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## Evidence of genetic and environmental influences on meristic variation in the rainbow trout, *Salmo gairdneri* Richardson

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Morphology, Variability, Taxonomy, Parentage, Temperature

### Synopsis

An investigation of the effect of parentage and temperature on the expression of selected meristic characters of rainbow trout, *Salmo gairdneri*, reveals statistical differences in the number of vertebrae, dorsal fin rays and anal fin rays among test batches of progeny of different parentage. Batches of fertilized ova of the same stock or parentage, when incubated at 9.5°C and 14.8°C, produced lower mean dorsal and anal fin ray counts and a higher mean pectoral fin ray count at the higher temperature. Incubation temperature had no significant effect on the number of vertebrae.

Significant statistical differences occurring in various characters among groups of rainbow trout of different parental origin provide convincing evidence of genetic inputs into meristic expression. However, the existence of both environmental and genetic inputs into meristic expression in rainbow trout necessitates further investigation before the meaning of observed meristic plasticity in rainbow trout can be resolved.

### Introduction

Ecophenotypic variation of meristic expression has been clearly demonstrated in many species of fishes (Hubbs 1922; Vladykov 1934; Tåning 1952; Lindsey 1954, 1958, 1962a; Seymour 1959; Barlow 1961) and is no less apparent in the rainbow trout, *Salmo gairdneri* Richardson (Mottley 1934, 1937; Orska 1957, 1962; Garside 1966; MacCrimmon &

Kwain 1969, Kwain 1975). Because of this phenomenon 'a shadow of uncertainty is always inherent in the use of meristic characters . . . in variational analysis' (Hubbs et al. 1974: 84). Recently, the factors controlling meristic expression in fishes have been shown to be exceedingly complex with a confusing interaction between environmental and genetic inputs existing in certain species (Ricker 1972, Lindsey & Harrington 1972, Ali & Lindsey 1974, Lindsey 1975).

Although ecophenotypic variation of certain meristic characters in rainbow trout has been studied and documented, little is known about the genetic constraints on meristic expression in this species. The importance of meristic characters in the identification of salmonid stocks (Neave 1944, Smith 1969, Ricker 1972) and the great variability of meristic expression among stocks or populations of rainbow trout (MacGregor & MacCrimmon 1976) necessitate further experimental work to provide insight into the genetic and environmental factors regulating the expression of these characters (Needham & Gard 1959). As an initial approach to this problem, a series of experiments were conducted to determine the effects 1) of parentage on meristic expression in rainbow trout, and 2) of temperature on the expression of selected meristic features.

### Methods and materials

#### A. Collecting and general culture techniques

Sexual products from adult rainbow trout were artificially taken at field location by the 'dry met-

hod' (Huet 1970) and the resultant fertilized ova transferred in jars to the University of Guelph for incubation within three hours of their fertilization. The ova were divided into experimental lots, placed in jars, and floated in the incubation waters until the temperatures equalized. The ova were then placed directly into trays of Heath vertical flow incubators (Huet 1970).

All eggs were incubated using well water supply (Hodson & Sprague 1975). The two test temperatures ( $9.5 \pm .3$  and  $14.8 \pm .1^\circ\text{C}$ ) were maintained by means of a thermostatically controlled holding tank below each incubator from which the water was lifted by submersible pumps to the uppermost incubation tray and run through the entire battery of trays before exit without change in temperature. The incubators were wrapped with heavy plastic to maintain dark conditions. Eggs were exposed to light from an overhead 40 watt bulb for an average of 10 minutes once daily during routine inspection and the removal of any dead eggs. There was no chemical treatment of water, eggs or fish.

At one week following complete hatch, the cleutheroembryos (Balon 1975) were transferred

to laboratory rearing tanks where they were maintained in the same water supply and at the same temperatures as during incubation but without controlled photoperiod. With the commencement of exogenous feeding the trout were fed daily with dry commercial pellets supplemented with frozen brine shrimp until sacrificed for examination (Table 1). Each 'batch' was coded relative to stock, parentage and incubation temperature (Table 1).

