UNIVERSITY OF TROMSØ UiT

FACULTY OF BIOSCIENCES, FISHERIES AND ECONOMICS
DEPARTMENT OF ARCTIC AND MARINE BIOLOGY

Life history strategies of a trimorphic population of Arctic charr (*Salvelinus alpinus* (*L.*)) in Skogsfjordvatn, northern-Norway

Picture: Sigrid Skoglund

Aslak Smalås

BIO-3910 Master`s thesis in Biology

May 2013

Ackonowledgements

First of all, I want to thank my family for their love to and appreciation for the nature and its resources, which made me adapt the same respect for nature's extraordinary magnificence. Most of all I want to thank my girlfriend, Synne, for the unconditional support, and for being a vent for frustration in difficult times. Your sacrifices in time and energy, so I could be able to finish this project and lots of others, are forever appreciated.

Thanks, to all the people in the Freshwater Ecology group that welcomed me with open arms. For the everlasting effort of keeping everybody enjoy, flourish and thrive in each other's company and for the numerous social activities. I want to thank Team Skogsfjordvatn aka. Laina´s crew of excellence, or in other words all the people that helped with the fieldwork. I want to thank the Master-Student-Team for the social and friendly environment. To the original group, thanks for an amazing trip to Britain, were we all become good friends and I'm sure we will look back upon the trip with a smile on our faces forever. To Marjorie, thank you for teaching me French fluidly in only a day in Scotland. To Kristin and Sigrid, I am sorry for given you a concussion one late evening at Skogsfjordvatn. Kristin, the everlasting effort of "just keep on going" regardless of what life throws at you, inspire. Sigrid, it was good that we were two when going to Sakhalin, it felt like it was us against the scary world of scientists. I want to show my appreciation for my office buddies and now good friends through two years. The endless hours spent in that "stinkin" office was more or less fun the whole time because of you guys. Thank you for your help, the discussions and the day-to-day conversations that made these two years flew by. John, Eirik and Øyvind I have enjoyed your company every day. Birgitte, Martin and Kristoffer, you have fitted in perfectly with the group. Birgitte don't set any more tables on fire, please. To all of you, good luck in the future.

Last, but not least I want to thank my two supervisors. Rune, I want to show my appreciation for your everlasting enthusiasm, your passion for not only your work, but also for my work and your "can do" positive attitude that rub of on everybody around you. Per-Arne, I want to thank you for the experienced coaching in the writing process, for your effort for the Freshwater Ecology group, it is indispensable, but most of all I want to thank you for your inspiring ambitions for us master students and the Freshwater Ecology group as a unit. Thank you for the trip to Britain and to Sakhalin. These two years have been a joyful journey.

Nothing in life is to be feared, it is only to be understood. Now is the time to understand more, so that we may fear less. – Marie Curie –

Aslak Smalås, Tromsø, May 2013.

Table of contents:

Summary

Polymorphisms are widespread throughout many different taxa of vertebrates. Discrete polymorphisms or morphs usually differentiate in morphology, ecology and life history, most likely driven by adaptations to different habitats and resources. For sympatric morphs to be able to maximize fitness in different niches and habitats, they may develop differences in several life history traits. Arctic charr (*Salvelinus alpinus* (L.)) is a good model species for verifying and understanding ecological driven polymorphism and speciation. Here, I address the life history traits of three sympatric living Arctic charr morphs in Skogsfjordvatn in northern Norway. The charr morphs differ in diet and habitat utilization; including one morph that feeds on benthic invertebrates and zooplankton in the littoral-pelagic zone (referred to as the LO-morph), a second that feeds on chironomids and small mussels in the profundal zone (PB-morph), and a third that also inhabits the profundal zone, but has a piscivorous diet (PP-morph). The littoral and the two profundal spawning morphs are differentiated in time and place of spawning and all morphs are genetically differentiated, indicating complete reproductive isolation. These morphs also had contrasting differences in numerous life history traits. Temperature and prey density differences between the profundal zone and the upper water layers led to that the two profundal morphs had distinctly lower growth rate than the LO-morph. The fast growth rate for the LO-morph led to a relative low age (~4.8 years) and a relatively large size (~21 cm) at maturity, which was intermediate compared to the other morphs. The two profundal morphs had totally contrasting life history traits even though abiotic factors and the growth rate in the first living years were similar. This indicates that they had adopted contrasting strategies for increasing fitness. The PB-morph matured at a young age (~3 years) and at a small body size (~8.5 cm) to be able to increase fitness by investing in reproduction early in life, leading to a shorter generation time and also decreasing the potential of being predated on. The PP- morph on the other hand, matured at an old age (~9.2 years) and a large body size (~26 cm). This delayed reproduction enables the PP-morph to increase fitness by investing in somatic growth to increase initial fecundity, and also to reach a body size were profitable prey (fish) might be available. Age at maturity also explain the difference in longevity between morphs. Fecundity and egg-size increased with body size both between and within morphs. The difference in trade-off regime between the PP and PB-morphs seems to be caused by adaptation to alternative trophic niches, and appears to be an important factor for the co-occurrence of two different morphs in the profundal zone.

Introduction

Polymorphisms are widespread throughout many different taxa of vertebrates, including examples from birds, amphibians, and fishes (Skulason and Smith, 1995). Polymorphisms are defined as discrete intraspecific morphs that utilize different resource niches, and which may have a varying degree of reproductive isolation (Smith and Skulason, 1996). Discrete polymorphisms or morphs usually differentiate in morphology, ecology and life history traits, most likely driven by different adaptations to different habitats and resources (Skulason and Smith, 1995; Smith and Skulason, 1996; Adams and Huntingford, 2004). In sympatry and parapatry, disruptive selection against intermediate phenotypes is suggested to be potent in diverging a population into different phenotypes exploiting different niches (Schluter, 2001; Doebeli and Dieckmann, 2003; Doebeli et al., 2005). For sympatric morphs to be able to maximize fitness in different niches, they may develop a difference in several life history traits. Some have even argued that differences in specific life history traits, like e.g. egg size, could promote divergence of a population (Leblanc et al., 2011). The role of morphology, body size, resource utilization and behavior for sympatric living morphs are well established in the literature (see: Skulason and Smith, 1995). In contrast, relatively little attention has been given to the specifically role of life history traits for sympatric morphs. Here, I address the life history traits of three sympatric living morphs in a freshwater fish population to be able to enhance the knowledge of its potential role in polymorphic systems.

Skulason and Smith (1995) suggest that the occurrence of different morphs is most evident in communities where interspecific competition is low, the potential for intraspecific variation of traits is high and the availability of open resource niches are large. Genetic variation, phenotypic plasticity and maternal effects are proposed to create the individual variation that is needed to adapt to a specific environment and exploit a novel resource niche (Skulason et al., 1999; West-Eberhard, 2005; Schluter, 2009; Schluter and Conte, 2009). Sympatric morphs could both emerge as phenotypic variabilities within a single gene pool, or as a differentiation of a gene pool into more than one, with some sort of reproductive isolation between the different phenotypes or morphs (Gislason et al., 1999; Parker et al., 2001). Reproductive segregation between sympatric morphs may occur due to e.g. assortative mating based on different phenotypic expressions (Doebeli et al., 2005). Differences in habitat selection between sympatric morphs could lead them to be exposed to different environments and selection pressures, which again can lead to fixation of different adaptive genes and could further lead to speciation (Skulason et al., 1999).

Life history theory aims to explain the evolution of different life-history traits adapted to different environments (Winemiller, 2005). An organism's life history strategy is defined by ontogenetic and reproductive traits that determine individual lifetime reproductive success (Roff, 1992). The selection pressure that creates variation in life history strategies between morphs comes from both abiotic factors like temperature, light, pH, etc., and biotic factors related to ecological interactions. The typical life history traits under selection are size at birth, growth schedule, age and size at maturity, number and size of offspring, age- and size specific reproductive investments, age- and size specific mortality rates and length of life (Stearns, 1992). An individual will experience energetic and developmental constraints on life history traits that make the optimization of all these traits difficult (Stearns, 1992). Life history traits are bound together by trade-offs due to these different constraints; an increase in energy allocation to one trait, would lead to decreased energy allocation to another trait (Roff, 1992; Stearns, 1992; Wootton, 1998). A classical trade-off exists between present reproduction and future growth (Wootton, 1998). For sympatric morphs, different selection pressure could lead to differences in trade-off regimes and as a consequence lead to differences in life history traits to be able to maximize fitness.

Fishes has evolved huge differences in numerous life history traits that are adapted to their ecological niche (Wootton, 1998). Also intraspecific differences in life history traits are large, and especially for many freshwater fish species, like e.g. sticklebacks, European whitefish, brown trout, Arctic charr, guppies and European perch (Rodd and Reznick, 1997; Klemetsen et al., 2003; Heibo et al., 2005; Østbye et al., 2006; Baker et al., 2008). Blanc and Lamouroux (2007) studied inter- and intraspecific differences in life history traits between 25 species of freshwater fish. They found that some life history traits, like growth rate, mortality rate and length of breeding season are more different within species than between species. The life history variations within species were suggested to come from great variation of abiotic factors affecting the different intraspecific populations (Blanck and Lamouroux, 2007). Temperature is one such abiotic factor. The temperature-size rule for ectotherms states that growing up at low temperatures will make individuals grow slower, mature at an older age, but still be larger at maturation than individuals in warmer temperatures (Arendt, 2010). Salinity, dissolved oxygen and light conditions in addition to temperature are all abiotic factors that could vary between lakes, but also between habitats in the same lake (Wetzel, 2001).

Any factor causing a change or a differentiation in mortality rates in a population will affect the life history traits of the population (Wootton, 1998). Predation is one such factor that could affect mortality rates in fishes, and thus affect the life history traits (see: Reznick et al., 1990; Johnson and Belk, 2001). High and unpredictable mortality rates in the adult stage of the life cycle select for increased reproduction early in life (Schaffer, 1979). High and unpredictable mortality rates in the juvenile stage of the life cycle in contrast select for decreased reproduction early in life and a longer adult life (Schaffer, 1979). Predation risk could force the prey population into less profitable habitats, but also force the prey species to allocate energy and attention to predator avoidance and thus alter life history traits indirectly (Griffiths, 1994; Bolnick and Preisser, 2005). There are many examples that inter- and/or intraspecific competition can affect life history of fishes (see: e.g. Mittelbach, 1988; Persson and Greenberg, 1990; Magnan et al., 2005). High competition for food resources could lead to poor growth for individuals within a population, which could affect many life history traits in addition to growth (Wootton, 1998). Relaxation of competitive pressure by switching to a different niche (Skulason and Smith, 1995), could alter life history strategies in order to be able to adapt to that novel niche. Switching from one habitat to another where the resource densities differ between them could also affect the expression of different life history traits.

In Arctic charr (*Salvelinus alpinus* (L.)) there are many examples of polymorphic systems that are believed to originate from an adaptive speciation process (Skulason et al., 1999; Jonsson and Jonsson, 2001; Klemetsen et al., 2003; Adams and Huntingford, 2004; Klemetsen, 2010). Some even argue that Arctic charr is the most polymorphic species in the world (Klemetsen, 2010). These Arctic charr morphs show very strong morphological, ecological and life-history differences (Klemetsen, 2010). The understanding of evolutionary processes, sympatric speciation and polymorphism in Arctic charr are mostly derived from three classical studies; lake Thingvallavatn in Iceland, Loch Rannoch in Scotland and lake Fjellfrøsvatn in Norway (Klemetsen, 2010). In lake Thingvallavatn there are described four distinct morphs, which are all found either in the pelagic or the littoral zone of the lake. These morphs differ in life history parameters like body size, fecundity and age and size at sexual maturation. These differences are believed to be an effect of dissimilarities in diet and habitat selection (Skulason et al., 1989; Sandlund et al., 1992). Loch Rannoch has three distinct morphs, which also segregate in the littoral-pelagic habitats (Adams et al., 1998). Fraser et al. (2008) found great differences in life history parameters like growth for the three different morphs as a consequence of the differentiation of their resource niche. In lake Fjellfrøsvatn there are two distinct morphs, one predominantly occupying the littoral-pelagic habitats, and the other being confined to the profundal habitat (Amundsen et al., 2008). These two morphs show significantly different life history traits from one another regarding time and place of spawning, growth, age and size at maturity, and fecundity and egg-size, suggested to be caused by difference in habitat and resource utilization (Klemetsen et al., 1997; Klemetsen et al., 2003).

Recently a polymorphic population of Arctic charr was discovered in lake Skogsfjordvatn, northern Norway. This population must originate from anadromous Arctic charr that invaded Skogsfjordvatn some time after the last ice age (10 000-12 000 years b.p). These ancestral charr assumedly segregated into different morphs either in sympatry or through multiple invasions to the lake (Knudsen, R., unpublished data). There are now three distinct morphs of Arctic charr in the lake; one inhabits the pelagic-littoral habitats, whereas two morphs inhabit the profundal. According to genetic analyses, the three morphs have a strong reproductive isolation from one another (Præbel, K. and Knudsen, R., unpublished data). They are also segregated in diet, morphology and parasite infection (Knudsen. R., unpublished data, Skoglund, S. in prep., Refsnes, B. in prep.). The morph that is utilizing the pelagic-littoral habitat is believed to be the ancestral invader and feeds mainly on zooplankton and zoobenthos, resembling monomorphic populations of Arctic charr elsewhere in northern Norway (Knudsen, R., unpublished data; Eloranta et al., 2013). This morph is named the littoral spawning omnivore morph, hereafter called LO-morph. One of the morphs that is utilizing the profundal zone feeds on soft bottom benthos similar to the profundal morph in Fjellfrøsvatn (see: Klemetsen et al., 1997). The last morph is mainly piscivorous and has a feeding habitat that is seldom seen for Arctic charr, since it utilizes the profundal zone to hunt for fish prey (Knudsen, R., unpublished data). These two morphs are named profundal spawning benthivore morph, hereafter called PB-morph, and profundal spawning piscivore morph, hereafter called PP-morph, respectively.

