

RESEARCH ARTICLE

Assessing Habitat Suitability for Juvenile Atlantic Salmon in Relation to In-Stream Restoration and Discharge Variability

Saija Koljonen,^{1,2} Ari Huusko,³ Aki Mäki-Petäys,⁴ Pauliina Louhi,⁵ and Timo Muotka^{5,6}

Abstract

In-stream restoration often aims at increasing the availability of the stream habitat suitable for salmonid fishes, thus creating potential for increased fish abundance. We assessed the success of in-stream restoration of River Kiiminkijoki, northern Finland, by combining River2D habitat hydraulic modeling and fish density monitoring at the same sites, with data from multiple restored and reference reaches for 3 years both before and after restoration. We modeled the effects of restoration on the area suitable (weighted usable area, WUA) for juvenile Atlantic salmon from post-hatching to age-1 fish. Wetted width in the restored reaches increased by 8.1% on average compared with only -0.2% change in the reference reaches. Habitat time series across 10 years showed significant

increases in the amount of suitable habitat under summer conditions for both age-0 and age-1 salmon. However, improvement of overwintering habitats was marginal or nonexistent. Densities of age-1 salmon showed no response to restoration. Low river discharge during the winter was correlated with low salmon densities the following summer. It thus appears that variability in wintertime discharge, and associated high interannual variation of WUA values, overrode the almost 20% increase in average post- versus pre-restoration summertime WUA. Our study shows that the combination of hydraulic modeling and biological monitoring is a promising approach to stream restoration assessment.

Key words: habitat modeling, River2D, river restoration, salmonid fishes, stream flow variation.

Introduction

Stream restoration has a diversity of purposes, but a common goal in northern temperate streams is the enhancement of salmonid fisheries. Restoration initiatives aim to increase the amount of stream habitat suitable for the target species, thus creating potential for increased fish abundance and production. Evidence for the success, or lack of it, of habitat enhancement projects is, however, inconclusive. A recent systematic review concluded that there is no rigorous evidence for the effectiveness of such constructions in increasing salmonid abundance (Stewart et al. 2009), whereas another meta-analysis reported that in-stream structures can increase salmonid density and biomass, although the response varied widely among species (Whiteway et al. 2010).

In Fennoscandia, numerous streams have been channelized to facilitate water transport of timber. In Finland alone, about 20,000 km of rivers were modified for timber floating. As floating became economically unfeasible, projects were initiated from the late 1980s onward to restore these rivers to their pre-channelization state. Restoration is controlled, designed, and implemented by regional environmental authorities, and it is conducted using excavators to add boulders to the stream bed, creating deflectors, boulder dams, weirs, and other enhancement structures (Muotka & Syrjänen 2007). The aim of using such structures is to modify flow patterns, resulting in a more diversified in-stream habitat (Thompson 2006). Indeed, these restoration structures do provide a wide array of habitat types suitable for juvenile salmonids. For example, large salmonids prefer deep, slowly flowing stream pools (e.g. Rosenfeld et al. 2000), and the size and number of such pools typically increase after restoration (Whiteway et al. 2010; White et al. 2011).

The few projects monitoring the success of these measures in Fennoscandian streams have used a rather rigorous Before-After-Control-Impact design to show that biological responses to restoration have been limited (Vehanen et al. 2010). More generally, several recent studies have shown that enhanced habitat diversity does not always translate to increased biodiversity, which may be regulated by other factors, such as flow-related and/or anthropogenic disturbances (Palmer et al.

¹Freshwater Centre, Finnish Environment Institute, FIN-40500, Jyväskylä, Finland

²Address correspondence to S. Koljonen, email saija.koljonen@environment.fi

³Kainuu Fisheries Research, Finnish Game and Fisheries Research Institute, FIN-88300, Paltamo, Finland

⁴Oulu Game and Fisheries, Finnish Game and Fisheries Research Institute, FIN-90570, Oulu, Finland

⁵Department of Biology, University of Oulu, FIN-90014, Oulu, Finland

⁶Natural Environment Centre, Finnish Environment Institute, University of Oulu, FIN-90014, Oulu, Finland

2010; Louhi et al. 2011). These factors may also be responsible for reduced salmonid populations rather than lack of in-stream habitat diversity. Therefore, the process of prioritizing restoration measures to improve salmonid populations may require the inclusion of other obstacles for successful restoration.

Physical habitat models are powerful tools for assessing changes in stream habitat at scales relevant to fish (e.g. Boavida et al. 2012). These models usually combine data on hydromorphological channel structure with habitat suitability indices to obtain the area of the stream habitat suitable (weighted usable area, WUA) for the target organism at a range of discharges. In restoration assessments, habitat models have focused on post-restoration evaluations or comparison of WUAs before versus after restoration (Gard 2009; Korsu et al. 2010). Most previous applications of habitat modeling to restoration have used the Physical Habitat Simulation system (PHABSIM) or related approaches, but recently more developed techniques, such as the River2D model (Steffler & Blackburn 2002), have gained growing interest. Two-dimensional models are considered superior to classical one-dimensional techniques (e.g. PHABSIM) because they take better into account local bed topography and substrate roughness and can therefore be used to model complex flow patterns (Gard 2009).

We assessed the success of in-stream restoration of River Kiiminkijoki, northern Finland, by combining habitat hydraulic modeling and salmon density monitoring at the same sites, with data from multiple restored and reference reaches both before and after restoration. The goal of the restoration was to increase the availability of in-stream habitats for young (age-0 and age-1) Atlantic salmon (*Salmo salar* L.) and thereby support the recovery of salmon in River Kiiminkijoki. We modeled the effects of restoration on the habitat suitable (WUA) for juvenile Atlantic salmon at different life stages from post-hatching to age-1 fish. We hypothesized that (1) the addition of in-stream structures should increase the availability of suitable microhabitats and, therefore, WUA for all phases of the early life of salmon and (2) if WUA increases, then so do densities of juvenile salmon; that is, the hydrological and biological improvements of restoration should go hand in hand.

Methods

Study Species

Atlantic salmon spend their juvenile phase in rivers before migrating to sea. After 1–4 years at sea, they return to their river of origin to spawn. In Finland, spawning occurs in late autumn (October). Fertilized eggs are covered with gravel, where they develop during the winter, until hatching in April to May. When most of the yolk sac has been consumed, the alevins emerge from the gravel into the open water. At that stage, they establish territories and start feeding on invertebrate prey. Before their first winter, age-0 salmon, also known as fry, have reached the length of 5–8 cm.

