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PROJECT 3-78-1312-I

STATUS AND DISTRIBUTION OF CUTTHROAT TROUT (*Salmo clarki lewisi*) IN GLACIER NATIONAL PARK, MONTANA

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PREFACE

The assumption comes naturally to many people that human beings should be managing the earth, and that they should do it largely, if not exclusively, for their own benefit. Likely enough, this premise describes the attitude of a large majority of our global citizens, although we hear increasingly from a coterie of idealists who regard it as arrogant and self-centered. These few suggest that it could be spiritually uplifting for men to broaden their view and concede that other living things have a right to space and survival .... The logic behind this reasoning is that sharing the earth is good business. There are solid reasons for preventing further extinctions .... Preserving species helps retain those management options we talk about, and a preliminary knowledge of man-earth relationships suggests that the more natural things are, the fewer mistakes will be made.... There ought to be some measure of safety in mechanisms that have worked satisfactorily through long periods of geologic time.

Durward Allen (1976)

SUMMARY OF PROPOSAL

Research is proposed to answer three basic questions: (1) to what extent have indigenous cutthroat trout populations in Glacier Park been genetically altered as a result of hybridization with stocked fish, (2) do undisturbed populations of native trout still exist in some park waters, and (3) what steps must be taken to preserve, or possibly restore, native cutthroat trout in selected waters?

Trout will be collected by gill nets and electrofishing equipment for comparative electrophoretic and morphomeristic analyses. Work will proceed in priority order on the North and Middle Forks of the Flathead River, the South Saskatchewan, and the Upper Missouri River drainages within the boundary of Glacier National Park.

A budget of approximately $44,000 is recommended for the 5.8-year project. Field investigations will commence in June 1978, and completion is expected in the spring of 1983. Included in the proposal are a general work plan and supplemental information summarizing much of what is presently known about the west-slope cutthroat trout.

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STATEMENT OF PROBLEM

The native subspecies of cutthroat trout, *Salmo clarki lewisi*, commonly referred to as the "westslope" cutthroat, has been severely depleted over most of its historic range, including the waters of Glacier National Park. Roscoe (1974) cites several causes for the decline of this unique subspecies, including: (1) loss of habitat from hydroelectric development and other floodplain disturbances; (2) competition with exotic species; and (3) hybridization with introduced fishes.

Some of these factors have contributed to the decline of indigenous trout populations in Glacier National Park. The widespread introduction of exotic species has profoundly disrupted the natural order of aquatic ecosystems in several park drainages. Native fishes have also been callously exposed to genetic contamination from hybridization with introduced trouts. Resident trout populations may, as a result, be less capable of surviving environmental stresses which periodically occur, due to genetic modification. The genetic "programming" of resident fish populations evolved through millenia of selective pressures, essentially by "trial and error." Gene pool alterations during the past half century brought about by fish stocking have not enhanced the long-term survival prospects of indigenous trout populations.

Rainbow trout, *S. gairdneri* (Richardson), were widely stocked in Glacier's lakes prior to World War II. Since both rainbow and cutthroat trout spawn in the spring, hybridization has occurred in several park drainages. Viable populations of rainbow trout persist today in some waters, mainly east of the Continental Divide. Their influence on native cutthroat populations is not presently known.

Of equal concern is the likelihood that native cutthroat populations have been affected by past introductions of other cutthroat subspecies. Several million Yellowstone cutthroats, for example, were released in park waters over a period of several decades through the late 1940's. More recent introductions probably included trout genetically similar to the indigenous subspecies, but the origins of some parent stocks have never been clearly established.

A bothersome aspect of the fish-stocking situation in Glacier Park is the presence of exotic species in a number of lakes for which there are no stocking records. These include lake trout, *Salvelinus namaycush* (Walbaum); lake whitefish, *Coregonus clupeaformis* (Mitchell); and, in some instances, Kokanee salmon, *Oncorhynchus nerka* (Walbaum). Since it is apparent that fish plantings in the park were not all documented, unrecorded introductions of cutthroat trout may also have occurred. Hence, uncertainties exist about the genetic integrity of cutthroat populations in virtually all park drainages where the species was historically present.

RESEARCH PLAN

Introduction

Any management plan aimed at perpetuating the genetic identity of the native cutthroat trout must proceed initially with the assumption that indigenous populations have been able to survive someplace free from human interference. Hopefully, this has been the case in certain remote areas of Glacier National Park. This means, populations which have not been genetically disturbed through hybridization with other trouts. In addition, a successful outcome requires that native populations remain in sufficient abundance to insure preservation of the full range of genetic diversity which characterized the indigenous gene pool.

Should viable populations of native cutthroats be located, two important benefits would immediately accrue: (1) designated waters harboring such populations could be managed intensively to insure the perpetuation of a unique and scientifically valuable native species; and (2) a reliable source would exist locally for brood stock which could later be used to re-establish the pure strain of *Salmo clarki lewisi* in disturbed ecosystems.

