Environmental manipulation of land-based farmed Arctic charr; effects on growth, feeding and maturation

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Abstract

Farming of Arctic charr takes mainly place in land-based farms applying intensive rearing methods with relatively high production costs. Depending on local conditions at each site, it is possible to regulate important environmental factors to improve productivity and well-being of the fish. Knowledge about how these different environmental factors affect various farming traits are therefore important to reduce production costs. The aim to this thesis was to investigate how rearing temperature, photoperiod, salinity and feeding rations can be used to enhance the production of land-based Arctic charr.

Rearing temperature is a highly effective tool to improve growth rate of Arctic charr. (Paper I). Juvenile Arctic charr reared at a constant temperature of 15 °C had mean weights that were 44 % and 78 % higher than fish reared at constant temperatures of 12 and 9 C, respectively. Attempts to transfer the Arctic charr down in rearing temperature as an effort to follow the drop in temperature optima for growth resulted in a consistently negative effects on the growth rate. High growth rates as observed at the higher temperature groups (Paper I) with subsequent high condition factor lead to higher incidence of maturation. Rearing of Arctic charr at periodic restricted feed rations (50 %) in Paper II led to full growth compensation (CG) of the farmed Arctic charr. Restricted feed groups had both higher feed intake and feed conversion efficiency during the re-feeding periods compared to the full ration group. Periodical feed restriction regimes had lower maturation level compared to full ration groups. The application of a six week short photoperiod within other ways continuous photoperiod improved long term growth rate of Arctic charr reared in freshwater (Paper III). Short day groups weighed 10.7–13.9 % more than the group reared on continuous light. Feed intake and feeding conversion efficiency increased following transfer to continuous light after a period of short day (Paper III) explaining the growth enhancement effect. Rearing salinity affected growth rate of Arctic charr and was higher for the lower salinity groups and maturation was lower and delayed (Paper

IV) in these same groups. Final weights of female Arctic charr reared at 17 ‰ were 19 % and 27 % higher than for the females in the 17-27 ‰ and 27 ‰ groups, respectively. Effort to induce the smoltification by application of a six week short day signal during early winter followed by transfer to continuous light (Paper IV) failed as no differences in neither gill NKA nor plasma Na^+ levels were detected compared with a control group kept at continuous light. Higher long term growth in the group receiving short day treatment in early winter is therefore likely linked to higher feed intake and or improved feeding efficiency following return to continuous light like demonstrated in Paper III rather than improved seawater tolerance for that group. Overall there appear to be an interactive effect on maturation from applying short-day photoperiod and subsequent rearing at higher salinity as GSI was higher in the short day groups reared at higher salinities.

In the thesis it has been demonstrated how rearing temperature, photoperiod, salinity and feeding ratio can affect farming traits like growth rate, maturation and feed conversion efficiency. High growth rate during juvenile phase as observed in the higher temperature groups (Paper I) can result in higher incidence of maturation during on growing period. Photoperiod manipulation and feed ration can be used as tools to improve growth and reduce maturation. Salinity has negative effect on growth rate but farmers with rich access to brackish water may get acceptable growth rates during on growing period. Future studies should focus on better preserving the potential high growth rate of Arctic charr during juvenile phase into the on growing period and establish protocols to improve the seawater tolerance of Arctic charr.

List of publications

Paper I.

Gunnarsson, S., Imsland, A.K., Árnason, J., Gústavsson, A., Arnason, I., Jónsson, J.K., Foss, A., Stefansson, S. and Thorarensen, H. (2011). Effect of rearing temperatures on the growth and maturation of Arctic charr (*Salvelinus alpinus*) during juvenile and on-growing periods. *Aquaculture Research*, 42: 211-229. doi:10.1111/j.1365-2109.2010.02615.x

Paper II.

Imsland, A.K. and Gunnarsson, S. (2011). Growth and maturation in Arctic charr (*Salvelinus alpinus*) in response to different feed rations. *Aquaculture.* 318 (3-4): 407-411. http://dx.doi.org/10.1016/j.aquaculture.2011.05.049

Paper III.

Gunnarsson, S., Imsland, A.K., Siikavuopio, S.I., Árnason, J., Gústavsson, A. and Thorarensen, H. (2012). Enhanced growth of farmed Arctic charr (*Salvelinus alpinus*) following a short-day photoperiod. *Aquaculture.* 350-353: 75-81. http://dx.doi.org/10.1016/j.aquaculture.2012.04.014

Paper IV.

Gunnarsson, S., Johansson, M., Gústavsson, A., Árnason, T., Árnason, J., Smáradóttir, H., Björnsson, B.Th., Thorarensen, H. and Imsland, A.K. (2013). Effects of short-day treatment on long term growth performance and maturation of farmed Arctic charr *Salvelinus alpinus* reared in brackish water. (Manuscript, submitted)

Summary of papers

Paper 1. Effect of rearing temperatures on the growth and maturation of Arctic charr (*Salvelinus alpinus*) during juvenile and on-growing periods.

The effect of rearing temperature on growth and maturation of Arctic charr (*Salvelinus alpinus*) was investigated. Arctic charr juveniles were reared for six months (phase I, October – April, size range 20-500 g) at constant temperature (9, 12 and 15 ºC) and at two temperature regimes where the temperature was changed in steps (T_{step}) with fish transferred either from 15 to 12 ºC or from 12 to 9 ºC during the rearing period. Following phase I, all groups were then reared at either 7 or 12 ºC for additional four months (phase II, size range 300-1000 g) and then slaughtered in August 2008. Overall growth rate was highest in the group reared at 15 ºC for the first six months of the trial with fish in this group being 44% and 78% heavier than fish reared at constant 12 or 9 ºC, respectively. The growth rate of the Arctic charr was reduced when transferred from higher to lower temperatures especially for groups previously reared at 15 ºC. There was a significant trend for higher gonadosomatic index (GSI) values at the end of the experiment for groups of fish that experience higher rearing temperatures during juvenile phase i.e. 4.18% (±0.79) and 7.29% (±0.89), for temperature groups 12 and 15 ºC, respectively compared to 2.49% (±0.74) for the 9 ºC group. Our results suggests that for production of fish > 1000 g, moderate or low temperatures (here 9 ºC) should be applied during the juvenile phase in order to reduce negative effects from maturation. Farmers with access to heat sources should accordingly choose more moderate rearing temperatures during juvenile stage especially if the fish is to be moved down in temperature regime during on-growing.

Paper II. Growth and maturation in Arctic charr (*Salvelinus alpinus*) in response to different feed rations.

Two groups of Arctic charr (Salvelinus alpinus) were reared in duplicate tanks supplied with freshwater, and subjected to two different ration levels, 100% (full ration) and 50% (half ration) for two six week periods during autumn (Sept.-Nov.) and winter (Dec-Feb.). Between and after the restricted ration periods all fish were fed full ration. After the first and second 42 day restricted feed periods, both sexes in the 50% had lower mean weight than the 100% group, but this size difference diminished as the trial progressed, and full growth compensation was seen for both males and females in the 50% group. Specific growth rates for both sexes were lower in the 50% group during the two reduced feeding periods, whereas growth was higher in the 50% group in the periods following re-feeding. No differences in growth were seen from May onwards. Feed conversion efficiency was higher in the 50% group during, and after, feed restriction, and daily feeding rate (F%) was higher in the 50% group in the periods subsequent to feeding restriction. In the following summer and autumn signs of lower maturation were seen for females in the feed restricted group. No differences were between the experimental groups in fillet water- and fat content. The present findings indicate that intermittent feeding during autumn and winter could be a cost-effective strategy for Arctic charr farmers in order to reduce feed costs and lower maturation.

