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Impacts of large seasonal hydropower-generated water level fluctuations on Arctic char (*Salvelinus alpinus*) recruitment in a Norwegian alpine reservoir



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This thesis is worth 60 study points

Abstract

Lake Møsvatn at Hardangervidda, South-Eastern Norway was developed for hydropower production in the early 19-hundreds. It is extensively regulated, with a regulation high of 18.5m and thus, comes into the category of highly impacted water resources. The reservoir is dominated by Arctic char (*Salvelinus alpinus*). The population is heavily harvested. Reports of a suspected decrease in abundance due to larger sizes and fewer individuals resulted in the present study, which aimed to investigate the population's health and eventually correlation to low water levels. Gillnetted Arctic char from two different years were investigated in the laboratory. Parameters from whole and dissected fish were sampled. Otoliths were used for age determination and data were sampled from organs in the abdominal cavity. Mean length and age was found to be increasing. Condition factor was rather low (mean<1). Co-findings indicate that post-spawners eat more than in-spawning individuals. Hatching time was explored. The littoral spawning population could be susceptible to the hydropower-generated annual water level drawdowns due to desiccation of roe. Year-class differences were found between years with high and low water levels, but the correlation was weak. Recruitment limitation might have confounding factors, such as water temperature. Wash-out of benthos from the littoral fauna may impact on food-webs and habitat competition. The Arctic char population might be left to feed on large pelagial zooplankton. Allover, the population seems to be bottom-up regulated by recruitment and food limitations.

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Foreword

Norwegian water resources have traditionally been dammed and developed for energy production. The ecological costs of hydropower production must be considered carefully to make sure that vulnerable aquatic ecosystems are not suffering from human impact. The European Union Water Framework Directive gives us guidance on how water resources should be preserved. In the case of highly impacted water resources, the human needs can potentially be prioritized due to economic benefits and less restrictions, although impacted water courses also require and demand preservation. This master's thesis explores the health of an Arctic char population of a large alpine hydropower reservoir in Norway and focuses on the impact from large water level fluctuations. The thesis is written independently, based on individual laboratory work and is part of a larger research project. Thanks to the contributors from LFI and USN, and thanks to the concept of ecology for such an interesting insight into nature and how it works. Front page photography: from the reservoir Lake Møsvatn.

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Introduction

The world is in need of renewable 'green' energy to meet the requirements set by international political agreements (IPCC 2021). One of the important renewable energy sources is hydropower, typically as high head, or run-of-the-river regulation systems. In Norway, high head hydropower has been the most important energy source because of the Norwegian steep topography with large alpine areas (nve.no). By January 2022, hydropower made up about 88% of the mean annual Norwegian energy production (137.9TWh of in total 157TWh) (nve.no, Feb 6, 2022). Of the larger Norwegian freshwater-sheds 70% are impacted by hydropower developments. Furthermore, 25% of the European hydropower is produced by Norwegian hydropower plants (miljostatus.miljodirektoratet.no, Feb 6, 2022). High head hydropower production typically consists of dammed headwater reservoirs that allow the downstream waterflow to be manipulated from the dam and diverted into one or more hydropower turbines. The rivers between the reservoirs and/or downstream, may be seminatural with manipulated flow. Sometimes those rivers are led through tunnels or pipes directly into the hydropower facility, leaving only residual and minimum flows in the river(s). Often there are several power plants per watercourse. Moreover, large alpine areas may be inundated by dams into reservoirs which will have non-natural water level fluctuations dictated by the hydropower production regime. Thus, although hydropower production is renewable, it comes at biological and ecological costs (Poff and Zimmerman 2010, Renöfält et al. 2010, Gillespie et al. 2015, Hirsch et al. 2017, Eloranta et al. 2018). High head systems with reservoirs in alpine areas may be particularly vulnerable to artificial inundation and fluctuating water levels due to scarce soil coverage, poor nutrition, and assemblages vulnerable to environmental changes. To mitigate ecological consequences, several countries have agreed on commitments to restore water resources through 'The European Union Water Framework Directive' (WFD). Hydropower reservoirs are characterized in the group of highly impacted water resources. Thus, the ecological costs comes in conflict with the beneficial effects to the human communities' needs (Hering et al. 2010).

Resident, natural fish species are known from both lentic and lotic ecosystems to be affected by habitat change and/or loss, egg desiccation and fish stranding. Those unnatural environmental changes is driven by hydropower generated water level fluctuations (Poff and Ward 1990, Johnsen et al. 2016, Klobucar et al. 2016, Carmignani and Roy 2017, Heggenes et al. 2017, Hirsch et al. 2017, Eloranta et al. 2018, Heggenes et al. 2021). Effects may depend on life stages and seasons. Lake resident fish species are adapted to relatively stable environments with some seasonal long-term fluctuations. Indeed, Nordic dimictic lakes tend to be stable by nature with respect to water surface levels and associated littoral ecology, although they experience predictable dynamic seasonal level and circulation periods. Several changes in ecosystems and long-term impacts of fish habitat quality and availability due to water level fluctuations in reservoirs have been documented (Sutela et al. 2002, Sutela et al. 2004, Eloranta et al. 2016, Johnsen et al. 2016, Sandlund et al. 2016, Hirsch et al. 2017, Eloranta et al. 2018). All life activities and distribution in fish (spawning, feeding, growth, survival/maintenance, sexual maturation, reproductive success and roe viability) may be affected by the environmental factors from hydropower impacts (Sutela et al. 2002, Johnsen et al. 2016, Carmignani and Roy 2017, Hirsch et al. 2017). Changes in lower trophic levels contribute to the impacts on fish populations and communities (Finger et al. 2007, Landry and Bernatchez 2010, Sandlund et al. 2016). The littoral ecology in reservoirs is particularly vulnerable, due to the biological and ecological effects of recurring drawdowns and potential desiccation of periodically water covered areas (Gracey and Verones 2016, Johnsen et al. 2016, Carmignani and Roy 2017).

Norwegian freshwaters were, after the last Ice Age, first colonized by the most cold-tolerant and stenothermic salmonid Arctic char (*Salvelinus alpinus*). Therefore, Arctic char has the widest distribution of all fish species in Norway, and is commonly a resident species in freshwater lakes (Borgstrøm and Hansen 2000). In a hydropower context the species may, however, be susceptible to changed and aggravated water level fluctuations, in particular with respect to recruitment (Saltveit and Brabrand 2002, Brabrand 2011, Johnsen et al. 2016). The Arctic char uses littoral areas as their spawning habitat in the fall. The eggs incubate at low water temperatures (<3°C) during winter, i.e., often below a cover of ice and

snow (Klemetsen et al. 2003, Budy and Luecke 2014). The eggs hatch during winter or in the following spring, and the shallow littoral areas then become the larval (alevin) nursery areas (Saltveit and Brabrand 2002, Klemetsen et al. 2003, Brabrand 2011, Johnsen et al. 2016). Later, as mobility increase, they typically move to profundal areas until the juveniles have matured and is about to spawn for the first time (Klemetsen et al. 2003). The species feeds on zooplankton or benthic fauna and insects (Amundsen et al. 1999, Budy and Luecke 2014).

Lake Møsvatn, at Hardangervidda in South-Eastern Norway, is by volume the eight largest reservoir in Norway (https://snl.no/vannmagasin_-_kraftverk#%20Norges_10_st%C3%B8rste_reguleringsmagasiner, Oct 18, 2022. Last updated Oct 13, 2022) and by power production capacity the fourth largest reservoir with a yearly mean capacity of 2282.28GWH (<https://www.nve.no/energi/analyser-og-statistikk/om-magasinstatistikken/>, Oct 18, 2022, last updated June 14, 2022). The fish community is dominated by Arctic char but also consist of brown trout (*Salmo trutta*) and European minnow (*Phoxinus phoxinus*). The reservoir is regulated by 18.5m (900-918.5masl) with registered water surface at 919.0masl at the map (<https://vann-nett.no/portal/#/waterbody/016-3-L>). The 0.5m from 918.0-918.5masl are not to be filled with exceptions of extreme flow scenarios (MPE 2015). Extensive littoral areas are affected by drawdown during winter and spring, the main season for hydropower production. These same areas may function as spawning habitats for Arctic char in the fall. Recurring winter and spring water level drawdown likely expose potential spawning grounds to air, ice, and snow during egg and early life stages (Brabrand 2011), but depending on when drawdown occurs and which altitudes functioning as spawning habitats. The sessile in-substratum egg incubation period is most vulnerable to desiccation. But also the larvae (alevin) stage, newly hatched alevins surviving on the yolk sac, are vulnerable (Saltveit and Brabrand 2002, Klemetsen et al. 2003). At this life stage they are susceptible to be stranded by fast receding water (Elliott and Elliott 2010) although they possibly move fast to profundal areas from spawning areas placed in steep topography (Klemetsen et al. 2003). The robustness increases when the alevins develop to fry. The yolk sac is then resorbed, and they feed external. The fry have developed better swimming skills and are more robust to physical

changes in the environment (Klemetsen et al. 2003, Brabrand 2011). The fry stays at profundal areas and grow into juvenile Arctic char that feed on profundal prey. Small sized fish, probably juveniles in addition to European minnows (*Phoxinus phoxinus*), are observed by echo sound in deep areas of lake Møsvatn (Saltveit and Brabrand 2002).

As soon as water drawdown closes and/or snow melt starts, often in May, the water surface level increases when the reservoir fills. The timing of the transition from receding to rising water levels may be critical for Arctic char recruitment, depending on the location of the spawning ground. This timing has been an important issue for the hydropower regulation and associated legislative demands and regulation (Brabrand 2011, MPE 2015). This critical timing period may be difficult to identify *in situ*, although theoretical models based on close monitoring of temperatures and degree-days may give an indication (Jungwirth and Winkler 1984, Wallace and Aasjord 1984, Bebak et al. 2000). However, *in situ* year class strength in relation to environmental conditions during the recruitment period, may shed light on potential causal mechanisms regulating recruitment. This is a frequent methodological approach in fisheries science (e.g., Ottersen and Loeng 2000, Grenouillet et al. 2001, Ottersen et al. 2006). Correlations between reservoir water level fluctuations and egg or alevin survival have been found in Arctic char (Cott et al. 2008, Zohary and Ostrovsky 2011, Eloranta et al. 2016). Similarly, other littoral dependent fish species populations have been found to suffer from drawdowns (Sutela et al. 2002, DeBoer et al. 2015, Klobucar et al. 2016, Carmignani and Roy 2017). On an anecdotal note, substantial annual variation in Arctic char catches is reported by local fishers, who suspect this may be related to winter lake drawdowns. Therefore, the objective of the present master's project was to explore potential consequences of annual water level fluctuations on recruitment of Arctic char in Lake Møsvatn with special focus on correlations with low water levels during spring. Brabrand (2011) suggested Arctic char in Lake Møsvatn may be recruitment limited via this mechanism. If so, deterioration of deposited eggs by exposure to temperatures below zero and desiccation would result in reduced abundance, i.e., year class strength (Brabrand 2011). Recruitment limitation has been observed in lake spawning salmonid populations in other reservoirs (Sutela et al. 2002, Johnsen et al. 2016).

Background: recruitment ecology

Spawning habitats and -behavior

Abiotic limnic parameters like temperature (stratification) and water chemistry may change in reservoirs and cascade into the biotic communities (Johnsen et al. 2016, Hirsch et al. 2017). Downstream of dams, the river-temperature may change due to manipulated water outlet/hydropower intake and discharge from the stratified reservoir (Hirsch et al. 2017, Heggenes et al. 2021). Water chemistry depends naturally on geology and nutrient leakage from the precipitation field and additionally local and/or airborne transported pollutants. Nutrient leakage and finer bottom sediments typically increases in regulated reservoirs compared to natural lakes, due to larger erosion risk (Johnsen et al. 2016, Espa et al. 2019, Cattaneo et al. 2021). Fish species may be left with degraded and low-quality habitats for recruitment and feeding. Species at lower trophic levels (i.e. invertebrate benthos) usually have disadvantage of the dry habitats, which may result in dietary and ontogenetic shifts in fish, to find replacing prey species in new habitats. Large regulation impacts often result in a dietary shift to more large planktonic species and less invertebrates or small fish. Invasive species or for the lake not-native species may be favored by changed environments and invertebrate community might become less diverse (Finger et al. 2007). The consequences are that the ecological balance in general and specifically in fish populations change. Such changes are prey availability, changed food and habitat competition and eventually changed predation pressure or indirectly reduction of recruitment.

Spawning habitats in the littoral zone used by fall-spawning species may become desiccated and frozen during winter drawdown. In particular this would be a risk in reservoirs with high difference between lowest regulated water level (LRW) and highest regulated water level (HRW). To know whether the spawning areas are exposed to such circumstances, the spawning sites and time must be known. Recruitment biology and life history traits are closely comparable in the two most common and widely distributed Norwegian freshwater resident salmonids, Arctic char and brown trout (*Salmo trutta*), despite differences in migration patterns and habitat selection (Klemetsen et al. 2003). Lake-resident brown trout

preferably migrate to spawn in lotic ecosystems (Saltveit et al. 2020). In some lakes brown trout are lake spawners and the spawning sites of the two species then can occur in the same areas (Saltveit and Brabrand 2002, Johnsen et al. 2016). Lake-resident Arctic char usually stay in the lake to spawn (Frost 1965, Low et al. 2011). Typically, spawning areas are found in a few meter wide fields parallel to the shoreline in relatively shallow littoral areas (Low et al. 2011). But also in steep areas (Klemetsen et al. 2003). Depths of spawning habitats are found at e.g. <124 cm and 1-21 m (Frost 1965, Low et al. 2011). Some populations spawn deeper. Rubin and Buttiker (1992) found spawning habitats down to 120m depth. Several places the Arctic char has been observed to develop different morphological variants inhabiting alternative spatial niches. These variants occur sympatric in the same ecosystem, separated by spawning habitats and spawning time. E.g., in deep lakes a profundal spawning Arctic char morph may occur sympatric to a littoral spawning population. (Frost 1965, Nordeng 1983, Hesthagen et al. 1995, Noakes 2008, Low et al. 2011, Alexeyev et al. 2014, Miller et al. 2015). The typical substrate preference is relatively large gravel, with common stone diameters about 1-5cm (Low et al. 2011, Johnsen et al. 2016). Larger stones and rocks in the spawning habitats are not unusual (Frost 1965, Kircheis 1976, Low et al. 2011). In regulated lakes the substrate typically becomes finer through time due to erosion and sedimentation. Thus, the natural spawning habitat and locations provide suitable larger gravel, may deteriorate gradually (Johnsen et al. 2016, Sandlund et al. 2016).

In spawning time, the female locates appropriate spawning sites and surrounding males compete about fertilizing the eggs. They can be aggressive towards other males. The large males are most aggressive, while smaller males are less interacting (Rudolfson et al. 2011). Sneakers are small males, that may fertilize the female's eggs in a short timespan while the larger males are busy defending the female against other large males. Some studies imply that these males seem to fertilize equally to the larger males. Therefore, they represent important contribution to the gene pool and variation (Rudolfson et al. 2011). However, the importance of sneakers' spawning competition ability is unclear. The delay that occurs between the release of female and male sneakers' gonads is unfortunate. Some milt

parameters increase the fluid velocity and help the egg and sperm to fuse. Fertilization ability is therefore increased when spawning occurs synchronized. Larger males in couple with a female on the particular spawning site would likely decrease the small sneakers' intraspecific recruitment competition (Turner 2002, Rudolfson et al. 2006, Rudolfson et al. 2011).

Individuals of Arctic char with a body size of 30 cm are able to move stones at the size of 4cm diameter with their tail as part of the spawning behavior (Fabricius and Gustafson 1954, Low et al. 2011), but they rather tend to shuffle eggs into cavities in the substrate than cover eggs with the substrate. Thus, spawning pits are often less visible as seen for example in brown trout spawning habitats (Klemetsen et al. 2003). Arctic char eggs are deposited on the substrate and are also found hidden in the interstitial spaces inside the substrate. The eggs might be detectable by diving at 5-15cm below the lake bottom (Low et al. 2011). Rather inconspicuous spawning pits with diameters up to 30cm have been found at Lake Fjorda in Norway (Johnsen et al. 2016). The often shallow, littoral spawning sites imply that Arctic char is naturally adapted to spawn in relatively stable lentic ecosystems i.e., not experiencing substantial drop of water level during winter. A corollary is that natural Arctic char spawning sites probably are vulnerable to high-intensive reservoir manipulation involving receding water levels in winter, with associated exposure to freezing temperatures and desiccation (Brabrand 2011, Hirsch et al. 2017). When spawning sites are found in areas with a steep bottom profile (Klemetsen et al. 2003), this will probably to some extent protect the vulnerable alevins and fry from water level drawdowns in late winter/early spring. The steep topography allows them to move faster and more easily to profundal areas after hatching even with less self-made movements (Klemetsen et al. 2003, Low et al. 2011).

In northern and/or alpine lakes in the Nordic countries most lakes are ice covered during the cold season and inverse stratification occurs. Inverse stratification means that the upper water layer under the ice cover holds temperatures in the range 0 - 4°C, while hypolimnion holds 4°C the entire winter. Summer and winter stratification makes these lakes stable by

nature, with the exception of spring and fall mixing periods. By regulation of the water surface, the inverse stratification would be disrupted. Spawning usually occurs in the duration of fall-circulation, at 4°C (Scott and Crossmann 1973, Jobling et al. 1998b). The exact time varies between populations and watercourses (Frantzen et al. 1997, Klemetsen et al. 2003, Alexeyev et al. 2014, Budy and Luecke 2014). Both early and late spawning may harm the egg viability due to narrow temperature tolerance at fertilization and the first days of zygote development. Ambient winter temperature in hatcheries are defined as 1 - 3°C (Jeuthe et al. 2016). Spawning at temperatures below 4°C (down to 0.75°C) has been observed but then with the cause of high egg mortality (Jeuthe et al. 2013, 2016). High temperatures have also been reported to be important to egg loss before the eyed stage (Jeuthe et al. 2013, 2016). By nature, the spawning is inhibited to occur at high temperatures by being synchronized to happen in late fall (October-November). In Arctic char farms spawning have been observed to be inhibited at the upper temperature limit of 10°C (Jobling et al. 1998b). In lakes where different sympatric populations are present, the spawning times differ between populations, and spring spawning may occur (Noakes 2008). If the population is profundal spawning, it may benefit of the 4°C hypolimnion. Littoral spawning populations benefit the fall or spring circulation period of 4°C. In cold freshwater lakes far north and/or in alpine areas, it is likely that main part of the spawning period occurs during the turnover in fall and that most of the egg incubation time happens at inverse stratification during winter. Possibly, the last part of the alevin stage overlaps with spring turnover (Jobling et al. 1998b, Klemetsen et al. 2003, Low et al. 2011, Budy and Luecke 2014).

