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Effects of Early Thermal Environment on Growth, Age at Maturity, and Sexual Size Dimorphism in Arctic Charr

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Abstract: The effects of early thermal environment on growth, age at maturity, and sexual size dimorphism in Arctic charr (*Salvelinus alpinus*) are investigated. This study is a 654-day long rearing trial split into two sequential experimental phases termed EP1 and EP2 and lasting 315 and 339 days, respectively. EP1 started at the end of the yolk sac stage when the experimental fish were divided into three groups and reared at different target temperatures (7, 10 and 12 °C). During EP2, all groups were reared at the same temperature (7–8 °C) until harvest (~1300 g). Growth rates increased with temperature from 7 to 12 °C, and at the end of EP1 the 12C group had 49.0% and 19.2% higher mean weight than groups 7C and 10C, respectively. Elevated early rearing temperatures were, however, found to cause precocious sexual maturation and reduce the long-term growth performance. At the end of EP2, the 7C group had 3.6% and 14.1% higher mean weight than 10C and 12C, respectively. Elevated early rearing temperatures had a much stronger effect on the maturity incidence of females, and while male-biased sexual size dimorphism (SSD) was found in all groups, the magnitude of SSD was positively associated with temperature.

Keywords: teleost fish; thermal plasticity; growth; puberty; sexual size dimorphism

1. Introduction

Temperature is the most important environmental factor influencing the development and growth rate in fish. Most species show rapid increase in growth rate as temperature increases, with growth peaking at an optimal temperature and then falling rapidly with higher temperature [1,2]. In addition to affecting growth rate, temperature can also modify a range of phenotypic traits, such as the development of the axial skeleton, muscle growth dynamics, age at puberty, and head shape [3–6].

The ability of organisms to express different phenotypes in response to environmental conditions is known as phenotypic plasticity. Fish have frequently been found to have a high level of plasticity during early life stages [7], and the responses to early conditions appear to be modified by epigenetic mechanisms, such as deoxyribonucleic acid (DNA) methylation [8]. A growing number of studies provide evidence that epigenetic mechanisms are associated with commercially important traits in aquaculture [9].

Arctic charr (*Salvelinus alpinus*) are among the most widespread fish species in the world. It is mainly distributed in Arctic and subarctic regions and is also found further south at high altitudes in many lakes in the Alps and Pyrenees [10]. The species is found both as anadromous and freshwater-resident forms [11] and hosts a remarkably diverse collection of phenotypes that vary considerably across its distribution range. Even within a single lake there may be up to four different sympatric morphs of Arctic charr [12]. As in other species of salmonids, male Arctic charr deploy alternative mating tactics. Small, early

maturing males often display sneaking spawning behavior while larger dominant males use guarding tactics and aggression towards potential competitors [13,14].

Early maturation and growth depression of males used to be one of the main economic obstacles for the Icelandic Arctic charr farming industry, but through domestication and selective breeding of the Hólar strain, problems associated with male maturation have decreased, with males now outperforming females in terms of growth [15,16]. Similar development has been observed in the Swedish Arctic superior® strain (Fisheries Board Research Station, Kälarne, Sweden) [17]. However, in Canada, where several strains of Arctic charr are farmed, preharvest maturation of males remains a problem, and production of all-female populations has been suggested as a countermeasure to improve the economic efficiency of the industry [18]. The biological response to a warming environment has generally been assumed to be independent of sex. Recent studies have, however, revealed sex-dependent effects of temperature on growth and maturity in a diverse array of animal species e.g., [5,19–21].

Several studies have examined the effect of temperature on the growth of Arctic charr [22–27]. While these short-term studies indicate that Arctic charr grow optimally at relatively high temperatures (12–18 °C), there is evidence to suggest that optimum temperatures for rearing to market size may be considerably lower because high rearing temperatures may lead to precocious maturation [28,29].

In Iceland, most Arctic charr farming takes place in brackish water on the volcanically active Reykjanes peninsula on the southwest coast. One of the qualities of this area with regards to land-based farming is the availability of relatively low-cost geothermal borehole water. However, in most areas in Reykjanes the supply of hot water is somewhat limited and is mainly used to elevate rearing temperatures from start-feeding up to the juvenile stages (<50 g). What prompted the present study were observations made by the fish farming company, Samherji Fiskeldi, over nearly two decades of land-based farming of Arctic charr in the Reykjanes area. The company's extensive dataset demonstrates clear differences in adult growing performances between groups originating from hatcheries using different thermal regimes. Thus, Arctic charr from a hatchery using low temperatures (7–8 °C) up to a size of about 100 g (Öxnalækur), tend to grow faster during the on-growing phase (up to ca. 1400 g) when compared with Arctic charr from another hatchery using elevated temperatures (10–12 °C) to enhance growth rates of juveniles up to a size of about 50 g (Staður, pers. obs.).

As the observed differences in the adult growing performance of Arctic charr originating from these two aforementioned hatcheries could potentially also be explained by other factors besides temperature, the present study was specifically designed to examine whether elevated early rearing temperatures may have a disproportionate effect on long-term growth performances and sexual maturation of Arctic charr at harvest. A second aim of the study was to examine the development of sexual size dimorphism in the Hólar Arctic charr strain, and whether the thermal plasticity in growth and age at maturity is sex dependent.

2. Materials and Methods

2.1. General Methods

The experimental fish were of mixed parentage and from the ninth-generation pedigree Arctic charr from the Hólar University College, NW Iceland. The breeding program was initiated in 1992 when wild Arctic charr from several lakes and rivers in Iceland were interbred with the purpose of creating an aquaculture strain that would mature late and grow fast [30]. Currently, all farmed Arctic charr in Iceland are of this origin. The fish used in this study were incubated at 3.5 °C in freshwater and hatched in February 2016.

The experiment was conducted at two locations. During early life stages (0.06 to ~100 g) the fish were reared in the Hólar University research facility Verid, at Sauðárkrókur, NW Iceland, and thereafter in the MFRI Aquaculture Research Station at Grindavík, SW Iceland.

