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Effects of fork length on the utilization distribution and habitat preferences of anadromous Arctic charr (Salvelinus alpinus) in a subarctic lake

Anders Kristoffer Halsvik Sandnes Natural resource management

Preface

This master's degree thesis was written in cooperation with a Akvaplan-NIVAs project that aim to study the migrational behaviour of the anadromous Arctic charr in a habitat highly influenced by human infrastructure. The project is led by leader of research and innovation in Akvaplan-NIVA Guttorm Christensen, who also served as co-supervisor to this thesis.

I wish to thank my supervisor Thrond O. Haugen for helping me out with heavy statistics, and setting up an alternative plan for me when everything turned upside down In march 2020. Kate Louise Hawley for almost always answering mails when Thrond was busy with other stuff, and Guttorm Christensen and Jenny Jensen for answering questions about ping rates and what was done in field. I also want to thank everybody that have been supporting me with help, meaningful conversations, laughter and cry the last 5 years at NMBU all until this final day.

Abstract

This was an acoustic telemetry study investigating lacustrine habitat utilization of anadromous population of Arctic charr (*Salvelinus alpinus*) located in Storvatnet in Hammerfest multiplicity northern Norway. Arctic charr's lacustrine habitat use lacks knowledge, and the aim of the study was to determine whether size-dependent effects occurred between habitat use in different seasons, and to find out to which extent the Arctic charr utilizes a part of the habitat that is planned to be filled out.

60 individuals of arctic charr were tagged with acoustic transmitters, and gently set back into the water where they were caught. These transmitters were constantly sending signals to a network of 13 receivers constantly logging signals from the transmitters. The signals were made into detailed position data revealing the position of the fish in the lake throughout the study period.

The results revealed differences in utilization distribution between different seasons. There was also a size-dependent effect for some of the seasons. The larger individuals had a low activity during the winter, a high activity in the spring, which continued into the summer before they migrated into the sea. When they came back in the fall they had a low activity, which continued through the spawning season. The smaller individuals also had a low activity during winter, and a high activity in summer, but for spring and fall the tendency was opposite of the larger ones, with low activity in spring, and high activity in autumn.

There was overlap between utilization distribution and filling area during all seasons, and for all sizes of fish. The probability of overlap was highest in the spring, and in this season increased with decreasing fish size. The probability was nevertheless relatively low for all sizes of fish and for all seasons peaking at about 25% probability for the smallest individuals in spring.

Due to the bad coverage of signals along the edge of the lake system, it is difficult to say whether if the findings on overlap are trustworthy. The fact that there is no research done on effects of filling on reproductive success of anadromous arctic charr, makes it even more difficult to predict to which extent the population will be affected by the filling. Further research on this topic is therefore recommended.

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1. Introduction

Establishment of human infrastructure in the habitats of wild animals often leads to habitat degradation or loss (Bulleri & Chapman, 2010; Polfus et al., 2011). With changes in climate and thus changing ecological prerequisites and additional loss of habitat, migrating species may be extra vulnerable since they depend on several different habitats (McNamara et al., 2010). Several species of fish from the family Salmonidae are anadromous, which brings about that they undertake migration to marine environments before returning to freshwater habitat to spawn or overwinter. The Arctic charr (*Salvelinus alpinus*) has a circumpolar distribution, and many populations in nearshore watercourses in arctic and subarctic regions are partly or fully anadromous (Klemetsen et al., 2003). When Arctic charr smolts migrate into salt seawater, they need to undergo a transformation; smoltification. This is a process that includes physiological, morphological and biochemical changes in the fish. (Aas-Hansen, 2004).

The benefits of choosing to migrate to sea, despite the huge changes in metabolism, may be great. The high primary production in the arctic oceans compared to the rather scarce production in arctic lakes, leads to a huge difference in prey species availability between the two habitats. That is why benefits of anadromous migrations are increasing with increasing latitude (Gross, 1987). Anadromous behaviour may also make the fish more vulnerable in face of changes in the ecosystems, since the anadromous fish species are dependent on both the marine environment and the freshwater environment. Anadromous salmonids are vulnerable to many anthropogenic disturbances such as physical barriers and degradation of estuarine habitats (Waldman et al., 2016). Pollutants such as polychlorinated biphenyls (PCB) and occurrence of salmon lice also represent disturbances for anadromous populations of Arctic charr (Aluru et al., 2004; Fjelldal et al., 2019). The Arctic charr populations of Norway are declining, and especially the anadromous populations have had a problematic population trend after 2000 (Anon., 2011). In addition to other disturbances, the Arctic charr is suggested a climate-change looser since it is sensitive to rising water temperatures (Lassalle & Rochard, 2009; Winfield et al., 2010).

Acoustic technology is a proven method to study behaviour of fish and other aquatic organisms in their natural habitat. The method provides detailed information beyond what can be observed from the surface, and is one of the few methods that may be used for tracking real-time movements of fish (Kessel et al., 2014). Passive acoustic telemetry evolved as a

method in the 1980s making it possible to collect detailed information about fish positions, and thus their behavioural ecology. This way of using acoustic technology also requires much less work from the researchers in field (McKibben & Nelson, 1986). Passive acoustic telemetry involves deploying acoustic signal receivers into the study area. They receive information from the transmitters in the fish, and are logging the information constantly. The data can be downloaded from the receivers when they are full, or whenever the study period is over (Kessel et al., 2014). The method is very suitable to study migration patterns, and behaviour in Arctic charr. Especially in their lacustrine phase, since the tagged fish never will be far away from a receiver (Bass et al., 2014; Mulder et al., 2018a). If the receivers are placed dense enough for a single signal from a transmitter to be detected on three or more receivers, the data can be triangulated and detailed data about the study objects positions are created (Smith, 2013).

