roughness inside
PALS by assigning roughness height values equal to the simulated post heights (i.e. 0.4m) to all topography points inside PALS. All other topography point features were assigned roughness height values equal to the weighted average roughness height estimate generated using the channel unit substrate size compositions. I exported the 2012 and restoration scenario topographies as a text files and modified them to be suitable for use with River 2D (Steffler and Blackburn, 2002).

I simulated flow patterns using River 2D, a two-dimensional, depth-averaged hydraulic modeling software package. I used the 2012 measured discharge and downstream water surface elevations as boundary conditions for both topographies because I did not simulate erosion or deposition at the upstream or downstream boundaries of the study site in the simulated restoration topography. Simulations continued until solution change between subsequent model steps was sufficiently small to consider the solutions converged, and I calibrated the 2012 solution by varying roughness height to minimize differences between inflow and outflow and the predicted and observed water surface DEMs.

The converged hydraulic solutions served as inputs for the rest of the NREI modeling process and I held all variables constant between the two simulations so that the only differences were based on topography. I converted the depth-averaged 2D hydraulic solutions to 2.5D solutions using the stream tubes model (Hayes et al., 2007). The stream tubes model divides River 2D solutions into tubes of equal discharge separated by cross sections and serves two purposes. First, this step allows the hydraulic solution to exhibit a vertical velocity gradient, which may be a more authentic representation of flow characteristics in natural channels. Second, the stream tubes themselves divide the stream space into cells needed for operation of the drift, foraging, and NREI models. Like a number of other NREI authors (e.g. Urabe et al., 2010; Jenkins and Keeley, 2010), I elected to assume drifting invertebrate concentrations were spatially uniform throughout the study site. This assumption is not realistic; however, I assumed the average measured drift concentration represents equilibrium between recruitment of drift from the benthos and drift depletion by foraging fish. I modeled spatial patterns of invertebrate drift concentration, steelhead
foraging, swimming costs, and NREI using models described in Hayes et al. (2007) with steelhead energetic parameters. The foraging and swimming costs models simultaneously estimated the energetic benefits and swimming costs of foraging, and the NREI was calculated by subtracting costs from benefits. I recorded each spatially explicit NREI prediction as an (x, y, nrei) point and TINned and rasterized the NREI values. I also exported depth and velocity rasters from the River 2D hydraulic solutions. I differenced the depth, velocity, and NREI rasters to compare current stream conditions with conditions under simulated restoration.

**Monitoring restoration with NREI**

I repeated NREI simulation in the study area using the 2013 topography, which represented topographic condition after PALS had been in place for six months, and I compared the 2012 and 2013 results to evaluate whether PALS were offering energetic benefits to fish. I simulated 2013 NREI using identical methods to 2012 NREI, except that I used the post-top and debris-top surveyed point features to explicitly account for PALS presence in the stream channel. I simulated PALS posts by adding true post heights from the topography surveys to the topography point feature closest to each PALS post. I simulated debris accumulation within PALS by adding 0.1m to any topography point feature contained within the polygon connecting PALS posts, because this value was consistent with field notes from the 2013 topography survey. Lastly, I assigned topography points inside PALS a roughness height value equal to the mean structure height for each PALS. Once PALS were explicitly modeled for the 2013 topography, I simulated flow patterns to convergence using the 2013 boundary conditions in River 2D, and I varied roughness heights until differences between inflow and outflow and observed and predicted water surface elevations were minimized.

Examining NREI differences between the two years required controlling for the effects of discharge on NREI by simulating NREI for both years at a common flow value. I chose to simulate the 2013 discharge over the 2012 topography using the calibrated 2012 hydraulic model (rather than vice versa) because the 2013 value was higher and I believed choosing the higher discharge would provide a larger wetted area in which to discern energetic contrasts
between years. I simulated flow patterns, drift dispersion, foraging, swimming costs, and NREI using the 2013 discharge value for both topographies, and I rasterized and exported the depth, velocity, and NREI predictions. I differenced depth, velocity, and NREI rasters to compare 2012 and 2013 stream conditions.

3.3 RESULTS

Modeling results from expected and post-restoration NREI simulations indicated increased depths near PALS in the study area and subsequent areal increases in slower velocities. Flow patterns creating these new depths and velocity combinations resulted in increased areas of higher-NREI habitat when comparing 2012 and the simulated restoration scenario. Results also predicted increased high NREI habitat in 2013 when compared to 2012, despite the lack of high-flow, channel-shaping events in the six months between the 2012 and 2013 topography surveys. NREI results indicate fish in the study area benefit from higher net rates of energy intake and possibly higher growth after PALS installation. Detailed results from each simulation are presented below.

