NRC Research Press

ARTICLE

Design and monitoring of woody structures and their benefits to juvenile steelhead (*Oncorhynchus mykiss*) using a net rate of energy intake model

C. Eric Wall, Nicolaas Bouwes, Joseph M. Wheaton, Stephen N. Bennett, W. Carl Saunders, Pete A. McHugh, and Chris E. Jordan

Abstract: Despite substantial effort and resources being invested in habitat rehabilitation for stream fishes, mechanistic approaches to designing and evaluating how habitat actions influence the fish populations they are intended to benefit remain rare. We used a net rate of energy intake (NREI) model to examine expected and observed changes in energetic habitat quality and capacity from woody debris additions in a 40 m long study reach being treated as part of a restoration experiment in Asotin Creek, Washington. We simulated depths, velocities, and NREI values for pre-treatment, expected, and post-treatment habitat conditions, and we compared pre-treatment versus expected and pre-treatment versus post-treatment simulation results. The pre-treatment versus expected topography simulations suggested treatment would increase energetically favorable area, mean NREI, and capacity in the study reach. Pre-treatment versus post-treatment comparisons yielded similar predictions, though to smaller magnitudes, likely due to the short time span and single high-flow event between pre- and post-treatment data collection. We feel the NREI modelling approach is an important tool for improving the efficacy of habitat rehabilitation actions for stream fishes.

Résumé : Malgré des efforts et ressources considérables affectés à la restauration d'habitats pour les poissons de cours d'eau, les approches mécanistes de conception de tels efforts et d'évaluation de leur influence sur les populations de poissons visées demeurent rares. Nous avons utilisé un modèle de taux net d'apport énergétique (NREI) pour examiner les modifications prévues et observées de la qualité et de la capacité énergétiques de l'habitat découlant d'ajouts de débris ligneux dans un tronçon de 40 m de longueur traité dans le cadre d'une expérience de restauration dans le ruisseau Asotin (Washington, États-Unis). Nous avons simulé les profondeurs, vélocités et valeurs du NREI pour obtenir les conditions de l'habitat prétraitement, prévues et post-traitement et avons comparé les résultats des simulations prétraitement et prévues, et prétraitement et post-traitement. La comparaison des simulations pour le relief prétraitement et prévu donne à penser que le traitement accroîtrait la superficie favorable sur le plan énergétique, le NREI moyen et la capacité dans le tronçon à l'étude. Les comparaisons des résultats de simulations prétraitement et post-traitement ont produit des prédictions semblables, mais de moindre envergure, probablement en raison de la courte période de temps et du fait qu'il n'y ait eu qu'un seul évènement de débit élevé entre la collecte des données pré- et post-traitement. Nous estimons que l'approche de modélisation du NREI est un outil important pour améliorer l'efficacité des efforts de restauration d'habitat pour les poissons de cours d'eau. [Traduit par la Rédaction]

Introduction

Restoration and rehabilitation of fish habitat have become commonplace throughout the world in response to degradation caused by anthropogenic activities (Roni et al. 2008). In fact, the number of documented restoration projects has grown exponentially in recent years, with annual restoration spending likely exceeding $1 billion in the United States alone (Bernhardt et al. 2005). Unfortunately, the benefits of restoration are rarely evaluated or demonstrated, and many projects either lack monitoring altogether or they lack monitoring plans designed with sufficient power to identify cause–effect relationships between implemented actions and intended outcomes (Bernhardt et al. 2005; Doyle and Shields 2012; Katz et al. 2007; Roni et al. 2008). For those projects that have been monitored, the lack of a fish response may stem from improper designs that were not tested with mechanistic models to better understand any intended biological benefits (Bennett et al. 2016).

Historically, the physical habitat simulation system (PHABSIM) has been the most prominent family of modelling approaches used to predict effects of habitat manipulation on fish populations (Milhous and Waddle 2012; Reiser et al. 1989; Tharme 2003). These models typically aggregate information from habitat suitability curves representing abiotic factors — mainly depth, velocity, and substrate — to calculate a species- and life-stage-specific habitat suitability index. Despite their prevalence, PHABSIM-type models have been criticized for their focus on physical habitat variables when it is well-documented that fish alter habitat selection behavior in response to other factors such as food availability (Rosenfeld

Received 21 March 2016. Accepted 24 August 2016.

C.E. Wall,* S.N. Bennett, W.C. Saunders, and P.A. McHugh. Watershed Sciences Department, Utah State University, 5210 Old Main Hill, Logan, UT 84322, USA; Eco Logical Research, Inc., P.O. Box 706, Providence, UT 84332, USA.
N. Bouwes. Eco Logical Research, Inc., P.O. Box 706, Providence, UT 84332, USA.
J.M. Wheaton. Watershed Sciences Department, Utah State University, 5210 Old Main Hill, Logan, UT 84322, USA.
C.E. Jordan. Northwest Fisheries Science Center, National Oceanic and Atmospheric Administration, 200 SW 35th Street, Corvallis, OR 97331, USA.
Corresponding author: C. Eric Wall (email: c.eric.wall@gmail.com).
*Present address: Department of Watershed Sciences, 5210 Old Main Hill, NR 210, Logan, UT 84322, USA.

Published at www.nrcresearchpress.com/cjfas on 27 September 2016.

et al. 2005). Additionally, most PHABSIM-type model applications have been limited to flow-related habitat manipulations rather than changes pertaining to temperature regime, food availability, or bedform.

More recently, net rate of energy intake (NREI) models have used a variety of habitat metrics (usually depth, velocity, invertebrate drift concentration, and temperature) in combination with foraging and bioenergetics models to characterize the energetic quality of fish habitat (Hayes et al. 2007; Jenkins and Keeley 2010; Wall 2014). NREI models predict the energetic trade-offs of potential foraging positions by subtracting the estimated metabolic costs of swimming from predicted foraging gains. By accounting for both biotic and abiotic factors, NREI models may overcome some limitations of approaches that only consider physical habitat variables when predicting habitat use. For example, NREI models revealed seasonal habitat limitation for Atlantic salmon (*Salmo salar*) (Nislow et al. 1999, 2000) and size-specific responses to temperature change for cutthroat trout (Jenkins and Keeley 2010), insights that would have been difficult to realize if only physical habitat variables had been considered. Despite their potential, NREI model application to investigate consequences of habitat manipulation for fishes remains rare. This is unfortunate because NREI models could help illuminate mechanistic processes linking project design and ecological principles thought to influence target fish populations, increasing the likelihood of project success and facilitating the extrapolation of restoration approaches to novel locations.

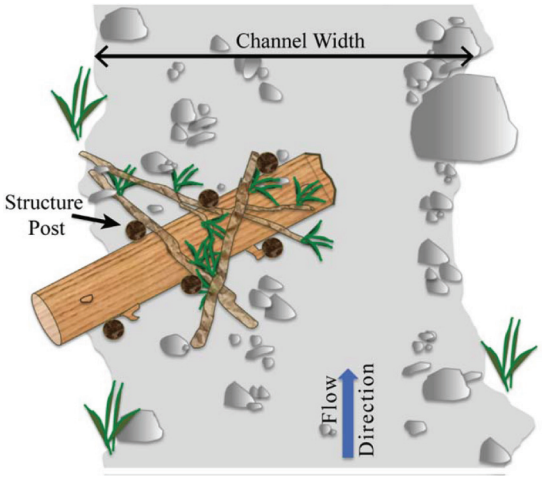
We used an adaptation of the NREI modelling approach described in Hayes et al. (2007) to link restoration design and fish energetics in the context of an ongoing stream restoration project in Asotin Creek, Washington, USA. First, we investigated the hypothesis that in-stream structures provide energetic benefits to juvenile steelhead (*Oncorhynchus mykiss*) at treatment sites by analyzing model predictions for pre-treatment and simulated post-treatment topographies. This part of our study demonstrates a method to examine mechanistic links between restoration design and target fish populations prior to project implementation. Second, we repeated the pre-treatment versus post-treatment analysis 6 months after large woody debris structures were installed, this time using the true post-treatment topography. This part of our study demonstrates use of NREI modelling as a tool to help understand and monitor channel response to in-stream structures after treatment.

Methods

Study area and restoration design

South Fork Asotin Creek is one of three streams involved in an experimental watershed restoration project designed to evaluate effectiveness of large woody debris structures as tools to increase salmonid production. The Asotin Creek basin is involved in an ongoing Intensively Monitored Watershed (IMW) project (Bennett et al. 2016) and is home to a steelhead population listed as threatened under the Endangered Species Act. Asotin Creek watershed is approximately 842 km² and is located in southeast Washington, USA. Asotin Creek is a tributary to the Snake River, characterized by coniferous forests and sagebrush steppe at higher and lower elevations, respectively. Our study occurred on a 40 m long section of South Fork Asotin Creek being treated as part of the overall restoration project. The Asotin Creek IMW restoration project uses a novel approach referred to as high-density large woody debris ($_{HD}$LWD). The $_{HD}$LWD method is described in detail in Camp (2015), but briefly, the method involves installation of woody structures using hand labor and focuses on building many small, dynamic structures with a decreased emphasis on structure stability relative to more permanent structure installation techniques. Wooden fence posts are driven into the stream bottom and used to temporarily secure logs in place, emulating woody debris recruited to the stream. Individual structures called bank-attached post-assisted log structures (PALS; Fig. 1), typically extend from the right or left bank to span 40%–70% of the total channel width. The restoration design hypothesized that a network of strategically placed PALS would act in concert to promote scour and deposition, creating a more complex array of habitat in treatment reaches (Wheaton et al. 2012). Potential stream channel responses included development of undercut banks, scour pools near the in-stream PALS ends, and eddy bar formation downstream of PALS (Fig. 2).

