Inter-population variation in brown trout (*Salmo trutta*) life-history- and migration strategies in a clay-affected river system: live fast, die young!

Variasjon i livshistorie- og vandringsstrategier mellom populasjoner av aure (*Salmo trutta*) i et leirepåvirket vassdrag: lev raskt, dø ung!

Erik Friele Lie og Thomas Sørensen

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River Leira at Homledalen

Preface

This thesis is part of our master degrees in Natural Resource Management at the Department of Ecology and Natural Resource Management (INA), University of Life Sciences (UMB).

The thesis was proposed by "Vannområde Leira-Nitelva" (the competent authority of Leira-Nitelva sub-district of Glomma River Basin District).

We are very glad to have got to know the river Leira (meaning "clay"), its fishy inhabitants and beautiful surrounding cultural landscape and deep forests. If this thesis somehow can contribute to conserve or even improve the qualities of this river and area – that would make us even happier.

All photos are by the authors if not otherwise stated.

Ås, December 2013

Erik Friele Lie   Thomas Sørensen

"Life histories lie at the heart of biology; no other field brings you closer to the underlying simplicities that unite and explain the diversity of living things and the complexities of their life cycles."

Stephen C. Stearns (1992)

Contents

Abstract

The objective of this study was to compare among-tributary variation in life-history and migration in brown trout (*Salmo trutta* L.) living in the Leira river system, Nannestad municipality. The results were to be discussed in both a general biological context as well as potential management implications, with special emphasis on the Water Framework Directive.

Data was sampled in four tributaries and one river station over six sampling rounds during 2012 and 2013. The fish were sampled using electrofishing and fyke nets. The fish were tagged with PIT-tags and the resulting mark-recapture data were modelled under a Cormack-Jolly-Seber model structure. Two PIT antennas were mounted to monitor large-scale migrations within the main river, but they did only function for a short period during the last part of the study. Scales were retrieved for age and growth analyses.

There were population differences in summer survival, second-and third-year growth and maturation sizes. In general, the Leira brown trout displayed a short life cycle, characterized by rapid early-life growth, early maturation and short life-span (< 6 years). There was a general trend with more rapid life cycles the further downstream. We suggest this gradient to be caused by increasing environmental stress (reduced water quality and increased inter-specific competition) downstream and possible lack of habitat. The population displaying the most rapid life cycle (Rotua) seems to have little suitable habitat for >0+ individuals and possibly also experience thermal stress in warm summers due to little vegetation coverage. An interesting find pertinent to management institutions is that we found no 0+ in the main river indicating that recruitment exclusively takes place in the tributaries. In accordance with this, we did find evidence of fluvial-adfluvial potamodromy, but the two larger tributaries seem to predominantly hold stationary or fluvial potamodromous individuals.

The findings are clearly in line with general life-history theory that predicts rapid early-life growth and high adult mortality in relation to juvenile mortality to result in early maturation. Furthermore, the unpredictable and highly variable Leira system favors early maturation and short life cycles with high reproductive effort.

Based on our findings the brown trout population density seem to provide information sensitive the water quality, but since there is an inter-specific competition aspect into this as well, an eventual brown trout water quality assignment index will need to take this into account. Since most migration interpretations in this thesis are only circumstantial a continuation of the PIT-antenna monitoring program should be secured so as to complete a full-year monitoring.

1. Introduction

Life-history traits are generally tightly linked to fitness and hence also to population viability (Stearns 1992). Understanding what is behind both temporal and spatial (i.e., among populations) variation in such traits is therefore pertinent to both ecological and evolutionary studies (Stearns and Hoekstra 2005). In the study of a species' life-history strategy there are many traits to consider. Size at birth, growth pattern, size- and age at maturation, semelparous- or iteroparous reproduction and longevity are some of the main features to evaluate (Stearns 1992). Either if you are working as a wildlife manager in terrestrial- or fish manager in aquatic environments a profound knowledge about an organism's life-history is crucial to be able to make good decisions and recommendations to management institutions regarding developments, stipulating quotas for game or preservation of nature resources. A profound knowledge of life-history aspects is particularly important regarding the latter when there is a general consensus that the environment is imposing detrimental threats like pollution, destruction of habitats and human-induced climate change (Primack 2012). When making management decisions, it is also important to understand the dynamics between environmental changes and the adaptations in the different species. A species or a population is considered to have local adaptations where certain trait values potentially would maximize fitness according to the current environmental conditions (Stearns and Hoekstra 2005). Human or natural alterations of the environment could lead to new adaptations for the species by "adjusting" certain traits to maximize fitness (Grant and Grant 1995, Haugen 2000). It is thus important to acknowledge the local adaptations in the involved populations when making management decision that affect habitat quality and/or harvesting regimes. In line with this, you must take into account that your decisions as a manager potentially could alter the current local adaptations in the species.

Life-history traits are considered evolutionary compromises between costs and benefits where the mean is to maximize fitness (Hutchings et al. 1999). The way these and other traits (e.g., behavioral traits like migration) combine, creates the diversity of life-histories that we see in nature (Stearns 1992). Life-history theory seeks to explain these major features of a life cycle and how they affect fitness through natural-selection processes (Stearns 1992, Campbell et al. 2008). These selection processes are believed to vary over different stages of the organisms' life cycle,

such as periods of high mortality rates, e.g. in early life stages, during winter-, draught-, and flood periods or post spawning period (Conover and Schultz 1997). The basic idea is that evolution through natural selection "favors" certain life-history traits, under given environmentally conditions, to enhance an organism's chances to survive and reproduce with success, i.e., the organism's fitness (Campbell et al. 2008), with a genetic and/or phenotypic basis (Roff 2002). The diversity of traits is bound together in constraining relationships of trade-offs (Stearns 1992). Moreover, measured phenotypical variations between populations could be a result of adaptations (i.e., genetic differentiation) and/or phenotypic plasticity (i.e., the same genotype has different phenotypic values across environmental gradients) (Schlichting and Smith 2002).

The diversity of life-histories among plants and animals are often very difficult to generalize because the natural world is so dynamic and stochastic both in time and space, which in turn will have a considerable effect on the demography of the populations (Charlesworth 1994, Haugen 2000), and the organisms have to constantly adapt to the changes in the environment (Campbell et al. 2008). These variations in life-history patterns and traits are not only common at species level but also at population- and individual level (Roff 2002), which has been observed in the family of Salmonidae, among others (Klemetsen et al. 2003, Jonsson and Jonsson 2011).

In many animals, migration and life-history are closely connected (Roff 2002). Migration is here distinguished from dispersal, which most often means a spreading of individuals away from others (Begon et al. 2006). Dispersal is a trait of greatest importance as regards species persistence and evolution, and is central in metapopulation theory (Clobert et al. 2001, Hanski and Gaggiotti 2004). Migration, as defined by Lucas and Baras (2001), is «a strategy of adaptive value, involving movement of part or all of a population in time, between discrete sites existing in an n-dimensional hypervolume of biotic and abiotic factors, usually but not necessarily involving predictability or synchronicity in time, since inter-individual variation is a fundamental component of populations». The potential benefits of migration give us three principal categories: reproductive, feeding and refuge migration (Lucas and Baras 2001). Hence, we can see how these are directly linked to important life-history traits like reproduction (timing and extent), growth and survival. However, there are also costs associated with migration, and whether the best

strategy is to stay or move depends on what gives the greatest fitness effect after benefits and costs have been balanced (Jonsson and Jonsson 1993). For instance, moving to a new habitat may mean better access to food, but at the same time it can increase the risk of predation.

Studies on life-history have been conducted on numerous species – both in aquatic- and terrestrial environments (Stearns 1992). Brown trout (*Salmo trutta* L.) is regarded to be well suited for these types of study (Olsen 2000), and an important freshwater fish receiving a lot of management attention in Norway (Qvenild 1994). The variability in growth, maturation and longevity, its diversity in migratory behavior- and strategy, great ability to move through steep rivers and disperse and establish populations in new watercourses, marked homing behavior and diverse environmental tolerances, make the brown trout to a species with one of the most diverse and complex life-histories (Jonsson 1989, Klemetsen et al. 2003, Jonsson and Jonsson 2011). Brown trout was earlier considered to be divided up in about 50 different species (Behnke 1986, Elliott 1994, Klemetsen et al. 2003), which gives an idea of the ecological variations in the brown trout (Elliott 1994).

The age and size at sexually maturation in brown trout varies greatly (Klemetsen et al. 2003), and the variation is especially high among individuals and populations where the fish has access to many potentially feeding habitats (Jonsson 1989, Jonsson and Jonsson 2011). Temperature plays an important role in the maturation and it has been observed a gradient in age from south to north in Europe (Jonsson and Jonsson 2011). In addition, it has been observed that brown trout mature at a higher age in cold mountain lakes than lowland sites (Jonsson et al. 1991b, Klemetsen et al. 2003). A general consensus states that an early maturation (i.e., small size and low age) increases the probability to reproduce before dying (Bell 1980). An early maturation in brown trout yields a short juvenile stage, which is considered to be a critical period with typically high mortality rate (e.g., predation, competition) (Bell 1980, Olsen 2000). Moreover, an early maturation could also mean less time spent in unfavorable habitats (e.g., feeding migrations in lakes and estuaries) relative to predation- and disease risk (Jonsson and Gravem 1985, Jonsson 1989, Klemetsen et al. 2003). The costs of early maturation include a shorter lifespan, probably due to high cost of reproduction in terms of post spawning mortality (Wootton 1998). In addition, an early maturation normally will decrease fecundity and egg size in female brown trout which will affect

the reproductive output (Gregersen et al. 2006). It has been found a positive correlation between both fecundity and egg size and the size of mature females, thus it is suggested that increased size therefore increases female fitness (Klemetsen et al. 2003). The maturity age and size also varies between the sexes where males usually mature at a younger age and more varied size than the females (Klemetsen et al. 2003). This corresponds with the often observed predominance of females among the migrating individuals in brown trout, suggesting that females have a higher selective benefit from a migration-induced higher growth rate than males (Klemetsen et al. 2003). Age at maturity is typically correlated with longevity where long lived brown trout matures at higher ages than those with a short life span (Jonsson and L'Abée-Lund 1993). It has also been observed a negative correlation between growth rate and age at maturity within brown trout populations (Alm 1959, Jonsson and Jonsson 2011). The longevity of brown trout is influenced by temperature (Pauly 1980). Accordingly, Jonsson et al. (1991a) found a significant trend on increased longevity towards north.

The brown trout is well-known for its migratory behavior, particularly its strong homing behavior – both anadromous and freshwater resident brown trout tend to return to their natal areas for spawning (Harden Jones 1968, Jonsson and Jonsson 2011). They also exhibit feeding migration, as when juveniles leave their natal stream to grow large in a nearby lake, and refuge migration to avoid periods of unfavorable conditions, like a stream drying out in the summer. The different habitat preferences change during the life cycle and individual fish can minimize fitness reduction if they move between these habitats at the right times (ontogenetic niche shifts) (Lucas and Baras 2001). Studies on brown trout also show examples of how life-history traits can affect migration patterns. For example, juvenile growth rate can have an effect on when or if a brown trout will smoltify and migrate to sea (Jonsson 1985). Migration should not be considered as a single strategy, but rather as a strategy that can be expressed along a continuum in time and space (Lucas and Baras 2001, Cucherousset et al. 2005). Anadromy gets much attention as a migratory strategy in brown trout, but potamodromy – migrations occurring entirely in freshwater – is a common and diverse trait in this species (Northcote 1997). All potamodromous categories, defined by Nothcote (1997), are found in brown trout: fluvial potamodromy refers to migration within a stream or river, fluvial-adfluvial potamodromy refers to migration between a main stem river and tributaries, lacustrine-adfluvial refers to migrations between a lake and rivers or streams

feeding that lake, and allacustrine potamodromy refers to the same except that the fish migrates to rivers or streams flowing out of the lake. The ultimate drivers behind all these migratory strategies remain enigmatic, but are likely to be complex and not necessarily congruent among different systems. Pertinent to management, migrations between habitats of different environmental qualities, such as good water-quality habitats in nursery streams versus lower water-quality habitats in main-river stretches utilized by larger individuals, impose challenges in terms of using brown trout as indicator species in water framework directive related monitoring programs.

In this study, we compare subpopulations of brown trout that all live at least most of their juvenile lives in respective tributaries that all empty into the same main river. The water quality, in terms of phosphorus loading and water turbidity, decreases as one moves down-stream. In particular, we will explore the following questions:

- Are there inter-population differences in life-history traits?
    - If so: Are there systematic associations between environmental conditions and life-history trait values?
- Are there inter-population differences in migration (i.e., fluvial-adfluvial potamodromy) tendency?
    - If so: Are there associations between life-history traits and migration tendency?

Finally, we will explore the management relevance of the findings.

2. Materials and methods

2.1. Study species

Our study species in this study on inter-population variation in life-history traits and migration is the brown trout (Figure 1). The study site is situated in an inland area (Figure 3) without access to coastal areas, and since the nearest accessible lake (Øyeren) is located several tens of kilometers downstream our study site, it is reasonable to assume that in this current system we are dealing with stream-dwelling brown trout. The latter will thus chiefly be described here although several, if not all, varieties overlap when it comes to life-history strategies.

The brown trout belongs in the family of Salmonidae. The species is iteroparous and it is identified as a fish with high ecological variability (Klemetsen et al. 2003). From having its origin chiefly in Europe and being confined to a few refuges during the last ice age it is now considered having a worldwide geographical distribution. The brown trout's success as a disperser is due to a wide environmental tolerance and migratory behavior, but the ultimate cause for the worldwide geographical distribution is introductions by humans (Klemetsen et al. 2003, Jonsson and Jonsson 2011).

Figure 1. Brown trout captured in Tøla during field work.

The brown trout is well known to have a wide variation in size, growth rate, food- and habitat preference both within and among water courses, and is considered to be one of the most well-adapted fishes in northern waters (Klemetsen et al. 2003, Jonsson and Jonsson 2011). The water temperature is one of the major factors that constraints the distribution of brown trout (MacCrimmon and Marshall 1968, Elliott 1994, Jonsson and Jonsson 2011). According to a study of Forseth et al. (2009) the lower- and upper temperature limit of for growth was measured to 5 °C and 23 °C, respectively, with the optimal growth temperature being about 13-18 °C, although Elliott et al. (1995) found a lower and upper temperature limit of 3.8 °C and 21.7 °C, respectively, through a water tank experiment. For the development of embryo the optimal temperature is between 0 °C and 15 °C (Elliott 1981, Jonsson and Jonsson 2011). Sufficient oxygen saturation in the water is also an important factor, especially during embryo development, and low water velocity with combination of sedimentation of silt and clay can be detrimental for embryo survival (Soulsby et al. 2001, Wood and Budy 2009, Jonsson and Jonsson 2011).

The brown trout normally starts its life cycle in a stream or a river, although spawning in lakes occurs occasionally in some populations (Scott and Irvine 2000, Brabrand et al. 2002, Klemetsen et al. 2003). Spawning occurs typically from September to December, but also as late as November to March, depending on altitude, latitude and water temperature (Armstrong et al. 2003). In addition, the time periods of incubation and endogenous larval feeding are both negatively temperature dependent (Crisp 1988, Elliott and Hurley 1998, Klemetsen et al. 2003). Hatching occurs in the successive spring, and during the first few weeks the alevins feed on their yolk sac before emerging from the gravel approximately 20 mm long (Klemetsen et al. 2003). The fry can be quite sedentary at first and will often start feeding in the proximity of the hatchery area, but if the environmental conditions are harsh, they can migrate to more favorable areas (Nordwall et al. 2001, Klemetsen et al. 2003). The young brown trout is known to be aggressive and territorial where intense competition for the resources is very common (Kalleberg 1958, Heland 1999, Lahti et al. 2001, Klemetsen et al. 2003).

The preference of habitat is related to physical factors such as substrate, water depth, water velocity and shelters (Heggenes 1989, Heggenes et al. 1999, Saltveit and Heggenes 2000). The choice of habitat depends on the availability and intraspecific competition often constrains the fry to utilize shallow areas close to shore while larger and older dominant individuals colonize

deeper and slow-flowing pools constituting more energy-conserving microhabitats (Bagliniere and Champigneulle 1982, Heggenes et al. 1999, Saltveit and Heggenes 2000). Studies have shown that brown trout juveniles prefer areas where the snout water velocity does not exceed 20 cm s^{-1}, and preferably between 0 and 10 cm s^{-1} (Greenberg et al. 1996, Heggenes et al. 1999, Heggenes 2002, Jonsson and Jonsson 2011). Another factor affecting not only the habitat choice, but also the diurnal activity, is seasonal variation in light and temperature (Jonsson and Jonsson 2011). While brown trout tend to be active throughout the day during the summer, this seems to change in the winter where the general activity level drops (Klemetsen et al. 2003, Jonsson and Jonsson 2011). Activity during winter is chiefly time spent on feeding and this is usually a nocturnal activity where the brown trout chooses slow-flowing areas as backwaters, pools and areas near the riverbank (Heggenes et al. 1993, Saltveit and Heggenes 2000). During day time it tends to seek to refuges in a coarse bottom substrate with overhead cover and snout water velocity close to 0 cm s^{-1} (Saltveit and Heggenes 2000).

After the yolk stage the fry are dependent on habitats that allow for catching drifting invertebrates with low risk of getting caught by other predators. Typically, at this stage the brown trout exploits coarse stony shallow areas with moderate water velocity where they can take shelter while monitoring the drift of invertebrates (Heggenes et al. 1999, Saltveit and Heggenes 2000, Klemetsen et al. 2003, Jonsson and Jonsson 2011). A coarse substrate also restrains the brown trout's aggressive behavior against other individuals because of visual isolation (Saltveit and Heggenes 2000).

The brown trout is an opportunistic predator where all types of benthos are potentially part of the diet, but this varies according to the size and the experience of the individuals (Bridcut and Giller 1995, Saltveit and Heggenes 2000, Klemetsen et al. 2003, Jonsson and Jonsson 2011). At the early stage of the brown trout's life span larvae of chironomids (Chironomidae) are very important in the diet and can become a bottleneck for the young of the year as the competition for the chironomids can be substantial, not the least from other species (Saltveit and Heggenes 2000).

As mentioned earlier the size, age at maturity and longevity vary greatly and are to a high extent connected together and with choice of habitat (Southwood 1977, 1988, Poff and Ward 1990, Jonsson and Jonsson 2011). In 4-year old fish a range in size from 20 gram for stream-dwelling individuals to 500-1000 gram for piscivorous and anadromous individuals is not unusual

(Jonsson and Sandlund 1979, Jonsson 1985, Klemetsen et al. 2003). There is an evident sexual difference in both size and age at maturity where males often attain maturity at smaller size and earlier age than females. According to Jonsson and Sandlund (1979) males can attain maturity with a size below 10 cm and one year of age. This is in accordance with the well-known sneak strategy in males where size is suggested to be an independent factor in reproductive fitness (Gross 1984, Jonsson and Jonsson 2011).

