Theor Appl Genet (1995) 90: 733–739

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Genetics of size and growth rate through sexual maturity in freshwater-reared coho salmon (*Oncorhynchus kisutch*)

Received: 12 August 1994 / Accepted: 22 September 1994

Abstract Genetic parameters of size through sexual maturity have been relatively unexplored for Pacific salmon. In this study, individually tagged coho salmon were raised in freshwater, and the heritabilities of size and growth rate were estimated at several intervals between 13 and 24 months of age (spawning). Heritability estimates for size were moderate to high from 13 to 19 months of age, ranging from 0.36 to 0.50, and lower from 21 months to spawning at 24 months, ranging from 0.17 to 0.32. Heritabilities of specific growth rates estimated over 3-month intervals were moderate from 16 to 21 months of age, ranging from 0.21 to 0.34. Genetic and phenotypic correlations between sizes measured at different ages were moderate to high, ranging from about 0.7 to 1.0. Correlations between growth rate and size indicated that the larger fish were the fastest growing between 16 and 19 months of age and were slower growing between 19 and 21 months of age.

Key words *Oncorhynchus kisutch* · Nested design Heritability · Freshwater · Growth rate

Introduction

Impediments to the rearing of salmonids particular to marine net-pen or cage culture include factors such as noxious marine algae (Horner et al. 1989; Mackenzie 1991) and increasing fears of the potential damages of coastal pollution and escaped cultured fish (Hindar et al. 1991; Webb and Youngson 1992). These considerations combined with the level of control possible in the freshwater rearing of salmonids may lure more producers to consider freshwater systems. However, the genetics of growth through maturity in freshwater systems has not been explored for salmon.

For accelerated coho salmon, adult size and sexual maturation are usually reached at 2 years of age (Donaldson and Brannon 1975). Growth during the second year of life is responsible for a 200–300% increase in length and greater than 80% of the total weight. Research on Pacific salmon concerning the genetic parameters for size and growth through maturity is limited (Withler and Beacham 1994).

Estimates of the genetic parameters for length and weight of coho salmon early in the second year of growth have been reported in the literature by Hershberger et al. (1990), and Withler and Beacham (1994). The estimates of Hershberger et al. (1990) are restricted to a single stock (derived from the Skykomish river), and because the fish were produced for sale at approximately 500 g, genetic parameters for size were not reported beyond 15 months of age. Additionally, both these studies were concerned with fish transferred to saltwater.

In 1988 the study presented here was begun to evaluate the genetic variation for size and growth rate in a stock of freshwater-reared coho salmon. In this paper, the results of a quantitative genetic analysis of growth and growth rate are presented based on the variation in a population of individually tagged fish from full- and half-sib families.

Materials and methods

In all cases the basic principles of laboratory animal care were followed.

The fish used as parents in this study were taken from the returns of the University of Washington accelerated coho stock returning in 1988 (to produce the BY 1988 experimental population). Mature 2-year-old coho were taken from the peak of the return between November 21 and December 2. For the BY 1988 population, each of 14 males was mated to multiple females (10 males were mated with 3 females, 3 males were mated with 2 females, and 1 male was mated with 4 females) for a total of 40 full-sib families nested within 14 half-sib groups.

Communicated by E. I. Eisen

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After fertilization of the eggs, from the water-hardening stage through hatching until transfer to troughs for first feeding in January, each full-sib family was maintained in a separate Heath incubator tray (Heath Techa Corp, Kent, Wash.) in a standard vertical stack at a constant temperature (10° ± 1°C). After hatching and development to the stage of yolk-sac absorption, alevins from each family were placed into one section of a 4.5 × 0.3 × 0.2-m trough divided into six sections. Each full-sib family was randomly culled to 500 individuals.

In February, 3 months after fertilization, one-half of the families were marked by adipose fin excision, and 2 families were combined into one container. The 2 families pooled after adipose fin excision were chosen to specifically exclude half-sib groups from sharing the same container. In April, 5 months after fertilization, 300 randomly chosen fish from each family were further marked with freeze brands (Mighell 1969) to uniquely identify each full-sib group, and all marked fish were combined into a single 27,000-l circular tank.

