Memo From

AMERICAN FISHERIES SOCIETY

DATE ______________________ TIME ____________ A.M. P.M.

TO ______________________

This is a copy of the new text that will appear on the last page of Chapter 8. It will face the first page of the color plates.

FORM 42102 RAPIDFORMS, INC., BELLMAWR, N.J. 08031

Color Plates: Illustrations by Joseph R. Tomelleri

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Memo From

AMERICAN FISHERIES SOCIETY

DATE 7-28-92 TIME ____ A.M. P.M.

TO Bob Behnke

Here is your copy of the index. If you have corrections or changes, please phone them to us as soon as possible. We plan to make final corrections and send the book to the printer early next week.

Sally Kendall

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Index

Principal entries for species and subspecies of western trout are made under the respective uninverted vernacular names. Asterisks (*) indicate that additional taxon-specific information on a subject can be found in species and subspecies accounts under the headings "description," "distribution," "life history and ecology," "status," "taxonomic notes," or "typical characters."

MD
MD CX
184 chewaucan basin
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Comma ok?
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JOBNAME: WESTERN TROUT PAGE: 13 SESS: 2 OUTPUT: Fri Jul 24 10:45:19 1992
/br2/305/team5/special/fish–west/4638tc–ind

Chapters 1-3

Revisions to Western Trout - June 1992

Keyed to circled red letters on the text annotated by Behnke
(Circled blue numbers denote previous queries to Behnke)

new files made w/page #s

* Page xi. Insert "a".

** Insert a new table of chromosome numbers on page xii in the front matter.

*** Insert new description of taxonomic characters on page xiii in the front matter.

(1) Page 2. Replace yellow sentence with:

Many former species names obviously have become synonyms of recognized species, but some names that are synonyms at the species level are available to designate subspecies--O. m. gairdneri is an example.

(2) Page 2. Add footnote superscript to the blue word:

clarki.[1]

* created new file

(3) Page 2. Delete yellow sentence. (a) Create footnote, to go on the first page following the references:

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

(b) Add to the references:

McDowall, R. M. 1991. The "-ii's" may have it at the end--patronyms should be amended only if demonstrably incorrect. New Zealand Natural Sciences 18:25-29.

(4) Page 3. Revise yellow phrase:

> ...Oregon, giving counts of 137[end]177 scales and 42 pyloric ceca for these fish.

(5) Page 6. Add parentheses around date: (1964)

(6) Page 8. Revise yellow material:

> The loss of teeth on particular bones in the mouth is one such irreversible change in character state. For example, a common ancester...

(7) Page 8. Revise yellow material:

> ...in their mouths; however, they have...

(8) Page 8. Delete parenthesis:

> ...teeth.

(9) Page 8. Run in:

> ...Mexican golden trout. Thus the loss of a complex...

(10) Page 8. Revise yellow material (but differently from Behnke):

> ...reconstructions because transitions in character state from presence to absence occur infrequently.

(11) Page 8. Start new paragraph at the blue "Most... ."

(12) Page 9. Revise yellow sentence:

> Thus, similar trends for higher gill raker number among lake forms in this case is evidence of convergent evolution, not an indication of close genetic relationship due to common ancestry.

(13) Page 9. Revise yellow sentence:

Much is yet to be learned about the times of phyletic branching, but my interpretation of available evidence suggests that all living forms of western trout arose from a common ancester as...

(14) Page 11. Insert page cross-reference.

(15) Page 14. Add to references:

LaRivers, I. 1964. A new trout from the Barstovian (Miocene) of western Nevada. Biological Society of Nevada Occasional Papers 3:1-4.

(16) Page 14. Revise yellow phrase:

Members of the catfish family Ictaluridae became extinct...

(17) Page 16. Revise yellow phrase:

...cutthroat trout probably occurred...

(18) Page 17. Revise yellow phrase:

The transfer of Yellowstone cutthroat trout from the Snake...

(19) Page 17. Revise yellow phrase:

...subspecies left disjunct...

(20) Page 17. Revise yellow passage:

...(type locality of bouvieri), and Crab Creek, Washington (both these populations have become extinct since they were discovered). The westslope populations above and below the falls have been isolated at least since the last discharge of glacial Lake Missoula 12,000-15,000 years ago. The upper and lower Yellowstone populations may have been separated 50,000 years or more. Nevertheless, virtually no differentiation has occurred within either subspecies.

(21) Page 18. Revise yellow phrase:

...introduced kokanee became the dominant game fish in Priest Lake and--before introductions of the opossum shrimp Mysis relicta--in Flathead, Pend Oreille, and Coeur d'Alene lakes, among others.

(22) Page 18. Make singular: kokanee.

(23) Page 18. Delete comma if it's there.

(24) Page 19. Revise yellow phrase:

...probably spread in...

(25) Page 19. Revise yellow phrase:

...Fort Rock, Malheur, Chewaucan, Warner Lakes, and Catlow basins...

(26) Page 19. Revise yellow phrase:

...basins had direct or indirect connections...

(27) Page 19. (a) Delete yellow sentence. (b) Start "(The Oregon..." sentence with a parenthesis and run it into the previous paragraph.

(28) Page 20. Revise yellow material; make new parenthetic paragraph:

(Some Canadian populations offer interesting problems. Trout in the British Columbia and Alberta headwaters of the Peace and Athabasca rivers, which drain to the Mackenzie River and the Arctic Ocean, resemble redband trout in coloration and spotting. They undoubtedly came from the Fraser system and, according to the scheme of colonization just outlined, should have reached the Mackenzie system in late- or postglacial times. However, I have seen recent, privileged data that suggest the headwater transfer occurred much earlier. Another population exists in the Liard River of the Mackenzie drainage. It could have come...

SUBSTITUTE FOR BOXED SENTENCE

However, Leon Carl (Ontario Ministry of Natural Resources, Maple) has sent me new evidence indicating that trout may have transferred from the Fraser to the Athabasca basin before or during the early stages of the last glacial period, about 64,000 years ago. As discussed more fully in Chapter 9, these fish have electrophoretic patterns that differ markedly from those of Fraser[end]Columbia redband trout and coastal rainbow trout.

(29) Page 20. Revise yellow sentence:

Coastal rainbow trout diverged from the redband line at some unknown time but probably relatively recently--possibly during the late Pleistocene (but prior to the most recent glacial period) and perhaps in California.