In both locations the fish were reared indoors in flow-through aquaculture systems. Salinity, oxygen, and temperature of the rearing water were measured daily, and pure oxygen was added to the inlet water to always maintain oxygen saturation close to 100%. The fish were reared under continuous light (LD 24:0) throughout the experiment. At Verid, the juveniles were fed commercial dry feed from Skretting A/S (Stavanger, Norway) up until a mean weight of about 30 g and thereafter they were fed dry feed (ECO-juvenile feed) from Laxá Feed mill Ltd. (Akureyri, Iceland). The feed was continuously provided in moderate excess by automatic feeders.

2.2. Experimental Design

2.2.1. Experimental Phase 1

In experimental phase 1 (EP1), three groups of Arctic charr were reared at different temperatures for 315 days, from the late alevin stage up to size of about 50 g. EP1 started on 21 March 2016, when about 2400 alevins were transferred from the Hólar University College breeding facility to the Verid. After the approximately 15-min transport time from Hólar Verid, the alevins were randomly distributed into 12 circular 20 L plastic tanks, where a growth experiment with three target temperatures (7, 10, and 12 °C) was carried out. The rearing temperature in each tank was gradually adjusted from the initial 3.5 °C to the target temperatures over a period of one week. The groups are subsequently referred to as 7C, 10C, and 12C. Initially there were 200 fish per tank, with triplicate tanks for groups 7C and 12C and sextuplicate tanks for group 10C. Most of the fry had started exogenous feeding by 7 April 2016, 11 days after the target temperatures were reached.

At the start of EP1 on 21 March 2016 (day 1) and on days 48 and 80, mean body sizes were estimated by measuring the bulk weight of 40 randomly sampled fish from each tank. On day 171, the number of fish was reduced to 100 per tank and all fish weighed individually as well as on subsequent measurement dates. On day 234, the fish were tagged intraperitoneally with passive, integrated transponder PIT-tags (Trovan, www.trovan.com, accessed 12 November 2021) under phenoxyethanol anesthesia (0.3 mL/L of water) and weighed. After tagging, the fish were transferred to eight 1 m³ rectangular fiberglass tanks. Each of groups 7C and 12C was randomly divided between two tanks, while group 10C was divided between four tanks. On day 315, the fish were all weighed and vaccinated by injection (Alpha Ject® 3000 Pharmaq AS, Overhalla, Norway).

During EP1, the mean rearing temperatures were 7.3 ± 0.04, 10.2 ± 0.06, and 12.1 ± 0.05 °C for groups 7C, 10C, and 12C, respectively. The salinity during this period fluctuated between 1 and 5 ppt, but the mean salinity was the same in all tanks, or 4.3 ppt.

2.2.2. Experimental Phase 2

Experimental phase 2 (EP2) was a direct 11-month sequel to EP1, designed to study the long-term effects of early temperature on commercially important traits in Arctic charr aquaculture. After the final measurements and vaccination on day 315 in EP1, the 10C and 12C groups were gradually acclimated to 7 °C over five days, while the 7C group remained at the same temperature.

During the first two months of EP2 the fish were kept at Verid, but on day 379 the fish belonging to each group were mixed into separate 400 L fish transport tanks and transported by truck 313 km to the MFRI Aquaculture Research Station. Upon arrival, the fish within each group were individually weighed and randomly distributed between two or four rectangular 3.2 m³ fiberglass tanks (7C and 12C in duplicate and 10C in quadruplicate tanks). Rearing conditions with approximately 8 °C and 22 ppt brackish water were maintained throughout EP2 and the fish were given no acclimation to the initial salinity change from 4 to 22 ppt. The fish were subjected to the abrupt increase in salinity from 4 to 22 ppt to resemble the farming practice of two of the largest Arctic charr producers on the Reykjanes peninsula (pers. obs.). After measurements on day 582, the fish were transferred to circular 5.6 m³ fiberglass tanks where they were reared until harvested on

day 654 (4 January 2018). In the final measurement of EP2, all fish except 34 individuals from each group were sacrificed by a sharp blow to the head and measured after bleeding. Thereafter, the sex was determined, and gonads weighed for each harvested fish. The fish that were not killed were measured as before.

From day 315 to 379, before the fish were transported to MFRI, the mean temperature in all groups was 7.2 ± 0.05 °C and the salinity was 4.1 ppt. After being transported to MFRI and until harvested on day 654, the mean temperatures were 8.4 ± 0.02, 8.3 ± 0.02, and 8.3 ± 0.02 °C in groups 7C, 10C, and 12C, respectively. At MFRI, the mean salinities in the respective groups were 22.3 ± 0.11, 22.5 ± 0.13, and 22.4 ± 0.11 ppt.

Throughout EP1 and EP2, the 10C group had twice as many total fish and replicates as the 7C and 12C groups. The experiment was designed this way to obtain a more reliable comparison between the growth trajectories of maturing and non-maturing fish.

2.3. Data Analysis and Statistical Methods

Body weight (W) was measured to the nearest g. Normality of distribution was assessed by the Shapiro–Wilk test. Gonad weight was measured to the nearest 0.01 g.

$$GSI = WG \times W^{-1} \times 100$$

where WG is the gonad weight and W is the total body weight. Males and females within each temperature group were sorted into three maturation stages based on their GSI at harvest. In accordance with the GSI of immature male Atlantic salmon [31], males having GSI < 0.2% were categorized as immature. Male maturation stages were based on the GSI frequency distributions within the 10C and 12C groups. Within groups 10C and 12C, there was a distinct cluster between 0.01% and 0.2% (immature, stage 0) and another cluster between 2% and 8% (stage 2). Only a small number of males (2–5 per temperature group) had a GSI between 0.2% and 2% (stage 1). Females having GSI < 0.35% were categorized as immature (stage 0) in accordance with reported GSI of immature Arctic charr and Atlantic salmon [15,32]. Those in the early stages of maturity with GSI between 0.35% and 3.5% were classified as stage 1, while those having GSI > 3.5% were classified as stage 2.

