Environmental Determinants of Spawning Location, and Density and Size of Age-0 Brown Trout *Salmo trutta* in a Small Boreal Stream

Leif Asbjørn Vøllestad

Abstract Brown trout *Salmo trutta* populations are common in small boreal streams in Scandinavia. Populations are often small and isolated. In this chapter, I summarized studies conducted for 8 years on a population of small-sized brown trout living in a small Norwegian boreal stream exposed to harsh winters (>5 months of ice cover) and low water levels during summer. Subsequently, I evaluated factors influencing local use of spawning areas and the distribution of age-0 individuals during autumn in a contiguous 1.4 km portion of the stream. Finally, I analyzed the local and temporal variation in individual length of the age-0 individuals during late fall and related distribution of age-0 brown trout to habitat qualities, including fish density and environmental factors varying at the catchment scale (i.e., discharge and temperature) or at the local scale (i.e., habitat characteristics summarized using principal component analysis and presence/absence of competitors). Spawning occurred throughout the stream, indicating that female brown trout were able to find small patches of suitable spawning habitat in most study sections. Age-0 brown trout were also found in all sections of the stream, with large variation among sections. General linear mixed effects models, with year as a random effect, indicated that variation in the second principal component was the main factor determining density of both mature and age-0 brown trout. However, the effect was in opposite direction for the two groups. Variation in length of age-0 brown trout was substantial, and associated with most of the measured parameters. There was a significant negative density effect, and this effect was exacerbated by the presence of alpine bullhead *Cottus poecilopus*. Both mature brown trout and age-0 juveniles utilized the full extent of the study area, leading to substantial phenotypic variation.

L. A. Vøllestad (✉)

Department of Biosciences, Centre for Ecological and Evolutionary Synthesis, University of Oslo, Oslo, Norway
e-mail: l.a.vollestad@ibv.uio.no; avollest@ibv.uio.no

1   Introduction

The brown trout *Salmo trutta* is one of the most widely distributed salmonid fishes in the world (Elliott 1994; Jonsson and Jonsson 2011; Lobón-Cerviá and Sanz 2018; Keeley 2019). The species is well documented; a search on the Web of Science using the search topic "Salmo trutta" OR "brown trout" on March 18, 2022, returned 10,271 hits. Most of the studies pertained to fisheries, and marine and freshwater biology. This suggests extensive interest in the species, mainly because of its value for recreational fishers but also historically as a commercial species. The brown trout is phenotypically very plastic, leading to a large number of life history types and morphologies, and broad variation in individual behavior. Consequently, controversies have arisen regarding species definitions and boundaries, evolutionary history, and ultimately, conservation and management of populations (Bernatchez 2001; Kottelat and Freyhof 2007; Jonsson and Jonsson 2011; Sanz 2018; Muhlfeld et al. 2019; Whiteley et al. 2019).

Brown trout have been translocated across the globe, and generally, the introductions have been successful (Elliott 1994; McIntosh et al. 2011). The species is phenotypically plastic, and the large growth plasticity throughout life seems to facilitate success as an invader (Budy et al. 2013). This plasticity is also evident within the native range, and even at very small geographic scales. Extensive translocation and stocking of brown trout and other salmonid fishes, present management challenges at a variety of spatial scales (Young et al. 2018; Hansen et al. 2019).

Brown trout are the most common freshwater fish in Norway (Huitfeldt-Kaas 1918), as anadromous sea trout along the coast, as lacustrine-adfluvial (lake dwelling/tributary spawning) populations in numerous lakes across the landscape, and as a large river- or small stream fluvial (river dwelling/spawning) and fluvial-adfluvial (river dwelling/tributary spawning) populations. Human translocations, starting more than 1000 years ago, have resulted in numerous populations at high elevations. In many small low-order headwater streams, isolated populations of small-sized brown trout are common. These populations are isolated by natural and anthropogenic barriers to migration (Jones et al. 2021). The dendritic nature of the riverscape, and the numerous barriers to dispersal, facilitate the development of genetically differentiated populations (Morrissey and de Kerckhove 2009; Vøllestad 2018).

This chapter is focused on brown trout in a small boreal headwater stream, commonly found in Norway. The brown trout population is isolated from the population in the downstream river by a semipermeable barrier (small waterfall) to upstream migration, and the stream is fed by an upstream bog–wetland system. Individuals are small and rarely exposed to harvesting (angling). However, these headwater populations of brown trout may contain large genetic diversity that has evolved over millennia, and understanding their population dynamics is important. My focus will be on the environmental factors that determine the choice of spawning location, habitat utilization by young-of-the-year (age-0) brown trout, and the factors affecting juvenile growth during their first summer.

2   The Study System

Brown trout were sampled extensively over a 1504-m portion of the small stream Bellbekken, during 2002–2009 (Fig. 1). Twenty-five contiguous sections were sampled annually. Sample section length varied from 32 to 96 m (mean section length = 60.2 m). Habitat varied from slow flowing, relatively deep sections to steeper (high gradient) areas with large rocks/boulders and substantial habitat heterogeneity (Table 1).

The stream has been used for the transport of timber (similar to most Norwegian streams and rivers) for generations and was historically modified for that use. Timber transport on this stream and most other Norwegian waterways was discontinued during the 1970s, and the stream has subsequently reverted to pre-transport conditions through natural geomorphological processes. Timber has been harvested from the catchment at regular intervals.

A small waterfall between Sections 1 and 2 prevents upstream migration of brown trout under most environmental conditions. Below the waterfall, the stream enters the larger river Julussa. In the upper part of the stream (above section 25), the stream enters a wetland and bog area. Brown trout may use this upstream area, but due to sampling limitations, these upper reaches were not included in the study. Previous studies suggested a weak, but statistically significant, genetic differentiation between brown trout upstream and downstream of the waterfall (Taugbøl 2008;
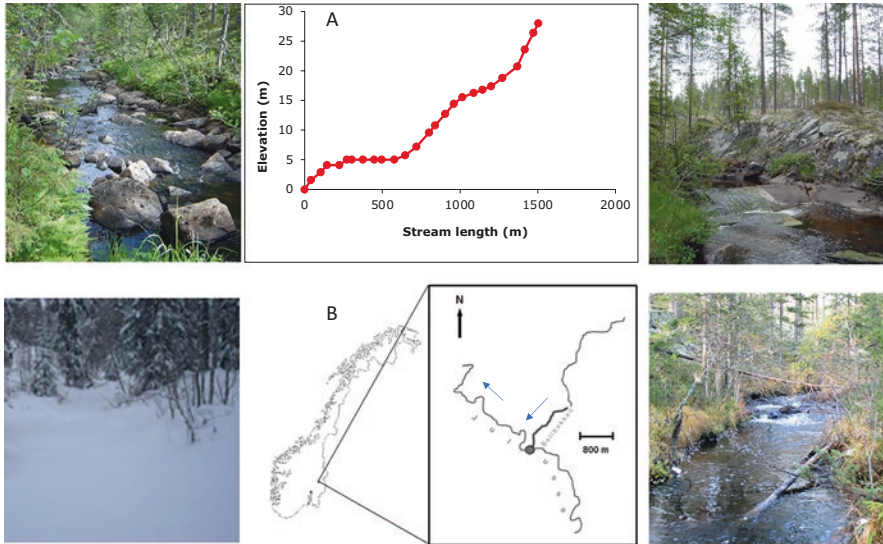

