

# **Non-native brook charr (*Salvelinus fontinalis*) in an urban fragmented stream:**

*Migration, growth, survival, and size at maturation*

**Marius Hassve**



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Marius Hassve

## Abstract

Hassve, M. (2012). Non-native brook charr (*Salvelinus fontinalis*) in an urban fragmented stream: Migration, growth, survival, and size at maturation. 60 pages including appendix.

**Key words:** *barrier, Hovinbekken, pools, temperature*

- Urbanization is a serious threat to stream ecosystems. Culverts fragment habitats, and can function as migration barriers. If migratory individuals are prevented to move between important habitats, this could potentially result in spatial variation in life-history traits.
- Brook charr (*Salvelinus fontinalis*) is an introduced salmonid species of North-American origin. It has shown to be mobile within systems, and its life history patterns to be phenotypic plastic. Despite being an unwanted species in the Norwegian fauna, it has received little attention as it has been considered to be a competition-weak species.
- In this study I tested the hypothesis that; <sup>a</sup> the degree of local-scale connectivity, including both natural- and man-made barriers, influences migration probability, and <sup>b</sup> owing to local-scale influence on within- stream section environmental conditions there are among-section differences in brook charr life history traits like growth, survival, and maturation.
- The hypothesis was tested in Oslo's most urban stream, Hovinbekken. The study stream was divided into four spatially separated sections, where individuals of brook charr were caught using electroshocking, tagged with PIT-tags, and recaptured, during an eighteen months period (2010-2012). Over five sampling occasions, in total 528 brook charr individuals were caught, of which 452 were tagged.
- Out of 143 recaptured individuals, 8 moved between stations. 6 of them moved between the two stations without natural or man-made barriers, a pattern attributed to spawning and winter-migration. 2 individuals moved in a downstream direction through culverts, none the opposite way. Upstream migration through natural and artificial fragmented landscape seems therefore to be absent, probably impossible.
- Growth, survival, and length at maturation varied at a temporal and spatial scale; the southernmost and most urban stations had highest growth rate for 0+, longer growth before stagnation, and matured at longer lengths, probably due to favorable temperature conditions. Survival probability seemed in general to be lowest over winter. Additionally, winter survival was size-dependent, i.e. larger fish having the highest survival. In contrast, and over summer, survival was negatively size-dependent. Spatial variation in size-dependent seasonal survival was found, and attributed to pool characteristics. Because of the inconsistency in size-independent spatial variation in survival, and the impossibility to determine age at sexual maturation, further research is needed to gain more knowledge of brook charrs life history traits in Hovinbekken.
- I also recommend continuing studying brook charr in Hovinbekken to obtain further knowledge for best management practice.

## Sammendrag

Hassve, M. (2012) Innført Bekkerøye (*Salvelinus fontinalis*) i en urban fragmentert bekk: Migrasjon, vekst, overlevelse, og størrelse ved kjønnsmodning. 60 sider inkludert vedlegg.

**Nøkkelord:** *barriere, Hovinbekken, kulper, temperatur*

- Urbanisering er en trussel mot elve-økosystem. Kulverter fragmenterer habitat, og kan således fungere som migrasjonsbarrierer. Om mobile individer blir hindret i å bevege seg mellom viktige habitat, kan dette resultere i romlig variasjon i livshistorietrekk.
- Bekkerøye (*Salvelinus fontinalis*) er en introdusert art i laksefamilien, opprinnelig fra Nord-Amerika. Den har vist seg å være mobil innad i systemer, og dens livshistorie å være fenotypisk plastisk. Til tross for at den er en uønsket art i norsk fauna, er den lite studert, trolig grunnet den generelle oppfatningen at den er konkurransesvak, og derav utøver liten biologisk trussel.
- Hypotesene testet i dette studiet var at <sup>a</sup>graden av lokal-skala konektivitet, inkludert både naturlige og menneskeskapte barrierer, påvirker muligheten for migrasjon, samt <sup>b</sup>grunnet småskala påvirkninger på lokale miljøforhold er det vekst, overlevelse, og kjønnsmodnings-relaterte forskjeller mellom seksjoner.
- Hypotesene ble testet i Oslos mest urbane bekk, Hovinbekken. Studieområdet ble videre inndelt i fire adskilte seksjoner. Bekkerøye ble fanget med elektrisk fiskeapparat, merket med PIT-tags, og gjenfanget iløpet av en atten måneder lang periode (2010-2012). Over totalt fem runder ble 528 enkeltindivider fanget, hvorav 452 merket.
- Av i alt 143 gjennfangede enkeltindivider ble 8 funnet å forflytte seg mellom stasjoner. 6 av disse hadde flyttet seg mellom de to stasjonene uten naturlige eller menneskeskapte barrierer, trolig henholdsvis gyte- og vintervandring. 2 individer vandret nedstrøms gjennom kulverter, ingen oppstrøms; oppstrømsvandring i det naturlige og menneske-fragmenterte miljøet synes således å være fraværende, trolig umulig.
- Vekst, overlevelse, og lengde ved kjønnsmodning varierte både over tid, og mellom stasjoner; Bekkerøye i de nederste og mest menneskepåvirkede stasjonene hadde best 0+ vekstrate, vekststagnerte senest, og var lenger ved kjønnsmoden tilstand, trolig grunnet mer gunstige temperaturforhold. Overlevelsessannsynlighet viste seg generelt å være noe lavere gjennom vinteren. Vinteroverlevelse var videre størrelsesavhengig, med høyere overlevelse for større individer. Sommeroverlevelsen derimot, var negativ størrelsesavhengig. Romlig variasjon i sesongmessig størrelsesavhengig overlevelse ble funnet, og har trolig en sammenheng med egnede kulper. Ettersom det ikke ble sett noe klart mønster i størrelsesuavhengig romlig overlevelse, samt at det ikke var mulig med sikkerhet å bestemme alder ved kjønnsmodning, er videre forskning nødvendig for å tilegne seg mere viten om livshistorietrekk for bekkerøye i Hovinbekken.
- Jeg foreslår også å fortsette å studere bekkerøye i Hovinbekken med bakgrunn i det å tilegne seg mere kunnskap og derav best mulig forvalte arten i fremtiden.

## Contents

|            |  |           |
|------------|--|-----------|
| <b>1</b>   | <b>Introduction</b> .....  | <b>6</b>  |
| <b>2</b>   | <b>Materials and Methods</b> .....   | <b>9</b>  |
| <b>2.1</b> | <b>Study system</b> .....  | <b>9</b>  |
| 2.1.1      | Bekkedalen north (station No1).....  | 12        |
| 2.1.2      | Bekkedalen south (station No2) .....   | 13        |
| 2.1.3      | Brobekk (station No3).....   | 14        |
| 2.1.4      | Risløkka (station No4).....  | 15        |
| <b>2.2</b> | <b>Study species</b> .....   | <b>16</b> |
| <b>2.3</b> | <b>Data Sampling</b> .....   | <b>18</b> |
| <b>2.4</b> | <b>Statistics</b> .....  | <b>22</b> |
| 2.4.1      | Capture-mark-recapture analyses .....  | 22        |
| 2.4.2      | Other statistical analyses.....  | 23        |
| <b>3</b>   | <b>Results</b> .....   | <b>25</b> |
| <b>3.1</b> | <b>Spatial variation in age distribution</b> .....   | <b>25</b> |
| <b>3.2</b> | <b>Spatio-temporal variation in (re)capture, survival, and migration probability</b> ..... | <b>26</b> |
| <b>3.3</b> | <b>Spatial variation in individual growth</b> .....  | <b>31</b> |
| 3.3.1      | Analysis of fall 0+ sizes.....   | 31        |
| 3.3.2      | Analysis of recaptured individuals .....   | 32        |
| <b>3.4</b> | <b>Spatial variation in maturation</b> .....   | <b>34</b> |
| <b>4</b>   | <b>Discussion</b> .....  | <b>36</b> |
| <b>4.1</b> | <b>Re(capture) probability</b> .....   | <b>36</b> |
| <b>4.2</b> | <b>Migration</b> .....   | <b>36</b> |
| <b>4.3</b> | <b>Life history traits</b> .....   | <b>39</b> |
| <b>5</b>   | <b>Management implications</b> .....   | <b>42</b> |
| <b>5.1</b> | <b>Further research</b> .....  | <b>45</b> |
|            | Acknowledgments .....  | 46        |
| <b>6</b>   | <b>Bibliography</b> .....  | <b>47</b> |
| <b>7</b>   | <b>Appendix</b> .....  | <b>54</b> |

## 1 Introduction

Urbanization threatens stream ecosystems (Morley & Karr, 2002; Paul & Meyer, 2001) and is expected to further increase worldwide (United Nations, 2008). Impervious surfaces, such as roads and other impenetrable artificial structures are known to be good predictors of urban land use and its subsequent consequences on streams (Paul & Meyer, 2001; Schueler, 1994). The effects are most often nonlinear (Allan, 2004), and several studies have documented negative effects when the percentage of imperviousness go beyond 10-20 % (Paul & Meyer, 2001; Wang, Lyons, & Kanehl, 2001; Wang, Lyons, Kanehl, Bannerman, & Emmons, 2000). Physical (vegetation, geomorphology, hydrology, and temperature), chemical (nutrient, metals, and pesticides) and biological alteration (invertebrates, algae, and fish), are some of the overall urbanization-related changes described (Paul & Meyer, 2001).

One of the major negative consequences of urbanization is habitat fragmentation (Delaney, Riley, & Fisher, 2010), “a landscape-scale process involving both habitat loss and the breaking apart of habitats” (Fahrig, 2003, p. 487). Fahrig (2003) stresses the importance of measuring fragmentation per se and habitat loss separately, since the latter has shown more negative effects on biodiversity than fragmentation itself. Though, for species that are dependent on moving between habitats, fragmentation can have devastating effects (Letcher, Nislow, Coombs, O'Donnell, & Dubreuil, 2007), since fragmentation of habitats can function as migration barriers (Warren & Pardew, 1998). Isolation, loss of genetic variation, and risk of extinction (Letcher et al., 2007; Wofford, Gresswell, & Banks, 2005) are potential outcomes.

Many fish species changes resource and habitat use as they grow (ontogenetic niche shift (Werner & Gilliam, 1984)). Habitat use at different ages, and different temporal scales, are described among others for Atlantic salmon (*Salmo salar*), brown trout (*Salmo trutta* (Heggenes, Baglinière, & Cunjak, 1999)), and brook charr (*Salvelinus fontinalis* (Johnson & Dropkin, 1996; Johnson, Ross, Dropkin, & Redell, 2011; Meyer & Gregory, 2000)).

Feeding migration at younger stages can decrease competition, and increase growth and survival (Northcote, 1978). Consequently, if important niches during later ontogeny are inaccessible this could affect growth and survival negatively. Einum, Sundt-Hansen, and Nislow (2006) found evidence for older juvenile Atlantic salmon to disperse from high-density areas. If this is the case for other salmonids, density-driven differentiation in growth and survival among stream stretches can result whenever density-dependent migration is

prevented, like in fragmented streams. In addition to biotic interactions, factors operating independent of current density (density independence) such as temperature and flow (abiotic factors) can also affect growth and survival (Xu, Letcher, & Nislow, 2010a, 2010b), as well as an interaction between the two (Carlson, Olsen, & Vøllestad, 2008; Vøllestad & Olsen, 2008). Growth and survival can further affect another life history trait; Hutchings (1993) found evidence for delayed reproduction when adult survival was high, while rapid growth favored early reproduction. In an isolated brook charr population in Massachusetts USA with high early survival, reproduction occurred at an earlier stage compared to the mainstem, with the result of smaller adult individuals (Letcher et al., 2007). One might therefore expect to find substantial between-section variation in sexual maturation in fragmented streams.

Habitats suitable for feeding and reproduction are often separated (Northcote, 1978), and upstream migration to spawning habitats is therefore relatively common (Lucas & Baras, 2001). If adults are unable to reach satisfactory spawning grounds, they might spawn in less optimal areas, potentially resulting in negative effects on a population level.

In fragmented systems, movement may be mainly downstream (Whiteley et al., 2010). Populations where key individuals migrate downstream, but are unable to return, may eventually go extinct (Thorstad et al., 2011). Ultimately, barriers can potentially select against migration behaviour favoring a resident life style. Such a selection has been found both in the only stream resident Atlantic salmon in Europe (Berg, 1985), and in a non-anadromous variant of rainbow trout (*Oncorhynchus mykiss* (Thrower, Hard, & Joyce, 2004)). In such a scenario populations will probably consist, more or less, of stationary individuals, depending on scale of movement defined.

In the event of a disturbance fish may move to refuge habitats (Schlosser & Angermeier, 1995), both in a downstream (Lucas & Baras, 2001), and upstream direction (Meisner, 1990). In this respect tributaries, woody debris (riparian vegetation), and pools are important habitats (Sedell, Reeves, Hauer, Stanford, & Hawkins, 1990). Pools may function as refugia in streams both during droughts and floods (Sedell et al., 1990), however, this might be dependent on fish size (Magoulick & Kobza, 2003). Since a refuge can operate at different spatial scales (Sedell et al., 1990), accessibility within a system or section could be a limiting factor, and migration necessary for persistence. Xu et al. (2010b) found a decreased survival for larger brook charr during low summer flows in small systems. In contrast, Hutchings, Pickle, McGregor-Shaw, and Poirier (1999) detected lower brook charr winter survival. Seasonal

variation in survival for different age classes of brook charr described by Carlson and Letcher (2003), suggests that size- and season specific survival rates are to be expected, especially in small streams modified by humans (loss of habitat and connectivity).

In streams, culverts are common crossing constructions. Culverts have both the potential to function as barriers to fish movement (Benton, Ensign, & Freeman, 2008; Gibson, Haedrich, & Wernerheim, 2005; Thompson & Rahel, 1998), and as passable units (Pluym, Eggleston, & Levine, 2008), thus bidirectional (Warren & Pardew, 1998). Culvert type (Langill & Zamora, 2002; Pluym et al., 2008), high velocity flow, high culvert slope, low water depth, culvert length, and high outlet hang (Degerman, 2008; Poplar-Jeffers et al., 2009), are some of the associated problems. Violations of one or more of these requirements for movement will therefore be expected to cause restricted mobility or none at all.

