REDBAND TROUT

RESILIENCE AND CHALLENGE IN A CHANGING LANDSCAPE

Oregon Chapter
American Fisheries Society

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Preface

In September 1996, 85 redband trout enthusiasts gathered at the Malheur Field Station in Harney County, Oregon for a workshop sponsored by the Oregon Chapter of the American Fisheries Society. All of us gathered to talk about the biology and status of redband trout, and to share our appreciation for this diverse fish. Concern about redband trout had been building in the region because of continued drought and the apparent decline of some populations, including the disappearance of redband trout in some streams such as Skull Creek in the Catlow Valley (Howell 1997). The status of redband trout throughout its range was considered to be precarious enough that it had been classified by the U.S. Fish and Wildlife Service as a candidate for being listed as an endangered species, though lack of information about its status or other factors had precluded listing. Although the candidate list had served as a warning sign about the status of species and populations, USFWS eliminated the list in 1996. It was in this climate that Phil Howell and Dave Buchanan organized the workshop on redband trout to compile information about the species, its management, and its status. The presentations at the workshop provided a broad perspective on redband trout such as life history and biology, systematics and classification, and history of management.

Shortly after the workshop, papers were solicited from the presenters for a publication. As is often the case, the idea of publishing a proceedings soon collided with the reality of getting papers submitted, sending them out for peer review, collecting comments from reviewers, sending manuscripts back to the authors for revisions, and getting papers back from authors. After a few years, this reality became further complicated by the retirement of the original editor and loss of momentum. A new effort was begun several years later and the drive to complete these proceedings began anew. A second lag occurred for several reasons, and once we regained a little progress, we were tempted at times to declare this the second edition of these proceedings and let readers wonder whether they had completely missed the first one. As we struggled through the last couple of years, we questioned whether or not to continue with our efforts to publish. However, as we solicited input from authors and other interested people, we heard about the need to collect and publish information about redband trout, and the need to provide a perspective on issues such as management of the species and questions pertaining to listing them under the federal Endangered Species Act.

Thirteen papers from the 1996 workshop are included in these proceedings. Most of them have been revised and updated to include recent data or to report on changes in management. Two additional papers that were not in the workshop have been included because we felt they would complement the other papers. It is our hope that these proceedings will provide a useful resource for those working with or interested in redband trout. Although the workshop used the term "inland rainbow trout" to describe populations of *Oncorhynchus mykiss* in the Columbia Basin east of the Cascade Mountains and those of the Northern Great Basin (including the Upper Klamath Lake Basin), we choose to use "redband trout" for these proceedings, following Behnke (1992, 2002).

Ten years have passed since the workshop and much has changed. We saw the long drought cycle of the 1990s pass, and we entered a period when flows generally have been higher, although dry years have been interspersed among the wet years. Redband trout were observed in downstream reaches of streams during years with adequate water, and adfluvial fish once again migrated between streams and lakes, such as the return of adfluvial redband trout in the Goose Lake basin. On the surface all would appear to be well with the redband trout. However, in the last 10 years many of the questions raised when redband trout were being considered for listing have yet to be answered, and little quantitative data have been collected in a method that allows an adequate assessment of the status of populations or life histories. Subsequently, knowledge is limited about the biology, life history, and status of redband trout throughout much of its range. As an example, the recent assessment of redband trout conducted by Oregon Department of Fish and Wildlife largely relied on biological opinion and anecdotal information about the distribution and relative abundance of stream populations. Although some measure of general status has been collected, little study has been made of individual populations or life histories. It is our hope that the papers in these proceedings will help to illuminate the world of redband trout: what we know, what we think we know, and what we clearly do not know about the species. In turn, we hope the papers will raise questions and will stimulate additional studies of redband trout, and will inspire an approach to studies and monitoring that not only examines the general abundance and distribution of redband trout populations, but also encompasses the diversity of their life histories.

The publication of these proceedings reflects the efforts of many people. Most importantly, we thank the authors for their contributions to the workshop and those who expanded and updated their papers at our request for this publication. We also thank them for their extreme patience in dealing with suggested edits and in waiting for their papers to be published. A large group of reviewers provided valuable assistance and service in insuring high quality papers, and we thank them for their efforts. Lisa Krentz and Andrew Talabere produced maps for several of the papers in these proceedings and their time, expertise, and patience are very much appreciated. The Oregon Chapter Executive Committee provided financial support for the workshop and continued to support publication of these proceedings. The Pacific Northwest Region of the U.S. Forest Service provided financial support for publication. Dave Buchanan and Phil Howell organized the workshop, solicited presenters, and initiated the effort to publish papers from the workshop presentations. Judy Maule assisted with layout early in the process. Many people helped to plan and organize the workshop and accompanying field trips. We particularly wish to acknowledge the efforts of Loretta Brenner, who was executive assistant for the Oregon Chapter AFS, Wayne and Patty Bowers, who were with ODFW in Hines, and Gary Ivey, who was the USFWS biologist at Malheur National Wildlife Refuge. Finally, the master fish artist, Joe Tomelleri, kindly allowed us to use his image of a Skull Creek redband trout for our cover.

One theme that runs through these papers is the tremendous diversity expressed by redband trout; from the habitats they inhabit (ranging from cold mountain rivers to high desert streams) to their diverse life histories that have allowed them to adapt to a wide range of environmental conditions. Ultimately, these proceedings are dedicated to the continued existence of this wonderful fish, an existence that will require vigilance and efforts from all of us.

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Introduction

The Wonder of Redband Trout

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"The only real voyage of discovery consists not in seeking new landscapes, but in having new eyes."—Marcel Proust

"You cannot make a better world unless you can imagine it so, and the first step toward change depends on the imagination's ability to perform this radical act of faith."—Ruth Ozeki

Every landscape holds a wealth of stories. Through the languages of geology, biology, and human culture we can begin to understand how the sequences of events have shaped the landscapes we see today. The way we tend to look at the landscape is naturally filtered through the lens of human culture, which in turn is colored by European settlement of the continent. In the Pacific Northwest, where this settlement period is short, the sense of time with which we assess change is often measured in decades, occasionally spanning a century or two. However, if you trace a biological story line it will stretch back thousands of years and will be rooted in the regional environment, giving you a picture of how large-scale changes have led to this moment. Thus, the stories can be a measure of how we live or fail to live within a landscape, and they can be a means to imagine the landscape we would like to leave to future generations.

