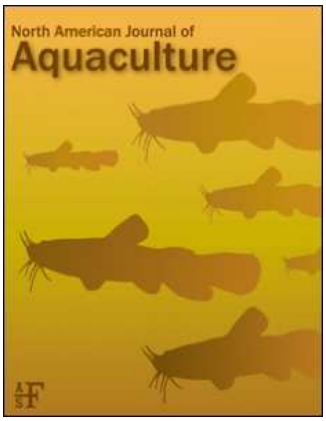

North American Journal of Aquaculture
Publication details, including instructions for authors and subscription information:
http://www.informaworld.com/smpp/title~content=t926380648

Genetic Gain for Growth and Delayed Sexual Maturation Using a Feral Strain of Anadromous Brook Trout

Andréane Bastien[a]; Guy M. L. Perry[bc]; Jean-Yves Savaria[ad]; Louis Bernatchez[b]; Céline Audet[a]
[a] Institut des Sciences de la Mer, Université du Québec à Rimouski, Rimouski, Quebec, Canada [b] Institut de Biologie Intégrative et des Systèmes, Université Laval, Quebec City, Quebec, Canada [c] State University of New York, Upstate Medical University, Syracuse, New York, USA [d] Department of Fisheries and Oceans Canada, Institut Maurice-Lamontagne, Mont-Joli, Quebec, Canada

Online publication date: 02 February 2011

To cite this Article Bastien, Andréane , Perry, Guy M. L. , Savaria, Jean-Yves , Bernatchez, Louis and Audet, Céline(2011) 'Genetic Gain for Growth and Delayed Sexual Maturation Using a Feral Strain of Anadromous Brook Trout', North American Journal of Aquaculture, 73: 1, 24 — 33
To link to this Article: DOI: 10.1080/15222055.2011.544609
URL: http://dx.doi.org/10.1080/15222055.2011.544609

North American Journal of Aquaculture 73:24–33, 2011

ISSN: 1522-2055 print / 1548-8454 online
DOI: 10.1080/15222055.2011.544609

ARTICLE

Genetic Gain for Growth and Delayed Sexual Maturation Using a Feral Strain of Anadromous Brook Trout

Andréane Bastien
Institut des Sciences de la Mer, Université du Québec à Rimouski, 310 Allée des Ursulines, Rimouski, Quebec G5L 3A1, Canada

Guy M. L. Perry[1]
Institut de Biologie Intégrative et des Systèmes, Université Laval, Quebec City, Quebec G1V 0A6, Canada

Jean-Yves Savaria[2]
Institut des Sciences de la Mer, Université du Québec à Rimouski, 310 Allée des Ursulines, Rimouski, Quebec G5L 3A1, Canada

Louis Bernatchez
Institut de Biologie Intégrative et des Systèmes, Université Laval, Quebec City, Quebec G1V 0A6, Canada

Céline Audet*
Institut des Sciences de la Mer, Université du Québec à Rimouski, 310 Allée des Ursulines, Rimouski, Quebec G5L 3A1, Canada

Abstract

A selective breeding program was initiated with a wild population of anadromous brook trout *Salvelinus fontinalis* from the Laval River, Quebec. The objective was to develop a new strain characterized by improved growth and reduced precocious sexual maturation. A control line was maintained by use of random within-family selection. Length and weight were measured and sexual maturity (mature or not mature) was determined at the end of the second year of growth (22 months of age). In the selected line, phenotypic variance, additive genetic variance, and heritability for weight within the selected families were reduced. A comparison between generations showed that fish weight at 22 months in the selected line increased by 23.1% from the F_1 to the F_2 generation and by 32.1% from the F_2 to the F_3 generation. The control line increased similarly in weight from the F_1 to the F_2 generation (34.7%) but not thereafter; this result was probably due to the domestication effect in the first generation after captivity. The proportion of fish that were immature at 22 months was 32.2% in the F_1 generation and increased to 61.4% by the F_3 generation in the selected line; the proportion immature did not change significantly after two generations in the control line (27.5%). Our results show that simultaneous selection for growth and late sexual maturation are compatible goals for brook trout breeding programs.

With the decline of Atlantic salmon *Salmo salar* populations in rivers of eastern Canada, sportfishing activities increasingly focus on anadromous populations of brook trout *Salvelinus fontinalis*. The genetic and biological characteristics of anadromous brook trout populations are largely unknown, but in the wild these populations present many traits that are attractive for

*Corresponding author: celine_audet@uqar.qc.ca
[1]Present address: State University of New York, Upstate Medical University, 3283 Weiskotten Hall, Syracuse, New York 13210, USA.
[2]Present address: Department of Fisheries and Oceans Canada, Institut Maurice-Lamontagne, 850 Route de la Mer, Mont-Joli, Quebec G5H 3Z4, Canada.
Received April 29, 2009; accepted August 9, 2010

fish producers. In an attempt to better understand the biology of anadromous brook trout populations and to investigate how they could be included in fish production programs, breeders from a feral population were captured in the Laval River (north shore of the St. Lawrence Estuary, Quebec). The current production of brook trout in Quebec is mainly designed for fish stock enhancement to support recreational fisheries. Legislation regarding enhancement by use of native strains in different administrative regions has increased the interest in developing new strains for brook trout production.

High growth rate and reduced incidence of precocious sexual maturation are standard breeding goals (Nilsson 1992; Winkelman and Peterson 1994; Gjedrem 2000; Kause et al. 2003). Fast-growing fish allow faster turnover at fish farms, which decreases production costs (Winkelman and Peterson 1994). Late sexual maturity allows fish to reach commercial size more rapidly since fish invest energy in growth instead of gametogenesis (Aksnes et al. 1986; Gjerde 1986); late maturation is also associated with reduced mortality and improved flesh quality (Nilsson 1992; Crandell and Gall 1993). A number of major commercial enterprises continue to suffer from a high incidence of precocious maturation (e.g., Glebe et al. 2003). In salmonid fishes, heritability (h^2) for growth and size at age tends to be moderate to high ($h^2 > 0.20$; Hershberger et al. 1990; Nilsson 1992; Rye and Refstie 1995; Chevassus et al. 2004; Perry et al. 2005b; Neira et al. 2006); therefore, genetic gain is often considerable (Gjedrem 2000). The h^2 of precocious maturation is also moderately high ($h^2 = 0.21$–0.39: Gjerde and Gjedrem 1984; 0.19–0.45: Nilsson 1992), suggesting that similar selective improvement is possible.