Fig. 1 The stream Bellbekken. (**a**) Stream profile of the sampled area of the stream Bellbekken. (**b**) Map of Norway, the stream Bellbekken and the larger downstream Julussa River. Arrows indicate the direction of streamflow, and the bold part of the stream Bellbekken indicates the sampled area. The pictures provide examples of stream sections, including a picture from winter when the stream is completely covered by ice and snow

Table 1 Habitat characteristics for the 25 contiguous sections of the stream Bellbekken (see Fig. 1), from the downstream to upstream section. PC1–PC3 are the mean loadings of the first three principal components from a principal component analysis. All habitat characteristics were measured at low streamflow in August 2004

Section	Length (m)	Slope	Transects (n)	Wetted width (m)	Mean depth (cm)	Exposed boulders (%)	Cover (%)	Undercut banks (%)	Underwater vegetation (%)	Substrate	Area (m²)	Wetted area (m²)	PC1	PC2	PC3
1	40	0.040	5	5.30	23.73	33.24	3.20	6.22	34.12	10.56	212.0	141.5	1.87	−1.06	0.73
2	64	0.020	8	4.63	17.70	30.61	18.39	20.51	36.93	8.86	296.0	205.4	0.68	0.37	0.32
3	40	0.030	5	3.80	30.88	9.82	14.48	19.20	27.92	8.88	152.0	137.1	−0.17	−0.66	−0.94
4	80	0.000	10	3.95	35.06	15.40	21.74	14.31	5.81	5.14	316.0	267.3	−1.58	−0.60	−0.19
5	48	0.020	6	4.75	26.03	17.97	17.62	19.95	15.80	6.62	228.0	187.0	−0.68	−0.32	0.38
6	32	0.000	4	4.13	52.08	0.00	23.93	37.45	0.00	4.85	132.0	132.0	−3.35	−0.62	−0.49
7	72	0.000	9	4.28	24.08	13.52	28.06	26.30	0.77	5.14	308.0	266.4	−1.96	0.36	0.19
8	72	0.000	9	4.50	29.03	20.88	19.62	19.66	0.00	4.12	324.00	256.36	−1.69	−0.07	0.52
9	48	0.000	6	3.75	25.00	14.50	14.85	30.25	0.00	4.00	180.00	153.90	−1.92	0.62	−0.36
10	80	0.000	10	4.15	17.59	24.39	19.39	20.33	0.57	4.24	332.00	251.03	−1.27	0.65	0.34
11	72	0.010	9	5.11	21.49	27.67	26.72	19.59	0.20	5.04	368.00	266.19	−1.34	0.28	1.30
12	72	0.020	9	5.22	14.12	18.38	5.41	11.54	35.12	8.57	376.00	306.90	1.28	−0.75	0.46
13	80	0.030	10	5.15	15.18	21.67	2.29	9.98	33.00	9.25	412.00	322.72	1.55	−0.81	0.42
14	40	0.030	5	4.80	14.62	18.78	1.20	17.58	32.92	9.56	192.00	155.94	1.35	−0.40	−0.01
15	64	0.030	8	7.88	14.11	24.85	2.44	10.83	39.90	8.71	504.00	378.76	1.66	−0.14	−0.54
16	56	0.030	7	4.29	13.67	28.69	1.57	17.27	38.79	8.79	240.00	171.15	1.48	0.18	−0.21
17	56	0.020	7	3.43	21.30	29.66	11.46	21.20	28.63	6.94	192.00	135.06	0.09	0.68	−0.68
18	72	0.010	9	3.67	16.69	11.90	23.26	23.26	11.70	5.93	264.00	232.58	−1.12	0.53	−0.53
19	56	0.010	7	3.93	21.90	18.17	15.66	22.60	0.54	5.74	220.00	180.02	−1.16	0.33	−0.16
20	56	0.010	7	3.79	13.87	13.21	8.93	14.47	11.76	7.21	212.00	183.99	0.05	−0.08	−0.60
21	72	0.020	9	3.83	10.89	20.49	5.46	14.43	37.60	7.98	276.00	219.45	1.14	0.12	−0.68
22	96	0.020	12	4.50	12.21	27.52	8.25	15.45	34.82	7.95	432.00	313.13	1.07	0.17	0.13

Section	Length (m)	Slope	Transects (n)	Wetted width (m)	Mean depth (cm)	Exposed boulders (%)	Cover (%)	Undercut banks (%)	Underwater vegetation (%)	Substrate	Area (m²)	Wetted area (m²)	PC1	PC2	PC3
23	48	0.060	6	4.42	16.75	29.15	3.65	16.27	48.32	9.17	212.00	150.20	1.65	−0.04	−0.18
24	56	0.050	7	4.07	19.01	36.51	5.96	17.00	35.69	9.07	228.00	144.75	1.26	0.35	−0.17
25	32	0.050	4	4.25	20.33	40.08	2.63	15.88	49.50	10.30	136.00	81.50	2.02	0.16	−0.16

Vøllestad et al. 2012). In fact, brown trout sampled in section 1 were more closely related to the brown trout in the river Julussa than to those upstream of the waterfall. Detailed genotypic analysis of several cohorts of brown trout suggested that a small number of individuals were immigrants from the downstream river Julussa (Serbezov et al. 2012b).

