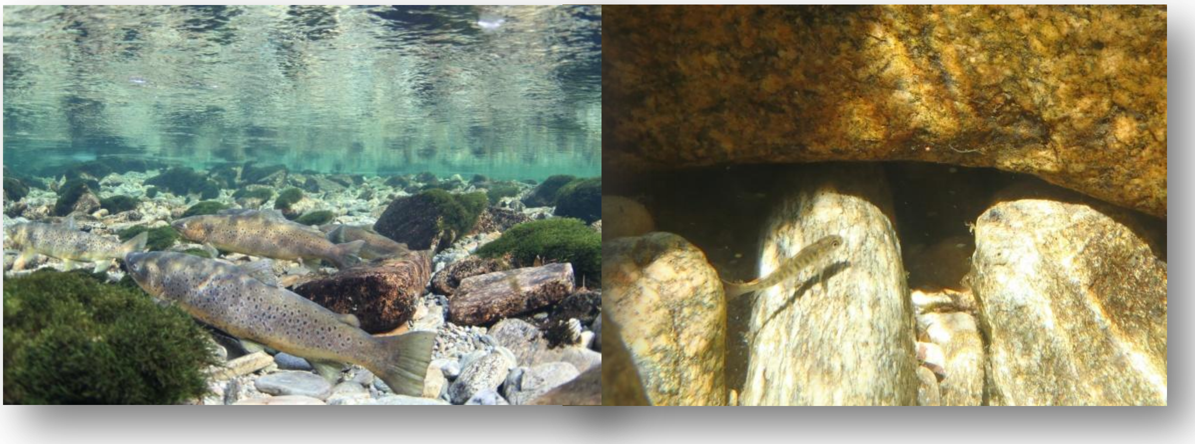
Spatial Distribution of Seatrout Spawning and the Effects on Juvenile Abundance in River Teigdalselva, Western-Norway



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[Front page: Left: Seatrout spawners in River Teigdalselva (Photo: Bjørn Barlaup). Right: Young of the year seatrout in River Teigdalselva (photo Eirik Straume Normann)**]**

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Abstract

The spatial distribution of seatrout spawning-grounds, microhabitat features and the resulting juvenile distribution were observed in a typical Western-Norwegian river. A total of 1870 squares within 187 cross-transects at 50 m distances were used to assess trout distribution in the 10 km long river. In October a total of 524 seatrout spawners were observed while snorkelling the length of the river. Spawners were found to be aggregated at 76 (40.6%) of the 187 transects in the river, and 50% of the spawners were found on 15 transects. One factor contributing to the observed skewed distribution was the non-uniform appearance of spawning areas which correlated significantly ($r = 0.32$, $p < 0.001$) with the distribution of spawners. Spawning area constituted 0.7‰ of the total area of 183 000 m^2.

The autocorrelation coefficient for spawning area showed continuous significance for only 1 lag (75 m), indicating patchiness in spawning area distribution. Young of the year (YOY) were more continuously distributed with significance for 5 lags in the autocorrelation. Spatial cross correlation between spawning area and YOY showed significant correlation in 6 transects downstream and 3 transects upstream. The number of YOY was higher at transects in the proximity of spawning area than transects remote from spawning area.

The analyses of the generalized additive models showed that the spatial distribution of YOY was significantly affected by the spatial distribution of both spawning areas (28.2% deviation explained, $p < 0.001$) and spawners (23.4% deviation explained, $p < 0.001$). Adding the habitat parameters, depth, velocity, substrate and shelter, to the model with spawning area showed that the interaction between substrate and shelter had the best fit with YOY distribution, followed by water velocity and depth. The full model explained a total of 59.3% of the deviance ($p < 0.001$, AIC = 1306). YOY length was negatively correlated with YOY abundance ($r = 0.30$, $p < 0.001$) indicating a strong density-dependent growth.

The present study gives a clear indication that the availability of spawning area and suitable nursery area set the limits for the number of seatrout potentially produced in the River Teigdalselva. The patchy distribution of spawning areas are also likely to apply for other Western-Norwegian rivers sustaining seatrout and the present findings are therefore likely to be of general interest. Moreover, the results found in the present study give some relevant information about expected usefulness and effective design of mitigation efforts to increase populations. Increasing spawning habitat is currently of particular interest in rivers where the original spawning areas have been destroyed by human activities.

Samandrag

Den romlege fordelinga av gyteområda til sjøauren, mikrohabitatkarakteristikk og den fylgjande fordelinga av ungfisk vart undersøkt i ei typisk vestnorsk elv. Totalt 1870 m^2 fordelt på 187 tversgåande transekt med 50 meters avstand vart undersøkt til å fastsetja fordelinga i den 10 km lange anadrome delen av elva. I oktober vart det utført gytefiskteljing ved snorkling av heile elva frå vandringshinderet til utløpet. Gytefisken vart funnen å vera opphopa på 76 (40.6%) av dei 187 transekta, og 50% av gytefisken vart funne på 15 transekt. Ein faktor som medverka til den ujamne fordelinga av gytefisk var tilgongen til gyteområde som samsvarte signifikant ($r = 0.32$, $p < 0,001$) med fordelinga av gytefisk. Gyteareal utgjorde 0.7‰ av det totale arealet på 183 000 m^2.

Autokorrelasjonskoeffisienten for gyteareal synte kontinuerleg signifikans for berre eitt transekt forseinking (75 m), noko som indikerer at gytinga ikkje skjedde i påfylgjande seksjonar. Fordelinga av gyteareal var difor klumpvis fordelt både på ein stor og liten skala. Årsyngelen hadde ei meir kontinuerleg fordeling med signifikans for fem transekt forseinking i autokorrelasjonen. Romleg krosskorrelasjon mellom gyteareal og årsyngel synte signifikans i seks transekt nedstraums og tre transekt oppstraums eit gjeve transekt. Talet på årsyngel var høgt på transekt i nærleiken av gyteområde og lågt på transekt som låg langt frå gyteområde.

Analysane av GAM-modellar syner at den romlege fordelinga av årsyngel er signifikant påverka av den romlege fordelinga av både gyteareal (28.2% deviasjon forklart, $p < 0,001$) og gytefisk (23.4% deviasjon forklart, $p < 0,001$). Ved å føya til habitatparametra, djup, straum, skjul og substrat, viste modellen med gyteareal at interaksjonen mellom substrat og skjul hadde den beste tilpassinga til fordelinga av årsyngel, fylgd av straum og djup. Heile modellen forklarte 59,3% av deviasjonen ($p < 0,001$, AIC = 1306). Lengda til årsyngelen var negativt korrelert med tettleik på transekta ($r = 0,30$, $p < 0.001$), noko som sterkt indikerar ein tettleiksavhengig vekst.

Det føreliggjande studiet gjev ein klår indikasjon på at tilgjengelegheita på gyteareal og passande oppvekstområde set grensene for sjøaureproduksjonen i Teigdalselva. Ei ujamn fordeling av gyteareal er mest truleg tilfelle i mange sjøaureførande vestlandselvar og resultata frå dette studiet er i så måte av generell interesse. Dessutan gjev resultatet her relevant informasjon om danninga av nye gyteområde og dei positive effektane ein kan forventa av slik innsats. Innsats for å auka gyteareal er av spesiell interesse i elvar der opphavlege gyteområde er øydelagt av menneskeleg aktivitet.

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1. Introduction

When starting this field work the main issue was to look for patterns in the distribution of young of the year (YOY) anadromous brown trout (*Salmo trutta*, hereafter called seatrout) and Atlantic salmon (*Salmo salar*) related to distribution of spawners and quality of the habitat. The salmonid spawners are known for their precise homing to their natal river they left as smolts (Hasler, 1996). Further, the females are very selective in their choice of spawning area as they seek out suited areas for egg survival based on water velocity, depth and substrate (Armstrong et al., 2003). These characteristics are a product of salmonid evolution (Fleming, 1996, Fleming, 1998). In Western Norway, the seatrout and the Atlantic salmon have been present since the last glacial age ended approximately 10 000 years ago (Ramberg et al., 2007), and have been important resources for humans since the stone age (Bøe, 1934).

Species which invest a lot of energy on their offspring, for example providing parental care, do often have low fecundity and mortality rates in early life stages (e.g. mammals) compared to species with high fecundity and little parental care (e.g. plants and many fish species). Species with high fecundity and a complex life cycle will often have the greatest loss of individuals in the early life stages (Caddy, 1991, Vermeij and Sandin, 2008, Morin et al., 1991). In the last years several papers have showed how populations are regulated in early life in salmonids (Einum and Nislow, 2005, Armstrong, 1997, Einum et al., 2006b, Imre et al., 2005, Jonsson et al., 1998, Lobon-Cervia and Mortensen, 2006, Teichert et al., 2011). These studies therefore suggest that the different life stages in salmonid populations should be looked into separately. Einum and Nislow (2005) showed how salmonid populations are regulated at small spatial scale in the first weeks after emergence. The dispersal is limited for these small salmonids, and the topography of the rivers may increase or decrease the dispersal length.

Different species have different explanations of fluctuations in population size and hence density. For roe deer (*Capreolus capreolus*) and elk (*Cervus elaphus nelsoni*) the regulating factors can be predation, winter mortality due to snow conditions and duration and time of birth (Melis et al., 2009, Smith and Anderson, 1998). Here it is likely that density-independent factors have the strongest effect on juvenile survival. For salmonids the regulating factors have been disputed over for many years. Early literature on brown trout ecology argued that cannibalism and fishing-mortality induced by fishermen were the most important factors regulating brown trout populations (Sømme, 1941). These and other density-independent factors were long seen as the regulating factors on salmonid populations. But as new results showed a stronger correlation with density-dependent factors there became a regime shift in the knowledge of juvenile salmonids ecology (Elliott, 1989, Elliott, 1993, Armstrong, 1997, Einum and Nislow, 2005, Einum et al., 2006b, Imre et al., 2005, Imre et al., 2010, Milner et al., 2003, Ward et al., 2007). For salmonids the first weeks after emerging from redds seem to be the phase when most of the density-dependent mortality occurs in their life cycle, and this period is often referred to as critical (Elliott, 1994). The literature mentioned above supports the explanation of density-dependent factors as the main factors affecting population size in salmonids.

The anadromous length of rivers varies enormously from few hundred meters to hundreds of kilometer. Nevertheless, the river can be occupied by one population or numerous metapopulation, and the regulation of populations will most likely not happen over their total extent because the entire river length is not accessible for juvenile salmonids due to restricted dispersal. Therefore, to understand the dynamics of population regulation it is not appropriate to use coarse scales. Fine scales should be examined to understand each rivers production potential and bottlenecks for production (Einum and Nislow, 2005, Einum et al., 2008a).

Atlantic salmon has been the object of many studies on population dynamic in early life stages (Armstrong and Nislow, 2006, Beall et al., 1994, Crisp, 1995, Davidson et al., 2010, Einum and Nislow, 2005, Einum et al., 2008a, Einum et al., 2006b, Nislow et al., 1999, Thorstad et al., 2010, Teichert et al., 2011). Some has also been performed on brown trout (Crisp, 1993, Elliott, 1989, Elliott, 1993, Lobon-Cervia and Mortensen, 2006). Relating spawning distribution to brown trout YOY density and growth has, however, never been carried out on a small spatial scale in a natural anadromous population. It is interesting to see if there are any differences between the close related salmonids. Therefore we designed a field study in a typical West-Norwegian glacial valley river, at a fine spatial scale. The study covered the whole anadromous length of the river and nearly all of the accessible area of the seatrout population. By electro-fishing the whole river reach, and assessing the spawning population, I wanted to find out to what extent the distribution of spawners affected the YOY distribution, and how far downstream and upstream migration could be expected. Habitat measurements were also done to see how much the habitat parameters water velocity, depth, substrate and shelter affected YOY residences. Causes of dispersal are discussed. In addition, length-measurements were taken of all caught fish to see if there was any relationship between growth and YOY densities. Further, mitigating efforts are proposed to increase the production in rivers with a skewed spawning distribution.

In western parts of Norway the situation for salmonids has gone from sustainable populations to near extinction in many rivers. The worst scenarios are experienced in the county of Hordaland. In this county there were no rivers open for fishing without extraordinary regulations in the 2010 season and the spawning population target for Atlantic salmon were not reached for any of the more than 30 salmon-rivers in the county (Anon., 2010). The situation for the seatrout is not as dramatic as for the Atlantic salmon, but declining populations has also led to the abandoning of fishing in many seatrout rivers (Anon., 2010). This study can, hopefully, participate in the knowledge of where to put in resources in the managements of rivers to increase their carrying capacity.

2. Materials and Methods

2.1 Study Site

The study was carried out in River Teigdalselva (Fig. 2.1), a tributary of the Vosso river in western Norway (60°42´N, 6°06´E). The study area was the approximately 10 km long river reach from Lake Evanger to Kråkefossen, which constitute a natural migration barrier for anadromous fish, and thus comprise the total anadromous length of the river. The river had an original drainage area of 145.7 km^2, of which, 58.8 km^2 have been transferred to the hydroelectric power station at Evanger. The remaining and present drainage is 87 km^2. As a result of the river regulation, the water discharge in the river is heavily modified (Barlaup, 2004). The water discharge is reduced with approximately 70% at the migration barrier (Fjellheim et al., 1994), and somewhat less reduced further downstream due to tributary streams and drainage from unregulated areas. Wetted area at 1 m^{3}s^{-1} is approximately 183 000 m^2 and detected spawning area 0.7‰ (129.5 m^2). There is no requested minimum water discharge to mitigate the loss of water to the power station, which results in frequent periods with very low water discharge, especially in winter. Also, transfer of water from the headwater lakes in the drainage area results in relative fast and great changes in discharge throughout the year.

The reduced water discharge is likely to have several negative impacts on the fish population in the river. The wetted area is reduced and episodes of low water discharge may cause redds and juveniles to strand and freeze during winter (Bradford, 1997, Hvidsten, 1985, Saltveit et al., 2001, Scruton et al., 2005). The reduced discharge has also caused extensive plant growth in the river`s only lake, Mestadvatnet, and thereby degraded the quality of the previous important spawning area at the outlet of Lake Mestadvatnet, and reduced the available fish habitat within the lake (Gabrielsen et al., 2009).

