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Life-history strategies in two subarctic lakes with polymorphic Arctic charr *Salvelinus alpinus* L. populations.

High across lakes stability in evolution of life-history strategies

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Abstract

Life history strategies of polymorphic Arctic charr in two sub-arctic lakes (Tårnvatn and Skøvatn) with similar environmental- and physiochemical conditions were studied. Disparities in life history traits may reflect ecological adaptations and is suggested an important factor in the incipient speciation process. In this region several lakes have polymorphic charr, and the designation of a fish to a morph-group was based on external morphology verified through genetic differences. The trimorphic population in Tårnvatn has one littoral omnivore (LO), a small-sized profundal benthivore (PB), and a large-sized profundal piscivore (PP) morph. Skøvatn has in addition to the LO-morph, a novel profundal zooplanktivore morph (PZ). The PZ-morph closely resembles the PB-morph in terms of external morphology (cryptic coloration, large eye-size, blunt snout) and several life-history traits. Compared with their sympatric LO-morph, the PZ- and PB-morphs had an early age (4 and 5 years) and size (<100 mm and <110 mm) at sexual maturity, similar as in two other nearby lakes. The PP-morph resemble a higher age at maturity compared to the co-occurring LO-morph. Intra-lake morph comparisons revealed also distinct disparities regarding population growth parameters calculated with von Bertalanffys' growth model. The different life-history trajectories regarding growth parameters and reproductive strategies between morph are reflected by divergent trophic niches. Thus, there are high across lakes stability in life-history traits among polymorphic Arctic charr populations occupying similar ecological niches in this region in northern Norway.

Keywords: Life-history, polymorphism, parallel evolution, Arctic charr, *Salvelinus alpinus*,

1 Introduction

Polymorphism is defined as the co-occurrence of two or more discrete intraspecific morphs that utilize different resource niches and show a varying degree of reproductive isolation (Skulason & Smith, 1995; Jonsson & Jonsson, 2001). Distinct morphs are usually differentiated in morphology, ecology and life-history traits, and life-history variations are significant components that may drive and maintain polymorphism (Skulason & Smith, 1995; Smith & Skulason, 1996). Polymorphisms are suggested to be found in systems with low interspecific competition, high potential for intraspecific variation of traits, and where opportunities for niche differentiation are large (Stearns, 1992; Skulason & Smith, 1995). Divergence into polymorphic populations is likely driven by adaptations to specific habitats, resource utilization and biotic interactions (Smith & Skulason, 1996; Adams & Huntingford, 2004). Realization of a new niche can occur either by niche specialization (Schluter, 2000) or niche expansion (e.g. Knudsen et al., 2006). The ability to establish in and exploit a niche is dependent on genetic variation, heredity and phenotypic plasticity (Skulason et al., 1999; West-Eberhard, 2005; Schluter, 2009; Schluter & Conte, 2009). Phenotypic plasticity is a trait where an organism can alter its phenotype in response to environmental changes (West-Eberhard, 1989; Roff, 1992; Skulason & Smith, 1995). Thus, phenotypic plasticity is an important factor in life history variation (Roff, 1992). Different environments favor unique sets of traits, so that natural selection on phenotypic traits (e.g. life history) will result in specific adaptations of an organism (West-Eberhard, 1989). High phenotypic similarity will increase competition, and thereby increase selection pressures against common- and intermediate phenotypes (Roughgarden, 1972; Skulason & Smith, 1995; Schluter, 2000). As a response to niche specialisation reproductive isolation might occur as a by-product by divergent natural selection (Dieckmann & Doebeli, 1999; Coyne & Orr, 2004). These barriers to gene flow are related to assortative mating, differences in spawning time as adaptations to the environment, and different habitat preferences (Skulason et al., 1999; West-Eberhard, 2005; Schluter 2009; Schluter & Conte, 2009).

Life history theory describes how natural selection and other evolutionary forces affect adaptations of an organism to the environment to optimize survival and reproduction (Roff, 1992; Stearns, 1992, 2000). The ultimate achievement by optimization of these life-history parameters is to maximize fitness (Roff, 1992). Typical fitness components, or life-history traits under selection, are growth patterns, age and size at maturity, fecundity, reproductive effort, size at birth and lifespan (Roff, 1992; Stearns, 1992, 2000). Any factor which cause a change or differentiation in mortality rates in a population will affect its life history (Wootton, 1998). Abiotic factors and biotic interactions, predation and competition in particular, are strong selective forces, which can alter an individual's life history (Wootton, 1998; Johnson & Belk, 2001). These factors seem to have the same effect across different species of

vertebrates (Skulason & Smith, 1995; Skulason et al., 1999) and insects (Lyn et al., 2011; Rotheray et al., 2016).

In fishes, typical life-history strategies under selection are growth, age- and size at maturity, and reproductive investments (Skulason & Smith, 1995; Jonsson & Jonsson, 2001). These traits are often plastic and indeterminate, as they are strongly influenced by environmental conditions (Weatherley & Gill, 1987; Wootton, 1998). Abiotic factors vary between different habitats within lakes. The littoral and upper-pelagic zones of subarctic dimictic lakes experience great fluctuations in temperature between seasons. In contrast, temperature in the profundal zone would remain relatively homogenous throughout the year (Wetzel, 2001). Water temperature and food availability are two main factors that may cause large variability in growth between populations subjected to different environments (Amundsen & Klemetsen, 1988; Hesthagen et al. 1995; Wootton, 1998). As temperature have a strong influence on physiological processes, a change of habitat can lead to contrasting selection pressures on life-histories (Wootton, 1998; Hesthagen et al., 2004; Fraser et al., 2008). Utilization of a habitat scarce on food resources would result in poor growth conditions, in contrast to a habitat with high food availability. Prey availability is important for growth, and resource richness is in general highest in the littoral zone with a variety of energetic profitable prey items, and scarce in the profundal with low prey abundance (Klemetsen et al., 1989). Some species can achieve sizes which enable piscivory or cannibalism, which further will enhance growth (Amundsen, 1994; Hammar, 2014) Thus, utilization of different niches can also lead to considerable variation in growth between populations (Jonsson et al., 1984; Weatherly & Gill, 1987).

Fish mature as they approach the asymptotic size which is constrained by the environmental conditions in which they occur (Jonsson & Jonsson, 1993). The food abundance and concomitant opportunities for growth have strong influence on maturation and reproduction. Growth rates and the maximum size achieved by a female individual is important for fecundity, as the number and size of eggs produced by a female increase with body size (Thorpe et al., 1994; Jonsson et al., 1996). Thus, highly nutritious niches may favor individuals that invest more in somatic growth in early life stages, and enable maturity at older ages and larger sizes, to increase fecundity. Individuals in less profitable habitats, exposed to high and unpredictable mortality rates due to predation or competition, should select for increased reproduction early in life (Schaffer, 1979; Stearns, 1992). The result is that the individual must confine with life history trade-offs between energy investments in somatic growth, reproduction, and survivorship (Stearns, 1992). Such trade-offs are important adaptations to the environment and might further strengthen reproductive isolation and the processes of divergent natural selection and speciation.

Postglacial lakes are evolutionary young systems where many occasions of sympatric polymorphisms are found in a number of freshwater fish species, including e.g. European whitefish *Coregonus lavaretus* L., three-spined stickleback *Gasterosteus aculeatus* L. and Arctic charr *Salvelinus alpinus* L. (Hindar &

Jonsson, 1993; Skulason et al., 1999; Klemetsen, 2010; Siwertsson et al., 2010). Arctic charr (hereafter charr) is a highly polymorphic species present in the Circumpolar region, and there are several studies on charr in polymorphic systems where sympatric speciation is suggested as their origin (Skulason et al., 1999; Jonsson & Jonsson, 2001; Klemetsen et al., 2003; Adams & Huntingford, 2004; Klemetsen, 2010). There are especially three classical studies on polymorphism and sympatric speciation in charr that have contributed to enhanced knowledge on these evolutionary processes: Thingvallavatn in Iceland, Loch Rannoch in Scotland and Fjellfrøsvatn in northern Norway (Klemetsen, 2010). The systems have four-, three-, and two sympatric charr morphs, respectively. All the studied morphs are suggested to have originated as a consequence of differentiation in resource niches, and they also reveal significant divergence. The different morphs have typically differences in life-history parameters such as growth and maturation (Skulason et al., 1989; Sandlund et al., 1992; Klemetsen et al., 1997; Adams et al., 1998; Fraser et al., 2008).

The polymorphic charr populations from Thingvallavatn and Loch Rannoch are segregated along the littoral-pelagic resource axis, which is found in many fish species exhibiting polymorphism (Klemetsen et al., 2003; Klemetsen, 2010). In Fjellfrøsvatn, however, one of the morphs predominantly occupy the littoral-pelagic habitats, whereas the other appears to be confined to the profundal habitat (Amundsen et al., 2008). The polymorphic charr population in Fjellfrøsvatn consists of a littoral-spawning omnivore morph with a similar ecology and life history as most charr populations in the region, and a small-sized profundal-spawning benthivore morph (Klemetsen et al., 1997; Knudsen et al., 2016). Recently, Smalås et al. (2013) reported evidence of a tri-morphic charr population in Skogsfjordvatn, another lake located in northern Norway. In addition to harboring two morphs equivalent to the LO- and PB-morphs found in Fjellfrøsvatn, Skogsfjordvatn also supports a profundal-spawning piscivore morph (PP). Further analysis revealed significant variations in their life-histories; The PB-morphs matured at young ages, was separated in time and place of spawning, low fecundity, and had significantly slower growth rates compared to the LO-morph. The PP-morph in Skogsfjordvatn had slow growth rates, but delayed maturation and matured at a high age and large sizes and high fecundity (Smalås et al., 2013).

Recently, possible polymorphic populations of charr were reported from another two lakes in northern Norway, Tårnvatn and Skøvatn (R.Knudsen pers.com). In Skøvatn, two morphs with similar morphological characteristics as the two morphs in Fjellfrøsvatn appeared to be present. In addition, Tårnvatn seemed to have a third morph which resembled the morphology of a piscivore-morph (PP), thus resembling the three-morph system in Skogsfjordvatn (see Smalås et al., 2013). Moccetti (2018) found evidence of segregation in trophic niche between all morph-populations in both Tårnvatn and Skøvatn. The two populations in Skøvatn consisted of a littoral-omnivore morph (hereafter LO) and a profundal-zooplanktivore (hereafter PZ), which names relates to their habitat and diet (Moccetti, 2018). The three populations in Tårnvatn consisted of a LO-morph, a profundal-benthivore (PB-morph) and a

profundal piscivore (PP-morph). These parallel evolutions of trophic ecologies indicate similar selection pressures, caused by abiotic and biotic factors (Siwertsson et al., 2016), thus one could expect morphs that utilize similar niches (eco-morph) to express similar life-histories (Schluter, 2009).

In this study I contrast the life-history parameters exhibited by the sympatric morphs in the two lakes, Skøvatn and Tårnvatn. I expect the sympatric living morphs to differ significantly in several life-history parameters such as age and size distribution, growth, age- and size at maturity, and fecundity. Furthermore, as the morphs in the lake seem to have relatively similar niche utilization (Mocchetti, 2018) as the studies from Fjellfrøsvatn (Klemetsen et al., 1997) and Skogsfjordvatn (Smalås et al., 2013) I predict these to express similar life-history strategies.

