Growth variation in brown trout
Salmo trutta across small spatial scales: effects of density dependence and habitat quality?

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Forord

Denne studien er en del av et større prosjekt ved CEES: *Spatial and temporal population structure and breeding system in stream-living brown trout: an integrated ecological and genetic approach*, som startet i1997.

Fisken i denne studien er samplet i perioden 2002-2003, hvor jeg ikke deltok. Jeg har gjort tilsvarende feltarbeid i 2004-2005.

Aller først vil jeg takke Asbjørn for muligheten til å skrive denne oppgaven. Han har alltid døren åpen for diskusjon. En hjertelig tusen takk til min bror, Thomas. Du har alltid hatt tid til en faglig diskusjon. Takk til Asbjørn, Thomas, Esben, Kjartan og Finn for å ha lest gjennom oppgaven og kommet med konstruktive tilbakemeldinger. Takk til min bror, Runar og Simen for korrekturlesing. Jeg vil også takke mine gode venner både på og utenfor bygget. En spesiell takk til Fußball-gutta, og Gry (evt Hege?). Disse Fußball-kampene har gjort tilværelsen de siste månedene mye enklere. Takk også til moder'n for finansiell og moralsk støtte.

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Abstract

The aim of this study was to investigate to what extent population density and small scale habitat variability affect somatic growth of resident, stream-living brown trout *Salmo trutta*. There is an ongoing debate whether density-dependent regulation of stream-living salmonids operates via mortality and emigration or growth. A capture-mark recapture study of brown trout was performed in Bellbekken, a small stream in east Norway. The 1.5 km stream was divided into 25 contiguous *Sites*. Trout movement was limited, and 76 % of the recaptures were caught at the same *Site* as the previous capture. Micro-habitat quality and trout density were estimated and used as predictors in the statistical modeling of instantaneous growth rate. Growth was estimated from length increments of recaptured fish, and from back-calculated lengths, determined from scale readings. A general linear model (GLM) showed that instantaneous growth rate was negatively related to length and age, and that immature fish grew better than mature fish. After adjusting for differences in length, age and the maturity state, ~40 % of the variability in growth was not accounted for. Some of this variability was related to *Site*, but most of it remained unexplained. Fish density and estimates of habitat quality accounted for roughly half of the variation explained by *Site*. The remaining variation could be related to other habitat variables which were not estimated, or alternatively that the habitat variables in this study were not measured at the most relevant spatial scale.

Introduction

'Habitat' is a widely used term, referring to spatial entities on very different scales (Barnard 2004). At the largest scale, habitat has a meaning similar to 'ecosystem' and refers to areas of the physical environment more or less distinct from other areas in a broad range of abiotic and biotic variables (e.g. lotic habitat and coral reef habitat). Habitat is also used on smaller scales within an ecosystem, referring to areas that are sufficiently different to appear quantitatively distinct (e.g. riffle and pool habitats within a stream). At an even finer scale, the term microhabitat is used for subdivisions of habitats that are relatively homogeneous and differ primarily in quantitative values of a small number of variables (e.g. deep and shallow water microhabitats within a pool) (Brett 1979, Wootton 1990, Barnard 2004).

Animals are generally associated with particular habitats and the distribution of animals across environmental gradients can often be interpreted as responses to habitat heterogeneity (Barnard 2004). Habitat selection and habitat use refer to the non-random use of space resulting from voluntary movements, and is a key process in the distribution patterns of organisms. This habitat selection is generally seen as the result of a trade-off between potential costs and benefits, with effects on survival, growth and reproductive success, and thereby on fitness (Patridge 1978, Barnard 2004). Fish, in particular, may restrict their activity to a well-defined area, and some may even defend a territory. Territorial behavior is associated with the presence of a defensible resource such as food or shelter. Alternatively, the area can be shared with other fish, forming a home range. The quality of the habitat in which a fish lives (e.g. resource availability and exposure to predators) is likely to affect its growth, survival and reproductive success (Wootton 1990, Barnard 2004).

This habitat dependency of fitness indeed applies to stream-dwelling salmonids, as lotic systems often display extensive spatial variation in environmental variables, such as current speed, water depth and substratum type. Such environmental variables typically affect the whole ecosystem, and hence the animal and plant fauna in the stream (Hynes

1970). Habitat use of stream-living salmonids is therefore often structured by spatial variation in these variables. Many lotic habitats are subject to strong temporal variation in water flow, and as water levels rise and fall, conditions change at each specific location (Heggenes 2002). Under such variable conditions, habitat selection must be dynamic, and individual fish must move between locations in response to changing conditions (Heggenes 2002).

Spatial variation in growth arises from and reflects underlying differences in quality among habitats (Bèlanger & Rodríguez 2002). However, if the fish moves around and utilizes different habitats, the effects of density and habitat quality upon growth can be masked (Rodriguez 2002). The "restricted-movement paradigm" (RMP) argues that many fish populations, and stream-living salmonids in particular, are sedentary, not moving beyond a short reach of the stream (20-50 m; Gerking 1959). Stream-living brown trout *Salmo trutta* seems to have a high degree of site fidelity (Solomon & Templeton 1976, Bachman 1984), although the validity of this view has been questioned (see review by Gowan et al. (1994)). Under the assumption of restricted movement, or site fidelity, variation in density and habitat quality on small spatial scales could potentially give rise to identifiable variation in the growth of stream-living trout.

The growth of fish is indeterminate and highly plastic (Wootton 1990). Individual growth is a fundamental element upon which a variety of life histories depend, e.g. body size in fish is strongly related to fecundity and competitive performance (Schaffer 2004), which again affects individual fitness. The trade-off between somatic and reproductive growth (Stearns 1992) results in reduced growth rate at the onset of maturation. This may result in initially fast-growing individuals which mature at an early age, being surpassed in ultimate size by slower growing fish, demonstrating that the difference in growth rates established in young fish does not necessarily persist throughout life (Wootton 1990). Organisms are not growing at their maximum possible rate (Conover & Present 1990, Blanckenhorn 2000), because of food shortage, or due to costs connected to high growth rates (Ali et al. 2003, Carlson et al. 2004). Potential costs of fast growth include increased predation risk (Lima & Dill 1990), reduced swimming performance (Gregory & Wood

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1998) and decreased adult longevity (Chippindale et al. 1994). These potential costs should translate into reduced survival of fast-growing individuals. If fish are able to move between habitats with different growth rates, compensatory growth (catch-up growth of small individuals in a cohort; Ali et al. (2003), Johnsson & Bohlin (2005)), has the potential to further enhance the masking of the habitat effects on growth.

Individual growth rates in stream-dwelling salmonids can potentially be regulated by shortage in food supply or territories (Elliott 1994). Newman (1993) argues that the distribution of individual growth rates should follow the distribution of foraging site qualitiy. The site quality model of Newman (1993) predicts that as density increases and additional trout occupy the lower quality sites mean growth will decrease; but the variance of growth will increase. The relationship between individual growth and density for stream-dwelling salmonids has often been described by a negative power curve (Grant & Imre 2005). In the comparative analysis of Grant & Imre (2005), 11 out of 15 populations with density dependent growth were best described by a negative power curve. The strongest relationship between density and growth was found at population densities <1 fish m^{-2}, when space limitation is unlikely, and individuals probably compete via exploitative competition. Three of the populations were adequately described by both a negative power curve and a linear regression, whereas only one population was best described by a linear regression. Detection of density dependence will be facilitated if the data span a wide range of densities and, most importantly, include very low densities (Jenkins et al. 1999).

Density-dependent reduction in individual growth rate has the potential to limit population growth, since individual fecundity is strongly correlated to body size. Generally, it is assumed that populations of stream-living salmonids are regulated primarily in the juvenile phase of the life cycle by mortality and emigration, to the extent that mean growth rates of resident survivors are unrelated to trout densities (Elliott 1990). However, density dependence in growth has been widely reported (Bohlin et al. 2002, Lorenzen & Enberg 2002, Vøllestad et al. 2002, Brännäs et al. 2004, Lobón-Cerviá 2005). Imre et al. (2005) suggest that population regulation can potentially be controlled

by mortality and emigration at high densities via interference competition, and by density-dependent growth via exploitative competition for stream drift at low densities.

There are a number of potential pitfalls when trying to chart out the relationship between growth of stream-living salmonids and density and environmental effects. Environmental factors and density tend to be confounded, and it can therefore be difficult to identify relationships by comparisons among streams, within a single stream, or among different years at the same location. Another problem is whether we are able to measure the important environmental variables affecting growth, at least at the appropriate scale. Moreover, growth is a very slow response compared to how dynamic habitat choice can potentially be, and even rare migrations on small scales could be sufficient to mask effects of habitat choice on growth (Rodriguez 2002, Lobòn-Cervià 2005).A condition for detecting growth variation caused by variation in habitat quality and density is that trout show high degree of site fidelity.

The objective of this study was to investigate whether there are measurable growth variations within and among cohorts of a stream-dwelling population of brown trout, and whether this variation can be explained by the local environmental conditions and population densities experienced by the fish. By doing a mark-recapture study through the whole stream of Bellbekken, I study growth variation in time and space and try to relate this to both abiotic- and biotic environmental characteristics.

Materials and Methods

Study area

This study was done in a small forest stream, Bellbekken, which drains into the river Rena, via Julussa in the Hedmark County, southeast Norway (fig1). Bellbekken is naturally stabilized by forest vegetation, particularly trees such as norwegian spruce *Picea abies*, scots pine *Pinus sylvestris* and downy birch *Betula pubescence*, which provide cover and allochtonous food for fish. Possible predators in the area are the dipper *Cinclus cinclus*, ducks *Mergus* spp., herons *Ardea cinerea* and mink *Mustela vison*. Bellbekken holds a landlocked population of brown trout above a waterfall at the outlet of the stream which presumably acts as a barrier for upward migration. One sampling site is located downstream of the waterfall, and although this site is in conjunction with Julussa, it is treated as a part of Bellbekken. The trout is the only self-sustaining fish species in the stream, although we have found a total of 7 alpine bullhead *Cottus poecilopus* above the waterfall during the period 1997-2005. No juvenile individuals of the alpine bullhead have ever been found, indicating that they are not reproducing in the stream. Studies on another bullhead species, *Cottus gobio*, report limited ability to move across a waterfall (Utzinger et al. 1998, Knaepkens et al. 2006). Therefore, we do not think that the alpine bullhead can swim across the waterfall, and suggest that the dipper, observed in the area, drop them by mistake when they settle to eat.

