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# Movement and growth of European grayling *Thymallus thymallus* in two Norwegian rivers

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# Contents

# Abstract

Growth rate and body size have long been used as surrogate measures of fitness, and particularly for fish. However, many organisms often show a lower growth rate than they are capable of. With an increase in growth rate the time spent feeding also has to increase, and although large body size provides protection against many predators, survival may be significantly lower for fast-growing individuals in the presence of predators. There might therefore be a trade-off between growth and survival, and movement is one trait that may be predicted to increase risk of predation exposure. Movement provides increased opportunity to select the most preferable habitats in terms of prey resources, and hence enable the individuals to track the spatiotemporal variation in environmental quality. Stream-living salmonids tend to have a limited territory at any given time, but the home range a fish utilizes throughout the year is much larger and overlapping with other individuals. Among the salmonids, one of the least well studied species with respect to movement patterns is the European grayling (*Thymallus thymallus*), which is the focal species of the present study. In the present study the aim was to test for correlations between growth rates (both juvenile and adult), post spawning migration distances, and activity during the growth season. This study was performed in two rivers situated in the central and south-eastern parts of Norway. During the period 2008 to 2010, 191 European grayling were caught, where 184 were suitable for growth analysis and 155 were radio-tagged. Radio tagged grayling were positioned once a week from early April until late November. For post spawning migration, model selection revealed that all fixed effects (location, sex, fish condition and body size) could be removed. Furthermore, model selection revealed that all fixed effects (sex, river, condition, body size, and year of capture) could be removed for the summer movement model. Thus, the results provided no evidence for a relationship between movement activity and growth. This conclusion assumes that there is a temporally consistent degree of movement activity between years for each individual grayling, which may be violated. Furthermore, this study does not take into account small-scale movements which may or may not be more important in influencing growth than large-scale movements are. Thus, studies incorporating data with a higher spatial resolution and which simultaneously measure growth and activity are required to corroborate my findings.

# Introduction

For many organisms, and particularly for fish, size and growth rate have long been used as surrogate measures of fitness (Schluter 1995). Therefore selection for rapid growth and a short juvenile period should be expected. However, many organisms often show a lower growth rate than they are capable of (Arendt 1997). With an increase in growth rate, the time spent feeding also has to increase. This will often result in reduced time spent vigilant (Caraco 1979), and although large size provides protection against many predators, survival may be significantly lower for fast-growing individuals in the presence of predators. Fish may therefore alter their behavior to spend more time in less risky, but less food rewarding habitats, causing reduced growth rates (Werner et al. 1983). Due to this potential trade-off between growth and survival, observed growth rate may be lower than what is physiologically possible in a given environment (Gotthard 2000). Furthermore, variation in growth rate can then be predicted to be correlated with traits that influence predation risk.

Movement is one trait that may be predicted to increase risk of predation exposure, but also to influence growth rates (Werner and Anholt 1993). It provides increased opportunity to select the most preferable habitats in terms of prey resources (Gowan and Fausch 2002), and hence enable the individuals to track the spatiotemporal variation in environmental quality (Fausch et al. 2002). Such a correlation between movement and growth has been found over either short time periods (days to weeks), small spatial scale (tens to hundreds of meters) or both (Grant and Noakes 1987; Skelly and Werner 1990; Martin-Smith and Armstrong 2002; Sundt-Hansen et al. 2009). However, less is known about the consistency of such patterns over larger temporal and spatial scales.

Salmonids tend to have a limited territory at any given time, but the home range a fish utilizes is much larger and overlapping with other individuals (Gerking 1959). Jonsson and Jonsson (1993) explains that partial migration (i.e., coexistence of migratory and resident individuals) occurs for several species. Movement is well studied in salmonids, especially for brown trout (Solomon and Templeton 1976) and Atlantic salmon (Cunjak and Randall 1993), and even coupled with growth (Sundt-Hansen et al. 2009). Thus, it seems clear that there exists a significant variation in the amount of movement shown by individual salmonids. Among the salmonids, one of the least well studied species with respect to movement patterns is the European grayling (*Thymallus thymallus*), which is the focal species of the present study. Like all species in the genus *Thymallus* (family Salmonidae), the European grayling favor cold, fast flowing and well oxygenated rivers as well as lakes. In Norway, grayling reach sizes of 60 cm and 3.5 kg. Age at first spawning depends on whether the population is from South, Central or Northern Europe. In the northern parts, spawning usually occurs after their third year of life. Spawning occurs in late May or early June, when the water temperature is around 4-

8 °C. Grayling have a small mouth, so that only the largest individuals include fish in their diet. They mainly feed on drifting plankton, insects and crustaceans (Northcote 1995; Pethon 2005; Kottelat and Freyhof 2007). Research on grayling movement and growth is limited. However, Northcote's (1995) review paper discussed some migration patterns and homing, and concluded that grayling undergo a complex migratory cycle which involves wintering habitat, feeding habitat and spawning habitat.

