

STUDIES ON THE COURSE OF GROWTH IN RAINBOW TROUT

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SUMMARY

The logistic function $y=(A+Be^{\lambda x})/(1+Ce^{\lambda x})$, which earlier has proved to fit the course of growth in broiler chickens and young bulls very accurately, was also found to describe the course of growth in rainbow trout during the period from 168 days of age to spawning very closely. Thus, the ratio between the sum of squares of deviations from the regression curve, based on the body weight means, and the total sum of squares was less than 2×10^{-5} . All the parameter estimates A, B, C, λ were significantly different from zero in each of the two sexes and three strains, one control (C) and two selection strains (Y and E). Selection for body weight at 364 days of age in strain Y caused a change in the *growth pattern* of the fish without giving any positive response in body weight at 364 days and earlier ages. This situation occurred because the positively correlated selection effects on A, C and λ were counteracted by the negatively correlated selection effect on B.

INTRODUCTION

The procedure of fitting a mathematical function to observed body weight data has been used as a tool by several biologists to be able to investigate the course of growth in greater detail than what is possible by analyzing "raw" body weight data. In fish, Refstie and Kittelsen (1976) reported that growth of trout and salmon appears to follow a typical exponential growth curve, at least up to sexual maturity, and that environmental changes affect the rate of growth but not the general shape of the response. Gall and Gross (1978) showed that growth rate of rainbow trout was nearly exponential at young ages but changed to become nearly linear at older ages. Liljedahl (1970, 1975) developed a mathematical function of the logistic type $y = (A+Be^{\lambda x})/(1+Ce^{\lambda x})$, which proved to fit observed body weight means of broiler chickens but also individual body weight data of young bulls during their growth period very closely.

In the present study, observed body weight means in rainbow trout during its age period from 168 days to spawning were fitted to the above logistic function. By means of this procedure, the course of growth was investigated more deeply.

MATERIALS AND METHODS

The body weight data used in the present investigation were obtained during the first six generations of a selection experiment with rainbow trout, conducted at the University of California, Davis, and including the following strains.

Strain C = control line reproduced by random mating.

Strain E = strain selected for egg size.

Strain Y = strain selected for body weight at 364 days of age.

The fish were weighted at 168, 192, 224, 252, 280, 308, 336 and 364 days of age, and at spawning (about 730 days of age). Age was calculated by taking the dam's spawning date as the birth day of her offspring i.e. the day of fertilization. The body weights from 168 to 364 days of age were recorded without identification of sex of the fish. Spawning was the only stage of development at which sex was identified and separate records of body weight in males and females therefore could be taken.

The logistic function, $y=(A+Be^{\lambda x})/(1+Ce^{\lambda x})$, was fitted to the means of body weight at the different age stages from 168 days to spawning for each of three strains, where y = body weight (g), x = age in days and A, B, C, λ = the parameters of the function. The Secant method (DUD) of the NLIN procedure of SAS (SAS, 1985) was used to estimate the parameters of the growth function.

RESULTS

The observed body weight means during the growth period from 168 days of age to spawning in the three strains are shown in Table 1 together with the deviations of the means for the two selection strains from the mean of the control strain. Thus, both the direct and the correlated responses for body weight in the period 168-364 days of age were small and negative.

Table 1. Body weight means at different age stages in the different strains

Age	Strain C		Strain E		E-C	Strain Y		
	N	Mean	N	Mean		N	Mean	Y-C
168 days	930	3.95	1670	3.86	-0.09	2500	3.78	-0.17
196 days	930	9.05	1670	8.75	-0.30	2500	8.62	-0.43
224 days	930	17.36	1670	16.39	-0.97	2500	16.31	-1.05
252 days	930	31.31	1670	28.49	-2.82	2500	28.16	-3.15
280 days	930	50.60	1670	47.98	-2.62	2500	47.38	-3.22
308 days	930	74.92	1670	69.74	-5.18	2500	69.82	-5.10
336 days	930	105.20	1670	98.60	-6.60	2500	98.60	-6.60
364 days	2273	140.29	4517	132.64	-7.65	5868	136.24	-4.05
spawn (♂♂)	246	904.05	586	930.59	26.54	282	946.34	42.29
spawn (♀♀)	455	866.79	1114	829.47	-37.32	527	870.84	4.05

The goodness of fit of the function to the observed body weight means during the period from 168 days to spawning in each strain was extremely good. Thus, the ratio between the sum of squares of deviation from regression (SSD) and the total sum of squares (SST) in each strain was less than 2×10^{-5} .