Paper III. Enhanced growth of farmed Arctic charr (*Salvelinus alpinus*) following a short-day photoperiod.

Both short and long term effects of short photoperiods on the growth and maturity of juvenile Arctic charr (*Salvelinus alpinus*) were investigated. The Arctic charr (240 individually tagged) were reared at a constant temperature (12°C) and on one of four different light regimes; continuous light (LD24:0) while three groups were exposed to a six week period of short day (LD8:16) either from 24th September –6thNovember (LD8:16Sep-Nov), 6th November – 19th December (LD8:16Nov-Dec) or 19 December

– 29 January (LD8:16Dec-Jan). Before and after the short photoperiod treatment the groups were reared on continuous light. The growth of the fish was monitored over a period of 11 months. At the termination of the experiment in September 2009, the body mass of the three groups receiving a short day period (LD8:16 Sep-Nov, LD8:16 Nov-Dec and LD8:16 Dec-Jan) was significantly higher (13.9%, 12.9% and 10.7% respectively) than that of the group reared on continuous light (LD24:0). The mean final weight of the three groups receiving the short photoperiod was not significantly different at the end of the trial. Therefore, the time of the year when the short photoperiod was applied did not appear to be of importance for the growth enhancement. The maturation rate was not significantly different at the end of the trial. The improved growth was mainly a result of a higher feed intake and improved feed conversion efficiency for the period following transfer of the charr from a short photoperiod to the continuous light. Application of such a winter photoperiod during the juvenile phase can, therefore, be used as a tool to increase the growth rate of farmed Arctic charr.

Paper IV. Effects of short-day treatment and salinity on growth in farmed Arctic charr (*Salvelinus alpinus* L.).

The effects of a short-day photoperiod, applied during the juvenile phase of Arctic charr *Salvelinus alpinus* in freshwater on smoltification and on the long term growth and maturity following transfer to dilute seawater (constant salinity of either 17 and 27 or increasing salinity in steps from 17-27) were investigated. Prior to salinity transfer, the juveniles were either reared at continuous light (C groups) or reared for six weeks on a short day (LD 8:16, S groups). Increased salinity had negative effect on growth, with female fish reared at 17 salinity weighing 19% and 27% more than the salinity-step group (17-27) and the 27 salinity group, respectively. The stepwise acclimation to salinity had limited advantage in terms of growth rate. Short photoperiod for six weeks (November to January) improved growth, but not seawater tolerance. Gill Na^+,K^+-ATPase activity and plasma Na^+ levels changed with time and had mismatching levels during the nine-month rearing in brackish water. Overall, there appear to be interactive effects on maturation from applying short-day photoperiod followed by rearing at higher salinities. Thus, a trend was seen for higher gonadosomatic index in the S groups reared at higher salinities. Plasma leptin varied with time and higher levels were concomitant with periods with high growth rate. It is concluded that changes in growth rates observed in the current study are mainly related to rearing salinity with higher growth rates at lower salinities. Short day photoperiod has some growth inducing effects but did not improve seawater tolerance. Farmers of Arctic charr using dilute seawater for land-based rearing should keep salinity at moderate and stable levels according to these results to obtain best growth.

Contents

1. Background

In 2012 the total human population on earth was over 7 billion and by every day the number rises by more than 200 thousand people. On a global scale aquaculture has been the fastest growing animal food growing sector (FAO, 2010). Aquaculture therefore plays an important role in meeting the needs of the growing world population. On a local scale aquaculture is frequently situated in rural areas providing jobs and resources to areas were job availability is scarce and income low. Aquaculture involves the farming of aquatic organisms such as fish, molluscs, crustaceans and aquatic plants. The diversification of the species farmed is high and the methods are also varied from *extensive farming* methods with low economic and technological level to *intensive farming* with high costs and advanced technology. Farming of Arctic charr (*Salvelinus alpinus* L.) is categorized as *intensive*. The bulk of production takes place in land-based farms where most environmental factors are controlled and the fish is fed manufactured feed pellets. This is a high cost production and the product is marketed and sold at the high-end market to consumers making demands for high quality product. The cost intensive farming methods call for constant strive to lower costs and maximize the output of the production without compromising the product quality. The overall aim of the study was to investigate the effect of four important environmental factors; temperature, photoperiod, salinity and feeding regimes and their effects on important farming traits such as growth, maturation and feed conversion efficiency.

1.1 Biology of Arctic charr

Arctic charr is a salmonid species of the genus *Salvelinus*. The Arctic charr has a circumpolar distribution in the Holarctic region (Maitland *et al.* 2007). It also has the northernmost distribution of all freshwater and anadromous fish species and it has been estimated that over 50.000 populations exist world-wide with most diversification in the Scandinavian countries (Klemetsen *et al*., 2003). The Arctic charr is extremely polymorphic in terms of ecology and phenotypic expression with large diversification in life history traits between and within different strains. These differences appear both in regard to specialisation to feed types (Jonsson and Jonsson, 2001) and size structured populations based on different competitive abilities (Persson *et al*., 2003). A good example for this diversification is found in Lake Þingvallavatn in Iceland that supports four trophic morphs of Arctic charr; two benthic morphs (small and large benthivorous charr) one which exploits pelagic waters (planktivorous charr) and the fourth piscivorous charr is found in both habitats (Snorrason *et al*., 1994).

Arctic charr is found in nature both as anadromous and as freshwater resident strains. Anadromous strains of Arctic charr typically stay in saline water during the summer months where they grow rapidly and attain significant adiposity in relatively short time (Rikardsen *et al*,. 2000). They then spend the rest of the year in fresh water either spawning in the late fall or living through fall and winter in the relatively food scarce and cold fresh water environment.

1.2 Farming of Arctic charr

Development of intensive farming methods of Arctic charr started in the 1980´s. Since then production of Arctic charr has increased slowly but steadily to reach about 6.000 tons. Iceland has been leading producer of Arctic charr with annual production of about 3.500 ton in 2012. Most of the charr produced in Iceland is exported fresh to either European or North American markets. Other countries with substantial production are Canada, Sweden and Norway, but most of the fish is sold in domestic markets.

The Arctic charr has several features that make it a prominent farming species. It has relatively good growth rates at low temperatures (Le Francois *et al*., 2002), it can be reared at high densities (Jørgensen *et al*., 1993) and has good flesh quality. The reason why the world production has remained moderately low is likely related to factors such as limited temperature tolerance, limited seawater tolerance, variable growth and limited markets for the products. The effort in research, development and marketing during the last 30 years has reduced these problems and secured the slow but steady growth in farming of Arctic charr.

In Iceland and Sweden selective breeding, based on the salmon model (Gjedrem, 1995) a combined family and individual selection, has been on-going since the mid 1980's. In both countries the breeding programs started by testing and selection of strains of Arctic charr with emphasis on fast growth and late maturation. After about seven generations substantial progress has been made to enhance growth and reduce early maturation in the farmed strains. In Sweden the production time of a given group has been shortened from 3.5 to 1.5 years and maturation reduced from over 70 % to less than 5 % for fish smaller than 1 kg (Eriksson *et al.*, 2010). In Iceland the progress from selective breeding is reported to be about 3-4 % weight gain per year and incidence of early maturation has dropped from about 20-30 % to less than 5 % for 1 kg Arctic charr (Svavarsson, 2007).

