

Small-scale dispersal and population structure in stream-living brown trout (*Salmo trutta*) inferred by mark–recapture, pedigree reconstruction, and population genetics

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Abstract: Many animals move among habitats, and even small-scale dispersal of individuals between habitat patches may have strong implications for population dynamics and structure. Here, we use long-term mark–recapture data combined with extensive genotyping and parentage assignment to investigate the importance of small-scale location change of resident brown trout (*Salmo trutta*) in a small stream (1500 m). During the first summer, juvenile fish dispersed downstream (mean displacement 200 m), with smaller juveniles dispersing longer distances. Downstream movement was also predominant during the first winter, but older fish moved little. This limited dispersal resulted in a significant isolation-by-distance structure for ages 1 and 2, but not for older age groups or for the mature fish. Individual pairwise relatedness coefficients decreased with waterway distance for mature fish during the 2002 and 2003 spawning seasons, but only weakly. Overall, between-site genetic differentiation was stronger for the younger age classes, and the signal decayed with age, indicating that the genetic structure observed in the stream is mainly driven by spatial aggregation of close relatives.

Résumé : De nombreux animaux se déplacent d'un habitat à l'autre et la dispersion, même à petite échelle, d'individus entre différentes parcelles d'habitat peut avoir d'importantes répercussions sur la dynamique et la structure des populations. Nous utilisons des données de marquage-recapture à long terme combinées au génotypage et à la détermination de la filiation de nombreux spécimens pour étudier l'importance des changements d'emplacement à petite échelle de la truite de mer (*Salmo trutta*) dans un petit cours d'eau (1500 m). Au cours du premier été, les poissons juvéniles se sont dispersés vers l'aval (déplacement moyen de 200 m), les juvéniles plus petits se dispersant sur de plus grandes distances. Les déplacements vers l'aval étaient également prédominants durant le premier hiver, bien que les poissons plus âgés se soient peu déplacés. Cette dispersion limitée s'est traduite par une structure d'isolement par la distance significative pour les groupes d'un et deux ans d'âge, mais non pour les groupes de juvéniles plus âgés ou les poissons matures. Les coefficients de corrélation par paire individuels montraient une faible diminution en fonction de la distance le long du cours d'eau pour les poissons matures durant les périodes de frai de 2002 et 2003. Dans l'ensemble, la différenciation génétique entre emplacements était plus forte pour les classes d'âges plus jeunes, le signal diminuant avec l'augmentation de l'âge, ce qui indique que la structure génétique observée dans le cours d'eau est principalement contrôlée par l'agrégation spatiale de parents proches.

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Introduction

Most animals move from time to time, but the temporal and spatial scales at which they move are highly variable (Dingle 1980; Queller and Goodnight 1989; Stenseth and Liddicker 1994). Dispersal is commonly defined as movement from the natal patch to the breeding patch or movement be-

tween alternative breeding patches (Clobert et al. 2001). However, a more general definition of dispersal is any movement between habitat patches that are separated by some unsuitable habitat — thus, dispersal constitutes movements that take an individual permanently away from its home range (Bowler and Benton 2005; Dingle and Drake 2007). In response to changes in habitat suitability or profitability, ani-

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imals move over small or large distances in search of food, mates, and shelter (Dingle and Drake 2007). Such dispersal may have important effects on population dynamics (Hanski and Gilpin 1991; Roff 2002). Further, such dispersal, given successful reproduction in the receiving patch, may lead to gene flow among patches (Hendry et al. 2004). Thus, the level and scale of dispersal have an impact on population structure (Schtickzelle and Quinn 2007). Costs and benefits of dispersal (including smaller-scale movement) are likely to be under selection (Bowler and Benton 2005). Therefore, to fully understand population-level processes, it is important to understand what drives individual variation in the scale and intensity of among-patch movement. Although movement at different spatial scales has been intensively studied in salmonid fishes (Elliott 1994; Hendry and Stearns 2004; Quinn 2005), the detailed dynamics of dispersal at small spatial scales are not well understood.

Juvenile salmon and trout, as well as adults of stream-resident populations, are primarily found in rivers and streams (Quinn 2005; Jonsson and Jonsson 2011), defending territories against same- or different-aged conspecifics (Keenleyside and Yamamoto 1962; Bachman 1984; Newman 1993). During the juvenile stage, the movement tends to be small-scale, but a small fraction of the individuals might undertake larger-scale movements, potentially leading to dispersal (Gowan et al. 1994; Rodríguez 2002; Morrissey and Ferguson 2010). Movement is generally downstream during early juvenile life, due to within-cohort competition for space (Steingrímsson and Grant 2003; Kaspersson and Höjesjö 2009), ontogenetic changes in habitat preference (Armstrong et al. 2003; Ayllón et al. 2010), or environmentally driven stochastic processes (Elliott 1994; Daufresne et al. 2005). The overall downstream dispersal is probably a result of passive displacement in addition to active movement. Recent experimental evidence shows that some of the early movement is due to density-dependent processes, but the scale at which this density dependence operates is highly variable (Morrissey and Ferguson 2010; Einum et al. 2011).

The extent of dispersal at various scales may translate into local-scale population structure. Because of their fragmented landscape, there is considerable spatial genetic structure within species of salmonid fishes. At the landscape scale, factors such as immigration history and barriers to gene flow generally lead to population differentiation. Such structuring may translate into patterns of isolation by distance (IBD; e.g., Castric and Bernatchez 2004), but not necessarily (Ferguson 1989; Castric and Bernatchez 2003; Dionne et al. 2009). At the local within-catchment scale, however, IBD genetic structure seems to be common — even at the scale of a few kilometres (Garant et al. 2000; Hudy et al. 2010; Kanno et al. 2011). This pattern is to be expected at this small scale given the very limited movement of many river-living salmonid fishes (see above).

In this study, we investigate dispersal patterns throughout life and the resulting population genetic structure of a resident brown trout (*Salmo trutta*) population by combining a long-term mark–recapture data set with pedigree and sibship reconstruction. In this way, we follow the recommendation of using a combination of direct (mark–recapture) and indirect (genotyping) methods (Wilson et al. 2004) to get a comprehensive picture of the extent of movement of both individuals

and alleles. The scale of this study (50–1500 m) is much smaller than almost all comparable studies available in the literature (but see Morrissey and Ferguson 2010; Kanno et al. 2011).

