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Does stocking eggs into boreal spawning rivers increase the abundance of brown trout parr?

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Running title: stocking brown trout eggs into boreal rivers

Abstract

Stocking with eggs has been widely used as a management measure to support degraded salmonid stocks. In Finland, Atlantic salmon and both sea-migrating and lake-migrating brown trout are stocked as eggs, alevins, fry, parr and smolt, while trout are also stocked as mature fish. The aim of this stocking is to improve catches and to support collapsed spawning stocks. We assessed the success of stocking with brown trout eggs in a study of seventeen Finnish boreal forest rivers, of which nine were subject to egg stocking. All rivers contained some naturally spawning trout. In sixteen rivers, including non-stocking years and unstocked rivers, egg stocking did not increase total (wild and stocked) density of 0-year-old parr. However, those rivers with higher existing trout densities in non-stocking years seemed to benefit most from stocking, suggesting some role of river-specific extrinsic factors affecting egg-to-parr survival. In one river monitored for 14 years, only a weak correlation was found between the total density of 0-year-old parr and the number of eggs stocked. However in nine parr samples from five rivers, the mean proportion of parr derived from stocked eggs was 40 %. Mean survival to first autumn parr of egg-stocked and wild individuals was 1.0 % and 3.3 %, respectively. Probable reasons for the detected low to moderate impact of egg-stocking are 1) large variation in total parr density between years and rivers, 2) low number of stocked eggs, 3) placing egg boxes and egg pockets in unsuitable microhabitats, and 4) unsuitable emergence time of egg-stocked individuals, or other extrinsic factors creating extra mortality. We recommend field and laboratory experiments to improve and standardize stocking methods, and monitoring the connection of wild spawning stocks and parr recruitment. Finally, we encourage fishery authorities to create clear management goals for threatened wild salmonid stocks.

Key words: alevin, Alizarin red, egg box, egg pocket, stock management, otolith, redd, *Salmo trutta*, survival

Introduction

Stocking of eggs or hatched alevins has been widely used as a management measure to support natural parr production of salmonid fishes in rivers (Prignon *et al.*, 1999) and lakes (Bronte *et al.*, 2002) or to expand their natural distribution range. Various methods have been used, including eggs in pipes that are pushed into gravel, egg boxes, and pouring eggs directly onto the bottom substratum (Barlaup and Moen, 2001; Kirkland, 2012). Eggs or alevins, rather than parr, have been used in stocking, as eggs are cheaper to stock than parr and are easy to transport (Johnson, 2004). Moreover, egg-stocked fish go through most phases of their life span in their natural environment, and thus experience natural selection, which could keep the genotypes and phenotypes of populations as near to natural as possible (Kirkland, 2012).

Globally, egg stocking has been used for stocks of the genus *Salmo* for more than a century (Kirkland, 2012). The success of the action could be estimated as egg-to-parr survival or as comparisons between different stocking methods. However, most studies are cases of one river, one year and one method (Beall *et al.*, 1994; Raddum and Fjellheim, 1995; Coghlan and Ringler, 2004), or are limited only to the alevin phase (Kirkland, 2012). Barlaup and Moen (2001) reviewed egg stocking or egg incubation methods, but could report egg/alevin survival only until alevin hatching and emergence.

In Finland, egg or alevin stocking has been used in the stock management of Atlantic salmon (*Salmo salar*), and sea-migrating and lake-migrating brown trout (*Salmo trutta*) for more than a century. From the 1980s or 1990s, egg or alevin stocking has been used annually as a recovery action for sea-migrating brown trout in rivers of the Finnish coast of the Baltic Sea, and in some years for Atlantic salmon in Finnish and Swedish rivers of the Bothnian Bay. However, the largest Finnish electrofishing dataset from egg-stocked rivers is available for brown trout in the southern Lake District. There, trout is stocked annually as eggs, alevins, emerged parr (fry), older parr, smolt or mature fish to improve recreational fishing catches and to support spawning stocks. Currently, wild spawning stocks of trout are small, and individual spawners are of small size and are probably mostly resident, non-migrating. Only very few trout of 70 cm long or more, i.e. migratory individuals, are now observed in Lake District rivers yearly (authors, unpublished). The mean length of the spawning redds of trout in the region is clearly smaller than in other boreal rivers still holding lake-migrating stocks (Syrjänen *et al*., 2014a). These observations indicate smaller-sized, probably resident, female spawners. Historically, spawners were 70 cm long and over 4 kg on average and were lake-migrating, and they were abundant in spawning rivers (Syrjänen and Valkeajärvi, 2010; P. Valkeajärvi, pers. comm). Thus, natural egg density is now most likely low. In Finland south from the Arctic Circle, lake-migrating brown trout is classified as endangered and sea-migrating trout as critically endangered in the 2010 Red List of Finnish Species (Rassi, 2010), and the main reasons for this are high fishing mortality in lakes (Syrjänen and Valkeajärvi, 2010) and in coastal areas (Kallio-Nyberg *et al*., 2007), along with river damming.

Here we assess the success of stocking of brown trout eggs in forest rivers in the Finnish Lake District. To reveal the impact on parr abundance, we evaluated the total autumnal density of 0-year-old trout in eight stocked (impact) and eight non-stocked (control) rivers. Secondly, for one river with 14 years of monitoring data, we analysed the relation between the yearly parr density and the number of eggs introduced. Thirdly, we estimated the proportion of stocked individuals in parr populations from nine parr samples from five rivers, and compared egg-to-parr survival of stocked and wild individuals in four of the five rivers.