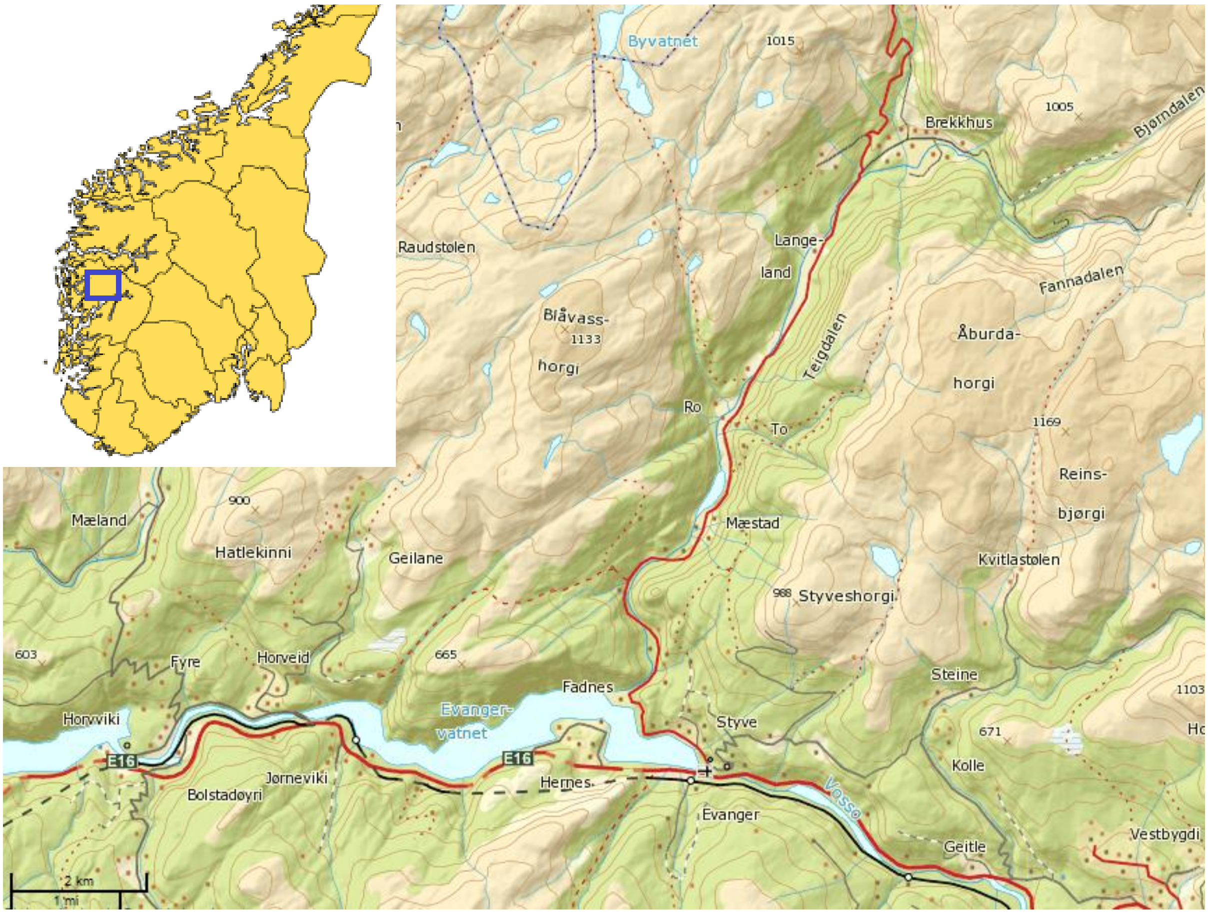

Figure 2.1: Map showing the location of the River Teigdalselva in western Norway. The outlet of the river is in the Lake Evangervatnet. Lake Mestadvatnet is located at Mestad 4 km upstream from Lake Evangervatnet. The River Teigdalselva and Lake Evangervatnet are both parts of the River Vosso watershed. Data derived from Statens Kartverk.

River Teigdalselva is characterized by long stretches with homogeneous substrate and slow flowing water, with some stretches of large boulders with small pools in between. The river reach upstream Lake Mestadvatnet is characterized by greater alluviums separated by steep rapids, while downstream pools and rapids dominates. The alluviums contain seemingly little or no shelters, except from the river banks where some refuge areas are available at average water discharge. However, at low water discharge the banks become dry land and much of the shelter habitat disappear. The rapid reaches is fast flowing and characterized by a substrate dominated by boulders and solid rocks and therefore contains no, or very few and small spawning areas.

During the 1990s, a number of restoration efforts were implemented to mitigate the negative effects of the reduced water discharge in River Teigdalselva. Basin weirs were made at four areas to compensate for loss of biotopes and create suitable habitat for fish. The weirs have an important function to sustain wetted areas in periods with very low water discharge, and the weirs will therefore generally have a positive effect on fish survival and recruitment. However, the weirs may favour seatrout over Atlantic salmon as the deep and slow-flowing habitat of the weir basins is not typically preferred by Atlantic salmon (Heggenes and Saltveit, 1990). The water velocity within the basins is typically low and gives little possibilities for spawning. In addition to the four weirs, there have been placed boulders in an approximately 100 m reach of the river in the upstream end of the weir basin at Fasteland. The boulders have led to much more heterogeneous flow and substrate conditions which have generated both important spawning and juvenile habitats.

Seatrout is by far the most dominant species in the river. There is also resident brown trout in the river but these are largely outnumbered by the seatrout. Atlantic salmon also frequently occurs and spawns in the river, but has been at a critical low population number after the collapse of the salmon in the whole Vosso river system in the late 1980`s. The seatrout population in the river system has also been reduced, but population size is not as critical low as it is for the Atlantic salmon. Seatrout and resident brown trout represent two different life-history strategies within the same species, and they may both contribute to the same gene pool (Elliott, 1994, Jonsson, 1985). Further the offspring of the two types are not possible to separate based on morphology. As a result, all trout juveniles are referred to as “seatrout” in the remaining part of the thesis. Aging of trout refer to the year they are hatched, where 0+ refer to one- summer old fish and 1+ and 2+ to two-, and three-summer old fish. Four distinct life cycles can be found in seatrout within a stream based on migration patterns. The first type is the resident form which spends their whole life in their natal stream. Second, there is a form which migrates inside the river system after the first year in the natal stream before returning as spawners. The third form is similar with the previous one except that the migrations are to a neighbouring lake. The fourth, and the main type in this thesis, is the estuarine or seatrout, migrating as smolts, to brackish or salt water (Elliott, 1994, Jonsson, 1985). Spawners in River Teigdalselva are represented by migrating and non-anadromous males and females. Seatrout usually smoltify at a certain size, and since growth is related to temperature and length of growing season it varies over latitudinal gradients. L’Abee-Lund et al. (1989) found that in Norway, from 58°N to 70°N age at smoltification varied from 1-8 years. Sea age at maturity and return to river varied from 1-13 years with females slightly older than males.

2.2 Spatial Distribution of Spawning

The spatial distribution of spawning was registered both by *in situ* counting of spawners, and by assessing suitable spawning habitat along the river. In River Teigdalselva there has been performed spawner census of seatrout and Atlantic salmon yearly since 1991 by LFI-Uni Environment. The spawners have been counted by one person snorkelling downstream and recording the number and size of spawners, and by recording the spatial position on a map. During counting, seatrout is sorted into four categories based on estimated size, < 1kg, 1-2kg, 2-3kg and > 3kg. In the period 1999-2011, it has been registered from 96-750 seatrout/yr, and 1-34 Atlantic salmon/yr in River Teigdalselva (Gabrielsen et al., 2009).

In 2009, the spawning census was carried out on 11 October by three persons (me and two experienced snorkelers from LFI-Uni Environment). The counting was performed near the peak spawning time for seatrout, and most of the spawning population is therefore expected to be at or near the spawning grounds. Further, the clear water and small size of the river makes snorkelling a very suitable method for assessing the spawning population. However, the method is still likely to underestimate the total spawning population, as some fish may hide and avoid being noticed by the snorkeler. Further, only fished that have been passed by the snorkeler are registered, to avoid multiple counts of the same fish.

Mapping of the size and spatial distribution of spawning areas were based on data from the spawning area assessment performed by LFI-Uni Environment. These data were based on the mapping of spawning areas and spawners during the 2004-2009 period and updated with a mapping of the spawning areas conducted during spring 2009 (16 April 09). The spawning habitat assessment was performed together with two experienced researchers who had previously conducted the counting of spawners in the river. The approximate area of river gravel used for spawning was assessed by wading, and the size (m^2) was then estimated and positioned on maps. Although the assessed spawning area is not a strict quantitative measure of egg deposition, a large spawning area is likely to reflect a high spawning activity, and thus serve as a proxy for egg deposition. These data on the size of the spawning areas were meant to be supplemented by a census of measuring the size of constructed redds planned to be carried out during late autumn, just after the spawning time, and while individual redds still are visible as light patches of disturbed gravel. Due to an unusual cold period in late autumn 2009, assessment of exact area of constructed redds made by the fish could not be performed in the time before the river froze up, and when the ice drift started, the riverbed became disturbed mechanically by the ice making it impossible to detect individual redds.

2.3 Field Work and Spatial Distribution of Fry

Assessment of fry distribution was performed by elctro-fishing. The field work was conducted from 24 June to 10 August 2010 at low water discharge. A total of 187 transects were investigated, all spaced at regular 50 m longitudinal intervals that were defined on beforehand and plotted on a map. At long stretches with few references in nature, Leupold® RX-600 Rangefinder was used to find the next transect to be fished. Each transect consisted of 10 squares each 1 m^2, that were divided evenly along the width of the river. Each square meter was fished thoroughly with a mobile electric system following Bohlin et al. (1989). The electric apparatus was programmed on high frequency and 1400 volt, to increase the catchability of small fish. Transects were usually approached against current. When going downstream, care was taken to avoid scaring fish at the next transect. Since the river width varied from about 5 to 50 m the way the fishing was performed shows the relative densities of juveniles between transects. The fish caught was identified to species, fork length measured to nearest millimetre and divided between YOY and older fish based on size distribution. Three distinct size classes of seatrout (≤58, 59-97, and ≥98) could be distinguished according to the length-frequency distribution of all seatrout captured during the study (N = 1673). In addition to the fish caught, it was noted how many fish that were observed but not caught on each square. These were added to the total number of fish during analyses (see Results). The number of the newly hatched 0+ was of primary interest, but the amount of older fish was also registered.

In each square meter substrate size, water velocity, depth and shelter were measured or quantified. Substrate size was measured using a metric measuring rod. Water velocity was measured using a velocimeter, taking the average speed of water at 2/3 height in the water column. Depth was measured using the handle on the landing net as a metric measuring rod. Shelter was assessed visually, where hollows deeper than 3 cm were quantified as shelters (Finstad et al., 2007). In this fieldwork shelter (defined as hollows > 3 cm) was a categorical variable divided between little, some and much shelter. Little shelter when less than ¼ of the square meter was covered with shelter-providing stones or vegetation, some when between ¼ and ¾ and much when over ¾ of the square meter provided shelter. Unlike Finstad et al. (2007) not only stones, but in addition vegetation, and then mainly *Fontinalis dalecarlica* and *F.antipyretica* (Lindstrøm; et al., 2004) were characterized as shelter. In some of these tufts there were many YOY and thoroughly fishing was needed to collect everyone (pers.obs).

Due to the fact that YOY can grow extremely fast in the first weeks of feeding it was important to do the field work over a short period. Time of hatching may differ along the examined reach of the river as a result of within-river variation in temperature and time of spawning. This was especially visible at the outlet of Lake Mestadvatnet in May 2010, where alevins were detected while still eyed eggs were present in the rest of the river (pers.obs).

In addition to seatrout census, there were planted 13000 Atlantic salmon eggs spread on five different locations as a part of the stock enhancement programme to save the endangered salmon population in the Vosso river system. The planting was coordinated by the Voss hatchery (http://vossklekkeri.no). The eggs came from the hatchery at Voss and the live gene bank in Eidfjord. The initial plan was to plant as much as 10 000 eggs at each location, and use this to examine the spatial distribution from the known planting locations. Due to high egg mortality prior to planting, locations and number of eggs were reduced. Eggs were planted in Vibert-boxes containing 1000 eggs each together with gravel of suitable size and buried in potential spawning habitat. Care was taken to avoid disturbance of existing seatrout redds at the locations. In July, when the alevins had emerged from redds in search for external food, the boxes were dug up and survival from eye egg stage recorded. Unfortunately the extent of the planting was too small to get any dataset worth analysing.

2.4 Statistical Analyses

All analyses were completed with the statistical software package R 2.10.0 for Windows (R Development Core Team, 2009). GAMs were from the mgcv library (Wood, 2001).

2.4.1 Distribution of Young of the Year, Spawning Area and Spawners

Before analysing, the total anadromous length of the river (Mestadvatnet excluded) was divided into 50 m sections corresponding to the transects that were electro-fished. Thus, the transects are located in the middle of each section, c. 25 m from the neighbouring section. The number of spawners and area of spawning habitat were then assigned to each of the position on the maps.

Bar plots were used to graphically illustrate YOY relative abundances along the river, and spawning area and distribution of spawners were included in the illustration. The effects of the biotic factors, i.e. distribution of spawners and spawning area, and the abiotic factors, i.e. water velocity, depth, shelter and substrate, on YOY seatrout density were then determined using generalized additive models (GAMs) from the mgcv library, since data exploration did not show any clear linear patterns between YOY density and the explanatory variables.

The river was treated as a one-dimensional line to investigate the spatial association between spawning activity and YOY densities. The approach is analogous to time series analyses and allows analysing spatial autocorrelation of YOY densities and spawning features. Spatial autocorrelations were plotted to describe how spawning area and YOY densities of each transect were related to those n lags (transects) away. This gives a general view of how far away one could expect to catch fish emerged from redds from the same section. Furthermore, cross-correlation was used to describe how the spawning area within a section influenced YOY densities in transects upstream and downstream from the given section.

The different habitat parameters were checked between YOY of salmon and trout, and between older salmon and trout. Summary was taken of each of the parameters in the different species and size classes and compared with a chi-square test for two or more independent samples.

2.4.2 Analysis of Fish-Length

Since the field work went over 18 days and the juveniles are in their best growing period in the river in their first period of external feeding (Elliott, 1975, Elliott, 2009), spatial length analyses were performed with respect to days after electrofishing started. Length related to density of YOY and days after field work start were analysed as a linear model with length as the log transformed response variable and density and days after field work as continuous explanatory variables.

2.5 Counts of Zero

In the electrofishing zero YOY were caught or observed on 1204 of the 1870 transects. High numbers of zeros in the YOY survey constitute a challenge to the analyses. Three main types of zeros occur in ecological data, true, false and naughty-noughts zeros (Austin and Meyers, 1996, Martin et al., 2005). True zeros are when a species is not present due to ecological processes, e.g. habitat is unsuitable, and when a species does not saturate its entire suitable habitat. False zeros occur when sampling is done in a suitable habitat but at e.g. wrong time of the day, and when the species is difficult to detect, catch or see (Martin et al., 2005, Zuur et al., 2009). Naughty-noughts are zeros due to sampling outside habitat range of the species. In this study the zeros are likely to be mainly of the first type. With the very limited dispersal YOY can have the first weeks after emergence, the problem of zero counts at suitable habitat is likely to occur. In addition, the sites may be located too far from redds to expect YOY appearance. Since the number of spawners has been reduced due to declining population in the River Vosso system (Barlaup, 2004, Barlaup, 2008), the last year’s production of YOY is possibly not as large as it could be. This will eventually lead to suitable habitat free of YOY. One could also expect some false zeros. When performing electrofishing there are many challenges one must cope with to get the highest catchability. The greatest challenges are high water velocity, depths over half a meter and high temperature. With 383 squares deeper than 50 cm and 105 squares with water velocities greater than 50 cm s^{-1} the chance of experiencing false zeros is high if YOY are present at the site.

Due to the large number of zeros an investigation of variance in YOY count data is necessary. When the mean is lower than the variance, and the variance is higher than 1.5 the general opinion is that there are too many zeros. In Poisson distribution variance should equal the mean (White and Bennetts, 1996). If one ignores zero-inflation two possible consequences can occur. Estimated parameters and standard errors may be biased and secondly the number of zeros can cause overdispersion (Zuur et al., 2009). There are several different distributions and families that could be used in GAM-analyses. In this study Poisson distribution was chosen as the most favourable model for analyses on transect levels due to the low number of zeros at this level. As a consequence of the great numbers of zeros on square meter level the analyses of YOY distribution related to habitat were carried out on transect level, in the same model as YOY distribution related to spawning area.

The continuous connection between transects causes independence between neighbouring transects which constitutes a challenge in the analyses. To overcome this challenge the river was treated as a continuous line and GAMs were used instead of generalized linear models. GAMs are applicable to likelihood-regression models, but the linear predictor in generalized linear models are replaced with the additive predictor. This is believed to strengthen the power of explanation of data, because the generalized additive models are described as data- rather than model-driven (Teichert et al., 2011). The model is especially useful in detecting non-linear covariate effects (Hastie and Tibshirani, 1990). In generalized linear models (GLMs) the relationship between the predictor and a continuous variable is specified by some explicit functional form, whereas in GAM non-parametric smoothers are used to describe the relationship (Crawley, 2007a). This is done without requiring us to specify any particular mathematical model to describe the non-linearity (Crawley, 2007b). Predictors in the YOY seatrout density model were spawning area or spawners, depth, water velocity, substrate and shelter (Nislow et al., 1999). Correlation tests were used to see if some of the habitat parameters were closely related. The tests revealed strongest correlation between substrate and shelter which were highly correlated ($p < 0.001$, $r = 0.28$). In the following analyses the interaction of shelter and substrate was used. GAMs were performed using a forward stepwise procedure. The first model starts with transect and spawning area. Then the model was tested with each of the habitat parameters. The one with the highest deviance explained was used as the basis for the next model. Each of the parameters was then added to the preceding model and the model with the highest deviation explained was retained. This was done until all of the parameters were in the model, and each model was tested against each other using Akaike`s information criterion (AIC). In turn, each of the parameters was removed from the final model to see which removal took away most of the deviation explained.