Stories are a composite of details that hold together to form a picture. Part of what drives us as biologists is a quest for details and specifics, but we should remember to pay attention to how these tell a story. Imagine looking at a painting and stepping closer to examine the detail. Each step closer reveals something new, but only because something else falls away in a blur. If you look closely enough you might be able to identify the path of a single bristle across the canvas. Although that detail is important and intriguing, it cannot stand alone. Isolate the brush strokes and you no longer have art. Similarly, if you focus only on details about a fish, such as genetics or abundance, you will miss the larger story.

The story of redband trout is a remarkable saga of a creature persisting for millennia in a landscape that has undergone immense geologic and hydrologic change. Redband trout range across the interior Pacific Northwest, living in a young and diverse environment shaped by volcanoes, continental glaciation, the great Missoula floods, and the formation and desiccation of large pluvial lakes. They share much of their range with salmon and are as much a part of the landscape, yet it is the salmon that has become the cultural icon of the region. However, in the Basin and Range country of Oregon, redband trout have survived where salmon could not, and it is here that redband trout have become a unique expression of their environment.

We think of redband trout in the High Desert as a species adapted to harsh conditions, living in streams with low flow and high temperature in summer and with freezing conditions in winter. However, the story of redband trout stretches far back in time and spans a diverse range of climatic and environmental conditions.

On a recent trip through the Fort Rock Basin, I thought about how much change redband trout had endured over a span of about 70,000 years. They arrived in this basin via the Deschutes River or across a low divide with the Klamath Basin, when the environment was considerably more lush than it is today. Forests of pine, spruce, and fir descended far down the slopes to meet the grassy foothills. If we were able to return to that scene, we would see a large, coldwater lake stretching out across the Fort Rock Basin, surrounded by rich productive wetlands in the shallow bays. We would easily recognize some of the animals inhabiting this landscape, even if a few seemed a little out of place. In the hills and prairies we would see bison roam, and deer and antelope graze. Rabbits and bighorn sheep would be seen in the grasslands and on the ridges. We would also see animals that are now extinct in this landscape: camels, llamas, mammoths, peccaries, musk oxen, and sabertooth tigers. The climate was cool and moist, with enough rain and snowmelt to fill the basin to depths of up to 200 feet. Large redband trout would be swimming in the lake, feeding on abundant prey such as tui chubs, and migrating up the streams in spring to spawn.

This picture of large lakes and a cool environment is often evoked as an almost static state in which redband trout in the Great Basin evolved. But in reality the evolutionary backdrop for the redband trout was a complex of climatic cycles and geologic events. Studies of sediment layers in lake basins can tell us about the general climate in increments of several thousand years, but the layers lack the detail to tell us about cycles of centuries or decades. Nonetheless, these studies indicate that the climate of the Pleistocene and early Holocene was punctuated by fluctuations of wet and dry periods, and that local climate may have deviated from the global pattern of climate change because of regional effects such as deflection of the jet stream. Periodic droughts in the Fort Rock Basin would cause the lake to evaporate. As the lake became shallow and alkaline, redband trout might have continued their adfluvial life history by using Paulina Marsh in all but the driest periods, when they may have been confined to tributary streams. Every generation would produce migrants that followed some evolutionary signal and kept pushing their range downstream until the climate cycled back and the basin filled again with water. These migrants would then find an environment where they could grow to a large size before ascending in the spring to seed the streams with their migratory legacy.

We cannot know how close to extinction the Fort Rock redband trout may have come in the past. Perhaps they were pushed to the brink during some of the worst droughts or by other events. One such conjunction of events occurred about 7,700 years ago, when Mount Mazama erupted. Because the lake was dry, most redband trout would have been residing in feeder streams, although some fish may have found suitable habitat in Paulina Marsh. For days, the sky must have been as dark as night while ash rained down on the landscape. When the skies finally cleared, ash coated the ground over a foot deep on the basin floor and up to several feet deep in the western uplands of the basin. Later, as rain and snowmelt washed the ash off the land, it would have covered gravels and transformed some sections of streams into a thick, chalky liquid. Seasonal floods would eventually clear the streams and clean the ash from the gravels, and the layer of ash on land would become buried beneath soils.

Redband trout have survived in the Fort Rock Basin for 70,000 years, enduring and repeatedly recovering from droughts, the eruption of Mount Mazama, and other dynamic events. How do we reconcile the fact that the cumulative actions of our modern times have pushed redband trout populations to dangerously low levels that rival or exceed those of the massive geologic and climatic events of the past?

Although the paths of redband trout and humans in the basin may have first crossed 13,000 years ago, it was not until European settlement that humans likely began to have major effects on redband trout. The early inhabitants of the basin settled on the shoreline of the lake during wet cycles and moved to other areas when the lake dried. Archeological investigations have revealed that these early people caught large numbers of tui chubs, presumably when the fish spawned in the shallows or became stranded. In contrast, few salmonid bones have been recovered at archeological sites in the basin. Although redband trout were no doubt seen in the lake or streams, they would have been difficult to catch in the deep areas of the lake or in the streams during the spring spawning migration, when flows would have been high.

European settlement and development came at a time when the range of redband trout was naturally constricted following the wet, cool climate of the Pleistocene. Within a short time span, our actions have affected every watershed and we have invaded the last refuges of redband trout, removing the natural buffers that protected these fish for millennia. Over the last 150 years we have dissected the landscape with our roads, cut timber from the slopes, turned large numbers of livestock loose through entire watersheds, changed the course of streams, diverted water out of the channels, and drained and diked the marshes. We have transported hatchery rainbow trout across divides and released them into redband trout waters, accomplishing in an afternoon what would have taken millennia to occur in Nature. And in some watersheds we defied the forces of Nature by introducing brook trout from the East. Now, in our relentless march across the landscape we are changing the global climate at an alarming rate, to which plants and animals may be unable to adapt. Consider this—if the width of this page represents the 70,000 years that redband trout have occupied the Fort Rock Basin, the span of European settlement would be the last 2/100 of an inch.

Despite these assaults, redband trout have somehow managed to persist. Perhaps the evolutionary history of redband trout has instilled them with the resilience to persist through these latest challenges. But resilience and persistence do not mean that redband trout are immune to extinction. Can our society learn to appreciate the amazing journey of these splendid fish and marvel at their ability to live within the confines of their landscape? Can we appreciate the tenacity to survive in a dynamic environment in an era when our society celebrates “new and innovative” more than “tried and true”? Although we are a product of our times, where political and social expediency often trump stewardship of the land, it seems the least we can do for redband trout is help them persist. Unlike the eruption of volcanoes or the uplift of fault blocks, we have some control over the trajectory of events affecting the landscape today. We can choose to provide some relief for redband trout.