Growth rate and late maturity may be conflicting traits for selection in salmonids; for example, body weight (BW) and the incidence of sexual maturation are positively genetically correlated in rainbow trout *Oncorhynchus mykiss* and Atlantic salmon (Thorpe et al. 1983; Gjerde and Gjedrem 1984; Martyniuk et al. 2003). However, genetic covariance is a function of underlying population-level genetic variation for an association between traits from pleiotropy, linkage, or both (Lynch and Walsh 1998), thus requiring case-by-case examination. Strong linkage, at least, might be circumvented in highly fecund species, where it is possible to choose genotypes with advantageous breeding values for both sexual maturity and growth among thousands of individuals (Kause et al. 2003).

Genetic change is realized by genetic shifts that occur in response to experimental selection as well as selection against individuals that fail to adapt to the aquacultural environment (Ruzzante 1994). Without an examination of unselected controls for comparison, it is not possible to differentiate the effects of the selection program from those of domestication, resulting in a false interpretation of gain (see Hershberger et al. 1990; Fleming et al. 2002). Several studies of salmonid evolution in new environments indicate very rapid progress towards a locally adapted state (Hendry et al. 2000; Quinn et al. 2000, 2001; Hendry 2001). Roberge et al. (2006) showed that only five to seven generations of artificial selection could lead to significant changes in gene expression between selection and control groups, and the average magnitude of the observed differences was approximately 20% for at least 1.4–1.7% of genes expressed at the juvenile stage. It could be surmised that selective gains in salmonid breeding programs are relatively rapid.

The objectives of this study were to examine the early stages of selection in anadromous brook trout and to distinguish the resulting genetic gain due to selection from the incidental genetic gain obtained via domestication. Since the low occurrence of early sexual maturation is a trait of commercial interest, a second objective was to test the h^2 of this characteristic in the Laval River strain. Finally, we estimated the relative changes in the quantitative genetic architecture of the above traits, including changes in the genetic correlation between growth and early sexual maturation resulting from selection.

METHODS

A selective breeding program was initiated with an anadromous strain of brook trout from the Laval River (Martin et al. 1997; Savaria 1998). From 1991 to 1993, wild breeders (F_0 generation) were captured in the Laval River near Forestville, Quebec (48°44′N, 68°05′W), and were brought to the Station Aquicole de l'Institut des Sciences de la Mer de Rimouski, Quebec (48°31′N, 68°28′W). In fall 1994, 12 crosses were made with six dams and eight sires to produce an F_1 generation. Eggs from each female were separated into two or three aliquots per female, and each aliquot was fertilized by a different male. Since the size of the wild population is unknown, the Quebec Ministry of Natural Resources and Wildlife restricted the capture of breeders for resource conservation reasons. However, microsatellite data confirmed the absence of inbreeding and showed relatively high heterozygosity in river brook trout (Martin et al. 1997) and in the F_2 control line (Boula et al. 2002; Perry et al. 2005a).

Selection began in 1996 on F_1 fish at 22 months of age (i.e., age 1). To maximize genetic gain, a combined between- and within-family selection protocol was used (Falconer and Mackay 1996) based on growth and on the absence of precocious sexual maturation. Fish that were immature at 22 months of age in the autumn were retained, and the largest of these were used as breeders for the next generation (F_2). The number of fish selected from the ith family (N_{si}) was determined according to the following equation:

$$N_{si} = \{[(x_i - X)/X] \times (N/K)\} + (N/K),$$

where x_i is the mean of weight for family i, X is the general mean weight for the population, N is the number of breeders considered necessary, and K is the number of families (Dubé and Blanc 1992). In the F_1 generation, 4.1–14.2% of fish were selected from the different families based on the specific family performance. In the F_2 generation, 11 full-sibling families were produced from the selected line, and 14.3% of that population was selected to produce the F_3 generation. In November 2001, 12 full-sibling F_3 families were produced from the F_2 breeders of

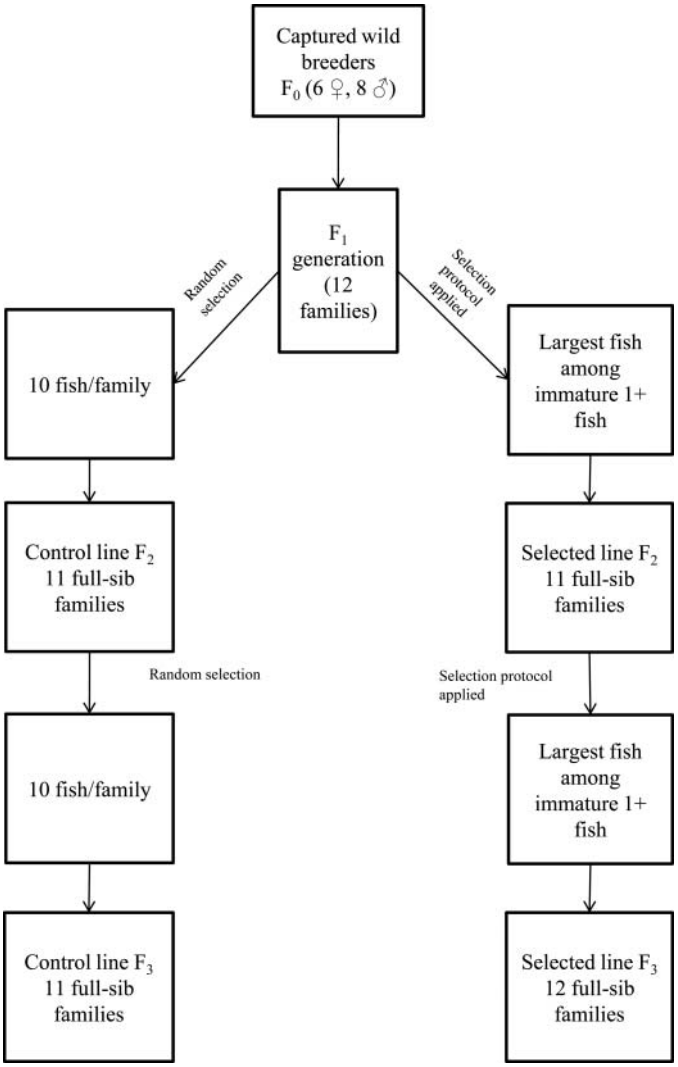

FIGURE 1. Mating design used for control and selected lines of Laval River strain anadromous brook trout in each generation (sib = sibling; 1+ fish = fish at 22 months of age).

the selected line. To differentiate between the effects of selection and domestication, a control group was maintained by using 10 randomly selected fish from each family in the F_1 population before the selection to create an F_2 control line (11 families from F_1 breeders). This pattern was repeated, and F_2 and F_3 control generations were formed with 11 random crosses (full siblings only) from control F_1 and F_2 breeders (Figure 1). Breeders for the F_2 and F_3 generations were only used once.

