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CUTTHROAT TROUT OF SOUTHERN ROCKY MOUNTAIN BASINS

Colorado River Cutthroat Trout *Oncorhynchus clarki pleuriticus*

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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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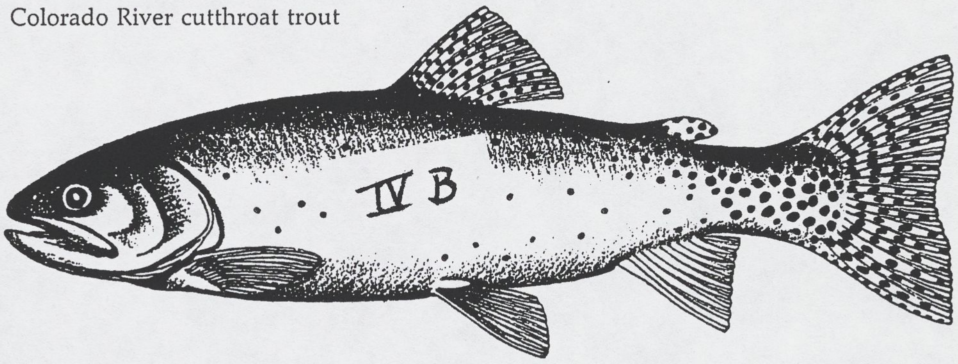
Colorado River cutthroat trout



Greenback cutthroat trout

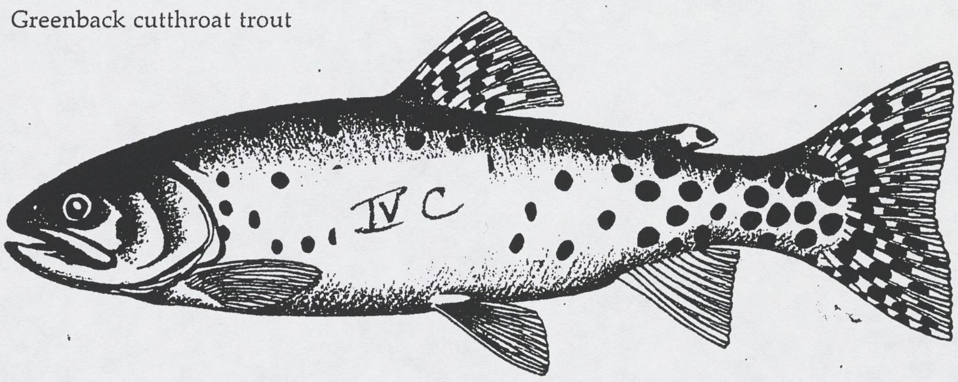
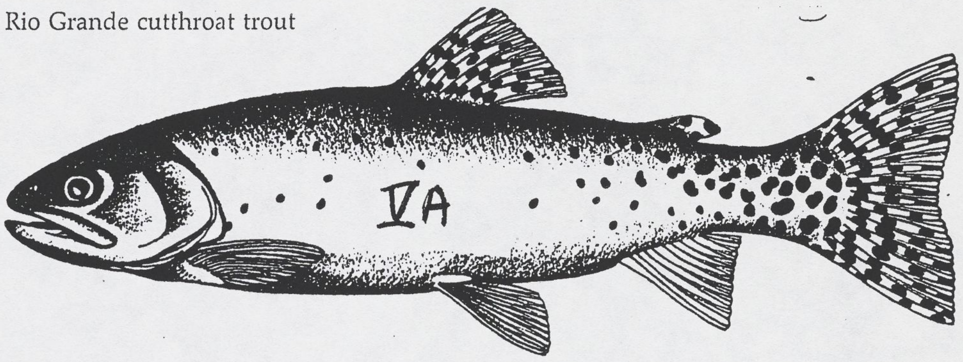


FIGURE 11.—Cutthroat trout of southern Rocky Mountain drainages.

Rio Grande cutthroat trout



Yellowfin cutthroat trout

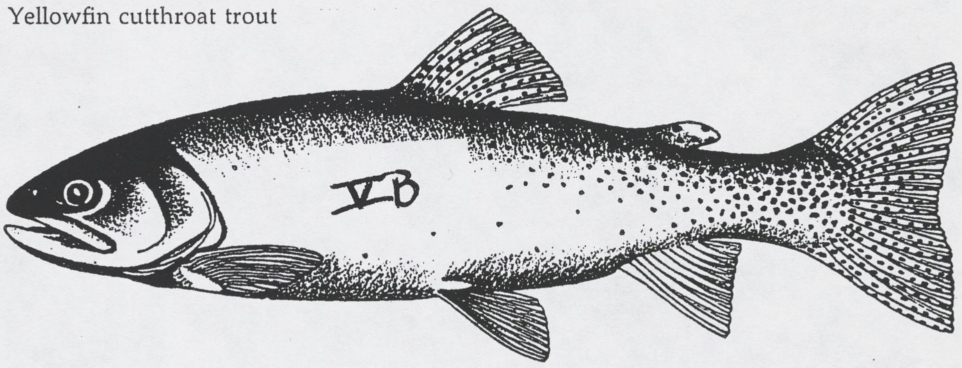


FIGURE 11.—Continued.