As a response to different temperatures and prey densities between the upper water layers and the profundal zone (Wetzel, 2001), I predict the LO-morphs in both lakes to exhibit faster growth than their sympatric profundal-dwelling morphs. The consequence for the different growth rates will be expressed in different strategies to increase fitness in the respective morph-populations. Secondly, I predict that the PB- and PZ-morph to mature at early ages and small sizes. As they invest relatively more energy into reproduction early in life, they will achieve small maximum sizes, thus resulting in low fecundities. Lastly, I predict the PP-population to delay maturation to higher age and larger size than LO-morph and invest energy in somatic growth to achieve a size which enables piscivory. As a result of large body-size, the PP-morph also will achieve highest fecundity.

2 Material and methods

2.1 Study sites

The two lakes examined in this study, Tårnvatn and Skøvatn are both located in Troms county, northern Norway (fig. 1, 2 a-b). Similar to most lakes in the region, Tårnvatn and Skøvatn are dimictic, oligotrophic, and usually ice covered for 6-7 months from November to May. The shore regions are mostly sandy and stony, with scarce emergent vegetation. Alpine landscape and deciduous forest dominate the drainage areas.

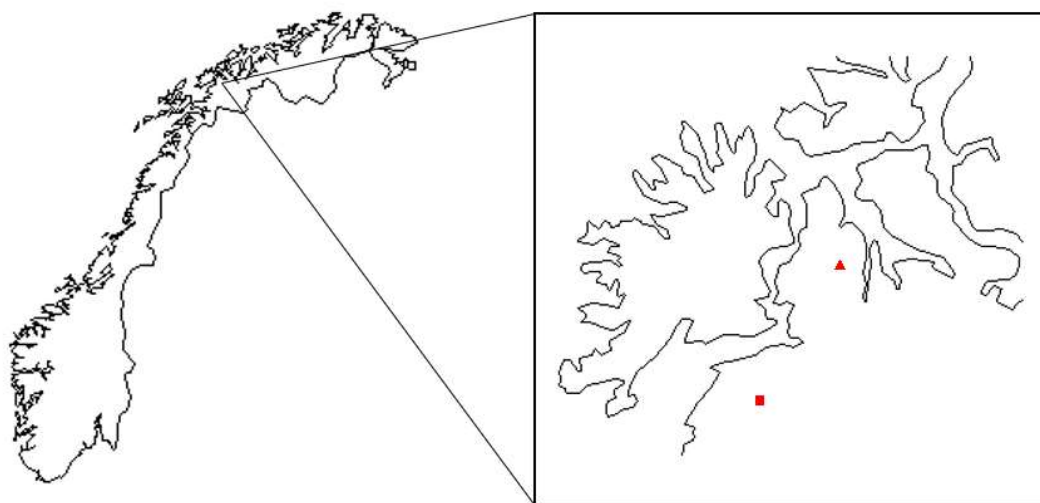


Figure 1: Location of the two study sites in Troms county, northern Norway; Tårnvatn (triangle), Skøvatn (square). The map was made in R (R Core Team, 2016).

Tårnvatn (fig. 2a) is 3.21 km² and 53 m deep, situated 107 m.a.s.l (Norges vassdrag- og energidirektorat, 2017; Scharthau et al., 2017). The drainage area is 34 km², and three rivers drain into the lake. The lake itself drains through river Tårnelv into Rossfjordvatnet, which is a brackish-water lake with open flow to the ocean. Migratory obstacles in the river prohibit fish moving upstream to reach Tårnvatn. In late October 2016, the secchi-depth was registered to be 8 meters, and the water temperature in the surface (depth ~1 meter) was measured to be 4 °C. The lake is typically oligotrophic with a total phosphorus and nitrogen levels to be 2.0 and 121 µg/l, respectively (Scharthau et al., 2017).

Tårnvatn is only accessible by a gravel road during the snow free period. There are no permanent settlements around the lake, only a few cabins. Any anthropogenic impacts on the lake are assumedly

low, which is supported by a recent national monitoring survey (Scharthau et al., 2017). The fish community in Tårnvatn consist of resident Arctic charr and brown trout *Salmo trutta* L..

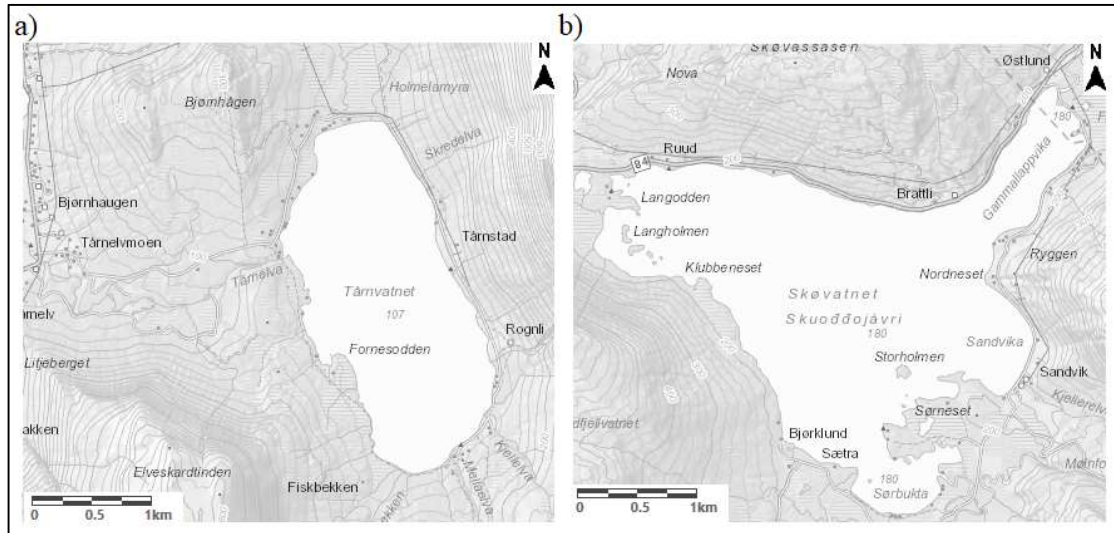


Figure 2 a) Lake Tårnvatn (69°18'30N, 18°21'56"E), and b) Lake Skøvatn (69°1'39"N, 17°53'4"E) (Norges vassdrag- og energidirektorat, 2017;)

Skøvatn (fig. 2b) is situated 180 m.a.s.l, with a surface area of 6.2 km², and a maximum depth of 119 m (Norges vassdrag- og energidirektorat, 2017). The drainage area is 51.59 km². Surface temperature (depth ~1 meter) was measured to 5.6 °C, and the secchi-depth was at 10 meters in late October 2016. The lake is easily accessible from a road passing on the northern end of the lake and a gravel- road leading around from the north-east to the south side. Some settlements, cabins and agricultural farms contributes to some humic influx to the lake, but the anthropogenic influences are assumed to be low. There are two inlet rivers to the lake, whereas the lake itself drains to Finnfjord through Skøelva river. There are no obstacles for fish migration between the lake and fjord, and both resident and migratory populations of Arctic charr and brown trout are present in the lake. Skøelva river also inhabit Atlantic Salmon *Salmo salar* L. which occasionally are caught in lake Skøvatn (Smalås & Henriksen, 2016). The classification of the watercourse as an anadromous salmonid- system causes specific regulations on the fishing in Skøvatn. The landowner's association conduct sales of fishing licenses to sports fishermen, but only landowners are allowed to fish with gillnets with maximum mesh size of 21 mm, knot to knot. As a measure to avoid catching anadromous salmonids, the top of the gillnets must be sunken 3 meters below the surface and are forbidden within a distance of 200 meters from the river outlet (Skøvatnet grunneierlag, 2017). In the late 1980's, it was concluded that the charr- population was stunted, and cultivating actions was made. From 1989 until recent, the landowners have performed an extensive outtake of small-sized charr, and more than 650 000 charrs have been removed (Smalås & Henriksen, 2016).

2.2 Fieldwork and sampling

Previous studies indicate that polymorphic Arctic charr populations occur in lakes within the region (Klemetsen et al., 1997; Smalås et al., 2013). These lakes have littoral spawning omnivore LO-morph that spawn in September through October, whereas a profundal spawning benthivore morphs (PB) and a profundal spawning piscivore morph (PP) are known to spawn from November to March (Klemetsen et al., 1997; Klemetsen, 2010; Smalås, 2013). Therefore, the field sampling was performed by the end of October with the aim to detect potential differences in spawning-time between the morphs. The fieldwork was conducted over a period of four days, with two nights fishing in Tårnvatn and one night in Skøvatn, from the 24th to the 27th of October 2016. Due to a recent survey in Skøvatn, which collected samples from all main habitats in the end of August 2016, I reduced the fishing effort in the littoral zone and excluded the pelagic zone in this lake. The data from the August survey were also included in this investigation.

Three types of gillnets were used for the fish sampling; multi-mesh sized benthic nets (BGO), multi-mesh sized floating nets (FGO), and standard mesh-size nets (SG). The BGO gillnets are 40m long and 1.5m deep, and are used in benthic habitats, i.e. both littoral and profundal zones. The FGO gillnets are 40m long and 6m deep floating nets that are used in the pelagic zone, fishing at the surface from 0-6 m depth. Both the BGO and FGO are divided in 8 panels with 5 m intervals, with mesh-sizes ranging from 10 to 45mm knot to knot (10, 12.5, 15, 18, 22, 26, 35 and 45 mm). Because of the variation in mesh-sizes, the BGO and FGO nets enable catches of a broad size-range on a small area, thus suitable to sample on a population level. The SG nets are 30m long, 1.5m deep and has one mesh-size throughout the whole net. These nets are used in all benthic habitats, to enhance the samples for specific size-groups if needed. All gillnets were put out during the evening and retrieved the following morning, giving each net approximately 12 hours of fishing. An overview of the fishing efforts is given in appendix a. The total catch from both BGO and SG nets was used in my analysis, as the supplement from the SG nets were essential to gather a decent sample size for the small-sized profundal Arctic charr morphs in both lakes.

Fish were assigned to a morph-population based on morphological characteristics; littoral-spawning omnivore (LO), profundal zooplanktivore/benthivore (PZ/PB) or profundal- piscivore (PP). The classification of individual fish to a specific morph was based on results from previous studies concerning polymorphic charr populations in this geographical region (Klemetsen et al., 1997; Smalås et al., 2013; Skoglund et al., 2015; Knudsen et al. 2016). These studies have shown strong relationship between the phenotype and genetic differences (Præbel et al., 2016; Simonsen et al., 2017). The LO-morph has a typical red-orange spawning color on the abdomen, a silvery side and dark color on its

back. The head shape is relatively small to their size, and the body shape is notably deeper compared to other morphs. The PZ/PB-morph was small-sized and had a paedomorphic appearance with parr-marks on their flanks at all life stages. They had a grey-yellow coloration, and the head shape was blunt and rounded. The eyes were large relative to their size. In Tårnvatn, the PB-morph also had some orange abdominal coloration. The PP-morph caught in Tårnvatn had a long, slim, and elongated body. The head was robust, with large jaws and sharp teeth on the jaw and tongue. The back and sides of the fish was dark grey or black in color, with pale red/orange spots. The abdomen in adult specimens had a dark orange coloration, and abdominal ventral fins were dark orange with a white stripe, similar to the spawning-coloration of LO-morph, (pictures of the morphs in appendix, i-j).