During the month of May increasing density in the rearing tank accompanied by rising temperatures (18°–19°C) created conditions that led to a bacterial epizootic. Treatment with a bactericidal solution reduced mortality. From each family 100 survivors were randomly chosen, moved to a different freshwater facility for further rearing and placed into a single concrete circular tank with a 35,500-l capacity in June 1990.

At approximately 1 year of age (all ages are given as post-fertilization) 25 of the 100 fish in each family were individually tagged with visual implant (VI) tags (Northwest Marine Technology). Two sample *t*-tests were performed to examine the effect of individual tagging on fish size.

During periodic sampling, from 20 to 50 fish in each family were measured for length and weight (including all individually tagged fish). Additionally, at these times 5 fish from each family were sacrificed for sex determination. Fish were sampled at 13 months, in December 1989, and at 16, 19 and 21 months and at spawning. Final length and weight measurements were made during spawning (November through December), or for those fish that did not sexually mature, on the final day of the spawning season. A sampling period lasted approximately 5 days. From 1 day prior to sampling and throughout the sampling period the fish were not fed in order to reduce variation due to different growth opportunities among the fish.

Length and weight data from each sample and growth rates between sampling periods were analyzed for genetic effects. Specific daily growth rate (SGR) was calculated from all individually tagged fish measured in consecutive samples ($SGR=(\log_{t1}-\log_{t0})$/no. of days, where t_1 and t_0 are sampling dates and no. of days is the number of days between t_1 and t_0). Growth rates for both length and weight were calculated. The 13-month to 16-month sample (SGRL1, specific daily growth rate for length between December and March; SGRW1, specific daily growth rate for weight between December and March) was the first interval, followed by the 16- to 19-month sample (SGRL2, SGRW2), the 19- to 21-month sample (SGRL3, SGRW3) and lastly, from 21 months to the spawning sample (SGRL4, SGRW4). Because the final maturation date was not the same for all fish, the first week in October 1990 when feeding was terminated was considered the end of the growing period, and growth rate calculations for the final interval were performed using this time interval for all fish.

Univariate analyses of variance (ANOVAs) were conducted to estimate the sire and dam components of variance for length, weight and growth rate (Becker 1984) using the SAS® GLM procedure. Multivariate analyses of variance (MANOVAs) were performed to estimate covariance components and genetic and phenotypic correlations between sample lengths, weights and growth rates (Grossman and Gall 1968) also using the SAS® GLM procedure. Growth rate and correlation estimates between samples were calculated using only observations from individually tagged fish measured in consecutive samples. Calculation of heritability estimates and their standard errors, and of the errors for genetic and phenotypic correlations was done following the methods of Becker (1984).

The effect of sex on size and growth rate was first examined by two sample *t*-tests on data taken at each sampling period, including all fish whose sex was known. The significance of the sex effect was also examined by inclusion in the ANOVA model. The full model utilized in the analysis of genetic parameters was:

$$Y_{ijkl}=u+C_l+S_i+D_{i(j)}+E_{ijkl}$$

where Y_{ijk} is the individual record, u is the overall mean, C_l is the effect of sex, S_i is the random effect of the **i th** sire, $D_{i(j)}$ is the random effect of the **j th** dam nested within the *i*th sire and E_{ijkl} is the random error. Probability values ≤0.05 were considered significant.

Results and discussion

The genetic parameter estimates reported here for size and growth rate during the second year were derived from a population raised entirely in freshwater. This was the first generation of this stock to be reared in captivity and wholly in freshwater.

Mortality during the second year accounted for a total of 107 fish, or approximately 2% of the population. However, of the 950 VI tags implanted in December 1989, only 605 (64%) were recovered in the final spawning sample. Most of the loss of tags was due not to fish mortality (57 VI-tagged fish died) but to the tag being lost from the fish recipient. Approximately 85% of the unrecovered tags were lost in this manner. Two sample *t*-tests (2-tailed) indicated no significant effect of the tags on growth for any sample.

Sample size, mean and standard deviation for length and weight are given in Table 1, and for growth rate in Table 2. Frequency distributions for some traits showed skewness, but because all distributions had a Pearsonian skewness coefficient between –3 and +3, no transformations were employed (Freund 1984). Although several contrasts between the sexes for length and weight were significant, no consistent trend was apparent (Table 1).

