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PROGRAM IN GENETICS
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Dear Bob,

Here is a copy of a manuscript I'm hoping to submit to Copeia in a month or so. It summarizes (at last!) my chromosome studies in rainbow, and some speculations based on the results. I would very much appreciate any comments you have on the manuscript.

Otherwise, things are going reasonably well. I am mostly funded by an NSF grant to work on producing polyploid and gynogenetic rainbow. Outside work, I have been doing some fly fishing for steelhead in the Snake, Grand Ronde and Salmon Rivers. That is a real experience! It seems like the runs are coming back somewhat thanks to the transport program around the dams.

Hope all is going well for you. I would appreciate copies of any recent papers you have put out.

Sincerely,

Gary Thorgaard

John D.

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L. Nelson

T. W. L.

CHROMOSOMAL DIFFERENCES AMONG RAINBOW TROUT POPULATIONS

Gary H. Thorgaard

ABSTRACT

Chromosome numbers varied from 58 to 64 among rainbow trout sampled from 29 locations 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 hatchery rainbow trout strains was not the most common type, but it was observed in fish from the upper Sacramento River system where most hatchery 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 - Straits 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; Behnke, 1979), 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; Gold, 1977; Wishard et al., 1982).

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 unique 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 hatchery and wild fish with a variety of life history patterns (Table 2). In most cases the fish sampled were native to the area sampled; exceptions are noted as footnotes in Table 2.

Most chromosome preparations were made from white blood cell cultures as previously described (Thørgaard, 1976). Chromosome preparations of some young fish were made by direct preparation from body tissues after colchicine injection (Kligerman and Bloom, 1977). Kidney chromosome preparations were analyzed from all the fish from Gilbert Creek, Fall Creek, and the Pit River in California, from three of the fish from the Gualala River, California, and from five of the fish from the 1978 Mad River, California sample. Intestinal chromosome preparations were analyzed from one Gualala River, California fish.

The karyotype of an individual fish was considered established after a minimum of three and usually at least five cells with a particular karyotype were counted.

RESULTS

Variation in chromosome number

Among the 290 rainbow trout examined chromosomally in this study, all but 5 had 104 major chromosome arms. The variation in chromosome number from 58 to 64 (Table 3) thus did not result from variation in the amount of genetic material. The differences apparently resulted from fusions of acrocentric chromosomes to form metacentrics or from fissions of metacentrics to form acrocentrics.

Although there have been reports of variation in chromosome number in cells with the same arm number within individual rainbow trout, I did not find extensive variation of this type in this or earlier studies (Thorgaard, 1976; 1977; Thorgaard and Gall, 1979). Chromosome numbers also did not seem to be tissue-dependent; fish analyzed from kidney chromosome preparations showed similar karyotypes to fish from the same or a nearby population analyzed from white blood cell cultures. For example, among the 1978 Mad River fish sampled, the one fish analyzed from white blood cell cultures had 64 chromosomes like four of the five analyzed from kidney preparations, and the two fish from Gilbert Creek, California, analyzed from kidney preparations had 59 chromosomes like many fish analyzed from white blood cell cultures from the nearby Rogue River, Oregon. The low level of variation within individuals, Hardy-Weinberg pattern of variation within populations (Thorgaard, 1976) and consistent differences between populations are in agreement with an inherited rather than a somatic basis for the chromosomal variation seen in this study.

The chromosomal variation showed a geographic pattern (Table 3). The most common karyotype among the populations studied had 58 chromosomes, including 46 metacentrics and submetacentrics, 2 subtelocentrics

and 10 acrocentrics (Fig. 2). This karyotype appears identical to those previously reported for some rainbow trout and for the closely related redband and golden trout (see Table 1). Two distinct 60 chromosome karyotypes were observed; fish with 44 metacentrics and submetacentrics, 4 subtelocentrics and 12 acrocentrics were observed in coastal Washington and British Columbia samples (Fig. 3, and see Fig. 2, Thorgaard, 1976) while fish with 44 metacentrics and submetacentrics, 2 subtelocentrics and 14 acrocentrics were found in southern Oregon and California (Fig. 4). Fish with more than 60 and as many as 64 chromosomes were found on the California coast (Fig. 5).

There were three triploids and two trisomics among the five fish which did not have 104 major chromosome arms. The triploids were all juveniles; one was sampled from the Mad River, California hatchery in 1977 and two others were sampled from the Pit River hatchery strain kept by the California Department of Fish and Game. Triploid rainbow trout have been observed previously in hatchery populations (Cuellar and Uyeno, 1972; Grammeltvedt, 1974) and may occasionally be present in high frequencies in individual families (Thorgaard and Gall, 1979).

Trisomic rainbow trout with 46 metacentric and submetacentric, 2 subtelocentric and 11 acrocentric chromosomes were found in samples from the Big Creek, Oregon hatchery population and from McGill Creek, California. As with the triploids found in this study, no detailed studies of these individuals were possible because the fish were discarded before the chromosome analyses were performed. Ohno (1970) and Davisson et al. (1972) have previously found viable trisomic trout.