What will future generations say about us? Will we be remembered as a society that realized how our actions were altering the global climate and causing the loss of species and environments, yet took only half-measures? Or will our time be remembered as a turning point? Will this be the moment when humans begin to nurture the environment and make changes to live more lightly on the Earth, to view landscapes as a source of nourishment rather than as a commodity? Around us are hopeful signs that good change is possible. Recent improvements in the Chewaucan and Goose Lake basins are helping adfluvial redband trout migrate upstream and downstream. Efforts are underway in other basins to improve habitat. But we will have to start doing more if redband trout are to survive the possible effects of climate change. Fish species in large rivers or with connections to the ocean have migratory responses that may allow them to adapt to climate change. In contrast, redband trout in the Great Basin or in other isolated streams have limited choices to respond to a climate change. We need to find the imagination and courage to create a landscape of high quality habitat and refuges that will provide choices for redband trout. As William Kittredge[1] wrote:

> We need to inhabit stories that encourage us to pay close attention, we need stories that will encourage us toward acts of the imagination that in turn will drive us to the arts of empathy, for each other and the world. We need stories that will encourage us to understand that we are part of everything, the world exists under our skins, and destroying it is a way of killing ourselves. We need stories that will drive us to care for one another and the world. We need stories that will drive us to take action.
>
> [from *Who Owns the West?*, 1996, Mercury House, San Francisco, pages 164–165]

Redband trout are a wonder. They tell a story of adaptation to a dynamic environment; they tell a story of living wholly within a landscape and becoming a part of that landscape, an expression of the landscape. But their decline tells another story about the collision of human culture and Nature, about our attempts to control the environment, and the drive to live beyond what the landscape can support. Their story will be part of our story. Redband trout continue to swim in the streams of the Fort Rock Basin, and if we give them a chance, large adfluvial fish may once again ascend from the floor of the basin on a spawning migration. That life history legacy is contained within redband trout, waiting to reappear. Yes, there are scientific and logical explanations for this phenomenon. Still, they are a wonder.

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[1] William Kittredge grew up on the MC Ranch in the Warner Valley. He has written often about how the valley was transformed by agricultural development, and the subsequent loss of the abundant natural life that the extensive wetlands had supported. His books include *Hole in the Sky, Owning It All,* and *We Are Not in This Together.*

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Malheur Field Station, September 1996

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Not in Picture: Dave Buchanan **[fearless photographer]**, ODFW; Mike Clady, USFS; Jeff Dambacher, ODFW; Rob Davies, USFS; Don Geisler; Bob Gresswell, USFS; Jim Harvey, USFS; Gary Ivey, USFWS; Tom Montoya, USFS; Clint Muhlfield, Montana DFWP; Jim Myron, OR Trout; Cynthia Tait, BLM; Tim Unterwegner, ODFW; Tim Walters, ODFW.

Redband Trout of the Northern Great Basin

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Abstract.—The redband trout *Oncorhynchus mykiss* of the Northern Great Basin are a rich complex of populations that cannot be neatly separated into subspecies with unique characters or precise geographic boundaries. Unlike monophyletic family trees, the evolutionary lines of the Northern Great Basin redband trout do not represent singular pathways of divergence leading to differentiated subspecies (as in cutthroat trout *O. clarkii*), but represent multiple routes of zoogeographic isolation and convergence. The Northern Great Basin redband trout illustrate the concept of polyphyletic origins and the problems of a taxonomy based on evolutionary relationships. This paper presents my view on the classification of these redband trout based on integrating evidence from meristic data, morphology, molecular genetics, zoogeography (patterns of dispersal and isolation), geologic history (isolating mechanisms, breakdown of geographic barriers), hatchery records (potential genetic contamination), and suggestions of adaptive traits. A strictly phylogenetic classification would recognize that three distinctly different ancestors gave rise to the present diversity of all redband trout found in the Northern Great Basin. A classification based on the shared evolutionary heritage for life in the large Pleistocene lakes that existed for tens of thousands of years in these basins would include all redband trout in the Northern Great Basin as a subspecies. This shared evolutionary ecology of a lacustrine life history encompasses a diversity of life histories including adfluvial migration and specialized predator-prey relationships that have continued to exist in lakes (e.g., Klamath and Goose lakes), in terminal marshes, and more recently in reservoirs (e.g., Threemile Reservoir in Catlow Basin).

The rainbow trout *Oncorhynchus mykiss* and cutthroat trout *O. clarkii* probably separated from a common ancestor by the end of the Pliocene, or about two million years ago. The evolutionary divergences leading to the existing subspecies of cutthroat trout are much simpler to interpret than those of *O. mykiss*, because the long isolation of about one million years among the four major subspecies of *O. clarkii* has allowed for clear-cut differentiation. This degree of differentiation in genetics and morphology among the major subspecies allows for the "minor" subspecies of cutthroat trout (evolving in past 100,000 years or so) to be confidently assigned to one of the major subspecies.

O. mykiss, in contrast, cannot be neatly separated into subspecies with unique characters or precise geographical boundaries. I believe this is the result of evolutionary lines that have alternated between isolation (and differentiation) and convergence, producing the mosaic of overlapping geographic divergences presently found in *O. mykiss*.

I have used the term redband trout for what I consider as primitive evolutionary lines of *O. mykiss* (Behnke 1992, 2002). My concept of redband trout comprises several diverse ancestral lines. That is, all redband trout cannot be traced to one common ancestor. The Northern Great Basin redband trout illustrates this concept of polyphyletic origins and the problems faced by a taxonomy that attempts to delineate evolutionary histories.

My latest opinion on the evolution and classification of rainbow and redband trout *O. mykiss* is presented in *Trout and Salmon of North America* (Behnke 2002). Further elaboration and details are presented here on a particular group, the redband trout of the Northern Great Basin.

The Northern Great Basin

The Great Basin of the western U.S. covers a vast area comprising many internal basins (Hubbs and Miller 1948). The Northern Great Basin, as defined here, encompasses six basins with indigenous redband trout and that portion of the Upper Klamath Basin that includes the Wood, Williamson, and Sprague rivers (Figure 1). Almost all of these basins are in south central Oregon, with southernmost extensions of the Upper Klamath and Goose Lake basins into California, the Warner Lakes basin into California and Nevada, and the Catlow and Guano Basins into Nevada. From the Miocene–Pliocene times to the present, climate change and volcanic and tectonic events have rearranged drainages and fish faunas. Remnants of a Miocene–Pliocene track that connected parts of the present Great Basin to the Snake River (which at that time flowed to the Pacific via the Klamath Basin) can be found in the Great Basin sucker genus *Chasmistes* and the endemic sucker genus *Deltistes*, both indigenous to the Upper Klamath Lake basin (Minckley et al. 1986). The continuity of these ancient genera attests that the Upper Klamath Lake basin has maintained a lacustrine environment since at least the Pliocene. All other basins of the Northern Great Basin had large lakes several times during the Pleistocene, including the last glacial epoch, starting from about 60,000 years ago up to about 10,000 years ago. The origins of the present redband trout in the Northern Great Basin can be traced to this period. I believe, however, that a redband trout ancestor was present in Upper Klamath Lake prior to the last glacial epoch. Unless otherwise cited, most of the historical information on geology, climate, and fish fauna is from Minckley et al. (1986).