Materials and methods

Hatchery stocks

The Finnish Game and Fisheries Research Institute (FGFRI) maintains twelve brown trout hatchery stocks from Finnish inland waters. In the Finnish Lake District there are two stocks: the Rautalampi stock from the Kymijoki watershed and the Vuoksi stock from the Vuoksi watershed (Fig 1). The Rautalampi hatchery stock was renewed by few migratory mature fish in 1990s from Lake Päijänne region, midst of the study area, but after that, no wild mature lake-migrating spawners have been caught in the rivers. First hatchery generation used in egg production in the beginning of 2000s were grown from the gametes of these wild fish. In 2000s, the hatchery stock has been renewed by wild parr sampled in the rivers of the Rautalampi watercourse, such as Taikinainen and Karinkoski which are included in this study as stocked rivers. Parr were grown to maturity in the hatchery. These originally wild fish were also used as spawners in the hatchery, but their eggs comprised 10 % of eggs used in this work, and 90 % of eggs were from the first or second hatchery generation. During 2006–2011, the Rautalampi stock has produced 40–60 litres of eggs annually, one litre containing 6555 eggs as an average between years (SD 482) (R. Kannel, FGFRI, pers. comm.), that have been stocked into some tens of rivers of the Kymijoki and the Kokemäenjoki watersheds (Fig. 1). Since 2008, trout eggs produced by the FGFRI have been marked by adding Alizarin red S to the egg tanks to create colour marks in alevin bones. Alizarin can then be detected in the fish otoliths in the laboratory, although the fish must be killed for this. The otoliths are analyzed under ultraviolet light with a fluorescent microscope, and a clear fluorescent area is seen in the centre of the otolith of an Alizarin-coloured fish.

Study rivers

The study area covers all the most important watercourses and approximately half of the most important free spawning rivers for brown trout in the Finnish Lake District. Seventeen rivers situated in the Kymijoki, Kokemäenjoki or Vuoksi watersheds were used in the study (Table 1). Some rivers were parts of the same watercourses, but were situated more than 10 km apart and separated by lakes; two egg stocking rivers, Taikinainen and Karinkoski, were situated only 200 m from each other but were separated by a large pool. Thus, 0-year-old brown trout were presumed not to move between the rivers. Average channel width of rivers was 5 to 100 m and mean discharge 1 to 150 $m^3 s^{-1}$. Twelve rivers were situated in a lake outlet and five rivers 0.5 to 10 km downstream from a lake. Upstream sections of the watercourses of most rivers consisted of a chain of lakes, and thus floods and movements of fine particles in the channels were mild. Channel bottoms comprised mainly stones of 10−100 cm in diameter, but also contained gravel. Large woody debris was sparse. All rivers were undammed. The riparian zones and catchment areas were mainly forest, and water quality was good or excellent. In one stocking river, Virtalankoski, lower water quality might restrict reproduction of brown trout (Table 1). Bottom ice occasionally formed in channels in winter.

All rivers had been dredged by narrowing their channels and removing or blasting boulders during previous centuries for timber floating, lowering lake surfaces or powering mills, but all have since been restored, except Kalkkistenkoski, Saajoki and Ohrajoki. In restoration since the 1980s, some boulders and stones were replaced in channels, channels were widened a little, and some spawning areas were created for trout with artificial gravel (see Muotka and Syrjänen, 2007). Dredging and restoration actions were usually less disruptive in large rivers than in small rivers. During the study period, light channel restoration was done in three stocked rivers, Taikinainen in 2002 and 2005, Karinkoski in 2002 and 2005, and Vihovuonne in 2007−2008, and in one unstocked river, Läsänkoski in 2004, 2006 and 2009. Low numbers of brown trout parr of 1 and 2 years old were introduced to some rivers during sampling years, but no parr of 0-year-old. No other management measures were applied to the channels. The availability to the study of appropriate unstocked rivers with no management measures was very restricted.

Wild fish stocks

Brown trout reproduces naturally, but not always annually, in all seventeen rivers. Two life history forms occur in most rivers, the common small-sized resident non-migrating form and the rare large-sized lake-migrating form. The natural trout egg density was estimated to be mainly 1–10 eggs m^{-2} in riffle sections based on counts and lengths of redds (see Syrjänen and Valkeajärvi, 2010). The total mean density of one year old or older parr was 4.5 individuals 100 m^{-2} in stocked rivers and 6.0 individuals 100 m^{-2} in unstocked rivers in electrofishing samples taken in September or October. As the density was low to moderate, and as the lake outlets supply abundant prey like filter-feeding insect larvae (Richardson and Mackay, 1991), competition from older parr was presumed not to affect the density of 0-year-old parr. Other fish species in the study rivers in order of appearance in electrofishing catches were bullhead (*Cottus gobio*), burbot (*Lota lota*), stone loach (*Barbatula barbatula*), perch (*Perca fluviatilis*), roach (*Rutilus rutilus*), pike (*Esox lucius*), bleak (*Alburnus alburnus*), grayling (*Thymallus thymallus*), ruffe (*Gymnocephalus cernuus*) and stocked or escaped rainbow trout (*Oncorhynchus mykiss* Walbaum).

Egg stocking methods

All egg stockings were actual management actions, not experimental treatments. The eggs were fertilized in hatcheries in September or October. The eggs of the Rautalampi stock were produced by the FGFRI Laukaa Fish Farm and used in the Kymijoki and Kokemäenjoki watersheds, and the eggs of the Vuoksi stock were produced by FGFRI Saimaa Fisheries Research and Aquaculture and used in the Vuoksi watershed. Stocking was done by hatchery personnel, by local river fishery organisers, or in some cases by research personnel, usually in March when eggs were in the "eyed" phase. Only some experts among the stocking personnel had experience of observing real trout redds in rivers. A tree sprout pipe of 60 mm in diameter and Whitlock-Vibert© plastic egg stocking boxes were used as stocking methods, often simultaneously in the same river, or only one method in one river through the study (Supplementary data). Both methods allow alevins to swim out freely. When using the pipe, some tens of egg pockets were created in the gravel beds in riffle sections of the upper parts of the rivers, and 100–200 mL of eggs were introduced into each hole in the gravel at a depth of 5–10 cm. With egg boxes, 100–200 mL of eggs were laid into each box, but not gravel. Each box was buried partly inside gravel and between stones of 10–20 cm of diameter, or just laid on the bottom surface with a weight. 10–30 egg boxes were used in each river. Water depth was 15–50 cm at sites with pipe egg pockets or egg boxes.

