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SHORT COMMUNICATION

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Dispersal of brown trout (Salmo trutta L.) fry in a low gradient stream - implications for egg stocking practices

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Abstract

Stocking of eggs is a common strategy to support declining or reintroduce extirpated salmonid populations. Data on how juveniles disperse from stocking points is crucial to be able to design efficient stocking programs. Detailed information of dispersal is limited for many salmonids, for example, brown trout. In this study, dispersal distance was measured at the end of the first growing season in a low gradient (0.7%) stream in Sweden where the trout population had been depleted. Eggs from 17 separate sets of parents were stocked as eyed eggs in March. During the following fall fry were sampled throughout the stream. The majority of the fry dispersed downstream and remained within a distance of 200 m from the stocking point with no difference between sizes of fry and the presence of a competing cohort or not. There was no dissimilarity in dispersal distances across offspring originating from different parents indicating absence of genetic influence. Our results suggest that, in streams similar to our study site, stocking points should be separated by approximately 330 m in order to avoid overlap in habitat use of fry from different stocking points and that the presence of competing cohorts, fry size and within population variability in dispersal can be neglected.

KEYWORDS

brown trout, dispersal, egg stocking, fry, salmonid, SNP

INTRODUCTION 1

In northern Europe, that is, Sweden, Norway and Finland, large numbers of brown trout (Salmo trutta), here after named trout, populations have become extirpated or threatened due to anthropogenic activities. In response, numerous restoration projects have been initiated, some of which include stocking of trout as fry, parr and adults, but also at earlier stages of their life cycle, for example, the eyed egg stage. Under appropriate conditions, stocking of eyed eggs has shown efficacy in some areas (Barlaup & Moen, 2001; Luhta, Huusko, &

Louhi, 2012; Syrjänen, Ruokonen, Ketola, & Valkeajärvi, 2015), but less is known about important parameters such as optimal distance between stocking points within a targeted restoration area. Improved understanding of the distance fry disperse after emergence will better equip managers to plan egg stocking projects that maximize survival of stocked individuals. Field studies focusing on the distance trout fry disperse from redds or stocking points are limited. However, some work has been conducted on Atlantic salmon (Salmo salar), here after named salmon. For instance Webb, Fryer, Taggart, Thompson, and Youngson (2001) sampled salmon fry 17 weeks after hatching in a

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river from a common stocking point and found that the maximum distance moved was 90 m upstream and 940 m downstream. Most fry had dispersed downstream within a distance of 380 m. Dispersal of fry is a function of habitat carrying capacity in terms of availability of food and shelter and the level of competition (Einum & Nislow, 2005; Finstad, Einum, Forseth, & Ugedsl, 2007; Grant, Steingrimsson, Keeley, & Cunjak, 1998; Milner et al., 2003). Rates and distances of dispersal of trout and salmon fry from the redd or stocking point have also been related to other factors including water velocity, parental origin and fry body length. When young salmonids initially leave the gravel they are sedentary, with low swimming ability. This makes fry vulnerable to high water velocity and they may easily be displaced in a downstream direction (Beall, Dumas, Claireaux, Barriere, &

Marty, 1994; Daufresne, Capra, & Gaudin, 2005; Elliott, 1987; Ottaway & Clarke, 1981). As a consequence dispersal distances should be greater in high- compared to low gradient streams. The findings of Webb et al., 2001 who studied dispersal at a gradient of 6%, is therefore probably not applicable to streams of lower gradient.

Furthermore, variation in dispersal patterns between and within populations has been observed for Chinook salmon (*Oncorhynchus tshawytscha*) (Bradford & Taylor, 1997) and salmon (Webb et al., 2001) fry. To our knowledge, within population variation in dispersal distance has not been studied in trout. Therefore, future studies aiming to produce generalized knowledge of trout dispersal would benefit from including multiple genetically separated groups. In field studies, Héland (1980) and later Elliott (1986) found that trout fry that had dispersed downstream were smaller than those that remained close to the redd. A negative relationship between fry body length and dispersal distances has also been documented in other salmonid species in experimental channels (Heggenes & Traaen, 1988).

The aim of this study was to explore dispersal distances of trout stocked as eyed eggs from emergence in spring until the following fall in a low gradient stream. To control for potential genetic variability in dispersal we stocked multiple groups of genetically separated siblings.

