Canadian Journal of Fisheries and Aquatic Sciences
Journal canadien des sciences halieutiques et aquatiques

**Net rate of energy intake predicts reach-level steelhead
(*Oncorhynchus mykiss*) densities in diverse basins from a
large monitoring program**

Journal:	<i>Canadian Journal of Fisheries and Aquatic Sciences</i>
Manuscript ID	cjfas-2015-0290.R2
Manuscript Type:	Article
Date Submitted by the Author:	30-Oct-2015
Complete List of Authors:	Wall, C.; Utah State University, Watershed Sciences; EcoLogical Research, Inc. Bouwes, Nicolaas; EcoLogical Research, Inc., Wheaton, Joseph; Utah State University, Watershed Sciences Saunders, W.; Utah State University, Watershed Sciences; EcoLogical Research, Inc. Bennett, Stephen; Utah State University, Watershed Sciences; EcoLogical Research, Inc.
Keyword:	FORAGING < General, HABITAT < General, MONITORING < General, MODELS < General, ENDANGERED SPECIES < General

SCHOLARONE™
Manuscripts

1
Net rate of energy intake predicts reach-level steelhead (*Oncorhynchus mykiss*) densities in diverse
2
basins from a large monitoring program
3

4
C. Eric Wall^{1,2}
c.eric.wall@gmail.com

5
Nicolaas Bouwes²
nbouwes@gmail.com

6
Joseph M. Wheaton¹
joe.wheaton@usu.edu

7
W. Carl Saunders^{1,2}
carl.saunders@usu.edu

8
Stephen N. Bennett^{1,2}
bennett.ecological@gmail.com

9
¹Watershed Sciences Department, Utah State University, 5210 Old Main Hill, Logan, Utah, 84322, USA

10
²Eco Logical Research, Inc., PO BOX 706, Providence, Utah, 84332

12
Corresponding Author:

13
C. Eric Wall

14
c/o Department of Watershed Sciences

15
5210 Old Main Hill, NR 210

16
Logan, UT 84322

17
540-220-8483

18
c.eric.wall@gmail.com

Abstract

Significant research effort has been devoted to understanding stream-dwelling salmonids' use of summer rearing and growth habitat, with a subset of studies focusing on foraging position selection and the energetic tradeoffs of differential habitat use. To date, however, cost-benefit analyses for most foraging model studies have focused on small sampling areas such as individual habitat units. To address this knowledge gap, we applied a mechanistic foraging model to 22, 100 – 400 m stream reaches from two watersheds within the Columbia River Basin. We found a strong, positive correlation ($R^2 = 0.61$, $p < 0.001$) between predicted carrying capacities and observed fish densities. Predicted proportion of suitable habitat was weakly correlated with observed fish density ($R^2 = 0.18$, $p = 0.051$), but the average net rate of energy intake prediction in sampling reaches was not a significant predictor of observed fish biomass. Our results suggest spatial configuration of habitat, in addition to quantity and quality, is an important determinant of habitat use. Further, carrying capacity predicted by the model shows promise as a habitat metric. We also evaluated the feasibility of applying this data-intensive modeling approach in a large-scale monitoring program to examine habitat quality and quantity. Though the approach can be computationally expensive, we feel the model's ability to integrate physical habitat metrics (e.g. depth, velocity) with important biological considerations like food availability and temperature is a benefit that far outweighs associated costs. We feel this modeling approach has great potential as a tool to help understand habitat use in drift-feeding fishes.

Keywords: Foraging model; Net energy intake; Net rate of energy intake; Salmonids; Steelhead trout; Drift-feeding; Carrying capacity; Habitat quality; Monitoring; Habitat

40 **Introduction**

41 Conservation and recovery of many lotic fishes depend on successful management and restoration of their
42 habitat. In the Columbia River Basin (CRB), for example, recovery efforts for listed salmon and steelhead
43 rely largely on restoration and changes in land management activities to improve tributary habitat for
44 freshwater rearing of juveniles (NOAA 2008; NPCC 2009; NMFS 2014). Extensive monitoring of
45 salmonid habitat is being conducted to evaluate whether habitat actions are resulting in habitat
46 improvements and to increase our understanding of fish–habitat relationships (Bouwes et al. 2011;
47 CHaMP 2014; Bennett et al. 2015). While this story is common to many imperiled species, the
48 development of transferable fish-habitat relationships remains elusive, and our record for improving
49 habitat quality via restoration or management is unclear (Rose 2000; Fausch et al. 2002; Roni et al. 2008).

50 A majority of the monitoring data collected to describe fish habitat has been linked to fish through
51 empirical models (e.g. Ahmadi-Nedushan et al. 2006). While relatively simple empirical approaches can
52 leverage large data sets to provide insight into fish-habitat associations, they often lack the experimental
53 manipulation necessary to identify causal mechanisms (Fausch et al. 1988). Empirical models may also
54 have limited transferability between systems, and they may lack the predictive ability to evaluate
55 alternative management scenarios (Nislow et al. 1999; see Bowlby and Roff 1986 for an example). In
56 contrast, mechanistic approaches investigate fish-habitat relationships by simulating the biological
57 processes thought to create observed patterns of fish distribution, and their predictions are often
58 corroborated by experiments (Fausch 1984; Hughes and Dill 1990). Mechanistic approaches allow
59 researchers to develop testable hypotheses about the mechanisms driving observed patterns, and validated
60 mechanistic models are more likely to be useful in novel locations and applications because they are
61 based on cause-effect relationships.

62 Habitat quality for salmonids can be described partly by the habitat's ability to support successful
63 foraging opportunities, as foraging is perhaps the most time consuming task an individual rearing

salmonid must accomplish to grow and survive (Harvey and Railsback 2014). Models that difference a fish's energy intake and swimming costs to estimate net rate of energy intake (NREI) have experienced success describing the energetic profitability of lotic environments (Rosenfeld et al. 2014). Fish consistently chose foraging positions with high NREI values in early modeling efforts (Fausch 1984; Hughes and Dill 1990), and newer studies have had success both predicting foraging locations for a variety of fish species (e.g. Guensch et al. 2001; Grossman et al. 2002) and estimating the capacity of a large pool (Hayes et al. 2007). Two recent studies, Jenkins and Keeley (2010) and Urabe et al. (2010), greatly expanded the spatial and temporal scales at which NREI models have been applied. These studies found positive correlations between NREI predictions and fish biomass, suggesting NREI is a useful indicator of habitat quality.

Most published NREI approaches measured depths, velocities, and invertebrate drift concentrations to estimate NREI. Hayes et al. (2007) extended previous modeling efforts to include hydraulic and drift dynamics in their NREI model, which used topography, discharge, drifting invertebrate concentration, temperature, and fish information as inputs. In addition, the Hayes et al. (2007) model outputs include spatially explicit NREI values that can be used with an estimate of territory size to estimate the carrying capacity of a modeled reach (we refer to this specific NREI variant as "Hayes NREI model" hereafter). The Hayes NREI model is arguably the most comprehensive NREI modeling approach published to date (Rosenfeld et al. 2014), and it broadens the range of management questions that can be addressed using NREI models to include actions that alter discharge regimes (e.g. dam releases), stream topography (e.g. stream restoration), or productivity (e.g. nutrient additions). Under the Hayes NREI modeling approach, spatially explicit foraging locations and carrying capacity estimates for multiple stream conditions and alternative management scenarios can be subject to hypothesis testing to further increase our understanding of fish-habitat relationships.

