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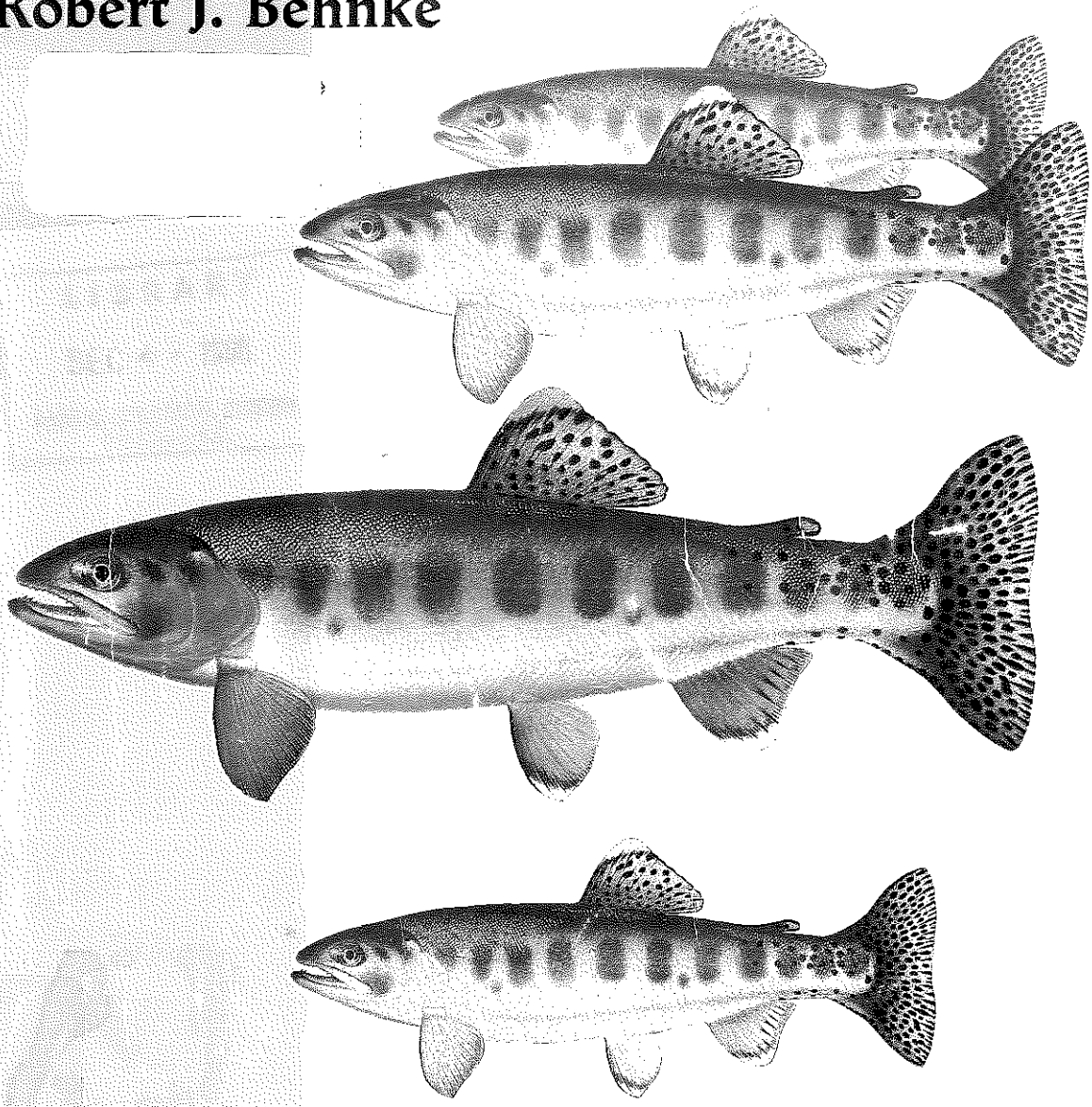
NATIVE TROUT
of Western North America

Robert J. Behnke



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PREFACE

This monograph distills many years of study of western North American trout. Its beginnings can be traced to the summer of 1957, when I accompanied the late Paul R. Needham on a trip from California to Alaska to obtain representative samples of western trout. The results of the 1957 and subsequent collections were compiled in an unpublished manuscript titled "The rainbow and cutthroat trouts of North America," which I wrote in 1963 while a graduate student at the University of California, Berkeley. In 1979, I prepared "Monograph of the native trouts of the genus *Salmo* of western North America" for the Denver regional office of the U.S. Fish and Wildlife Service. The 1979 monograph summarized and interpreted collections and observations of western trout made over more than 20 years. It was intended as a basic outline for government agencies on the diversity, classification, distribution, and current status of indigenous trout of western North America. The Fish and Wildlife Service distributed some photocopies of that monograph, and the Lakewood, Colorado, regional office of the U.S. Forest Service produced a typeset version. Although not an official publication, the monograph stimulated considerable interest and supplies of it were soon exhausted. Continuing demand led to an expanded and updated version prepared for the Denver regional office of the Fish and Wildlife Service in 1981. In that revision, I greatly augmented the biological and ecological information to provide—independently of formal taxonomic designations—a rationale for preserving genetic diversity at the subspecific and population levels. Funds were not available to publish that report, and the present monograph is a revised and updated version of the 1981 work.

The taxonomic accounts in this volume are based on examination of several thousand specimens. The collections I made through 1963 are deposited with the California Academy of Sciences, and arrangements are being made to house my later specimens in museums at The Ohio State University and the University of Colorado. Some changes in classification occurred since the 1979 monograph. To simplify classification, I recognized two species of rainbow trout in the 1979 report: *Salmo gairdneri* for the phylogenetically more advanced coastal group, and *S. newberrii* (misspelled *newberryi* in 1979) for all the more primitive forms, which I call redband trout. Because no infallible demarcation exists between all

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coastal rainbow trout and all forms of redband trout, I reclassified all redband trout as subspecies of *Salmo gairdneri* in the 1981 revision.

The major changes in classification in the present version concern transfer of all western North American trout from the genus *Salmo* to the genus *Oncorhynchus* and the change in species name of rainbow trout from *S. gairdneri* to *O. mykiss*, as summarized by Smith and Stearly (1989) and adopted by the American Fisheries Society's Committee on Names of Fishes (Robins et al. 1991). The change from *Salmo* to *Oncorhynchus* results in a classification more correctly reflecting phylogenetic relationships as depicted by Behnke (1968) and Kendall and Behnke (1984).

The replacement of *gairdneri* with *mykiss* for the rainbow trout species follows the Law of Priority of the International Code of Zoological Nomenclature. There is no longer any reasonable doubt that the rainbow trout of North America and the rainbow trout of Kamchatka (Siberia) belong to the same species (Mednikov and Akhundov 1975; Okazaki 1984, 1985). The Kamchatkan rainbow trout was named *Salmo mykiss* by Walbaum in 1792, and the North American rainbow trout was named *S. gairdneri* by Richardson in 1836. If *mykiss* and *gairdneri* belong to the same species, then *mykiss*, by the rule of priority, has precedence over *gairdneri*—although *gairdneri* can still be used as a subspecies name for redband trout of the upper Columbia River basin.

The species and subspecies discussed in this monograph are listed after the Preface. Two species recognized in the American Fisheries Society's "Common and Scientific Names of Fishes from the United States and Canada" (Robins et al. 1991) are reduced to subspecies—*Oncorhynchus aguabonita* to *O. mykiss aguabonita* and *O. apache* to *O. gilae apache*. I believe this classification better reflects phylogeny.

The present diversity of western trout evolved in response to different selective factors operating in different geographical regions. Prominent specializations are associated with anadromy and with fluvial and lacustrine environments. Within each of these broad categories, further adaptations have fine-tuned life histories to favor survival in relation to local climates, streamflows, temperatures, predators, prey, and coexisting fish species. The interplay of selective factors has produced the great diversity inherent among populations of western trout. This diversity is a resource that has rich potential for application in fisheries management. During the past 100 years, much intraspecific diversity in western trout has been lost. Some of the loss was caused by environmental degradation, but most can be attributed to fisheries management policies of state and federal agencies whose programs, historically, have ranged from benign neglect to outright extermination of native trout. Especially devasting have been widespread introductions of nonnative salmonid species. Interior subspecies of cutthroat trout now retain only a small fraction of their original distribution, abundance, and diversity.

In recent years, conservation biology and the preservation of biodiversity have received much attention. The values of intraspecific diversity to fisheries management have been well publicized in several major works on themes that include fish gene pools (Ryman 1980), stock concepts (special issue of the *Canadian Journal of Fisheries and Aquatic Sciences*, 1981, volume 38, number 12), and population genetics and fisheries management (Ryman and Utter 1987). A 1991 symposium sponsored by the North Atlantic Treaty Organization addressed genetic conservation of salmonid fishes; the proceedings will be published in 1993 or 1994. One of my goals in writing "Native Trout of Western North America" is to accelerate preservation and enhancement efforts to maintain and use the biodiversity of western trout. To attain this goal, I have treated a wide range of subjects, including some for which I lack in-depth expertise. I recognize the tension between rigorous scientific documentation and professional judgement based on experience and inference in fisheries management. I have tried to make it clear if I have based a position on well-documented sources or on circumstantial evidence and professional judgement. Scientists in certain disciplines undoubtedly will find flaws in my interpretation of their specialties. In mitigation, I point out that most flaws and oversimplifications occur in a larger context of making or emphasizing a major point. One of my recurring themes is that protection, restoration, and enhancement programs may be unnecessarily delayed or abandoned because of demands for a "scientifically sound" basis to justify an action. For example, opponents of a change in multiple-use practices designed to restore riparian habitat on federal lands may demand that expected benefits to target species be precisely quantified in terms, say, of increases in abundance and biomass. But for complex natural systems containing considerable uncertainty, no method or model can be expected to accurately predict the effects of environmental change on a target species. A model can transform unknown, uncertain, and stochastic events into deterministic events, but the results are unlikely to emulate biological reality. Accurate predictions can result only when a tight cause-and-effect relationship is determined by a precisely regular pattern, and little such regularity exists in natural aquatic systems.

Although the resulting change in biomass or abundance may not be accurately predictable, any environmental change that modifies any factor such as temperature or streamflow toward a species' optimum range will increase that species' niche volume. I use the terms niche volume and niche overlap frequently in this monograph to illustrate a point or a concept. I am not a niche theoretician, but I have found Hutchinson's (1957) abstract concept of a niche hypervolume with n dimensions of biotic and abiotic components to be very helpful in thinking about evolutionary ecology. In particular, I frequently resort to Hutchinson's concepts of the fundamental niche and the realized niche, and of how the volume of a fundamental niche is contracted into a realized niche by interactions of coexisting species. Readers interested in applications of niche theory to fisheries biology may consult the debate between Kerr (1980) and Werner (1980) and the concise review published by Wootton (1990).

The importance of theory (and experimentation) notwithstanding, the interpretation of niche and other ecological changes in nature still must rely heavily on informed professional judgment. During my 35 years of work with western trout, I have seen this invaluable resource dwindle much faster than scientific knowledge about it has grown. So much must be done in so short a time to protect the remaining genetic diversity of these fishes that I cannot responsibly suspend judgments about trout biology and management in the

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hope that irrefutable data might one day be collected. I have not done so in this monograph, though I recognize the risk of error. If protective management of these species cannot be based on informed professional judgment, many native stocks will disappear before science can vouch for their unique value.

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The black-and-white illustrations used in this monograph were prepared by Lynn Bjork. Color drawings of fish shown on the plates were executed by Joseph Tomelleri. The California golden trout on the front cover (paperback copies) and dust jacket is the type specimen of the species then called *Salmo roosevelti* Evermann, drawn from life by the eminent artist Charles B. Hudson. It is reproduced from the "Nineteenth biennial report of the State Board of Fish Commissioners of the State of California, for the years 1905–1906," published in 1907. Edwin Pister provided a copy of Hudson's work.

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COMMON AND SCIENTIFIC NAMES OF FISH SPECIES

Throughout this monograph, fish species are referred to by their common names in nontaxonomic contexts. Their respective scientific names follow.

alewife ..... *Alosa pseudoharengus*
Alvord chub ..... *Gila alvordensis*
Apache trout[a] ..... *Oncorhynchus gilae*
Arctic char ..... *Salvelinus alpinus*
Arctic grayling ..... *Thymallus arcticus*
Atlantic salmon ..... *Salmo salar*
Bear Lake sculpin ..... *Cottus extensus*
Bonneville cisco ..... *Prosopium gemmifer*
Borax Lake chub ..... *Gila boraxobius*
brook trout ..... *Salvelinus fontinalis*
brown trout ..... *Salmo trutta*
bull trout ..... *Salvelinus confluentus*
Chihuahua chub ..... *Gila nigrescens*
chinook salmon ..... *Oncorhynchus tshawytscha*
chum salmon ..... *Oncorhynchus keta*
coho salmon ..... *Oncorhynchus kisutch*
common carp ..... *Cyprinus carpio*
creek chub ..... *Semotilus atromaculatus*
cutthroat trout[a] ..... *Oncorhynchus clarki*
Dolly Varden ..... *Salvelinus malma*
fathead minnow ..... *Pimephales promelas*
Gila trout[a] ..... *Oncorhynchus gilae*
inconnu ..... *Stenodus leucichthys*
June sucker ..... *Chamistes liorus*

kokanee[b] ..... *Oncorhynchus nerka*
lake trout ..... *Salvelinus namaycush*
lake whitefish ..... *Coregonus clupeaformis*
lenok ..... *Brachymystax lenok*
longnose dace ..... *Rhinichthys cataractae*
longnose sucker ..... *Catostomus catostomus*
Mexican golden trout ..... *Oncorhynchus chrysogaster*
northern squawfish ..... *Ptychocheilus oregonensis*
Pacific salmon ..... *Oncorhynchus* spp.
pink salmon ..... *Oncorhynchus gorbuscha*
rainbow trout[a] ..... *Oncorhynchus mykiss*
redside shiner ..... *Richardsonius balteatus*
Rio Grande chub ..... *Gila pandora*
roundtail chub ..... *Gila robusta*
sockeye salmon ..... *Oncorhynchus nerka*
steelhead[c] ..... *Oncorhynchus mykiss*
tui chub ..... *Gila bicolor*
Utah sucker ..... *Catostomus ardens*
white sucker ..... *Catostomus commersoni*

---

[a] Subspecies names are given on pages xvi–xvii.
[b] Landlocked form of sockeye salmon, remaining all its life in fresh water.
[c] Anadromous form of rainbow (and redband) trout.

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TAXONOMY OF WESTERN NORTH AMERICAN TROUT

Four species of native western trout are recognized for purposes of this monograph. Three of them have recognizable subspecies, some of which have not yet been formally named. Taxa are listed below in the order of their treatment in this monograph.

Order Salmoniformes,[a] Family Salmonidae,[b] Genus *Oncorhynchus*[c]

Cutthroat trout ..... *Oncorhynchus clarki*[d]
- coastal cutthroat trout ..... *O. c. clarki*
- westslope cutthroat trout ..... *O. c. lewisi*
- Yellowstone cutthroat trout ..... *O. c. bouvieri*
- finespotted Snake River cutthroat trout ..... *O. c.* subsp.
- Lahontan cutthroat trout ..... *O. c. henshawi*
- Paiute cutthroat trout ..... *O. c. seleniris*
- Humboldt cutthroat trout ..... *O. c.* subsp.
- Alvord cutthroat trout ..... *O. c.* subsp.[e]
- Whitehorse cutthroat trout ..... *O. c.* subsp.
- Bonneville cutthroat trout ..... *O. c. utah*
- Colorado River cutthroat trout ..... *O. c. pleuriticus*
- greenback cutthroat trout ..... *O. c. stomias*
- Rio Grande cutthroat trout ..... *O. c. virginalis*
- yellowfin cutthroat trout ..... *O. c. macdonaldi*[f]

Rainbow trout ..... *Oncorhynchus mykiss*
- Columbia River redband trout ..... *O. m. gairdneri*[g]
- California golden trout ..... *O. m. aguabonita*
- Kern and Little Kern golden trout ..... *O. m. gilberti*
- Sacramento redband trout ..... *O. m. stonei*
- coastal rainbow trout ..... *O. m. irideus*[g]
- Kamchatkan rainbow trout ..... *O. m. mykiss*[g]

Gila and Apache trout ..... *Oncorhynchus gilae*
- Gila trout ..... *O. g. gilae*
- Apache trout ..... *O. g. apache*

Mexican golden trout ..... *Oncorhynchus chrysogaster*

Mexican populations of uncertain classification .....
(Río Yaqui, Río Mayo, Río San Lorenzo, and Río del Presidio)

---

[a] Other North American families in the Salmoniformes: Esocidae (pikes), Umbridae (mudminnows), Argentinidae (argentines), Bathylagidae (deepsea smelts), Opisthoproctidae (spookfishes), and Osmeridae (smelts).

[b] Other North American genera in the Salmonidae: *Coregonus* and *Prosopium* (20 species of whitefishes and ciscoes), *Salmo* (Atlantic salmon and brown trout), *Salvelinus* (Arctic char, bull trout, brook trout, Dolly Varden, and lake trout), *Stenodus* (inconnu), and *Thymallus* (Arctic grayling).

[c] Other North American species of *Oncorhynchus*: pink salmon, chum salmon, coho salmon, sockeye salmon, and chinook salmon.

[d] The anadromous form is called sea-run cutthroat trout.

[e] Probably extinct as pure form.

[f] Extinct.

[g] The anadromous form is called steelhead.

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CHROMOSOMES OF WESTERN NORTH AMERICAN TROUT

Chromosome numbers offer intriguing but ambiguous evidence of phylogenetic relationships among native western trout. Forms of cutthroat trout that seem, on other grounds, to be evolutionarily younger have fewer chromosomes, whereas more recent forms of rainbow trout have more chromosomes.

	Diploid number of	
Species and subspecies	Chromosomes	Chromosome arms
Cutthroat trout		
Coastal cutthroat trout	68	104
Westslope cutthroat trout	66	104
Yellowstone cutthroat trout and all other subspecies	64	104
Rainbow trout		
Columbia River redband trout	58	104
California golden trout	58	104
Kern and Little Kern golden trout	58	104
Sacramento redband trout	58	104
Coastal rainbow trout	58–64	104
Kamchatkan rainbow trout	58–60	104
Gila and Apache trout	56	106
Mexican golden trout	60	104
Other Mexican trout	?–64	104

TAXONOMIC CHARACTERS

In Parts II–IV of this monograph, frequent reference is made to counts of meristic characters useful in the identification of western trout. Most descriptions of species and subspecies begin with a summary of these character counts, listed in the telegraphic style used for formal taxonomic publications, but the counts are mentioned frequently in the narrative text as well. The following notes describe how the counts are made. All counts traditionally are made on the left side of the fish.

Basibranchial teeth Count includes all basibranchial teeth found after the basibranchial area is stained with alizarin red and allowed to stand overnight.

Gill rakers Count includes all (even rudimentary) anterior gill rakers on the upper and lower arms of the first arch. When they have diagnostic value, counts of posterior gill rakers on the first arch also are given.

Pyloric caeca Count includes the bodies of all caeca found after the intestine is unwound from the stomach and laid out.

Scales in the lateral series Counted longitudinally along the second row of scales above the lateral line. The count extends from the scale in contact with the pectoral girdle to the scale at the end of the hypural plates. The end of the hypural plates is marked by the crease that forms when the caudal fin is flexed. (Standard length is measured to this crease as well.)

Scales (or scale rows) above the lateral line Counted obliquely down and back from the dorsal midline toward the lateral line. The count extends from the first detectable scale immediately in front of the dorsal fin to—but not including—the lateral line.

Vertebrae Counted on X-ray photographs.

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SYMBOLS AND ABBREVIATIONS

The following symbols and abbreviations are used in this monograph.

°C	degrees Celsius or centigrade	m	meter
cm	centimeter	mg	milligram
g	gram	s	second (time)
kg	kilogram	sp.	species (singular)
km	kilometer	spp.	species (plural)
L	liter	subsp.	subspecies

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PART I

Relationships, History, and Biology

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1

CLASSIFICATION

Biological classification is the science and art of arranging the results of evolution in a hierarchical scheme. Ideally, such a scheme reflects degrees of relatedness. Taxonomy is the application of general classification principles to naming organisms in accordance with international rules of zoological nomenclature. These rules provide for stable nomenclature but they do not concern the interpretation of evolutionary evidence for the construction of phylogenetic classifications. Systematics comprises research on evolutionary differentiation, which provides the evidence for phylogenetic classification, the representation of evolutionary relationships (Behnke 1989a). For example, systematic studies recently revealed, beyond reasonable doubt, that the rainbow trout of the Kamchatka Peninsula in Siberia and the rainbow trout of North America are indistinguishable and should be recognized as a single species. The rules of taxonomy dictate that the first name published for either former species is the valid name for the combined species. Therefore, because the name *mykiss* given to Kamchatkan rainbow trout in 1792 predates the name *gairdneri* (1836) given to North American rainbow trout, it is the valid name for the merged species. The name *gairdneri* becomes a synonym of *mykiss* at the species level (although it still is available for use as a subspecies name). Over the years, my ideas on systematics and taxonomy have been most influenced by the publications of Ernst Mayr. Except that I place less emphasis than Mayr on reproductive isolation as a character state for the classification of salmonid fishes, I am in general agreement with his methods, principles, and philosophy as delineated by Mayr and Ashlock (1991).

All the native species of North American trout, as well as the Kamchatkan rainbow trout, were placed in the genus *Salmo* when they were described originally. *Salmo* also includes Atlantic salmon and Eurasian species of trout. Systematists have concluded recently that North American trout have a greater affinity with Pacific salmon, genus *Oncorhynchus*, than with Eurasian trout (Smith and Stearley 1989). Consequently, all the species described in this monograph have been moved to *Oncorhynchus*; Old World species (including brown trout, which has been introduced in North America) remain in *Salmo*. Throughout this monograph, I use *Salmo* when I discuss the taxonomic history of North American species, but I use *Oncorhynchus* otherwise.

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TAXONOMIC HISTORY

From 1792 to 1972 about 50 species of western trout were described in the literature. The fifth edition of the American Fisheries Society's "Common and Scientific Names of Fishes from the United States and Canada" (Robins et al. 1991) lists only five species of western trout exclusive of the Mexican golden trout, which is beyond the range considered for that list. I have further reduced the number of full species to four, including the Mexican golden trout. Many former species names obviously have become synonyms of recognized species, but some names that are synonyms at the species level are available to designate subspecies—*O. m. gairdneri* is an example.

The first published binomial name applicable to any western trout was Walbaum's 1792 description of *Salmo mykiss*, the rainbow trout of Kamchatka. In 1836, Richardson described a rainbow trout from the Columbia River as *Salmo gairdneri* and a cutthroat trout from a lower Columbia River tributary as *Salmo clarki*.[1] Thus, the oldest name for any member of the rainbow trout species is *mykiss*, and Kamchatka is the type locality for the name. Richardson's *Salmo clarki* was undoubtedly based on a specimen of coastal cutthroat trout from the lower Columbia River basin; Trotter and Bisson (1988) have deduced that its type locality is the North Fork of the Lewis River. Therefore, when the species *Oncorhynchus clarki* is divided into subspecies, *O. clarki clarki* becomes the subspecific designation of the coastal cutthroat trout.

The type specimen on which the name *gairdneri* is based came from Fort Vancouver, Washington, 160 km up the Columbia River. It was almost certainly a steelhead making its upstream spawning migration. As I discuss later, however, two subspecies of rainbow trout have steelhead spawning runs up the Columbia River—coastal rainbow trout to the Cascade Range, and redband trout to the basin east of the Cascades. For the taxonomically correct use of *O. mykiss gairdneri* to designate one of these subspecies, I follow Jordan and Evermann (1896), who were the first revisers of the taxon *gairdneri*. They redefined *gairdneri* based on a collection of steelhead from the Columbia River near Astoria, Oregon, giving counts of 137–177 lateral-series scales and 42 pyloric caeca for these fish. These characters indicate the name *gairdneri* should be assigned to the inland redband trout of the Columbia River basin. Coastal rainbow trout typically have 120–140 scales in the lateral series and about 50–60 pyloric caeca. Gibbons first named the coastal form of rainbow trout *Salmo iridea* in 1855, based on a young steelhead from San Leandro Creek, a tributary to San Francisco Bay, California. I recognize steelhead and resident forms of the coastal rainbow trout (defined by low scale counts, high pyloric caecal counts, and a profusion of small irregular spots on the body) as *O. mykiss irideus*.

The first attempt to treat all known western trout in a comprehensive taxonomic arrangement resulted in an 1861 monograph by George Suckley, a

[1]Richardson used *–ii* endings for both species. According to Bailey and Robins (1988), the single *–i* ending is required by current rules of nomenclature (International Commission on Zoological Nomenclature 1985). McDowall (1991), however, has disagreed with this interpretation of the rules.

U.S. Army surgeon and naturalist who collected many western trout specimens while participating in the Pacific Railroad Survey of the 1850s. His manuscript was not published until after his death (Suckley 1874). Suckley proposed the name *Oncorhynchus* to separate Pacific salmon from rainbow and cutthroat trout. He recognized that the cutthroat trout he found in the upper Missouri River near Great Falls, Montana, were identical to the cutthroat trout encountered on the other side of the Continental Divide in the Clark Fork drainage of the Columbia River basin—a fact that eluded subsequent authors.

From about 1880 to 1930, the work of David Starr Jordan and his associates completely dominated all trout classification. The reputation of Jordan as an eminent ichthyologist, educator, and statesman caused his publications to be considered the ultimate authority on the subject. However, Jordan frequently changed his opinion on the classification of western trout.

Early in his career Jordan recognized two basic forms of western trout—cutthroat trout and rainbow trout. His confusion began when he encountered specimens of redband trout (inland rainbow trout) from the Columbia and Sacramento basins. These fish muddled his attempts to arrive at a taxonomy reflecting evolutionary relationships. Jordan envisioned an Asian cutthroat trout ancestor that invaded North America and dispersed inland. According to this line of reasoning, the creation of Shoshone Falls on the Snake River 30,000–60,000 years ago separated the progenitors of coastal cutthroat trout and inland cutthroat trout; the inland cutthroat then dispersed down the Colorado River and crossed the Sierras to evolve into the California golden trout, a transitional form between cutthroat and rainbow trout. Jordan's theory had the coastal rainbow trout evolving in the Sacramento basin and later giving rise to the fine-scaled rainbow (i.e., redband) trout in the Columbia basin. At the time, around the turn of the century, this evolutionary reconstruction seemed to explain the distribution and diversity of western trout. We now know, however, that cutthroat trout never extended their range below the Grand Canyon of the Colorado River and therefore could not have crossed the Sierras to evolve into golden trout. (Jordan mistakenly assumed that the Apache trout of Arizona was a form of the Colorado River cutthroat trout.)

Jordan first used *Salmo purpuratus* (a name Pallas had given to Kamchatkan rainbow trout in 1814) for cutthroat trout, but he switched to *S. mykiss* when he found that *mykiss* had priority. About 1896, Jordan received a specimen of Kamchatkan rainbow trout and realized it was not a member of the cutthroat trout species. (He believed it was most closely related to Atlantic salmon.) Jordan and Evermann (1898) adopted Richardson's scientific name for cutthroat trout, *S. clarki*.

In his early work Jordan classified all western trout as one, two, or three species. In 1895 he regarded all western trout as a single species, *S. mykiss*, believing that the life history distinctions between steelhead and resident rainbow trout were under direct environmental control and lacked a hereditary basis (Jordan 1895). The collections of resident redband trout during the Columbia River expedition of Gilbert and Evermann (1894) and of California golden trout obviously caused Jordan considerable confusion. In the first volume of the great reference work "The Fishes of North and Middle America,"

Jordan and Evermann (1896) classified western trout into three species: (1) cutthroat trout *Salmo mykiss*, with 10 subspecies including *S. mykiss gibbsi*, which was based on the redband trout of the middle Columbia basin; (2) steelhead *S. gairdneri*, with two subspecies, one for anadromous steelhead and one for the Kamloops trout of the upper Columbia River and Fraser River systems; and (3) Coast Range rainbow trout *S. irideus*, with five subspecies including the golden trout *S. irideus aguabonita*. The uncertainty of this classification is apparent from Jordan and Evermann's statement (1896:491): "It is not unlikely, that when the waters of the Northern Hemisphere are fully explored, it will be found that all the black-spotted trout of America, Europe, and Asia are forms of one species, for which the oldest name is *Salmo trutta* Linnaeus."

Evidently, when Jordan became frustrated with his attempts at an orderly system of classification that reflected phylogeny, he began to recognize almost every described form as a full species. His last recorded classification (Jordan et al. 1930) listed 32 full species, which are presently referable to the diversity within rainbow and cutthroat trout.

Snyder (1940) published a classification of western trout that combined Jordan's steelhead series and Coast Range rainbow series into one rainbow series, but he still listed 12 full species of rainbow trout. In addition, Snyder's cutthroat series contained nine full species. Miller (1950) described *Salmo gilae* from the Gila River drainage of New Mexico and also arranged all western trout into two evolutionary groupings or series. This relegated many of the species recognized in Snyder's classification to subspecies and increased the number of species and subspecies in the cutthroat series from 9 to 12.

Needham and Gard (1959) described collections of trout from California and Mexico. The major significance of their work was the discovery of the Mexican golden trout in three river systems draining to the Gulf of California. Under the "two series" theory of western trout evolution, Needham and Gard originally treated the Mexican golden trout as a form of rainbow trout. When it became apparent that the characteristics of the Mexican golden trout diverge greatly from those of any known rainbow or cutthroat trout, Needham and Gard (1964) described the Mexican golden trout as a new species, *S. chrysogaster*.

The most recently described species of western trout is *Salmo apache*, named by Miller (1972a) for a trout native to a few headwater tributaries of the lower Colorado River basin in Arizona. The Apache trout, the Gila trout, and the Mexican golden trout are native to certain areas of the lower Colorado basin and the Gulf of California. Their position in respect to the phylogeny of rainbow and cutthroat trout is not clear but, as discussed later, all available evidence indicates that they represent early branching from the lineage leading to rainbow trout.

Also unclear is the phylogenetic position of the trout I call redband trout, which are native to the Sacramento basin, Columbia basin, upper Klamath Lake basin, and several separate Oregon desert basins. In my 1979 report I classified all redband trout as a separate species, *Salmo newberrii*. I made it clear, however, that this was done solely for practical purposes. Such a classification makes it simpler to emphasize the great range of diversity associated with various groups of redband trout. For the present work I have included all redband trout in *O. mykiss* because it is impossible to draw clear boundaries between redband and coastal rainbow trout. Some populations, such as the rainbow trout of Eagle Lake, California, cannot definitely be assigned to either the coastal rainbow or the redband trout evolutionary lines. Intermediate populations probably resulted from ancient hybridization between coastal rainbow and interior redband trout in the Sacramento and Columbia basins.

The inclusion of redband trout (and California golden trout) with rainbow trout makes *O. mykiss* an extremely variable species. For example, based on my examinations of more than 1,000 specimens of coastal rainbow and redband trout, mean numbers of vertebrae range from 59 or less to 65 or more, mean lateral-series scale counts from less than 120 to more than 180, and mean numbers of pyloric caeca from 30 or less to 60 or more. Among populations, diploid chromosome numbers range from 58 to 64, and coloration and spotting patterns exhibit a great array of differences. Comparable morphological variability is also found among the 14 subspecies of cutthroat trout; moreover, the biochemical genetic variation is many times greater among subspecies of cutthroat trout than among forms of rainbow–redband trout.

PRINCIPLES AND METHODS OF CLASSIFICATION

The goal of most animal classification is to construct a hypothetical phylogeny of a group that represents the most likely evolutionary stages leading to the group's present species and subspecies. Figure 1 is such a representation for western trout of the genus *Oncorhynchus*.

Evolutionary sequences cannot be known with certainty, only approximated. To achieve the best approximation, taxonomists evaluate evidence from different disciplines, including anatomical characters, genetic and chromosome data (including DNA variation), distribution patterns, and life history and behavioral traits. By comparing characteristics along a series of related taxa, they infer which states of the character are primitive and which are derived. Taxonomists are especially interested in unique evolutionary changes—changes in character state that occur only in one phylogenetic branch—because these can be used to mark points of divergence and trace evolutionary progression through a phylogeny to its end points (living species and their subspecies). The characters that best reflect phylogenetic branching are irreversible and not subject to independent evolution in more than one line. The loss of teeth on particular bones in the mouth is one such irreversible change in character state. For example, a common ancestor that gave rise to the minnow family Cyprinidae and the sucker family Catostomidae lost dentition on the jaws and on the bones within the mouth. All species of minnows and suckers reflect this phylogenetic event by lacking teeth on their jaws and in their mouths; however, they have developed a great diversity of pharyngeal teeth. Basibranchial teeth occur as vestiges in some Gila, Apache, and redband trout. From this it can be assumed that all Gila, Apache, and redband trout had a common ancestor with basibranchial teeth. However, a shared primitive character does not indicate the branching sequence for separate lines leading from the ancestral form to the living forms. The gap between the evolutionary lines of Gila trout and rainbow trout in Figure 1 denotes that, on the available evidence, the branching point of

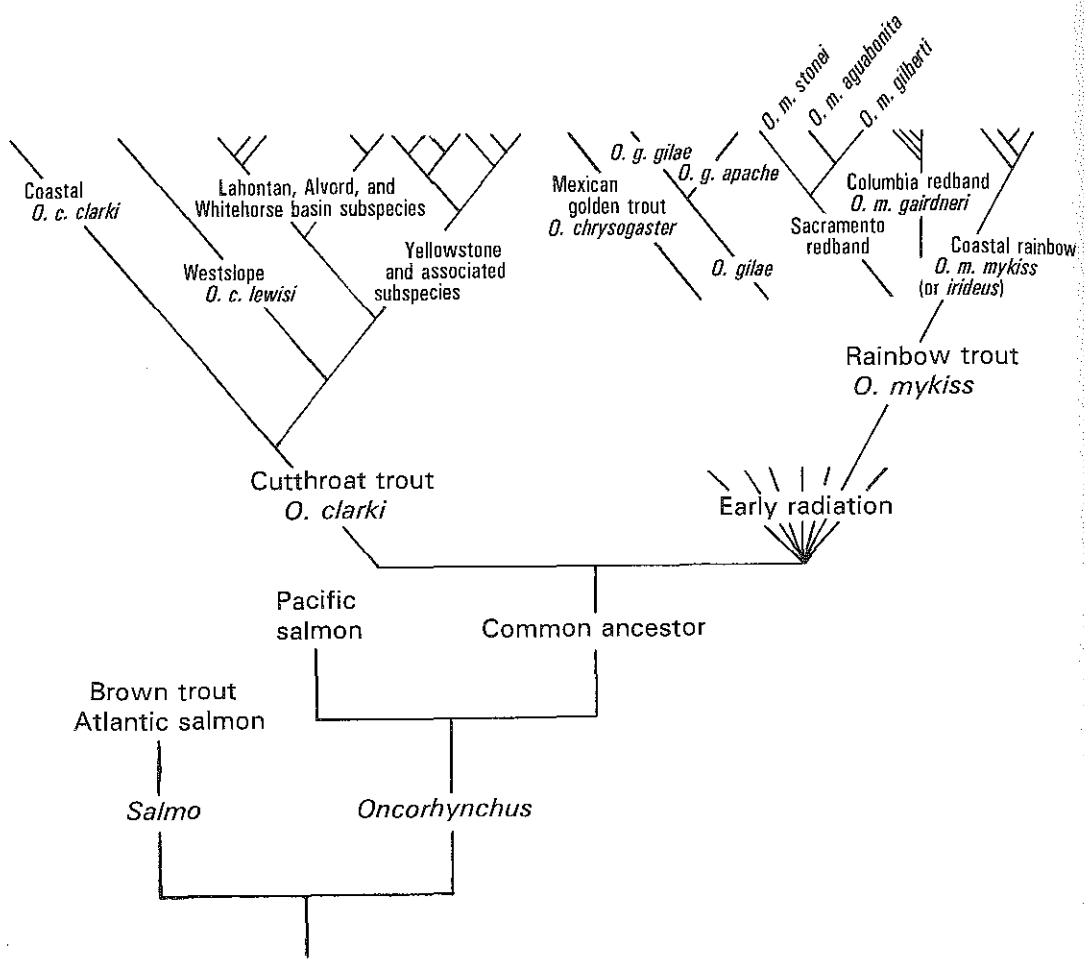

FIGURE 1.—Hypothesized phylogeny of western trout. Unconnected lines have uncertain connecting points.

the Gila trout–Apache trout evolutionary line from the rainbow–redband line is not known. This is also true for the Mexican golden trout line. Thus, the loss of a complex character state such as teeth—a traditional taxonomic criterion commonly known as Dollo's rule (Mayr and Ashlock 1991)—often is insufficient for phylogenetic reconstructions because vestigial intermediate character states may persist in some evolutionary lines.

Most meristic characters (characters that have countable elements in a series) used in western trout taxonomy are subject to convergence (independent evolution of similar character values in separate lines) when all taxa are considered. Some trends can be deduced when taxa assumed on some basis to be more primitive (e.g., Mexican golden trout, Gila and Apache trout, and Sacramento redband trout) are compared with forms assumed to be the most "modern" or derived form (e.g., coastal rainbow trout). Such comparisons of

trout indicate that low numbers of meristic elements (vertebrae, fin rays, pyloric caeca, gill rakers) represent the primitive state and higher numbers the advanced state. These characters change independently within several lines and have limited usefulness for phylogenetic reconstruction. With such data, overall similarity of the various forms can be compared, but overall similarity of characters cannot be used to construct a phylogeny of western trout unless other evidence establishes the primitive and advanced states of the characters used. For example, trout that evolve in a large lacustrine environment, where planktonic food items are small, typically have more gill rakers than similar forms adapted to streams. This has happened with cutthroat trout native to the Lahontan basin of Nevada and redband trout native to some of the Oregon desert basins. Thus, similar trends toward more gill rakers among lake forms in this case is evidence of convergent evolution, not an indication of close genetic relationship due to common ancestry. Without a sound appreciation of which character states are primitive and which are derived within a group of organisms, even sophisticated multivariate computer programs, which are increasingly used to process great amounts of taxonomic data, generate phylogenetically misleading classifications.

The amount of unique evolutionary change that can be detected in various evolutionary lines depends in general (with many exceptions) on the length of time a particular line has been separated from its sister group or closest related line (that is, the elapsed time since they separated from a common ancestor): Much is yet to be learned about the times of phyletic branching, but my interpretation of available evidence suggests that all living forms of western trout arose from a common ancestor as recently as 2 million years ago—a mere wink on the geological time scale. With such recent evolution, the phylogenetic branches leading to living forms would not be expected to have accumulated many unique derived characters.

The western trout probably have been given more intensive genetic study by protein electrophoresis (a means of separating proteins for identification) than any other similar group of fishes. An evaluation of all evidence confirms that western trout are all closely related to each other. The electrophoretic evidence generally agrees with my phylogenetic interpretation of western trout (Loudenslager et al. 1986; Behnke 1988c). There are some discrepancies; for example, the electrophoretic data indicate that the westslope cutthroat trout is more closely related to rainbow trout than to Yellowstone cutthroat trout (Reinitz 1974). With evolutionary divergences on the order of 50,000 years or less, few, if any, genetic changes detectable by electrophoresis should be expected to occur. Consequently, some of the recently evolved subspecies of cutthroat trout cannot be validated by electrophoresis even though they may exhibit considerable morphological divergence. Also, in contrast to the great amount of morphological variability among the various forms of rainbow, redband, and golden trout in *O. mykiss*, electrophoretic variation is slight. Thus, some evolutionary lines may exhibit considerable divergence in that part of their genome governing morphology but exhibit very little change in the part of the genome that can be sampled by electrophoresis. Phelps and Allendorf (1983) failed to detect any genetic divergence between two species of sturgeon in the

genus *Scaphirhynchus* when they electrophoretically analyzed proteins governed by 37 gene loci.

A variety of new techniques, such as mitochondrial DNA (mtDNA) analysis, can contribute new data on genetic differentiation. Sometimes these data avoid the problem of which is the primitive and which is the derived state. Bernatchez and Dodson (1990) used mtDNA analysis to show that sympatric populations of lake whitefish in many lakes of northern Maine and eastern Quebec represent distinct evolutionary lines that have dispersed from two glacial refugia. That is, the sympatric pairs of populations represent two monophyletic evolutionary lines that have come into contact. In a previous electrophoretic study of sympatric whitefish populations in Maine lakes, Kirkpatrick and Selander (1979) failed to detect the true ancestral origins of the populations. The preliminary results from DNA analysis of western trout that I have seen are discussed in the accounts of species and subspecies.

The chromosomes of western trout have also been well studied. Because of the great variation and independent evolution in different trout lines, attempts to associate chromosomal changes with phylogeny have not been very informative. Chromosomal change within a monophyletic group of animals often involves the fusion of single-arm (acrocentric) chromosomes into double-arm (metacentric) chromosomes (Robertsonian fusion). Thus, the total number of chromosomes is reduced but the number of arms remains the same. In this evolutionary trend, a higher number of chromosomes is the primitive condition and a lower number the derived condition. Chromosomal evolution in cutthroat trout follows the typical progression from higher to lower numbers (see page xviii). The coastal cutthroat trout has a diploid complement of 68 chromosomes, the westslope cutthroat trout has 66, and the Yellowstone cutthroat trout (and the other subspecies derived from it) has 64 (Loudenslager and Thorgaard 1979). The rainbow–redband line, however, appears to have followed a reverse sequence. The Sacramento and Columbia River redband trout, believed most primitive based on distribution and morphology, have 58 chromosomes. Coastal rainbow trout from the Columbia River northward have modal values of 60 chromosomes, but past mixing of stocks is apparent in populations whose individuals have 58, 59, or 60 chromosomes. South of the Columbia River, coastal rainbow trout tend to have higher numbers (60–62), and some California populations have 64 chromosomes (Thorgaard 1983). The Gila and Apache trout have 56 chromosomes with 106 chromosomal arms (all other western trout karyotypes have 104 arms). The Mexican golden trout has 60, and trout native to the Río Yaqui and Río Mayo in northern Mexico, which morphologically resemble Gila trout, have 64 chromosomes (T. Uyeno, National Science Museum [Tokyo], and R. R. Miller, University of Michigan, unpublished). Such a pattern is very perplexing when one attempts to construct a phylogeny of karyotypes. Obviously no single process, such as Robertsonian fusion, was followed throughout the western trout phylogeny. The number 64 evidently was achieved independently three times—by interior cutthroat trout, coastal rainbow trout (some California populations), and the trout of the Río Mayo and Río Yaqui.

There is much yet to be learned regarding the evolution of western trout and the branching sequences in their phylogeny. It is premature to make definitive pronouncements on the subject.

For characterization of taxa, it is best to take an eclectic approach: use available evidence from all methods. The use of morphological characters such as coloration, spotting, and meristic elements can be criticized because of the influence environmental conditions may have on these characters. However, most experiments that induced changes in the numbers of vertebrae, scales, and fin rays were performed in laboratories under extreme conditions of temperature, light, or dissolved oxygen concentration during embryonic development. In nature, most trout spawn and the embryos develop under comparable environmental regimes in all geographical areas. Thus, when consistent differences are found in any character between geographically disjunct groups of trout, it can be assumed that these differences have a hereditary basis. This matter was discussed by Schreck and Behnke (1971) and Hickman and Behnke (1979).

In contrast to meristic characters, morphometric characters—measures of body dimensions and their proportions—are subject to considerable nonhereditary influence. Relative head and jaw lengths, body depths, and other comparative measurements of trout change markedly with age and growth. Koops and Mann (1975) demonstrated great differences in body proportions between genetically identical rainbow trout raised under three different environmental regimes. I have found no consistent clear-cut differences in the shape of the body or relative position of body parts in any of the western trout. The Gila and Apache trout apparently have a genetic basis for a body that is deeper and fins that are longer than those of other western trout, and cutthroat trout tend to have relatively longer jaws than rainbow trout, but these characters are of limited usefulness as diagnostic criteria because of their range of variability and overlap.

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2

ORIGINS AND DISTRIBUTIONS

The Salmonidae is a primitive teleost family whose relationships to other families in the order Salmoniformes are not well understood (Lauder and Liem 1983). The family might have originated with a tetraploid event (doubling of chromosomes) in the Cretaceous Period about 100 million years ago. Without better evidence from the fossil record, one can only speculate about the time of origin based on primitive character states reflected in the skeletons of salmonid fishes and supported by biochemical evidence.

The earliest fossil definitely attributed to Salmonidae is *Eosalmo driftwoodensis* from Eocene deposits (40–50 million years old) in British Columbia (Wilson 1977). This fossil looks superficially like a grayling (subfamily Thymallinae), but Wilson (1977) and Cavender (1986) believed it represents the subfamily Salmoninae. It is probable that the family Salmonidae had evolved into three subfamilies—Salmoninae (trout and salmon), Thymallinae (graylings), and Coregoninae (whitefishes)—by the Eocene Epoch.

Based on the evidence of evolution summarized by Kendall and Behnke (1984), I believe the subfamily Salmoninae divided into two main branches, probably during the Oligocene Epoch 30–40 million years ago. One branch led to the genera *Hucho, Brachymystax,* and *Salvelinus,* and the other to *Salmo* and *Oncorhynchus*. The separation of the ancient *Salmo* progenitor into an Atlantic Ocean group (*Salmo*) and a Pacific Ocean group (*Oncorhynchus*) probably occurred by mid-Miocene times about 15 million years ago.

From a possible Cretaceous origin of Salmonidae to the presumed Miocene origin of *Oncorhynchus,* several factors influenced speciation, distribution, and extinction. Foremost among them were the geological and climatic history of the earth, marked by volcanism, earth movement and uplift, alternating periods of warm and cold climates, alternating arid and pluvial periods, and rearrangement of drainage basins. For example, a cooling trend during the latter Miocene Epoch (5–10 million years ago) allowed southward movement of salmonid fishes in western North America, a movement represented by upper Miocene–lower Pliocene fossils in California, Nevada, Oregon, and Idaho (LaRivers 1964; Cavender and Miller 1972, 1982; Kimmel 1975; Smith 1975, 1981; Taylor and Smith 1981; Smith and Miller 1985; Cavender 1986). Cavendar (1986) and

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Minckley et al. (1986) reviewed the influences of geology and climate on fishes through time.

My survey of the literature suggests the following scenario. By the end of the Miocene Epoch (5 million years ago), the ancestral form of *Oncorhynchus* in the Pacific Ocean drainages of North America had evolved into two distinct but closely related lines, one leading to modern Pacific salmon and the other to modern western trout. (Fossils representing the trout line have been classified in the genera *Salmo, Parasalmo,* and *Rhabdofario,* though all would be called *Oncorhynchus* in current classifications.) During the late Pliocene Epoch (about 2–3 million years ago), drastic changes and extinctions occurred in the fish fauna of western North America. Members of the catfish family Ictaluridae became extinct west of the Continental Divide, where the family Centrarchidae (sunfishes)—abundantly represented by Miocene and Pliocene fossils—persisted only as a single species in the Sacramento River basin. About this time, inland species of the Pacific salmon line, as well as some taxa in the trout lineage, declined. Their places were taken during the subsequent Pleistocene Epoch by progenitors of modern western trout.

Also during the late Miocene and early Pliocene epochs, unusual salmonid species existed in western North America. *Smilodonichthys rastrosus,* known from Pliocene fossils of Oregon and California, may have represented a highly specialized species derived from *Oncorhynchus,* but it was so different from any known salmonid that Cavender and Miller (1972) described it as a new genus. *Smilodonichthys rastrosus* attained lengths to about 2 m, had more than 100 gill rakers on its first arch, and lacked teeth except for a large fang on the premaxillary. By the late Miocene, fish of the Eurasian genus *Hucho* had migrated from Asia to become established in western North America, as evidenced by Idaho fossils (Smith and Miller 1985). These Idaho *Hucho* fossils were first described as a new genus, *Paleolox* (Kimmel 1975). Evidently, *Hucho* became extinct in North America during the Pliocene. Cavender (1980) reported fossil *Salvelinus* from Nevada "at least 10 million years old." Probably these Miocene *Salvelinus* also became extinct in North America during the Pliocene. The present western North American species of this genus (bull trout, Arctic char, and Dolly Varden) represent more recent immigration from Asia.

During colder periods of the Pliocene and Pleistocene, trout occurred farther south than in historical times. The locality for the fossil named *Salmo australis,* described by Cavender and Miller (1982) from the Lake Chapala basin of southwestern Mexico, is near 20° north latitude and about 400 km south of the present range of salmonid fishes.

GENESIS OF PRESENT DISTRIBUTIONS

The separation of the ancestral lines leading to cutthroat trout on one hand and to rainbow trout and associated species on the other may have occurred by the late Pliocene. The separation of the three main evolutionary branches of cutthroat trout—the coastal (68 chromosomes), westslope (66), and Yellowstone (64) subspecies—probably occurred by early to mid-Pleistocene times. Isolation of Lahontan cutthroat trout from a 64-chromosome ancestor probably occurred soon after the separation of the 66- and 64-chromosome lines. The rainbow trout of Kamchatka is essentially identical to North American coastal rainbow trout. The Kamchatkan populations represent a recent dispersal from North America, and the separation and genetic isolation of Asian from North American rainbow trout probably dates back no more than 15,000 years (Lindsey and McPhail 1986). No living form of western trout can be considered a disjunct relict dating to the Miocene or Pliocene analogous to the isolated but related species of paddlefishes (family Polyodontidae) and suckers (Castostomidae) found today in China and North America.

The modern distribution of native trout, before the era of stocking and transplantation, is shown in Figure 2.

Cutthroat Trout

Although the phylogenetic branching sequences leading to the present North American species and subspecies of cutthroat trout probably occurred more than a million years ago, in the mid-Pleistocene and earlier, most present distributions were determined by events of the last glacial period and postglacial times (from about 70,000 years ago to the present). At the borders of glaciated regions, for example, ice dams formed great lakes that often created changes in drainage relationships. Lake Missoula was formed by one such ice dam that formed across the Clark Fork River near present Lake Pend Oreille, Idaho. At maximum size the lake was about 8,000 km^2 in area, 300 m in depth, and 2,130 km^3 in volume. According to Waite (1980), Lake Missoula rose and broke through its ice dam about 40 times during the last glaciation, releasing catastrophic floods that swept across eastern Washington and created the present channeled scablands. The present disjunct distribution of westslope cutthroat trout in the Lake Chelan drainage of Washington, the John Day drainage of Oregon, and the Salmon and Clearwater drainages of Idaho may have resulted from Lake Missoula and its floods (and subsequent elimination of intervening populations by redband trout, of which more later).

The three major lineages of cutthroat trout evolved in association with the Columbia River basin. Coastal cutthroat trout spread south to California and north to Prince William Sound, Alaska, and they rarely occur far inland. The extension of westslope cutthroat trout across the Continental Divide to the South Saskatchewan and upper Missouri river drainages and the trans-Divide extension of Yellowstone cutthroat trout from the upper Snake to the Yellowstone drainage occurred in postglacial times. This is apparent from the glacial geological history of the areas involved, the lack of differentiation between populations across the Continental Divide, and the absence of indigenous cutthroat trout in downstream refugia such as the Black Hills of South Dakota and Wyoming.

A Yellowstone cutthroat ancestor moved from the Snake River drainage into the Lahontan basin during the mid-Pleistocene, after which the Lahontan cutthroat line developed and diversified as late-Pleistocene pluvial conditions in the basin alternately waxed and waned. Transfers of a Yellowstone cutthroat ancestor from the upper Snake River drainage into the Bonneville basin may

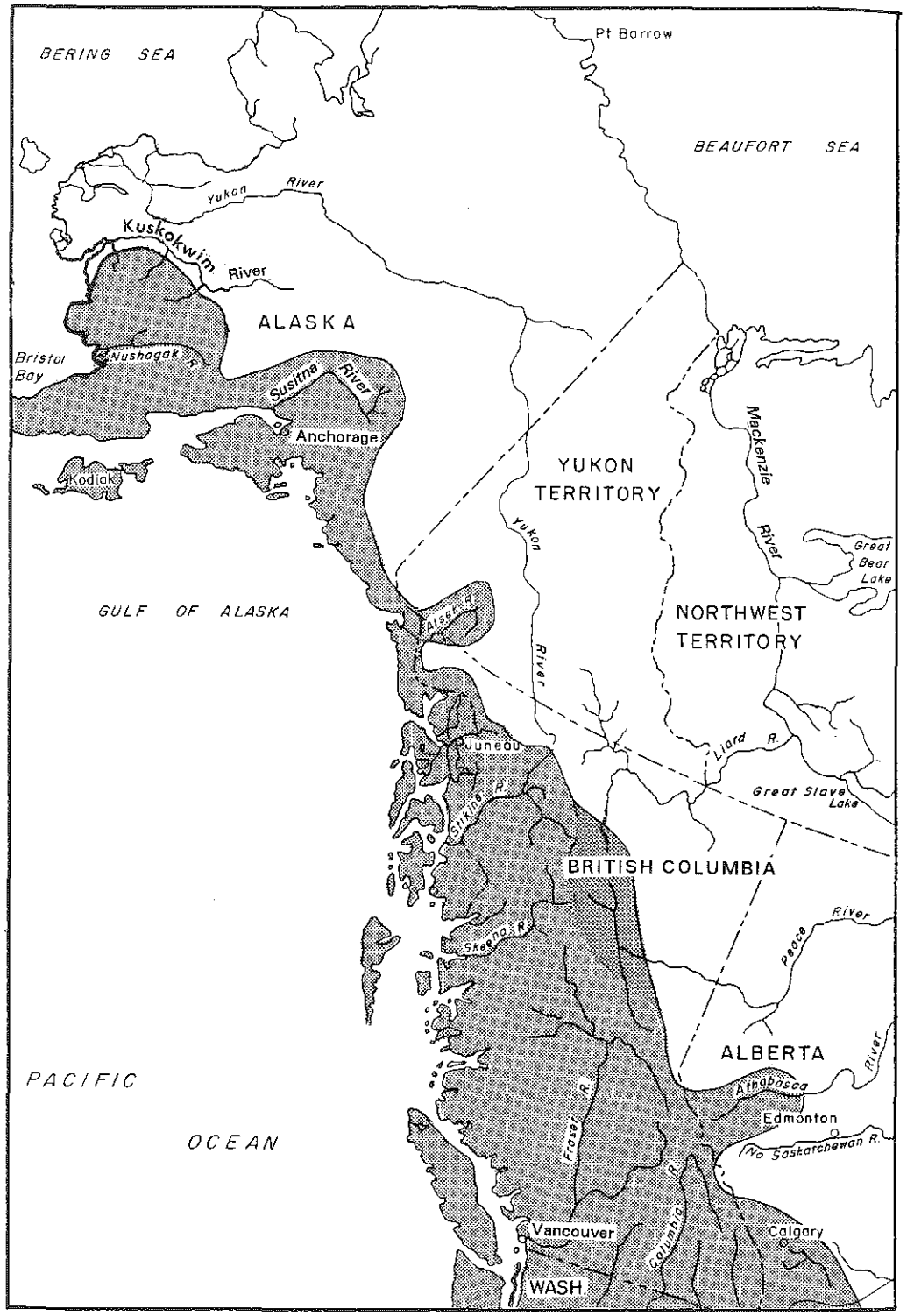

FIGURE 2.—Composite distribution of native trout in western North America at approximately the end of the 19th century.

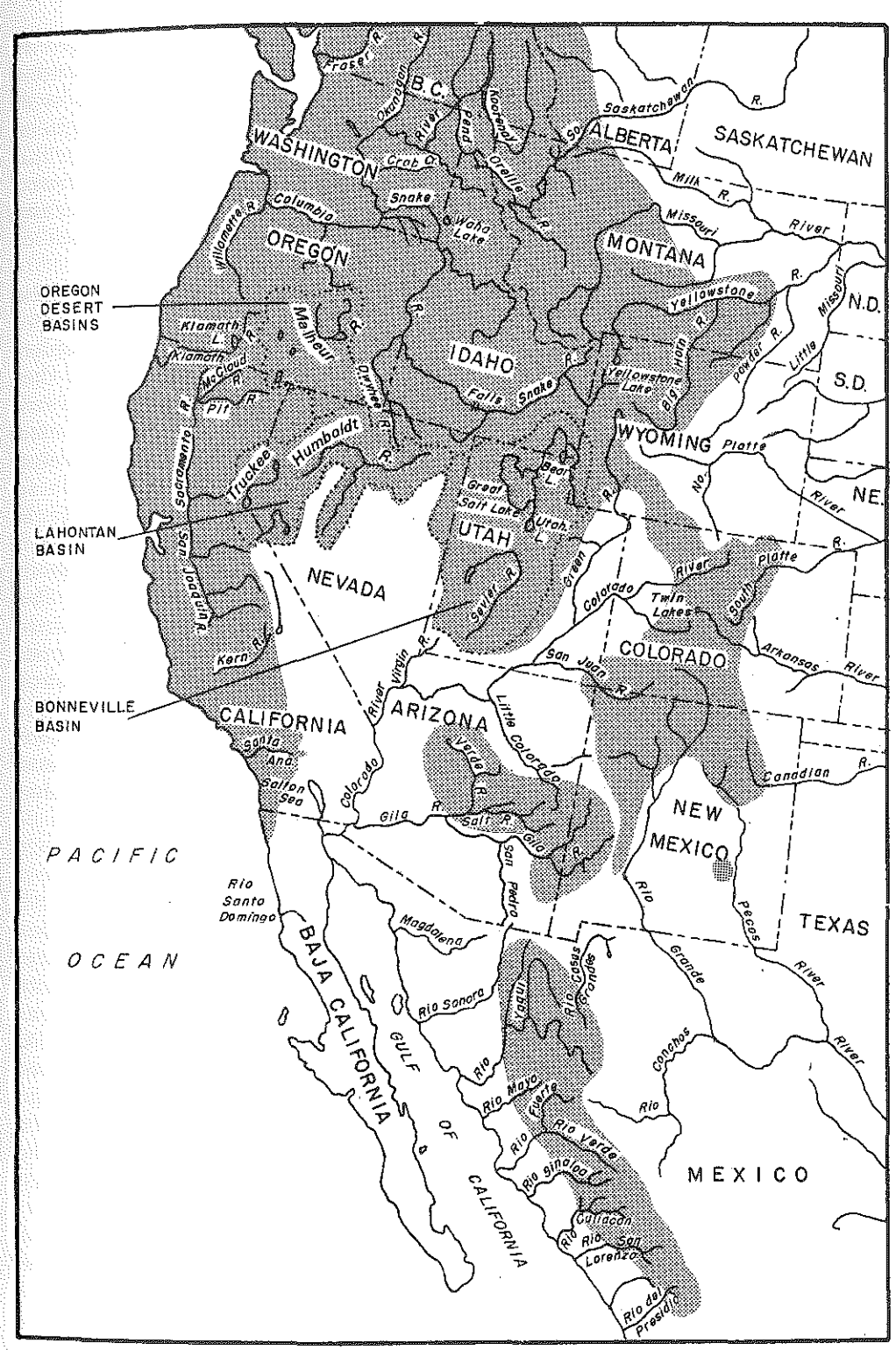

FIGURE 2.—Continued.

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have occurred as recently as 30,000 years ago, when the Bear River changed its course and became a tributary to Lake Bonneville. The transfer of Yellowstone cutthroat trout from the Snake River to the Green River of the Colorado River basin may have occurred earlier in the last glacial period or during a preglacial period (based on coloration differences between the Yellowstone River and Colorado River subspecies). Once in the Colorado basin, cutthroat trout crossed the Continental Divide to become established in the South Platte and Arkansas river headwaters (greenback subspecies) and in the Rio Grande basin of Colorado and New Mexico (Rio Grande subspecies).

During the last glacial period, barrier falls formed on major tributaries in the upper Columbia basin—on the Kootenay River near Libby, Montana; on the Clark Fork–Pend Oreille and Spokane rivers near the Washington–Idaho border; and on the Snake River near Twin Falls, Idaho. Malde (1965) estimated that Shoshone Falls on the Snake River was created between 30,000 and 60,000 years ago. Populations of the Yellowstone subspecies of cutthroat trout were isolated above Shoshone Falls, and groups of the westslope subspecies were isolated above falls in the Kootenay, Clark Fork, and Spokane drainages. Both these subspecies left disjunct relict populations in lower areas: westslope cutthroat trout in the Lake Chelan and John Day drainages; Yellowstone cutthroat trout in Waha Lake, Idaho (type locality of *bouvieri*), and Crab Creek, Washington (both these populations have become extinct since they were discovered). The westslope populations above and below the falls have been isolated at least since the last discharge of glacial Lake Missoula 12,000–15,000 years ago. The upper and lower Yellowstone populations may have been separated for 50,000 years or more. Nevertheless, virtually no differentiation has occurred within either subspecies. Thus, it becomes obvious that the distinctive subspecies themselves—westslope cutthroat trout representing the 66-chromosome line and Yellowstone cutthroat trout representing the 64-chromosome line—separated from a common ancestor well before the last glacial period.

Rainbow Trout

No forms of rainbow trout or kokanee (populations of sockeye salmon that live permanently in fresh water) are indigenous to sections of the Kootenay, Clark Fork, Spokane, and Snake river drainages above barrier falls. The only other salmonine fish native to these areas is the bull trout, and even bull trout are not native above Shoshone Falls on the Snake River. About 50,000 to 70,000 years ago, before they were blocked by falls or ice-dammed lakes, these river sections should have been accessible to ancestral rainbow trout (as well as Pacific salmon) if they were ever present in the basin. Yet no modern rainbow trout or kokanees occurred above barrier falls until they were introduced there by humans during the past 100 years. Once introduced, these fish have done very well: rainbow trout have largely replaced westslope cutthroat trout in the upper Kootenay, Clark Fork, and Spokane drainages, and introduced kokanee became the dominant game fish in Priest Lake and—before introductions of the opossum shrimp *Mysis relicta*—in Flathead, Pend Oreille, and Coeur d'Alene lakes, among others. No indigenous population of Yellowstone cutthroat trout

persists below Shoshone Falls. Thus it can be surmised that rainbow trout (and kokanee) did not occur in the upper Columbia River area before the barrier falls developed 50,000–70,000 years ago.

Phylogenetic evidence suggests that the rainbow trout group was restricted to the region south of the Columbia River until the late Pleistocene. The most primitive trout I associate with the rainbow trout phylogeny (after the protorainbow and protocutthroat forms separated) are found near the Gulf of California. They include Mexican golden trout, Gila and Apache trout, and other Mexican rainbowlike trout. These trout share primitive characters such as cutthroatlike coloration and low meristic values, but they are well differentiated from one another, which leaves little doubt that they originated long before the last glacial period. The next most primitive forms in the rainbow trout group, in my opinion, are found in the Sacramento–San Joaquin river basin and include the California golden trout of the Kern River drainage and the Sacramento redband trout of the upper McCloud River. Their degree of differentiation also indicates origins prior to the last glaciation.

Rainbow trout probably spread in the Columbia River between 50,000 and 32,000 years ago, the interval between the formation of upriver barrier falls and the next (and last) glacial advance (Tahoe stage). Glacial periods have been pluvial periods in western North America, times when rivers have flooded, valleys have filled with lakes, and drainage patterns have changed. Valleys of the Great Basin—now deserts with a few remnant lakes and internally draining streams—gained connections with one another and with external river systems. Today, redband trout whose greatest affinities are with the Columbia River fauna live in relict waters of the isolated Fort Rock, Malheur, Chewaucan, Warner Lakes, and Catlow basins in central and southeastern Oregon. These basins had direct or indirect connections to the Columbia basin during glaciopluvial periods, the last of which peaked around 32,000 years ago and again around 18,000 years ago (Minckley et al. 1986). The Oregon basin redband trout differ from their Columbia River counterparts in having more gill rakers (an adaptation to lacustrine life) and a preponderance of a primitive allele for the enzyme lactate dehydrogenase (the *LDH-B2*100* allele; Berg 1987). This amount of divergence suggests that the Oregon populations became isolated from the Columbia populations during the early phase of the Tahoe glaciation—which means that redband trout were in the Columbia basin by 32,000 years ago. (The Oregon populations are treated more fully in Chapter 9. The only trout in the more easterly Alvord, Whitehorse, Lahontan, and Bonneville basins are cutthroat trout, described in Chapter 7.)

By the time glaciers retreated about 15,000 to 10,000 years ago, a redband trout was dominant over cutthroat trout in the Columbia basin below barrier falls. A series of glacial lakes left in the Okanagan Valley by retreating ice allowed fish to move between the upper Columbia and upper Fraser river basins in present-day British Columbia (McPhail and Lindsey 1986). This relatively recent connection explains the virtually identical form of redband trout, commonly called Kamloops trout, in the upper parts of both basins.

Some Canadian populations offer interesting problems. Trout in the British Columbia and Alberta headwaters of the Peace and Athabasca rivers, which

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drain to the Mackenzie River and the Arctic Ocean, resemble redband trout in coloration and spotting. They undoubtably came from the Fraser system and, according to the scheme of colonization just outlined, should have reached the Mackenzie system in late- or postglacial times. However, Leon Carl (Ontario Ministry of Natural Resources, Maple) has sent me new evidence indicating that trout may have transferred from the Fraser to the Athabasca basin before or during the early stages of the last glacial period, about 64,000 years ago. As discussed more fully in Chapter 9, these fish have electrophoretic patterns that differ markedly from those of Fraser–Columbia redband trout and coastal rainbow trout. Another population exists in the Liard River of the Mackenzie drainage. It could have come either from the Fraser River or the Stikine basin, which drains to the Pacific (McPhail and Lindsey 1986). I have not examined these fish and do not know if they are redband or coastal rainbow trout.

Coastal rainbow trout diverged from the redband line at some unknown time, but probably relatively recently—possibly during the late Pleistocene (but prior to the most recent glacial period) and perhaps in California. Although it spread southward into Mexican waters, its more dramatic expansion was north to the Kuskokwim River in Alaska and westward to Kamchatka. This dispersal most likely occurred during the late Pleistocene when the Bering Land Bridge existed. Thus, the evolution of the rainbow trout complex has been associated with northward movement of more phylogenetically advanced forms. First came the rainbowlike forms of the Gulf of California and desert Southwest, then the golden–redband group of the Sacramento–San Joaquin Valley, then redband trout of the Columbia and upper Fraser rivers, and finally the coastal rainbow trout of rivers around the north Pacific Ocean. With a few minor exceptions, all modern redband and rainbow trout are restricted to Pacific Ocean drainages (including the desert basins of Oregon during pluvial periods). The small populations of redband trout in the upper Mackenzie basin have been mentioned. Needham and Gard (1959) reported rainbow trout from the Río Casas Grandes, a discontinuous stream in the Rio Grande basin of Mexico. These fish appear identical to Mexican rainbowlike trout native to the Río Yaqui, which flows to the Gulf of California. The headwaters of the two drainages are in close proximity. The Casas Grandes may have acquired trout by headwater transfer, but human transfer is more likely. Eagle Lake, California, is a disjunct segment of the Lahontan basin and contains a Lahontan fish fauna with the exception of the Eagle Lake rainbow trout. I assume that Lahontan cutthroat trout inhabited Eagle Lake until a postglacial warm period 8,000–4,000 years ago (Minckley et al. 1986), when the lake's one spawning tributary may have become intermittent. A cooler, wetter period 4,000–2,000 years ago (Allison and Bond 1983) provided the opportunity for Pit River rainbow trout to reach Eagle Lake by headwater transfer.

The broad overlap of rainbow and cutthroat trout niches (particularly those of nonanadromous populations), which generally prevents these species from coexisting in the same habitat, suggests the ancestors of the two species evolved in isolation from each other. The vulnerability of Yellowstone cutthroat trout and its derivatives in the Great Basin and the Colorado, Rio Grande, and South

Platte basins to replacement by introduced rainbow trout suggests their ancestors lacked a coevolutionary phase with rainbow trout. The coexistence of coastal cutthroat and coastal rainbow trout, and (to a more limited extent) of westslope cutthroat and redband trout probably reflects behavioral and ecological changes evolved in recent geological time.

My interpretation of the origins and distributions of cutthroat and rainbow trout differs considerably from that of Jordan (1894a). Jordan believed a cutthroat trout ancestor (coastal cutthroat trout) came from Asia and moved up the Columbia River basin. One branch became isolated above Shoshone Falls and evolved into the Yellowstone cutthroat trout, which then crossed the Continental Divide, moved down the Missouri River and up the South Platte, recrossed the Continental Divide to the Colorado River, moved down to the lower Colorado River, and crossed the Sierra Mountains to evolve into the California golden trout, which, in turn, evolved into rainbow trout—all during the last glaciation. In light of what we now know about geological and glacial histories, the fossil record, present distribution patterns, and the amount of evolutionary divergence in western trout, Jordan's scenario is fanciful although much neater than what I offer.

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3

ELEMENTS OF TROUT BIOLOGY AND MANAGEMENT

I present a general discussion of trout biology here to avoid repetition of information in the taxon accounts. No attributes of reproduction, feeding, growth, migration, or other aspects of life history are consistently unique to any species or subspecies of western trout. Special adaptations are associated with populations rather than with taxa. Different selective pressures acting on the same taxon of trout may result in very different ecological adaptations. This point can be readily illustrated with cutthroat trout of the Bonneville basin and redband trout of the Oregon desert basins.

Between 25,000 and 30,000 years ago the Bear River lost its connection to the Snake River and became a tributary to pluvial Lake Bonneville (Malde 1965), which thereby received cutthroat trout. At maximum level Lake Bonneville was about the size of present-day Lake Michigan and it covered much of Utah; now, it is represented by a remnant, Great Salt Lake. During the existence of Lake Bonneville, the Bear River remained a large drainage. Selective pressures acted on cutthroat trout of the basin to create two ecological types, one adapted to the great lake and the other to tributary streams. The length of evolutionary time was not sufficient for the lake and stream populations to develop clear-cut differences in structure and appearance, so all cutthroat trout native to the Bonneville basin are classified as a single subspecies. Nevertheless the two forms acquired pronounced ecological differences that influenced their present status. The fish specialized to live in the great lake proved ill-adapted to the stream environments left after Lake Bonneville declined. They were extremely vulnerable to displacement by nonnative trout stocked in the basin during the past 100 years. There is no documented example of the lake-selected form persisting in coexistence with any nonnative species of trout. On the other hand, the cutthroat trout native to flowing waters in the Bear River drainage became adapted over eons to harsh and fluctuating environments of desert basin streams, and in several areas of the drainage they remain the dominant trout. In 1976 I surveyed the Thomas Fork and Smith Fork of the Bear River drainage near Cokeville, Wyoming. These frequently turbid streams are characteristic of the foothill region, and they appear marginal for trout at best. A person with a

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general knowledge of trout biology would predict that only brown trout could maintain populations in them, yet I found the native cutthroat trout were completely dominant in all sections sampled; brown trout were restricted to two small, cold, clear tributaries. Thus, differing selection pressures on segments of the same subspecies led to subtle hereditary differences that are ecologically significant, even if they cannot be quantified by current methods.

In the desert basins of southern Oregon and northern Nevada, redband trout regularly encounter water temperatures that kill other trout. Numerous experiments have demonstrated the obvious: brook, brown, rainbow, and cutthroat trout are coldwater fish that typically experience stress when water temperatures rise above 22°C. With gradual increases in temperature (1–2°C per day), loss of equilibrium and death can be expected to occur at about 28–29°C. Nevertheless, I have found native redband trout in intermittent desert streams thriving in water of 28.3°C. They were actively feeding at this temperature, and those I caught on flies fought vigorously when hooked, indicating considerable energy reserves. The tolerance of exceptionally high temperatures shown by these redband populations evolved through natural selection in streams of hot, arid regions over thousands of years.

HABITAT, NICHE, AND ENVIRONMENT

Experienced anglers have a good understanding of trout habitat even if they do not think of it in technical terms. They know that trout are not randomly and equally distributed, so they do not cast a stream randomly. Instead, they seek out certain combinations of flow, velocity, depth, and cover that identify areas where trout tend to gather. This example of how an expert angler interprets visual cues to assess habitat quality illustrates the attributes of professional judgment; it also introduces the problem of habitat quantification. Attempts to accurately measure habitat quality by abstracting innumerable subtle, complex, and interacting factors into a few discrete components that can be expressed as a number or a formula must confront the severe limitations imposed by oversimplification.

A biological niche is the role of a species in its community. It comprises all the interactions of that species with its physical, chemical, and biotic environments during all stages of its life history. The physical, chemical, and biotic attributes of a stream environment include the quality, flow, velocity, and temperature of the water; substrate; channel morphology; and all the plants and animals living in or associated with the stream. The environment determines the abundance of the species. Habitat is the result of environmental features that can be expressed as depth, flow, velocity, and cover, which in different combinations attract different life history stages of a species. Habitat is an important determinant of abundance but is not the sole determinant.

Habitat Constraints

In many circumstances, especially in high-gradient streams, trout abundance may be constrained more by physical habitat than by food. Trout require

four kinds of habitat during the various stages of their life history: spawning habitat, nursery or rearing habitat, adult habitat, and overwintering habitat. Deficiencies in any one of the four will limit populations.

Where spawning gravels are extensive enough, trout typically produce more young than the population can absorb. Fecundity is about 1,800 to 2,200 eggs per kilogram of female body weight, but a stable population can be maintained if only two progeny from each pair of spawning parents survive to reproduce themselves. This leaves a tremendous surplus of young fish expendable to natural mortality. Before any effort is made to improve spawning habitat or to stock supplementary embryos, managers should ascertain that poor spawning success truly limits population size.

Spawning success may be severely limited in high-gradient streams where the current carries off suitable spawning gravel, leaving behind a substrate of boulders and rubble. In lower parts of watersheds, reproduction typically is restricted by high sediment loads that blanket redds with silt, a common problem in watersheds suffering from accelerated erosion. Because sediment loads are greatest during spring runoff and thus have their greatest negative effect on reproduction of spring-spawning native trout, accelerated erosion can favor populations of fall-spawning nonnative brook and brown trout over the native western trout.

After hatching and during the first months of life, trout need rearing habitat with protective cover and water of low velocity. Such habitats occur along the margins of streams and in spring seeps, side channels, and small tributaries. High-gradient, high-velocity streams may lack suitable nursery sites, in which case few fish survive to their second year even though spawning success may be high. Ottaway and Clarke (1981) and Ottaway and Forest (1983) demonstrated that newly emerged brown trout and Atlantic salmon are apt to be swept away during high-flow periods. Nehring (1986) compared year-class abundances of rainbow and brown trout with flow regimes in several Colorado streams. He found strong positive correlations between year-class abundance and lower-than-normal flows during the emergence period (and for several weeks thereafter), and strong negative correlations between abundance and higher-than-normal flows during the same period. As with spawning habitat, however, there can be too much rearing habitat. Excessive recruitment into a population where young and adult fish compete for a common food supply results in short-lived, slow-growing individuals and a population whose biomass is tied up in small, young fish.

The survival rate greatly increases after young trout attain lengths of 125–150 mm, typically in the second year of life. At this stage they relocate to riffle areas; later, they establish territories in deeper waters such as those of pools or undercut banks. By the time they reach adulthood, stream trout generally live at depths of 0.3 m or greater in areas where slow waters for resting (0–0.1 m/s) are juxtaposed with fast waters that carry food and where protective cover is provided by boulders, logs, overhanging vegetation, or undercut banks.