### B. Meristics

Thirty-nine specimens from each of the 9 batches were preserved in formaline and subsequently cleared and stained as outlined by Hollister (1934). Following the definitions of MacGregor & MacCrimmon (1976), the fork length and numbers of dorsal, caudal, pectoral and pelvic fin rays, vertebrae, branchiostegal rays and fork length were determined. Counts of fin rays and vertebrae in parent fish were determined from radiographs;

Table 1. Parentage, incubation temperature, time to complete hatch, and age and length at sacrifice for each of the batches examined.

Stock	Batch Parentage	Code	Incubation Temperature	Time Complete Hatch (days)	Age Sacrificed (days)	Fork Length Sacrificed (mm)
Saugeen Fall	male 1 x female 1	SB1	9.5 C	37	104	29.12
	male 2 x female 2	SC1	9.5 C	37	104	28.50
	male 2 x female 2	SC2	14.8 C	21	103	61.02
	pooled ova	SM1	9.5 C	37	107	29.56
	pooled ova	SM2	14.8 C	21	107	60.47
Normandale Fall	male 1 x female 1	FB1	9.5 C	39	90	28.21
	male 2 x female 2	FC1	9.5 C	39	75	27.65
	pooled ova	FM1	9.5 C	39	94	28.09
	pooled ova	FM2	14.8 C	21	68	27.20

pectoral and pelvic fins were removed and placed flat against the x-ray plate.

### C. Parentage experiment

On November 2, 1974, two pairs of rainbow trout were taken from the fallspawning run of rainbow in Saugeen River at Denny's Dam, Southampton (SB1, SC1). Similarly, on November 14 and 29, 1974, two pairs were taken from the fallspawning stock at the Provincial Fish Hatchery at Normandale, Ontario (FB1, FC1). Each pair was stripped on location and the resultant ova incubated in separate trays in the identical water supply at a controlled temperature of  $9.5^{\circ}\text{C} \pm 0.3^{\circ}\text{C}$ . Parent fish were sacrificed, marked and frozen for future meristic examination. The progeny were cleared, stained and meristic counts made when they reached suitable size (Table 1). The following comparisons were used to determine the direct effect of parentage on each meristic character: FB1 vs FC1, SB1 vs SC1. The midparent values for meristic features of the parent fish were then related to those of the progeny through correlation coefficients (Strickberger 1968).

### D. Effect of temperature

On November 14, 1974 a random sample of newly-fertilized eggs was taken from a pooled supply of fertilized ova resulting from the artificial spawning of a number of parents from the fallspawning stock at the Normandale Provincial Fish Hatchery, Ontario. Similarly, a mixed lot of eggs resulting from a cross of two males and three females of the Saugeen fallspawning run were taken on November 2, 1974. Eggs of each stock were divided into two equal portions and reared in a vertical incubator at  $9.5^{\circ}\text{C} \pm 0.3^{\circ}$  (FM1, SM1) and  $14.8^{\circ}\text{C} \pm 0.1^{\circ}\text{C}$  (FM2, SM2). The resultant progeny were subsequently cleared and stained for examination (Table 1). The following statistical comparisons were carried out for each meristic character: SM1 vs SM2, FM1 vs FM2, SM1 vs FM1, SM2 vs FM2.

In order to obtain a more precise estimate of the effect of temperature on known meristic features of individual parents than is possible with pooled eggs, the progeny of a single pair of Saugeen stock were reared at the two test temperatures and ex-

amined (SC1 vs SC2) by the previously described procedures.