(30) Page 20. Revise yellow sentence:

This dispersal most likely occurred during late~~- and postglacial times as ice retreated from coastal waters~~ Pleistocene when the Bering Land Bridge existed.

(31) Page 20. Revise yellow phrase:

...forms of the Gulf of California and desert Southwest,...

(32) Page 23. Revise yellow phrase; paragraph indent:

Between 25,000 and 35,000 years ago...

(33) Page 23. Add yellow reference:

(Malde 1965),

(34) Page ~~23~~ 25. Correct spelling: circumstances.

(35) Page 28. Revise yellow phrase:

Nehring (1980) reported biomasses of 620 and 784 kg/hectare for rainbow and brown trout combined in two no-kill-regulation sections...

(36) Page 29. Revise yellow line:

...overwintering habitat downstream. (Typically, dams that benefit trout store peak runoff to...

(37) Page 29. Revise yellow phrase:

...and such mutual adjustments can be made by species...

(38) Page 29. Change "stream segment" to "habitat".

(39) Page 30. Add sentences to end of paragraph:

> In any case, most trout streams already have established populations of various species and opportunities for niche packing in such habitats are limited. ~~The use of~~ niche packing has its greatest potential ~~for~~ stocking lakes and reservoirs where natural reproduction is very low or nonexistent.

use in/of

(40) Page 32. Change "for" to "on".

(41) Page 32. Change "crop is" to "crops of".

(42) Page 32. Delete the material set off by em-dashes, and the em-dashes themselves. Ignore Behnke's insertion here.

(43) Page 32. Add sentences to end of paragraph.

> A more fundamental limitation of models is that they can generate consistently precise and accurate predictions only when natural patterns are highly regular--but natural systems are highly irregular. If stochastic variation is built into models, the models become much more realistic but much less precise.

(44) Page 32. Revise yellow phrase:

> ...evaluations therefore remains very...

(45) Page 32. Revise yellow phrase:

> ...could ever predict...

(46) Page 32. Check that "chubs" has been pluralized.

(47) Page 34. Add quotation marks: "preferences".

(48) Page 34. Revise yellow material:

...may initiate spawning activity by coastal cutthroat and rainbow trout from late December through April; actual spawning typically occurs when daily maximum temperatures reach 6-9°C.

(49) Page 35. Delete "hatchery:

...races of trout under...

(50) Page 36. Check that the hand-written changes in two lines have been made.

(51) Page 38. Add word space if it's not there already.

(52) Page 38. Revise yellow phrase:

...phase is more than offset by the...

(53) Page 38. Revise yellow phrase:

Mortality usually is high...

(54) Page 38. Add new paragraph:

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

days

(55) Page 39. Insert "other".

(56) Page 40-41. Revise yellow sentences:

On the other hand, sympatric races within subspecies have developed differences in the time or place of spawning that keep them reproductively isolated. Summer and winter runs of steelhead may occur in the same river (Leider et al. (1984), but they retain their genetically based fidelity to run timing when they do. In...

(56a) Page 41. (a) Insert new sentence:

Yellowstone cutthroat trout in Yellowstone lake also seem to have developed genetic affinities for inlet or outlet spawning (Bowler 1975).

(b) Add new citation to reference list:

Bowler, B. 1975. Factors influencing genetic control in lakeward migrations of cutthroat trout fry. Transactions of the American Fisheries Society 104:474-482.

(57) Page 41. Delete "out" if it's still in.

(58) Page 43. Revise yellow phrase:

Most of the brown trout in...

(59) Page 43. Revise yellow phrase:

...feeding habits and growth, not with a different...

(60) Page 43. Revise yellow sentence:

The population of brown trout called "ferox" In Lough Melvin, Ireland, however, is genetically distinct from other populations of brown trout in that lake, as shown by Ferguson and Mason (1981).

(61) Page 44. Change "they are" to "it is" if not already changed.

(62) Page 44. Make past tense: provided.

(63) Page 46. Add hyphen if still missing.

(64) Page 46. Change (Clark 1980) to (Clark and Alexander ~~1984~~). 1985)a

(65) Page 46. Insert "genetic": genetic changes....

(66) Page 47. Delete entire yellow paragraph.

(67) Page 47. Adjust placement of comma if not already done.

(68) Page 48. Revise yellow phrase:

...invertebrates that had fallen into the water. have?

(69) Page 48. Make "Interactions" plural if it's not already.

(70) Page 49. Insert "trout": cutthroat trout.

(71) Page 49. Revise yellow phrase:

...cutthroat trout: Pierce 1984a, 1984b).

(72) Page 49. Delete reference:

...Apache trout.

(73) Page 49. Add reference:

...brown trout (Robinson and Tash 1979).

(74) Page 50. Revise yellow phrase:

...trout may be the westslope...

(75) Page 50. (a) Delete "even" if it's still there.

(b) Revise blue phrase (after the em-dash):

--indeed, cutthroat markedly declined,...

(76) Page 50. Revise yellow phrase:

The Lahontan cutthroat trout of Pyramid Lake and the Gerrard strain of Kamloops redband trout of Kootenay Lake are prime examples, but the principle of predator[end]prey coevolution extends to all salmonines, such as lake trout...

(77) Page 51. Revise yellow phrase:

For the form of redband trout tested, however,...

(78) Page 51. Revise yellow phrase:

...trout by fly-fishing when...

(79) Page 53. Delete "in" if it's still around.

(80) Page 54. Break sentence:

...trout diet. Many workers...

(81) Page 54. (a) Add new sentences to the end of the paragraph:

However, most fishery biologists have overlooked an invertebrate source of potentially great magnitude. This is the hyporheic fauna, the asemblage of aquatic invertebrates that live and forage below ground in the water table of floodplains (Stanford and Gaufin 1974). This assemblage, which includes caddisflies, mayflies, and stoneflies, can extend more than a kilometer from a river channel (J. Ward, Colorado State University, personal communication). Recruitment from the hyporheic fauna could help explain the Allen paradox.

; Stanford and Ward 1988).

(b) Add citation to References:

Stanford, J. A., and A. R. Gaufin. 1974. Hyporheic communities of two Montana rivers. Science (Washington, D.C.) 185:700-702.

(82) Page 55. Extend sentence:

...of the habitat and make previously inaccessible food available.