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Figure 1. Oregon basins of the Northern Great Basin and the Upper Klamath Basin.

Harney Basin

The Harney Basin was part of the upper Columbia River basin until it was isolated by lava flows about 18,000 years ago. A large lake formed in the basin during the latter part of the last glacial period. This lake desiccated by about 8,000 to 10,000 years ago into two terminal lakes. Harney Lake receives the drainage of Silver Creek, but the high alkalinity of the lake is lethal to fishes. Malheur Lake receives the Donner und Blitzen River drainage from the south and the Silvies River drainage from the north. In most years, Malheur Lake maintains a sufficient volume to allow habitation by redband trout migrating from the Donner und Blitzen River. Such trout could be called adfluvial (migrating between river and lake), but trout cannot survive in the shallow, warm water of Malheur Lake during drought years. Thus, sporadic periods of desiccation would select against a more fixed pattern of migratory behavior (as, for example, in steelhead) and favor a flexible, opportunistic life history that can greatly expand its foraging range during periods of increased volume of the lake.

The native fish fauna of the Harney Basin consists of 10 species, all of which occur in the upper Columbia Basin, as would be expected from their relatively recent connection of about 18,000 years ago. Bisson and Bond (1971) detailed a more recent event that transferred fishes from the John Day River drainage (mid Columbia Basin) into the Silvies River.

To assess the degree of purity of contemporary redband trout compared to the original native trout, I examined museum specimens collected before the stocking of hatchery trout became widespread. J. O. Snyder collected six specimens each from Silver Creek and the Silvies River in 1904 (Snyder 1908). These specimens have 20–24 gill rakers (Table 1). This is the only morphological character that differs from typical middle and upper Columbia Basin redband trout *O. m. gairdneri*, which generally have 17–20 gill rakers. Other morphological characters (counts of scales, vertebrae, and pyloric caeca) are typical of redband trout in the middle and upper Columbia Basin (Table 1). This similarity would be expected because the Harney Basin has been separated

Table 1. Range and means (in parentheses) for five morphological characteristics of redband trout in Great Basin streams and in the Upper Klamath and upper Pit River basins.

Basin, population	Year (s)	n	Gill rakers	Scale rows above lateral line	Scales in lateral series	Pyloric caeca	Vertebrae
			Morphological character				
Harney							
Silver Creek	1904	6	20–24 (22)	(32)	150–152	37–40	64–66 (65)
Silvies River	1904	6	20–24 (21)				64–66 (65)
Silver Cr, Silvies R.[a]	1972	48	(20)	(29–30)	(136–144)	(39–42)	(64–65)
Smyth Creek	1968, 1972	25	18–22 (20)	(32)	(148)	33–45 (38)	63–66 (65)
Catlow							
Threemile Creek	1968	10	20–22 (21)	28–33 (30)	129–146 (139)	30–46 (37)	62–65 (64)
Fort Rock							
Silver Creek	1897	3	20–22 (21)	31–35	145–148		63,64
Buck Creek	1904	6	19–22 (20)	28–33 (30)	137–145 (142)		63–64(64)
Buck Creek	1968	10	17–21 (20)	(31)	(142)	38–62 (47)	63–65 (64)
Bridge Creek	1968	24	19–23 (21)	29–34 (31)	137–158 (145)	36–53 (43)	62–66 (64)
Upper Klamath							
Lake, Williamson R.	1855, 1883	4	20–23	32–35	142–148	45–58	63–65
Upper Sprague R.[b]	1968, 1970	33	17–21 (19)	29–33 (30,31)	129–144 (133–139)	36–56 (46–48)	62–65 (62–63)
Goose Lake/Pit River							
Cottonwood Creek	1904	6	21–24 (23)	(30)	(139)		61–64 (63)
Thomas Creek	1968	15	19–23 (21)	(30)[c]	(132–136)[c]		
Lassen Creek	1968	38	18–24 (20)			35–54 (42–43)[d]	
Davis Creek	1968	12	18–24 (21)	(33)	(147)		
Warner Lakes							
Honey Creek	1904	8	23–24 (23)	(31)	(147)		61–63 (62)
Honey Creek	1968	19	20–24 (22)	(29)	(133)	35–54 (45)	62–64 (63)
Chewaucan							
River	1897, 1904	8	20–23 (22)	28–33 (30)	133–148 (142)		63–64 (64)
Elder Creek	1968	28	19–24 (21)	27–33 (30)	136–154 (143)	33–46 (40)	61–65 (63)
Dairy Creek	1970	10	19–22 (21)	(30)	(135)	40–58 (46)	61–64 (63)

[a] Dairy and Sawmill creeks (Silver Creek drainage); Crooked, Camp, and Myrtle creeks (Silvies River drainage).
[b] Trout and Whitworth creeks; also includes samples from Butte Creek in Siskiyou County, California.
[c] Combined values for Thomas and Lassen creeks.
[d] Combined values for Thomas, Lassen, and Davis creeks.

from direct connection to the upper Columbia Basin for only about 18,000 years.

To assess a hybrid influence from hatchery rainbow trout, I assumed that all or virtually all hatchery stockings over many years were with stocks derived from coastal rainbow trout *O. m. irideus*, which differ meristically from redband trout. Coastal rainbow trout generally have lower counts of gill rakers (18–20) and scales in the lateral series (125–135) and above the lateral line (25–30), and higher counts of pyloric caeca (45–55) than redband trout. Although the sample size of the 1904 collections is small and limited to two sites, it does provide an approximation of the original redband trout in Harney Basin. In 1968 and 1972, I collected redband trout from six streams in the three major drainages of Harney Basin: Silver Creek, Silvies River, and the Donner und Blitzen River (Smyth Creek). Most of the streams I sampled were readily accessible, some in popular recreation areas with a long history of stocking with hatchery rainbow trout. I was somewhat surprised to find that the trout I collected appeared to be redband trout in coloration (yellowish tints on body), parr marks (more elliptical than rounded), and spotting (generally larger, sparser spots more concentrated dorsally). Their meristic characters were slightly lower in counts of gill rakers, scales, and vertebrae, intermediate between values found in the 1904 specimens and hatchery rainbow trout, suggesting a hybrid influence. The most isolated collection was from Smyth Creek, on private land (Figure 1), and these fish were generally most like the 1904 specimens (Table 1). Smyth Creek may not have been stocked with hatchery fish, or at least should have been least exposed to hybridization with hatchery rainbow trout.