Here, I studied different life history traits of the three sympatric Arctic charr morphs in Skogsfjordvatn. I will contrast the life history parameters that these morphs exhibit, compare their life history traits to other populations of Arctic charr found elsewhere and compare the findings to general life history theory. Based on the knowledge about these morphs habitat utilization and resource niche and, knowledge from other Arctic charr systems, I expect them to differ significantly in the life history traits studied here; time and place of spawning, growth, age- and size at maturity, fecundity and egg size. Due two differences in temperature and prey densities between the profundal and the upper water layers (Wetsel, 2001), it is expected that the LO-morph has a faster growth rate than the two other morphs. Due to the difference in growth rate, habitat and diet it is expected that the different morphs would have different strategies for increasing fitness; the PB-morph is expected to mature at a young age and thus a small body size, invest relatively more energy in reproduction early in life leading to a low maximal body size and as a consequence of a small body size have low fecundity and small eggs. The PP-morph is expected to mature at an older age in order to invest energy in somatic growth to be able to reach a size where piscivory is efficient, and thus a relatively large size at maturity, reach the largest maximal body size because of its diet, and as a consequence of body size have the highest fecundity and largest eggs. The LO-morph is expected to mature at a relatively young age, however, at a relatively large body size due to high growth rate, have intermediate age and size at maturity relative to the other morphs and thus intermediate fecundity and egg-size.

Materials and methods

Study site and sampling

The study site was Lake Skogsfjordvatn on the island Ringvassøya in Troms County, northern Norway. The lake is 13.6 km^2 and about 10 km long and is situated 20 meters above sea level. The lake is considered to be an old fjord from the last ice age (10 000 -15 000 years ago) (Norges vassdrag- og energidirektorat, 2010). The main basin is between 60-65 meters deep and the lake has a maximum depth of about 100 meters. The lake is dimictic, oligotrophic, poor in calcareous compounds and is slightly affected by humic influx. It is usually ice-covered from December to early June. The drainage area is dominated by alpine landscape and birch forests, and there is also a few farms on the eastern side of the lake. Gillnet fishing by local people has been conducted for a long time. The outlet river from Skogsfjordvatnet is only 1 km long, with no major obstacles for anadromous fish (Norges vassdrag- og energidirektorat, 2010). This leads to a fish community that consists of both anadromous and freshwater-resident fish populations. The fish species present in Skogsfjordvatn are anadromous and resident salmonids: Arctic charr (*Salvelinus alpinus* (L.)), brown trout (*Salmo trutta* (L.)) and Atlantic salmon (*Salmo salar* (L.)). There is also a population of three-spined stickleback (*Gasterosteus aculeatus* (L.)), and a small population of the catadromous European eel (*Anguilla anguilla* (L.)). Gillnet fishing has revealed that the anadromous populations of salmonids are very limited.

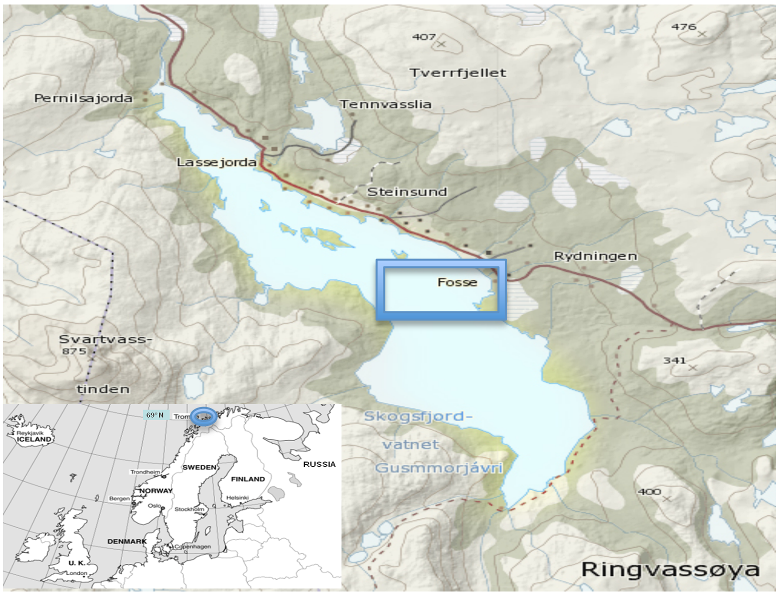

Fig. 1. The small map is a map of northern Europe with the location of Skogsfjordvatn. The larger map showing Skogsfjordvatn where the blue square marks the area of the survey fishing. (from Google-maps).

The fieldwork was done over 2-3 days once a month (except July) from May 2011 until January 2012. We used gillnets in all three habitats of the lake and the gillnets were set out at approximately the same sites each time (fig. 1). The gillnets were set out in the afternoon and taken up in the morning the next day, giving each gillnet around 12 hours of fishing at every set. We used three different types of multi-mesh sized gillnets, one type called BGO, that is 40 m long and 1.5 m deep, used in the benthic areas both in the littoral zone (0-15 m) and the profundal (>20 m). The second one is called FGO, it is 40 m long and 6 m deep and is used in the pelagic zone. The two types of gillnets have a range of mesh sizes in 5 m intervals from 10 to 45 mm knot to knot. The third type of multi-mesh sized gillnets is called NORDIC net, it is 30 m long, 1.5 m deep and with a range of mesh sizes in 2.5 m intervals from 5 to 55 mm knot to knot and is also used in the benthic areas. We also used a fourth type of gillnet in this survey, called standard sized gillnets (SG) which are 30 m long, 1.5 m deep and only one mesh size throughout the whole net. This last gillnet type is also used in the benthic areas.

Table.1. Overview of fishing efforts in the survey period, with the distribution of fishing efforts in different habitats and type of gillnet used.

Habitat (depth)	**Gillnet type**	**Number of nights fishing**
Littoral (1-15m)	BGO	35
	NORDIC	3
	SG	4
Profundal (25m)	BGO	13
	NORDIC	2
	SG	8
Profundal (35m)	BGO	21
	NORDIC	3
	SG	13
Profundal (45m)	BGO	16
	NORDIC	2
	SG	17
Profundal (60m)	BGO	1
Pelagic (0-6m)	FGO	12
Total:		150

All captured fish were sampled and recorded, but here only the Arctic charr procedures will be described. In the field laboratory the individual fish was given a number and divided into three different morph groups by its external looks. Littoral spawning omnivore morph (LO) has a relatively small head, red to orange spawning color on the abdomen and a silvery body color. Profundal spawning benthivore morph (PB) has a small body size, an inflated gas bladder, the adults have par marks along the side of the body and a relatively blunt and rounded head. Profundal spawning piscivore morph (PP) has a relatively large and elongated head, dark grey or black body color with white spots along the side of the body. The PP- morph also has a relatively slim and elongated body shape and sharp teeth on the tongue and the palate.

In the field a photo was taken for morphological studies, the fish was weighed (g), the fork-length of each fish was measured (mm), otoliths were taken for age determination and a sample of the gills was taken for genetic studies. Thereafter the fish's body cavity was opened and the stomach, swim bladder, intestine and gonads of sexual mature female fish were sampled. The sex and stage of sexual maturity of each fish was decided by examining the gonads, and the stage of sexual maturity was classified in three groups; 1) juvenile or immature, 2) sexually mature and spawning this following breeding season and 3) sexually mature, but not spawning the following breeding season or already spent. Parasites in the body cavity were classified by species and counted. Samples from liver and muscle tissue were taken for stable isotope analysis and the coloration of the flesh was noted.

Laboratory analysis

Age determination

The age determination was done by analyzing the sagittal otoliths, which are located in the inner ear of the fish. The otoliths consist of calcium carbonate and the accretion rates of calcium carbonate vary with the growth rate of the fish (Holden and Raitt, 1974). In subarctic areas the growth pattern of fishes vary within the year, with typically good growth in the summer and slow growth in the winter. This pattern is also shown in the otoliths, where the opaque winter-growth zones differ significantly from hyaline summer-growth zones (Holden and Raitt, 1974). Hence, it is possible to distinguish between these zones and thus determine the age of the fish. The otolithes were preserved in 96 % ethanol, and later analyzed under a stereo microscope after being put in glycerol to make the difference in growth zones more visible (see: Holden and Raitt, 1974). The surface reading method was used and the otholiths were classified according to their quality, i.e. how easily the different growth zones distinguish from each other. The otoliths with the poorest quality were analyzed multiple times by different readers or ignored and classified as unreadable. The few unreadable otoliths were taken out of the sample, since age determination was impossible.

Fecundity measurements

Gonads of sexual mature female fish were collected in the field from August through January, was weighed and preserved and stored in Gilson`s fluid (100 ml 60% alcohol, 800 ml water, 15 ml 80% nitric acid, 18 ml glacial acetic acid, 20 g mercuric chloride) (Holden and Raitt, 1974). The glasses with the gonads and Gilson`s fluid were shaken to loosen the ovarian tissue from the eggs and to ensure that the preservative got into contact with all the eggs (see: Holden and Raitt, 1974). In the laboratory the gonads were re-weighed to look for deviations from the measurements taken in the field and how the Gilson preservation affected the oocytes. We estimated the total number of eggs (i.e. clutch size) for each individual fish using a gravimetric method described in Holden and Raitt (1974). We counted a sub-sample of 1- 2 grams of eggs and then used the following equation to estimate total clutch fecundity; **F = nG/g** where F = fecundity, n = number of eggs in the subsample, G = total weight of the ovaries, g = weight of the subsample in the same units (Holden and Raitt, 1974).

The fish that were selected for egg size measurements were all collected within a month prior to spawning time for the different morphs, so that differences in spawning time would not affect the egg-size. Fifteen oocytes from each fish were randomly picked out for egg size measurements. They were measured to the nearest 0.01 mm using a stereo microscope. We also measured the size of oocytes from fish collected in other months to see if the development of the oocytes varies within the morphs or between morphs.

Statistical analysis

Growth

Growth or length at age data were analyzed using a von Bertalanffys growth model. This growth model is well established for estimating individual growth in fish populations and has been used widely for many years (see: Chen et al., 1992; Lester et al., 2004). It is especially good describing individual somatic growth after the individuals have reached sexual maturity, however not as well describing somatic growth pre-maturity (Lester et al., 2004). The von Bertalanffys growth model assumes that somatic growth rate decreases as the individuals grows, the equations can be as following:

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

where t is time or age of the fish, l is the length of the fish, L_∞ or “L infinity” is the asymptotic length where growth is zero, K is the growth coefficient or the rate of how fast the L_∞ is achieved, and t_0 is the age where size equals zero and is included to adjust the equation for the initial size of the individual. The three parameters L_∞, K and t_0 have to be estimated with a nonlinear regression. This was done for all three morphs.

The difference in von Bertalanffy curves where pairwise tested between the morphs using a Welch-two-sample-t-test.

Age and size at maturity

Logistic regression with immature and mature fish as binomial variables was used to analyze and interpret the data regarding age and length at sexual maturity. Logistic regression produces a sigmoid curve fitted to the observed values,

$$\mathbf{p_x = e^{(b_0+b_1x)}/(1+e^{(b_0+b_1x)})}$$

where P is the probability that an individual is sexual mature, **x** is the age or length interval, b_0 and b_1 are parameters that define the shape and intercept of the fitted sigmoid curve.

We have two predictor variables (morph and age/length) predicting the response variable (proportion sexual mature). To be able to decide which generalized linear model that describes the observed response variables best, the Akaike information criterion (AIC) was used. This is a tool used to measure goodness of fit of a statistical model, effectively describing how much information that is lost using a particular model. Five different models were tested, all were different combinations of the two predictor variables predicting the response variable. The model that had the lowest value of AIC or the model that lost the least amount of information was morph:age (AIC = 27.1) and morph:length (AIC = 30.96). This model describes the response variable → Proportion sexual mature = dependent on both morph and age or length (morph*age/ or length) or in other words; the chance of an individual is sexually mature depend on the morph and the length or the age of the individual. The model was also tested with a chi square test on the residual deviance and the degrees of freedom to determine if the model fitted the observed value in a satisfying way. The null hypothesis, which is in this case the selected model cannot be rejected if the P-value of the chi square test > 0.05. The chi square test is performed as following in R → 1 – pchisq (residual deviance, degrees of freedom) → The result of the chi square test was → P = 0.999999 for morph:age and 0.999999 for morph:length. This means that we have no evidence against the null hypothesis and cannot reject the model.

