Effects of Inbreeding on Rainbow Trout Populations

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ABSTRACT

An approach for measuring inbreeding depression on the basis of differences between inbred and outbred half-sib family groups is described. Using this method, estimates of inbreeding depression in populations of rainbow trout (*Salmo gairdneri*) following one generation of brother-sister mating was calculated for three production traits—percent egg hatchability, percent fry survival from swim-up to 150 days, and weight at 150 days. The inbreeding depression estimates obtained from male and female half-sib families were 1.7 and 4.4% for percent egg hatchability, 22.2 and 16.1% for percent fry survival, and 12.0 and 9.8% for weight at 150 days, respectively. Estimates for fry survival and weight at 150 days were significant at $P < 0.01$ while egg hatchability estimates were nonsignificant. Following one generation of full-sib mating, the calculated effect of inbreeding on the number of live fish and total weight of fish at 150 days of age showed a reduction of 16.1 and 24.4% in female families and 22.1 and 31.4% in male families, respectively. The difference between inbreeding depression estimates derived from male and female half-sib groups provide a measure of the maternal influence.

Generalized trends of increasing depression with increasing levels of inbreeding from $F = 0.125$ to $F = 0.50$ were significant for weight at all ages from 77 to 150 days, but were nonsignificant for percent hatchability or percent fry survival. Inbreeding depression estimates for weight are considered to be minimum estimates because higher mortality rates in the inbred families resulted in lower fish density during the rearing period and, therefore, compensatory growth which reduced the weight difference between inbred and outbred families.

The intensive culture of small populations of a domestic species with the attendant selection of individuals best suited to a specific use inevitably leads to increased inbreeding. Estimates of the effects of inbreeding studied in many domestic and laboratory species have shown that fitness traits (traits associated with general vigor such as growth rate, survival and body conformation) are frequently reduced by increasing levels of inbreeding, whereas simply inherited (one locus and two-locus system) traits are little affected by the level of inbreeding (Wright 1922; Falconer 1960; Robertson 1954). Little information is available on the effects of inbreeding in fish species. Moav and Wohlfarth (unpublished) observed a 15% reduction in relative growth rate in full-sib mated carp (*Cyprinus carpio*). Moav and Wohlfarth (unpublished) also reported that a large proportion of the inbred carp displayed a variety of dorsal fin anomalies which they attributed to the inbreeding. Deformities in fry of rainbow trout (*Salmo gairdneri*) associated with one generation of brother-sister mating have also been reported by Aulstad and Kittelsen (1971). Abnormal body curvature in one family observed after resorption of the yolk sack resulted in death of all affected fry within a short time. Ryman (1970), who studied Atlantic salmon (*Salmo salar*), reported a tendency toward lower recapture frequencies of marked fish from inbred families, suggesting the existence of lower survival in these families. Inbreeding depression estimates of 5.12% and 0.44% per 10% inbreeding on 150-day fry weight and formalin tolerance in rainbow trout (*Salmo gairdneri*) were reported by Bridges (1971). Von Limbach (1970) and Bridges (1972) also reported a reduction in egg hatchability and fry livability in inbred rainbow trout. Menasveta (1961), studying hybrids between the University of Washington and Lake Chelan rainbow trout, found higher mortality and lower growth rate in the University of Washington strain than in the hybrid.

METHODS

The Fish Genetics Laboratory initiated a program in 1969 to measure the effects of inbreeding in rainbow trout, using inbred lines available at the laboratory. The problem was examined by measuring the mean

