VARIATION IN GROWTH OF HATCHERY REARED ARCTIC CHARR, SALVELINUS ALPINUS (L.)

BY

MICHAEL H. PAPST

A Thesis
Submitted to the Faculty of Graduate Studies
in Partial Fulfillment of the Requirements
for the Degree of

DOCTOR OF PHILOSOPHY

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ISBN 0-612-13432-6

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VARIATION IN GROWTH OF HATCHERY REARED ARCTIC CHARR, *Salvelinus alpinus* (L.)

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A Thesis submitted to the Faculty of Graduate Studies of the University of Manitoba in partial fulfillment of the requirements for the degree of

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ABSTRACT

Wild Arctic charr populations and groups of hatchery reared Arctic charr exhibit a high degree of phenotypic plasticity. Phenotypes include a slow growing dwarf form and a fast growing form. The rate of increase in variation in charr weight was positively correlated with increasing mean weight, with mean weight explaining over 95% of the variation. Under hatchery rearing conditions of constant water temperature and excess rations, groups of Arctic charr exhibit a high degree of consistency in the rate of increase in variation. The growth pattern of charr is established early in life, but is not affected by time of hatch or time of first feeding. Ration level does affect variation in weight. Charr groups fed a restricted ration have a lower variation. Rearing density had no effect on the rate of increase in variation in charr weight. A small number of slow growing male charr mature early, but early sexual maturation is not a significant factor affecting the rate of increase in variation in weight. Small slow growing charr do not have a poorer gross nutritional state than faster growing charr. Offspring sired by slow growing early maturing charr do not exhibit a different rate of increase in variation in weight than charr sired by faster growing large charr.

It was concluded that growth depensation in hatchery reared charr results primarily from the expression of several phenotypes

which differ in their growth rate (polyphenism). Ration level is one environmental factor which can trigger a change in charr polyphenism and thereby affect the rate of growth depensation.

ACKNOWLEDGEMENTS

First and foremost, I would like to thank Dr. T. A, Dick for his patience and guidance throughout the course of this study and during the preparation of this manuscript. I would also like to express my appreciation to the members of my committee for their advice and assistance.

I would like to thank the staff of the Rockwood Aquaculture Research Centre who helped make this study possible.

A special thank you is extended to Dr. M. G. Boyer for introducing me to the world of research and to Mr. P. H. Sutherland for his special support.

Finally I would like to thank my wife Diane and my children Victoria, Henry and Joseph, whose love and patience made this work possible.

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GENERAL INTRODUCTION

VARIATION IN GROWTH OF HATCHERY REARED ARCTIC CHARR, SALVELINUS ALPINUS (L.)

A number of studies have examined the biology of sympatric charr populations (Jonsson & Hindar 1982; Johnson 1983; Nordeng 1983; Svedang 1990). In most cases, sympatric charr populations are segregated into one small and one large form, commonly referred to as dwarf and normal charr respectively. Often three coexisting forms are found, segregating the population into anadromous, small and large freshwater resident forms. Forms may differ in several aspects of life history including; feeding ecology; growth rate; size and age at maturity; morphology. Resident charr forms generally have lower growth rates, are younger and smaller in size at maturity then anadromous forms (Nordeng 1983).

Based on rearing and transplant experiments Nordeng (1983) hypothesized that coexisting forms of Arctic charr can arise from the same gene pool and that an individual may manifest all three forms during its lifetime. Svedang (1990) reported that between coexisting dwarf and large forms of charr in central Sweden, the dwarf form was dominant for growth and maturation. Nordeng (1983) concluded that the segregation of different forms was dependent on the individual charr's genetic constitution and access to food. An

analysis of the offspring of hatchery reared small resident forms, large resident forms and anadromous forms had similar percentages of each of the forms (Nordeng 1983)(Table 1).

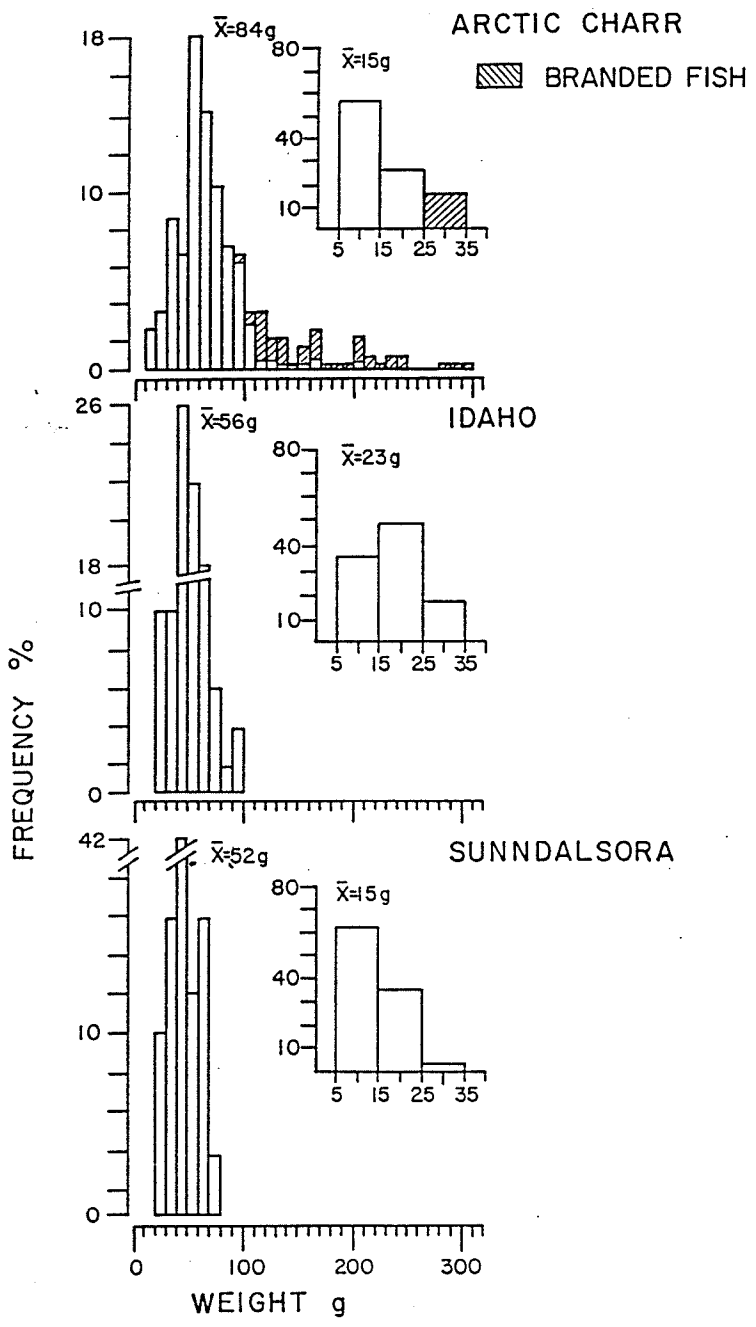
Variation in growth of Arctic charr cultured under hatchery conditions has been documented (Papst and Hopky 1983; Jobling & Wandsvik 1983; Jobling 1985; Jobling & Reinsnes 1986; Jobling & Reinsnes 1987). Characteristically weight distributions of hatchery reared charr are skewed due to groups of charr with fast and slow growth rates (Papst and Hopky 1983)(fig 1). It has been inferred by some authors that this variation in growth results primarily from social interaction between individual fish (Jobling & Wandsvik 1983; Jobling 1985; Jobling & Reinsnes 1986; Jobling & Reinsnes 1987). Changes to the rearing environment have been interpreted as having an effect on variation in growth by changing the degree or nature of social interactions (Christianson and Jobling 1990; Jobling and Baardvik 1994; Jorbensen and Jobling 1993).

Brown (1946) was the first author to use the phrase "size hierarchy effect" in relation to fish growth, but the mechanism(s) responsible for establishing size hierarchy effects in fish populations are still debated (Koebele 1985). Brown (1957) postulated that stress due to interactions between dominant and subordinate fish was responsible for the observed variance in growth rates in a size hierarchy. Magnuson (1962) concluded that

Table 1. Parental crosses and percentage of offspring for different "forms" (phenotypes) of Arctic charr; small resident charr (SR), large resident charr (LR) and anadromous charr (A). Charr were from Overvatn (Salangen river system) in northern Norway. Table based on material presented in Nordeng (1983).

Parental cross	Number Charr	Percent Offspring		
		SR	LR	A
SR X SR	2705	67.9	10.8	21.3
LR X LR	1629	66.9	11.5	21.6
A X A	4046	62.9	14.2	22.9

Figure 1. Weight frequency distributions at the beginning (inserts) and end of an 85 day growth trial for a group of Arctic charr and for groups of rainbow trout (Idaho and Sunndalsora strains). Figure adapted from Papst and Hopky (1983).


ARCTIC CHARR
BRANDED FISH
IDAHO
SUNNDALSORA
X̄=84g
X̄=15g
X̄=56g
X̄=23g
X̄=52g
X̄=15g
FREQUENCY %
WEIGHT g
0
100
200
300
5
15
25
35
10
40
80
18
26
42

both Brown's experiments were not conducted at maximum ration and that the hypothesis that growth differences in fish hierarchies results
from physiological stress was incorrect. Magnuson (1962) working with medaka Oryzias latipes) concluded that both disproportional food acquisition and genetic differences could account for individual variations in fish growth weight. Koebele (1985) working with juvenile cichlids (Tilapia zillii), concluded that dominant-subordinant relationships, were responsible for disproportional food acquisition and thus mediated growth rate in size hierarchies.

Most of the research on fish size hierarchy effects has been conducted in aquaria, with small numbers of fish. The relationship between these experiments and commercial scale aquaculture has not been demonstrated. Studies of the variation in growth of hatchery reared Arctic charr have not attempted to evaluate variation in the terms of the known ability of wild populations to produce coexisting forms.

Polyphenism is a term used to describe the situation in which one genotype produces two or more discrete phenotypes in response to an environmental signal (Stearns 1989, 1992). Polyphenism in the production of phenotypes of charr with different growth rates would result in variability in individual charr weights in a population even

if that population resulted from a small gene pool. Balon (1984)

proposed that charr could adopt alternative life history styles: unstable (low competition) environments were suggested to favour dwarf, generalist charr while stable competitive ones allow the development of large specialists. There is no reason to assume that hatchery reared Arctic charr would not express polyphenism similar to that observed in wild charr populations. The observed growth depensation in hatchery reared charr might therefore be a result of polyphenism.

The unanswered question is how much variation in size observed in hatchery reared Arctic charr results from variation in life history (polyphenism) and how much results from the effects of size hierarchy. Understanding the principal factors causing variation in growth of hatchery reared Arctic charr is important to hatchery operators as it will determine if genetics or genetic/environmental interactions in the rearing systems, will have the greatest effect on variation in growth. Furthermore an understanding of variation in growth of hatchery reared Arctic charr may provide insight into the development and segregation of coexisting forms of wild Arctic charr populations.

A comparison of the effects of genetic and fish culture factors on the variance in fish weights of test populations requires a method which allows comparisons among treatments where

significantly different mean weights of fish occur. The coefficient of variation (CV=standard deviation/mean X 100) of the distribution of individual fish weights has been used to describe treatment effects and changes in the variation of fish weights over time (Purdom 1974). Comparisons of CV are confounded by differences in the final mean weight of the test groups (Purdom 1974). A model to describe variance in fish weight which is not confounded by differences in final group mean weights or differences in initial variance has been proposed (Arnason et al. 1992). The application of the model to test changes in variance in weight with the growth of families and strains of charr has yet to be reported. The model may also have uses in determining the significance of genetic and rearing variables on variation in fish weight.

The present study examines the development of variation in weight as test groups grow and the effects of culture factors such as ration (amount of food fed) and density on variation in weight. Development of variation in weight was examined in several full-sib families of Arctic charr and in groups from both anadromous and resident forms. The relationship between variation in life history (size and age at maturity) and variation in weight of hatchery reared charr was examined.

CHAPTER 1

Early growth and variation in weight in hatchery reared Arctic charr (Salvelinus alpinus L.)

ABSTRACT

Many Arctic charr populations exhibit phenotypic plasticity, with the occurrence of two or more forms. Arctic charr reared under controlled conditions exhibit a large variation in body weight and form. A full sib family of Arctic charr reared under hatchery conditions showed increased variation in individual body weight over time, with increasing mean fish weight explaining most of the increased variation. This relationship between increasing variation in weight and increasing mean weight is established shortly after first feeding with some charr having consistently low growth rates. A small number of these slow growing charr became sexually mature 522 days post fertilization. All these individuals were males and removing them from the distribution of charr body weights did not significantly change the distribution. A significant number of charr exhibited no gonad development and could not be sexed. This group of charr appeared to have a significant effect on the weight distribution. Sampling of a maturing hatchery brood stock originating from a single full sib mating, supports the conclusion that small maturing males occur in hatchery charr populations but do not appear to significantly contribute to the observed variation in charr weights.

INTRODUCTION

Arctic charr reared under hatchery conditions exhibit a positive correlation between the $\log_e$ increase in variance in fish weight and the $\log_e$ mean weight of the population (Arnason et al. 1992; Papst et al. 1992). This relationship between increasing variance in fish weight and increasing mean weight appears to develop early in the life history of the hatchery reared charr (Papst et al. 1992). These observation are consistent with the observations of Balon (1980), that shortly after first feeding charr could be divided into "glutton" forms and "hunger" forms, with "glutton " forms being noticeably larger and deeper in body form. The difference in size between the "glutton" and "hunger" forms increased as the charr aged, even after all charr had initiated exogenous feeding (Balon 1984). Physiological (genetic) factors have been identified as important in determination of slow growth rates of "stunted" hatchery reared charr (Jobling & Reinsnes, 1986).

Rearing and transplantation experiments have suggested that three coexisting forms of Arctic charr can arise from the same gene pool (Nordeng 1983). The three forms include a small or dwarf form, a large resident form and a large anadromous form (Nordeng 1983). These forms differ in their growth rate, sex ratios and time of first sexual maturity (Nordeng 1983). It is not clear whether the variation in weight observed in hatchery reared charr is an expression of the

same phenotypic plasticity demonstrated by wild charr populations. Early maturation amongst small male hatchery reared Arctic charr has been reported and these charr may represent an expression of the dwarf early maturing phenotype of charr, observed in wild populations (Papst & Hopky 1983).

In the present study the development of variation in weight in a full sib family of hatchery reared Arctic charr was observed from the time of first feeding in order to determine if variation in weight develops consistently from early in the life history as suggested by earlier studies (Papst et al. 1992). The effect of the dwarf maturing and non maturing phenotypes on variation in weight was also examined.

MATERIALS AND METHODS

Charr used in this experiment were members of two full sib families, originating from a first generation hatchery brood-stock developed from spawn taken from the Fraser River Labrador, Canada (de March & Baker 1990; Papst & Hopky 1984). The families were identified as LAc 1 and LAc 2. Family LAc 2 was a random sample of family number 7, described by Tompkins (1989).

Experiments were conducted at the Rockwood Aquaculture Research Centre, located 65 km north of Winnipeg Manitoba, Canada and operated by The Department of Fisheries and Oceans.

Family LAc 1 (Assessment of growth and variation)

Charr were reared in 61-l fiberglass tanks connected to a common bio-filter at a water temperature of 10°C, oxygen saturation was maintained at 80%. Charr were fed commercial rainbow trout feed (Martins Feed Mill, Elmira, Ontario, Canada) by hand four times daily during the period from 0830h to 1600h. No feeding occurred on census days. The amount of food fed was calculated using commercial feeding tables (Hilton & Slinger 1981) and the ration was adjusted every census day based on changes in the total wet weight of fish in each tank.

The growth experiment was 389 days and ended 522 days post fertilization. From 133 days PF to 196 days PF, a destructive sampling method was used to measure the wet and dry weights of individual charr and all charr were reared in a single tank. Charr were censuses by placing all the charr in a 2.0 l plastic pail and taking two dip net samples at random, using a 7 cm aquarium dip net. This sampling procedure produced two samples of approximately 25 charr each. Charr were fixed in a 5% formalin solution after being killed with an overdose of anesthetic (2-phenoxyethanol). After fixing, individual charr were dried on a paper towel and weighed on an electronic balance to the nearest 0.05 mg. Charr were then placed on individual glass slides and the hardened yolks removed. The slide containing the alevin and yolk were dried to a constant weight in an electric oven at 85 ^{o}C . The glass slides were cooled in a desiccator and the dried charr alevin, yoke and glass slide were weighted on an electronic balance to the nearest 0.05 mg. A correction factor was established to convert formalin fixed weights to wet weights (wet weight = -0.01 + 0.96 (formalin weight)), by weighing a group of fish before and after fixing .

From 210 days PF to 468 days PF individual charr wet weights were measured on days 272, 311, 313, 361, 388, 424, and 452, by anaesthetizing the fish with 2-phenoxyethanol, shaking off excess water and weighing individual charr to the nearest 0.05g on an electronic balance. The total weight of the charr in the tank was

determined by weighing all of the charr in a tared volume of water.

Three hundred and thirteen days PF two replicate samples of 150 charr were removed from the population and a random sample of approximately 70 charr from each of these replicate groups were individually weighed. A random sample of 16 fish in each group was marked with an individual hot wire brand. The two replicates were placed in separate 61 l tanks connected to a common bio-filter. Individual charr wet weights in both groups were measured periodically from 313 days PF to 468 days PF.

After the census on day 468 each of the two groups were divided randomly in two new groups and the resulting four groups placed into four separate 61 l tanks connected to a common bio-filter. All the charr from the four tanks were pooled after 54 days and a single random sample of 131 charr was killed with an overdose of 2-phenoxyethanol and individually weighed on an electronic balance. Gonads were removed from a random sub-sample of 75 charr and individually weighed. A maturity index (MI = gonad weight / body weight X 100) for each charr was calculated. Charr were sexed by examining the gonads.

Mean specific growth rate for the interval between two weighings was calculated using the formula:

$$G = 100(\log_e W_t - \log_e W_{t'}) / (t - t') \quad [1]$$

where G is specific growth rate (%/day), W_t is mean weight in g at time t, $W_{t'}$ is g mean weight at the previous weighing time (t'), and (t-t') is the time in days between weighing.

The effect of treatment on increase in variance of fish weights was tested using a linear variance model (Arnason et. al. 1992):

$$Y = b_0 + b_t X_1 + b_w X_2 \quad [2]$$

where $Y = \log_e (S_t^2 - S_0^2)$, X_1 is $\log_e t$, X_2 is $\log_e W_t$, b_t and b_w are the time and weight model coefficients. $S_t^2 - S_0^2$ is the increase in variance in fish weight to time t from the start of the growth trial at time 0.

Where $\log_e$ time was not significant, b_t was assumed to have a value of zero:

$$Y = b_0 + b_w X_2 \quad [3]$$

Expected coefficients of variation $E(CV_t)$ for weight distributions at time t were calculated using the linear variance model (Arnason et al. 1992):

$$E(CV_t)=((S_0^2/W_t^2)+e^{b^\circ t}{}^{b}{}^{t}W_{t\,w-2})^{0.5} \quad [4]$$

Throughout this study mean fish weights were expressed as the mean (± the standard deviation) and the variance model coefficients were expressed as (± the standard error). The coefficient of Variation (CV) for fish weight distributions were calculated using:

CV=(standard deviation weight/mean weight)X100 [5]

All data analyses were preformed using the Statistical Analysis System (SAS Institute Inc. ,Box 8000, Cary, NC) as implemented by the Freshwater Institute computer services.

Family LAc 2 (Assessment of maturity)

Family LAc 2 was reared initially at 10 °C as part of the growth experiments described by Tompkins (1989) . Rearing conditions were the same as those used for family LAc 1. At an age of approximately 1 year two groups of 100 charr were transferred to 61-l tanks at a water temperature of 6.4 °C. After 182 days, both groups of charr were transferred to a single 1500-l brood-stock tank. Thirty days after the transfer all the charr were Individually weighed by anaesthetizing the charr with 2-phenoxyethanol, shaking off excess water and weighing to the

nearest 0.1g on an electronic balance.

After 510 days, all surviving charr were individually weighed, fork length measured, sexed and gonads weighed following the procedure used for family LAc 2.

RESULTS

Family LAc 1

The mean dry alevin weight in family LAc 1 133 days PF was 4.7(1.3)mg and the yolk dry weight was 1.5(1.2)mg . Yolk weights were highly variable with a CV of 78.5 %. Alevin dry weights were less variable than yolk weights with a CV of 28.3%. The mean percent of total dry body weight which was yoke was 27.1% and ranged from a low of 1.4 to 60.6%. There was a significant (P=0.001) negative correlation between yoke dry weight and alevin dry weight, with dry alevin weight explaining approximately 54% (r^2=0.54) of the observed variance in yoke dry weight (fig. 2).

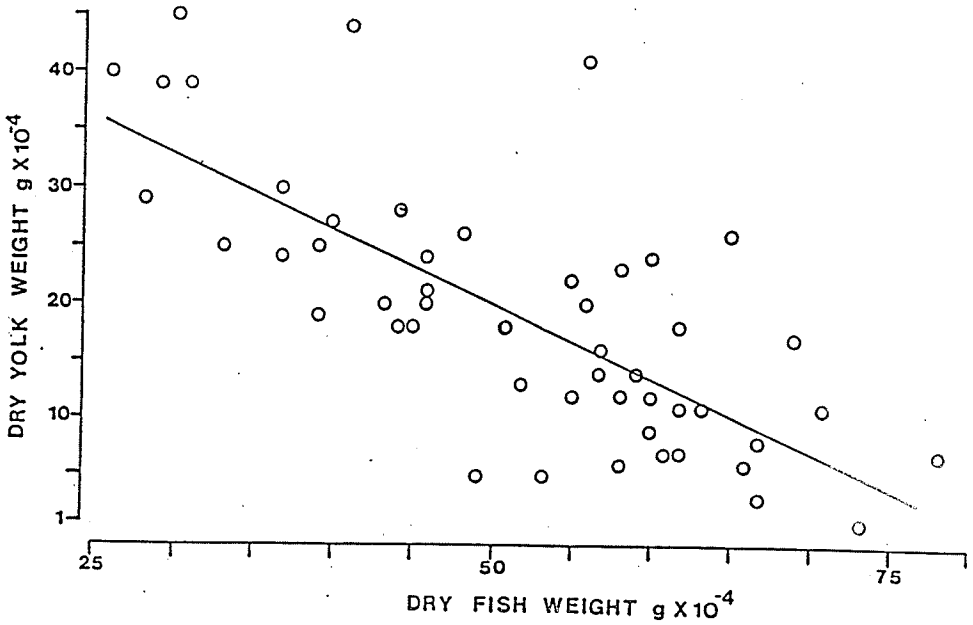
Alevin mean wet weight increased from 66.1(9.7)mg to 502.3(179.0)mg during the period from 133 to 196 days PF (Table 2). The mean dry weight of alevins increased from 6.2(1.1)mg to 79.5(33.3)mg during the same time period. The CVs increased for both the wet and dry alevin weight distributions between 133 and 196 days PF, with the majority of the increase occurring between 133 and 160 days PF (Table 2).

Mean charr wet weight increased from 0.7(0.3) to 5.2 (2.2)g, from 210 to 311 days PF (Table 3). The mean weights of the two groups of charr taken from the population 313 days PF were 5.8(7.3)g and 5.1 (2.0)g (Table 3). There was a marked difference in

Table 2. Mean (± standard deviation) and coefficient of variation (CV) of the distribution of charr wet and dry weights in family LAc 1 from 133 to 196 days post fertilization (PF).

Days PF	number Fish	Weight			
		Wet		Dry	
		Mean (±Sd) mg	CV %	Mean (±Sd) mg	CV %
133	50	66.1 (9.7)	14.7	7.1 (0.9)	12.7
160	49	97.8 (36.2)	37.0	9.8 (3.9)	39.8
168	49	165.4 (64.5)	39.0	18.8 (8.0)	42.9
181	50	274.3 (104.0)	38.2	46.6 (21.0)	45.1
196	46	502.3 (179.0)	35.6	76.8 (33.0)	43.0

Figure 2. Regression of dry charr yolk weight versus dry charr body weight for family LAc 1, 133 days post fertilization (PF).


DRY YOLK WEIGHT g X10-4
40
30
20
10
1
25
50
75
DRY FISH WEIGHT g X10-4

the variances of the two groups on day 313 but by the end of the growth trial 468 days PF variances were similar in the two groups (Table 3).

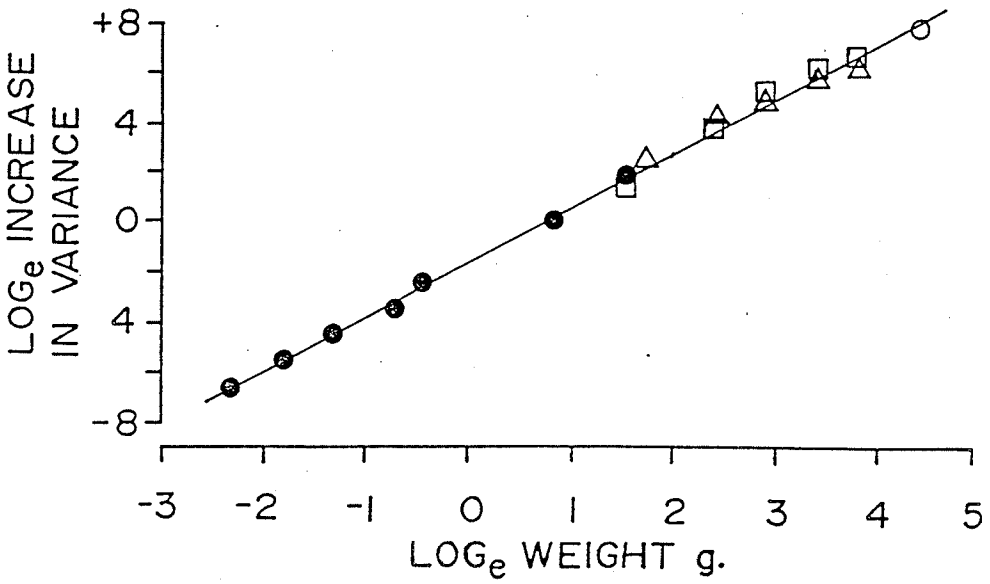
A significant (P=0.01) positive correlation was observed between the $\log_e$ increase in the variance of fish weight and the $\log_e$ mean fish weight of the charr in family LAc 1 during the time period from 133 to 311 days PF (Fig.3). There was a significant (P=0.01) positive correlation between the $\log_e$ increase in variance of fish weight and the $\log_e$ mean fish weight from 133 to 468 days PF (Fig. 3). There was a non significant (P=0.90) contribution of $\log_e$ time to the variance model [3] for the time period from 133 to 311 days PF and a non significant (P=0.89) contribution of $\log_e$ time to the variance model for the time period 133 to 468 days PF. Using the sub-variance model [4], assuming $\log_e$ time to be zero, Log_e mean weight explained over 99% (r^2=1.00) for both time periods. The b_o coefficients were -1.82(0.07) and -1.76(0.06) for the 133 to 313 and the 133 to 468 days PF time periods respectively. The b_w coefficients were 2.11(0.05) and 2.14(0.02) for the 133 to 313 and the 133 to 468 days PF time periods respectively.