Fig. 1. Plan view post-assisted log structure illustration from the Asotin Creek restoration project design report. [Colour online.]

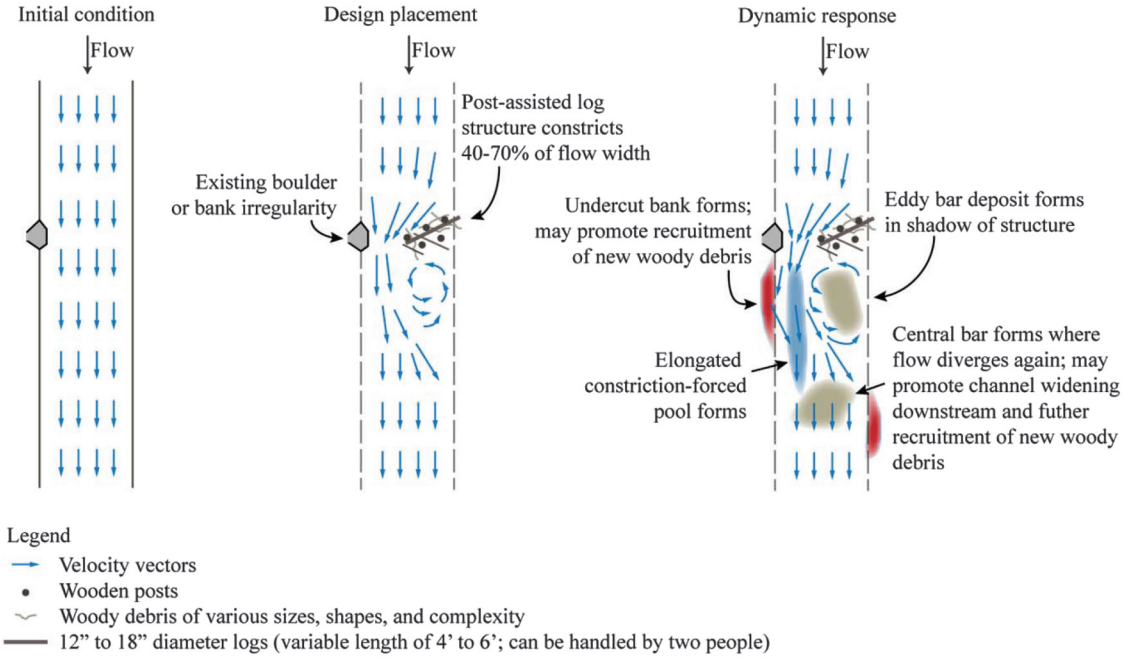


Modelling approach overview

We used an adaptation (Hayes et al. 2012) of the NREI modelling approach described in Hayes et al. (2007) to predict NREI and carrying capacity in the study reach under three habitat conditions: pre-treatment, expected topography, and post-treatment. We collected pre-treatment topographic data in early July 2012, prior to the restoration, which began in late July 2012 and continued through September of the same year. To simulate and analyze a treatment effect in the NREI model, we manipulated the pre-treatment topographic data to mimic hypothesized responses to restoration (e.g., scour and deposition). We refer to the simulated post-treatment topography as the "expected topography" hereinafter. In late winter 2013, 6 months after the restoration actions were completed, we collected as-built post-treatment topographic data to allow pre-treatment versus true post-treatment analyses.

We used a hydraulic model to simulate depths and velocities throughout the study reach, and we used the Stream Tubes program to prepare hydraulic model outputs for the foraging and swimming costs models. While Hayes et al. (2007) modelled dispersion of drifting prey items, we simplified drift modelling by assuming invertebrate drift concentrations (expressed as individuals·m^{-3}) were constant throughout the reach. Depth and velocity predictions from the hydraulic model served as inputs to foraging and swimming costs models that estimated the energetic profits of foraging and costs of swimming, respectively, at thousands of potential foraging locations throughout the study reach. The swimming costs model uses temperature, fish size, and water velocity as inputs, and the foraging model uses those three plus water depth, invertebrate drift concentration, size of drifting invertebrates, and height of foraging above the streambed. Gross rate of energy intake (GREI) predictions from the foraging model were adjusted to account for 30% losses due to wastes (Hughes et al. 2003; Hayes et al. 2007), and the model predicted NREI by subtracting swimming costs (SC) from adjusted GREI (i.e., NREI = (GREI × 0.7) – SC). Resulting NREI estimates have units of Joules per

Fig. 2. Example of hypothesized response to post-assisted log structure (PALS) 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 the installed structure and again at the second flow diversion. (Note: 1 inch = 2.54 cm; 1 foot = 0.304 m.) [Colour online.]



second and are estimates of the net energy balance a drift forager could obtain per unit time of foraging effort at each modelled foraging location. Finally, we generated an estimate of how many fish the reach could support by systematically comparing NREI predictions throughout the reach to a user-set minimum allowable value (see section on Pre-treatment topography, hydraulics, and NREI modelling below for more information).

The model simulated foraging, predicted NREI, and estimated carrying capacity for the pre-treatment, expected, and post-treatment topographies while holding invertebrate drift concentration, temperature, and fish size constant to isolate the influence of channel shape (e.g., as a result of restoration) on fish energetics and reach capacity as predicted by the model. We assessed spatial variation of depth, velocity, and NREI predictions for the pre-treatment versus expected and pre-treatment versus post-treatment topographies. We also compared predicted NREI distributions and carrying capacities for the same paired scenarios. The pre-treatment versus expected comparison was used to assess mechanistic links between the restoration design and fish populations prior to restoration. The pre-treatment versus post-treatment assessment was used to investigate energetic consequences of habitat manipulation resulting from the PALS treatments.

Pre-treatment topography, hydraulics, and NREI modelling

We collected a network of 3D points and breakline features (Bouwes et al. 2011) on 23 July 2012 using a total station (Nivo 5C, Nikon Corporation, Tokyo, Japan) to describe the shape of the stream channel and flood plain under pre-treatment conditions. We recorded the wetted perimeter, estimated discharge, and identified and delineated channel unit boundaries (Bouwes et al. 2011). For each channel unit, we visually estimated the percentage 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), cobble (64–250 mm), boulder (250–4000 mm), and bedrock (>4000 mm). We processed topographic data with GIS software to create digital elevation models (DEMs) of the stream channel and water surface and to generate polygon shapefiles for delineated channel units. Cell size in the resulting DEMs was 0.1 m by 0.1 m.

We modelled steady-state flow conditions using River2D and the methodology described by Steffler and Blackburn (2002). We used raster cell center coordinates from the streambed DEM as River2D's topographic inputs. We summed the products of the channel unit areas and substrate coverage percentages to estimate the portion of the 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 the study area. As an example, a reach with 50% coarse gravel and 50% cobbles would receive a roughness height estimate of 0.0985 m. We distributed River2D's computational nodes uniformly throughout the study area at an approximate spacing of 0.25 m, with inflow and outflow boundaries receiving additional nodes spaced approximately 0.1 m apart. Hydraulic modelling assumed no losses or gains from groundwater or tributaries, and we varied roughness height until differences between inflow and outflow and between predicted versus observed water levels were minimized.

We prepared the pre-treatment hydraulic model solution for the NREI model with the Stream Tubes program (Hayes et al. 2007). The Stream Tubes program divides flow laterally and vertically to create tubes of equal discharge separated longitudinally by cross-sections where NREI calculations occur. Users define the number of vertical and lateral stream tubes, the longitudinal distance between cross-sections, and the number of NREI estimates per cross-section. Using the recommendations of Kelly et al. (2012), we selected 14 horizontal stream tubes, five vertical stream tubes, 0.3 m cross-section spacing, resulting in 143 longitudinal cross-sections and 37 NREI estimates per cross-section. These values resulted in an NREI point density of approximately 60 estimates per square metre while satisfying the recommended settings and offering a balance of computational performance and spatial resolution. We also selected the default Stream Tubes setting for output with a logarithmic vertical velocity profile.

Table 1. Summary of net rate of energy intake (NREI) model inputs.

NREI model input	Value
Mean steelhead fork length	0.109 m
Mean steelhead mass	18.03 g
Invertebrate drift concentration	1.9 individuals·m^{-3}
Stream temperature	15.0 °C

To parameterize invertebrate drift concentration in the NREI model, we sampled invertebrate drift on 11 August 2011. We deployed two drift nets (1000 μm mesh, 40 cm tall × 20 cm wide mouth opening) side-by-side in a riffle near the upstream end of our study reach. Nets sampled drift between 1000 and 1230 h, were suspended 2 cm above the streambed to prevent benthic invertebrates from crawling in, and also extended above the water surface to capture drifting terrestrial invertebrates. Using a depth rod and a Marsh-Mcbirney Model 2000 Flo-mate (Marsh-Mcbirney Inc., Maryland, USA), we measured water depth and velocity in each net mouth at the time of deployment and at the end of sampling. We measured velocity at a point centered laterally in the net mouth and at 60% of the depth from the water surface to the bottom of the net mouth. At the end of sampling, we transferred net contents to jars containing 95% ethanol. In the lab, we pooled the nets' contents and sorted individuals into 3 mm family-level size classes. Volume of water filtered by each net was calculated as mean net depth (m) × net width (m) × mean net mouth velocity (m·s^{-1}) × sampling duration (s). We calculated drift concentration by dividing the total number of invertebrates in both nets by the total volume of water filtered (Table 1). Measured drift concentration later served as an input to the foraging model, which uses drift concentration to predict capture success. After predicting capture successes, the foraging model calculates the energy content of captured prey items in Joules as described in Hughes et al. (2003) using equations from Smock (1980).

