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REVIEWS

Synthesis of habitat restoration impacts on young-of-the-year salmonids in boreal rivers

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Abstract River restoration offers the potential to enhance biological integrity, often measured as fish population changes. We used a meta-analytical approach to synthesize density responses to in-stream habitat restoration by young-of-the year (YOY) brown trout and Atlantic salmon in 28 rivers (overall 32 restoration projects) in Finland. We also examined which local and watershed-scale factors most influenced restoration success. Finally, we conducted an expert survey to obtain an independent estimate of a sufficient density enhancement for restoration to be considered successful. Despite strong context-dependency, habitat restoration had an overall positive effect on YOY salmonid density. When compared to target levels derived from the expert survey, density responses mainly reached the minimum expected success rate, but remained short of the level considered to reflect distinct success. Variability in restoration responses of trout was linked mainly to river size, predominant geology, water quality and potential interspecific competition (trout vs. European bullhead). Fishing mortality tended to obscure positive effects of restoration and stocking by YOY fish affected negatively trout's response to restoration,

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supporting a shift towards self-sustainable schemes in fisheries management. These results imply that habitat restoration is a useful approach for improving the ecological and conservational status of salmonid populations in boreal rivers. To further improve the success rate, and thereby public acceptance, of restorations they need to be complemented by other management measures that enhance the potential for the recovery of threatened salmonid populations.

Keywords Atlantic salmon · Brown trout · Habitat improvement · Juvenile salmonids · Meta-analysis · River restoration

Introduction

River restoration is undertaken worldwide to restore degraded habitats, ecosystem processes, biotic communities and the services they provide. Traditionally, restoration has been species-driven, recreating channel forms believed to be favorable for a particular species or species group (Clarke et al. 2003; Palmer et al. 2010). In-stream habitat restoration then aims at increasing habitat availability for the target species, potentially enhancing fish productivity and reproduction, particularly of the declining salmonid populations (Roni et al. 2008; Stewart et al. 2009; Koljonen et al. 2012).

Salmonid fishes are widely regarded as indicators of stream restoration success (Roni et al. 2008). For instance, almost two-thirds of project managers in Washington State reported some type of salmon survey or count as the primary measure for evaluating their projects, and the top four biological measures were all salmonid related (Bash and Ryan 2005). Although the nature of evaluation data varies widely (Bash and Ryan 2005), it typically includes some type of monitoring, results of which often remain in grey literature or completely unpublished (but see Roni and Quinn 2001; Louhi et al. 2016). The synthesis of these data would provide valuable knowledge of restoration success and the factors affecting it (Stewart et al. 2009; Thomas et al. 2015).

Previous studies on in-stream restoration success have generally reported an increase in streambed and flow diversity (e.g. Muotka and Syrjänen 2007; Marttila et al. 2016a; Poppe et al. 2016) and salmonid rearing habitat (e.g. Korsu et al. 2010; Koljonen et al. 2012). However, studies focusing on salmonid reproductive success and juvenile abundances have shown highly variable responses. For example, Stewart et al. (2009) argued that the high variability of salmonid responses does not support widespread use of in-stream restoration structures, particularly in larger streams. In a review from northern Europe, Nilsson et al. (2015) showed that only one of the five papers that studied fish populations demonstrated a positive response to in-stream restoration. Similarly, Luhta et al. (2012) found slightly positive, but stream-specific effects on the density of young-of-the-year (YOY) brown trout. In contrast, Whiteway et al. (2010) and Roni et al. (2008) concluded that in-stream habitat improvement generally benefits juvenile salmonids, although the responses vary widely among species and life stages.

The inconsistency of biological responses results partly from differences in habitat enhancement practices (Palm et al. 2007; Louhi et al. 2016) but it also raises the question of whether other regional and local factors might enhance or constrain the biotic recovery of restored sites (Palmer et al. 1997; Muhar et al. 2016). Environmental variables are linked to biological productivity at variable spatial scales and may therefore shape the restoration outcome (Palmer et al. 1997). Properties of the surrounding catchment (e.g. geomorphology and river basin size) influence in-stream conditions (discharge, water temperature and chemistry, sedimentary processes and input of allochthonous material; Foldvik et al. 2017) which in turn play an important role in defining whether a restoration project meets its ecological goals. Species interactions and fishing mortality may also alter salmonid densities and overwhelm any positive effects of restoration (Palmer et al. 1997; Whiteway et al. 2010). Although several studies have emphasized the potential importance of these factors (Roni et al. 2008; Bernhardt and Palmer 2011), tests of their relative role based on extensive field data are largely missing (Kail et al. 2012; Lorenz and Feld 2013).

In Fennoscandia, the earliest stream restoration attempts took place about 40 years ago, with the aim of improving the spawning and nursery areas for salmonids, particularly brown trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*), in rivers channelized for timber floating. More recently, improving the overall ecological status of rivers has become a key objective of restoration, endorsed by the implementation of the EU Water Framework Directive (WFD) and associated legal obligations. In Finland, 35% of total river length still remains below the minimum goal of good ecological status (SYKE 2013). In many cases, achieving this goal requires habitat restoration that should lead to a measurable increase in ecological quality. Prioritizing restoration efforts requires better understanding of their potential to improve river status (Lorenz and Feld 2013).

