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Impact of environmental factors on the growth and maturation of farmed Arctic charr

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Abstract

Farming of Arctic charr mainly takes 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 is important to reduce production costs. This review shows how rearing temperature, photoperiod, salinity and feeding rate can affect farming traits such as growth rate, maturation and feed conversion efficiency of Arctic charr. High growth rate during juvenile phase when the fish are reared at higher temperatures can result in higher incidence of maturation during the on-growing period. Overall, more moderate rearing temperature regimes seem to result in better long-term growth rates. Photoperiod manipulation and feed ration can be used as tools to improve growth and reduce maturation. It is possible to rear Arctic charr successfully up to market size in salinities up to c. 27–28 ppt. However, extended rearing resulted in higher ratio of sexually mature fish at 29 than at 25 possibly linked to higher rearing temperatures in brackish water. 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.

Key words: Arctic charr, environmental manipulation, land-based farming, seawater tolerance, sustainable aquacultue, temperature.

Introduction

The Arctic charr has a circumpolar distribution in the Holarctic region (Maitland *et al.* 2007; Fig. 1). It has the northernmost distribution of all freshwater and anadromous fish species, and it is estimated that over 50 000 populations exist worldwide with most diversification in the Scandinavian countries (Klemetsen *et al.* 2003). The production of Arctic charr has increased slowly but steadily during the last 30 years to reach 6000–10 000 metric tons (MT, Sæther *et al.* 2013, 2016). Iceland is the leading producer of Arctic charr with an annual production of 4280 MT in 2017, and further expansion is planned. Most of the charr produced in Iceland is exported fresh to either the European or the North American markets. Other countries, such as Canada, Sweden and Norway, produce Arctic charr mainly for domestic markets.

Farming of Arctic charr

Arctic charr has several features that make it a good species for farming in colder climates. It has relatively good growth rate at low temperatures (Le François *et al.* 2002; Gunnarsson *et al.* 2011; Siikavuopio *et al.* 2013), it can be reared at high densities (Jobling *et al.* 1993a; Jørgensen *et al.* 1993) and flesh is perceived of high quality (Gines *et al.* 2004; Gunnarsson *et al.* 2012). Several aspects of the farming cycle and the attributes of Arctic charr as food are important to the species sustainability as farmed product. No antibiotics or other medical products are used in Arctic Charr farming in Iceland, and it has not been genetically modified (GMO) in any way. Consumer preference tests done by Matís in Iceland (https://issuu.com/matisohf/docs/iceland_arctic_charr) revealed that consumers rate the product as a high-quality product with excellent taste. The

Figure 1 Map showing the global distribution of Arctic charr inclusive of all nominate subspecies and closely related "species" considered to belong to this group in the narrow sense (http://www.grida.no/resources/7758).

carbon footprint of the farming is very low and around 20% lower than farming of Atlantic salmon in Norway (http://www.avs.is/media/skyrslur/2013_10_30_Iceland_Arctic_Charr_final.pdf). Arctic Charr is as rich in protein as cod but higher in unsaturated fatty acids. Vitamin D content of the fillet is high so 100 g of fillet would suffice to cover the recommended daily allowance for vitamin D. The polyunsaturated fatty acids of Arctic Charr are mostly long-chain omega-3 fatty acids. Arctic Charr is very low in sodium (http://www.matis.is/media/matis/utgafa/33-11-Naeringargildi-sjavarafurda.pdf).

Eriksson *et al.* (2010) reviewed the status of Arctic charr farming in Sweden and concluded that, in order to develop a significant charr industry in Sweden, Iceland and Norway, an effort would be required to develop the markets. Furthermore, factors such as limited tolerance to high temperatures, limited seawater tolerance and morphological variations between strains are all factors that limit the production of Arctic charr (Guðmundsdóttir 2017). Nonetheless, the slow but steady growth in the production of Arctic charr and the limited production volume has maintained market prices relatively constant. The market price of fresh Arctic charr has reached more than twice the market price of Atlantic salmon showing the high-quality and consumer preferences in markets where the species is well known (Thorarinsdottir 2013).

Breeding programmes for Arctic charr have been in place in Iceland and Sweden for the past 30 years (Svavarsson 2007; Eriksson *et al.* 2010). In both countries, fish were collected from several wild populations and compared before selecting the populations with the best production performance to start up the breeding programmes. 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). Through selective breeding and other measures, the productions costs of Arctic charr in Sweden have been reduced by at least 40% compared to the years before 2000 (Eiriksson *et al.* 2010). In Iceland, the progress of selective breeding is reported to be about 3–4% weight gain per year and the incidence of early maturation has dropped from about 20–30% to less than 5% for 1 kg Arctic charr (Svavarsson 2007).

Most of the Arctic charr production in Iceland is in coastal land-based farms with good access to brackish (15–25 ppt) water at stable temperatures. The juvenile production is all in freshwater, but in Iceland, the fish are commonly transferred to brackish water at a size of 50–150 g (Árnason *et al.* 2014; Gunnarsson *et al.* 2014). The land-based farms offer varying degrees of possibilities of controlling environmental factors such as rearing temperature, salinity and photoperiod. In Sweden, the majority of Arctic charr farms are in large, semi-oligotrophic freshwater lakes in the northern half of the country (Eriksson *et al.* 2010).

In Canada, the potential for selective breeding in several strains has been investigated (Ditlecadet *et al*. 2006, 2009; Blackie *et al.* 2011; Norman *et al.* 2011, 2014). Two natural populations from geographically distant locations and phylogenetic lineages have been the primary contributors to the Arctic charr being produced in the Canadian industry (Blackie *et al.* 2011): the Nauyuk Lake system in Nunavut and the Fraser River in Labrador. These strains were established from limited numbers of founders in the 1970s and 1980s (Lundrigan *et al.* 2005). Blackie *et al.* (2011) found that broodstocks from the Nauyuk Lake broodstocks showed greater differentiation from each other than did Fraser River broodstocks, which could be attributed to differences in the number of founders. The genetic variability in two farmed strains in Quebec (Buteux and Fraser) was investigated by Ditlecadet et al. (2006). They found that the two strains had significantly different allelic and genotypic distribution and that the genetic variability was lower in the Quebec domesticated strains than in wild populations of the same species. In a later study (Ditlecadet *et al.* 2009) with the same farmed strains, it was found that faster-growing families had significantly lower relatedness coefficients than slower-growing families. Recently, Nugent *et al.* (2017) presented a single nucleotide polymorphism (SNP) linkage map for Arctic charr based on genetic sequencing of 85 full-siblings, and their parents, from the Fraser strain.

Effects of environmental factors on growth of Arctic charr

Farms where fish are reared in net cages have limited possibilities of regulating environmental factors. However, in land–land-based farms there may be some room for adjustment of rearing environment depending on the local conditions (Thorarensen & Farrell 2011). Farms applying recirculation technology have, at least in principle, the possibility to regulate most of the environmental factors affecting growth and feeding although economic considerations may limit what is feasible, for example, in terms of temperature control. Similarly, farms with access to geothermal heat or hot effluent water from industrial plants may have possibilities of regulating rearing temperature. However, most farms have limited practical possibilities of regulating rearing conditions. Photoperiod and light can be controlled both in tanks and in net cages. Most Arctic charr farmers in Iceland have light over tanks, reportedly to increase feed intake during the night. This has, however, not been studied in any detail. Under these conditions, fish may mature during any season which suggests that the lights are strong enough to affect biological clocks, even in outdoor tanks. Sound knowledge of the impact of different environmental factors on important farming traits is therefore critical so they can be manipulated to secure high productivity and competitiveness for farming and matching the needs of a given species.