This method of separation into distinct morph populations was suitable for the majority of the catch. However, deviations from these distinct categories was found, and these individuals was marked as uncertain. These few individuals were placed with the population which they phenotypically resembled the most. In Skøvatn, we registered three fish that was categorized as potential anadromous charr due to their silvery- coloration and large size at age. These individuals were omitted from the data due to their deviant life-history and low sample size.

2.3 Laboratory analysis

Fork-length and weight was measured to the nearest 1mm and 0.1g precision. Otoliths were taken out and stored on ethanol for age determination. The abdomen of each fish was cut open from the pelvic fins, to anus. The sex and stage of maturity of each individual was decided by examining the gonads. The stage of sexual maturity was categorized in three groups; 1- juvenile or immature, 2- sexually mature that should spawn the current breeding season, 3- sexually mature, but already spent. The latter group also include “resting” individuals.

Category 1 female individuals are recognized by small, orange ovaries occupying only a small area posterior in the abdomen, whereas in males, two transparent sperm ducts are barely noticeable between the stomach and swim bladder. Category 2 females have large oocytes filling most of the abdomen, whereas males have large, white sperm sacks along the full interior length of the fish. Category 3 female spent spawner had both fresh- and residual roe in different sizes, and blood-filled oviduct along the intestine. Mature female fish which would not spawn this season was recognized by some blood in the oviduct, and dark/black residual roe left in abdomen. Category 3 males might have some milt left in the sperm ducts, but considerably less, and appear bloodier. Gonads from sexually mature female fish were sampled for further analysis of fecundity.

2.3.1 Age determination

The sagittal otoliths located at the inner ear of the fish was used for age determination. These were taken out and stored on small container with 96 % ethanol. The otoliths consist of calcium carbonate and are

regarded to be an accurate method for age determination, as the accretion rate of calcium carbonate vary with the growth rate of the fish (Holden & Raitt, 1974). Growth rates of fish in subarctic areas vary within the year, with enhanced growth during summer, whereas it decreases in winter. This seasonal variation in growth creates a significant difference between dark opaque winter-growth zones, and broader white hyaline summer-growth zones (Holden & Raitt, 1974). Thus, counting the winter-zones of the otoliths is an easy and precise way to determine the age of salmonid fish. The otoliths were submerged in glycerol to make the difference in growth zones more visible, before they were surface-read under a stereo-microscope, counting the opaque zones from center and outwards (Holden & Raitt, 1974).

2.3.2 Fecundity measurements

Gonads from sexually mature female fish were preserved and stored in glass containers with Gilson's fluid (100ml 60% alcohol, 800ml water, 15ml 80% nitric acid, 18ml glacial acetic acid, 20g mercuric chloride). Each container was shaken to dissolve the ovarian tissue, and to ensure all eggs got in contact with the preservative, and further to facilitate separation and handling of the oocytes for clutch-size analysis (Holden & Raitt, 1974; Smalås et al., 2013).

The total number of oocytes for each individual female was calculated by a gravimetric method described in Holden & Raitt (1974). The whole gonads were weighed, before a subsample on 1-2 grams was counted. Subsamples were weighed with a precision of 0.0001g. The clutch fecundity was estimated by the following equation;

$$F = n * G / g$$

where F = fecundity, n = number of oocytes in the subsample, G = total weight of the ovaries, g = weight of the subsample (Holden and Raitt, 1974). I used grams as the weight unit in my analysis. Oocytes of the mature PB/PZ-morph female individuals were counted directly, as the total amount of oocytes rarely exceeded 60.

We do not have precise knowledge for when spawning takes place for each morph population in Tårnvatn and Skøvatn. Thus, oocyst/embryo development could have reached different stages, and egg-size analysis was therefore not considered useful.

2.4 Data- and statistical analysis

All statistical analyses were conducted in R, version 3.3.1 (R Core Team, 2016).

2.4.1 Length and age distribution

The length and age distributions were tested between the sympatric morph-populations in Tårnvatn and Skøvatn, and between similar eco-morphs across the two lakes; *LO* vs *LO*, and *PB* vs *PZ*. These tests were conducted with Welch's two sample t-test. This test calculates the mean and the variance of the parameter and compares these values between populations. Welch's t-test is useful to test on "unpaired" or "independent" samples, as it is designed for unequal variances and unequal sample sizes.

2.4.2 Growth

The growth rate was calculated for each morph, in each lake using von Bertalanffy's growth model. The model is well known and widely used for growth estimates of fish populations (Lester et al., 2004). The von Bertalanffy growth model uses non-linear least-square (nls) regression to estimate maximum length, growth rate, and the age where size equals zero (t_0). The equation is as follows;

$$l_t = L_{\infty}(1 - e^{-K(t-t_0)})$$

where l is the length, and t is the time (age) of the fish. L_{∞} ("L infinity") is the asymptotic maximum length of the fish estimated by the model. The growth coefficient, K , describes the rate, i.e. how fast the individual obtains maximum length. The age where size equals zero, t_0 , adjusts the equation for the initial size of the individuals. The parameters were calculated with the *nls* function in R. Critics of this model point at problems when describing somatic growth pre-maturity (Enberg et al., 2008). The model describes individual somatic growth post-maturation better, as it assumes that somatic growth rates decrease due to reproductive investment (Lester et al., 2004; Enberg et al., 2008).

2.4.3 Condition

The condition-factor (Kf) was calculated with the equation

$$Kf = \text{weight (gram)} * 100 / (\text{length (cm)})^3,$$

and then tested between the sympatric morph-populations in Tårnvatn and in Skøvatn, and between eco-morphs across lakes with Welch's two-sample t-test.

2.4.4 Age and size at maturity

Logistic regression was used to analyze age and length at sexual maturity for each morph population. Immature and mature individuals were used as binomial variables, with age and length as response variables. Logistic regression produces a sigmoid curve to fit the observed values and enable us to calculate the proportion of mature fish in a population at a given age or length interval.

$$p_x = e^{(b_0 + b_1 x)} / (1 + e^{(b_0 + b_1 x)})$$

From the equation, p is the probability of an individual being sexual mature, and x is the age or length interval. The parameters b_0 and b_1 define the shape and intercept of the sigmoid curve that is fitted to the data. These calculations were performed with the *glm* function in R.

The values for A_{50} and L_{50} , i.e. the age and length, respectively, where 50 % of the population are sexual mature, were extracted by the use of the *MASS*-package (Venables & Ripley, 2002) and *dose.p* function in R. The package works on generalized linear models, when logistic regression is performed with a binomial variable. The output from these calculations were then plotted as a line against the observed data spots with the *ggplot2*-package (Wickham, 2009).

2.4.5 Fecundity

Mean number of oocytes and the fecundity range was estimated for each morph population, in addition to the mean number of oocytes per body-length of the fish, and the gonadosomatic index (GSI). The GSI is the gonad mass as a proportion of body mass.

3 Results

3.1 Length and age frequency distribution

In Tårnvatn, a clear differences in length frequency distributions between the three morph populations was found (appendix, b; t-test, $p < 0.001$)(fig. 3), additionally to the two populations in Skøvatn (appendix, b; t-test, $p < 0.0001$). In both lakes, the LO-morph had a wide size-range, with many intermediate and some large sized individuals. There was a reduced frequency of charr in the length-groups between 15 and 19 cm in Tårnvatn, which coincides with the age-classes 4-6-year (fig.4). The LO-population in Skøvatn also expressed low frequency of small-sized individuals in the size groups from 8 to 17 cm. The PB- and PZ-population had a significantly smaller size-distribution range, and no individuals exceeding 17 or 13 cm, respectively. Thus, across the two lakes there is significantly different pattern in size frequency distribution between the PB- and PZ-populations. In contrast, none individuals smaller than 12 cm was registered for the PP-population, whereas several exceeded 40 cm (fig.3). It is a noticeable difference in frequency of mature individuals within the PB- and PZ-population, in contrast to all the other sympatric populations.

A general population structure in fishes would consist of a high frequency of young and small-sized individuals, following a steady reduction towards older and larger individuals. My data show that I miss the youngest and smallest size groups. This is a result of the equipment used which are known to have a low catch-efficiency of fish smaller than 10 cm length.

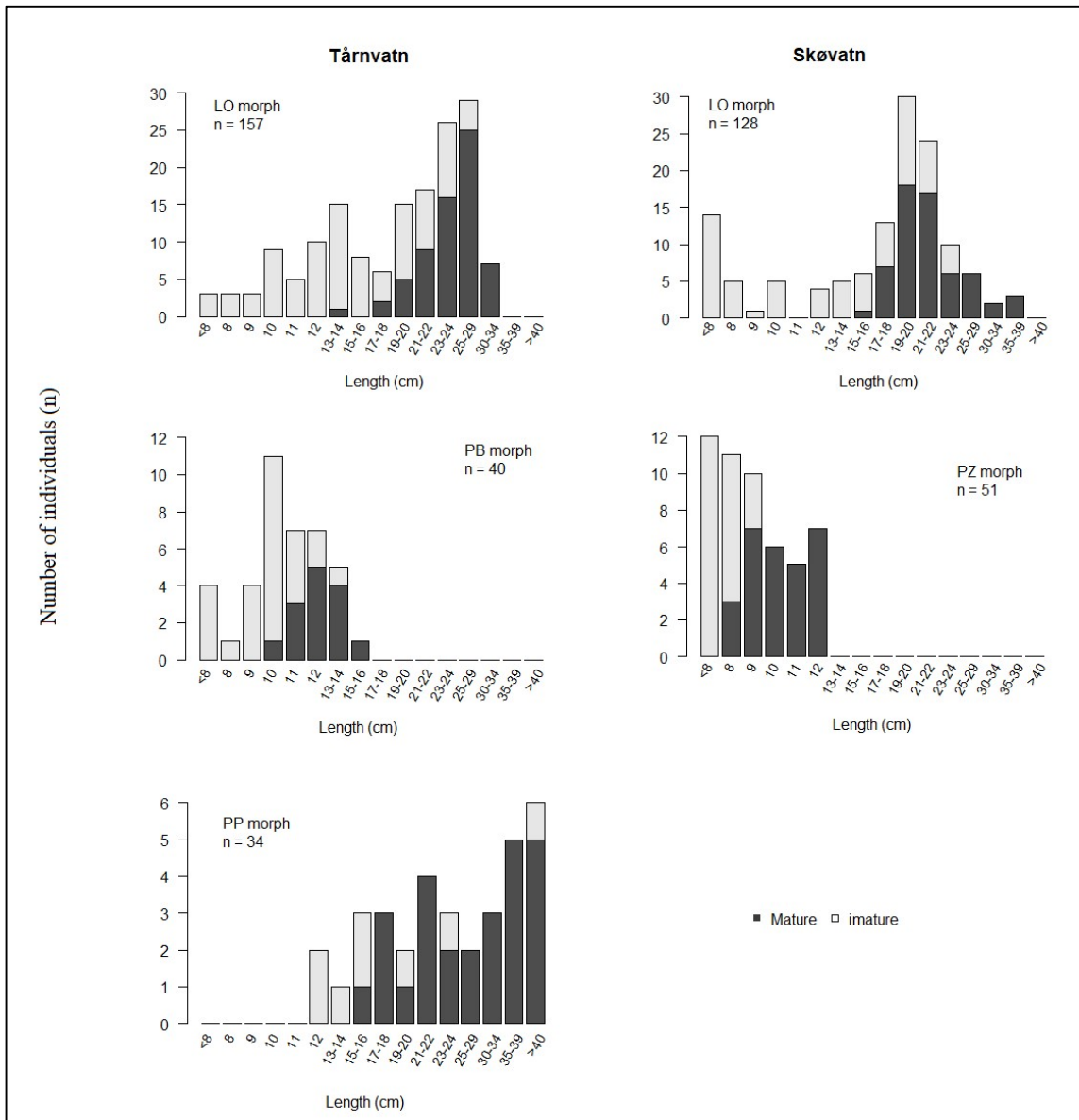


Figure 3: Length distribution of the three morph populations from Tårnvatn (left column), and two morph populations from Skøvatn (right column), split up in immature (light shaded) and mature (dark) individuals. Notice the unequal scaling of the y-axis