Individuals in the population are small, rarely reaching ages >6 years and lengths >20 cm (fork length, FL) (Olsen and Vøllestad 2003; Vøllestad et al. 2012). Fish density and individual growth rates are relatively low (Vøllestad et al. 2002). Analysis of long-term mark-recapture data for brown trout aged 1+ have shown that density and temperature interact to control growth performance, and growth was more affected by density for younger than older brown trout (Bærum et al. 2013). Data also suggested that growth in general is resource limited, and individual growth variation, particularly in the early years of life, had a relatively high heritability (h^2 varying from 0.16 to 0.31, with significant maternal and paternal effects; Serbezov et al. 2010b). Slow-growing brown trout are small at maturity (Olsen and Vøllestad 2005). For example, males were predicted to mature at 3.1 y and 142 mm (FL); females were generally older and larger at first maturation (3.5 y and 147 mm, FL). Larger individuals within an age group had a higher probability of being mature (Olsen et al. 2014).

Long-term mark-recapture data have suggested that survival rate is density dependent, but survival is also influenced by density-independent and stochastic factors (Olsen and Vøllestad 2001; Carlson et al. 2008). Further, there was no strong evidence for the "big-is-better" hypothesis that suggests that survival is higher for larger fish. Rather, there was a tendency for survival to be better for the average sized fish within each age class (Carlson et al. 2008). However, we found that both mating and reproductive success increased with increasing body size for both males and females (Serbezov et al. 2010a). We used both genetic and demographic data to evaluate the effective population size (Ne) of the population, using a variety of methods (Serbezov et al. 2012a, b). Most estimates of Ne were around 100, indicating that the population is relatively small. However, the data also suggested some gene flow from the larger population in the downstream Julussa River into the Bellbekken population.

3 General Methods

3.1 Fish Sampling

Brown trout were sampled using the same backpack electrofishing apparatus and methods during all years. Here, I analyze samples collected during September–October each year in the period 2002–2009. September–October is a period where individual growth is strongly reduced (Vøllestad et al. 2002), but not necessarily zero, due to the low water temperature. Sampling was conducted just prior to the

spawning season, to avoid disturbing the fish during the actual spawning. I assumed that most mature brown trout had moved to or toward their selected spawning location during that period. This assumption is based on a set of observations. During some additional sampling periods later in autumn, mature female and male trout were observed throughout the stream. We also observed post-spawned females distributed throughout the stream. Further, during early summer (June) small-sized juveniles were observed throughout the stream (Vøllestad, unpublished observations). For three cohorts, we used the observation of where potential parental fish (all genotyped) were observed during spawning, together with observation of where genotyped offspring were found the next autumn, to infer the dispersal during the first summer of life (Vøllestad et al. 2012). The results indicated a weak, but significant, downstream dispersal during the first summer. Taken together, I am confident that spawning happened throughout the length of the stream.

All sections within the stream Bellbekken were usually sampled within 1 week. Environmental conditions were stable (i.e., low streamflow and no/limited precipitation) during sampling. However, the stream drains a catchment containing bogs, wetlands, and coniferous forests leading to leaching of humic substances. The brownish-colored water and low transparency reduced visibility and led to reduced catchability, particularly for small brown trout.

On a given sampling occasion, brown trout were collected in each section using electrofishing from the downstream to the upstream limit at least three times (i.e., the removal method; White et al. 1982, Bohlin et al. 1989). Capture probabilities for age-0 individuals are generally low and variable in this and similar streams (see Lund et al. 2003; Carlson et al. 2008), and therefore, they were not included in the density estimates. Number of captured age-0 individuals per section can, however, be used as a relative measure of abundance. All fish were returned to the section of capture when all passes were completed. The relative density of age-0, and mature males and females was estimated as the total number captured within a section divided by the wetted area of the section ($n\ m^{-2}$).

Brown trout were the most abundant species present in each section. However, during some years a small number of alpine bullhead *Cottus poecilopus* were observed in some sections. In a previous study in a nearby river, we documented a significant overlap in diet for the alpine bullhead and the brown trout (Holmen et al. 2003), leading to the potential for negative competitive interactions (Vøllestad et al. 2002). Presence or absence of alpine bullhead was therefore used as a predictor variable in statistical analyses (see later).

Fork length of all fish was measured (nearest mm), and after handling, individuals were allowed to recover and were subsequently released within the section of capture. The age-0 individuals could usually be differentiated from the older fish based on length alone. A small number of scales were removed from larger fish (> 6 cm) for later age analysis in the laboratory. The sex of the mature fish could be easily distinguished during the spawning season based on external characteristics and presence of running milt and mature eggs (often clearly discernible).

3.2   Habitat Characteristics

Several habitat variables potentially important for the distribution and performance of the brown trout were measured in each section (Table 1). To get a general description of each section, transects (n = 188) were placed at 8-m intervals along the studied stream. At each transect, a measuring tape was stretched perpendicular to the streamflow to record total wetted width. Each transect was divided into 50-cm long sample stations. Depth was measured to the nearest cm at the middle of each sample station.

For each 50-cm sample station, a quadrate with a size 50 times 50 cm was visually inspected and an estimation was made of the following habitat characteristics:

1. The percentage of substrate, such as large boulders that were not submerged in water, hereafter called "exposed boulders." This reduces the overall available habitat within a section, but may also act as security habitat for fish.
2. The percentage of cover that is composed of undercut banks, hereafter called "undercut banks."
3. The percentage of the area covered by a canopy or large instream woody debris (such as large trees and branches), hereafter called "cover."
4. The percentage of the substrate covered with underwater vegetation (mosses and algae).
5. The dominant substrate type was classified according to a modified Wentworth scale (following Heggenes 1988).

For each of the 25 sections, the average slope was calculated as the total vertical displacement within a study section (m) divided by the total length of the section (m). The slope parameter provided an approximate idea of the water velocity in that section. The steepest part of the stream had a slope of 6%, whereas some sections had a slope of 0% (see Table 1).

The habitat classification was only performed once (in August 2004), at a time when the water level was low and stable. Means were estimated for all habitat characteristics in each of the 25 sections (Table 1). Many of the habitat characteristics measured in Bellbekken are strongly correlated (Table 2), indicating that they could not all be included as predictor variables in statistical analyses. To have a set of uncorrelated parameters describing the habitat in each section, I performed a principal component analysis (PCA). I extracted the three first principal components from the PCA which explained in total 73.3% of the habitat variability in the stream (Table 3). The loading matrix suggested that most parameters were associated with the first principal component (PC1; Table 3); therefore, it was not possible to extract one or two particular parameters that could easily convey information on important habitat characteristics. I therefore decided to use the mean loadings of the three first principal components for each section as predictors in subsequent statistical analyses.