Because the egg incubation and development takes place in winter, the eggs are susceptible to temperatures below zero additional to desiccation during winter drawdown (Eloranta et al. 2016, Johnsen et al. 2016, Hirsch et al. 2017). Incubation time runs through several months (Jobling et al. 1998b, Klemetsen et al. 2003, Budy and Luecke 2014) and depends on temperatures. In alpine Scandinavian lakes the littoral spawning sites would hold ambient winter temperature (1-3°C) in the upper stratification layer under the ice. (Dumas et al. 1992, Baroudy and Elliott 1994, Jobling et al. 1995, Jobling et al. 1998b, Atse et al. 2002,

Koops and Tallman 2004, Janhunen et al. 2010, Budy and Luecke 2014, Jeuthe et al. 2016). At deeper spawning areas (under the threshold of the hypolimnion) the water would hold 4°C. Water temperatures and oxygen saturation is crucial to salmonid egg development, especially to the cold-stenotherm Arctic char (Budy and Luecke 2014, Klobucar et al. 2016). Survivals of fry, through alevin stage, have in the experimental study of Atse et al. (2002) been reported to be five times higher in low temperatures compared to high temperatures. Oxygen is highly correlated to water temperature, and reported oxygen saturation levels from Arctic char farms are e.g., >70% (Frantzen et al. 1997), >90% (Frantzen et al. 2004) and 98% (Jeuthe et al. 2016). Mortality in early life stages is high and have different causations, among others, thermal stress and egg quality (Jeuthe et al. 2013). Mortality have also been found correlated to acidification in the context of Aluminum poisoning, e.g. low spring and summer pH were associated with weak year classes (Hesthagen et al. 1995). Aluminum is known to affect the oxygen exchange through the cell surface and is highly soluble and biological obtainable when pH is low. Young life stages of Arctic char, i.e. eggs and alevins are more vulnerable to acidification than adults (Johnsen et al. 2016). Examples on management actions to improve spawning grounds for Arctic char in accordance with acidification in Norway are shown by text and video at <https://www.vannportalen.no/vannregioner/innlandet-og-viken/aktuelt-for-vannregion-innlandet-og-viken/se-video-fra-utflyging-av-gytegrus-i-oyangen/>.

Development

In wild Arctic char, the incubation time from spawned eggs to the fry stage can vary with different variables, such as ice-coverage time, water temperature, spawning depth and -habitat, spawning time of the year, egg size and female size (Klemetsen et al. 2003, Budy and Luecke 2014). The fry first feed after several months of egg incubation in darkness after some weeks of alevin stage, i.e. the larvae stage while the yolk resorbs (Klemetsen et al. 2003, Budy and Luecke 2014). When the swimming ability is sufficient to catch small-sized zooplankton they leave the littoral area and develop to independently feeding fry (age 0+) in the profundal zone where they live as juvenile fish. The lake morphology and topography impact the development process and feeding choice for the 0+ fry (Klemetsen et al. 2003).

In small resident freshwater populations of wild Arctic char, individuals mature at 2-6 years of age (Johnsen et al. 2016), while anadromous Arctic char mature at 4-8 years (Nordeng 1983). Sizes vary by age between different populations, so does maturation. When conditions are limited by competition, maturation may occur at smaller sizes (Adams and Huntingford 1997, Klemetsen et al. 2003). When the population becomes less abundant maturation may occur at larger ages. Farmed Arctic char develops faster due to commercial profit demands, and feeding fry stage occurs earlier than in the wild (Frantzen et al. 1997, Jobling et al. 1998b). However, studies of hatcheries and fish farms have useful data with high accuracy and environmental control. They give useful information on biological responses, and lend themselves to do controllable experimental designs (Atse et al. 2002, Frantzen et al. 2004, Janhunen et al. 2010, Jeuthe et al. 2013, 2016).

Already a year previous to the spawning year, development of new oocytes starts in early spring. Light and darkness may affect the progress of maturation (Frantzen et al. 2004). In polar areas the Arctic char is exposed to more light during the summer months with intensive daily light exposure by the midnight sun phenomenon. Manipulation of day lengths impacted on maturation (Frantzen et al. 2004). Thus, there is a possibility that long time with ice coverage may delay the maturation. Alpine Norwegian lakes are usually ice covered several months, often November-May. Exposure to high summer temperatures during female gonadal development have been found to impact the egg size and quality i.e., lipid and hormonal composition (Jobling et al. 1995, Tveiten et al. 1998, Jeuthe et al. 2013) (Tab. 1 below). Female size has been shown to correlate with egg size and egg quality have been found to impact the viability (Klemetsen et al. 2003). Jeuthe et al. (2013) found results indicating that reproductive effectiveness increased with female age up to six years and then stabilized. Furthermore, larger females developed larger eggs (Jeuthe et al. 2013) and larger eggs resulted in larger alevins with less remaining yolk. Larger individuals with less yolk indicates a more advanced developed alevin stage at hatching, and they are likely to consume the yolk sac more rapidly (Jeuthe et al. 2016). Thus, in wild populations larger alevins with less yolk would be more robust.

Food competition and seasonal feeding behavior

In lakes inhabiting the two salmonids brown trout and Arctic char, interspecific feeding competition may occur. Brown trout would by nature defend a diet of larger invertebrates in littoral feeding habitats. Large benthos is needed to increase growth rates before they become piscivorous (Borgstrøm and Hansen 2000) and feed on small Arctic char and to a less degree possibly minnows (Museth et al. 2003) in profundal habitats (Saltveit and Brabrand 2002). In Møsvatn brown trout become piscivorous at the age of eight to nine years and sizes above 30cm (Saltveit and Brabrand 2002). A common consequence from reservoir regulation is that the invertebrate diversity decrease, and that large invertebrate prey are replaced with large zooplankton. Especially the littoral fauna is vulnerable to such impacts (Finger et al. 2007, Sandlund et al. 2016, Murphy et al. 2019). Large zooplankton may also feed on smaller zooplankton and might be a competitor to plankton feeding fish species. When littoral fauna is disrupted, the brown trout are forced towards a more planktonic diet. Similar dietary shift towards more zooplanktons and ontogenetic shift towards pelagic habitat use occurs in Arctic char populations with lack of benthic fauna. Thus, more interspecific competition occurs in the pelagic feeding habitat (Borgstrøm and Hansen 2000). However, the Arctic char consume zooplankton in lack of larger invertebrates more effectively than the brown trout and is more flexible to change between different habitats of the lake and between different diets (Cavalli 2002, Saltveit and Brabrand 2002, Klemetsen et al. 2003, Sandlund et al. 2016). Intraspecific competition in the Arctic char population would occur if the population becomes overcrowded or prey becomes limited (Saltveit and Brabrand 2002, Klemetsen et al. 2003). In fall, Arctic char may eat roe at the spawning areas. Therefore, even immature individuals can be found in the spawning habitats. With respect to recruitment, availability of appropriate small prey is synchronized with hatching time and increased temperature and light exposure that gives rise to the production in spring (Borgstrøm and Hansen 2000). Prey availability largely impacts the individual growth of Arctic char (Cavalli 2002). In alpine lakes, small planktonic crustaceans have been found important in the 0+ fry-diet, while insects (e.g. *Chironomidae spp.*) are naturally important prey species from the age of three years (Cavalli 2002).

Patterns of the combined vertical temperature and vertical trophic level stratification may influence the time spent in water sufficiently cold to permit full development of gametes (Tab. 1). Especially in reservoirs, where insect supply in the diet often is replaced with zooplankton, intense feeding behavior on plankton may cause more foraging in too warm water (Jobling et al. 1995). Temperatures during development of gametes above 12°C may impair, and perhaps even inhibit gonadal development (Jobling et al. 1998a, Jeuthe et al. 2019). According to Gillet (1991) the upper temperature limit during vitellogenesis for Arctic char females to produce viable eggs is 8-10°C with an absolutely maximum at 11-12°C (Tab. 1). The female Arctic char are more susceptible to high temperatures when the temperature is held constant than in a more variable environment (Jeuthe et al. 2013). In natural lakes the summer temperatures are systematically varied by vertical temperature stratification. Thus, the prey availability impacts the selection of feeding habitats and therefore the temperatures during sexual maturation and development of gonads.

Lipid reserves are stored during summer, before the Arctic char almost cease feeding before spawning (Imsland and Gunnarsson 2011). Anadromous Arctic char does not feed at all during over-wintering in freshwater (Jobling et al. 1998a, Heggenes et al. 2017) while the resident freshwater Arctic char has been found to feed some at very low temperatures (Klemetsen et al. 2003). Jobling et al. (1998a) found that anadrome post spawners lose approximately 50-55% (males) and 80% (females) of the deposited lipid storage during the winter. Additional to external factors as prey availability and temperatures (Jobling et al. 1998b, Cavalli 2002), the seasonal growth patterns are internal regulated by hormones (Tveiten et al. 1998). It is likely that the sexual development in lake resident Arctic char can be inhibited by scarce lipid deposition during summer as it is found in anadrome strains of the species (Jobling et al. 1998a, Imsland and Gunnarsson 2011). If so, the gonadal development will stop at stage IV. The developmental stages I, II, III, IV, V, VI and VII-II are explained in the methods. In situations when the development is paused at stage IV, the fish will eventually cease feeding as the fall progresses and winter anorexia is initiated (Frantzen et al. 1997, Jobling et al. 1998a, Tveiten et al. 1998). Food deprivation in spring has been shown to cause compensatory feeding and growth later on, and may also cause limited or

delayed gonadal development (Imsland and Gunnarsson 2011). A negative correlation between relative growth rate and maturation has been found, and lipid storage during the summer season seems crucial (Adams and Huntingford 1997).

Incubation times and temperature impacts

The high contents of neutral lipids in salmonid eggs, are suggested to be linked to long incubation time (Jobling et al. 1998a). Egg incubation in Arctic char occurs under ice coverage during winter, typically at 1-3°C (Jeuthe et al. 2016) for several months (Klemetsen et al. 2003, Budy and Luecke 2014). Different studies use different incubation temperatures due to local circumstances and experimental focus. The degree-days incubation time calculations vary accordingly. For the further sections we define egg incubation time as the number of degree-days from spawning to hatching or calculate it into number of days of a specific temperature. Sometimes the term 'eyed-stage' is used for the embryo stage before hatching. The eyed stage confirm that fertilization has succeeded and occurs approximately the half-way of degree-days to hatching. After hatching, the larvae have a yolk sac attached. This stage is called the alevin stage. The alevins have no or little self-movement and stay at the spawning site. The alevin stage has some mystery around it due to lack of information on what happens from hatching until feeding fry. Elliott and Elliott (2010) defines it as an after-larvae-stage staying in the gravel, while Klemetsen et al. (2003) might be understood in the direction of less sessile alevins which might be movable if the water streams and/or topography allow them to leave the spawning area. The incubation time as the degree-days from fertilization through all stages until first feeding fry is less reported and the degree-days during all stages are usually not given in the same studies. Therefore, we have calculated some of the intervals ourselves by use of the most appropriate temperature ranges despite some differences in thermal conditions.

In the wild, the incubation starts with spawning, which is likely to be 4°C. Further on, the incubation time would be in the range 0 - 4°C for most of the process with a possible exception of the alevin stage while the temperatures can be increasing to e.g. 4°C. Incubation time from spawning to hatching normally takes about 450-450 degree-days,

depending on temperature (Jobling et al. 1998b, Janhunen et al. 2010, Jeuthe et al. 2016). In Atse et al. (2002) eggs were held at constant incubation temperature 4.5°C in darkness until hatchment. Then the temperature was increased by 0.5°C pr day through the alevin stage until first feeding. The temperature rise was stopped at 8°C. The study focused on survivals in water with different temperatures and salinity. Survivals at the different stages (24 hours after spawning, eyed stage, hatching, and first feeding) were counted. In Atse et al. (2002) the estimated degree-days were defined as the time when 50% of the total number of individuals (or eggs) had reached the specific stage. This differs from e.g. Jeuthe et al. (2016), where the hatching day was defined as the day when 90% of the eggs were hatched. Unfortunately, Atse et al. (2002) only reported the degree-days from fertilization to first feeding fry, which were 627±13 degree-days. The result was similar to all experimental groups. Relatively high temperatures were used. In comparison, Jeuthe et al. (2013) reported the incubation time from spawning to hatching and included the specification of the eyed stage. Ice-covered freshwater alpine lakes in Norway might fit the degree-day-scheme and temperatures used in Nordic experimental studies, e.g. Jeuthe et al. (2013, 2016), Jeuthe et al. (2019) and (Jobling et al. 1998b), Janhunen et al. (2010). Those studies might be useful for degree-day calculations in wild cold-water Arctic char populations.

Several studies have explored the importance of incubation temperature, e.g. Janhunen et al. (2010) who compared the development at optimal (2°C) and extremely stressful (7°C) incubation temperature. Rate of viable and largely developed alevins by hatching (larger individuals with less remaining yolk) were higher at 2°C incubation temperature. The embryos at eyed stage were also found larger and more successfully developed. Other studies show similar results (Jobling et al. 1998b, Jeuthe et al. 2016). Furthermore, hatching rate is reported higher in lower compared to higher temperatures, 47% by 6°C to 65% by 3°C (de March 1995). Thus, it seems that low temperatures (as occur in the wild in ice covered lakes) delay the development in time (Jobling et al. 1998b) but reduce the number of degree-days (Janhunen et al. 2010). Furthermore, the eyed stage and alevin stage become larger and more successfully and completely developed with fewer development failures and less variation between individuals (Janhunen et al. 2010, Jeuthe et al. 2016).

The low temperature scheme in Janhunen et al. (2010) (2°C until hatching) seems appropriate for modelling wild Arctic char populations in Northern alpine lakes with incubation process going on under the ice during winter. The degree-days of alevin period (from hatching to feeding fry) was unfortunately not reported. Information from Atse et al. (2002) might therefore supply the total degree-day calculations of the total development process.

In respect to degree-day calculations, Janhunen et al. (2010) found the eyed stage to occur after 222-224 degree-days by 2°C incubation temperature, compared to 343-355 degree-days at a 7°C (Tab. 1). Hatching occurred after 450-483 degree-days at 2°C compared to 702-708 degree-days at a 7°C (Tab. 1). Results close to the observations in Janhunen et al. (2010) is reported by Jeuthe et al. (2013), where the eyed stage occurred after approximately 220 degree-days (Tab. 1). This study focused at the most on mortality of eggs until eyed stage and how egg sizes and quality correlated to female age. Therefore they reported only the number of degree-days until the eyed stage. In Jeuthe et al. (2016) hatchment occurred in the range 370-530 degree-days for six batches with different temperature treatments during the experiment. The variability in the duration of the experiment makes it less useful for modelling wild-population incubation time.

Calculated incubation time from eyed stage to hatching would take 228-259 degree-days, given the information in Jeuthe et al. (2016) and Janhunen et al. (2010). The duration of the alevin stage i.e., degree-days from hatching to first feeding, is more difficult to find. However, it might be calculated from the results of Atse et al. (2002) and Janhunen et al. (2010) despite different use of temperatures which makes the calculation less precise (Tab. 1). To supply calculations of the duration of the alevin stage, knowledge about brown trout alevins might be useful. The brown trout alevins have been found to consume the yolk sac in 52 days (Ojanguren et al. 1996). With knowledge of hatching time of the Arctic char population, incubation temperatures for the duration of alevin stage can be calculated more precise. With knowledge of the different incubation times, the seasons for desiccation

vulnerability can be interpreted more precisely. The conclusions of such findings, then can be implemented into the management and regulation regime of the reservoir.

Table 1. Temperature preferences of the Arctic char through different life stages.

Life stage/process	Preferences	Limiting factors	Duration	Selected references
Sexual maturation	4-8°C	Delayed >8°C Disrupted or inhibited >11-12°C	From early spring through the entire summer and early fall. First spawners in wild freshwater populations are about 2-6 years.	(Gillet 1991, Jobling et al. 1998a, Jobling et al. 1998b, Jeuthe et al. 2019)
Spawning and fertilization	4°C	Egg mortality observed at high and low temperatures (2-0.75°C and >10°C)	3-4 weeks	(Jobling et al. 1998b, Jeuthe et al. 2013, 2016)
Egg incubation from spawning to hatching	0.5-4°C	Delayed >6-7°C. Egg mortality >10°C	Eyed stage: 222-224 °C-days. Spawning-hatching: 450-483d°C	(Janhunen et al. 2010, Jeuthe et al. 2013)
Alevin stage	4-6°C	>8°C	614-640 °C-days from fertilizing to first feeding. Calculated by combining references to be 157-164°C-days from hatching to first feeding	(Atse et al. 2002, Janhunen et al. 2010)
Feeding, growth, maintenance, and survival	7-8°C, large individuals may feed and grow at temperatures towards 0°C	Reduced juvenile growth at >12-15°C. Temperatures from 21-22°C and above, are lethal to juveniles.	Spring/summer: body lipids are deposited. Fall: feeding cease before recruitment. Winter: starvation. Survival by use of deposited body lipid storage.	(Jobling et al. 1998a, Tveiten et al. 1998, Imsland and Gunnarsson 2011)

Study area

Geolocation, lake morphology and hydrology

The studied reservoir is located at Hardangervidda in South-Eastern Norway (Fig. 4), in watershed area #016 (*'Skiensvassdraget'/'Langesundfjorden'*) at 919masl (<https://atlas.nve.no>). Hardangervidda is a Norwegian National Park which is a large, protected mountain area due to its vulnerable alpine nature and several endangered or near threatened species. The total area of the main watershed #016 (Fig. 1 and 4) is 1504.2 km². The yearly water flow supplying the reservoir from the surroundings is 1565.35 million m³ and the residence time is one year. The reservoir volume is 1573.523 million m³ (<https://atlas.nve.no/>). Surface areas of the reservoir depends on the water level and range from 78km² to 28km², mean depth is 20m and maximum depth is 68.5m (<https://vann-nett.no/portal/#/waterbody/016-3-L>). The main rivers into the reservoir are Kvenna, Hondle and Skinåi (Fig. 2). The main river from the reservoir is the regulated river Måna, that flows east ca 730 altitude meters via six hydropower plants and several installations (Fig. 3) to Lake Tinnsjø (altitude 190masl, area 51km², mean depth 190m, maximum depth 460m, volume 9700 million m³, residence time 2.9 years, watershed area 3768.91 km², and 3339.29 million m³ water supply per year). The regulation regime of the dam and thus, the water level in the reservoir Lake Møsvatn is mainly dictated by the downstream hydropower station needs and restrictions on the water levels in the regulated Lake Tinnsjø and its outflowing river Tinnelva (Fig. 3).