Study organism

Brown trout is endemic to Europe, Western Asia and the Atlas mountains of North Africa, but has been successfully introduced into at least 24 countries outside Europe (Elliott 1994). It is one of the most studied fish species, partly because of its commercial and recreational interest. In the Northern Hemisphere, spawning has been recorded in all months from October to March, but the usual spawning time in most populations is November through December (Elliott 1994). Spawning usually takes place in clean gravel in running fresh water, although lake spawning populations do occur (Klemetsen et al. 2003). After hatching in the spring, the alevins (yolk-sac larvae) 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 (Elliott 1994). The swim-up larvae disperse from the nest and establish feeding territories (Elliott 1994), and enter a critical period with high mortality. The trout nearly always spends the first year of its life cycle within the natal stream, but the habitats of the subsequent life stages vary considerably between populations (natal stream, larger rivers, lakes, or the sea; Cucherousset et al. 2005). In many sea-trout populations, duration of the sea period differs between individuals, corresponding to large intra-population variability in age and size at maturity (Hendry et al. 2004). High intra- and interpopulation variability exists for many life-history traits in brown trout (L'Abèe-Lund et al. 1989, Jonsson & L'Abèe-Lund 1993, Vøllestad et al. 1993, Klemetsen et al. 2003), and the polytypic nature of the trout has caused about 50 morphological variants to be described as different species (Behnke 1986). Stream-dwelling trout represent an excellent study organism for studying individual growth rates as they apparently show a high degree of site fidelity and can be individually tracked.

Habitat characteristics

A range of 1.5 km of the stream was divided into 25 contiguous sites with different lengths (table 1). To model growth rate as a function of habitat, several habitat variables expected to be important for the distribution of fish and growth (Heggenes et al. 1999) were quantified (table 1). The values of these habitat variables are averages from each site: The stream was divided into transects at regular intervals (8 m), the number of transects per site being proportional to the length of the site, where a measuring tape was stretched perpendicular to the water flow. Each transect was sub-divided into areas of 50*50 cm. Values are averaged over areas within a transect and over transects within a site. *Depth* was measured to the nearest cm at the middle of each area, and a visual estimation was made of: *Dry land*,(i.e.) the percentage of the substratum not submerged in water; *Cover*, (i.e.) the percentage canopy cover and instream woody debris; *Overhang*, (i.e.) overhanging streambed; *Vegetation*, (i.e.) the percentage of the substratum covered with moss and algae; *Substrate*, (i.e.) the dominant substrate type, classified according to a modified Wentworth scale (Heggenes 1988), using categories from sand (size group 4) up to large boulders (size group 11).
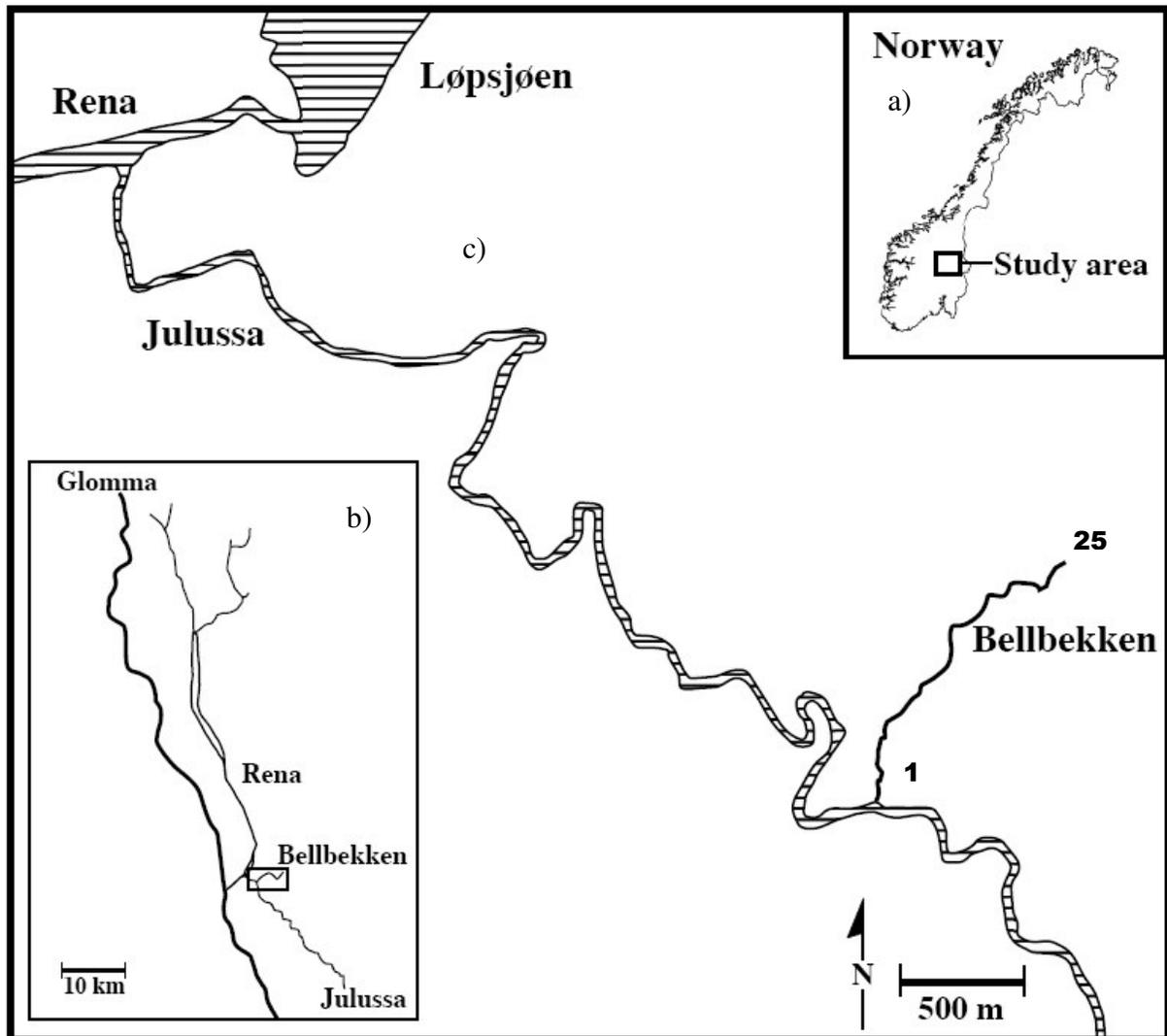
Figure 1. Map of the study area. (a) Position of the study area in Norway. (b) The river system. (c) Bellbekken, the stream of study, draining via the river Julussa and into the river Rena. Fish were sampled in the sites 1-25, Site 1 is in conjunction with Julussa, while Site 25 is furthest upstream.

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Table1. Environmental variables measured at the study sites.

Site	Length (m)	Slope	transects	Width (m)	Depth (cm)	Dry land (%)	Cover (%)	Overhang (%)	Vegetation (%)	Substrate	Wetted area
1	40	0.04	5	5.3	23.7	33.2	3.2	6.2	34.1	10.6	141.5
2	64	0.02	8	4.6	17.7	30.6	18.4	20.5	36.9	8.9	205.4
3	40	0.03	5	3.8	30.9	9.8	14.5	19.2	27.9	8.9	137.1
4	80	0	10	4.0	35.1	15.4	21.7	14.3	5.8	5.1	267.3
5	48	0.02	6	4.8	26.0	18.0	17.6	20.0	15.8	6.6	187.0
6	32	0	4	4.1	52.1	0.0	23.9	37.5	0.0	4.9	132.0
7	72	0	9	4.3	24.1	13.5	28.1	26.3	0.8	5.1	266.4
8	72	0	9	4.5	29.0	20.9	19.6	19.7	0.0	4.1	256.4
9	48	0	6	3.8	25.0	14.5	14.9	30.3	0.0	4.0	153.9
10	80	0	10	4.2	17.6	24.4	19.4	20.3	0.6	4.2	251.0
11	72	0.01	9	5.1	21.5	27.7	26.7	19.6	0.2	5.0	266.2
12	72	0.02	9	5.2	14.1	18.4	5.4	11.5	35.1	8.6	306.9
13	80	0.03	10	5.2	15.2	21.7	2.3	10.0	33.0	9.3	322.7
14	40	0.03	5	4.8	14.6	18.8	1.2	17.6	32.9	9.6	155.9
15	64	0.03	8	7.9	14.1	24.9	2.4	10.8	39.9	8.7	378.8
16	56	0.03	7	4.3	13.7	28.7	1.6	17.3	38.8	8.8	171.2
17	56	0.02	7	3.4	21.3	29.7	11.5	21.2	28.6	6.9	135.1
18	72	0.01	9	3.7	16.7	11.9	23.3	23.3	11.7	5.9	232.6
19	56	0.01	7	3.9	21.9	18.2	15.7	22.6	0.5	5.7	180.0
20	56	0.01	7	3.8	13.9	13.2	8.9	14.5	11.8	7.2	184.0
21	72	0.02	9	3.8	10.9	20.5	5.5	14.4	37.6	8.0	219.5
22	96	0.02	12	4.5	12.2	27.5	8.3	15.5	34.8	8.0	313.1
23	48	0.06	6	4.4	16.8	29.2	3.7	16.3	48.3	9.2	150.2
24	56	0.05	7	4.1	19.0	36.5	6.0	17.0	35.7	9.1	144.8
25	32	0.05	4	4.3	20.3	40.1	2.6	15.9	49.5	10.3	81.5
mean	60.16	0.02	7.5	4.5	21.1	21.9	12.2	18.5	22.4	7.3	209.6

Slope: A transparent water-filled hose was stretched between adjacent transects, holding the hose under the stream surface in the upper transect, and over the stream surface in the lower transect. The vertical separation between the water column surface in the hose and the surface of the stream in the lower transect was measured. The *Slope* variable was calculated as the total vertical separation within the site divided by the total length of the site:

$$Slope = \frac{\sum_{t=2}^{T} h_t}{d},$$

where *T* is the total number of transects within the site, h_t is the measured vertical separation between transects *t* and *t*-1, and *d* is the horizontal length of the site.

The habitat classification was only performed once at each location (in August 2004), when the water level was relatively low. The different habitat quality variables were strongly correlated (table 2), for instance *Slope* and *Vegetation*, and *Slope* and *Substrate* had correlation coefficients (r) of 0.9, whereas *Cover* was negatively correlated with *Vegetation* and *Substrate* with correlation coefficients of -0.8. Because of the high correlation among environmental variables a principal component analysis (PCA) was performed on the habitat variables (table 3). The rationale behind a PCA is to identify which combinations of variables explain the largest amount of variation in the multivariate data set, and thereby reduce the dimensionality of the set of data variables. In sum, the first three principal components explained 90 % of the total variation in the habitat variables. The first principal component explained 65 % of the total habitat variation, to which all variables contributed almost equally. In the second principal component, explaining an additional 14 % of total variation, stream width was the most contributing factor. Stream depth and width contributed most to the third principal component, which explained about 11 % of the remaining variation in the measured habitat variables.