Despite of the many studies done on migration, habitat use and feeding behaviour of the anadromous Arctic charr when it exploits its marine habitat (i.e. (Berg & Berg, 2011; Harris et al., 2020; Moore et al., 2016), their behaviour and habitat use while overwintering in lacustrine waters remain poorly characterized (Mulder et al., 2018b). For Arctic charr feeding behaviour and activity can variate with size and stage of the fish. Sexually mature individuals of anadromous Arctic charr have been proved to more or less cease foraging when returning to the lake after the seaward migration in summer. The younger post-smolts on the other hand, continue foraging after their return (Rikardsen et al., 2003). This size-dependent difference in feeding behaviour makes it likely to believe that there is also a size-dependent difference in movement activity. A recent study from Labrador in Canada showed that a size-dependent difference in activity with shorter individuals being more active than longer ones during winter (Mulder et al., 2018a).

The lake Storvatnet in Hammerfest northern Norway is known for being inhabited by fastgrowing individuals of Arctic charr (Torrissen & Barnung, 1991). These are anadromous, and some of them may gain an impressive size. The lake is situated in the middle of town, making it vulnerable to pollution and other anthropogenic disturbances (Kramvik, 2014). The local authority of Hammerfest (Hammerfest commune) and The Norwegian Public Road Administration (Statens vegvesen) have put forward plans to upgrade the road RV94 through Hammerfest town. These plans include an upgrade of the area around Storvatnet as an urban green space (Anon., 2021). To enable establishment of a promenade around the lake, filling masses into the lake is required, and therefore part of the plan. This may constitute a threat to

the spawning grounds of the Arctic charr, which are believed to be located close to the shore in this lake (Rikardsen et al., 1997).

In this study, I am analysing position data from acoustic telemetry in Storvatnet collected during 2010 to 2012. In line with Mulder et al (2018), I hypothesize there is a negative correlation between fish size and winter activity in the anadromous Arctic charr in Storvatnet. In addition, I will aim to find out to which extent it occurs overlap between individual Arctic charr's utilization distributions and the planned filling of the project area. I will later discuss whether if the establishment of Storvatnet as a green area in Hammerfest may constitute a threat to anadromous Arctic charr in the lake.

2. Materials and methods

2. 1. Study area

Storvatnet (70°39'44 N, 23°42'30 E) is a small lake (0,23 km²) situated 7 meters above sea level in Hammerfest municipality, Troms and Finnmark County, northern Norway. It is oligotrophic, cold-monomictic and shallow, with its deepest point at 17 m, and an average depth at 9 m (figure 1). The watercourse drains into the sea through a 200 m long river stretch which constitutes an open passage for migratory fish. All inlet streams of significant size are blocked for migration by waterfalls. The total water catchment area for this watercourse is 42.87 km², with an annual inflow of 53.55 million m^3 (NVE, 2021). The lake is situated in the middle of Hammerfest municipality, with suburban and urban surroundings. The outlet stream drains into the sea in the middle of the harbour area of Hammerfest, which means that the marine surroundings also are affected by human infrastructure to a great extent. These polluted areas are exploited by the Arctic charr during its seaward migration (Jensen et al., 2016). High concentrations of lead (Pb) polycyclic aromatic hydrocarbons (PAH16) and polychlorinated biphenyls (PCB17) have been detected in sediments of this harbour area, with levels reaching 83.55 mg/kg for lead, PAH-levels reaching 0.20 mg/kg and PCB-levels 53.46 mg/kg (Rambøll, 2013). These pollutants may leak into the seawater. In addition, there are other sources to pollution in the harbour area such as discharge of household sewage, snowdumps, landfills, and frequent shipping traffic (Kramvik, 2014). The region is subarctic, with short but light summers, and long cold winters. The lake is normally covered with ice from November to May-June, and in winter the whole water column has water temperatures below 1 °C. After ice out in early summer, the water temperature rapidly increases to 12 °C in July (Rikardsen et al., 2000). In addition to Arctic charr, the fish community in Storvatnet also

holds brown trout and three-spined sticklebacks (*Gasterosteus aculeatus*), European eels (*Anguilla anguilla*), and Atlantic salmon (Rikardsen et al., 1997).

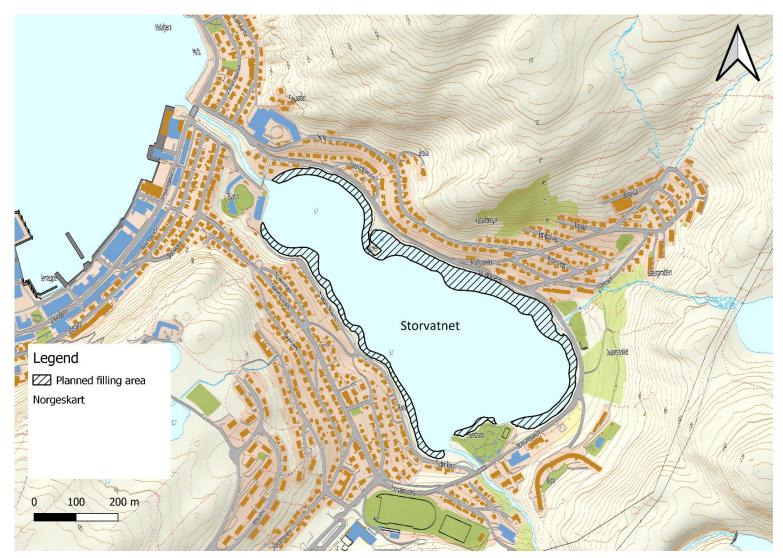


Figure 1: Map of Storvatnet with filling area.

As part of the plans to upgrade the road RV94, Hammerfest commune and The Norwegian Public Road Administration (Statens vegvesen) have planned to establish a green space around Storvatnet (Anon., 2021). In that occasion it is necessary to fill masses into the lake to enable the establishment of a promenade around the lake. According to the sketch of the landscape plan (Appendix I) a quite comprehensive filling into the lake has been planned. This will affect the littoral zone, especially along the northeast shore of the lake (figure 2).