Table 1 Mean ± standard deviation for length and weight for males and females. The coefficient of variation (CV) is based on the mean and standard deviation over all fish measured

Trait	Males	Females	CV (%)
Length (cm)			
13 months**[a]	29.5 ± 1.7 (379)	29.3 ± 1.6 (433)	5.7
16 months**	36.0 ± 2.1 (377)	35.5 ± 1.9 (399)	5.8
19 months	41.8 ± 3.3 (357)	41.7 ± 3.2 (420)	7.9
21 months	46.5 ± 3.9 (345)	47.0 ± 3.9 (399)	8.4
Spawn[b]	49.7 ± 4.4 (504)	49.7 ± 4.0 (536)	8.3
Weight (g)			
13 months*	319.5 ± 58.7 (379)	314.0 ± 55.3 (433)	18.2
16 months	554.9 ± 102.6 (377)	538.4 ± 95.0 (399)	18.8
19 months	887.9 ± 211.7 (357)	858.7 ± 198.1 (420)	24.1
21 months	1,423.0 ± 362.3 (345)	1,374.9 ± 358.5 (399)	25.3
Spawn**	1,561.5 ± 437.7 (504)	1,465.6 ± 385.5 (536)	27.1

[a] Asterisks indicate significant differences between males and females. * indicates significance at 0.05 level and ** at 0.01 level

[b] Spawning measurements were made before gametes were stripped on males and females

[c] Numbers in parentheses give the number of animals from which mean and standard deviation were calculated

Table 2 Mean ± standard deviation for specific growth rate (SGR) of length and weight (all values $\times 10^{-3}$).

Trait	Mean ± SD (n^a)
SGRL	
13–16 months	1.85 ± 0.30 (731)
16–19 months	1.70 ± 0.48 (656)
19–21 months	1.82 ± 0.53 (629)
21 months-spawn	1.28 ± 0.54 (574)
SGRW	
13–16 months	5.13 ± 1.07 (731)
16–19 months	5.00 ± 1.60 (656)
19–21 months	7.38 ± 2.07 (629)
21 months-spawn	1.20 ± 2.71 (574)

[a] Numbers in parentheses give the number of animals from which mean and standard deviation were calculated

Table 3 Heritability estimates based on variance components due to sires (h^2_{sire}) and dams (h^2_{dam}) for length and weight at each sample, and for growth rate at each interval

Age/Interval	Length		Weight	
	h^2_{sire}	h^2_{dam}	h^2_{sire}	h^2_{dam}
13 months	0.36 ± 0.28	0.82 ± 0.28	0.43 ± 0.31	0.83 ± 0.28
16 months	0.50 ± 0.31	0.69 ± 0.24	0.49 ± 0.33	0.85 ± 0.28
19 months	0.50 ± 0.34	0.90 ± 0.29	0.45 ± 0.32	0.85 ± 0.28
21 months	0.32 ± 0.25	0.69 ± 0.24	0.17 ± 0.22	0.77 ± 0.26
Spawn[a]	0.26 ± 0.24	0.72 ± 0.26	0.19 ± 0.24	0.90 ± 0.30
SGR 3	0 ± 0.14	0.65 ± 0.22	0 ± 0.11	0.51 ± 0.19
SGR 4	0.34 ± 0.24	0.54 ± 0.19	0.27 ± 0.18	0.31 ± 0.14
SGR 5	0.21 ± 0.15	0.25 ± 0.12	0.25 ± 0.16	0.23 ± 0.12
SGR 6	0 ± 0.11	0.75 ± 0.25	0.14 ± 0.12	0.20 ± 0.12

[a] Spawning measurements were made before gametes were stripped on males and females

Variance components and heritability estimation

Size at age

The mean squares and variance component estimates for length and weight were calculated from ANOVAs for each sample. Significance of the sex effect was variable, as was expected from the *t*-tests. In all cases the dam effect was significant and the dam variance component was greater than the sire variance component.

The heritabilities for length and weight for each sample were estimated from both sire and dam components of variance (Table 3). Because of incubation space limitations, the number of sires used in this study was small, and one consequence was a lack of significant heritability and genetic correlation estimates. The standard errors associated with heritability and genetic correlation estimates can be reduced somewhat by increasing the number of individuals measured per family, but as shown by Klein et al. (1973) the number of families is overwhelmingly important. Therefore, the estimates presented here, while based on the intraclass correlation of paternal half-sibs and so relatively unbiased (Falconer 1981), should be considered cautiously, and in comparison with estimates from other populations. Table 4 provides mean values, coefficient of variation, sample size and heritability estimates of weight at age for a variety of salmonids raised in freshwater or saltwater.