### E. Data analysis

Meristic data were placed on keypunch cards and analyzed on the University IBM 370/155 computer, using existing programs. Standard descriptive statistics such as means, variances and standard deviations were calculated using raw data. The statistical analysis was set up so that parentage was nested within stock since these two variables are hierarchically related. Temperature and stock were treated as factorial variables with two levels ( $9.5^{\circ}\text{C}$  and  $14.8^{\circ}\text{C}$ ). A multivariate analysis of variance (program SC1M06) was then executed. By this computation, in conjunction with Scheffe's test (Snedecor & Cochran 1967), it was possible to determine if a given character differed statistically at the 0.05 and 0.01 levels among stocks, among parentage or as a response to incubation temperature. The entire analysis was conducted using reciprocal transformations, thereby ensuring homogeneity of variance.

## Results

### A. Parentage experiment

A high correlation existed between the midparent and progeny counts of dorsal fin rays, anal fin rays, pectoral fin rays and vertebrae (Table 2), although these correlations could not reliably be tested statistically. Because of erosion of the principal caudal rays in the parent Normandale fish, this meristic character was dropped from the analysis.

Significant differences in certain meristic characters occurred between 'batches' of progeny of different parental origin (Table 3), although all 'batches' were incubated under the same conditions (Table 1). The two 'batches' of Saugeen stock (SB1, SC1) differed significantly in the number of dorsal, caudal and branchiostegal rays (right side) and in the number of vertebrae. Similarly, the two Normandale 'batches' (FB1, FC1) varied significantly in the number of pectoral fin rays, anal fin rays and vertebrae. Significant differences occurred only when the combination of parental counts for the given character differed between 'batches' (Tables 2, 3).

Table 2. Descriptive statistics, frequency distributions and midparent: progeny correlation coefficients of meristic characters among experimental 'batches' (SB1, SCl, FB1, FCl) of rainbow trout.

Character	Batch §	Frequency	Mean	$S_{\bar{x}}$	Character	Batch §	Frequency	Mean	$S_{\bar{x}}$						
<b>Dorsal Rays</b>					<b>Vertebrae</b>										
		Count					Count								
		15	16	17	18		60	61	62	63	64	65			
SB1 male		*				SB1 male				*					
female						female			*						
progeny		4	31	4	16.00	0.07	progeny		9	21	8	1	63.03	0.12	
SC1 male				*							*				
female				*							*				
progeny		3	14	18	4	16.59	0.13	progeny		17	19	3	63.64	0.10	
FB1 male		*								*					
female			*							*					
progeny		21	18		15.46	0.08	progeny		1	28	9	1	62.25	0.09	
FCl male		*								*					
female			*							*					
progeny		12	12	1	15.72	0.08	progeny		1	34	4		61.08	0.06	
Midparent: progeny correlation (r) = 0.95					Midparent: progeny correlation (r) = 0.94										
<b>Pectoral Rays</b>					<b>Branchiostegal Rays (Total)</b>										
		Count					Count								
		13	14	15			20	21	22	23	24				
SB1 male		*				SB1 male		*							
female			*			female		*							
progeny		21	16	2	13.51	0.10	progeny		3	4	31	1	21.77	0.11	
SC1 male			*							*					
female			*							*					
progeny		12	24	3	13.66	0.09	progeny		3	6	13	7	10	22.38	0.20
FB1 male		*								*					
female			*							*					
progeny		10	24	5	13.87	0.10	progeny		4	9	25	1	21.59	0.12	
FCl male		*								*					
female			*							*					
progeny		26	13		13.33	0.08	progeny		8	8	22	1	21.43	0.15	
Midparent: progeny correlation (r) = 0.81					Midparent: progeny correlation (r) = 0.55										
<b>Pelvic Rays</b>					<b>Anal Rays</b>										
		Count					Count								
		9	10				13	14	15	16					
SB1 male		*				SB1 male		*							
female			*			female		*							
progeny		3	36		9.92	0.05	progeny		13	25	1	14.69	0.08		
SC1 male		*							*						
female			*						*						
progeny		2	37		9.95	0.04	progeny		2	12	21	4	14.69	0.12	
FB1 male		*							*						
female			*						*						
progeny		1	38		9.97	0.03	progeny		3	32	4	15.03	0.07		
FCl male		*							*						
female			*						*						
progeny		3	36		9.90	0.04	progeny		6	27	6	14.00	0.09		
Midparent: progeny correlation (r) = 0.31					Midparent: progeny correlation (r) = 0.83										

\* parental value; § refer to Table 1;  $S_{\bar{x}}$ , standard error.