Since exotic strains of cutthroat trout have at one time or another been stocked in most park lakes capable of sustaining fish, the possibility exists that genetically "pure" populations of native trout no longer occur in Glacier Park. This would complicate any program aimed at restoring the best possible representation of the native subspecies, but this situation would not necessarily eliminate prospects for re-establishing a trout essentially identical to the indigenous strain. Under this circumstance, the objective would be to judiciously manage populations which show the least influence from hybridization with other species or subspecies, and assume that selective pressures will, over the long term, re-establish a population gene pool similar to that which existed prior to human interference. However, it would be unwise to rely totally on that assumption. While it may be expedient to protect trout populations that have been altered only slightly, it would be inadvisable to utilize parent stocks from these populations for restoring indigenous cutthroat trout to disturbed ecosystems. If "pure" populations of native trout cannot be located inside Glacier National Park, it would be better to seek cooperation with other agencies and attempt to develop a genetically pure brood stock of "westslope" cutthroat trout from another area for reintroduction to the park.

Regardless of the course of action ultimately chosen, it is first necessary to gain a clear understanding of the extent to which resident trout populations have been genetically disturbed. This does not promise to be an easy task since the implied prerequisite is the capability for discriminating hybrid influences as far as forty generations advanced.

Purpose and Scope

This research will document the genetic variability of cutthroat trout populations in Glacier National Park. The approach will be examination of selected physical and biochemical parameters that are genetically transmitted. Results of the study will provide a rationale for managing cutthroat trout in park waters where the goal is to perpetuate the indigenous species.

Objectives

Objectives of the study are to:

1. Examine stocking records to identify park waters which may not have been stocked and could, therefore, contain genetically undisturbed populations of cutthroat trout.

2. Identify from stocking records waters where gene pool contamination has likely influenced native cutthroat trout populations.

3. Attempt to identify park waters excluded from the natural range of cutthroat trout, but which now contain the species, in order to locate specimens which characterize introduced strains.

4. Collect 30 cutthroat trout from each designated water as categorized above.

5. Examine samples of cutthroat trout by means of electrophoretic analyses to observe possible differences in the protein behavior of specific body tissues.

6. Examine samples of cutthroat trout from selected park waters for significant differences in morphological and meristic characteristics.

7. Consolidate the morphological and electrophoretic data and formulate conclusions about the genetic status of cutthroat trout populations in park waters.

8. Make recommendations for management of this species in Glacier National Park, and identify additional research needs.

Methods

Study Design. Field work will be undertaken in priority order on the North Fork, Middle Fork, Hudson Bay, and Upper Missouri River drainages. Individual waters have been assigned a priority within each drainage. Lakes containing exotic fishes, and which have a history of intensive trout stocking, are less likely to contain stable populations of indigenous fishes. Conversely, headwater lakes which escaped stocking show promise, particularly in situations where effective downstream barriers exist. No effort will be made to examine all park waters in the present study.

Field Procedures. Trout will be collected from lakes by horizontal gill nets and hook-line fishing. A DC shocking boat will be used where conditions allow. A small rubber raft and canoe will be used to facilitate work on lakes. Stream collections will be made with a backpack electroshocker.

Each trout will be measured for total length (millimeters), weighed (grams), and a scale sample will be collected from the right lateral line region. Color transparencies will be taken of representative fish from each sample population for later reference. Trout will be identified by a numbered tag fixed to the lower jaw. Fish will be opened by a ventral slit to expose the viscera; a sex determination will be made and a piece of the liver will be removed (approximately one square centimeter). A similar-sized piece of muscle tissue will be cut from the right side. The right eye of each specimen will also be removed. The pieces of liver, muscle tissue, and the eye from each trout will be placed in a small plastic bag in the field, with each sample bearing an identification tag corresponding to the trout number. The tissue samples will be placed in a portable ice-chest for temporary storage, and later transferred to a freezer to await electrophoretic analyses.

After removal of these tissues in the field, the fish will be placed in plastic bags containing 10 percent formalin. Specimens will later be transferred to rigid containers and preserved in buffered 10 percent formalin.

Laboratory Tests. Historically, fish systematists have relied upon an examination of selected meristic and morphometric features as their principal diagnostic tool. Where taxonomic relationships are distinct, as at the genus or species level, this approach works quite well and often can be performed without highly sophisticated methods. However, as taxonomic affinities draw closer together, as in subspecies differentiations, or in the case of intraspecific hybrids, morphological criteria become more difficult to use as a diagnostic tool. Although physical features can still be used with moderate sensitivity to discriminate at the subspecies level, more skill is required and larger sample sizes are needed for reliability.

Recently, a great deal of effort has been given to the development of biochemical tests for use in fish systematics. One of the more promising techniques is starch-gel electrophoresis, a method developed in the mid-1950's but which has only recently found widespread application in fish genetics (Gall, et al., 1976; Utter, Allendorf, and Hodgins, 1973; Utter, Allendorf, and May, 1976). An excellent review of the potentials and limitations of biochemical genetic studies in fishes is presented by Utter, Hodgins, and Allendorf (1974).

The methodology to be followed in this study is based on the premise that a combination of morphometric and biochemical techniques will lead to more definitive conclusions than would be possible through either approach alone. By combining information obtained from stocking records with electrophoretic and morphometric data, it should be possible to resolve the genetic background of cutthroat populations in Glacier's waters, and more important, to document the occurrence of undisturbed populations if any still exist in the park.

Meristic-Morphometric Analyses: Murphy (1974) examined meristic and morphometric features in cutthroat trout collected from several drainages in Wyoming, Montana, Idaho, Utah, and Nevada. Included were samples of Yellowstone cutthroats, "westslope" cutthroats, and hybrids of these related subspecies. Two meristic features were found to differ with enough consistency to permit reliable separation of the Yellowstone and "westslope" forms. Population samples of the Yellowstone cutthroat showed higher average numbers of both gill rakers and pyloric caeca (See Table 2, page 18).