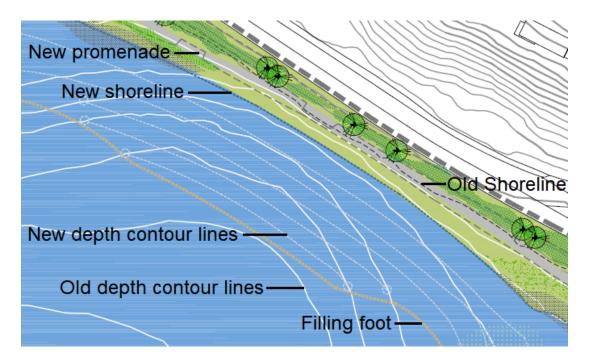


Figure 2: Excerpt from the sketch of the landscape plan showing the filling and the planned promenade in Storvatnet. Picture based on sketch of landscape plan made by Sigrid Rasmussen, Asplan Viak. The whole sketch is showed in appendix I.

2. 2. Study species

Arctic charr is a species of fish in the family Salmonidae. Though it has many similarities with its more famous relatives the brown trout (Salmo trutta) and the Atlantic salmon (Salmo salar), it is less thoroughly researched than these. The Arctic charr has a circumpolar prevalence and is found in many freshwater systems throughout northern parts of North-Amerika, Europe and Asia (Johnson, 1980). In fact, it is the species of freshwater fish with the northernmost prevalence, and in many alpine and Arctic lakes, it is the only fish species present (Klemetsen et al., 2003). The species appears through a myriad of different morphs. In nearshore watercourses in the far north, many of the populations are partly or fully anadromous, which means that they stay in the marine environment for a time during summer to exploit marine feeding resources (Berg & Berg, 1989; Berg & Berg, 1993; Klemetsen et al., 2003). This gives the individuals that choose to migrate out from the freshwater system, an increased growth, and they gain more weight than the individuals that choose to stay in the lake or river (Berg & Berg, 2011; Rikardsen, 2005). Furthermore, it is giving the anadromous individuals an increased fitness, which explains why this trait has prevailed through evolution (Jonsson & Jonsson, 1993). This is especially important for females since fecundity and egg size in salmonids increases with body length (Crespi & Teo, 2002).

The great span of life history traits in anadromous Arctic charr are well studied, especially in North-America (Dempson et al., 1984; Graigner, 1953; Harris et al., 2020; Johnson, 1989), and they vary a lot among populations. This includes factors like; the proportion of the population choosing to migrate to marine areas; timing of migration onset and return, migration distance, habitat useage whilst at sea, mean age at first migration and diet during the marine phase (Dempson et al., 2002; Klemetsen et al., 2003; Moore, 1975). In contrast to the anadromous migrating pattern of salmon and trout, the anadromous Arctic charr only stays in the sea during the summer season, and has to migrate back to freshwater before the rivers freeze in autumn (Klemetsen et al., 2003). This includes even juveniles and non-spawning adults who has to get back to freshwater presumably to avoid high salinity in combination with seawater temperatures below 0 °C (Johnson, 1980; Klemetsen et al., 2003). However more recent studies done on riverine anadromous arctic charr in Northern Norway and Canada have shown that the charr may exploit estuarine waters even in Winter (Harwood & Babaluk, 2014; Jensen & Rikardsen, 2008; Jensen & Rikardsen, 2012).

1. 4. Spawning and lacustrine habitat use

The majority of Artic charr individuals that undertake seaward migration in Storvatnet are expected to return to the lake by mid-August (Jensen et al., 2016). During their freshwater residency, some of the mature individuals will also spawn. Depths of the spawning grounds vary a lot between populations, but the most common spawning grounds are on shallow gravel at less than five meters depth (Klemetsen et al., 2003). In Storvatnet, the spawning period is believed to last from mid-September to mid-October (Rikardsen et al., 1997).

Several studies have shown that the charr avoid eating upon arrival in their residential lake. In fact, in some cases there is evidence supporting that they may not feed at all during their lacustrine residency (Boivin & Power, 1990; Dutil, 1986; Rikardsen et al., 2003). However, the non-feeding charr keep their energy reserves impressively high throughout the winter. Dutil (1986) found that non-reproductive charr of the Nauyuk lake, northern Canada, in average lost 30 % of their energy reserves throughout a 10-month period of lacustrine residency. The non-reproductive fish managed to recover fully after less than 60 days at sea the following summer. Due to the lack of feeding during winter residency, spawning may constitute a considerable energy cost for the anadromous arctic charr. In Dutil's study, the loss of energy turned out to be vast for spawners, who had a net energy loss of 52 % in 12 months. These findings show that overwintering and spawning required so much energy from the fish, that one seaward migration during summer was far from enough to recover the

energy loss from the previous year. The anadromous charr from this lake are also known to abstain from seaward migration the summer prior to spawning which gives the spawning individuals an additional inconvenience through their forsaken opportunity to restore energy loss (Dutil, 1986). In these extreme Arctic conditions, most charr individuals skip yearly spawning, and need a minimum of two summers to restore energy reserves sufficient for spawning again. Dutil (1986) found that larger fish tended to use more time than smaller fish to fully recover after spawning

After spawning, the Arctic charr stays calm, and use as little energy as possible throughout the winter. Their movement activity declines when the lake surface freezes, and keeps at a low level throughout the ice-covered period. Activity in spring and autumn is correlated with daylight hours suggesting that charr may feed under the ice cover as an energy conservation strategy. (Mulder et al., 2018a) However, movement intensity in winter is negatively correlated with size of the charr, whereas summer activity increase with increasing body size. Regardless, considerable individual variations occur (Mulder et al., 2018a). The overwintering Arctic charr strive to keep themselves in cold waters (0.5-2 °C), and mainly occupies the middle and upper water column. The reason why they prefer cold waters is believed to be a strategy to minimize metabolic cost and thus energy expenditure (Mulder et al., 2018a).