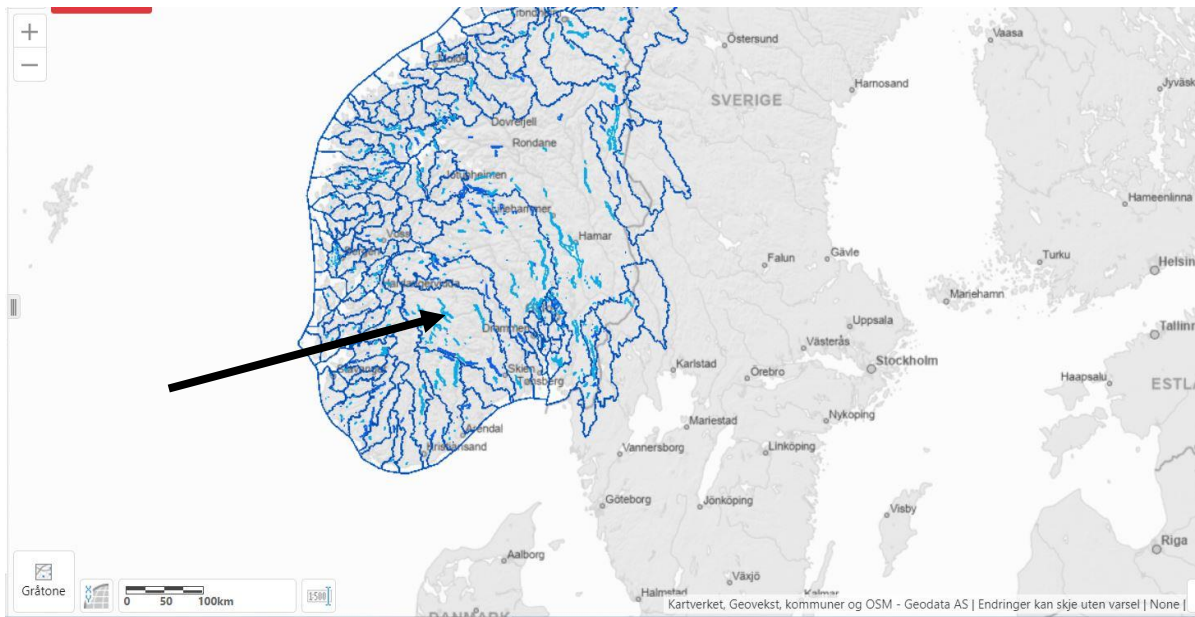


Figure 1. Geographic location of the watershed area 016 where reservoir Møsvatn is the headwater for the downstream hydropower industry.

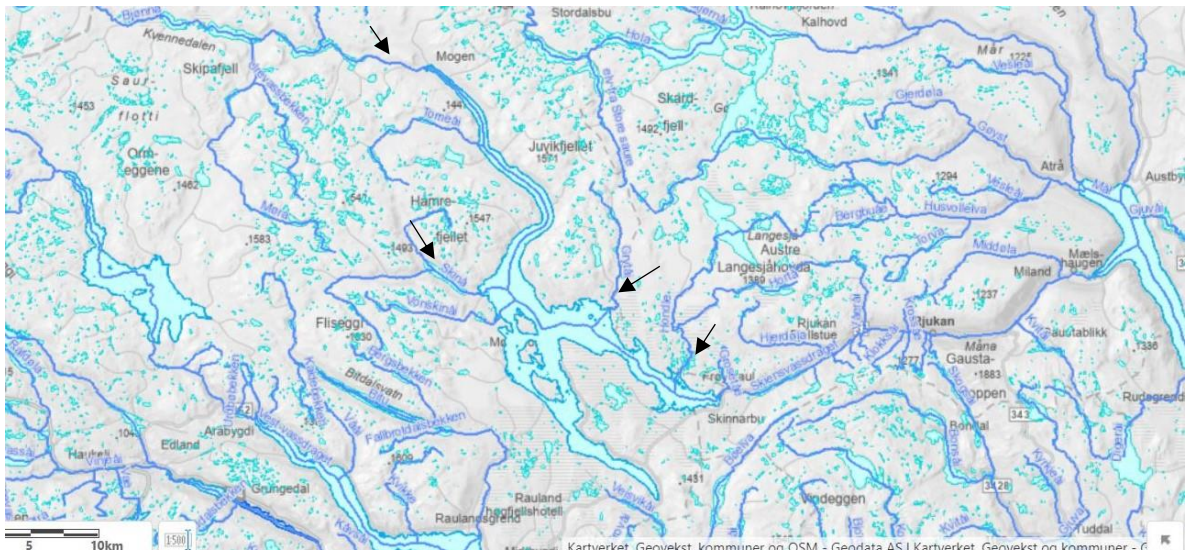


Figure 2. Main rivers into the reservoir. Marked with arrows: Kvenna, Skinåi, Grtåi and Hondle.

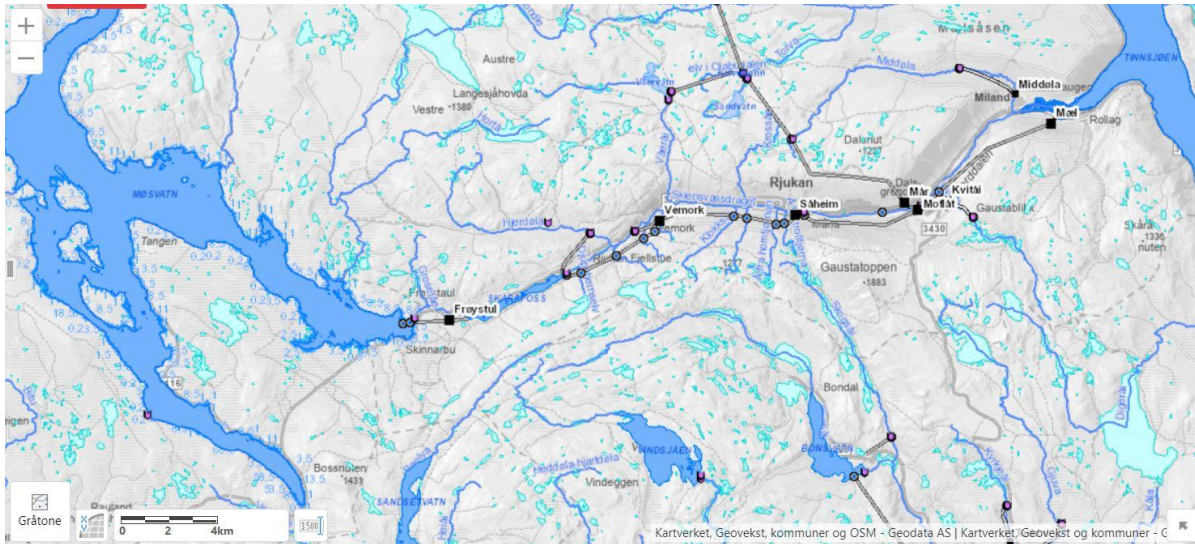


Figure 3. Power production developments in the river Måna from lake Møsvatn to lake Tinnsjø.

The area is alpine (above 800masl and more or less above the threshold for tree-growth) (Fig. 4). More exactly, the reservoir is located at 919masl according to the map, although HRW is 918.5masl, according to the legislation rules (MPE 2015). LRW is 900masl (Fig. 5) and has not been changed the entire time from the beginning of the dam development. Due to erosion risk, the water surface level is seldom risen above 918.0masl (Fig. 5). The concession expresses that only in extreme flow situations the upper half meter (918.0-918.5masl) is allowed to be filled and then only in situations in danger of flow damage downstream the dam and further down the watercourse (MPE 2015). The dam owners (Øst-Telemarkens Brukseierforening (ØTB)) record water levels. In addition, chemical, physical and ecological parameters have been monitored for several years (<https://vanmiljo.miljodirektoratet.no/>). The main water chemistry sample station by the dam, is geolocated at EREF89, UTM33N: 125283E 665037N. Additionally, several other sample stations have been administrated to monitor micro-flora and -fauna, benthos, and other biota (<https://vanmiljo.miljodirektoratet.no/>) (Fig. 4). Through the lifetime of the reservoir, extensive amounts of bottom sediments have been moved. The purpose of the sediment movements has been to increase the water flow between the different parts of the basin and distribute the waterflow more evenly with increased regulation efficiency as the result (Brabrand 2011). The movement of masses, additionally sedimentation, erosion, and

recurring impacts from annually water level changes, have changed the bottom topography and sediment composition. Possibly, parts of the old Arctic char spawning habitats have been deteriorated (Brabrand 2011, Reckendorfer et al. 2019).

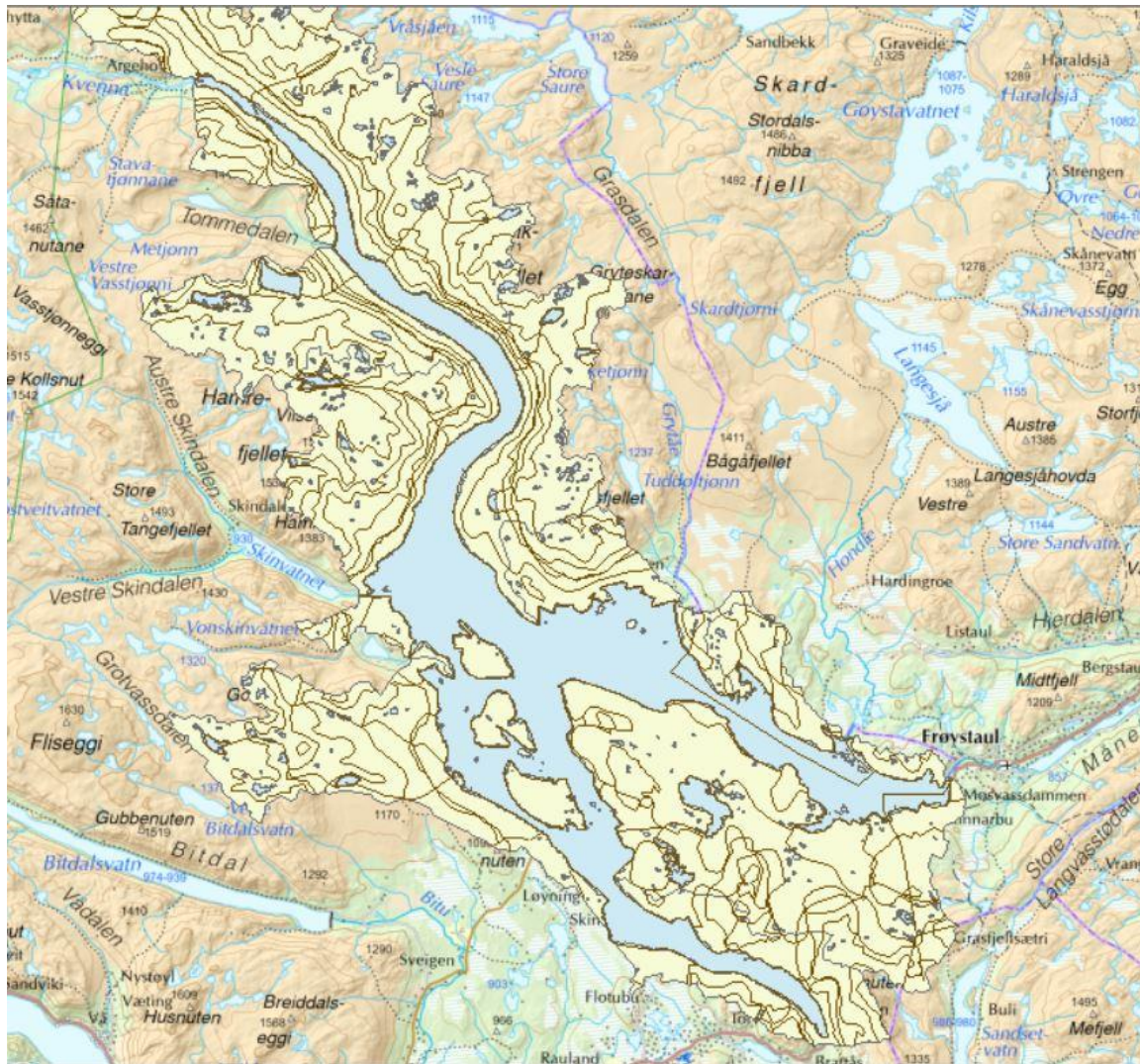


Figure 4. Local watershed (in yellow) (Area 374.91km²) to the Lake Møsvatn reservoir. Source: Regime model from the Norwegian Energy Resources and Energy Directorate (NVE). Source for altitude curves in the precipitation field is Norwegian Institute of Bioeconomy Research (NIBIO). The water chemistry sample station close to the dam construction is georeferenced EREF89, UTM33N: 125283E 665037N (<https://vanmiljo.miljodirektoratet.no/>). All GIS datasets are downloaded from <https://kartkatalog.geonorge.no/>.

Dam development – historical changes of the lake morphology

Lake Møsvatn has been regulated from 1906-11. Hydropower development started in 1903. Before damming, there were three natural lakes: Lake Møsvatn (902masl), Lake Martinsfjorden (904masl), and Lake Kromvatn (905masl). Thus, the Møsvatn reservoir has three main bodies of water with more shallow areas in-between (Brabrand 2011). The first hydropower concession permitted HRW to be 912masl and LRW to be 900masl. These restrictions were in effect until new concessions replaced them in 1908, 1942 and 2015 (MPE 2015). In 1908 the dam construction was improved (<http://www.otb.no/naturen-i-arbeid/>). Furthermore, a channel with 500 meters length and four meters width was built between two parts of the waterbody: the previous Lake Martinsfjorden and Lake Møsvatn. This improvement allowed for tapping of more water to hydropower production. HRW was at the same time increased with 2.5 meters, to 914.5masl (Brabrand 2011). The channel was cleaned and expanded to seven meters width in 1940-41. In 1942 HRW was raised to 918.5masl in a new concession reaffirmed in 1948 and valid for 60 years (MPE 2015). A concession describing those upper four meters (914.5-918.5masl) was issued in 2015 and will be valid for thirty years or until eventually ecological consequences demands new restrictions and replaces it (MPE 2015). Further improvements and clean-ups of the channels were done in 1948, 1956 and 1994. The last improvement (1994) increased the water flow between the main reservoir Lake Møsvatn and the two others by removing 20000 m³ of bottom sediments (Brabrand 2011). Additional 5000 m³ of sediments were removed from three smaller channels, i.e., a 500 meters long channel in the previous outlet of Lake Kromvatn and at two other locations. Thus, the bottom topography and substrate quality, especially in the areas between the previous Martinsfjorden (the southern narrow arm, map in fig. 4 and 5) and the main reservoir, were changed (Brabrand 2011).

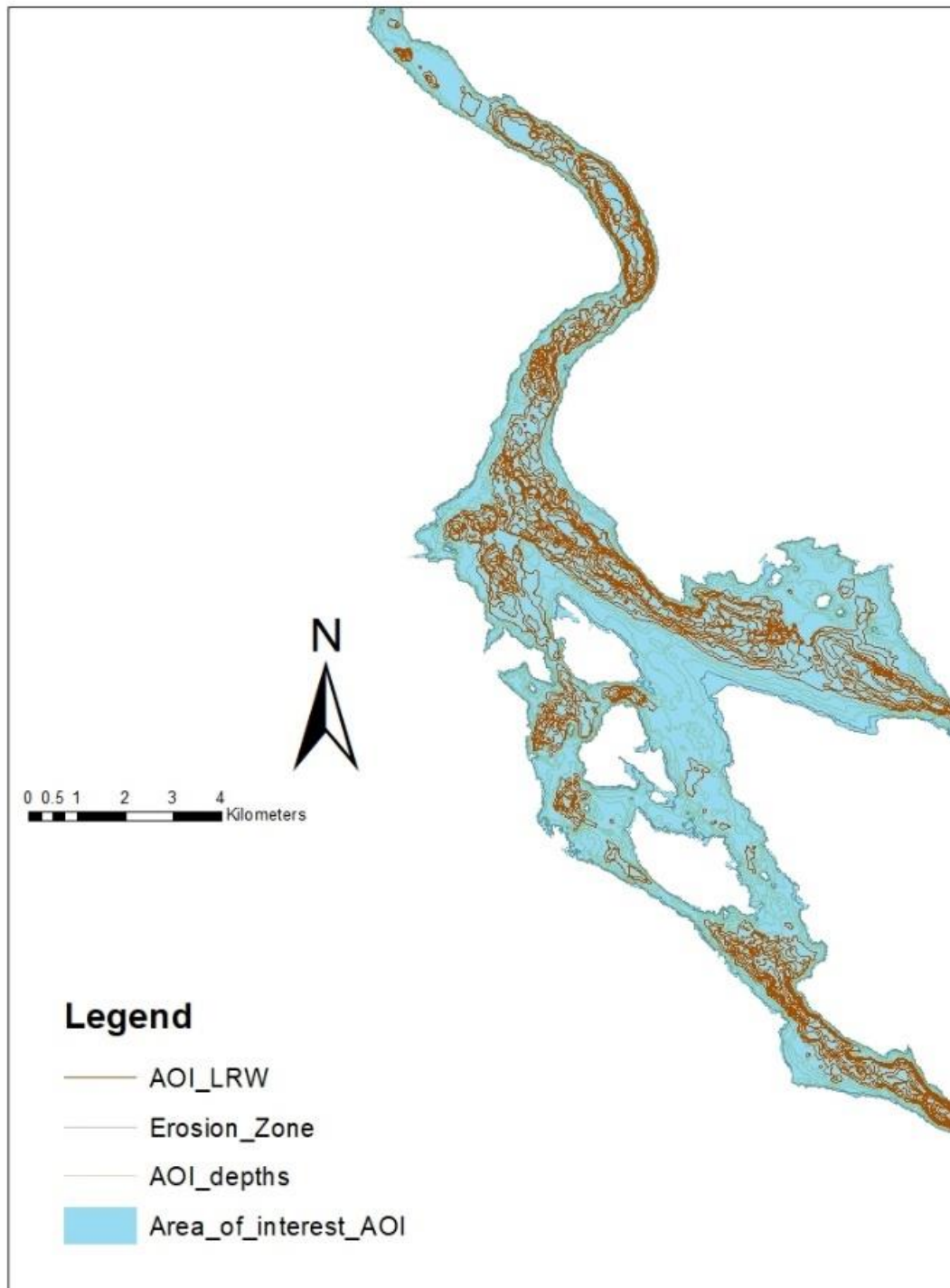


Figure 5. Lake Møsvatn with depth curves. Red curves are all depths from LRW and below ($\leq 900\text{masl}$). Each depth curve represents four meters. Dataset source is Norwegian Energy Resources and Energy Directorate (NVE) downloaded from <https://kartkatalog.geonorge.no/>.

Geology and water chemistry

The bedrock consists of mixed magmatic minerals, acidic migmatite in the North-Western part and several rock types with different pH in the South-Eastern part (Norwegian Geological Survey (NGU)) (fig. 6). In alpine areas, the soil layer often is very thin and poor in nutrition. Thus, the bedrock types dictate a large part of the natural lake pH and minerals, by leakage into the water. Mean water pH in lake Møsvatn was 6.45 in 2016. Older data show almost similar, or slightly lower results (mean pH 6.41). Mean calcium level was 1.35mg/l based on older data. We are studying a very oligotrophic lake, with TOC values often recorded <2 and all available data are <5 (<https://vanmiljo.miljodirektoratet.no/>). The sedimentation and water level fluctuations have impacted the ecological responses, which can be observed in the composition of species, especially the invertebrate fauna, and in fish abundance. Lake Møsvatn have a stable pH between six and seven and the water chemistry does not reflect any acidification problems (<https://vanmiljo.miljodirektoratet.no/>).