Table 2. Correlation matrix of the measured habitat variables used in the modelling of growth. Significant correlations ($P_\alpha < 0.05$) in bold type.

	Slope	Width	Depth	Cover	Overhang	Vegetation	Substrate
Slope	1.000	0.239	-0.380	**-0.756**	**-0.534**	**0.873**	**0.878**
Width		1.000	-0.222	-0.316	**-0.461**	0.302	0.320
Depth			1.000	**0.567**	**0.601**	**-0.527**	-0.459
Cover				1.000	**0.661**	**-0.828**	**-0.819**
Overhang					1.000	**-0.610**	**-0.663**
Vegetation						1.000	**0.927**
Substrate							1.000

Table 3. A Principal component analysis of the habitat variables. The first three principal components, explaining 90 % of the total variation in the habitat variables were used as predictors in modelling growth.

Eigenvalue	4.574	0.959	0.742	0.325	0.215	0.123	0.062
Percent	65.339	13.705	10.597	4.648	3.070	1.762	0.879
Cum Percent	65.339	79.044	89.641	94.289	97.360	99.121	100.000
Eigenvectors							
Slope	0.405	0.333	0.255	0.081	0.346	-0.730	-0.016
Width	0.207	-0.785	0.493	0.309	0.013	-0.030	0.020
Depth	-0.306	0.227	0.779	-0.436	-0.199	0.065	-0.121
Cover	-0.423	-0.096	0.043	-0.052	0.886	0.151	-0.021
Overhang	-0.373	0.347	0.199	0.814	-0.108	0.057	0.151
Vegetation	0.437	0.222	0.104	0.191	0.141	0.482	-0.679
Substrate	0.437	0.204	0.183	-0.075	0.157	0.451	0.708

Sampling and treatment of fish

The 25 sites were sampled using a backpack electrofishing apparatus (S. Paulsen, Trondheim, Norway) during three sampling sessions, one in September/October 2002 and two in 2003, in June/July and September/October, respectively. Parts of the stream have been sampled since 1997 but sampling of the whole stream began in autumn 2002. Due to extensive ice cover in October 2002 fishing efficiency was low, reducing the precision of density estimates. The sampling session in September 2003 was interrupted because of heavy rain, and postponed to late September/early October when conditions were better. Each site was electrofished upstream three times in a standardized manner, with a resting period between fishing bouts (the removal method; (Zippin 1956, Zippin 1958, White et al. 1982, Bohlin et al. 1989)). The whole study area could be sampled; the deepest area in the stream is 110 cm-although some sites were harder to fish due to dense canopy and instream cover. Block nets were used during the sampling session in autumn 2002, but after this session the use of block nets was discontinued (due to logistic reasons). The removal method is effective when the capture efficiency is high enough to reduce the population size substantially during each bout. In

addition, assumptions of a closed population, equal catchability for all individuals, and equal catchability among the removals, should be met (Bohlin et al. 1989). These assumptions of the removal method will only be partially met in field studies, and are possible sources of sampling bias. Peterson et al. (2004) evaluated the removal method for estimating the abundance of stream-dwelling salmonids and found that it overestimated three-pass capture efficiency by 39 % and underestimated fish abundance by 88 %.

After sampling, the trout were anaesthetized with benzocaine before tagging, measuring of fork length (L_F, to the nearest mm) and scale sampling for age determination. Determination of sex and maturation was done visually, and could only be done on mature individuals in autumn. Passive integrated transponder tags (PIT-tags; Prentice 1990) were used to mark the fish, by insertion into the body cavity of the fish using a syringe. In addition, the adipose fin was clipped for visual identification of recaptured fish. The one-summer-olds (0^+) and the smallest one-year-olds (1) were tagged by injection of a coloured elastomer material (Visible Implant Elastomer) just under the skin (Frederick 1997, Olsen & Vøllestad 2001b). Tagging an individual fish with specific colours at specific places makes individual identification possible. Scales were taken from an area just above the lateral line between the adipose and the dorsal fin (Jonsson 1976, Devries & Frie 1996) when captured for the first time. In total, 2147 captures of trout were done during the three sampling sessions (autumn 2002, spring 2003 and autumn 2003), of these 528 were recaptures. Some of these recaptures were tagged before the sampling sessions in 2002-2003. After handling, the fish were placed in a bucket with stream water for recovery. All fish were released back into the sites from which they were captured. Handling mortality was apparently low, approximately 1 % of the trout died during electrofishing and handling.

Data treatment

Fish was sampled from all 25 sites, of which one (site 1) is located beneath the waterfall at the outlet of the stream. The fish in this site has the possibility to enter Julussa River and interact with other species but they do not have significantly different growth compared to the other sites, and is included as a part of Bellbekken.

Age of captured fish was estimated in two ways; from the distinct smallest modes in length-frequency plots for the youngest fish and from scale readings for older fish. A length-frequency approach may be used to distinguish between different age groups provided that the

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length distribution of each age group is unimodal, and that the modes of different age groups have little overlap (Bagenal & Tesch 1978). Individuals within the smallest mode in the autumn sessions (35-65 mm) were assigned to the age group 0^+, whereas individuals within the smallest mode in the spring session (45-90 mm) were assigned to the age group 1. Doubtful assignments, in the upper range of the smallest modes (>60 mm and >80 mm respectively), were confirmed by scale readings. Age was estimated as the number of annuli (transition zone between poor and good growth, corresponding to the start of a new growth season) in the scales from scale readings using a microfilm reader (Jonsson & Stenseth 1976).

Growth was estimated in two ways; empiric growth and back-calculated growth. For all fish older than 1 year, I have used instantaneous growth rates based on length increments between time t_1 and t_2:

$$g = \frac{\log(L_F(t_2)) - \log(L_F(t_1))}{t_2 - t_1} * 100,$$

where $L_F(t)$ is empiric or back-calculated length at time t. Empiric growth rate (per day) is found from the actual length measurements of recaptured fish at each capture. Length of 0^+ at the end of the growing season is used as a proxy for growth rate in the first growth season. Back-calculated growth was calculated from estimated lengths at earlier ages, based on scale readings (Francis 1990). The relationship between the size of calcified structures and body length of fish has been widely used in fisheries science to estimate body size at a younger age by back-calculation (Casselman 1990, Francis 1990, Ricker 1992). Back-calculation analyses are based on the correlation between the scales and length increment of the fish. By identifying growth rings on the fish scales, length at earlier ages of an individual fish can be estimated provided that the relationship between fish length and scale radius is known. To establish this relationship, a regression of fish length (L_{Fc}) on scale radius (S_c) was done (0^+ excluded from the regression since scale samples are missing for trout in their first summer). A linear regression was the best fit for this relationship (fig 2) and the intercept was significantly different from zero (95 % CL for the intercept: 19.42-26.26) .Therefore, from scale and fish lengths, the estimated fork lengths at previous ages were determined by the Fraser-Lee equation (Francis 1990, Ricker 1992) giving the best linear fit to the data:

$$L_{Ft} = 22.840 + (L_{Fc} - 22.840) * \frac{S_t}{S_c},$$

Where L_{Fc} is length at capture, S_c is scale radius at capture, S_t is scale radius at time t, and 22.840 is the intercept from the regression of body length on scale radius (in occular units) (fig 2). Back-calculated growth rates are calculated per season. Growth at different ages of each fish was calculated from lengths at subsequent ages obtained from back-calculation. Growth in the fifth growth season, log (L_5)-log (L_4), was not calculated due to low sample size (n = 21).

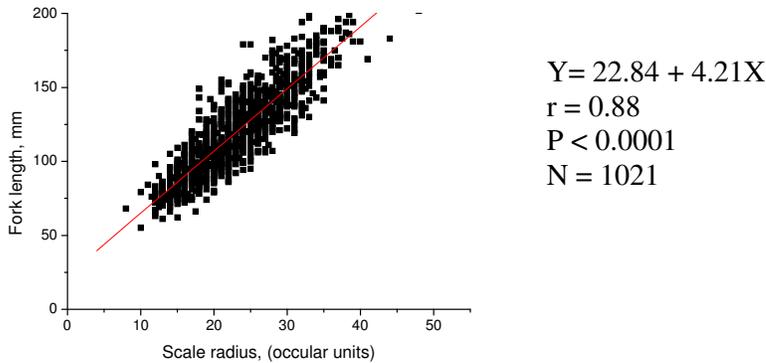Y= 22.84 + 4.21X
r = 0.88
P < 0.0001
N = 1021

Figure 2. A linear regression of body length on scale radius with the intercept significantly different from zero implying that the Fraser-Lee equation is the best method for back-calculation of lengths (Francis 1990).

Fish caught at the same site in both sampling sessions in 2003 (n = 120) are analysed separately, and will be referred to as the *Site confirmed dataset*. For these fish, the assumption of site fidelity is more reliable, whereas for fish recaptured at a different site from where it was tagged it is clearly not. To test for fish movements, all registered recaptures with known capture and recapture site for the period 1997-2004 were used (n=1896).

Trout density was estimated using the successive removal method (Zippin 1956, Zippin 1958) following Bohlin et al. (1989). In addition, several proxies for fish density were used: number of fish caught during the three removals per square meter (n/m^2), and the sums of fork lengths squared and cubed per square meter ($\sum L_F^2/m^2$ and $\sum L_F^3/m^2$ respectively). As density-dependent growth arises from competition for food or space, the measure of fish density should correspond to the allometric relationship between fish size and the processes of

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competition (Post et al. 1999). Large fish, have a higher capacity to deplete food resources than smaller fish, can feed at a higher rate due to faster swimming, and have better visual acuity (Wootton 1990). In addition, large fish can more easily suppress smaller fish through aggressive behaviour (Wootton 1990). Because of this asymmetric competitive ability, the use of numerical abundance alone may be inappropriate as a measure of the experienced competition (Post et al. 1999).

The majority of studies detecting density-dependent growth have found the relationship to be best described by a negative power curve (Imre et al. 2005). A simple regression of growth (log-transformed to obtain normal distribution of data) against estimated density, on the *Site confirmed dataset*, showed no relationship between growth and density (r_{21} = - 0.1, P =0.8). A simple regression of growth against log (estimated density) did not show a markedly better relationship (r_{21} = - 0.1, P = 0.7), and I therefore used the untransformed densities in all the anlyses. The models with untransformed density had homogeneous residuals around the mean: hence a transformation was not necessary.

Analyses
The analyses were done in JMP, Statistical Discovery Software, SAS Institute.