Study River and Restoration Measures

We conducted the study in River Kiiminkijoki, a 170-km long, free-flowing river in northern Finland with mean annual flow of 44 m³/s (see Fig. S1, Supporting Information). The mean of the lowest annual daily discharge is 6.25 m³/s and the mean highest daily discharge is 367 m³/s. One-third of the peatland-dominated catchment (total of 3,845 km²) is drained for forestry purposes. The river water is slightly acidic (pH range: 5–7) with high concentrations of humic substances (mean total organic carbon [TOC]: 14 [5–28] mg/L; mean water color: 155 [33–682] mgPt/L). Nutrient concentrations are moderate and highly variable (total P: 35 [6–100] µg/L; total N: 531 [40–1,600] µg/L) (Environmental Information System HERTTA, Finnish Environment Institute). The river is permanently ice-covered for approximately 4 months (December to April) and the spring flood peaks soon after the ice break-up in late April. The mean discharge is 12 m³/s during the ice-covered period, whereas in summer (June to September) it is 28 m³/s.

River Kiiminkijoki was channelized for timber floating by the early 1950s. Some rapids, however, were left unmodified, remaining in a hydromorphologically natural state. Timber floating ceased by the end of the 1960s, and a comprehensive restoration project in 2003 aimed to enhance fish habitat availability, with the goal of reestablishing naturally spawning Atlantic salmon populations. Historically, the river supported moderately high stocks of Atlantic salmon: in the beginning of the twentieth century, more than 3,000 kg of salmon were annually harvested from the river. Loss of natural heterogeneity and increased amount of humic substances, together with over-fishing, extirpated the native salmon population of River Kiiminkijoki by the end of the 1970s. By the late 1990s, the water quality of River Kiiminkijoki could be considered adequate for the reestablishment of salmon.

Field Measurements and Ecohydraulic Modeling

We selected three channelized reaches (60–115 m long; 37–70 m wide) to assess in-stream restoration effects and, correspondingly, three unmodified reaches (60–110 m long; 30–80 m wide) for reference. Within each study reach, we quantified geographically referenced river bed topography before (July 2003) and after restoration (July 2004/2005) with a total station (SOKKIA Set 4010, Sokkia Topcon Co., Kanagawa, Japan) during minimum summer flows. In deep, non-wadable areas, we used an inflatable boat. We divided each study reach into regularly (by every 3 m) spaced cross-sections, taking measurements at 3-m intervals along each section. We measured additional points where distinct transitions appeared in the river bed, such as large boulders or abrupt alterations in bed elevation, resulting in high point density in areas of topographic complexity and lower density in topographically simpler areas (Wheaton et al. 2010). The total amount of points per reach ranged from 700 to 1,700, depending on reach length and width, and river bed complexity. To specify local bottom roughness for hydraulic modeling, we estimated dominant substrate size at each measurement

point using a modified Wentworth scale (Vehanen et al. 2010).

We entered the field data into River2D (Steffler & Blackburn 2002) to create a hydraulic model for each reach. River2D is a depth-averaged finite-element procedure for hydraulic modeling of natural streams. First, we entered the georeferenced topographic data into River2D to construct a terrain model over each restored and reference reach, both before and after restoration. The terrain model was based on a triangular network of elements, with elements (cells) ranging from 0.13 to 1.21 m², yielding a total of 4,400–20,800 elements per reach. We interpolated field-measured substrate sizes to obtain a substrate index for every grid element of the model. Then, we used a two-dimensional hydraulic model available in River2D to calculate local water depths and velocities ($0.6 \times \text{depth}$) over the study reach at six flow conditions: 2, 10, 20, 40, 60, and 100 m³/s.

We then applied life stage-specific (age-1) habitat preference criteria (HPC) for depth, velocity, and substrate preference by Atlantic salmon (Mäki-Petäys et al. 2002, 2004) to translate values of the modeled habitat variables in each cell into preference values, ranging between 0 and 1, separately for each variable. These were then converted to combined suitability indices, calculated as the geometric mean of variable-specific values. Finally, we computed WUA, an index of habitat value, as a product of the combined suitability indices and the area associated with each cell of the River2D grid, summed over the entire reach. WUA values at flow levels other than the modeled ones were determined by linear interpolation from the six calibrated flow models. Thus, the end product of the modeling procedure was a quantitative estimate of the potential suitability of habitat for age-1 salmon before and after restoration.

To assess restoration success through time, we selected a 10-year period (1997–2006) of discharge monitoring in River Kiiminkijoki (Environmental Information System HERTTA, Finnish Environment Institute) and estimated WUAs for different life stages of juvenile (age-0 and age-1) salmon using average weekly discharges under both channelized and restored conditions. We started our assessment from early June when alevins emerge from the gravel and start their active life. The weekly mean discharge and the corresponding WUA values were calculated from this point onward for the next 16 months. We used the summer HPCs of age-0 salmon from early June to late October (first-summer life stage) (Mäki-Petäys et al. 2002), thereafter the winter HPCs, until the onset of spring flood in May (first-winter life stage) (Mäki-Petäys et al. 2004). To continue following the same cohort, we then applied the HPCs of age-1 Atlantic salmon from early June to late October of the subsequent year (second-summer life stage). We did not perform modeling for the spring floods as no published information on the HPCs of juvenile salmon under such conditions is available.

We tested the change in the WUAs for different life stages of salmon using a generalized linear mixed model (GLMM), which allows incorporation of fixed factors and random effects that control for correlation in data arising from grouped observations (Pinheiro & Bates 2000). We included treatment

(restored vs. reference) as a fixed factor and reaches as random effect (i.e. random reaches within larger restored reaches) to deal with the spatial nonindependence of the reaches. We included a first-order temporal autocorrelation across times to exclude any possible effect of year on within-reach measurements. All data were logarithmic transformed prior to analysis. Statistical significance was tested using *F*-statistics in lme function (nlme library) in the free software R 2.9.2 (R Development Core Team 2009). In this design, a significant period \times treatment interaction indicates a difference between treatments in how they vary from before to after restoration. We used the same GLMM design to test for the effects of restoration on the wetted width of the river. For this purpose, channel width was measured to the accuracy of 1 m at 10 cross-channel transects in each study site, both before and after restoration, at a range of discharges from the wintertime-low (about 2 m³) to summertime-high (40 m³) flows.

