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Long-term monitoring reveals the success of salmonid habitat restoration

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Abstract

The growing concern on declining salmonid populations has resulted in numerous restoration projects with variable responses worldwide. In this spatially replicated multi-year study, we assessed the long-term (12 years post-restoration) effects of in-stream habitat restoration (i.e. addition of boulders or large woody debris (LWD) together with boulders) on densities of three age-classes of juvenile brown trout in six forest streams in northern Finland. LWD combined with boulders was more beneficial, particularly for the larger trout (age-2 and older), than were boulder structures alone, indicating that the more diverse habitat created by LWD may have provided a safeguard against drought for the larger fish. Density of age-0+ trout showed a significant long-term increase in boulder-restored sections, providing evidence that log structures may need to be complemented by stony enhancement structures to guarantee the availability of suitable stream habitat for all trout age-classes. As trout densities are known to exhibit inherently wide inter-annual variability that tracks climatically-induced hydrological variation, long-term post-restoration monitoring that encompasses extreme hydrological events is critical for evaluating the success of restoration projects.

Key-words: long-term monitoring, in-stream restoration, brown trout, *Salmo trutta* L.

INTRODUCTION

The growing concern for the loss of biodiversity and ecosystem services has resulted in numerous restoration projects worldwide during the past decades (SER 2004). Traditionally, stream restoration has been based on the premise that if stream habitat heterogeneity increases, organisms will recolonize the restored habitat, that is, physical and biological improvements are related (Palmer et al. 1997). Using this assumption as a guideline, fisheries management has a long tradition of constructing in-stream structures, such as weirs, flow detectors and boulder dams, to enhance the recovery of declining salmonid populations (Thompson 2006; Jonsson and Jonsson 2011). For example, timber floating in the forested areas of Finland ceased in the late 1970s. Restoration of thousands of kilometers of boreal streams channelized for timber floating during the first half of the 20th century mainly aims to improve in-stream habitat conditions for salmonid fishes due to their high economical value (Nilsson et al. 2015; Vehanen et al. 2010).

Recent evidence suggests, however, that biological communities respond weakly to stream habitat restoration (e.g. Jähnig et al. 2010; Miller et al. 2010; Palmer et al. 2010). Indeed, even substantial improvement of the physical habitat has not always translated into beneficial outcomes; two recent meta-analyses on the efficiency of in-stream restoration structures reported the overall benefits to be equivocal or non-existent (Thompson 2006; Stewart et al. 2009), whereas yet another one reported generally positive responses by salmonid fishes (Whiteway et al. 2010). For boreal streams, in-stream restoration has consistently enhanced stream habitat heterogeneity, with decreased flow velocities and increased bed complexity (e.g. Muotka and Syrjänen 2007; Gardeström et al. 2013), whereas biotic responses have been weak or completely lacking for most species (Nilsson et al. 2015).

These controversial outcomes have been explained partly by the restored habitat structures being degraded through time, resulting in fading biological responses within a few years after restoration (Palmer et al. 2010; Whiteway et al. 2010). However, recent evidence from boreal streams showed individual restoration structures to have changed little 10-20 years post-restoration, although substrate variability was still lower in the restored than in near-pristine streams (Marttila et al. 2015). A similar result was obtained by White et al (2011) for six Colorado mountain streams 21 years after they were restored using log drop structures. A minimum monitoring period of ten years has been suggested for judging the success of a restoration scheme, based on the argument that a restored site should experience variable climatic events and discharge conditions during the monitoring period (Kondolf and Micheli 1995), spanning preferably several fish generations (Johnson et al. 2005). Nevertheless, the volume of long-term studies able to identify the performance trajectory of stream restoration projects is low; monitoring that exceeds five years is already rare and a monitoring period exceeding ten years is exceptional. Some recent monitoring studies do span relatively long post-restoration periods (e.g. White et al. 2011; Pierce et al. 2013; Scrimgeour et al. 2015) but even these are based on repeated snapshot samples rather than on a trajectory approach whereby the same sites are followed regularly (often annually) through time.

We assessed the long-term (12 years post-restoration) effects of in-stream habitat restoration measures on the densities of three age-classes of juvenile brown trout (*Salmo trutta* L.) in six forest streams in northern Finland. All six streams were channelized to facilitate water transport of timber in the 1950s and 1960s, and restored by addition of logs and large boulders in 2001. In this spatially replicated multi-year study, we assessed whether the densities of juvenile trout were enhanced after restoration compared to unmodified (i.e. channelized) control sections. Furthermore, we assessed the relative effectiveness of two restoration structures to test whether the use of large woody debris produced any added long-term benefits compared to stony enhancement structures. Large wood modifies stream habitats by, for example, controlling the processes that shape the channel structure,

and by increasing the volume of stream pools and the retention of organic matter and nutrients (Roni et al. 2014). As many of these modifications are either directly or indirectly beneficial for stream salmonids, it is not surprising that large wood has often substantially enhanced salmonid habitat in streams (e.g. Roni et al. 2008; White et al. 2011). We therefore expected addition of both large wood and boulders to bring greater long-term benefits to trout populations than mere addition of boulders.