2. 2. Capture and tagging

The charr were sampled using two different methods. The 5th of November 2010, a beach seine was used to catch fish in the lake, while on 6th of June 2011, a fyke net situated in the outlet stream, was used to catch sea-ward migrating fish. This migration trap consisted of a fyke and two small-meshed leading nets (figure 3). Thirty fish were caught in November 2010, and thirty in June 2011 [mean fork length (L_F) 427 mm, range 274-575 mm (figure 3)]. All fish were tagged with acoustic transmitters [models: V9-2L (9x29 mm, 4.7 g in air, 2.9 g in water, signal output 146 dB re 1 µPa at 1 m, estimated battery life 778 days), V13TP-1L (13x48 mm, 13 g in air, 6.5 g in water, signal output 147 dB re 1 µPa at 1 m, estimated battery life 1095 days), V13-1L (13x36 mm, 11g in air, 6 g in water, signal output 147 dB re 1µPa at 1 m, estimated battery life 1095 days), or V16P-4L (16x71 mm, 26 g in air, signal output 150 dB re 1 µPa at 1 m, estimated battery life 1095 days), Vemco, Inc., Canada, vemco.com].

The 30 fish tagged in November 2010 were tagged with V13-1L and V16P-4L. These transmitters had ping rate 2200-2600, meaning that they transmit a signal every 2200 to 2600 second. The 30 fish tagged in June 2011 were tagged with V9-2L and V13-TP. These tags

were programmed to ping every 30-90 second for 90 days, followed by 270 days with a lower ping rate at 2200-2600. This was done to secure a high amount of data from the summer when the fish move more, but to prevent the receiver memory becoming full over winter (Hawley, 2021). The V13TP-1L recorded and transmitted water pressure (depth) and temperature in addition to the tag code information, whereas the V16P-4L did not measure temperature. The V9-2L and V13-1L tags only transmitted tag code information (Jensen et al., 2016).



Figure 3: This picture shows how the migration trap looks. It consists of a ruse attached to two small meshed leading nets. The fish is trapped inside the fyke net, before it is taken to a tube for measurements and the surgical attachment of the transmitter. Photo: Martin A Svenning, NINA

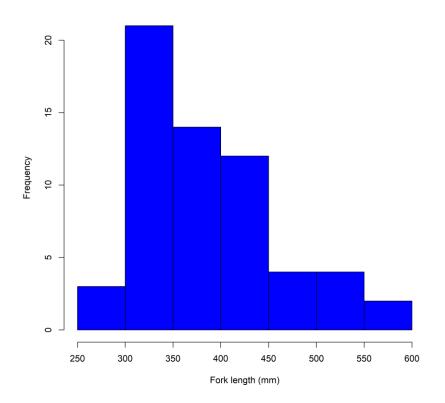


Figure 4: Fork length distribution for the tagged Arctic charr individuals (n=60)

After the fish were caught, they were anesthetized with clove oil, before tagging (Iversen et al., 2003). When the individual fish reached complete anesthesia, it was placed in a tube with head and gills submerged in fresh water. A 2-3 cm long incision was made in the ventral surface posterior to the pelvic gridle with a disinfected scalpella. Thereafter, the transmitter was gently pushed into the abdominal cavity through this incision. After inserting the tags, the incision was closed with 2-3 independent silk sutures (3-0 Ethicon). The fish were also externally tagged with a modified Floy tag (Floy Tag, Inc., Seattle, USA) at the base of the dorsal fin to enable return of the tags upon possible recapture. A net cage in the water was used to make sure the fish recovered properly before releasing. When the fish were showing normal behavior, i.e. calmly keeping vertical position or swimming around, they were released into the river or lake where they were caught (Jensen et al., 2016).(Christensen, 2020)

2. 3. Tracking

Ten acoustic receivers (model VR2-W, Vemco, Inc.) were placed at 5 m depth in the lake held in place by a rope attached to an anchor and buoy. The receivers were operative from

November 2010 to June 2014. Tagged fish were monitored continuously as long as they were within the range of the omnidirectional detection range. In addition, temperature and water pressure recordings was monitored through the tags that enabled this. Testing of the tag signal range revealed that signals from the transmitters could be detected by the receivers at 200-1000 m distance in seawater (Jensen et al., 2016).

The acoustic receivers were deployed in a system with low and even distance to each other in 5 different deployments (figure 5). This enabled detection of single ping signals on multiple receivers. If a signal from a transmitter is detected on three or more of the receivers, the exact position of the tagged fish may be detected by triangulating (Smith, 2013). In this study, I used the positional data from triangulating to make detailed models over the charrs utility distribution in the lake.

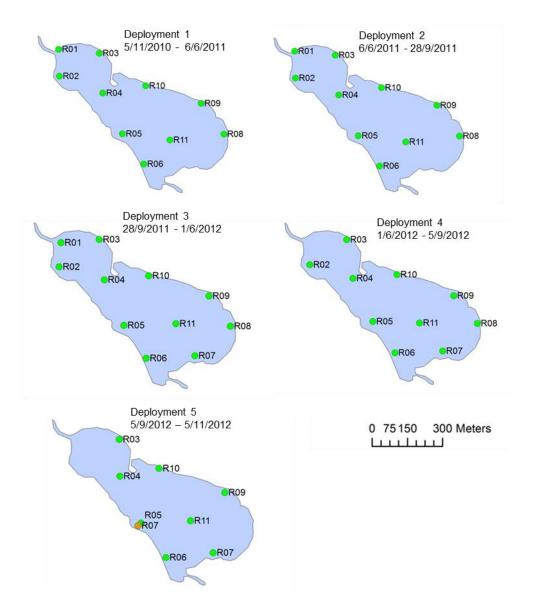


Figure 5: Positioning of acoustic receivers in Storvatnet in the 5 different deployments. R01 to R11 refers to the receiver ID. Map made by Kate Hawley.

Seaward migration times was defined as the time of the first ping signal registered on a receiver in the sea, and equivalent, the first ping signal registered in the lake defined the returning date. The marine residency time was defined as the period from the first to the last registration on a receiver at sea, and only for fish later returning to the lake.

2.3 Seasons

The seasons were defined as Spring (week 16-24), summer (week 25-32), fall (week 33-38), spawning (week 39-44) and winter (week 45-15). These times were chosen because of the Arctic climate, and thus long winters and short summers. The parameter "4seasons" was defined the same, but with the "fall" and the "spawning season" merged together as "fall". The spawning season was determined according to local observations (Christensen, 2020).