Consistent with its northerly distribution (Maitland *et al.* 2007), Arctic charr is also among the most cold-adapted freshwater and/or anadromous fish species in the world (Baroudy & Elliott 1994; Sinnatamby *et al.* 2015). Despite their association with cold environments, Arctic charr exhibit the widest natural distribution of all salmonids and some recent studies have indicated that different populations of Arctic charr may differ in their response towards environmental factors. Sinnatamby *et al.* (2015) studied phenotypic variation in inferred growth and field metabolic rates in young-of-the-year Arctic charr across eastern and central Canada and revealed higher growth in high-latitude populations demonstrating the significant ability of the species to utilize different thermal regimes with different growing season lengths. In Iceland, studies have revealed differences in growth performance of different populations (Pétursdóttir & Eyþórsdóttir 1993; Eyþórsdóttir *et al.*, 1993). Larsson *et al.* (2005) found differences in growth performance among Arctic charr populations in Sweden, but no indication of thermal adaptation. This review focussed the impact of environmental factors on the growth and maturation in farmed Arctic charr discussion the response to environmental factors in farmed populations. We are fully aware that these responses may differ in different wild populations (Pétursdóttir & Eyþórsdóttir 1993; Larsson *et al.* 2005; Sinnatamby *et al.* 2015), but this is outside the scope of this review which focuses on the response in farmed Arctic charr.

The main objective of this review was to discuss how the farmers of Arctic charr can use and manipulate environmental factors to improve the productivity of their farms. In a recent review by Sæther *et al.* (2016), the water quality requirements for land-based farming of Arctic charr were reviewed. Accordingly, the present review focuses on manipulation of temperature, photoperiod, salinity and feeding regimes and their effects on growth, feeding and maturation of farmed strains of Arctic charr.

Rearing temperature

A good number of studies have examined the effect of temperature on the growth of Arctic charr, and the results suggest that the optimum temperature for growth for juveniles is between 12 and 18°C (Swift 1964; Lyytikäinen *et al.* 1997; Larsson & Berglund 1998, 2005; Larsson *et al.* 2005; Jobling *et al.* 2010; Gunnarsson *et al.* 2011; Table 1). However, Arctic charr will grow at temperatures as low as 0.3°C (size range: 200–300 g, Brännäs & Linnér 2000; size range: 2–25 g, Borgstrøm *et al.* 2015) and the upper limits for growth are near 20°C (size range: 1–5 g, Lyytikäinen *et al.* 1997; size range: 15–26 g, Thyrel *et al.* 1999). Most of these studies were performed on small fish over a relatively short period of time and provide only limited information on the effect of temperature on the long-term growth of Arctic charr up to market size. For most species, the optimum temperature for growth decreases with increasing size of fish (Hallaråker *et al.* 1995; Björnsson & Tryggvadóttir 1996; Imsland *et al.* 1996, 2001a,b, 2006, 2008; Aune *et al.* 1997; Jonassen *et al.* 1999). Long-term studies on the growth of Arctic charr also suggest that the optimum temperature for growth of the fish is reduced as the fish grow larger (Gunnarsson *et al.* 2011; Siikavuopio *et al.* 2013; Table 1). In Figure 2, we summarize the results of several growth studies of two Icelandic aquaculture populations and one wild population of Arctic charr performed between 1997 and 2000. The long-term growth of fish was consistently as good or even better at 9°C than at 15°C. Similarly, Pétursdóttir and Eyþórsdóttir (1993) found about equal growth of fish when reared at 8–12°C (Fig. 3), but lower gonadosomatic index at 5 and 9°C compared to 14°C (Fig. 4). These results suggest that there are small differences in long-term growth performance between 8 and 15°C for Arctic charr up to 800 g, considerably lower temperature than the results of the short-term studies suggest. These findings concur with the experience of some Icelandic fish farmers who choose to grow Arctic charr at 8–9°C, even if higher temperatures are available, claiming that growth at this temperature is equally good and that there are less problems with diseases than at higher temperatures (Benedikt Kristjánsson, Íslandsbleikja Fish Farm, pers. comm.). Another reason that favours the use of lower temperatures in Arctic charr aquaculture is that growth rate is maximized a few degrees below the temperature giving maximum feed intake (Jobling 1994; Imsland *et al.* 2006; Handeland *et al.* 2008). Feed conversion efficiency can, therefore, improve if the rearing temperature is lowered slightly below the optimum temperature for growth.

Table 1 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		
0.5–25 g	15°C	Lyytikäinen *et al.* (1997), Larsson and Berglund (1998)
<50 g	>15°C	
20–150 g	12–18°C	Siikavuopio *et al.* (2013)
	12–16°C	Jobling *et al.* (2010)
	14–16°C	Swift (1964), Thyrel *et al.* (1999), Larsson and Berglund (2005), Larsson *et al.* (2005)
50–200 g	15°C	Siikavuopio *et al.* (2013)
On-growing		
100–500 g	8–12°C	Pétursdóttir and Eyþórsdóttir (1993)
	15°C	Gunnarsson *et al.* (2011)
>500 g	7–12°C	Gunnarsson *et al.* (2011)
	8–12°C	Pétursdóttir and Eyþórsdóttir (1993)

During growth to market size, the feed intake of Arctic charr can cycle (Pálsson *et al.* 1992) resulting in periods where growth rate is reduced or the fish even lose weight (Sæther *et al.* 1996; Tveiten *et al.* 1996; Damsgård *et al.* 1999). This is also in line with the experience of Icelandic charr farmers where fish reared at a constant temperature under continuous light, go through periods where feed intake and growth rate are reduced (Hjalti Bogason, Íslandsbleikja Fish Farm, pers. comm.), especially in farms that grow the fish to a market size of 1.5 kg or more. These growth cycles may, to some extent, be linked to maturation since maturing fish grow faster than immatures early in spring and then feed intake and growth of maturing fish is reduced in late summer and autumn (Pálsson *et al.* 1992; Sæther *et al.* 1996; Tveiten *et al.* 1996; Damsgård *et al.* 1999).