The farming procedure of Arctic charr is in many ways similar to that for Atlantic salmon with the exception that the on-growing phase of Arctic charr does not take place in full strength seawater due to limited seawater tolerance. In Iceland the bulk of the Arctic charr production during on-growing takes place in coastal land-based farms with rich access to brackish water with stable rearing temperatures. The rearing of juveniles (up to 50-70 g) takes place in land-based freshwater farms followed by on-growing phase in either land-based farms, or net-pens offering varying degrees of possibilities to control environmental factors such as rearing temperature, salinity and photoperiod. In Sweden the farming of Arctic charr takes mainly place in net pens located in nutritionally poor freshwater reservoirs, formed by damning rivers for hydropower production (Eriksson *et al.*, 2010). In these there are limited possibilities to control the environmental factors but the productions costs are lower compared to land-based farms.

1.3 Environmental effects and farming traits

To secure good and even growth rates of farmed species it is fundamental to achieve acceptable productivity. Growth rate of fish is a complex phenomenon and is often the result of interaction between several internal and external factors. In the wild there is seasonality in feeding and growth both in landlocked and anadromous strains with the majority of growth within a few weeks period in the summer (Jobling *et a*l., 1998). The observed growth spurt in wild stocks is mainly dependent on food availability even though frequently during the same period (summer) there are rising temperatures and extended photoperiods. Depending on the local conditions, fish farmers often have the possibility to control or regulate one or more environmental factors and feed can be supplied in excess. Experiments have indicated that seasonal cycles persist for Arctic charr in feed intake and growth rate even when they are held at either constant rearing temperature (Damsgård *et al.*, 1999; Tveiten *et al.*, 1996) or constant temperature and photoperiod (Pálsson *et al.*, 1992; Sæther *et al.*, 1996). These observed variations can partly be explained by maturation processes (Damsgård *et al.*, 1999; Sæther *et al.*, 1996; Tveiten *et al.*, 1996). Immature Arctic charr displayed delayed and less rapid reduction in feeding and growth and Tveiten *et al.*, (1996) report that this was observed once a threshold condition of 1.4-1.5 was attained. They suggested that the fish become anorexic once energy reserves have been replenished for overwintering and in the case of maturing fish to complete gonadal growth during the maturation process.

Farms applying recirculation technology have the possibility to regulate most of the environmental factors affecting growth and feeding. Rearing temperature can often be regulated in land-based farms with access to geothermal heat or hot effluent water from industrial plants. Photoperiod and lighting can be controlled in indoor facilities and with additional light over tanks in outdoor facilities. Sound knowledge about how different environmental factors affect important farming traits is therefore critical so they can be manipulated to secure high productivity and competitiveness for farming of a given species.

Under natural conditions Arctic charr experiences large changes in environmental factors such as temperature and photoperiod throughout the year. Photoperiod is known to affect various important farming traits such as the growth rate (Mortensen and Damsgård, 1993) and the timing of maturation (Frantzen et al., 2004) of Arctic charr. There is a marked difference in the feeding and growth related to day length and the general trend is that feeding is highest during spring and early summer when days become longer (Tveiten et al., 1996; Johnston, 2002, Paper III). Arctic charr also show seasonal differences in sweater tolerance (Finstad *et al*,. 1989; Arnesen *et al.*, 1993b) and this has limited the farming of Arctic charr to either freshwater or to farming sites with access to brackish water.

Brett (1979) defined the scope of growth (G_{scope}) giving the maximum amount of energy from food available for growth, maintenance and other activities as the difference between the maximum ration (R_{max}) and the maintenance ration (R_{maint}). As the size of fish increases, both the R_{max} and the R_{maint} decline. However since the R_{max} declines at a higher rate compared to R_{maint} the surplus energy available for growth (G_{scope}) reduces with increasing fish size. In the farming situation it is therefore especially important to take advantage of this relatively higher G_{scope} during the first feeding and juvenile stage compared to the on-growing. Environmental factors such as rearing temperature or photoperiod are also more manageable during the earlier stages while the fish is being farmed in indoor facilities, biomass is lower and kept in smaller rearing units. Changes in abiotic factors such as rearing temperature, photoperiod, salinity and feeding regimes will affect the rates of food consumption and the metabolism and therefore affect the growth rate of the fish. In the project we designed four studies, each dealing with a major abiotic factor and its influence on important farming traits of Arctic charr i.e. rearing temperature, photoperiod, salinity and feeding regimes.

1.3.1 Rearing temperature

Fish are ectothermic and temperature has great influence on growth rate, feeding and maturation processes. While metabolic rates increase with increasing rearing temperature the food intake for given fish size typically increases with increasing temperature to reach a peak, falling rapidly beyond that. The difference between food intake and metabolism indicates the resources available for growth. Growth increases with increasing temperature to reach a plateau and then declines and the temperature at which growth in optimized is called optimum temperature for growth. The optimal temperature for growth is however a few degrees lower than the optimum temperature for maximum feed ingestion (Jobling, 1994). Feed conversion efficiency is therefore improved if the rearing temperature is lowered slightly below the optimum temperature for growth. Feed costs are amongst the single highest cost factors in aquaculture. For the fish producer it is therefore not sufficient to know at which point optimal growth is achieved but he also need to know what conditions give the most efficient feed utilization. Growth-rations curves reveal an estimate for the growth rates and feed ration levels leading to greatest feed utilization for a given rearing temperature. It should be considered that rates of feeding that result in greatest feed utilizations are lower than those resulting in maximum growth and the amounts of ingested food resulting in most efficient feed utilizations vary with rearing temperatures (Jobling, 1994).

Larsson *et al.* (2005) reported lower and upper temperature limits for growth of seven Arctic charr populations to vary between 1.7 to 5.3 and 20.8 to 23.2 °C whereas maximum growth rate was observed in the range from 14.4 to 17.2 °C. In the same study it was also demonstrated that there was no geographical or climatic trend in growth performance among the seven populations tested. Arctic charr from large piscivore fish showed higher growth rates than populations feeding on zoobenthos or zooplankton in the wild. This concurs with the observed growth potential of different strains to be used for selective breeding in Sweden (Eriksson *et al.*, 2010) and Iceland (Eyþórsdóttir *et al.*, 1993) with piscivore strains having the greatest growth potential. Larsson and Berglund (1998) and Larsson (2005) reported that growth efficiency of

Arctic charr is maximised at temperatures lower than 10 °C. Studies on preference temperature also indicate that Arctic charr in nature prefer optimum temperatures associated with improved feeding efficiency rather than optimal growth (Larsson 2005; Larsson *et al.*, 2005; Mortensen *et al.*, 2007).

Table I. Optimal rearing temperature for growth for different ontogenic groups and size classes of Arctic charr.

Size of Arctic charr	**Optimal temperature for growth**	**Reference**
Broodstock	4-6 °C	Jobling *et al.* 2010
Eggs	4-6 °C	Jobling *et al.* 2010
Yolk sac -first feeding stage	6-8 °C	Jobling *et al.* 2010
Juveniles		
< 50 g	>15 °C	Siikavuopio *et al.* (2013)
20 – 100 g	12-18 °C	Jobling *et al.* 2010:
	14-16 °C	Larsson *et al.* 2005;Thyrel et al. 1999
50-200 g	15 °C	Siikavuopio *et al* (2013)
100 – 500 g	8-12 °C 15 °C	Pétursdóttir and Eyþórsdóttir, 1993 Paper I
>500 g	7-12 °C 8-12 °C	Paper I Pétursdóttir and Eyþórsdóttir, 1993