To satisfy the model's temperature and fish size inputs, we used a combination of IMW monitoring data, underwater video, and snorkeling observations. We estimated an appropriate summer baseflow temperature by taking the mean of 15 min readings from in-stream temperature loggers on the day of a summer electrofishing survey in the study reach (Table 1). Electrofishing was conducted as part of separate ongoing IMW research. Mean steelhead length and mass from the electrofishing survey were used to satisfy the model's fish size input requirements (Table 1). Through video and snorkeling, we observed fish maintaining positions close to the bed where water velocity was slower (E. Wall, personal observation), so we chose 5 cm as the height above the bed for NREI calculations.

We estimated pre-treatment NREI and carrying capacity using the process described in Kelly et al. (2012), summarized below. Starting with the most upstream cross-section, the model estimated NREI and evaluated predictions relative to a user-set minimum value. We used NREI ≥ 0.0 J·s^{-1} as our threshold for fish placement because this value implies fish maintaining mass. If the highest NREI prediction on the cross-section being evaluated equaled or exceeded the user-set threshold, the model recorded that position as being capable of supporting a fish and moved to the next downstream cross-section to repeat the process. Once all cross-sections were evaluated, the number of locations recorded as being capable of supporting fish served as an estimate of carrying capacity for the reach. Given that fish need an energy surplus (i.e., NREI > 0.0 J·s^{-1}) to grow and reproduce, our selected threshold of 0.0 J·s^{-1} might seem too low. However, fish in the study reach are often observed to lose mass over summer baseflow conditions, which suggests that a low threshold such as 0.0 J·s^{-1} is appropriate for modelling energetics during a potentially stressful period.

Table 2. Summary of topographic change characteristics associated with post-assisted log structures in pilot experiments.

Change characteristic	Observed range (m)	Mean value (m)	*n*
Erosion length	3.0–19.0	10.4	10
Erosion width	0.5–3.7	2.3	10
Erosion depth	0.05–0.7	0.3	10
Deposition length	2.0–8.0	3.9	12
Deposition width	1.0–3.5	1.9	12
Deposition height	0.1–0.8	0.2	12

Expected topography, hydraulics, and NREI modelling

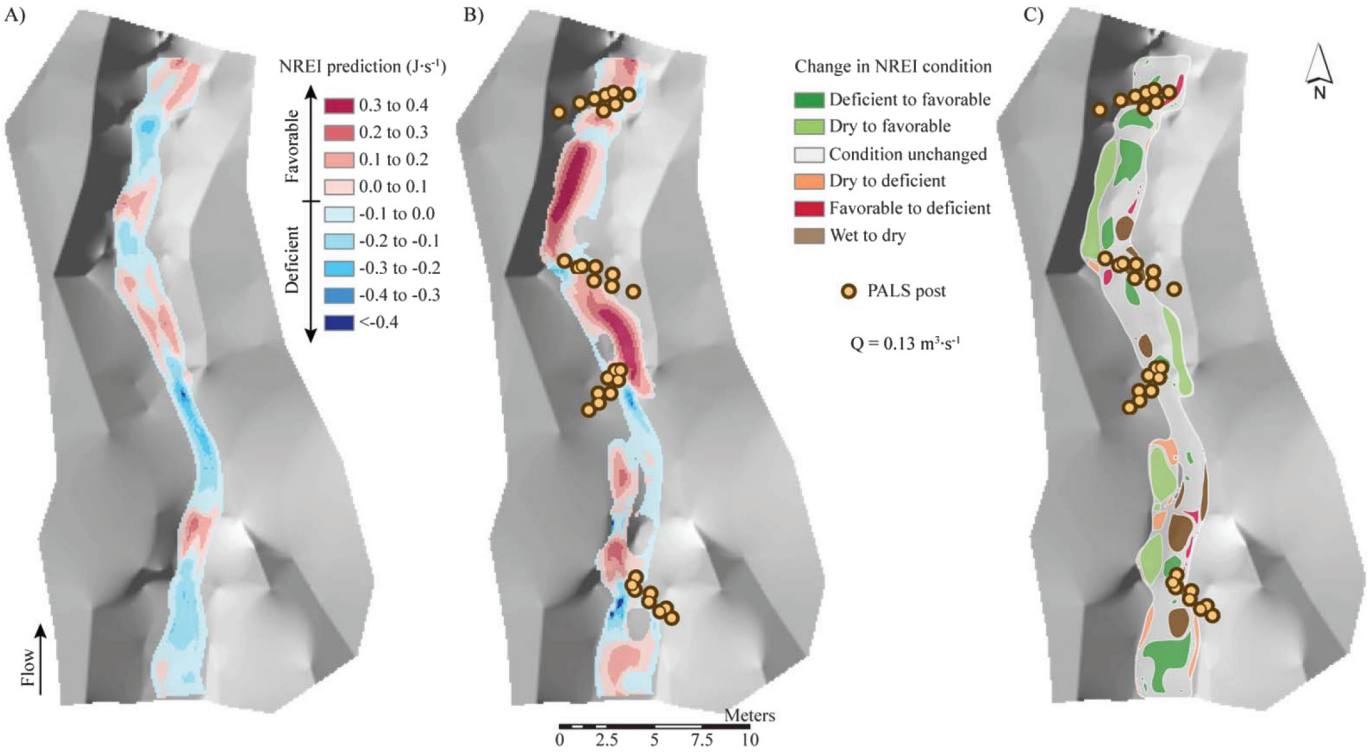
We integrated information from multiple sources to create the reach's expected (i.e., simulated post-treatment) topography. First, we summarized results from 1-year-old pilot PALS experiments in the Asotin Creek basin by measuring the length, width, and depth or height of PALS-related erosional or depositional features using GIS software (Table 2). We characterized feature lengths by measuring along each feature's centerline in the streamwise direction. We characterized feature widths by taking the mean of multiple measurements across each feature in the cross-stream direction. We characterized feature depth (or height) by measuring erosional or depositional magnitude in four to five locations near the deepest (or highest) points and calculating the mean. Second, we manipulated the pre-treatment DEM in a manner consistent with the pilot experiment summaries to create the expected post-treatment topography for NREI simulation. To accomplish this, we referenced the restoration design for intended PALS locations and their hypothesized channel responses (Fig. 2), and then we simulated erosional and depositional magnitudes consistent with the pilot experiment summaries in those locations. We simulated the individual PALS posts by adding 0.4 m, the mean post height in pilot PALS experiments, to DEM cell elevations where posts were to be installed. We added 0.3 m to the elevation of any raster cell in the interior of the modelled PALS to simulate debris accumulation at PALS bases. Woody debris woven through real-life PALS increases flow resistance, so we increased roughness height in the simulated PALS interiors to 0.4 m, the mean height of PALS posts. Because the summary of the pilot PALS experiments took place after PALS had been in place 1 year, the finished expected topography should be considered to represent potential channel change after about 1 year with sufficient high-flow periods to drive channel restructuring.

We estimated flow patterns for the expected topography in River2D using identical methods as for the pre-treatment flow simulation, reusing the pre-treatment boundary conditions (e.g., discharge and water surface elevation) during hydraulic modelling. Stream Tubes, NREI modelling, and estimation of carrying capacity were all conducted with identical input values as for the pre-treatment simulations.

Post-treatment topography, hydraulics, and NREI modelling

We collected true post-treatment data on 13 February 2013, 6 months after PALS installation. We used identical surveying and discharge measurement methods as for the pre-treatment data collection to describe post-treatment streambed topography and estimate discharge. We also collected (*XYZ*) points on the top-center of each installed PALS post, on the bank-side and stream-side endpoints of the top layer of woody debris spanning each PALS, and around PALS bases. We began with a DEM interpolated from the (*XYZ*) points collected on the streambed and floodplain and augmented the surface using (*XYZ*) points collected in or on PALS to account for PALS in the post-treatment DEM post hoc. To account for individual PALS posts, we added the surveyed post heights to DEM cell elevations where PALS had been installed. We

Fig. 3. Net rate of energy intake (NREI) predictions for the pre-treatment (A) and expected (B) topographies and associated categorical NREI condition changes (C). [Colour online.]



raised DEM cell elevations in PALS interiors by 0.1 m, the mean debris accumulation at PALS bases at the time of the post-treatment survey. To account for increased flow resistance through PALS, we increased roughness height in PALS interiors to the mean height of each structure.

We estimated flow patterns for the post-treatment topography using identical methods as for the pre-treatment flow simulation, except that we used the post-treatment boundary conditions (i.e., discharge, downstream water surface elevation). Stream Tubes, NREI modelling, and estimation of carrying capacity were conducted with identical input values as for the pre-treatment and expected topography simulations. Pre- and post-treatment topography surveys were conducted at different discharges ($Q = 0.13$ and 0.24 $m^3 \cdot s^{-1}$, respectively). To enable a pre- versus post-treatment comparison at a single discharge value (i.e., to control for the effects of discharge on NREI and carrying capacity predictions), we resimulated hydraulics, NREI, and carrying capacity for the pre-treatment topography at the higher discharge using the calibrated pre-treatment hydraulic model.