The specific growth rate, *g*, for the *Site confirmed dataset* (fish caught twice at the same site during the two sampling sessions of 2003) were right-skewed and therefore $\log_{10}$ transformed for a better fit to the ANOVA assumptions of normal distribution and uniform variance before being analysed. Growth was modelled using general linear models (GLM). Model selection was based on Akaike information criterion (AIC), the model with the lowest AIC value was considered to offer a markedly better description of the data if the difference in AIC values was > 2 (Motulsky 2004). Growth, log (g), was modelled in the following manner:

1. First, I included Length, Age and the maturity state of the fish as covariates in the model, since they are parameters that we know affects growth, especially in organisms with indeterminate growth such as fish (Wootton 1990). These parameters will be referred to as the basic model.
2. I added *Site* (a nominal variable) to the basic model .

3. I added the first three principal components to the basic model together with the different proxies for density. Only one density parameter was included at a time, and the density parameter and the principal components resulting in the lowest AIC value in a stepwise regression was selected as the best model at this stage.

4. I added the habitat variables to the basic model together with the different proxies for densitiy. Only one density parameter was included at a time, the habitat variables and the density parameter resulting in the lowest AIC value in a stepwise regression was selected as the best model at this stage.

5. I added all the density variables (one by one) together with the basic model. The model with the lowest AIC value was considered as the best model at this stage.

6. I forced all habitat variables together with one density parameter at a time to the basic model. The density parameter resulting in the model with lowest AIC value was selected as the best model at this stage. This model was built to see how much of the site effect was captured by all the measured habitat-variables.

First-year growth was estimated as the length of 0^+ at the end of the growth season and analysed in the same way as described above, but I did not use the covariates *Length*, *Age* and *Maturation*, since I only have length at the end of the growth season for these individuals, which are of the same age and have not yet matured. First year growth was therefore modeled with just *Year* as a covariate, and then *Site,* density and habitat were added as described above.

When modeling variation in growth by age from the back-calculated data, length at the beginning of the growth period, i.e. L_1 for growth in the second season, L_2 for growth in the third season, and so on, was included in the model as a covariate together with age, because of the overestimation of length at age (see results). Maturation was not included in any models for temporal variation in growth, because I do not know the maturity history of the fish. In addition, cohort was included as a covariate when modeling back-calculated growth.

Results

Fish movements

Of the recaptured trout in the period 1997-2004, 76 % were recaptured at the site of previous capture, and 87 % were recaptured within 1 site upstream or downstream from the previous capture (fig 3), and I refer to the 76 % caught at the same site twice as "residents".
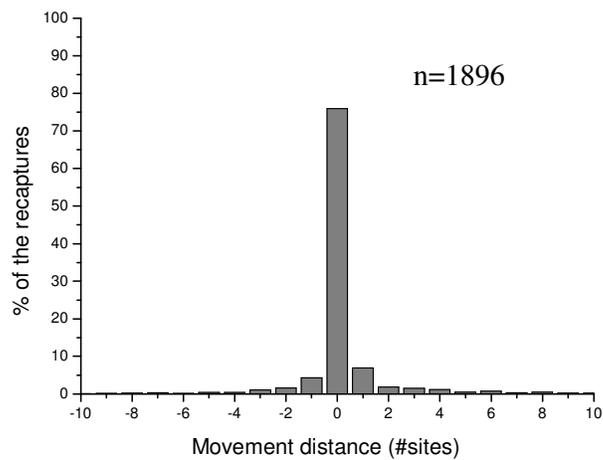

Figure 3. Movement distances of recaptured fish. Positive values refers to upstream movement and negative values refers to downstream movement.

For non-residents, there appears to be no relationship between the time between captures and the distance moved (fig 4, left panel). The proportion of residents was rather independent of the time between captures when this was ≤ 600 days (fig 4, right panel). The proportion of residents was lower when time between captures was longer (fig 4, right panel), but the estimate of 17 % for >800 days is based on only 6 fish, and is therefore highly uncertain.
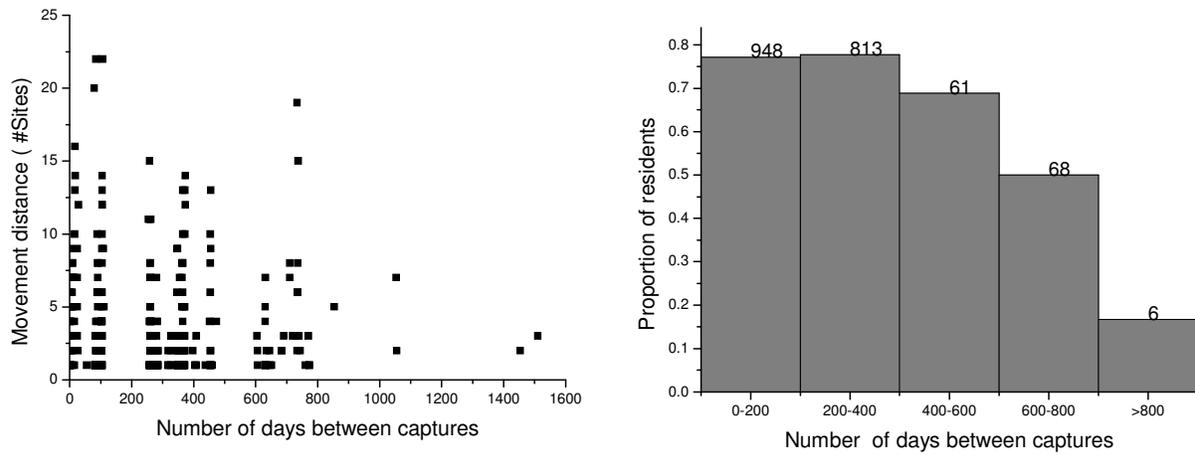

Fig 4. Left panel: The relationship between the distance moved and the time between captures.
Right panel: The proportion of residents against the time between captures.

Population description

Most of the fish captured during the three sampling sessions were less than 20 cm long (the largest was from autumn 2002 and was 222 mm) and none were older than 6 years (fig 5). 0^+ could not be sampled in the spring session due to their small size. The low catch of 0^+ in the autumn of 2002 relative to the catch of one-year olds in the following spring suggests that there is low catchability for 0^+ individuals.
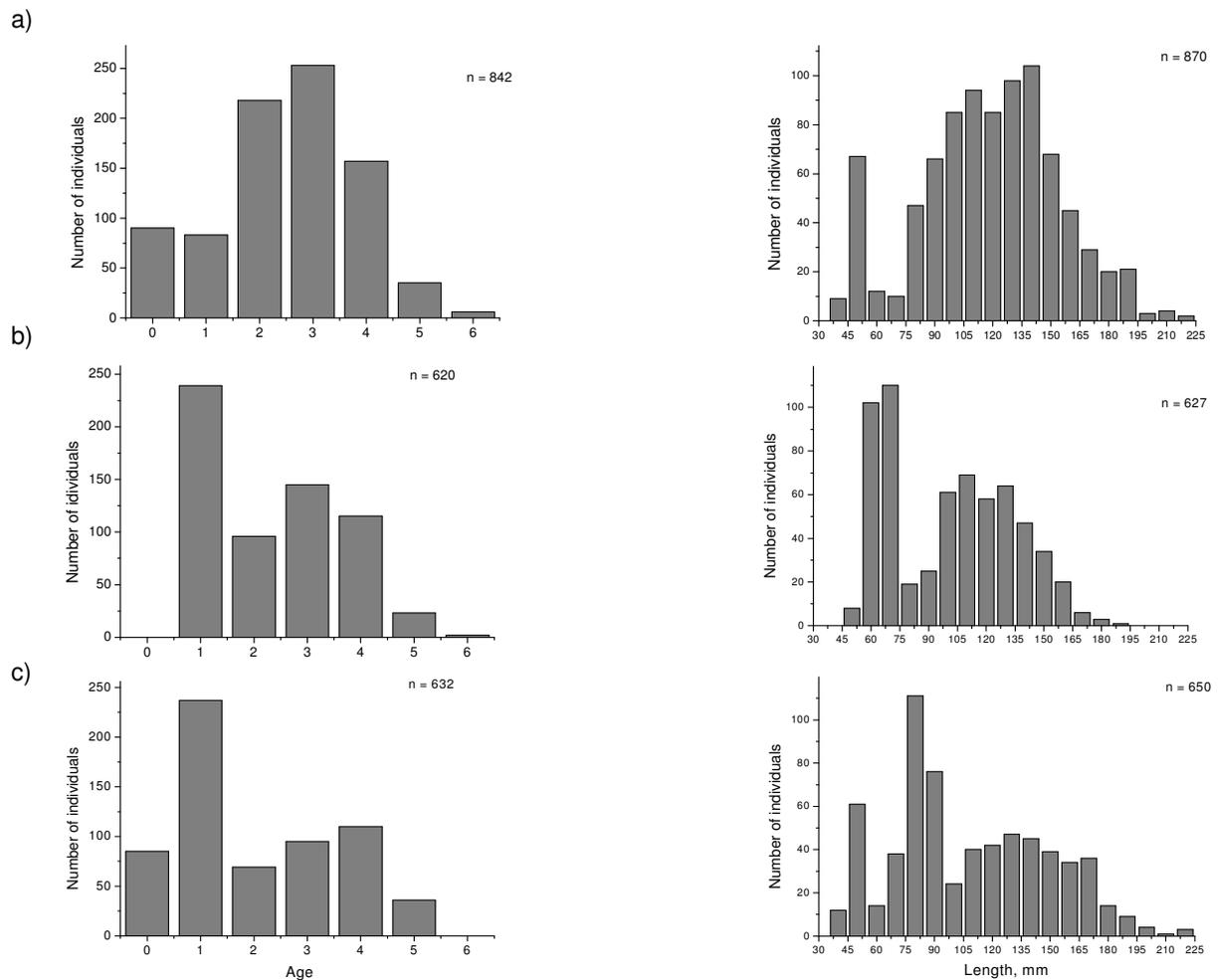

Figure 5: Age and length (mm) distributions for all three sampling periods; autumn 2002 (a), spring 2003 (b) and autumn 2003 (c). Sample size differs for the age and length distribution within a period because age could not be determined for all individuals.

