



Hedmark University College

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## Master thesis

Habitat selection and longitudinal distribution patterns of sympatric sub-adult trout (*Salmo trutta*) and grayling (*Thymallus thymallus*) in two large northern rivers.



Master in Applied Ecology

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## Abstract

Compared with wadeable streams there is little knowledge on habitat selection and distribution patterns of sub-adult fish in large rivers, because fish sampling and habitat measurements in large rivers are methodically challenging and require a high effort in order to reduce bias. In my thesis I studied habitat selection and longitudinal distribution patterns of sub-adult (<3 years, sorted by: 0+, 1+ and 2+) trout (*Salmo trutta*) and grayling (*Thymallus thymallus*). Fish sampling and habitat measurements were conducted with transects (approx. 500 m in length) in two large river sections (>10 km) that differed in valley confinement and gradient. Habitat selection were analyzed with AICc model selection, while longitudinal distribution patterns were analyzed by testing if fish abundance had a linear or non-linear response to distance from the upmost spawning ground. Segregation in habitat preference between sub-adult trout age-classes indicated intraspecific competition, whereas trout 0+ had a low abundance in areas with high substrate coarseness in contrast to trout 2+. Abundance of sub-adult grayling was associated with areas of reduced valley confinement and river gradient. This caused grayling 0+ and grayling 1+ to have an increasing non-linear relation to distance from the upmost spawning ground in the confined and high gradient river Otta. A similar distribution pattern was observed for trout 0+ in Otta, in contrast to trout 2+ which displayed a simple linear decrease in abundance from the upmost spawning ground. In the unconfined low gradient river Lagen, none of the species age-classes expressed a distribution pattern related to distance from the upmost spawning ground, indicating that the effects of a high valley confinement and river gradient in Otta was the predominant drivers of longitudinal distribution patterns.

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**Key words:** distribution patterns, habitat selection, large rivers, Gudbrandsdalslågen, Otta, *Salmo trutta*, *Thymallus thymallus*

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# 1. Introduction

The species composition of lotic ecosystems is strongly influenced by physical habitat, which is defined by large scale drivers including; geology, climate, geomorphology and vegetation (Frissell, Liss, Warren, & Hurley, 1986). However, human alterations of freshwater ecosystems caused by hydropower production, agriculture, industry and other society needs have had a severe impact on many rivers (Poff & Ward, 1989; Müller, 1996; Poff et al., 1997; Ward, Tockner, & Schiemer, 1999; Allan, 2004; Freeman, Pringle, & Jackson, 2007; Döll, Fiedler, & Zhang, 2009). The impact of anthropogenic effects on lotic ecosystems is generally most noticeable in larger rivers (main channel >2 meters deep, wetted width >30 meter, mean annual discharge >30 m<sup>3</sup> s<sup>-1</sup>) and lakes due to their high economical and social value (Postel, 2000). In order to mitigate for the wide range of river alterations, several measures have been implemented to preserve and restore habitat quality, hydrological functions and connectivity. However, each river differs to some degree in the way they respond to anthropogenic changes, which causes management agencies to depend on extensive watershed and river assessments to understand and predict the effects of river alterations (Pess et al., 2003; Roni & Quimby, 2005; Palmer, 2009). Additionally, management agencies must cope with the fact that there is still a much uncertainty linked to many different fish species` habitat preferences and life history-dynamics in large rivers. Compared with smaller rivers, streams and tributaries (i.e. wadeable streams), fish sampling and habitat measurements in large rivers are methodically challenging and require a high effort in order to reduce bias (De Leeuw et al., 2007; Tomanova, Tedesco, Roset, Berrebi dit Thomas, & Belliard, 2013). As a result, wadeable streams have been studied to a greater degree than larger rivers, especially studies that examine the distribution and composition of different juvenile fish species`. Understanding the role of wadeable streams is of great importance, however knowledge gained from such studies is not necessarily transferable to larger rivers. A better understanding of habitat preferences, spatial distribution and migration patterns of sub-adult fish in large rivers is therefore of crucial importance in order to understand and predict the potential impact of river alterations. This is also explicitly emphasized as objectives in the “Hydropower and connectivity in inland rivers” (RIVERCONN) project, which was designed based on the implementations of the EU water framework directive (WFD) (Directive 2000/60/EC).

My study describes habitat preferences and longitudinal distribution patterns of sympatric sub-adult (<3 years) trout (*Salmo trutta*) and grayling (*Thymallus thymallus*) over larger spatial scales, in two large and connected northern rivers; Gudbrandsdalslågen (hereby Lagen) and Otta. These rivers are highly different in valley confinement and river gradient, with Lagen representing a slow flowing, un-confined, low-gradient river and Otta a fast flowing, high- to medium-confined, high-gradient river. Just downstream of migration barriers in the upmost parts of the study area in both rivers there is a large spawning ground for grayling and trout. This design entailed for a study area where I could assume a certain overview of each species' upmost area of sub-adult distribution, even though adult fish downstream movement from upper areas of the rivers has been documented (Junge, Museth, Hindar, Kraabøl, & Vøllestad, 2013).

As with other fish species' within lotic ecosystems, habitat preferences and distribution patterns of sub-adult trout and grayling have mainly been described in wadeable streams and experimental stream channels (Maki-Petäys, Muotka, Huusko, Tikkanen, & Kreivi, 1997; Sempeski, Gaudin, & Herouin, 1998; Greenberg, 1999; Roussel & Bardouet, 2002; Vehanen, Huusko, Yrjana, Lahti, & Maki-Petäys, 2003; Jones & Tonn, 2004; Nykanen & Huusko, 2004; Heggenes & Wollebæk, 2013). Studies conducted on sub-adult trout and Atlantic salmon (*Salmo salar*) in larger rivers indicate that the most important habitat feature is access to cover structures (i.e.: substrate cavities, woody debris, undercut river banks and aquatic vegetation), which is similar to the results of studies conducted in wadeable streams. However, substrate cavities associated with coarse substrates (cobble and boulders) seems to be of even greater importance in larger rivers (Heggenes & Saltveit, 1990; Greenberg, Svendsen, & Harby, 1996). The abundance of younger trout age-classes are also known to differ with depth, whereas young of the year trout (trout 0+) and to some degree trout 1+ prefer shallower edge habitats than trout 2+, which are assumed to be caused by intraspecific competition and predation risk (Heggenes & Saltveit, 1990; Greenberg et al., 1996; Greenberg, 1999; Heggenes & Wollebæk, 2013). Knowledge of habitat preferences for grayling sub-adults in large rivers is based on behavioral studies and point sampling, and these studies show that sub-adult grayling prefer shallow edge habitat with water velocities of 10-20 cm s<sup>-1</sup> (Northcote, 1995; Sempeski & Gaudin, 1995; Greenberg et al., 1996; Nykanen & Huusko, 2003).

In my study I conducted fish sampling with an electrofishing boat, and was therefore able to conduct larger transects (approx. 500 m) and effectively cover the distance of two larger stream systems (>10 km). Because the start of my study sections in both rivers was in the

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approximate upmost area of distribution for sub-adults, I was also able to describe cross gradient longitudinal downstream distribution patterns from the upmost spawning ground. Studies conducted in wadeable streams and experimental stream channels indicate that water velocity influences the level of downstream displacement of sub-adult trout and grayling (Ottaway & Clarke, 1981; Ottaway & Forrest, 1983; Bardonnet, Gaudin, & Persat, 1991). It has therefore been speculated that valley confinement and river gradient, which are two of the primary determinants of water velocity and substrate coarseness (Bisson & Montgomery, 1996; Benda et al., 2004), may have a strong effect on the downstream displacement of post-emergent trout and grayling. If such downstream displacement does occur, then there should be noticeable differences in the longitudinal distribution patterns of sub-adults between Lagen and Otta, because of the large differences in valley confinement and river gradient between these two rivers.

More specifically my study attempts to answer the following questions:

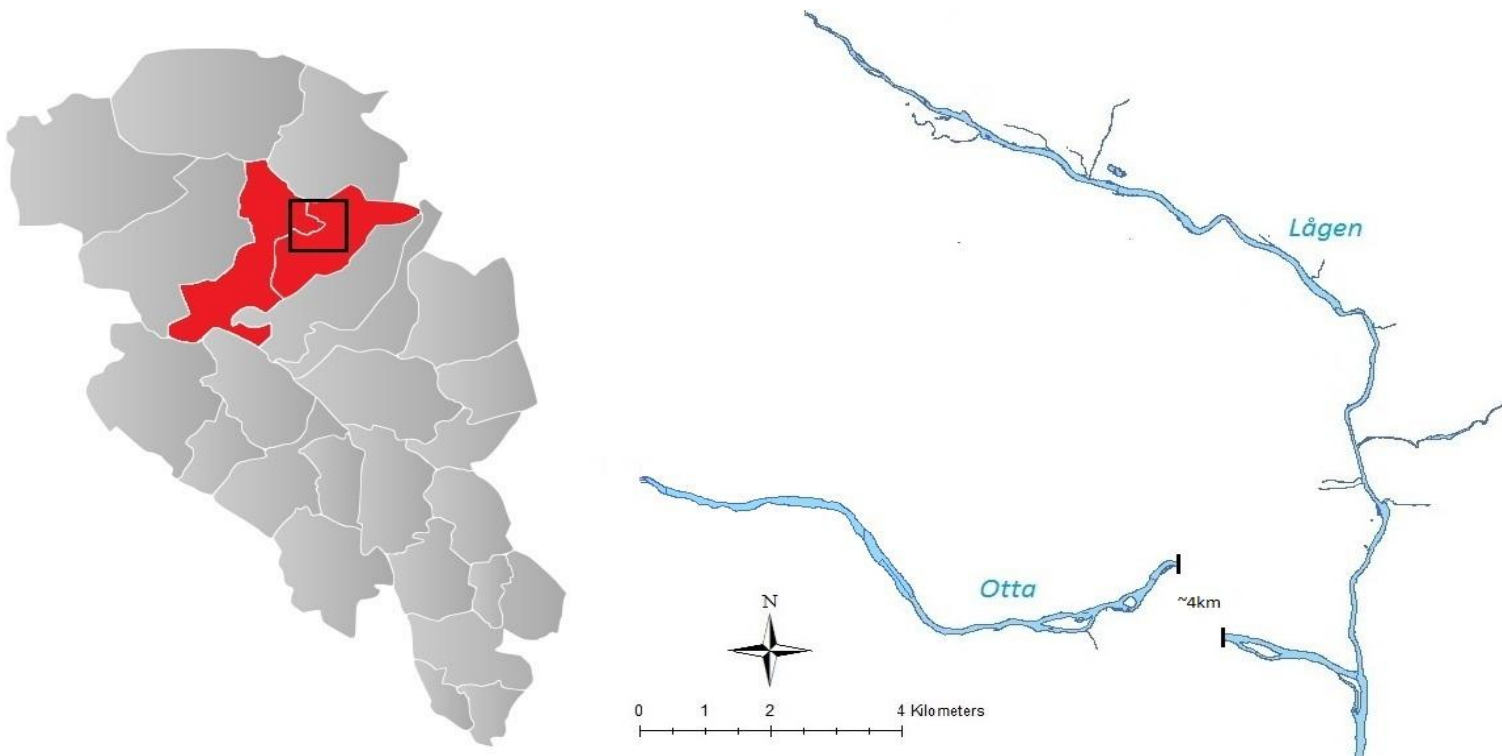
- A. What habitat conditions are associated with sub-adult trout and grayling in large northern rivers?
  - Prediction 1: Density of sub-adult trout is expected to be positively associated with coarse substrates.
  - Prediction 2: Density of sub-adult grayling is expected to be positively associated with low levels of valley confinement and river gradient, and a shallow edge habitats.
  
- B. Is there a difference in habitat preference between age-classes of sub-adults?
  - Prediction 1: I expect that known factors such as intraspecific competition and predation risk would cause segregation within sub-adult trout, whereas trout 0+ were expected to be associated with shallower edge habitats than trout 1+ and trout 2+.
  - Prediction 2: Intraspecific competition is not known to occur within grayling sub-adults. I therefore did not expect difference in habitat preference between sub-adult grayling age-classes.
  