As an overall goal for my master thesis, I studied the effect of habitat fragmentation on brook charr movement in an urban landscape. The observational study was done with the use of capture-mark-recapture method over an eighteen months period, in the stream Hovinbekken, Oslo, Norway. In field, length, weight, and sex were registered to also study brook charr life history patterns, since such information is relevant regarding management of a non-native species.

This thesis is a highly relevant urban-ecological topic, both on general grounds but also for the study system in particular, since a partly re-opening of the study system is in progress. In this respect I hope my thesis will be a part of the assessment criteria for further opening plans, since there are important aspects to take into consideration before restoring the study system closer back to its pristine state.

More specifically my study tests the following hypothesis:

- a. the degree of local-scale connectivity, including both natural- and man-made barriers, influences migration probability.
- b. owing to local-scale influence on within- stream section environmental conditions there are among-section differences in brook charr life history traits like growth, survival, and maturation.



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## 2 Materials and Methods

### 2.1 Study system

This study was conducted in the first/second order stream Hovinbekken, Oslo County, Norway (60° N, 10° E (Figure 1)). The catchment area is 11 km<sup>2</sup>, and drains through forest and urban land (Beschoner, 2010) on its way to Akerselva, where the stream enters through a large culvert (Hvoslef, Nilsen, Tønsberg, Gulbrandsen, & Johnsen, 2004). Total stream length is 8.3 km (NVE, s.a.), and estimated average water discharge 0.18 m<sup>3</sup>/s (Oslo kommune vann- og avløpsetaten, 2011). Hovinbekken is Oslo's fourth largest watershed (Hartwig, Tønsberg, Nilsen, Johnsen, & Hvoslef, 2010), but still a small system in a broad scale.

The stream, which is the most closed waterway in Oslo (Hvoslef et al., 2004), was divided into four study sections: Bekkedalen north (station No1), Bekkedalen south (station No2), Brobekk (station No3), and Risløkka (station No4), all of them located in the upper part of the system (Figure 1). Three sections are isolated, caused by culverts placed underneath roads. Each station is classified after Bisson, Buffington, and Montgomery (2006) classification system, as pool-riffle reaches (more detailed and specific station characteristics described later). The amount of imperviousness increases downstream from station No1 to No4 (Figure 1).

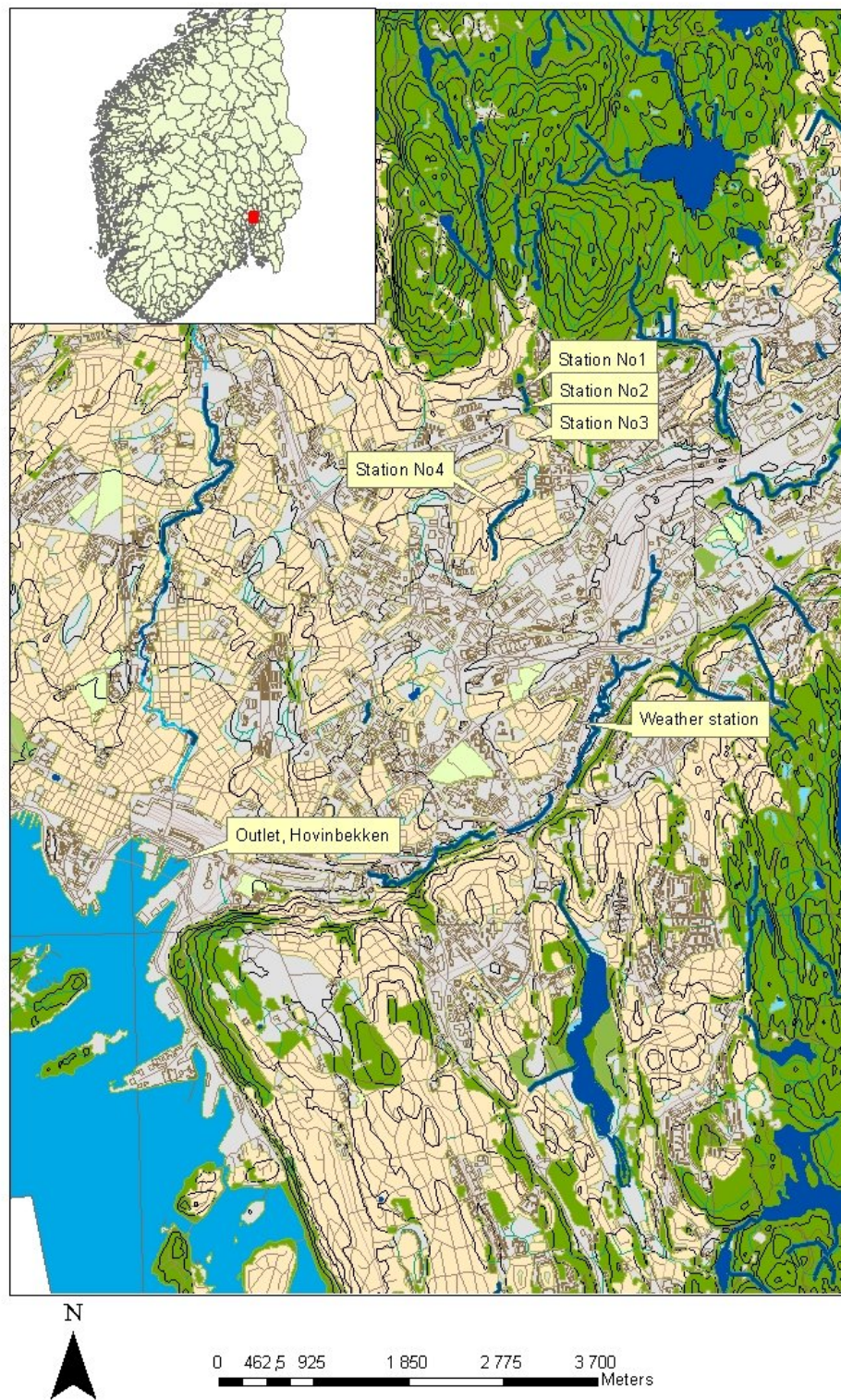
In total, 452 brook charr individuals were tagged, and 143 recaptured (186 when including fish recaptured more than once), during five periods from fall 2010 to early spring 2012. Number of brook charr tagged varied among stations and over years (Table 1), with the lowest number of caught/tagged fish in station No1 and No2 during last field work period (Appendix 1A, Table 1). Untagged individuals (n=76) were mainly those too small, and those only included in the length distribution (Appendix 1A).

**Table 1.** Number tagged and number of recaptures, in four study stations and over 5 sampling rounds in stream Hovinbekken.

| Date       | Station | Number tagged | Number recaptures |
|------------|---------|---------------|-------------------|
| 29.09.2010 | 1       | 25            | -                 |
|            | 2       | 49            | -                 |
|            | 3       | 53            | -                 |
| 06.05.2011 | 1       | 12            | 4                 |
|            | 2       | 18            | 13                |
|            | 3       | 14            | 12                |
|            | 4       | 13            | -                 |
| 27.09.2011 | 1       | 19            | 10                |
|            | 2       | 18            | 9                 |
|            | 3       | 27            | 10                |
|            | 4       | 29            | 4                 |
| 10.11.2011 | 1       | 16            | 12                |
|            | 2       | 19            | 29                |
|            | 3       | 37            | 19                |
|            | 4       | 61            | 15                |
| 22.03.2012 | 1       | 9             | 0                 |
|            | 2       | 7             | 4                 |
|            | 3       | 11            | 18                |
|            | 4       | 15            | 27                |
| Total      |         | 452           | 186               |

Section 4 was first implemented in the study 06.05.2011.

The biological and ecological status in Hovinbekken is not good, but varies along the stream gradient. Ecological status indices that use data abundance on mayflies (Ephemeroptera), stoneflies (Plecoptera), caddies flies (Trichoptera (EPT taxa)), and average pollution tolerance for benthic invertebrates (ASPT index) showed decreasing biodiversity and increasing pollution downstream the system (Bækken, Bergan, Eriksen, & Lund, 2011). Biological (algae) and chemical analysis (phosphorus and nitrogen) show similar results (Beschorner, 2010). Water quality can therefore be seen as a chemical barrier for downstream movements to Akerselva, supported by no detection of brook charr in the southernmost station measured by Bækken et al. (2011).



**Figure 1.** Study system (mostly underground and not seen) with specific study stations. Top left: Overview map of southern parts of Norway with Oslo marked in red square. The river to the left of Hovinkbekken is the more known Akerselva.

### 2.1.1 Bekkedalen north (station No1)

The uppermost station (UTM 32 (N, E) 6646880, 0601721), located at an altitude 185 meters above sea level, and with the steepest stream gradient (2.6°). The 44.9 meter long stretch (119 m<sup>2</sup> total area) is surrounded by a unique valley consisting of deciduous species requiring warm and mild climate such as hazel,



**Figure 2.** Bekkedalen north, station No1.

elm, and ash, but also more typical species for the area, birch, spruce, and pine (75 % canopy cover). Bekkedalen north is a natural system (Figure 2) with well conserved riparian vegetation, though not more than 6 pieces of woody debris was found in the wetted part.

**Table 2.** Habitat classification, Bekkedalen north, station No1.

| Variables                    | Pools                 | Riffles               | Undercut banks       |
|------------------------------|-----------------------|-----------------------|----------------------|
| Numbers                      | 4                     | 3                     | 2                    |
| Mean length (m)              | 2.25 ± 0.38 SD (n=4)  | 11.97 ± 8.83 SD (n=3) | 1.5 ± 0.85 SD (n=2)  |
| Mean width (m)               | 2.93 ± 0.59 SD (n=7)  | 2.58 ± 0.65 SD (n=8)  | 0.24 ± 0.09 SD (n=7) |
| Total area (m <sup>2</sup> ) | 25.98                 | 93.41                 | 0.67                 |
| Mean depth (m)               | 0.32 ± 0.12 SD (n=12) | 0.15 ± 0.07 SD (n=15) |                      |
| Max depth (m)                | 0.47                  | 0.28                  |                      |

**Table 3.** Substrate classification, Bekkedalen north, station No1.

| Substrate  | Percent |
|------------|---------|
| 0.1-10 cm  | 50      |
| 10.1-30 cm | 20      |
| >30 cm     | 30      |



### 2.1.2 Bekkedalen south (station No2)

Located upstream the highly trafficked road Trondheimsveien (UTM 32 (N, E) 6646701, 0601738). The station is at an altitude 171 meters above sea level, and stream gradient is 1.9°. The stretch is 87.5 meters long (190 m<sup>2</sup> area), including a 29.8 meter long side channel (riffle) with limited large fish habitat. Riparian conditions are similar as for Bekkedalen north (75 % canopy cover), but with significant more woody debris (30 pieces). Out of 6 smaller woody debris jams, one creates a larger dammed pool (Appendix 2B), with the deepest single depth registered at all stations (Table 4). Similar as for station No1, 50 % of the substrate is sand and small gravel (Table 5). The stream enters a culvert visually low in gradient, medium sized in length (Appendix 3C), and with low outlet hang. Though, low water depth, no substrate, and elevated velocity caused by a narrow culvert width (Appendix 4D), probably makes the culvert only passable downstream.



**Figure 3.** Bekkedalen south, station No2.

**Table 4.** Habitat classification, Bekkedalen south, station No2.

| Variables                    | Pools                 | Riffles               | Undercut banks       |
|------------------------------|-----------------------|-----------------------|----------------------|
| Numbers                      | 6                     | 6                     | 4                    |
| Mean length (m)              | 2.98 ± 2 SD (n=6)     | 11.61 ± 9.48 SD (n=6) | 1.5 ± 0.31 SD (n=4)  |
| Mean width (m)               | 2.44 ± 0.9 SD (n=8)   | 1.91 ± 0.59 SD (n=18) | 0.28 ± 0.1 SD (n=11) |
| Total area (m <sup>2</sup> ) | 47.47                 | 142.25                | 1.96                 |
| Mean depth (m)               | 0.35 ± 0.12 SD (n=17) | 0.13 ± 0.07 SD (n=31) |                      |
| Max depth (m)                | 0.55                  | 0.35                  |                      |

**Table 5.** Substrate classification, Bekkedalen south, station No2.

| Substrate  | Percent |
|------------|---------|
| 0.1-10 cm  | 50      |
| 10.1-30 cm | 20      |
| >30 cm     | 30      |

### 2.1.3 Brobekk (station No3)

The stream flows through a residential area (UTM 32 (N, E) 6646395, 0601732), at an altitude of 152 meters above sea level, with a 1.04° stream gradient. The 52.5 meter long stretch (102 m<sup>2</sup> area) are surrounded by a narrow riparian buffer zone, and the vegetation is less diverse than in station No1 and No2, including alder,



**Figure 4.** Brobekk, station No3

chestnut, birch, and some conifers, and smaller shrubs (45 % canopy cover). In total five pieces of woody debris was found. Frequent repeated sequences of pools and riffles are found in this stretch (Table 6), and substrate sizes are close to evenly distributed of different size classes (Table 7). Brobekk is the only station having a tributary potential function as refugia. Height difference between station No3 and No4 indicates that brook charr not are able to move upstream the longest and steepest culvert (there are several culverts between these stations).