3. Results

3.1 Distribution of Spawners

During the spawning census, spawning seatrout were registered on 76 (40.6%) of the 187 transects in the river, and 50% of the spawners were found on 15 transects. There were several sections of the river extending over 500 m without spawners. Thus, spawning fish were not uniformly distributed, but were found aggregated within the river (Fig 3.1). There were also more spawners in the upper half of the river (upstream Lake Mestadvatnet), than in the lower part of the river (343 seatrout, 3.17 per transect, above Lake Mestadvatnet vs. 181, 2.29 per transect, below). A total of 524 seatrout and 3 Atlantic salmon were recorded.

The distribution of spawners was corresponded with the spatial distribution of spawning areas. A correlation test between distribution of spawner and spawning area showed a significant relationship ($r = 0.32$, $p < 0.001$).

3.2 Results of Electrofishing

A total number of 1301 YOY seatrout, 28 YOY Atlantic salmon, 372 1+ and older trout and 54 1+ and older salmon were caught during electrofishing. In addition, 365 YOY and 500 1+ and older fish were observed but not caught. As YOY seatrout vastly outnumbered YOY Atlantic salmon (YOY Atlantic salmon constituted only 2.1% of the total numbers of YOY caught), all observed YOY were assumed to be seatrout. The resulting analyses are therefore consequently performed on the total numbers of YOY seatrout (caught + observed).

On a square level, it was found YOY seatrout on 666 (35.6%) of the 1870 squares that were electrofished, with the maximum number of YOY seatrout found on a square being 20 individuals. On a transect level, it was found YOY seatrout on all but six (96.8%) of the 187 transects, with the median number of individuals per square being 7 and the highest number being 47 (Fig. 3.1). Seatrout 1+ and older were found on 494 (26.4%) of the squares (max: 41 individuals) and on 157 (84%) of the transects (median: 3 individuals, max: 48 individuals).

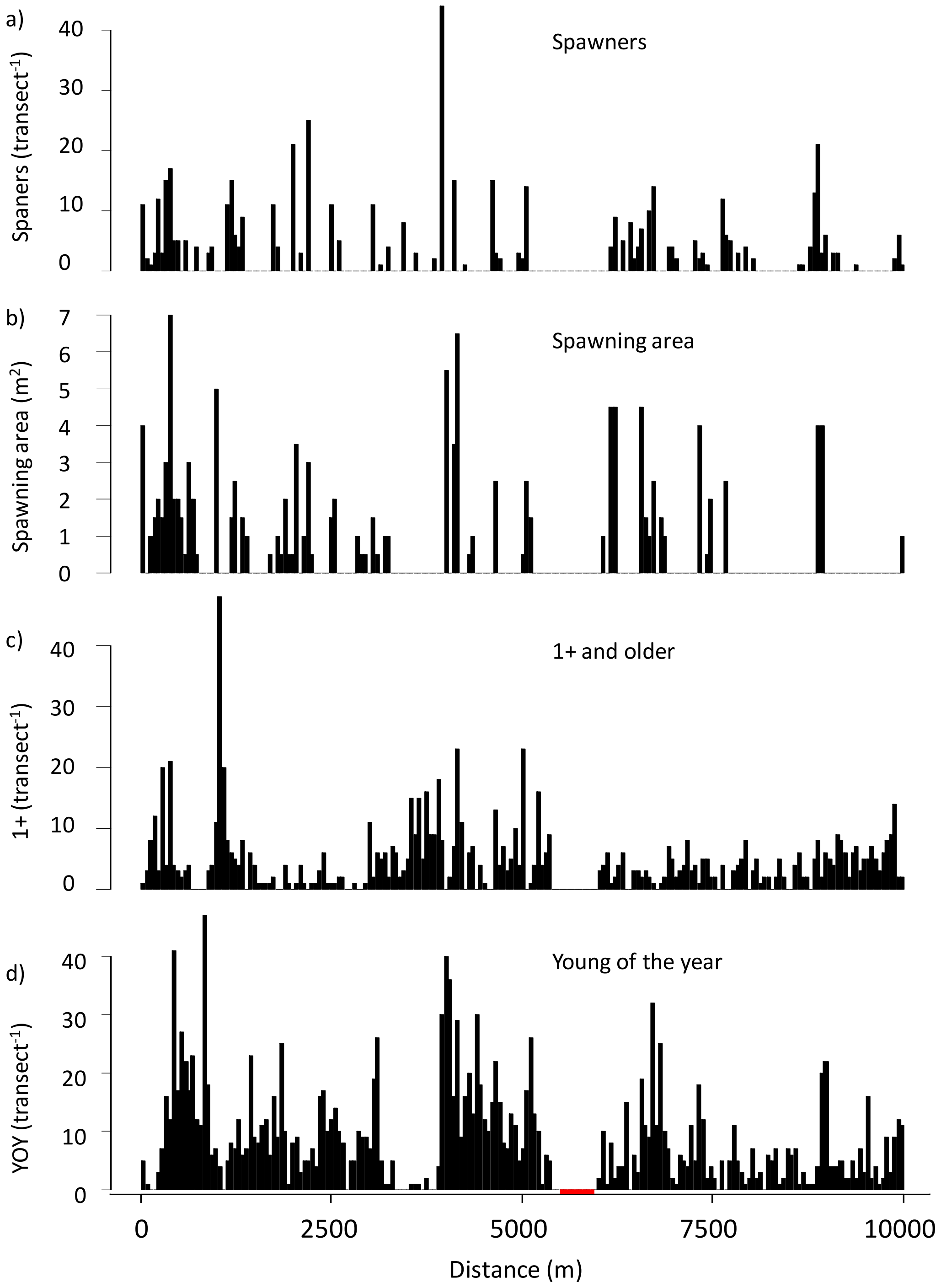

Figure 3.1: a) Distribution of spawners **(b)**, spawning areas **(c)**, 1+ and older trout and Atlantic salmon **(d)** and young of the year seatrout in River Teigdalselva. Distance is given in meter from the migration barrier to the outlet into Lake Evangervatnet. The red line indicates placement of Lake Mestadvatnet, where no measures were performed.

3.3 Distribution of YOY Related to Spawners, Spawning Area and Habitat

From Fig. 3.1, many of the transects with high densities of YOY appear to be aggregated within the river, and also appears to coincide with the spatial distribution of spawning areas and spawners. For example, the density of YOY were reasonably high in most of the transects in the area downstream the migration barrier (Kråkefossen), where there also was found a high availability of spawning habitat and a high density of spawners. There was also found very high YOY densities at, and downstream, Fasteland (ca 4000 m downstream Kråkefossen), which constitute the largest aggregated spawning area in the river, and the area which had the highest aggregation of spawners. YOY densities were generally low in the lower parts of the river (from 7 500 - 10 000 m below Kråkefossen), with the notable exception of high densities at two transects about 9000 m downstream Kråkefossen, which also is one of the few areas with spawning habitat in this part of the river. Conversely, YOY densities were generally low in the longer sections of the river where spawning habitat was absent.

The analyses of GAMs show that the spatial distribution of YOY is significantly affected by the spatial distribution of both spawning areas and spawners. Spawning area and spawners were tested separately. In Table 1 distribution of spawning area (model1) and spawners (model2) are compared in terms of deviance explained in YOY distribution, and AIC-values of the different models. Distribution of spawners explained 23.1% of the deviance in YOY distribution ($r^2 = 0.161$, $p < 0.001$), while positions of spawning area explained 28.2% of the deviation ($r^2 = 0.223$, $p < 0.001$) at transect level. For each model the habitat parameters, substrate and shelter, depth and velocity, were added in correct order according to deviance explained and AIC value. The effect of shelter was cancelled out when tested along with the interaction of shelter and substrate. In model1 (Fig. 3.2) the interaction between substrate and shelter had the best fit with YOY distribution, explaining 24.4% of the deviance in addition to spawning area ($r^2 = 0.428$, $p < 0.001$). Further, velocity explained 5.9% more of the deviance ($r^2 = 0.467$, $p < 0.001$), and depth 0.8% more ($r^2 = 0.499$, $p < 0.001$). The AIC values went down for each step in the model, while all parameters stayed significant. For model 2 the interaction between substrate and shelter explained 29.1% of the deviance ($r^2 = 0.401$, $P < 0.001$) in addition to spawners. Further, water velocity explained 5.6% more of the deviance ($r^2 = 0.429$, $p < 0.001$), and depth 2.3% more ($r^2 = 0.456$, $p < 0.001$). The AIC values for model 2 went down for each step, and all parameters stayed significant. Although model 2 had more deviance explained than model 1, model1 had the lowest AIC score and was taken for the best fit model. When testing this model backwards by taking one and one factor out of the model, the removal of the interaction between substrate and shelter causes the greatest loss of deviance explained (-12.5%), making this the most important correlates of local densities.

Average depth of transects varied from 2.8 cm to 83.5 cm (median 30.9 cm). Velocity varied from 1.3 to 104 cm s^{-1} on transects level (median 14.3 cm s^{-1}). Substrate varied from 0.25 to 55.5 cm on transects level (median 9.7 cm). Shelter varied from 1 to 2.9 on transects level (median1.8). The median of 1.8 shows that less than half of the transects had some or much shelter.

Table 3.1: YOY distribution is explained by spawning area (spawnarea) and spawners. The two GAMs are then extended with habitat parameters (substrate and shelter, depth and velocity). Spawnarea = spawning area. The analyses were carried with family = poisson. Full R-output can be found in Appendix II.

Model 1	Deviance (%)	AIC
gam(YOY~s(spawnarea)+s(meter))	28.2	1683
gam(YOY~s(spawnarea)+s(meter)+s(substrate,shelter))	52.6	1387
gam(YOY~s(spawnarea)+s(meter)+s(substrate,shelter)+s(velocity))	58.5	1317
gam(YOY~s(spawnarea)+s(meter)+s(substrate,shelter)+s(velocity)+s(depth))	59.3	1306
Model 2		
gam(YOY~s(spawners)+s(meter),family=poisson)	23.1	1754
YOY ~ s(spawners) + s(meter) + s(substrate, shelter)	52.2	1397
YOY ~ s(spawners) + s(meter) + s(substrate, shelter)+s(velocity))	57.8	1332
YOY ~ s(spawners) + s(meter) + s(substrate, shelter)+s(velocity)+s(depth)	60.1	1311

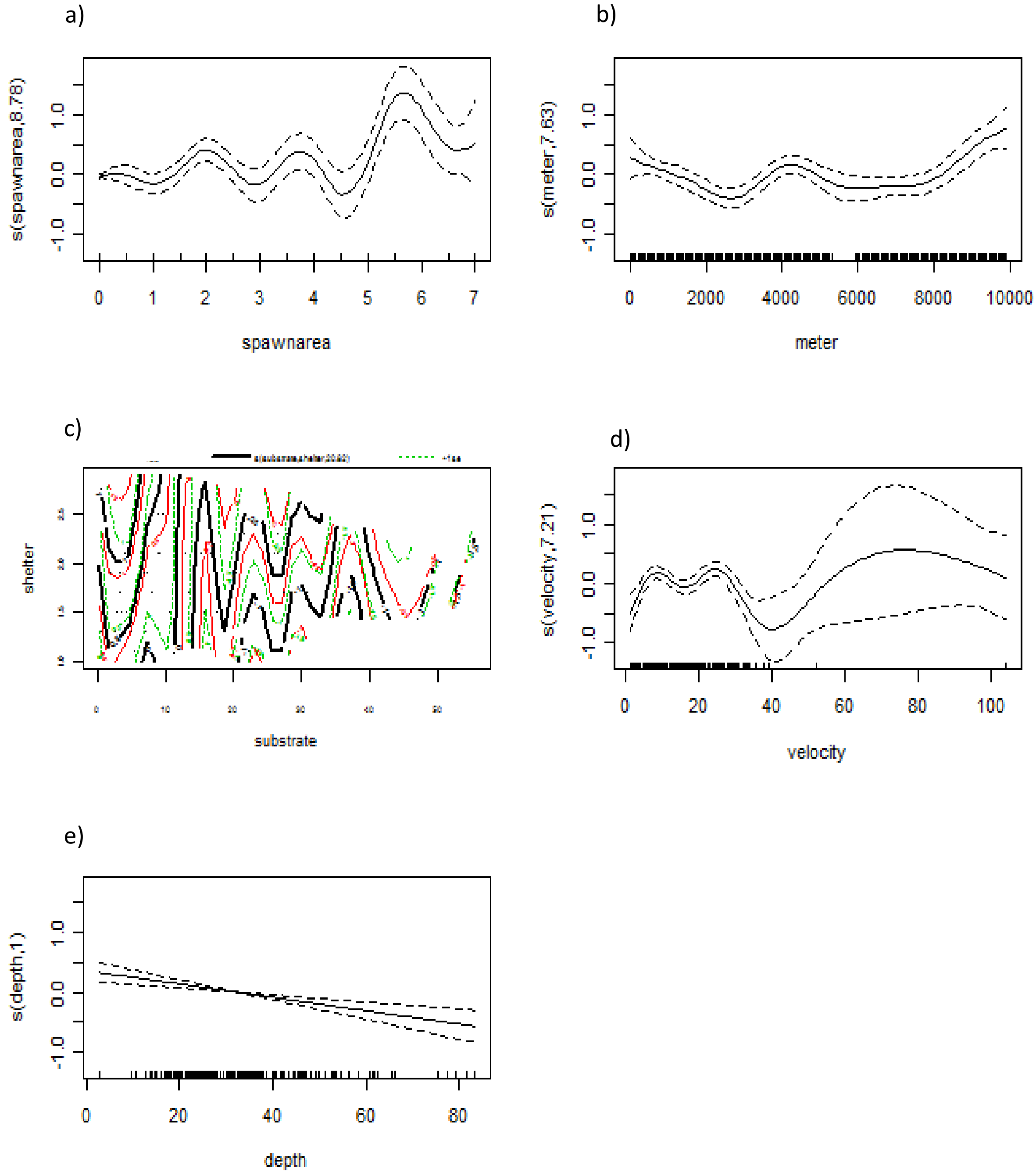

Figure 3.2: Panel of the different explanation variables in the GAM model 1. **a)** Smoother of spawning area related to YOY distribution. Area from 0-7 m^2 at the x-axis shows that larger area at a transect gives more YOY in the vicinity. **b)** The distribution of YOY related to meter from the migration barrier. The gap on the X-axis is Lake Mestadvatnet where no measurements were performed. **c)** Distribution of YOY related to substrate and shelter which were strongly correlated. YOY was most frequent found at transects with average substrate size below 10 cm size. The x-axis shows substrate size in cm and the y-axis shelter where 1 relates to little shelter and 3 to much shelter. **d)** Smoother of velocity related to YOY distribution. Velocity is given in cm s^{-1}. **e)** Smoother of depth related to YOY distribution. Depth is given in cm. Dotted lines are standard deviations.