Genetic data on Harney redband trout are found in the doctoral dissertations of Berg (1987) and Currens (1997)[1]. The best allozyme trait differentiating *O. m. gairdneri* from *O. m. irideus* is the allelic frequency for the enzyme lactate dehydrogenase at the B2 locus (LDH-B2*). The 100 allele (LDH-B2*100) is characteristic of *O. m. irideus* (and most hatchery rainbow trout) and typically occurs with 80–100% frequency. In contrast, the 76 allele (LDH-B2*76) predominates in *O. m. gairdneri* at about 50–100% frequency in various populations. Assessing a hybrid influence in Harney Basin redband trout is problematic because we do not know the frequency of the 76 allele in the original redband trout. In addition, the earliest form of *O. m. gairdneri* in the Columbia Basin lacked the 76 allele, or had it at low frequencies, similar to *O. m. irideus* (Currens et al. 1990). The earliest redband trout that moved from the upper Columbia Basin into the Harney Basin (about 50,000 years ago or earlier) would be expected to have had the 100 allele. Redband trout arriving in the basin later should have brought in high frequencies of the 76 allele, until the outlet to the Columbia Basin was blocked and the Harney Basin became isolated about 18,000 years ago. In five samples from the Donner und Blitzen drainage, Currens (1997) found a 5–33% occurrence of the 76 allele, with the lowest frequency probably indicating a hatchery rainbow trout. He also sampled two sites on Sawmill Creek (Silver Creek drainage, Figure 1) and reported frequencies of the 76 allele at 20% for the headwater sample and 10% for the downstream area.

The lower section of Sawmill Creek is along a road in a high-use recreational area and received regular stockings of hatchery rainbow trout in the past. I collected specimens from Sawmill Creek in 1972 and noted that these samples showed the most obvious hybrid influence of my Harney Basin collections (Behnke 1992). Berg (1987) sampled three streams in the Silvies drainage and found that the 76 allele occurred at frequencies of 34–53%. The higher frequencies of LDH-B2*76 allele in the Silvies drainage is in agreement with a later transfer of interior Columbia redband trout (characterized by high frequencies of the 76 allele) from the John Day drainage into the Silvies drainage (Bisson and Bond 1971).

Catlow and Guano Basins

With regard to invasion of fishes, the Catlow and Guano Basins are the most isolated basins of the northern Great Basin. Besides the native redband trout, only the tui chub *Gila bicolor* is known to be native. Speckled dace *Rhinichthys osculus* have been found only in Skull Creek, but these were probably introduced as a forage fish into a reservoir near the mouth of the creek. The maximum lake level reached in the Catlow Basin during the last glacial epoch was below a visible outlet channel to the Harney Basin that is evidently from an earlier glacial period and is too precipitous for fish to navigate. Redband trout are found in Threemile, Skull, and Home creeks, small streams that drain the east side of the basin, and in Rock Creek, the largest stream in the basin, which drains from the west (Figure 1).

The Catlow redband trout likely derived from a headwater transfer from the Donner und Blitzen drainage. The Catlow and Harney redband trout are morphologically and genetically quite similar. In 1968, I collected 10 specimens from Threemile Creek that had meristic characteristics generally similar to the 1904 Harney Basin samples, with the exception of fewer scales in the lateral series for the Catlow redband trout (Table 1).

Currens (1997) sampled three sites on Home Creek, two in a lower section and one in the upper section. From upstream to downstream, the frequency of the LDH-B2*76 allele was 13%, 11%, and 5%. If the transfer of trout from the Harney Basin occurred early in the last glacial period (about 30,000–50,000 years ago), I would expect lower frequencies of the 76 allele than would have occurred about 18,000 years ago. At about that time the Harney Basin lost its connection to the Columbia Basin, thereby blocking further entry of the recent form of *O. m. gairdneri* that had high frequencies of the 76 allele. However, small populations such as the redband trout in Catlow Valley streams are subjected to genetic bottlenecks over thousands of generations, whereby allelic frequencies of the ancestral founder can undergo large changes.

In 1968, I observed large redband trout (about 1–2 kg) in Threemile Reservoir attempting to negotiate the silted delta on a spawning migration up the creek. Studies of these redband trout found that they fed on tui chub in the reservoir and grew rapidly (Kunkel 1976; Kunkel and Hosford 1978). The biomass of redband trout in the reservoir (530 kg) was severalfold greater than that in Threemile Creek (60 kg). Silt essentially filled the reservoir in the late 1970s, but the reservoir was dredged in 1998 and enlarged in 1999 to provide redband trout habitat. Prior to the reservoir filling with sediment, an attempt was made to establish a brood stock of Threemile Creek redband trout in a ranch pond for artificial propagation. However, offspring of wild trout are difficult to rear in hatcheries geared for production of domesticated hatchery rainbow trout, and the propagation of these native redband trout was unsuccessful. A few offspring of the Threemile Creek redband trout were sent to the USFWS Bozeman Fish Technology Center for feeding trials. The most efficient food conversion and growth of "ordinary" rainbow trout occur at about 15°C. In contrast, the highest feeding efficiency of the Threemile Creek redband trout occurred at 19°C, which was the highest temperature used in the trials (Dwyer et al. 1981).