(83) Page 55. Rewrite yellow passage:

...benefit from artificial habitat improvements. For example, the growth and biomass of trout (mainly brown trout) decreased in a zone of the main Au Sable River, Michigan, when pollution abatement markedly reduced the influx of nutrients and, consequently, the production of invertebrate prey. Intensive additions of instream habitat devices failed to reverse the decline of this trout population (Alexander et al. 1979), which appears to be food-limited.

(84) Page 55. Revise blue material:

Substrate diversity influences invertebrate abundance, as pointed out earlier, but an increase in invertebrate production can generally come about only from an increase in primary production, which is governed by light and nutrients. If a small headwater stream is overgrown with vegetation,...

(85) Page 55. Extend sentence:

...production, as ~~alluded to in~~ suggested by the Au Sable example just above.

(86) Page 55. Add paragraph indent.

(87) Page 55. Revise blue material:

...only doubled. The likely explanation of this seeming anomaly is that the trout in tiny Berry Creek had been obtaining barely more than maintenance rations before the experiment. Suppose a fish required 5 g of food daily just to replace the energy lost to normal metabolism, but it was able to obtain only 6 g, leaving but 1 g for growth. Then a doubling of daily consumption to 12 g would provide 7 g above maintenance requirements for net production. The maintenance energy needs of fish should be kept in mind whenever food enhancement programs are designed and evaluated.

(88) Page 56. Change date from 1975 to 1978.

(89) Page 57. (a) Revise yellow material:

Under such conditions, larger trout cannot meet their maintenance requirements (which are inflated because the fish must spend more time foraging for small items); they begin negative growth (loose weight) and suffer a high mortality rate, leaving a population with a truncated size and age distribution. Studies of feeding, growth, and population dynamics cited in this chapter make it clear that trout restricted to small food items form populations characterized by small maximum individual sizes and young maximum ages that very few fish exceed. Only when trout have adequate access to larger prey, such as fish and crawfish, can they avoid feeding competition with smaller trout and sustain positive growth (Behnke 1989c).

(b) Add new citation to references:

Behnke, R. J. 1989c. We're putting them back alive. Trout, Autumb 1989:46-61.

(90) Page 59. Add references:

(a) Yellow: ...Montana (Roscoe 1974),...

(b) Blue: ...Nebraska (Van Velson 1977),...

(91) Page 59. Revise start of sentence:

Westslope cutthroat...

(92) Page 60. (a) Change yellow reference to Clapp et al. (1990).

(b) Delete blue sentence.

(93) Page 60. Merge the two sentences:

...are uncommon, probably because food of appropriate size is rare,...

The double-spaced material on pages 13-14 can be imported directly into the main document

(94) Page 60. (a) Delete the blue material.

(b) Add the following, starting with a new paragraph:

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

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

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

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

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

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

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

(c) Add four references to the bibliography: Allen (1969), Beard and Carline (1991), Carline et al. (1991), and Riley (1992). Cards are attached to the reference section.

(95) Page 60. Revise yellow sentence:

Trout mobility may be limited in lakes.

(96) Page 60. (a) Convert subhead to first-order (all caps):

INFLUENCES OF HATCHERY FISH

(b) Revise Contents accordingly

(97) Page 60. Revise blue sentence:

Introductions of hatchery fish have been reported to have varied effects on wild trout in streams.

(98) Page 61. Revise yellow phrase:

...microhabitats, and the hatchery trout...

(99) Page 61. Revise yellow phrase:

...wild trout increased almost threefold in one section, and the relative degrees of recovery indicated that hatchery rainbow trout had had a greater negative effect on wild rainbow trout than on wild brown trout.

(100) Page 61. Extend blue sentence:

...sections, and no significant movement of wild or hatchery fish between sections.

(101) Page 61. (a) Make new paragraph.

(b) Add hyphen.

(c) Substitute "neither" for "not".

(102) Page 62. (a) Delete or ignore yellow material.

(b) Add blue material:

...should be expected. But if stocking elevates total trout density by some substantial amount for some substantial time, wild trout are likely to be displaced. How far these "stressed" fish might move and what might be their fates are unknown.

<u>This completes the current round of revisions through Chapter 3. Numbering starts over again with Chapter 4.</u>

Chapters 4-8

Revisions to Western Trout - June 1992

Part II: Cutthroat Trout

✓(1) Page 64. Revise yellow phrase:

...that would allow them to coexist with those forms and with nonnative trout species.

✓(2) Page 64. Revise yellow phrase:

...13 subspecies that I tentatively recognize...

✓(3) Page 66. (a) Delete yellow parentheses (two).

(b) Convert blue brackets to parentheses (two).

✓(4) Page 72. Extend sentence:

...in Sweden, and Scott and Crossman (1973) noted successful introductions of the species in Laurentian lakes of Quebec.

✓(5) Page 76. Revise yellow phrase:

...Washington, labeled "Salmo crescentis" in the collection,...

✓(6) Page 76. Delete blue sentence.

✓(7) Page 78. Revise yellow phrase:

...those in some Vancouver...

✓(8) Page 78. Revise and extend the material:

...such as the numerous gill rakers for feeding on zooplankton shown by Crescent Lake fish and the high number of basibranchial teeth characteristic of the Lake Sutherland population. (The nature of lacustrine selection for more abundant basibranchial teeth is unknown, but it also is expressed in lake populations of Yellowstone and Lahontan cutthroat trout.)

(9) Page 79. Flag reference problem; RJB says help is on the way.

(10) Page 80. Revise yellow phrase:

...gave as the Washington state record cutthroat trout a Crescent Lake specimen...

(11) Page 81. Revise yellow phrase:

...the only critical hybridization experiment with...

(12) Page 81. Revise yellow sentence and add new one:

Also, he found no sex ratio differences between hybrids and the offspring of pure parental matings. In other fish groups such as sunfishes (genus Lepomis), a predominance of one gender among hybrids indicates a partially developed fertility barrier between parents.

(13) Page 82. Revise yellow phrase:

...of the cutthroat trout in...

(14) Page 84. Change date from (1979) to (1976).