The Hayes NREI model uses either a 1D or 2D hydraulic model to produce NREI and carrying capacity predictions. While 1D hydraulic models may be more cost effective to implement, they do not capture spatial complexities in flow patterns as well as 2D hydraulic models. Most large-scale fish habitat monitoring programs do not collect the data necessary to develop 2D or even 1D hydraulic models (EPA 2006; Moore et al. 2008; Heitke et al. 2010). However, advances in the application of high resolution surveying technologies using precise instruments (e.g. total stations, real-time kinematic GPSs, light detection and ranging, etc.) have allowed for the collection of XYZ data sets that can be interpolated into continuous topographic models such as digital elevation models (DEM; Bangen et al. 2014). The high resolution DEMs are appropriate inputs to 2D hydraulic models, such as the one used in the Hayes NREI model. In addition, most fish habitat monitoring programs do not sample invertebrate drift, which is a critical input to NREI models. Recently, the Columbia River Habitat Monitoring Program (CHaMP) was developed to characterize habitat for Chinook salmon (*Oncorhynchus tshawytscha*) and steelhead (*O. mykiss*) in wadeable streams in watersheds throughout the Columbia River Basin (Bouwes et al. 2011; CHaMP 2014). The protocol requires the use of a total station (or other tools to collect XYZ data) to capture stream topography. The program also collects discharge estimates, invertebrate drift concentrations, and stream temperature data (Bouwes et al. 2011). The CHaMP protocol was designed, in part, so approaches like the Hayes NREI model could be applied in a fish habitat monitoring context to improve understanding of fish-habitat relationships (Bouwes et al. 2011; Rosenfeld et al. 2014). Currently the program samples approximately 500 reaches per year in the Columbia River Basin.

Assuming reach-level NREI capacity predictions can be scaled up to reliably estimate population-level capacity (e.g. using network extrapolation models; Isaak et al. 2014), the NREI modeling framework also holds promise within population modeling and general stock assessment contexts. Recovery planning for threatened or endangered salmonids in the CRB, for instance, has relied heavily on population models which require stage-specific estimates of carrying capacity (Moussalli and Hilborn 1986; Mobrand et al. 1997; Sharma et al. 2005; Scheuerell et al. 2006). In addition to filling this baseline information need,

NREI models offer a basis for simulating population performance under alternative habitat restoration scenarios because NREI-based capacity is built upon a mechanistic link to habitat. This also highlights the potential for using NREI to estimate a parameter (i.e. capacity) central to fishery management from a season of data rather than from decades of population monitoring (e.g. Hilborn and Walters 1992). Despite these promising applications, the Hayes NREI model has not yet been tested in longer, more complex study reaches, nor across multiple, diverse study reaches.

In order for the Hayes NREI model to be applicable to larger management questions, larger scale applications are necessary. In this paper, we expand the application of this model to multiple, continuous stream segments in order to investigate relationships between reach-scale habitat characteristics and carrying capacity. We used data collected by CHaMP to demonstrate the use of NREI models at spatial scales typically surveyed to monitor fish populations. Our goal was to test the ability of the Hayes NREI model to predict juvenile steelhead carrying capacity and observed density at 22 stream reaches throughout the CRB. Our specific objectives were to: (1) demonstrate/test the feasibility of using the Hayes NREI model at the reach scale, (2) convert reach-level NREI values into juvenile steelhead abundance (i.e. predicted carrying capacity), density, and biomass predictions, (3) calculate the average NREI value for each CHaMP reach using this model, (4) determine if the predicted density of juvenile steelhead was correlated with juvenile steelhead density observed at each reach, and (5) determine if average NREI was correlated with juvenile steelhead biomass observed at each reach.

Materials and methods

We used an adaptation of the Hayes NREI model that includes sub models for estimating gross rate of energy intake (GREI) and swimming costs (SC). The model ultimately calculates NREI as the difference of these quantities after adjusting GREI to account for losses due to wastes (i.e. $NREI = (0.7 \times GREI) - SC$; Hughes et al. 2003). Here, we used the same hydraulic and NREI model components, but simplified modeling of invertebrate drift by assuming it is spatially uniform. We collected the physical habitat,

temperature, invertebrate drift, and fish size data necessary to parameterize and run this NREI variant through an intensive field sampling campaign focused on steelhead populations of significant conservation concern.

Study reaches

We surveyed 22, 100 – 400 m stream reaches in two basins (Figure 1) involved in ongoing research and monitoring as part of CHaMP and ongoing Intensively Monitored Watershed projects (Bennett et al. 2015). The John Day River watershed in north central Oregon, USA ($n = 13$ reaches) drains a large portion of northeastern Oregon (approximately 20 700 km²) before joining with the Columbia River. 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 in southeastern Washington, USA ($n = 9$) drains approximately 842 km² of land 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 fish species, including US Endangered Species Act (ESA)-listed steelhead, the focal species of this study. We collected data between 21 June and 27 September, 2011.

Field data collection

We sampled fish populations to estimate steelhead abundance and mean size. We herded fish downstream into seines using an electrofishing machine set on a low setting (approximately 1000 V). We weighed and measured fish to the nearest 0.1 g and 1 mm, respectively. Fish with a fork length greater than 70 mm received a passive integrated transponder tag or had a fin clipped so they could be identified when recaptured. Mark and recapture events occurred on consecutive days, and we estimated steelhead abundance using the bias-adjusted Lincoln-Petersen mark-recapture model (Chapman 1951).

We calculated mean water temperature from in-stream temperature loggers (13 reaches) or with handheld thermometers (9 reaches). For reaches with in-stream temperature loggers, we calculated the average of

15-minute temperature readings over the course of the fish sampling event. For all other reaches we averaged temperature measures from the start and end of fish sampling. Because we sampled fish during summer baseflows, modeled temperatures can be considered typical for summer baseflow conditions.

We deployed two drift nets (1000 μm mesh, 40 cm x 20 cm mouth opening) at each reach to quantify the number, size distribution, and composition of drifting invertebrates. We placed nets side-by-side within the thalweg of a riffle near the upstream boundary of each study reach, suspended 2 cm above the streambed to prevent benthic invertebrates from crawling in. We also ensured net tops extended above the water surface to catch drifting terrestrial invertebrates. We collected drift samples during daylight conditions between 0830 and 1900 hrs., and sample durations ranged from three to five hours (Bouwes et al. 2011). Previous work suggested drifting invertebrate concentrations would be more constant at this time of day relative to samples collected during twilight conditions, and it also indicated juvenile steelhead are most actively feeding at these times (Weber 2009; Weber et al. 2014). We measured water depth and velocity in each net mouth when we deployed them using a Marsh-McBirney Model 2000 Flo-mate (Marsh-McBirney Inc., Maryland, USA) and a depth rod. We measured velocity at a point centered laterally and at 60% of the depth from the water surface to the bottom of the net mouth. We measured velocity again at the conclusion of sampling and then transferred net contents to jars containing 95% ethanol. We calculated the volume of water filtered by each net as *net depth (m) x net width (m) x average net mouth velocity ($\text{m}\cdot\text{s}^{-1}$) x sampling duration (s)*. In the lab, we pooled each pair of drift nets and sorted contents into 3 mm family-level size classes. We calculated drifting invertebrate concentration by dividing the total number of invertebrates from the pooled sample by the total volume of water filtered by both nets.