To provide a visual summary of the changes to in-stream habitat structure, we performed a principal component analysis (PCA) on the measured habitat variables (depth, water velocity, and substrate size) and their coefficients of variation. We ran separate analysis for wadable stream areas and the main channel to examine whether the structural shifts following restoration were similar in these two main habitat types.

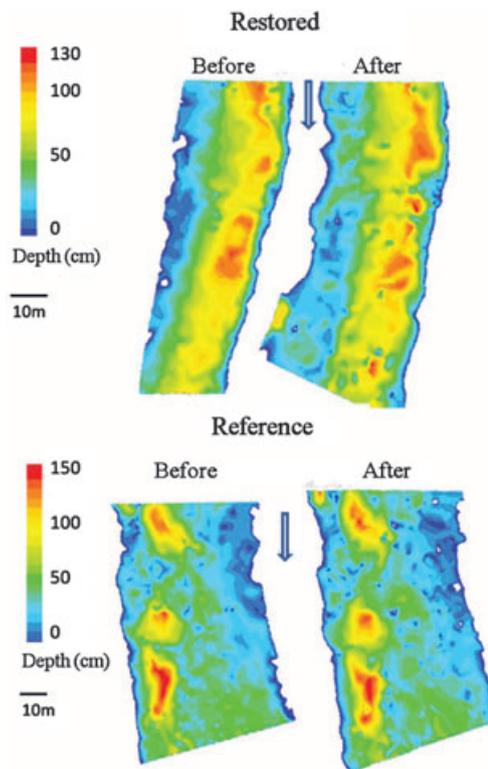


Figure 1. Spatial distribution of water depth, modeled by River2D, in one of the restored reaches before and after restoration at 20 m³/s. Corresponding maps are also shown for the nearest reference reach before and after restoration of the target reach. Arrow indicates direction of the flow.

Monitoring Densities of Juvenile Atlantic Salmon

As the Atlantic salmon population in River Kiiminkijoki was initially nonexistent, each study reach was stocked with age-0 salmon (64–80 mm, 2–5 g) at equal density (10 fish 100 m⁻² amounting to 2,500–7,000 fish per reach, depending on reach area) every September, starting in 2000 and continuing until 2005. This stocking density is well within the range of

densities of age-0 salmon in Finnish streams (Romakkaniemi 2008). The stocked fish originated from Kainuu Fisheries Station, northeastern Finland, and they represented the original stock of the nearby River Simojoki. From 2001 to 2006, we estimated salmon densities by three-pass electrofishing trials in late summer (August; i.e. 1 month prior to stocking) each year in three sampling sites (60–100 m²) per reach. Densities

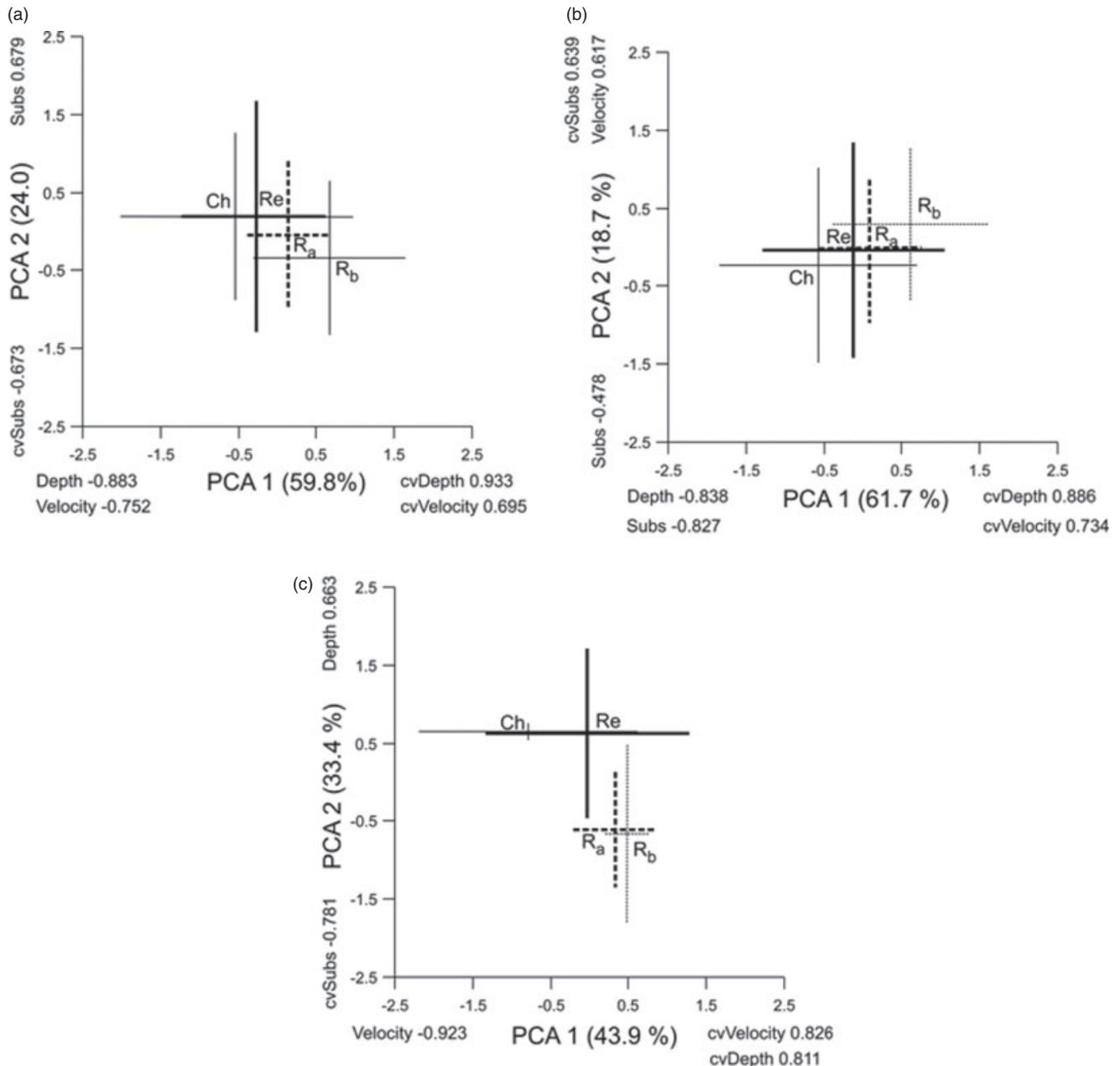


Figure 2. PCA on in-stream habitat variables of the study reaches at 20 m³/s. Mean PCA scores (± 1 SD) are presented for channelized (Ch), restored (Re), and reference sites (R_b—reference before restoration; R_a—after restoration). All data points included (a), only wadable areas (mainly less than 70 cm deep) included (b), and only main channel areas included (c). Key habitat variables with their loadings are given below each axis.