The growth cycles of Arctic charr are not only related to maturation status, since immature fish also show growth cycles (Jobling 1987; Sæther *et al.* 1996; Damsgård *et al.* 1999). For wild fish, these cycles may balance the need to acquire quickly the necessary energy to survive long winters without undue exposure to predation while foraging, especially in the marine environment. The growth cycles of immature fish are caused by variations in feed intake and they are maintained under constant temperature and photoperiod conditions, suggesting that they are driven by endogenous rhythm (Jobling 1987; Sæther *et al.* 1996). There also appears to be some form of regulatory mechanism, a lipostat of sorts (Frøiland *et al.* 2010, 2012), that reduces feed intake once the fish have reached a certain level of adiposity. At higher temperatures, the cycles may be shorter (6 months at 10°C) (Jobling 1987) than at lower temperatures (12 months at 4°C) (Sæther *et al.* 1996) which suggests that temperature could modulate the length of the cycles. Fulton's condition factor (K) can be an indicator of the different energy reserves especially when

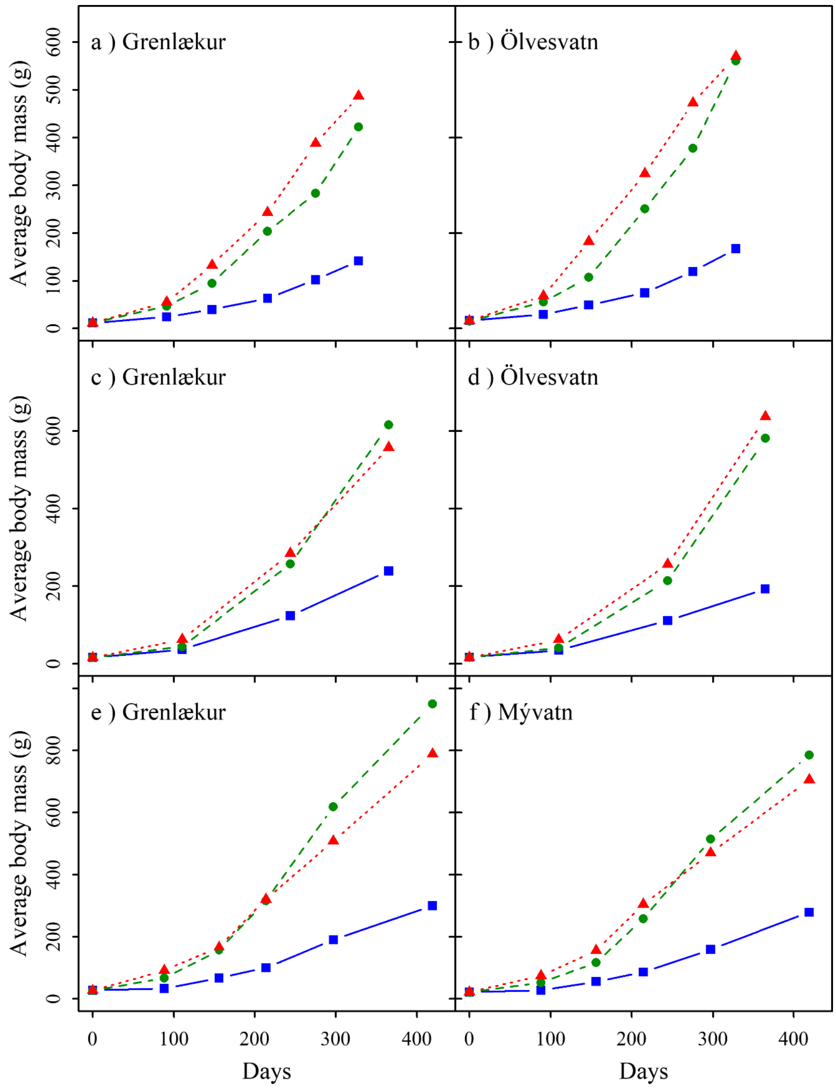

Figure 2 Results from three growth studies on Arctic charr populations at different temperatures. The first experiment was conducted in 1997–1998 (a and b), the second experiment was conducted in 1998–1999 (c and d) and the third experiment was conducted in 1999–2000 (e and f). The populations Grenlækur and Ölfusvatn were the populations chosen for the Icelandic Arctic charr breeding programme and are the F2–F3 generations from wild ancestors. The Mývatn population is the F1 generation from wild parents. Each population was tested in either duplicate (a, c, d) or one tank (b), with 90–100 fish in each tank 2-m^3 tank. All experiments commenced in early October. Prior to that time, all groups were reared at 8–10°C. The fish were fed in excess, twice each day. (a) –■–, 5°C; --●--, 10°C; ··▲··, 15°C. (e) –■–, 5°C; --●--, 9°C; ··▲··, 13°C.

comparing fish of similar sizes. The *K* of Arctic charr increases as they grow and the rate at which the *K* increases is proportional to temperature between 5 and 14°C (Gunnarsson *et al.* 2011). Therefore, fish reared at higher temperatures may reach earlier the level of adiposity where feed intake and growth are reduced and this, in turn, could explain why the growth cycles are shorter at higher temperatures (Jobling 1987; Sæther *et al.* 1996). However, it is not clear whether the set points of adiposity, whether they do in fact exist, are the same at all temperatures. It is of interest to look at the results of Gunnarsson *et al.* (2011) in this context. They found that when charr were transferred from 15 to 12°C, the fish almost stopped growing while fish maintained at 15°C continued to grow well (Fig. 5). In contrast, the growth rate of fish transferred from 12 to 9°C slowed only slightly (Fig. 5) compared with fish maintained at 12°C. The *K* in the group reared at 15°C was higher at the time of transfer than in the 12°C group which may suggest that the 'set point' of the 'lipostat' is lower at 12 than at 15°C. Another possibility is that *K* reached at 15°C exceeded the lipostat value for growing at 12°C, while the *K* reached during growth at 12°C was not only lower but also under the threshold that would reduce the growth rate for fish at both 9 and 12°C. In this case, the 'set point' of the 'lipostat' is not necessarily lower at 12 than at 15°C but just not reached.

Since the optimum temperature for growth is reduced as the fish become larger, it may be possible to maximize growth by reducing the rearing temperature progressively as the fish grow. The growth of Atlantic halibut, *Hippoglossus hippoglossus* L. (Aune *et al.* 1997), turbot, *Scophthalmus maximus*, and Atlantic cod, *Gadus morhua* (Imsland *et al.* 2007, 2008), has been improved by 18–20% compared with fish reared at constant temperature by applying a strategic

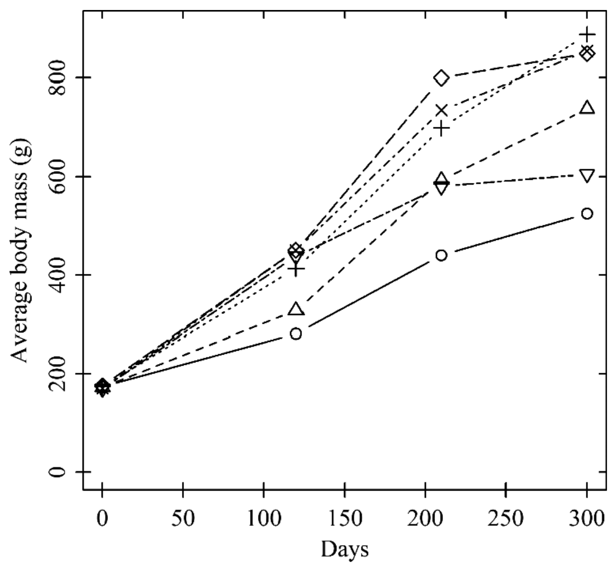

Figure 3 Results from a growth experiment conducted in Iceland in 1991–1992 (redrawn from Pétursdóttir & Eyþórsdóttir 1993; Eyþórsdóttir *et al.* 1993). The fish come from several different populations sampled in different locations around Iceland in autumn 1990. F1 generation from wild parents. Each temperature treatment was tested in duplicate with 50 fish in each tank. All populations were reared in equivalent conditions at temperatures 4, 6, 8, 10, 12 and 14°C. –○–, 4°C; -△-, 6°C; ··+··, 8°C; -×-, 10°C; –◇–, 12°C; ·▽·, 14°C.