Materials and methods

The brown trout

Brown trout breed in fresh water during autumn and winter, utilizing clean gravel in running water (Klemetsen et al. 2003; Jonsson and Jonsson 2011). After hatching in spring, the alevins remain in the nest for several weeks until the end of the yolk-sac stage and then emerge from the gravel as fry to start feeding exogenously. Mortality is high during the first few weeks after emergence (Elliott 1994). Juvenile trout establish feeding territories, and the possession of a territory can be crucial for surviving this critical period (Elliott 1994). Trout may remain in their natal stream throughout their lives, whereas in some populations fish migrate to larger rivers, lakes, or the ocean to feed (Jonsson 1989; Cucherousset et al. 2005).

Study system

Brown trout were sampled from a small forest stream (Bellbekken) in southeast Norway (61°15'N, 11°51'E; see figure 1 in Olsen and Vøllestad 2001a) during the period 2002–2007. Twenty-five contiguous stream sections were used as permanent study sites. Site length varied from 32 to 96 m (mean = 60.2 m), spanning in total 1504 m. There is a small waterfall between station 1 and station 2 preventing upstream migration under most conditions and leading to weak but significant genetic differentiation between trout upstream and downstream of the waterfall (Taugbøl 2008). Below the waterfall the stream enters the larger river Julussa. Long-term tagging studies indicate that some individuals from Bellbekken disperse downstream into the Julussa (L.A. Vøllestad and E.M. Olsen, unpublished data), but only one tagged individual has ever been detected moving upstream past the waterfall. Hence, downstream migrants are lost from the population.

Individuals in this population rarely reach ages greater than 6 years and lengths over 20 cm (Vøllestad et al. 2002; Olsen and Vøllestad 2003, 2005). Fish density and growth rates are relatively low. Long-term mark–recapture studies have shown that survival rate is density-dependent, but also that it is strongly influenced by stochastic factors (Olsen and Vøllestad 2001a; Carlson et al. 2008). In addition, growth rate seems to be density-dependent, although the evidence for this is less strong than for survival (Vøllestad et al. 2002). Based on long-term demographic and genetic methods, the per-generation effective population size (N_e) in Bellbekken has been estimated at ~100 individuals (Serbezov et al. 2012a, 2012b).

Fish sampling

The trout population was sampled with a backpack electrofishing apparatus during early summer (June) and just prior to the spawning season in autumn (late September to early October) from the autumn of 2002 to 2009 (the main effort during 2002–2006). All sites within the stream were usually sampled within a 4- to 5-day period. Sampling was always

performed under good conditions (i.e., low water flow and stable weather conditions). At a given sampling occasion, each site was fished systematically and thoroughly from the downstream to the upstream limit at least three times (i.e., the removal method; White et al. 1982; Bohlin et al. 1989). Brown trout abundance (excluding age-0 fish) at each site and sampling occasion was estimated using the Zippin multiple-pass removal method (Bohlin et al. 1989). Estimated total abundance for all sites pooled for the different sampling periods varied between 895 and 1413 individuals (for details see Carlson et al. (2008)).

Passive integrated transponder (PIT) tags (Prentice et al. 1990) were used to individually mark all brown trout that were larger than ~50 mm. Occasionally, some fish were individually tagged by injection of a coloured elastomer material just under the skin (Olsen and Vøllestad 2001b). Irrespective of tagging method, trout were anaesthetized with benzocaine prior to tagging. The adipose fin (or a small clip from the caudal fin) was removed and stored in 1.5 mL tubes with 96% ethanol for later genotyping. The fin clip was also used as an external marker indicating that the fish had been captured and tagged previously. At first capture, a few scales were removed for age determination. The fork length of all fish was measured (to the nearest mm), sex was noted for sexually mature fish during the autumn sessions, and tag number was read for all previously tagged fish. After handling, the fish were allowed to recover and then released at the site of capture. During the spring sampling, fish could be classified into the 0+ and 1+ age-class based on length alone. Based on identical genotyping profiles and compatible age estimates and length measurements, we were also able to identify individual fish that had previously been caught and genotyped but not marked, or had lost their tag, and then were recaptured subsequently.

Genotyping

Genotyping data used for this analysis are from Serbezov et al. (2010a), and methods are detailed therein. In brief, DNA was extracted from the collected tissue samples using a salt-based method similar to that outlined in Aljanabi and Martinez (1997). Tissue samples from a total of 4440 individuals were genotyped for 15 loci that amplified well and were polymorphic (see Serbezov et al. 2010a). Polymerase chain reaction (PCR) amplification was performed in one triplex (SSaD71, SSaD85, and SSaD170), one duplex (CA060177 and TAP2B) and the rest of the loci in simplex, as these loci amplified best at slightly different conditions. The following protocol was used for each sample: 1.0 μ L DNA template, 10 mmol·L⁻¹ NH₄ reaction buffer, 0.03–0.05 μ L *Taq* DNA polymerase (Bioline), 0.24–0.5 μ L 50 mmol·L⁻¹ MgCl₂, 0.3 μ L dNTP, 0.3–0.5 μ L of each primer, and mqH₂O to a total volume of 10 μ L. For the triplex PCR reaction, 1.5 μ L of DNA template was used for a total of 15 μ L reaction volume. Cycling conditions consisted of an initial denaturation step at 94 °C for 2–5 min, followed by 30–35 cycles of denaturation at 92–95 °C for 30–45 s, primer annealing at 55–66 °C for 30–45 s, and sequence extension at 68–72 °C for 30 s to 2 min, and a final extension step for 5–10 min. The duplex was run with a “touch-up” type program consisting first of 20 cycles where the annealing temperature started at 60 °C and increased by 0.5 °C after each

cycle to reach 70 °C, followed by 15 additional cycles with annealing temperature set at 60 °C. Samples were subsequently electrophoresed on an ABI Prism 3100 Genetic Analyzer and analyzed with GeneScan Analysis and Genotyper Softwares (Applied Biosystems) and on an ABI 3730 DNA Analyzer and then analyzed with GeneMapper 3.7 software (Applied Biosystems). As the length of the alleles differed slightly between the two genetic analyzer machines, a plate of 96 individuals was genotyped on both to calibrate the results. Between 12% and 24% of the individuals were genotyped more than once at a particular locus, allowing us to estimate and systematize genotypic error (Hoffman and Amos 2005).