Evaluating design hypotheses

Hydraulic models predicted increased mean depth and depth variability for the restoration scenario (mean depth = 0.14m, standard deviation = 0.10) when compared to predictions based on the 2012 topography (mean depth = 0.1m, standard deviation = 0.06) (Figures 3.3, 3.4). On average, wetted raster cells were predicted to be 0.05m deeper in the restoration scenario.
Fig. 3.3: River 2D depth prediction changes. Green shades indicate areas predicted to be shallower, and purple shades indicate areas predicted to be deeper in the simulated restoration.
Fig. 3.4: Modeled study site depth distributions using 2012 (dark gray) and simulated restoration (white) topographies.

The majority of the commonly wetted area between the two topographies displayed decreased predicted velocities when comparing 2012 and the simulated restoration scenario, and the distribution of predicted velocities experienced a commensurate shift toward lower values (Figures 3.5, 3.6). The mean 2012 velocity prediction was 0.52 m/s (standard deviation = 0.28), while the mean velocity prediction for the simulated restoration was 0.35 m/s (standard deviation = 0.23). On average, wetted raster cells were predicted to be 0.08 m/s slower in the restoration scenario. Locations with increased predicted velocity in the restoration scenario tended to be PALS-adjacent, and most displayed increased velocity because they had been dry (i.e. velocity was zero) in the 2012 topography.
Fig. 3.5: River 2D velocity prediction changes. Green shades indicate areas predicted to be faster, and blue shades indicate areas predicted to be slower in the simulated restoration.
Fig. 3.6: Modeled study site velocity distributions using 2012 (dark gray) and simulated restoration (white) topographies.

Results indicated a larger number of relatively high NREI locations for the simulated restoration when compared to the 2012 results, in addition to increased variability in NREI predictions (Figures 3.7, 3.8). The mean NREI prediction in 2012 was -0.03 J/s (standard deviation = 0.10), while the mean prediction for the simulated restoration was 0.06 J/s (standard deviation = 0.13). Whereas predicted velocity tended to decrease in the majority of the commonly wetted channel, predicted NREI tended to increase (Figure 3.7). Two noticeable exceptions occurred downstream of the first and second PALS where simulated aggradation caused these locations to become shallower or dry in the restoration scenario. On average, NREI raster cells were predicted to increase 0.07J/s when comparing the 2012 and simulated restoration topographies. A greater proportion of stream area changed from insufficient NREI values to sufficient NREI values than vice versa following simulated restoration, and much of the new habitat created by PALS had sufficient NREI to support fish (Figure 3.9).
Fig. 3.7: NREI prediction changes. Red shades indicate areas predicted to change positively after simulated restoration. Blue shades indicate areas predicted to change negatively after simulated restoration.
Fig. 3.8: Modeled study site NREI distributions using 2012 (dark gray) and simulated restoration (white) topographies.

**Monitoring restoration with NREI**

Hydraulic models predicted a slight increase in both the mean site depth and variability in depths after six months of PALS presence. The mean 2012 depth prediction was 0.13m (standard deviation = 0.07), while the mean depth prediction in 2013 was 0.15m (standard deviation = 0.08) (Figures 3.10, 3.11). In general, areas predicted to be deeper in 2013 were located near the in-channel ends of PALS, while areas predicted to be shallower were near the bank-side ends of PALS or inside the structures themselves (Figure 3.10). On average, depth raster cells were predicted to be 0.03m deeper in 2013 than in 2012.
Fig. 3.9: Changes in NREI condition after simulated restoration.

Change in NREI condition by area
- Insufficient to sufficient NREI
- Dry to sufficient NREI
- NREI condition unchanged
- Dry to insufficient NREI
- Sufficient to insufficient NREI
- Wet to dry

Q = 0.13 m³/s
Fig. 3.10: River 2D depth prediction changes. Green shades indicate areas predicted to be shallower, and purple shades indicate areas predicted to be deeper based on the 2012 and 2013 topographies.

$Q = 0.24 \text{ m}^3/\text{s}$
Hydraulic models predicted a decrease in the mean site velocity and an overall increase in the number of relatively slower locations after six months of PALS presence (Figure 3.13). The mean velocity prediction in 2012 was 0.66m/s (standard deviation = 0.36), while the mean prediction in 2013 was 0.54m/s (standard deviation = 0.32). While areas near the in-channel ends of PALS were generally predicted to have increased velocities, the majority of the site displayed decreased predicted velocity (Figures 3.12, 3.13). On average, velocity raster cells were predicted to be 0.04m/s slower in 2013 than in 2012.
Fig. 3.12: River 2D velocity prediction changes. Green shades indicate areas predicted to be faster and blue shades indicate areas predicted to be slower based on the 2012 and 2013 topographies.