To calculate A_{50}, age where 50 % of the population is sexual mature, and L_{50}, length where 50 % of the population is sexual mature, for the three morphs, the logistic regression parameters b_0 and b_1, were used.

$$\mathbf{A\ (or\ L)_{50} = -b_0/b_1}$$

Fecundity

Number of eggs produced by a female has a statistical normal distribution around an average. To be able to analyze and interpret these data a linear regression model and ANOVA (analysis of variance) were used. Regression analysis have a few important assumptions: the variance of the residuals has to be constant and independent of each other, in addition the residuals has to be normally distributed. Whether the three assumptions were fulfilled, was tested by using a diagnostic tool-plot in R. The model that fitted best and where all the assumptions of a linear regression analysis were met, was a nlog-nlog model of the response variable number of eggs, and the predictor variable length of the fish. When this was established I tested if there was an interaction between the two predictor variables length of the fish and morph. This was done by a two-way analyze of variance. The two-way ANOVA established a significant ($P = 0.00166$) interaction aspect between the two predictor variables that describes the response variable. Hence, we had to treat the two predictor variables together and not independently form each other to be able to explain the response variable.

Eggsize

Egg-size of different female individuals are also statistical distributed normally around an average egg-size. As for fecundity, ANOVA (analyze of variance) and linear regression were used to interpret egg-size data. The same assumptions had to be fulfilled regarding the regression analysis for egg-size as for fecundity. The model that fitted the observed values best was the natural logarithm (nlog) of the predictor variable length. Then a two-way ANOVA was used to be able to test for an interaction between the two predictor variables length and morph. This established no evidence against the null hypothesis ($P= 0.3468$), which was no interaction amongst the two predictor variables. No interaction means that the two predictor variables (length of the fish and morph) should be treated independently of each other to be able to describe the response variable (egg-size). Whether both predictor variables or only one of the two should be included was tested using Aikake Information Criterion or more precisely stepAIC function in R. This established that the only predictor variable that should be included in the model was the length of the fish, and thus ignoring the predictor variable of morph. I also converted the diameter or more precisely the radius of the eggs to volume using the following formula:

$$V=(4\pi r^3)/3.$$

Results

Age and length distribution

A comparison of the age and length distributions of the three different morphs revealed large differences between them (fig 2). The oldest individuals of the PP-morph was 17 years old, for the LO-morph the oldest individual was 12 years and for the PB- morph the oldest individual was 11 years. The length distribution was quite similar between the LO- and PP-morphs, but the PP-morph had a higher frequency of fish >30 cm (fig 2). However, the largest difference in length distribution occurred between the PB-morph and the two others. The largest individual of the PB-morph was 15 cm, whilst the two other morphs had individuals well over 40 cm.

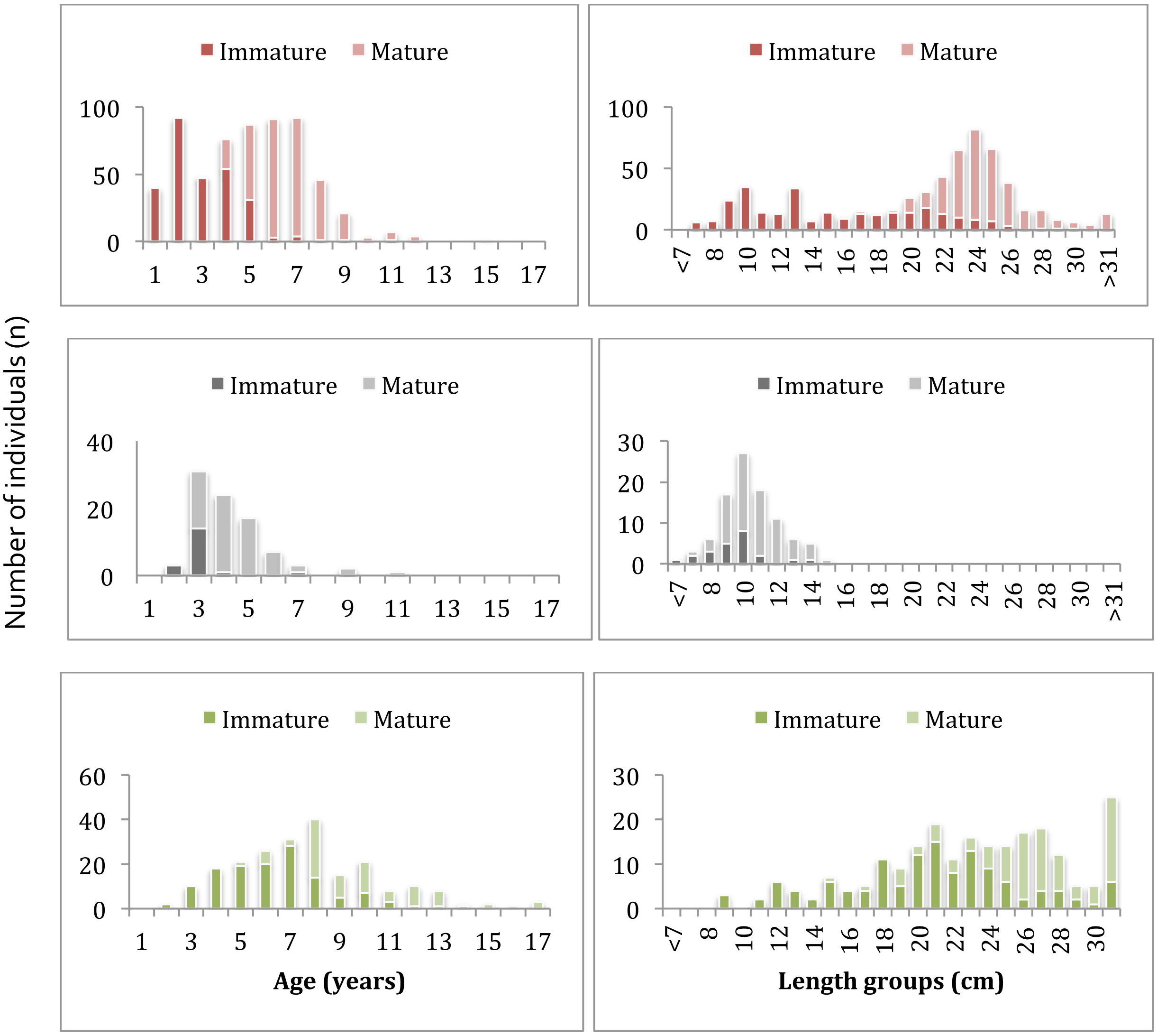

Fig 2. Age- (left) and length- (right) distribution for the three different morphs split up in sexual immature (dark shaded) and mature (light shaded) individuals. On the top panel: LO-morph (n= 608 and n= 623 for age- and length distribution, respectively), middle panel: PB (n= 88 and n= 118) and lower panel: PP (n= 218 and n= 223).

Time and place of spawning

Time and place of spawning were distinctly different between the morphs. The LO-morph spawns in the littoral zone, whilst the two other morphs seem to spawn in the profundal zone since the two profundal morphs never were caught in the littoral zone and all ovulating individuals were caught in the profundal zone both for the PB- and the PP-morph. Apparently, the LO-morph mainly spawned in the beginning of October, and all caught females had spawned when sampled in November (table 2). The PB-morph appeared to spawn mainly from late November to early December, and all females had spawned by January (table 2). For the PP-morph, a few individuals spawned in October, a few in November and a few had spawned early December, and all individuals were done with the spawning by the beginning of January (table 2).

Table 2. Proportion of spent individuals from the mature portion of the populations from August to January for the three different morphs.

Morph	n	August	September	October	November	December	January
LO	194	0	0	86	100	100	100
PB	62	0	0	0	17	80	100
PP	58	0	0	13	12	17	100

Growth

The LO-morph had the best growth of all morphs up to 7-8 years of age, however after this age the growth curve flattened and the LO-morph reached an intermediate maximal body size compared to the two other morphs ($L_\infty = 33.3$ cm) (fig. 3, table 3). The PB-morph had the slowest growth and the growth curve flattened at a young age compared to the other morphs. The PB-morph reached also the smallest maximal body size ($L_\infty = 13.8$ cm) (fig. 3, table 3). The PP-morph had relatively slow growth up to the age of 7-8 years, but the growth curve did not flattened out as for the LO-morph, this let to that the PP-morph reached the largest body size of all morphs ($L_\infty = 40.3$ cm) (fig. 3, table 3). The pairwise Welch-two-sample-t-test showed that there was a significant difference in the estimated growth curves between the PB- and the LO-morphs ($P < 0.01$), and between the PB- and the PP-morphs ($P < 0.0001$), whereas the growth curves were not significantly different between the LO- morph and the PP- morph ($P > 0.05$) (table 3).

Table 3. The von Bertalanffys growth parameters (± SD) for the three different morphs, where L_∞, is the asymptotic length of the fish where growth is zero, K, is the growth coefficient and t_0, is the estimated age where the length of the fish is zero. P-values for the Welch-two-sample-t-test of difference in growth curve.

Morph	n	L_∞ ± SD	K ± SD	t_0 ± SD	PB	PP
LO	539	33.3 ± 1.1	0.2 ±0.01	-0.52± 0.14	0.001061	0.509
PB	74	13.8 ± 2.3	0.28 ± 0.2	-1.68± 2.5	-	-
PP	183	40.3 ± 5.3	0.11 ± 0.04	-1.43± 1.08	2.012e-05	-

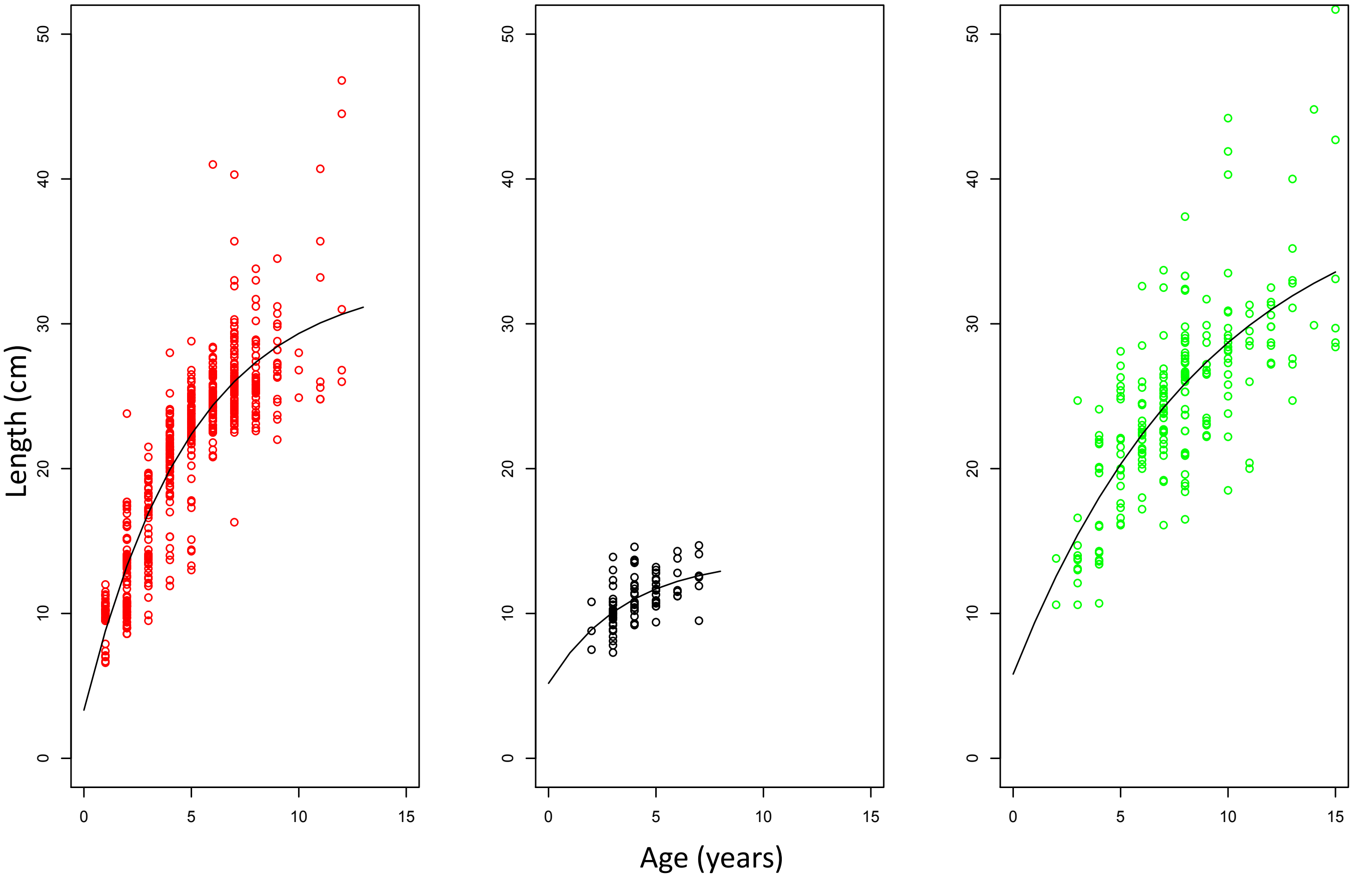

Fig. 3. Growth (age at length) for the three different morphs with von Bertalanffys growth model fitted to the observed values (black lines). To the right: LO-morph (n = 539); middle: PB-morph (n = 74) and to the right: PP-morph (n = 183). For the LO-morph, the age groups 10 years and older were put together (≥10) in the model estimations due to low sample size for these age classes. The same apply for the PP-morph regarding the age groups 15 years and older.