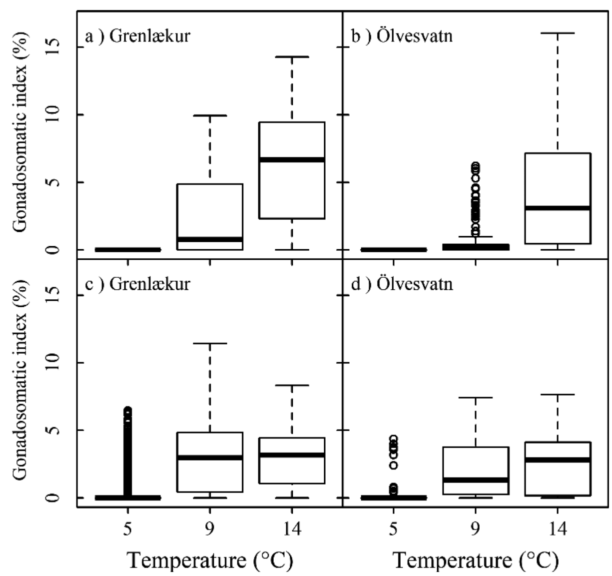

Figure 4 The gonadosomatic index of Arctic charr reared at three different temperatures. (a, b) Results from the experiments shown in Fig. 2a,b. (c, d) Results from the same experiment as shown in Fig. 2c,d. The points shown outliers.

reduction in temperature reflecting the progressive change in optimum temperature as the fish grow. A similar approach was tested for farmed Arctic charr (Gunnarsson *et al.* 2011) but with no long-term production gain since the growth of fish reared at progressively lower temperatures resulted in a consistently lower growth rates than in fish kept at constant temperature.

Photoperiod

Photoperiod is one of the physical environmental factors that can be regulated in Arctic char farming to improve productivity through various physiological processes such as the feed intake (Pálsson *et al.* 1992; Sæther *et al.* 1996; Tveiten *et al.* 1996; Gunnarsson *et al.* 2012), growth (Mortensen & Damsgård 1993; Gunnarsson *et al.* 2012) and maturation (Frantzen *et al.* 2004; Liu & Duston 2019). In land-based farms in Iceland, Arctic charr is most commonly reared under continuous light, both during the juvenile stage and the on-growing phase by placing artificial light above the water surface of each tank.

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 (Jørgensen & Johnsen 2014; Hawley *et al.* 2017). However, Arctic charr held in controlled environment, including constant photoperiods and stable water temperatures, also display seasonal cycles in food intake and growth (Pálsson *et al.* 1992; Sæther *et al.* 1996; Tveiten *et al.* 1996). Growth of Arctic charr is often stimulated following changes in day length, and the growth of fish in changing photoperiod may be better than in fish kept in constant photoperiod. Thus, Duston *et al.* (2003) reported lower maturation rate and increased proportion of high-value fish (>1 kg) in Arctic charr that were exposed to long photoperiod (LD18:6) for 42 days during winter followed by a short (LD8:16) or natural photoperiod compared with fish reared under constant long days. 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 in between periods of continuous light compared with a group reared at continuous light. Gunnarsson *et al.* (2012) reported that Arctic charr given a 6-week short photoperiod between periods of continuous light improved long-term growth rate of Arctic charr reared in freshwater (Fig. 6a) compared with fish kept in continuous light. However, a change from short days to long days does not necessarily result in increased growth, as Bottengård and Jørgensen (2008) found no immediate increase in growth in Arctic charr after transfer from short days to

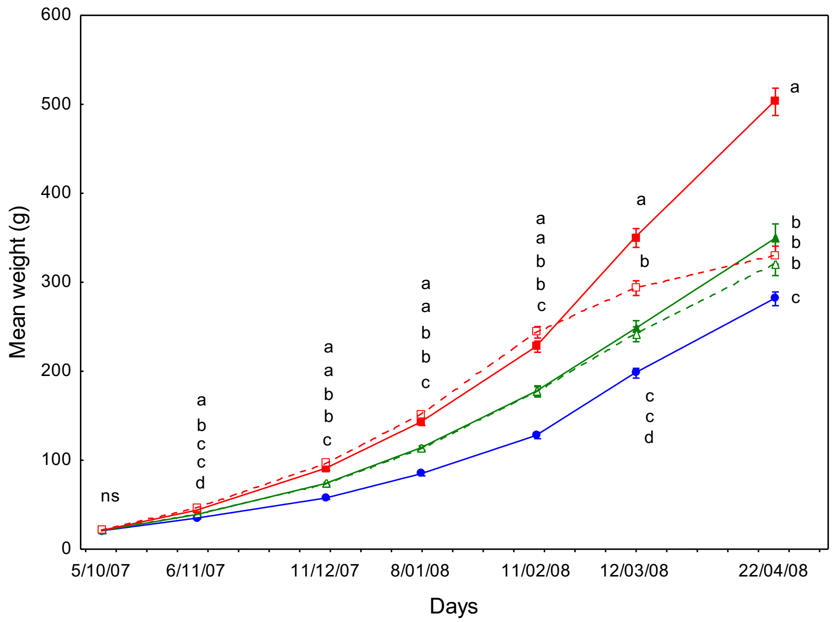

Figure 5 Mean weight of juvenile Arctic charr reared at three constant temperatures and two different temperature steps. Different letters indicate statistical differences. Different letters indicate statistical differences. Modified from Gunnarsson et al. (2011). Temperature was changed in February in the 12–9°C and the 15–12°C groups. [symbol], 9°C; [symbol], 12°C; [symbol], 12–9°C; [symbol], 15°C; [symbol], 15–12°C.

continuous light in late winter. It is not clear whether this photostimulation of growth could be dependent of temperature or season in Arctic charr, whereas such temperature-dependent photostimulation has been indicated in Atlantic salmon (Imsland *et al.* 2017). Hence, it appears as if the growth of Arctic charr might be less sensitive to acute photostimulation than other salmonids (Imsland *et al.* 2017). Aarseth *et al.* (2010) suggested that this may indicate a much stronger endogenous component in the seasonal regulation of appetite and growth in the high-latitude Arctic charr than in more temperate species, such as the Atlantic salmon.

The effect of photoperiod on the fish is generally mediated through the diurnal cycles of the hormone melatonin which is expressed during darkness and while expression is suppressed in daylight (Falcon *et al.* 2010). The plasma melatonin profiles of Arctic charr mirror closely the prevailing photoperiod (Strand *et al.* 2008). At high latitudes, plasma melatonin levels in Arctic charr are constantly low during the summer when feeding activity is high, and high during the dark winter when, in nature, they eat little (Strand *et al.* 2008). Aarseth *et al.* (2010) found that, in Arctic charr, the feed intake, growth and the timing of the seasonal growth rhythm were not affected when summer plasma melatonin levels were artificially increased and the authors concluded that melatonin did not have any direct effect on the somatotropic axis in the Arctic charr. Nonetheless, the melatonin profile reflects the seasonal photoperiod cycle that Arctic charr are exposed to (Strand *et al.* 2008), and therefore, it seems likely that this hormonal system is involved in the regulation and control of the seasonal changes in feed intake and growth.