A common finding in studies on fish examining the relationship of fish size and rearing temperatures on growth is that growth rates are lower and optimum temperature for growth ($T_{opt}G$) shifts to lower temperatures as fish increase in size (Aune *et al.*, 1997; Björnsson and Tryggvadóttir, 1996; Hallaråker *et al.*, 1995; Imsland *et al*., 1996; Imsland *et al*., 2001a; Imsland *et al*., 2001b; Jonassen *et al*., 1999). Indications for ontogenic differences in thermal optima from egg to juvenile phase have been reported for Arctic charr (Jobling *et al*., 1993; Siikavuopio *et al*., 2013; see also table I). Pétursdóttir and Eyþórsdóttir (1993) revealed that 200-1000 g 1+ Arctic charr grew best at temperatures in the range 8-12 °C and in another experiment testing growth of Arctic charr of three size classes (60, 350 and 960 g) some evidence was established for lower optimal temperature for the larger fish (Pétursdóttir unpublished data). The findings of different temperature optima for different size classes together with the downward trend of the optimal temperature for growth with size can be summarized in so called "stepwise-temperature-hypothesis" ($T_{steps,}$ Imsland *et al*., 1996). In aquaculture some forms of stepwise temperature control is widely used to enhance fish growth and consequently improve overall production output by rearing the fish at near optimum temperatures for growth or feed conversion efficiency. Instead of using constant rearing temperatures, "temperature-steps" are applied where the fish is reared at optimum temperatures for a given size class. The possible benefits of temperature-step use compared to constant temperature has been verified experimentally in Atlantic halibut, *Hippoglossus hippoglossus* L., with 18% gain in three months (Aune *et al.,* 1997), turbot, *Scophthalmus maximus*, and Atlantic cod, *Gadus morhua*, with achieved growth gain of up to 20% (Imsland *et al*., 2007; Imsland *et al*., 2008). Such an approach of utilizing the changing temperature optima with size has been tested for Artic charr (Paper I) but with no long term production gain. Moving the Arctic charr down to lower rearing temperature consistently resulted in a negative effect on growth rate masking out any previous weight gain from rearing at higher temperatures.

1.3.2 Photoperiod

Photoperiod is one of the most important environmental factors entraining various physiological variables and is known to have profound effect on the feed intake

(Pálsson *et al.*, 1992; Sæther *et al.*, 1996; Tveiten *et al.*, 1996; Paper III), growth (Mortensen and Damsgård, 1993; Paper III) and maturation in Arctic charr (Frantzen *et al.*, 2004). Species living at high latitudes like Arctic charr experience large seasonal changes in environmental factors such as temperature and photoperiod with subsequent seasonal fluctuations in food intake and body condition (Bairlein and Gwinner, 1994; Loudon 1994). Seasonal changes in feed intake, growth and maturation are termed endogenous that appear even if the Arctic charr is held in constant environment but they are entrained by external factors like photoperiod. An important physiological factor behind these endogenous rhythms in feeding and growth may be the energy status of the Artic charr with reduced feeding once sufficient energy stores have been reached to overwinter in colder and feed depleted environments (Tveiten *et al.*, 1996). Development of maturation also affects the feed intake and growth with increasing feeding and growth during the early stages of maturation and reduced feeding during the later stages (Sæther *et al.*, 1996; Tveiten *et al.*, 1996). Most populations of Arctic charr are autumn spawners but the developmental process leading to maturation starts several months earlier (Tveiten *et al.*, 1998; Frantzen *et al.*, 2004; Rikardsen *et al.*, 2004). As the Arctic charr is a species living at higher latitudes, photoperiod is the main environmental signal synchronizing the maturation process. Photoperiod is therefore an important tool that can be used in farming of Arctic charr to manipulate the maturation time of broodstock or arrest or delay the maturation during on-growing. How and when the photoperiod is changed is of importance. Altering of the photoperiod during early phase of maturation is more likely to result in stronger synchronization of both ovulation and spermiation rather than alter the proportion of maturing Arctic charr (Frantzen *et al.,* 2004). However Duston *et al.* (2003) reported lower maturation ratio and increased proportion of high value fish (> 1 kg) for Arctic charr that was exposed to long photoperiod (LD18:6) for 42 days during winter followed by a short (LD8:16) or natural photoperiod compared with Arctic charr reared under constant long days.

As mentioned, photoperiod is one of the abiotic factors that can be regulated and controlled to some degree in aquaculture but little is known about the possibilities of improving productivity through photoperiod manipulation of stocks in farming of Arctic charr. In land-based farms, Arctic charr is most commonly reared under continuous light, both during the juvenile stage and the on-growing phase in outdoor tanks, by placing artificial light above the water surface of each tank. For salmonids it is well established that photoperiod can be used to either enhance or delay the time of maturation (Bromage *et al.,* 2001) and photoperiod is also used in commercial fish farming to postpone or reduce the ratio of maturing fish. Feeding behaviour is affected by photoperiod and the general trend is that increased or extended photoperiods lead to increased feeding and growth (Boeuf and Le Bail, 1999: Boeuf and Falcon, 2001). For fish that rely on visual feeding, longer days give the fish increased chance to find and capture prey. In nature the Arctic charr displays highest growth rate during spring and summer but this period also coincides with high availability of food sources and increasing water temperatures. Arctic charr held in controlled environment including continuous artificial light and stable water temperatures still display seasonal cycles in food intake and growth (Pálsson *et al.*, 1992; Sæther *et al.*, 1996; Tveiten *et al.*, 1996). In experiments where fish are reared at different photoperiods but given equal opportunity to access feed (fed for equal number of hours during the light phase) there are differences in growth. There is a marked difference in the feeding and growth of Arctic charr related to day length and the general trend is that feeding is highest during spring and early summer when days become longer (Tveiten *et al.*, 1996; Johnston, 2002). Mortensen and Damsgård (1993) reported that Arctic charr (4-50 g) reared at constant short or long days grew equally well but a group of fish reared for a period on a short photoperiod followed by long photoperiod showed a significant increase in growth. In a long term study Siikavuopio *et al.* (2009) reported a 25-30% higher growth rate of wild Arctic charr held under culture condition and exposed to intervals of short day length within a continuous light compared to a group reared at continuous light.

1.3.3 Seawater tolerance

Anadromous salmonids migrate between freshwater and seawater. *Salvelinus* species are typically less anadromous than their counterparts belonging to the *Salmo* species (Hoar, 1988). The general assumption is that anadromous strains of Arctic charr stay in the marine environment for a period of a few weeks during spring or summer and then return to fresh water. It has however been reported that an anadromous riverine strain of Arctic charr spent on average 40 days in estuary and 25 days in sea, during the winter months (Jensen and Rikardsen 2008; Jensen and Rikardsen 2012). It should also be kept in mind that there are differences in the osmoregulatory capacity between landlocked and anadromous strains of Arctic charr (Eliassen *et al.,* 1998) and between different anadromous strains (Jørgensen and Arnesen, 2002). When conducting research on seawater tolerance of Arctic charr the origin of the fish should therefore be considered. For the anadromous Arctic charr they typically grow rapidly during the marine phase and increase their adiposity before moving back to freshwater (Rikardsen *et al*., 2000). On return to freshwater the Arctic charr either spawn during the fall or overwinter in the cold and often food scarce environment where they enter a catabolic state until the next seawater entrance (next spring/summer).

While still in freshwater prior to migrating to seawater anadromous salmonids adapt to the habitat change by transformation referred to as smoltification involving various behavioural, morphological and biochemical changes (Wedemeyer *et al*., 1980). Development of smoltification is primarily initiated by environmental zeitgebers, photoperiod and temperature (Duston and Saunders, 1990; Björnsson *et al*., 1995; Stefansson *et al*., 2007). Increase in day length induces hypoosmoregulatory capacity of Arctic charr, reaching a peak in early summer (Finstad *et al*., 1989). The smoltification process in Arctic charr is little affected by rearing temperature (Bottengard and Jørgensen, 2008), possibly in part explained by reduced thermal sensitivity of the Na^+, K^+-ATPase pumps as an adaptation of organisms living in cold environment (Galarza-Munoz *et al*., 2011). In farming of Atlantic salmon the manipulation of photoperiod is frequently used to induce smoltification, involving a long day "summer" photoperiod interrupted with a "winter" period of short day length to produce out-of-season smolts (Björnsson and Bradley, 2007). For wild Arctic charr the transition between the freshwater and seawater can be an annual event in adult life (Halvorsen *et al.*, 1994) while for Atlantic salmon the smoltification is a once in lifetime event. Similarly the Arctic charr seem to reverse smoltification with a preparatory phase while still in seawater involving up regulation of the gills from actively secreting ions to a state of actively absorbing ions before entering fresh water (Bystriansky *et al.*, 2007).

