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Growth and Movement in Brown Trout (*Salmo trutta) in two Norwegian Rivers*

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Contents

Abstract

In the present study, using stream-dwelling brown trout (*Salmo trutta*) as a model species, movement through the summer and autumn in two large Norwegian rivers, River Glomma and River Gudbrandsdalslågen, was observed. In addition fish from each river were sampled for age and growth analysis. The aim of the study was to test for which individual characteristics (sex, body mass, body condition factor, tagging site and cohort) that influenced movement and to test for correlations between growth rates (both immature and mature) and movement (movement during the growth season and spawning migration) on a large spatiotemporal scale.

Model selection showed that body condition was negatively related to movement during the growth season and that there was a difference in movement activity between the two rivers. Female body size had a positive effect on the activity level shown for movement during the growth season and spawning period; however no such relationship was found for males. As this relationship has not been shown before in salmonids, the reason for this pattern remains unknown. However, one might speculate that it is related to differences between the two sexes in size-specific energy requirements associated with spawning. Neither movement during the growth season nor spawning migration could be predicted from growth rates experienced as juveniles. This indicates that variation in movement among individuals is not temporally consistent throughout life in brown trout.

Sammendrag

Bevegelse hos stedfast brunørret (*Salmo trutta*) ble observert gjennom sommeren og høsten i to store norske elver, Glomma og Gudbrandsdalslågen. I tillegg ble fisk fra hver elv aldersbestemt og analysert for vekst gjennom skjellesing. Hensikten med studiet var å se om noen av brunørretens individuelle karaktertrekk (kjønn, kroppsvekt, kroppskondisjon, merkeplass og kohort) påvirket bevegelse og å teste for en korrelasjon mellom vekstrate (både hos umodne og kjønnsmoden individer) og bevegelse (bevegelse i vekstsesongen og gytevandring) på en stor romlig- og tidsskala.

Modellseleksjon viste at kroppskondisjon var negativt korrelert med bevegelse i vekstsesongen og at det var en forskjell i hvor mye populasjonene beveget seg i de to elvene. Kroppsvekt hos huer hadde en positiv effekt på bevegelse i vekstsesongen og gytevandringen. Kroppsvekt hadde ikke lignende effekt for hanner. Ettersom dette forholdet ikke har blitt vist før hos laksefisk, kan man bare spekulere i årsaken. Likevel kan man tenke seg at forskjeller i forhold til størrelsesspesifikke energibehov assosiert med gytinga kan være ulikt mellom kjønnene. Verken bevegelse under vekstsesongen eller gytevandringen kunne bli forutsett fra vekstrater erfart som juvenil. Dette indikerer at variasjon i bevegelse blant individer ikke er konstant over tid gjennom livet til brunørreten.

Introduction

For animals, movement is one of the primary behavioral patterns (Kahler et al. 2001). Movement permits animals to respond to their physical habitat, conspecifics and other biotic parameters in their environment in order to increase their fitness. These movements occur over many scales of space and time (Dingle 1996; Kahler et al. 2001). One group of organisms that are commonly considered to be suitable model organisms for movement is stream fish, since longitudinal movement is easy to model in one single dimension, and hence this reduces model complexity. Furthermore, stream fish can be efficiently sampled and individually tagged and be observed in their natural environment (Knouft and Spotila 2002; Rodriguez 2002). Many salmonid populations inhabit streams throughout the majority of their lives. Movement on a seasonal scale like spawning migration and moving between wintering and feeding habitats are typical characteristics of salmonid life histories (Jonsson and Jonsson 2011). Stream-dwelling salmonids however, have for a long time been characterised as having restricted movement throughout their entire lifespan (Gerking 1959). Although some forms of movement like spawning migration are recognized, the focus has been on the restricted territories the fish establish for feeding during the summer months (Gowan et al. 1994). Research during the lasts decades, using radio telemetry to study movement, has revealed that stream-dwelling salmonids have more variable movement patterns than first anticipated and can move from a few meters to many kilometres (Höjesjö et al. 2007; Jonsson and Jonsson 2011). The home range over a season can therefore be much larger and overlap substantially among individuals (Höjesjö et al. 2007), indicating a complex social structure. Most organisms have to move through a mosaic environment where they try to optimise foraging and safety. Thus, they cannot spend all of their time in a limited spatial patch since their needs change over a single day and a year (Barraquand and Benhamou 2008). The major focus regarding influences on movement has been in relation to environmental factors like water levels and temperature (Popoff and Neumann 2005; Zimmer et al. 2010), but there is also an increasing interest in the influence of individual characteristic on movement.

Movement is a trait that may be predicted to increase the risk of predation exposure, but also to influence growth rates. Tracking the spatiotemporal variation in environmental quality can have a positive influence on growth rates (Werner and Anholt 1993). Active individuals might find more energetically profitable areas or locations that minimise energy cost (Dieterman et al. 2012), and as a result mobile individuals may show more rapid growth than immobile

individuals (Forseth et al. 1999; Jonsson 1985). Growth rate has long been used as a surrogate measure for fitness (Schluter 1995). As a result of the positive fitness consequences of having a high growth rate one should thus expect selection for rapid growth and maturing at an early age (Arendt 1997). However, growth often fluctuates noticeably and in nature one often observes an intermediated growth (Elliott 1994; Gotthard 2000). Substantial intra-cohort variation in body size is often displayed in stream-resident salmonids; this may give selection a basis to act on (Elliott 1994). For an organism to increase its growth rate it has to increase its food intake (i.e. the time spent feeding). This will likely increase the time spent moving around and reduce the time spent vigilant. Sedentary individuals may benefit from keeping more cryptic and have a lower mortality rate (Biro et al. 2006; Lankford et al. 2001). Therefore in the presence of predators a fish may alter its behaviour to feed in less risky habitats, although the habitat may be less food rewarding (Werner et al. 1983). Support has been for movement affecting growth in salmonids, where mobile fish grew faster (Grant and Noakes 1987; Kahler et al. 2001; Naslund 1990; Steingrimsson and Grant 2003). Martin-Smith and Armstrong (2002) found that growth was positively correlated to the degree of movement between areas of a stream, on a small spatial scale (meters). However, most of these studies have looked at the relationship on a small spatial scale and little is known about the correlation between movement and growth in river-dwelling salmonids on a large spatial scale.