### B. Effect of temperature

Temperature had a significant effect upon certain meristic characters. The number of dorsal, anal and branchiostegal rays (right side) decreased significantly whereas the number of pectoral fin rays increased significantly at the higher incuba-

tion temperature (Tables 3, 4). The number of caudal fin rays decreased significantly at the higher incubation temperatures in one 'batch' of Saugreen stock (SC), but there was no significant change in the number of vertebrae, pelvic fin rays or in the remaining branchiostegal ray counts between the two incubation temperatures.

Table 3. Statistical significances in meristic characters due to parentage and temperature.

Comparison <sup>§</sup>	Treatment	Character								
		Do	Ca	P1	P2	An	BR	BL	Bt	Vt
Sb1 vs SC1	Parentage	*	**				*			**
Fb1 vs FC1	Parentage			*		**				**
SM1 vs SM2	Temperature	*		**		**	*			
FM1 vs FM2	Temperature	*		**		**				
SC1 vs SC2	Temperature	*	**	**		**	*			

§ refer to Table 2; \*\* significant .01 level; \* significant .05 level.

Key to abbreviations: Do, dorsal; P1, pectoral; P2, pelvic; An, anal; BR, branchiostegal rays (right side); BL, branchiostegal rays (left); BT, branchiostegal rays (total); Vt, vertebrae.

Table 4. Descriptive statistics of meristic characters from selected experimental 'batches' (SM, SC, FM) of rainbow trout, each incubated at 9.5°C and 14.8°C.

Batch <sup>§</sup>	Incubation Temperature	Statistic	Character								
			Do	Ca	P1	P2	An	BR	BL	BT	Vt
SM1	9.5°C	mean	16.15	19.10	13.10	9.92	15.31	11.18	11.23	22.41	62.44
		$S_{\bar{X}}$	0.10	0.06	0.09	0.06	0.12	0.09	0.09	0.15	0.11
SM2	14.8°C	mean	15.69	19.08	14.15	10.13	14.18	10.85	10.92	21.77	62.82
		$S_{\bar{X}}$	0.10	0.10	0.10	0.07	0.12	0.13	0.13	0.22	0.13
SC1	9.5°C	mean	16.59	20.51	13.77	9.95	14.69	11.18	11.21	22.39	63.64
		$S_{\bar{X}}$	0.13	0.10	0.09	0.04	0.12	0.11	0.11	0.20	0.10
SC2	14.8°C	mean	16.08	19.64	14.36	10.0	13.72	10.80	11.03	21.82	63.64
		$S_{\bar{X}}$	0.10	0.11	0.08		0.13	0.09	0.11	0.16	0.17
FM1	9.5°C	mean	15.39	19.0	13.97	10.13	14.36	10.95	11.18	22.13	62.85
		$S_{\bar{X}}$	0.11		0.06	0.05	0.11	0.08	0.10	0.16	0.09
FM2	14.8°C	mean	15.08	19.0	14.72	10.08	13.90	10.90	10.95	21.85	62.62
		$S_{\bar{X}}$	0.13		0.08	0.04	0.11	0.11	0.11	0.21	0.13

§ refer to Table 2.

Key to abbreviations: Do, dorsal; P1, pectoral; P2, pelvic; An, anal; BR, branchiostegal rays (right side); BL, branchiostegal rays (left); BT, branchiostegal rays (total); Vt, vertebrae.

Table 5. Vertebral counts including and excluding fish with abnormal vertebrae.