2 | MATERIALS AND METHODS

2.1 | Study site

The study was conducted in the third order stream, Falåströmsbäcken (64°50′47.5″ N 18°34′52.9″ E), in the Ume- and Vindel River catchment and supports both anadromous and resident life histories (Figure 1). The study site extended for 1,540 m between the two lakes. The upstream lake has an area of 14.1 km², which provides stable flow conditions with a mean annual flow of 1.3 m³ s⁻¹. During the study period, discharge ranged between 0.9–3.3m³ s⁻¹ in 2015 and 0.5–3.1m³ s⁻¹ in 2016. The mean thalweg depth and width of the stream was 0.5 and 11.9 m, respectively, with a consistent gradient of 0.7% without any occurrence of cascades or pools. The size range of stream bed substrate was 0.1–80 cm (median = 30 cm). Surface flow was consistent throughout the stream and was predominated by riffles. Thus, the stream provided a total 18,326 m² of trout habitat. During the 19th century, the stream was channelized for timber floating resulting in the extirpation of trout and the rest of the local fish community. After timber floating was discontinued during the 1970s and the habitat was restored, most of the naturally occurring fish species recolonized the stream with the exception of trout. Bullhead (*Cottus gobio*) is now the predominant species in the stream, but perch (*Perca fluviatilis*), burbot (*Lota lota*), pike (*Esox Lucius*), roach (*Rutilus rutilus*) and brook lamprey (*Lampetra planeri*) also occur.

2.2 | Egg production

In October 2014 and 2015, adult anadromous trout ascending from the sea were caught at a fish collecting facility located close to the outlet of the Ume- and Vindel River in the Baltic Sea (Figure 1). Nine separate pairs of males and females were combined in each of the study years. Tissue samples from all individuals were collected and analysed for single nucleotide polymorphism (Vignal, Milan, SanCristobal, & Eggen, 2002) to be able to assign offspring back to their parents. Adults were stripped of gametes to produce nine sets of genetically unique siblings each year. The fertilized eggs were kept under normal rearing conditions until stocking at the eyed stage in March the following year. Families 1–9 were stocked in 2015 with the exception of family number seven which was not stocked due to a low rate of egg fertilization. Families 10–18 were stocked in 2016 (Table 1).

2.3 | Stocking

In March 2015 and 2016, approximately 33,600 eggs were evenly stocked in the stream at three different stocking points, 86, 893 and 1,198 m downstream from the upstream lake (Figure 1). At each stocking point, batches of $11,200 \pm 1,000$ eggs were stocked containing individuals from three unique sets of siblings (Table 1). As family seven was excluded from stocking in 2015, an additional set of eggs from family nine was stocked to maintain consistent stocking densities between stocking points. At the stocking point, a perforated plastic crate ($0.6 \times 0.4 \times 0.3$ m) was placed on top of the stream bed (Figure 2). Four Whitlock-Vibert boxes (Barlaup & Moen, 2001) were evenly filled with eyed eggs where after they were placed on the bottom of each crate. The crates were then completely loaded with washed sorted gravel, 4–6 cm in diameter, to promote water exchange.

2.4 | Sampling

Electrofishing was conducted between August 18th-20th in 2015 and August 16th-18th in 2016. The full study reach was sampled



FIGURE 1 Map showing the location of the stream Falåströmsbäcken in the Ume- and Vindel River catchment in northern Sweden. Numbers indicate the location of the three stocking points. Lake Österavan can be seen on the left and lake Ruskträskkalven on the right. Black arrow indicates direction of streamflow

with a single pass using a battery driven back pack electroshocker (Hans Grass IG600, Hans Grass Inc., Germany) that generated 600 V. In the study area, the electroshocker used, commonly generate a low probability of catching juvenile trout (p < .25). Additionally, the substrate, predominated boulder with numerous interstitial spaces, further decreased the catch efficiency. This electroshocker was used due to its design and low weight which allows the operator to swiftly move long distances in difficult terrain. As we were interested in comparing relative abundance by collecting a subsample of the population rather than estimating the absolute number of trout in the study area, the anode was swept at approximate intercepts of two meters both laterally and longitudinally. When a trout was caught, total body length was measured (mm) and section of the anal-fin was removed and stored in alcohol before the trout was returned to the stream. The distance (m) from the outlet of the upstream lake was recorded for each sampled trout.