In this study, the standard errors of the heritability estimates were large, particularly for estimates based on the sire variance components. None of the heritability estimates based on sire variance components were significantly different from zero. The heritability estimates derived from dam components of variance were mostly significant (Table 3) and all larger than estimates based on the sire variance components. The magnitude of the difference between estimates based on sire and dam variance components indicates a substantial influence of dominance, epistatic, maternal or common environmental effects from the incubation and fry rearing stage, or some combination of these effects. While maternal and common environmental effects generally dissipate over the first 120 days (Kincaid 1972; Iwamoto et al. 1982), it has been suggested that these effects can have an impact on salmon throughout the life cycle (Sylven et al. 1991). In this population, although the effect of egg size (a maternal effect) was significant in the 10-month sample (Silverstein and Hershberger 1994), for the 13-month sample the simple correlations between egg size and length and weight were not significant. Common environmental effects also would not be expected to be a large factor because they appeared to have diminished in earlier samples (Silverstein and Hershberger 1994). Dominance and epistatic effects, however, cannot be ruled out in this study. In other studies of heritability of size at age in salmonids where a measure of dominance effects was possible, dominance effects have been found (Gall 1975; Gunnes and Gjedrem 1978; Gjerde and Gjedrem 1984; McKay et al. 1986b; Gall and Huang 1988; Gjerde and Shaeffer 1989; Nilsson 1992). However, in the population studied here the magnitude of differences between sire and dam estimates of heritability were larger than most found in the literature, suggesting that non-additive effects may play a bigger role in this population. It cannot be determined from this study if this is common to coho salmon in general or whether it is peculiar to the population studied.

The heritability estimates for size at age in the BY 1988 population based on sire components of variance were quite high for both length and weight through the 19-month sample, from 0.36 to 0.50, and dropped to between 0.17 and 0.32 in the last 5 months (Table 3). Two other reports give heritability estimates for length and weight of coho salmon beyond 1 year of age (Hershberger et al. 1990; Withler and Beacham 1994; see Table 4). The estimates for size at 15 months of age of Hershberger et al. (1990) were lower than those found in this study. The fish in that experiment were raised in sea water net-pens, and greater environmental variation encountered in sea water rearing may have reduced the proportion of variance attributable to additive genetic sources. Recent work by Sylven et al.

Table 4 Phenotypic parameters and heritabilities (based on sire components of variance) of weight in several salmonid species at different ages[a]

Species	Age[b]	Mean (g)	CV(%)	h^2	Method of estimation[c]	Number of families[d]	Author(s)
Saltwater							
Coho salmon	15 months (1978)e	283.2	31.3	0.33	HS	20S:40D	Hershberger et al. 1990
	15 months (1985)	429.8	37.5	0.20	FS	35–40F	Hershberger et al. 1990
	22 months	144.0	54.3	0.61	HS	30S:60D	Withler and Beacham 1994
	34 months	569.3	31.9	0.59	HS	30S:60D	Withler and Beacham1994
Rainbow trout	24 months	2,497.0	28.8	0.21	HS	47S:249D	Gjerde and Schaeffer1989
	30 months	3,922.4	25.6	0.16	HS	35S:131D	Sylven et al. 1991
Atlantic salmon	35 months (1973)	4,960.0	31.7	0.10	HS	31S:57D	Gunnes and Gjedrem1978
	35 months (1974)	5,630.0	28.2	0.36	HS	32S:87D	Gunnes and Gjedrem1978
Freshwater							
Rainbow trout	13 months	650.3	18.7	0.26	HS	54S:18D	Crandell and Gall 1993
	15 months	900.0	18.2	0.40	HS	54S:18D	Crandell and Gall 1993
	18 months	1,379.9	18.7	0.33	HS	54S:18D	Crandell and Gall 1993
	21 months	1,973.3	19.0	0.24	HS	54S:18D	Crandell and Gall 1993
	25 months (post-spawn)	2,260.4	21.1	0.21	HS	54S:18D	Crandell and Gall 1993
	30 months	133.5	41.9	0.38	FS	34S:34D, 68F	McKay et al. 1986
	48 months	416.1	31.7	0.27	FS	34S:34D, 68F	McKay et al. 1986
	18 months	693.7	42.5	0.13	HS	39S:113D	Sylven and Elvingson1992
	30 months	2,329.7	35.4	0.12	HS	39S:113D	Sylven and Elvingson1992
	30 months	2,639.0	20.3	0.27	HS	35S:131D	Sylven et al. 1991
Arctic charr	24 months	313.3	40.2	0.44	FS	29F	Nilsson 1990
	30 months	764.2	33.3	0.40	FS	29F	Nilsson 1990
	36 months	888.7	33.8	0.49	FS	29F	Nilsson 1990
	24 months	326.7	36.1	0.34	FS	36S:32D, 95F	Nilsson 1992
	30 months	422.2	39.0	0.39	FS	36S:32D, 95F	Nilsson 1992
	36 months	651.2	36.4	0.52	FS	36S:32D, 95F	Nilsson 1992