3.4 Spatial Correlation Tests for YOY and Spawning Area

GAM analyses revealed stronger correlation between YOY and spawning area than YOY and spawners. Spatial autocorrelation analyses for spawning area (Fig. 3.3) and YOY (Fig. 3.4) showed strong autocorrelation for YOY, but weaker for spawning area. The correlation was significant for lags 1 to 5 for YOY distribution, with decrease in significance as distance increases. Spatial autocorrelation for spawning area shows only significant for 1, 3 and 7 for spawning area. Spatial autocorrelation of YOY and spawning area show how densities of nearby transects affect the density of a given transect. Further it shows that YOY is more spread than spawning area and that the densities of YOY at one transect is more related with YOY densities at neighbouring transects. Spawning area shows more patchiness and, hence, little continuity. Cross-correlation analyses were carried out between YOY densities and spawning area and showed a strong spatial connection for the two, from -3 to +6 (150 meter upstream to 300 downstream), which generally drops with distance (Fig. 3.5). Thus, transects with spawning activity in a section nearby had a higher YOY density.

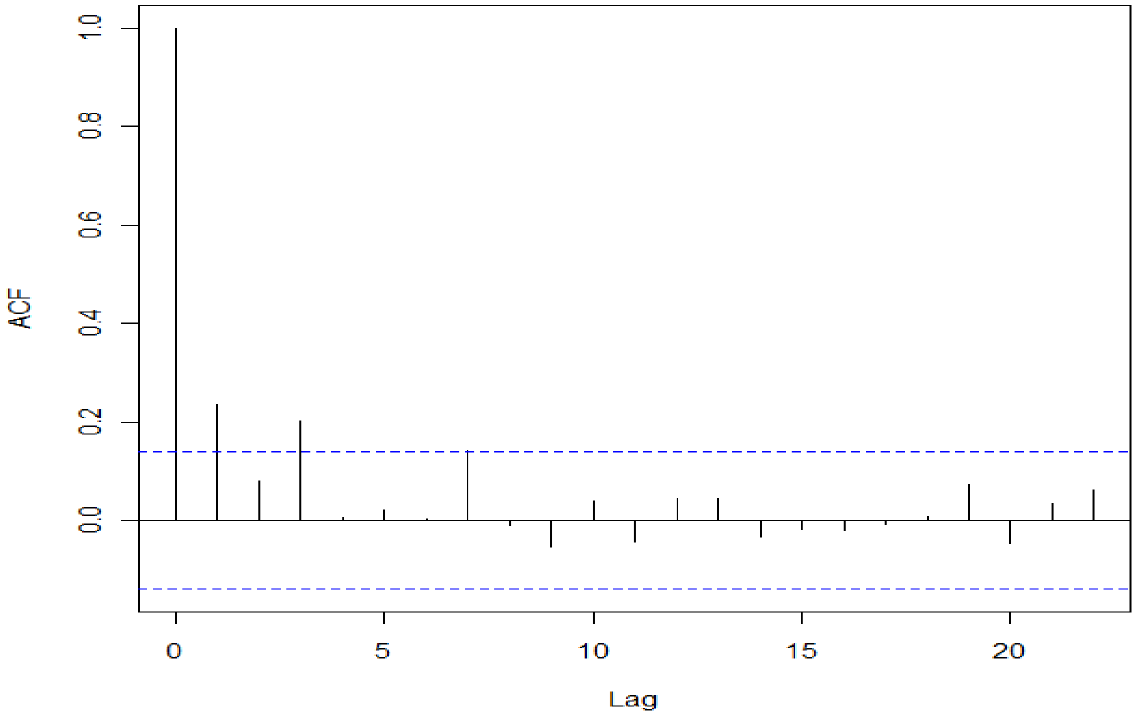

Figure 3.3: Spatial autocorrelations for spawning area in the River Teigdalselva. Lags are measured in 50m sections. Significance of only 1 section continuously shows a strong patchiness in spawning area locations, and indicate few areas with spawning occurring in two adjacent transects. Dashed lines show 95% confidence interval.

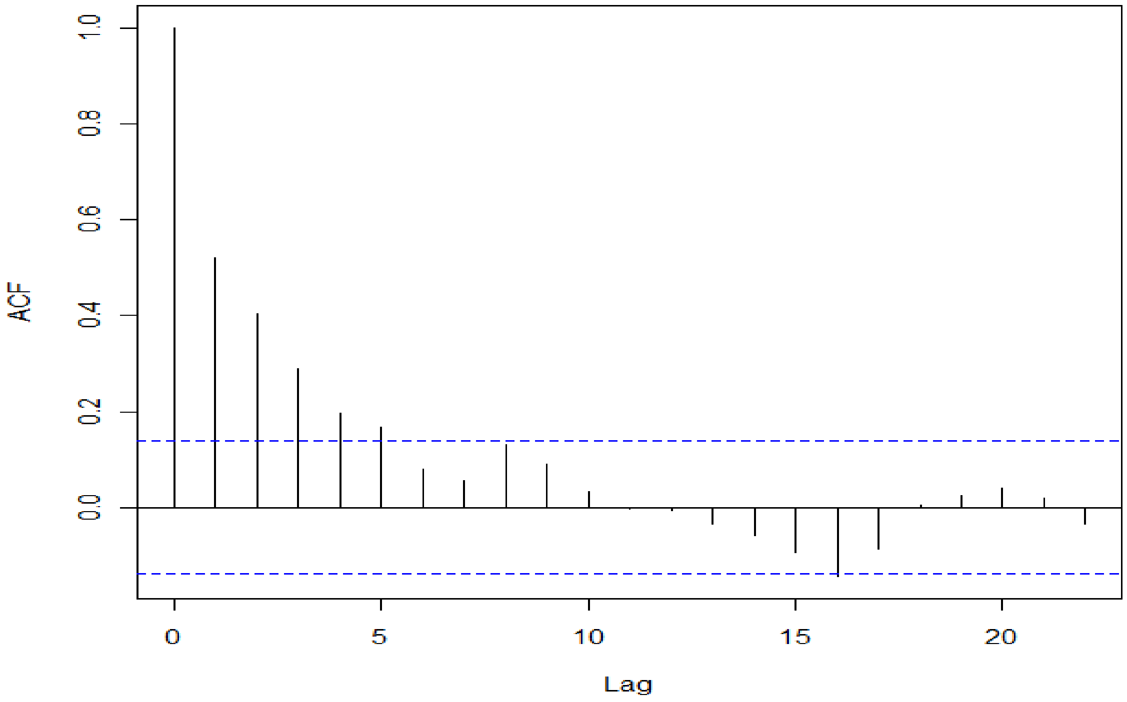

Figure 3.4: Spatial autocorrelations for young of the year seatrout densities in River Teigdalselva. YOY is more continuously distributed than redd area (Fig. 3.3) with significance for the 5 first lags. Lags are measured in sections of 50m. Dashed lines show 95% confidence interval.

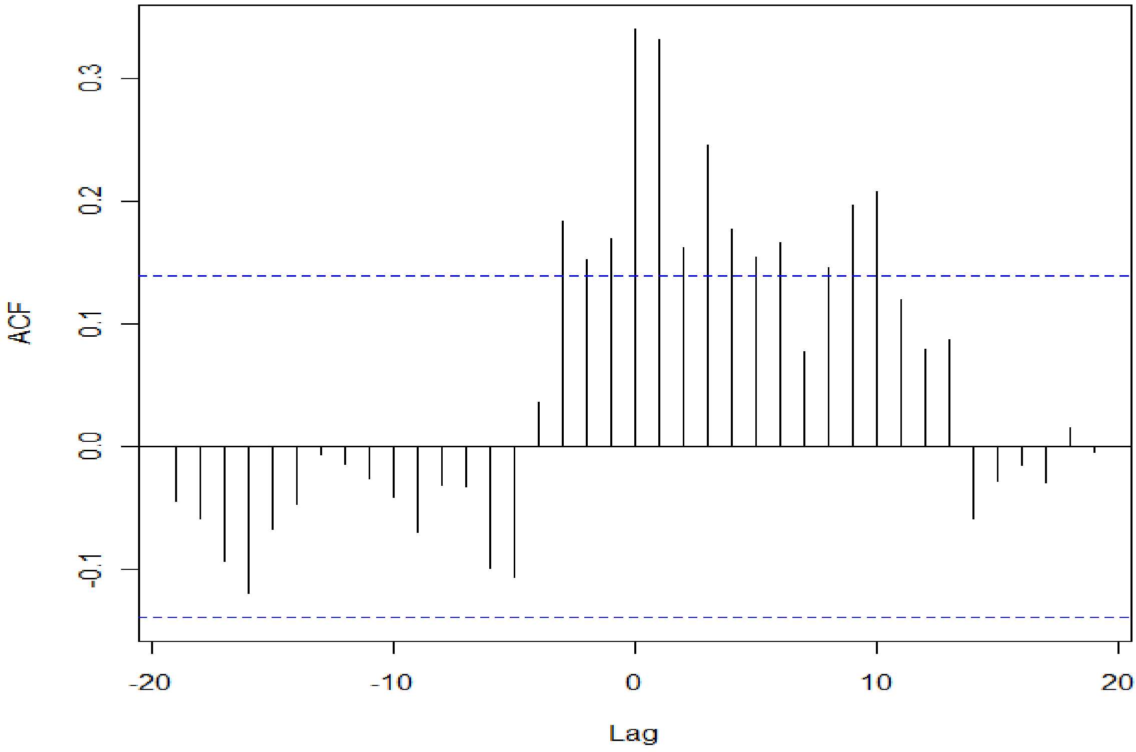

Figure 3.5: Spatial cross-correlation between seatrout young of the year (YOY) densities and spawning area. Lags are measured in sections of 50m. Positive lags are correlations between spawning area in a given section and seatrout YOY densities downstream of these. Dashed lines show 95% confidence interval.

3.5 Differences in Habitat Occupied by YOY and Older Fish, and Seatrout and Salmon

Figures 3.6 to 3.9 show the distribution of YOY and older fish according to the different habitat parameters (depth, substrate, water velocity and shelter). From the descriptive part of the habitat investigation the patterns are clear. YOY is overrepresented at low depths, fine substrate, low water velocity and areas with much shelter available. Older trout are overrepresented at intermediate depths, coarse substrate, low- and intermediate water velocity and more overrepresented at areas with much shelter than YOY.

Older trout preferred slightly shallower water than older salmon (mean 31.34 and 35.43 respectively). When it comes to shelter 83% of old trout and 81% of YOY were caught or seen at squares containing some or much shelter.

A chi-square test showed significant difference ($p < 0.05$) in mean water velocity of occupied habitat between YOY seatrout and salmon (8.45 and 20.93 respectively). The other habitat parameters (substrate, shelter and depth) gave no significant difference. The same pattern were seen in the analyses of older trout and salmon with significant difference in velocity ($p < 0.05$, mean = 9.806 and 24.20 respectively). Since statistical analyses were carried out at transect level, the results of the square meter survey are showed in figures (3.6-3.9).

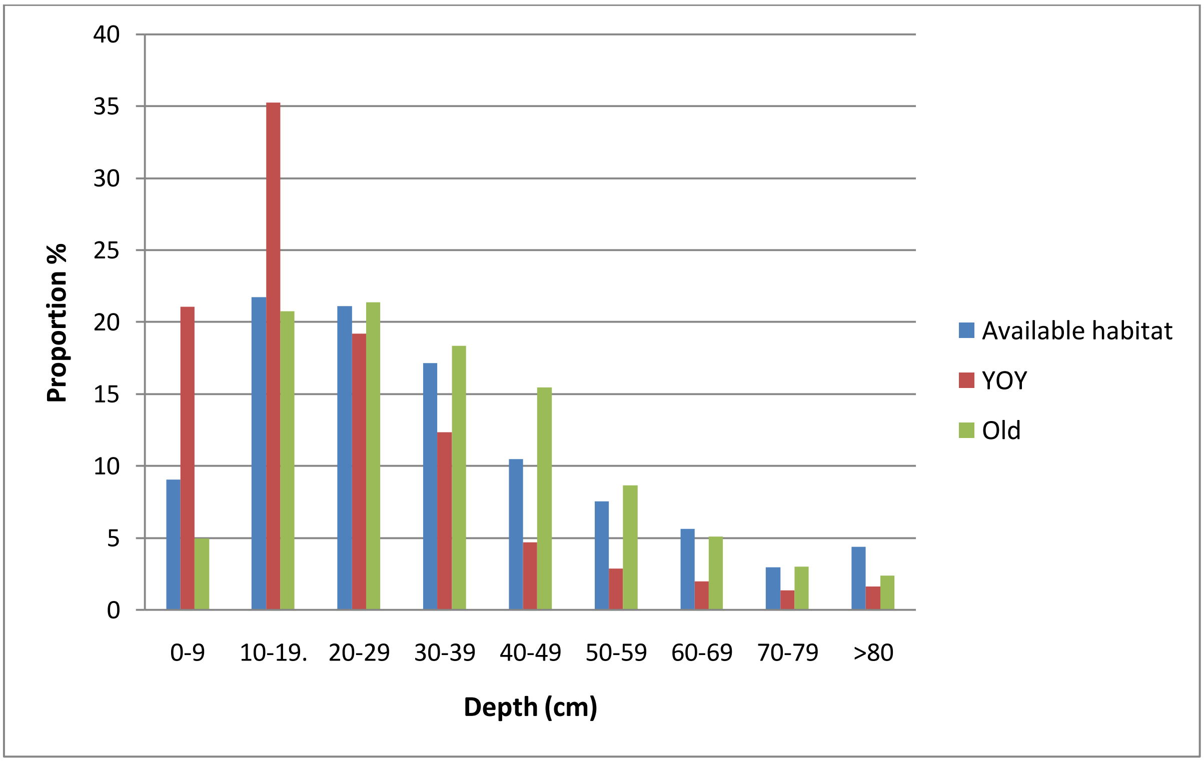

Figure 3.6: YOY related to depth. YOY is overrepresented at the shallow areas, and underrepresented in the deep areas, while older trout is overrepresented at medium depths and underrepresented at shallow and deep areas. Available habitat means the squares fished in the survey (1870 squares).

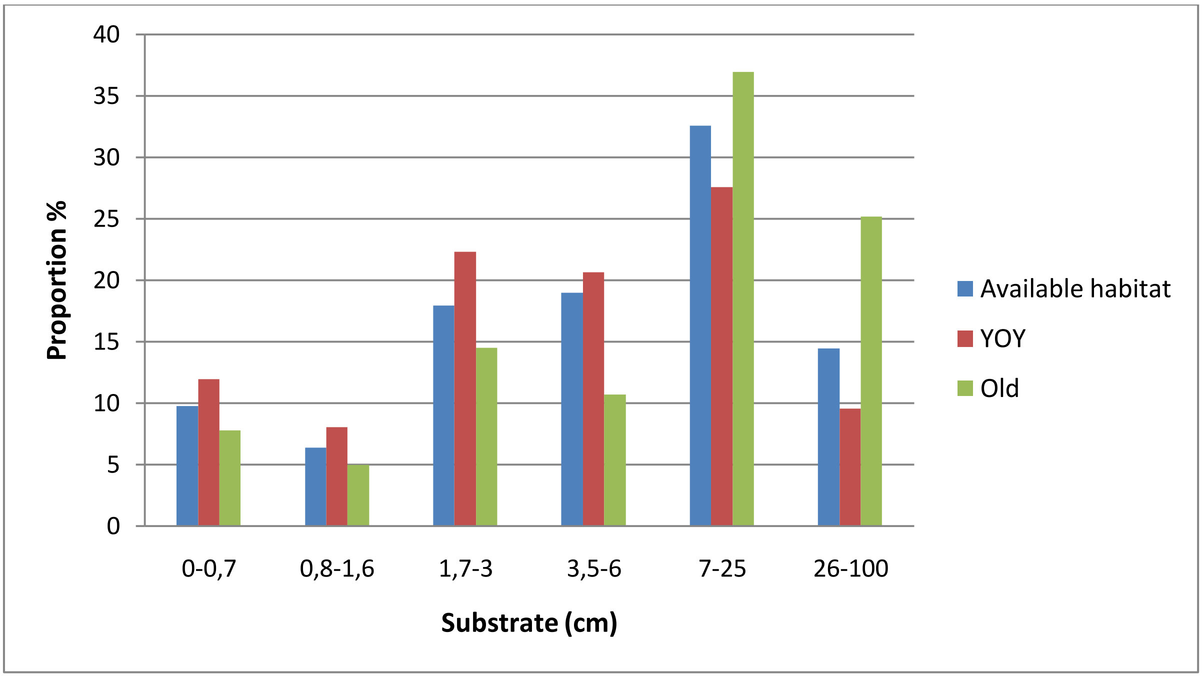

Figure 3.7: YOY and older fish preference for substrate. YOY is overrepresented at fine substrate and underrepresented in areas with coarse substrate, while older fish is overrepresented in areas with coarse substrate and underrepresented in areas with fine substrate. Available habitat means the squares fished in the survey (1870 squares). Substrate classification modified after Wentworth (1922).