Analysis

We assessed differences between pre-treatment and expected topographies and between pre-treatment and post-treatment topographies using four analyses. First, we mapped categorical NREI prediction changes to provide spatial context for changed areas of the study reach. For example, we delineated areas that had pre-treatment NREI < 0.0 $J \cdot s^{-1}$ (i.e., areas where the model predicted fish should lose mass; hereinafter "energetically deficient") but were predicted to provide at least a maintenance ration (i.e., predicted NREI ≥ 0.0 $J \cdot s^{-1}$; hereinafter "energetically favorable") following simulated or actual restoration. Second, we compared pre-treatment versus expected and pre-treatment versus post-treatment carrying capacity predictions to examine how changes in topography might influence fish abundance. Third, we differenced the depth, velocity, and NREI prediction rasters to characterize the spatial arrangement and magnitude of changes in these metrics resulting from changes to topography and the PALS structures themselves. Fourth, we examined distributions of depth, velocity, and NREI predictions to look for shifts following the simulated or actual topographic changes. Simulations for the pre-treatment versus expected analyses were conducted using the pre-treatment discharge, while simulations for the pre-treatment versus post-treatment analyses were conducted using the post-treatment discharge.

Results

Pre-treatment versus expected topography

Approximately 22 m^2 (33%) of the pre-treatment wetted area was predicted to be energetically favorable. This figure increased to approximately 48 m^2 (63%) after simulating restoration, an increase of 118% by area. Approximately half of the newly created energetically favorable habitat resulted from previously dry areas being eroded during simulated treatment, with the remainder having changed from being energetically deficient in the pre-treatment simulation to being energetically favorable in the expected topography (Fig. 3C). The increase in favorable habitat coincided with an increase in predicted carrying capacity from 71 to 127 fish, an increase of 79%.

Changes to River2D depth predictions were primarily concentrated in areas of simulated erosion and deposition, though the model also predicted slight pooling upstream of three of the four simulated PALS (Fig. 4A). Depth predictions for the expected topography displayed a higher (i.e., deeper) mean (0.14 m) and increased variability (standard deviation (SD) = 0.10 m) when compared with pre-treatment simulation predictions (mean = 0.10 m, SD = 0.06 m; Figs. 5A). On average, wetted raster cells were predicted to be 0.05 m deeper in the expected topography simulation.

The majority of the pre-treatment wetted channel was predicted to experience slower velocities following simulated restoration, with the exceptions primarily being areas of simulated erosion that had previously been dry (i.e., velocity = 0.0 $m \cdot s^{-1}$;

Fig. 4. Spatial arrangement and magnitude of changes to depth (A), velocity (B), and NREI (C) predictions for the pre-treatment versus expected topography assessment. [Colour online.]

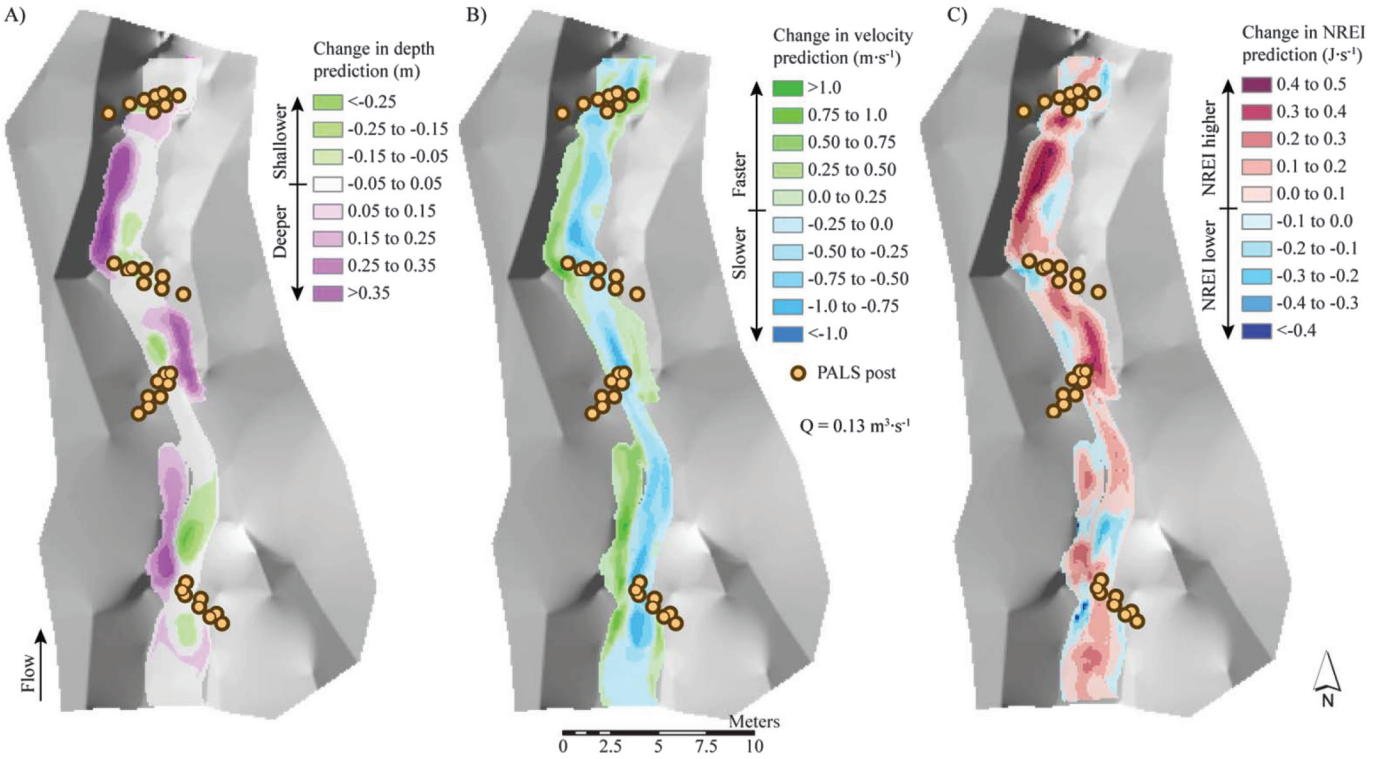


Fig. 4B). Velocity predictions for the expected topography displayed lower mean (0.35 m·s^{-1}) and variability (SD = 0.23 m·s^{-1}) compared with predictions for the pre-treatment topography (mean = 0.52 m·s^{-1}, SD = 0.28 m·s^{-1}; Fig. 5B). On average, wetted raster cells were predicted to be 0.08 m·s^{-1} slower under the expected topography conditions.

Deeper and slower flow patterns generally resulted in increased NREI predictions for the expected topography relative to the pre-treatment simulation (Fig. 4C). The mean NREI prediction improved from a net negative value (–0.03 J·s^{-1}) to a net positive value (0.06 J·s^{-1}) following simulated restoration (Fig. 5C). Predictions for the expected topography also displayed slightly higher variability (SD = 0.13 J·s^{-1}) compared with pre-treatment predictions (SD = 0.10 J·s^{-1}). On average, raster cell NREI values were predicted to be 0.07 J·s^{-1} higher in the expected topography simulation.

Pre-treatment versus post-treatment topography

Approximately 24 m^2 (30%) of the pre-treatment wetted area was predicted to be energetically favorable, as compared with 47 m^2 (52%) for the true post-treatment topography and flow conditions, an increase of 96%. While a small portion of the newly created favorable habitat resulted from erosion in the study reach, the majority changed from being energetically deficient under pre-treatment topography conditions to being energetically favorable after restoration (Fig. 6C). Predicted carrying capacity increased from 81 to 107 fish, an increase of 32%.

Changes to River2D depth predictions were primarily concentrated in areas of erosion and deposition (Fig. 7A), though the effects were smaller for the pre-treatment versus post-treatment comparison than for the pre-treatment versus expected topography comparison. Post-treatment depth predictions displayed a higher mean (0.15 m) and increased variability (SD = 0.08 m) when compared with pre-treatment predictions (mean = 0.13 m, SD = 0.07 m; Fig. 8A). On average, wetted raster cells in the post-treatment simulation were predicted to be 0.03 m deeper following restoration.