2.5 | Analysis

From the tissue samples collected, a random subset of 92 and 91 samples were genotyped in 2015 and 2016, respectively, representing roughly every second caught individual. A 96 SNP panel developed for trout of the region was used for genotyping samples to assess parentage. DNA was extracted from fin samples using QIAsymphony DSP, Qiagen LLC, Maryland, USA. Genotyping was performed using Biomark HD, Fluidigm INC, San Francisco, USA. The software ML-RELATE (Kalinowski, Wagner, & Taper, 2006) was used to assign offspring back to their parents and stocking point. Analysis of dispersal distance was conducted using the software Minitab 19, Minitab LLC, Pennsylvania, USA. Data were log-transformed to meet the assumption of normal distribution and equal variances. To test if dispersal distance differed between stocking points, years and parental origin, mixed effect model was used with year and stocking point and the interaction (yearXstocking point) as fixed effects and parental origin

 TABLE 1
 Data of stocking points, stocked families, sampled size from SNP analyses, body length and dispersal of brown trout in the stream

 Falåströmsbäcken in 2015 and 2016

Year	Stocking point	Family ID #	Sampled fry, N	Median total body length (mm)	Median dispersal (m)	Max dispersal (m)	Portion of upstream dispersal (%)
2015	1	1	15	92	83	124	33
2015	1	2	7	103	72	139	0
2015	1	3	12	92	50	131	8
2015	2	4	13	86	96	160	0
2015	2	5	17	85	52	95	0
2015	2	6	5	89	57	75	0
2015	-	7 ^a	-	-	-	-	-
2015	3	8	17	84	83	206	47
2015	3	9	6	89	78	192	33
2016	1	10	3	90	85	86	100
2016	1	11	29	83	76	240	41
2016	1	12	16	92	84	1,175	13
2016	2	13	2	80	215	247	0
2016	2	14	5	75	85	290	40
2016	2	15	5	78	93	114	60
2016	3	16	12	86	79	109	33
2016	3	17	12	81	104	290	58
2016	3	18	7	65	64	99	14

^aFamily number seven was not stocked due to a low rate of egg fertilization.

as random effect. Spearman correlation was used to test if dispersal distance was correlated to fry body length.

3 | RESULTS

3.1 | Sampling

Stocking crates were retrieved and contents were investigated in late June each year. In both years, few dead eggs were observed, indicating low egg mortality. In 2015 and 2016, electrofishing resulted in a total catch of 169 (size range: 70-112 mm; mean size: 90 mm) and 208 (size range: 62-108 mm; mean size: 85 mm) age 0+ trout fry, respectively. During the second year, 228 (size range: 118-228 mm; mean size: 160 mm) age 1+ individuals from the cohort stocked in 2015 were caught evenly throughout the study area, implying potential intraspecific competition from elder trout for the cohort stocked in 2016. We assumed that the cohort stocked in 2015 did not experience any competition from older cohorts given that all fish sampled were assigned to a known parent. Hence, patterns of dispersal in 2015 and 2016 were influenced by different levels of intraspecific competition. Even if stocked at equal numbers, the number of sampled individuals per family varied from 5 to 17 in 2015 and 2 to 29 in 2016 (Table 1). Although stocked at twofold density, only six individuals was sampled from family nine.

3.2 | Dispersal

Dispersal occurred both in an upstream and downstream direction. Median family specific dispersal distance ranged between 52 and 215 m (Table 1, Figure 3). Maximum family specific dispersal distance ranged between 68 and 290 m except two individuals from family 12 at stocking point one in 2016 that dispersed 506 and 1,175 m downstream. When pooling all individuals from 2015 and 2016, 73% had dispersed in a downstream direction. 90% of the downstream dispersers were caught within a distance of 130 m downstream from the stocking point and 90% of the upstream dispersers were caught within a distance of 200 m upstream from the stocking point. The total linear stream length where most individuals from a given stocking point would be found was therefore 330 m. Neither of the factors, year (F = 1.10, p = .317), stocking point (F = 0.26, p = .778), interaction (yearXstocking point) (F = 0.57, p = .581) or parental origin (F = 1.26, p = .222) had significant effects on dispersal distances. Similarly, there were no significant effect of total body length on dispersal distance (r = -0.011, p = .877).