Batch <sup>§</sup>	Incubation Temperature	Percentage Mortality	Number fish with abnormal vertebrae	Vertebral count (all fish)		Vertebral count excluding fish with abnormal vertebrae	
				Mean	s*	Mean	s*
SM1	9.5	6.0	0	62.49	.68		
SM2	14.8	29.3	14	62.84	.79	62.81	.68
SC1	9.5	23.2	12	63.64	.63	63.63	.63
SC2	14.8	36.9	20	63.63	1.04	63.75	.69
FM1	9.5	29.4	0	62.85	.55		
FM2	14.8	69.6	0	62.62	.82		

§ Refer to Table 1. \* Standard deviation.

(SC) batch towards a more typical value of 19 at the higher test temperature.

As mortality increased markedly at the higher incubation temperature in all batches (Table 5), the possibility exists that selective mortality may have been the cause of meristic differences. However, Lindsey (1962a) stated that variations in the numbers of serial structures are probably not caused primarily by differential mortality, while Lindsey & Harrington (1972) demonstrated entirely non-genetic vertebral variation in the self-fertilizing *Rivulus marmoratus* as a response to different rearing temperatures. Nevertheless, genetic determination of meristic characters both within and among populations or races has been demonstrated in various species (Barlow 1961).

In the present study, the significant statistical differences which occurred in various characters among groups of rainbow trout of different parental origin, when incubated under identical conditions (Table 4), provide convincing evidence of genetic input into the expression of meristic characters. In addition, a high correlation between the midparent value and progeny mean was found for the numbers of dorsal fin rays and vertebrae. Despite the low number of degrees of freedom ( $df = 2$ ), the correlation between midparent and progeny counts in dorsal fin ray counts is statistically signifi-

cant. Similarly, the correlation in vertebral counts is only .01 away from statistical significance. Notwithstanding sample size restrictions, the data suggest that inheritance of meristic expression is most probable. A similar trend in the relationship of parent: progeny vertebral counts can be observed in Orska's (1962) data when the control lots of progeny are compared to the parental counts.

The heritable nature of meristic expression in fish is not understood since surprisingly few investigations have been undertaken. It is not presently known whether the phenotypic response of meristic features reflects a corresponding change in the genetic factors regulating them. Hence, certain of the meristic expressions of the parental trout herein examined may have been the result of an environmental response without a corresponding genetic shift and thus were not the heritable expression. Were the genotypic expressions of each character known for the parent fish, the observed midparent:progeny correlations could either improve or break down. Schroder (1965, in Fowler 1970) concluded that the number of dorsal fin rays in *Mollienesia* were inherited in a polygenic manner. The fact that many meristic characters are expressed in a species-specific fashion also points to an inheritable nature of these features.

Genetic differences in meristic features of rain-

bow trout stocks have been ascribed by previous investigators. Neave (1944) found genetic differences among three stocks of rainbow trout in the Cowichan River, B.C.; by rearing fertilized ova of the stocks under the same conditions he concluded that hereditary factors affect the number of oblique scale rows and the number of pored scales in the lateral line. Smith (1969) noted that certain meristic characters, particularly the number of vertebrae, were strongly heritable. Behnke (1972) suggested that the two spawning runs described by Dodge & MacCrimmon (1971) are likely genetically distinct and Ricker (1972) described several genetic differences occurring among many stocks of Pacific salmon and steelhead trout.

The present study has empirically identified both environmental and genetic influences on expression of selected meristic characters of rainbow trout. Because rainbow trout can successfully develop under a variety of environmental regimes (0.3° C – 15.5° C; Dodge & MacCrimmon 1971, Scott & Crossman 1973) the significance of the considerable meristic plasticity of this species (Needham & Gard 1959, MacGregor & MacCrimmon 1976) cannot be fully resolved until precise breeding experiments are carried out. Crosses among parents of known meristic expression will provide invaluable information regarding the heritable nature of meristic characters in rainbow trout.