While these two parameters may be most useful for detecting hybrid influences in trout collected from Glacier's waters, other meristic and morphological features may be considered at the discretion of the investigators.

Electrophoretic Procedures: The method to be used in these studies is horizontal starch-gel electrophoresis, incorporating refinements described by Utter, et al. (1974) and Utter and Hodgins (1970). The procedure involves maceration of a tissue sample in an appropriate chemical buffer and subsequently drawing these across a gel strip by application of an electrical current. Depending upon the type of buffer system used, the amount of electrical current, and other variables, the protein complexes present in the tissue will migrate at different rates across the electrically charged field. A skilled interpreter can often identify the types of proteins present and compare these with samples obtained from similar tissues in other fish. Such comparisons may provide valuable clues about the evolutionary affinities between different populations since the protein systems being examined are genetically determined.

Time Frame

The study will require five seasons of intensive field work to complete. Work will commence in the spring of 1978 and continue at least through 1982. Park drainages will be investigated according to the following schedule:

TABLE 1. Field Work Schedule, 1978-82.

	Calendar Year				
Drainage	1978	1979	1980	1981	1982
North Fork	xxxxxxx	xxxxxxx			
Middle Fork		xxxxx			
Hudson Bay		xxxxxxxx	xxxxxxxx	xxxxxxxx	
Upper Missouri				xxxxxxx	xxxxxxx

Completion of field work is expected by fall 1982, and a final report will be submitted the following spring. Annual progress reports will be prepared and may include interim management recommendations.

Project Administration

Responsibilities for the various phases of the study are delegated to the following individuals:

Dr. Leo Marnell, National Park Service, Glacier National Park, West Glacier, Montana 59936. Overall study coordinator. Will be responsible for field data collection.

Dr. Robert J. Behnke, Colorado State University, Fort Collins, Colorado 80521. Principal advisor on zoogeography and systematics of trout. Has primary responsibility for meristic-morphometric analyses.

Dr. Fred W. Allendorf, University of Montana, Missoula, Montana 59812. Primarily responsible for electrophoretic analyses.

BUDGET -- STATUS AND DISTRIBUTION OF CUTTHROAT TROUT IN GLACIER NATIONAL PARK, 1977-82.

	Fiscal Year						Account		
Expenditure Category	1977	1978	1979	1980	1981	1982	Aq. Ecol. Account	Suppl. Funds	Total
Field Operations									
Major Equipment*	4,630	3,680	-	-	-	-	8,310	-	8,310
Maint./Repl. Exp.	-	-	100	100	300	-	500	-	500
Vehicle	-	1,000	1,000	1,000	1,000	1,000	5,000	-	5,000
Pack Stock	-	300	300	300	300	300	1,500	-	1,500
Seasonal Aid	-	-	2,480	2,800	3,000	3,100	11,380	-	11,380
Supplies-Mat.	-	250	250	250	250	250	1,250	-	1,250
Contract Investigations									
Morphometric-Meristic Analyses - Colorado State University									
Salary - Prin. Investig.	-	500	500	500	500	1,000	-	3,000	3,000
Student Asst, 280 hrs	-	700	700	700	700	700	-	3,500	3,500
Travel	-	300	300	300	300	300	-	1,500	1,500
Electrophoretic Analyses - University of Montana									
Salary - Prin. Investig.	-	500	500	500	500	1,000	-	3,000	3,000
Lab Tests	-	800	800	800	800	800	-	4,000	4,000
Travel	-	200	200	200	200	200	-	1,000	1,000
TOTAL / YEAR	4,630	8,230	7,130	7,450	7,850	8,650	27,940	16,000	43,940
Aquatic Ecol. Acct.	4,630	5,230	4,130	4,450	4,850	4,650	27,940	-	
Suppl. Funds	-	3,000	3,000	3,000	3,000	4,000	-	16,000	

*Major Equipment

1977	
DC Backpack Shocker	1,000
Electrofishing Boat	3,500
1 pr Chest Waders	50
Scales, 0-2 kg	30
Length Board	50
	4,630
1978	
Gill Nets	950
E-F Boat Fixtures	1,500
2 pr Chest Waders	100
Scales, 0-10 kg	30
Rubber Raft	175
Canoe	350
Portable Freezer	25
Generator, 1500 W	550
	3,680

SUPPLEMENTAL INFORMATION

Westslope Cutthroat Trout
Salmo clarki lewisi

SUPPLEMENTAL INFORMATION

Administrative Status

The Montana "westslope" cutthroat trout was at one time listed as an "endangered" species in the U.S. Department of Interior Redbook. However, in 1973 its classification was changed to "status undetermined" due to confusion which arose over the taxnomic relationship between this subspecies and a similar trout in the Yellowstone Basin. Although the systematics of the cutthroat complex remains somewhat confused, the indigenous subspecies found in Glacier National Park should be regarded as "endangered" until sufficient information becomes available to alter this assessment. The validity of a species or subspecies must not obstruct protective measures for rare animals. Rather, the major consideration should be that the animal represents a unique biological entity which may be in danger of extinction (Behnke and Zarn, 1976).