For salmonids, it is well established that photoperiod can be used to either advance or delay the time of maturation (Bromage *et al.* 2001) and photoperiod is also used in commercial fish farming to postpone or suppress maturation. As discussed above, plasma melatonin profiles of Arctic charr have been found to mirror environmental photoperiod (Strand *et al.* 2008). Further, in other teleosts, melatonin has been found to influence the release of luteinizing hormone (LH) from the pituitary cells in vitro (Khan & Thomas 1996), reduce dopamine levels which would result in increased LHb secretion (Popek *et al.* 2005) and suppress annual testicular function (Bhattacharya *et al.* 2007). However, less is known about these control mechanisms of melatonin in Arctic charr and we suggest that this aspect of sexual maturation control should be investigated in future studies.

Salinity tolerance

Anadromous salmonids migrate between freshwater and seawater. However, *Salvelinus* species are typically less anadromous than the *Salmo* species (Spares *et al.* 2012, 2015). Anadromous strains of Arctic charr stay in the marine environment for a period of a few weeks during spring or summer, often near the estuaries making sorties into the sea and then returning to freshwater. Thus, an anadromous riverine strain of Arctic charr may spend about 40 days in the estuary and 25 days at sea during the summer (Jensen & Rikardsen 2008, 2012). Under natural conditions, the seawater tolerance of Arctic charr is limited to this short time each year (Finstad *et al.* 1989; Arnesen *et al.* 1993b). It should also be kept in mind that there are differences in the

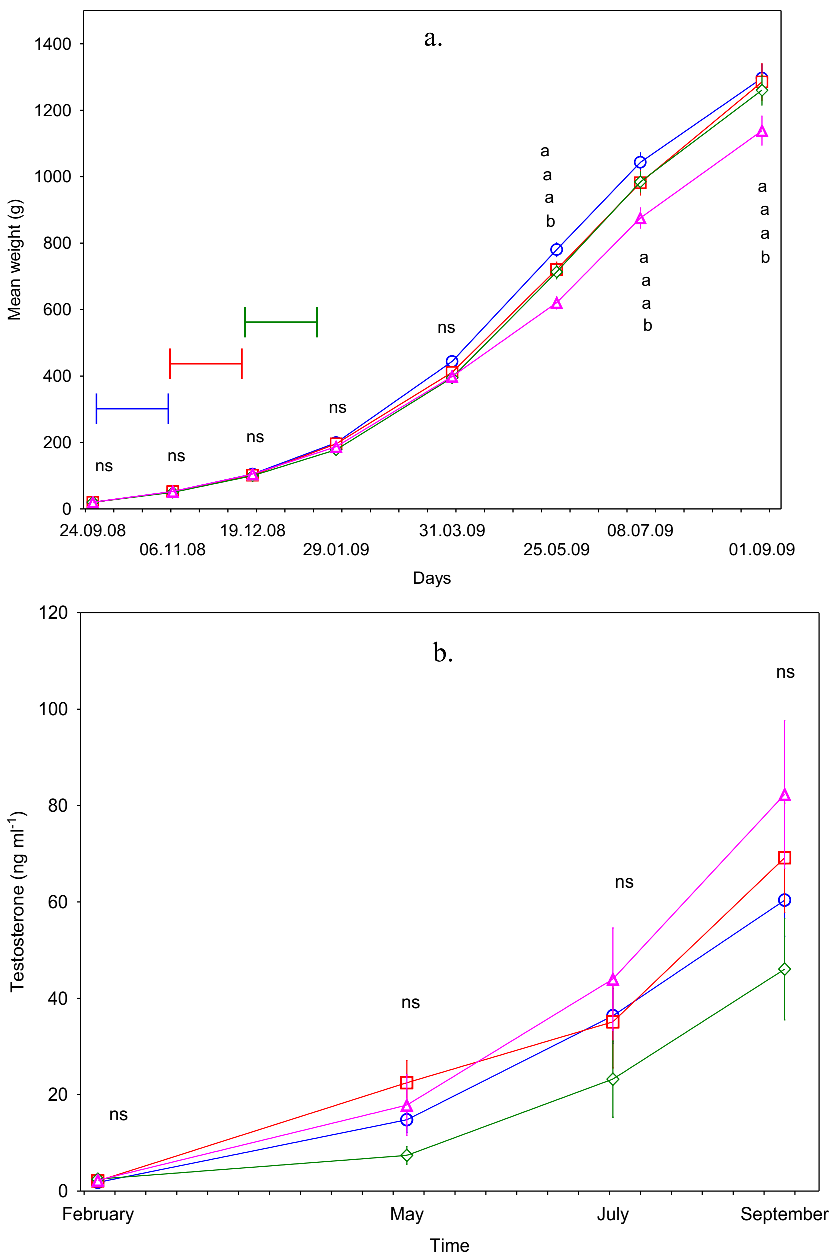

Figure 6 (a) Mean weight of juvenile Arctic charr reared under four different photoperiod treatments. Different letters indicate statistical differences. (b) Mean plasma testosterone values, of tagged female juvenile Arctic charr, reared under four different photoperiod treatments. Different letters indicate statistical differences. Modified from Gunnarsson et al. (2012). ○, LD 8:16 Sep–Nov; □, LD 8:16 Nov–Dec; ◇, LD 8:16 Dec–Jan; △, LD 24:0.

osmoregulatory capacity between landlocked and anadromous strains of Arctic charr (Eliassen *et al.* 1998), between different anadromous strains (Jørgensen & Arnesen 2002) and within rearing strain (Chiasson *et al.* 2014). 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 first part of the marine phase and increase their adiposity before moving back to freshwater (Rikardsen *et al.* 2000). Thus, the anadromous charr may return to the lake after only 5–6 weeks in the sea, because the potential to maintain a high growth rate in the sea is reduced (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 until the next seawater entrance (next spring/summer).

The development of hyperosmoregulatory capacity is, to some degree, similar in Arctic charr and in Atlantic salmon (Halvorsen *et al.* 1994). Anadromous salmonids adapt to the habitat change by a transformation referred to as smoltification which involves various behavioural, morphological and biochemical changes (Wedemeyer *et al.*

1980). As for Atlantic salmon, the development of seawater tolerance for Arctic charr also takes place, while the fish are still in freshwater (Arnesen *et al.* 1992; Staurnes *et al.* 1992; Nilssen *et al.* 1997). 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 primarily a once in lifetime event. Improved seawater tolerance in salmonids is linked to increases 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 h of seawater challenge tests (Björnsson & Bradley 2007). The onset of smoltification in salmonids is primarily initiated by changes in environmental photoperiod and temperature that act as cues for the initiation of the process (Duston & Saunders 1990; Björnsson *et al.* 1995; Stefansson *et al.* 2007). However, the salinity tolerance of Arctic charr may not be under as strict environmental control as it is in other salmonids. The increasing day length during spring induces the hypoosmoregulatory ability of Arctic charr under natural conditions. Finstad *et al.* (1989) and Jørgensen & Johnsen (2014) suggest that, as in other salmonids, the smoltification of Arctic charr is essentially an endogenous rhythm, modulated by photoperiod, which acts as a zeitgeber. However, photoperiod does not necessarily change the salinity tolerance of Arctic charr. A study showed that exposing Arctic charr to a 6-week short day period during early winter followed by continuous light did not result in measurable differences in neither gill NKA nor plasma Na^+ levels when compared with a control group kept at continuous light at 27 ppt during the on-growing phase (Gunnarsson *et al.* 2014, Fig. 7a,b). There is also evidence to suggest that the smoltification process in Arctic charr is less affected by rearing temperature than it is in Atlantic salmon (Bottengård & Jørgensen 2008). The NKA pumps in Arctic charr gills show little temperature sensitivity which may be an adaptation to cold environment (Galarza-Munoz *et al.* 2011).