The majority of $E(CV_t)$ values estimated from the variance sub-model fitted to the weight data for the 133 to 313 days PF period were within 5% of the observed CV values over the 133 to 465 days PF time period (Fig. 4A). The weakest agreement occurred

Table 3. Mean (± standard deviation) and coefficient of variation (CV) of the distribution of charr wet weights in family LAc 1 from 210 to 468 days post fertilization (PF).

Days PF	Tank Number	Number Fish	Weight Mean(±Sd) g	Weight CV %
210	1	104	0.7(0.3)	42.9
272	1	101	2.3(0.9)	39.3
311	1	80	5.2(2.2)	42.3
313	2	68	5.8(1.8)	53.6
	3	68	5.1(2.0)	39.0
361	2	129	12.5(7.6)	60.4
	3	129	11.8(6.6)	55.9
388	2	127	19.1(10.3)	53.9
	3	129	21.5(12.6)	58.5
424	2	129	32.3(16.5)	51.0
	3	129	34.0(18.5)	54.4
452	2	136	46.8(23.6)	50.4
	3	133	49.4(26.5)	53.6
468	2	127	57.1(27.6)	48.3
	3	126	56.3(29.5)	52.4

Figure 3. Relationship between the $\log_e$ increase in variance of charr weights and the $\log_e$ mean charr weight for family LAc 1; solid dots represent census from 133 to 311 days post fertilization (PF); open triangles and boxes represent census from 313 to 468 days PF, for tanks 2 and 3; the open circle represents the random sample taken 522 days PF. Line indicates values predicted from the variance model (equation 3) fitted to the data from 133 to 311 days PF, with b_0 and b_w coefficients of -1.86 and 2.07, respectively.


+8
4
0
4
-8
LOGe INCREASE IN VARIANCE
-3
-2
-1
0
1
2
3
4
5
LOGe WEIGHT g.

immediately following the division of the family into the two sub-groups (Fig. 4A). The difference between the CV for the weight distribution of the random sample taken 522 days PF and the $E(CV_t)$ was 1.2%. The majority of $E(CV_t)$ values estimated from the variance sub-model fitted to the data form 133 to 465 days PF were within 5% of the observed values (Fig. 4B). The difference between the CV of the weight distribution of the random sample taken 522 days PF and the $E(CV_t)$ was 8.1%.

Twelve of the 32 fish which were individually marked on day 313 PF were identified at the end of the growth trial (468 days PF, Table 4). The ranking of marked charr based on individual body weight, within each tank, changed little over the 155 days (Table 4 Fig.5A & B). The individual charr growth rates ranged from 0.8 to 2.0 %/day (Table 4). The majority of marked charr had individual growth rates in the range of 1.4 to 1.7 %/day (Table 4).

The mean weight of 131 charr randomly selected from all the surviving members of family LAc 1 522 days PF was 93.6(45.4)g and the CV of the weight distribution was 48.5%. The mean weight of the 75 charr sampled for sexual maturity was 100.7(47.1) and the CV of the weight distribution was 46.6% (Fig 6). Fourteen of the 75 charr could not be sex but the male:female sex ratio of the remaining charr was 1.2:1. The average maturity index (MI) for male charr was 1.2%, while the mean MI of female charr was 0.3%. Seven charr had

Figure 4A. The difference between the observed coefficient of variation (CV) and the estimated CV ($E(CV_t)$) for the weight distribution for family LAc1 for each of the sampling days. $E(CV_t)$ values are calculated from the variance model fitted to the weight data from 133 to 313 days PF.

Figure 4B. The difference between the observed coefficient of variation (CV) and the estimated CV ($E(CV_t)$) for the weight distribution for family LAc1 for each of the sampling days. $E(CV_t)$ values are calculated from the variance model fitted to the weight data from 133 to 468 days PF.

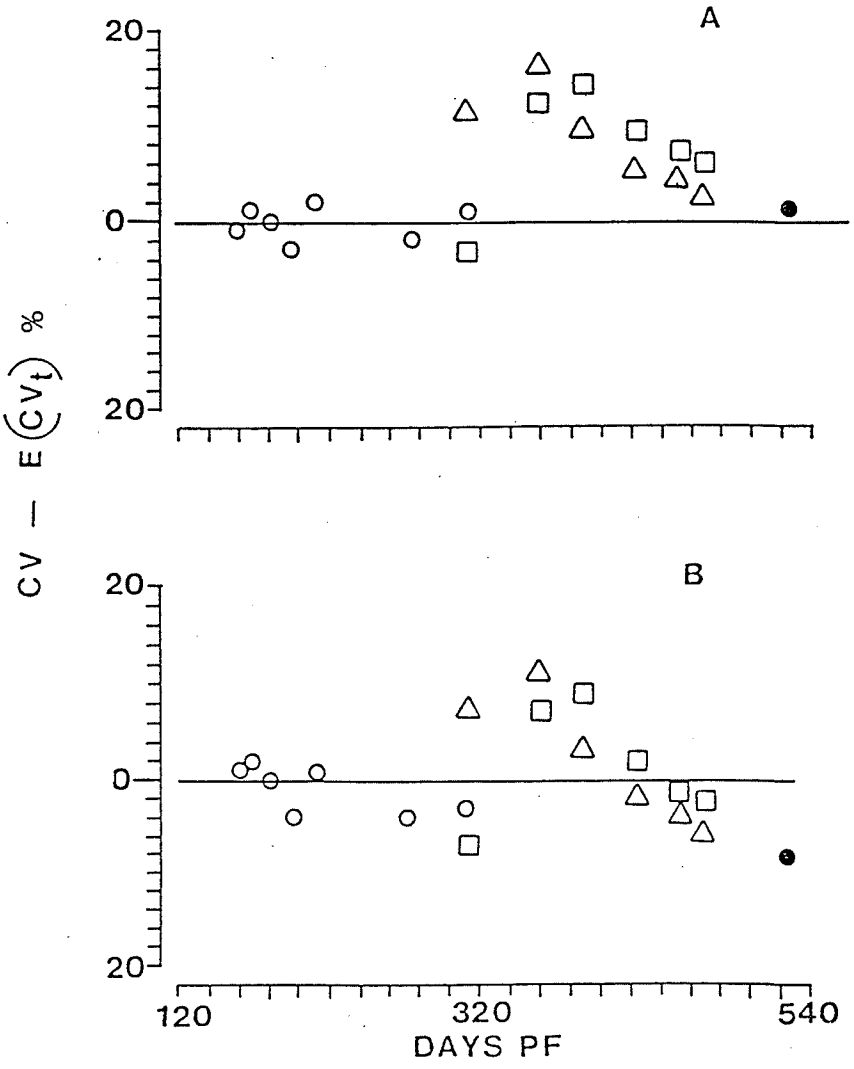

A
B
20
0
20
20
0
20
120
320
540
DAYS PF
CV − E(CVt) %

Table 4. Change in wet body weight of individually marked charr in family LAc 1 from 313 to 468 days post fertilization (PF). Charr were ranked according to their body weights, from heaviest to lightest in each of the marked groups and the specific growth rate (SGR) over the time period was calculated for each fish. Charr identification (ID) number refers to tank number . charr number.

Charr ID Number	313 Days PF Weight g	Rank	468 Days PF Weight g	Rank	Change in Rank	SGR %/Day
Tank 2						
2.1	5.6	5	73.9	3	2	1.7
2.2	8.6	2	81.1	1	1	1.4
2.3	6.5	3	49.2	4	1	1.3
2.4	2.9	6	10.2	6	0	0.8
2.5	5.7	4	33.6	5	1	1.1
2.6	10.8	1	80.1	2	1	2.0
Tank 3						
3.1	4.7	5	57.6	5	0	1.6
3.2	4.9	4	58.6	4	0	1.6
3.3	5.8	2	62.0	3	1	1.5
3.4	2.4	6	15.4	6	0	1.2
3.5	7.1	1	89.0	1	0	1.6
3.6	5.0	3	65.6	2	1	1.7

Figure 5A. Individual branded charr weights on census days in tank 2 and the mean weight ± standard deviation (SD), 95% and 5% quantiles for the distribution of charr weights of charr family LAc 1. Branded charr identified by ID number.

Figure 5B. Individual branded charr weights on census days in tank 3 and the mean weight ± standard deviation (SD), 95% and 5% quantiles for the distribution of charr weights of charr family LAc 1. Branded charr identified by ID number.

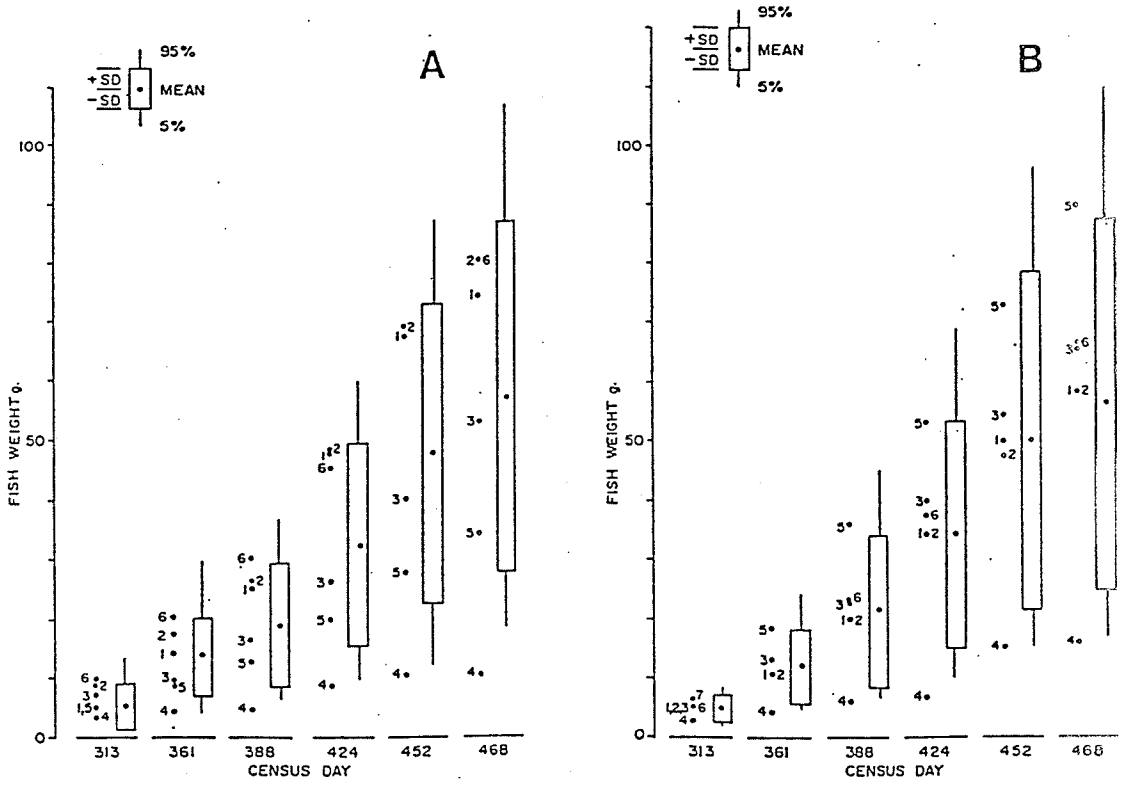
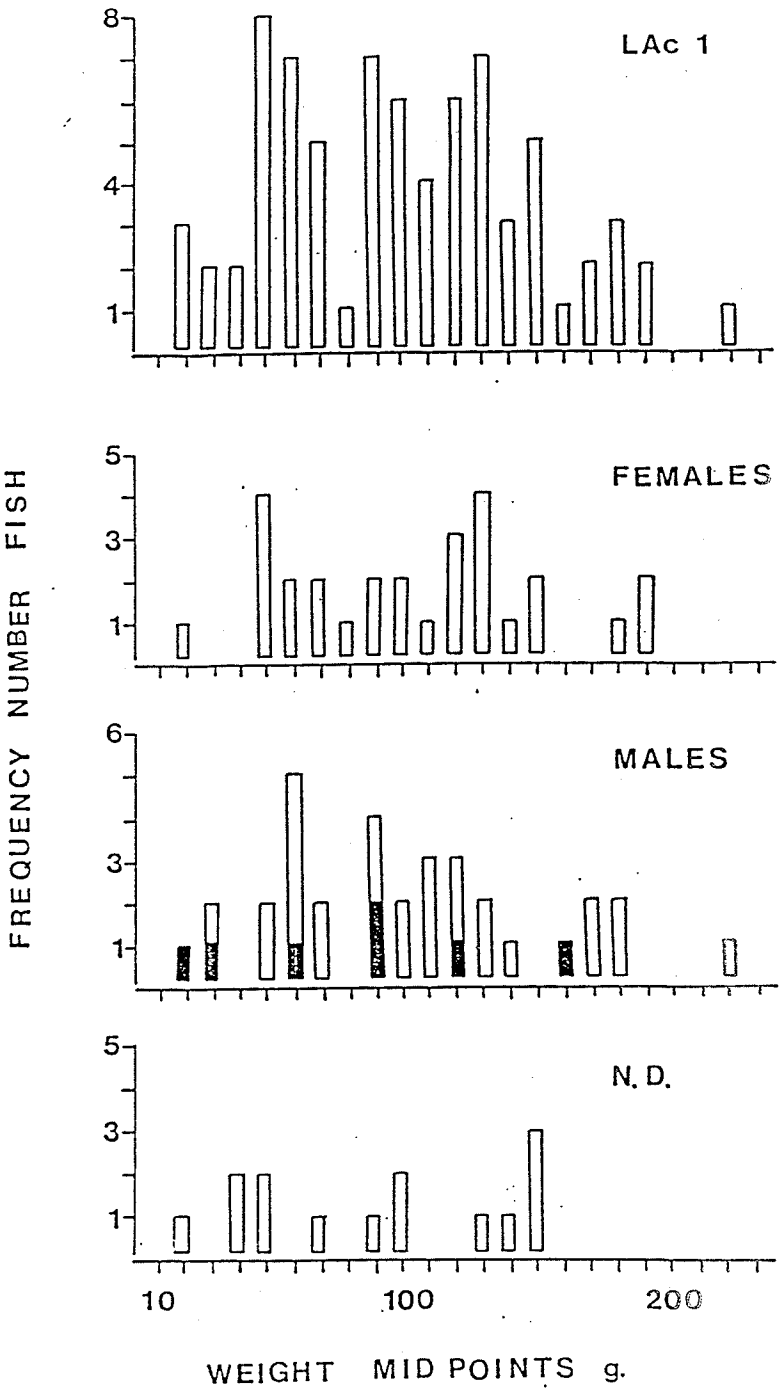

A
B
95%
+SD
-SD
MEAN
5%
FISH WEIGHT g.
0
50
100
313
361
388
424
452
468
CENSUS DAY

Figure 6 . Weight distributions of all charr, female charr, male charr and charr with no gonad development (N.D.) in family LAc 1, 522 days PF, filled in columns represent charr with a maturity index (MI = gonad weight/charr weight X 100) of 2% or greater.


LAc 1
FEMALES
MALES
N. D.
FREQUENCY NUMBER FISH
WEIGHT MID POINTS g.
10
100
200

a MI of 2% or greater, all were males and the mean weight of these charr was 81.7(47.6)g (Fig. 6). The mean weight of immature male charr was 106.4(49.0)g and the sample mean weight of charr minus mature charr was 102.7(47.0)g. Removing the mature male charr from the weight distribution changed the CV from 46.6 to 45.7%.

Family LAc 2

Six hundred and seven days PF the mean weight of the charr in family seven was 230.4(200.5)g , the CV of the charr weight distribution was 87.0 %. After being reared for an additional 510.0 days (1117 days PF) the mean charr weight for family 7 had increased to 539.0(427.6)g, the CV of the weight distribution was 79.3% (Fig. 7). The male: female sex ration was 1.8:1 and 21 charr (15%) could not be sexed. The mean weight of male charr was 579.1 (420.0)g and the CV of the weight distribution was 72.5% (Fig. 7). The mean weight of female charr was 660.8 (430.1)g and the CV of the weight distribution was 65.1% (Fig. 8). The distribution of male and female body weights were not significantly different (P = 0.7 Kolmogorov - Smirnov Test). The mean weight of the charr which could not be sexed was 144.1(139.3)g and the CV of the weight distribution was 96.7% (Fig. 8).

The mean MI for male charr was 8.8% while the mean MI for female charr was 3.9% . Half the charr in family LAc 2 had MIs

Figure 7. Weight distribution of family LAc 2, 1,117 days PF.

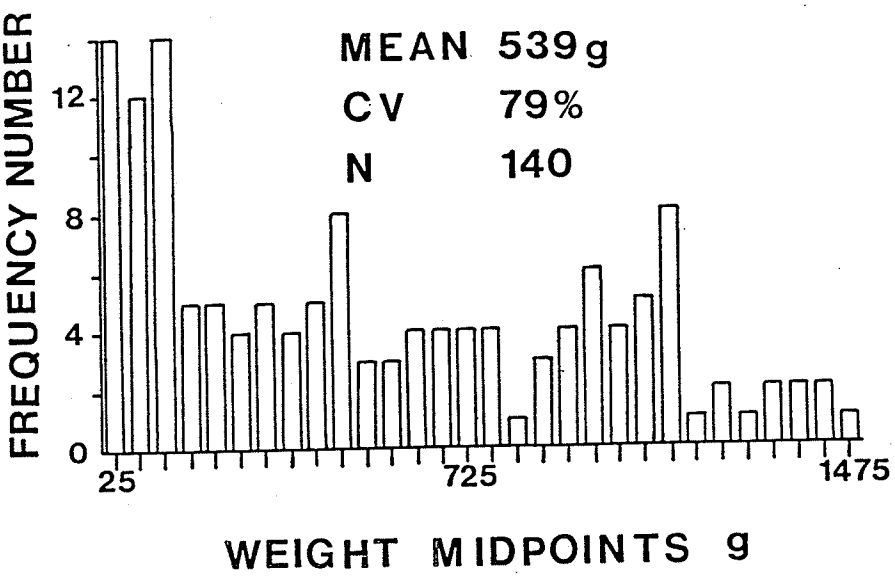
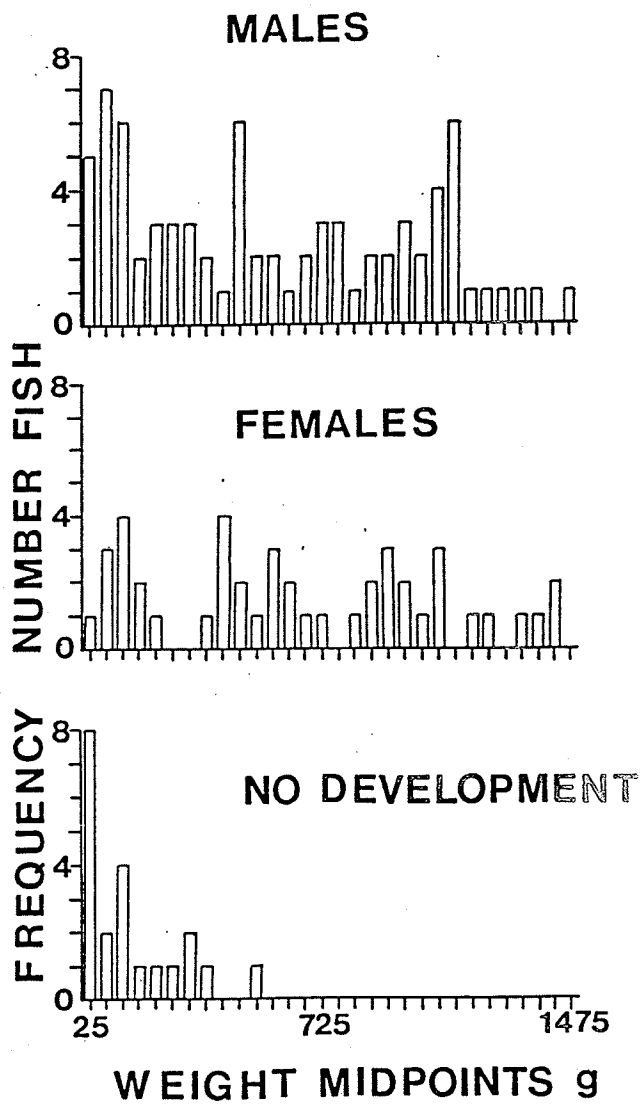
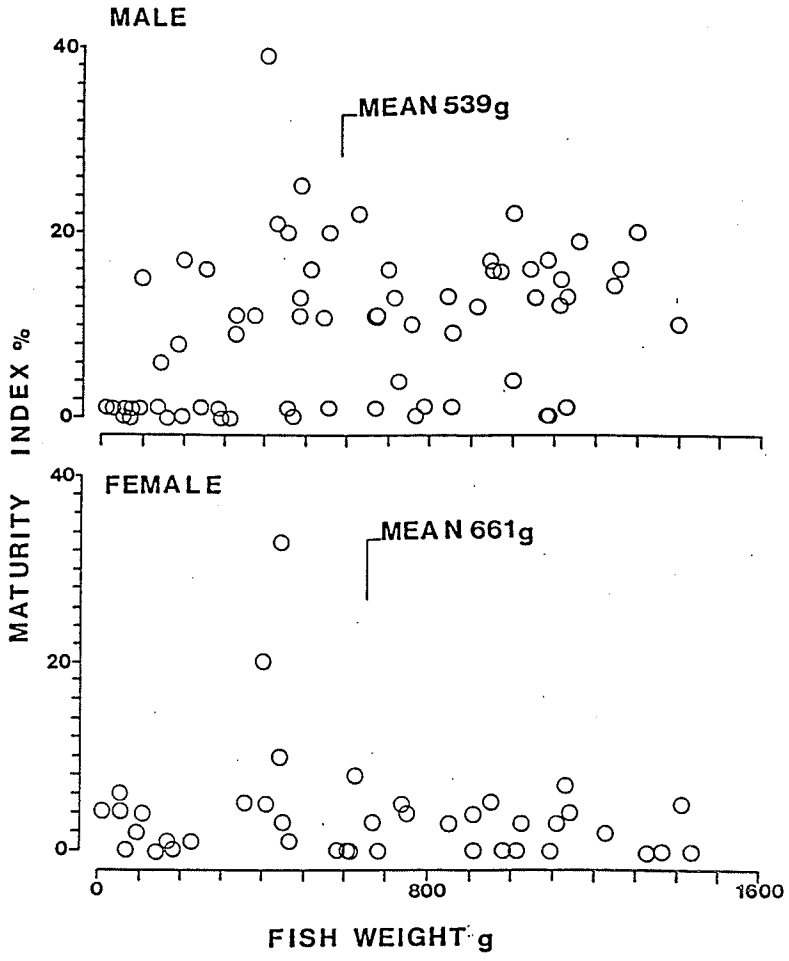

FREQUENCY NUMBER
12
8
4
0
MEAN 539g
CV 79%
N 140
25
725
1475
WEIGHT MIDPOINTS g

Figure 8. Weight distribution of family LAc 2, 1,117days PF by sex. No development refers to charr which could not be sexed due to a lack of gonad development.


MALES
FEMALES
NO DEVELOPMENT
NUMBER FISH
FREQUENCY
8
4
0
25
725
1475
WEIGHT MIDPOINTS g

greater than 2% of these 43 were females and 27 were males (Fig. 9). The mean weight of the maturing males was 634.0(418.6) g with a CV of 66.0%, while the mean weight of maturing females was 752(371.9)g with a CV of 49.9%. Seventeen male charr had MI values less than 2%, while 33 females had MI values less than 2%. Twenty charr could not be sexed due to a lack of gonad development. The mean weights of male and female charr with MI values of less than 2% were 701.7(457.0) and 352.0(372.4)g respectively. The CVs of the weight distributions for male and female charr with MI values less than 2% were 65.1 and 105.5% respectively. The mean weight of the 20 charr which could not be sexed due to a lack of gonad development was 136.3 (138.1)g, with a CV of 101.3%.

Figure 9 . Maturity index (MI = gonad weight/body weight X 100) versus charr body weights in family LAc 2, 1,117days PF by sex.


MALE
40
20
0
MEAN 539g
MATURITY INDEX %
FEMALE
40
20
0
MEAN 661g
0
800
1600
FISH WEIGHT g

DISCUSSION

Variation in charr body weights increases with the increasing mean weight of the population corroborating other data (Arnason et al 1992; Papst et al 1992) for hatchery reared Arctic charr. The results of my study are consistent with the conclusion that individual charr growth patterns are established early in the life history. Little change in rank occurred within the marked groups of charr during the growth trial.

During the first few years of life, variability in length and weight of a year class of fish tends to increase and this increasing variability is referred to as growth depensation (Ricker 1979). This suggest that growth dispensation may begin early in the life history and that the variation in individual charr weights continues to increase as the population grows.