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

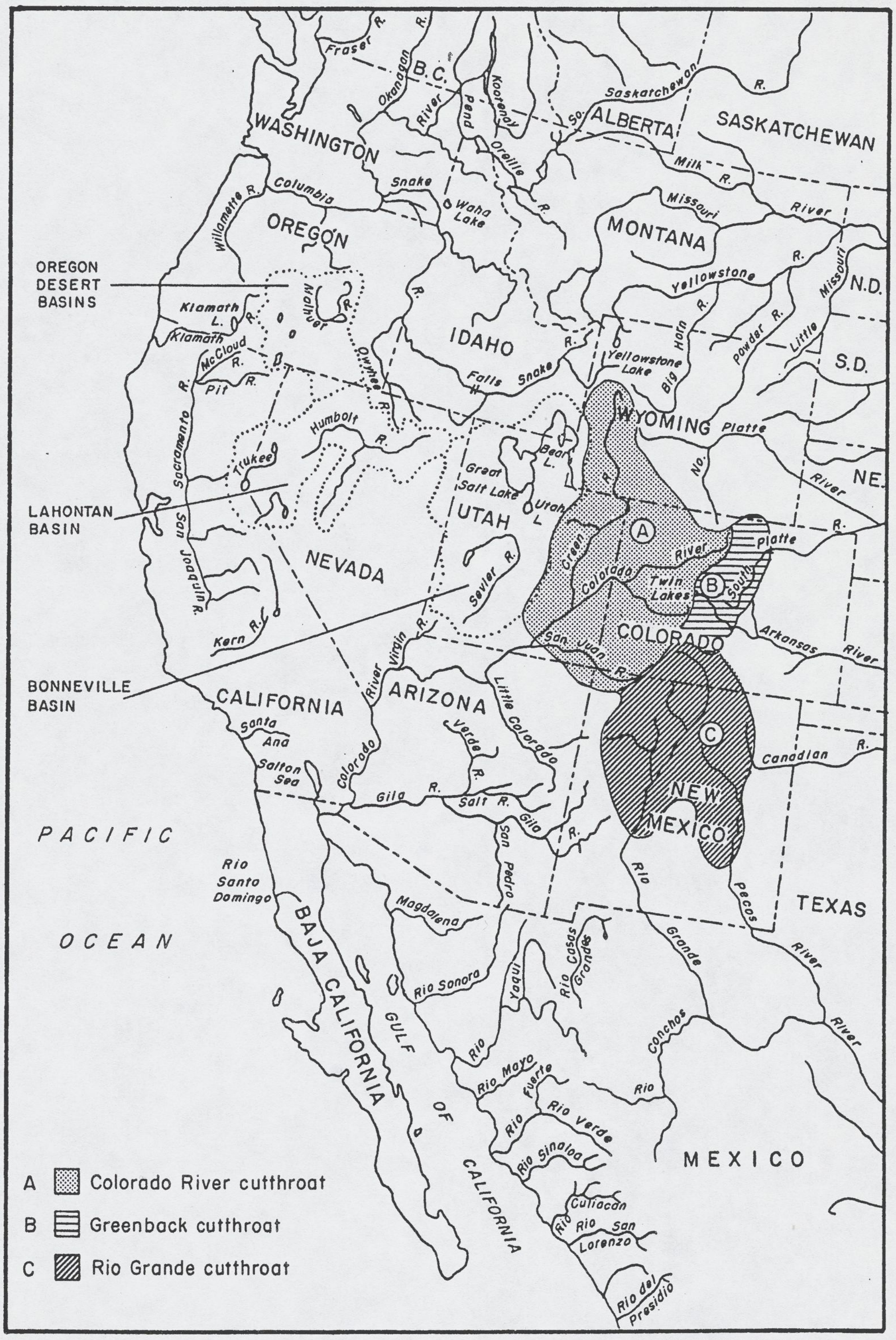


FIGURE 12.—Distributions of Colorado River cutthroat trout, greenback cutthroat trout, and Rio Grande cutthroat trout.