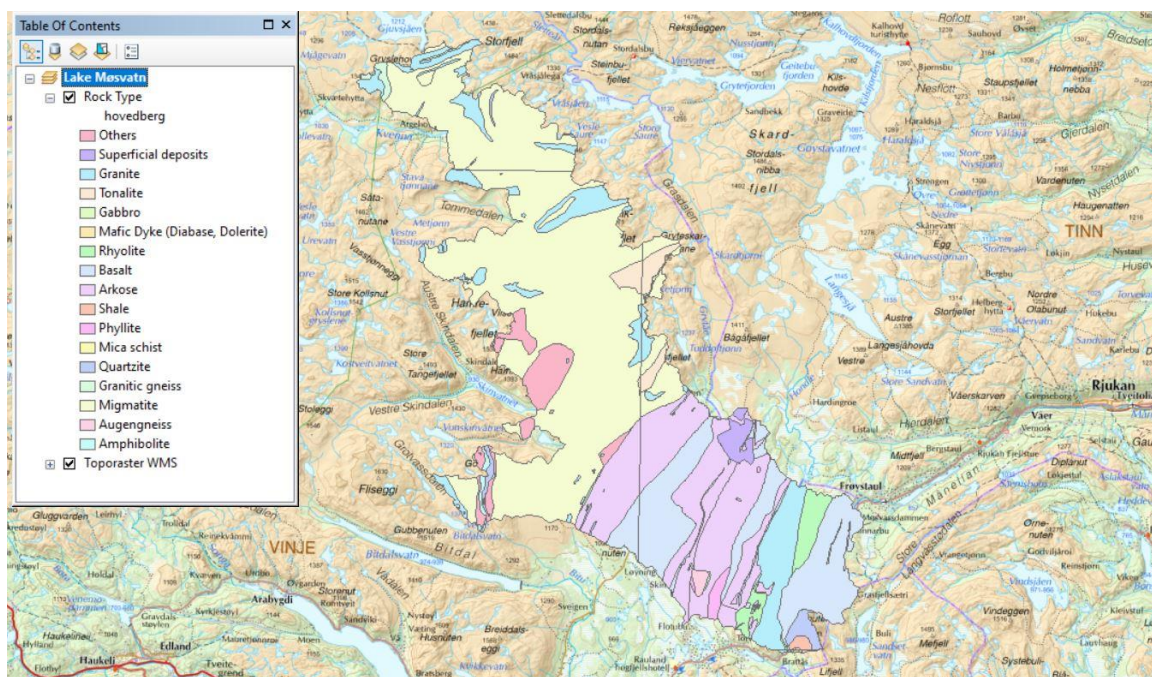


Figure 6. Local bedrock geology in the watershed surrounding the reservoir. In the North-Eastern part, the bedrock contains mainly migmatite while the South-Western part consists of a mixture of several rock types e.g., arkose, basalt, granite, and rhyolite. Dataset source is Norwegian Geological Survey (NGU) downloaded from <https://kartkatalog.geonorge.no/>

According to the Norwegian guidelines for the Water Framework Directive (WFD), the lake is located to eco-region Southern Norway and water-region Vestfold and Telemark (<https://vann-nett.no/portal/#/waterbody/016-3-L>). The water chemistry fits the National water category L304 (lime-poor/very clear) (personally calculated from the Norwegian WFD guidelines). The difference in water type from <https://vann-nett.no/portal/#/waterbody/016-3-L>, which puts the lake into the category L204, probably comes from the climate zone, i.e. the registered climate zone is 200-800masl, while the correct climate zone is alpine (above 800masl). However, this difference doesn't impact the classification of ecological health notably. Furthermore, the lake has to be classified in the group of highly impacted water resources (SMVF) due to its importance for energy supply (Direktoratgruppen Vanndirektivet 2018).

Ecology and fish assemblage

According to Huitfeldt-Kaas (1935): '*Der Einfluss der Gewasserregulierungen auf den Fischbestand in Binnenseen*', cited in Saltveit and Brabrand (2002), Brabrand (2011), Lake Møsvatn was inhabited by brown trout only, until the middle of the 1930ies. Arctic char then immigrated from lakes in the surrounding area, where it had been stocked by man. Later, probably in the 1970ties (Quenlid 2004), the invasive European minnow was introduced by accident (Hesthagen and Sandlund 2016, Hesthagen and Sandlund 2018, Lyche Solheim et al. 2019). For brown trout, Saltveit and Brabrand (2002) found important recruitment habitats in the large inflow rivers, especially Kvenna. Still, some brown trout stocking has been considered necessary to maintain the abundance. Annually, 3500 fry (0+) and 700 yearlings (1+) have been stocked since 1959. Since 1973, the farmed juveniles come from Tunhovd-stock (Saltveit and Brabrand 2002). The stocked trout, of non-native origin, do not appear to reproduce successfully. Genetic studies indicate that the native strains of brown trout in Lake Møsvatn is naturally reproduced in the main inflowing rivers Kvenna, Hondle and Skinåi (Heggenes and Røed 2006). Arctic char has not yet been stocked, but has been suggested by Brabrand (2011) as one alternative to management actions, because Arctic char reproduction appears to have been reduced in recent years. The Arctic char mainly spawns in the littoral areas (above) (Brabrand 2011). Also young brown trout have

been observed in the same nursery habitats, suggesting some lake spawning individuals (Saltveit and Brabrand 2002), which is also reported from earlier times by Huitfeldt-Kaas (1935).

Food webs and invertebrate fauna

In Lake Møsvatn, the littoral ecology has become disturbed for all trophic levels due to the reservoir regulation, and as seen in other reservoirs, the food webs have been changed. Although the zooplankton and benthos communities in Lake Møsvatn still contains several species (<https://vanmiljo.miljodirektoratet.no/>), comparison of data (e.g. <https://vanmiljo.miljodirektoratet.no/>) from different periods of time indicates biotic changes in lower trophic levels, i.e. invertebrate fauna (Saltveit and Brabrand 2002, Lyche Solheim et al. 2019). Common prey species replacing the natural but disturbed benthos in reservoirs, are large crustaceans (Fig. 7), e.g. *Gammarus lacustris*, *Eurycerus lamellatus* and the *Triopsidae* (Borgstrøm and Hansen 2000, Sandlund et al. 2016). *Gammarus lacustris* are often important prey to brown trout until they have grown large enough to become piscivorous (Borgstrøm and Hansen 2000). Brown trout have been found by Saltveit and Brabrand (2002) to be piscivorous at about 25 – 30 cm in Lake Møsvatn. *Lepidurus arcticus* is an important prey crustacean to Arctic char (Saltveit and Brabrand 2002) and adult individuals of the species have been found in Lake Møsvatn in 1930 and 1964 (vanmiljo.miljodirektoratet.no). Their egg stage probably benefits from dry and frozen environments (Sandlund et al. 2016), and is therefore well adapted to the fluctuating water levels in heavily regulated reservoirs. Because of hydropower impacts, the amount of available benthos is reduced in the littoral areas. The zooplankton community also change due to sedimentation and changed substrate quality. In Møsvatn e.g. *Eurycerus lamellatus* might have been favored with increase of more fine-particular substrate (Saltveit and Brabrand 2002). Interspecific competition between Arctic char and brown trout for the planktonic species in the pelagic zone will typically increase with such ecological changes. In lakes with high minnow densities, minnow would likely represent additional prey competition to the salmonids, and with higher consequences when the diet alters towards more planktonic species (Fig. 7) (Cavalli 2002, Sandlund et al. 2016, Jensen et al. 2017). On

the other hand, minnow may also, at least in some cases, supply the diet to piscivorous brown trout (Museth et al. 2003). In Lake Møsvatn the minnow population was found by Saltveit and Brabrand (2002) to be rather abundant in deep water together with small sized, probably Arctic char juveniles. Large brown trout might eat small sized Arctic char, and both salmonids may appear to be cannibalistic and eat juveniles or fry of their own species from sizes below 30 cm (Saltveit and Brabrand 2002, Kahilainen et al. 2019). The minnow and small Arctic char might constitute important prey to large piscivorous brown trout, which also has been pronounced as an important management goal for the reservoir (Saltveit and Brabrand 2002, Sandlund et al. 2016).

FOOD WEB – THE AQUATIC FAUNA IN LAKE MØSVATN

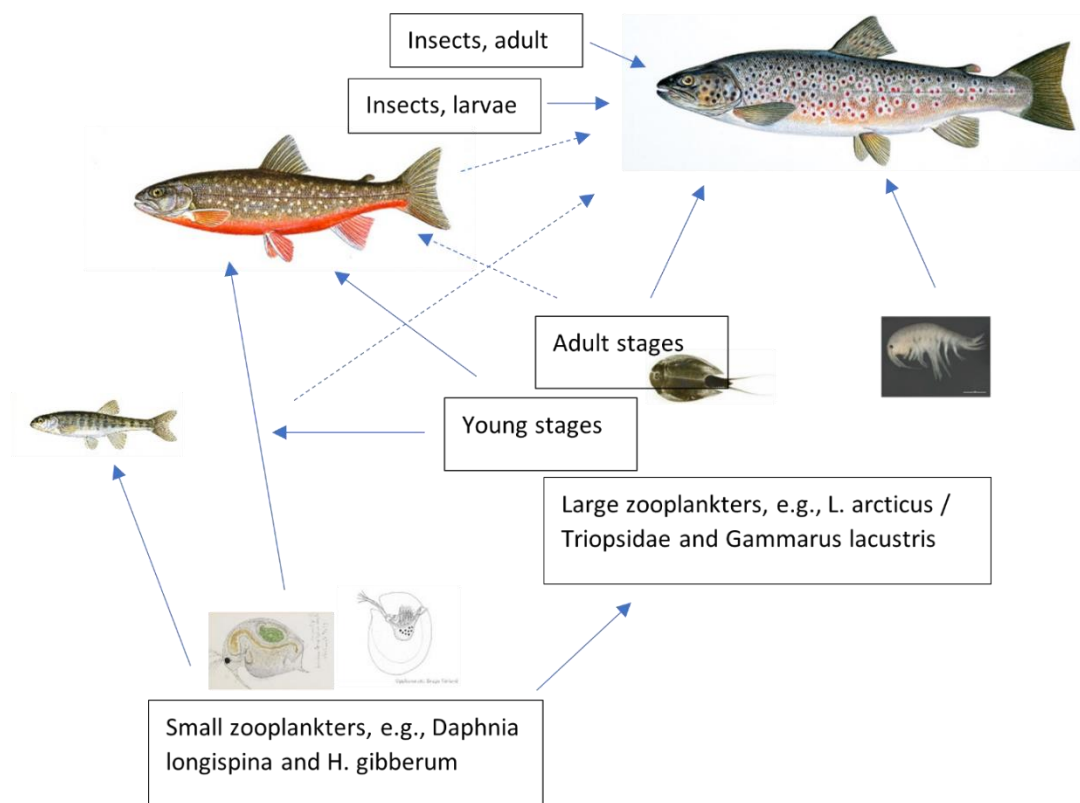


Figure 7. Examples of the food-web in Lake Møsvatn. Several species at the lower trophic levels exist and the species in the figure must be seen as examples from the different taxa.

Hydropower production impacts

The Møsvatn reservoir surface elevation, ranging from 900-918.5masl, is mainly a result of hydropower production (Lyche Solheim et al. 2019). The used and/or potential spawning areas in the reservoir have never been systematically investigated or mapped for the whole reservoir, although field studies and excursions have been conducted (Brabrand 2011). Brabrand (2011) pointed out that spawning by Arctic char in general tend to take place in shallow littoral areas (above) and in late fall when the Møsvatn reservoir typically is nearly full, i.e., 914.5-918.5masl. It was suggested that reservoir drawdowns during the egg stage likely would lead to reduced recruitment because of egg exposure (freezing, drying). The until now final concession for the reservoir (MPE 2015) considers the upper four meters of surface water levels (914.5-918.5masl) to be the most important issue. Restrictions on drawdowns during winter, demands the water surface level to be filled to the altitude of 914masl as soon as possible in spring, and maintain water surface at that altitude until December 1 (MPE 2015). What happens to the eggs when drawdown occurs after Dec. 1, but still before the hatching/alevin stage, is not known. The concession and hearing debate imply that the Arctic char is important to the local people.

As explanatory factor for any recruitment problems in Arctic char, Brabrand (2011) suggests the annually recurring water level fluctuations during the egg stage. This hypothesis generated the concession renewal in 2015. Several regulation restrictions were implemented (below) (MPE 2015). A new 'Energy Law' (<https://lovdata.no/dokument/NL/lov/1990-06-29-50>) in 1991 opened for export of hydropower from Norway, and increasingly more hydropower has been exported from Norway. Consequences are, among others, that there are now earlier and more drawdowns/fluctuations in hydropower reservoirs. The regulation of Lake Møsvatn has been typical for Norwegian reservoirs. If not restricted, a major drawdown appears early in the fall/winter transition and continues during the winter months, dictated by high power prices in Europe. Drawdown continues until snowmelt in spring (fig 8).

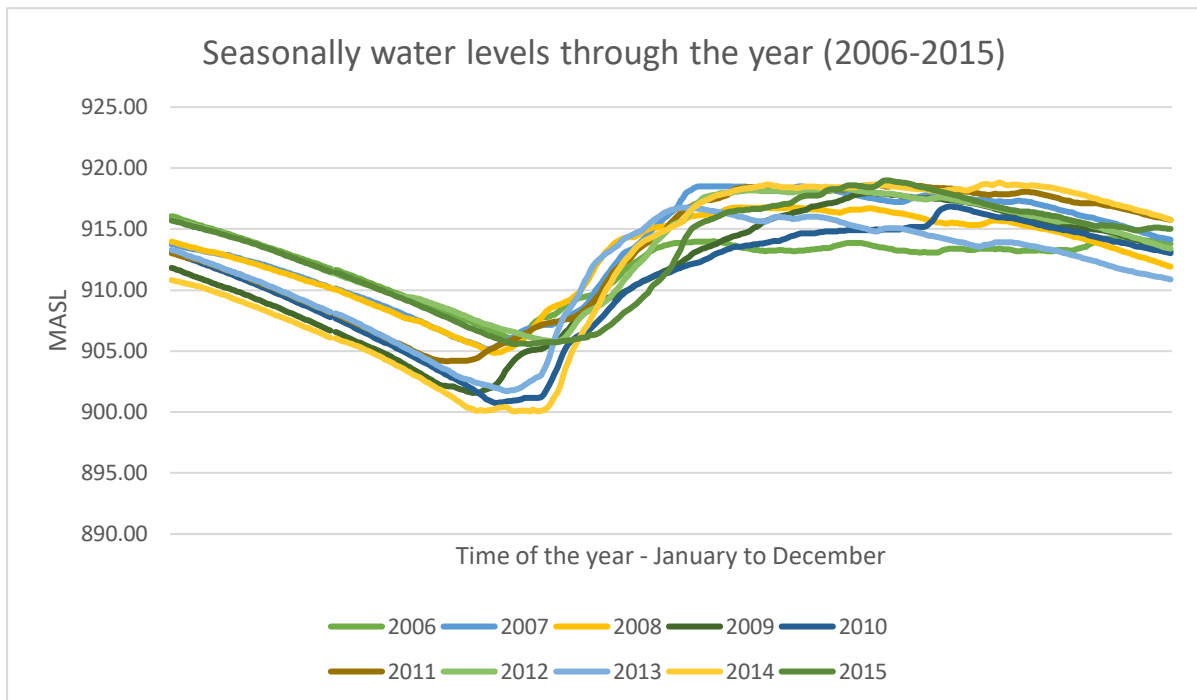


Figure 8. Water levels the ten years of hatching seasons of the present study's samples. The drawdown pattern is typical for Norwegian high head reservoirs after increased energy export from 1991 and further on.

The current concession restrictions for Lake Møsvatn after 2015 (MPE 2015) are briefly summed up below:

- All water supply from the inflow rivers in spring should be used to fill the reservoir as fast as possible up to 914masl and 914masl should be approached before May 1.
- From May 1, until December 1, the water level should be changed as little as possible, and preferably be kept at or above 914masl.
- On December 1, the water level is allowed to drop below 914masl.
- The upper 0.5 meter (918.0 - 918.5masl), is for flow limitation downstream the reservoir only, due to erosion risk. Thus, normal HRW is 918.0masl.
- The reservoir's fish populations should be evaluated every five years. The recent focus have been on the Arctic char population due to the reported recruitment decrease in Brabrand (2011).

- Annually stocking of brown trout should be continued to maintain the population despite reduced recruitment.
- Arctic char population is, and should be, harvested by the local people as income supply. This inhibits over-crowded populations, but abundance must be monitored. Potentially, stocking may be an alternative if research reports conclude with recruitment reduction.

This master's thesis evaluates the period before the last concession from 2015 and is a supplement to the required evaluation program of the ecological situation in the reservoir. The focus is mainly on the Arctic char recruitment and how it potentially may be affected by water level fluctuations and temperatures, in particular during the egg-alevin-fry stages. Other ecosystem parameters are assessed in the context of a holistic ecosystem-based management point of view.

Methods

Water levels

Vulnerability by desiccation during drawdown might be represented by observations of eyed Arctic char eggs between HRW and LRW (Brabrand 2011, Hirsch et al. 2017). Although mortality in Arctic char eggs are naturally high (Jeuthe et al. 2013), observations above LRW would prove spawning in areas that are likely to be desiccated during egg incubation in winter or alevin development in spring. Earlier studies in the area have discussed the problem and the issue is important in respect to the formula of future concessions and to weight human benefits against the ecological costs in another legislation (Saltveit and Brabrand 2002, Brabrand 2011). Clear correlation between water levels and year class strengths have not yet been found. The reservoir has been monitored for several years. The present study explores the hypothesis of potential correlation between water levels and recruitment. The last ten years of the regulation regime before the concession of 2015 is in focus. Those years were the hatching years of the individuals in the two samples of the study, sample 1 and sample 2 (caught in 2016 and 2019, respectively). The data for the years 2009-2014 were extra relevant to compare with each other, because the age classes of those years were close (5-7-years-old). Relevance of comparison between the two samples were higher in close year classes due to a 'normal' population structure and observed natural mortality above six - seven years. The water levels approach LRW in April and May at an annually basis, and recurring drawdowns seem to occur about the same times of the year (Fig 8). We have explored the hatching time by calculating degree-days and interpreted the water level data obtained from ØTB. Minimum altitude level for spawning area and the duration of time when the water level must cover that altitude was calculated. Data of maturation stage and stomach contents from the samples supplied the calculations with information. The reservoir was managed according to the old rules before the concession from 2015 during the hatching years of the sampled individuals of the present study.

Field sampling

The sampling was in large degree conducted by local fisheries, who work with fishery supplemental to their other jobs. They sampled 227 fishes by bottom gill nets with 57 mm (knot-to-knot) mesh size the two sampling years (124 in 2016 and 103 in 2019). Further four fishes were obtained from field workers from USN. The fishing took place in fall, during the assumed spawning period (October-November). Mean October levels for each of the ten years was in the range 913.3-918.4. Thus, the material used in the present study is a sample of the reservoir's spawning population, taken in 2016 and 2019. The gill nets were set in rows consisting of 3-4 net units, i.e., 75-100 meters long rows, starting at approximately one meter depth and ended at about 15-20 m depth. It is likely that the nets have reached LRW (900masl) some places and approached it other places depending on the slope. Thus, spawning ground should have been hit provided the spawning areas are above LRW. The accurate sample times of each individual fish is unknown in the timespan of the 3-4 weeks from mid-October to first week of November (2016). Due to unforeseen circumstances, the sampling took place about 2-3 weeks later in 2019, i.e., last week of October to mid-November. First, the sample size in 2019 was too low, i.e. $n < 100$, and thirty-one individuals were added later on, from another local fisher. These individuals were meant for the ordinary food consumer market and therefore, the fisher had already gutted and cleansed them. Weight and gonadal/stomach assessments were therefore not available from these individuals. However, the age determination was the most important and the sample size became sufficiently large ($n=107$) for the correlation analyses. The analyses of sexes, maturation and stomach contents were thus taken with a lower sample size than the water level – age correlation analyses. When those factors were crossed, the individuals missing data on one variable were excluded. Samples from previous years were stored at Laboratory of Freshwater Ecology and Inland Fishery (LFI) at Natural History Museum, University of Oslo (UiO), and we received the frozen fish from 2016 at USN in fall 2019. The representant from LFI who brought the fish to USN, instructed the biology laboratory method. A field team from USN brought the sample from 2019 frozen to us, and the fish were stored at the university until analyses took place.