Yamagishi (1969) concluded that behavioral interactions result in an increasing CV for the distribution of individual fish weights and that completely random behavioral interactions resulted in unchanged CV. Purdom (1974) reached the same conclusion but recommend the use of the coefficient of variance (CV^2), since in genetic terms variance of a population is more relevant than standard deviation. Jobling (1985) concluded that growth depensation in Arctic charr was a result of behavioral interactions

and that these interactions occurred even when food supplies were not limiting. Jobling (1986) concluded that genetic factors were also important in determining the slow growth of small "stunted" charr and that interactions tended to exacerbate interactions between small and large charr determining the degree of growth depensation.

In the growth study with family LAc 1 the CV of the weight distribution initially increased significantly from 14.7 to 37.0% (133 to 160 days PF) and was 43.2% 311 days PF when the population was divided. The variance model fitted to the early growth data predicted a gradually increasing CV for the weight distribution and accurately predicted the CV of the population 522 days PF. Significant differences among estimated and observed CVs occurred when family LAc 1 was randomly divided into two tanks but began declining shortly there after. Clearly the growth pattern of family Lac 1 was effected by the change in rearing environment but once affected the family's growth pattern returned over time to the pattern of growth and growth depensation established earlier in the life history.

Although the results of this study do not eliminated the possible affects of social interaction on variation in growth, the results more strongly support the conclusion that the growth pattern of family Lac1 was primarily affected by genetic factors,

which tend to produce a predictable increase in variability in weight (depensation) as weight increased. Only when the rearing environment is significantly altered does this growth pattern change. This conclusion is be consistent with the hypothesis that variation in size in charr populations results from members of a population adopting alternative life history styles with resulting different growth patterns early in life (Balon 1984).

Weight distributions for families Lac 1 and Lac 2 were not significantly skewed. This suggests that variation in charr weights in these families did not result from the "shooting" phenomenon described by Wohlfarth (1977) for cultured carp, sunfish and catfish populations.

The occurrence of small mature males in family LAc 1, 522 days PF is consistent with early observations of hatchery reared Arctic charr (Papst & Hopky 1984). Overall however the early maturing male charr did not significantly affect the weight distribution of family LAc 1. The variation in time and size of maturation observed in this study is consistent with the conclusions of Nordeng (1984), that charr from a single gene pool can produce several phenotypes (forms) which differ in age and size at maturity.

These results are further supported by the observed variation in size and maturity in family LAc 2. Immature females and charr

which could not be sexed contributed significantly to the lower portion of the weight distribution in family LAc 2. Mature males and females were generally distributed throughout the weight range of charr in family LAc 2 .

Results from this study support the conclusion that early sexual maturation among small charr is not a significant factor in determining the growth pattern of hatchery reared Arctic charr groups.

CHAPTER 2

Effect of hatching time and time of first feed on variation in weight in hatchery reared Arctic charr (Salvelinus alpinus L.).

ABSTRACT

The rate of increase in variation in individual body weights of hatchery reared arctic charr was not affected by the time of hatch. A single variance model could be fitted to growth data from an early and a late hatch subgroup of the same group of hatchery reared Arctic charr. Increasing mean weight explained almost all of the observed increase in variation in charr body weight over the growth period. Two initial feeding patterns were observed among the hatchery reared charr, with some charr initiating feeding on the bottom, while others initiated feeding in the water column. The rate of increase in variation in body weight did not differ amongst these feeding types when the groups were reared separately. The rate of increase in variation in weight of groups of hatchery reared Arctic charr begins early in its life history. Time of hatching and initial feeding habits do not appear to significantly influence the rate of increase in variance with charr growth.

INTRODUCTION

Results from Chapter 1 demonstrated that a significant positive correlation was established early in the growth of hatchery reared Arctic charr between the $\log_e$ increase in variance of fish weight and the $\log_e$ mean fish weight. The increasing mean weight of the population of charr explained most of the observed variation in fish weight.

Balon (1984) concluded that the two forms or phenotypes of Arctic charr (dwarf & normal) resulted from differences in the early developmental strategies. The "dwarf" form exhibiting a longer combined embryonic and alevin phase than the "normal" form. "Dwarf" forms were reported to initiate exogenous feeding long before yolk reserves were exhausted (Balon 1980 & 1984).

The observation that the rate of increase in variation in weight of hatchery reared arctic charr is established early in the life history and is largely constant over much of its life history suggest that the degree of weight variation results from differences in the early rate of development of individuals. Two important stages in the development of hatchery reared fish are the times of hatching and first feeding.

The objective of this experiment was to investigate the effect of time of hatching and time of first feeding on variation in weight of hatchery reared Arctic charr.

MATERIALS AND METHODS

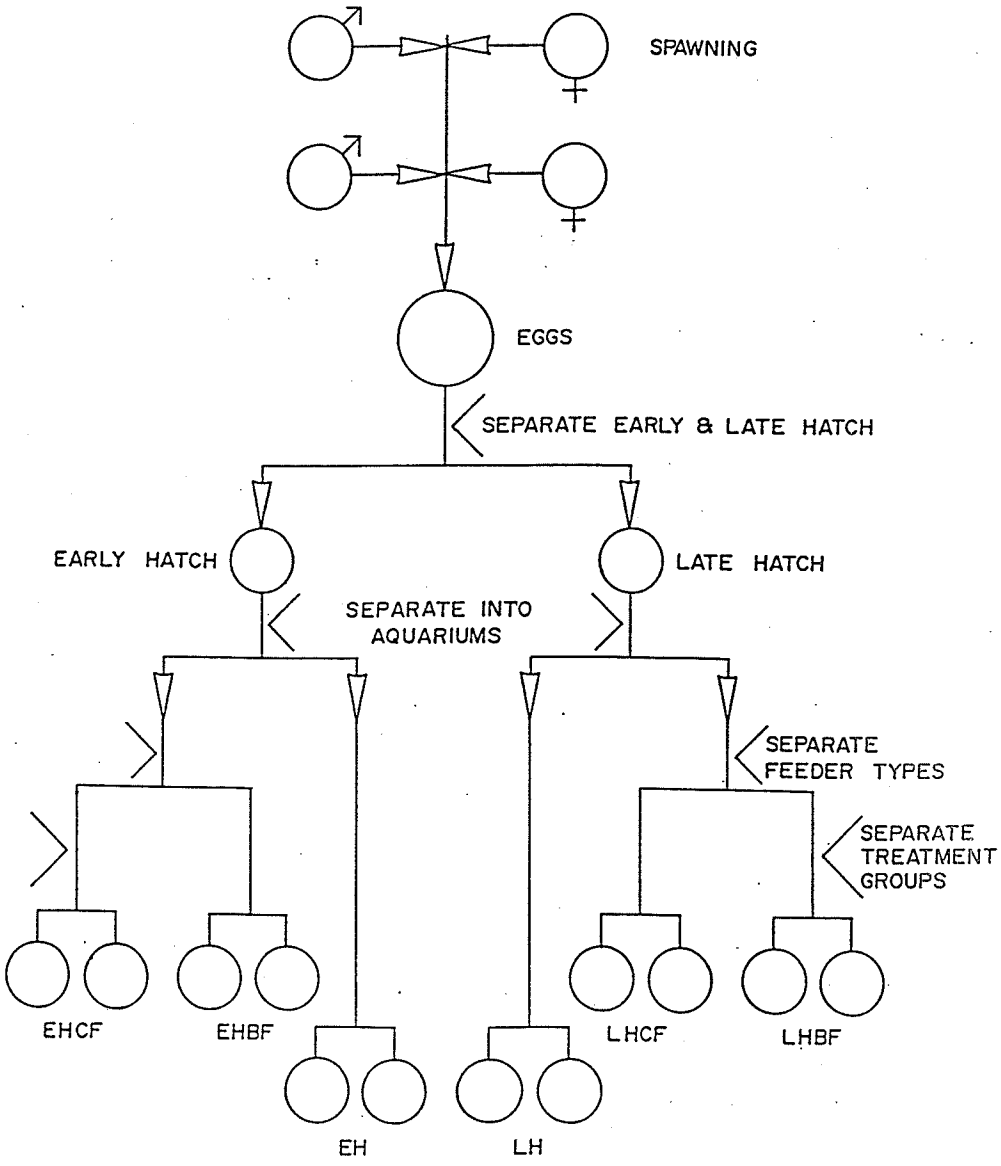
This experiment was conducted at the Rockwood Aquaculture Research Centre and the statistical analysis of the results was as described in Chapter 1.

Charr for this experiment were taken from a hatchery brood-stock of the Nauyuk Lake strain. Early rearing and development of this strain has been described by Papst and Hopky (1984). The gametes from two males and two females were combined and incubated in a vertical incubator at 6 °C.

The experimental design is given in Figure 10. The first 50% of the eggs to hatch were separated from the unhatched eggs and were designated the early hatch (EH) treatment group. The last 50% of the eggs to hatch were designated the late hatch (LH) treatment group. One hundred and ten days post fertilization (PF) , two random replicate samples of the EH and LH charr groups were placed in 2 - l aquariums supplied with aerated hatchery water, from a common bio-filter at a temperature of 10 °C. A small amount of a commercial semi-moist salmon starter diet (Bioproducts, Inc. Warrenton Oregon USA) was fed to each of the charr groups 4 times a day.

Once each day from 110 to 122 days PF the feeding activity of

Figure 10. Experimental design for effect of hatch and feeding time on variation in charr body weights. The six treatment groups of charr were, early hatch (EH), late hatch (LH), early hatch column feeding (EHCF), early hatch bottom feeding (EHBF), late hatch column feeding (LHCF) and late hatch bottom feeding (LHBF).


SPAWNING
EGGS
SEPARATE EARLY & LATE HATCH
EARLY HATCH
LATE HATCH
SEPARATE INTO AQUARIUMS
SEPARATE FEEDER TYPES
SEPARATE TREATMENT GROUPS
EHCF
EHBF
LHCF
LHBF
EH
LH

the charr in each aquarium was observed for a five minute period to assess when the charr had initiated feeding. At the end of this time period (122 days PF) one EH group and one LH group were transferred to separate 61 - l fibreglass tanks connected to a common bio-filter. The remaining EH and LH groups were each divided in two, by removing charr feeding in the water column from charr feeding on the bottom. The charr were removed over a 5 hour period, using a small aquarium net with approximately 30 minutes between nettings. After this removal procedure no charr were observed feeding in the water column in either aquarium. Four groups of charr were used in the experiment; an early hatch column feeding (EHCF) group; an early hatch bottom feeding (EHBF) group; a late hatch column feeding (LHCF) group; a late hatch bottom feeding (LHBF) group. The EH, LH, EHCF,EHBF, LHCF and LHBF charr groups were reared in separate 61 - l tanks connected to a common bio-filter, at a water temperature of 10 ^{0}C for 49 days.

Two random groups of 75 charr were taken from each of the six treatment groups 171 days PF and placed in separate 61-l tanks connected to a common bio-filter, at a water temperature of 10 ^{0}C and using the rearing methods described in Chapter 1. Charr were reared under these conditions for 150 days.

Individual charr weights were measured 110, 117 and 122 days PF by placing all the charr from a treatment group in a 1 - l plastic

pale and removing a single dip net sample from the pail with an aquarium dip net. Charr were fixed in a 5% formalin solution after being killed with an overdoses of anesthetic (2-phenoxyethanol). After fixing, individual charr were dried on a paper towel and weighed on an electronic balance to the nearest 0.05 mg.

During the 150 days from 171 to 321 days PF, the wet weight of individual charr were measured on days 171, 211, 232, 253, 253, 296 and 321, by anesthetizing the charr with 2-phenoxyethanol, shaking off excess water and weighing individual charr to the nearest 0.05g on an electronic balance.

RESULTS

The percent yolk (dry weight) at the first census 110 days PF, in the EH group was 54.6% , while it was 49.0% in the LH group. Yolk weights were not significantly (P = 0.17 Kruska-Wallis) different between the EH and LH charr groups 110 days PF. Charr weights less the yoke weights in the Eh and LH groups were significantly (P = 0.01 Kruska-Wallis) different between the EH and LH groups 110 days PF (Table 5). Charr were not observed feeding from 110 to 116 days PF, but were observed feeding on day 117 PF. No food was observed in the intestine of the charr sampled 110 days PF, where as 40.0% of the EH and 87.5% of the LH charr sampled 117 days PF had food in their intestine (Table 5).

The percent yolk in both the EH and LH groups declined during the period from 110 to 117 days PF (Table 5). Yolk weights and charr weights less yolks of the EH and LH groups were not significantly (P>0.50 Kruskal-Wallis) different at day 117 PF (Table 5).

During the 150 day growth trial period 171 and 321 days PF, specific growth rates of the two EH charr groups were 2.2 and 2.3 %/day, while during the same period the specific growth rates of the two LH groups were 2.2 and 2.1 %/day (Table 6). The CV of the weight distributions of the two EH groups increased from 22.3

Table 5. Mean (± Standard deviation) dry charr, yolk and charr with yolk weights; percent yolk (yolk weight/body weight X 100) and percent charr feeding (number of charr with food in intestine/number of charr X 100); 110, 117, and 122 days post fertilization (PF) for the six treatment groups; early (EH) and late (LH) hatching; column (EHCF & LHCF) and bottom (EHBF & LHBF) feeding.

Group	Days PF	N[1]	Weight Mg. Mean (± Sd)			Percent	
			Charr	Yolk	Charr & Yolk	Yolk	Feeding
EH	110	17	6.72(0.95)	8.14(1.33)	14.86(1.56)	54.6	0
LH	110	16	7.88(1.10)	7.54(1.02)	15.42(1.44)	49.0	0
EH	117	15	8.43(1.26)	4.33(0.92)	12.75(1.43)	34.0	40.0
LH	117	12	8.71(0.72)	4.80(0.99)	13.51(0.86)	35.4	87.5
EHCF	122	21	10.06(2.05)	2.66(1.41)	12.72(2.31)	20.8	73.0
EHBF	122	22	11.03(1.24)	2.58(0.96)	13.61(1.65)	18.6	100.0

[1]Number of charr sampled

Table 6. Mean charr weights (± Standard deviation), coefficient of variation (CV) and specific growth rate (SGR), 171 and 321 days post fertilization, for the six treatment groups; early (EH) and late (LH) hatching; column (EHCF & LHCF) and bottom (EHBF & LHBF) feeding.

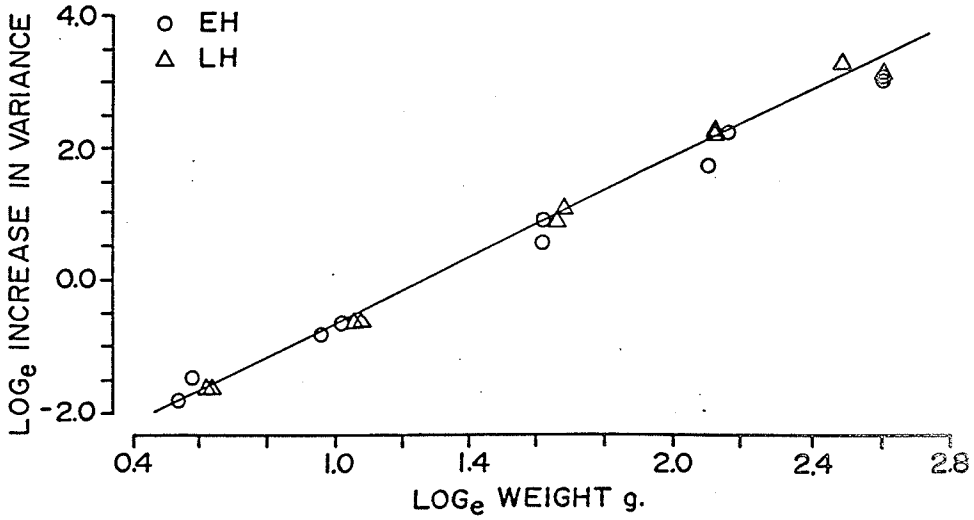
Group	Tank No.	Day 171 charr weight		Day 321 charr weight		SGR %/day
		Mean (±Sd) g.	CV %	Mean (± Sd) g.	CV %	
EH	1	0.48 (0.11)	22.3	13.57 (4.31)	31.8	2.2
EH	2	0.46 (0.13)	27.2	13.38 (4.49)	33.6	2.3
LH	1	0.48 (0.13)	26.9	13.40 (4.49)	33.5	2.2
LH	2	0.51 (0.13)	25.5	11.97 (4.95)	41.3	2.1
EHCF	1	0.57 (0.14)	24.3	12.90 (4.61)	35.7	2.1
EHCF	2	0.54 (0.13)	23.3	12.29 (4.66)	37.9	2.1
EHBF	1	0.54 (0.12)	21.4	13.37 (5.44)	40.7	2.1
EHBF	2	0.57 (0.14)	24.6	11.96 (5.35)	44.7	2.1
LHCF	1	0.52 (0.13)	24.3			
LHCF	2	0.52 (0.13)	24.3	14.82 (6.57)	44.3	2.2
LHBF	1	0.46 (0.16)	34.8	12.62 (6.73)	53.3	2.2
LHBF	2	0.46 (0.13)	28.9	12.08 (5.42)	44.9	2.2

and 27.2% to 31.8 and 33.6% during the 150 day growth trial (Table 6). The CV of the weight distributions of the two LH groups increased from 26.9 and 25.5% to 33.5 and 41.3% during the 150 day growth trial (Table 6).

A significant (P = 0.01) positive correlation was observed between the $\log_e$ increase in variance in charr weight and $\log_e$ mean charr weight for the EH and LH treatment groups (Fig. 11). Log_e mean charr weight explained over 99% (r^2 =1.0) of the variance when the variance sub-model [3] assuming the effect of $\log_e$ time to be zero, was fitted to the results of the 150 day growth trial. There was a non significant (P = 0.70) contribution of $\log_e$ time to the variance model [2]. No significant (P = 0.30) tank or weight by treatment (P = 0.06) interaction effects were observed. In summary there were no treatment differences on the b_0 or b_w coefficients of the variance model [3] and a common model could be fitted to both the EH and LH groups (Fig. 11).

The percent yolk of the EHCF,EHBF, LHCF and LHBF 122 days PF ranged from 23.2 to 17.6 % (Table 5). The distributions of yolk weights among the 4 groups of charr 122 days PF were not significantly (P= 0.43 Kruskal-Wallis) different (Table 5). Weight distributions of the charr in the 4 treatment groups were not significantly (P = 0.09 Kruskal-Wallis) different 122 days PF (Table 5).

Figure 11. Log_e increase in variance in charr weight versus the log_e Mean charr weight, for the early (EH) and Late (LH) hatching treatment groups during the growth trial period. Line indicates values predicted from the common variance model with b_o and b_w coefficient values of -3.23(0.11) and 2.49(0.06), respectively.


4.0
2.0
0.0
-2.0
LOGe INCREASE IN VARIANCE
o EH
Δ LH
0.4
1.0
1.4
2.0
2.4
2.8
LOGe WEIGHT g.

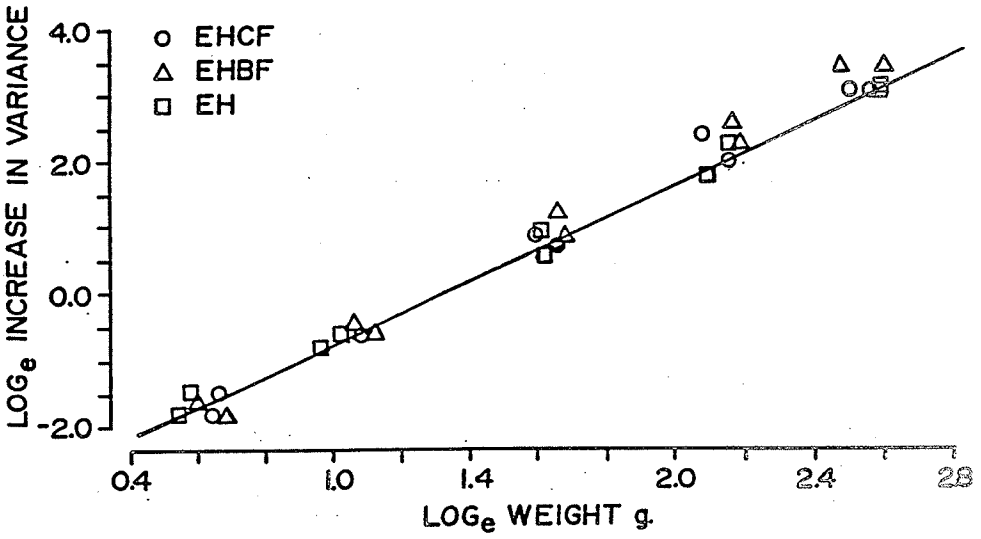
During the 150 day growth trial from 171 to 321 days PF specific growth rates among the EHCF, EHBF, LHCF and LHBF treatment groups ranged from 2.1 to 2.2 %/day (Table 6). The CV for the charr weight distributions for all the treatment groups increased during the growth trial period (Table 6).

A significant (P = 0.01) positive correlation was observed between $\log_e$ increase in variance and the $\log_e$ mean weight for the EHCF and EHBF treatment groups (Fig. 12). There was a significant (P = 0.01) tank effect in the EHBF treatment group.

A common variance sub-model [3] , assuming the effect of $\log_e$ time to be zero, could be fitted to the $\log_e$ increase in variance and the $\log_e$ mean charr weight data for the EHCF & EH treatment groups (fig. 12). The b_0 and b_w coefficient for the variance sub-model [3] were -3.07(013) and 2.32(0.07) respectively. There was a non significant (P = 0.11) treatment effect and $\log_e$ mean charr weight explained over 99% (r^2 = 0.99) of the observed variance in individual charr weight.

A significant (P = 0.01) positive correlation was observed between the $\log_e$ increase in variance and $\log_e$ mean weight for the LHCF and LHBF treatment groups (Fig. 13). The analysis for the LHCF treatment group was not complete since one tank was destroyed due to a mechanical failure after the third census.

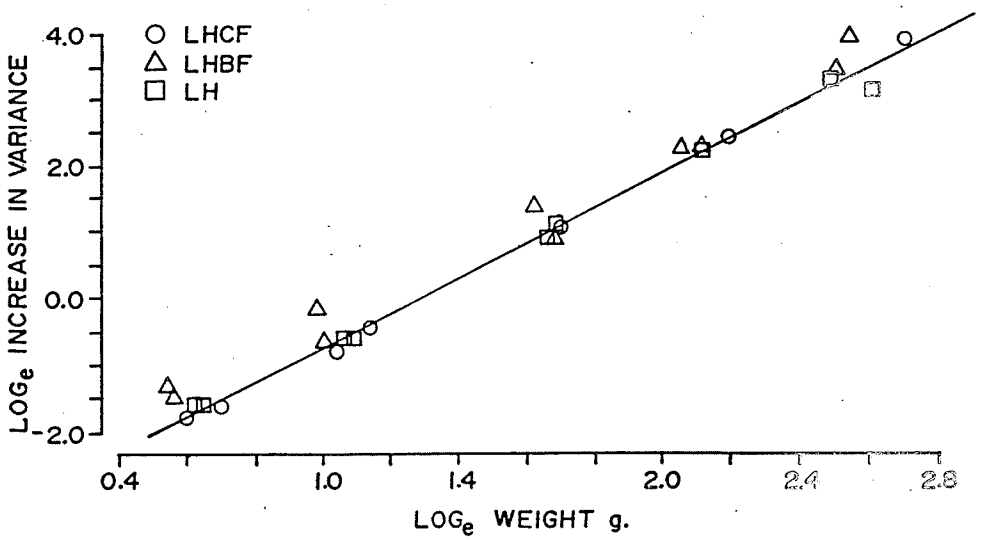
Figure 12. Log_e increase in variance in charr weight versus the log_e Mean charr weight, for the early hatch (EH), early hatch column (EHCF) and early hatch bottom, feeding groups during the growth trial period. Line indicates values predicted from the common variance model fitted to the data from the EH and EHCF groups, with b_0 and b_w coefficient values of -3.07(0.13) and 2.32(0.07), respectively.


LOGe INCREASE IN VARIANCE
4.0
2.0
0.0
-2.0
o EHCF
Δ EHBF
□ EH
0.4
1.0
1.4
2.0
2.4
2.8
LOGe WEIGHT g.

A common variance sub-model [3] assuming the effect of $\log_e$ time to be zero, could be fitted to the $\log_e$ increase in variance in individual charr weight and the $\log_e$ mean charr weight data from the LHBF and LH treatment groups (Fig. 13). The model coefficients b_0 and b_w were -3.23(0.17) and 2.49(0.10) respectively. There was a non significant ($P = 0.17$) treatment effect and $\log_e$ mean weight explained 99% ($r^2 = 0.99$). of the observed variance.

A single variance sub-model [3] assuming the $\log_e$ time to be zero could be fitted to the results from the EH, LH, LHBF and EHCF growth trials. Log_e mean fish weight explained over 99% (r_2=1.00) of the observed variance. The model coefficients b_0 and b_w were -3.23(0.17) and 2.49(0.10) respectively. There was a non significant ($p = 0.14$) treatment effect and a non significant ($P = 0.23$) treatment by weight interaction effect. In summary the variance sub-model [3] assuming the effect of $\log_e$ time to be zero, could be fitted to 4 of the 6 treatment groups. The LHCF treatment group could not be included in the analysis since one of the replicate tanks was destroyed and the EHBF treatment could not be included since there was a significant tank effect.

Figure 13. Log_e increase in variance in charr weight versus the log_e Mean charr weight, for the late hatch (LH), late hatch column (LHCF) and late hatch bottom, feeding groups during the growth trial period. Line indicates values predicted from the common variance model fitted to the data from the LH and LHBF groups, with b_o and b_w coefficient values of -3.23(0.17) and 2.49(0.10), respectively.


LHCF
LHBF
LH
4.0
2.0
0.0
-2.0
LOGe INCREASE IN VARIANCE
0.4
1.0
1.4
2.0
2.4
2.8
LOGe WEIGHT g.