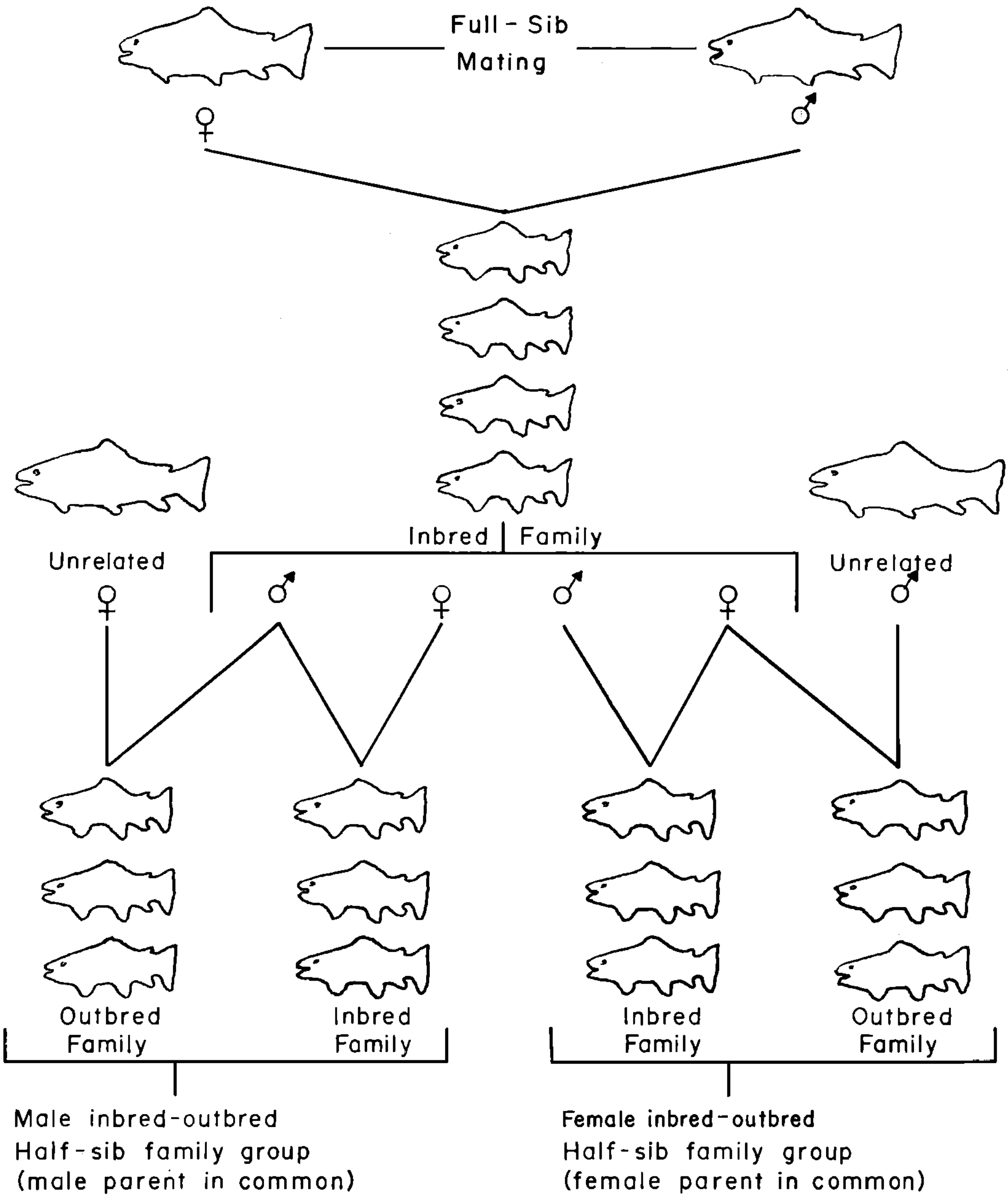

FIGURE 1.—*Diagram of the mating procedure for producing inbred and outbred half-sib families where the inbred family is produced from a full-sib mating (brother-sister) and has an inbreeding coefficient of* $F = 0.375$.

deviation between full-sib members of inbred and outbred half-sib families (Fig. 1) reared as contemporaries.

Female inbred-outbred families were produced by dividing the spawn of individual females into two lots. One lot was fertilized by a full brother to produce an inbred full-sib family and the second was fertilized by a randomly-selected unrelated male from the same base population from which the female came to produce an outbred family. The level of inbreeding obtained in a specific family was dependent on the previous inbreeding history of the mates. Assuming no prior history of inbreeding, the inbreeding coefficient (F) from one generation of brother-sister mating would be $F = 0.25$, from two generations $F = 0.375$, and from three generations $F = 0.50$. The inbreeding coefficient from a mating of two unrelated individuals would be $F = 0.0$. In situations where previous inbreeding has occurred, but the level is unknown the calculated coefficient would not be strictly correct but would still reflect the relative increase in homozygosity resulting from one generation of full-sib mating. The mating procedure used to generate male inbred-outbred half-sib families was to fertilize the eggs of two females with milt from a single male (Fig. 1). All full-sib families were reared separately in the standardized rearing environment of the Fish Genetics Laboratory to 150 days of age. Characteristics of the standardized rearing environment were temperature, 11 ± 1 C; pH, 7.6–7.8; water hardness, 426 ppm hardness as $CaCO_3$, 634 ppm total hardness; incubation equipment, Heath overflow type with each tray subdivided into six compartments; and rearing container, a 17-liter circular polyethylene tub with 2.27 liters per minute gravity inflow. Initial loading density was 300 fry at 42 days of age with the maximum fish load per tank limited to 1 kg during the test period.