Normality of distribution was assessed by the Shapiro–Wilk test. A three-way mixed model analysis of variance (ANOVA), with replicate tanks as the random variable and temperature and sex as fixed variables, was used to test for possible differences in mean W between temperature groups. Differences in mean W between maturity groups were analyzed separately for males and females, using a two-way ANOVA with replicates (random) and maturity stage (fixed). Significant differences in the aforementioned ANOVA analysis were followed by Tukey's HSD tests. Differences in mean W between males and females within each temperature group were tested using a two-way mixed ANOVA with replicates (random) nested within sex (fixed). Significant gender differences in the mean W were followed by Student's t-tests.

The significant variation of the sex ratio from 1:1 was determined using the χ^2 goodness-of-fit test. Data are presented as mean $\pm$ S.E. All statistical analyses were performed using R version 4.1.1 (the R foundation for statistical computing; www.r-project.org, accessed 25 August 2021).

3. Results

3.1. Mortality

During the first part of EP1, until fish numbers were reduced on day 171, the mortality rates were 5.0%, 2.2%, and 4.2% in the 7C, 10C, and 12C groups, respectively. From that point until the end of EP2 at day 654, the mortality rates were 6.8%, 5.6%, and 9.5% in the same groups, respectively.

3.2. Growth, Puberty, and Sexual Size Dimorphism (SSD)

The initial mean body weight (W), as estimated from bulk weights on day 1, was not significantly different among the groups ($p > 0.05$). The effect of temperature on growth was

already evident on day 48, when the mean body weights of all groups were significantly different ($p < 0.05$, Figure 1). During EP1, the differences in body weight continued to increase, and at the end of EP1 on day 315, the mean weights in groups 7C, 10C, and 12C were 40.4 ± 0.9, 54.9 ± 0.9, and 66.6 ± 1.0 g, respectively (Figure 1).
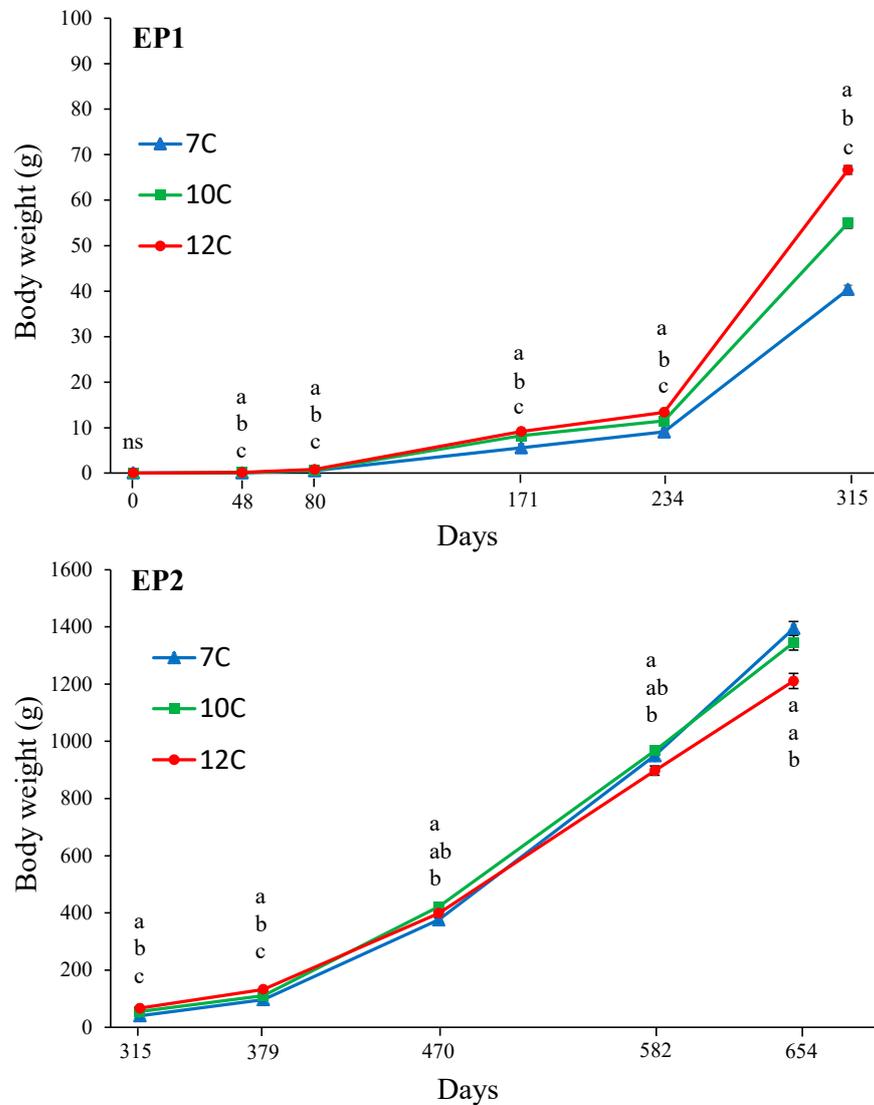

Figure 1. Mean growth in W of Arctic charr reared at three different temperature regimes: 7C (▲), 10C (■), and 12C (●) during the juvenile stage in experimental phase 1 (EP1). Experimental phase 2 (EP2) started on day 315 when the temperature was adjusted to 7 °C in all groups. In all groups the salinity was increased from 4 to 22 ppt on day 379 after the fish had been transported from the Verid to MFRI research station. Different lower-case letters denote significant differences between groups at the 5% level of significance.

During the first two months of EP2, after all groups were acclimated to 7 °C, the temperature-induced size differences established during EP1, between groups 7C, 10C, and 12C, were maintained. However, during the following three months, the 10C group had the highest growth rate and became significantly heavier than 12C on day 582 ($p < 0.05$). By day 582, the 7C group had transcended the 12C group, and had a significantly higher W than 12C at harvest ($p < 0.05$). During the final growing period from day 582 to 654, group 7C also transcended the 10C group and had the highest W at the end of EP2 (1395 ± 24 g). The 10C group ranked a close second with a final W of 1340 ± 26 g, while the 12C group had a final W of 1211 ± 26 g (Figure 1).