Fish density (ind/m^2), estimated using the removal method, (appendix 1-3), was estimated for each of the three sampling sessions, mean density (95 % CL) was 0.19 ind/m^2 (0.18-0.20), 0.17 ind/m^2 (0.15-0.20), and 0.16 ind/m^2 (0.14-0.18), respectively. Density could not be estimated for all sites in all periods due to low catchability. Differences between sites were larger than differences between sessions, but the precision of the estimates differed markedly between sites. Precision of estimates for each site varied between sessions (Fig 6).

a)
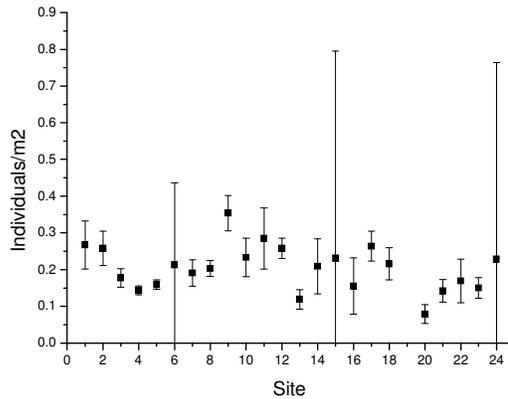
b)
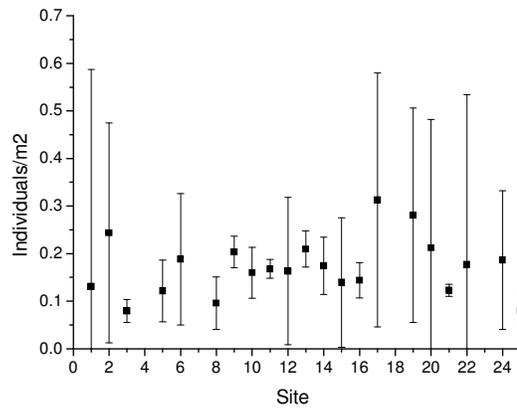
c)

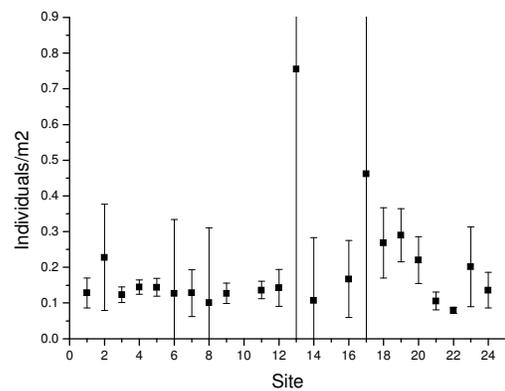Figure 6. Estimated trout densities with 95 % CL within autumn 2002 (a), spring 2003 (b) and autumn 2003 (c). Density could not be estimated for some sites and periods. All age groups were included in the analysis.

The correlation between density estimates in successive sessions was low (r_{20} = 0.19, P = 0.7, for the relationship between density in the two autumn sessions). Some of the density

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estimates had extremely low precision (fig 6), resulting in weak correlations between density estimates.

Empirical growth

The fork length of 0^+ individuals at the end of the growth season was used as a proxy for first year growth. Simple one-way factor analyses showed that mean 0^+ length was significantly different between sites (oneway ANOVA, $F_{22,152} = 1.77$, P = 0.024) and did not differ significantly between years (oneway ANOVA, $F_{1,173} = 2.64$, P = 0.1). The length of 0^+ was significantly positively correlated with the slope variable (linear regression, $r_{175} = 0.27$, P = 0.0002), although the relationship was weak.

The model with only *Site* and *Year* as predictors was selected as the best model, using the AIC criterion. The model explained 22.9 % of the variation in length (table 4). Site alone explained 20.4 % of the variation in length (table 4), the habitat variables or principal components explained considerable less (table 4).

Table 4. Models with 0^+ length at the end of the growth season as the response variable. Year was included in the model as a covariate, after which *Site*, the first three principal components (+density) and the habitat variables (+density) were added separately to see which model that best explained the rest-variation after accounting for the year effect. Model in bold is the best model by AIC criterion.

Model	R^2	Df	F	P	AIC
Year	0.015	1,173	2.64	0.1	608
Site	0.204	22,152	1.77	0.02	578
Year+Site	**0.229**	**23,151**	**1,95**	**0.01**	**508**
Year+1Pc+3Pc+$\sum L^3/m^2$	0.105	4,170	4.98	< 0.001	527
Year+Slope+Depth+Substrate+$\sum L^3/m^2$	0.140	5,169	5.48	0.0001	525

A linear regression revealed a negative correlation between the log transformed growth rate (Y) and length of the fish at the beginning of the growth period, $Y = 0.344 - 0.002 * L_F(t_1)$, ($r_{120} = -0.7$, P < 0.0001) (fig 7, left). Growth also decreased with increasing age (oneway ANOVA, $F_{4,115} = 31.5$, P < 0.0001); one-year old trout grew significantly better than older age groups, and the 2-year-olds differed from 4-year-olds in growth (All pairs Tukey-Kramer P < 0.05)(fig 7, right). Only 4 individuals are included as 5-year-olds in the analysis, therefore growth of this group is highly uncertain.
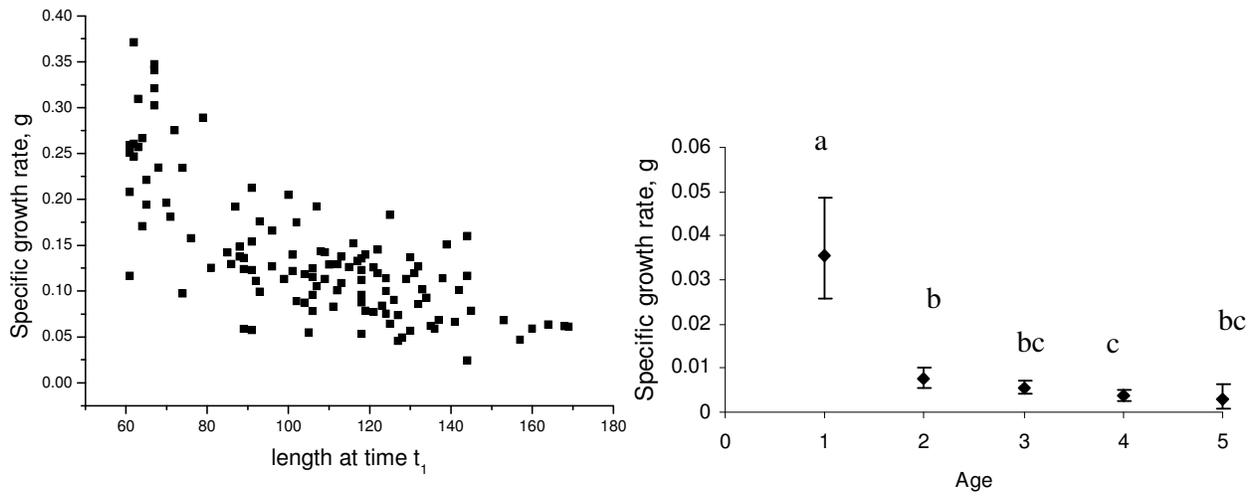
Figure 7. Specific growth rate decreases with inreasing length (left) and age (right) of the fish. (right): The mean specific growth rates together with 95 % confidence limits are shown for the different age groups. Levels not connected by same letter are significantly different. Estimates from 1-factor ANOVAs on $\log_{10}$ transformed values.
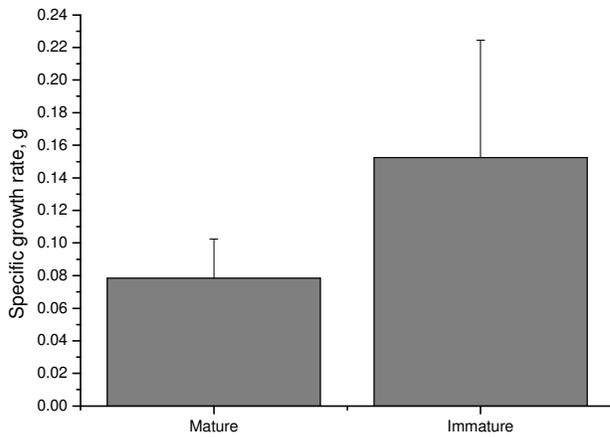

Figure 8. Mean specific growth rate + standard deviation for mature (n = 23) and immature (n = 97) fish.

The specific growth rate, (g), was significantly lower for the mature than for the immature individuals (Oneway ANOVA, $F_{1,118} = 35.0$, $P < 0.001$; fig 8). Sex-dependent variation in growth rate could not be tested due to low sample size, and the sexed individuals were therefore pooled.

The basic model with the covariates alone (*Age*, L*ength* and S*tage*) explained 59.9 % of the variation in the specific growth rate in the *Site confirmed dataset* (table 5). Adding *Site* to the basic model as a predictor variable increased the explained variation in growth to 70.7 %, and this model had the lowest AIC score of all models tested. Least square means for *Site* (from model 2 in tab 5) with 95 % CL are shown in figure 9. Width and Overhang together with the covariates explained 63.3 % of the variation in growth, (model 3 in table 5). Adding the best explaining parameter for density, namely $\sum L_F^3/m^2$, increased the explained variation to 63.8 % (model 4 in table 5), not changing the AIC score. The covariates, the first principal component and $\sum L_F^3/m^2$ explained 61.5 % of the variation in growth rate (model 6 in table 5) whereas the covariates together with $\sum L_F^3/m^2$ explained 60.2 % of the variation in growth (model 7 in table 5). When all habitat variables, in addition to $\sum L_F^3/m^2$, were forced together with the basic model (model 8 in table 5), 64.9 % of the variation in growth was explained. Site explained about twice as much of the residual variation (not explained by the covariates) as all the environmental variables and the best density proxy estimate. Estimates of the parameters from model (8) in table 5, with all the habitat variables and $\sum L_F^3/m^2$, are listed in table 6.

Table 5: The table lists different models explaining variation in the specific growth rate (from the *Site confirmed dataset*), L = length at time t_1, A = age, M = maturation, Pc_1 = 1.principal compontent. The best model by AIC criterion is in bold type.

Model		R^2	Df	F	P	Aic
1	L+A+M	0.599	6,113	28.18	<0.0001	-265
2	**L+A+M+ Site**	**0.707**	**30,89**	**7.16**	**<0.0001**	**-274**
3	L+A+M+ Width + Overhang	0.633	8.111	23.93	<0.0001	-271
4	L+A+M+Width+Overhang+$\sum L^3/m^2$	0.638	9,110	21.53	<0.0001	-271
5	L+A+M+ Pc_1	0.609	7,112	24.88	<0.0001	-266
6	L+A+M+$\sum L^3/m^2$ + Pc_1	0.615	8.111	22.16	<0.0001	-266
7	L+A+M+ $\sum L^3/m^2$	0.602	7.112	24.22	<0.0001	-263
8	L+A+M+Slope+Width+Depth+ Cover+Overhang+Vegetation+ Substrate+$\sum L^3/m^2$	0.649	14,105	13.88	<0.0001	-265
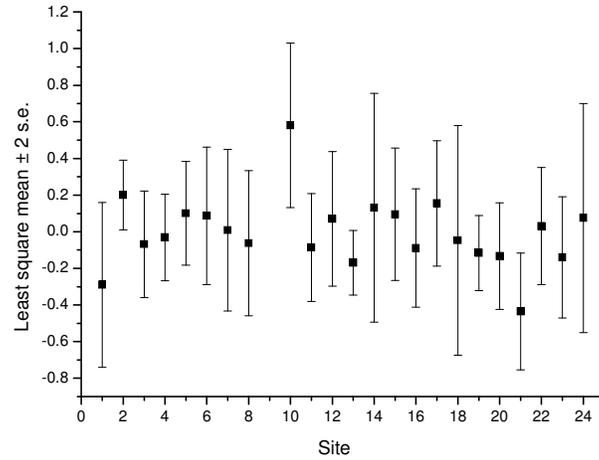
Figure 9. Least square mean growth rate (log(g)) for the various sites adjusted for the covariates *Length*, *Age* and *Maturation*. ± 2 s.e. Estimates are from model 2 in table 5.