The aim of this study was to provide a more complete understanding of the success (or lack of it) of in-stream restoration in enhancing juvenile salmonid densities and of the factors that influence restoration success. Instead of assessing restoration responses on a case-by-case basis, our study synthesizes data from multiple restoration projects. We focused on YOY fish because their occurrence and densities are considered to indicate successful reproduction and fry survival (Lorenz et al. 2013). Our study focuses on the two salmonid species (brown trout; Atlantic salmon) important in Finnish streams and rivers but the results should be useful for fisheries managers in other boreal streams where largely similar techniques have been used for salmonid habitat enhancement. By using an extensive electrofishing database, we examined (1) whether restoration enhanced juvenile salmonid densities; (2) whether these two species with partly different habitat requirements (see Armstrong et al. 2003; Jonsson and Jonsson 2011) responded differently to similar restoration measures, (3) whether these improvements, if any, were considered sufficient by stream managers and fisheries experts, and (4) which in-stream and watershed-scale factors influenced salmonid responses to restoration.

Materials and methods

Study sites and study design

The dataset consisted of electrofishing surveys collected by our research partners in 28 rivers across 1978–2014. We included all surveys that provided data on salmonid densities for at least 2 years before and 2 years after restoration for a given site (overall number of restoration sites 88, a total of 1196 electrofishing surveys; Table S1). Time between the first and the last sampling year for a site varied from 6 to 33 years. The rivers are located in 17 watersheds across Finland (60°–68° N, 22°–30° E) and they are either medium-sized (river basin size 100–1000 km^2, 15 rivers) or large (1000–10,000 km^2, 12 rivers) lowland rivers, with one small river (29.8 km^2) being also included. Drainage areas of the study rivers were dominated by peatland (8 rivers), mineral soil (17 rivers) or clay (3 rivers).

Hydromorphological degradation of the study sites was mainly caused by channelization for timber floating between the late nineteenth and mid-twentieth century. Rivers were straightened and narrowed, and boulders were removed from the channel, to facilitate timber floating (Nilsson et al. 2015; Syrjänen et al. 2018). Our dataset represents typical Fennoscandian running water habitats, including a wide environmental gradient in terms of size, water chemistry, stream gradient and catchment land use (mainly forestry) intensity, excluding only the smallest headwater streams (< 5 m wide) where timber floating was not practiced.

Restoration measures

As road transport of timber became economically feasible, timber floating largely ceased by the end of the 1970s. Soon thereafter, the first efforts were launched to restore the structural complexity of the rivers. To date, the majority of channelized rivers has been restored, in some cases more than once (Nilsson et al. 2015; Syrjänen et al. 2018). Usually this means returning boulders back into the river and adding in-stream structures, such as boulder dams and flow deflectors, to modify the flow and scour patterns. In addition, side channels are re-opened to increase the availability and connectivity of riverine habitats, providing more refuge areas for juvenile salmonids during adverse flow conditions (Yrjänä 1998; Nilsson et al. 2005). Also spawning gravel is routinely added in suitable places (in terms of water depth and current velocity) immediately after restoration to enhance the establishment of self-sustaining salmonid populations. In Finland, restoration projects usually target the entire main stem of river networks, with the activities focusing mainly on riffle and run sections of the rivers. Accordingly, most of the projects included in our study aimed at restoring all, or at least several, riffle-pool sequences within a river.

Study species and estimation of juvenile densities

Brown trout was the target species of restoration in most of our study rivers (n = 27, Table S1) whereas salmon was the main target species in only seven rivers (Table S1). Populations of Atlantic salmon and brown trout included in our study contain both sea-running and freshwater populations. Both species belong to the 2010 Red List of Finnish Species and are classified as vulnerable to critically endangered (Rassi et al. 2010). Originally, salmon occurred in 20 rivers along the Finnish Baltic coast, but nowadays indigenous, self-sustaining salmon stocks are only found in rivers Tornionjoki and Simojoki (HELCOM 2011). Brown trout is distributed throughout Finland but its numbers have decreased drastically, and original, self-supporting migratory stocks are rare. Migratory and resident trout may occur and reproduce within the same river system (Huusko et al. 2018) but their exact proportions in any specific population are unknown to us.

Fish data were collected in wadeable riffles following the Finnish electrofishing standard (Vehanen et al. 2013). The area of an electrofishing site was typically 100–300 m^2 and data for replicate sites, if any, within a river section were pooled. Fish sampling focused on riffles because several studies in the same geographical area have shown that while larger fish tend to occupy deeper stream pools, the youngest size classes of both brown trout (Mäki-Petäys et al. 1997) and Atlantic salmon (Mäki-Petäys et al. 2005) are mainly found in riffle sections of rivers. An increased fish density in the restored study sites might reflect behavioural responses by fish (immigration to the best available habitats) rather than demographic responses within a restored reach. However, in another study (Syrjänen et al. 2014), we counted the number of spawning redds in eight of the trout rivers included in this survey, and about 60% of the electrofishing sites in these eight rivers contained redds with eggs. In the rest 40% of the sites, redds were observed within tens of metres from the electrofishing sites. We therefore believe it is safe to assume that the wild YOY fish in our electrofishing catches had mainly emerged within the same river section.