2. 4. Statistical Analyses

Fish data and position data from Microsoft Excel was read into R version 4.0.5 (Team, 2020) (REF) as CSV-files for further analysis. Several different candidate models were adapted for the different response variables including various combinations of explanatory factors and covariates to estimate the response. AIC (Akaike information criteria) tables were constructed, and the models were then ranked according to their AICc value. The model attaining the lowest AICc value would be the candidate model explaining the variation in the dataset most effectively, i.e., having the most optimal balance between explained variation, precision and deviation among candidate models (Anderson, 2007).

Weekly kernel-based 50% utilization distribution (UD50) and 95% utilization distribution (UD95) were estimated for every fish using the package "adehabitatHR" (Calenge & Fortmann-Roe, 2020) in R. Overlap between 50% utilization distribution polygon (HR-50) and filling area polygon (FA) using the "gIntersection" and "gArea" from the library "rgeos". The probability of overlap between UD50 and FA (Pr(overlap(FA) was estimated as:

Pr(overlap(FA)=Area(intersect(UD50,FA))/Area(UD50)

Candidate models exploring effects from fish length and seasonal aspects on Pr(overlapFA) were fitted using generalized linear mixed effects models (glmer – lme4 library) (Bates et al., 2015). In these analyses, a logit link was used for linearization where number of positions that were included in the individual weekly UD50-estimates was used as weighting factor. ID was used as random effect to account for ID-related dependency variation in the response variable.

3. Results

3. 1. Seaward migration times

A total of 55 of the tagged charr undertook an anadromous migration the first summer in 2011. Of these 35 returned to Storvatnet after the seaward migration. In 2012, all 34 individuals detected undertook the second seaward migration. 25 of these successfully returned to Storvatnet afterwards. The average amount of days spent outside of the lake was 48 (SD \pm 5) and 46 (SD \pm 3) the respective years 2011 and 2012. The number of days spent outside of the lake varied from 16 to 65 in 2011. In 2012, it varied from 41 to 56 days. The first migratory fish left the lake 21.05 in 2011 and 27.03 in 2012. The last migratory fish left

the lake 24/06 in both years. The first detection of returning fish in the lake in 2011 was 12.06, and 21.05 in 2012. The last fish returned 04.08 in 2011 and 29.07 in 2012. The average outmigration days was 2 June (SD \pm 8 days) and 31 May (SD \pm 7 days) respectively, and the average returning date was 21 July (SD \pm 8 days) and 16 July (SD \pm 4 days) respectively (Jensen et al., 2016).

3. 4. Depth use

All position data from fish with tags measuring pressure (depth) were plotted in a violin plot (figure 6). This reviled a tendency towards a more surface-orientated behaviour in the summer months, than in the winter months.

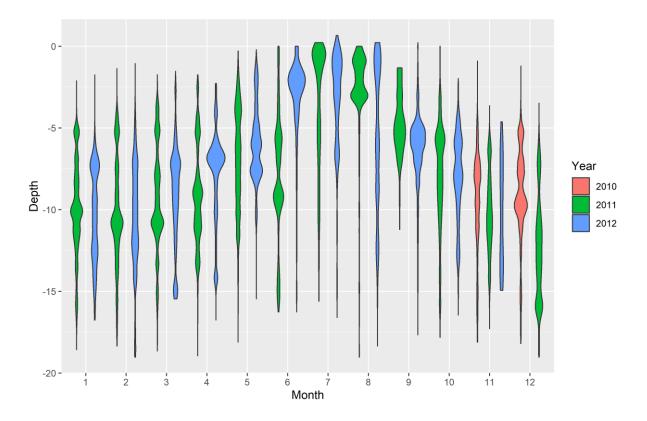


Figure 6: Violin plot showing usage of different depths by anadromous Arctic charr in Storvannet for every month throughout the study period.

3. 3. Utilization distribution

3.3.1 50% utilization distribution (UD50)

The model selection revealed that log(FL)*season was clearly the most supported model among the 6 models tested for 50% utility distribution (Table 1). This was also the model with the highest number of estimated parameters, resulting in a parameter estimate model with 10 parameters (Table 2). Whereas spring in interaction with log-scaled fork length had a positive effect on UD50, fall in interaction with log-scaled fork length had a strong negative effect. This indicates that fish with a low measured fork length have larger utilization distributions in the autumn than the longer measured individuals, whereas in the spring, the opposite effect is present.

Table 1: Result of AIC-based model selection for UD50. The models are ranked according to AICc. In addition the model shows the number of estimated parameters (K), Δ AICc model likelihood AICc weight, log-likelihood (LL) and cumulative Weight.

Modnames	К	AICc	ΔAICc	ModelLik	AICcWt	LL	Cum.Wt
log(FL)*season	12	3634.3988	0.000	1.0000	1.0000	-1805.13	1
log(FL)+season	8	3669.4463	35.047	0.0000	0.0000	-1826.69	1
log(FL)*4season	10	3682.5111	48.112	0.0000	0.0000	-1831.21	1
log(FL)+4season	7	3711.5238	77.125	0.0000	0.0000	-1848.74	1
log(FL	4	4582.8980	948.499	0.0000	0.0000	-2287.44	1
1	3	4590.3479	955.949	0.0000	0.0000	-2292.17	1

Table 2: Parameter estimates and effect tests (Anova) for the most supported UD50 model (table 1). FL = fork length, intercept = log(FL*season[fall]

		Parameter	estimates		Effec	t test	I	
	Term	Estimate	SE	Effect	F	Df	Df.res	Р
Fixed	Intercept	8.6257	1.8429	log(FL)	0.2178	1	47.63	0.6429
	log(FL)	-1.4267	0.3125	season	290.2866	4	2186.95	< 0.00001
	season[Spring]	-11.6097	1.9526	log(FL)*season	10.8128	4	2188.83	< 0.00001
	season[Summer]	-6.7726	2.19					
	season[Winter]	-8.6551	1.8342					
	season[Spawning]	-6.0823	2.1277					
	log(FL)*season[Spring]	1.9698	0.3308					
	log(FL)*season[Summer]	1.2082	0.3717					
	log(FL)*season[Winter]	1.3399	0.311					
	log(FL)*season[Spawning]	0.9695	0.361					
Random	Among-ID	0.01245						
	Within analysation	0.29392						

The prediction plot of the selected model visualises how the fork length interreacted with the different seasons (figure 7). It is clear that the 50% utilization distributions during winter was small compared to the other seasons, and independent of fork length. During spawning season, the 50% utilization distributions was generally small too, in contrast to in summer where it was generally large. For both summer and spawning season increasing fork length

gave a slight decreasing 50% utilization distributions but with a larger confidence interval for summer.