Age at sexual maturity

Age at sexually maturity was significantly different between the three morphs (fig. 4, table 4). For the BP- morph, some individuals became sexually mature already at the age of 3 years, whereas from the age of 4 years and older practically all of the individuals were mature. The age where 50 % of the population first reached sexual maturity was estimated at 3.2 years (GLM: p = 0.009) (fig. 4, table 4). For the LO- morph individuals started to mature at the age of 4 years, and at age 6 and older almost all individuals were sexually mature. The estimated age where 50 % of the population first reached sexual maturity was 4.8 years (GLM: p = 0.005) (fig. 4, table 4). For the PP- morph the earliest individuals that reached sexual maturity were 5 years old. However, 100 % maturation did not occur before the age class of 15 years, and the estimated age for 50 % maturity was 9.2 years for the PP-morph (GLM: 0.003) (fig. 4, table 4). Females sexually matured on average about 1 year later than males for the LO-morph and PP-morph, but the age at maturity was more similar between females and males from the PB-morph (table 4).

Table 4. Age at 50 % sexual maturity (A_{50}) (± SD), P-value for the difference in slopes for the generalized linear model (GLM), number of individuals (n), z-statistic for the GLM-slope and the age at 50 % maturity (A_{50}) (± SD) for the different sexes for the three different morphs.

Morph	**n**	**A_{50} ± SD**	**P-value GLM**	**Z-statistic (Age*morph)**	**A_{50} ± SD (Females)**	**A_{50} ± SD (Males)**
LO	593	4.8 ± 3.0	0.00519 **	2.795 on 33 d.f.	5.1 ± 2.7	4.3 ± 1.4
PB	89	3.2 ± 2.2	0.00897 **	2.613 on 33 d.f.	3.3 ± 2.0	3.0 ± 0.1
PP	217	9.2 ± 2.0	0.00315 **	2.953 on 33 d.f.	9.5 ± 1.7	8.6 ± 2.3

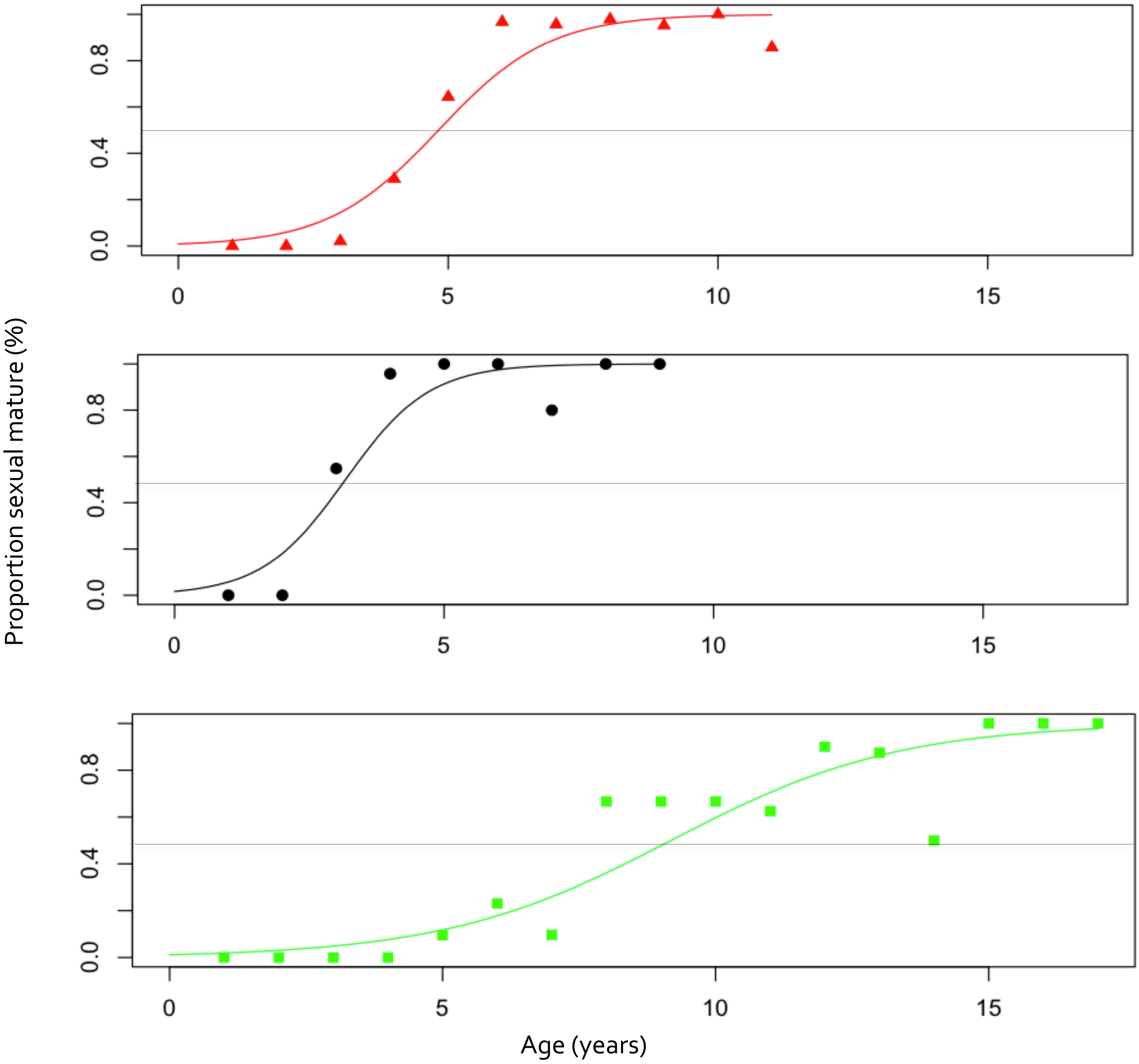

Fig. 4. Observed (dots) and fitted generalized linear regression (lines) of the proportion sexual mature individuals at age for the three different morphs. Top: LO-morph in red, n = 593; middle: PB-morph in black, n = 89; bottom: PP-morph in green, n = 217.

Length at sexual maturity

The length at first sexual maturity was also significantly different between the three morphs (fig. 5, table 5). For the PB-morph the first individual reached sexual maturity already at 7.3 cm and the length that the PB-morph first reached 50 % maturity (L_{50}) was around 8.5 cm. The first LO- morph individual reached sexual maturity at the length of 14.3 cm and the calculated L_{50} were around 21.2 cm of length for the LO-morph (table 5). For the PP-morph the first individual reached maturity at the length of 16.6 cm and the calculated L_{50} for the PP-morph were 26.0 cm of length (table 5). The females were significantly larger than males at maturity for the LO- and PP-morph, but in contrast the males were distinctly larger than females for the PB-morph (table 5).

Table 5. The length at 50 % sexual maturity (L_{50}) (± SD), P-value for the difference in slopes for the generalized linear model (GLM), number of individuals (n), z-statistic for the GLM-slope and length at 50 % maturity (L_{50}) (± SD) for the different sexes for the three different morphs.

Morph	**n**	**L_{50}**	**P – value GLM**	**Z-statistic (Length*morph)**	**L_{50} (Females)**	**L_{50} (Males)**
LO	593	21.2 ± 2.7	0.00009 ***	3.852 on 56 d.f.	21.7 ± 5.5	19.9 ± 3.4
PB	89	8.5 ± 2.5	0.000163 ***	3.728 on 56 d.f.	8.0 ± 4.3	9.1 ± 1.9
PP	217	26.0 ± 3.0	0.000196 ***	3.644 on 56 d.f.	27.1 ± 4.3	23.8 ± 3.7

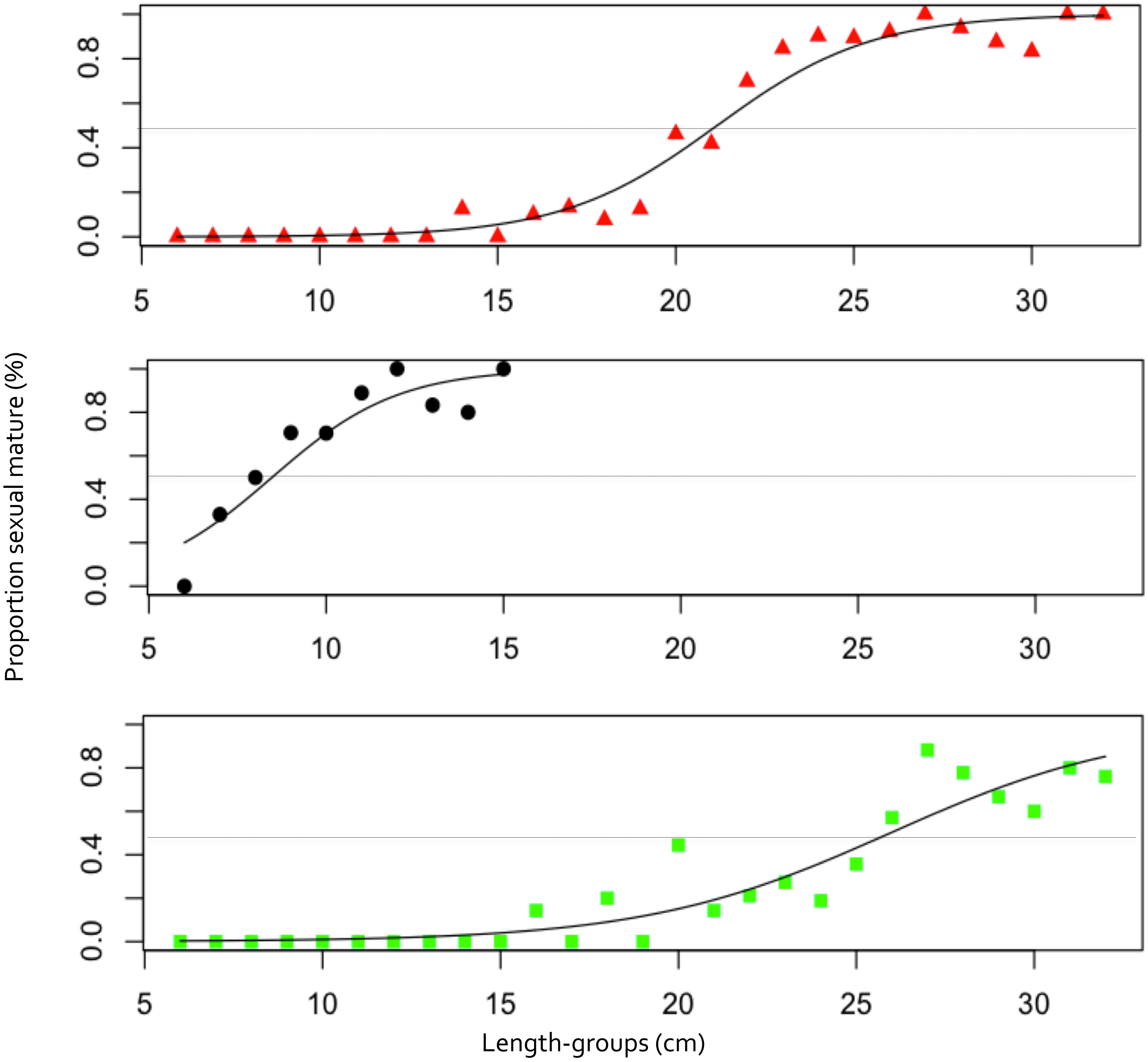

Fig. 5. Observed (dots) and fitted generalized linear regression (lines) of the proportion that is sexual mature by length-groups (1 unit equals 1 cm) for the three different morphs. The last length group is pooled individuals above a length of 32 cm (>32). Top: LO-morph in red, n = 539; middle: PB-morph in black, n = 89; bottom: PP-morph in green, n = 217.

Fecundity

Mean number of eggs produced for each morph in Skogsfjordvatn was distinctly different from one another (table 6). Females from the LO- morph, PB-morph and PP- morph had on average around 611, 48 and 810 eggs, respectively. Mean number of eggs per gram total fish weight was significantly different between the three morphs (table 6). The PB- morph produced the highest number of eggs per gram fish weight and the PP-morph the least amount of eggs per gram fish weight. The gonadosomatic Index (GSI) showed similar values for all three morphs in Skogsfjordvatn. The numbers of eggs an individual produce (fecundity) were mostly dependent on a function of length (volume) of the fish, however fecundity had an additional effect of which morph the individual derived from (ANOVA → $P > 0.001$) and thus an interaction between length and morph had to be included into the linear model (ANOVA → $P = 0.0016$). Fecundity was significantly different between the PB- morph and the LO- moprh ($P = 0.009$) and between the PB- morph and the PP- morph ($P = 0.0008$), but not between the LO- morph and the PP- morph (0.433).

Table 6. Gonadosomatix index (GSI ± SD), mean number of eggs with fecundity range, mean number of eggs/kg body weight (± SD) and sample size (n) for the three different morphs in Skogsfjordvatn.