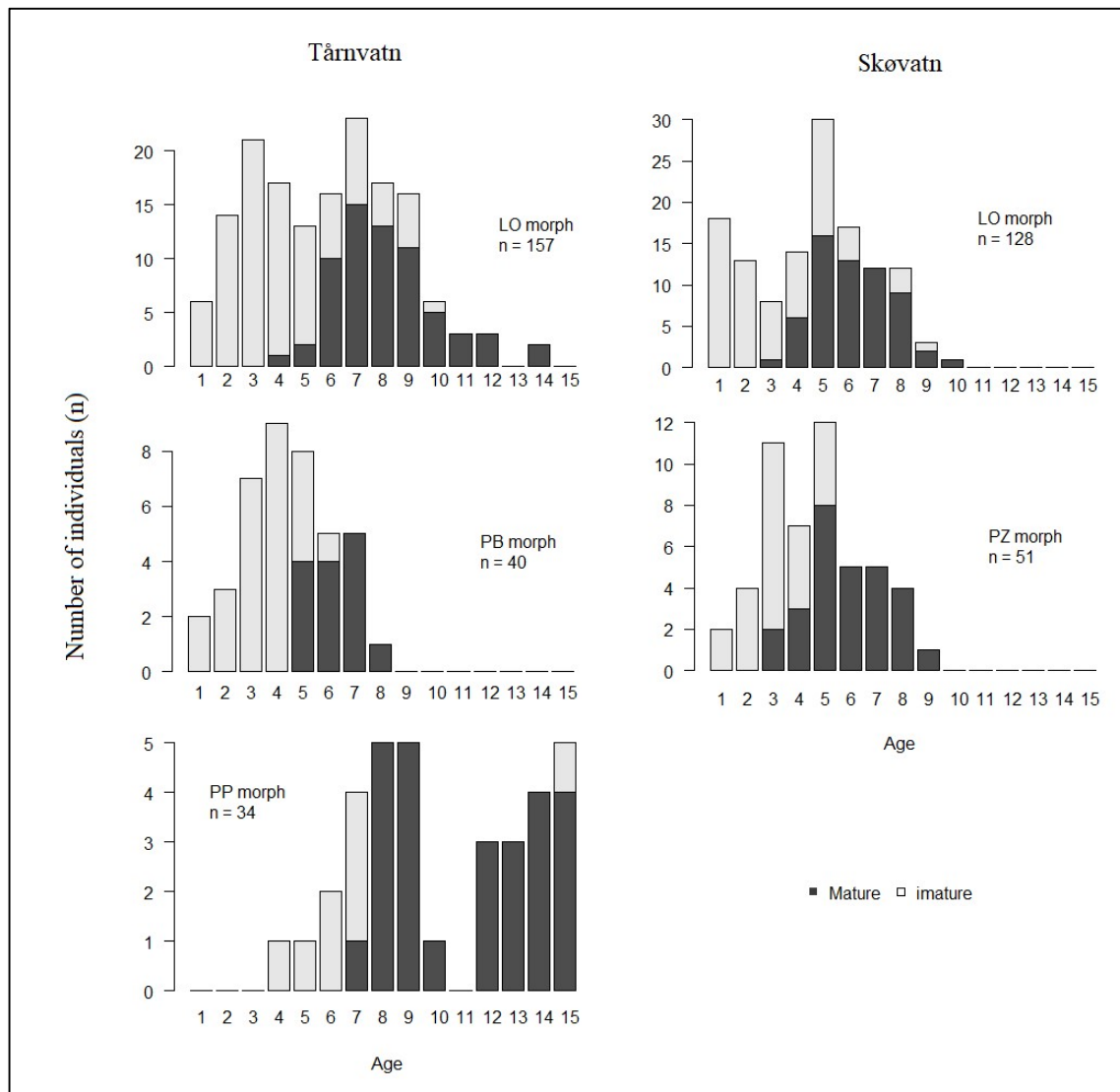


Figure 4: Age distribution of the three morph populations from Tårnvatn (left column), and two morph populations from Skøvatn (right column), split up in immature (light shaded) and mature (dark) individuals. Notice the unequal scaling of the y-axis

3.2 Growth and condition

3.2.1 Growth

In Tårnvatn, the LO-morph had the fastest growth of all morphs up to 6 – 8 years of age, and then the growth curve flattened out towards an asymptotic maximum length (fig. 3, table 1; $L_{\infty} = 28.8$ cm). The PP-morph grew to a larger size, and had the highest maximum length estimated from the model (fig. 3, table 1; $L_{\infty} = 108.1$ cm). The model plot shows an approximately linear growth curve for the PP-morph. Thus, von Bertalanffy growth model does not provide a good fit of the observed data for this population, which also is reflected in the model parameters in table 1. The PB-morph had the lowest maximum

length of the morph populations in Tårnvatn ($L_{\infty} = 16.9$ cm), and differed significantly compared to both the LO-, and PP- morph (fig. 3).

In Skøvatn, the growth of LO-morph flattens out around lengths close to 22 cm at 7-8 years of age, which is somewhat lower than the estimated maximum length of the model (table 1; $L_{\infty} = 33.9$ cm). The maximum length for the PZ-morph suggested by the model was higher than the observed (fig. 3, table 1; $L_{\infty} = 16.3$ cm).

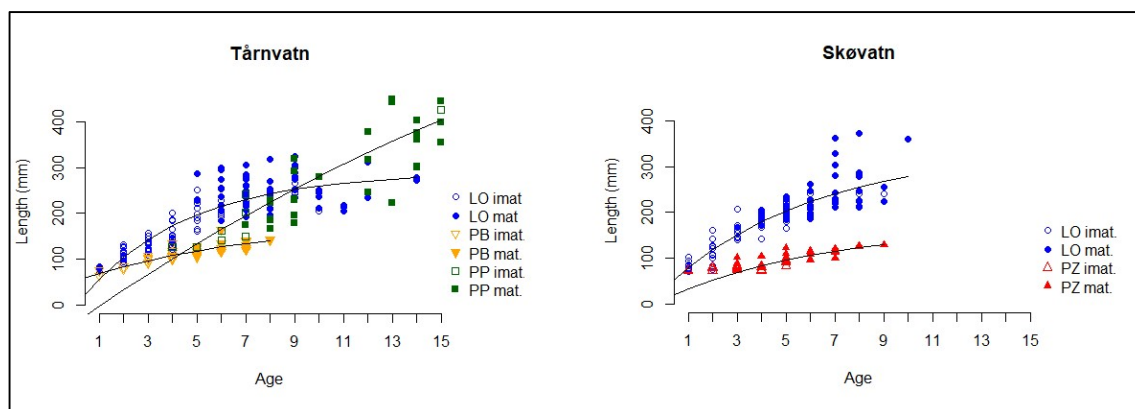


Figure 5: Observed individual size (length at age) for each population in the two lakes. Open symbols represent immature individuals, whereas filled symbols represents mature. Dark lines are the estimated von Bertalanffy's growth model for each of the morph-populations

Table 1: The calculated von Bertalanffy growth parameters for each morph population in Tårnvatn and Skøvatn. L_{∞} is the asymptotic length, K is the growth coefficient and t_0 is the estimated age where length equals zero, and the sample size n .

Lake	Morph	n	L_{∞} (cm) \pm SE	$K \pm$ SE	t_0
Tårnvatn	LO	157	28.8 ± 1.53	0.229 ± 0.035	-0.36
	PB	40	16.9 ± 3.28	0.172 ± 0.093	-1.95
	PP	34	108.1 ± 217	0.0337 ± 3.074	1.09
Skøvatn	LO	128	33.9 ± 3.98	0.162 ± 0.041	-0.65
	PZ	51	16.3 ± 5.96	0.1662 ± 0.173	-0.36

Across lake comparison of eco-morphs revealed similar growth patterns between the LO-morphs, and between the PB- and PZ-morph (fig. 5, table 1). LO-morphs grew well until ages of 6-8 years, after which the growth curves flatten out at relatively similar maximum lengths. Although the PB-morph in Tårnvatn had a slightly higher maximum length compared to the PZ-morph in Skøvatn, the growth curves of the two populations express similar growth trajectories.

3.2.2 Condition

The condition-factor differed significantly between LO- and the two profundal morph-populations in Tårnvatn, and between the LO- and PZ-morph in Skøvatn (table 2, t-test, $p < 0.001$). However, the condition-factor did not differ significantly between the PB- and PP-morph in Tårnvatn (table 2, t-test, $p = 0.427$).

Across lakes comparisons revealed that the condition-factor between the LO-morphs in Tårnvatn and Skøvatn was similar (table 3, t-test, $p > 0.05$), although the condition of the LO-morph in Skøvatn was higher. The condition-factor between the PB-morph in Tårnvatn and the PZ-morph in Skøvatn was also similar (table 3, t-test, $p = 0.663$).

Table 2: Welch two-sample t-test on condition-factor between the sympatric populations in Tårnvatn, and in Skøvatn.

Lake	X vs Y	t-stat	df	p-val	Mean of X	Mean of Y
Tårnvatn	LO vs PB	5.5252	100.59	<0.0001	0.9979	0.8882
	LO vs PP	4.0418	68.808	< 0.001	0.9979	0.9072
	PB vs PP	-0.79829	66.965	0.4275	0.8882	0.9072
Skøvatn	LO vs PZ	8.094	94.881	< 0.0001	1.03	0.88

Table 3: Welch two-sample t-test on condition-factor between the two LO-morphs, and between the PB- and PZ-morph in Tårnvatn and Skøvatn.

Tårnvatn vs Skøvatn	t	df	p-val	Mean Tv	Mean Sv
LO vs LO	1.8239	272.65	0.069	0.998	1.027
PB vs PZ	-0.43652	87.885	0.6635	0.888	0.879

3.3 Maturity

3.3.1 Length at sexual maturity

Length where 50 % of population reached sexual maturity (L_{50}) differed between all the morph populations (fig. 6, table 4). As expected, the PB-morph in Tårnvatn matured at the smallest size (table 4). However, it was unexpected to find the PP-morph to mature at a smaller size than the LO-morph (table 4). This result is explained by the skewed sample size distribution of the PP-morph, which cause a bad fit of the model: most of the fish we caught were mature, and very few small-sized individuals in this population. The difference in L_{50} were significant between the three populations (appendix, f; glm, $p < 0.05$). The PZ-morph in Skøvatn matured at significantly smaller size than the LO-morph (fig. 6, appendix, f; glm, $p < 0.05$).