In our previous study (Vehanen et al. 2010), we used a spatially and temporally replicated Before-After-Control-Impact –design to assess the short-term effects (three years before and three years after) of restoration on brown trout densities and growth. This study was based on the same study design, but expands the recovery period of fish populations to 12 years after restoration. In Vehanen et al (2010), any potentially positive effects of restoration were overwhelmed by an extreme drought soon after the in-stream structures were installed. We now hypothesized that after a much longer recovery period, trout populations might gradually be achieving the full potential of the restoration scheme. Therefore, we expected trout densities to have increased from the drought, and also from the pre-restoration period. We expected this to be particularly evident in reaches where large wood was used for restoration because, in addition to many other advantages, large wood may provide safeguard for fish against extreme drought (Vehanen et al. 2010). Finally, we assessed whether the initial restoration structures had endured through the 12-yr post-restoration period.

MATERIAL AND METHODS

Study sites and study design

The study was conducted in six headwater streams in the Oulujoki watercourse, northeastern Finland (64 °N, 28 °E; Fig.1). These second-order forest streams have a mean annual flow of 0.29–

0.70 m³ s⁻¹ and mean width of 3–5.5 m. All the streams were channelized for timber floating in the 1950s and 1960s and they had therefore lost part of their structural complexity. Prior to restoration, the streams supported natural brown trout populations in sparse densities (mean of 1.6 age 0+ fish 100 m⁻²), a vast majority of them being resident (T. Vehanen, unpublished). Other fish species in these streams are grayling, *Thymallus thymallus* (L.), European bullhead, *Cottus gobio* L., stone loach, *Barbatula barbatula* (L.), minnow, *Phoxinus phoxinus* (L.), and burbot, *Lota lota* (L.) which all occur in very low densities (for more information of the study streams, see Vehanen et al. 2010).

Three 300 to 1100 m long reaches in each of the six streams, separated by at least 300-m long deep, slow-flowing sections, were selected for this study. The variable reach length was dictated by natural variability of stream morphology. A 350 m² study section was selected for fish monitoring in each study reach. Monitoring of fish densities started in June 1999. In late summer 2001, one randomly selected reach in each stream was restored to its full length using stones (cobbles and boulders), another one using stones + large woody debris (LWD) while the third reach was left unmodified as a control. Thus, our study followed a randomised-block design where each treatment was applied to one experimental unit (reach) in each block (river), in a randomised order (see Fig. 1. for an example).

Restoration measures are described in detail in Vehanen et al. (2010), and we therefore provide only a short summary here. Restoration work was mostly conducted using an excavator. Cross-sectional weirs were created using boulders (25-100 cm) in one of the reaches, and both logs (ø 30-40 cm) and boulders in the other restored reach. Both types of weirs were placed at intervals of five times the stream width, and the distance was adjusted by the slope of the river (Cowx and Welcomme 1998). Boulders removed from the stream during channelization and placed along stream margins were returned to the channel, and logs were anchored to riverbanks. Some individual boulders were

also placed between the weir structures, much like in a natural stream. In addition, spawning gravel (ϕ 0.5–5 cm) was added to each restored reach to create spawning grounds of 1–2 m². With the average gravel bed size (1.5 m², 20 cm thick), this resulted in 0.9 gravel beds and 1.4 m² added gravel per 100 m² of restored stream. The restoration measures used followed closely Finnish stream restoration protocols (Yrjänä 1998), with the exception that the use of large wood in stream restoration has been uncommon in Finland until very recently. These measures are known to be highly effective in enhancing streambed complexity (Muotka and Syrjänen 2007), thus increasing habitat availability for juvenile salmonids (see Koljonen et al. 2013). In channelized reaches, no weirs were created or spawning gravel added, i.e. they remained intact.

Stream habitat measurements

Vehanen et al. (2010) reported results from a habitat survey in all study sections before and immediately after the restoration work during late summer low-flow conditions. They showed that restoration created deeper and slower-flowing sections with higher habitat heterogeneity. This was indicated by, for example, substantially higher coefficient of variation of water velocity and higher depth, especially in sections with added wood.