- C. What are the differences in longitudinal distribution patterns of sub-adult trout and grayling between two rivers?
  - Prediction 1: Because sub-adult trout are known to utilize substrate cavities as cover from water velocity I do not expect sub-adult trout to have any longitudinal distribution patterns in Otta and Lagen, because habitats with coarse substrates were evenly distributed in both rivers.
  - Prediction 2: Because sub-adult grayling are not known to utilize substrate cavities, I expect sub-adult grayling to have a positive non-linear distribution in Otta (i.e. rapid increase in abundance in the lower areas of Otta where valley confinement and river gradient has decreased). I do not expect grayling to have any pattern of longitudinal distribution in Lagen due to the generally low level of valley confinement and river gradient.

## 2. Area description

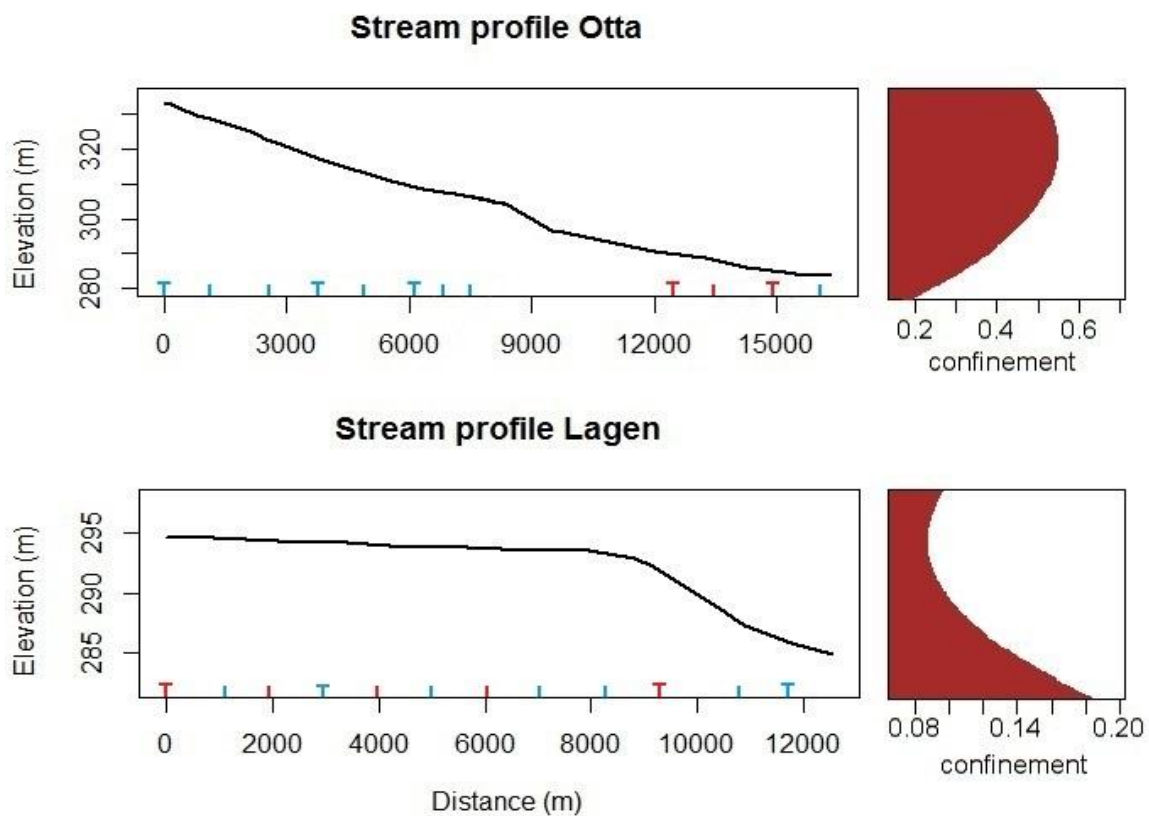
The river Lagen in Oppland County has its source in Lesjaskogsvatnet (611 m.a.s.l) in the municipality Lesja at the most northern part of the valley Gudbrandsdalen and ends up in Norway's largest lake, Lake Mjøsa, in Lillehammer municipality. Lagen is 204 km long with a watershed of 11459 km<sup>2</sup>, which counts for approximately 70% of lake Mjøsa's watershed. The Otta River has its source in the southern part of Lake Djupvatnet (1016 m.a.s.l) in Stranda municipality in Møre & Romsdal County and it joins with Lågen in the confluence near Otta city in the municipality Sel. Otta is the largest tributary to Lagen and Otta actually has a larger annual discharge than Lagen at the confluence of these two rivers. Otta is 147 km long and has a watershed of 4011 km<sup>2</sup>. River Bøvra in Lom municipality is Otta's largest tributary, while rivers like Måråa, Vulu, Tora, Glitra, Framruste, Ostri, Skjøli and Aura are other important tributaries higher up in the Otta watershed (Figure 1).

My study area was from the Lagen/Otta confluence and continued approximately 12 km upstream in Lagen and 15 km upstream in Otta. The Lagen reach had a low river gradient (overall slope of -0.08 m per 100 m in study area) and were predominantly unconfined by the valley. The main riverbed substrate composition was dominated by sand and gravel, but with frequent occurrence of coarse boulders along the riverbank. Historically, Lagen was a more meandering river with greater floodplain connectivity than it is today. Today, the river is channelized and large boulders have been introduced in order to improve riverbank stability. How these alterations have affected the fish populations in Lagen is unknown since there are little data collected prior to this period. The study area of river Otta has a medium to high river gradient channel (overall slope of -0.31 m per 100 m in study area) with a greater heterogeneity in different habitat-types (i.e. pool, run, riffle and glide) than Lagen. Riverbed composition is dominated by coarse substrates (i.e. cobble and boulder) in the upper half of the study area, while the lower parts close to the confluence with Lagen has an increasing level of gravel and pebble. The study area of Otta starts at Eidefossen hydropower-plant (annual average discharge of 111 m<sup>3</sup> s<sup>-1</sup>), which was built at an already existing natural migration barrier (Huitfeldt-Kaas, 1918). The effects of hydropower are the most noticeable of anthropogenic influences in my study area of Otta, but road building and riverbank reinforcement has also led to input of large boulders along the riverbank.





**Figure 1:** Study area; Map of the two rivers Lågen and Otta with the river-systems position in Oppland County. Note: 4km of Otta between 8 and 12 km are not included since this area was not sampled.



**Figure 2:** Stream profile (decrease in elevation with distance) in Otta and Lågen. Markers along the x-axis shows starting position of each transect, whereas blue = 1 transect and red = 2 transects, T = additional backpack electroshocker transects. On the right side of the stream profile is the non-linear valley confinement-patterns associated with river gradient at the given elevation.

## 2.1 Species description within study area

Both rivers have a viable population of trout and grayling (Museth et al., 2011). The appreciation and importance of the two species' (e.g. for anglers), including unique riverine landscape features throughout the entire Lagen watershed have resulted in a total of 26 tributaries and 7 individual reaches to be protected by the Norwegian Protection Plan for River Systems (L'Abée-Lund et al., 2009 ). There are no accurate estimates of the two species' population-size in the two rivers within my study area, but Otta is considered to have at higher density of trout than Lagen. Other species within my study area are the common minnow (*Phoxinus phoxinus*) and the introduced crucian carp (*Carassius carassius*). Both trout and grayling are often characterized by migrating subpopulations, where migrations are conducted to reach spawning grounds, feeding areas and over-wintering habitats (Nykänen, Huusko, & Mäki-Petäys, 2001; Klemetsen et al., 2003). However, the two species do have considerable different life-histories, with trout spawning in autumn (Jonsson & Jonsson, 2011) and grayling spawning in spring / early summer (Nykänen et al., 2001). The two species' are also known to mainly utilize different over-wintering habitats, even though they do occasionally overlap (Nykänen et al., 2001; Klemetsen et al., 2003; Nykänen, Huusko, & Lahti, 2004). Trout can become piscivorous when they achieve lengths > 13-15 cm (Campbell, 1979; L'Abée-Lund, Langeland, & Sægrov, 1992), which together with stronger intraspecific competition cause trout populations to have greater heterogeneous individual growth patterns than grayling (L'Abée-Lund et al., 1992; Northcote, 1995).

## **3. Materials and methods**

### **3.1 Background**

In 2008 - 2010, the Norwegian Institute of Nature Research (NINA) at Lillehammer conducted an environmental impact assessment (EIA) in Lagen and Otta (Museth et al., 2011), because there was a proposal to re-develop Eidefossen hydropower-plant in Otta. This proposed change would alter the winter-flow from today's interval of 30-50 m<sup>3</sup> s<sup>-1</sup> down to a minimum flow of 10 m<sup>3</sup> s<sup>-1</sup> and a minimum summer-flow of 20 m<sup>3</sup> s<sup>-1</sup> within the first 10 km of Otta. The induced increased knowledge of spawning sites, population structure and adult migratory patterns of trout and grayling (Junge et al., 2013). However, it was concluded that a monitoring program to study the effects of the hydropower development was necessary, e.g. how the minimum flow section would affect sub-adult trout and grayling abundance and distribution.

### **3.2 Habitat measurements**

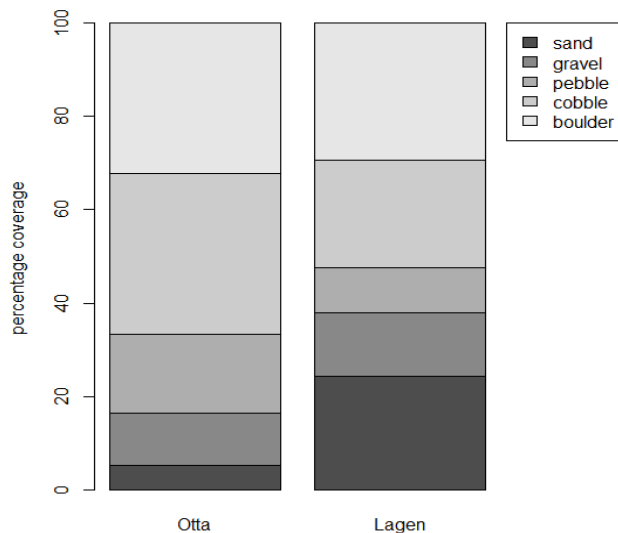
The size of the two study systems and potential biases in catchability of fish determined what type and scale of variables that were collected to predict distribution of sub-adult trout and grayling. Both study sections were long (> 10 km) and included areas that were highly challenging to perform fish sampling and habitat measurements. This was especially the case in parts of Otta, which has rapids classified as high as level 5 for experienced rafters. Because of these challenges, my study focused on describing broad scale distribution patterns of sub-adult trout and grayling (age 0+ to 2+) and linking their distribution and abundance to a longitudinal scale and habitat measurements recorded within a certain habitat-type (e.g. pool, run, riffle, glide etc).



**Photo 1:** Launching the electrofishing-boat in the upmost transect of river Otta.

To describe habitat conditions associated with sub-adult trout and grayling distribution in the two rivers, we conducted fish sampling and physical habitat description in 500 meter transects located as close to the riverbank as possible (Lagen:  $n=17$ , Otta:  $n=15$ ). Transects were identified using aerial photos ArcMap (ESRI, 2012) with the goal of selecting transects that were relatively similar in physical conditions along the entire transect length (i.e. no distinct changes in flow patterns, river gradient, and/or river width). However, in some parts of the rivers, Otta especially, it was difficult to find sections that were similar across the entire 500 meter transect length. This caused some transect to have shorter lengths (i.e., the shortest transect was 360 m). The high river gradient character of Otta and lack of locations to launch the el-boat also made it impossible to sample a segment of  $\approx 4$  km in length (8 – 12 km from Eidefoss). Some areas that were easily accessible were sampled twice, once at each side of the river if the habitat conditions differed between each side, but all transects were treated as independent sample units. Valley confinement and downstream distance were measured using GIS, while river gradient was calculated from earlier measurements conducted by the Norwegian Water Resources and Energy Directorate (NVE). Valley confinement is the ratio between valley floor width and river width and provides information of a rivers general appearance. Rivers that are highly confined by the valley are associated with low river sinuosity, high velocities and coarse substrates, while rivers that are unconfined are more meandering or branching with low velocities and fine substrates (Bisson & Montgomery,

1996). River gradient is the average channel slope in each river segment (Slope = (elevation upstream end of reach - elevation downstream end of reach) / reach length) and is expressed as meters/ distance at an index appropriate to the scale of the area (Bisson & Montgomery, 1996; Montgomery & Buffington, 1998). Downstream distance was measured as the river length from the start of the study area to the start of each transect within that river. At the scale of this study, distance itself does not determine fish distribution, but it was used for descriptive purposes of longitudinal distribution patterns. At each transect the following additional predictors were measured: substrate coarseness, velocity, slope of the riverbank (hereafter “bank slope”) and aquatic vegetation. Substrate was visually measured as percent coverage of each substrate type (% of: sand (<2 mm), gravel (2-16 mm), pebble (16-65 mm), cobble (65-300 mm) and boulders (>300 mm) (Platts, Megahan, & Minshall, 1983; Bain, Finn, & Booke, 1985; Cowx, O’Grady, Gibson, Hillier, & Whalen, 1998) (Figure 3).