It is adult habitat that limits the population biomass of resident trout in most streams. That is, spawning and rearing habitats are adequate, and the food supply would support a greater biomass of trout if more adult habitat were

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present. This was demonstrated experimentally on a section of Lawrence Creek, Wisconsin, by Hunt (1976). Originally, the experimental section consisted mainly of shallow riffles. Invertebrate production was good, and small brook trout, mostly yearlings, were abundant, but the section held few larger, older trout. The stream was artificially constricted to create a narrower, deeper channel, and overhanging structures were constructed along the banks. The total food supply decreased because the substrate area was reduced, but trout biomass doubled and the numbers of larger, age-2 and older trout increased almost fourfold.

Binns and Eiserman (1979) developed a model to predict trout biomass in Wyoming streams based on the relative importance of various environmental factors. Of these factors, the annual flow regime has the greatest influence on trout biomass, according to the model. The "best" flow regime has no great difference between maximum and minimum flows during the year: the low base flow of late summer is at least 55% of the annual average daily flow, which keeps the optimum habitat sites under water. When the base flow drops below about 25% of the average daily flow in most trout streams, much of the undercut bank and desirable shoreline habitat is exposed as water levels recede. The best Wyoming trout streams, according to Binns and Eiserman, have nitrate levels of 0.15–0.25 mg/L, invertebrate abundances of more than 5,000 organisms/m^2, summer water temperatures of 10–18°C, stable streambanks, and abundant protective cover, which may include stands of submerged aquatic vegetation. These are the characteristics of a meandering, spring-fed stream with vigorous riparian vegetation.

Overwintering habitat is very important to fish, but it often is ignored when a river is evaluated for trout habitats. With allowance for the severity of winter conditions, overwinter survival is related to the amount of deep water with low current velocity and protective cover, such as occurs in deep pools with large boulders and rootwads or areas with deep beaver ponds (Bjornn 1971; Bustard and Narver 1975). In some headwater streams with poor overwintering habitat and severe winter conditions, trout leave in the fall to overwinter in larger streams at lower elevations. Such behavior is common in many populations of cutthroat trout native to headwater tributaries in the Salmon River drainage of Idaho.

Biomass in Streams

If spawning, rearing, and overwintering habitats are not limiting, and if adult habitat allows a trout population (or populations of two or more species) to expand until it reaches the limit of the food supply, how much trout biomass can a stream sustain? Any "maximum biomass" must fluctuate as annual climatic variations affect flow and temperature regimes, and it is influenced by variations in production of stream invertebrates and the relative contribution of terrestrial food. Nevertheless, the question has practical relevance because one objective of wild trout management programs is to increase the carrying capacity of present environments as a means of increasing trout production, and also because one purpose of flow recommendations for regulated rivers is to maintain fish populations downstream from dams.

Some of the largest trout biomasses occur in the spring-fed streams in the limestone areas of Pennsylvania: values as high as 630 kg/hectare in Big Springs Creek and 785 kg/hectare in Falling Spring Branch have been recorded (Graff and Hollender 1980). Nehring (1980) reported biomasses of 620 and 784 kg/hectare for rainbow and brown trout combined in two no-kill regulation sections of the South Platte River near Denver. These high values were attributed to years of good winter flow releases (1.4 m^3/s or greater) from an upstream reservoir, which maintained overwintering habitat downstream. (Typically, dams that benefit trout store peak runoff to augment low summer base flows.) Finally among the top records, McDowell (1986) measured a 1,105-kg/hectare combined biomass of brown trout (88%) and rainbow trout (12%) in a section of Sand Creek, a low-gradient, spring-fed stream in northeastern Wyoming. This may be about the upper limit of trout biomass that a stream with ideal habitat and abundant food can maintain, at least temporarily.

As these examples suggest, trout biomass usually is greatest where two or more species coexist. Here, the concepts of fundamental and realized niches (Hutchinson 1957) must be considered: the sum of two or more realized niches in the same environment should be greater than a single "fundamental" niche in that environment. For example, if only rainbow trout occur in a stream, they occupy all the habitats that represent their fundamental niche in that stream. If they occur with brown trout, the brown trout dominate the deepest pools and streambank areas, and the rainbow trout are more restricted to the riffles and open-channel reaches. The fundamental niches of the two species contract into realized niches in response to overlap of their fundamental niches. The contraction of potential niche into realized niche is an adaptive strategy to minimize direct competition between ecologically similar species, and such mutual adjustments can be made by species (such as brown and rainbow trout) that have no phylogenetic history of coevolution. Coexistence tends to force a change in strategy from generalist to specialist in regard to habitat selection and feeding preference. A result of specialization is more efficient use of both habitat and food. The better efficiency allows two coexisting trout species to maintain more biomass in a habitat than one species by itself. However, managers who might wish to maximize biomass by packing as many trout species as possible into a stream should remember the dangers of hybridization. Cutthroat trout in particular are vulnerable to hybridization with other trout species, a process that already has cost them much of their geographical range and biological integrity. In any case, most streams already have established populations of various species, and opportunities for niche packing in such habitats are limited. Niche packing has its greatest potential use in stocking of lakes and reservoirs where natural reproduction is very low or nonexistent.

Although many trout populations are limited by the availability of spawning, rearing, adult, or overwintering habitat, others are constrained by food availability. Nehring (1987) provided a case in point from Colorado. In the Fryingpan River below Ruedi Reservoir, annual fall sampling between 1972 and 1982 indicated 40–80 kg of brown trout and 15–230 kg of rainbow trout per hectare. The quantities varied from year to year, but the long-term average for the two species combined was less than 200 kg/hectare. During the 1970s, the

opossum shrimp *Mysis relicta* was introduced and became abundant in Ruedi Reservoir. In 1982 mysids began to wash out of the reservoir with water released into the Fryingpan River below the dam. The addition of this abundant, easily captured, and relatively large organism to their diet caused the trout to soar in growth and biomass. By the fall of 1986, the combined biomass of brown and rainbow trout was estimated at 961 kg/hectare (254 kg brown trout and 707 kg rainbow trout). This fivefold increase from the premysid era occurred with no change in habitat and no change in flow regime.

Habitat Enhancement

In recent years, stream habitat enhancement projects designed to increase salmonid biomass have been popular in fisheries management. Federal, state, and provincial agencies are committing considerable amounts of funding and personnel to enhancement projects and techniques, and groups of private citizens are increasingly involved with habitat improvement. The basic premise for habitat enhancement is that a particular population is limited mainly by habitat, not by food. The premise probably is correct in most cases; whereas the "best" streams have trout biomasses of hundreds of kilograms per hectare, the overall average for hundreds of western streams for which data are available is only 54 kg/hectare (Platts and McHenry 1988). It should be noted, however, that a stream channel modified to have more optimum habitat for trout generally does not have more stream invertebrates; instead, it provides trout with additional living space in which they can exploit more of the existing invertebrates for food. Conversion of riffle habitat to pool habitat (a common modification) usually decreases aquatic insect production—but not always. A Quebec study by Burgess and Bider (1980) provided an apparent exception. A section of a small brook trout stream was modified by rock and log dams until it had a 50:50 pool-to-riffle ratio, and large woody debris and rafts of alder branches were placed in strategic areas for cover. Trap samples indicated a slight but unquantified increase of emerging insects in the improved section compared with the control section; meanwhile, crawfish and brook trout biomass increased about 2.5 times in the improved section. The trout and crawfish increase can be attributed to the added pool habitat, but the increase in emerging insects may have resulted from the added woody debris. Elliot (1986) showed a sharp reduction in insect biomass (about 60%) after a small Alaskan stream was cleared of debris, followed by a fivefold increase in biomass after debris was reestablished. Two points are worth making with respect to food supply and habitat enhancement. First, whether or not a habitat project will increase invertebrate production for trout may depend on the kinds of structure added. Second, before a large investment is made in a particular stream improvement, it may be worth checking that the existing food base will support a larger biomass of trout.

Knowledge of habitat, niche, and environment allows data to be quantified for predictive purposes, but development of general models of trout biology still is rudimentary. It is not always possible to envision how a trout population will be affected by certain known changes in flow and temperature regimes resulting from a dam or water diversion project, or to know which environmental factors

favor trout over nongame fishes or native trout over nonnative trout. In the model developed by Binns and Eiserman (1979) for predicting trout biomass in Wyoming streams, a qualitative element relied on professional judgment, which increased the model's accuracy in the region known well by the authors. When this model was tested in an Ontario trout stream, however, all predictive accuracy was lost (Bowlby and Roff 1986).

The most encompassing environmental influences on trout populations in streams are flow and temperature regimes. Wesche and Rechard (1980) reviewed methods of evaluating flows in relation to trout abundance, and Fausch et al. (1988) reviewed models that predict standing crops of stream fishes based on habitat variables. The practical limitations of the models developed to date are that they do not handle combined effects of habitat variables very well, and they are even poorer at accommodating biological factors such as species interactions. For example, I know of no current model that could have predicted the demise of native cutthroat trout over so much of the species' range during the past 100 years or the dominance that native cutthroat trout retain over introduced species in sections of the Humboldt River drainage of the Lahontan basin and the Bear River drainage of the Bonneville basin. A more fundamental limitation of models is that they can generate consistently precise and accurate predictions only when natural patterns are highly regular—but natural systems are highly irregular. If stochastic variation is built into models, the models become much more realistic but much less precise.

The role of professional judgment in habitat evaluations therefore remains very strong. In the 1960s, well before habitat modeling came to the fore, the Nebraska Game and Parks Commission successfully predicted that fencing Otter Creek to halt its degredation by cattle would boost production of rainbow trout that migrate to Lake McConaughy, where they grow and mature (Van Velson 1977, 1978). What were not predicted, and what no habitat model could ever predict, were the magnitude of the increase in rainbow trout production and the faunal shifts that accompanied that increase. In 1974, only 5 years after the fencing program began, more than 20,000 young rainbow trout migrated from Otter Creek to Lake McConaughy. Not only did the fish assemblage change from one dominated by suckers and chubs to one dominated by trout, the dominant species of trout changed. During 1957–1966, the fish fauna of Otter Creek consisted of 1% rainbow trout, 17% brown trout, 22% white sucker, and 60% creek chub. The 1974–1976 samples revealed striking changes—to 97% rainbow trout, 2% brown trout, 0.5% white sucker, and 0.5% creek chub. This dramatic restructuring of fish fauna can be attributed to changes in the environment that favored rainbow trout over other species in competition for food, space, and reproduction, and it was effected solely by excluding cattle from the riparian zone. Qualitatively we can learn from the Otter Creek example that changes from warmer to colder water temperatures, from turbid to clear water, and from silt to gravel or rocky substrate act to increase the niche volume of rainbow trout, but precise translations of niche volume changes to changes in species abundance and biomass still cannot be expected.

The Otter Creek example illustrates the role of professional judgment and of quantitative versus qualitative approaches for environmental assessment, as

discussed by Fryer (1987), and it is relevant to habitat restoration projects. An agency, influenced by user groups such as the livestock or forest products industry, may demand that "scientifically sound" studies be undertaken to quantify the benefits to a trout population before an action is taken. For example, a quantitative study of relative impacts of wild and domestic animals on a stream may be required before authorization is given to restore riparian vegetation. Such a study would needlessly waste funds and delay implementation. Any management action resulting in changes in the aquatic environment that tend to optimize components of the trout niche volume (temperature, water quality, cover, substrate) will be beneficial. Precisely how beneficial can only be known during the several years in which the environmental changes are realized and the trout population reaches a new equilibrium level. Implicit in all this, however, is that sound professional judgement must be based not only on practical experience and critical thinking, but also on an understanding of theories, principles, and paradigms and how they apply to particular situations. Essentially, sound professional judgement reflects an ability to correctly interpret patterns of regularity and to understand the limitations of observed past regularities for making accurate predictions.

REPRODUCTION

Spawning by native western trout shows greater intraspecific than interspecific variation, as is the case with variation in other general phases of trout life histories. Any attempt to quantify spawning characteristics in the hope of defining species-specific differences has an excellent chance of failing. The differences documented in the literature are, by and large, not genetically based, but reflect the size of the fish and the environment in which it reproduces. For example, Harper (1978) compiled detailed data on the spawning of Apache trout, and Rinne (1980) did so for Gila trout. The "preferences" for depth, velocity, and substrate that could be established from these data are not species-specific; rather, they represent only the limited range of options offered in the small streams where the observations were made. The spawning characteristics of any species of trout of comparable size in these streams would most likely be identical to those found for Apache and Gila trout.

Seasonality

All western trout evolved to spawn during the spring season, stimulated by rising water temperatures. Spawning time varies greatly in different regions, depending on temperature and flow regimes. Along the Pacific coast in areas of moderate winter climate, water temperatures of about 3–6°C may initiate spawning activity by coastal cutthroat and rainbow trout from late December through April; actual spawning typically occurs when daily maximum temperatures reach 6–9°C. Temperature controls on spawning may be superimposed on genetic controls, which are revealed when local races are exposed to similar environmental stimuli. For example, Leider et al. (1984) reported about a 2-month difference in mean spawning time of native summer-run steelhead

(mid-February) and winter-run steelhead (mid-April) in Gobar Creek, a tributary to the Kalama River in Washington. Hatchery stocks of both steelhead runs also spawn in Gobar Creek—about a month earlier than their respective wild counterparts (probably due to hatchery selection). Dodge and MacCrimmon (1970) described two spawning runs of introduced rainbow trout from Lake Huron into Bothwell Creek, Ontario. The A run entered the creek from late October to mid-February and spawned mainly from January 15 through February 5. The B run entered from mid-February to early May and its spawning peaked between March 16 and April 16. The temperature regime in Bothwell Creek during spawning and egg incubation of the A run must be considerably below the norm for rainbow trout.

The genetic control of spawning time is readily modified, as shown by the rapid selection for fall-spawning races of trout under hatchery conditions and the earlier spawning times characteristic of hatchery races of steelhead. I know of no example, however, of fall-spawning hatchery trout that established fall-spawning wild populations. Evidently, the fish revert to spring spawning when subjected to natural temperatures and photoperiods. Also, eggs spawned in the fall by any of the western trout probably would all die if exposed for several winter months to temperatures near freezing. The eggs and embryos of spring-spawning species appear to be less tolerant of low water temperatures than eggs and embryos of fall-spawning species.

Some wild populations of rainbow and cutthroat trout, however, do spawn in the fall in rivers with unusual thermal characteristics. Introduced populations of rainbow trout spawn in the fall in the Firehole River, Yellowstone National Park (Kaya 1977), and in tributaries to the North Platte River, Nebraska (Van Velson 1974, 1978). I have examined specimens of cutthroat trout taken on spawning redds in November in a tributary to the upper Snake River, Idaho. In all of these populations, the fish move from cold autumn waters into warmer spring-fed waters. In general, spring-spawning species can be stimulated to spawn in the fall if fish with mature gonads move from colder to warmer waters. Spring-spawning trout must have their gonads in an advanced stage of development by autumn anyway if they are to spawn the following spring. Typically, winter is a time in which energy reserves are expended for body maintenance, and significant gonad development does not occur.

Environmental Constraints

All native western trout evolved to spawn in flowing waters that circulate dissolved oxygen through the redd. Embryos need the most oxygen when their development is most rapid, which occurs just before hatching at a time of rising water temperatures. Most rivers during the spring have supersaturated levels of dissolved oxygen (9–12 mg/L or more), which is more than adequate for developing trout eggs. The crucial figure, however, is the oxygen concentration at the surface of the developing egg, which depends on the permeability of the redd. When gravels become clogged by fine sediment, water flow through the redd is impeded and less dissolved oxygen reaches the embryos. Chapman (1988) described the characteristics and unique features of the egg pocket within

salmonid redds, and he reviewed studies of embryo mortality in relation to the percentage of fine sediment in a redd. The greatest mortality due to sedimentation may occur during the period from hatching to emergence rather than earlier (Chapman 1988; MacKenzie and Moring 1988). In any case, excessive sediment accumulation in redds limits reproductive success in watersheds characterized by accelerated erosion. Stocking eggs in Vibert boxes or some other hatching device does not protect the eggs from sediment, and the practice may encourage fungal and bacterial growths that can kill eggs (Harshbarger and Porter 1979, 1982). Only watershed rehabilitation that reduces erosion will increase reproductive success in streams with sedimentation problems.

In a few cases cutthroat and rainbow trout successfully reproduce in lakes without access to tributary streams. There, environmental limits on reproduction are imposed by a lack of spawning substrate and by poor circulation of highly oxygenated water through the substrate. In Rocky Mountain National Park, Colorado, stocking of hatchery trout in lakes ceased in 1967. It was assumed that lakes without suitable spawning tributaries would no longer have cutthroat or rainbow trout once the last stocked fish died. In the 1970s, James Mullan and Bruce Rosenlund of the U.S. Fish and Wildlife Service found several year-classes of cutthroat trout (and cutthroat × rainbow hybrids) in several park lakes that lacked spawning tributaries. Evidently, spawning had been occurring on gravel bars in the lakes near outlets where upwelling of water through the substrate was likely. The very small amount of suspended sediment in these lakes allowed adequate oxygen to reach the embryos despite extremely slow water circulation through the gravel. Cutthroat trout also spawn in lakes without inlet or outlet streams in Glacier National Park (Marnell et al. 1987).

Some lakes in Rocky Mountain National Park are barren of trout despite having excellent spawning tributaries. These lakes are at high elevations where cold weather delays spawning time until late July or early August. The low incubation temperature and sharp September decline in temperature do not allow accumulation of the approximately 330 Celsius temperature units (sum of average daily temperatures above 0°C) necessary for hatching, plus the additional 300 units needed between hatching and emergence, before winter sets in. In park lakes with slightly more favorable regimes, reproduction is successful only in years with warmer, extended summers (B. Rosenlund, personal communication).

Spawning Frequency

It is commonly assumed that sexually mature trout soon perish if they do not spawn but instead resorb the products of their gonads. Although I do not know of any experimental studies of this subject, I doubt that resorption is lethal. Volodin (1980) reviewed data on egg resorption for about 30 species of fish and concluded that resorption does not increase mortality and may even be beneficial by recycling nutrients in the body. The association of mortality with egg resorption has been fostered by the stocking of hatchery rainbow trout in lakes without access to adequate spawning areas. Sexually mature trout 2–3 years old are commonly observed in such lakes, but very few of these fish are

alive the following year. The explanation is that through inadvertence, domesticated rainbow trout have been bred for a short life span because they have been selected for rapid growth and early maturity. Very few survive for more than 1 year in the wild after reaching sexual maturity, whether they spawn or not.

The age and size at first spawning of western trout, as well as their fecundity, vary greatly and are influenced by both environmental and hereditary factors. Relative fecundity ranges from about 1,200 to 3,200 eggs per kilogram of body weight. Total fecundity—eggs per female—increases with fish size, but relative fecundity tends to decrease in larger, older fish, partly because the eggs are larger. More rapid early growth tends to induce earlier sexual maturation as well as a shorter life span. Nevertheless, hereditary disposition for older age at first sexual maturation has evolved in certain anadromous and lacustrine populations even though their marine or lake environments support the rapid and sustained growth of juveniles. In these populations, the greater natural mortality associated with an extended juvenile growth phase is more than offset by the greater fecundity of larger spawning adults.

In streams, most western trout first spawn 2–4 years after their parents had spawned. If males and females first spawn at different ages, males consistently tend to mature a year sooner. Mortality usually is high after first spawning, and first spawners provide the bulk of the fecundity in most trout populations. Typically, more females than males are repeat spawners. Lacustrine populations of rainbow and cutthroat trout commonly have a 2-year repeat-spawning cycle. The duration between successive spawnings depends on the rate of energy accumulation in postspawning fish, hence on food abundance and length of growing season. Only 5–20% of most steelhead runs are repeat spawners; however, Dodge and MacCrimmon (1970) reported that 75% of the A run and 52% of the B run of Lake Huron rainbow trout spawning in Bothwell Creek were repeat spawners. Perhaps the absence of large ocean predators from Lake Huron accounts for the greater postspawning survival there.

Arctic char offer an extreme salmonine example. Dutil (1986) described the reproductive cycle of an anadromous Arctic char population in Nauyuk Lake near the Canadian Arctic Circle, where thermal conditions are very rigorous. These fish feed in the Bering Sea during summer, where they have only 50 days or so to accumulate nearly all their annual energy. In late summer they return to fresh water for spawning, during which females lose up to 46% of their energy reserves; the fish then overwinter in the lake for 10 months. Under these conditions, individuals require more than 2 years between successive spawnings. Evolutionary selective pressures on Arctic populations favor long life, large adult size, and many repeat spawnings (Craig 1985).

Reproduction in Harsh Environments

In some rivers with limited spawning habitat, trout may use small, intermittent tributaries for reproduction. This tactic is successful if the tributary flows until the young are able to move to the main stream. Once the young acquire some swimming facility, declining flows stimulate their downstream movement, and massive losses from stranding are avoided (Erman and Leidy

salmonid redds, and he reviewed studies of embryo mortality in relation to the percentage of fine sediment in a redd. The greatest mortality due to sedimentation may occur during the period from hatching to emergence rather than earlier (Chapman 1988; MacKenzie and Moring 1988). In any case, excessive sediment accumulation in redds limits reproductive success in watersheds characterized by accelerated erosion. Stocking eggs in Vibert boxes or some other hatching device does not protect the eggs from sediment, and the practice may encourage fungal and bacterial growths that can kill eggs (Harshbarger and Porter 1979, 1982). Only watershed rehabilitation that reduces erosion will increase reproductive success in streams with sedimentation problems.

In a few cases cutthroat and rainbow trout successfully reproduce in lakes without access to tributary streams. There, environmental limits on reproduction are imposed by a lack of spawning substrate and by poor circulation of highly oxygenated water through the substrate. In Rocky Mountain National Park, Colorado, stocking of hatchery trout in lakes ceased in 1967. It was assumed that lakes without suitable spawning tributaries would no longer have cutthroat or rainbow trout once the last stocked fish died. In the 1970s, James Mullan and Bruce Rosenlund of the U.S. Fish and Wildlife Service found several year-classes of cutthroat trout (and cutthroat × rainbow hybrids) in several park lakes that lacked spawning tributaries. Evidently, spawning had been occurring on gravel bars in the lakes near outlets where upwelling of water through the substrate was likely. The very small amount of suspended sediment in these lakes allowed adequate oxygen to reach the embryos despite extremely slow water circulation through the gravel. Cutthroat trout also spawn in lakes without inlet or outlet streams in Glacier National Park (Marnell et al. 1987).

Some lakes in Rocky Mountain National Park are barren of trout despite having excellent spawning tributaries. These lakes are at high elevations where cold weather delays spawning time until late July or early August. The low incubation temperature and sharp September decline in temperature do not allow accumulation of the approximately 330 Celsius temperature units (sum of average daily temperatures above 0°C) necessary for hatching, plus the additional 300 units needed between hatching and emergence, before winter sets in. In park lakes with slightly more favorable regimes, reproduction is successful only in years with warmer, extended summers (B. Rosenlund, personal communication).

Spawning Frequency

It is commonly assumed that sexually mature trout soon perish if they do not spawn but instead resorb the products of their gonads. Although I do not know of any experimental studies of this subject, I doubt that resorption is lethal. Volodin (1980) reviewed data on egg resorption for about 30 species of fish and concluded that resorption does not increase mortality and may even be beneficial by recycling nutrients in the body. The association of mortality with egg resorption has been fostered by the stocking of hatchery rainbow trout in lakes without access to adequate spawning areas. Sexually mature trout 2–3 years old are commonly observed in such lakes, but very few of these fish are

alive the following year. The explanation is that through inadvertence, domesticated rainbow trout have been bred for a short life span because they have been selected for rapid growth and early maturity. Very few survive for more than 1 year in the wild after reaching sexual maturity, whether they spawn or not.

The age and size at first spawning of western trout, as well as their fecundity, vary greatly and are influenced by both environmental and hereditary factors. Relative fecundity ranges from about 1,200 to 3,200 eggs per kilogram of body weight. Total fecundity—eggs per female—increases with fish size, but relative fecundity tends to decrease in larger, older fish, partly because the eggs are larger. More rapid early growth tends to induce earlier sexual maturation as well as a shorter life span. Nevertheless, hereditary disposition for older age at first sexual maturation has evolved in certain anadromous and lacustrine populations even though their marine or lake environments support the rapid and sustained growth of juveniles. In these populations, the greater natural mortality associated with an extended juvenile growth phase is more than offset by the greater fecundity of larger spawning adults.

In streams, most western trout first spawn 2–4 years after their parents had spawned. If males and females first spawn at different ages, males consistently tend to mature a year sooner. Mortality usually is high after first spawning, and first spawners provide the bulk of the fecundity in most trout populations. Typically, more females than males are repeat spawners. Lacustrine populations of rainbow and cutthroat trout commonly have a 2-year repeat-spawning cycle. The duration between successive spawnings depends on the rate of energy accumulation in postspawning fish, hence on food abundance and length of growing season. Only 5–20% of most steelhead runs are repeat spawners; however, Dodge and MacCrimmon (1970) reported that 75% of the A run and 52% of the B run of Lake Huron rainbow trout spawning in Bothwell Creek were repeat spawners. Perhaps the absence of large ocean predators from Lake Huron accounts for the greater postspawning survival there.

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1975; Erman and Hawthorne 1976). Where a particularly harsh environment has been a regular feature of a region for thousands of years, certain reproductive adaptations could be expected under specific conditions. Coffin (1981) provided information on reproduction by the Humboldt form of Lahontan cutthroat trout in an arid region of unstable and highly fluctuating streamflows. A spawning run from a reservoir entered Willow Creek, Nevada, from April 8 to May 28, peaking on May 11. The maximum daily water temperature in Willow Creek during the peak of the run was 15.5°C, and it reached 26.6°C by the end of the run (both maxima are well above any temperatures I have seen reported for other runs of spring-spawning salmonids). The actual spawning evidently occurred in headwater tributaries fed by snowmelt. These tributaries, however, typically are dry or intermittent by midsummer. Under such an environmental regime, rapid embryonic development should have a survival advantage. Coffin (1981) reported that fertilized eggs of the Willow Creek cutthroat trout were taken to a hatchery where hatching occurred in 23 days at 11°C (254 temperature units), an unusually short time. The lack of more comprehensive information prevents a confident conclusion that the Willow Creek cutthroat trout possesses a genetic adaptation for rapid embryonic development, but such an adaptation would be the expected result of natural selection in an unusually harsh environment.

By contrast, trout reproducing in another harsh environment—an alpine lake—do not seem to have been selected for rapid embryonic development, at least not within 20–25 generations. Cutthroat trout and rainbow trout were introduced into previously fishless Emerald Lake, Colorado, in 1888–1890 (Lentsch 1985; Van Velson 1985), and subsequently the two species have hybridized to produce a broad base of heterozygosity. The reproductive environment of Emerald Lake, at an elevation of about 3,100 m, is severe. Spawners enter the inlet stream about mid-June when daily water temperatures typically fluctuate between 1 and 4°C. Spawning begins at daily mean temperatures of 2–3°C. Maximum temperatures in late July and August do not much exceed 6°C. By late summer the inlet stream becomes intermittent. Spawning also occurs in the outlet area of Emerald Lake, where more than twice as many temperature units accumulate during the spawning-to-emergence period than in the inlet stream, but the lake level drops in mid or late summer to expose most of the spawning habitat in the outlet area. Eggs from both inlet and outlet spawners have been hatched at the Colorado Division of Wildlife's Bellvue hatchery. Hatchery foreman Tom Mandis told me that both groups hatched at 330 temperature units when incubated at 12°C, which is typical of all forms of rainbow trout raised at the hatchery. If a hereditary adaptation has occurred in the reproduction of the Emerald Lake trout, it may be the ability to spawn and begin egg incubation at temperatures considerably below the norm for most rainbow and cutthroat trout.

Reproductive Isolation

A fascinating aspect of reproduction concerns reproductive isolation, or the lack of it, between various sympatric forms of western trout. In general, the only large-scale instance of reproductive isolation between sympatric species occurs between coastal rainbow trout and coastal cutthroat trout from California to Alaska; on a smaller scale, it also occurs between redband trout and westslope cutthroat trout in some Columbia River drainages in Idaho and Oregon. Whenever hatchery rainbow trout have been stocked outside their native range, however, they almost always have hybridized with various native subspecies of cutthroat, Gila, and Apache trout. On the other hand, sympatric races within subspecies have developed differences in the time or place of spawning that keep them reproductively isolated. Summer and winter runs of steelhead may occur in the same river (Leider et al. 1984), but they retain their genetically based fidelity to run timing when they do. In Kootenay Lake, British Columbia, three distinct groups of redband trout (Cartwright 1961; Hartman 1969; Andrusak 1981), as well as three races of kokanee (Vernon 1957), keep their identities by spawning in separate tributaries. Neave (1944) described three races of reproductively isolated rainbow trout (two steelhead runs and a resident population) in the Cowichan River on Vancouver Island; oddly, he could find no clear-cut separation between the races in time and place of spawning. Even these brief examples illustrate the amount of intraspecific diversity that can be lost when a large segment of a reproductive habitat is lost to fish.

Reproductive isolation may be developing within the previously mentioned trout population of Emerald Lake, Colorado. First stocked 100 years ago (1890–1892), the now-hybridized rainbow × cutthroat population spawns in both the inlet and outlet areas. Fish born in the two areas exhibit different age–growth characteristics, causing them to behave as two separate populations. Tagged repeat spawners from the inlet and outlet spawning sites have exhibited virtually 100% fidelity in returning to the site where they previously spawned (Lentsch 1985; Van Velson 1985). Yellowstone cutthroat trout in Yellowstone Lake also seem to have developed genetic affinities for inlet or outlet spawning (Bowler 1975). Reproductive isolation between sympatric stocks of the same species increases the abundance of the species by generating specialized populations that, in combination, more fully exploit their environment than a single generalized stock.

Some cases of apparent reproductive isolation may actually reflect local environmental influences on gonadal maturation. Rainbow trout of Lake McConaughy, Nebraska, may migrate and spawn in the fall, or the same fish may spawn in the spring as a repeat spawner (Van Velson 1974). The timing of reproduction probably depends on when fish move from the colder North Platte River into warmer, spring-fed tributaries: if they make this movement in the fall, spawning begins then. Snyder (1917) described two distinct spawning runs of Lahontan cutthroat trout from Pyramid Lake, Nevada, up the Truckee River. The first run migrated from the lake in the late fall and consisted of large trout called redfish. As this run waned, smaller trout called tommies ran up the river. Perhaps two distinct and reproductively isolated groups of Lahontan cutthroat were native to Pyramid Lake, but I believe that only a single population was involved. The differences in the timing of the runs and the size of the fish can be attributed to repeat spawners (redfish) and first spawners (tommies).

Steve McMullin, Montana Fish and Game Department biologist, informed

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me that a small run of cutthroat trout leaves Flathead Lake in November, but the bulk of the spawning migration begins in February. These runs may be explained by different responses to environmental stimuli in relation to gonadal development between repeat spawners and first spawners, or they could be based on hereditary differences. Fish that migrate farther to spawn would be expected to start their migration sooner. Separated by their homing instincts, distinct and reproductively isolated races characterized by early or late migration might result, similar to the winter- and summer-run races of steelhead.

AGE AND GROWTH

Age and growth of trout are governed by complex and incompletely known interactions of heredity and environment. Trout have indeterminate growth: the potential to grow as long as they live. Life span has a hereditary basis (mainly determined by age at sexual maturity) but is also enormously influenced by environmental factors that affect rates of growth and metabolism. Typically, slower growth (lower metabolic energy expenditure) results in older age at sexual maturity and longer life. A striking example of this phenomenon concerns hatchery brook trout introduced into Bunny Lake, California, where some individuals lived for 24 years—about six times the normal life span of the source stock (Reimers 1979). The harsh, cold environment and sparse food supply of Bunny Lake caused extremely slow growth and greatly delayed gonadal development.

An environmentally extended life span also can be acquired by older individuals that exploit a new food supply, thus avoiding competition with younger, smaller fish in the population. Campbell (1979) investigated the occurrence of ferox trout (large specimens of brown trout) in Scottish lakes. The ferox trout typically occurred in nutrient-poor lakes with Arctic char. Most of the brown trout in these lakes grew slowly and generally had a maximum life span of 6–8 years. A few individuals near the end of their normal life span, however, began to feed on Arctic char. Evidently this new food resource rejuvenated them, increasing their growth rates and extending their maximum life spans to 15 years or more. Arctic char themselves demonstrate the phenomenon of rejuvenation, especially in lakes where they are the only fish species present. There, some individuals become cannibalistic and attain much greater size and age than are typical of the population (Skreslet 1973). Rejuvenation is associated with changed feeding habits and growth, not with a different genetic expression. The population of brown trout called "ferox" in Lough Melvin, Ireland, however, is genetically distinct from other populations of brown trout in that lake, as shown by Ferguson and Mason (1981).

The maximum life span of most native western trout in most environments is 6–7 years. The span is extended where the annual metabolic energy expenditure is low as a result of cold water, short growing season, or sparse food supply. For example, whereas the typical maximum age of the cutthroat trout native to Yellowstone Lake is 7–8 years, I have collected 11- and 12-year-old fish derived from Yellowstone Lake parents in the frigid waters of South Gap Lake, Wyoming, at 3,310 m elevation; they resembled 3–4-year-old trout in Yellowstone Lake.

Although a genetic factor influences maximum life span, it is often obscured by environmental factors. Typically, the older the age at sexual maturity, the longer the life span. Environments that nurture rapid and sustained growth (oceans and large lakes) selectively impress a hereditary basis for older age (and much larger size) at sexual maturity. Thus, races of large steelhead that spend two or more years in the ocean before maturing, and races of large Kamloops trout such as those in Kootenay Lake, have a genetic basis for sexual maturation at an advanced age. Conversely, hatchery selection of domesticated strains of trout has produced a genetic basis for rapid growth, early sexual maturity, high fecundity, and—unavoidably—a short life span.

Size

Like longevity, maximum size is subject to environmental modification, but ultimately it is under genetic control. The large sizes attained by some races of western trout, even in nonnative waters, illustrate the inheritance of maximum size.

Among cutthroat trout, the Lahontan subspecies historically grew about twice as large as any other subspecies. The official size record for cutthroat trout is a 19-kg fish from Pyramid Lake, Nevada, but unofficial reports of specimens as large as 28 kg are attributed to the former commercial and subsistence fisheries in that lake (Hickman and Behnke 1979).

In the rainbow trout group, fish of great size are noted among summer-run steelhead of the Skeena River drainage, British Columbia, the steelhead migrating up the Snake River, Idaho, and the redband (Kamloops) trout of large lakes in the upper Columbia and upper Fraser river basins, particularly those lakes that have abundant populations of suitable forage fish such as kokanee. The record rod-caught steelhead weighed 19.1 kg and was taken near Bell Island, Alaska (Hart 1973). The proximity of Bell Island to the mouth of the Skeena River suggests the record fish originated in the Skeena drainage. Kamloops trout of the Gerrard strain in Kootenay Lake attain weights of 12 kg or more in their native environment but have reached much greater size when stocked into other lakes. Kootenay Kamloops trout stocked into Lake Pend Oreille, Idaho (where small kokanees provided abundant forage), reached 15 kg at 4 years of age and 17 kg at 5 years. A specimen of Kootenay trout stocked into Jewel Lake, British Columbia, attained a weight of 23.7 kg (Scott and Crossman 1973).

Other sources of hereditary specializations for large size among the native western trout include rainbow trout of Eagle Lake, California; trout native to Upper Klamath Lake, Oregon; rainbow and cutthroat trout native to Crescent Lake, Washington; Bonneville cutthroat trout (Bear Lake stock); and rainbow trout of Lake Iliamna, Alaska. These populations represent some of the sources of natural genetic diversity among western trout that exhibit older ages at maturity and large maximum sizes.

Growth

Growth rate is directly influenced by growth hormones (Agellon et al. 1988) and some enzymes (Reinitz 1977), which may be controlled by only a few genes, but it is very unlikely that growth rate is determined simply by the actions of

"fast-growth" or "slow-growth" alleles. Nevertheless, selective breeding of fast- or slow-growing fish can permanently change average growth rates within a hatchery population (Tave 1986). An obvious, though less well-documented, corollary is that size-selective mortality, by preventing fish of certain sizes from reproducing, also can change a population's genetic tendencies for growth. This corollary has raised concerns that fishing, which is inherently size-selective, can degrade (from the fisher's viewpoint) the growth characteristics of an exploited population. Ricker (1981) adduced that the ocean fisheries for Pacific salmon off British Columbia, which selectively harvests the larger (fast-growing or late-maturing) fish before they reproduce, has reduced the average growth rates of all targeted species. Silliman (1974) subjected *Tilapia mossambica* to intensive size-selective mortality by removing the fastest-growing fish and leaving the slowest-growing to reproduce. A genetic change to slower growth was effected among males (but not females) after only three generations.

Efforts to demonstrate genetic consequences of recreational fishing have not been successful, however, and I know of no valid evidence that selective angling mortality has ever caused hereditary changes in the growth rate of wild trout. Published evidence to this effect is misleading. Favro et al. (1979, 1980, 1982) attributed the slow growth of brown trout observed after 1973 in a section of the Au Sable River, Michigan, to selective removal by anglers of larger trout from the population. They used the output from computer models to support their contention that a genetic change caused slower growth. The major problem with their genetic model, as pointed out by Nelson and Soulé (1987), is that it treated fecundity as age-dependent, but size-independent: the fastest-growing fish were assigned the same fecundity as the slowest-growing fish at the same age. When realistic size-dependent fecundity is incorporated into the model, the hypothetical trout population rapidly runs to fixation for the fastest-growing genotypes, regardless of the level of angling mortality (Nelson and Soulé 1987). In the Au Sable River, moreover, predators account for a much greater proportion of annual mortality than do anglers, and predation mortality is selective for smaller trout (Alexander 1976). Thus, as a selective factor, predation should exert a much greater influence against slow growth than angling mortality does against fast growth. The actual reason for the slower growth of Au Sable brown trout after 1973 was a reduction in nutrient input to the river after effluents from a sewage lagoon and a fish hatchery ceased (Clark and Alexander 1985).

As the trout species most vulnerable to angler exploitation, cutthroat trout might be expected to show angler-induced selection for slower growth in wild populations. Cutthroat trout native to Yellowstone Lake and the Yellowstone River were exposed to heavy exploitation for many years until regulations instituted in 1973 protected larger fish and greatly reduced angling mortality. Presently, the general maximum size of Yellowstone cutthroat trout is the same as the maximum size reported for the virgin population by the first anglers in Yellowstone National Park (about 56 cm and 2 kg).

It would be counterproductive to breed fast-growth strains of hatchery trout in an attempt to produce a trout of superior survival capabilities for stocking into natural waters. Whether a strain of fish is selected for rapid growth or not, genetic changes accumulated over several generations in a hatchery environment—where artificial diets are abundant, water temperatures and flow are controlled at optimal levels, and predation (apart from minor cannabalism) is absent—undermine growth and survival under natural conditions where stocked fish must capture and assimilate natural food organisms in competition with other fish species. For example, Dwyer and Piper (1984) evaluated the performance of two strains of domestic hatchery rainbow trout and two strains of wild rainbow trout stocked into two Montana ponds in which angling was allowed. In the hatchery, fed a hatchery diet, the domestic strains exhibited better growth and food conversion than the wild strains. Once stocked into the ponds and exposed to natural conditions, however, the wild and domestic strains showed strikingly different mortality rates. After 2 years, no hatchery trout remained alive in either pond, whereas a considerable number of wild trout continued to thrive.

The native trout of Henry's Lake, Idaho, is the Yellowstone cutthroat trout, but the lake has a long history of stocking with nonnative trout, including rainbow × cutthroat hybrids. The hybrid is particularly popular among anglers because of its rapid growth and large average size: it averaged 451 mm in the 1982 fishery (compared with 416 mm for the native cutthroat trout) and 589 mm in the 1982 spawning run (versus 471 mm for the native: Rohrer 1983). The native cutthroat trout shows virtually no hybrid influence on its taxonomic characters, based on my own examination of specimens and on more extensive data supplied by Richard Wallace, University of Idaho. If the fast-growing hybrid were truly superior in terms of survival, persistence, and dominance, then the native cutthroat trout of Henry's Lake would have been hybridized, if not eliminated altogether, long ago. Its persistence demonstrates that the native trout is better adapted to Henry's Lake than the hybrid genotype, and that growth rate is not a deciding factor in its success. (The Idaho Department of Fish and Game now stocks sterile hybrids in Henry's Lake to reduce the hybridization threat to native fish: Rohrer 1983).

The empirical evidence is that bigger is not always better in relation to survival and success of a genotype. The growth process of wild trout in natural environments is complex. Although growth is ultimately under genetic control, innumerable environmental factors can be expected to overwhelm the expression of heredity. Growth of wild trout in diverse environments is not yet readily explained on the basis of quantifiable genetic determinants.

FOOD AND FEEDING

All trout are opportunistic feeders that consume a wide range of organisms from among those available in particular habitats. Alexander and Gowing (1976) and Bernard and Holmstrom (1978) detailed the great range of foods eaten by rainbow, brown, and brook trout in different environments, showing that trout typically prey on the organisms most available at any given time. It would be futile to seek some unique hereditary distinction by analyzing the diet of a particular trout in an environment where it is the only trout species. Only when two or more species or forms coexist and their fundamental niches are con-

tracted into realized niches do genetically based feeding tendencies become apparent (Trojnar and Behnke 1974). For example, when juvenile rainbow trout (steelhead) and juvenile coho salmon occur together, the trout feed mainly in riffle areas and the salmon in pools (Johnson and Ringler 1980). This habitat partitioning results in little dietary overlap or competition for food: steelhead feed predominantly on aquatic invertebrates and coho salmon feed predominantly on terrestrial invertebrates that have fallen into the water. Glova and Mason (1977) found this same relationship between juvenile coho salmon, which occupied pools, and coastal cutthroat trout.

Species Interactions

How two species subdivide a habitat depends a great deal on context. In Nicholas's (1978b) study of resident rainbow and resident coastal cutthroat trout coexisting in the upper Willamette River, Oregon, cutthroat trout predominated in riffles and rainbow trout in pools, and cutthroat trout exhibited the slower growth and shorter life span. Nilsson and Northcote (1981) characterized 17 allopatric and 10 sympatric populations of coastal rainbow trout and coastal cutthroat trout in lakes of British Columbia. In the absence of cutthroat trout, allopatric rainbow trout fed on invertebrates throughout the lake, from the substrate surface to the water surface. They grew more rapidly and attained greater maximum size than allopatric cutthroat trout, which fed mainly in the open waters but also preyed on fish (sculpins and sticklebacks). In the 10 lakes with sympatric populations, rainbow trout fed mainly in open water and at the surface, whereas cutthroat trout used more of the shore zone and larger cutthroat trout became highly piscivorous; further, cutthroat trout exhibited more rapid growth and larger maximum size than sympatric rainbow trout. In Crescent Lake, Washington, however, sympatric coastal rainbow and coastal cutthroat trout both fed predominantly on kokanee after attaining a size of about 36 cm. Although both species attained large maximum sizes, rainbow trout were larger (maximum, 9 kg, versus 5.5 kg for cutthroat trout: Pierce 1984a, 1984b).

Brown trout and native Apache trout coexist in Big Bonito Creek, Arizona. Apache trout are most active during the day and brown trout at dusk and after dark. In laboratory experiments with brine shrimp, Apache trout was the more active feeder in bright daylight but it ceased to feed in starlight, whereas the brown trout continued to feed in starlight. The brown trout was much more cover-oriented than the Apache trout. In two sections of the stream brown trout outnumbered Apache trout by 20:1 and 4:1 in electrofishing samples, yet 22 hours of daytime fly-fishing yielded 55 Apache trout and only 4 brown trout (Robinson and Tash 1979). This great differential vulnerability to angling between native western trout and brown trout is a factor that trout managers should recognize. The selective removal of native trout, even under light angling pressure, will act to favor brown trout.

Piscivory

Although western trout generally are omnivorous, they vary considerably in their degree of piscivory. In general, stream-dwelling trout prey less on other fish than lake dwellers. The least piscivorous native trout may be the westslope cutthroat trout. Normally a stream dweller, the westslope subspecies also occurs naturally in Pend Oreille, Priest, and Coeur d'Alene lakes, Idaho. Even in those lakes it did not become markedly piscivorous when kokanees were introduced and became an important forage resource—indeed, cutthroat trout markedly declined, probably because kokanees monopolized the zooplankton on which it fed.

In lakes where they have coexisted with an abundant fish fauna through thousands of years, trout have developed both their greatest degree of piscivory and their greatest sizes. The Lahontan cutthroat trout of Pyramid Lake and the Gerrard strain of Kamloops redband trout of Kootenay Lake are prime examples, but the principle of predator–prey coevolution extends to all salmonines such as lake trout in the Great Lakes and the brown trout subspecies native to the Caspian Sea basin (Berg 1948).

Temperature Effects

Most laboratory experiments indicate that trout reduce and finally cease feeding as water temperatures rise to between 22 and 25°C (Dickson and Kramer 1971). As temperatures approach 21°C, other species of fish may gain a competitive advantage over trout in using a common food supply. Reeves et al. (1987) raised juvenile steelhead and redside shiners separately and together in laboratory streams. When water temperatures were 12–15°C, production of young steelhead was the same with and without redside shiners, whereas shiner production markedly declined when steelhead were present. At 19–22°C, steelhead production declined by 54% when redside shiners were present, whereas shiner production was the same with or without steelhead. Obviously, temperature has important influences on the realized niche of trout.

Experimental studies indicate that most salmonid fishes have an optimum feeding temperature (at which growth and assimilation of food are best) of 13–16°C (Dwyer et al. 1981, 1983a, 1983b). An exception to this rule comes from unpublished data given to me by Pat Dwyer (U.S. Fish and Wildlife Service, Fish Cultural Development Center, Bozeman, Montana) on feeding and growth efficiency of redband trout from an Oregon desert basin (Three Mile Creek, Catlow Valley). Young redband trout that weighed less than 2 g at the start of trials gained less than 5 g each at 13 and 16°C during 140 days, versus almost 8 g for fish at 19°C; the growth curves for different temperatures greatly diverged during the last 30 days of the trials. Also of interest was the curve relating accumulated temperature units to growth (temperature units per centimeter of growth). With other forms of rainbow (and brook) trout tested at the Bozeman Center, this curve is U-shaped; more temperature units are required per centimeter of growth at both low (4 and 7°C) and high (19°C) temperatures than at more optimal temperatures of 10–16°C. For the form of redband trout tested, however, the curve was still declining at 19°C, indicating that optimum growth efficiency for this subspecies lies at some higher temperature (which was not

tested). As previously noted, I have caught desert redband trout by fly-fishing when water temperatures exceeded 28°C, an indication that the fish were actively feeding at these high temperatures. (The feeding responses of these redband trout at low temperatures were similar to those of other fishes tested at the Bozeman Center: feeding intensity declined rapidly at 4–6°C, and although feeding continued at lower temperatures, growth essentially ceased at 4°C.)

The concept of functional feeding temperatures—the temperature range over which fish continue to feed and gain weight—is useful in perceiving subtle hereditary differences among fishes. Both low and high ends of the temperature spectrum are of importance in this regard, but temperate-latitude fishes that normally encounter near-freezing winter temperatures are most likely to express functional differences at higher temperatures. Upper lethal temperatures for trout are very similar; when determined by the same laboratory method (different methods give different results), lethal temperatures for various taxa of trout usually cluster within 1°C of each other (e.g., Lee and Rinne 1980; Sonski 1982, 1984). Differences among trout in the range of functional feeding temperatures thus reflect degrees to which fish can continue to function as their upper lethal temperature is approached. One measure of functionality is the metabolic scope for activity (Fry 1947), the difference between maximum metabolic rate (usually represented as oxygen consumed during forced exercise) and resting metabolic rate at a given temperature. Scope for activity is an index of short-term energy reserves. A trout with a broader functional temperature range than another should have a greater scope for activity at high temperatures. Hochachka (1961) and Dickson and Kramer (1971), for example, showed that domesticated hatchery rainbow trout have less scope for activity at near-lethal temperatures than wild rainbow trout.

Trout do not necessarily have broad functional temperature ranges in circumstances where they might be expected to have them. Introduced rainbow trout have been established for many generations in the Firehole River, Yellowstone National Park. The Firehole River receives effluent from several thermal springs and may reach temperatures as high as 29.5°C during the low-flow summer period (Kaya 1978). It might be assumed that natural selection has created a race of thermally adapted rainbow trout in the Firehole River, but this seems not to have happened. Kaya (1978) confirmed in laboratory experiments that upper incipient lethal temperatures, the temperatures at which 50% of the experimental fish died within 1 week, did not differ between Firehole River rainbow trout and two hatchery strains of rainbow trout: they were about 26°C, influenced somewhat by acclimation temperatures. The tests indicated that these rainbow trout would survive less than 2 hours at 29.5°C and about 7 hours at 27.8°C. When temperatures were raised by 1°C per week, feeding ceased at 23–24°C, well below lethal temperatures. Although laboratory tests are not necessarily accurate guides to fish performance in the field, Kaya's experiments suggest that rainbow trout could not survive the highest temperatures in the Firehole River; rather, the fish probably seek out cooler refugia, which are available along the river. Whereas thousands of years of adapting to a desiccating environment have enabled Oregon desert redband trout to feed at high temperatures, 60–70 years (about 20 generations) seem to have been too few for rainbow trout to expand its functional temperature range in the Firehole River.

Feeding and growth are stimulated more by a fluctuating temperature than by a constant temperature. Spigarelli et al. (1982) compared the feeding and growth rates of three groups of adult brown trout in three different temperature regimes during a 57-day period. One group was reared with a daily regular cycle of 9–18°C (mean, 12.5°C), the second group was reared at a constant temperature of 13°C, and the third group was maintained in an arrhythmic temperature regime of daily fluctuations and a gradual increase of daily mean temperatures (range, 4–11°C; 57-day mean, 7.7°C). The trout were fed alewives to satiety twice a day. At the end of 57 days, the mean food consumption and weight gain per individual reared in the daily 9–18°C cycle were by far the best: 752 g and 163 g, respectively. Fish reared at a constant 13°C consumed 459 g and gained 104 g, on average, while fish in the arrhythmic temperature regime consumed 476 g and gained 94 g. In constant-temperature trials at the Bozeman Fish Cultural Development Center (Dwyer et al. 1981, 1983a, 1983b), trout raised at 7–8°C had only 20% as much growth as trout raised at 13°C after 140 days, but the brown trout tested by Spigarelli et al. grew about as well at fluctuating low temperatures as they did at a constant 13°C. Evidently, diurnally fluctuating temperatures promote more efficient conversion of temperature units to growth than do constant temperatures, presumably by stimulating greater food consumption. Konstantinov and Zdanovich (1986) also found more rapid growth with fluctuating temperatures than with constant temperatures for several species of fish.

Stream Foraging

Trout in streams typically feed more on drifting larvae of aquatic insects than on insects dwelling on substrates. Drift of aquatic insects is influenced by flow, temperature, season, and the species involved, but maximum drift density typically occurs at night with peaks around dusk and dawn (Bishop and Hynes 1969; Elliot 1970; Hynes 1970; Waters 1972). When interspecific and intraspecific competition is intense or benthic food availability is great, salmonids may pick invertebrates off substrates. Unless the prey organism is large, such as some species of stoneflies, however, drift feeding is more energy efficient. The papers just cited record that in small streams (5–10 m wide) with good riparian vegetation, 50% or more of the total diet of trout during the summer months of peak feeding may be invertebrates of terrestrial origin. This often-large terrestrial component of diets makes it difficult to directly relate instream invertebrate production to trout production. Nevertheless, several studies have concluded that trout production is too high to be explained by instream invertebrate production alone. This phenomenon is commonly known as the Allen paradox (Hynes 1970). Some of the discrepancy between trout production and instream invertebrate production probably involves terrestrial input into the trout diet. Many workers believe it is due more to limitations of sampling techniques, which often do not recover invertebrates occurring deep in the substrate (Allan 1983; Winters 1988). However, most fishery biologists have overlooked an invertebrate source of potentially great magnitude. This is the hyporheic fauna,

the assemblage of aquatic invertebrates that live and forage below ground in the water table of floodplains (Stanford and Gaufin 1974; Stanford and Ward 1988). This assemblage, which includes caddisflies, mayflies, and stoneflies, can extend more than a kilometer from a river channel (J. Ward, Colorado State University, personal communication). Recruitment from the hyporheic fauna could help explain the Allen paradox.

Despite the apparently high consumption of annual invertebrate production by stream salmonids, most studies agree that salmonids do not influence density, biomass, or species composition of aquatic insects; predation takes only surplus production, and the characteristics of stream invertebrate communities show no change when salmonids are removed from a stream section (Allan 1982; Culp 1986). On the other hand, when Wilzbach et al. (1986) modified a small stream in Oregon to enlarge the area used by feeding cutthroat trout, fish growth increased and invertebrate drift decreased, ostensibly because predation depressed invertebrate abundance. The authors concluded that in most natural streams, structural complexity prevents salmonids from feeding efficiently and taking more than surplus production. As discusssed earlier in this chapter, surplus invertebrate production often is adequate for the existing fish population; in western streams of high gradient, trout populations are more commonly limited by habitat. Where habitat is limiting, increased fish biomass should be expected from the addition of instream structures that increase the amount and quality of the habitat and make previously inaccessible food available. Conversely, a food-limited population would not be expected to benefit from artificial habitat improvements. For example, the growth and biomass of trout (mainly brown trout) decreased in a zone of the main Au Sable River, Michigan, when pollution abatement markedly reduced the influx of nutrients and, consequently, the production of invertebrate prey. Intensive additions of instream habitat devices failed to reverse the decline of this trout population (Alexander et al. 1979), which appears to be food-limited.

Substrate diversity influences invertebrate abundance, as pointed out earlier, but an increase in invertebrate production can generally come about only from an increase in primary production, which is governed by light and nutrients. If a small headwater stream is overgrown with vegetation, canopy removal allows more sunlight to reach the water, which increases primary and secondary production (Murphy and Hall 1981; Murphy et al. 1981). Artificial enrichment also may stimulate production, as suggested by the Au Sable example just above. Black Earth Creek, Wisconsin, a stream organically enriched by sewage effluent, had a reported annual trout production of about 400 kg/hectare, which was three to four times greater than unenriched trout streams of the area (Brynildson and Mason 1975; Alexander and Ryckman 1976).

Warren et al. (1964) dripped a sugar solution (sucrose, a normal product of primary production) into test sections of Berry Creek, a very small Oregon stream. The sucrose stimulated massive production of bacteria, which were consumed by aquatic insects. The end result was more than a sevenfold increase in the production of cutthroat trout, although trout food consumption only doubled. The likely explanation of this seeming anomaly is that the trout in tiny Berry Creek had been obtaining barely more than maintenance rations before

the experiment. Suppose a fish required 5 g of food daily just to replace the energy lost to normal metabolism, but it was able to obtain only 6 g, leaving but 1 g for growth. Then a doubling of daily consumption to 12 g would provide 7 g above maintenance requirements for net production. The maintenance energy needs of fish should be kept in mind whenever food enhancement programs are designed and evaluated.

The addition of nitrate and phosphate to nutrient-limited lakes may enhance salmonid production. Fertilization of Great Central Lake, Vancouver Island, with these nutrients during 1970–1973 increased production of phytoplankton and zooplankton severalfold; the survival of juvenile sockeye salmon rose 2.6 times and the number of returning adults rose more than 7 times (Le Brasseur et al. 1978). Fertilization undoubtedly benefited sockeye salmon in Great Central Lake, but the links in the species' food web and the great increase in returning adults are not well understood.

Optimal foraging theory holds that feeding organisms attempt to maximize energy intake while minimizing energy expenditure. According to this theory, trout presented with different-size foods of equal edibility, nutritional value, and ease of capture will select the largest organisms they can handle and swallow easily. Experienced anglers know, however, that feeding trout often ignore larger flies presented to them but strike at rather precise imitations of a tiny insect. Ringler's (1979) laboratory studies suggest an explanation for this contradiction of optimal foraging theory. Ringler conducted feeding trials with prey organisms ranging in size from tiny (brine shrimp) to medium (small crickets and mealworms) to large (large crickets and mealworms). Wild brown trout fed brine shrimp on the first day continued to select, or prefer, brine shrimp on the second day when medium and large food items were introduced. True size selection of prey, as predicted by optimal foraging theory, was not fully manifested until the fourth and fifth days after the medium and large food items were introduced.

In natural streams, one insect species typically predominates in the drift at a time. Trout apparently fix on this species to the near exclusion of all other particles in the drift and on the surface; only after extended exposure to new images of larger organisms is the trout's fixation on the original feeding stimulus weakened. If this explanation is true, then the degree of selective feeding by trout will be inversely related to the diversity in size, shape, and color of organisms in the drift. Individual trout vary considerably in their ability to learn to feed on a new, energetically more favorable food item (Ringler 1985), and trout do select the largest individuals of a species in the drift when preying on a single species (Winters 1988). Thus trout seem to follow the spirit of optimal foraging, if not the letter.

In most streams, the overwhelming majority of aquatic insects—whether expressed in terms of diversity, biomass, or production—are small. When tiny organisms are the only important food supply for trout of all sizes in a stream, the older, larger fish are energetically disadvantaged; a food supply that is adequate for maintenance and growth of a yearling trout of 100 g may not be adequate for an age-3 trout of 300 g. Under such conditions, larger trout cannot meet their maintenance requirements (which are inflated because the fish must

spend more time foraging for small items); they begin negative growth (lose weight) and suffer a high mortality rate, leaving a population with a truncated size and age distribution. Studies of feeding, growth, and population dynamics cited in this chapter make it clear that trout restricted to small food items form populations characterized by small maximum individual sizes and young maximum ages that very few fish exceed. Only when trout have adequate access to larger prey, such as fish and crawfish, can they avoid feeding competition with smaller trout and sustain positive growth (Behnke 1989c).

MOVEMENTS AND MIGRATIONS

I define migration as an extended, directional movement that is an integral part of the life cycle, such as a spawning migration from the ocean or a lake up a river or the migration of young downstream to the ocean or lake. I use the term movement to denote motion of a less predictable nature over small distances, such as the movements of trout to riffle areas for feeding. I recognize the problems involved in using simple definitions to characterize fish behavior in nature, because some behavior is difficult to categorize. In large Pacific coast rivers, for example, salmon deposit great numbers of eggs in limited areas during a brief time each year. Many of these eggs become food for other fish species. Not only may rainbow trout resident near a spawning tributary make short movements to capitalize on this annual food bonanza, but rainbow trout populations from a distant downstream lake or river section may make annual excursions to follow salmon to the spawning grounds. I am not aware of published studies of such extended excursions, which might qualify as migrations, but I have observed them in the Brooks Lake–Naknek Lake system of Alaska, and I have heard many first-hand accounts of large rainbow trout moving with salmon spawning runs in the Iliamna Lake system. All of these lakes are noted for the large size of their rainbow trout, whose populations have coevolved with abundant salmon runs (primarily sockeye salmon). Presently, I can only speculate that a behavioral pattern has evolved to make best use of resources provided by salmon—a supply of eggs in rivers during the summer and fall and a year-round supply of juvenile salmon in lakes.

Spawning Migrations

Genetically based differences in anadromous spawning migrations allow distinctive populations of a species to coexist. Some reproductive isolation is accomplished by different timing of spawning runs. The homing instinct that returns fish to their natal streams also isolates spawning groups within the same drainage basin. These evolutionary strategies promote a diversity of discrete stocks whose collective specializations exploit a river system's resources in time and space more thoroughly than a single stock could do (Leider et al. 1984). The result is increased abundance of the species through more effective use of the total environment. When a dam blocks a network of major spawning tributaries, a significant part of an andromous species' genetic diversity is lost. The original

diversity of numerous spawning stocks cannot be maintained by hatchery propagation below the dam.

Steelhead may migrate thousands of kilometers at sea between the time they enter the ocean as smolts and the time they return to their natal river as spawners. Sea-run cutthroat trout are not known to move into the open ocean; instead, their annual 2–3-month sojourn in salt water is mainly confined to bays, estuaries, and shallow inshore areas. In Washington, discovery of genetic differences between coastal cutthroat trout populations separated by areas of deep ocean water indicates that deep open seas act as a barrier to gene flow (Utter et al. 1980).

The longest known spawning migrations of native western trout were made by steelhead that spawned in the upper Columbia River, British Columbia, and in the upper Snake River near Twin Falls, Idaho. The upper Columbia run was blocked by Grand Coulee Dam in 1939 and the upper Snake River run by Hells Canyon Dam in 1964 (Fulton 1970). These runs extended upriver almost 1,600 km from the ocean. Sea-run coastal cutthroat trout do not make long spawning migrations, rarely going more than about 100 km from the ocean. Some spawning runs of westslope cutthroat trout from Flathead Lake, Montana (Roscoe 1974), and of nonnative rainbow trout of Lake McConaughy, Nebraska (Van Velson 1977), cover 150 km or more.

Movements by Resident Trout

A fascinating phenomenon is the genetic control of movements made by young fish spawned in inlets and outlets of lakes. Working with cutthroat trout in Yellowstone Lake, Raleigh and Chapman (1971) demonstrated a genetic basis for upstream movement of young produced by outlet spawners and for downstream movement of young produced by inlet spawners. Northcote (1962) presented evidence that the directional movement of young rainbow trout hatched in the inlet and in the outlet of Loon Lake, British Columbia, was mainly under environmental control, but he later modified this conclusion (in Kelso et al. 1981) when hereditary upstream and downstream movements were documented for rainbow trout newly emerged from inlets and outlets of two lakes. The trout in Emerald Lake, Colorado, discussed previously, may be at an incipient stage of evolution into inlet and outlet runs (the population has been established for less than 100 years); however, according to sampling data (Lentsch 1985), a large proportion of the newly emerged fish in the outlet area move downstream over a falls and are lost to the population. Evidently, about 25 generations have not been sufficient for natural selection to fix the appropriate upstream movement in progeny of the outlet spawners.

Resident stream trout may undertake considerable movement (or migration) in some circumstances. In small tributary streams exposed to severe winter conditions, trout commonly migrate downstream to overwinter in larger, deeper areas. Westslope cutthroat trout native to Idaho's Salmon River drainage may make overwintering migrations of more than 160 km (Bjornn and Mallet 1964; Bjornn 1971). If movement or migration had survival advantages during the

evolution of native trout in a particular drainage, the trout will have such movement or migration programmed into their life history.

Large brown trout in the South Branch Au Sable River, Michigan, make extensive movements, as documented by Clapp et al. (1990) with radio-tagged fish. In this river, trout longer than 450 mm are uncommon, probably because food of appropriate size is rare, forcing these fish to search substantial areas of the river to find it.

For stream populations of trout lacking a strong hereditary basis for directed movement—which includes most nonanadromous, resident stream populations—the concepts of movement most generally accepted today are similar to those expressed by Allen (1969). During their first year of life, trout are thought to disperse from areas of high density to areas of low density. Because suitable spawning areas are uncommon and nonrandomly distributed in most streams, this dispersion is a logical strategy to distribute the population more uniformly among available habitats, thereby exploiting the carrying capacity of the whole stream.

Once juveniles begin to establish territories and home ranges in their second year of life, their movements are thought to be much reduced. Adults are considered to be rather sedentary, making only short feeding excursions within their home ranges. Extended movements such as those made by large brown trout in the Au Sable River (Clapp et al. 1990) are thought to be unusual exceptions to the general rule.

Recent studies of brook trout in four small Colorado streams (Riley 1992) and of brown trout in a Pennsylvania stream (Beard and Carline 1991; Carline et al. 1991) suggest that "further research" is necessary before more definitive conclusions can be drawn about trout movement in streams. In the Colorado study, adult brook trout moved much more than would be predicted from our contemporary concepts. In the Pennsylvania study, brown trout moved much less than expected. Beard and Carline (1991) concluded that the significantly higher densities of all age-groups in Pennsylvania stream sections with the best spawning habitat reflected lack of movement from areas of high trout density to areas of low density.

A basic explanation for these deviations from expected movement patterns might be that that the option to move or not move at any life stage is determined by the potential survival advantage of one option over the other. In the high-elevation, high-gradient streams of Colorado, where productivity is low and environmental regimes are harsh, brook trout populations are likely to encounter periods of severe food shortage. If they do not move, they are more likely to die of starvation than they are if they search for greater opportunities. In the Pennsylvania stream, young brown trout may not have reached some critical density at which the probability of death from local competition exceeds the risks of extended movement.

Obviously, no general rules of movement apply to all resident trout populations in all streams. The factors influencing movement or lack thereof are likely to be site specific.

Stream sections a few kilometers long sometimes are placed under special angling regulations to reduce fishing mortality. Significant differences in size, age, and abundance of trout between protected and contiguous unprotected sections have been documented (Behnke and Zarn 1976; Graff and Hollender 1980; Nehring 1980). Such differences could not arise if most fish moved randomly between stream sections or if fish of all size-classes actively dispersed from high- to low-density areas.

Much is yet to be learned about movement in resident stream populations, but the generality can be made that a high proportion of adult trout in most streams fit the traditional concept of home range residency and limited upstream or downstream movement. This principle allows different management options, such as protective regulations, to be applied to different sections of the same stream.

Trout mobility may be limited in lakes. In the 1960s and early 1970s, Yellowstone Lake angling regulations consisted of a 356-mm size limit and a three-fish bag limit. The native cutthroat trout was heavily exploited. In September 1971, when I participated in sampling the lake, very few trout longer than 356 mm were found in the lake's heavily fished northern end. Our samples from the south end, which received light use, contained numerous trout 356–460 mm long. It was apparent that cutthroat trout were not uniformly dispersed throughout Yellowstone Lake and that movement of certain populations was circumscribed within definite areas of the lake.

INFLUENCES OF HATCHERY FISH

Introductions of hatchery fish have been reported to have varied effects on wild trout in streams. Miller (1954) found that hatchery cutthroat trout experienced high and relatively rapid mortality when stocked into Gorge Creek, Alberta. In this high-gradient stream, native cutthroat trout occupied all of the suitable microhabitats, and the hatchery trout had to move continually in search of resting sites. The stocked fish suffered high mortality within a few days from exhaustion associated with acidosis.

Vincent (1987) presented evidence that stocking catchable-size hatchery rainbow trout depressed the abundance of wild brown and rainbow trout in the Madison River, Montana. After stocking ceased, the abundance and biomass of wild trout increased almost threefold in one section, and the relative degrees of recovery indicated that hatchery rainbow trout had had a greater negative effect on wild rainbow trout than on wild brown trout. On the other hand, when Marshall (1973) examined the effect of hatchery trout on wild trout in the Poudre River, Colorado, he found no differences in size and abundance of wild brown and rainbow trout in stocked and unstocked sections, and no significant movement of wild or hatchery fish between sections.

The apparent contradictions in the studies cited above can be resolved in light of different environments, different stocking densities, and different rates of removal of the hatchery trout by anglers, which in turn influenced the movement of stocked and wild trout. The Madison River is a large river typical of a run habitat (generally intermediate between riffle and pool habitat in depth and velocity). Hatchery trout were stocked at high density; in some sections there may have been an instantaneous doubling of the biomass. Removal of

hatchery fish by anglers was low (about 20%). The large, deepwater environment of the Madison River did not demand excessive movement of the hatchery trout to find resting habitat and they could survive for some time. The unnatural density created by the hatchery trout probably stressed the wild trout, who defended their territories until eventually abandoning them and moving on, as observed by Bachman (1984) for brown trout in a Pennsylvania stream. In the Poudre River, each stocking of hatchery trout equaled about 10% of the biomass of the wild trout in the stocked section. Up to 90% of the hatchery trout were harvested by anglers, most of them within a few days of stocking.

A general conclusion is that if a wild-trout stream "must" be stocked with catchable trout and the artificial density created by stocking is neither high nor long-lasting, little effect on wild trout should be expected. But if stocking elevates total trout density by some substantial amount for some substantial time, wild trout are likely to be displaced. How far these "stressed" fish might move and what their fates might be are unknown.

PART II

Cutthroat Trout

EX5004-000037-TRB

4

CUTTHROAT TROUT
Oncorhynchus clarki

The common name cutthroat trout is generally used for all forms of *Oncorhynchus clarki*. Evidently, the name was popularized by Charles Hallock, editor of *Forest and Stream*, the leading sporting journal of the late 19th century. The first published reference to cutthroat trout that I am aware of is in a paragraph by Hallock in the October 4, 1884, issue of the *American Angler* (volume 6, number 14). Hallock used the name to describe the trout he caught in Rosebud Creek, a tributary to the Yellowstone River south of Columbus, Montana. David Starr Jordan, America's most eminent ichthyologist, railed against the use of the pejorative word cutthroat for the trout he greatly admired. He believed the cutthroat trout was a much finer and more beautiful fish than the rainbow trout and stated that it should be the predominant trout of fish culture (Jordan 1891). Goode (1888) wrote: "Hallock and other recent writers have applied to it the horrible name Cut Throat Trout, which it is hoped will never be sanctioned in the literature." (Goode also objected to the "ridiculous" name Dolly Varden trout, also to no avail.)

The cutthroat trout has the greatest North American distribution of all western trout species. A single coastal subspecies occurs from southern Alaska to northern California, and many subspecies are found in the interior.

Behnke (1988c) divided *O. clarki* into four major subspecies and 10 minor subspecies, based on the magnitude of phylogenetic divergence. The recognition of subspecies facilitates management by dividing a highly variable, widely distributed species into many smaller units associated with particular drainage basins or geographical areas. Although some of the subspecies, such as *stomias* (greenback) and *pleuriticus* (Colorado River), might logically be combined, I have not done so because of their historical value and their use in modern management and restoration programs. These programs are urgent because most recognizable groups of cutthroat trout have undergone marked declines during the past 100 years.

REASONS FOR DECLINE

Except for the westslope cutthroat trout, native to the Salmon and Clearwater drainages in Idaho and to the John Day River drainage in Oregon, interior

EX5004-000038-TRB

cutthroat trout evolved apart from rainbow and redband trout, and they lack innate isolating mechanisms that would allow them to coexist with those forms and with nonnative trout species. When rainbow trout have been introduced into the interior waters where cutthroat trout is the only native trout (which includes virtually the entire distribution of interior cutthroat trout), mass hybridization has almost invariably followed. Brown trout have commonly replaced interior cutthroat trout in the larger rivers, and the eastern brook trout is now the most common small-stream trout in the West. Of the 13 subspecies that I tentatively recognize for interior (noncoastal) cutthroat trout, 2 are believed extinct as pure populations (yellowfin cutthroat trout of Twin Lakes, Colorado, and Alvord basin cutthroat trout), 10 have suffered catastrophic declines, and 2 are holding their own, neither replaced by nor hybridized with nonnative species throughout most of their known ranges. Both of the persisting subspecies are undescribed. One is the finespotted cutthroat trout native to the upper Snake River, Wyoming, where it remains the dominant trout in the drainage from Jackson Lake to Palisades Reservoir. The other is the Whitehorse cutthroat trout of Willow and Whitehorse creeks, two small streams that drain onto a high desert just east of the Alvord sump in Oregon. No other fish live in these streams, but the modern range of the Whitehorse subspecies is small and severely degraded.

The dramatic decline of interior cutthroat trout across their entire range can be appreciated by reading 19th-century accounts of their great abundance. If one were to revisit the sites of most of these accounts (Bear River, Utah Lake, upper Colorado River, Green River, Rio Grande, Lake Tahoe, Truckee River), only nonnative trout would be found. The greatest abundance of pure interior cutthroat trout occurs in Yellowstone Lake and the Yellowstone River drainage above the falls in Yellowstone National Park.

It is astounding how rapidly native cutthroat trout can vanish after nonnative trout become established. I observed the virtual replacement of cutthroat trout by brook trout within 5 years in Black Hollow Creek, a small tributary to the Poudre River near Fort Collins, Colorado. In 1967, Black Hollow Creek was treated with rotenone to remove brook trout after a barrier dam was constructed, and in 1968 it was stocked with greenback cutthroat trout, the native subspecies. The population increased and flourished. In 1972, however, two brook trout were found above the barrier. The numbers of brook trout increased yearly thereafter and the cutthroat population declined. When we electrofished Black Hollow Creek in the fall of 1977, we found a dense population of brook trout, but not a single cutthroat trout. A few greenback cutthroat trout, possibly from an upstream refuge, appeared in Black Hollow Creek samples in 1978.

Cutthroat trout still enjoy a selective advantage over nonnative trout in many high-altitude headwaters, evidently because they function better in colder waters. Although most of these populations that I have examined have been exposed to hybridization and are not pure native trout, they do maintain the appearance of native trout and should be recognized and managed as such. In these situations the remnant native populations may be extremely vulnerable to replacement after environmental disturbance.

In 1972, I made a collecting trip in Montana with George Holton (Montana Fish and Game Department) in search of westslope cutthroat trout populations. These cutthroat trout had been found in the headwaters of a small stream tributary to the Smith River during a 1968 survey, when brook trout occurred farther downstream. The watershed was clear-cut in the intervening years and all vegetation was removed from the streambanks. Consequently, erosion, sediment load, and water temperatures greatly increased. In 1972, when we electrofished the stream to its source, we found only brook trout. A neighboring watershed was also clear-cut except for a small segment of the uppermost headwaters; there, we found only native cutthroat trout in the pristine section and predominantly brook trout where the stream flowed through the spoils of the clear-cut.

PROPAGATION OF CUTTHROAT TROUT

A definitive history of trout culture in America has yet to be written. Regular publications on the subject began after the establishment of the American Fish Culturist's Association (precursor of the American Fisheries Society) in 1870 and the U.S. Fish Commission in 1871. However, as pointed out to me by W. J. Wiltzius, historian of fish culture in Colorado (Wiltzius 1985), information about mid-19th-century aquaculture can be found in commercially published books and newspapers of the era--including accounts of unsuccessful efforts to propagate brown trout and other European salmonids in New York some 20 years before the "official" 1883 date for the introduction of brown trout to North America.

The earliest propagation of cutthroat trout is unknown but probably occurred in California or Utah. Livingston Stone was dispatched to California in 1872 by the newly created U.S. Fish Commission to find a source of salmon eggs for propagation and distribution. Stone's western experiences were recorded in the first (1874) report issued by the U.S. Fish Commission. He was impressed by Salt Lake City's municipal hatchery, which propagated the native Bonneville cutthroat trout. Stone did not mention how long the Salt Lake City hatchery had been in operation before 1872. In California, the Lahontan cutthroat trout was being propagated in a private hatchery by 1867 or 1868. The first report of the California State Fish Commission, for 1870–1871, mentioned that the Comer brothers had operated a hatchery for the previous 3 years on the Truckee River, where they hatched more than 3 million eggs (Leitritz 1970). The Comers may have been taking eggs from Pyramid Lake cutthroat trout during spawning runs in the Truckee River.

The first cutthroat trout propagated in a federal hatchery were the greenback and yellowfin subspecies, which were obtained from sympatric populations in Twin Lakes, Colorado, in 1891 and cultured at the Leadville National Fish Hatchery. Annual reports of the U.S. Fish Commission of the late 19th and early 20th centuries indicated that all the presently recognized subspecies of cutthroat trout (with the possible exception of the yellowfin) were treated as a single entity--the black-spotted trout. Almost from the beginning of cutthroat trout propagation at the Leadville Hatchery, two Colorado subspecies, the

greenback subspecies of the eastwardly draining Arkansas River system (Twin Lakes) and the Colorado River cutthroat trout from the western side of the Continental Divide, were mixed together as black-spotted trout to be stocked out and shipped to other states.

The Bozeman (Montana) National Fish Hatchery was constructed in 1898 and began to propagate two additional subspecies of cutthroat trout: Yellowstone from Henry's Lake, Idaho, and westslope from the Madison River, Montana. As at Leadville, subspecies were mixed together for propagation and distribution as black-spotted trout.