Similar habitat surveys were repeated in August 2014 at a closely corresponding water level in all 18 study sections. Transects perpendicular to the flow ($n = 20$ –30 per site) were placed in 2–3-m intervals across each study section and measurements of water depth (cm), mean flow velocity (cm s⁻¹ at 0.6 * depth) and relative proportions of substrate size classes (modified Wentworth scale: fine sediments= <0.7 mm, sand=0.7–2 mm, fine gravel=2–8 mm, gravel=8–16 mm, small pebble=16–32 mm, pebble=32–64 mm, small cobble=64–128 mm, cobble=128–256 mm, small boulder=256–512 mm, boulder=512–1024 mm, boulder/bedrock ≥ 1024 mm) were recorded at about 1-m intervals along each transect. In addition to hydromorphological variables, we also estimated the percentage

cover of aquatic macrophytes (mainly mosses, particularly *Fontinalis* spp.) in a 1.0 m² quadrat around each survey point, and the amount of large wood (diameter > 5cm; m³ ha⁻¹) within each stream section.

In the 2014 surveys, we also visually estimated the physical condition of the constructed weirs and spawning sites, and their functioning in, for example, creating or enlarging a pool or increasing potential spawning area. These were rated into three categories using a classification system modified from Frissell and Nawa (1992): success, impaired or failed. When constructed weirs had largely remained physically intact and were roughly functioning as intended, they were considered as 'success'. A weir remaining in its original location but partly impaired (e.g. boulders had shifted from their initial position) and appearing largely ineffective, was considered 'impaired'. A weir or spawning site washed downstream, severely fragmented or armored, and thus unable of achieving its initial objective, was classified as 'failure' (Frissell and Nawa 1992). Evaluation of the physical condition of each structure was made by a person involved also in the 2001 post-restoration survey.

Fish monitoring

Monitoring of trout densities started in 1999, two years before restoration. Sampling was conducted in late-summer flow conditions in August each year, always by the same field crew, using three-pass electrofishing surveys. Fish were counted, measured for total length and weight, and then returned to their initial position in the stream. Scale samples were taken to estimate trout age. Densities of juvenile trout were analysed by age group: age-0+, age-1+, and age-2+ and older. Brown trout in our study area typically mature at the age of 2-3 years (Öhlund et al. 2008; Korsu et al. 2010). Densities of brown trout by age group were estimated using the software PROGRAM CAPTURE (model Zippin; Otis et al. 1978).

Statistical analyses

We used Principal Component Analysis (PCA) in 'vegan' package (Oksanen et al. 2013) in the R statistical environment to visualize differences in habitat characteristics among boulder-restored, LWD-restored and channelized sections, using transect means and CVs for depth, flow, macrophyte cover, and weighted average of substratum size. Although PCA is considered unsuitable for long and non-linear environmental gradients, it provides a very effective summary on data (such as ours) where gradient for most variables are reasonably linear (e.g. Gauch 1982). In the late summer and autumn 2002, one year after restoration, discharges were record-low (once-in-50-years drought), and remained so through the winter of 2002-2003 in most of northern Finland (Finnish Environment Institute 2002; 2004). Trout densities in our study streams collapsed during the drought and remained very low for several years following it (Vehanen et al. 2010). We therefore analysed trout densities for three separate time periods: 1999–2000 (before restoration), 2001–2006 (age 0+), 2001–2007 (age 1+), and 2001–2008 (age 2+) (drought impact, staggered by age class), and 2007–2013 (age 0+), 2008–2013 (age 1+), and 2009–2013 (age 2+) (long-term restoration impact). Electrofishing surveys were initially conducted three times a year (see Vehanen et al. 2010) but starting from 2007, sampling was reduced to one late-summer (August) survey each year; we therefore used only data from the late-summer survey for all study years in data analyses. All sections were considered independent experimental units, as trout migration among sections was very low; only 1.5 % of recaptured fish (N=1871; average capture rate 55 %) were found outside their original section in a mark-recapture study where trout larger than 10 cm were marked with dye marks indicating the site of the first capture (for more detail, see Vehanen et al. 2010).

The effects of the two restoration measures (boulders only, LWD + boulders) on densities of each age group were analysed by fitting a generalized linear mixed model with a negative binomial distribution (function `glmer.nb` in package `lme4` in R; Bates et al. 2014). Treatments (different

restoration measures) and the three time periods (before restoration, drought, and long-term restoration impact) were included as fixed factors, and sections nested within streams and years as random effects in the model. For all models, random effects were evaluated according to Zuur et al. (2009), and were found to improve the fit of the model (subsequent comparisons of log-likelihoods). All comparisons were made against the before-restoration period (1999-2000) and the channelized (no added structures) treatment (intercept); we thus focused on significant period x treatment interactions that indicate a difference from before-restoration conditions relative to channelized sections after restoration. Additional analyses were performed to compare differences in density among the drought-impact and long-term restoration impact -periods to assess if fish densities exhibited a long-term trend of restoration benefits despite being initially reduced by the drought.