2.2. Study system

The study was conducted in the river Leira with tributaries (south-east Norway, 60°20'N, 10° 98'E) (Figure 3A). From an elevation around 700 meters in Gran municipality, Oppland county, the river runs 100.7 km to its outlet around 100 meters above sea level in river Nitelva, just upstream the large lake Øyeren (NVE 2013). Mean water discharge in the outlet is 13.3 $m^3 s^{-1}$ (Pettersson 2005). The total catchment area comprises 662.6 km^2 (NVE 2013), of which 380 km^2 is covered in marine deposits, including thick layers of clay (Vannregion Glomma 2012). The higher parts are dominated by conifer forests, mainly on granite or syenite rock, or moraine deposits (NGU 2013a, b). This area consists of many lakes and the water here is clear. The river enters the area of marine deposits, which is dominated by agriculture, at Vollaugmoen about 200 meters above sea level. Downstream from here the water gets more and more turbid. Average concentration of suspended sediment at Krokfoss is calculated to be 122 mg L^{-1} (Bogen et al. 2002). However, the sediment transport varies a lot within and among years. In general, the sediment transport follows the fluctuations in water discharge, which because of hardly permeable grounds in the catchment area tends to increase rapidly after rainfall and snowmelt. The wettest periods are in the fall, and five months have an average temperature below freezing (Figure 2). Leira is mostly slow-flowing after Vollaugmoen, interrupted by some waterfalls. After Krokfoss there are no more waterfalls and the river gets highly meandering toward its outlet. Leira is a protected water course and there are no power stations in the river, which is virtually unregulated (Nannestad kommune 2009).
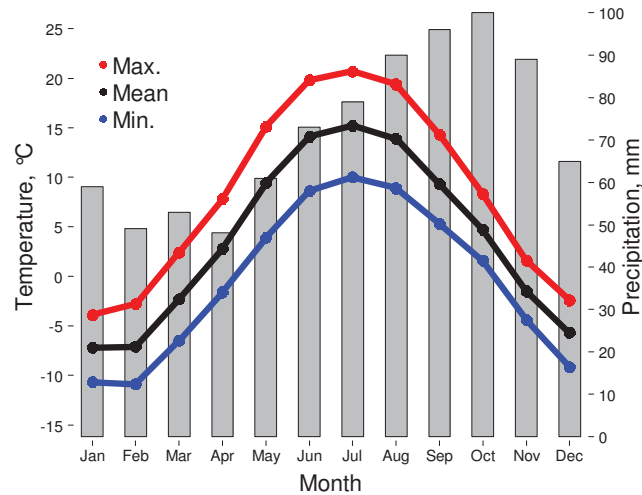
Figure 2. Mean (black), average of maximum (red) and average of minimum (blue) air temperature, and average precipitation (grey bars) at Gardermoen (5-6 km east of Leira, see Figure 3). Data from Meteorologisk Institutt (2013).

This study focuses on the lower middle parts of the river, in Nannestad municipality, Akershus county (Figure 3B). Within this area, four stations in separate tributaries were chosen for fish sampling and tagging. Those are (from north to south): Tøla (TØL), Eskerudbekken (ESK), Rotua (ROT) and Nordbybekken (NOR). The stations are given the same name as the stream they are part of. One short stretch of the main river was also electrofished in all sampling rounds. This station was named Kringlerstryket (KRI). All stations will be described in more details below. In addition, three stretches of the main river (LEI_1, LEI_2 and LEI_3) were electrofished with boat at one occasion (see 2.3.1. Fish sampling). The main river is within the study area classified as a fifth order river upstream the conjunction with Rotua and as a sixth order river downstream (NVE 2013). Downstream from this river stretch there are several waterfalls which may act as migration barriers for fish. The landscape is characterized by large fields intersected with a number of ravines formed by streams eroding in the marine deposits. Eutrophication is considered a problem in this part of Leira, and the extent of it increases in a downstream direction (Borch et al. 2008, Haaland and Gjemlestad 2012). The main anthropological sources are thought to be agriculture runoff and sewage, in addition to the natural source of phosphorus in the clay.
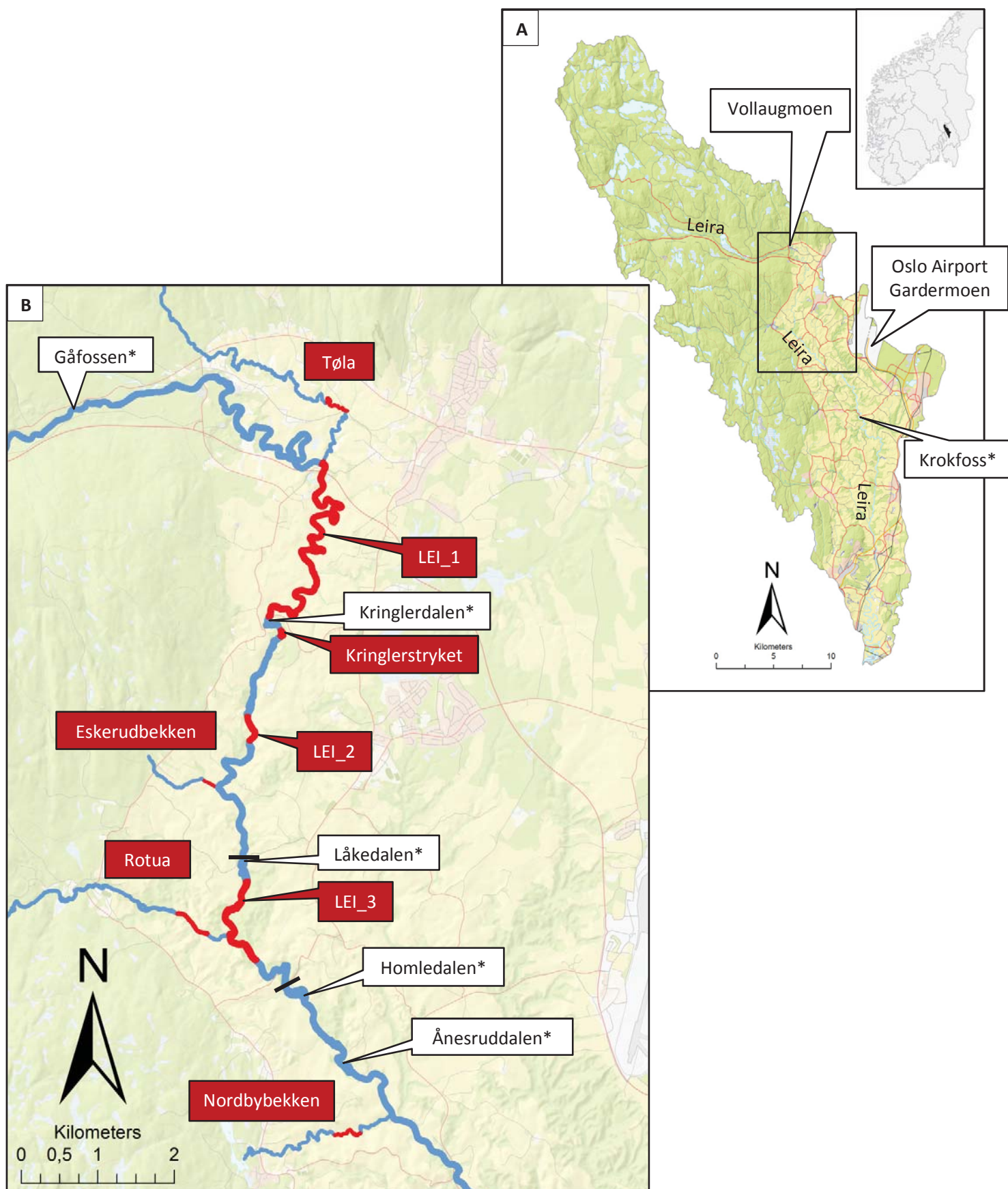
Figure 3. Maps showing the catchment area of Leira (**A**) and the study area (**B**). Stretches that were electrofished are marked in red. The asterisks (*) indicate main river waterfalls. The black lines at Låkedalen and Homledalen indicate the location of PIT antennas. Map source: Statens Kartverk (The Norwegian Mapping Authority).

The lower part of Leira has a very high diversity of fish species by Norwegian standards, due to the fact that it runs into the lake Øyeren. This lake holds the highest number of fish species (ca. 25) of any lake in Norway (Brabrand 2002). In the middle part of Leira the diversity is lower. During the study, six other species were observed in addition to trout. Eurasian minnow (*Phoxinus phoxinus*) and European brook lamprey (*Lampetra planeri*) were found in the main river and in all the tributaries. Alpine bullhead (*Cottus poecilopus*) was found in the main river and all tributaries apart from Nordbybekken. In Eskerudbekken, one individual of arctic char (*Salvelinus alpinus*) (in bad condition) was found. Chub (*Leuciscus cephalus*) and ruffe (*Gymnocephalus cernuus*) (one individual) were found only in the main river, downstream Låkedalen. Common dace (*Leuciscus leuciscus*) is also believed to be found here (Toverud 2001), but was not found by us. According to local inhabitants, Northern pike (*Esox lucius*) is found all the way up to the Ånesruddalen waterfall, possibly as far upstream as Låkedalen (pers. comm. Karl Henrik Laache, 01.10.2013).

Habitat characterizations were performed in May and June 2013. The characterization results are summarized in Table 1 and in the following paragraphs. The descriptions of the stations are more or less subjective and approximate for many of the dimensions, but nonetheless they should give a correct impression of the stream sections in question, particularly for comparisons among the stations. All the characterizations were performed by us. The dimensions that were characterized may vary by many factors, especially as a result of water discharge. The water discharge in the main river at Kringlerdalen (available from the Norwegian Water Resources and Energy Directorate) the day of characterization is therefore given as a proxy of water discharge in the tributaries. Stream gradient within a station was calculated using the length of the station, as measured in field, together with approximate elevation difference obtained from digital map with a contour interval of one meter (The Norwegian Mapping Authority, www.norgeskart.no). The structure of a stream section was separated into pools and riffles. Temperature recorders (iButton® Thermochron DS1921Z-F5) were mounted in all stations during June 2013 to October 2013. The recorded temperatures are plotted in Figure 4 together with air temperature data from the weather station at Gardermoen. Unfortunately, the Nordbybekken temperature logger did not provide data due to technical problems.
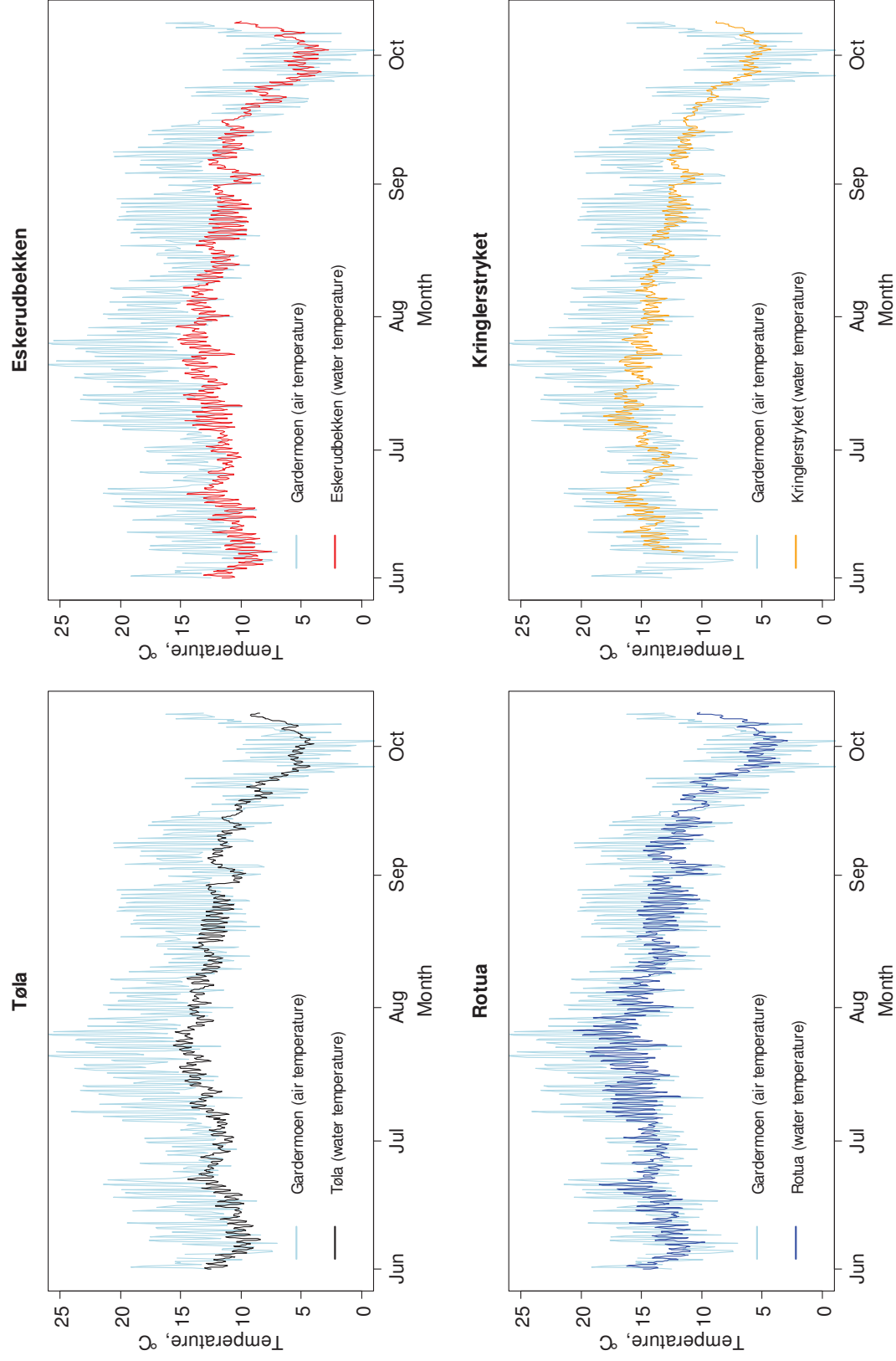
Figure 4. Water temperatures from four of the stations and air temperature from Gardermoen from June to October 2013. Water temperatures are based upon measurements every second hour, air temperature is based upon measurements every sixth hour.

Table 1. Values obtained from habitat characterizations of the sampling stations in Tøla, Eskerudbekken, Rotua and Nordbybekken.

		Tøla[a]	Eskerudbekken[b]	Rotua[c]	Nordbybekken[c]
River order[d]		3[e]	2[e]	5[e]	2[e]
Total length (m)		454.5	178	494	428.5
Gradient (°)		0.13	0.97	1.04	2.01
Area (m^2)		2137	514	6689	1461
Distribution of substrate particle size (%)	< 2 mm	46	14	< 1	21
	2-64 mm	48	62	7	9
	64-256 mm	4	17	29	22
	> 256 mm	2	7	64	48
Overhanging vegetation cover (%)		86	94	25	94
Undercut banks (% of total bank length)		20.6	19.7	1.4	8.9
Large woody debris per 100 m^2		5.3	8.0	0.3	5.3
Woody debris jams per 100 m^2		2.7	5.8	0.1	3.9
Number of	Pools	8	6	4	17
	Riffles	7	6	4	17
Mean length (m)	Pools	43.4 ± 24.3 SD	9.6 ± 4.0 SD	12.9 ± 3.6 SD	10.9 ± 10.5 SD
	Riffles	15.4 ± 7.5 SD	20.1 ± 15.6 SD	110.6 ± 80.3 SD	14.9 ± 12.1 SD
Mean width (m)	Pools	4.6 ± 0.6 SD	2.9 ± 1.2 SD	10.4 ± 4.1 SD	3.6 ± 1.2 SD
	Riffles	4.8 ± 0.6 SD	2.9 ± 0.7 SD	13.8 ± 5.6 SD	3.1 ± 1.3 SD
Total area (m^2)	Pools	1600	171	568	723
	Riffles	537	343	6120	739
Mean depth (m)	Pools	0.74 ± 0.24 SD	0.55 ± 0.16 SD	0.89 ± 0.21 SD	0.67 ± 0.26 SD
	Riffles	0.48 ± 0.07 SD	0.19 ± 0.04 SD	0.42 ± 0.08 SD	0.29 ± 0.09 SD
Max depth (m)	Pools	1.45	1.05	1.45	1.60
	Riffles	0.95	0.30	0.90	0.55

[a]Date of characterization: 30.05.2013 (discharge at Kringlerdalen: 11.8 m^3/s)

[b]Date of characterization: 31.05.2013 (discharge at Kringlerdalen: 10.6 m^3/s)

[c]Date of characterization: 06.06.2013 (discharge at Kringlerdalen: 12.8 m^3/s)

[d]Strahler (1957)

[e]NVE (2013)

2.2.1. Tøla

Tøla (Figure 5) is the northernmost of the tributaries included in the study. Most of it drains areas above marine deposits, but the sampling station was located below this boundary. Here, the stream is mostly slow-flowing and the substrate is dominated by fine-grained particles. Undercut banks are common and woody debris jams somewhere form impoundments.

Figure 5. Woody debris jam in Tøla.

The riparian zone is narrow, but mostly intact. It is dominated by grey alder (*Alnus incana*) and bird cherry (*Prunus padus*). The station ends at a large culvert under a road, where a tributary named Åsbekken enters, and starts 100-200 meters downstream the point where another tributary, Vikka, enters. The lowest parts of these two tributaries were included in the third sampling round, in October 2012. In total, 52 and 18 trout were captured and tagged in Vikka and Åsbekken, respectively.

2.2.2. Eskerudbekken

Eskerudbekken (Figure 6) is the smallest of the four tributaries. The station ends at the outlet into Leira. A small waterfall, potentially a fish migration barrier, marks the start. The riparian vegetation is dominated by grey alder and bird cherry. Overhanging vegetation is substantial and so is woody debris within the stream. Gravel dominates the substrate and undercut banks are common.

Figure 6. Eskerudbekken.

2.2.3. Rotua

Figure 7. Rotua.

Rotua (Figure 7) is by far the largest of the tributaries. Its sources comprise several lakes upon the woody hills and most of its stretches are located above the marine deposits limit. The sampling station though is located below this limit, ending about 300 meters upstream the outlet and starting where the tributary Elgbekken enters. The sampling station is characterized by long riffles with coarse substrate. The riparian zone is also here dominated by grey alder and bird cherry, but the vegetation is more varied, with elements of Norway spruce (*Picea abies*), birch (*Betula pubescens*) and rowan (*Sorbus aucuparia*). Overhanging vegetation and woody debris are far scarcer than in the other tributaries.

2.2.4. Nordbybekken

Figure 8. Nordbybekken.

Nordbybekken (Figure 8) originates from two small lakes just above the marine deposits limit. The stream therefore runs almost entirely through marine deposits. This is particularly apparent in the lower part, where clay is common in the substrate and the water easily gets turbid by suspended particles. Also, the amount of overhanging vegetation and woody debris is substantial

here. Grey alder and bird cherry dominate the riparian vegetation. The stream runs through a ravine, occasionally with very steep sides. In the middle of the station there is a steep section of small step pools which may be hard for fish to pass.