The rearing protocol was identical for all generations. Fertilized eggs were incubated in darkness. Each family was incubated separately in individual trays with screened bottoms to allow the upwelling of water through the eggs during incubation and to allow inflow from the upstream side during fry rearing. Each incubation tank contained 11 trays. During incubation, heaters were used to maintain the temperature at 4°C. At hatching, the temperature was gradually increased (by 1°C per week) to 8°C until natural temperature reached the same level (beginning of June). Each family was maintained in its individual tray until the initiation of exogenous feeding. Heaters were then removed, and fish were raised in freshwater under natural photoperiod and temperature conditions (minimal temperature [1.2°C] was reached in February; maximal temperature [15°C] was reached in September). When fish reached 17 months of age, salinity was gradually increased (at a rate of 2 $g \cdot L^{-1} \cdot d^{-1}$) to approximate the salinity of estuarine seawater (final salinity = 20 g/L) for the summer (June–August). In August, fish were returned to freshwater. Except for age-0 fish, all other age-groups spent the summer at 20-g/L salinity as described above. Fish were fed commercial pellets, and the feeding rate (percentage of BW per day) was adjusted according to fish age and water temperature (Savaria 1998).

When exogenous feeding was well established (March–April), fish from all families were randomly transferred from individual trays into sections in evenly divided, 0.03-m^3 tanks with separators (3 families/tank, 1 family/section). Family sets were randomly selected. At this stage, fish were too small to be marked. Each family was therefore kept in a tank section until fish reached approximately 1.5 g. At this point (June–July), pelvic fin clips were applied for familial identification (right fin, left fin, both fins, or unmarked) and groups of four families were transferred to larger tanks (0.5 m^3), where they remained for the rest of the study period. Again, family sets were randomly selected. Fin markings were verified every 3–4 months, and unidentifiable fish were removed. In the F_3 generation, 10 families/line were followed, and length and weight were measured monthly from May to September 2002 (20 fish/family) and again in January 2003 (20 fish/family) and April 2003 (100 fish/family) to monitor growth. All fish were anesthetized (3-aminobenzoic acid ethyl ester at 0.16 g/L) before being measured. Weight was measured to the nearest 0.1 g, and fork length (FL) was measured to the nearest 0.1 cm. Fulton's condition factor (K; Barton 1996) was calculated as:

$$K = (\mathrm{BW}/\mathrm{L}^3) \times 100,$$

where BW is the body weight (g) and L is the FL (cm). In November 2003, when fish were 22 months old, FL and BW were measured in all individuals for each control and selected family (approximately 70 fish/family for the F_3), and the status of sexual maturation was determined via the presence of milt or eggs after gentle pressure was manually applied to the abdomen. Sexual maturation was treated as a binary variable: a value of 1 was assigned to mature males or females, and a value of 0 was assigned to immature fish. Mature males and females were grouped together since early maturation causes a diversion of energetic resources and reductions in flesh quality in both sexes (Aksnes et al. 1986). Sampling of fish at sexual maturity from each line and each generation was conducted as described previously for the F_3 generation. The number of fish differed among generations since the number of families was different.

Throughout the study, fish were healthy and we encountered no problems in maintaining any of the families, lines, or generations. Once fish reached the exogenous feeding stage, the number of fish was standardized among families (1,000 individuals). Regular random culls within families were used to maintain appropriate stocking conditions in the rearing facility (<30 kg of fish/m^3).

Normality of data was verified by Kolmogorov–Smirnov tests (Sokal and Rohlf 1995). When data were not normally distributed, a suitable exponential transformation was obtained via a Box–Cox transformation macro (M. Friendly, York University, Toronto, Ontario). For the September, January, and April sampling times, we tested for tank effects on the experimental groups by use of two-way analyses of variance (ANOVA; GLM procedure in the Statistical Analysis System; SAS 1998), the two factors being full-sibling family and rearing tank.

Realized h^2 in this population was estimated from phenotypic gain by use of the breeder's equation ($h^2 = R/S$; where R = response to selection [the difference of the mean phenotypic value between the offspring of the selected parents and the whole parental generation before selection] and S = selection differential; Falconer and Mackay 1996). Genetic variance components were estimated separately within the F_3 control and selected groups by employing restricted maximum likelihood (REML) in Parameter Estimation (PEST) software version 3.0 (Groeneveld et al. 1990) and Variance Component Estimation (VCE) software version 4.2 (Groeneveld 1994). Genetic variances and genetic covariance were estimated using PEST and VCE. Estimated breeding values, variances and covariances, h^2, and genetic correlations (r_a) were calculated in VCE. Genetic variance parameters were estimated for BW, K, and precocious maturation by means of a bivariate animal model of the form:

$$\mathbf{y}_i = (\mathbf{X}_i\mathbf{b}_i) + (\mathbf{Z}_i\mathbf{a}_i) + \mathbf{e}_i,$$

where $\mathbf{y}$ is the vector of phenotypic observations on trait i (BW or K), $\mathbf{X}$ is the incidence matrix for trait i, $\mathbf{b}$ is the vector of fixed effects (rearing tank), $\mathbf{Z}$ is the incidence matrix of random (fish) effects for trait i, $\mathbf{a}$ is the vector of random fish effects (breeding values) for trait i, and $\mathbf{e}$ is the vector of random error for trait i.

Relationships among fish were limited to the parent–progeny relationship between the F_2 and F_3 generations since pedigree records beyond this immediate point were not available. Heritability estimates and SE values for maturation in the control and selected populations were estimated on the observed binary scale and then transformed to the liability scale by using the transformation of Roff (1997):

$$h^2 = h^2(0, 1)p(1 - p)/z^2,$$

where $h^2(0,1)$ is heritability on the binary scale in each population, h^2 is heritability on the underlying liability scale, p is the proportion of mature individuals, and z is the point on the normal curve corresponding to p. The variable z is calculated as

$$z = \exp(-0.5x^2)/\sqrt{2\pi},$$

where

$$x = [\text{sign}(0.5 - p)][1.238c(1 + 0.0262c)]$$

and

$$c = \sqrt{-\log_e[4_p(1 - p)]}$$

Heritability values for the complete set of traits (BW, K, and precocious maturity) were compared by using a t-test (Satterthwaite's approximation for unequal variances in the Statistical Analysis System; SAS 1998) to determine general trends in genetic variance between selected and control lines.