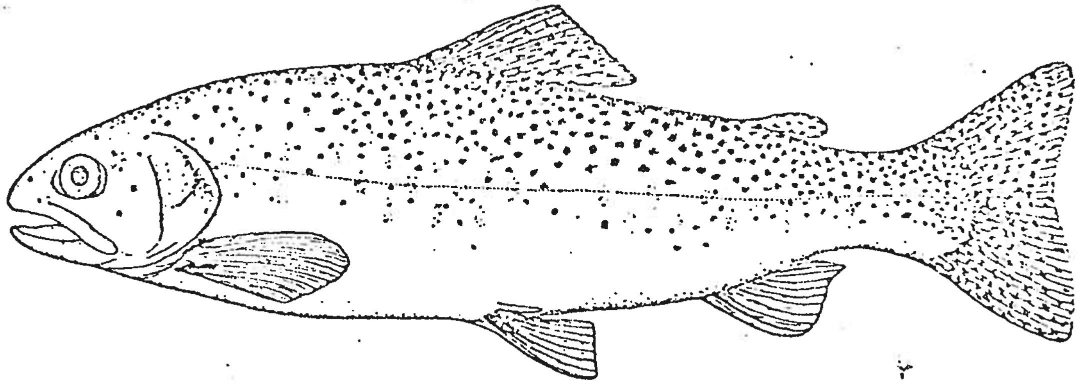
Description

Recognition of subspecies within the polymorphic cutthroat trout complex has little validity on the basis of morphological characteristics (Behnke, 1971). Although slight differences in pigmentation are discernible for some subspecies (Behnke, 1967, 1971; Behnke and Zarn, 1976; Murphy, 1974; Miller, 1972), behavioral nuances evolved through millenia of geographic separation may be a more appropriate basis for taxonomic divisions.

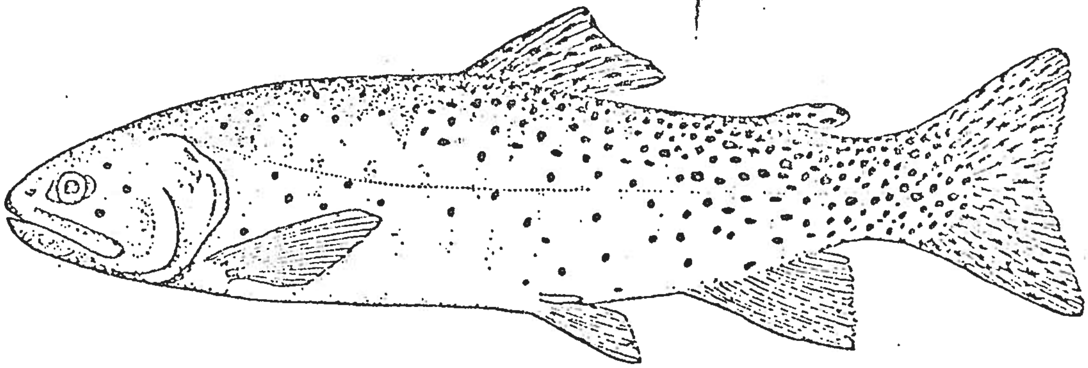
Despite close phenotypic similarities, "pure" populations of some subspecies exhibit distinctive markings which can be recognized by trained persons. Differences in spotting patterns cannot, however, be consistently relied upon to discriminate hybrids and intergrades; hence, the utility of this approach may be limited in some field situations.

Stocking records for Glacier National Park indicate that indigenous trout have been exposed to hybridization with the Yellowstone cutthroat, and also with rainbow trout. Although both the westslope and Yellowstone cutthroats exhibit a wide range of natural variability, the former trout can usually be recognized by its characteristic pattern of small irregularly shaped spots, mainly in the caudal peduncle region. The dense spotting pattern often extends anteriorly to the head, concentrating above the lateral line. Relatively few spots are seen below the lateral line anterior to the anal fin (Figure 1a). In contrast, the pure form of Yellowstone cutthroat typically has large roundish spots distributed laterally over most of the body. The spots are noticeably fewer in number, but more may extend below the lateral line (Figure 1b).

Meristic characteristics for the westslope subspecies have been compared with the Yellowstone trout by Roscoe (1974). Although a distinction is made between westslope (i.e., Upper Columbia River), Upper Missouri, and southern Saskatchewan populations, Roscoe concluded that all three populations represented *lewisi*. When meristic features of *lewisi* were compared with the Yellowstone trout, only



A. Westslope cutthroat trout (*Salmo clarki lewisi*).



B. Yellowstone cutthroat trout (*Salmo clarki* sp.).

Figure 1. Spotting patterns of the westslope and Yellowstone subspecies of cutthroat trout. (Adapted from Roscoe 1974)

two obscure characteristics separated populations of the two subspecies. Yellowstone cutthroats exhibited a higher average number of pyloric caeca and typically possessed more basibranchial (hyoid) teeth (Table 2). The latter characteristic is perhaps the most discriminating feature between these very similar trouts.

Rainbow × cutthroat hybrids also present problems of visual recognition, especially beyond the F_1 generation where the natural range of variability for either species could obscure the influence of hybridization. For example, it had long been thought that rainbow trout stocked during the early 1900's in Yellowstone Lake perished and that the indigenous cutthroat fishery had escaped genetically intact. Recent studies, however, suggest that rainbow trout hemoglobin may be present in the Yellowstone cutthroat fishery. Evidently, this influence has persisted in the population as a result of hybridization that occurred more than half a century ago (Wydoski, et al., 1976).

