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Dr. Robert Behnke
Department of Fish and Wildlife Biology
Colorado State University
Fort Collins, CO 80523

Dear Dr. Behnke,

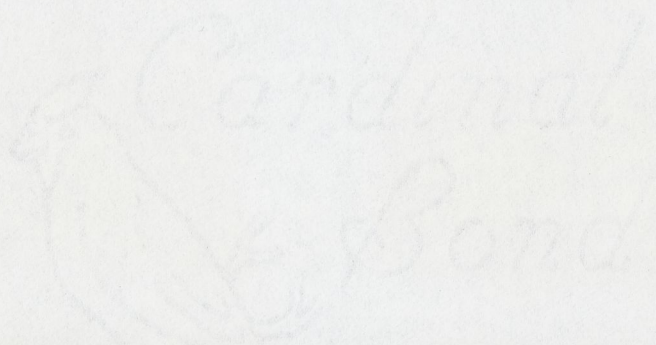
I am about to begin my M.S. research project under Dr. Carl Schreck and Dr. Hiram Li. The principle objective of the project is to determine whether the resident rainbow trout and steelhead in the mainstem of the Deschutes River are genetically segregated into different races. The two types are being managed under this assumption. Because I also will be extensively sampling the tributaries of the lower Deschutes, especially those areas isolated above waterfalls, I also have the opportunity to investigate these populations for ties to the redband trout group. I have tried to design the investigation in order to look at both questions.

I have enclosed a draft of my research proposal for your inspection. I would very much appreciate your comments, criticisms, and suggestions about the design of the project and especially my choice of characters. Thank you very much for your consideration and I look forward to your response.

Sincerely,

Kenneth Currens

Kenneth P. Currens



M.S. Research Proposal

A Genetic Investigation of Resident and Anadromous Rainbow Trout
(Salmo gairdneri) in the Deschutes River, Oregon

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Introduction

Evolution requires genetic diversity. One of the basic problems of evolutionary biology is to document and explain the genetic diversity between and within species. This has important practical consequences: a basic goal in managing species for protection or harvest is to preserve genetic diversity and allow for future adaptive and economic potential (California Gene Resources Program 1982).

Rainbow trout (Salmo gairdneri) are a genetically diverse (Selander and Johnson 1973) and adaptable (Rounsefell 1958) species with recreational importance. Because anadromous salmonids tend to return to their natal streams to spawn, gene flow between populations is minimized and localized populations may be adapted to their home streams systems (Schaffer and Elson 1975, Ridell and Legett 1981, Ridell et al. 1981). However, different populations have different migratory tendencies. Rainbow trout may be non-migratory, living out their lives within hundreds of yards of where they hatched, migratory within streams but not into the ocean, or anadromous (Rounsefell 1958, Behnke 1979, Cargill 1980). Genetically segregated races of nonanadromous rainbow trout may occur in most streams of the Pacific Coast (Shapovalov and Taft 1954, Rounsefell 1958) but the presence of nonanadromous rainbow in a stream does not indicate genetic segregation. Nonanadromous rainbow trout may be the progeny of anadromous or nonanadromous parents (Shapovalov and Taft 1954). Furthermore, decreases in

precision of homing to tributaries within a stream system relative to the river itself may prevent the isolation of nonanadromous and anadromous rainbow trout that is necessary for the evolution of racial differences. Hence, within a complex stream system, steelhead and nonanadromous rainbow trout may be genetically segregated from each other and those of other tributaries in varying degrees or not at all.

As early as 1936, Mottley (1936) recognized that should anadromous and nonanadromous rainbow trout be genetically distinct, conservation of the two forms might require separate treatments and he posed the fundamental question that yet needs to be answered: to what degree is the phenotypic variation between nonanadromous and anadromous rainbow trout genetically or environmentally determined. Neave's (1944) evidence of inherited differences in meristics and migratory behavior between steelhead and a resident population of lake rainbow trout from the Cowichan River, B.C., is the most often cited evidence for genetic separation of the two forms (Ricker 1972). Briggs (1953) believed that because nonanadromous rainbow trout spawn in smaller tributaries and shoaler water, spatial separation accounted for resident races, but did not give evidence for either mechanism. Likewise, Shapovalov and Taft (1954) note that not only may resident races of rainbow trout live in steelhead streams but all combinations and permutations of spawnings and offspring between steelhead and nonanadromous rainbow trout may occur depending on stream conditions. In most stream systems where both forms exist,

the question is still unanswered (Withler 1972).

