

Predicting the efficiency of multi-stage selection in the breeding of rainbow trout

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A method is presented for predicting the genetic superiority of rainbow trout (*Salmo gairdneri*) selected by multi-stage selection for body mass at ten months of age. Trout selections are currently based on successive gradings for body width at 2, 4 and 6 months of age, followed by successive weighings for body mass at 8 and 10 months. Such multi-stage selection distorts the initial multivariate distribution, making it difficult to describe the consequences of selection in the later stages. The selection practiced is, however, intermediate to two extreme forms of selection. Basing approximate calculations on values of input parameters intermediate to those of the extreme methods of selection is proposed.

'n Metode word voorgelê vir die voorspelling van die genetiese meerderwaardigheid van reënboogforelle (*Salmo gairdneri*) wat aan multi-stadiumseleksie vir liggaamsmassa op 10-maande-ouderdom onderwerp is. Forelseleksies geskied tans op grond van opeenvolgende graderings van liggaamsbreedte op 2-, 4- en 6-maande-ouderdom en opeenvolgende wegings van liggaamsmassa op 8 en 10 maande. Sulke multi-stadiumseleksie vervorm die oorspronklike veelveranderlike verdeling en bemoeilik dus beskrywing van die gevolge van seleksie in die latere stadia. Die seleksie wat beoefen word is egter deur twee uiterste vorms van seleksie begrens. Benaderde berekeninge in terme van waardes van insetparameters tussen die waardes van die uiterstes word voorgestel.

Keywords: Correlated responses, point of truncation, selection intensity.

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Introduction

Multi-stage selection for quantitative traits within a given generation in the breeding of rainbow trout (*Salmo gairdneri*) is facilitated by the need to periodically reduce the stocking densities of ponds. The selection procedure consists of three successive gradings for body width (G_2 , G_4 and G_6) and two successive weighings for body mass (M_8 and M_{10}). The subscripts indicate the age of the fish in months. At each stage the selection objective (M_{10}) is the same, but different information is used and a different intensity of selection is applied. The purpose of this paper is to suggest an approximate method for predicting the genetic superiority of multi-stage-selected rainbow trout.

Material and Methods

A system of 40 'Port-A-Pool' ponds, 3.0 m in diameter and 1.2 m in height, with adjustable settings for depths and flow rates was used for this study at the Aquaculture Research Unit of the University of Stellenbosch.

Fish were hatched as full-sib families in July and about 2500 fish per family, at an average individual mass of 2 g, were placed in a pond. Thirty such full-sib families were placed in separate ponds. The fish were graded on a within-family basis in hand-held box graders at two-monthly intervals. Starting at two months of age, when the average individual mass was about 12 g (G_2), 600/2500 were selected. At an average mass of 50 g (G_4), 300/600 were selected, and at an average mass of 150 g (G_6), 200/300 were selected. The criterion of selection in grading was the maximal body width of each individual and was chosen in preference to body mass because individual weighing and identification at these early stages is impractical due to the high numbers involved.

At 8 months of age, the fish were anaesthetized with benzocaine and were weighed individually. They then weighed

approximately 300 g (M_8) and 100/200 were selected for body mass on a within-family basis. Finally, they were weighed individually at 10 months of age (M_{10}) when they weighed about 700 g. At this stage 10/100, five males and five females, were selected. The best 10/30 families were then selected on family mean body mass.

It is of interest to predict the rate of genetic improvement in body mass at 10 months of age as a result of this procedure. Selection for one variate will reduce the genetic and phenotypic variances of subsequently measured variates and will also affect the covariances between them. These adjustments must be taken into account when predicting genetic superiority.

Cochran's (1951) formula (10) for the variance in Y after selection for X can be expressed as

$$V(y) = \sigma_y^2 [1 - \rho_{xy}^2 i(i-t)],$$

where ρ_{xy}^2 = the phenotypic correlation between X and Y ,
 t = the point of truncation in standard deviation units, and
 i = the mean of individuals with values exceeding the point of truncation, in standard deviation units.

The notation $s = i(i-t)$ is used below.

Cunningham (1975) has shown that if there are any three normally distributed variates whose mutual covariances are known, and if truncation selection is applied to one of them, the covariances adjusted for the effects of selection can be obtained from a generalization of Cochran's (1951) formula (10) as follows: Let the variates be z_i , z_j and z_k and their covariances be σ_{ij} , σ_{ik} and σ_{jk} . A general expression for a covariance after truncation selection for z_i is:

$$\sigma_{jk}^* = \sigma_{jk} - \sigma_{ij} \sigma_{ik} s / \sigma_i^2 = \sigma_j \sigma_k (\rho_{jk} - \rho_{ij} \rho_{ik} s).$$

Cunningham (1975) has also shown how this formula can be used to adjust a whole matrix of covariances for selection on any one variate. This procedure is followed here.