Morph	**n**	**GSI ± SD**	**Mean number of eggs (Fecundity range)**	**Mean number of eggs/kg fish ± std.**
LO	35	11.6 ± 2.5	610.6 (320-1139)	3149.6 ± 254
PB	23	10.4 ± 2.3	48.0 (32-78)	4262.4 ± 198
PP	13	9.9 ± 3.8	809.8 (212-1835)	2372.3 ± 328

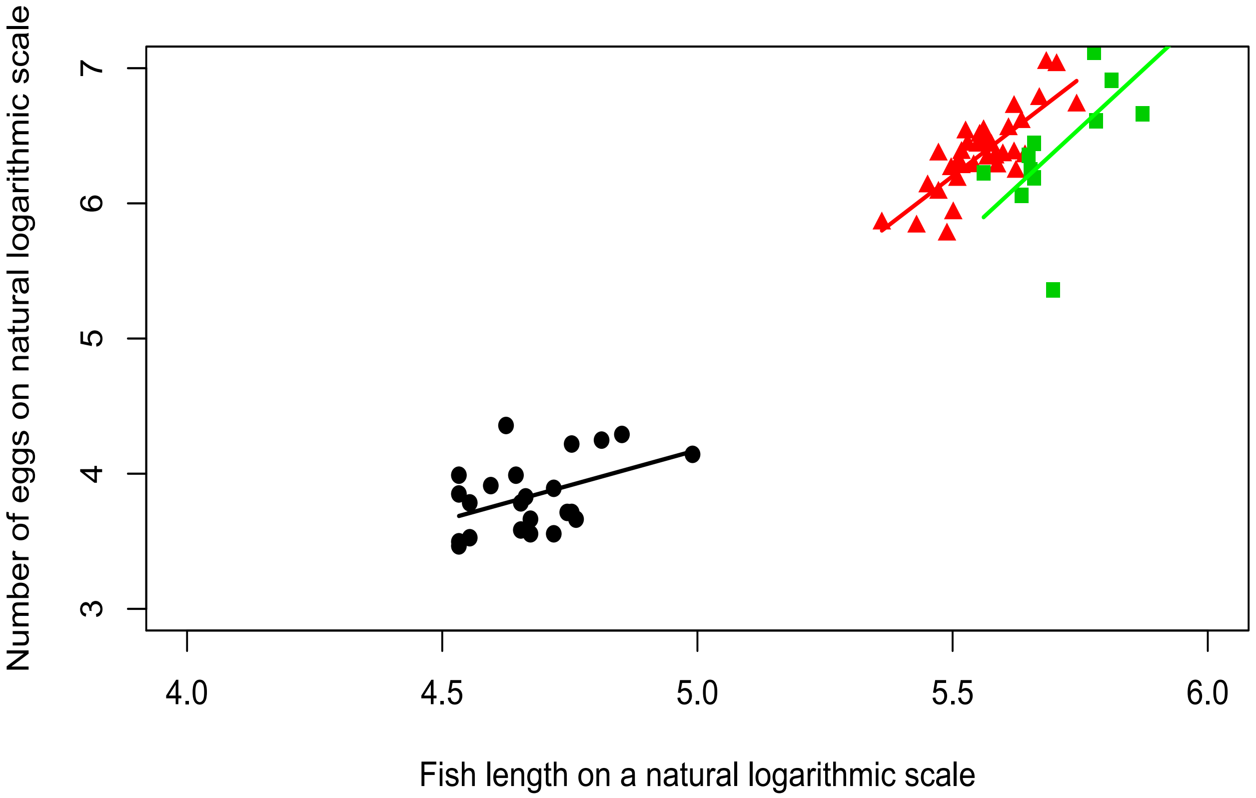

Fig. 6. Number of eggs as a function of fish length for the three different Arctic charr morphs in Skogsfjordvatn (LO-morph in red triangles, n= 35; PB-morph in black sircles, n= 23; PP in green crosses, n= 13). The lines describe the estimated relationship between the number of eggs and body length for the three different morphs (Black = PB, red= LO and green = PP).

Egg-size

The PB-morph had the smallest mean egg-diameter (3.12 mm) and the PP-morph the largest (4.54 mm), with the LO-morph having intermediate mean egg-diameter (4.24 mm). The difference in mean egg-size was even clearer when recalculated to volume. PB-morph had a mean egg volume of 15.9 mm^3, LO-morph 39.9 mm^3 and PP-morph 48.9 mm^3. The egg size of the PB-morph was only 32 % of the size of the eggs from the PP-morph. An analysis of variance test showed that mean egg-diameter was significantly different between the morphs ($P < 0.001$, $F = 51.57$, d.f. 2 and 45). From a linear model analysis, egg-diameter was found to increase significantly with fish size ($P = 0.00347$). An Analyze of variance to test if there was an additional effect of morph, ignoring the predictor variable of length of the fish did not show significant importance ($P = 0.1084$).

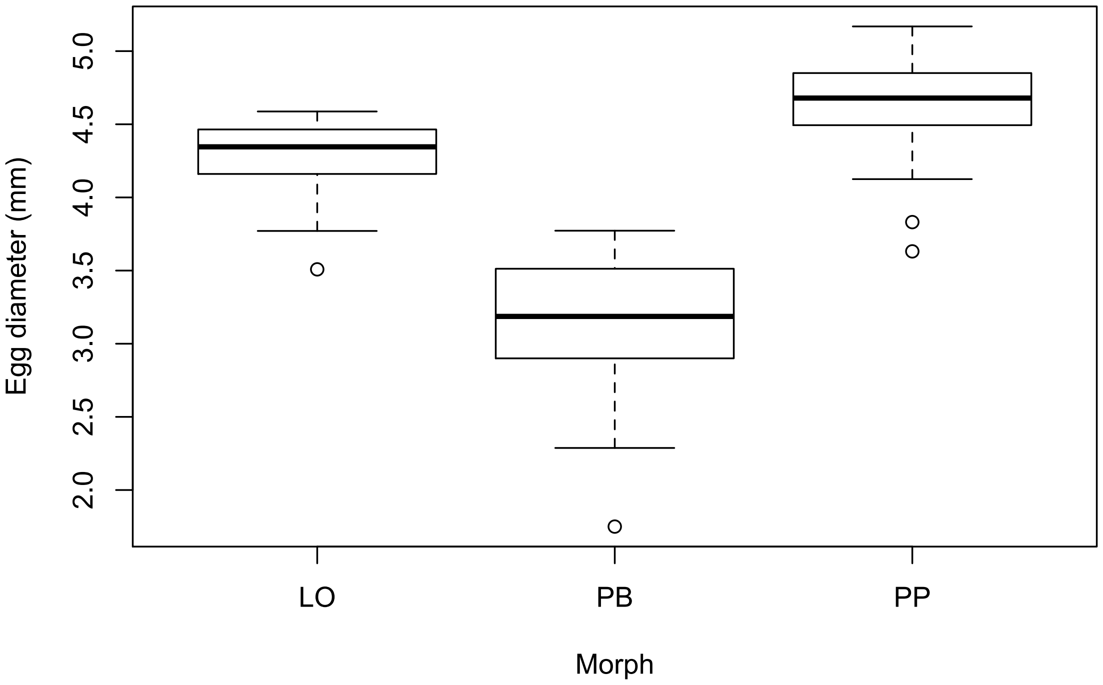

Fig. 7. The egg-size in diameter for the PB-morph (n = 24), LO-morph (n = 12) and PP-morph (n = 13). The boxes showing the median (thick line), the interquartile (box), values that are up to 1.5 times different form the interquartile (whiskers) and outliers (circles).

Discussion

Time and place of spawning

The difference in time and place of spawning indicates that the three Arctic charr morphs in Skogsfjordvatn are reproductively isolated from one another. Genetic analysis of the three morphs in Skogsfjordvatn verifies this (K. Præbel et al., unpublished data). The LO-morph seems to spawn in the middle of October in the littoral zone. This coincides with the majority of Arctic charr populations in subarctic areas (Klemetsen, 2010). The two profundal morphs spawned later in the year in the profundal zone. Apparently, the highest spawning frequencies occurred from late November to early December and from late December to early January for the PB-morph and PP-morph, respectively. The profundal morph in Fjellfrøsvatn also spawned later than the littoral morph similar to the present findings. However, in Fjellfrøsvatn the profundal morph spawned as late as in February-March (Klemetsen et al., 1997; Klemetsen, 2010), i.e. approximately two-three months later than the PB-morph in Skogsfjordvatn. Klemetsen et al. (1997) suggests that profundal living Arctic charr morphs develop different spawning seasons compared to their sympatric morphs. Due to less variation in temperature and light conditions in the profundal zone compared to the littoral zone the exact timing of the spawning season may vary between profundal morphs of Arctic charr (Klemetsen et al., 1997). Fjellfrøsvatn and Skogsfjordvatn is only approximately 95 km from each other and thus it is reasonable to assume that the temperature regime in the lakes do not differ significantly. In Fjellfrøsvatn, Klemetsen et al. (1997) found that eggs laid in the profundal zone experienced on average 1.5°C warmer water temperature during the ice covered season compared to eggs laid in the littoral zone and thus eggs in the profundal zone need less time to develop than eggs in the littoral zone. This could compensate for at least some of the time lag between the profundal morph and the littoral morph in Fjellfrøsvatn (Klemetsen et al., 1997), and also compensate for the time lag between the two profundal morphs and the LO-morph in Skogsfjordvatn.

Growth and Maturity

The von Bertalanffys growth- curve was significantly different between the PB-morph and the two others, but not distinctly different between the LO-morph and the PP-morph. However, the estimated slope parameters (L_∞, K and t_0) were different between all three morphs. The LO-morph had the fastest growth of all three morphs, and grew to a relatively large body size. The exhibited growth pattern of the LO-morph seems to coincide with other littoral-pelagic living Arctic charr populations (e.g. Klemetsen et al., 1997; Fraser et al., 2008). The von Bertalanffys model parameters L_∞ and K for the LO-morph had intermediate values compared with other Arctic charr populations in general (Vøllestad and L´Abèe-Lund, 1994). In some populations of Arctic charr and other salmonids it is common to see an ontogenetic niche shift, from feeding on zooplankton via benthic invertebrates to fish as the fish grow larger (Forseth et al., 1994; Keeley and Grant, 2001). Such niche-shifts seem also to apply for the LO-morph in Skogsfjordvatn, however piscivory does not seem to be valid in a very large degree for the LO-morph. This could also be seen out of the LO-morphs low asymptotic length (L_∞), but some large individuals do become piscivorous (Knudsen, R., unpublished data).

The length at age shows that the PB-morph had slower growth and achieved the smallest body size compared to the two other morphs in Skogsfjordvatn. This pattern of slow growth and small maximum body size is also seen for other profundal morphs, both in Arctic charr (see: Hindar and Jonsson, 1982; Hesthagen et al., 1995; Klemetsen et al., 1997; Alekseev and Pichugin, 1998; O'connell and Dempson, 2002), and other fish species like European whitefish (*Coregonus lavaretus*) (Kahilainen et al., 2003; Siwertsson et al., 2010).

The PP-morph had a slow growth rate compared to the LO-morph in Skogsfjordvatn, but it still reached the largest body size of all three morphs due to large longevity and continued growth up to old age classes. Piscivorous and cannibalistic populations or individuals of Arctic charr grow in general to a larger maximum body size than populations or individuals that exploit other lacustrine food resources (Svenning and Borgstrom, 2005; Klemetsen, 2010). This is also true for other salmonids like e.g. brown trout (Jonsson et al., 1999; Klemetsen et al., 2003, and references therein). To my knowledge, there has not been described any other reproductively isolated piscivore morph of Arctic charr that utilizes the profundal zone as their main feeding habitat. However, there is reported a piscivore form in Gander Lake that mostly is caught quite deep in the lake throughout the year (on average > 40 m) (Power et al., 2005), but to my knowledge the reproductive behavior is not described. This form grows to a similar body size (max = 42 cm) and has similar longevity (17 years) as the PP-morph in Skogsfjordvatn (Power et al., 2005). In addition, there are a few other piscivore morphs of Arctic charr that utilize the littoral-pelagic habitats like e.g. the PI-morph from Thingvallavatn on Iceland and the piscivorous morph from Loch Rannoch, Scotland (Sandlund et al., 1992; Adams et al., 1998). The piscivorous morph from Loch Rannoch shows strikingly similar growth trajectory and von Bertalanffys growth parameters as the PP-morph from Skogsfjordvatn (see: Fraser et al., 2008), whereas the PI-morph from Thingvallavatn does not (see: Sandlund et al., 1992).

Also age and size at sexual maturity were significantly different between all three Arctic charr morphs in Skogsfjordvatn. This was expected due their great differences in resource utilization and habitat selection. The LO-morph had intermediate age (A_{50} = 4.8 years) and size (L_{50} = 21 cm) at maturity compared to the other two morphs. This age and size at maturity seems common for Arctic charr populations elsewhere (Vøllestad and L´Abèe-Lund, 1994). The Fjellfrøsvatn littoral Arctic charr morph also mainly utilizes the littoral-pelagic habitats and has a similar diet as the Skogsfjordvatn LO-morph (see: Knudsen et al., 2006; Knudsen, R. unpublished data), and they also show a similar age (5 years) and size at maturity (Klemetsen et al., 1997). The Sirdalsvatn "normal" morph which also lives sympatrically with a profundal living "dwarf" morph, also have a similar age at maturity as the LO-morph in Skogsfjordvatn (Hesthagen et al., 1995).