2.2.5. Kringlerstryket

Kringlerstryket (Figure 9) in the main river Leira was not habitat characterized in detail as the other stations. The station is no longer than 100 meters and has many of the same characteristics as the station in Rotua, but with even less overhanging vegetation and woody debris.

Figure 9. Kringlerstryket.

2.3. Fish tagging and data acquisition

A total of 1091 trout were captured (including recaptures) between May 2012 and October 2013 (Table 2). Out of these, 799 were tagged with individual passive integrated transponder (PIT) tags. In total, 54 of the tagged fish were later recaptured and their PIT-tag successfully scanned. The 243 trout not tagged were either small (< 120 mm) or captured in the last sampling round. Length structures based on capture site and sampling round are shown in Figure 10 and Figure 12.

2.3.1. Fish sampling

The fish were captured using a portable backpack electroshocking gear (Steinar Paulsen: 1983 FA2 No. 7, 700/1400 volt, 35-70 Hz, pulsed-DC) (Figure 11). This is one of the most important sampling gears for fish in wadeable running waters (Bohlin et al. 1989, Forseth and Forsgren 2009). The catchability and risk of injury is affected by a range of environmental factors, the size of the fish (Bohlin et al. 1989, Borgstrøm and Qvenild 2000) and the experience and skills of the personnel (Forseth and Forsgren 2009). It has been demonstrated that the catchability increases exponentially with the fish size (Bohlin et al. 1989).

During a sampling round all stations were electrofished once (one pass) in an upstream direction by two or three persons. One person performed the electroshocking and the fish were retrieved using dip nets handled by all in the personnel. The captured fish were stored in a black 20 liters bucket. The person with the shocking gear walked in front and performed electroshocking in pulses of five to ten seconds. To maintain sufficient temperature and oxygen-levels fresh water was regularly added to the bucket with fish. Large leafs were added on the surface to minimize visual stress for the fish and preventing it from jumping out of the bucket. In addition, the density of fish carried in the bucket was held low – also to minimize the stress.

Table 2. Overview of number of brown trout captured, tagged, recaptured and captured, but not tagged during the study.

Sampling round	Date	Station	No. captured	No. tagged	No. recaptured	No. captured, not tagged
1	29-30.05.12	TØL	30	30	-	-
	29.05.12	ESK	-	-	-	-
	28.05.12, 26.06.12	ROT	32	32	-	-
	30.05.12	NOR	5	5	-	-
	30.05.12	KRI	4	4	-	-
2	14.08.12	TØL	34	33	1	-
	14.08.12	ESK	36	34	-	2
	15.08.12	ROT	37	36	1	-
	15.08.12	NOR	4	4	-	-
	16.08.12	KRI	2	2	-	-
3	01-02.10.12, 08.10.12, 23-26.10.12	TØL	155	140	4	13
	01.10.12, 23-25.10.12	ESK	66	59	7	-
	08.10.12	ROT	33	14	2	17
	24.10.12	NOR	4	3	1	-
	01.10.12	KRI	2	2	-	-
4	17.06.13	TØL	14	7	1	6
	18.06.13	ESK	16	14	2	-
	18.06.13	ROT	15	13	-	2
	19.06.13	NOR	6	6	-	-
	19.06.13	KRI	3	3	-	-
5	10-11.09.13	TØL	40	36	3	3
	11.09.13	ESK	19	12	1	6
	11-13.09.13	ROT	153	137	7	10
	13.09.13	NOR	10	8	2	-
	10.09.13	KRI	9	8	-	1
Boat	30.09.13	LEI_1	110	97	-	13
	01.10.13	LEI_2	30	28	-	2
	01.10.13	LEI_3	36	32	-	4
6	09.10.13	TØL	74	-	8	66
	09.10.13	ESK	58	-	6	52
	10.10.13	ROT	35	-	5	30
	10.10.13	NOR	8	-	2	6
	09.10.13	KRI	11	-	1	10
Sum		KRI	31	19	1	11
Sum		TØL	347	246	17	88
Sum		ESK	195	119	16	60
Sum		ROT	305	232	15	59
Sum		NOR	37	26	5	6
PIT antenna in Låkedalen			-	-	2	-
PIT antenna in Homledalen			-	-	-	-
Sum		All	1091	799	56	243
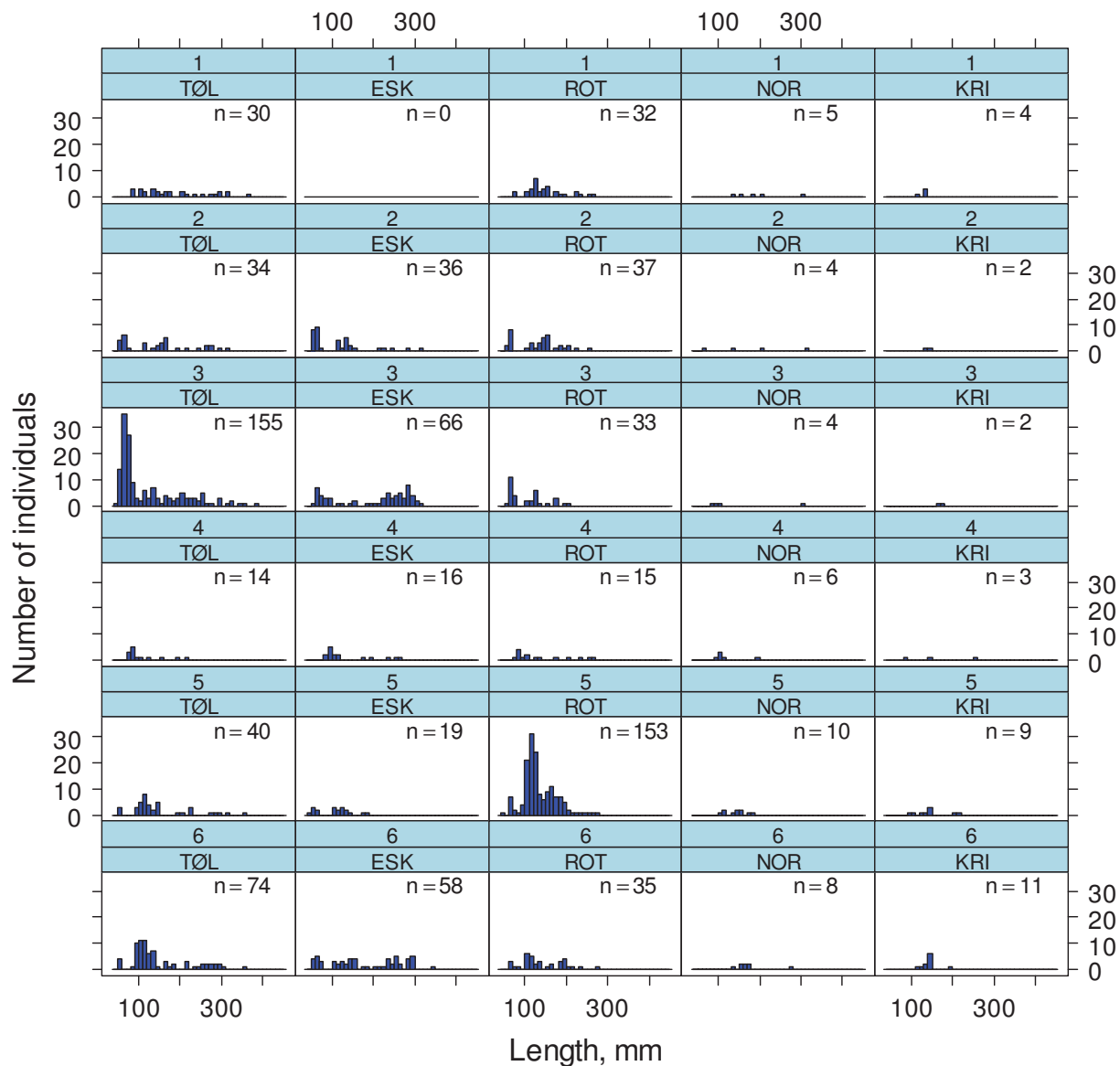
Figure 10. Length histograms for brown trout based on station and sampling round (number provided in the top row of the respective panel headers).

Figure 11. Electrofishing in Rotua.
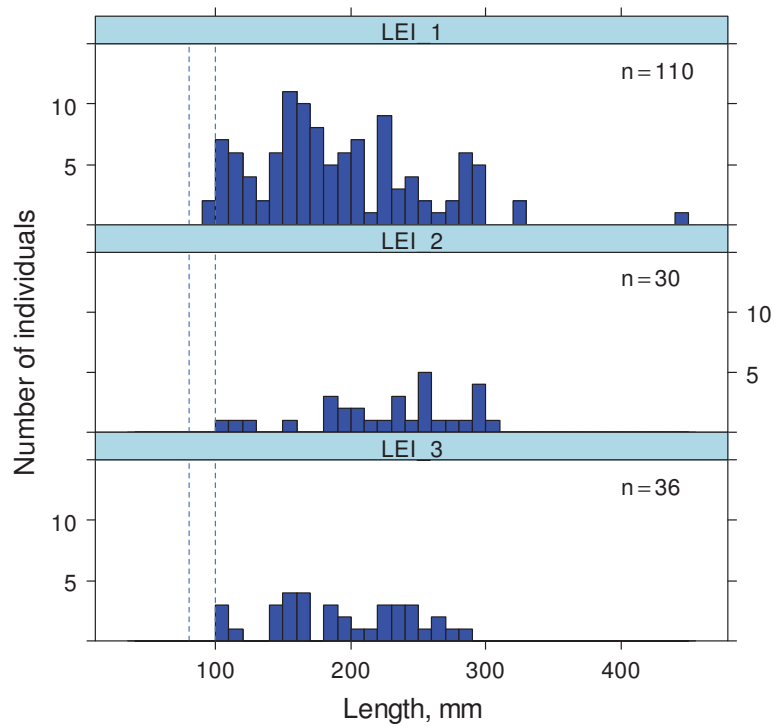
Figure 12. Station-specific length histograms of brown trout captured during electrofishing with boat in Leira. The dashed lines represents the smallest and largest upper length limit for October 0+ brown trout in the tributaries, as decided from length distributions based on station and year.

Figure 13. Electrofishing with boat in Leira.

During the field work, we experienced difficulties in using the portable shocking device in the main river due to high water velocity and discharge. We therefore decided to use a boat with integrated electroshocking gear for one of the sampling rounds (Figure 13). This was achieved by hiring expertise from Norwegian Institute for Nature Research (NINA). This method was performed by drifting more or less passively downstream, and two persons (i.e., the two of us) were placed on each side of the bow where both controlled the electroshocking independently of each other and also captured the fish using dip nets. One person (Jon Museth, NINA) held the boat on course with the bow facing downstream by using a set of oars. The fish were contained in two 50 liters water tanks where fresh water was added regularly to keep the oxygen level high and the temperature low. The method is described in detail in Museth et al. (2013). Because the electroshocking device in the boat recorded the number of seconds it was giving pulses, we were able to get a rough estimate of fish density in terms of number of fish captured per minute of electroshocking. Station LEI_1 resulted in 2.64 brown trout per minute (if considering only the most upstream stretch of this station the number gets 3.66 per minute), LEI_2 resulted in 2.82 per minute, and LEI_3 resulted in 1.26 per minute.

During field period number three (October 2012), a fyke net originally designed for eel (*Anguilla anguilla*) was used in each tributary (two in Rotua) to capture spawning individuals of brown trout (Figure 14). This catching gear had an entrance with a funnel that lead the fish into an enclosed area that hinder escape after entrance. The fyke nets were used four nights in each of the streams, except in Rotua, where it was used three nights only because of difficulties with high water discharge. The fyke net was placed in a pool or behind a rock in a backwater with low water velocity to prevent captured fish from getting exhausted and stressed by the currents. The fyke net was fixed to the stream bottom using rebars and rocks, and we stretched chicken wire from the stream edges to the fyke net to lead the fish into the trap. This passive capture technique is dependent on the organism being in activity (Borgstrøm and Qvenild 2000), which was the case for the migratory brown trout heading for the spawning areas. According to Borgstrøm and Qvenild (2000) the fyke net will in theory have approximate equal catchability for fish larger than a certain size to a upper limit dependent on the diameter of the funnel.

Figure 14. Set-up of fyke net in Rotua. Photo: Thrond O. Haugen.

2.3.2. Measurements and tagging procedure

Following capture, the fish were measured and tagged. The fish were held in a black 20 liter plastic bucket with fresh water that got supply of oxygen from an air pump. The fish was sedated by moving it to a plastic bucket with benzocaine in an ethanol solution with mixing ratio of 5-7 ml per 10 liter of water. The brown trout was regarded sedated when showing no reflex to a gentle pressure to the caudal peduncle. The sedated fish was then moved over to the measuring board where the total length was measured. An ethanol-disinfected PIT tag was inserted into the fish after first applying a 2-3 mm surgical incising into the abdominal cavity between the pelvic fins using a scalpel (Figure 15). The size of the PIT tag used was selected based on the fish size. For fish in the 70-120 mm length interval 12.0 mm x 2.12 mm PIT tags (HDX ISO 11784/11785) manufactured by Oregon RFID (http://www.oregonrfid.biz/) were used. For fish larger than 120 mm a 23 mm long and 3.65 mm in diameter PIT-tag was used (ISO 11784/11785 compatible, Oregon RFID). Before insertion of the tag the unique numeric ID code was read from the tag using a handheld HDX/FDX reader (Agrident APR 350, http://www.agrident.com/Products/APR350.html). Fish smaller than 50 mm were not tagged.

Figure 15. Use of scalpel before PIT tag is inserted.

The sex and maturity stage was also registered if possible. Finally, the adipose fin was cut to ease the separation of the marked individuals from the unmarked during field rounds two through six. From field round three through five we also took samples of 4 to 10 scales from fish >120 mm. The scales were dried in envelopes holding information about each individual. The scales were collected from the area above the lateral line between the dorsal fin and adipose fin, corresponding to the area where the first few scales usually form (Borgstrøm 2000). The fish was then placed in a bucket holding fresh water to recover from the anesthesia. When the trout was able to swim actively on its own it was released back to the stream in an area with low turbulence and water velocity, preferably in the proximity of where

it was captured. All the recaptures were registered during field round two through six. None of the individuals in round six was tagged.

According to Roussel et al. (2000), "the PIT tag itself is an encapsulated glass cylinder that consists of an integrated circuit chip, chapacitor and antenna coil, which needs an external energy source to operate. An electromagnetic field generated by the reading device (e.g., handheld or a PIT antenna) induces current in the antenna coil which energizes the integrated circuit, which transmits its signal to the reading device." PIT tagging has been used in CMR studies since the mid-1980s, and is a powerful tool today when monitoring mobile fishes like salmonids (Acolas et al. 2007). Generally speaking, many studies have shown a high tag retention rate, and no significant effect on the mortality- and growth rate (Ombredane et al. 1998, Gries and Letcher 2002), although some studies have shown opposing results (Sigourney et al. 2005, Dieterman and Hoxmeier 2009).

2.3.3. PIT antennas

Two stations with PIT antennas were placed in the main river in July 2013 to identify potential migratory pattern among the individuals of brown trout. One was placed in Låkedalen (Figure 16) which is situated in the middle section of the study area between the stream Eskerudbekken and Rotua, while the second antenna was placed in Homledalen which is in the lower section of the study area between Rotua and Nordbybekken. These areas were picked on the basis of minimizing the risk of damage to the antenna unit in case of high water discharge and maximize the potential rate of detection, but also based on which areas in the main river we considered important regarding pollution in terms of leakage of nutrients from agricultural land and sewage. The two antennas were mounted as horizontal loops at the bottom. Both were wired to remote tuner boards that were connected to an antenna reader box (TIRIS RI-CTL MB2A; Oregon RFID, USA) and supplied with an 110Ah 12V battery or a 12 V charger (Vanson 60W) attached to the mains, creating a magnetic field in the antenna loop, covering the total water column. When a tagged fish passed over the antenna loop the tag was energized, and the antenna number, date, time, and tag number were recorded by the reader box (Zydlewski et al. 2006). The PIT antennas' ability to detect the tagged brown trout was dependent on that the fish swam close to the antenna loop that covered the riverbed. According to Roussel et al. (2000) the antennas can detect tags from a distance up to one meter, but when we tested the device in the field the detection distance was no more than 25-30 cm. The antennas in Låkedalen and Homledalen were operative from September 4th and

November 12th 2013, respectively, and were still running when this thesis got published December 16th 2013.

Figure 16. Installation of PIT antenna in Låkedalen.

November 12th 2013, respectively, and were still running when this thesis got published December 16th 2013.

Figure 16. Installation of PIT antenna in Låkedalen.

2.3.4. Age determination and back-calculation of growth

To determine the age and back-calculate the growth of the brown trout, we used the scales collected during sampling round three through five. For some individuals, we only had samples of regenerated scales. Regenerated scales are usually assumed to be unusable when analyzing growth and age because the growth data prior the regeneration of the scale is "eroded". In agreement with the supervisor, we decided to use regenerated scales with the assumption that the first growth year was "lost". The scales were placed between two microscope slides and an image was recorded by using a stereoscopic microscope (Leica MS5, 16x magnification) with a mounted digital camera (Leica DFC320, 0.63x magnification), and the image-capture program Image-Pro Express version 6.3.0.531 for Windows XP/Vista (Media Cybernetics, Inc.).

Image-Pro Express was further used to assign age and back-calculate the growth of each specimen. To do so, we measured the radius of the scale, from the focus to the outer edge, followed up by locating and marking the transition between the outer edge of the winter growth and the beginning of the spring growth, known as the "winter zone" (Figure 17). The winter- and summer growth were identified from areas with small inter-circuli distances and wide inter-circuli distances, respectively. Together they represent one growth year and each of the "winter zone" markings represent a completed year of life (Haraldstad 2011). The distance from the focus to each completed year of life in addition to the measurement of the distance from the focus to the

Figure 17. Scale with two winter zones, sampled from brown trout in Rotua.

outer edge of the scale was used in an equation to back-calculate growth in all the years since hatching. The growth of the scale is considered to be a proportional reflection of the growth of the fish (Borgstrøm 2000). The summer- and winter bands are both comprised of circuli. As

the fish grows the circuli accumulates on the scale (Dahl 1910, Borgstrøm 2000). A low growth rate gives few circuli and also a short distance between them. This is normally the case in the winter when access to food is low compared to spring and summer. Many circuli with long distance between them is a typical sign of good growth (Dahl 1910, Borgstrøm 2000).

2.3.5. Meteorological data

Meteorological data was obtained from the Norwegian Meteorological Institute and their climate database "eKlima" (Meteorologisk Institutt 2013). Air temperatures were retrieved from a weather station at Gardermoen (No. 4780) and snow data from the weather station at Ukkestad (No. 4740). Since no data was available for ice cover on rivers and streams, snow cover data was used as a proxy for this. "Snow-off day" was defined as the day in the spring when snow for the first time did not cover the entire ground. Short periods with snow cover later in the spring were ignored, so was periods with bare ground in the winter. "Bare-ground days" was defined as the number of days from snow-off day to the first day of lasting snow cover in the following autumn.