Sex Chromosomes

The heteromorphic sex chromosomes found in male rainbow trout in southwest Washington (Thorgaard, 1977a) and in a California hatchery

population (Thorgaard and Gall, 1979) were apparent in most of the male rainbow trout sampled from Alaska to California (Table 3; see pair 23, Fig. 4 and pair 21, Fig. 5). Although many of the males with three or four subtelocentric chromosomes appeared to have heteromorphic sex chromosomes, they were often difficult to classify (Thorgaard, 1977). Consequently, fish with three or four subtelocentrics were routinely placed in the "uncertain" category as to sex chromosome type (Table 3). Among the fish of known sex which could be classified as chromosomally "XY" or "XX", only 2/93 females appeared XY, while 19/108 males appeared XX (see pair 24, Fig. 2). Several such atypical males were found previously (Thorgaard, 1977). Some populations (Karluk River, Alaska; Butte Creek, California; and West Fork San Luis Rey River, California) had especially high frequencies of atypical males. In addition, in several populations in which the sex of the fish sampled was not known (Pit River, California and Moosehead Creek, California) no individuals with sex chromosome heteromorphisms were found.

DISCUSSION

Patterns of Chromosomal Variation

This study and previous investigations (Table 1) have demonstrated considerable chromosomal variation within the rainbow trout species. Chromosome numbers vary at least from 58 to 64 (some studies suggest an even greater range) and the differences are associated with centric fusions and/or fissions.

This study demonstrated that the variation shows a geographic pattern. A 58 chromosome karyotype is the most common type over the species range. Fish with as many as 64 chromosomes are common on the California coast. Two groups of 60 chromosome fish are present; a northern group is found in the Puget Sound - Straits of Georgia region and a southern group is in southern Oregon and northern California. The northern 60 chromosome fish have two more submetacentrics and two fewer acrocentrics than the southern group; the groups may differ by a pericentric inversion.

The 60 chromosome karyotype in Oregon and California fish (Fig. 4) appears identical to that found in most previous studies of rainbow trout (Table 1). These previous results probably reflect the common origin of most hatchery rainbow trout strains from trout native to the McCloud River, a Sacramento River tributary in northern California (Needham and Behnke, 1962; MacCrimmon, 1971). Samples in this study from near the McCloud River (samples 26, 28, and 29) had fish with the karyotype typical of hatchery rainbow trout. Several previous studies showing rainbow trout with $2n = 58$, rather than $2n = 60$, karyotypes (Wilmot, 1974; Busack et al., 1980) were of fish with non-McCloud River origins.

The differences among populations in this study should, for the most part, reflect natural differences within the rainbow trout species. Some populations I sampled had a mixed origin, however (Table 2), and

reflect this by showing increased chromosomal variation within the population. The Mad River, California hatchery winter steelhead (samples 16a and 16b), for example, had extensive variation both within and between year-classes (Table 3). This probably reflects their mixed origin from Mad River and Eel River winter steelhead; the year-class difference could reflect different relative contributions of the two stocks. Similarly, the variation in the Cowlitz River, Washington winter steelhead (samples 7c and 7d) may reflect their mixed origin from native Cowlitz fish (probably $2n = 58$) and introduced Chambers Creek, Washington winter steelhead (predominantly $2n = 60$). The late-spawning Cowlitz winter steelhead (sample 7e) didn't show any variation, probably because their late spawning time prevented any introgression with the introduced Chambers Creek steelhead. These differences among Cowlitz River steelhead demonstrate how chromosomes might be used to trace ancestry in some rainbow trout populations.

In some other cases it is more difficult to assess the significance of intrapopulation variation. Based on planting histories I would predict that the variation in Rogue River steelhead (sampled 13a and 13b) may be natural, but that the variation in rainbow trout in the Mount Palomar region in Southern California (samples 19 and 20) may reflect introgression between native fish (possibly with $2n = 64$) and introduced rainbow trout. The West Fork San Luis Rey population (sample 20) seems more likely to be of predominately native origin than the Pauma Creek population (sample 19).

Further study is needed to determine more exactly where the natural "transition zones" in chromosome number in rainbow trout are located on the Pacific Coast. Past introductions of fish from hatcheries may make such determinations difficult in some cases.

Chromosomal Variation Compared to Life History, Morphological and Protein Variation

Steelhead returning from the ocean at different times of the year (summer and winter) could be compared chromosomally in two rivers with little history of past introductions: the Quinault River, Washington (samples 6a and 6b) and the Rogue River, Oregon (samples 13a and 13b). The fish from the Rogue and Quinault differed chromosomally, but summer and winter steelhead from each river were similar. This is consistent with studies of protein variation (Utter and Allendorf, 1977; Chilcote et al., 1980) and morphology (Behnke, 1972) suggesting that there are not large genetic differences between summer and winter steelhead from the same river system. These results suggest that the different times of return may have evolved independently in the different river systems.

The chromosomal differences observed among rainbow trout populations in this study do not correspond closely to the morphological and protein differences found among populations in other studies. Morphological comparisons of populations suggest that there may be two major groups: the interior (upper Columbia and Fraser river systems) and redband populations, and the coastal populations. The interior/redband group is characterized by finer scales, lower pyloric caecal counts and brighter colors than the coastal rainbow (Behnke, 1972; Gold, 1977; Behnke, 1979). The major protein allele frequency differences (at the LDH-4 and SOD loci) are between interior rainbow trout populations and coastal populations (Utter and Allendorf, 1977; Allendorf and Utter, 1979). Protein studies suggest that the redband populations are not a single evolutionary group; some populations show similarities to coastal rainbow trout (Utter and Allendorf, 1977) while others show similarities to inland populations

(Wishard et al., 1982). Chromosomally, the interior rainbow trout populations (samples 21-24 in this study, and the Deschutes River, Oregon fish studied by Wilmot [1974], Table 1) and possible redband populations (see Table 1 and samples 15, 25, and 27 in Tables 2 and 3) are characterized by a 58 chromosome karyotype. However, many coastal rainbow trout populations, which differ from the interior populations in morphology and protein allele frequency, also have fish with apparently identical $2n = 58$ karyotypes. Variation in chromosome number from 58 to 64 was observed among coastal rainbow trout populations for which no marked morphological or protein allele frequency differences have been found.