Flow

Meters

Change in velocity prediction (m/s)

-1.25 to -1.0
-1.0 to -0.75
-0.75 to -0.50
-0.50 to -0.25
-0.25 to 0.0
0.0 to 0.25
0.25 to 0.50
0.50 to 1.0
1.0 to 1.25
>1.25

Q = 0.24 m³/s
Foraging and NREI models predicted increased mean site NREI and a shift in the distribution of predicted NREIs toward higher values in 2013 (Figure 3.15). Mean NREI prediction in 2012 was -0.05 J/s (standard deviation = 0.12), while the mean prediction in 2013 was 0.015 J/s (standard deviation = 0.12). Areas predicted to have decreased NREI tended to be areas where velocities were predicted to increase, but the majority of the wetted area had higher NREI predictions in 2013 (Figures 3.14, 3.15). On average, NREI raster cells were predicted to be 0.05 J/s higher in 2013 than in 2012. As in the simulated restoration, a greater proportion of habitat shifted from insufficient to sufficient than vice versa. When compared to the simulated restoration, a greater proportion of habitat had unchanged NREI condition after six months of PALS presence (Figure 3.16).
Fig. 3.14: Predicted NREI changes. Red shades indicate areas predicted to change positively and blue shades indicate areas predicted to change negatively based on the 2012 and 2013 topographies.
3.4 DISCUSSION

The approach used here is a significant advance in efforts to link fish performance and restoration activities through the design, implementation, and monitoring stages of a restoration project. In the past, fish response to many restoration projects was either not evaluated or results could not clearly document effectiveness (Bernhardt et al., 2005; Roni et al., 2008; Thompson, 2006; but see Gowan and Fausch, 1996), making it difficult to learn from outcomes and apply lessons learned to future endeavors. Under these circumstances, modeling provides a convenient framework for investigating restoration because it encourages practitioners to formulate explicit functional hypotheses linking restoration plans and project goals and then allows them to test those hypotheses.
Fig. 3.16: Changes in NREI condition after 2013 restoration.
The prediction that PALS and their accompanying geomorphic changes alter flow patterns in a manner energetically beneficial to fish while food, temperature, and discharge are held constant is novel. Both sets of NREI simulations suggested improved NREIs after PALS installation, but benefits were highest when comparing 2012 to the simulated restoration scenario, presumably because topographic changes in the simulated restoration were of greater magnitude than those the stream actually experienced in the short time between the 2012 and 2013 topography surveys. I expect energetic conditions may continue to improve in the study site as future high-flow events cause further changes to the stream channel. Sundbaum and Naslund (1998) and Gustafsson et al. (2012) both found that wood in streams promoted visual isolation among conspecifics, reducing aggressive behavior and energy spent defending territories, also resulting in overall increases in net energy intake. Their findings suggest another reason that the presence of PALS may provide energetic benefits for study area steelhead, albeit via a different mechanism than in this study.

The use of wood and other instream structures to improve fish habitat is a widely applied stream restoration approach. However, despite their use throughout decades of management, there remains much debate about their effectiveness at improving fish abundance. For example, a recent review (Stewart et al., 2009) and meta-analysis (Whiteway et al., 2010) arrived at different conclusions about the effectiveness of instream structures for improving salmonid abundance. In a well-documented, long-term pair of studies, Gowan and Fausch (1996) and White et al. (2011) found persistent, long-term increases of both trout abundance and biomass in treatment sections relative to controls more than 20 years after installation of instream structures. However, their results indicated increases were primarily due to immigration rather than increased recruitment, survival, or growth in treatment sections, suggesting that abundances increased without any apparent benefit to fish performance or fitness. In contrast, this study suggests PALS could improve fish NREI, a metric potentially related to growth. Further monitoring of the Asotin Creek restoration with NREI models could potentially provide evidence of increased fish performance to accompany any abundance increases.
The modeling approach described here provides a straightforward and flexible methodology for incorporating design hypotheses and results from pilot experiments in NREI simulations. Having results from pilot restoration experiments is certainly convenient and can lend simulations a degree of realism, but the overall modeling process could easily be extended to situations where this information is not available so long as potential outcomes or structural features to be modeled can be realistically represented with (x, y, z) coordinates. Compared to similar modeling approaches, the modeling in this study is comparable to PHABSIM-type approaches when considering time invested in sampling and analysis, but it has advantages over PHABSIM-type and other preference-based approaches because it relates physical habitat structure to net rate of energy intake, an intuitive and biologically meaningful metric. Similarly, comparing restoration scenarios using differenced NREI rasters and before-and-after NREI distributions is a simple and intuitive approach for visualizing how different habitat configurations might influence fish.