Differences between the inbred and outbred full-sib families of a half-sib group were interpreted by the model in equation 1:

$$D = I + P + E; \qquad (1)$$

D = difference in mean value of a trait measured in inbred and outbred full-sib families;

I = effect due to inbreeding;

P = effect due to differential production potential of the two unrelated mates of the common parent (called maternal effect in male half-sib families and paternal effect in female half-sib families);

E = random error.

Since random selection of mates was used to produce a half-sib family, there was an equal opportunity for the outbred mate to be better or worse than the inbred mate. This procedure for choosing mates results in P being a random effect with a mean of zero when averaged over a large number of half-sib families. Similarly, E is a random effect with a mean of zero. The practice of rearing the inbred and outbred families as contemporaries provided a means for removing environmental effects from consideration in measuring inbreeding depression. Under these circumstances equation 1 reduces to equation 2:

$$D = I. \qquad (2)$$

The use of deviations between the half-sib families under these conditions provides a clean estimate of the effect of inbreeding when averaged over a large number of half-sib families.

The specific calculation for measuring inbreeding depression was the deviation between inbred and outbred full-sib families within half-sib family groups calculated by equation 3:

$$D_j = X_{oj} - X_{ij}; \qquad (3)$$

D_j = deviation observed in the jth half-sib family;

X_{oj} = mean of the outbred full-sib family ($F = 0.0$) from the jth half-sib family group;

X_{ij} = mean of the inbred full-sib family from the jth half-sib family group.

The percent inbreeding depression was then calculated by the equation:

$$\text{Percent inbreeding depression} = \frac{X_{oj} - X_{ij}}{X_{oj}}. \qquad (4)$$

The above procedure was applied to each of the traits measured, which included *percent hatch*: percent of fertilized ova surviving to hatch; *percent fry survival*: percent of swim-up fry surviving to 150 days of age (post-fertilization); *attained weight*: mean fish weight at 77, 84, 91, 105, 112, 125, and 150 days of age. The total family was counted and weighed at each age.

		Male Parent Line				
		1	2	3	4	5
Female Parent Line	1	F=0.500	F=0.125	F=0.250	F=0.188	F=0.000
	2	F=0.125	F=0.375	F=0.250	F=0.188	F=0.000
	3	F=0.250	F=0.250	F=0.313	F=0.1875	F=0.000
	4	F=0.188	F=0.188	F=0.188	F=0.313	F=0.000
	5	F=0.000	F=0.000	F=0.000	F=0.000	F=0.000

FIGURE 2.—*Diagram of mating design used in experiment 2 to produce half-sib family groups. Each row corresponds to a female half-sib family group (common female parent) while each column corresponds to a male half-sib family group (common male parent). Inbreeding coefficients* (F) *for each possible mating are shown in the body of the matrix.*

Experiment 1

During the 5-year period 1969–73, a total of 103 female and 67 male inbred-outbred half-sib families at the $F = 0.25$ level of inbreeding were evaluated through 150 days of age. Weight was evaluated at three ages in the 1969 and 1970 year classes, but was changed to five ages in the 1971, 1972, and 1973 year classes. Percent hatch and percent survival from swim-up to 150 days was calculated for all five year classes. At swim-up each family was reduced to 300 fry. This reduction process was done at random except that individuals with obvious deformities were excluded.

Experiment 2

In the fall of the 1972 spawning season, half-sib family groups were produced by mating individual females to five males selected on the basis of relatedness to each female to produce a set of five full-sib families. Each of these families then possessed differing levels of inbreeding from zero to $F = 0.50$ and collectively formed a half-sib family group. These families were generated by using a five by five design (Fig. 2); each of the five males was mated to the five females in one set of the mating design to form five male half-sib family groups (columns in Fig. 2) and five female half-sib family groups (rows in Fig. 2). These families were reared as contemporaries in the standardized rearing environment to 150 days of age. The resulting deviations between full-sib families at different levels of inbreeding within the half-sib family groups provided a means for measuring the increasing effects of inbreeding with increasing levels of homozygosity. The mating design was replicated four times, but high levels of egg and fry mortality reduced this study to a total of 23 pairs, covering a range in level of inbreeding from $F = 0.125$ to $F = 0.50$. The criterion for measuring inbreeding effects was the deviation between inbred and outbred full-sibs within each half-sib family group and inbreeding level, as shown in equations 3 and 4.