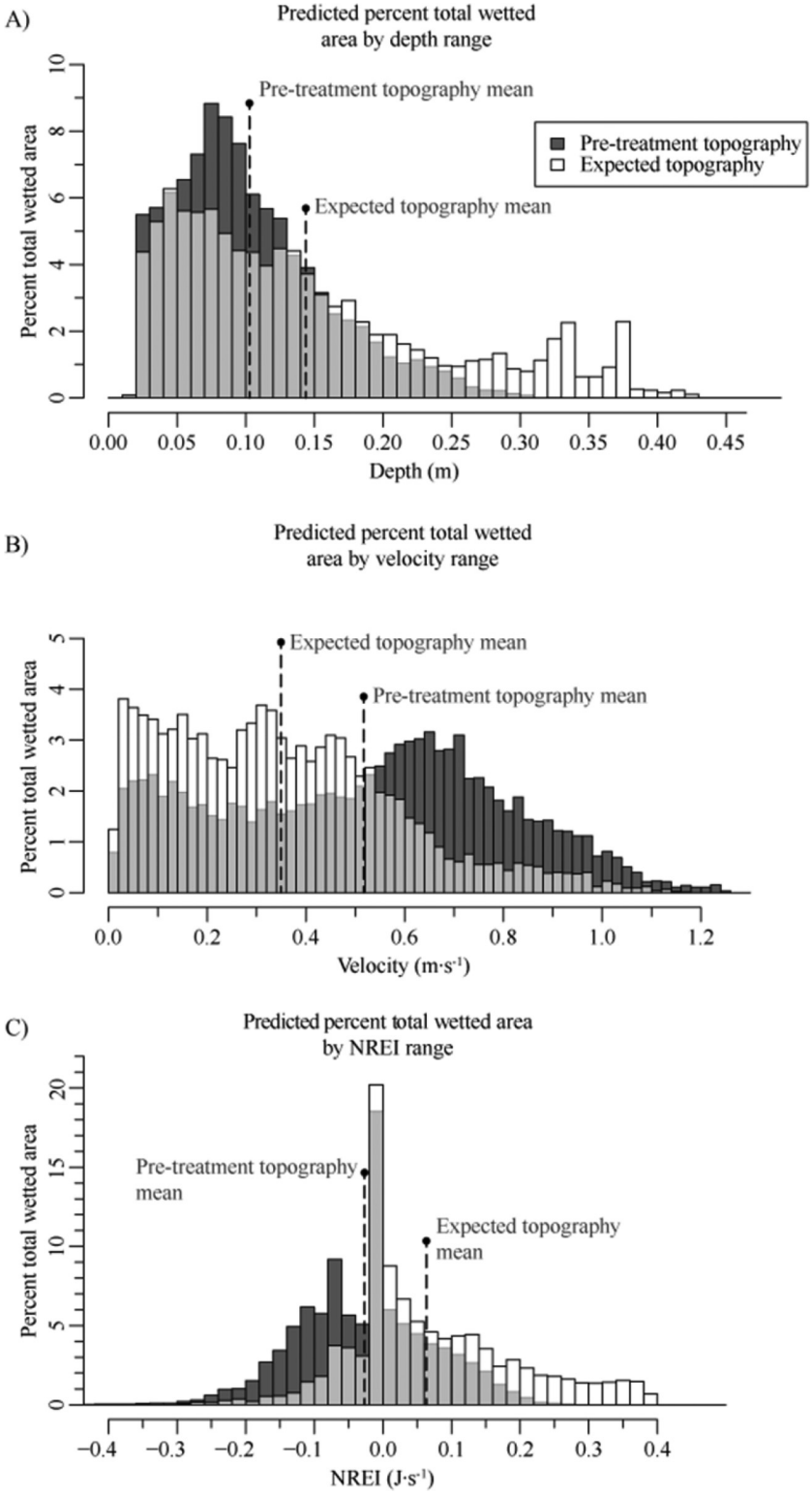
The majority of the wetted channel was predicted to experience slower velocities after restoration, with the exceptions primarily being areas that had previously been dry (Fig. 7B). Velocity predictions for the post-treatment topography displayed lower mean (0.54 m·s^{-1}) and variability (SD = 0.32 m·s^{-1}) compared with the pre-treatment predictions (mean = 0.66 m·s^{-1}, SD = 0.36 m·s^{-1}; Fig. 8B). On average, wetted raster cells in the post-treatment simulation were predicted to be 0.04 m·s^{-1} slower than those in the pre-treatment simulation.

The NREI model predicted increased mean NREI for the study reach and a shift in the distribution of predicted NREIs toward higher values after treatment (Figs. 7C, 8C). Mean NREI prediction increased from –0.05 to 0.015 J·s^{-1} (SD = 0.12 J·s^{-1} for both distributions; Fig. 8C). The majority of the wetted area had higher NREI predictions after treatment (Fig. 7C). On average, raster cells were predicted to be 0.05 J·s^{-1} higher after treatment.

Discussion

Foraging and bioenergetics modelling approaches, such as the NREI modelling described here, hold promise in providing a mechanistic prediction of how salmonids forage and occupy streams at multiple scales (Rosenfeld et al. 2014). NREI models have been demonstrated to predict individual foraging positions (Guensch et al. 2001; Hayes et al. 2007; Hughes and Dill 1990), fish biomass in pool and riffle channel units (Jenkins and Keeley 2010), fish biomass in 30–450 m long stream segments (Urabe et al. 2010), and fish density in 100–400 m stream reaches (Wall et al. 2016). Estimates of NREI are often based on depth and velocity measurements (e.g., Urabe et al. 2010), providing a static representation of habitat that can be time-consuming to collect. However, some studies have coupled NREI and hydraulic models (e.g., Booker et al. 2004; Guensch et al. 2001; Hayes et al. 2007; Wall et al. 2016) to offer a powerful and flexible framework for investigating alternative habitat conditions that may be influenced by flow management or restoration (Hayes et al. 2016).

Fig. 5. Depth (A), velocity (B), and NREI (C) prediction distributions for the pre-treatment versus expected topography assessment. Light gray indicates areas of overlap in the two distributions.



Large wood is commonly used to improve stream fish habitat throughout the world (Roni et al. 2015), including in the Pacific Northwest where woody debris addition is one of the most common restoration approaches (Katz et al. 2007). While structures are often engineered to withstand large flood events or create specific geomorphic and hydraulic responses, quantitative predictions of how the resulting structures might impact fish are rare. To help address this shortcoming, we have used NREI modelling to offer mechanistic insight into the hydraulic and energetic consequences of installing PALS-type wood structures to improve stream habitat for drift-feeding steelhead. To investigate the restoration's anticipated fish response, we modelled and then con-

Fig. 6. NREI predictions for the pre-treatment (A) and post-treatment (B) topographies and associated categorical NREI condition changes (C). [Colour online.]