Subs—dominant substrate size; cvSubs—coefficient of variation for substrate size; Velocity—mean water velocity; cvVelocity—coefficient of variation for water velocity; cvDepth—coefficient of variation for water depth. Eigenvalues for each axis in all ordinations exceeded 1.0. Percent variation explained is given below each axis (in parentheses).

were estimated using the removal method (Bohlin et al. 1989). We then used the mean across the three sites as an estimate of the reach-scale density of juvenile salmon in restored versus reference reaches.

We tested the impact of restoration on Atlantic salmon density using GLMM. We included three independent categorical variables as fixed factors: (1) period (B), “before” (temporal control) versus “after” restoration; (2) treatment (TR), defining “restored” versus “reference” (spatial control); and (3) sampling times (T) nested within periods (T(B)), allowing the time series structure of the data to be taken into account (3-year data for each “before” and “after” period). We fitted sampling sites as random effects to control for the nonindependence of observations within sites. In this design, interest lies mainly in the interaction (B × TR), which, if significant, implies a long-lasting pulse impact of restoration. All data were logarithmic transformed prior to analysis. We tested the statistical significance of period, treatment, sampling times, and period × treatment interaction using *F*-statistics in lme function (nlme library) in the free software R 2.9.2. (R Development Core Team 2009).

Results

Habitat Structure

Wetted width of the restored reaches increased by 8.1% on average (compared to only −0.2% change in the reference reaches). This change was also indicated by a significant interaction term (Treatment [restored vs. control] × Period [before vs. after restoration]) in GLMM ($F_{[1,469]} = 12.27, p < 0.001$). A visual inspection of the spatial distribution of habitat variables indicated that the restored reaches were structurally more similar to the reference than channelized reaches (Fig. 1). Reference reaches remained practically unmodified between the two sampling occasions. These results are summarized in the PCA ordination demonstrating restoration-induced changes to habitat structure (Fig. 2). Changes in the deeper, main channel areas were insubstantial, whereas the shallower areas along river margins resembled the reference reaches following restoration (see also changes to individual habitat variables, Fig. S1).

Habitat Suitability for Juvenile Salmon

The estimated amount of suitable habitat (WUA; m^2 per 100 m river length) peaked in all study reaches and salmon life stages at below $20 m^3/s$. Most of the areas with high WUA scores were located along the river margins, both before and after restoration, whereas restoration measures had only limited impact in the mid-channel sections of the river (Fig. 3). Restoration increased WUA almost consistently, whereas reference reaches exhibited similar WUA values between the two surveys (Fig. 4). Habitat time series across 10 years, summarized as net WUA benefit of restoration, exhibited significant increases in the amount of summertime rearing habitat for both age-0 ($F_{[1,4]} = 27.53, p = 0.006$) and

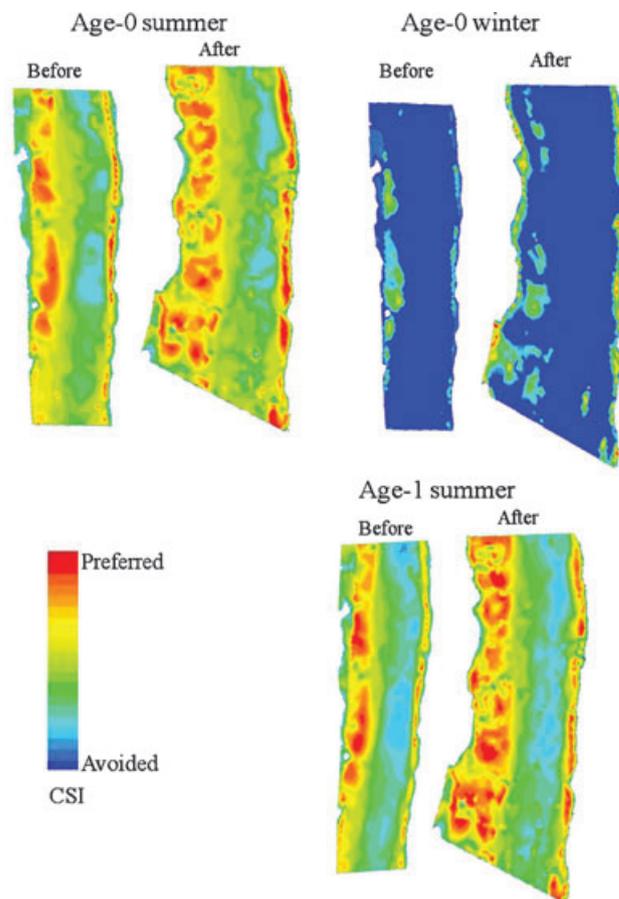


Figure 3. Combined habitat suitability (CSI: depth, velocity, and substrate; red = preferred, blue = avoided habitat) maps for age-0 salmon in summer, age-0 salmon in winter, and age-1 salmon in summer in one of the restored reaches (same reach as in Fig. 1) modeled by River2D at $20 m^3/s$.

age-1 ($F_{[1,4]} = 37.88, p = 0.004$) salmon. The life stage-specific increase in suitable habitat varied on average from 300 to $1,000 m^2$ per 100 m river length (Fig. 5). However, restoration-induced benefits to winter habitats of age-0 salmon were nonsignificant ($F_{[1,4]} = 0.78, p = 0.428$), with one study reach indicating even negative wintertime net (before vs. after restoration) WUA values (Figs. 4 & 5).