In 1902, personnel of the Spearfish (South Dakota) National Fish Hatchery discovered that vast numbers of cutthroat trout eggs could be taken at Yellowstone Lake as spawning trout ascended a few small tributary streams, where they were readily trapped. From about 1905 to 1955, the Yellowstone Lake cutthroat trout was the dominant subspecies propagated. A record 43,500,000 eggs were taken in 1940 and distributed to state and federal agencies and to private individuals and organizations in all the western states. Because of such large-scale propagation and widespread distribution, the common name Yellowstone cutthroat became widely established for virtually all interior cutthroat trout.

All the western states with native cutthroat trout established their own propagation programs, which usually relied on eggs from wild populations in lakes or reservoirs. Most of these brood-stock lakes had been stocked with Yellowstone cutthroat trout and rainbow trout so that hybrids, scarcely resembling the native trout, were widely stocked as "native" trout throughout the West. Most of the interior subspecies of cutthroat trout were propagated in state, federal, or private hatcheries at one time or another. Moreover, exchanges among all these hatcheries thoroughly mixed races from different geographical areas.

In the late 19th century, after fish culturists learned how relatively simple it was to obtain and hatch millions of trout eggs, fisheries in the United States entered an era typified by what might be called the Johnny Appleseed mentality. All that needed to be done was to "seed" baby trout and salmon in waters all over the country with the Biblical admonition to be fruitful and multiply. Environmental limitations governing a species' distribution and abundance were not given much thought. Reports of the U.S. Fish Commission during this period document that chinook salmon were stocked in Great Salt Lake and in the Mississippi River. Miners in Nevada pleaded to have common carp sent to them because the native Lahontan cutthroat trout sold for the outrageous price of up to 40 cents a pound. (The miners promised they would do their best to control the trout population and make the waters safe for carp.)

Would-be stockers had only to write to their congressman or to the U.S. Fish Commissioner and free fish would be delivered. The U.S. Fish Commission and some states had their own railroad cars to transport and deliver fish. The recipient merely took a bucket to the station and met the train. During this period, which lasted until World War II, individuals and clubs obviously made innumerable unrecorded introductions of varieties of cutthroat (mainly from

Yellowstone Lake), rainbow, brook, and brown trout supplied by the U.S. Fish Commission and state agencies.

The U.S. Forest Service and National Park Service also ran their own fish propagation and distribution programs in some areas. The "seeding" of headwater streams with eyed eggs or fry became a standard part of fisheries management programs in western states, and this practice continued in some areas into the 1970s. The string of packhorses and mules transporting their cargo through remote mountain areas became a romantic image of fisheries management. The loss of the Paiute cutthroat trout from its type locality, Silver King Creek above Llewellyn Falls in the Lahontan basin of California, was due to an inadvertent stocking of rainbow trout fingerlings during a headwater seeding operation in 1949.

In many areas of the West, such large-scale and indiscriminant introductions have made finding pure native trout populations extremely difficult today. So much unrecorded stocking took place that hardly a stream or lake in the country is known with certainty to be untouched by it. A few of my own experiences illustrate the consideration that must be given to the influence of past stocking in regard to native trout.

During my master's thesis research on the Lahontan cutthroat trout, I noted that the three type specimens of *Salmo evermanni* in the Stanford University collection were, in fact, Lahontan cutthroat trout. *Salmo evermanni* was named for a trout found in 1907 in the headwaters of the Santa Ana River, California, above a barrier falls. Old stocking records, found in the biennial reports of the California Fish Commission, revealed that 6,000 Lahontan cutthroat trout, from eggs taken at Lake Tahoe, were stocked into the Santa Ana River in 1895, and 17,500 were stocked in 1896; the records note that 15,000 of these were stocked "above the falls." Thus, *Salmo evermanni* is not a valid species but a synonym of *Oncorhynchus clarki henshawi* (Benson and Behnke 1961).

In 1958, there was much excitement over the discovery of greenback cutthroat trout in the headwaters of the Big Thompson River in Rocky Mountain National Park. The greenback subspecies was thought to be extinct at the time. Although no one knew how to recognize a greenback trout, the newly found fish was undoubtedly a cutthroat trout. The Big Thompson River was part of the subspecies' historical range (South Platte basin), it was isolated, and no stocking records were known for it. This circumstantial evidence resulted in a news release by the U.S. Fish and Wildlife Service announcing the discovery of a subspecies of trout long believed extinct. The bubble of excitement burst when handwritten notes found in Park Service files disclosed that the Estes Park Sportsmen's Association had stocked 140,000 "spotted native" trout in 1922 and 130,000 trout in 1923 in the Big Thompson headwaters. The trout had been given to the Sportsmen's Association by the Estes Park State Fish Hatchery and were of unknown origin.

When I examined specimens from the present population in the headwaters of the Big Thompson River, however, I was surprised to find that the trout were not Yellowstone cutthroat trout, as stocked fish were expected to be, but were relatively "good" greenback trout only slightly hybridized. I concluded that these isolated waters already had an abundant native trout population when the

hatchery fry were stocked, and virtually none of the nonnative fry had survived. So, if trout already existed in the river, why was it stocked? Richard Delong, one of my graduate students, once interviewed an elderly resident of Estes Park who participated in the stockings of 1922 and 1923. The veteran stocker recalled that traveling from Estes Park to the headwaters of the Big Thompson River required two days and two crossings of the Continental Divide by pack train. No one knew if trout were native to the stream because the area was so remote that none of the sportsmen had ever fished it. This stocking was motivated by the Johnny Appleseed desire to seed all headwater areas with fry and trust they would grow, multiply, and increase trout abundance throughout the watershed.

In 1967, Wyoming Game and Fish Department personnel found only cutthroat trout in a series of lakes in the Green River drainage near Pinedale. A falls on the drainage protects the watershed from invasion by introduced trout. Wyoming records revealed no stocking of these lakes, and it was assumed that a stronghold of the rare, native Colorado River cutthroat trout had been discovered. In 1969, I examined specimens collected from these lakes and, from their appearance and taxonomic characters, recognized that they were introduced Yellowstone Lake cutthroat trout. Subsequently, notes discovered in the local office of the U.S. Forest Service revealed that these originally fishless lakes had been stocked with Yellowstone cutthroat trout by the Civilian Conservation Corps in 1937.

Introductions occasionally have preserved a unique race of trout now extinct in its original environment. Hickman and Behnke (1979), for example, described the discovery of the original Pyramid Lake race of the Lahontan cutthroat trout outside its native range. During the summer of 1977, Hickman found a population of unusual trout in a small stream on Pilot Peak on the Utah–Nevada border. I positively identified them as Lahontan cutthroat trout (Hickman and Behnke 1979). Undoubtedly they were introduced, because Pilot Peak is in the Bonneville basin. We determined that Lahontan cutthroat trout had been in this small stream since before 1930; thus they were introduced during a period when the only Lahontan cutthroat trout used in propagation came from Pyramid Lake. This discovery has special significance to fish culturists because the Pyramid Lake race of Lahontan cutthroat trout was probably the largest of all trout native to western North America. It is a genetic resource of great potential.

In recent years interest in endangered species and preservation of rare native fauna has stimulated attempts to propagate pure, native subspecies of cutthroat trout. The interior cutthroat trout most commonly raised (mainly in federal and Wyoming state hatcheries) is the finespotted cutthroat trout native to the upper Snake River, Wyoming. Most cutthroat trout propagation relies on eggs taken from wild fish, but the Wyoming Game and Fish Department has developed a semidomesticated race of finespotted cutthroat trout at its Auburn Hatchery, where a brood stock maintained for more than 30 years has been selected for early spawning. A concern for this and other hatchery brood stocks developed from wild stocks is loss of genetic variability. Allendorf and Phelps (1980), for example, found that a Montana stock of westslope cutthroat trout

suffered a 57% reduction in the proportion of polymorphic gene loci (loci with more than one allele) after only 14 years of hatchery cultivation.

The coastal cutthroat trout has fared better than the interior subspecies in maintaining its integrity under hatchery conditions. Virtually all propagation of coastal cutthroat trout occurs in Washington and Oregon, where the coastal and interior subspecies have historically been separated in propagation to some degree. In areas where coastal cutthroat trout are known to hybridize with rainbow trout, however, the stocking of hatchery trout may be a significant factor in the breakdown of reproductive isolation between rainbow and coastal cutthroat trout. Crescent Lake, on Washington's Olympic Peninsula, was once famed for its fishery of large native rainbow and cutthroat trout. In the 1950s, after great numbers of hatchery rainbow trout and Yellowstone cutthroat trout had been introduced over many years, hybrid specimens became dominant in the lake's only spawning tributary of Crescent Lake. The implications of this are discussed later.

In contrast to the rainbow trout, the cutthroat trout has rarely become naturalized much beyond its original distribution. Nilsson (1971) wrote that "a couple" of stocks of cutthroat trout were established in Sweden, and Scott and Crossman (1973) noted successful introductions of the species in Laurentian lakes of Quebec. Also, within their native range, cutthroat trout were excluded from many headwater lakes at high elevations by falls; many such lakes now are regularly stocked with cutthroat trout by fisheries agencies. The modern association of cutthroat trout with originally fishless mountain lakes and their rarity in their original range have given rise to an erroneous belief held by many anglers that the natural distribution of interior forms of cutthroat trout was restricted to remote, high-elevations lakes.

EX5004-000041-TRB

5

CUTTHROAT TROUT OF COASTAL BASINS

Coastal Cutthroat Trout *Oncorhynchus clarki clarki*

TYPICAL CHARACTERS

Coloration silvery to brassy with yellowish tints. Outline of spots irregular (not rounded). Scales in the lateral series typically 140–180, but 120–140 for some coarse-scaled resident stocks; 30–40 scale rows above the lateral line. Gill rakers 15–21, typically 17–18; short and blunt. Pyloric caeca 25–55, mean values about 40. Vertebrae 59–64, typically 61–62.

DESCRIPTION (Plate 1; Figure 3)

The coastal cutthroat trout differs from all other trout by its profusion of small to medium-size spots of irregular shape (not round, as on most interior cutthroat trout subspecies), which are distributed more or less evenly over the sides of the body, onto the head, and often onto the ventral surface and anal fin. Of all interior subspecies, only the Lahontan cutthroat trout has spots distributed like those of the coastal subspecies, but the spots of Lahontan cutthroat trout are larger, rounder, and fewer. The spots on coastal cutthroat trout are densely packed. Qadri (1959) demonstrated that specimens of coastal and westslope cutthroat trout can be reliably separated by quantifying the differences in their spots. Snyder (1940) counted 26–71 spots on the head and 322–577 on the body of coastal cutthroat trout.

The coastal form does not develop the brilliant colors of some interior subspecies. Sea-run individuals are silvery, and the silvery skin deposits often obliterate or mask body spots. Resident freshwater fish tend to be darker with a coppery or brassy sheen. Pale yellowish colors may appear on the body, and the lower fins may be yellow to orange-red. A rose tint is sometimes apparent on the sides and ventral region of sexually mature fish, especially in lake-dwelling stocks.

Its distinctive spotting pattern is the only morphological character that

EX5004-000042-TRB

5

CUTTHROAT TROUT OF COASTAL BASINS

Coastal Cutthroat Trout *Oncorhynchus clarki clarki*

TYPICAL CHARACTERS

Coloration silvery to brassy with yellowish tints. Outline of spots irregular (not rounded). Scales in the lateral series typically 140–180, but 120–140 for some coarse-scaled resident stocks; 30–40 scale rows above the lateral line. Gill rakers 15–21, typically 17–18; short and blunt. Pyloric caeca 25–55, mean values about 40. Vertebrae 59–64, typically 61–62.

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EX5004-000043-TRB

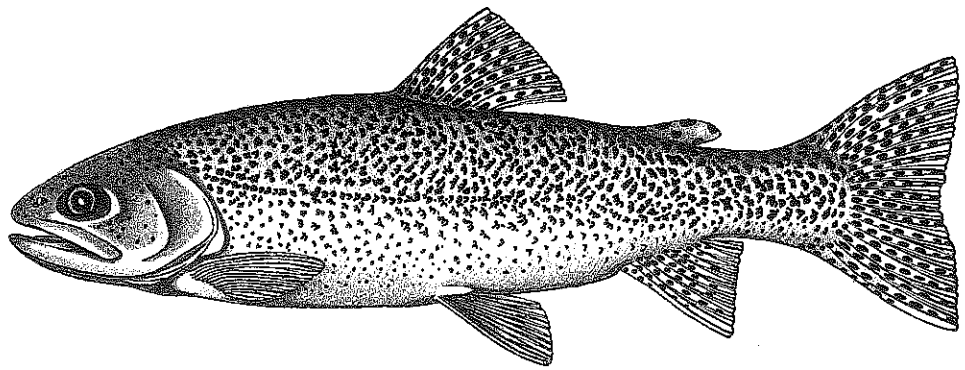

FIGURE 3.—Coastal cutthroat trout.

obviously separates coastal cutthroat from the interior subspecies. Other trends in differentiation, however, can be used to separate most coastal from most interior cutthroat trout and also from rainbow and redband trout.

The gill rakers of coastal cutthroat trout typify those of predaceous species. They are slightly fewer (usually 17–18 versus 18–20, but with much overlap) than the gill rakers of nearly all other cutthroat and rainbow–redband trout, and they are short and blunt rather than long and attenuated. Juveniles of coastal cutthroat and coastal rainbow trout can be separated by their parr marks—those of cutthroat trout are typically more narrow or oblong than the rounded parr marks of typical coastal rainbow trout (McConnell and Snyder 1972).

My taxonomic data are based on examination of 277 coastal cutthroat specimens from 22 localities scattered throughout the range of the subspecies, from northern California to southern Alaska, supplemented by recent collections from Vancouver Island and the works of Schultz (1936), Snyder (1940), DeWitt (1954), Hartman (1956), and Qadri (1959). I have compared samples from sea-run populations, populations isolated in small streams above barrier falls, and lake-dwelling populations to assess the variability found within a subspecies of such broad geographical distribution and diverse ecological form.

I have found that coastal populations with direct access to the sea (typical sea-run cutthroat trout) are morphologically similar throughout their entire range, showing no evidence of clinal variation in characters between northern and southern populations. Among isolated resident populations, considerable divergence is apparent in such characters as the numbers of scales and basibranchial teeth. The morphological divergence of these isolated populations,

like that of interior populations isolated from each other for several thousand years, has resulted in much variation within the subspecies.

The scale count in the lateral series ranges from 140 to 180 in coastal cutthroat trout free to migrate to and from the sea. Mean values consistently fall between 150 and 160. From two Oregon streams isolated by barrier falls, I took samples that differ from each other by 40 scales: 30 specimens from Grassy Lake Creek, Clatsop County, have 117–138 (mean, 126) scales in the lateral series; 15 specimens from Bible Creek, Tillamook County, have 148–184 (167) scales. Hatchery rainbow trout, which have fewer lateral scales than cutthroat trout, were stocked into the Grassy Lake Creek watershed, and some hybridization probably has occurred. Two of the 30 specimens lack basibranchial teeth (absence of such teeth is a rainbow trout character), but the vertebral count of 59–62 (60) is the lowest of any of my samples of coastal cutthroat trout, indicating that hybrid influence from rainbow trout is slight.

A northern California sample from an isolated population in Penn Creek, Patrick's Point State Park, which appears to be pure cutthroat trout in all other respects, has scale counts similar to the Grassy Lake Creek fish. Eleven specimens from Penn Creek have 118–135 (mean, 126) lateral-series scales. Schultz (1936) mentioned that two forms of coastal cutthroat trout have been observed in the Puget Sound drainages of Washington—a normal form with 143–180 scales in the lateral series and 30–36 scales above the lateral line, and a coarse-scaled form with 120–140 (usually 125–130) lateral-series scales and 25–29 scales above the lateral line. It was not stated whether the two forms occurred together.

When typical ranges of variability are given for a widely distributed species or subspecies, many exceptions should be expected. Hundreds of populations with atypical characters, like those of Grassy Lake Creek and Penn Creek, probably occur throughout the large range of coastal cutthroat trout.

Typically, vertebrae in the coastal subspecies number from 60 to 64, averaging 61–62, which is characteristic of the species as a whole.

Gill rakers number from 15 to 21; most mean values are near 18. My lowest counts are from the Penn Creek sample, 15–18 (mean, 17), and my highest counts are from museum specimens of the cutthroat trout from Crescent Lake, Washington, labeled "*Salmo crescentis*" in the collection, 13 of which have 18–21 (19) gill rakers.

Pyloric caeca number from about 25 to 55, averaging about 40, which is similar to counts for other subspecies of cutthroat trout except those in the Lahontan basin. DeWitt (1954) found 23–60 (mean, 40) caeca in 71 coastal cutthroat specimens from several northern California localities.

Basibranchial teeth are usually present but difficult to observe. These very small teeth lie between the gill arches on the floor of the pharynx on the membranous basibranchial plate. Basibranchial teeth are not present, or at least were not seen by me, in cutthroat trout at the time they emerged from redds at lengths up to about 25 mm. The smallest specimen in which I have found a basibranchial tooth was 37 mm. These teeth continue to increase in number until the fish grow to lengths of 70–100 mm.

DeWitt (1954) found that 6 of 79 California coastal cutthroat specimens

EX5004-000044-TRB

lacked basibranchial teeth, but he mentioned that some specimens had an appearance suggestive of hybridization. He counted from 1 to 34 (mean, 9) basibranchial teeth in the 73 specimens with these teeth, which is similar to tooth counts for my samples from California to Alaska (means ranged from 5 to 15) with one notable exception. The highest number of basibranchial teeth I found in any coastal cutthroat was in a sample of nine museum specimens from Lake Sutherland, Washington, where two species had been described, *Salmo jordani* and *S. declivifrons* (Meek 1899). I found the Lake Sutherland specimens to be typical of coastal cutthroat trout except for the high number of basibranchial teeth, 15–52 (mean, 29)—about twice the number found in any other sample.

I believe that pure coastal cutthroat trout have basibranchial teeth, and that the absence of these teeth indicates hybridization with rainbow trout. This opinion is based on 110 specimens of coastal cutthroat trout from remote areas of Alaska and British Columbia where, I assume, the influence of stocking has been nil. All 110 specimens have basibranchial teeth. In samples from Washington and Oregon, where stocking of hatchery fish has been heavy, I found specimens without basibranchial teeth. For example, 4 of 17 specimens from Gate Creek, a tributary of the McKenzie River, Oregon, lack basibranchial teeth. Campton and Utter (1985) verified rainbow × cutthroat hybridization in two Puget Sound streams by electrophoretic analysis.

Besides the loss of basibranchial teeth, hybrids may differ in coloration, spotting pattern, and numbers of scales, caeca, and vertebrae. Where coastal hybrids are found, there is seldom the hybrid swarm typical of interior waters. That is, although gene flow may occur between coastal cutthroat and coastal rainbow trout, reproductive isolation typically does not break down completely.

In 1979 I visited streams on the west coast of Vancouver Island, where I made several collections of the native trout. In lower reaches of these streams, steelhead and coastal cutthroat trout coexist. Above barrier falls in some of the streams, a resident trout occurs that represents a rainbow × cutthroat hybrid (predominantly rainbow trout; Parkinson et al. 1984). The rainbow and cutthroat trout niches broadly overlap. Coexistence of rainbow and coastal cutthroat trout in Pacific coastal streams (and of rainbow and interior cutthroat trout in the Salmon and Clearwater drainages of Idaho) depends on maintenance of reproductive isolation. In small streams with limited niche diversity and insufficient space to allow their physical separation at spawning, cutthroat trout and rainbow trout appear unable to resist crossbreeding, and a hybrid swarm results if they come into contact.

In 1981, Robert Smith (U.S. Fish and Wildlife Service, retired), a keen observer of western trout, sent me specimens from the headwaters of Mussel Creek, Oregon, about 24 km north of the mouth of the Rogue River. Smith wrote that steelhead and sea-run cutthroat trout occur in the lower reaches of Mussel Creek but that a "strange" trout lives in the upstream reaches. The strange specimens are rainbow × cutthroat hybrids. Evidently, limited habitat diversity in upper Mussel Creek resulted in hybrid swarms like those in some Vancouver Island streams.

DISTRIBUTION

The northern (and western) extent of coastal cutthroat trout distribution is the Prince William Sound area of southern Alaska, bounded by Gore Point on the Kenai Peninsula. The southern limit is the Eel River, California (Figure 4). Coastal cutthroat trout occur on all the numerous islands with suitable habitat off the coast of British Columbia and southern Alaska. Typically, they do not occur far inland—usually less than 150 km from the coast. The farthest natural inland penetration is in the headwaters of the Skeena River, British Columbia. Throughout this range, both sea-run and nonmigratory stocks are found. Many of the nonmigratory stocks live in lakes and show morphological specializations for lacustrine life, such as the numerous gill rakers for feeding on zooplankton shown by Crescent Lake fish and the high number of basibranchial teeth characteristic of the Lake Sutherland population. (The nature of lacustrine selection for more abundant basibranchial teeth is unknown, but it also is expressed in lake populations of Yellowstone and Lahontan cutthroat trout.)

TAXONOMIC NOTES

The unique karyotype (68 diploid chromosomes) and several unique alleles detected by electrophoresis (Leary et al. 1987; Allendorf and Leary 1988) indicate the unity of coastal cutthroat trout and its long isolation from other subspecies. This evidence is the basis for recognizing *O. clarki clarki* as one of the four major subspecies of cutthroat trout (Behnke 1988c).

All coastal cutthroat trout are currently recognized as a single subspecies. In the past, other species or subspecies have been named that are now considered to be synonymous with *O. clarki clarki*. Jordan (1896) named *Salmo gairdneri crescentis* from Crescent Lake, Washington. The type specimen lacks basibranchial teeth, which led Jordan to associate it with the fine-scaled steelhead rather than with the cutthroat trout. I examined the type specimen of *crescentis* (Stanford University number 11863) and verified that it has no basibranchial teeth. However, the Stanford collection includes six other *crescentis* specimens, collected in 1909, five of which have basibranchial teeth. All other characteristics of the type specimen and the six 1909 specimens are typical of coastal cutthroat trout. I also examined six specimens of Crescent Lake cutthroat trout collected in 1899, borrowed from the Field Museum of Natural History in Chicago, and all of them have basibranchial teeth (2–12). As a group, all the Crescent Lake cutthroat specimens show lateral-series scale counts of 150–162 (mean, 155), gill raker counts of 18–21 (19), and vertebral counts of 62–65 (63). The gill raker and vertebral counts are the highest I have encountered in any sample of coastal cutthroat trout.

Meek (1899) named another species of trout from Crescent Lake, *Salmo bathoeceter*, which was reputed to live only in deep water. I can find nothing in Meek's description or in the specimens borrowed from the Field Museum (collected by Meek) that indicates any difference between *bathoeceter* and *crescentis*. I conclude that both *crescentis* and *bathoeceter* are synonyms of *O. c. clarki*. Pierce (1984a, 1984b) studied the trout of Crescent Lake during 1981–1982.

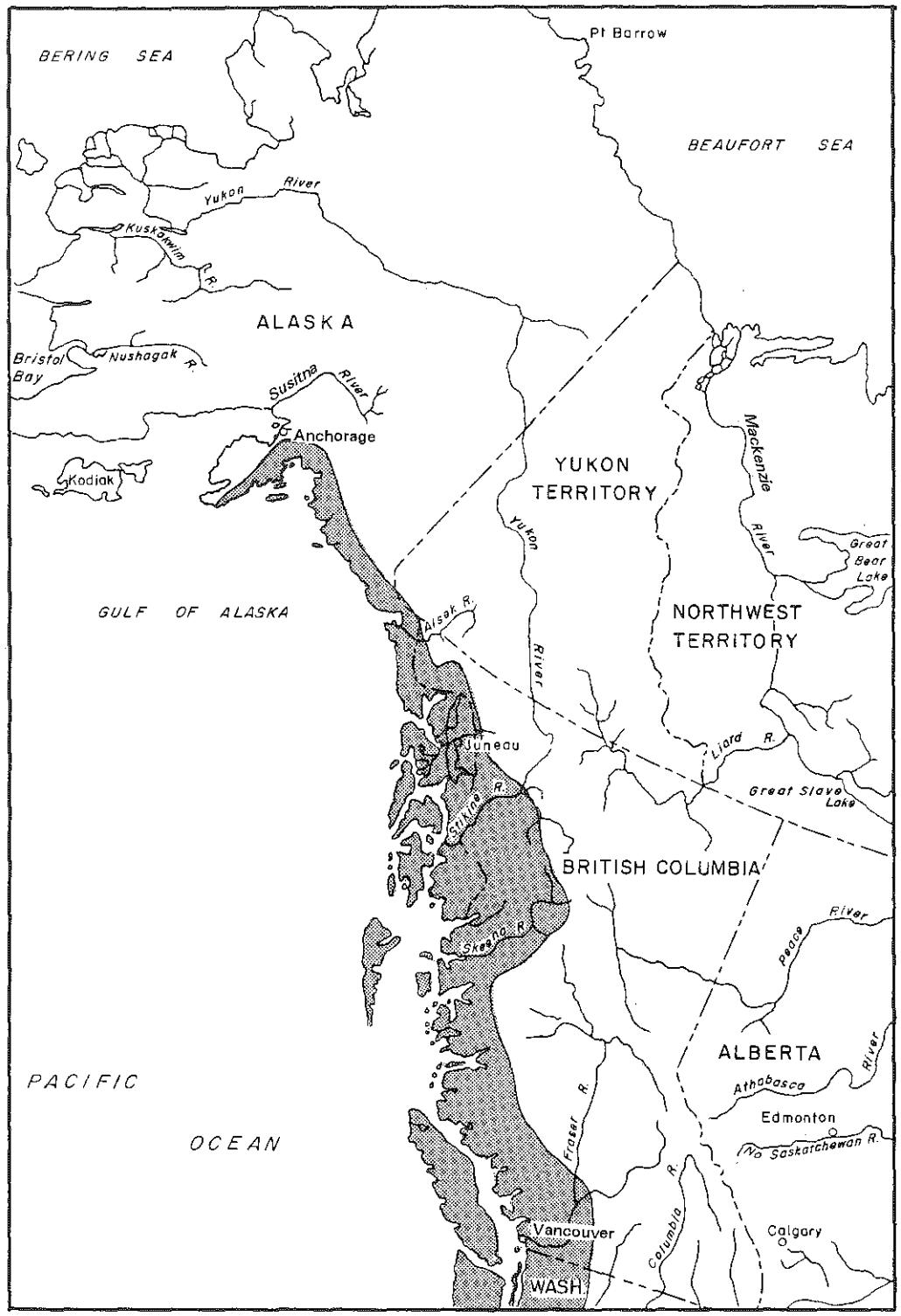

FIGURE 4.—Distribution of coastal cutthroat trout.

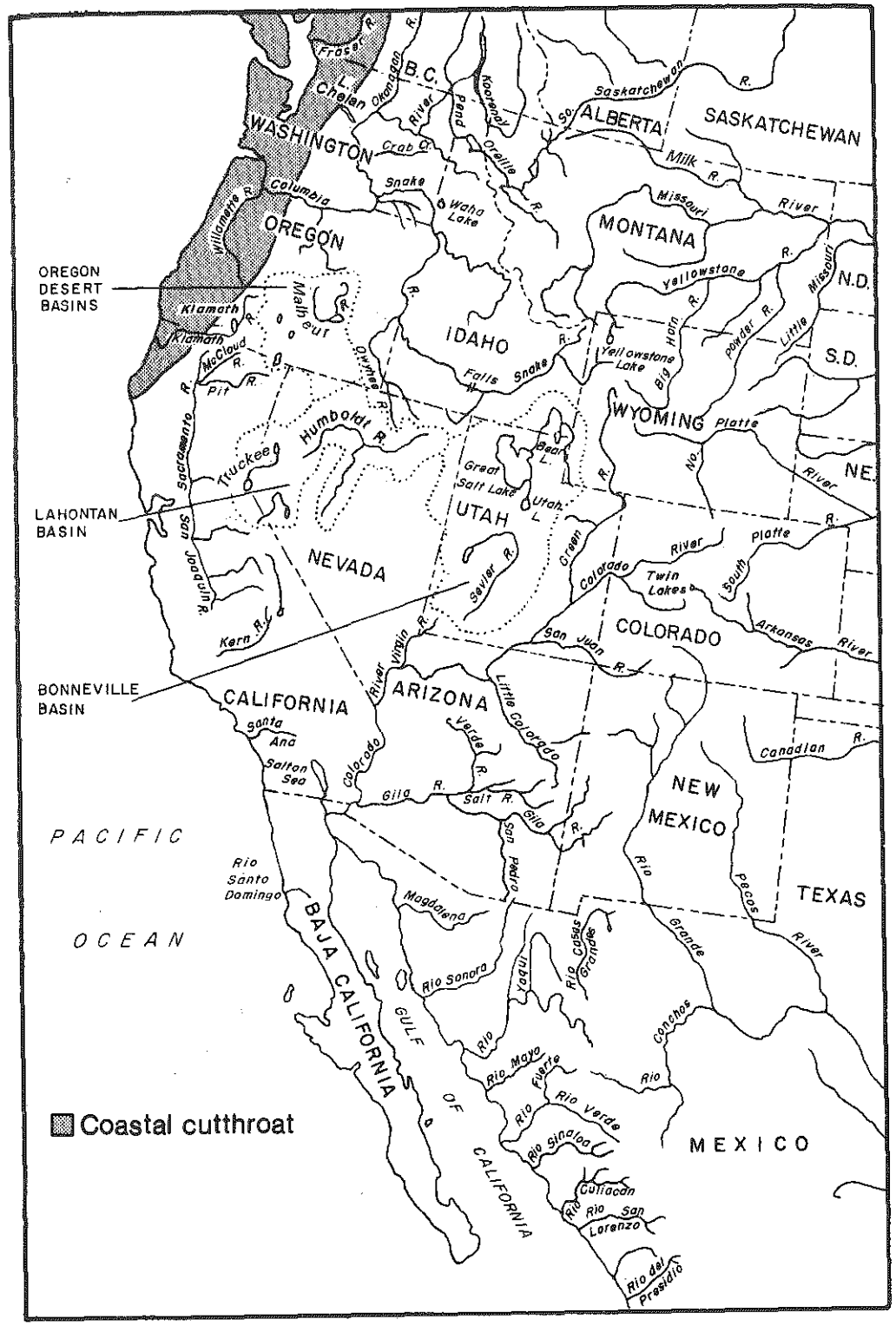

FIGURE 4.—Continued.

He found that native cutthroat trout still maintain a small population in the lake by reproducing in the outlet stream. Barnes Creek, the only spawning tributary to Crescent Lake, now contains a rainbow × cutthroat hybrid swarm. It is likely that two reproductively isolated populations of cutthroat trout originally occurred in Crescent Lake, one spawning in Barnes Creek and one in the outlet stream. Differences in their life histories may have generated the belief that they represented two species. From a practical viewpoint, sympatric populations with different life histories should be managed separately even if they are not recognized as different taxa.

Crescent Lake is a deep body of water covering 1,960 hectares in Olympic National Park, Washington. It is isolated from the sea by barrier falls. In the late 19th century the lake was famous for its large native cutthroat trout and rainbow trout (named *Salmo gairdneri beardsleei*: Jordan 1896). Wydoski and Whitney (1979) gave as the Washington state record cutthroat trout a Crescent Lake specimen of 5.45 kg. During the 20th century human attempts to improve on nature included a massive stocking program that introduced millions of hatchery rainbow trout, Yellowstone cutthroat trout, and kokanee into Crescent Lake, whose major tributary was blocked and polluted. The results were disastrous to the native trout. The U.S. Fish and Wildlife Service studied the situation in the 1940s and 1950s. A 1949 report by L. R. Garlick ("Report of Fishery Investigations, Lake Crescent, Olympic National Park with Management Recommendations") and a 1953 report by Z. E. Parkhurst and M. A. Smith ("Report on the Management of the Beardsley Trout Fishery of Lake Crescent, Olympic National Park") assumed cutthroat × rainbow hybrids were common among the Crescent Lake trout. Color photographs accompanying Parkhurst and Smith's report, however, show a typical rainbow trout (the Beardsley trout) and a typical cutthroat trout (*crescentis*) taken from the outlet spawning run. The more recent study by Pierce (1984a, 1984b) revealed that hybridization is limited to Barnes Creek and that the hybrids are mainly resident in the creek (only 3 of 47 adult trout sampled from the lake were of Barnes Creek origin). Pure native rainbow trout and pure native cutthroat trout have persisted by spawning in different parts of the outlet area.

From the 1953 report by Parkhurst and Smith, it is obvious that the concept of genetic uniqueness was not yet appreciated among fisheries managers. The recommendations of the report were to forget about the native trout, because they were hybridizing and difficult to propagate, and to stock Crescent Lake with large numbers of a "good strain" of hatchery rainbow trout. The implications were that nothing of value would be lost because the native Beardsley strain was a typical rainbow trout and the *crescentis* cutthroat was a typical coastal cutthroat trout. Entirely overlooked was the value of the Beardsley strain as a large, lake-adapted predator (which I discuss later).

Meek (1899) named two additional species, *S. jordani* and *S. declivifrons*, for what apparently is a single coastal cutthroat trout population native to Lake Sutherland, which lies immediately east of Crescent Lake. Examination of Meek's data and of the specimens he used in his description (borrowed from the Field Museum) does not indicate more than one form of cutthroat trout in Lake Sutherland. However, this trout is slightly differentiated, as reflected by the high number of basibranchial teeth (15–52; mean, 29) in 10 specimens and the below-average scale counts (135–158; mean, 146). Much stocking has occurred in this century, and the purity of the present cutthroat trout is unknown.

To my knowledge, the only critical hybridization experiment with coastal cutthroat trout was the master's thesis research of Hartman (1956), who crossed coastal cutthroat trout from Chilliwack Lake with interior Kamloops (redband) trout from Cultus Lake, British Columbia. The chromosome numbers of the parent species, although not considered by Hartman, should be 68 and 58, typical of coastal cutthroat and interior redband or Kamloops trout. This is the maximum difference between various forms of cutthroat and rainbow–redband trout. Hartman actually found slightly higher viability among hybrids than among the offspring of pure parental matings. For his thesis, Hartman did not have time to make second-generation crosses to determine the fertility of the hybrids, but he told me in 1961 that the hybrids were backcrossed with both rainbow trout and cutthroat trout and were fully fertile. Also, he found no sex ratio differences between hybrids and the offspring of pure parental matings. In other fish groups such as sunfishes (genus *Lepomis*), a predominance of one gender among hybrids indicates a partially developed fertility barrier between parents.

Where coastal cutthroat and rainbow trout coexist, they are ecologically separated at spawning by the preference of cutthroat trout for smaller tributary streams and of rainbow trout for main river channels. The introduction of hatchery rainbow trout could bridge this ecological separation in some streams and bring about hybridization and gene flow between the two species.

Carl Bond (Oregon State University) told me that two populations of coastal cutthroat trout occur in Triangle Lake, in Oregon's Siuslaw River drainage. One population spawns in late winter (typical of coastal cutthroat trout) and the other in May. This might be either a natural situation or the result of introductions of a stock whose genetically based spawning time differs from that of the native population. Odell Lake, Oregon, has two populations of kokanee, both introduced, which do not hybridize because of differences in the time and place of spawning (Averett and Espinosa 1968).

Utter et al. (1980), reviewing electrophoretic studies of coastal cutthroat trout, reported genetic differentiation between sea-run populations in Puget Sound, where the mouths of rivers are separated by areas of deep water. Apparently, deep-water areas are avoided by coastal cutthroat trout during their foraging in salt water and can act as an effective block to gene flow between populations.

LIFE HISTORY AND ECOLOGY

As a sport fish, the coastal cutthroat trout is less popular than the larger and more glamorous steelhead. This is reflected in the volume of literature, both popular and scientific, about each species. Detailed life history data were not published until Sumner's (1953, 1962) papers on the cutthroat trout of Sand Creek, Oregon. Hartman and Gill (1968) discussed the ecological preferences of juvenile rainbow and cutthroat trout, thereby providing some insight into the

mechanisms of niche separation. Giger (1972) gave comprehensive life history data on the cutthroat trout populations of several Oregon rivers. Armstrong (1971) discussed the age, growth, feeding habits, and migrations of the cutthroat trout in Eva Lake, Alaska. Andrusak and Northcote (1971) and Schutz and Northcote (1972) studied the feeding habits and spatial distribution of cutthroat trout occurring with Dolly Varden in British Columbia. Idyll (1942) studied the feeding habits of cutthroat, rainbow, and brown trout in the Cowichan River, British Columbia. Bustard and Narver (1975) studied winter habitat of cutthroat trout and coho salmon in British Columbia. Nicholas (1978b) delineated the winter habitat preference of coastal cutthroat trout in the Willamette River watershed and the interactions of these fish with rainbow trout. Narver (1975) published notes on the ecology of cutthroat trout in Great Central Lake, Vancouver Island. Nilsson and Northcote (1981) provided life history and ecological information on coastal cutthroat and rainbow trout in several British Columbia lakes with allopatric or sympatric populations. Cutthroat trout were much more predaceous than rainbow trout and attained a larger maximum size where they coexisted in the British Columbia lakes studied. In Crescent Lake, Washington, however, rainbow trout (the Beardsley strain) attain a larger maximum size than cutthroat trout, perhaps because they evolved from a steelhead ancestor and were preadapted as a limnetic predator. Trotter (1989) has produced the most recent and inclusive compilation of life history information on coastal cutthroat trout.

The sea-run cutthroat trout of Oregon typically migrate to salt water in the late spring or early summer at age 2 or age 3 and at a size of 175–225 mm, although some individuals in a population may never go to sea. Evidently, coastal cutthroat trout do not travel in the open ocean, preferring to concentrate in bays, estuaries, and along the coast. In salt water they feed intensively on crustaceans and fish and grow at a rate of about 25 mm per month. After 2 to 5 months in the sea, they return to rivers. Their typical spawning period is late winter to early spring, but it may extend into May. The timing of the migrations, age at migrations, length of time spent in the sea, and spawning time vary among stocks and geographical areas.

Sea-run coastal cutthroat trout attain a maximum age of about 10 years. They grow slowly after first spawning at age 3 or age 4. The fall runs of cutthroat trout, as they congregate off the mouths of rivers and run up the rivers, provide highly popular local fisheries for West Coast anglers. These fish are commonly known as harvest trout because most of the runs coincide with the harvest season. Washington (1977) concluded that the cutthroat trout is the third-most popular game fish caught in marine waters of the Pacific Northwest, after coho and chinook salmon (virtually all steelhead are caught in fresh water). Fish making up the fall run range from about 250 to 450 mm, and their maximum size is about 550 mm and 2 kg; exceptional fish approach 3 kg.

Like cutthroat trout in general, the coastal subspecies is vulnerable to overexploitation by angling. In Sand Creek, which is little used by anglers, survival was 30% between the first and second spawning, 17% between the second and third spawning, and 12% between the third and fourth spawning. In five Oregon rivers subjected to heavy angling pressure, the estimated survival

ranged from 5 to 26% between the first and second spawning. Johnson (1976) discussed the problem of angler overexploitation of coastal cutthroat trout and the need for stricter regulations on sport fisheries. Predation at sea may be a significant cause of natural mortality. Giger (1972) reported that 58% of the wild cutthroat and 67% of the hatchery cutthroat trout taken from the Alsea River estuary in 1970 had scarring indicative of predator attacks.

Although the coastal cutthroat trout has been propagated in large numbers in Oregon and Washington, only in recent years has some thought been given to making better use of its genetic diversity in fishery programs. Professional indifference to native stocks has been detailed by Crawford (1979) in a history of coastal cutthroat propagation by the Washington Game Department, which began a hatchery program for sea-run cutthroat trout in 1958. Eggs were taken from sea-run cutthroat trout of three rivers and mixed together, and young from these crosses were stocked in many rivers. The hatchery on Beaver Creek supplied especially large stockings made in an attempt to establish a sizable run for egg-taking operations. Returns were poor, however, so 100,000 eggs from Oregon (Alsea River sea-run cutthroat trout) were thrown into the pot. In 1967 and 1968, crosses were made with steelhead, which thoroughly bastardized the stock. Returns continued to be poor. From an average of about 10,000 smolts released annually, returns of adults to the Beaver Creek hatchery were 24 in 1976 and 14 in 1977. The failure of Beaver Creek hatchery stock caused some personnel of the Washington Game Department to realize that a successful hatchery program for sea-run cutthroat trout must be based on appreciation of the genetic diversity of native populations.

Johnson (1976) and Johnson and Mercer (1976, 1977) discussed the Washington Game Department's use of two stocks in its cutthroat trout propagation program. One stock returns from the sea in September and October, the other in December and January. Giger (1972) found considerable natural straying of sea-run fish between streams. Consequently, genetic mixing of coastal cutthroat stocks of close proximity and with similar life histories may not undermine propagation programs to the extent that mixing of steelhead or salmon stocks would. Of potentially greater significance is the stocking of hatchery rainbow trout in streams where both cutthroat trout and steelhead exist. This could lead to a breakdown in reproductive isolation if the domestic rainbow trout bridged the spatial gap and any spawning-time gap between steelhead and cutthroat trout, thus stimulating hybridization.

Hybrid cutthroat trout should not be regarded as inferior by definition. Donaldson et al. (1957) crossed a hatchery strain of coastal cutthroat trout with a wild strain. When the hybrid was stocked in Echo Lake, Washington, it returned from three to six times more fish than either of the parental races. These interesting results suggest some practical use of genetic diversity.

Coastal cutthroat trout can be highly predaceous. Idyll (1942) found that cutthroat trout had a higher percentage of fish in their diets than either rainbow or brown trout in the Cowichan River, British Columbia. Studies by Armstrong (1971) in Alaska and by Andrusak and Northcote (1970, 1971) in British Columbia revealed that when coastal cutthroat trout live with Dolly Varden, the cutthroat trout is the more predaceous species by far. Ricker (1941) found

cutthroat trout to be the major predator on young sockeye salmon in Cultus Lake in 1940. Nilsson (1971) showed more rapid growth and more predaceous feeding habits for cutthroat than for rainbow trout in a British Columbia lake. These results were further detailed and verified by Nilsson and Northcote (1981).

Interactions between nonmigratory coastal cutthroat and rainbow trout in the same stream or lake are variable. In the Willamette River, Oregon, Nicholas (1978b) found that rainbow trout were dominant and grew more rapidly than cutthroat trout. In British Columbia, Nilsson and Northcote (1981) found that cutthroat trout were more predaceous and attained a greater maximum size than rainbow trout in the same lake, but that rainbow trout were behaviorally dominant over cutthroat trout of comparable size. Narver (1975) reported on a 2-year creel survey of Great Central Lake, Vancouver Island, in which the anglers caught 324 cutthroat trout to 23 rainbow trout. This prompts the question: What environmental factors act to favor cutthroat trout over rainbow trout in Great Central Lake? The lake has extremely low values for nutrients and primary production, so perhaps the native coastal cutthroat trout is a more effective predator (mainly on young sockeye salmon and sticklebacks) in such an environment.

In view of their predatory nature and long maximum life span (to at least 10 years), it is strange that trophy coastal cutthroat trout of 8–9 kg or more are unknown. Dymond (1932) gave a maximum size of 7.7 kg for lake-dwelling coastal cutthroat but provided no documentation. This size has been repeated in the literature even though the lake in question has never been identified or the record verified.

The coastal cutthroat trout, as well as the interior subspecies, appears to be highly vulnerable to logging activities. Clear-cutting of forests in Oregon led to increased sedimentation, reduced cover, and greater maximum water temperature in streams, which combined to depress cutthroat trout populations for 6–8 years, although coho salmon populations rebounded rapidly after clear-cutting ended (Moring and Lantz 1975; Ringler and Hall 1975).

STATUS

The coastal cutthroat trout is considered a single subspecies throughout its entire range. Although numbers of coastal cutthroat trout have drastically declined in many areas because of environmental alterations (mainly logging), and although the threat of hybridization exists for many stocks, this is by far the most widely distributed and abundant of any subspecies of cutthroat trout. "Abundance," however, is a relative term when the subject is the conservation status of native fish. Nehlsen et al. (1991) considered almost all native populations of sea-run cutthroat trout in California, Oregon, and Washington to be at some risk of extinction, and they cited pervasive, continuing declines in stock size as the reason for this risk.

6

CUTTHROAT TROUT OF THE COLUMBIA AND MISSOURI BASINS

We now know that cutthroat trout native to the middle and upper Columbia River basin, the South Saskatchewan drainage, and the upper Missouri and Yellowstone systems are represented principally by two highly divergent subspecies: westslope cutthroat trout *Oncorhynchus clarki lewisi* and Yellowstone cutthroat trout *O. c. bouvieri* (Marnell et al. 1987; Behnke 1988c); an undescribed fine-spotted subspecies occupies the upper Snake River drainage (Figure 5). The westslope and Yellowstone subspecies represent the most ancient divergence of inland cutthroat trout. Their phylogenetic separation is estimated to be of mid-Pleistocene origin (Behnke 1988c). The evolutionary paths leading to *lewisi* and *bouvieri* evidently were associated with the upper Columbia River (*lewisi*) and the Snake River (*bouvieri*). The original separation of these ancestral lines may have occurred south of the area presently drained by the Snake, however. This possibility arises because soon after the *lewisi* and *bouvieri* lines diverged, the *bouvieri* ancestry gave rise to another lineage that was isolated in the Lahontan basin and became *O. c. henshawi*. The precise area where *lewisi* and *bouvieri* separated thus awaits resolution of mid-Pleistocene drainage patterns.

Until the 1970s, attempts to classify the inland subspecies produced confusion. The Lewis and Clark expedition first recorded cutthroat trout in 1805, along the upper Missouri River at the "Great Falls of the Missouri." In 1853, George Suckley, a surgeon with the Pacific Railroad survey, returned to the site visited by Lewis and Clark and caught specimens on an artificial fly (Suckley 1874). These specimens were described as *Salar lewisi* by Girard (1856). Thus the type locality established for the name *lewisi* is the upper Missouri River near Great Falls, Montana. Because the same cutthroat lineage is native to the South Saskatchewan, Kootenay, Clark Fork, and St. Joe drainages, all of these cutthroat trout are classified as the subspecies *lewisi*.

Jordan and Evermann (1896) were aware that cutthroat trout had made a transfer across the Continental Divide from the Snake River drainage to the Yellowstone River drainage via Two Ocean Pass. They assumed these fish had dispersed down the Yellowstone River to its junction with the Missouri, then upstream to the headwaters of the Missouri. Under this misconception, they

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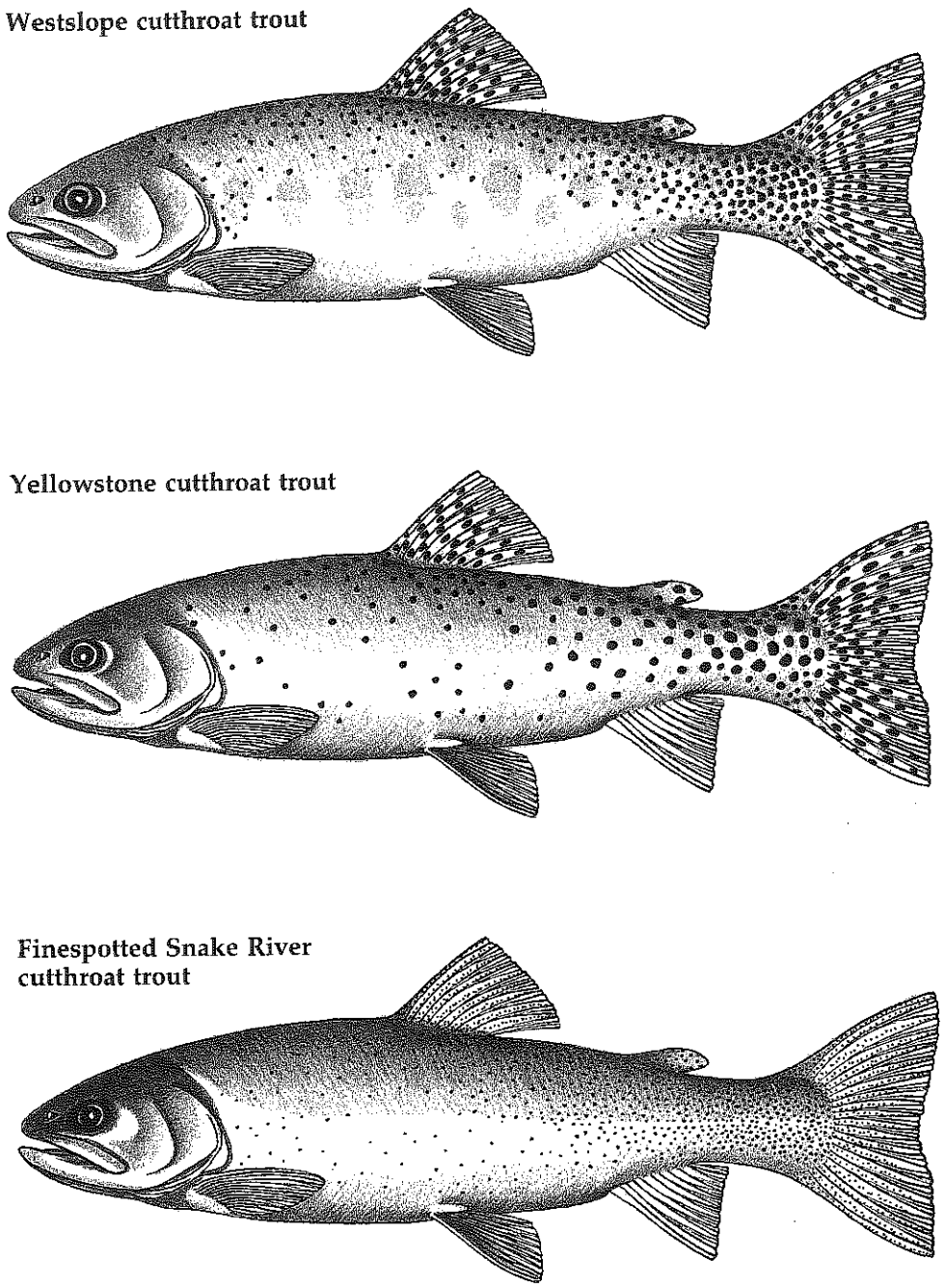

FIGURE 5.—Cutthroat trout of the Columbia and Missouri basins.

applied the name *lewisi* to Yellowstone cutthroat trout, not understanding that the cutthroat trout native to the upper Missouri and Yellowstone drainages represented two highly differentiated subspecies.

Jordan and Evermann (1896) recognized all cutthroat trout as subspecies of *Salmo mykiss*. *Salmo mykiss lewisi* was designated for cutthroat trout of the Snake River above Shoshone Falls and of the Yellowstone and upper Missouri drainages. Below Shoshone Falls, in the middle Columbia basin to the Cascade Mountains, they recognized the "silver trout" *S. m. gibbsi* (in reality a redband trout). They did not attempt to classify the trout native to the Kootenay, Clark Fork, and St. Joe drainages. In their 1902 book, Jordan and Evermann incorrectly assumed that the distribution of the coastal cutthroat trout (subspecies *clarki*) extended east of the Cascades to Shoshone Falls and "into the headwaters of the Pend Oreille" (Clark Fork drainage of Montana). This raised a problem with their earlier classification, which recognized various cutthroat subspecies. Two of those subspecies, *gibbsi* and *clarki*, had been assumed to coexist over a vast range in the middle Columbia basin. To resolve this problem, they upgraded all of their earlier subspecies to full species (Jordan and Evermann 1902).

It is now apparent that the trout classification of Jordan and Evermann, which persisted essentially unchallenged into recent times, was based on insufficient, misleading data. The confusion that frustrated later workers' attempts to classify inland cutthroat trout of the Columbia and Missouri basins is exemplified by Schultz (1935, 1941). Using Jordan and Evermann's division of cutthroat trout into coastal (*clarki*) and "Yellowstone" (*lewisi*) forms, Schultz believed he had found various hybrids and transitional types among the inland cutthroat trout of Washington and of Glacier National Park. Unable to make much sense of the diversity he observed, he concluded that all inland cutthroat trout should be grouped as the subspecies *lewisi*, to which he assigned the common name Yellowstone cutthroat trout.

During the 1970s, studies based on morphology, electrophoresis, and karyotyping all agreed that the Yellowstone cutthroat trout and the westslope cutthroat trout represent two long-divergent lines of evolution. The name *lewisi* was clearly fixed for westslope cutthroat trout, so the Yellowstone cutthroat trout required a new subspecific designation. The oldest name strictly associated with the large-spotted cutthroat trout of the Snake and Yellowstone drainages is *bouvieri*, given by Bendire (1882) to the trout native to Waha Lake, Idaho. Waha Lake and Crab Creek, Washington (the native trout of Crab Creek was named *eremogenes* by Evermann and Nichols 1909), are the only localities in the middle Columbia basin where the large-spotted Yellowstone form of cutthroat trout was found by early collectors (both populations are extinct today). Both the Crab Creek drainage and Waha Lake lie in independent basins that today lack direct connections to the Columbia basin. Evidently, they became physically isolated before any form of rainbow trout could reach them. In other waters below Shoshone Falls, later-invading forms of redband trout eliminated and replaced all populations of *bouvieri* where they came in contact.

If Waha Lake overflowed, it would spill into the Clearwater River drainage south of Lewiston, Idaho, and thence into the Snake River. If the Crab Creek basin overflowed, it would spill into the Columbia River above the confluence

with the Snake. The occurrence of Yellowstone cutthroat trout in Waha Lake and Crab Creek indicates the once-broad distribution of this subspecies throughout the Snake and middle Columbia drainages. Presently, the native cutthroat trout of the Salmon and Clearwater drainages is the westslope subspecies, but there seems little doubt that a Yellowstone ancestor came to Waha Lake via the Clearwater River. Such a scenario requires Yellowstone cutthroat trout to be the original native of the Salmon and Clearwater drainages, subsequently to be eliminated when redband trout invaded this region. With the Yellowstone form gone, the westslope cutthroat trout gained access to the Salmon and Clearwater drainages, probably via headwater stream transfer from the Clark Fork drainage, and it has persisted to the present in coexistence with redband trout. Although both the Waha Lake and Crab Creek cutthroat trout are now extinct, the lack of significant differentiation between museum specimens of these trout and between other fish species common to Waha Lake and Crab Creek indicates that these basins were isolated no longer ago than the latest glaciation during a period from about 20,000 to 60,000 years ago. In any event, the overall similarity of the Yellowstone-type cutthroat trout native to Crab Creek, Waha Lake, and the upper Snake and Yellowstone drainages justifies their classification as a single subspecies, for which *bouvieri* is the oldest name.

The contiguous and disjunct distributions of westslope and Yellowstone cutthroat trout are shown in Figure 6 (page 78). The finespotted Snake River cutthroat trout of the upper Snake basin is enigmatic, as will be seen in the subsequent account of this undescribed subspecies.

Westslope Cutthroat Trout *Oncorhynchus clarki lewisi*

TYPICAL CHARACTERS

Spots small, irregular in outline (nonrounded), similar in shape and size to the spots of coastal cutthroat trout. Few spots on anterior body below lateral line. Coloration variable, generally silver with yellowish tints, but bright yellow, orange, and especially red colors can be expressed to a much greater extent than on coastal or Yellowstone cutthroat trout. Vertebrae 59–63, typically 60–61. Scales in the lateral series typically 150–200 or more, mean values generally 165–180. Specimens from Salmon and Clearwater drainages and some British Columbia populations have the highest lateral-series counts, averaging more than 200. Pyloric caeca typically 25–50, with mean values of 30–40. Upper Missouri basin specimens generally have lowest caecum counts. Gill rakers typically 17–21, mean values usually 18–19; posterior gill rakers on first arch absent or weakly developed.

DESCRIPTION (Plate 1; Figure 5, page 74)

Westslope cutthroat trout tend to have fewer meristic elements (vertebrae, pyloric caeca, gill rakers) than Yellowstone cutthroat trout, but the variation in meristic counts within each subspecies and the overlap in counts between subspecies are considerable. The two subspecies have distinctive spotting patterns and coloration differences, however, and experienced observers can use these characters to identify the subspecies and approximate the relative purity of a stock.

Millions of Yellowstone cutthroat trout have been stocked in the range of the westslope subspecies during the past 80 years. Cutthroat trout with pronounced, large, round spots and brownish yellow coloration are due to those introductions. Hybridization between the two subspecies can produce a complete spectrum of spotting and coloration. Hybridization with rainbow trout can be detected by the appearance of spots on the top of the head and on the anterior body below the lateral line, as well as by reduced scale counts, increased caecal counts, and loss of basibranchial teeth (Marnell et al. 1987).

The distribution of spots on westslope cutthroat trout is, in general, typical of interior cutthroat subspecies. The area within an arc extending from the origin of the pectoral fin to a point just above the lateral line and downward to the origin of the anal fin usually has very few or no spots. This spotting pattern was illustrated by Hanzel (1959), Brown (1971), and Campbell (1971) and it is consistent throughout the subspecies' range. Coloration is under some environmental influence because some of the pigments deposited in the skin are derived from food. Westslope cutthroat trout, however, has a genetic basis for bright

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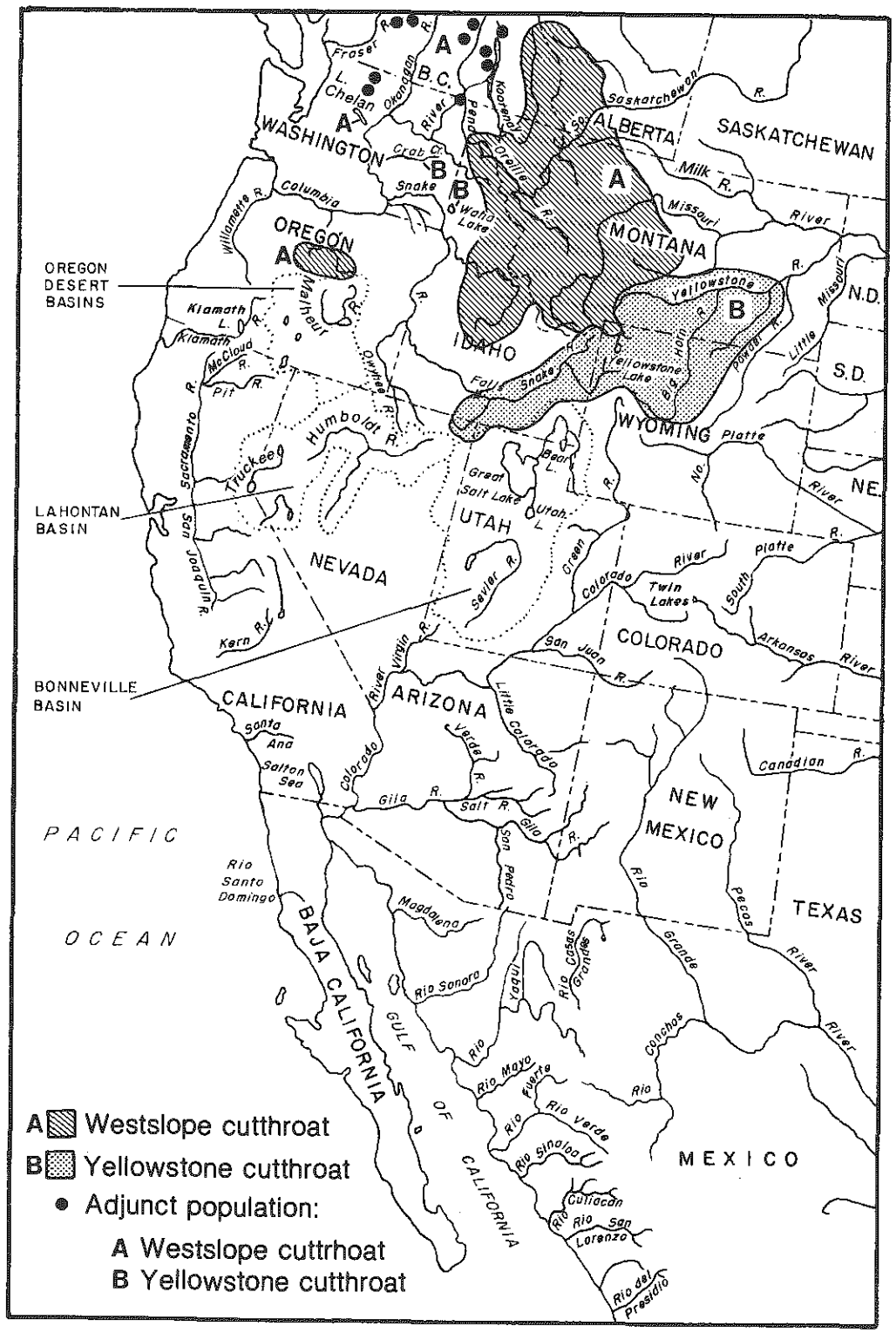

FIGURE 6.—Distributions of westslope and Yellowstone cutthroat trout.

coloration, particularly for red hues of varying intensity that are best developed on lacustrine males during the spawning season. In extreme examples, the whole ventral region may be crimson. The Yellowstone subspecies does not express these colors so intensely on the sides and belly.

Westslope cutthroat trout have 66 chromosomes, based on Loudenslager and Thorgaard's (1979) work with fish from the Montana Fish and Game Department's brood stock, which originated from a tributary of Hungry Horse Reservoir. This karyotype is intermediate between those of coastal cutthroat trout (68) and Yellowstone cutthroat trout (64).

Electrophoretic data for proteins derived from many gene loci diverge substantially between westslope and Yellowstone cutthroat trout (Reinitz 1974; Leary et al. 1987; Marnell et al. 1987; Allendorf and Leary 1988); indeed, differences are greater between these subspecies than between westslope cutthroat and rainbow trout. This divergence among alleles at several gene loci is so great that Allendorf and Leary (1988) proposed that westslope and Yellowstone cutthroat trout be recognized as separate species. Mitochondrial DNA comparisons, however, agree with other systematic and zoogeographical evidence that all subspecies of cutthroat trout are more closely related to each other than any of them is to rainbow trout (Gyllensten and Wilson 1987).

DISTRIBUTION

The original distribution of westslope cutthroat trout is not known with certainty. I consider the mountain cutthroat trout of British Columbia, named *Salmo clarki alpestris* by Dymond (1931), to represent disjunct populations of *lewisi*. The known native range of westslope cutthroat trout includes the upper Missouri basin (main river and all tributaries) downstream to about Fort Benton, Montana, about 60 km below Great Falls, as well as headwaters of the Judith, Milk, and Marias rivers, which join the Missouri downstream from Fort Benton. Except for some headwaters in northwestern Wyoming and southern Alberta, the entire Missouri basin distribution of the subspecies is in Montana (Figure 6, page 78).

West of the Continental Divide, in the Columbia River basin, the subspecies' natural distribution includes the upper Kootenay River above the falls near Libby, Montana, extending into the river's British Columbia headwaters, and above barrier falls on some Idaho tributaries of the Kootenay. The original distribution embraced the entire Clark Fork drainage of Montana and Idaho downstream to falls on the Pend Oreille River near the Idaho–Washington border. Westslope cutthroat trout are native to the Spokane River above Spokane Falls and into Idaho's Coeur d'Alene and St. Joe drainages. An apparent anomaly is the occurrence of westslope cutthroat trout in the Salmon and Clearwater drainages of Idaho's Snake River system, where the Yellowstone subspecies might be expected as the native form. As previously discussed, the Yellowstone form probably was the original cutthroat trout of the Salmon and Clearwater drainages, based on its historical occurrence in Waha Lake, but was displaced by redband trout. Thereafter, transfers from the Clark Fork drainage established westslope cutthroat trout in the Salmon and Clearwater drainages,

where it managed to coexist with anadromous redband trout. No cutthroat trout are known to be native to other major Snake River tributaries below Shoshone Falls, such as the Wood, Weiser, Boise, Payette, Owyhee, and Malheur rivers. There, the redband is the only known native trout.

Below the barrier falls that originally isolated westslope cutthroat trout in the upper Columbia basin, the subspecies occurs westward to the Cascade Mountains as disjunct populations, including those of the mountain cutthroat trout ("*alpestris*") of British Columbia. In recent years I have documented the natural occurrence of the westslope form in the Lake Chelan drainage, Washington, where a falls prevented natural invasion by rainbow trout, and in the John Day River drainage, Oregon (Behnke 1988c). Twenty-four specimens collected in 1979 and 1980 from eight streams afford proof that westslope cutthroat trout are indigenous to the John Day drainage. I identified the John Day fish from their spotting pattern and coloration. Rose, orange, and yellow tints on some of these fish would not be expected on specimens of Yellowstone cutthroat trout living in small streams. The spots are irregular in outline and arranged over the body in the typical westslope pattern, although they are somewhat larger than spots typical of the pure subspecies elsewhere. The larger spots may reflect an ancient mixing of westslope and Yellowstone forms in the middle Columbia basin, or they may result from slight hybridization with redband trout. I identified 1 of the 24 specimens as a cutthroat × redband hybrid, based on its lack of basibranchial teeth, erratic spotting pattern, and lower scale counts, so limited gene flow is occurring between the species; but the absence of hybrid swarms indicates that gene flow is not pronounced. Six of the eight collections of cutthroat trout contain specimens of redband trout, and four contain bull trout. Robert Smith, who made the collections, observed that only cutthroat trout occurred in the uppermost headwaters, but that they were joined farther downstream by redband and bull trout. Steelhead also spawn and rear in some of the downstream areas. Thus, three groups of native *Oncorhynchus* trout coexist in the John Day drainage: cutthroat trout and resident and anadromous redband trout.

The occurrence of disjunct populations in the middle Columbia basin may be the result of late-Pleistocene flooding from glacial Lake Missoula. Several times during the last glacial epoch, ice dams backed up the Clark Fork River to form an enormous lake; these dams periodically burst, causing floods of incredible magnitude across eastern Washington (Waite 1980). Conceivably, other undocumented populations of westslope cutthroat trout occur in the middle Columbia basin. Reports of U.S. Fish and Wildlife Service surveys of the Columbia River made during 1948–1950 contain a few brief references to cutthroat trout in the middle Columbia basin (Bryant and Parkhurst 1950): for example, "rainbow trout and cutthroat trout are reported from the North Fork of Ahtanum Creek" (a tributary to the Yakima River), and "cutthroat, rainbow, Dolly Varden, whitefish, and kokanee are also present and extensively fished in the Wenatchee River watershed." Cutthroat trout were also reported from the Chewack River, which flows to the Methow River and thence to the Columbia north of Lake Chelan and south of the confluence of the Columbia River with the Okanogan River. More solid evidence of indigenous westslope cutthroat trout in

mid-Columbia tributaries was provided by James Mullan in the form of specimens and collection data. Mullan, Kenneth Williams, and other biologists have conducted surveys of mid-Columbia tributaries in recent years. The headwaters of the Wenatchee, Entiat, and Methow rivers are difficult to reach and only the Methow drainage has been relatively well surveyed to date. Cutthroat trout were recorded in 19 of the 27 Methow tributaries sampled. Although the drainage has been stocked with both rainbow and cutthroat trout for many years, the widespread occurrence of cutthroat trout indicates that the westslope subspecies is native to the Methow River drainage, and probably also native to the Wenatchee and Entiat drainages. My examination of rainbow and cutthroat trout from the Methow drainage revealed considerable hybridization between the species. If this degree of hybridization had been ongoing for thousands of years, I would not expect to find typical cutthroat trout phenotypes still existing. The stocking of nonnative forms of both rainbow and cutthroat trout probably has broken down the historically established reproductive isolation between the two species. Cutthroat trout and the native bull trout are restricted to the coldest sections of streams. The collection data for the Methow drainage indicates that where introduced brook trout have become established, cutthroat and bull trout are eliminated. Westslope cutthroat trout may be native to the Lost River group of streams of the Snake River Lava Plateau. These Idaho streams originate in the Lost River Mountains and sink into the ground before they reach the Snake River, so fish in the headwaters are completely isolated from those in lower rivers. These headwaters are contiguous with headwaters of the Salmon River. The native trout of these streams are unknown, and any future study will have to deal with the problem of introductions. Hayden (1872) mentioned a small-spotted cutthroat trout in one of the Lost River streams (Medicine Lodge Creek). Hubbs and Miller (1948) believed the cutthroat trout of the Snake River Lava Plateau represents an undescribed subspecies.

I examined 10 specimens collected in 1934 from one of these isolated drainages (Irving Creek); these specimens are in the University of Michigan collection. They appear to be hybrids of native trout with rainbow trout or Yellowstone cutthroat trout (or both). The question of the native trout of the Lost River streams remains open. The other fish species native to these streams—bull trout and cottid sculpins—are also found in the Salmon River drainage but not in the upper Snake River. My interpretation is that Pleistocene volcanic eruptions eliminated all fish life from these streams and buried their connections with the upper Snake River. Subsequently, headwater stream transfers from the Salmon River system established the present fauna. If this is true, westslope cutthroat trout would be the native trout of the Lost River streams unless the transfer occurred at a time when Yellowstone cutthroat trout inhabited the Salmon River drainage.

TAXONOMIC NOTES

I characterize westslope cutthroat trout mainly by its distinctive spotting, and I group all cutthroat trout native to the upper and middle Columbia, South Saskatchewan, and upper Missouri basins, which share this spotting, as one

subspecies. As previously discussed, the identification based on spotting pattern is corroborated by a distinctive karyotype (66 chromosomes) and electrophoretic data. The subspecies *lewisi* represents a major divergence in the phylogeny of the species.

The earliest name for any member of this wide-ranging group is *Salar lewisi*, used by Girard (1856) for specimens caught in the Missouri River near Great Falls, Montana. *Oncorhynchus clarki lewisi* (Girard) thus is the correct subspecific name.

Montana biologists recognized long ago that the cutthroat trout native to the westward-draining Clark Fork (*lewisi*) differed in appearance from the Yellowstone Lake cutthroat trout (*bouvieri*), and they used the common name westslope cutthroat in referring to Clark Fork fish. However, *lewisi* was mistakenly believed to be the correct classification for the Yellowstone cutthroat, and the westslope form was assumed to be an undescribed species or subspecies.

Hanzel (1959) presented photographs depicting the differences in spotting between Yellowstone and upper Missouri cutthroat trout, but he did not discuss the taxonomic implications of these differences. Zimmerman (1965) demonstrated that the cutthroat trout on both sides of the Continental Divide in the Clark Fork and upper Missouri drainages are identical (this observation was also made by George Suckley in the 1850s), but he did not compare these fish with Yellowstone cutthroat trout. Weisel (1955) considered the Yellowstone and upper Missouri cutthroat trout to be the subspecies *lewisi*, but he classified the westslope form as *Salmo clarki clarki* (coastal cutthroat trout). Brown (1971) applied *Salmo clarki* (without subspecies) to all the native cutthroat trout of Montana, then presented photographs of Yellowstone and westslope cutthroat that clearly showed their distinctly different spotting.

Idaho biologists also recognized differences between cutthroat trout native to the Spokane and Clark Fork drainages (*lewisi*) on one hand, and hatchery cutthroat stocks derived from Henry's Lake or Yellowstone Lake (*bouvieri*) on the other hand. Some of these biologists called *lewisi* the "north Idaho cutthroat."

Despite its wide distribution and long separation from other subspecies of cutthroat trout, the westslope evolutionary line has not given rise to any other subspecies that have survived into modern times. In contrast, the evolutionary line leading to Yellowstone cutthroat trout (whose representatives have 64 chromosomes) has produced 12 subspecies, all by geographical isolation (Behnke 1988c).

The subspecies *alpestris* is considered a synonym of *lewisi* because it is part of a broad but sporadic band of disjunct westslope populations extending from the John Day River drainage into British Columbia. Moreover, the range of *alpestris* in British Columbia was completely covered by glacial ice until about 10,000 years ago. Although it is generally agreed that *alpestris* is a synonym of *lewisi*, some clarification is necessary to correct previous misuses of these names. Qadri (1959) and Carl et al. (1967) considered *alpestris* to be a synonym of *lewisi*, but their classification of *lewisi* followed Schultz (1935, 1941), who included both westslope and Yellowstone cutthroat trout as *lewisi*. Dymond (1932) published a color plate of "Yellowstone cutthroat trout, *Salmo clarkii lewisi* (Girard)," which was reprinted in Carl et al. (1967). The specimen depicted represents the

cutthroat trout native to the Kootenay and Flathead drainages of British Columbia and is a typical westslope fish (*lewisi*). Dymond (1931, 1932) noted that the Kamloops rainbow trout (which he recognized as a full species, *Salmo kamloops*) is the common trout in the upper Columbia drainage of British Columbia, and that cutthroat trout occur only as a few relict populations, typically above falls that isolate them from contact with rainbow trout. He found the same form of cutthroat trout in a few Fraser basin sites; presumably the fish reached there by headwater transfer.

Probably influenced by their distribution pattern, Dymond (1931) lumped all these disjunct populations of *lewisi* together and named them the "mountain cutthroat trout, *Salmo clarkii alpestris*." He provided some taxonomic data for a few specimens from two localities, Isaac Creek and Canyon Creek. The most diagnostic character of *alpestris* is a high number of scales in the lateral series—200–230, according to Dymond (1931, 1932). I counted 195–207 lateral-series scales on four specimens from Isaac Creek, borrowed from the University of British Columbia and the Royal Ontario Museum. I also found high numbers of basibranchial teeth (15–40) and of pored scales in the lateral line (145–150); lateral line scales typically number less than 130 on most rainbow and cutthroat trout. If all populations of *alpestris* exhibit these divergent characters, their common ancestor must have differentiated significantly from *lewisi* before the present distribution was attained. I consider this highly unlikely (where would such a common ancestor have existed in isolation from *lewisi* during the last glacial epoch?), and I regard the Isaac Creek population as a very local divergence of a small, isolated population.

LIFE HISTORY AND ECOLOGY

The westslope cutthroat trout practices one of three lifestyles over its range: it migrates between lakes and streams, it migrates between small tributaries and main rivers, or it remains a nonmigratory resident of tributaries (Liknes and Graham 1988). This subspecies is native to all the large lakes of the upper Columbia basin in Idaho and Montana (Coeur d'Alene, Priest, Pend Oreille, and Flathead lakes). Cutthroat trout from these lakes may migrate upstream 150 km or more to spawning grounds, where spawning occurs from March to July. The young typically spend 2 or 3 years in the stream before migrating to the lake at lengths of 175–225 mm. After 1 to 3 years in the lake, sexual maturation occurs, typically at age 4 or 5 and at lengths of 300–400 mm. An average maximum weight is about 1.5 kg.

Of the migratory river fish that spawn in tributaries, some may remain there during the summer months, but most return to the main river soon after spawning. All members of these populations overwinter in main river channels (Liknes and Graham 1988). Tagged fish have shown annual movements of more than 150 km within a river system (Bjornn and Mallet 1964; Bjornn 1971). This migratory pattern is prevalent among stocks of westslope cutthroat trout native to the Salmon River drainage, where it may help to partition niches with sympatric steelhead.

In contrast to other subspecies of cutthroat trout, the westslope form does

not appear to be highly predaceous on other fish. Roscoe (1974) and Liknes and Graham (1988) summarized the literature on its feeding habits. Most of the food studies involved populations in large lakes with abundant forage fish, yet rarely were fish consumed. Introduced kokanee became abundant in all the large upper Columbia lakes of Idaho and Montana but had a negative effect on westslope cutthroat trout. In Lake Pend Oreille, westslope cutthroat trout drastically declined because of competition with kokanee for zooplankton. In contrast, native piscivorous bull trout attained record weights in Lake Pend Oreille after kokanee was introduced, and the Gerrard race of large Kamloops redband trout from British Columbia's Kootenay Lake (where they feed on native kokanees) attained weights to 17 kg only 5 years after their introduction into Lake Pend Oreille (Behnke 1988b).