Individual sampling protocol

During July, August, and December 2019, we investigated the individual samples from each of the two years in the biology laboratory at the University of South-Eastern Norway, campus Bø. We conducted measurements of length and weight by the metric scale, to the nearest millimeter and gram. As the fish was still whole, a vertical dorsal cut into the neck, 1-2 cm behind the skull bone, gave access to assess the muscle color, and classify it as red (R), light red (LR) or white (W). Next, a vertical cut from the front of the skull bone towards the eye (Fig. 11), opened up caput to detect and sample the otoliths from the area beside/beneath the brain (Fig. 11). After detecting the otoliths and picked them out with a pair of tweezers, we put them into paper envelopes to store dry for later age determination. To assess stomach fullness, sexes, and sexual matureness (Fig. 12 and 13), we opened the abdominal cavity from the gut and forward, by use of a knife or a pair of scissors. We noted all data at the individual paper envelopes, also containing the pair of otoliths and scales. Scales were sampled with a scalpel from the lateral side of the individual, above the lateral line in front of the adipose fin (Fig. 10). Scale sampling was to eventually complement otolith age determination, particularly in young individuals but were not necessary to use. Scales have been found to be less appropriate for age determination in adults (Howland et al. 2004).

Consecutively as we sampled data from each individual in the laboratory, we assessed the stomach upfill in the 200 individuals of which it was possible. The scale 0-12 was used. Zero is empty and twelve is full and stretched stomach (LFI, personal comm.). Esophagus was cut in the anterior end, and the intestines was cut closely behind the attachment to the stomach. Additional to amount of food eaten, we logged number of eggs in the stomach and the approximate proportion of the stomach filled with eggs (in % of all stomach content), to document egg predation. Records of egg predation implies that the fish has been caught when it stayed at the spawning areas, i.e. it confirmed that spawning place and time was hit. The stomach content data would also indicate any cessation of feeding prior to spawning, also confirming pre- or in-spawning time. Food cessation is assumed to appear before spawning and more or less to continue during winter (Tveiten et al. 1998).

After laboratory work, we dried the otoliths at ambient room temperature. Pairs of otoliths from one-by-one individual in each paper envelope, also containing all sampled data from the individual. To determinate the age, we put each pair of two otoliths into a small glass jar and added 85% ethanol. The otoliths were investigated visually by using a Zeiss ocular, preferably with a black background. Annual winter growth in the otoliths were counted from its visually detectable dark rings in the white otolith (Fig. 9) (Howland et al. 2004, Aymes et al. 2016).

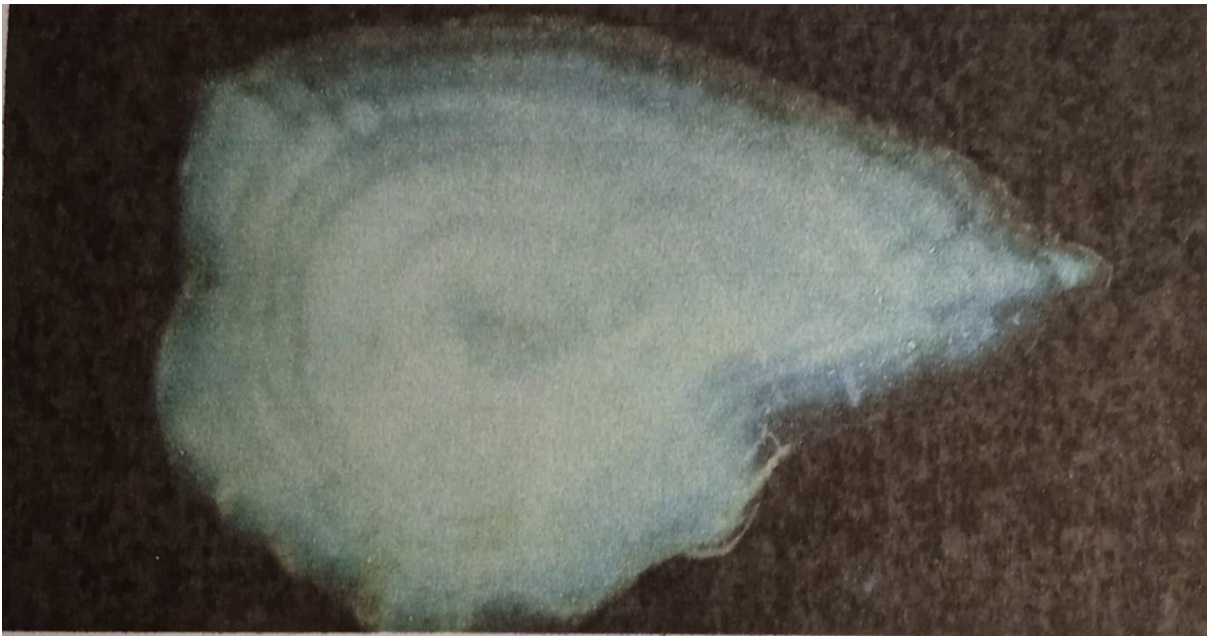


Figure 9. Otolith with dark winter growth and light summer growth. Counting rings from the core determine the individual's age. The otoliths of Arctic char are thick and can be difficult to 'read'.



Figure 10. Sampling of scales from the left lateral side above the lateral line, in front of the adipose fin.



Figure 11. The cutting method we used to find the otoliths and pick them out from beneath the brain. Starting the cut in front of the skull bone and end it by the eye (left). Caput was bend forward (right) and a pair of tweezers were used to pick out the pair of otoliths one by one.

The gonadal development was determined according to (Dahl et al. (1917) *Trout and trout waters in Norway*, cited in cited in Johnson and Matzow (1979) and in Hesthagen et al. (1995), with illustration (Fig. 12) published at <https://www.miljolare.no/aktiviteter/vann/natur/vn12/fiskekompendiet/full.php>). The scale I to VII-II (Fig. 12) was used. The method was originally developed for trout but is also appropriate to the close related Arctic char, although not necessarily to fish species which is not part of the salmonids (*Salmonidae spp.*). The development stages have a nomenclature using the roman numerals I to VII and VII-II. Early gonads are small (stage I and II). If sampled in summer/fall, these are young and immature individuals that have not spawned previous seasons and will not mature the present season. Gonadal maturation evolves further to the developing stages III and IV in which the gametes prepare for spawning the coming season. Gonads in those stages fill more than half of the length of the abdomen. In stage IV, the gametes (i.e. oocytes or spermatozoa) are visibly larger. The final development, vitellogenesis, is observable in stages V and VI, before spawning with increased egg/sperm size. During the vitellogenesis (stages V and VI, fig. 12) the oocyte size increase notably and separates. In the last part of stage V and in stage VI, the eggs and milt can release from the gut by using a soft pressure on the ventral side of the body. The content of lipids, proteins and hormones evolve in stage V and VI. During vitellogenesis the oocyte nucleus also develops. The yolk develops in the cytoplasm in stage VI and is the last development stage before the fish is ready for spawning (Frantzen et al. 1997). Stage VII are post-spawners or individuals during spawning. The degrading gonads gradually resorbs and disappear from the abdomen. Because of the early onset of immature gonads preparing for the next season, gonads at an early development stage are detectable at the same time as maturing gonads. The post-spawners are therefore grouped as stage VII-II to illustrate the appearance of remains of old gonads and new growth of early developing gonads at the same time (Frantzen et al. 1997).

HUNN	STADIUM	HANN	
	I		GJELDFISK Skal ikke gyte kommende høst
	II		
	III		GYTEFISK Skal gyte kommende høst
	V		
	VII-II		UTGYTT FISK Tidligere gytere
← Bukhulens lengde →		← Bukhulens lengde →	

Figure 12. Classification figure for gonadal development assessments in brown trout and Arctic char (Dahl et al. 1917, cited in Jonsson and Matzow 1979), published at miljolare.no, (7.10.22). The text in the figure is unfortunately in Norwegian. The columns are, translated (from left): female, stage, male. The rows in the fourth column are, translated: immature fish that are not spawning the coming fall, spawning fish that are going to spawn the coming fall, post-spawners that have already spawned. The text in the bottom row indicates how large proportion of the abdominal cavity the gonads cover in female and male fish, respectively.



Figure 13. Female Arctic char with gonads on development stage VI (left). At late in stage VI, when the female is ready to spawn and when spawning is going on (overlapping with stage VII-II), the eggs are easy to be stroked out of the gut opening (right). In this case the eggs were stored on a glass vial to another project.

For statistical analyses we used the free software *R* (Venables and Smith 2012), using the menu-driven add-on package RCommandrPluginNMBU version 4.1.1 (Liland 2017). We also used Microsoft 365, Apps for enterprise Excel version 2209 for data sampling and supplying the statistics and figures. Statistical analyses and tests are described more detailed in the result chapter consecutively as results are presented. For maps, we used ArcGIS version 10.7.1 and data-set resources downloaded from <https://kartkatalog.geonorge.no/>. We used datasets from NGU, NVE and NIBIO.

Results

Samples

Arctic char caught by night with gillnet fishing in two different sample years, i.e. 2016 (sample 1) and 2019 (sample 2), represented the material. In total, the samples contained $n=231$ individuals. From sample 1, $n=124$ and from sample 2, $n=107$.

Sample 1

Two individuals from sample 1 were not age determined because the otoliths could not be found. The remaining individuals from sample 1 which were possible to age determine ($n=122$), made up the sample in analyses with respect to recruitment year.

Eight individuals from sample 1 were less confidently sex determined due to lack of gonadal development at the time of capture. The lengths of those individuals with small and less developed gonads ranged from 230 to 261 mm. Four of the individuals were five years old. The other ages were four, six, and five years. We logged six individuals as males due to small but, however, detectable gonads. In the remaining two individuals, found to be five years old, the gonads were not detectable, and we logged the sexes as unknown (NA). From sample 1, the remaining number of individuals available for analyses of sexes and sexual maturation was $n=122$

Sample 2

In all, from sample 2 ($n=107$) we found otoliths in 104 individuals that were successfully age determined. In two of the discarded individuals we did not find the otoliths and in the last one, the otoliths were too thick to be age determined. The remaining sample for water level correlation analyses was $n=104$.

Four fish (one female and three males) from sample 2 had very small gonads, although they were of the larger individuals, with lengths 294 mm, 281 mm, 259 mm, and 272 mm. Age determination indicated they were old fish compared to the sample 2 mean, which was 6.26 years. They were 11, 11, 7, and 9 years old, in respectively order to the lengths (above). Their gonadal status was VII-II (post-spawners). The accuracy of gonadal determination of those individuals were lower than rest of the sample, due to old gonads that already had started the resorption process and they were difficult to distinguish from immature individuals. The combination with their ages put them in the post-spawner group. Further one individual did not have detectable gonads and was also excluded from the sexual maturation analyses. Thirty-one fishes were gutted and cleansed before the sample came to USN. Those were excluded from the variables describing sexes, sexual maturation, and stomach fullness. Remaining available individuals from sample 2 for statistical analyses including gonadal development were $n=72$ and remaining individuals for stomach contents were $n=76$.

Summed up, age determined individuals from sample 1 was $n=122$, age determined individuals from sample 2 were $n=104$, sexual determination and gonadal status assessments were conducted on $n=116$ individuals from sample 1 and $n=72$ individuals from sample 2. Stomach fullness were assessed in $n=124$ individuals in sample 1 and $n=76$ in sample 2.

Stomach fullness and egg predation

Sample 1

A large proportion (53 individuals = 42.74%) of sample 1 ($n=124$) had empty stomachs. This indicates that the population was in the duration of spawning and that the winter starvation was about to start. Very small amounts of food in the stomach (level 1 on the scale (0-12)) was found in 25% = 31 individuals and 12.9% = 16 individuals were assessed to level 2 at the scale, i.e., they had eaten something but not much. For stomach fullness level three and four 3.23% = 4 individuals and 5.65% = 7 individuals respectively, were counted. Frequency

of level 5-11, i.e., about half or more of the stomach was filled with something, was in the range 1-3 individuals or 0.8-2.4% of the sample. Of the sample, 21 individuals = 16.94% had eaten eggs, which indicate that they in some degree stay at the spawning ground not only to reproduce but also to feed. In stomach fullness level one and two, the number of eggs eaten ranged from one to six and ranged from 50-100% of the food content in the stomach. In stomach fullness level three, one individual had eaten 24 eggs. This represented 100% of the stomach content. One individual with level four had eaten 15 eggs, which represented 60% of the food eaten. At level five and six, one individual at each of the levels had eaten 11 and 29 eggs, which both was 100% of the stomach content. On level eight, three individuals had eaten only eggs (i.e., 100%) and the number of eggs they had eaten were 24, 30 and 39. At stomach fullness level nine, one individual had eaten 39 eggs, which was the only content (100%) in the stomach. At level ten, one individual had eaten seven eggs (60% of the stomach content) and one fish had eaten 71 eggs (100% of the stomach content). Parasite cysts (one or more) were found in the stomach skin in 97 individuals = 78.23% of the sample, versus 27 individuals = 21.77% with no cysts. In 48.39% of sample 1 (62 individuals) the muscle tissue was light red (LR). Red (R) muscle color was found in 34 individuals = 27.42%, and 28 individuals = 22.58% of sample 1 had white (W) muscle tissue color.

Sample 2

Empty stomachs were found in 16 individuals, 21.33% of sample 2 (n=75). Stomach fullness of levels one and two consisted of eight individuals (10.67%) each. Eleven individuals (14.67%) were reported in each of the levels three and four. Eight (10.67%), seven (9.33%) and six individuals (8%) had middle full stomach fullness (levels five, six and seven, respectively). Only one individual from sample 2 had eaten eggs, and the individual had not eaten anything else, i.e. 100% of the stomach fullness were eggs. The eggs had started to degrade, and the content was impossible to separate into single countable eggs. The stomach fullness level of that individual was seven. Parasite cysts were found in the stomach skin in 44 individuals (58.67%) versus not found in 31 individuals (41.33%) of sample 2. The muscle color (n=105) of sample 2 was red (R) in 24 individuals (22.86%), light

red (LR) in 37 individuals (35.24%) and white (W) in 44 individuals (41.9%) of sample 2. For one individual the data on muscle tissue color was not obtained, due to human error.

Age distribution

Mean age of the individuals in sample 1 was 5.45 years. Median was 5 years. Standard deviation was 0.9883826. Mean age of the individuals in sample 2 was 6.26 years. Median age was 6 years. Standard deviation was 1.5264350. Shapiro-Wilk normality test indicated that both age distributions were skewed (Fig. 14), i.e. did not fit the normal distribution according to the given parameters (sample 1: $W = 0.75202$, $p = 4.503 \times 10^{-13}$ and sample 2: $W = 0.92086$, $p = 0.00001089$). The age distributions (Fig. 14) were skewed towards older individuals with a mode at 5 years for sample 1 and 5-7 years for the sample 2. The range of ages were 4-10 years in sample 1 and 4-11 years in sample 2. To test for any change in age between the samples, the two age distributions were compared using a Welch two-sample t-test for unequal variances. The analysis indicated older fish in sample 2 ($t = -4.6379$, $p = 0.000006962$). Thus, the age distribution has changed: sample 2 consisted of significantly more individuals with larger age than sample 1 (Fig. 14). Furthermore, the range implies that maturation does not occur before the individuals are at least four years old (Fig. 14). The age classes five and six years were notably larger than the other age classes in sample 1. In sample 2 the age classes four to eight were more evenly distributed (Fig. 14).

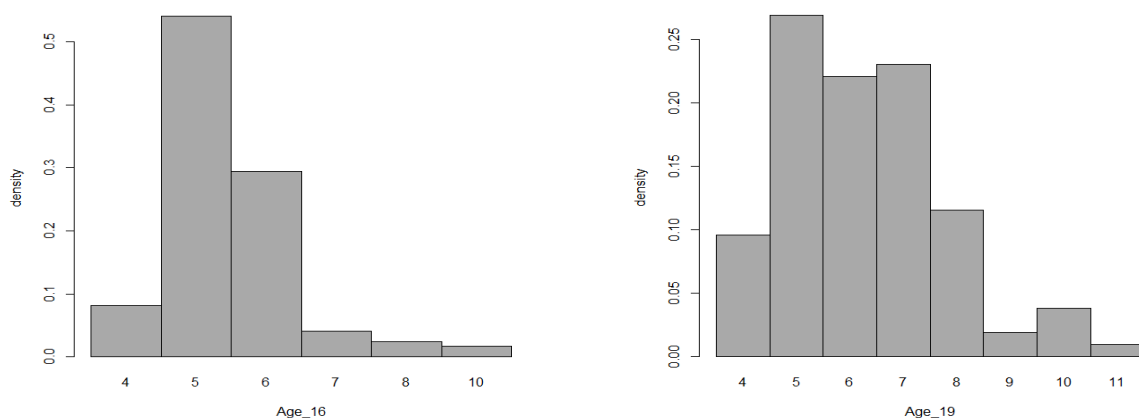


Figure 14. Density histograms of ages in the two samples. The histograms peaks at five years. For sample 1 (2016) a large proportion of the mature population is five and six years old. In sample 2 (2019) the year classes from five to seven are more evenly distributed. Both samples lack individuals below four years age. From the low but present four-years-old age class and peak in the five-year-old age class, we assume that the adult Arctic char mature at about four to five years age.

Distribution of sexes and gonadal development

The distribution of sexes was about equal in sample 1 with 48% female and 52% male fish (Fig 15) and skewed with more males in sample 2. Sample 2 contained 31% female and 69% male individuals (Fig. 15). The sum of individuals that did not have abdominal contents or was not sexual assessable were excluded, which reduced sample size for sample 2 to n=70.