Evidence for other anadromous salmonids is equally confusing. Ricker (1938, 1940, 1959) noted "residual" sockeye salmon (Oncorhynchus nerka) - nonmigratory offspring of anadromous parents - and speculated on their role in the evolution of landlocked kokanee salmon. However, anadromous sockeye salmon can develop from kokanee populations when migration to sea is possible (Foerster 1947). The two freshwater and one anadromous forms of the Arctic charr (Salvelinus alpinus) have been considered ecological variants of a uniform gene pool (Brenner 1980, Nordeng 1983) and also reproductively isolated species forms (Behnke 1972, 1980, Savvaitova 1980). Freshwater resident brown trout (Salmo trutta) of the Tweed River are largely from anadromous parents (Campbell 1977). Whether brown trout migrate or not depends on the availability of food in the stream, but genetic differences are important where selection favors one or the other forms (Jonsson 1982).

Selection may favor resident populations of rainbow trout through barriers to upstream migration. Studies of rainbow trout above and below waterfalls provide evidence for genetic differentiation of resident and migratory trout that may be useful for investigating the forms where they occur sympatrically. Northcote et al. (1970) showed meristic and electrophoretic differences between rainbow trout above and below falls. Differences in migratory behavior for these trout have a genetic basis in current response (Northcote 1969, 1981) that has been

correlated to differences between lactate dehydrogenase (LDH-4) isozymes (Northcote and Kelso 1981). Functional and physiological differences between the particular liver lactate dehydrogenase isozymes are also correlated to superior swimming performance (Tsuyuki and Williscroft 1973, 1977).

Whether differences in proteins are, in fact, the result of natural selection, as these correlations suggest, or not, is a controversial and unanswered question. However, the analysis of geographical patterns of genetic variation in protein systems as measured by electrophoresis may be used to identify and characterize different populations (Utter et al. 1974, Allendorf and Utter 1979, Utter et al. 1980). The method has been successful in stock characterization studies of salmonids on the Columbia River (Milner 1977, Milner and Teel 1979, Milner et al. 1980, Milner et al. 1981, Wishard and Seeb 1983). Because the protein systems are chosen on the basis of known patterns of simple inheritance and electrophoretic analysis offers an ease of detection and an abundance of data (Utter et al. 1980), the method is an important but complementary tool to other methods in genetic investigations.

Other methods of determining genetic segregation include analysis of chromosome number and morphology and the classical taxonomic measurements of meristic and morphometric characters. Organisms are characterized cytogenetically by chromosome number and morphology. Where variation exists, the use of such karyotypic differences may allow racial identification of fishes

(Roberts 1967). Thorgaard (1983) has reviewed the chromosomal differences among populations of rainbow trout and speculated on their evolutionary significance.

Phenotypic variation in meristic and morphometric characters of the Salmonidae has allowed taxonomists to identify species and unique populations as well as to infer evolutionary relationships (Rounsefell 1962). An extensive literature records the variation found in rainbow trout (see Needham and Gard 1959, Behnke 1972, 1979, 1981). The use of variation in meristic and morphometric characters to infer genetic segregation, however, must consider the effect of environmental differences on the characters. Differences in temperature, light, and dissolved oxygen during development, as well as heredity, produce a variety of meristic responses (see Mottley 1937, Taning 1952, Vernon 1957, Seymour 1959, Kwain 1975).

Because environmental influences may also explain phenotypic variation in anadromy and residency of rainbow trouts, defining the environmental conditions that are associated with the presence or absence of each life history form may also provide clues to how or why they occur. Southwood (1977) has emphasized that a habitat-oriented classification of ecological strategies would help unify the diverse disciplines of population biology. Similarly, Warren and Liss (1983) note that because a system, its environment, and its elements interpenetrate, and the behavior of a system is jointly determined by the interactions of its elements and environments, which lead to qualitative changes in the system,

systems are best defined not by measurements of performances but by the potential capacities of the environments within which they evolved. Such theoretical perspectives help explain the observations that environments that influence life history differences, rather than general environmental variables, are most important in explaining the genetic variability in salmonids (Utter et al. 1980). If we view residency and anadromy as a life history system, then the potential capacities of their environments - the streams - are best approximated by watershed classification (Warren and Liss 1980) and such a scheme may provide explanations for how and why the life history forms occur when and where they do.