In the present study movement through the summer and autumn in brown trout in two large Norwegian rivers, River Glomma and River Gudbrandsdalslågen, was observed. Fish from each river were tagged with radio transmitters and sampled for age and growth analysis. The data on movement and growth of individual fish allowed me to address two issues: First I tested whether the amount of movement during the growth season or spawning migration was correlated with individual characteristics (sex, body mass, body condition factor, tagging site and cohort) recorded during tagging. Second, using back-calculations based on scale samples, I examined whether growth rates experienced earlier in life (as juvenile or the last year prior to tagging) were correlated with movements during the growth season or spawning migration. Some studies have tested whether heterogeneity observed in the movement pattern among mature fish is constant over time in an individual's life (Morrissey and Ferguson 2011). If so, this may suggest that correlations between growth and movement may be maintained throughout life, with different individuals consistently differing in their choice with regard to the trade-off between growth and survival.

Method

Telemetry data and fish scale samples were provided by the Norwegian Institute for Nature Research (NINA) division in Lillehammer (courtesy of Dr. Jon Museth). The telemetry study was approved by the National Animal Research Authority in accordance with national legislation.

Study sites

Brown trout were monitored and sampled from the two rivers Glomma and Gudbrandsdalslågen situated in the south-eastern part of Norway. The study site in River Glomma consisted of a 85 kilometer reach between Røstefossen in Os municipality (6932775 N, 616537 E) and Høyegga in Alvdal municipality (6877763 N, 595286 E). Røstefossen power station prevents any upstream movement and Høyegga is set as delimitation for the study site in Glomma (Museth et al. 2012).

The study site in River Gudbrandsdalslågen consisted of a 54.5 kilometer reach between Rostenfallene in Sel municipality (6859695 N, 521680 E) and Harpefoss in Sør-Fron municipality (6827814 N, 544579 E). Harpefoss power station works as a migration barrier whereas Rostenfallene is a natural barrier is a natural barrier to upstream migration. In addition to the reach between Rostenfallene and Harpefoss, 15 km of the major tributary River Otta was included (i.e. up to the migration barrier at Eidefoss power plant)(Museth et al. 2009).

Both rivers support multispecies fish communities, the study section of River Gudbrandsdalslågen contain grayling (*Thymallus thymallus*), brown trout (*Salmo trutta*) and European minnow (*Phoxinus phoxinus*). In addition, the following species are found in River Glomma: whitefish (Coregnus lavaretus), pike (*Esox lucius*), perch (*Perca fluviatilis*), roach (*Rutilus rutilus*), European minnow, bullhead (*Cottus poecilopus*), burbot (*Lota lota*), and brook lamprey (*Lampetra planeri*) (Museth et al. 2012).

Study organism

Brown trout (*Salmo trutta*), belongs in the family Salmonidae (Elliott 1994). Brown trout can be divided into three forms; lake-run brown trout, sea-run brown trout and resident brown trout (Pakkasmaa and Piironen 2001). Although the different forms have different habitat requirements and movement behaviors, they belong to the same population and have the ability to interbreed (Arnekleiv and Ronning 2004). Stationary brown trout has an ontogenetic life cycle that consists of four stages; alevin (hatched individuals with yolk sac), fry (emerging individuals), parr (older juveniles) and mature individuals (Elliott 1994). Habitat preference changes with size, life stage and season. Larger individual favor deeper stream areas than smaller individuals, fry prefers more aquatic vegetation than parr and substrate preference varies through the season (MakiPetays et al. 1997). Brown trout is an opportunistic feeder and diet and varies with season, age, size, habitats and among individuals. Small individuals feed on zoobenthos, terrestrial insects and occasionally zooplankton. Only the individuals that have reached a length of about 15 cm or more may become fully or partial piscivor (L'Abée-Lund et al. 1992). Northern populations of brown trout have a larger feeding activity in the spring and early summer, when water temperatures is increasing, than during other parts of the year (Klemetsen et al. 2003). Their breeding season in my study areas lasts from late September to mid October.

Fish capture and telemetry

In River Glomma 47 fish were captured between April and October 2010 from 12 different localities. In River Gudbrandsdalslågen a total of 201 fish from 40 localities were caught during three different periods; April to September 2008, March to November 2009 and April to November 2010. The fish were caught through cooperation with local anglers and were kept in fish traps at the tagging site for a maximum of three days before tagging. All fish were anaesthetized to surgical level by water administrated 2-phenoxyethanol (0.7 ml l^{-1}) for two to three minutes prior to tagging. The anaesthesia resulted in a loss of voluntary and involuntary muscle movement. The handling time lasted between three to eight minutes such that the anaesthetic did not need to be sustained. Throughout the procedure oxygenated water was pumped over the gills (Museth et al. 2011). For immature fish internal radio transmitters was used and for spawning fish an external radio transmitter was applied (model F1960, F1970, Museth et al., 2012). The external transmitter was positioned laterally above the lateral line on the right side of the dorsal fin. Wires coated with plastic were attached through the dorsal

musculature to secure the transmitter (Bridger and Booth 2003). For immature fish internal transmitters (model F1830, F1580, F1170 (coil)) were surgically implanted in the peritoneal cavity through a ventral incision made in front of the pelvic fin. The fish were placed with the ventral side upwards in a V-shaped operation device. Two to three sutures were used to close the incision. After the operation, for both the internal and the external transmitters, the fish were immediately placed in a recovering tub with fresh water from the river. Although it took between 1.5 to 4 minutes for the fish to recover, it was kept in the tub 15-30 minutes to be monitored prior to release (Museth et al. 2012).