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 ●●●)

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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 ●●●). 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. after

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 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 ●●●)

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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 ●●●). 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 Grande, an isolated tributary in the Guzman basin, which once had a connection to the Rio Grande (Needham and Gard 1959), but 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.

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DESCRIPTION (Figure 11, page ●●●)

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 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 intro-

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duction 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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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 rainbow trout *O. m. irideus*. *Oncorhyncus 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 Pleistocence 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).

Mackenzie
Peace
Laird

north
Bering
refugia
L. MB.
Kamchatka

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 sequences of dispersion and differentiation of rainbow and redband trout are far

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[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).

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 predominately have the *LDH-B2*76* allele

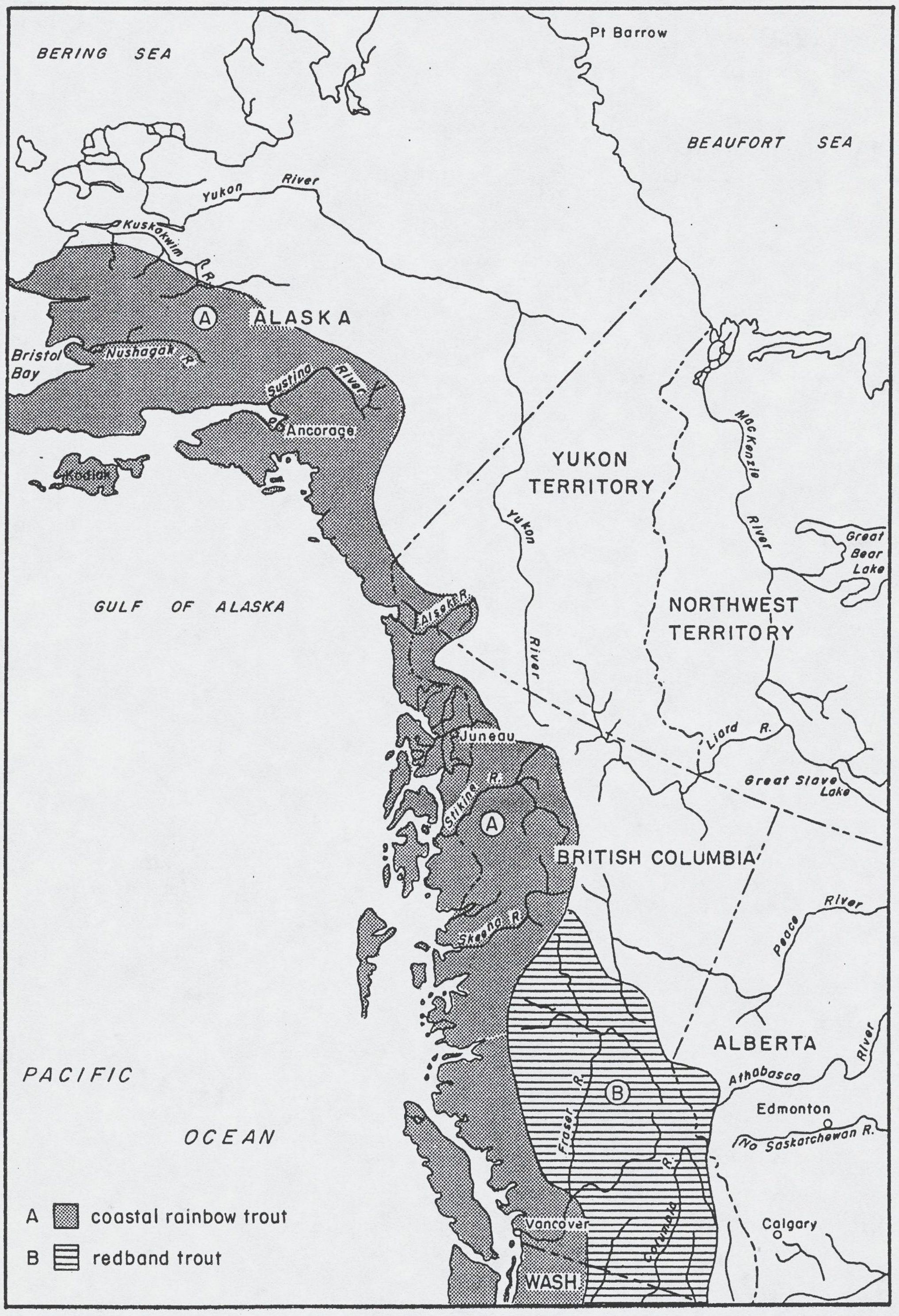

FIGURE 13.—Distributions of coastal rainbow trout and redband trout.