Hubbs and Miller (1948) pointed out the considerable isolation between the Guano and Catlow basins. They reproduced a photograph of a channel cut through lava, indi-

[1]Allele designations in Currens (1997) follow the standards of international nomenclature (Shaklee et al. 1990). Synonymous designations by Berg (1987) are: Ldh 75 = LDH-B2*76; Gpi 150 = GPI-B1*138; Lgg 60 = PEPB-1*69.

cating that glacial Lake Guano drained northward to the Catlow Basin, but this connection was probably of an earlier (mid-Pleistocene) connection. An endemic subspecies of chub is the only known fish native to the Guano Basin. Evidently, the Catlow redband trout never had access to the Guano Basin. The headwaters of Guano Creek maintains high quality trout habitat. Stocking records of ODFW indicate that Lahontan cutthroat trout *O. c. henshawi* from Willow Creek of the Whitehorse (or Coyote Lake) Basin were released in Guano Creek in 1957, followed by more Lahontan cutthroat (probably of Heenan Lake, California origin) in 1969, 1973, 1976, and 1978. Rainbow trout were stocked in Guano Creek in 1957, 1962, 1963, 1964, and 1969. I expected to find a hybrid swarm in Guano Creek when I visited the stream in 2006 with ODFW biologists. I was surprised to find that of the many specimens I examined in the field, none was an obvious hybrid. Variation in spotting patterns indicated that the present population was derived from different parental sources, but an influence from rainbow trout was not obvious in the external appearance of the Guano Creek fish. This suggests to me that a form of Lahontan cutthroat trout was already well established in Guano Creek before the first recorded stocking in 1957. In their discussion of the Catlow Basin, Hubbs and Miller (1948) mention "local testimony" (probably from 1939) of a transplant of Alvord cutthroat trout *O. c. alvordensis* from Trout Creek. Because all of the streams in the Catlow Basin contained native redband trout, troutless Guano Creek most likely would have been the stream where Alvord cutthroat were transplanted. Such a transplant would have occurred prior to about 1928, when rainbow trout were stocked into Trout Creek and hybridized the Alvord cutthroat out of existence. I contacted historian Bruce Gilinski, who has studied the history of this area, concerning the presence of trout in Guano Creek before 1957. Mr. Gilinski recalled that as a boy, he and his grandfather camped at the headwaters of Guano Creek soon after WW II (ca. 1946–1947) and they caught trout. I believe there is a strong possibility that the trout caught by Mr. Gilinski were derived from an early transplant of the now extinct Alvord cutthroat. If so, what remains of the Alvord subspecies is incorporated into the trout now found in Guano Creek.

Fort Rock Basin

Three native fishes, redband trout, tui chub, and speckled dace, are found in the Fort Rock Basin. Redband trout are found in the three perennial streams of the basin, Silver, Buck, and Bridge creeks (Figure 1), but in Silver Creek are found only in the lower section downstream of Thompson Reservoir. Brook trout *Salvelinus fontinalis* have replaced the redband trout in the headwaters of Silver Creek. In Buck Creek brook trout were more abundant than redband trout in a sample of fish collected at a road crossing in July 2006. I had not found brook trout in Buck Creek during several previous samplings.

I examined three museum specimens collected in 1897 from Silver Creek and six specimens collected in 1904 from Buck Creek, and in 1968, I collected specimens from Buck and Bridge creeks (Table 1). The most distinctive trait of the 1904 specimens from Buck Creek is that four of the six have basibranchial teeth—a typical key character used to distinguish rainbow trout (basibranchial teeth absent) from cutthroat trout (teeth present). I have found basibranchial teeth in about 3% of all the specimens of northern Great Basin redband trout I have examined. In contrast, 30% of the 1968 Buck Creek specimens and 17% of the Bridge Creek specimens had basibranchial teeth. Basibranchial teeth were not found in specimens collected in Silver Creek in 1897. I suspect that basibranchial teeth occurred at low frequency in the ancestral redband trout that came into the basin but that the frequency increased because of bottlenecks in the small population in Buck Creek.

Redband trout in Buck and Bridge creeks appear to have remained virtually pure, with no or only very slight influence from hatchery rainbow trout. The 1968 specimens from Buck Creek have virtually identical meristic counts as the 1904 specimens (Table 1), with the exception of a lower frequency of basibranchial teeth. The meristic values of the Bridge Creek specimens are similar to those from Buck Creek but with slightly fewer pyloric caeca (Table 1). The relatively high counts of pyloric caeca in Fort Rock redband trout, compared to other populations, suggest that its ancestor came from the Upper Klamath Basin, probably via a headwater transfer in the area of Sycan Marsh, where a low divide presently separates the two basins. A linkage of ancestry between Upper Klamath and Fort Rock redband trout is also supported by genetic data (Currens 1997). The 112 allele for aconitate hydratase (sAH*112), is found at low frequencies only in redband trout of the Upper Klamath and Fort Rock basins (Buck and Bridge creeks) and in no other form of rainbow or redband trout.

Upper Klamath Lake basin

Although the Upper Klamath Basin now drains to the Pacific Ocean via the Klamath River, its native fish fauna, except for three (perhaps four) species of lampreys (*Lampetra*), is derived from the Great Basin (Moyle 2002). Until the end of the Pliocene, about two million years ago, the ancient Snake River flowed to the Pacific Ocean through parts of the Upper Klamath Basin. At about the same time, the Pit River (including the present Goose Lake basin) was a tributary to the Upper Klamath Basin. Lava flows then diverted the Pit River to the Sacramento Basin and changed the course of the Snake River (Minkley et al. 1986). During much of the Pleistocene, Upper Klamath Lake was part of pluvial Lake Modoc, which had a maximum surface area of about 284,000 ha (Dicken 1980). Later in the Pleistocene, the pluvial lake cut through a lava flow and created a connection to the Pacific Ocean via the Klamath River. Downcutting of the outlet eventually resulted in the present Upper Klamath Lake (including Agency Lake) with a surface area of almost 33,000 ha and an average depth of only 2.4 m.

Agency Lake (about 3,500 ha) is connected to the main body of Upper Klamath Lake by a channel and is commonly considered as a separate lake. Spawning runs of the large lacustrine redband trout from Agency Lake spawn in the Wood River. The Williamson River and tributary springs are the spawning grounds for the large redband trout of Upper Klamath Lake.

The connection to the Pacific Ocean allowed for invasions of lampreys, and provided access for the coastal form of steelhead that could have influenced the evolution of the Upper Klamath redband trout. Otherwise, all of the nine species of Catostomidae, Cyprinidae, and Cottidae are derived from inland, not coastal drainage connections. Seven of these nine species are endemic to the basin, including the endemic sucker genus *Deltistes*. Only the ubiquitous tui chub and speckled dace are found in other basins. Although most of the Upper Klamath Basin fish species have been long isolated from their ancestors (since Pliocene–early Pleistocene), the ancestor(s) of the redband trout apparently gained access to the basin via headwater transfers much later, perhaps in mid to late Pleistocene. The native redband trout lacks clear-cut morphological and genetic divergence from other *O. mykiss*.