Geomorphic data were collected using methods described in detail by Bouwes et al. (2011). The shape of the stream channel and adjacent floodplain, the wetted perimeter, and channel unit boundaries were described by collecting topographic (XYZ) points with a total station. Topographic data were stratified to

be focused at vertices of changes in bed form, resulting in more points collected near complex topography and breaks in slope (Bangen et al. 2014). Breaklines (e.g. top of bank, toe of bank, edge of water, bankfull) were also collected to improve surface quality and reduce the overall number of points necessary to represent the channel and floodplain topography (Lane et al. 1994; Brasington et al. 2003). We quantified substrate size composition in each channel unit by visually estimating the percent of substrate in each of seven size categories based on a simplified Wentworth scale: fines (< 0.06 mm), sand ($0.06 - 2$ mm), fine gravel ($2 - 16$ mm), coarse gravel ($16 - 64$ mm), cobbles ($64 - 250$ mm), boulders ($250 - 4000$ mm), and bedrock (> 4000 mm). We estimated discharge using the U.S. Environmental Protection Agency's protocol (Peck et al. 2001).

Modeling framework

We modeled steady-state flow conditions at study reaches using River2D and the methodology described by Steffler and Blackburn (2002). We processed topographic data with GIS software to create polygon shapefiles for channel units and 10 cm digital elevation models (DEMs) of the stream channel and the water surface. Raster cell coordinates from the stream channel DEMs served as topography inputs for River2D. We summed the products of channel unit areas and substrate size percentages to estimate the portion of each reach covered by the seven substrate size classes. We weighted the coverage portions by their corresponding size class midpoints, excluding bedrock, and summed the results to estimate reach-level roughness height. For example, a reach with 50% coarse gravel and 50% cobbles received a roughness height estimate of 0.0985 m. We distributed computational nodes for flow calculations uniformly throughout study reaches at an approximate spacing of 0.25 m, with inflow and outflow boundaries receiving additional nodes at an approximate spacing of 0.1 m. Modeling assumed no losses or gains from groundwater or tributaries.

We collected spatially explicit depth and velocity measures for hydraulic model calibration and validation at two reaches, CC1 and NFAC1. Using a depth rod and a Marsh-McBirney Model 2000 Flo-mate, we

recorded depths and velocities every 0.25 m on existing monumented cross sections spaced roughly 15-20 longitudinal meters apart. We collected these depth-velocity pairs at two discharges using the higher discharge for calibration and the lower discharge for validation. This resulted in between 60 and 110 depth-velocity pairs for each of the two flow scenarios in the CC1 and NFAC1 reaches. We varied roughness height until differences between inflow and outflow and predicted versus observed depths and velocities were minimized for the calibration discharge, and then we simulated the lower discharge and compared model predictions to the validation datasets.

We prepared River2D solution files for the NREI model with the Stream Tubes program (Hayes et al. 2007). The Stream Tubes program divides flow vertically and laterally to create tubes of equal discharge separated longitudinally by cross sections on which NREI calculations occur. Users define the numbers of vertical and lateral stream tubes, the longitudinal spacing of cross sections, and the number of NREI estimates to be calculated on cross sections in a reach (Kelly et al. 2012). Increasing the numbers of stream tubes or cross sections can provide increased prediction resolution, but at the cost of computational efficiency. We based the number of vertical and lateral stream tube divisions on mean reach depth and width, respectively (Table 2), and we used constant 0.2 m spacing between cross sections because these values offered a balance of spatial resolution and computational efficiency while satisfying the cross section spacing recommendations in Kelly et al. (2012). We selected the model's default setting for vertical velocity profile—logarithmic—which allows modeled flow to be slower near the bed and faster near the surface.

The model calculates NREI by estimating gross rate of energy intake with the foraging model, accounting for losses due to wastes, and then subtracting swimming costs (Hughes et al. 2003; Hayes et al. 2007). A search area that accounts for fish swimming ability, prey size, and reactive distance to prey is multiplied by water velocity to describe search volume. The density of drifting invertebrates is multiplied by search volume to describe prey encounter rate. Successful predation events are a proportion of the prey

encountered (i.e. success is not 100% of prey observed). We assumed a 55% foraging success rate for steelhead, a figure identical to the success rate Hughes et al. (2003) observed for brown trout (*Salmo trutta*). Fish were assumed to hold foraging positions 5 cm from the streambed (described below), and swimming costs were estimated based on velocities at this vertical location. Other physiological functions used in NREI calculations were size- and temperature-dependent, and based on *O. mykiss* specific parameters (Hayes et al. 2007).

We simulated NREI and estimated carrying capacity using an adaptation of the Hayes et al. (2007) approach described by Kelly et al. (2012). In short, the model estimates NREI for fish of a given size on the cross sections created by the Stream Tubes program. Users define the number of equally-spaced NREI estimates that will be calculated along cross sections in a study reach. Users also define the height above the streambed at which these estimates will occur. Starting with the highest NREI value on the most upstream cross section, the NREI prediction is compared to a user-defined minimum acceptable value. If the predicted value meets or exceeds the minimum allowed, the model records this location as being able to support a fish and moves to the next downstream cross section where the test is repeated. After processing the last cross section in the reach, the model provides an estimate of carrying capacity by counting all locations recorded as being able to support fish.

We set other NREI model inputs using a variety of resources. To satisfy the NREI model's fish size inputs, we used the mean length and weight from each reach's fish sampling event. For each study reach, we used a number of NREI estimates per cross section that provided, on average, roughly one NREI estimate every 10 cm along cross sections. We observed through video and snorkeling that fish typically maintained positions close to the bed, where water velocity was slower, but also in close proximity to each other (E. Wall, personal observation). Thus, we chose 5 cm as the height above the bed for NREI calculations, and 10 cm as the minimum allowable distance between fish in the model. Choosing a fish territory size smaller than the cross section spacing leaves cross section spacing as the governing variable

determining minimum distance between fish. We were interested in how many fish each reach could support, so we chose a minimum acceptable NREI of $0.0 \text{ J} \cdot \text{s}^{-1}$. By definition, a fish achieving NREI of $0.0 \text{ J} \cdot \text{s}^{-1}$ is neither gaining nor losing weight according to the model. Outputs from River2D, the NREI model, and the results of fish placement are shown in Figure 2 for the NFAC1 reach. After estimating NREI and carrying capacity, we calculated density by dividing carrying capacity estimates by the wetted areas predicted by River2D, and we calculated biomass ($\text{g} \cdot \text{m}^{-2}$) for study reaches by multiplying reach density ($\text{fish} \cdot \text{m}^{-2}$) by mean reach fish weight (g). Thus, our NREI-based estimates of capacity are implicitly defined by a fish's ability to maintain weight during the summer.

We also evaluated relationships between reach-level NREI summary statistics and fish abundance data by examining reach-level collections of NREI estimates in three ways. First, we compared the total number of suitable NREI locations in a reach (those with NREI estimates greater than or equal to $0.0 \text{ J} \cdot \text{s}^{-1}$) to observed reach fish abundance. Second, we divided the number of suitable locations by the total number of NREI estimates to calculate the proportion of suitable NREI locations and compared this value to observed fish density. Third, we calculated the mean NREI estimate and compared this value to observed biomass. We treated negative NREI estimates as zeros when calculating the mean (as in Urabe et al. 2010).