(15) Page 88. Insert new material at the yellow mark:

The original separation of these ancestral lines may have occurred south of the area presently drained by the Snake, however. This possibility arises because soon after the lewisi and bouvieri lines diverged, the bouvieri ancestry gave rise to another lineage that was isolated in the ~~in the~~ Lahontan basin and became O. c. henshawi. The precise area where lewisi and bouvieri separated thus awaits resolution of mid-Pleistocene drainage patterns.

(16) Page 88. Revise blue sentence as the start of a new paragraph:

Until the 1970s, attempts to classify the inland subspecies produced confusion. The Lewis and Clark...

(17) Page 90. Revise yellow phrase:

...into the Columbia River above the confluence with the Snake.

(18) Page 94. Revise yellow phrase:

...evidence that all subspecies of cutthroat trout are more closely related to each other than any of them ~~are~~ is to rainbow trout (Gyllensten and Wilson 1987).

(19) Page 95. Revise yellow phrase:

...lack of basibranchial teeth, erratic spotting pattern, and lower scale counts, so limited gene...

(20) Page 97. Revise yellow phrase:

The other fish species native...

(21) Page 98. Change date from (1956) to (1965).

(22) Page 99. Change Carl et al. date from (1971) to (1967) [two yellow places].

(23) Page 99. Change Schultz date from 1939 to 1935 [blue].

(24) Page 101. Change to singular: Kokanee....

(25) Page 102. Revise yellow material:

...documented by Bjornn and Johnson (1978). Angling...

(26) Page 103. Revise yellow material:

...when stocked together in waters where natural reproduction does not occur, will produce more fish, more biomass,...

(27) Page 103. Extend blue sentence:

...in mountain lakes stocked with trout.

(28) Page 104. Revise yellow phrase:

Their living areas include...

(29) Page 104. Delete blue sentence.

(30) Page 105. Revise yellow phrase:

...selective factors--including their fish communities (especially the predaceous bull trout, present in Glacier Park but not in Yellowstone Lake), forage organisms, cestode parasites, and morphometries--that could give...

(31) Page 109. Change "caecum" to "caecal".

(32) Page 111. Revise yellow phrase:

On the south side...

(33) Page 114. Insert "trout": cutthroat trout.

(34) Page 115. Rewrite yellow sentence:

The finespotted Snake River cutthroat trout is electrophoretically indistinguishable from Yellowstone cutthroat trout, but its spots more closely resemble those of westslope cutthroat trout in size and shape.

(35) Page 116. Make plural: populations...

(36) Page 117. Extend yellow sentence:

...longnose dace (which is rare).

(37) Page 125. Revise yellow phrase:

...fish could move freely...

(38) Page 126. Change date from 1972 to 1972b.

(39) Page 129. Change yellow reference:

...Kiefling (1974a, 1974b),...

(40) Page 132. Insert "probably":

...Snake River probably during...

(41) Page 135. Break and revise yellow sentence:

...cutthroat trout evolved. The adaptive values of spotting pattern and abundant pyloric caeca are unknown, but within salmonine groups, species and subspecies that are more piscivorous tend to have more pyloric caeca (Behnke 1968). Numbers of vertebrae...

(42) Page 137-138. Revise yellow phrase:

...in water level (Benson and Thompson 1987), which could have provided opportunities for isolation and incipient speciation; the subspecies in the Humboldt River drainage probably originated in this way.

(43) Page 138. Revise blue phrase:

...Tahoe was most likely based on intrapopulation differences in size and age between first spawners and repeat spawners, and on apparent differences in color between sexually mature and immature fish.

(44) Page 138. Change date from (Behnke 1972) to (Behnke 1972b).

(45) Page 139. Revise yellow material:

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

The original Pyramid Lake population of Lahontan cutthroat trout disappeared in the 1940s after it lost its access to Truckee River spawning grounds. In their last spawning run...

(46) Page 139-140. (a) Rewrite blue paragraph:

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

(b) Check that tui chub is in the master species list (front matter).

(47) Page 140. Revise yellow phrase:

...agencies have exhibited little interest to date in...

(48) Page 143. Change date from Snyder (1933) to Snyder (1933b).

(49) Page 143. Revise yellow phrase:

...furthermore, according to electrophoretic data, Paiute cutthroat...

(50) Page 144. Change date from (1933) to (1933b).

(51) Page 145. Change date from (1933) to (1933b).

(52) Page 145. Revise blue phrase:

...Paiute cutthroat trout...

(53) Page 145. Revise blue phrase:

...to designate the Paiute trout first as endangered and then as threatened.

(54) Page 150. Revise yellow phrase:

Data from small samples of Quinn drainage cutthroat trout, supplied to me by Patrick Coffin (Nevada Department of Wildlife) and Dennis Shiozawa (Brigham Young University), have...

(55) Page 150. Delete blue sentences. Substitute:

If, as I suspect, cutthroat trout in the Quinn and Humboldt drainages share a common origin, the unique mitochondrial DNA of the Humboldt fish must have developed after the two drainages separated.

(56) Page 150-151. Delete entire yellow section on TAXONOMIC NOTES.

(57) Page 153. Revise yellow phrase:

...withdrawals dry up many streams, leaving little habitat for native trout.

(58) Page 153. Revise blue material:

...Carlin and Deeth now have no trout because the environment is highly degraded. The Humboldt cutthroat trout nominally receives the same protection under the Endangered Species Act as the Lahontan cutthroat trout, yet most degradation of its habitat has occurred on federal lands. Grazing problems are serious enough to generate some publicity. A 1988 General...

(59) Page 153. Insert new sentence:

The decline of the Quinn River cutthroat trout from livestock-induced habitat destruction was cited in a Newsweek magazine feature article on public land management in the West (September 30, 1991). Since 1980,...

(60) Page 153. Delete blue paragraph and substitute the following:

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

(61) Page 154. Revise yellow phrase:

...first collected cutthroat trout...

(62) Page 161. Add subspecies name: Chasmistes liorus mictus,....

(63) Page 162. Revise, extend, and add to the yellow sentence:

As of mid-1992, to my knowledge, nothing was being done to preserve what remains of the Alvord cutthroat genotype, including implementation of a proposed land exchange that would place upper Virgin Creek in federal ownership. As the federal agency designated to preserve the diversity of freshwater fishes through administration of the Endangered Species Act, the U.S. Fish and Wildlife Service should take a leadership role in the restoration of the Alvord cutthroat phenotype.

(64) Page 163. Revise yellow phrase:

...assumed pluvial lake....