**Figure 3:** Level of total percentage coverage for the five different substrate-types in rivers Otta and Lagen.

Additionally, water velocity and bank slope (slope from the riverbank to thalweg, indicating depth at edge habitat) were subjectively categorized as low, moderate, high (velocity) and shallow, medium, steep (bank slope). Aquatic vegetation was registered by visually interpreting the level of presence (coverage and height) and categorized from “A” (no vegetation) to “D” (continuous coverage over entire transect length + height  $\approx$  >50% of water depth). Since these measurements were subjectively measured, a research assistant and I collected these data simultaneously and values were averaged. Other cover-structures, such as in-stream dead wood and undercut river-banks were not measured because they were rare.

### 3.3 Fish sampling

Fish sampling was conducted with an electrofishing boat (hereafter el-boat) between the 11<sup>th</sup> and 23<sup>rd</sup> of September. El-boat fishing is a technique developed in the USA to survey fish populations in large rivers and lakes. In contrast to electrofishing with a backpack electroshocker, which use is confined to wadeable areas, the el-boat can be used over a large area and wide range of habitats with high efficiency depending upon river conditions. The el-boat supplies an electrical current to the anodes that are positioned in the water in front of the boat using droppers attached to adjustable poles. This creates an electric field between the anodes and cathode (metallic cords) that are positioned at the front of the hull. Fish that are within the power field are stunned so that they can be netted by one of two net-handlers standing in the front of the boat. Catchability with an el-boat is more or less determined by the same premises as electrofishing with a backpack electroshocker: 1) the fish must be within the electric field, 2) the fish must be stunned, 3) the fish must be spotted by net-handlers, and 4) the net-handler must be able to catch the fish with a net. Different probabilities can be associated with each of these four events ( $P_1$  to  $P_4$ ). If we assume these events to be independent, the probability of catching one individual fish  $P_i$  may be expressed as:  $P_i = P_{i,1} * P_{i,2} * P_{i,3} * P_{i,4}$  (Zippin, 1958; Bohlin, Hamrin, Heggberget, Rasmussen, & Saltveit, 1989). If one of these probabilities equals 0, then the fish will have a catch-probability of 0 even if some of the other probabilities are high. As an example: a fish living in cover (e.g., rock cavity) may have a high probability of being affected by the field of electricity, but it will not be spotted by the angler if it cannot be observed because of the cover structure. Therefore having a low  $P_{i,3}$  causes the fish to have a low total catch-probability.

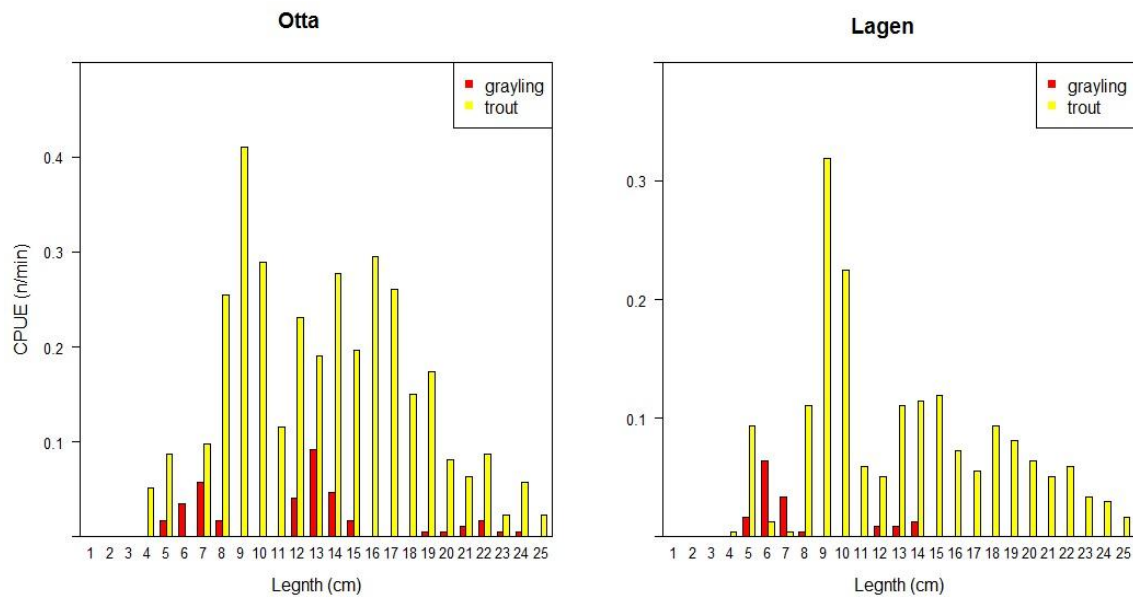


**Photo 2:** Fish sampling in one of the lower areas of river Otta. Photo by: Ketil Sandviken G.D. (Gudbrandsdølen).

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Many factors affect catchability when using an el-boat. Especially important when targeting smaller fish is water conductivity, velocity, depth, turbidity, and substrate coarseness (Bayley & Austen, 2002). Due to the voltage differential across fish length, smaller fish tend to be less susceptible to electrofishing than larger fish, and it is therefore often necessary to use a higher pulse frequency and voltage to catch smaller fish (Bohlin et al., 1989). With the el-boat used in this study it is possible to adjust the frequency and voltage according to the target size of the fish you sample and conductivity. However; with lower connectivity it becomes more difficult to compensate with higher voltage due to the higher resistance in the water (Bohlin et al., 1989; Hill & Willis, 1994). During the fish sampling in this study the average ambient conductivity (measured close to the surface using a conductivity meter) was  $0.53\mu\text{S}/\text{m}$  (microsiemens per meter) in Otta and  $1.01\ \mu\text{S} / \text{m}$  in Lagen, which is considered as low. Differences in surface velocity may also affect catchability, since the window of time from observation to netting the fish becomes shorter with increased velocity. However, increased velocity would also gain the net-handlers an advantage since fish will have less time to detect the incoming electric field (or visually detect the boat or sound coming from the generator) and thus escape before being stunned (Bayley & Austen, 2002). An increase in depth and/or turbidity will potentially have a stronger negative effect on the catchability of smaller fish, because they are more difficult to visually detect. With coarse substrates the water-flow is broken to a higher degree close to the riverbed (Dinehart, 1999). This provides water-flow refuges which allow smaller fish to stay close to the riverbed often in between rock cavities, even if they are stunned, making them more difficult to detect and net.

Captured fish were identified to species (grayling and trout) and length measured before released back to the river. Length-frequency histograms were used to estimate maximum annual growth rate in order to group fish into age-classes (0+, 1+, 2+ and >2+) (figure 4). Maximum annual growth rate in both rivers was estimated to 55 mm/yr for trout and 80 mm/yr for grayling. Differences in individual growth rates may cause some individuals to be misclassified, especially sub-adult trout that have a lower annual growth rate than grayling during their first two to three growth seasons. Differences in growth rates may therefore cause overlapping age-class estimates, which were supported to some degree in a small selection of trout between 46-64 mm (Otta: n=16; Lagen: n=14) that were aged using otoliths. In this sample of sub-adult trout, the largest 0+ in Otta was 55 mm and the smallest 1+ was 51 mm, while in Lagen the largest 0+ was 56 mm and the smallest 1+ was 55 mm.



**Figure 4:** Length distribution of trout and grayling in Otta and Lagen in relation to CPUE, showing peak occurrences used to estimate the two species' age-classes. Note that catchability for 0+ is noticeably lower than 1+ for both species and that grayling 1+ had a low CPUE in Lagen while grayling 2+ had a low CPUE in Otta and was not caught in Lagen.

Since we were expecting some catch biases with the el-boat, especially regarding size selectivity, I performed additional fish sampling with a backpacker apparatus (transects: Otta  $n=5$ , Lagen  $n=4$ ). This sampling was conducted according to standard methods (Zippin, 1958; Bohlin et al., 1989) with  $3 \times$  successive removal on a 50 meter long stretch within selected el-boat transects that had wadeable areas. The only exception from the standard method was that sampling was conducted by one person and not by the recommended minimum of two persons. By conducting  $3 \times$  successive removal it is possible to estimate the catchability of each species age-class including their population size and fish density (number of fish per square meters). According to (Bohlin et al., 1989) it is necessary to catch at least 50 fish in order to gain valid confidence intervals of population size and catchability when fish sampling with  $3x$  successive removal. I was unable to catch 50 fish, partially since only one person conducted the sampling. Therefore estimates of fish/m<sup>2</sup> caught using the backpack shocker was only used to describe and discuss potential biases in the el-boats catchability. Transects sampled with the backpacker apparatus were also habitat classified for substrate coverage, aquatic vegetation, and surface velocity ((measured by timing how long it took for a wine cork to float past 50 meters (replicated 3 times and averaged)).



The following formula was used to calculate population size and number of fish per square meters (Bohlin et al., 1989):

$$N = \frac{6X^2 - 3XY - Y^2 + T\sqrt{Y^2 + 6XY - 3X^2}}{18(X - Y)}$$

**Fish per square meters = N / (length \* width of transect)**

Where  $c_1$  = number of fish at first session,  $c_2$  = number of fish at second session,  $c_3$  = number of fish at third session.  $X = 2c_1 + c_2$ ,  $Y = c_1 + c_2 + c_3$ .  $N$  = population size.

### 3.4 Statistical analysis

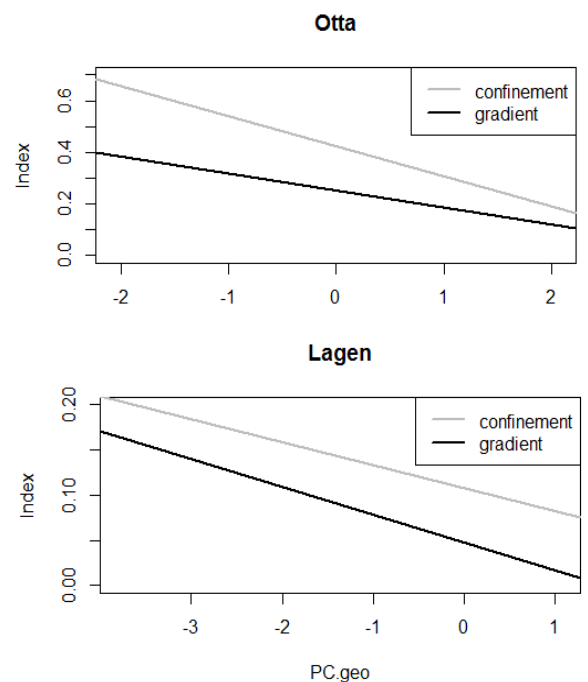
The basis for objectively ranking models and statistical model selection was performed with Akaike Information Criteria for small sample sizes ( $AIC_c$ ),  $AIC_c = AIC + ((2k(k + 1) / (n - k - 1)))$ , where  $n$  = sample size (Burnham & Anderson, 2002). This second order bias correction for AIC (Sugiura, 1978; Hurvich & Tsai, 1989) penalizes extra parameters more than standard AIC, and was therefore considered appropriate for this study. AIC model selection is based on relative differences between models, meaning that the approximation of the “best model” is gained from the difference in the AIC value between selected candidate models (Burnham & Anderson, 2002). The models are ranked using delta AIC ( $\Delta AIC$ ) ( $\Delta AIC = \Delta_i = AIC_i - AIC_{min}$ ), where  $AIC_i$  is the value for model  $i$ , and  $AIC_{min}$  is the value for the best model.  $\Delta AIC$  provides a method for ranking models, with models with low  $\Delta AIC$  having more support than models with high  $\Delta AIC$ . Models with  $\Delta AIC$  values  $< 2$  have considerable support, models with  $\Delta AIC$  values between 2-7 have less support, while models with a  $\Delta AIC$  value  $> 10$  have little support (Burnham & Anderson, 2002; Burnham, Anderson, & Huyvaert, 2011). I considered models with  $\Delta AIC < 2$  to have considerable support, while models with a  $\Delta AIC$  value between 2 and 4 were regarded as partially supported. Additionally, the Akaike weights (AIC weight), which indicates the probability of one model being the best model relative to the set of candidate models, were used to compare each models strength of evidence (Burnham & Anderson, 2002). I also determined the importance of each predictor across all models with a  $\Delta AIC$  value  $< 4$  by quantifying the variable importance value. This number provides information on how important one variable is for the respective species age-class relative to other predictors included in candidate models with a  $\Delta AIC$  value  $< 4$  (Burnham & Anderson, 2002). R-squared ( $R^2$ ) or the coefficient of determination was also included to assess model fit.