RESULTS AND DISCUSSION

Experiment 1

The effects of inbreeding at the $F = 0.25$ level found in male and female half-sib families were summarized by year class (Tables 1 and 2) to demonstrate the repeatability of inbreeding estimates in the traits measured. Examination of the annual depression estimates by trait measured show that all fall within a small range except the male weight estimates in 1972 (Table 1) where the small sample size resulted in negative estimates. Mean deviations in the percent hatch indicated a nonsignificant reduction of embryos in both the paternal and maternal comparisons due to inbreeding. Percent hatch was an extremely variable trait, with deviations within half-sib families ranging from –50.8 to 71.6% in the male groups and from –40.4 to 34.8% in the female groups.

The effect of inbreeding on percentage fry survival was much more pronounced. Mean depressions of 22.2 and 16.1% for male and female families were both highly significant ($P < 0.01$). In both inbreds and

TABLE 1.—*Inbreeding depression measured in male half-sib families by year class for nine egg and fry characteristics (inbreeding level* F = *0.25). Asterisks denote significance at* P ⩽ *0.05** or P ⩽ *0.01**.*

Year class	Measurement	Trait: Hatch	77-day weight	84-day weight	91-day weight	105-day weight	112-day weight	126-day weight	150-day weight	Fry survival
1969	Number of families	11		11			11		11	11
	Outbred mean	75.9%		0.37g			0.72g		1.46g	68.4%
	Inbred depression	5.7%		0.06g			0.10g		0.25g	18.1%
	Standard error	5.9%		0.03g			0.04g*		0.11g*	8.4%
	Percent depression	7.5%		16.2%			13.9%		17.1%	26.5%
1970	Number of families	21		21			21		21	19
	Outbred mean	63.9%		0.45g			1.00g		2.23g	57.1%
	Inbred depression	10.8%		0.05g			0.19g		0.32g	18.2%
	Standard error	7.3%		0.04g			0.09g*		0.18g	6.6%*
	Percent depression	16.9%		11.1%			19.0%		14.3%	31.9%
1971	Number of families	19	24		24	24		24	24	19
	Outbred mean	53.2%	0.27g		0.41g	0.64g		1.12g	1.91g	64.8%
	Inbred depression	−12.4%	0.04g		0.07g	0.10g		0.19g	0.30g	5.4%
	Standard error	6.9%	0.02g*		0.03g**	0.04g*		0.06g**	0.15g	6.3%
	Percent depression	−23.3%	14.8%		17.1%	15.6%		16.8%	15.7%	8.3%
1972	Number of families	2	2		2	2		2	2	2
	Outbred mean	60.2%	0.49g		0.86g	1.28g		2.19g	3.39g	74.5%
	Inbred depression	15.4%	−0.12g		−0.07g	−0.09g		−0.22g	−0.48g	11.2%
	Standard error									
	Percent depression	25.6%	−24.5%		−8.1%	−0.8%		−10.0%	−14.2%	15.0%
1973	Number of families	3	9		9	9		7	9	9
	Outbred mean	46.2%	0.48g		0.92g	1.59g		2.87g	5.22g	79.1%
	Inbred depression	−8.6%	0.08g		0.14g	0.21g		0.25g	0.41g	22.3%
	Standard error	13.6%	0.04g		0.08g	0.15g		0.19g	0.47g	9.9%
	Percent depression	−18.6%	16.7%		15.2%	13.2%		8.8%	7.9%	28.2%
TOTAL	Number of families	56	35	32	35	35	32	33	67	60
	Outbred mean	61.5%	0.34g	0.42g	0.57g	0.92g	0.90g	1.56g	2.43g	65.5%
	Inbred depression	1.1%	0.04g	0.05g	0.08g	0.12g	0.16g	0.18g	0.29g	14.5%
	Standard error	4.0%	0.02g**	0.03g	0.03g**	0.06g*	0.06g**	0.06g**	0.10g**	3.7%**
	Percent depression	1.7%	12.0%	12.9%	14.2%	12.7%	17.5%	11.6%	12.0%	22.2%

outbreds, the largest losses occurred while the fry were starting to feed but mortality continued at a higher level in the inbred groups until 105 days of age; thereafter, few losses were observed in either group. This observation suggests that genetically unfit individuals are purged from the population by 105 days of age (about 0.9 g mean weight). No definitive information is available on the differential survival of inbred fish at later life stages.