In both methods, 6 000–30 000 (approximately 0.9–4.6 L) of eggs were used per river and year, and the stocking density was 1–10 eggs m^{-2} for riffle sections. The number of stocked eggs per river corresponds to the number of eggs from approximately 5–22 kg of mature female trout biomass including eggs, or from 1–5 migrating females with mean size of 4–5 kg. The mean wet mass of eggs produced by FGFRI hatchery females is 15 % of the mass of a large female including eggs, and the mean wet mass of an egg of a large female is 0.11 g (Turkka and Arkko, 2004).

In the box stocking method, the boxes were removed from the channels in June, when the number of dead eggs or alevins was always 20 or less per box. No accumulation of fine particles in boxes was detected in any river.

Collection of three data sets

In the sixteen-river dataset, the total (wild + stocked) density of 0-year-old parr was used as the dependent variable. Density was estimated by electrofishing two to five constant sampling areas, total 300–800 m^2 per river, mainly by the three-pass-removal method, in September or October. River-specific catchability values were used. The gears used were backpack Geomega FA4 or FA3, backpack Deka Lord 3000, and Lugab with aggregator. The same gear was used in each river through the study. Approximately 80 % of the artificial egg pockets and egg boxes were situated inside the electrofishing sampling areas or less than 20 m upstream, and the other 20 % were located 20–50 m upstream. Data were collected from 2000 to 2011, but the number of sampling years per river was 4–12. The number of stocking years and the number of non-stocking years were both 2–10 per stocked river. Unstocked rivers were sampled in exactly the same years as stocked rivers. Thus, yearly fluctuation in environmental factors, like river flow at the time of electrofishing, should not have any noticeable effect on the final results of the impact, as regional floods or droughts occur simultaneously in most or all of the study rivers. The total number of density observations was 122.

In the Simunankoski data set, electrofishing was done in 1996 and from 1999 to 2011. In this river, there were ten stocking years and four non-stocking years, and 10 000–30 000 eggs were stocked per stocking year. This corresponds to the egg number of 2–5 migrating females.

In the otolith dataset, nine parr samples yielding a total of 198 individuals of 0-year-old parr were taken from five rivers (Table 1) in September-October 2009 to 2012, each sample consisting of 5–30 fish. The otoliths were removed and analyzed in the laboratory, and the proportions of individuals derived from stocked eggs and of wild individuals were calculated. To estimate survival of egg-stocked and wild individuals, the size of habitat area suitable for 0-year-old parr was estimated for four rivers from map measurements and field observations made during electrofishing and redd counting, but Kalkkistenkoski Rapids was too large (Table 1) and spatially too complicated for such estimates. Each of the four rivers was bordered by a lake or a large pool at its upper and lower end, so each river length was measured precisely. The size of suitable habitat area was calculated using the Internet service Paikkatietoikkuna (www.paikkatietoikkuna.fi) by three field assistants independently, and average values were used. Riffle area shallower than 1 m was classified as suitable habitat, but boat routes were excluded. The numbers of egg-stocked and wild parr were estimated by multiplying the density estimates for both groups from electrofishing samples by the size of the suitable habitat area.

The sample size of otoliths per river was restricted because we limited killing a threatened species, as wild individuals were also expected to occur in the samples. Thus, discussion of results from proportional occurrence and survival estimates is mainly on the means among the five rivers.

The number of wild eggs was estimated by redd counting and measuring, done by wading in the same four rivers and for the same year classes in October-November, prior to egg stocking in March. Three rivers were waded completely, and Simunankoski to a depth of 1–1.5 m, by experienced personnel. Redd tail lengths were measured with a ruler stick. Clear redd-shaped pits were classified as redds, but small and unclear pits were carefully dug out, and if 1−2 eggs were found the pit was identified as a redd (see Syrjänen *et al.*, 2014a). The fork length of a spawned female trout (L, cm) was estimated for each redd from the redd tail length (q, cm) as ln $L = 0.60 \cdot \ln q + 0.86$ (modified from Crisp and Carling, 1989). The egg number (E) buried by the female in her redd was calculated from the female fork length (L, mm) as $E = 0.006266 \cdot L^{2.048}$ (Elliott 1995). Egg numbers in redds were summed for each river. To account for mortality of wild eggs during winter, 90 % of wild eggs were assumed to survive until March (see Syrjänen *et al*., 2008), the time of egg stocking. Survival was calculated as the proportion of parr numbers in autumn from egg number in March, separately for wild and stocked eggs and parr.

Data analysis

The data from sixteen rivers were first analysed using a general linear model with maximum likelihood (ML) and restricted maximum likelihood (REML) (IBM SPSS statistics v20) methods. The total (wild + stocked) density of 0-year-old parr was explained by the fixed effect of the river type (stocked, unstocked). The fixed effect of stocking year (stocking, non-stocking) was nested within a river type, as only the stocked rivers were stocked. To control for regional conditions, such as water quality, weather or fishing restrictions that could affect general trout abundance within the region, river pair was fitted as a fixed factor, a pair meaning a stocked river and a nearby unstocked river. General yearly variation was taken into account by fitting year as a fixed factor. To control for the non-independence of the subsequent observations from the same rivers over time, identity of the river was fitted as a random factor. Models were chosen by AIC (from ML models), and parameter estimates were obtained with REML. The model selection was performed on the subset of possible models that contained factors relevant to our study questions (stocking). As stocking was nested within the river type, no model contained effects of stocking without river type. The egg stocking method (pipe or box) could not be included as a factor, as the data were unbalanced for this factor, and both methods were often used simultaneously (Supplementary data).

To explore further the determinants of stocking success, we analysed whether the overall parr density in non-stocking years (proxy for natural parr density of the river), number of eggs stocked and their interaction could affect parr density in stocked rivers. After standardization to a mean of zero, these effects were fitted as continuous covariates. This REML model included also a random effect of river identity, and year as a fixed factor. Note that since non-stocked rivers were not considered in this analysis, fitting a regional factor was not meaningful (i.e. since fitting single site within each region).

In the Simunankoski data set, the correlation of the total (wild + stocked) autumnal density of 0-year-old parr and the number of eggs stocked was analyzed in 14 observation years.

In the otolith dataset, survival between egg-stocked and wild individuals was analysed with paired samples t-test, and correlation in survival between the two groups was analyzed with seven observations (Kalkkistenkoski excluded).