I attribute the weak development of piscivory by westslope cutthroat trout to the coevolution of this trout with two fish-eating species, the bull trout and the northern squawfish. By specializing as invertebrate feeders, westslope cutthroat trout have avoided direct feeding competition with these voracious predators. The introduction of nonnative fishes, however, along with environmental alterations, has disrupted the historical harmony of the native trout with its physical and biological environment, causing dramatic declines in the distribution and abundance of westslope cutthroat trout throughout most of its range. Kokanee and lake trout are particularly detrimental to lacustrine stocks of cutthroat trout. The kokanee, with its numerous gill rakers, monopolizes the zooplankton of lakes, and the lake trout is an effective predator on cutthroat trout. Besides kokanee and lake trout, the lake whitefish has become established in several lakes with indigenous westslope cutthroat trout. This whitefish feeds effectively on both zooplankton and benthos. Combinations of nonnative fish species, often in concert with nonnative mysid shrimp, have greatly reduced the abundance of native cutthroat trout in all of the large lakes of Idaho and Montana and in Lake Chelan, Washington.

The northern squawfish has adapted well to unnatural environments such as reservoirs and appears to coexist with nonnative fishes. Consequently, its populations have surged in many areas. An apparent relationship between the increase of northern squawfish and the decline of native cutthroat trout in lower-elevation waters of the Spokane and Clark Fork drainages can be easily misinterpreted. Cutthroat trout abundant in a particular area 100 years ago but gone today do not owe their demise to northern squawfish, which were there for many thousands of years. Instead, changes in flow regimes and water quality due to water development and land use practices, and the establishment of brook trout in small tributaries and of brown trout, rainbow trout, and an assortment of nonnative fishes in main streams, caused the cutthroat trout to disappear.

Throughout much of its range, the westslope cutthroat trout has been replaced by the brook trout in small headwater streams. In streams where both species coexist, the cutthroat trout predominates in higher-gradient reaches with higher water velocities (Griffith 1988).

As is true of cutthroat trout in general, the westslope subspecies is vulnerable to exploitation by anglers. Conversely, a population can rapidly

respond to protective angling regulations with a dramatic increase in abundance and survival of older, larger fish, as documented by Bjornn and Johnson (1978). Angling pressures of no more than 30 to 40 hours per hectare per year are apt to overexploit cutthroat trout in a stream, but populations respond markedly to relief from such angling intensities.

The intraspecific diversity of westslope cutthroat trout can be exploited for management purposes, as discussed by Trojnar and Behnke (1974). In 1971–1972, while Trojnar was a graduate student, we studied the interactions of the finespotted Snake River cutthroat trout and a partially hybridized stock of greenback cutthroat trout in a small Colorado lake. The two avoided direct competition by partitioning the food supply. The implication was that well-differentiated stocks of a species tend to specialize when living together, thereby using the food supply more efficiently and producing more total biomass than could one stock alone. In 1972, George Holton of the Montana Department of Fish, Wildlife, and Parks arranged to duplicate the Colorado study by stocking five Montana lakes with westslope and Yellowstone cutthroat trout. Preliminary observations (the study could not be followed for long) indicated no obvious difference in growth or survival of the two subspecies in the lakes, but they fed on different groups of invertebrates, and the angler catch at any one time was predominantly one subspecies or the other. From this we can presume that westslope and Yellowstone cutthroat trout, when stocked together in waters where natural reproduction does not occur, will produce more fish, more biomass, and a higher catch rate than either could alone, and that the interaction between the two will result in a more consistent fishery in mountain lakes stocked with trout. Such introductions of nonnative species or subspecies should not be made in watersheds where pure westslope populations exist or in lakes where natural reproduction occurs.

STATUS

From 1966 to 1973, the U.S. Department of the Interior issued an annual redbook of endangered species. In the early volumes the Montana westslope cutthroat trout, "*Salmo* sp.," was listed as an endangered species, but that was changed to "status undetermined" in later editions because of taxonomic confusion. It should now be clear that the Montana westslope cutthroat trout is *Oncorhynchus clarki lewisi*, and that the range of the subspecies is much greater than the Clark Fork drainage of Montana.

Liknes and Graham (1988) stated that pure populations of westslope cutthroat trout presently occur in 2.5% of the subspecies' historical range in Montana. This figure is based on stream length. Because most of the streams where pure westslope populations occur are small headwaters, the spatial reduction in distribution is far greater than the 2.5% figure indicates.

Although the westslope cutthroat trout has vanished from most of its once-vast range, certain areas exist where essentially pure native westslope populations are relatively common. Such populations have been exposed to hybridization, but they show little or no outward sign of hybridization; that is, phenotypically they are westslope forms. Their living areas include tributaries to

the Salmon and Clearwater drainages, the upper St. Joe River of Idaho, and much of the Flathead River drainage above Flathead Lake, Montana. The areas where westslope cutthroat trout are still the dominant trout, however, make up only a small fraction of the subspecies' original distribution.

Subtle but significant ecological differences in westslope populations can be noted in relation to their sympatric occurrence with redband or rainbow trout. In the John Day, Salmon, and Clearwater drainages, the westslope cutthroat trout has been coevolving with redband trout for thousands of years and has obviously developed ecological distinctions that favor reproductive isolation between the two species. Above the falls on the Kootenay, Pend Oreille, Clark Fork, and Spokane–St. Joe drainages, and in the upper Missouri and South Saskatchewan drainages, redband trout is not native, and hybridization has occurred almost universally after rainbow trout became established. I know of only two places where native westslope cutthroat trout and introduced rainbow trout occur sympatrically with little or no hybridization: in a small area of the Flathead River above Flathead Lake, where westslope cutthroat trout is the dominant trout (Liknes and Graham 1988); and in Sixteen Mile Creek, a Missouri River tributary north of Bozeman, Montana, where I caught numerous brown trout, rainbow trout, and native cutthroat trout in 1983. These rare exceptions should be studied for the insights they might give into the subtle environmental differences that allow westslope cutthroat trout to persist with nonnative trout.

Cutthroat trout from Yellowstone Lake (*bouvieri*) were widely stocked throughout the range of westslope cutthroat trout. In Glacier National Park, when both subspecies were introduced into previously barren lakes, hybrid swarms developed; but in lakes with native westslope populations, introduced Yellowstone cutthroat trout did not survive and hybridization did not occur (Marnell et al. 1987; Marnell 1988). Evidently, thousands of years of prior residence endowed the native westslope populations with selective advantages over the nonnative subspecies. The lakes of Glacier Park and Yellowstone Lake differ in several selective factors—including their fish communities (especially the predaceous bull trout, present in Glacier Park but not in Yellowstone Lake), forage organisms, cestode parasites, and morphometries—that could give one subspecies an advantage over the other in its home waters. Glacier Park remains the major stronghold of pure westslope populations, and Yellowstone Park serves a similar function for Yellowstone cutthroat trout. The largest lake in Glacier Park, Lake McDonald, however, now holds only a remnant population of westslope cutthroat trout; the dominant fish are nonnative kokanee, lake whitefish, and lake trout (Marnell 1988).

In Idaho the most widely stocked cutthroat trout is the Yellowstone cutthroat trout of Henry's Lake, which is slightly hybridized with rainbow trout. Many millions of Henry's Lake cutthroat and rainbow trout have been stocked throughout the range of westslope cutthroat trout for decades. Now, very few Idaho westslope populations have not been exposed to hybridization.

The Montana Department of Fish, Wildlife, and Parks has established a relatively large propagation and stocking program for westslope cutthroat trout. The original hatchery brood stock was taken from a tributary to Hungry Horse Reservoir (before Hungry Horse Dam was constructed, this area of the South

Fork Flathead River was used by westslope spawning runs from Flathead Lake). During the first 15 years, genetic bottlenecks occurred and the hatchery brood stock lost much of its original heterozygosity (Allendorf and Phelps 1980). Since then, more attention has been given to the genetics of brood-stock management in Montana, and periodic infusions of wild gametes are made to maintain heterozygosity and reduce the dangers of domestication (Allendorf and Leary 1988).

Beginning in 1903 when eggs were first taken from Lake Chelan, the Washington Game Department (now the Washington Department of Wildlife) propagated and stocked pure westslope cutthroat trout without knowing the subspecific identity of its "Cascade" or "intermontane" cutthroat trout. Until relatively recently, no one was aware that the westslope cutthroat trout is native to Washington and Oregon. For example, Wydoski and Whitney (1979) regarded the coastal cutthroat trout as the only cutthroat subspecies native to Washington, and they described westslope cutthroat trout as an introduced subspecies.

During the past 50 years most of the stocking of lakes in the Cascade Mountains has been from westslope brood stocks of Twin Lakes and Kings Lake. The Kings Lake fish represent pure westslope stock from Priest Lake, Idaho (Crawford 1979). The Twin Lakes fish were most probably derived from the native westslope cutthroat trout of Lake Chelan, but documentation of the original introduction into Twin Lakes is lacking. I have examined samples of both the Twin Lakes and Kings Lake fish and found them to be excellent representatives of pure westslope cutthroat trout.

Washington also, for many years, propagated and stocked a hybrid westslope cutthroat × rainbow trout from Dumphkey Lake, a tributary to Lake Chelan originally barren of fish. Crawford (1979) stated that the trout of Dumphkey Lake (which he spelled "Dumpka" Lake) were of Lake Chelan origin. Cranford (1912) recalled that while he was superintendent of hatcheries, he stocked Dumphkey lake with young steelhead in 1904 and with Lake Chelan cutthroat trout in 1906. When Cranford visited Dumphkey Lake in 1911, he found that the cutthroat and rainbow trout had hybridized to produce a "splendid trout." Cranford was so impressed with the hybrid that he instituted an egg-taking operation at Dumphkey Lake so that "many streams in the State will be stocked with the best and gamiest trout in the world" (Cranford 1912).

Yellowstone Cutthroat Trout *Oncorhynchus clarki bouvieri*

TYPICAL CHARACTERS

Spots medium-large, pronounced, rounded in outline. Distribution of spots on body somewhat similar to that of westslope subspecies, concentrated on caudal peduncle, except Yellowstone Lake fish have spots more evenly distributed over sides of body. Coloration yellowish brown, silvery, or brassy. Bright golden-yellow, orange, or red colors absent. Rose tints may appear on body of mature fish. Vertebrae 60–63, typically 61–62. Scales in the lateral series 150–200, typically 165–180. Pyloric caeca 25–50, typically 35–43. Gill rakers 17–23, typically 19–20 (but higher in Yellowstone Lake fish).

DESCRIPTION (Figure 5, page 74)

The cutthroat trout native to Yellowstone Lake was stocked by the millions from about 1905 to 1955 in many waters outside the subspecies' range, and it may be encountered as a nonnative cutthroat trout in states throughout the West. The Yellowstone Lake stock is the most widely known form of the subspecies, but it differs from other populations in having spots more or less evenly distributed over the sides of the body (sometimes onto the ventral region), more gill rakers (18–23; mean, 21), well-developed rakers on the posterior side of the first gill arch, and more basibranchial teeth (mean, 22). Some of these distinctive traits evidently reflect natural selection in lakes. They were used by Marnell et al. (1987) in a meristic index by which Yellowstone cutthroat trout of Yellowstone Lake origin and westslope cutthroat trout native to Glacier Park could be accurately identified and hybridization between the two subspecies could be assessed. I emphasize that this meristic index is specific to Yellowstone Lake trout. It will not effectively distinguish westslope cutthroat trout from most non-Yellowstone Lake populations of *bouvieri*. The meristic characters of stream populations of Yellowstone cutthroat trout native to the upper Snake and Yellowstone river drainages differ only slightly from typical values for westslope cutthroat trout.

The sharp divergence sometimes expressed by a local isolated population of a subspecies is seen in the cutthroat trout of Sedge Creek in Yellowstone National Park. Sedge Creek is a tributary to Yellowstone Lake but separated from it by geothermal activity that has created Turbid Lake, a barrier to fish passage. The isolation of Sedge Creek trout from Yellowstone Lake trout is not of great geological age, because no fish could have inhabited the Yellowstone Plateau until glacial ice receded approximately 8,000 years ago. Sedge Creek cutthroat trout have only a few spots on the caudal peduncle and closely resemble the type specimen of Yellowstone cutthroat trout from Waha Lake,

Idaho. In nine specimens from Sedge Creek, I counted 52–63 (mean, 58) pyloric caeca, which, except for some Lahontan cutthroat trout, are the highest caecal counts recorded for pure cutthroat trout (Sedge Creek has never been stocked, according to park records). Bulkley (1963) also found marked differences in spotting, coloration, and basibranchial tooth numbers between Sedge Creek and Yellowstone Lake cutthroat trout. Loudenslager and Kitchin (1979), however, could not find a single difference between the two populations in electrophoretic patterns representing 22 gene loci. Apparently, very slight genetic differentiation has resulted in conspicuous differences in spotting pattern and in the number of pyloric caeca in the small Sedge Creek population. This situation recalls the isolated discrepant population of westslope cutthroat trout in Isaac Creek, discussed earlier.

DISTRIBUTION

Yellowstone cutthroat trout had a much greater distribution before redband trout invaded the middle Columbia River basin in the late-glacial period. After it was replaced by redband trout in the Snake River system, the subspecies was limited to the Snake River above Shoshone Falls, to the Yellowstone River drainage downstream to the Tongue River, and to two (now extinct) isolated populations in Waha Lake, Idaho, and Crab Creek, Washington (Figure 6, page 78).

The type locality for *bouvieri* is Waha Lake, an isolated lake near Lewiston, Idaho, close to the Washington border. Formerly, Waha Lake was linked with the lower Snake River by the Clearwater River drainage. Cutthroat trout most likely reached Crab Creek via a headwater transfer from the Palouse River drainage (the last major tributary to the Snake River before its confluence with Columbia River). From this it can be assumed that Yellowstone cutthroat trout was the original native trout of the entire Snake River system; it was replaced, however, by redband trout below Shoshone Falls in the Snake and by westslope cutthroat trout in the Salmon and Clearwater drainages.

Above Shoshone Falls the Yellowstone cutthroat trout is native to all the Snake River system except for waters between Jackson Lake and Palisades Reservoir, where the finespotted Snake River cutthroat trout exists. Before Palisades Reservoir was constructed, the native trout of the main Snake River from Palisades to Shoshone Falls could have been the finespotted subspecies, the Yellowstone subspecies, or both. The evidence is confusing on this question. All the tributaries to the Snake River between Palisades and Shoshone Falls (Henry's Fork, Portneuf, Raft, and Goose rivers) have Yellowstone cutthroat trout as the native trout.

Yellowstone cutthroat trout exist today in Pacific Creek, which joins the Snake River just below Jackson Lake. The subspecies undoubtedly invaded the Yellowstone drainage from Pacific Creek, crossing to Atlantic Creek of the Yellowstone system via Two Ocean Pass, an access route that is still open. The customary description of Two Ocean Pass, based on Evermann's 1893 observations as recounted by Jordan and Evermann (1896) and many other authors, is in error. Along the Continental Divide, North Two Ocean Creek precisely splits

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into branches that become Pacific Creek, a Snake River tributary, and Atlantic Creek, a Yellowstone tributary. There are no barriers between the Snake River and Yellowstone Lake via this route. When visiting the area in 1967, however, I concluded from age and size distributions and taxonomic examination of specimens that Yellowstone Lake cutthroat trout run up to the head of Atlantic Creek for spawning but do not enter Two Ocean Creek or Pacific Creek. The trout of Two Ocean and Pacific creeks are nonmigratory stream fish. Reproductive isolation between resident Pacific Creek fish and migratory Yellowstone Lake fish (spawners and juveniles) in Atlantic Creek is indicated by differences in posterior gill raker development on the first gill arch. Pacific Creek specimens have only a few, weakly developed posterior rakers, typical of resident stream populations.

On the south side of Two Ocean Pass, South Two Ocean Creek flows through a complex network of beaver ponds while the main flow goes into Atlantic Creek. Evermann believed the transcontinental passage route was via South Two Ocean Creek, which could only occur during high flows. Evidently, in following Pacific Creek to its headwaters, he was led astray by a dead-end, spring-fed branch and did not see the connection between Pacific and Atlantic creeks via North Two Ocean Creek.

After the ice on the Yellowstone Plateau melted about 8,000 years ago, cutthroat trout became established in Yellowstone Lake. Since then they have established several subpopulations that remain reproductively isolated by homing on natal tributaries to reproduce. In the Yellowstone drainage, Yellowstone cutthroat trout spread down the Yellowstone River (and up all the tributaries encountered) as far as the Tongue River. The Powder River, the next downstream tributary, was barren of native trout when reached by the first collectors, so it appears that this subspecies did not disperse in the Missouri basin beyond the confines of the Yellowstone drainage.

TAXONOMIC NOTES

There is no doubt that Yellowstone cutthroat and westslope cutthroat trout represent highly differentiated subspecies. Because the name *lewisi* is fixed for the upper Missouri basin cutthroat trout, which is identical to westslope cutthroat trout, another name must be assigned to the Yellowstone form. The earliest name applied to cutthroat trout characterized by large, rounded spots in either the Snake River or Yellowstone basins was *Salmo purpuratus bouvieri*, used by Bendire (1882) for the cutthroat trout native to Waha Lake, Idaho.

In Bendire's original description of *bouvieri* he stated that: "... in some instances, the whole belly is red." I have never observed bright red on Yellowstone cutthroat trout, so perhaps "shades of pink" might be a more accurate description. The color of live cutthroat trout native to Waha Lake cannot be confirmed because the population is extinct. The spotting pattern of westslope cutthroat trout—small, irregularly shaped spots—is highly consistent throughout the subspecies' range. The large, round spots on Waha Lake cutthroat trout align it with the Yellowstone cutthroat evolutionary line, despite

the red belly mentioned by Bendire. (However, spotting patterns are not a wholly reliable guide to identification, as I discuss shortly.)

Jordan and Evermann (1902) published an illustration of "*Salmo bouvieri*" of Waha Lake showing a cutthroat trout with a few large round spots, mainly on the caudal peduncle. They gave a lateral-series scale count of 173. I examined one museum specimen of *bouvieri* from Waha Lake in the collection of the California Academy of Sciences and counted 157 scales in the lateral series. This specimen has 17 gill rakers, 61 vertebrae, and a spotting pattern conforming to the illustration in Jordan and Evermann. It is my judgment that the California Academy's collection number 28359 contains five additional specimens of *bouvieri* from Waha Lake. These were part of a larger collection, number 735, sent from Indiana University (no date). Collection 735 was originally shipped from Walla Walla, Washington, but the records list no name or date. In the introduction to Bendire's 1882 paper, D. S. Jordan wrote that "the U.S. National Museum has recently received from Captain Bendire a very fine series of fishes from the neighborhood of Fort Walla Walla." It appears Jordan brought Bendire's Walla Walla collection (at least collection 735) to Indiana and later to California, where it is now part of the California Academy of Sciences' ichthyology collection. Besides the more inclusive collection numbers, each trout specimen has an individually numbered tag. The specimens numbered 3559, 3560, 3563, 3564, and 3565 of collection 28359 are Yellowstone cutthroat trout with medium-size rounded spots sparsely distributed and concentrated on the caudal peduncle (specimen 3566 is a redband trout). Specimen 3562 is the one labeled as "*S. mykiss*, Waha Lake." It appears that the five cutthroat trout specimens of unknown locality are topotypes (specimens of *bouvieri* collected at the type locality) from Waha Lake. Specimen 3561 may have been retained at the National Museum as the holotype of *bouvieri*.

I have provided these details because *bouvieri* is extinct in Waha Lake, and the only museum specimens designated from Waha Lake of which I am aware are the holotype and specimen 3562 in the California Academy's collection. The meristic characters I recorded from the five California Academy specimens are vertebrae, 61–63 (mean, 62); gill rakers, 19–21 (20); scales above the lateral line, 45–52 (48); scales in the lateral series, 160–181 (168); pyloric caeca, 26–35 (31); basibranchial teeth, 5–12 (7). Perhaps the DNA of museum specimens will be analyzed one day for its conformance with the DNA of Yellowstone cutthroat trout.

The cutthroat trout of Crab Creek, Washington, named *Salmo eremogenes* by Evermann and Nichols (1909), appears to be identical to *bouvieri* and I consider *eremogenes* a synonym for *bouvieri*. Crab Creek, an isolated stream of the eastern Washington scablands, is part of the Moses Lake basin, an isolated drainage within the Columbia basin. Apparently, Crab Creek cutthroat trout persisted as a relict population protected from contact with the later-invading redband trout. As with the Waha Lake trout, the Crab Creek trout population is extinct and very few specimens exist in museums—only three more than 100 mm long. The lower Crab Creek drainage lies in the path of flood waters from glacial Lake Missoula, which suggests that westslope cutthroat trout would have been its native trout. The large, rounded spots on *eremogenes* specimens, however,

clearly align Crab Creek cutthroat trout with the Yellowstone subspecies. The most plausible route for a Yellowstone ancestor into the Crab Creek drainage was observed during an exploratory survey I made with Richard Wallace (University of Idaho) in April 1989. About 10 km southwest of the Spokane airport and southward, we noted areas where the headwaters of Crab Creek and the Palouse River drainage are separated by an almost imperceptible divide. No native trout has been documented for the Palouse River drainage; however, given the relict population of Crab Creek cutthroat trout, it is logical to suppose that the Yellowstone form was also the native trout of the adjoining Palouse drainage. A barrier falls occurs on the Palouse River a short distance upstream from its confluence with the Snake River. Apparently, redband trout were not native above the falls and did not naturally eliminate Yellowstone cutthroat trout from the Palouse drainage, as occurred in all other Snake River tributaries below Shoshone Falls. Stocking of rainbow trout (plus brown trout and brook trout) during the past 100 years, however, seems to have accomplished the same end result. Although native cutthroat trout are unknown in the Palouse drainage, it is hoped that some still persist and will be discovered to test my hypotheses about their identity and the origin of the Crab Creek cutthroat trout.

Although patterns of body spots often can be used to distinguish Yellowstone from westslope and other cutthroat trout subspecies, their reliability is undermined by a major, unresolved problem: the size, shape, and distribution of spots on trout (of any species) can markedly change with very slight overall genetic change in a population. For example, Skaala and Jorstad (1987, 1988) studied a brown trout population with unusual spotting patterns in a Norwegian lake. One form had a spotting pattern that was normal for the species. A second form exhibited fine spots similar to those of the finespotted Snake River cutthroat trout. A third form had spotting intermediate between the normal and fine spotting patterns. Breeding experiments revealed that this striking variation in spotting is controlled by two codominant alleles at one gene locus.

Ambiguities associated with spotting patterns hinder the interpretation of cutthroat trout identities. The finespotted Snake River cutthroat trout is electrophoretically indistinguishable from Yellowstone cutthroat trout, but its spots more closely resemble those of westslope cutthroat trout in size and shape. The McBride Lake cutthroat trout, propagated and stocked in Montana (McMullin and Dotson 1988), is a pure Yellowstone cutthroat trout but has a spotting pattern somewhat intermediate between those of a typical Yellowstone and a typical westslope cutthroat trout. The true genotype of McBride Lake cutthroat trout is apparent in the coloration of adult fish. Large specimens I have examined from lakes express the typical dull yellowish, brassy appearance of Yellowstone cutthroat trout rather than the bright coloration of the westslope subspecies.

Throughout its vast range, the westslope cutthroat trout has a spotting pattern that is very consistent in comparison with the variation found in other subspecies. I have never observed large, roundish, sparse spots in a westslope population. The possibility must be recognized, however, that the native cutthroat trout of Waha Lake, on which the name *bouvieri* is based, could have been westslope cutthroat trout with a highly aberrant spotting pattern.

Unless DNA analysis can be done on museum specimens of Waha Lake cutthroat trout, the strongest evidence that the Yellowstone cutthroat trout was the original trout in the Salmon and Clearwater drainages and the native trout of Waha Lake will come from discoveries of relict populations in isolated sections of the Salmon, Clearwater, or Palouse drainages. Initial field distinctions between Yellowstone and westslope cutthroat trout can be based on spotting pattern and coloration, and later confirmed by electrophoresis. Electrophoresis, however, cannot distinguish native from introduced populations of Yellowstone cutthroat trout, and meristic comparisons will be necessary for that purpose. I assume that all Yellowstone cutthroat trout stocked in the Salmon, Clearwater, and Palouse drainages of Idaho came from Yellowstone Lake or Henry's Lake. Both these stocks differ from other populations of the subspecies in having more numerous and relatively well-developed posterior rakers on the first gill arch and more numerous basibranchial teeth (mean, about 20).

In the summer of 1990, U.S. Forest Service workers made two collections of cutthroat trout from the Little Salmon River drainage, Idaho, that looked different from westslope cutthroat trout native to the Salmon River watershed. The specimens were sent to Richard Wallace for examination. Wallace kindly sent me copies of his data and notes on these specimens.

Five specimens from Clayburn Creek have 19–21 (mean, 20) gill rakers, 10–11 posterior gill rakers, and 7–37 (18) basibranchial teeth. The specimens have large, round spots distributed all over the body, typical of cutthroat trout from Yellowstone and Henry's lakes. Wallace and I agree that the Clayburn Creek specimens are introduced Yellowstone cutthroat trout. A sample of nine fish from Trail Creek represents a native population. This sample has 15–18 (16) gill rakers, 0–2 (0.3) posterior gill rakers, and 3–23 (10) basibranchial teeth. Also, the number of pyloric caeca, 30–37 (33), is less than expected in Yellowstone Lake or Henry's Lake fish (40–42). The positive identification of the Trail Creek cutthroat trout as Yellowstone or westslope cutthroat must await electrophoretic analysis. The spots are indistinct, of moderate size, and concentrated on the posterior part of the body. Based on examination of the preserved specimens and with no information on life colors, Wallace could not rule out the possibility that the Trail Creek cutthroat trout represents a westslope population with an atypical spotting pattern.

LIFE HISTORY AND ECOLOGY

Most of what is known of the life history of Yellowstone cutthroat trout is based on the populations of Yellowstone Lake (Cope 1956, 1957a, 1957b, 1957c; Bulkley 1961). Because Yellowstone Lake fish have been widely propagated and stocked, the role of cutthroat trout in fisheries management is largely based on the performance of this stock of the Yellowstone subspecies. This focus has produced misconceptions about the ecological variability found in the species as a whole. For thousands of years, cutthroat trout evolved in Yellowstone Lake with only one other fish—the longnose dace (which is rare). Such narrow evolutionary programming with respect to other fish species, combined with the highly stable and oligotrophic environment of Yellowstone Lake, makes the

Yellowstone Lake cutthroat trout ill-adapted to successfully coexist with other fish species or to thrive in the unstable environments where it has been introduced.

The comparative unsuitability of Yellowstone Lake fish became evident in a Montana trout stocking program that now uses McBride Lake *bouvieri*. McBride Lake is a 9.3-hectare body of water in the northeastern section of Yellowstone Park, and its native cutthroat trout have been subjected to far different selective pressures from those of Yellowstone Lake. The McBride Lake fish showed significant increases in growth, survival, and natural reproduction when stocked in lakes and reservoirs that formerly received cutthroat trout derived from Yellowstone Lake (McMullin and Dotson 1988).

The longnose sucker, introduced in 1923, and the redside shiner, first recorded in 1957, now are both abundant in Yellowstone Lake. The redside shiner is mainly restricted to littoral areas, but the longnose sucker has spread through most of the lake (Gresswell and Varley 1988). When these two species become established in lakes and reservoirs elsewhere, they are generally regarded as threats to salmonids because they compete for food. In Yellowstone Lake, however, they have had no detectable effect on cutthroat trout (Gresswell and Varley 1988). I do not attribute this to the innate competitive ability of the native cutthroat trout so much as to the unique environment of Yellowstone Lake—its depth, morphometry, temperature, and invertebrate forage organisms—to which the native cutthroat trout has become supremely adapted. The environment favors the cutthroat trout niche to such an extent that its volume has not been reduced by overlap with the sucker and shiner niches.

Yellowstone cutthroat trout, in general, appears to feed more on fish than does westslope cutthroat trout. Above Shoshone Falls in the Snake River and in the Yellowstone drainage, bull trout and northern squawfish were historically absent, and cutthroat trout were the only large predators. In Goose Creek, Nevada, the last major tributary to the Snake River above Shoshone Falls, I found that fish remains made up almost 100% of the stomach contents of cutthroat trout over 300 mm.

In the main Snake River, just upstream from Shoshone Falls, cutthroat trout in the 6–7-kg size range have been reported by anglers and Idaho Department of Fish and Game personnel. I once examined two specimens from this area that weighed about 2 kg. My attention was called to them because they were spawning in November, a remarkably early date for reproduction. Spring-spawning trout normally enter the fall–winter period with gonads at an advanced state of maturity, thus they are ready to spawn as soon as water temperatures rise. The two specimens collected on November 19 were taken from a spawning redd in a spring-fed tributary with a constant 9°C temperature. Evidently, the movement from the colder Snake River into the warmer waters of the tributary provoked the November spawning. These large trout above Shoshone Falls are cutthroat × rainbow hybrids (based on my specimens), but the cutthroat phenotype predominates. The large fish were silvery, which obscured the spotting pattern to such an extent that I could not decide if the original cutthroat ancestor was the Yellowstone or the finespotted subspecies.

Other reports of Yellowstone cutthroat trout reaching 5 to 10 kg or more in the Rocky Mountain region may be based on hybrids. Yellowstone Lake cutthroat trout were stocked into Strawberry Reservoir, Utah, soon after its creation, and a 12.3-kg "cutthroat" is recorded from this reservoir (Platts 1957). Varley and Gresswell (1988) stated that a 14.6-kg Yellowstone trout was "reported" caught from Strawberry Reservoir in 1948, but Leo Lentsch (Utah Division of Wildlife Resources) told me that there is no evidence of such a large trout from that reservoir. The Strawberry Reservoir cutthroat trout that I examined in 1972 was a hybrid between Yellowstone Lake cutthroat trout and rainbow trout, but the Yellowstone ancestry predominated. The largest well-documented hybrid is a Yellowstone cutthroat × rainbow trout of 13.8 kg caught by an angler in Ashley Lake, near Kalispell, Montana (*Kalispell Weekly News*, May 19, 1982). Information sent to me by Fred Allendorf (University of Montana, July 20, 1982) revealed that electrophoretic analysis of this record specimen showed 50% rainbow trout alleles and 50% Yellowstone cutthroat trout alleles at eight gene loci. Further analysis of 44 specimens of Ashley Lake hybrid trout by Allendorf indicated 55% rainbow trout alleles, 40% Yellowstone cutthroat trout alleles, and 5% westslope cutthroat trout alleles (the westslope cutthroat trout is the only trout native to the Flathead River drainage in the Kalispell area).

The maximum age of Yellowstone cutthroat trout is variable and greatly influenced by environmental factors, but not notably different from the maxima of other subspecies. In Yellowstone Lake the general maximum age is about 7, but fish of 8 and 9 years of age occasionally have appeared in spawning runs since protective regulations greatly reduced mortality from angling (Gresswell and Varley 1988). Another result of reduced angling mortality has been an increase in the average age of spawners. In a Yellowstone Lake tributary, Clear Creek, the average age of spawners increased from 3.9 years in 1966 to 5.6 years in 1983, mainly because the number of repeat spawners increased (Gresswell and Varley 1988). (It is noteworthy that overexploitation occurred in Yellowstone Lake during the 1960s with an annual angling pressure of less than 15 angler-hours per hectare: Varley and Gresswell 1988.) In South Gap Lake, Wyoming, I examined introduced Yellowstone Lake cutthroat trout of ages 10 and 11. South Gap Lake is in the Snowy Range at an elevation of about 3,400 m, where it probably has about 90 ice-free days per year. In this frigid regime, metabolism and growth processes are slowed and life span is extended. At ages 10 and 11, these trout were only 280–325 mm long.

The cutthroat trout of South Gap Lake were also remarkable for the average number of their basibranchial teeth: 33, versus 22 for the source Yellowstone Lake stock. This increase may have been due to a founder effect or to the longer time required to reach lengths of 60–100 mm, when the definitive number of teeth is attained. This is the only example, among many comparisons, of a significant difference between basibranchial teeth counts of parental and introduced populations.

As discussed, redband trout completely replaced Yellowstone cutthroat trout wherever they came in contact below Shoshone Falls. Like westslope cutthroat trout, the Yellowstone subspecies did not coevolve with rainbow or redband trout, and sympatric populations of native Yellowstone fish and introduced rainbow trout are extremely rare. One noteworthy exception occurs

EX5004-000060-TRB

in the 200-km reach of the Yellowstone River below Yellowstone Falls. This large-river environment provides niche diversity which, in theory, should promote the coexistence of cutthroat and rainbow trout, yet the major factor allowing sympatry is reproductive isolation based on differences in time of spawning (Clancy 1988 and personal communications). Spawning by native cutthroat trout peaks in June in many tributaries. Rainbow trout, however, spawn only in late winter, and only in spring-fed creeks with warmer temperatures than elsewhere. In small tributaries to the Yellowstone River with resident trout populations, I have found hybrid swarms derived from the two species.

STATUS

Compared with most other cutthroat subspecies, Yellowstone cutthroat trout could be said to be doing well, particularly if comparisons were made in relation to past and present total abundance rather than to total distribution and preservation of diversity within the subspecies. This relative success is mainly due to the numbers of native cutthroat trout in Yellowstone Lake and in the entire Yellowstone River drainage above the falls in Yellowstone Park. Recent population estimates of adult trout (longer than 350 mm) in 35,400-hectare Yellowstone Lake ranged from 1 million to 4 million (Varley and Gresswell 1988), representing a total biomass of roughly 1,000,000–2,000,000 kg.

Of the other large lakes (larger than 1,000 hectares) in which Yellowstone cutthroat trout was native, Henry's Lake retains a dominant and abundant population of these fish (slightly hybridized); the Yellowstone form has, however, been replaced by rainbow trout downstream in the Henry's Fork River. Whether the native trout of Jackson Lake on the Snake River was the Yellowstone or the finespotted subspecies is unknown. Cutthroat trout drastically declined in Jackson Lake after lake trout became established.

In tributaries to the Yellowstone River downstream from Yellowstone Park, Yellowstone cutthroat trout have been largely replaced by brook, brown, and rainbow trout and by hybrid rainbow × cutthroat trout populations. In the upper Snake River drainage, the subspecies persists in Heart Lake and other waters above Jackson Lake, but how it and finespotted cutthroat trout were historically distributed in various sections of the upper Snake drainage is unknown. The persistence of a thriving population of large Yellowstone cutthroat trout in Heart Lake is noteworthy because lake trout have long been established there.

Between Shoshone Falls and Palisades Reservoir, the Yellowstone cutthroat trout persists in some Snake River tributaries but has been replaced in others. For example, rainbow trout is now the dominant trout in the Henry's Fork, but the native cutthroat trout is dominant in the Teton Fork, its major tributary. Where the Yellowstone subspecies persists in the Snake drainage of Idaho, special angling regulations have been effective in increasing the abundance and proportion of older fish (5–7 years old) in populations (Thurow et al. 1988).

Before egg-taking operations ceased at Yellowstone Lake, 818 million eggs of the native cutthroat trout were taken between 1899 and 1957, peaking at 43.5 million in 1940 (Gresswell and Varley 1988). Presently, hatchery propagation of Yellowstone cutthroat trout is carried out in Idaho (Henry's Lake stock), Wyoming (South Paintrock Creek stock), and Montana (McBride Lake stock). The Wyoming Game and Fish Department introduced Sedge Creek trout into barren sections of the Thoroughfare River, a headwater tributary to the Yellowstone River, to extend the range of this unique race of Yellowstone cutthroat trout.

In 1985 a population of illegally introduced brook trout was found in Arnica Creek, a tributary to Yellowstone Lake. Chemical treatment in 1985 and 1986 apparently eliminated these brook trout, which were the only nonnative salmonid fish occurring in the Yellowstone drainage above the falls (Gresswell and Varley 1988).

EX5004-000061-TRB

Finespotted Snake River Cutthroat Trout *Oncorhynchus clarki* subsp.

TYPICAL CHARACTERS

The most diagnostic trait of the undescribed finespotted Snake River cutthroat trout is its unique spotting. This subspecies has the smallest spots of any trout native to western North America. The spots are profuse and resemble a heavy sprinkling of ground pepper on the sides of the fish. Its other characters are similar to those of Yellowstone cutthroat trout, except for a tendency toward more yellowish colors and orange or red lower fins.

DESCRIPTION (Figure 5, page 74)

When I first compared samples of the Yellowstone cutthroat trout from headwaters of the Snake River (Heart Lake) with samples of finespotted cutthroat trout from more isolated localities, I found significant differences in some characters. However, as I analyzed more samples from throughout the ranges of the finespotted and Yellowstone cutthroat trout in the upper Snake River drainage, all clear-cut distinctions between the two subspecies broke down except for the consistent difference in spotting.

Heavy stocking of rainbow trout and Yellowstone cutthroat trout has occurred within the range of the finespotted cutthroat trout. In more recent times, finespotted cutthroat trout propagated in large numbers at the Jackson (Wyoming) National Fish Hatchery and at Wyoming Game and Fish Department hatcheries have been stocked into the range of Yellowstone cutthroat trout in the upper Snake drainage. Thus, it can be assumed that some hybridization has occurred and some of the variability in taxonomic characters may be secondary.

Despite introductions of rainbow trout and forced mixing between the two cutthroat subspecies, the two forms of native cutthroat trout remain phenotypically distinct and are still the dominant trout in most of their native ranges above Palisades Reservoir in the Snake River drainage. In six samples of finespotted cutthroat trout, Murphy (1974) found lateral-series scale counts ranging from 136 to 188 with mean values of 153–176. Pyloric caeca numbered from 32 to 51 and averaged 39–46. Vertebrae numbered from 60 to 65 with means of 61–63. Basibranchial teeth ranged from 4 to 30 and averaged 12–18. This high degree of variation may indicate some hybrid influence in the stocks sampled. Differences among samples and observations on size- and age-groups from different localities clearly show that the finespotted Snake River cutthroat trout is not a homogeneous entity. Instead, it consists of many reproductively isolated stocks living in a continuous environment.

The basic coloration of the finespotted cutthroat trout, like that of the

Yellowstone cutthroat trout, is predominantly yellowish brown, sometimes with purple and silvery tones. Faint rose tints may appear on mature fish, and the lower fins typically are orange or red. The distribution of spots on the body is similar to that of interior cutthroat trout generally, with the greatest concentration on the caudal peduncle and above the lateral line anterior to the dorsal fin.

DISTRIBUTION

The distribution of the finespotted Snake River cutthroat trout is most unusual in overlapping that of another cutthroat subspecies, the Yellowstone. All other extant cutthroat subspecies are geographically isolated from each other (the extinct yellowfin trout, however, occurred sympatrically with greenback cutthroat trout in Twin Lakes, Colorado).

The present known distribution of the finespotted cutthroat trout extends in the Snake River drainage from below Jackson Lake downstream to Palisades Reservoir, encompassing all tributaries from the Gros Ventre River to the Salt River. Below Jackson Lake, the first three tributaries—Pacific Creek, Buffalo Fork, and Spread Creek—contain Yellowstone cutthroat trout as the native trout. Populations of both subspecies occur in the Gros Ventre, the Yellowstone form in headwater tributaries and the finespotted form in the rest of the drainage. I have not encountered an area where the two forms exist together in the same habitat. Somehow they are able to partition the upper Snake River drainage and avoid hybridization.

Before a dam was constructed to raise the level of Jackson Lake, fish could move freely between the lake and the Snake River below it. Whether the Yellowstone cutthroat trout, the finespotted cutthroat trout, or both were native to Jackson Lake is unknown. The Yellowstone cutthroat trout appears to be the common trout above the lake. Large numbers of finespotted cutthroat trout of hatchery origin have been stocked into Jackson Lake and the Snake River above it, confounding the original distribution patterns of the two subspecies.

The original downstream distribution of the finespotted subspecies has been obscured by the dam that created Palisades Reservoir. From below the reservoir downstream to Shoshone Falls, the Yellowstone cutthroat trout is the native trout in all tributaries from which I have examined specimens.

How this intermingled distribution of two distinct forms of closely related cutthroat trout originated and how the subspecies have persisted without hybridizing into a single intermediate form despite forced mixing are two of the most fascinating unanswered questions of cutthroat trout systematics and biology.

TAXONOMIC NOTES

A biological species is usually defined by its ability to maintain reproductive isolation when it occurs together with a closely related form. The recognition of distinct but closely related forms as species or subspecies is generally based on the degree of reproductive isolation between them. If two geographically isolated forms are capable of hybridization, it is assumed that they would

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hybridize if they occurred together and they are recognized as subspecies of one species. If two forms maintain their distinctions when sympatric, as do the finespotted and Yellowstone cutthroat trout in certain areas of the Snake River drainage, usually they are recognized as separate species.

I do not believe reproductive isolation is complete between Yellowstone and finespotted cutthroat trout. The transition and overlap in taxonomic characters and the occasional specimen with intermediate spotting indicate that occasional hybridization and limited gene flow do occur. The electrophoretic study of Loudenslager and Kitchin (1979) showed no differences between several samples of finespotted Snake River cutthroat trout and large-spotted cutthroat trout from the Snake and Yellowstone drainages. Overall genetic similarity of proteins from 23 gene loci ranged from 0.995 to 1.0. Further electrophoretic analysis by Leary et al. (1987) and by Allendorf and Leary (1988) confirmed that the finespotted cutthroat trout and the Yellowstone cutthroat trout are identical at the many gene loci surveyed. However, the finespotted Snake River cutthroat trout does indeed represent an evolutionary and ecological reality. Because of this, it should be regarded as a distinct subspecies. Probably it was derived from the Yellowstone cutthroat trout evolutionary line in recent geological times. I have previously discussed the problem of recognizing species solely on the basis of reproductive isolation (Behnke 1972b, 1989a).

When I first became familiar with the finespotted cutthroat trout, its spotting led me to consider as its direct ancestor a coastal cutthroat trout that had penetrated the upper Snake River before Shoshone Falls was formed but after the Yellowstone form was established there. The chromosomes of the finespotted cutthroat trout proved to be identical to those of Yellowstone cutthroat trout, however, and that theory of origin was discarded (Behnke 1970). I also considered that the direct ancestor may have been westslope cutthroat trout that accompanied a stream transfer from the upper Salmon River across the present Snake River Lava Plateau but dismissed that explanation after genetic data demonstrated the extremely close relationship between the finespotted and Yellowstone cutthroat trout. The finespotted cutthroat trout probably originated from the Yellowstone cutthroat trout during the last glaciation in the upper Snake River area.

J. D. Love, of the U.S. Geological Survey and the University of Wyoming, is an authority on the geological history of the upper Snake River and Yellowstone area. As he explained to me, ancestral cutthroat trout had several opportunities during the late Pleistocene epoch to fractionate in isolated, glacially dammed lakes and landslide lakes of the upper Snake basin. Evidently, after thousands of years of separation, the ancestral Yellowstone cutthroat trout and the new form, both slightly differentiated during isolation, came together again; but instead of freely hybridizing, they spatially partitioned the upper Snake River environment and maintained their distinctions through reproductive isolation. Once the two lines were in contact, evolutionary mechanisms governed by natural selection probably emphasized their spotting differences.

Why was such a distinctive trout not described by early ichthyologists? Apparently because its restricted distribution caused the finespotted form to be overlooked. Jordan, Evermann, and Gilbert collected fish in the upper Snake

River drainage between 1889 and 1895. Jordan came down the Snake River from its headwaters at Heart Lake to President Camp above Jackson Lake. Evermann came over the Continental Divide and down Pacific Creek. In these localities, only the Yellowstone cutthroat trout collected by Jordan and Evermann are native. Evermann and Gilbert collected farther downstream at Portneuf and Henry's Fork rivers, which also have only Yellowstone cutthroat. Many years later, Baxter and Simon (1970) presented a photograph of the finespotted Snake River cutthroat trout and mentioned that it had never been formally described but was worthy of recognition.

It is possible that the diagnostic spotting differences between the finespotted and the Yellowstone cutthroat trout are determined by two alleles at one gene locus, as found for brown trout by Skaala and Jorstad (1988).

LIFE HISTORY AND ECOLOGY

Kiefling (1978) comprehensively reviewed the life history and ecology of the finespotted Snake River cutthroat trout. In the Snake River from Jackson Lake to Palisades Reservoir, these trout support a major sport fishery. Formerly, they made up 97–99% of the trout catch of Palisades Reservoir, but an outbreak of nematode parasites of the genus *Philonema* has severely affected the reservoir population in recent years. Data I have seen from a 1975 investigation by the Idaho Department of Fish and Game suggested that cutthroat trout still made up 84% of the reservoir catch. Subsequent to the onset of the epizootic, the unpublished Idaho studies revealed that the brown trout population and its contribution to the catch have increased, primarily because brown trout feed less on the zooplankton crustacean that serves as an intermediate host for the parasite.

The greater vulnerability of cutthroat than of brown trout to angling can be illustrated by comparing the angler catch and the gill-net samples at Palisades Reservoir in 1975. Cutthroat trout made up 84% and brown trout made up 15% of the angler catch; but only 28% of the gillnetted trout were cutthroat trout.

As mentioned, the finespotted cutthroat trout is not a single homogeneous stock in the Snake River drainage but consists instead of discrete populations. These populations follow two basic lifestyles. Migratory fish spend most of their lives in the main Snake River and return to tributaries to spawn. Nonmigratory stocks reside in tributary streams. The population structures and the interactions between discrete stocks are complex and perhaps of a delicate balance easily upset by environmental modifications. Because of the importance of the finespotted Snake River cutthroat trout to Wyoming's fishery program, studies of its ecology have been conducted by the Wyoming Game and Fish Department, leading to reports by Wiley (1969) and Kiefling (1974a, 1974b), and the definitive report by Kiefling (1978).

As discussed by Trojnar and Behnke (1974), the evolutionary programming of the finespotted Snake River cutthroat trout, influenced by sympatry with a variety of fish species in a big-river environment, has resulted in a trout with a wide range of adaptive responses that allow for successful introductions in diverse environments. After the study by Trojnar of this subspecies in a

Colorado lake (Trojnar and Behnke 1974), Sekulich (1974) continued the study of the finespotted cutthroat trout's adaptability to new environments by following its growth and feeding habits in three reservoirs on the Uinta Indian Reservation, Utah. In different environments, the subspecies opportunistically exploits the major available food resources and readily changes from benthic to limnetic to surface feeding. At a size of 300 to 350 mm, it prefers large organisms like fish and crawfish, if available, and its growth rate rapidly increases. I have raised finespotted cutthroat trout in a small pond in Fort Collins, Colorado, where fish supplied with abundant crawfish reached 550 mm and 2 kg in their fourth year.

Hazzard and McDonald (1981) discussed the use of the finespotted Snake River cutthroat trout in Colorado fisheries programs. Mullan (1975) indicated that the subspecies may not be well adapted to life in small streams because he found that fish stocked in small streams on the Uinta Indian Reservation, Utah, were in poor condition.

The finespotted Snake River cutthroat trout is now extensively propagated in hatcheries and widely distributed outside its original range. I believe that as more studies are made on introduced stocks of this trout, along the lines of the research by Trojnar and Behnke (1974) and Sekulich (1974), the stereotype of cutthroat trout held by fisheries managers, which is based on Yellowstone Lake fish, will change. The genetic diversity found within the species, as manifested by ecological and life history specializations, can have significant practical applications in fisheries management.

STATUS

The finespotted Snake River cutthroat is the only subspecies of cutthroat trout more abundant now than it was historically. There has probably been no marked reduction in abundance within its known historical range, and widespread propagation and introduction outside that range have increased its numbers.

The hatchery stock of finespotted cutthroat trout has produced excellent results in a variety of waters, including lakes and reservoirs of different types, sizes, elevations, and associated fish species, as well as the Green River below Flaming Gorge Reservoir. This success in different environments indicates the broad adaptability of the hatchery stock. Such adaptability appears to contradict the implications of a genetic analysis of this stock by Robb Leary (University of Montana), which revealed low heterozygosity. A 1986 report from Leary to the Jackson (Wyoming) National Fish Hatchery analyzed the products of 72 gene loci in the Auburn hatchery stock used by the Wyoming Game and Fish Department and in the Jackson hatchery stock, which was derived from Auburn stock (virtually all nonnative populations of finespotted Snake River cutthroat trout are derived from the Auburn stock). Heterozygosity scores of 0.021 (Jackson hatchery) and 0.025 (Auburn hatchery) were found. The proportion of polymorphic loci was 0.046 (3 of 72 loci were polymorphic in both hatchery stocks). Such extremely low values might be considered indicative of genetic bottlenecks and inbreeding. This should not be surprising, because the Auburn

hatchery stock was derived from relatively few individuals in the 1950s and has been selectively bred for early spawning (December) and other hatchery-preferred traits. In view of the low heterozygosity and unpromising history of the hatchery stock, the success of finespotted cutthroat trout stocked in diverse environments seems anomalous. It would be of interest to infuse wild gametes into this hatchery stock and observe if "adaptiveness" could be further improved.

Probably all finespotted cutthroat stocks have been exposed to hybridization with both Yellowstone cutthroat trout and rainbow trout, but they have resisted the effects of hybridization to an amazing degree. Hybridlike specimens are most common in disturbed habitats such as the unstable environment at the mouth of Spread Creek. For practical purposes, the purity of any stock of finespotted cutthroat trout can be judged by the uniformity of the spotting pattern.

7

CUTTHROAT TROUT OF THE GREAT BASIN

As defined by Hubbs and Miller (1948), the Great Basin of the western United States consists of many separate, internal drainage basins without present connections to the ocean. Figure 7 illustrates those basins known to have native trout. The cutthroat trout native to the Lahontan, Bonneville, Alvord, and Whitehorse basins are derived from the Yellowstone phylogeny (64-chromosome group) but represent distinctly different times of invasion (Behnke 1988c).

Cutthroat trout became established in the Lahontan basin long before the last glacial epoch, perhaps during the mid-Pleistocene Epoch, based on fossil evidence. The modern Lahontan cutthroat trout is the most direct descendant of the early colonization. It now is the most distinctive of the Great Basin cutthroat trout, ranking as one of the four main subspecies of *Oncorhynchus clarki*. It gave rise to four other subspecies in the late Pleistocene: the Alvord and Whitehorse forms in satellite basins north of the Lahontan; and the Humboldt and Paiute forms in subbasins within the Lahontan.

Cutthroat trout are recent immigrants to the Bonneville basin, arriving there from the upper Snake River probably during the last glacial period. Modern Bonneville cutthroat trout are only slightly differentiated from Yellowstone cutthroat trout, and they constitute a minor subspecies.

During the last ice age about 10,000 to 70,000 years ago, and during previous Pleistocene periods of glaciation, large lakes existed in these separate basins. The largest of the ancient lakes was Lake Bonneville, which at maximum level was approximately the size of present-day Lake Michigan. Lake Lahontan attained the size of present-day Lake Erie. Bull trout and northern squawfish did not become established in Great Basin waters, and cutthroat trout were the only large predatory fish among many species of minnows and suckers in the ancient lakes. An evolutionary programming to specialize as a large lake predator is particularly imprinted in the genotype of the Lahontan cutthroat trout.

About 8,000 years ago, the large lakes of the Great Basin shrank to about their present conditions, leaving behind only a few remnant waters such as Pyramid Lake, Nevada, and Great Salt Lake, Utah. Cutthroat trout that had become large lacustrine predators were ill-adapted to life in the small streams to

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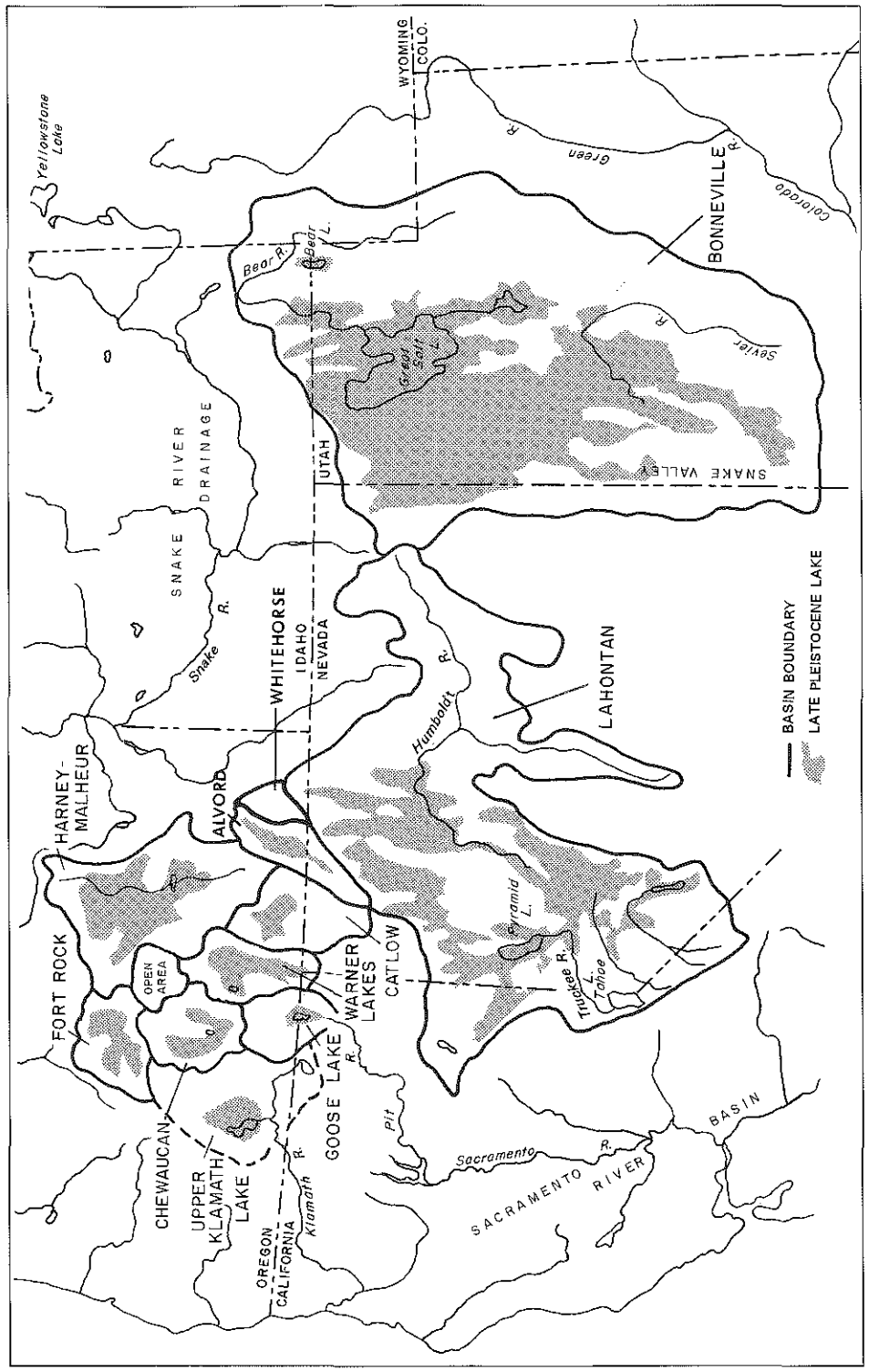


FIGURE 7.—Segments of the Great Basin known to have native trout. Shaded areas indicate the approximate maximum extent of late Pleistocene lakes. Cutthroat trout are native to the Lahontan, Bonneville, Alvord, and Whitehorse basins. Redband trout are native to the other basins.

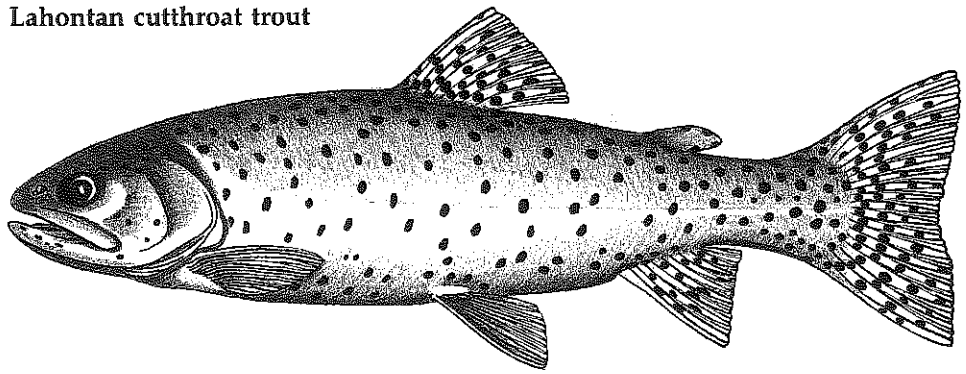
which they became restricted. They were able to persist in remnant populations until recent times, but they have shown themselves poorly suited to competition with nonnative stream trout, and most of their remnants have disappeared since nonnative trout were introduced to the Great Basin.

Unlike most of their lacustrine relatives, the cutthroat trout native to the two largest river systems in the Great Basin—the Humboldt River drainage of the Lahontan basin and the Bear River of the Bonneville basin—have resisted replacement by nonnatives. Evidently, they had specialized to fluvial rather than lacustrine environments, and I believe their ancestors were nonmigratory stream trout, even during the time of the ancient lakes. The semiarid climate of the past several thousand years has imposed unstable temperatures and fluctuating flows on the Humboldt and Bear river drainages. Many of the habitats where native cutthroat trout still flourish in these two drainages would be considered marginal or submarginal trout waters by most standards (Behnke 1981). Under such rigorous conditions, the native trout have been able to hold their own against intruders.

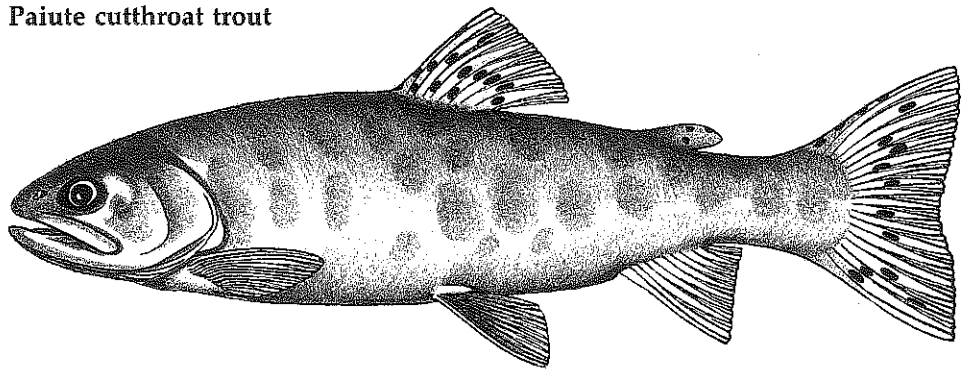
The Lahontan basin cutthroat trout exemplify the need to preserve not merely taxonomic status but genetic diversity. The ecological adaptations of the native trout of the Lahontan basin are diverse, allowing remnant forms to exploit environments ranging from permanent lakes to unstable streams. This diversity points out a serious flaw in arguments, such as those in the General Accounting Office's report to the U.S. Congress (July 2, 1979), that the U.S. Endangered Species Act should be amended to protect only those species that are endangered or threatened throughout all or a significant portion of their ranges. If local populations and subspecies are ignored until a species as a whole becomes endangered or threatened, much of the species' genetic diversity will be lost, never to be recovered.

Figure 8 illustrates the Great Basin subspecies of cutthroat trout, and Figure 9 shows their distributions.

Lahontan cutthroat trout



Paiute cutthroat trout



Humboldt cutthroat trout

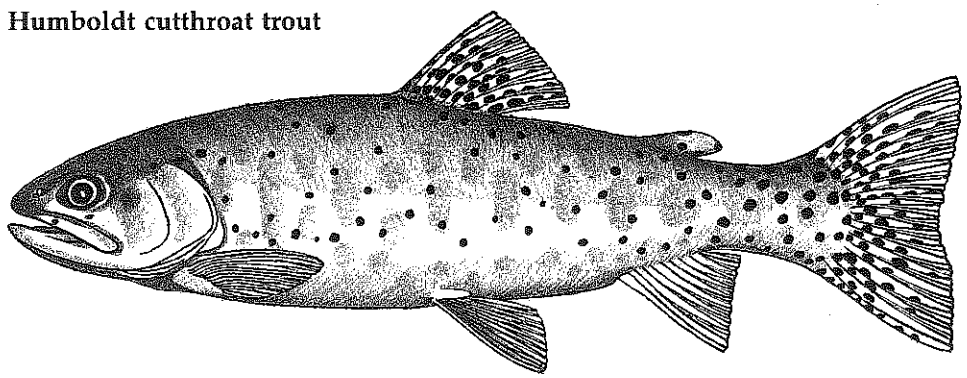
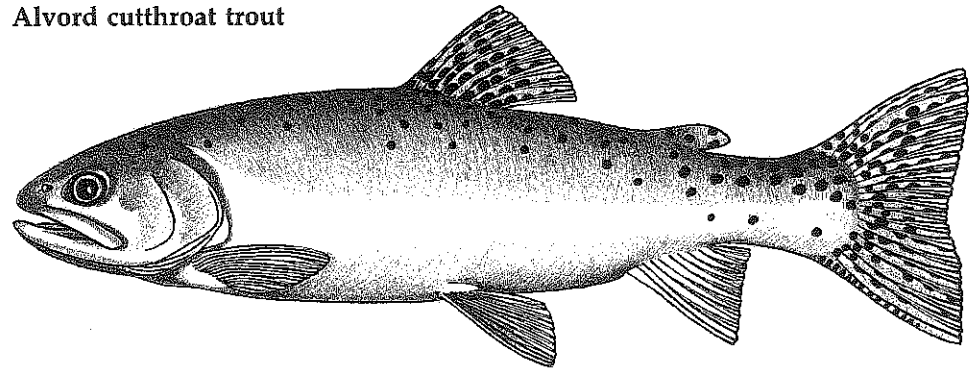
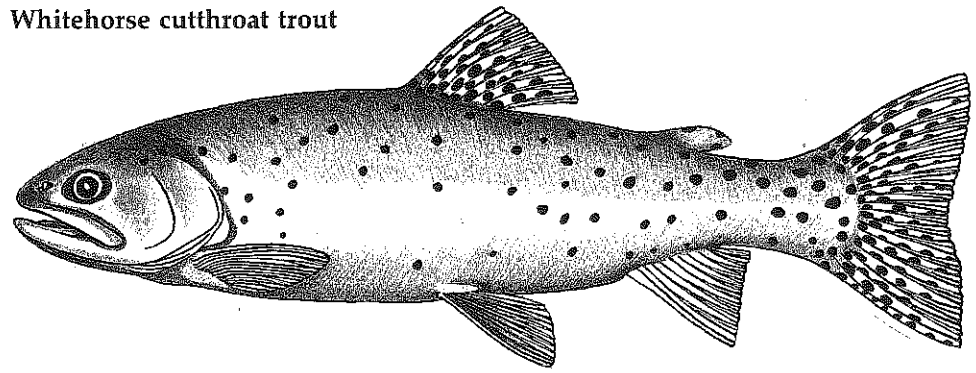


FIGURE 8.—Cutthroat trout of the Great Basin.

Alvord cutthroat trout



Whitehorse cutthroat trout



Bonneville cutthroat trout

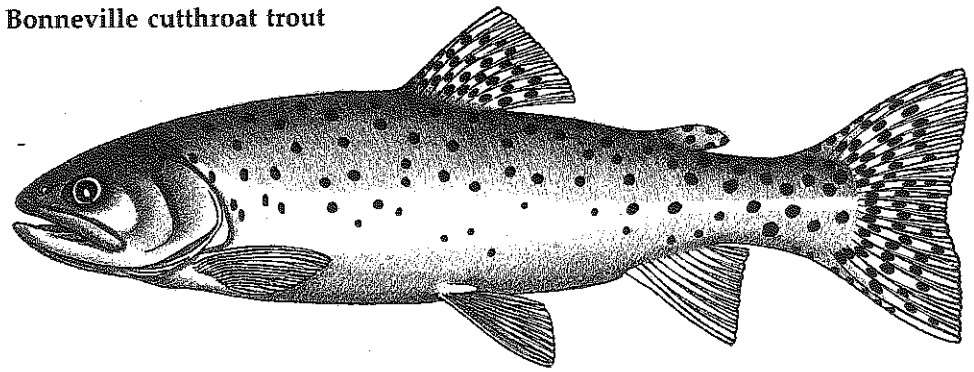


FIGURE 8.—Continued.

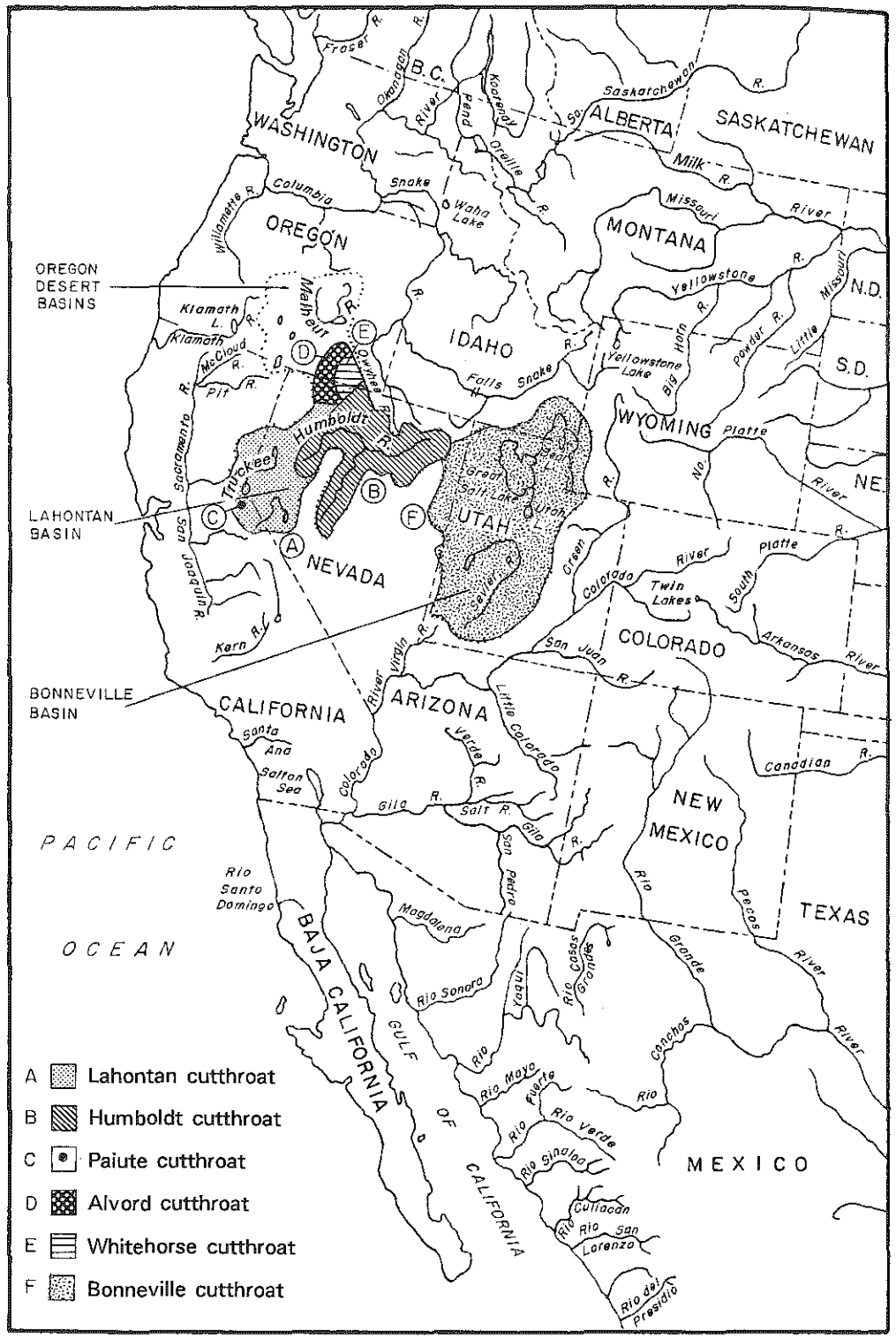


FIGURE 9.—Distributions of Great Basin cutthroat trout.

Lahontan Cutthroat Trout *Oncorhynchus clarki henshawi*

TYPICAL CHARACTERS

A combination of three characters distinguishes Lahontan cutthroat trout from all other subspecies of cutthroat trout: the spotting pattern of medium-size to large, rounded spots more or less evenly distributed over the sides of the body, on top of the head, and often on the abdomen; the most gill rakers of any cutthroat or rainbow trout, 21–28, averaging 23–26; and the abundance of pyloric caeca, 40–75 or more, typically averaging more than 50.

DESCRIPTION (Plate 2; Figure 8, page 108)

The spotting pattern of Lahontan cutthroat trout is most similar to that of coastal cutthroat trout, except that the spots on Lahontan fish are larger, rounded in outline, and less numerous. In lake-living populations, silvery guanine deposits in the skin can transform the spots from medium-size or large and rounded to small and star-shaped. The coloration is generally dull, like that of Yellowstone cutthroat trout, but red colors may appear on the sides and cheeks of Lahontan fish. Snyder (1917) likened the opercula of spawning males from Pyramid Lake to "glowing coals."

The number of pyloric caeca in Lahontan cutthroat trout is generally higher than in any other subspecies. Mean values of 45 or more are rare in populations of other subspecies, but Lahontan cutthroat trout typically have more than 50 (17 specimens from Donner Creek, Utah, averaged 66 caeca). Numerous gill rakers facilitate planktonic feeding in lakes, the habitats in which Lahontan cutthroat trout evolved. The adaptive values of spotting pattern and abundant pyloric caeca are unknown, but within salmonine groups, species and subspecies that are more piscivorous tend to have more pyloric caeca (Behnke 1968). Numbers of vertebrae, typically 60–63, and lateral-series scales, typically 150–180, are similar to those of Yellowstone cutthroat trout. Basibranchial teeth are generally well developed. Specimens from Independence Lake, California, that I examined had more than 100 basibranchial teeth densely packed like bristles on a brush—another example of an isolated population developing a character to extremes.

The Lahontan cutthroat trout shares the Lahontan basin with the Paiute cutthroat trout and the Humboldt cutthroat trout. The Paiute cutthroat trout is differentiated solely by the absence of spots on its body. The Humboldt cutthroat trout differs from the Lahontan subspecies mainly in having fewer gill rakers (average, 21) and fewer scales.

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DISTRIBUTION

The range of Lahontan cutthroat trout when Europeans reached the region was the Lahontan basin exclusive of the Humboldt River system, which had its own cutthroat subspecies (Figure 9, page 110). The Lahontan cutthroat trout was the native trout of the Truckee, Carson, Walker, and Quinn rivers, although as discussed later, the Quinn River cutthroat trout may have been derived from the Humboldt River. The Lahontan subspecies was also native to Lake Tahoe and to Pyramid, Walker, Donner, Independence, and Summit lakes. Summit Lake now lies in a separate basin isolated from the Lahontan basin by a lava flow that diked off a former Lahontan tributary stream. Native Lahontan cutthroat trout are extinct in Tahoe, Pyramid, Walker, and Donner lakes, but they still occur in Independence and Summit lakes, and the Summit Lake trout has been extensively propagated as a source of pure *henshawi*.

TAXONOMIC NOTES

The Lahontan cutthroat trout of Pyramid Lake apparently attained the largest maximum size of all western North American trout. When Frémont's expedition reached Pyramid Lake in January 1843, Indians brought trout to his camp. The long trek across an expanse of barren country may have influenced Frémont's opinion of the Lahontan cutthroat trout, which he referred to as "Salmon-trout" and about which he wrote (Frémont 1845): "Their flavor was excellent—superior, in fact, to that of any fish I have ever known. They were of extraordinary size—about as large as the Columbia River salmon—generally from 2 to 4 feet in length."

By 1870, the large size of Lahontan cutthroat trout had attracted the attention of fish culturists in California, and trout from Independence Lake and the Truckee River were being propagated in private hatcheries and by the California Acclimatization Society. The earliest literature indicated a general belief that two forms or species of Lahontan cutthroat trout occurred in all of the lakes: a brown or black form and a silver form. In 1870, one of the first tasks of the newly created California Fish Commission was to classify the Lahontan cutthroat trout. Specimens of brown and silver trout from Lake Tahoe and the Truckee River were sent to Seth Green, a famous fish culturist, who pronounced them "landlocked salmon," not trout.

The name *Salmo henshawi* was given by Gill and Jordan in 1878 in the second edition of Jordan's textbook "Manual of the Vertebrates," based on a specimen from Lake Tahoe sent by the naturalist H. W. Henshaw. Adhering to the common belief in two species of Lahontan cutthroat trout, Jordan at first used the name *henshawi* to designate the silver trout of Lake Tahoe, and he recognized the black Tahoe trout as *S. tsuppitch* (*tsuppitch* is a synonym of *Oncorhynchus kisutch*, the coho salmon). Later, Jordan and Evermann (1896) designated the black trout as *S. mykiss henshawi* and noted that the silver trout of Lake Tahoe did not deserve separate taxonomic recognition. Shortly thereafter, however, they named the silver trout *S. clarki tahoensis* (Jordan and Evermann 1898). Snyder (1917) described two distinct spawning runs of cutthroat trout from Pyramid Lake up the Truckee River, but he believed only one species was involved.

Whether or not the black and silver trout represented two forms of Lahontan cutthroat trout native to Lake Tahoe and Pyramid Lake has never been adequately answered. Ancient Lake Lahontan underwent several long-term fluctuations in water level (Benson and Thompson 1987), which could have provided opportunities for isolation and incipient speciation; the subspecies in the Humboldt River drainage probably originated in this way. Based on my examination of specimens, I conclude that only a single subspecies, *henshawi*, should be recognized. The type specimen of *tahoensis* does not differ in any way from *henshawi* (Jordan's gill raker count of 18 for *tahoensis* is in error; there are actually 25 gill rakers on the first left gill arch in the type specimen). I could find no real indication of more than one form of cutthroat trout in the many collections I examined from the Truckee (including Lake Tahoe and Pyramid Lake specimens), Carson, and Walker river drainages. The belief that there were two species of native trout in Lake Tahoe was most likely based on intrapopulation differences in size and age between first spawners and repeat spawners, and on apparent differences between sexually mature and immature fish. Until 1931, California Department of Fish and Game hatcheries separately propagated *henshawi* and "*tahoensis*."

As previously mentioned, the *Salmo evermanni* described from headwaters of the Santa Ana River, California, was based on *henshawi* introduced from Lake Tahoe. Snyder (1914, 1917) described three additional species of trout from the Lahontan basin: *S. regalis*, the royal silver trout of Lake Tahoe; *S. smaragdus*, the emerald trout of Pyramid Lake; and *S. aquilarum*, the Eagle Lake trout. I have published my opinion elsewhere that *S. smaragdus* is based on an introduced rainbow trout and that *S. regalis* is based on hatchery-produced cutthroat × rainbow hybrids (Behnke 1972b). The Eagle Lake trout, however, is of considerable interest. Eagle Lake is isolated from the Lahontan basin but once was a tributary to it, and the native fish fauna are all Lahontan species except for the trout, which belongs to the rainbow–redband evolutionary lineage. The most logical explanation of this distribution is that the original trout of Eagle Lake was Lahontan cutthroat trout, which disappeared during a dry cycle that eliminated spawning tributaries. Later, headwater transfer brought a form of redband or rainbow trout to Eagle Lake from the Pit River drainage.