Table 2 Correlation matrix for the measured habitat parameters is used for describing the habitat in the different sections. The average values for each section were used. Significant correlations are indicated in bold

	Wetted width (m)	Mean depth (m)	Exposed boulders (%)	Cover (%)	Undercut banks (%)	Underwater vegetation (%)	Substrate
Slope	0.239	−0.381	**−0.653**	**−0.756**	**−0.534**	**0.873**	**0.878**
Wetted width (m)		−0.222	−0.218	−0.316	**−0.461**	0.302	0.320
Mean depth (m)			**0.515**	**0.567**	**0.601**	**−0.528**	**−0.459**
Exposed boulders (%)				**−0.497**	**−0.538**	**0.610**	**0.536**
Cover (%)					**0.661**	**−0.828**	**−0.819**
Undercut banks (%)						**−0.610**	**−0.663**
Underwater vegetation (%)							**0.927**

Table 3 Principal component analyses for the habitat characteristics for the stream Bellbekken. Eigenvalues and eigenvector loadings for the three first principal components are given

	PC1	PC2	PC3
Eigenvalue	3.006	1.086	1.036
Percent	42.944	15.508	14.797
Eigenvectors			
Mean depth (cm)	−0.3763	−0.4752	−0.0661
Width (m)	0.0797	−0.3586	0.8628
Exposed boulders (%)	0.2888	0.5825	0.4166
Cover (%)	−0.4477	0.1792	0.1576
Undercut banks (%)	−0.3129	0.5081	−0.0331
Underwater vegetation (%)	0.4858	−0.0450	−0.1860
Substrate	0.4841	−0.1185	−0.1308

3.3 Water Temperature and Streamflow

Water temperature directly and indirectly influences fish growth and development (Kamler 1992; Wootton 1998). In the stream Bellbekken, the mean daily water temperature was estimated from readings taken 8–10 times a day with submerged HOBO loggers from May–October during 2002, 2004, and 2005. For the remaining years, direct measurements of water temperature were not available; however, mean monthly air temperature measurements at a weather station located approximately 4 km from the stream (at Rena city; data supplied by the Norwegian Meteorological Institute) and water temperature during June–September 2002, 2004, and 2005 were found to be positively correlated ($r^2 = 0.85$, $P < 0.001$). Therefore, I used air

temperature as a proxy for average water temperature during the brown trout growth season. Mean monthly air temperature predictably became positive in April, reaching a maximum between 12 and 20 °C during July, and decreased to below zero again in November (Fig. 2), but interannual air temperature varied substantially during the study period. In particular, variation was greatest during July, the month when discharge normally reached base-streamflow conditions.

Discharge has not been measured directly in Bellbekken; therefore, I accessed daily discharge measurements ($m^3 s^{-1}$) from a stream in the same vicinity (the river Frya) to serve as a proxy for variation in discharge in Bellbekken. Data were available through the Norwegian Water Resources and Energy Directorate (www.nve. no). From these data, I annually extracted the maximum discharge during spring (usually May) as an index of the size of the spring flood (primarily snow-melt) and minimum discharge during the summer season (June–August) as an index of drought severity (Vøllestad and Olsen 2008). Mean summer discharge served as a metric describing habitat availability during summer and potential transport of drifting food items (Table 4).
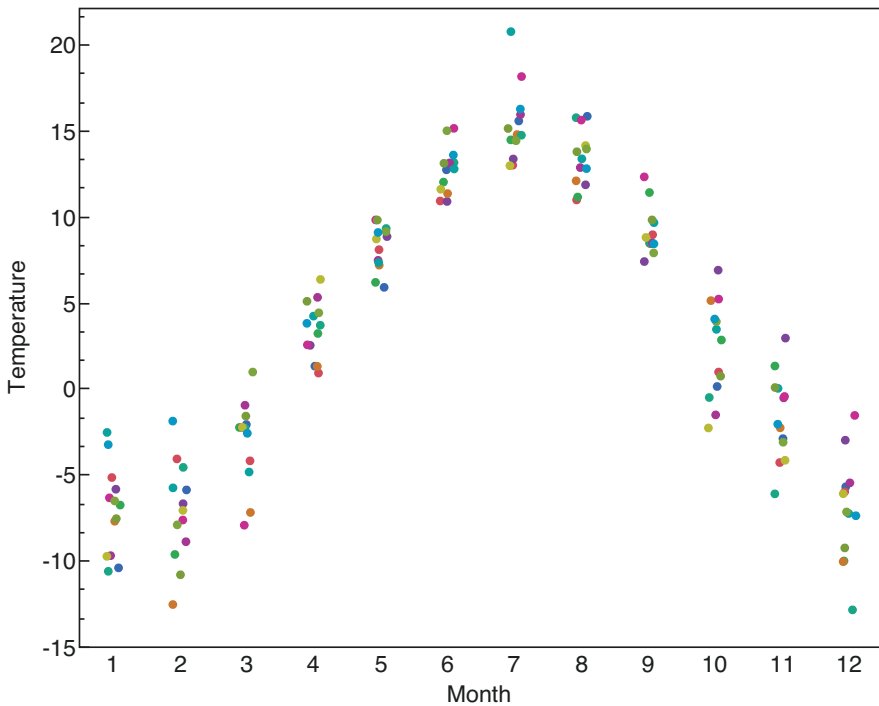

Fig. 2 Mean monthly air temperature (°C) at the Rena meteorological station, 2002–2009. Different years are in different colors

Table 4 Variation in streamflow ($m^3 s^{-1}$), based on measurements in river Frya (data from www. nve.no). Estimated mean and minimum summer streamflow, and maximum streamflow during spring are presented

Year	Mean summer streamflow	Minimum summer streamflow	Maximum spring streamflow
2002	0.92	0.04	11.85
2003	1.42	0.05	14.95
2004	1.03	0.04	14.87
2005	0.80	0.01	14.62
2006	1.44	0.02	14.62
2007	0.68	0.04	8.54
2008	1.37	0.02	15.54
2009	1.20	0.03	13.55

3.4 Analyses

I used a general linear mixed model (glmm) approach with model selection to evaluate the effects of environmental variables measured at different temporal and spatial scales on the observed variation in density of mature (males and females) and age-0 brown trout, and length of the age-0 individuals. To assess variation in the distribution of mature brown trout, I first tested for the variation in numbers among sections, using year as random variable. In a subsequent model, I then included section as a fixed effect. Finally, I evaluated which factors at the local scale best described the distribution by exchanging the section effect with various covariates. The full model included several fixed effects describing each section: slope ($m \cdot m^{-1}$) and the mean of the three first principal components. No interaction effects were included in the analyses. Year was included in all three analyses as a random variable to account for some unmeasured variation.