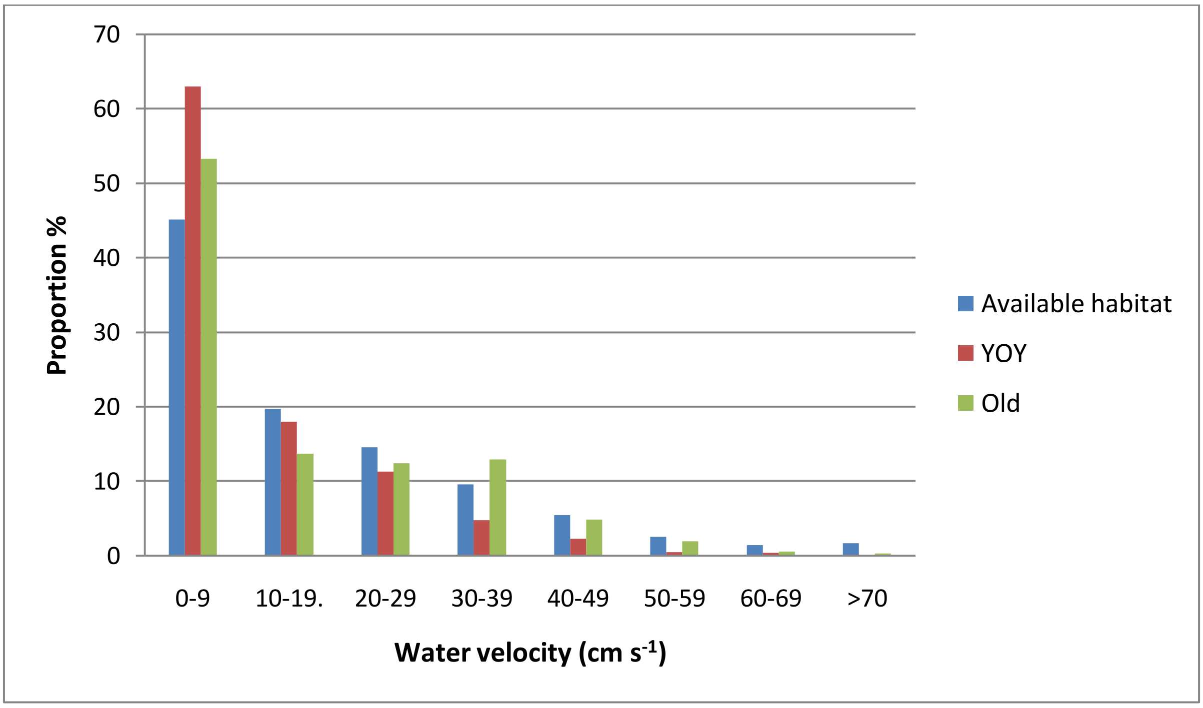

Figure 3.8: YOY and older fish related to water velocity. YOY is overrepresented at low water velocities and underrepresented at high velocities, while the opposite is the case for older fish. Available habitat means the squares fished in the survey (1870 squares).

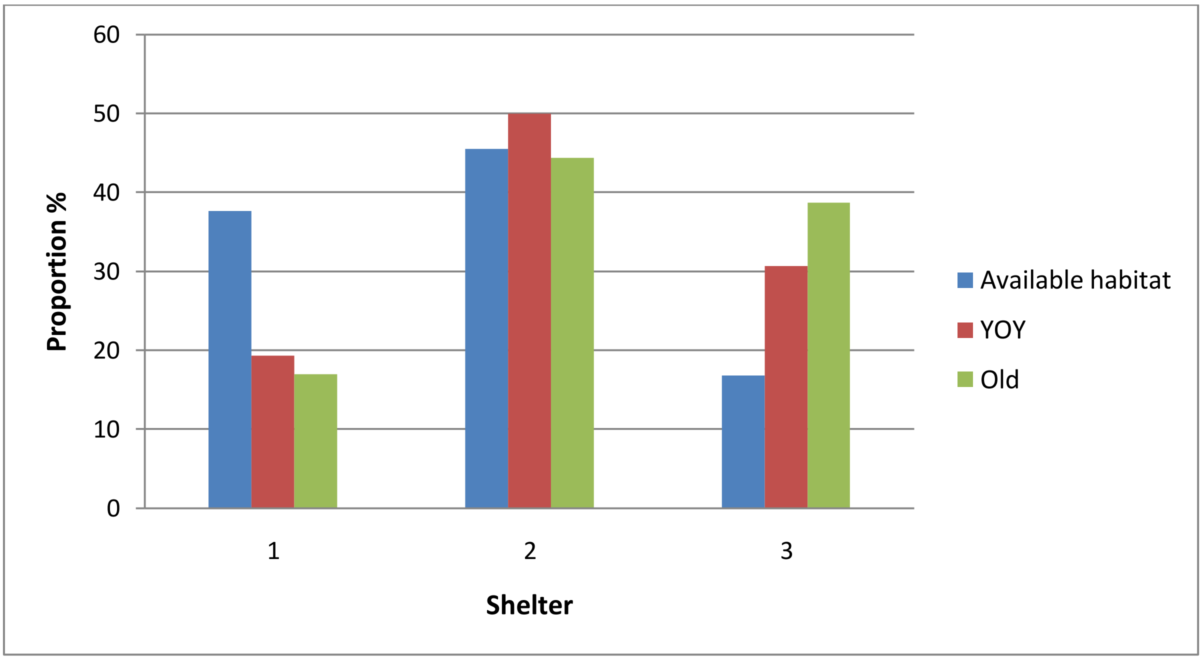

Figure 3.9: YOY and older fish related to shelter availability. YOY is overrepresented in areas with some or much shelter, while older fish is only overrepresented in areas with much shelter. The categories of shelter is divided between 1 which means less than ¼ of the square covered with shelter-providing substrate, 2 which means between ¼ and ¾ and 3 which means more than ¾ of the square covered with shelter-providing habitat. Available habitat means the squares fished in the survey (1870 squares).

3.6 Length Analyses

Length of trout varied from 25 to 196mm, with two outliers on 262 and 320 mm. According to the length distribution, YOY was defined from 25 – 58 mm (Fig. 3.10). The largest ones could be resident brown trout or seatrout with a higher age at smoltification than usual. The size distribution of YOY ranged from 25 to 58 mm (median = 37 mm, mean = 37.7 mm ± 5.5 SD). YOY length was negatively correlated with YOY abundance ($r = 0.30$, $p < 0.001$).

Figure 3.11 shows the effect of density on YOY growth. The pattern displays a negative relationship between density and length. Effects of density on growth were tested for using a linear model. The linear model for YOY length related to YOY abundance and date after field work start was significant ($p < 0.001$) (Fig. 3.12, Table 3.2).

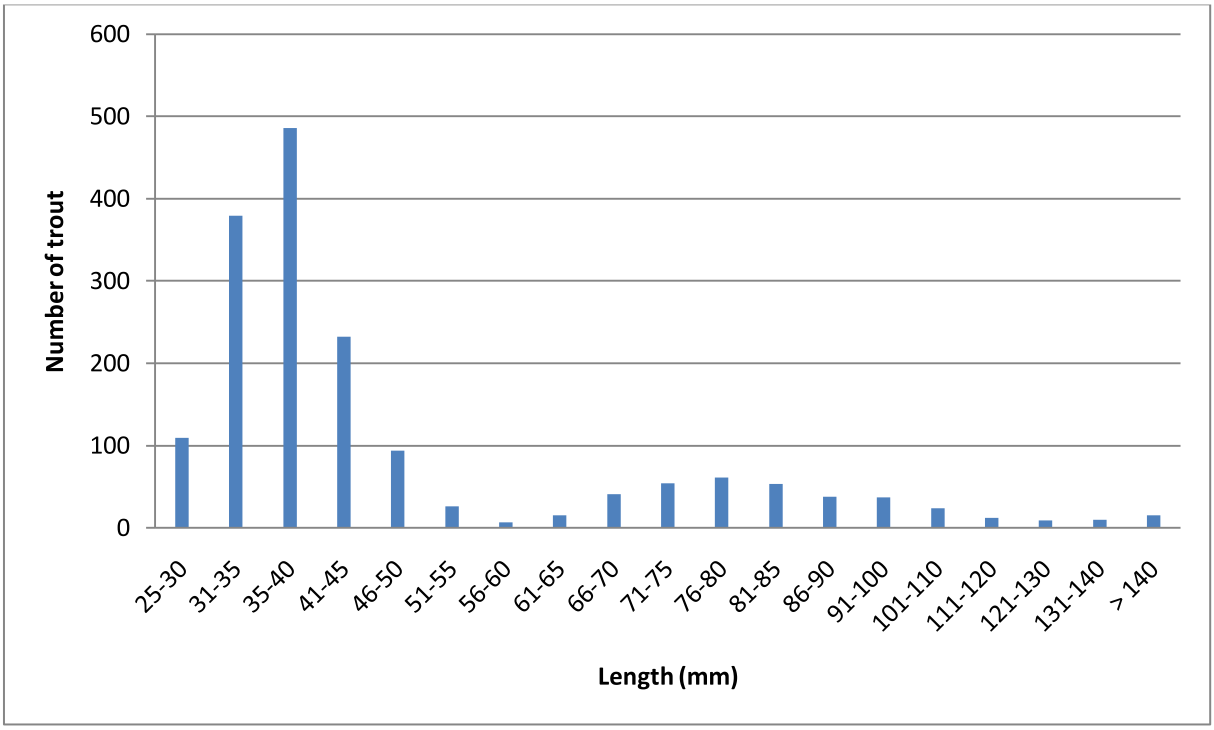

Figure 3.10: Length distribution of trout caught (n = 1673). Young of the year group was defined between 25 and 58 mm. From 25 to 90 mm the interval is 5, whereas between 91 and 140 the interval is 10. Fish with length > 140 is summarized in the last bar.

Table 3.2: Linear model output for model lm (log (length) ~ density + date)). The full model had 167 degrees of freedom and $p < 0.001$.

Coefficient	Std.error	t-value	p-value
(intercept)	0.01976	180.75	< 0.001
Density	0.011545	-2.078	0.039
Date	0.001377	7.551	< 0.001

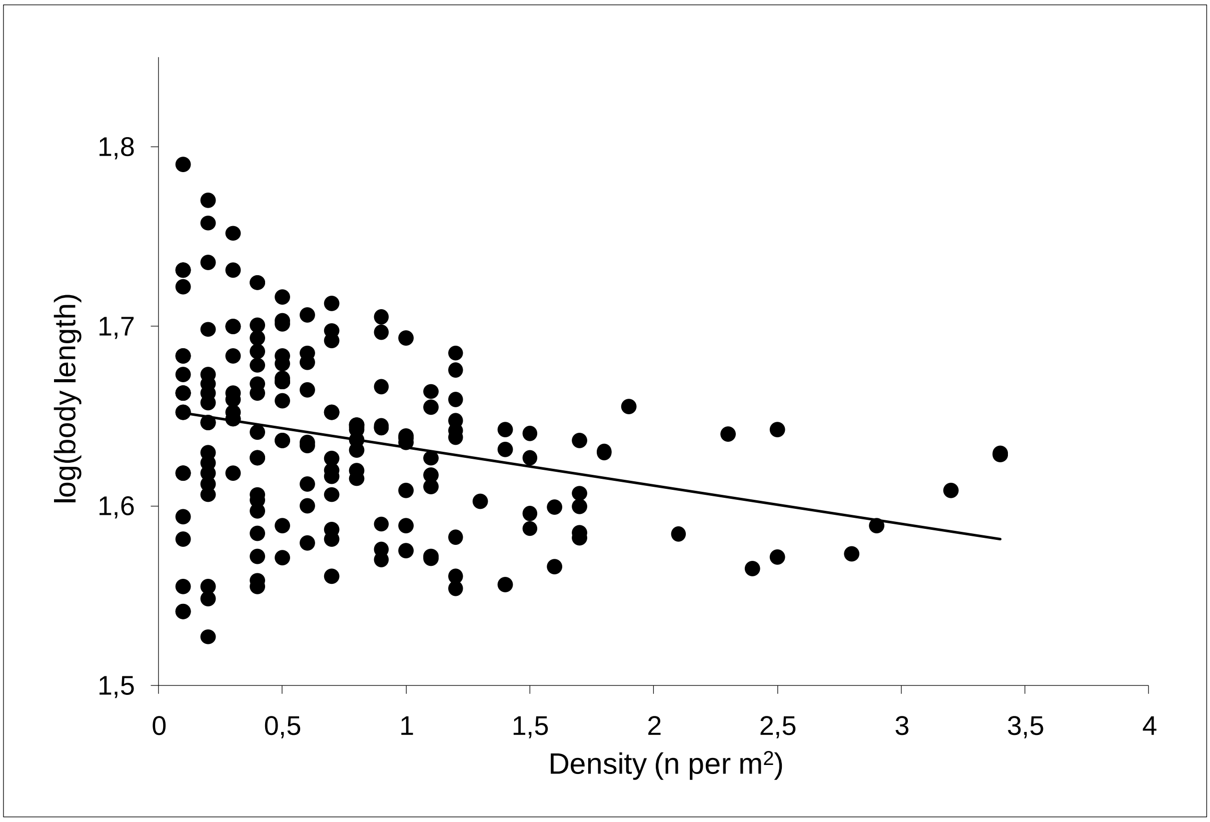

Figure 3.11: YOY transect abundance plotted against log-transformed mean body lengths of YOY caught at the same transect. Least squares regression line ($y = -0{,}0213x + 1{,}604$) shows how body length decreases when density increases.