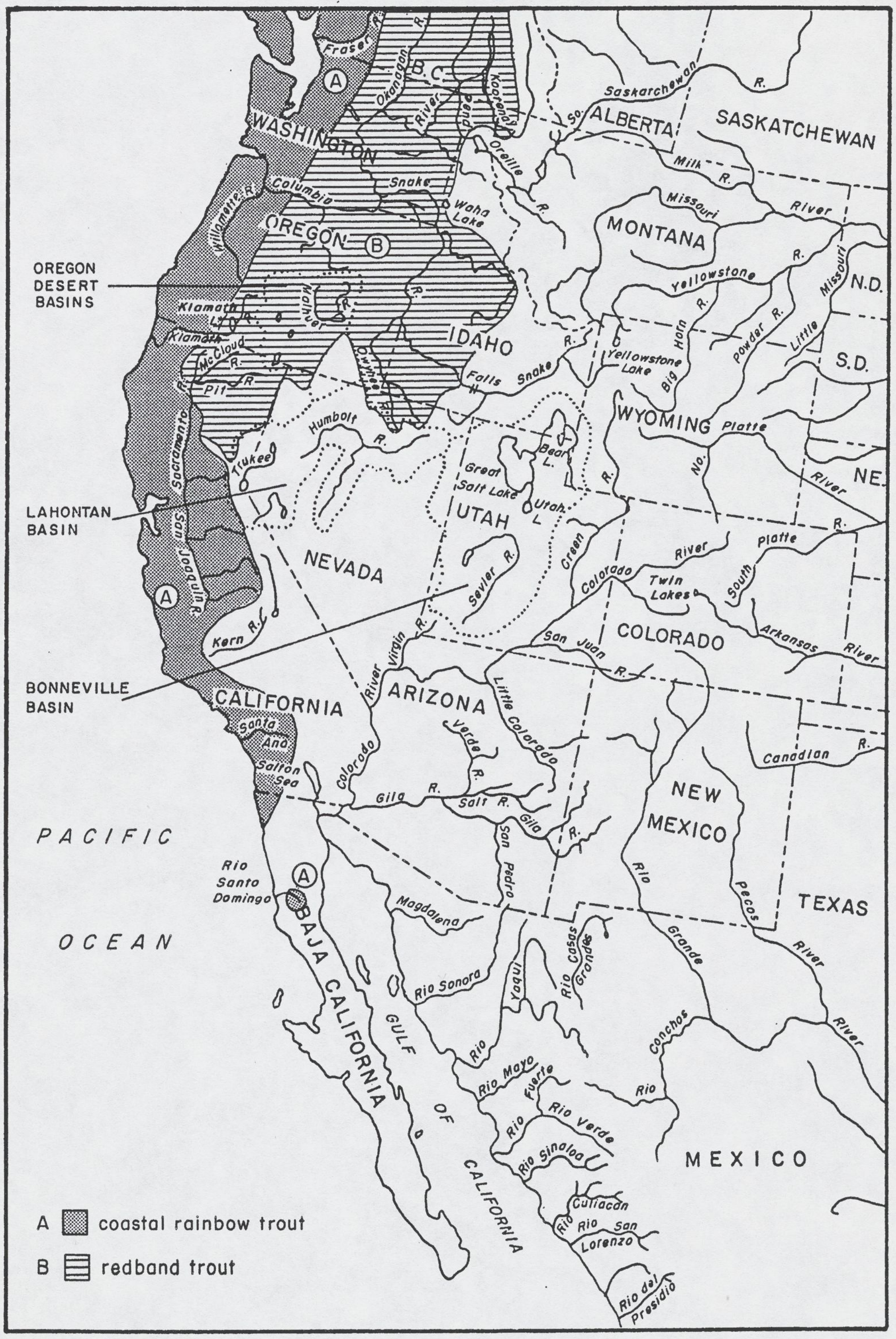

FIGURE 13.—Continued.

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 that carry predominantly 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.

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 for 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 size. 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 Jewell 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 temperature 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 DISTRIBUTION

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 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 Columbia River basin east of the Cascades and to the upper Fraser River basin (including Kamloops trout, resident stream forms, and steelhead) as *Oncorhychus 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 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.