At seven ages ranging from 77 to 150 days, weight reduction due to inbreeding was significant in both sex groups at all ages. The mean reduction due to inbreeding (Tables 1 and 2) increased with increasing age. This trend was expected considering that these measurements were taken at a series of age intervals on the same families. Since growth occurs as a function of body mass at the beginning of a particular growth period, any deviation between the inbred and outbred weight at the end of one growth period would be expected to increase in each subsequent growth period. Mean depression in weight at 150 days of age was 12.0% for male families and 9.8% for female families. These values are considered to be conservative estimates because even though families were reared in identical containers with uniform initial fish densities, the decreased survival of inbred fry resulted in proportionally fewer fish in the containers with inbred families toward the end of the study. This reduced fish number would produce somewhat more favorable densities in the inbred families resulting in the trend toward an increased percent depression in later growth periods being reduced. The percent inbreeding depression for each growth period obtained (Tables 1 and 2) suggests that the percentage difference in weight was increasing through 112 days and thereafter decreased; however, this trend was not statistically significant to 150 days. The 112 day age corresponds to the age at which fish mortality stopped.

The effects of inbreeding in the maternal and paternal family groups were markedly different; the male estimates were larger in all traits except percentage hatch. These dif-

TABLE 2.—*Inbreeding depression measured in female half-sib families by year class for nine egg and fry characteristics (inbreeding level* F = *0.25). Asterisks denote significance at* P ≤ *0.05** *or* P ≤ *0.01**.*

		Trait								
Year class	Measurement	Hatch	77-day weight	84-day weight	91-day weight	105-day weight	112-day weight	126-day weight	150-day weight	Fry survival
1969	Number of families	14		14			14		14	14
	Outbred mean	77.5%		0.36g			0.73g		1.53g	68.7%
	Inbred depression	7.2%		0.04g			0.09g		0.19g	18.4%
	Standard error	2.6%*		0.01g**			0.03g*		0.09g	6.5%
	Percent depression	9.3%		11.1%			12.3%		12.4%	26.8%
1970	Number of families	37		37			37		37	33
	Outbred mean	55.0%		0.46g			1.04g		2.50g	59.7%
	Inbred depression	3.0%		0.03g			0.14g		0.24g	15.8%
	Standard error	2.4%		0.02g			0.05g**		0.10g*	4.1%**
	Percent depression	5.5%		6.5%			13.5%		9.6%	26.5%
1971	Number of families	30	38		38	38		38	38	30
	Outbred mean	65.2%	0.27g		0.44g	0.68g		1.21g	2.15g	63.0%
	Inbred depression	2.8%	0.02g		0.03g	0.05g		0.10g	0.16g	3.5%
	Standard error	2.4%	0.01g**		0.01g*	0.02g*		0.03g**	0.06g**	3.9%
	Percent depression	4.3%	7.4%		6.8%	7.4%		8.3%	7.4%	5.6%
1972	Number of families	3	3		3	3		3	3	3
	Outbred mean	34.8%	0.42g		0.76g	1.14g		1.99g	3.07g	94.5%
	Inbred depression	−3.8%	0.01g		0.09g	0.14g		0.27g	0.40g	4.4%
	Standard error	14.1%	0.01g		0.03g	0.11g		0.17g	0.26g	4.2%
	Percent depression	−10.9%	2.4%		11.8%	12.3%		13.6%	13%	4.7%
1973	Number of families	7	11		11	11		9	11	11
	Outbred mean	56.3%	0.48g		0.92g	1.60g		2.92g	5.12g	81.2%
	Inbred depression	−5.7%	0.08g		0.16g	0.25g		0.46g	0.60g	6.3%
	Standard error	3.3%	0.01g**		0.03g**	0.06g**		0.11g**	0.49g	5.0%
	Percent depression	−10.1%	16.7%		17.4%	15.6%		15.8%	11.7%	7.7%
TOTAL	Number of families	91	52	51	52	52	51	50	103	91
	Outbred mean	61.3%	0.32g	0.43g	0.56g	0.90g	0.95g	1.57g	2.53g	65.9%
	Inbred depression	2.7%	0.03g	0.03g	0.06g	0.10g	0.13g	0.18g	0.25g	10.6%
	Standard error	2.8%	0.01g**	0.01g*	0.01g**	0.02g**	0.04g**	0.04g**	0.02g**	2.4%**
	Percent depression	4.4%	9.6%	7.4%	11.1%	10.9%	13.2%	11.3%	9.8%	16.1%