Densities of Juvenile Salmon

The annual fish catch was dominated (ca. 75%) by age-1 salmon (mean size: 116 mm, range: 86–134 mm) stocked the previous year. However, about 20% (180 individuals) represented natural reproduction. The average size of these age-0 fish was 55 mm (range: 42–64 mm). Only 25 fish older than age-1 (up to 178 mm) were captured during the monitoring period.

Densities of age-1 salmon showed no response to restoration, but followed the same trajectory in the reference and restored reaches, both before and after restoration (see nonsignificant interaction term in Table 1). Salmon densities

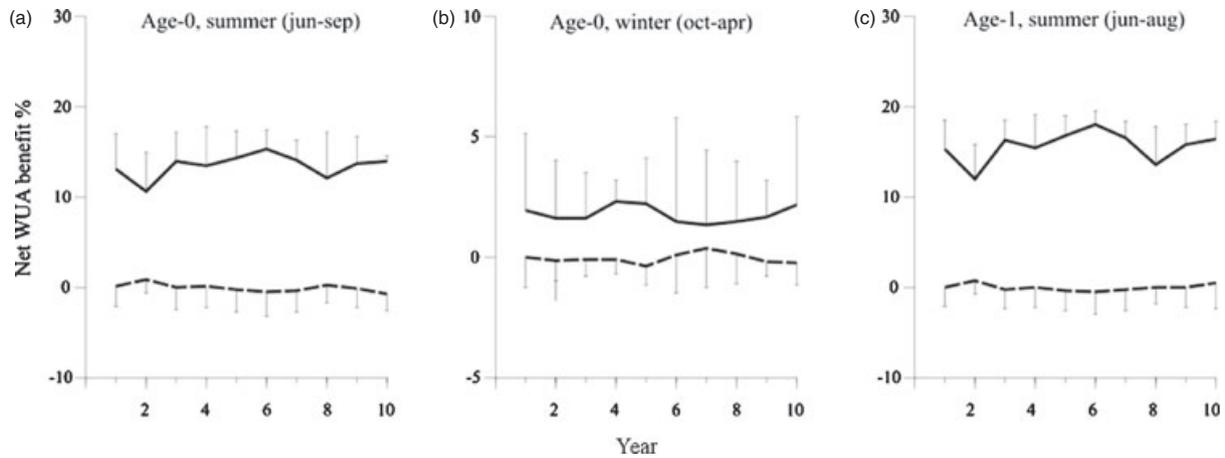


Figure 4. Before–after restoration differences (means \pm 1 SD) in the WUAs (net WUA benefit % = percent change in $WUA_{After} - WUA_{Before}$ vs. WUA_{Before}) for the early life stages of salmon in the restored (continuous line) and reference reaches (broken line). Values of WUA were calculated for each life stage and reach ($n = 3$ for each treatment by year combination) by using weekly discharge values over 10 water years (1997–2006) of River Kiiminkijoki.

appeared to track stream discharge during the preceding winter (October–March/early April); low flows during the winter were reflected as low fish densities the following summer (Fig. 6). Correlation between the average wintertime discharge and late-summer population density (annual mean across six study sites) was relatively high ($r_s = 0.62$), albeit nonsignificant ($p = 0.18$, $n = 6$ years).

Discussion

The goal of in-stream restoration of River Kiiminkijoki was to improve the in-stream habitat for juvenile Atlantic salmon. Most corresponding attempts use in-stream structures to add complexity to channelized stream bed and thereby increase the availability of microhabitats for juvenile fish. In the case of River Kiiminkijoki, these measures had a distinct, though relatively modest, effect on the amount of habitat suitable for salmon. This was mainly caused by restoration measures being effective at river margins, thereby increasing the area where water depth and velocity remained suitable for salmon at most flow conditions.

Intuitively, an increase in WUA should result in increased salmonid abundance, but we did not observe this in our electrofishing surveys. It is possible that our monitoring period, with 3 years before and 3 after restoration, was too short to detect an impact. It has been suggested that the post-restoration time frame for detecting salmonid response should span several fish generations, amounting to at least 5 (and preferably more) years (Johnson et al. 2005). Nevertheless, our results correspond well with the recent meta-analysis by Stewart et al. (2009) who showed that the use of in-stream structures for salmonid enhancement is not supported by scientific evidence. Interestingly, Whiteway et al. (2010) reached a very different conclusion in their meta-analysis, showing a significant increase in salmonid density and biomass following the in-stream restoration. The effect varied between

species, but one of the strongest positive responses was detected for Atlantic salmon. However, despite a positive overall response to restoration, no habitat variable emerged as a significant correlate of fish density. Thus, the habitat factors limiting salmonid density are likely to be site specific, rendering the search for generally important causal factors potentially unrewarding.

Restoration structures used in Fennoscandia seem to provide scope for salmonid population enhancement, but this potential is frequently obscured by variability, natural or human-induced, in landscape-level or regional factors that overwhelm local restoration efforts (Vehanen et al. 2010). Lack of suitable spawning habitat has been raised as one of the reasons for the weak response by salmonids to management actions. Stream channels in Fennoscandia have naturally low sediment supply rates, causing these streams to have initially limited amount of spawning gravel (Rosenfeld et al. 2011). Indeed, Palm et al. (2007) demonstrated that adding gravel enhanced densities of age-0 brown trout in Swedish streams (Pedersen et al. 2009). However, the effects of gravel additions may be more complex than that because they may induce increased density-dependent mortality at later life stages (Einum et al. 2008).