DISCUSSION

Although there was a variation in the time of hatching for the experimental charr population, a common variance model could be fitted to both the EH and LH treatment groups. Log_e mean charr weight explained most of the variation in weight over the growth trial period. Variation in hatching time does not appear to affect the rate of increase in variation in fish weight over time.

Two distinct feeding patterns were observed amongst the larvae charr, one group of charr feeding in the water column and the other on the bottom. The two feeding patterns were observed in both the EH and LH groups. The percentage of charr feeding differed between the EH and LH treatment groups 117 days PF, with the EH group having 50% fewer charr feeding as the LH group. The EH, LH, LHBF and EHCF groups could be fitted with a common variance model with Log_e mean weight explaining almost all of the observed variance in fish weight. As with time of hatch the pattern of initial feeding does not appear to affect the rate of increase in variance in fish weight.

The significant tank effect in the EHBF group resulted from a significant difference in the b_0 (intercept) coefficient between the two replicates of this group, the b_w (slopes) of the two replicates were not significantly different. The variance model is sensitive to

small variations between replicates, which can affect the estimates of the b_0 coefficient (Arnason et al. 1992). The estimated b_w coefficient for the variance model fitted to the EHBF group was 2.74(0.02), compared with 2.32(0.07) for the EHCF, EH common model and 2.49(0.09) for the EH, LH, LHBF, EHCF common model. The possible significance of the higher value for b_w for the EHBF group was unclear since the significant tank effect prevented a statistical comparison. However the data from the two EHBF tanks appeared to fall within the same range as the EHCF and EH groups (Fig.12).

The results of this experiment support the conclusion that the rate at which variation in body weight changes with time is established early in the life history and most of the increase in variation in weight over time can be explained by increasing mean fish weight. Although differences were noted in the weight of charr, yolks, time of first feeding and the pattern of initial feeding these differences in development rates did not affect the rate of increase in variation in fish weight.

The results of this experiment support the conclusion that charr populations exhibit polyphenism early in their life history (Balon 1984). Further the results of this experiment suggest that growth depensation is not affected by variations in hatching time, time of first feeding or initial feeding pattern.

CHAPTER 3

Effect of ration on the variation in fish weight of hatchery reared Arctic charr(Salvelinus alpinus L.)

ABSTRACT

The effect of ration size on variation in charr weight in a full-sib family of hatchery reared Arctic charr was investigated by feeding replicate test populations three different ration levels and observing the effect on the rate of increase in variance in fish weight over time. Over an initial mean weight range of 1.0 to 20g, ration level had a small, but statistically significant effect on the rate of increase in variance in fish weight. Log_e mean weight explained the majority of the observed variance in fish weight. For the growth period from a mean weight of approximately 20 to 95g the charr fed the lowest ration had a lower variation in fish weight and produced a lower percentage of small fish then did charr fed at the highest ration. These results are consistent with other studies which suggest that charr populations produce a higher percentage of "dwarf" forms when food is abundant. Therefore the differences observed in this experiment in the rates of increase in variance in weight at different ration levels might be an example of the phenotypic plasticity of Arctic charr. Alternatively these differences may be linked to the significantly longer time for charr fed the low ration groups to achieve the target weight or it may result from behavioral differences between individuals in tanks at the different ration levels.

INTRODUCTION

Balon (1984) suggested that dwarf Arctic charr occurred in wild populations during periods when food was not limited. Nordeng (1983) observed that the amount of food fed to hatchery reared Arctic charr prior to release affected the percentage of "dwarf" fish occurring in the population. Higher ration levels tended to produce populations with a higher percentage of "dwarf" fish (Nordeng 1983).

Hatchery reared charr might be expected to respond to a restricted ration level by exhibiting an increased variance in fish weights due to competition among individuals in the tank. However, Ryer and Olla (1991ab) suggested that under restricted ration conditions schooling fish do not exhibit much aggressive behaviour.

The purpose of this experiment was to investigate the effect of ration level on variation in body weight.

MATERIALS AND METHODS

This experiment was conducted at the Rockwood Aquaculture Research Centre and the statistical analysis of the results was as described in Chapter 1.

The experiment was divided into two time periods. The first period was the time required for the mean weights of charr to increase from approximately 1.0 to 20g. The second period was the time required for the mean weight of charr to increase from approximately 20 to 100g. The same charr were used throughout the experiment.

Arctic charr used in this experiment originated from the mating of a single male and female charr from the Nauyuk Lake brood-stock. The brood-stock were originally received in January 1978 as eggs from Nauyuk Lake on the Kent Peninsula, N.W.T. Canada. The biology of the wild population has been described in detail by Johnson (1980). Seventy five charr were randomly selected from the stock population and assigned randomly to tanks. During the first time period there were 12 tanks consisting of four replicate tanks at 3 different ration levels. During the second time period the number of tanks was reduced to 6 and consisted of 2 replicates at each of the 3 ration levels. The two replicates used in the second time period were randomly selected from the 4 replicate tanks at

each ration level used in the first period.

The water temperature and oxygen saturation were maintained at 10°C and 80% respectively. Charr were fed commercial rainbow trout feed (Martins Feed Mill, Elmira, Ontario, Canada) by hand four times daily during the period from 0830h to 1600h. No feeding occurred on census days. The ration was calculated using commercial feeding tables (Hilton & Slinger 1981) and it was adjusted every census day based on changes in the total wet weight of fish in each tank. Three ration levels were created by feeding tanks 50, 100 or 150 percent of the table values.

During the first time period charr were reared in 21l fiberglass tanks connected to a common bio-filter. Charr were reared in 60l tanks during the second experimental period and these were also attached to a common bio-filter.

Charr were censuses by anesthetizing and individually weighing all charr in a tank. The total weight of fish in each tank was also measured by weighing all the charr from a tank in a tared pail of water. Dead charr were removed daily but were not replaced. Ration was not adjusted until the next census.

During the first time period charr were censused monthly. Individual charr weights were not routinely measured during the

second time period, but feeding rates were adjusted monthly based on the total wet weight of charr in each group.

RESULTS

The first growth period ended after 181, 188 and 258 days for the 150%, 100% and 50% treatment groups respectively (Table 7). All charr groups achieved or exceeded the target mean weight of 20g , except in the 100% treatment where three groups failed to achieve the target weight by the time the growth period was ended (Table 7). Mortalities during the first growth period ranged from zero to eight charr except for charr group number two at the 50% ration level, where all the charr were killed due to a tank drain failure (Table 7).

During the first growth period the CV for the weight distribution increased in all of the charr groups (Table 7). The smallest increases in CV for the weight distributions occurred in groups 3 and 4 at the 50% ration level, where the increases were 3.8 and 2.0%, respectively while the CV increase in charr group number 1 at the 50% ration level was 12.6% (Table 7). CV increases in the weight distributions of the other charr groups were generally less variable than those observed at the 50% treatment level (Table 7).

The second growth period ended 279, 341 and 504 days after the start of the experiment for the 150%, 100% and 50% ration levels respectively (Table 7). Final mean weights ranged from 84.6 to 98.1 g (Table 7). The CV for the weight distributions of all treatment groups increased during the second growth period. The

Table 7. Mean (± Standard deviation) charr weight and coefficient of variation (CV) for the three ration level treatment groups, at the beginning of the growth trial (day 0), at the end of the first growth period and at the end of the second growth period.

Tank Number	Number Charr	weight Mean(± Sd) g.	CV %	Number Charr	Weight Mean(± Sd) g.	CV %	Number Charr	Weight Mean(±Sd) g.	CV %
				Ration level 150 %					
	Day 0			Day 181			Day 279		
1	75	0.7 (0.1)	20.2	71	20.2 (6.1)	30.2	71	84.6 (50.7)	59.9
2	75	0.7 (0.2)	24.7	67	21.4 (6.8)	32.0	66	98.1 (56.8)	57.7
3	75	0.7 (0.2)	24.7	75	22.6 (7.8)	34.3	00	00.0 (00.0)	00.0
4	75	0.7 (0.1)	20.2	70	24.2 (6.8)	28.2	00	00.0 (00.0)	00.0
				Ration level 100%					
	Day 0			Day 188			Day 341		
1	75	0.6 (0.1)	23.6	69	19.3 (6.4)	33.1	75	92.1 (47.4)	51.5
2	75	0.7 (0.1)	20.2	73	16.6 (5.4)	32.4	70	89.5 (42.2)	47.4
3	75	0.6 (0.1)	23.6	72	20.3 (7.6)	37.5	00	00.0 (00.0)	00.0
4	75	0.7 (0.1)	20.2	75	18.7 (6.3)	33.5	00	00.0 (00.0)	00.0
				Ration level 50%					
	Day 0			Day 258			Day 504		
1	75	0.7 (0.1)	23.6	69	20.8 (7.5)	36.2	67	95.2 (40.5)	42.5
2	75	0.6 (0.1)	22.5	00	00.0 (0.0)	00.0	00	00.0 (00.0)	00.0
3	75	0.6 (0.2)	25.0	71	22.0 (6.3)	28.8	00	00.0 (00.0)	00.0
4	75	0.7 (0.1)	22.7	74	22.5 (5.6)	24.7	73	85.4 (29.2)	34.3

highest CV values for the weight distributions occurred at the 150% ration level and the lowest occurred at the 50% ration level (Table 7). The charr fed the 150 % and 100% ration contained a higher percentage of small charr than the two charr groups at the 50% ration level (Fig. 14). Numbers of charr in the test groups ranged from a low of 66 to a high of 73 (Table 7). The less variable groups at the 50% ration level did not experience a significantly higher mortality rate than the charr groups at other ration levels (Table 7).

A significant (P=0.01) positive correlation was observed between the $\log_e$ increase in variance of fish weight and the $\log_e$ mean charr weight for each of the charr groups, during the first growth period at all of the ration levels (Fig. 15). Log_e mean charr weight explained over 95% ($r^2 > 0.95$) of the observed variance. There was a non significant ($P = 0.29$) contribution of $\log_e$ time to the variance model [2] at the 100% ration level. The sub-model for variance in fish weight [3] assuming the effect of $\log_e$ time to be zero was used to compare the increase in $\log_e$ variance in charr weight at the different ration levels over the first growth period. There was a significant treatment (ration level) by $\log_e$ mean weight interaction effect (non-parallelism) among the treatment groups (Fig. 15). However there was a non significant treatment by $\log_e$ mean weight interaction effect when only the 50% and 150% ration levels were compared (Fig. 15). There was a significant

Figure 14. Charr weight frequency distributions at the end of the second growth trial period for the 50% ration level (R50), the 100% ration level (R100) and the 150% ration level (R150) treatment groups; each treatment group was replicated and tank (TK) numbers are shown on the right of the graph.

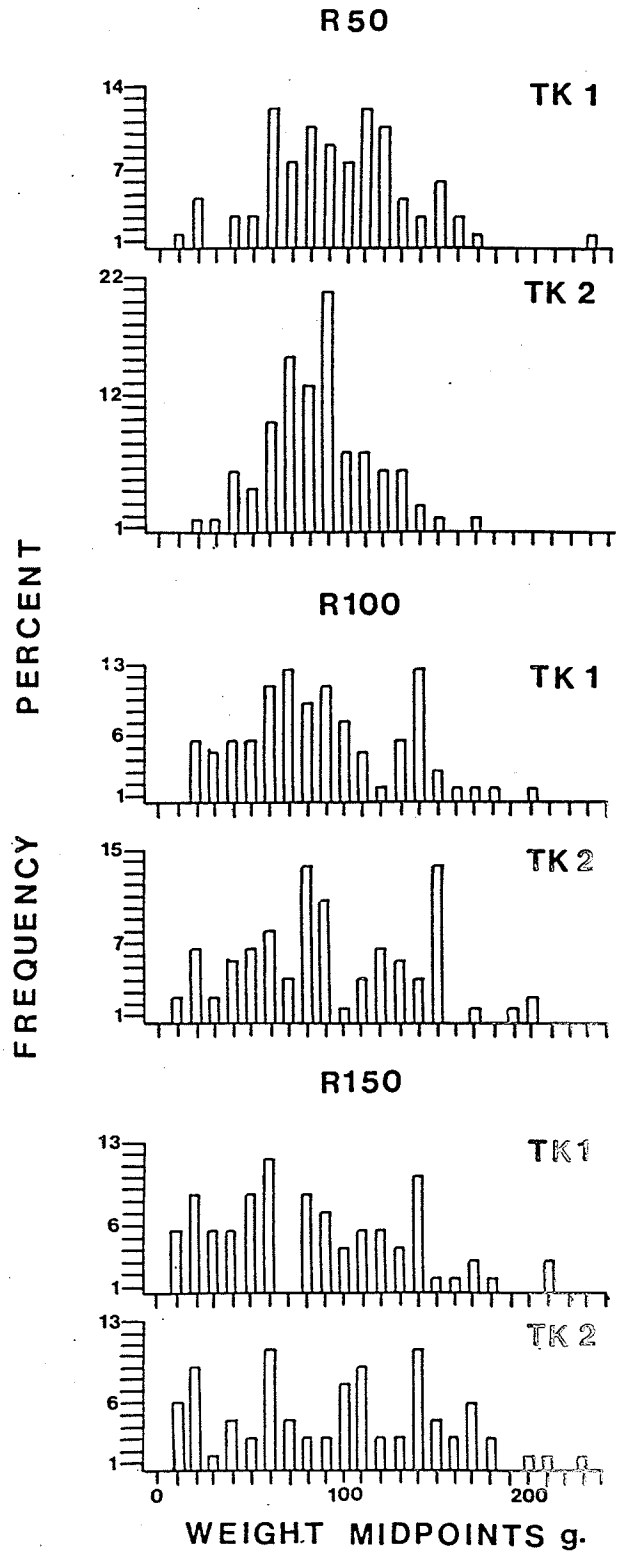
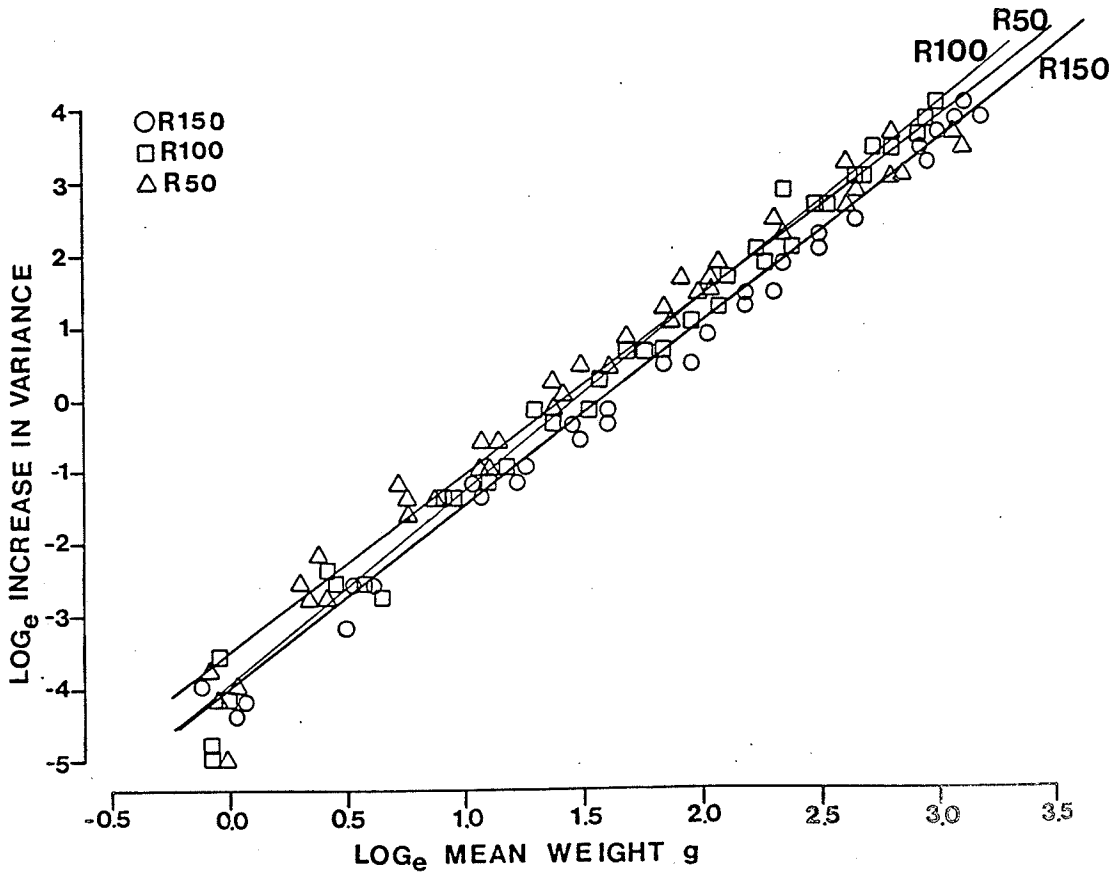

R50
TK 1
14
7
1
TK 2
22
12
1
R100
TK 1
13
6
1
TK 2
15
7
1
R150
TK1
13
6
1
TK 2
13
6
1
0
100
200
FREQUENCY PERCENT
WEIGHT MIDPOINTS g.

Figure 15. Log_e increase in variance in charr weight versus the log_e mean charr weight, for the first growth trial period, for the 50% (R50), 100% (R100) and 150% (R150) ration levels. Solid lines indicate values predicted from the common variance model fitted within each ration level; b_0 coefficients for the R50, R100 and R150 groups were -3.58(0.16), -3.90(0.18) and -4.03(0.15), respectively; the b_w coefficients for the R50, R100 and R150 groups were 2.38(0.08), 2.60(0.09) and 2.39(0.07), respectively.

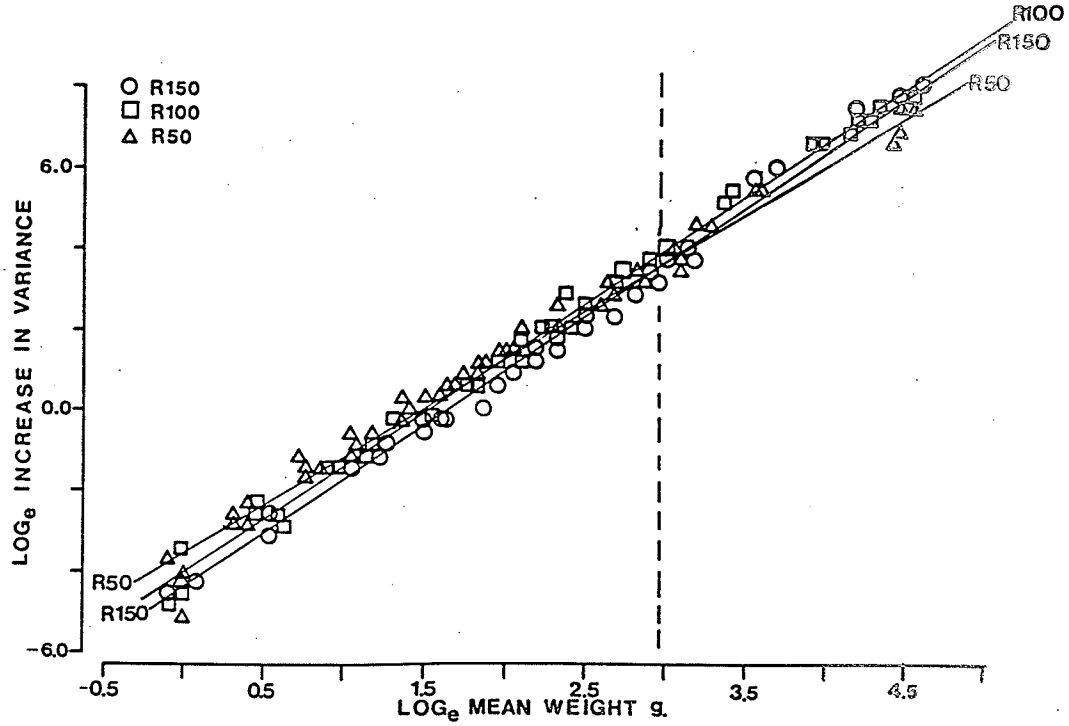

R50
R100
R150
OR150
□R100
△R50
4
3
2
1
0
-1
-2
-3
-4
-5
LOGe INCREASE IN VARIANCE
-0.5
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
LOGe MEAN WEIGHT g

($P = 0.01$) treatment (ration level) effect on the $\log_e$ increase in variance in fish weight when the 50% and 150% ration levels were compared. The b_w coefficients for the 150% and 50% ration levels were 2.52(0.05) and 2.47(0.05), respectively.

There was a significant ($P=0.01$) positive correlation between $\log_e$ increase in variance of fish weight and the $\log_e$ mean fish weight over the whole experiment (periods 1 & 2) for the two charr groups at each of the three ration levels (Fig. 16). There was a significant treatment (ration level) by $\log_e$ weight interaction effect (non-parallelism) among the treatment groups (Fig. 16). The b_w coefficients (slopes) for the variance models for the 50, 100 and 150% ration levels were 2.48(0.04), 2.67(0.04) and 2.65(0.04), respectively. These values were not markedly different than the values observed during the first growth period for the 50 and 100% ration level groups.

Estimated CV ($E(CV_t)$) values for the weight distributions of the three treatment groups were calculated assuming a mean charr weight of 90g, which correspond to the approximate mean weight of the groups at the end of the second growth trial. $E(CV_t)$ values were calculated using coefficient values from both the variance

Figure 16. Log_e increase in variance in charr weight versus the log_e mean charr weight, for both the first and second growth periods, for the 50% (R50), 100% (R100) and 150% (R150) ration levels, the vertical broken line represents the separation between growth periods one and two. Solid lines indicate values predicted from the common variance model fitted within each ration level; b_0 coefficients for the R50, R100 and R150 groups were -3.68(0.10), -4.09(0.10) and -4.29(0.10), respectively; the b_w coefficients for the R50, R100 and R150 groups were 2.48(0.04), 2.67(0.04) and 2.65(0.04), respectively.


R100
R150
R50
O R150
□ R100
△ R50
6.0
0.0
-6.0
LOGe INCREASE IN VARIANCE
R50
R150
-0.5
0.5
1.5
2.5
3.5
4.5
LOGe MEAN WEIGHT g.

model [2] including $\log_e$ time as a covariate and the sub-model [3] assuming $b_t = 0$. Estimates were calculated using the coefficients derived from the fitting of the models to the first growth trial period and using coefficients derived from the combined first and second growth trial periods (Table 8). $E(CV_t)$ values calculated from the variance model coefficients derived from the growth data from the combined first and second growth trial periods were more similar to the observed CV values then were $E(CV_t)$ values calculated using the coefficients derived from the first period growth data alone (Table 8). $E(CV_t)$ values for the 50% ration level group were smaller than the $E(CV_t)$ values for the other treatment groups in all cases except were the sub-model [3] coefficient values were estimated using the data from only the first growth trial period (Table 8).

Table 8. Comparison of Estimated CV ($E(CV_t)$) and an average observed CV (standard deviation/mean X 100) values, of the distribution of charr weights in the 50% (R50), 100% (R100) and 150% (R150) treatment groups; assuming a target weight of 90g. $E(CV_t)$ values were estimated using both the full variance model [2] including $\log_e$ time as a variable and the variance sub - model [3] assuming $b_t = 0$; models were fitted to growth data from the first part of the growth trial and from the combined data from part one and two .

Variance model	Treatment group	$E(CV_t)$ @ 90g. %	Observed CV %	Difference CV - $E(CV_t)$
		First Growth Trial		
[2]	R 50	27.0	38.4	+ 11.4
	R100	101.9	49.5	- 52.4
	R150	55.8	58.8	+ 3.0
[3]	R 50	40.7	38.4	- 2.3
	R100	54.6	49.5	- 5.1
	R150	34.0	58.5	+ 24.5
		First and Second Growth Trial		
[2]	R 50	35.1	38.4	+ 3.3
	R100	54.5	49.5	- 5.0
	R150	59.4	58.5	- 0.6
[3]	R 50	39.2	38.4	- 0.8
	R100	55.7	49.5	- 6.2
	R150	55.9	58.8	+ 2.9

DISCUSSION

The slow growth of charr fed at the 50% ration level confirms that this ration level is limiting to growth. The relatively small difference in growth between the 100 and 150% ration level suggests that the 150% treatment was approaching or had exceeded the maximum ration level for the charr under the experimental cultural conditions. Both the CV values for the weight distributions at the end of the experiment and the results of the variance model analysis confirm an effect of ration on variation in charr growth, with the charr groups fed a restricted ration exhibiting the lower variation in weight. These results are consistent with Nordeng's (1983) observation that an increased amount of food increased the resident (small) fraction of a charr population. However the 100 and 150% ration level charr groups in this experiment contained some of the largest charr and there was no indication that these ration levels resulted in a reduced number of anadromous (large) charr as observed by Nordeng (1983). The charr groups fed at the 50% ration exhibited an overall more normal weight distribution with fewer small and fewer larger individuals than the charr groups fed at the 100 and 150% ration levels.

The significantly longer time it took charr fed at the 50% ration level to achieve the target mean weight may explain the observed differences in variation in weight. However the b_w (slope)

coefficient of the variance models fitted to the first part of the growth trial to a target weight of 20g and the model fitted to all the growth trial data did not differ significantly for the 50 and 100% ration level groups. It was only the 150% ration level group which exhibited a significant change (increase) in the value of the b_w coefficient between the two growth periods.

The reduced variation in charr weights in the groups fed a restricted ration might also result from a reduction in aggressive behaviour by dominant charr. Ryer & Olla (1991 ab) reported a decline in aggressive behaviour with reduced feeding levels, particularly with schooling fish. However it has also been suggested that low feeding levels result in an increased level of aggression among fish (Symons 1968), with dominant fish tending to more actively prevent access to food by other members of the group.

A restricted ration level did affect the degree of variation in weight observed in the charr groups in this experiment, although the results of this experiment do not demonstrate the mechanism by which this effect occurs. Control of ration levels is relatively easy to implement under culture conditions and may provide some method of controlling weight variation in cultured groups of Arctic charr. The slow growth of charr on a restricted ration would make the use of a restricted ration over all of the growth cycle uneconomical but it might be possible to use a restricted ration levels at selected

times during the production cycle to control variation in weight in groups of culture Arctic charr.