Pedigree and sibship reconstruction

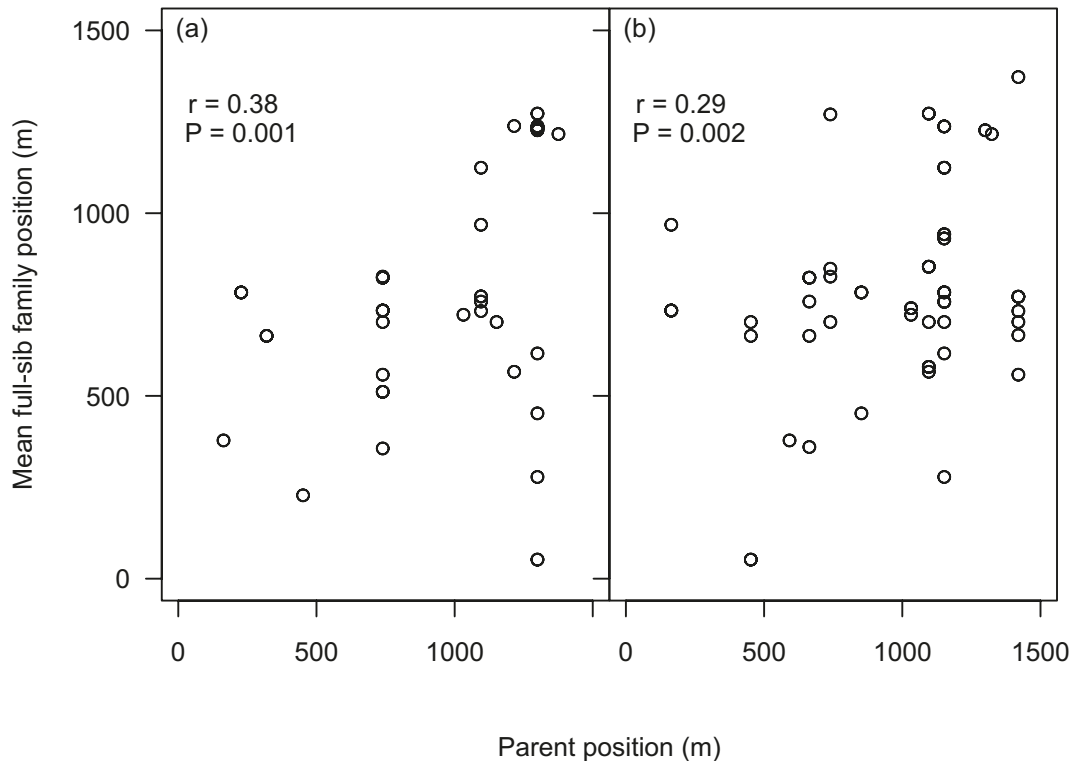
We used COLONY v. 2.0 (Wang 2004; Jones and Wang 2010) to perform pedigree reconstruction to assess the distribution of individuals from full-sib families and thus infer the extent of movement of 0+ and older trout. Both males and females in the population were allowed to be polygamous when constructing the sibship families, as both sexes have been shown to be polygamous in this population (Serbezov et al. 2010a). The differences in location of pairs of full-sib individuals were assessed to infer their distribution relative to the redd site (see below). Individuals larger than ~5 cm were also tagged so that the distribution of these full-sibs could be assessed over several seasons by recaptures; this mainly relates to individuals captured and genotyped as 1+ or older. This analysis was done for all full-sib families with $n \geq 2$.

Because the water in the Bellbekken is slightly turbid, it was not possible to visually locate spawning areas or spawning activity to know with certainty where the different individuals were spawned (i.e., the redd location). We therefore used the position of the mother during the autumn sampling period each year (2002–2004) as the redd location. If a mother had not been assigned, the redd location was considered unknown. We evaluated alternatives to this method; these were using male location when the mother was not known or the mean position of full-sibs based on COLONY. Based on the typical salmonid mating system, we expected males to move more than females within and among seasons (Hutchings and Gerber 2002), as male fitness will mostly be determined by the number of mates (Fleming 1998), and males may be expected to move longer distances to find more mates. We estimated the mean position of full-sib families and tested if this was correlated with maternal or paternal location during sampling (Fig. 1). Mean position of full-sib families was more strongly correlated with maternal position ($r_{80} = 0.38$, $P = 0.001$) than with paternal position ($r_{118} = 0.29$, $P = 0.002$).

Isolation by distance

Under migration–drift equilibrium, populations are expected to exhibit a significant correlation between their genetic and geographic distance (i.e., IBD; Wright 1943). This means that populations in close proximity to each other should be genetically less differentiated because of stronger gene flow among them than among populations further apart. We tested for IBD signals for the various age classes sampled during different years. To have reasonable sample sizes, indi-

Fig. 1. Within-stream position of full-sib families (estimated as the mean position for families where $n \geq 2$) relative to the position of the assigned (a) mother and (b) father. Position is given as the stream distance upstream the confluence with the river Julussa. Regression statistics are also given.



viduals from adjacent sampling locations had to be pooled (see Supplemental Table S1¹). If 20 or more individuals of one age-class were sampled at a site, we used the midpoint of this site as the geographical position of the sample. In cases where fewer than 20 individuals were sampled at a site, these individuals were pooled with the individuals captured at the adjacent upstream site, and the midpoint of the two sites was designated as the geographical position of the sample. To arrive at sufficient sample sizes without compromising geographical precision, we pooled individuals from a maximum of three sites. Pairwise F_{ST} values were calculated between individuals of the same age sampled at the same sampling event (early summer; autumn), and thus we used only sampling events where at least two samples (consisting of one, two, or three sites) with more than 20 individuals had been achieved. Although we obtained pairwise F_{ST} values for fish from the 0+ to 4+ age classes, the IBD analysis was performed only for 1-, 2-, and 3-year-old fish, as there were too few pairwise F_{ST} values for 0+ and 4+ fish (≤ 11). In total, 4079 individuals were used for the IBD analysis.