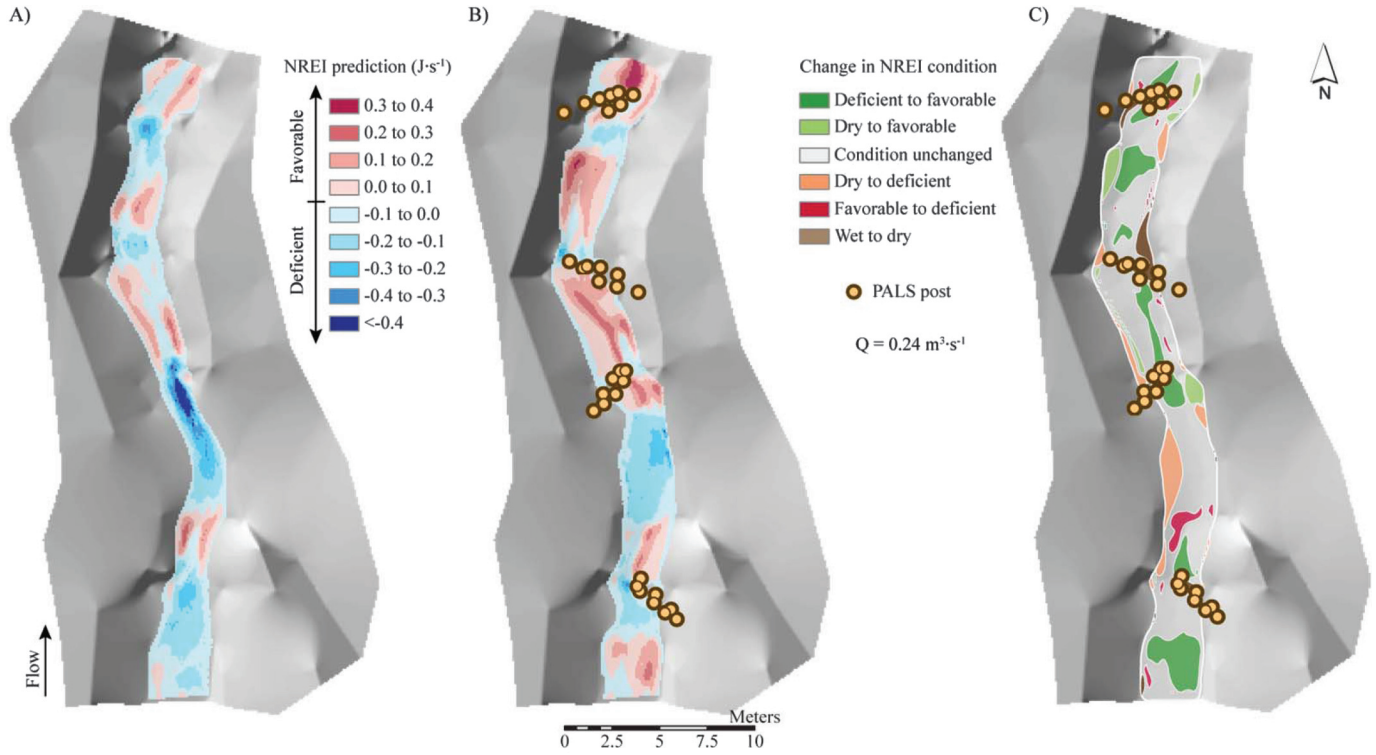
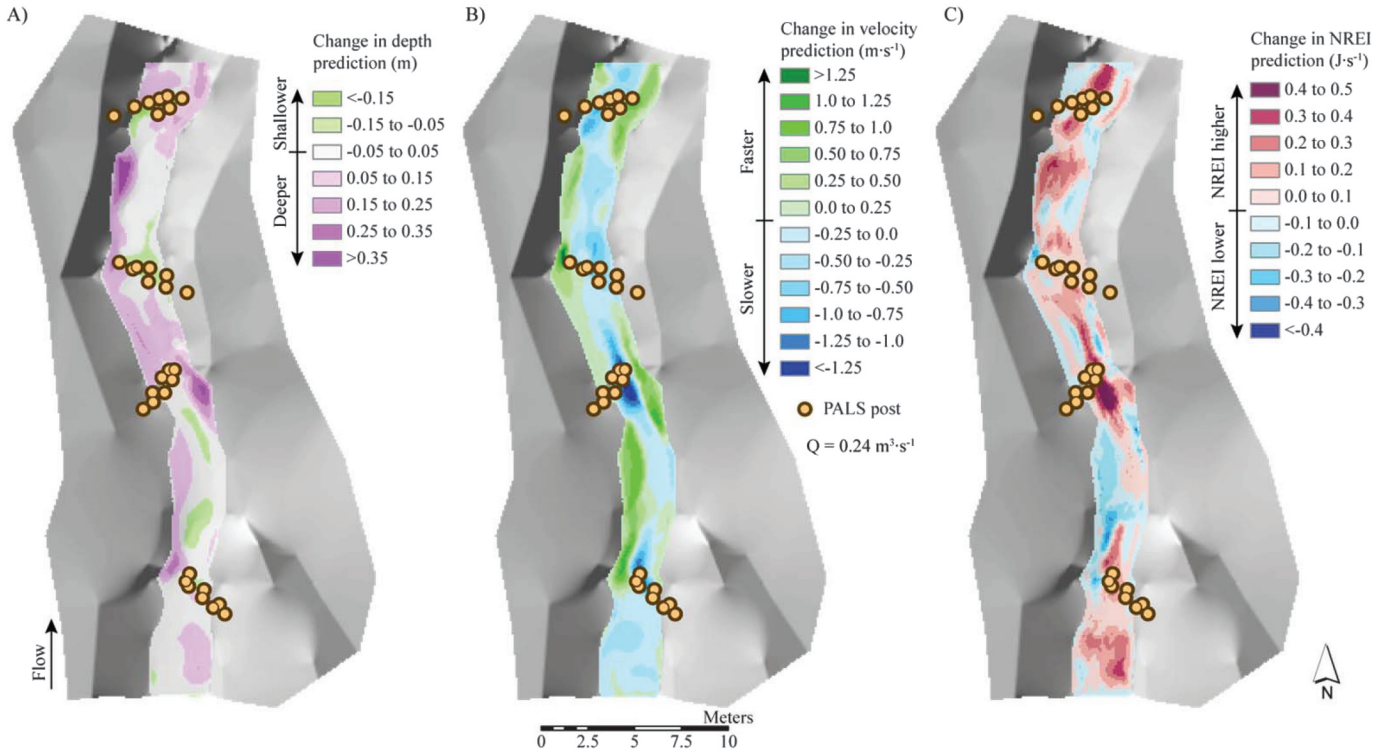
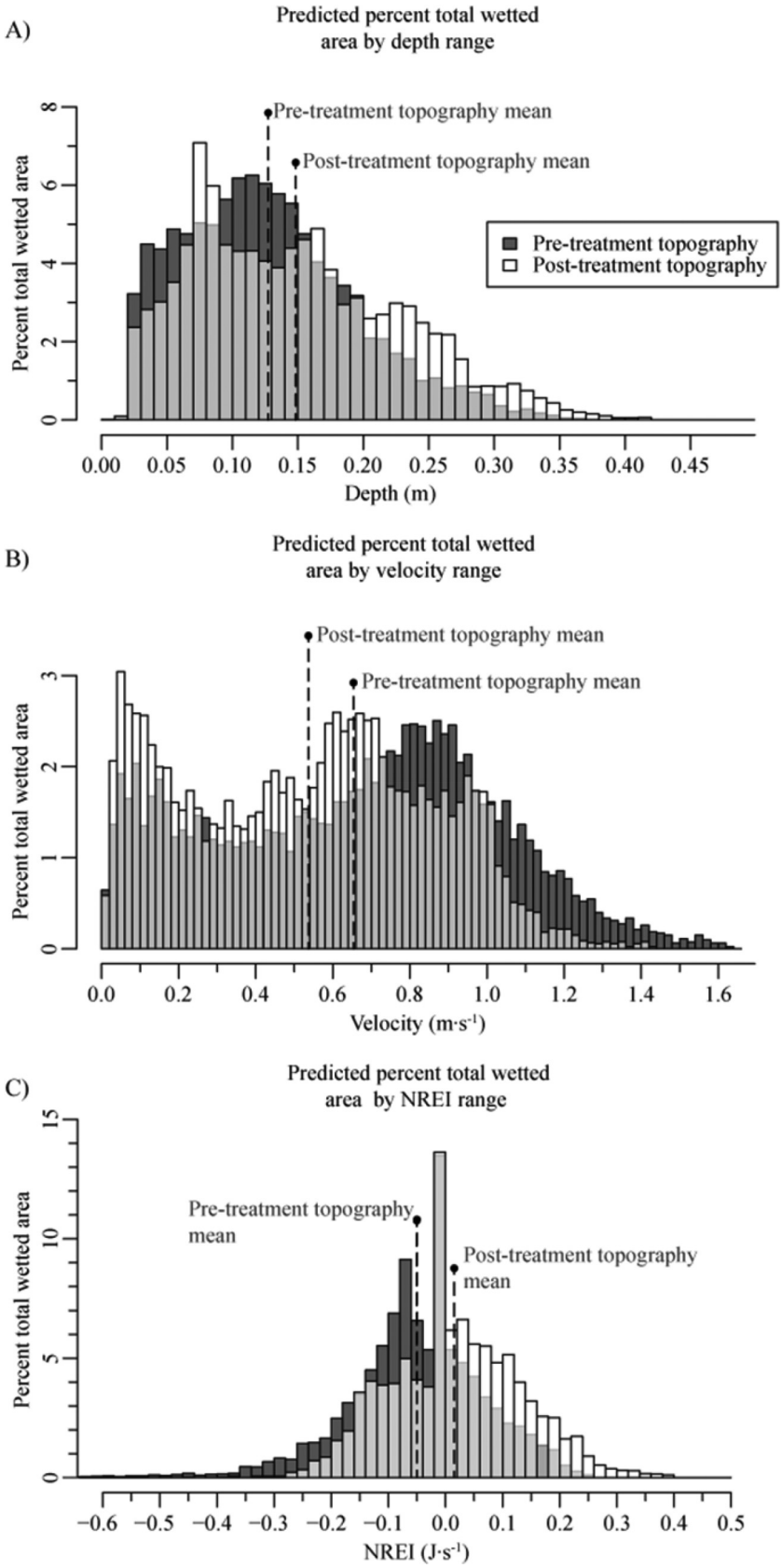


Fig. 7. Spatial arrangement and magnitude of changes to depth (A), velocity (B), and NREI (C) predictions for the pre-treatment versus post-treatment topography assessment. [Colour online.]



trasted hydraulics and NREI for pre-treatment, expected (i.e., simulated post-treatment), and actual post-treatment habitat conditions. We used raster differencing to quantify the areas and magnitudes of changes to depth, velocity, and NREI, and we used classification of categorical NREI changes (e.g., from dry to energetically favorable) to provide further context. Holding fish size, temperature, and prey concentration constant across simulations, our results suggested restoration increased energetically

Fig. 8. Depth (A), velocity (B), and NREI (C) prediction distributions for the pre-treatment versus post-treatment topography assessment. Light gray indicates areas of overlap in the two distributions.



favorable reach area, mean NREI, and rearing capacity in the study area. Our results demonstrate that NREI modelling can improve understanding of how proposed habitat actions might influence target fish populations, which can be difficult and costly to assess empirically in a before–after project implementation context.

The effects of wood structures on both physical stream habitat and fish populations have been studied extensively (Roni et al. 2015; Stewart et al. 2009; Whiteway et al. 2010). For example, in a 211-study meta-analysis, Whiteway et al. (2010) concluded in-stream structures generally increased mean depth, cover, wetted surface area, and salmonid density and biomass in treatment areas. While studies have reported generally positive effects of in-stream structures on salmonids (Roni et al. 2015), the question of how or why fish density increases in response to in-stream structures is still a growing area of research. Large wood has been shown to provide velocity shelters (Shirvell 1990) fish can exploit to minimize metabolic costs of swimming and maximize NREI (Fausch 1993). In-stream structures have also been credited with promoting visual isolation and reducing defended territory sizes (Imre et al. 2002), thus decreasing time and energy expended during aggressive behaviors and ultimately increasing NREI (Gustafsson et al. 2012; Sundbaum and Näslund 1998). Another possible explanation for energetic benefits provided by in-stream structures is that deeper foraging habitat created by some in-stream structures (e.g., pools) provides important and scarce foraging areas for relatively larger individuals in otherwise shallow streams where foraging may be limited by depth availability (i.e., where reactive distance exceeds stream depth; Rosenfeld and Taylor 2009). In addition to velocity shelters, visual isolation, and new or different foraging opportunities, wood in streams can also provide fish cover. Kawai et al. (2014) found that accounting for cover (woody materials, grasses, undercut banks) improved an already significant predictive model relating observed biomass and NREI. Their findings suggest that further study of the interactive effects of both cover and energetic improvements provided by in-stream structures may be warranted.