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## Discussion

The use of meristic features as taxonomic characters has been a subject of considerable controversy in ichthyology since the early experiments of Schmidt as described in Vladykov (1934) which demonstrated environmental modification of vertebral counts in both *Salmo trutta* and *Zoarces viviparus*. Subsequently, the ecophenotypic plasticity of meristic characters in many other species has been documented experimentally (Lindsey 1954, 1958, 1962a, 1962b, Orska 1957, Seymour 1959). Since good taxonomic characters are not, ideally, readily modifiable by the environment (Blackwelder 1967), considerable doubt has thus been cast on the reliability of meristic features in fishes.

Mottley (1934, 1937) was the first investigator to demonstrate the environmental modification of meristic features in *Salmo gairdneri*. More recently, Orska (1957) found that fertilized ova of rainbow trout, when subjected to rapid and intense temperature changes at different stages of development, exhibited considerable deviations in the average number of vertebrae, dorsal, anal and pectoral fin rays. Significantly, she observed two and later three 'phenocritical periods' (Orska 1962) in which the average number of vertebrae would respond either positively or negatively to a higher incubation temperature, and concluded that, during the developmental period in which both truncal and caudal somites are formed, the number of vertebrae is greatly modifiable by incubation temperature. Garside (1966) found that the number of vertebrae decreased at successively higher sustained incubation temperatures and were significantly affected by oxygen concentration. MacCrimmon & Kwain (1969) observed a significant effect of light intensity upon the number of vertebrae and dorsal and anal fin rays of rainbow trout; while Kwain (1975) found a significant interaction between the effects of light and temperature on meristic characters, although temperature was the major factor involved.

In published meristic studies on rainbow trout, Garside (1966) and Kwain (1957) used pooled fertilized ova of mixed parental origin whereas Orska (1957, 1962) used the progeny of single parental pairs. Recognizing that the results of these experiments using different methodology may not be strictly comparable, our examination of the effects of incubation temperature on meristic fea-

tures used both methods but found that, where general trends exist, no difference in the overall results occurred. The average number of dorsal and anal fin rays decreased at the higher incubation temperature in all experiments, a phenomenon previously noted by both Orska (1957) and Kwain (1975). The latter author also observed increases in the number of pectoral fin rays at the higher temperature although Orska (1957) reported that there were both slight increases and decreases in these counts in fish exposed to higher incubation temperature.

The lack of significant response by the number of vertebrae to incubation temperature in the present study is of particular interest because of its contradiction to previous findings (Mottley 1937; Orska 1957, 1962; Garside 1966; Kwain 1975) where the number of vertebrae in rainbow trout decreased with increased incubation temperature. In the present study there was a sharp rise in the number of fish with abnormal vertebrae at the higher temperature, a fact also observed in *Salmo gairdneri* by Orska (1957), Garside (1966) and Kwain (1975). Consequently, we thought that the observed anomalous response may have been the result of incorrectly counting the abnormal vertebrae, the possibility having been previously noted by Garside (1966). However, when the fish with abnormal vertebrae were removed from the present analysis, virtually identical means were obtained (Table 5). Thus it would seem that the response of vertebral counts to incubation temperature in the rainbow trout is either not as plastic as originally believed, or perhaps that fish with different genetic histories may respond differently. Such a phenomenon is recorded by Ali & Lindsey (1974) who found different vertebral count responses to incubation temperature among batches of medaka (*Oryzias latipes*) of different parental origin (most batches responded in a U-shaped fashion to increased incubation temperatures, whereas some responded in a declivous manner and yet others showed no response at all).