In the present study the aim was to test for correlations between growth rates (both juvenile and adult), post spawning migration distances, and activity during the growth season. Can patterns of growth be linked to movements on a seasonal/annual scale and over a spatial scale of kilometers? And can movement activity among individuals of older age classes be predicted from growth rates experienced as juveniles? If so, this would suggest that correlations between growth and movement may be maintained throughout life, with different individuals consistently differing in their choice with regard to the growth/survival trade-off. Other interesting questions that will be addressed are whether factors such as population (two rivers studied), sex and fish condition have an effect on movement activity or post spawning migration distance. Because of the one-dimensional nature of streams and rivers, such habitats have been the most productive for animal movement studies (Skalski and Gilliam 2000). European grayling in Norwegian rivers are thus well suited for such studies.

## Materials and methods

**Study sites**

   This study was performed in two rivers situated in the central and south-eastern parts of Norway. More specifically, two substantial river sections without migration barriers constituted the study area. In River Glomma, a 65 km long reach between Røstefossen in Os municipality (6932775 N, 616537 E) and Høyegga in Alvdal municipality (6877763 N, 595286 E). Correspondingly, in River Gudbrandsdalslågen, the 53 km reach between Rosten in Sel municipality (6859695 N, 521680 E) and Harpefoss in Sør-Fron municipality (6827814 N, 544579 E) in addition to the lower 15 km in the tributary River Otta made up the study area.

**Fish capture and telemetry**

   During the period April-October in 2010, 92 European grayling were caught in River Glomma, and 99 grayling were caught during the periods April-May 2008, April-June 2009 and April 2010 in River Gudbrandsdalslågen. All individuals were measured for body size (fork length, ± 1 mm) and mass (± 5 g), and the capture date and location of capture was recorded. Most fish (155) were subsequently radio-tagged and all fish had scale samples taken before being released. Out of the 191 scale samples, 184 were suitable for growth analysis. Radio tagged grayling were positioned once a week, and twice a week during the spawning period within areas where spawning sites were known or indicated by fish behavior. In all three years, during the period from early April to late November, the fish were located by telemetry and assigned to 500 m river zones. Some fish had tags that were still active and could be located the year after tagging, but only the data from the year of tagging was used in this study. All tagged fish were likely to be spawning fish, as European grayling become mature at their third year and will spawn every year after the beginning of their fourth year of life (Hellawell 1969).

   Fish were caught and tagged at a total of 28 localities in the two rivers. However, some localities were merged due to their spatial proximity ($\leq$ 1500 m). In River Glomma eight localities were defined as tagging sites (reduced from the original nine), and in River Gudbrandsdalslågen 15 localities were defined (reduced from the original 19). The tags used were both internal and external radio transmitters manufactured by Advanced Telemetry Systems (ATS). Individual fish with a mass more than 550 g were tagged with an internal transplant (model F1830), whereas smaller individuals were tagged with either an internal transplant (model F1580) or external attachment (model F1970). The transmitters were in all cases less than 2% of the fish body mass (Mellas and Heynes 1985; Thorstad et al. 2000). All fish used in this study were anaesthetized by water administered 2-phenoxyethanol (0.7 ml l$^{-1}$) before they were placed in a cylindrical tube with well oxygenated water (external transmitters),

or placed with the ventral side upwards in a V-shaped operation device (internal transmitters), for swift attachment of the transmitters.

A Challenger Receiver (model R2100, manufactured by Advanced Telemetry Systems, USA) and a three-element folding Yagi antenna (model 12762) were operated from a car, and occasionally on foot. The telemetry study was approved by the National Animal Research Authority in accordance with national legislation. All telemetry data and fish scales were provided by NINA Lillehammer (Jon Museth).