For both types of transmitters the general "2% rule", where the weight of the transmitter should not exceed 2% of the fish body mass in air, was applied (Winter 1996). The transmitters were provided by Advanced Telemetry Systems (ATS). A Challenger Receiver (model R2100) manufactured by ATS (USA) and a three-element folding Yagi antenna (model 12762) were operated from a car, and occasionally on foot (Museth et al. 2011).

The radio tagged fish were positioned once a week, and twice a week during the spawning period (specified below). During each positioning each fish was assigned to a 500 meter river zone.

In addition to the tagging, fork length (±1 mm), body mass (±5g) and sex (through external characters) were recorded. A scale sample for ageing and growth analysis was taken from each individual. Moreover, capture date, tagging site and whether the fish appeared to be spawning the subsequent fall or not was recorded. According to Museth et al. (2011) there are indications that a large fraction of the sexually mature part of the population spawn every year, for both rivers. It is however possible that some individuals will not spawn and this can be a source of error. To minimize this error, particular attention was given to the movement pattern ahead of the spawning period and the concentration of radio tagged so non-spawning individuals could be excluded.

Fish scale analysis

Scale-reading is a validated method for age estimation of brown trout (Rifflart et al. 2006). As a fish grow the growth is reflected in the scale, through rings called circulii laid down from the center of the scale (Nordeng and Jonsson 1978). Food availability and temperature changes cause circulii to be laid down at different rates, resulting in differences between summer and winter zones (Fig. 1). Age is given by the number of winter zones. The distances between winter zones are used to back-calculate growth every year of life, assuming direct proportion between scale radius and fish (Lea, 1910),

$$L_i = (S_i/S_c)L_c \tag{i}$$

, where L_c og S_c refer to fish body length and scale radius at the time of capture, respectively. L_i and S_i are the corresponding measurements at the time of formation of the *i*th scale mark for winter i = 1, 2,…, n. (Francis 1990)

To minimize the errors in the age determination process each individual scale was read twice. A Nikon Ri1 camera fitted to a microscope was used to photograph the scales. The scale reading was done with Image Pro Plus.

A total of 296 fish scale was read; there were however numerous scale samples only containing replacement scales, which had to be excluded. Thus growth estimates were available from a total of 203 individuals.

Fig. 1 Picture of a brown trout scale. The black line represent the anterior transect which is followed when reading of age. From the center of the scale eight winter zones are evident.

Definition of movement- and growth measurements

Movement measurements

Average daily large scale movement during the growth season (hereafter termed summer movement) was defined to include the months May, June and July in both rivers. The period was chosen to exclude potential migration from winter habitat to summer habitat, as well as the spawning migration. The spawning period is between September 15th and October 15th in River Glomma and between September 25th and October 15th in River Gudbrandsdalslågen (Museth et al. 2012; Museth et al. 2011) There is large variation among individuals regarding the start of spawning migration relative to actual spawning. Spawning migration may occur immediately; prior to spawning or it may start as early as August. Thus by excluding data from August and onwards I avoid including spawning migration into the summer movement measurement. The absolute distance between two consecutive positionings divided by the number of days in the interval was used as a measure of minimum distance moved per day. The average was then calculated from these measures for each individual. The other measure of movement was spawning migration distance. Spawning migration distance was defined as the largest absolute distance between the most downstream and the most upstream position observed during the whole observation period (i.e. May – October)

Growth measurements

Juvenile growth during the first four years of their lives was measured as the estimated body size achieved at the end of age one to age four (mm year^{-1}). Brown trout in the two rivers mature at age 5-6 around 30 cm (Jon Museth, pers. comm.). After the first sexually maturation growth declines as most of their available resources are spent on reproduction (Reznick 1983). Mature growth was defined as growth (mm year^{-1}) the year before tagging.

Statistical analysis

I first test whether the amount of movement during the growth season or spawning migration were correlated with individual characteristics (sex, body mass, body condition factor, tagging site and cohort) recorded during tagging. The full models consisted of the fixed effects sex (S), river (R), body condition factor (K) and body mass (W). In addition to the main effects of these fixed effects, I also included the possibility for different effects of body mass between males and females through an interaction term between S and W. Cohort and tagging site were entered as random factors.

Thus, the full model for movement (M, either representing summer movement or spawning migration) is given as

$$M_i = \alpha + \beta_1 K_i + \beta_2 R_i + \beta_3 S_{i\,+} \beta_4 W_i + \beta_5 G_i W_i + a_{j,k} + \varepsilon_i \qquad\qquad \text{(ii)}$$

The index i denotes individuals, α and β are the parameters for the fixed factors and $a_{j,k}$ represents the random factors cohort and tagging site.

The body condition factor K was calculated according to the Fulton formula (Sømme 1954) as

$$K = (100 \times W)/L^3 \qquad\qquad \text{(iii)}$$

,where L is the length of the fish (cm) and W designates the body mass (g).

For summer movement, number of observations did not have a statistically significant effect and was thus not included in the analysis.

To test for growth (immature and mature), the full model consisted of the fixed effects spawning migration, summer movement, sex, river and body mass. Cohort and tagging site were entered as random factors. To avoid overly complex models, no interaction was considered.