The occurrence of IBD was tested by correlating genetic distances ($F_{ST}/(1 - F_{ST})$; Rousset 1997) with geographic distances, measured as the linear distance along the stream measured in metres. The association of the matrices was assessed using a Mantel test as implemented in the “ade4” package for R 2.6.2 software (R Development Core Team 2008). The level of significance for the correlation coefficient was evaluated performing 10 000 permutations.

For the mature fish, the sample sizes allowed us to perform similar IBD analyses based on F_{ST} values only for the 2002 and 2004 spawning seasons (see Supplemental Table S2¹). We therefore used the individual-based approach to assess the spatial pattern of among-individual relatedness in the spawning population. We used SPAGeDi v. 1.3 (Hardy and Vekemans 2002) to calculate Queller and Goodnight’s (1989) estimator of pairwise relatedness and relate these estimates to the spatial distribution of the spawners.

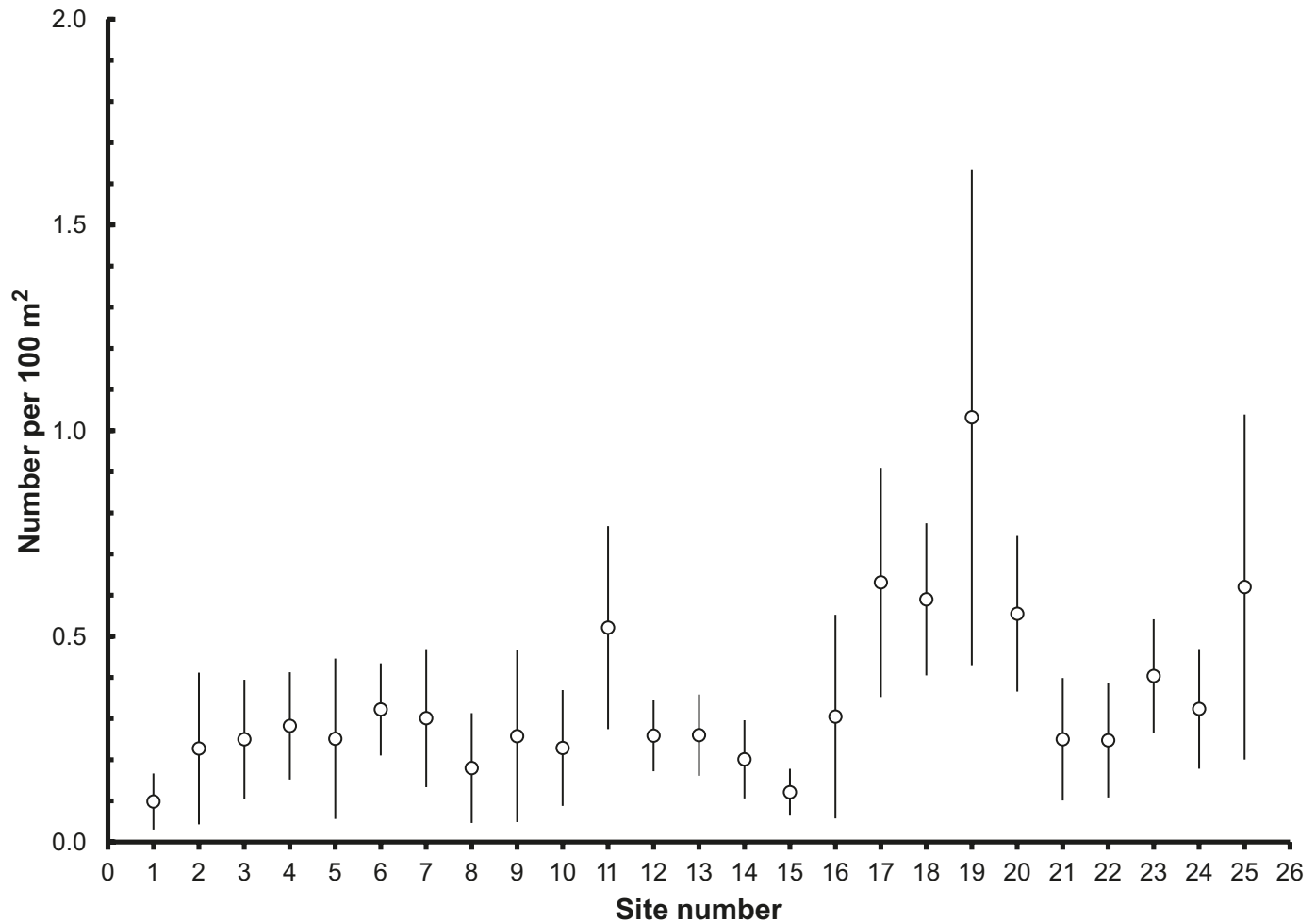
Results

Mature male and female trout were found throughout the length of the stream during all spawning seasons (2002–2009; Fig. 2), indicating that patches of suitable spawning habitat are found scattered throughout the stream. However, there were some areas with significantly higher densities of mature fish (especially stream site 19) (analysis of variance on ln-transformed densities; $F_{[24,175]} = 7.36$, $P < 0.001$). Spawning activity and redds were not directly observed.

A total of 1856 individuals belonging to the three cohorts that emerged during 2003–2005 were sampled. Of these, 156 young-of-the-year (0+) trout, sampled during the autumn season, were assigned to their mother. Assuming that the observed position of the assigned mother was close to the actual redd, the juveniles tended to disperse downstream (mean overall position relative to redd position was -200 m (95% confidence limit, CL: -272 , -129 m). Absolute distance moved (whether upstream or downstream) ranged between 0

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/f2012-073>.

Fig. 2. Mean (\pm standard deviation, SD) number of reproductively mature male and female brown trout per 100 m² observed at the various locations in the stream Bellbekken during the autumn seasons of 2002–2009. Stream sections are numbered from downstream to upstream.



and 1324 m, with a mean of 348 m. Based on the family structure assessed using COLONY, we estimated the pairwise differences in position (in metres along the stream) of all possible full-sib pairs (Fig. 3). More than 55% of the full-sib pairs were found less than 100 m apart. Overall, the smaller 0+ fish tended to have moved longer distances downstream from the inferred redd location than the larger fish (Fig. 4; $r_{156} = 0.208$, $P = 0.009$).