**Table 6.** Habitat classification, Brobekk, station No3.

| Variables                    | Pools                 | Riffles               | Undercut banks        |
|------------------------------|-----------------------|-----------------------|-----------------------|
| Numbers                      | 6                     | 6                     | 4                     |
| Mean length (m)              | 3.59 ± 1.37 SD (n=6)  | 5.16 ± 3.07 SD (n=6)  | 1.63 ± 0.49 SD (n=4)  |
| Mean width (m)               | 1.89 ± 0.64 SD (n=11) | 1.99 ± 0.64 SD (n=14) | 0.28 ± 0.05 SD (n=10) |
| Total area (m <sup>2</sup> ) | 39.1                  | 62.93                 | 1.79                  |
| Mean depth (m)               | 0.26 ± 0.06 SD (n=17) | 0.12 ± 0.05 SD (n=21) |                       |
| Max depth (m)                | 0.35                  | 0.21                  |                       |

**Table 7.** Substrate classification, Brobekk, station No3.

| Substrate  | Percent |
|------------|---------|
| 0.1-10 cm  | 40      |
| 10.1-30 cm | 30      |
| >30 cm     | 30      |

#### 2.1.4 Risløkka (station No4)

At the last station (UTM 32 (N, E) 6645688, 0601524), the stream flows through an urban neighborhood (including park-landscape, houses and a road). The stretch is 99.4 meters in length (224 m<sup>2</sup> area) and contains few, but large pools (Table 8).



Figure 5. Risløkka, station No4

Sand and small gravel dominates the substrate (Table 9). Stream gradient is low (0.42°), and at an altitude of 117 meters above sea level. The riparian corridor is less developed than in the three other stations (some alder, birch, conifers and shrubs, 10 % canopy cover in total), and runoff, and erosion from the riverbank is therefore more likely to occur (Figure 5). Not surprisingly no woody debris was found in the stream channel. Partly embankment of the riverbank (Appendix 5E) makes the stream flow more controlled and channelized, resulting in loss of natural excavation. Still the channel is slightly meandering.

Table 8. Habitat classification, Risløkka, station No4.

| Variables                    | Pools                 | Riffles               | Undercut banks    |
|------------------------------|-----------------------|-----------------------|-------------------|
| Numbers                      | 4                     | 3                     | 3                 |
| Mean length (m)              | 9.15 ± 2.57 SD (n=4)  | 20.93 ± 14.8 (n=3)    | 1.63 ± 0.93 (n=3) |
| Mean width (m)               | 2.61 ± 0.87 SD (n=10) | 2.1 ± 0.56 (n=12)     | 0.34 ± 0.13 (n=7) |
| Total area (m <sup>2</sup> ) | 96.78                 | 127.02                | 1.62              |
| Mean depth (m)               | 0.31 ± 0.08 SD (n=17) | 0.13 ± 0.06 SD (n=20) |                   |
| Max depth (m)                | 0.5                   | 0.19                  |                   |

Table 9. Substrate classification, Risløkka, station No4.

| Substrate  | Percent |
|------------|---------|
| 0.1-10 cm  | 65      |
| 10.1-30 cm | 30      |
| > 30 cm    | 5       |

## 2.2 Study species

Brook charr (Figure 6) is a salmonid species of North American origin (Hesthagen & Sandlund, 2007). It occurs in a large variety of water environments, including streams, and are often found in the uppermost part of a watershed (Jonsson, 2006). It is a rock-and gravel nester (Jonsson, 2006), shown to prefer deep and low flow sites for spawning (Cucherousset, Aymes, Poulet, Santoul, & Céréghino, 2008; Essington, Sorensen, & Paron, 1998). It spawns in autumn (Grande, 1964), normally around 12-25 cm long (Jonsson, 2006), and has an iteroparous life strategy (Letcher et al., 2007). Brook charr has the potential to be either anadromous or resident (Carlson, Hendry, & Letcher, 2007), territorial or not (Grant & Noakes, 1988), and even within systems it shows tremendous variation in mobility (Gowan & Fausch, 1996; Hutchings & Gerber, 2002; Riley, Fausch, & Gowan, 1992). Normal size is 25-30 cm, 150-250 gram (Jonsson, 2006), and growth can be affected by multiple density dependent and density independent factors such as, microhabitat and food availability (Fausch, 1984), intraspecific competition (Marchand & Boisclair, 1998), and density (Utz & Hartman, 2009), and stream flow (Xu et al., 2010a) and temperature (Drake & Taylor, 1996; Xu et al., 2010a). Regarding habitat requirements, Sotiropoulos, Nislow, and Ross (2006) found pools and low-velocity locations to be important during summer. In winter, pools (Cunjak & Power, 1986), often containing woody debris (Meyer & Gregory, 2000), have shown to be preferred habitats, while different preferences in velocity and substrate size during summer and autumn are described for different age classes by Johnson et al. (2011). Even though pools seem like a key habitat, habitat heterogeneity seem of great importance for brook charr, since it at least to some degree require different microhabitats under different conditions and seasons.





**Figure 6.** Largest brook charr (in weight) caught during field work (32.3 cm, 384 gram).

Brook charr was introduced in Norway during two main periods, late 19<sup>th</sup>-early 20<sup>th</sup> century, and in 1970s-80s. Today it has a restricted distribution centered around south/south-east parts. The second introduction round was motivated by acidification problems in southern parts of Norway. Many brown trout populations got extinct during this period and brook charr, that tolerates lower pH than brown trout, was introduced in order to maintain fish populations even in acidified systems (Hesthagen & Sandlund, 2007). Even though the species has existed in our fauna for a while, we know surprisingly little about its biology under Norwegian conditions.

Brook charr is the only species registered in the study system over the last decade (Bremnes & Saltveit, 2002; Bækken et al., 2011). This species has probably been present in allopatry since the 1970s, and has most likely spread naturally from the upper part of the watershed over time.

## 2.3 Data Sampling

A total of 528 brook charr individuals were caught using electroshocking (Steinar Paulsen: 1983 FA2 No. 7, 700/1400 volt, 35-70 Hz, pulsed-DC). Out of three electroshocking gears described, this gear caused least harm to the fish (Forseth & Forsgren, 2008). Both catchability and injury depends on environmental factors (Forseth & Forsgren, 2008). For brook charr specifically, electrofishing have shown low mortality (Riley et al., 1992), but also to cause injuries with increasing length (Hollender & Carline, 1994). Larger fish has also been found to have higher catchability (Borgström & Qvenild, 2000), a pattern tested in my study (see chapter 3.2 and 4.1). Regarding behavioral responses, Gowan and Fausch (1996) found no significant change in brook charr movement after electroshocking.

All sections were passed once at each occasion, in an upstream direction. Three persons with dip nets were strategically placed in the locality (Figure 8). The captured fish were temporarily held in plastic buckets at low densities to minimize stress. Water was changed regularly to maintain satisfactory oxygen levels (external oxygen supply was also added).

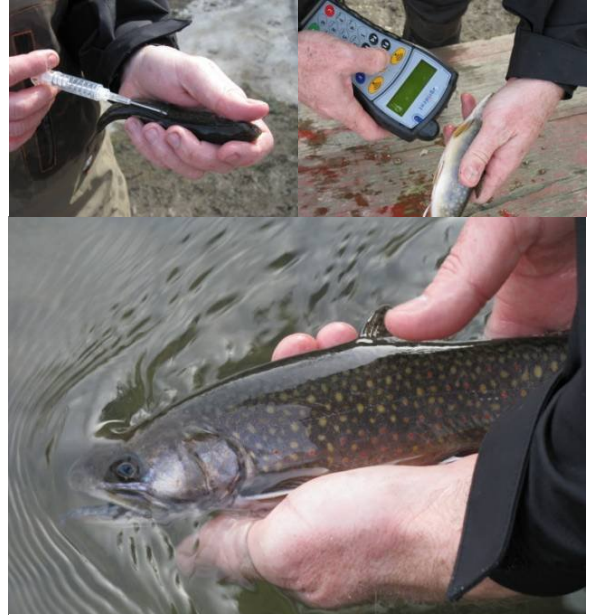


Figure 7. Handling procedure during fieldwork.



Figure 8. Electroshocker (me), supervisor, and study colleague searching for brook charr in station No3.

After capture, the fish was anaesthetized with benzokain, before an individual Passive Integrated Transponder (PIT) tag was surgically implemented. Only fish larger than 70 mm were tagged, either in the dorsal muscle (individuals >80mm), or in the body cavity (individuals <80mm). Two different PIT tags was used, Biomark HPT12 (12.5 MM 134.2 kHz ISO FDXB), and OregonRFID (9 MM 134.2 kHz ISO FDXB). The scanners used to identify individual codes during recapture, were a handheld Biomark FS2001F-ISO, and a handheld FDX reader for the OregonRFID tags (immobilization not needed). At three occasions the two scanners seemed to disturb each other, resulting in unidentifiable codes.

PIT tag procedure is a well known and described method. Ombredane, Bagliniere, and Marchand (1998) found a low percentage of tag loss on brown trout, while Dieterman and Hoxmeier (2009) results showed a higher loss proportion on both brown trout and brook charr. More specifically for brook charr, tag positioning had a significant effect, with 100 % retention for marks in the dorsal muscles, and 70% retention in the body cavity. Ombredane et al. (1998) and Prentice, Flagg, and McCutcheon (1990) did not detect any significant effects on growth and survival of tagged salmonids. In addition, Prentice et al. (1990) found no negative PIT tag effects on swimming behaviour.

During handling time, length (total length), weight (to the nearest gram), and sex (when possible), were determined, for further statistical analyses. Sex was determined by external characterizations mainly during fall sampling occasions (time period when maturation stage most consistently can be determined), i.e., close to/after spawning.

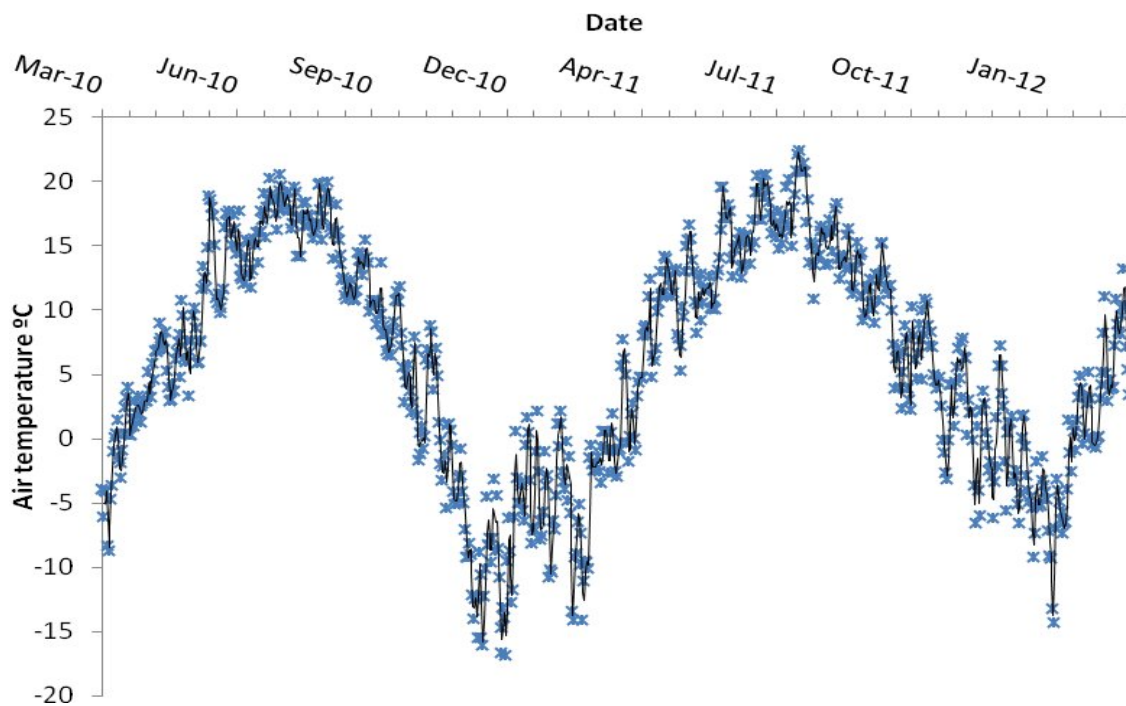
After recovery, all individuals were released to the same stream unit as they were caught. One fish only was documented dead due to sampling and handling stress.

A GPS (GARMIN 60CSx) was used for measuring height specifications (source of error), coordinate specification, and to be certain that the same area was electrofished at each sampling period. Start and endpoints were defined according to natural transition points, either because of artificial constructions (culverts), or in the transition zone where one channel reach naturally turned into another.

Map over the study system was made by the use of ARCGIS, version 10 (FKB data). Since the system more or less runs in culverts underground, only parts of the system are visual (Figure 1).