Thus the full models for juvenile growth (G, immature or mature) is given as

$$G_i = \alpha + \beta_1 M + \beta_2 R_i + \beta_3 S_i + \beta_4 W_i + a_{j,k} + \varepsilon_i \qquad \text{(iv)}$$

All statistical analyses were conducted using the statistical software R, v. 2.15.0 (R Development Core Team 2012)

To test for an effect of cohort and tagging site, I first compared the models with the same fixed effects, but with different random structures using the package nlme in R (Pinheiro et al. 2009). I compared four models; the random structures to the mixed effect models were *cohort/tagging site* and *cohort* and *tagging site* respectively. To compare the four models the function linear mixed effects (lme) were used with the mixed effect models, and the generalized least square function (gls) was applied for the linear model. All the calculations were based on REML and compared with ANOVA and I selected the best random structure based on likelihood ratio tests (Zuur et al. 2009).

To compare the different fixed effects structure a model selection approach was used to obtain the optimal model (Zuur et al. 2009). The calculations were based on maximum likelihood (ML) and compared using likelihood ratio tests. Fixed factors were removed until no further model simplification could be made without causing a significant ($P<0.05$) decrease in log-likelihoods. After finding the optimal model the models were refitted with REML and validated.

The residuals for the full model for both spawning migration and summer movement showed heteroscadasticity relative to body mass and sex. The function varPower was therefore applied to stabilise the variables according to body mass ($P<0.0001$ for both models). The form argument of the function varPower was also incorporated to allow for dissimilar variation between the two sexes (Zuur et al. 2009). The stabilisation was successful (visually assessed).

The residuals for the growth models showed no signs of heteroscadasticity and no weights argument was specified.

Result

Summer movement

In general brown trout from both rivers showed a tendency for low summer movement; 61% moved an average of 40 meter or less per day. There was some variation among individuals as 12% moved 100 meters or more per day and 8% moved 150 meters or more per day. Median summer movement for River Glomma and River Gudbrandsdalslågen was 61 meters and 27 meters per day, respectively (Fig. 2).
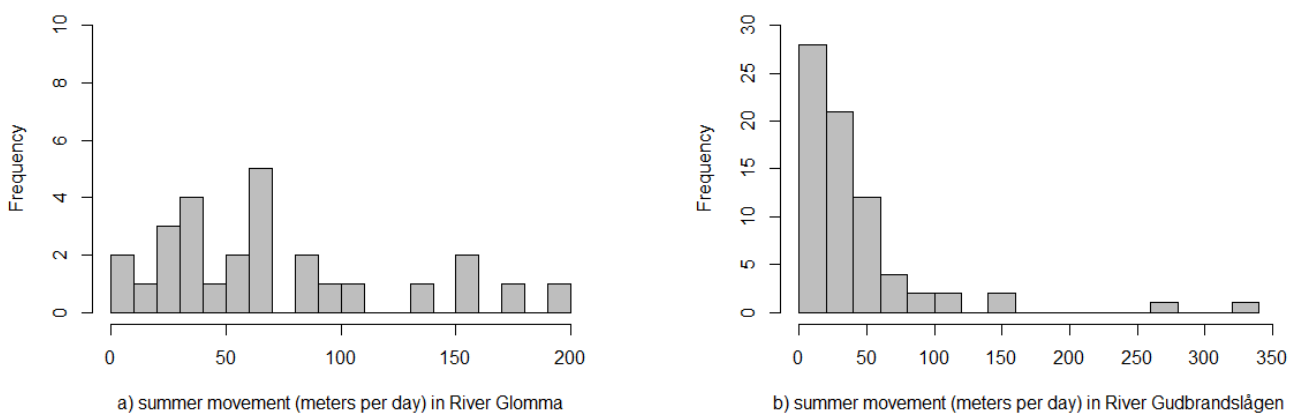

Fig. 2 The distribution of summer movement of brown trout in **(a)** River Glomma and **(b)** River Gudbrandsdalslågen.

The comparison of models with different random structures showed no indication of a cohort effect or an effect of tagging site on summer movement (P≥0.9998). The model selection showed that year of capture was not statistically significant in explaining summer movement (P=0.1287) and it was therefore removed from the model. No remaining terms could be removed (P≤0.0447). The main terms population and body condition factor K and the interaction between body mass and sex were significantly related to summer movement (table 1). The brown trout in River Gudbrandsdalslågen was estimated to move on average 39 meter per day less than those in River Glomma. K was negatively related to summer movement which may indicate that a fish in good condition move less. Body mass was positively related to summer movement for females, which indicates that larger females tend to move more in the summer than smaller females. For males no such relationship was found (Fig. 3a)

Table 1 Summary table of a gls model, describing variation in summer movement (meters) of brown trout in River Glomma and River Gudbrandsdalslågen. N=78 individuals.

	Estimates	SE	T	*P*
Intercept	230.25	51.20	4.49	<0.0001
Population2[1]	-39.19	11.17	-3.47	0.0009
Body mass	0.003	0.02	0.16	0.8706
Sex2[2]	-88.52	32.06	-2.76	0.0073
Fish condition	-167.97	60.1	-2.79	0.0066
Body massxSex2[3]	0.16	0.06	2.52	0.0140

[1] Estimate for River Gudbrandsdalslågen relative to the intercept (i.e. that for River Glomma).