ferences ranging from 2.7 to 74.3% occurred as a result of the inclusion of maternally-influenced differences in the paternal estimates but not in the maternal estimates. Maternal effect would be expected to be appreciably larger than paternal effects during the early period of life because of the influence of embryo size and quantity and the quality of yolk materials which are almost entirely determined by the female during egg formation. The formation of maternal half-sib families from a random half of the eggs of a single female maximized the uniformity of the eggs used in each of the female matings. In paternal families, however, the range in size and general quality of the eggs varied at random, depending on the particular female selected. Inbreeding would be expected to have a depressing effect on maternal influence where the female was herself inbred (Falconer 1960); however, none of the females used in the present comparisons were inbred. Even though the reduction in growth due to inbreeding was lower in maternal estimates, the reduced variability in female families (attributed directly to the exclusion of maternal effects) resulted in a higher level of significance at a given age for female than for corresponding male estimates.

Experiment 2

Further studies were conducted in 1973, to examine the effect of increasing levels of inbreeding using maternal half-sib families containing five full-sib families, four at different levels of inbreeding and one outbred (Fig. 2). Deviations from the outbred full-sib family were calculated and summarized by level of inbreeding (Table 3). The considerable difficulty encountered in rearing the higher level inbreds accounts for the low number of comparisons at the $F = 0.50$ and $F = 0.375$ levels of inbreeding. The entire half-sib family group containing a full-sib family of $F = 0.375$ or $F = 0.50$ inbreeding was produced from an inbred female. This means of half-sib family production introduces the effects of inbreeding from two sources (Falconer 1960); inbreeding of the zygote and inbreeding from the maternal envi-

TABLE 3.—*Effects of increasing levels of inbreeding in seven juvenile traits in rainbow trout measured as deviations (outbred family mean minus inbred half-sib family mean) from maternal comparisons. Asterisks denote significance at* $P \leqslant 0.05^*$ *or* $P \leqslant 0.01^{**}$.

Level of inbreeding	Number of pairs	Trait						
		Hatch	Survival	77-day weight	91-day weight	105-day weight	126-day weight	150-day weight
$F = 0.50$	1							
Outbred mean		43.5%	87.6%	0.42g	0.83g	1.51g	2.64g	4.61g
Inbred depression		–3.9%	9.4%	0.12g	0.25g	0.46g	0.53g	1.00g
Percent depression		–9.0%	11.0%	29.0%	30.0%	30.0%	20.0%	21.7%
$F = 0.375$	2							
Outbred mean		72.1%	77.6%	0.40g	0.80g	1.47g	2.73g	4.72g
Inbred depression		4.0%	3.1%	0.09g	0.26g	0.47g	0.63g	0.99g
Percent depression		5.5%	4.0%	23.0%	33.0%	32.0%	23.0%	21.0%
$F = 0.25$	11							
Outbred mean		56.3%	81.2%	0.48g	0.92g	1.60g	2.92g	5.12g
Inbred depression		–5.7%	6.3%	0.08g	0.16g	0.25g	0.46g	0.60g
Standard error		3.3%	5.0%	0.01g**	0.03g**	0.06g**	0.11g**	0.22g*
Percent depression		–10.1%	7.7%	16.7%	17.5%	15.6%	15.7%	11.6%
$F = 0.1875$	4							
Outbred mean		70.9%	81.2%	0.39g	0.80g	1.48g	2.78g	4.70g
Inbred depression		–1.2%	11.7%	0.06g	0.13g	0.21g	0.22g	0.08g
Standard error		4.6%	9.1%	0.01g**	0.06g	0.11g	0.21g	0.34g
Percent depression		–1.7%	14.4%	15.4%	16.3%	14.2%	7.9%	1.8%
$F = 0.1250$	5							
Outbred mean		53.8%	80.6%	0.46g	0.90g	1.62g	2.87g	5.27g
Inbred depression		2.4%	2.0%	–0.01g	–0.04g	–0.11g	–0.11g	–0.45g
Standard error		9.5%	7.7%	0.03g	–0.05g	0.07g	0.10g	0.37g
Percent depression		4.5%	2.5%	0.0%	–4.4%	–6.8%	–3.8%	–8.5%

ronment producing the ova. Both sources of inbreeding affect the mean value of a trait measured from an inbred female family. The deviation between inbred and outbred families of a half-sib family group, however, measures only the inbreeding caused by inbreeding of the zygote (assuming no significant interaction between the two sources of inbreeding effects). A division of the effects attributable to each of these sources of inbreeding was not attempted here because of the small sample number and the incompleteness of the design resulting from the low hatch and low fry survival.