Table 6: Estimates of the parameters in model 8 from table 5 with standard error and P values.

Term	Estimate	Std error	P
Intercept	-1.4297	0.4664	0.0028
Length (t_1)	-0.0088	0.0032	0.0074
Age [2-1]	-0.3862	0.1278	0.0032
[3-2]	0.0197	0.1053	0.8517
[4-3]	0.0231	0.0991	0.8164
[5-4]	0.2183	0.2018	0.2817
Maturation [Immature]	0.0924	0.0525	0.0812
$\sum L^3/m^2$	$-4.886e^{-8}$	$2.264e^{-7}$	0.8295
Slope	-2.9819	4.7310	0.5299
Width	0.0590	0.0482	0.2230
Depth	-0.0029	0.0056	0.6017
Cover	0.0074	0.0067	0.2670
Overhang	0.0152	0.0078	0.0543
Vegetation	0.0076	0.0068	0.2684
Substrate	-0.0255	0.0540	0.6376

The coefficient of variation of growth rate, *CV (g)*, was calculated for each site with sufficient sample size, $n \geq 3$. *CV (g)* was not correlated with the different proxies for density (fig 10). The number of individuals caught per square meter (N/m^2) and estimated population size (Est ind / m^2), was negatively correlated with CV (*g*) whereas the sums of fork lengths squared ($\sum L_F^2/m^2$) and cubed ($\sum L_F^3/m^2$) both had a positive correlation with *CV (g)* (Fig 10).

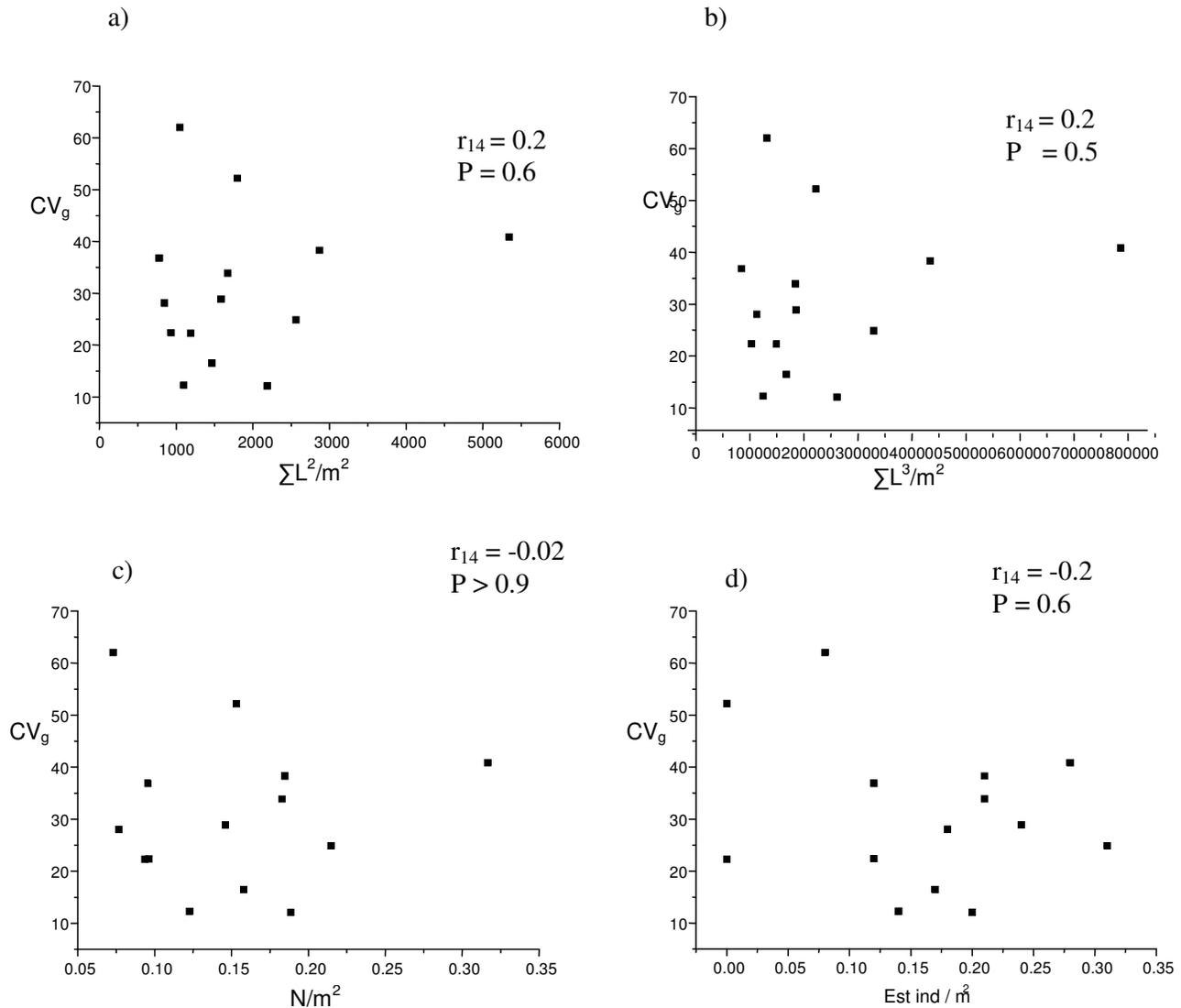a)   b)

Fig 10. Correlations of the coefficient of variation in growth within sites and several density variables, sums of fork lengths squared (a) and cubed (b) per square meter, number of individuals caught during three fishing bouts per square meter (C) and the estimated population density per square meter (d).

Back-calculated growth

Back-calculated lengths were significantly larger than the observed lengths for all ages (non-overlapping 95 % confidence intervals) for mean empiric lengths in autumn when growth assumedly stops and mean back-calculated length at annulus formation in early spring.
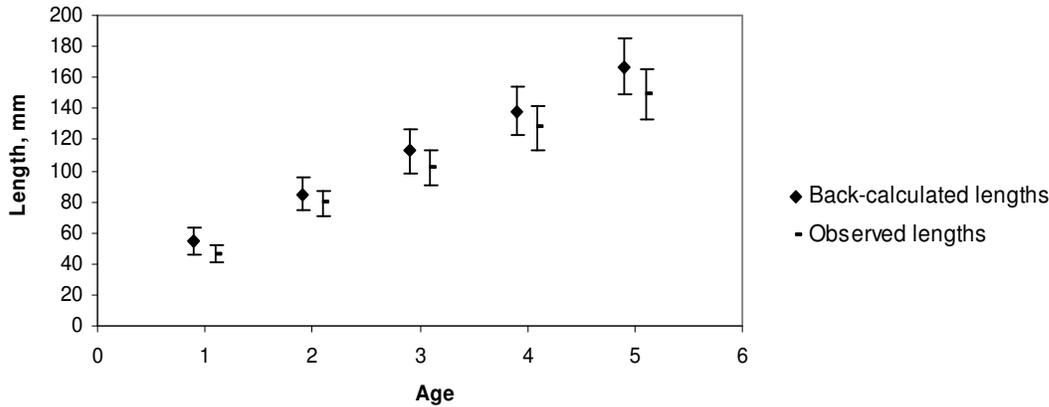

Figure 11: Mean (± std) estimated back-calculated lengths (at annulus formation in early spring) compared with the mean observed lengths in late autumn for all ages.

Although mean back-calculated lengths were higher than mean observed lengths for all ages (fig 11), the method works fairly well to estimate the lengths at previous ages. The variability in length increased with age for both the back-calculated and empiric lengths. The difference between the mean back-calculated and observed lengths increased with age, but the relative difference was largest for the one-year-olds. The relative difference between back-calculated and observed length was 0.15, 0.07, 0.09, 0.08 and 0.11 for the 5 age groups respectively.

Growth modeling on the back-calculated data was done in a similar manner as for the *Site confirmed dataset*. Length at the beginning of the growth period, *Cohort* and *Age* were used as covariates when modeling growth rate in the second growth season. Growth in the third and fourth growth season was modelled in the same way, except Cohort was not included as a covariate for these responses (because of few cohorts for these responses). Density was not added in any model of temporal variation in growth, since I do not have density estimates for all the years. The covariate (L_i), length at the start of the growth season, always explained most of the variation in growth, whereas the predictor variables (*Site*, habitat variables and principal components) were of minor importance. For the growth rate in the second growth period, $log\ (L_2)\text{-}log(L_1)$, two models could not be distinguished by the AIC criterion (model 1 and 3 in table 7), the least square mean for *Site* from (1) in table 7 are shown in fig 12, and the estimates of the parameters from model 3 in table are shown in table 8.

Table 7. Specific growth rate (back-calculated) in the second, third and fourth growth season. The best model by AIC criterion is in bold type.

Response	Model	R^2	Df	F	P	AIC
$\log(L_2)-\log(L_1)$	**1 L_1+C+A +Site**	**0.535**	**33,862**	**30.0**	**<0.0001**	**-4391**
	2 L_1+C+A+ 1.P+2.P+3.P	0.518	12,883	79.2	<0.0001	-4384
	3 L_1+C+A+	**0.522**	**12,883**	**80.3**	**<0.0001**	**-4390**
	Slope+Depth+Substrate					
$\log(L_3)-\log(L_2)$	**4 L_2+A+Site**	**0.200**	**28,565**	**5.0**	**<0.0001**	**-3221**
	5 L_2+A+1.P+3.P	0.170	6,587	20.0	<0.0001	-3211
	6 L_2+A+Depth	0.169	5,588	24.0	<0.0001	-3213
$\log(L_4)-\log(L_3)$	**7 L_3+C+A+Site**	**0.297**	**29,239**	**3.5**	**<0.0001**	**-1557**
	8 L_3+A +1.P+3.P	0.235	8,260	10.0	<0.0001	-1544
	9 L_3+A+ Depth	0.236	6.262	13.5	<0.0001	-1549

Figure 12: Least square mean growth ± 95 % CL at the different sites, after adjusting for the baseline model (L_1, C, A) in model 1 table 7.
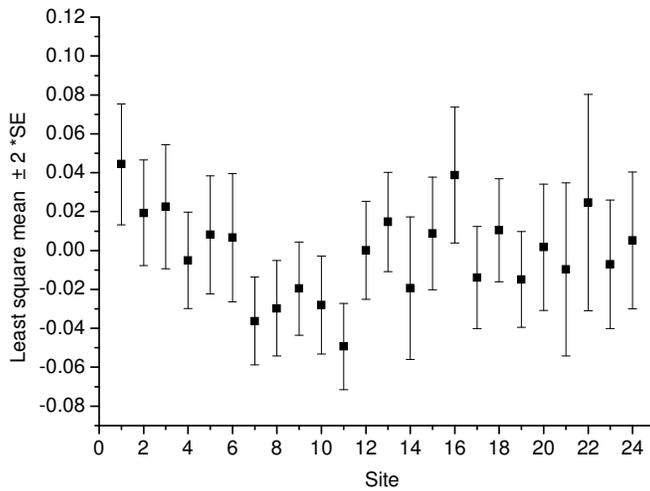
Table 8: The table lists the variables with estimate, std error and P-value, from model 3 in table 7.