Results

We used the sixteen-river dataset to test several different combinations of explanatory factors; using AIC as a selection criterion, the best model contained effects of river identity, river type, and stocking nested within river type (Table 2). We therefore restrict our results and discussion to this model, which is sufficiently parsimonious but still captures the details of our setup (effects of stocking and effects due to control and stocked rivers).

Among the sixteen rivers, the type of river (stocked, unstocked) did not affect trout density ($F_{[1,18.056]}$ = 0.003, P = 0.959); mean density (from estimated marginal means) was 11.3 in stocked rivers and 11.6 individuals 100 m^{-2} in unstocked rivers. Moreover, the effect of stocking was weak in the stocked rivers ($F_{[1,111.760]}$ = 0.850, P = 0.430); mean density was 12.9 in stocking years and 9.7 in non-stocking years (Fig. 2). Thus, the average, but non-significant, effect of egg stocking was approximately 3 individuals 100 m^{-2} (see also Supplementary data). River identity affected densities (variance 85.87, standard error of the mean 37.76, Wald Z = 2.274 P = 0.023) and the variation in the parr density between rivers and years was large (Fig. 2).

We also found that higher levels of egg stocking (number of eggs) increased parr densities in stocked rivers (b = 0.00578, SE = 0.00205, $F_{1, 11.432}$=7.984, P = 0.016), although the average natural parr density did not indicate a significant effect on yearly parr density (b = 0.919, SE = 0.637, $F_{1, 4.105}$=2.085, P = 0.221). However, interaction of stocking and natural density indicated that at high natural densities the egg stocking was more effective in increasing the total parr density (b = 0.000102, SE = 2.164 x 10^{-5}, $F_{1, 9.972}$ =22.341, P = 0.001). River identity did not affect variation in parr density (Wald Z = 1.338, P = 0.181), but we did find an effect of year ($F_{1, 8.602}$=4.373, P = 0.021).

In Simunankoski Rapids, the Spearman correlation coefficient between the number of eggs stocked and the total (wild + stocked) parr density was positive but non-significant when the four non-stocking years were included (r = 0.434, P = 0.121, n = 14), or excluded (r = 0.523, P = 0.121, n = 10) (Fig. 3).

According to otolith analysis, the average proportion of individuals originating from egg stocking was 39.9 %, (range 0−100 %) in the nine samples from five rivers. In three samples, the proportion was remarkably high, 77−100 % (Table 3). Average egg-to-parr survival of egg-stocked and wild individuals from time of egg stocking (usually March) to September-October was 1.0 %, (range 0−2.6) and 3.3 % (0−9.0), respectively (Table 3). No difference was detected in survival between egg-stocked and wild trout (t_6 = 1.57, P = 0.168). If the two samples smaller than 20 fish were excluded, the average proportion of egg-stocked individuals was 49.2 % (range 5.0−100), and the average egg-to-parr survival of egg-stocked and wild individuals was 1.2 % (0.3−2.6) and 2.3 % (0−6.8), respectively. The survival estimates for egg-stocked and wild individuals did not correlate (Spearman r = -0.179, P = 0.702, n = 7).

Discussion

Efficiency of trout egg stocking

Using a 12-year dataset of egg-stocking and population estimates from 16 rivers, and a data set of ten stocking years from one river of these, we found rather low average effectiveness of brown trout egg stocking in rivers in the Finnish Lake District. Moreover, according to otolith analysis the egg-to-parr survival was low, even though the proportion of marked otoliths in parr samples was higher than expected with respect to the two other data sets.

Although egg stocking is widely used, its effectiveness at increasing parr abundance has rarely been assessed. In another field experiment with brown trout eggs made in northern Finland, stocking had a positive impact on parr density, but only in sites without natural parr (Niva *et al.*, 2012). However, the design of this earlier study lacked non-stocking years at stocked rivers, and the eggs were poured directly to the channel substratum.

Why is egg-stocking apparently ineffective in Finland?

There are several possible reasons for the low to moderate average effectiveness of egg stocking. First, large annual and spatial variation in total parr density lowered the possibility to detect an impact of stocking by reducing the test power. The variation is probably due to annual variation in egg-to-parr survival of wild and/or egg-stocked individuals and in wild egg production. Survival in the hatching and/or emergence period may be particularly affected by temporal and spatial fluctuations in factors like water temperature (Jensen and Johnsen, 1999; Sternecker *et al*., 2014), floods (Jensen and Johnsen, 1999), food supply, and fish predation (Brännäs, 1995). In addition, distribution of 0-year-old salmonids may be patchy (Beall *et al.*, 1994; Einum *et al.*, 2011), and the location of high and low density patches may change from year to year. Catchability during electrofishing is affected by river flow level at the time of sampling (Ugedal *et al*., 2008), but our sixteen-river design included river pairs with nearby control rivers, which should have decreased any effects of interannual differences in discharge. Enlarging the total sampling areas electrofished would also diminish this problem by producing more accurate information about yearly parr densities, but labour resources for this are usually not available.

Second, number of stocked eggs per occasion was low, corresponding to only few large females. Third, mean survival of stocked eggs to first autumn parr was low. This may be partly a consequence of placing egg boxes and egg pockets in unsuitable microhabitats, producing extra mortality. The stocking procedure was not standardized, as stocking personnel changed between rivers and years, and the skills of the persons varied. Alternatively, the timing of hatching and/or of emergence of egg-stocked individuals may differ from the natural population, as the timing of egg fertilization is decided by hatchery personnel, perhaps starting the egg incubation period before or after the peak spawning period of natural populations. As a result, the timing of emergence in spring may differ between the egg-stocked population and the natural population, which may result in different survival between the two groups depending on temporal fluctuation of mortality factors. In addition, the length of the “spawning period” of hatchery fish, i.e. the time when the fish are milked and eggs are fertilized, is normally only some hours, but the length of the spawning period of a natural brown trout stock may well be weeks. Thus, the emergence period could be shorter in an egg-stocked population (see Syrjänen *et al.* 2008) than in a natural population in the same river, which in turn may create more yearly fluctuation in mortality of the egg-stocked population at emergence. In other words, if environmental factors during the short emergence period happen to be optimal, so that water temperature and discharge are optimal, prey are abundant and fish predation is low, then egg stocking may be effective. But if the environmental factors during emergence are sub-optimal, egg stocking may have only a negligible impact on the total parr density. In a natural population, the longer emergence period could equalize the impact of these temporally varying mortality factors. Indeed in our parr otolith data, the large temporal and spatial variation in proportion of egg-stocked individuals in samples (Table 3) and the lack of correlation between survival of wild and egg-stocked individuals support these hypotheses.