Relative size differences between males and females, indicative of sexual size dimorphism (SSD), were analyzed from tagging on day 234 until the fish were harvested at the end of EP2 (Figure 2). In all groups the degree of SSD increased between measurements, except during the last period in the 12C group ($p < 0.05$). Growth of the sexes diverged earlier with increasing temperature. Males in the 12C group were already significantly larger than females when the fish were PIT tagged on day 234, whereas in the 10C and 7C groups, significant differences between sexes were first observed on day 470 (Figure 2; $p < 0.05$). At harvest on day 654, the relative differences in body weights between males and females were 11.6%, 17.3%, and 17.5% in groups 7C, 10C, and 12C, respectively. However, when fish with GSI above indicative puberty thresholds were excluded (>0.2% and >0.35%, for males and females, respectively), the gender differences were reduced to 9.8%, 13.1%, and 3.3% in the 7C, 10C, and 12C groups. The overall number of males and females did not differ significantly from a 1:1 ratio in any group ($\chi^2 < 3.84$, $p > 0.05$).
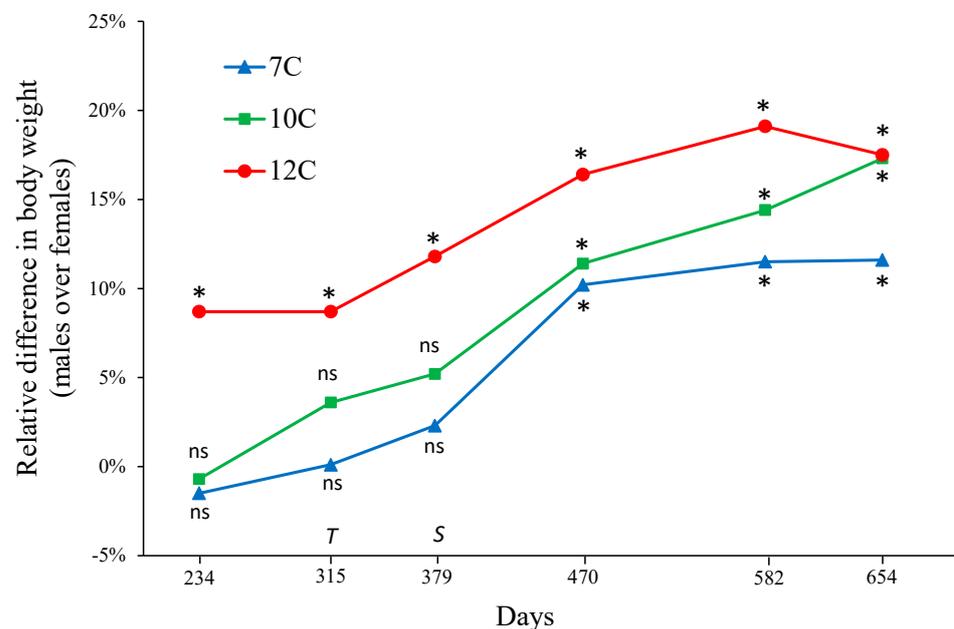

Figure 2. Body weight (W) progression of Arctic charr males relative to their female counterparts from tagging on day 234 until harvest on day 654. From day 0 until day 315 the groups were reared at three target temperatures, 7C (▲), 10C (■), and 12C (●). On day 315 all groups were acclimatized to 7 °C (*T*) and reared at 7–8 °C until harvest on day 654. On day 379 all groups were subjected to a salinity change from 4 to 22 ppt (*S*). Asterisks indicate significant differences in W at the 5% level of significance. Non-significant differences in W are indicated (ns).

In Table 1, males and females from each group are sorted and grouped based on GSI at harvest. At harvest, the overall mean GSI values of males in the 7C, 10C, and 12C groups were 0.23 ± 0.09, 0.77 ± 0.12, and 1.02 ± 0.20%, respectively, while the respective mean GSI values of females were 0.26 ± 0.01%, 1.31 ± 0.19%, and 2.46 ± 0.40% (Table 1).

Table 1. Male and female Arctic charr from each group sorted into three maturation stages according to GSI at harvest on day 654. Mean GSI within each maturation stage (GSI), number of fish within each stage (n). Mean body weights (W) $\pm$ $_{S.E.}$ at tagging on day 234 (W_5) and harvest at day 654 (W_{10}). No males had GSI from 0.6% to 2.0% and no females had GSI from 0.8% to 3.5%.

Group	Maturation Stage	GSI Range	GSI (%)	n	W_5 (g)	W_{10} (g)
Male						
7C	0	<0.2	0.10 ± 0.003	112	9.1 ± 0.31	1483 ± 39
7C	1	0.2–2	0.44 ± 0.14	2	6.4 ± 1.0	1465 ± 145
7C	2	>2	7.6 ± 1.60	2	11.3 ± 2.9	600 ± 78
7C	Overall	0.01–8.2	0.23 ± 0.20	116	9.17 ± 0.3	1478 ± 36
10C	0	<0.2	0.09 ± 0.002	223	11.5 ± 0.3	1564 ± 26
10C	1	0.2–2	0.43 ± 0.07	5	12.0 ± 1.5	1254 ± 208
10C	2	>2	5.8 ± 0.34	31	12.0 ± 0.6	812 ± 61
10C	Overall	0.01–8.1	0.77 ± 0.12	262	11.5 ± 0.3	1449 ± 28
12C	0	<0.2	0.09 ± 0.003	106	14.1 ± 0.4	1411 ± 34
12C	1	0.2–2	0.37 ± 0.009	2	13.4 ± 1.0	1831 ± 39
12C	2	>2	6.3 ± 0.289	18	14.4 ± 1.0	810 ± 65
12C	Overall	0.01–7.7	1.02 ± 0.20	126	14.0 ± 0.4	1326 ± 35
Female						
7C	0	<0.35	0.24 ± 0.01	109	9.2 ± 0.3	1345 ± 33
7C	1	0.35–3.5	0.45 ± 0.04	12	9.4 ± 1.1	950 ± 107
7C	2	>3.5	-	0	-	-
7C	Overall	0.06–0.9	0.26 ± 0.001	121	9.1 ± 0.3	1306 ± 32
10C	0	<0.35	0.27 ± 0.002	144	11.2 ± 0.4	1372 ± 32
10C	1	0.35–3.5	0.43 ± 0.007	86	11.8 ± 0.5	1107 ± 38
10C	2	>3.5	9.1 ± 0.62	29	12.8 ± 0.8	857 ± 68
10C	Overall	0.12–14.4	1.31 ± 0.19	259	11.7 ± 0.3	1226 ± 24.4
12C	0	<0.35	0.29 ± 0.01	34	12.5 ± 0.6	1365 ± 55
12C	1	0.35–3.5	0.43 ± 0.01	56	13.4 ± 0.5	1185 ± 48
12C	2	>3.5	10.2 ± 0.59	24	12.2 ± 0.7	626 ± 45
12C	Overall	0.14–14.5	2.46 ± 0.40	114	12.8 ± 0.3	1113 ± 38