Across lakes comparison revealed that the L_{50} was similar between PB- and PZ-morph (appendix, g; glm, $p = 0.18$), and between the two LO-morphs (appendix, g; glm, $p = 0.87$). A larger proportion of the LO- and PZ-morph in Skøvatn mature at smaller sizes than the LO- and PB-morph in Tårnvatn, respectively (fig. 6, table 4). Apart from the PP-morph in Tårnvatn, there was a trend that males in a population matured at smaller sizes than females, although these differences did not differ significantly (appendix, h; glm, $p > 0.25$).

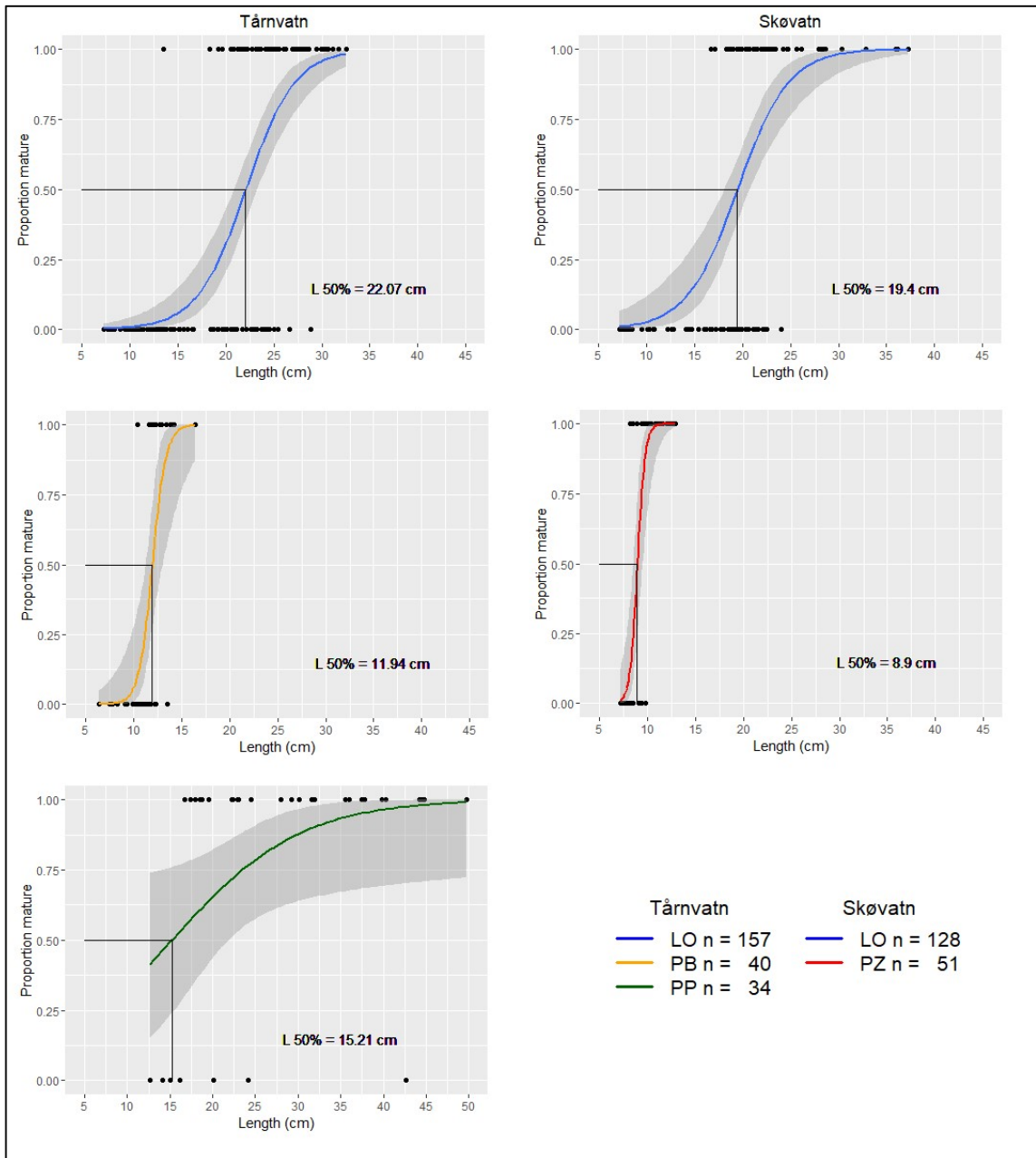


Figure 6: Observed (dots) and fitted generalized linear regression (curves) of the proportion of sexual mature individuals by length (cm) for each morph of Arctic charr in Tårnvatn and Skøvatn. The dark-shaded area in affiliation with the curve represents the standard error (SE) for the model. Black, straight lines mark the L50 value in each plot.

Table 4: Length at 50 % sexual maturity (L_{50}) for each morph of Arctic charr in Tårnvatn and Skøvatn and between the sexes within these, with standard error for the models ($\pm SE$), and the sample size n . Lengths are given in cm.

<i>Lake</i>	<i>Morph</i>	<i>n</i>	$L_{50} \pm SE$	$L_{50} \pm SE$ (Females)	$L_{50} \pm SE$ (Males)
<i>Tårnvatn</i>	LO	157	22.1 ± 0.58	22.5 ± 0.64	21.8 ± 1.03
	PB	40	11.9 ± 0.34	12.2 ± 0.58	11.7 ± 0.38
	PP	34	15.2 ± 4.42	14.4 ± 6.42	17.4 ± 4.95
<i>Skøvatn</i>	LO	128	19.4 ± 0.61	20.6 ± 0.83	18.3 ± 0.76
	PZ	51	8.9 ± 0.21	9.4 ± 0.19	8.4 ± 0.16

3.3.2 Age at sexual maturity

The age where 50 % of the population reached sexual maturity (A_{50}) varied between the sympatric morphs in both lakes (fig. 6, table 5). However, the A_{50} -models only revealed significant difference between the PP- and PB-morph in Tårnvatn (appendix, c; glm, $p = 0.039$). The difference in A_{50} between the LO- and PB-morph was close to significant (appendix, c, glm $p = 0.057$), whereas between the LO- and PP-morph the models overlapped (appendix, c; glm, $p = 0.45$). In Skøvatn the A_{50} models revealed a overlap between the LO- and PZ-morph, thus they seem to mature at relatively similar ages (appendix, c; glm, $p = 0.138$). Across lakes comparison showed that A_{50} was similar between the PB- and PZ-morph (appendix, e; glm, $p = 0.25$), and the LO-morphs (appendix, e; glm $p = 0.87$). In most cases, the males matured earlier than the females, although not significantly (appendix, d; glm, $p > 0.4$). This trend was not as strong in Tårnvatn as in Skøvatn, where the difference in A_{50} -values between the sexes were 2 and 1.5 years for the LO- and PZ-morph, respectively (table 4).

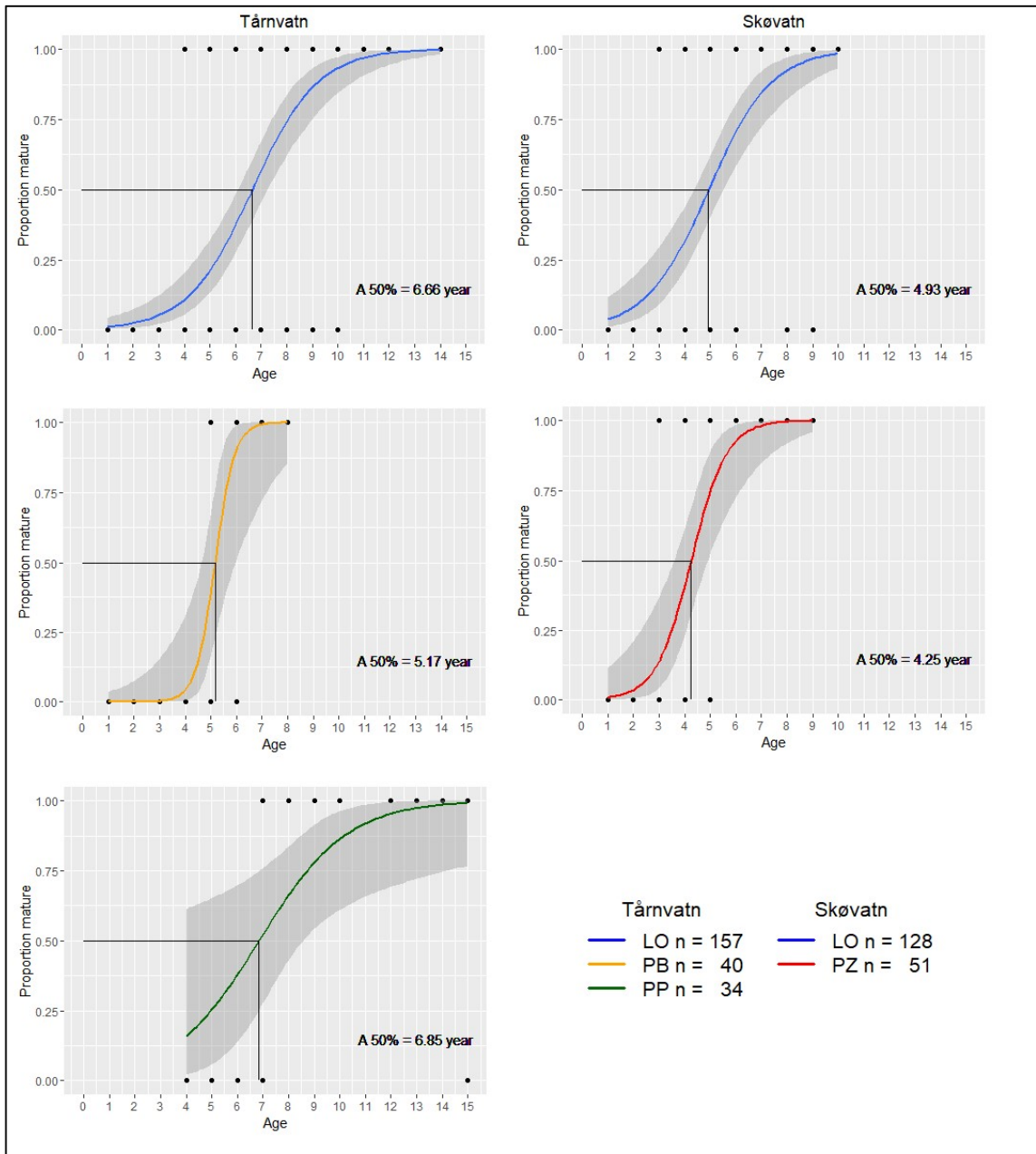


Figure 7: Observed (dots) and fitted generalized linear regression (curves) of the proportion of sexual mature individuals at age of each morph of Arctic charr in Tårnvatn and Skøvatn. The dark-shaded area in affiliation with the curve represents the standard error (SE) for the model. Black, straight lines mark the A50 value in each plot.