The patterns of genetic diversity, should they exist, that biochemical, chromosomal, meristic, and morphometric characters may reveal and the evolutionary or adaptive significance of the differences between anadromous and nonanadromous rainbow trout have not been determined. Presumably, the differences reflect an evolutionary premium on adaptability in a species that has been subjected to isolation by the movements of glaciers or other geological events (Moyle 1976). Interpretations of electrophoretic data conclude that separation of populations by migratory races or life histories is not of major evolutionary importance within the taxon (Allendorf 1975). Behnke (1972) has found no consistent taxonomic differences or clinal trends in comparisons of coastal resident and nonanadromous (steelhead) populations of rainbow trout, but he speculates that as we continue to investigate the

genetics of nonanadromous behavior we will find examples of complete genetic segregation of the two life-history forms as well as transitional areas where environment influences partial genetic segregation. By determining the complete or partial genetic segregation and environments where nonanadromous rainbow and steelhead occur together, we can not only gain a better understanding of the genetic diversity and adaptive significance of these life-history forms but an appreciation for the future potential of the species.

Deschutes River Rainbow Trout

The Deschutes River is one of the few streams in Oregon that supports substantial numbers of native nonanadromous rainbow trout and a wild steelhead run (Fessler 1972). These nonanadromous rainbow trout occur both sympatrically with steelhead in the mainstem of the lower Deschutes and isolated above barrier waterfalls in various tributaries. Several populations of native resident rainbow trout above waterfalls, the native nonanadromous rainbow of the mainstem Deschutes, and the wild summer steelhead are morphologically distinct from each other in body shape and coloration as well as migratory habits. The mainstem nonanadromous rainbow, known as "redsides" (Bond 1973), have traditionally been considered and are presently managed as a separate resident race from the steelhead. However, spawning areas and times may overlap substantially in some years and male

residual hatchery steelhead, which develop a typical redside appearance, have been observed spawning with female steelhead (Fessler 1972). The isolated populations of rainbow trout above waterfalls may also be completely nonmigratory, or contribute immigrants to rainbow trout or steelhead gene pools below the barriers. Whether phenotypic differences in these trouts reflect environmental differences, racial separation, or past evolutionary ties with the ancient inland redband trout group (Utter and Allendorf 1977, Behnke 1979) is not known.

Evidence of genetic segregation of resident and steelhead rainbow trout in the Deschutes River is mixed. Karyotypes of 14 rainbow indicated no difference between mainstem anadromous and nonanadromous forms (Wilmot 1974). An electrophoretic study did not distinguish mainstem resident rainbow trout from steelhead except in one tributary, but the study was flawed by very low sample sizes and too few enzyme systems (Chilcote 1976). Comparisons of the melting and reassociation properties of DNA of both forms also failed to show any differences (Gharrett 1975). Scale analysis indicates that resident rainbow grow faster than steelhead (Fessler 1973) but does not show a genetic basis. Although both forms show a vernal decrease in coefficients of condition, those of resident rainbow trout raised in hatcheries with steelhead appear to be consistently higher (Aho and Fessler 1975). Resident rainbow trout and steelhead raised under normal photoperiods and constant water temperature displayed similar migration characteristics when released (Fessler 1973). On the

other hand, offspring of captured and spawned resident rainbow trout were raised in a similar environment as steelhead at Round Butte Hatchery and they displayed only a weak tendency to migrate when released (Aho and Fessler 1975). Unfortunately, the suspected residents were released at a significantly smaller mean size (15.3cm) than the steelhead (19.0 to 21.0cm), a factor that is known to have a marked effect on residualism in Deschutes River hatchery steelhead (Fessler 1972, 1973). No comprehensive taxonomic study of the Deschutes River rainbow trouts has yet been undertaken.

Statement of Objectives

Objective: To determine whether the resident rainbow trout and anadromous rainbow trout in the Deschutes River are genetically segregated into different races.

Subobjective 1: To determine genetic and phenotypic differences between the resident rainbow trouts and steelhead where they occur sympatrically and isolated by barriers in the mainstem and tributaries of the Deschutes River.

Subobjective 2: To determine the genetic or environmental basis for the phenotypic differences between the resident and steelhead rainbow trouts.