The ratio of fish having GSI above indicative puberty thresholds increased with temperature in both sexes. However, while the male maturity (GSI > 0.2%) increased only slightly with temperature (3.5%, 13.7% and 15.9% in 7C, 10C, and 12C, respectively), the female maturity (GSI > 0.35%) increased much more dramatically with rising temperature (9.9%, 44.4%, and 70.2% in the respective temperature groups, Figure 3).

Overall, maturing males and females had higher W at day 234 than immature fish. However, at harvest on day 654, the size rank was reversed and the fish in immature stages had the highest W (Table 1). The effects of sexual maturation on growth can be observed in greater detail when the relative size differences of immature and maturing fish are compared retrospectively from tagging on day 234 until harvest. When compared with immature males, second-stage mature males in the 10C and 12C groups were generally larger during the juvenile stage. However, the maturing males showed depressed growth as early as one year before harvest and weighed 63% and 54% less than the immature males in the 10C and 12C groups, respectively (Figure 4).
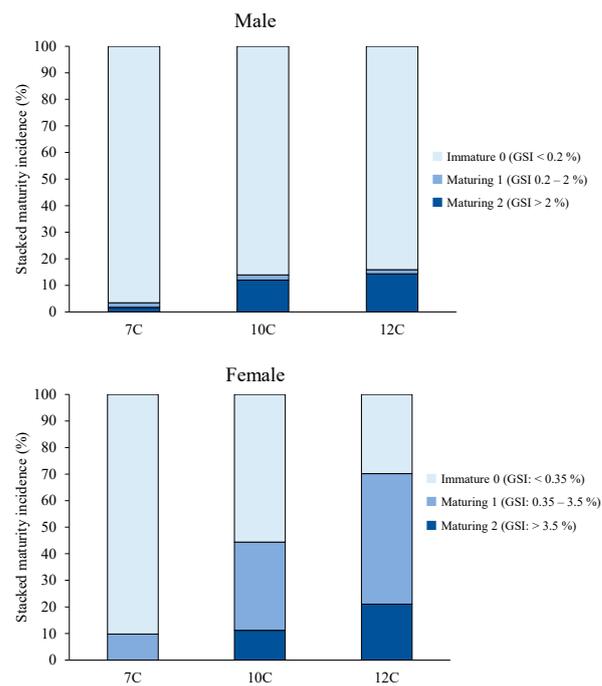
Figure 3. Harvest maturity incidence (%) in male and female Arctic charr reared at 7, 10, and 12 °C during the juvenile stage. Mean GSI values within each maturation class are shown in Table 1.
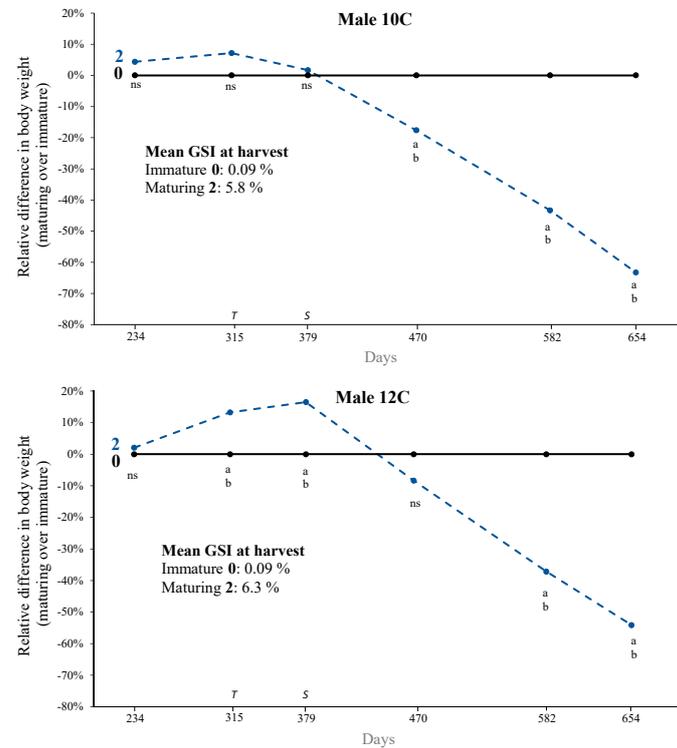

Figure 4. Body weight (W) progression of immature male Arctic charr in experimental groups 10C and 12C, relative to maturing conspecifics. The maturity stages are based on gonadosomatic indices (GSI) at harvest on day 654. Immature males in stage 0 had GSI from 0.01% to 0.2%, while those in stage 2 had GSI > 2%. Males in maturity stage 1 are excluded from this analysis due to low numbers of individuals. On day 315 all groups were acclimatized to 7 °C (*T*) and reared at 7–8 °C until harvest. On day 379 all groups were subjected to an abrupt increase in salinity from 4 to 22 ppt (*S*). Different lower-case letters denote significant differences between groups at the 5% level of significance.