It will be difficult to determine why the chromosomal differences among the populations do not correspond to the morphological and protein differences that are seen. Different selective factors and/or different instances of random genetic drift were apparently involved in the different types of divergence. There are several ideas about the significance of chromosomal change in evolution. Chromosome rearrangements might represent random events facilitated by small population size and inbreeding (Bickham and Baker, 1980), might influence the expression of genes and promote adaptive evolution (Wilson et al., 1974), or might serve as isolating mechanisms to promote the genetic divergence of groups (White, 1978). The role that chromosome rearrangements have played in the evolution of rainbow trout populations is unknown at this time.

Sex Chromosomes

Comparison of the chromosomes of male and female rainbow trout in this study supported earlier observations (Thorgaard, 1977a; Thorgaard and Gall, 1979) of a heteromorphic sex chromosome pair in male, but

not female, rainbow trout. However, 19/108 males with two subtelocentric chromosomes showed no evidence of the sex chromosome heteromorphism; several such "XX males" were found previously (Thorgaard, 1977a). The males lacking the sex chromosome heteromorphism were concentrated in certain populations (Butte Creek, California; West Fork San Luis Rey River, California and Karluk River, Alaska) and are likely to be present in several other populations (Pit River, California and Moosehead Creek, California) in which no evidence of any sex chromosome heteromorphism was found among fish of unknown sex. It is noteworthy that populations lacking the sex chromosome heteromorphism were located near the limits of the species range or in isolated headwater streams.

These results are consistent with an intraspecific polymorphism in the sex chromosome pair in rainbow trout. Heteromorphic sex chromosomes are usually believed to evolve from morphologically identical homologs (Ohno, 1967; Singh et al., 1976); some populations in the species may have retained the primitive characteristic of undifferentiated sex chromosomes, while most have become fixed for, or have a high frequency of, a rearrangement which differentiated the Y chromosome morphologically from the X. Further study of the nature of the Y chromosome rearrangement and its distribution in populations should be interesting.

Chromosomes and Evolutionary Relationships

The observation that the 58 chromosome karyotype, rather than the 60 chromosome type, was the most common over the species range of the rainbow trout was rather surprising. An apparently identical karyotype is also characteristic of the golden and redband trout and is found in the Kamchatka trout, which may represent an Asiatic form of rainbow trout (Table 1). Future studies might reveal differences among these

58 chromosome karyotypes, but the simplest assumption is that they are homologous. This would suggest that the common ancestor of all these groups shared the 58 chromosome karyotype.

If the common ancestor had 58 chromosomes then rainbow trout with higher chromosome numbers must have arisen by centric fission. Centric fusion has usually been believed to be much more common in evolution than centric fission (Sturtevant and Novitski, 1941; Matthey, 1973; Baker et al., 1975) but there are several well-documented examples of centric fission (Yosida et al., 1979; Fryns et al., 1980). I previously proposed that the 58 chromosome karyotype in rainbow trout was derived from the 60 chromosome karyotype by centric fusion (Thorgaard, 1976). Gold (1977) proposed that the 58 chromosome karyotype in golden and redband trout was derived from the 60 chromosome rainbow trout karyotype by centric fusion.

The karyotypes found in rainbow trout are distinct from those in most other western North American trout. The various cutthroat trout subspecies have $2n = 64-70$ but the same number of major chromosome arms as the rainbow, golden and redband trout. Coastal cutthroat (*Salmo clarki clarki*), with $2n = 68-70$ (Simon, 1964; Gold et al., 1977) and West-slope cutthroat (*S. c. lewisi*), with $2n = 66$ (Loudenslager and Thorgaard, 1979) both have many more chromosomes with minor short arms than the rainbow trout. The Yellowstone cutthroat (*S. c. bouvieri*) and Lahontan cutthroat (*S. c. henshawi*) have 64 chromosomes and none with minor short arms (Gold et al., 1977; Loudenslager and Thorgaard, 1979); they lack a subtelocentric chromosome pair (sex chromosome pair) corresponding to that in rainbow, golden and redband trout. The extent of homology between $2n = 64$ cutthroat and rainbow trout otherwise is

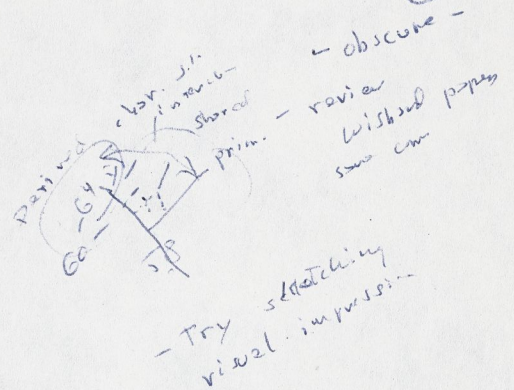
difficult to assess without improved chromosome banding techniques. Both S. apache (Miller, 1972) and S. gilae (Beamish and Miller, 1977) have $2n = 56$ karyotypes distinct from those in rainbow trout.

The simplest general explanation of chromosomal evolution in rainbow trout is that the common ancestor to rainbow, golden and redband trout had 58 chromosomes and lacked a sex chromosome heteromorphism in males. Centric fissions and pericentric inversions led to the present variation within rainbow trout of from 58 to 64 chromosomes with 104 major chromosome arms and 2 to 4 minor arms on subtelocentric chromosomes. The Y chromosome differentiated from the X in most populations so that males showed heteromorphic sex chromosomes; some populations retain the primitive, undifferentiated Y chromosome in high frequency.