Through time, the pairwise distance among full-sibs increased (Fig. 3; Spearman rank correlation of median location version time, $r_8 = 0.875$, $P = 0.020$). Most full-sib pairs, however, remained within 200 m of each other.

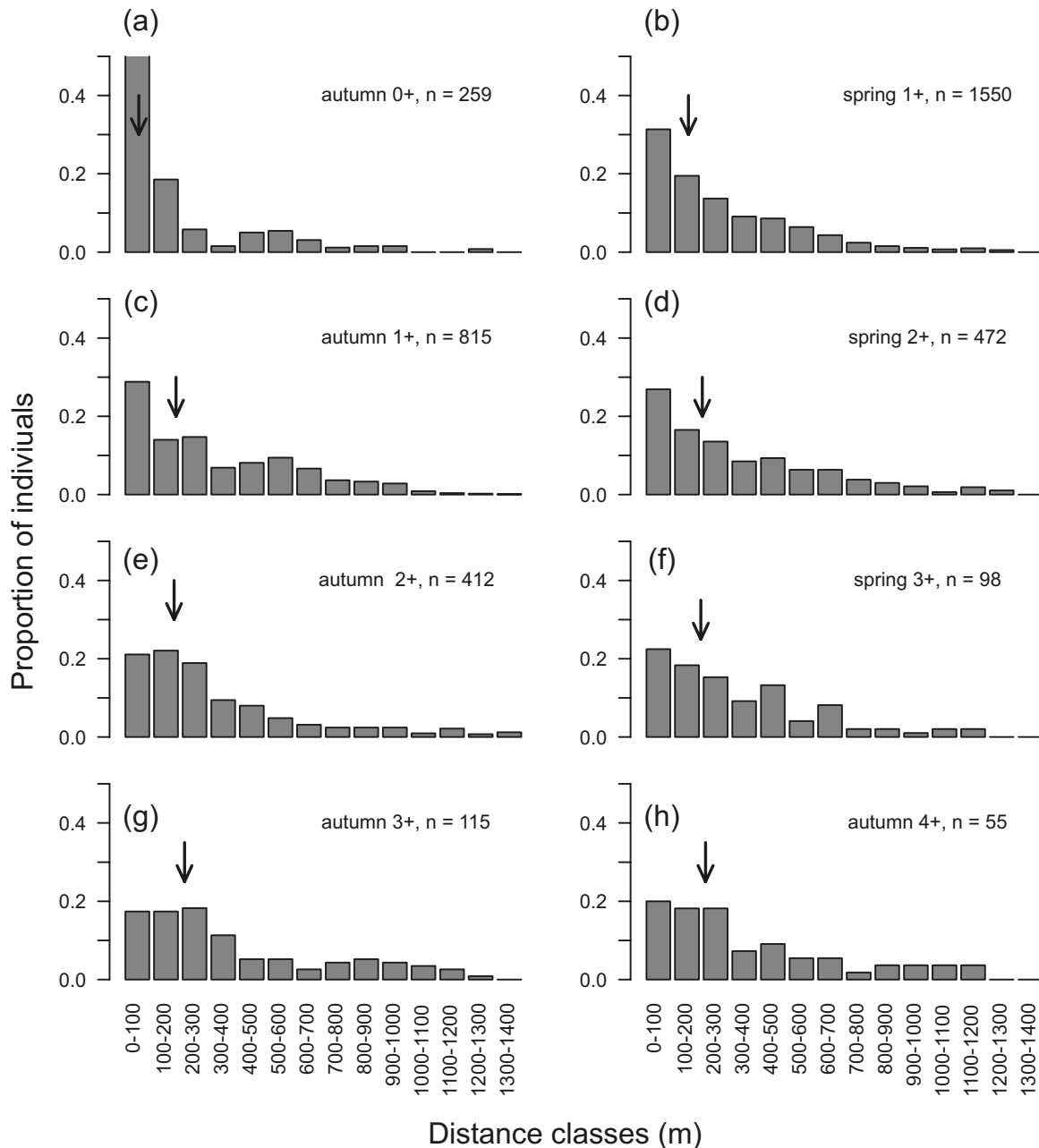
The between-season movement of the older age classes of trout was further inferred from direct observations of the location of marked and recaptured trout of the various age classes (from age 1 trout during spring until age 6 trout during spring; Table 1). We focused on the shortest time interval possible given by our data (i.e., movement during summer (spring to autumn) or winter (autumn to spring)). During the first winter (from 0+ in autumn to 1+ in spring), the fish tended to move downstream. In general, fish did not move between sections between subsequent time periods (1506 of 2201 observations of the same fish over two consecutive sampling sessions were in the same section), but there was a tendency for upstream dispersal for some of the time periods

even if the dispersal distances were short. Actually, there was a general upstream dispersal during the summer period (significant in four out of five comparisons). Dispersal distance overall did not differ between differently sized fish of the same age within these time periods; all regression coefficients were nonsignificant ($P > 0.05$).

In total, 703 pairwise comparisons of F_{ST} were estimated for fish belonging to age classes 0–4, with a mean F_{ST} (\pm standard error, SE) of 0.0071 ± 0.0004 . We performed the IBD analysis for the immature age classes (1+, 2+, and 3+; see Olsen and Vøllestad 2003; Serbezov et al. 2010a) for the spring and autumn seasons separately (Fig. 5; see Supplemental Table S1¹ for details about sampling structure and samples sizes). There were clear IBD signals for the 1+ and 2+ trout, both during spring and autumn. Based on 10 000 permutations of the data, these signals were clearly significant (Fig. 5). There was, however, no clear IBD structure for the 3+ fish. As evidenced by the level of the estimated mean F_{ST} values, the overall genetic structure became less strong over time (Fig. 6).