Our study used a combination of spatially explicit hypotheses and measurements to evaluate how changes to channel shape and site hydraulics as a result of wood structure installation would influence spatially explicit NREI values and capacity. Because abundance for this ESA-listed population of anadromous *O. mykiss* can be heavily influenced by factors outside the study area (e.g., ocean rearing and mainstem Columbia River migration conditions; Schaller et al. 2014), and because assessments of restoration effectiveness require long-term monitoring commitments (e.g., Bennett et al. 2016), we could not validate our pre- versus post-restoration predictions using actual fish observations. The post-treatment predicted capacity was less than the corresponding prediction for the expected topography; however, this is not surprising because the study reach's PALS rely on channel-shaping flow events to effect topographic change (Bennett et al. 2016), and only one moderate flow event occurred in the short period between pre- and post-treatment data collection. Thus, we anticipate additional capacity increases as the channel continues to evolve in response to restoration. We also note that because our modelling does not include other possible benefits of wood (e.g., predator refugia, competition mitigation), our estimates of salmonid habitat quality improvement may be conservative.

As suggested by others (Hayes et al. 2016; Rosenfeld and Taylor 2009), the interaction of food availability and hydraulics is critical to the prediction of habitat use by salmonids. We assumed that drift concentration (individuals·m^{-3}) was constant throughout the study reach, an assumption that has been made by other studies as well (e.g., Hughes and Dill 1990; Jenkins and Keeley 2010; Urabe et al. 2010), often in small systems where high relative roughness creates turbulence that encourages hydraulic mixing (Leung et al. 2009). Nonetheless, our assumption may underestimate fine-scale drift variation in the study area (Shearer et al. 2002), and treating drift concentration as constant also ignores the effects of drift depletion by foraging fish, possibly inflating both ambient food availability and rearing capacities in the model. An alternative viewpoint, however, is that the drift samples collected for this research were collected in the presence of active competition for food resources, suggesting the drift value we used in our simulations inherently represents the results of competition (Rosenfeld et al. 2014). An important clarification about the assumption of constant drift concentration is that it still allows for variability in prey encounter rates throughout the reach due to spatial variability in hydraulics. For example, because drift concentration is standardized to water volume in the model, it allows high-velocity areas with correspondingly high discharge throughput to convey greater numbers of drifting prey items compared with lower throughput areas. Nonetheless, our capacity predictions may be optimistic if exploitative competition strongly regulates drift densities. Regardless, however, our assumption of uniform drift was a trade-off necessary to facilitate the development of an NREI framework that could be applied here and as part of broader monitoring and modelling contexts.

We believe our NREI modelling approach to be flexible and capable of lending valuable modelling insights to applications dealing with different restoration goals or spatiotemporal extents than those presented here. For example, in addition to hydraulics and physical habitat, both temperature and drift concentration are explicitly accounted for in the model, so restoration projects focusing on water temperature (e.g., restored riparian shading) or having the potential to alter food regimes (e.g., carcass additions; Claeson et al. 2006) could easily implement our approach as long as expected responses could be predicted (e.g., Heat Source; Boyd and Kasper 2003) or observed changes could be documented. Investigating the energetic consequences of different discharge regimes would also be possible, and recent research highlighted the interplay of variable discharge and drift rates in NREI modelling (Hayes et al. 2016). While we chose to consider our pre- and post-treatment simulations as end points representing the sum effects of multiple, channel-forming events, our approach could also be used to investigate or document intermediate steps along a channel's response to treatment. Inclusion of hydraulics, temperature, food availability, and fish size as inputs is a clear strength of NREI modelling because it allows for evaluation of the relative importance of these inputs in different seasons, under contrasting regimes, or across systems. For example, Nislow et al. (1999, 2000) and Jenkins and Keeley (2010) were able to identify seasonal differences in the quantity of suitable habitat available for Atlantic salmon and cutthroat trout (*Oncorhynchus clarkii*), respectively. In a study investigating the relative influence of food availability and physical habitat structure on energetic habitat quality, Rosenfeld and Taylor (2009) offered that nutrient addition may be as, or more, cost-effective than adding in-stream structures, but that combining both might provide the most benefits because of their synergistic, rather than additive, effects. With regards to spatial extent, our simulations were limited to a single reach of the Asotin Creek IMW experimental restoration. However, we believe a strategic combination of detailed NREI modelling and rapid assessment techniques could aid in monitoring habitat change over large areas. As one potentially fruitful area of future research, detailed NREI modelling might highlight important geomorphic features or feature sequences (e.g., pools or the transition zones between fast and slow water areas, respectively) that are often associated with high NREI values. Rapid assessments inventorying habitat or cataloging habitat change could then be used to provide energetic context over larger spatial extents. By simply manipulating the inputs of interest or strategically combining NREI model outputs with other data sources and analyses, we believe NREI modelling can provide valuable insight into fish energetics across a variety of applications and spatial extents.

Our modelling approach provides a straightforward and flexible methodology for using NREI simulations to explore the influence of physical habitat on fish energetics both before and after project implementation. Incorporating results from pilot restoration experiments lent realism to our simulations, but our approach could be extended to investigate any design feature that can be represented realistically with 3D topography. In addition, NREI simulation could also be used to investigate alternative temperature, food availability, or discharge scenarios. Simulations used in the spirit of our approach should be designed to mimic planned restoration actions as closely as possible, and they should be coupled with explicit, testable hypotheses about potential responses of the stream environment and fish populations to planned treatments. To have maximum value and avoid spurious interpretation, such an effort should be combined with appropriate monitoring efforts in a design–predict–interpret adaptive management framework (Bouwes et al. 2016) to improve understanding of proposed habitat actions and maximize chances for project success.

Acknowledgements

Financial support for this work was provided by the Asotin Creek Intensively Monitored Watershed project 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 authors thank Reid Camp and Andy Hill for providing field support that made this project possible and Eric Goodwin for support with the Stream Tubes program and the foraging model. We are also thankful for the thoughtful comments of two anonymous reviewers on an earlier version of this manuscript.

References

Bennett, S., Pess, G., Bouwes, N., Roni, P., Bilby, R.E., Gallagher, S., Ruzycki, J., Buehrens, T., Krueger, K., Ehinger, W., Anderson, J., Jordan, C., Bowersox, B., and Greene, C. 2016. Progress and challenges of testing the effectiveness of stream restoration in the Pacific Northwest using intensively monitored watersheds. Fisheries, **41**(2): 92–103. doi:10.1080/03632415.2015.1127805.

Bernhardt, E.S., Palmer, M.A., Allan, J.D., Alexander, G., Barnas, K., Brooks, S., Carr, J., Clayton, S., Dahm, C., Follstad-Shah, J., Galat, D., Gloss, S., Goodwin, P., Hart, D., Hassett, B., Jenkinson, R., Katz, S., Kondolf, G.M., Lake, P.S., Lave, R., Meyer, J.L., O'Donnell, T.K., Pagano, L., Powell, B., and Sudduth, E. 2005. Synthesizing U.S. river restoration efforts. Science, **308**(5722): 636–637. PMID:15860611.

Booker, D.J., Dunbar, M.J., and Ibbotson, A. 2004. Predicting juvenile salmonid drift-feeding habitat quality using a three-dimensional hydraulic–bioenergetic model. Ecol. Model. **177**(1–2): 157–177. doi:10.1016/j.ecolmodel.2004.02.006.

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 for salmonid habitat surveys within the Columbia Habitat Monitoring Program. Project #2011-006. The Integrated Status and Effectiveness Monitoring Program.

Bouwes, N., Bennett, S., and Wheaton, J. 2016. Adapting adaptive management for testing the effectiveness of stream restoration: an intensively monitored watershed example. Fisheries, **41**(2): 84–91. doi:10.1080/03632415.2015.1127806.

Boyd, M., and Kasper, B. 2003. Analytical methods for dynamic open channel heat and mass transfer: methodology for heat source model Version 7.0 [online]. Oregon Department of Environmental Quality, Portland, Oregon. Available from http://www.deq.state.or.us/wq/TMDLs/tools.htm.

Camp, R. 2015. Short Term Effectiveness of High Density Large Woody Debris in Asotin Creek as a Cheap and Cheerful Restoration Action. M.S. thesis, Department of Watershed Sciences, Utah State University, Logan, Utah.

Claeson, S.M., Li, J.L., Compton, J.E., and Bisson, P.A. 2006. Response of nutrients, biofilm, and benthic insects to salmon carcass addition. Can. J. Fish. Aquat. Sci. **63**(6): 1230–1241. doi:10.1139/f06-029.

Doyle, M.W., and Shields, D.F. 2012. Compensatory mitigation for streams under the Clean Water Act: reassessing science and redirecting Policy1. J. Am. Water Resour. Assoc. **48**(3): 494–509. doi:10.1111/j.1752-1688.2011.00631.x.

Fausch, K.D. 1993. Experimental analysis of microhabitat selection by juvenile steelhead (*Oncorhynchus mykiss*) and coho salmon (*O. kisutch*) in a British Columbia stream. Can. J. Fish. Aquat. Sci. **50**(6): 1198–1207. doi:10.1139/f93-136.