**Fish scale analysis**

To analyze the fish scales, they were first photographed with a Nikon Ri1 camera fitted to a microscope. The analysis itself was done with Image Pro Plus. Based on winter and summer growth zones (sclerites), age of the fish and the scale growth for every year was estimated (fig. 1). Based on these estimates, body sizes at age were back-calculated for individual fish assuming proportional growth where the ratio between body size and scale radius is assumed to be constant through life (Francis 1990; Pierce et al. 1996). The grayling scales are somewhat irregular compared to scales from other salmonid fish species like salmon and trout. It was decided that the best distance to measure the scales was to choose the second outermost edge to the right (anterior transect, fig. 1). One reason for this is that this distance in most scales is perfectly linear when drawing a line from the center to the edge of the scale (compared to the diagonal transect).
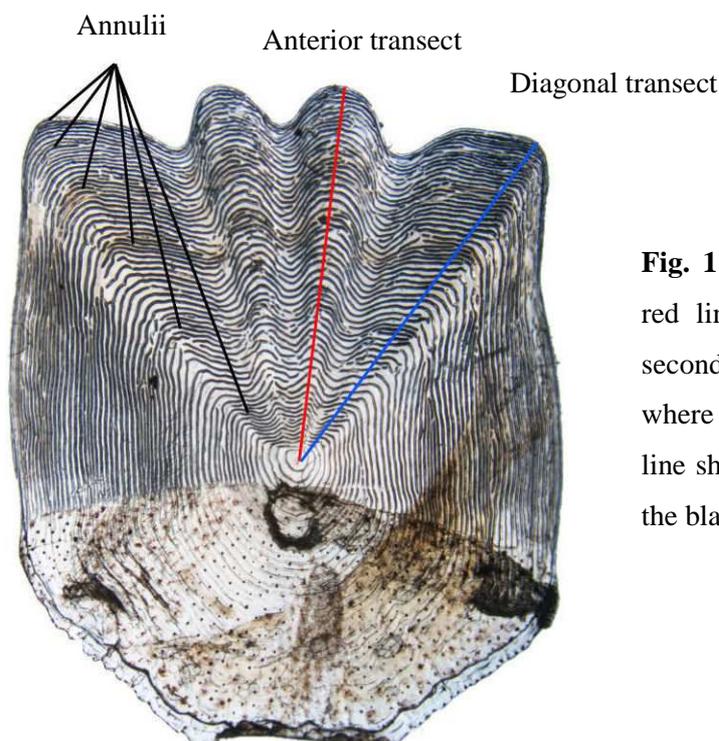


**Fig. 1** A typical European grayling scale. The red line from the center of the scale to the second outermost edge (anterior transect) is where the measurements were taken. The blue line shows the diagonal transect (not used), and the black lines indicate the annuli.

**Movement and growth measurements**

First, the distance of the post spawning migration was calculated, which was defined as the largest absolute distance between positions observed during the spawning period and the growth period. In River Glomma the combined spawning and summer period was between May 13th and October 4th, while in River Gudbrandsdalslågen this period was between May 25th and September 30th. The reason for the different start dates of these calculations was that spawning commenced during late May in River Glomma, and in early June in River Gudbrandsdalslågen, respectively (Museth et al. 2011, 2012). Any fish tagged after mid May (Glomma) or late May (Gudbrandsdalslågen), or lost before the end of September were excluded, giving a total sample size of 100 individuals.

Furthermore, the average daily large-scale movement in the rivers over the growth season (defined to include the months of July, August and September) was calculated, hereafter termed summer movement. For each interval between two observations for a fish, the distance moved and the number of days in the interval was used to calculate minimum distance moved per day. The average was then calculated from these intervals for each fish. This period was chosen to exclude potential post spawning and winter migrations. Any fish tagged after June or lost before the end of September were excluded, giving a total sample size of 101 individuals.

In this study, juvenile growth was defined as the estimated body size achieved at the end of their third year of life. After this, fish growth (mm year$^{-1}$) declined (fig. 2), as they became mature and spent resources on reproduction. It was possible to estimate growth data for 178 fish.