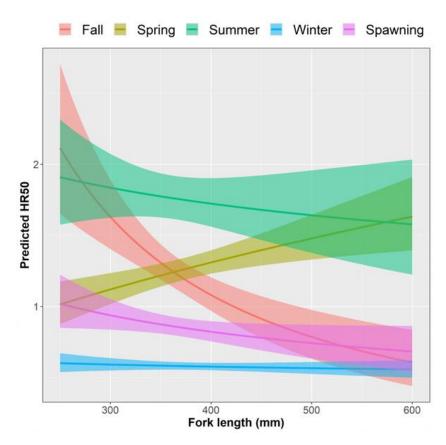


Figure 7: Prediction plot over the selected model (table 2) showing differences in areal (ha) of 50% utility distribution on fork length through different seasons.

3.3.2. 95% utilization distribution (HR95)

Like for UD50, the model selection for HR95 revealed that log(FL)*season was clearly the most supported model among the tested models (Table 3). This model also had 10 estimated parameters which is the highest number among the alternative models tested (Table 6).

Table 3: Result of AIC-based model selection for HR95. The models are ranked according to AICc. In addition, the model shows the number of estimated parameters (K), Δ AICc model likelihood AICc weight, log-likelihood (LL) and cumulative Weight.

Modnames	К	AICc	ΔAICc	ModelLik	AICcWt	LL	Cum.Wt
log(FL)*season	12	2850.99	0.00	1.0000	1.0000	-1413.41	1.0000
log(FL)*4season	10	2878.35	27.36	0.0000	0.0000	-1429.11	1.0000
log(FL)+season	8	2881.50	30.50	0.0000	0.0000	-1432.71	1.0000
log(FL)+4season	7	2901.66	50.66	0.0000	0.0000	-1443.80	1.0000
log(FL)	4	3714.12	863.13	0.0000	0.0000	-1853.05	1.0000
1	3	3716.33	865.34	0.0000	0.0000	-1855.16	1.0000

		• • • • • • •			с	* * * * *			
	Pasrametre est	imates		Effect test					
	Term	Estimate	SE	Effect	F	Df	Df.res		
Fixed	Intercept	8.3469	1.9308	log(FL)	0.2178	1	47.63	0.6	
	log(FL)	-1.0879	0.3276	season	273.6012	4	1735.16	< 0.0	
	season[Spring]	-10.6476	2.0339	log(FL)*season	9.6817	4	1737.7	< 0.0	
	season[Summer]	-7.0548	2.2308						
	season[Winter]	-6.5455	1.9186						
	season[Spawning]	-6.7564	2.2967						
	log(FL)*season[Spring]	1.8336	0.3448						
	log(FL)*season[Summer]	1.2421	0.3789						
	log(FL)*season[Winter]	0.9857	0.3255						
	log(FL)*season[Spawning]	1.1014	0.3903						
Random	Among-ID	0.01668							
	Within analysation	0.28451							

Table 4: Parameter estimates and effect tests (Anova) for the most supported HR95 model (table 3). FL = fork length, intercept = log(FL*season[fall]

The prediction plot visualises how the fork length interreacted with the different seasons (Figure 8). The 95% utilization distributions during winter were small compared to the other seasons, and independent off fork length. HR95 during spawning season also lacked a significant effect of fork length. In spring there was a positive correlation between fork length and HR95, and in fall the opposite tendency occurred. During summer the model showed a slight increase in HR95 with increasing fork length, but it had a too large confidence interval to be significant.

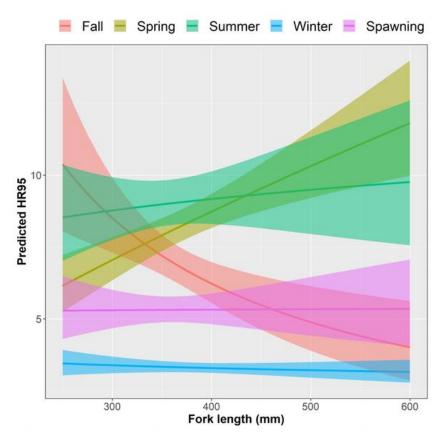


Figure 8: Prediction plot over the selected model (table 4) showing differences in areal (ha) of 95% utility distribution on fork length through different seasons.

3. 4. Overlap between UD50 and planned filling area

Model selection with the AIC-method brought out that scale(FL)*season was the most supported model to explain differences in overlap between UD50 and filling in the different seasons (Table 7). Again, the model with the highest number of estimated parameters, was selected, resulting in a parameter estimate model with 10 parameters (Table 8).

Table 5: Result of AIC-based model selection for overlap between UD50 and the planned filling. The models are ranked according to AICc. In addition, the model shows the number of estimated parameters (K), ΔAICc model likelihood AICc weight, log-likelihood (LL) and cumulative Weight.