4 | DISCUSSION

Although approximately 67,000 eggs were stocked, merely 377 young of the year trout were captured. Also, the number of sampled

individuals per family varied considerably. The low and variable number of caught trout might be explained by poor and differential survival among families. As the number of dead eggs remaining in the crates upon retrieval was low and as VW-boxes kept egg predators out, most mortality probably occurred post hatching. If all stocked individuals would have had survived and settled evenly throughout the stream, the density of fry would sum up to approximately 1.8 ind./m². However, as dispersal was limited, initial density must have been several times higher and may have caused exaggerated intraspecific competition and subsequent fry mortality (Milner et al., 2003) with the addition of predation from other fish species. The low numbers of captured trout might not only explained by fry mortality or predation but also by the sampling methodology applied, including sparse sweeps with the anode and the use of an electroshocker that generate low probability to catch juvenile trout.

At the sampling occasions, the majority of trout had a limited dispersal distance of 200 m from the stocking point and the most common course of dispersal was in a downstream direction. This corresponds with the findings in other studies on trout, for example,



FIGURE 2 Schematic drawing showing the egg stocking set-up at each of three stocking points in the stream Falåströmsbäcken in the Ume- and Vindel River catchment in northern Sweden 2015 and 2016. The gravel that was loaded into the perforated plastic crate is not shown in the figure

Daufresne et al. (2005) and Elliott (1986), who found that the vast majority of trout fry dispersed in a downstream direction 0-28 days after emergence measured in traps located approximately 10 m upstream and downstream from the redd. However, to our knowledge, no earlier studies have investigated the dispersal distances of trout fry during equivalent time periods as our study has, and at similar distances from the redd, therefore accurate comparable data are lacking. Nonetheless, similar studies have been conducted on Atlantic salmon. In France, Beall et al. (1994) reported slightly longer dispersal distances compared to the current study. Here, 71% of salmon that hatched in March were observed within 200 m downstream from the stocking point in April. However, in June, 68% were observed within 900 m downstream from the stocking point. Additionally, Webb et al. (2001) who studied salmon in Scotland that hatched in May observed most dispersals restricted to within 380 m downstream from the stocking point in August and September. It is likely that local streamflow characteristics are also an important factor controlling dispersal distances. Building on this, the gradient of the study streams in Beall et al. (1994) and Webb et al. (2001), 11% and 6%, respectively, were higher compared to the current study (0.7%) which might partly explain the different dispersal distances observed. Alternatively, it is possible that salmon naturally exhibit longer dispersal distances from their hatch location compared to trout.

As we conducted the study in an open system without migration barriers, it is possible that fry could have dispersed to the upstream or downstream lake which might potentially bias our data. However, as lakes in this region contain high density of predators, for example, perch and pike, young of the year trout should avoid entering these habitat and probably few of our stocked trout did enter the lakes. This assumption is supported by the dispersal distances observed from individuals stocked at the site located in the middle of the stream (site number two). No individuals from this site were observed dispersing further than 290 m even though they had the possibility to disperse several hundred meters more in both upstream and downstream directions.



FIGURE 3 Data from fish sampling in 2015 (solid circles) and 2016 (open circles). Each data point indicates one individual and horizontal lines specific sets of siblings. Vertical line at 0 m indicate location of stocking points. Positive values indicate downstream dispersal and negative values upstream dispersal. Family seven was not used in the study It should be pointed out that the dispersal distances observed could be influenced by the specific carrying capacity and habitat quality of our study site (Finstad et al., 2007; Grant et al., 1998), as well as high initial fry density near the egg-crates that could have promoted dispersal due to competition (Einum & Nislow, 2005; Elliott, 1986; Milner et al., 2003). A lower number of stocked eggs might therefore have resulted in shorter dispersal distances. As the crates containing the eggs were placed on top of the streambed, emerging fry were likely exposed to higher water velocity compared to if the fry would have emerged naturally from the stream bed. This might have resulted in slightly longer dispersal distances than what would have been expected from a natural redd. However, as the gradient was low and boulders were abundant, providing numerous flow refuges, we assumed this effect to be minor.