Term	Estimate	Std error	P
Intercept	0.7965	0.0967	<0.0001
Length, L_1	-0.0084	0.0003	<0.0001
Cohort [1998-1997]	0.0078	0.0254	0.8
[1999-1998]	-0.0399	0.0117	0.0007
[2000-1999]	-0.0196	0.0105	0.0607
[2001-2000]	0.0391	0.0110	0.0004
Age [2-1]	0.0084	0.0865	0.9
[3-2]	0.0417	0.0106	<0.0001
[4-3]	0.0127	0.0107	0.2
[5-4]	-0.0082	0.0211	0.7
Slope	-0.5127	0.3986	0.2
Depth	0.0009	0.0004	0.0373
Substrate	0.0135	0.0032	<0.0001

Discussion

I found considerable variation in growth among trout in a small stream. Most of this variability was caused by differences in length, age and maturity. Estimates of trout density did not explain any significant part of the residual growth variability, but ~25 % of it was accounted for by the *Site* variable. Measures of habitat quality accounted for some of the variation in growth but not as much as the *Site* variable, even though habitat quality was measured on the same spatial scale.

One assumption for studying habitat and density effects upon individual growth is limited movement between habitats, as mobile individuals may interact with habitat heterogeneity (Rodriguez 2002) to swamp any effects of habitat and density on growth (Newman 1993). Mobility effects the energetic costs of the individual (Forseth et al. 1999) and hence growth, susceptibility to predation (Gilliam & Fraser 2001) and mortality (Elliott 1994). The ideal free distribution predicts that spatial scale will affect the intensity of density-dependent growth: at small spatial scales, movement of fish will equalize growth rates between patches differing in density and intrinsic quality (Barnard 2004). Clearly, the perception of mobility depends on the time and space over which movement is monitored. Nevertheless, movement in this study seemed to be restricted, as 76 % of all recaptures were never caught at different sites, hence justifying the investigation of density dependence at the spatial scale of *Sites*. The proportion of 'residents' was almost constant when the time between captures was in the period of 0-600 days, and decreased rapidly from 600 days and onwards. This result argues that the fish in this study are stationary in the first period of their life (at least after being tagged, usually as 1^+ or 2^+), and that the mobility increases with the age of the fish, which makes the analyses on young fish more reliable. This increase in the proportion of mobile individuals after 600 days coincides with mature individuals moving to spawning grounds, since most fish are tagged as 1^+ or 2^+, and most fish in this stream mature at the age of 3 (Olsen & Vøllestad 2005).

There was considerable variation in individual growth rates in this study of which the age, length and state of maturation of the fish were the most important explanatory variables. Growth decreased with increasing length, age and with the onset of maturation. These variables are strongly correlated in indeterminately growing organisms, as long fish are also old and mature. The scope for growth decreases with increasing length of the fish (Wootton 1990), and as a fish is getting old and mature, it allocates most of the energy to reproduction at the expense of growth (Wootton 1990). Density and its proxies were weakly related to

growth in this study. The sums of fork lengths squared was negatively related to growth, but the estimate in the model was close to zero.

Studies indicate that intraspecific competition is an important factor for explaining variation in growth in stream-living brown trout (Jenkins et al. 1999, Nordwall et al. 2001, Bohlin et al. 2002), but density-dependent growth could not be detected in this study. Ray & Hastings (1996) concluded that searching for density-dependent processes are more often hindered by inappropriate spatial scaling than by short time series and low test power. Despite the supposedly limited movement in this study, the sample scale in this study (site) may be too small to detect density dependence. Jenkins et al. (1999) suggest that the sampling area should be at least 100 m^2 to adequately capture the average trout density experienced by the individual fish over the growth period. Food availability (invertebrate drift) may be affected by trout upstream and therefore depending more on the trout density at a larger spatial scale. Even though the average density was in the range where detection of density dependence is most easily detectable (Jenkins et al. 1999), the range of density in this study may be to low to detect density dependence.

The residual-variation after accounting for age, length at the start of the growth period, and maturation, were best explained by *Site*. The habitat variables and density as predictors explained about half as much of the residual variation in specific growth rate as *Site*, and the model with the first principal component explained even less of the variation than the model with the habitat variables as predictors. First year growth was also best explained by *Site*. Habitat and density only explained about half as much of the variation in growth as *Site*. If the measured habitat variables and density perfectly reflect the variability in growth potential between sites, they should explain as much of the variation in growth as *Site*, since they are measured on the same spatial scale. Plausible reasons for why they do not, are that important microhabitat variables may not have been measured, or at least not at the relevant scale. It is therefore not unexpected that *Site* explains more of the residual-variation. Migration between sites should, however, affect the estimated relationship between *Site* and growth and habitat variables and growth in a similar way. The habitat qualities were all measured under low water level, and even if the relative variation in habitat quality are assumed to be the same at all water levels, habitat selection could vary between different water flows (Heggenes 2002). The principal components explained little of the variation in growth compared to the habitat

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variables: This means that they are not good substitutes for the habitat variables, even if the first three principal components capture 90 % of the variation in the habitat variables.

Given the result of restricted movement in this study, there should be a high correlation between densities in subsequent sessions. The correlations are weak and more importantly, the precision of the density estimates are low, maybe too low for detecting density dependence in growth, even if present. Newman (1993) argues that trout are forced to select sites of less quality as trout density increases, resulting in an increase in the number of slower growing fish, which results in an increase in the variance of growth. The coefficient of variation (CV) in growth in this study had only weak relationships with the different density variables. The correlation between CV (g) and estimated density was negative, which is the opposite of what Newman (1993) predicted for a system with density-dependent growth. Within the framework of Newman's site quality model, the coefficient of variation in growth in this study gave no indication of density dependence being of importance for growth in Bellbekken.

Density dependence in individual growth rate is a potentially powerful mechanism of population regulation since both survival and fecundity are typically positively related to body size. Density-dependent growth may regulate population size through at least two mechanisms. First, density dependence in the growth and condition of underyearlings may translate into density-dependent survival over the first winter, when trout lose mass. Second, because the fecundity of brown trout is positively related to female body size, density dependence in the growth and condition of adult fish should limit the egg production of a population (Grant & Imre 2005).

Environmental factors and density tend to be confounded and should be replicated in time and space, and if possible complemented by experimental manipulations at the appropriate spatial scales. At a given spatial scale, density-dependent growth will be weaker across space than across time. This is because individuals can switch between patches in space but not between patches in time. However, as spatial scale increases, individuals will not be able to sample more distant patches, and the possible masking effect of movement will be reduced. Jenkins et al. (1999) found density dependent growth at the scale of whole sections (340-500 m) but not at the scale of individual segments (5-31m). Vøllestad et al. (2002) studied growth variation among streams in the same river system as in this study, and found evidence of density and

habitat dependence on growth rate. The variance in both density and habitat quality are larger among streams than within a single stream (as they are measured on larger scales). This scale dependence could be a reson for why Vøllestad et al (2002) find density-dependent growth whereas I do not. Hence there is a possibility that by increasing the spatial scale in this study, by fusing sites, density-dependent growth could be detected, as well as a stronger relationship between habitat quality and growth. However, if movements of fish between sites in this study are limited in the way the results suggest, the spatial scale of *Site* used in this study may be appropriate. This, and the fact that mean densities in this study coincides with the range Jenkins et al. (1999) propose as where the detection of density dependent growth is most easily detectable, suggests that the spatial scaling in this study, when it comes to size of sampling units (sites) and range in density, is appropriate for detecting density-dependent growth. Therefore, I propose that mortality rather than density-dependent growth may be a controlling factor in this system. Olsen and Vøllestad (2001a) studied monthly trout survival in Bellbekken, and found survival to be relatively low. They did not include age-effects in their models, but nevertheless their results show that there are high mortality rates for trout in Bellbekken, which also the age distribution in this study reflects. Hence, there is a possibility that high mortality is reducing trout densities to levels where density-dependent growth does not operate. Einum et al. (2004) argue that big eggs are an indication of density dependence, whereas small eggs points to low competition and density independent factors as regulating mechanisms. In a study of egg size in several streams in this river system, Bellbekken had smaller eggs than the average egg size (Olsen et al. 2003), indicating little competition.

The mean back-calculated length in this study was significantly larger than the mean observed length for all ages, but the relative difference was largest for the one year olds. If trout growth stagnates in autumn and there is no growth between sampling sessions in autumn and spring, observed and back-calculated lengths should not be systematically different from each other. Even though models of salmonid thermal performance predict a lower temperature limit for growth and food consumption of approximately 5°C (Elliott 1994), there is evidence that salmonids are able to feed and grow at temperatures close to 0°C during winter (Finstad et al. 2004). Growth beyond the observed growth period, between sampling sessions in spring and autumn, may therefore explain the difference between mean back-calculated and observed length at each age. An alternative explanation for this pattern is size-selective mortality, with higher mortality of the smaller individuals (the 'bigger is better hypothesis'; Sogard 1997). The relative difference being largest for the youngest age group points to size-selective

mortality as the more plausible explanation, since size selective mortality is generally more important at young ages (Elliott 1994, Wootton 1990, Sogard 1997, Meyer & Griffith 1997, Einum et al. 2004), while it is less obvious why duration of the growth season should be age-dependent. Methodical error may also contribute to the discrepancy between back-calculated and observed length. The regression between scale and fork length is analysed on fish older than 0^+. A different relationship of the scale-fork length for the youngest age group could lead to the relative difference between back-calculated and observed length for one-year-olds being largest.