Modnames	К	AICc	ΔAICc	ModelLik	AICcWt	LL	Cum.Wt
scale(FL)*season	11	52981.27	0.00	1	1	-26479.58	1
scale(FL)*4season	9	53045.88	64.61	<0.0001	<0.0001	-26513.90	1
scale(FL)+season	7	53064.29	83.02	<0.0001	<0.0001	-26525.12	1
scale(FL)+4season	6	53129.47	148.20	<0.0001	<0.0001	-26558.72	1
scale(FL)	3	61619.76	8638.48	0	0	-30806.87	1
1	2	61620.25	8638.98	0	0	-30808.12	1

	Pasrametre est	imates	Effect test					
	Term	Estimate	SE	Effect	Chisq	Df	Р	
Fixed	Intercept	-2.32318	0.08246	scale(FL)	4.3852	1	0.03625	
	scale(FL)	-0.18685	0.08933	season	8891.2505	4	<0.0001	
	season[Spring]	0.90611	0.02854	scale(FL)*season	99.0701	4	<0.0001	
	season[Summer]	-0.48284	0.0322					
	season[Winter]	-0.07689	0.02834					
	season[Spawning]	0.21538	0.03311					
	scale(FL)*season[Spring]	0.02077	0.03804					
	scale(FL)*season[Summer]	0.275	0.04439					
	scale(FL)*season[Winter]	-0.01335	0.03757					
	<pre>scale(FL)*season[Spawning]</pre>	0.07782	0.04177					
Random	Variance among-ID	0.3343						

Table 6: Parameter estimates and effect tests (Chisq) for the most supported model predicting overlap between UD50 and planned filling (table 5). FL = fork length, intercept = log(FL*season[fall]

The prediction plot over the selected model showed that overlapping between HR 50 and the planned filling area was most prevalent, in the spring, and increasing with decreasing fork length (Figure 9). The overlap during spawning season also increased with decreasing fork length, but never exceeded

18% even for the shortest individuals. The planned filling area is though used more during the spawning season than in summer, fall and winter.

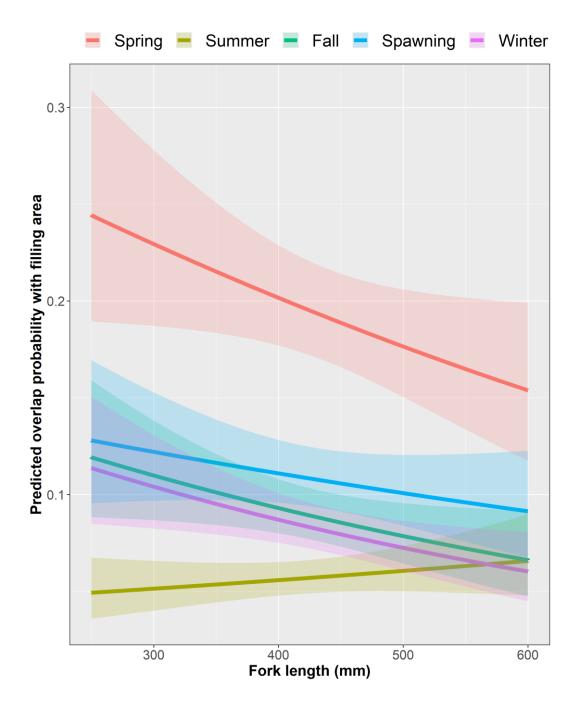


Figure 9: Prediction plot over the selected model (table 7) showing differences in overlap between 50% utility distribution and the planned filling area through the different seasons. Overlap is shown as a decimal number.

4. Discussion

The results from this study revealed that anadromous individuals of Arctic charr from lake Storvatnet had a size-dependent usage of lacustrine habitat between different seasons. The amount of size-dependency varied between seasons, and for some seasons the size dependent effect did not occur. The littoral area, which is planned to be filled out, was exploited by Arctic charr of all sizes, but was most important for smaller fish, especially in the spring. The filling area was used slightly more in the spawning season than in the summer autumn and winter.

4. 1. Lacustrine habitat utilization

Fork length had significant impact on utilization area for certain seasons, but a size-dependent effect on winter activity was not detected neither using 50% weekly utility distributions (figure 7) nor 95% weekly utility distributions (figure 8). On the contrary, the size of the weekly utilization distributions of Arctic charr in Storvatnet during winter season was independent of fork length. For all sizes off tagged fish included in this study, the winter activity was low. This result did not support my hypothesis that winter activity would decrease with increasing fork length. Nevertheless, the results revealed size-dependent effects on utilization distribution for other seasons. Longer fish had clearly larger utility distributions in the spring, both measured as 95% UD and 50% UD. In the autumn, a clear opposite effect was detected with activity increasing with decreasing fork length. This indicates that before the seaward migration in summer, the larger individuals increase their activity more than the smaller individuals, whereas in autumn, the larger individuals calm down faster than the smaller individuals. Rikardsen et al. (2003) found that mature anadromous arctic charr with longer fork lengths ceased foraging after return to Storvatnet, while the smaller immature anadromous arctic charr continued foraging after freshwater arrival. If we assume that increased utilization distribution correlates with increased foraging, the last finding is in line with what Rikardsen et al. (2003) found in the same lake.

For the seasons spawning and summer, the effect of fork length was less clear (figure 7) and 7). When analysed with 95% utilization distribution, the utilization areas seemed to be larger with increasing fork length for both summer and spawning season, but this tendency was not significant due to the large confidence intervals. When analysed with 50% utilization distribution, the tendency is opposite, with decreasing size of utilization distribution with

increasing fork length for both Summer and spawning seasons. Both models showed that the utilization distributions in summer are about twice the size of those during the spawning season.

The overlap model showed that the area of the planned filling in the littoral region of the lake was used the most in the spring, and the probability of overlap between UD50 and Filling increased with decreasing fork length (figure 9). Except for in the spring, the probability of overlap was highest during spawning season, closely followed by winter and fall. In summer there was a low probability of usage of the planned filling area.

If we look at the models in coherence, we see that even though smaller individuals of anadromous Arctic charr utilises smaller areas during spring (figure 7), they are dominating in the planned filling area, in the same period. The planned filling covers most of the littoral zone around the lake. This tells us that there is a clear size dependency in choice of habitat in the spring. Smaller individuals utilize small areas, and remain in the littoral in the spring, while larger individuals utilize larger areas, and are less dependent on the littoral zone. This niche differentiation between different sized charr may be a result off differential prey selection. It is shown from other studies that different sizes of Arctic charr prefers different species of prey (Dempson et al., 2002; Rikardsen et al., 2000).

Another tendency that occurs when comparing the two models is that even though the utilization distributions during spawning season are small compared to those of the other seasons (figure 7), they overlap more with the planned filling area than most of the other seasons, only spring activity is higher within this area (figure 8). The slight tendency towards a higher exploitation of the planned filling area during spawning season, is therefore amplified by the fact that utilization distributions during spawning seasons are generally small.