As not all fish were located every week, the number and length of observation intervals varied. It was tested if this affected post spawning migration and summer movement, but there was no significant effect of the number of observations.
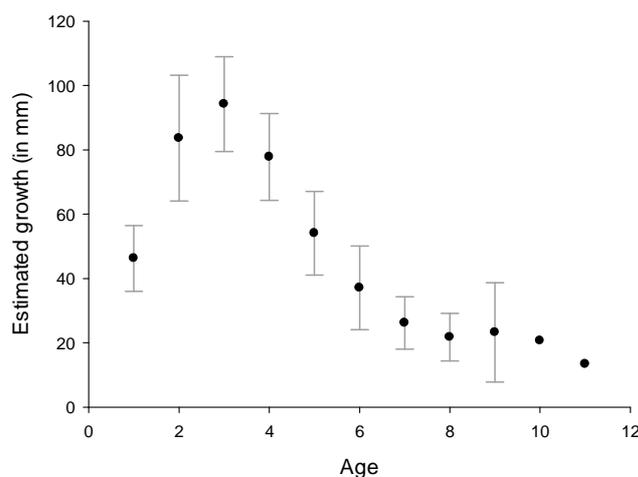


**Fig. 2** Estimated annual growth (mm during preceding year) for European grayling in the rivers Glomma and Gudbrandsdalslågen. Dots represent mean growth, lines are ±SD.

**Statistical analyses**

All statistical analyses were conducted using the statistical software R, v. 2.12.1. (R Development Core Team 2011). We used a model selection approach to obtain the best models according to Zuur et al. (2009). For post spawning migration, the full model consisted of the fixed effects sex, location of capture, fish condition (K) and body size, whereas cohort was entered as a random effect. For summer movement, the full model consisted of the fixed effects sex, river, year of capture, fish condition (K) and body size, with location of capture and cohort entered as random effects. The reason for entering location of capture as a fixed effect for post spawning migration was that this effect is probably more important than the effect of the difference between the rivers.

Variation in growth rates as dependent variables were then modeled. Growth post maturation was modeled with estimated total body size the year before capture, post spawning migration, summer movement, sex and river as fixed effects, and location of capture and cohort as random effects. For juvenile growth, fixed effects were summer movement, post spawning migration, sex and river, and location of capture and cohort as random effects. Since the measurement of post spawning migration and summer movement were correlated (61.6%), a VIF test was done to see if both explanatory variables could be included in the same model. The GVIF value was 1.61, and it was decided to include both variables. The limit for not including both is when the GVIF value is above 2 (Zuur et al. 2010).

# Results

**Post spawning migration**

Most fish performed a fairly short post spawning migration, with 45% migrating 3 km or less. Some fish, however, migrated much longer distances, with 24% migrating more than 10 km. Only a few individuals (8%) migrated more than 20 km (fig. 3).

The best model for post spawning migration is a simple linear model, compared to the model with one random effect ($\Delta$AIC = 2.00). Model selection revealed that all fixed effects could be removed (p = 0.06 for location, p > 0.29 for sex, condition and body size) from the model of post spawning migration distance.
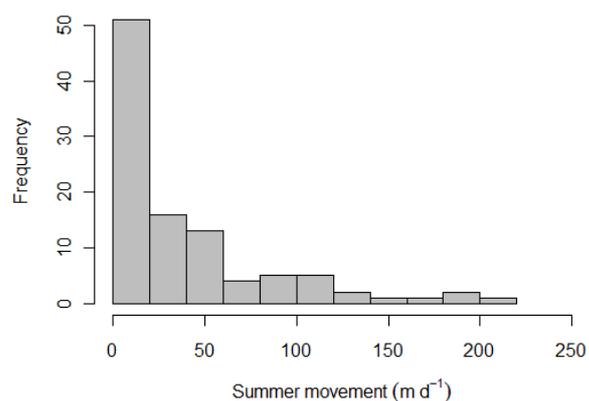
**Summer movement**

As expected, most fish performed a fairly restricted summer movement, with 66.3% moving 40 meters per day or less. Some fish, however, were much more active, with 11.9% moving more than 100 meters per day. Only a few individuals (4.9%) travelled more than 150 meters per day (fig. 4).

The simple linear model was considerably better than the three mixed effect models ($\Delta$AIC $\leq$ 2.00). As for post spawning migration, model selection revealed that all fixed effects (sex, river, condition, body size, and year of capture) could be removed (p > 0.19 for all). Hence, none of the factors investigated seemed to affect summer movement (fig. 5).
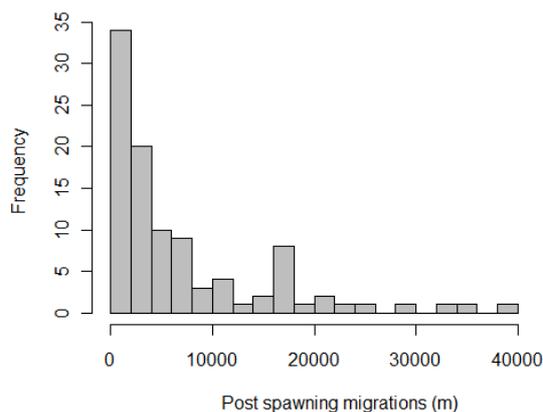


**Fig. 3** The distribution of spawning migration distances in European grayling in River Glomma and River Gudbrandsdalslågen.