It is my hope that continued NREI modeling in the Asotin Creek watershed will build upon the dataset used here as current and future treatment sites begin to change or continue changing in response to PALS and other structure types being implemented in the Asotin Creek basin. This study suggests mechanistic links between stream channel changes caused by PALS and juvenile steelhead NREI values in treatment sites. Continued topographic monitoring, combined with the restorations current pre- and post-treatment fish monitoring data, could provide further support for mechanistic links between fish performance and abundance increases in response to ongoing restoration efforts in the Asotin Creek basin.
CHAPTER 4
CONCLUSION

Recent efforts linking mechanistic foraging and habitat selection models to fish populations (e.g. Hayes et al., 2007; Jenkins and Keeley, 2010; Urabe et al., 2010) reinforced the idea that net energy intake models have potential to help improve understanding of the habitat needs of fish. Hayes et al. (2007) demonstrated that NREI models can reasonably predict fish abundance, while both Jenkins and Keeley (2010) and Urabe et al. (2010) found that NREI predictions were positively correlated with habitat quality as indicated by fish biomass per unit of area. Despite these favorable results, NREI model application remains rare, especially at spatial scales typical of monitoring and recovery efforts in the northwestern United States. In this thesis, I attempted to contribute to efforts expanding the application of NREI models with the hope of improving our current understanding of both NREI models themselves and fish-habitat relationships in the context of threatened fish populations in the Columbia River basin.

In the first chapter, I investigated patterns between NREI predictions and fish populations. This study was motivated by recent research that expanded the spatial and temporal scales of NREI model application and suggested the possibility that NREI models could be used to help understand differences in fish habitat quality at scales relevant to monitoring and recovery efforts (Hayes et al., 2007; Jenkins and Keeley, 2010; Urabe et al., 2010). The Hayes et al. (2007) model in particular has a number of features that make it well-suited to this purpose, and the Columbia Habitat Monitoring Program (CHaMP) has intentionally collected monitoring data to support this type of effort. Using CHaMP data as inputs, I extended the Hayes et al. (2007) model to reach scales at multiple sites in two watersheds and found a positive correlation between fish densities predicted by the model and observed fish densities at study sites. In contrast to other NREI research, however, the proportion of suitable foraging locations and the mean NREI site values were generally not well correlated with fish biomass. Despite this fact, I believe the positive correlation between observed and
predicted fish densities is a valuable contribution to the body of NREI research and reinforces the notion that NREI has potential as a tool to help researchers and managers better understand fish-habitat relationships. The NREI modeling process as implemented here is both time- and cost-intensive. However, since the completion of this research, CHaMP has already worked to make this modeling approach more efficient by improving the automation of three of the most time-intensive steps: data preparation, hydraulic modeling, and cross section placement.

In my second chapter, I demonstrated a process by which restoration design, hypotheses, and monitoring can be investigated using NREI models. This chapter builds upon the suggestion by Hayes et al. (2007) that NREI could be used to quantify habitat availability, by extending NREI concepts to evaluate alternative restoration designs and then monitor restoration progress through time. My results suggested that post-assisted log structures, as described in Wheaton et al. (2012), can provide energetic benefits to fish. This analysis is important for two reasons: first, my findings agreed with restoration hypotheses, providing support for the associated projects and a broader understanding of how the restoration might influence fish; second, I demonstrated a process by which researchers, managers, and restoration practitioners can mechanistically evaluate restoration plans, a step in the design process that is rarely undertaken (but see Wheaton et al., 2004a,b for examples dealing with restoration of spawning habitat). While I found the modeling approach to be high in complexity, this type of modeling is not out of reach if proper input data sets can be obtained.

I expect that this research will aid in the continued development of NREI modeling and mechanistic investigations into benefits of restoration. Though I found some aspects of the NREI modeling undertaken here to be time- and cost-intensive, improvements have already been made to make the modeling more approachable and to greatly improve usability. Overall, the combined efforts of this thesis bolster the opinion that NREI model predictions are relevant to fish in the context of fish-habitat investigations.
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