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

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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 (Plate 5; Figure 14)

Resident stream populations are found throughout the range of the redband trout east of the Cascades in the Columbia 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

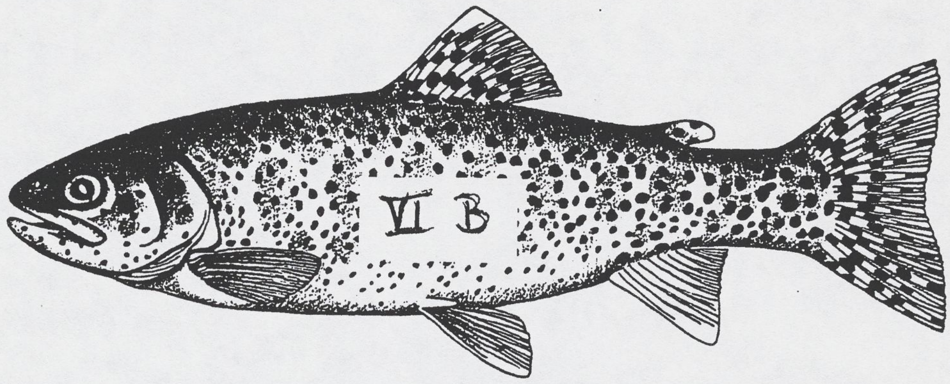

FIGURE 14.—Columbia River redband trout.

basin above Hell's Gate; and headwater areas of the Mackenzie River basin (Peace and Athabasca drainages), where headwater transfers evidently occurred from the upper Fraser system. 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 electrophoetic 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 temperature. 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.

POPULATIONS IN 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

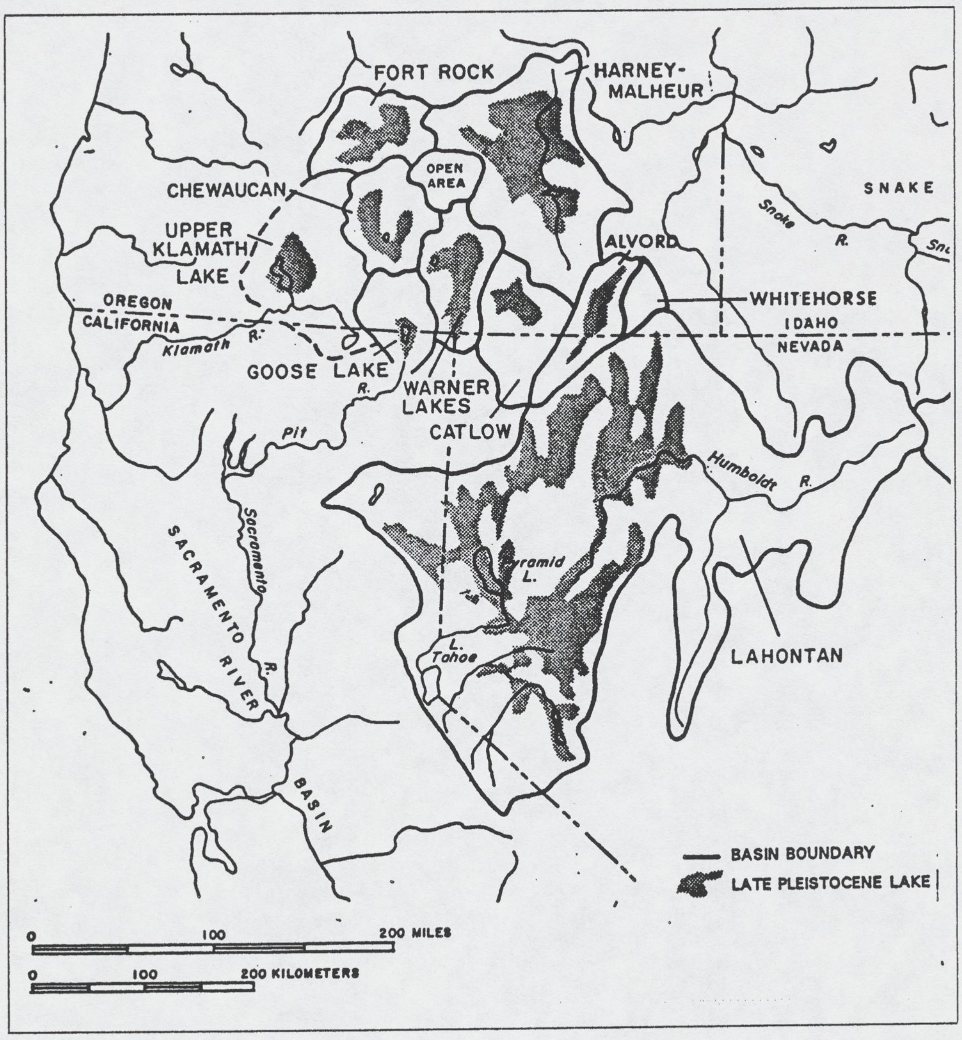

FIGURE 15.—Oregon desert basins.