LIFE HISTORY AND ECOLOGY

Behnke and Zarn (1976) and Gerstung (1988) summarized the pertinent literature on Lahontan cutthroat trout life history. The subspecies is an opportunistic feeder whose life history characteristics are greatly influenced by the environment. For example, the population (slightly hybridized with rainbow trout) in Blue Lakes, California, was the parental stock for the Heenan Lake population, yet the two show clear-cut differences in condition, growth, age at maturity, and feeding. These differences demonstrate what can happen when the same genotype is exposed to different environments (Calhoun 1944a, 1944b). They also underscore the need for caution in attempts to assign a genetic basis to subtle ecological differences.

During the postglacial desiccation of Lake Lahontan, Pyramid Lake retained

the largest array of the basin's fish fauna. The stock of Lahontan cutthroat trout indigenous to Pyramid Lake thus had the longest history of coevolution with fish prey, and I believe it possessed more of the genetic attributes necessary to achieve large size than any other stock of the subspecies. Summit Lake, a recent source of Lahontan cutthroat trout for Pyramid Lake, has no native fish other than *henshawi*. The Heenan Lake stock of the subspecies, commonly propagated in hatcheries and also added to Pyramid Lake, first was isolated from the Carson River and therefore is adapted to rivers, not to lakes.

The original Pyramid Lake population of Lahontan cutthroat trout disappeared in the 1940s after it lost its access to Truckee River spawning grounds. In their last spawning run from Pyramid Lake in 1938, Lahontan cutthroat trout averaged 9 kg (Sumner 1940). The world record sport-caught cutthroat trout from Pyramid Lake weighed 18.6 kg, but when I first visited the Paiute Indian Reservation at Pyramid Lake in 1958, it was a common belief among the older tribal members that trout larger than 18 kg had been caught regularly in the tribal fishery. Also, Wheeler (1969) cited the testimony of Fred Crosby, who acted as an agent for the tribal fishery, that a 28-kg trout was caught in 1913.

During the past 20 years, millions of Lahontan cutthroat trout from Summit and Heenan lakes have been stocked in Pyramid Lake, but few trout of more than 9 kg have been produced. Larger Summit Lake fish become piscivorous in Pyramid Lake, and the abundance of fish prey in the lake, particularly of tui chub, may be greater today than it was previously because predation pressure from trout and white pelicans *Pelecanus erythrorhynchos* is lower now. Nevertheless, Summit Lake cutthroat trout rarely exceed a weight of 6–7 kg and an age of 7 years in Pyramid Lake (Sigler et al. 1983), whereas the native race probably reached ages of 10–11 years (Behnke 1986a). The introduced stocks lack the genetic potential for growth characteristic of the endemic race.

To successfully use the genetic diversity in remnant *henshawi* stocks to create a large lake predator, managers should seek fish with delayed maturation. In lakes with abundant food, fish spawning for the first time at age 5 or 6 will attain a greater maximum age and reach a much greater maximum size than fish first spawning at 2 or 3.

A small sample of the original Pyramid Lake genotype apparently still exists, available for use, in Donner Creek on Pilot Peak along the Utah–Nevada border. The Donner Creek population of Lahontan cutthroat trout was introduced (Pilot Peak is in the Bonneville basin) sometime before 1952—probably around the turn of the century, according to local testimony. Until the 1950s the only Lahontan cutthroat trout stocked in Nevada came from Pyramid Lake (Hickman and Behnke 1979). Discovered by workers with the Utah Division of Wildlife Resources and the U.S. Bureau of Land Management in 1977, the present Donner Creek population does not carry the complete evolutionary heritage of the Pyramid Lake race. The original stocking must have involved relatively few fish, and the selection factors in tiny Donner Creek are very different from those of Pyramid Lake. The Donner Creek population is maintained by the Utah Department of Wildlife Resources, but state and federal agencies have exhibited little interest to date in exploiting this genetic resource (Behnke 1989b).

Information on the cutthroat trout stocked in Pyramid Lake in recent times was presented by Sigler et al. (1983) and by Coleman and Johnson (1988). The high alkalinity tolerance of Lahontan cutthroat trout, which allows it to thrive in saline and alkaline lakes inhospitable to other trout, has long been recognized as a subspecies attribute of practical value to fisheries management. Galat et al. (1985) investigated the histological changes in organs of Lahontan cutthroat trout in lakes of differing salinity and alkalinity and speculated on the physiological adaptations that give this fish its unusual tolerance.

STATUS

The Lahontan cutthroat trout was formerly listed as an endangered species under the 1973 Endangered Species Act. Its status was changed to threatened in 1975 to legalize angling and facilitate management. The original Pyramid Lake population became extinct in the lake as a result of the first U.S. Bureau of Reclamation project. The Newlands Irrigation Project, begun in 1905, diverted water at Derby Dam on the Truckee River 48 km above Pyramid Lake. Until about 1920, sufficient water passed over Derby Dam to support natural reproduction in the river below. As more and more water was diverted, reproduction diminished, and the last spawning run occurred in 1938; no native trout appeared in the river thereafter. The native trout of Lake Tahoe became extinct around 1940 after most of the suitable spawning tributaries were dewatered or dammed and lake trout had become a dominant species. The Walker Lake stock has been maintained in a hatchery since 1948, when flows in the Walker River were so reduced from irrigation diversions that natural reproduction became impossible.

The Lahontan cutthroat trout still exists in Independence Lake, despite a long history of introductions of nonnative salmonids. In recent years the California Department of Fish and Game has propagated the Independence Lake cutthroat trout, and a new brood stock is now established in Heenan Lake (Gerstung 1988). The Summit Lake cutthroat trout was in peril from the effects of overgrazing on Bureau of Land Management lands in the watershed. The only spawning tributary carried a heavy sediment load that created a delta at the mouth, and a bulldozer was required to open the stream to spawning (Behnke and Zarn 1976). Subsequently, fencing and grazing controls were imposed and the situation dramatically improved (Dahlem 1979; Coffin 1988).

Gerstung (1988) and Coffin (1988) listed all known populations of *henshawi*, both native and introduced, in California and Nevada.

Paiute Cutthroat Trout *Oncorhynchus clarki seleniris*

TYPICAL CHARACTERS

The only trait distinguishing Paiute from Lahontan cutthroat trout is the absence of spots on the body. All other characters are typical of the Lahontan subspecies.

DESCRIPTION (Plate 3; Figure 8, page 108)

The Paiute cutthroat trout was derived in relatively recent geological times from Lahontan cutthroat trout after a population was isolated in Silver King Creek, a tributary to the East Carson River, Alpine County, California. The Paiute subspecies can be described as a Lahontan cutthroat trout without spots, but even the lack of spotting is not an absolute character. Up to nine faint spots were found on the type specimens of Paiute cutthroat trout used by Snyder (1933b) for the description of *Salmo seleniris* (Ryan and Nicola 1976). I have observed specimens of the remnant *henshawi* population isolated in the uppermost headwaters of the East Carson River that have virtually no spots on the body. Such specimens would be classified as *seleniris* if found in Silver King Creek.

All the meristic characters of Paiute cutthroat trout are typical of Lahontan fish: lateral-series scales, 150–180; vertebrae, 60–63; pyloric caeca, 50–70; gill rakers, 21–27 (mean, 24). The assumption that Paiute cutthroat trout is more closely related to Lahontan cutthroat trout of the Carson River drainage than to Lahontan populations in other drainages is supported by the electrophoretic studies of Busack (1978) and Busack and Gall (1981); furthermore, according to electrophoretic data, Paiute cutthroat trout of the Silver King drainage were less similar to an introduced Paiute population in Cottonwood Creek, southern California, than to the Lahontan population of the East Carson drainage.

In terms of genetic relatedness, Paiute cutthroat trout is one of the minor subspecies derived from Lahontan cutthroat trout (Behnke 1988c), but it is the only species or subspecies of western trout that consistently has no obvious spots on the body.

DISTRIBUTION

The distribution of the Paiute cutthroat trout is unique in that the subspecies is not native to its type locality above Llewellyn Falls in Silver King Creek (Figure 9, page 110), but was introduced there in 1912 by sheepherders (Behnke and Zarn 1976; Ryan and Nicola 1976; Busack 1978). When Snyder (1933b) described *seleniris*, he believed it was native only to the headwaters isolated by Llewellyn

Falls. Virgil Connell, a stockman who pastured sheep in the Silver King watershed, later provided the information that no fish existed above Llewellyn Falls until transplanted from below the barrier in 1912. This transplant was fortunate, because by 1933 the trout below Llewellyn Falls represented a rainbow × cutthroat hybrid swarm (Behnke 1960).

Two isolated tributaries to lower Silver King Creek, Coyote Valley and Corral Valley creeks, also had Paiute cutthroat trout (Vestal 1947). These streams may have been stocked from lower Silver King Creek as early as the 1860s by loggers. In 1946, Paiute cutthroat trout collected mainly from Corral Valley and Coyote Valley creeks were transported and stocked in the North Fork of Cottonwood Creek, Mono County, California (Vestal 1947). A few transplants from Cottonwood Creek also have been made.

In 1949, rainbow trout were inadvertently stocked in Silver King Creek above Llewellyn Falls, and a hybrid swarm had developed there when I examined specimens in 1964. The cutthroat trout in Corral Valley and Coyote Valley creeks were also hybridized by 1964. Two small headwater tributaries to upper Silver King Creek—Four Mile Canyon and Fly Valley creeks—still had unhybridized Paiute cutthroat trout, which were used to restock Silver King Creek after it was treated with rotenone to kill off the hybrids in 1964. Some hybrids survived the treatment, and the effects of hybridization (indicated by spots on the body) gradually spread through the population again. The rotenone treatment was repeated in 1976 but was again ineffective (Behnke 1987b).

TAXONOMIC NOTES

Snyder (1933b) described the Paiute cutthroat trout as a full species, *Salmo seleniris*. As already discussed, however, the genetic relationship between *seleniris* and *henshawi* is very close. The subspecies category historically has been used to identify a geographically isolated group of organisms rather than to reflect a degree of evolutionary divergence. The name *seleniris* has been widely used in the literature and has been entered into the *Federal Register* to designate the Paiute trout first as endangered and then as threatened. It has been incorporated into the management plans of the California Department of Fish and Game and the U.S. Forest Service. Undoubtedly, the Paiute cutthroat trout has benefited from being recognized as a subspecies rather than as a mere race of Lahontan cutthroat trout.

LIFE HISTORY AND ECOLOGY

Behnke and Zarn (1976) and Behnke (1987b) reviewed ecological aspects of the Paiute cutthroat trout, and Diana and Lane (1978) studied the subspecies' movement and distribution in Cottonwood Creek. Like their Lahontan cutthroat trout ancestors, Paiute cutthroat trout are vulnerable to replacement by or hybridization with nonnative trout, and they must be maintained in isolation if they are to be preserved.

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STATUS

In 1975, the classification of Paiute cutthroat trout under the 1973 Endangered Species Act was changed from endangered to threatened, in part to permit management plans that called for rotenone treatment. The hybrid population in Silver King Creek had reappeared after the 1964 rotenone treatment, and for several years electrofishing was used in an effort to remove all fish with more than five spots on the body. This proved ineffective, so the stream was again treated with rotenone in 1976, but hybrids again reappeared. A monitoring program continues on Silver King Creek and on the North Fork of Cottonwood Creek. A few small populations have been established in eastern California in Cabin, Stairway, and Sharktooth creeks (Behnke 1987b).

Because the native range of Paiute cutthroat trout was always small (the smallest of any currently recognized subspecies of cutthroat trout), it would not take much in the way of introductions in new waters to increase its relative abundance. On the other hand, with so few viable populations, it would not take much in the way of inadvertent or illegal introductions of nonnative trout to cause its extinction.

Humboldt Cutthroat Trout *Oncorhynchus clarki* subsp.

TYPICAL CHARACTERS

Similar to Lahontan cutthroat trout except for fewer gill rakers: 18–24 (mean, 21) versus 21–28 (24); also, the Humboldt cutthroat trout tends to have fewer scales in the lateral series and above the lateral line.

DESCRIPTION (Figure 8, page 108)

The subspecies in the Humboldt River drainage has not been formally named. I became aware of a group of native trout differentiated from Lahontan cutthroat trout when I examined museum specimens collected by J. O. Snyder in the Lahontan basin from 1911 to 1915. Cutthroat trout native to the Truckee, Walker, and Carson drainages consistently differed from those of the fourth major drainage, the Humboldt River, in the number of gill rakers.

Ancient Lake Lahontan reached its maximum level about 13,000 years ago and then commenced to shrink (Benson and Thompson 1987). The Walker River drainage was the first to be isolated from the rest of the basin, about 12,000 years ago according to the lake level chronology of Benson and Thompson (1987). It was followed by the Truckee, Quinn, and Carson–Humboldt drainages, in that order, as the lake level dropped from about 1,330 m to about 1,180 m between about 13,000 and 10,000 years ago. During years of high precipitation in modern times, the Carson and Humboldt drainages still maintain an ephemeral connection via their overlapping sinks. Thus, the differentiation of Humboldt cutthroat from other Lahontan cutthroat trout cannot be attributed to recent isolation of the Humboldt drainage; instead, its origin must go back to an earlier period.

Previously, I compiled gill raker counts of all Lahontan basin cutthroat trout examined to 1964. In comparing 161 specimens of the Lahontan subspecies with 137 specimens of Humboldt trout from 20 localities, I found that Lahontan cutthroat trout has 21–28 gill rakers with a mean of 24, and that the Humboldt cutthroat trout has 18–24 gill rakers with a mean of 21. More extensive collections of both subspecies since 1964 have confirmed this separation.

In a more quantitative study, Hickman (1978) used a discriminant function analysis of 16 characters to quantify the differences between Bonneville cutthroat trout and several other subspecies. He included 35 specimens of Lahontan and 32 specimens of Humboldt cutthroat trout. The analysis separated Lahontan specimens from Humboldt fish with 100% accuracy.

Besides the difference in gill raker numbers, the Humboldt cutthroat trout tends to have fewer scales in the lateral series and above the lateral line than Lahontan cutthroat trout. Most mean values for lateral-series scale counts range between 140 and 150 in Humboldt samples. Trout from Gance Creek in the

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North Fork Humboldt drainage are particularly coarse-scaled. On 17 specimens, I counted 117–140 (mean, 126) scales in the lateral series. Large numbers of nonnative trout were stocked in the Humboldt drainage, and all populations of Humboldt trout probably have been exposed to hybridization, first with Lahontan cutthroat trout (stocked in large numbers until the 1920s) and later with Yellowstone Lake cutthroat trout and rainbow trout. Unlike most other regions where native subspecies of interior cutthroat trout have been replaced or thoroughly hybridized with nonnative trout, the Humboldt cutthroat trout has resisted hybridization with and replacement by nonnative trout to an amazing degree (Behnke 1981). Basibranchial teeth are usually the first character to reflect hybridization with rainbow trout. Among interior cutthroat trout in general, the more obvious effects of hybridization (changes in spotting and coloration) are not apparent until about 50% or more of the population lacks basibranchial teeth. Of 121 specimens of Humboldt cutthroat trout more than 100 mm long that I collected from several localities, basibranchial teeth were present in 115, or 95%.

Pyloric caeca number from 40 to 70 and average 50–60, which is similar to values for Lahontan cutthroat trout. Six specimens from Hanks Creek, a tributary to the Marys River (eastern headwaters of Humboldt drainage), have the highest number of caeca: 55–69 (mean, 65). Vertebrae number 60–63, which is also similar to counts for the Lahontan subspecies.

There are subtle but not clear-cut differences in spotting patterns and coloration between Humboldt and Lahontan cutthroat trout. Spots typically are fewer on Humboldt trout and more concentrated posteriorly on the body. Only rarely are spots found on the abdomen. The coloration generally is dull, typically with brassy, copper, or burnished silver colors predominating. Light yellow with some pink tints may appear on the side of the body. The ventral region is white or gray, and the lower fins are brownish but may develop faint pink tints. Smith (1984) published two color photographs of Humboldt cutthroat trout.

Based on allele frequencies as determined by electrophoresis, the Humboldt cutthroat trout is very similar to Lahontan cutthroat trout (Loudenslager and Gall 1980). Williams and Shiozawa (1989), however, showed that mitochondrial DNA differed distinctly between the two subspecies (only two Humboldt specimens were analyzed, however). An April 1990 report by R. N. Williams, "Genetic analysis and taxonomic status of cutthroat trout from Willow Creek and Whitehorse Creek in southeastern Oregon," submitted to the Portland, Oregon, office of the U.S. Fish and Wildlife Service, verified the unique mitochondrial DNA of Humboldt cutthroat. This report also includes data from electrophoretic analysis of enzymes representing 72 gene loci. To date, mitochondrial DNA and meristic characters have distinguished Humboldt from Lahontan cutthroat trout better than enzyme profiles.

DISTRIBUTION

The Humboldt cutthroat trout once was native throughout the Humboldt River drainage of eastern Nevada (Figure 9, page 110), but it is now restricted to numerous small streams. The current known distribution was given by Coffin

(1983, 1988). The independent, isolated basins immediately south of the Humboldt drainage lacked trout, and early settlers stocked many barren streams in the Toiyabe Mountains with Humboldt cutthroat trout from the Reese River (Hubbs and Miller 1948). Coffin (1983) listed two streams in the Smoky Valley basin that contain Humboldt cutthroat trout, evidently the result of early introductions.

The nature of cutthroat trout in the Quinn River, an isolated stream in northern Nevada, is ambiguous. Data from small samples of Quinn drainage cutthroat trout, supplied to me by Patrick Coffin (Nevada Department of Wildlife) and Dennis Shiozawa (Brigham Young University), have 20–21 gill rakers (modal counts), typical of Humboldt cutthroat trout. However, Williams's 1990 report to the U.S. Fish and Wildlife Service, mentioned above, indicated that the mitochondrial DNA of two samples of Quinn drainage cutthroat trout is typical of the Lahontan, not the Humboldt subspecies. Recent geological research at the University of Nevada, conveyed to me by Coffin (personal communication, December 19, 1990), indicates that the Humboldt River once flowed to the Quinn River before changing course to its present terminus in the Humboldt sink. If, as I suspect, cutthroat trout in the Quinn and Humboldt drainages share a common origin, the unique mitochondrial DNA of the Humboldt fish must have developed after the two drainages separated.

LIFE HISTORY AND ECOLOGY

An evolutionary history of survival in the watersheds of the Humboldt drainage, where the native trout has been subjected for several thousand years to an unstable environment characterized by flood–drought cycles, has produced an adaptable genotype well suited to environmental extremes. This evolutionary heritage appears to be the most logical explanation of the Humboldt cutthroat trout's resistance to replacement by and hybridization with nonnative trout. Brook, brown, and rainbow trout are mainly established in the "best" trout streams in the Ruby Mountains, where watersheds are well vegetated and streamflows are relatively stable year-round. In contrast, the Humboldt cutthroat trout dominates streams in the poorer watersheds, where flows are highly unstable.

I have caught Humboldt cutthroat trout in late summer from small streams that had no flowing water, only shrinking pools separated by long reaches of dry streambed; yet debris from spring floods had caught in tree branches 2 m above the dry bed. Humboldt cutthroat trout thrive in Frazer and Sherman creeks where summer temperatures of 26°C have been recorded. Whether Humboldt cutthroat trout have evolved temperature adaptations different from those of Lahontan cutthroat trout is not known. Vigg and Koch (1980) measured a maximum upper lethal limit of only 23°C for Lahontan cutthroat trout, but the tested fish were held without food up to 381 hours (16 days) at constant temperatures before they perished, which may have affected the results.

During high-runoff years, Humboldt cutthroat trout from headwater tributaries often enter two irrigation reservoirs in the drainage: Willow Creek Reservoir between Tuscarora and Midas, and Jiggs Reservoir south of Elko.

These reservoirs are turbid, eutrophic bodies of water seemingly unsuited for cutthroat trout. The Humboldt subspecies nevertheless attains weights of 2–3 kg in these unlikely environments. In contrast, brook and rainbow trout stocked in Willow Creek Reservoir had low survival rates, and the few that survived for 1 year lost weight (W. Nisbet and P. Coffin, Nevada Department of Wildlife, personal communication). It is not known if the Humboldt cutthroat trout is similar to the Lahontan subspecies in its tolerance of high alkalinity, but this tolerance is a trait of the Lahontan fish fauna in general. The Humboldt cutthroat trout may have other unusual tolerances that help it to prosper in turbid, eutrophic waters.

STATUS

Coffin (1988) listed 92 streams with a combined 433 stream kilometers that contained Humboldt cutthroat trout. The abundance of most populations is limited by habitat volume and quality. Many streams are reduced to a few seep pools by late summer. Others are affected by mining activity. Most of the watersheds are badly overgrazed by livestock and suffer from heavy irrigation diversions. Long-term survival of native cutthroat populations in most Humboldt drainage tributaries is precarious. The most secure population, inhabiting the largest area, is in the headwaters of the Marys River, where the drainage originates in the Jarbidge Primitive Area of the Humboldt National Forest.

In arid-land watersheds characteristic of much of the Humboldt drainage, irrigation withdrawals dry up many streams, leaving little habitat for native trout. All of the sites where Snyder (1917) collected native trout from 1911 to 1915 along the main Humboldt River and in a few tributaries between Carlin and Deeth now have no trout because the environment is highly degraded. The Humboldt cutthroat trout nominally receives the same protection under the Endangered Species Act as the Lahontan cutthroat trout, yet most degradation of its habitat has occurred on federal lands. Grazing problems are serious enough to generate some publicity. A 1988 General Accounting Office report (GAO/RCED-88-105) on public rangelands featured two Humboldt drainage streams, Pearl and Tabor creeks, to illustrate livestock damage to trout streams on federal lands. The decline of the Quinn River cutthroat trout from livestock-induced habitat destruction was cited in a *Newsweek* magazine feature article on public land management in the West (September 30, 1991). Since 1980, 5 of the 10 known populations of Quinn River drainage cutthroat trout, which are of special systematic and evolutionary significance, have become extinct on Bureau of Land Management lands because of continued livestock abuse of watersheds (Coffin, personal communication).

The 1988 General Accounting Office report mentioned above described some hopeful initiatives taken by cattlemen's associations, in cooperation with the Bureau of Land Management and state fish and wildlife agencies, to develop less-destructive grazing systems. Such progressive attitudes toward public lands have been sorely lacking in the Lahontan basin.

Cutthroat Trout of the Alvord and Whitehorse Basins

The Alvord and Whitehorse basins are contiguous, internally draining depressions lying immediately north of the Lahontan basin and extending from northwestern Nevada into southeastern Oregon (Figure 7, page 106). Considerable new information on these basins and their fishes has become available since I wrote the first draft of this monograph in 1979 and discussed the Alvord and Whitehorse basin trout in a 1981 publication. The new information has altered my earlier conclusions on the origins of these native cutthroat trout.

Carl Hubbs and his family first collected cutthroat trout in the Alvord and Whitehorse basins in 1934. Hubbs and Miller (1948) mentioned a history of ancient lakes in the Alvord basin extending back to Miocene times. At maximum level during the late Pleistocene, Lake Alvord extended on a north–south axis for 166 km and had a surface area of 12,766 km^2 (Snyder et al. 1964). Miocene sunfish fossils (family Centrarchidae) are common in the basin (R. R. Miller, University of Michigan, personal communication, and my 1972 personal observations in the area). After the Miocene fish fauna became extinct, the Alvord basin evidently remained well isolated from surrounding drainages. The modern fish fauna represents only two ancestral invasions. One resulted in evolution of the Alvord chub, which is well differentiated from its nearest living relative, tui chub, and probably represents a Pliocene or early Pleistocene invasion (Hubbs and Miller 1948, 1972). (The Borax Lake chub was derived from the Alvord chub by isolation within the basin since the desiccation of Lake Alvord; Williams and Bond 1980.) The other invasion brought cutthroat trout from the Lahontan basin during the late Pleistocene, but perhaps prior to the last glacial epoch; the Alvord cutthroat trout now is subspecifically distinct from its Lahontan predecessor.

Brandon Curry (Purdue University), who conducted graduate research on the geology of the Summit Lake basin, provided me with information on connections that allowed cutthroat trout to transfer from the Lahontan basin into the Alvord basin. Curry concluded that Mahogany Creek, now tributary to Summit Lake of the Lahontan basin, once flowed into Virgin Creek of the Alvord basin. An alluvial fan then developed, diverting Mahogany Creek into the Lahontan basin. Later, 15,000–20,000 years ago, a landslide blocked Mahogany Creek and formed Summit Lake, creating an independent basin. Based on the taxonomic characters of the Alvord cutthroat trout (lower pyloric caecal counts and sparse spotting pattern compared with contemporary Lahontan cutthroat trout), I assume that if a Lahontan ancestor gained access to the Alvord basin via Mahogany Creek, they probably did so before or during an early stage of the last glacial period as Mahogany Creek shifted back and forth between the Lahontan and Alvord basins; thus, cutthroat trout became established in the Alvord basin much before the formation of Summit Lake. Summit Lake cutthroat trout are

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essentially undifferentiated from other Lahontan populations, whereas Alvord cutthroat exhibit obvious distinctions. The Alvord cutthroat trout is now presumed extinct in its pure form.

Little geological history is known for the Whitehorse basin, whose designation follows Russell (1903). The map of Pleistocene Great Basin lakes by Snyder et al. (1964) neither indicates a lake in the Whitehorse basin nor includes this basin as part of the Great Basin. Antelope Creek and Twelvemile Creek of the Whitehorse basin are incorrectly depicted on this map as connected to Crooked Creek, a tributary to the Owyhee River of the Columbia basin. Presently, the sump of the Whitehorse basin is ephemeral Coyote Lake on a playa at 1,233 m elevation. Almost certainly, a relatively large, shallow, late-Pleistocene lake occurred in the Whitehorse basin, which probably overflowed into Lake Alvord via Sand Gap, a depression in the rim separating the two basins. The present minimum elevation of Sand Gap is 1,270 m. This elevation is higher than the minimum elevation of 1,266 m along the rim separating the Whitehorse and Columbia River basins, but that rim has no obvious notch or depression to indicate past overflow. I assume that, over thousands of years, at least 20 m of soil and sand have been deposited at the outlet channel leading from the Whitehorse to the Alvord basin at Sand Gap. The maximum elevation of Lake Alvord was about 1,240 m. The steep gradient below Sand Gap indicates the overflow was a cascade, which would have prevented Lake Alvord fish from entering the Whitehorse basin. This conclusion is supported by the absence of the Alvord chub in the Whitehorse basin. The only fish native to the Whitehorse basin is the cutthroat trout, which most likely was derived from the Lahontan basin via headwater transfer from the Quinn River drainage. If the previously mentioned Quinn–Humboldt river system was a reality during the late Pleistocene, then the Whitehorse cutthroat trout was derived from an early evolutionary stage of the Humboldt cutthroat before the unique Humboldt complement of mitochondrial DNA evolved, because Whitehorse cutthroat trout have mitochondrial DNA typical of Lahontan cutthroat trout.

The other possible origin of Whitehorse cutthroat trout is via headwater transfer from the Trout Creek drainage of the Alvord basin. The degree of similarity between Humboldt and Whitehorse cutthroat trout (apart from their mitochondrial DNA) favors an origin from a Humboldt-like ancestor.

Alvord Cutthroat Trout *Oncorhynchus clarki* subsp.

TYPICAL CHARACTERS

Differs from Lahontan cutthroat trout in spotting pattern, typically having fewer than 50 spots scattered mainly above the lateral line (see Figure 3 in Behnke 1981, a photograph of museum specimens from Virgin Creek and Trout Creek collected in 1934). It also differs from the Lahontan subspecies in having lower lateral-series scale counts (126–151; mean, 137); fewer pyloric caeca (34–49); and feeble development of basibranchial teeth (absent in about 50% of the specimens collected in 1934).

DESCRIPTION (Figure 8, page 109)

The description of the Alvord cutthroat trout is based mainly on examination of 30 specimens collected from Virgin Creek, Nevada, by Carl Hubbs on August 3, 1934 (University of Michigan Museum of Zoology number 13052). They range from 75 to 154 mm in total length. Hubbs's Virgin Creek collections also contain rainbow trout, which had been stocked as fingerlings in the fall of 1933, according to his field notes. Evidently, the 1933 stocking of rainbow trout was the first introduction of this species in Virgin Creek, and the cutthroat trout collected in 1934 are assumed to represent pure Alvord cutthroat trout. Hubbs also collected trout from several sites in Trout Creek in 1934. I examined 26 of these specimens and found them to be mainly hybrids with rainbow trout. Hubbs's field notes mention that rainbow trout were stocked 5 years earlier in Trout Creek.

Meristic characters are: gill rakers, 20–26 (mean, 24); scales in the lateral series, 126–151 (137); scales above the lateral line, 33–37 (35); pyloric caeca, 34–49 (42); vertebrae, 59–63 (62); dorsal fin rays, 9–10 (10); anal fin rays, 9–11 (10); pectoral fin rays, 13–14 (14); pelvic fin rays, 8–9 (9); right branchiostegal rays, 9–10 (10); left branchiostegal rays, 9–11 (10). Basibranchial teeth are absent in 10 of 19 specimens more than 100 mm long.

Hubbs's field notes mention a "deep rose band" on the sides and rose color on the opercula of the larger Virgin Creek specimens. Larger specimens of cutthroat trout (partially hybridized) collected in upper Virgin Creek in 1984 and 1985 by Nevada Department of Wildlife biologists and by Robert Smith exhibited intense rose coloration over the sides of the body, much more intense than is typical of Great Basin cutthroat trout.

In 1985 and 1986, upper Virgin Creek specimens that most resembled cutthroat trout were selected for electrophoretic analysis (Tol and French 1988). Although rainbow trout alleles were detected at about 50% of the loci analyzed, the five diagnostic cutthroat trout alleles all had frequencies identical to those of

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Lahontan cutthroat trout. Evidently, the Alvord cutthroat trout was not isolated long enough from Lahontan stock to evolve diagnostic alleles at the loci assessed. Genetic differentiation from Lahontan cutthroat trout is adequately expressed in phenotypic appearance and meristic characters to warrant subspecific status.

DISTRIBUTION

After Lake Alvord dried up, the Alvord cutthroat trout was restricted to a few streams with perennial flow in the Virgin–Thousand Creek drainage and the Trout Creek drainage (Figure 9, page 110). Extinction rapidly followed the introduction of rainbow trout.

TAXONOMIC NOTES

In 1984, many years after the Alvord cutthroat trout was pronounced extinct, Nevada biologists made a rare find while surveying upper Virgin Creek above a rock slide that evidently had blocked upstream migration of the rainbow trout introduced in 1933. There, on the Wilson Ranch, they found a few large, reddish trout among numerous rainbow trout. In 1985, Robert Smith caught about 50 trout while fly-fishing in upper Virgin Creek. Most of them were typical of rainbow trout in appearance, but three large specimens 318, 445, and 498 mm in total length resembled cutthroat trout. I examined these three specimens and found 22, 22, and 23 gill rakers; 34, 35, and 35 scales above the lateral line; 129, 140, and 144 scales in the lateral series; and 40, 44, and 46 pyloric caeca—all similar to values found in the 1934 specimens. Two of the fish lacked basibranchial teeth and the third had one tooth. In view of the feeble development of basibranchial teeth in the 1934 specimens, I believe these three specimens represented the last pure or virtually pure individuals of the Alvord cutthroat trout.

I aged these specimens at 5, 6, and 7 years. It is likely that rainbow trout gained access to upper Virgin Creek in the 1970s, and by the mid-1980s only a relatively small proportion of the population retained a 50% or greater cutthroat trout heredity.

No scientific name for this native cutthroat has been recognized, although Sigler and Sigler (1987:357) listed the "Alvord cutthroat trout, *S. c. alvordensis* (undescribed)." Their *alvordensis* is a nomen nudem because it is not proposed with a formal description of the new taxon. Nevertheless, it is the manuscript name given by Hubbs for the specimens he collected in 1934 and is an appropriate name for this subspecies.

LIFE HISTORY AND ECOLOGY

Although no life history studies were made of the Alvord cutthroat trout before its presumed extinction as a pure form, the three specimens collected in 1985 indicate the subspecies could reach sizes and ages that are above average for any trout. Such growth characteristics are consistent with long selection in a large lacustrine environment, a selection process that also left the Alvord cutthroat trout unprepared to resist replacement by rainbow trout in the small streams of the Alvord basin.

STATUS

According to Hubbs's field notes, Trout Creek was first stocked with rainbow trout about 1929. Most of the specimens collected from lower Trout Creek in 1934 were obvious hybrids. A November 1989 letter I received from Harold Egoscue of Grantsville, Utah, whose family had pastured sheep in the Trout Creek watershed, confirms this chronology of hybridization. Egoscue wrote that he first caught what appeared to be typical rainbow trout in lower Trout Creek in 1934. By 1941, most of the trout caught were rainbow trout or obvious hybrids. The last fish resembling a cutthroat trout was caught by Egoscue in 1964 in the upper section of Big Trout Creek. In 1972, I collected specimens in both Little and Big Trout creeks to the headwaters and found no indication of any cutthroat trout influence in any of the specimens, which appeared to be typical rainbow trout in all respects. I stopped collecting at an unimproved road crossing, thinking I had reached the uppermost headwaters. In 1984, however, J. L. Perry of Eugene, Oregon, sent me a specimen he caught more than a kilometer above that road crossing. This specimen is predominantly of rainbow trout heredity but does exhibit a rainbow × cutthroat trout spotting pattern. Also, on page 150 of the sixth edition of "The New Henning's Guide to Fishing in Oregon" (1984, Flying Pencil Publications), it is said of Trout Creek that "Small, unique Alvord cutthroat inhabit the bracing upper waters of this creek ... There is not a lot of water in the upper creek, and the trout above are generally under 8 inches and darkly speckled." Although it is doubtful that any pure Alvord cutthroat trout remain, it might be possible to recreate the phenotype of the original trout by establishing and selectively breeding a new population from the most cutthroatlike specimens found in this headwater section.

Extinction of the Alvord cutthroat trout in the Virgin River drainage proceeded as in the Trout Creek drainage. Hubbs recorded that rainbow trout were first introduced in Virgin Creek in 1933. Six Virgin Creek specimens (Oregon State University number 3834) collected in 1970 near the site of Hubbs's 1934 collection are typical rainbow trout showing no evidence of cutthroat trout heredity. Rainbow trout were probably stocked in upper Virgin Creek above the barrier rock slide in the 1970s, and hybridization soon began there as well. By 1984–1986, only a small proportion of the fish had phenotypes resembling cutthroat trout, and electrophoretic data for these fish revealed about 50:50 occurrence of rainbow trout and cutthroat trout alleles. In October 1986, 60 of these cutthroatlike trout were removed from Virgin Creek and transplanted into Jackson Creek in the Lahontan basin, which was fishless at that time (Tol and French 1988). By continually selecting future Jackson Creek specimens that most closely resemble the Alvord cutthroat trout in spotting pattern and coloration, it should be possible to approximate the phenotype of this extinct form, even though a large proportion of rainbow trout alleles would remain.

A formal listing of the Alvord cutthroat as endangered or threatened may have to await resolution of the controversy over whether or not a hybridized population qualifies for listing under the U.S. Endangered Species Act (Goodman 1990; Fergus 1991; O'Brien and Mayr 1991). A precedent exists: the June sucker of Utah Lake is listed as endangered yet it now exists only as a hybrid with the Utah sucker. (Miller and Smith 1981 designated a new subspecies name for the hybrid, *Chasmistes liorus mictus*, to distinguish it from the extinct June sucker.) Nevertheless, attorneys of the U.S. Department of the Interior have issued three opinions since 1981 that hybridized taxa or populations do not qualify for listing under the Endangered Species Act. These opinions did not have the force of law and they have been withdrawn (*New York Times*, March 12, 1991), but they did nothing to protect biotic diversity while they were extant. As of mid-1992, to my knowledge, nothing was being done to preserve what remains of the Alvord cutthroat genotype, including implementation of a proposed land exchange that would place upper Virgin Creek in federal ownership. As the federal agency designated to preserve the diversity of freshwater fishes through administration of the Endangered Species Act, the U.S. Fish and Wildlife Service should take a leadership role in the restoration of the Alvord cutthroat phenotype.

Whitehorse Cutthroat Trout *Oncorhynchus clarki* subsp.

TYPICAL CHARACTERS

Differs from Alvord Lake basin subspecies in having fewer gill rakers (typically 19–23 versus 22–25), more scales in the lateral series (typically 140–155 versus 125–145), more pyloric caeca (typically 40–58 versus 35–48), and better development of basibranchial teeth (averaging 5–6 and present in about 95% of specimens).

DESCRIPTION (Plate 3; Figure 8, page 109)

The description of the Whitehorse cutthroat trout is based on 68 specimens collected during 1934–1983 from Willow Creek, 57 specimens collected during 1969–1983 from Whitehorse Creek, and 26 specimens collected during 1972–1983 from Little Whitehorse Creek.

Willow Creek and Whitehorse Creek are completely isolated from each other, but I assume that periods of above-average precipitation produced connections between them at some time during the past few thousand years, allowing exchanges of their cutthroat trout. Populations native to the two isolated drainages differ slightly, and the limited mitochondrial DNA analysis performed to date indicates that mixing of the Willow and Whitehorse populations has been extremely limited since the desiccation of the assumed pluvial lake in the basin. A dirt road crosses Little Whitehorse Creek, making it the most probable site for introductions if nonnative trout had ever been stocked in the basin. Little Whitehorse Creek connects to Whitehorse Creek during high flows, and trout can move throughout the drainage where perennial flows occur.

In 68 specimens from Willow Creek, I counted 59–64 (mean, 62) vertebrae, 18–23 (21) gill rakers, 36–55 (44) pyloric caeca, 36–45 (40) scales above the lateral line, and 139–163 (150) scales in the lateral series. Basibranchial teeth, numbering 1–13 (6), were found in 130 of 136 specimens examined from both the Willow and Whitehorse drainages. Almost all specimens have 9 pelvic fin rays, and branchiostegal rays range from 9 to 11. Vertebral counts for a combined sample of 102 specimens range from 59 to 64 (62).

Whitehorse and Little Whitehorse creek specimens are meristically similar to the Willow Creek samples: gill rakers, 18–24 (22); pyloric caeca, 35–52 (43); scales above the lateral line, 34–43 (38); scales in the lateral series, 131–164 (147). The spotting pattern is somewhat similar to those of the Alvord cutthroat trout in Virgin Creek and the Humboldt drainage cutthroat trout. The spots are relatively large and sparsely distributed, tending to concentrate posteriorly and above the lateral line anteriorly. The coloration is similar to that of Lahontan and Humboldt cutthroat trout—dull silvery or brassy, with indistinct rose tints in the

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region of the lateral line on sexually mature fish. Smith (1984) published a color photo of the Whitehorse cutthroat trout.

DISTRIBUTION

For thousands of years this trout has been restricted to the Willow and Whitehorse creek drainages of Malheur and Harney counties, Oregon (Figure 9, page 110). No other species of fish is found in this basin, which argues for a long period of isolation from all surrounding drainages and a headwater transfer of an ancestral cutthroat trout either from the Lahontan or Alvord basin. A transplanted population exists in Antelope Creek, a Whitehorse basin stream without fish prior to the 1971 introduction.

TAXONOMIC NOTES

Hubbs and Miller (1948) recognized "Alvord" cutthroat trout as an undescribed subspecies, but their material included representatives of both the Alvord and Whitehorse basins. They did not examine the taxonomic characters that distinguish the two groups of fish.

Wilmot (1974) counted 64 chromosomes in cutthroat trout from Whitehorse Creek, a number common to Lahontan and Yellowstone cutthroat trout. Tol and French (1988) concluded that the cutthroat trout of the Whitehorse basin (which they called the Coyote basin) were most likely introduced by humans from the Quinn or Humboldt river drainages because of the similarities among these populations. However, differences in counts of pyloric caeca and scales between Humboldt and Whitehorse cutthroat trout strongly argue against an origin by recent introduction. Mitochondrial DNA analysis by Williams and Shiozawa (1989) also indicates that Whitehorse basin cutthroat are native, not introduced. Nine specimens from Willow Creek and four specimens from Whitehorse Creek had mitochondrial DNA patterns typical of Lahontan cutthroat trout; five Whitehorse Creek specimens, however, had a pattern not yet found in any other sample of cutthroat trout.

As they did for the Alvord cutthroat trout, Sigler and Sigler (1987:358) listed a nomen nudem subspecies for the Whitehorse trout: "Unnamed subspecies, *S. c. smithi*, undescribed." The designation *smithi* is a manuscript name that I inadvertently supplied to the Siglers.

Whether or not a Whitehorse basin subspecies should be recognized is still uncertain. Sufficient evidence is not yet at hand to favor one of various explanations of its ancestral origin or to estimate the time of its isolation. The most reasonable origin involves a headwater transfer from Quinn River drainage of the Lahontan basin; but at the time of the transfer, was the Quinn River cutthroat trout an early evolutionary stage of the Lahontan or of the Humboldt subspecies? If a transitional gradient of characters indicates a Humboldt–Quinn–Whitehorse evolutionary line, then the Quinn and Whitehorse cutthroat trout should be included with the Humboldt subspecies.

Genetic data on degree of relatedness provide important evidence for determining the taxonomic status of any unique form such as the Whitehorse cutthroat trout, but they should not be regarded as the sole or ultimate basis for recognition of taxa. The recent papers by Avise (1990) and Meyer et al. (1990) demonstrate the limitations of current quantitative genetic techniques for assessing taxon validity.

LIFE HISTORY AND ECOLOGY

The most interesting life history aspect of Whitehorse basin cutthroat trout is their ability to live under extreme conditions. Their evolutionary adaptations to an unstable arid-land environment are probably comparable to those of Humboldt cutthroat trout of the Lahontan basin and Bear River cutthroat trout of the Bonneville basin. During July 1988, Robert Smith (personal communication) recorded minimum and maximum daily temperatures in Willow Creek with an Orvis stream thermometer. Minimum temperatures of 15.5°C occurred at dawn, and maximum temperatures over three days were 29.5–30°C. No trout were observed at the site of the recordings, but they were seen above and below the area, where maximum daily temperatures were believed comparable. It is likely that the Whitehorse basin cutthroat trout has evolved physiological adaptations to exist at extreme temperatures.

STATUS

Although the Whitehorse cutthroat trout has not been replaced by nonnative trout in its original range and a new population has been established in Antelope Creek, its populations have suffered from the effects of livestock grazing. Most of the Willow Creek and Whitehorse Creek watersheds are on Bureau of Land Management lands grazed by domestic livestock. The problem, typical of arid rangelands, is that green vegetation is limited to riparian areas of stream channels by midsummer. Cattle then concentrate along the streams, causing damage to trout habitat by eliminating riparian vegetation, destabilizing banks, and silting the water. A livestock exclosure fence along a section of Whitehorse Creek demonstrated what the stream habitat could become throughout the drainage if protected from livestock. Within the fence, lush riparian vegetation stabilized the banks and provided cover. Outside the fence, during my visit in 1972, was a barren wasteland. Robert Smith recently informed me that conditions have continued to deteriorate. In 1990 the Bureau of Land Management excluded livestock from the Willow and Whitehorse drainages for a 3-year period.

Williams et al. (1989) listed the Whitehorse cutthroat trout as a species of "special concern." Whitehorse basin populations are classified as *O. c. henshawi* by state and federal agencies, so they should qualify for the same protection afforded Lahontan cutthroat trout under the Endangered Species Act.

Bonneville Cutthroat Trout *Oncorhynchus clarki utah*

TYPICAL CHARACTERS

Similar to Yellowstone cutthroat trout, from which it differs mainly in its larger, more evenly distributed spots on the sides of the body and in generally fewer scales in the lateral series.

DESCRIPTION (Figure 8, page 109)

The cutthroat trout native to the Bonneville basin comprises three slightly differentiated groups associated with (1) the Bonneville basin proper, including the Ogden, Provo, Weber, and Sevier river drainages, (2) the Snake Valley region of Utah and Nevada on the western extremity of the basin, and (3) the Bear River drainage (Figure 10). Because of the high degree of intrabasin variability and the close relationship to Yellowstone cutthroat trout, the Bonneville cutthroat trout cannot, at present, be unambiguously separated from the Yellowstone subspecies. The major difference is that Bonneville fish tend to develop larger, more pronounced spots that are more evenly distributed on the sides of the body rather than concentrated posteriorly. Spots on the Snake Valley cutthroat trout, although fairly evenly distributed, typically are smaller and more profuse.

Scales in the lateral series typically number from 140 to 180, averaging between 150 and 170. The lowest counts are for Snake Valley fish, and the highest counts are for Bear River drainage specimens. Pyloric caeca number from about 25 to 55 or more; mean values are about 35 except for the Bear River drainage samples, which typically average more than 40 caeca (52 in Bear Lake fish). Gill rakers typically number from 16 to 21 (mean, 18–19), except Snake Valley cutthroat trout have 18–24 (20–22).

Snake Valley fish have profuse basibranchial teeth—6–90, averaging 20–28. Most other samples of Bonneville cutthroat trout average 5–10 basibranchial teeth, the exception being the collection from Willow Creek, a small, isolated stream south of Salt Lake City, which has an average of 19. Vertebral counts tend to be slightly higher (typically 62–63 versus 61–62) than in other subspecies. The generally dull coloration of Bonneville fish is typical of Great Basin cutthroat trout.

It was formerly believed that pure populations of Bonneville cutthroat trout were extinct (Cope 1955; Platts 1957; Sigler and Miller 1963). Identification of pure populations labored under two handicaps—the absence of an adequate description of the subspecies and the single, misleading illustration of this subspecies published by Jordan (1891). The illustration was based on an atypical Utah Lake fish in which silvery pigments induced by the alkaline environment had reduced the spots to a few small speckles.

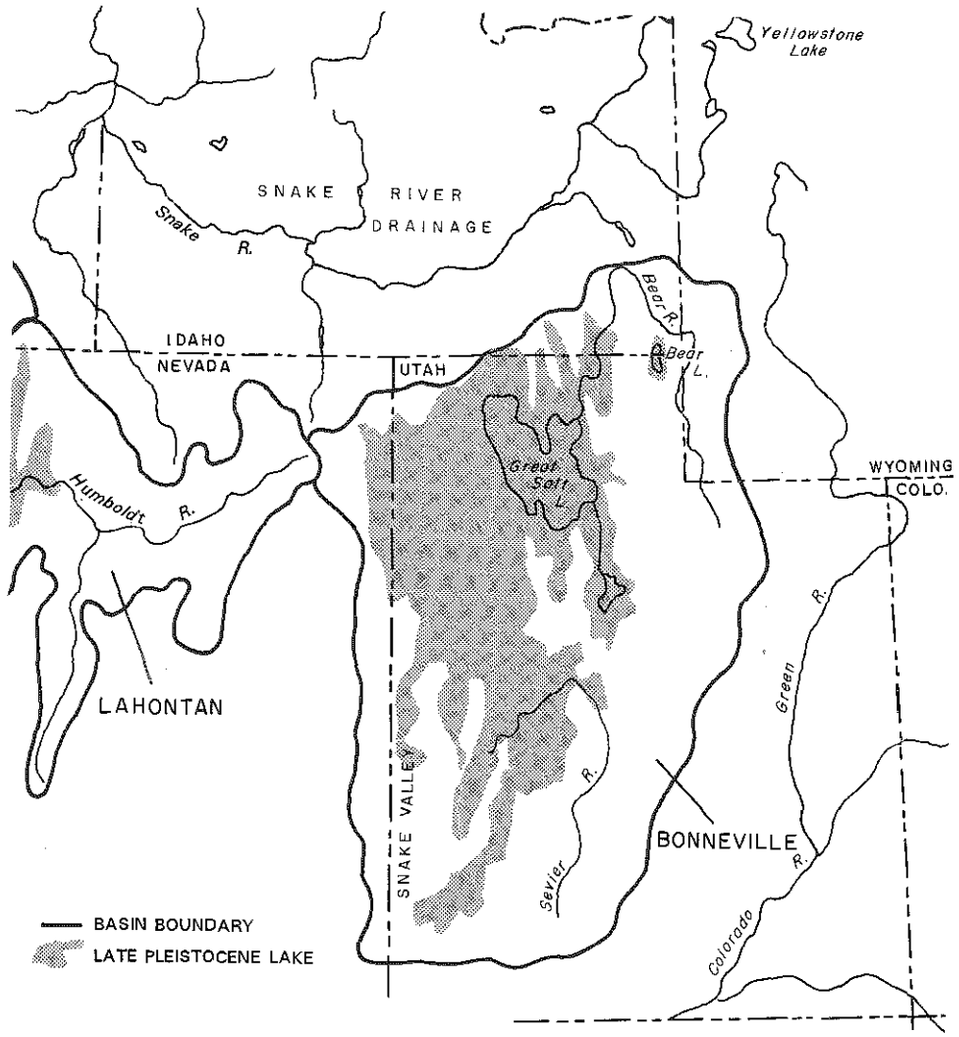

FIGURE 10.—Bonneville basin.

To establish a diagnosis of Bonneville cutthroat trout, I examined 27 ancient museum specimens from the Bonneville basin. I first noticed variation within the subspecies when I studied more recent collections from Pine Creek on the western slope of Mount Wheeler, Nevada. The Pine Creek cutthroat trout, which are derived from the Snake Valley section of the basin, differed sharply from the old museum specimens, particularly in having more gill rakers and basibranchial teeth. I also found lesser but still notable differentiation, especially in counts of scales and pyloric caeca, between the museum specimens and cutthroat trout native to the Bear River drainage.

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Murphy (1974) and Hickman (1978) further examined some of this variation among cutthroat trout of the Bonneville basin. Their theses (which include my Snake Valley and Bear River data from unpublished reports) and electrophoretic analyses by Loudenslager and Gall (1980) and Martin et al. (1985) supported the differentiation of Bonneville cutthroat trout into three groups: a Bear River group (electrophoretically identical to Yellowstone cutthroat trout), a Snake Valley group, and a group associated with the Bonneville basin proper (which shares an allele with some Colorado River cutthroat trout).

DISTRIBUTION

The Bonneville basin, covering about 132,650 km^2, is the Great Basin's largest basin and once contained the largest of its ancient lakes (Figure 10). At maximum size Lake Bonneville extended over 51,840 km^2 and had a depth of about 300 m (Snyder et al. 1964). The native cutthroat trout occurred in all suitable waters of the basin after the desiccation of Lake Bonneville (Figure 9, page 110).

It has been assumed that the ancestral cutthroat trout did not gain access to the Bonneville basin until relatively recent geological times, perhaps as recently as 30,000 years ago, when the Bear River lost its connection with the upper Snake River and drained instead into the Bonneville basin (Hickman 1978; Behnke 1988c). The evidence of genetic differentiation of the Bonneville cutthroat trout into three subgroups, however, could be used to argue that an ancestral cutthroat trout was established in the basin before the Bear River joined it, and that the present taxon *utah* is of multiple origin. Bonneville fish species of the genera *Iotichthys, Chasmistes, Gila,* and *Prosopium* are endemic to the basin, demonstrating that ancestors of the present species were in the basin long ago, perhaps dating back to the Pliocene Epoch or earlier.

After the Bear River changed course and entered the Bonneville basin, the greatly augmented inflow increased the size of Lake Bonneville until it spilled over at Red Rock Pass to connect to the Snake River. Because most of the Bear River drainage was never submerged by ancient Lake Bonneville (just as most of the Humboldt drainage was not covered by Lake Lahontan), its cutthroat trout continued to adapt to fluvial conditions during their recent evolution—except for those in Bear Lake.

The differentiation of Snake Valley cutthroat trout can be explained by fluctuating levels of Lake Bonneville. Like ancient Lake Lahontan, Lake Bonneville apparently had four major fluctuations during its most recent existence. Snake Valley was a bay of ancient Lake Bonneville when the lake was high, but it was isolated from the rest of the basin at other times.

Cutthroat trout were distributed in all suitable waters of the basin when Europeans reached the region. About 100 years ago, cutthroat trout from the Snake Valley region were stocked in fishless streams in neighboring isolated basins between the Bonneville and Lahontan basins (Hubbs et al. 1974). One of these early introductions persisted in Pine Creek on Mount Wheeler, and several subsequent transplants of Pine Creek stock have established a few additional populations in small streams in these separate basins (Duff 1988).

Bonneville cutthroat trout also exist in two headwater streams, Reservoir Canyon and Water Canyon creeks, that drain to the Santa Clara River of the Virgin River drainage of the lower Colorado River basin. It is not known whether these populations are native or introduced. Miller (1961) cited an "old-timer" who claimed cutthroat trout were in the Santa Clara River at Pine Valley, Utah, in 1863. I visited Pine Valley in 1958 and 1973. Only a slight, gentle divide separates the Bonneville and Santa Clara drainages, so headwater transfer is a plausible explanation for the occurrence of Bonneville cutthroat trout in the Santa Clara drainage. On the other hand, none of the early fish collections from the Virgin River basin were reported to include trout. If trout were native to the headwaters of the Santa Clara drainage, they should have spread in all suitable waters throughout the Virgin River drainage.

TAXONOMIC NOTES

In the early literature, Bonneville cutthroat trout were referred to as *Salmo virginalis*. This erroneous use of the name *virginalis* was pointed out by Snyder (1919) in a footnote to his paper on Bear Lake whitefishes and also by Jordan (1920). The earliest name given to a trout strictly of the Bonneville basin is *Salmo utah,* assigned by Suckley (1874). Suckley merely wanted to differentiate the cutthroat trout of Utah Lake from the rest of the Bonneville cutthroat trout, which he identified as *S. virginalis*. Utah Lake trout, because of their silvery coloration and large size, appeared quite distinct from the trout in mountain streams. Although Suckley meant to apply the name *utah* only to Utah Lake trout, Utah Lake is in the Bonneville basin, and if all Bonneville cutthroat trout are recognized as one subspecies, the correct name is *O. c. utah*. Many common names have been applied to the Bonneville cutthroat trout. It is often referred to as the Utah cutthroat trout. The common name Bonneville cutthroat trout is more accurate because not one but three cutthroat subspecies are native to the state of Utah (Bonneville, Colorado River, and Yellowstone), and the native range of the Bonneville cutthroat trout extends into Wyoming, Idaho, and Nevada.

Electrophoretic studies reflect a pattern of diversity suggesting multiple ancestral origins of the Bonneville cutthroat trout. Limited mitochondrial DNA analyses of Bonneville cutthroat trout by Williams and Shiozawa (1989) also suggest diverse origins or multiple, independent mitochondrial DNA mutations in the basin. Eight specimens from Bear Lake had three mitochondrial DNA patterns among them; eight specimens from the Bear River drainage had three patterns, two of them different from Bear Lake results; and seven specimens from the Sevier River drainage had two patterns, both different from the others. The Bear Lake and Bear River samples shared some mitochondrial DNA features with Yellowstone cutthroat trout, but none of the Bonneville specimens shared such features with seven Colorado River cutthroat trout from Current Creek, Utah. Much work remains to be done before the phylogeny and intraspecific relationships of Bonneville cutthroat trout can be interpreted with confidence.

LIFE HISTORY AND ECOLOGY

As I have pointed out (Behnke 1981, 1988c), cutthroat trout of the Bear River drainage (including Bear Lake) are, in their ecological adaptations, very different from other Bonneville cutthroat trout. For example, Bear River and Bear Lake fish are the only forms of this subspecies able to persist in their native waters with introduced nonnative trout. Also, Bear Lake cutthroat trout express delayed maturation, long life span, piscivorous feeding habits, and overwinter growth that make them valuable in put-grow-and-take stocking programs (Nielson and Lentsch 1988, and unpublished).

The studies by Nielson and Lentsch have provided life history data on Bear Lake cutthroat trout in Bear Lake and in four reservoirs where they were introduced. In Bear Lake, 20% of the smaller fish (mean length, 250 mm), 80% of the larger fish (mean, 350 mm), and 95% of the largest specimens (mean, 550 mm) fed on fish. The main fish species consumed by cutthroat trout in Bear Lake were Bonneville cisco and Bear Lake sculpin, both endemic to Bear Lake. Evidently, Bear Lake cutthroat trout readily switch to other forage fishes in other waters. In Mantua Reservoir the abundant fathead minnow proved the favorite prey, and 90% of Bear Lake cutthroat trout with an average size of 333 mm were piscivorous.

Nielson and Lentsch (1988) mentioned that 1987 cutthroat trout spawners from Bear Lake were 4–11 (mean, 7) years old, and that fish 6 years old and older made up 92% of the spawning population. Repeat spawning is rare (less than 4% of all spawners), so almost all the 6-year and older fish were spawning for the first time. Details of the 1988 spawning runs are given in "The Bear Lake cutthroat trout enhancement program, annual performance report 7-26-R-14" (Utah Department of Wildlife Resources), and are based on marked fish of known age. The ages and (parenthetically) numbers of fish for each age-group in the 1988 spawning run were as follows: age 3 (3), age 4 (3), age 5 (75), age 6 (20), age 7 (114), age 8 (80), age 9 (54), age 10 (3).

In new waters, growth rates can be expected to differ, as can the age of first maturation. Preliminary results reported by Nielson and Lentsch indicate that Bear Lake cutthroat trout show more rapid early growth in reservoirs and mature earlier at modal ages of 4–6 years. This is still older than the modal maturation ages of 2–3 years typical of most hatchery trout currently stocked in reservoirs for put-grow-and-take fisheries. This difference can be important in relation to maximizing returns of stocked trout and for producing trout of trophy size.

Nielson and Lentsch also cited the catchability and survivability of Bear Lake cutthroat trout stocked in new waters. Equal numbers and sizes of Bear Lake cutthroat trout and Strawberry Reservoir cutthroat trout (Yellowstone cutthroat × rainbow trout hybrids) were stocked into Strawberry Reservoir, yet anglers caught 10 times more Bear Lake cutthroat trout.

The most abundant prey species in Bear Lake, the Bonneville cisco, is available in greatest concentrations during its peak spawning in January. Bear Lake cutthroat trout are able to exploit this resource and continue growing through the winter. Other cutthroat trout, rainbow trout, brown trout, and brook trout typically cease to grow when water temperatures decline to 4°C and lower. The ability of Bear Lake cutthroat to continue growing at these temperatures in waters where forage fish are available could be of practical significance to fisheries managers.

STATUS

Duff (1988) reviewed the status and management of Bonneville cutthroat trout. He listed 41 native and introduced pure populations of the subspecies in Utah, Wyoming, Idaho, and Nevada. Thirty-nine of those populations occur in 302 km of streams, and two populations are native to lakes: Bear Lake, Utah–Idaho (28,200 hectares), and Alice Lake, Wyoming (93 hectares), both in the Bear River system. Duff summarized the various state and federal management plans for this subspecies, and he expressed an optimistic view of its future—certainly much more optimistic than was possible 30 to 40 years ago when the Bonneville cutthroat trout was assumed to be extinct. The Bear Lake form, in particular, is the focus of large-scale hatchery production and stocking in new waters. This signifies a markedly expanded role of Bonneville cutthroat trout in fisheries management and a new awareness of the value of the genetic diversity found in native cutthroat trout.

The Bear Lake cutthroat trout is an example of a population whose superb adaptations to unique environmental conditions have allowed it to resist hybridization with and replacement by nonnative trout. Yellowstone cutthroat trout, Yellowstone cutthroat × rainbow trout hybrids, and rainbow trout were stocked for decades in Bear Lake. The only two spawning tributaries to the lake, St. Charles Creek and Swan Creek, have long been degraded by land-use practices and irrigation diversions. These circumstances led McConnell et al. (1957) to conclude that the native cutthroat trout of Bear Lake no longer existed, having been replaced by "a mixture of several subspecies of cutthroat and rainbow trout." About 10 years ago I examined specimens from Bear Lake and compared them with museum specimens from the lake and with cutthroat trout from the Bear River drainage. I was surprised to find no evidence of hybridization among their taxonomic characters. Subsequently (in 1983), 52 Bear Lake specimens were examined electrophoretically, and no rainbow trout alleles were observed in any of the fish (Nielson and Lentsch 1988).

Because of severely limited habitat for natural reproduction, Bear Lake cutthroat trout occurred in low numbers before the advent of the large-scale hatchery program. Estimated angler catch increased from 500 in 1973 to more than 14,000 in 1985 after hatchery supplementation (Nielson and Lentsch 1988).

The Wyoming Game and Fish Department has established a hatchery brood stock of native Bear River cutthroat trout, derived from Raymond and Giraffe creeks, at their Daniel hatchery. Only the native cutthroat trout is now stocked in the Bear River drainage of Wyoming.

The Utah Division of Wildlife Resources recently has significantly modified its fisheries programs from traditional stocking of catchable trout to an emphasis on preservation and enhancement of the state's native fish fauna. Extensive restoration and enhancement projects have benefited both the Colorado River

cutthroat trout and the Bonneville cutthroat trout. Dale Hepworth, Regional Fisheries Manager, Cedar City, provided me with an update (to August 1991) of the status of native and transplanted (restored) populations of Bonneville cutthroat trout and a copy of a management plan and status report on the native cutthroat trout of Dixie National Forest. This report reviews the progress made and future plans to protect and restore native Bonneville and Colorado River cutthroat trout in Dixie National Forest. The work represents a joint state–federal effort. I cite this Utah example to illustrate a hopeful trend in state and federal agencies that reflects a higher degree of understanding and appreciation, or stewardship, of native fishes.

8

CUTTHROAT TROUT OF SOUTHERN ROCKY MOUNTAIN BASINS

Colorado River Cutthroat Trout *Oncorhynchus clarki pleuriticus*

TYPICAL CHARACTERS

Differs from previous subspecies in its higher scale counts (170–205+ in lateral series, 38–48+ above lateral line) and its disposition to develop brilliant red, orange, and golden-yellow coloration. However, Colorado River cutthroat trout cannot be separated from greenback cutthroat trout on the basis of these characters.

DESCRIPTION (Plate 4; Figure 11)

A striking change in the coloration of native cutthroat trout occurs between the Bonneville, upper Snake River, and Yellowstone River drainages on one hand, and the Green River–Colorado River basin on the other. In some areas of adjacent headwaters, it is possible to know that one has crossed a divide into the Green River drainage when the somber hues of Bonneville or Yellowstone cutthroat trout are replaced by the brilliant colors of Colorado River cutthroat trout.

Coloration is best developed on sexually mature males from lakes. Besides the reds along the lateral line, the entire ventral region may be bright crimson, and the lower sides of the body are golden yellow. The genetic basis for bright coloration was passed via an ancestral Colorado River cutthroat trout to its descendant greenback and Rio Grande subspecies. The spotting pattern is variable. Fish in tributaries to the upper Green River in Wyoming typically have relatively small or moderate-size spots (as small as or smaller than the pupil of the eye) distributed on the sides of the body mainly on the caudal peduncle and above the lateral line anterior to the dorsal fin, as they are on interior cutthroat trout in general. The spots are pronounced and rounded. In the Little Snake

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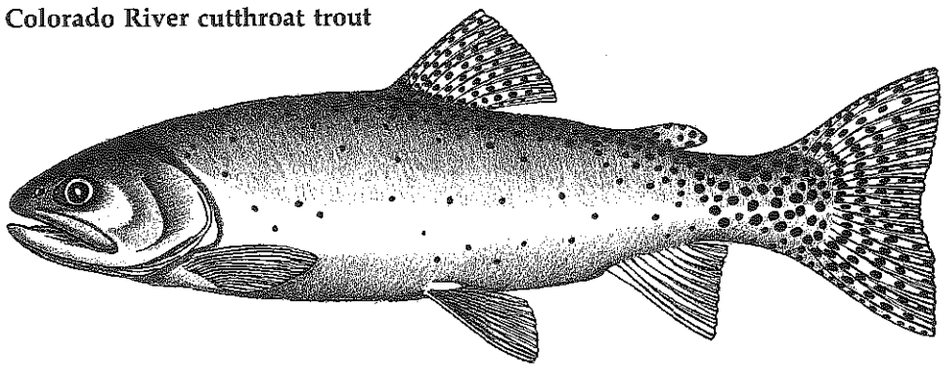
Colorado River cutthroat trout



Greenback cutthroat trout

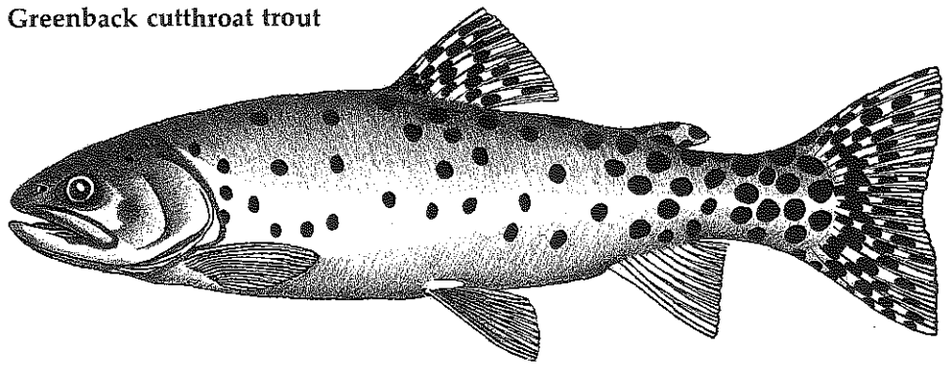
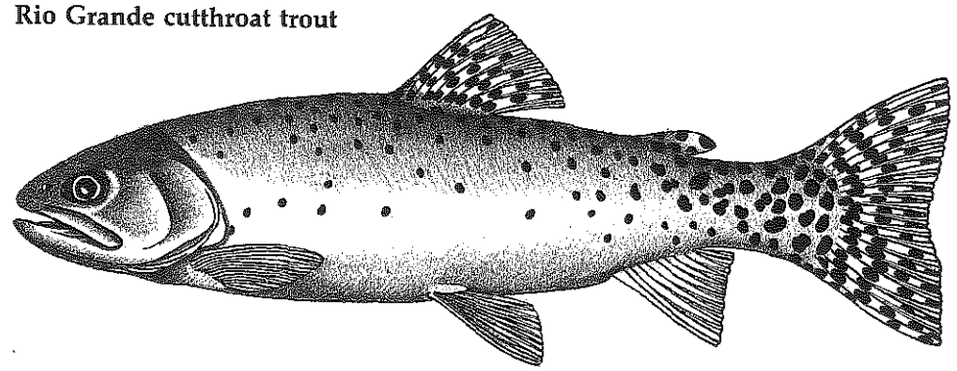


FIGURE 11.—Cutthroat trout of southern Rocky Mountain drainages.

Rio Grande cutthroat trout



Yellowfin cutthroat trout

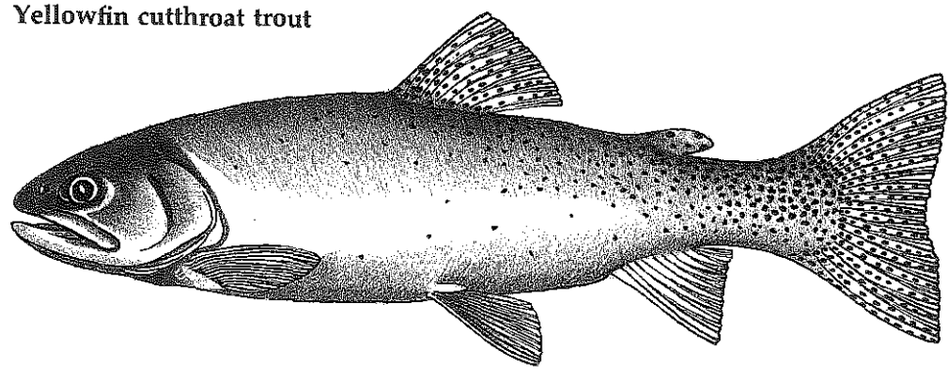


FIGURE 11.—Continued.

River drainage, tributary to the Yampa River, native cutthroat trout have larger spots quite similar to those of greenback cutthroat trout (Binns 1977).

The Colorado River and the greenback cutthroat trout consistently exhibit the highest scale counts of all subspecies. Lateral-series scales range from 170 to well over 200. Pure populations of Colorado River cutthroat trout should average more than 180 scales in the lateral series and more than 43 scales above the lateral line. Vertebrae typically number from 60 to 63 with mean values of 61 or 62. Gill rakers number from 17 to 21, averaging 19. Pyloric caeca typically number from 25 to 45 and average 30 to 40. Binns (1977) characterized Colorado River cutthroat trout in Wyoming, and Martinez (1988) presented data on this subspecies in Colorado.

DISTRIBUTION

The early 19th-century range of the cutthroat trout native to the upper Colorado River basin covered a large area, but it was discontinuous and probably had been for several thousand years. Warm, sediment-laden waters in the Green River below the present town of Green River, Wyoming, and in the Colorado River below Rifle, Colorado, likely confined trout to cooler, clearer tributaries most of the time. The resulting discontinuous distribution probably explains the differences in spot sizes between specimens from various parts of the drainage.

This subspecies is native to the upper Colorado River basin above the Grand Canyon (Figure 12). Its natural distribution has been assumed to be bounded to the west by the Dirty Devil (Frémont) River of Utah (Behnke and Benson 1980) and to the south by the San Juan River drainage of Colorado, New Mexico, and Arizona. During 1991, Glen McFaul of Mesa, Arizona, sent me color photographs of cutthroat trout he had caught in East Boulder Creek of the Escalante River drainage, Utah, which drains to the Green River south of the Frémont River. Through the cooperation of regional fisheries manager Dale Hepworth, I examined specimens of the East Boulder Creek cutthroat trout, and I have no doubt that they are Colorado River cutthroat trout. It cannot be known with certainty that this subspecies is native and not introduced in the Escalante drainage, but to reach the mouth of the San Juan River, cutthroat trout would have had to move past the mouth of the Escalante. Although the Colorado River cutthroat trout is not generally recognized as native to Arizona, it almost certainly occurred in a few streams of the San Juan drainage in the Chuska Mountains near the New Mexico border. Old records of this subspecies from the headwaters of the Little Colorado River and from the White River, Arizona, are based on specimens of Apache trout (Miller 1972a).

TAXONOMIC NOTES

Cope (1872) described *Salmo pleuriticus* from specimens he examined from the Green River near Fort Bridger, Wyoming, the South Platte River, and the Yellowstone River. He also listed *pleuriticus* from the Rio Grande and Bonneville basins. The basis for Cope's description of a new species was a keel he observed

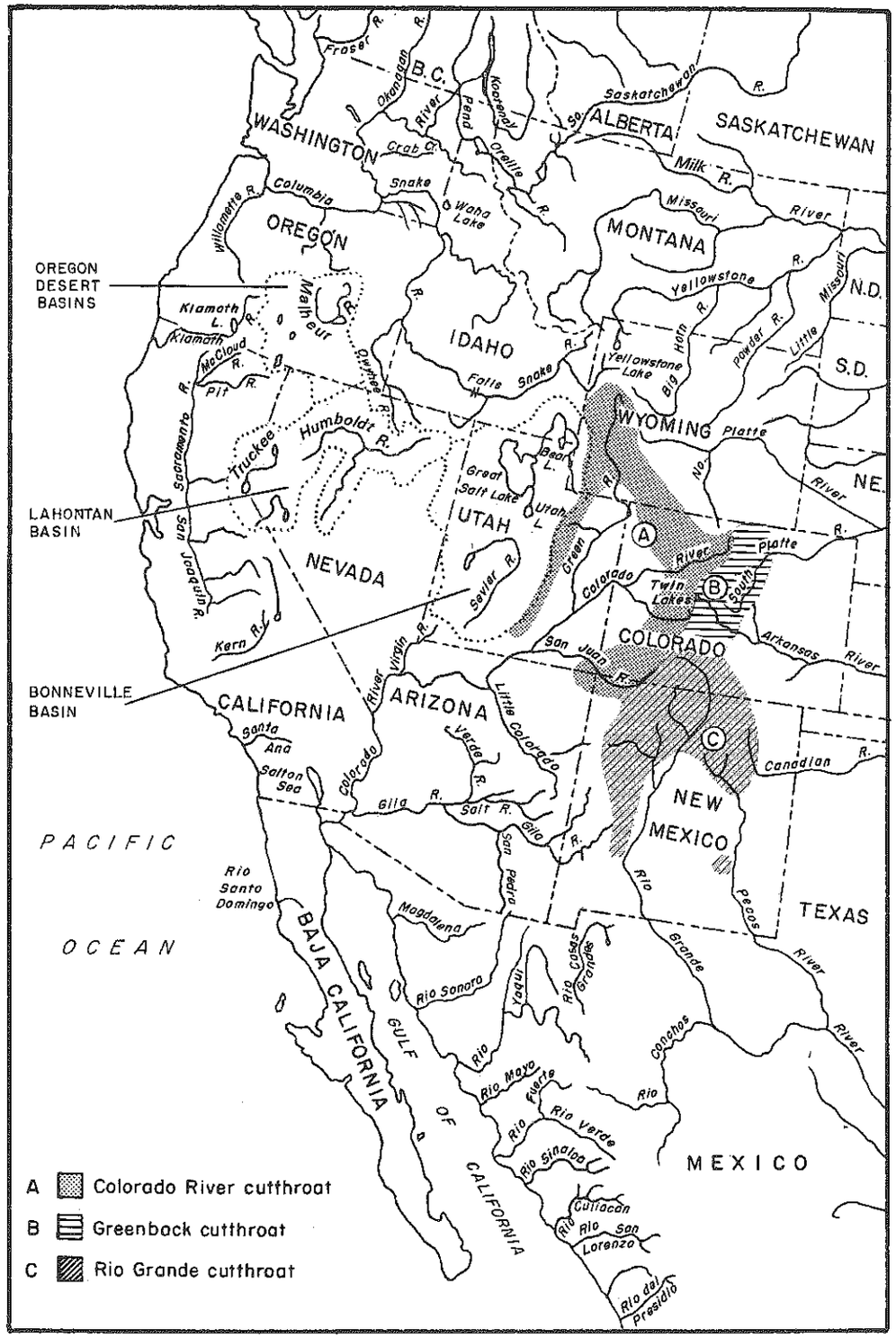


FIGURE 12.—Distributions of Colorado River cutthroat trout, greenback cutthroat trout, and Rio Grande cutthroat trout.

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along the midline of the skull in the specimens he grouped as *pleuriticus*. This character proved to be an artifact caused by improper preservation; the frontal bones of dehydrated specimens evidently distorted to form a ridge. Because a name had not been previously proposed for the cutthroat trout of the Colorado–Green river basin, Cope's *pleuriticus* became the valid name in Jordan's (1891) revision, which applied *pleuriticus* solely to the Colorado River basin cutthroat trout, and this usage has continued to the present.

An unpublished 1989 report submitted by R. F. Leary and F. W. Allendorf (University of Montana) to the U.S. Fish and Wildlife Service, Denver, gave electrophoretic data for Colorado River cutthroat trout in Williamson Lakes, California, a population that had been transferred from Trappers Lake, Colorado, in 1931. Allele frequencies at two gene loci—L-iditol dehydrogenase (*IDDH-1*36*) and malic enzyme (*MEP-1*100*)—distinguished this population from Yellowstone cutthroat trout. If the diagnostic value of these alleles can be confirmed for other Colorado River stocks, they will be a valuable identification tool.

LIFE HISTORY AND ECOLOGY

As did most inland forms of the species, Colorado River cutthroat trout evolved in isolation from rainbow and other trout. This evolutionary Achilles' heel left the subspecies vulnerable to hybridization with rainbow trout and to replacement by brook trout and brown trout. The native cutthroat trout rapidly disappeared from the main streams of the upper Green and upper Colorado rivers and their major tributaries after nonnative trout were introduced. Events in the Gunnison River, Colorado, afford a typical example. Rainbow trout were first introduced in the Gunnison in 1888 with the stocking of 10,000 fry. By 1897, the Gunnison was famous for a rainbow trout fishery that included fish up to 5 kg, and the native cutthroat trout had virtually disappeared (Wiltzius 1985).