Interestingly, we also found that those rivers that already had higher natural density of trout seemed to benefit most from stocking. This suggests a role for external factors that reduce survival of both wild eggs and/or parr, but also effectiveness of egg stocking. This result could indicate that the parr densities are far from carrying capacity in the study rivers. If carrying capacity is a limiting factor, we would expect to see negative or diminishing effects of stocking on overall density in rivers with high natural reproduction. Then in some cases, egg stocking may be very important to maintain parr production, as the highest proportions of egg-stocked parr were 77−100 % in three otolith samples. In extreme cases (such as Myllynkoski), without egg stocking the species might even disappear from the river (Table 3).

Egg-to-parr survival of stocked and wild individuals

In six published egg stocking case studies of rivers, the survival estimates for Atlantic salmon from egg to first fall parr vary strongly, as the range was approximately 0−20 % (Table 4). However, many of these stockings were probably experimental actions done by skilful experts, not hatchery personnel perhaps partly lacking knowledge of the proper microhabitat for eggs. Our result for average egg-to-parr survival of 1 % is low, but not unusual, compared to the published results. In wild populations in the other six studies, the survival of brown trout or Atlantic salmon from egg to first fall parr was mainly 1−5 % (Table 4), so the mean survival in our study of 3 % is well within the published range. Hence the survival estimates for wild and stocked individuals seem to be quite similar, but encompass a wide natural range. Thus in general, egg stocking could be a valid method to boost degraded stocks.

Unfortunately, we could not observe survival during the alevin or emergence period, but Syrjänen *et al.* (2008) observed high survival of eggs until hatching (83−98 %) in an egg incubation experiment in rivers Arvajanjoki and Rutajoki in the Kymijoki watershed with eggs from the same Rautalampi hatchery stock as used in this work. In that earlier study, eggs were again mainly from the first or second hatchery generation, but survival was very high. In Barlaup and Moen's (2001) review, average survival of salmonid eggs, mainly of the genus *Salmo*, was 67 %, (range 6−98 %, n of sites/rivers=31) to hatching, and 57 % (range 5−98 %, n=10) to emergence. In our study, egg boxes never included appreciable numbers of dead eggs or alevins in June, but some dead eggs or alevins may have decomposed and disappeared from the boxes. However, the occurrence of significant mortality could rather occur during and immediately after the emergence period (Brännäs, 1995). The boxes might not have mimicked natural egg pockets, especially in their shallow burial. In this scenario, when alevins leave the boxes they might occupy the surface of gravel beds instead of being inside beds between particles. On the gravel surface they could then face higher predation or unsuitably high water velocity.

We could not compare results from different stocking methods. Harshbarger and Porter (1982) compared the pipe and the box methods, and concluded that pipes produced higher average egg-to-parr survival than Whitlock-Vibert© boxes (29 % vs. 8 %, respectively). However in that study, boxes accumulated large amounts of sand, and the sediment volume correlated positively with egg mortality. Rigorous comparisons of different methods by field experiments and in artificial channels with reasonable spatial and temporal scales are needed.

Stock-recruitment connections

Only local information about the number of eggs laid by the natural spawning stock and about the stock-recruitment relationship can provide an accurate basis for egg or parr stocking into a particular river, but unfortunately this information is usually lacking, as it is for our study rivers. Supportive egg stocking will increase parr abundance only if the number of eggs produced by the natural spawners is clearly less than the number that yields the highest parr abundance. Globally, only few appropriate stock-recruitment curves have been created for the genus *Salmo*. In Black Brows Beck, sea-migrating brown trout parr density peaked at 60 eggs m^{-2} (Elliott, 1994). In the River Imsa, Atlantic salmon smolt number was highest at both 6 and 60 eggs m^{-2} (Jonsson, Johnson and Hansen, 1998). In the Nivelle River, Atlantic salmon parr density was highest at 5 eggs m^{-2} of riffle habitat (Dumas and Prouzet, 2003), and in Girnock Burn, an egg density of 3.4 eggs m^{-2} yielded the highest smolt number (Buck and Hay, 1984). A wide range in the optimal egg density estimates between studies and rivers may result from variation in sampling methods, quality of physical parr habitats, prey supply, smoltification age, or survival between rivers. In the Finnish Lake District, annual monitoring of spawning stocks, estimates of egg-to-parr survival for both wild and stocked individuals, and creation of stock-recruitment estimates are needed for better management of collapsed salmonid stocks.