Although the Upper Klamath Basin redband trout is not strongly differentiated from *O. mykiss* in general, nor from other Northern Great Basin redband trout in particular, it is the only form of *O. mykiss* that maintains distinct lacustrine and fluviatile populations in sympatry. I base this conclusion on meristic distinctions I found between four ancient specimens in the collection of the U.S. National Museum representing the lacustrine form and on 33 specimens representing the fluviatile form collected from three streams in 1968 and 1970. One of the museum specimens was taken from Upper Klamath Lake in 1855 and is the type specimen for "*Salmo newberrii*" (Behnke 1992). The other three specimens were collected from the Williamson River in 1883. The streams sampled in 1968 and 1970 were Whitworth and Trout creeks (Sprague River drainage, Figure 1) and Butte Creek, a disrupted part of the Upper Klamath Basin in Siskiyou County, California.

Although the sample size is only four, there is virtually no overlap of several meristic characters with samples from contemporary fluviatile populations (Table 1). Another distinctive trait of the lacustrine specimens is 12–14 branchiostegal rays. The fluviatile specimens have 9–13 (mean = 11) branchiostegal rays, which is typical for both rainbow and cutthroat trout. The degree of differentiation between the lacustrine redband trout and the resident stream populations clearly indicates that the redband trout evolutionary history in the basin selected for two life histories—a resident stream form and a migratory (adfluvial) lake form. This is similar to the evolution of distinctive adfluvial and fluviatile forms of cutthroat trout in the Lahontan Basin, which has also maintained a continuous lacustrine environment probably since the Pliocene, as evidenced by the lacustrine sucker genus *Chasmistes* of Pyramid Lake.

It is not known if the fluviatile form, with its distinctive meristic traits, occurs in all drainages in the Upper Klamath Basin. For example, in the Lahontan Basin, the fluviatile form of cutthroat trout with diagnostic meristics is restricted to the Humboldt and Quinn river drainages (Behnke 1992, 2002).

There are no unique genetic markers that can diagnose Upper Klamath redband trout as a whole, but some alleles that occur sporadically in Upper Klamath redband trout also occur in redband trout of Goose Lake (and Warner and Chewaucan) basins, such as the tripeptide aminopeptidase 69 allele (PEPB-1*69) and sAH*112 allele also found in Fort Rock redband trout. These alleles are essentially otherwise unknown in all other *O. mykiss*.

The lacustrine form of Upper Klamath Lake redband trout is famed for its large size, with the largest angler-caught fish reported as 11 kg and 86 cm in 1956 (Messmer and Smith 2007, this volume). A spawned-out redband trout measured 94 cm and was estimated to have weighed almost 14 kg before spawning.

Millions of hatchery rainbow trout were continuously stocked in Klamath and Agency lakes and their tributaries for about 50 years starting in 1928 (Messmer and Smith 2007, this volume) and considerable unrecorded stocking probably occurred before 1928. With such massive stocking of hatchery rainbow trout, the persistence of the native redband trout genotype might be questioned. Fortunately, two strong selective factors favor the native redband trout over nonnative hatchery rainbow trout to such an extent that very few of the nonnative trout survived to reproduce.

First, Upper Klamath Lake is hypereutrophic and experiences dense blooms of blue-green algae when the shallow lake warms in the summer, during which pH rises to 9.5–10.5 (Falter and Cech 1991)—conditions that are lethal to nonnative trout. In September 1990, I had the memorable experience of catching and releasing a splendid redband trout from Pelican Bay of Upper Klamath Lake that measured 64 cm and over 2 kg. At the time, the water of Pelican Bay resembled warm, green pea soup.

Second, *Ceratomyxa shasta* occurs in Upper Klamath Lake. This myxosporean parasite is highly lethal to trout that lack resistance. The native redband trout coevolved with this pathogen and is resistant to its effects. Studies conducted in the 1960s demonstrated that few hatchery rainbow trout were surviving in the lake and later studies confirmed the presence of *C. shasta* (Messmer and Smith 2007, this volume). Stocking of hatchery fish into the lake was stopped in 1980. Although I doubt that the lacustrine form of Upper Klamath Lake redband trout could persist in absolute purity, I believe the strong selective factors favoring the native trout have maintained a genotype with little influence from hatchery rainbow trout.

Goose Lake, Warner Lakes, and Chewaucan basins

The redband trout of Goose Lake, Warner Lakes, and Chewaucan basins have a common origin and share distinctive morphological and genetic traits. Goose Lake can be considered as a "semi-isolated" basin of the Northern Great Basin. During extended periods of high precipitation in historical times, the lake level rose and overflowed into the headwaters of the Pit River in California. Seven of the eight native fish species in the Goose Lake basin also occur in the Pit River. The distinctive native redband trout of the Goose Lake basin also occurs in the upper Pit River drainage, but only in tributaries upstream of the confluence with Fall River (e.g., Davis Creek). The native redband trout in the Pit River basin downstream of Fall River and throughout the northern Sacramento River system is sharply differentiated from the Goose Lake redband trout both morphologically and genetically. The Upper Klamath–Pit River–Sacramento basin connection is a plausible explanation for the great diversity found in redband trout native to the upper Sacramento River basin, especially the Goose Lake basin redband trout, the most differentiated redband of the Northern Great Basin. This morphological and genetic differentiation indicates an ancient origin and a long isolation of the Goose Lake redband trout and derivatives found in the Warner Lakes and Chewaucan basins. Besides the redband trout, tui chub, and speckled dace, the Warner Lakes basin also has an endemic species of sucker, *Catostomus warnerensis*. The Chewaucan Basin has been long isolated from invasion of fishes from other basins. The redband trout evidently entered the basin from the Goose Lake or the Warner Lakes basin via headwater transfer. The only other native species in the Chewaucan Basin are the tui chub and speckled dace.

Meristic characters of the native redband trout present prior to introductions of hatchery rainbow trout are based on six specimens collected in 1904 from Cottonwood Creek (Goose Lake), eight specimens collected in 1904 from Honey Creek (Warner Lakes basin), and eight specimens collected in 1897 and 1904 from the Chewaucan River. The museum specimens have mean values of 22 or 23 gill rakers (Table 1), which I assume should occur in any remnant pure populations.

In 1968, I collected specimens from Thomas, Lassen, and Davis creeks in the Goose Lake basin (Figure 1). Gill raker counts in these recent collections were reduced from those of the museum specimens and reflect the influence of a long history of stocking hatchery rainbow trout in these streams.

The meristic characteristics of recent redband trout in the Warner Lakes basin are based on specimens collected in 1968 from Honey Creek (Figure 1). These redband trout retained high gill raker numbers, but the average scale counts were lower than the averages in the 1904 specimens (Table 1). However, specimens in the Oregon State University collection that were collected in the 1980s from Deep and Willow creeks (Figure 1) had reduced gill raker counts (17–22, mean = 20).