Analyses of variance were used to compare the phenotypic values of lines and families within lines (selected or control) for traits in the F_2 and F_3 generations (Sokal and Rohlf 1995). Tukey's test was used to compare post hoc differences among means when variances were homogeneous, and the Games–Howell test was used when variances were heterogeneous ($P < 0.05$; see Sokal and Rohlf 1995).

RESULTS

Realized Gain in Control and Selected Lines

Mean weight increased through the generations for both the control and selected groups. The entire F_1 cohort was considered to be a control since no selection had been imposed prior to this point. In the control line, weight increased by 36 g from the F_1 to the F_2 generation (34.7%) but only by 6 g from the F_2 to the F_3 generation (4.0%); thus, the total increase in weight was 42 g (41%; Table 1). The phenotypic variance in the F_2 generation was significantly greater for the control line than for the selected line (Figure 2). No difference in weight for the F_3 generation was observed between the selected and control groups in the first months. As fish reached 15 months of age, however, the selected fish were significantly heavier than the control fish (Table 2). Significant family effects were present in both the selected and control groups in September, January, and April ($P < 0.001$). As in the F_2 generation, phenotypic variability among families in the F_3 generation was higher in the control group (Figure 3), which contained both heavier and lighter families, than in the selected group. The average weights in the different families at 15 months of age (April 2003) demonstrated a pattern similar to that observed for fish at 8 months of age (September 2002). Tank effects were negligible for all traits.

In the control line, there were no apparent changes in early sexual maturity after two generations. However, selection led to a decrease in the proportion of early sexual maturity at 22 months over generations; the proportion of fish that were immature at

TABLE 1. Mean weight (SD in parentheses) and number of brook trout per generation and number of fish selected (at 22 months of age) to contribute to the next generation for control and selected groups ($P = 0.02^*$; $P < 0.001^{**}$; *P*- values indicate ANOVA comparisons between control and selected lines; *n* randomly selected = the number of individuals selected for production of the succeeding generation; *n* selected as immature fish = the number of immature individuals selected for production).

Generation	Weight (g)	Total *n*	Immatures *n*	Immatures (%)	♂ *n*	♀ *n*	*n* randomly selected in population	*n* selected as immature fish
				Control line				
F_1	103.8 (45.9)	2,106	679	32.2	786	641	120	201
F_2	139.8 (68.5)	491	199	40.5	169	123	90	
F_3	145.8 (54.4)	546	150	27.5	221	175		
				Selected line				
F_2	127.8 (54.9)*	524	283**	54.0	106	135		75
F_3	168.9 (55.2)**	632	388**	61.4	123	121		

22 months was 32.2% in the F_1 generation, while in the F_3 generation 27.5% of the control group and 61.4% of the selected group were immature at 22 months. Weight comparisons at the time of selection (22 months, November) showed an increase of 24 g from the F_1 to the F_2 generation (23.1%) and 41 g (32.1%) from the F_2 to the F_3 generation. Thus, the total weight increase in the selected line was 65 g (62.7%) from the F_1 to the F_3 generation (Table 1).

Additive Genetic Variance and Heritability among Selected and Control Lines after Two Generations of Selection

Realized h^2 (F_2 to F_3) for BW at 22 months (November) was estimated as 0.83 for the F_3 generation of the selected group, and h^2 for the control line (0.86) compared favorably with the realized h^2 for the selected line. Realized h^2 for percentage of immature fish was estimated as 0.16 for the F_3 generation of the selected group. Heritability estimates calculated using REML for the F_3 generation were generally high ($h^2 > 0.40$; Table 3). Genetic variance for weight and *K* was higher in the control group than in the selected line (Table 3). Genetic correlation between weight and *K* was high and positive ($r_a > 0.80$) except in April, when r_a was significantly lower in the F_3 selected line than in the F_3 control group (as indicated by nonoverlap of r_a estimates, including SE).

The analysis of genetic variance–covariance of precocious maturation and weight at 22 months in the F_3 population indicated high h^2 (>0.30) for both characters in both the selected and control lines. However, the h^2 of weight appeared to be considerably higher in the control group than in the selected line (Table 3). In contrast, h^2 estimates for precocious maturation, while nearly overlapping, were actually higher in the selected line than in the control line (selected: $h^2 \approx 0.80$; control: $h^2 \approx 0.50$). All h^2 estimates may be partially biased upwards due to dominant genetic variance (Falconer and Mackay 1996). Estimates of r_a between precocious maturation and weight were also highly divergent; r_a was highly negative in the controls (−0.94), indicating that precociously mature fish had poor genetic value for growth, but r_a (mean ± SE) was marginally positive in the selected line (0.05 ± 0.03; Table 3). Heritability values for the complete set of traits (BW, *K*, and precocious maturity) were marginally lower in the selected line than in the control line ($t = 2.01$, $P = 0.0638$).

We also compared the observed values of gains in growth and the predicted efficacy of the selection scheme given the intensity of selection and the above estimates of h^2 variance using

TABLE 2. Mean (SD in parentheses) weight and condition factor (*K*), for the F_3 generation in selected and control groups of brook trout over the sampling year. Probabilities (*P*) for ANOVA comparisons between control and selected lines are indicated.

Group	Date	Weight (g)	*P*	*K*	*P*
Selected	Sep 2002	11.1 (3.1)	0.576	1.058 (0.090)	0.334
Control		11.3 (4.6)		1.051 (0.073)	
Selected	Jan 2003	30.4 (13.7)	0.187	0.926 (0.071)	0.006
Control		29.0 (15.4)		0.950 (0.101)	
Selected	Apr 2003	33.7 (15.0)	0.005	0.935 (0.404)	0.920
Control		32.2 (16.5)		0.937 (0.084)	
Selected	Nov 2003	168.9 (55.2)	0.000	1.081 (0.096)	0.024
Control		146.8 (54.4)		1.093 (0.091)	

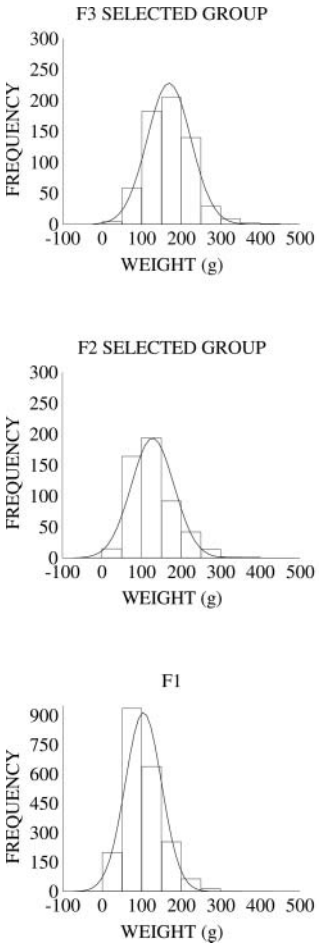

FIGURE 2. Distribution of weights at 22 months of age for brook trout in the F_1, F_2, and F_3 generations.