Hanzel (1959) noted that F_1 rainbow × cutthroat hybrids in Montana waters often display a faint slash under the "throat," a pale margin on the anal fin, and small to intermediate spots along the lateral line. Roscoe (1974) states that pelvic fin ray counts may also be useful for detecting the influence of rainbow trout hybridization in cutthroat populations. Pure cutthroat trout almost invariability have nine (occasionally eight) developed rays in the pelvic fins. Since rainbows typically have ten rays, the presence

TABLE 2. Meristic Comparisons of Three Cutthroat Trout Populations.

Cutthroat trout geographic populations	Number of vertebrae	Gill rakers	Scales above lateral line	Scales on lateral line	Pyloric caeca	Basi-branchial teeth
Salmo clarki lewisi						
West-slope waters						
NW Montana						
Range	59 - 62	17 - 24	38 - 46	149 - 182	24 - 48	1 - 24
Mean	60.8	19.3	41.2	165	36.6	7.7
Upper Missouri River Basin						
Range	60 - 62	18 - 22	37 - 50	147 - 204	25 - 44	1 - 14
Mean	60.8	19.4	42.3	173	33.3	6.4
South Saskatchewan River Basin						
Range	59 - 63	15 - 21	31 - 40	137 - 178	23 - 50	1 - 23
Mean	60.9	17.9	37.9	158	38.6	8.0
Salmo clarki sp.						
Yellowstone River Basin						
Range	59 - 63	18 - 23	37 - 53	146 - 188	33 - 60	2 - 53
Mean	61.6	20.5	43.4	169	44.8	22.0

Adapted from Roscoe (1974) with modifications by Behnke (*personal communication*).

of cutthroats with more than nine pelvic fin rays is a good indication of genetic influence from rainbow trout.

Range and Distribution

The native range of *S. c. lewisi* is bounded on the west by the Pend Oreille and Coeur d'Alene River valleys reaching across northern Idaho into Washington. Similar specimens have been reported from the Lake Chelan area along the east slope of the Cascades (Behnke, *personal communication*). From there, it ranges into the Salmon and Clearwater drainages, tributary to the lower Snake River in central Idaho. From that point, *lewisi* extends northward through the Clark Fork and Flathead River valleys of western Montana and into the Kootenai drainage of southeastern British Columbia.

East of the Continental Divide, this subspecies is sparsely distributed in portions of the Upper Missouri Basin, occurring in the Beaverhead, Gallatin, and Madison River systems. It is indigenous to the mainstem Missouri River above Fort Benton, Montana, although isolated populations may occur in some tributaries downstream to the confluence of the Musselshell River. In the South Saskatchewan drainage, *lewisi* extends from the St. Mary Valley along the east slope of Glacier National Park northward to the Bow River in southern Alberta, Canada. (See map, Figure 2)

Roscoe (1974) reports that pure populations of *lewisi* still exist in Poorman and Ross Creeks (Clark Fork drainage) and in the