It is assumed that the multivariate distribution at the start is normal, but it is appreciated that selection based on successive gradings and weighings distorts this normality. The degree of distortion will depend on the intensities of selection and on the correlations between the successive variates.

The basic requirement of quantitative theory regarding truncation selection from a normal distribution will, therefore, not be met and this makes it difficult, at successive screenings, to define the intensity of selection (i) and the truncation point (t), and hence to calculate the consequences of selection by the well-known formulae.

The problems of distortion of the normality of distribution and of determining the appropriate intensities of selection seemed insurmountable until we considered the possibility of setting empirical limits to the selection which could be applied.

At one extreme, consider the multi-stage selection as though it was selection for different traits in different populations. Because selection for one trait will have no effect on the other traits, either in the intensities of selection or in the normality of the distributions, the following array of proportions selected, viz. 600/2500, 300/600, 200/300, 100/200 and 10/100, will yield appropriate values of i , t , and s . These are given in Table 1.

Table 1 Intensities of selection, points of truncation, and s values, as though selection was for different traits in different populations

Proportion selected	i	t	s
600/2500	1.295	0.706	0.763
300/600	0.798	0.000	0.637
200/300	0.545	-0.431	0.532
100/200	0.798	0.000	0.637
10/100	1.755	1.282	0.831

At the other extreme, consider selection for the same trait in the same population, first the proportion 600/2500, then (as though there were no previous selection) 300/2500 (the 'best' 300 of the remaining 600 being in fact the same individuals as in the original 2500), followed by 200/2500, 100/2500 and finally 10/2500. The values in Table 2 are the truncation points (t'), the intensities (i'), and the s' values determined in the usual way.

Table 2 Intensities of selection and points of truncation, and s values, as though selection was successive selection for the same trait

Proportion selected	i'	t'	s'
600/2500	1.295	0.706	0.763
300/2500	1.667	1.175	0.820
200/2500	1.858	1.405	0.842
100/2500	2.154	1.751	0.870
10/2500	2.962	2.652	0.917

The values needed for the calculation of the efficiency of the multi-stage selection must be somewhere between the values for the extremes calculated above. For any variate used in selection, the calculation could be completed if a point of truncation, t'' , and a selection intensity, i'' (two values of the standardized variate), were known. We simply used $t'' = \frac{1}{2}(t + t')$ and $i'' = \frac{1}{2}(i + i')$ — and hence $s'' = i''(i'' - t'')$ — in our calculations.

In the absence of appropriate data for parameter estimation, values for the between-family and within-family components of variance and within-family estimates of heritability were reconstructed using known means together with realistic coefficients of variation and intraclass correlation coefficients. Naturally, these values should be used with care but we felt justified in using them to a limited extent in planning. The estimates for the five criteria of selection are given in Table 3.

Table 3 Generated data for the five criteria of measurement in rainbow trout, viz. body width at three ages and body mass at two ages. The subscripts indicate the age of fish in months

Criterion of measurement	Mean	Phenotypic variance		Within-family h^2
		Between-family	Within-family	
G_2	5 mm	0.025	0.975	0.026
G_4	10 mm	0.160	3.840	0.042
G_6	15 mm	0.450	8.550	0.053
M_8	300 g	303.750	1721.250	0.176
M_{10}	700 g	2205.000	8820.000	0.250

Following Cunningham (1975), a simplified supermatrix M (see Table 4), can be constructed using the data in Table 3, together with estimates of the required phenotypic and genetic correlations between the criteria of measurement. In our case the supermatrix is simplified in that the C matrix is a scalar. This is the within-family genetic variance, and is coincidentally equal to the between-family phenotypic variance for M_{10} . It is, in fact, the product of the within-family phenotypic variance for M_{10} and its within-family heritability. This implies also that Cunningham's G matrix is reduced to a vector here.

Table 4 Supermatrix M at start, based on within-family estimates of variance and covariance

0.9750	0.9673	0.8658	4.0949	4.6347	0.0746
0.9673	3.8400	2.8655	16.263	18.407	0.3774
0.8658	2.8655	8.5500	36.393	54.922	0.9474
4.0949	16.263	36.393	1721.2	1948.2	245.47
14.6347	18.407	54.922	1948.2	8820.0	2205.0
0.0746	0.3774	0.9474	245.47	2205.0	2205.0

The analysis proceeds in a stepwise manner starting with the first grading (G_2). We want to predict the effect of selection for G_2 on M_{10} and determine the consequent adjustment of the variances and covariances of the supermatrix, M .