Results

Field survey summary

In total, we surveyed more than 4 km of stream in support of our NREI assessment (Table 1) and observed considerable contrast in NREI drivers across reaches. Sample reaches ranged widely in size, spanning an order of magnitude in width (1.8 – 14.9 m) and two to three orders of magnitude in discharge ($0.031 - 1.257 \text{ m}^3 \cdot \text{s}^{-1}$). Invertebrate drift also showed wide variation, approximately 50-fold, across the 22 survey reaches. Despite the wide variation in NREI drivers, fish density showed considerably less

contrast. Through mark–recapture (approximately 4600 tagged fish across reaches), we estimated reach-level densities (i.e. abundance / reach area) that centered between 0.4 and 1.4 fish · m⁻² at most reaches.

Flow simulation

Hydraulic model outputs for the NFAC1 reach were more accurate than those for the CC1 reach, which showed bias in depth predictions for the validation discharge (Figures 3 and 4). However, positive relationships between model predictions and measured depths and velocities indicated that both models preserved major depth and velocity patterns in the two study reaches. Mean absolute depth and velocity errors for the CC1 model were 0.05 m and 0.18 m·s⁻¹ at the calibration discharge (Figure 3A and 3B) and 0.07 m and 0.16 m·s⁻¹ for the validation discharge, respectively (Figure 3C and 3D). Mean absolute depth and velocity errors for the NFAC1 model were 0.05 m and 0.20 m·s⁻¹ for the calibration discharge (Figure 4A and 4B) and 0.04 m and 0.19 m·s⁻¹ for the validation discharge, respectively (Figure 4C and 4D). Mean absolute errors for NFAC1 equaled or exceeded those for CC1 in three of four cases, but the NFAC1 model did a better job overall at preserving flow patterns, indicated by a slope of ca. 1.0.

NREI predictions

Across all reaches, NREI predictions ranged from -12 J·s⁻¹ to 1.4 J·s⁻¹. Every reach had negative NREI predictions, and 17 of the 22 reaches also had a negative median NREI value. The range of mean predicted NREI values (treating negatives as zeros) spanned more than an order of magnitude with the smallest and largest predictions being 0.002 J·s⁻¹ and 0.21 J·s⁻¹, respectively. The model predicted every reach as being able to support fish, though predictions showed a considerable range of densities (0.3 fish·m⁻² – 3.2 fish·m⁻²).

Relationship between NREI and observed fish abundance

A linear regression between observed and NREI-predicted fish densities was significant ($R^2 = 0.61$, $p < 0.001$; Figure 5). However, NREI-predicted density (a.k.a. capacity) exceeded observed density at all but

one reach. We found the total number of suitable NREI locations at a reach was not well correlated with observed abundance. While the regression of observed density on the proportion of suitable NREI locations was marginally significant ($R^2 = 0.18$, $p = 0.051$; Figure 6A), it explained only a minor portion of the variability in observed fish density across the 22 reaches. Mean NREI was not a significant predictor of fish biomass in the study reaches (Figure 6B).

Discussion

We have demonstrated that the Hayes NREI model can be readily applied beyond the habitat unit scale to the reach level using habitat data collected by the CHaMP monitoring protocol. We designed this study to test the feasibility of applying this NREI model with a few simplifying assumptions (e.g. uniform drift concentration) at spatial scales typically surveyed to monitor fish populations (e.g. 100 – 400 m stream reaches). We estimated NREI, carrying capacity, and fish density, and found a strong, positive correlation between predicted carrying capacity and observed fish density across 22 reaches in 2 basins. This effort significantly increases the spatial scales of typical NREI modeling research, and it demonstrates that habitat quality can be inferred from a mechanistic model. Our study also provides managers with an example of an alternative approach to assessing the viability of fish populations listed under the ESA and it suggests NREI modeling could be used to better understand the effectiveness of stream restoration. To our knowledge, this is both the first use of fine-scale topographic surveys to drive NREI modeling for a large number of reaches at relatively large spatial scales, and the first use of NREI modeling as a tool in long-term monitoring programs such as CHaMP to evaluate habitat quality and quantity.

Several previous studies suggested fish use habitat at a variety of spatial scales in relation to energetic costs and benefits. For example, fish foraged in positions predicted to offer high NREI values in both individual channel units (Hughes and Dill 1990) and a 250 m stream reach (Guensch et al. 2001). Reach-level NREI summary statistics were also shown to be significant predictors of fish biomass in pool and riffle channel units (Jenkins and Keeley 2010) and in 30 – 150 m long stream reaches (Urabe et al. 2010).

Corroborating the idea that NREI estimates are relevant to fish, we found NREI-predicted carrying capacity to be significant as a predictor of observed fish density. We believe estimating carrying capacity with the Hayes NREI approach will allow for a better understanding of the effectiveness of habitat restoration actions and fish population responses.

We assumed reaches predicted to have higher carrying capacity would also have higher fish density in agreement with ideal free distribution theory (Fretwell 1969). While we found predicted and observed densities were highly correlated, we also found densities to be far lower than predictions made by the NREI model. Predicted steelhead densities may have exceeded observed densities for several reasons. First, steelhead in both study basins are considered to be substantially depressed relative to historical levels, so much so that they are protected under the ESA (NOAA 2011). Reasons for the depressed populations may include factors outside our study areas. Second, whereas we modeled the single dominant species in our study reaches, other drift-feeding species were present and may have fed on invertebrate drift to an extent that could reduce resources available to steelhead. Third, it's possible that our chosen NREI threshold value for fish placement of $0.0 \text{ J} \cdot \text{s}^{-1}$, which implies fish are at least able to maintain weight, could be too low because fish need greater-than-maintenance NREI to support growth and reproduction. However, we commonly observe fish that do not gain weight, in fact many lose weight, during baseflow periods of summer, so a neutral fish placement threshold value may be a reasonable assumption to represent survival through this potentially stressful period. Finally, we assumed invertebrate drift was uniform throughout each reach, effectively ignoring reach-level effects of drift depletion by foraging fish and possibly inflating the total amount of invertebrate drift available to fish in the model. Despite these limitations, the model still successfully accounted for nearly 2/3 of variation in observed fish density in two distant and distinct basins.

One reach in our study appeared to exert heavy influence on the relationship between observed and predicted fish densities. However, because we are validating a simulation model with observed data,

rather than developing a predictive relationship that could be dramatically altered by influential points, we believe inclusion of this influential point is important to test the NREI model under a broader range of conditions. Despite its heavy influence, this study reach had the highest observed and predicted densities, indicating that the NREI model positioned it correctly amongst the 22 reaches. The modeled relationship did not change dramatically when we excluded this reach from the regression (i.e. the slope and intercept were similar; Figure 5), but the regression did account for a smaller portion of variation in observed fish density ($R^2 = 0.61$ when included; $R^2 = 0.24$ when excluded). We also excluded from regression the single reach where observed densities were higher than predicted densities, as this point was detected as an outlier because it was outside the 95% prediction interval. We still, however, observed a similar relationship (slope = 0.41, intercept = -0.04, $R^2 = 0.73$, $p < 0.0001$) to the regression including all 22 study reaches. Interestingly, this reach also had the smallest mean fish length (61 mm) and the highest observed temperature, suggesting that behavioral and allometric relationships may not be extrapolated across all size classes of fish or to all environmental settings.