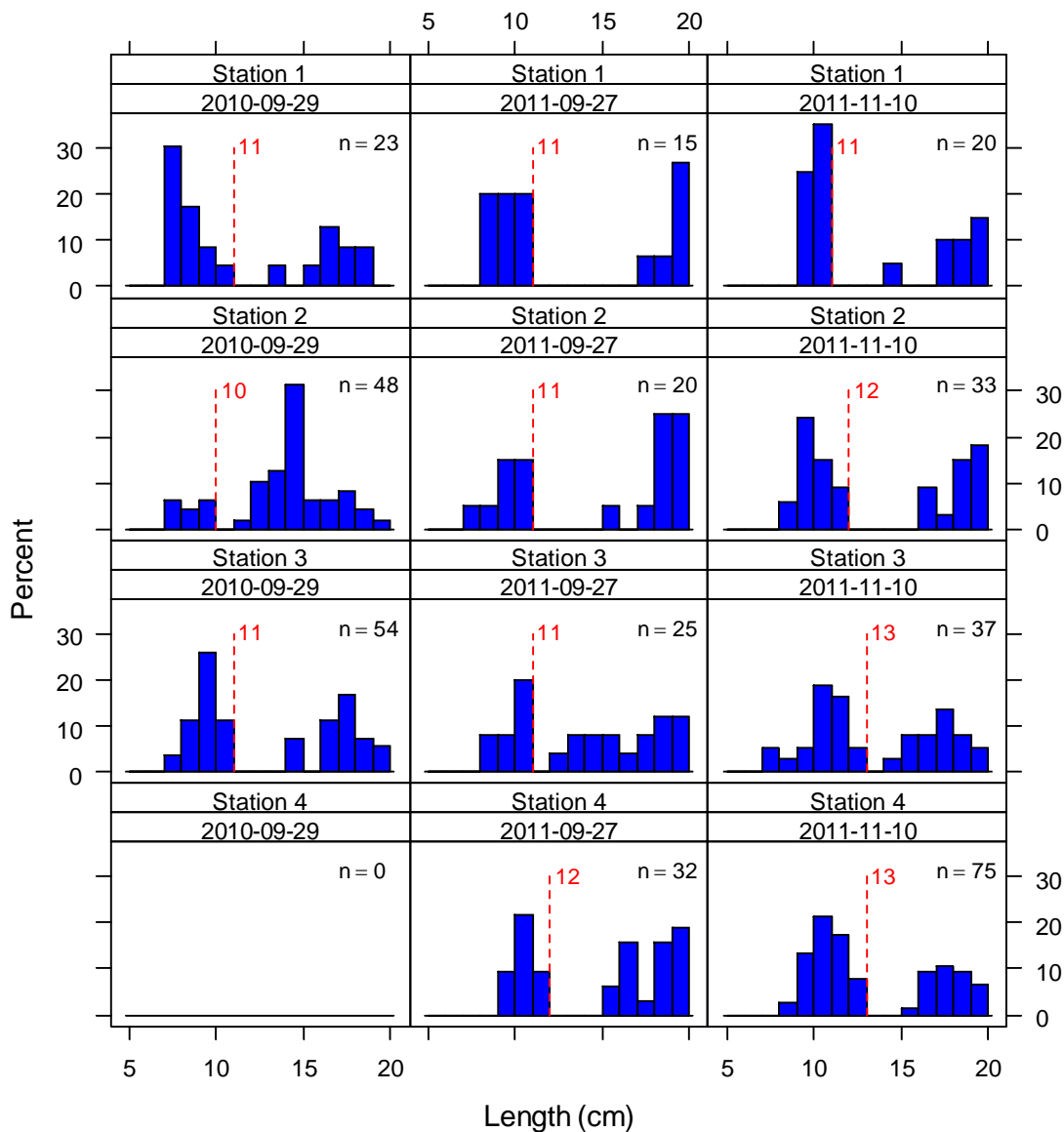
Regarding environmental variables, daily median air temperature (Figure 9) from the nearest functional weather station, Alna (Figure 1), was downloaded from meteorological institute from March 2010 to March 2012 (Meteorological Institute, 2012). Temperature for the study period was used in the individual growth rate model (recaptured individuals). Air temperature has been shown to be a good proxy for stream temperature, explaining 80-85 % of the variation in water temperature (Almodóvar, Nicola, Ayllón, & Elvira, 2012).

In addition, habitat characteristics (Table 2 – 9) were measured during March 2012. Substrate, woody debris (larger than 10 cm in diameter, and 1 meter in length), debris jam, numbers of pools, riffles, and undercut banks, canopy cover, and riparian condition were determined by visually inspection, while length, width, and depth data, were determined using tape measure and a PVC tube with markings (five centimeter intervals) from five centimeters up to two meters.



**Figure 9.** Daily median air temperature with added trendline from March 2010 to March 2012.

Age was primarily determined from the length distribution (Figure 10), and verified by inspection of otoliths (representative sample). Because of high growth variance for larger individuals, it was not possible to specifically age determine individuals older than 0+ (under yearlings). A size limit was drawn between the max length of 0+ and minimum length of 1+ (and larger), for each station and season separately. 0+ growth seemed to vary among stations and therefore site-specific upper-size limits was applied (dashed lines in Figure 10).



**Figure 10.** Length distributions for the four stations during three fall sampling rounds (2010 and 2011). Dashed lines represent upper size limits for 0+ assignments (in cm).

## 2.4 Statistics

Statistical analysis in my master thesis has been done after finding the most parsimonious model based on AIC values (Anderson, 2008; Burnham & Anderson, 2002). Models were based on ecological knowledge; all possible combinations of predictor variables have therefore not been fitted.

### 2.4.1 Capture-mark-recapture analyses

Analysis of capture-mark-recapture data was done by the use of program MARK (6.1). A multi-strata approach was used, where each individual was connected to the respective stations where it was caught by a capture history of either 1, 2, 3 or 4 in each sampling occasion. If an individual was not recaptured during a sampling occasion it was given the value zero (0 not caught, 1 caught in station No1, 2 caught in station No2, 3 caught in station No3, and 4 caught in station No4).

This use of a mark-recapture model can be illustrated in a "fate diagram" (Figure 11), where it is possible to follow various possible outcomes in a capture history from first tagging occasion  $k$  through the next tagging occasions ( $k+1$ ,  $k+2$  and so on). According to Arnason-Schwarz parameterization (Arnason, 1973), the different probability parameters can be described as follows;

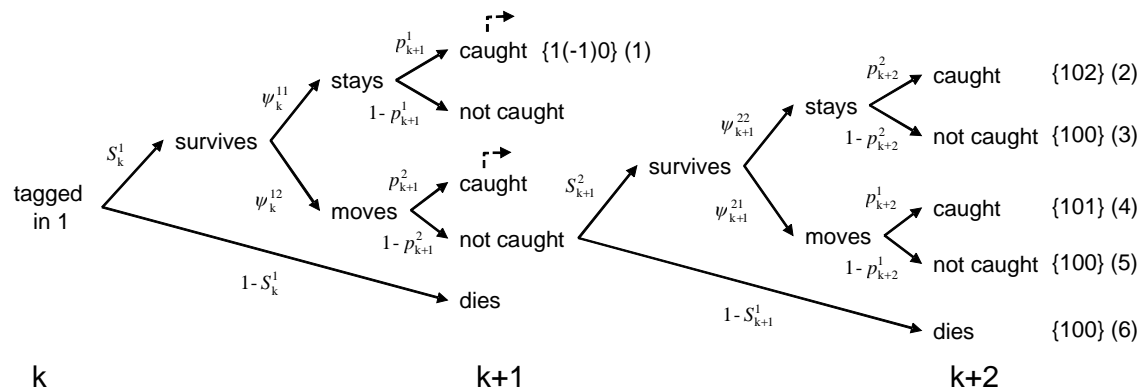
- $s_k^1$  = survival probability from  $k$  to  $k+1$  for individuals first caught in station No1.
- $\psi_k^{12}$  = dispersal probability from station No1 to No2 from  $k$  to  $k+1$ .
- $\psi_k^{11}$  = probability of staying
- $p_k^1$  = probability of being captured at  $k$

Examples of capture histories are given in brackets to the right in Figure 11; 0, not caught; 1 caught, in station No1; 2 caught in station No2; - 1 caught in station No1, and died during capture process.

The maximum-log likelihood method was applied to fit the parameters. All parameters could have been set as either constant or time-dependent during all sampling occasions, but they can



also be estimated as functions of covariates of interest. The covariates can add more ecological relevance to the model, and can both be occasion specific (e.g. temperature and density), and individual specific (e.g. size).



**Figure 11.** Fate diagram with corresponding conditional Arnason-Schwarz (CAS) parameterization.

Movements between stations were not very pronounced in my study system. When studying the movement pattern it was easily revealed that, except for two individuals, dispersal activity occurred between station No1 and No2. Because of this all other psi parameters (probability of movement) were fixed to zero.

#### 2.4.2 Other statistical analyses

All my statistical analyses were performed in R (2.14.2).

Based on recapture data, a growth analysis was fitted using generalized additive models (GAM, gam procedure in R, MGCV package), where thin-plate regression was used to look at interaction effects between multiple covariates (Wood, 2003), amongst others, temperature. In this respect did literature search not reveal any clear answers for lower temperature limit regarding brook charr growth (including Dr. Jeffrey Alexander Hutchings pers. communication). Therefore, a median air temperature of 2 °C was set in agreement with supervisor as a minimum temperature required for growth, due to brook charrs apparent preference for cold water (Schofield & Keleher, 1996).

In this method, response surface was fitted as a function of n-dimensional predictor variables where the surface complexity is selected by means of generalized cross-validation (GCV) procedures (Gu & Wahba, 1991). Hence, the parameter under estimation is estimated degrees of freedom (edf), i.e. number of surface knots.

Ordinary contingency-table based chi-square statistics (chisq.test-procedure in R) was used to explore differentiation in age distribution among stations and years.

Generalized linear models (GLM, glm procedure in R) were used to fit maturation models, where each individual was assigned 1 if mature, and 0 if immature. Estimates of length at maturation (i.e., length at 50% probability of being mature, L50) and corresponding confidence bounds were retrieved by applying the most supported GLM to the dose.LD50 procedure, (package doBY).

The maturation assignment described above (1 mature, 0 immature) was also done to test if migration was dependent on station specific density. Density was calculated by area pool instead of total area since pools are important for brook charr (Cunjak & Power, 1986; Meyer & Gregory, 2000; Sotiropoulos et al., 2006). This model was fitted because of short time span of the study, and as a consequence that density dependent migration was non-estimable in MARK. All models were fitted using logit-link and maximum likelihood method.

Analyses of 0+ size differentiation among stations and year was performed by fitting linear models, with subsequent analysis of variance (ANOVA, using the lm and anova procedures in R).

For candidate models that differed less than 4 in AICc, model averaging was undertaken (if not otherwise mentioned) using the modav procedure in the AICcmodavg library (Anderson, 2008).



### 3 Results

#### 3.1 Spatial variation in age distribution

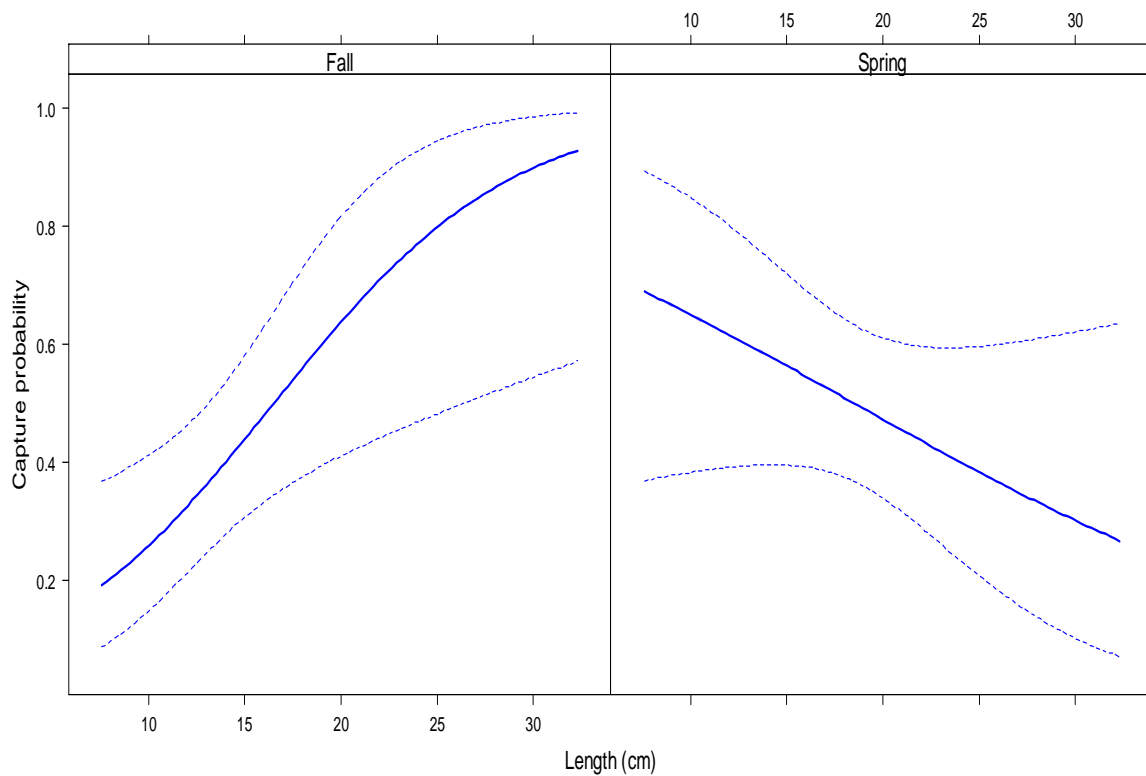
There was a significant among-station variation in age distribution during September 2010, but not in 2011 (Table 10). When pooling data from both years there was a weak significant age differentiation ( $\chi^2=9.27$ ,  $df = 3$ ,  $p = 0.026$ ). The age differentiation in 2010 could be due to over- and under-representation of age groups in respective stations (Table 10).