The PB-morph had the youngest age (A_{50} = 3.2 years) and smallest size (L_{50} = 8.9 cm) at maturity amongst the three morphs in Skogsfjordvatn. The age and size at maturity for the PB-morph is at the very low end of the scale for Arctic charr populations in general (Vøllestad and L´Abèe-Lund, 1994; Klemetsen et al., 2003). However, the age and size at maturity is similar to the profundal morph in Fjellfrøsvatn, and these two morphs also have similar growth trajectories, feeding niches and habitat utilization (see: Klemetsen et al., 1997; Klemetsen et al., 2006; Knudsen et al., 2006; Knudsen, R. unpublished data). Also the SB Arctic charr morph in Thingvallavatn has similar age and size at maturity as the PB-morph in Skogsfjordvatn, although they have different habitat and diet niche utilizations (Sandlund et al., 1992). Hence, the size at maturity for the PB-morph seems to be very small for Arctic charr as a species, although not unique. These findings support Klemetsen et al. (2003) in that there seem to be a lower threshold for size at sexual maturation of Arctic charr females around 7 cm. To my knowledge there has not been found mature females below this size in any "dwarf" populations of Arctic charr. The fecundity of 7 cm female Arctic charr are very low (around 30 eggs or fewer), and this is suggested to be a determining factor for the lower size limitations of adult female Arctic charr (Klemetsen et al., 2003). However, as these fishes are extremely plastic (Klemetsen, 2010), there might be female individuals maturing at an even smaller size. One potential candidate may be the extremely deep living, small-sized charr form in Tinnsjøen, Norway (Søreide et al., 2006), but this still remains to be explored.

The PP-morph matured at the oldest age (A_{50} = 9.2 years) and largest size (L_{50} = 26 cm) of the three Arctic charr morphs in Skogsfjordvatn. Contrasting the PB-morph, the PP-morph was at the very high end of the typical scale regarding age at maturity, whereas the size at maturity was more intermediate compared to other populations of Arctic charr (Vøllestad and L´Abèe-Lund, 1994). When comparing the PP-morph to other profundal living Arctic charr morphs (i.e. the Fjellfrøsvatn profundal morph and the Sirdalsvatn dwarf morph), especially the age, but also the size at maturity is high (see: Hesthagen et al., 1995; Klemetsen et al., 1997). If we compare these findings to other piscivore morphs, independent of habitat utilization, the age at maturity still seems to be high for the PP-morph, but the size at maturity seems to coincide. For example the age and size at maturity for the PI-morph in Thingvallavatn is 5.7 years and 25.6 cm, respectively (Sandlund et al., 1992) and for the piscivore morph in Loch Rannoch the age and size at maturity is 8.9 years and around 25 cm (Fraser et al., 2008).

The somatic growth of fishes seems in general to be very flexible and the same species may show very different patterns of growth in different environments (Wootton, 1998). The growth trajectories for the different morphs in Skogsfjordvatn could be explained by different factors, both abiotic and biotic. One of the most important factors affecting growth for fishes in general is the trade-off between reproduction and somatic growth (Stearns, 1992; Wootton, 1998). Growth rate could affect age and size at maturity and conversely, age and size at maturity could thus affect growth. Before maturation, all acquired energy is available for maintenance and growth, but when maturation sets in, energy allocated to gonads, secondary sexual characters and reproductive behavior has to be prioritized (see: Wootton, 1998). This leads to less energy for i.e. somatic growth (Wootton, 1998). This means that the timing of first reproduction often will affect the average lifetime growth rate and the achieved maximum body size of fishes. Life history theory states that early maturation is beneficial because there is a higher probability of surviving until maturity, since they spend a decreased period of time at a juvenile stage (Stearns, 1992). In addition, early maturation will increase fitness since it would lead to shorter generation time for those individuals that mature early compared to individuals that mature later (Stearns, 1992). However, if delaying maturity permits further growth, and fecundity increases with size, then delayed maturity leads to higher fecundity at first reproduction. Maturity should be delayed until the fitness gains of early maturation are outweighed by the increased fecundity from delaying maturation (Stearns, 1992).

The two morphs that utilize the profundal zone, and thus experience similar abiotic factors, have obviously adopted different strategies for age and size at maturity: The PB-morph is maturing at a young age and small body size and the PP-morph is maturing at an older age and larger body size. At the age when the PB-morph reaches maturation the growth rate seems to go towards zero, which suggests that all available energy is used on maintenance and reproduction leaving no energy to allocate to further growth. Also the somatic growth before the PB-morph matures is lower than for the PP-morph. This further suggests that the energy intake rate of the PB-morph is low. Life history theory states that one should mature early if there is no fitness gain of delaying maturation (Stearns, 1992). The energy intake rate for the PB-morph is apparently so low that investing in further growth will not increase fecundity enough to be able to outweigh the fitness gain of maturing early. The PB-morph increases fitness by earlier maturation, shorter generation time and assumedly a shorter period of time exposed to predators before maturation. This again could lead to the observed small maturation and maximum body size for the PB-morph. Arctic charr morphs elsewhere show the same pattern, where small morphs mature earlier than sympatric living larger ones (e.g. Jonsson et al., 1988).

The PP-morph delays maturation and invests in somatic growth apparently in order to increase fecundity and thus increase fitness by higher initial fecundity (i.e. fecundity at first reproduction). The PP-morph, contrasting the PB-morph, seem to grow relatively well also after reaching the reproductive age, which could indicate that the food resources are so abundant and energy rich that they can invest in growth simultaneously with allocating energy to maintenance and reproduction. This reflects that for a piscivore morph there would be a potential for further growth after maturation due to the possibility of including larger and larger prey as they grow, and the body size constraints are therefore not as evident as for the other morphs (Fraser et al., 2008). Hence, for the PP-morph it seems like delaying maturation would increase fecundity sufficiently to be able to outweigh the fitness gain of maturing earlier. In addition, the PP-morph has to invest more in growth to be able to reach a size where piscivory is possible and effective. When this size is reached, fish prey are a much more profitable food resource than chironomids and small mussels (e.g. Kerr, 1971), which are the diet for the PB-morph.

The LO-morph was somewhere in the middle regarding both age and size at maturity, as they delayed maturity a bit longer than the PB-morph, but not as long as the PP-morph. However, the LO-morph reached almost the same size at maturity as the PP-morph, thus in much shorter time. Life history theory predicts that relatively fast growth in the juvenile stage compared to the adult stage of an individual selects for maturation early in life (Hutchings, 1993, and references therein), however size at maturity could vary. The fast growth of this morph compared to the other morphs in Lake Skogsfjordvatn, leads to that the selected size at maturation is achieved relatively early in life and much sooner than for the PP-morph. The relative high growth rate before the age at maturation compared to the growth rate post age at maturation for the LO-morph, suggest that the LO-morph matures at a size where foraging efficiency is optimized, and energy is allocated to reproduction instead of somatic growth (see: Fraser et al., 2008).

There are other factors besides the trade-off between reproduction and somatic growth that could affect growth rate, maximal body size and age and size at maturity. Temperature could be an important environmental factor affecting the growth rate of fish, as low temperatures slow down metabolic processes involved in somatic growth (Wootton, 1998). The temperature regime in the profundal zone of lakes is relatively homogenous throughout the year compared to the littoral- and upper pelagic zone which has temperatures that fluctuate greatly between seasons (Wetzel, 2001). In lakes in northern Norway the temperature seldom exceeds 8°C in the profundal zone (see: Huang, 2011; Mousavi and Amundsen, 2012). The maximum growth for Arctic charr is suggested to occur between of 14.4 and 17.2°C (Larsson et al., 2005). This is within the range for the upper water temperatures during the summer in Skogsfjordvatn (see: Christensen, 1994). Larsson et al. (2005) studied climatic trends in eleven Arctic charr populations and found that there was no geographical or climatic trend in growth performance among populations of Arctic charr. Thus, there was no indication of thermal adaptations that would differ between different populations of Arctic charr (Larsson et al., 2005). Assumedly there would not be any differentiating thermal adaptations between the different morphs in Skogsfjordvatn, although this could not be verified here. Therefore, based on the temperature differences between the profundal zone and the upper water layers, it is logical that the two profundal morphs had slower growth than the LO-morph. However, energetic growth efficiency for Arctic charr seems to decrease with increasing temperatures (Larsson and Berglund, 2005). This suggests that the two profundal morphs in Skogsfjordvatn need less energy to be able to grow than the LO-morph. Wootton (1998) states that when nutrition intake rates are low, growth will increase with decreasing temperatures. Also growth capacity was suggested to be higher in the profundal morph in Fjellfrøsvatn compared with the littoral morph (Klemetsen, 2010). The relatively less profitable habitat that is the profundal zone (Wetzel, 2001) could thus be inhabited by profundal adapted Arctic charr morphs as a consequence of low energy needs for these morphs.

There are several ecological interactions that could decrease energy availability for growth of fishes (Wootton, 1998), including for example an increase in competition for food resources, low densities of prey or increased attention given to predator avoidance (e.g. Mittelbach, 1988;

Bolnick and Preisser, 2005). There is so far no evidence that there is a difference in competitive pressure between the Skogsfjordvatn morphs that would explain that the two morphs in the profundal zone had slower growth compared to the LO-morph. The predation risk could on the other hand be highest in the profundal zone due to the presence of the PP-morph. This could indirectly affect the individual growth of the PB-morph and juveniles of the PP-morph in a negative way, by allocating energy to predator avoidance instead of somatic growth (Bolnick and Preisser, 2005, and references therein). However, in Fjellfrøsvatn where no specialized profundal predator such as the PP-morph is present, the profundal morph still has a similar growth pattern as the PB-morph in Skogsfjordvatn (see: Klemetsen et al., 1997). Furthermore, the presence of piscivorous brown trout and birds in the upper water layers likely leads to a relative high predation risk for the LO-morph (see: Klemetsen, 1989; Persson, 2007). Hence, between-habitat differences in predation pressure are likely not important for the growth differences between the LO-morph and the two profundal morphs.

Maximal body size could also be affected by different factors other than age and size at maturity. There is for example evidence that there is an optimum prey size for gape-limited fish predators such as Arctic charr, defined by amongst other factors the per capita energy gain of the predator (see: e.g. Werner, 1974; Mittelbach, 1981). In that respect, Fraser et al. (2008) proposed an interesting hypothesis, suggesting that the constraints in maximum body size arise from the food particle size utilized by individual Arctic charr. A narrow size distribution of small sized prey like zooplankton (0.01 – 0.3 cm) and benthic invertebrates (0.1 – 3.5 cm), will select for a body size where the foraging efficiency for this prey types is large (Fraser et al., 2008). The prey size distribution is much broader for piscivorous Arctic charr (4 – 50 cm; Maitland, 2004), and therefore the foraging efficiency will remain high over a wide range of body sizes (Fraser et al., 2008). The PB-morph utilizes small-sized soft bottom benthos, the LO-morph predominantly feeds on littoral invertebrates and zooplankton while the PP-morph is mainly piscivorous (Knudsen, R., unpublished data). These differences in the diet niche of the three morphs in Skogsfjordvatn are likely to cause maximum body length constraints on the PB- and LO-morphs, but in less degree on the PP-morph and may thus partly explain the difference in maximum body length, especially in respect to the large L_∞ of the PP-morph.

According to life history theory, another factor that could determine age and size at maturity is the instantaneous mortality rates at different ages and sizes (Wootton, 1998). The LO-morph may experience heavy predation in the juvenile stage from cannibalistic charr and fish-eating trout and birds. It could therefore be vital for LO-morph individuals to grow to a size where the predation risk is reduced, and as a consequence maturation would be delayed until that size is achieved (see: e.g. Reznick and Endler, 1990). There is no evidence that the predation risk for the PB-morph would differ significantly with different sizes or ages, since all size-groups of the PB-morph could potentially be predated on by adults of the PP-morph (Knudsen, R., unpublished data). This assumption is based on the observations that cannibalistic Arctic charr on average may utilize fish prey that are 22-30% of their own length (Amundsen, 1994; Amundsen et al., 1995). This further suggests that the longer the PB-morph lives, the higher the probability of being predated on by the PP-morph will be. Hence, in this predation scenario, early reproduction will indeed increase fitness for the PB-morph. However, the Fjellfrøsvatn profundal morph showed similar age and size at maturity without any known predation risk (see: Klemetsen et al., 1997). This again suggests that the size at maturity for the PB-morph is already at a minimum and the selection pressure in form of predation does not further force the size at maturity to be even lower, as could be anticipated from life history theory (Stearns, 1992). Juvenile or small individuals of the PP-morph are assumedly also at predation risk from cannibalistic individuals of its own kind (Knudsen, R., unpublished data). Apparently, the PP-morph has adopted a contrasting strategy in the trade-off between growth and reproduction compared to the PB-morph. The PP-morph invest energy in somatic growth to be able to reach a size outside the predation window, and therefore postpone reproduction (see: e.g. Reznick and Endler, 1990), while the PB-morph try to "escape" predation by investing in reproduction early in life, reducing the time before reproduction and thus lowering the chance of being predated on.

As expected, age and length at sexually maturity were different between the sexes within the different morphs, the females usually maturing at a later age and a larger size. However, the females of the PB-morph matured at a smaller size, although at an older age than the males, partly contradicting general life history theory (see: Bell, 1980). Female gonads are energetically more costly to produce, but more importantly the large size difference between sperm cells and eggs leads to that male fish can have many more times the number of gametes than females at the same size (Wootton, 1998). Therefore, it should be more favorable for a female to delay maturation in order to increase body size and thereby increase fitness. The fitness consequences for male fishes in general are not as prominent in respect to increased body size. An important exception of this general rule is in situations where there is a strong mating competition between the males (see: Wootton, 1998). This could suggest that the PB-morph males has some sort of competition for females or mating behavior that selects for a greater body size, but this does not seem very likely as there were an overweight of females in the PB-morph population. A more likely explanation could be that there is a difference in survival or growth that selects for a slight differentiation in size and age at maturity between the sexes of the PB-morph. The low densities of nutrition in the profundal zone could explain why females of the PB-morph mature at a smaller size and older age than males, the females may be forced to invest all available energy into reproduction and thus there is no energy left to invest in somatic growth, whilst males could invest one fraction to reproduction and one fraction to somatic growth.