CHAPTER 4

Effect of rearing density on the early growth of juvenile Arctic charr (*Salvelinus alpinus* L.)

ABSTRACT

Arctic charr from the same full-sib family were reared under two different densities for 97 days at 10 °C. In one treatment density was adjusted every two weeks by means of a tank enclosure to a density of 50kg/m^3. In the other treatment the density was allowed to increase as fish biomass increased to 50kg/m^3. Density had no significant effect on the variation observed in individual fish weights over the course of the growth trial. Density had a significant effect on the relationship between fish weight and specific growth rate. The increasing density treatment had an overall higher mean specific growth rate of 0.1%/day.

INTRODUCTION

In intensive aquaculture, the density at which a fish species can be stocked is an important factor in determining the economic viability of a production system. Wallace et al. (1988) and Baker and Ayles (1990) reported that the growth rate of Arctic charr was higher at densities of 30 to 40 kg fish/m^3 than they were at lower densities.

Wallace et al. (1988) hypothesized that higher rearing densities inhibited the development of aggressive behaviour amongst the fry and stimulated the development of schooling behaviour. Jobling (1985) claimed that social interactions were important determinants in the growth of Arctic charr and that a reduction in aggressive interactions could reduce the large variation in individual growth rates often reported in cultured charr populations. Neither Wallace et al. (1988) nor Baker and Ayles (1990) determined if increased density reduced variation in individual fish weights within the test populations.

The aim of the present study was to examine the effect of density on variation in individual fish weight of juvenile charr and the effect of high density (50 kg/m^3 or greater) on the overall mean fish growth rate.

As a fish population grows the density expressed as biomass per unit of water volume changes. To carry out controlled density experiments involves removing animals at selected time intervals during the experiment to reduce densities (Refstie 1977) or conducting the growth trial in a series of separate experiments (Wallace et al. 1988). These methods of adjusting density make it difficult to determine the effect of density on the variation in individual fish weights. Typically in commercial fish production systems, an initial density of fish is established by estimating the final density the culture system can support, and allowing the population to "grow into" the target density.

In the present study, an adjustable tank enclosure was used to maintain a density of greater than 50 kg/m^3 in one treatment. A simple model was used to compare changes in the variation in individual fish weights over time. Arctic charr fry were used because fish of this size have a high growth rate. The test population was formed from a single full-sib family to reduce genetic effects.

MATERIALS AND METHODS

Fish used in this study were members of a full-sib family of hatchery reared Arctic charr, originating from a first generation hatchery brood-stock (Papst and Hopky 1984). Experiments were conducted at the Rockwood Aquaculture Research Centre located 65 km north of Winnipeg, Manitoba, Canada. The fish used in this experiment were actively feeding and had a mean weight of 2.6 g. Each tank was stocked with 75 fish selected at random from the source population.

Fish were reared in round 21 l fibreglass tanks, all connected to the same bio-filter. Four tanks were selected at random and fitted with an adjustable screen cage (mesh size of 3mm), which allowed the culture volume of the tank to be adjusted. Based on the total wet weight of the fish population in the tank, the cages were adjusted every 14 days to ensure a fish density of 50 kg/m^3. Fish densities in four other tanks, not fitted with cages, increased to 50 kg/m^3 by the end of the experiment (day 97).

The water temperature and oxygen saturation were maintained at 10^{o}C and 80 percent, respectively. Fish were fed commercial rainbow trout feed, (Martins Feed Mill, Elmira, Ontario, Canada) by hand four times daily during the period from 08:30 hours to 16:00 hours. No feeding occurred on census days. The amount of food fed

was calculated using commercial feeding tables (Hilton and Slinger 1981) and the ration was adjusted every census day based on changes in the total wet weight of fish in each tank.

Individual charr weights were measured bi-weekly by anesthetizing the fish with 2-phenoxyethanol, shaking off excess water and weighing the fish to the nearest 0.05 g on an electronic balance. The total weight of the population was determined by weighing all the fish in a tank in a tared volume of water. Sample results throughout this paper are summarized by the mean (± the standard deviation).

Mean specific growth rate over the interval between 2 weighings was calculated using [1] from Chapter 1 and the effect of treatment on the increase in variance of fish weights was tested using the linear model [2] Chapter 1.

Treatment effects on growth rates were assessed by using an analysis of covariance of the relationship between growth rate and fish weight as described by Brett (1979) and the equation:

$$\log_e G = a + b \log_e W_t \qquad [6]$$

where G = specific growth rate (%/day) over the time interval t' to t, W_t is the mean weight (g) at time t, and a and b are the intercept and

slope, respectively, of the growth relationship.

The coefficient of variation (CV) for the charr weight distributions were calculated as described in Chapter 1.

RESULTS

The mean density of charr in the tanks without enclosures was 8.7 kg/m^3 on day 0 and increased to a mean density of 50.8 kg/m^3 on day 97. The mean density of charr in the tanks with enclosures was adjusted every two weeks to approximately 50 kg/m^3 (Fig. 17).

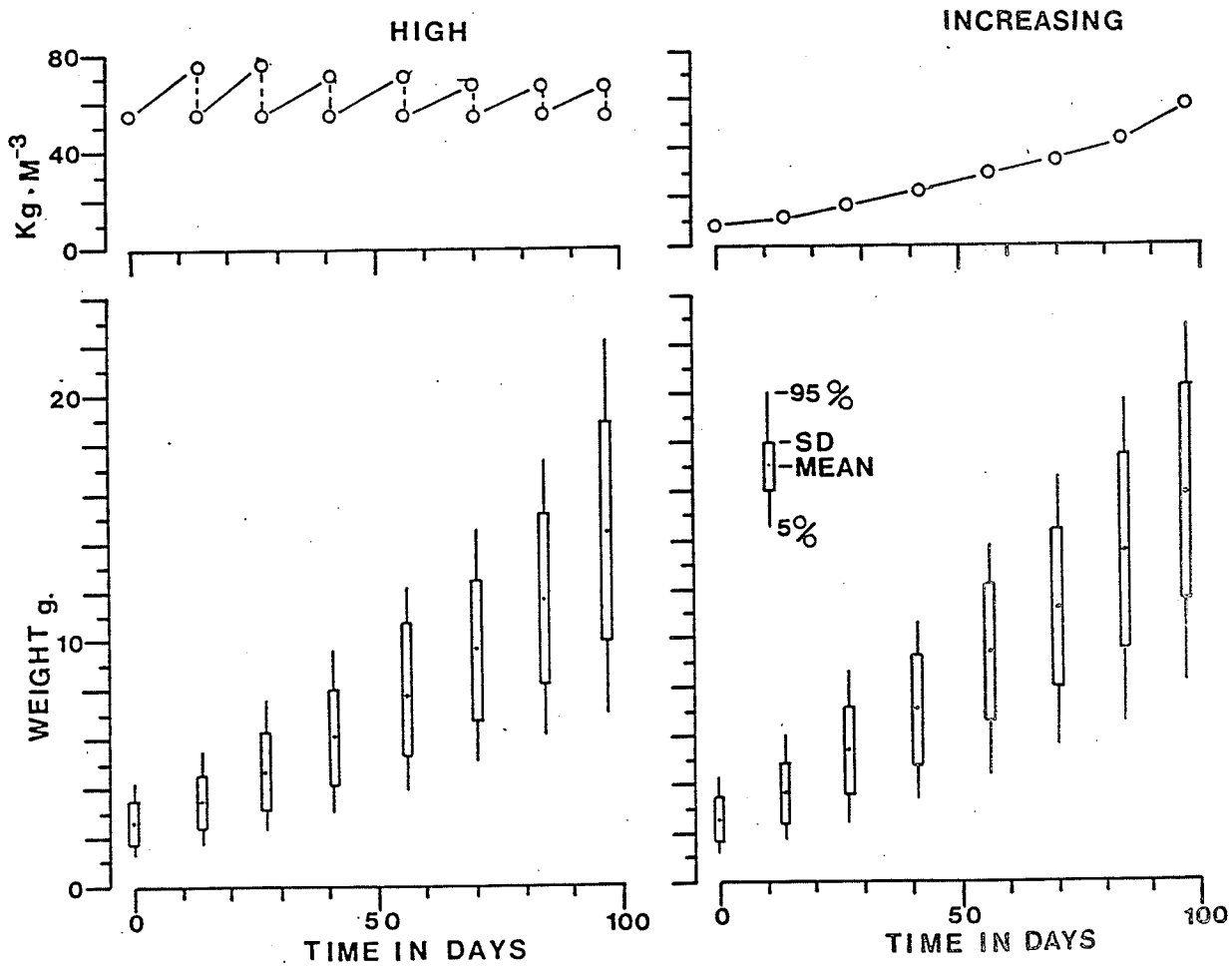
The overall mean weight of charr in tanks without enclosures was 2.6 (0.9) g on day 0 and increased to 15.7 (4.1) g by day 97 (Table 9) (Fig. 17). The overall mean weight of charr in tanks with enclosures was 2.6 (0.9) g on day 0 and increased to 14.4 (4.5) g by day 97 (Table 1) (Fig. 1). No significant ($P = 0.36$) differences were found among charr weights in any of the tanks at the beginning of the experiment (day 0). On day 97 mean charr weight in the tanks without enclosures (increasing density) was significantly ($P < 0.01$) greater than that in the tanks with enclosures (fixed density). Mean charr weights between replicate tanks within a treatment were not significantly different on day 97 ($P > 0.05$).

Over the 97 days of the experiment the specific growth rate of the charr population in the tank without enclosures (increasing density) was 1.5 %/day, while the specific growth rate of charr in the tanks with enclosures (high density) was 1.4 %/day (Table 9).

Table 9. Mean charr weight (± standard deviation) and coefficient of variation (CV = standard deviation/mean X 100) of the distribution of individual charr weights for the increasing (Inc.) treatment and the high density treatment groups on day 0 and day 97; the specific growth rate (SGR) for each group for the 97 day growth trial period.

Treatment	Tank	Mean Charr weight g.		CV %		SGR
		Day 0	Day 97	Day 0	Day 97	%/day
Inc.	1	2.8 (1.0)	16.8 (4.9)	36.6	29.0	1.5
	2	2.5 (0.9)	15.2 (4.5)	35.2	39.7	1.5
	3	2.7 (1.0)	16.1 (4.0)	38.8	24.9	1.5
	4	2.5 (0.9)	15.7 (4.1)	35.0	25.9	1.6
High	1	2.4 (0.8)	14.4 (4.2)	32.7	29.0	1.4
	2	2.6 (1.0)	14.3 (5.0)	38.6	35.1	1.4
	3	2.6 (0.8)	15.0 (4.6)	31.6	30.5	1.4
	4	2.6 (0.9)	13.8 (4.2)	34.8	30.4	1.4

Figure 17. Change in density and mean charr weight with time for the high and increasing density treatments.Vertical lines represent 5 and 95% quantiles for the distribution of charr weights.


HIGH
INCREASING
80
40
0
Kg · M-3
20
10
0
WEIGHT g.
95 %
SD
MEAN
5%
0
50
100
TIME IN DAYS
0
50
100
TIME IN DAYS

A significant ($P < 0.01$) negative correlation was observed between $\log_e$ specific growth rate and $\log_e$ mean charr weight within each treatment ($r^2 = 0.72$ increasing density, $r^2 = 0.75$ high density) (Fig. 18). No significant differences ($P > 0.40$) were observed between replicates within treatments. A significant ($P = 0.01$) $\log_e$ weight by treatment interaction effect was observed showing that the linear relationships between $\log_e$ specific growth rate and $\log_e$ weight for treatments were not parallel (unequal b in [6]).

A significant ($P = 0.01$) positive correlation was observed between the $\log_e$ increase in the variance of fish weight and the $\log_e$ mean charr weight (Fig. 19). There was a significant ($P < 0.01$) contribution of $\log_e$ time to the variance model [2] even after $\log_e$ weight was accounted for. The model incorporating $\log_e$ mean weight and $\log_e$ time explained 98% ($r^2 = 0.98$) of the observed variance. No significant $\log_e$ weight by treatment ($P = 0.58$) or $\log_e$ time by treatment ($P = 0.81$) interaction effects were observed and there was no significant ($P = 0.67$) difference between the adjusted treatment means. In summary, there were no treatment differences on any of the coefficients of the variance model [2] and a common model could be fitted to both treatments (Fig. 19).

The CV for the distribution of charr weights in the increasing density treatment declined slightly from 36.2% on day 0 to 29.9% on

Figure 18. The specific growth rate (SGR) - mean charr weight relation for the increasing and fixed (high) density treatments. The regression for the increasing density was $\log_e(SGR) = 1.20 - 0.34 \log_e$ (mean charr weight) with a $r^2 = 0.72$. The regression for the fixed density was $\log_e(SGR) = 1.61 - 0.48 \log_e$ (mean charr weight) with a $r^2 = 0.75$.

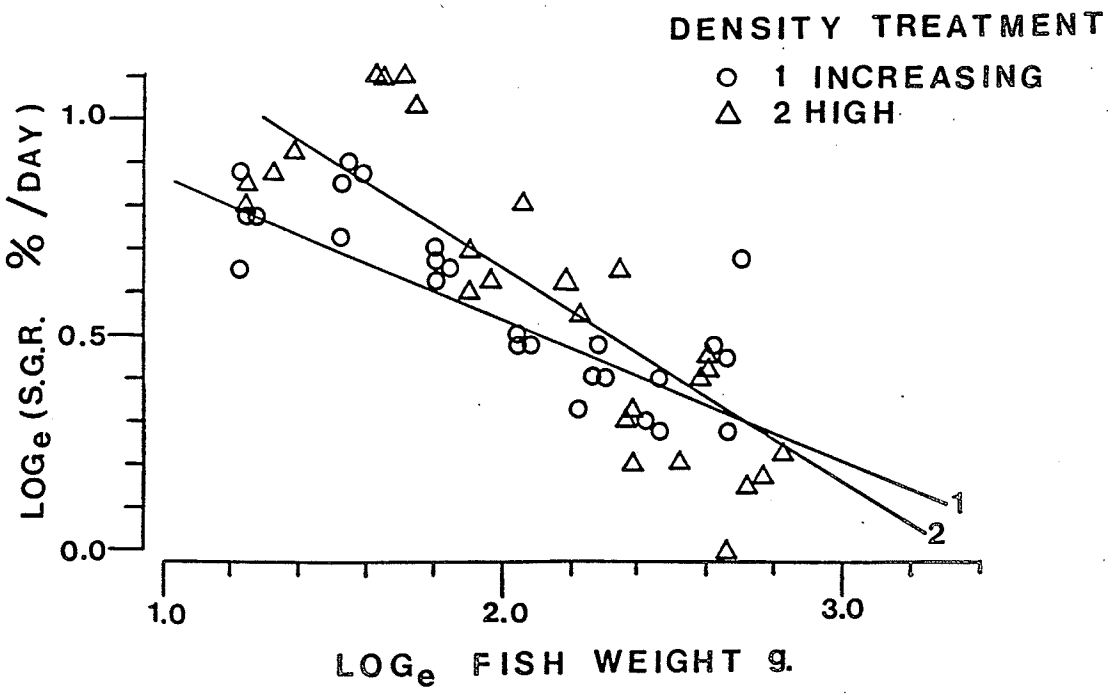
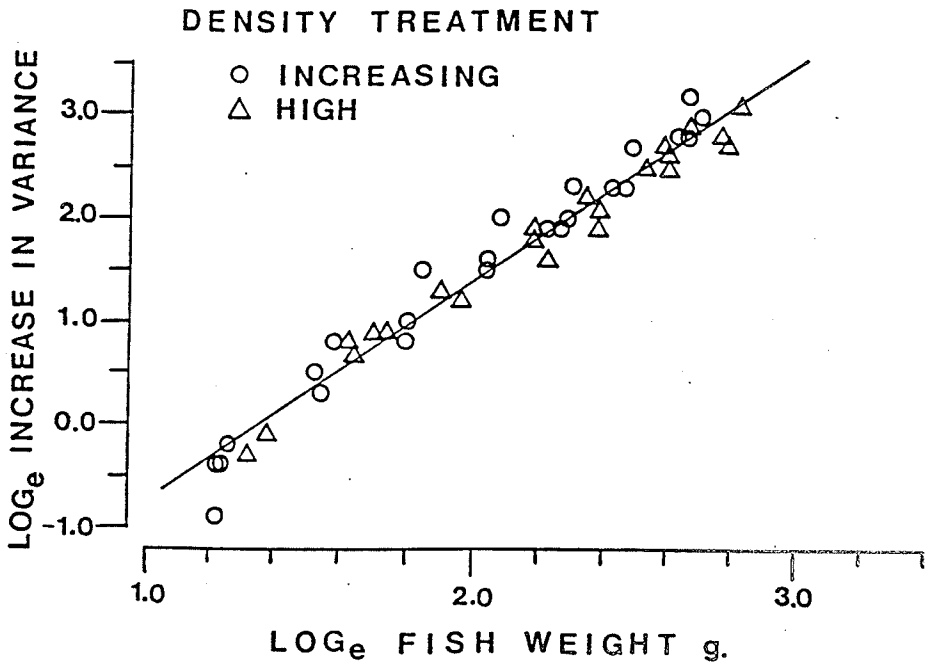
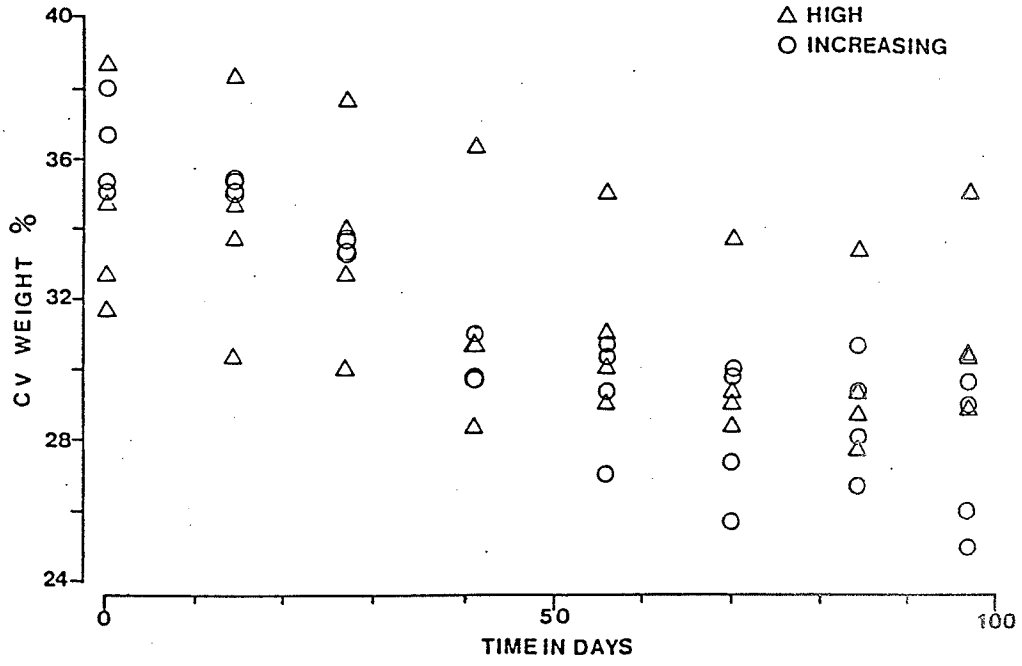

DENSITY TREATMENT
1 INCREASING
2 HIGH
LOGe (S.G.R. % /DAY)
1.0
0.5
0.0
1.0
2.0
3.0
LOGe FISH WEIGHT g.
1
2

Figure 19. Linear regression of $\log_e$ increase in variance in charr weight versus $\log_e$ mean charr weight ($r^2 = 0.97$). The fitted common line for both treatments (ignoring a small but significant contribution of $\log_e$ time) was $\log_e$ (increase in variance) = - 3.02 + 2.2 $\log_e$ (mean charr weight).


DENSITY TREATMENT
INCREASING
HIGH
LOGe INCREASE IN VARIANCE
3.0
2.0
1.0
0.0
-1.0
1.0
2.0
3.0
LOGe FISH WEIGHT g.

day 97 (Table 9). The CV for the distribution of charr weights in the high density treatment also declined from 34.4% on day 0 to 31.3% on day 97 (Table 9). No trends were observed in the coefficient of variation for the distribution of charr weights in either treatment over the course of the experiment (Fig. 20).

Figure 20. Changes in the coefficient of variation CV (standard deviation/mean) for the distribution of individual charr weights in each tank for each census day.


△ HIGH
○ INCREASING
CV WEIGHT %
40
36
32
28
24
0
50
100
TIME IN DAYS

DISCUSSION

The overall difference in specific growth rate between treatments was 0.1 %/day and the difference in final mean charr weight was 1.3 g. Given the marked difference in rearing density, these results confirm the conclusions of earlier studies (Wallace et al. 1988, Baker and Ayles 1990) that Arctic charr can be reared at high densities.

The lack of a significant treatment effect for the model analyzing the relationship between weight and variance suggests that density had no affect on the variance of individual charr weights. The lack of a trend for the coefficient of variation in weight distribution for both treatments also suggests that high density culture does not reduce size variation. These observations do not support the prediction (Wallace et al. 1988) that high density culture of Arctic charr would reduce size variation.

The results from this study do not remove the possibility that social interactions are responsible for variation in growth of Arctic charr, for it could be argued that density does not affect social interaction. However, it is unlikely that social interaction would have had a consistent effect in all the tanks and amongst treatments. It would seem much more likely that the observed variation in individual Arctic charr weights is primarily affected by

genetic factors and that the increase in variance for charr weights, observed over the course of a growth trial, results principally from the increasing mean weight of the populations.

The significant negative correlation between mean charr weight and specific growth rate is consistent with that reported by Brett (1979) as occurring generally with salmonids. The slopes for the linear relationship between $\log_e$ weight and $\log_e$ specific growth rate for the increasing density treatment (-0.34) and the high density treatment (-0.48) were similar to the -0.41 value suggested by Brett (1979) as common to salmonids. Brett (1979) suggested that environmental factors would affect the intercept of the relationship but not the slope. These results clearly show that density significantly affects the relationship between size and growth rate. This is new information and has important implications for the use of the relationship between size and growth rate. Jobling (1985) hypothesized that feeding rates and social interaction were important factors affecting the relationship between size and specific growth rate of cultured Arctic charr. Our results suggest that the effect of density must be considered when interpreting size and growth rate relationships.

CHAPTER 5

Variation in weight in full-sib families of hatchery reared Arctic charr (*Salvelinus alpinus* L.).

ABSTRACT

Arctic charr reared under intensive culture conditions exhibit a large variation in individual body weight. Full-sib families exhibited a significant ($P = 0.01$) positive correlation between $\log_e$ increase in variance for fish weight and the $\log_e$ mean fish weight. Over 95% of the variation in weight was explained by the mean fish weight and elapse time. The relationships between the $\log_e$ increase in variance for fish weight, the $\log_e$ mean fish weight and the $\log_e$ elapse time for the families were not significantly ($P = 0.58$) different. Only a small percentage of fish were maturing sexually 700 days after fertilization. Neither sexual maturation nor sexual dimorphism appeared to contribute significantly to the observed variation in weight in any of the families.

INTRODUCTION

Arctic charr (Salvelinus alpinus) reared under intensive culture conditions exhibit a large variation in body weights (Papst and Hopky 1983). Jobling (1985) concluded that social interactions were responsible for observed increases in the variation in weight of groups of Arctic charr. Papst et al. (1992) observed that rearing Arctic charr at a fixed density of 50 kg/m^3 had no significant effect on the variation in individual fish weights and that the majority of the variation was explained by increasing mean weight and rearing time. While investigating the factors leading to stunting in hatchery reared Arctic charr Jobling and Reinsnes (1986) concluded that the physiological growth potential of stunted Arctic charr was lower than normal individuals in the absence of any social interaction.

Phenotypic plasticity is a general term used to describe all types of environmentally induced phenotypic variation (Stearns 1989). Natural Arctic charr populations often exhibit a significant degree of phenotypic plasticity, often occurring in several coexisting forms which differ in size and time to sexual maturity (Svedang 1990). Papst and Hopky (1983) found that the occurrence of early maturation small, male Arctic charr contributed significantly to the variation in individual body weights of a graded mixed population reared under intensive aquaculture conditions.

Variation in charr weights within a group of hatchery reared charr might result from a variation in the success of individuals in obtaining food. One would expect the gross nutritional state of charr that were not successfully feeding due to social interaction or other factors to be low. Jensen (1980) observed that an index based on the water content of the gut of charr was highly correlated with the energy content of the charr and therefor a measure of the gross nutritional state of individual charr. This gut index was not correlated with charr size in wild populations (Jensen 1980).

The present study examines the growth and variation in growth of six full-sib families of Arctic charr to determine how variation in body weight changes over time and with growth. The degree to which early maturation, sexual dimorphism and variation in the gross nutritional state contribute to variation in body weight was examined.

MATERIALS AND METHODS

Fish stocks

Charr used in this study were members of six full-sib families of hatchery reared Arctic charr, originating from the Fraser River, Labrador, Canada (de March and Baker 1990). Families one and two were from a first generation hatchery reared brood-stock from a 1981 spawn taken from the wild population. The remaining families were from a second generation hatchery reared brood-stock from a 1980 wild spawn take. Experiments were conducted at the Rockwood Aquaculture Research Centre located 65km north of Winnipeg Manitoba, Canada. Eggs were incubated at 6.4 °C and fry were transferred to tanks 131 days post fertilization (PF).

Growth Trial

Between 162 and 169 days PF 150 to 140 actively feeding fry were transferred to 21-l fibreglass tanks. Families one, two and three had three replicates and families four, five and six had two replicates. The charr were acclimatized for approximately two weeks prior to the growth trial which commenced 190 days PF, with a census of all tanks. After 112 days charr were transferred to 61-l fibreglass tanks and the growth trial was continued for 94 days. In total the growth trial lasted 206 days and ended 396 days PF. Throughout the growth trial the water temperature was 10°C.