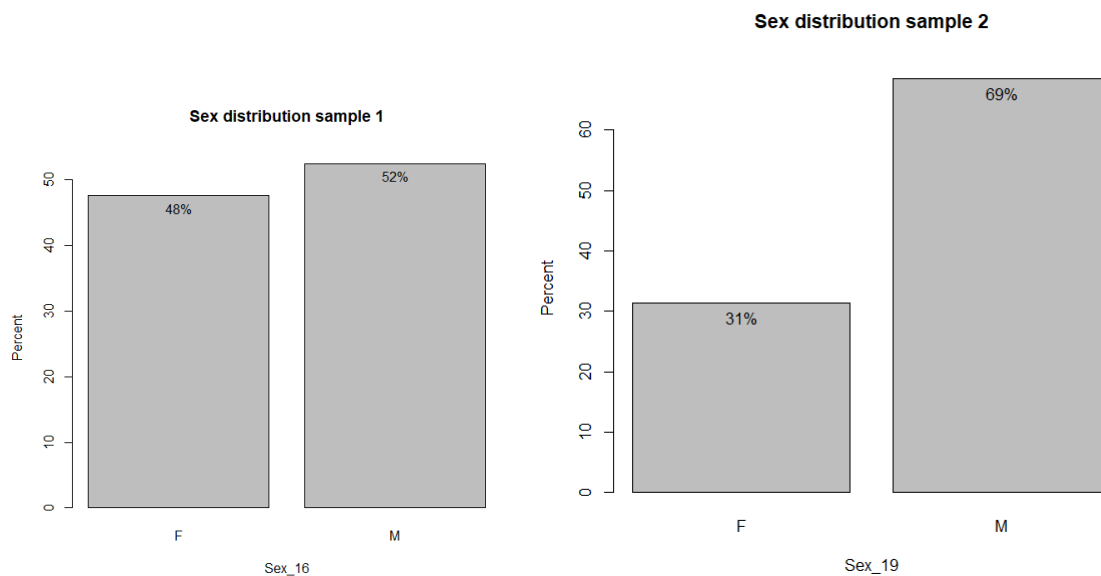


Figure 15. Distributions of sexes, female (F) and male (M), in Arctic char from sample 1 (2016) and sample 2 (2019). The sample sizes are n=122 in sample 1 and n=70 in sample 2.

The distributions of sexual maturation (Fig. 16) indicate large proportion of sample 1 to be close upon to the spawning period, with stage V (31%) and VI (38%) and less (13%) post spawners (stage VII-II) in comparison. Early stages: stage I, II and IV, were represented with

6%, 4% and 7%, respectively, of the sample. No individual was at stage III. More post-spawners were found in sample 2 (36% of the sample). Stage I, II, III, IV, V and VI ranged from 9-13% (stage I and V: 9% each, stage II: 13%, stage III, IV and VI: 11% each) (Fig. 16).

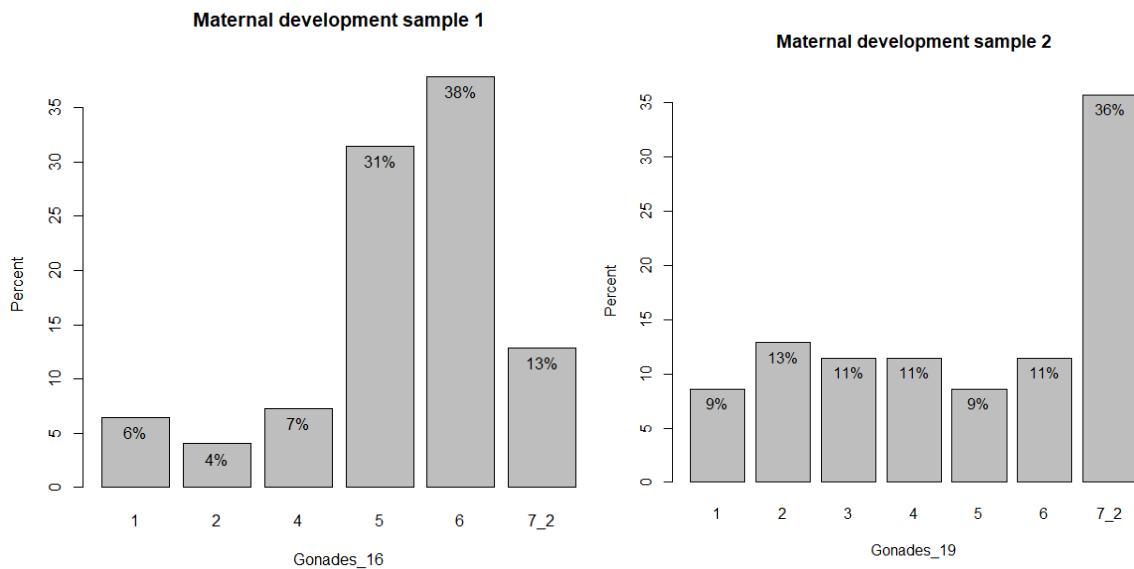


Figure 16. Maternal development for sample 1 (2016) and sample 2 (2019). Sample 2 was cut down to n=70 due to missing abdominal contents. N=124 for sample 1.

The spawning time seems to be better hit in 2016 than 2019, due to the larger proportion of post-spawners in 2019 (36% compared to 13% in 2016). The information about maturation contributes to confirm that spawning time and habitats were found. The age distribution with no individuals less than four years, implies that four years was the lowest maturation age in this Arctic char population at the time of sampling.

The stomach fullness data support that sample 1 was close upon spawning with a large proportion of empty stomachs (42.74%). Contrarily, only 21.33% were found with empty stomachs in sample 2 (above). Feeding is theoretically, ceased previous spawning and stay low during the spawning period and throughout the winter. This pattern was found in

sample 1 which contained 69% individuals at maturation stage V and VI. In sample 2, containing more post-spawners the stomach fullness was larger, i.e. fewer individuals with empty stomachs. Thus, after spawning it seems like feeding in this Arctic char population increases despite winter is coming (Fig. 17 and 18). Gonadal development was tested against stomach fullness in R using chi-square quantile distribution (Fig. 17 and 18).

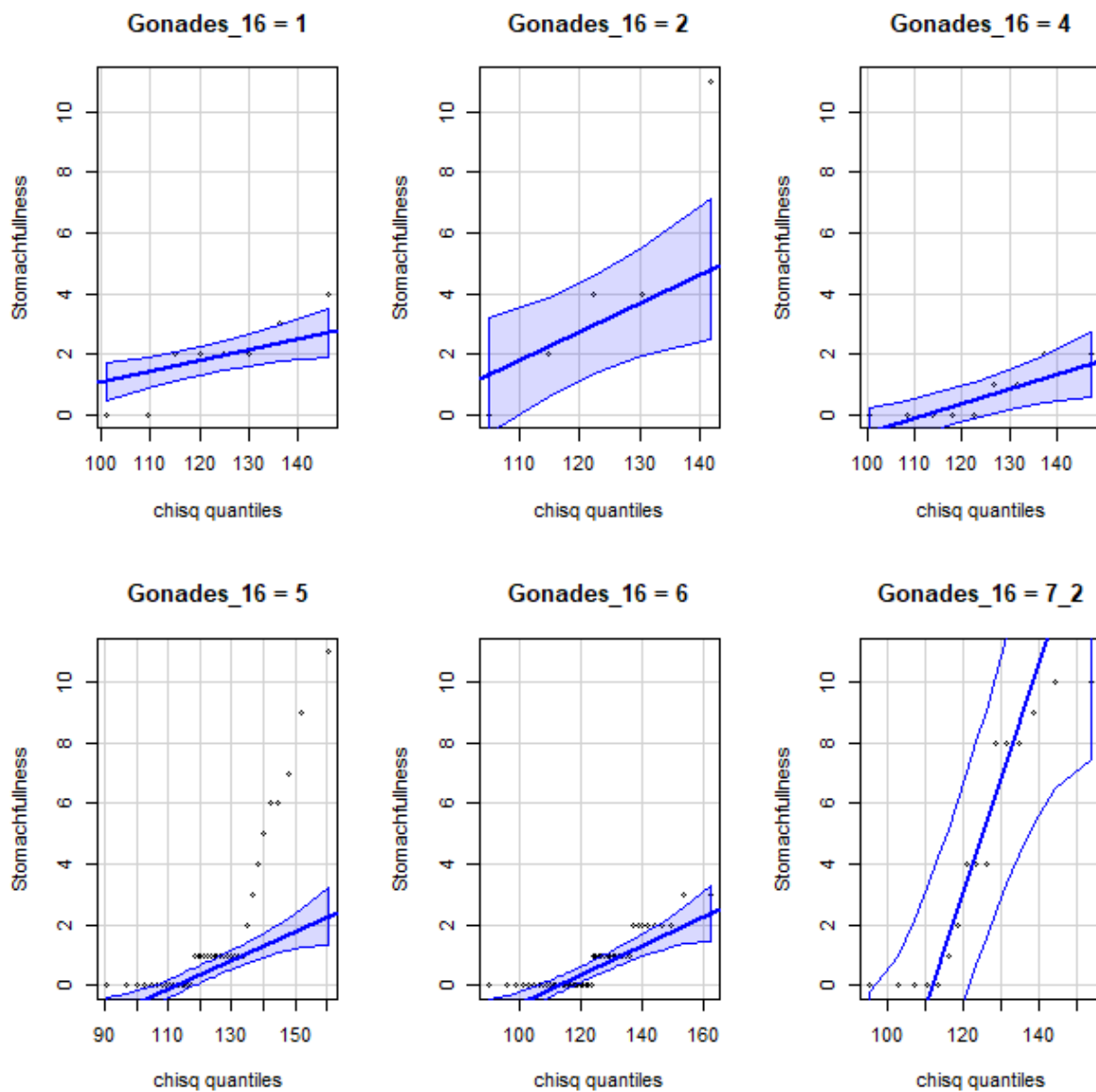


Figure 17. Feeding through the seasonal maternal development in the local lake Møsvatn Arctic char population, sample 1. N=124, expressed by stomach fullness (scale 1-12) and chi-square quantiles of the sample.

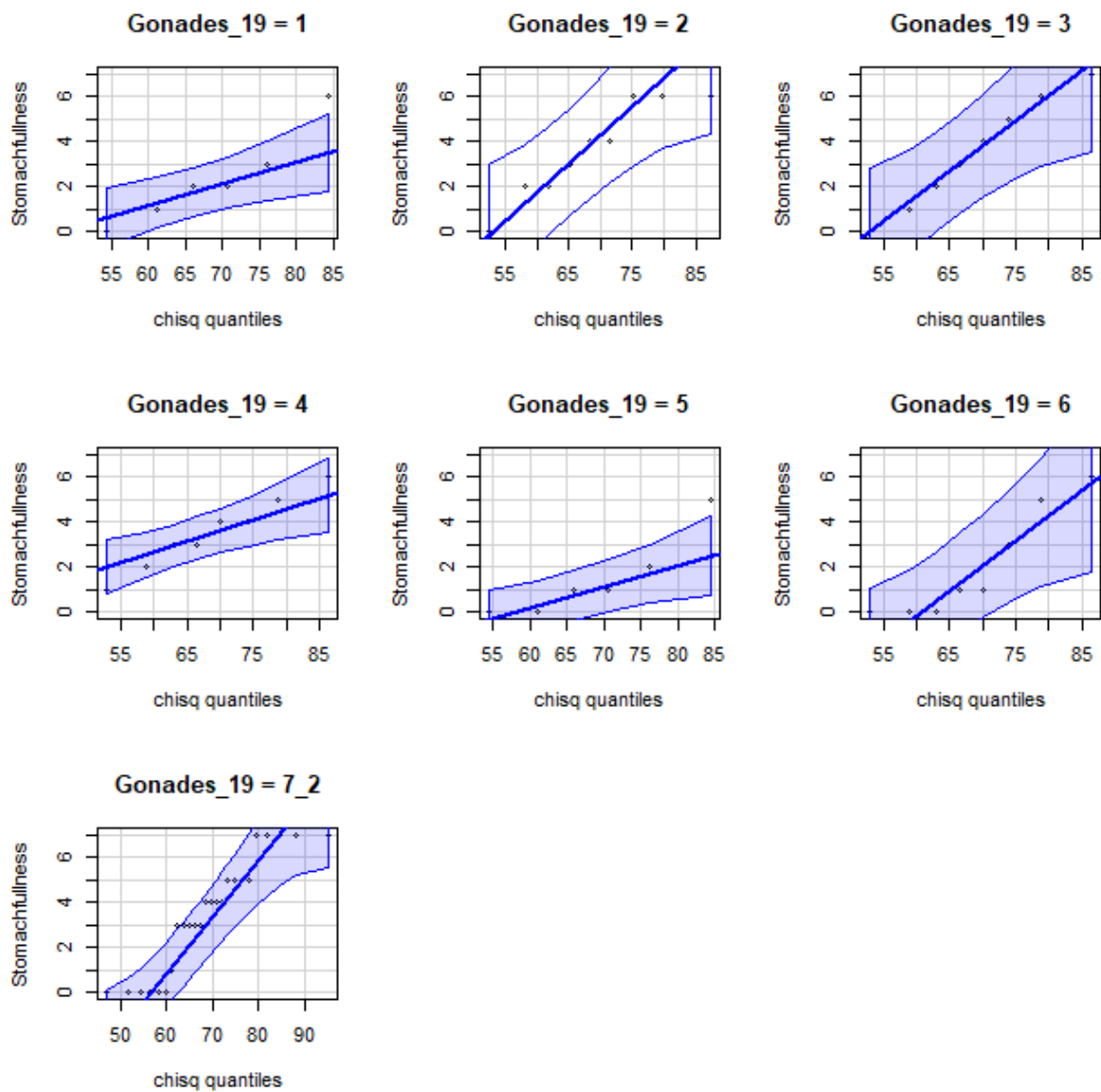


Figure 18. Feeding activity through the seasonal maternal development in the lake Møsvatn Arctic char population, sample 2. N=70. Expressed by stomach fullness (scale 1-12) and chi-square quantiles of the sample.

Growth

Empirical growth

Mean length for all individuals in sample 1 was 259.5 mm and median 247 mm. Standard deviation was 17.73953. The mean lengths of the specific age classes were, four years (n=10): 244.3mm, five years (n=66): 244.3mm, six years (n=36): 257.3mm, seven years (n=5): 251.4mm, eight years (n=3): 267.3mm and ten years (n=2): 274.5mm (Fig. 19). For sample 2 the mean length of all individuals was 272.3mm and median was 271.5mm. Standard deviation was 24.79069. Mean lengths in the specific age classes were, four years (n=10): 244.6mm, five years (n=28): 257.5, six years (n=23): 268.8, seven years (n=24): 283.0mm, eight years (n=12): 295.3mm, nine years (n=2): 296mm, ten years (n=4): 303.8mm and eleven years (n=1): 294.0mm (Fig. 19).

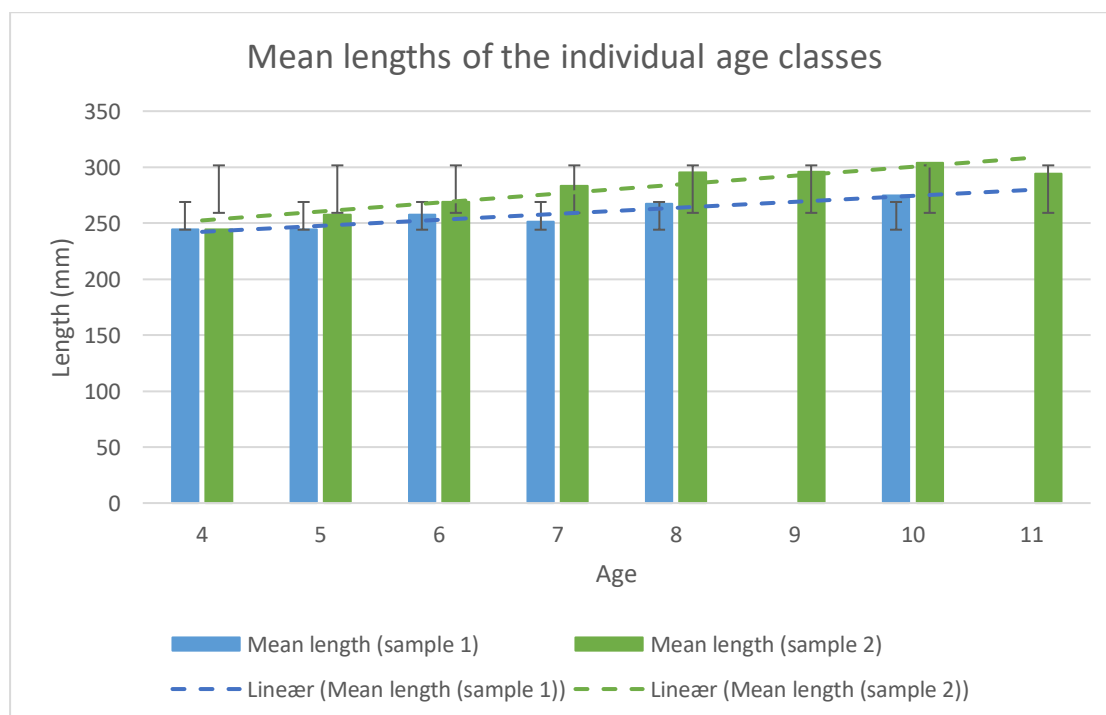


Figure 19. Empirical growth showed by mean lengths of the specific age classes with standard deviations (from whole sample) and linear regression line. Blue is sample 1 and green is sample 2.

Annually growth in length appears to be somewhat better in sample 2 compared to sample 1. Pearson's product-moment correlation analysis was used to find the correlation between length and age. The data for sample 1 resulted in a clearly significant correlation ($t = 4.1778$, $p = 0.00005615$). The correlation coefficient was, however, surprisingly low, with $r = 0.356$. The same test for the sample 2 data resulted in $t = 8.72$, and $p = 5.459 \times 10^{-14}$. Correlation coefficient was $r = 0.65$ and relatively high. The result shows significant and a relatively high correlation between age and length, especially in sample 2. The difference in lengths between the samples was compared by using two sample t-test. The difference between sample 1 and sample 2 was significant, $p = 0.0002013$. According to the data (e.g. the mean lengths of the individual age groups, fig. 19), and the significant difference between samples, one may conclude that the individuals in sample 2 were significantly longer than the individuals in sample 1.

Fulton's Condition factor, K .

The condition was calculated by Fulton's Condition Factor, $K = 100W/L^3$, where W is total weight in grams of the whole fish and L is length in centimeters (Fig.20) (Kurkilahti et al. 2002). For sample 1, all individuals contained abdominal organs and thus, all individuals ($n=124$) were included in the conditional calculation which required length and weight. Mean K for sample 1 was 0.99, median K was 0.98 and standard deviation was 0.10227687. Sample 2 lacked weight for thirty-one individuals and the condition factor was calculated for the remaining $n=76$ individuals. Mean K in sample two was 0.88, median was 0.87 and standard deviation was 0.07881461. For both samples, there were a few individuals with no determined age (above). Therefore, the sum of sample sizes (n) for K in individual age classes is not equal to the total sample sizes n , for sample 1 and sample 2 across ages. Fulton's Condition Factor, K (Fig. 20) were calculated for the individuals in all age classes in both samples. In sample 1, four-years-old individuals had the mean condition factor $K = 0.96$, in five-, seven-, and eight-years-old individuals mean K was 0.98 in each age class, in six-years-old individuals mean $K = 1.02$, and ten-years-old individuals had the mean condition factor $K = 0.96$. In sample 2, the four-, five-, and ten-years-old individuals had each a mean condition factor $K = 0.88$, six-years-old individuals had the mean condition factor $K =$

0.89, in seven-years-old individuals mean $K = 0.91$ and in eight-years-old individuals mean $K = 0.85$. In nine years old individuals mean $K = 0.84$ and in the eleven years old individual in sample 2, K was 0.73 (Fig 20).