Variation in number of age-0 individuals at the end of the season was evaluated using the same approach as for the mature brown trout. After having identified the best model (see below), I assessed the effect of density of mature trout on the density of age-0 individuals. Finally, I assessed the influence of Alpine bullhead (presence-absence) on age-0 brown trout density.

The effect of environmental variables on length of the age-0 brown trout at the end of the growth season was evaluated using variables measured either at the annual scale (streamflow and water temperature) or at the specific section scale (habitat characteristics: PC1–3, slope, brown trout density, and presence/absence of alpine bullhead in a given section during a given year). Only the interaction between brown trout density and presence/absence of alpine bullhead was included in the modelling, and year was included as a random factor to account for among-year variation not accounted for by the predictor variables. Before doing the main analyses, I evaluated what would be the best descriptor of the influence of streamflow and brown trout density. Streamflow was estimated at the annual scale, as either minimum or mean summer streamflow, or maximum observed streamflow (during April–May) (Table 3). Density was either estimated as the total number of brown

trout per section or per area (wetted area), or total number of age-0 brown trout per section. I determined the appropriate explanatory variables and the best model explaining variation in age-0 brown trout size using standard model selection (Burnham and Anderson 1998). I started with the full model, comparing all potential combinations of response variables.

All statistical modelling was performed in the JMP statistical environment (SAS Institute Inc. 2020–2021). I used the Akaike Information Criterion adjusted for small sample size (AIC$_c$) (Akaike 1974) for the model selection, following Burnham and Anderson (1998). The model giving the lowest AIC$_c$ value was selected as the most parsimonious and was used for inference.

4 Results and Discussion

4.1 *Mature Fish*

During the 8 years of study, the total number of spawning brown trout in the study area in stream Bellbekken varied between a low of 101 and a high of 215 individuals. The male–female ratio varied around 1:1; females dominated some years, and males were most abundant in other years. Mean length of mature females (± SE) was 151 ± 1 mm, and males averaged 168 ± 1 mm (Fig. 3), and differences were statistically significant (ANOVA; $F_{1, 1016} = 159.3$, $P < 0.001$). Mean length of males was also more variable than that of the females (Levene's test, $F_{1, 1294} = 44.9$, $P < 0.001$). Despite a relatively small range in length for mature individuals of both sexes, sexual selection driven by female mate choice and male–male competition has been documented in this population (Serbezov et al. 2010a).

During spawning, female brown trout choose spawning locations based on availability of suitable spawning substrate (i.e., clean gravel; see review by Jonsson and Jonsson 2011) and subsequently she build a redd with a variable number of nests for egg deposition (Fleming 1998; Esteve 2005). Small-sized brown trout like those found in the stream Bellbekken spawn between 112–330 eggs (Olsen and Vøllestad 2003, Vøllestad unpublished data), and these eggs may be deposited in 1–3 nests (Fleming 1998) over 1–3 days. In the stream Bellbekken, the number of males and females in a given section was positively correlated ($r = 0.76$, $P = 0.03$), suggesting that the males may distribute themselves depending on the availability of females. However, because the females may complete actual spawning in just a few days and males may be sexually active for weeks (Fleming 1998; Esteve 2005; Jonsson and Jonsson 2011), the males may reposition repeatedly during the spawning season.

The number of mature brown trout varied among sections (Fig. 4), and the glmm model with section as fixed effect explained approximately 39% of the variation. Although suitable spawning sites were available throughout the study area, some sections with a greater than average density of mature fish did occur. For example, in section 19 there was a relatively large area with suitably-sized gravel and greater
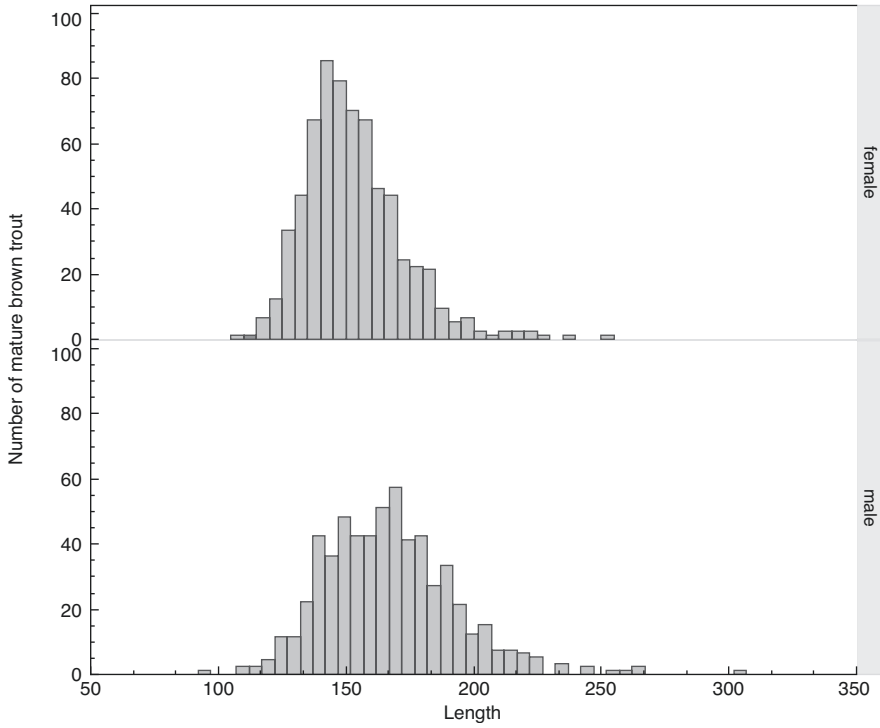
Fig. 3 Length distribution (fork length; mm) of mature male and female brown trout sampled in the stream Bellbekken during autumn (September–October) 2002–2009

than average number of mature fish. Although this type of gravel occurred throughout the stream, it was usually limited to small patches.

The best model for explaining the variation in number of mature brown trout had PC2 as the only explanatory variable, and the next best model also included the effect of slope (Table 5). Density of mature fish increased significantly with increasing values of PC2 (Fig. 5). PC2 was positively correlated with proportion underwater vegetation (various mosses; Bryophyta) and exposed boulders (not submerged) and negatively correlated with depth (Table 3). Results suggested that the brown trout selected shallow areas with cover (often underwater vegetation, see Mäki-Petäys et al. 1997) and structure; however, this model explained only 18.5% of the variation in density of mature brown trout. In contrast, the glmm with only section as fixed effect explained more of the variation (adjusted R^2 = 0.39; see above).