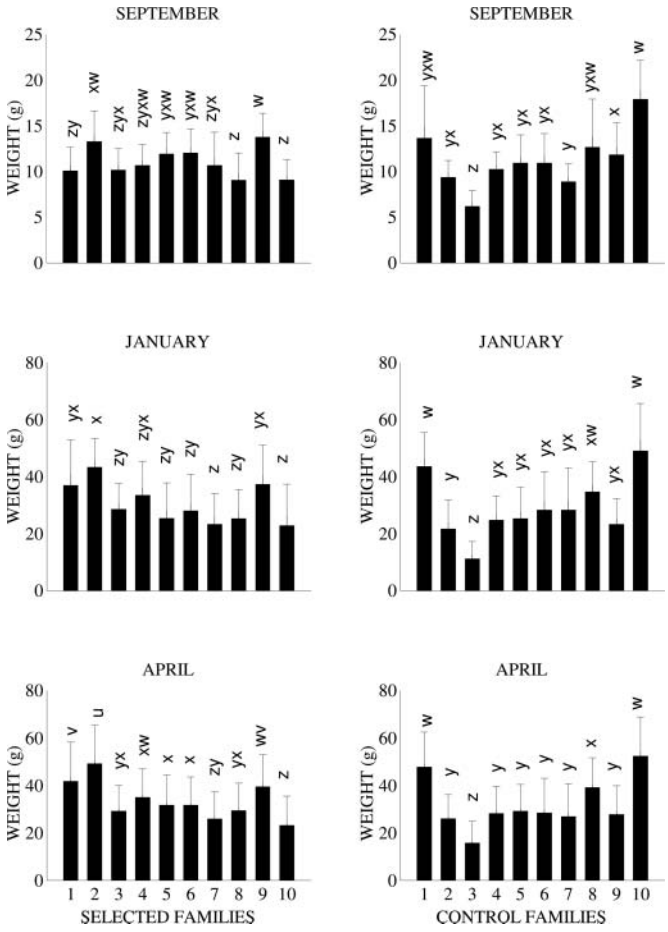

FIGURE 3. Mean (±SD) weight (g) at 8 months (September 2002), 12 months (January 2003), and 15 months of age (April 2003) for brook trout in F_3 control families (right panels) and families subjected to selection (left panels). The phenotypic SD per family is shown. Different letters (z–u) indicate significant differences ($P < 0.05$) among families.

the derived breeder's equation ($R_p = ih^2\sigma_p$, where R_p = phenotypic response, i = intensity of selection, and σ_p = phenotypic SD; Falconer and Mackay 1996). For weight at an approximate selection intensity of 10%, R_p was 50.6 g (1.282 × 0.86 × 45.9) in the F_2 generation and 59.5 g (1.282 × 0.86 × 54) in the F_3 generation, translating to realized improvements of approximately 47.4% and 69.0% of R_p. These calculated values are higher than the observed increases of 24 g (23.1%) from the F_1 to the F_2 generation and 41 g (32.1%) from the F_2 to the F_3 generation. Thus, while we obtained a very good response to

TABLE 3. Mean (SE in parentheses) heritability estimates (h^2) and genetic correlations (r_a; correlation between the given character and weight) for weight, condition factor (K), and precocious maturation for the F_3 generation in selected and control brook trout of different ages (months). Restricted maximum likelihood was used to calculate h^2.

			Selected families		Control families	
Character	Date	Age (months)	h^2	r_a	h^2	r_a
Weight	Sep 2002	8	0.494 (0.179)		0.679 (0.175)	
K			0.490 (0.178)	0.858 (0.128)	0.827 (0.168)	0.921 (0.064)
Weight	Jan 2003	12	0.589 (0.190)		0.830 (0.242)	
K			0.433 (0.167)	0.980 (0.055)	0.610 (0.209)	0.985 (0.035)
Weight	Apr 2003	15	0.660 (0.192)		0.651 (0.185)	
K			0.671 (0.200)	0.689 (0.170)	0.582 (0.180)	0.964 (0.027)
Weight	Nov 2003	22	0.497 (0.019)		0.860 (0.093)	
Precocious maturation			0.482 (0.018)	0.054 (0.029)	0.306 (0.160)	−0.940 (0.140)

selection, its full potential was apparently not achieved based on those predictions. We calculated the expected gain in reducing maturation (i.e., increasing the percentage of immature fish), also by using the derived breeder's equation, since linear methodologies appear to generally confer equivalent power in analysis. By treating p as 0.01 ($i = 3.960$) in standard truncation tables to approximate the intended intensity of complete selection ($s = 1.0$) against precociously mature individuals and by using σ_2^p and h^2 from the REML analysis in the control line (see above), we estimated a predicted R_p of 0.55 ($3.96 \times 0.306 \times 0.455$). Realized gain ($G_R = p_{F1} - p_{F2}$) using the simple linear interpretation (see Lopes et al. 2000) was calculated as 0.22 between the F_1 and the F_2 generation and 0.074 between the F_2 and the F_3 generation; these values translate to a G_R of 40% and 13%, respectively, in the reduction of precocious maturation, for a total G_R of 53%. Both predicted and realized responses to selection for precocious maturation were very similar.

DISCUSSION

Selection Effects at Younger Ages (F_3 Families)

There was little difference in weight between selected and control fish until 15 months posthatch, and there was no pattern before 7 months. Although the best-performing families could be detected as early as 8 months posthatch, Silverstein and Hershberger (1994) found that egg size still had a significant effect on fish size after 10 months of age in coho salmon *Oncorhynchus kisutch*. Early identification of superior families would be very useful for reducing production costs, minimizing time to market, and improving homogeneity (Vandeputte et al. 2002; see Winkelman and Peterson 1994).