[2] Estimate given for females relative to the intercept (i.e. that for males)

[3] Estimate given for body mass effect in females relative to the main effect (i.e. that for males).
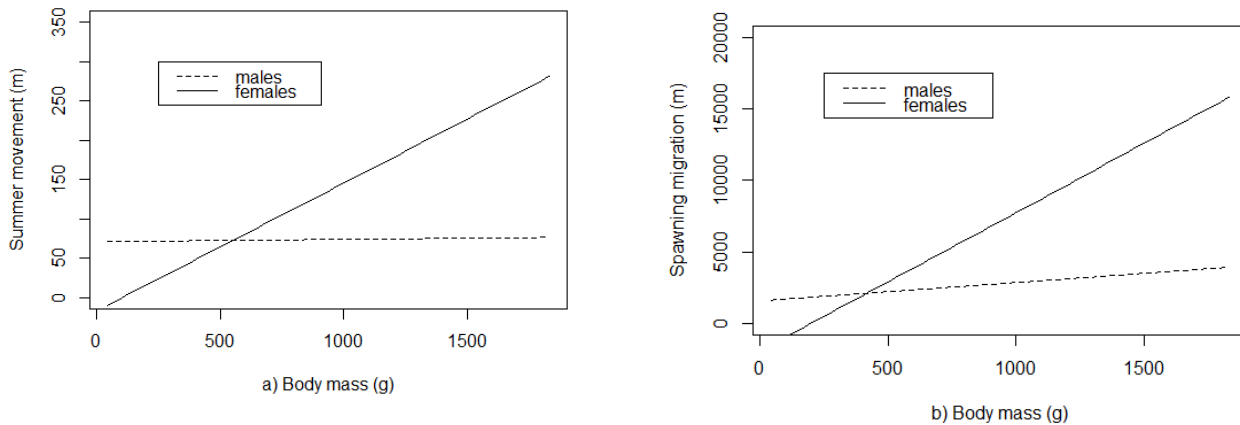

Fig 3. The estimated relationship between body mass and movement for male and female brown trout during **a)** summer movement and **b)** spawning migration.

Spawning migration

Individual spawning migrations varied from staying within one zone to moving 24 kilometres (Fig 4). During the spawning period 40.5% of the brown trout were relatively stationary; either staying within one 500 meter zone or moving between two 500 meter zones. A large proportion, 80.2% of the brown trout moved 5 kilometres or less, while 7.7% moved more than 10 kilometres. The median spawning migration was 1.5 kilometres.
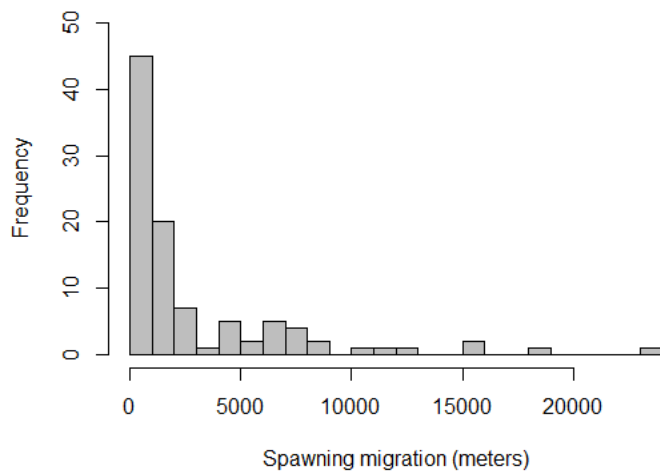

Fig. 4 The pooled distribution of spawning migration distances in brown trout in River Glomma and River Gudbrandsdalslågen.

The comparison of models with different random structures showed no indication of a cohort effect or an effect of tagging site on spawning migration (P≥0.1704). The main terms capture year, K and population were removed as they were not statistically significant in explaining spawning migration distance (P≥0.4480). No remaining terms could be removed (P≤0.032). There was a significant interaction between body mass and sex. Body mass was positively related to spawning migration for females. For males no such relationship was found (Table 2, Fig. 3b).

Table 2 Summary table of a gls model, describing variation in spawning migration distance (meters) of brown trout in River Glomma and River Gudbrandsdalslågen. N=98 individuals.

	Estimates	SE	T	*P*
Intercept	1551.56	950.48	0.92	0.1059
Body mass	1.29	1.40	1.63	0.3599
Sex2[1]	-3533.12	1793.50	-1.30	0.0518
Body mass x Sex2[2]	8.43	3.37	2.50	0.0140

[1] Estimate given for females relative to the intercept (i.e that for males)

[2] Estimate given for body mass effect on females relative to the main effect (i.e. that for males)

Juvenile growth

Juvenile growth was fairly normally distributed for all the four age classes, with few individuals showing either very low or very high growth (Fig 5a-d)

The comparison of models with different random structures showed no evidence of a cohort effect or an effect of tagging site on juvenile growth at either age one, two, three or four (P≥0.1947), hence the gls model was used in the model selection. The model selection showed that none of the main terms sex, summer movement, spawning migration, body mass or population were significantly explaining juvenile growth for any age (P≥0.2019).