Results suggested that there is a suitable spawning habitat throughout the stream. This was supported by observations made while sampling, where small patches of suitable gravel and reasonable streamflow were observed throughout the stream. Furthermore, the generally small size of the male and female brown trout suggests that relatively small gravel in small patches will be adequate for digging redds and depositing the relatively few eggs (Ottaway et al. 1981; Gauthey et al. 2017). Indeed,
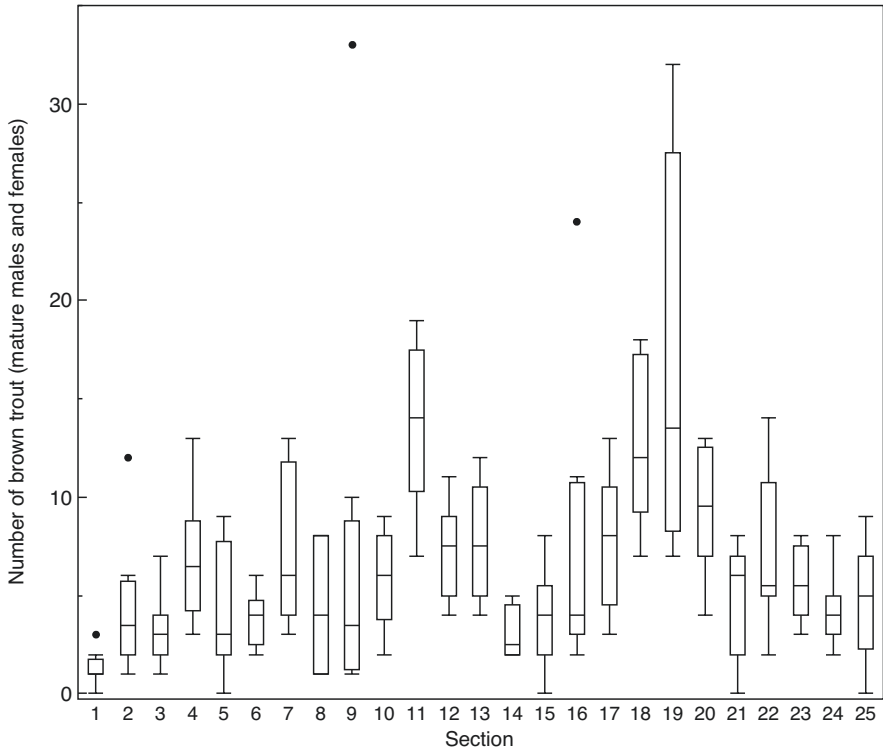
Fig. 4 Number of mature brown trout (female and male) in the different sections of the stream Bellbekken

Table 5 Selection of the best model explaining variation in the density of mature brown trout (males and females) in the stream Bellbekken. (a) The full model and the five best models are presented, with the best model given in bold. The best model is the one with the lowest AIC_c-value. AIC_c, ΔAIC_c, and rank are given. Year was always included as a random variable. Year was used as a random effect. (b) Parameter estimates ($\pm$ SE) for the best model; $R^2 = 0.162$ adjusted $R^2 = 0.185$, $n = 200$, the random year effect accounted for 5.11% of the total variance

(a) Model selection			
Parameters	AIC_c	ΔAIC_c	Rank
Slope + PC1 + PC2 + PC3	−814.0	22.7	6
PC2	**−836.7**	**0**	**1**
PC2 + PC3	−827.2	9.5	3
PC1 + PC2	−824.4	12.3	4
Slope + PC2	−832.2	4.5	2
Slope + PC1 + PC2	−824.0	12.7	5

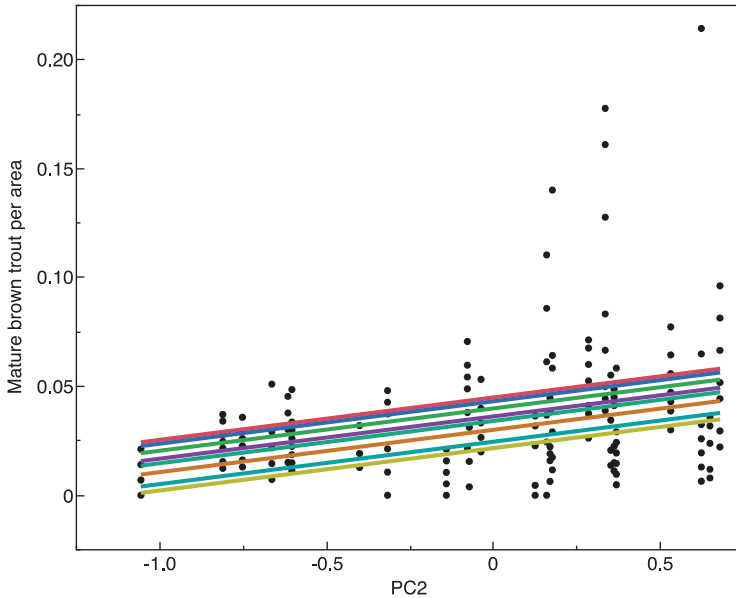| (b) Parameter estimates					
Parameter	Estimate	SE	DF	t-ratio	P
Intercept	0.034	0.003	7.02	11.511	<0.001
PC2	0.019	0.004	191	4.91	<0.001

Fig. 5 Relationship between the number of mature brown trout (males and females) and proportion of undercut banks and exposed boulders (as summarized in PC2; see Tables 1 and 3 for details). The regression lines are for the different years (2002–2009), based on a random year effect (random intercept) in a general linear mixed model

average fecundity of a female brown trout in Bellbekken is approximately 280 eggs (Olsen and Vøllestad 2003). This limited number of eggs may be deposited in a small number of nests (batches), probably within the same redd (see Jonsson and Jonsson 2011). We never observed spawning directly, and these small-sized fish probably spawn at dusk or dawn to reduce predation risk (Jonsson and Jonsson 2011). Apparently, brown trout captured in this study were sheltering close to spawning sites.

4.2 Young of the Year Brown Trout—Variation in Numbers

Density of young-of-the-year (age-0) brown trout was generally low, and relative density varied spatially from a mean of almost zero in section 9, to 4–5 individuals per 100 m^2 in section 1 and 12. A glmm model with section as fixed effect and year as random effect explained 34.5% of the variation in density of age-0 brown trout.