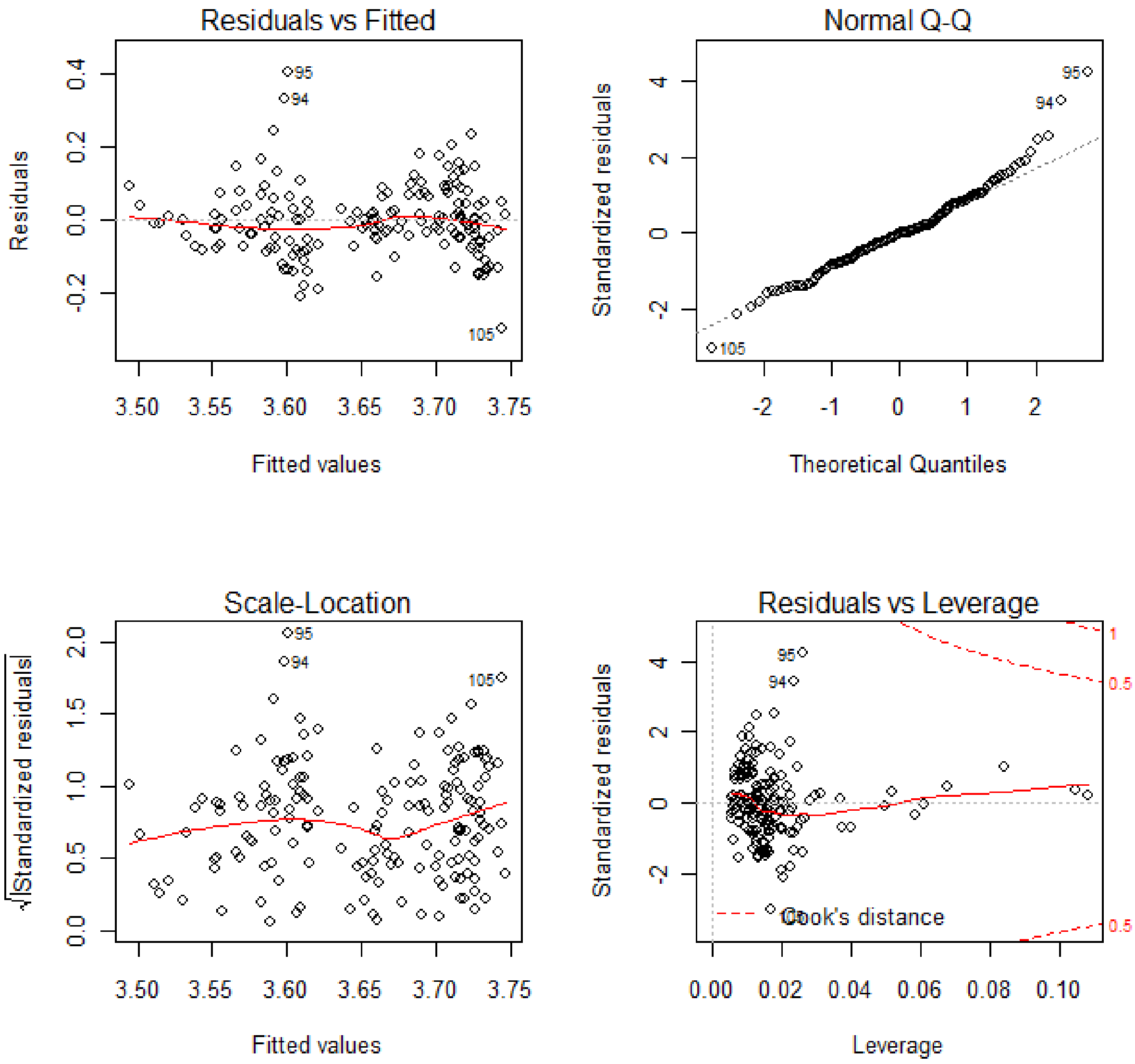

Figure 3.12: Plot of the linear growth model in Table 2. The Q-Q-plot shows a linear pattern between standardized residuals and the theoretical model which shows a good fit to the linear model.

4. Discussion

4.1 Spatial Distribution of Seatrout Spawning

The spatial distribution of seatrout spawning-grounds, microhabitat features and the resulting juvenile distribution were observed throughout a typical western Norwegian river, containing natural population of seatrout along with a nearly extinct population of Atlantic salmon. The effects of spatial distribution of spawners on offspring performance and distribution have received increased interest the last years; these studies have been exclusively performed on Atlantic salmon. Both experimental manipulations with artificial redds to simulate spawning (Einum and Nislow, 2005, Einum et al., 2008a, Einum et al., 2008b), and studies of natural population of salmonids (Finstad et al., 2010, Foldvik et al., 2010, Teichert et al., 2011) have been performed to investigate the effects on offspring performance. The present study aims to contribute to the knowledge on wild salmonids ecology by using seatrout as the target species.

The results from the snorkelling showed that the seatrout spawners had patchy distribution during the spawning period. The spawners most likely aggregated at or close to spawning grounds and were observed at low numbers or were absent from areas without available spawning habitat. This pattern is reflected in the results from the spawning survey where the autocorrelation coefficient for spawning area showed only continuously significance for 1 lag (75 m), which indicates that spawning did not happen in continuously sections. Thus the distribution was patchy on a global, as well as a local scale (Fig. 3.1b). Since spawners distribute themselves according to the presence or absence of available spawning areas, the patchy distribution of spawning areas cause spawners to be non-uniformly distributed. This is illustrated by the fact that 69% (0.82 m^2 $section^{-1}$) of the spawning areas was located upstream of Lake Mestadvatnet whereas only 31% (0.5 m^2 $section^{-1}$) was located downstream of the lake. The total size of the recorded spawning area was 129.5 m^2, which only constitute 0.7‰ of the total wetted area. The latter has been measured to 183 000 m^2 at 1 m^3s^{-1} water discharge (Gabrielsen et al., 2011). The following discussion focuses on both biotic and abiotic factors that may contribute to the observed patchy distribution of spawning areas, and the subsequent distribution of YOY and possible consequences for stock recruitment.

4.2 Salmonid Spawning Biology as a Factor Causing Spatial Distribution of Spawning Areas

The patchy distribution of spawning habitat, which has been discovered both in the survey on spawning population and registration of spawning area, can have several causes. The female choose the redd location and the distribution of redds is therefore a result of the females selection of spawning habitat (Armstrong et al., 2003). Typical spawning habitat for seatrout comprises water velocities in the range 15-75 cm s^{-1}, substrate sizes of 8-128 mm, depths often below 1 m and no more than 8-12% of fine materials less than 1 mm in diameter (Chapman, 1988, Crisp and Carling, 1989, Shirvell and Dungey, 1983). Size of the spawning population is likely to impact to what extent spawning areas are used. A large spawning population is likely to occupy a larger portion of the total available spawning area than a low density spawning population. This can be argued because the salmonid spawning biology is characterized by a fierce competition between males, but also competition between females for good spawning areas (Fleming, 1996). On spawning grounds with a small area available, subdominant females are likely to migrate away from competition to find unoccupied spawning areas with less competition. Redd area assessment are therefore used as a method to indirectly measure the size of the spawning population (Foldvik et al., 2010). In a dense spawning population it is therefore more likely that a larger portion of the total available spawning habitat will be used.

When performing the survey on spawning population the procedure is to float down the river and count every passing fish, and then note on a map where the fish passed you. This is usually done in October before the fish enters the spawning sites. The problem with this method is that the observed location of the fish is not necessarily the position of the spawning ground. Often the spawners can be encountered in pools because that is where they find shelter and stay until they spawn. Pools are not areas for spawning since both seatrout and salmon prefer depths of 6-82 cm (Armstrong et al., 2003). However, the pools occupied by the spawners are normally not far away from the spawning grounds, and often spawning occurs at the outlet of pools. But in an experiment layout like this with sections of 50 meters, the distance between residence and spawning ground will be a mismatch that reduces the accuracy of the models used. As previous studies have shown both salmon and seatrout have a three phased migration pattern in the river (Finstad et al., 2005, Økland et al., 2001, Östergren et al., 2011). First there is migration where the fish reach the area in the river close to the spawning site, second, a phase of searching with movements up and down the river nearby the spawning ground, and third a phase of holding when the fish stays still until it is ready to spawn (Økland et al., 2001). The research of spawning population is generally done in the third period. Then the fish is calm and it is often easy to count. Differences in the results using either redd area or spawners indicate a difference in position of spawners and redd area even close up to spawning time. Counting of spawners was performed October 11th 2009. The seatrout in River Teigdalselva is believed to spawn in the middle of October, thus the counting was done very near spawning time (Barlaup, 2008).

Stock-recruitment curves for salmonids are usually found to reach an asymptote indicating that the carrying capacity for producing juveniles and smolt is reached (Armstrong, 1997, Jonsson et al., 1998, Barrowman and Myers, 2000). The mechanism leading to asymptotic shape of the curve is likely density-dependent competition at various life-stages. Jonsson et al. (1998) found that density-dependence is present in early life stages in Atlantic salmon, but not in adult stages at sea. The asymptotic shape of the stock-recruitment curve occurs when there is a maximum population size regulated by density-dependent factors like exploitation and interference. This was indicated by increasing loss-rates from eggs to adults for egg-densities, as 73% of the loss-rates were explained by variation in egg density, thus female density on the spawning ground could be a decisive factor in regulation of production (Jonsson et al., 1998). In the present study, the analyses of the relationship between length and density show a clear pattern of density-dependent growth in YOY (Fig. 3.11). The areas where density-dependence heavily affects YOY growth are likely to have reached the carrying capacity. In River Teigdalselva this is likely to occur at the largest spawning areas.

4.3 Abiotic Factors Causing Spatial Distribution of Spawning Areas

The size of the total available habitat which corresponds to the female preferences will be a function of geomorphology and flow patterns (Kocik and Ferreri, 1998). In Norway, the glaciers in the ice ages made the land as we see it today, due to geological properties of the rock types (Ramberg et al., 2007). River Teigdalselva lies in a typical glacier valley (U-shaped). Between the ice ages floods and avalanches can alter the geomorphology in the rivers (Lamberti et al., 1991). A normal flood may not contribute to these changes on small temporal scales, but great floods, like the one in November 2005 in western Norway, can alter river beds if the river beds are composed of deposits, and hence change positions of suitable spawning area (Einum et al., 2006a). Habitat quality along the river may vary considerably.

Rapids with water velocities of more than 200 cm s^{-1} (LFI-Uni Environment unbubl. data) some places are followed by pools of water flow < 5 cm s^{-1}, whereas substrate size varies from the finest silt to solid rock.

In the analyses the observed spawning area was used as a proxy for egg numbers in the sections. There was detected spawning area on 63 of 187 transects and 50% of the spawning area was found in 15 sections.

During the last years (i.e. after 2005) there have been no major floods in River Teigdalselva. It is therefore reasonable to assume that the morphology and the spawning habitat of the river have been stable. This is also supported by the observations done during the spawning surveys which indicate little between year variation in the positioning of spawners and spawning areas (B. Barlaup & H. Skoglund pers. obs.). The number of spawners, and their distribution along the river reach was quite similar in the spawning population of 2009 as in 2008, when assessment of spawning area was performed. The winter of 2009-2010 was of the cold type and large amounts of ice had scrambled down the river with mechanical disturbance of the river bed as the result. This disturbance did not seem to have any influence on the survival of eggs in the discovered redds, but redds were hard to discover. The events caused the assessment of redds from the 2009 spawning population impossible to carry out. The analyses would have been a little more accurate if the redds could have been spotted exactly, but most likely the difference between the two years will have little to say for the final result, which the explanation of 28.2% of the deviance in YOY distribution shows.

4.4 YOY Distribution

YOY is more evenly distributed than spawners and spawning area. Also the spatial autocorrelation coefficient showed significance for 5 lags of YOY distribution. Thus the distribution of YOY is also patchy, but not as patchy as the spawning. Four stretches from 600 to 1050 meters long are without discovered spawning. It could still be that, within these stretches, some very small areas have suitable spawning habitat that were not recorded. This is considered the most likely explanation for the observed distribution of YOY. However, the major part of YOY found in these stretches have most likely dispersed downstream from spawning areas, since upstream dispersal for juvenile salmonids is expected to be limited both in frequency and distance during the first weeks after emergence (García De Leániz et al., 2000). Further the cross correlation showed continuously significance for 6 lags downstream and 3 lags upstream transects which reflects a distribution distance of 150 m upstream and 300 meter downstream. This is longer distances than recorded from other study performing the same analyses (Foldvik et al., 2010) where cross correlation propose a significant relation between the two of only 3 lags of 25 m downstream transects. There could be differences between salmon and trout in dispersal. Several studies on YOY Atlantic salmon have demonstrated that the dispersal from the spawning area is limited in the period after emergence (Crisp, 1995, Einum and Nislow, 2005, Einum et al., 2008a, Foldvik et al., 2010). It is uncertain whether this is due to reduced mobility and dispersal ability or whether it reflects a low motivation for dispersal. High sensitivity to predation may for example cause dispersal to be especially risky, so that fry avoid dispersal if they are not forced. The greater differences found in the present study could also result from the habitat downstream important spawning areas such as the areas 350 and 4000m downstream the migration barrier. These spawning areas lie in the upstream ends of water basins created by weirs. The basins are characterized by homogeneous substrate with generally little shelter. Here dispersal for YOY could be easier than over heterogeneous habitat with many hinders which may decrease the dispersal length (Kocik and Ferreri, 1998). Another explanation can be that the newly emerged YOY had had more time to disperse in this research design than in the corresponding studies. The dispersal ability in the early weeks is most of all related to size. In this study YOY had a mean length of 37.7 mm which is similar to the length of Atlantic salmon in other studies, with 40 mm (Foldvik et al., 2010) and 38 mm (Teichert et al., 2011) recorded. The time to disperse seems not to be the explanation of the dispersal. However, the low densities of YOY found at transects in some parts of the river shows that dispersal is limited. From figure 3.1 the pattern is clear when comparing the distributions of spawning area and YOY, thus the number of YOY at transects downstream large spawning areas decreases with distance. Yet another explanation can be found to explain the YOY distribution. The size of the spawning area is likely to decide the length of distribution. A small spawning area with low densities of YOY will likely cause little need for dispersion, while large spawning areas will most likely cause higher abundance of YOY in the proximity to the spawning area, thus individuals that disperse from high density areas to areas with lower density will have an advantage when it comes to growth. Therefore one should expect dispersal of a greater extent from large spawning areas than small.

In figure 3.1 the field work results are summarized. The YOY distribution shows that YOY is represented in the whole river, but at some places in very low numbers. One example is the stretch from 3 100 to 3 900 (see also Appendix I) where almost no YOY is caught or observed. Compared with spawning area in the same figure the reason seems clear. No spawning area was recorded from the stretch. The areas with large spawning areas coincides also well with high numbers of YOY according to the figure.

YOY distribution in River Teigdalselva was best explained with substrate and shelter and water velocity. One should expect the distribution of spawning area as the best explaining factor. However, the patchy distribution of spawning area and yet dispersal by 6 lags from the autocorrelation the quality of the habitat becomes a better explanation. Some places false zeros, fish present in the square but not caught, or spawning area in the downstream end of transects can cause YOY to be caught at the first transect downstream not at the one where spawners were located. At transect level YOY is found where they are because of spawning occurring in the proximity. At square level YOY density is primarily explained by habitat quality at the specific square, since suitable habitat supports YOY appearance. Habitat should therefore be measured at small spatial scales, even down to square meter level, as in this study, when rivers are classified by site quality.

4.5 Length, Species and Preferable Habitat

YOY abundance had significant effects on YOY lengths. Figure 3.11 shows how the growth is declining with abundance in transects and revealing evidence for density-dependent growth in the wild seatrout population. Scatter plot suggest a concave relationship with most of the reduced growth occurring at low abundances (< 1 YOY m^{-2}). Several explanations have been proposed to be responsible for this pattern. The two main explanations is exploitation competition for drifting prey (Imre et al., 2005, Imre et al., 2010) and spatial competition (Ward et al., 2007). In the first weeks after hatching YOY salmonid need small areas to sustain growth, but as body weight increases quickly the demand for more food and larger areas increases (Lobon-Cervia and Mortensen, 2006). The exact cause of the density-dependent growth observed in the present study has not been detected, and the debate concerning this issue shows how difficult this is.

The different incubation temperature during the egg stage could bias the length of YOY throughout the river. The temperature at the outlet of Lake Mestadvatnet was believed to be higher due to the properties of water (heaviest at 3.98°C), and observed alevins in May, while only eyed eggs were present in the river, supports this (pers.obs). Temperatures of a lake may increase slower after the ice break than in the river reaches, which minimizes the effects of earlier hatching. However, the effects of the earlier hatching on time of emergence are described as being small (Syrjanen et al., 2008).

There seem to be differences in preferable habitat between seatrout and salmon in both under yearling and older life stages. The greatest differences are the water velocity where seatrout has preference for lower than 10 cm s^{-1}, while salmon YOY and older salmon are more tolerable for higher snout velocities (water velocity experienced by the fish at its territory), but older salmon prefer slightly higher snout velocities. Few YOY salmon were caught and results from the survey should be handled with care, but it can indicate that even YOY salmon prefer higher snout velocities than YOY seatrout. From previous studies (Heggenes et al., 1999, Maki-Petays et al., 1999) these result is as expected. Maybe one should expect older trout to stay at habitat with higher velocities, but older trout seem to prefer areas with the right combination of depth and velocity. This means low velocity and deep water (Shirvell and Dungey, 1983). In River Teigdalselva there are few deep areas, but many areas are wide and slow flowing. The problem dealing with these areas is the catchability of older than YOY fish. Fine substrate with little shelter forces the older fish to flee the area before paralysed by the electricity. This is well explained by catch of older trout against substrate and shelter. Water depths preferred were similar for the YOY groups.