The development of hyperosmoregulatory capacity is to some degree similar in Arctic charr as for Atlantic salmon (Halvorsen *et al.*, 1994). As for Atlantic salmon, the development of seawater tolerance for Arctic charr takes place while the fish are still in freshwater (Arnesen *et al.*, 1992; Staurnes *et al.*, 1992; Nilssen *et al.*, 1997). The transition from hyper-osmoregulation (ion absorption) to hypo-osmoregulation (ion excretion) requires changes in the osmoregulatory mechanism to maintain homeostasis. In freshwater the fish has to respond to influx of water and losses of ions by producing high amounts of diluted urine and by uptake of ions in gill tissue and partly in intestine. In seawater water leaks out and ions flow into the cells due to gradients. The fish responds to this by drinking seawater and actively taking up ions and water in the intestine and by extrusion of excessive Na^+ and Cl^- over gill epithelium while divalent ions are excreted in the kidney. The gills are the major site for excretion of ions to maintain homeostasis, and the hypo-osmoregulatory capacity is linked to differentiation of gill chloride cells that are rich in ion transport proteins (Evans *et al.*, 2005). Improved seawater tolerance is linked to increase in Na^+, K^+-ATPase activity (NKA) in the gill tissue (McCormick *et al.*, 1996; Nilsen *et al.*, 2003; Stefansson *et al.*, 2012) and common indicators to evaluate the smolt quality in Atlantic salmon involve assessment of increase in branchial NKA and measurement of monovalent plasma ions following 24-72 hours seawater challenge tests (Björnsson and Bradley, 2007). These tools in addition to assessment of physical and behavioural changes in the smolting juveniles are used to time the appropriate window for seawater transfer, avoiding or reducing problems such as mortalities and growth reductions (stunting).

Salinity of the rearing water has an effect on the growth and food intake of various fish species (Boeuf and Payan 2001; Imsland *et al*., 2001a). For Arctic charr (200-300 g) Mortensen and Lund (1991) reported highest growth at 20 ‰ for fish reared at salinities between 17-32 ‰. Due to the limited and seasonal seawater tolerance of Arctic charr (Arnesen *et al*.,1993a,b; Finstad *et al*., 1989) the bulk of production of farmed fish (on growing) takes place in either freshwater or brackish water. The Arctic charr tolerates full strength seawater (33-35 ppt.) during the approximately 2 month period following seaward migration period in mid-summer but with reduced photoperiod in the late summer/fall the Arctic charr undergo desmoltification (Finstad *et al*., 1989). The Arctic charr seem to cope well at any time of the year in brackish water < 20 ppt but with reduced growth and feed conversion efficiency with increased salinities (Arnesen *et al*., 1994; Finstad *et al*., 1989; Paper IV). Brackish water in the range from 15-28 ppt is successfully used during the on-growing period of Arctic charr in Iceland.

1.3.4 Restricted feeding

Feed costs make up one the highest single factors in production of salmonids as for many other species. It is therefore of high importance for the fish farmer to ensure that largest amounts of the feed is consumed and that the consumed feed is utilized efficiently for somatic growth. There are various factors that can affect growth rate, feed intake and feed utilization efficiency in aquaculture and three important factors have been addressed earlier; rearing temperature, photoperiod and salinity. Feeding techniques, i.e. spread of feed in time and space, are also important in this respect. In nature the Arctic charr experience large seasonal fluctuations in environmental factors and food availability. Anadromous Arctic charr show rapid growth and can double their body weight and increase their body lipids during their stay in seawater in the summer (Jørgensen *et al*., 1997; Jobling *et al*., 1998). After migration back to freshwater they have to adapt to prolonged periods of fasting and have to rely on the body reserves acquired during the previous summer to survive until next growth period (Boivin and Power 1990; Jørgensen *et al*., 1997). Farmed Arctic charr held at stable rearing temperature and photoperiod and fed in excess still show seasonal changes in appetite and growth (Pálsson *et al*., 1992; Sæther *et al*., 1996; Tveiten *et al*., 1996) indicating an endogenous growth rhythm. Farmers of Arctic charr have been reporting uneven growth rate during on-growing period (Strategy report; the Icelandic Aquaculture Association, 2009). In the farming situation it should therefore be of interest to use controlled feeding schedules to shorten the periods with little or no growth and extend periods with high growth rates leading to overall higher productivity and slaughter yield. Different feeding regimes can be used as a tool in aquaculture to control growth rate, feed intake, feed utilization efficiency, maturation, and slaughter quality.

The term compensatory growth (CG) is use to describe a phase of accelerated growth in a period where favourable conditions have been restored after a period of growth depression (Ali *et al*., 2003). The CG is frequently characterized by either full or partial compensation. Full compensation involves that fish which have previously experienced growth depression attain the same size at the same age as control group when favourable conditions are restored whereas for partial compensation the growth deprived fish show relatively rapid growth rates but do not reach the same size as the control fish (Ali *et al*., 2003). The length in time or the severity of the feed restriction has an effect on the outcome of trials and whether the fish can partly or fully compensate for the weight loss when reverted to full feeding (Jobling *et al*., 1993; Jobling and Koskela, 1996). Factors like rearing temperature interplay in determining the effect from different restricted feeding regimes since higher rearing temperatures lead to higher metabolic rates making the window narrower for applying restricted feeding if the aim is full compensation after feeding to satiation is restored. Studies have shown that compensatory growth is partly a result of hyperphagia (Ali *et al*., 2003; Paper II), a state where the feed intake of the previously feed deprived or restricted group is significantly higher than for a group that has been fed ad libitum.

Hyperphagia response was reported for Atlantic salmon when feeding was restored after a period of feed restriction (Bull *et al*., 1997). Arctic charr in hyperphagia state consumed 1.5 – 2.0 % body mass day^{-1} while controls had feed intake of 1.0-1.4 % of body mass day^{-1} (Miglavs and Jobling 1989).

In aquaculture the aim should be to develop feeding routines with sufficient food deprivation or restrictions to evoke compensatory growth followed by a long enough period with enough feed availability to allow for a full compensatory growth compared with continuously fed fish. Sea bream (*Sparus aurata*) juveniles (initial weights 6.4 g) subjected to different levels of restricted feeding or feed deprivation in a 48 day trial were unable to catch up with control group that was fed continuously to satiation (Eroldogan *et al*., 2008) and similar results were reported by Ali and Jauncey (2004). Groups of turbot showed full compensatory growth when fed 0.35 % and 0.38 % compared to control fed 1.0 % of body weight per day for 41 day followed by full ration for 34 days (Sæther and Jobling, 1999). Compensatory growth can partly be explained by improved feed utilization. Working with single individual fish in tanks Miglavs and Jobling (1989) found improved feed conversion efficiency for Arctic charr when returned to normal feeding after a period with restricted feeding and similar response was reported for Atlantic cod by Jobling *et al*. (1994). Hansen *et al*. (2012) reported that feed cost could be drastically reduced for juvenile Atlantic cod fed periodically restricted feed rations compared continuously fed fish without compromising biomass growth. Quinton and Blake (1990) reported improved feed conversion efficiency for rainbow trout undergoing compensatory after 3 weeks of restricted feeding. Boujard *et al*. (2000) reported that compensatory growth in rainbow trout was caused by improved growth efficiency but not higher feed intake. In contrast Speare and Arsenault (1997) found no differences in growth efficiency between groups of rainbow trout undergoing compensatory growth compared with control group in a 7 week trial.