The golden and redband trout, although apparently karyotypically identical to many rainbow trout and closely related to them on the basis of electrophoretic studies (Utter and Allendorf, 1977; Wishard et al., 1982), share many meristic and morphological characteristics with cutthroat trout (Schreck and Behnke, 1971; Gold, 1977). Several numerical taxonomic studies have demonstrated that golden and redband trout are phenotypically more similar to cutthroat trout than rainbow trout (Legendre et al., 1972; Gold, 1977). However, these similarities may reflect primitive or ancestral characteristics that these groups have in common (Miller, 1972; Behnke, 1979). As Miller (1972) discussed, primitive features can cause misinterpretations when estimating evolutionary relationships; groups that share them may simply have retained them over a long period from a common ancestor. Many meristic and morphological characteristics of golden and redband trout, like the $2n = 58$ karyotype, were probably present in the common ancestor of the golden, redband and

rainbow trout. The similar high mountain, small stream environment shared by the golden trout and many redband and cutthroat trout may have provided similar selection pressures to retain the primitive characters. For example, Moyle (1976) has discussed how sexual selection may have favored the bright coloration of the golden trout in the Sierras.

Morphological and chromosomal changes in some rainbow trout probably reflect shifts away from the ancestral condition. Perhaps redband trout should be thought of as a broad group of rainbow trout retaining certain ancestral characteristics rather than as a distinct phylogenetic line.



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Table 1

Previous chromosome studies of rainbow trout and some related trout¹.

Study	Species (strain)	Material	Modal chromosome number (Number of individuals studied)	Chromosome arm number	Number of subtelocentric chromosomes observed	Intraindividual Robertsonian variation?
Wright, 1955	Rainbow trout, <u>Salmo gairdneri</u> (hatchery rainbow)	blastula squashes	60	-	-	-
Bungenberg de Jong, 1955	Rainbow trout (hatchery rainbow)	blastula squashes	60	-	-	-
Lieder, 1956 in Simon and Dollar, 1963	Rainbow trout (hatchery rainbow)	blastula squashes	60	-	-	-
Simon and Dollar, 1963	Rainbow trout (hatchery rainbow from several sources)	blastula squashes	60	104	2	-
Simon, 1964	Rainbow trout (steelhead, Soos Cr., WA)	blastula squashes	60	104	?	-
	Rainbow trout (steelhead, Minter Cr., WA)	blastula squashes	60-64	?	?	-
Ohno et al., 1965	Rainbow trout (hatchery rainbow)	embryo, liver, spleen, kidney, ovary, and testis squashes	58-62(12) ²	104	-	+

Table 1 (continued)

Previous chromosome studies of rainbow trout and some related trout.

Study	Species (strain)	Material	Modal chromosome number (Number of individuals studied)	Chromosome arm number	Number of subtelocentric chromosomes observed	Intraindividual Robertsonian variation?
Heckman et al., 1971	Rainbow trout (hatchery rainbow)	cultured leukocytes	60	104	-	+
Cuellar and Uyeno, 1972	Rainbow trout (hatchery rainbow)	gill squashes	60(17),90(1)	104	2-3	-
Fukuoka, 1972	Rainbow trout (hatchery rainbow)	air-dried kidney	60(5),58(1)	104	2	-
Grammeltvedt, 1974	Rainbow trout (hatchery rainbow)	cultured leukocytes	59-63(15)	104(?)	2	?
Muramoto, et al., 1974	Rainbow trout (hatchery rainbow "oceanic form")	air-dried kidney	60(5)	104	2	-
Ohno, 1974	Rainbow trout (hatchery rainbow)	-	56-68 ³	104	?	+
Wilmot, 1974	Rainbow trout (hatchery rainbow, winter steelhead)	-	60	104	2	-

Table 1 (continued)

Previous chromosome studies of rainbow trout and some related trout.

Study	Species (strain)	Material	Modal chromosome number (Number of individuals studied)	Chromosome arm number	Number of subtelocentric chromosomes observed	Intraindividual Robertsonian variation?
Wilmot, 1974	Rainbow trout (summer steel-head from Deschutes and Siletz R., OR. and Clearwater R., ID.)	kidney squashes, leukocyte cultures	58(16)	104	2	-
Vasil'yev, 1975	Rainbow trout (hatchery rainbow)	kidney	62(9), 60(1)	104	2	+
Raicu and Taisescu, 1977	Rainbow trout (introduced wild rainbow)	air-dried kidney, spleen gill, liver	60(3), 58(1), 61(1), 62(1)	100-106	-	-
Thorgaard and Gall, 1979	Rainbow trout (hatchery rainbow)	cultured leukocytes	60(1), 59(4), 89(3), 90(3)	104	2-3	-
Busack et al., 1980	Rainbow trout (Eagle Lake, CA)	cultured leukocytes	58(4)	104	2	-
Kaidanova, 1980	Rainbow trout (hatchery rainbow)	blastula squashes	60-62	104	?	?
Miller, 1972	Golden trout, <u>Salmo aguabonita</u>	gill squashes	58	104	2	-
Wilmot, 1974	Golden trout	gill	58	104	2	-

Table 1 (continued)

Previous chromosome studies of rainbow trout and some related trout.

