ANALYSIS OF GROWTH CURVES IN RAINBOW TROUT USING RANDOM REGRESSION

L.R. McKay, L.R. Schaeffer and I. McMillan
CGIL, Animal and Poultry Science, University of Guelph, Guelph, Ontario, Canada N1G 2W1

INTRODUCTION

Heritability estimates for weight of rainbow trout (Oncorhynchus mykiss) vary, depending on age, strain, population structure and estimation method (Tave, 1993). Heritabilities may change systematically with age. Selection response may be maximized if selection is applied when heritability is highest.

When repeated measurements have been taken on the same individuals, growth curves over time can be calculated for individuals. Random regression methods have been used to estimate genetic parameters for milk lactation curves in dairy cattle (Jamrozik and Schaeffer, 1997). Similar methodology can be used to estimate genetic parameters for growth curves.

MATERIALS AND METHODS

Population structure. Three generations of rainbow trout were examined. The 1991 year class (91 YC) consisted of three diverse strains of naturally spring-spawned rainbow trout described by Quinton (2001). These strains were crossed to produce the 94 YC and the 96 YC, which in turn, produced the 98 YC and the 99 YC. Factorial mating systems were used to produce the 94 YC, 96 YC, 98 YC and 99 YC. Exact parentage was determined for three year classes using DNA fingerprinting (96 YC and 99 YC) or separate fry tanks (98 YC). A total of 64 dams and 65 sires were used to produce these three year classes.

Rearing conditions. All year classes were reared at the Alma Aquaculture Research Centre at a water temperature of 8.5 °C ± 1 °C, under a simulated natural photoperiod. Dissolved oxygen levels were monitored regularly and remained above 7 mg/l. Through the life cycle, tanks of fish were weighed every 2 to 6 weeks up to the beginning of the spawning season in the third year. Rations were changed every 1 to 2 weeks to reflect biomass of each tank. Fish were culled regularly to maintain similar densities across tanks and year classes within each phase of the life cycle.

Data collection. Fish in the second and third generations were tagged with Passive Integrated Transponder (PIT) tags between 291 and 501 days post-fertilization and weighed individually every 3 months until 909 to 1043 days. Each fish was weighed 6 to 10 times, unless it died prematurely. A total of 9324 records on 1253 pedigreed fish (96 YC, 98 YC and 99 YC) and 1322 records on 221 fish (94 YC) were included in the analysis.

Statistical analysis. The random regression model (RRM) was

\[ y_{ijklmn} = (YC \times SM \times AC)_{ijkl} + f_1(a_{ijk}, n, age) + f_2(p_{ijk}, n, age) + e_{ijklmn} \]
where \( y_{ijklm} \) is weight at a given age on fish \( l \), from year class (YC) \( i \), sexual maturity group (SM) \( j \) and age class (AC) \( k \); \( f_1(a_{ik}, n_1, \text{age}) \) is a random regression function of age for additive genetic values of individuals of order \( n_1 \) (i.e. the highest order polynomial was \( n_1 = 1 \)); \( f_2(p_{ik}, n_2, \text{age}) \) is a random regression function of age for animal permanent environmental effects of order \( n_2 \); and \( e_{ijklm} \) is a residual effect.

In this study, \( n_1 = n_2 = 4 \). There were 4 YC. Sexual maturity groups were 2M, 3M, 4M, 3F, 4F and U, with M for males, F for females and U for immature at 4 years or died immature, and 2, 3 and 4 being the year of age when they matured. Residual variances were assumed to differ according to age class (AC). There were 54 age classes of 14 days each. Standardized (between –1 and +1) ages, \( x \), were calculated from age in days as \( x = \frac{(\text{age}-291)}{753} \times 2 - 1 \).

The random regression function for additive genetic effects was then

\[
f_1(a_{ik}, n_1, \text{age}) = a_{i1} + a_{i2}x + a_{i3}x^2 + a_{i4}x^3.
\]

Hence for each fish, four coefficients were estimated. The variance-covariance matrix of the random regressions was \( G \) of order 4 for the additive genetic effects and \( P \) of order 4 for the permanent environmental effects. Additive genetic relationships were utilized tracing all fish back to 91 YC or to unknown parents. Eight phantom parent groups were formed for unknown parents (Quaas, 1988).