Guensch, G.R., Hardy, T.B., and Addley, R.C. 2001. Examining feeding strategies and position choice of drift-feeding salmonids using an individual-based, mechanistic foraging model. Can. J. Fish. Aquat. Sci. **58**(3): 446–457. doi:10.1139/f00-257.

Gustafsson, P., Greenberg, L.A., and Bergman, E. 2012. The influence of large wood on brown trout (*Salmo trutta*) behaviour and surface foraging. Freshw. Biol. **57**(5): 1050–1059. doi:10.1111/j.1365-2427.2012.02767.x.

Hayes, J.W., Hughes, N.F., and Kelly, L.H. 2007. Process-based modelling of invertebrate drift transport, net energy intake and reach carrying capacity for drift-feeding salmonids. Ecol. Model. **207**(2–4): 171–188. doi:10.1016/j.ecolmodel.2007.04.032.

Hayes, J.W., Goodwin, E., Hay, J., Shearer, K.A., and Kelly, L.H. 2012. Minimum flow requirements of trout in the Mataura River: comparison of traditional habitat and net rate of energy intake modelling. Cawthron Report 1957.

Hayes, J.W., Goodwin, E., Shearer, K.A., Hay, J., and Kelly, L. 2016. Can weighted useable area predict flow requirements of drift-feeding salmonids? Comparison with a net rate of energy intake model incorporating drift–flow processes. Trans. Am. Fish. Soc. **145**(3): 589–609.

Hughes, N.F., and Dill, L.M. 1990. Position choice by drift-feeding salmonids: model and test for Arctic Grayling (*Thymallus arcticus*) in subarctic mountain streams, interior Alaska. Can. J. Fish. Aquat. Sci. **47**(10): 2039–2048. doi:10.1139/f90-228.

Hughes, N.F., Hayes, J.W., Shearer, K.A., and Young, R.G. 2003. Testing a model of drift-feeding using three-dimensional videography of wild brown trout, *Salmo trutta*, in a New Zealand river. Can. J. Fish. Aquat. Sci. **60**(12): 1462–1476. doi:10.1139/f03-126.

Imre, I., Grant, J.W., and Keeley, E.R. 2002. The effect of visual isolation on territory size and population density of juvenile rainbow trout (*Oncorhynchus mykiss*). Can. J. Fish. Aquat. Sci. **59**(2): 303–309. doi:10.1139/f02-010.

Jenkins, A.R., and Keeley, E.R. 2010. Bioenergetic assessment of habitat quality for stream-dwelling cutthroat trout (*Oncorhynchus clarkii bouvieri*) with implications for climate change and nutrient supplementation. Can. J. Fish. Aquat. Sci. **67**(2): 371–385. doi:10.1139/F09-193.

Katz, S.L., Barnas, K., Hicks, R., Cowen, J., and Jenkinson, R. 2007. Freshwater habitat restoration actions in the Pacific Northwest: a decade's investment in habitat improvement. Restor. Ecol. **15**(3): 494–505. doi:10.1111/j.1526-100X.2007.00245.x.

Kawai, H., Nagayama, S., Urabe, H., Akasaka, T., and Nakamura, F. 2014. Combining energetic profitability and cover effects to evaluate salmonid habitat quality. Environ. Biol. Fishes, **97**(5): 575–586. doi:10.1007/s10641-013-0217-4.

Kelly, L.H., Hay, J., Hughes, N.F., Goodwin, E., and Hayes, J.W. 2012. Flow related models for simulating river hydraulics, invertebrate drift transport, and foraging energetics of drift-feeding salmonids: user guide (version 1.1) [online]. Available from http://www.cawthron.org.nz/media_new/publications/pdf/2014_05/ForagingUserManual_1.pdf.

Leung, E.S., Rosenfeld, J.S., and Bernhardt, J.R. 2009. Habitat effects on invertebrate drift in a small trout stream: implications for prey availability to drift-feeding fish. Hydrobiologia, **623**(1): 113–125. doi:10.1007/s10750-008-9652-1.

Milhous, R.T., and Waddle, T.J. 2012. Physical Habitat Simulation (PHABSIM) Software for Windows (v.1.5.1).

Nislow, K.H., Folt, C.L., and Parrish, D.L. 1999. Favorable foraging locations for young Atlantic salmon: application to habitat and population restoration. Ecol. Appl. **9**(3): 1085–1099. doi:10.1890/1051-0761(1999)009[1085:FFLFYA]2.0.CO;2.

Nislow, K.H., Folt, C.L., and Parrish, D.L. 2000. Spatially explicit bioenergetic analysis of habitat quality for age-0 Atlantic salmon. Trans. Am. Fish. Soc. **129**(5): 1067–1081. doi:10.1577/1548-8659(2000)129<1067:SEBAOH>2.0.CO;2.

Reiser, D.W., Wesche, T.A., and Estes, C. 1989. Status of instream flow legislation and practices in North America. Fisheries, **14**(2): 22–29. doi:10.1577/1548-8446(1989)014<0022:SOIFLA>2.0.CO;2.

Roni, P., Hanson, K., and Beechie, T. 2008. Global review of the physical and biological effectiveness of stream habitat rehabilitation techniques. N. Am. J. Fish. Manage. **28**(3): 856–890. doi:10.1577/M06-169.1.

Roni, P., Beechie, T., Pess, G., and Hanson, K. 2015. Wood placement in river restoration: fact, fiction, and future direction. Can. J. Fish. Aquat. Sci. **72**(3): 466–478. doi:10.1139/cjfas-2014-0344.

Rosenfeld, J.S., and Taylor, J. 2009. Prey abundance, channel structure and the allometry of growth rate potential for juvenile trout. Fish. Manage. Ecol. **16**(3): 202–218. doi:10.1111/j.1365-2400.2009.00656.x.

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

Rosenfeld, J.S., Bouwes, N., Wall, C.E., and Naman, S.M. 2014. Successes, failures, and opportunities in the practical application of drift-foraging models. Environ. Biol. Fishes, **97**(5): 551–574. doi:10.1007/s10641-013-0195-6.

Schaller, H.A., Petrosky, C.E., and Tinus, E.S. 2014. Evaluating river management during seaward migration to recover Columbia River stream-type Chinook salmon considering the variation in marine conditions. Can. J. Fish. Aquat. Sci. **71**(2): 259–271. doi:10.1139/cjfas-2013-0226.

Shearer, K.A., Hayes, J.W., and Stark, J.D. 2002. Temporal and spatial quantification of aquatic invertebrate drift in the Maruia River, South Island, New Zealand. N.Z. J. Mar. Freshw. Res. **36**: 529–536. doi:10.1080/00288330.2002.9517108.

Shirvell, C.S. 1990. Role of instream rootwads as juvenile coho salmon

(*Oncorhynchus kisutch*) and steelhead trout (*O. mykiss*) cover habitat under varying streamflows. Can. J. Fish. Aquat. Sci. **47**(5): 852–861. doi:10.1139/f90-098.

Smock, L.A. 1980. Relationships between body size and biomass of aquatic insects. Freshw. Biol. **10**: 375–383. doi:10.1111/j.1365-2427.1980.tb01211.x.

Steffler, P., and Blackburn, J. 2002. River2D: Two-dimensional depth averaged model of river hydrodynamics and fish habitat [online]. Available from http://www.river2d.ca/Downloads/documentation/River2D.pdf.

Stewart, G.B., Bayliss, H.R., Showler, D.A., Sutherland, W.J., and Pullin, A.S. 2009. Effectiveness of engineered in-stream structure mitigation measures to increase salmonid abundance: a systematic review. Ecol. Appl. **19**(4): 931–941. doi:10.1890/07-1311.1. PMID:19544735.

Sundbaum, K., and Näslund, I. 1998. Effects of woody debris on the growth and behaviour of brown trout in experimental stream channels. Can. J. Zool. **76**(1): 56–61. doi:10.1139/z97-174.

Tharme, R.E. 2003. A global perspective on environmental flow assessment: emerging trends in the development and application of environmental flow methodologies for rivers. River Res. Appl. **19**(5–6): 397–441. doi:10.1002/rra.736.

Urabe, H., Nakajima, M., Torao, M., and Aoyama, T. 2010. Evaluation of habitat quality for stream salmonids based on a bioenergetics model. Trans. Am. Fish. Soc. **139**(6): 1665–1676. doi:10.1577/T09-210.1.

Wall, C.E. 2014. Use of a net rate of energy intake model to examine differences in juvenile steelhead (*Oncorhynchus mykiss*) densities and the energetic implications of restoration. M.S. thesis, Department of Watershed Sciences, Utah State University, Logan, Utah.

Wall, C.E., Bouwes, N., Wheaton, J.M., Saunders, W.C., and Bennett, S.N. 2016. Net rate of energy intake predicts reach-level steelhead (*Oncorhynchus mykiss*) densities in diverse basins from a large monitoring program. Can. J. Fish. Aquat Sci. **73**(7): 1081–1091. doi:10.1139/cjfas-2015-0290.

Wheaton, J., Bennett, S., Bouwes, N., and Camp, R. 2012. Asotin Creek intensively monitored watershed: restoaration plan for Charley Creek, North Fork Asotin, and South Fork Asotin creeks. Eco Logical Research.

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