Several studies have identified stream discharge as a key factor regulating salmonid populations (e.g. Lobon-Cervia 2007), and a positive relationship between winter discharge and densities of Atlantic salmon has been detected in other boreal rivers as well (Gibson & Myers 1988; Hvidsten 1993). During low discharges, most of the habitat along stream margins remains unavailable, decreasing the overall availability of overwintering habitats. It thus appears that variability in discharge, and associated high interannual variation in WUA values, overrode the almost 20% average increase in post- versus pre-restoration WUA. Alternatively, restoration measures focusing on stream edges may have been poorly targeted and adding in-stream structures to mid-channel sections might produce greater benefits. Nevertheless, adding

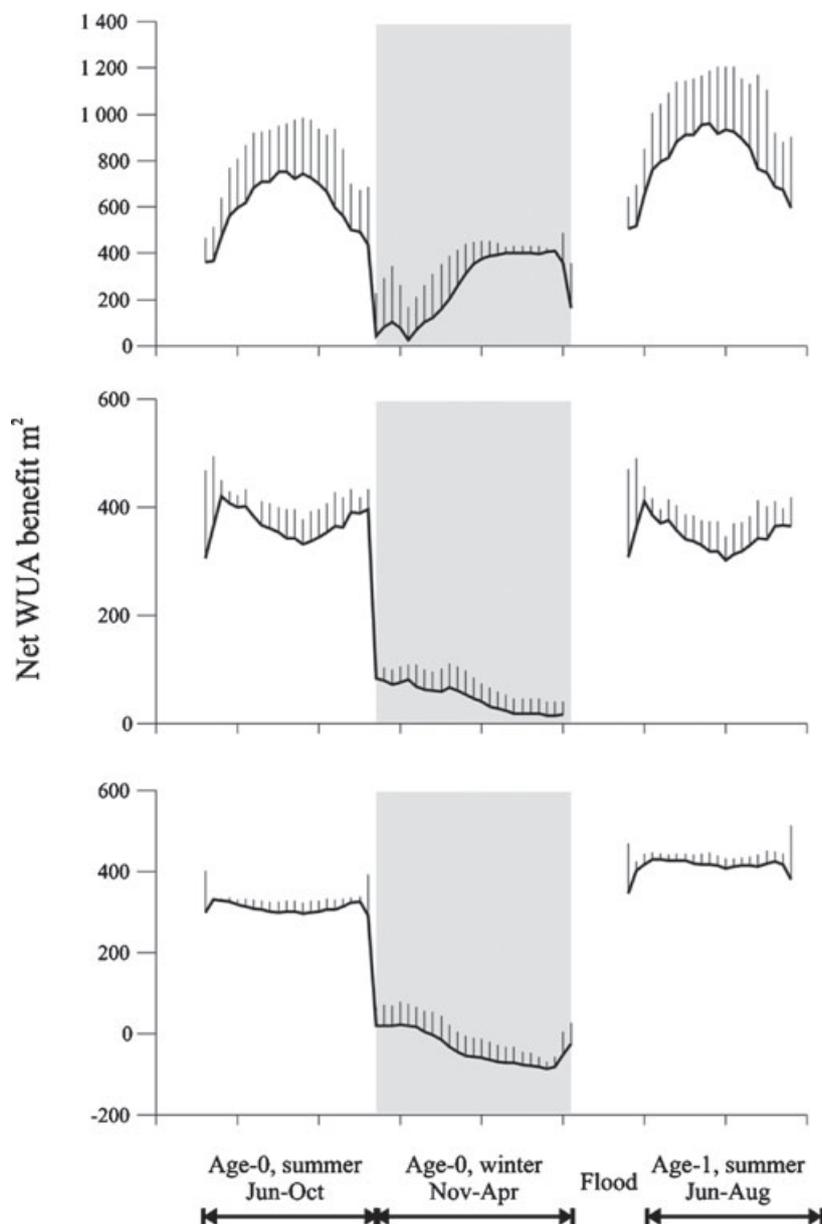


Figure 5. After versus before restoration differences in WUAs (net WUA benefit [m^2] = $\text{WUA}_{\text{After}} - \text{WUA}_{\text{Before}}$) for the early life stages of salmon in the three restored reaches of River Kiiminkijoki. Values of WUA are expressed for each week (means \pm 1 SD) from hatching until age-1+ autumn, modeled using weekly discharge values over 10 years (1997–2006) of River Kiiminkijoki. Gray shading indicates winter.

large boulders to mid-channel sections would have increased suitable (deep, fast-flowing) area mainly for large fish, whereas closer to stream edges they created suitable rearing habitat for juvenile salmon.

There is ample evidence that lack of winter habitat may be a critical bottleneck for salmonid populations (Cunjak 1996; Huusko et al. 2007). In our earlier study, the paucity of wintertime habitat caused temporary mass loss, followed by fast catch-up growth in late spring, by age-0 brown trout (Koljonen et al. 2012). One might thus expect increased habitat complexity through in-stream restoration to enhance the overwintering success of juvenile salmon. Nonetheless, we

observed a dramatic shortage of wintertime WUA in River Kiiminkijoki, irrespective of in-stream restoration. This suggests that although restoration did improve the summertime rearing conditions for salmon, it failed to improve the overwintering habitat. As we did not directly monitor the movement of salmon, we cannot be confident if they stayed within the same reach throughout the winter. In one of the few studies following individually tagged salmon through the winter, Linnansaari and Cunjak (2010) documented considerable emigration at the onset of winter but high site fidelity through the rest of the winter. In another study, Palm et al. (2009) concluded that while a majority of detected movements by brown trout in a

Table 1. Generalized linear mixed model on the effects of in-stream restoration on density of age-1 Atlantic salmon (no. individuals 100 m^{-2}) before versus after restoration of River Kiiminkijoki.

Source of variation	Density		
	df	F	p
Before versus After = B	1,24	1.52	0.230
Among treatments = TR	1,4	0.02	0.894
Times (B) = T(B)	1,24	0.86	0.362
B \times TR	1,24	1.11	0.302

Sites were included as a random variable (i.e. random sites within larger restored reaches), and other factors were treated as fixed.