Finally, we investigated whether there was any geographic genetic structure for the mature fish during each spawning season. Owing to the relatively low samples sizes, this was only possible for the 2002 and 2004 spawning seasons. There was no significant IBD signal; however, the slope was nega-

Fig. 3. Pairwise difference in within-stream position of full-sib individual brown trout for different age classes and seasons from (a) 0+ during autumn to (h) 4+ during autumn. Differences in position are grouped into 100 m bins, and the arrow indicates the median. n = total number of pairwise comparisons.



tive (Mantel tests, autumn 2002: $r = -0.011$, $n = 28$, $P = 0.493$; autumn 2004: $r = -0.091$, $n = 15$, $P = 0.752$). Using pairwise relatedness coefficient, there were significant but very weak negative correlations between relatedness and distance in 2002 ($r = -0.036$, $n = 11\ 112$, $P < 0.0001$) and 2003 ($r = -0.023$, $n = 8913$, $P = 0.028$), but not so during 2004 ($r = 0.0001$, $n = 17768$, $P = 0.989$) (Supplemental Fig. S2¹).

Discussion

Using direct and indirect methods, we show the scale and extent of dispersal of individual brown trout in a small stream. Overall, most fish did not perform location changes

between two consecutive sampling sessions. However, the extensive genotyping followed by parentage assignment and mark–recaptures showed that there was an overall small-scale downstream dispersal of juvenile fish during the first year after emergence. The smaller fish tended to move longer distances than larger fish belonging to the same cohort. After the juvenile phase, trout movement was very limited but in the upstream direction. Limited dispersal and aggregation of full-sib individuals lead to an IBD genetic structure at this very small spatial scale (≈ 1500 m). The IBD signal was evident for 1+ and 2+ fish, but disappeared at older ages.

Based on the total data set, it was evident that most fish did not change locations within a given season. In total, 1506 of 2201 individuals were observed at the same sam-

Fig. 4. Dispersal distance (m) from the inferred redd position of differently sized (fork length, mm) 0+ brown trout captured during autumn (pooled for 2003–2005).

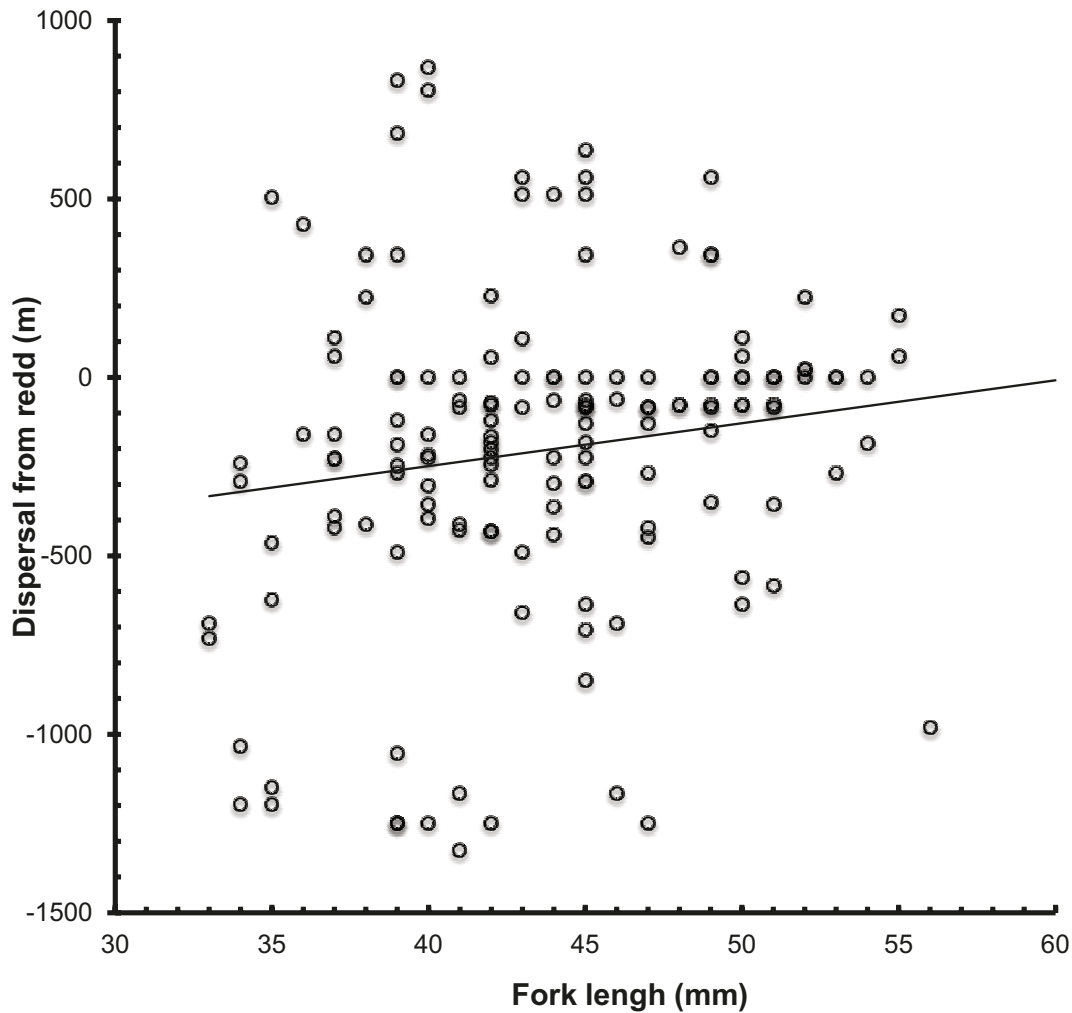


Table 1. Mean (± 2 standard error, SE; m) observed difference in position (Position 1 – Position 2) along the stream for brown trout of different ages observed at two consecutive time periods (spring or autumn season).