[a] The statistics shown here were taken either directly from the cited articles or were calculated from data provided within the article
[b] Where ages were given in years in the original article, they were converted as closely as possible to months
[c] HS, half-sib; FS, full-sib
[d] S follows the number of sires used, D follows the number of dams used, and F follows the number of families
[e] Numbers in parentheses refer to broodyear populations when one article provides estimates for more than one broodyear population

(1991) showed higher heritabilities for weight several months prior to sexual maturation in rainbow trout raised in freshwater than for siblings raised in saltwater (Table 4), and they suggest that variation in osmoregulatory capacity may have influenced this result.

The high heritability estimate for mature size in coho salmon reported by Withler and Beacham (1994; Table 4) came from the mixed rearing of several coho populations under severe feed restriction. It may be that the feed restriction enhanced the expression of genetic variation, since other experiments on some of the same populations yielded lower estimates for the heritability of size when feed was not as limited (Swift 1991; as cited in Withler and Beacham 1994).

Reported heritability estimates for size beyond 1 year of age in other salmonids reared in freshwater have been variable, ranging between about 0.2 and 0.5 (see Table 4). Though few reports give heritabilities for size at multiple ages, the estimates given here for coho salmon are within the range reported for other species near maturation, and are slightly higher than most reported heritabilities for size more than 6 months before maturation.

In this study a drop in heritability estimates as the fish grew older was documented. There is no clear pattern of decline in other studies reporting heritability over multiple samplings, though both increases and declines have been reported (Table 4). In Arctic charr, Nilsson (1990) found heritability estimates for length and weight increased from 2 to 3 years. In the study on rainbow trout by McKay et al. (1986) the lower estimates of heritability all came in later samples when the rainbow trout were 4 years of age. In a study by Crandell and Gall (1993) as well, the heritability estimates for weight declined during the second year from a 15-month high of 0.40 to a spawning sample low of 0.21. O'Flynn et al. (1992) estimated heritability of length in two stocks of Atlantic salmon several months after transfer to saltwater and then again 6 months prior to sexual maturation. In one stock the heritability decreased from 0.15 to 0.13, yet in the other it increased from 0.18 to 0.29.

One factor that may have contributed to the lower heritability estimates for size in later samples in this work was feeding regime. From 16 months until the fish ceased feeding prior to sexual maturation, daily rations were set

Table 5 Genetic correlations estimates (upper triangle) based on the sire components of variance (r_G sire) and phenotypic correlation estimates (lower triangle) (*N.C.* non-calculable due to negative value within a square root)