River gradient and valley confinement were correlated in both rivers (Pearson's  $r = 0.80$  in Lagen and  $0.58$  in Otta), which was expected as river gradient increases with increased valley confinement (Bisson & Montgomery, 1996). Therefore, PCA (principal component analysis) was used to combine these two variables into a new variable for each river called "PC.geo". In both rivers, the river gradient and valley confinement decreased with an increase in PC.geo. Therefore an increase in CPUE with PC.geo would indicate an increase in CPUE with a decrease in valley confinement and river gradient (Figure 5). Velocity had a strong relationship with PC.geo and was therefore disregarded from statistical modeling because PC.geo was viewed as the primary determinant of velocity. To transform the measurements of substrate coverage to substrate coarseness, each of the five substrate classes was ranked from 0 (sand) to 5 (boulders) and combined to an average value for each transect (Cowx et al., 1998). Even though valley confinement and river gradient are primary determinants of substrate coarseness (Bisson & Montgomery, 1996), PC.geo did not correlate with substrate coarseness in any of the two rivers. This is likely the cause of boulders that has been introduced to reinforce the riverbank at specific places in both rivers. Variable "aquatic vegetation" was not used due to generally low occurrence. Additionally, 2 transects in Lagen were not used in AICc model selection due to high levels of aquatic vegetation which could cause potential disturbance of other predictors. Trout  $>3$  years was not incorporated as predictor for potential predation / cannibalism, since this variable was highly correlated with substrate coarseness (Pearson's  $r = 0.68$  in Lagen and  $0.83$  in Otta). Finally I ended up with 3 non-correlated variables, which could be used to predict fish distribution: "PC.geo" (numeric), "bank slope" (numeric) and "substrate coarseness" (categorical).

**Table 1:** Linear models used in AICc model selection.

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<b>m0=lm(y ~ 1)</b>
<b>m1=lm(y ~ Substrate coarseness)</b>
<b>m2=lm(y ~ PC.geo)</b>
<b>m3=lm(y ~ Bank slope)</b>
<b>m4=lm(y ~ Substrate coarseness + PC.geo)</b>
<b>m5=lm(y ~ Substrate coarseness + Bank slope)</b>
<b>m6=lm(y ~ PC.geo + Bank slope)</b>
<b>m7=lm(y ~ Bank slope + Substrate coarseness + PC.geo)</b>



**Figure 5:** Relation of valley confinement and river gradient with PC.geo

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To describe patterns of longitudinal distribution patterns, all species age-classes were initially tested with quasiPoisson models (due to overdispersion) to see if CPUE had a relation to distance from the upmost spawning ground. This was conducted by using actual count data as response while effort (time) was incorporated to the model as an “offset” covariate (Shono, 2008; Coxe, West, & Aiken, 2009; Hazin et al., 2012). By plotting CPUE in relation to distance I could visually examine the nature of this relationship (simple or higher-order polynomial). By constructing models from simple to higher-order polynomials (variable “distance” squared with a maximum integer of 3) I used ANOVA to test if models with higher-order polynomials described the relationship between distance and fish abundance better than a linear model. Since generalized linear models has no direct analogue to  $R^2$ , I used  $R^2_{\text{deviance}}$  ( $1 - (\text{deviance higher-order polynomial} / \text{deviance linear model})$ ) which functions as a pseudo  $R^2$  for generalized linear models (Coxe et al., 2009). By doing this I could see how high the proportional reduction of deviance was between higher-order polynomials and the linear model. Note that  $R^2_{\text{deviance}}$  does not provide the model’s goodness of fit, unlike standard  $r^2$  gained from ordinary least squares (OLS) regression, since  $R^2_{\text{deviance}}$  represents a proportional reduction in deviance between two models (Coxe et al., 2009). Species age-classes where the linear model did not have a relation to distance were also tested with higher-order polynomials. Whereas, if a higher-order polynomial model had a significant difference from the linear model, than the higher-order polynomial would be compared with the null-model. If the higher-order polynomial was distinguishable from the null-model, then the distribution of that model were used further in descriptive statistics.

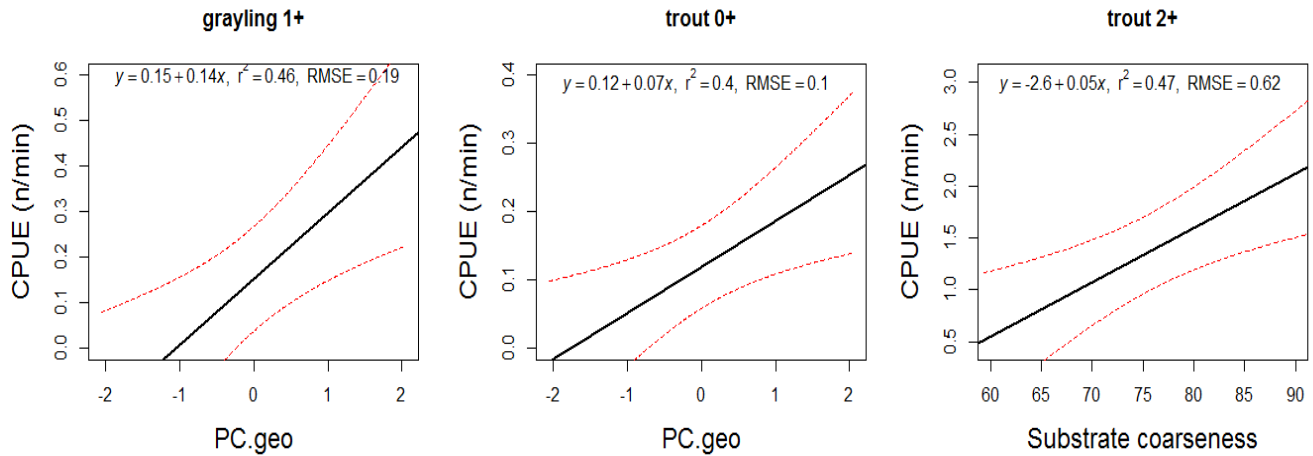
All statistical analysis were conducted in R (R.core.team, 2014).

## 4. Results

### 4.1 AIC model selection

In the Otta River (table 2), there were five models with considerable support (i.e.  $\Delta\text{AICc} < 2$ ) predicting the abundance of grayling 0+, where the best model (model 3) had a 1.25× higher likelihood than the second best model (model 4). Model 3 also explained almost an equal amount of variation ( $R^2 = 0.47$ ) as model 4 ( $R^2 = 0.45$ ) with one less predictor. Covariates PC.geo ( $y = 0.1 + 0.6x$ ) and bank slope had the highest variable importance values of 0.48 (PC.geo) and 0.47 (Bank slope) (figure 8). The model set for grayling 0+ also included the null model as partially supported (i.e.  $\Delta\text{AICc} = 2 - 4$ ), which had a 3.8 × lower likelihood than the best model. Grayling 1+ had only one model with considerable support (model 4), which had a 4 × higher likelihood than the next best model (model 2). Variable PC.geo ( $y = 0.15 + 0.14y$ ) was the only predictor in model 2 ( $R^2 = 0.46$ ) and was also included together with substrate coarseness ( $y = 1.03 + 0.012x$ ) in model 4 ( $R^2 = 0.65$ ). PC.geo also had the highest variable importance value of 0.97 which was 1.3 × higher than substrate coarseness (figure 8).

There were 3 models with considerable support predicting the abundance of trout 0+ in the Otta River, with the most support for model 2 which had a 1.5 × higher likelihood than the second best model (model 4). Variable PC.geo ( $y = 0.12 + 0.07x$ ) had the highest variable importance (0.88) (figure 8) and was included in all 3 models predicting trout 0+. Model 1 was the only model with considerable support predicting the abundance of trout 2+, and had a 4.2 × higher likelihood than the next best model (model 4). Substrate coarseness ( $y = -2.6 + 0.05x$ ) had a variable importance value of 0.95 which was more than 5 times higher than the other predictors (figure 8). Grayling 2+ and trout 1+ were the two species age-classes in Otta where only the null model had considerable support.

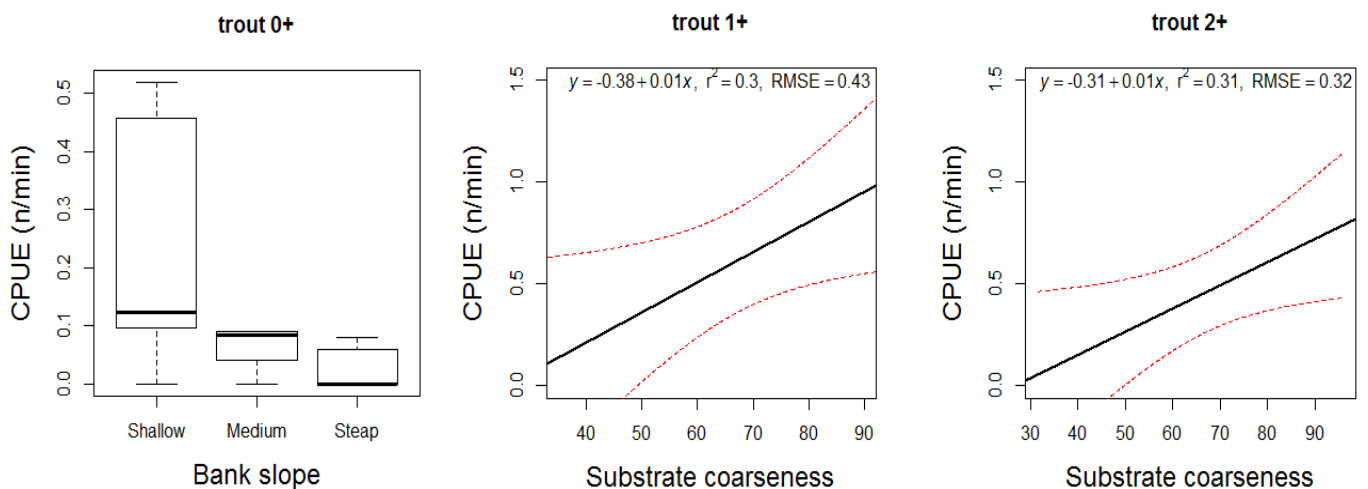


**Figure 6:** CPUE of grayling 1+, trout 0+ and trout 2+ in Otta in relation to covariates that were included in models with best support and that had the highest variable importance value (see figure 8). Presented with best fit line (solid, black line) and confidence intervals (dashed red lines) together with intercept, slope,  $R^2$  and root mean square error (RMSE).

**Table 2:** AICc model selection for Otta including models with  $\Delta AICc < 4$ . K = number of parameters in the model,  $\Delta AICc$  = deviation relative to the best model for each response variable, AICc weight = the probability of one model to be estimated as the best of the candidate set, and  $R^2$  = model fit.