Table 5: Age at 50 % sexual maturity (A_{50}) for each morph of Arctic charr in Tårnvatn and Skøvatn, and between the sexes within these, with standard error for the models ($\pm SE$), and the sample size n .

<i>Lake</i>	<i>Morph</i>	<i>n</i>	$A_{50} \pm SE$	$A_{50} \pm SE$ (Females)	$A_{50} \pm SE$ (Males)
<i>Tårnvatn</i>	LO	157	6.7 ± 0.28	6.5 ± 0.34	7.0 ± 0.49
	PB	40	5.2 ± 0.23	5.2 ± 0.46	5.0 ± 5.41
	PP	34	6.9 ± 0.95	7.0 ± 0.07	7.3 ± 1.29
<i>Skøvatn</i>	LO	128	4.9 ± 0.28	5.5 ± 0.40	4.4 ± 0.33
	PZ	51	4.3 ± 0.28	5.0 ± 5.54	3.5 ± 0.28

3.4 Spawning time and fecundity

In Tårnvatn, none of the morphs had spawned prior to my field-sampling, i.e. end of October. However, the LO-morph showed signs of ongoing spawning during the sampling period (severe egg-shedding, pers.obs.). Of the sexually mature individuals from each of the three morph-populations, 96 % of the LO-morph were caught in the littoral or pelagic zone, and over 90 % of the PB- and PP-morphs were caught below 15 m depth (table 6). The two morphs in Skøvatn were segregated in time of spawning. All mature individuals of the LO-morph had spawned prior to our fieldwork, i.e. end of October. None of the mature PZ-individuals that was caught had signs of recent egg-shedding at this time, and all of these were caught below 15 m depth (table 6). Although these results only represent a snap-shot data, they indicate that the PZ-, PB-, and PP-morph resides and utilize deeper habitats than the LO-morphs, that might also include spawning habitat.

Table 6: Habitat and number of mature individuals caught from each morph of Arctic charr, and the sample size *n*.

Lake	Morph	<i>n</i>	Littoral	Pelagic	Sub-littoral	Profundal 1	Profundal 2
			(1 – 8 m)	(0 – 6 m)	(~15 m)	(~25 m)	(~35 m)
Tårnvatn	LO	49	27	20	2	-	-
	PB	11	1	-	-	6	4
	PP	17	1	-	3	13	-
Skøvatn	LO	48	31	13	3	1	-
	PZ	17	-	-	10	6	1

The fecundity of females revealed clear differences between the populations (table 7, fig. 8 a,b). The PZ and PB-morphs had very low number of oocytes (mean: 55-78) compared with their sympatric morphs (mean >293). Even though the mature females of LO- and PP-morph are of relatively similar sizes, there was a clear difference in the fecundity and number of oocytes per body length of the fishes between them (table 7, fig. 8a). The sample size of mature female individuals with oocytes from the PB- and PP-morph was scarce (*n*=2 and *n*=3), thus not sufficient for statistical analysis.

Table 7: Mean fecundity and fecundity range, gonadosomatic index (GSI), mean number of oocytes/mm body-length and sample size (*n*) of ripe female individuals from each of the populations of Arctic charr from Tårnvatn and Skøvatn.

Lake	Morph	<i>n</i>	Mean fecundity	GSI	Mean number of
			(fecundity range)		oocytes/mm body-length
Tårnvatn	LO	26	639.27 (170 – 1626)	8.2 %	2.33
	PB	2	77.50 (72 – 83)	8.2 %	0.64
	PP	3	293.00 (129 – 456)	5.7 %	1.12
Skøvatn	LO	0	-	-	-
	PZ	13	55.23 (42 – 82)	4.9 %	0.51

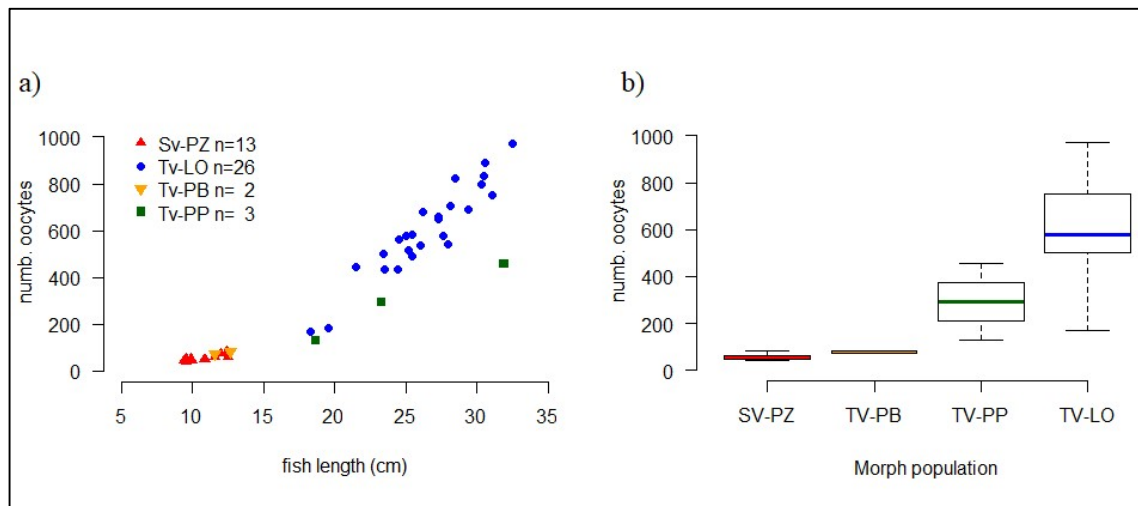


Figure 8: a) Number oocytes against body-length (cm), in four of the morph populations. b) Fecundity range of four of the morph of Arctic charr; Skøvatn PZ (red), Tårnvatn PB (orange), Tårnvatn PP (darkgreen), and Tårnvatn LO (blue). Centre line of boxes represents the median, the box defines the inter quartile range (IR) and represents the values $\pm 25\%$ from the median (2nd and 3rd quartile). The whiskers (in b) define the main part of the distribution, excluding outliers and defined as $1.5 \cdot IR$.

4 Discussion

Phenotypic differences in life-history strategies are observed in several vertebrate species, including reptiles, amphibians, and birds (Skulason & Smith, 1995). These differences are expressed in adult size, growth, age- and/or size at maturation and reproduction and the cause of these variations relates to resource competition and habitat utilization. It has frequently been observed that restricted resource availability causes a reduction in growth and small adult size in insects, reptiles, and several fish species (Colins et al., 1993; Rotheray et al., 2016; Trudel et al., 2001; Kahilainen et al., 2003). In subarctic freshwater systems, limited resource availability is often related to specific habitats within lakes, such as the profundal zone. Several fish species in subarctic lakes have consistently developed similar life-history strategies, such as small adult size, maturation at low age and small size, and low fecundity, as adaptations to the extrinsic environment.

There were clear and consistent differences in several life-history parameters such as age and size distribution, growth, age- and size at maturity, and fecundity of the sympatric morphs in Skøvatn and Tårnvatn. More specifically, the littoral spawning omnivore LO-morphs in both lakes had the fastest growth rate and matured at a medium size and age compared to their sympatric profundal-dwelling morphs. In contrast, the PB-morph from Tårnvatn and the PZ-morph from Skøvatn matured at early ages and small sizes and had low growth-rates. The PP-morph had a slow but steady growth rate but did not delay maturation to higher age and larger size compared to the LO-morph. These results coincide with life-history pattern elsewhere and supported by relatively similar niche utilization (Mocchetti, 2018) across lakes as Fjellførsvatn (Klemetsen et al., 1997) and Skogsfjordvatn (Smalås et al., 2013). These consistent life-history patterns among sympatric morphs may be a response to different environmental variables (e.g. temperatures) and prey densities between the upper water layers and the profundal zone.

4.1 Length and age distributions

The length distributions of the sympatric morphs in Tårnvatn and Skøvatn revealed clear differences between the populations. The LO-morphs in both lakes mostly consisted of intermediate and large sized individuals, a result which corresponds to several lake-systems (Klemetsen et al., 1997; Klemetsen et al., 2003; Hammar, 2014). The low frequencies of fish in the length groups 15 – 19 cm in Tårnvatn may indicate increased competition within the length groups below 15 cm. The LO-population in Skøvatn also expressed low frequency of small-sized individuals in the size groups from 8 to 17 cm. This result probably relates to an intensive fishing-effort to reduce the fish-stock performed by the local land-owners but may also relate to competition within juvenile or small-sized groups. The PB- and PZ-morph was consistently smaller than the sympatric LO-morph, and these results coincides with other systems of sympatric charr morphs (Klemetsen et al., 1997; Hammar, 2014; Markevich et al., 2017). The overlap in size-distribution between the PB-/PZ-morph and the LO-morphs in the respective lake, was minor. Thus, the PB- and PZ-morph express a clear phenotypic difference. These differences become more

protruding when seen in relation with the age-distributions of the respective morphs. These results reveal that the sympatric morphs in Tårnvatn and Skøvatn have fairly similar age distributions, except from the PP-morph in Tårnvatn. The PP-morph mostly consisted of large sized individuals, and no individuals below 12 cm length was recorded. This demonstrate a potential uncertainty of separating the different morph populations at small sizes.

The clear differences in size-distributions between the sympatric populations indicate different strategies between the populations in terms of growth and reproduction. The small, or absent, size overlap between mature individuals in the sympatric populations

4.2 Growth

There were clear signs of divergent growth trajectories between sympatric upper-water and deep-water morph-populations in the two lakes, Skøvatn and Tårnvatn. These differences are related to their different niche and habitat utilizations (*sensu* Moccetti, 2018). The LO-morphs in the two lakes had high growth rates and achieved intermediate sizes as they utilized the littoral-pelagic habitat and had a broad dietary niche (see Moccetti, 2018). This is seen in other comparable studies in lakes from the same region (Klemetsen et al., 1997; Knudsen et al., 2006; Smalås et al., 2013). The deep-water benthivorous PB-morph in Tårnvatn had a much slower growth and achieved the smallest body size of the sympatric occurring morphs. It was predominantly caught below 20 m depth and fed on profundal benthos (Moccetti, 2018). These results are described in previous studies from the same region (Klemetsen et al., 1997; Smalås et al., 2013), and other studies on small-sized charr morphs (Jonsson et al., 1988; Hammar, 2014). The growth trajectories for the two small-sized profundal populations studied here coincide with the PB-morphs from Fjellfrøsvatn (Klemetsen et al., 1997) and Skogsfjordvatn (Smalås et al., 2013). The PB-morph in Tårnvatn and the PZ-morph in Skøvatn closely resembled each other in growth: the parameters from the von Bertalanffy growth-model are almost identical, thus express similar growth trajectories, although the observed size and condition factor of the PB-population in Tårnvatn was somewhat larger. Hypothesis for exploiting the profundal habitat has addressed release of interspecific competition, predation, and parasitism as possible causes (Knudsen et al., 2016). This hypothesis could apply for the PB-morph in Tårnvatn, as it manages to exploit the profundal resources with low parasite infections, although in the presence of a piscivore-morph (Moccetti, 2018). The piscivore PP-morph had the slowest growth but attained the largest size of all the populations in Tårnvatn, due to its high longevity and continuous growth. This corresponds to the PP-morph in Skogsfjordvatn (Smalås et al., 2013). Moccetti (2018), showed that small-sized PP-morph utilizes profundal benthic prey, and further indicated that the PP-morphs change their diet through an ontogenetic niche shift to piscivory/cannibalism when they achieve a size threshold around 20 cm length. The PP-morph is the second incident of a large-sized, profundal utilizing piscivore form described from a northern Norwegian lake, after Skogsfjordvatn (Smalås et al., 2013). Although the

growth parameters from von Bertalanffy's model are dissimilar between the PP-morph from Skogsfjordvatn and the PP-morph from Tårnvatn the growth trajectories closely resemble each other (Smalås et al., 2013). The von Bertalanffy growth model parameters for the PP-morph in Tårnvatn did not provide reasonable information: a brief calculation with the estimated growth coefficient in relation to the high asymptotic size from the model ($> 1\text{m}$) indicate that the PP-morph would achieve the asymptotic length after 200 years. The observed growth of the PP-morph seems linear and does not decline as the population matures, which is observed in the other sympatric populations, and previous studies (Smalås et al., 2013; Hammar, 2014). A higher sample-size could have helped register a more realistic maximum size for the PP-morph, and also helped reducing the large standard errors for this growth-model.