Parr abundance of boreal lake-migratory stocks

Historically in the Finnish Lake District rivers, egg density was most probably much higher than now, as there were annually tens or hundreds of lake-migrating female spawners per river, and the mean female size was over 4 kg (Syrjänen and Valkeajärvi, 2010; P. Valkeajärvi pers. comm). Currently, fishing mortality in lakes prevents the maturation and spawning of lake-migrating individuals. In rivers, observations of large (i.e. migratory) individuals returning from lakes are very few (authors, unpublished). Syrjänen *et al.* (2014b) marked 5762 stream trout of length 14−65 cm and mainly wild, with Carling or t-anchor tags in rivers of the Kymijoki watercourse . As tag controls, 933 tag observations were made on marking rivers prior to possible lake migration, 107 observations on lakes, and 1 observation of a mature fish in the marking river returned from lake migration to spawn. In lake tag returns, the average length of caught trout was 47 cm, and no fish reached a length of 70 cm. Thus, the egg number is most likely limiting the parr number now, but other factors, like environmental conditions or predation, will also affect egg and parr survival. The highest reported average densities of 0-year-old brown trout in autumn electrofishing samples over several years in Finland were 120 individuals 100 m^{-2} in the Kivikoski Rapids in Arvajanjoki in 1984−1993 (Syrjänen and Valkeajärvi, 2010) and 43 individuals 100 m^{-2} in the River Kitkajoki in the northern Oulankajoki watershed in 1987−1994 (Mäki-Petäys *et al.*, 2000). In both cases, the female spawners were mainly lake-migrating and 50−80 cm (1.5−7 kg) in size. In the upper part of Vindelälven in North Sweden, the average density of 0-year-old brown trout was 61 individuals 100 m^{-2} in the 6 km long main reproduction site of a lake-migrating brown trout stock in 2006−2012 (M. Bidner, Ekom AB, Sweden, pers. comm.). In six tributaries of Lake Vättern in Sweden, the among-river average was 61 individuals 100 m^{-2}, but 146 in the best river Röttleå, in 2000−2012, and spawners were mainly migratory from Lake Vättern (Olsson and Johansson, 2013). In our study including the best trout rivers in the Finnish Lake District, the average density was only 11 individuals 100 m^{-2} including egg-stocked individuals.

Management goals for wild migratory salmonids

To conclude, our results emphasize that collapsed and strongly harvested stocks of migratory salmonids cannot easily be stimulated by egg stocking alone. The action might raise parr density significantly if higher numbers of eggs were used, and if the stocking methods were improved. However, stocking of tens of litres of eggs per river would need financial and labour resources not available, and the current supply of eggs in hatcheries is insufficient. But standardization of the egg stocking methods, as has been done in egg incubation experiments by developing standardized egg sandwich (Pander *et al.*, 2009) and floating box (Pander *et al.*, 2010) methods, could produce more accurate information about the effect of the action, or perhaps higher survival of egg-stocked individuals. On the other hand, continuous stocking of eggs, parr or smolts into waters where individuals could reproduce naturally, raises question about the goals of fishery management (see Youngson *et al.*, 2003). Stocking, even of eggs, may change the genotype of stocks if the practice continues for decades or centuries.

In Finland, the benefits of current egg stocking practices are at best moderate. Moreover, stocking of parr and smolts has only produced weak yields during recent decades according to tag returns from trout in the Finnish Lake District (Syrjänen *et al.*, 2011) or in the Finnish coast of the Baltic Sea (Kallio-Nyberg *et al*. 2007), or from Atlantic salmon in the Baltic Sea

(Kallio-Nyberg *et al*. 2013). Nor has another common management action, channel restoration, succeeded in restoring brown trout spawning stocks, or raising parr abundance (Muotka and Syrjänen, 2007; Syrjänen and Valkeajärvi, 2010; Vehanen *et al.*, 2010), or appreciably improving parr habitat quality (Huusko and Yrjänä, 1997; Korsu *et al.*, 2010). If wild salmonids stocks in Finland are to recover, we recommend that fishery administrations should create clear management goals for wild salmonid stocks, and decrease fishing mortality by regulation of lake or coastal sea fishing effort.

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Table 1. The rivers used in the different study designs (16r=16 rivers, SR=Simunankoski Rapids, o=otolith analysis), pair number in design 16s, watershed (K=Kymijoki, Ko=Kokemäenjoki, V=Vuoksi), location in lake outlet (y=yes, n=no), geographical location, size, and selected mean water chemistry characteristics in the 17 study rivers in southern Finland in 2000−2011. Tot-P values may be overestimations for Ohrajoki (tributary), as water samples were taken from its main river Pengerjoki.

River	Used in design	River pair	Water-shed	Lake outlet	Latitude (N)	Longitude (E)	Mean channel width (m)	River order	pH	Tot-P ($\mu g \bullet l^{-1}$)
Stocked rivers										
Kalkkistenkoski	16r, o	1	K	y	61° 17’	25° 35’	105	6	7.2	7
Myllynkoski	16r, o	2	K	y	61° 44’	26° 08’	15	4	7.0	8
Muuramenjoki	16r, o	3	K	y	62° 08’	25° 41’	19	4	6.9	9
Taikinainen	16r	4	K	y	62° 36’	26° 19’	90	4	6.9	6
Karinkoski	16r	5	K	n	62° 36’	26° 19’	90	4	6.9	6
Simunankoski	16r, SR, o	6	K	y	62° 23’	26° 11’	42	5	6.9	7
Virtalankoski	16r	7	Ko	n	62° 18’	24° 44’	14	4	5.9	23
Vihovuonne	16r	8	V	y	62° 24’	28° 43’	85	5	6.9	6
Unstocked rivers										
Läsänkoski	16r	1	K	y	61° 54’	26° 54’	38	4	6.8	11
Arvajanjoki	16r	2	K	y	61° 41’	25° 10’	12	3	6.6	4
Saajoki	16r	3	K	n	61° 59’	25° 24’	4	3	6.1	16
Koivujoki	16r	4	K	n	63° 23’	26° 23’	15	3	6.8	13
Ohrajoki	16r	5	K	n	62° 22’	25° 06’	7	3	6.0	26
Huopanankoski	16r	6	K	y	63° 33’	25° 02’	20	4	6.9	12
Multianjoki	16r	7	Ko	y	62° 25’	24° 44’	10	3	6.2	14
Puuskankoski	16r	8	K	n	61° 34’	26° 43’	25	5	7.0	5
Additional stocked river										
Sahankoski	o		K	y	63° 08’	25° 57’	40	4	7.0	12

Table 2. Model selection for the best predictive model for the total density of 0-year-old brown trout parr across 16 rivers. -2LL denotes twice the log likelihood whereas AIC denotes Akaike information criteria (smaller is better). The best model is highlighted with bold.

Model	Model equation	-2 LL	AIC
1	y=river pair+river type+stocking(river type)+year+riverID	937.219	985.219
2	y=river type+stocking(river type)+year+riverID	943.154	977.154
3	y=river pair+river type+stocking(river type)+riverID	958.602	984.602
4	y=river pair+river type+year+riverID	939.536	983.536
5	**y=river type+stocking(river type)+riverID**	**963.669**	**975.669**

Table 3. Number of sampled 0-year-old brown trout (N) per river, proportion of individuals originating from egg stocking (E), and estimated survival of egg-stocked (S_E) and wild (S_W) individuals from March through to September-October. ND = No data.