Fish densities were counted from the raw data or compiled from reports. If a site was fished by multiple-pass removal, catchability values were used (Table S1). For one-pass method, fish densities (individuals/100 m^2) represented a direct catch or were generated using a river-specific or regional catchability (see Junge and Libosvarsky 1965). As we focused on density responses within a river, it was important to ensure that the estimation method was consistent across years within a river, whereas methodological differences between rivers should not bias our results (Whiteway et al. 2010; Thomas et al. 2015). Electrofishing methods were always the same before and after restoration and, in most cases, surveys before vs. after were conducted by the same field crew.

Our synthesis of YOY density responses was based on project-level data. A ‘project’ was defined as a compilation of restoration efforts within the same river and time period. If different sites within a river were restored at different times (i.e. $\geq$ 5 years between restoration efforts), they were considered as distinct projects (identified with different letters in Table S1).

Assessing restoration success: expert opinion

One of our aims was to examine whether the restoration-induced increase in YOY densities (if any) was sufficient to designate a restoration project successful from the salmonid fisheries perspective. Therefore, we conducted a questionnaire survey among the key Finnish water managers and fisheries/environmental consultants, both governmental and private, to identify appropriate target levels for YOY salmonid densities. An e-mail survey was sent to 25 recipients in different environmental agencies across Finland. They were selected to our survey because of their experience and expertise in river restoration and/or monitoring of fish densities in different regions. We asked the recipients to (1) define the minimum improvement in YOY salmonid (salmon and/or trout) density needed to designate a restoration effort successful, and (2) to shortly describe the restoration projects they have been involved in. Seventeen recipients replied to our survey, the response rate being 68%. The two most frequently stated indicators of success, representing different levels of expected improvement, were: (1) 1.1 $\times$ pre-restoration density (i.e. 10% increase; often defined as ‘any improvement indicates success’), and (2) 2 $\times$ pre-restoration density (‘distinct success’).

Potential factors affecting restoration outcome

The following factors that might potentially regulate restoration success were compiled for each project and were associated with the electrofishing data (Table S1):

(1) *Recovery time*, classified into four phases: before restoration, 1–4 years (short term), 5–8 years (middle term) and > 8 years (long term; up to 19 years) after restoration.
(2) *Latitude* as an indicator of geographical location.
(3) *River basin size*: medium 100–1000 km^2 and large 1000–10,000 km^2 (obtained from national database HERTTA managed by the Finnish Environment Institute, http://www.syke.fi/en-US/Open_information).
(4) *Predominant geology:* peatland or mineral soils (HERTTA).
(5) *Water quality* variables calculated as average values across the most recent 10 years (HERTTA; Tables SI and S2). Data on total phosphorus (totP) and pH were from the whole calendar year, whereas oxygen saturation (O_2%) was recorded for the winter months only (November to April). The water quality variables included in the analysis were assumed to potentially influence egg survival during the winter and thus YOY densities (Crisp 1996).
(6) The presence of *migratory obstacles* downstream of a restored site; indicator of habitat connectivity.
(7) Annual data on *stocking* of eggs, alevins and YOY. If no stocking was conducted, all observations of YOY were assumed to indicate natural reproduction.
(8) *Fishing pressure*: fishing forbidden or only catch-and-release (CR) fishing allowed; fishing allowed on license.
(9) *Species interactions*, density of a potential predator, burbot (*Lota lota*) and a competitor, European bullhead (*Cottus gobio*); data on these species were available for 21 rivers.

We used annual data on migratory obstacles, stockings, fishing pressure and species interactions, thus taking into account possible changes in these variables during the monitoring period.

Unfortunately, most projects did not include measurements of stream habitat structure so we were unable to include it as an explanatory variable in our meta-analysis. Nevertheless, we have made such measurements in several previous projects, the very consistent outcome being that the way river restoration is being conducted in Finland considerably enhances in-stream habitat heterogeneity (e.g. Muotka and Syrjänen 2007; Vehanen et al. 2010; Marttila et al. 2016a; see also similar results from Swedish streams, Polvi et al. 2014).

Statistical analysis

To synthesize restoration responses between two ‘treatments’ (before vs. after restoration) from multiple projects (n = 30 for trout and n = 7 for salmon), we used random effects model with restricted maximum likelihood estimator (REML; function rma in package metafor; Viechtbauer 2010). REML is recommended when differences in sampling methods and sample characteristics may introduce variability among true effects (Viechtbauer 2010). Mean difference between study treatment means (after–before mean densities) was compiled from each study and used to calculate the grand mean effect size and its bootstrapped 95% confidence intervals, separately for trout and salmon. Sample size (i.e., number of sampling sites in a project) was always equal between the two ‘treatments’, and the mean values were counted from the site-level data. We used an unweighted meta-analysis, because the use of empirically-based weighting in random-effects meta-analysis has been questioned recently (Shuster 2010; Shuster et al. 2010). There is also often ecological justification for using unweighted meta-analysis (e.g. Gruner et al. 2017). In our case, weighted analysis would have given undue emphasis on studies with very low salmonid numbers both before and after restoration, resulting in spuriously precise estimates of effect size (see Stewart 2010).

Models on the potential factors affecting restoration outcome were only constructed for trout because of the low number of salmon rivers (n = 7). YOY trout densities in medium and large-sized rivers (n = 26) 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). In our basic model, treatment (before and after restoration) was included as a fixed factor, and sites nested within rivers and years since restoration (before and after) as random effects. For all models, random effects were evaluated according to Zuur et al. (2009) and were found to improve fit of the model (comparisons of log-likelihoods). Comparisons were made either against the before-restoration period (for variables with the same value both before and after restoration; i.e., river basin size and predominant geology) or against the before-period × a variable (presence of migratory obstacles, fishing pressure, stockings, presence of European bullhead or burbot. For water chemistry variables and latitude, interaction was not included in the models to avoid any bias caused by varying numbers of fishing surveys in before vs after periods.