Gain per Generation

The gain in weight and the reduction in precocious maturation were different for the selected and control groups. Mean weight increased in the selected line by 23.1% after one generation (F_1 to F_2) and by 32.1% after the second generation (F_2 to F_3). In comparison, Charo-Karisa et al. (2006) observed that selection in Nile tilapia *Oreochromis niloticus* produced a growth response of 34.7% from the F_0 to the F_1 generation and 14.9% from the F_1 to the F_2 generation. In coho salmon, a 60% increase in weight was observed after four generations of family selection (Hershberger et al. 1990). Friars et al. (1995) observed cumulative gains in the market size of Atlantic salmon after they used mass and index selection over two generations in a high-grilse stock. Most of the genetically controlled gain in weight from the F_1 to the F_2 generation in the present study may have resulted from incidental domestication selection or adaptation since a large increase in weight from the F_1 to the F_2 generation (34.7%) occurred in the control line, whereas almost no increase was observed from the F_2 to the F_3 generation (4.0%). The large difference in weight from F_1 to F_2 in both groups might partially be due to improvements in feeding protocol. The wild strain used to initiate this experiment had a different feeding behavior that prompted us to adjust the first-feeding protocol and to switch from floating to sinking pellets for older fish. The tank effect was evaluated at three different periods after families had been mixed and was found to be negligible. However, it was not tested during the first feeding period, when families were raised in individual trays. Thus, the possibility that some tank effect in early life could have influenced the growth trajectory in some families cannot be excluded. Nevertheless, care was taken to randomly assign trays among families at spawning so that each of the three incubation tanks contained both control and selected families.

Phenotypic variance for weight was generally lower in the selected line than in the control line: SD steadily decreased from the F_1 to the F_3 generation. Glover et al. (2001) suggested that selection via mortality during first feeding might play a role in an inadvertent domestication selection scheme. Moreover, Hershberger et al. (1990) also observed a significant domestication effect that continued for four generations in coho salmon. The response to the selection for age at first sexual maturation was also clearly present by the F_3 generation in our study. The proportion of fish that were immature at 22 months increased from 32.2% in the F_1 generation to 61.4% in the F_3 generation, demonstrating the accuracy of the combined selection scheme for this trait. There was no concomitant increase in the proportion of immature fish occurring in the control line, suggesting that selection for this trait was effective.

Heritability

Estimates of the h^2 of morphological traits tend to be high (>0.30) in salmonids (Winkelman and Peterson 1994; Gjedrem 2000; Kause et al. 2003; Martyniuk et al. 2003; Perry et al. 2005b; Thériault et al. 2007; Carlson and Seamons 2008). Our estimates for the control and selection lines were also very high ($h^2 = 0.40$–0.85), possibly representing the partial effects of dominance, residual maternal variance, or both in the full-sibling families (Lynch and Walsh 1998). However, the lack of clear trends in variance and covariance parameters among traits during ontogeny suggests that any dominance or maternal overestimation effects were unbiased with respect to line. Notably, h^2 estimates for weight in the selected and control lines differed more in September and January but less in April (at 15 months of age), perhaps suggesting a decrease in the maternal effect during the first year of growth. Overall, h^2 values for the complete set of traits (BW, K, and precocious maturity) were marginally lower in the selected line than in the control line. However, our high h^2 estimates might also have been partially affected by overestimation related to (1) the small number of full-sibling families used or (2) unknown relationships between parents higher in the pedigree. While we cannot exclude that different results in terms of exact values could have been obtained with a higher number of founding families, we consider it very unlikely that the relatively small sample sizes in our study would be the main factor causing the significant differences between strains. On the contrary, small sample sizes will increase

the variance around the estimates and result in a reduced power to detect real differences.

Two generations of selection appear to be sufficient to produce significant differences in the proportion of fish showing early sexual maturation. Our estimates of h^2 for precocious maturation were roughly in the range of values reported for other species of salmonids ($h^2 = 0.21$–0.39 for rainbow trout: Gjerde and Gjedrem 1984; 0.19–0.45 for Arctic char *Salvelinus alpinus*: Nilsson 1992), but notably the estimates of genetic variance for precocious maturation appeared to be actually lower in the control line than in the selected group, although the SE associated with the estimate of h^2 for precocious maturation in the F_3 control group was unusually high compared with other estimates. Genetic variance for this trait in the two groups may be closer than is immediately apparent. There are several explanations for these findings. Firstly, selection may have culled out specific dominant genotypes (leaving others intact) rather than having increased additive genetic variance; our full-sibling variance estimates were not capable of discriminating between dominant and additive genetic variance. Secondly, phenotypic differentiation between the lines may have been caused by the apparent deterioration of genetic associations between weight and precocious sexual maturation resulting from, or coupled with, selection for weight (Lynch and Walsh 1998).

Interaction between Traits

The high detected r_a between weight and K in our study showed that the gene expressions of these characteristics are strongly associated, which has also been found elsewhere (Su et al. 2002; Martyniuk et al. 2003; but see Neira et al. 2004).

Coupled selection for high growth and late sexual maturation is typically presumed to be incompatible because of negative genetic and phenotypic associations between the growth rate or size at age and the age at sexual maturity (Thorpe et al. 1983; Gjerde and Gjedrem 1984; Rye and Gjerde 1996; Quinton et al. 2002; Martyniuk et al. 2003). However, such relationships are not uniformly observed (Huang and Gall 1990; Crandell and Gall 1993), and we detected radical sign changes in r_a for the selection line compared with the control line. Part of this deviation might be related to the relatively small numbers of families; however, our genetic variance component estimates were fairly consistent by trait within groups. Inbreeding might cause such radical changes (Phillips et al. 2001), but we did not observe a significant reduction in genetic diversity in controls relative to wild fish, suggesting that the number of breeders used and the absence of crosses between siblings were sufficient to avoid significant inbreeding effects. Indeed, in wild brook trout from the Laval River, the average heterozygosity at microsatellite loci was 0.65, which translates to an inbreeding coefficient ($F = 1 - H_e$, where H_e = expected heterozygosity; Hartl and Clark 1997) of 0.35 (Martin et al. 1997). In the control F_2 captive population, an average heterozygosity of 0.61, which translates to an F-value of 0.39, was estimated at microsatellite loci (Boula et al. 2002). Finally, Perry et al. (2005a) quantified an average heterozygosity of 0.64 (an F-value of 0.36) in the control F_3 generation. On the other hand, the narrow demographic passes at the F_1–F_2 and F_2–F_3 junctures could have caused drift at functional loci instead of markers, thereby fixing alleles with antagonistic or neutral effects on weight and maturation. Thus, it is possible that the two lines could have diverged in allele frequencies at functional loci, affecting the traits under selection while maintaining similar genetic variance. Our estimates of r_a between BW and precocious maturation in the control group, presumably representative of their association in the absence of selection, were generally in line with negative r_a values between age at maturation and growth rate in other salmonid systems.