(65) Page 165. Delete entire yellow paragraph.

(66) Page 169. Add to and revise yellow material:

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

(67) Page 169. Revise blue phrase:

Their theses (which include my Snake Valley and Bear River data from unpublished reports) and electrophoretic...

(68) Page 178. Revise yellow phrase:

...resulting discontinuous distribution...

(69) Page 179. Change date from (Miller 1972) to Miller (1972a).

(70) Page 179. Revise yellow phrase:

...a population that had been transferred...

(71) Page 179. Revise blue phrase:

Allele frequencies at two gene loci--L-iditol dehydrogenase (IDDH-1*63) and malic enzyme (MEP-1*100)--distinguished this population...

NOTE: The L in L-iditol is small cap. <cm;1>|<cm;0>

(72) Page 185. Revise yellow phrase:

...greenback cutthroat trout are...

(73) Page 187. Revise yellow parenthetic phrase:

...(with "basihyal" teeth, assumed to mean basibranchial teeth)...

(74) Page 187. End sentence and omit blue phrase:

...lacks basibranchial teeth.

(75) Page 187. Revise yellow phrase:

...Casas Grande, an isolated tributary in the Guzman basin, which once had a connection to the Rio Grande...

(76) Page 187. Revise blue phrase:

...in Mexico, which I consider doubtful, it would be...

(77) Page 187. Truncate existing sentence and add a new yellow one:

...Conchos. If cutthroat trout were native to the Guzman basin, remnant populations would be expected in the headwaters of the Mimbres drainage, New Mexico.

(78) Page 188. (a) Add new material at yellow mark:

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...

(b) Add to the list of species on page viii:

Rio Grande chub .... Gila pandora

(79) Page 190. Revise yellow passage:

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...

(80) Page 192. Revise yellow phrase:

...trout obtained by Jordan...

(81) Page 195. Revise yellow phrase:

Jordan (1922) stated in his autobiography that the yellowfin...

(82) Page 195. Code blue name with acute accent: Jaff[acu]e (1902),...

Chapters 9-14

Revisions to Western Trout - Parts III-V

June 1992

(1) Page 199. Revise yellow passage:

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...

(2) Page 199. Fix yellow dates: (1879); (1889).

(3) Page 200. Change yellow date from 1972 to 1972b.

(4) Page 201. Revise blue material:

The most primitive living species linked to redband trout--Gila[end]Apache and Mexican golden trout--are associated with the Gulf of California, so it is likely that ancestral redband trout reached the Sacramento[end]San Joaquin basin from the south during the second half of the Pleistocene Epoch. Spreading through the 750-km-long valley, these fish began differentiating into distinctive populations, of which several persist today at the northern (McCloud drainage) and southern (Kern drainage) ends of the basin. From a still somewhat primitive assemblage of redband trout in California,...

(5) Page 201. Revise yellow phrase:

...southward to close the loop back to the northern Sacramento basin.

(6) Page 201. Revise blue phrase:

...upper Fraser basin and possibly into the Athabasca system (but see below).

(7) Page 201. Revise yellow phrase:

...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).

✓(8) Page 201. (a) Insert new paragraphs at green mark:

New information[2] 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 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[end]San Joaquin basin, the redband trout of the Columbia and Fraser basins, and coastal rainbow trout.

(b) Create footnote 2 (add to the footnote page after references):

[2]Carl, L. M., 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).

(8a)
✓ (8) Page 201. Revise blue phrase:

...shows distinctive morphological tendencies, it embraces...

✓(9) Page 201. Revise yellow phrase:

...whereas some early museum...

(10) Page 201. Add blue parenthetic phrase:

...basins (collected before hybridization with rainbow trout occurred) average...

(11) Page 202. Delete paragraph break and run sentence in.

(12) Page 202. Add new material at the yellow mark:

Redband[end]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, ~~as discussed shortly,~~ (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.

(13) Page 202. Start new paragraph at the blue mark and revise as follows:

Genetic analyses have not yet indicated much distinction among subspecies of rainbow and redband trout, but they have revealed differentiation within the Columbia[end]Fraser redband group, which is morphologically and meristically uniform. Although mitochondrial DNA...

(14) Page 202. Delete yellow words: ...most genetic work...

(15) Page 202. Revise blue phrase:

...has involved electrophoretic...

(16) Page 202. Revise yellow phrase:

...locus; their...

(17) Page 202. Extend blue phrase:

...not yet clear, though they contributed to the unique characterization of Athabascan trout (Carl, personal communication).

(17a) Page 202. Revise green phrase:

Allendorf (1975) and Utter and Allendorf (1977) were the first to show...

(18) Page 203. Revise yellow material:

...Athabasca River (Carl, personal communication). Furthermore, the *100 allele predominates in Sacramento basin redband trout, ~~and~~ in coastal rainbow trout. Thus there as well as 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,...

(19) Page 203. Revise blue material:

...recent development. This development postdates the initial spread of redband trout in the Columbia[end]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.

(20) Page 203. Revise yellow phrase:

...allele consists of Columbia[end]Fraser redband trout.

(21) Page 203. Revise blue phrase:

...could be redband or rainbow trout of any stock; phenotypic analysis backed...

(22) Page 203. Delete yellow sentence.

(23) Page 204: Revise yellow phrase:

Today, the greatest potential for hybridization between redband and coastal rainbow trout occurs in...

(24) Page 205: Revise yellow phrase:

...with redband trout are...

(25) Page 207. Replace yellow sentence with the following:

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.

(26) Page 209. Delete yellow line if it is duplicated in the computer record.

(27) Page 209. Blue: change "Cascade" to "Columbia".

(28) Page 209. Yellow: change "ceca" to caeca".

(29) Page 209-210. Insert missing line, if it has been lost from computer record.

...are more similar to each other than either is to other groups of O. mykiss. If full species recognition were given...

(30) Page 211. Delete yellow line if it is duplicated in the computer record.

(31) Page 211. Revise blue line:

Myron Green, Stone's assistant of several years at the Fish Commission, then became superintendent of the Commission's trout...

(32) Page 212. Change yellow phrase from "(Behnke 1990)." to "Behnke (1990)."

(33) Page 212. Change blue "Shelby" to "Shebley".

(34) Page 212. Revise yellow phrase:

...introductions of different steelhead races that maintained...