In contrast to Urabe et al. (2010), we found mean NREI was not correlated with observed juvenile steelhead biomass. We also expected the proportion of suitable NREI estimates to be a better predictor of fish density than the mean NREI value; however, proportion of suitable NREI values was only weakly correlated to observed density. In view of these results, we believe the spatial configuration of habitat, in addition to its energetic profitability, needs to be examined when assessing relationships between NREI predictions and observed fish density. This concept can be highlighted by considering two streams with identical sets of NREI values that happen to be in different spatial arrangements. Depending on the spatial configuration of suitable NREI values, the two streams might be expected to support different numbers of territorial fish (Figure 7) even though they would have the same mean NREI estimate and proportion of suitable NREI predictions. Thus, carrying capacity estimates, as predicted by a fish placement system, may provide a better synthesis of the diverse spatial distribution of NREI values throughout a reach than simple summary statistics to illuminate patterns of habitat use.

Our assumption of spatially uniform invertebrate drift has two key implications. First, we did not use the drift model to simulate spatially variable prey concentrations. Therefore, drift in the model might have displayed lower small-scale spatial variation than may actually occur (Shearer et al. 2002), especially in habitat units where invertebrates might be expected to settle (e.g. long, slow pools or runs). Second, as mentioned previously, we did not simulate depletion of drifting prey items by drift-feeding fish. Ignoring the influence of drift depletion could inflate food concentrations in the model and result in higher carrying capacity predictions, suggesting capacity estimates could be considered an upper limit to fish density under food-rich conditions. However, an alternative viewpoint is that drift samples quantify the drifting invertebrate prey items remaining in the drift after competition has occurred, suggesting that competition is implicitly represented by the drift values we used in this study (Rosenfeld et al. 2014).

Spatially explicit modeling of drift dispersion and depletion has been demonstrated (Hayes et al. 2007), but it requires collection and processing of many spatially explicit drift samples along with calibration of a drift model. It's possible that modeling drift dispersion and depletion by foraging fish might have improved fish density predictions in this study. We attempted, but were unable, to achieve close agreement between drift model predictions and spatially explicit drift samples at the CC1 and NFAC1 reaches using this approach, hence the adopted assumption of uniform drift in this study (Wall 2014).

Consumption by foraging fish, substrate movement, invertebrate swimming ability, and invertebrate drifting behavior influence concentrations of prey items in the drift and further complicate drift modeling (Rader 1997). Of these, only consumption by foraging fish is explicitly accounted for by the Hayes et al. (2007) drift model. In addition, much of the information needed to parameterize models like the Hayes et al. (2007) drift model is unavailable for most taxa (Rosenfeld et al. 2014). While evidence exists that hydraulic mixing in turbulent streams homogenizes drift (Leung et al. 2009), spatially uniform invertebrate drift concentration is likely a poor assumption (see Shearer et al. 2002) despite its near-ubiquity in NREI modeling research (e.g. Jenkins and Keeley 2010; Urabe et al. 2010). Modeling

approaches for predicting spatially variable invertebrate drift warrant continued development and future research (Anderson et al. 2013).

Rather than relying on observed depths and velocities, the Hayes NREI model uses hydraulic model predictions to calculate NREI. A small number of previous studies used flow simulations to provide depth and velocity estimates for NREI modeling (e.g. Guensch et al. 2001; Booker et al. 2004), but the majority of studies measured depths and velocities in the field (e.g. Urabe et al. 2010). Using flow simulations to provide depth and velocity inputs for NREI models, rather than measuring them in the field, can provide depth and velocity estimates with equal or lower error than field-measured values (Pasternack et al. 2006) at increased spatial resolution. This increased spatial resolution carries over to the spatial resolution of NREI estimates as well. For example, depending on cross section width, we typically attained over 20 NREI estimates per square meter in this study. By comparison, other recent studies (e.g. Jenkins and Keeley 2010; Urabe et al. 2010) achieved less than five predictions per square meter. In addition to increased spatial resolution, flow simulations can also provide depth and velocity estimates under different discharge or topographic scenarios, allowing modelers to investigate the influence of flow regulation (e.g. Hayes et al. 2007) or changes to channel structure (e.g. planned restoration) on spatial patterns of NREI predictions or predicted capacities (Rosenfeld et al. 2014; Wall 2014). For these reasons, the Hayes NREI model shows great potential to help large-scale monitoring programs evaluate fish habitat quality and quantity from an energetic perspective by comparing NREI distributions and capacity estimates.

A main goal of our study was to evaluate the feasibility of applying the Hayes NREI approach in a large-scale monitoring program to help evaluate fish habitat quality and quantity. While we were able to apply the Hayes NREI model in multiple reaches, each study reach required considerable time and effort, despite having topography, temperature, and invertebrate drift data already collected by CHaMP. Simulating flows and then modeling stream tubes, foraging, and NREI usually required between one and

422 four days once the inputs had been collected. We spent the majority of that time in River 2D and the
423 Stream Tubes program. While River 2D produced acceptable depth and velocity predictions in the study
424 reaches, other hydraulic modeling platforms might offer improved automation and efficiency to help
425 speed modeling efforts. For example, hydraulic models accepting raster inputs as topography data sets
426 exist and are both convenient and efficient because many topographic data sets are in raster formats. In
427 fact, since completion of this study, CHaMP has automated the Delft3D model to produce 2.5D output in
428 raster format and has implemented the model across all CHaMP reaches, greatly increasing NREI
429 modeling efficiency. One-dimensional hydraulic models are also an option and can be more cost effective
430 than 2D models, but they do not capture as much spatial complexity of habitat as 2D models. Regardless,
431 they can still provide valuable information regarding relative differences between NREI or capacity
432 predictions from different reaches or habitat scenarios. The Stream Tubes program successfully divided
433 cross sections into tubes of equal discharge, but it did exhibit some problems in areas with complex flow
434 patterns, around sharp bends, or near islands. In addition, fine cross section spacing such as the values
435 used in this study made stream tube placement more difficult, greatly increasing the manual oversight
436 required to prepare reach data. Stream tubes are currently needed to take advantage of the Hayes et al.
437 (2007) drift dispersion model; however, the assumption of spatially uniform invertebrate drift
438 concentration greatly simplifies drift calculations in the model and alleviates the need for stream tubes.
439 While the drift, foraging, and NREI models usually did not require user intervention, these models still
440 took between 35 minutes and 13 hours (mean processing time was roughly 3 hours) on 32-bit personal
441 computers with 4 gigabytes of random access memory. Any single change to model inputs (e.g. a change
442 in temperature) required re-simulation and the same time investment over again. Unfortunately, the net
443 effect of these complications makes calibration, validation, and sensitivity analysis extremely difficult, if
444 not impossible, especially if hundreds of reaches are to be simulated, as is the case for CHaMP. A final
445 challenge to widespread implementation is that the model is currently limited to a single modeled fish size
446 per simulation. Moving the model to an individual-based modeling system might allow for simulations of

multiple size classes simultaneously, and it would benefit future studies considering the importance of size hierarchies in structuring populations.