During the second year, we observed individuals in the study area that were stocked the prior year but no difference in dispersal pattern between years was detected. This suggests that density and inter cohort completion had no effect on dispersal at our study site. Older cohorts would probably have had an effect on dispersal if food and habitat was scarce. Given that the overall low abundance of trout, and that only one older cohort was present, this was probably not the case at our study site. Webb et al. (2001) found a significant effect of family origin and dispersal distance in salmon fry. The density of individuals from three sets of stocked siblings differed within 14 specific stream sections, with large variations in habitat, extending from the stocking point and 389 m downstream. However, no test of differences in average dispersal distance between families was reported. As we were only interested in range, and average dispersal distance, we did not estimate density within specific stream sections. Nevertheless, it is unlikely that large variations did occur between sections, due to a low degree of habitat variability at our study site. Hopefully, future studies would clarify if the pattern observed by Webb et al. (2001) also applies to trout. As we measured range of and average dispersal distance of 17 different sets of siblings, at three stocking points and across 2 years we are confident that any dissimilarity between families was negligible. Therefore, between family variability is likely not an important factor in egg stocking practices for similar streams and trout populations of comparable evolutionary history. Forthcoming studies that includes multiple populations of mixed evolutionary background will clarify if between family variability in dispersal exists. Data from this study revealed no relationship between fry body length and dispersal distance. This is in contrast with a number of previous studies on salmon and trout. For instance, Webb et al. (2001) observed decreasing fry body length with increasing downstream distance from the stocking location. Likewise, Héland (1980) found that fry that dispersed downstream were smaller than individuals that did not disperse. Also, Heggenes and Traaen (1988) noted that the probability of fry dispersing from the stocking location was higher for small individuals. Perhaps the differing result in the present study is due to the larger size of fry. For instance, the mean body lengths of the two groups of trout included in the study by Heggenes and Traaen (1988) were c. 32 mm and c. 43 mm and the salmon in Webb et al. (2001) were c. 48 mm. In contrast, trout in the present study had a family

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specific median body length of 75-103 mm. Larger body lengths increase the ability to withstand high water velocity (Heggenes & Traaen, 1988). Probably, water velocity at our low gradient study site was not enough to displace such large individuals. Large size of fry at our study site might be a consequence of low density ant subsequent competition. Given the patterns of fry dispersal, planning for stocking of eggs should consider the distance between stocking locations to maximize the use of habitat. Our results suggest that in streams of low gradient and predominated by boulders, a distance of approximately 330 m provides sufficient stream length to prevent individuals from different stocking points competing for the same habitat. Although it was not evaluated in the present study, streambed substrate might also influence dispersal of fry. Interstitial spaces between pieces of gravel is possibly more suitable for fry when compared to boulders due to limited access of lager sized predators or competitors, thereby likely reducing fry dispersal. However, abundant boulders provide a lot of flow refuges, when compared to smaller substrate, which also play an important role in reducing fry dispersal. The outcome of these potential contradictory effects of substrate size on fry dispersal is not easy to conclude and is an interesting topic for future research. In an evaluation of trout egg stocking in Finland, Syrjänen et al. (2015) found that stocking was rather ineffective. They stated that one contributing factor of failure could be the placing of egg in unsuitable microhabitat causing unnatural high mortality. As habitat characteristics influence risk of displacement, stocking points should be located with consideration to this. Heggenes and Traaen (1988), who studied swimming ability of emerging trout fry found that the critical velocity for displacement was 0.15–0.19 ms⁻¹. Stocking should therefore not be conducted at locations where water velocities exceeds 0.15 ms⁻¹ to avoid exaggerated downstream displacement and associated mortality. Our recommendation is therefore to stock eggs in habitat predominated by low gradient riffles, as were the case in the present study. The stocking of eggs has more challenges to it than simply minimizing overlap in habitat use of fry from different stocking points. As eggs are a limited resource, an important task is to find the optimal number of eggs to stock at each site to utilize the full carrying capacity but to also not to cause exaggerated densitydependent fry mortality. Future studies should therefore aim to provide guidelines for the optimal number of eggs to stock in various stream habitats. In addition, similar data on dispersal from other common stocking practices, for example, stocking fry or older fish, would also benefit forthcoming stocking activities.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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