	K	AICc	$\Delta AICc$	AICc weight	$R^2$
<b>Grayling 0+</b>					
m3=lm(y ~ Bank slope)	3	-10,995749	0	0,26944091	0,4724871
m4=lm(y ~ Substrate coarseness + PC.geo)	3	-10,36868	0,6270688	0,19692338	0,4499672
m6=lm(y ~ PC.geo + Bank slope)	4	-9,924787	1,0709624	0,15772735	0,5849248
m1=lm(y ~ Substrate coarseness)	3	-9,647427	1,3483218	0,13730273	0,2555789
m2=lm(y ~ PC.geo)	2	-9,323984	1,6717652	0,1168004	0,2393527
m0=lm(y ~ 1)	1	-8,402019	2,5937297	0,07366179	0
<b>Grayling 1+</b>					
m4=lm(y ~ Substrate coarseness + PC.geo)	3	-1,218652	0	0,72438323	0,6451532
m2=lm(y ~ PC.geo)	2	1,248913	2,467566	0,21093239	0,4604497
<b>Grayling 2+</b>					
m0=lm(y ~ 1)	1	-30,31084	0	0,63754347	0
m1=lm(y ~ Substrate coarseness)	2	-27,56635	2,74449	0,16164091	0,02873427
m2=lm(y ~ PC.geo)	2	-27,19554	3,1153	0,13428607	0,00442472
<b>Trout 0+</b>					
m2=lm(y ~ PC.geo)	1	-18,024616	0	0,37251182	0,4021662
m4=lm(y ~ Substrate coarseness + PC.geo)	2	-17,205434	0,8191821	0,24731868	0,5105024
m6=lm(y ~ PC.geo + Bank slope)	3	-17,199763	0,8248529	0,24661842	0,6412426
<b>Trout 1+</b>					
m0=lm(y ~ 1)	1	32,06573	0	0,57196575	0
m2=lm(y ~ PC.geo)	2	34,84193	2,776202	0,14273334	0,02667875
m1=lm(y ~ Substrate coarseness)	2	34,89908	2,833354	0,13871232	0,02296319
m3=lm(y ~ Bank slope)	3	35,54382	3,478092	0,10048747	0,2092662
<b>Trout 2+</b>					
m1=lm(y ~ Substrate coarseness)	2	36,26334	0	0,75913296	0,4683893
m4=lm(y ~ Substrate coarseness + PC.geo)	3	39,12245	2,859113	0,18174787	0,5013156

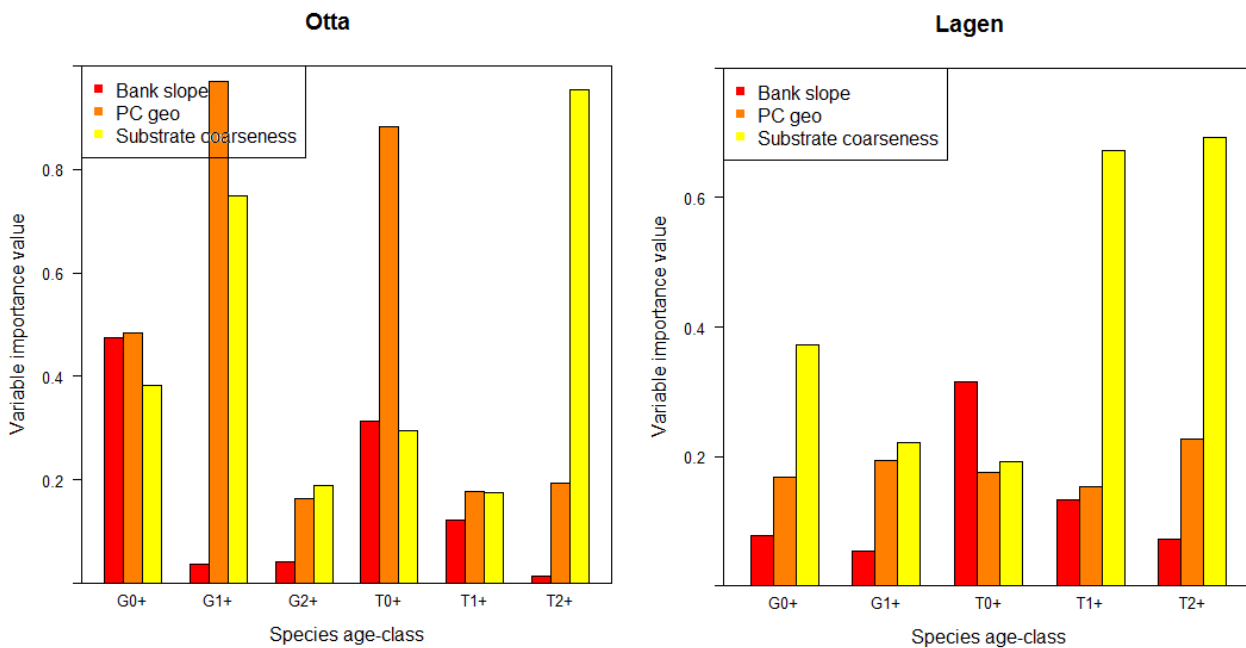
In Lagen (table 3) trout 1+ and trout 2+ were the only species age-classes where the null-model did not have considerable support. There were 1 model with considerable support and 3 models with partial support predicting the abundance of trout 1+ in Lagen, whereas model 1 had a  $3 \times$  higher likelihood than next best model (null model). For models predicting trout 1+ abundance, the covariate substrate coarseness ( $y = -0.38 + 0.015x$ ) had a variable importance value of 0.67, which was  $2 \times$  higher than bank slope (figure 8). Bank slope was also the only covariate in model 3 (ranked as the fourth best model), which explained an almost equal amount of variation ( $R^2 = 0.32$ ) compared to model 1 ( $R^2 = 0.30$ ). Trout 2+ also had model 1 as the only model with considerable support and 3 additional models with partial support, where model 1 had a  $3 \times$  higher likelihood than the second best model (null model). The covariate substrate coarseness ( $y = -0.31 + 0.011x$ ) had the highest variable importance value of 0.69 for models predicting trout 2+, which was more than  $3 \times$  higher than the other predictors (figure 8). There was considerable uncertainty among models predicting trout 0+ abundance, where the best model (null model) had a  $1.8 \times$  higher likelihood than model 3 which was the second best model. Bank slope had the most noticeable variable importance value (0.31) (figure 8), and was the only predictor in the second best model ( $R^2 = 0.32$ ). There were 2 models with considerable support for grayling 0+ abundance (null model and model 1), where model 1 had a  $1.4 \times$  times lower likelihood than the null model. Substrate coarseness ( $y = 0.37 - 0.004x$ ), which was the single predictor in model 1, had the highest variable importance value of 0.31 (figure 8). Only the null model predicting grayling 1+ abundance had considerable support, with model 2 and 3 as partially supported.



**Figure 7:** CPUE of trout 0+, trout 1+ and trout 2+ in relation to covariates that included in models with considerable support and with highest variable importance value in Otta (see figure 8). Linear models are presented with best fit line (solid, black line) and confidence intervals (dashed red lines) together with intercept, slope,  $R^2$  and root mean square error (RMSE). Boxplot with median (horizontal line), first and third quartiles (box) and  $1.5 \times$  interquartile range (whiskers).

**Table 3:** AICc model selection for Lagen including models with  $\Delta AICc < 4$ . K = number of parameters in the model,  $\Delta AICc$  = deviation relative to the best model for each response variable, AICc weight = the probability of one model to be estimated as the best of the candidate set, and  $R^2$  = model fit.

Grayling 0+	K	AICc	$\Delta AICc$	AICc weight	$R^2$
m0=lm(G0+-1)	1	-1,9740083	0	0,44909457	0
m1=lm(G0+-Substrate coarseness)	2	-1,2694666	0,7045417	0,31575375	0,152235
m2=lm(G0+-PC.geo)	3	0,8202141	2,7942223	0,11106575	0,02550873
<b>Grayling 1+</b>					
m0=lm(G1+-1)	1	-23,338235	0	0,57038841	0
m1=lm(G1+-Substrate coarseness)	2	-21,098902	2,239333	0,18616828	0,06089909
m2=lm(G1+-PC.geo)	3	-20,771528	2,566708	0,15805824	0,04017793
<b>Trout 0+</b>					
m0=lm(T0+-1)	1	-8,617092	0	0,42862602	0
m3=lm(T0+-Bank slope)	3	-7,441735	1,175356	0,23815139	0,3217976
m2=lm(T0+-PC.geo)	2	-6,027099	2,589993	0,11740015	0,03868679
m1=lm(T0+-Substrate coarseness)	2	-5,866128	2,750964	0,10832138	0,02831498
<b>Trout 1+</b>					
m1=lm(T1+-Substrate coarseness)	2	25,16616	0	0,5490333	0,3032857
m0=lm(T1+-1)	1	27,40504	2,238879	0,17923893	0
m4=lm(T1+-Substrate coarseness +PC.geo)	3	28,5571	3,390939	0,10075479	0,3228501
m3=lm(T1+-Bank slope)	3	28,60565	3,439487	0,09833851	0,320655
<b>Trout 2+</b>					
m1=lm(T2+-Substrate coarseness)	2	16,97744	0	0,53989052	0,3083009
m0=lm(T2+-1)	1	19,32468	2,347246	0,16695814	0
m4=lm(T2+-Substrate coarseness +PC.geo)	3	20,06102	3,083586	0,11553496	0,3413594
m2=lm(T2+-PC.geo)	2	20,26257	3,285137	0,10445931	0,1389435



**Figure 8:** Variable importance value for variable substrate coarseness, PC.geo and bank slope ordered by species age-classes in Otta and Lagen. G = grayling with age-class, T = trout with age-class.

## 4.2 Patterns of longitudinal fish distribution

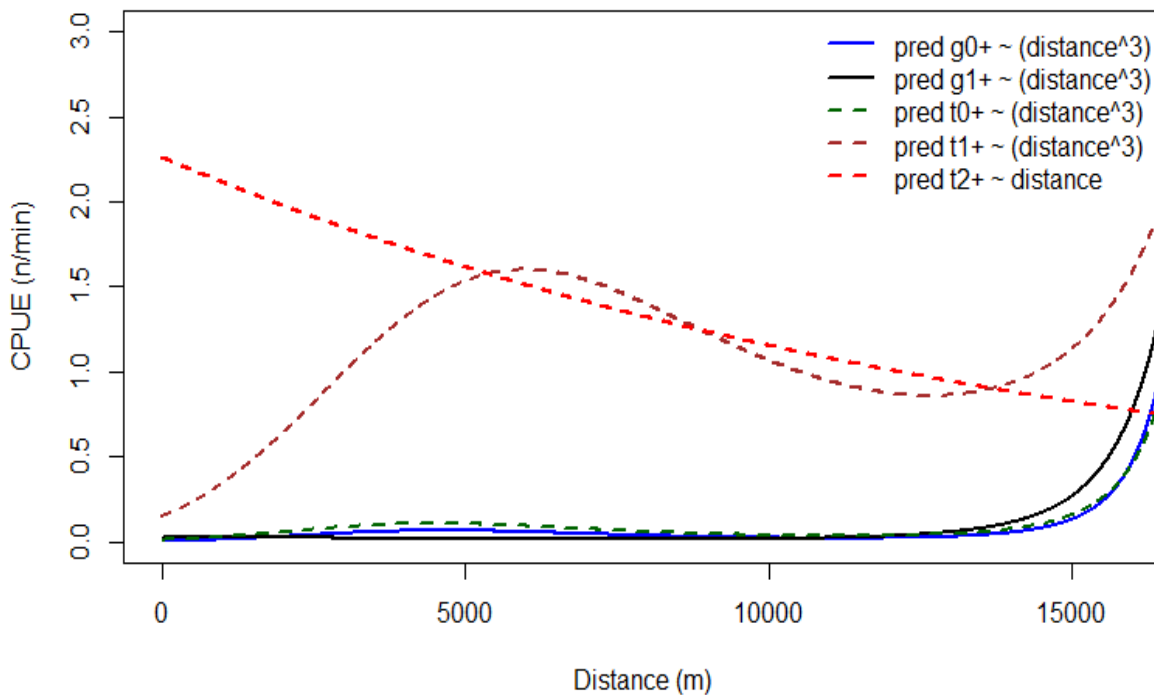
In Otta, the CPUE of grayling 0+ ( $p = 0.082$ , Pearson's  $r = 0.48$ ) and grayling 1+ ( $p < 0.01$ , Pearson's  $r = 0.56$ ) increased with distance from the most upstream transect. By providing higher predictive power to the linear model ( $y \sim \text{distance}$ ) the CPUE for these grayling age-classes improved based on  $R^2_{\text{deviance}}$  with a cubic model ( $y \sim \text{distance} + \text{distance}^2 + \text{distance}^3$ ) (table 4, figure 9). For grayling 2+, none of the models with higher order terms explained more variation nor improved model fit relative to the linear model. The CPUE of trout 0+ increased with distance ( $p = 0.014$ , Pearson's  $r = 0.54$ ) while there was a trend for trout 1+ increasing with distance ( $p = 0.171$ , Pearson's  $r = 0.37$ ). Trout 2+ was the only species age-class in Otta where CPUE decreased with distance from the most upstream transect ( $p = 0.011$ , Pearson's  $r = -0.63$ ). Model fit for trout 0+ and trout 1+ improved with a cubic model ( $y \sim \text{distance} + \text{distance}^2 + \text{distance}^3$ ), while trout 2+ was best described by a linear model (table 4, figure 9). In Lagen, none of the species age-classes had a strong relation with distance from the most upstream transect. Additionally, when providing higher predictive power to the linear model, none of the higher-order polynomials could achieve a significant difference from the linear model in any species age-class.