	13 months		16 months		19 months		21 months		Spawning Sample	
	Length	Weight	Length	Weight	Length	Weight	Length	Weight	Length	Weight
13 months										
Length		0.97 ± 0.05	1.02 ± 0.06	1.03 ± 0.09	0.89 ± 0.17	0.87 ± 0.21	0.88 ± 0.23	1.07 ± 1.08	0.96 ± 0.24	0.82 ± 0.41
Weight	0.92 ± 0.01		0.93 ± 0.09	1.03 ± 0.05	0.86 ± 0.17	0.88 ± 0.17	0.74 ± 0.32	0.93 ± 0.87	0.79 ± 0.29	0.77 ± 0.39
16 months										
Length	0.89 ± 0.01	0.85 ± 0.02		0.97 ± 0.03	0.91 ± 0.08	0.89 ± 0.11	0.95 ± 0.11	1.27 ± 1.35	0.97 ± 0.12	0.95 ± 0.27
Weight	0.81 ± 0.02	0.88 ± 0.01	0.95 ± 0.01		0.90 ± 0.10	0.89 ± 0.11	0.85 ± 0.18	1.12 ± 0.99	0.89 ± 0.17	0.91 ± 0.22
19 months										
Length	0.81 ± 0.02	0.78 ± 0.03	0.87 ± 0.01	0.86 ± 0.02		1.00 ± 0.0	1.01 ± 0.05	1.42 ± 1.55	1.03 ± 0.07	1.09 ± 0.28
Weight	0.73 ± 0.03	0.77 ± 0.03	0.81 ± 0.02	0.85 ± 0.02	0.96 ± N.C.		0.97 ± 0.07	1.33 ± 1.35	0.98 ± 0.09	1.08 ± 0.26
21 months										
Length	0.74 ± 0.03	0.71 ± 0.03	0.80 ± 0.02	0.79 ± 0.02	0.93 ± 0.01	0.91 ± 0.01		1.03 ± 0.08	1.04 ± 0.05	0.98 ± 0.09
Weight	0.67 ± 0.03	0.69 ± 0.03	0.74 ± 0.02	0.77 ± 0.02	0.87 ± 0.01	0.90 ± 0.01	0.96 ± N.C.		1.28 ± 1.12	1.11 ± 0.50
Spawn										
Length	0.70 ± 0.03	0.68 ± 0.03	0.77 ± 0.02	0.77 ± 0.02	0.90 ± 0.01	0.87 ± 0.01	0.97 ± 0.00	0.94 ± 0.01		1.01 ± 0.05
Weight	0.64 ± 0.03	0.67 ± 0.03	0.74 ± 0.03	0.77 ± 0.02	0.85 ± 0.02	0.87 ± 0.02	0.92 ± 0.01	0.93 ± 0.01	0.95 ± 0.01	

at 1.5% wet body weight of fish, and the entire ration was delivered at one feeding. Before 16 months, fish had been fed to apparent satiation three times daily. Possibly the restricted ration hindered expression of genetic differences in size between families. Nevertheless, it is interesting to note that in the report by Withler and Beacham (1994) restricted rations appeared to have the opposite effect and enhanced expression of genetic variation between families.

Growth rate

The sire mean squares for SGRL1, SGRW1 and SGRL4 were not significant, and the sire variance components for these measures were negative. In all other measures of specific growth rate the sire effect was significant, and the sire variance component was positive. In all measures of growth rate the dam mean squares were significant, and the variance components were positive.

The heritability estimates for the SGR1 interval based on the sire component of variance were small and negative, but they were quite high for the dam estimates. In the two succeeding intervals both the sire and dam estimates were positive, moderate and similar in magnitude. In the final interval, the heritability estimate for SGR4 in length returned to a small negative value based on the sire component of variance, yet again was positive and high based on the dam component. The heritability estimates for SGRW in the final interval were lowly based on both sire and dam variance component estimates.

Few other studies have investigated the heritability of growth rate. In this study specific growth rate had the highest heritability (based on the sire components of variance) at the 16- to 19-month interval. The estimate for heritability was high enough to suggest that selection on growth rate during this interval could result in improvements in growth rate and size. However, this interval also marks the beginning of the period that fish in this study were put on restricted rations, and restricted rations may be necessary for expression of additive genetic variation in growth rate. Nilsson (1992) reported that heritability estimates for specific growth rate of Arctic charr were high from 1.5 to 2 years and that over subsequent intervals (2–2.5 years and 2.5–3 years) heritabilities decreased considerably; no data were shown, and details concerning the feeding regime were not provided.

Genetic and phenotypic correlations

The estimates of genetic correlation between length and weight within a sampling period were all high for both sire and dam genetic correlations, ranging from 0.92 to 1.03 (Table 5, only sire data shown). Across sampling periods, the genetic correlations involving length and weight were high for samples occurring in sequence, and diminished as samples were further apart.

Phenotypic correlations, r_P, between length and weight within a sampling period were high (from 0.92 to 0.96, Ta-

ble 5). Between adjacent samples, r_p's between length and weight were also high and decreased in steps as sampling periods were further apart, like genetic correlation estimates.