While neither Hayes et al. (2007) nor this study performed a full sensitivity analysis on the Hayes NREI model, the influence of parameter uncertainty on the predictions of foraging models can be useful to guide future research or direct data collection efforts to improve model accuracy. In a formal sensitivity analysis of his NREI model, Addley (1993) found NREI predictions to be sensitive to the fish's reactive distance to prey, estimates of the energy content of prey items, and invertebrate drift concentration used in the model. Detailed observations of foraging fish indicate that capture success declines rapidly with increasing distance from a fish's focal point and with velocity (Hill and Grossman 1993; Hughes et al. 2003; Piccolo et al. 2008b), rather than experiencing uniformity throughout the capture area as is commonly assumed (Rosenfeld et al. 2014). A review of foraging model research indicated that the functions governing capture success, which are dependent upon reactive distance, and the models used to predict swimming costs are two of the most influential components in NREI models (Rosenfeld et al. 2014). However, the spatial distribution, dispersal, and production of drift within modeled reaches may be the largest uncertainty faced by foraging modelers (Rosenfeld et al. 2014). In light of these findings and the result that gross energy intake predictions typically dwarf predicted swim costs (Hill and Grossman 1993; Piccolo et al. 2008a), empirical functions to more accurately predict capture success while taking into account velocity and distance from the fish's focal point are needed. Advances in predicting capture success would improve NREI prediction accuracy and, therefore, our ability to discern relative differences in habitat profitability. However, if accurate growth predictions are also of research interest, then both capture success functions and swim costs models will need to be improved. In this case, future research should also focus on models that can accurately predict the energetic costs of swimming in a turbulent environment (Rosenfeld et al. 2014). Full sensitivity analysis of the Hayes NREI model would require sensitivity analysis of the approach's submodels, including performance of the hydraulic modeling package used, the Stream Tubes program, and the drift dispersion model.

The Hayes NREI model provides a substantial contribution to the NREI modeling approach. The model addresses criticisms of habitat suitability approaches (e.g. exclusion of food in habitat selection; Rosenfeld and Boss 2001), and provides a mechanistic understanding of how certain habitat variables influence habitat quality and quantity (Rosenfeld et al. 2014). However, the model works at a fine spatial scale and can be computationally expensive, making it difficult to implement across large-scale monitoring programs. We believe improved model efficiencies, once achieved, will greatly increase the use of NREI predictions in habitat assessments where supporting data have been collected. We also believe the NREI modeling approach has great potential to provide an energetics context to questions of fish habitat quantity and quality.

Acknowledgements

Support was provided by the Snake River Salmon Recovery Board, the Utah State University School of Graduate Studies via a Presidential Fellowship, and the Bonneville Power Administration through grants to the Integrated Status and Effectiveness Monitoring Program (BPA Project ISEMP: 2003-017) and the Columbia Habitat Monitoring Program (BPA Project CHaMP: 2011-006). The faculty, staff, and students of Utah State University's Watershed Sciences Department were integral in the development, execution, and completion of this work. Eric Goodwin provided support for the Stream Tubes program and the foraging model. Pete McHugh and two anonymous reviewers provided valuable feedback on an earlier version of this manuscript.

References

- Addley, R.C. 1993. A mechanistic approach to modeling habitat needs of drift feeding salmonids. M.Sc thesis, Department of Civil and Environmental Engineering, Utah State University, Logan, UT.
- Ahmadi-Nedushan, B., and six coauthors. 2006. A review of statistical methods for the evaluation of aquatic habitat suitability for instream flow assessment. *River Research and Applications* **22(5)**:503-523.
- Anderson, K.E., Harrison, L.R., Nisbet, R.M., and Kolpas, A. 2013. Modeling the influence of flow on invertebrate drift across spatial scales using a 2D hydraulic model and a 1D population model. *Ecological Modeling* **265**:207-220.
- Bangen, S.G., Wheaton, J.M., Bouwes, N., Bouwes, B., and Jordan, C. 2014. A methodological intercomparison of topographic survey techniques for characterizing wadeable streams and rivers. *Geomorphology* **206**:343-361.
- Bennett, S.N., Pess, G., Bouwes, N., Roni, P., Bilby, R., Gallagher, S., Ruzycski, J., Buehrens, T., Krueger, K., Ehinger, W., Anderson, J., and Jordan, C. 2015. Progress and challenges of testing the effectiveness of stream restoration in the Pacific Northwest using Intensively Monitored Watersheds. *Fisheries* **In review**.
- Booker, D.J., Dunbar, M.J., and Ibbotson, A. 2004. Predicting juvenile salmonid drift-feeding habitat quality using a three-dimensional hydraulic-bioenergetic model. *Ecological Modeling* **177**:157-177.
- Bouwes, N., Moberg, J., Weber, N., Bouwes, B., Bennett, S., Beasley, C., Jordan, C.E., Nelle, P., Polino, M., Rentmeester, S., Semmens, B., Volk, C., Ward, M.B., and White, J. 2011. Scientific protocol

- 511 for salmonid habitat surveys within the Columbia Habitat Monitoring Program. Project #2011-
512 006, The Integrated Status and Effectiveness Monitoring Program.
- 513 Bowlby, J.N., and Roff, J.C. 1986. Trophic structure in southern Ontario streams. *Ecology* **67**:1670-1679.
- 514 Brasington, J., Langham, J., and Rumsby, B. 2003. Methodological sensitivity of morphometric estimates
515 of coarse fluvial sediment transport. *Geomorphology* **53**:299-316.
- 516 CHaMP. 2014. Scientific protocol for salmonid habitat surveys within the Columbia Habitat Monitoring
517 Program. Prepared by the Integrated Status and Effectiveness Monitoring Program and published
518 by Terraqua, Inc., Wauconda, WA.
- 519 Chapman, D.G. 1951. Some properties of the hypergeometric distribution with applications to zoological
520 sample censuses. University of California Press, Berkeley.
- 521 EPA, U. S. 2006. Wadeable streams assessment: a collaborative survey of the nation's streams. United
522 States Environmental Protection Agency, Office of Water, Washington, DC. EPA 841-B-06-002
523 December 2006.
- 524 Fausch, K.D. 1984. Profitable stream positions for salmonids - relating specific growth-rate to net energy
525 gain. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **62**:441-451.
- 526 Fausch, K.D., Hawkes, C.L., and Parsons, M.G. 1988. Models that predict standing crop of stream fish
527 from habitat variables: 1950-85. U.S. Department of Agriculture, Forest Service, Pacific
528 Northwest Research Station, Portland, OR.
- 529 Fausch, K.D., Torgersen, C.E., Baxter, C.V., and Li, H.W. 2002. Landscapes to riverscapes: Bridging the
530 gap between research and conservation of stream fishes. *Bioscience* **52**:483-498.
- 531 Fretwell, S.D. 1969. On territorial behavior and other factors influencing habitat distribution in birds II.
532 Sex ratio variation in the dickcissel (*Spiz american Gmel*). *Acta Biotheoretica* **19**:37-52.