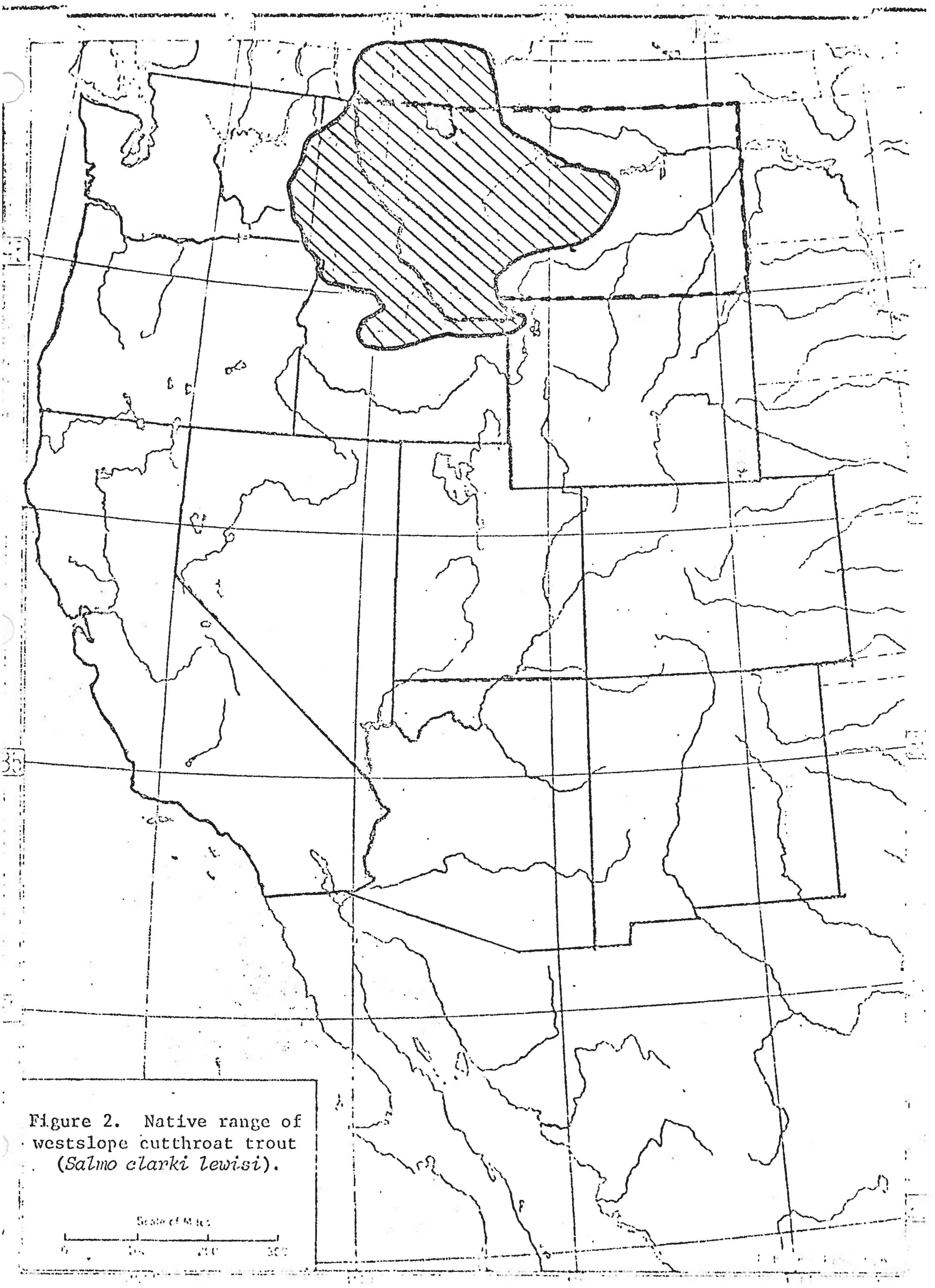


Figure 2. Native range of westslope cutthroat trout (*Salmo clarki lewisi*).

South Fork of Granite Creek (Pend Oreille drainage). In the upper Flathead drainage, populations were also found in the Spotted Bear River and in Upper Trwin Creek. Other headwater streams near Glacier Park that may contain indigenous populations of *lewisi* are Gateway, Crow, and Griffen Creeks, all tributary to the South Fork of the Flathead River above Hungry Horse Reservoir. Reinitz (1974) found essentially pure populations of *lewisi* in Bear Trap, Shave Gulch, Alice, and Little Stoney Creeks in Montana's Bitterroot Mountains, and in Ward Creek near the Montana-Idaho border downstream from Flathead Lake. Varley (*personal communication*) reports that relict populations of *lewisi* may also exist in the extreme western portion of Yellowstone National Park.

There is no certified brood stock of pure westslope cutthroat presently in captivity. Trout derived from stocks indigenous to the South Fork of the Flathead River above Hungry Horse Dam are maintained at the state hatchery in Arlee, Montana, but some authorities are skeptical about the genetic history of these fish (Larry Peterson, George Holton, *personal communication*).

Zoogeography

All interior subspecies of cutthroat trouts derived from a common ancestor. While *Salmo clarki* probably differentiated prior to the last glacial epoch, events associated with the Wisconsin glaciations seemingly had the most to do with the distribution and subspeciation of the cutthroat complex (Behnke, 1972). An excellent zoogeographic account of this species throughout the northwest interior portion of its range is presented by Roscoe (1974).

It is assumed that the ancestral lineage of interior cutthroat trouts derived from an aboriginal form distributed throughout the network of Pacific Northwest coastal streams. That trout is now represented by the coastal subspecies *Salmo clarki clarki*, which significantly has a diploid chromosome number four higher than is reported for any other subspecies of cutthroat. The primitive interior trout evidently differentiated after being physically isolated from its coastal precursor, and subsequently dispersed throughout several interior basins, including the lower Columbia, Yellowstone, Colorado, and Bonneville drainages. The ancestral "prototype" is believed to have been characterized by relatively few spots, fairly large in size, distributed laterally along the caudal peduncle and tail. This contention is supported by the present-day occurrence of several disjunct populations of large-spotted cutthroats in restricted portions of the Columbia River Basin. These relict populations are presumed to be descendents of the ancestral large-spotted fish that gained access to this drainage ahead of the rainbow trout. Evidently, these cutthroats survived only in areas where physical barriers protected them from displacement by the latter species. This scenario suggests that existing populations of large-spotted trouts in the Yellowstone Basin and portions of the Snake River have their affinities with relict populations interspersed throughout the Columbia Basin (Murphy, 1974).

The "westslope" subspecies *lewisi*, characterized by a profuse pattern of small irregularly shaped spots, evolved more recently. Differentiation from the large-spotted form very likely occurred during the most recent glacial period in an area where the rainbow trout was absent. Geologic evidence suggests that this could have taken place in the Clark Fork drainage (Upper Columbia River Basin) while the area was inundated by glacial Lake Missoula.

Glacier Lake Missoula, one of several immense ice-front lakes formed by the Cordillian Ice Sheet, afforded the ideal environment for differentiation of *lewisi*. The 2,900-square-mile expanse of water is claimed by Bretz, et al. (1956) to have flooded at least seven times due to repeated ice-dam failures along its northwest shore. Such conditions presumably allowed the ancestral cutthroat to invade the area and become isolated by physical barriers during the terminal stages of the lake's existence. Although Lake Missoula conceivably existed 70,000 years ago, *lewisi* probably emerged within the past 15,000 years. The final withdrawal of this vast lake occurred from seven to ten thousand years ago, leaving Flathead and Pend Oreille Lakes behind as remnants.