As for the males, the maturing females in the 10C and 12C groups were generally somewhat larger than the immature females during the juvenile stage, but over the course of the experiment there was a progressive decline in the relative size difference between immature and maturing females, until the immature females transcended the maturing females and became significantly larger than females in maturation stages 2 and 1 on days 582 and 654, respectively (Figure 5).
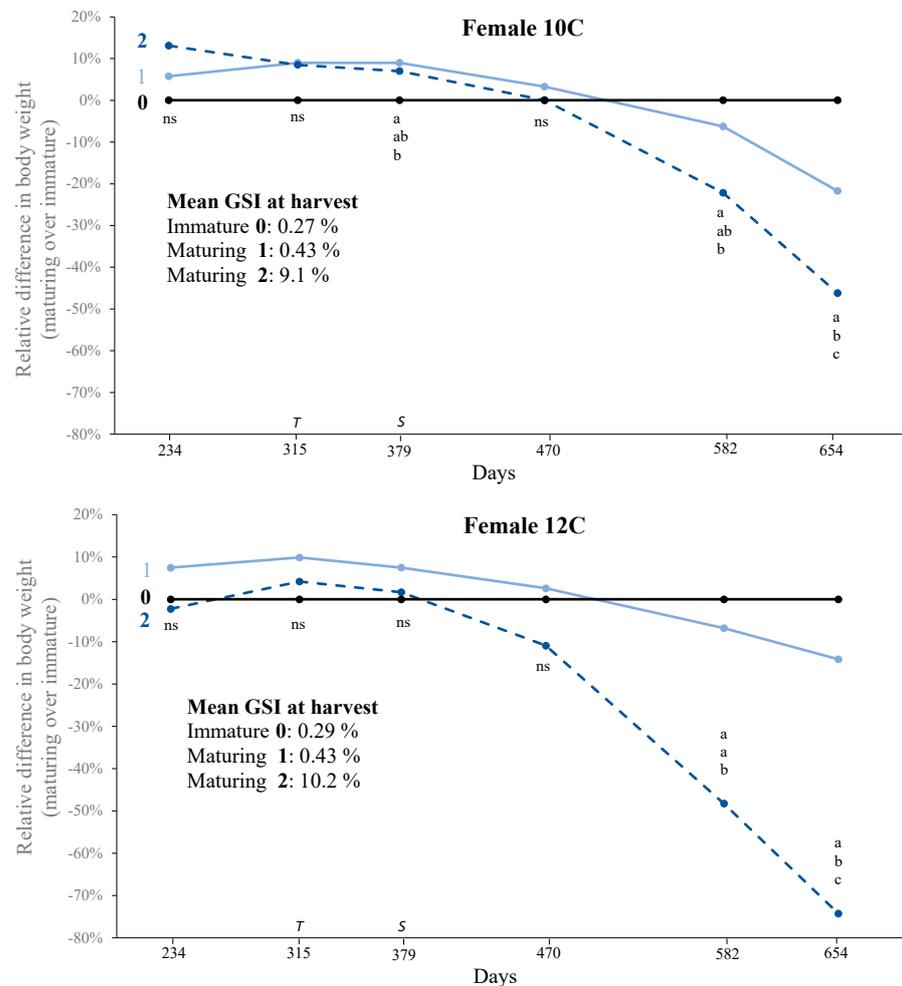

Figure 5. Body weight (W) progression of immature female Arctic charr in experimental groups 10C and 12C, relative to maturing conspecifics. The maturity stages are based on gonadosomatic indices (GSI) at harvest on day 654. Immature females in stage 0 had GSI within 0.15% and 0.35%, while females in stages 1 and 2 had GSI from 0.35% to 3.5%, and >3.5%, respectively. On day 315 all groups were acclimatized to 7 °C (*T*) and reared at 7–8 °C until harvest. On day 379 all groups were subjected to an abrupt increase in salinity from 4 to 22 ppt (*S*). Different lower-case letters denote significant differences between groups at the 5% level of significance.

While the rearing temperatures during EP1 influenced the overall growth trajectory as shown in Figure 1, the results are very different when all maturing fish are excluded from the analysis (Figure 6). Thus, temperature during EP1 had little or no effect on the growth of immature females during EP2 and females from all temperature groups had similar mean body weights at harvest (1345–1372 g, Figure 6A). However, the early thermal environment may have affected the on-growing performance of immature males, as immature 12C males had the highest mean body weight at the start of EP2 but a significantly lower body weight (1411 ± 34) than immature 10C males at harvest (1564 ± 26 g, $p < 0.05$, Figure 6B). The immature 7C males also transcended the 12C males and had the second highest body weight at harvest (1483 ± 39).
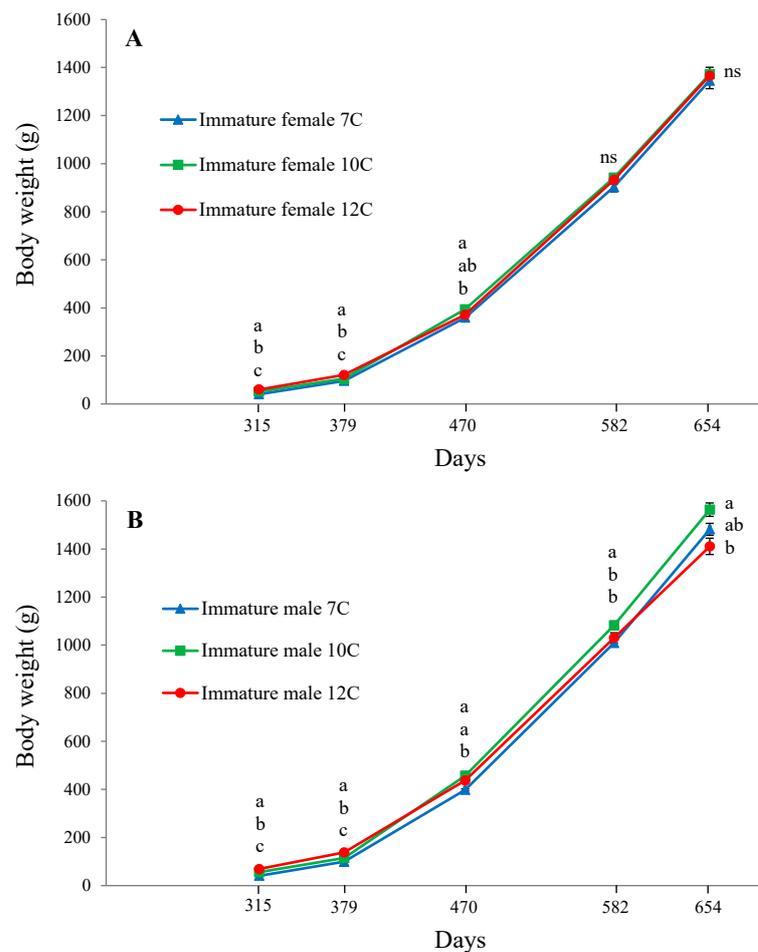
Figure 6. Mean growth in W of immature females (**A**) and males (**B**) during EP2. The 10C and 12C groups were subjected to a decrease in temperature from 10 and 12 °C to 7 °C on day 315, while group 7C remained at 7 °C. In all groups the salinity was increased from 4 to 22 ppt on day 379 after the fish had been transported from Verid to MFRI research station. Different lower-case letters denote significant differences between groups at the 5% level of significance.