Today, trout that resemble Colorado River cutthroat trout usually are found in isolated headwater streams. In the foothills of Wyoming's Green River drainage, however, several populations of native cutthroat trout that are only slightly hybridized occur in severely degraded streams (Behnke and Zarn 1976; Binns 1977). The unstable environments that characterized these foothill streams over the past several thousand years may have selected for a resilient form of the native subspecies here, as analogous conditions did with the cutthroat trout native to the Humboldt and Bear river drainages.

Historically, cutthroat trout reached large sizes in the Colorado River basin; unverified reports of fish weighing 8–10 kg or more exist. An anonymous article titled "Trout in the Rocky Mountains," published in *Forest and Stream* magazine in 1878 (9[25]:268–269), mentioned that although the greenback cutthroat trout was abundant on the east slope of the Colorado Rockies, anglers would have to travel west to the Colorado River basin if they desired large trout.

STATUS

Pure populations of Colorado River cutthroat trout are gone from most of the expansive range they inhabited 100 years ago. Williams et al. (1989) listed this subspecies as a taxon of "special concern."

Binns (1977) developed a genetic purity rating system ranging from A (pure) to F (obvious hybrids) to facilitate protection and management of Colorado River cutthroat trout in Wyoming. Martinez (1988) modified Binns's system to rate populations of this subspecies in Colorado, and she noted an alarming trend for populations monitored in the last decade. Twelve of 36 stream populations showed evidence of increased hybridization, and two populations had been replaced by brook trout.

In Trappers Lake, Colorado, the largest formerly pure population of Colorado River cutthroat trout is now becoming hybridized with rainbow trout (Martinez 1988). I had considered the Trappers Lake cutthroat trout to be pure, based on specimens collected in 1970. This diagnosis was verified by Gold et al. (1978). Since then, evidently, rainbow trout have gained access to Trappers Lake, probably from a tributary lake.

Fortunately, pure Trappers Lake fish were shipped to California in 1931 and stocked in Williamson Lakes, where they still exist. A joint effort by the Colorado Division of Wildlife, the California Department of Fish and Game, the U.S. Fish and Wildlife Service, the National Park Service, and the U.S. Forest Service, under the guidance and inspiration of California Fish and Game biologist Phil Pister, resulted in the reintroduction of pure Trappers Lake stock in Colorado. This effort culminated in 1987, when about 300 trout from Williamson Lakes were stocked in Bench Lake in the Colorado River drainage of Rocky Mountain National Park (Martinez 1988; Pister 1988).

Greenback Cutthroat Trout *Oncorhynchus clarki stomias*

TYPICAL CHARACTERS

Similar to Colorado River cutthroat trout but tending to have larger spots and more scales (typically more than 45 scales above the lateral line and more than 185 in the lateral series).

DESCRIPTION (Figure 11, page 140)

The cutthroat trout native to the South Platte and Arkansas drainages tend to exaggerate the basic spotting pattern and the large number of scales of their Colorado River ancestor. The greenback cutthroat trout typically has the largest spots and the most scales of any subspecies of cutthroat trout.

Scale counts from what I consider to be pure greenback collections average from 44 to 53 above the lateral line and from 189 to 217 (mean values) in the lateral series. Numbers of vertebrae and pyloric caeca are about the same as in Colorado River cutthroat trout. Like the Colorado River subspecies, greenback cutthroat trout often develop brilliant coloration.

DISTRIBUTION

Greenback cutthroat trout originally occurred in mountain and foothill headwaters of the South Platte and Arkansas river drainages (Figure 12, page 143). The range lies almost entirely within the state of Colorado except for a few headwater tributaries of the South Platte in a small area of southeastern Wyoming. No trout are native to the North Platte drainage.

TAXONOMIC NOTES

The origin of the type specimens used to describe *stomias* is confused. In the same publication in which he named *plueriticus*, Cope (1872) named *Salmo stomias* based on specimens collected from what he believed to be the "South Platte River at Fort Riley, Kansas"—but the South Platte River drainage does not enter the state of Kansas. In later publications Cope stated that the type locality of *stomias* was the Kansas River at Fort Riley—yet the Kansas River has no native trout.

The confusion originated with an Army expedition under the command of F. T. Bryant, which traveled from Fort Riley, Kansas, to Fort Bridger, Wyoming, and back again in 1856. W. R. Hammond, a surgeon, accompanied the expedition and made natural history collections that included two specimens of cutthroat trout. The expedition traversed parts of the Kansas, North Platte,

South Platte, and Green river drainages in Kansas, Nebraska, Wyoming, and Colorado. Cutthroat trout could have been collected only in the Green or South Platte drainages. All the specimens Hammond collected were simply labeled "Fort Riley, Kansas," the terminus of the expedition, and shipped to the Philadelphia Academy of Sciences, where Cope later examined the two specimens of cutthroat trout on which he based the name *stomias*.

Jordan (1891) redefined *stomias* and limited the name to the cutthroat trout native to the South Platte and Arkansas river drainages. Jordan also appears to have been the first to use the common name greenback for this trout in the literature. Actually, *stomias* specimens do not have any more green on their backs than do any other subspecies of cutthroat trout.

The differentiation between greenback and Colorado River cutthroat trout is slight and best explained by a recent separation. Cutthroat trout probably invaded the South Platte basin via a headwater stream transfer from the Colorado River basin. The cutthroat trout is the only species of native fish common to the two basins. Greenback cutthroat trout presumably entered the Arkansas drainage by a later transfer from the South Platte, but other scenarios are possible; the direction of transfers could have been reversed, for example. There is a gentle divide at Trout Creek Pass between the South Platte and Arkansas drainages.

LIFE HISTORY AND ECOLOGY

The rapid disappearance of greenback cutthroat trout after the introduction of nonnative trout suggests they are among the most vulnerable of all cutthroat trout to displacement. The only naturally occurring populations of the pure subspecies occur in small headwater areas above barrier falls.

The greenback cutthroat trout of Twin Lakes suffered a fate common to the subspecies throughout its range. In the 19th century Twin Lakes was noted for abundant greenback cutthroat trout. Then, in the 1890s, rainbow, brook, and lake trout and even Atlantic salmon were introduced to the lakes. When Juday (1906) sampled Twin Lakes in 1902 and 1903, rainbow trout had become dominant. Even some of the specimens he identified as greenback cutthroat trout I found to be hybrids when I examined them at the U.S. National Museum. Within a few generations of the rainbow trout introduction, the greenback cutthroat trout was extinct in Twin Lakes.

Greenback cutthroat trout seldom attain a large size. About 1 kg seems to be a typical maximum size given by most old accounts. However, when stocked in a small pond with abundant food on the Fort Carson Military Reservation, Colorado, some greenback cutthroat trout increased in weight from about 100 g to 2 kg in 3 years (Stuber et al. 1988), so optimum conditions can promote growth to a relatively large size.

An interesting life history trait, evidently an adaptation to coldwater reproduction, was reported by Dwyer and Rosenlund (1988) for the greenback population native to the uppermost headwaters of the Little South Poudre River, Colorado. In this high-elevation habitat (about 3,200 m), greenback cutthroat trout do not spawn until July. Normally, such late spawning would not allow

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sufficient time for trout eggs to hatch and fry to emerge and start feeding before winter conditions set in. When eggs from the Little South Poudre population and from a population native to Cascade Creek (Arkansas River drainage) were incubated in 8°C water at the Saratoga (Wyoming) National Fish Hatchery, the Cascade Creek eggs hatched in 39 days (312 temperature units)—a typical rate for trout species in general—but the Little South Poudre eggs completed hatching in only 32 days (256 temperature units).

STATUS

The greenback cutthroat trout was listed as endangered under the 1973 Endangered Species Act until 1978, when its status was changed to threatened. Only five naturally occurring pure populations are known to have survived into recent times. Brood stocks were developed from these sources, and subsequent introductions established many new populations in 12 streams (81 km) and five lakes (44 hectares) by 1987 (Dwyer and Rosenlund 1988; Stuber et al. 1988). New introductions have continued, thus making the recovery program for the greenback cutthroat trout one of the more successful examples of restoration of an endangered or threatened form of life.

Most of the restoration in lakes has occurred in Rocky Mountain National Park. After all nonnative trout are eliminated from a lake by chemical treatment, hatchery-reared greenback cutthroat trout are stocked. When a population becomes self-sustaining by natural reproduction, the lake is opened to angling under catch-and-release (no-kill) regulations. This management strategy has received very favorable media coverage.

Rio Grande Cutthroat Trout *Oncorhynchus clarki virginalis*

TYPICAL CHARACTERS

Differs from greenback and Colorado River cutthroat trout by having fewer scales (typically 150–180 in the lateral series and 35–45 above the lateral line) and by the irregular shape of spots on the caudal peduncle.

DESCRIPTION (Plate 4; Figure 11, page 141)

Two forms of the Rio Grande cutthroat trout exist, one associated with the Rio Grande proper of Colorado and New Mexico, and the other with the upper Pecos River in New Mexico (Figure 12, page 143). The Pecos form has the larger spots, which are more typical of greenback cutthroat trout, and more scales in the lateral series, averaging about 175. Smith (1984) provided color photographs of both forms.

Vertebrae typically number 61–62. Pyloric caeca number 30–50, slightly higher than counts for the greenback and Colorado River subspecies. Basibranchial teeth are weakly developed. One of two specimens collected in 1872 from the Rio Puerco, New Mexico, lacks basibranchial teeth, and the other has only two microscopic vestiges of them.

Rio Grande cutthroat trout develop colors like those of greenback and Colorado River cutthroat trout—rich reds, oranges, and golden yellows—but somewhat less intensely than the other subspecies. Adult Rio Grande fish have large, close-set spots on the caudal peduncle. These spots tend to be club-shaped rather than rounded, suggesting that several smaller spots have coalesced.

DISTRIBUTION

Two major unknowns concerning the native range of Rio Grande cutthroat are its southern extension into Texas and Mexico and its eastern extension into the Canadian River drainage.

Cope (1886) reported on two specimens of cutthroat trout (with "basihyal" teeth, assumed to mean basibranchial teeth) collected from an unknown drainage of southern Chihuahua, Mexico, at an elevation of "7,000 to 8,000 feet" near the boundaries of Sinaloa and Durango. Mexican golden trout occur in the Pacific drainage streams of this area, but this subspecies lacks basibranchial teeth. A rainbowlike trout also occurs in westward-flowing streams in the region, and a population (probably introduced from the Río Yaqui) exists in the headwaters of the Río Casas Grandes, an isolated tributary in the Guzman basin, which once had a connection to the Rio Grande (Needham and Gard 1959), but

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these fish also lack basibranchial teeth. Cope's specimens have been lost and their identification is unverified. Jordan and Evermann (1896, and other publications) give the range of the Rio Grande cutthroat trout as "southward to Chihuahua, Mexico" based on Cope's record. If a Rio Grande cutthroat trout ever occurred or still occurs in Mexico, which I consider doubtful, it would be in the headwaters of the Río Conchos. If cutthroat trout were native to the Guzman basin, remnant populations would be expected in the headwaters of the Mimbres drainage, New Mexico.

Rio Grande cutthroat trout once might have existed in the Rio Grande basin of Texas, although this was never verified by collections. A suggestive article by J. W. Daniel titled "Salmonidae in Texas" appeared in *Forest and Stream* magazine in 1878 (10[48]:339). Daniel, who served in Texas during the Civil War, had a "distinct recollection" of catching "speckled trout" from the Devils River, a Rio Grande tributary in Val Verde County, and from the Limpia River, a tributary to the Pecos in Jeff Davis County. Daniel also mentioned he caught trout in the Rio Bonito in Lincoln County, New Mexico. The Rio Bonito, which did contain Rio Grande cutthroat trout during the Civil War, is a tributary to the Pecos and represents the southernmost known distribution of cutthroat trout in the Pecos drainage in historical times (Behnke 1988d). Rio Bonito trout were transplanted to Indian Creek on the western slopes of Sierra Blanca Peak in south-central New Mexico, north of Almagordo, where they still exist. They have the large spots typical of the Pecos form and about 175 scales in the lateral series. Evidence that the Indian Creek trout are not native but were introduced from the Rio Bonito is based on testimony of local people, gathered by former U.S. Fish and Wildlife Service biologists Robert Azevedo and Terry Merkel, and on the drainage of the creek to the White Sands desert (Tularosa basin), long isolated from any contact with the Rio Grande.

Another article in *Forest and Stream* in 1878, by N. A. Taylor (10[13]:236), claimed that "brook trout" occurred in the Limpia River, Texas. The Limpia River was described as a "clear, cool, sparkling stream flowing through a region about 5,000 feet in elevation" (Davis Mountains). Garrett and Matlock (1991) reviewed the historical reports of cutthroat trout in Texas and used distributional evidence for the Rio Grande chub to conclude that the Rio Grande cutthroat trout probably was native to Texas in historical times. Rio Grande chub and Rio Grande cutthroat trout have similar distributions in New Mexico. In Texas, the Rio Grande chub occurs only in Little Aguja Creek, a tributary to the Pecos River in the Davis Mountains. Little Aguja Creek is close to the Limpia River, the stream reported to have "brook trout" in 1878. The only stream containing a self-reproducing trout population in Texas today is McKittrick Creek on Guadalupe Mountain. Those fish are rainbow trout.

The occurrence of native trout in the Canadian River basin has not been verified by accounts of early explorers or by museum specimens. The headwaters of the Canadian River system, which drain the east slopes of the Sangre de Cristo Mountains in northern New Mexico and southern Colorado, contain much excellent trout habitat. Cutthroat trout introductions in the Canadian drainage were made as early as 1907, according to records of the New Mexico Department of Fish and Game.

Probably the most convincing evidence that Rio Grande cutthroat trout are native to the Canadian River drainage is an anonymous article in an 1877 issue of *Forest and Stream* (9[4]:67) titled "Rio Grande trout." The author claimed that the finest fishing for Rio Grande trout was found in the headwaters of the Vermejo River. He made this claim while describing his fishing experiences in Colorado (perhaps also in northern New Mexico), where the only Vermejo River is a tributary to the Canadian River.

In historical times the southern limit of Rio Grande cutthroat trout has been the Las Animas River drainage, a tributary to the Rio Grande in southwestern New Mexico (about 33°N latitude). This is also the southernmost known natural distribution of cutthroat trout.

The distribution of pure populations of Rio Grande cutthroat trout in New Mexico was presented in the May–June 1977 issue of *New Mexico Wildlife* magazine. A map in that article erroneously shows Little Blue Creek as a tributary to the Pecos drainage. Little Blue Creek is in the Canadian River drainage.

TAXONOMIC NOTES

As with its distribution, confusion surrounds the nomenclature of the Rio Grande subspecies. In 1853, members of a Pacific Railroad Survey preserved specimens of cutthroat trout from what is now called Ute Creek at Fort Massachusetts in the San Luis Valley of Colorado. Girard (1856) described *Salar virginalis* on the basis of these specimens and gave the locality as "Utah Creek." A few years later more specimens were taken and preserved at Fort Garland, near Sangre de Cristo Creek. Cope (1872) examined these specimens and named a new species, *Salmo spilurus*, from "Sangre de Cristo Pass." Both Ute Creek and Sangre de Cristo Creek are tributaries to Trinchera Creek, and it can be assumed that Girard's *virginalis* and Cope's *spilurus* represent the same form of cutthroat trout. Although Cope knew of Girard's description of *virginalis*, he believed *spilurus* was a valid species because it was "not so slender." Cope believed *Salmo pleuriticus* (the Colorado River cutthroat trout) also inhabited the Rio Grande drainage around Fort Garland.

Jordan (1891) mistakenly assumed that the type locality of *virginalis* ("Utah Creek") was in the Bonneville basin of Utah, so he used the name *virginalis* for the Bonneville cutthroat trout and *spilurus* for the Rio Grande cutthroat trout. This usage continued in the literature until Snyder (1919) recognized the error. Jordan (1920) further elaborated on this correction in nomenclature.

Most of the early literature on Rio Grande cutthroat trout mentions two forms, one small-spotted and the other large-spotted. As discussed, there are two forms of Rio Grande trout, but the large-spotted form is isolated in the Pecos basin, and the two forms do not occur together. I can find no evidence from examination of hundreds of specimens that two distinct forms of cutthroat trout ever occurred together in the Rio Grande River. Although there may be some factual merit in these early observations, I believe they were based on differences within the Rio Grande form associated with size, age, and environment, not on two genetically distinct, coexisting forms.

The early descriptions of Rio Grande cutthroat by Girard and Cope cannot be used to successfully identify the subspecies. Jordan (1891) provided some taxonomic data and illustrations of specimens, but he concluded that the Rio Grande cutthroat trout is "wholly identical" to the Colorado River cutthroat trout except for having fewer scales.

Jordan believed the greenback cutthroat trout gave rise to the Rio Grande subspecies, which then gave rise to the Colorado River subspecies; in the process, fish transferred from the Arkansas drainage to the Rio Grande drainage to the upper Colorado River basin. It is more likely that the Rio Grande cutthroat trout was derived from the Colorado River basin (Gunnison or San Juan drainage) via a headwater transfer, but its derivation from the greenback trout of the Arkansas River drainage may have been possible in the Poncha Pass area at the north end of the San Luis Valley.

The close similarity of Colorado River, greenback, and Rio Grande cutthroat trout indicates a late-Pleistocene isolation of the three subspecies. Fossil evidence of cutthroat trout in the Rio Grande basin might indicate a much earlier occurrence of an ancestral form. Rogers et al. (1985) described what they believed to be cutthroat trout fossils dating back 740,000 years (mid-Pleistocene) from the San Luis Valley, Colorado. Bachhuber (1989) found cutthroatlike fossils dating back 130,000 years in the Estancia basin of central New Mexico, which lies between the Rio Grande and Pecos drainages. If these mid- to late-Pleistocene fossils actually are cutthroat trout, I believe they represent a more primitive form that became extinct and that was not the direct ancestor of the Rio Grande cutthroat trout (Behnke 1988c).

LIFE HISTORY AND ECOLOGY

As with other interior subspecies, the Rio Grande cutthroat trout is highly vulnerable to replacement by nonnative trout. Also, it is vulnerable to angling and may suffer differential fishing mortality where it shares waters with another trout. Behnke and Zarn (1976) noted that the native cutthroat trout was dominant over the brown trout in the Rio Chiquito near Taos, New Mexico, before the Rio Chiquito became a public fishing stream. Soon after this stream received significant angling pressure, however, the brown trout became the dominant species.

STATUS

The Rio Grande cutthroat trout, or a trout that typifies this subspecies, is rare throughout its original range in Colorado and New Mexico. Stefferud (1988) reviewed its status in New Mexico and discussed management plans developed by state and federal agencies. Most Rio Grande cutthroat populations are found in small headwater streams. Many suffer from habitat problems caused by livestock grazing. Some streams have no physical barriers separating cutthroat trout in headwaters from rainbow trout and hybrids occurring lower in the watersheds. In contrast to most Rocky Mountain waters, where the eastern

brook trout is the most serious threat to native cutthroat trout in small streams, the brown trout seems to be the greatest threat in New Mexico.

The New Mexico Department of Game and Fish is developing a hatchery program to rear Rio Grande cutthroat trout, and the U.S. Fish and Wildlife Service has hatched eggs from the Indian Creek population (Stefferud 1988). The Colorado Division of Wildlife has also been active in restoring these native trout. Several transplants have been made in recent years, most of them derived from pure populations found in streams on the Forbes Trichera Ranch near the type locality for the subspecies *virginalis*.

Williams et al. (1989) listed Rio Grande cutthroat trout in the "special concern" category.

Yellowfin Cutthroat Trout *Oncorhynchus clarki macdonaldi*

TYPICAL CHARACTERS

Seven specimens of yellowfin cutthroat trout collected in 1889 with greenback cutthroat trout from Twin Lakes, Colorado, differ from the greenback subspecies in having more gill rakers (20–22 [mean, 21] versus 18–21 [19]), fewer scales in the lateral series (159–185 [175] versus 170–202 [189]) and above the lateral line (mean, 42, versus 48), and silvery coloration with small, irregularly shaped spots versus bright coloration with large, round spots.

DESCRIPTION (Figure 11, page 141)

The original description of the yellowfin cutthroat trout by Jordan and Evermann (1890), essentially repeated by Jordan in 1891, does not provide convincing evidence that two distinct groups of cutthroat trout existed in Twin Lakes. If only the original description and literature accounts of the yellowfin cutthroat trout were consulted, the reality of this subspecies could be questioned. That is, it might be concluded that yellowfin cutthroat trout were nothing more than unusual specimens of greenback cutthroat trout.

The 1889 Twin Lakes collections are represented in museums by seven specimens of yellowfin and eight specimens of greenback cutthroat trout. In 1902 and 1903, Juday (1906) also collected trout from Twin Lakes, which are now represented by 13 specimens of greenback cutthroat trout in the U.S. National Museum. The seven yellowfin cutthroat trout obtained by Jordan in 1889 are believed to be the only specimens of this trout in existence; five of them are in the National Museum, and two, formerly in the Stanford University collection, are now at the California Academy of Sciences. Critical examination of the 7 yellowfin and 21 greenback specimens leaves no doubt that the two subspecies were distinct and living sympatrically in Twin Lakes in 1889.

Although long-preserved, the specimens remain in good condition, and they agree with the illustrations and descriptions in Jordan (1891). The small, star-shaped spots and silvery coloration of the yellowfin cutthroat trout are very dissimilar to the pronounced, large, rounded spots and dark coloration of the greenback subspecies. All of the specimens are between 150 and 300 mm, so differences in appearance are not due to size. As mentioned, the yellowfin specimens have more gill rakers and fewer scales than the greenback fish from Twin Lakes.

DISTRIBUTION

Yellowfin cutthroat trout are known only from Twin Lakes, Colorado (Arkansas River drainage). Propagation of this subspecies was carried out by the

Colorado Fish Commission beginning in 1885 and by the Leadville National Fish Hatchery from 1892 until at least 1897. No state or federal records, however, document introductions of these fish. Presumably, most were returned to Twin Lakes.

In the March 8, 1890, edition of *Field and Farm,* a journal published in Denver, Gordon Land, the Colorado state fish commissioner, wrote that the yellowfin cutthroat trout was not restricted to Twin Lakes but was also found in all tributaries in the upper Arkansas River drainage. Land claimed that he had spawned yellowfin cutthroat trout in Chalk Creek, a tributary of the Arkansas. No museum specimens or other evidence supports his view of the subspecies' distribution.

TAXONOMIC NOTES

It is possible that an ancient headwater stream transfer brought an ancestor of Colorado River cutthroat trout from the Colorado River drainage into the Arkansas River drainage above Twin Lakes, and that two ecologically distinct groups of cutthroat trout then evolved reproductive isolation and avoided hybridization in Twin Lakes. Speculation is all that can be contributed on this matter, however, for there is no clear-cut evidence to indicate whether the yellowfin trout was native to Twin Lakes or introduced from the Colorado River basin by humans.

Twin Lakes was a popular resort area, but the earliest reports on its trout fishing mention only the small greenback cutthroat trout (Behnke and Wiltzius 1982). Charles Hallock's *Sportsman's Gazetteer and General Guide,* published in 1877, mentioned that Twin Lakes trout were small (greenback cutthroat trout), but that anglers interested in larger trout could hike over Tennessee Pass to the Eagle River drainage to fish for larger trout (Colorado River subspecies).

The first record of a large, silvery trout in Twin Lakes is found in the 1885–1886 report of the Colorado fish commissioner, John Pierce. Pierce claimed that a trout with yellow coloration and with yellowish flesh, reaching a weight of 4.5 kg, was found in Twin Lakes. It was believed the trout spawned before the ice was off the lake. Pierce mentioned that an attempt was made to transplant this trout into Island Lake on Grand Mesa. His comments were republished in the 1885 report of the U.S. Fish Commission and were instrumental in the decision to construct a federal hatchery near Twin Lakes at Leadville.

LIFE HISTORY AND ECOLOGY

The large size of yellowfin cutthroat trout attracted the attention of anglers. The subspecies reputedly attained weights of 5–6 kg and was piscivorous. Jordan (1891) mentioned that its flesh was light colored because of its diet, whereas greenback cutthroat trout in Twin Lakes fed mainly on crustaceans and had red flesh. There was a general belief that hybridization between the two forms was avoided because yellowfin cutthroat trout spawned earlier and in the lake, whereas greenback cutthroat trout spawned later and in tributary streams. There is little doubt that two distinct populations of cutthroat trout occurred

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together in Twin Lakes, where they occupied different niches and were reproductively isolated.

STATUS

The yellowfin cutthroat trout probably has been extinct in Twin Lakes since about the turn of the century, although U.S. Fish Commission reports indicate "yellowfin trout" were held at the Leadville Hatchery until 1905. Nonnative trout were introduced to the lakes in large numbers in the 1890s. Juday's collections of 1902 and 1903 included no yellowfin cutthroat trout; they were dominated instead by rainbow trout, and greenback × rainbow hybrids made their first appearance. The Twin Lakes greenback cutthroat trout soon followed the yellowfin subspecies into extinction. The U.S. Fish Commission report for 1905 is the last record of yellowfin cutthroat trout at the Leadville hatchery. A common belief held that introduced yellowfin cutthroat trout persisted until the 1930s in Island Lake on the Grand Mesa. The report of the U.S. Fish Commission for 1931 mentions that the U.S. Forest Service was propagating yellowfin cutthroat trout on the Grand Mesa. Beginning in 1899 and for several years thereafter, both the Leadville National Hatchery and the Colorado Fish Commission obtained cutthroat trout eggs from "lakes on the Grand Mesa," including Island Lake. Evidently, the attempt to establish yellowfin cutthroat trout in Island Lake, mentioned in Pierce's 1885–1886 report, was behind the belief that yellowfin trout occurred there. As pointed out by Behnke and Wiltzius (1982), however, the Grand Mesa is in the Colorado River basin, and it is assumed that waters of the Grand Mesa contained the Colorado River cutthroat trout. There is no evidence that Island Lake was barren of trout before 1885.

Jordan (1922) stated in his autobiography that the yellowfin cutthroat trout was "successfully introduced into France from eggs shipped from the Mount Massive, Leadville, Hatchery." The source of this half-true story of transoceanic propagation is Jaffé (1902), who operated a hatchery at Sandfort, Germany. Jaffé recounted that he received 10,000 eggs of yellowfin cutthroat trout (la truite à nageoires jaunes) from the U.S. Fish Commission in 1899, stating that the eggs were taken from "La Mesa, Colorado." This is verified in the U.S. Fish Commission report for 1899 and for 1902, when an additional 20,000 cutthroat eggs collected from Grand Mesa lakes were shipped to Jaffé. The Commission reports, however, do not identify these shipments as yellowfin cutthroat trout, only as "black-spotted" trout.

Jaffé distributed his "yellowfin" trout to other hatcheries in Germany and offered to supply this new fish to French hatcheries. He concluded that "the establishment of the species seems almost certain." However, no further information on the fate of these advertised fish (most likely Colorado River cutthroat trout from the Grand Mesa) shipped to Germany in 1899 and 1902 has come forward since Jaffé's 1902 publication.

Thus, the yellowfin cutthroat trout remains a great ichthyological mystery, as to both its origin and its ultimate fate. The remote possibility that a lost yellowfin population lingers on as the result of some early, unrecorded introduction is intriguing and has stimulated several expeditions—all, so far, fruitless. Yet believers are not wanting, perhaps urged on by accounts such as the following. In the June 1891 issue of *Sports Afield* there is a photo (reproduced by Wiltzius 1985) showing three large trout that I identify as yellowfin cutthroat trout. No other form of trout in Colorado in 1891 would have had such a spotting pattern with a profusion of very small spots concentrated on the caudal peduncle. The *Sports Afield* text stated that the trout were caught in a ranch pond near Buena Vista, downstream on the Arkansas River below Twin Lakes. The 1891 photo is evidence that unrecorded introductions of yellowfin cutthroat trout were made by the Colorado Fish Commission in 1885–1886, and probably for some years thereafter. Might any offspring of those early introductions be lurking in some remote water, waiting to make their finder famous?

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Color Plates: Illustrations by Joseph R. Tomelleri

Differences in spotting between these illustrations and the typical patterns shown in the text figures exemplify the variation that can occur among isolated populations of the same taxon.

PLATE 1: Coastal cutthroat trout *Oncorhynchus clarki clarki*, premigratory sea-run fish from Sweet Creek, Siuslaw River drainage, Oregon.

Westslope cutthroat trout *Oncorhynchus clarki lewisi* from Cottonwood Creek, John Day River drainage, Oregon.

PLATE 2: Lahontan cutthroat trout *Oncorhynchus clarki henshawi* from East Fork Creek, California.

PLATE 3: Paiute cutthroat trout *Oncorhynchus clarki seleniris* from Silver King Creek, California.

Whitehorse cutthroat trout *Oncorhynchus clarki* subsp. from Willow Creek, Oregon.

PLATE 4: Colorado River cutthroat trout *Oncorhynchus clarki pleuriticus* from Mitchell Creek, Colorado.

Rio Grande cutthroat trout *Oncorhynchus clarki virginalis* from Padre Creek, Pecos River drainage, New Mexico.

PLATE 5: Upper Klamath redband trout *Oncorhynchus mykiss "newberrii"* from Deming Creek, Upper Klamath Lake basin, Oregon.

California golden trout *Oncorhynchus mykiss aguabonita* from Cottonwood Creek, California.

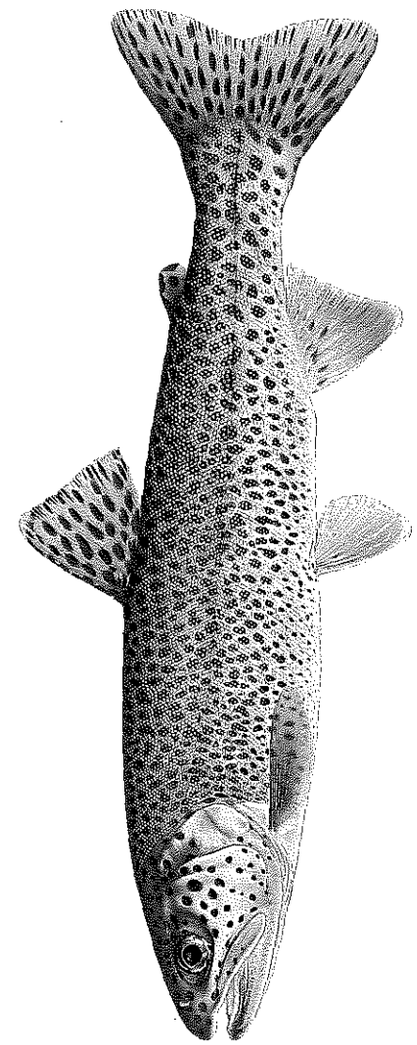
PLATE 6: Little Kern golden trout *Oncorhynchus mykiss gilberti* (or *whitei*) from Willow Creek, Little Kern River drainage, California.

Coastal steelhead *Oncorhynchus mykiss irideus* from the North Umpqua River, Oregon.

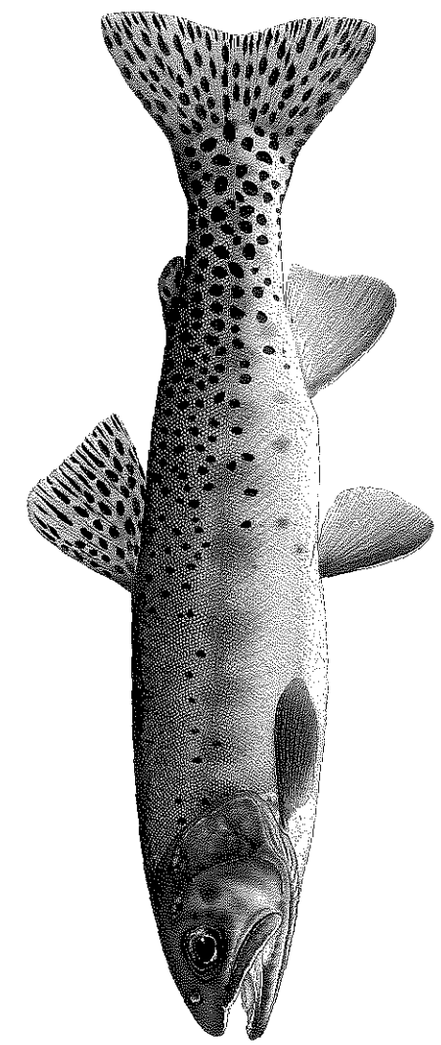
PLATE 7: Coastal rainbow trout *Oncorhynchus mykiss irideus* from the MacKenzie River, Oregon.

PLATE 8: Gila trout *Oncorhynchus gilae gilae* from Iron Creek, New Mexico.

Apache trout *Oncorhynchus gilae apache*, brood fish from the Williams Creek National Fish Hatchery, White River, Arizona.



Coastal cutthroat trout *Oncorhynchus clarki clarki*



Westslope cutthroat trout *Oncorhynchus clarki lewisi*

PLATE 1

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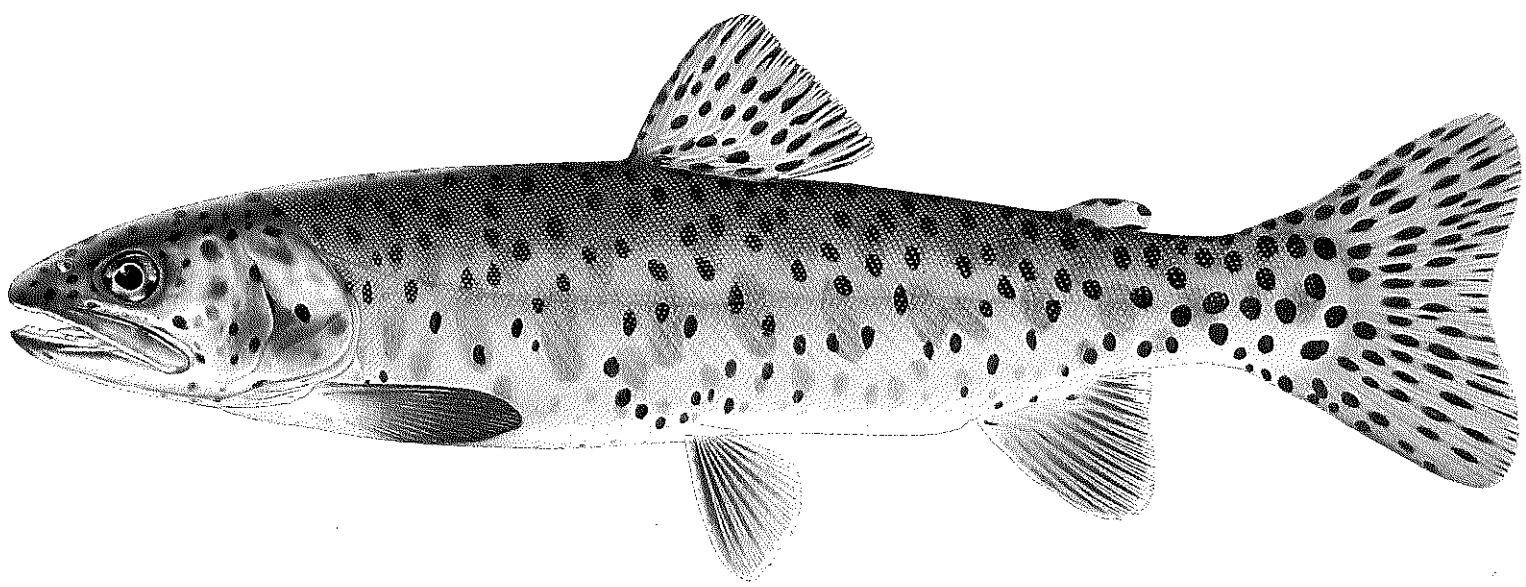
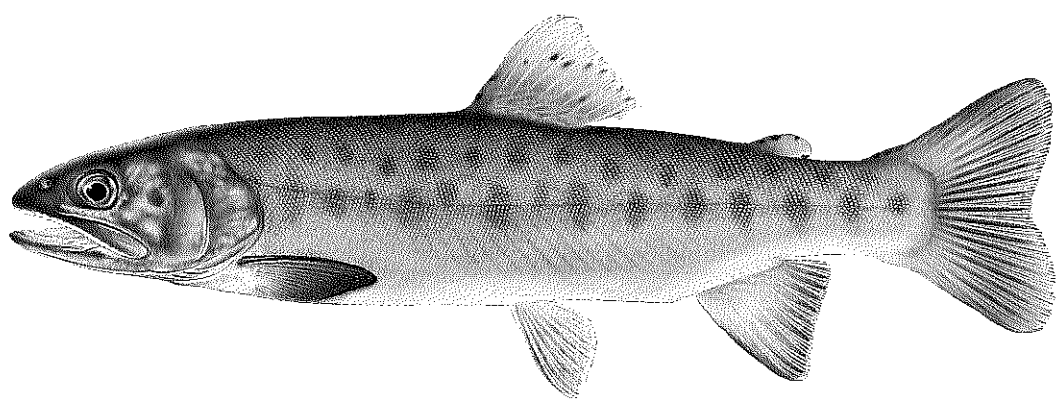
PLATE 2

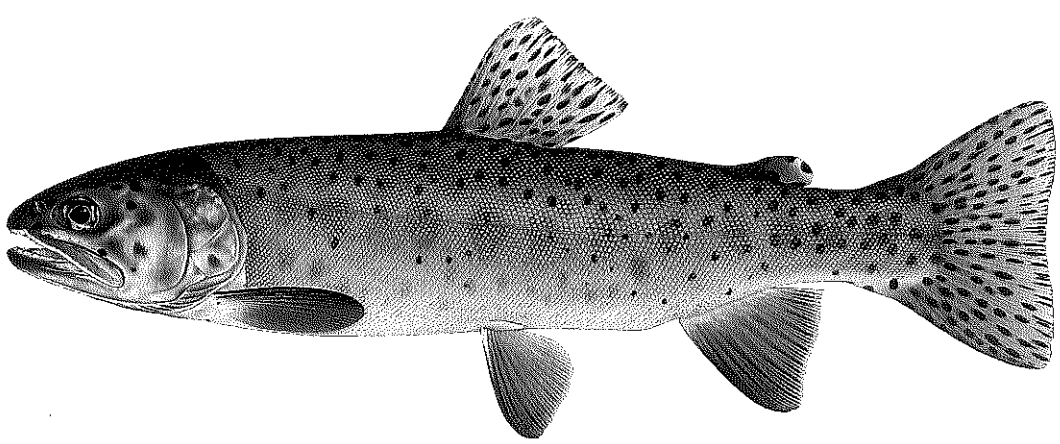


Lahontan cutthroat trout *Oncorhynchus clarki henshawi*

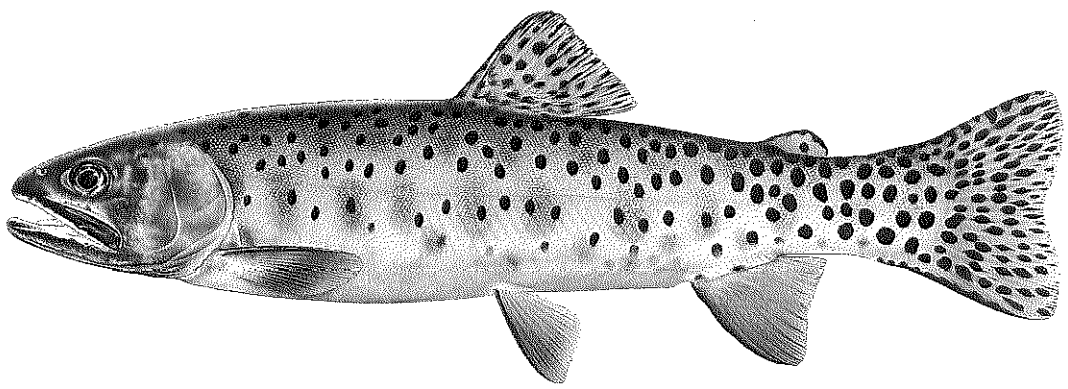
PLATE 3



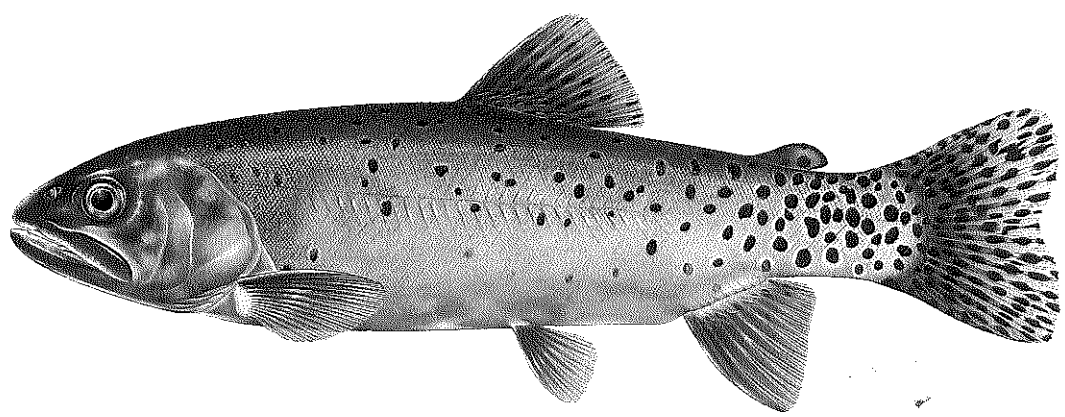
Paiute cutthroat trout *Oncorhynchus clarki seleniris*



Whitehorse cutthroat trout *Oncorhynchus clarki* subsp.

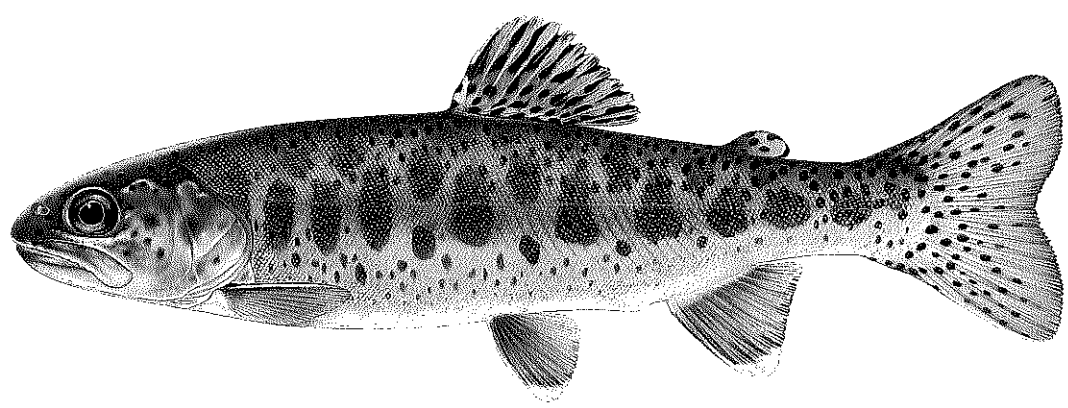


Colorado River cutthroat trout *Oncorhynchus clarki pleuriticus*

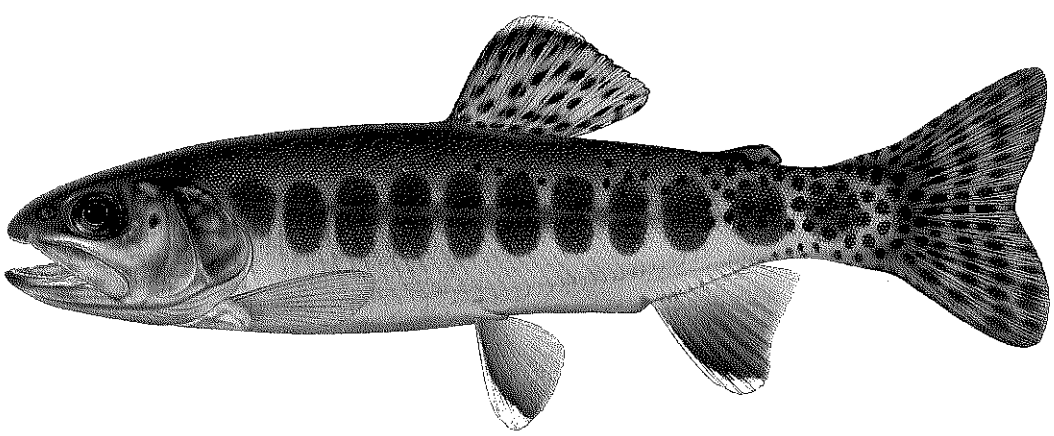


Rio Grande cutthroat trout *Oncorhynchus clarki virginalis*

PLATE 4



Upper Klamath redband trout *Oncorhynchus mykiss "newberrii"*



California golden trout *Oncorhynchus mykiss aguabonita*

PLATE 5

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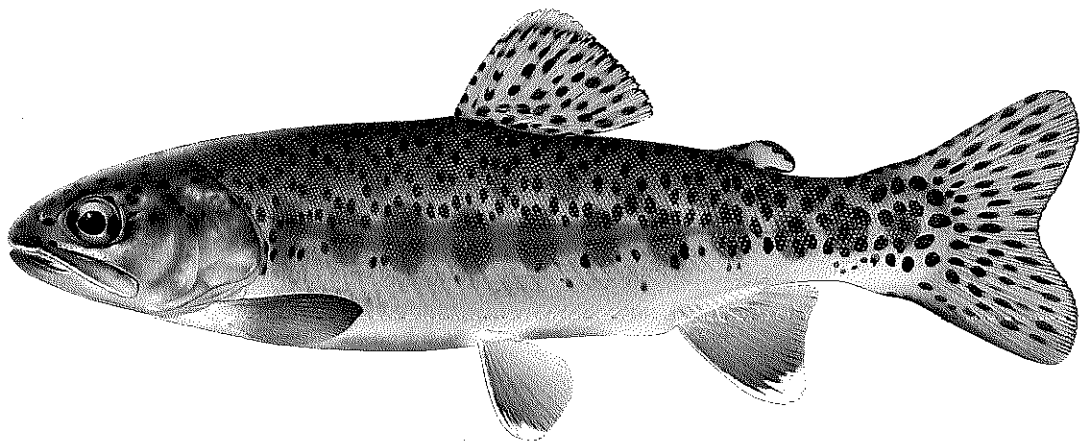
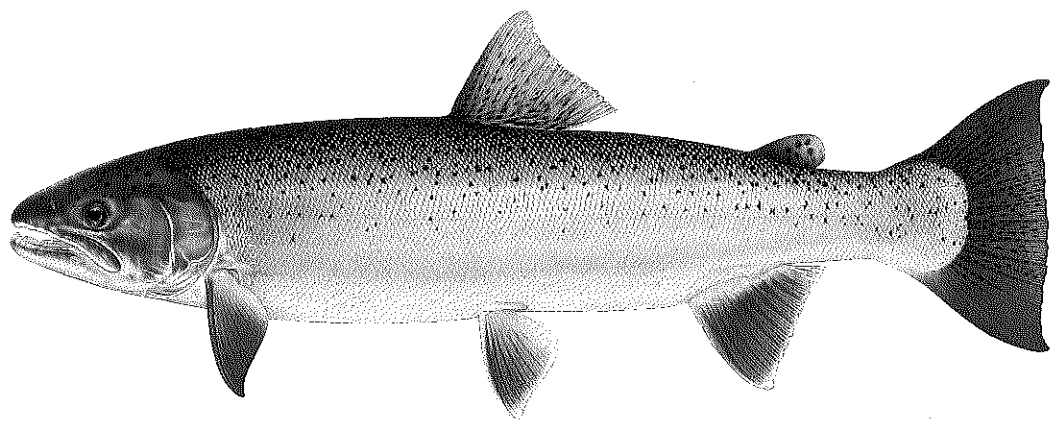
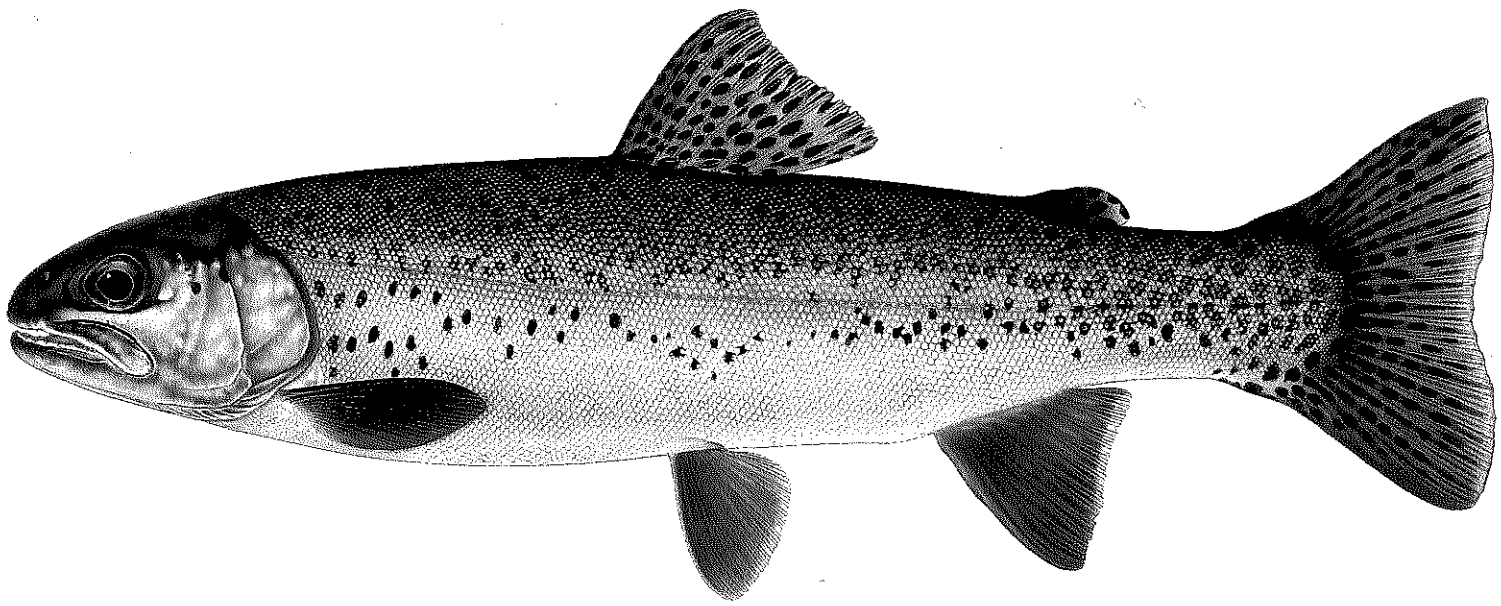


Little Kern golden trout *Oncorhynchus mykiss gilberti*

PLATE 6

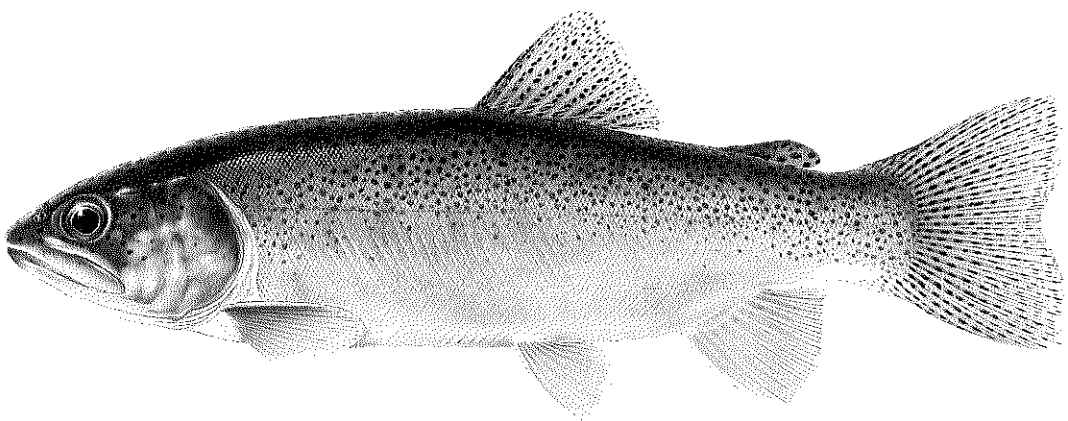


Coastal steelhead *Oncorhynchus mykiss irideus*

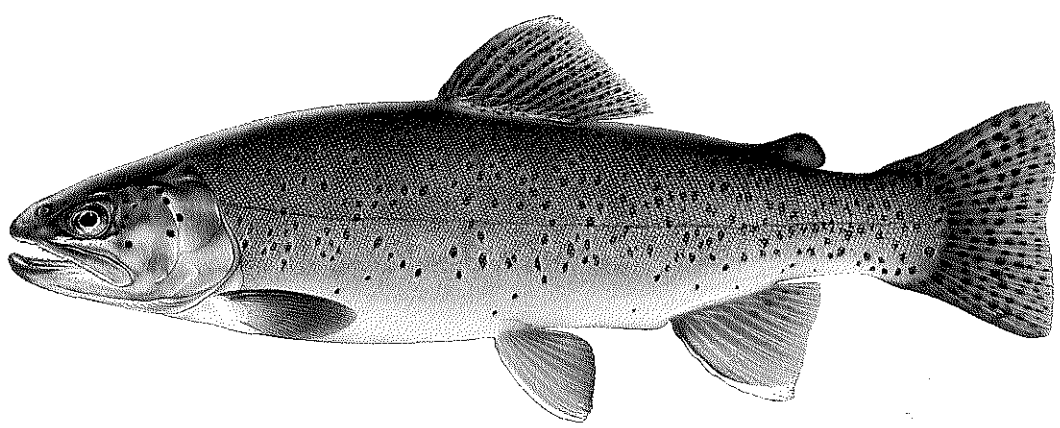


Coastal rainbow trout *Oncorhynchus mykiss irideus*

PLATE 7



Gila trout *Oncorhynchus gilae gilae*



Apache trout *Oncorhynchus gilae apache*

PLATE 8

PART III

Rainbow Trout

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9

RAINBOW AND REDBAND TROUT
Oncorhynchus mykiss

Assemblages of taxonomic characters associated with distribution patterns suggest to me that at least three major evolutionary groups are manifested in the present diversity found in the trout commonly called rainbow trout (Figure 1, page 8). A common ancestor of these groups branched from the primitive cutthroatlike trout lineage and diverged to produce all extant forms of rainbow and redband trout, the Mexican golden trout, and the Gila and Apache trout.

Although apparently only one ancestor was involved in the original separation from cutthroat trout, its complex radiation has made placement of branching points leading to each of the extant forms difficult. Most of the distinctive characters used to classify the more primitive forms of noncutthroat trout are shared primitive characters of little value in establishing phylogenetic branching sequences. Much of the evidence from karyotypes and electrophoresis is also ambiguous, perhaps because there were few long periods of geographic isolation comparable to those that resulted in the divergences of the four major subspecies of cutthroat trout. Where a lineage was long isolated, as in the Gila River system, clear-cut differentiation from all other noncutthroat trout is apparent in the taxonomic characters and karyotypes of modern descendants. In general, however, differentiation among evolutionary lineages of noncutthroat trout is not marked, making any attempt to classify the modern diversity into species and subspecies highly provisional and open to individual interpretation.

The groups sharing the most primitive traits are associated with ancestral distributions radiating from the Gulf of California. These are the Gila and Apache trout of the Gila River system, the Mexican golden trout, and other rainbowlike trout indigenous to waters on the mainland of Mexico. These trout are treated separately from rainbow and redband trout in later chapters.

In the species *Oncorhynchus mykiss* I include three major groups: (1) the redband trout of the Columbia River basin, both east of the Cascade Mountains and in the upper Fraser River basin (classified as *O. mykiss gairdneri*); (2) the redband trout of the Sacramento River basin, which is divided into two Kern River drainage subspecies, *O. m. aguabonita* and *O. m. gilberti*, and the McCloud River subspecies (provisionally denoted as *O. m. stonei*); and (3) the coastal

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rainbow trout *O. m. irideus*. *Oncorhynchus m. mykiss* of east Asia is also considered a coastal rainbow trout.

Other forms of *O. mykiss*—such as the redband trout native to Oregon desert basins, Upper Klamath Lake, the Pit River drainage, and Eagle Lake, California—cannot be consistently distinguished from the three groups listed above. Presently, their classification is a matter of personal preference and professional judgment.

Compared with other rainbow trout, the redband trout subspecies of the Sacramento and Columbia river basins share cutthroatlike trout characters such as brighter coloration, larger and sparser spots, elliptical parr marks, more numerous scales, fewer pyloric caeca, and vestigial basibranchial teeth. I use the term redband trout for subspecies of both basins, but as noted in Figure 1, it is not known if they arose from a single ancestor or if they represent separate branchings off a line leading to the more advanced coastal rainbow trout.

Classifiers of the trout I include as *O. mykiss* have wavered from recognizing many species to regarding all as a single species. In the 1880s, Jordan first considered all rainbow trout a single species after puzzling over resident (nonmigratory) forms and anadromous steelhead. When Jordan discovered that some of the steelhead ascending the Columbia River had more scales in the lateral series (140–180) than did coastal rainbow trout (120–140), he recognized two species: *Salmo gairdneri*, the fine-scaled steelhead of the Columbia River, and *S. irideus*, the coarse-scaled rainbow trout along the Pacific Coast.

When, in the 1890s, Jordan studied and described the California golden trout (as subspecies *aguabonita*, assigned first to cutthroat trout and then to rainbow trout) and two subspecies of fine-scaled trout resident in the McCloud River (*stonei*, assigned to *S. gairdneri*, and *shasta*, assigned to *S. irideus*), he became confused about the classification of western trout in general and of rainbow trout in particular. This confusion was heightened by the trout collected from the Columbia River basin by Gilbert and Evermann (1894). From Shoshone Falls of the Snake River westward to the Cascade Range, Gilbert and Evermann encountered resident populations of fish that seemed to bridge the gap between interior cutthroat and coastal rainbow trout. These fish had scale counts closer to those of cutthroat trout (140–170) and often had traces of a cutthroat mark, but (like rainbow trout) they lacked basibranchial teeth. The form associated with the Columbia River basin east of the Cascade Range was dubbed the silver trout and classified as a subspecies of cutthroat trout, *Salmo mykiss gibbsi*, by Jordan and Evermann (1896). Jordan (1892) conferred still another name, *Oncorhynchus kamloops*, on the Kamloops trout native to lakes in the upper Columbia River and Fraser River basins of British Columbia. A year before he died, Jordan (in Jordan et al. 1930) recognized 16 species in his classification of rainbow, redband, and California golden trout, although he then believed the Kamloops trout of British Columbia was synonymous with *gairdneri* (the redband trout of the Columbia River). Dymond (1932) continued to recognize *kamloops* as a species separate from *gairdneri*.

The trout native to the upper Klamath Lake basin and to several desiccating basins of southern Oregon were long a mystery. Cope (1879) first called them rainbow trout but later (1889) considered them to be cutthroat trout. Snyder (1908) classified these Oregon desert basin trout as cutthroat trout.

In the 1930s and 1940s, many experimental data demonstrated that taxonomic characters such as the numbers of scales and vertebrae could be modified by incubating eggs at different temperatures. Most fishery workers then followed the lead of Mottley (1934a, 1934b, 1936b, 1937) in regarding all forms of rainbow trout (except *aguabonita*) as a single species, *Salmo gairdneri*, and assuming that variations in their characters were mainly environmentally induced and not reflections of evolutionary divergence. Needham and Gard (1959) and MacCrimmon (1971) essentially lumped all noncutthroat trout of western North America as a single species.

From examination of museum specimens, I discovered consistent differences in scale counts between rainbow trout native to the upper Sacramento River basin of California, to the Oregon desert basins, and to the upper Columbia River basin on one hand, and rainbow trout native to coastal drainages on the other. These differences were too great, too consistent, and too widespread to be explained by direct environmental influence. Although I recognized the reality of divergent groups of rainbow trout, I first believed that interior rainbow trout originated from hybridization between interior forms of cutthroat trout and coastal rainbow trout when the two species came into contact after the last glacial period. This opinion was expressed in a paper on the origin of hatchery rainbow trout from the McCloud River (Needham and Behnke 1962).

Collections of trout specimens in northern California and southern Oregon in 1968, combined with studies of the California golden trout, led me to conclude that the interior noncutthroat trout—from the California golden trout of the Kern River drainage in south-central California to the mountain Kamloops trout in the headwaters of the Columbia River basin in British Columbia—represented a more primitive stage of rainbow trout evolution. I noted general trends in these interior forms for yellow and orange coloration, a trace of a cutthroat mark, vestigial basibranchial teeth, and pronounced white or yellow tips on the dorsal, anal, and pelvic fins. Also, compared with coastal rainbow trout, they tended to have higher scale counts, fewer pyloric caeca, and elliptical rather than rounded parr marks. I grouped these interior populations under the name redband trout.

I have expressed my opinion on the evolutionary reality of redband trout in several publications (Behnke 1970, 1972b, 1981, 1986b, 1988b; Schreck and Behnke 1971). Part of my confidence in the group's integrity lies in the constellation of characters listed above, although, as I discuss shortly, none of those characters discriminates redband trout absolutely from other taxa. Another part of my confidence stems from the largely coherent history that can be constructed for the group. The most primitive living species linked to redband trout—Gila–Apache and Mexican golden trout—are associated with the Gulf of California, so it is likely that ancestral redband trout reached the Sacramento–San Joaquin basin from the south during the second half of the Pleistocene Epoch. Spreading through the 750-km-long valley, these fish began differentiating into distinctive populations, of which several persist today at the northern (McCloud drainage) and southern (Kern drainage) ends of the basin. From a still somewhat primitive assemblage of redband trout in California, a group moved

farther north, arriving at the Columbia River during or just before the time of the last major glacial advance, some 30,000 years ago. High water levels during the pluvial climate of this era provided access to the now-isolated basins of eastern and central Oregon. Some redband trout moved into and among these basins, developing adaptations to lake conditions, and spreading southward to close the loop back to the northern Sacramento basin. Other redband trout moved up the Columbia River, colonizing its tributaries to the limits posed by barrier falls, and following the retreating glaciers into the Columbia's northern headwaters, where they found ways into the upper Fraser basin and possibly into the Athabasca system (but see below). Meanwhile, the coastal subspecies of rainbow trout arose, perhaps in the Sacramento basin, and spread both south to Mexico and north to Alaska, from where the subspecies moved to the Kamchatkan Peninsula in Asia during late- or postglacial times. Such a history is consistent with the modern distribution of redband and coastal rainbow trout (Figure 13). No geographical patterns of differentiation suggest that coastal rainbow trout survived the last glacial period in a northern refugium (Beringia), although other salmonids did so (Lindsey and McPhail 1986).

New information[1] sent to me by Leon Carl (Ontario Ministry of Natural Resources, Maple) in April 1992 raises serious doubts about the scenario outlined above for the late- and postglacial entries of redband trout into the Columbia and Fraser drainages and their subsequent transfer from Fraser headwaters to the Athabasca River. The Athabascan trout have some basic redband characters (such as large, coarse spotting, yellowish colors, and 40 pyloric caeca) but they have low scale counts (means of 31 scales above the lateral line and 132 in the lateral series). Based on the low scale counts and electrophoretic distinctions, Carl and his colleagues concluded that the trout native to the Athabasca drainage in Alberta are not derived from any form of redband trout presently known in the Fraser and Columbia drainages or from any form of coastal rainbow trout. Rather, these fish represent a more primitive form of redband trout that gained access to the Athabasca drainage before the last glacial period—64,000 years ago or earlier—and survived the last ice advance in a glacial refuge. In support of this conclusion, Carl et al. cited the occurrences of two subspecies in the Athabasca drainage that are derived from the Fraser or Columbia basins: the undescribed Jasper longnose sucker *Catostomus catostomus* ssp. and the Banff longnose dace *Rhinichthys cataractae smithi*.

If a form of redband trout lived in the Fraser basin before the last glacial period, it would be expected to occur in the Columbia basin then as well. If it did, redband trout should have had access to areas above the present barrier falls on the Kootenay, Pend Oreille, Spokane, and Snake rivers and also to Lake Chelan, Waha Lake, and Crab Creek. No native redband trout met the first European visitors to these areas, however, and the cutthroat trout that are there imply a very long-term absence of redband trout.

Much is yet to be learned about this subject, and my opinions about the

[1]L. M. Carl, C. Hunt, and P. E. Ihssen. A taxonomic study of the Athabasca rainbow trout, *Oncorhynchus mykiss*. Manuscript (1992) submitted for journal publication as Ontario Ministry of Natural Resources contribution 92.08 (Carl, personal communication).

sequences of dispersion and differentiation of rainbow and redband trout are far from definitive. With obvious reservations concerning the Athabascan populations, I recognize three evolutionary groups within the modern *Oncorhynchus mykiss*, as suggested previously. From least to most advanced, these are the redband trout of the Sacramento–San Joaquin basin, the redband trout of the Columbia and Fraser basins, and coastal rainbow trout.

Although the redband group as a whole shows distinctive morphological tendencies, it embraces a great deal of variation that discourages firm taxonomic boundaries around and within the group. For example, redband trout from Sheepheaven Creek, California, average 16 gill rakers (Gold 1977)—the lowest sample mean known for any form of cutthroat or rainbow trout—whereas some early museum specimens of redband trout from Oregon desert basins (collected before hybridization with rainbow trout occurred) average around 23 gill rakers. Mean numbers of vertebrae range from 59–60 in California golden trout to 64–66 in upper Columbia basin fish. If all the data I have gathered on redband trout were to be quantitatively treated in the computer program used by Gold (1977), the lines depicting redband trout would largely encompass coastal rainbow trout at one extreme and cutthroat trout at the other. Thus it is impossible at present to quantitatively diagnose and clearly separate all redband trout from all coastal rainbow trout on the basis of any morphological character. Redband–rainbow distributions are essentially continuous throughout the species' range. In contrast to the long isolation that promoted development of the four major cutthroat trout subspecies, gene flow probably has occurred among all forms of *O. mykiss*, which would have hindered clear-cut differentiation among them. Coastal rainbow trout have a geographically long interface with redband trout (Figure 13), and Columbia–Fraser redband trout extending south through the Oregon desert basins could have mixed with Sacramento redband trout in Goose Lake and the Pit River in northern California.

Genetic analyses have not yet indicated much distinction among subspecies of rainbow and redband trout, but they have revealed differentiation within the Columbia–Fraser redband group, which is morphologically and meristically uniform. Although mitochondrial DNA research is gaining prominence in salmonid biology, most genetic work done with western trout over the past 20 years has involved electrophoretic analysis of enzymes, which provides indirect clues about the genetic makeup of individuals and populations. Particular attention has been given to the enzyme lactate dehydrogenase (LDH) because it shows detectable variation in biochemical structure among trout populations, reflecting the action of different alleles at the *B2* locus of the *LDH* gene (denoted *LDH-B2** in current genetic nomenclature: Shaklee et al. 1990). The two most common alleles at this locus in the rainbow–redband fauna are denoted **100* and **76* (*LDH-B2*100* and *LDH-B2*76* in the full notation), named for the electrophoretic behavior of the variant enzymes they encode. Minor alleles (alleles occurring with low frequencies in populations) have been detected at the *LDH-B2** locus; their relevance to the history of rainbow and redband trout is not yet clear, though they contributed to the unique characterization of Athabascan trout (Carl, personal communication).

Allendorf (1975) and Utter and Allendorf (1977) were the first to show that redband trout of the Columbia River predominantly have the *LDH-B2*76* allele

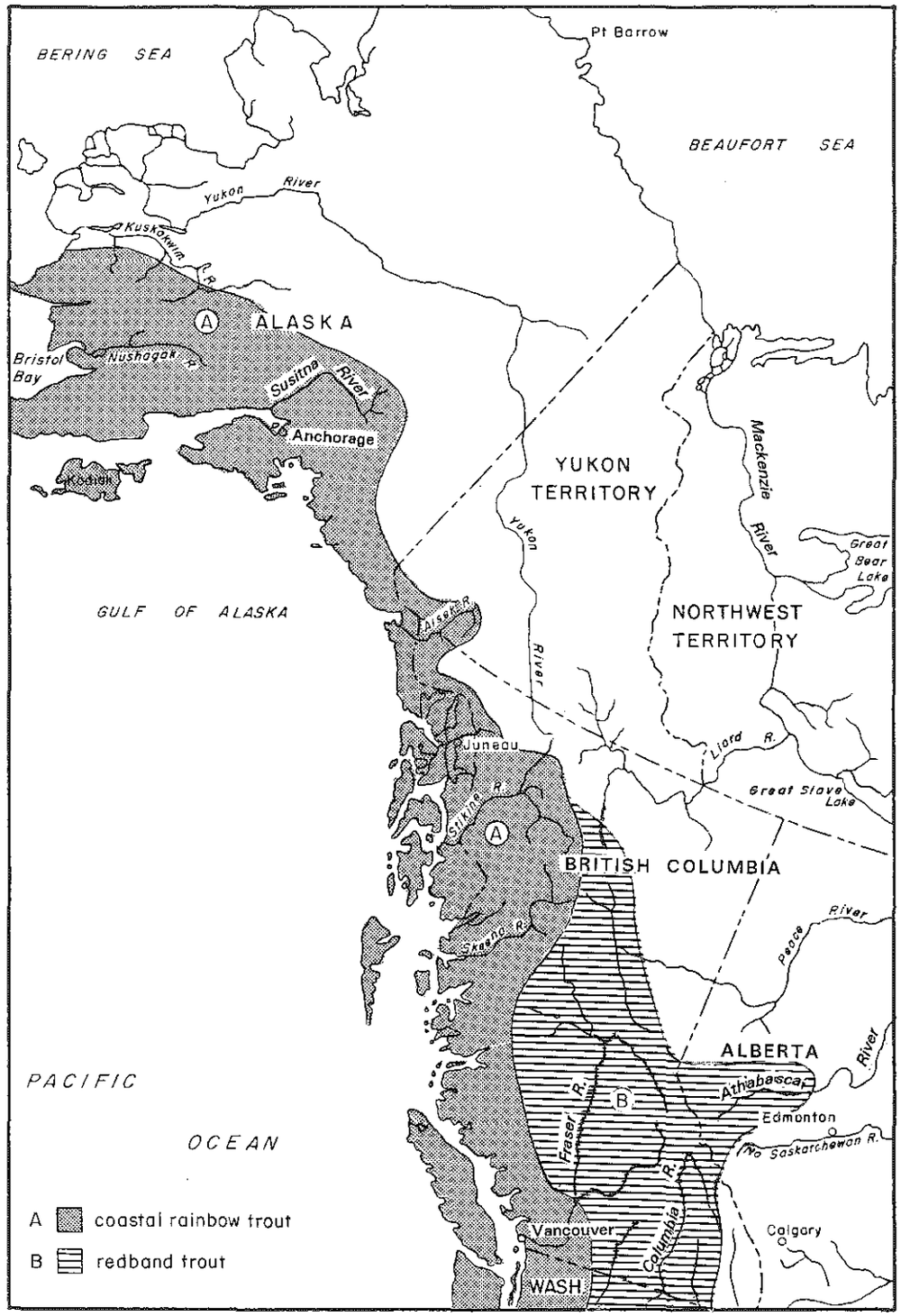

FIGURE 13.—Distributions of coastal rainbow trout and redband trout.

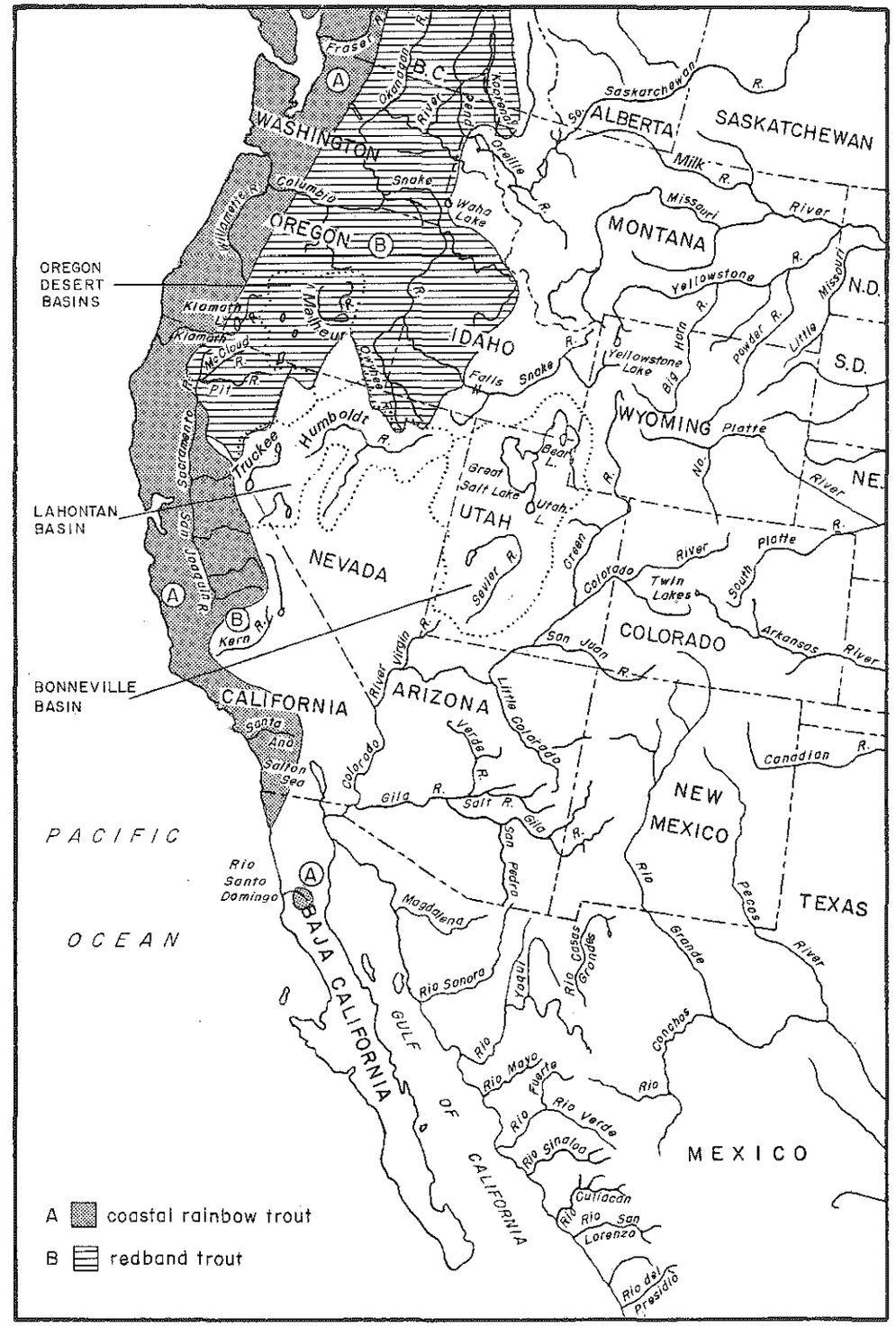

FIGURE 13.—Continued.