Unlike other GLMM´s, the model for recovery time was constructed for both salmon and trout. The model included the four time periods (before restoration, short, middle and long after restoration) as fixed factor, and sites nested within rivers and calendar year of restoration as random effects. Density responses between time periods were compared using each relevant time period as an intercept.

To relate fish density responses to expert opinions about restoration success we used a subset of 13 trout projects with reasonable pre-restoration densities (> one individual per 100 m^2). We thus excluded sites where trout were only sporadically observed before restoration. The expected response rates (minimum level of improvement; distinct success) derived from expert opinions were made commensurate with our density data by multiplying mean pre-restoration densities of each project by 1.1 or 2, respectively.

Results

Overall effects of restoration on salmonids

The overall effects of restoration were positive for both species, but the response was significant only for trout. Mean effect sizes (calculated as mean difference across studies between after–before densities) were, however, closely similar: 4.32 (95% CI = 1.14–7.50, n = 30,) for trout and 5.06 (95% CI = − 2.28–12.39, n = 7) for salmon (Fig. 1). The mean density of young-of-the-year brown trout was 3.09 fish 100 m^{-2} (range: 0–19) before restoration and 7.14 (0–31) after

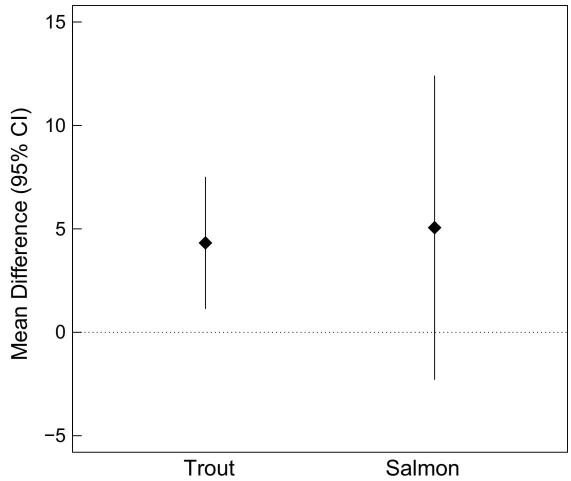


Fig. 1 Mean effect sizes, calculated as mean difference between study treatment means (after–before mean densities ± 95% bootstrap confidence intervals) for the effect of restoration on YOY brown trout (n = 30 restoration projects) and Atlantic salmon (n = 7) densities

it. Corresponding values for Atlantic salmon were 1.23 (range: 0–8) and 5.66 (0–15) fish 100 m^{-2}, respectively. Thus, we can say with 95% confidence (assuming a random effects model) that the effect of restoration on trout densities was at least slightly positive, whereas confidence limits for salmon overlap zero and therefore the restoration impact, cannot be considered significant. The trout response was positive (although not always significantly so) in 23 and negative in seven projects (Fig. 2a). Salmon response was positive in six projects and negative in one (Fig. 2b). The test for heterogeneity suggested no heterogeneity among true effects (trout: Q = 19.22, $df = 29$, $p = 0.916$; salmon: Q = 4.15, $df = 6$, $p = 0.656$).

Level of improvement in relation to experts' expectations

When the overall improvement in trout densities was compared to that expected by stream managers and other experts, the minimum success rate (1.1 × pre-restoration density; mean expected effect size = 0.73) was mostly exceeded (8 projects exceeded, 5 did not). However, the level considered as distinct success (2 × pre-restoration density; mean expected effect size = 7.27) was mostly not achieved (4 projects achieved, 9 did not).

Local and regional determinants of salmonid response

GLMM results indicated that salmon responses did not vary among the three post-restoration time periods. For trout, densities recorded shortly after restoration were somewhat higher than in the two subsequent periods (Table 1), whereas middle and long-term periods did not differ from each other.

Several environmental variables modified the responses of YOY trout to restoration. First, trout density response was more positive in mid-sized than in large rivers (Table 2). Trout response was also related to predominant geology and was less positive in rivers draining peatland-dominated catchments than in those surrounded by mineral soils. Compared to rivers draining mineral soils, rivers on peatland-dominated catchments had higher concentration of phosphorus and lower levels of pH and wintertime O_2 saturation (Table S2). Total phosphorus was negatively and wintertime oxygen saturation positively associated with trout density responses (Table 3). YOY trout response to restoration was also related to site location, with more positive responses in southern than northern Finnish rivers (Table 3).