RESULTS

In-stream habitat structure

A before vs. immediately after comparison of habitat characteristics in three of the study streams showed a decrease in water depth at all three sites, but the change was lowest in the LWD-restored sites (Table 1). The most drastic change to stream habitat structure was the loss of aquatic vegetation (mainly mosses) in the boulder-restored sites. By 12 years post-restoration, mosses had recovered fairly well in the boulder-restored sites, but remained low in the LWD-restored sites. Another distinct (and persistent) change caused by restoration was the increase of wood in LWD-restored sites (Table 1).

The first two axes of the Principal Component Analysis (PCA) on the 12-yrs post-restoration habitat data explained together 58.9 % of total variation of the original habitat variables (PCA1: 37.5%, eigenvalue 3.38; PCA2: 21.4%, eigenvalue 1.93; Fig. 2). Restoration-induced differences in the stream habitat were still distinct, with only the boulder-restored sites overlapping slightly with channelized sites in the ordination space. The LWD-restored sites were characterized, expectedly, by a substantially higher amount of wood and somewhat deeper stream pools. The channelized sections were characterized by a high cover of aquatic macrophytes and near lack of wood. Boulder-restored sections were intermediate in most respects, showing very low among-section variability (Fig. 2).

Qualitative observations of restoration structures

Visual observations showed that restoration structures had partly deteriorated over the 13 post-restoration years. Most (53 %) of the weirs constructed from both LWD and boulders had remained intact and were therefore considered as successes (Table 1). None of the LWD+ boulder -weirs was rated as failure. The majority (56 %) of boulder weirs were rated as impaired, mainly because some of the boulders had shifted from their initial position. Finally, 17 % of the boulder weirs were rated as failures because the initial construction was difficult to recognize (Table 1). All of the added gravel beds had disappeared and were therefore considered as failures (Table 1).

Trout densities

Densities of all age classes, and particularly of age-0+, showed considerable inter-annual variation (Fig. 3; see also Table S1 in supplementary material). In the boulder-restored sections, density of age-0+ trout showed a significant long-term increase and doubled itself, likely reflecting a long-term restoration impact (Fig. 3a, Table 3). In the LWD-restored sections, age-0+ densities first decreased in half, bordering at significance (drought vs. before restoration), but increased thereafter

significantly (drought vs. long-term response) (Table S1), possibly indicating a long-term positive response to restoration once the impact of drought was alleviated (Table 3). Age-1+ trout density also increased significantly in the LWD-restored sites, but only in the long run (Fig. 3b, Table 3). Age-2+ (and older) trout in the LWD+boulder sections first increased slightly (no drought effect), then continued to increase in the long term and multiplied their density by 2.8 times (Fig. 3c, Table 3, Table S1). No significant responses to mere addition of boulders were detected for either age-1+ or age-2+ trout (Table 3).

DISCUSSION

River restoration has become a widely-accepted approach to improve the well-being of stream organisms and ecosystems. With limited resources and funding, it is tempting to assume that simply increasing habitat heterogeneity will enhance the declining populations of salmonid fishes. However, quantitative reviews on the effectiveness of in-stream restoration on stream-dwelling salmonids have yielded inconclusive results (Stewart et al. 2009; Whiteway et al. 2010; Kail et al. 2015). In our study on the relative effectiveness of two restoration structures, three important results emerged: (i) restoration structures had generally positive but variable effects on all age classes of brown trout; (ii) the use of large wood combined with boulders was more beneficial than boulder additions alone, particularly for larger trout; (iii) long-term monitoring exceeding 10 years is needed to detect the outcome of a restoration project, as any shorter monitoring period will easily be obscured by natural hydrological fluctuation.

The positive restoration impact of LWD additions on older trout suggests that habitat availability was at least partly limiting these age groups. The LWD-restored sections were not only