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whereas coastal rainbow trout predominantly carry the **100* allele. Other workers have confirmed this generality but added some important details. At several places around the periphery of the redband trout range in and near the Columbia River basin, populations have been found with a preponderance of the **100* allele. According to descriptions of the authors or my own observations, these fish all are phenotypically "correct" redband trout. Such populations occur in the Oregon desert basins (Berg 1987); in the White River, a tributary to the Deschutes River isolated by barrier falls (the **76* allele predominates elsewhere in the Deschutes basin: Currens et al. 1990); and in the headwaters of the Athabasca River (Carl, personal communication). Furthermore, the **100* allele predominates in Sacramento basin redband trout, as well as in coastal rainbow trout. Thus there is no doubt that a predominance of the **100* allele is the primitive condition in this species and that a high frequency of the **76* allele, characteristic of most Columbia and Fraser basin redband trout, is a recent development. This development postdates the initial spread of redband trout in the Columbia–Fraser system, the colonization of Oregon desert basins by redband trout, and the origin of coastal rainbow trout. High frequencies of the **76* allele could have originated either within the Columbia basin or outside it; the latter alternative implies a second invasion of the Columbia River by redband trout.

For my practical purposes, the genetic analyses imply that a population of rainbow–redband trout with a preponderance of the *LDH-B2*76* allele consists of Columbia–Fraser redband trout. A population with a high frequency of the **100* allele, however, could be redband or rainbow trout of any stock; phenotypic analysis backed by knowledge of collection locality will be needed to identify the sample.

Virtually all redband trout examined to date have 58 chromosomes, but coastal rainbow trout may have from 58 to 64 chromosomes, and the number may vary within the same population (Thorgaard 1983, and personal communication). Thus, chromosome analysis can be an ambiguous guide to subspecies identification.

Hybridization and gene flow between interior redband and coastal rainbow trout probably occurred during and after the last glacial epoch. Only in areas isolated by barriers was it likely that ancestral redband trout underwent no genetic mixing with coastal rainbow trout (none, at least, until hatchery rainbow trout were introduced). These areas include the South Fork of the Kern River (California golden trout), the headwaters of the McCloud River (Sacramento redband trout), and perhaps certain isolated headwaters in the Columbia River basin in British Columbia (the mountain Kamloops trout of Dymond 1932), where native trout are conspicuously differentiated from coastal rainbow trout. Today, the greatest potential for hybridization between redband and coastal rainbow trout occurs in the vicinity of the Cascade Mountains and their extensions into British Columbia. These mountains roughly separate coastal rainbow trout to the west from redband trout to the east (Figure 13). Transitions in meristic characters and in allele frequencies at the *LDH-B2** locus occur in steelhead populations in tributaries to the Columbia River in the Cascade Mountains. For example, although Schreck et al. (1986) grouped the steelhead of

Fifteenmile Creek (eastern Cascade tributary) with redband steelhead (all populations east of Cascades), these fish resemble coastal rainbow trout in their full suite of taxonomic characters more than they do other redband steelhead from east of the Cascades; also, they form the only winter-run redband steelhead (all others are summer-run). As other examples, I have examined *O. mykiss* specimens from resident native populations in small tributaries to the Klamath River (below Klamath Lake) and in the Rogue River, and from headwater streams in southern California, where only coastal rainbow trout would be expected to occur. These specimens exhibit some characters typical of interior redband trout. Such a situation makes it very difficult, if not impossible, to divide rainbow and redband trout into subspecies comparable to those of allopatric cutthroat trout subspecies. For fisheries management the major significance of separate evolutionary lines leading to coastal rainbow and interior redband trout does not concern correct taxonomy. Rather, it concerns differences in the adaptive specializations the two forms acquired over several thousand years of evolution and how those differences can be accommodated in management programs.

Coastal rainbow trout are distributed along the North American coast from the Kuskokwim River of Alaska to Baja California. Detailed data on the taxonomic characters of the native trout throughout most of this range are lacking, and one can only speculate on the relative influence of redband trout hybridization in the evolutionary history of the coastal rainbow trout.

Anadromous steelhead populations are found in both coastal rainbow and redband trout groups. The only steelhead I presently classify with redband trout are those ascending the Columbia River east of the Cascade Range and those in the Fraser River above Hell's Gate. It is possible that redband steelhead once occurred in the upper Sacramento River basin and in the upper Klamath Lake drainage, but I have no evidence of this.

Some nonmigratory redband populations native to the Columbia River and Oregon desert basins have the genetic potential to become effective piscivores and attain large sizes. The Gerrard race of Kamloops (redband) trout native to Kootenay Lake, for example, evolved with kokanee. After introduced kokanee became abundant in Pend Oreille Lake, Idaho, Kootenay Kamloops trout were stocked there and attained weights to nearly 17 kg in 5 years (Scott and Crossman 1973; Behnke 1988b). This same race of Kamloops trout stocked in Jewel Lake produced fish to nearly 24 kg.

The world record angler-caught rainbow or redband trout is a 19.1-kg steelhead caught off Bell Island, Alaska (Hart 1973). I assume this record Alaska steelhead was a summer-run fish of the Skeena River basin, hence a form of coastal rainbow trout. The Babine River, a major tributary to the Skeena River, which enters the Pacific Ocean just south of the Alaska–British Columbia border, is noted for its large summer-run steelhead. Hart (1973) mentioned a 19.5-kg steelhead netted off Port Simpson just north of the mouth of the Skeena River.

As with other trout lineages, the significance to fisheries management of the large Kamloops trout of Kootenay Lake involves its peculiar evolutionary specializations. Relatively few lakes contain rainbow or redband trout that have evolved with kokanee for several thousand years, along the way acquiring the

adaptations necessary to become an effective predator on these landlocked sockeye salmon. Except for Crescent Lake, Washington, virtually all such lakes occur in the upper Fraser and upper Columbia river basins and are inhabited by Kamloops trout. Kokanees are widely propagated throughout the West for introductions in large lakes and impoundments. Typically, where introduced kokanees have flourished, the rainbow trout (or cutthroat trout) fishery has declined because kokanees outcompeted the trout for zooplankton; kokanees, with their more numerous gill rakers, can remove smaller crustaceans from the water column more effectively than can trout (Schneidervin and Hubert 1987). To establish a trophy trout fishery in kokanee lakes, management is well advised to introduce a preadapted kokanee predator such as the Kootenay Kamloops trout.

In the Oregon desert basins and in the arid regions of the Owyhee drainage (Columbia River basin) of southern Oregon, western Idaho, and northern Nevada, the redband trout has evolved adaptations to live in extremely harsh environments characterized by great extremes of water temperature and flow. In most of these situations, hatchery strains of rainbow trout are not effective predators or competitors. For many lakes characterized by warm summer temperatures and abundant nongame fish populations, fisheries management consists of periodic eradication of all fish and restocking with hatchery rainbow trout. A more innovative management approach would draw on the genetic diversity found in some redband trout populations and attempt to convert forage fish into trophy trout.

ORIGINS AND DISTRIBUTIONS

Their loss of basibranchial teeth and lower number of chromosomes indicate that rainbow and redband trout are phylogenetically more advanced than cutthroat trout. Also, their absence (before stocking) from areas above the major barrier falls in the Columbia River basin and from the most isolated sections of the Great Basin, where cutthroat trout are indigenous, indicates that the redband–rainbow lineage developed in North America after the cutthroat line. However, the general time period and geographic area involved in the separation of the noncutthroat evolutionary line from a primitive cutthroatlike ancestor, and the subsequent radiation of this line into groups of redband and coastal rainbow trout, are largely matters of speculation (Behnke 1988b).

An Asiatic origin of the rainbow–redband group could be hypothesized based on the assumptions put forth by Neave (1958), who proposed that the genus *Oncorhynchus* was derived from the genus *Salmo* in basins draining into the western Pacific Ocean during the Pleistocene. The fossil record reveals that *Oncorhynchus* appeared well before the Pleistocene, but Neave's speciation model might be applicable to the original separation of the rainbow–redband group from a cutthroatlike ancestor or the subsequent separation of coastal rainbow trout from redband trout.

If its center of origin was Asia, however, the rainbow–redband line left no evidence of it. The rainbow trout of Kamchatka appears to be a recent derivative of the coastal rainbow trout that migrated from North America during the late Pleistocene when the Bering Land Bridge existed. There is no evidence in taxonomic characters to suggest that the Asian rainbow trout is a primitive relict of an early stage of evolution in the rainbow–redband line. Of living forms, the most primitive noncutthroat trout appear to be the Gila and Apache trouts of the Gila River basin and the Mexican golden trout. The available evidence indicates that the ultimate origins of redband and rainbow trout lay near the Gulf of California.

In general, the most primitive living representative of the rainbow–redband group is the Sheepheaven Creek trout native to the headwaters of the McCloud River, above a series of barrier falls, at the north end of the Sacramento basin, California. Certainly the rainbow–redband group did not originate in Sheepheaven Creek. The McCloud distribution reflects an interior dispersal of the earliest primitive invaders of the Sacramento basin, which became isolated and protected from contact with the later-invading coastal rainbow trout.

The most inland penetration of redband trout in the Columbia River basin occurs in the Kootenay River. MacCrimmon (1971) drew the upstream limit at the British Columbia–Idaho border, but the actual native distribution extends upstream to the barrier falls on the Kootenay River between Troy and Libby, Montana (Allendorf et al. 1980).

The great majority of steelhead originally ascending the Columbia River must have been redband steelhead (only a relatively small part of the basin lies west of the Cascades). These interior runs have dwindled and many local races are extinct because of dams, irrigation, and land use practices. Although hatchery propagation of middle Columbia basin redband steelhead occurs on a massive scale, hatcheries can neither maintain the genetic diversity of wild stocks nor recreate the diversity of extinct stocks.

Hatchery rainbow trout derived mainly from coastal steelhead are also widely stocked throughout the ranges of western trout. These hatchery fish have led to hybridization with most populations of resident redband trout in the upper Sacramento River basin, the Oregon desert basins, and much of the Columbia River basin. Campton and Johnston (1985) described the hybrid influence from introduced hatchery rainbow trout on resident redband populations native to the Yakima River drainage.

Undoubtedly, a considerable amount of the original genetic diversity of both the Sacramento and Columbia redband trout has been lost during the past 100 years.

TAXONOMIC HISTORY

According to the international rules of zoological nomenclature, if all rainbow and redband trout are treated as a single species, their scientific species name must be *mykiss* because that was the first name applied to any member of the species. Richardson's 1836 description of *Salmo gairdneri* was based on a steelhead taken at Fort Vancouver, Washington, about 160 km from the mouth of the Columbia River. Although Fort Vancouver is west of the Cascade Mountains, most steelhead migrating past that point are headed for spawning areas east of the Cascades, where most of the Columbia basin lies, so the type

specimen most likely was a redband steelhead. Jordan and Evermann (1896) redefined *gairdneri* from a sample of steelhead taken from the Columbia River near Astoria, Oregon. The redescription included counts of 137–177 lateral-series scales and 42 pyloric caeca, which associates the name *gairdneri* with redband trout native to the Columbia River basin east of the Cascade Mountains. Thus, I recognize the rainbow or redband trout native to the Columbia River basin east of the Cascades and to the upper Fraser River basin (including Kamloops trout, resident stream forms, and steelhead) as *Oncorhynchus mykiss gairdneri*.

I essentially follow Jordan's usage of the name *irideus* for the coarse-scaled coastal rainbow trout, based on Gibbons's 1855 description of *Salmo iridea* from San Leandro Creek, tributary to San Francisco Bay. I classify coastal rainbow trout from California to Alaska as *O. m. irideus*.

The oldest name describing any of the redband forms native to the Sacramento River basin is *S. mykiss aguabonita*, given by Jordan in 1892 for the California golden trout native to the South Fork of the Kern River and Golden Trout Creek. In 1894 Jordan named *Salmo gairdneri shasta* and *S. irideus stonei* for resident trout native to the McCloud River. The names *shasta* and *stonei* are based on the same form of trout, which is somewhat intermediate between the extreme form of redband trout native to the McCloud River above barrier falls (Sheepheaven Creek population) and the coastal rainbow trout—indicating that hybridization occurred when the redband and coastal rainbow trout came into contact in the Sacramento basin.

The trout native to the main Kern River was named *S. gairdneri gilberti* by Jordan in 1894. The Little Kern golden trout was named *S. whitei* by Evermann in 1906. Schreck and Behnke (1971) pointed out that *gilberti* and *whitei* represent only slightly differentiated forms and suggested that *whitei* should be considered a synonym of *gilberti*. Undoubtedly, *aguabonita* and *gilberti* are more closely related to each other than either is to other groups of *O. mykiss*. If full species recognition were given for *aguabonita*, then *gilberti* should be a subspecies of *aguabonita* rather than of *mykiss*. However, the relationships of *aguabonita* and *gilberti* are phylogenetically close to other forms of *O. mykiss*, and their classification as subspecies of *O. mykiss*—*O. m. aguabonita* and *O. m. gilberti*—seems to me the most appropriate classification. I do not object to recognizing the Little Kern golden trout as *O. m. whitei*, however. The listing of *whitei* under the Endangered Species Act has promoted a successful recovery program for this form.

PROPAGATION

According to common belief, the hatchery rainbow trout was derived from a nonmigratory trout of the McCloud River—the Shasta rainbow trout. Needham and Behnke (1962) reviewed the U.S. Fish Commission's fish culture operations on the McCloud River from 1879 to 1888, based on the notes of Livingston Stone, director of the McCloud station. We pointed out that during the years of egg taking, the McCloud River drainage had both a steelhead run (probably a coastal rainbow trout) and resident populations of fine-scaled trout

(redband trout). Stone stated that he obtained small trout in tributary streams and large trout (up to 5 kg) that appeared late in the year (November–December) in the McCloud River. Both the small (redband) tributary trout and the large (coastal steelhead) trout were caught, kept in holding ponds, and indiscriminately spawned together. Because of the size differential, it can be assumed that most of the genetic background of these hatchery rainbow trout came from coastal steelhead.

Dollar and Katz (1964), hewing to the common belief about the origins of hatchery rainbow trout, concluded that all hatchery stocks are derived from the McCloud River, and that no substantial mixing with other sources occurred until 25,000 steelhead eggs from Skagit River, Washington, were brought into the Manchester, Iowa, federal hatchery in 1925. This, however, is far from the complete story. The very first propagation of rainbow trout was of coastal rainbow trout from the San Francisco Bay area, not from the McCloud River. In the first U.S. Fish Commission Report for 1872–1873, Stone recounted the propagation of rainbow trout (called "California brook trout") by the California Acclimatization Society, a quasi-public organization established to develop a state fish culture program until the California Fish Commission could assume responsibility. Leitritz (1970) has also provided historical information on this early propagation of rainbow trout.

It seems that San Francisco facilities for hatching trout eggs were established in 1870 in the city hall basement and on the University of California (Berkeley) campus. Until 1873, all rainbow trout eggs were obtained from wild populations of the San Francisco Bay region. Other sources, such as Kelsey Creek on Clear Lake (1873–1874), were also used before any eggs from McCloud River trout were taken. The first California shipments of rainbow trout outside the region (to New York and Michigan in 1875–1876 and to Japan in 1877) were not McCloud River trout. Some history on a contemporaneous, private hatchery operation of J. B. Campbell (and Myron Green, brother of Seth Green) was given by Wales (1939) and MacCrimmon and Gots (1972). Campbell constructed his hatchery on Campbell Creek near its junction with the McCloud River. It is not known if the eggs sold by Campbell to the California Fish Commission were mainly redband trout, mainly coastal steelhead, or a hybrid mixture of the two. The first propagation of McCloud River trout by Campbell occurred in 1877. In 1878, McCloud rainbow trout eggs were shipped to Seth Green to raise at his Caldonia, New York, hatchery.

In 1879, Livingston Stone took over Campbell's operation for the U.S. Fish Commission and moved the hatchery to Crooks Creek (now Greens Creek), a tributary to the McCloud 4 km below Campbell Creek. Myron Green, Stone's assistant of several years at the Fish Commission, then became superintendent of the Commission's trout propagation program on the McCloud River. From 1880 to 1888, about 2.5 million rainbow trout eggs were shipped from the McCloud hatchery to federal and state hatcheries, and brood stocks were established in federal hatcheries in Wytheville, Virginia, and Northville, Michigan. Soon afterward egg sources multiplied. From 1895 to 1900, great numbers of coastal steelhead from Redwood Creek, California, and from the Willamette, Klamath, and Rogue rivers of Oregon were propagated in federal hatcheries.

Further documentation of hatchery rainbow trout origins is available in Behnke (1990).

Scott et al. (1978) discovered that the first rainbow trout established in New Zealand (in 1883) came from a private hatchery that used steelhead eggs from Sonoma Creek, a tributary to San Francisco Bay. Kinunen and Moring (1978) discussed the origins of six strains of rainbow trout propagated in Oregon hatcheries and concluded that only one of these strains could be considered native to Oregon. Busack et al. (1979) and Busack and Gall (1980) examined the origins and genetic background of hatchery strains of rainbow trout in California.

Thus, the overwhelming majority of hatchery brood stocks of rainbow trout maintained around the world originated mainly from various mixtures of coastal steelhead. Redband trout of the McCloud River made only a minor contribution during hatchery operations there during 1877–1879 (J. B. Campbell) and from 1880 to 1888 (U.S. Fish Commission). In California alone, 169 hatcheries and egg-taking stations drew on diverse populations of rainbow trout from 1870 to 1960 (Shebley 1922; Leitritz 1970). Exchanges of fish and eggs among state, federal, and private hatcheries mixed these rainbow trout stocks with little regard to their ancestry.

Possibly the genetic diversity of the various stocks that formed the present strains of hatchery rainbow trout provided a basis for rapid domestication. Hatchery propagation of rainbow trout is more recent than that of brook trout and much more recent than that of brown trout, yet rainbow trout are easier to rear in hatcheries.

Some of the original genetic profiles of hatchery stocks have been manifested in rainbow populations established outside their native range. The two discrete runs of rainbow trout spawning in a tributary to Lake Huron, previously discussed, may be derived from chance introductions of different steelhead races that maintained their genetic identity. Lake McConaughy, Nebraska, has a steelheadlike rainbow trout developed from introductions in the North Platte River drainage many years ago, probably before the complete domestication of hatchery strains (Van Velson 1974, 1978).

A discussion of the origins of domesticated hatchery strains is largely of academic interest, although it may also be useful in genetic considerations of hatchery characteristics such as disease resistance. Once a race of trout has been thoroughly domesticated by rigorous selection to perform well under hatchery conditions, the genetic changes that have taken place favoring growth and survival under artificial conditions are detriments to survival under harsh natural conditions, particularly in competition with other fish species.

10

REDBAND TROUT OF NORTHERN BASINS

Columbia River Redband Trout *Oncorhynchus mykiss gairdneri*

TYPICAL CHARACTERS

Variable but generally differentiated from coastal rainbow trout by larger spots, more-elliptical parr marks that often include dorsal and ventral supplementary rows (as in cutthroat trout), a tendency for yellow and orange tints on the body, a trace of a cutthroat mark, and light-colored tips on dorsal, anal, and pelvic fins. Vertebrae typically 63–66 (mean, about 64); pyloric caeca typically 30–50 (mean, about 40); lateral-series scale counts variable from about 130 to about 170 (means, 135–160).

DESCRIPTION (Figure 14)

Resident stream populations are found throughout the range of the redband trout east of the Cascades in the Columbia River basin. Lacustrine populations, commonly called Kamloops trout, occur in lakes in the upper Columbia and upper Fraser river basins. Some steelhead populations once migrated almost 1,600 km from the sea to the Snake River below Shoshone Falls and to the upper Columbia River in British Columbia. Both of these long-distance runs have been lost because of dams. Considerable variability in life history and in taxonomic characters is found in this group of trout. An extreme form of Columbia redband is the mountain Kamloops trout, named *Salmo kamloops whitehousei* by Dymond (1931), who based his description on populations in British Columbia probably long isolated from coastal rainbow trout.

DISTRIBUTION

I somewhat arbitrarily define the distribution of Columbia River redband trout to include the Columbia River basin east of the Cascades to barrier falls on the Kootenay, Pend Oreille, Spokane, and Snake rivers; the upper Fraser River

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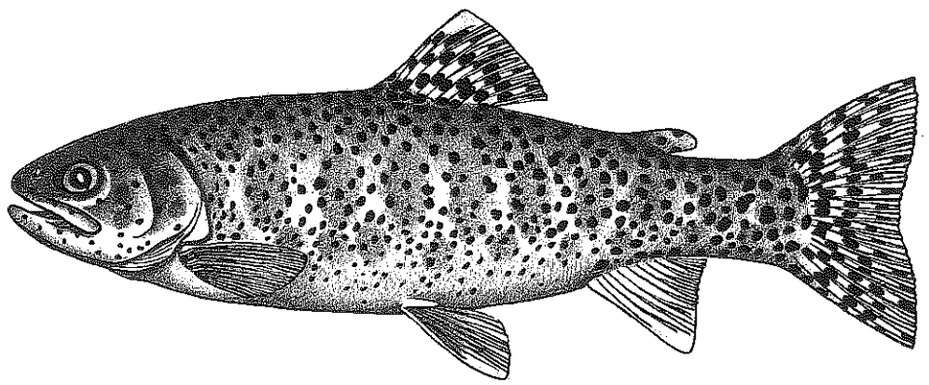

FIGURE 14.—Columbia River redband trout.

basin above Hell's Gate; and Athabasca headwaters of the Mackenzie River basin, where headwater transfers evidently occurred from the upper Fraser River system. Rainbow trout native to the MacKenzie's Liard and Peace drainages may be redband trout derived from the Fraser system or coastal rainbow trout from the Skeena or Stikine basins (Lindsey and McPhail 1986). The native trout of the Oregon desert basins and the Upper Klamath Lake basin are considered to be a more primitive form of redband derived from the Columbia River basin, distinguished by the *LDH-B2*100* allele. The native redband trout of each basin has its own peculiarities. All forms could be placed in the subspecies *gairdneri*, or several new subspecies could be recognized.

A peculiar form of redband trout is native to the Wood River drainage of Idaho, a tributary to the Snake River below Shoshone Falls. The fish fauna of the Wood River appears to have been long isolated from communication with the Snake River (Hubbs and Miller 1948). Gilbert and Evermann (1894) reported cutthroat trout from the Big and Little Wood rivers near Shoshone, Idaho. I examined three of these specimens collected in 1892, two from the Big Wood River (Stanford University number 2040) and one from the Little Wood River (2023). They are redband trout. The Big Wood River specimens have severe vertebral deformities (fusion), perhaps as a result of toxic mining pollution, and are of limited use for taxonomic analysis. The Little Wood River specimen has 37 scales above the lateral line, 169 scales in the lateral series, 64 vertebrae, and 19 gill rakers.

A long history of heavy stocking of hatchery rainbow trout in the Big and Little Wood river drainages, combined with environmental changes, makes the persistence of the native genotype doubtful. In 1988, I examined 10 specimens (93–177 mm, total length) collected from the Big Wood River above its confluence with the East Fork. They have a peculiar appearance marked by a deep body, short head and jaw, thick maxillary, and short fins. The parr marks and spotting pattern are more typical of redband trout than of hatchery (coastal) rainbow trout, but the scale counts are low: 29–32 above the lateral line and only 116–135 in the lateral series.

The evolutionary isolation of the Wood River indicates that its native redband trout should have the primitive *LDH-B2*100* allele. This also is the allele carried by hatchery rainbow trout, so electrophoretic analysis of lactate dehydrogenase may not be useful for an assessment of stock purity.

TAXONOMIC NOTES

My classification of a group (or groups) of trout of the rainbow trout evolutionary line as the subspecies *O. m. gairdneri* essentially follows the redescription of *gairdneri* by Jordan and Evermann (1896), who acted as the first revisers of the name. The name *gairdneri* is associated with Columbia River redband trout. The subspecies *O. m. gairdneri* is here applied to the Columbia River and Fraser River redband trout and all closely related forms derived from it. This subspecies includes steelhead populations, populations adapted to lakes (Kamloops trout), and resident stream populations.

Berg (1987) and Williams et al. (1989) classified the Columbia River redband trout as *O. m. gibbsi*. This classification is similar to Jordan and Evermann's (1896) subspecific designation for redband trout east of the Cascades, except that Jordan and Evermann classified *gibbsi* as a subspecies of cutthroat trout. Jordan and Evermann (1896) fixed Richardson's 1836 description of *gairdneri* with Columbia basin redband trout. The 1836 description of *gairdneri* has priority over Suckley's 1858 description of *gibbsi*, and *gairdneri* is the correct subspecies designation for the redband trout of the Columbia and Fraser basins.

Dymond (1931, 1932) recognized the native trout of the upper Columbia and upper Fraser basins in British Columbia as a full species, *Salmo kamloops*. Dymond knew that some British Columbia Kamloops trout are quite distinct from coastal rainbow trout and that they must represent a real evolutionary divergence, but he was not aware that trout sharing a common ancestry with Kamloops trout are widespread in the Columbia basin as resident stream populations and as steelhead populations. Nor was he aware of the transitional forms whose taxonomic characters prevent clear-cut separation between the coastal rainbow and interior redband trout.

LIFE HISTORY AND ECOLOGY

Practical aspects of the diversity of Columbia redband trout include the hereditary basis for large size associated with lake-dwelling Kamloops trout and some steelhead races. The steelhead that historically migrated to the middle and upper Columbia basin were summer-run fish but consisted of numerous discrete stocks. Many of these stocks are now extinct because of dams blocking the paths to their ancestral spawning grounds; some of the lost stocks migrated almost 1,600 km from the sea, to above Arrow Lakes in British Columbia and to Shoshone Falls on the Snake River in Idaho (Fulton 1970). Two major extant

groups (A and B) of steelhead are commonly recognized in the Snake River. The A group enters the Columbia River before mid-August, the B group somewhat later, but both reach Ice Harbor Dam on the Snake River at about the same time. Steelhead of the B group are larger, averaging about 5–7 kg with maximum size near 16 kg. The A and B groups maintain reproductive isolation from each other by homing to specific tributaries. Actually, both the A and the B groups consist of numerous reproductively isolated stocks.

The arid-lands redband trout, mainly known from the Owyhee and Malheur river drainages, possesses the hereditary basis to function at high temperatures. As discussed, I have caught the native redband trout in Chino Creek, Nevada, by fly-fishing in water of 28.3°C. I also caught the same form of trout under similar conditions in Swamp Creek, Oregon, in intermittent, stagnant pools. A similar form of redband trout but with a lacustrine evolutionary heritage (and *LDH-B2*100* allele) is native to the Oregon desert basins.

The Columbia River redband trout evidently replaced the interior cutthroat trout in most areas where they came into contact. Widespread sympatric occurrence of both native redband and native cutthroat trout is known only in the Salmon and Clearwater drainages of Idaho and, to a lesser extent, in the John Day drainage of Oregon and in headwaters of the Wenatchee and Methow drainages, Washington.

STATUS

In the Columbia basin the original genetic diversity of resident and anadromous stocks of redband trout has been impoverished by land and water use practices and the stocking of nonnative forms of rainbow trout. Special Publication 10 of the American Fisheries Society (Schwiebert 1977) documents the decline and demise of many races of salmon and steelhead in the past 40 years because of dams and environmental degradation.

REDBAND TROUT OF OREGON BASINS

Native trout occur in several internal basins of southern Oregon: Malheur, Catlow Valley, Fort Rock, Chewaucan, and Warner Lakes (Figure 15). The Goose Lake basin can be considered a disrupted part of the Sacramento River basin because Goose Lake has overflowed to the Pit River in historical times. The Upper Klamath Lake basin now drains to the Klamath River, but its fish fauna and geological history reveal former connections to interior drainages. The native trout of these basins were long confused. Snyder (1908) and Hubbs and Miller (1948) believed them to be cutthroat trout. There is no doubt that the native trout of the Oregon internal basins are redband trout derived from the Columbia River. These basins all contained large lakes in late-Pleistocene times. At high lake levels, the Fort Rock and Malheur basins had direct connections to the Columbia River system, and Goose Lake flowed to the Sacramento basin as it occasionally does now. Thus, both Columbia redband trout and Sacramento redband trout have had access to the Oregon basins. Evolution for several thousand years in the Pleistocene lakes of each basin resulted in higher gill raker numbers than are found in either the Columbia or Sacramento redband trout.

The oldest name, exclusive of *gairdneri*, applied to any redband trout is *Salmo newberrii* for the trout specialized for lacustrine conditions in Klamath Lake. This form is well differentiated from other groups of both redband and coastal rainbow trout and could be recognized as a subspecies, *O. m. newberrii*.

UPPER KLAMATH LAKE

Upper Klamath Lake was once a larger body of water with connections to other internal drainages, as can be perceived from its fish fauna (Hubbs and Miller 1948; Smith 1977). A redband trout probably entered the upper Klamath watershed from interior connections contemporary with the establishment of the bull trout and the tui chub. After the lake cut an outlet to the Pacific Ocean via the Klamath River, it became smaller as the outlet trenched down.

A trout collected in Klamath Lake by Dr. Newberry in 1855 as part of the Pacific Railroad Surveys was illustrated and briefly described as *Fario gairdneri* by Girard in the survey report. Shortly thereafter, Girard (1858) changed his mind and wrote that the Klamath Lake specimen is not *gairdneri* but a new species, "*Fario* or *Salmo newberrii*." Girard gave no real details on how *newberrii* differs from *gairdneri* except to mention that it has yellowish-white coloration on the ventral surface. The type specimen (number 578) is still in good condition in the collection of the U.S. National Museum. I counted 65 vertebrae, 20 gill rakers, about 45 pyloric caeca, 32 scales above the lateral line, and 142 scales in the lateral series for the type of *newberrii*. Three National Museum specimens collected in 1883 from the Williamson River, a tributary to Klamath Lake, are of

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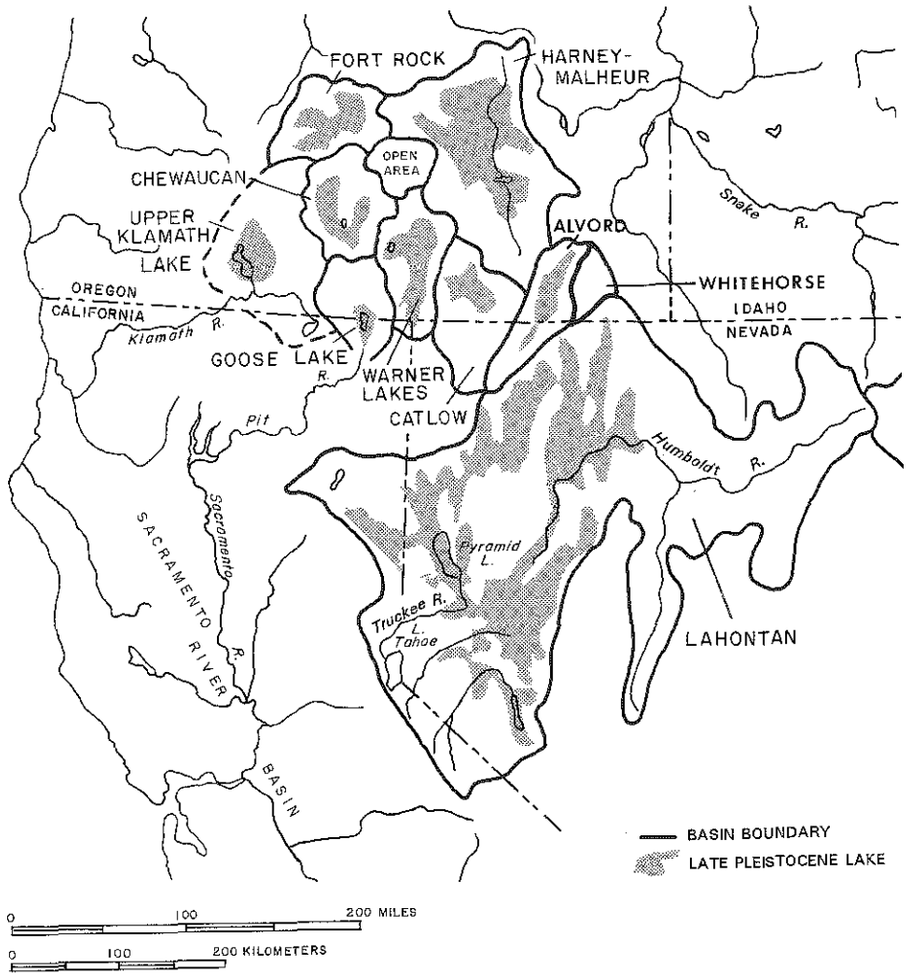

FIGURE 15.—Oregon desert basins.

the same form of trout. These specimens have 63 (two fish) and 65 (one) vertebrae; 21, 22, and 23 gill rakers; about 50, 56, and 58 pyloric caeca; 33–35 scales above the lateral line; and 146–148 scales in the lateral series. Another character separating the Upper Klamath Lake trout from other western trout is their high number of branchiostegal rays. The four specimens from the Upper Klamath watershed have 12–14 branchiostegal rays; two specimens have 12 rays (both left and right sides), and two have 13–14 rays.

Anadromous steelhead runs are native to the Klamath River, and it is possible that, as in the Columbia River basin, these runs were composed originally of both coastal rainbow and redband trout (until the upper Klamath River was blocked by Copco Dam). The data I have on Klamath River steelhead

indicate they are coastal rainbow trout and quite distinct from the native lacustrine trout of Upper Klamath Lake. Snyder (1931) found an average of 62 vertebrae in 175 specimens of Klamath River steelhead. In three specimens from Spencer Creek, tributary to the Klamath below Klamath Lake, I found 62 vertebrae, 11–12 branchiostegal rays, 17–20 gill rakers, 28 scales above the lateral line, and 133–137 scales in the lateral series. The closest affinities of *newberrii* appear to lie with the redband trout native to the Oregon desert basins.

In 1968 and 1970, I collected 25 trout in the upper Klamath basin from Whitworth and Trout creeks (Sprague river tributaries), and Donald Seegrist, U.S. Forest Service, collected eight specimens from Butte Creek, a disrupted part of the upper Klamath basin in Siskiyou County, California. These recent collections represent resident stream populations that differ from the 19th-century specimens discussed above, suggesting that two distinct groups of redband trout are native to the upper Klamath basin—one adapted to lakes and the other to streams. A stream form is shown in Plate 5.

Compared with museum specimens from Upper Klamath Lake, the recent collections from small streams have low gill raker counts (17–21, averaging 19), low scale counts (means of 30–31 above the lateral line and 133–139 in the lateral series), fewer branchiostegal rays (9–13, mainly 11), an indication of lower vertebral counts (62–65, averaging 62–63), and pyloric caecal counts of 36–56 (mean, 46–48). The specimens in the recent collections have typical redband coloration with yellow and orange tints, elliptical parr marks with supplementary rows, and a trace of a cutthroat mark.

Of 37 specimens examined from the upper Klamath basin, only one specimen, from Whitworth Creek, has a basibranchial tooth.

It is probable that a large measure of the original genotype of the lake-adapted trout in Upper Klamath Lake remains intact. Upper Klamath Lake is eutrophic and experiences intense blooms of the blue-green alga (or bacteria) *Aphanizomenon flos-aquae*. During bloom periods, pH rises to 9.5–10.5, rarely dropping below 9.0 (Falter and Cech 1991). An endemic bacterial disease, highly lethal to nonnative rainbow trout, is another selective factor favoring the native genotype.

In September 1990, Denny Rickard, a resort owner and guide at Upper Klamath Lake, took me on the lake to observe the trout. In clear-water sections influenced by spring flows, hundreds of large, robust trout from about 1 to 5 kg could be readily observed. In shallow (2-m) Pelican Bay, in the midst of a bloom (I estimated a Secchi disk clarity of about 40 cm), I caught a magnificant trout of 640 mm and 2.3 kg. Bowing to Rickard's wishes, I released the fish and the opportunity to compare the present Upper Klamath Lake trout with data from historical specimens of *newberrii*. Regardless of how much of the original genotype persists, the Upper Klamath Lake trout represents a highly significant unit of diversity among redband trout.

DESERT BASINS

Between the Columbia River basin to the north and east, the Klamath basin to the west, and the Sacramento River and Lahontan basins to the south, eight

separate desert basins have native trout. Cutthroat trout are the natives in the easternmost of these, the Whitehorse and Alvord basins; redband trout occupy the other six. I use the names given by Hubbs and Miller (1948) for these basins: Malheur, Catlow Valley, Fort Rock, Chewaucan, Warner Lakes, and Goose Lake. During the Pleistocene the basins contained large lakes (portrayed in U.S. Geological Survey map I-416, Pleistocene lakes in the Great Basin) where redband trout occurred with an array of cyprinid fishes and suckers.

Some taxonomic data on these trout were given by Snyder (1908). His lateral-series scale counts for various samples are about 15 to 20 scales higher than mine for the same specimens, probably because he believed the fish were cutthroat and biased his scale counts accordingly. Following Snyder, Hubbs and Miller (1948) assumed that the trout native to these basins were derived from a cutthroat trout, but they believed that the native trout had become thoroughly hybridized with hatchery rainbow trout.

The museum specimens I have been able to find of the desert basin redband trout are rather sparse (2–3 specimens per sample). A few specimens were collected by Evermann in 1897, the rest by Snyder in 1904. The specimens are in the U.S. National Museum collection and in the Stanford University collection, now part of the California Academy of Sciences' fish collection. In 1968, 1970, and 1972—with the assistance of Donald Seegrist of the U.S. Forest Service, Ray Simon of the U.S. Fish and Wildlife Service, and Richard Wilmot and Peter Bisson, then graduate students at Oregon State University—I collected trout from all six desert basins, the upper Klamath basin, the upper Sacramento basin, and the Columbia River basin (tributaries to the Malheur and Owyhee rivers of Snake River drainage). I attempted to resample the sites visited by Snyder in 1904 to assess the relative hybrid influence occurring since the original collections.

I was surprised to find a predominantly native redband trout still occurring in many streams of the Oregon desert basins, although a hybrid influence is indicated by the fewer gill rakers in recent collections.

Malheur Basin

When the large Pleistocene lake in the Malheur basin declined about 8,000 years ago, it left two shallow, remnant bodies of water on the valley floor: Harney Lake and Malheur Lake. The Malheur basin is the largest of the Oregon desert basins and contains the greatest amount of trout habitat. Silver Creek drains from the north into Harney Lake, the Silvies River drains from the north into Malheur Lake, and the Donner und Blitzen River drains into Malheur Lake from the south. The fish fauna of the Malheur basin is little differentiated from the Columbia River fauna, suggesting a rather broad and geologically recent connection of ancient Malheur Lake to the Malheur River (Columbia basin). Berg (1987) found a relatively high frequency (34–53%) of the *LDH-B2*76* allele in three populations of redband trout in the Silvies River drainage, indicating that the more recently derived form of Columbia redband trout gained access to the Malheur basin after the other Oregon desert basins became isolated from

invasion. Bisson and Bond (1971) discussed probable transfers of fish from the upper John Day River (Columbia basin) into the Malheur basin.

In 1904, J. O. Snyder collected trout from Silver Creek and from the Silvies River. I examined six of Snyder's specimens from each of these sites and found 64–66 vertebrae (averaging 65 in each collection) and 20–24 gill rakers (means, 21 for Silvies River and 22 from Silver Creek). I counted 37–40 pyloric caeca in three specimens from Silver Creek and obtained mean values of 32 scales above the lateral line and 150–152 scales in the lateral series.

Recent collections examined include 25 specimens from Smyth Creek (Donner und Blitzen drainage), 34 specimens from Dairy and Sawmill creeks (Silver Creek drainage), 13 specimens from Crooked and Camp creeks, and 14 specimens from Myrtle Creek (Silvies drainage). The recent specimens most like those collected by Snyder in 1904 came from Smyth Creek. They have 18–22 (mean, 20) gill rakers, 63–66 (65) vertebrae, 33–45 (38) pyloric caeca, and averages of 32 scales above the lateral line and 148 in the lateral series. The mean values in the other recent samples are: gill rakers, 20; vertebrae, 64–65; pyloric caeca, 39–42; scales, 29–30 above the lateral line and 136–144 in the lateral series. The samples from Dairy Creek and Sawmill Creek (adjoining tributaries along roadsides in a popular recreation area) appear to be the most heavily hybridized, but even these specimens still retain the predominant redband trout appearance with tints of yellow and orange and distinctive parr marks.

Based on my limited information, I conclude that the original redband trout of the Malheur basin, before stocking of hatchery rainbow trout, were characterized by averages of 21–22 gill rakers, about 65 vertebrae, 37–40 pyloric caeca, 32 scales above the lateral line, and about 150 scales in the lateral series. None of the 92 specimens examined from the Malheur basin has basibranchial teeth.

It is not known if pure populations of native trout persist in the Malheur basin. The purest of recent collections from Smyth Creek was made at the downstream limits of trout distribution in July 1968, when 25 dead and dying specimens were taken from a pool in the largely intermittent stream, obviously suffering from high temperatures and oxygen depletion. These hazards are constantly faced by desert basin trout, and they select for genotypes adapted to unstable environments—which probably explains why arid-region redband trout have so successfully resisted hybridization.

Catlow Valley

The Catlow Valley basin lies south of the Malheur basin and is separated from the Alvord basin to the east by the Steens Mountain range. There is little trout habitat left in Catlow Valley, and native trout inhabit only a few small streams.

I know of no ancient museum specimens of native Catlow Valley trout. My analysis is based on 10 specimens collected from Three Mile Creek in 1968. They have 62–65 (mean, 64) vertebrae, 20–22 (21) gill rakers, 30–46 (37) pyloric caeca, 28–33 (30) scales above the lateral line, and 129–146 (139) scales in the lateral series. None has basibranchial teeth.

The native trout and the few other native fish species in Catlow Valley are

most likely derived from the Malheur basin, perhaps from a direct connection during the maximum lake level stage when the lake in Catlow Valley was tributary to the Malheur basin. The Catlow Valley (Three Mile Creek) redband trout appear similar to the original Malheur basin trout, but have slightly fewer scales and vertebrae.

Trout also occur in Home Creek and Roaring Springs, north of Three Mile Creek. The trout of Three Mile Creek was established in a private ranch pond (Kunkel and Hosford 1978).

Fort Rock Basin

At maximum lake levels the Fort Rock basin, lying west of the Malheur basin, once drained into the Deschutes River via the Crooked River. An impressive outlet channel is still visible. The Fort Rock basin is contiguous with the upper Klamath basin to the southwest and the Chewaucan basin to the south. Silver Lake, an alkaline body of water barren of fish life, is the remnant of the basin's large Pleistocene lake. All present trout habitat of which I am aware is in headwater areas of Buck, Bridge, and Silver creeks, tributary to Paulina Marsh. In 1968, native redband trout were found in upper Buck and Bridge creeks, but only brook trout were found in tributaries to Silver Creek.

I examined six museum specimens collected by Snyder in 1904 from Buck Creek. The outstanding feature in this collection is the presence of basibranchial teeth in four specimens. Of all the redband samples I have examined, basibranchial teeth were common only in the Sheepheaven Creek trout of the northern Sacramento basin (in about half of the specimens). I found no basibranchial teeth in three specimens collected by Evermann in 1897 from Silver Creek. The other taxonomic characters of the six Buck Creek specimens collected in 1904 are 63–64 (mean, 64) vertebrae, 19–22 (20) gill rakers, 28–33 (30) scales above the lateral line, and 137–145 (142) scales in the lateral series. The three specimens from Silver Creek collected in 1897 have 63 (two fish) and 64 (one) vertebrae; 20, 21, and 22 gill rakers; 31–35 scales above the lateral line; and 145–148 scales in the lateral series. The trout populations native to the Buck, Bridge, and Silver creek drainages have probably been isolated from each other for several thousand years and have undergone slight differentiation from each other.

In 1968, 10 redband trout from Buck Creek and 24 from Bridge Creek were collected. The Buck Creek specimens show almost no difference from those taken in 1904 in vertebrae (63–65; mean, 64), gill rakers (17–21; 20), and scales (average, 31 above the lateral line and 142 in the lateral series). Only 3 of the 10 recent specimens possess basibranchial teeth. Pyloric caeca number 38–62 (47). There appears to be a slight hatchery rainbow trout influence in the present Buck Creek trout, as indicated by the apparent reduction in basibranchial teeth and the extreme range of caecal counts.

The trout in the headwaters of Bridge Creek appear to be less influenced by hybridization. This sample of 24 specimens has 62–66 (64) vertebrae, 19–23 (21) gill rakers, 29–34 scales above the lateral line, 137–158 (145) scales in the lateral series, and 36–53 (43) pyloric caeca. Four of the 24 specimens have basibranchial teeth.

The original native trout of the Fort Rock basin are assumed to be characterized by an average of 64 vertebrae, 20–21 gill rakers, 30–32 scales above the lateral line, 140–145 scales in the lateral series, and 40–45 pyloric caeca. Basibranchial teeth probably occurred in half or more of the original Buck Creek trout, but they occurred in lesser frequencies in the trout of the Bridge and Silver Creek drainages.

Chewaucan Basin

The Chewaucan basin is between the Warner Lakes basin to the east, the upper Klamath basin to the west, the Fort Rock basin to the north, and the Goose Lake basin to the south. The two remnants of its Pleistocene lake—Summer Lake and Abert Lake—are highly alkaline and barren of fish life. The Chewaucan River drainage, tributary to Abert Lake, contains several good trout streams.

I examined two specimens collected by Evermann in 1897 and six specimens collected by Snyder in 1904 from the Chewaucan River. They have 20–23 (mean, 22) gill rakers, 63–64 (64) vertebrae, 133–148 (142) scales in the lateral series, and 28–33 (30) scales above the lateral line. One of the eight specimens has basibranchial teeth.

In 1968, 28 specimens were collected from Elder Creek, and 10 specimens were collected in 1970 from Dairy Creek in the Chewaucan drainage. Both sites have easy access and receive relatively high recreation use. Undoubtedly, heavy stocking with hatchery trout has occurred over the years. I was surprised to find that the trout in Elder and Dairy creeks did not resemble hatchery rainbow trout but were quite typical of native redband trout in coloration, spotting, and parr markings. The Elder Creek specimens have 61–65 (63) vertebrae, 19–24 (21) gill rakers, 136–154 (143) scales in the lateral series, 27–33 (30) scales above the lateral line, and 33–46 (40) pyloric caeca. Two of 20 specimens (more than 100 mm in length) have basibranchial teeth. The Dairy Creek sample has 61–64 (63) vertebrae, 19–22 (21) gill rakers, 40–58 (46) caeca, an average of 30 scales above the lateral line, and 135 scales in the lateral series. Two of 10 Dairy Creek specimens have basibranchial teeth.

A slight hybrid influence is indicated by the fewer gill rakers of recent specimens compared with the museum specimens, and perhaps by the lower scale counts and higher caecal counts in the Dairy Creek trout. These populations, however, predominantly retain the native genotype and should be considered as representatives of the native trout of the Chewaucan basin.

The closest relationships of the Chewaucan basin redband trout probably are with the redband trout native to the Goose Lake and Warner Lakes basins.

Warner Lakes Basin

The Warner Lakes basin is east of the Chewaucan basin, west of the Catlow Valley basin, and contiguous on its southwestern side with the Goose Lake basin. The Warner Lakes are remnants of an elongated Pleistocene lake that filled the valley floor, extending about 100 km along a north–south axis.

I examined eight specimens collected by Snyder in 1904 from Honey Creek.

They have 61–63 (mean, 62) vertebrae. Their scales average about 31 above the lateral line and about 147 in the lateral series. Seven specimens have 23 gill rakers and one has 24 (mean, 23). This is the highest gill raker count obtained for any sample of desert basin redband trout, but the original trout of the Goose Lake basin probably had similar numbers.

Nineteen specimens collected from Honey Creek in 1968 reveal a hybrid influence: their gill rakers were reduced to 20–24 (22), and their scale counts were reduced to an average of 29 above the lateral line and 133 in the lateral series. They have 62–64 (63) vertebrae and 35–54 (45) pyloric caeca. Recent Warner Lakes basin collections from Deep and Willow creeks, now in the Oregon State University collection, are still more hybridized. Eight Willow Creek specimens have 17–22 (20) gill rakers, and six Deep Creek specimens have 20–21 (20) gill rakers. I tentatively construe the original Warner Lakes trout as having 62–63 vertebrae, about 23 gill rakers, 30–32 scales above the lateral line, about 145–150 in the lateral series, and about 40 pyloric caeca. No basibranchial teeth were found in any specimen from the Warner Lakes basin, whose native trout may have been identical to the Goose Lake basin trout.

Goose Lake Basin

The Goose Lake basin is contiguous with the upper Klamath basin on the west, the Chewaucan basin on the north, and the Warner Lakes basin on the east. Goose Lake at higher levels has occasionally connected to the headwaters of the Pit River (upper Sacramento River basin) during historical times (Hubbs and Miller 1948), so the Goose Lake basin can be considered a semidisrupted part of the upper Sacramento basin.

I found six specimens collected by Snyder in 1904 from Cottonwood Creek to be very similar to the specimens from Honey Creek of the Warner Lakes basin. The Cottonwood Creek specimens have 21–24 (mean, 23) gill rakers and 61–64 (63) vertebrae, and they average 30 scales above the lateral line and 139 scales in the lateral series. From recent collections I examined 38 specimens from Lassen Creek, 15 from Thomas Creek, and 12 from Davis Creek. All three samples have been influenced by hybridization with hatchery rainbow trout, as reflected by gill raker counts of 18–24 with means of 20 (Lassen Creek), 21 (Thomas Creek), and 21 (Davis Creek). Pyloric caeca number from 35 to 54, with mean values of 42–43. Davis Creek specimens have higher-than-expected scale counts, averaging 33 above the lateral line and 147 in the lateral series (the other samples average 30 scales above the lateral line and 132–136 scales in the lateral series). Of the 71 specimens examined from the Goose Lake basin, 2 (1 from Thomas Creek and 1 from Davis Creek) have basibranchial teeth.

11

REDBAND TROUT OF THE SACRAMENTO BASIN

California Golden Trout *Oncorhynchus mykiss aguabonita*
Kern and Little Kern Golden Trout *Oncorhynchus mykiss gilberti*
Sacramento Redband Trout *Oncorhynchus mykiss stonei*

The coloration and other taxonomic characters of redband trout in the Sacramento River basin are the most variable of all geographical groups of redband trout (Plates 5, 6; Figure 16), which indicates that these fish are derived from more than one ancestral form. In the northernmost section of the basin, in the headwaters of the Pit River drainage, the native trout is similar to redband trout in the desert Goose Lake basin to the north, which is to be expected because of the recent connections between Goose Lake and the Pit River. At the southern extreme is one of the most strikingly colored trout in the world—the California golden trout of the South Fork Kern River.

The relationships of the California golden trout to the redband trout, particularly the links between trout native to the nearby main Kern River in the southern basin and to Sheepheaven Creek in the northern basin, were discussed by Schreck and Behnke (1971). Additional taxonomic data on golden trout were given by Gold and Gall (1975a, 1975b) and Gold (1977). Berg (1987) presented electrophoretic data for many populations of upper McCloud redband trout in the north and upper Kern golden trout in the south. Sacramento basin fish overwhelmingly carry the *LDH-B2*100* allele, as do coastal rainbow trout and other redband populations other than those in the interior Columbia and Fraser river basins.

California golden trout represent extremes in coloration and character values. This subspecies has the fewest vertebrae (58–61, averaging 59–60), the highest scale counts (35–45 above the lateral line and 150–210 in the lateral series), and the fewest pyloric caeca (20–40; mean, 31) known for trout of the redband evolutionary line. The Little Kern golden trout (often called subspecies *whitei*) and the main Kern redband trout (*gilberti*) were considered one subspe-

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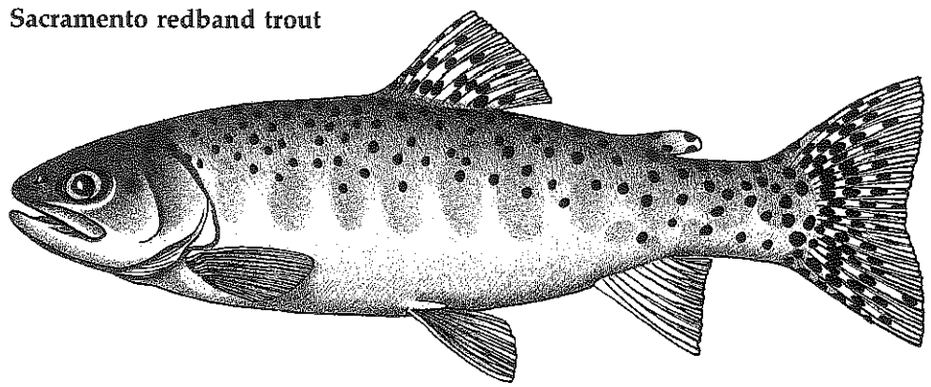
Sacramento redband trout



California golden trout

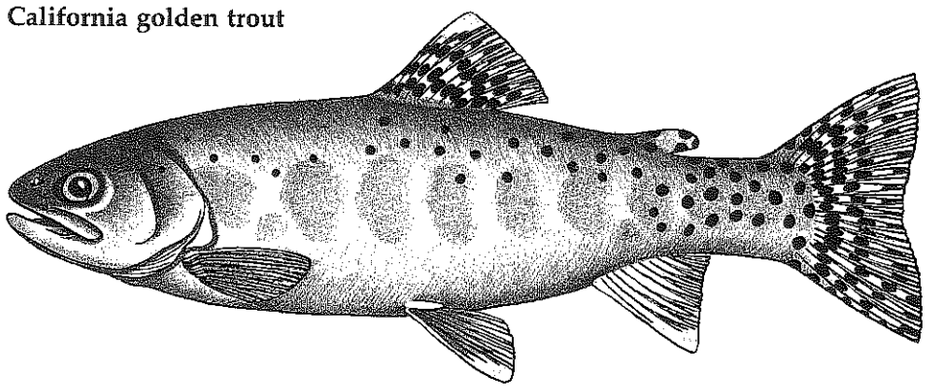


FIGURE 16.—Redband trout of the Sacramento basin.

cies (*gilberti*) by Schreck and Behnke (1971). They differ from California golden trout in having less-intense coloration, more vertebrae (59–63; mean, 60–61), fewer scales (means, 155–160 in the lateral series and about 35 above the lateral line), and more pyloric caeca (typically 35–40). I have never found basibranchial teeth in specimens of California golden trout, but they do occur occasionally in Kern and Little Kern specimens. Three of 10 specimens collected from the Kern River in 1893 and 1904 have basibranchial teeth. Some specimens from the Kern and Little Kern drainages have an unusual pattern of tongue dentition, with inner rows of teeth beside the normal row along the edge of the tongue. Such tongue dentition also occurs in some Sheepheaven Creek redband trout.

The occurrence of two subspecies (*aguabonita* and *gilberti*) and perhaps a third (*whitei*) in the Kern system reflects successive invasions by redband trout in the San Joaquin drainage. The Kern River has had sporadic connections to the San Joaquin via Lake Tulare into historic times, but environmental barriers along this route apparently allowed only occasional migrants to reach the upper Kern.

The first trout to become established in the upper Kern drainage probably reached there well before the last glacial epoch. This primitive form of Sacramento redband trout also left remnants in the headwaters of the McCloud River at the northern end of the Sacramento–San Joaquin basin.

The South Fork Kern River and Golden Trout Creek were the Kern drainages most isolated from successive invasions of trout from the San Joaquin. Thus subspecies *aguabonita* is assumed to have evolved with the least influence from later invaders. The Little Kern River is isolated by a falls from the main Kern, so its form of golden trout (*"whitei"*) should have been more influenced by later invaders than *aguabonita* but less so than trout of the main Kern (*gilberti*). Nevertheless, the oldest museum specimens of Little Kern and Kern trout, collected before nonnative rainbow trout were stocked in the drainage, showed no differences in meristic characters (Schreck and Behnke 1971). The taxa *whitei* and *gilberti* were based on virtually indistinguishable specimens, and they are very closely related, if not identical. If they are to be separately recognized, *whitei* and *gilberti* should be subspecies of the same species. The listing of *whitei* (as a subspecies of *O. aguabonita*) under the Endangered Species Act, first as endangered and then as threatened, has been instrumental in preserving and restoring remnant populations of pure Little Kern golden trout.

Evidently, except for the semi-isolated Kern River drainage, coastal rainbow trout replaced redband trout in the southern Sacramento River basin (San Joaquin drainage). The redband trout, or at least a strong redband influence, persisted in the northern part of the basin as far south as the Feather River, according to the descriptions and scale counts given by Rutter (1908).

The primitive redband trout that first invaded the Sacramento basin is probably best represented today by the population isolated in tiny Sheepheaven Creek of the upper McCloud River drainage. Gold (1977) gave a comprehensive description of the Sheepheaven trout based on 25 specimens. I have examined 21 specimens from Sheepheaven Creek, and my data essentially agree with Gold's except that I found basibranchial teeth in a higher proportion of specimens (11 of 21 versus 9 of 25). The Sheepheaven Creek trout are not highly colored. They typically exhibit light or dull yellow tints on the sides and have a

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faint yellow cutthroat mark. In numbers of vertebrae (60–63; mean, 61), scales in the lateral series (153–174; 162), and pyloric caeca (29–42; 36), they are similar to the Kern–Little Kern golden trout. Sheepheaven Creek redband trout have the fewest gill rakers of any western trout (14–18; 16).

Sheepheaven Creek is an isolated segment of the upper McCloud drainage, and the ancestors of its trout probably gained access to the McCloud headwaters before the river's present series of barrier falls was formed. I have examined specimens from other tributaries to the upper McCloud above the falls (Tate, Edson, Trout, Raccoon, and Moosehead creeks); although these specimens share one or more characters with Sheepheaven Creek trout, they differ in others. Berg (1987) also found relatively large differences in allele frequencies among upper McCloud redband trout populations. Some of this variability may be the result of introductions of and hybridization with hatchery rainbow trout. Basibranchial teeth were found in 1 of 3 Trout Creek specimens, 3 of 15 Moosehead Creek specimens, and 1 of 16 Edson Creek specimens.

In the McCloud River below the barrier falls, meristic characters again vary greatly among trout of different tributaries. In the 12 specimens used by Jordan in his description of the taxa *stonei* and *shasta*, I found 61–64 (mean, 63) vertebrae, 17–22 (20) gill rakers, 28–35 (32) scales above the lateral line, 139–160 (146) scales in the lateral series, and 10–13 (12 right and 12 left) branchiostegal rays. The branchiostegal ray count in Sheepheaven Creek trout is 8–11 (10 right and 10 left). The characteristics of the specimens used by Jordan to name *stonei* and *shasta* might serve to diagnose the subspecies *stonei* and, in general, to profile redband trout of the McCloud and Pit river drainages. However, there is great variability in numbers of vertebrae, scales, and pyloric caeca among populations in several other tributaries of the McCloud and Pit rivers. The use of *stonei* as a subspecies for redband trout of the upper Sacramento basin (or only the McCloud drainage) has some practical value, but it must be recognized that *stonei* is not a biological subspecies—only a practical one. Moreover, there is no way to classify the mosaic of diversity found in upper Sacramento basin redband trout into one or more good subspecies comparable to the classification of native trout of the upper Kern drainage into the subspecies *aguabonita* and *gilberti*. I believe the great variability exhibited by upper Sacramento redband trout represents a mixture of two or more ancestral forms of redband trout, as well as a coastal rainbow trout influence in some populations.

Snyder collected six specimens from the headwaters of the Pit River at the mouth of Joseph Creek in 1904. They have 62–63 (63) vertebrae, 19–23 (21) gill rakers, and 138–155 (148) scales in the lateral series—comparable to Jordan's "type" specimens of *stonei* and *shasta* from the McCloud River, and also comparable to the redband trout of the Goose Lake basin. In intervening areas, however, patterns of variability randomly occur without a smooth transition. For example, in tributaries to the McCloud River, mean vertebral counts range from 61 in 20 specimens from Hawkins Creek to 64 for 23 specimens from Clairborne Creek. Most pyloric caecal counts for McCloud and Pit river drainage redband trout average 40–45, as is common for most Columbia basin redband trout; but in the lower Pit River drainage, collections from a series of tributaries (Kosk, Snowslide, Nelson, Burney, and Hat creeks and the Lost River) have caecal counts higher than those for typical coastal rainbow trout (53–79). In coloration and most other characters, the specimens from these creeks are redband trout, but they have large, roundish spots on the body reminiscent of cutthroat trout.

I examined 10 specimens from the South Fork of Parker Creek in the northern headwaters of the Pit River. They have 62–66 (64) vertebrae, 19–23 (21) gill rakers, 37–49 (43) pyloric caeca, and an average of 33 scales above the lateral line and 149 in the lateral series. Even after a long history of stocking with hatchery rainbow trout, the trout in South Fork Parker Creek closely resemble the museum specimens collected by Snyder from headwaters of the Pit River. Basibranchial teeth occur in about 5% of the specimens from the Pit River drainage.

TAXONOMIC NOTES

Despite the variability in numbers of vertebrae, scales, and pyloric caeca, populations from diverse geographical areas exhibit a transition between extreme forms. The only groups with some clear-cut distinctions are those long isolated from contact with other redband trout and from contact with coastal rainbow trout, such as the South Fork Kern golden trout, the Kern–Little Kern golden trout, and the unnamed Sheepheaven Creek trout.

As previously discussed, I recognize the California golden trout as a subspecies of rainbow trout, *O. m. aguabonita*. Although I group the Kern and Little Kern golden trout as one subspecies (*gilberti*), they could be recognized as separate subspecies (*gilberti* and *whitei*, respectively)—provided they are kept together in the same species. The common practice of placing them in different species (*O. aguabonita whitei* and *O. mykiss gilberti*) creates a taxonomic incongruity. The incongruity disappears if *aguabonita*, *gilberti*, and *whitei* are all considered subspecies of *O. mykiss*.

I use *O. m. stonei* only as a practical catchall category to group the great variability found in the McCloud and Pit river drainages. The redband trout native to Sheepheaven Creek is sufficiently differentiated to justify recognition as a new subspecies, but the name would be applicable only to the Sheepheaven population.

LIFE HISTORY AND ECOLOGY

Pure populations that persist as isolated relicts, such as the California golden trout in the South Fork Kern River and the redband trout of Sheepheaven Creek, are vulnerable to replacement by nonnative trout. Evidently, long isolation of California golden trout resulted in a lack of competitive ability. I know of no example where introduced California golden trout were able to coexist with brook trout or brown trout, or where preexisting California golden trout avoided hybridization with introduced rainbow or cutthroat trout.

The Eagle Lake trout, which may have a mixed redband–coastal rainbow ancestry, has an evolutionary history as a lacustrine predator on tui chub. It has long been propagated in hatcheries (the population in Eagle Lake is maintained

by artificial propagation). Only in recent years, however, has the Eagle Lake trout been stocked into new waters with follow-up evaluations of its suitability. Rawstron (1977) reported that when stocked into Berryessa Reservoir, the Eagle Lake trout yielded 50% more biomass to the creel than did a hatchery strain of Kamloops redband trout. Eagle Lake fish are treated more fully in Chapter 12.

STATUS

The California Department of Fish and Game's Committee on Threatened Trout has been active in protecting and enhancing the survival of various forms of native trout. The redband trout of Sheepheaven Creek has been transplanted to barren streams. The California golden trout has been widely stocked in western states and is more abundant now than it was historically, although it can maintain pure populations by natural reproduction only if rainbow or cutthroat trout are not stocked with it. Many, if not most, self-reproducing California golden trout populations in the Rocky Mountain region are hybridized. In the South Fork Kern River, the abundance and distribution of California golden trout have been drastically reduced because of the invasion of brown trout. Attempts (apparently successful) have been made to eliminate the brown trout by chemical treatment and barrier construction in the headwaters of the South Fork Kern River.

The Kern–Little Kern golden trout is listed as a federally threatened species under the subspecies name *whitei*. Until a few years ago, pure populations of this subspecies persisted in only a few headwater tributaries (Upper Soda Springs Creek, Deadman Creek, and Wet Meadows Creek). During recent years, a continuing program of reintroductions has established several new populations in the Little Kern drainage.

12

RAINBOW TROUT OF COASTAL BASINS

Coastal Rainbow Trout *Oncorhynchus mykiss irideus*

TYPICAL CHARACTERS

Heavily spotted with irregularly shaped spots both above and below the lateral line. Scales in the lateral series 120–140. Pyloric caeca 40–70, typically averaging about 55. Vertebrae 61–65, averaging 62–64. A rose-red lateral band present at some stage of the life cycle. Parr marks rounded; dorsal and ventral supplemental rows reduced or absent.

DESCRIPTION (Plates 6, 7; Figure 17)

No set of character values distinguishes all coastal rainbow trout from all trout of redband evolutionary lines. Considerable genetic interchange between coastal rainbow and interior redband trout in the Columbia and Sacramento basins has probably occurred during and since the last glacial period, and many populations of rainbow trout do not conform to the typical diagnosis stated above. Coastal rainbow trout exhibit weak clinal trends at best; that is, northern populations do not consistently have more scales or vertebrae than do southern populations. This lack of geographical differentiation argues against an isolation of coastal rainbow trout in the northern Beringia refugium during the last glacial epoch.

Among 166 Alaska specimens from 10 localities where I collected with the late P. R. Needham in 1957, vertebrae numbered 60–65 and averaged 62 (Bedlam Lake on the Kenai Peninsula) to 63 (Alagnak River and Brooks Lake on the Alaska Peninsula). Lateral-series scales numbered 111–146, averaging 122 for 20 Bedlam Lake fish to 137 for 16 Brooks Lake specimens. Gill rakers numbered 17–24, averaging 19–20. All the Alaska samples came from resident populations.

In the Yukon Territory coastal rainbow trout occur in headwaters of the Alsek River, which enters the Pacific Ocean just north of the Alaska–British

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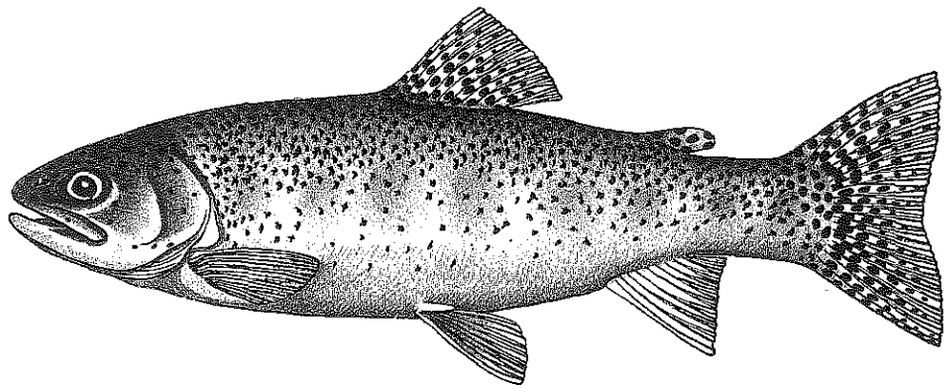

FIGURE 17.—Coastal rainbow trout.

Columbia border (Figure 13, pages 166–167). Seventeen specimens from Kathleen Lake of the Alsek drainage have 63–66 (mean, 64) vertebrae, 15–20 (18) gill rakers, and 126–138 (131) lateral-series scales. These heavily spotted trout have spots extending about halfway below the lateral line.

A typical coastal steelhead population is represented by a sample of 30 smolts from the Coquihalla River, a tributary to the lower Fraser River near Hope, British Columbia. These smolts have 111–138 (125) scales in the lateral series, 62–65 (64) vertebrae, and 18–22 (19) gill rakers. Thirty resident rainbow trout from the Salmonberry River, a tributary to the Nehalem River just south of the Columbia River drainage, Oregon, have 117–143 (127) lateral-series scales, 62–64 (63) vertebrae, and 17–20 (18) gill rakers. Meristic data presented by Schreck et al. (1986) for many coastal steelhead populations of the Columbia River basin west of the Cascade Mountains fall within the ranges mentioned above.

From the Klamath River southward steelhead seem to have fewer vertebrae. Snyder (1931) counted 60–65 (mean, 62) vertebrae in 175 Klamath River steelhead. I examined seven specimens from the Russian River, nine from the San Lorenzo River, and five from Waddell Creek, California. These southern steelhead have low vertebral counts (60–63; means, 61–62) as well as low scale counts (117–132; means, 121–124). Of the rainbow trout discussed by Needham and Gard (1959), only their sample from San Pablo Creek, tributary to San Francisco Bay of the lower Sacramento River basin, can be considered typical coastal rainbow trout. The San Pablo Creek specimens have 61–65 (63) vertebrae and 121–153 (133) scales in the lateral series.

Toward the southern extremity of the range of natural distribution, peculiar

characters appear in rainbow trout populations. An unusual trout occurs in Pauma Creek, a headwater tributary to the San Luis Rey River on Mount Palomar in southern California, which is near the southernmost historical limit of steelhead distribution. The trout of Pauma Creek exhibit yellowish colors on the sides of the body with occasional orange tints on the ventral surface and pronounced light-colored tips on the dorsal, anal, and pelvic fins. The parr marks are elliptical with supplementary smaller marks, either round or oval, ventral to them. These traits are characteristic of redband trout, but in nine specimens of Pauma Creek trout I found 62–63 (62) vertebrae, 122–140 (131) lateral-series scales, and 17–19 (18) gill rakers—typical of coastal rainbow trout. The pyloric caecal counts of 34–54 (42), however, are more typical of redband trout. Berg (1987) presented electrophoretic data on San Luis Rey rainbow trout (probably Pauma Creek specimens) that showed no distinct differences in allele frequencies from those of coastal rainbow trout.

A pond at the headwaters of Pauma Creek has long been stocked with hatchery rainbow trout, so a hatchery influence must be suspected. However, the unique appearance of Pauma Creek trout and their low pyloric caecal numbers suggest they represent the native trout of this region, differentiated from the typical coastal rainbow trout. Pauma Creek is isolated from the San Luis Rey River by a series of falls. The native trout isolated in its headwater areas may represent the earliest invaders, perhaps hybrids of coastal rainbow and redband trout resulting from the first contact of these forms or coastal rainbow trout at an early stage of divergence from the redband line.

A trout native to the Río Santo Domingo drainage of Baja California has been transplanted to the nearby Río San Rafael. Its ancestry is probably similar to that of the Pauma Creek rainbow trout—a mixture of primitive forms of redband and coastal rainbow trout. This trout was described as a new species, *Salmo nelsoni*, by Evermann (1908). More complete descriptions of the Santo Domingo trout were given by Snyder (1926) and Needham and Gard (1959). In an electrophoretic analysis, Berg (1987) found that the Santo Domingo trout shares all the most common alleles with coastal rainbow trout, although it does have a unique rare allele at a locus that codes the enzyme creatine kinase. (Rare alleles often are found in small, isolated populations.) The native trout of the Río Santo Domingo typically have 61–62 vertebrae (low for coastal rainbow trout) and 125–140 scales in the lateral series. Needham and Gard (1959) mentioned that 1 of their 25 specimens has three basibranchial teeth, a character not found in any other specimen of coastal rainbow trout that I have examined. I counted 46, 47, and 53 pyloric caeca in three Santa Domingo trout. Although the Baja California rainbow trout lacks diagnostic taxonomic characters by which it can consistently be separated from other coastal rainbow trout, Mexican fisheries agencies regard it as an endemic subspecies, *Oncorhynchus mykiss nelsoni*. If subspecies recognition serves to preserve a unique population by stimulating habitat enhancements and transplants into new waters, as has been the case with *nelsoni*, then such recognition has practical if not taxonomic merit.

The southernmost distribution of rainbow trout occurs in streams tributary to the Gulf of California in Durango and Sinaloa provinces of Mexico. Needham and Gard (1959) presented data for fish collected from tributaries of the Río del Presidio and the Río San Lorenzo. The Río del Presidio marks the southernmost

natural occurrence of any extant species of the family Salmonidae. Collections were made there at about 24°N latitude, just north of the Tropic of Cancer and slightly to the south of the native occurrence of *Oncorhynchus masou* in Taiwan.

Much stocking of hatchery rainbow trout has occurred in Mexico, beginning with a shipment of 33,000 eggs from the McCloud River in 1888, so the possible influence of introductions must be taken into account. The characters of the Mexican rainbow trout discussed by Needham and Gard (1959) are distinctive, and I do not regard them as derived from hatchery introductions. The trout of the Río del Presidio and Río San Lorenzo drainages differ from each other, and both differ from the Río Santa Domingo trout of Baja California. The mainland Mexican trout (including trout native to the Río Yaqui and Río Mayo, north of the distribution of Mexican golden trout) diverge from coastal rainbow trout much more than do the Baja California trout.

Needham and Gard (1959) presented data on 23 specimens from the Río Tabacatiado and 27 specimens from the Río Hondo, headwater tributaries to the Río del Presidio. These trout are characterized by high vertebral counts, 63–66 (mean, 64), and relatively high lateral-series scale counts, 125–150 (137 and 138). I counted 33–43 (37) pyloric caeca in 10 specimens of Río Tabacatiado trout, and 34 and 37 caeca in 2 specimens of Río Hondo trout. These characteristics are similar to those of Columbia River basin redband trout.

Needham and Gard (1959) described trout from the Río Truchas, a headwater tributary to the Río San Lorenzo just north of the Río del Presidio drainage. The Río Truchas trout are characterized by low vertebral counts of 58–63 (61) in 17 specimens and high lateral-series scale counts of 133–161 (149). I counted 31–39 (33) pyloric caeca in five Río Truchas specimens. The Río Truchas trout also have pronounced white tips on the dorsal, anal, and pelvic fins. These characteristics bear similarities to those of Sacramento basin redband trout. The unusual characters of the Río Truchas trout may represent hybridization between a Mexican golden trout ancestor and the peculiar rainbow trout of the Río del Presidio.

The three drainages immediately to the north of the Río San Lorenzo—Río Culiacan, Río Sinaloa, and Río Fuerte—have the Mexican golden trout. The trout native to the Río Mayo and Río Yaqui, north of the range of the Mexican golden trout, have a spotting pattern and coloration somewhat similar to those of Gila trout but differ considerably in chromosome numbers and allele frequencies (Loudenslager et al. 1986; Berg 1987).

Thorgaard (1983) presented extensive data on rainbow trout chromosomes. The predominant diploid number of coastal rainbow trout chromosomes is 58 (as in redband trout), although populations characterized by 60 chromosomes are common, and Thorgaard found 64 chromosomes in some northern California steelhead. It appears that some coastal rainbow trout have evolved higher chromosome numbers by splitting a two-arm (metacentric) chromosome into two one-arm (acrocentric) chromosomes. Thus, in rainbow trout the chromosome complement of 58 is primitive and the higher numbers are more advanced. Many populations are variable (polymorphic) for chromosome numbers, which attests to mixing between chromosomal races. No consistent differences in allele frequencies, morphology, or meristic characters are associated with chromosomal races of coastal rainbow trout.

Obviously, it is difficult to characterize and classify coastal rainbow trout—but not so difficult as defining and classifying the diversity of redband trout.

DISTRIBUTION

The northernmost populations of coastal rainbow trout occur in southern tributaries to the Kuskokwim River, Alaska, south of the mouth of the Yukon River (Figure 13, pages 166–167). Robert Smith of Central Point, Oregon, sent me two specimens of rainbow trout he caught in August 1981 in the Goodnews River, the next drainage south of the Kuskokwim. They have the typical spotting pattern of coastal rainbow trout, and their scale counts are typical of the subspecies (24 and 28 above the lateral line; 124 and 128 in the lateral series). Also, they have 41 and 47 pyloric caeca. Smith noted yellowish colors, traces of a cutthroat mark, and light-colored tips on the dorsal, anal, and pelvic fins in some specimens he caught in the Goodnews and Togiak rivers. The native rainbow trout occurs there with the northern subspecies (*malma*) of Dolly Varden and with Arctic char in some lakes.

The southernmost limit of rainbow trout is the Río del Presidio, Mexico. I do not regard the Río del Presidio trout as coastal rainbow trout, however. Instead, I would assign the southernmost distribution of the subspecies either to the Baja trout of the Río Santo Domingo or, for those who prefer to recognize the Baja trout as the subspecies *nelsoni*, to the Otay River drainage southeast of San Diego.