The difference in growth trajectories for the morphs utilizing different habitats (hereby the littoral-pelagic *versus* the profundal) in the Tårnvatn and Skøvatn are related to the strong segregation in dietary niches among the sympatric morphs (Mocchetti, 2018). Prey availability is important for growth opportunities and growth rates, and resource richness decreases from the littoral, to the pelagic, and lowest in the deep-water areas in subarctic lakes (Klemetsen et al., 1989; Kahilainen et al., 2003). This would imply that the LO-morph should achieve the largest body-size of these populations, which is not the case as the PP-morph achieves a larger observed size. Fraser et al. (2008) hypothesized that the size of food particles utilized by Arctic charr will constraint its maximum body size. Thus, piscivorous individuals will have a larger size distribution of potential prey than individuals which utilize zooplankton or benthic invertebrates (Smalås et al., 2013 and references therein). This leads to a high foraging efficiency with increasing size of the piscivores (Fraser et al., 2008), that could explain large sizes of the PP-morph in Tårnvatn. The PP-morph experience a boost in their growth at 7-9 years of age and approximately 19 cm of length. This can be explained by the ontogenetic niche shift within the PP-morph, where they perform a diet shift from profundal benthos to fish at these sizes (Mocchetti, 2018). A shift to a large-sized energy-rich prey such as fish, results in increased growth (Hammar, 2014; Borgstrøm et al., 2015). Lack of such a niche-shift for the strict benthivore PB-morph may explain the observed divergent growth patterns between the PP- and PB- morphs that live under identical abiotic factors in the profundal zone in Tårnvatn.

The LO- and PZ-morph in Skøvatn show remarkable differences in growth, even though they express close to 50 % zooplanktivore dietary niche overlap (Mocchetti, 2018). The relative difference in prey abundance between habitats, parasitism, and disease, in addition to the contrasting abiotic factor between the two environments, may cause this large difference in growth rates. The PZ-morph was mainly caught at depths below 15 m and expressed a novel foraging strategy where it feed on zooplankton (Mocchetti, 2018). It had a slow growth and attained a significantly smaller body-size compared to its sympatric conspecific, an observation which resembles the sympatric charr populations

in Fjellfrøsvatn (Klemetsen et al., 1997). The PZ-morph seem to occupy the lower pelagic zone which is less abundant on prey than the upper pelagic zone. However, it might be more favorable than a strict profundal-benthic diet (Mocchetti, 2018). This strategy to reside at deeper-water may result in less predation pressure from avian predators and piscivore fish on the PZ-morph, as there seems to be few true piscivores in deep-water areas in Skøvatn. This suggests that the PZ-morph might divert less energy towards predator avoidance, while at the same time it manages to feed on pelagic resources. On the other hand, several zooplankton species functions as intermediate hosts for food-transmitted parasites. The large proportion of zooplankton in the diet revealed high parasite infections which influence growth by requiring energy from its host, in addition to costly immune-responses (Halvorsen & Andersen, 1984; Knudsen & Klemetsen, 1994; Bush et al., 1997). Fishes with low resource availability may not cope with this additional energy cost associated with parasite infection (Bush et al., 1997). Our field observations revealed very skinny and slender individuals, and the condition factor for the PZ-morph was significantly lower than its sympatric conspecific LO-morph. Thus, there are several indications such as low growth rates and high parasite burdens, which suggests that the PZ-population suffers from energetic constraints. Although, the two sympatric populations have approximately similar longevities, and mature at approximate same age, their size at maturity is very different. The somatic growth in fishes can be significantly restricted at the onset of maturation as energy resources will be directed to production of gonads and reproductive activity (Reznick & Endler, 1982).

The conclusion is that the eco-morphs in the two lakes, which exploits similar niches, develop similar life-history strategies based on adaptations to abiotic factors, although their dietary niches and biotic interactions might differ. Thus, this could be another example of parallel evolution of life-histories adapted to a profundal life-style.

4.3 Maturity

Utilization of contrasting environments influence maturation, thus the sympatric populations have developed different life-history strategies to maximize fitness through reproduction. The LO-morphs in the two lakes mature at intermediate age and size, and these results coincides with other studies of Arctic charr (Klemetsen et al., 2010; Smalås et al., 2013). In contrast, the sympatric PB- and PZ-morphs in the respective lakes mature at lower ages, and at small size. These results address the strong effects of abiotic factors, niche utilization, and the energetic cost of reproduction. These results further coincide with studies on small-sized profundal charr-morphs from Fjellfrøsvatn (Klemetsen et al., 1997), Skogsfjordvatn (Smalås et al., 2013), Vangsvatn (Jonsson & Hindar, 1982) and Thingvallavatn (Jonsson et al., 1988). Although the PB- and PZ-morph seem to mature at a slightly older age, their size-parameters are similar. These results were unexpected as I predicted the PB- and PZ morph to mature at even lower ages, and reveal more contrasting maturation strategies in terms of age with their sympatric LO-morph. For instance, the LO- and PZ-population in Skøvatn have approximately similar longevities

(9 and 10 years) and mature at the same age. The major difference between them is the size at maturity, which indicate that size is a more important factor on maturation than the age. This can further be related to trade-off regarding fecundity.

The contrasting maturation strategies between the two profundal-populations in Tårnvatn, where the PP-morph mature at a higher age and larger size than the PB, address different trade-offs between population subjected to the same environmental factors. As the PB-morph mature, the growth nearly stops, suggesting that most of the available energy resources are directed towards maintenance and reproduction. In contrast, the PP-morph delay maturation and invest more into somatic growth, probably to perform an ontogenetic niche shift. Thereby it can grow relatively well after maturation as it may feed on large energy-rich resources, such as fish. The PP-morph therefore can invest in somatic growth simultaneously with allocation of energy to reproduction. These results can also explain the large variation in longevity between the two morphs; the PP-morph live almost twice as long as the PB-morph (15 *versus* 8 years) according to my sample.

The PP-morph from Tårnvatn matures at a lower age and a smaller size than the PP-morph from Skogsfjordvatn (Smalås et al., 2013), and the difference in length at maturity is quite large. This was not in accordance with my hypothesis of delayed maturation in favor of somatic growth. I have already mentioned the poor fit of the models of maturation (A_{50} and L_{50}), due to a skewed distribution of age and size, in addition to a low sample size for this population. The models suggest a L_{50} value of 15 cm for the PP-morph from Tårnvatn, which is lower than the suggested size-threshold to initiate piscivory (~20 cm, Moccetti, 2018). It would be contradictory to the strategy of achieving a size to enable piscivory before maturation, if they mature just too small to achieve this size-threshold. Growth trajectories for the sympatric morph-populations show that the growth become asymptotic when individuals mature. As the PP-population obviously continues to grow post maturation, from a size below the ontogenetic niche shift, this suggests that they have sufficient prey resources available to support both investment in somatic growth and the process of reproduction. Therefore, I suggest that the poor fit of the maturation-models for the PP-morph give an inconclusive view of the populations maturation strategy.

The females in all morph-populations, except for the PP-morph in Tårnvatn, matured at larger sizes than the males. The energetic cost to produce large gonads, in addition to the space needed in the body cavity, limits the number of gametes within females in contrast to males (Wootton, 1998). This suggests size as a more important factor to maturation than age for females, as increased body-size leads to increased fecundity, thus also fitness. Therefore, females seem to delay maturation and invest more in somatic growth to enhance fecundity,

The core of life-history theory aims to find the strategy which increases fitness in each trait (Stearns, 1992). For the PB- and PZ-morph, there is no fitness gain to delay maturation further. Relations between growth and the dietary niche described by Moccetti (2018) suggests that there's little opportunity for further growth, thus also to increase fecundity. On the other hand, the PP-morph should delay maturation until it reaches a size which enable it to feed on large and more energetic prey, and thereby increase fitness by an increased fecundity later in life. Another point presented by Hammar (2014) is the effect of a cannibalistic predator. Juveniles of the PP-morph are subjected to the same predator risk in the profundal habitat as the PB-morph, thus growth of both morphs are negatively affected. This can further cause a delay in the maturation for the PP-morph as it may allocate more energy towards predator avoidance and spend more time to achieve a large size.

Instantaneous mortality rates at specific age or size-range in a population could affect and determine age- and size at maturity according to life history theory (Wootton, 1998). Predation is a factor which can influence these parameters as the body-size of an individual set limitations for possible predators (see growth discussion). The LO-morph which reside in shallow waters are exposed to avian predators in addition to piscivore/cannibalistic charr and trout. Therefore, it could be favorable to achieve a size which minimize the predation risk before the onset of maturation (Smalås et al. 2013, and references therein). Smalås et al. (2013) further discuss that the PB-morph in Skogsfjordvatn would be subjected to predation in all age- and size intervals in the presence of a piscivore-fish. Therefore, early maturation for the PB-morph would be a favored strategy to increase fitness. This hypothesis can also apply in Tårnvatn where there is evident signs of a PP-morph (Moccetti 2018). However, LO-morphs which achieve large sizes are also known to switch to piscivory/cannibalism (Forseth et al., 1994; Keely & Grant, 2001). This in addition to the presence of brown trout could imply that predation could affect the maturation strategies also for the Skøvatn system.

These results address life history trade-offs a population must encounter in adaptations to different environments; present or future growth or reproduction. This study revealed three distinctly different strategies of maturation between the sympatric populations in Tårnvatn and Skøvatn. The LO-morphs in both lakes mature at intermediate and large size, which can reduce predation risk and achieve a high fecundity. The PB- and PZ-morph mature at smaller sizes and lower ages than their sympatric conspecifics, and thereby increase the chance of reproduction due to predation risk and instantaneous mortality. The PP-morph delay maturation and invest in somatic growth to achieve a body-size which enable piscivory, thus enhance fecundity with larger body sizes later in life.