**Table 4:** Species age-classes in Otta where the higher order model achieved a significant improvement in  $R^2_{\text{deviance}}$  compared to the linear model, indicating a non-linear relation to distance from the most upstream transect.

Species age-class	ANOVA: non-linear model vs. linear model	
	p-value	$R^2_{\text{deviance}}$
Grayling 0+	0.036	0.55
Grayling 1+	0.027	0.42
Trout 0+	0.028	0.41
Trout 1+	0.018	0.48



### Downstream distribution of subadult grayling & trout in Otta

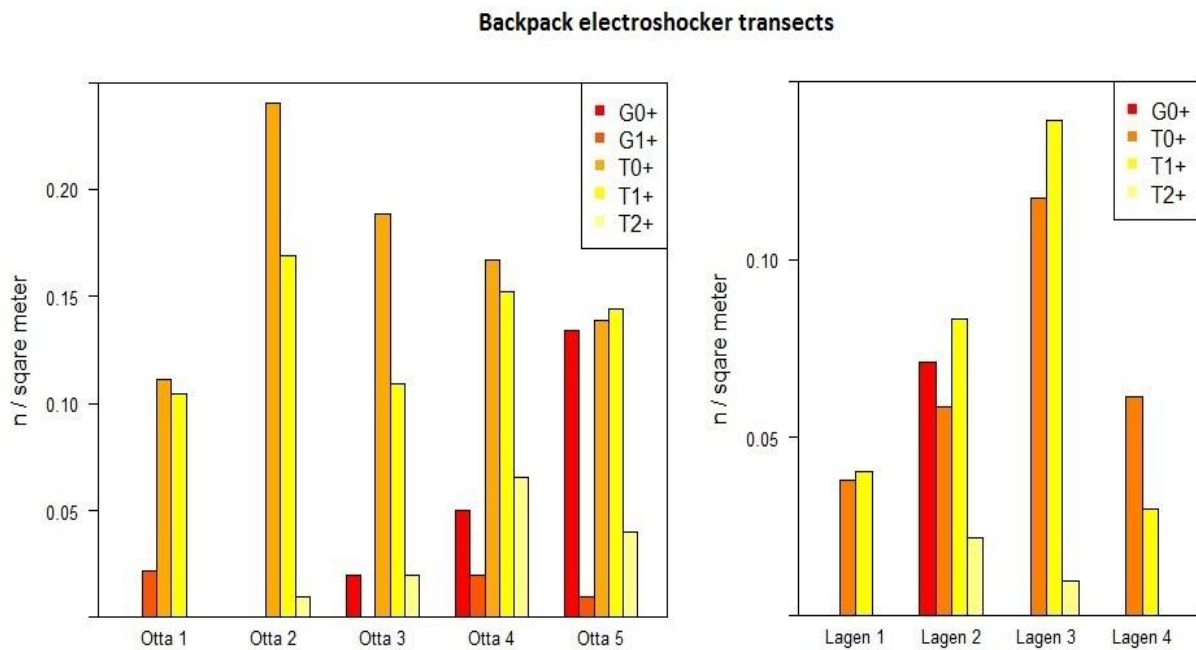


**Figure 9:** CPUE of all species age-classes in Otta (except grayling 2+) with predicted line of selected model. g = grayling with age-class, t = trout with age-class.

### 4.3 Fish sampling with backpack electroshocker

In Otta, grayling 0+ was caught with increasing numbers in the lower transects (figure 10) which was coherent with the el-boat results. Grayling 1+ had a maximum fish density of  $0.02 / \text{m}^2$  which was  $6.5 \times$  lower than the maximum fish density of grayling 0+ (figure 10). Since the el-boat caught an almost equal amount of grayling 0+ and grayling 1+, these differences with the backpack electroshocker may indicate that grayling 1+ were positioned in deeper areas and / or further from the riverbank than grayling 0+. The reason for this is that the backpack electroshocker transects were confined to a maximum depth of 0.5 meters and conducted within 2 meters from the riverbank, while the el-boat covered a minimum of 4 meters from the riverbank regardless of depth. Trout 0+ and trout 1+ had a fish density between  $0.11 / \text{m}^2$  to  $0.28 / \text{m}^2$  within every backpack electroshocker transect, while trout 2+ had a maximum density of  $0.07 / \text{m}^2$  (figure 10). This may indicate that trout 2+ were positioned in deeper areas and / or further from the riverbank than trout 0+ and trout 1+. In Lagen, grayling 0+ were the only grayling age-class that was caught with the backpack electroshocker, all in the same transect (Lagen 2). This transect stood out as the only transect with a high level of aquatic vegetation (level D) and the lowest level of substrate coarseness

and surface velocity (appendix: table 1). The highest level of trout 0+ and trout 1+ were caught in transect “Lagen 3” (figure 10). This transect had the highest substrate coarseness and the highest surface velocity relative to other transects (appendix: table 1). Note that “Lagen 2” had the second highest level of trout 0+ and trout 1+, as well as the highest level of trout 2+ (figure 10) indicating that trout may have a more generalist approach to preferred type of cover structure than grayling. Trout 2+ also had a much lower fish density than trout 0+ and trout 1+ in Lagen, indicating that trout 2+ had a lower abundance in shallower edge habitat.



**Figure 10:** Number of sub-adult grayling and trout per square meter (m<sup>2</sup>) in Otta and Lagen based on fish sampling with a backpacker apparatus (see fig 2 for transect position). G = grayling with age-class, T = trout with age-class.

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## 5. Discussion

This study was conducted to describe differences in habitat preference and longitudinal distribution patterns of sub-adult trout and grayling in two large northern rivers, which were highly different in valley confinement and river gradient. Below I discuss my results and compare them with other findings on sub-adult habitat preference and distribution patterns. I also discuss research implications for future studies and habitat monitoring in relation to the planned development of Eidefossen hydropower-plant in Otta. Since sampling of fish in large rivers is methodically challenging, I have also added a section that describes some of the most important biases that may have influenced my results.

### 5.1 Habitat

Shelter (e.g., substrate cavities) availability has shown to be an important factor predicting sub-adult trout abundance. However, intraspecific competition and risk of predation can also segregate the abundance of young trout age-classes. This have been observed in studies where trout 0+ preferred shallow edge-habitats dominated by pebble and cobble, while the upper sub-adult age-classes had an increasingly strong preference for deeper edge-habitats dominated by boulders (Heggenes & Saltveit, 1990; Greenberg et al., 1996; Maki-Petäys et al., 1997; Maki-Petäys, Vehanen, & Muotka, 2000; Roussel & Bardonnnet, 2002; Jonsson & Jonsson, 2011; Heggenes & Wollebæk, 2013). My study supported such segregation in habitat niche, since abundance of trout 2+ were strongly associated with coarse substrates in both rivers while trout 0+ had a stronger relation to reduced levels of valley confinement and river gradient in Otta and bank slope in Lagen. It were also noticeable that none of the habitat variables could define habitat preference of trout 1+ in Otta, even though this species age-class had the highest CPUE. Therefore I speculate that this species age-class may represent a transition phase from shallow edge habitat to deeper edge habitat with coarser substrates in my study area of Otta. The low density of trout 2+ caught the backpack electroshocker also support a spatial segregation because backpack electrofishing were confined to wadeable areas and was conducted within 2 meters from the riverbank.

As expected, the habitat preference of grayling 0+ and 1+ in Otta were positively associated with PC.geo, indicating a preferred habitat with reduced valley confinement and river gradient. This is partially consistent with other findings associating sub-adult grayling to shallow edge habitats (Bardonnnet et al., 1991; Sempeski & Gaudin, 1995; Greenberg et al., 1996; Sempeski et al., 1998; Nykänen et al., 2001) because low levels of valley confinement

and river gradient are associated with shallow areas and low water velocities (Bisson & Montgomery, 1996; Benda et al., 2004). The results from the el-boat sampling showed evidence of high uncertainties linked to habitat preference for sub-adult grayling in Lagen. However, the only backpack electroshocker transect in Lagen where grayling 0+ was caught had high levels of aquatic vegetation (Lagen 2). Even though aquatic vegetation were uncommon in Lagen, this observation indicates that the presence of aquatic vegetation can affect habitat choice for sub-adult grayling.

## 5.2 Longitudinal distribution

The longitudinal distribution of each species, age-class in Otta (apart from grayling 2+) displayed strong associations with distance from the upmost spawning ground. Grayling 0+ and grayling 1+ showed a positive non-linear pattern of longitudinal distribution, where the abundance of grayling 0+ and grayling 1+ increased in the lower areas of Otta where the level of valley confinement and river gradient were reduced. The abundance of these age-classes were not expected to be so low within the first 8 km downstream of Otta, especially since there are at least 4 grayling spawning grounds within this area (Museth et al., 2011) (appendix: figure 1). The distribution pattern of grayling sub-adults in Otta might indicate a post-emergent downstream movement, which have been observed in trap studies of medium sized rivers and observed in artificial stream channels (Bardonnnet & Gaudin, 1990; Bardonnnet et al., 1991; Grimardias, Faivre, & Cattaneo, 2012). However, none of these studies have been able to identify how far downstream post-emergent grayling may distribute from spawning grounds. Even though there are several spawning grounds within my study area of Otta, the rapid increase of sub-adult grayling abundance in the lower parts of Otta may indicate a severe downstream movement of post-emergent grayling in this system. Additionally, since I found no longitudinal distribution patterns for sub-adult grayling in Lagen, the longitudinal distribution patterns of sub-adult grayling in Otta may indicate that post-emergent grayling are more susceptible to migrate (intentional behavior) or potentially drift (unintentionally) further downstream in rivers with high levels of valley confinement and river gradient.

Increased downstream displacement of post-emergent trout entering their initial free-feeding stage has been observed in studies conducted in experimental stream channels (Ottaway & Clarke, 1981; Ottaway & Forrest, 1983). However, I expected that sub-adult trout in the upper part of Otta (0-8 km) would utilize the cavities in the coarse substrates of this area as cover from the high velocities. This would cause trout to have a random longitudinal distribution with distance, but this was not the case since all age-classes of sub-adult trout had a linear or

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non-linear relation to distance from the upmost transect in Otta. Trout 0+ expressed the same distribution pattern as grayling 0+ and 1+, with a positive non-linear distribution where abundance increased rapidly in the lower section of Otta. Trout 1+ also had a non-linear increase with distance but with a much earlier increase in abundance than trout 0+, while trout 2+ were the only species age-class that decreased with distance in Otta. The distribution pattern of trout 0+ may therefore be an indication of a much higher downstream movement of post-emergent trout than expected, where trout migrate or drift downstream before displacing in habitats with a lower velocity.