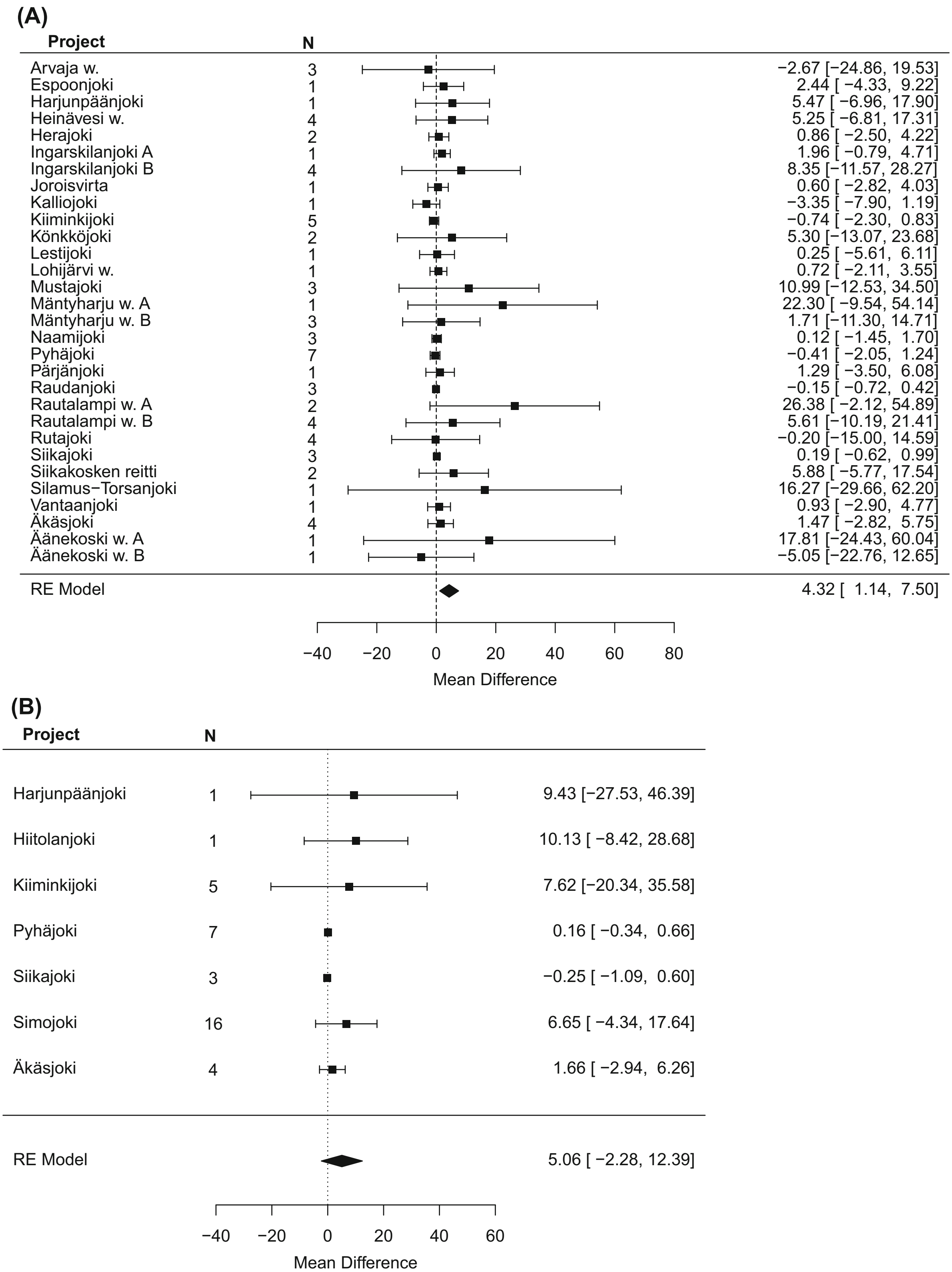
Our results also suggested that fishing regulations may influence trout responses to restoration. Trout density responses were more positive at sites where trout fishing was completely prohibited or only catch-and-release fishing was allowed compared to sites where fishing was allowed on license (Table 2). The effect of fishing regulations was not very strong, however, as the interaction only bordered at significance. We also found a negative interaction between trout density response and stocking of alevins/YOY, indicating that attempts to increase density through artificial colonization had an opposite effect. Stocking of eggs had no effect on trout responses (Table 2).

Restoration did not change densities of burbot ($z = -1.656$, $p = 0.098$), and neither did this piscivore affect the responses of trout to restoration (Table 2). European bullhead responded positively to restoration ($z = 2.082$, $p = 0.037$) and its presence reduced the response of trout (Table 2).

Discussion

Stream restoration offers the potential to enhance biological integrity, often measured as fish population changes (Jungwirth et al. 2000). Our synthesis of in-stream restoration projects in Finland demonstrated a highly context-dependent, but on average positive effect of restoration on YOY salmonid density. The positive overall response was significant for brown trout, but not for Atlantic salmon. Also the previous synthesis by Roni et al. (2008) and Whiteway et al. (2010) showed that although in-stream habitat improvements were generally beneficial for juvenile salmonids, responses varied between species. Interestingly, Whiteway et al. (2010) suggested that Atlantic salmon responded more than did brown trout. In our study, the size and direction of the effect sizes showed that the two species responded almost similarly to restoration. The difference in statistical significance likely reflects differences in sample size: the lower number of salmon projects resulted in greater variation in effect size. While this mainly results from the low number of remaining salmon rivers, it is also possible that restoration designed to support juvenile trout may not serve the habitat requirements of Atlantic salmon equally well. Although the juvenile stages of the two species have largely similar habitat requirements, there are also important differences. For example, brown trout are known to prefer deeper stream areas with moderate to low water velocities, whereas young Atlantic salmon tend to occupy faster-flowing and shallower stream areas (Heggenes 1996; Armstrong et al. 2003). Also the scarcity of overwintering habitats may restrict salmon populations even if summertime rearing habitats are improved (Palm et al. 2007; Koljonen et al. 2012). Such species-specific differences in habitat use and preference need to be better incorporated into restoration designs in the future.