Our selective breeding program decreased the rate of precocious sexual maturity, improved growth, and resulted in genetic coupling between these traits relative to unselected controls, although the full potential of selection was apparently not reached based on observed and predicted responses. Despite this, genetic gain was substantial, being more than double what has been observed in other salmonids (Kincaid et al. 1977; Gjedrem 1979, 2000; Hershberger et al. 1990; Charo-Karisa et al. 2006; Neira et al. 2006). Indeed, responses from salmonid selection schemes average 15% (Gjedrem 2000), which is much less than we observed. Still, there are currently no comprehensive selection schemes for the commercial aquaculture of brook trout and there are few genetically improved lines of any salmonid species in use anywhere in the world today (1–2% globally) despite the potential for massive economic returns (Gjedrem 2000). The combined improvement in growth and precocious maturation—coupled with the apparently rapid attenuation of domestication effects—suggests greater amenability to commercial rearing in Laval River strain brook trout than in other salmonid populations, and our results indicate that there is ample opportunity for bidirectional or simultaneous genetic improvement in this strain.

ACKNOWLEDGMENTS

The authors are grateful to Nathalie Morin and France Béland for helpful technical assistance and valuable advice and to Benjamin Laplatte, Annie Chalifour, and Marc-Antoine Dion for technical assistance. This work was supported by research grants from the Quebec Nature and Technology Research Fund–Society of Research and Development in Continental Aquaculture; the Quebec Ministry of Agriculture, Fisheries, and Food; and the Quebec Aquaculture Network.

REFERENCES

Aksnes, A., B. Gjerde, and S. O. Roald. 1986. Biological, chemical and organoleptic changes during maturation of farmed Atlantic salmon, *Salmo salar*. Aquaculture 53:7–20.

Barton, B. A. 1996. General biology of salmonids. Pages 29–86 *in* W. Pennell and B. A. Barton, editors. Principles of salmonid culture. Developments in aquaculture and fisheries science, volume 29. Elsevier, New York.

Boula, D., V. Castric, L. Bernatchez, and C. Audet. 2002. Physiological, endocrine, and genetic basis of anadromy in the brook charr, *Salvelinus*

fontinalis, of the Laval River (Québec, Canada). Environmental Biology of Fishes 64:229–242.

Carlson, S. M., and T. R. Seamons. 2008. A review of quantitative genetic components of fitness in salmonids: implications for adaptation to future change. Evolutionary Applications 1:222–238.

Charo-Karisa, H., H. Komen, M. A. Rezk, R. W. Ponzoni, J A. M. van Arendonk, and H. Bovenhuis. 2006. Heritability estimates and response to selection for growth of Nile tilapia (*Oreochromis niloticus*) in low-input earthen ponds. Aquaculture 261:479–486.

Chevassus, B., E. Quillet, F. Krieg, M-.G. Hollebecq, M. Mambrini, A. Fauré, L. Labbé, J.-P. Hiseux, and M. Vandeputte. 2004. Enhanced individual selection for selecting fast growing fish: the "PROSPER" method, with application on brown trout (*Salmo trutta fario*). Genetics Selection Evolution (Versailles) 36:643–661.

Crandell, P. A., and G. A. E. Gall. 1993. The genetics of body weight and its effect on early maturity based on individually tagged rainbow trout (*Oncorhynchus mykiss*). Aquaculture 117:77–93.

Dubé, P., and J.-M. Blanc. 1992. Élevage des salmonidés, fascicule 2: americanélioration génétique. [Salmonid production, volume 2: genetic improvement.] Quebec Council of Fisheries and Aquaculture, Quebec. (In French.)

Falconer, D. S., and T. F. C. Mackay. 1996. Introduction to quantitative genetics, 4th edition. Pearson Education, Harlow, UK.

Fleming, I. A., T. Agustsson, B. Finstad, J. I. Johnsson, and B. T. Björnsson. 2002. Effect of domestication on growth physiology and endocrinology of Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 59:1323–1330.

Friars, G. W., J. K. Bailey, and F. M. O'Flynn. 1995. Application of selection for multiple traits in cage-reared Atlantic salmon (*Salmo salar*). Aquaculture 137:213–217.

Gjedrem, T. 1979. Selection for growth rate and domestication in Atlantic salmon. Zeitschrift fuer Tierzeuchtung und Züchtungsbiologie 96:56–59.

Gjedrem, T. 2000. Genetic improvement of cold-water fish species. Aquaculture Research 31:25–33.

Gjerde, B. 1986. Growth and reproduction in fish and shellfish. Aquaculture 57:37–55.

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

Glebe, B., P. Harmon, and C. Quinton. 2003. Early and ongoing studies on maturation of cage-reared Atlantic salmon in the Bay of Fundy. Bulletin of the Aquaculture Association of Canada 103(1):13–18.

Glover, K. A., J. B. Taggart, Ø. Skaala, and A. J. Teale. 2001. Comparative performance of juvenile sea trout families in high and low feeding environment. Journal of Fish Biology 59:105–115.

Groeneveld, E. 1994. A reparameterization to improve numerical optimization in multivariate REML (co)variance component estimation. Genetics Selection Evolution 26:537–545.

Groeneveld, E., M. Kovac, and T. Wang. 1990. PEST, a general purpose BLUP package for multivariate prediction and estimation. Pages 488–491 *in* Proceedings of the 4th world congress on genetic applied to livestock production. Garzi Press, Madrid.

Hartl, D. L., and A. G. Clark. 1997. Principles of population genetics, 3rd edition. Sinauer, Sunderland, Massachusetts.

Hendry, A. P. 2001. Adaptive divergence and the evolution of reproductive isolation in the wild: an empirical demonstration using introduced sockeye salmon. Genetica 112–113:515–534.