(34a) Page 213. Start new paragraph at "A discussion...".

(35) Page 214. Close parens: "160)."

(36) Page 219. Correct spelling: "newberrii."

(37) Page 219. Revise yellow phrase:

...collected in Klamath Lake by...

(38) Page 219. Blue: Change "River" to "Lake".

(39) Page 219. Revise yellow sentence:

Three National Museum specimens collected in 1883 from the Williamson River, a tributary to Klamath Lake, are of the same form of trout.

(40) Page 220. Revise yellow phrase:

Compared with museum specimens from Upper...

(41) Page 221. Make the yellow species name continuously italic (retain hyphen):

flos-aquae

(42) Page 225. Revise yellow phrase. Note spelling change for Kunkel:

The trout was established in a private ranch pond (Kunkel and...

(43) Page 226. Correct number: ...63[end]65;...

(44) Page 229. Correct spelling: Pyloric...

(45) Page 230. Add sentence to end of paragraph:

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.

(46) Page 233. Correct numbers: 62[end]66.

(47) Page 234. (a) Insert new sentences at the yellow marker:

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.

(b) Start new paragraph at the blue "I use O. m. stonei...".

(48) Page 236. Mark "irideus" for italics: irideus.

(49) Page 236. Revise blue phrase:

Parr marks rounded; dorsal and ventral...

✱ (50) Page 236. Revise yellow phrase:

...between coastal rainbow and interior redband trout in the Columbia and Sacramento basins during and since...

has probably occurred

(51) Page 237. Correct yellow number: "62[end]65".

(52) Page 238. Revise yellow phrase:

...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.

(53) Page 244. Change date from 1972 to 1972b.

(54) Page 247. Correct spelling: McConaughy.

(55) Page 249. Revise yellow line:

...River; and Shedko (1991) on mitochondrial DNA analysis. Savvaitova et al. (1973) compiled and summarized taxonomic and biological information on...

(56) Page 249. Delete all blue material.

(57) Page 252. Revise yellow phrase:

...rainbow trout may have evolved...

(58) Page 257. Correct word: introduced.

(59) Page 258. (a) Revise yellow material:

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...

(b) Add to the master species list (front matter, page vii):

Chihuahua chub .... Gila nigrescens

(60) Page 258. Revise blue phrase:

...Yates, University of New Mexico, unpublished...

(61) Page 259. Revise yellow phrase:

...drainage in the Guzman basin,...

(62) Page 260. Make plural: habitats.

(63) Page 260. Revise blue material:

I called Propst and found out that the paper had just come out in Southwestern Naturalist.

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 Mescalero 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%.

(64) Page 260. Delete "[give reference]," start new paragraph, and revise yellow sentence:

The catastrophes of 1989 caused the U.S. Fish and Wildlife Service's Gila Trout Recovery Team to develop a new conservation strategy.

(65) Page 260. Eliminate paragraph break and run in.

(66) Page 270. Change "Rio Grande" to "Guzman".

(67) Page 271-272. Move the two yellow paragraphs to the start of Chapter 14.

(68) Page 274. Replace yellow sentence with new material:

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).

(69) Page 274. Revise yellow phrase:

...views that lack a sound understanding...

(70) Page 274. Start new paragraph, with new material, at the blue marker:

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...

(71) Page 275. Revise yellow phrase:

...programs to insure that practices do not violate...

(72) Page 275. Replace blue material with new text:

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.

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 time 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...

(73) Page 276. Add sentence at blue mark, then begin new paragraph:

These biologists should not confuse quantitativeness with biological reality, nor should they be intimidated by modern technologies.

Given the great...

(74) Page 276. Revise yellow phrase; add new sentence:

...measure, the importance of professional judgment in fisheries conservation and management cannot be overemphasized. The need for judgment extends well beyond the interpretation of genetics data, as I have stressed elsewhere in this monograph. Any attempt...

(75) Page 276. Revise blue phrase:

...progressive programs for native trout management...

Chapter 4

Cutthroat Trout Oncorhynchus clarki

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

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

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

4.22.92

programs are urgent because most recognizable groups of cutthroat trout have undergone marked declines during the past 100 years.

REASONS FOR DECLINE

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

The dramatic decline of interior cutthroat trout across their entire range can be appreciated by reading 19th-century accounts of their great abundance. If one were to revisit the sites of most of these accounts (Bear River, Utah Lake, upper Colorado River, Green River, Rio Grande, Lake

Tahoe, Truckee River), only nonnative trout would be found. The greatest abundance of pure interior cutthroat trout occurs in Yellowstone Lake and the Yellowstone River drainage above the falls in Yellowstone National Park.

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

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

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

PROPAGATION OF CUTTHROAT TROUT

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

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

The first cutthroat trout propagated in a federal hatchery were the greenback and yellowfin subspecies, which were obtained from sympatric populations in Twin Lakes, Colorado, in 1891 and cultured at the Leadville National Fish Hatchery. Annual reports of the U.S. Fish Commission of the late 19th and early 20th centuries indicated that all the presently recognized subspecies of cutthroat trout (with the possible exception of the yellowfin) were treated as a single entity--the black-spotted trout. Almost from the beginning of cutthroat trout propagation at the Leadville Hatchery, two Colorado subspecies, the greenback subspecies of the eastwardly draining Arkansas River system (Twin Lakes) and the Colorado River cutthroat trout from the western side of the Continental Divide, were mixed together as black-spotted trout to be stocked out and shipped to other states.

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

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

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

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

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

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

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

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

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

When I examined specimens from the present population in the headwaters of the Big Thompson River, however, I was surprised to find that the trout were not Yellowstone cutthroat trout, as stocked fish were expected to be, but were relatively "good" greenback trout only slightly hybridized. I concluded that these isolated waters already had an abundant native trout population when the hatchery fry were stocked, and virtually none of the nonnative fry has survived. So, if trout already existed in the river, why was it stocked? Richard Delong, one of my graduate students, once interviewed an elderly resident of Estes Park who participated in the stockings of 1922 and 1923. The veteran stocker recalled that traveling from Estes Park to the headwaters of the Big Thompson River required two days and two crossings of the Continental Divide by pack train. No one knew if trout were native to the stream because the area was so remote that none of the sportsmen had ever fished it. This stocking was motivated by the Johnny Appleseed desire to seed all headwater areas with fry and trust they would grow, multiply, and increase trout abundance throughout the watershed.