Whether restoration is considered successful relates partly to expectations by various interest groups (Marttila et al. 2016b); a failure for one can be a success for another (Baker and Eckerberg 2016). A prerequisite for evaluating whether restoration has been effective is that project goals have been accurately defined a priori (Miller et al. 2016). In this study, we conducted an expert survey to identify their definitions for success. Comparing the observed trout responses to expected response rates indicated that


(A)
Project
N
Arvaja w. 3 −2.67 [−24.86, 19.53]
Espoonjoki 1 2.44 [−4.33, 9.22]
Harjunpäänjoki 1 5.47 [−6.96, 17.90]
Heinävesi w. 4 5.25 [−6.81, 17.31]
Herajoki 2 0.86 [−2.50, 4.22]
Ingarskilanjoki A 1 1.96 [−0.79, 4.71]
Ingarskilanjoki B 4 8.35 [−11.57, 28.27]
Joroisvirta 1 0.60 [−2.82, 4.03]
Kalliojoki 1 −3.35 [−7.90, 1.19]
Kiiminkijoki 5 −0.74 [−2.30, 0.83]
Könkköjoki 2 5.30 [−13.07, 23.68]
Lestijoki 1 0.25 [−5.61, 6.11]
Lohijärvi w. 1 0.72 [−2.11, 3.55]
Mustajoki 3 10.99 [−12.53, 34.50]
Mäntyharju w. A 1 22.30 [−9.54, 54.14]
Mäntyharju w. B 3 1.71 [−11.30, 14.71]
Naamijoki 3 0.12 [−1.45, 1.70]
Pyhäjoki 7 −0.41 [−2.05, 1.24]
Pärjänjoki 1 1.29 [−3.50, 6.08]
Raudanjoki 3 −0.15 [−0.72, 0.42]
Rautalampi w. A 2 26.38 [−2.12, 54.89]
Rautalampi w. B 4 5.61 [−10.19, 21.41]
Rutajoki 4 −0.20 [−15.00, 14.59]
Siikajoki 3 0.19 [−0.62, 0.99]
Siikakosken reitti 2 5.88 [−5.77, 17.54]
Silamus−Torsanjoki 1 16.27 [−29.66, 62.20]
Vantaanjoki 1 0.93 [−2.90, 4.77]
Äkäsjoki 4 1.47 [−2.82, 5.75]
Äänekoski w. A 1 17.81 [−24.43, 60.04]
Äänekoski w. B 1 −5.05 [−22.76, 12.65]
RE Model 4.32 [1.14, 7.50]
−40 −20 0 20 40 60 80
Mean Difference
(B)
Project
N
Harjunpäänjoki 1 9.43 [−27.53, 46.39]
Hiitolanjoki 1 10.13 [−8.42, 28.68]
Kiiminkijoki 5 7.62 [−20.34, 35.58]
Pyhäjoki 7 0.16 [−0.34, 0.66]
Siikajoki 3 −0.25 [−1.09, 0.60]
Simojoki 16 6.65 [−4.34, 17.64]
Äkäsjoki 4 1.66 [−2.94, 6.26]
RE Model 5.06 [−2.28, 12.39]
−40 −20 0 20 40 60
Mean Difference

◀**Fig. 2** Forest plots showing the effect of in-stream habitat restoration on **a** brown trout density in 30 projects (w. = watercourse) and **b** on Atlantic salmon density in seven projects. 'Mean difference' refers to mean difference between study treatment means (after–before mean densities ± 95% bootstrap confidence intervals). Diamond illustrates the grand mean effect size (and its bootstrapped 95% confidence intervals) calculated from project-specific mean differences. N = number of study sites within a project

restoration projects had largely reached the minimum success level, but remained short of distinct success. A few respondents expressed very high expectations for restoration, suggesting that a successful project should bring the fish population back to its natural, pre-channelization state (> 30 individuals/100 m^2). This highly ambitious goal was rarely achieved, as post-restoration trout densities remained mainly lower than those typically observed in near-pristine streams in Finland (Syrjänen et al. 2015). On the other end of the continuum, one respondent suggested that, for endangered populations, such as the landlocked form of Atlantic salmon and sea-running populations of brown trout (Rassi et al. 2010), even a slight increase is significant. Indeed, even low returns from restored reaches may contribute to the overall viability of a fish population (Waldman et al. 2016).

Studies reporting post-restoration recovery times of stream fishes are rare (Thomas et al. 2015). Our results

Table 1 Parameter estimates from the generalized linear mixed models examining differences in YOY salmonid densities between time periods (short after restoration vs before restoration, middle and long term after restoration)

	Trout				Salmon			
	Estimate	SE	z value	P	Estimate	SE	z value	*p*
Intercept (Short)	0.736	0.393	1.872	0.061	0.432	0.694	0.623	0.534
Before	− 0.713	0.128	− 5.586	**< 0.001**	− 1.024	0.244	− 4.201	**< 0.001**
Middle	− 0.377	0.165	− 2.278	**0.023**	− 0.138	0.297	− 0.465	0.642
Long	− 0.395	0.165	− 2.39	**0.017**	0.028	0.434	0.064	0.949