**Fig. 4** The distribution of summer movement in European grayling in River Glomma and River Gudbrandsdalslågen.
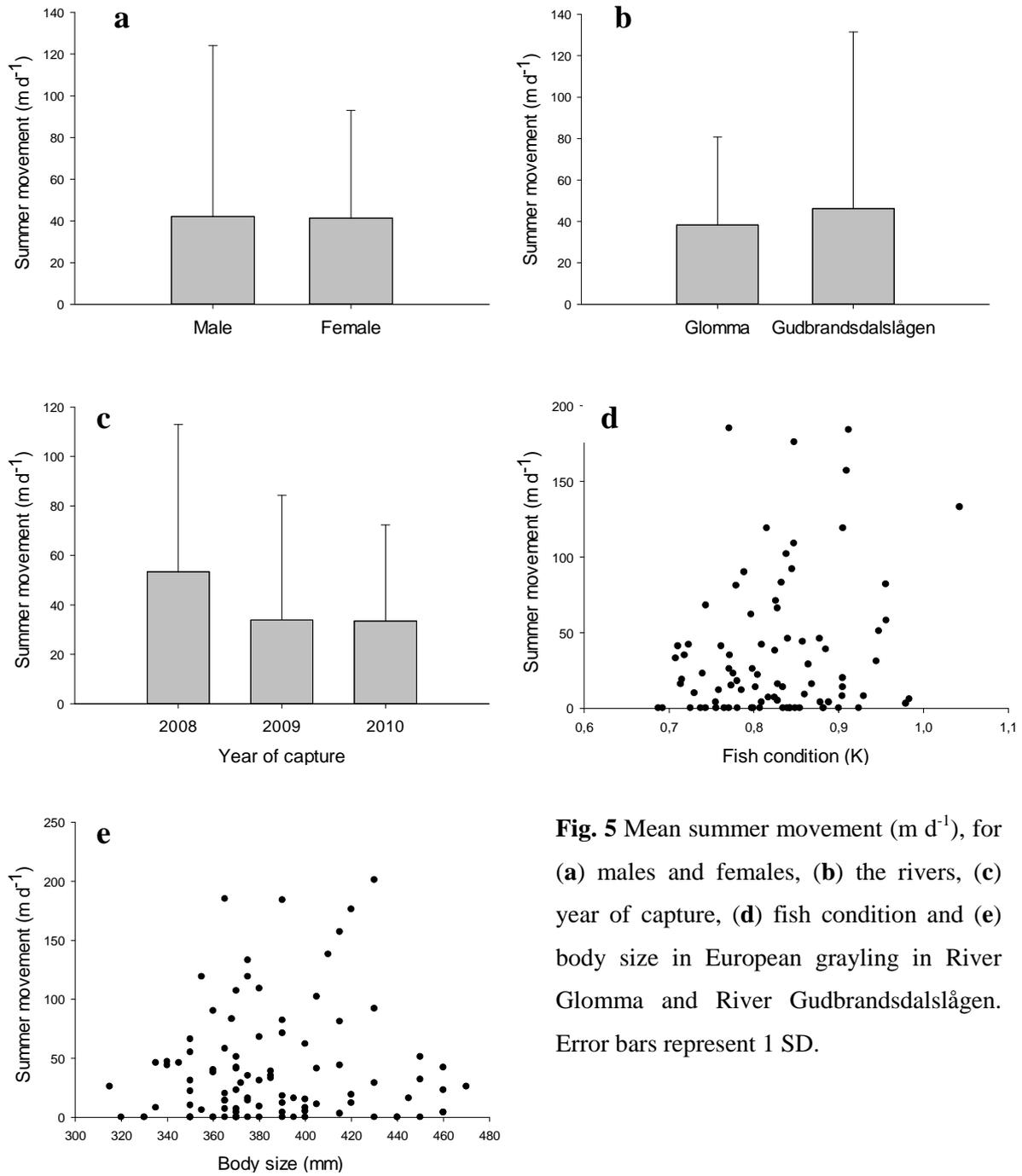
**Fig. 5** Mean summer movement (m d$^{-1}$), for (**a**) males and females, (**b**) the rivers, (**c**) year of capture, (**d**) fish condition and (**e**) body size in European grayling in River Glomma and River Gudbrandsdalslågen. Error bars represent 1 SD.
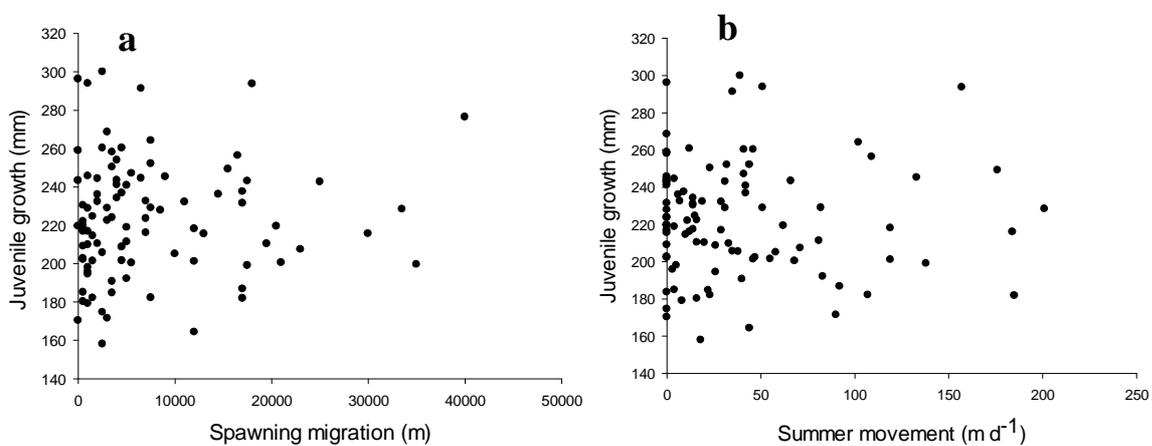
**Juvenile growth**