Density of age-0 brown trout can be influenced by numerous habitat quality metrics. However, the best glmm model explaining the variation in density only comprised the second principal component as an explanatory variable (Table 6). The density of age-0 brown trout was negatively related to PC2, in direct opposition to

Table 6 Selection of the best general linear model explaining variation in the density of age-0 brown trout in the stream Bellbekken. (a) The full model and the five best models are presented, with the best model given in bold. The best model is the one with the lowest AIC_c-value. AIC_c, ΔAIC_c, and rank are given. Year was always included as a random variable. Year was used as a random effect. (b) Parameter estimates (± SE) for the best model; $R^2 = 0.189$, adjusted $R^2 = 0.158$ $n = 200$, the random year effect accounted for 14.36% of the total variance

(a) Model selection			
Parameters	AIC_c	ΔAIC_c	Rank
Slope + PC1 + PC2 + PC3	−837.1	22.7	6
PC2	**−862.0**	**0**	**1**
PC3	−853.6	8.4	4
Slope	−860.6	1.4	2
Slope + PC1	−851.9	10.1	5
Slope + PC2	−857.7	4.3	3

(b) Parameter estimates					
Parameter	Estimate	SE	DF	t-ratio	P
Intercept	0.021	0.004	7.01	45.11	0.001
PC2	−0.011	0.004	191	3.15	0.002

the result found for the distribution of mature brown trout. This may indicate that small-sized juvenile trout avoid areas with large numbers of larger fish, either to avoid competition for space or because of different preferences during this time. To assess the influence of mature brown trout on the density of age-0 brown trout, the number of mature individuals was included as an explanatory variable in the model; however, it was not statistically significant (parameter estimate: 0.016 ± 0.067, $P = 0.617$). Similarly, the presence/absence of the Alpine bullhead was not a statistically significant explanatory variable in the model (parameter estimate -0.003 ± 0.003, $P = 0.332$).

Habitat selection by juvenile brown trout can be both dynamic and relatively flexible (Heggenes 1996, 2002). We have earlier observed that juvenile brown trout disperse from the redd location during the first summer (Vøllestad et al. 2012), and habitat requirements vary according to life stages of brown trout (Jonsson and Jonsson 2011). Thus, habitat use just prior to the spawning season may be different than habitat use during other seasons.

4.3 Young of the Year Brown Trout—Variation in Size

During the 8-year study, the mean length of the age-0 brown trout at the end of the growth season (September–October) varied from a low of 42 ± 7 mm to a high of 51 ± 5 mm and differences were statistically significant (ANOVA, $F_{7, 813} = 17.5$, $P < 0.001$). More specifically, individuals varied from <35 mm to >60 mm (Fig. 6);
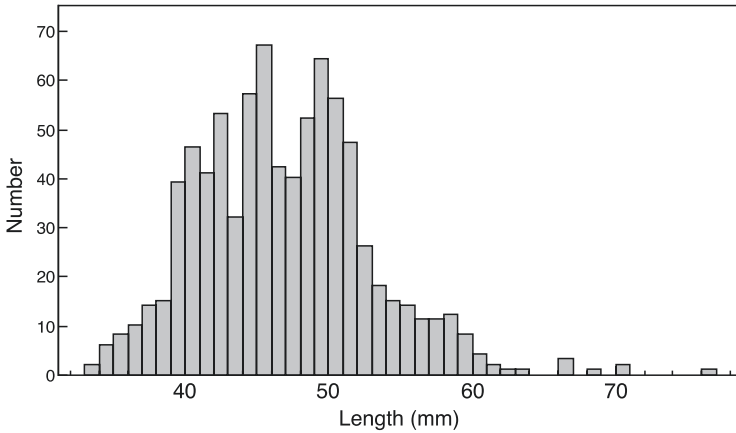
Fig. 6 Length distribution (fork length; mm) of age-0 brown trout (all years pooled) sampled in the stream Bellbekken during autumn (September–October) 2002–2009

however, individuals >65 mm may actually be age-1 brown trout that were erroneously classified as age-0 (however, included in further analyses).

Juvenile growth, and thus length at the end of the growth season, may be affected by numerous factors at a variety of scales. For example, broad-scale factors, such as streamflow (m^3 s^{-1}) and temperature, are relevant at the stream scales. Further, growth may also depend on environmental factors relevant to microhabitats utilized by individuals.

At the section scale in the present study, individual brown trout were assumed to have lived most of the first summer relatively close to the location of capture (in the same section). The effect of section slope (proxy for water velocity), the three first principal components (PC1–3) based on the habitat measures, brown trout density, and the presence or absence of alpine bullhead were tested in a glmm. Year was always used as a random factor (random intercept) in the analyses to account for among-year variation in unmeasured factors influencing growth (such as variation in primary and secondary productivity).

First, I evaluated mean summer flow, minimum summer flow, and maximum spring flow in a glmm to determine which discharge metric explained the most of among-year variation in individual age-0 length. Based on the AIC_c-criterion, minimum summer flow was the better fit to data ($\Delta AIC_c < 6.0$ units than for the two other metrics) and were thus used in the final modelling.

Second, I used a glmm with year as a random effect to assess metrics for brown trout density as a predictor, comparing density estimated as the total number of brown trout or total number of age-0 per section, or density as the number of age-0 juveniles per m^2. The total number of brown trout (all age classes) per section was the best explanatory factor with a ΔAIC_c value <16.0 units than for the two other metrics. The best model explained 17.9% of the variation in age-0 length.

Table 7 Selection of the best model explaining variation in the length of age-0 brown trout in the stream Bellbekken. (a) The full model and the five best models are presented, with the best model given in bold. The best model is the one with the lowest AIC_c-value. AIC_c, ΔAIC_c, and rank are given. Year was always included as a random variable. (b) Parameter estimates ($\pm$ SE) for the best model is presented; $R^2 = 0.316$, adjusted $R^2 = 0.309$ $n = 811$, the random year effect accounted for 13.66% of the total variance

(a) Model selection			
Parameters	AIC_C	ΔAIC_C	Rank
N(trout)*Sculpin + Streamflow + Temperature + PC1 + PC2 + PC3 + Slope	4902.6	2.4	2
N(trout)*Sculpin + Streamflow + Temperature + PC2 + PC3 + Slope	**4900.2**	**0**	**1**
N(trout)*Sculpin + Streamflow + PC1 + PC2 + PC3 + Slope	4906.1	5.9	4
N(trout)*Sculpin + Streamflow + Temperature + PC2 + PC3	4906.2	6.0	5
N(trout)*Sculpin + Streamflow + PC2 + PC3 + Slope	4903.7	3.5	3