Subobjective 3: To classify the distribution of resident rainbow trout and steelhead trout in the Deschutes River according to habitat.

Materials and Methods

Study Area

The Deschutes River drains 10,400 square miles of northern central Oregon, or 11% of the total area of the state. Much of the drainage was once utilized by anadromous and nonanadromous salmonids, but since the 1950s, the Pelton-Round Butte Dam complex has limited salmon and steelhead spawning to the tributaries and mainstem of the lower 100 miles of river (Figure 1). Within this area, the Warm Springs River, White River, and Shitike Creek are the only tributaries with substantial year-round flows and each of these originates on the eastern slope of the Cascade Range. Other westside tributaries of the Deschutes are Nena Creek and Wapinitia Creek. Eastside tributaries drain Oregon's high plateau and include Trout Creek, Bakeover Creek, and Buckhollow Creek. These smaller tributaries are characterized by varying degrees of intermittent flow and use by both resident and steelhead rainbow trout. Of all these, only the White River is entirely blocked to upstream migration of steelhead by waterfalls two miles from its mouth, although it does support populations of native resident rainbow trout.

Subobjective 1: To determine genetic and phenotypic differences between resident rainbow trouts and steelhead where they occur sympatrically and isolated by barriers in the tributaries and

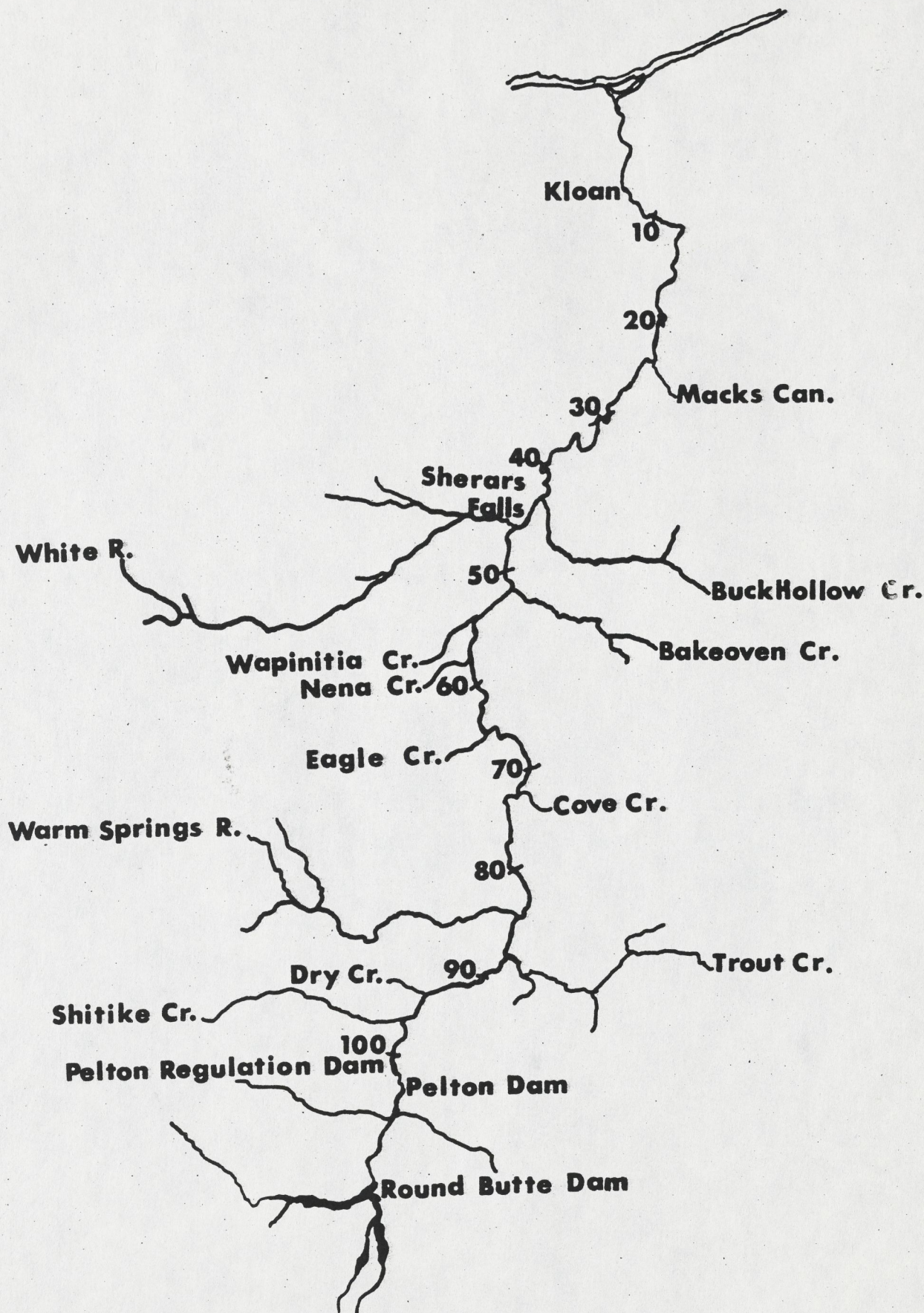


FIGURE 1. Lower 100 miles of the Deschutes River.

mainstem of the lower Deschutes River.

Ho: No differences exist between the rainbow trouts of the Deschutes River other than that some become anadromous and some do not.

Task 1.1: Collect resident and anadromous rainbow trout where they occur sympatrically and where they are isolated by barrier waterfalls.

Rainbow trout will be collected from all major tributaries of the lower Deschutes, as well as the mainstem of the river. Small and intermittent tributaries will be sampled if it appears that they support juvenile rainbow trout of either or both life history types. Populations of rainbow trout above waterfalls will be sampled for all known locations where the waterfall is a known or suspected barrier to upstream migration. A partial list of sampling areas (Table 1) based on information collected from maps, popular and scientific literature, interviews with biologists, and discussions with anglers will be further refined.

Important assumptions must be met. 1) Populations of rainbow trout to be sampled are native, wild fish. Because a selected fishery exists on summer steelhead in the Deschutes, wild steelhead may be identified by the absence of clipped fins and other hatchery marks. Stocking records will be reviewed to determine the extent of introductions into tributaries where nonanadromous rainbow trout will be collected. 2) Collected rainbow trout may be successfully partitioned into anadromous and nonanadromous life history types. This is the major sampling