Norman *et al.* (2011) investigated the genetic basis of salinity tolerance in Arctic charr. They used a genome-scan approach to map quantitative trait loci (QTL) correlated with variation in four salinity tolerance performance traits and six body size traits. Comparative genomics approaches were used to infer whether allelic variation at candidate gene loci (e.g. ATP1α1b, NKCC1, CFTR and cldn10e) could have underlain observed variation. Among the salinity tolerance performance QTL, trait co-localizations occurred on chromosomes 1, 4, 7, 18 and 20, while the greatest experimental variation was explained by QTL on chromosomes 20 (19.9%), 19 (14.2%), 4 (14.1%) and 12 (13.1%). Variation in salinity tolerance capacity could, therefore, be mapped to a subset of Arctic charr genomic regions that significantly influence performance in a seawater environment and the study provided a foundation for more detailed candidate gene-based experiments**.** The detection of QTL on linkage group 12 was consistent with the hypothesis that variation in salinity tolerance may be affected by allelic variation at the ATP1α1b locus. IGF2 may also affect salinity tolerance capacity as suggested by a genome-wide QTL on linkage group 19. More recently, Norman *et al.* (2014) found that that intraspecific variation in salinity tolerance capacity correlated with differential expression of immune response genes.

Anadromous Arctic charr can tolerate full-strength seawater (33–35 ppt) for approximately 2-month period during summer but appear to lose this ability in late summer/fall (Finstad *et al.* 1989). However, Arctic charr appear to tolerate brackish water at any time of year. Comparing the growth of Arctic charr (200–300 g) reared at salinities between 17 and 32 ppt, Mortensen and Lund (1991) found the highest growth rate at 20 ppt. Similar findings were found by Chiasson *et al.* (2014) that investigated possible family × environmental interactions in growth and survival in the Canadian Frasier strain by reared either in freshwater or in 20 ppt for 1 year. They found that some families reared at 20 ppt outperformed their freshwater counterparts, but the evidence of significant treatment (FW vs. 20 ppt) by family interaction for each trait also suggests that rearing at brackish water (here 20 ppt) does influence the growth performance among families differentially. In a related study, Chiasson *et al.* (2015) tested whether previously identified quantitative trait loci (QTL) for body weight and condition factor were detectable across a commercial broodstock (Frasier strain) reared in both freshwater and brackish water (20 ppt). They identified variation in body weight QTL across multiple families of Arctic charr and this, combined with moderate heritability and genetic correlations between full-sibs reared in fresh and brackish water environments, indicates there is potential for genetic improvement of growth in both environments. In another study, Gunnarsson *et al.* (2014) found that Arctic charr maintain high NKA activity and relatively stable levels of plasma Na^+ at 27 ppt, although growth rate was lower at 27 ppt than at 17 ppt. Similarly, Árnason *et al.* (2014) reported lower long-term growth at 29 ppt than at 25 ppt. Due to the limited and seasonal seawater tolerance (Finstad *et al.* 1989; Arnesen *et al.* 1993a, b), most of the production of Arctic charr (on-growing) takes place either in freshwater or in brackish water. In Iceland, the bulk of the Arctic charr farming takes place in brackish water (15–27 ppt) during on-growing (Árnason *et al.* 2014; Gunnarsson *et al.* 2014).

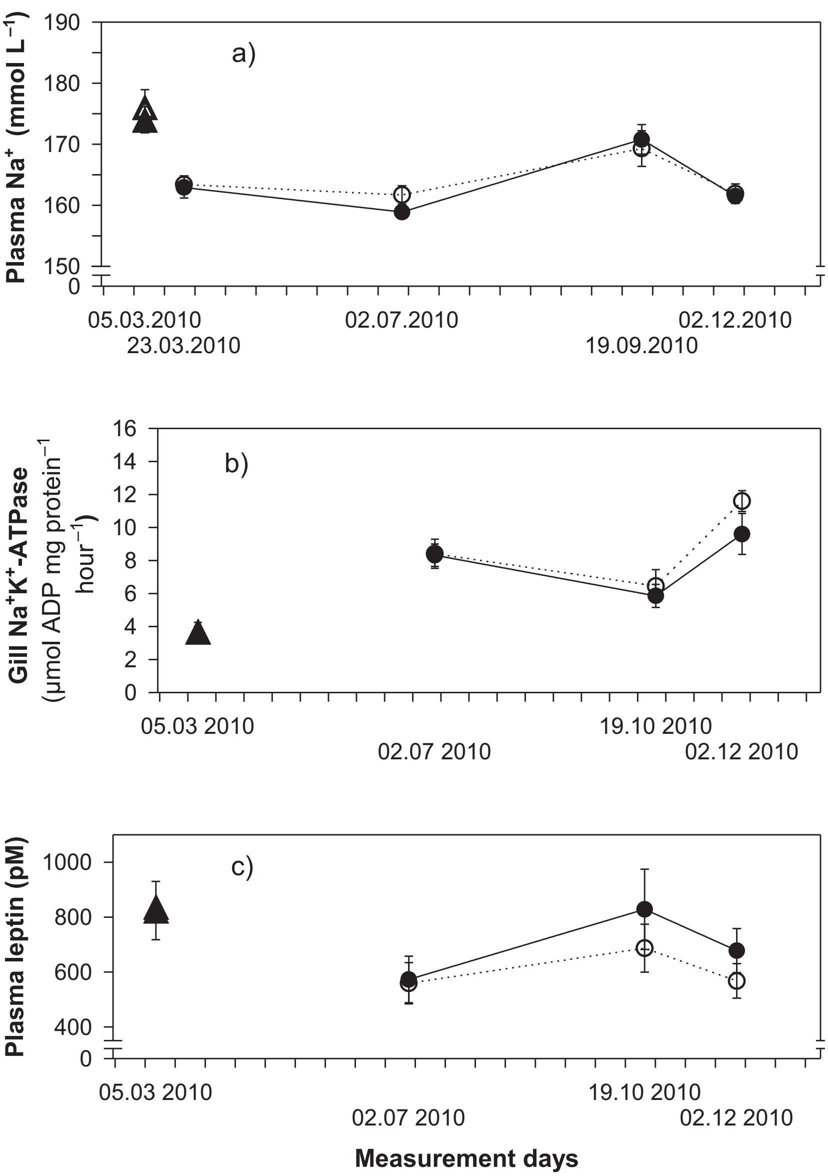

Figure 7 Mean (a) plasma sodium, (b) gill NKA activity and (c) plasma leptin of untagged juvenile Arctic charr at different measurement dates in the period from March to December 2010. The Arctic charr was reared in freshwater for 100 days and then reared in seawater (27 salinity) for the following 9 months. Two photoperiod regimes: S groups (●) were given short day (LD8:16) from 24 November to 5 January but then returned to continuous light. C groups (---○---) were held at continuous light at all times. The first data points are from Arctic charr following 24-h seawater challenge test (30 salinity), S group (▲) and C group (△), while the subsequent samplings are from the 27 salinity treatment. Modified from Gunnarsson et al. (2014).