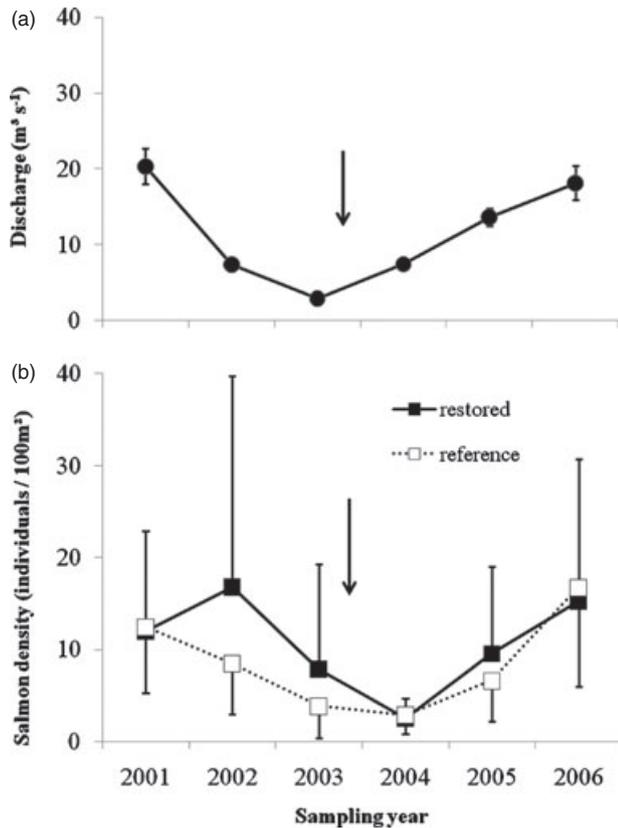


Figure 6. Mean ($\pm 95\%$ CL) river discharge (a) and mean ($\pm 95\%$ CL) density of age-1 Atlantic salmon (b) in electrofishing surveys in the restored ($n = 3$) and reference ($n = 3$) reaches. Arrow indicates the timing of restoration in 2003.

north Swedish river were very short ($11 \pm 3\text{ m}$, mean \pm SE), most undetected individuals likely conducted stream scale movements of up to several kilometers. The likelihood of long-distance movements during the winter is also related to fish size, such that larger fish are more likely to abandon their summer habitats (Heggenes et al. 1993; Hiscock et al. 2002). However, the large fish in these two studies were substantially larger than age-1 salmon in River Kiiminkijoki, and we believe that most of the age-0 fish stocked at our study reaches in the autumn remained within the same reach until next summer. Moreover, even fish that might have abandoned the riffles

during the winter likely returned to the best feeding sites in summer, so wintertime movements alone cannot explain the lack of a positive density response by age-1 salmon.

Our study shows that the combination of two-dimensional hydrodynamic modeling and biological monitoring bears promise as a tool for in-stream restoration assessment. Monitoring of fish densities, even when based on pre- versus post-restoration design with multiple treatment and reference sites, may not allow a reliable detection of restoration impacts because of the inherently high variability of salmonid populations and typically short monitoring periods. Habitat hydraulic modeling provides an important link between geomorphologic change and its ecohydraulic implications (Wheaton et al. 2010). To this end, habitat modeling may provide a useful device for post-evaluation of restoration projects (Gard 2006; Korsu et al. 2010) or as a means of comparing alternative restoration designs prior to the onset of a project.

Implications for Practice

- In-stream restoration aiming at the enhancement of salmonid fisheries in northern boreal areas should focus on increasing the availability of sheltering habitats for overwintering fish.
- Broad-scale regional factors, such as low wintertime discharge, may override any positive effects of local restoration efforts, at least in a short temporal perspective.
- Long-term biological monitoring with data from multiple restored and reference reaches for several years both before and after restoration, combined with habitat hydraulic modeling, provides a promising tool for the assessment of stream restoration success.

Acknowledgments

We are grateful to O. van der Meer for field and modeling assistance. We also acknowledge the late P. Kreivi for his efforts on the early stages of this study. A. Huhmarniemi assisted in the electrofishing surveys. Our research was funded by the Foundation for Research of Natural Resources in Finland (to A.M.-P.), Maj and Tor Nessling Foundation (to A.M.-P.), University of Oulu (Thule Institute; to T.M.), and Academy of Finland (to T.M.). We are grateful for the comments made by two anonymous reviewers and D. Ryder on a previous version of the manuscript.

LITERATURE CITED

- Boavida, E., J. M. Santos, R. Cortes, A. Pinheiro, and M. T. Ferreira. 2012. Benchmarking river habitat improvement. *River Research and Applications* in press.
- Bohlin, T., S. Hamrin, T. G. Heggberget, G. Rasmussen, and S. J. Saltveit. 1989. Electrofishing – theory and practice with special emphasis on salmonids. *Hydrobiologia* **173**:9–43.
- Cunjak, R. 1996. Winter habitat of selected stream fishes and potential impacts from land-use activity. *Canadian Journal of Fisheries and Aquatic Sciences* **53**:267–282.