Fecundity and Egg-size

Number of eggs produced was significantly different between the PB-morph and the two other morphs in Lake Skogsfjordvatn. As expected, the difference was mostly explained by the size difference between the morphs, but the number of eggs produced by the PB-morph had an additional effect of morph regardless of body length. This could indicate different adaptations regarding fecundity between the PB-morph and the two other morphs in Skogsfjordvatn. However, a more likely explanation is that there is a confounding effect of the difference in egg-size between the PB-morph and the two other morphs. The PB-, LO- and PP-morph had relative to each other the lowest, intermediate and highest absolute fecundity, respectively. The totally opposite picture was true for number of eggs per kilogram body weight (i.e. the relative fecundity), where the PP-morph had the lowest and the PB-morph had the highest value of eggs/kg. This is most likely due to the observed difference in egg-size between the three morphs and does not reflect difference in energetic investment to the gonads, since the GSI (Gonadosomatic Index) was not significantly different between the morphs. However, it is evident that there is a trade-off between egg-size and fecundity, which acts differently between the three morphs.

Lets assume that a random female individual from the PB-morph is mature at age 3 years and produce on average 50 eggs every year until it reaches the age of 8 years and then dies, which would indicate a lifetime fecundity of around 600 eggs. This shows that the PB-morph would have a lifetime fecundity that is less than the fecundity in one breeding season for the LO-morph and the PP-morph. However, the difference in generation time needs to be taken into consideration. For simplicity reasons, we can assume that survival of the offspring until they can reproduce by them self is 100 percent and that the different morphs only reproduce once, the PB-morph at 3 years and the PP-morph at 9 years. After 3 years: the PB- and PP-morph would have produced 50 and 0 offspring, respectively. After 6 years: the PB- and PP-morph would have produced 50^2 = 2500 and 0 offspring, respectively. After 9 years: the PB- and PP-morph would have produced 50^3 = 125 000 and 809 offspring, respectively. If we assume that they can reproduce many times the difference would be even greater after 9 years. In this thought experiment it is quite easy to see that difference in age-specific mortality rates and longivety between the different morphs would have dramatic effect on fitness.

As expected, also the egg-size was significantly different between the three morphs. However, results show that this difference is only a function of the length differences between the morphs. On average the PB-, LO- and the PP-morph had the smallest-, intermediate- and largest eggs, respectively, compared to each other. The volume of the eggs of the PB-morph was only 32 percent of that of the PP-morph on average. In general for salmonids, larger eggs have higher energy content than smaller eggs (e.g. Thorpe et al., 1984; Einum and Fleming, 1999). In addition, smaller eggs lead to smaller juveniles at hatching than larger eggs for Arctic charr (Leblanc et al., 2011). This suggests that the PB-morph in Skogsfjordvatn is smaller already at hatching than the two other morphs. Larger juveniles at hatching may eat larger sized prey, survive starvation for a longer period of time and have fewer predators than small juveniles (Wootton, 1998). This suggests that hatchlings from the PB-morph have higher mortality rates than hatchlings for the other two morphs in Skogsfjordvatn.

For salmonids in general, egg-size and absolute fecundity increases with body length, however, relative fecundity decreases (see: Wootton, 1998; Einum and Fleming, 1999; Thorpe et al., 1984). This general life history assumption seems to be true for all morphs in Skogsfjordvatn, where absolute fecundity increases and egg-size and relative fecundity decreases from the smallest sized morph (PB) to the largest sized morph (PP), but also within morphs where fecundity increases from small sized individuals to larger ones. Lacustrine populations of Arctic charr are suggested to have a clutch size of approximately 3000 eggs per kilogram body weight (Pethon, 2005), and have a egg-size range between 3.5 - 5.0 mm (Johnsen, 1980). Klemetsen et al. (2003) also indicates a lower limit of egg-size for Arctic charr around 3.5 mm. The LO-morph had a similar average number of eggs per kilogram (3150 eggs/kg) as the suggested number for Arctic charr in general, and an egg-size within the given range for Arctic charr. The Fjellfrøsvatn littoral morph is reported to have an annual fecundity range between 278-480 eggs per individual (Klemetsen, A., unpublished data in Klemetsen et al., 2006), which is distinctly less than the range of annual fecundity for the LO-morph in Skogsfjordvatn (320-1139), even though size differences between these two morphs are less evident (see: Klemetsen et al., 1997 for body size of mature individuals). However, the egg-size for the LO-morph (4.2 mm) was distinctly smaller than the egg-size for the littoral morph in Fjellfrøsvatn (5.3 mm) (Klemetsen, A., unpublished data in Klemetsen et al., 2006).

This suggests that the LO-morph invests its energy to increase fecundity at the expense of egg quality, whilst the littoral morph in Fjellfrøsvatn invest more energy in each egg at the expense of fecundity. The PB-morph had significantly higher relative fecundity than the suggested general number of 3000 eggs per kilogram fish for Arctic charr and smaller average egg-size than the given range of Arctic charr, also smaller than the smallest egg-size reported by Klemetsen et al. (2003). This indicates that egg-size of Arctic charr could be much more variable than formerly assumed. The profundal morph in Fjellfrøsvatn had a similar fecundity range (18-69 eggs; Klemetsen et al., 2002) as the PB-morph, however, the lower limit in fecundity is somewhat smaller than for the PB-morph. This could be related to the observation that the mean egg size of the profundal morph in Fjellfrøsvatn (3.8 mm) (Klemetsen et al., 2003) was larger than for the PB-morph in Skogsfjordvatn (3.2 mm). This suggests that the trade-off regime between egg-size and fecundity is somewhat different between these two morphs.

The Gonadosomatic Index (GSI) was quite equal between the three morphs in Skogsfjordvatn. The GSI values for the Skogsfjordvatn morphs falls in the range of the reported GSI values for a number of populations of Arctic charr (Vøllestad and L´Abèe-Lund, 1994), however at the very low end of the range for all three morphs. Life history theory predicts that fish that mature relatively early and at a small body size should invest relatively more in annual reproduction than its conspecifics that mature later and at a bigger body size (Fraser et al., 2008). The gonadosomatic index (GSI) for the three morphs in lake Skogsfjordvatn did not support this theory, as the PB-morph did not invest more energy than the other morphs into gonads. However, this was also true for the small benthivorous morph in Thingvallavatn, this morph had lower GSI than the other morphs in Thingvallavatn (Sandlund et al. 1992). This pattern could also be due to low energy intake rates and thus it is possible that there is not enough energy to be able to increase the relative energy to gonads. Therefore these morphs invest relatively more energy to enhance fecundity at the expense of egg-size, evidently to be able to increase fitness.

Conclusion and future perspectives

As hypothesized, there were great differences in life history traits between the three different Arctic charr morphs in Skogsfjordvatn. These different life history strategies reflect their differences in habitat and diet utilization, and in most cases the adopted traits could be predicted by life history theory (see: Stearns, 1992; Wootton, 1998). Both different abiotic and biotic factors seemed to influence the differences in life history traits. Temperature dissimilarities between the upper water layers and the profundal zone in Skogsfjordvatn seem to be important for the growth rate of the different morphs. The two profundal morphs, that experience lower temperature in the growth season, have lower growth rates than the LO-morph at least in the pre-adult stages. Difference in age and size at maturity was furthermore important to explain growth differences in the adult stages of their life cycle. The trade-off between reproduction and somatic growth seems to differentiate the two profundal morphs in lifetime growth rate, maximal body size and age and size at maturity. The PB-morph increases fitness by maturing early and the size at maturation was thus quite small, leading to low growth rate and a small maximum body size. In contrast, the PP-morph invests in somatic growth for a longer time to be able to utilize fish prey effectively, and when this size limit for piscivory is achieved they seem to grow quite well as a consequence of their large-sized and nutritious diet. This leads to an old age at maturity and a larger maximum body size than for the PB-morph. The difference in size at maturation also explains their dissimilarities in fecundity and egg-size. As predicted by life history theory both fecundity and egg-size increased with the size of the female fish, both between morphs and also within each morph. As a consequence, smaller individuals apparently invest relatively more energy to enhance fecundity at the expense of egg-size compared to larger individuals that invest relatively more energy into each egg.

One interesting aspect of this research is to see another evidence of a profundal niche for the Arctic charr. The niche of utilizing the nutrition poor profundal zone for the whole life cycle is now found in an increasingly number of lakes. These Arctic charr morphs feed exclusively on soft bottom benthos like chironomids and small mussels. This niche seems also to produce very similar life history traits between lakes as the profundal morph from Fjellfrøsvatn and the PB-morph from Skogsfjordvatn show almost identical life history strategies. The only slight difference between them is the relative investment in fecundity and egg-size, where the PB-morph in Skogsfjordvatn seems to invest a little more energy in fecundity at the expense of egg-size compared to the profundal morph in Fjellfrøsvatn that invests more energy in each egg. One cannot eliminate the possibility that these morphs originate from the same population although it does not seem very likely due to the lakes historical origin and geographical distance. This could mean that the experienced selection pressure is so similar between these two morphs that they are a product of two different sympatric/parapatric speciation processes or in other words a product of parallel evolution.

However, the novelty of this system is the occurrence of a second Arctic charr morph in the profundal zone. To my knowledge there has never been described two different Arctic charr morphs in the profundal zone of lakes, and the PP-morph has thus a life history strategies that is seldom to see for Arctic charr. It seems like the split between the PB-morph and the PP-morph is related to trade-off differences in energy allocation between somatic growth and reproduction at different ages and sizes. In Fjellfrøsvatn the profundal morph was caught in the profundal zone throughout the year, while in monomorphic populations there is very few individuals of Arctic charr in the profundal zone during the ice covered season. Therefore, it seems like the PP-morph is dependent of the presence of the PB-morph to be able to exist, because one can assume from other systems, that the only fish prey in the profundal zone during the ice covered season is the PB-morph and thus at least from December to May the only prey for the PP-morph is the PB-morph. This has led to a year around piscivore niche in the profundal zone, however, further research need to be conducted to be able to understand why a piscivorous morph has emerged in Skogsfjordvatn and not in Fjellfrøsvatn.

References

Adams, C.E., Fraser, D., Huntingford, F.A., Greer, R.B., Askew, C.M., Walker, A.F. 1998. Trophic polymorphism amongst Arctic charr from Loch Rannoch, Scotland. J Fish Biol **52**, 1259-1271.

Adams, C.E., Huntingford, F.A. 2004. Incipient speciation driven by phenotypic plasticity? Evidence from sympatric populations of Arctic charr. Biol J Linn Soc **81**, 611-618.

Alekseev, S.S., Pichugin, M.Y. 1998. A new form of charr *Salvelinus alpinus* (Salmonidae) from Lake Davatchan in Transbaikalia and its morphological differences from sympatric forms. J Ichtyol **38**, 292-302.

Amundsen, P.-A. 1994. Piscivory and cannibalism in Arctic charr. J Fish Biol **45**, 181-189.

Amundsen, P.-A., Damsgard, B., Arnesen, A.M., Jobling, M., Jorgensen, E.H. 1995. Experimental evidence of cannibalism and prey specialization in Arctic charr, *Salvelinus alpinus*. Envir Biol Fish **43**, 285-293.

Amundsen, P.-A., Knudsen, R., Klemetsen, A. 2008. Seasonal and ontogenetic variations in resource use by two sympatric Arctic charr morphs. Envir Biol Fish **83**, 45-55.

Arendt, J.D. 2010. Size-fecundity relationships, growth trajectories, and the temperature-size rule for ectotherms. Evolution **65**, 43-51.

Baker, J.A., Heins, D.C., Foster, S.A., King, R.W. 2008. An overview of life-history variation in female threespine stickleback. Behaviour **145**, 579-602.

Bell, G. 1980. The costs of reproduction and their consequences. The American Naturalist **116**, 45-76.

Blanck, A., Lamouroux, N. 2007. Large-scale intraspecific variation in life-history traits of European freshwater fish. J Biogeogr **34**, 862-875.

Bolnick, D.I., Preisser, E.L. 2005. Resource competition modifies the strength trait-mediated predator-prey interactions: a meta-analysis. Ecology **86**, 2771-2779.

Chen, Y., Jackson, D.A., Harvey, H. H. 1992. A comparison of von Bertalanffy and polynomial functions in modelling fish growth data. Can J Fish and Aq Sci **49**, 1228-1235.

Christensen, G.N. 1994. Selective predation by pelagic Arctic charr, *Salvelinus alpinus* (L.), in the oligotrophic lake Skogsfjordvatnet (Northern Norway). Master thesis, University of Tromsø, pp. 69 (in Norwegian).

Doebeli, M., Dieckmann, U. 2003. Speciation along environmental gradients. Nature **421**, 259-264.

Doebeli, M., Dieckmann, U., Metz, J.A., Tautz, D. 2005. What we have also learned: adaptive speciation is theoretically plausible. Evolution **59**, 691-695.