**Table 10.** Contingency table of September age groups in the four stations in both 2010 and 2011. Corresponding  $\chi^2$ -statistics are provided each year respectively.

| 2010    |     | Age group        |     |      |         | 2011 |      | Age group       |      |     |  |
|---------|-----|------------------|-----|------|---------|------|------|-----------------|------|-----|--|
|         |     | 0+               |     | >0+  |         |      |      | 0+              |      | >0+ |  |
| Station | obs | exp              | obs | exp  | Station | obs  | exp  | obs             | exp  |     |  |
| 1       | 14  | 8.9              | 11  | 16.1 | 1       | 9    | 8.8  | 22              | 22.2 |     |  |
| 2       | 8   | 17.4             | 41  | 31.6 | 2       | 8    | 7.7  | 19              | 19.2 |     |  |
| 3       | 28  | 23.8             | 39  | 41.2 | 3       | 9    | 10.5 | 28              | 26.5 |     |  |
| 4       |     |                  |     |      | 4       | 13   | 12   | 29              | 30   |     |  |
|         |     | $\chi^2 = 13.64$ |     |      |         |      |      | $\chi^2 = 0.46$ |      |     |  |
|         |     | df = 2           |     |      |         |      |      | df = 3          |      |     |  |
|         |     | p = 0.001        |     |      |         |      |      | p = 0.930       |      |     |  |

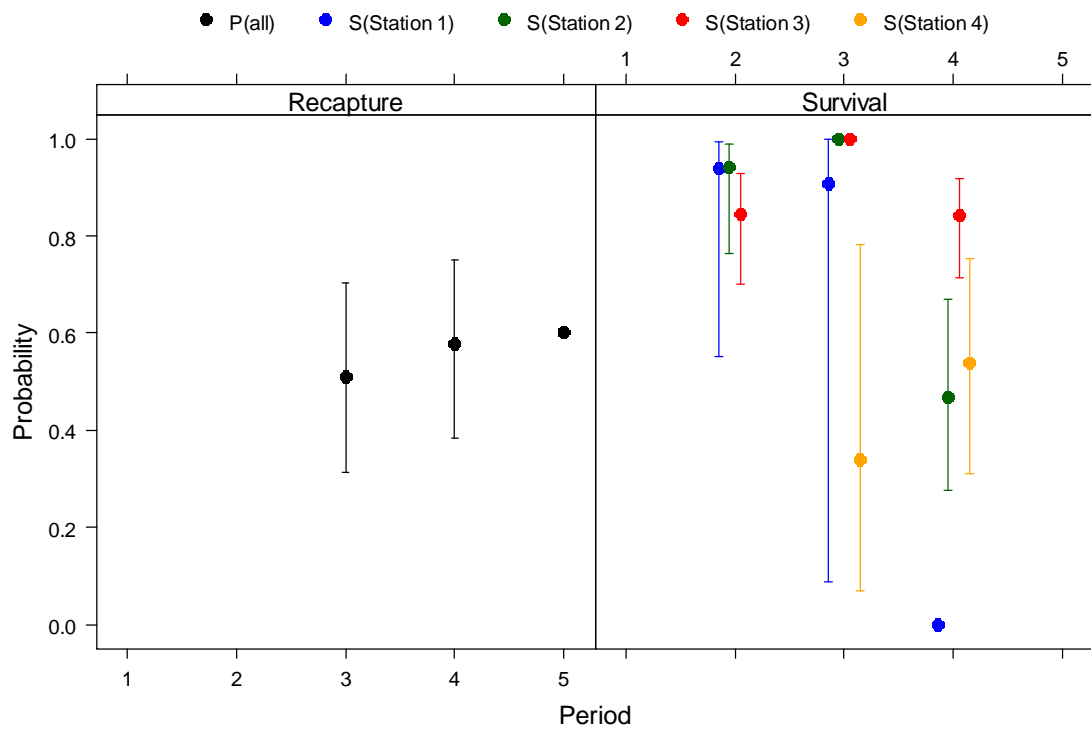
### 3.2 Spatio-temporal variation in (re)capture, survival, and migration probability

(Re)capture was most parsimoniously modeled without station effects, but varied according to sampling season and fish size; (re)capture probability increased with increasing fish size during fall sampling rounds and decreased with increasing fish size during spring sampling rounds (Figure 12).



**Figure 12.** (Re)capture probability as a function of season and brook charr size. Dashed lines represent 95% confidence bounds.

For tagging ages older than 2, recapture probability was generally high and stable (0.5-0.6), while survival probability (tagging ages older than 1) varied both between sampling seasons, and stations (Figure 13); Station No3 appears to have a high and stable survival rate, while the most pronounced change was observed from period 3 (November 2011) to period 4 (March 2012), in station No2, and especially in station No1 where apparently no tagged individuals survived over the winter. Seemingly, station No4 had a medium-low survival probability both through fall 2011 (period 2-3), and through winter 2012 (period 3- 4). Survival over winter seemed in general to be lower than during other seasons.



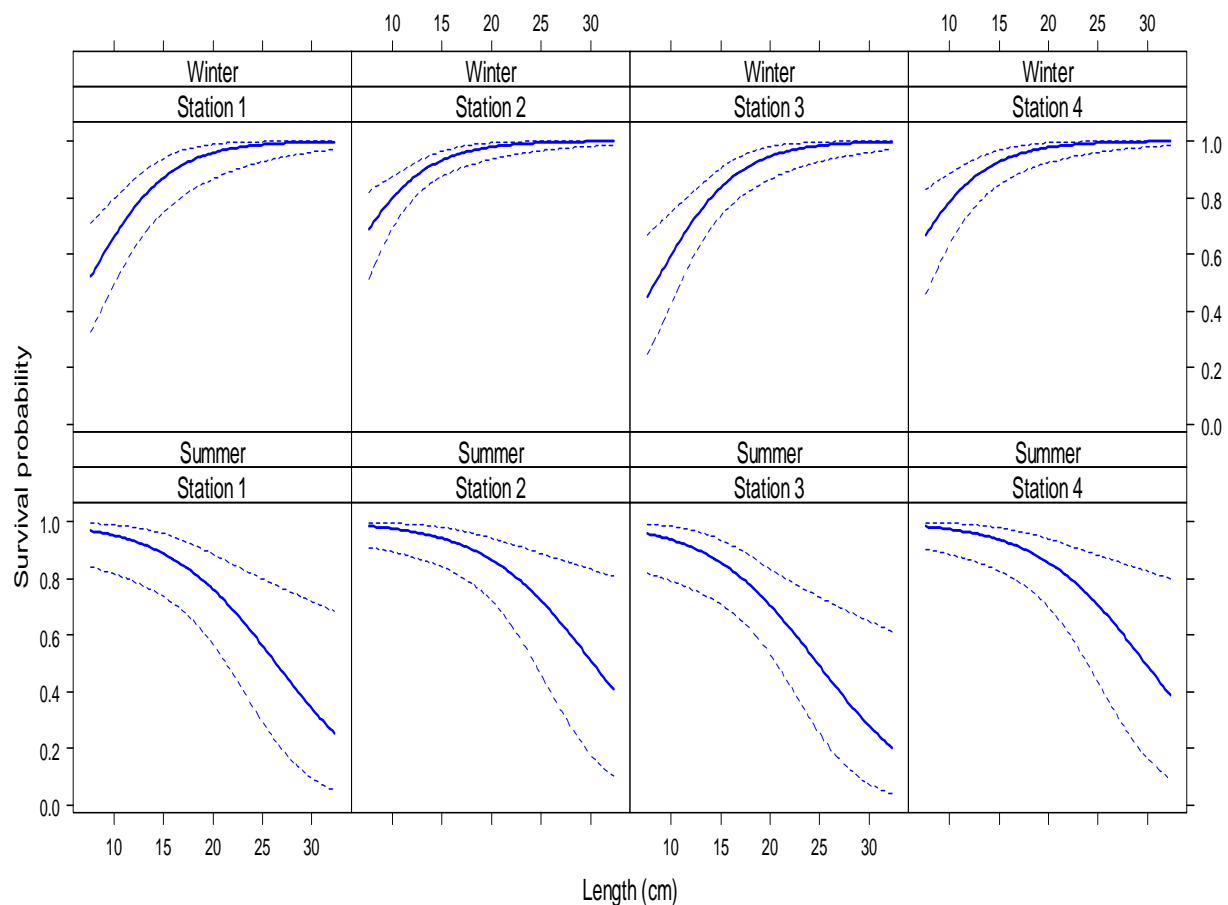
**Figure 13.** Recapture probability for tagging age >2, and survival probability for tagging age >1 (estimates following after marking periods). Error bars represent 95% confidence bounds.

The CAS model with the highest support had an AIC value that was 6.8 units lower than the second best model, and had an AIC weight of 0.88 (Table 11).

**Table 11.** Model selection table for models that had AICc weights larger than zero. np= number of parameters, St=station specific, L=individual length, t=time specific. For the psi parameters, St1 → St2 and St2 → St1 migration only were modeled as the remaining psi estimates were fixed to zero.

| Model  | AICc    | Delta AICc | AICc Weights | Model Likelihood | np | Deviance |
|--|---------|------------|--------------|------------------|----|----------|
| {S(a1(St+season*L),a2(St*t))p(a1(season*L),a2(t))psi(St*L*t)}                | 828.353 | 0.000      | 0.88273      | 1                | 26 | 773.648  |
| {S(a1(St+season*L),a2(St*t))p(a1(L),a2(t))psi(St*L*t)}                       | 835.116 | 6.763      | 0.03         | 0.034            | 25 | 782.616  |
| {S(a1(density+season*L),a2(season*density))p(a1(season*L),a2(t))psi(St*L*t)} | 835.536 | 7.183      | 0.02432      | 0.0276           | 20 | 793.936  |
| {S(a1(St+season*L),a2(St*t))p(a1(t*L),a2(t))psi(St*L*t)}                     | 836.050 | 7.697      | 0.01882      | 0.0213           | 31 | 770.190  |
| {S(a1(St+season*L),a2(St*t))p(a1(season+L),a2(t))psi(St*L*t)}                | 836.854 | 8.501      | 0.01259      | 0.0143           | 26 | 782.148  |
| {S(a1(St*season*L),a2(St*t))p(a1(L),a2(t))psi(St*L*t)}                       | 837.472 | 9.119      | 0.00924      | 0.0105           | 28 | 778.331  |
| {S(a1(St+season*L),a2(St*t))p(a1(t+L),a2(t))psi(St*L*t)}                     | 837.598 | 9.245      | 0.00868      | 0.0098           | 27 | 780.679  |
| {S(a1(density+season*L),a2(St*t))p(a1(t*L),a2(t))psi(St*L*t)}                | 838.173 | 9.820      | 0.00651      | 0.0074           | 29 | 776.801  |
| {S(a1(season*L),a2(St*t))p(a1(L, fixedSt4),a2(t))psi(St*L*t)}                | 839.656 | 11.303     | 0.0031       | 0.0035           | 22 | 793.721  |
| {S(a1(density*season*L),a2(St*t))p(a1(t*L),a2(t))psi(St*L*t)}                | 839.842 | 11.489     | 0.00283      | 0.0032           | 30 | 776.230  |
| {S(a1(density+season*L),a2(season+density))p(a1(t*L),a2(t))psi(St*L*t)}      | 843.478 | 15.125     | 0.00046      | 0.0005           | 24 | 793.175  |
| {S(a1(density+season*L),a2(season*density))p(a1(t*L),a2(t))psi(St*L*t)}      | 843.759 | 15.406     | 0.0004       | 0.0005           | 25 | 791.259  |
| {S(a1(season*L),a2(St*t))p(a1(L, fixedSt4),a2(t))psi(St*L*t)}                | 845.254 | 16.901     | 0.00019      | 0.0002           | 25 | 792.754  |
| {S(a1(density+season*L),a2(season+density))p(a1(season*L),a2(t))psi(St*L*t)} | 846.025 | 17.672     | 0.00013      | 0.0001           | 20 | 804.425  |
| {S(a1(density+season),a2(St*t))p(a1(t*L),a2(t))psi(St*L*t)}                  | 849.676 | 21.323     | 0.00002      | 0                | 27 | 792.757  |

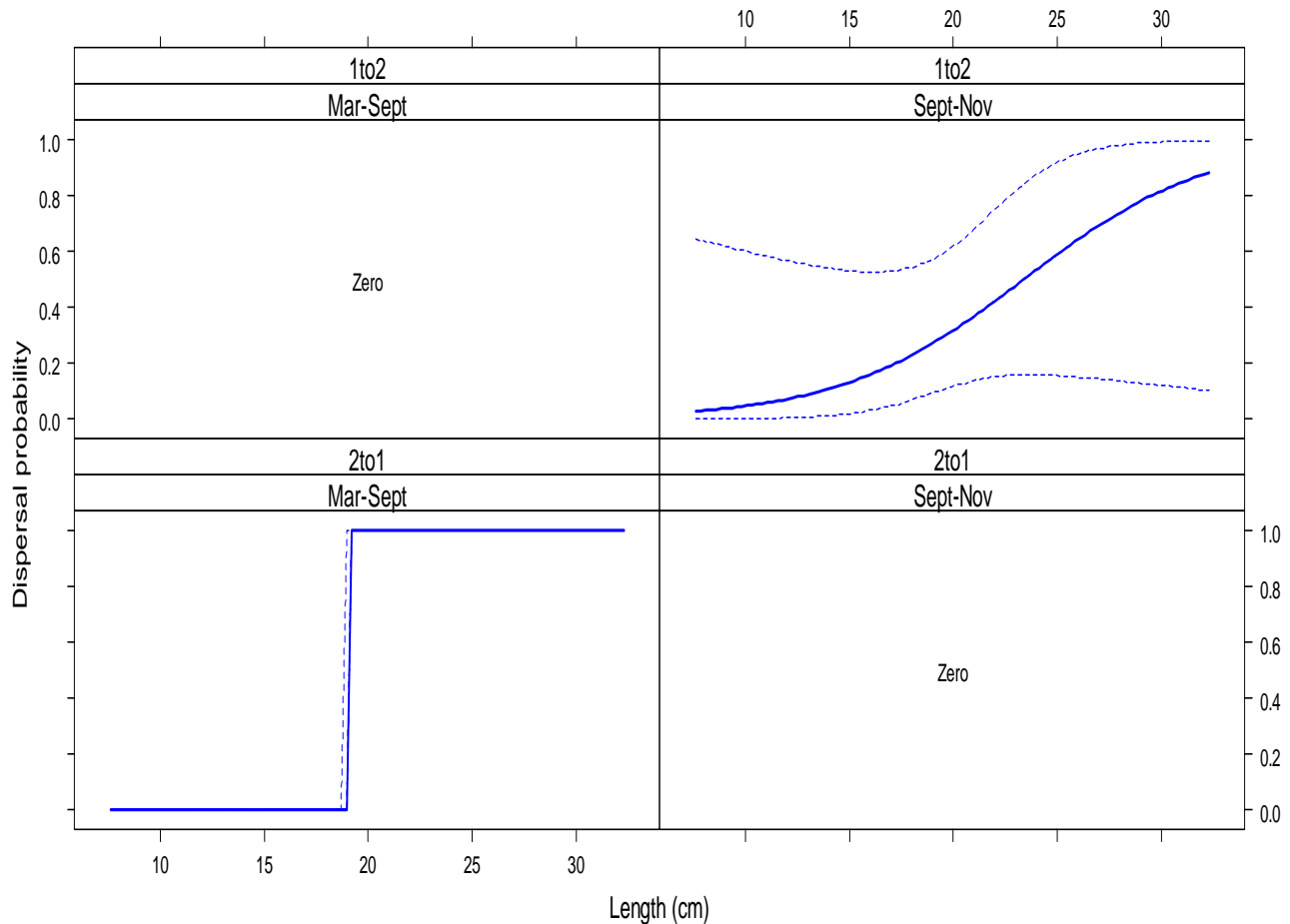
According to the most supported CAS model (Table 11), winter survival for brook charr in Hovinbekken was positively associated with fish size, while summer survival was negatively correlated with fish size (Figure 14). There was high support for among-station differentiation in size-specific survival for both winter and summer periods; smaller individuals in station No1 and No3 seemed to have lower winter survival probability than smaller individuals in station No2 and No4. Over summer, larger individuals in station No1 and No3 seemed to have lower survival probability than larger conspecifics in station No2 and No4 (Figure 14). There was little support for density dependent survival as the best model. Including density as a survival effect only received an AICc weight of 0.02 (Table 11).