This chronology accounts for the incipient distribution of *lewisi* throughout the Upper Columbia Basin and explains its occurrence in the westslope waters of Glacier National Park. Roscoe (1974) theorizes that postglacial erosion and ice retreats contributed to headwater transfers along the Continental Divide near

Glacier Park, which allowed *lewisi* to cross over into portions of the Upper Missouri and southern Saskatchewan drainages. This means of dispersal across the Divide is also implied by the work of Zimmerman (1965) and Reinitz (1974) who independently concluded that cutthroat populations indigenous to all three drainages of Glacier Park represent the subspecies *lewisi*.

Taxonomy

The cutthroat trout is the extreme example of a "polytypic" species among freshwater fishes. It is represented by a complex of geographically disjunct populations which have adapted to a variety of habitats over a vast area. *Salmo clarki* is a valid species because the various geographic populations will interbreed if given the opportunity. Yet they have maintained their genetic identity in all situations where they have historically coexisted with closely related species.

Because early systematists had no comprehension of the range of morphological variability that could exist within a species, it was inevitable that their reliance on the traditional approach of "typological" species identification would lead to taxonomic confusion. Although many misconceptions have been dispelled by recent geologic and zoogeographic evidence, an adequate systematic account of the ubiquitous cutthroat complex is still lacking.

Cutthroat trout were first observed in 1806 by Lewis and Clark in the vicinity of Great Falls, Montana (Roscoe, 1974). Half a century later, specimens collected from this locale during the early railroad surveys were described by Girard (1856) as *Salar lewisi*. Subsequent collections of similar black-spotted trouts were made from the Gallatin River (Hayden, 1872), headwater tributaries of the southern Saskatchewan River, including the St. Mary River near Glacier Park (Jordan, 1878), the Madison River (Jordan, 1889), and the Beaverhead River in Montana (Evermann, 1891). Although the affinities of these widely dispersed groups were obscure at the time, similarities were recognized by Suckley (1873) among populations distributed throughout the Upper Missouri Basin. It was also noted that cutthroat trout from the Clark Fork drainage of eastern Washington closely resembled those found in the Upper Missouri (Cooper, 1870).

Recent investigations have led to the discovery of several relict forms of cutthroat trouts throughout other interior basins of the western United States. The status, distribution, and probable affinities for several of these subspecies are described by Behnke and Zarn (1976).

Much of the early confusion over the taxonomic status of the "westslope" cutthroat derives from the misconception that cutthroat populations found in the Upper Missouri Basin evolved from the Yellowstone cutthroat, and further, that those found east of the Continental Divide in Montana were instrinsically different from the subspecies inhabiting westslope waters of the Upper Columbia Basin.

Roscoe (1974) attributes this quandary to the mistaken belief of Jordan and Evermann (1902) that the various subspecies of cutthroat trout differentiated along a geographic continuum. Their contention was that the coastal subspecies of cutthroat trout (*S. clarki clarki*) extended inland to Shoshone Falls via the Columbia and Snake River systems, and differentiated into a single widespread subspecies, *lewisi*, above Shoshone Falls. It was their hypothesis that *lewisi* entered the Yellowstone Basin via the Snake River, crossed the Continental Divide near Two Ocean Pass, and subsequently extended northward into the Upper Missouri Basin. The slight morphological differences seen in populations from the Upper Missouri were interpreted as being geographic variations of the Yellowstone phenotype.

Recent information reveals that the scenario proposed by Jordan and Evermann was only partially correct. Hanzel (1959) found no evidence, for example, that cutthroat populations indigenous to the Upper Missouri ever extended below the confluence of the Musselshell River. Clarification of the affinities and dispersion routes for cutthroat trout in this area has recently been provided by several studies involving morphometric analyses (Zimmerman, 1965; Murphy, 1974; Roscoe, 1974) and starch-gel electrophoretic techniques (Reinitz, 1974; Peterson, 1976). The evidence suggests that cutthroat populations of the Upper Missouri did not evolve from the Yellowstone subspecies, but rather invaded from westslope waters by crossing the Continental Divide, possibly in the vicinity of Glacier National Park.

These revelations created chaos in the taxonomic order of the cutthroat trout complex. The name *lewisi*, previously associated with the Yellowstone cutthroat, instead must apply exclusively to the "westslope" subspecies. The *Law of Priority* (ICZN, 1964) makes this mandatory since the latter was assigned that name by Girard (1856). This means that a new subspecies name must be designated for the Yellowstone cutthroat. It is also evident that the term "westslope" is a misnomer since the same subspecies is indigenous to the east slope as well (i.e., Upper Missouri and southern Saskatchewan basins). Perhaps the ultimate irony is reflected in Behnke's (1974) caveat that the so-called "westslope" cutthroat may be more endangered east of the Continental Divide.

Stocking History in Glacier Park

The introduction of exotic fishes into the waters of Glacier National Park began shortly after the turn of the century. Efforts to "improve" fishing by such means were promoted by local sportsmen's groups, commercial entrepreneurs, and the early railroads. Some local ranchers also carried out their own private trout-stocking programs in portions of the park.

The earliest form of artificial enhancement of Glacier's fishery involved the transplanting of trout from one water to another, a practice which inevitably led to the establishment of fish in previously barren lakes. Primitive fish culturing operations had their beginnings during the first quarter of the century, producing millions of eyed eggs and fry for introduction into Glacier Park. In 1918, the National Park Service collaborated with the U.S. Bureau of Fisheries (predecessor of the U.S. Fish and Wildlife Service) in the construction of a fish hatchery near the East Glacier Hotel at the park's eastern boundary. This facility operated for several years, producing fingerling-sized fish for planting park waters; brook trout, golden trout, and grayling were produced.