River	Year	N	E (%)	S_E (%)	S_W (%)
Myllynkoski	2011	22	100	0.3	0.0
Muuramenjoki	2011	30	77	1.1	0.4
Muuramenjoki	2012	30	27	1.7	6.8
Sahankoski	2010	5	0	0.0	9.0
Sahankoski	2011	26	31	0.8	1.5
Simunankoski	2009	28	25	0.7	3.9
Simunankoski	2010	30	80	2.6	1.2
Kalkkistenkoski	2009	20	5	ND	ND
Kalkkistenkoski	2010	7	14	ND	ND
Mean			40	1.0	3.3

Table 4. Mean survival estimates (S, %) from egg until first fall parr of egg-stocked and wild individuals of brown trout or Atlantic salmon in published papers. LAS=landlocked Atlantic salmon, AS=Atlantic salmon, BT=brown trout. *=until first winter, †=until 1st July.

Species	River	S (%)	Author
Egg-stocked			
LAS	Salmon River	0	Coghlan and Ringler, 2004
AS	Beaver Brook	0.8	Johnson, 2004
AS	a Scottish stream	11.1−14.8	Egglishaw and Shackley, 1980
AS	Bjørnbettelva	2−24	Einum and Nislow, 2005
AS	Ekso	c.a. 10−20	Raddum and Fjellheim, 1995
AS	a French stream	11.8*	Beall *et al*., 1994
Wild			
BT	Rutajoki	0.7−5.1	Syrjänen, Sivonen and Sivonen, 2014a
BT	Black Brows Beck	2−5	Elliott, 1994
BT	Wilfin Beck	1−5	Elliott, 1994
BT	Kernec Brook	5	Bagliniere *et al.*, 1994
AS	Tobique River	3.8	Gibson *et al.*, 2009
AS	Nivelle River	1.0	Dumas and Prouzet, 2003
AS	Catamaran Brook	30.7†	Cunjak and Therrien, 1998

Supplementary data. Total (wild and egg-stocked) density of 0-year-old brown trout (individuals per 100 m^2) in eight stocked rivers and eight unstocked rivers in southern Finland in egg stocking (s) years and non-stocking (non-s) years in design 16r, number of observation years (N), and stocking method used.

River	River pair	Density in s years			Density in non-s years			Egg stocking method
		Mean	Range	N	Mean	Range	N	
Stocked rivers								
Kalkkistenkoski	1	9	3−14	2	15	15−16	2	Box, pipe
Myllynkoski	2	8	2−20	6	2	0−4	2	Box, pipe
Muuramenjoki	3	10	6−14	2	14	1−23	10	Box
Taikinainen	4	7	6−8	2	2	0−4	2	Box, pipe
Karinkoski	5	10	2−19	2	13	7−19	2	Box, pipe
Simunankoski	6	38	16−58	9	22	14−38	3	Pipe, box
Virtalankoski	7	2	0−6	3	2	0−4	9	Box
Vihovuonne	8	2	0−4	2	6	1−10	3	Box, pipe
Mean		11			9			
Unstocked rivers								
Läsänkoski	1	8	1−14	2	8	0−15	2	
Arvajanjoki	2	17	2−30	6	20	16−24	2	
Saajoki	3	3	1−5	2	5	0−15	10	
Koivujoki	4	12	5−19	2	8	7−9	2	
Ohrajoki	5	12	0−24	2	10	6−14	2	
Huopanankoski	6	7	1−14	9	5	1−11	3	
Multianjoki	7	19	6−40	3	35	4−77	9	
Puuskankoski	8	3	0−5	2	2	0−3	3	
Mean		10			11			

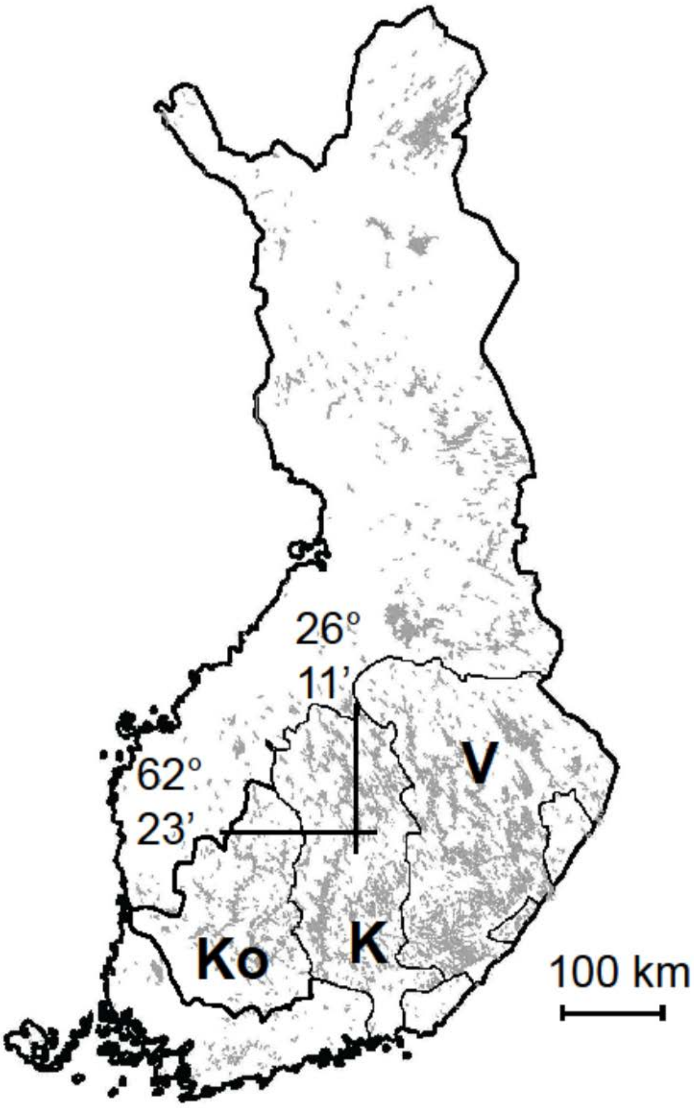

Figure 1. Location of the the Kokemäenjoki (Ko), Kymijoki (K) and Vuoksi (V) watersheds in southern Finland. The location of the Simunankoski Rapids is shown with latitude and longitude values. Lakes are shown in grey.