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

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

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

Phelps (1980), for example, found that a Montana stock of westslope cutthroat trout suffered a 57% reduction in the proportion of polymorphic gene loci (loci with more than one allele) after only 14 years of hatchery cultivation.

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

In contrast to the rainbow trout, the cutthroat trout has rarely become naturalized much beyond its original distribution. Nilsson (1971) wrote that "a couple" of stocks of cutthroat trout were established in Sweden, (4) (7) Also, within their native range, cutthroat trout were excluded from many headwater lakes at high elevations by falls; many such lakes now are regularly stocked with cutthroat trout by fisheries agencies. The modern association of cutthroat trout with originally fishless mountain lakes and their rarity in their original range have given rise to an erroneous belief held by many anglers that the natural distribution of interior forms of cutthroat trout was restricted to remote, high-elevations lakes.

(7) Scott & Crossman (1974): 180, "About 1942 cutthroat (it) was introduced in Laurentian lakes in Quebec. It succeeded but began to appear in the fishermen's catch only in 1966" – This introduction also mentioned by Canadian authors in article on "genetic conservation – something like that" in TAFS or Fisheries a few (2-3) years ago. – but "rarely become naturalized" doesn't change.

Chapter 5

Cutthroat Trout of Coastal Basins

Coastal Cutthroat Trout Oncorhynchus clarki clarki

TYPICAL CHARACTERS

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

DESCRIPTION (Plate 1; Figure 3)

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

The coastal form does not develop the brilliant colors of some interior subspecies. Sea-run individuals are silvery, and the silvery skin deposits often obliterate or mask body spots. Resident

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freshwater fish tend to be darker with a coppery or brassy sheen. Pale yellowish colors may appear on the body, and the lower fins may be yellow to orange-red. A rose tint is sometimes apparent on the sides and ventral region of sexually mature fish, especially in lake-dwelling stocks.

The distinctive spotting pattern is the only morphological character of coastal cutthroat that differs from the interior subspecies. Other trends in differentiation, however, can be used to separate most coastal from most interior cutthroat trout and also from rainbow and redband trout.

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

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

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

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

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

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

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

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

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

Basibranchial teeth are usually present but difficult to observe. These very small teeth lie between the gill arches on the floor of the pharynx on the membranous basibranchial plate. ~~I stain the area with alizarin-red and allow the specimens to stand overnight before examining them under a binocular microscope.~~ Basibranchial teeth are not present, or at least were not seen by me, in cutthroat trout at the time they emerged from redds at lengths up to about 25 mm. The smallest specimen in which I have found a basibranchial tooth was 37 mm. These teeth continue to increase in number until the fish grows to lengths of 70[end]100 mm.

DeWitt (1954) found that 6 of 79 California coastal cutthroat specimens lacked basibranchial teeth, but he mentioned that some specimens had an appearance suggestive of hybridization. He counted from 1 to 34 (mean, 9) basibranchial teeth in the 73 specimens with these teeth, which is similar to tooth counts for my samples from California to Alaska (means ranged from 5 to 15) with one notable exception. The highest number of basibranchial teeth I found in any coastal cutthroat sample was for nine museum specimens from Lake Sutherland, Washington, where two species had been described, Salmo jordani and S. declivifrons (Meek 1899). I found the Lake Sutherland specimens to be typical of coastal cutthroat trout except for the high number of basibranchial teeth,

Check date for Meek 1989 in refs — corrected 1899

15[end]52 (mean, 29)--about twice the number found in any other sample.

I believe that pure coastal cutthroat trout have basibranchial teeth, and that the absence of these teeth indicates hybridization with rainbow trout. This opinion is based on 110 specimens of coastal cutthroat trout from remote areas of Alaska and British Columbia where, I assume, the influence of stocking has been nil. All 110 specimens have basibranchial teeth. In samples from Washington and Oregon, where stocking of hatchery fish has been heavy, I found specimens without basibranchial teeth. For example, 4 of 17 specimens from Gate Creek, a tributary of the McKenzie River, Oregon, lack basibranchial teeth. Campton and Utter (1985) verified rainbow [24] cutthroat hybridization in two Puget Sound streams by electrophoretic analysis.

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

In 1979 I visited streams on the west coast of Vancouver Island, where I made several collections of the native trout. In lower reaches of these streams, steelhead and coastal cutthroat trout coexist. Above barrier falls in some of the streams, a resident trout occurs that represents a rainbow [24] cutthroat hybrid (predominantly rainbow trout; Parkinson et. al. 1984). The rainbow and cutthroat trout niches broadly overlap. Coexistence of rainbow and coastal cutthroat trout in Pacific coastal streams (and of rainbow and interior cutthroat trout in the Salmon and Clearwater drainages of Idaho) depends on maintenance of reproductive isolation. In small streams with limited niche diversity and insufficient space to allow their physical separation at spawning, cutthroat trout and rainbow trout appear unable to resist crossbreeding, and a hybrid swarm results if they come into contact.

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

DISTRIBUTION

The northern (and western) extent of coastal cutthroat trout distribution is the Prince William Sound area of southern Alaska, bounded by Gore Point on the Kenai Peninsula. The southern limit is the Eel River, California. Coastal cutthroat trout occur on all the numerous islands with suitable habitat off the coast of British Columbia and southern Alaska. Typically, they do not occur far inland--usually less than 150 km from the coast. The farthest natural inland penetration is in the headwaters of the Skeena River, British Columbia. Throughout this range, both sea-run and nonmigratory stocks are found. Many of the nonmigratory stocks live in lakes and show morphological specializations for lacustrine life, such as more numerous gill rakers for feeding on zooplankton.

TAXONOMIC NOTES

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

All coastal cutthroat trout are currently recognized as a single subspecies. In the past, other species or subspecies have been named that are now considered to be synonymous with O. clarki

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

Meek (1899) named another species of trout from Crescent Lake, Salmo bathoeceter, which was reputed to live only in deep water. I can find nothing in Meek's description or in the specimens borrowed from the Field Museum (collected by Meek) that indicates any difference between bathoeceter and crescentis. I conclude that both crescentis and bathoeceter are synonyms of O. c. clarki. Pierce (1984a, 1984b) studied the trout of Crescent Lake during 1981[end]1982. He found that native cutthroat trout still maintain a small population in the lake by reproducting in the outlet stream. Barnes Creek, the only spawning tributary to Crescent Lake, now contains a rainbow [24] cutthroat hybrid swarm. It is likely that two reproductively isolated populations of cutthroat trout originally occurred in Crescent Lake, one spawning in Barnes Creek and one in the outlet stream. Differences in their life histories may have generated the belief that they represented two species. From a practical viewpoint, sympatric populations with different life histories should be managed separately even if they are not recognized as different taxa.