**Figure 14.** Survival probability as a function of brook charr size, season, and station. Dashed lines represent 95 % confidence bounds.

In general, there was little among-station dispersal during the study period (n=8). Only two brook charr moved between artificially fragmented stations, both in a downstream direction from station No2, to station No3 and No4. As estimated from the most supported CAS-model, the most evident dispersal took place between station No2 and station No1 (Figure 15). Three individuals from station No2 ascended to station No1 during March-to-September 2011, while three individuals descended to station No2 during September-to-November 2011. Both these migration activities were positively related to fish size (Figure 15).

I found no difference in probability of migration, depending on station specific density (binomial model= $\chi^2_{1,10}=0.05$ ,  $p=0.82$ ).



**Figure 15.** Between station dispersal probabilities as a function of brook charr size and period. Dashed lines represent 95 % confidence bounds.

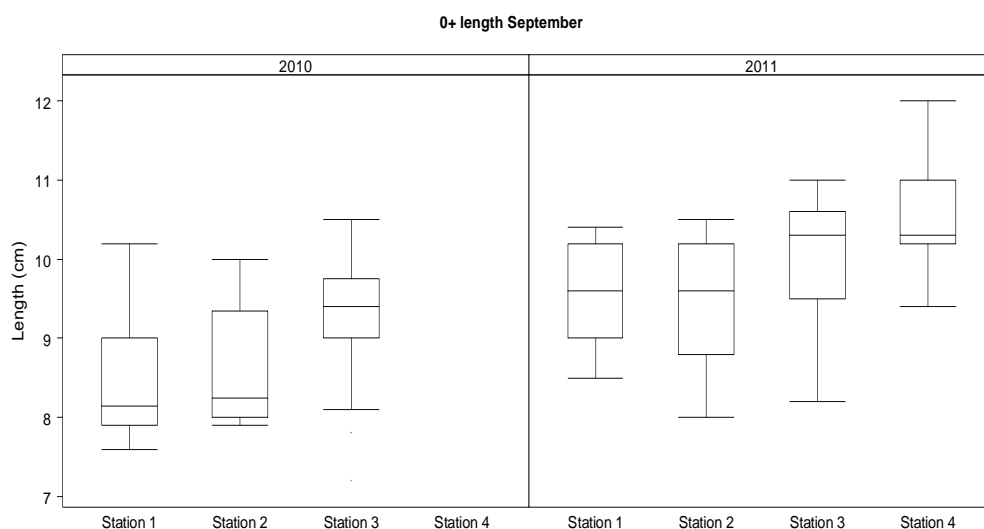
### 3.3 Spatial variation in individual growth

#### 3.3.1 Analysis of fall 0+ sizes

There was a significant difference in 0+ sizes among stations and the two years (two-way anova,  $p_{\text{station}} < 0.0001$ ,  $p_{\text{year}} = 0.0002$ ; Table 12). The linear model showed that 0+ growth was better in 2011 than in 2010. In addition, the two southernmost stations (station No3 and No4), had larger 0+ than the two northernmost stations (station No1 and No2 (Figure 16)).

**Table 12.** Parameter estimates and corresponding test statistics for the linear model testing station and year effects on September 0+ sizes. Effect levels are provided in square brackets and default level (intercept) constitutes station No1 in 2010. Model test statistics:  $F = 13.22$ ,  $df = 4/84$ ,  $p < 0.0001$ ;  $R^2 = 0.36$ .

| Parameter estimates |       |       | Test statistics |    |        |        |        |          |
|---------------------|-------|-------|-----------------|----|--------|--------|--------|----------|
| Parameter           | coef  | SE    | Term            | df | SS     | MSS    | F      | p-values |
| Intercept           | 8.583 | 0.190 | Station         | 3  | 25.403 | 8.468  | 12.393 | <0.0001  |
| Station[2]          | 0.062 | 0.270 | Year            | 1  | 10.723 | 10.723 | 15.694 | 0.0002   |
| Station[3]          | 0.685 | 0.222 |                 |    |        |        |        |          |
| Station[4]          | 1.168 | 0.313 |                 |    |        |        |        |          |
| Year[2011]          | 0.811 | 0.205 |                 |    |        |        |        |          |



**Figure 16.** Boxplot showing station-specific size distributions of 0+ during late September for both 2010 and 2011. Boxes entail 50 % of the observations; horizontal lines within boxes comprise medians, while whisker represents 10<sup>th</sup> and 90<sup>th</sup> percentiles.

### 3.3.2. Analysis of recaptured individuals

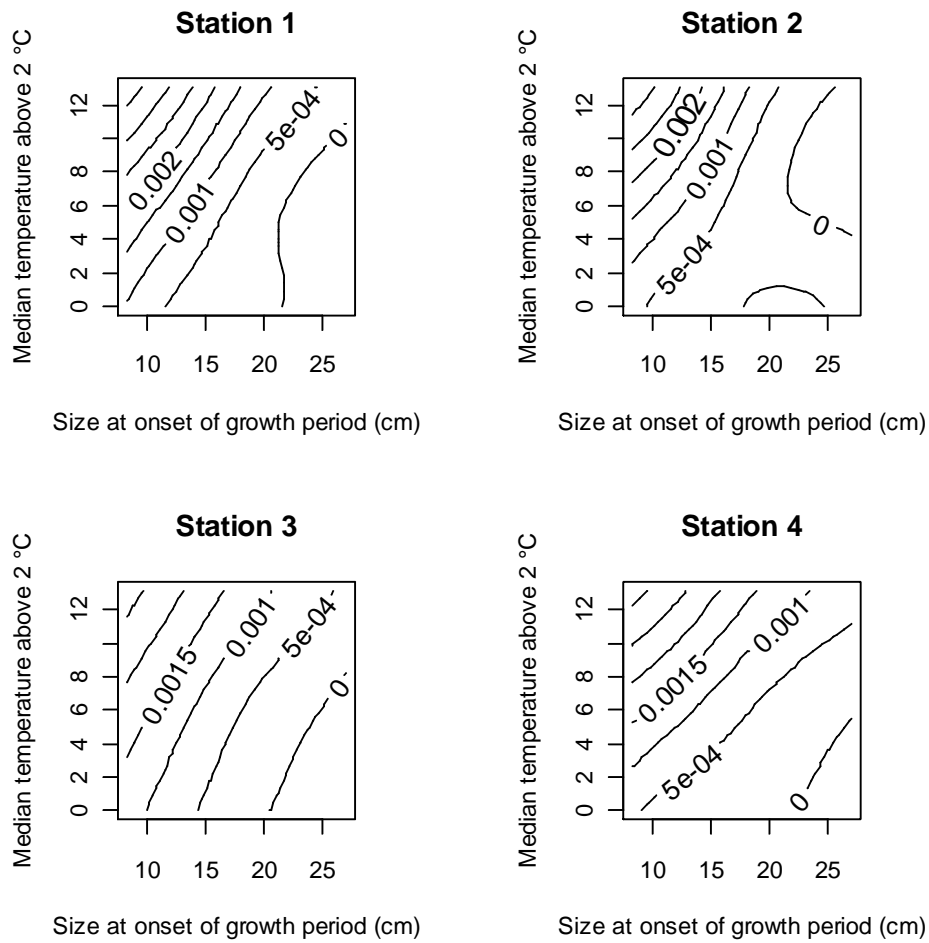
The most supported specific growth rate model showed that there was a spatial variation in growth response towards median air temperature (above 2 °C) and initial size (Figure 17). This model was only slightly better since a similar model without station effect had an AIC value just 1.2 units higher. However, model averaging was not an issue here as there were no common parameters due to all  $s(L1, \text{median temp})$  surfaces were station-specific in the most supported model. Not surprising, brook charr from all stations had very similar response pattern; specific growth rate (per day) increased with decreasing initial size, and increasing median temperature. Individuals in station No1 and No2 had faster growth in the beginning, but they seemed to stagnate at smaller lengths than individuals in station No3 and No4. Also, temperature seemed to have a higher effect on specific growth rate in station No4 than in the other stations as the growth isoclines have a less steep slope in this specific station (Figure 17).

There was no significant growth rate difference between migratory and stationary individuals during growth period (one-way anova:  $F = 0.761$ ,  $df = 1,184$ ,  $p = 0.384$ ).

**Table 13.** Parameter estimates and corresponding test statistics for the most supported GAM model fitted to predict individual specific growth rate from initial size, median air temperature above 2°C, experienced during the growth period and station. Edf = estimated degrees of freedom. The model explained 75.4 % of the deviance. The  $s()$ -notation relates to the thin-plate smoother where non-linear interaction effect among variables included in parentheses is modeled.

| Parameters                                    | Linear parameters |         | Thin-plate estimates |        | test statistics |          |
|---|-------------------|---------|----------------------|--------|-----------------|----------|
|   | coef              | SE      | edf                  | Ref.df | F               | p-values |
| Intercept                                     | 0.00067           | 0.00004 |                      |        | 15.93           | <0.0001  |
| $s(L1, \text{median temp})[\text{Station 1}]$ |                   |         | 3.599                | 3.917  | 38.2            | <0.0001  |
| $s(L1, \text{median temp})[\text{Station 2}]$ |                   |         | 3.872                | 3.991  | 26.88           | <0.0001  |
| $s(L1, \text{median temp})[\text{Station 3}]$ |                   |         | 3.245                | 3.687  | 39.71           | <0.0001  |
| $s(L1, \text{median temp})[\text{Station 4}]$ |                   |         | 3.664                | 3.941  | 21.89           | <0.0001  |





**Figure 17.** Spatial variation in specific growth rate (per day) as a function of size and median air temperature (above 2 °C). Isoclines represent the contours of the specific growth rate response.

### 3.4 Spatial variation in maturation

A generalized linear model (GLM) fitted all the fall-period data, revealed a significant effect of body length (slope =  $0.633 \pm 0.068$  SE – (logit-scale)) on probability of being mature. This over-all model for the whole population yields an expected size at maturation (i.e., when the probability of being mature is 50%) at a size of  $20.22 \pm 0.24$  (confidence bounds) cm.

The most supported maturation model (Table 14) that included size, station, and year as potential predictors of maturation, revealed an additive structure where the intercept of the size was highly differentiated among stations (i.e., Length + Station), and that the length slope varied between the two years covered by the study (i.e., Length \* Year). The model parameters along with test statistics is provided in Table 15 and model predictions are displayed in Figure 18; i. e. the two southernmost stations (station No3 and No4) showed a probability of maturation at longer lengths for both years compared to the two northernmost stations (station No1 and No2).

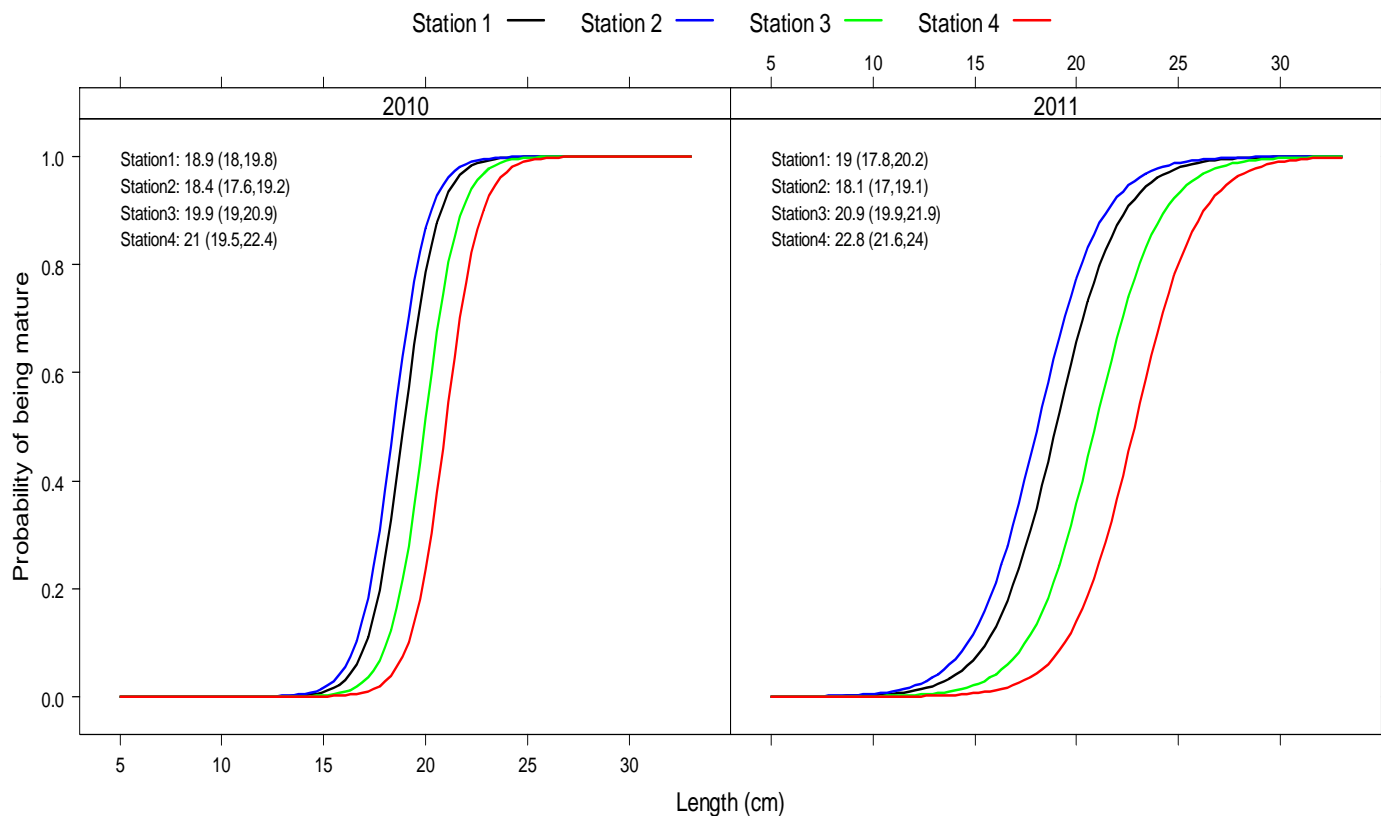
**Table 14.** Ordered AIC-table showing the AIC-support for fitted maturation models (logit-models). Response is a binominal variable whereas 1 denotes “mature” and 0 “immature”.