The longitudinal distribution of sub-adult trout in Otta can be compared with findings of drift feeding salmonids distribution in New Zealand (Jellyman, 1994) and Alaska (Hughes & Reynolds, 1994; Hughes, 1998), where the mean length of trout and grayling increased upstream. A potential explanation for such large scale distribution patterns may be linked to fish size and their required daily ration. LaPerriere (1983) discovered that in subarctic rivers the drift density of invertebrates increased upstream, and linked the source of increased invertebrate drift concentration to be positively correlated with velocity. This could explain the gradual decrease in abundance of trout 2+ with distance in Otta, whereas trout may perform an additional upstream migration within its first three life-years in order to reach areas with a higher velocity and drift density of invertebrates in order to accommodate for the higher required daily ration.

The understanding of how habitat alterations effects adult fish species' home ranges in large rivers is increasing as a result of telemetry and catch-mark-recapture (CMR) studies. Studies conducted by NINA Lillehammer in Otta/Lagen and the river Søndre-Rena in Hedmark County Norway, shows that adult grayling have home-ranges that far exceeds the average home-range of other species like trout and pike (*Esox lucius*) (Taugbøl, Museth, Berge, & Borgerås, 2004; Museth et al., 2011; Junge et al., 2013). Even though grayling have larger adult home-ranges, we may still be underestimating the total life-history home-range of this species, since early life-history downstream migrations may be more important than first expected. These potential downstream migrations may also be affected by anthropogenic changes in river habitat. Studies conducted on trout and grayling migrations response to loss of connectivity, have primarily focused on adult spawning-migration and trout smolt survival in relation to dams (Linløkken, 1993; Jepsen, Aarestrup, Økland, & Rasmussen, 1998; Arnekleiv, Kraabøl, & Museth, 2007). However, dams also reduce upstream water velocities and river surface gradient, creating a more slow flowing river reservoir (Pringle, 1997). These changes may have a large effect on grayling and trout in rivers with high levels of valley

confinement and river gradient, because any form of post-emergent downstream migration or drift may come to an abrupt halt once it reaches the river reservoir. Apart from potentially disturbing a large part of trout and grayling life-history home range, other consequences such as increased predation on sub-adult riverine fish in river reservoirs could be severe depending on the rivers species composition. Within a reservoir the succession of fish communities may favor less riverine adapted species' such as; pike (*Esox lucius*) and perch (*Perca fluviatilis*) (Kubečka, 1993), which are all specialist piscivores that can adapt to forage in both the littoral, pelagic and profundal zone of a river reservoir (Jepsen, Beck, Skov, & Koed, 2001; Brosse, Grossman, & Lek, 2007). The proposed reduction of minimum water-flow in the first 10 km from Eidefossen in Otta may also have an effect on sub-adult fish. For grayling this is not expected to have a severe impact on post-emergent downstream movement due to high overflow during floods that often occur when grayling fry hatch. However, reducing the minimum winter-flow to  $10 \text{ m}^3 \text{ s}^{-1}$  is expected to have a severe effect on the sub-adult trout population. Even though water flow will be altered to accommodate for trout spawning, the reduction of water flow during winter and early spring may cause a strong reduction in habitat availability which may result in an increased intraspecific competition. The reduced water levels during winter will also reduce the water velocity within the 10 km long influence area. Regardless if the distribution pattern of trout 0+ in Otta is a result of intentional downstream migration or unintentional drift, I expect that any form of post-emergent downstream movement will be severely affected by the alteration in minimum winter-flow.

### **5.3 Potential study biases**

Sampling with a backpack electroshocker was conducted to identify potential biases of el-boat catchability, and these samples did explain some results. The abundance of trout 0+ caught with a backpack electroshocker implies that there was not just an overall underestimation of this species age-class compared to the upper two age-classes of trout (see figure 4), but that certain habitat features may also have had an effect on the catchability of trout 0+. This was especially noticeable in the upper areas of Otta (0-8 km) where trout 0+ had a similar abundance in the backpack shocker transects (Otta 1 – Otta 3) compared with transects in the lower parts of Otta (Otta 4 and 5). In comparison; the first 8 el-boat transects only had a combined CPUE (n/min) average of 0.06 compared with the last 7 el-boat transects that had a combined CPUE (n/min) average of 0.19. This can potentially be explained by the combination of coarse substrates and high water velocities affecting the net-handlers ability to detect trout 0+, which could also be relevant for sub-adult grayling <2 years and potentially

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trout 1+. Additionally the high abundance of trout 2+ in the upper areas of Otta may also have caused the net-handlers to reach a saturation point in catch effectiveness (Schoenebeck & Hansen, 2005), which again could have affected the catchability of trout and grayling <2 years. However the backpack electroshocker transects in the upper parts of Otta were confined to a few wadeable areas with lower velocities and finer substrates (lower percentage of boulders) than the overall appearance of this area. These transects may therefore have been conducted in more favorable trout 0+ habitats, and less favorable trout 2+ habitats. In Lagen the abundance of sub-adult grayling must be considered as underestimated in many of the el-boat transects with a shallow bank slope, fine substrates (sand) and without aquatic vegetation. The reason for this is observations of grayling 0+ that displayed a shoal like behavior in these areas, with shoals up to 30 individuals that we were not able to catch during normal sampling speeds with the el-boat (slightly faster than the surface velocity). Because size of fish is an important factor when electrofishing (Bohlin et al., 1989), the study was conducted in mid September in order to let young of the year trout and grayling to utilize as much of the growth season as possible. However, river dwelling trout and grayling  $\geq 2$  years are known to conduct a migration to overwintering habitats (slower flowing pool habitats) during late autumn, a behavior expected to be controlled by water temperature and daylight duration (Heggenes & Saltveit, 1990; Nykänen et al., 2001; Nykänen et al., 2004; Heggenes & Wollebæk, 2013). Even though such migrations have yet to be documented for grayling and trout <2 years in larger river, the time of year when this study was conducted may be a potential bias for sub-adults habitat selection and longitudinal distribution patterns. This may also be one of the reasons for the el-boats low catchability of grayling  $\geq 2$  years in both rivers.

#### **5.4 Reserch implications and future monitoring**

By performing fish sampling and habitat characterization in transects over larger spatial scales it is possible to develop a general estimate of sub-adult fish abundance and distribution patterns in these two large northern rivers. This method provides information that sampling at smaller spatial scales cannot describe to the same degree, such as the large scale effects of gradient and valley confinement. Catch biases and a high effort are constraints, but these challenges must be accepted in order to gain quantitative information from large riverine ecosystems. Based on the findings in my study I request more research on the subject of fish migration within younger age-classes in larger rivers, as I consider this to be of crucial interest for the science and management of large northern lotic ecosystems.

This study was partially conducted to assess the suitability of using an el-boat in Otta/Lagen and to gain a certain reference point of sub-adult abundance and distribution for future monitoring. Further assessments and studies prior to the re-development of Eidefossen hydropower-plant are necessary to describe temporal variation and to gain higher precision. Additionally, even though the distribution patterns found in Otta indicate that fish abundance may be affected by more than physical habitat, it is advised to conduct el-boat fish sampling with 2 or 3 × successive removal (Meador, 2005) in each habitat-type (e.g. run, riffle, pool, glide etc). This is in order to gain an estimate of the different species age-classes catchability in these habitats which can be used to correct for certain catch biases.

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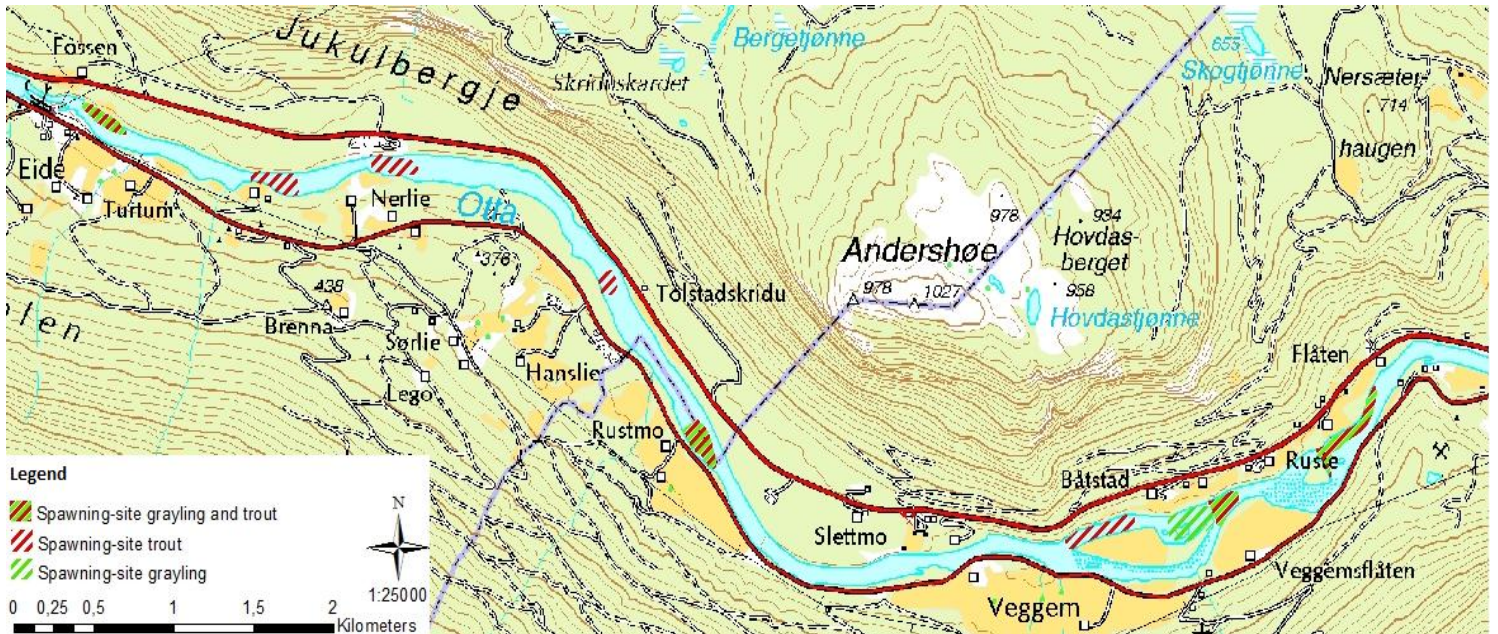
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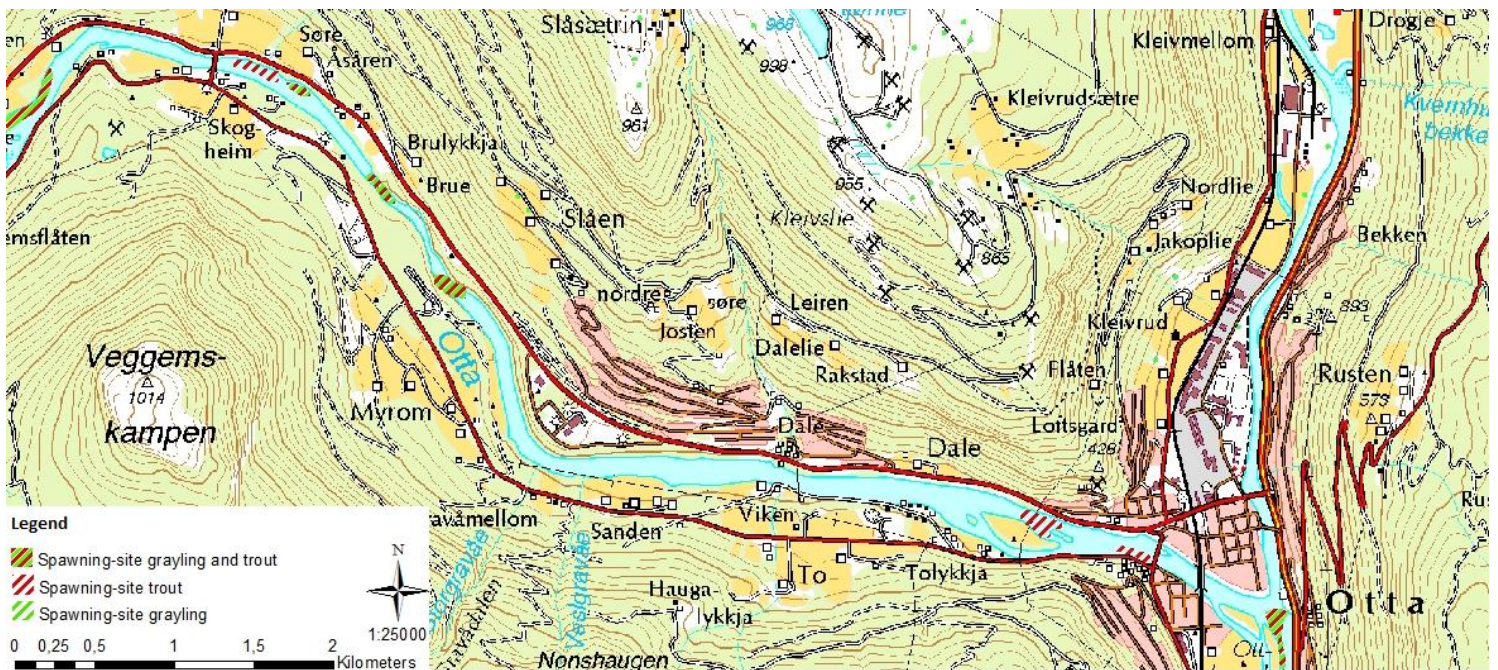
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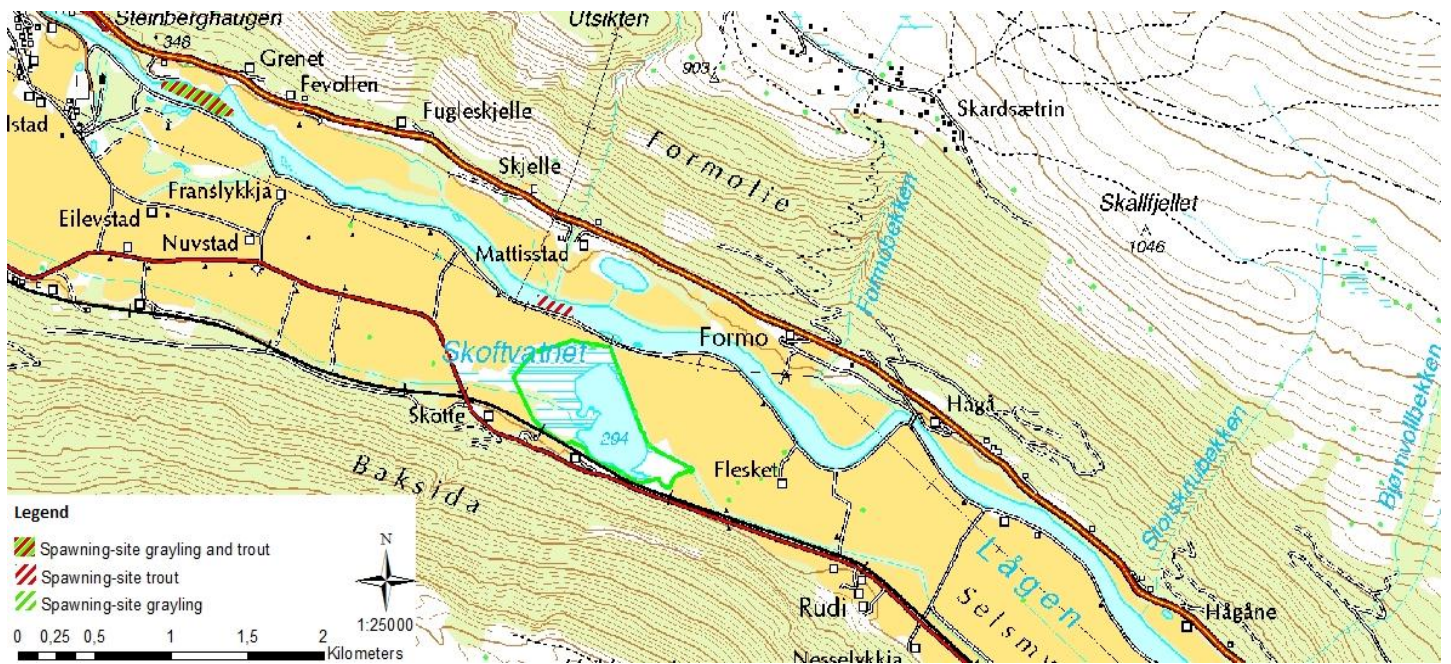
## 7. Appendix