2.4. Data analyses

2.4.1. Capture-mark-recapture analyses

The capture-mark-recapture (CMR) data were analyzed using the software MARK version 6.1 (White and Burnham 1999). Due to a low recapture rate (54 out of 799 marked individuals were recaptured once or more) the data did not allow for advanced model structures with many parameters to be estimated. Even though the sampling design was a multi strata one (sensu Arnason 1973), we collapsed all spatial structure and used an ordinary Cormack-Jolly-Seber (CJS) approach (Lebreton et al. 1992) with station identity as a group effect. This could be justified by the fact that none of the recaptured individuals were recaptured in other stations than the one they were initially tagged. CJS models account for variation in recapture probabilities (p), but cannot separate mortality from emigration when estimating survival probabilities. Hence, survival estimates under this modeling approach constitute "apparent survival", denoted ϕ (phi). Owing to just one recapture in Kringlerdalen, data from this station was not included in the CMR analyses. Neither was the two individuals recorded by PIT antenna.

A CJS analysis is conducted based on individual capture histories that comprise an array of 1s and 0s, one number for each sampling occasion. A "1" denotes that the individual has been recaptured at a given occasion and a "0" that it was not recaptured. Under the assumptions that all capture histories are independent and individuals within a group (e.g., age group and/or station) behave similarly probabilities for recapture and apparent survival can be estimated at given occasions/periods using the maximum log likelihood method (Lebreton et al. 1992).

The parameterization of CJS models can be visualized in a fate diagram (Figure 18). From the fate diagram, we can follow individuals tagged at occasion k that are captured and released at subsequent occasions. In the diagram, we follow the Markovian steps describing survival and recapture processes involved over four capture occasions (Figure 18A). ϕ_1 represents the apparent survival probability between the first sampling to the second occasion. p_2 represents the recapture probability at occasion 2. In panel B of Figure 18, parameterization with a tagging-age structure is demonstrated. Here, $\phi_{a=1}$ represents survival over the first period following tagging. This parameter can be estimated to be similar over all survival periods (but only for newly tagged individuals) or to vary over all periods (i.e., $\phi_{a=1,k}$). The same applies to the p-parameter.

Parameters were fitted using the maximum log likelihood method. All parameters can in theory be estimated as being constant over all occasions/periods or time dependent. In addition, and more ecologically relevant, the parameters can be estimated as functions of covariates of interest. These covariates can both be occasion-specific (e.g., density, water discharge) and individual-specific (e.g., size). The most supported model structure was selected based on AICc (Burnham and Anderson 1998).
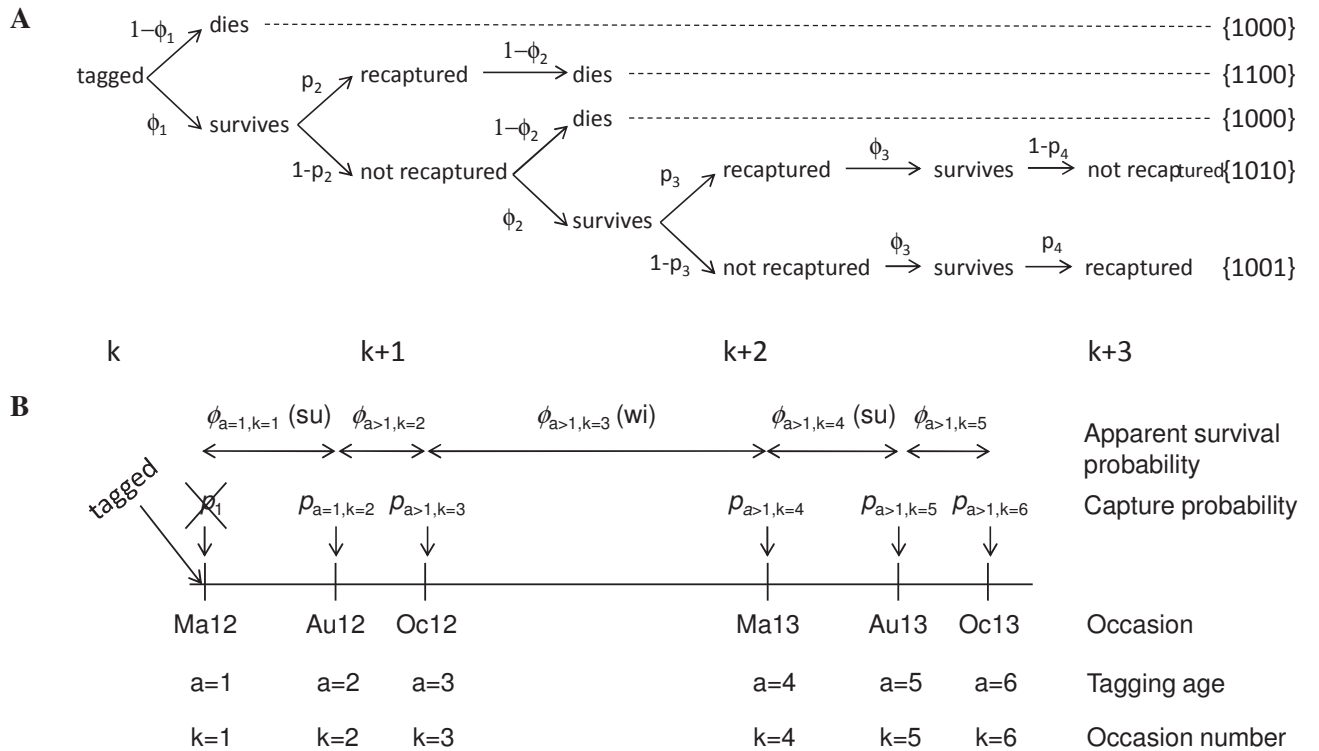
Figure 18. A: Fate diagram with corresponding Cormack-Jolly-Seber parameterization. **B**: An example parameterization for the current study setting under an age-structured model. p_1 cannot be estimated due to lack of preceding tagging information. su=summer, wi=winter, Ma=May, Au=August, Oc=October

2.4.2. Other statistical analyses

All other statistics other than CMR-modelling was conducted using R (R Development Core Team 2012).Sex-specific among-station differences in age distribution were tested using contingency-table χ^2-tests under the null-expectation of homogenous distribution. This was done using the chisq-procedure in R.

Effects from various continuous (e.g., temperature and length of growth season) and categorical (e.g., station/stream) variables on back-calculated growth rates and various size responses were quantified by fitting generalized linear models (GLM) (MacCullagh and Nelder 1989) using the glm-procedure in R. Corresponding anova effect tests were retrieved using the anova-procedure in R. Post-hoc contrast test conducted to explore among-group level differences (i.e., among stations) were performed using the Tukey Honest Significant Difference test (Yandell 1997) using the TukeyHSD-procedure in R.

Model selection was conducted using Akaike's Information Criterion (AIC) (Akaike 1974). This model selection tool avoids multiple testing and favors models that best balance bias and precision under the principle of parameter parsimony maximization (Burnham and Anderson 1998).

3. Results

3.1. Capture-mark-recapture analyses

3.1.1. Goodness of fit

Program RELEASE goodness of fit tests showed no sign of lack of fit as all GOF-tests provided p-values larger than 0.05 (Table 3). We therefore concluded that core assumptions behind the CJS-model were fulfilled and continued with further analyses.

Table 3. Goodness of fit test statistics for fully time-dependent CJS-model. Test 2 tests for deviation from assumptions relevant for the survival process and test 3 for the recapture process.

Group	Test 2			Test 3		
	χ^2	df	p	χ^2	df	p
TØL	0.71	3	0.87	0.00	3	1.00
ESK	4.03	2	0.13	3.79	3	0.29
ROT	0.71	1	0.40	0.00	2	1.00
NOR	0.94	1	0.33	0.00	1	1.00
All	6.38	7	0.50	3.79	9	0.92

3.1.2. Apparent survival (phi) and recapture (p) probabilities

The fitting of candidate models to the CMR data resulted in two most supported models with fairly similar AICc values. The ten most supported models are listed in Table 4. Since the difference between the top two models was marginal, we have chosen to present beta parameter estimates from both of them (Table 5 and Table 6). The model structure for recapture probability is identical for all of these ten models and was selected under a fully time-dependent apparent survival model.

Table 4. Model selection table for the ten most supported CMR models. Par.=Number of parameters estimated, su=summer (round 1-2 & 4-5), au=autumn (round 2-3 & 5-6), w=winter (round 3-4), L=Length, -L=Length effect not estimated, D=Discharge, 1=Parameter fixed to 1

	Model	AICc	Δ AICc	AICc weight	Model Likelihood	Par.	Deviance
1	{phi(su(stream*L(NOR-L)),au(1),w(L+L²))p(L+D*stream,ESK(intercept+L))}	416.509	0	0.325	1	12	392.016
2	{phi(su(stream+stream*L(NOR(1)),au(1),w(L+L²))p(L+D*stream,ESK(intercept+L))}	416.908	0.400	0.266	0.819	13	390.333
3	{phi(su(stream+L),au(stream+L),w(stream+L²))p(L+D*stream,ESK(intercept+L))}	419.042	2.534	0.092	0.282	11	396.626
4	{phi(su(TØL&ESK(.)ROT(L)NOR(1)),au(1),w(L+L²))p(L+D*stream,ESK(intercept+L))}	419.854	3.346	0.061	0.188	11	397.438
5	{phi(su(stream*L(ESK(Lsq))(NOR-L)),au(1),w(L+L²))p(L+D*stream,ESK(intercept+L))}	420.035	3.527	0.056	0.172	13	393.459
6	{phi(su(.)(NOR(1)),au(1),w(L+L²))p(L+D*stream,ESK(intercept+L))}	420.515	4.006	0.044	0.135	10	400.168
7	{phi(su(.),au(1),w(L+L²))p(L+D*stream,ESK(intercept+L))}	421.302	4.794	0.030	0.091	10	400.956
8	{phi(su(small.fish(<150mm).density),au(1),w(L+L²))p(L+D*stream,ESK(intercept+L))}	421.900	5.392	0.022	0.068	11	399.484
9	{phi(su(stream*L(ESK&NOR-L),au(1),w(L+L²))p(L+D*stream,ESK(intercept+L))}	422.435	5.926	0.017	0.052	12	397.942
10	{phi(su(L),au(.),w(L+L²))p(L+D*stream,ESK(intercept+L))}	423.195	6.687	0.011	0.035	11	400.779

The most supported model differentiated between apparent summer, autumn and winter (including spring) survival (Table 5). Apparent summer survival probability was fitted with a common intercept for all stations, but different effects of length at tagging. In Nordbybekken, there was no evidence for a length effect on apparent summer survival. Due to short survival period, apparent autumn survival was fixed to 1 for all stations. It should be mentioned that similar close-to-one parameter estimates resulted when fitting constant apparent autumn survival. For apparent winter survival, all populations had similar quadric effects of length at tagging. The most supported recapture probability model structure entailed a common intercept and common effect of fish length, but with stream- and sampling-round-specific effect of water discharge, except for Eskerudbekken that had a constant recapture probability.

The second-most supported model had differential stream intercepts and length effects for apparent summer survival (Table 6). For Nordbybekken, apparent summer survival was fixed to 1. Model structure was otherwise identical to the most supported model.

The second-best model was not able to estimate the intercept for apparent summer survival in Eskerudbekken, and none of the models were able to estimate a reliable length effect on apparent summer survival for this station.

Table 5. Beta estimates (logit scale) from the most supported CMR model (model 1). SU=Summer (round 1-2 & 4-5), AU=Autumn (round 2-3 & 5-6), WI=Winter (round 3-4).

Parameter	Term(season)[stream]	Estimate	SE	LCL	UCL	
phi	intercept(SU)[All]	2.485	1.211	0.112	4.858	
phi	length(SU)[TØL]	0.306	0.804	-1.269	1.882	
phi	length(SU)[ESK]	37.036	84.244	-128.082	202.154	
phi	length(SU)[ROT]	-1.267	0.843	-2.920	0.386	
phi	intercept(AU)[All]	0.000	0.000	0.000	0.000	FIXED
phi	intercept(WI)[All]	1.243	0.189	0.873	1.613	
phi	length(WI)[All]	1.415	0.725	-0.006	2.836	
phi	length²(WI)[All]	-1.422	0.731	-2.854	0.010	
p	Intercept[All]	-2.270	0.253	-2.765	-1.775	
p	length[All]	0.209	0.177	-0.138	0.555	
p	intercept[ESK]	0.902	0.391	0.137	1.667	
p	discharge[TØL]	-0.292	0.245	-0.772	0.189	
p	discharge[ROT]	-1.220	0.334	-1.875	-0.564	
p	discharge[NOR]	-0.541	0.539	-1.598	0.516	

Table 6. Beta estimates (logit scale) from the second-most supported CMR model (model 2). SU=Summer (round 1-2 & 4-5), AU=Autumn (round 2-3 & 5-6), WI=Winter (round 3-4).

Parameter	Term(season)[stream]	Estimate	SE	LCL	UCL	
phi	intercept(SU)[TØL]	2.465	1.746	-0.956	5.886	
phi	intercept(SU)[ESK]	28.398	0.000	28.398	28.398	
phi	intercept(SU)[ROT]	1.592	0.837	-0.048	3.233	
phi	length(SU)[TØL]	0.297	0.805	-1.280	1.875	
phi	length(SU)[ESK]	1876.521	0.000	1876.521	1876.521	
phi	length(SU)[ROT]	-0.864	0.631	-2.101	0.374	
phi	intercept(SU)[NOR](AU)[All]	0.000	0.000	0.000	0.000	FIXED
phi	intercept(WI)[All]	1.265	0.195	0.883	1.647	
phi	length(WI)[All]	1.520	0.737	0.076	2.964	
phi	length^2(WI)[All]	-1.532	0.745	-2.991	-0.073	
p	Intercept[All]	-2.214	0.254	-2.712	-1.715	
p	length[All]	0.197	0.177	-0.150	0.544	
p	intercept[ESK]	0.843	0.392	0.074	1.611	
p	discharge[TØL]	-0.275	0.247	-0.760	0.210	
p	discharge[ROT]	-1.377	0.402	-2.164	-0.590	
p	discharge[NOR]	-0.482	0.488	-1.438	0.474	

The recapture probability was negatively correlated with discharge and positively correlated with fish length (Figure 19). The model fitted the data best when not accounting for a discharge effect in Eskerudbekken.
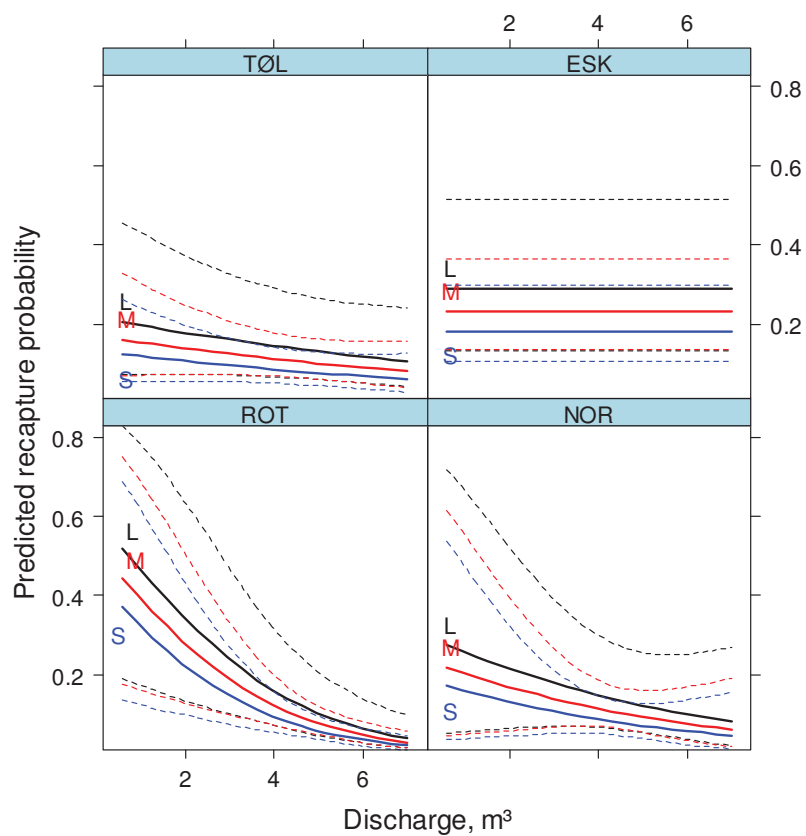
Figure 19. Predicted recapture probabilities in different stations, based on discharge and brown trout length. 95 % confidence intervals are shown with dashed lines. L=Large-sized trout (300 mm), M=Medium-sized trout (200 mm), S=Small-sized trout (100 mm).

According to the most supported model, fish length had a weak positive effect on apparent summer survival probability in Tøla, and a negative effect on the same trait in Rotua (Figure 20). However, the confidence intervals are wide for both stations. Apparent summer survival seems to be relatively high for all length classes in Nordbybekken. The model did not manage to calculate reliable apparent summer survival probabilities for Eskerudbekken.
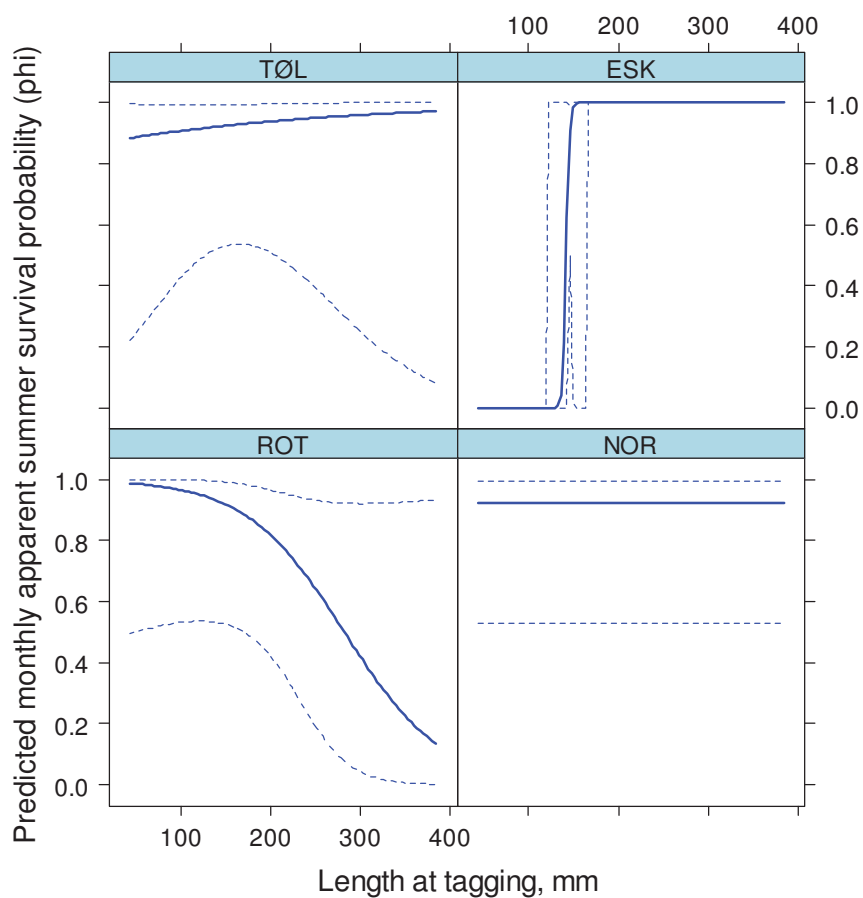
Figure 20. Predicted monthly apparent summer survival probability as an effect of brown trout length, based on the most supported model. 95 % confidence intervals are shown with dashed lines.