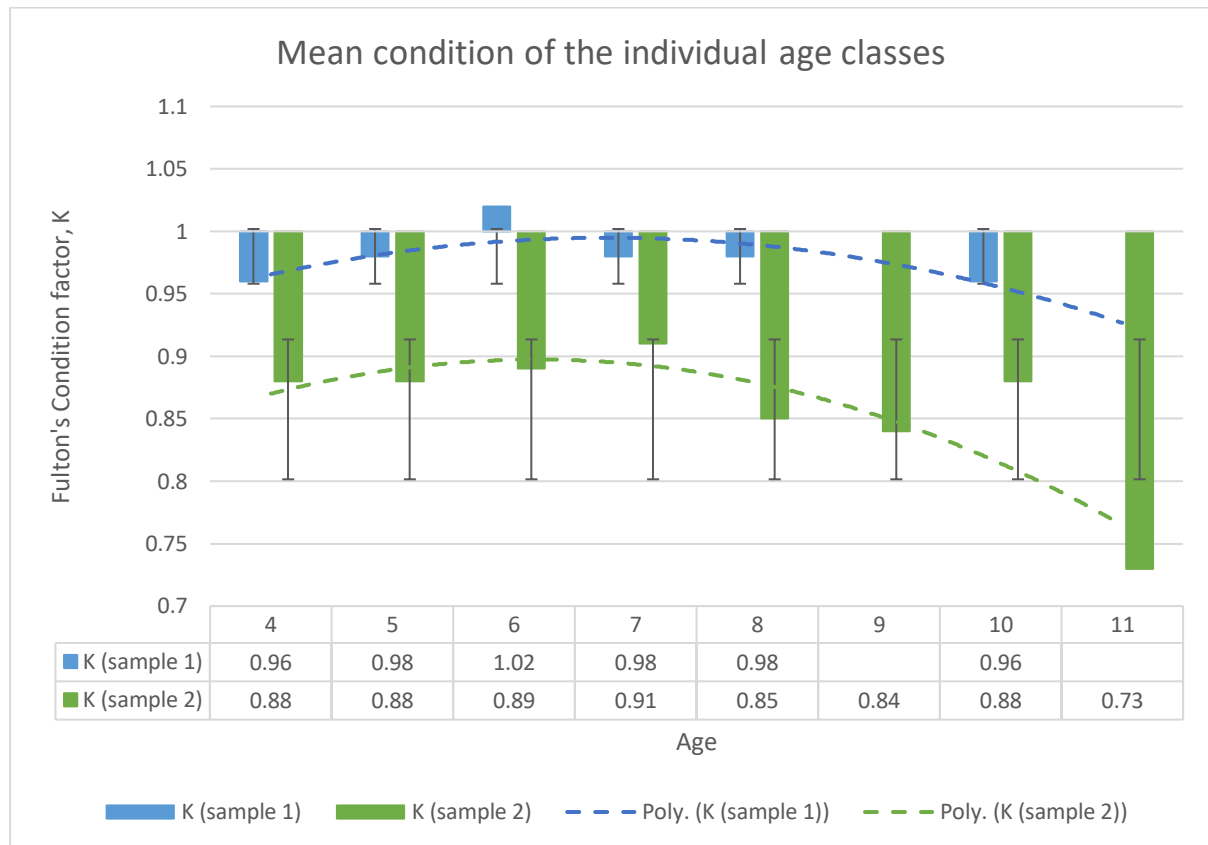


Figure 20. Fulton's condition factor, K . Sample one in blue bars and sample two in green bars. Standard deviation is from the whole sample.

Age distribution and reservoir water level correlation

We investigated a potential correlation between reservoir water levels and year class strength, i.e., the number of individuals (as indicated by year class strength) that were hatched in respective years at different water levels. The samples represent individuals that have survived the winter drawdown the hatching year and the low water levels during spring the same year. The hatching year was back calculated from age determination of mature adults sampled on spawning areas. Juveniles staying in profundal areas are safe

from the low water levels. By the species annual cycle, they return to the spawning areas after maturing. Thus, the sampled fish had survived for four or more years, until they were adults and participated in the spawning.

Hatching time and incubation times to different development stages

With the 2°C water temperature approach during egg incubation (Janhunen et al. 2010) the egg incubation time should be about 450-483 degree-days from spawning to hatching. From the results (above) we found the mature individuals to spawn in late October, closely before ice covering. The hatching occurs around ice-break in spring, and the alevins use about further 157-164 degree-days to resorb the yolk sac. The alevin period may be calculated from a 4°C scheme, (i.e., 19-21 days) provided the timing to be close after ice-off. Fish farms have an accurately calculated fertilization date, which is not exactly detectable *in situ* studies (Tab. 2). Because the duration of spawning is 3-4 weeks and begins during the autumn mixing at 4°C. Therefore, we subtracted the incubation time by a period estimated to 14 days with higher water temperature during spawning. With information obtained from literature (Tab. 1 and 2) and data from the two samples (above) we found that the Arctic char eggs in Lake Møsvatn are likely to hatch in May (fig 21). Fig. 21 shows the timeline for calculations of the number of days after spawning the different development stages occur throughout the season. It begins with spawning in middle of October at ca. 4°C (October 15 set as day 1) and then continues in accordance with a 2°C temperature scheme. Eyed stage occurs around January 20, after 210-225 degree-days, or 98 days. The further development goes on until hatching occurs after 211-226 days in the last three weeks of May, totally 450-483 degree-days subtracted the estimated 14 days from October. Development of movable and feeding fry with resorbed yolk sac is less precisely described at ambient lake temperatures. From written sources (Tab. 1 and 2) and calculations (above) it should last for about 19-21 days provided the spring mixing have started and water temperature of 4°C.

Table 2. Degree-day calculations and duration of the different life stages.

Stadium	Duration from spawning/fertilization to the stage. (Degree-days at the given temperature).	Temperatures used for calculations. Based on ambient Nordic ice-covered lake temperatures.	Estimated number of days $\chi = \frac{\text{degree days}}{\text{Celsius degrees}}$	Season for the development stage to occur in Lake Møsvatn	Selected references
Initial incubation time/ the duration of spawning/fertilization	56 degree-days	4°C	Ca. 14 days	During last half of October	(Jobling et al. 1998b, Jeuthe et al. 2016) and ambient water temperature in late fall / preferred fertilization temperature
Eyed stage	222-224 degree-days	2°C	111-112 (subtracted 14 days from initial incubation)	January 20.	(Janhunnen et al. 2010)
Hatching	450-483	2°C	225-241 (subtracted 14 days from initial incubation)	Three last weeks of May	(Janhunnen et al. 2010)
Alevin		4°C	225-241 plus 19-21 days (subtracted 14 days from initial incubation)	First half of June	(Atse et al. 2002, Janhunnen et al. 2010)
Feeding fry	614-640	4°C (profundal areas and/or during spring mixing)			(Atse et al. 2002, Janhunnen et al. 2010)

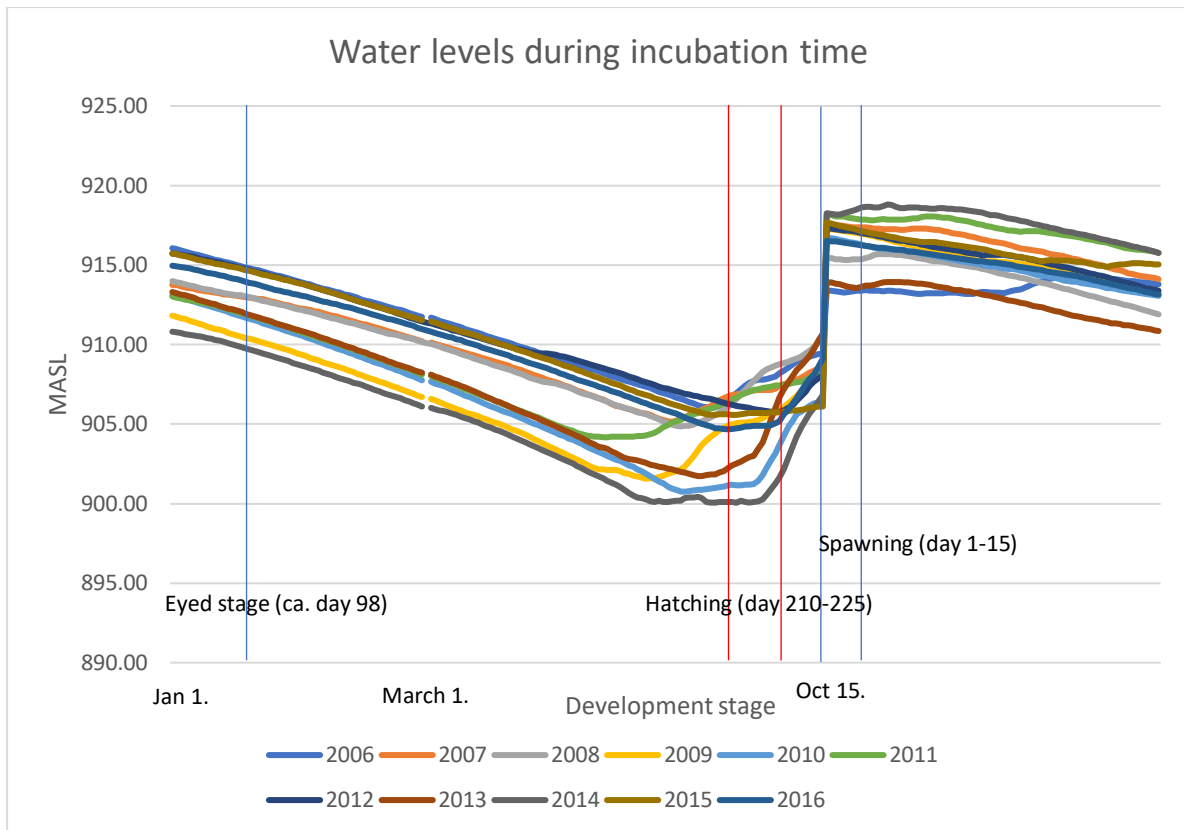


Figure 21. Water levels and incubation time for different development stages. October 15 (day 1) simulates estimated spawning (fertilization) time, (between the right blue vertical lines). Spawning was from the data found to occur in last half of October. Eyed stage was calculated to occur in the end of January, after about 97 days (left blue vertical line). Hatching was found most likely to take place from middle of May, after 210-225 days or 7-7.5 months (between the two red vertical lines) and alevin period lasts for further ca. 20 days provided 4°C water temperature (until day 220-245). Thus, the finally developed movable and feeding fry are ready after ca. 8 months. It is not known exactly how and when the alevins move to the profundal area and how vulnerable they are. The alevins are reported differently, to stay in gravel or spawning areas and to move fast into profundal areas. Sufficient water level is required to save them from stranding.

Year-class strengths and water levels

Hatching years were back calculated from the ages of adult fish sampled at the spawning sites. The correlation analyses were focused on the ten hatching years (2006-2015) and the years when the two samples contained year-classes close to each other and were comparable, i.e., five- to seven-years-old individuals. Year classes of both samples were

compared to each other and correlated to water levels (Fig. 22 and 23). Those six recruitment years with comparable age-classes (2009-2014) included the two years with the lowest water levels during all ten years (2006-2015). Previous reports from LFI (Brabrand 2011) also focused on six years periods. The two years with lowest minimum water levels for February, March, and April were 2009 and 2014. Five-years-old individuals from sample 2 were hatched in 2014 and seven-years-old individuals from sample 1 were hatched in 2009. The main hypothesis of this study, that weaker year class strengths could potentially correlate with low water levels during winter or spring in the hatching year, was visualized in fig. 22 and fig. 23.

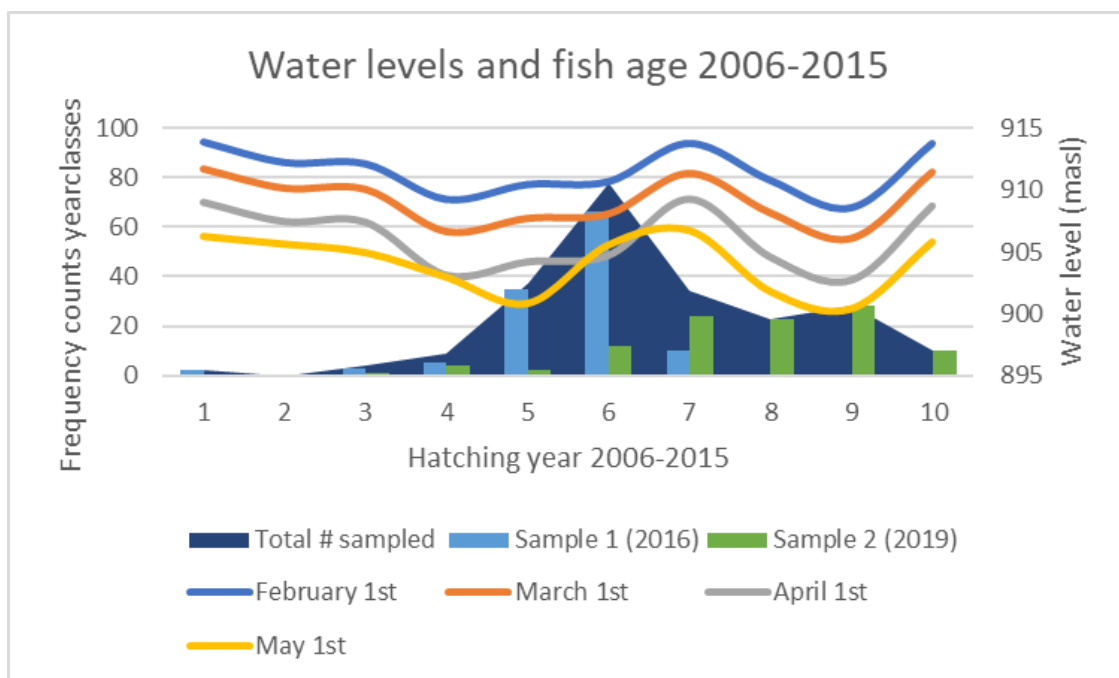


Figure 22. Water levels first day of each winter/spring month (right y-axis) and number of recruits (left y-axis) each of the investigated hatching-years (x-axis), the ten-year period 2006-2015. Hatching year number 1 on the x-axis is 2006 and hatching year number 10 is 2015.

Year-class strength (recruitment) in the six hatchment years of five- to seven- years old individuals (2009-2014) and water levels were grouped into two-meters altitude intervals (Fig. 23). However, some years of the real water-level data had no records with minimum water levels exactly in those intervals (zero hatched individuals in the data-table in fig. 23).

The water levels were therefore, adjusted to use real recorded minimum water levels and calculated mean water levels. Statistical analyses were conducted by using those water levels as threshold between groups of years with low versus high water levels. The lowest minimum water level reported in February was in the interval 906-908masl. In March it was below 904masl and in April, water levels drop towards LRW (904-900masl.) (Fig. 23).

Notably, the water level was never high in March and low in February, or vice versa in the same year. Survived individuals of March and April would have been survived February the same year. The water levels dropped continuously during spring until the water supply from surroundings were held back and water level started to increase relatively fast, usually in May. At minimum water levels below 904masl in March, 33 hatchments survived and at minimum water levels below 904masl in April, 91 hatched individuals survived. In comparison, 124 individuals survived the water level interval 904-906masl in March and 66 hatched individuals survived the similar water level interval in April. Thus, 906-904masl seems to have sufficed for survival in spring (March and April). The water levels in April are always low but, all water levels have resulted in survivals.

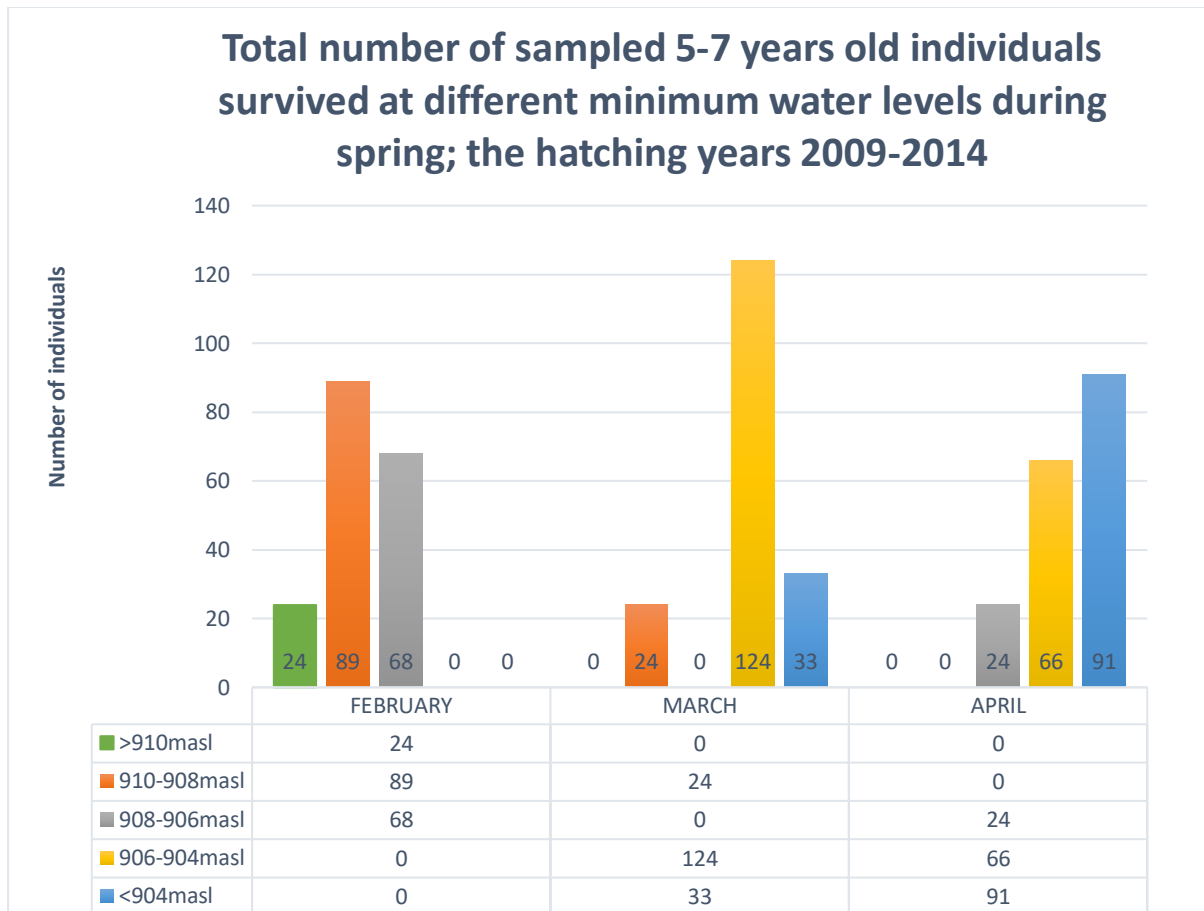


Figure 23. Number of survived individuals from age classes 5-7 years, during different water levels in February, March, and April for the six years 2009-2015. The zero individual hatchment in March for water levels 908-906masl has its explanation from the water level data in March. None of the investigated years had minimum water level in that interval in March. Similar conditions explain the other zero bars in the figure.

It seemed important to find a specific critical lowest minimum water level. And it was important to test whether the year classes born in years with low minimum water levels are weaker compared to year classes born in years with higher minimum water levels. These issues were approached in two different ways after interpreted the visualized data in fig. 22 and 23.