4. Discussion

In the present study, long-term growth, and development of Arctic charr were monitored over 21 months, from the late yolk-sac stage to adult size. The study, which was carried out in two sequential experimental phases, shows how the early thermal environment can influence important physiological traits of Arctic charr.

At the beginning of the study, alevins were acclimatized to 7, 10 or 12 °C and reared at these temperatures for 315 days, or until vaccination at mean weight 40–66 g. The direct thermal effects on growth were clearly demonstrated during EP1, where growth rate increased with rising target temperatures from 7 to 12 °C. However, in the following 339 days of EP2, or after the groups were all acclimatized to 7 °C, early rearing at 10 and 12 °C was found to have long-term consequences from a farming perspective, with higher incidence of preharvest maturation, which in turn resulted in suppressed growing performances when compared with the 7C group.

In a recent study, Gunnarsson et al. [29] demonstrated similar effects of rearing temperature in the size range from 20 to 500 g on the incidence of puberty and subsequent growth in Arctic charr. While the present study demonstrates long-term effects of early rearing temperature from the late alevin stage to about 50 g size, another question at hand is how early in ontogeny does temperature influence the age at maturity and adult growth? In fish, there are many examples demonstrating that environment during early

development influences phenotypic traits later in life [8,33], and in salmonids, these include reproductive investment [34], thermal acclimation capacity [35,36], growth [37–39], and sex determination [40]. It can thus be hypothesized that the age at puberty of the Arctic charr in the present study may have been influenced by temperature as early as on the alevin stage. However, further research is required to provide more detailed information as to how heated water should be utilized in Arctic charr farming without causing losses associated with early maturation.

Temperature has been found to influence growth and age at maturity of Arctic charr in the absence of temperature changes [28,41]. In the present study, however, the temperature drop at the end of EP1 may have affected the growth of the 10C and 12C groups during EP2. Gunnarsson et al. [29] found that a 3 °C reduction in temperature at the higher end of the thermal range induced long-lasting growth disturbances for Arctic charr. Several studies have demonstrated that thermal performance curves are not fixed within species but can shift along the temperature-axis because of phenotypic plasticity [42–44]. It is therefore possible that the early rearing at 10 and 12 °C in the present study may have caused an upward shift in thermal range and optimal temperature for growth. When transferred to low or medium on-growing temperatures (such as 7–8 °C in the present study), these warm-adapted fish may have been reared at the low end of their thermal range and their growth may have suffered accordingly. The observed long-term growth depression of the immature 12C males, as shown in Figure 6B, may indeed suggest that this may have been the case for the Arctic charr males in this study. On the other hand, the absence of such an effect for immature females may suggest gender differences in the plasticity of the early thermal response of Arctic charr.

In salmonids, puberty has often been found to have opposite effects on growth, with increased somatic growth and appetite during the early stages when the gonads are small, and negative effects when large energetic investments are directed to gonadal growth. In Arctic charr and Atlantic salmon, pubertal growth spurts have been found to be associated with sex steroid levels [32,45]. The reported growth divergence of immature and maturing Arctic charr is highly variable, i.e., some studies have reported enhanced growth of maturing charr [46–49], while others have indicated small or no divergence between immature and maturing charr [50–53]. In the present study, the relationship between growth and age at puberty was clearly observed when the growth of maturation groups was compared retrospectively. It was found that fast growing juveniles during EP1 had a propensity for early maturation. This is consistent with previous studies on Arctic charr [54], as well as studies on other fish species e.g., [55–57]. However, in contrast to these earlier studies where the initial growth advantage was maintained up until the advanced stages of puberty, the maturing individuals in the present study displayed growth reduction long before the fish allocated significant energy reserves to gonadal growth.

Gonadosomatic indices of immature female Arctic charr and Atlantic salmon have typically been found to be <0.35% [15,32]. In the present study, females that seem to have been in the early stages of gonadal recrudescence at harvest, with a mean GSI of 0.43%, had markedly lower growth rates than the immature charr during EP2. This suggests that the immature females may have started outperforming the maturing females before the GSI of the maturing females surpassed 0.35%, or even as early as nine months before harvest. Based on previous work, the GSI of immature male Arctic charr is typically <0.1%. However, a histological examination is needed for correct classification of pubertal stages and a GSI in the range of 0.1–0.2% has not been found to be exclusive to maturing males [58]. In the present study, males having GSI in the range of 0.1–0.2% showed a similar growth performance as those having GSI < 0.1% (data not shown). On the other hand, maturing males having GSI in the range of 2–8% at harvest began showing reduced growth when they were on average between 60 and 120 g, or roughly 11 to 9 months before harvest. Thus, with regards to the developmental stage at which puberty began having negative effects on growth, it seems that sexual maturation elicited a gender-neutral effect.

Many factors, including temperature, salinity, photoperiod, and adiposity, are known to influence the development of sexual maturation and growth in Arctic charr [41]. It is therefore difficult, with any degree of certainty, to identify factors that caused the early growth restriction of maturing individuals in the present study. However, Duston et al. [59] found that relative differences in growing performances of maturing and non-maturing Arctic charr are greatly influenced by the photoperiod. In the present study the Arctic charr was reared under continuous light (LD 24:0) from the late alevin stage up to harvest size over a period of 654 days, and unlike most previous studies reporting similar or higher growth rates of maturing Arctic charr, the fish in this study did not show any prominent seasonal growth cycles. Thus, while the rearing environment in this study may have prevented the maturing fish from showing pubertal growth spurts, it may have allowed for a relatively even growth among the immature individuals.