Conclusion

In this study I have used empiric growth rates and growth rates estimated from back-calculated length at age data to model spatial and temporal growth. Variation in growth was best modeled by the length of the fish at beginning of the growth period, age, and the maturation of the fish. The habitat variables measured in this study explained much less of the variance in growth than the *site* variable, indicating that there are significant effects at the *Site* level, not explained by the environmental variables measured. Nevertheless, a model with the habitat variables together with the length, age and maturity of the fish, explained more of the variation in growth than just these covariates alone. In this study, growth was not density-dependent. The low range in density in this study could be a reason for not detecting density dependence. Sampling at a larger scale could possibly increase the chance of detecting density-dependent growth by avoiding individuals moving between sampling units obscuring the effect of density on growth, but movement in this study was limited. The density estimates vary in precision, and the precision may be too low for detecting density-dependence in growth. Underestimation of population size due to methodological bias in the removal method could also be a reason for not detecting density-dependent growth. The prediction of density increases leading to a decrease in mean growth but an increase in the coefficient of variation was not supported.

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Appendix 1. Population density estimates (y), and different proxies for density per square meter for autumn 2002.

Site	Season	Year	N	N/m^2	Est pop size(y)	$(y)/m^2$	SE(y)	$SE(y)/m^2$	Est catchability (p)	SE(p)	$\sum L_F^2/m^2$	$\sum L_F^3/m^2$
1	Autumn	2002	33	0.23	37.85	0.27	4.62	0.03	0.50	0.12	4913.81	34.72
2	Autumn	2002	47	0.23	52.97	0.26	4.84	0.02	0.52	0.10	3099.87	15.09
3	Autumn	2002	23	0.17	24.30	0.18	1.75	0.01	0.62	0.12	2564.30	18.71
4	Autumn	2002	37	0.14	38.35	0.14	1.63	0.01	0.67	0.09	1997.24	7.47
5	Autumn	2002	29	0.16	29.80	0.16	1.19	0.01	0.70	0.09	2108.82	11.27
6	Autumn	2002	18	0.14	28.17	0.21	14.72	0.11	0.29	0.21	2252.94	17.07
7	Autumn	2002	45	0.17	50.80	0.19	4.80	0.02	0.51	0.10	2695.80	10.12
8	Autumn	2002	49	0.19	52.06	0.20	2.76	0.01	0.61	0.08	2779.08	10.84
9	Autumn	2002	50	0.32	54.46	0.35	3.70	0.02	0.57	0.09	4605.19	29.92
10	Autumn	2002	50	0.20	58.58	0.23	6.58	0.03	0.47	0.10	2532.56	10.09
11	Autumn	2002	60	0.23	75.82	0.28	11.07	0.04	0.41	0.10	3414.27	12.83
12	Autumn	2002	73	0.24	79.22	0.26	4.30	0.01	0.57	0.07	2146.14	6.99
13	Autumn	2002	34	0.11	38.48	0.12	4.25	0.01	0.51	0.12	1345.46	4.17
14	Autumn	2002	27	0.17	32.61	0.21	5.82	0.04	0.44	0.14	2038.84	13.07
15	Autumn	2002	31	0.08	87.56	0.23	106.73	0.28	0.14	0.19	1210.59	3.20
16	Autumn	2002	21	0.12	26.54	0.16	6.55	0.04	0.41	0.17	1984.49	11.60
17	Autumn	2002	33	0.24	35.65	0.26	2.76	0.02	0.58	0.11	4035.06	29.88
18	Autumn	2002	44	0.19	50.16	0.22	5.11	0.02	0.50	0.10	2724.84	11.72
19	Autumn	2002	29	0.16	-	-	-	-	-	-	2523.83	14.02
20	Autumn	2002	13	0.07	14.50	0.08	2.34	0.01	0.53	0.18	1309.02	7.11
21	Autumn	2002	28	0.13	31.17	0.14	3.38	0.02	0.53	0.12	1910.55	8.71
22	Autumn	2002	42	0.13	53.07	0.17	9.26	0.03	0.41	0.12	1884.99	6.02
23	Autumn	2002	21	0.14	22.59	0.15	2.10	0.01	0.59	0.13	2132.52	14.20
24	Autumn	2002	15	0.10	33.08	0.23	38.74	0.27	0.18	0.26	1726.85	11.93
25	Autumn	2002	16	0.20	18.16	0.22	2.98	0.04	0.51	0.17	3742.42	45.92

Appendix 2. Population density estimates (y), and different proxies for density per square meter for spring 2003.

Site	Season	Year	N	N/m^2	Est pop size(y)	$(y)/m^2$	SE(y)	$SE(y)/m^2$	Est catchability(p)	SE(p)	$\sum L_F^2/m^2$	$\sum L_F^3/m^2$
1	Spring	2003	8	0.06	18.51	0.13	32.27	0.23	0.17	0.36	681.20	80981.40
2	Spring	2003	30	0.15	50.08	0.24	23.73	0.12	0.26	0.17	1588.24	185251.81
3	Spring	2003	10	0.07	10.89	0.08	1.65	0.01	0.57	0.20	1047.68	131671.08
4	Spring	2003	25	0.09	-	-	-	-	-	-	1189.36	148989.65
5	Spring	2003	18	0.10	22.74	0.12	6.06	0.03	0.41	0.18	933.90	102911.89
6	Spring	2003	18	0.14	24.86	0.19	9.11	0.07	0.35	0.20	1674.36	213935.37
7	Spring	2003	28	0.11	-	-	-	-	-	-	1100.26	126818.42
8	Spring	2003	19	0.07	24.62	0.10	7.04	0.03	0.39	0.18	1015.28	131963.75
9	Spring	2003	29	0.19	31.30	0.20	2.56	0.02	0.58	0.11	2185.85	261055.45
10	Spring	2003	33	0.13	40.15	0.16	6.71	0.03	0.44	0.13	1214.60	138407.86
11	Spring	2003	42	0.16	44.69	0.17	2.61	0.01	0.61	0.09	1465.87	167927.38
12	Spring	2003	30	0.10	50.08	0.16	23.73	0.08	0.26	0.17	934.05	104257.68
13	Spring	2003	59	0.18	67.70	0.21	6.20	0.02	0.50	0.09	1671.41	184685.31
14	Spring	2003	23	0.15	27.18	0.17	4.71	0.03	0.46	0.15	1643.49	193412.54
15	Spring	2003	31	0.08	52.84	0.14	25.83	0.07	0.26	0.17	859.00	101897.91
16	Spring	2003	22	0.13	24.65	0.14	3.17	0.02	0.52	0.14	1277.90	149208.24
17	Spring	2003	27	0.20	42.25	0.31	18.03	0.13	0.29	0.17	2160.12	254040.69
18	Spring	2003	26	0.11	-	-	-	-	-	-	910.47	97722.73
19	Spring	2003	32	0.18	50.55	0.28	20.30	0.11	0.28	0.16	1827.84	215673.40
20	Spring	2003	22	0.12	39.05	0.21	24.79	0.13	0.24	0.20	1398.49	164526.38
21	Spring	2003	26	0.12	27.00	0.12	1.41	0.01	0.67	0.10	971.95	103633.54
22	Spring	2003	24	0.08	55.54	0.18	55.89	0.18	0.17	0.21	882.86	103774.96
23	Spring	2003	20	0.13	-	-	-	-	-	-	1460.74	177487.44
24	Spring	2003	19	0.13	27.00	0.19	10.53	0.07	0.33	0.20	1370.97	171853.82
25	Spring	2003	6	0.07	6.54	0.08	1.28	0.02	0.57	0.26	824.23	95111.96

Appenix 3. Population density estimates (y), and different proxies for density per square meter for autumn 2003.

Site	Season	Year	N	N/m^2	Est pop size (y)	$(y)/m^2$	SE(y)	$SE(y)/m^2$	Est catchability (p)	SE(p)	$\sum L_F^2/m^2$	$\sum L_F^3/m^2$
1	Autumn	2003	16	0.11	18.16	0.13	2.98	0.02	0.51	0.17	1154.20	155714.12
2	Autumn	2003	32	0.16	46.77	0.23	15.27	0.07	0.32	0.15	1601.01	185347.73
3	Autumn	2003	16	0.12	16.92	0.12	1.48	0.01	0.62	0.14	1417.47	177587.02
4	Autumn	2003	36	0.13	38.65	0.14	2.69	0.01	0.59	0.10	2058.03	282362.01
5	Autumn	2003	25	0.13	26.94	0.14	2.34	0.01	0.58	0.12	1434.04	177743.35
6	Autumn	2003	10	0.08	16.69	0.13	13.70	0.10	0.26	0.29	969.01	123549.30
7	Autumn	2003	26	0.10	34.10	0.13	8.73	0.03	0.38	0.16	1279.24	173850.96
8	Autumn	2003	13	0.05	25.86	0.10	26.90	0.10	0.21	0.27	614.34	78681.39
9	Autumn	2003	18	0.12	19.61	0.13	2.22	0.01	0.57	0.15	1878.88	260956.88
10	Autumn	2003	20	0.08	-	-	-	-	-	-	962.37	121663.92
11	Autumn	2003	35	0.13	36.26	0.14	3.27	0.01	0.55	0.11	1160.12	133109.77
12	Autumn	2003	33	0.11	43.67	0.14	7.93	0.03	0.42	0.13	1637.59	236319.14
13	Autumn	2003	54	0.17	243.87	0.76	430.50	1.33	0.08	0.15	1933.17	247203.08
14	Autumn	2003	10	0.06	16.69	0.11	13.70	0.09	0.26	0.29	652.13	81775.11
15	Autumn	2003	18	0.05	-	-	-	-	-	-	326.19	30949.35
16	Autumn	2003	21	0.12	28.58	0.17	9.25	0.05	0.36	0.18	1099.16	124665.59
17	Autumn	2003	29	0.21	62.39	0.46	50.26	0.37	0.19	0.19	2563.81	328976.88
18	Autumn	2003	48	0.21	62.50	0.27	11.46	0.05	0.39	0.12	2272.21	305175.26
19	Autumn	2003	44	0.24	52.24	0.29	6.71	0.04	0.46	0.11	5344.83	786427.51
20	Autumn	2003	34	0.18	40.54	0.22	6.05	0.03	0.46	0.12	2869.53	434147.71
21	Autumn	2003	21	0.10	23.20	0.11	2.74	0.01	0.54	0.14	781.87	84573.14
22	Autumn	2003	24	0.08	24.85	0.08	1.29	0.00	0.67	0.11	847.50	112917.84
23	Autumn	2003	23	0.15	30.33	0.20	8.42	0.06	0.38	0.17	1798.26	221988.83
24	Autumn	2003	17	0.12	19.71	0.14	3.57	0.02	0.48	0.17	1309.75	157753.37
25	Autumn	2003	17	0.21	-	-	-	-	-	-	3425.15	482948.61