characterized by deeper pools and higher amount of wood, but they also created more complex habitat in terms of substrate, depth and current. Furthermore, the LWD-structures persist well through time, indicating that changes in habitat structure are long-lasting (White et al. 2011; Roni et al. 2014). Large wood is known to control the physical processes that shape channel structure, increase pool volume and the retention of organic matter and nutrients (Roni et al. 2014). Placement of large wood has been successfully used to enhance salmonid habitat in channelized rivers elsewhere (Gowan and Fausch, 1996; Lehane et al. 2002; Roni et al. 2008; White et al. 2011). The amount of added wood per reach was on average $20\text{--}30\text{ m}^3\text{ ha}^{-1}$, which is clearly more than reported for most Finnish forest streams (Muotka and Syrjänen, 2007), but still substantially lower than the $100\text{ m}^3\text{ ha}^{-1}$ recommended by Kail et al. (2007). Despite the relatively low amount of added wood, the availability of pools, a key habitat structure for larger salmonids (e.g. Harvey et al. 1999; Roni and Quinn 2001), was increased. Pools are particularly important as wintertime habitat for larger salmonids, and their low availability has been suggested to limit the overwintering success of juvenile salmonids (e.g. Cunjak 1996; Mäki-Petäys et al. 1997; Weber et al. 2013). In our study streams, the added wood comprised of anchored logs without branches or twigs, and unanchored whole-tree trunks that facilitate the formation of debris dams have been reported to be even more effective as an in-stream restoration structure (Kail et al. 2007; Helfield et al. 2007). Overall, our results support those of Gardeström et al. (2015) in that the mere addition of stony enhancement structures does not modify the stream habitat sufficiently but larger particles (large boulders, large wood) is also needed for stronger ecological responses.

Drought is considered as a disturbance in flowing waters, causing both direct (e.g. water withdrawal, loss of habitat for aquatic organisms, and loss of stream connectivity) and indirect (e.g. deterioration of water quality, alteration of food resources, and changes in species interactions) effects on stream ecosystems (Lake 2003). In this study, densities of all trout age-classes in all

treatments were strongly reduced by the drought a year after the restoration, albeit less so for age-2+ than younger trout (Vehanen et al. 2010). Larger trout showed a tendency towards recovery almost immediately after the drought, and the positive response became stronger (and significant) through time. This indicates that the more diverse habitat created by LWD additions provided a safeguard against drought for the larger fish. Several previous studies have identified discharge variability as a key factor regulating stream salmonid populations (e.g. Elliott 1987; Lobon-Cervia 2007), and drought has been reported to cause a decline in population densities (Matthews and Marsh-Matthews 2003; White et al. 2008). Drought also decreases stream surface area, thereby causing potentially severe intercohort competition (Magoulick and Kobza 2003). According to recent climate change scenarios, extreme hydrologic conditions are likely to occur more often than previously, potentially modifying the amount and quality of salmonid habitats (Poff et al. 2002; Battin et al. 2007). Not only the magnitude of the change in discharge regimes but also the timing of extreme flood and drought events may have profound consequences on trout populations. Northern latitudes are predicted to experience shorter winters with more variable precipitation events and an increasing proportion of precipitation falling as rain (IPCC 2013). This forces stream organisms to cope with harsh wintertime conditions at a highly vulnerable life stage, i.e., eggs developing within gravel beds (Nilsson et al. 2015). Recent evidence indicates that regional climatic variability may overwhelm any effects of localized management efforts (e.g. Straile et al. 2003; Battin et al. 2007; Weber et al. 2013), strongly emphasizing the importance of placing local restoration efforts on a wider regional context, with the goal of ensuring habitat availability (e.g. drought refugia) for salmonids and other stream biota under variable flow conditions.

The response of age 0+ -trout differed from the older age classes as their density increased only in the boulder-restored sections long after restoration. In fact, age-0+ densities during the drought decreased more in the LWD-restored sections than in the other two treatments, Small trout (< 7cm)

usually occupy shallow (20-30 cm), slow-flowing (<50 cm/s) stream areas (Armstrong et al. 2003), whereas older trout prefer deeper stream pools ('the bigger fish-deeper habitat' relationship; Mäki-Petäys et al. 1997), often displacing younger trout to suboptimal habitats (Kaspersson et al. 2010; Louhi et al. 2014). Similar to our results, Langford et al. (2012) reported the density of age 0+ trout to be negatively correlated with the amount of LWD, due mainly to the deeper stream habitat they created. Further, in an experimental study, Gustafsson et al. (2014) detected a positive growth response to wood additions by larger, but not by small (age-0+) brown trout. Thus, addition of wood cannot be considered as an all-embracing solution to salmonid habitat restoration but should be complemented by the use of stony enhancement structures to ensure availability of suitable stream habitat for all trout age-classes.

The LWD-restored sections had a substantially lower cover of aquatic macrophytes compared to the boulder-restored sections. In our study sites, macrophytes consisted mainly of mosses that use rhizoids to anchor themselves to the substrate, and they were likely better able to attach onto the coarser surface of boulders than of logs. Aquatic mosses may be important habitat particularly for smaller fish, as they create shelter from the current (Eklöv and Greenberg 1998; Heggenes and Saltveit 2002). Our streams are dominated by *Fontinalis* spp mosses which often form extensive moss beds that cover large areas of the stream bed (Muotka and Virtanen 1995). Louhi et al. (2011) reported low responses of benthic macroinvertebrates, the main food resource of salmonids, to in-stream restoration, explaining this partly through the slow renewal of aquatic bryophytes in recently restored streams. Mosses also contribute importantly to key ecosystem processes, such as organic matter retention (Muotka and Laasonen 2002; Koljonen et al. 2013). Consequently, the low cover of aquatic bryophytes in restored streams may have far-reaching effects on benthic invertebrates, and eventually on underyearling trout, due to reduced availability of shelter and food.