Hendry, A. P., J. K. Wenburg, P. Bentzen, E. C. Volk, and T. P. Quinn. 2000. Rapid evolution of reproductive isolation in the wild: evidence from introduced salmon. Science (Washington, D.C.) 290:516–518.

Hershberger, W. K., J. M. Myers, R. N. Iwamoto, W. C. McAuley, and A. M. Saxton. 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.

Huang, N., and G. A. E. Gall. 1990. Correlation of body weight and reproductive characteristics in rainbow trout. Aquaculture 86:191–200.

Kause, A., O. Ritola, T. Paananen, E. Mäntysaari, and U. Eskeline. 2003. Selection against early maturity in large rainbow trout *Oncorhynchus mykiss*: the quantitative genetics of sexual dimorphism and genotype-by-environment interactions. Aquaculture 228:53–68.

Kincaid, A. L., W. R. Bridges, and B. von Limbach. 1977. Three generations of selection for growth rate in fall-spawning rainbow trout. Transactions of the American Fisheries Society 106:621–628.

Lopes, U. V., D. A. Huber, and T. L. White. 2000. Comparison of methods for prediction of genetic gain from mass selection on binary threshold traits. Silvae Genetica 49:50–56.

Lynch, M., and B. Walsh. 1998. Genetics and analysis of quantitative traits. Sinauer, Sunderland, Massachusetts.

Martin, S., J.-Y. Savaria, C. Audet, and L. Bernatchez. 1997. Microsatellites reveal no evidence for inbreeding effects but low inter-stock genetic diversity among brook charr stocks used for production in Québec. Bulletin of the Aquaculture Association of Canada 97(2):21–23.

Martyniuk, C. J., G. M. L. Perry, H. K. Mogahadam, M. M. Ferguson, and R. G. Danzmann. 2003. The genetic architecture of correlations among growth-related traits and male age at maturation in rainbow trout (*Oncorhynchus mykiss*). Journal of Fish Biology 63:1–19.

Neira, R., N. F. Dìaz, G. A. E. Gall, J. A. Gallardo, J. P. Lhorente, and R. Manterola. 2006. Genetic improvement in coho salmon (*Oncorhynchus kisutch*) I: selection response and inbreeding depression on harvest weight. Aquaculture 257:9–17.

Neira, R., J. P. Lhorente, C. Araneda, N. Díaz, E. Bustos, and A. Alert. 2004. Studies on carcass quality traits in two populations of coho salmon (*Oncorhynchus kisutch*): phenotypic and genetic parameters. Aquaculture 241:117–131.

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

Perry, G. M. L., C. Audet, L. Bernatchez. 2005a. Maternal genetic effects on adaptive divergence between anadromous and resident brook charr during early life history. Journal of Evolutionary Biology 18:1348–1361.

Perry, G. M. L., C. M. Martyniuk, M. M. Ferguson, and R. G. Danzmann. 2005b. Genetic parameters for upper thermal tolerance and associated growth-related traits in rainbow trout (*Oncorhynchus mykiss*). Aquaculture 250:120–128.

Phillips, P. C., M. C. Whitlock, and F. Fowler. 2001. Inbreeding changes the shape of the genetic covariance matrix in *Drosophila melanogaster*. Genetics 158:1137–1145.

Quinn, T. P., M. T. Kinnison, and M. J. Unwin. 2001. Evolution of Chinook salmon (*Oncorhynchus tshawytscha*) in New Zealand: patterns, rate and process. Genetica 112–113:493–513.

Quinn, T. P., M. J. Unwin, and M. T. Kinnison. 2000. Evolution of temporal isolation in the wild: genetic divergence in timing of migration and breeding by introduced Chinook salmon populations. Evolution 54:1372–1385.

Quinton, C. D., S. M. Moghadasi, L. R. McKay, and I. McMillan. 2002. Genetic parameters of body weight, female spawning date, and age at sexual maturation in rainbow trout. *In* Proceedings of the 7th world congress on genetics applied to livestock production. INRA (Institut National de la Recherche Agronomique), Montpellier, France.

Roberge, C., S. Einum, H. Guderley, and L. Bernatchez. 2006. Rapid evolutionary changes of gene transcription profiles in farmed Atlantic salmon. Molecular Ecology 15:9–20.

Roff, D. A. 1997. Evolutionary quantitative genetics. Chapman and Hall, New York.

Ruzzante, D. E. 1994. Domestication effects on aggressive and schooling behavior in fish. Aquaculture 120:1–24.

Rye, M., and B. Gjerde. 1996. Phenotypic and genetic parameters of body composition traits and flesh colour in Atlantic salmon, *Salmo salar* L. Aquaculture Research 27:121–133.

Rye, M., and T. Refstie. 1995. Phenotypic and genetic parameters of body size traits in Atlantic salmon *Salmo salar* L. Aquaculture Research 26:875–885.

SAS (Statistical Analysis System Institute). 1998. SAS version 8.1. SAS Institute, Cary, North Carolina.

Savaria, J.-Y. 1998. Amorce d'un programme de sélection génétique chez deux souches d'ombles de fontaine en fonction des critères de croissance et de l'âge à la maturation sexuelle. [Initiation of a breeding program based on improved growth and reduced precocious sexual maturation in two strains of brook trout.] Master's thesis. Université du Québec à Rimouski, Quebec. (In French.)

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

Sokal, R. R., and F. J. Rohlf. 1995. Biometry, 3rd edition. Freeman, New York.

Su, G.-S., L. E. Liljedahl, and G. A. E. Gall. 2002. Genetic correlations between body weight at different ages and with reproductive traits in rainbow trout. Aquaculture 213:85–94.

Thériault, V., D. Garant, L. Bernatchez, and J. J. Dodson. 2007. Heritability of life history tactics and genetic correlation with body size in a natural population of brook charr (*Salvelinus fontinalis*). Journal of Evolutionary Biology 20:2266–2277.

Thorpe, J. E., R. I. G. Morgan, C. Talbot, and M. S. Miles. 1983. Inheritance of developmental rates in Atlantic salmon, *Salmo salar* L. Aquaculture 33:119–128.

Vandeputte, M., E. Quillet, and B. Chevassus. 2002. Early development and survival in brown trout (*Salmo trutta fario* L.): indirect effects of selection for growth rate and estimation of genetic parameters. Aquaculture 204: 435–445.

Winkelman, A. M., and R. G. Peterson. 1994. Genetic parameters (heritabilities, dominance rations and genetic correlations) for body weight and length of Chinook salmon after 9 and 22 months of saltwater rearing. Aquaculture 125:31–36.