The planting of "catchable"-sized trout rose to prominence with the advent of modern hatchery facilities capable of rearing fish beyond the fingerling stage. Indeed, a large federal hatchery was constructed in 1947 at Creston, Montana, solely for the purpose of raising trout to stock Glacier Park. This facility was also used later to supply fish for other Montana waters. Trout stocking in Glacier Park was discontinued in the late 1960's.

The past management philosophy and public attitudes toward fish stocking in Glacier Park are exemplified in a memorandum prepared by a National Park Service employee in 1925, which states in part:

> ...in all, about two million eggs have been planted during the past four years .... we also receive fry and fingerling trout through the State of Montana and the federal hatchery at Bozeman .... recently a U.S. Fisheries car arrived at Glacier Park with about one hundred thousand large brook

> trout fingerlings. We feel that the success of this venture is due to Mr. *Smith*, who sponsored the idea. Without his assistance and cooperation, we could not have attained the results of which we are all justly proud (*sic*) .... the increasing number of tourists means that we must expand these activities....

The crusade to enhance sport-fishing opportunities in Glacier Park apparently obscured concern for the natural order of the park's aquatic ecosystems. Several exotic species have become established, including the brook trout (*Salvelinus fontinalis* Mitchell), native to the Great Lakes area and eastern interior regions of the continent. Rainbow trout, also exotic to Montana, are likewise present, mainly on the east side of the park. Rainbows, however, have not been particularly successful in Glacier's extremely cold high-gradient streams.

Exotic species which have more recently invaded park waters include the Kokanee salmon, lake trout, and lake whitefish. Competition with indigenous species for food and space is ocurring, and in the case of the lake trout, predation could also be a factor. Native species appear to be on the decline in some waters where exotic fishes are present. Cutthroat trout, in particular, have come under pressure in several of the large glacial lakes which drain to the North and Middle Forks; serious declines are indicated in McDonald, Bowman, and Kintla Lakes, all of which harbor introduced populations of lake trout, lake whitefish, and Kokanee salmon.

Stocking records do not adequately explain the occurrence of some of these species in park waters. It appears from old file correspondence that lake trout and lake whitefish were introduced into some lakes shortly after World War II, although records are not available to verify this. Lake trout occur naturally in a few lakes east of the Continental Divide, but they are exotic to the west slope. The species was established in the lower Flathead system and Whitefish Lake about 1910, and while a few lake trout were reported in a state creel census conducted on the North Fork during the 1960's (Bob Domrose, *personal communication*), it is unlikely that they gained access to park waters via the small high-gradient streams which drain from these lakes. Thus, circumstantial evidence strongly suggests that both lake trout and lake whitefish were directly introduced into park waters.

Kokanee salmon undoubtedly invaded some of the park's westslope waters via the Flathead River system. This species was successfully established in Flathead Lake nearly 40 years ago, and large spawning runs later developed in both the South and Middle Forks of the Flathead River. However, the presence of Kokanee salmon in some isolated lakes of Glacier Park can likewise only be explained by stocking.

Importance of Genetic Factors

Only recently has serious attention been paid to the significance of genetic factors in the province of applied fisheries management. There is mounting evidence that inheritable traits play an important role in the adaptability of fishes to the peculiar conditions of their environment and, moreover, that native fisheries are, with proper management, capable of producing a higher-quality angling experience to sportfishermen than artificially maintained fisheries (Butler, 1975; Behnke and Zarn, 1976; Bjornn, 1975).

The ecological stability of indigenous fisheries makes complete sense when one considers the evolutionary dynamics involved. Darwinian theory predicts that stresses placed on a species in one part of its geographic range will lead ultimately to the evolution of a population gene pool which imparts the highest survival value under the existing conditions. Inheritable traits which enhance survival can be expected to be well represented in the population. Conversely, genetically transmitted traits which reduce prospects for survival among individuals tend to be suppressed in the population by pressures of natural selection. From this it follows that two geographically disjunct populations of a given species will diverge genetically if they exist for a long period under vastly different circumstances. Harsh conditions evoke increased selectivity, and if divergence is extreme, differentiation into separate species may occur given sufficient time. Under less demanding conditions (i.e., where selective pressures are reduced), genetic drift may yield different strains, races, or subspecies.

Environmental adaptability is not the only mechanism that is genetically determined in fish populations. There is a growing body of evidence suggesting that genetically transmitted modes of behavior are important determinants of subtle but significant differences in life history specializations between species and even within a given species complex. Spatial and temporal isolating mechanisms between sympatric species, which may be peculiar to certain geographic locations, reflect long-term associations which have evolved a genetic basis. An example is the reproductive isolation that exists between rainbow trout and the westslope cutthroat in the Salmon and Clearwater drainages of central Idaho. In this part of its range, the westslope cutthroat evolved sympatrically with rainbow trout (steelhead) and has been able to maintain its identity (i.e., does not hybridize with rainbow trout). All other known populations of westslope cutthroat trout readily hybridize with rainbow trout. This is because the two species did not historically coexist elsewhere throughout their respective ranges (Roscoe, 1974), and hence, have not evolved the necessary behavior mechanisms to remain separated.

Other studies have affirmed the importance of genetic factors as determinants of niche separation at both the inter- and intra-specific levels (Andrusak and Northcote, 1970; Cordone and Nicola, 1970; Nilsson, 1963; Trojnar and Behnke, 1974).

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