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 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.

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.

see plate

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 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. 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 the headwaters of Buck and Bridge creeks, but only eastern 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, 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 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 Lake 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

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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

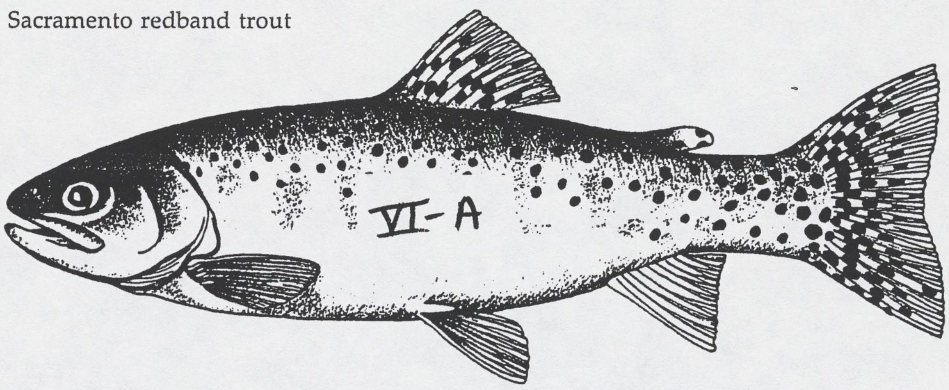
California Golden Trout *Oncorhynchus mykiss aguabonita*
Kern and Little Kern Golden Trout *Oncorhynchus mykiss gilberti*
Sacramento Redband Trout *Oncorhynchus mykiss stonei*

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 (Plate 6; Figure 16), which indicates they 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-

Sacramento redband trout



California golden trout

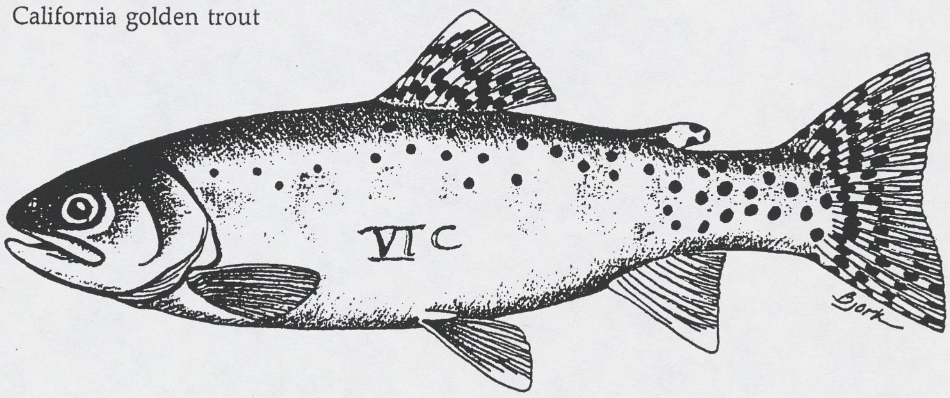


FIGURE 16.—Redband trout of the Sacramento basin.

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 of golden trout in the Kern River drainage is likely the result of two or more invasions. Prior to the last glacial epoch, an early invasion of a primitive redband trout may have populated both the Kern River and headwaters of the McCloud River. The trout established in headwaters of the South Fork of the Kern (which became California golden trout) was more isolated from later invasions of other redband trout and coastal rainbow trout than was the Kern–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 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 between 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 (Plate 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.

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 Columbia border (Figure 13, page ●●●). Seventeen specimens from Kathleen Lake of the Alsek drainage have 63–66 (mean, 64) vertebrae, 15–20 (18) gill

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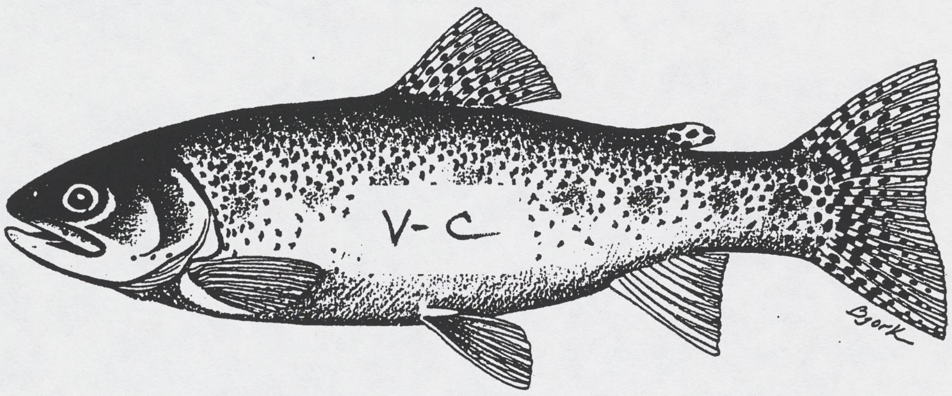

FIGURE 17.—Coastal rainbow trout.