For Arctic charr, there is still little, and fragmented, information on the effect of salinity on the maturation processes. Árnason *et al.* (2014) found indication that rearing Arctic charr at 25 ppt delays the onset of maturation by c. 4 months compared with rearing at 29 ppt. Similarly, Gunnarsson (2014) also reported that gonad growth in Arctic charr was stimulated by rearing in 27 ppt compared with 17 ppt. Sexual maturation is known to slow somatic growth in salmonids (Damsgård *et al.* 1999; Berglund *et al.* 2006; Duston *et al.* 2007). The immature Arctic charr in the study of Gunnarsson *et al.* (2014) had 35.6% higher final mean weight than maturing fish and the elevated gonadosomatic index levels in the 27 ppt group may therefore have been a causative factor for their slower growth compared with the 17 ppt group. Atse *et al.* (2002) found that female broodstock of Arctic charr kept in seawater during the summer months produced larger eggs containing more lipids and proteins than eggs from female broodstock in freshwater. Similarly, survival of eggs and embryos from broodstock in seawater was higher than that of fish in freshwater. 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 brackish water (29 ppt, Árnason *et al.* 2014; 27 ppt. Gunnarson *et al.* 2014) may have had similar effects of mild stress leading to advanced maturation.

Compensatory growth and restricted feeding

Feed costs make up one of the highest single factors in the production of salmonids as for many other species. It is therefore of importance for the fish farmer to ensure that the feed is consumed and is utilized efficiently for somatic growth. 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 few weeks 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 & Power 1990; Jørgensen *et al.* 1997). The term compensatory growth (CG) refers to a phase of accelerated growth following a period of little or no growth when food has been withheld (Ali *et al.* 2003). Following refeeding after a period of starvation, fish going through CG may reach full compensation of growth compared with fish fed ad libitum (Ali *et al.* 2003). The length of time or the severity of the feed restriction has an effect on the outcome of trials, whether the fish can partly or fully compensate for the weight loss when reverted to full feeding (Jobling *et al.* 1993b; Jobling & Koskela 1996; Savoie *et al.* 2017). Factors such as rearing temperature are important in determining the effect of restricted feeding regimes on CG since higher rearing temperatures lead to higher metabolic rates which, in turn, may make the window narrower for applying restricted feeding if the aim is to reach full compensation in growth. Studies have shown that compensatory growth is partly a result of hyperphagia (Ali *et al.* 2003; Imsland & Gunnarsson 2011), a state where the feed intake of the previously feed-deprived or feed-restricted group is significantly higher than for a group that has been fed ad libitum. The hyperphagia response was reported for Atlantic salmon when feeding was restored after a period of feed restriction (Bull & Metcalfe 1997). Hyperphagic Arctic charr may consume nearly twice as much food as do controls fed ad libitum (Miglavs & Jobling 1989).

In addition to consuming more food, fish may show improved feed utilization during periods of CG. Miglavs and Jobling (1989) found improved feed conversion efficiency for Arctic charr when returned to normal feeding after a period of 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 with 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. Savoie *et al.* (2017) found that long fasting (39 and 61 days) during summer in juvenile (80–120 g) brook charr (*Salvelinus fontinalis*) resulted in full CG and adjustment in both growth and several physiological indicators (feed conversion ratio, organosomatic index, digestive enzymatic activities) were more pronounced. The authors suggested that CG in juvenile brook charr takes place in two stages after a long starvation period: (i) restoration of the digestive system followed by enzyme activities (trypsin and chymotrypsin) and (ii) rebuilding of somatic tissues. However, not all studies have reported improved feed utilization during periods of CG. 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. Further, not all studies have shown benefits of restricted feeding and compensatory growth. For example, sea bream (*Sparus aurata*) juveniles were unable to catch up with a control group that was fed continuously to satiation (Ali & Jauncey 2004; Eroldogan *et al.* 2008).

Cassidy *et al.* (2016) deprived juvenile Arctic charr (Canadian Nauyuk strain) of food for 101 days and then fed to satiety for 126 days. The refeeding period resulted in compensatory growth, with a partial compensation of body mass. The feed deprivation period leads to a decrease in hepatosomatic index (HSI) and intestinal somatic index (ISI). HSI and ISI were then gradually replenished during early refeeding, following a lag phase prior to the compensatory growth response. mRNA transcripts regulating protein degradation via the autophagy pathway (cathepsin D and cathepsin L) in muscle were upregulated during feed restriction and downregulated after refeeding allowing for greater protein accretion in muscle, facilitating compensatory growth. The same research group later studied possible adjustment of protein metabolism in fasting Arctic charr (Cassidy *et al.* 2018) of the Canadian Fraser strain. They found no observable effects of food deprivation on the protease activities in any of the tissues measured (red and white muscle, liver, heart and gills) with the exception of liver, where the ubiquitin–proteasome pathway seemed to be activated during fasting conditions. The authors speculated whether Arctic charr regulate protein metabolism during food deprivation to conserve proteins.

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. Tveiten *et al.* (1998) reported that maturing Arctic charr reduced feeding once a 'threshold condition' in the range of the condition index (K) 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 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). In mammals, appetite is regulated through a hypothalamic integration of stimulatory (orexigenic) and inhibitory (anorexigenic) factors. Although major gaps exist in our understanding of the control of food intake in fish, the regulation seems to involve the same signalling molecules (hormones, neuropeptides) as in mammals (Frøiland *et al.* 2010). Recently, Striberny *et al.* (2014) investigated the possible involvement of altered gene expression of brain neuropeptides in seasonal appetite regulation of Arctic charr. They found that the non-feeding Arctic charr (May, January) had a lower expression of the anorexigenic centrally expressed leptin (LepA1), melanocortin receptor 4 (MC4-R) and leptin receptor (LepR) in hypothalamus and a higher expression of the orexigenic neuropeptide Y (NPY) and agouti-related peptide (AgRP) in mesencephalon, than the feeding charr (July). The peptide hormone leptin is produced and secreted from adipose tissue of mammals and appears to function as an adiposity signal, being anorexigenic, with plasma leptin levels decreasing with loss of fat tissue, for example, due to food restriction (Maffei *et al.* 1995). There are indications that leptin has similar anorexigenic function in fish (Murashita *et al.* 2011; Striberny *et al.* 2014), 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 (Kling *et al.* 2009; Frøiland *et al.* 2012; 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). Higher levels of leptin have been found to be concomitant with periods where the overall growth rate of Arctic charr was highest (Gunnarsson *et al.* 2014, Fig. 7c). 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 with the use of restricted feeding routines, given that the fish can reach full growth compensation in the periods with full feeding. Application of periodically restricted feed rations (50%) of 6 weeks followed by full ration feeding (100%) in Arctic charr between 20 and 200 g led to full growth compensation (CG) (Imsland & Gunnarsson 2011). Periods of food restrictions can affect the maturation rate of Arctic charr although results are contrasting. Jobling *et al.* (1993b) reared Arctic charr (initial size range: 28–31 g, final size range: 236–452 g) at different intervals of either food deprivation or full ration and found no effect on maturation ratio when beginning the food restriction in May prior to maturation in the following autumn. In contrast, Imsland and Gunnarsson (2011) reported that periodical feed restriction regimes proved to be effective in reducing the incidence of maturation with lower mean gonadosomatic index (GSI) and plasma testosterone (T) levels (Fig. 8) during the final stages of maturation in the feed-restricted group (Fig. 8). Recently, Liu and Duston (2019) found that food deprivation under LDN in fall (October–November) had no significant effect on maturation (♀:52%; ♂:42%) but was more effective during winter (December–January), significantly reducing maturity in both sexes (♀:32%; ♂:15%). 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). In general, fish undergoing compensatory growth may utilize energy and nutrients for growth that otherwise would utilized for reproduction (Ali *et al.* 2003).