Table 1. Tentative list of tributaries of the Deschutes River to be sampled for resident and anadromous rainbow trout.

	Westside Tributaries	Eastside Tributaries
	mainstem of river	
	Warm Springs River	Trout Creek
	Shitike Creek	Bakeoven Creek
Sympatric	Nena Creek	Buckhollow Creek
Populations	Wapinitia Creek	
	White River and its	Foley Creek
Isolated	tributaries	(Trout Creek)
Populations	Nena Creek	

problem of the project. Anadromous salmonids are most successfully distinguished from resident forms by scale analysis (Shapovalov and Taft 1954, Bagenal et al. 1973). However, because this research project will require large sample sizes (100 specimens per sampling area for electrophoresis alone), the use of adults for all experiments is logistically infeasible and environmentally unacceptable. I will use adults where necessary but I also propose to collect juvenile rainbow trout and to tentatively partition the two forms by analyzing otolith nuclei. Rybock et al. (1975) showed that size of otolith nucleus is positively correlated to size of dam and could be used to successfully partition wild juvenile steelhead and resident rainbow trout in the Deschutes River. However, Rybock et al. (1975) assumed genetic segregation of the two forms. No evidence exists to show that the mechanism behind the correlation is genetic. The value of such tentative partitioning will be tested against any apparent differences in genetically controlled characters between adults and known resident fish. At worst, the analysis of otolith nuclei provides an estimate of the relative proportion of parental resident rainbow trout and steelhead in the sampled area of stream.

Task 1.2: Determine if biochemical differences exist between the rainbow trout and steelhead where they occur sympatrically and where they are isolated by waterfalls.

Electrophoretic analysis of enzyme systems will be used to test for the presence of biochemical differences between groups of

if not
no
correlation
at
all

rainbow trout. Isozyme frequencies for the enzyme systems will be treated as a characteristic of the group. One hundred juvenile rainbow trout will be collected from each area and for each life history type. Juveniles will be immediately frozen on dry ice. Prior to electrophoresis, eye, liver, and muscle tissue will be removed from the fish. Methods for starch gel electrophoresis will largely follow May (1975, 1980). As many enzyme systems as possible will be tested for variation between groups of trout (Table 2).