Applying periods of restricted feeding in farming Arctic charr could also be of interest regarding the relationship between adiposity, feed intake and maturation. As already mentioned farmers of Arctic charr frequently complain about uneven growth under farming conditions. Tveiten *et al.* (1998) reported that maturing Arctic charr reduced feeding once a “threshold condition” in the range of 1.4-1.5 was attained suggesting that fish become anorexic once sufficient energy reserves were obtained for overwintering and or maturation. Studies have indicated that there is a lipostatic regulation of feed intake for various salmonids species such as Atlantic salmon (Johansen et al., 2001; 2002; 2003), chinook salmon (Shearer *et al*., 1997) and for Arctic charr (Tveiten *et al*., 1998; Frøiland *et al*., 2012) although a comprehensive understanding of the endocrine control of lipid homeostasis is still lacking (Leaver et al., 2008). The peptide hormone leptin is produced and secreted from adipose tissue of mammals and appears to function as an adiposity signal in mammals, being anorexigenic, with plasma leptin levels decreasing with loss of fat tissue e.g. due to food restriction (Maffei *et al*., 1995). Data on fish indicate a similar anorexigenic function of leptin (Murashita et al 2011), but on the other hand, leptin appears to be expressed mostly in liver of salmonids fish and its plasma levels increase rather than decrease during periods of fasting or food restriction (Frøiland *et al*., 2012; Kling *et al*., 2009; Trombley *et al*., 2012). Fuentes *et al.* (2012) suggested that for fine flounder (*Paralichthys adspersus*) plasma leptin levels are linked to nutritional status, controlling appetite and limiting physical activity in periods of natural food shortage. In Arctic charr, leptin seems to be involved in the long-term regulation of energy homeostasis, but does not function as an adiposity signal (Frøiland *et al*., 2010; 2012). Restricted feeding reduces growth and adiposity (Einen *et al*., 1999; Shearer *et al*., 2006) but if applied for a short time during the window of "critical decision point" for maturation it can lead to delayed maturation with little effects on the final weight due to compensatory growth during the following full feeding period (Taranger *et al*., 2010). It could therefore be hypothesized that it is possible to reduce the observed growth fluctuations in farming of Arctic charr by involvement of restricted feeding routines given that the fish can reach full growth compensation in the periods with full feeding.

2. Aims of the study

Farming of Arctic charr takes mainly place in land-based facilities applying intensive rearing methods. The cost of such production is high both due to building and running costs. It is possible to regulate important environmental factors, depending on local conditions at each site, to improve productivity and well-being of the fish. Detailed knowledge about how these different environmental factors affect important farming traits are therefore important. Such information can be used by current farmers to make the most of their farms and aid future farmers in choosing good farming sites and optimize their farming routines. The following four themes are studied with the overall purpose to develop a basis for development of a more cost effective rearing strategies for land-based farming of Arctic charr.

- Effects of rearing temperatures regimes during juvenile phase on long term growth, feeding and maturity. If environmental manipulations such as heating of water are applied early in the rearing phase when biomass is relatively small, a substantial economic return could possibly be achieved from such investments by allowing maximum growth capacities. However, a prerequisite for economic relevance implies that the growth advantage achieved during the juvenile phase can be maintained onto the on-growing phase. We investigate this possibility.

- Effect of restricted feeding for growth, feeding efficiency and maturation in Arctic charr. Can periodical restricted feeding be used as a tool for improving productivity i.e. attain similar growth but use less resources in terms of feed costs? In addition explore possible benefits in terms of reduced maturation effects.

- Long term effects of a short term photoperiod manipulation during juvenile phase for important farming traits. Can application of a 6 week short photoperiod in early winter within an otherwise continuous light, induce long term growth and reduce maturation?

- Effects of photoperiod treatment and different salinity regimes on growth rate of Arctic charr. Explore the potential benefits from applying a short day photoperiod within an otherwise continuous light to induce smoltification prior to transfer to brackish water and long term effects on growth and maturation. Does a step vice increase in salinity regime improve growth during on-growing period?

3. Methods and research parameters

3.1 Fish stock and rearing conditions

The fish used in the experiments came from the Icelandic breeding program for Arctic charr at Hólar University College (Iceland). For every experiment (Papers I – IV) a randomly selected subsample from one year class was used. Common pre-experimental rearing conditions at Hólar breeding station a near constant rearing temperature of 6-8 °C and continuous light.

All the experimental work to place in Verið research station at Sauðárkrókur, North Iceland, where the experiment took place in a three year period from September 2007 to December 2010. The rearing tanks used during the experiments (Papers I, II and III) were green square fiber plastic tanks with rounded corners and active rearing volume of 700 L. For experiments in Paper IV the freshwater phase tanks were green square fibre plastic tanks with rounded corners and active rearing volume of 1.500 L and the seawater phase was performed in four green square fibre plastic tanks with rounded corners and active rearing volume of 7.000 L. All the experimental work took place in indoor facilities with artificial light.

All tanks for the experiments were supplied with aerated and oxygenated freshwater originating from the local ground well. The seawater supply (Paper IV) was either aerated and oxygenated seawater (water inlet at a depth of about 25 m), or seawater mixed with the local freshwater source. The water flowed through system with a partial reuse with a 100% exchange rate of water every 4 hours and 25 minutes. Oxygen saturation and temperature were registered daily in the effluent water.

3.2 Experimental setup and sampling

In the experiments the effects rearing temperature, photoperiod, feeding regime and salinity on important farming traits of Arctic charr. In the farming situation all these factors and more are constantly interplaying to varying degree affecting the outcome of experiments. To strengthen the possibilities to analyse and evaluate the effects from different environmental factors focus was on testing the effects from single environmental factor while striving to keep conditions in other ways constant between different environmental factors. All treatments were also run in replicates to reduce the effects from possible tank effects.

The fish in the experiments were weighed and length measured at 4 - 10 week intervals, depending on the duration of the study and experimental design. In general, two days prior to each weighing the fish were not fed. For all experimental groups the Arctic charr was individually tagged intraperitoneally with Trovan® Passive Transponder tags. The Arctic charr were weighed to the nearest 0.1 g and length measured to the nearest 0.1 cm. Prior to the measurements the fish were anaesthetized. At termination of the experiments, the individually tagged fish were slaughtered, sex was assessed and gonad of each fish weighed to calculate the individual gonadosomatic index (GSI).

4. Results and discussion

4.1 Effects on growth and maturation

The farmed strain of Arctic charr used for the experiments in the current study has been selectively bred for over twenty years with an emphasis on improving growth rate and reduce early maturation. Incidence of early maturation has dropped from being in the range of about 20-30 % to less than 5 % for a 1 kg Arctic charr but in the same time the growth rate has improved substantially (Svavarsson, 2007). Producers of Arctic charr have different targets regarding slaughter size and as the farmer aims for larger fish or the rearing time is extended the greater the risk for negative effects from sexually maturation. Development of maturation affects the feed intake and growth with increasing feeding and growth during the early stages of maturation and reduced feeding during the later stages (Sæther *et al.*, 1996; Tveiten *et al.*, 1996). Even though early maturation has been significantly reduced with selective breeding in the farmed Arctic charr population used in the current study, reducing the negative effects on the productivity and the product quality it is important to take account of maturation when studying growth traits.