In our previous study based on a shorter monitoring period (three years before and three after restoration; Vehanen et al. 2010), we found few detectable effects on brown trout populations in either of the restoration schemes. Only age 2+ and older fish benefited from the added LWD which seemed to provide some safeguard against the extreme drought. With a much longer monitoring period of this study, we were able to detect positive outcomes of LWD on all age classes of juvenile trout. This highlights the critical need for long-term monitoring for the evaluation of stream restoration success, particularly if the target species have a relatively long reproductive cycle and exhibit naturally high population variation related to hydrological variability; obviously, salmonid fishes are a prime example of lotic species with these characteristics (Elliott 1987; Lobon-Cervia 2007). The outcomes from shorter-term monitoring programs are likely to be highly context-dependent, varying in response to timing of the monitoring period in relation to hydrological and other environmental variability, thus confounding the reliable detection of restoration success (or lack of it) (Feld et al. 2011).

Despite the generally positive restoration impact, the densities of trout were still low in all restored reaches twelve years after restoration. For example, the mean density of age 1+ trout in LWD-restored sections was 3.0 fish 100 m⁻², which is close to the values reported for other restored streams in adjacent watersheds (Luhta et al. 2012). Obviously, if the initial population density of the target species is very low in all parts of the river system, it cannot be expected to colonise the restored habitat via natural immigration (Johnson et al. 2005; Hughes 2007). Therefore, the improvement of summertime rearing habitat is unlikely to be a successful restoration strategy unless accompanied by other management actions. The restoration attempts monitored by us failed to provide trout with improved spawning conditions: of all the added structures, spawning grounds clearly deteriorated through time (see also Marttila et al. 2015). Palm et al. (2007) showed that carefully positioned gravel beds may indeed enhance the reproductive success of brown trout.

However, boreal streams are naturally gravel-poor (Rosenfeld et al. 2011) and excessive addition of spawning gravel, or stocking of young salmonids, to restored streams may lead to increased mortality at older age classes beyond the limits of carrying capacity (Einum et al. 2008). Although our study sites are not seriously stressed by land use activities, and water quality should not be limiting to trout, it may well be that much higher population densities cannot be achieved in these naturally unproductive forest streams. Nevertheless, our results do suggest that in-stream restoration may be a successful strategy to safeguard trout populations from the vagaries of climate-change induced hydrological variability. To show that this really is the case, long-term monitoring of trout populations is needed to ascertain that the monitoring period will include hydrological extremities (spates, drought). To this end, even 12 years of post-restoration monitoring (as in this study) may be too short, and results from any shorter periods may lead to biased conclusions and inappropriate management recommendations.

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Figure legends

Fig. 1. Location of the study streams in River Oulujoki basin, eastern Finland. One stream is shown as an example of treatment positioning within streams; treatments were positioned in a randomized order within each block (stream). Three 300 to 1100 m long study reaches in each of the six streams were separated by at least 300-m long deep, slow-flowing sections.

Fig. 2. Principle component analysis of the in-stream habitat structure. Each polygon encloses all observations for a treatment. Arrows indicate the relative importance and direction of change of each variable. Solid line = channelized sections, dashed line = boulder-restored sections, dotted line = LWD+boulder restored sections.

Fig. 3. Mean densities of brown trout of A) age-0+, B) age-1+ and C) age-2+ and older in the late summer electrofishing surveys from 1999 to 2013. Open circles = channelized sections, grey circles = boulder-restored sections, black circles = LWD+boulder -restored sections. Solid line indicates the timing of restoration in July 2001 (end of the before period), dot-dash line indicates the onset of the drought-impact period in 2002, dashed line indicates the end of the drought-impact period (2001–2006 (age 0+), 2001–2007 (age 1+), and 2001–2008 (age 2+) (drought impact, staggered by age class), and the onset of the final monitoring period (long-term restoration impact; 2007–2013 (age 0+), 2008–2013 (age 1+), and 2009–2013 (age 2+)). For the ease of interpretation, only mean values are shown; for information about standard errors around the means, see Table S2 (supplementary material).

Table 1. Mean (± 1 SE) values for the key in-stream habitat characteristics of each restoration treatment at summer low-flow conditions before, a year after and 12 years after the restoration. – no data available.