The most supported model estimated a combined apparent winter survival probability for the four stations (Figure 21). It shows a positive effect of fish length up to a point between 150 and 200 mm, and a strong negative effect beyond these lengths, but the uncertainty is greatest for the largest lengths.
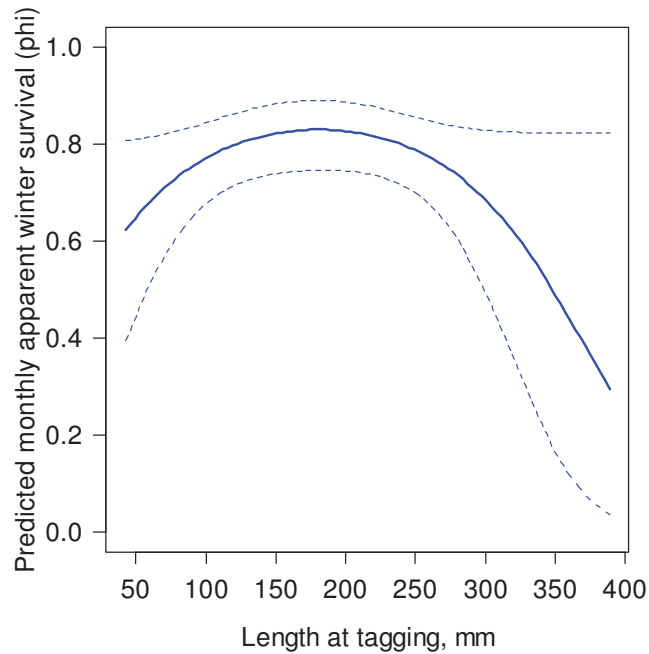
Figure 21. Predicted monthly apparent winter survival probability, for all stations combined, as an effect of brown trout length. 95 % confidence interval is shown with dashed lines.

3.2. Growth analyses

3.2.1. Empirical length

Age-specific empirical length

Length-at-age differed among stations (Figure 22). However, the data material is scarce for ages 4 and 5 and varies among stations. No brown trout were determined to be older than 5 years and few reached lengths beyond 300 mm. The only significant length differences were found between brown trout in Tøla and Rotua. Two- and three-year old brown trout in Tøla were on average 25 and 39 mm longer than brown trout at the same age in Rotua, respectively (Tukey HSD post-hoc tests: $p < 0.001$ and $p = 0.004$).
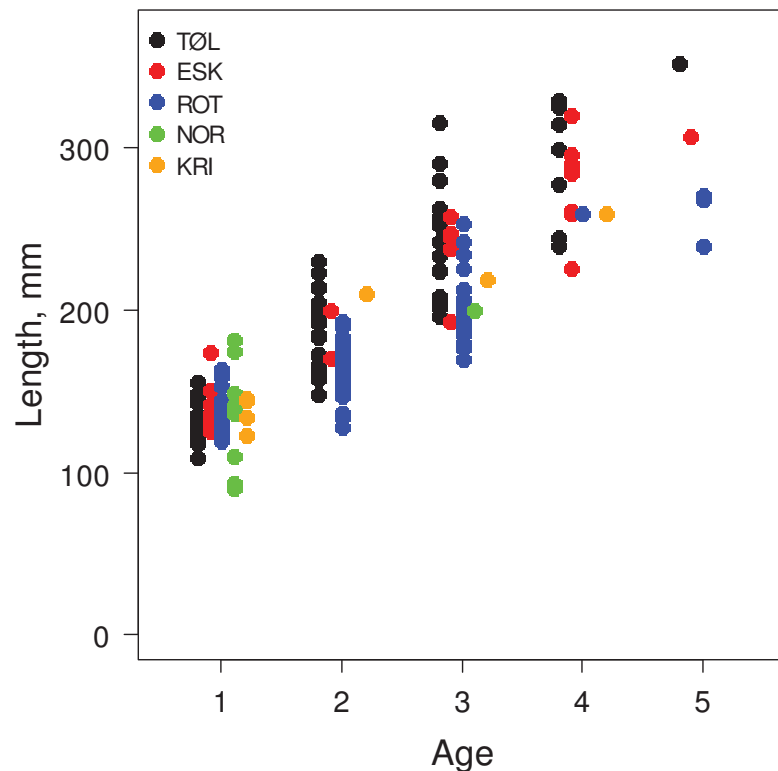
Figure 22. Empirical growth in five Leira brown trout populations in 2012 and 2013. Age was determined from scale analysis.

October 0+ length

The number of 0+ brown trout captured in October 2013 was considerable lower than in October 2012 (Figure 23). No 0+ were captured in Nordbybekken, Kringlerstryket or during boat electrofishing in the main river.
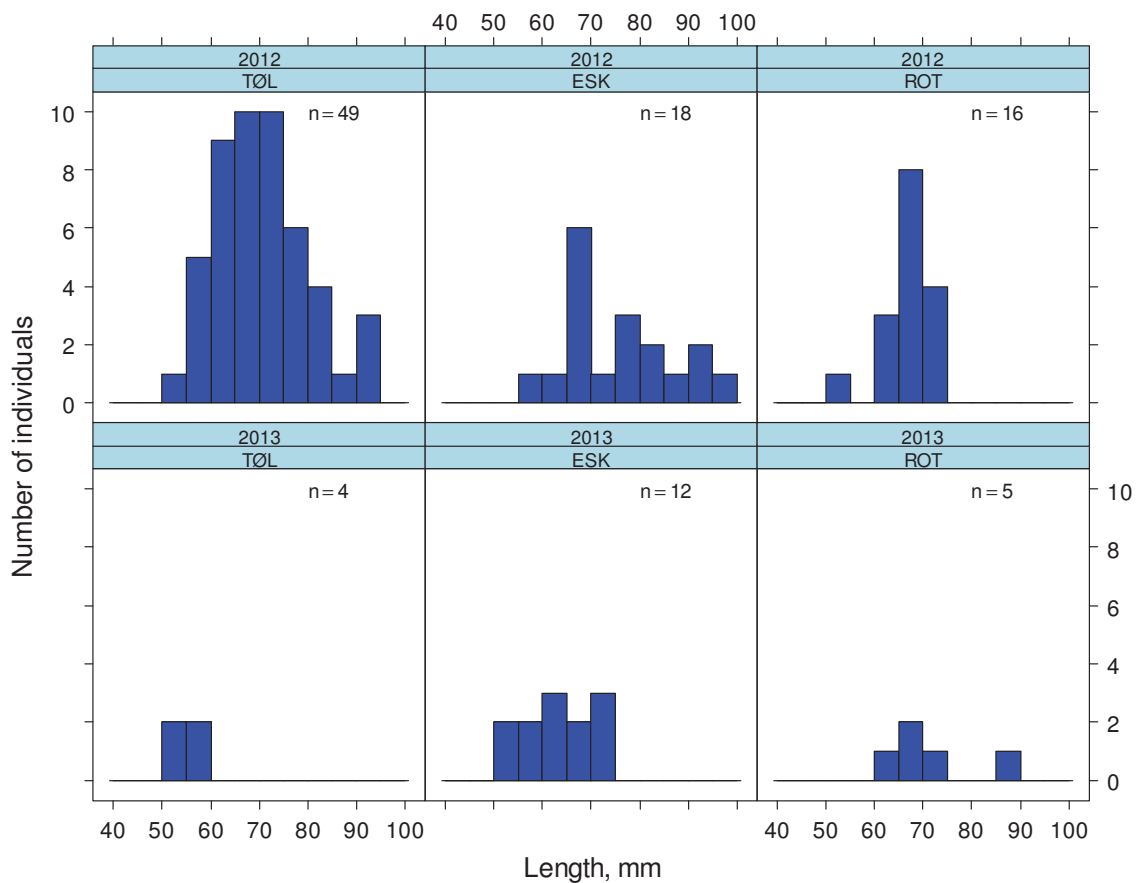
Figure 23. Length distributions for October 0+ brown trout captured in Tøla, Eskerudbekken and Rotua in 2012 and 2013.

The variation in 0+ lengths (Figure 23) was best explained by a fully factorial model with station and year as explanatory variables (Table 7). There were significant differences to be found both between stations and year (Table 8 and Figure 24).

Table 7. AIC table for models fitted to the empirical October 0+ length data.

Model	df	AIC
Station*Year	7	760.300
Station+Year	5	768.729
Year	3	768.991
Constant	2	774.985
Station	4	777.712

Table 8. Parameter estimates and corresponding ANOVA test statistics for the linear model testing station and year effects on October 0+ lengths. $R^2_{adj} = 0.171$.

Parameter estimates			
Parameter	Estimate	SE	p
Intercept[ESK,2012]	76.889	2.125	<0.001
Station[ROT]	-9.389	3.097	0.003
Station[TØL]	-5.603	2.484	0.026
Year[2013]	-12.389	3.359	<0.001
Station*Year[ROT,2013]	18.089	5.711	0.002
Station*Year[TØL,2013]	-2.147	5.767	0.710

ANOVA test				
Effect	df	SS	MSS	F	p
Station	2	122.8	61.42	0.756	0.472
Year	1	999.4	999.43	12.301	<0.001
Station*Year	2	1010.8	505.40	6.220	0.003
Residuals	98	7962.3	81.25		
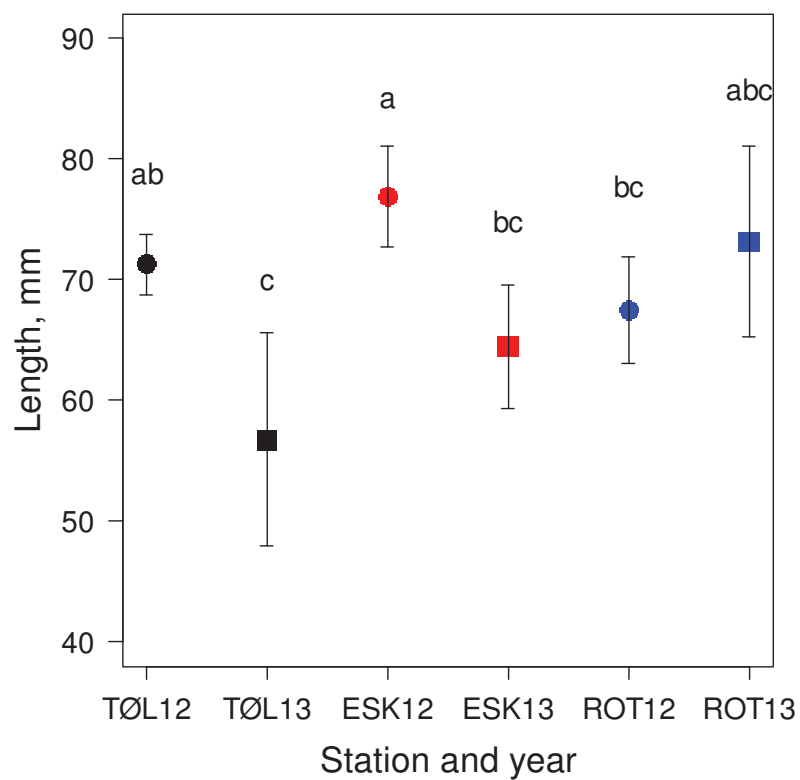
Figure 24. Predicted October 0+ lengths with 95 % confidence interval (vertical bars), as function of station and year. Different letters indicate significant difference (based on Tukey HSD post-hoc tests). Predictions were derived from the most supported model – provided in Table 8.

3.2.2. Back-calculated length and growth analyses

In general, the brown trout in the Leira system show rapid growth during their first two years of life (Figure 25). Differences in growth among stations for the three first years are presented in Figure 26.
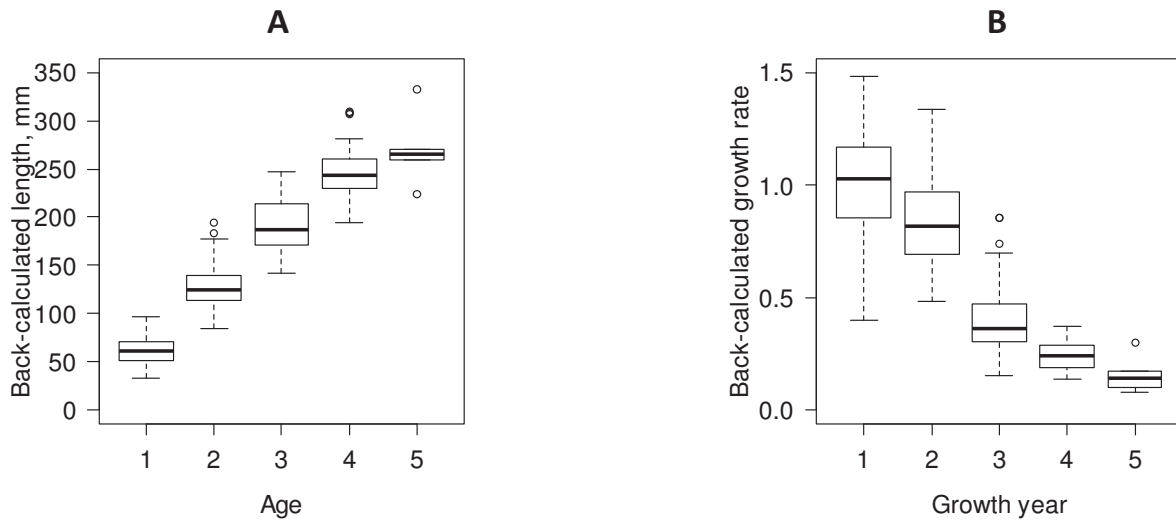
Figure 25. Box-and-whiskers plots of back-calculated length as function of age (**A**), and back-calculated growth rate as function of growth year (**B**). The boxes entail 50% of the observations and the whiskers span 90% of the observations. Thick horizontal lines represent the median value.
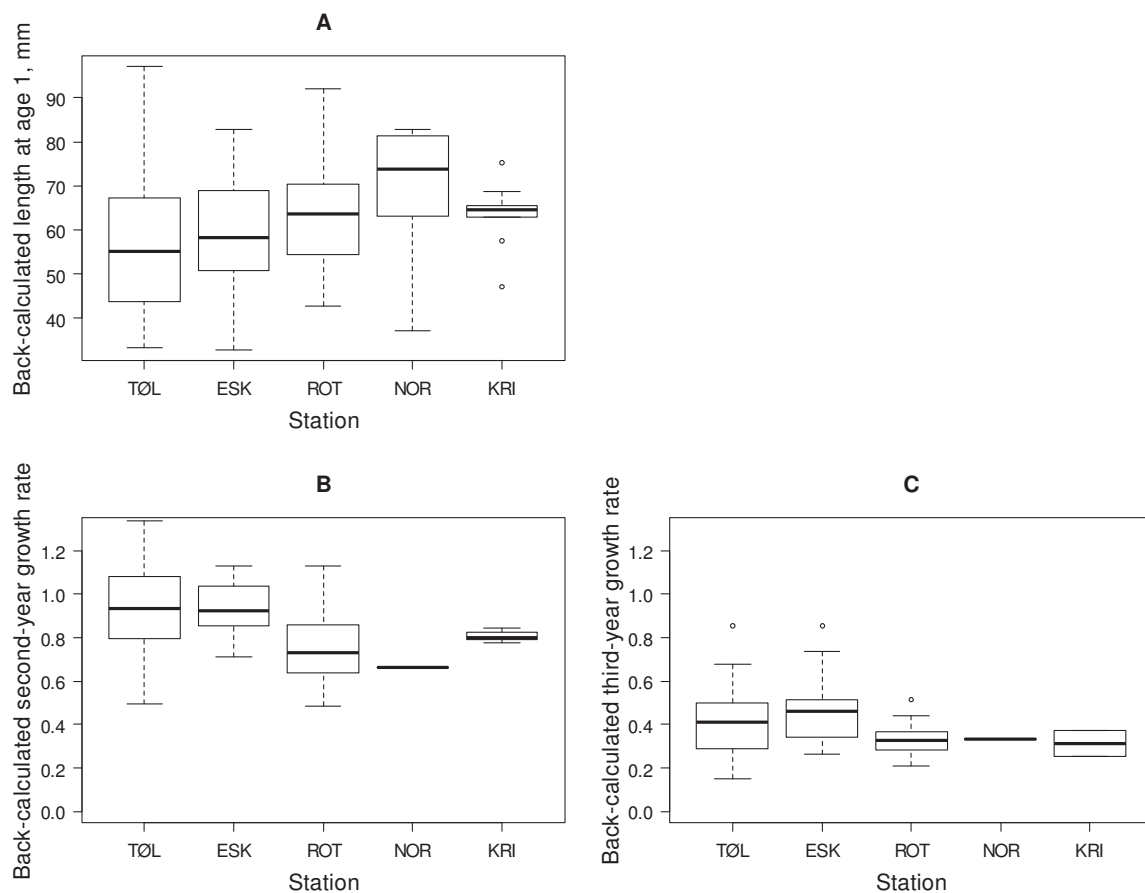
Figure 26. Box-and-whiskers plots of back-calculated length at age 1 as function of station (**A**), back-calculated second-year growth rate as function of station (**B**), and back-calculated third-year growth rate as function of station (**C**). The boxes entail 50% of the observations and the whiskers span 90% of the observations. Thick horizontal lines represent the median value.

Length at age 1

Variations in back-calculated length at age 1 were best explained by two nearly equally supported models fitted effects from March and April temperatures, and March and June temperatures, respectively (Table 9). Both models explain almost 28 % of the variation – a relatively high value for growth models with two explanatory variables. The two models have almost identical AICc values, and we have therefore chosen to present parameter estimates and plots derived from both models (Table 10-Table 11 and Figure 27-Figure 28). According to the models, mean March temperature has a large positive effect on length at age 1, but the effect seems to be reduced by high April or June temperatures. However, if the mean March temperature is low, then high April or June temperatures seem to have a positive effect on length.

Table 9. The ten most supported models, based on AICc, to explain variations in back-calculated length at age 1.

Model structure	df	AICc	ΔAICc	AICc weight	Log Likelihood
Mean temperature March*Mean temperature April	5	1518.12	0	0.22	-753.90
Mean temperature March*Mean temperature June	5	1518.14	0.02	0.22	-753.91
Mean temperature March*Mean temperature April+Mean temperature May	6	1520.25	2.13	0.08	-753.90
Mean temperature March*Mean temperature April*Mean temperature July	7	1521.43	3.31	0.04	-753.42
Snow-off day	3	1522.50	4.38	0.03	-758.18
Snow-off day*Station	11	1522.91	4.79	0.02	-749.73
Snow-off day*Mean temperature summer	5	1523.86	5.74	0.01	-756.77
Mean temperature March*Station	11	1524.15	6.03	0.01	-750.35
Snow-off day+Sum temperature summer	4	1524.21	6.09	0.01	-758.00
Snow-off day+Mean temperature May	4	1524.24	6.12	0.01	-758.01

Table 10. Parameter estimates and corresponding ANOVA test statistics for the general linear model testing the effect of mean March and April temperatures on back-calculated length at age 1. $R^2_{adj} = 0.278$.