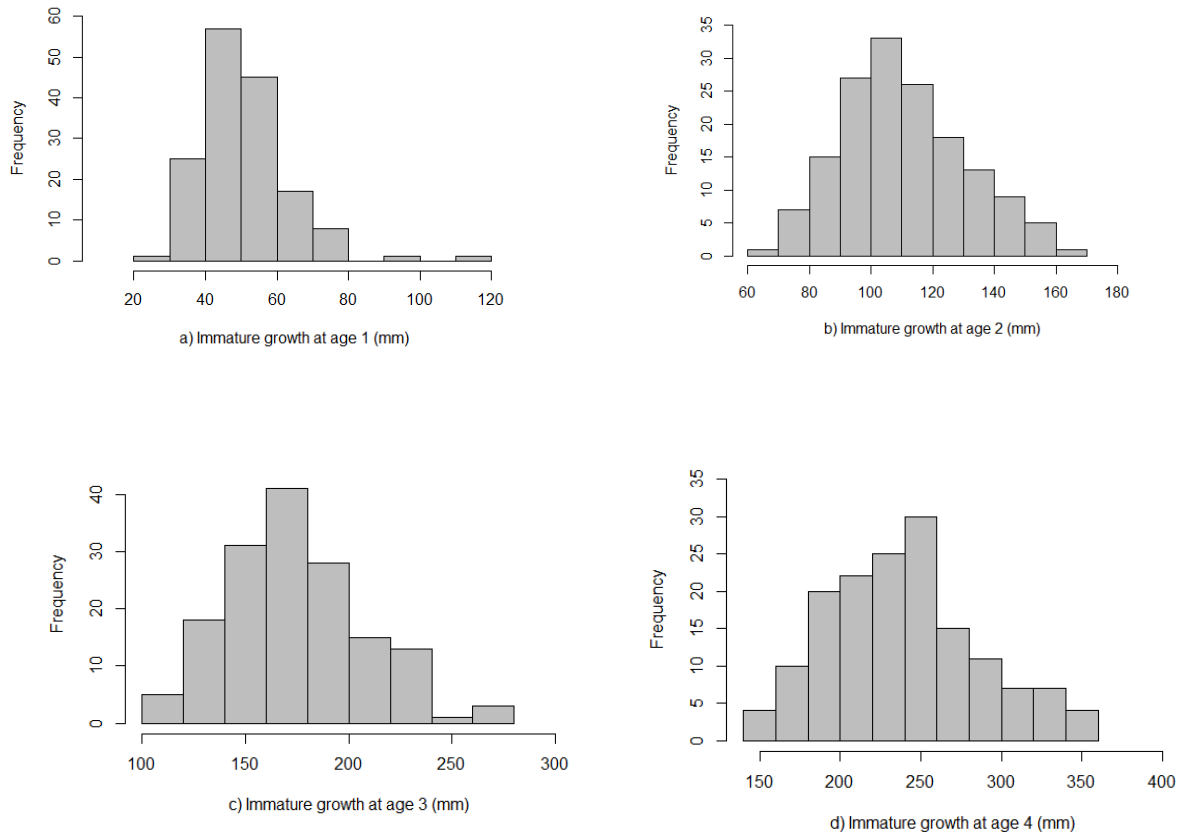**Fig 5.** The pooled distribution of juvenile growth mean±sd for brown trout, for both rivers at **a)** age 1; 51±12 mm **b)** age 2; 111±20 mm **c)** age 3; 174±33 mm and **d)** age 4; 239±45 mm

Mature growth

Mature growth was fairly normally distributed with a mean of 43±2 mm per year and a mean of 34±3 mm per year in the rivers Glomma and Gudbrandsdalslågen, respectively (Fig 6a-b).
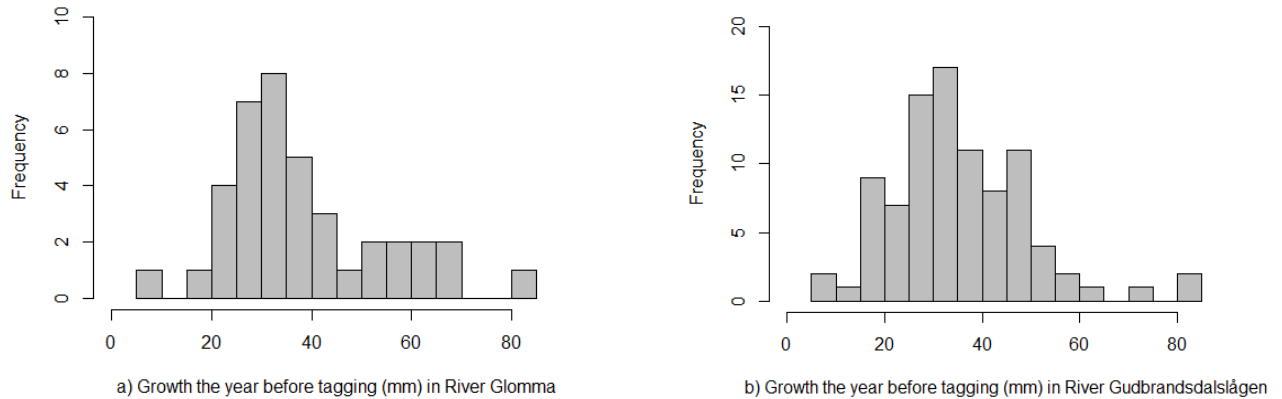

Fig 6. The distribution of mature growth (mm) in **a)** River Glomma and **b)** in River Gudbrandsdalslågen.

There was no indication that tagging site influenced growth after maturation (P=0.9998). Cohort was almost significant (P=0.0501), but the gls model was used in the model selection that followed. The fixed factors summer movement, spawning migration, sex and body mass and did not influence adult growth (P≥0.154). Population could not be removed as it proved significant (P<0.001), reflecting the higher growth in River Glomma than in River Gudbrandsdalslågen.

Discussion

Overall, this study showed that brown trout were relatively stationary as the highest proportion of the fish showed a tendency for low movement activity during the summer months (Fig. 2). The same trend was apparent for spawning migration distance (Fig. 4). This is consistent with other findings, with a large resident part and a smaller mobile part in the fish population (Heggenes et al. 1991; Hesthagen 1988; Knouft and Spotila 2002; Solomon and Templeton 1976). Gowan et al. (1994) however have questioned the terms sedentary and mobile fractions in a population. Movement behaviour may be more plastic, allowing an individual to switch between strategies according to the environment. Harcup et al. (1984) tracked a sample of a fish population for two years and recorded that individuals adapted the degree of movement: mobile fish became resident and the other way around. A common movement pattern for stream salmonids is a high turnover rate, but short movement distance (Gowan and Fausch 1996). This kind of movement pattern may be characterized as ranging behaviour where the individuals leave their current habitat to monitor and seek similar habitats with better feeding opportunities on a large spatial scale (Gowan and Fausch 2002). These kinds of normal exploratory trips may suggest that the use of area is larger than commonly estimated (Smithson and Johnston 1999).