Both the 21-l and 61-l tanks were connected to common bio-filters. Charr were fed commercial rainbow trout feed (Martins Feed Mill, Elmira, Ontario Canada) by hand four times daily during the period from 0830h to 1600h. No feeding occurred on census days. The amount of food fed was calculated using commercial feeding tables (Hilton & Slinger 1981) and the ration was adjusted every census day based on changes in total wet weight of fish in each tank.

Individual charr weights were measured approximately every 30 days by anesthetizing the fish with 2-phenoxyethanol, shaking off excess water and weighing 75 fish to the nearest 0.05g on an electronic balance. The total weight of the population was determined by weighing all the charr in a tank in a tared volume of water.

Mean specific growth rate over the interval between two weighings and the effect of treatment on the variance in charr weights were determined using the methods described in Chapter 1.

Family effects on growth rates were assessed by using an analysis of covariance of the relationship between specific growth rate and the mean charr weight as described in Chapter 4.

At the conclusion of the 206 day growth trial, two random samples of 75 charr were taken from each of the families and these

charr groups were reared for 101 days at a water temperature of 10 °C in separate 61-l tanks. After the 101 day period families were transferred to150 -l tanks at 6.4 °C and reared for an additional 203 days. At the end of the 206 day growth period (700 days PF), 75 charr from each family were killed with an overdose of 2-phenoxyethanol. Individual lengths and weights were measured and the sex of each charr was determined by examining the gonads. A random sub-sample of 35 charr from each family was used to determine the maturity Index (wet weight of gonad/ wet charr weight X 100). The stomach and intestines (gut) were also removed from each of the 35 charr in the random samples. The gut samples from each charr were placed in individual plastic bags and frozen at -25°C. After storage for approximately 60 days the guts were thawed and washed with distilled water. The guts were then blotted dry with a paper towel and weighed to the nearest 0.001 g on an electronic balance. Guts were then placed in individual pre-weighed tinfoil trays and heated in a drying oven at 80°C for 24 hours. After cooling in a desiccator the guts were individually weighed to determine a dry gut wet. A gut index (GI) was calculated (GI= dry gut weight/wet gut weight X 100) following the method described by A. J. Jensen (1980).

RESULTS

The mean charr weight in all the families increased by approximately 40.0 g over the 206 day growth trial (Table 10). The overall mean growth rates for the families were similar and ranged from a high of 2.4%/day to a low of 2.2%/day (Table 10).

The coefficient of variation (CV) for the distribution of individual charr weights for families 1 & 6 changed little during the growth trial, while the CV for families 2 & 5 increased and the CV for families 3 & 4 declined (Table 10). Charr weight distributions for the families were not strongly skewed on day 0 and changed little over the course of the growth trial (Table 10).

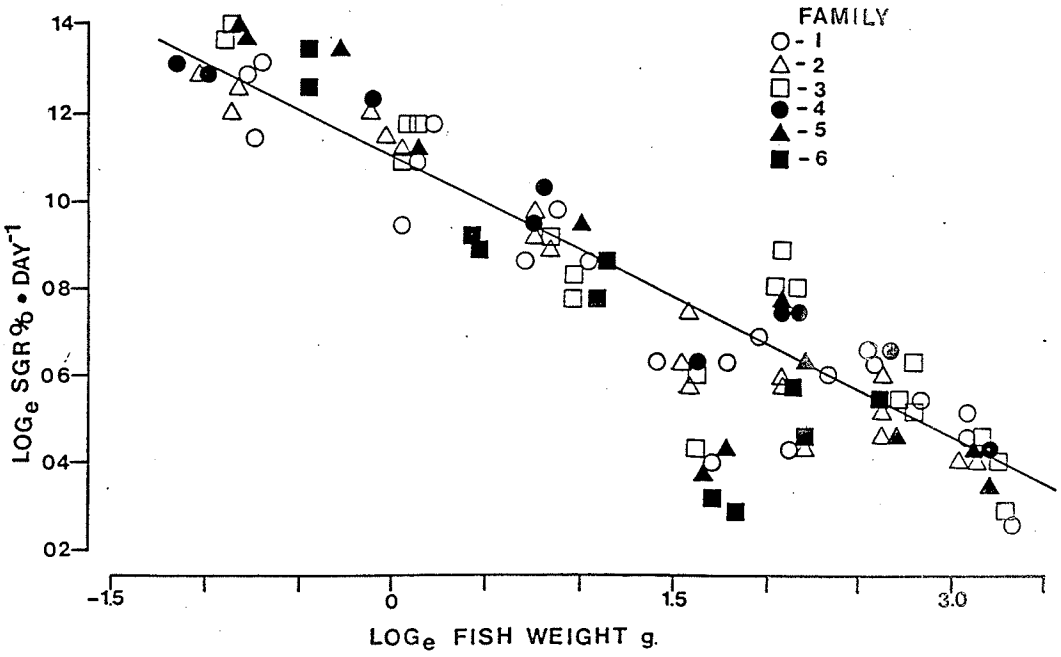
At the start of the growth trial mean weights were not significantly ($P > 0.05$) different among replicates except for replicate two in family 3 and replicate 2 in family 4. The actual differences in mean weights was small (Table 10). At the end of the growth trial there were no significant differences among replicates except in family 1, where replicate 1 was significantly ($P = 0.05$) smaller than the other two replicates (Table 10).

A significant ($P < 0.01$) negative correlation was observed between $\log_e$ specific growth rate and $\log_e$ mean weight for each of the families (Fig 21). No significant differences ($P > 0.50$) were

Table 10. Mean charr weight (± Standard deviation); coefficient of variation (CV = standard deviation/mean X 100) and skew (Sk) for the charr weight distribution; at the start (day 0) and the end (day 206) of the growth trial for the six families of charr. Specific growth rate (SGR) over the 206 day growth trial.

Tank	Number	Weight Day 0				Number	Weight Day 206			SGR
	Charr	Mean (± Sd) g.		CV %	Sk	Charr	Mean (± Sd) g.		CV %	Sk	%/day
					Family 1						
1	111	0.45	(0.12)	26.4	+0.22	82	39.7	(11.1)	27.9	+0.13	2.2
2	131	0.46	(0.13)	26.9	+0.14	75	42.5	(10.5)	24.7	+0.00	2.2
3	126	0.48	(0.13)	27.1	+0.13	81	46.1	(12.7)	27.6	+0.51	2.2
					Family 2						
1	152	0.39	(0.14)	35.5	+0.20	84	40.3	(16.1)	40.0	+0.00	2.3
2	120	0.35	(0.14)	40.6	+0.11	79	37.9	(18.0)	47.5	-0.08	2.3
3	141	0.39	(0.14)	36.1	+0.14	80	39.9	(19.7)	49.2	+0.29	2.3
					Family 3						
1	111	0.43	(0.12)	28.1	-0.12	76	45.9	(9.7)	21.2	-0.38	2.3
2	122	0.40	(0.13)	32.4	+0.13	81	44.1	(11.4)	25.9	-0.72	2.3
3	126	0.41	(0.12)	28.6	+0.11	81	45.9	(13.1)	28.4	-0.79	2.3
					Family 4						
1	93	0.37	(0.14)	37.0	+0.39	71	45.9	(12.5)	27.1	-0.47	2.3
2	73	0.31	(0.14)	44.9	+0.29	68	44.9	(12.2)	27.1	-0.28	2.4
					Family 5						
1	86	0.43	(0.11)	24.2	-0.03	82	42.0	(14.6)	34.7	-0.24	2.2
2	81	0.44	(0.14)	30.9	+0.14	80	43.6	(16.6)	38.0	+0.01	2.2
					Family 6						
1	85	0.64	(0.19)	29.3	-0.22	74	39.9	(11.4)	28.5	-0.66	2.0
2	81	0.62	(0.17)	28.0	-0.06	79	41.1	(11.7)	28.6	-0.56	2.0

Figure 21. The specific growth rate (SGR) - mean charr weight relation for six families during the 206 day growth trial. The common regression for the families was $\log_e(SGR) = 1.06(0.06) - 0.24(0.03) \log_e$ (mean charr weight).


FAMILY
1
2
3
4
5
6
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12
10
08
06
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02
LOGe SGR % • DAY-1
-1.5
0
1.5
3.0
LOGe FISH WEIGHT g.

observed between replicates and no significant ($P > 0.50$) family differences were observed. A common model could be fitted to all of the growth trial data.

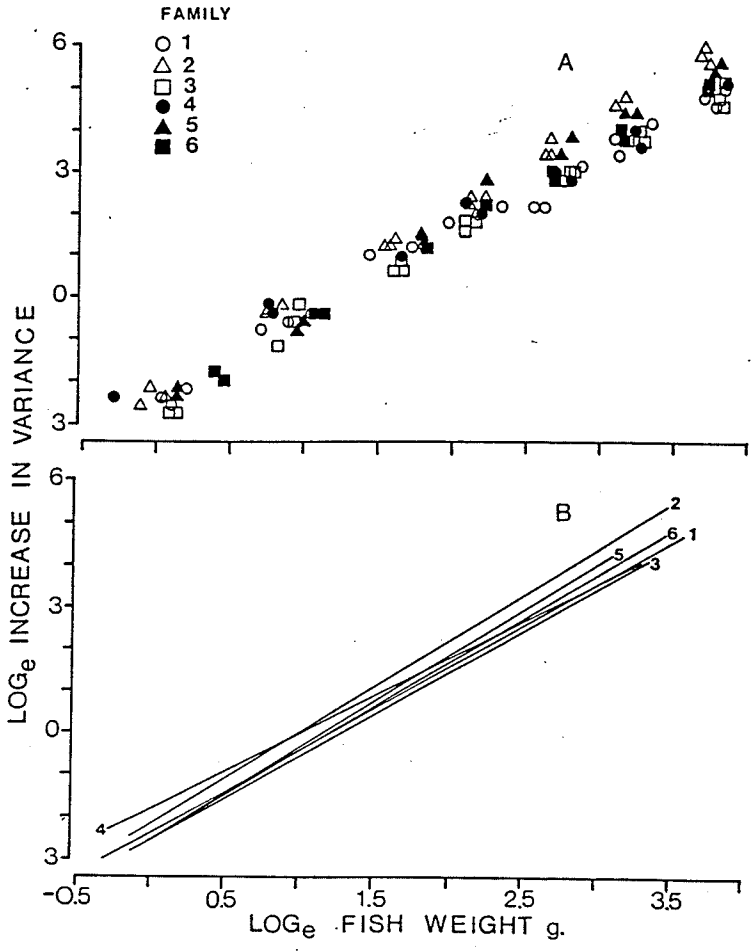
A significant ($P = 0.01$) positive correlation was observed between the $\log_e$ increase in the variance of charr weight and the $\log_e$ mean charr weight for each family (Fig. 22A & B). A significant ($P = 0.01$) $\log_e$ mean weight by family interaction effect was observed, as family regressions were not parallel.

There was a significant ($P > 0.01$) contribution of $\log_e$ time to the variance model [2] even after $\log_e$ weight was accounted for in all families except families 2 & 5. The model incorporating $\log_e$ mean weight and $\log_e$ time explained 99% ($r^2 = 0.99$) of the observed variance. No significant $\log_e$ weight by family ($P = 0.07$) or $\log_e$ time by family ($P = 0.50$) interaction effects were observed and there was no significant ($P = 0.58$) difference between the adjusted family means. There were no family differences for any of the coefficients of the variance models [2] and therefore a common model could be fitted to all the families. Although $\log_e$ time did not contribute significantly to the variance model in families 2 & 5, removal of these families from the analysis did not change the values of the coefficients.

Figure 22A. Log_e increase in variance in charr weight versus log_e mean charr weight during the 206 day growth trial, for the six charr families.

Figure 22B. Linear regressions of log_e increase in variance in charr weight versus log_e mean charr weight for each of the six charr families:

family	b_o	b_w	r^2
1	-2.52(0.23)	2.01(0.09)	0.99
2	-2.39(0.11)	2.29(0.05)	1.00
3	-2.67(0.20)	2.05(0.08)	0.99
4	-1.62(0.13)	1.77(0.05)	1.00
5	-2.62(0.17)	2.17(0.07)	0.99
6	-2.69(0.17)	2.07(0.07)	0.99


FAMILY
1
2
3
4
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6
A
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3
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3.5
LOGe FISH WEIGHT g.

Estimated coefficients of variation (ECV_t) for the distribution of charr weights for each family were calculated from the fitted variance models [2] for each family and compared with the measured CV values (Fig. 23). For the most part ECV_t values were within 5% of the measured values. ECV_t values were also calculated for the random samples of 75 charr measured 700 days PF (Fig. 23). Estimated values generally agreed with measured values except for family 2 and one replicate in family 1 (Fig. 23).

Seven hundred days PF the mean charr weight for the families ranged from 210.2 (55.6) to 159.9 (49.3)g (Table 11). The CV for the weight distributions ranged from 39.3 to 21.4 % (Table 11). The distributions of charr weights for all of the families were negatively skewed, expect for family 4which was positively skewed (Fig. 24). The mean weight of family 3 was significantly (P=0.05 Tukey's studentized range test) larger than the mean weights of families 5 and 6. There were no other significant differences between the mean weights of the six families.

The mean weights of male charr among the families ranged from 200.2 (52.4) to 158.7 (85.2)g (Table 11). Whereas female charr mean weights ranged from 218.1 (52.4) to 186.3 (23.0) g (Table 11). Male charr weight distributions in families 1 and 2 were significantly (P = 0.05 Kolmogorov-Smirnov) different than the distributions of female charr weights. Male charr weight

Table 11. Mean charr weight (± standard deviation), coefficient of variation (CV = standard deviation/mean X 100) of charr weights and sex ratio of a random sample of charr from; each of the six families (family sample) 700 days PF; male and female charr from each family and charr which could not be sexed due to a lack of gonad development (ND).

Family	Sample	Number Charr	Weight Mean (± Sd) g.	CV %	Sex ratio M:F
1	Family	74	193.4(41.3)	21.4	1.5:1
	Males	33	183.5(46.9)	25.6	
	Females	22	211.1(30.7)	14.5	
	ND	19	190.2(36.7)	19.3	
2	Family	72	189.1(74.4)	39.3	0.7:1
	Males	29	158.7(85.2)	53.7	
	Females	42	212.1(57.1)	27.0	
	ND	1	108.6(.)		
3	Family	73	210.2(55.6)	26.4	0.7:1
	Males	29	198.3(59.0)	29.8	
	Female	44	218.1(52.4)	24.0	
	ND	0			
4	Family	72	192.3(50.5)	26.3	1.1:1
	Males	37	200.2(59.0)	26.2	
	Females	34	188.0(42.1)	22.4	
	ND	1	46.5(.)		
5	Family	75	172.9(66.0)	38.2	1.4:1
	Males	42	169.8(65.1)	38.3	
	Females	30	189.2(56.9)	30.1	
	ND	3	53.4(39.7)	74.2	
6	Family	73	159.9(49.3)	30.8	4.0:1
	Males	32	170.8(46.1)	27.0	
	Females	8	186.3(23.0)	12.4	
	ND	33	143.0(52.1)	36.4	

Figure 23. Difference between the observed coefficient of variation (CV = standard deviation/ mean X 100) and the estimated coefficient of variation ($E(CV_t)$ for each of the groups of charr in each family, for each of the census days (clear symbols) during the 206 day growth trial (190 to 396 days post fertilization (PF) and the sample of 75 charr (solid symbols) measured 307 days after the start of the growth trial (497 days PF).

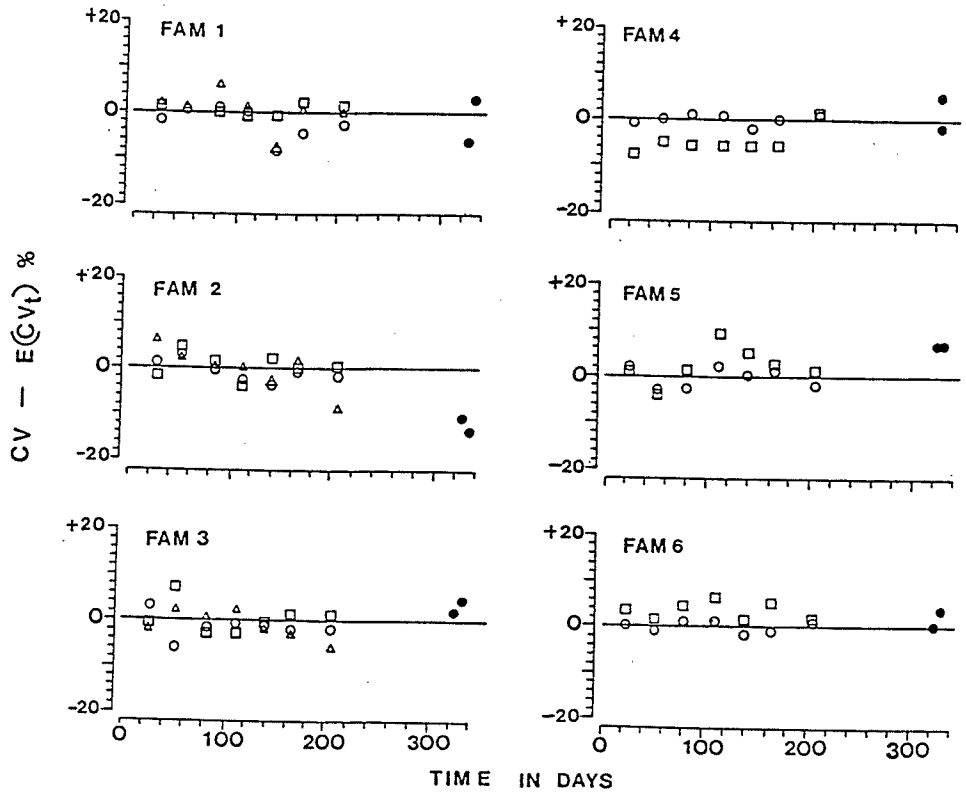
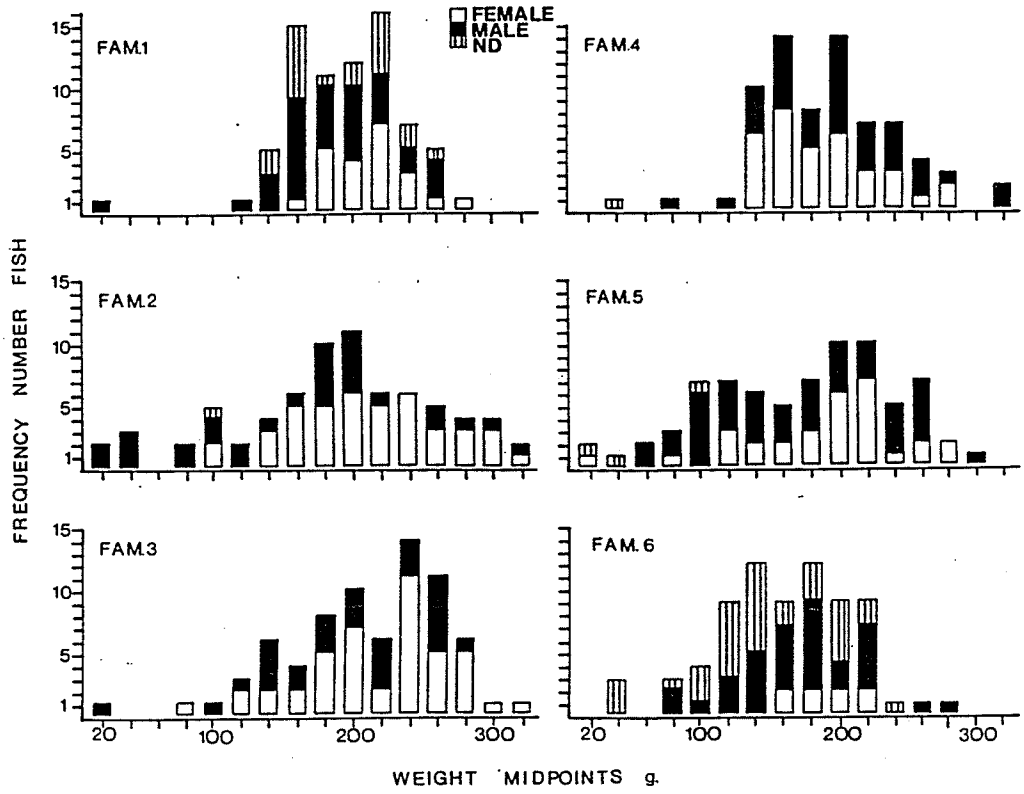

FAM 1
FAM 4
FAM 2
FAM 5
FAM 3
FAM 6
+20
0
-20
CV − E(Cvt) %
0
100
200
300
TIME IN DAYS

Figure 24. Distribution of individual charr weights, in each of the six families, by sex, 700 days post fertilization (PF).


FEMALE
MALE
ND
FAM.1
FAM.2
FAM.3
FAM.4
FAM.5
FAM.6
FREQUENCY NUMBER FISH
WEIGHT MIDPOINTS g.
1
5
10
15
20
100
200
300

distributions were not significantly different than female charr weight distributions in families 3, 4, 5, and 6. The CVs for the weight distributions of males was higher than that for females in all six families (Table 11). Males were amongst the smallest and largest charr in each of the families (Fig. 24).

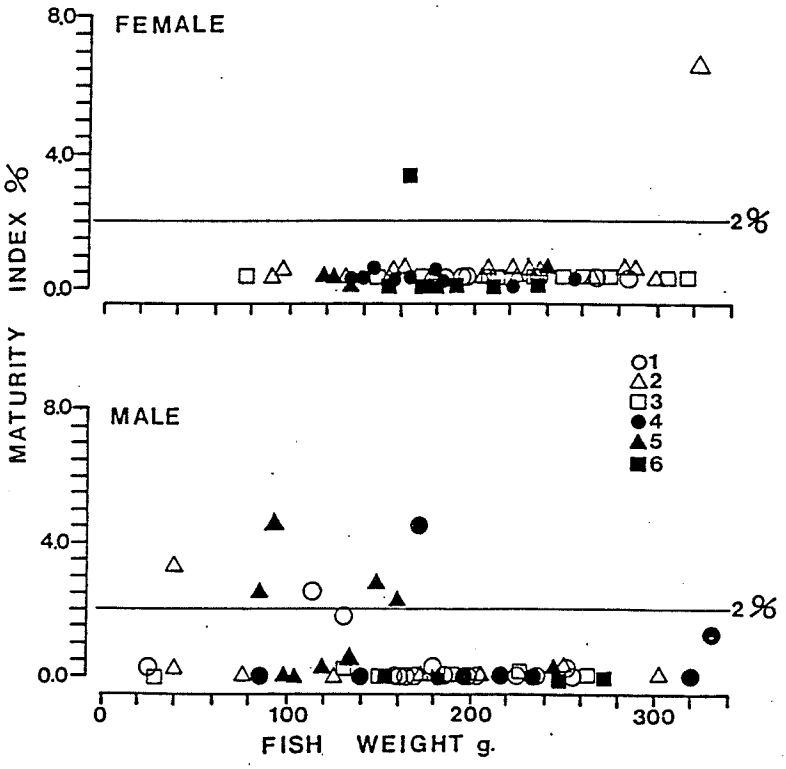
The sex ratio (males:females) of the charr amongst the families ranged from 4.0 : 1 to 0.7 : 1 (Table 11). The 4.0 : 1 ratio was observed in family 6 which contained the largest number of charr which could not be sexed due to a lack of gonadal development. Charr with no gonadal development appeared throughout the weight distribution of charr in family 6, while charr showing no gonadal development tended to be amongst the smaller charr in families 2, 4 and 5 (Fig. 24). All the charr in family 3 exhibited some gonad development (Table 11)

The mean maturity index of both males and females was less than 1% in all six families (Table 12). Seven males and two females had maturity indices greater than 2% (Fig. 25). Four of the males with maturity indices higher than 2% occurred in family 5, where they made up 20% of the males sampled. No males with maturity indices of 2% or greater were observed in either family 3 or 6 (Fig. 25). The two females with maturity indices higher than 2% were observed in families 6 and 2 (Fig. 25). Both females with maturity indices greater than 2% had body weights greater than 100g. Charr

Table 12. Mean charr weight (± standard deviation) and mean maturity index (MI = gonad weight/body weight X 100) by sex for charr in the maturity sub-sample of the six families, 700 days post fertilization (PF).

Family	Sex	Number Charr	Weight mean(± Sd) g	Mean MI %
1	Male	18	176.7(54.0)	0.3
	Female	7	220.7(42.5)	0.2
2	Male	13	176.6(90.4)	0.5
	Female	19	210.5(66.6)	0.7
3	Male	13	185.9(62.9)	0.1
	Female	22	218.4(55.4)	0.2
4	Male	15	207.2(54.8)	0.4
	Female	20	186.5(40.2)	0.3
5	Male	20	172.5(55.4)	0.7
	Female	15	191.2(44.4)	0.3
6	Male	12	176.6(53.8)	0.0
	Female	7	185.0(24.6)	0.5

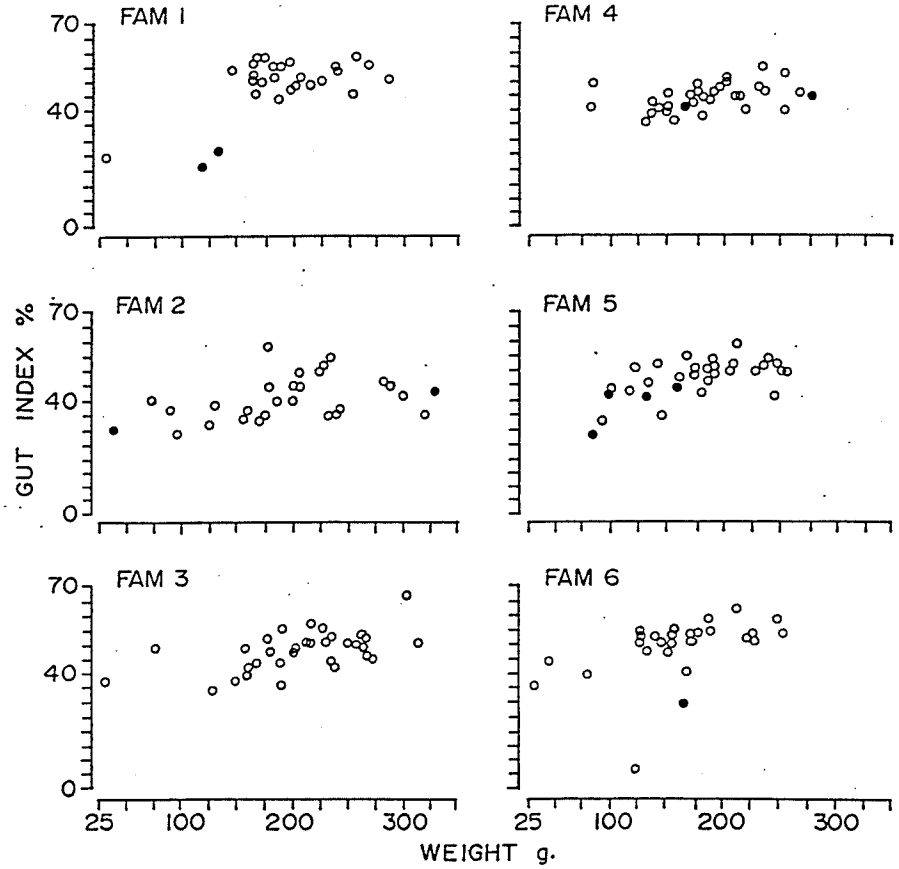
Figure 25. Maturity index (MI = gonad weight/ body weight X 100) versus body weight, for female and male charr in the maturity sub sample of each of the six families, 700 days post fertilization (PF).