- 533 Grossman, G.D., Rincon, P.A., Farr, M.D., and Ratajczak, R.E. 2002. A new optimal foraging model
534 predicts habitat use by drift-feeding stream minnows. *Ecology of Freshwater Fish* **11**:2-10.
- 535 Guensch, G.R., Hardy, T.B., and Addley, R.C. 2001. Examining feeding strategies and position choice of
536 drift-feeding salmonids using an individual-based, mechanistic foraging model. *Canadian Journal*
537 *of Fisheries and Aquatic Sciences* **58**:446-457.
- 538 Harvey, B.C., and Railsback, S.F. 2014. Feeding modes in stream salmonid population models: is drift
539 feeding the whole story? *Environmental Biology of Fishes* **97**:615-625.
- 540 Hayes, J.W., Hughes, N.F., and Kelly, L.H. 2007. Process-based modeling of invertebrate drift transport,
541 net energy intake and reach carrying capacity for drift-feeding salmonids. *Ecological Modeling*
542 **207**:171-188.
- 543 Heitke, J.D., Archer, E.K., and Roper, B.B. 2010. Effectiveness monitoring for streams and riparian areas:
544 sampling protocol for stream channel attributes. Unpublished paper on file at:
545 <http://www.fs.fed.us/biology/fishecology/emp>.
- 546 Hilborn, R., and Walters, C.J. 1992. Quantitative Fisheries Stock Assessment: Choice, Dynamics and
547 Uncertainty/Book and Disk. Springer Science & Business Media.
- 548 Hill, J. and Grossman, G.D. 1993. An energetic model of microhabitat use for rainbow trout and rosyside
549 dace. *Ecology* **74**:685-698.
- 550 Hughes, N.F., and Dill, L.M. 1990. Position chioce by drift-feeding salmonids: Model and test for Arctic
551 Grayling (*Thymallus arcticus*) in subarctic mountain streams, interior Alaska. *Canadian Journal*
552 *of Fisheries and Aquatic Sciences* **47**:2039-2048.

- 553 Hughes, N.F., Hayes, J.W., Shearer, K.A., and Young, R.G. 2003. Testing a model of drift-feeding using
554 three-dimensional videography of wild Brown Trout, *Salmo trutta*, in a New Zealand river.
555 Canadian Journal of Fisheries and Aquatic Sciences **60**:1462-1476.
- 556 Isaak, D.J., and nine coauthors. 2014. Applications of spatial statistical network models to stream data.
557 Wiley Interdisciplinary Reviews: Water 1(3):277-294.
- 558 Jenkins, A.R., and Keeley, E.R. 2010. Bioenergetic assessment of habitat quality for stream-dwelling
559 cutthroat trout (*Oncorhynchus clarkii bouvieri*) with implications for climate change and nutrient
560 supplementation. Canadian Journal of Fisheries and Aquatic Sciences **67**:371-385.
- 561 Kelly, L.H., Hay, J., Hughes, N.F., Goodwin, E., and Hayes, J.W. 2012. Flow related models for
562 simulating river hydraulics, invertebrate drift transport, and foraging energetics of drift-feeding
563 salmonids: user guide (version 1.1). Cawthron Report 922.
- 564 Lane, S.N., Chandler, J.H., and Richards, K.S. 1994. Developments in monitoring and modeling small-
565 scale river bed topography. Earth Surface Processes and Landforms **19**:349-368.
- 566 Leung, E.S., Rosenfeld, J.S., and Bernhardt, J.R. 2009. Habitat effects on invertebrate drift in a small
567 trout stream: implications for prey availability to drift-feeding fish. Hydrobiologia **623**:113-125.
- 568 Mobrand, L.E., Lichatowich, J.A., Lestelle, L.C., and Vogel, T.S. 1997. An approach to describing
569 ecosystem performance “through the eyes of salmon”. Canadian Journal of Fisheries and Aquatic
570 Sciences **54**:2964-2973.
- 571 Moore, K., Jones, K., and Dambacher, J. 2008. Methods for stream habitat surveys: Aquatic Inventories
572 Project, Oregon Department of Fish & Wildlife, Corvallis, OR. Unpublished paper on file at:
573 <http://oregonstate.edu/dept/ODFW/freshwater/inventory/pdffiles/habmethod.pdf> 67p. .

- 574 Moussalli, E., and Hilborn, R. 1986. Optimal stock size and harvest rate in multistage life history models.
575 Canadian Journal of Fisheries and Aquatic Sciences **43**:135-141.
- 576 Nislow, K.H., Folt, C.L., and Parrish, D.L. 1999. Favorable foraging locations for young Atlantic salmon:
577 Application to habitat and population restoration. Ecological Applications **9**:1085-1099.
- 578 NMFS. 2014. NOAA's National Marine Fisheries Service, Northwest Region, Endangered Species Act
579 Section 7(a)(2) Supplemental Biological Opinion. Consultation on remand for operation of the
580 federal Columbia River Power System. NOAA Fisheries Log Number: NWR-2013-9562.
- 581 NOAA. 2008. Supplemental Comprehensive Analysis of the Federal Columbia River Power System and
582 Mainstem Effects of the Upper Snake and other Tributary Actions.
- 583 NOAA. 2011. Five-year Review: Summary & Evaluation of Middle Columbia River Steelhead.
- 584 NPCC. 2009. Northwest Power and Conservation Council. Columbia River Basin fish and wildlife
585 program: 2009 amendments. Document no. 2009-09, Northwest Power and Conservation
586 Council, Portland, Oregon. Available: [www.nwcouncil.org/fw/program/program-2009-09-](http://www.nwcouncil.org/fw/program/program-2009-09-amendments/)
587 [amendments/](http://www.nwcouncil.org/fw/program/program-2009-09-amendments/) September 2013.
- 588 Pasternack, G.B., Gilbert, A.T., Wheaton, J.M., and Buckland, E.M. 2006. Error propagation for velocity
589 and shear stress prediction using 2D models for environmental management. Journal of
590 Hydrology **328**:227-241.
- 591 Peck, D.V., Lazorchak, J.M., Klemm, D.J., and Branch, R.E. 2001. Western pilot study field operations
592 manual for wadeable streams.
- 593 Piccolo, J.J., Hughes, N.F., and Bryant, M.D. 2008a. Development of net energy intake models for drift-
594 feeding juvenile coho salmon and steelhead. Environmental Biology of Fishes **83**:259-267.

- 595 Piccolo, J.J., Hughes, N.F., and Bryant, M.D. 2008b. Water velocity influences prey detection and capture
596 by drift-feeding juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (*Oncorhynchus*
597 *mykiss irideus*). *Canadian Journal of Fisheries and Aquatic Sciences* **65**:266-275.
- 598 Rader, R.B. 1997. A functional classification of the drift: traits that influence invertebrate availability to
599 salmonids. *Canadian Journal of Fisheries and Aquatic Sciences* **54**:1211-1234.
- 600 Roni, P., Hanson, K., and Beechie, T. 2008. Global review of physical and biological effectiveness of
601 stream habitat rehabilitation techniques. *North American Journal of Fisheries Management*
602 **28**:856-890.
- 603 Rose, K.A. 2000. Why are quantitative relationships between environmental quality and fish populations
604 so elusive? *Ecological Applications* **10**:367-385.
- 605 Rosenfeld, J.S., and Boss, S.M. 2001. Fitness consequences of habitat use for juvenile cutthroat trout:
606 energetic costs and benefits in pools and riffles. *Canadian Journal of Fisheries and Aquatic*
607 *Sciences* **58**:585-593.
- 608 Rosenfeld, J.S., Bouwes, N., Wall, C.E., and Naman, S.M. 2014. Successes, failures, and opportunities in
609 the practical application of drift-foraging models. *Environmental Biology of Fishes* **97**:551-574.
- 610 Scheuerell, M.D., Hilborn, R., Ruckelshaus, M.H., Bartz, K.K., Lagueux, K.M., Haas, A.D., and Rawson,
611 K. 2006. The Shiraz model: a tool for incorporating anthropogenic effects and fish-habitat
612 relationships in conservation planning. *Canadian Journal of Fisheries and Aquatic Sciences*
613 **63**:1596-1607.
- 614 Sharma, R., Cooper, A.B., and Hilborn, R. 2005. A quantitative framework for the analysis of habitat and
615 hatchery practices on Pacific salmon. *Ecological Modeling* **183**:231-250.