Summer movement

The model for movement in the growth season yields several results. The result indicates that there is less movement in River Gudbrandsdalslågen than in River Glomma (Table 1). The variation in movement in the growth season between rivers may reflect differences in environmental factors like temperature, water discharge and distribution among different habitats – which is reflected in the movement activity between rivers in the growth months. As specific environmental variables have not been recorded and taken into consideration in this study it is difficult to infer which abiotic variables may be most important.

There was also evidence for effects of individual characteristics on movement within populations as the body condition factor (K) was negatively correlated to summer movement (Table 1). There are two potential explanations for this result. First, K may be related to dominance. Studies have shown how dominant individuals reside in the most profitable feeding or breeding areas, and exclude subordinates (Fox et al. 1981; Krebs 1971). Furthermore, Hansen and Closs (2009) demonstrated that subordinate individuals relocated at a higher frequency to other pools than individuals of higher social rank. A reason for the

higher relocation rate can be a "department rule" where a decline in the individual's energy reserves will make the individual more willing to take risks for higher food intake (Railsback et al. 1999). Dominant individuals that reside in the most profitable feeding sites will have a higher food intake and grow faster, because relocation does not always result in higher growth rates (Fausch 1984; Hansen and Closs 2009; Höjesjö et al. 2002). The spatio-temporal distribution of resources has been shown to influence dominance (Grand and Grant 1994; Martin-Smith and Armstrong 2002). Within the 500 meter zone that is applied in this study there can be very different micro – and mesohabitats. Dominance is likely to work on a much smaller spatial scale than what is used in this study, which perhaps makes it more unlikely that dominance is affecting the pattern we see between K and summer movement. An alternative mechanism may be effects of K on food requirement. The relationship between summer movement and K can reflect that individuals in poor body condition must be more active and search for improved resources (Gowan and Fausch 1996; Mesick 1988; Naslund et al. 1993; Nordeng 1983). Hilderbrand and Kershner (2004) found a negative relationship between mobility and condition in stream-dwelling Bonneville cutthroat, this correlation was however in relation to fish of similar lengths in the general population. Mobile and resident individuals did not differ in condition or growth the following year. Due to the spatial scale in this study food requirements may be a more probable cause for the negative relationship between K and summer movement activity than dominance.

Movement activity in females is dependent on body mass, as body mass has a positive effect on the distance moved. Body mass did not influence the distance moved for males (Fig. 3a). To my knowledge, the present study is the first to test for a relationship between sex and body mass on summer movement in salmonids, and the reason for this pattern remains unknown. One might speculate that it is related to differences between the two sexes in size-specific energy requirements associated with spawning. Large females may move more than small ones because they need more energy to account for higher energetic needs to produce more eggs. In general, increased feeding provides larger energy reserves for use during gonadal development (Jonsson et al. 1996). In a study done on brown trout, where both resident morphs and anadromous morphs were taken into consideration, the relative gonadal investment increased with female size. This relationship was not evident for males (Jonsson and Jonsson 1997). In a review by (Fleming 1996) mature Atlantic salmon females (anadromous) were found to invest between 20-25% of their body mass into gonads, whereas mature males (anadromous and parr) only invested 3-6% and 9% of their body mass prior to

spawning, respectively. Thus, the relationship between body mass and sex in relations to summer movement in this study may be a reflection of differences in gonadal investment between the sexes. However, as stated above, one can only speculate as nothing is known about the in gonadal investment between the sexes in the two study-systems.

Spawning migration distance

The potential for movement in both rivers is great as there are no barriers to movement over a large scale. This is reflected in the fact that some of the individuals in River Gudbrandsdalslågen moved more than 20 km to the spawning area and in River Glomma the corresponding figure was over 11 km.

For spawning migration distance there is a positive relationship with body mass for females, however this relationship was not found for males (Fig 3b.). Jørgensen et al. (2008) devised a bioenergetics model for the Northeast Arctic cod stock (*Gadus morhua*) that showed the same relationship for females, where the distance migrated increased with female body size. They only focused on females as the selection pressure on male body size is not well known.

Larger anadromous fish are known to move further upriver than smaller conspecifics of srealmonids (L'Abée-Lund 1991; Schaffer and Elson 1975). Jonsson and Jonsson (2006) examined whether natural tip length had any impact on the distance moved upstream in anadromous brown trout in nine rivers. They did find a trend that there was a positive relationship between standard fish length and distance moved for anadromous fish. No differences were found between males and females.

This effect of body size may be explained by size-specific differences in energetic demands related to swimming, as the cost of swimming is reduced with increased body size (Ware 1978). Thus, overall there may be reasons to believe that given an advantage of long spawning migrations, the optimal migration distance may depend on body size. However, it is not clear why this should differ between sexes, and the reason for the observed differences in effect of body size on spawning migration between males and females in the present study therefore remains unknown.