FEMALE
MALE
8.0
4.0
0.0
2%
MATURITY INDEX %
1
2
3
4
5
6
0
100
200
300
FISH WEIGHT g.

weights for males with maturity indices of 2% or higher ranged from 39.2g (family 2) to 172.6g (family 4) (Fig. 25). One male charr in each of families 2 and 4 had maturity indices greater then 1% (Fig. 25).

There was a non significant ($P > 0.50$) correlation between charr body weight and GI in any of the families (Fig. 26). Generally the GI varied little over the range of body weights examined. The smaller charr from families 1, 5 and 6 had lower GIs (Fig. 26). Charr with MI values of 1% or greater, had GI values less than their family mean GI value. However not all charr with GI values below the family mean had high MI values (Fig. 26).

Figure 26. Gut index (GI = wet gut weight/dry gut weight X 100) versus body weight for the sub sample of charr from each of the six families, 700 days post fertilization (PF); solid dots represent charr with a maturity index (MI = gonad weight/body weight X 100)of greater than 1% and clear dots represent charr with a MI of less than 1%.


FAM 1
FAM 4
FAM 2
FAM 5
FAM 3
FAM 6
GUT INDEX %
70
40
0
25
100
200
300
WEIGHT g.

DISCUSSION

The small differences between overall growth rates of the families during the growth trial and the lack of a significant family effect for the model analyzing the relationship between fish mean weight and specific growth rate suggest that there was little difference in growth performance among families. The significant negative correlation between fish mean weight and specific growth rate is consistent with that reported for other salmonids (Brett 1979).

The lack of an increase in the positive skewness of the weight distributions suggests that the families did not exhibit the "shooter" phenomena associated with some cultured fish populations (Wohlfarth 1977). Increases in variance of the weight distributions of the test families were associated with the occurrence of both slow growing and fast growing fish.

Growth in weight of charr populations in this study were characterized by an increase in variance with time. This pattern of fish growth has been termed "growth depensation" (Brett 1979). Growth depensation in groups of hatchery reared Arctic charr has been attributed to behaviourial interaction (Jobling 1983) and to a combination of genetic factors and behaviourial interactions (Jobling 1986). The presence of behaviourial interactions has been

associated with increasing CV values (Brett 1979, Yamagishi 1969). Only family two in the present study exhibited an increasing CV for the weight distribution.

The lack of a significant family effect for the model analyzing the relationship between weight and variance suggest that there was little difference among families in the way variance of individual fish weights increased over the growth trial. Results suggest that the increase in variance for fish weights, over the course of the growth trial, resulted principally from the increasing mean weight of the populations.

The variance model successfully predicted the CV for the weight distribution of the random samples except for family 2 where the model significantly over predicted the CV. Despite the lack of a family effect in the variance model, factors not included in the model appear to affect the variance in weight in family 2.

Lack of sexual maturation and lack of a significant difference between the mean weights of males and females in this study were consistent with the results reported by Tompkins (1989). However the observation that males comprise the majority of small individuals suggests that sexual dimorphism may be a factor in variation in weight, to a limited extent. Svedang (1990) and Nordeng

(1983) observed that natural dwarf populations tend to be predominantly males. The lack of sexual maturation and the infrequent occurrence of precocious maturation in the families is consistent with Tompkins' (1989) conclusion that sexual maturation was not a factor in variation in weight.

Lack of a significant correlation between body weight and GI is consistent with the results reported by Jensen (1980) for natural Arctic charr populations. A trend toward lower GI values for sexually maturing Arctic charr is also consistent with the results reported by Jensen (1980).

Jensen (1980) reported a strong correlation between the gut index and the gross nutritional state of Arctic charr, resulting from the deposition of fat around the gut. If the variation in weight observed in the Arctic charr used in this study resulted primarily from social interaction which prevented some charr from feeding, one would expect to find a correlation between fish weight and the GI or at least a strong tendency toward lower GI values in small animals. In the present study if one removes the charr known to be sexually maturing, few charr had GI values markedly lower than the mean value for the family. There appears to be little evidence that smaller slower growing animals are in a nutritionally deprived state, with less storage of fat.

The results from this study do not eliminate the possibility that social interactions are responsible for variation in weight in cultured Arctic charr populations, as it could be argued that social interaction affects were consistent across families and that social interactions did not effect the gross nutritional state of individuals. However, it would seem much more likely that variation in weight is primarily affected by the degree of expression of phenotypic plasticity. The results of this study suggest that the degree of phenotypic plasticity expressed in the rearing environment used in this study, varied little amongst the families tested.

CHAPTER 6

Variability in weight of hatchery reared Arctic charr (Salvelinus alpinus L.), sired by slow growing early maturing male charr.

ABSTRACT

Hatchery reared Arctic charr populations often contain charr, which grow slowly throughout their life. Some but not all of the slow growing "dwarf" hatchery charr may also exhibit early sexual maturity. In the present study, the growth and variation in weight of the progeny of a dwarf male charr by large female charr (SMXLFM) cross was compared with the progeny of its half-sib, large male by large female (LMXLFM) cross. A significant positive correlation was observed between the $\log_e$ increase in variance of fish weights and the $\log_e$ mean weight of the test groups, during a 235 day growth trial period at 10°C. A common variance model could be fitted to the growth trial results of both treatment groups, with $\log_e$ mean weight explaining over 95% of the observed increase in variation in weight. After a 617 day cold water rearing period (1067 days PF), few sexually mature charr were observed in either of the treatment groups, with the majority of the charr exhibiting no gonad development. However the progeny of the SMXLFM cross contained more mature charr, than the progeny of the LMXLFM cross. Only a few of the mature charr weighed less than 100g.

INTRODUCTION

Hatchery reared Arctic charr often contain slow growing charr, which grow significantly slower than the rest of the population from early in their life history (Chapter 1). Papst and Hopky (1983) reported that Arctic charr reared in an intensive aquaculture system had a percentage of the charr which grew slowly and a number of these charr were early maturing males. Variability in life histories, including age and size at maturity, have often been observed in wild charr populations (Nordeng 1983). In hatchery rearing trials of wild charr, Nordeng (1983) observed that crosses of small resident charr, large resident charr and anadromous charr produced similar percentages of dwarf progeny and the small resident form was the dominant form. Svedang (1990) observed that the growth of hybrid charr produced from dwarf charr by normal charr crosses were intermediate to the performance of normal by normal or dwarf X dwarf crosses. Otolith measurements from wild charr populations suggest that males developing into slow growing dwarfs do so throughout their life history, but female charr developing into dwarfs vary in their growth rates.

In the present study, variation in body weight amongst a group of charr, sired from two small early maturing charr were compared with a half-sib group sired by two large charr.

MATERIALS AND METHODS

The experiment was conducted at the Rockwood Aquaculture Research Centre located 65km north of Winnipeg Manitoba, Canada. Two treatment groups of charr were formed by spawning two small early maturing male charr and two large male brood-stock charr with the same two large hatchery brood-stock charr. The brood-stock charr came from the same Labrador brood-stock used to produce the full-sib families in Chapter 5. The small male charr originated from the smallest fraction of a graded group of 3 year old Labrador hatchery charr stock. The mean weights of the two small male charr were 120 and 90g. The mean weights of the hatchery brood stock were over 1000g.

Eggs were incubated at 6.4 ^{o}C and the growth trial began 215 days PF at an approximate mean charr weight of 2.0g. At the start of the growth trial, three random replicate groups of 100 charr each were taken from the two treatment groups and placed in separate tanks. The growth trial lasted 235 days and ended 450 days PF. Throughout the growth trial the water temperature was 10^{o}C and charr were reared in 21-l tanks connected to common bio-filters. Charr were fed commercial rainbow trout feed (Martins Feed Mill, Elmira, Ontario Canada) by hand four times daily during the period from 0830h to 1600h. No feeding occurred on census days. The amount of food fed was calculated using commercial feeding tables

(Hilton & Slinger 1981) and the ration was adjusted every census day based on changes in total wet weight of fish in each tank.

During the growth trial the 6 groups of charr were sampled on days 270, 314, 338, 369, 409 and 450 PF. Individual charr weights were measured by anesthetizing the charr with 2-phenoxyethanol, shaking off excess water and weighing the charr to the nearest 0.05 g on an electronic balance. Total weight of each group of charr was determined by weighing all the charr in a tank in a tared volume of water. Sample results throughout this paper are summarized by the mean (± the standard deviation).

Mean specific growth rates over the interval between two weighing and the effect of treatment on the variance in charr weights were determined using the methods described in Chapter 1.

At the end of the growth trial (450 days PF) each of the charr groups were transferred to 150-l tanks at a water temperature of 6.0 °C and were reared for 617 days. At the end of this cold water rearing period the charr were 1067 days old. All the charr in each group were killed with an overdose of anesthetic and weighed to the nearest 1.0g on an electronic scale. The sex of charr in a sub-sample of 50 charr from each of the six groups were determined by dissecting the charr. Charr were classified as mature if milt or eggs could be expelled when hand pressure was applied to the

charr's abdomen.

RESULTS

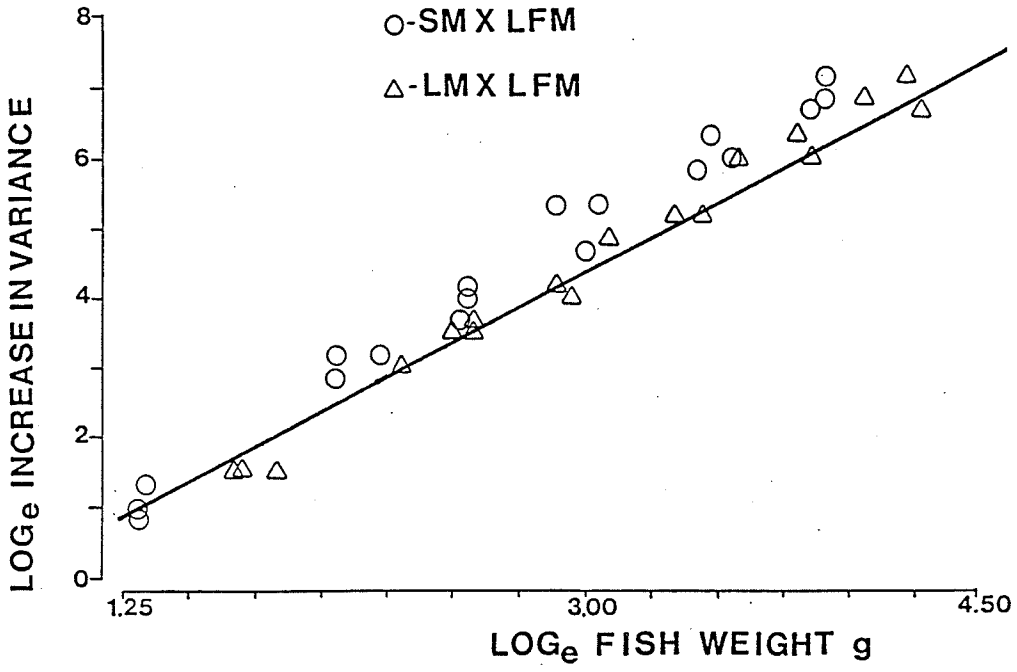
There was little difference in the specific growth rates among the six charr groups, with specific growth rates among the groups over the course of the growth trial ranging from 1.4 to 1.5 %/day. The coefficient of variation (CV) for the weight distributions of the treatment groups all increased during the growth trial from 214 to 450 days PF (Table 13). The largest increases in CV occurred in two of the SMXLFM replicate groups (Table 13).

There was a significant ($P = 0.001$) positive correlation between the $\log_e$ increase in variance of charr weight and the $\log_e$ mean weight of the charr in each of the groups (Fig. 27). Log_e mean weight explained over 95% ($r^2 > 0.95$) of the observed variance in each of the treatment groups. There was a non significant ($P = 0.30$) contribution of $\log_e$ time to the variance model [2] for the SMXLFM charr group and a significant ($P = 0.02$) contribution of $\log_e$ time to the variance model [2] for the LMXLFM group. The sub-model for variance in fish weight [3] assuming the effect of $\log_e$ time to be zero was used to compare the increase in $\log_e$ variance in charr weight over the growth trial period. There was a non significant ($P = 0.43$) treatment effect between the small male and large male sired groups. There was a non significant ($P = 0.19$) treatment by $\log_e$ mean weight interaction

Table 13. Mean weight (± standard deviation) and coefficient of variation (CV = standard deviation/mean weight) for the distribution of individual charr weights in the small male X large female (SMXLFM) and the large male X large female (LMXLFM) treatment groups, 214, 450 and 1067 days post fertilization (PF).

Tank	Day 214		Day 450		Day 1067	
	Weight (±Sd) g.	CV %	Weight (±Sd) g.	CV %	Weight (±Sd) g.	CV %
SMXLFM						
1	1.6 (0.4)	25.0	50.9 (37.3)	73.3	458 (178)	39
2	1.6 (0.4)	25.0	47.3 (27.1)	57.3	406 (178)	44
3	1.6 (0.5)	31.3	50.3 (31.6)	62.8	386 (199)	52
LMXLFM						
1	2.0 (0.6)	30.0	57.5 (29.4)	51.1	423 (189)	45
2	2.0 (0.6)	30.0	71.6 (29.2)	40.8	429 (175)	41
3	2.0 (0.6)	30.0	68.2 (34.8)	51.0	411 (195)	47

Figure 27. Log_e increase in variance in charr weight versus log_e mean charr weight for the small male charr X large female charr (SM X LFM) and the large male charr X large female charr (LM X LFM) treatment groups. The solid line indicates values predicted from the common variance model fitted to the growth trial results from both treatment groups, with b_0 and b_w coefficients equal to - 2.07 and 2.15 respectively.


○-SM X LFM
△-LM X LFM
LOGe INCREASE IN VARIANCE
8
6
4
2
0
1.25
3.00
4.50
LOGe FISH WEIGHT g

effect. In summary there was no significant difference in the rate of increase in variance between the small male and large male sired groups.

During the cold water rearing period from 450 to 1067 days PF the CVs of the charr weight distributions of the six groups all decreased slightly, except for the LMXLFM tank 2 group which remained constant (Table 13). Charr weights of the groups were not significantly ($P = 0.22$, Kruskal-Wallis test) different at the end of the cold water growth period 1067 days PF (Table 13; Fig. 28). The 10 percentile value for the SMXLFM tanks 1,2 and 3, were 218,120 and 140 g ,respectively. The 10 percentile value for the LMXLFM tanks 1,2 and 3 were 166.162 and 119 g ,respectively.

The charr weights of the 50 charr sub-samples from the end of the cold water growth period were not significantly ($P = 0.50$, Kruskal-Wallis test) different (Table 14). The majority of charr in the 50 charr sub-samples of the groups had no gonad development and were classified as undeveloped (ND) (Table 14). A slightly higher number of females than males were identified in each of the groups (Table 14). Twelve of the 150 charr sampled from the SMXLFM group were sexual mature, while 2 of the 150 charr sampled from the LMXLFM group were sexually mature (Table 14). The mean weight of the 12 mature charr from the SMXLFM group was 374(182)g, with mature charr weights ranging from 55 to 654 g. The weights of the

Figure 28. Distribution of charr weights tanks 1,2 and 3 for the small male charr X large female charr (SM X LFM) and large male charr X large female charr (LM X LFM) treatment groups 1067 days post fertilization (PF).

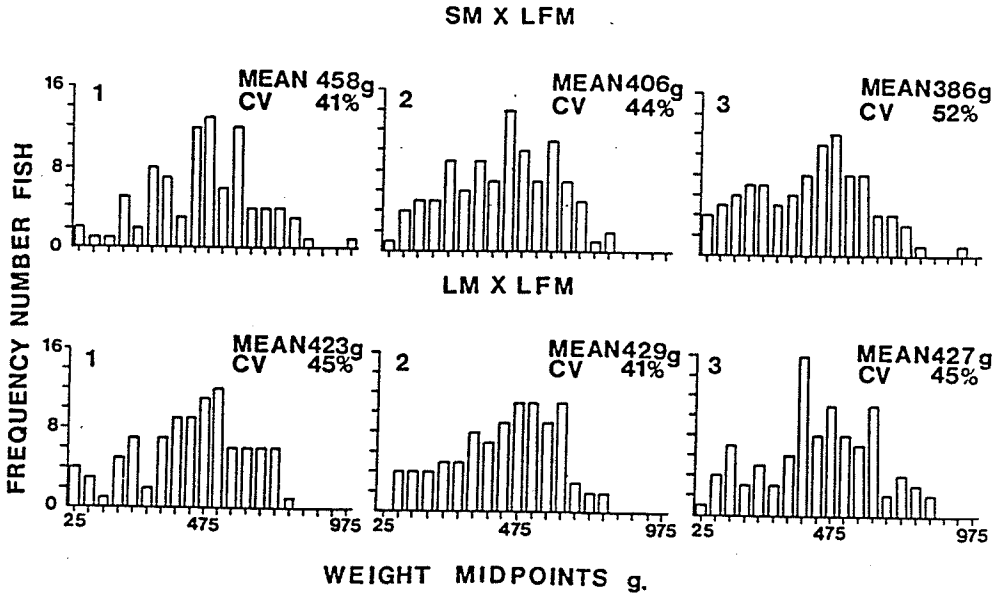

SM X LFM
MEAN 458g
CV 41%
1
MEAN406g
CV 44%
2
MEAN386g
CV 52%
3
LM X LFM
MEAN423g
CV 45%
1
MEAN429g
CV 41%
2
MEAN427g
CV 45%
3
FREQUENCY NUMBER FISH
16
8
0
25
475
975
WEIGHT MIDPOINTS g.

Table. 14 Mean charr weight (± Standard deviation), number of male, female, undeveloped (ND) and mature charr for sub samples of the small male charr X large female charr (SMXLFM) and large male charr X large female charr (LMXLFM) treatment groups, 1067 days post fertilization (PF).

Tank	Weight g. Mean (±Sd)	Number of Charr					
		Sample	Males	Females	ND	Mature	
						Males	Females
SMXLFM							
1	467(187)	50	9	11	30	3	0
2	404(191)	50	4	10	36	0	4
3	410(178)	50	8	15	27	4	1
LMXLFM							
1	403(184)	50	5	17	28	0	0
2	401(184)	50	6	17	27	0	0
3	411(195)	50	4	14	32	0	0

2 mature male charr in the LMXLFM group were 83 and 270g.

DISCUSSION

The significant positive correlation between $\log_e$ increase in variance of charr weight and the $\log_e$ mean charr weight observed in this study is consistent with the results from the previous growth trial with hatchery reared Arctic charr reported in Chapters 1 through 5. The lack of a significant difference between the correlations observed between the group of charr sired by the small early maturing males and the group sired by the large brood stock males, suggests that the paternal effect on variation in growth of hatchery reared charr is low. Unfortunately small early maturing female charr are not present in the blood-stock population at the Rockwood Aquaculture Centre. Efforts to assess the maternal effects on variation in growth will require the rearing of small female charr, which are often culled as a part of normal hatchery operations before they mature.

The observation that more of the progeny sired by the small early maturing male were sexually mature at 1067 days PF, suggests that there was a paternal effect on the age of maturation, although the numbers of mature charr in both groups were small. The observation that all the smallest mature charr were males, but few small charr showed sexual development is consistent with other growth trial results (Chapter 1 and 5) and is consistent with the conclusion, that early sexual maturation is not an important factor

affecting variation in growth of hatchery reared Arctic charr.

If the small slow growing charr phenotype observed in hatchery studies is analogous with the small resident or dwarf forms described by Nordeng (1983), then the results of this study agree with observations that all forms produce similar percentages of dwarfs when the charr are reared under hatchery conditions (Nordeng 1983). However the results of my study appear inconsistent with Svedang's (1990) observations that the growth performance of hybrid progeny from dwarf by normal charr crosses was less than the growth of normal by normal charr crosses and higher than the dwarf by dwarf crosses. Direct comparisons of my study with that reported by Svedang (1990) are difficult as he frequently size graded during the experiment and the growth performance of dwarf and non dwarf sired hybrid groups were not reported separately.

Results of my study suggest that hatchery operators using small males as brood stock would not increase the variance in charr weights, but might experience an increase in the number of early maturing charr. Studies to assess the paternal effects on growth are recommended.

CHAPTER 7

Relationship between increasing variance in charr weight and increasing mean weight in groups of hatchery reared Arctic charr (*Salvelinus alpinus* L.)

ABSTRACT

The increase in mean charr weight in groups of hatchery reared Arctic charr explains the majority of the increased variance in charr weights as a group of charr grows. A significant correlation is observed between the $\log_e$ increase in variance in weight and the $\log_e$ mean charr weight. In the present study the intercepts (b_o) for the regression of $\log_e$ increase in variance in weight on $\log_e$ mean weight for groups of charr originating from different strains and from anadromous and nonmigratory forms of charr ranged from -4.26(0.16) to -1.48(0.48), while the slopes (b_w) ranged from 2.82(0.13) to 1.85(0.04). Log_e mean charr weight was observed to account for over 95% of the observed variance in the $\log_e$ increase in variance for charr weights, during hatchery growth trials conducted at 10°C. A common variance model could be fitted to growth trial data from the progeny of batch and family groups originating from the same strain of Arctic charr.

INTRODUCTION

Groups of Arctic charr reared under hatchery conditions exhibit similar correlations between $\log_e$ increase in variance in charr weight and $\log_e$ mean charr weight, with $\log_e$ mean charr weight explaining the majority of the observed variation (Arnason et al. 1992; Chapters 1 through 6). This relationship develops early in the life history and appears to remain constant over much of the life history of charr reared under hatchery conditions (Chapters 1 through 6). This relationship can be used to examine the effect of different rearing conditions on variation in charr weights and to examine differences in variation amongst different strains or forms of charr (Arnason et al. 1992).

The present study examined the relationship between increasing variance in charr weight and mean charr weight over several growth trial periods for hatchery charr originating from two anadromous strains and one nonmigratory form.

MATERIAL AND METHOD

All growth trials were conducted at the Rockwood Aquaculture Research Centre located 65km north of Winnipeg Manitoba, Canada. Charr eggs were incubated at 6.4 °C and the growth trials were conducted at 10 °C in tanks connected to common bio-filters. Charr were fed commercial rainbow trout feed (Martins Feed Mill, Elmira, Ontario Canada) by hand four times daily during the period from 0830h to 1600h. No feeding occurred on census days. The amount of food fed was calculated using commercial feeding tables (Hilton & Slinger 1981) and the ration was adjusted based on changes in total wet weight of fish in each tank. On census days individual charr weights were measured by anesthetizing the charr with 2-phenoxyethanol, shaking off excess water and weighing the charr to the nearest 0.05 g on an electronic balance. Total weight for a group of charr was determined by weighing all the charr in a tank in a tared volume of water. Sample results throughout this paper are summarized by the mean (± the standard deviation) and the coefficient of variation (CV) was calculated as described in Chapter 1.

The Nauyuk Lake anadromous and nonmigratory stocks of Arctic charr used in this study originated from a 1978 spawn taking of charr from the Nauyuk Lake system, Kent Peninsula, NWT, Canada (Papst and Hopky 1984). The charr used in this study were from a

second generation brood stock. The biology of the wild Nauyuk Lake charr population has been described by Johnson (1980). Batch groups refer to charr resulting from the combining of spawn from five or more males and females, while families refer to charr resulting from a single male female spawning.

Two random samples of 75 charr were reared from each cross.

Results of the growth trials from the present study were compared with results from Tompkins (1989) and from Chapter 5 including both Nauyuk Lake and Labrador strains of Arctic charr. The Labrador strain originated from spawn collected in 1980 from an anadromous stock of charr from the Fraser River in Labrador, Canada (Baker 1983). All growth trial data were based on at least two replicates and did not include data where there was significant ($P < 0.05$) tank or tank by weight interaction effects.

Mean specific growth rate over the interval between two weighings was determined using the methods described in Chapter 1. The relationship between the $\log_e$ increase in the variance of charr weights and the $\log_e$ mean charr weight was analyzed using the variance sub model [3] described in Chapter 1.

RESULTS

The length of the growth trials ranged from 134 to 213 days and mean starting weights ranged from 4.6(0.6) to 2.2(1.4) g (Table 15). Growth trials included; two batch groups one each from the Nauyuk Lake anadromous and nonmigratory forms; 2 families from the Nauyuk Lake anadromous form; 2 families from the Nauyuk Lake Nonmigratory group; 1 nonmigratory male by anadromous female family.