Habitat parameters measured in this study are considered extra important for young salmonids than older individual (Heggenes et al., 1999). For young trout water velocity and depth seems like the most important factors explaining occupied habitat.

4.6 Effects of Hydropower Development and Other Human-Induced Changes

Hydrological changes experienced after regulation to hydropower production are commonly related to water discharge, velocity, and temperature and ice conditions (Johnsen et al., 2010). River Teigdalselva went through great changes when becoming regulated. The main change was reduction in water discharge especially in the uppermost end of the anadromous reach.

Some of the spatial distribution of spawners and spawning areas we see today is a result of these changes. In some places in the river earlier used spawning habitats may be avoided due to low water discharge. A study on water velocity and spawning habitat revealed a lower limit of 15-20 cm s^{-1} and an upper limit related to size of which salmonids preferred to spawn (Crisp and Carling, 1989, Kondolf and Wolman, 1993). In the present study it was found long distances where the river has a substrate suitable for spawning, but the fish will not use these areas as the water velocity is lower than 15 cm s^{-1} even with relatively high water discharge during spawning time.

The reduced water discharge due to the regulation is likely to have had negative impacts on fish production in River Teigdalselva (Barlaup, 2004). There is no doubt that the regulation has affected juvenile production, but habitat improvements such as boulders and building of weirs have been tried to dampen the negative impacts. On Fasteland (4000 m downstream Kråkefossen) abundance of YOY and older fish has been recorded since 1991 by electro-fishing. At the station there were added boulders along the river bed, where the previous substrate was gravel. This station has had the highest seatrout density of YOY (e.g. 2008 with 85.7ind pr. 100 m^2) and older individuals (2008: 53.4 individuals 100 m^{-2})(Gabrielsen et al., 2009). In the present study, the Fasteland spawning area also was the area with the highest abundance of spawners. Long stretches are dominated by fine gravel. These results indicate the huge potential to increase spawning and juvenile production by river restoration efforts based on adding gravel to create spawning areas and boulders to create shelter for juvenile fish (Barlaup et al., 2008). Previous studies, and the present one, have showed how juvenile seatrout are overrepresented in some habitats, showing a positive correlation between the preferred habitat and density (Palm et al., 2007, Pulg et al., 2011). Since YOY have some specific demands for habitat quality, habitat surveys should be performed in rivers with a known patchy spawning distribution. Efforts to increase spawning areas should therefore be put in at areas where there is existing suitable habitat for juveniles, but the carrying capacity for the area is not reached. The general opinion is that future efforts to increase populations should focus on improvements of environmental condition (Johnsen et al., 2010, Fjellheim et al., 2003).

With generally little water discharge throughout the summer in River Teigdalselva (Fjellheim et al., 1994) the upstream migration of seatrout can be delayed. The building of weirs, to mitigate the loss of water to hydropower and natural migration barriers are factors affecting upstream migration in salmonids (Thorstad et al., 2008). These factors can result in potentially loss to the population (Thorstad et al., 2008). Especially the weirs, which constitute the largest changes in the river, are prominent constructions reducing water current. For seatrout this may not causing any reduction in production (Flodmark et al., 2006), but for salmon which prefer higher water velocities and hence higher water discharge this may have negative impacts on population size (Armstrong et al., 2003, Bremset, 2000).

4.7 Methodological Considerations Concerning Electrofishing

One of the main errors in this study is the electrofishing and the use of the equipment. Beforehand I practiced in another river to avoid any start problems in the study. This was done to become as good as possible before start, avoiding increasing my skills too much during the study, thus get a biased result. When fishing one and one square meter the most important is to approach the square from downstream and be especially aware when the first pulse is sent. Then one has to be quick to catch the fish before it drifts away with the current. The starting point of the electro-fishing was also discussed before start. I started on a fish rich spot at Fasteland, 3500 meters downstream the migration barrier, and fished each square meter thoroughly. This was done to avoid getting no fish at transects with very few, but still present YOY. The time spent fishing on one square meter varied according to what extent shelter was available and hence catchability of the fishes, but the mean time spent on each transect both fishing and measuring the variables was approximately 40 min. The general method used to estimate density, hence population size, of juveniles in rivers is to fish 100 square meters along the river bank (e.g. 4 x 25 meters) three times. The fishing is done three times to catch as many fishes as possible, because some are always paralysed out of site or reach (Sandlund et al., 2011). In these studies the competence of the field workers are important, due to the quantitative estimates of fish density to detect changes in population size over years (Forseth and Forsgren, 2009). This study was not quantitative, but relative, hence the skills of the fisher were less important. I fished 10 square meter in each transect irrespective of river width, thus it would have been difficult to fish the correct square meter several times. The fish has to wake up after the electrocution before re-fishing the square, and this would obvious lead to a lot of extra time spent on the study, exceeding the limited time to perform such a study. Electro-fishing, therefore, were performed with one fishing round at each square meter, and the fishing was performed by the same person all the time, and as similar as possible from square to square.

Temperature measurements from 2003 to 2010 in River Teigdalselva in the field work period showed a mean temperature between 13 and 17°C (LFI-Uni Environment unpubl. data). The level of activity of the fish increases with temperature and the catchability decreases with the possibility to escape. At temperatures over 12°C electro-fishing in quantitative estimates is consequently stopped due to low catchability. In River Teigdalselva the temperatures was generally high in the three weeks of field work, thus the number of especially fish older than YOY could be underestimated. Smaller fish is worse to paralyse, hence catch, than bigger ones, but the ability to escape rules out this factor, thus it is easier to catch YOY than older fish. In conclusion, I think the set up of the field work, and the performance, was sufficient to get a clear picture of the relative abundances of YOY and older fish in the field work period.

The field work had to be carried out in the summer, to catch the YOY within a couple of months after emergence from redds. July and August was chosen to have greatest chances of carry through the field work without long periods of heavy precipitation and floods. Difficulties in this period generally, and electro-fishing specially, is first of all related to temperatures and floods. Water discharge is a limiting factor in electrofishing. Too deep or fast flowing water at the fishing grounds will put an effective stop to electro-fishing. The sight at depths over 50 cm is strongly reduced, even in clear waters, when there are currents in the surface. Because of the regulation of the river heavy rain one day will not cause flood for many days, but the water discharge will increase and sink rapidly and would be fishable approximately 2-3 days after a heavy rain. Fortunately the weather stayed fine the whole field work period with only minor precipitation. Unfortunately the temperatures were high which challenged the electro-fishing to a great extent. Catch of especially older fish was lower than it could have been at more sufficient temperatures.

4.8 Concluding Remarks

The present study gives a clear indication that the availability of spawning area and suitable nursery area puts the limits for fish production in seatrout. The patchy distribution of spawning leads to stretches with low densities or absence of YOY, due to the limited dispersal of under-yearlings (Beall et al., 1994, Einum and Nislow, 2005, Einum et al., 2008a, Foldvik et al., 2010). This shows that even some mobile organisms do not distribute after the ideal free distribution, due to the fact that mobility is limited in some life-stages. For seatrout the distribution ability is limited in the first weeks after emergence, but different habitat is believed to affect the length of possible distribution. The access to spawning habitat is most certainly the factor which explains most of the carrying capacity and spawning target (egg m^{-2}) for rivers. The spawning target can be theoretically reached without reaching the carrying capacity if density-dependent mortality occurs. This indicates that in some rivers with little spawning area there is a potential to increase the population, by creating more spawning habitat. Efforts to increase spawning habitat is especially of current interest in rivers where the original spawning areas are destroyed by human activities (Johnsen et al., 2010). This study also provides some information to what extent density affect YOY growth.

This study has showed that a thorough mapping of spawning habitat and nursery habitat can give information about factors that are important for defining the production potential for the River Teigdalselva. The observed patchy distribution of spawning areas is likely a general feature of West-Norwegian rivers inhabitated by seatrout. In rivers where original spawning areas are reduced or destroyed by human activity, mapping of spawning areas and subsequent restoration of spawning areas can be an important means to mitigate population declines. The knowledge of population-regulating effects found in the present study can add valid information concerning how to shape and optimize such mitigation efforts.

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6. Appendices

Appendix I:

Raw data for transects. The transects from 109 to 120 were at Lake Mestadvatnet where no measurements were taken. Meter is meter from the migration barrier. Transect are cross-fished sites of 10 m^2 with 50 meter distance between. YOY = young of the year, and refers to young of the year trout and salmon. Trout and salmon ≥1+ refer to trout and salmon one year or more since hatching. Depth is the mean of depth at each transect, measured in cm. Velocity is the mean water velocity at each transect, measured in cm s^{-1}. Substrate is the mean substrate at each transect, measured in cm. Shelter is the mean shelter availability at each transect, measured in categories of 1, 2 and 3, where 1 means less than ¼ of the square covered with shelter providing substrate, 2 means between ¼ and ¾ of the square covered with shelter providing substrate, and 3 means more than ¾ of the square covered with shelter providing substrate. Spawning area is assed spawning area in 2008. Spawners are seatrout spawners assessed by snorkelling 11th October 2009.

Meter	Transect	YOY trout	YOY salmon	Trout ≥1+	Salmon ≥1+	Depth	Velocity	Substrate	Shelter	Spawning area	Spawners
0	1	3	0	1	0	24,10	10,3	12,4	2,8	4	11
50	2	0	0	1	1	31,4	5,9	25,3	1,6	0	2
100	3	0	0	3	1	37	16,3	23,65	1,9	1	1
150	4	0	0	5	1	23	13,1	30,95	2	1,5	3
200	5	3	0	1	0	66,3	7	21,8	1,8	2	12
250	6	6	0	4	0	28,9	25	23,3	2	1,5	3
300	7	12	0	2	0	24,8	26	26,05	2,1	3	15
350	8	8	0	13	0	32,8	15,5	26,6	2,3	7	17
400	9	34	1	3	0	18,2	9,4	9,85	2,4	2	5
450	10	15	1	2	0	22,9	8,1	10,7	1,5	2	5
500	11	25	1	1	0	15,1	14,8	5,7	1,8	1,5	0
550	12	18	1	1	2	10,7	17	4	2	0,5	5
600	13	15	0	1	0	23	7	2,81	1,6	3	0
650	14	12	0	0	0	14,9	25	4,65	1,6	2	0
700	15	11	1	0	0	17,5	33,3	4,9	1,2	0,5	4
750	16	11	0	0	0	36,7	15,8	4,65	1,2	0	0
800	17	35	1	0	0	13,9	22,4	4,05	1,7	0	0
850	18	12	0	3	0	16,1	24,3	3,3	1,3	0	3
900	19	6	0	2	0	61,9	5,5	3,71	1,5	0	4

950	20	7	1	8	1	35,6	8	9,705	2,4	5	0
1000	21	2	0	6	0	33,3	14,3	26,55	2,1	0	0
1050	22	0	0	12	0	31,3	19,7	39,2	1,9	0	0
1100	23	5	1	0	1	27	7,7	25,13	2,2	0	11
1150	24	8	0	3	2	27,4	17,9	14,5	2,4	1,5	15
1200	25	5	0	0	0	36,8	12,2	1,872	1,5	2,5	6
1250	26	7	0	3	1	25,2	15,1	10,16	1,8	0	4
1300	27	5	0	6	0	43,4	21,2	3,63	1,6	1,5	9
1350	28	6	0	0	0	44,8	9,4	5,91	1,1	1	0
1400	29	12	0	0	0	25,6	22,5	4,15	1,6	0	0
1450	30	8	0	1	0	18,3	28,6	5,2	1,6	0	0
1500	31	8	0	0	0	17,7	26,9	5,1	1,3	0	0
1550	32	10	0	1	0	14,2	32,3	4,7	1,3	0	0
1600	33	11	0	1	0	18,3	29	4,4	1,2	0	0
1650	34	4	0	1	0	53,3	13,3	5,73	1,6	0,5	0
1700	35	14	0	0	0	49,1	1,6	3,97	1,9	0	11
1750	36	9	0	0	0	44,3	104	3,7	1,5	1	4
1800	37	16	0	0	0	9,5	23,1	4,1	1,8	0,5	0
1850	38	7	0	1	0	16,8	18,1	8	1,2	2	0
1900	39	1	0	0	0	40	10,3	2,94	1,2	0,5	0
1950	40	4	3	0	0	20,5	12,9	3,2	1,2	0,5	21
2000	41	6	0	1	0	21,5	15,4	4,24	1,4	3,5	0
2050	42	2	0	3	0	33,5	10,8	12,31	1,4	0	3
2100	43	4	3	1	0	36	10,4	5,2	1,7	1	0
2150	44	4	0	0	0	9,8	30,8	2,17	1,3	3	25
2200	45	6	0	1	0	33,7	11,1	11,91	1,6	0,5	0
2250	46	1	0	0	0	62,4	8	7,23	1,3	0	0
2300	47	16	0	3	0	40,7	12,1	4,06	2,1	0	0
2350	48	17	0	0	1	26,8	12,3	3,75	1,6	0	0
2400	49	7	0	0	0	22	17,3	3,75	1,3	0	0
2450	50	5	0	0	0	33,6	13,6	4,15	1,2	1,5	11
2500	51	9	0	1	0	19,9	25,6	7,1	1,2	2	0
2550	52	10	0	1	0	34,4	12,8	13,43	1,7	0	5
2600	53	8	0	1	0	45,6	8,3	11,51	1,7	0	0
2650	54	0	0	0	0	18,7	12,5	4,05	1,5	0	0
2700	55	4	0	0	0	23,8	8,8	3,6	1,2	0	0
2750	56	4	0	0	0	26,4	7,7	14,1	1,3	0	0
2800	57	10	0	0	0	17,3	15,6	4	1,3	1	0
2850	58	2	0	0	0	18,7	12,5	1,86	1	0,5	0
2900	59	9	0	1	0	15	23,7	2,67	1,3	0,5	0
2950	60	7	0	0	0	30,9	10,6	3,02	1,5	0	0
3000	61	15	0	2	0	45,9	7,1	7,71	1,9	1,5	11
3050	62	24	0	4	2	33,8	12,7	5,66	2,3	0,5	0
3100	63	5	0	5	1	18,2	25,8	11,63	1,8	0	1
3150	64	1	0	5	0	37	8	17,48	1,9	1	0