Here, $b = \text{Cov}(G_2, T_{M_{10}}) / \sigma_{G_2}^2$
 (where T = the true breeding value of an individual)
 $= (h_{G_2} r_{E_{2,10}} h_{M_{10}} \sigma_{G_2} \sigma_{M_{10}}) / \sigma_{G_2}^2$

so, $\sigma_I^2 = b^2 \sigma_{G_2}^2$
 $= (h_{G_2} r_{E_{2,10}} h_{M_{10}} \sigma_{M_{10}})^2$

and $R = i \sigma_I$
 $= i h_{G_2} r_{E_{2,10}} h_{M_{10}} \sigma_{M_{10}}$
 $= \text{expected genetic superiority in } M_{10} \text{ as a result of truncation selection for } G_2.$

Now, $\text{Var}(T) = C$ in the supermatrix, and the accuracy of selection, $r_{TI} = \sigma_I / \sigma_T$.

Again, following Cunningham (1975), the variances and covariances of the whole supermatrix, M , can be adjusted for the effects of selection on G_2 as follows: Let the ratio of the selection parameter, s , to the variance of the prior index, σ_I^2 , be $w = s / \sigma_I^2 = s / b^2 \sigma_{G_2}^2$.

Now define a vector, x' = the first row of M scalar-multiplied by b , so that the necessary adjustments can be made as follows:

$$M^* = M - xx'w.$$

The first row and the first column of the adjusted supermatrix, M^* , are now discarded and the effects of selection for G_4 can be analysed by repeating the cycle described above.

A listing of a computer program performing these calculations (written in Pascal) is available from the authors.

Results and Discussion

Any results or discussion we might offer would be suspect in so far that these would necessarily be based on the hypothetical values used for the input parameters. However, a purpose of this paper is to show that the consequences of selection of the two extreme forms of selection (shown in Tables 5 and 7) are not drastically different. This encouraged us to use values

Table 5 The effects of multi-stage selection in rainbow trout on the within-full-sib-family phenotypic and genetic variances, the accuracy of selection and the expected genetic superiority at 10 months of age of those selected. Calculations as for different traits in different populations

Measure- ment	i	Phenotypic variance	Genetic variance	Accuracy r_{TI}	$R_{M_{10}}$
	—	8820	2205	—	—
G_2	1.295	8803	2205	0.002	0.1 g
G_4	0.798	8758	2205	0.004	0.1 g
G_6	0.548	8603	2205	0.006	0.2 g
M_8	0.798	7327	2182	0.129	4.8 g
M_{10}	1.755	1238	1715	0.507	41.6 g

Table 6 The effects of multi-stage selection in rainbow trout on the within-full-sib-family phenotypic and genetic variances, the accuracy of selection and the expected genetic superiority at 10 months of age of those selected. Calculations based on intermediate selection parameters

Measure- ment	i''	Phenotypic variance	Genetic variance	Accuracy r_{TI}	$R_{M_{10}}$
	—	8820	2205	—	—
G_2	1.295	8803	2205	0.002	0.1 g
G_4	1.232	8746	2205	0.004	0.2 g
G_6	1.202	8506	2205	0.006	0.3 g
M_8	1.476	6806	2172	0.130	9.0 g
M_{10}	2.358	521	1649	0.511	56.1 g

Table 7 The effects of multi-stage selection in rainbow trout on the within-full-sib-family phenotypic and genetic variances, the accuracy of selection and the expected genetic superiority at 10 months of age of those selected. Calculations as for the same trait in repeated selections

Measure- ment	i'	Phenotypic variance	Genetic variance	Accuracy r_{TI}	$R_{M_{10}}$
	—	8820	2205	—	—
G_2	1.295	8803	2205	0.002	0.1 g
G_4	1.667	8745	2205	0.004	0.3 g
G_6	1.858	8510	2205	0.006	0.5 g
M_8	2.154	6840	2173	0.130	13.1 g
M_{10}	2.962	566	1654	0.510	70.5 g

for the input parameters intermediate to those of the extreme forms of selection in our planning; see Table 6.

As a sample of a conclusion reached on the basis of the approximate results in Table 6, note that the gains in selection due to the gradings G_2 , G_4 and G_6 are tiny compared to the gain to weighing at 8 months and (more especially) at 10 months. However, were the management requirements to be met by random reduction in the number of fish per pond at 2, 4 and 6 months, the expected genetic superiority of those selected would then be 41.3 g or about 75% of that of fish selected by the multi-stage method. Our conclusion was that the early grading should be retained in the selection program.

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