In the study short and long term effects of four environmental factors, temperature, photoperiod, salinity and feeding regimes on growth rate of farmed Arctic charr was investigated. The overall findings show how each of these factors can be manipulated to improve growth rate and productivity. It was also demonstrated that rearing temperature, feeding rations and salinity can affect the incidence of maturation of the Arctic charr (Papers I, II and IV).

Manipulation of rearing temperature was a highly effective tool to improve growth of juvenile Arctic charr (Paper I). After 6 month rearing at elevated temperatures (October–April), Arctic charr reared at a constant temperature of 15 °C had mean weights that were 44 % and 78 % higher than fish reared at constant temperatures of

12 and 9 C, respectively. These results are in line with several other studies showing that optimal rearing temperature for growth of juvenile Artic charr is in the range from 14 to 15 C (Swift 1964; Jobling 1983; Lyytikainen *et al*., 1997; Larsson and Berglund 1998, 2005; Larsson *et al*., 2005). The observed differences in the growth rate between the three temperatures (9, 12 and 15 °C) decreased as the fish grew larger (Paper 1). Attempts to transfer the Arctic charr down in rearing temperature as an effort to follow the drop in temperature optima for growth resulted in a consistently negative effects on the growth rate. Previously it has been demonstrated that substantial growth enhancement can be achieved by following the drop in optimum temperature for species like Atlantic halibut (Aune *et al.,* 1997) and turbot (Imsland *et al*., 2007; 2008). High growth rates as observed at the higher temperature groups in Paper I with subsequent high condition factor and induction of early maturation has been reported for several salmonids species (Rowe and Thorpe, 1990; Simpson, 1992; Berglund, 1995). In Paper I it was concluded that for successful long term rearing of Arctic charr it is advantageous to rear the Arctic charr at moderate rearing temperatures during juvenile phase to reduce the negative effects from early maturation during the on growing period.

Application of periodic restricted feed rations (50 %) in Paper II led to full growth compensation (CG) of the farmed Arctic charr. These results are in line with previous experiments performed on Atlantic cod (Jobling *et al*., 1994) and turbot (Sæther and Jobling, 1999) reporting full growth recovery after restricted feeding. In contrast, partial CG as a result of starvation was previously reported for the Arctic charr (Jobling *et al*., 1993), as well as in other species such as Alaska yellowfin sole, *Pleuronectes asper* (Paul *et al*., 1995), Atlantic halibut (Foss *et al*., 2009 and Heide *et al*., 2006), black rockfish, *Sebastes schlegeli* (Oh *et al*., 2008) and Atlantic salmon, (Imsland *et al*., 2011; Stefansson *et al*., 2009). An important factor affecting the outcome in trials with restricted feeding or starvation periods is the length in time or the severity of the feed restriction and if the fish can partly or fully compensate for the weight loss when reverted to full feeding (Jobling *et al*., 1993; Jobling and Koskela, 1996). The contrast between current findings and those of Jobling *et al.* (1993)

working with Arctic charr is most likely related to different experimental set-up, as the Arctic charr were starved for different periods of time in the experiment of Jobling *et al.* (1993), whereas feed was only periodically restricted in the current study (Paper II). Periodical feed restriction regimes proved to be effective in reducing the risk of high incidence of maturation (Paper II) with lower mean gonadosomatic index (GSI) and plasma T levels during the final stages of maturation in the feed restricted group. Similar results have been presented for Atlantic salmon (Thorpe *et al.*, 1990), Chinook salmon, *Oncorhynchus tshawytscha* (Shearer *et al.*, 2006) and Atlantic halibut (Foss *et al.*, 2009). The current results are in contrast to those of Jobling *et al.* (1993) who reared Arctic charr at different intervals of either food deprivation or full ration and found no effect on maturation ratio. In general, fish undergoing compensatory growth may utilize energy and nutrients that otherwise would be available for reproduction. Ali *et al.* (2003) noted that food restriction resulted in a subsequent lower rate of maturation despite a compensatory restoration of lipid levels or body mass, which is in line with current findings in Paper II.

The application of a six week short photoperiod within other ways continuous photoperiod improved long term growth rate of Arctic charr reared in freshwater (Paper III). The groups receiving the short day signal weighed 10.7–13.9 % more than the group reared on continuous light. This is in agreement with the previous findings that increased or extended photoperiods lead to enhanced growth in fish (Boeuf and Le Bail, 1999: Boeuf and Falcon, 2001). These results are also in line with the findings of (Mortensen and Damsgård, 1993 and Siikavuopio et al., 2009) that reported a similar weight increase for Arctic charr that reported increased growth after subsequently 6 and 8 weeks rearing on a short day length and then returned to continuous light. The application of a six week short day period did not have any effects on sexual maturation compared to Arctic charr kept at continuous light (Paper III). The short day photoperiod groups had improved growth compared to the group on constant continuous light while there were no differences in GSI or testosterone values between the different groups. A sub group in paper IV received a similar short day period and was before and after reared at continuous light (S group) with the aim to induce smoltification. For the S group (short day) charr in Paper IV there was an earlier rise in GSI compared with the C group fish (continuous light). The different response with regard to maturation in Paper III and IV are most likely linked to the fact that the Arctic charr in Paper IV was reared during on-growing in brackish water and as already mentioned salinity had some inductive effects on maturation. The maturation processes in fish are known to be rhythmic in nature with photoperiod acting as a *zeitgeber* (Boeuf and Falcon, 2001). The short-day photoperiod for six weeks in Paper IV could therefore have acted as a synchronizing signal adding to the salinity effects on the maturation process for the Arctic charr in Paper IV.

Long term rearing at three different salinity regimes (Paper IV) revealed that growth rate was lower for the higher salinity groups. Final weights for female Arctic charr reared at 17 ‰ were 19 % and 27 % higher than for the females in the 17-27 ‰ and 27 ‰ groups, respectively complying with earlier reports about lower growth at elevated salinities (Duston *et al.*, 2007; Mortensen and Lund, 1991). The effort to induce or synchronize the smoltification by induced photoperiod (application of a six week short day signal during early winter followed by continuous light, Paper IV) did not result in measurable differences in neither gill NKA nor plasma Na^+ levels when compared with a control group kept at continuous light during the whole experimental period.. Overall higher long term growth in the group receiving six weeks short day treatment in early winter (Paper IV) is therefore more likely linked to higher feed intake and or improved feeding efficiency following return to continuous light like demonstrated in Paper III. The overall increase in NKA throughout the experimental period for the Arctic charr in Paper IV contrasts most previous reports of the limited and seasonal seawater tolerance of Arctic charr (Arnesen *et al.*,1993b; Finstad *et al.*, 1989).

The lower and delayed maturation at lower salinity regimes (Paper IV) despite higher growth rates in these groups are in contrast to results in Paper I and Paper II. Atse *et al.* (2002) reported that rearing Arctic charr in coastal seawater conditions during summer months were more favourable than rearing in freshwater with respect to reproductive success as females in seawater produced larger eggs with higher protein and lipid content and male milt had higher spermatozoa concentration. Long term rearing of Arctic charr at intermediate salinities like in Paper IV is likely to impose some osmoregulatory stress due to limited seawater tolerance of Arctic charr. Stress can have various effects on reproduction depending on when in the life cycle it is experienced and the severity and duration of the stressor (Schreck, 2010). The decision of salmonids whether or not to mature is taken several months prior to final maturation stage. Rainbow trout had advanced ovulation when exposed to mild stressor during late or the whole vitellogenic period (Schreck *et al.,* 2001). The rearing of Arctic charr at 27‰ in Paper IV may have had similar effects of mild stress leading to advanced maturation in this group.