	Depth cm <i>Mean $\pm$ S.E.</i>	Velocity cm s ⁻² <i>Mean $\pm$ S.E.</i>	Vegetation cover % <i>Mean $\pm$ S.E.</i>	LWD (m ³ m ⁻²) <i>Mean $\pm$ S.E.</i>
<i>Before</i>				
Channelized	20.2 $\pm$ 1.0	-	37.9 $\pm$ 3.8	-
Boulder	23.4 $\pm$ 1.5	-	41.7 $\pm$ 3.3	-
LWD+boulder	22.1 $\pm$ 1.4	-	23.9 $\pm$ 2.7	-
<i>Immediately after</i>				
Channelized	12.1 $\pm$ 0.5	21.3 $\pm$ 1.3	27.8 $\pm$ 2.1	0
Boulder	14.7 $\pm$ 0.6	23.8 $\pm$ 1.8	14.6 $\pm$ 1.2	0
LWD+boulder	18.5 $\pm$ 1.0	21.8 $\pm$ 1.9	19.2 $\pm$ 1.9	6.5 $\pm$ 0.3
<i>Long after</i>				
Channelized	16.6 $\pm$ 0.6	27.5 $\pm$ 1.2	33.3 $\pm$ 2.3	0
Boulder	21.4 $\pm$ 0.7	29.4 $\pm$ 1.3	34.4 $\pm$ 1.9	0
LWD+boulder	23.2 $\pm$	25.4 $\pm$ 1.3	22.0 $\pm$ 2.1	7.9 $\pm$ 0.3

Table 2. Number (and %) of weirs rated as success, impaired or failure in each of the two types of restoration schemes. For spawning sites, only the percent of observations is reported.

Class	Boulder–restored	LWD+boulder–restored	Spawning sites
	n (%)	n (%)	%
Success	5 (27.8)	9 (52.9)	0
Impaired	10 (55.6)	8 (47.1)	0
Failure	3 (16.7)	0 (0)	100
Total	18	17	100

Table 3. Parameter estimates from the generalized linear mixed model explaining variation in density of three age-classes of juvenile brown trout, given as treatment contrasts. All comparisons were made against the before-restoration period (1999-2000) and the channelized (no added structures) treatment (intercept). Other treatments were boulder additions and LWD+boulder (LWD+b) additions. Other time periods were drought impact (2001–2006 (age 0+), 2001–2007 (age 1+), and 2001–2008 (age 2+), and long-term restoration impact (age 0+: 2007–2013; age 1+: 2008–2013, and age 2+: 2009–2013). Only interaction terms are reported as main effects are uninterpretable under this design. Significant interaction P-values (< 0.05) are given in bold, and P-values bordering at significance (< 0.10) are in italics.

	Age 0+			Age 1+			Age 2+ and older		
	<i>Estimate ± S.E.</i>	<i>t</i>	<i>P</i>	<i>Estimate ± S.E.</i>	<i>t</i>	<i>P</i>	<i>Estimate ± S.E.</i>	<i>t</i>	<i>P</i>
Intercept	-5.22 ± 0.99	-5.25	<0.001	-3.95 ± 0.56	-7.07	<0.001	-4.34 ± 0.45	-9.72	<0.001
Drought x boulder	0.54 ± 0.78	0.69	0.490	0.59 ± 0.44	1.34	0.182	0.60 ± 0.40	1.50	0.133
Long-term x boulder	1.48 ± 0.74	2.00	0.045	0.67 ± 0.43	1.55	0.120	0.41 ± 0.41	1.00	0.319
Drought x LWD+b	-1.38 ± 0.75	-1.84	<i>0.066</i>	0.40 ± 0.43	0.93	0.355	0.74 ± 0.39	1.88	<i>0.060</i>
Long-term x LWD+b	-0.13 ± 0.72	-0.18	0.858	0.86 ± 0.41	2.09	0.036	1.10 ± 0.40	2.73	0.006
Drought vs. long-term boulder*	0.94 ± 0.56	1.68	<i>0.094</i>	0.08 ± 0.38	0.21	0.834	-0.19 ± 0.30	-0.64	0.520
Drought vs. long-term LWD+b*	1.25 ± 0.55	2.26	0.024	0.47 ± 0.36	1.31	0.191	0.36 ± 0.28	1.27	0.206

* Comparisons were made against drought period 2001–2006 (age 0+), 2001–2007 (age 1+), and 2001–2008 (age 2+) and the channelized (no added structures) treatment (intercept).