As expected, juvenile growth distribution seemed to be fairly normally distributed, with few individuals showing very low growth and a few with high growth (fig. 6).

When testing which factors that may affect juvenile growth, the model including both location of capture and cohort were considerably better than models with just one or no random effects ($\Delta$AIC $\leq$ 3.8). Model selection revealed that river, sex, post spawning migration and summer movement could be removed (p > 0.24 for all). Thus, none of the fixed effects seem to affected juvenile growth (fig. 7).
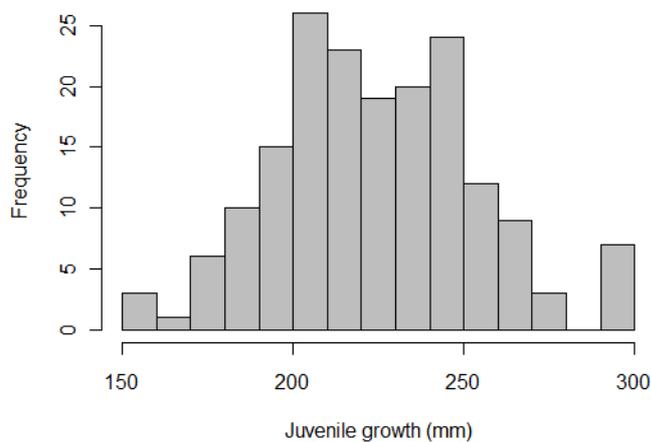


**Fig. 6** Distribution of juvenile growth for European grayling in River Glomma and River Gudbrandsdalslågen.



**Fig. 7** Distribution of juvenile growth with respect to (**a**), post spawning and (**b**), summer movement in European grayling in the rivers Glomma and Gudbrandsdalslågen.

**Growth post maturation**

As expected, the body size of the fish affected its growth, and the term is necessary in the model selection (fig. 8). When testing which factors affect growth the year before tagging (mature growth), the models including both random effects were considerably better than models with just one or no random effect ($\Delta$AIC $\leq$ 8.3). Model selection revealed that summer movement, post spawning migration and river could be removed from the model (p > 0.37). In contrast, sex and estimated body size the year before capture could not be removed (p < 0.0001 for both).

This model was refitted with all data that had the required information (i.e. increasing the sample size from 90 to 147 individuals). For this new model only cohort was included as a random effect ($\Delta$AIC $\leq$ 4.1), but the same fixed effects remained significant. According to this model, growth decreased with size, and growth was slightly better for males than for females (Table 1).