The effect of inbreeding on the percentage hatch (Table 3) was inconclusive because the deviations from the outbred family means were erratic, probably due to the small number of families involved. At three of the five inbreeding levels, the inbred families had a larger hatching percentage. In percentage fry survival, the inbred families had lower (but nonsignificant) levels of survival at all inbreeding levels. An apparent trend for increasing depression with increasing levels of inbreeding was not significant (Table 4).

Effect of inbreeding on weight at the five ages (77–150 days) showed two basic trends. First, the percentage inbreeding depression decreased as age increased from 77 to 150 days at all levels of inbreeding. This trend in the data is an anomaly largely explained by the higher fry mortality observed in inbred lots, which lowered fish density and thus reduced competition for the available space and food. The growth of the remaining fry reared at a lower fish density would give the

TABLE 4.—*Regression of percent depression on level of inbreeding percent of seven juvenile traits within the range* $F = 0.125$ *to* $F = 0.50$. *Asterisks denote significance at* $P \leqslant 0.05^*$ *or* $P \leqslant 0.01^{**}$.

Trait	Percent hatch	Percent fry survival	Attained weight at day				
			77	91	105	126	150
Regression coefficient	–0.178	–0.060	0.663	0.849	0.913	0.607	0.796
t-test	0.68	0.033	4.0**	3.0*	3.3**	2.8*	4.3**
Variation due to linearity (%)	13.5	3.5	85	75	78	72	86

TABLE 5.—*Calculated inbreeding depression in weight of fish and number of fish at 150 days of age due to the joint effects of egg hatchability, fry survival, and attained weight at* F = *0.25.*

Trait	Female		Male	
	Out-bred	In-bred	Out-bred	In-bred
Starting number of eggs	1000	1000	1000	1000
Percent egg hatchability	61.3	61.3	61.5	61.5
Number of sac-fry	613	613	615	615
Percent fry survival	65.9	55.3	65.5	51.0
Number fingerlings (150 days)	404.0	339.0	402.8	313.7
Mean fish weight (g at 150 days)	2.53	2.28	2.43	2.14
Total fish weight (g)	1022.0	772.9	978.9	671.2
Percent reduction in inbred:				
by weight		24.4		31.4
by number		16.1		22.1

appearance of decreasing effect of inbreeding depression, as suggested by the trend seen in this experiment. Second, a significant trend of increasing depression with increasing level of inbreeding was seen at all five ages ($P < 0.05$—see Table 4), with linearity accounting for 72 to 85% of the variation. At the lower level of inbreeding ($F = 0.125$), inbreds were larger than outbreds at the older ages. However, the lower fish density in the inbred families, as shown by lower fry survival in these groups, could have permitted compensatory growth which obscured the expected growth depression.

The accumulative effect of inbreeding depression of egg hatchability, fry survival, and 150-day weights on resulting total weight and total number of fish produced at 150 days of age, was calculated by using the mean inbreeding effects measured at the $F = 0.25$ level of inbreeding from Tables 2 and 3, is shown in Table 5. The effect of inbreeding on egg hatchability was nonsignificant and is included as a zero effect. The combined effects of the remaining two traits at an inbreeding level equivalent to one generation of full-sib mating reduced the total weight of fish produced at 150 days of age by 24.4% in female families and 31.4% in male families.

Although the levels of inbreeding that exist in the most widely used strains of rainbow trout are unknown, it must be assumed that they are increasing and often not trivial. A number of methods are available to the fish breeder to minimize the rate of inbreeding. Some of these methods are: (1) maintenance of large random breeding populations (more than 100 breeding pairs); (2) periodic introduction of fish from different sources; (3) avoidance of full or half-sib mating through identification of individual families; and (4) inter-strain hybridization. One or more of these basic approaches can readily be adapted to most brood stock situations.

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