Significant *p* values are in bold

Table 2 Results of generalized linear mixed models examining YOY brown trout responses to treatment × explanatory variable interactions ('treatment' referring to before vs. after restoration) Comparisons were made either against the before-restoration period (explanatory variables with the same value both before and after restoration; i.e., river basin size and predominant geology) or against the before-period × a variable (presence of migratory obstacles, fishing pressure, stockings, presence of European bullhead or burbot). Only interaction terms are reported, as the main effects are uninterpretable under this design

Source (intercept in brackets)	Model intercept	Estimate for treatment × variable	SE	z value	*p*
Size: medium (vs. large)	− 0.759	1.129	0.238	2.199	**0.028**
Geology: peat (vs. mineral)	0.731	− 2.588	0.393	− 3.304	**< 0.001**
Obstacles: present (vs. absent)	0.162	− 0.166	0.517	0.987	0.324
Fishing pressure: forbidden/CR (vs. allowed on license)[a]	− 0.355	0.888	0.288	− 1.882	0.06
Stockings					
Eggs (vs. no stockings)	− 0.05	0.674	0.486	− 0.386	0.70
Alevins/YOY (vs. no stockings)	− 0.05	− 0.033	0.45	− 2.56	**0.01**
European bullhead	− 2.256	− 0.916	0.025	− 3.823	**< 0.001**
Burbot	− 1.265	− 0.324	0.241	1.761	0.078

Significant *p* values are in bold. See more details on explanatory variables in the text

[a]CR = catch-and-release fishing

Table 3 Parameter estimates from the generalized linear mixed models examining effects of covariates on YOY trout density responses

	Model intercept	Estimate for treatment	SE	z value	*p*
Latitude	− 0.582	− 1.36	0.344	− 3.958	**< 0.001**
TotP	0.818	− 0.038	0.019	− 2.024	**0.043**
Winter-O_2%	− 0.191	0.832	0.304	2.735	**0.006**
pH	− 2.992	0.428	1.452	0.295	0.768

Significant *p* values are in bold

suggested that trout densities were higher immediately after restoration than during later phases. Similarly, Höckendorff et al. (2017) reported an initially high fish response that stabilized approximately 7 years after restoration. One explanation for fading trout responses could be a gradual deterioration of gravel beds after restoration (e.g. Marttila et al. 2016a). Louhi et al. (2016) reported that only long-term monitoring (up to 10–12 years) of trout densities revealed the success of in-stream habitat restoration while short-term monitoring (3 years post-restoration) of the same sites yielded less encouraging results (Vehanen et al. 2010). In any case, the inherently large interannual variability of salmonid populations (Roni et al. 2002; Muotka and Syrjänen 2007; Louhi et al. 2016) makes the detection of restoration responses challenging and requires monitoring that spans several fish generations (Kondolf and Micheli 1995; Roni et al. 2015). Some of our data spanned almost 20 years post-restoration, enabling us to examine the long-term trajectory of the restoration outcome. Although the year of restoration was considered as a random effect in our analyses, the fact that the recovery periods among our study rivers were not synchronized may have influenced our capacity to detect temporal trends.

The strongest positive responses for trout were recorded in mid-sized rivers. This finding supports the view that restoration is more challenging in larger rivers: the larger the river, the more complex are the environmental issues associated with the upstream drainage basin (National Research Council 1992). Similarly, Stewart et al. (2009) concluded that in-stream structures may be less effective in larger rivers than in smaller streams, whereas Whiteway et al. (2010) showed no difference in density responses between different-sized streams.

The weaker responses by trout in peatland-dominated river basins may be related to acidity caused by humic substances (Laudon and Buffam 2008). While the range of water quality variables at our study sites was typical of Finnish rivers, the use of mean values may have hindered us from detecting the lowest seasonal values that may have obscured restoration responses. Total phosphorus was negatively related to trout response, possibly indicating the limiting effect of even slight nutrient enrichment on the capacity of juvenile trout to respond positively to restoration. Several previous studies have concluded that in-stream habitat restoration is unlikely to be successful unless water quality is controlled at the watershed scale (e.g. Haase et al. 2013; Mueller et al. 2014; Roni et al. 2015). While poor water quality may have reduced the beneficial effects of habitat restoration in some of our study rivers, it is likely that water quality was mainly sufficient to allow positive development of salmonid populations.

We detected a geographical structure in trout responses to restoration, with trout densities responding more positively in southern than in northern Finnish rivers. Geographic patterns in restoration responses are likely interrelated to other natural and anthropogenic characteristics of the rivers addressed in this study. However, they may also stem from potential differences in restoration procedures and the time needed for biotic recovery (related to, for example, fish generation length) in different parts of the country.

Few previous studies have examined the effect of fishing pressure on restoration outcome (but see Gowan and Fausch 1996). We used river-specific information on fishing regulations as a proxy of fishing pressure. Our results suggest that fishing mortality may obstruct the positive effects of habitat restoration and stricter fishing regulations are needed to support population recovery (Binns 2004). The effect of fishing regulations remained relatively weak, however, possibly because of the low number of sites where fishing after restoration was either completely forbidden or only catch-and-release fishing was allowed. Habitat enhancement may trigger increased angler interest, causing intensified fishing pressure after restoration (Binns 2004), and migrating salmonids are exposed to fishing mortality also during the lake (or sea) phase (Syrjänen et al. 2018). Therefore, even when habitat restoration may seem to have failed, restoration may allow a higher success rate if constraints related to strong fishing pressure are mitigated (Bond and Lake 2003).