Juvenile growth

Sex was not significant in explaining any of the variation in immature growth at any age; this is consistent with earlier observations in salmonids where immature male and female brown trout grew at equal rates (Dittman et al. 1998; Jonsson 1989)

Neither summer movement nor spawning migration could be predicted from growth rates experienced as juveniles. Such an effect might have been predicted if growth and movement are positively correlated, and variation in movement among individuals is temporally consistent throughout life. However, this latter assumption may be violated as fish change their behavior throughout life due to ontogenetic shifts (Elliott 1994). Movement abilities are likely to vary considerably as a fish gets larger (Ims and Hjermann 2001; Roff 1991), and there are changes in energy stores and mortality risks (Einum et al. 2006). As stated by Werner et al. (1983) ontogenetic change in resource use among fish is nearly universal. Early life-stages show a tendency for density-dependent dispersal with strong juvenile territoriality (Einum and Nislow 2005). In later age classes differences in movement have been found between males and females (Hutchings and Gerber 2002), between dominant and subordinate individuals (Höjesjö et al. 2007) and among different size classes (Skalski and Gilliam 2000). Few studies take into consideration movement through the entire life cycle of fish. Morrissey and Ferguson (2011) followed one cohort of brook charr (*Salvelinus fontinalis*) in order to study movement throughout the life cycle in Freshwater River. They did not find any evidence of temporally consistent intra-population heterogeneity in movement. Biro and Ridgway (2008) looked at repeatability of foraging tactics in young lake-dwelling brook trout. The repeatability in foraging tactics (pursuit of prey vs. sit-and-wait) was significant: active individuals tended to be active and sedentary individuals tended to stay put, but although the effect was significant, estimated repeatability was relatively low. They concluded that low repeatability indicates considerable within-individual variance in foraging activity over time. Sih et al. (2004) argued that more field studies are needed to discover the extent to which repeatable differences (personality) exists in behaviour, and to infer more about their stability over a life time. This issue has not been studied in brown trout, making it difficult to conclude whether the absence of a relationship between movement and growth in the present study is because these two are not causally related, or whether there are no temporally consistent differences among individuals in movement rates.

Mature growth

In contrast to immature growth, river was a significant factor in explaining some of the variation in mature growth, as mature individuals in River Glomma grew 9 mm more than mature individuals in River Gudbrandsdalslågen the year before tagging (Fig 6 a-b). The difference in mature growth between rivers may be linked to different allocation and quantity of good feeding habitats. Within a population, different growth rate patterns can be shown for different year classes, due to environmental parameters and fish density (Carlson and Letcher 2003; Cucherousset et al. 2005). In this study cohort was almost significant in explaining some of the variation within mature growth. Lack of a significant cohort effect may be due to a small sample size for each year class, which makes it difficult to detect any variance across cohorts.

In the two rivers mature growth was not influenced by sex. For Atlantic salmon, there is abundant support that growth rates differ between mature males and females (Thorpe, 1977). It has been speculated that the variation in growth rates reflects differences in foraging behaviour between the sexes (Holtby and Healey 1990). Differences in foraging behaviour between males and females have not been shown for brown trout, however Greenberg and Giller (2001) found evidence for variation in habitat utilization between mature males and females, independent of size. Neither was mature growth influenced by movement in the growth season. Although there were differences between individuals regarding movement, as the results for summer movement have shown, different strategies may not necessarily mean unequal gain in growth (Wilson 1998).

The distanced covered by a fish during the spawning season could not be linked to the differences in growth experienced by each individual, neither could summer movement. Such an effect could have been predicted if growth and movement were positively correlated. Like juvenile growth, the mature growth model assumes that variation in movement among individuals is temporally consistent throughout life. However, a temporal consistency in the spawning migration distance each year for every individual brown trout has not been proven earlier for brown trout or summer movement. A better estimate for mature growth may be the growth the same year as tagging. The decision to migrate have been linked to growth the same

year, but only for juvenile individuals migrating from natal streams (Acolas et al. 2012) or migrating to new growing environments (Cucherousset et al. 2006; Jonsson 1985).

Fish scale analysis

The growth estimates from scales may also be a source of error as the assumptions for the Lea-Dahl's proportional hypothesis are often violated (Francis 1990; Zivkov 1996). Growth is a complex self-regulating process which will continuously change throughout ontogeny (Zivkov 1996). One assumption is that fish scales are laid down at length zero, However scales are usually formed when the fish is at a minimum length of around 40 mm for brown trout (Jonsson 1976) and some fish may not have reached this minimum length during first growth season and scales are therefore not laid down before the second growth season (Berg and Jonsson 1990). Moreover, at the onset of maturation there will be a trade-off between somatic growth and reproductive investment which will result in stagnated growth (Reznick 1983). These two factors make it difficult to estimate the correct age and growth rate for an individual. Age is often underestimated in older brown trout and the same goes for growth (Berg and Jonsson 1990; Jonsson 1976). Both growth and age estimates may therefore in this study be underestimated. The Lea-Dahl's proportional hypothesis should only be considered a rough aid to estimate growth and the results must be handled accordingly (Nordeng and Jonsson 1978).

One study conducted by Johal et al. (2001) have compared different methods of back-calculating using silver carp (*Hypophthalmichthys molitrix*). They found no significant differences among dissimilar models. Heidarsson et al. (2006) compared the Dahl-Lea model and the Fraser-Lee model (tries to account for the body growth before scale formation) by using Atlantic salmon smolt. They tested if predicted lengths by the two models differed with observed lengths, which is one of the criterion suggested by Francis (1990) for validating different back-calculating models. The comparison suggested that that the accuracy for the Dahl-Lea model is acceptable in back-calculation, although the model overestimated smolt length to some degree. However, the Fraser-Lee model overestimated smolt length even more. It has been argued that one should include both sex and age to get better estimates (Francis 1990; Kielbassa et al. 2011).

Conclusion

The movement pattern for brown trout in the two Norwegian rivers investigated is consistent with previous studies: A large part of the population was found to have a sedentary life style with short distance moved. However, some individuals have long range movement in the growth period and during spawning migration. Consequently, it is important to study movement on a larger scale to avoid biased results against low movement activity. Large spatial scale studies should incorporate environmental data in addition to individual characteristics and more studies are needed to investigate the interaction between sex and body mass on movement.

Stream-living populations have traditionally been considered as a unit of identical individuals (Greenberg and Giller 2001). This assumption is however ignorant as this study and other studies have shown. Brown trout show a high variability in biology and ecology and future studies should take into account individual variation instead of treating it as background noise.

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