- Einum, S., K. Nislow, J. Reynolds, and W. Sutherland. 2008. Predicting population responses to restoration of breeding habitat in Atlantic salmon. *Journal of Applied Ecology* **45**:930–938.
- Gard, M. 2006. Changes in salmon spawning and rearing habitat associated with river channel restoration. *International Journal of River Basin Management* **4**:201–211.
- Gard, M. 2009. Demonstration flow assessment and 2-D modeling: perspectives based on instream flow studies and evaluation of restoration projects. *Fisheries* **34**:320–329.
- Gibson, R. J., and R. A. Myers. 1988. Influence of seasonal river discharge on survival of juvenile Atlantic salmon, *Salmo salar*. *Canadian Journal of Fisheries and Aquatic Sciences* **45**:344–348.
- Heggenes, J., O. M. W. Grog, O. R. Lindas, J. G. Dokk, and J. D. Armstrong. 1993. Homeostatic behavioural responses in changing environment: brown trout (*Salmo trutta*) become nocturnal at night. *Journal of Animal Ecology* **62**:295–308.
- Hiscock, M. J., D. D. A. Scruton, J. A. Brown, and C. J. Pennel. 2002. Diel activity patterns of juvenile Atlantic salmon (*Salmo salar*) in early and late winter. *Hydrobiologia* **483**:161–165.
- Huusko, A., L. Greenberg, M. Stickler, T. Linnansaari, M. Nykänen, T. Vehanen, S. Koljonen, P. Louhi, and K. Alfredsen. 2007. Life in the ice lane: the winter ecology of stream salmonids. *River Research and Applications* **23**:469–491.
- Hvidsten, N. A. 1993. High winter discharge after regulation increases production of Atlantic salmon (*Salmo salar*) smolts in the River Orkla, Norway. *Canadian Special Publication of Fisheries and Aquatic Sciences* **118**:175–177.
- Johnson, S. L., J. D. Rodgers, M. F. Solazzi, and T. E. Nickelson. 2005. Effects of an increase in large wood on abundance and survival of juvenile salmonids (*Oncorhynchus* spp.) in an Oregon coastal stream. *Canadian Journal of Fisheries and Aquatic Sciences* **62**:412–424.
- Koljonen, S., A. Huusko, A. Mäki-Petäys, H. Mykrä, and T. Muotka. 2012. Body mass and growth of overwintering brown trout in relation to stream habitat complexity. *River Research and Applications* **28**:62–70.
- Korsu, K., A. Huusko, P. K. Korhonen, and T. Yrjänä. 2010. The potential role of stream habitat restoration in facilitating salmonid invasions: a habitat-hydraulic modeling approach. *Restoration Ecology* **18**:158–165.
- Linnansaari, T., and R. A. Cunjak. 2010. Patterns in apparent survival of Atlantic salmon (*Salmo salar*) parr in relation to variable ice conditions throughout winter. *Canadian Journal of Fisheries and Aquatic Sciences* **67**:1744–1754.
- Lobon-Cervia, J. 2007. Numerical changes in stream-resident brown trout (*Salmo trutta*): uncovering the roles of density-dependent and density-independent factors across space and time. *Canadian Journal of Fisheries and Aquatic Sciences* **64**:1429–1447.
- Louhi, P., H. Mykrä, R. Paavola, A. Huusko, T. Vehanen, A. Mäki-Petäys, and T. Muotka. 2011. Twenty years of stream restoration in Finland: little response by benthic macroinvertebrate communities. *Ecological Applications* **21**:1950–1961.
- Mäki-Petäys, A., J. Erkinaro, E. Niemelä, A. Huusko, and T. Muotka. 2004. Spatial distribution of juvenile Atlantic salmon (*Salmo salar*) in a subarctic river: size-specific changes in a strongly seasonal environment. *Canadian Journal of Fisheries and Aquatic Sciences* **61**:2329–2338.
- Mäki-Petäys, A., A. Huusko, J. Erkinaro, and T. Muotka. 2002. Transferability of habitat preference criteria of juvenile Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* **59**:218–228.
- Muotka, T., and J. Syrjänen. 2007. Changes in habitat structure, benthic invertebrate density, trout populations and ecosystem processes in restored forested stream: a boreal perspective. *Freshwater Biology* **52**:724–737.
- Palm, D., E. Brännas, F. Lepori, K. Nilsson, and S. Stridsman. 2007. The influence of spawning habitat restoration on juvenile brown trout (*Salmo trutta*) density. *Canadian Journal of Fisheries and Aquatic Sciences* **64**:509–515.
- Palm, D., E. Brännas, and K. Nilsson. 2009. Predicting site-specific overwintering of juvenile brown trout (*Salmo trutta*) using habitat suitability index. *Canadian Journal of Fisheries and Aquatic Sciences* **66**:540–546.
- Palmer, M. A., H. Menninger, and E. Bernhardt. 2010. River restoration, habitat heterogeneity and biodiversity: a failure of theory or practice? *Freshwater Biology* **55**(Suppl. 1):205–222.
- Pedersen, M. L., E. A. Kristensen, B. Kronvang, and H. Thodsen. 2009. Ecological effects of re-introduction of salmonid spawning gravel in lowland Danish streams. *River Research and Applications* **25**:626–638.
- Pinheiro, J. C., and D. M. Bates. 2000. *Mixed-effect models in S and S-PLUS*. Springer-Verlag, New York.
- R Development Core Team. 2009. *A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna. ISBN 3-900051-08-9 (available from <http://www.r-project.org>).
- Romakkaniemi, A. 2008. Conservation of Atlantic salmon by supplementary stocking of juvenile fish. Academic PhD dissertation. University of Helsinki, Finland. 43p.
- Rosenfeld, J. S., D. Hogan, D. Palm, H. Lundqvist, C. Nilsson, and T. J. Beechie. 2011. Contrasting landscape influences on sediment supply and stream restoration priorities in Northern Fennoscandia (Sweden and Finland) and coastal British Columbia. *Environmental Management* **47**:28–39.
- Rosenfeld, J. S., M. Porter, and E. A. Parkinson. 2000. Habitat factors affecting the abundance and distribution of juvenile cutthroat trout and coho salmon. *Canadian Journal of Fisheries and Aquatic Sciences* **57**:766–774.
- Steffler, P., and J. Blackburn. 2002. Two-dimensional depth averaged model of river hydrodynamics and fish habitat, introduction to depth averaged modeling and user's manual. University of Alberta, Edmonton, Canada.
- Stewart, G. B., H. R. Bayliss, D. A. Showler, W. J. Sutherland, and A. S. Pullin. 2009. Effectiveness of engineered in-stream structure mitigation measures to increase salmonid abundance: a systematic review. *Ecological Applications* **19**:931–941.
- Thompson, D. M. 2006. Did the pre-1980 use of in-stream structures improve streams? A re-analysis of historical data. *Ecological Applications* **16**:784–796.
- Vehanen, T., A. Huusko, A. Mäki-Petäys, P. Louhi, and T. Muotka. 2010. Effects of habitat rehabilitation on brown trout (*Salmo trutta*) in boreal forest streams. *Freshwater Biology* **55**:2200–2214.
- Wheaton, J. M., J. Brasington, S. E. Darby, J. E. Merz, G. B. Pasternack, D. A. Sear, and D. Vericat. 2010. Linking geomorphic changes to salmonid habitat at a scale relevant to fish. *River Research and Applications* **26**:469–486.
- White, S. L., C. Gowan, K. D. Fausch, J. G. Harris, and W. C. Saunders. 2011. Response of trout populations in five Colorado streams two decades after habitat manipulation. *Canadian Journal of Fisheries and Aquatic Sciences* **68**:2057–2063.
- Whiteway, S. L., P. M. Biron, A. Zimmermann, O. Venter, and J. W. A. Grant. 2010. Do in-stream restoration structures enhance salmonid abundance? A meta-analysis. *Canadian Journal of Fisheries and Aquatic Sciences* **67**:831–841.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Frequency distributions for dominant substratum size (Wentworth scale), water depth, and water velocity in one restored (treatment) site and one reference site (same sites as in Fig. 1) in River Kiiminkijoki. White bars represent the before-restoration state, and gray bars represent the after-restoration state. Depth and velocity are classified at 10 cm and 10 cm/s intervals, respectively. All data points included.

Figure S2. Same as Figure S1, but only wadeable stream areas included.