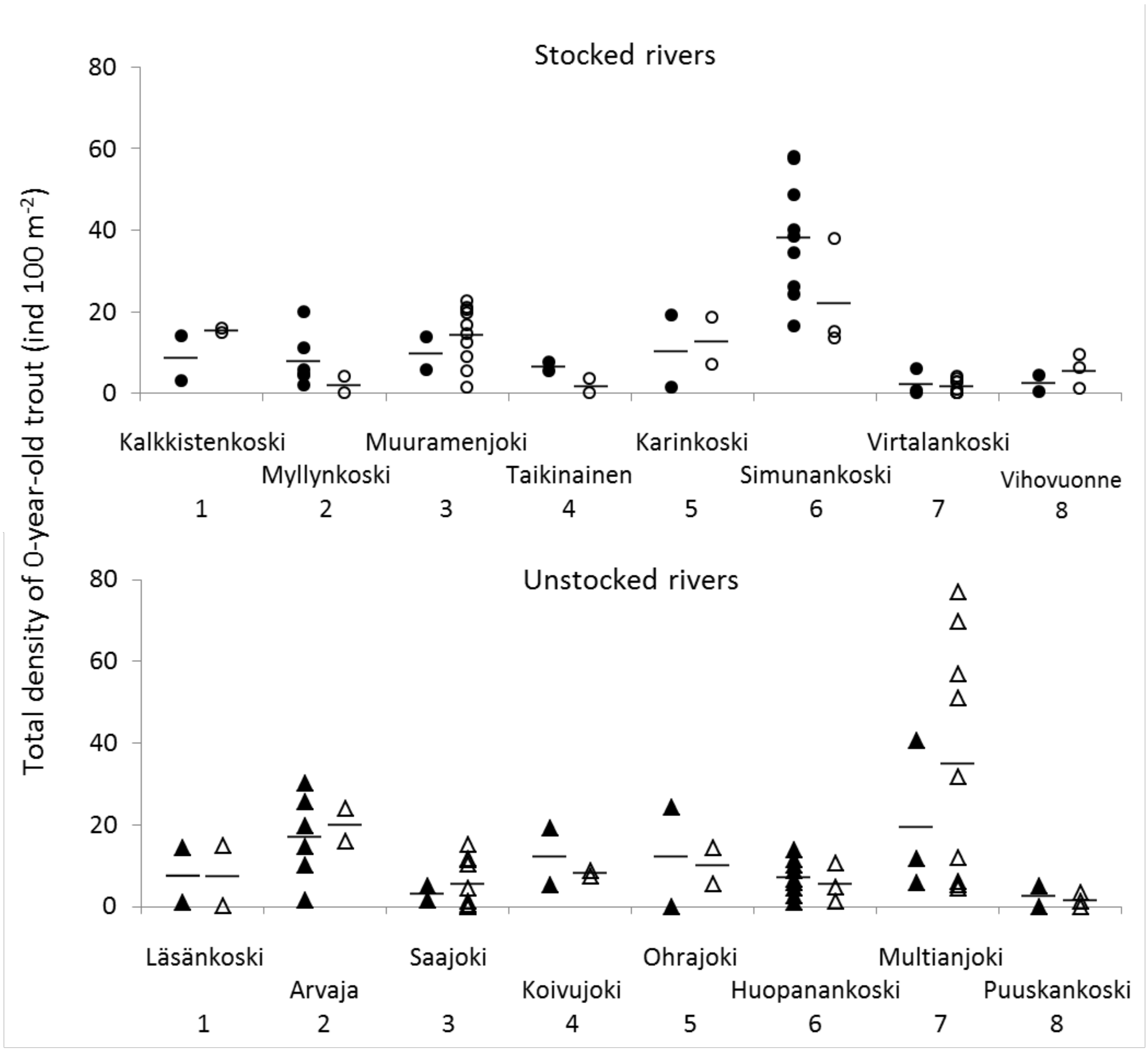

Figure 2. Total (wild and egg-stocked) autumnal density of 0-year-old brown trout parr in sixteen rivers in the Finnish Lake District in 2000−2011. Black symbols indicate yearly parr density in stocked and unstocked (control) rivers in stocking years, and open symbols indicate parr density in non-stocking years. Line symbols indicate average values in each river in stocking years and non-stocking years. Numbers below river names indicate river pairs.

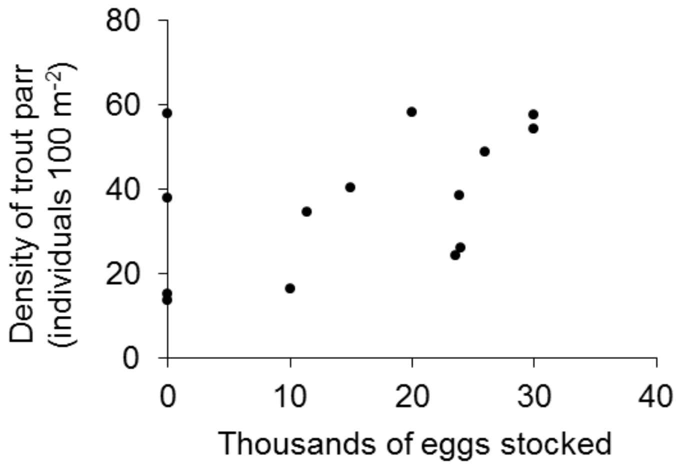

Figure 3. Total (wild and egg-stocked) annual density of 0-year-old brown trout parr related to the number of eggs stocked in Simunankoski Rapids in years 1996 and 1999−2011. Spearman r = 0.434, P = 0.121. Eggs were stocked in spring and the river was electrofished in the following autumn of the same calendar year.