Study	Species (strain)	Material	Modal chromosome number (Number of individuals studied)	Chromosome arm number	Number of subtelocentric chromosomes observed	Intraindividual Robertsonian variation?
Gold and Gall, 1975	Golden trout	air-dried kidney	58	104	2	+
Miller, 1972	Redband trout, <i>Salmo</i> sp.	gill	58	104	2	-
Wilmot, 1974	Redband trout	several	58	104	2	-
Gold, 1977	Redband trout	air-dried kidney	58	104	2	-
Vasil'yev, 1975	Kamchatka trout, <i>Salmo mykiss</i> , (migratory form)	gill, kidney	60-62(16)	108	0	+
	Kamchatka trout (fresh-water form)	gill, kidney	58-60(17)	104	2	+
Gorshkova, 1980	Kamchatka trout	gill	58	104	2	-

¹ Some of my results on chromosome variation in rainbow trout have already been published (Thorgaard, 1976, 1977a, 1977b). These results are combined with my more recent findings in this report to facilitate description of the geographic pattern of chromosome variation in the species.

² Chromosome numbers from 58 to 65 (with 104 chromosome arms) were observed within individuals.

³ Chromosome numbers observed within individuals; modal numbers are not given.

Table 2

Rainbow trout populations sampled in this study. Past introductions of non-native rainbow trout into some populations are discussed in the footnotes; the other populations are presumed to be predominantly of native origin.

	Location (see Fig. 1)	Type ¹	Sample (Adults or Young, date)	Sample obtained through
1.	Karluk R., AK (57°35'N, 154°20'W)	W, FS	A, 11/76	John Murray, Alaska Dept. of Fish and Game (ADFG)
2.	Naha R., AK (55°35'N, 131°35'W)	W, FS	A, 10/76	Don Siedelman, ADFG
3.	Keogh R., B.C. (50°40'N, 127°20'W)	W, WS	A, 2/77	Eric Parkinson, British Columbia Fish and Wildlife
4.	Big Qualicum R., B.C. (49°23'N, 124°37'W)	H, WS	Y, 12/77	Dick Harvey, Fisheries and Oceans, Canada
5.	Chambers Cr., WA ² (47°11'N, 122°32'W)			Fred Utter, Fred Allendorf National Marine Fisheries Service, Peter Davenport Washington Dept. of Game (WDG)
	5a ^{3,4}	H, WS	A, 4/75-11/75	
	5b	H, WS	A, 2/76	
6.	Quinault R., WA (47°21'N, 124°17'W)			Terry Wright, Quinault tribal biologist
	6a	W, SS	A, 6/76	
	6b	W, WS	A, 1/77	
7.	Cowlitz R., WA ⁵ (46°29'N, 122°44'W)			Harold Fisher-Benson, WDG
	7a ³	H, SS	A, 2/75	
	7b	H, SS	A, 2/76	
	7c ²	H, WS	A, 2/75	
	7d	H, WS	A, 2/76	
	7e ⁶	H, LWS	A, 5/76	
8.	Washougal R. ^{6,7} , (45°38'N, 122°10'W)	H, SS	A, 2/76	Peter Davenport, WDG
9.	Big Cr., OR (46°9'N, 123°35'W)	H, WS	Y, 12/76	Ray Sheldon, Oregon Dept. of Fish and Wildlife (ODFW)

Table 2 (continued)

	Location (see Fig. 1)	Type ¹	Sample (Adults or Young, date)	Sample obtained through
10.	Siletz, R., OR (44°50'N, 123°45'W)	H, SS	Y, 12/76	Homer Clendenon, ODFW
11.	Alsea R., OR (44°25'N, 123°34'W)	H, WS	Y, 12/76	Paul Groman, ODFW
12.	N. Umpqua R., OR (43°17'N, 123°21'W)	H, SS	A, 3/77	Jerry Bower, ODFW
13.	Rogue R., OR (42°40'N, 122°40'W)			Mike Evensen, ODFW
	13a	H, SS	A, 8/76	
	13b	H, WS	Y, 3/77	
14.	Gilbert Cr., CA (41°59'N, 124°12'W)	W, WS	Y, 4/78	California Dept. of Fish and Game (CDFG)
15.	Butte Cr., CA ⁸ (41°30'N, 124°2'W)	W, R	Y, 7/79	CDFG
16.	Mad R., CA ⁹ (40°53'N, 124°00'W)			Bob Will, CDFG
	16a	H, WS	Y, 5/77	
	16b	H, WS	Y, 5/78	
17.	Gualala R., CA (38°46'N, 123°31'W)	W, WS	Y, 4/78	CDFG
18.	Fall Cr., CA (37°3'N, 122°5'W)	W, WS	Y, 6/78	CDFG
19.	Pauma Cr., CA ¹⁰ (33°21'N, 116°57'W)	W, R	A, 5/79	John Hewitson, Encinitas, California
20.	W. Fk. San Luis Rey R., CA ¹¹ (33°20'N, 116°48'W)	W, R,	A, 6/79	John Deinstadt, Larry Bottroff, CDFG
21.	Loon Lk., B.C. (51°10'N, 121°10'W)	W, R	A, 6/77	Eric Parkinson, British Columbia Fish and Wildlife
22.	Columbia R., (Wells Dam) WA ¹² (47°57'N, 119°52'W)	H, SS	A, 1/77	Gary Treffrey, WDG
23.	Snake R., WA ³ (46°35'N, 118°0'W)	?, SS	A, 1/75, 8/75	Jim Mighell, NMFS

Table 2 (continued)