Overall, the growth advantage of maturing fish during the juvenile stage started diminishing rapidly after the fish were transferred from 4 to 22 ppt. This is likely to have occurred because high salinity stimulates gonad growth in Arctic charr [15,16,60]. While the physiological mechanisms behind the effects of salinity on maturity are unclear, it has been suggested that the effect may be stress related [41]. Stress can influence reproduction of fish in many ways, depending on duration and the severity of the stressor, as well as the developmental stage in which the stress is encountered. Moreover, stress experienced during one developmental phase can have an effect during later phases [61]. It is therefore likely that the abrupt increase in salinity experienced on day 379 as well as the prolonged exposure to 22 ppt may have enhanced the effect of the early thermal environment on growth and age at maturity. Taking into consideration that most farmed Arctic charr in Iceland are reared in brackish water during the on-growing phase (>100 g), further studies on the effects of salinity on pre-harvest maturity may be warranted.

While the present study contrasts previous findings with regards to the relative growth differences of maturing and immature Arctic charr, the results are in broad agreement with empirical studies on the growth dynamics of early- and late-maturing fish. Usually, adult body sizes are found to be negatively correlated with the age at maturity, e.g., [5,62,63], and this phenomenon is frequently discussed in the context of the temperature size rule (TSR) which describes the plastic response of ectotherms, whereby individuals from colder areas grow slower, mature later, and become larger than individuals from warmer areas [64–66].

4.1. Sexual Size Dimorphism (SSD)

Sex-dependent variation in the age at puberty is found in many animal species. Usually, members of the larger sex mature later than members of the smaller sex, and the magnitude of SSD is often positively correlated with sex differences in the age at maturity [67]. Sexual size dimorphism is therefore commonly regarded as an important aspect in aquaculture and has prompted scientists to find methods to produce mono-sex populations using only the gender that grows faster and matures later [68]. From an aquaculture perspective, the males in the present study outperformed the females in all groups. However, the effect of early thermal environment on maturity was different between the sexes, with the females displaying a steeper increase in maturity with rising temperature than the males (see Figure 3 and Table 1). Liu and Duston [53] reported similar results in the Canadian Fraser River strain of Arctic charr, where maturity rates were strongly temperature dependent, especially in female charr reared under continuous light. Moreover, Gunnarsson et al. [29] found that temperature had positive effect on gonad growth in females but not males. These results, like the present study, suggest that the need for mono-sex production in Arctic charr farming may to some extent depend on the rearing temperature. This may also apply to other species, as recent studies have demonstrated that salmonids [69,70], European perch (*Perca fluviatilis* L.) [71], lake whitefish (*Coregonus clupeaformis*) [72], as well as animals of other classes [73,74], show intraspecific latitudinal variations in SSD. Much of this variation is thought to be caused by sex differences in body size plasticity. However, laboratory studies, such as the present study, have rarely been conducted, and as

biogeographic studies of SSD are based on field samples, it has often not been possible to distinguish between the effect of slow evolutionary divergence and sex-specific differences in phenotypic plasticity [75].

Many studies have suggested that SSD is established at the onset of puberty in parallel with an increase in sex hormone secretions [76,77]. In the present study, during the last six months of EP2 (day 470 to 654) the 7C group displayed a relatively modest degree of male-biased SSD in comparison with the 10C and 12C groups, indicating that physiological processes associated with sexual maturation may underlie the development of male-biased SSD during EP2. It should, however, be noted that all groups displayed the most rapid divergence in gender sizes during the juvenile stage. During this period, the degree of SSD was positively correlated with temperature, and while the 7C and 10C groups did not show significant SSD at tagging (~10 g), the males in group 12C had already become 8.7% larger than the females. In a recent study, temperature was found to influence SSD in chinook salmon (*Oncorhynchus tshawytscha*) as early as the alevin stage, where the sexes did not differ at 10 °C, but males were heavier than females at 15 °C [78]. In the same study, a female-biased SSD was observed at the adult stage, and the authors speculated that a head start on growth by the males may underlie their maturation at a smaller size. This hypothesis is not supported by the present study, as males tended to reach puberty at a larger size than females despite faster growth during the juvenile phase. Thus, the relative importance of early SSD with regards to the development of sexual maturation is currently uncertain.

4.2. Implications of the Experimental Set-Up

When discussing the results of this study from an aquaculture perspective, it is important to note that the Arctic charr juveniles were reared in small tanks (20 L) during the first 234 days (up to 10–13 g). In these tanks the juveniles showed normal growth rates for the first few months from the initiation of exogenous feeding, but eventually they outgrew the tanks and showed depressed growth towards the end of the period in which they were kept in the small tanks (see Figure 1). Based on unpublished data for the growth of juvenile Arctic charr reared at 10 °C in larger tanks at the MFRI research station, the time length of EP1 was approximately two months longer than it would have been if the juveniles had been reared in larger tanks. This temporary growth restriction does not seem to have influenced the growth potential of the experimental fish since the long-term growth performances were similar to those found in previous studies with Hólar strain Arctic charr [15,16]. However, the prolonged duration of EP1 may have enhanced the effects of temperature on growth because temperature can influence the age at maturity independently of growth [5]. Despite this shortcoming, the results agree with extensive data collected for nearly two decades by the commercial Arctic charr and salmon farming company Samherji Fiskeldi, which has consistently demonstrated slower adult growth in groups reared at elevated temperature during the juvenile stage.

5. Conclusions

The present study demonstrates that Arctic charr has a high degree of thermal plasticity, as rearing temperatures over a period of 315 days from the end of the yolk-sac stage until ~50 g can profoundly influence long-term growth performances and the incidence of precocious maturity at harvest. Unlike previous studies, where maturing Arctic charr have been found to grow similarly or faster than their immature conspecifics up to the advanced stages of maturation, the present study showed a marked growth depression during the early stages of puberty. Although the physiological mechanisms behind the early growth reduction of maturing fish are not clear, the study indicates that it may be salinity related, and as most of the Arctic charr farming in Iceland takes place in brackish water, the results are obviously of applied interest. The results of the present study may also be relevant from a global warming perspective, as elevated temperatures during the juvenile stage are observed to lead to a lower age at maturity and most likely also to a reduced maximum size.

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