Parameter estimates			
Parameter	Estimate	SE	p
Intercept	63.508	4.023	<0.001
Mean temperature March	9.629	2.016	<0.001
Mean temperature April	-1.781	0.906	0.051
Mean temp. March*Mean temp. April	-1.986	0.585	0.001

ANOVA						
Effect	df	Deviance	Resid. df	Resid. Deviance	F	p
Mean temperature March	1	8780.7	193	27877	64.402	<0.001
Mean temperature April	1	264.6	192	27612	1.941	0.165
Mean temp. March*Mean temp. April	1	1570.5	191	26041	11.519	0.001
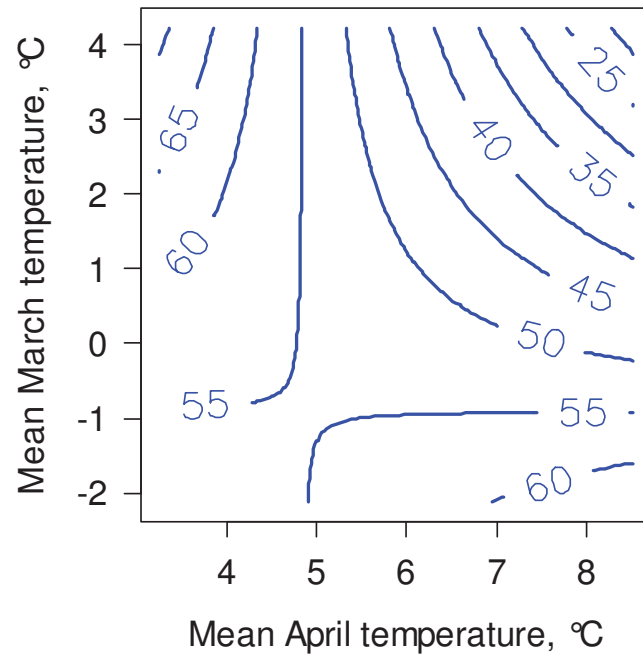
Figure 27. Predicted back-calculated length at first winter (shown as isoclines) as function of mean March and April air temperatures. Predictions were derived from the most supported model – provided in Table 10.

Table 11. Parameter estimates and corresponding ANOVA test statistics for the general linear model testing the effect of mean March and June temperatures on back-calculated length at age 1. $R^2_{adj} = 0.278$.

Parameter estimates			
Parameter	Estimate	SE	p
Intercept	42.268	24.583	0.087
Mean temperature March	40.558	10.420	<0.001
Mean temperature June	0.783	1.731	0.652
Mean temp. March*Mean temp. June	-2.929	0.799	<0.001

ANOVA test						
Effect	df	Deviance	Resid. df	Resid. Deviance	F	p
Mean temperature March	1	8780.7	193	27877	64.397	<0.001
Mean temperature June	1	1.1	192	27875	0.008	0.930
Mean temp. March*Mean temp. June	1	1832.0	191	26043	13.436	<0.001

Figure 28. Predicted back-calculated length at first winter (shown as isoclines) as function of mean March and June air temperatures. Predictions were derived from the second-most supported model – provided in Table 11.
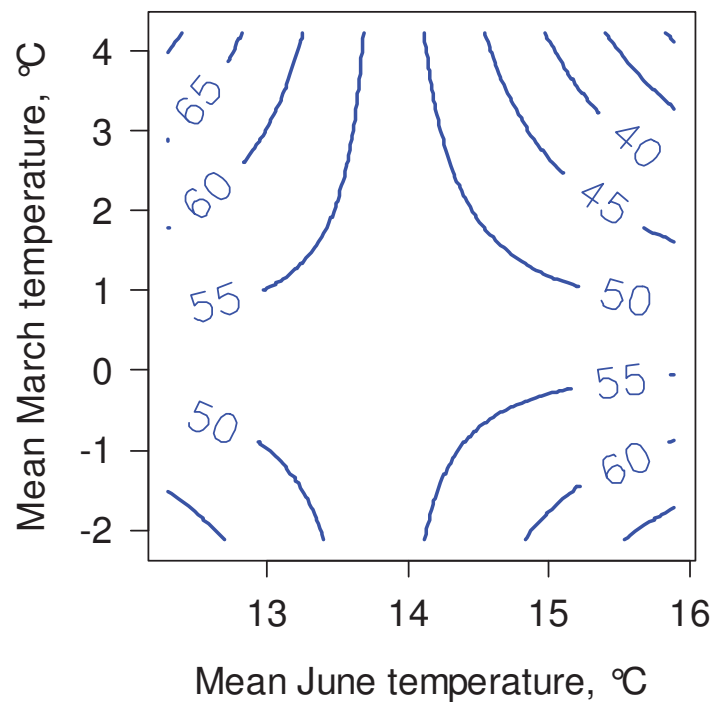
Second-year growth

Variations in back-calculated second-year growth were best explained by an additive model taking into account snow-off day and station (Table 12). Station was included in all of the five most supported models. The most supported model predicts high second-year growth rates for later snow-off days (Table 13, Figure 29 and Figure 30). The growth is apparently better in Tøla and Eskerudbekken than in Rotua and Kringlerstryket, with Nordbybekken being the station with the lowest second-year growth rate. However, confidence intervals for Nordbybekken and Kringlerstryket are large.

Table 12. The ten most supported models, based on AICc, to explain variations in back-calculated second-year growth rate.

Model structure	df	AICc	ΔAICc	AICc weight	Log Likelihood
Snow-off day+Station	7	-80.61	0	0.32	47.88
Snow-off day*Station	10	-79.16	1.45	0.16	50.75
Bare ground days+Station	7	-78.61	2.00	0.12	46.88
Snow-off day+Station+Mean summer temperature	8	-78.31	2.30	0.10	47.90
Snow-off day*Station+Mean summer temperature	11	-77.64	2.97	0.07	51.24
Snow-off day	3	-76.34	4.28	0.04	41.29
Mean summer temperature +Station	7	-76.32	4.29	0.04	45.74
Snow-off day+Mean summer temperature	4	-75.56	5.06	0.03	41.98
Bare ground days	3	-75.47	5.14	0.02	40.86
Mean February temperature	3	-75.27	5.34	0.02	40.75

Table 13. Parameter estimates and corresponding ANOVA test statistics for the general linear model testing the effects of snow-off day and station on back-calculated second-year growth rate. $R^2_{adj} = 0.286$.

Parameter estimates			
Parameter	Estimate	SE	p
Intercept[ESK]	0.581	0.135	<0.001
Snow-off day	0.004	0.001	0.006
Station[KRI]	-0.101	0.103	0.329
Station[NOR]	-0.269	0.165	0.106
Station[ROT]	-0.121	0.058	0.039
Station[TØL]	0.010	0.054	0.857

ANOVA test						
Effect	df	Deviance	Resid. df	Resid. Deviance	F	p
Snow-off day	1	0.833	103	2.800	33.375	<0.001
Station	4	0.331	99	2.470	3.314	0.014
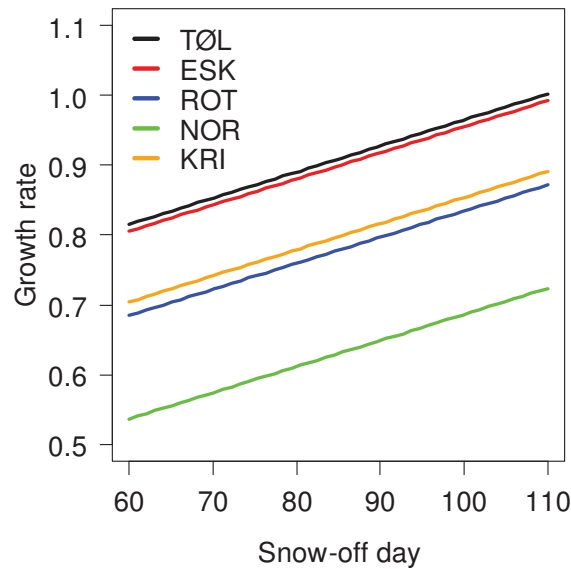
Figure 29. Predicted second-year growth rate as a function of snow-off day and station. Predictions were derived from the most supported model – provided in Table 13.
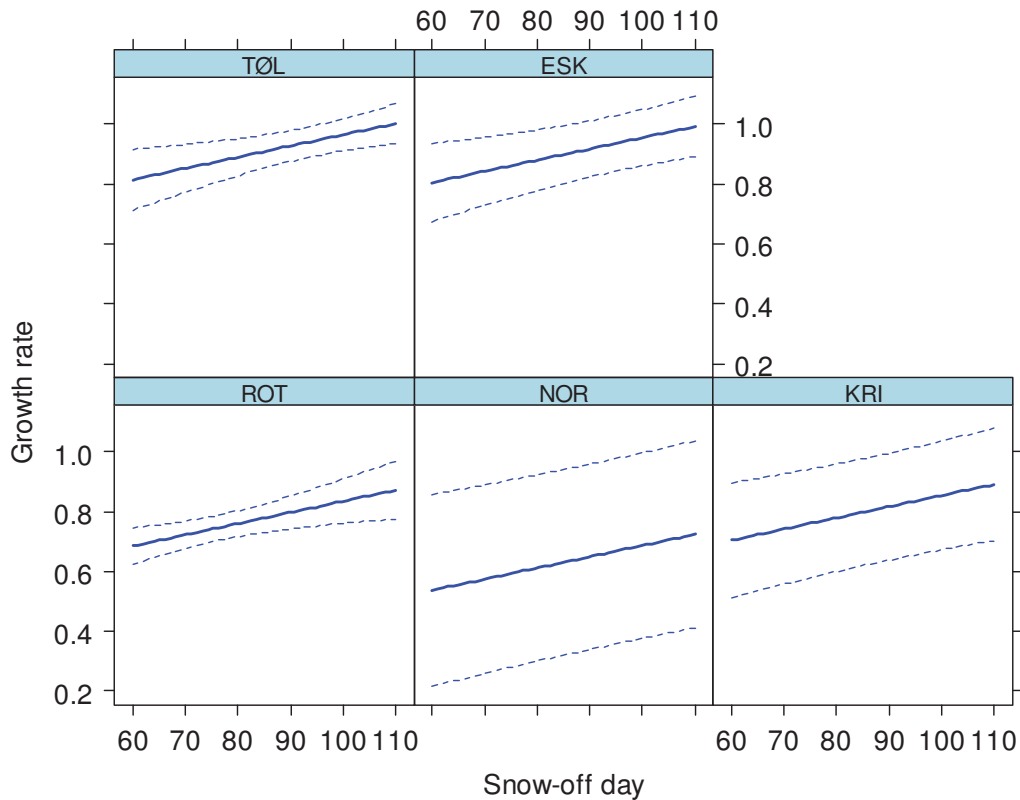
Figure 30. Predicted second-year growth rate as a function of snow-off day and station. Each station is here plotted separately with 95 % confidence interval (dashed lines). Predictions were derived from the most supported model – provided in Table 13.

Third-year growth

Variations in back-calculated third-year growth rate were best explained by only taking number of bare ground days into account (Table 14). According to this model, the number of bare ground days has a weak negatively effect on third-year growth (Table 15 and Figure 31). The second- and third-most supported models also include one explanatory variable only – snow-off day and station, respectively. Snow-off day and bare ground days are correlated ($r = -0.872$, $p < 0.001$), and the effect of snow-off day on third-year growth is relatively similar to the effect of snow-off day on second-year growth. The third most supported model shows a significant difference in third-year growth between brown trout in Eskerudbekken and Rotua (Table 16 and Figure 32).

Table 14. The ten most supported models, based on AICc, to explain variations in back-calculated third-year growth.

Model structure	df	AICc	ΔAICc	AICc weight	Log Likelihood
Bare ground days	3	-57.30	0	0.15	31.86
Snow-off day	3	-56.44	0.86	0.10	31.43
Station	6	-55.79	1.50	0.07	34.67
Mean temperature July+Mean August temperature	4	-55.37	1.92	0.06	32.04
Mean March temperature	3	-55.25	2.05	0.06	30.83
Station+Mean winter temperature	7	-55.19	2.11	0.05	35.65
Snow-off day+Mean summer temperature	4	-55.13	2.16	0.05	31.92
Mean July temperature	3	-54.89	2.40	0.05	30.66
Bare ground days+Station	7	-54.63	2.66	0.04	35.37
Sum summer temperature	3	-53.91	3.38	0.03	30.17

Table 15. Parameter estimates and corresponding ANOVA test statistics for the general linear model testing the effects of bare ground days on back-calculated third-year growth. $R^2_{adj} = 0.067$.

Parameter estimates			
Parameter	Estimate	SE	p
Intercept	1.013	0.267	<0.001
Bare ground days	-0.003	0.001	0.025

ANOVA test					
Effect	df	Deviance	Resid. df	Resid. Deviance	F	p
Bare ground days	1	0.113	59	1.257	5.327	0.025
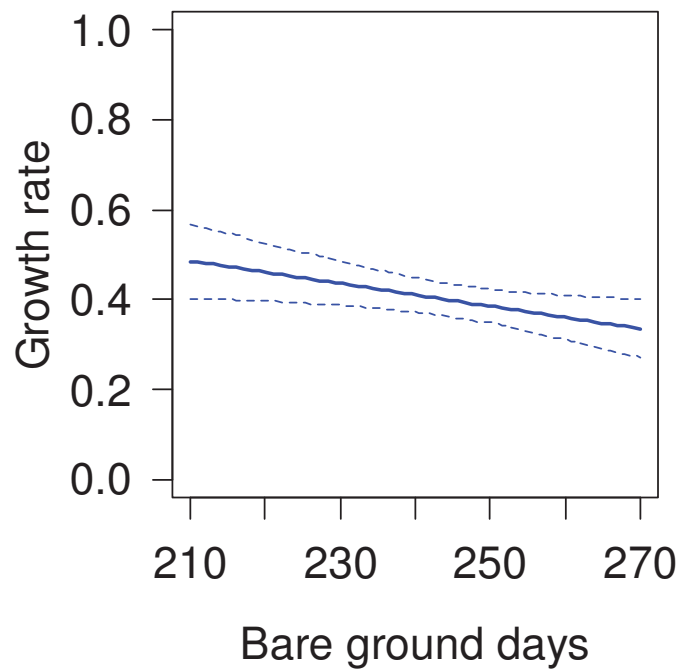
Figure 31. Predicted third-year growth rate with 95 % confidence interval (dashed lines), as a function of bare ground days. Predictions were derived from the most supported model – provided in Table 15.

Table 16. Parameter estimates and corresponding ANOVA test statistics for the general linear model testing the effects of station on back-calculated third-year growth. $R^2_{adj} = 0.104$.

Parameter estimates			
Parameter	Estimate	SE	p
Intercept[ESK]	0.486	0.038	<0.001
Station[KRI]	-0.173	0.108	0.116
Station[NOR]	-0.151	0.148	0.313
Station[ROT]	-0.155	0.050	0.003
Station[TØL]	-0.071	0.048	0.143

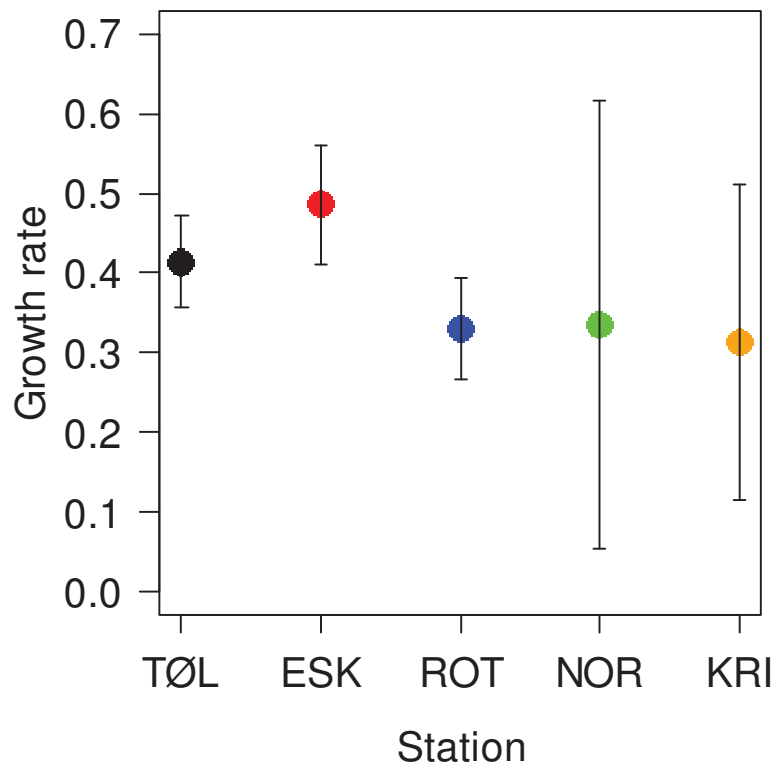| ANOVA test						
Effect	df	Deviance	Resid. df	Resid. Deviance	F	p
Station	4	0.224	56	1.146	2.740	0.037

Figure 32. Predicted third-year growth rate with 95 % confidence interval (vertical bars), as a function of station. Predictions were derived from the third-most supported model – provided in Table 16.

3.3. Maturity

3.3.1. Age at maturity

There was a significant among-station variation in age distribution of mature males (Table 17). In general, mature males in Rotua were younger than in Tøla and Eskerudbekken.

Table 17. Contingency table with expected (Exp) and observed (Obs) numbers of mature males in different age classes, with corresponding χ^2-statistics.

Station	Exp/Obs	Age				
		1	2	3	4	5
TØL	Exp	1.5	4.2	5.8	2.7	0.8
	Obs	0	5	8	2	0
ESK	Exp	1.1	3.1	4.2	2.0	0.6
	Obs	2	1	3	5	0
ROT	Exp	1.3	3.7	5.0	2.3	0.7
	Obs	2	5	4	0	2
χ^2 = 17.164		df = 8		p = 0.028		

Our data had few age-determined mature females, and we found no significant among-station variation in age distribution for this group (Table 18).

Table 18. Contingency table with expected (Exp) and observed (Obs) numbers of mature females in different age classes, with corresponding χ^2-statistics.