**Table 1** Summary of the linear mixed effect model with only cohort as random effect. This shows that only the initial length before that year and the sex affect growth the year prior to capture.

|  | Estimate | t | P |
|---|---|---|---|
| Intercept | 141.86 | 13.09 | < 0.0001 |
| Body size | -0.28 | -10.04 | < 0.0001 |
| Sex (male) | 4.51 | 2.17 | 0.0315 |
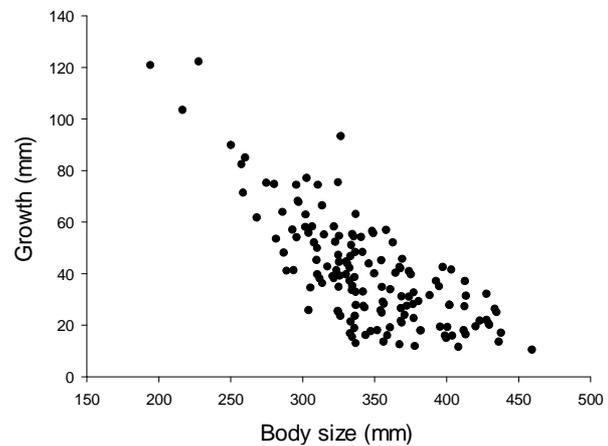


**Fig. 8** The estimated body size of European grayling in River Glomma and River Gudbrandsdalslågen the year before tagging with respect to growth the year before tagging.

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# Discussion

My results indicate that there is no relationship between juvenile growth, summer movement and the distance of post spawning migrations in European grayling. For juvenile growth there also seems to be no significant difference between the sexes, or between fish in two studied rivers. For post spawning migration distance, neither fish condition nor body size showed any significant effect. Similarly, neither river, fish condition, body size, nor year of capture has any significant effect on summer movement. After maturation, the growth was slightly better for males than for females.

**Growth**

Acolas et al. (2012) found that increased growth rates in juvenile brown trout was positively correlated to observed migration rate, probability of migration and winter survival. Furthermore, they concluded that body size was not a key factor for the decision to migrate. This may support my findings that adult post spawning migration distance is not affected by body size. The model for growth after maturation showed no significant effect of post spawning migration distance. This suggests that there is no correlation between how far an adult migrates after spawning and the subsequent growth rate that it achieves. However, because the data for this analysis consisted of growth rate for one year and post spawning migration distance in the subsequent year, this assumes that that there is a temporally consistency in the length of post spawning migration between the years for each individual grayling. This assumption is likely violated as such consistency is not previously known for grayling.

Similarly, the test of a relation between juvenile growth and summer movement activity relies on the assumption of individual differences in activity that are consistent throughout life, since my measures of activity were at the adult stage. This assumption will not be true if individuals differ in how their movement activity changes throughout their lives, or are influenced to different extents by predator presence or other external factors. It is likely that fish will change their behavior in many ways through different stages of their life cycle. Morrissey and Ferguson (2011) concluded that for brook char, "heterogeneity in individual movement of adults is not representative of patterns of movement throughout the life cycle". If this conclusion is also valid for European grayling, my design would fail to find positive relations between movement and growth even if such relationships are present within years.

**Post spawning migration**

The number of suitable spawning habitats for European grayling is likely to be limited due to specific habitat requirements for their eggs in terms of water velocity and gravel size (Fabricius and Gustafson 1955; Gonczi 1989; Maitland and Campbell 1992) . Requirements for suitable summer

habitats may be less specific, so that larger sections of the rivers will likely be utilized during summer. There is an indication that the overwintering site selected by the fish will affect the distance of the post spawning migration. The reason we did not get a significant result for location of capture is that there is a large number of localities (23), and most contain very few fish (mean number of fish at each location ± SD is 6.7±4.5). Thus it is reasonable to assume that distances to suitable summer habitats will vary among different spawning habitats. However, I have not been able to test whether the distance of the spawning migration affects the post spawning migration distance, but it seems that grayling prefer spawning habitats close to the winter habitat. Taking account of the spawning migration distance or the spawning site location will reveal if the overwintering location has an effect on the post spawning migration. European grayling in the British Isles migrate from slow flowing river sections to faster flowing tributaries to spawn (Maitland and Campbell 1992), and Arctic grayling in North America have been recorded to spawn in the main river under the turbid conditions of spring flood (Schallock 1965). Such floods occur every year in both River Glomma and River Gudbrandsdalslågen, and will affect suitable spawning habitat for grayling.