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Fig.1. Location of the study streams in River Oulujoki basin, eastern Finland. One stream is shown as an example of treatment positioning within streams; treatments were positioned in a randomized order within each block (stream). Three 300 to 1100 m long study reaches in each of the six streams were separated by at least 300-m long deep, slow-flowing sections.

101x71mm (300 x 300 DPI)

SUPPLEMENTARY MATERIAL

Table S1. Mean (± 1 SE) densities (100 m^{-2}) of the three brown trout age classes (age 0+, 1+, and 2+ and older) in each treatment throughout the monitoring period. Solid line indicates the timing of restoration in July 2001 (end of the before period), dot-dash line indicates the onset of the drought-impact period in 2002, dashed line indicates the end of the drought period (2001–2006 (age 0+), 2001–2007 (age 1+), and 2001–2008 (age 2+) (drought impact, staggered by age class), and the onset of the final monitoring period (long-term restoration impact; 2007–2013 (age 0+), 2008–2013 (age 1+), and 2009–2013 (age 2+)).

Age 0+ <i>Year</i>	Channelized		Boulder		LWD+boulder	
	<i>Mean</i>	<i>S.E.</i>	<i>Mean</i>	<i>S.E.</i>	<i>Mean</i>	<i>S.E.</i>
1999	2.17	1.93	0.18	0.18	5.20	1.66
2000	6.13	4.21	2.70	1.37	3.43	1.19
2001	1.74	1.67	2.17	1.73	0.71	0.42
2002	4.49	3.45	1.69	1.52	1.77	0.92
2003	2.38	2.19	0.72	0.45	0.43	0.23
2004	3.52	2.67	0.52	0.33	1.57	1.31
2005	1.04	0.68	4.02	1.80	1.45	0.88
2006	3.60	3.60	1.06	0.47	2.83	1.49
2007	4.25	4.25	2.25	1.74	8.13	5.15
2008	3.32	3.19	0.52	0.45	5.41	3.50
2009	2.61	2.56	3.09	2.10	1.99	1.35
2010	3.64	3.48	5.50	3.00	8.02	6.18
2011	0.35	0.35	2.57	1.47	1.99	0.98
2012	0.59	0.59	1.39	1.32	0.68	0.62
2013	3.30	1.52	4.25	1.83	6.14	2.06
Age 1+ <i>Year</i>	Channelized		Boulder		LWD+boulder	
	<i>Mean</i>	<i>S.E.</i>	<i>Mean</i>	<i>S.E.</i>	<i>Mean</i>	<i>S.E.</i>
1999	2.97	1.14	2.44	0.93	3.82	2.07
2000	2.56	1.26	0.90	0.31	3.94	2.06
2001	5.41	3.47	2.82	1.30	3.56	0.99
2002	1.93	1.03	1.32	0.48	2.10	1.09
2003	1.25	0.68	1.82	0.89	2.24	0.80

2004	0.61	0.21	0.79	0.30	1.24	0.556
2005	1.26	0.74	0.91	0.44	2.60	1.82
2006	2.32	0.60	3.22	1.28	4.77	2.00
2007	0.96	0.47	1.23	0.47	4.27	2.07
2008	1.83	0.92	1.79	1.50	5.46	2.38
2009	3.03	2.01	1.96	0.88	4.79	2.58
2010	1.23	0.73	1.59	1.32	1.95	0.70
2011	1.28	0.81	1.98	1.54	1.89	0.94
2012	1.73	1.11	2.04	1.31	2.85	1.21
2013	0.34	0.34	2.77	2.51	1.19	0.83

Age 2+ and older	Channelized		Boulder		LWD+boulder	
	<i>Mean</i>	<i>S.E.</i>	<i>Mean</i>	<i>S.E.</i>	<i>Mean</i>	<i>S.E.</i>
1999	1.36	0.42	0.99	0.49	0.84	0.35
2000	1.99	0.58	1.16	0.38	1.16	0.35
2001	0.85	0.37	0.78	0.28	1.41	0.66
2002	1.38	0.78	1.45	0.60	1.69	0.62
2003	0.71	0.21	1.08	0.52	1.07	0.34
2004	1.20	0.67	0.76	0.42	0.96	0.29
2005	0.61	0.25	1.14	0.31	1.40	0.50
2006	1.16	0.38	1.42	0.43	1.59	0.80
2007	0.47	0.18	0.63	0.32	0.70	0.33
2008	0.45	0.39	0.78	0.52	1.83	0.88
2009	1.61	0.67	2.44	1.82	4.68	2.38
2010	1.15	0.62	0.64	0.26	3.64	1.91
2011	0.63	0.35	1.50	1.14	1.28	0.58
2012	0.94	0.32	0.76	0.62	1.53	0.55
2013	1.68	1.01	1.88	1.09	3.30	1.84