Task 1.3: Determine if differences in chromosome number exist between the resident rainbow trouts and steelhead where they occur sympatrically and where they are isolated by waterfalls.

Resident rainbow trout and steelhead will be captured from each of the major sampling areas and transported live to Oregon State University's Smith Farm. The specimens may be either juveniles or adults depending on the technique of chromosome preparation employed. Fish chromosome methodology is reviewed by Denton (1973) and Blaxhall (1975). I have chosen two methods. Kligerman and Bloom's (1977) method of chromosome preparation from solid tissues is fast, inexpensive, and may be used successfully on small fish. However, it does not offer as many metaphases as other methods and requires sacrificing the fish. Thorgaard (1976) has refined a method of leucocyte culture, which does not require sacrificing the fish, that provides many metaphases but is also time consuming. Since conservation of wild steelhead is an important consideration in this project, this latter method will

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Table 2. Tentative list of enzymes and the loci coding for them that will be used to differentiate resident rainbow trout from steelhead.

Enzyme	Abbreviations	No. of Loci
Aspartate aminotransferase	AAT	
Aconitase	ACO	
Adenosine deaminase	ADA	
Alcohol dehydrogenase	ADH	
α -Glycerophosphate dehydrogenase	AGP	2
Creatine kinase	CK	2
Glyceraldehyde-3-phosphate dehydrogenase	GAPDH	4
Isocitrate dehydrogenase	IDH	4
Lactate dehydrogenase	LDH	5
Malate dehydrogenase	MDH	4
Malic enzyme	ME	
Peptidase 1	GL	2
Peptidase 2	LGG	
Phosphoglucose isomerase	PGI	3
Phosphoglycerate kinase	PGK	
Phosphoglucomutase	PGM	2
Phosphomannose isomerase	PMI	
Sorbitol dehydrogenase	SDH	
Superoxide dismutase	SOD (T0)	
Transferrin		
Xanthine oxidase	XO	

be emphasized.

Task 1.4: Determine if differences in meristics and morphometrics exist between resident rainbow trouts and steelhead where they occur sympatrically and where they are isolated by waterfalls.

Adult resident and steelhead rainbow trout will be collected from the mainstem and tributaries where they occur sympatrically. Juveniles will be collected from areas where identification of life history type is certain. Preservation and determination of characters will follow the methods of Hubbs and Lagler (1957). This method of morphometric measurements will be compared with measurements obtained by a recently-developed method of truss measurements using a digitized computer pad (Winans 1983). A tentative list of important meristic and morphometric characters has been constructed from reviews of salmonid systematic literature and personal communication with Dr. Carl Bond, ichthyologist at Oregon State University (Table 3). Dr. Robert Behnke, ichthyologist at Colorado State University, has also been asked to comment on the selection. - G D E C R

Subobjective 2: To determine the genetic or environmental basis for the phenotypic differences between resident and steelhead trouts in the Deschutes River.

Ho: Phenotypic differences between resident rainbow trout and steelhead that occur sympatrically and isolated by barrier waterfalls are due to differences in available environments.

Task 2.1: Determine whether differences in growth rates between

Table 3. Tentative list of meristic and morphometric characters that may be useful in differentiating resident rainbow trout and steelhead.

Meristic Characters.

Number of vertebrae
Number of scales in lateral line series
Number of rows of scales above and below the lateral line
Number of gill rakers
Number of branchiostegal rays
Number of fin rays in dorsal, anal, pelvic, pectoral, and caudal fins
Presence or absence of basibranchial teeth
Number of pyloric caeca

Morphometric Characters

Head depth, width, and length
Width of orbit and least interorbital width
Snout to anterior insertion of pectoral fins
Snout to anterior insertion of pelvic fins
Maximum body width and depth
Relative distance of adipose from dorsal and anal fins
Size and shape of caudal, pectoral, pelvic, anal, and dorsal fins
Length of maxillary

Coloration

Number, size, and shape of parr marks
Distribution of spotting
Colors along lateral line
Colors of fins
Colors on operculum

resident and steelhead rainbow trout are genetically or environmentally determined.

Task 2.2: Determine whether differences in meristic and morphometric characters between resident and steelhead rainbow trout are genetically or environmentally determined.