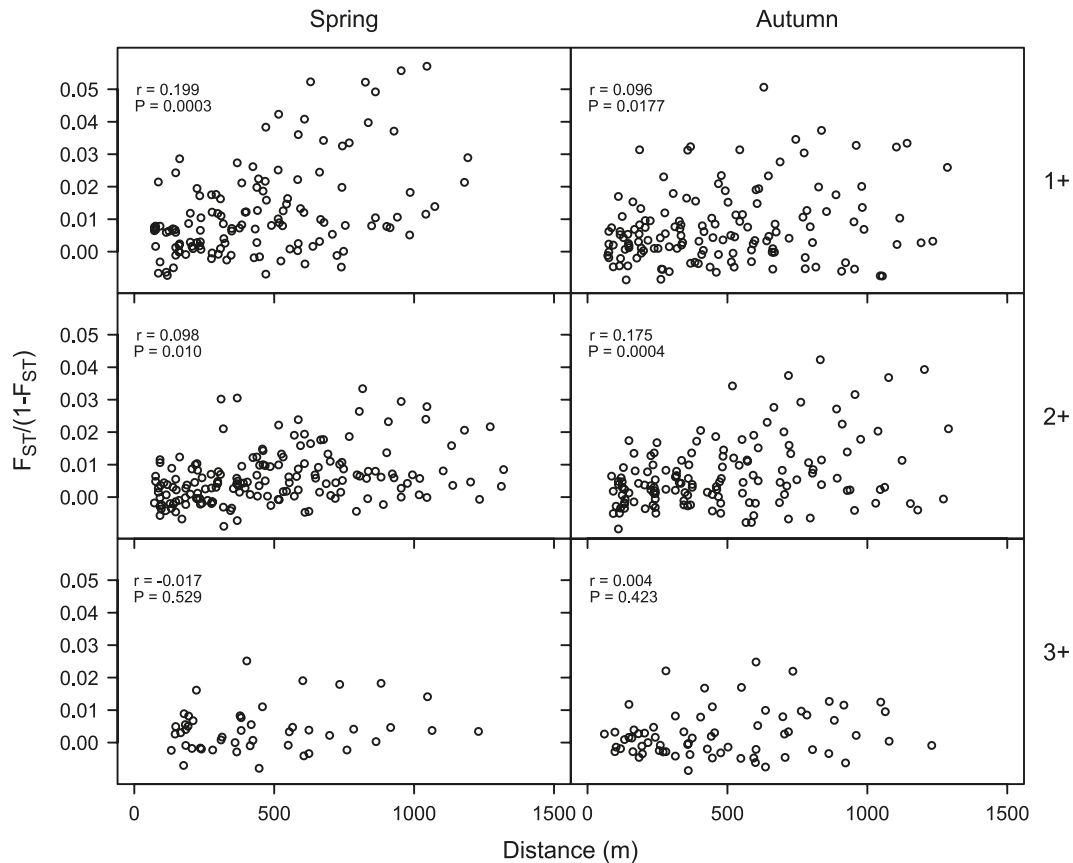
Age and season	<i>n</i>	Position 1 – Position 2	<i>t</i> test	<i>P</i>
0+ autumn to 1+ spring	43	-124 \pm 74	3.35	0.002
1+ spring to 1+ autumn	202	38 \pm 19	4.05	<0.001
1+ autumn to 2+ spring	271	6 \pm 20	0.63	0.530
2+ spring to 2+ autumn	390	35 \pm 18	4.01	<0.001
2+ autumn to 3+ spring	332	-4 \pm 16	0.44	0.660
3+ spring to 3+ autumn	277	22 \pm 15	2.85	0.005
3+ autumn to 4+ spring	199	7 \pm 17	0.81	0.422
4+ spring to 4+ autumn	170	23 \pm 20	2.34	0.020
4+ autumn to 5+ spring	86	-22 \pm 42	1.05	0.296
5+ spring to 5+ autumn	74	39 \pm 54	1.44	0.154
5+ autumn to 6+ spring	35	-70 \pm 57	1.82	0.178

Note: Negative values indicate downstream movement. Tests for deviations from 0 dispersal are also given (*t* statistic, *P* value).

pling location on consecutive sampling sessions. Moreover, when a fish did move, it was generally to a neighboring location. This dispersal pattern clearly conforms to the classical “restricted-movement paradigm” of stream-resident fishes (Gerking 1959; Gowen et al. 1994), with the majority of the individuals in the population being stationary. Similar scales

of movement occur in the brook char (i.e., brook trout, *Salvelinus fontinalis*) (Hudy et al. 2010; Morrissey and Ferguson 2010) and may be a general trait for such small-sized resident populations of salmonid fishes. However, as noted before (Rodríguez 2002), a minor proportion of each population may be more mobile. As we have reported elsewhere (Carl-

Fig. 5. Relationship between observed geographic distance (m) between sampling station midpoints and estimated genetic distance ($F_{ST}/(1 - F_{ST})$) for pairwise between-station comparisons of different brown trout age groups (age 1+, 2+, and 3+) during spring and autumn sampling. The results from the Mantel tests (r) with associated P values based on 10 000 iterations are also given.



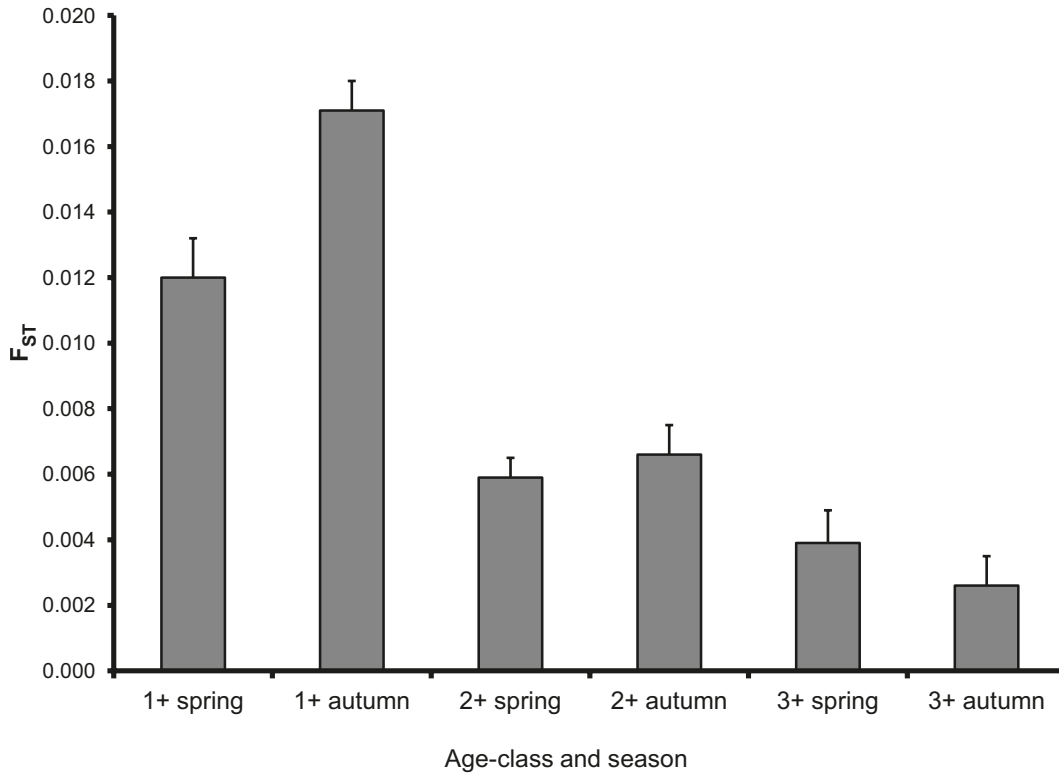
son et al. 2008), some individual trout disperse over longer distances both upstream into more lentic habitats and downstream past waterfalls.