Coastal rainbow trout extend farther north, farther south, and farther inland than coastal cutthroat trout (see Figure 4, pages 66–67). Steelhead populations occur throughout the range of coastal rainbow trout except in the northern and southern extremities. The northwestern limit of steelhead in North America has generally been assumed to be the southern drainages of the Alaska Peninsula. However, Constance Iten (National Marine Fisheries Service, Seattle), who helped compile an atlas of marine resources, pointed out to me a steelhead record for Point Heiden on the north side of the peninsula. The "Alaska habitat management guide: Southwest Region, volume 1," published by the Alaska Department of Fish and Game (1985), lists the Sandy River, Bear River, King Salmon River, and Steelhead Creek in the Point Heiden region as containing steelhead. The present southern limit of steelhead distribution is Malibu Creek, California. Historically, steelhead occurred to the Otay River just north of the Baja California border (Barnhart 1986). All of the present southernmost steelhead populations of Malibu Creek, Santa Clara River, Ventura River, and Santa Ynez River are at risk of extinction, according to Nehlsen et al. (1991).

The coastal rainbow trout has been successfully established in suitable waters all over the world. MacCrimmon (1971, 1972) detailed the worldwide distribution of rainbow trout but lacked details of rainbow trout in Iran. I have observed established rainbow trout populations in streams of the Zagros Mountains (Tigris River basin) and in the Zayanderud River (internal basin) in Iran. In streams of the Caspian Sea basin with native brown trout, introduced

rainbow trout have not been able to establish populations. Competitive exclusion of introduced rainbow trout by native brown trout generally occurs in European waters as well.

TAXONOMIC NOTES

Historically, *Salmo irideus* or *S. gairdneri irideus* referred to resident, nonanadromous rainbow trout. It is now obvious that all anadromous steelhead and all resident rainbow trout did not arise from two distinct evolutionary lines; rather, the two ecological forms have given rise independently to each other in various forms of rainbow and redband trout. The type locality of *irideus* is San Leandro Creek, a tributary to San Francisco Bay. The type specimen of *irideus* was a juvenile coastal steelhead. Thus, the subspecies *O. m. irideus* designates all coastal rainbow trout from California to Alaska, both steelhead and resident populations.

As discussed, some trout populations have characters intermediate between those of coastal rainbow and interior redband trout. The trout native to Eagle Lake, California, is another such example. Commonly classified as the subspecies *aquilarum*, the Eagle Lake rainbow trout has no morphological, meristic, or electrophoretic distinctions useful for distinguishing it from other subspecies of rainbow trout (Busack et al. 1980). Eagle Lake, an isolated part of the Lahontan basin, has a fish fauna made up of typical Lahontan species with the exception of the trout. Its original trout, when it was directly connected to Lake Lahontan, should have been the Lahontan cutthroat trout. After the final desiccation of Lake Lahontan, a warmer, drier period probably left spawning streams dry and eliminated the Lahontan cutthroat trout from Eagle Lake. A subsequent cooler, wetter period then resulted in a headwater transfer from the Pit River (upper Sacramento River basin) drainage into the Eagle Lake basin, and a trout that may have represented a mixture of coastal rainbow and redband trout gained access.

Snyder (1917) described the Eagle Lake rainbow trout as *Salmo aquilarum*. There is nothing in Snyder's original description to clearly separate the Eagle Lake trout from other rainbow trout. I counted 136–140 lateral-series scales on the four specimens collected by Snyder from Eagle Lake. Needham and Gard (1959) based their description of the Eagle Lake trout on eight large specimens taken in 1951. They reported 19–21 (mean, 20) gill rakers—I found 16–19 (18) in the four original specimens collected by Snyder—61–65 (64) vertebrae, and 133–155 (143) lateral-series scales.

I examined 20 small specimens of Eagle Lake trout raised at the Crystal Lake, California, hatchery in 1957. These specimens, cultured from eggs taken during the spawning run of Eagle Lake trout in Pine Creek, have 16–21 (18) gill rakers, 61–64 (62) vertebrae, and 122–142 (131) lateral-series scales. Busack et al. (1980) found 17–21 (19) gill rakers, 58–63 (62) vertebrae, 126–153 (138) lateral-series scales, 33–74 (55) pyloric caeca, and 58 chromosomes among the Eagle Lake trout they examined; electrophoretic analysis revealed no gene loci different from those of other rainbow trout. The Eagle Lake rainbow trout is widely propagated in hatcheries in western states for put-grow-and-take stocking in lakes and reservoirs. If fisheries managers find it useful to designate an unusual form of rainbow trout as a subspecies to distinguish it from other forms of rainbow trout propagated in hatcheries, then the name *aquilarum* has some practical value. It must be recognized, however, that forms such as *nelsoni* and *aquilarum* do not satisfy any definition of a subspecies based on degree of distinction from all other subspecies of a species (Weins 1981).

In my opinion the royal silver trout of Lake Tahoe, *S. regalis*, and the emerald trout of Pyramid Lake, *S. smaragdus*, described from the Lahontan basin, were products of hatchery introductions (Behnke 1972b). The trout of Crescent Lake, Washington, named *S. gairdneri beardslei* by Jordan, is a specialized lacustrine form isolated in Crescent Lake. Like the Kootenay Lake Kamloops trout, the Beardsley rainbow trout coevolved with kokanee and is a specialized predator on kokanees. Undoubtedly, it has evolved subtle behavioral and physiological differences worthy of fishery management consideration, but it does not differ taxonomically from typical coastal rainbow trout.

LIFE HISTORY AND ECOLOGY

The most significant life history attribute of coastal rainbow trout is the widespread occurrence of steelhead populations. Great life history variability is found among steelhead populations. Steelhead populations can be broadly divided into summer-run and fall- or winter-run fish, depending on when the spawning migration enters fresh water. This is an oversimplification, however. Steelhead probably enter fresh water somewhere in their range during every month of the year. Spring–summer runs enter fresh water typically from May through August and move upstream to hold over until the following spring to spawn. Fall runs typically enter from September through November and spawn in the spring. Some rivers have later winter runs (December–March) that spawn soon after they enter fresh water. In different parts of the range, spawning may occur from January to June. Spring- and summer-run steelhead enter fresh water with immature gonads. Late winter-run steelhead have gonads that are almost fully mature by the time they ascend rivers.

The timing of runs has a genetic basis (Neave 1944, 1949; Smith 1969; Ricker 1972), and reproductive isolation exists between the stocks. How races of steelhead originated, and how races maintain reproductive isolation when they occur in the same river, are not well understood. In the Cowichan River, British Columbia, two distinct runs of steelhead and a resident rainbow trout coexist, according to Neave's studies, without clear-cut separation in the time and place of their spawning.

Leider et al. (1984) described the spawning characteristics of four sympatric steelhead populations in the Kalama River drainage (Columbia River tributary), Washington. The Kalama River has native populations of winter-run and summer-run steelhead; in addition, winter and summer runs are supplemented with nonnative hatchery stock. Some separation occurs in the times and places of spawning among the four populations, but the native winter- and summer-run populations maintain their identities despite large numbers of spawning hatchery fish. A greater reproductive success of native than of hatchery

steelhead in the Kalama River was deduced by Chilcote et al. (1986) and confirmed (with a different rationale) by Campton et al. (1991).

With many exceptions, summer-run steelhead spawn in the upper or headwater parts of river basins or in river sections accessible during the high flows of early summer. The evolutionary divergence of an anadromous species into discrete races enlarges its use of the environment and increases its productivity. The evolution of distinct seasonal races is a widespread phenomenon not only among trout, salmon, and char, but in other anadromous species such as lampreys and sturgeons as well. Many distinct local races of steelhead, particularly of summer-run stocks, have been lost because of dams, pollution, irrigation practices, and environmental changes.

Steelhead typically spend 2–3 years in fresh water before smolting and migrating to the ocean. After 1–3 years of ocean life, steelhead return to spawn in their home waters, typically in their 4th or 5th year of life. Generally, the largest steelhead are those with the longest oceanic phase (2–3 years or more). Each race has different life history characteristics, a variability summarized by Withler (1966).

Steelhead may spawn more than once, although survival to a second spawning is generally low. Most steelhead runs include 10–20% repeat spawners, but this percentage decreases in runs migrating the farthest upriver (only 1–3% of redband steelhead runs to Idaho's Salmon and Clearwater rivers are repeat spawners).

There is now a general awareness that hatchery propagation of steelhead, which historically mixed stocks indiscriminately, can be a significant factor in breaking down separation among races. A large gap remains, however, between perception of the problem and implementation of programs that avoid mixing of hatchery and wild steelhead. Barnhart (1975) presented a general review of steelhead management.

Nonanadromous or resident populations occur throughout the range of the coastal rainbow trout, often inhabiting the same streams used by spawning steelhead. Rainbow trout generally spawn in the spring, but spawning occurs from December–January to May–June in various parts of the range. Leider et al. (1984) found that spawning by the four steelhead populations in the Kalama River extended over 6 months (hatchery summer steelhead spawned first and native winter steelhead spawned last).

Hatchery selection has developed fall-spawning strains of nonanadromous rainbow trout, so spawning can occur in almost any month, given the diverse hatchery strains now available. In nature, however, it appears that fall-spawning rainbow trout revert to spring spawning, responding to increases in temperature and day length. Unusual cases also exist. Rainbow trout from Lake McConaughy, Nebraska, migrate up the North Platte River in the fall and spawn in warmer tributary streams in October and November (Van Velson 1974, 1978), for example, and rainbow trout in the Firehole River of Yellowstone National Park spawn in fall and winter where hot springs provide normal spring-spawning temperatures (Kaya 1977).

The largest rainbow trout are generally those that mature at the oldest ages. This is an important consideration for producing trophy rainbow trout from

stocking programs. The age at sexual maturation is under both genetic and environmental control (Ricker 1972). Domesticated hatchery rainbow trout have been selected for rapid growth and early maturation, which results in a shortened life span. A long evolutionary history in a large-lake environment where selection has favored large, predatory trout should provide a stock with genetically delayed maturity, as in the case of large Kamloops trout in Kootenay Lake.

STATUS

The coastal rainbow trout as a whole is doing well. Because it has been established all over the world and is profusely propagated in hatcheries, the subspecies likely has reached record abundance. Still of concern to management is the maintenance of genetic diversity in the multitudinous native steelhead races (Nehlsen et al. 1991) and in the unique life history forms of resident populations.

Kamchatkan Rainbow Trout *Oncorhynchus mykiss mykiss*

Around 1740, the naturalist George Wilhelm Steller wrote a manuscript (published posthumously in 1774) describing the Pacific salmon, char, and trout he observed on the Kamchatkan Peninsula. Stellar used the common names of the local people, which were later copied by Walbaum to formally describe the new species. Three names were formally proposed for the Kamchatkan trout: *Salmo mykiss* by Walbaum in 1792, and *S. purpuratus* and *S. penshinensis* by Pallas in 1814. The older Russian literature used *penshinensis* for the anadromous steelhead form and *mykiss* for the nonanadromous rainbow trout. Until recent times it was not known if more than one species of trout is native to Kamchatka.

In the absence of evidence concerning relationships, Jordan initially believed the Kamchatkan trout was a cutthroat trout and used the name *Salmo purpuratus* (later *S. mykiss*) as the name for North American cutthroat trout. Around 1896, Jordan received the head and skin of a large specimen of Kamchatkan steelhead. From this specimen he concluded that *mykiss* was not a cutthroat trout but was instead closely related to the Atlantic salmon *S. salar*. In the addenda to the third volume of Jordan and Evermann's (1898) work on the fishes of North America, the scientific name for cutthroat trout was changed from *S. mykiss* to *S. clarki*.

I examined the specimen of Kamchatkan trout received by Jordan many years earlier, which is in the Stanford University collection (number 12011). It is typical in all respects of North American steelhead, which would be expected on zoogeographical evidence—all Kamchatkan species of Pacific salmon, Arctic grayling, Arctic char, and Dolly Varden also occur in northwestern North America. In 1960, I examined seven specimens of Kamchatkan trout in museums in Moscow and Leningrad. I concluded that only one species of trout is native to Kamchatka, represented by both resident and anadromous forms, and that it is very closely related to the rainbow trout of North America (Behnke 1966). I reported vertebral counts of 57–59 for the museum specimens. I later learned that a mix-up had occurred in the X-ray films I examined, and that my counts were based on another species (probably the lenok, another Siberian salmonid). The Kamchatkan trout actually has 61–65 vertebrae, typically 62–63, similar to most North American coastal rainbow trout.

Since my 1966 paper on *S. mykiss*, numerous additional papers have been published, most of them in the Soviet journal *Voprosy Iktiologii* (translated into English as *Journal of Ichthyology*). Articles from *Voprosy Iktiologii* on Kamchatkan trout available in English include Maksimov (1971, 1972, 1976) on reproductive biology, ecology, and life history; Kokhmenko (1972) on food habits; Mina (1973) on techniques of aging; Savvaitova (1975) on population structure; Vasilyev (1975) and Gorshkova and Gorshkov (1985) on chromosomes; Alekseyev and Sviridenko (1985) on a new distribution record from Shantar Island; Savvaitova

et al. (1989) on taxonomic characters of *mykiss* from the Kishimshina River; and Shedko (1991) on mitochondrial DNA analysis. Savvaitova et al. (1973) compiled and summarized taxonomic and biological information on Kamchatkan rainbow trout. Mednikov and Akhundov (1975) studied DNA hybridization in resident, anadromous, and hatchery rainbow trout of Russia and North America.

North American rainbow trout have long been propagated in hatcheries in the former Soviet Union. Steelhead from Oregon were also imported, mainly in an attempt to establish runs in the Caspian and Black seas.

TYPICAL CHARACTERS

Vertebrae, 61–65 (means, 62–63); scales in the lateral series, 125–135; scales above the lateral line, 24–29; pyloric caeca, 25–60 (35–50); gill rakers, 16–22 (typically 19). Coloration, spotting, and general appearance are similar to those of coastal rainbow trout.

DESCRIPTION

Most Kamchatkan steelhead populations average 40–45 pyloric caeca, and resident populations average 34–51 caeca. Considerable geographical variability occurs in the number of caeca.

Studies of DNA hybridization, mitochondrial DNA analyses, and limited biochemical analysis confirm the close relationship between Kamchatkan and North American rainbow trout.

The chromosomes of 17 specimens from the Kamchatka River were studied by Vasilyev (1975), who counted 57–63 chromosomes in various cells (modal values, 58 and 60) and 104 chromosomal arms. Gorshkova and Gorshkov (1985) found a diploid number of 58 chromosomes with 104 arms in steelhead and resident populations of Kamchatkan trout. This is the most frequent karyotype of North American rainbow and redband trout. Vasilyev (1975) reported modal counts of 60–62 chromosomes with 108 arms in three Kamchatkan steelhead populations (origin not stated), but I regard these counts as dubious.

DISTRIBUTION

Beyond the Kamchatkan Peninsula, rainbow trout have been recorded from the Commander Islands east of Kamchatka and sporadically in the Okhotsk Sea basin as far south as the mouth of the Amur River along the mainland. The distribution records outside of Kamchatka probably represent migrating or straying Kamchatkan steelhead rather than established native populations. Alekseev and Sviridenko (1985) did document purportedly resident populations in rivers of Big Shantar Island (in the Okhotsk Sea near the Asiatic mainland north of the Amur River mouth). These authors suggested that rainbow trout may be competitively excluded by lenok in waters of the Asiatic mainland, but this assumption is doubtful. Chereshnev (1990) published a survey of the fish fauna in drainages to the Okhotsk Sea north of the Uda River. The Uda contains species of the salmonid genera *Brachymystax* and *Hucho*, but the northern rivers

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do not—nor do they contain rainbow trout. (The rivers barren of rainbow trout include the Penzhina, which has been generally listed as the northernmost river containing Kamchatkan *mykiss,* though this record is based on a secondhand account in Berg 1948.)

The distribution of Kamchatkan trout is most likely explained by events during the last glacial period when ocean levels were lower and a land bridge connected the Chukotsk Peninsula to the Seward Peninsula of Alaska.

TAXONOMIC NOTES

Before my 1966 publication, Russian scientists treated the Kamchatkan trout as two species—*mykiss,* the resident form, and *penshinensis,* the steelhead form. All recent Russian literature agrees that only one species, *mykiss,* should be recognized, and that resident and anadromous forms are expressions of life history and ecological differentiation within a single species. Resident rainbow trout and steelhead in North America are interpreted in the same way.

Because there is no longer any reasonable doubt that the rainbow trout of Kamchatka and North America are members of one species, the oldest and therefore the valid species name is *O. mykiss.* Although the name *gairdneri* is a synonym of *mykiss* at the species level, *gairdneri* may be used for subspecies designation, as I have done to classify the redband trout of the Columbia and Fraser basins.

The application of *mykiss* to North American rainbow trout came into use after Okazaki (1984, 1985) showed that ocean-caught steelhead, presumed to represent both North American and Kamchatkan fish, were electrophoretically alike. Okazaki did not present electrophoretic data on known Kamchatkan trout, however, and the results of this work do not document a mutual allelic identity for Kamchatkan and North American coastal rainbow trout. I have no reason to doubt that when detailed electrophoretic analysis is performed on Kamchatkan rainbow trout, the allele variation will fall entirely within the range of North American coastal rainbow trout. This raises the question of subspecific recognition for Kamchatkan rainbow trout and North American coastal rainbow trout. Provisionally, I group all native Asian rainbow trout as *O. m. mykiss* to denote their geographic separation, but I recognize that no known taxonomic characters separate *mykiss* from *irideus.*

LIFE HISTORY AND ECOLOGY

Based on the references cited previously, Kamchatkan steelhead are most common in rivers on the west coast of the peninsula. The maximum age is reported to be 8 years for steelhead and 9 years for residents. Steelhead spend 1–4 years (generally 2–3) in fresh water and 1–4 years (generally 2–3) in the ocean, which is comparable to steelhead populations in the northern part of their North American range. A length of about 1 m and a weight of about 10.5 kg may be attained by the largest Kamchatkan steelhead.

To date, seasonal races of steelhead comparable to the summer and fall or winter runs in North America have not been documented. Spawning migrations

begin about mid-August in southern rivers of Kamchatka and are under way until November in northern rivers. Some evidence suggests that the Bolshaya River may contain a spring run, just before spawning, in addition to the run in late summer and early fall. Spawning occurs from April through June. A coastal form may exist, feeding in estuaries and coastal areas like sea-run coastal cutthroat trout. In the absence of sea-run cutthroat trout, Kamchatkan rainbow trout may have evolved ecological forms that fill the niche used by cutthroat trout along the Pacific coast of North America.

Lake Azabachye (Kamchatka River basin) has a lacustrine form of rainbow trout. With increasing size, the Lake Azabachye trout becomes highly predaceous. The bulk of its diet consists of smelt, sticklebacks, juvenile sockeye salmon, and char.

STATUS

The Kamchatkan rainbow trout is more common and widespread than formerly believed. I find nothing in the Soviet literature regarding threats to its environment or problems with overexploitation. Although the Kamchatkan rainbow trout has been proposed for propagation and introduction into new waters in the former Soviet republics, I am not aware of any large-scale programs now in progress.

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PART IV

Southwestern Trout

13

TROUT OF GULF OF CALIFORNIA BASINS

In addition to the previously discussed trout native to the Río del Presidio and Río San Lorenzo of Mexico, three groups representing major evolutionary divergences have ancestral origins associated with dispersal from the Gulf of California. These are the Mexican golden trout, native to three drainages north of the Río San Lorenzo; the trout native to the Río Mayo and Río Yaqui; and the Gila and Apache trout of New Mexico and Arizona (Figure 18). I assume that the Gila and Apache trout originated from a common ancestor after this ancestor gained access to the Gila River basin.

Trout native to Gulf of California drainages are the most recently named, and the least known, of western North American trout. Gila trout were described only in 1950, Mexican golden trout in 1964, and Apache trout in 1972. The other Mexican trout have not been formally described. Many unknowns surround the position of all these fish in the phylogeny of western trout.

I previously suggested (Behnke 1970; Schreck and Behnke 1971) that Gila and Apache trout may be most closely related to primitive forms of rainbow trout (California golden and redband trout) because of their yellow coloration, the low numbers of their vertebrae and pyloric caeca, and the pronounced light-colored tips on their dorsal, anal, and pelvic fins. The relationship may be correct, but the diagnosis is based on shared primitive characters, which cannot be arranged as primitive and derived character states, and this makes any discussion of phylogenetic branching points largely speculative.

Of these southwestern fish, the trout of the Río del Presidio is the least differentiated morphologically from the Columbia basin redband trout, which suggests that it is the most recently established form, perhaps dating from the late Pleistocene. The Mexican golden trout on one hand and the Gila and Apache trout on the other represent the most divergent groups, indicating the longest isolation from all evolutionary lines of rainbow trout, perhaps dating from the early to the mid-Pleistocene. The trout of the Río Yaqui and Río Mayo is intermediate in its degree of divergence from Columbia and Sacramento subspecies of redband trout—more divergent than the Río del Presidio trout but less so than the Gila–Apache and Mexican golden trout. The trout native to the

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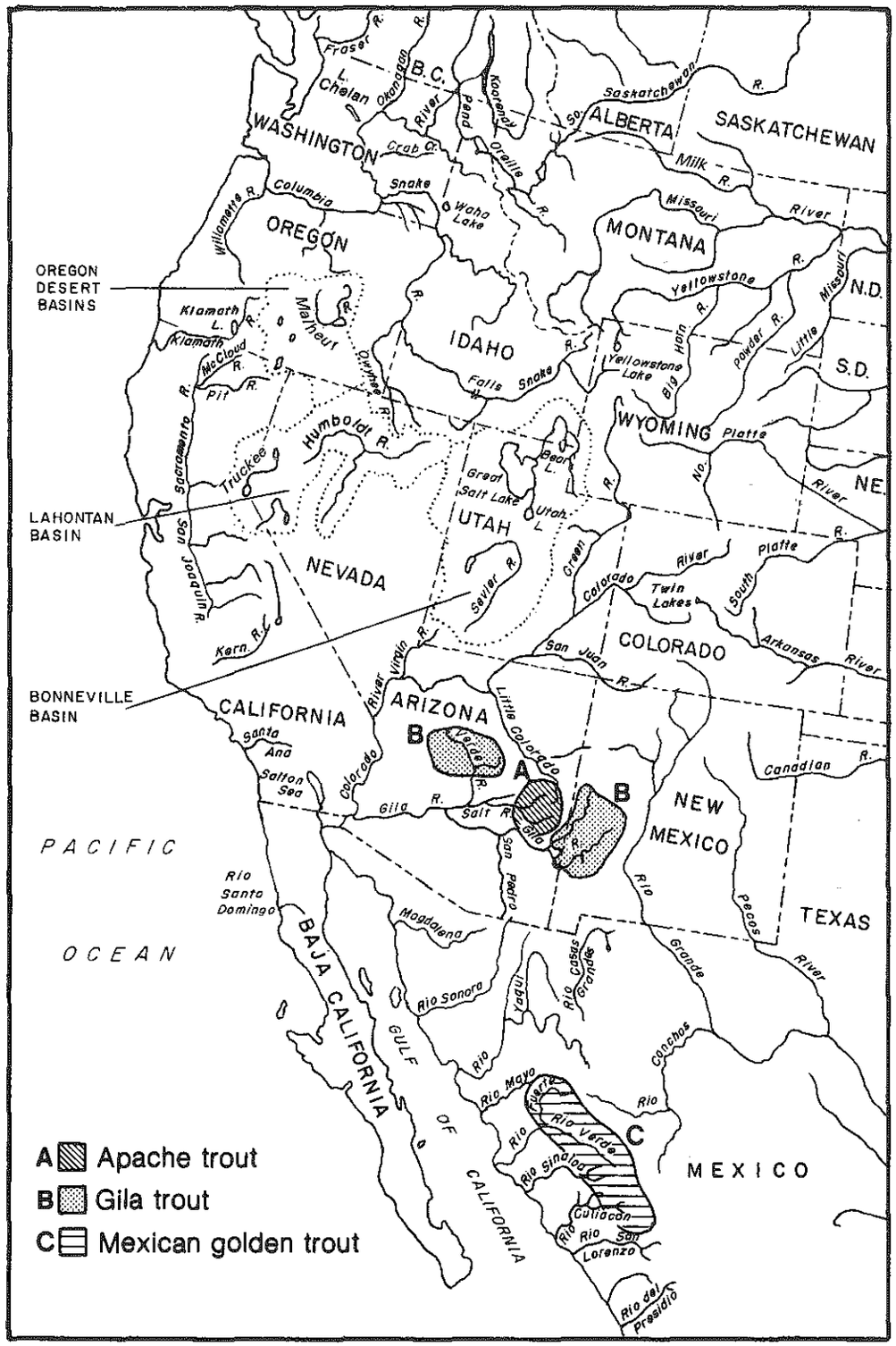

FIGURE 18.—Distributions of southwestern trout.

Río San Lorenzo drainage may represent another independent line from the Gulf of California, or it may be the result of hybridization between Mexican golden trout and Río del Presidio trout.

The colder climate during the major glacial epochs of the Pleistocene would have provided opportunities for southward movement of various evolutionary lines. Such a movement may be represented by *Salmo australis*, described by Cavender and Miller (1982) from fossil material of presumed Pleistocene age from the Chapala basin (Río Lerma drainage), about 400 km south of the present distribution of trout in headwaters of the Río del Presidio. The descendants of the earliest invasions would be expected to reflect the greatest divergence from contemporary forms of coastal rainbow and redband trout. An alternative view, based on the opinion that the Gila–Apache trout and the Mexican golden trout represent the most primitive forms of noncutthroat trout, is that the Gulf of California was an area of major speciation, and that northward movement along the Pacific Coast from the Gulf played a role in shaping the present diversity of rainbow trout. Both southward and northward dispersals probably occurred.

Gila Trout *Oncorhynchus gilae gilae*

Native trout have long been known from the Gila River basin of New Mexico and Arizona. In 1950, Miller described the Gila trout as *Salmo gilae*, and in 1972, he described the Apache trout as *S. apache*. Since then, data from karyotyping, electrophoresis, and mitochondrial DNA comparisons have substantiated the close genetic relationship of Gila and Apache trout (much closer than the relationship among the four major subspecies of cutthroat trout). To reflect this consanguinity, I recognize the Gila and Apache trout as two subspecies of one species.

TYPICAL CHARACTERS

Lateral-series scale counts, 135–165 (means, 150–155); vertebrae, 59–63 (60–61); pyloric caeca, 25–45 (32–35), except the Spruce Creek population has a mean value of 48. Coloration yellowish with diffuse pink–red tinges along the lateral line in mature males and a yellowish cutthroat mark. Profusion of small spots on body, mainly above the lateral line. Gila trout differ from Apache trout most consistently in having smaller and more numerous spots.

DESCRIPTION (Plate 8; Figure 19)

The deeper, more truncated bodies and longer fins of Apache and Gila trout separate them from other western trout. Besides the difference in spotting patterns, the Gila trout differs from the Apache trout in its red or pink hues (essentially absent during the entire life of Apache trout) and by its retention of parr marks in older age-classes.

Basibranchial teeth are found in some specimens of Gila trout from Spruce Creek, New Mexico, and are present in museum specimens from the Verde River drainage of Arizona.

Beamish and Miller (1977) first reported on the chromosomes of Gila trout after examining cells from four specimens of the Main Diamond Creek population raised at the Sterling Springs Hatchery, Arizona. Subsequent analyses have agreed that Gila and Apache trout have a diploid number of 56 chromosomes and a total arm number of 106, which distinguishes them from all forms of cutthroat trout (64–68 chromosomes) and rainbow trout (58–64 chromosomes, 104 chromosomal arms).

DISTRIBUTION

The distribution of Gila trout before European colonization of the region is not known with certainty. Some of the unusual aspects of its distribution were

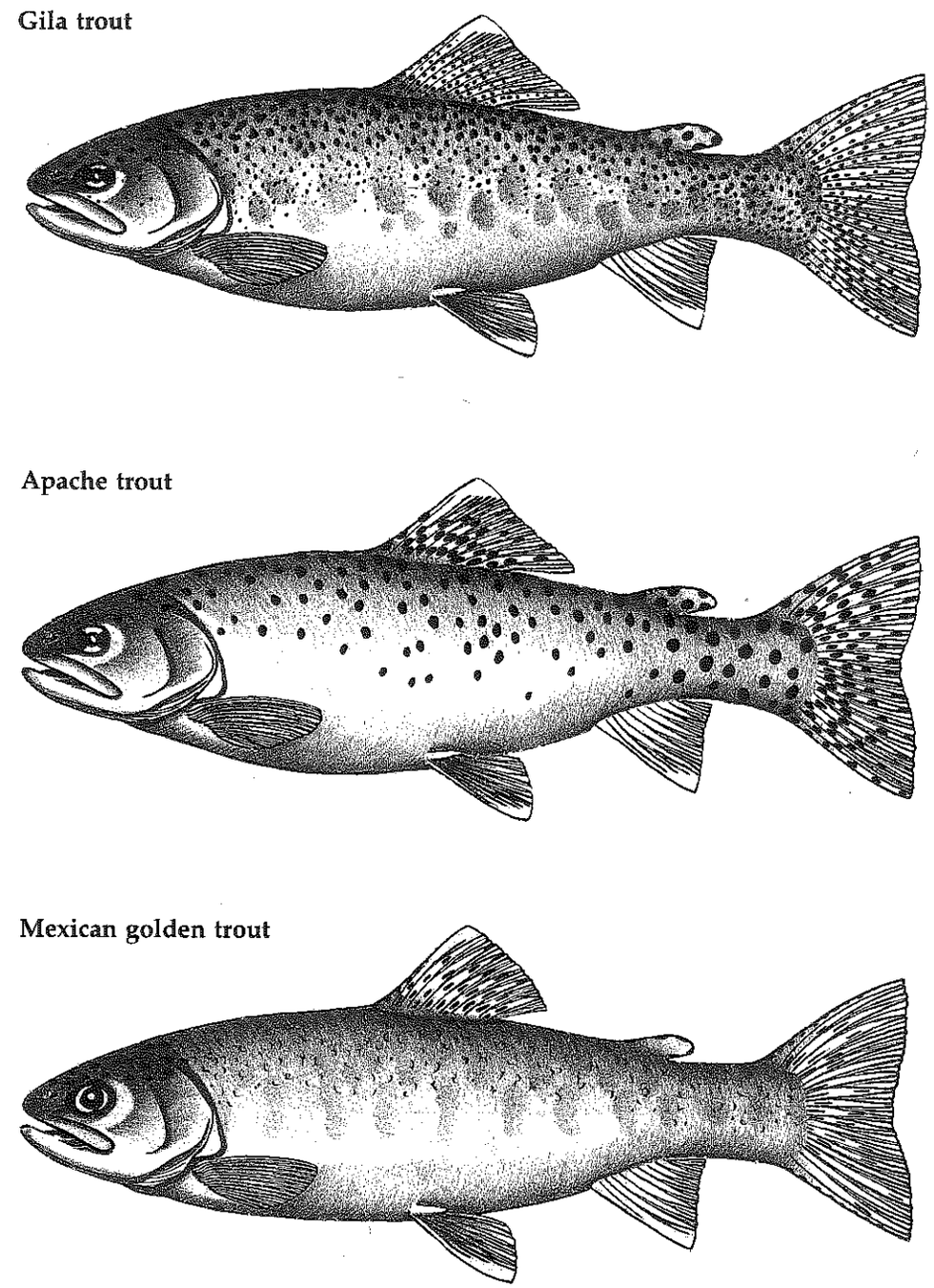

FIGURE 19.—Trout of Gulf of California drainages.

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discussed by Miller (1972a) and Behnke and Zarn (1976). Until recent years, its population centers were disjunct, one in western New Mexico, the other in central Arizona (Figure 18); the only extant population in Arizona has been introduced. When Miller (1950) described the Gila trout, he believed its historical distribution was the upper Gila River basin of New Mexico. He regarded the population in Spruce Creek of the San Francisco River drainage, a major tributary to the Gila along the New Mexico–Arizona border, as introduced. Gila trout are reputed to be native to Eagle Creek, Arizona, a tributary to the Gila west of the San Francisco drainage (Minckley 1973), and should have been native to at least part of the San Francisco drainage. Gila trout of Spruce Creek differ from other populations, which indicates long isolation rather than a recent introduction.

Gila trout were also native to the Verde and probably to the Agua Fria drainages, both tributary to the Salt River segment of the Gila River basin in central Arizona (Behnke and Zarn 1976). Minckley (1973) pointed out that the unusual distribution of Gila trout has much in common with a subspecies of roundtail chub. Rinne (1976) presented an excellent discussion of geological and climatic changes in the present Gila River basin in relation to the distribution of chubs of the genus *Gila*. It is likely these events were also responsible for the differentiation and distribution of Gila and Apache trout.

Sublette et al. (1990) noted a mention in the 1848 Emory Survey report of a "trout" in the Mimbres River drainage, New Mexico, which abuts the Gila drainage. The Mimbres is a tributary in the Guzman basin, a disrupted segment of the Rio Grande basin. I suspect, however, that this early reference to "trout" was based on the Chihuahua chub. Presently, an introduced population of Gila trout occurs in McKnight Creek in the Mimbres drainage.

TAXONOMIC NOTES

The morphological and meristic characters and the karyotypes of Gila and Apache trout substantiate a close relationship. Divergence from a common ancestor in the Gila River basin probably occurred during the mid to late Pleistocene. Loudenslager et al. (1986) presented data from electrophoretic analysis of 36 gene loci for four populations of Gila trout and five populations of Apache trout, which were compared with Río Mayo (Mexican) trout, two populations of hatchery rainbow trout, and three subspecies of cutthroat trout (Lahontan, Yellowstone, and Colorado River). The index of genetic similarity between Apache and Gila trout was 0.93. Genetic similarity was 0.86 between Gila trout and rainbow trout and 0.85 between Apache trout and rainbow trout. The genetic similarity of Gila and Apache trout (grouped together) to cutthroat trout (three subspecies grouped) was 0.72. The Río Mayo trout had genetic similarities of 0.90 to rainbow trout and 0.81 to Gila and Apache trout. Preliminary results of mitochondrial DNA analysis indicate close similarities between Gila and Apache trout, and closer similarity of these two forms to rainbow than to cutthroat trout (B. R. Riddle and T. L. Yates, University of New Mexico, unpublished data).

Thus, morphological and genetic studies agree that Gila and Apache trout are closely related to each other and that both have greater affiliations with rainbow than with cutthroat trout. Future taxonomic revisions, based on quantitative genetic data and the lack of reproductive isolation, might classify Gila and Apache trout as subspecies of rainbow trout. *Oncorhynchus gilae* is more of a practical than a biological species, although it does have a singular karyotype.

LIFE HISTORY AND ECOLOGY

The life history and ecological information on Gila trout are of limited value for diagnosing anything unique about the subspecies. Any trout species living in the small, mostly intermittent streams now inhabited by Gila trout probably would be comparable to them in growth, maturation rate, fecundity, feeding habits, and the like. The largest Gila trout collected in the wild that I have observed was a 330-mm specimen from South Diamond Creek. Individuals in the formerly abundant population in Main Diamond Creek almost never exceed 225 mm. Their small size is due to the tiny, harsh environments in which they are restricted, not to genetic dwarfism.

Rinne (1980) published a detailed account of spawning by Gila trout, and Sublette et al. (1990) provided an updated summary of information on their biology.

STATUS

Native populations of Gila trout now occur in Main Diamond, South Diamond, McKenna, and Iron creeks (upper Gila River tributaries) and Spruce Creek (San Francisco River Drainage), all in New Mexico. Introduced populations occur in McKnight Creek (Mimbres River drainage in the Guzman basin, New Mexico); in Sheep Corral, Little, Big Dry, Trail Canyon, and Woodrow Canyon creeks (Gila drainage, New Mexico); and in Gap Creek (Verde River drainage, Arizona). These are all small headwater streams. Native distribution occurs in about 15 km of five streams, and introduced distribution in about 25 km of six streams.

The problems of maintaining remnant populations of an endangered species in very small habitats include coping with natural catastrophes such as drought, fire, and flood. All these factors have severely stressed Gila trout in recent years. Propst et al. (1992) documented recent problems faced by Gila trout. In July 1989, a fire ignited during severe drought swept the Main Diamond Creek watershed and burned much of the South Diamond Creek watershed. As a precautionary measure, biologists removed 566 Gila trout from Main Diamond Creek to the Mescalaro National Fish Hatchery; 202 of these fish were subsequently stocked in McKnight Creek, which itself had lost 95% of its Gila trout population because of drought. The precautionary transfer was well advised, for in August a large flood scoured the Main Diamond watershed, producing ash-laden debris flows that eliminated all the remaining fish from the creek. Floods also reduced the Gila trout population in South Diamond Creek by 95%. In Arizona, years of low flow reduced the Gap Creek population to six adults

and it is assumed that this small stream cannot maintain a viable population of Gila trout.

The catastrophes of 1989 caused the U.S. Fish and Wildlife Service's Gila Trout Recovery Team to develop a new conservation strategy. In the future, restoration will be attempted in a larger segment of a drainage and include several tributaries capable of serving as refugia during times of natural catastrophes.

In 1989, the Gila trout was proposed for downlisting from endangered to threatened status (Williams et al. 1989). This proposal was withdrawn after the impacts of the catastrophes were evaluated. The Gila trout is the only trout currently listed as endangered under the Endangered Species Act. Other trout formerly listed as endangered (Little Kern golden, Apache, Lahontan, Paiute, and greenback cutthroat trout) have been downgraded to threatened status.

Apache Trout *Oncorhynchus gilae apache*

TYPICAL CHARACTERS

Deep, compressed body; golden-yellow or olive-yellow body coloration; pronounced, moderate-size, rounded or oval spots more or less evenly distributed over sides of the body and onto top of the head. Dorsal fin typically the largest of any western trout. Vertebrae, 58–61 (means, 59–60); lateral-series scales, 135–170 (150–155); pyloric caeca, 21–44 (27–33). About 5% of some populations possess basibranchial teeth.

DESCRIPTION (Plate 8; Figure 19, page 213)

The spotting differences between Apache and Gila trout can be compared with the differences between subspecies of cutthroat trout. The Apache trout has a spotting pattern similar to that of most interior cutthroat trout subspecies except that the spots tend to be slightly smaller and they occur anteriorly below the lateral line more or less evenly over the sides of the body and on top of the head. The Gila trout more resembles the finespotted Snake River cutthroat trout in its spotting pattern.

The Apache trout typically has brighter golden-yellow colors than does the Gila trout, but it usually lacks red or pink on the body. The Apache trout has a distinctive horizontal band of dark pigment across the iris, which produces a masklike effect.

Although environmental, nongenetic influences can alter trout morphology to create large overlap among taxa, Apache and Gila trout typically differ from other western trout in at least three respects. Their body form is deeper, chunkier, and more compressed; they have longer fins; and their dorsal fin originates farther posteriorly on the body. The dorsal fin of Apache trout is the longest (depressed length) of all western trout, and the Gila trout typically has the longest adipose fin.

The taxonomic description of Apache trout given by Miller (1972a) has been greatly supplemented by Rinne (1985) and Rinne and Minckley (1985), who provided comprehensive morphometric and meristic data on many populations of the subspecies.

DISTRIBUTION

The 19th-century distribution of Apache trout, based on Miller's (1972a) examination of museum specimens, included the White and Black river drainages (headwaters of the Salt River division of the Gila River basin), the headwaters of the Little Colorado drainage, and the Blue River (specimen from

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KP Creek) in the San Francisco River drainage. These streams are all close to each other in the White Mountains of Arizona (Figure 18, page 210). The estimated distribution of Apache trout comprised about 950 km of stream habitat (Recovery Plan draft, 1977). This was reduced to about 50 km of small, headwater tributaries before restoration efforts began.

The original distribution patterns of Gila and Apache trout present perplexing questions to zoogeographers. For example, if the Apache trout occurred in headwaters of the Salt River, what kept it from becoming the native trout in the Verde and Agua Fria drainages, which are tributaries to the Salt River, instead of Gila trout?

TAXONOMIC NOTES

Cope and Yarrow (1875) and later Jordan (1891) classified Apache trout with the Colorado River cutthroat trout, *O. clarki pleuriticus*. They did not know that the range of the Colorado River cutthroat trout did not extend to the Grand Canyon. When Miller (1950) described *Salmo gilae*, he provisionally included Apache trout with *gilae*. After examining more specimens, Miller (1972a) separated the Apache trout as a distinct species, *Salmo apache*. He believed the most likely origin of Apache trout was from a cutthroat trout ancestor isolated in the headwaters of the Little Colorado drainage.

As discussed under Gila trout, the very close relationship of Apache and Gila trout indicates a mid- to late-Pleistocene separation from a common ancestor in the Gila basin. In turn, that common ancestor was more aligned with rainbow trout than with cutthroat trout.

In suggesting that Gila and Apache trout and Mexican golden trout originated as hybrids, Needham and Gard (1964) erroneously assumed that rainbow and cutthroat trout came into contact in the lower Colorado River basin. Analyses of karyotypes, gene loci, and mitochondrial DNA disprove the hybrid-origin theory.

Rinne et al. (1985) reported on a hybridization experiment between female hatchery-reared Apache trout and male hatchery rainbow trout. In a 1981 trial, only six fish hatched from 300 fertilized eggs; of these, only two survived to the fingerling stage. In a 1983 hybridization trial involving 200 fertilized eggs, five fish hatched and three of them were deformed (lordosis). These experiments suggest strong reproductive incompatibility between Apache trout and rainbow trout. I suspect, however, that the results are atypical. Only two female Apache trout and two male rainbow trout were used; possibly their sperm and eggs were abnormal, immature, or overmature, or the researchers failed to make all reciprocal crosses for comparisons. The morphometric and meristic comparisons of Apache trout, rainbow trout, and suspected hybrids by Rinne and Minckley (1985), the electrophoretic analysis of suspected hybrids by Loudenslager et al. (1986), and my examination of numerous hybrid specimens from several White Mountain streams discount the existence of a sterility barrier that prevents hybridization between Apache trout and rainbow trout in nature. Robert David (U.S. Fish and Wildlife Service, Alchesay–Williams Creek National Fish Hatchery, White River, Arizona) told me of a rainbow × Apache trout hybrid experiment, incorporating both sexes of both species, conducted at the Alchesay hatchery. No evidence of infertility in the hybrid cross was found. In 1991, 2-year-old hybrids of both sexes, with developing gonads, were being raised at the hatchery and a second generation was to be attempted. I have a color photograph of a hybrid whose phenotype is predominantly that of a rainbow trout.

LIFE HISTORY AND ECOLOGY

Harper (1978) and Rinne (1978) presented comprehensive information on the biology and habitat of Apache trout, but no unique attributes were found. Alcorn (1976) conducted temperature tolerance tests with fingerling Apache trout. After acclimation, the temperature was raised 2–3°C every 2 days. In three of four test groups, feeding ceased and signs of distress were apparent at temperatures of 20.1–21.2°C. The fourth group did not cease feeding until temperatures reached 23.5°C. Total mortality occurred between 23.5 and 24.0°C. No other species were tested under identical conditions, so the meaning of these data is uncertain. Lee and Rinne (1980) found no differences in the critical thermal maximum (measured by raising the temperature 1°C per hour until equilibrium was lost) between Apache, Gila, rainbow, brown, and brook trout. All of the fish lost equilibrium at about 29.5°C. Lee and Rinne also mentioned that they and others had observed Apache and Gila trout feeding at 23°C in streams. Thus, there is no hard evidence that Apache trout (or Gila trout) differ from other trout in their temperature tolerances.

Robinson and Tash (1979) reported on feeding by Apache trout in relation to light intensity. They also discussed the much greater vulnerability of Apache trout than of brown trout to angling exploitation when the two live together in the same stream.

Apache trout are essentially restricted to small headwater streams at high elevations (above 1,800 m) in the White Mountains. In addition, several recreational lakes on the Fort Apache Reservation are stocked with Apache trout. In small streams Apache trout rarely exceed 300 mm, but in hatcheries and in lakes they can reach at least 2 kg.

STATUS

In 1975, the status of the Apache trout was changed from endangered to threatened under the Endangered Species Act to facilitate a management program that included recreational angling. Because of concern and respect for a symbol of their biological heritage, members of the White Mountain Apache Tribe have long practiced stewardship of Apache trout on the 600,000-hectare Fort Apache Reservation. The U.S. Fish and Wildlife Service, in cooperation with the tribe, has undertaken a large-scale propagation program designed to replace rainbow trout with Apache trout in waters on the reservation (Hansen and David 1989). This program calls for stocking both fingerling trout (mainly for put-and-grow fisheries in impoundments) and catchable trout (for put-and-take fisheries). The goal is to annually stock 219,000 fingerlings or subcatchable fish

and 257,000 catchable fish (larger than 200 mm). To reach this goal will require a large hatchery brood stock. Along with the unavoidable selection for certain hatchery-favored characteristics (disease resistance, artificial diet assimilation, tolerance of high-density rearing, etc.), program managers have decided to select for males that sexually mature at a younger age (age 2 versus age 3) (Hansen and David 1989). Ironically, to accomplish its grand goal of restoring Apache trout and delisting the species under the Endangered Species Act, this large-scale propagation program will sacrifice the trout's natural genetic diversity.

For large-scale catchable trout production, there may be no cost-effective, efficient alternative to artificial selection and hatchery rearing. If catchable trout are stocked into waters where pure wild populations of Apache trout do not exist, then no negative effect should be expected. For fingerling stocking, however, the goal should be to maintain the natural genetic diversity of wild populations. This could be accomplished by stocking fish from several pure populations in a productive impoundment (in an attempt to maximize heterozygosity) and using the surviving spawners to obtain sperm and eggs. If such a heterozygous wild brood stock were maintained under natural conditions, it could also serve to increase the heterozygosity of the hatchery brood stock and promote more rapid selection for efficient rearing under artificial conditions.

I have discussed the failure of the U.S. Fish and Wildlife Service's attempt to develop a hatchery brood stock of Lahontan cutthroat trout (Behnke 1989b). As selection for hatchery life increased, poststocking survival in nature decreased to a point of no return. It is to be hoped that the preservation of intraspecific genetic diversity will be incorporated into any restoration program based on hatchery propagation.

Mexican Golden Trout *Oncorhynchus chrysogaster*

TYPICAL CHARACTERS

Sides of body with light golden yellow coloration. Orange on ventral surface. Spots small, irregularly shaped, sparse and diffuse, mainly restricted to area above the lateral line. Vertebral counts of 56–59 and pyloric caecal counts of 10–30 (means, 21–23) are the lowest found in any western North American trout. Branchiostegal rays 8–10; pelvic rays 9.

DESCRIPTION (Figure 19, page 213)

The Mexican golden trout was first described and illustrated by Needham and Gard (1959), who formally named it in 1964.

The basic characters of the Mexican golden trout are generalized primitive characters retained from an ancestor common to it and rainbow trout. Miller (1972a) claimed the Mexican golden trout represents the most primitive living species of western trout. Needham and Gard, however, found no basibranchial teeth in the 100 or so specimens they examined. Thus, the evolutionary branch leading to the Mexican golden trout must have lost this primitive feature. Robert R. Miller and T. Uyeno (personal communication and unpublished data) found a diploid number of 60 chromosomes and a total arm number of 104 for Mexican golden trout. As previously discussed, this karyotype does not appear to be primitive in relation to the 56 chromosomes of Gila and Apache trout. The chromosome number of Mexican golden trout is assumed to have evolved independently and is not homologous with that of some coastal rainbow trout, which also possess a diploid number of 60 chromosomes.

Lateral-series scale counts reported by Needham and Gard (1959) are variable. They range from 115 to 158 and average 126–142 in different samples.

DISTRIBUTION

The Mexican golden trout is known only from headwater tributaries to the Río Culiacan, Río Sinaloa, and Río Fuerte, all tributaries to the Gulf of California in Durango and Sinaloa, Mexico (Figure 18, page 210).

TAXONOMIC NOTES

In their original publication, Needham and Gard (1959) considered Mexican golden trout to be a form of rainbow trout. They attributed the highly divergent characters of these trout to environmental influences. After I had accumulated several years of data on thousands of specimens of many forms of western trout,

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it became obvious that the unique characters of Mexican golden trout could not be explained by environmental influences. Instead, they represent a distinct and highly divergent evolutionary line. This point was accepted by Needham and Gard in their 1964 description of the Mexican golden trout as a new species. They proposed a hybrid origin whereby cutthroat trout and rainbow trout in the lower Colorado River basin gave rise to the Mexican golden, Gila, and Apache trout. A hybrid origin for Gila and Apache trout can be dismissed, as previously discussed.

LIFE HISTORY AND ECOLOGY

Needham and Gard (1959) presented some descriptions of habitat, but no other biological information is known. Smith (1984) described angling for Mexican golden trout.

STATUS

Needham and Gard (1959) and Needham's field notes reveal that much environmental deterioration and loss of habitat has occurred, which has greatly reduced the distribution and abundance of this trout. The potential threat from hybridization with introduced rainbow trout is not known, but R. R. Miller related to me that a reservoir at the headwaters of the Río Fuerte is stocked with rainbow trout that might escape into the Río Fuerte during high-water periods. Smith (1984, and personal communication regarding 1990 field trip) found Mexican golden trout to be virtually absent from streams near roads or human habitation; the fish are exploited by various methods to the point of local extinction.

Other Mexican Trout

Trout that have not been formally classified occur in drainages of the Río Yaqui, Río Mayo, and Río Casas Grandes in Mexico (Figure 18, page 210). Needham and Gard (1959) presented data on collections from the Río Yaqui and Río Casas Grandes drainages. Although the Río Casas Grandes is an isolated segment of the Guzman basin, it closely adjoins tributaries of the Río Yaqui, and the trout of both drainages appear identical. Natural headwater transfer or (more likely) human transfer could account for the Casas Grandes trout.

Needham and Gard discussed a collection of specimens from Black Canyon, a headwater tributary to the Río Yaqui, and from the Río Seco, tributary to the Río Casas Grandes. These trout have light-yellowish coloration with a yellow cutthroat mark, a strong red band on the side, and a bright red-orange tip on the dorsal fin (essentially identical to color photos of Río Mayo trout). The parr marks are elliptical with supplementary rows. Vertebrae number from 58 to 61 (mean, 60), and lateral-series scale counts average 138 in the Black Canyon sample and 146 in the sample from the Río Seco.

Trout of the Río Yaqui and Río Mayo trout have a diploid number of 64 chromosomes with 104 arms (R. R. Miller and T. Uyeno, personal communication), quite distinct from the karyotype of Gila trout. As previously discussed, electrophoretic analysis (Berg 1987; Loudenslager et al. 1986) revealed a genetic similarity of 0.81 between Río Mayo trout and Gila and Apache trout, and a similarity of 0.90 between Río Mayo trout and coastal rainbow trout.

The trout native to the Río Yaqui and Río Mayo probably represent a primitive form of rainbow–redband trout that independently evolved a derived karyotype. That is, their diploid number of 64 is not homologous with the 64 chromosomes of coastal rainbow trout in northern California.

Nothing has been published on trout in the Río Mayo. They were first discovered by University of Arizona students on a field trip in 1975. Trout were observed both above and below Basasechic Falls in the Río Caudamean, tributary to the Río Mayo. The Río Mayo drainage is between the Río Yaqui drainage to the north and the Río Fuerte to the south.

Much is yet to be learned about the distribution and classification of Mexican trout. The report of Cope (1886) on a trout with basihyal (basibranchial) teeth collected near the junction of Durango, Sinaloa, and Chihuahua is still a mystery. Our incomplete understanding of Mexican trout is not surprising in view of how little we know about evolutionary relationships and classification of the native trout in such well-studied areas as the Columbia and Sacramento river basins.

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PART V

Epilogue

14

PRESERVATION OF TROUT DIVERSITY

The native trout of western North America cannot be reduced to a neat classification of species and subspecies that accurately reflects all the degrees and nuances of evolutionary relationships. Realistically, we can only attempt to approximate the major and minor branching sequences of western trout phylogeny, based on critical evaluation of all evidence of relationships.

It can be assumed that no system of classification of western trout will ever receive universal agreement. My advice to fishery biologists, managers, and administrators is to avoid taxonomic anxiety and concentrate instead on recognizing that particular forms of trout are native to particular areas, and that these forms are differentiated from each other. The sum total of this differentiation represents the biodiversity of western trout—a genetic resource still to be integrated into fisheries management programs. The biodiversity of western trout should be recognized as a natural resource, but one that has been historically neglected, squandered, and depleted.

The original intent of this monograph was to fill the perceived need for an identification guide to the species and subspecies of western trout and to provide some supplementary information on distribution and status. Over the years, it has evolved into a celebration of wild, native trout, and one of its goals is to stimulate preservation of trout diversity by emphasizing the practical benefits to fisheries management available among the remnants of this diversity. This emphasis on the preservation of biodiversity nicely complements the contemporary "mission" or "vision statements" of resource agencies. Translating good intentions into effective policies and programs—moving from words to deeds, from generalities to specifics—is difficult, however. The credibility and success of conservation and management programs depend on the depth of knowledge of the subject matter.

The November–December 1989 issue of *Fisheries* contains two articles germane to this work: "Fishes of North America, endangered, threatened, or of special concern" (Williams et al. 1989) and "Extinctions of North American fishes during the past century" (Miller et al. 1989). Two subspecies of cutthroat trout, the yellowfin and the Alvord, are listed as extinct. Eight additional

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subspecies of cutthroat trout, eight subspecies (most of them unnamed) of rainbow trout, and the Gila, Apache, and Mexican golden trout are recognized as endangered, threatened, or of special concern by the American Fisheries Society's Endangered Species Committee (Williams et al. 1989). Nehlsen et al. (1991) listed 214 stocks of Pacific salmon, steelhead, and coastal cutthroat trout at risk of extinction in California, Oregon, Idaho, and Washington. Of these, 101 are considered to be at high risk and 18 may already be extinct.

The listing of taxa (species and subspecies) in need of protection is only the first step, however, toward the implementation of an effective program to preserve biodiversity, because most of the significant differences in life history and ecological adaptation are associated with "nontaxa" at the stock or population level. The 1989 emergency listing of winter-run chinook salmon of the Sacramento River under the Endangered Species Act and the 1991 petitions for listing spring, summer, and fall runs of chinook salmon of the Snake River drainage of Idaho, sockeye salmon of the Salmon River, Idaho, and coho salmon of the Columbia River basin are focusing attention on the rationale for protecting individual stocks. The importance of significant units of diversity within a species or subspecies is being recognized. The dilemma facing the fisheries profession is that petitions to formally list 100 or more stocks, races, or populations that are "legally" entitled to protection under the Endangered Species Act will likely result in a backlash and weakening of the Act through a legislative redefinition of the smallest taxonomic level the Act can protect.

Fisheries managers must avoid a public reaction against what might be perceived as overly zealous applications of the Endangered Species Act, yet not be immobilized by fear of a backlash. They can find a middle ground by clearly defining the uniqueness of stocks, races, and populations, and prioritizing the most significant units in relation to extinction risks and "irreplaceability." By irreplaceability, I refer to the degree of difference in life history among intraspecific populations. For example, winter-run Sacramento chinook salmon form the only population of their species that has a hereditary basis to spawn in the spring. This particular unit of diversity within *Oncorhynchus tshawytscha* is irreplaceable by any other unit of the species. The original Pyramid Lake cutthroat trout, representing a population of *O. c. henshawi*, and the Bear Lake cutthroat trout, representing a population of *O. c. utah*, are irreplaceable units of their subspecies because of their unique evolution as keystone predators in large lakes. No other populations of these subspecies would be expected to duplicate the life histories of the native populations if stocked into Pyramid Lake or Bear Lake, nor to attain the maximum size or original abundance of the native populations. The life histories and great maximum size of the Gerrard population of Kootenay Lake redband trout and the summer-run race of Skeena River steelhead should be recognized as irreplaceable units of diversity within *O. mykiss*.

A summer-run steelhead population that became extinct because of pollution in a particular river drainage might be considered replaceable—provided pollution were abated—if populations of summer-run steelhead in neighboring drainages essentially duplicated the life history of the extinct population in time of run, distance from ocean, time of spawning, freshwater life, and ocean life.

The question of replaceability or irreplaceability concerns the degree of differences in all aspects of life history, and it can be answered only by comparing a particular unit of diversity with all other units of the species or subspecies.

A common contention of those opposed to protection of units below the species level, especially of diversity at the stock level, is that intraspecific diversity is nonadaptive and replaceable by other members of a species or by closely related species. This thesis has its origins in the saltation theory of evolution proposed by geneticists in the early 1900s. According to that theory, new species arise from old species by single macromutations; intraspecific variation is due to micromutations that are random, nondirectional, and not subject to natural selection. This form of saltation theory was rejected by evolutionary biologists after landmark publications by Dobzhansky (1937), Huxley (1942), and Mayr (1942) reaffirmed the basic principles of Darwinian evolution: (1) variation among individuals of an interbreeding population; (2) surplus reproduction; (3) differential survival of variants due to natural selection; and (4) gradual accumulation of many small differences. The idea that intraspecific variation is nonadaptive has persisted nonetheless, and it was well articulated by Tucker (1979). But the ability of native Lahontan cutthroat trout to grow larger in Pyramid Lake than any introduced successor, the ability of redband trout in Oregon basins to function at high temperatures that would kill most other trout, and the ability of fluvial Bonneville cutthroat trout to outcompete stocked invaders in marginal habitats are but three of many examples described in this monograph of irreplaceable stock-level adaptations that thoroughly refute the views espoused by Tucker—views that lack a sound understanding of evolutionary biology.

To effectively counter arguments that intraspecific variation is nonadaptive, biologists involved with the preservation of biodiversity must be knowledgeable about evolutionary theory and understand that adaptiveness in the evolutionary sense is synonymous with survival. Members of each population, completely or largely isolated from gene exchange with other populations of the same species, will become better adapted to survive (maintain maximum abundance) in their native environment than any new immigrant to that environment. Therefore, the maintenance and restoration of trout and salmon species, especially of anadromous populations, over the long term must be based on preserving the maximum amount of intraspecific diversity. Attempts to increase abundance by massive production of genetically altered hatchery stocks (of nonnative origins in relation to the waters stocked) should not be regarded as replacements. Wild populations may, in some cases, be supplementable, but they are not replaceable. Goodman (1990) pointed out that massive hatchery propagation and stocking has been a major cause of the decline and endangerment of wild races. He called for federal regulation of salmonid hatchery programs to insure that practices do not violate the Endangered Species Act by further jeopardizing the existence of declining wild stocks proposed for listing and protection under the Act.

Once the rationale for the preservation of intraspecific diversity is established and effectively communicated, the problem of defining intraspecific units, especially irreplaceable stocks and populations, must be addressed. The use of

biochemical and genetic techniques to quantify genetic differentiation, such as electrophoresis of proteins to assess alleles at gene loci, measuring divergences in mitochondrial DNA, and sequencing of amino acids in protein molecules, will bring very powerful analytical tools to bear on these problems. But there is great danger in relying only on such methods to determine a population's uniqueness. Present analytical techniques of quantitative genetics sample only that part—less than 1%—of the genome consisting of structural genes, the genes that code detectable molecular products. The other 99+% of the genome consists of regulatory genes that activate and deactivate the structural genes and thus program all life history traits. Differences quantified in the structural genome are unrelated to differences in life history traits determined by the (unsampled) regulatory genome.

The following three examples illustrate the current limitations of quantitative genetics for interpreting irreplaceable units of biological diversity.

Under human selection, domestic dogs *Canis familiaris* have diverged from wolves *C. lupus* during the past 10,000 years—about the same amount of time that has been available for diversification in many trout populations. Despite the great morphological differences among breeds of dogs and between dogs and wolves, no variation in structural genes has been found among these groups (Wayne and O'Brien 1987). A person told that chihuahuas or English bulldogs are completely adequate replacements for retrievers or setters as hunting dogs because these breeds are genetically identical would consider the statement false and ludicrous. The same person, however, might accept a statement that summer and winter runs of steelhead are not hereditarily based units of intraspecific diversity because no consistent pattern of genetic differentiation has been detected between them. Such a conclusion would be just as erroneous for steelhead as it would be for dogs.

Lake Victoria, Africa, contains a species flock of cichlid fishes classified into about 200 species representing 20 genera. The long-standing problem of how all these species originated has stimulated genetic research in recent years (Avise 1990; Meyer et al. 1990). Several genes as well as mitochondrial DNA have been closely analyzed for 14 species in 9 genera. Victoria cichlids have habitat specializations that range from papyrus swamps to open waters and feeding specializations to exploit every resource from detritus and algae to mollusks and fishes. Nevertheless, the 14 species analyzed showed less quantitative genetic diversity than the human species—which itself exhibits less intraspecific differentiation than many other vertebrates. As with dogs, genetic analysis of Victoria cichlids provides an insufficient and misleading measure of biodiversity.

A Florida subspecies of seaside sparrow *Ammodramus maritimus nigrescens* recently became extinct. This form was distinctive enough to once be considered a full species, the dusky seaside sparrow *A. nigrescens* (AOU 1983). In discussing the application of mitochondrial DNA (mtDNA) data to wildlife management, Wirgin et al. (1991) referred to these birds, stating: "Although they were morphologically distinct, their mtDNA genotypes showed close affinity to those of other seaside sparrow populations; therefore, efforts to preserve the Florida gene pool would not have been warranted." Perhaps preservation of the Florida seaside sparrow was not warranted. This dubious line of reasoning, however,

would have a devastating effect on conservation if it were applied to cichlid species flocks, to races of trout and salmon, or to any group whose adaptations have evolved too recently to be reflected in the structural genome.

As the preceding examples indicate, successful programs for preserving biodiversity will rely on biologists who have some fundamental understanding of how evolution by natural selection works and where the limits of genetic quantification lie with respect to defining intraspecific diversity. These biologists should not confuse quantitativeness with biological reality, nor should they be intimidated by modern technologies.

Given the great gap between our ability to measure and our ability to understand what we measure, the importance of professional judgment in fisheries conservation and management cannot be overemphasized. The need for judgment extends well beyond the interpretation of genetic data, as I have stressed elsewhere in this monograph. Any attempt to associate environmental or habitat components with fish abundance for predictive purposes is limited by the regularity of the system under study. Most natural aquatic systems are characterized by high irregularity, and the irregularities of complex interactions and interrelationships determine the limits of accurate prediction. No methods, models, or rules can transform uncertain or unknown processes into deterministic events; "more data" cannot change this fact of nature. The most successful fisheries biologists will be those who develop the knowledge, experience, and expertise upon which professional judgment is based. Perhaps it will take a new generation of people filling agency positions before the goals of wild, native trout management propounded in this monograph can be fulfilled. I hope, however, that my efforts will stimulate more rapid adoption of progressive programs for native trout management by sowing the seeds of ideas and concepts which, properly cultivated and developed, should bear a rewarding harvest.

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GLOSSARY

acrocentric chromosome A chromosome with the centromere at one end, giving the chromosome the appearance of having one arm. (Compare *metacentric chromosome.*)
allele An alternative form of a gene. Alleles of the same gene differ from each other in details of their DNA sequence; thus they code slightly different sequences of amino acids in a protein. This sometimes changes the protein's character enough that variant proteins can be detected by electrophoresis, giving clues about which alleles an organism possesses.
allopatric Occurring in different areas; not overlapping in distribution.
anadromous Living some of life in the sea but returning to fresh water to spawn.

basibranchial teeth Teeth borne on the median ventral plate overlying basibranchial bones between the gill arches.
benthic Living on or in the substrate of a stream or water body.
biomass The weight of organisms in a defined area or volume. The biomass of fish usually is expressed (in the metric system) as kilograms per hectare (kg/hectare).
branchiostegal rays Bony processes that support the membranes enclosing the gill chamber, below the operculum (gill cover).

caudal On or toward the posterior or tail end of an animal.
caudal peduncle The usually narrower region of a fish's body between the anal fin and the caudal fin.
centromere Constricted portion of a chromosome at which the chromosome strands are joined during chromosome duplication and by which the chromosome is attached to the spindle during cell division.
cline A consistent change in a morphological or genetic character over a geographic range, such as an increase in number of vertebrae from south to north or from lowlands to highlands within an animal's range.
convergence Independent development of the same or similar values of a character in separate evolutionary lines.

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cover Anything that provides visual or physical protection for an animal. Cover for fish includes vegetation that overhangs the water, undercut banks, rocks, logs and other woody debris, turbulent water surfaces, and deep water.

derived character A character state judged to be younger than some comparable character within an evolutionary lineage. (Compare *primitive character*.)

deterministic Not subject to random (chance) variation. A deterministic process or model proceeds at fixed rates, and its outcome can be calculated if the initial state is known. (Compare *stochastic*.)

diploid Having two sets of chromosomes per nucleus, one set from each parent. (Compare *tetraploid*.)

disjunct Separated in space. A species' distribution becomes disjunct when intervening populations of a once-continuous distribution disappear. If disjunct populations remain isolated long enough, they may accumulate enough differences to evolve into sister species.

DNA Deoxyribonucleic acid, the hereditary material of genes. Most DNA is organized into chromosomes within cell nuclei, but about 1% of a cell's DNA resides in mitochondria. Modern analytical techniques allow DNA fragments to be compared between individuals and species, providing a powerful taxonomic and systematic tool. (Compare *mitochondrial DNA*.)

dorsal On or toward the back of an animal. (Compare *ventral*.)

drift (insects) The aggregate of terrestrial and aquatic insects drifting passively downstream with the current, both at the surface and suspended in the water column.

electrophoresis The movement of charged particles in response to an electric current. Proteins carry electric charges, so proteins in a sample of blood or other tissue can be separated in an electric field and then identified. Because each protein—and each variant of a protein—is uniquely coded by DNA, electrophoretic analysis of proteins provides evidence of an organism's genetic makeup. Presently, fewer than 1% of a fish's genes can be identified by protein electrophoresis. Fragments of DNA also can be separated by electrophoresis.

endemic Restricted to a locality or region; found nowhere else.

eyed egg A fish egg in which the dark pigment of the embryonic eyes is visible through the shell.

fecundity Number of eggs produced by a female during a breeding season. *Total* or *absolute fecundity* is the number of eggs produced by a female without reference to her size. *Relative fecundity* is the number of eggs produced per unit weight (gram or kilogram) of female.

flow Volume of a fluid or gas moving past a point per unit time, measured (in the metric system) as cubic meters per second (m^3/s). Water flow in streams is often called *discharge*. (Compare *velocity*.)

food conversion The total weight of feed given to a fish during a specified time divided by the weight gained by the fish during the same period. The lower the quotient, the better the conversion of feed to flesh. This is the aquacultural use of the term; in ecology, the inverse ratio is used (weight gained divided by weight eaten) and often called "feeding efficiency."

fundamental niche The role a species would play in an ecosystem if it were constrained only by its genetic makeup. The fundamental niche is an abstract concept, because a species is never unconstrained by physical, chemical, or biological factors in its environment, but the concept facilitates an understanding of a species' potential ecological role in various circumstances. A practical approximation of the fundamental niche is the sum of all roles a species plays in all contexts throughout its geographic range. (Compare *realized niche*.)

gene The segment of DNA that codes formation of a particular protein.

genome The complete set of an organism's genes.

genotype The genetic constitution of an organism. (Compare *phenotype*.)

gill rakers Bony processes arrayed along gill arches. The rakers divert solid objects from the respiratory gill filaments and also trap food particles from the water.

habitat The place where an organism lives and grows. Habitat usually is defined in terms of physical attributes such as space, structure, water flow, energy, and temperature; key chemical features such as salinity and acidity often are included. In less formal usage, habitat sometimes embraces biological elements such as characteristic plant or animal groups. (Compare *microhabitat*.)

hybrid swarm A population made up wholly or predominantly of hybrids between species, showing evidence of two or more generations of hybridization and of backcrossing to the parental species.

hyporheic Below the streambed, where interstitial water moves by percolation. In areas of coarse, unconsolidated soils, the hyporheic zone extends laterally from the stream into the groundwater.

hypurals Expanded haemal spines of the posterior vertebrae. Hypurals help support the caudal fin rays.

karyotype The structural characteristics of chromosomes in a cell, including total number of chromosomes, numbers of acrocentric and metacentric chromosomes, and number of chromosome arms, among other diagnostic features; also, a composite photograph or drawing of the chromosomes from one nucleus.

lacustrine Living in or relating to lakes.

lateral line The longitudinal series of scales bearing pores of the seismosensory system, the system that detects pressure waves in water caused by moving objects.

lateral series The scales along the length of the fish two rows up from the lateral line.
limnetic Within the water column of a lake or reservoir.
locus The location of a gene on a chromosome. "Locus" (plural, loci) and "gene" often are used interchangeably.

maxillary (maxilla) The posterior bone on either side of the upper jaw. (Compare *premaxillary*.)
meristic character A morphological character that has countable elements in a series (e.g., scales, vertebrae, fin rays). (Compare *morphometric character*.)
metacentric chromosome A chromosome with the centromere some distance from an end, giving the chromosome the appearance of having two arms. Some metacentric chromosomes were formed by the fusion of two acrocentric chromosomes. (Compare *acrocentric chromosome*.)
microhabitat The site (within a habitat) occupied by an organism at any point in time. Microhabitats are characterized by the same physical and chemical variables—depth, current, temperature, salinity, etc.—used to describe habitats. (Compare *habitat*.)
mitochondria Subcellular organelles in which high-energy chemical bonds are formed to drive biochemical reactions throughout the body. Mitochondria are self-replicating and contain DNA.
mitochondrial DNA (mtDNA) DNA housed within mitochondria. All mtDNA molecules are inherited from the mother and they are identical within an individual, though they may vary among individuals. Mitochondrial DNA molecules are smaller than nuclear DNA molecules and hence easier to analyze; they also mutate more readily, facilitating diagnosis of individuals and species.
monophyletic Having a common ancestor. (Compare *polyphyletic*.)
morphometric character A measurable (as opposed to countable) morphological character (e.g., body length, eye diameter, caudal peduncle depth). (Compare *meristic character*.)

niche See *fundamental niche* and *realized niche*.

parr A young trout or salmon actively feeding in fresh water. The term (plural, parr) usually is applied to young anadromous salmonids before they migrate to the sea. Parr typically have a distinctive series of dark, vertically elongated "hash" marks along each side of their bodies. These parr marks are lost when the fish move to the sea as smolts. (Compare *smolt*.)
pharyngeal teeth Teeth on bones of the fifth (last) branchial arch in the pharynx (throat) of fish. Unlike most fishes, whose pharyngeal teeth are on the ceratobranchial (ventral) part of the arch, trout have tiny teeth on the epibranchial (dorsal) part of the arch.
phenotype The physical appearance or properties of an organism. (Compare *genotype*.)

phylogenetic Based on natural evolutionary relationships.
piscivore An animal that feeds on fishes.
piscivory Predation on fishes.
pluvial Relating to a time of wet climate caused by high precipitation (snow and rain) and low evaporation. During pluvial periods, streamflows are strong and lake levels are high.
polyphyletic Not sharing a common ancestor. Said of taxa (especially genera) that are morphologically similar but are known or suspected to be derived from different lineages. (Compare *monophyletic*.)
premaxillary (or premaxilla) The anterior-most bone on each side of the upper jaw, usually bearing teeth. In trout, the premaxillary is followed by the maxillary; in many of the more advanced fishes, the premaxillaries form the entire border of the upper jaw. (Compare *maxillary*.)
primary production Plant production resulting from photosynthesis. Algae account for most of the primary production in aquatic systems. (Compare *secondary production*; see *production*.)
primitive character A character state judged to be older than some comparable character state within an evolutionary lineage. (Compare *derived character*.)
production The elaboration of plant or animal biomass per unit area or per unit time or, most often, both (e.g., kilograms per hectare per year). *Total production* is the sum of all new biomass created by growth and reproduction in the defined space and time. *Net production* is total production minus the biomass lost to mortality and metabolism.
pyloric caecum (or cecum) A tubular pouch extending from and opening into the posterior stomach or anterior intestine. (Plural: caeca or ceca.)

realized niche The role a species actually plays in a particular ecosystem or habitat. A species' realized niche expands, contracts, or qualitatively shifts as physical, chemical, or biological factors (constraints) are subtracted from or added to its environment. (Compare *fundamental niche*.)
redd A nest excavated in gravel, consisting of a depression dug by a fish for egg deposition (and then filled) and associated gravel mounds. Redd usually refers specifically to the nests made by salmonids.
relative fecundity See *fecundity*.

salmonid Any member of the family Salmonidae, which includes the salmon, trout, chars, whitefishes, ciscoes, inconnu, and grayling of North America.
salmonine Any member of the subfamily Salmoninae (family Salmonidae), which includes all the salmon, trout, and chars of North America, but not whitefishes, ciscoes, inconnu, or grayling.
scope for activity The difference between an animal's maximum metabolic rate and its resting ("standard") metabolic rate. The greater the difference, the greater the animal's ability to mobilize energy for attack, flight, or other burst of activity.
secondary production Animal production resulting from consumption of live or dead plant matter (primary consumption). Because many animals are

omnivorous, secondary production sometimes is considered to include all animal production—of secondary consumers (predators) as well as of primary consumers. (Compare *primary production*; see *production*.)

sister groups Two evolutionary lineages that share a more recent common ancestor than either shares with other lineages.

smolt A young anadromous trout or salmon undergoing physiological changes that will allow it to adapt from life in fresh water to life in the sea. The smolt stage follows the parr stage; it begins as, or shortly before, the fish starts its downstream migration, and it is completed by the time the fish leave brackish estuaries for the sea. In the process of "smoltification," the fish loses its parr marks and becomes silvery or more adultlike in coloration. Smolts that cannot or do not reach the sea may revert to parr status and remain in fresh water for another year. (Compare *parr*.)

stochastic Subject to random (chance) variation. A stochastic process or model proceeds at rates that can vary unpredictably, and its outcome can be calculated only in terms of probabilities. (Compare *deterministic*.)

sympatric Occurring in the same area; overlapping in distribution.

systematics The study of evolutionary diversity and relationships among organisms.

taxon Any formal taxonomic unit or category of organisms (subspecies, species, genus, family, etc.). Plural: taxa.

taxonomy The application of formal classification principles to the naming of organisms.

temperature unit One degree (Celsius or Fahrenheit) in average daily temperature above a specified reference temperature. The reference temperature usually is the freezing point of water (0°C or 32°F). An average temperature of 11°C over a 24-hour period represents 11 Celsius temperature units. A fish embryo developing at average temperatures of 5°C on day 1, 5°C on day 2, and 6°C on day 3 accumulates 16 temperature units over the three days. An embryo developing at successive daily temperatures of 3, 4, 4, and 5°C also accumulates 16 temperature units, but over four days. Because developmental rates of cold-blooded animals like fishes are under the strong influence of temperature, fish of the same species tend to reach similar stages of development when they have accumulated similar numbers of temperature units, even though development proceeds more rapidly at higher than at lower temperatures.

tetraploid Having four sets of chromosomes per nucleus, representing a doubling of chromosomes with respect to the normal diploid number (two sets) of either the parents or more ancient progenitors. (Compare *diploid*.)

velocity Rate of movement (distance per time) measured in the metric system as meters per second (m/s). (Compare *flow*.)

ventral On or toward the abdominal side of an animal. (Compare *dorsal*.)

year-class A group of animals of the same species born in the same year.

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Principal entries for species and subspecies of western trout are made under the respective uninverted vernacular names. Asterisks (*) indicate that additional taxon-specific information on a subject can be found in species and subspecies accounts under the headings "description," "distribution," "life history and ecology," "status," "taxonomic notes," or "typical characters."

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