4.4 Spawning and fecundity

None of the populations in Tårnvatn had spawned prior to field-sampling, although it appeared to be ongoing for the LO-morph, and not for the PB- and PP-morph. Thus, segregation in spawning time between the sympatric populations in Tårnvatn as was seen in Fjellfrøsvatn (Klemetsen et al., 1997; Knudsen et al., 2006) and Skogsfjordvatn (Smalås et al., 2013). In contrast, the LO-morph in Skøvatn had spawned prior to the sampling in October, whereas the PZ-morph had not. Thereby this indicate segregation in spawning time between the LO- and PZ-morph in Skøvatn. The sympatric populations occupy different habitats, thus indicate different preferences for spawning sites (Klemtesen et al., 1997; Smalås et al., 2013). My results might indicate that the sympatric populations in both lakes are reproductively isolated in terms of spawning habitat, where the LO-morph spawn in the littoral, whereas the PB-, PP-, and PZ-morph was found to reside at deeper water. However, these are only to be considered as indications as there are no specific knowledge concerning the respective spawning sites, or time, for the profundal morphs in Tårnvatn and Skøvatn.

Segregation in spawning time between the sympatric morphs in Skøvatn indicated in this study might further be explained by spatial segregation as adaptations to the abiotic factors in their habitat. Development of oocytes are closely linked to temperatures (see Klemetsen et al., 1997). Thus, temperature variations between the littoral *versus* sub-littoral/profundal habitat influence embryo development: eggs laid in the profundal zone will experience relatively warmer temperatures during winter compared to eggs of the LO-morph, and the development to embryo/larvae proceed faster. Klemetsen et al. (1997) suggests that the difference in temperature between the littoral and profundal spawning grounds to some extent can be compensated with difference in spawning time. My results, seen in relation to the work of Moccetti (2018) indicate an incomplete segregation by depth between the sympatric morphs in Skøvatn. The populations express large zooplanktivore diet overlap (Moccetti 2018), which might indicate a microhabitat segregation in the vertical pelagic zone in terms of temperature preferences. Similar incidents of ecological segregation within the pelagic habitat have been found in Arctic charr in North American lakes (Power et al., 2005), and in other fish species (Turgeon et al., 1999; Gjelland et al., 2007; Helland et al., 2008).

The LO-morphs in Tårnvatn had the highest fecundity of the sympatric populations, whereas fecundity of the PP-morph was intermediate. This was not in accordance with my hypothesis, as I expected the PP-morph, which achieve the largest body-size, to have highest fecundity. This result contrasts with the studies from Skogsfjordvatn, where Smalås et al. (2016) revealed that the PP-morph had the highest fecundity as a result of largest body-size. The PB- and PZ-morph had much lower fecundities compared to both the LO- and PP-morph in Tårnvatn. These results have a clear resemblance to previous studies from Fjellfrøsvatn (Klemetsen, 2003; Knudsen et al., 2006), Skogsfjordvatn (Smalås et al., 2016) and Sirdalsvatn (Hesthagen et al., 1995), where the respective PB-morph mature at a low age and small size,

which results in low fecundity. Although these results suffer from a small sample-size, they express the general differences between the populations as expected due to their size differences. As the absolute fecundity for salmonids increases with body length in general (see Wootton, 1998), the fecundity of the PB-and PZ-morph are constrained by their sizes as a trade-off in other life-history traits discussed above. The higher fecundity in the PB-morph compared to the PZ-morph can be explained by their ecology. Parasite infections observed in the PZ-morph (Moccetti, 2018) can reduce fecundity of the host due to energetic constraints.

The different fecundities between the sympatric morph populations in Tårnvatn and Skøvatn resembles previous studies on Arctic charr morph populations (Klemetsen et al., 2003; Smalås et al., 2013, 2016). The studies from Fjellfrøsvatn and Skogsfjordvatn revealed clear reproductive isolations between the sympatric morphs (Knudsen et al., 2006; Smalås et al., 2013,2016), which is an important factor for divergent natural selection as it reduces gene flow (Nosil, 2012). These results support the theory that utilization of habitats with similar abiotic factors drives the evolution of similar strategies in terms of fecundity and spawning time, across lakes.

5 Conclusions

My results reveal clear segregation in life-history strategies in terms of growth, maturation, and fecundity between the sympatric populations studied. The disparities between the sympatric populations in Tårnvatn and Skøvatn are suggested to result from adaptations in trophic ecology (see Moccetti, 2018), and differing abiotic factors between upper water layers and the profundal zone. The present results correspond to previous studies of polymorphic Arctic charr populations in the same region (Klemetsen et al., 1997; Smalås et al., 2013, 2016). The PP-morph in Tårnvatn is the second report of a piscivore/cannibalistic charr morph in a subarctic lake which seems to mainly reside in the profundal habitat. A complementary study of the inter-annual growth within the sympatric populations in Tårnvatn, to achieve a more fine-scaled view on the dietary niches, would be of great interest. A study with a larger sample of the populations, at different times of the year, could further increase knowledge of the life-history traits studied here, and obtain accurate knowledge of time and place of spawning for each morph.

The findings in this study suggest that, although the dietary niches are dissimilar (Moccetti, 2018), adaptation to environments with corresponding abiotic factors can lead to parallel evolution of similar life-history strategies. This is consistent with the reports from several authors (Jonsson & Jonsson, 2001; Klemetsen, 2003, 2010; Knudsen et al., 2016), which suggests that these processes are stable across lakes.

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Appendix

a) Overview of fishing efforts, its distribution in different habitats, and gillnets used.

<i>Lake</i>	<i>Habitat (depth)</i>	<i>Gillnet type</i>	<i>Number of nets</i>	<i>Number of nights fishing</i>
<i>Tårnvatn</i>	Littoral (1-12m)	BGO	3	2
		SG	2	2
	Profundal (15m)	BGO	2	2
		SG	9	2
	Profundal (25m)	BGO	2	2
		SG	9	2
	Profundal (35m)	BGO	2	2
		SG	9	2
	Pelagic (0-6m)	FGO	2	1
	<i>Skøvatn</i>	Littoral (1-12m)	BGO	3
Profundal (15m)		BGO	2	1
		SG	9	1
Profundal (25m)		BGO	2	1
		SG	9	1
Profundal (35m)		BGO	2	1
		SG	9	1

b) Welch two-sample t-test on length frequency distribution between sympatric populations in Tårnvatn, and in Skøvatn

Lake	X vs Y	t-stat	df	p-val	Mean of X	Mean of Y
Tårnvatn	LO vs PB	14.287	187.14	< 0.0001	19.8	11.1
	LO vs PP	-4.0845	38.277	< 0.001	19.8	27.7
	PB vs PP	-8.7952	34.975	< 0.0001	11.1	27.7
Skøvatn	LO vs PZ	14.473	163.09	<0.0001	18.5	9.5

c) Generalized linear model (GLM) with a bimodal distribution, testing for interaction of age and morph on maturation (A50) between the sympatric populations in Tårnvatn, and in Skøvatn

Lake	Morph	z-val	p-val	Null dev	Res dev	AIC
Tårnvatn	LO vs PB	1.906	0.057	318.32 on 230 df	170.12 on 225 df	182
	LO vs PP	-0.075	0.45	318.32 on 230 df	170.12 on 225 df	182
	PB vs PP	2.057	0.039	318.32 on 230 df	170.95 on 225 df	182
Skøvatn	LO vs PZ	1.482	0.138	252.31 on 181 df	155.13 on 178 df	163

d) Generalized linear model (GLM) with a bimodal distribution, testing for interaction of age and sex on maturation (A50) within the populations in Tårnvatn, and in Skøvatn

Lake	morph	n	z-val	p-val	Null dev	Res dev	AIC
Tårnvatn	LO	157	-0.594	0.552	212.98 on 156 df	125.62 on 153 df	134
	PB	40	0.005	0.996	51.796 on 39 df	16.159 on 36 df	24
	PP	34	-0.006	0.995	37.1 on 33 df	21.131 on 30 df	29
Skøvatn	LO	128	0.804	0.422	176.95 on 127 df	112.99 on 124 df	121
	PZ	51	-0.007	0.994	70.21 on 50 df	28.688 on 47 df	37

e) Generalized linear model (GLM) with a bimodal distribution, testing for interaction of age and lake on maturation (A50) between the two littoral- and small-profundal eco-morphs from Tårnvatn and Skøvatn.

<i>Tårnvatn / Skøvatn</i>	<i>z-val</i>	<i>p-val</i>	<i>Null dev</i>	<i>Res dev</i>	<i>AIC</i>
<i>LO vs LO</i>	-0.167	0.87	395.69 on 287 df	244.59 on 284 df	253
<i>PB vs PZ</i>	1.149	0.25	125.641 on 90 df	54.996 on 87 df	63

f) Generalized linear model (GLM) with a bimodal distribution, testing for interaction between length and morph on maturation (L50) between the sympatric morphs in Tårnvatn, and in Skøvatn.

<i>Lake</i>	<i>morph</i>	<i>z-val</i>	<i>p-val</i>	<i>Null dev</i>	<i>Res dev</i>	<i>AIC</i>
<i>Tårnvatn</i>	<i>LO vs PB</i>	2.184	0.029	317.11 on 229 df	177.4 on 224 df	189
	<i>LO vs PP</i>	-2.869	0.004	317.11 on 229 df	177.4 on 224 df	189
	<i>PB vs PP</i>	2.724	0.006	317.11 on 229 df	179.21 on 224 df	191
<i>Skøvatn</i>	<i>LO vs PZ</i>	0.0719	0.002	252.31 on 181 df	139.25 on 178 df	147

g) Generalized linear model (GLM) with a bimodal distribution, testing for interaction of length and lake on maturation (L50) between the two littoral-, and between the two small-sized profundal eco-morphs in Tårnvatn and Skøvatn.

<i>Tårnvatn / Skøvatn</i>	<i>z-val</i>	<i>p-val</i>	<i>Null dev</i>	<i>Res dev</i>	<i>AIC</i>
<i>LO vs LO</i>	0.158	0.87	394.51 on 286 df	233.71 on 283 df	242
<i>PB vs PZ</i>	-1.328	0.18	125.614 on 90 df	52.931 on 87 df	61

h) Generalized linear model (GLM) with a bimodal distribution, testing for interaction between sexes and length on maturation (L50) in each morph-population in Tårnvatn, and in Skøvatn.

<i>Lake</i>	<i>morph</i>	<i>n</i>	<i>z-val</i>	<i>p-val</i>	<i>Null dev</i>	<i>Res dev</i>	<i>AIC</i>
<i>Tårnvatn</i>	LO	157	-1.141	0.254	211.91 on 155 df	117.05 on 152 df	125
	PB	40	0.488	0.626	51.796 on 39 df	27.924 on 36 df	36
	PP	34	-0.324	0.746	37.1 on 33 df	29.022 on 30 df	37
<i>Skøvatn</i>	LO	128	0.585	0.559	176.95 on 127 df	110.23 on 124 df	118
	PZ	51	0.382	0.703	70.21 on 50 df	17.795 on 47 df	26

i) A typical LO-morph (upper), and a mature female (middle) and male (bottom) PZ-morph from Skøvatn



j) LO- (upper), PB- (middle), and PP-morph (bottom) from Tårnvatn. The PB-morph is a mature female with ripe oocytes, whereas the LO- and PP specimens are males.