Other meristic responses to incubation temperature detected in this study, not previously measured, present further evidence of ecophenotypic variation, notably a decrease in both the number of branchiostegal rays and the number of caudal fin rays at the higher test temperature. The caudal fin ray count, generally considered to be the most constant of rainbow trout meristic features, decreased from an inordinately high mean of 20.5 for Saugeen



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## Chromosomal Differences Among Rainbow Trout Populations

GARY H. THORGAARD

Chromosome numbers varied from 58 to 64 among rainbow trout sampled from 29 locations ranging from Alaska to California. The differences were associated with centric fusions or fissions; the chromosome arm number was constant at 104 while the chromosome number varied. A 58 chromosome karyotype similar to that found in the golden and redband trout was the most commonly observed karyotype over the species range. The similar karyotypes in the rainbow, golden and redband trout suggest that these groups are closely related. If their common ancestor also had 58 chromosomes then chromosomal changes in some rainbow trout since that time may have been associated with centric fissions.

The 60 chromosome karyotype with two subtelocentric chromosomes that has been commonly found in domestic rainbow trout strains was not the most common type, but it was observed in fish from the upper Sacramento River system where most domestic rainbow trout strains originated and in fish from the southern Oregon and northern California coasts. Fish with 60 chromosomes, including four subtelocentric chromosomes, were found in the Puget Sound-Strait of Georgia area while fish with up to 64 chromosomes were found on the California coast.

Most males showed a morphological difference between the X and Y chromosomes but a number of males with no apparent sex chromosome heteromorphism were observed. These fish were particularly common in some populations; these may represent areas in which the rearrangement resulting in a morphological difference between the X and Y has not become fixed in the population.

THE rainbow trout (*Salmo gairdneri*) is native to the Pacific Coast of North America from Mexico to Alaska and has been widely introduced around the world (MacCrimmon, 1971; Sheppard, 1972). A variety of life history (Withler, 1966), meristic and morphometric (Needham and Gard, 1959; Behnke, 1972, 1979, 1981) and protein (Utter and Allendorf, 1977; Allendorf and Utter, 1979) differences have been observed among rainbow trout populations. These differences have raised questions about the relationships of the rainbow trout and the closely related golden and redband trout (Behnke, 1972, 1979, 1981; Gold, 1977; Wisard et al., 1983).

Chromosomal variation has also been observed in rainbow trout (Table 1). Chromosome numbers from 56 to 68 have been reported; the most commonly reported chromosome number has been 60. The variation appears to involve rearrangements (centric fusions and fissions, sometimes termed Robertsonian rearrangements) which change the chromosome number while conserving the chromosome arm number at 104. Similar chromosome rearrangements are

common in other salmonid fish species (Simon, 1963; Roberts, 1970; Gold, 1977; Loudenslager and Thorgaard, 1979) and in other animals (White, 1973). The variation in chromosome number with constant arm number in salmonids is unusual because of reports that it may be found within individual fish (Ohno et al., 1965; Roberts, 1968, 1970; Davisson et al., 1973; Gold and Gall, 1975).

This report describes the results of chromosome analyses of 290 rainbow trout from 29 locations covering much of the species range. Chromosome numbers from 58 to 64 were found in rainbow trout with 104 chromosome arms; the variation showed a geographic pattern that may reflect the evolutionary relationships among the populations.

### MATERIALS AND METHODS

Chromosomes of rainbow trout from 29 locations covering most of the natural species range along the Pacific Coast of North America (Fig. 1) were studied. With the help of many individuals and agencies, I was able to sample

ELECTROPHORETIC EVIDENCE FOR A GENETIC ADMIXTURE OF  
NATIVE AND NONNATIVE RAINBOW TROUT IN THE  
YAKIMA RIVER, WASHINGTON

DONALD E. CAMPTON AND JAMES M. JOHNSTON

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Bob,

I thought you might like  
a reprint of this paper.

Thank you for the opportunity  
to visit with you in October.  
I enjoyed the visit very much.  
I met Jim Shackle for the  
first time in November, and  
~~parents~~ learned first hand that →

all the superlatives you had for  
him were true. Meeting Jim was  
one of the high points of a meeting  
we both attended in Florida.

my address after April 1 is:

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Best regards,

Don