The high correlations found between length and weight within a sampling period are in accord with all other studies reporting such correlations in salmonids of any age (Gunnes and Gjedrem 1978; Refstie and Steine 1978; Iwamoto et al. 1982; Gjerde and Gjedrem 1984; Nilsson 1992).

The decrease in genetic and phenotypic correlations of size at different ages as the measurements occurred further apart in time found in this study has been shown in other studies examining such correlations for Atlantic salmon (Naevdal et al. 1978) and rainbow trout (Naevdal et al. 1979; Crandell and Gall 1993). Nevertheless, the correlations between samples for length and weight reported here were higher over the entire second year than has been found in other studies. The high, significant correlations found in this population suggest that selection for size at 13 months or earlier (see below) would give a substantial correlated response in size at later ages.

Both phenotypic and genetic correlations of SGRL2 and SGRW2 with size (data not shown) were moderate to high (0.4 to 0.9), especially size from 16 months onward. Furthermore, the correlations were positive and many were significant, suggesting that although mean growth rate was low during this period (Table 2) larger animals were faster growing between 16 and 19 months and remained the largest fish through maturity. Conversely, genetic correlations of size with SGRL3 and SGRW3 were mainly negative (data not shown), and the phenotypic correlation estimates for size prior to 19 months with SGRL 3 and SGRW3 were small and negative. Nevertheless, from 21 months to spawning the phenotypic correlations were small and positive. Although the phenotypic correlations are small, they suggest that the growth rate of larger fish was lower and that smaller fish were growing the fastest from 19 to 21 months.

The parameters measured in this study show no large departures from estimates made previously on other salmonids, however the heritabilities and correlations presented are high. The effect of the freshwater environment was not tested but, in general, it appears that genetic parameter estimates on freshwater-reared populations are higher; the estimates given here support this trend. Furthermore, genetic correlations between pre-smolt growth and post-smolt growth (smoltification is the transformation enabling salmonids to osmoregulate in saltwater) in salmon transferred to saltwater are low to moderate, ranging from 0.35 to 0.70 (Hershberger et al. 1990; Withler and Beacham 1994). Withler and Beacham (1994) have suggested that the low genetic correlations indicate different genetic control of growth in fresh and saltwater. In this experimental population, maintained in freshwater after smolting, the genetic correlations of size as pre-smolts with 21-month size were high, ranging from 0.84 to 1.10 (Silverstein 1993). This indicates that genetic control of growth was similar from as early as 6 months of age through 21 months and that earlier selection for size should give a correlated response in size at later ages.

This study has demonstrated good growth and substantial genetic variability for size and growth rate of coho salmon grown in freshwater. The rapid gains achieved with coho salmon raised in saltwater, where heritability estimates were lower (Hershberger et al. 1990), suggest that similar or better gains could be realized in freshwater.

Acknowledgements The authors thank G. Yokoyama, T. Vu, I. Ahn J. Myers and E. Mooney for assistance with fish rearing and data collection. This research was funded by U.S.D.A. Grant No. 87-CSRS-2-3219. University of Washington, School of Fisheries, Seattle, Wash., USA.

References

Becker WA (1984) Manual of quantitative genetics, 4th edn. Academic Enterprises, Pullman, Wash.

Crandell PA, Gall GAE (1993) The genetics of age and weight at sexual maturity based on individually tagged rainbow trout (*Oncorhynchus mykiss*). Aquaculture 117:95–105

Donaldson LR, Brannon EL (1975) The use of warmed water to accelerate the production of coho salmon. Fisheries 1:12–15

Falconer DS (1981) Introduction to quantitative genetics, 2nd edn. Longman, New York

Freund JE (1984) Modern elementary statistics. Prentice Hall, Englewood Cliffs, N.J.

Gall GAE (1975) Genetics of reproduction in domesticated rainbow trout. J Anim Sci 40:19–28

Gall GAE, Huang N (1988) Heritability and selection schemes for rainbow trout: body weight. Aquaculture 73:43–56

Gjerde B, Gjedrem T (1984) Estimates of phenotypic and genetic parameters for carcass traits in Atlantic salmon and rainbow trout. Aquaculture 36:97–110

Gjerde B, Shaeffer LR (1989) Body traits in rainbow trout. II. Estimates of heritabilities and of phenotypic and genetic correlations. Aquaculture 80:25–44