| Model structure     | df | AICc   | $\Delta$ AICc | AICcWt | LogLikelihood |
|---------------------|----|--------|---------------|--------|---------------|
| Length*Year+Station | 7  | 240.34 | 0             | 0.61   | -113.05       |
| Length+Station      | 5  | 242.41 | 2.07          | 0.22   | -116.14       |
| Length+Station+Year | 6  | 244.43 | 4.09          | 0.08   | -116.13       |
| Length*Station      | 8  | 244.51 | 4.17          | 0.08   | -114.11       |
| Length+Station*Year | 8  | 247.78 | 7.44          | 0.01   | -115.74       |
| Length*Station*Year | 14 | 250.64 | 10.3          | 0      | -110.89       |
| Length*Year         | 4  | 283.85 | 43.52         | 0      | -137.89       |
| Length              | 2  | 284.07 | 43.73         | 0      | -140.02       |

**Table 15.** Logit parameter estimates (some are model averaged according to AICc weight in table 14) and corresponding likelihood ratio test statistics for the most supported (see Table 14) GLM fitted the maturation data. p-values have been derived under the assumption that term-specific deviances are  $\chi^2$ -distributed (Hastie & Pregibon, 1992).

| Parameter estimates |          |       | LRT test statistics |    |          |     |           |          |
|---------------------|----------|-------|---------------------|----|----------|-----|-----------|----------|
| Parameter           | Estimate | SE    | Term                | df | Deviance | df  | Residuals | p-values |
| Intercept           | -22.556  | 4.761 | Length              | 1  | 287.81   | 500 | 280.05    | <0.0001  |
| Length              | 1.05*    | 0.31* | Year                | 1  | 0.25     | 499 | 279.79    | 0.614    |
| Year[2011]          | 9.11*    | 5.83* | Station             | 3  | 47.53    | 496 | 232.26    | <0.0001  |
| Station[2]          | 0.586    | 0.499 | Length*Year         | 1  | 6.15     | 495 | 226.11    | 0.013    |
| Station[3]          | -1.236   | 0.496 |                     |    |          |     |           |          |
| Station[4]          | -2.471   | 0.556 |                     |    |          |     |           |          |
| Length*Year[2011]   | -0.55*   | 0.27* |                     |    |          |     |           |          |

\*model averaged



**Figure 18.** Prediction plot of the probability of being mature as a function of brook charr size, station and year. The predictions have been retrieved from the GLM-logit model presented in Table 15. Numbers displayed in the figure represent station- and year-specific size at maturation estimates ( $\text{Pr}(\text{mature})=0.5$ ) with corresponding confidence bounds.

## 4 Discussion

There was in general little spatial movement, and the only dispersal activity through natural and man-made barriers took place in a downstream direction; i.e. *<sup>a</sup>the degree of local-scale connectivity, including both natural- and man-made barriers, influenced migration probability in Hovinbekken.*

Growth, survival, and length at maturation varied at a temporal and spatial scale and were attributed to *<sup>b</sup>local-scale influence on within- stream section environmental conditions.* Based on this data, my hypotheses were confirmed.

### 4.1 (Re)capture probability

The recapture probability was consistently high. (Re)capture probabilities increased with increasing brook charr size during fall sampling rounds, while the opposite pattern was seen during spring. Only the fall pattern is consistent with general findings (Borgstrøm & Qvenild, 2000). One potential explanation for the observation could be a temperature related change in behaviour; i. e. concealment behaviour (Meyer & Gregory, 2000) when water is cold (spring), and that larger individuals acts more bold close to spawning.

The importance with these findings is their discovery, since patterns like this in general needs to be accounted for to obtain reliable results.

### 4.2 Migration

Consistent with other findings (Gowan & Fausch, 1996; Kanno, Vokoun, & Letcher, 2011; Riley et al., 1992; Rodríguez, 2002) brook charr in Hovinbekken consists of both sedentary and migratory individuals. In total 8 out of 143 tagged brook charr individuals were found to perform movement between stations. Isolated, a stationary and immobile life style seems to be most common, consistent with the “restricted mobility paradigm” (Gerking, 1959; Gowan, Young, Fausch, & Riley, 1994). Though, the study design makes total control of movement impossible as a proportion of the tagged individuals was not recaptured (Figure 13). In addition to mortality, this could be due to faulty equipment (i.e. mark loss, see chapter 2.3), or emigration from the system. There is therefore not unreasonable to suggest that there is, at least to a point, a higher degree of mobility in Hovinbekken than detected.

The migration activity from station No2 to station No1 (no natural or artificial barriers) are most likely related to spawning. Upstream spawning migration is consistent with both general (Lucas & Baras, 2001), and more specific findings for brook charr (Kanno et al., 2011). The probability of dispersal increased drastically with size (Figure 15), i. e. mature fish seemed more prone to move. In total three brook charr individuals moved in an upstream direction, before late September 2011 (brook charr spawning season is in September-October (Jonsson, 2006)).

Since this migration pattern most likely is fitness-related, I believe brook charrs apparently restricted mobility is not due to a selection against migration; individuals moving furthest upstream a system will probably have the potential to distribute their offspring more evenly through the system (i.e. flushed downstream during spring flow).

No evidence of density dependent migration was found. Density effects on migration can however not be disregarded as my study covers too short a time span for drawing general inferences with respect to density effects. In addition, it is important to correctly distinguish between the functional habitat available and the actual habitat utilized by brook charr when testing for density effects.

Available spawning substrate seemed to be similar for the two stations in question (Table 3 and 5), while the amount of deeper areas which has shown to be used by brook charr regarding spawning (Essington et al., 1998), actually seemed to be better in station No2 (Table 2 and 4, Appendix 2B). It therefore seems unlikely that, regarding habitat features, station No1 is more suitable for spawning. More likely, it could be explained by more groundwater supply into the system, which is also considered to be an important factor regarding brook charr spawning (Essington et al., 1998); the amount of groundwater input in station No1 is not known, but during the last sampling round, survival was drastically reduced (Figure 13); owing to clear evidence of iron precipitation in groundwater springs dredging into station No1 and No2 (Appendix 7G), I believe the apparently high mortality may be due to oxidation of iron (II), a highly toxic phenomenon associated with groundwater (Teien, Garmo, Åtland, & Salbu, 2008), and that, if this acts at a local scale, station No1 would have a higher groundwater supply (no tagged individuals survived in station No1, while only a reduction in survival was seen in station No2 during last sampling round).

If station No1 has higher spawning ground qualities, I would in the first place expect to find more 0+ individuals there during fall sampling rounds. On the other side, station No2 is

larger, and has a more heterogeneous environment (i.e. cover) important for younger brook charr (Johnson et al., 2011). The number of 0+ observed did not vary much over years in these two specific stations; though in both 2010 and 2011, station No1 had more 0+, both than expected, and compared to station No2 in total (Table 10). This could be due to chance (i. e. striking evidence for age differentiation over years), but when taking station size into account, I find it more likely that it is because station No1 is a preferred spawning habitat.

A potential explanation for why spatial variation in recruits was not more evident could be due to high juvenile density dependent mortality caused by restricted mobility at an early life stage, or dispersal later in the juvenile stadium as a response of high density, as shown for Atlantic salmon (Einum et al., 2006; Finstad, Einum, Sættem, & Hellen, 2010). I find the first explanation most likely, because of brook charr's apparently stationary life style.

Between late September and mid November 2011 three brook charr individuals moved downstream from station No1 to station No2. As for the upstream migration, a positive relationship with fish size was evident (less steep slope, Figure 15). I therefore suggest that station No2 is a better overwintering area; a large, and deep (largest depth registered, Table 2) debris dam pool (Appendix 2B) was present in station No2 during the study period. In contrast with other pools in station No1 and No2, I find this pool to be more suitable as refugia because of its heterogeneous environment, its size, and its potential to maintain sufficient water amount even during low flow. This is strengthened with the observation that station No2 seemed to have higher winter survival probability for smaller brook charr than station No1 (Figure 14), and further supported by findings that stream depth (Kanno, 2010), and pools (Cunjak & Power, 1986; Sotiropoulos et al., 2006) are important habitats. Even though no density effects on survival was found, I believe competition-related mortality due to limitation in suitable pools during harsh conditions is more likely to occur in station No1, and that smaller individuals during winter pays the price; brook charr will most likely increase its aggressiveness when needed.

The two individuals moving through culverts moved in a downstream direction (from station No2 to station No3 and No4), centering all migratory behaviour in station No2. The observation could possibly be due to chance, but other causes cannot be disregarded. More importantly it shows how brook charr are able to recolonize areas downstream if necessary. Kanno et al. (2011) found that presence of barriers probably affected the direction of movement. Therefore, a one-way movement may indicate that culverts act as physical

upstream barriers for brook charr. Though, both the culvert (Appendix 3C & 4D), and the natural fall downstream station No2 (Appendix 6F), are most likely physical barriers; upstream movement has therefore most likely never existed in this part of the stream.

### 4.3 Life history traits

Analyses of fall 0+ sizes revealed that brook charr was larger in 2011 than in 2010 (Table 12, Figure 16). The age distribution model (Table 10) detected in total more brook charr in September 2010 than in September 2011. Though, station No2 had exactly the same 0+ September density over years, and still fall size was larger in 2011. Inter-cohort competition, as documented in Hagstrøm (2012), seems in the first place like a more likely explanation. Though, longer time series is needed, and the apparently slightly higher size-independent density in station No1 2011 compared to 2010, leads me over to another possible explanation for the observed growth differences.

Temperature has been found to affect brook charr growth (McCormick, Hokanson, & Jones, 1972.; Xu et al., 2010a). While Drake and Taylor (1996) did not find any significant change in 0+ growth in relation to spring temperature, Ries and Perry (1995) and Xu et al. (2010a) revealed that an increase in spring temperature may increase individual growth rate in general. When looking into air temperature data, 2011 had a higher spring temperature (March-to-May), than 2010, with the most pronounced temperature difference in April (average daily median temperature 3.6° higher in 2011). In addition, the growth rate model (Figure 17) revealed that specific growth rate increased with both increasing temperature and decreasing size.

I believe temperature, as a density independent factor, explains how brook charr in Hovinbekken may have gotten a head-start (early hatching, longer growth season) in 2011 compared to 2010, which resulted in larger individuals during fall; Observation of a newly hatched brook charr already during last sampling round in the extraordinary warm March 2012 supports this hypothesis.

The two southernmost stations, No3 and No4, had larger 0+ fall sizes than the two northernmost ones. Since the same pattern was observed on a two year temporal scale (station No4 not included in 2010), this probably means that growth conditions for first growth season are somewhat better in the two low gradient reaches. Both these stations have less developed

riparian vegetation (higher water temperature expected (Degerman, 2008)), and perhaps less groundwater supply (colder water). When modeling, temperature seemed to affect growth in station No4 more than in other stations; unless temperature exceeded the upper limit for brook charr during summer (higher metabolic costs), I believe temperature explained (at least some) of the growth variance between stations. Variables such as area pools (most in station No4), tributary junction effects (Kiffney, Greene, Hall, & Davies, 2006) as the only tributary was in station No3, and lower reach-gradients, can though not be excluded as potential explanations for the observed spatial 0+ growth differentiation.

In contrast with previous findings, and from 0+ of age, individuals in the two uppermost stations showed a faster specific growth rate than individuals in station No3 and No4 (Figure 17). This could perhaps be due to a compensatory growth response (smaller individuals shown to have higher growth rate), or perhaps just that they grow faster in a short period before stagnating as spawning-time approaches (growth stagnation seemed to occur at smaller lengths in station No1 and especially in station No2). No quantitative measures were performed regarding specific age determination using otoliths, though when studying one specific individual growth rate pattern, evidence that spawning apparently can occur from 1+ of age is evident, provided sufficient growth (individual 3D9 IBF 22A0832 captured 06.05.2011 in station No4; 14.4 cm; recaptured 27.09.2011; 23 cm; mature).

Surprisingly, even though my results suggest a higher growth rate for all stations in 2011 in addition to increased length at maturation for the two southernmost stations, the two northernmost ones exhibited approximately same lengths at maturation as in 2010 (Figure 18). Possible explanations for this could be shorter growth season, and/or differentiation in breeding regimes, with the northernmost stations exhibiting a preference for maturation at smaller sizes, i.e. less maturation size plasticity. The latter has been found in a genetically isolated brook charr population (Letcher et al., 2007).

As already mentioned, length at maturation varied between stations. Both growth and survival have been found to affect maturation patterns (Haugen, 2000; Hutchings, 1993, 1996). One should keep in mind that the survival probabilities estimated in my study can be affected by emigration, or perhaps refuge seeking. The latter is a possible reason for the seasonally stable but medium-low survival probability for brook charr in station No4 (Figure 13); brook charr were seen actively seeking into culverts (both upstream and downstream) when electroshocking, possible leading to an underestimation of survival. Such a phenomenon was



not observed in the other stations, were brook charr not caught immediately, most often were driven into the pool next to its originally stream position, and caught there.