	Location (see Fig. 1)	Type ¹	Sample (Adults or Young, date)	Sample obtained through
24.	Clearwater R., ID (46°31'N, 116°17'W)	H, SS	Y, 10/77	Bob White, Bill Klontz, Univ. of Idaho
25.	Pit R., CA ⁸ (41°00'N, 121°35'W)	H, R	Y, 5/78	CDFG
26.	McGill Cr., CA (41°03'N, 121°58'W)	W, R	Y, 6/78	CDFG
27.	Moosehead Cr., CA ⁸ (41°11'N, 121°48'W)	W, R	A, 11/78	CDFG
28.	N. F. Little Squaw Cr., CA (40°45'N, 122°29'W)	W, R	A, 11/78	CDFG
29.	Battle Cr., CA ¹³ (40°24'N, 122°8'W)	H, FS	A, 1/79	Doug Dysart, U. S. Fish and Wildlife Service

- ¹ Type: H or W indicates hatchery or wild origin; SS, FS, WS, LWS indicate the time of return from the ocean, if the fish were steelhead (summer, fall, winter or late winter). R indicates the fish were resident rainbow trout.
- ² Chambers Cr. hatchery stock is a mixture of fish from various Puget Sound streams, the Nemah River on the Washington Coast, and possibly others (Royal, 1973).
- ³ These results were previously reported in Thorgaard (1976).
- ⁴ These fish were the progeny of matings involving a limited number of parents, and were kept at the NMFS Montlake Laboratory, Seattle.
- ⁵ Summer steelhead in the Cowlitz River are the result of introductions of Washougal River (Skamania) summer steelhead. Chambers Creek winter steelhead were introduced into the Cowlitz system in the 1960's. The May-spawning late winter steelhead stock originated from a native Cowlitz stock (Harold Fisher-Benson, WDG, personal communication).
- ⁶ These results were previously reported in Thorgaard (1977a).
- ⁷ Washougal River (Skamania) summer steelhead hatchery stock originated from fish from the Washougal and Klickitat Rivers in Washington (Jack Ayerst, WDG, personal communication).
- ⁸ Identified by Behnke (1979) as probable resident redband trout populations.
- ⁹ Mad River winter steelhead hatchery stock originated as a mixture of fish from the Mad and Eel Rivers in California (Bob Will, CDFG, personal communication).

- 10 Pauma Creek probably originally had a native rainbow trout population (Eigenmann, 1892) but it seems likely that historical and recent introductions of rainbow trout may have influenced the genetic background of the native population (Behnke, 1979).
- 11 West Fork San Luis Rey River probably originally had a native rainbow trout population (Eigenmann, 1892) but may have been planted with hatchery rainbow trout in the 1890's (Larry Bottroff, CDFG, personal communication).
- 12 Probably mostly of upper Columbia River origin, although there may have been some mixing of Washougal hatchery stock with the Wells Dam hatchery stock (Gary Treffrey, WDG, personal communication).
- 13 Battle Creek hatchery stock originated from upper Sacramento system steelhead, but these fish were mixed with Kamloops trout in the early 1960's, and with Nimbus hatchery steelhead (of mixed Washougal and Eel origins) in the 1970's. The impact of these introductions is unknown.

Table 3 (continued)

Chromosomal differences among rainbow trout populations

Population	Type ¹	No. of fish with chromosome number									Sex chromosome types among fish of different sexes								
		58	59	60	61	62	63	64	3n	Males			Females			Unknown			
										XY	XX	?	XY	XX	?	XY	XX	?	
10. Siletz R., OR	SS	4									3				1				
11. Alsea R., OR	WS	2									2				1				
12. N. Umpqua R., OR	SS	10									9	1							
13a Rogue R., OR	SS	2	6	5								1			6		1	5	
13b Rogue R., OR	WS		2	3							3	1			1				
14. Gilbert Cr., CA	WS		2								1				1				
15. Butte Cr., CA	R	4										3			1				
16a Mad R., CA	WS			1	3	1	1		1		1		2		1	3			
16b Mad R., CA	WS				1				5		1				5				
17. Gualala R., CA	WS								4		1		1		2				
18. Fall Cr., CA	WS								2		1							1	
19. Pauma Cr., CA	R			1	4	1					3		1		1				1
20. W. Fk. San Luis Rey R., CA	R				1	3	2	3			1	4			1	2	1		
<u>Interior populations</u>																			
21. Loon Lk., B.C.	R	5									3	1			1				

Table 3 (continued)

Chromosomal differences among rainbow trout populations

Population	Type ¹	No. of fish with chromosome number									Sex chromosome types among fish of different sexes								
		58	59	60	61	62	63	64	3n	Males			Females			Unknown			
										XY	XX	?	XY	XX	?	XY	XX	?	
22. Columbia R., WA	SS	14	1	1							4		1		11				
23. Snake R., WA	SS	6															3	3	
24. Clearwater R., ID	SS	2																2	
<u>Upper Sacramento Populations</u>																			
25. Pit R., CA	R	4							2									3	3
26. McGill Cr., CA	R		3	3							4			2					
27. Moosehead Cr., CA	R	5																5	
28. N. F. Little Squaw Cr., CA	R			5							2			1			2		
29. Battle Cr., CA	FS		3	2	1										6				

¹ Type: SS, FS and LWS indicate the time of return from the ocean if the fish were steelhead (summer, fall, winter or late winter). R indicates the fish were resident rainbow trout.

FIGURE LEGENDS

- Fig. 1. Native distribution of the rainbow trout (MacCrimmon, 1971; Behnke, 1972) and locations sampled in this study.
- Fig. 2. Karyotype of $2n = 58$ male rainbow trout from Butte Creek, California.
- Fig. 3. Karyotype of $2n = 60$ female rainbow trout from Big Qualicum River, British Columbia.
- Fig. 4. Karyotype of $2n = 60$ male rainbow trout from McGill Creek, California.
- Fig. 5. Karyotype of $2n = 64$ male rainbow trout from Fall Creek, California.