- 616 Shearer, K.A., Hayes, J.W., and Stark, J.D. 2002. Temporal and spatial quantification of aquatic
617 invertebrate drift in the Maruia River, South Island, New Zealand. *New Zealand Journal of*
618 *Marine and Freshwater Research* **36**:529-536.
- 619 Steffler, P., and Blackburn, J. 2002. Two-dimensional depth averaged model of river hydrodynamics and
620 fish habitat. *River2D user's manual*, University of Alberta, Canada.
- 621 Urabe, H., Nakajima, M., Torao, M., and Aoyama, T. 2010. Evaluation of habitat quality for stream
622 salmonids based on a bioenergetics model. *Transactions of the American Fisheries Society*
623 **139**:1665-1676.
- 624 Wall, C.E. 2014. Use of a net rate of energy intake model to examine differences in juvenile steelhead
625 (*Oncorhynchus mykiss*) densities and the energetic implications of restoration. M.Sc thesis,
626 Watershed Sciences Department, Utah State University, Logan, UT.
- 627 Weber, N. 2009. Development of a salmonid food availability monitoring protocol. M.Sc thesis,
628 Watershed Sciences Department, Utah State University, Logan, UT.
- 629 Weber, N., Bouwes, N., Jordan, C.E., and Jonsson, B. 2014. Estimation of salmonid habitat growth
630 potential through measurements of invertebrate food abundance and temperature. *Canadian*
631 *Journal of Fisheries and Aquatic Sciences* **71**:1158-1170.

632

633 **Tables and Figures**

634 *Tables*

635 Table 1. General characteristics of the 22 study reaches at the time of sampling. Standard error of mean
636 weight is shown in parenthesis. CC = Charley Creek, NFAC = North Fork Asotin Creek, SFAC = South
637 Fork Asotin Creek, and MFJDR = Middle Fork John Day River.

Reach Name	Mean Wetted Width (m)	Mean Thalweg Depth (m)	Wetted Area (m ²)	Water Surface Gradient	Drift Density (No·m ⁻³)	Discharge (m ³ ·s ⁻¹)	Mean Steelhead Weight (g)
CC1	3.4	0.22	604	0.009	0.6	0.263	13.4 (0.53)
CC2	3.6	0.20	557	0.023	1.2	0.180	13.9 (0.62)
CC3	3.4	0.19	633	0.029	1.0	0.212	16.2 (0.77)
CC4	3.5	0.22	619	0.021	2.0	0.220	19.1 (1.00)
NFAC1	7.9	0.35	1654	0.017	1.1	0.718	19.7 (1.51)
NFAC2	6.9	0.34	1418	0.008	0.7	0.662	26.4 (1.96)
SFAC1	4.7	0.20	857	0.018	10.5	0.120	16.6 (0.69)
SFAC2	3.7	0.22	635	0.029	1.9	0.146	18.0 (0.75)
SFAC3	4.9	0.20	876	0.028	2.1	0.103	19.4 (1.28)
Bridge Ck.	3.0	0.13	368	0.015	7.4	0.058	21.4 (3.83)
Hidaway Ck.	4.1	0.25	532	0.006	0.7	0.050	11.7 (1.0)
Camas Ck.	12.9	0.43	3537	0.004	2.2	0.290	17.1 (1.19)
Rock Ck.	6.7	0.50	1579	0.004	2.4	0.472	3.5 (0.18)
Service Ck.	2.1	0.32	233	0.002	0.5	0.183	13.9 (0.91)
Clear Ck.	10.3	0.37	2271	0.008	0.2	0.420	26.3 (2.50)
Thirtymile Ck.	6.1	0.29	999	0.008	7.4	0.125	28.0 (3.76)
Cummings Ck.	1.8	0.18	184	0.022	0.9	0.050	5.8 (0.66)
Granite Ck.	14.3	0.36	4683	0.018	0.6	1.033	6.9 (0.40)
Pine Ck.	6.1	0.20	773	0.007	5.1	0.031	11.5 (1.49)
SF Deer Ck.	2.0	0.35	268	0.007	0.7	0.245	20.1 (4.24)
MFJDR1	14.9	0.41	6056	0.004	1.3	1.257	42.7 (3.85)
MFJDR2	7.0	0.48	1268	0.004	1.3	0.370	27.4 (2.08)

640 Table 2. Stream tube and cross section spacing assignment criteria. Numbers of vertical and lateral stream
 641 tubes were based on stream size. Cross sections spacing (not shown in table) was 0.2 m for all reaches.

Vertical stream tube assignment		Lateral stream tube assignment	
<u>Mean thalweg depth</u>	<u>Vertical stream tubes</u>	<u>Mean wetted width</u>	<u>Lateral stream tubes</u>
≤ 0.25 m	5	≤ 6 m	1 per 0.25 m mean wetted width
> 0.25 m	1 per 0.05 m mean thalweg depth	> 6 m	1 per 0.33 m mean wetted width

642

643 *Figures*

644 Figure 1. Locations of the 22 study reaches in the Asotin Creek (A) and the John Day River (B)
645 watersheds.

646

647 Figure 2. River 2D depth and velocity predictions (A), predicted spatial variation in NREI (B), and predicted spatial variation in NREI showing
 648 predicted fish locations (C) for the NFAC1 reach.

Figure 3. Hydraulic model calibration (top) and validation (bottom) results for the CC1 reach depth (left) and velocity (right) predictions. One-to-one line shown in dashed grey.

Figure 4. Hydraulic model calibration (top) and validation (bottom) results for the NFAC1 reach depth (left) and velocity (right) predictions. One-to-one line shown in dashed grey.

Figure 5. Linear regression between observed and predicted steelhead densities. Results for the CC1 and NFAC1 reaches are shown by the star and diamond, respectively. One-to-one line shown as light grey with long dashes. Short-dashed, dark grey line represents removal of the reach with highest observed and predicted densities.

Figure 6. Observed steelhead density vs. proportion of suitable NREI locations (A). Observed biomass vs. mean predicted NREI (B).

Figure 7. Two stream segments, differing only in the spatial configuration of suitable habitat, illustrate the role of habitat configuration in determining stream capacity. The stream segments below could have identical mean NREI and proportion of suitable habitat, but might support different numbers of territorial fish because of the spatial arrangement of acceptable foraging locations.