**Summer movement**

This study does not take into account small scale movements which may or may not be more important for European grayling than large-scale movements. Very different micro- and mesohabitats are likely to exist within each 500 meter zone. In some river sections, long stretches may contain suitable feeding habitats, whereas in other sections suitable habitats may be much more patchy. If an individual fish occupy a part of the river with a large continuous feeding habitat, it may most likely be stationary, whereas an individual fish in a more patchy habitat will be forced to move more frequently. A result of this may be that summer movement might not be consistent between years for individual fish.

Museth et al. (2012) did show that there is some genetic variation between the different parts of my study area in Glomma, and Junge (2011) could show the same for Gudbrandsdalslågen. Both concluded that the small genetic difference is caused by "isolation-by-distance" and that the grayling in each of the rivers do not consist of separate spawning populations. My data also show that there is a substantial movement of grayling in the river. The spawning biology of grayling may play a role in this. Northcote (1995) mentions that female graylings do not construct redds, and that the eggs are lodged about 3 cm into the gravel. After emerging the fry are small and weak swimmers. Both eggs and fry are therefore subject to passive downstream drift, and combined with subsequent active migration the fish might end up in very different sections of the river for their first winter. Both the genetic studies and the possible large downstream drift of juveniles might explain the random pattern in grayling movements. Several studies have reported reproductive homing for both European (Witkowski and Kowaleski 1988; Kristiansen and Doving 1996) and Arctic (Vincent-Lang 1990) grayling. However, these patterns seem complex and with much regional variation. Less is known

about habitat fidelity for feeding habitats and other trophic migrations. Most spawning migration studies have been conducted in tributaries to big rivers or lakes. There is reason to assume that reproductive homing is less strong in systems where the grayling spawn in the main river like River Gudbrandsdalslågen and upper parts of River Glomma, as physical and chemical cues might be more homogenous. Because of this, even trophic migrations might vary from year to year for any individual fish. In young Atlantic salmon the downstream movement patterns are well studied (Fleming and Einum 2011), and Naesje et al. (1986) found significant drift of both cisco (*Coregonus albula*) and whitefish (*C. lavaretus*) larvae during the spring flood in Gudbrandsdalslågen. However, little is known about downstream migrations of young European grayling. Important causal mechanisms for movement in other studies have been identified as temperature (Zimmer et al. 2010), water flow (Popoff and Neumann 2005), environmental heterogeneity (Gowan et al. 1994) and anti-predator behavior (Young 1995). Without accounting for these factors in the present study it may be difficult to link summer movement to both growth and other variables.

**Fish scale analysis**

One source of error in the study is likely to be growth estimation of the fish. Although there are several guidelines when it comes to determining age and growth based on fish scales, there is no true model that fits all fish species. Hurley et al. (1997) concluded that the diagonal transect of the scale is harder to read compared to the anterior transect in ctenoid scales (fig. 1). They also discussed that there is in many cases a significant difference between back-calculated lengths when using the different transects, however this is not likely to affect the growth assessment. In this study we have reasons to believe that the second outermost edge from the right (anterior transect) is the best choice in European grayling, as it is observed to be the less irregular than the diagonal transect or any other edge (fig. 1). In addition, the radius to this edge is easier to read compared to any other edge. Horka et al. (2010) found that it is common to underestimate age when reading grayling scales, as the annuli formation can be hard to detect during the later years when the growth rates of the fish decreases. However, this problem was mostly avoided in this study as we were mainly interested in the early growth of the fish, and the first few winter annuli formations were easily identified. Zivkov (1996) reported that there are several problems with the assumption of proportional growth when back-calculating fish growth. They found that the ratio between fish length and scale radius will differ both between fish and within fish dependent on age. As a result of compensatory growth in fish, this ratio, in particular, varies a lot for juvenile fish from year to year. In this study this problem was mostly avoided as the fish length after the third year of growth was used as an estimate of juvenile growth rate. Any compensatory growth in the juvenile period is therefore not likely to affect my results.

In the two Norwegian rivers investigated, as well as in many other rivers, fish movement and growth is determined by variation in both environmental and life-history. On the large spatiotemporal

scale used in this study, any connection between summer movement and growth may be difficult to find. Migration models are probably more suitable with data that include such large-scale movements, whereas during the summer when grayling are more stationary, models may call for much more detailed movement registrations. Thus, studies incorporating data with a higher spatial resolution and which simultaneously measure growth and activity are required to corroborate my findings.

## Acknowledgements

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