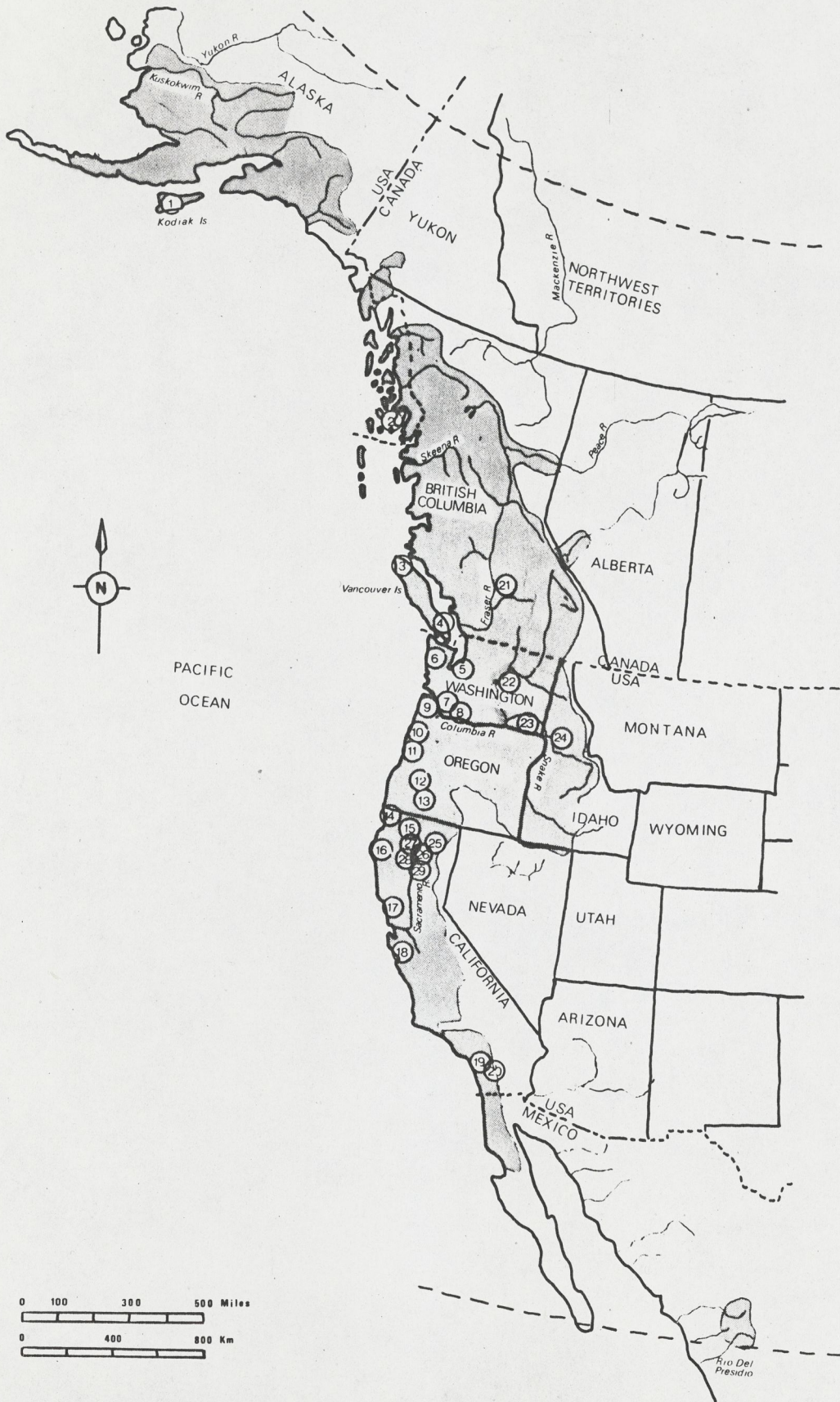


Fig. 1

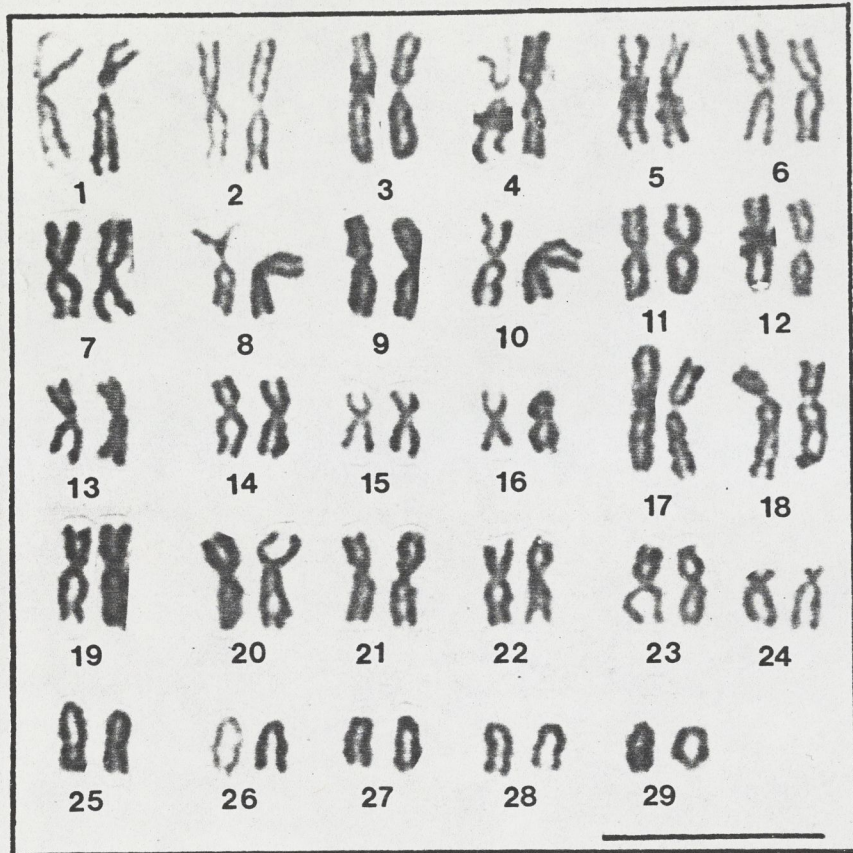


Fig. 2

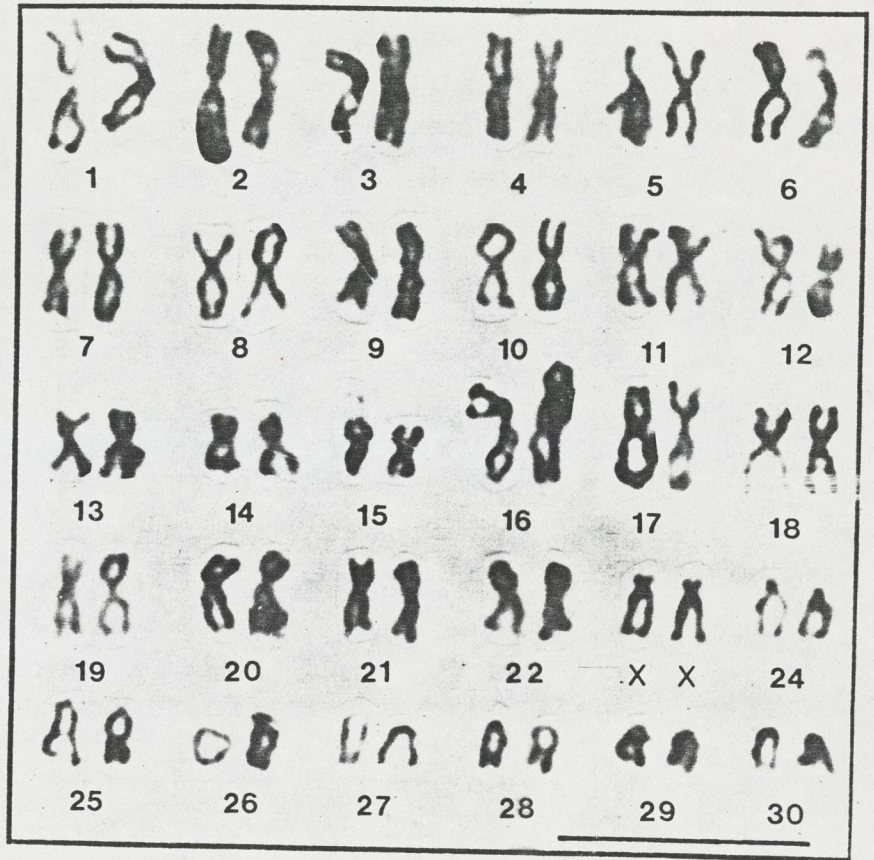