Station	Exp/Obs	Age				
		1	2	3	4	5
TØL	Exp	0.0	1.5	5.0	2.0	0.5
	Obs	0	1	5	3	0
ESK	Exp	0.0	0.5	1.7	0.7	0.2
	Obs	0	0	1	1	1
ROT	Exp	0.0	1.0	3.3	1.3	0.3
	Obs	0	2	4	0	0
χ^2 = 9.067		df = 6		p = 0.170		

3.3.2. Length at maturity

The length distribution for mature individuals varied greatly among stations for both sexes (Figure 33). Accordingly, the most supported model analysing variation in length of mature fish comprised an additive station and sex effect (Table 19). Parameter estimates from this model are presented in Table 20. As visualised in the prediction plot (Figure 34), mature individuals in the upper tributary stations (Tøla and Eskerudbekken) were larger than in the lower ones. The same upstream-downstream pattern was apparent also for the main-river stations (i.e., LEI_1 and LEI_2 > LEI_3).
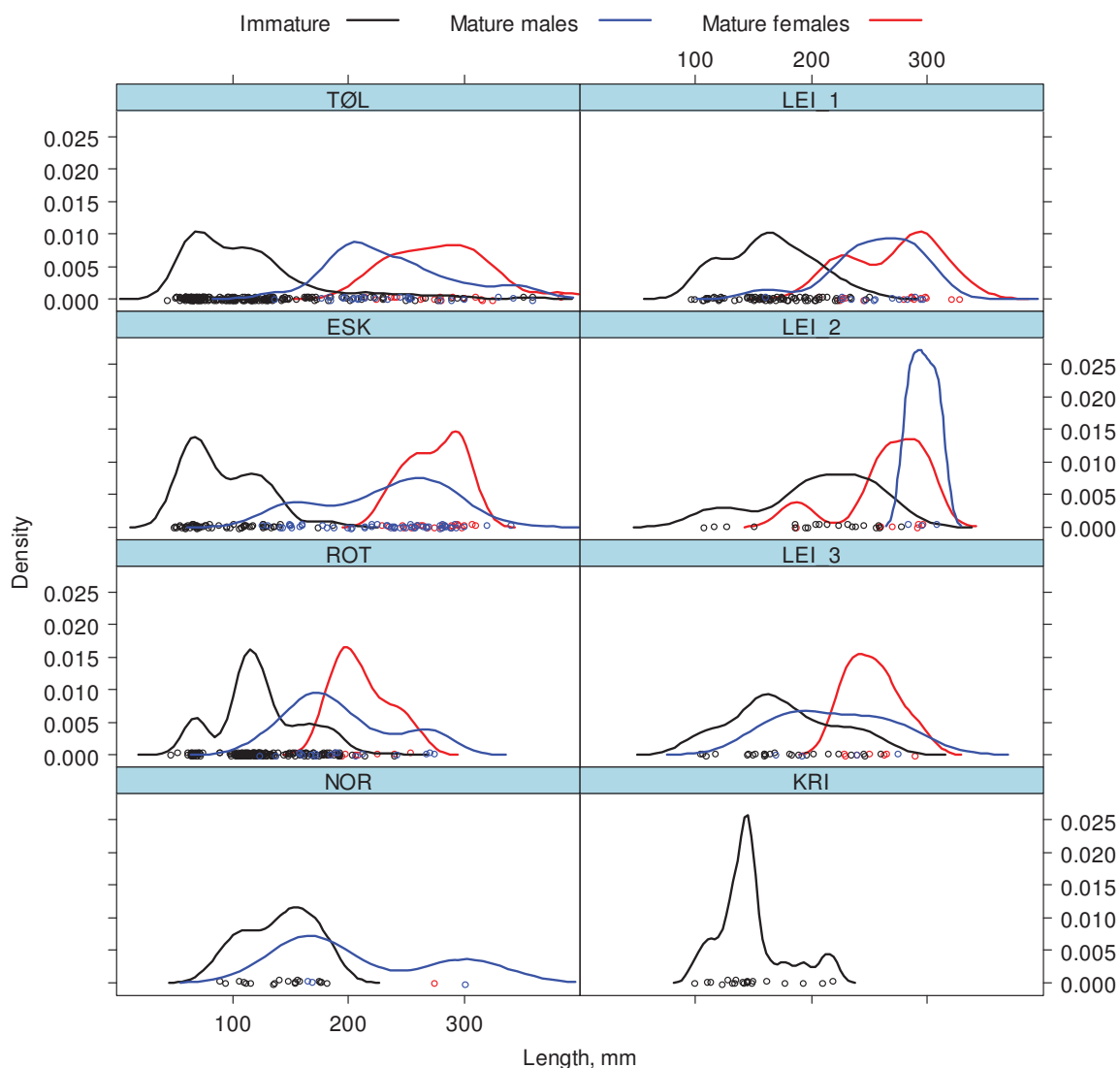

Figure 33. Density plot based on length, of immatures, mature males and mature females in each of the stations.

Table 19. AIC table for models fitted to the data of length of mature fish.

Model structure	df	AIC
Sex+Station	9	2192.266
Sex*Station	15	2195.112
Station	8	2207.941
Sex	3	2211.840
Constant	2	2230.184

Table 20. Parameter estimates and corresponding ANOVA test statistics for the general linear model testing the effect of sex and station on length of mature brown trout. $R^2_{adj} = 0.195$.

Parameter estimates			
Parameter	Estimate	SE	p
Intercept[ESK,Female]	264.702	7.138	<0.001
Sex[Male]	-29.096	6.908	<0.001
Station[LEI_1]	18.543	10.190	0.070
Station[LEI_2]	18.727	16.031	0.244
Station[LEI_3]	-13.758	15.314	0.370
Station[NOR]	-15.380	24.128	0.525
Station[ROT]	-45.832	10.611	<0.001
Station[TØL]	7.534	8.857	0.396

ANOVA test						
Effect	df	Deviance	Resid. df	Resid. Deviance	F	p
Sex	1	53140	205	514563	23.938	<0.001
Station	6	72794	199	441768	5.465	<0.001
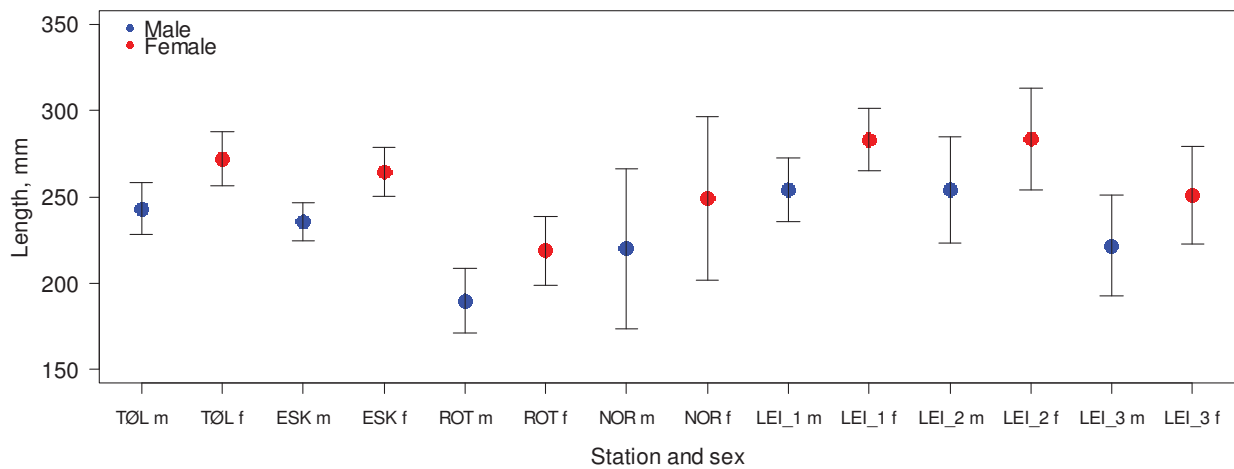
Figure 34. Predicted length of mature males and females as a function of station. Predictions were derived from the most supported model – provided in Table 20.

3.4. Migration

Only two individuals were encountered at another location than the one they were tagged in. They were also the only individuals recorded by the PIT antennas. One brown trout tagged in Eskerudbekken 25.10.2012 was recorded by the PIT-antenna in Låkedalen 05.11.2013. One brown trout tagged in the northernmost station in the main river (LEI_1) 30.09.2013 was recorded by the PIT antenna in Låkedalen 26.10.2013.

4. Discussion

In our study on brown trout inter-population life-history variation in the Leira river system, we found evidence of significant among-stream variation in most traits. The key findings were differential summer survival (low in Rotua), differential individual growth (less sustained growth in lower stations) and differential maturation (earlier maturation in lower stations). In addition, but less convincing, we found evidence of differential degree of fluvial-adfluvial potamodromy. These findings will be discussed in light of life-history theory, habitat- and environmental gradients in the river system.

4.1. Variation in survival

According to the most supported models, apparent summer survival is quite different among stations, but the uncertainties here are large (Figure 20). Tøla and Nordbybekken seem to provide a high summer survival probability for all length classes. Both these streams are characterized by a relatively good access of deep pools (Table 1). This can be crucial for brown trout survival in hot and dry summers. Under such conditions the water-covered area available for fish and drifting food is reduced, which in combination with low oxygen concentrations and high temperature can increase mortality (Elliott et al. 1997, Jonsson and Jonsson 2011). Also, one can imagine that less water in the stream will make the fish more vulnerable to terrestrial predators, e.g. mink (*Mustela vison*), which is present in this area (Heggenes and Borgstrøm 1988). Pools can provide needed refuges from such detrimental factors. It should be mentioned that the summer of 2013 was very dry, and this could be a possible explanation of the low number of 0+ captured in autumn 2013. Tøla and Nordbybekken also provide considerable shelter opportunities due to well-developed vegetation canopy, and good access to large woody debris and undercut banks, which have been found to have a significant positive effect on survival in brown trout (Finstad et al. 2007). In Rotua, this kind of shelter is much scarcer, and the pool frequency is also considerable lower (Table 1). Furthermore, the summer temperature in Rotua is notably higher, and with considerably higher diel variation, than Tøla and Eskerudbekken (Figure 4). More solar radiation because of less overhanging vegetation cover is probably the most important reason for this. These observations can be part of the explanation why the survival probability is lower in

Rotua. However, it is important to keep in mind that what we have estimated is *apparent* survival. Only one stretch in every station was electrofished. In Rotua, this stretch account for approximately 4.3 percent of the total stream length. It is plausible that small-scale within-stream movements result in low encounter rate. Within the station there are few good spawning grounds, due to the dominating substrate being too coarse, so a possible explanation could be that mature individuals migrate further upstream to more suitable spawning grounds. Or, they migrate downstream into Leira (for summer/winter refuges). The same within-stream movement may as well be the case for Tøla, but the access to suitable spawning substrate is higher here than in Rotua.

Our models were not able to calculate good estimates of apparent summer survival probability for brown trout in Eskerudbekken. The reason is probably little data. No individuals were captured there during the first sampling round and the majority was captured in the two autumn rounds, which included large proportions of mature individuals and yearlings. However, the models predicted low survival probability in small Eskerudbekken individuals and high probability in large individuals. Eskerudbekken was regarded the easiest stream to cope with in relation to recaptures and internal migration. The reasons for this were low discharge and that we sampled all the entire area from the outlet up to a waterfall considered to block further upstream fish movement. Non-recaptured individuals are therefore very likely to have either died or emigrated to the main river. Our deduction is that Eskerudbekken is a pronounced nursery tributary where mature brown trout enter, spawn, and leave in autumn. The yearlings probably emigrate before their first winter or during early spring in their second year. This explains the low over-summer apparent survival of small individuals (Figure 20). If survival is zero for small individuals (as indicated in the figure) – the population would be in big problems! Early emigration from the natal stream as an adaptation to avoid detrimental hydrological conditions is known from other salmonid streams (Borgstrøm and Heggenes 1988, Titus and Mosegaard 1989, 1992). Eskerudbekken is small with few deep pools and drought and bottom freezing might be a limiting factor during summer and winter, respectively.

The selected winter-survival model predicted survival to decrease from lengths around 200 mm and beyond – in all study tributaries Figure 21. The increase in mortality rate for larger (i.e., older) individuals, a process called ageing (e.g., Partridge and Mangel 1999), is most likely a

result of post-reproductive mortality, considered a cost of reproduction. These findings are in accordance with the scale-reading results of short life spans and early maturity in the Leira brown trout populations. A survival cost of reproduction has been documented in many salmonids studies (Bell 1980, Hutchings et al. 1999, Dmitriew 2011). Investment in current reproduction is a trade-off situation resulting in diminished probability for future reproduction (Stearns 1992). Hutchings et al. (1999) showed that reproductive males and females of brook trout (*Salvelinus fontinalis*) have significantly larger over-winter lipid depletion than non-reproductive individuals, and that this depletion strongly affects over-winter survival. They also provided evidence that lipid losses increase with increasing body size in reproducing individuals, but not for non-reproducing individuals. This is especially evident in post-spawning males who normally have the highest over-winter lipid depletion.

A lower winter survival rate for small individuals is as expected – the disadvantages of being small are many. One is the combination of lower energy reserves and higher metabolism (Biro et al. 2004). Small individuals live under a higher risk of predation (Milinski 1993), and will often loose against larger, more dominant conspecifics in the competition for the most favorable positions in the stream (Bohlin 1977, Jonsson and Jonsson 2011). Another mortality factor that can be highly relevant in Leira is flooding. Floods are most detrimental for alevins and during the first week of emergence, but juveniles are vulnerable to floods throughout their first year (Jensen and Johnsen 1999, Jonsson and Jonsson 2011). A flood may not kill the fish, but displace it further downstream to less favorable conditions. Such a flood displacement scenario may not only affect displaced individuals' survival (imposed by poorer conditions), but will also affect our apparent survival estimates as displaced individuals will be modelled as dead (unless reappearing in the station at later sampling rounds).

4.2. Variation in growth

In general, the brown trout in the Leira system showed rapid growth in their first two year of life (Figure 25). It should be emphasized that growth is a complex process influenced by a wide range of factors – both biotic and abiotic (Baerum et al. 2013). This is especially valid in poikilothermic organisms with indeterminate growth, like brown trout (Blueweiss et al. 1978, Baerum et al.

2013), where ontogenetic niche shifts coupled with migrations play an important role in the growth pattern (Fuiman and Higgs 1997).

Rotua brown trout constitute the most divergent individuals when it comes to growth. Unlike second- and third-year growth, first-year growth in Rotua individuals was just as good as in Tøla and Eskerudbekken (Figure 26). In Rotua, we observed many suitable habitats (i.e., shallow areas with coarse substrate and low water velocity (Heggenes et al. 1999)) for brown trout 0+, even in periods with little precipitation and thus low water discharge. However, as mentioned earlier there was a rather low availably to pools in Rotua. This may comprise a limiting factor for larger than 0+ individuals in this stream and thus partly explain the less sustained growth pattern. Furthermore, since Rotua individuals have a low age at maturation (Table 17 and Table 18) they will likely face growth costs and thus result in the observed reduction in post 0+ growth (Figure 26).

Spring conditions seem to play an important role in first-year growth of Leira brown trout. All the best models predicting length at age 1 include either mean March temperature or snow-off day (Table 9). Around March, the yearlings of brown trout are still positioned in the gravel, either as eggs or as newly hatched alevins, feeding of their yolk sac (Klemetsen et al. 2003). Size of alevins and fry is considered to be important in areas that are regarded as unfavorable in terms of resource competition (i.e., food and habitat) (Biro et al. 2004), as the subsequent winter can be a survival bottleneck as a consequence of lipid depletion as pointed out with rainbow trout (*Onchorhynchus mykiss*) (Biro et al. 2004). According to Flemming and Gross (1990) and Jonsson and Jonsson (1999), the yolk-to-body tissue conversion efficiency decreases with increasing temperature. As a consequence, larval size at hatching decreases with increasing incubation temperature. Based on this, we hypothesize that high March and April temperatures are negative for the alevin development and hence first-year growth (Figure 27).

The model explaining length at age 1 by March and April temperatures is only slightly better (in practice identical) than the model using March and June temperatures (Table 9). The predictions from this second-most supported model (Figure 28) could in part be related to the interplay between food availability and temperature. Brown trout has an optimal temperature for growth around 15 °C (Forseth et al. 2009), and if periods with this temperature coincides with an

abundance of food, this will be very beneficial for growth. Furthermore, temperatures in excess of the evolved optimum value will increase metabolic rates and reduce maximum consumption rates, and if coinciding with low food availability this can be detrimental for growth (Arendt 1997, Biro et al. 2007). An early spring (i.e., high March temperature) could mean early hatching of insects (Lillehammer 1986, Brittain and Eikeland 1988, Lillehammer et al. 1989). If so, the newly hatched brown trout would not be able to utilize this food source because they still reside in the gravel. A warm summer (i.e., high June temperature) could then be detrimental for the growth of the now emerged fry, because they have missed the peak of drifting insects and in addition have to cope with high temperatures that increase food demand.

In general, one would expect an early spring and a long growth season to have a positive effect on fish growth rate in temperate regions. However, our results for second- and third-year growth showed the contrary, suggesting a late spring and a short growth season yield a positive effect on growth (Figure 29, Figure 30 and Figure 31). Our best explanation is that the mechanism behind this is much the same as discussed for first-year growth: If a late spring delays the peak time of invertebrate drift, and this means that the peak coincides with the period of optimum growth temperature for brown trout, then it may be beneficial for growth. Lillehammer (1986) found evidence that the incubation time for stoneflies (Plecoptera) showed great variation as a consequence of different temperature regimes. This finding was also supported by a study of Elliott (1988) on stoneflies in Britain. We do not know the diet of Leira brown trout, but similar temperature effects as the one reported in stoneflies are probably relevant to most potential food item invertebrates in this river system.

Due to the one-pass sampling strategy applied in this study, our density estimates constitute minimum values. In addition, we do not have access to historical data on fish density. Hence, exploring effects from experienced density on individual growth is not possible and this must be kept in mind when discussing the growth results. Individual growth in brown trout has repeatedly been demonstrated to be density-dependent (Jenkins Jr et al. 1999, Grant and Imre 2005, Jonsson and Jonsson 2011), so not being able to explore this potential effect is unfortunate.

As stated earlier, all brown trout in this study system (except Nordbybekken) lives in sympatry with at least three other species – Eurasian minnow, alpine bullhead and European brook lamprey, so interspecific resource competition is likely at play. Unfortunately, we do not possess adequate density data of these other fish species. Hence, exploring interspecific effects on brown trout growth is not feasible for our data. Olsen (2000) found evidence in his Ph.D. thesis that brown trout living in sympatry with alpine bullhead reached maturation early and did not become either big or old. However, he did not find evidence of a negative growth effect from alpine bullhead.

On the whole, there is a gradient in growth rate where growth decreases downstream. This pattern is especially evident in second- and third-year growth rate (Figure 29 and Figure 32). The pattern can be spurious, but since it appears both within the main river as well as for the tributaries this could potentially reflect influence from a gradient mechanism. As the environmental condition in terms of degree of clay quantity, turbidity and eutrophication increases downstream (Haaland et al. 2011, Haaland and Gjemlestad 2012), one can suggest that the lower growth rate in downstream individuals are caused by a larger environmental-induced stress for these individuals (Bash et al. 2001). Inter-specific competition is also likely to increase downstream, as the number of fish species increases. Below the Låkedalen waterfall cyprinids like chub and common dace are found.