First, correlation analysis (Spearman's rank) was done by using mean water levels in March for all years compared to the pooled sample recruitments those years. The test showed

negative covariance ($r = -0.41$). February water levels were also tested and gave less covariance and we stayed with March water levels. Second, recruitment on low water levels were compared to recruitment on high water levels, using real minimum water level in March as threshold between groups. The ten years-period was split into five years with relatively low water levels and five years with higher water levels. The five years with lower water levels were 2009, 2010, 2011, 2013, 2014. The five years with higher water levels were 2006, 2007, 2008, 2012, 2015. By exploring the exact water level data from the dataset, we defined the threshold for low water levels through spring to be $<908.5\text{masl}$ in February and $<905\text{masl}$ in March. Similarly, $>908.5\text{masl}$ in February and $>905\text{masl}$ in March were set as threshold for minimum water levels to be defined as high water levels. The threshold water level for March was in the approximated interval of suspected critical water levels and split the ten years into two equal groups of five years in each. During the five years with low water levels, 157 recruits from the pooled samples were hatched and survived until matureness. The mean per year was 31.4 individuals. During the five years with higher water levels, 50 recruits survived until maturity. Mean was 10 recruits each year (Tab 3).

The five years with low versus the five years with high (above) water levels in February and March during the sample period were compared using Welch two-sample t-test and the difference in recruitment on low versus high water levels was above but close to significance level ($p=0.0597$). Comparison of recruitment were done for the two years with the lowest minimum water levels, i.e. $<903.5\text{masl}$ in March (Tab. 4) and recruitment in the nearest age-classes. This means a comparison of recruitment of the five-to-seven-years old individuals of the two samples (Tab. 4). Two-sample Welch test was used, the difference in means was above but close to significance level ($p = 0.0878$).

Table 3. Recruitment on five years of high vs five years of low water levels in February and March across a ten-years period of time, using all age-data (back calculated and pooled).

	Minimum 'low' water levels: February <908.5 masl, March <905 masl	Minimum 'high' water levels: February >908.5 masl, March >905 masl
Sum recruits (survival)	157	50
Number of years (n)	5	5
Mean recruits per year	31.4	10
Standard deviation	22.2216111	15.41644144

Table 4. Recruits from the age classes 5-7-years-old individuals from both samples, born in the two years with most extreme water levels compared to recruits born the year before and after.

5-7 years-old	Minimum water levels: February <907masl, March <903.5masl	Minimum water levels: February >907masl, March >903.5masl
Sum recruits (survival)	33	148
Number of years (n)	2	4
Mean recruits per year	16.5	37
Standard deviation	16.26346	20.08316

Discussion

Year-class strength correlation to reservoir water levels

The present study focused on the reproductive ecology of Arctic char with especially emphasis on the correlation to annually recurring water level fluctuations due to hydropower production. When mature age-classes close to each other (5-7year-class strengths) are compared by pooled frequency data of individuals that have survived spring seasons with minimum water levels in March below vs above 903.5masl, the test gives signal of a difference, however above significance level. When the pooled frequency data are shared into two groups of five years each, with March minimum water levels below and above 905masl, the test also give signal but above significance level. The p-values were relatively close significance levels and imply a weak correlation. When the whole sample are compared with mean March water levels by Spearman's rank test, the data showed relatively low negative correlation ($r = -0.41$). Thus, across all years in which individuals have been hatched, the frequency of hatchments does not correlate well with the water levels. However, there might be a low covariance between survival rate and minimum water levels. Interpretation of the results indicate that if there is a critical minimum winter/spring water level above the existing LRW (900masl), this is most likely to be 905masl. However, it seems more likely that the recruitment depends less on water levels and that confounding factors might impact the population density.

Spawning habitats and incubation times

Spawning area and spawning time

Habitat loss has been discussed to have impacted the recruitment (Brabrand 2011). According to the analyses of critical water levels (above) there seem to be less loss of spawning habitats than first suspected. Interspecific spawning habitat competition is probably low or not existing. Assumed that the spawning habitats of the local Arctic char population are located around 905masl., the water levels in fall are sufficient high to cover the area. Thus, intraspecific spawning habitat competition in fall might also be excluded. Assessments of habitat quality was out of the scope of this study. Thus, whether the

population's spawning sites have changed because of reduced quality of the bottom substrate are left to further research. Reported fishing places and intensity (number of nets in a row) imply that most of the altitudes that catch up spawning areas have been sampled. I.e., from one meter below water level surface at spawning time (October) and down to LRW (900masl). Mean October water levels ranged from 913.3masl to 918.36masl for 2006-2015. Exact fishing places are not reported but cover shorelines of several parts of the reservoir. Spawning habitats and time seem to be hit with good approximation. Due to the analyses of hatching frequency at different water-levels, the Arctic char probably spawn at altitudes up to 905.0masl. Thus, the previous hypothesized spawning habitats at around 908-910masl (Brabrand 2011) might be rejected unless eggs and/or spawning pits are detected at such high altitudes. The habitat loss stays closer to LRW. Roe predation and observations of maternal stages support that spawning ground and time were hit by fishing. The larger proportion of roe predation in sample 1 and larger proportion of post-spawners in sample 2, indicate that spawning time was hit better in 2016 than 2019. The observations of maternal stage and roe predation are supported by the observations of starvation at the time of sampling in 2016. Together with reports given about fishing time and the circumstances that caused fishery later in fall for sample 2 than for sample 1, the picture seems clearer. Thus, we can now with high confidence assume that the spawning most likely occurs in the last half of October.

Hatching time and incubation times to different life stages

The calculated incubation time from spawning to hatching seem to be notably longer than estimated by Brabrand (2011). The calculations summed up from different literature in the present study indicate an incubation time from spawning to hatching to be about 7-7.5 months and the results by Janhunen et al. (2010) is selected as the most appropriate comparable incubation scheme to Nordic cold-water lakes with an incubation temperature of 2°C. However, some modified to natural lake situations with 4°C in fall and spring. The incubation time were in Janhunen et al. (2010) 450-483 degree-days. Thus, the altitude found likely to be the critical low water level during winter and spring must be covered by water all winter and during spring until May. How long the alevins stay on spawning areas

and at exactly which time they are finally developed to fry after hatching is not surely known. Neither is it exactly known how they reach the profundal areas they use for feeding during the juvenile period until matureness. Due to the local climate and the hatching time, calculated to happen in May about the same time as ice-break, alevins would possibly develop in the duration of three weeks at 4°C and be able to use water streams during the spring circulation after ice-break to move towards the profundal areas provided the younger stages are not frozen or desiccated. The water level manipulation in May have in the reservoir often been comprehensive and one should have in mind that the alevins are likely to be vulnerable to fast receding water for a time into the summer months and that they in general are vulnerable to fast changing water level fluctuations (Eloranta et al. 2016, Eloranta et al. 2018). According to the results of this study, the crucial minimum water level may appear around the altitude 905masl. The crucial time for the spawning area to be water covered seem to be the entire ice-covered period, from October to May. Thus, this study may lead to a recommendation to rise the lower regulated water level (LRW), e.g. to 905masl.

Population structure and health

Distribution of sexes and gonadal development

Sample 1 is equally distributed between sexes (52% males and 48% females) and sample 2 is skewed towards males (69% males and 31% females). Males may have a delay in seasonal maturation compared to females. Because sample 2, according to anecdotally reporting, was taken a couple of weeks later in fall than sample 1, the sex-related delay of maturation might be a part of the causation, but this is not certain. If so, a sex-related skewness in maturation can confound to low recruitment success. If the population itself is skewed with a larger proportion of males, it also might cause less recruitment due to less spawned eggs and thus, less embryos and lower recruitment. Sexual maturation in Lake Møsvatn was found to occur around the age of four. This result fits with literature about freshwater resident wild Arctic char populations (Nordeng 1983). Some individuals, especially in sample two were apparently not mature at ages that were unreliable old to not be part of the spawning population of this iteroparous species. The gonads could have been so

degenerated that they were not detectable, i.e., in post-spawners and the coming gonads correspondingly small. Another explanation might be that the individuals had failed to mature that particular season. It is known that some individuals do not spawn each year due to the energy cost. Especially when food is limited (Jobling et al. 1998b). High summer temperatures due to e.g., climate change also can inhibit maturation (Jobling et al. 1995, Klobucar et al. 2016). Because the onset of gonadal maturation starts already in spring a year previous to spawning, the development of female oocytes might have suffered from the very warm summer in 2018 (<https://seklima.met.no/>) and this can have resulted in low maturation rate of females and thus lower proportion of females at the spawning sites in 2019. This hypothesis can be supported by the lower rate of egg predation in 2019 despite more individuals with more stomach content in general, although the very degraded eggs found in the one individual imply that the spawning time were done and eventually eggs eaten would have been digested.

Age distributions and suggested long-time impact on the population structure

The age-class of five-years-old individuals was notably larger than the other age-classes in sample 1, while the age-classes were more evenly distributed in sample 2 with the mean above six years. The data indicates with high confidence that the spawning population have become older ($p < 0.001$). The age distribution combined with matureness exploration show that matureness occurs at the age of at least four years. Due to the strength of four-years age-classes, which were lower than the five-years age classes in both samples, parts of the lake's Arctic char population likely mature at five-or-six-years age. In previous studies (Brabrand 2011) the four-years age-class was the largest in a sample from 1998 and furthermore, the five-years age-class was the largest from a sample in 2010. Thus, the results of the present study combined with previous research of the same spawning population (Brabrand 2011), strongly indicate a spawning population that is ageing with time despite intensive harvesting. Eventually, the pattern of larger year-classes at a higher age can be explained by a population maturing for the first time at a higher age. The juveniles are systematically not sampled, because they are not staying at spawning ground in fall but stay in profundal areas until maturing.

These results imply a less abundant population, as was expected. The older and longer individuals might, hypothetically, prey on small juvenile fish and could inhibit the Arctic char population to be overcrowded. Predation impact from cannibalism is not observed except egg predation. The expressed management goal for the reservoir is a top-down regulated ecosystem with brown trout as the top predator (Saltveit and Brabrand 2002). The same mechanisms would be functional with Arctic char as top predator. The brown trout population has not been the focus in this study. However, the salmonids must be seen in a competition context with overlapping niches and management should include both species in reference to each other.

Although the stomach contents were not taxonomic determined and recorded in this study, the diet have been observed planktonic for several years (Saltveit and Brabrand 2002, Brabrand 2011). Planktonic stomach contents were also observed in sample 1 and 2, despite the exception of diet records. Such a planktonic diet supports the hypothesis of recruitment limitation by high summer temperatures. Because the population would need intensive plankton predation in the pelagial during gonadal development in summer they may not stay sufficiently long time in stratification layers with low temperatures in the deep and oocyte development may fail (Sutela et al. 2002, Eloranta et al. 2018). A trend going in the direction of more planktonic predation would in most cases not be possible to give the growth rate needed for the fish to become piscivorous (Borgstrøm and Hansen 2000, Kahilainen et al. 2019).

The population of spawning individuals in reservoir Møsvatn showed significant increase in mean length during the three years between sample 1 and sample 2 (2016-2019). As hypothesized by reports and communication with the local fisheries (Brabrand 2011) the increased length may be a consequence of decreased abundance. However, the fish are of moderate size with rather low condition factor. Samples taken from the spawning population, as the sample in this study, do not represent the total Arctic char population in the reservoir but the population of adult mature individuals. As found by Saltveit and

Brabrand (2002) small sized individuals and juveniles stay in profundal areas. What happens in the profundal area is not known. One should be cautious conclude with recruitment limitation without a more systematically investigation of the growth areas for juvenile fish. Furthermore, a less abundant population may have different causations. Higher mortality of juveniles due to predation from larger fishes would approach a good ecosystem health. Unfortunately, it is more likely that eventually decrease in density is caused by losses in early life stages or less reproduction. Lack of maturation or low fertilization success or egg/alevin mortality from fast changing water levels in spring may confound with diet and feeding habitat limitation (Sutela et al. 2002, Linløkken and Sandlund 2015, Eloranta et al. 2018).

Co-findings and alternative population-regulating factors

Co-findings of this study strongly indicate that the population is food limited. The population's condition is conspicuous low. Fulton's condition factor K was in mean below 1.0 for all age-classes except six-years old individuals in sample one. The condition factor was overall lower in sample two than in sample one. The samples were caught at the time of the season when the individuals are going into the most critical survival period of their adult life cycle, and they were supposed to have stored bodyfat during summer to survive the cold season with less food consumption. The Arctic char has been found to feed at very low temperatures and freshwater resident Arctic char may feed more during winter than anadromous (Klemetsen et al. 2003, Elliott and Elliott 2010, Eloranta et al. 2016). Results from the stomach fullness assessments in this study imply that the population feeds after spawning, due to more stomach contents in post-spawners than in less sexual developed individuals. Whether this observed feeding activity is behavioral compensation to low degree of lipid reserves stored through the summer season is not known although it might be reasonable (Imsland and Gunnarsson 2011). These co-finding was briefly introduced from the present study. It may be hypothesized that post-spawning feeding behavior might covariate with low condition factor. Inhibition of female maturation is found to correlate with poor lipid resources and feeding behavior to catch up for extended winter starvation has been found (Imsland and Gunnarsson 2011). Thus, lack of lipid storage through the

feeding season may contribute to the hypothesis of eventually lack of female sexual maturation by food limitation.

Loss of littoral habitats might impact also on feeding habitats. In the present population the stomachs contain most planktonic prey, and it is reasonable that the Arctic char feeds in the pelagial due to lack of benthos (Saltveit and Brabrand 2002, Brabrand 2011, Kahilainen et al. 2019). In further research of the population it would be useful to taxonomy-classify the stomach contents, to monitor eventually bottom-up effects from food limitation.

Typically, benthic fauna become less diverse in reservoirs and prey benthos are replaced with zooplankton. The decrease of benthic diversity leads to more interspecific competition and species that might usually is separated by feeding habitats now may share planktonic diet in larger degree. However, in competition of planktonic species between Arctic char and brown trout, the Arctic char will sustain as the most effective zooplankton predator and the trout is more likely to become a predator on larger crustaceans and insects or become the top predator eating piscivorous prey (Klemetsen et al. 2003, Kahilainen et al. 2019). Probably, among important confounding variables to the potent changes of abundance in the salmonids of the lake, is general ecological changes due to changes often found in aquatic ecosystems occurring when a lake is highly impacted by water level manipulation, as is the case in Lake Møsvatn. In ultra-oligotrophic lakes on high altitudes inhabited by Arctic char, the planktonic community health and in particular zooplankton communities should be included in the fish management program (Cavalli 2002).

Management plan and further research

To mitigate the general management goals of sustainable and healthy fish ecology and preferably self-recruiting populations, the regulation regime and its consequences must regularly be evaluated. Attractive fisheries for income supply are preferred (MPE 2015), i.e. good conditioned populations of large piscivore brown trout and Arctic char. To mitigate this management goal, the community needs a sufficient number of small prey fish, i.e.

Arctic char (Saltveit and Brabrand 2002) without becoming overcrowded. Brabrand (2011) is not concerned of neither the competition from European minnow nor an overcrowded Arctic char population. The minnow has been found by Museth et al. (2003) to mainly be eaten by trout during a narrow time-span in spring during their spawning period. Because this study is based only on fish caught in fall, we cannot know by certain the ecological function neither of the European minnow nor the small sized juvenile Arctic char (Saltveit and Brabrand 2002, Brabrand 2011). All fish species in lake Møsvatn (*S. alpinus*, *S. trutta* and *P. phoxinus*) have in other studies been found to reproduce and feed in littoral habitats (Saltveit and Brabrand 2002, Johnsen et al. 2016). Depending on how large the winter drawdown is, it may affect the egg and alevin survival in autumn spawners that use the littoral zone as spawning and nursery areas. Water level changes in spring should be slowed down to mitigate the vulnerable alevins in spring when they need to move towards the profundal zone. Especially, because young individuals are more vulnerable to fast water level changes than slower changes more similar to natural water level fluctuations.

The Arctic char population may benefit a rise of LRW to e.g. 905masl. Exactly mapping of spawning habitats may be subject for further investigation. Eventually, stocking of Arctic char yearlings (0+) may be an alternative. A cannibalistic strain then wisely might be considered. However, first the profundal areas serving as feeding area for juvenile fish would be recommended to update. To supply this study of casually harvested spawning population, a systematically sampling of the whole Arctic char population at different places and several depths through different habitats, e.g. using NS-EN 14757:2015 in addition to echo-sounding and/or electro-fishing from boat is recommended. More exact age distribution for the whole population and potentially new locations of spawning habitats and further adaptations to a changed ecosystem may be mapped. Alternatively, supplying the further research of this long-term-impact-study, which depends on collaboration with fisheries, with a mark-recapture design, can be a useful approach to estimate the population density. Furthermore, the benthic fauna should be included more intensively in the monitoring program.

Conclusions

The adult mature spawning population of Lake Møsvatn consists of individuals with a mean age and length that have become longer and older. Longer individuals were found in the sample from 2019 than in the sample from 2016. Fulton's condition factor is overall low, below one for both samples in all, and have become lower with time from 2016 to 2019.

The Arctic char population in the lake appear to mature for first spawning at age four or more. Dominant year classes have become older with time. In 2016, the five-years-old year-class dominated and in 2019, the three year-classes five-to-seven-years dominated. Those age-classes were more evenly distributed, and the two populations had different age-distributions. The dominant year class in sample 2016 was recruited in 2001, and in 2019 the dominating year classes were recruited consecutively during the years 2012-2014.

Although the statistical analyses gave low correlation between water levels and recruitment frequency, comparisons between year class strengths and reservoir surface water levels suggest there to be a difference between recruitment in years with high and low water levels. The water level 905.0masl seems to be the eventually crucial water level limit to be water covered the entire season. Degree-day calculations found the hatching time to be in May. After hatching the alevins are vulnerable for about further three weeks. Therefore, LRW should be risen to 905masl.

From the age and sex distributions, stomach fullness data, contributed by the maturation data, and condition factor data the population may seem to suffer from food limitations and inhibition of female sexual maturation. Those variables may confound, and causations can be environmental.

Co-findings of stomach fullness that may confound with maturation stage data, imply post spawning individuals to feed towards winter. These findings may confound with the low condition factor to start compensating feeding behavior in late fall to catch up eventually lack of lipid storage before over-wintering. These indications may explain eventually low female maturation rate because the population is forced to stay in the heated epilimnion to feed on plankton during summer. High summer temperatures may inhibit the development of the current year's gonads. The same pattern would be likely to occur from feeding habitat competition due to lack of littoral benthos and littoral feeding habitat losses. The population parameters altogether, imply a bottom-up regulated population of adult Arctic char, with recruitment and/or food limitation as the main factors.

New hypotheses generated from this study is:

- The population is food limited with the potential causations in a lack of large invertebrate fauna and/or loss of feeding habitats.
- Food limitation cause an ontogenetic shift from invertebrate fauna to more zooplankton. The population is forced to stay in temperature stratified water-layers with higher temperatures than optimal, to feed on zooplankton. This leads to failure of oocyte development, which has an impact on recruitment.
- The incubation time is notably longer than previously estimated. The data imply hatchment to occur in May and the young life stages to be vulnerable for a substantially longer period than expected.
- The spawning habitats are located at a lower altitude than previously expected. The data imply the spawning area to be located around the altitude 905masl.
- Post-spawners start to eat in late fall towards the cold season.

Appendix

Appendix 1: Raw data

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