Crescent Lake is a deep body of water covering 1,960 hectares in Olympic National Park, Washington. It is isolated from the sea by barrier falls. In the late 19th century the lake was famous for its large native rainbow and cutthroat trout. Wydoski and Whitney (1979) gave the Washington state record as a Crescent Lake specimen of 5.45 kg. During the 20th century human attempts to improve on nature included a massive stocking program that introduced millions of hatchery rainbow trout, Yellowstone cutthroat trout, and kokanee into Crescent Lake, whose major tributary was blocked and polluted. The results were disastrous to the native trout. The U.S. Fish and Wildlife Service studied the situation in the 1940s and 1950s. A 1949 report by L. R. Garlick ("Report of Fishery Investigations, Lake Crescent, Olympic National Park with Management Recommendations") and a 1953 report by Z. E. Parkhurst and M. A. Smith ("Report on the Management of the Beardsley Trout Fishery of Lake Crescent, Olympic National Park") assumed cutthroat [24] rainbow hybrids were common among the Crescent Lake trout. Color photographs accompanying Parkhurst and Smith's report, however, show a typical rainbow trout (the Beardsley trout) and a typical cutthroat trout (crescentis) taken from the outlet spawning run. The more recent study by Pierce (1984a, 1984b) revealed that hybridization is limited to Barnes Creek and that the hybrids are mainly resident in the creek (only 3 of 47 adult trout sampled from the lake were of Barnes Creek origin). Pure native rainbow trout and pure native cutthroat trout have persisted by spawning in different parts of the outlet area.

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

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

To my knowledge, the only experimental hybridization with coastal cutthroat trout was the master's thesis research of Hartman (1956), who crossed coastal cutthroat trout from Chilliwack Lake with interior Kamloops (redband) trout from Cultus Lake, British Columbia. The chromosome numbers of the parent species, although not considered by Hartman, should be 68 and 58, typical of coastal cutthroat and interior redband or Kamloops trout. This is the maximum difference between various forms of cutthroat and rainbow[end]redband trout. Hartman actually found slightly higher viability among hybrids than among the offspring of pure parental matings. For his thesis, Hartman did not have time to make second-generation crosses to determine the fertility of the hybrids, but he told me in 1961 that the hybrids were backcrossed with both rainbow trout and cutthroat trout and were fully fertile. Also, he found no difference in the sex ratios of hybrids and the offspring of pure parental matings.

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

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

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

LIFE HISTORY AND ECOLOGY

As a sport fish, the coastal cutthroat trout is less popular than the larger and more glamorous steelhead. This is reflected in the volume of literature, both popular and scientific, about each species. Detailed life history data were not published until Sumner's (1953, 1962) papers on the cutthroat trout of Sand Creek, Oregon. Hartman and Gill (1968) discussed the ecological preferences of juvenile rainbow and cutthroat trout, thereby providing some insight into the mechanisms of niche separation. Giger (1972) gave comprehensive life history data on the cutthroat trout populations of several Oregon rivers. Armstrong (1971) discussed the age, growth, feeding habits, and migrations of the cutthroat in Eva Lake, Alaska. Andrusak and Northcote (1971) and Schutz and Northcote (1972) studied the feeding habits and spatial distribution of cutthroat trout occurring with Dolly Varden in British Columbia. Idyll (1942) studied the feeding habits of cutthroat, rainbow, and brown trout in the Cowichan River, British Columbia. Bustard and Narver (1975) studied winter habitat of cutthroat trout and coho salmon in British Columbia. Nicholas (1978b) delineated the winter habitat preference of coastal cutthroat trout in the Willamette River watershed and the interactions of these fish with rainbow trout. Narver (1975) published notes on the ecology of cutthroat trout in Great Central Lake, Vancouver Island. Nilsson and Northcote (1981) provided life history and ecological information on coastal cutthroat and rainbow trout in several British Columbia lakes with allopatric or sympatric populations. Cutthroat trout were much more predaceous than rainbow trout and attained a larger maximum size where they coexisted in the British Columbia lakes studied. In Crescent lake, Washington, however, rainbow trout (the Beardsley strain) attain a larger maximum size than cutthroat trout, perhaps because they evolved from a steelhead ancestor and were preadapted as a limnetic predator. Trotter (1989) has produced the most recent and inclusive compilation of life history information on coastal cutthroat trout.

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

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

Like cutthroat trout in general, the coastal subspecies is vulnerable to overexploitation by angling. In Sand Creek, which is little used by anglers, survival was 30% between the first and second spawning, 17% between the second and third spawning, and 12% between the third and fourth spawning. In five Oregon rivers subjected to heavy angling pressure, the estimated survival ranged from 5 to 26% between the first and second spawning. Johnson (1979) discussed the problem of angler overexploitation of coastal cutthroat trout and the need for stricter regulations on sport fisheries. Predation at sea may be a significant cause of natural mortality. Giger (1972) reported that 58% of the wild cutthroat and 67% of the hatchery cutthroat trout taken from the Alsea River estuary in 1970 had scarring indicative of predator attacks.

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

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

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

Coastal cutthroat trout can be highly predaceous. Idyll (1942) found that cutthroat trout had a higher percentage of fish in their diets than either rainbow or brown trout in the Cowichan River, British Columbia. Studies by Armstrong (1971) in Alaska and by Andrusak and Northcote (1970, 1971) in British Columbia revealed that when coastal cutthroat trout live with Dolly Varden, the cutthroat trout is the more predaceous species by far. Ricker (1941) found cutthroat trout to be the major predator on young sockeye salmon in Cultus Lake in 1940. Nilsson (1971) showed more rapid growth and more predaceous feeding habits for cutthroat than for rainbow trout in a British Columbia lake. These results were further detailed and verified by Nilsson and Northcote (1981).

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

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

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

STATUS

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