Specific growth rates during the growth trials ranged from 1.3 to 1.8 %/day (Table 15). The initial CV of the random samples of a charr group often differed significantly, for example family 1 of the anadromous by anadromous cross differed by 39.9% (Table 15). However the final CV values of the two random samples generally differed by less than 5% (Table 15).

There was a significant ($P < 0.01$) positive correlation between the $\log_e$ increase in variance for charr weight and the $\log_e$ mean charr weight in each of the groups (Table 16). There were no significant tank or tank by weight interaction effects within groups, however there were significant ($P = 0.01$) interaction effects when a common model was fitted to all the groups. Common models could be fitted amongst the anadromous by anadromous and

Table 15. Mean charr weight(±Standard deviation), coefficient of variation (CV) and specific growth rate (SGR) for Nauyuk Lake hatchery reared Arctic charr, reared as part of growth trials at 10°C, days refer to length of growth trial. Batch charr groups were formed by combining the spawn of several males and females, while family groups were formed from the crosses of single male and female charr.

Charr Group	Tank	Days	Growth Trial Weight Mean(± Sd) g. Start		End		CV % Start	End	SGR %/day
Anadromous male X Anadromous Female									
Batch	1	213	2.3	(0.7)	36.0	(23.7)	30.4	65.8	1.3
	2	213	2.2	(1.4)	33.6	(18.8)	63.6	55.9	1.3
Family 1	1	186	4.6	(0.6)	69.1	(30.9)	13.0	44.7	1.5
	2	186	3.4	(1.8)	69.7	(28.5)	52.9	40.9	1.6
Family 2[1]	1	186	2.6	(0.7)	73.1	(28.2)	26.9	38.6	1.8
	2	186	2,5	(0.5)	63.7	(23.4)	20.0	36.7	1.7
Nonmigratory male X Nonmigratory Female									
Batch	1	213	3.0	(1.5)	73.1	(28.2)	50.0	38.6	1.5
	2	213	2.6	(1.0)	68.1	(39.7)	38.5	58.3	1.5
Family 1	1	186	3.3	(1.5)	67.0	(23.6)	50.0	35.2	1.6
	2	186	2.6	(1.0)	60.8	(22.4)	38.5	36.8	1.7
Family 2[1]	1	134	2.9	(1.1)	21.3	(12.0)	37.9	56.3	1.5
	2	134	2.6	(1.0)	20.9	(9.0)	38.5	43.1	1.6
Nonmigratory male X Anadromous Female									
Family 1[1]	1	186	3.5	(0.8)	78.2	(32.6)	22.9	41.7	1.7
	2	186	3.5	(0.5)	73.7	(31.3)	14.3	42.5	1.6

[1] Related half-sib families

Table 16. Variance model (equation 3) coefficients (±Standard error), for the correlation between the $\log_e$ increase in variance in charr weights and $\log_e$ mean charr weight; for Nauyuk Lake hatchery reared Arctic charr, reared at 10°C. All correlations used were significant ($P<0.01$), and the result of fitting the model to two replicate groups, batch charr groups were formed by combining the spawn of several males and females, while family groups were formed from the cossing of a single male and female charr and common refers to the common variance models for the anadromous and nomigratory groups.

Charr Group	Coefficients				r^2
	b_0	(± SE)	b_w	(±SE)	
Anadromous male X Anadromous Female					
Batch	-3.95	(0.35)	2.82	(0.13)	1.00
Family 1	-2.99	(0.70)	2.03	(0.24)	0.99
Family 2[1]	-2.08	(0.74)	2.00	(0.26)	0.96
Common	-2.51	(0.43)	2.14	(0.15)	0.97
Nonmigratory male X Nonmigratory Female					
Batch	-1.93	(0.27)	2.21	(0.09)	0.99
Family 1	-2.34	(0.63)	2.06	(0.23)	0.97
Family 2[1]	-1.43	(0.68)	1.86	(0.30)	0.95
Common	-1.48	(0.48)	1.98	(0.21)	0.98
Nonmigratory male X Anadromous Female					
Family 1[1]	-2.39	(0.29)	2.13	(0.09)	1.00

[1] Related half-sib families

the nonmigratory by nonmigratory groups (Table 16). Estimates of the variance model coefficient b_0 (intercept) ranged from -3.95 (0.35) to -1.43 (0.68) and estimates of the coefficient b_w ranged from 2.82 (0.13) to 1.86 (0.30) (Table 16). The b_0 and b_w coefficients of the model fitted to the nonmigratory male by anadromous female family were between the estimates for the anadromous by anadromous and the nonmigratory by nonmigratory group common models (Table 16). A common variance sub-model [3] could be fitted to the half-sib families suggesting there was little difference in the rate of increase in variance of charr weights in these related families (Table 16).

Log_e mean charr weight explained 95% ($r^2 = 0.95$) or more of the observed variation in the increase in variance in charr weights over the growth trial (Table 16).

Estimates of the b_0 and b_w coefficients from the models fitted to the growth data reported by (Tompkins 1989) were within the range of estimates from the growth trials in the present study (Table 17). Only 2 of the four Nauyuk Lake families and 1 of the 3 Labrador families reported by Tompkins (1989) could be used, as these were the only families where there were non significant ($P < 0.05$) tank or tank by weight interaction effects . The b_w coefficient estimate of 1.85 (0.04) for the growth data from family 8 of the Labrador strain report by Tompkins (1989), is the lowest estimate

Table 17. Variance model (equation 3) coefficients (±Standard error), for the correlation between the $\log_e$ increase in variance in charr weights and $\log_e$ mean charr weight, for hatchery reared Arctic charr, reared at 10°C. All correlations used were significant ($P<0.01$), results are for cases where the model was fitted to two or more replicate groups without interaction effects. Batch groups were from crosses of several males and females, while family groups were formed from crosses of a single male and female charr and common refers to the common variance models for the charr group.

Charr Group (Source of Data)	Coefficients b_0 (± SE)	b_w (±SE)	r^2
Nauyuk Lake			
Anadromous male X Anadromous Female (Present Study)			
Batch	-3.95 (0.35)	2.82 (0.13)	1.00
Common	-2.51 (0.43)	2.14 (0.15)	0.97
Anadromous Male X Anadromous Female (Tompkins (1989))			
Family 2	-4.26 (0.16)	2.72 (0.07)	0.99
Family 3	-2.86 (0.34)	2.61 (0.15)	0.96
Nonmigratory male X Nonmigratory Female (Present Study)			
Batch	-1.93 (0.27)	2.21 (0.09)	0.99
Common	-1.48 (0.48)	1.98 (0.21)	0.98
Labrador Charr			
Anadromous male X Anadromous Female (Present Study)			
Batch	-2.41 (0.49)	2.29 (0.19)	0.98
Anadromous male X Anadromous Female (Chapter 5)			
Family 3	3.12 (0.12)	2.00 (0.05)	1.00
Family 6	1.54 (0.09)	2.02 (0.04)	1.00
Anadromous male X Anadromous Female (Tompkins 1989)			
Family 8	-2.35 (0.11)	1.85 (0.04)	1.00

for any of the groups tested (Table 17). Estimates for the b_w coefficient for the Labrador strain were in the same range as the estimates for the Nauyuk Lake strain but were amongst the lower values observed (Table 17).

DISCUSSION

The lack of a significant group effect for charr originating from the Nauyuk Lake anadromous group and nonmigrating group suggests that the rate at which variance in charr weight increases with growth within these groups is the same. Although a lack of parallelism prevented the statistical comparison of the anadromous and nonmigrating groups, the variance model coefficient b_w (slope) was similar for all the groups. The fact that a common model could be fitted to the half-sib related families supports the conclusion that the rate of increase in variance in charr weight is similar for the two groups of Nauyuk Lake charr, when reared under hatchery conditions. Due to the small number of families examined in this study and the limited size of the gene pool of the original wild brood-stock it is not possible to generalize to the wild populations.

The similarity of values for the coefficients of the variance model amongst the various charr groups studied as part of this study and reported by Tompkins (1989), suggests that the rate of increase in variance in charr weight is similar amongst all the charr groups regardless of the original source stock, when the charr are reared under common hatchery rearing conditions.

The results of my study does not remove the possibility that

social interactions are responsible for some of the observed variation in growth within a group of charr. However, it seems unlikely that social interaction would have had a consistent effect across groups. It would seem more likely that the observed variation in weight of hatchery reared charr is primarily affected by genetic and environmental factors. Results of my study suggest that these factors are similar amongst the charr groups tested.

GENERAL DISCUSSION

The results of the experiments reported as part of this study suggest a consistency in variation in weight of Arctic charr groups reared under hatchery conditions. The rate of increase in variation in charr weight was positively correlated in all cases with the increasing mean weight of the test charr groups, with mean weight accounting for the vast majority of the observed variation in weight. This relationship is exhibited early in the life history of hatchery reared charr and remains constant throughout the period of highest growth rate, from 0.5 to 100g. The hypothesis that growth depensation in charr results primarily from the production of several phenotypes which differ in their growth rate (polyphenism), would be consistent with the results of this study. Jobling and Reinsnes (1986) concluded that growth depensation in charr was in part a result of the slow growth of a "stunted" or dwarf phenotype. Results of the present study expands the conclusions of Jobling and Reinsnes (1986) suggesting that growth depensation under constant rearing conditions is primarily a result of differences in growth rates of several phenotypes (forms), including the dwarf form.

A hypothesis that growth depensation results primarily from polyphenism is consistent with Nordeng's (1983) observations that different charr groups produced similar percentages of dwarf and normal forms of charr and with the observed similarity in the rate

of increase in variance in weight observed for the different families and strains of charr used in this study. Polyphenism is often associated with an environmental "trigger" which can change the types or numbers of phenotypes produced by a common genotype (Stearns 1989). The observation in this study that ration level affected the rate of increase in variation in weight with time, with increased ration levels resulting in an increase in the numbers of the small, slow growing phenotype, suggests that ration might be one "trigger" controlling polyphenism in charr. This conclusion would be consistent with Nordeng's (1983) observations that feeding level changed the number of dwarf charr produced by groups of wild charr reared in a hatchery and would also be consistent with the hypothesis that wild charr populations produce different phenotypes in response to environmental conditions (Balon 1984). The observation in this study that the rate of growth depensation is determined early in the life history of charr is consistent with the hypothesis that the "decision" on the numbers of alternative phenotypes expressed by a charr population is determined early in the life history (Balon 1983).

The lack of effect of rearing density on variation in weight observed in this study suggests that density is not important in determining the pattern of growth depensation in charr. It also raises questions about what effect behavioral interactions have on growth depensation. One would have anticipated that the

extremes in density used in this study would have resulted in some change to the rate of interactions. Both the lack of a density effect and the consistency of the rate of growth depensation observed in this study, suggest that the effect of social interactions on growth depensation in hatchery reared charr is not significant. However this does not imply that social interactions do not occur or that social hierarchies are not established in groups of hatchery reared charr, rather that these social interactions are not a primary factor in determining the pattern of growth depensation.

The results of this study regarding the lack of effect of differences in hatching time, time of first feeding and initial feeding behaviour on growth depensation, point to the need to be able to test the effect of variability in different traits on growth depensation. Without the variance model used in this study to test the effect of variation in hatching time or time of first feeding on growth depensation, one could have mistakenly concluded that such obvious variability contributed to growth depensation. The results of this study also demonstrate the difficulty of assessing the effects on growth depensation by the analysis of trends in CV or CV^2. Both of which are difficult to model, are confounded by treatment effects on growth rate and are obscured by initial variance effects and are highly variable (Arnason et al. 1992). The ability to calculate expected CV values from the variance model and compare these to observed CV values provides a method of detecting time periods

where factors not included in the variance model temporarily affect the variance in weight of the population. The results of this study suggest that the use of a variance model as recommended by Arnason et al. (1992) is an effective method of testing the effect of different genetic traits and environmental conditions on growth depensation.

If the hypothesis that growth depensation in hatchery reared charr is largely the result of growth rate polyphenism, then perhaps the rate of growth depensation is altered by various environmental triggers. As noted above, the results of this study suggest that ration level is a trigger. However, reducing ration level to reduce the expression of the dwarf phenotype is not a practical strategy for commercial aquaculturists, since reduced ration levels significantly reduce overall growth. Other environmental factors may also act as triggers to the expression of different charr phenotypes, for example water temperature and photo-period. Aquaculturists interested in changing the rate of growth depensation in hatchery reared Arctic charr should experiment with the manipulation of such possible triggers for polyphenism.

Griffiths (1994) proposed a model to explain the variability of size structure in wild charr populations. An important element of this model was the response to food availability and prey size. Results of this study regarding the ability of charr populations to

produce fast and slow growing phenotypes and to adjust the numbers of these types in response to ration level are consistent with Griffiths' (1994) model for wild populations. Further, the results of this study suggest that hatchery rearing experiments with charr can provide valuable insight into the factors affecting polyphenism in wild populations. For example, the results of the dwarf sire experiments conducted in this study suggest that growth polyphenism is maternally inherited.

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APPENDIX I

SAMPLE VARIANCE MODEL FITTING PROCEDURE.

FITTING PROCEDURE FOR THE VARIANCE MODEL

Results of the growth trials of the Nauyuk Lake anadromous male by anadromous female families from chapter 7 are used to demonstrate the fitting procedure used for the variance model [2] and the variance sub-model [3]. From the sample Statistical Analysis System (SAS) printouts, the anadromous X anadromous, families 1, and 2 from Chapter 7 are identified as fam 4 and fam 7, respectively. The following abbreviations are used: TK represents Tank values; LWT represents $\log_e$ mean charr weight; LT represents $\log_e$ time; LDS represents the $\log_e$ increase in variance in charr weight.

SAMPLE FITTING PROCEDURE

Step 1: Testing the tank effects within a family (treatment)

Tank effects within family groups were tested using the SAS Proc GLM procedure by sorting the data by family and setting the class statement to tank (TK). For the variance model [2] the SAS statements were:

```
PROC GLM;
BY FAM;
CLASS TK;
```

MODEL LDS = LWT LT TK LWT X TK LT X TK/SOLUTION;

The Proc GLM statements for testing the variance sub-model [3] were:

PROC GLM;
BY FAM:
CLASS TK;
MODEL LDS = LWT TK LWT X TK/SOLUTION;

Type III sums of squares were used to test the significance of the $\log_e$ weight, $\log_e$ time and interaction effects. For example in fam 4, when the variance sub-model [3] was tested there was a significant ($P > 0.0001$) LWT ($\log_e$ weight) effect, a nonsignificant ($P > 0.4957$) tank (TK) effect and a nonsignificant ($P > 0.5997$) interaction effect (Fig. A1).

The variance model [2] including $\log_e$ time showed a non significant $\log_e$ time effect in fam 4.

Analysis of the results for the other anadromous family (fam 7) were similar to those observed with fam 3 (Fig. A2). Based on this analysis tank results within families were pooled for the analysis of family effects.

Figure A1. SAS output for step 1 of the sample variance sub-model [3] analysis of the results from family 4 (see text) were:

a - significant $\log_e$ mean weight (LWT) effect

b - nonsignificant tank (TK) effect

c - nonsignificant interaction effect.

d - b_0 ($\pm$SE) -2.99(0.70)

e - b_w ($\pm$SE) 2.30(0.24)

The SAS System

---------- FAM=4 ----------

General Linear Models Procedure

Dependent variable: LDS

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	3	50.05907184	16.68635728	68.11	0.0001
Error	6	1.46993419	0.24498903		
Corrected Total	9	51.52900602			

R-Square	C.V.	Root MSE	LDS Mean
0.971474	14.40007	0.49496367	3.43722980

Source	DF	Type I SS	Mean Square	F Value	Pr > F
LWT	1	49.88481328	49.88481328	203.62	0.0001
TK	1	0.09909633	0.09909633	0.40	0.5483
LWT*TK	1	0.07516223	0.07516223	0.31	0.5997

Source	DF	Type III SS	Mean Square	F Value	Pr > F
LWT	1	50.01458159	50.01458159	204.15	0.0001 a
TK	1	0.12878661	0.12878661	0.53	0.4957 b
LWT*TK	1	0.07516223	0.07516223	0.31	0.5997 c

Parameter		Estimate	T for H0: Parameter=0	Pr > |T|	Std Error of Estimate
INTERCEPT		d -2.993998421 B	-4.29	0.0051	0.69735229
LWT		e 2.302167610 B	9.79	0.0001	0.23512124
TK	204	-0.725822688 B	-0.73	0.4957	1.00107936
	221	0.000000000 B	.	.	.
LWT*TK	204	0.185690355 B	0.55	0.5997	0.33524540
	221	0.000000000 B	.	.	.

NOTE: The X'X matrix has been found to be singular and a generalized inverse was used to solve the normal equations. Estimates followed by the letter 'B' are biased, and are not unique estimators of the parameters.

Figure A2. SAS output for step 1 of the sample variance sub-model [3] analysis of the results from family 7 (see text) were:

a - significant $\log_e$ mean weight (LWT) effect

b - nonsignificant tank (TK) effect

c - nonsignificant interaction effect

d - b_0 ($\pm$SE) -2.08(0.74)

e - b_w ($\pm$SE) 2.00(0.26)

The SAS System

---------- FAM=7 ----------

General Linear Models Procedure

Dependent Variable: LDS

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	3	42.61671282	14.20557094	45.95	0.0002
Error	6	1.85491476	0.30915246		
Corrected Total	9	44.47162758			

R-Square	C.V.	Root MSE	LDS Mean
0.958290	16.43450	0.55601480	3.38321666

Source	DF	Type I SS	Mean Square	F Value	Pr > F
LWT	1	42.39855192	42.39855192	137.14	0.0001
TK	1	0.01986932	0.01986932	0.06	0.8083
LWT*TK	1	0.19829159	0.19829159	0.64	0.4537

Source	DF	Type III SS	Mean Square	F Value	Pr > F
LWT	1	42.08552845	42.08552845	136.13	0.0001 a
TK	1	0.21796658	0.21796658	0.71	0.4333 b
LWT*TK	1	0.19829159	0.19829159	0.64	0.4537 c

Parameter		Estimate	T for H0: Parameter=0	Pr > |T|	Std Error of Estimate
INTERCEPT		d -2.077920753 B	-2.81	0.0306	0.73863290
LWT		e 1.995929592 B	7.63	0.0003	0.26162650
TK	206	-0.896700897 B	-0.84	0.4333	1.07030259
	217	0.000000000 B	.	.	.
LWT*TK	206	0.294200907 B	0.80	0.4537	0.36734845
	217	0.000000000 B	.	.	.

NOTE: The X'X matrix has been found to be singular and a generalized inverse was used to solve the normal equations. Estimates followed by the letter 'B' are biased, and are not unique estimators of the parameters.

Step 2: Testing family effects

Family effects were tested using the SAS proc. GLM procedure. The proc GLM statements for the variance sub-model [3] the proc GLM were:

PROC GLM;

CLASS FAM;

MODEL LDS = LWT FAM LWT X FAM/SOLUTION;

Analysis of results of the growth trial for families 4 and 7 showed a significant ($P > 0.0001$) $\log_e$ weight effect, a non significant ($P>0.2310$) family effect and a nonsignificant ($P>0.2876$) interaction effect (Fig. A3). Therefore a common variance sub-model [3] could be fitted with coefficients values for b_0 and b_w of -2.51 (0.46) and 2.14 (0.16), respectively (Fig. A3).

Step 3: Test for the effect of repeated-measures

The SAS statements used to test the variance sub-model [3] using a repeated-measures model repeated were:

Figure A3. An example of SAS output for step 2 of the variance sub-model [3] analysis with:

a - the significant $\log_e$ mean weight effect

b - the nonsignificant family (Fam) effect

c - the nonsignificant interaction effect

d - $b_0(\pm SE)$ -2.51(0.46)

e - $b_w(\pm SE)$ 2.14(0.16)

The SAS System

General Linear Models Procedure

Dependent Variable: LDS

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	3	92.29795229	30.76598410	132.42	0.0001
Error	16	3.71726841	0.23232928		
Corrected Total	19	96.01522070			

R-Square	C.V.	Root MSE	LDS Mean
0.961285	14.13413	0.48200547	3.41022323

Source	DF	Type I SS	Mean Square	F Value	Pr > F
LWT	1	91.92369150	91.92369150	395.66	0.0001
FAM	1	0.09313588	0.09313588	0.40	0.5356
LWT*FAM	1	0.28112492	0.28112492	1.21	0.2876

Source	DF	Type III SS	Mean Square	F Value	Pr > F
LWT	1	92.22104260	92.22104260	396.94	0.0001 a
FAM	1	0.36020139	0.36020139	1.55	0.2310 b
LWT*FAM	1	0.28112492	0.28112492	1.21	0.2876 c

Parameter		Estimate	T for H0: Parameter=0	Pr > |T|	Std Error of Estimate
INTERCEPT		d -2.507013296 B	-5.43	0.0001	0.46189650
LWT		e 2.140648367 B	13.51	0.0001	0.15846078
FAM	4	-0.835900756 B	-1.25	0.2310	0.67132682
	7	0.000000000 B	.	.	.
LWT*FAM	4	0.250193307 B	1.10	0.2876	0.22744583
	7	0.000000000 B	.	.	.

NOTE: The X'X matrix has been found to be singular and a generalized inverse was used to solve the normal equations. Estimates followed by the letter 'B' are biased, and are not unique estimators of the parameters.

```
PROC GLM;
CLASS FAM TK;
MODEL  LDS = FAM TK (FAM) LWT LWT X FAM/SOLUTION;

TEST H=FAM E=TK(FAM);
```

There was a nonsignificant (P>0.1347) family effect using the type III mean square values for Family(tank) as the error term (Fig. A4).

Since the results of the repeated-measures model agrees with the completely randomized model (step 2) the results of the randomized model were reported for families 4 and 7.

In summary it was concluded that there was a nonsignificant family effect between families 4 and 7.

Figure A4. SAS output for repeated-measures model with:

a - nonsignificant family (Fam) effect when the type III mean square values for TK(Fam) are used as the error term.

The SAS System

General Linear Models Procedure

Dependent Variable: LDS

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	5	92.41691794	18.48338359	71.91	0.0001
Error	14	3.59830276	0.25702163		
Corrected Total	19	96.01522070			

R-Square	C.V.	Root MSE	LDS Mean
0.962524	14.86627	0.50697300	3.41022323

Source	DF	Type I SS	Mean Square	F Value	Pr > F
FAM	1	0.01458710	0.01458710	0.06	0.8152
TK(FAM)	2	0.25956450	0.12978225	0.50	0.6141
LWT	1	91.86713096	91.86713096	357.43	0.0001
LWT*FAM	1	0.27563538	0.27563538	1.07	0.3180

Source	DF	Type III SS	Mean Square	F Value	Pr > F
FAM	1	0.35450707	0.35450707	1.38	0.2598
TK(FAM)	2	0.11896565	0.05948282	0.23	0.7964
LWT	1	92.06047877	92.06047877	358.18	0.0001
LWT*FAM	1	0.27563538	0.27563538	1.07	0.3180

Tests of Hypotheses using the Type III MS for TK(FAM) as an error term

Source	DF	Type III SS	Mean Square	F Value	Pr > F
FAM	1	0.35450707	0.35450707	5.96	0.1347 a

Parameter		Estimate	T for H0: Parameter=0	Pr > |T|	Std Error of Estimate
INTERCEPT		-2.474636030 B	-4.95	0.0002	0.49958346
FAM	4	-0.776251961 B	-1.06	0.3061	0.73082423
	7	0.000000000 B	.	.	.
TK(FAM)	204 4	-0.199156440 B	-0.62	0.5446	0.32073799
	221 4	0.000000000 B	.	.	.
	206 7	-0.089571137 B	-0.28	0.7850	0.32215245
	217 7	0.000000000 B	.	.	.
LWT		2.145157836 B	12.81	0.0001	0.16745621
LWT*FAM	4	0.248346911 B	1.04	0.3180	0.23981487
	7	0.000000000 B	.	.	.

NOTE: The X'X matrix has been found to be singular and a generalized inverse was used to solve the normal equations. Estimates followed by the letter 'B' are biased, and are not unique estimators of the parameters.

Standard error estimates for the variance sub-model [3] coefficients b_0 and b_w for were obtained from the proc GLM procedure using the statements:

```
PROC GLM;
CLASS FAM;
MODEL LDS = FAM FAM X LWT/NOINT SOLUTION;
```

For families 4 and 7 the b_0 ($\pm$ SE) coefficient values were -3.34 (0.49) and -2.51 (0.46), respectively (Fig. A5). The b_w ($\pm$SE) coefficient values for families 4 and 7 were 2.39 (0.16) and 2.14 (0.16), respectively (Fig. A5).

Figure A5. SAS output of variance sub-model [3] coefficients and standard errors for family 4 and family 7.

a - Family (Fam 4) b_{o4} = -3.34(0.49)

b - Family (Fam 7) b_{o7} = -2.51(0.46)

c - Family (Fam 4) b_{w4} = 2.39(0.16)

d - Family (Fam 7) b_{w7} = 2.14(0.16)

The SAS System

General Linear Models Procedure

Dependent Variable: LDS

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	4	324.89040186	81.22260047	349.60	0.0001
Error	16	3.71726841	0.23232928		
Uncorrected Total	20	328.60767027			

R-Square	C.V.	Root MSE	LDS Mean
0.961285	14.13413	0.48200547	3.41022323

Source	DF	Type I SS	Mean Square	F Value	Pr > F
FAM	2	232.60703666	116.30351833	500.60	0.0001
LWT*FAM	2	92.28336520	46.14168260	198.60	0.0001

Source	DF	Type III SS	Mean Square	F Value	Pr > F
FAM	2	17.78382776	8.89191388	38.27	0.0001
LWT*FAM	2	92.28336520	46.14168260	198.60	0.0001

Parameter			Estimate	T for H0: Parameter=0	Pr > |T|	Std Error of Estimate
FAM	4	a	-3.342914052	-6.86	0.0001	0.48716662
	7	b	-2.507013296	-5.43	0.0001	0.46189650
LWT*FAM	4	c	2.390841674	14.65	0.0001	0.16316185
	7	d	2.140648367	13.51	0.0001	0.15846078