3200	65	1	0	2	1	26	18,2	11,85	1,7	1	4
3250	66	2	0	4	0	33,5	15,1	8,1	2,4	0	0
3300	67	0	0	4	0	20	13,6	13,55	1,7	0	0
3350	68	0	0	0	0	19,4	17,4	21,28	1,8	0	0
3400	69	0	0	0	0	42,4	16	45,35	2	0	8
3450	70	0	0	0	4	25,7	18,4	14,9	2,4	0	0
3500	71	1	0	5	0	25,1	7,6	15,28	2,1	0	0
3550	72	1	0	5	0	31,1	21,4	28,05	1,9	0	3
3600	73	0	0	4	0	22,2	27,8	14	2	0	0
3650	74	0	0	3	0	24	33,8	20,4	2,1	0	0
3700	75	2	0	12	0	24,2	21	12,4	2,4	0	0
3750	76	0	0	4	1	21,1	24,3	19,5	2,2	0	0
3800	77	0	0	2	0	21,8	33,8	17,2	2,6	0	2
3850	78	4	0	8	1	19,6	35,5	9,73	2,5	0	0
3900	79	23	0	8	0	21,8	26,3	9,08	2,1	0	44
3950	80	28	0	0	0	53,8	4,7	4,1	1,3	5,5	0
4000	81	27	0	2	0	42,5	12,45	2	1,4	0	0
4050	82	16	0	0	0	42,5	12,3	2,1	1,2	3,5	15
4100	83	29	0	10	0	30,9	14	3,4	1,9	6,5	0
4150	84	9	0	6	0	34,1	13,5	3,75	1,5	0	0
4200	85	14	0	0	0	54,6	10,2	1,82	1,2	0	1
4250	86	17	0	6	0	24,6	20	5,15	1,4	0,5	0
4300	87	12	0	7	0	21,8	52,2	4,4	1,5	1	0
4350	88	28	0	0	0	23,2	21,8	2,35	1,8	0	0
4400	89	12	0	4	0	22,2	20,4	4,71	1,3	0	0
4450	90	10	0	1	0	22,6	14	4,32	1,4	0	0
4500	91	8	0	0	0	31,8	6,3	0,25	1,8	0	0
4550	92	11	0	0	0	46,6	6,4	2,14	1,7	0	15
4600	93	17	0	13	0	52,9	10,4	6,1	2,9	2,5	3
4650	94	10	0	4	0	28,2	8,1	5,88	2,1	0	2
4700	95	3	0	7	0	30,7	25	8,93	2,3	0	0
4750	96	7	0	3	0	31,2	1,8	9,02	2,5	0	0
4800	97	10	0	2	0	34,9	6	11,5	2,7	0	0
4850	98	9	0	5	0	27,8	20,1	10,4	2,6	0	0
4900	99	4	0	2	0	22,3	30,6	9,3	2,1	0	3
4950	100	1	0	6	0	24,6	30,8	20,5	2,2	0,5	2
5000	101	15	0	0	0	35,6	11,4	6,6	2,2	2,5	14
5050	102	17	0	1	0	19,1	7,5	2,07	1,9	1,5	0
5100	103	10	0	0	0	23,8	9,2	0,93	1,6	0	0
5150	104	5	0	0	0	37,9	12,6	6,35	1,4	0	0
5200	105	0	0	2	0	60,8	2,5	8,03	1,6	0	0
5250	106	5	0	2	0	48,1	3,5	0,93	1,5	0	0
5300	107	2	0	3	0	83,5	2,4	3,42	1,7	0	0
5950	108	1	0	0	0	46,7	2	0,65	1,3	0	0
5400	109	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

5450	110	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
5500	111	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
5550	112	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
5600	113	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
5650	114	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
5700	115	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
5750	116	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
5800	117	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
5850	118	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
5900	119	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
5950	120	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
6000	121	8	0	1	0	23,5	3,2	0,46	1,8	1	0
6050	122	1	0	2	0	35,2	3	2,91	1,8	0	0
6100	123	7	0	0	0	49,8	2,9	2,41	2,6	4,5	4
6150	124	2	0	0	0	58,5	1,6	1,65	1,9	4,5	9
6200	125	3	0	1	0	79,4	2,2	13	2,1	0	0
6250	126	3	0	0	0	45,4	4,7	8	2,5	0	5
6300	127	11	0	0	0	44,9	8,3	6,15	2,5	0	0
6350	128	0	0	0	0	40,6	12,1	8,05	1,7	0	8
6400	129	6	0	1	0	37,8	3,4	7,4	1,9	0	2
6450	130	2	0	1	0	81,6	1,5	3,31	1,3	0	4
6500	131	14	1	1	0	19,4	11,5	3,11	1,8	4,5	7
6550	132	10	2	0	0	14,1	24	4,5	2	1,5	0
6600	133	7	2	0	0	19,7	15,6	4,11	1,4	1	10
6650	134	18	1	0	0	9,8	21,8	2,49	1,6	2,5	14
6700	135	11	0	0	1	33	22,6	6,5	1,6	0	0
6750	136	23	1	0	0	17,4	7,3	4,5	1,9	1,5	0
6800	137	8	2	1	0	21,4	19,7	4,7	1,7	1	0
6850	138	5	0	3	0	30,5	24,1	20,2	1,8	0	4
6900	139	2	0	1	0	53,7	5,7	40,7	1,9	0	4
6950	140	1	0	1	1	61,5	14,7	38,2	1,8	0	2
7000	141	6	0	0	0	34,3	9,6	45	1,6	0	0
7050	142	5	0	0	0	23,4	16,3	27,5	1,7	0	0
7100	143	4	0	5	1	38,8	4,1	22,25	1,9	0	0
7150	144	9	0	0	0	39,9	5,9	32,65	1,6	0	0
7200	145	4	0	1	0	53,4	1,3	3,92	2	0	5
7250	146	9	0	0	5	20,5	12,8	6,2	1,7	4	2
7300	147	9	2	0	2	37,3	26,8	21,6	2,3	0	3
7350	148	1	2	1	5	27,4	15,9	6,95	1,9	0,5	1
7400	149	4	0	0	6	32,5	20,8	7,3	1,9	2	0
7450	150	2	0	2	2	45,9	7,8	6,3	1,7	0	0
7500	151	0	0	0	1	77,6	2,2	5,5	1,1	0	0
7550	152	5	0	1	0	75,5	1,6	17,05	2,4	0	12
7600	153	0	0	0	0	42,3	2	10,4	1,6	2,5	6
7650	154	5	0	0	0	38	13,1	5,45	1,8	0	5

7700	155	9	0	3	0	2,8	5,3	5,3	2	0	0
7750	156	4	0	3	1	23,3	33,8	11,4	1,4	0	3
7800	157	3	0	1	0	47,3	25,4	22,4	1,1	0	0
7850	158	1	0	3	0	51,3	13,7	15,75	1,5	0	4
7900	159	1	0	0	0	21,7	32,7	17,7	1,5	0	0
7950	160	3	0	0	0	27,3	28,4	12,45	1,6	0	2
8000	161	1	0	4	0	25,1	20,8	23,7	2	0	0
8050	162	3	0	0	0	33,5	11,3	20,45	1,9	0	0
8100	163	0	0	0	0	25,4	15,5	28,55	1,4	0	0
8150	164	5	0	0	0	30,2	19	15,75	1,8	0	0
8200	165	5	0	0	0	34,3	7,6	16,75	2,1	0	0
8250	166	7	0	0	0	40,2	4,9	40	1,6	0	0
8300	167	1	0	1	0	43,5	13,2	41,3	2	0	0
8350	168	2	0	1	0	29,5	21,1	55,5	2,2	0	0
8400	169	6	0	0	0	56,3	15,2	13,4	1,7	0	0
8450	170	4	0	0	0	41,6	9,1	28,7	1,8	0	0
8500	171	4	0	2	0	33,6	7,1	19,7	2,3	0	0
8550	172	0	0	1	0	35,9	18,2	33,75	1,8	0	1
8600	173	3	0	1	0	27,3	17	18,5	1,8	0	1
8650	174	0	0	1	0	40,7	37,7	23,15	1,1	0	0
8700	175	1	0	0	0	37,3	30,1	20,75	1,6	0	4
8750	176	1	0	2	1	52,8	8,2	36	2	0	13
8800	177	2	0	5	1	46	11	24,4	1,6	4	21
8850	178	12	0	2	0	12,7	17,3	12,3	2	4	3
8900	179	18	0	5	1	27,2	28,3	19	2	0	6
8950	180	3	1	2	1	16,1	21,9	27,4	2	0	0
9000	181	4	0	2	0	38	26,5	31,05	1,7	0	3
9050	182	2	0	5	0	33,9	39,1	17,5	1,8	0	3
9100	183	5	0	4	0	37,3	24,9	18,5	1,6	0	0
9150	184	1	0	4	0	29,5	29,7	28,5	1,7	0	0
9200	185	2	0	1	0	37,3	29	52,7	1,7	0	0
9250	186	4	0	2	1	30,1	30,9	29,2	2,4	0	0
9300	187	1	0	3	0	27,9	13,8	33,2	2	0	1
9350	188	5	0	1	0	34,3	8,3	26,75	1,8	0	0
9400	189	2	0	2	0	26,5	15,3	28,9	2	0	0
9450	190	7	0	3	0	22,7	5,4	28	2,3	0	0
9500	191	2	0	2	0	26,7	16,7	39,25	1,9	0	0
9550	192	3	0	1	0	42,2	19,2	37,5	2,2	0	0
9600	193	1	0	1	0	33	38	39,5	1,9	0	0
9650	194	2	0	4	0	65,6	13,5	36,75	1,8	0	0
9700	195	9	0	4	0	36,4	18,9	31,5	2	0	0
9750	196	2	0	3	0	21,7	26,2	21,5	2,1	0	0
9800	197	6	0	7	1	35,5	24,4	15,5	2	0	2
9850	198	10	0	0	2	20,2	33,1	19,2	1,9	0	6
9900	199	7	0	1	0	30,9	25,1	24,5	2,6	1	1

Appendix II

R-output from the GAM and length analyses.

Output from R in model 1 in the GAM-analyses.

```
Formula:
YOY ~ s(spawnarea) + s(meter)

Parametric coefficients:
              Estimate    Std. Error  z value     Pr(>|z|)
(Intercept)   2.07848     0.02706     76.82       <2e-16 ***

Approximate significance of smooth terms:
                    edf    Ref.df  Chi.sq  p-value
s(spawnarea)        8.717  8.717   154.6   <2e-16 ***
s(meter)            8.538  8.538   159.7   <2e-16 ***

R-sq.(adj) =  0.223   Deviance explained = 28.2%
UBRE score = 4.5496  Scale est. = 1       n = 187

Formula:
YOY ~ s(spawnarea) + s(meter) + s(substrate, shelter)

Parametric coefficients:
              Estimate    Std. Error  z value     Pr(>|z|)
(Intercept)   1.95684     0.03077     63.6        <2e-16 ***

Approximate significance of smooth terms:
                        edf         Ref.df      Chi.sq      p-value
s(spawnarea)            8.817       8.817       62.59       3.50e-10 ***
s(meter)                8.125       8.125       71.24       3.22e-12 ***
s(substrate,shelter)    22.538      22.538      222.71      < 2e-16 ***

R-sq.(adj) =  0.428   Deviance explained = 52.6%
```

```
UBRE score = 2.9679  Scale est. = 1         n = 187



Formula:
YOY ~ s(spawnarea) + s(meter) + s(substrate, shelter) + s(velocity)

Parametric coefficients:
                   Estimate      Std. Error     z value       Pr(>|z|)
(Intercept)        1.93698       0.03113        62.22         <2e-16 ***

Approximate significance of smooth terms:

                          edf            Ref.df         Chi.sq            p-value
s(spawnarea)              8.721          8.721          78.27         2.57e-13 ***
s(meter)                  5.672          5.672          40.74         2.28e-07 ***
s(substrate,shelter)      23.004         23.004         249.41        < 2e-16 ***
s(velocity)               7.568          7.568          75.02         2.90e-13 ***

R-sq.(adj) =  0.467   Deviance explained = 58.5%
UBRE score = 2.5898  Scale est. = 1         n = 187



Formula:
YOY ~ s(spawnarea) + s(meter) + s(substrate, shelter) + s(velocity) +
    s(depth)

Parametric coefficients:
                   Estimate      Std. Error     z value       Pr(>|z|)
(Intercept)        1.93172       0.03125        61.82         <2e-16 ***

Approximate significance of smooth terms:
                          edf            Ref.df         Chi.sq        p-value
s(spawnarea)              8.776          8.776          63.54         2.19e-10 ***
s(meter)                  7.604          7.604          53.64         5.36e-09 ***
```

```
s(substrate,shelter)    20.800    20.800    179.88    < 2e-16 ***
s(velocity)             7.183     7.183     39.37     1.98e-06 ***
s(depth)                1.000     1.000     17.63     2.69e-05 ***

R-sq.(adj) =  0.499   Deviance explained = 59.3%
UBRE score = 2.5306  Scale est. = 1         n = 187
```

```
                                df          AIC
YOY~s(Spawners)+s(Meter)        18.25597    1683.558
+s(Substrate,Shelter)           40.47928    1387.791
+s(Velocity)                    45.96502    1317.076
+s(Depth)                       46.36407    1306.014
```

Output from R in model 2 in the GAM-analyses

```
Formula:
YOY ~ s(spawners) + s(meter)

Parametric coefficients:
              Estimate    Std. Error    z value    Pr(>|z|)
(Intercept)   2.09253     0.02683       78     <2e-16 ***

Approximate significance of smooth terms:
              edf         Ref.df        Chi.sq     p-value
s(spawners)   8.394       8.394         44.61      6.3e-07 ***
s(meter)      8.824       8.824         209.02     < 2e-16 ***

R-sq.(adj) =  0.161   Deviance explained = 23.1%
```

```
UBRE score = 4.9306  Scale est. = 1         n = 187


Formula:
YOY ~ s(spawners) + s(meter) + s(substrate, shelter)

Parametric coefficients:
                Estimate     Std. Error    z value      Pr(>|z|)
(Intercept)     1.94711      0.03119        62.42       <2e-16 ***

Approximate significance of smooth terms:
                        edf          Ref.df       Chi.sq       p-value
s(spawners)             8.591        8.591        33.59        7.7e-05 ***
s(meter)                8.501        8.501        121.30       < 2e-16 ***
s(substrate,shelter)    24.670       24.670       251.55       < 2e-16 ***

R-sq.(adj) =  0.401   Deviance explained = 52.2%
UBRE score = 3.0187  Scale est. = 1         n = 187


Formula:
YOY ~ s(spawners) + s(meter) + s(substrate, shelter) + s(velocity)

Parametric coefficients:
                Estimate     Std. Error    z value      Pr(>|z|)
(Intercept)     1.92916      0.03149       61.27        <2e-16 ***

Approximate significance of smooth terms:
                        edf          Ref.df       Chi.sq       p-value
s(spawners)             8.401        8.401        25.29        0.00181 **
s(meter)                8.047        8.047        81.50        2.58e-14 ***
s(substrate,shelter)    24.202       24.202       262.17       < 2e-16 ***
s(velocity)             7.548        7.548        69.61        3.44e-12 ***

R-sq.(adj) =  0.429   Deviance explained = 57.8%
```

```
UBRE score = 2.6698  Scale est. = 1         n = 187
```

```
Formula:
YOY ~ s(spawners) + s(meter) + s(substrate, shelter) + s(velocity) +
    s(depth)

Parametric coefficients:
                   Estimate     Std. Error    z value      Pr(>|z|)
(Intercept)        1.92486      0.03152       61.07        <2e-16 ***

Approximate significance of smooth terms:
                          edf          Ref.df       Chi.sq       p-value
s(spawners)               8.255        8.255        24.41        0.00231 **
s(meter)                  8.330        8.330        92.10        2.66e-16 ***
s(substrate,shelter)      21.838       21.838       150.56       < 2e-16 ***
s(velocity)               7.331        7.331        49.54        2.53e-08 ***
s(depth)                  7.315        7.315        32.68        3.98e-05 ***

R-sq.(adj) =  0.456   Deviance explained = 60.1%
UBRE score = 2.5562  Scale est. = 1         n = 187
```

	df	AIC
YOY~s(Spawners)+s(Meter)	18.21805	1754.811
+s(Substrate,Shelter)	42.76163	1397.284
+s(Velocity)	49.19681	1332.039
+s(Depth)	54.06909	1310.801

Output from R in the linear model describing growth related to density and day after field work start

```
Call:
lm(formula = log(length) ~ density + date)

Residuals:
Min         1Q          Median      3Q          Max
-0.293691   -0.061735   -0.001552   0.051416    0.406823

Coefficients:
            Estimate    Std. Error  t value     Pr(>|t|)
(Intercept) 3.571716    0.019760    180.753     < 2e-16 ***
Density     -0.023991   0.011545    -2.078      0.0392 *
Date        0.010398    0.001377    7.551       2.68e-12 ***

Residual standard error: 0.09756 on 167 degrees of freedom
Multiple R-squared: 0.3147,             Adjusted R-squared: 0.3065
F-statistic: 38.35 on 2 and 167 DF,     p-value: 1.971e-14
```