Bayesian estimation methods via Gibbs sampling were used to estimate \( G \) and \( P \) and the residual variances for the 54 age classes. Two chains of 20,000 samples each were run and 3000 samples discarded as the burn-in period. The estimates were the average of every 31\(^{st}\) sample after burn-in. The results for \( G \) and \( P \) are shown in Table 1 and can be used to generate variances for any age in the interval 291 to 1043 days. If \( x \) is the desired standardized age, then

\[
z = \begin{pmatrix} 1 \\ x \\ x^2 \\ x^3 \end{pmatrix}, \quad \text{and the genetic variance for that age would be } z'Gz.
\]

### Table 1. Estimates of (co)variance matrix of random regression coefficients for genetic (G) and permanent environmental (P) effects

<table>
<thead>
<tr>
<th>Element</th>
<th>G</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 1</td>
<td>10827.461</td>
<td>40130.8</td>
</tr>
<tr>
<td>1 2</td>
<td>11160.787</td>
<td>70980.3</td>
</tr>
<tr>
<td>1 3</td>
<td>14.187</td>
<td>14950.5</td>
</tr>
<tr>
<td>1 4</td>
<td>-2.155</td>
<td>-18228.9</td>
</tr>
<tr>
<td>2 2</td>
<td>11507.434</td>
<td>142565.4</td>
</tr>
<tr>
<td>2 3</td>
<td>14.628</td>
<td>55995.8</td>
</tr>
<tr>
<td>2 4</td>
<td>-2.223</td>
<td>-19425.2</td>
</tr>
<tr>
<td>3 3</td>
<td>0.018</td>
<td>67576.4</td>
</tr>
<tr>
<td>3 4</td>
<td>-0.003</td>
<td>26311.2</td>
</tr>
<tr>
<td>4 4</td>
<td>0.0046</td>
<td>28979.1</td>
</tr>
</tbody>
</table>
The estimated \( G \) and \( P \) were used to construct and solve mixed model equations for estimates of \((YC \times SM \times AC)\) subclasses (growth curves) and estimated breeding values for all fish.

Comparisons were made between pairs of YC x SM growth curves and tested for significant differences at each age class containing observations for both categories.

**RESULTS AND DISCUSSION**

**Genetic parameters.** Variances were expected to increase with overall size, and therefore, with age of the fish. Both genetic variance (GV) and permanent environmental variance (PEV) increased steadily throughout the age range, but PEV increased at a faster rate than GV after 430 days post-fertilization, indicated by the random regression coefficients for \( G \) and \( P \) (Table 1). Residual variances (RV) were quite low until 700 days, after which they increased.

Combining GV, PEV and RV for each age, computed heritabilities peaked at 0.49 around 390 to 430 days post-fertilization (Figure 1). Afterwards, heritability declined to less than 0.1 after 950 days, due to the proportionately larger increases in PEV and RV relative to GV. PEV began to increase more rapidly than GV shortly after the 2M males began maturing. As individuals began to mature, growth rates appeared to reflect maturation status more than genetic potential for growth.

![Figure 1. Heritability as a function of age](image)

**Growth of sex-maturation categories.** Figure 2 shows the growth curves for 2M, 3M and 3F groups for the 96 YC. These curves are representative of other year classes. Early maturing males (i.e. 2M) grew rapidly before 2 years. Around 2 years, mature males stopped growing. After the spawning season, at least some of the early maturing males began to grow again. Males and females maturing at 3 years (3M and 3F) grew steadily until after well past 2 years.

F-tests of individuals at single time periods confirmed that growth patterns were different for different SM categories. For the 96 YC, 2M males were significantly (p<0.05) heavier than later maturing fish from 330 to about 700 days. 3M and 3F fish were significantly (p<0.5) heavier than 2M males from 760 to 950 days.
In this study, early maturing males exhibited improved growth compared with non-maturing cohorts up to the age of sexual maturation, suggesting that the maturation process is associated with accelerated growth. Crandall and Gall (1993) reported similar findings.

CONCLUSION
The random regression model proved useful in evaluating individual growth data for a rainbow trout population. This technique allowed characterization of age trends for heritability and comparison of growth curves for different SM categories. Further refinement could include fitting logistic functions to the SM growth curves (Su et al., 1994).

In this population, selection for improved growth would be most efficient just after 1 year of age, since heritability for growth is highest at this point. Such selection could lead to increased rates of early male maturation, since early maturing males were heaviest at this age. A selection strategy based on weight around 1 year, but with consideration of age at sexual maturation would be necessary to avoid problems of early maturation.

If production fish are marketed prior to sexual maturation, populations of males, particularly early maturing males would be expected to out-perform mixed or all-female populations.

REFERENCES