(b) Parameter estimates					
Parameter	Estimate	SE	DF	t-ratio	P
Intercept	18.57	16.81	5.30	1.10	0.317
Trout density	−0.14	0.02	802.0	−6.62	<0.001
Alpine bullhead (absent)	0.14	0.44	800.6	0.32	0.752
Trout density * alpine bullhead (absent)	0.09	0.02	799.8	4.19	<0.001
Streamflow	111.39	71.28	5.1	1.56	0.178
Slope	12.85	16.40	799.8	0.78	0.434
PC2	−1.653	0.41	799.0	−3.69	<0.001
PC3	1.84	0.40	799.8	4.63	<0.001
Temperature	2.29	1.187	5.3	1.96	0.104

The full model included numerous potential explanatory variables (Table 7). In addition to the random year effect, an interaction effect between alpine bullhead presence/absence and brown trout density was included because results from prior studies have suggested competitive interaction occurs between alpine bullhead and brown trout (Vøllestad et al. 2002; Holmen et al. 2003). The model that best fit the data, based on the AIC_c-criterion, contained all parameters except PC1 (Table 7a), but several of the explanatory variables were not significant (Table 7b). The full model was the second-best model, and a model without temperature and PC1 was the third-best model. The best model explained 30.9% of the variation in age-0 length. The random year effect accounted for 13.8% of the variance.

Length (and thus growth over the summer) of brown trout differed depending on habitat quality at the section scale (Table 7). Length increased with increasing stream width (PC3) and decreased with increasing proportion of cover and exposed boulders (PC2). Another interesting result from this analysis was the significant interaction between the presence/absence of alpine bullhead and brown trout density. Length was negatively correlated with brown trout density, and density
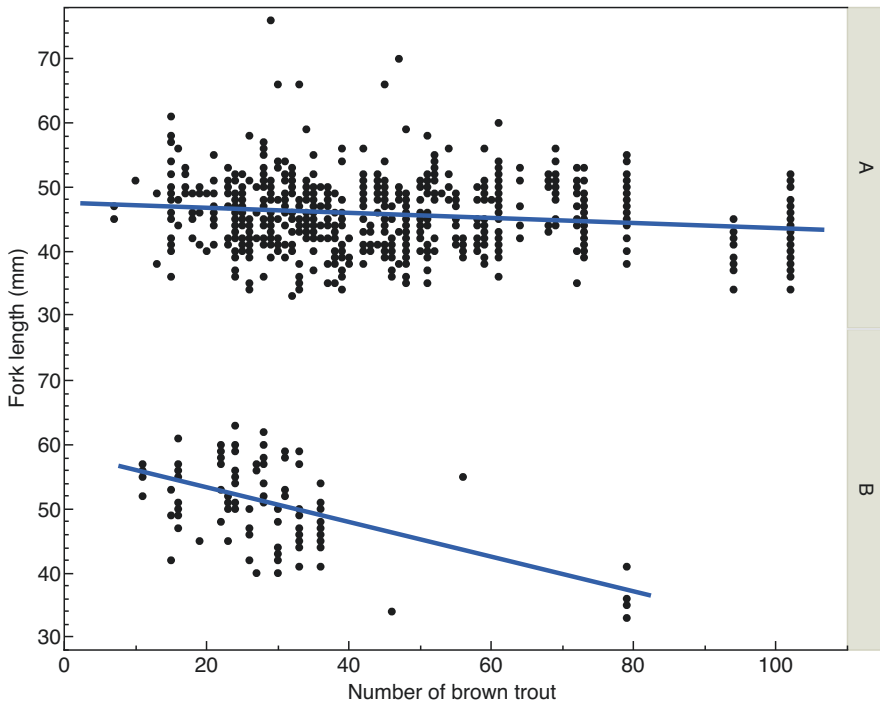
Fig. 7 Relationship between fork length (mm) of age-0 brown trout during autumn (September–October) and the total number of brown trout per section, for sections and year combinations without (**a**) or with (**b**) alpine bullhead present. Regression lines are given

dependence was significantly stronger in the presence of the alpine bullhead than when the alpine bullhead was not present (Fig. 7).

The observation that size of age-0 brown trout was smaller in sections with alpine bullhead than in sections without suggests an overall competitive interaction between the alpine bullhead and brown trout. Brown trout fry may avoid microhabitats with bullhead. For example, behavioral avoidance reactions have been documented in experimental situations (Gaudin and Heland 1984; Bardonnet and Heland 1994; Gaudin and Caillere 2000). Furthermore, evidence suggests that the alpine bullhead and brown trout compete for food, and potentially also for space (Olsen and Vøllestad 2001; Holmen et al. 2003). In addition, bullhead may be predators of small brown trout (Andreasson 1980). Taken together, the alpine bullhead may have a strong negative effect on the juvenile brown trout.

The degree to which observed size differences are important for population growth rate and resilience is poorly understood. For example, previous research has documented that early size does not have a predictable consequence for early survival of brown trout (Lund et al. 2003; Carlson et al. 2008). However, if the size differences established during the first summer are retained later in life, then these differences may translate into divergences in individual fitness. Moreover,

fast-growing fish may mature at a younger age, or at a larger size (Olsen and Vøllestad 2005; Olsen et al. 2014). A long-term study on small-sized and stream-dwelling brook trout *Salvelinus fontinalis* has documented that the size distribution determined in early life is indeed maintained throughout life (Letcher et al. 2011). Results from previous research have revealed a strong maternal effect on juvenile size, in addition to measurable heritability (additive genetic effect) (Serbezov et al. 2010b). This suggests that maternal decisions as to when to mature and where to spawn may affect fitness. A significant paternal effect on juvenile length was also apparent, presumably manifested through male mate choice (Serbezov et al. 2010b). In general, therefore, the stream Bellbekken appears to have substantial capacity for retaining phenotypic variation in juvenile size (and thus growth). The weak and variable strength and direction of selection, both driven by differences in survival and growth, may help maintain phenotypic and genotypic variation. Maintaining habitat heterogeneity is probably a prerequisite for maintaining this diversity, and thus for population resilience (see Young et al. (2018) for a discussion).

5 Concluding Remarks

In this small boreal stream, mature and age-0 brown trout were distributed throughout most of the stream, and were thus exposed to fine-scale variation in environmental conditions. Such fine-scale environmental diversity can result in variation in phenotypic traits, such as growth and size, at broader spatial scales, and associated diversity in survival, maturity, and fecundity. More generally, phenotypic and genotypic variation contribute to population resilience and persistence of small populations (low effective population size).

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