Adult fish from each of the selected sampling areas will be captured and held for spawning at Oregon State University's Smith Farm. Breeding experiments under controlled or identical hatchery environments will be conducted to test the null hypothesis. Families from each of the selected sites will be constructed by mating a predetermined number of males and females. Number will depend on the availability of tanks, number of required eggs, and determining an appropriate sample size. Eggs from each matings will be pooled and randomly divided into three replicate groups for each of the populations of interest. Eggs from each replicate group will be hatched in separate incubation trays and raised under identical conditions. Length, weight, and selected important meristic and morphometric characters determined by Task 1.4 will be measured on 20 fish from each group at monthly intervals from swim-up to the termination of the experiment. All morphometric and meristic measurements will be made on the fry at the end of the experiment and the fry will be preserved for analysis of otoliths and electrophoresis.

Subobjective 3: To classify the distribution of resident rainbow trout and steelhead trout in the Deschutes River according to

habitat.

Ho: No difference exists in the habitat of resident rainbow trout and the habitat of steelhead.

Task 3.1: Employ techniques of watershed classification to classify the habitats of resident rainbow trout and steelhead where they occur sympatrically and where they are isolated by barriers.

Techniques of watershed classification are still being developed. Warren and Liss (1983) suggest that a watershed may be classified hierarchically by the greater system of which it is a part and by the capacities of its subsystems, including the water, climate, substrate, biota, and cultural systems. Approximations of these subsystem capacities are the stream network, slope, and drainage patterns, annual precipitation, bedrock lithology, soil type, topographic relief, riparian vegetation, presence or absence of fish species and aquatic invertebrates, and the degree of human use. Approximations of the greater system are especially important to the anadromous salmonid when we consider the distance to saltwater, presence or absence of an estuary, and the overall difficulty of the journey.

Watershed classification will take three steps. 1) Initial classification of the Deschutes River drainage will use general information available from geological, topographic, vegetation, fish distribution, and water resource maps. This will provide an approximation of the types of habitat and different environmental capacities in the drainage. The information will be

used to further refine the sampling scheme by constructing an area frame of habitat classes. This will not only allow more complete coverage of different environments but also the potential to identify environments with similar capacities - or streams that might serve as replicate samples. 2) Detailed classification of the tributaries and mainstem that will be sampled will begin by preparing a comprehensive list of characters that approximate subsystem capacities and determining as much of that information as possible from maps. Aerial photographs will also be used. Finally, critical information, such as the presence of waterfalls, of either or both resident and steelhead rainbow trout, intermittent streams, and estimates of the variety, intensity, and duration of environment perturbations will be verified in the field. 3) Multivariate clustering and discriminant analysis will determine relationships of habitat classes.

Task 4.1: Analyze data to determine whether any genetic differences between the groups of rainbow trout and steelhead show racial differences.

Univariate and multivariate analysis of data will be used to determine whether any significant genetic differences exist between the rainbow trout groups, which characters best distinguish the different groups, how similar or different the groups are, and how differences in habitat or environmental capacity may be related to the distribution of phenotypes and genotypes of rainbow trout. Samples collected in different years

will be tested for homogeneity with chi-square tests of contingency and pooled if low levels of heterogeneity are indicated. The significance of differences between means of two populations for meristics and karyotypes will be tested using t-tests, with appropriate adjustments for unequal sample sizes. Significant differences in growth rates or change in morphological characters will be tested using F test of homogeneity of regression (Steel and Torrie 1980). Significant differences in isozyme frequencies will be determined by whether confidence intervals of the most common homozygous genotype overlap or not and by χ^2 tests. Nei's (1978) measure of genetic distance will be used to quantify the differentiation between populations. Discriminant analysis will also be used to test the hypothesis that all groups of rainbow trouts are homogeneous and to determine the cumulative percent variation for each of the characters. Canonical analysis will provide graphic representation of the relationships and cluster analysis will be used to construct dendrograms of the relationships (Sneath and Sokal 1973).

Significance of this Research

The results of this investigation will provide systematic data for several possibly unique groups of rainbow trout in the Deschutes River drainage. Because both anadromous and nonanadromous life history types are targets of a prized wild trout fishery in the mainstem of the Deschutes, knowledge of the genetic segregation of the two forms is important to their

conservation and management. In addition, because this study will genetically describe several populations of unstudied native resident rainbow trout above barriers in the tributaries, this information will provide important baseline data in assessing the impacts of introductions were these tributaries to be opened to naturally spawning steelhead or considered for stocking. Such information may be particularly important now for the White River.

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