Movement was most pronounced during the first summer of life, and most movement was in a downstream direction. A predominantly downstream movement soon after emergence from the redd is common for juveniles of salmonid species (Steingrímsson and Grant 2003; Morrissey and Ferguson 2010; Einum et al. 2011), and experimental studies show that the dispersal is more rapid at higher water velocities (Crisp 1991; Daufresne et al. 2005). This movement may be induced by the need to search for feeding territories and to avoid competition leading to density-dependent growth and mortality; individuals unable to acquire a territory close to their site of emergence must move to find a suitable territory. Thus, the mobile individuals are expected to have lower competitive ability (Daufresne et al. 2005). Displacement of subordinate individuals may lead to smaller and weaker individuals dispersing farther downstream than larger and stronger individuals (Heggnes and Traaen 1988; Elliott 1994; Daufresne et al. 2005). In our study, smaller fish tended to move farther downstream during the first summer. However, in a comparable study on brook trout, no such size-dependent variation in dispersal was found (Hudy et al. 2010). In theory, such water-flow-driven downstream displacement of emerging fry has been suggested as an important mechanism for population regulation through impacts

on recruitment (Cattaneo et al. 2002; Lobón-Cerviá and Rincón 2004).

For juvenile trout, downstream dispersal was common also during the first winter. For all fish older than age 1 in all seasons, movement between stations was uncommon, but most dispersal activity tended to be in the upstream direction. Furthermore, a few individuals moved greater distances. This indicates that there is little need for the fish to move long distances to find a new territory as they grow larger. Researchers have suggested that habitat preference changes with ontogeny and larger fish prefer deeper and slower flowing water (Mäki-Petäys et al. 1997; Heggnes 2002; Ayllón et al. 2010). The stream studied here is small but exhibits large within-station variability in habitat types and structural heterogeneity. By making short displacements (at scales <50 m), individuals can access new habitat types.

We observed a weak but significant IBD structure for the trout belonging to the younger age classes, but the strength of the IBD signal decreased with time and was not evident for trout older than 2 years of age. Interestingly, the IBD structure was observed at a very small spatial scale — much smaller than reported previously. For salmonid fishes, IBD genetic structure is common in landscapes with opportunity for movement of individual and alleles (for a review, see Hendry et al. 2004). Brown trout populations in particular tend to be highly genetically differentiated because of the effects of barriers to movement and because of the strength of

Fig. 6. Within age-class and season variation in genetic distance (F_{ST} + standard error, SE) for brown trout in the stream Bellbekken.

natal homing in this species (Allendorf et al. 1976; Ryman et al. 1979; Ferguson 1989). Genetic structuring with strong isolation by distance signals is evident in systems without barriers to movement and at scales varying from several kilometres to hundreds of kilometres (Carlsson et al. 1999; Griffiths et al. 2009; Kanno et al. 2011). In this study, we found significant IBD structure at a scale of hundreds of metres, distances much smaller than previously documented. Detection of an IBD signal at these small scales likely requires more detailed small-scale sampling than used in previous studies.

But how is this IBD signal established? One way this may occur is if close kin (full-sibs) aggregate. Here we show that during early life, closely related individuals (full-sibs) are found relatively close together, with the aggregation becoming looser with time. Such close association of close kin has been repeatedly documented for brown trout (Hansen et al. 1997; Carlsson et al. 2004; Vera et al. 2010), as well as for other salmonids (Mjølnørød et al. 1999; Hudy et al. 2010). Grouping of close kin such as half-sib and full-sib families may lead to genetic structure (Allendorf and Phelps 1981; Hansen et al. 1997) and potentially an IBD signature. Further, if individual fish exhibits precise natal homing during reproduction, the IBD signature will strengthen. Natal homing at the population scale is common in trout and salmon (Stabell 1984; Hendry et al. 2004), and natal homing at very small spatial scales has also been documented (Halvorsen and Stabell 1990; Armstrong and Herbert 1997; Carlsson and Carlsson 2002). In our study, we have no evidence for natal homing, and there was no strong IBD signature for the mature fish sampled during spawning. However, there was a weak tendency for the more closely related mature fish to be

found more closely together than unrelated fish during spawning. Also, mature fish found more closely together in this stream are more likely to mate with each other compared with fish from more distant locations (Serbezov et al. 2010a).

To conclude, we have observed significant IBD signature for young trout at spatial scales spanning 50–1500 m. This structuring seems to be due to spatial aggregation of closely related individuals. What are the implications of such a small-scale genetic structuring? We have previously shown that this small population contains substantial additive genetic variance for important life history traits (length-at-age) (Serbezov et al. 2010b). Further, mark–recapture studies have documented highly variable and weak selection on length (Carlson et al. 2008). Also, allelic diversity is rather high and is retained over time even if the effective population size is low ($N_e \approx 100$; Serbezov et al. 2012a, 2012b). Our study stream is small, but it exhibits large habitat heterogeneity (Olsen and Vøllestad 2001a). Aggregation of close kin in space may expose different families to variable selection and may even lead to genotype–environment correlations. This may lead to increased genetic variability within the population even if some variation is lost locally. More studies should clearly focus on small scales to understand the evolutionary dynamics of small populations at all spatial scales.

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