4.2. Potential effects of establishing green areas around Storvatnet

The overlap between 50% utilization distribution and filling area was analysed and the results revealed that the area is utilized, but not to a very great extent. Despite the tendency towards increased activity in the filling area during spawning season, the overlap probability never exceeded 17%, (figure 9). If we assume that the arctic charr spawn within their 50% utilization distribution during spawning season, the probability that Arctic charr in Storvatnet spawn within the filling area is lower than the probability for that they will spawn outside of this area. The negative effects on the Arctic charr's reproductive success caused by the filling

will therefore most likely be small, if present at all. If in addition filling masses will be of a type that enables spawning, it may even be possible that the filling will enhance spawning opportunities. This is assumed because sedimentation has been reported to deteriorate former healthy spawning grounds (Bjørn, 2021).

The planned filling area was more important for the smaller individuals in the spring. Almost one out of four of the shortest individuals included in the study had a 50% utility distribution that was overlapping with the filling area. This implies that the planned filling area is an important area for smaller individuals of anadromous Arctic charr prior to the seaward migration. A filling will decrease the size of the shallow littoral zone (Appendix I), and may constitute a moderate threat to small individuals' spring behaviour.

The filling will make the lake a bit smaller, the littoral zones will become steeper and the bottom substrate within the filling will be changed. The statistical results from this study, and the available background information is not enough to predict whether if the filling will have a negative or positive effect on the anadromous Arctic charr population in Storvatnet.

4.3. Management relevance

Due to negative population trends of anadromous Arctic charr in Storvatnet, strict fishing rules have been applied. The results from this study can be used to predict which size classes of Arctic charr that are more active during different seasons of the year. This knowledge should be adapted into the fishing rules if the fishing management want to fish more of certain size classes of fish, and preserve others. For example; if the goal is to preserve large individuals of anadromous Arctic charr, there is a possibility to open fishing during mid-summer. We know from this study that larger charr move less after arrival from the seaward migration, and from Rikardsen et al. (2003), we know that they also cease foraging after arriving to the lake. The opposite effect is shown for smaller individuals, they maintain a high activity level and continue foraging after arrival in fresh water. Therefore, fishing in the lake after mid-summer would give higher probability of catching smaller individuals. Adapting fishing season to the knowledge about size-dependent activity would reduce bycatch of unwanted size classes.

The study is also showing when the Arctic charr in Storvatnet have the lowest probability of using the planned filing area (Figure 8). This knowledge should be used when determining when to start filling masses in this area. Figure 8 shows that the filling area has a low overlap

with UD50 during summer. I therefore suggest that the measure with filling masses into the lake should be conducted during summer season.

4.3. Shortcomings, study weaknesses and suggestions of improvements

The mayor problem with this current study is that the VPS results and thus the position data that constitute the basis of all statistics done in this thesis is less trustworthy along the edge of the system. This weakens the actual explanatory effect of the last model, and makes it even more difficult to conclude with anything when it comes to overlap between UD and Filling area. The filling area is exactly along the edges were the VPS-results are less trustworthy.

Tracking fish over several years, and analysing data with the use of fork length as a key parameter, could be problematic since the fish continues to grow after tagging and measuring. In this study, I doubt that this is a problem since tracking ceased within 3 years after the first fish was tagged.

Arctic charr is known for being a species where differences in life history traits are very large between different populations (Klemetsen et al., 2003). This implies that there is a need for knowledge about the local population to be able to do the right actions. In this study there were uncertainties associated with the spawning season and spawning areas. I found documentation on both, but it was approximate, and difficult to find and verify the source behind the knowledge. To get a better picture of where the spawning occurs in the lake, and at what time, a combination of acoustic telemetry and acoustic recordings would secure more accurate results. The method that was used by Bolgan et al. (2018) would be more secure. In that manner it is possible to verify when and where the spawning activity happens.

A topic within restoration ecology which as far as I can see lacks knowledge, is success criteria for restoration of Arctic charr spawning grounds. This may be caused by the earlier mentioned variation in life history traits. I tried to find out if Arctic charr would have problems with spawning if the spawning grounds became to steep. Unfortunantely I didn't find any literature about this, and therefore couldn't say anything about if the steeper littoral would have an impact on the reproductive success of spawning Arctic charr in Storvatnet after the filling is made. With that said, Storvatnet would be the perfect system to study effects of filling, change in bottom substrate, and other changes related to establishment of human infrastructure affecting spawning grounds of Arctic charr. If the green space around Storvatnet becomes a reality this is a good opportunity for such study.

4.4. further investigations

To increase knowledge about how Arctic charr utilizes its habitat as a response to man made changes in the environment, I recommend that a similar study should be conducted after the green space around Storvatnet is established. But before that, the before data should be improved, so that a good picture of before and after effects may be detected. A such study would probably establish firm knowledge on where and when spawning happens, and seek to quantity the spawning success. This in combination with the telemetry data could give an indication of spawning success in the lake before the planned works. The study could then be repeated after the filling, as a comparison and to access the effects. In general, it would be interesting to know more about the species requirements to spawning grounds. Preferences on environmental factors on the spawning grounds such as depth, stone size of gravel and steepness of the spawning grounds should be investigated closer.

4. 5. Concluding remarks

This study revealed that anadromous individuals of Arctic charr have a size-dependent utilization of their lacustrine habitat in Storvatnet. The amount of size-dependency varied between seasons, but was not present during winter, in contrast to what was hypothesized. The planned filled area was exploited during all seasons, and by all sizes of charr, but was clearly most used in the spring and by individuals of Arctic charr. In general, it was relatively low overlap between UD50 and filling area making it likely that the population of Arctic charr in Storvatnet most likely will not be very negatively affected by the filling. Nevertheless, there are uncertainties due to lack off knowledge about Arctic charr's requirements to spawning habitat.

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Norges miljø- og biovitenskapelige universitet Noregs miljø- og biovitskapelege universitet Norwegian University of Life Sciences Postboks 5003 NO-1432 Ås Norway