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 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 Culican, 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. 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 Kuskowim. 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. 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 *Oncoryhynchus 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 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.

Arctic char

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; Alekseev 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 the 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 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 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

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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

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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

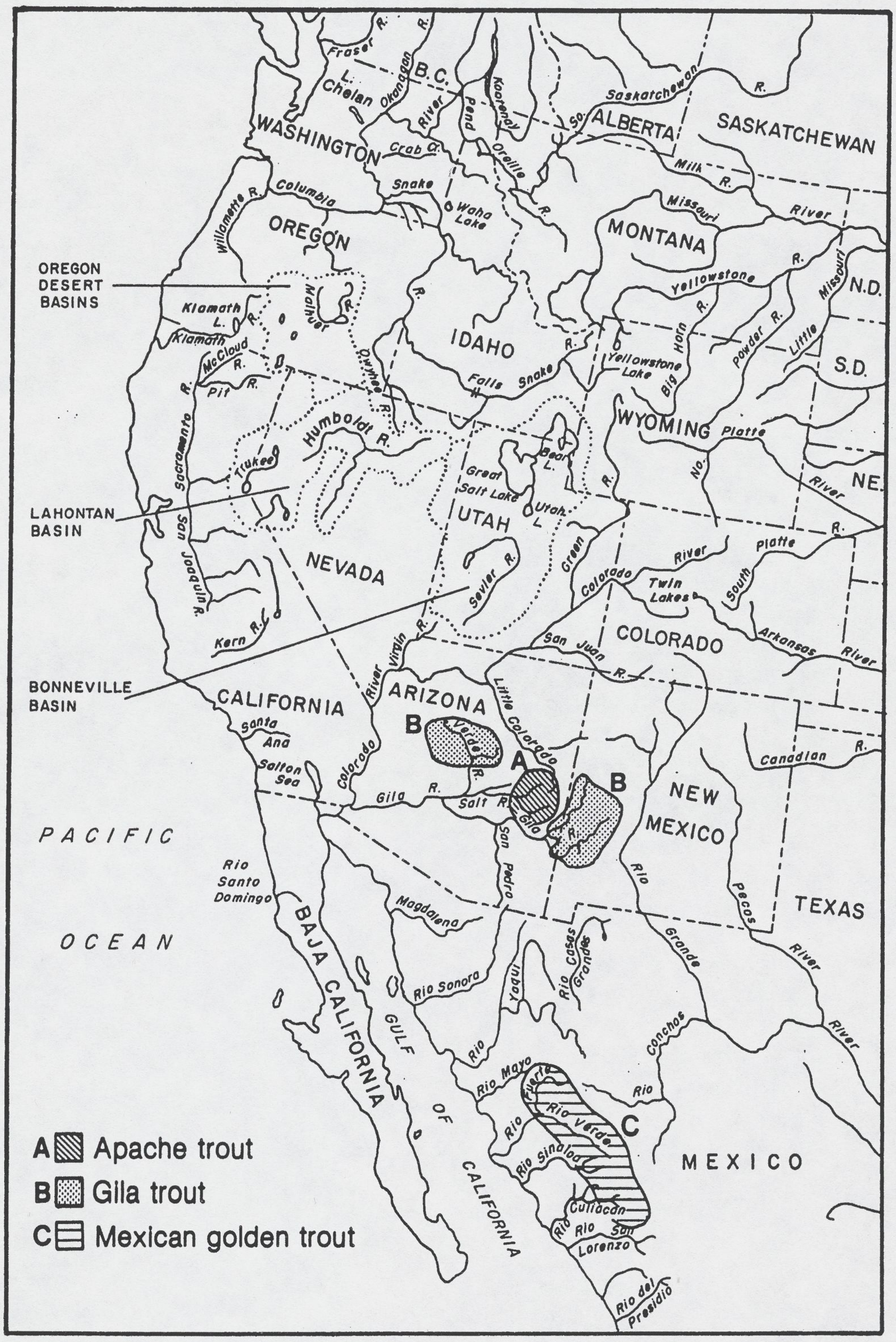


FIGURE 18.—Distributions of southwestern trout.