Conclusions: Strategies for advancing Arctic charr farming

In this article, we have discussed the short- and long-term effects of four environmental factors, temperature, salinity, photoperiod and feeding regimes, on several important farming traits of Arctic charr. 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 challenges in farming of Arctic charr are to ensure stable and even growth and reduce negative effects from maturation. The high-latitude Arctic charr has strong endogenous rhythms in terms of feeding, growth and maturation that endure even though various environmental factors are manipulated in fish farms.

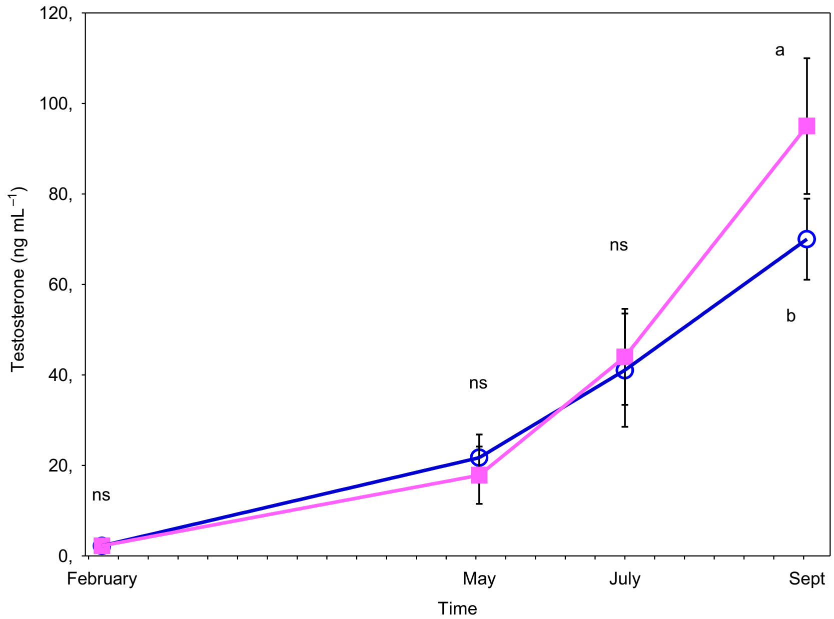

Figure 8 Mean (±SE) plasma values of testosterone (T) of individually tagged female Arctic charr reared at two feeding regimes. Different letters indicate significant difference between the experimental groups. Modified from Imsland and Gunnarsson (2011). ○, 50% ration; ■, 100% ration.

Rearing temperature is a highly effective tool to improve growth rate of Arctic charr, and the optimum temperature varies with the size of fish and development (Pétursdóttir & Eyþórsdóttir 1993; Thyrel *et al.* 1999; Larsson *et al.* 2005; Jobling *et al.* 2010; Gunnarsson *et al.* 2011; Siikavuopio *et al.* 2013). The combination of high temperatures and high growth rate during the juvenile phase can induce early maturation during the on-growing phase so for production of fish >1 kg, moderate (≤10°C) or low temperatures should be applied during the juvenile phase in order to reduce negative effects from maturation. 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). Accordingly, to maximize feed utilization farmers of Arctic charr should choose more moderate rearing temperatures (<10°C) especially during juvenile stage. High-latitude species such as 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 & Gwinner 1994; Loudon 1994). Photoperiod can be applied in the farming environment, entraining various physiological variables and affecting the feed intake (Pálsson *et al.* 1992; Sæther *et al.* 1996; Tveiten *et al.* 1996; Gunnarson *et al.* 2012), growth (Mortensen & Damsgård 1993; Gunnarsson *et al.* 2012) and maturation in Arctic charr (Frantzen *et al.* 2004). 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 to alter the proportion of maturing Arctic charr (Frantzen *et al.* 2004). The general trend is that increased or extended photoperiods lead to increased feeding and growth (Tveiten *et al.* 1996; Boeuf & Le Bail 1999; Boeuf & Falcon 2001; Johnston 2002). Variable photoperiod shifting between periods with long day and short day has been shown to have growth-inducing effects compared with rearing at continuous light (Mortensen & Damsgård 1993; Siikavuopio *et al.* 2009; Gunnarsson *et al.* 2012). Arctic charr is most commonly reared under continuous light throughout the both during the juvenile stage and the on-growing phase, but future studies are required on application of alternate photoperiods to enhance growth. Especially, how photoperiod manipulation can be used to reduce or work against the endogenous growth rhythm in Arctic charr resulting in periods with growth halt and reduced productivity.

Salvelinus species are ranked as least anadromous compared with their counterparts belonging to the *Salmo* species (Spares *et al.* 2015). Rearing of Arctic charr in seawater or dilute seawater is of interest as it opens up for net-pen rearing in the sea and farming in coastal land-based facilities with dilute seawater resources. In Iceland, Arctic charr has been successfully farmed during on-growing in land-based facilities with dilute seawater in the range from 18 to 27 ppt. Development of hyperosmoregulatory capacity of Arctic charr takes place while the fish are still in freshwater (Arnesen *et al.* 1992; Staurnes *et al.* 1992; Nilssen *et al.* 1997). The smoltification process of Arctic charr is likely under endogenous rhythm, but photoperiod is acting merely as a zeitgeber altering the timing of the smoltification (Jørgensen & Johnsen 2014). Photoperiod manipulation as a method to synchronize or induce smoltification is not part of the current production routines prior to rearing in dilute seawater. The salinity tolerance of Arctic charr is positively correlated to body size (Johnston 2002), so size at the day of transfer to seawater is of importance. The Arctic charr seem to cope well at any time of the year in brackish water (15–27 ppt) but with reduced growth and feed conversion efficiency with increased salinities (Finstad *et al.* 1989; Arnesen *et al.* 1994; Gunnarsson *et al.* 2014). Brackish water in the range from 15 to 27 ppt is successfully used during the on-growing period of farmed Arctic charr in Iceland, but with some negative effects in terms of higher ratio of maturing fish in groups at higher salinity (29 ppt Árnason *et al.* 2014; 27 ppt Gunnarsson *et al.* 2014).

Feed costs make up one the highest single factors in the production of Arctic charr as for many other species. Good feed utilization is therefore an important element in successful Arctic charr farming. There are many factors that affect growth rate, feed intake and feed utilization efficiency in Arctic charr farming as we have discussed such as rearing temperature, photoperiod and salinity. Feeding techniques such as rearing Arctic charr at periodically restricted feed rations can be an effective tool to reduce feeding costs. Periodical feed restrictions followed by full ration can improve the overall feed conversion efficiency and reduce early maturation compared with the full ration groups (Imsland & Gunnarsson 2011).

Future studies in the field should be directed at investigating how the growth advantage of farmed juvenile Arctic charr reared at optimum temperature can be transferred successfully into the on-growing period without the observed negative effect on growth (Gunnarsson *et al.* 2011) when transferred down in temperature regime 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 water or seawater. Future studies should also address the question of genetic variability inside and among Arctic charr populations and discuss whether these genetic traits could affect the phenotypic plasticity and the responses of phenotypic traits to modulation of environment to optimize productivity as well-being of fish.

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