Einum, S., Fleming, I.A. 1999. Maternal effects of egg size in brown trout (Salmo trutta): norms of reaction to environmental quality. Proc Roy Soc B **266**, 2095-2100.

Eloranta, A.P., Knudsen, R., Amundsen, P.-A. 2013. Niche segregation of coexisting Arctic charr (*Salvelinus alpinus*) and brown trout (*Salmo trutta*) constrains food web coupling in subarctic lakes. Freshw Biol **58**, 207-221.

Forseth, T., Ugedal, O., Jonsson, B. 1994. The energy budget, niche shift, reproduction and growth in a population of Arctic charr, *Salvelinus alpinus*. J Anim Ecol **63**, 116-126.

Fraser, D., Huntingford, F.A., Adams, C.E. 2008. Foraging specialisms, prey size and life-history patterns: a test of predictions using sympatric polymorphic Arctic charr (*Salvelinus alpinus*). Ecol Freshw Fish **17**, 1-9.

Gislason, D., Ferguson, M., Skulason, S., Snorrason, S.S. 1999. Rapid and coupled phenotypic and genetic divergence in Icelandic Arctic char (*Salvelinus alpinus*). Can J Fish Aq Sci **56**, 2229-2234.

Griffiths, D. 1994. The size structure of lacustrine Arctic charr (Pisces, Salmonidae) populations. Biol J Linn Soc **51**, 337-357.

Heibo, E., Magnhagen, C., Vollestad, L.A. 2005. Latitudinal variation in life-history traits in Eurasian perch. Ecology **86**, 3377-3386.

Hesthagen, T., Hindar, K., Jonsson, B., Ousdal, J.O., Holthe, H. 1995. Effects of acidification on normal and dwarf Arctic charr *Salvelinus-alpinus* (L) in a Norwegian lake. Biol Conserv **74**, 115-123.

Hindar, K., Jonsson, B. 1982. Habitat and food segregation of dwarf and normal Arctic charr (*Salvelinus-alpinus*) from Vangsvatnet Lake, western Norway. Can J Fish Aq Sci **39**, 1030-1045.

Holden, M.J., Raitt, D.F.S. 1974. Manual of fisheries science. FAO Fish Tech Pap pp. 115.

Huang, X. 2011. A high-resolution temperature record from lakes of the Lofoten islands, nortwestern Norway based on a new uk temperature calibration from in situ measurements. Master thesis, University of Massachusetts Amherst, pp. 105.

Hutchings, J.A. 1993. Adaptive life histories effected by age-specific survival and growth rate. Ecology **74**, 673-684.

Johnson, J.B., Belk, M.C. 2001. Predation environment predicts divergent life-history phenotypes among populations of the livebearing fish *Brachyrhaphis rhabdophora*. Oecologia **126**, 142-149.

Johnson, L. 1980. The Arctic charr, *Salvelinus alpinus*. In *Charrs, salmonid Fishes of the Genus Salvelinus* (ed. Balon, K.), pp. 15-98. W. Junk, The Hague.

Jonsson, B., Jonsson, N. 2001. Polymorphism and speciation in Arctic charr. J Fish Biol **58**, 605-638.

Jonsson, B., Skulason, S., Snorrason, S.S., Sandlund, O.T., Malmquist, H.J., Jonasson, P.M., Gydemo, R., Lindem, T. 1988. Life-history variation of polymorphic Arctic charr (*Salvelinus-alpinus*) in Thingvallavatn, Iceland. Can J Fish Aq Sci **45**, 1537-1547.

Jonsson, N., Næsje, T.F., Jonsson, B., Saksgård, R., Sandlund, O.T. 1999. The influence of piscivory on life history traits of brown trout. J Fish Biol **55**, 1129-1141.

Kahilainen, K., Lehtonen, H., Kononen, K. 2003. Consequence of habitat segregation to growth rate of two sparsely rakered whitefish (*Coregonus lavaretus* (L.)) forms in a subarctic lake. Ecol Freshw Fish **12**, 275-285.

Keeley, E.R., Grant, J.W.A. 2001. Prey size of salmonid fishes in streams, lakes and oceans. Can J Fish Aq Sci **58**, 1122-1132.

Kerr, S.R. 1971. Prediction of fish growth efficiency in nature. J Fish Board Can **28**, 809-814.

Klemetsen, A. 2010. The charr problem revisited: exceptional phenotypic plasticity promotes ecological speciation in postglacial lakes. Freshw Rev **3**, 49-74.

Klemetsen, A., Amundsen, P.-A., Muladal, H., Rubach, S., Solbakken, J.I. 1989. Habitat shifts in a dense, resident Arctic charr *Salvelinus alpinus* population. Physiology and Ecology Japan*,* Special Volume **1**, 187–200.

Klemetsen, A., Amundsen, P.-A., Dempson, J.B., Jonsson, B., Jonsson, N., O'Connell, M.F., Mortensen, E. 2003. Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. Ecol Freshw Fish **12**, 1-59.

Klemetsen, A., Amundsen, P.-A., Knudsen, R., Hermansen, B. 1997. A profundal, winter-spawning morph of Arctic charr *Salvelinus alpinus* (L.) in lake fjellfrøsvatn, northern Norway. Nordic J Freshw Res **73**, 13-23.

Klemetsen, A., Elliott, J.M., Knudsen, R., Sorensen, P. 2002. Evidence for genetic differences in the offspring of two sympatric morphs of Arctic charr. J Fish Biol **60**, 933-950.

Klemetsen, A., Knudsen, R., Primicerio, R., Amundsen, P.-A. 2006. Divergent, genetically based feeding behaviour of two sympatric Arctic charr, *Salvelinus alpinus* (L.), morphs. Ecol Freshw Fish **15**, 350-355.

Knudsen, R., Klemetsen, A., Amundsen, P.-A., Hermansen, B. 2006. Incipient speciation through niche expansion: an example from the Arctic charr in a subarctic lake. Proc Roy Soc B **273**, 2291-2298.

Larsson, S., Berglund, I. 2005. The effect of temperature on the energetic growth efficiency of Arctic charr (*Salvelinus alpinus* L.) from four Swedish populations. J Therm Biol **30**, 29-36.

Larsson, S., Forseth, T., Berglund, I., Jensen, A.J., Naslund, I., Elliott, J.M., Jonsson, B. 2005. Thermal adaptation of Arctic charr: experimental studies of growth in eleven charr populations from Sweden, Norway and Britain. Freshw Biol **50**, 353-368.

Leblanc, C.A. 2011. The importance of egg size for the diversity of salmonids. Phd, Oregon State University, pp. 139.

Lester, N.P., Shuter, B.J., Abrams, P.A. 2004. Interpreting the von Bertalanffy model of somatic growth in fishes: the cost of reproduction. Proc Roy Soc B **271**, 1625-1631.

Magnan, P., Proulx, R., Plante, M. 2005. Integrating the effects of fish exploitation and interspecific competition into current life history theories: an example with lacustrine brook trout (*Salvelinus fontinalis*) populations. Can J Fish Aq Sci **62**, 747-757.

Maitland, P.S. 2004. Keys to the freshwater fish of Britain and Ireland. FBA Special Publication, Far Sawrey, Cumbria: Freshwater Biological Association.

Mittelbach, G.G. 1981. Foraging efficiency and body Size - a study of optimal diet and habitat use by bluegills. Ecology **62**, 1370-1386.

Mittelbach, G.G. 1988. Competition among refuging sunfishes and effects of fish density on littoral-zone invertebrates. Ecology **69**, 614-623.

Mousavi, S.K., Amundsen, P.-A. 2012. Seasonal variations in the profundal Chironomidae (Diptera) assemblage of a subarctic lake. Bor Envir Res **17**, 102-112.

Norges vassdrag- og energidirektorat. 2010. Skogsfjordelva. 200/1 NVE.

O'connell, M.F., Dempson, J.B. 2002. The biology of Arctic charr, *Salvelinus alpinus*, of Gander Lake, a large, deep, oligotrophic lake in Newfoundland, Canada. Envir Biol Fish **64**, 115-126.

Parker, H.H., Noonburg, E.G., Nisbet, R.M. 2001. Models of alternative life-history strategies, population structure and potential speciation in salmonid fish stocks. J Anim Ecol **70**, 260-272.

Persson, L., Amundsen, P.-A., De Roos, A.M., Klemetsen, A., Knudsen, R., Primicerio, R. 2007. Culling prey promotes predator recovery—alternative states in a whole-lake experiment. Science **316**, 1743-1746.

Persson, L., Greenberg, L.A. 1990. Interspecific and intraspecific size class competition affecting resource use and growth of perch, *Perca-Fluviatilis*. Oikos **59**, 97-106.

Pethon, P., 2005. Aschehougs Store Fiskebok. **5.** Edition. H. Aschehoug & Co. A/S, Oslo.

Power, M., O'Connell, M.F., Dempson, J.B. 2005. Ecological segregation within and among Arctic char morphotypesin Gander Lake, Newfoundland. Envir Biol Fish **73**, 263-274.

Refsnes, B. In prep. Differences in parasite infection in a polymorphic Arctic charr population in a subarrctic lake, northern Norway. Master thesis, University of Tromsø.

Reznick, D.A., Bryga, H., Endler, J.A. 1990. Experimentally induced life-history evolution in a natural-population. Nature **346**, 357-359.

Rodd, F.H., Reznick, D.N. 1997. Variation in the demography of guppy populations: The importance of predation and life histories. Ecology **78**, 405-418.

Roff, D.A. 1992. Evolution of life histories: theory and analysis. Chapman and Hall, New York, USA.

Sandlund, O.T., Gunnarsson, K., Jonasson, P.M., Jonsson, B., Lindem, T., Magnusson, K.P., Malmquist, H.J., Sigurjonsdottir, H., Skulason, S., Snorrason, S.S. 1992. The Arctic charr *Salvelinus-alpinus* in Thingvallavatn. Oikos **64**, 305-351.

Schaffer, W.M. 1979. Equivalence of maximizing reproductive value and fitness in the case of reproductive strategies. PNAS USA **76**, 3567-3569.

Schluter, D. 2001. Ecology and the origin of species. TREE **16**, 372-380.

Schluter, D. 2009. Evidence for Ecological Speciation and Its Alternative. Science **323**, 737-741.

Schluter, D., Conte, G.L. 2009. Genetics and ecological speciation. PNAS USA **106**, 9955-9962.

Siwertsson, A., Knudsen, R., Kahilainen, K.K., Praebel, K., Primicerio, R., Amundsen, P.-A. 2010. Sympatric diversification as influenced by ecological opportunity and historical contingency in a young species lineage of whitefish. Evol Ecol Res **12**, 929-947.

Skoglund, S. 2013, in prep. Morphological divergence of three sympatric Arctic charr (*Salvelinus alpinus* (L.)) morphs in Skogsfjordvatn. Master thesis, University of Tromsø.

Skulason, S., Smith, T.B. 1995. Resource polymorphisms in vertebrates. TREE **10**, 366-370.

Skulason, S., Snorrason, S.S., Jonssson, B. 1999. Sympatric morphs, populations and speciation in freshwater fish with emphasis on Arctic charr. Evol Biol Div **70**, 70-92.

Skulason, S., Snorrason, S.S., Noakes, D.L.G., Ferguson, M.M., Malmquist, H.J. 1989. Segregation in spawning and early life-history among polymorphic Arctic charr, *Salvelinus-alpinus*, in Thingvallavatn, Iceland. J Fish Biol **35**, 225-232.

Smith, T.B., Skulason, S. 1996. Evolutionary significance of resource polymorphism in fishes, amphibians, and birds. Annu Rev Ecol Syst **27**, 111-133.

Stearns, S.C. 1992. The evolution of life histories. Oxford University Press, New York, USA.

Svenning, M.A., Borgstrom, R. 2005. Cannibalism in Arctic charr: do all individuals have the same propensity to be cannibals? J Fish Biol **66**, 957-965.

Søreide, F., Dolmen, D., Hindar, K. 2006. Den mystiske dypvannsfisken i Tinnsjøen. Fauna **59**, 122-129 (In Norwegian with an English summary).

Thorpe, J. E., Miles, M. S., Keay, D. S. 1984. Developmental rate, fecundity and egg size in Atlantic salmon, *Salmo salar* L. Aquaculture **43**, 289-305.

Vøllestad, L.A., L'Abée-Lund, J.H. 1994. Evolution of the Life-History of Arctic Charr *Salvelinus alpinus*. Evol Ecol **8**, 315-327.

Werner, E. E. 1974. The fish size, prey size, handling time relation in several sunfishes and some implications. J Fish Board Can **31**, 1531-1536.

West-Eberhard, M.J. 2005. Developmental plasticity and the origin of species differences. PNAS USA **102**, 6543-6549.

Wetzel, R.G. 2001. Limnology; lake and river ecosystems. **3.** Edition. Elsevier Academic press, San Diego.

Winemiller, K.O. 2005. Life history strategies, population regulation, and implications for fisheries management. Can J Fish Aq Sci **62**, 872-885.

Wootton, R.J. 1998. Ecology of Teleost Fishes. **2.** Edition. Kluwer, London.

Østbye, K., Amundsen, P.-A., Bernatchez, L., Klemetsen, A., Knudsen, R., Kristoffersen, R., Naesje, T.F., Hindar, K. 2006. Parallel evolution of ecomorphological traits in the European whitefish *Coregonus lavaretus* (L.) species complex during postglacial times. Mol Ecol **15**, 3983-4001.