Grossman M, Gall GAE (1968) Covariance analysis with unequal subclass numbers: component estimation in quantitative genetics. Biometrics 24:49–59

Gunnes K, Gjedrem T (1978) Selection experiments with salmon. IV. Growth of Atlantic salmon during two years in the sea. Aquaculture 15:19–33

Hershberger WK, Myers JM, Iwamoto RN, McAuley WC, Saxton AM (1990) Genetic changes in the growth of coho salmon (*Oncorhynchus kisutch)* in marine net-pens, produced by ten years of selection. Aquaculture 85:187–197

Hindar K, Ryman N, Utter F (1991) Genetic effects of cultured fish on natural fish populations. Can J Fish Aquat Sci 48:945–957

Horner RA, Postel JR, Rensel JE (1989) Noxious phytoplankton blooms in western Washington USA waters. In: Graneli E et al. (eds) Toxic marine phytoplankton; 4th Int Conf. Elsevier Science Publ, New York, pp 171–176

Iwamoto RN, Saxton AM, Hershberger WK (1982) Genetic estimates for length and weight of coho salmon during freshwater rearing. J Hered 73:187–191

Kincaid HL (1972) A preliminary report on the genetic aspects of 150-day family weights in hatchery rainbow trout. In: (eds) West Proc 52nd Annu Conf West Assoc State Game Fish Comm., Portland, Oregon, pp 562–565

Klein TW, DeFries JC, Finkbeiner CT (1973) Heritability and genetic correlation: standard errors of estimates and sample size. Behav Genet 3:355–364

MacKenzie L (1991) Toxic and noxious phytoplankton in Big Glory Bay, Stewart Island, New Zealand J Appl Phycol 3:19–34

McKay LR, Ihssen PE Friars GW (1986) Genetic parameters of growth in rainbow trout, *Salmo gairdneri,* as a function of age and maturity. Aquaculture 58:241–254

Mighell JL (1969) Rapid cold-branding of salmon and trout with liquid nitrogen. J Fish Res Board Can 26:2765–2769

Naevdal G, Holm M, Leroy R, Moller D (1978) Individual growth rate and age at first sexual maturity in Atlantic salmon. Fiskeridir Skr Ser Havunders 16:519–529

Naevdal G, Holm M, Leroy R, Moller D (1979) Individual growth rate and age at sexual maturity in rainbow trout. Fiskeridir Skr Ser Havunders 17:1–10

Nilsson J (1990) Heritability estimates of growth-related traits in Arctic charr (*Salvelinus alpinus*). Aquaculture 84:211–217

Nilsson J (1992) Genetic parameters of growth and sexual maturity in Arctic charr (*Salvelinus alpinus*). Aquaculture 106:9–19

O'Flynn FM, Friars GW, Bailey JK (1992) Development of a selection index to improve market value of cultured Atlantic salmon (*Salmo salar*). Genome 35:304–310

Refstie T, Steine TA (1978) Selection experiments with salmon. III. Genetic and environmental sources of variation in length and weight of Atlantic salmon in the freshwater phase. Aquaculture 14:221–234

SAS (1990) User's Guide: Statistics. Version 6, First Edition, SAS Institute Inc., Cary, NC, USA

Silverstein JT (1993) A quantitative genetic study of size, growth rate and timing of sexual maturation in coho salmon (*Oncorhynchus kisutch*). PhD thesis, University of Washington, Seattle, Wash.

Silverstein JT, Hershberger WK (1994) Genetic parameters of size pre- and post-smoltification in coho salmon (*Oncorhynchus kisutch*). Aquaculture 128:67–77

Sylven S, Rye M, Simianer H (1991) Interaction of genotype with production system for slaughter weight in rainbow trout (*Oncorhynchus mykiss*). Livest. Prod Sci 28:253–263

Sylven S, Elvingson P (1992) Comparison of rainbow trout (*Oncorhynchus mykiss*) strains for body weight, length and age at maturity in different Swedish production systems. Aquaculture 104: 37–50

Webb JH, Youngson AF (1992) Reared Atlantic salmon, *Salmo salar* L. in the catches of a salmon fishery on the west coast of Scotland. Aqua Fish Mange 23:393–397

Withler RE, Beacham TD (1994) Genetic variation in body weight and flesh colour of the coho salmon (*Oncorhynchus kisutch*) in British Columbia. Aquaculture 119:135–148