Survival probability through winter seemed in general to be lower than through other seasons (Figure 13). The general idea has been that mortality is highest during winter (Carlson & Letcher, 2003), with larger fish having higher survival, a “paradigm” challenged by Carlson et al. (2008). Studies are inconsistent (Carlson et al., 2008), but Hutchings et al. (1999) detected varying though relatively high brook charr winter mortality, while Meyer and Griffith (1997) found higher survival for larger 0+ brook charr sizes; in my study stream winter survival showed to be positively size-dependent (Figure 14). Since larger fish in general has lower metabolic costs and higher energy reserves (Schultz & Conover, 1999), this could be favorable in Hovinbekken during winter. Spatial variation regarding seasonal size-dependent survival was, as mentioned earlier, detected; I suggest that smaller fish in station No4 has a slight survival advantage over smaller ones in station No3, due to area suitable pools.

In contrast, summer survival in my study was negatively dependent on fish size (i.e. large fish had reduced survival). This is consistent with Xu et al. (2010b) discoveries for larger brook charr in a small tributary in Massachusetts U.S.A, and can be attributed to low summer flow (Xu et al., 2010b), and/or perhaps high temperature combined with lack of cold water refugia. No flow measures have been done during summer, though the two stations with presumably lowest summer mortality for larger brook charr had either largest area of functional pools (station No4, Table 8), or the deepest and most heterogeneous pool (station No2, Appendix 2B), indicating its importance for both smaller and larger size classes during both summer and winter.

Angling cannot be excluded as a potential factor for decreasing summer survival for larger fish; Angler prefers larger individuals thus leading to size-biased selection. One should be aware of that recent research has revealed that faster-growing individuals have shown to be more vulnerable to fishing, independent of size (Biro & Post, 2008). Also, shallow water and high clarity in all stations, provides an opportune hunting spot for terrestrial and avian predators, Mink (*Mustela vison*) predation on salmonids have been found to be a significant mortality cause in small streams (Heggenes & Borgstrøm, 1988), and ice cover to function as protection during winter (Carlson et al., 2008). This seems though like a less likely explanation due to the general spatial consistency in survival probability over larger areas.

As in my study, brook charr life history characteristics have shown to be phenotypic plastic, and to vary even within a system (Hutchings, 1996). Because of its variation it is difficult to see a clear context relating survival to maturation. It is though more clearly regarding growth; brook charr in station No3 and No4 were larger at 0+, growth stagnated later, and lengths at maturation were longer. I believe that fast growing individuals are able to mature one year earlier (1+) than individuals with slower growth, and that this differs on a spatial scale. This will give us more knowledge of brook charrs life history traits, though remains to be tested.

## 5 Management implications

Surprisingly, and contrary to Stranko et al. (2008), the apparently most anthropogenically affected station seemed to be a well-functioning brook charr section. Small human made changes can actually be positive at low levels (Allan, 2004); my results indicate that such a positive effect on growth occurred. Increased temperature is a pattern related to urbanization (Paul & Meyer, 2001), and elevated summer temperature has shown to be negative for brook charr (Xu et al., 2010b). Even though optimal temperature can vary even within a species (Forseth, Jonsson, & Damsgård, 1995), all species faces an upper temperature limit, for brook charr around 20-24° (MacCrimmon & Campbell, 1969; Meisner, 1990; Stranko et al., 2008). Since the combined effects of an ongoing climate change and urbanization are predicted to be critical for fish (Nelson et al., 2009), negative effects are to expect in the future, not only for brook charr living in the southernmost stations in Hovinbekken, but also for other urban fish communities sensitive for changes.

Even though spatial differences in migration and life history traits was found, all stations seemed to possess habitats required at different ontogenetic stages (Table 2-10, Appendix 1A). Upstream-movement through artificial barriers may therefore not be as critical as proposed, especially not on a short term. Future research should emphasize if the suggested downstream-biased gene-flow can have a negative population effect on a longer term. If brook charr in Bekkedalen becomes extirpated (e. g. iron (II) hydroxide leaching or emigration), station No1 and No2 will most likely only be naturally recolonized if there exists brook charr further upstream the watershed. The subpopulations in Bekkedalen can thus function as an important (but unstable) source area for stations downstream, and should therefore be managed accordingly. The intact riparian zone and in-stream habitat

heterogeneity is probably a key element for preservation, and potentially the explanation why not all individuals died during this spring (recent observations from locals confirm that the area has got a high density of 0+).

Since invasive species are considered a serious threat to biodiversity (Gurevitch & Padilla, 2004), presence of a non-native species will complicate management practice. The native species in Hovinbekken was probably *Salmo trutta* (Bergan & Bækken, 2011), but brook charr is currently the only species present. Although brook charr is considered a competition-weak species and little negative effect have been detected in Norway (Berger, Hesthagen, Fløystad, Jensås, & Hamstad, 2004), negative effects and/or interactions with native salmonids are described in both America (Levin, Achord, Feist, & Zabel, 2002; Peterson, Fausch, & White, 2004) and Europe (Cucherousset et al., 2008; Korsu, Huusko, & Muotka, 2007). Dominance of brook charr is thus most likely to occur in small streams (Öhlund, Nordwall, Degerman, & Eriksson, 2008), probably such as in Hovinbekken.

Brook charr in Hovinbekken have shown to exhibit downstream movements. If further restored (including improved water quality), Hovinbekken can potentially function as a dispersal corridor, either to Akerselva, or directly into the sea, depending on the future choice of outlet. Since brook charr is defined as a species with high risk of negative effects on native biodiversity (Gederaas, Salvesen, & Viken, 2007), a trade off regarding increasing connectivity versus risk of spread of an invasive species should be carefully evaluated, since a restored system potentially can serve as inhabitable areas, and refuge, for native species in Akerselva. This is particularly pertinent, having the emission disaster in Akerselva, winter 2011 in mind. Anyway, in this specific case, and according to Fausch, Rieman, Dunham, Young, and Peterson (2009) conceptual framework, restoration back to its pristine state will not be recommended when brook charr still exists in the system. At present, a complete reopening would probably neither be socially accepted or economically feasible, and will also interfere with public legislations, if no preventive measures are implemented (Lovdata, 2012).

Even though occasionally neglected, persistence of non-native species should be taken into account in accordance with the European water framework directive (Vandekerckhove & Cardoso, 2010). One possible way to deal with this is through eradication programs. Habitat complexity in streams can though make eradication difficult (Peterson et al., 2004). Toxins (Gresswell, 1991), and electrofishing (Meyer, Lamansky, & Schill, 2006) are examples of two used methods. Regarding electroshocking it has to be repeated over time, or else it might lead

to a compensatory response for the species in question (Meyer et al., 2006). Good planning and accurate handling is thus important to minimize risk of an unsuccessful implementation; in this specific case study, a catchment scale project is probably necessary, since brook charr probably exist in other localities upstream Hovinbekken. In this respect acceptance from the public can be a challenge, and probably also often neglected. Even though protection of biodiversity should be the critical element, it is important to see management in a holistic view, including ecological, social, and economic considerations.

Another alternative to eradication is to put effort into dispersal hindering. Creation of a bidirectional barrier downstream the system (if restored), will allow us to further study brook charr without risking further spread, which in a longer time perspective can be important for future management of non-indigenous freshwater species; further biological and ecological knowledge may allow us to apply this knowledge in predicting the potential spread of an invasive species and thus its effects. I suggest this approach.

A reopening will first of all temporarily open lost habitats, and connect isolated sections. Thereafter, if allowed, will the dynamic flow regime again create naturally fluvial geomorphological variations along the riverscape and reinforce ecological integrity. Today's open stream stretches contains in general high quality habitat patches, with a varying riparian corridor. Despite its potential as a growth predictor, re-creation of a riparian buffer zone should be an integral part of the restoration project, since riparian vegetation reduces temperature, runoff, and bank erosion, and increases litter, and wood input (Degerman, 2008), with positive cascading effects on a long term; although landscape scale factors are considered to be the major factor affecting stream conditions, local riparian zone plays a major role, and have shown to be well as important (Allan, 2004; Roth, Allan, & Erickson, 1996; Stauffer, Goldstein, & Newman, 2000).

For the future, planners should continue to emphasis on a natural heterogeneous environment rather than engineered parklands, since the latter not necessarily creates sustainable fish habitats. Plans for the restoration of Hovinbekken will therefore have to incorporate practices from both land and water management to ensure satisfactory future stream integrity. Increased stream health will further benefit fish, whether brook charr, *Salmo trutta*, or both are present in the future.

## 5.1 Further research

- Continue capture-mark-recapture method to obtain longer time series for even more reliable estimates (i. e look for trends and test for potential density dependent effects)
- Measure habitat variables (and flow) under different conditions (seasons) and include them in analysis
- Detailed study (observational) of brook charr microhabitat utilization
- Use of temperature logger in different stations for including accurate temperature in analysis
- Quantitative age determination by the use of otoliths to accurately determine age at sexual maturity
- Testing for metapopulation ecology
- Include/investigate sections even further downstream (including inside culverts) to reveal its southern boarder
- A more detailed examination of culverts and the natural water fall to be absolutely certain about its upstream passability
- Placement of a pit-antenna to detect all potential movements
- Analyses with focus on gene flow, and genetic differentiation in potentially genetically isolated subpopulations
- Examination of lakes, streams, and tributaries upstream Hovinbekken to reveal brook charr presence on a catchment scale

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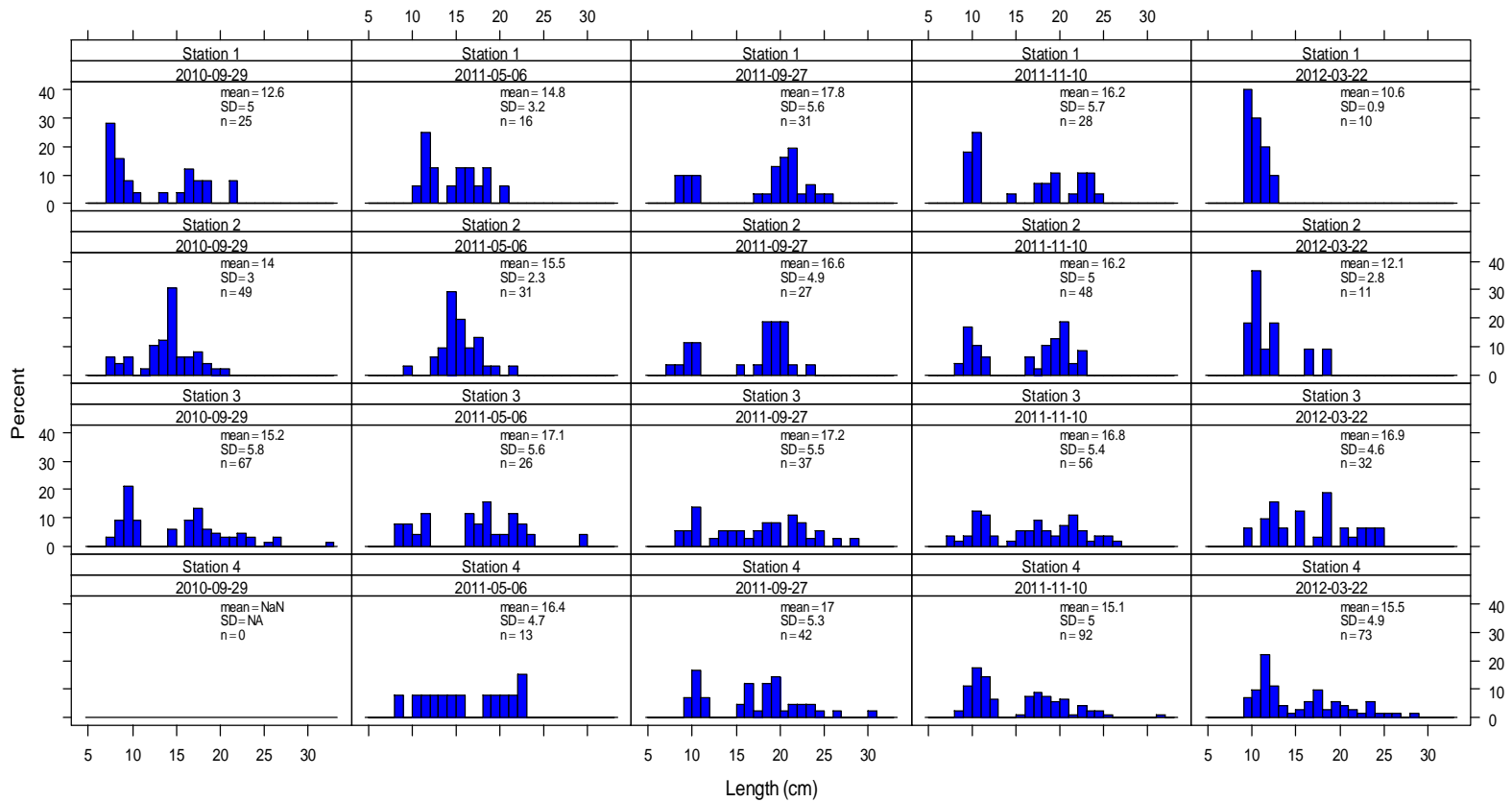
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## Appendix Appendix 1



**Figure A.** Length distribution for all brook charr caught (including tagged, untagged, and recaptured individuals) in the four study stations (n=714).

**Appendix 2**

**Figure B.** Debris dam pool according to Bisson et al. (2006) in station No2.



### Appendix 3



**Figure C.** Culvert upstream Trondheimsveien (downstream station No2).

#### Appendix 4



**Figure D.** Culvert downstream Trondheimsveien (downstream station No2).



**Appendix 5**

**Figure E.** Unnatural hardening of the riverbank in station No4.



**Appendix 6**

**Figure F.** Natural waterfall (around 10-11 meters) between station No2 and No3.

**Appendix 7**

**Figure G.** Iron (II) hydroxide observed in several locations in Bekkedalen.