4.2 Condition factor and feeding responses

Arctic charr held at constant environment with regard to rearing temperature and photoperiod has been reported to have endogenous rhythm with regard to feed intake and growth. Similarly farmers of Arctic charr held in land-based farms at stable rearing temperature have also reported growth fluctuations. Such observed growth variations have been partly related to maturation development (Damsgård *et al*., 1999; Sæther *et al*., 1996; Tveiten *et al*., 1996; Paper I and IV). The endogenous growth rhythms for immature fish have also been linked to the Arctic charr reaching a threshold condition factor of 1.4-1.5 (Tveiten *et al*., 1996). They suggested that the fish become anorexic once energy reserves have been replenished for overwintering and in the case of maturing fish to complete gonadal growth during the maturation process. In the experiments in Paper I the condition factor of the Arctic charr increased throughout the experiment and peaked in August. The repeated growth halt following the transfer of Arctic charr down in rearing temperature could be partly explained by this theory of sufficient energy reserves reached prior to the transfer down in rearing temperature as fish reared at higher temperatures had an overall higher CF throughout the study. In that way the transfer down in rearing temperature may have acted as a winter signal on the Arctic charr that had already replenished their energy reserves. The observed decline in CF following the transfer of the 15 C groups to lower temperatures is attributed to reduced weight gain in relation to length increment. Such a positive growth in length during periods with little or no muscle growth seems to be a general phenomenon in fish undergoing fluctuating (seasonal) changes in temperature or feed abundance (Nicieza and Metcalfe, 1997; Stefansson *et al.*, 2009). In Paper III the CF increased progressively in all the treatments during the first 10 months of the experiment to reach a value in the range from 1.5 – 1.6 with the exception of a slight drop in CF for the LD24:0 group in the period from 31st of March to 25th of May. From July to September there was a drop in condition factor but this can in most part be attributed to increased maturation in the same period. Feed intake, feed conversion efficiency and growth increased following transfer to continuous light after a period of short day (Paper III) in line with the results from other studies that have shown that increasing day length stimulates feed intake and growth of fish (Mason *et al.*, 1991, Boeuf and Le Bail, 1999 and Sonmez *et al.*, 2009). Salinity had significant effect on feeding rate (Paper IV) with more food consumed at lower salinity but no differences in the feed conversion efficiency in line with results by Duston *et al.* (2007). The adverse effect of salinity on feeding rate in Paper IV indicates that the higher salinity produced significant stress on the Arctic charr. In contrast to the findings in Paper IV, Arnesen *et al.* (1993a) reported that a transfer of 150 g Arctic charr in April from freshwater to salinity in the range from 10-35 did not affect growth or feed intake during a 30-day experimental period. In an another study Arctic charr (size 20-27 cm) were reared at three different salinities (0, 20 and 35) during winter (December-January, 59 days), higher growth and feed intake was observed in freshwater and 20 salinity than in fish reared at full salinity (Arnesen *et al.*, 1993b), but no such differences were detected when the experiment was repeated during summer (June-July). The observed differences in feeding rate in Paper IV are most likely related to insufficient osmoregulatory ability even though the observed blood plasma Na^+ levels and gill NKA activity did not indicate such impaired hypo-osmoregulatory capacity. In the feed trial reported in Paper II the restricted feed groups had both higher feed intake and feed conversion efficiency during the re-feeding periods compared to the full ration group. Hyperphagia has been shown to be one of the main mechanisms involved when fish undergo compensatory growth (Ali *et al.*, 2003). Hyperphagic response was reported for Atlantic salmon when feeding was restored after a period of feed restriction (Bull *et al.*, 1996). For Arctic charr in hyperphagic state consumed 1.5 – 2.0 % body mass day^{-1} while controls had feed intake of 1.0-1.4 % of body mass day^{-1} (Miglavs and Jobling, 1989).

5. Conclusions and future perspectives

The short and long term effects of four environmental factors, temperature, salinity, photoperiod and feeding regimes, on several important farming traits of Arctic charr were investigated. Intensive aquaculture is a high cost production so information regarding optimal rearing conditions resulting in high growth rate of the fish but in the same time maintaining good product quality is important to secure competitive production. The main objective in the thesis was to cast some light on how the farmers of Arctic charr can use and manipulate these environmental factors to improve the productivity of their farms.

Rearing temperature is a highly effective tool to improve growth rate of Arctic charr. (Paper I). Juvenile Arctic charr reared at a constant temperature of 15 °C had mean weights that were 44 % and 78 % higher than fish reared at constant temperatures of 12 and 9 C, respectively. Attempts to transfer the Arctic charr down in rearing temperature as an effort to follow the drop in temperature optima for growth resulted in a consistently negative effects on the growth rate. High growth rates as observed at the higher temperature groups (Paper I) with subsequent high condition factor lead to higher incidence of maturation. The results suggests that for production of fish > 1 kg, moderate or low temperatures (here 9 ºC) should be applied during the juvenile phase in order to reduce negative effects from maturation. Farmers with access to heat sources should accordingly choose more moderate rearing temperatures during juvenile stage especially if the fish is to be moved down in temperature regime during the on-growing.

Rearing of Arctic charr at periodic restricted feed rations (50 %) in Paper II led to full growth compensation (CG) of the farmed Arctic charr. Restricted feed groups had both higher feed intake and feed conversion efficiency during the re-feeding periods compared to the full ration group. Periodical feed restriction regimes had also lower maturation level compared to full ration groups. Periodical feed restriction could therefore be an effective tool to improve productivity in Arctic charr farming.

The application of a six week short photoperiod within other ways continuous photoperiod improved long term growth rate and reduced maturation of Arctic charr reared in freshwater (Paper III). Short day groups weighed 10.7–13.9 % more than the group reared on continuous light. Feed intake and feeding conversion efficiency increased following transfer to continuous light after a period of short day (Paper III) explaining the growth enhancement effect.

Growth rate of Arctic charr was higher for the lower salinity groups and maturation was lower and delayed (Paper IV). Final weights of female Arctic charr reared at 17 ‰ were 19 % and 27 % higher than for the females in the 17-27 ‰ and 27 ‰ groups, respectively. Effort to induce the smoltification by application of a six week short day signal during early winter followed by transfer to continuous light (Paper IV) failed as no differences in neither gill NKA nor plasma Na^+ levels were detected compared with a control group kept at continuous light. Higher long term growth in the group receiving short day treatment in early winter is therefore likely linked to higher feed intake and or improved feeding efficiency following return to continuous light like demonstrated in Paper III rather than improved seawater tolerance for that group. Overall there appear to be an interactive effect on maturation from applying short-day photoperiod and subsequent rearing at higher salinity as GSI is higher in the S groups reared at higher salinities. The high leptin levels are concomitant with periods of high growth rate, but plasma leptin did not correlate to CF. The changes in growth rates observed in the current study are probably interrelated result of the rearing environment (rearing salinity and photoperiod) and rate of sexual maturation.

Future studies could be directed at investigating how the great growth advantage of farmed juvenile Arctic charr reared at optimum temperature can be transferred successfully into the on-growing period without the observed "stunting" when transferred down in temperature regime (Paper I) and negative effects from induced early maturation. Studies of interest could include interacting effects of different environmental factors such as rearing temperature and photoperiod and their effects on growth and maturation as well as further investigations exploring the effects of feeding regimes on important farming traits. The theme in these studies should focus on how the great scope of growth during the juvenile phase can be extended into the on-growing period. Future studies should also focus on better understanding the development of smoltification of Arctic charr and how this can be manipulated to improve the performance of Arctic charr during on-growing in brackish- or seawater.

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