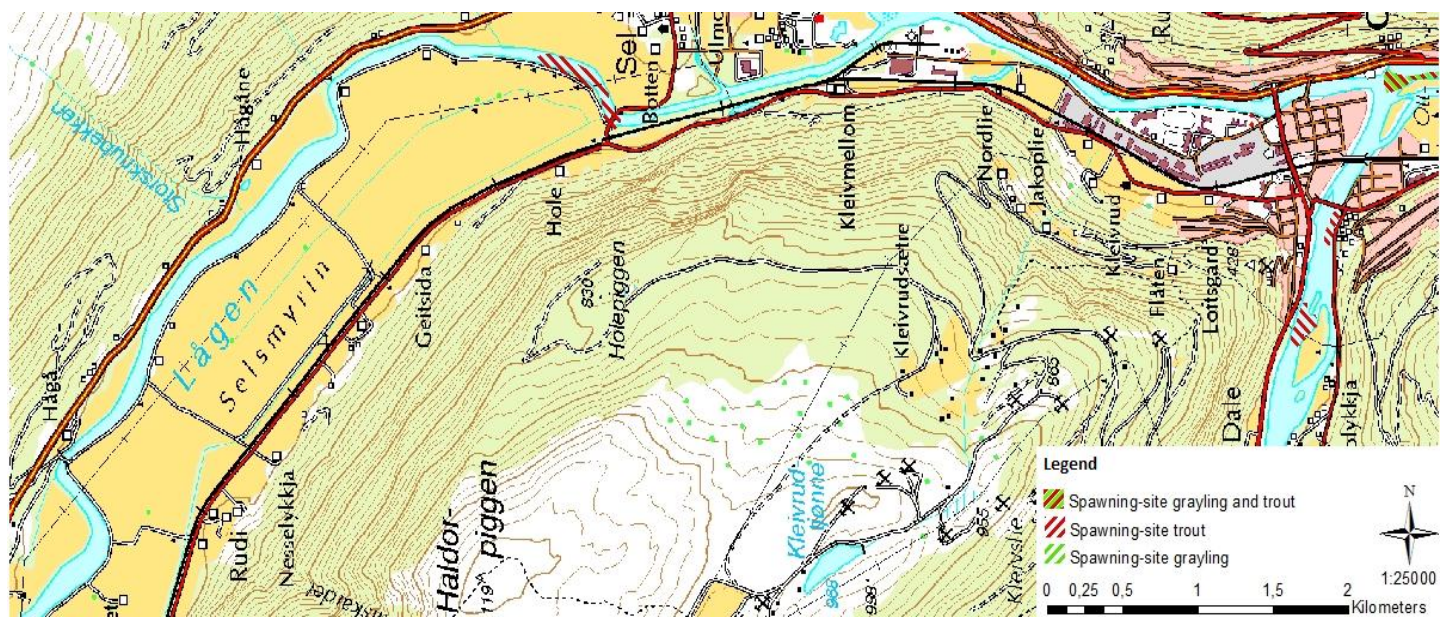
**Figure 1:** Locations of known spawning grounds in study area of Otta (0 – 8 km)



**Figure 2:** Locations of known spawning grounds in study area of Otta (8 – 17 km)



**Figure 3:** Locations of known spawning grounds in study area of Lagen (0 – 5 km)



**Figure 4:** Locations of known spawning grounds in study area of Lagen (5 – 12 km) (map rotated 90° to the left).

**Table 1:** Habitat characteristics in transects conducted with a backpack electroshocker.

Transect	UTM 32		Surface velocity m/s	m <sup>2</sup>	Aquatic vegetation	Percentage substrate cover					Substrate coarseness
	V	N				Sand	Gravel	Pebble	Cobble	Boulder	
<b>Lagen 1</b>	523586	6856759	0,41	125	0	20	40	30	10	0	38,4
<b>Lagen 2</b>	525453	6855824	0,39	100	4	85	5	0	5	5	27,4
<b>Lagen 3</b>	528643	6852526	0,71	100	1	5	20	15	40	20	66,4
<b>Lagen 4</b>	528760	6848499	0,55	125	1	10	15	15	55	5	63,4
<b>Otta 1</b>	519108	6850038	0,48	100	0	0	10	35	40	15	70,4
<b>Otta 2</b>	520901	6850313	0,41	100	0	5	10	30	40	15	68,4
<b>Otta 3</b>	522102	6850607	0,39	125	0	5	5	30	45	15	71,4
<b>Otta 4</b>	528332	6848541	0,51	100	0	5	15	10	35	35	73,4
<b>Otta 5</b>	528723	6846907	0,55	100	1	10	15	15	40	20	66,4



**Table 2:** Habitat characteristics in the el-boat transects conducted in Otta.

Transect	Percentage substrate cover					Substrate coarseness	Bank slope	Aquatic vegetation	Confinement	Level of gradient pr 100 meters
	Sand	Gravel	Pebble	Cobble	Boulder					
<b>1w</b>	0	5	5	40	50	87	steep	0	0,52910053	0,3
<b>2w</b>	0	0	0	30	70	94	medium	0	0,51507937	0,22727273
<b>3e</b>	5	5	5	55	30	80	steep	0	0,44602356	0,40847458
<b>4e</b>	10	15	15	25	35	72	medium	0	0,69789699	0,28
<b>5w</b>	0	15	25	15	45	78	medium	0	0,52649614	0,2773913
<b>6w</b>	5	15	20	45	15	70	shallow	0	0,47364739	0,49659091
<b>7w</b>	10	10	35	40	5	64	shallow	1	0,37795347	0,23333333
<b>8e</b>	15	20	20	40	5	60	steep	0	0,54951797	0,23333333
<b>9e</b>	0	20	15	30	35	76	medium	1	0,57773941	0,25686275
<b>9w</b>	0	15	5	50	30	79	medium	0	0,57773941	0,25686275
<b>10e</b>	0	10	15	45	30	79	medium	0	0,28037811	0,16736842
<b>10w</b>	10	20	15	30	25	68	medium	1	0,28037811	0,16736842
<b>11e</b>	0	0	0	10	90	98	steep	0	0,16713853	0,192
<b>11w</b>	10	8	32	35	15	67,4	shallow	1	0,16713853	0,192
<b>12w</b>	15	8	47	25	5	59,4	shallow	0	0,18941403	0,11587302

**Table 3:** Habitat characteristics in the el-boat transects conducted in Lagen.

Transect	Percentage substrate cover					Substrate coarseness	Bank slope	Aquatic vegetation	Confinement	Level of gradient per 100 meters
	Sand	Gravel	Pebble	Cobble	Boulder					
<b>1e</b>	10	35	30	10	15	57	medium	0	0,087449959	0,005555556
<b>1w</b>	15	30	30	5	20	57	medium	0	0,087449959	0,005555556
<b>2</b>	45	15	0	30	10	49	medium	1	0,101969323	0,013846154
<b>3e</b>	45	15	0	25	15	50	shallow	0	0,105015332	0,024166667
<b>3w</b>	45	10	0	25	20	53	shallow	2	0,105015332	0,024166667
<b>4</b>	50	35	10	2	3	34,6	shallow	4	0,089824519	0,024166667
<b>5e</b>	0	0	5	15	80	95	steep	0	0,084521621	0,026250000
<b>5w</b>	0	0	5	10	85	96	steep	0	0,084521621	0,026250000
<b>6</b>	50	5	10	25	10	48	steep	2	0,094824353	0,022000000
<b>7e</b>	80	5	0	7	8	31,6	shallow	0	0,088949368	0,028750000
<b>7w</b>	10	0	5	30	55	84	steep	0	0,088949368	0,028750000
<b>8</b>	50	10	0	20	20	50	medium	0	0,071002117	0,033698630
<b>9</b>	0	15	15	30	40	79	steep	0	0,07686608	0,090588235
<b>10e</b>	0	20	15	40	25	74	shallow	0	0,170245351	0,093333333
<b>10w</b>	0	25	10	45	20	72	shallow	1	0,170245351	0,093333333
<b>11w</b>	0	0	0	35	65	93	steep	0	0,198456686	0,111910112
<b>12w</b>	10	20	30	35	5	61	shallow	0	0,129722195	0,092000000