The parameter estimates of the function and their asymptotic standard deviations are shown in Table 2. All parameters estimated from each set of body weight means were significantly

different from zero ($P < 0.01$) with B and C being highest for strain C, intermediate for strain E and lowest for strain Y. On the opposite, the parameter estimates for A and λ were highest for strain Y, intermediate for strain E and lowest for strain C. For each strain by sex combination, the asymptotic correlations between A and λ on one hand and B and C on the other hand were close to -1 while being close to 1 between A and λ and between B and C. From the function, it can be mathematically induced that parameters A, B and λ have a positive effect while C has a negative effect on body weight (y). Thus, in terms of the effect of increasing body weight, the asymptotic correlations between A, B and λ on one hand and C on the other hand were close to -1 while being close to 1 for any of the combinations between A, B and λ .

Growth rate in an infinitesimal age interval (dx) can be estimated from $dy/dx = (B-AC)\lambda e^{\lambda x}/(1+Ce^{\lambda x})^2$.

By putting $d^2y/dx^2=0$, the growth rate maximum and the inflexion body weight can be estimated. Thus, $(dy/dx)_{max} = \lambda(B/C - A)/4$, $y_{inflexion} = (B/C + A)/2$ when $x = -\ln C/\lambda$.

Further, the upper asymptote $y_{x=\infty} = B/C$ is an extrapolated estimate of the adult body weight. These derived growth characteristics are shown in Table 3. When females 500-506 days and males 511-520 days old they attained a growth rate maximum of 2.71-2.85 g/day and 2.81-3.08 g/day respectively. At this age, body weight was 436.9-460.1 g in females and 481.5-501.1 g in males.

Table 2. Parameter estimates and their asymptotic standard deviations

	Strain	A	B	C	λ
Female	C	-18.54±3.74**	3.068±0.701**	32.68 ⁻⁴ ±69.2 ^{-5**}	11.31 ⁻³ ±59.2 ^{-5**}
	E	-16.02±3.37**	2.594±0.591**	29.15 ⁻⁴ ±62.0 ^{-5**}	11.59 ⁻³ ±59.4 ^{-5**}
	Y	-14.00±2.57**	2.121±0.395**	23.00 ⁻⁴ ±40.1 ^{-5**}	12.15 ⁻³ ±48.9 ^{-5**}
Male	C	-18.80±3.81**	3.148±0.726**	32.07 ⁻⁴ ±68.2 ^{-5**}	11.23 ⁻³ ±59.8 ^{-5**}
	E	-16.67±3.55**	2.792±0.658**	27.40 ⁻⁴ ±59.0 ^{-5**}	11.34 ⁻³ ±61.3 ^{-5**}
	Y	-14.40±2.67**	2.232±0.426**	22.05 ⁻⁴ ±39.4 ^{-5**}	11.98 ⁻³ ±50.0 ^{-5**}

Table 3. Some growth characteristics derived from the parameter estimates

	Strain	Inflexion point		Upper Asymptote	Fitted BW at spawn	
		Growth rate	Age			
Female	C	2.7076	505.86	460.06	938.67	869.44
	E	2.6243	503.72	436.86	889.67	828.17
	Y	2.8454	499.83	454.21	922.42	871.71
Male	C	2.8082	511.49	481.47	981.73	903.75
	E	2.9353	520.31	501.07	1018.82	930.57
	Y	3.0755	510.62	499.03	1012.47	947.46

CONCLUSION AND DISCUSSION

The direct and indirect effects of selection in strain Y and indirect effects of selection in strain E proved to be small and most often negative. However there were clear and consistent differences in all the four growth parameters between the three strains. Thus, when taking the directions of change of the parameters which would increase body weight at a given age into consideration, strain Y had the most favourable and strain C the most unfavourable values of parameters A, C and λ while, on the other hand, strain C had the most favourable and strain Y the most unfavourable values of B. Consequently, the parameter values for strain E were consistently intermediate between those for strain Y and strain C. This means that selection caused a clearcut change in the *growth pattern* of the fish without giving rise to any significant direct or indirect response in body weight. If assuming that the genetic correlations between the parameters are similar to the phenotypic correlations, this result would be expected because the positively correlated selection effects on A, C and λ were counteracted by the negatively correlated selection effects on B. This is in agreement with the results and conclusions of Liljedahl (1975) in an investigation on the growth curve of identical bull twins, in which A, C and λ were found to be genetically compatible with each other but incompatible with B. Thus, selection for body weight might be regarded as selection for a complex of components some of which are positively correlated, and other negatively correlated. This may be exemplified as follows. The expected growth rate maximum was attained 7-8 months before spawning. At this time, the gonads usually start to grow with an accelerating rate. Consequently, an age-determined negative correlation between growth rate of somatic tissues and growth rate of the reproductive organs originates.

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