Fig. 3

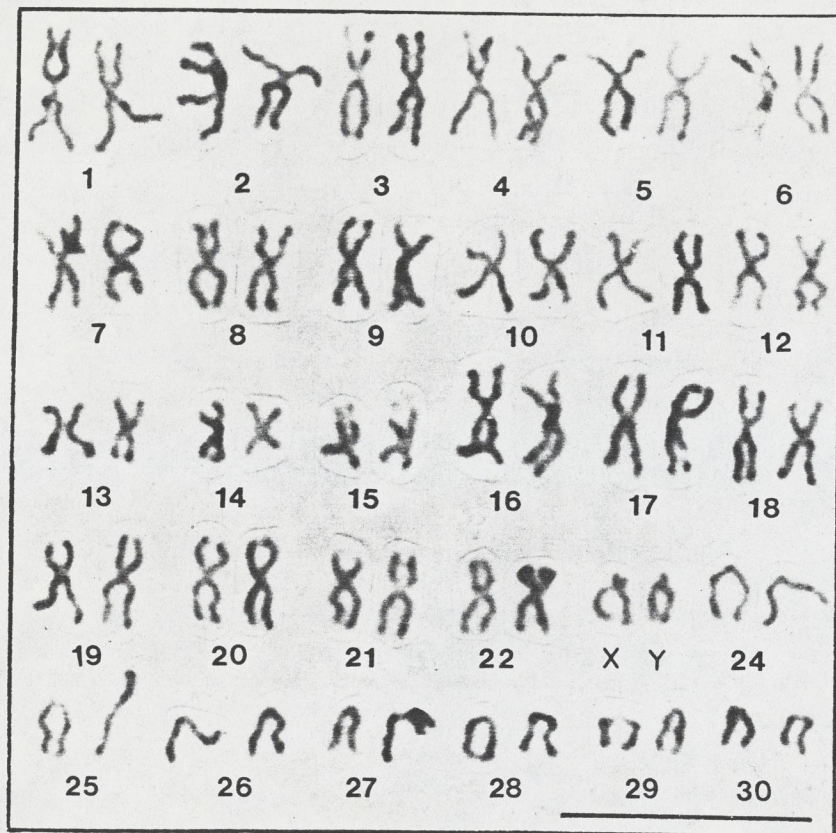


Fig. 4



Fig. 5

FIRST CLASS



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