Leira is a river which carries large amounts of clay particles, and the load is especially large after heavy rainfall and extensive snowmelt. The effects of suspended sediment on riverine fish have been investigated in many studies, and the findings have revealed negative effects on growth (Ryan 1991, Wood and Armitage 1997). There can be several underlying mechanisms. Shaw and Richardson (2001) experimentally tested the effects of sediment pulse duration on stream invertebrates and rainbow trout fry. In their study, total abundance of benthic invertebrates and family richness declined as sediment pulse duration increased. This can be an indirect negative effect of fine sediment on fish growth, by reducing the availability of prey. However, even though they found that the family richness of drifting invertebrates also declined, they found that the abundance of drifting invertebrates increased as sediment pulse duration increased, solely because of an increase in abundance of chironomids – an important prey for trout. They

concluded that such indirect effects of fine sediment on trout growth were of minor importance compared to more direct effects, such as impaired vision leading to reduced prey capture success (Barrett et al. 1992, Vogel and Beauchamp 1999).

Brown trout can be sensitive to biotic interactions with other fish species (Degerman and Sers 1992, Eklov et al. 1999). The presence of both predators and competitors may decrease energy intake and increase energy consumption, hence reduce growth (Jonsson and Jonsson 2011). The presence of predators may result in a shift in habitat use, both spatially and temporally (more nocturnal activity) (Alvarez and Nicieza 2003).

4.3. Variation in maturity

In general, brown trout in Leira mature early and at small sizes (i.e., at ages 1-3 years and 2-3 years in males and females, respectively). As just discussed, brown trout in Leira also display rapid first-year growth and have short life-time expectancy. This is in accordance with life-history theory, where fast growth, early maturation and short life-span link together (Alm 1959, Stearns and Koella 1986, Hutchings 1993, Roff 2002). Similar life-history strategies are also found elsewhere in brown trout stream populations (Jonsson 1985, 1989, Olsen 2000).

As already stated, Rotua brown trout have a relatively good first-year growth, but then they slow down and 2- and 3-year old individuals are significantly smaller than in Tøla (Figure 22). From this we would expect that brown trout matures earlier in Rotua. This was supported by the age distribution of mature males (Table 17), where we found mature Rotua individuals to be significantly younger than individuals in both Tøla and Eskerudbekken, and also smaller than mature Tøla and Eskerudbekken individuals (Figure 33 and Figure 34). The survival in Rotua individuals was also consistent with the observed maturity pattern, as a high mortality rate of older individuals relative to younger ones favor early reproduction, and to devote a large proportion of resources the subsequent years to reproduction, thus leading to small adult body sizes (Kozłowski and Uchmanski 1987).

As for growth, we observed a gradient in maturity size throughout the system, with decreasing size from upstream towards downstream (Figure 33 and Figure 34). These findings, we suggest,

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could be a result of an increasingly stochastic and hostile environment as one moves downstream, which favors early maturation to secure reproduction, as postulated in Roff (2002). The Leira system in general qualifies to the characteristic stochastic environment, with its large and rapid fluctuations in discharge and the resulting changes in sediment transport. This could partly explain the general life-history strategy in this system. In Rotua, where this life-history strategy is most extreme, the fluctuations in temperature (Figure 4) add another dimension to the instability.

4.4. Migration

We believe the study tributaries are widely used as spawning and nursery habitats for Leira brown trout. As mentioned, we found clear signs of spawning migration from the main river to Eskerudbekken. There are also other signs pointing toward extensive fluvial-adfluvial potamodromy in this system. The fact that no 0+ brown trout were captured in the main river indicates that very limited, if any at all, spawning takes place here. A high proportion of mature individuals in the tributaries in autumn also support this. Poor spawning habitats within the main river, at least in the lower reaches, might be the main reason for this migratory pattern. Brown trout have certain habitat requirements for their spawning area, associated with water velocity, depth, substrate, cover, oxygen and temperature (Armstrong et al. 2003). Its preferred particle size in the spawning substrate lies broadly in the range 5-128 mm and it avoids sites with uniform particle size (Armstrong et al. 2003, Jonsson and Jonsson 2011). The main river is mostly slow-flowing with fine-grained sediments. Some potential spawning habitats are probably present in the main river too, but the large transport of fine sediments here can be problematic for eggs and alevins (Lisle and Lewis 1992, Soulsby et al. 2001). Fine sediments can prevent sufficient permeation of oxygen into the interstitial spaces within the gravel where the eggs are buried, and efficient removal of metabolic waste (Armstrong et al. 2003). In addition, clay particles may reduce oxygen uptake for the embryos by creating a low-permeability seal around the eggs and/or physically block the micro-pore canals in the egg membrane (Greig et al. 2005). For brown trout alevins, fine sediments can cause problems both because of reduced oxygen availability and because intergravel movements get blocked (Sternecker and Geist 2010). We find it unlikely that there are good spawning habitats in the main river downstream from where we sampled, since

eutrophic conditions and sediment concentration increases downstream (Haaland and Gjemlestad 2012).

Apart from one tagged individual in the main river upstream Kringlerdalen that subsequently got recorded by the PIT-antenna in Låkedalen, we have no indications of large-scale migration within the system. Long migrations are energetically costly and potential benefits of large-scale migrations in this system, which will involve passing one or more waterfalls, may not outweigh the costs (Kinnison et al. 2001, Kinnison et al. 2003). The fact that no brown trout were recaptured in another tributary than the one in which they got tagged is a sign of strong homing behavior in this system – a well-known behavior in brown trout (Harden Jones 1968, Jonsson and Jonsson 2011). Based on our findings, we are more inclined to suggest small-scale migratory pattern to be widespread, as indicated when discussing spawning migration in the tributaries. We suggest the low recapture rate is partly due to small-scale migrations resulting in a reduced probability of recaptures within the station. Especially in the larger tributaries, Rotua and Tøla, we find it likely that there are individuals that never or seldom enter the main river. If they do, we would have expected to have some recaptures in the main river, especially during the boat electrofishing survey in which relevant stretches of the main river were surveyed for both these tributaries. The low growth pattern in Rotua brown trout could indicate that they stay their entire life within the stream. Possibly, benefits from migrating to the main river become less pronounced for the lower reaches of the main river – due to low abundance of relevant habitats, poorer water quality and competition from other species.

In contrast, Eskerudbekken individuals seem to spend a great proportion of their life time in the main river allowing for a more endured growth rate. The reason why larger brown trout do not reside in this tributary year-round is probably because of lack of suitable habitats due to its small size. In addition, the main river in this area may provide relatively unstressing environments compared to further downstream, where the environment is more hostile (i.e., more interspecific competition and poorer water quality). Unfortunately, during the boat electrofishing survey, we did not get access to main river sections located in the vicinity of the outlet of Eskerudbekken. We expect brown trout from this tributary to reside in this area, and indeed we did get a PIT antenna registration of an Eskerudbekken individual at Låkefossen – about 1 km downstream the tributary outlet. Rotua and Tøla may provide sufficient habitats year-round and also have own

tributaries which can be utilized by the fish. However, it is not unlikely that these streams are utilized for spawning by brown trout individuals otherwise residing in the main river. Such a partial migration pattern is well-known from coastal streams, where a part of the population migrates to sea and others, of both sexes, stay (Jonsson 1989, Jonsson and Jonsson 1993).

4.5. Conclusion

To wrap up our general findings, our study has shown that the general life-history strategy in brown trout from this part of the Leira river system is fast early-life growth, early maturation and a relatively short life span. There was inter-population variation within this life-history strategy with Rotua individuals displaying the most rapid life-history and a general increase in life-history rapidness as one moves downstream the main river. Brown trout in the upper parts are larger and have better and more persistent growth (Figure 22, Figure 29 and Figure 32). Age and length of mature fish also decreased downstream, both among stations in the tributaries and among main-river stations (Table 17, Figure 33 and Figure 34). Although we do not have precise estimates of brown trout density, we have clear indications of decreasing density downstream. Most evident was the low density in Nordbybekken and the southernmost main river station (LEI_3). We hypothesize that these observed gradients in life-history traits and density reflect adaptations to the prevailing downstream environmental gradients of increased eutrophication, turbidity and number of fish species.

Our findings suggest that small-scale migrations in the system are common and differ some in type among populations (Figure 35). Eskerudbekken brown trout displays fluvial-adfluvial potadromy in the form of spawning migration. In the larger tributaries, Rotua and Tøla, within-stream migrations are likely to take place. Although further research is required to make well-built conclusions, large-scale migrations in the system seem unlikely. The migration patterns can be explained by habitat characteristic and are reflected in life-history.
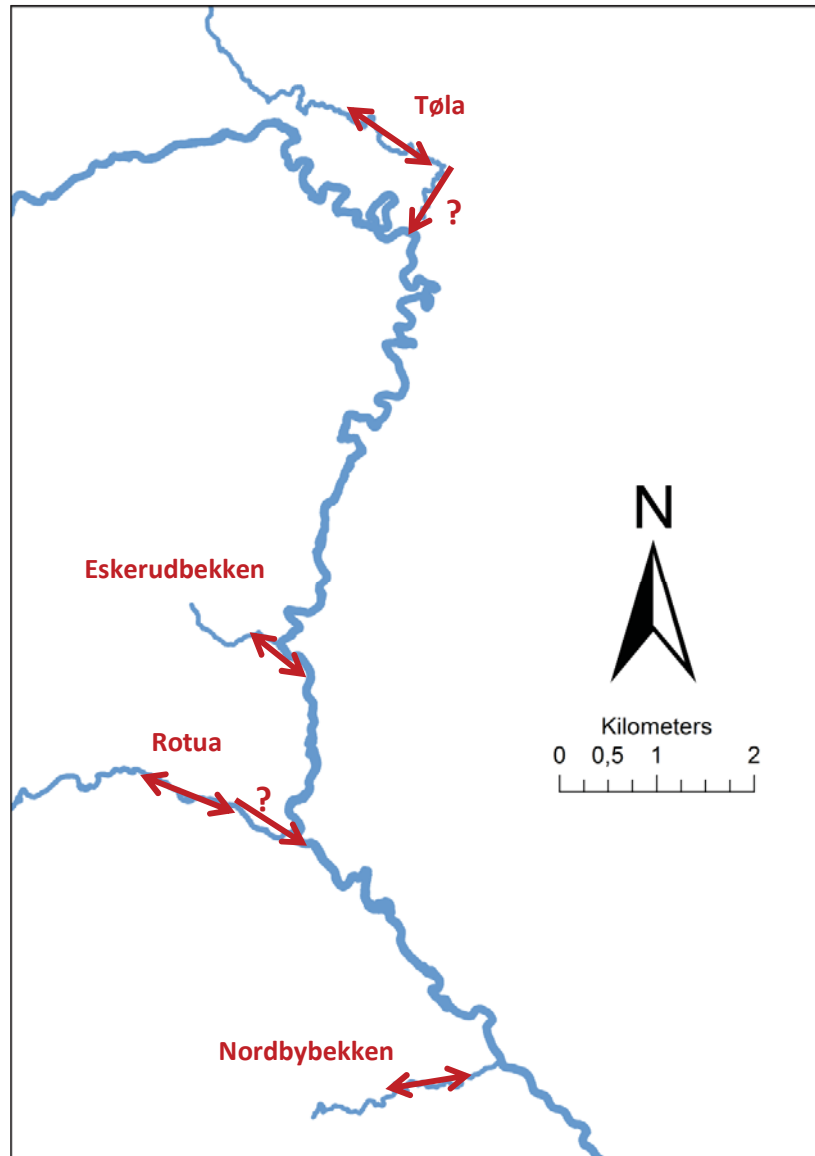
Figure 35. Schematic illustration of our hypothesized migration patterns of brown trout in the middle part of the Leira river system.

4.6. Shortcomings and further research

The recapture probability was low, yet estimable, in this study. There might be several reasons for this. As expected, the probability increased with increasing fish size (Figure 19) (Bohlin et al. 1989, Borgstrøm and Skaala 1993). There was also a clear relationship between the recapture probability and water discharge. This was especially true for the largest tributary, Rotua, which became quite cumbersome to electrofish at high discharges. In addition to the difficulty of

covering all areas in the large quantities of water, high discharge was often accompanied by large amounts of suspended particles which made the water highly turbid, thus making it hard to perceive the fish. Dealing with a large population size and dispersal will also affect the recapture probability. This is especially valid for the Cormack-Jolly-Seber modelling approach undertaken in our study (Lebreton et al. 1992). A basic principle of this CMR-study is that we are dealing with apparent survival as stated earlier. It has already been stated that the mobility can be severe in brown trout. This has its complications both during and between field rounds. During a field round it is conceivable that the fish get startled and swim out of the station. This may be more common in the spring and summer when they are more active (Forseth and Forsgren 2009). In the autumn, when the temperature drops, the brown trout tends to be more nocturnal and it is more likely to remain in the shelter in the daytime regardless of any disturbances (Forseth and Forsgren 2009).

Between field rounds it is plausible to assume a movement out of the station for various reasons (e.g., foraging, altered behavior, avoiding unfavorable condition or spawning), especially considering the fact that only a fraction of each stream was electrofished. It was a considerable distance between the stations, which made it difficult to capture possible movements within the system. This was particularly true for Tøla and Rotua where a movement upstream is not inconceivable. In addition, two of the stations in the main river, the two PIT antennas in Låkedalen and Homledalen, were only (more or less) operative from September 4th and November 12th, 2013, respectively. Another key issue is that during electrofishing with boat in the main river we were not able to cover a section in Leira where Eskerudbekken empties into. As earlier stated we are rather sure of an evident seasonally migration pattern between Eskerudbekken and the main river, and electrofishing adjacent to the inlet of the stream could have confirmed our suggestions. One of our study objectives was to identify any large-scale migration in the system. In a system like this, with apparently extensive fluvial-adfluvial potamodromy behavior among brown trout, and since we got some ambiguous results on this matter, it would be interesting to identify a migrating pattern on a smaller scale. In this context it would be appropriate to add more stations, either by a set-up of PIT antennas (assuming they would function) in each stream to capture internal movement, alternatively it is possible to modify the stations with electrofishing, going from one to several stations in each stream.

An adjustment in the electrofishing method as described in Forseth and Forsgren (2009), which gives good measurement of population density, could give stronger data to model density effects on the different trait values. Since we only had one station in each tributary, and the fact that in each field round we only electrofished the stretch one time, we attained no minimum estimates on brown trout density with low power for testing density effects on life-history trait values. However, we did see some indications of variation in density.

One aspect in the life-history of brown trout in Leira that have not been considered to any extent is inter-population differences in reproductive effort in terms of fecundity and size of eggs. A natural cause for this was the low number of captured mature females during the field work. In theory, we would expect inter-population differences since we found a gradient of decreasing length downstream and size is an important trait regarding reproductive effort (Jonsson and Jonsson 2011). An extensive study on this matter would to some degree complement our understanding of the life-history of brown trout in Leira.

Use of scales for age determination and back-calculation of yearly growth is regarded a very useful tool, but also a tool where a quality control is appropriate. Error in both measurements and reading of the scales is common and would result in error in interpretation of the data. A typical mistake is to underestimate the age of the fish, which is very common and often impossible to avoid in stunted fish without having other biological texture with information about the age (e.g., otoliths). We do, however, not think there is an underestimation problem for the Leira populations as the age structure very much reflects the high mortality rate observed in this system.

The set-up with the PIT antennas in this study did not work in our favor, resulting in perhaps more questions than answers regarding the migratory behavior of brown trout in Leira. Assuming they will function properly in the future, this project should continue, creating a time series which would probably remove some of the gaps in the knowledge about large-scale migration of brown trout in Leira.

A different and interesting aspect would be to do a research on potential gene flow among stations and detect any existence of in-stream genetic differentiation in potentially isolated sub-populations. This will add a different view on migration in the system, in terms of gene flow.

4.7. Management implications

The objective of the EU Water Framework Directive is to establish a framework for the protection of water bodies (European Commision 2000). The management of water bodies shall be holistic and knowledge-based, and for inland surface water the main goal is that all water bodies shall, if not heavily modified, obtain or maintain at least "good ecological status" within a given time. Having failed to find a reliable quality element for ecological quality assignment in this system it has been proposed to use brown trout as an indicator species (Haaland et al. 2011).

The brown trout is often associated with cold, clean and clear water, and does not thrive very well under warm, eutrophic and turbid conditions (Jonsson and Jonsson 2011), as illustrated in this study. It should therefore be well suited as an indicator of good water quality. This is supported by a study of Eklov et al. (1998), which compared stream fish communities between 1960s and 1990s in southern Sweden in relation to improved water quality. One of their main findings was that brown trout abundance and distribution had increased as an effect of better water quality, including higher oxygen concentrations. Our finding of a gradient in brown trout life-history strategy and density accompanied by an environmental gradient adds further support to the brown trout's suitability as an indicator species. Therefore, an expansion downstream of the brown trout distribution in Leira and/or an increase in abundance of existing populations could be interpreted as a result of improved water quality. However, since there is an inter-specific competition aspect into this as well, an eventual brown trout water quality assignment index will need to take this into account. In general, the use of brown trout as an indicator requires knowledge about its local life-history. This study has contributed to such knowledge, and one finding is that 0+ brown trout are likely to be present in the tributaries only – an important issue to consider when interpreting brown trout data from a monitoring station in the main river. However, if this age class later is to be found here it could be a clear sign of improved water quality. One cannot be totally sure if an individual captured in a given monitoring station has not spent most of its life under a better water quality elsewhere in the river system. However, we believe the probability is small since

long migrations are unlikely and especially if the station is not located in the vicinity of a high-water quality tributary. Further research could help clarify this.

An important finding of our study is the importance of the tributaries as spawning and nursery habitats. During the fieldwork, we surveyed most of the streams in the study area without detecting brown trout to a significant degree. Wise management of tributaries that do hold brown trout is therefore essential for the conservation of the Leira population, which should be regarded a metapopulation where tributaries are important source populations. An important aspect of this management is riparian management. We observed that the riparian zones were virtually intact along all our tributary-stations. We stress the importance of letting them remain so. Riparian zones serve several functions important for fish: They stabilize the stream bank and greatly decrease erosion (Beeson and Doyle 1995), can attenuate floods by absorbing and storing water during and after high flow (Mitsch and Gosselink 2000), can help maintain good water quality by filtering, binding and transforming sediments, nutrients and pollutants (Barling and Moore 1994, Naiman and Decamps 1997), and they are crucial for fish food and habitat. By providing woody debris they can increase fish production both directly for fish by providing habitat and indirectly by providing habitat for invertebrates which serve as food for fish (Gregory et al. 1991, Degerman et al. 2004). Finstad et al. (2007) even suggested that that increased shelter availability may select for larger fish, because negative effects of shelter reduction increases with fish body size. Such an effect is probably welcomed by fishermen. Riparian zones also provide shelter in terms of overhanging vegetation, which in addition can have a positive effect on stream temperature, regarding brown trout, by reducing solar radiation in warm summer periods (Cross et al. 2013).

In summary, management decisions must be based on knowledge of the brown trout life-history and its link to migration and habitat use. One must be aware that implementation of management decisions that change the environment is likely to affect life-history adaptations for the populations involved. There is a dynamic interplay between a species' life-history and its environment, and humans and human actions comprise important components of this environment.

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