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 *Oncorhynchyus 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.

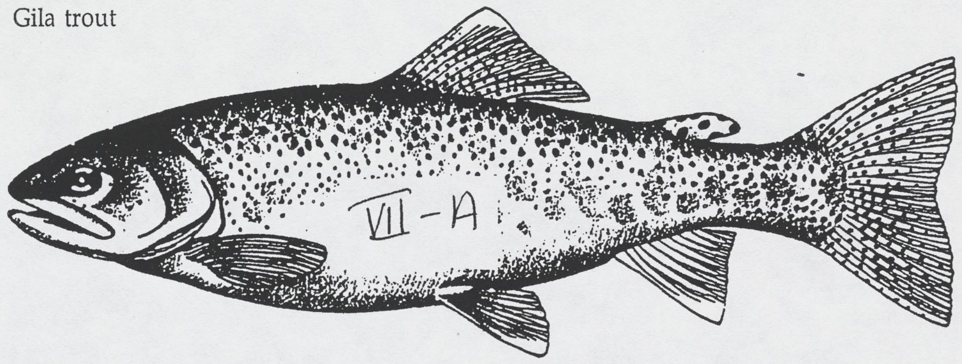
Basibranchial teeth are found in some specimens of Gila trout from Spruce Creek, New Mexico, and are present in museum specimens from the Verde River drainage of Arizona.

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).

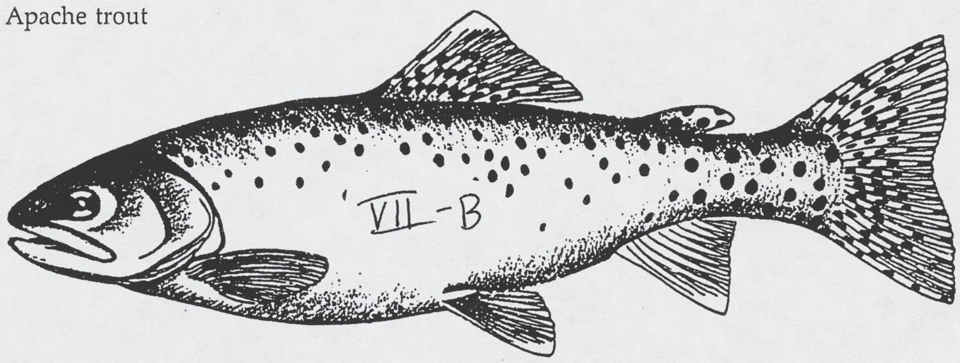
DISTRIBUTION

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

Gila trout



Apache trout



Mexican golden trout

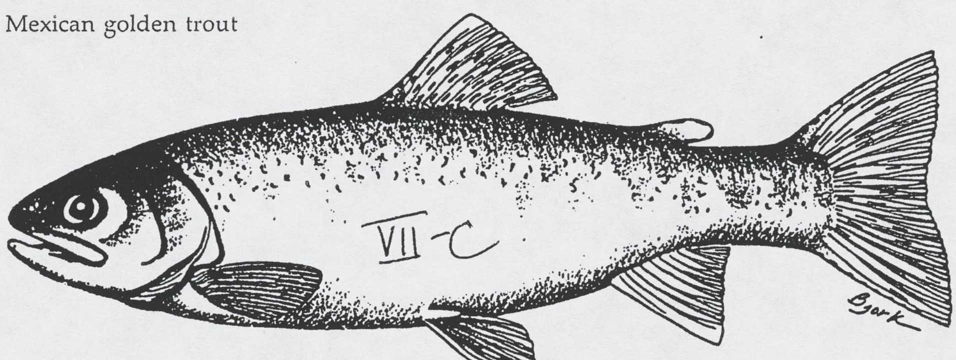


FIGURE 19.—Trout of Gulf of California drainages.

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 the 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. *Oncorhyncus 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.

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DESCRIPTION (Plate 8; Figure 19, page ●●●)

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

KP Creek) in the San Francisco River drainage. These streams are all close to each other in the White Mountains of Arizona. 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 hererozygous 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.

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DESCRIPTION (Figure 19, page ●●●)

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.

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, 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. 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

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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 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 the 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.

much less than

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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MD (scan)

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 most 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 ray A bony process that supports the membranes enclosing the gill chamber, below and behind 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 a similar character in separate evolutionary lines.

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 water depth.

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 it 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 that 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, 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 Bones (haemal arches) associated with the last, modified vertebral element (urostyle) that help support the caudal fin.

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 in the middle, 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, streamflow is 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 new 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.