Recovering salmonid populations may be vulnerable to predators and competitors (Ward et al. 2008) and increased densities of predators may be associated with low recruitment of salmonids (Ward et al. 2008; Luhta et al. 2012). It remains unclear, however, if and how habitat restoration influences potential predators and competitors of juvenile salmonids (Nilsson et al. 2005). We did not find any effect of a potential predator (burbot) on salmonids, and neither did this species seem to benefit from restoration. Instead, European bullhead responded positively to restoration and its presence reduced the positive effect of restoration on trout. Brown trout and bullhead occupy partly similar niches and are therefore potential competitors. Previous studies have reported variable results on competitive interactions between bullhead and salmonids (Louhi et al. 2014, and references therein) but our results suggest that competition between these two species may be asymmetric, with bullhead limiting trout's response to restoration. Restoration efforts rarely target nonsalmonid fishes and any responses by these species to in-stream restoration are therefore poorly known. In one of the few exceptions, Roni (2003) examined the effects of large woody debris (LWD) on several benthic fishes, including two *Cottus* species, in 29 North American streams. Densities and mean lengths of the species examined did not differ between restored vs. reference reaches although the length of reticulate sculpin (*C. perplexus*) was positively related to the amount of LWD. Clearly, more research on the responses of non-target fish species to stream habitat enhancement is needed.

In-stream restoration is often supported by stocking, also referred to as assisted colonization (Stoll et al. 2013). Although this is a controversial measure, its use may be justified for species with scattered distributions, particularly if the target species has disappeared completely from a river (Luhta et al. 2012; Stoll et al. 2013). In Finland, stockings of Atlantic salmon and migratory brown trout have been conducted for more than a century (Luhta et al. 2012; Syrjänen et al. 2015). Since stocking is often undertaken within a few years after restoration, it might seem an obvious explanation for the temporary post-restoration density increase of trout. However, stockings were either ineffective (eggs) or negatively related (alevins/YOY) to restoration outcome, thus supporting previous findings that the benefits of current stocking practices are moderate at best (Luhta et al. 2012; Syrjänen et al. 2015). High numbers of stocked YOY may attract predators (Ward and Hvidsten 2011) and cause density-dependent mortality during the parr stage (Einum et al. 2008), thus rendering stocking an ineffective or even detrimental tool for fisheries management. In the near future, we may see a paradigm shift in salmonid management whereby expensive stockings are replaced, either partly or entirely, with measures that address directly the factors that limit the recovery of threatened fish populations (Ministry of Agriculture and Forestry 2012).

Habitat restoration likely has a higher potential to improve local fish production if dispersal to and from the restored site is unrestricted (Gowan and Fausch 1996). However, trout response in our study was unrelated to downstream migratory obstacles. Stoll et al. (2013) noted that to test the importance of barriers appropriately information on passability, not simply presence, of migration obstacles is needed. They also found that the spatial extent of dispersal was surprisingly limited; species not present within 5 km up- or downstream of a restored reach were unlikely to colonize the site within a few years (Stoll et al. 2013). Unfortunately, information on the distance and abundance of source populations was unavailable for most of our study sites.

Assessing merely YOY density responses may lead to partial misinterpretation of the restoration outcome. For example, lack of spawners may prevent populations from reaching the full restoration potential. Furthermore, parr-to-smolt survival may vary between restored rivers, regardless of their potential for YOY recruitment. Previous studies have reported variable results among fish life stages (Roni et al. 2008), and some observations suggest that larger salmonids may in fact be more responsive to habitat restoration than are juveniles (Gowan and Fausch 1996; White et al. 2011). In boreal streams, main concerns are related to the lack of spawning and overwintering habitats (Palm et al. 2007; Koljonen et al. 2012; Marttila et al. 2016a). Indeed, better results could be achieved by using more variable restoration material, such as spawning gravel and wood. Particularly the addition of large wood may considerably enhance the rearing capacity of stream habitat for salmonid fishes (Jones et al. 2014), often resulting in better survival and higher abundance of salmonids in restored reaches (Johnson et al. 2005; Louhi et al. 2016; Thompson et al. 2018).

The overall amount of new habitat created through restoration was insufficiently reported and therefore was not considered in our density estimations. Koljonen et al. (2012) and Lepori et al. (2005) showed that restoration may increase the wetted width of a reach considerably (up to 40%), thereby increasing habitat availability per reach (Korsu et al. 2010). Therefore, even if reach-scale density remains unaltered, total numbers of YOY trout may increase after restoration (Lepori et al. 2005; Nilsson et al. 2015).

Despite considerable context-dependency, our meta-analysis provides evidence that salmonid densities have generally benefitted from stream habitat restoration. This suggests that stream restoration has potential to enhance the recovery and conservation of salmonid populations. Density responses of brown trout reached the minimum success rate, but remained lower than what the experts perceived as distinct success. Restoration success was linked to watershed-scale factors, such as water quality, geographical location and river size, as well as to fishing regulations and interspecific competition. Many of these factors have been highlighted in previous studies, but testing their role based on a meta-analytical approach is a novel contribution. Our study supports the notion that restoration is more likely to be successful if the watershed-scale context is considered. Finally, we emphasize that well-planned fisheries management, especially as it relates to fish stocking and fishing regulations both in the river and in feeding areas, is critical for the sustainable development of threatened migratory fish stocks.

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