Of the redband trout I collected from the Chewaucan Basin (Elder and Dairy creeks, Figure 1), the Elder Creek sample had reduced gill raker counts from the 1904 specimens (Table 1), indicating a hybrid influence. Scale counts were similar to the counts I made on the 1904 specimens from the Chewaucan River. The Dairy Creek specimens also had reduced gill raker counts and reduced numbers of scales in the lateral series compared to the 1904 specimens (Table 1). Elder Creek and, especially, Dairy Creek have easy access, are popular recreational fishery sites, and have a long history of stocking with hatchery rainbow trout. Dairy Creek received annual stocking of hatchery trout until 1997 (Bowers et al. 1999). It is surprising that much, probably most, of the native genotype has persisted, especially in phenotypic appearance. The elliptical parr marks, larger spots, and yellowish body coloration, typical of redband trout, still characterize the redband trout of Elder and Dairy creeks and most of the populations of Northern Great Basin redband trout I have seen. Besides the occurrence of redband trout in the Chewaucan River drainage, an isolated population is known from Foster Creek (Bowers et al. 1999), which drains toward Summer Lake (Figure 1). In July 2006, I accompanied ODFW biologists for sampling of Foster Creek. Its small size, isolation, and difficult access suggest that the Foster Creek redband trout has not been influenced by nonnative trout. In external appearance, these trout represent a pure population of Chewaucan redband trout whose ancestors gained access to Foster Creek from ancient Lake Chewaucan more than 10,000 years ago. The two terminal lakes in the basin, Abert and Summer lakes, are too alkaline for fish life and have been isolated since the end of the last glacial period, when the large pluvial lake in the Chewaucan Basin desiccated.

The populations of redband trout in the Goose Lake, Warner Lakes, and Chewaucan basins that were sampled for genetic analysis by Berg (1987) and Currens (1997) have been long exposed to stocking with hatchery rainbow trout and potential hybridization to varying degrees. However, the genetic data were similar to the morphological evidence in showing the high degree of differentiation of the native redband trout of the Goose Lake, Warner Lakes, and Chewaucan basins and the persistence of native genotypes.

The glucose-6-phosphate isomerase 138 allele (GPI-B1*138) is diagnostic for the native redband trout of the three basins, and likely occurred at or near 100% frequency in the original redband trout before introductions of hatchery rainbow trout. This allele was extremely rare or absent in all other *O. mykiss* analyzed by Currens (1997), but was found at 80–100% frequencies in samples from Beaver, Camp, Cox and Thomas creeks of the Goose Lake basin. Berg (1987) found the 138 allele at 45–95% frequencies in samples from Crane, Thomas, and Buck creeks of the Goose Lake basin, and at 60–85% frequencies in samples from the upper Pit River and lower Goose Lake (Lassen, Davis, Parker, Joseph, and East creeks). In other samples from the Pit River below the confluence with Fall River and from the rest of the Sacramento River basin, the only samples with the 138 allele (1% frequency) were from the upper McCloud River (Berg 1987).

In the Warner Lakes basin, the frequency of the 138 allele was 87% in redband trout from an upstream section of Honey Creek and 75% in redband trout from a downstream section (Currens 1997). The frequency of this allele was 57% in Deep Creek specimens, and was 45 and 70% in two collections from Willow Creek. In the Chewaucan Basin, the frequency of the 138 allele was 75% in redband trout from Elder Creek, 53% in redband trout from Dairy Creek, and 46% in trout from Augur Creek, a tributary of Dairy Creek (Currens 1997).

The GPI-B1* allelic frequencies of contemporary samples can be assessed relative to an assumed 100% occurrence in the original redband trout of the three basins and, combined with comparisons to morphological data (especially gill raker counts), can be useful in evaluating degrees of hybridization between the native redband trout and introduced rainbow trout. For example, of redband trout sampled in recent times from the Warner Lakes basin, the gill raker counts of those from Honey Creek were more similar to the museum specimens (Table 1) than those from Deep and Willow creeks (17–22). The frequency of the 138 allele was also higher in the Honey Creek samples than in samples from Deep and Willow creeks (Currens 1997), suggesting a higher degree of hybridization in the latter streams.

Another genetic marker that probably occurred at high frequencies in the original native trout of the three basins is PEBP-1*69. The 69 allele occurred at 11–47% frequencies (Berg 1987) and at 47–81% frequencies (Currens 1997) in streams of the Goose Lake basin. In Thomas Creek, the only site sampled in both studies, the frequency of the 69 allele was 47%. The frequency of the 69 allele in four tributaries of the upper Pit River and lower Goose Lake was 15–45% (Berg 1987). Low frequencies of the 69 allele (10–13%) occurred in four samples from the Warner Lakes basin (Currens 1997). In the Chewaucan Basin, the frequency of the 69 allele was 10% in specimens from Dairy Creek, compared to 71% in redband trout from Elder Creek. This same allele is found commonly, but sporadically in the Upper Klamath Basin redband trout and occurred at 8% frequency in redband trout from Buck and Bridge creeks of the Fort Rock Basin (Currens 1997). Although the frequencies of the 69 allele in the original populations are not known, it appears that random genetic drift and genetic bottlenecks, in addition to hybridization, have influenced frequencies in contemporary populations.

Discussion and Conclusions

I classified all of the Northern Great Basin redband trout as *O. m. newberrii* in my recent book (Behnke 2002). Bowers et al. (1999) also used the subspecies *newberrii* for these same trout. "*Salmo*" *newberrii* was described in 1858 for the redband trout of Upper Klamath Lake (Behnke 1992). No other species or subspecies names have been proposed for the redband trout of the other basins of the Northern Great Basin. Although classification of all Northern Great Basin redband trout as one subspecies has practical merit, it must be recognized that three distinctly different ancestors gave rise to the present diversity. For a strictly phylogenetic classification, *newberrii* would include only Upper Klamath and Fort Rock redband trout. Different subspecies names would be used for the redband trout of the other basins.

The trout native to the Harney Basin was derived from the Columbia River basin redband trout *O. m. gairdneri* and has been isolated in the Harney Basin for only about 18,000 years. A more recent transfer from the John Day drainage into the Silvies drainage also brought more of the "modern" *O. m. gairdneri* (with high frequencies of LDH-B2*76 allele) into the Harney Basin. The Catlow Basin redband trout is similar to the Harney redband trout from which it is derived, and the redband trout of the Fort Rock Basin was derived from the Upper Klamath Basin. Redband trout in the Goose Lake, Warner Lakes, and Chewaucan basins are the most distinctly differentiated form of redband trout and best conform to the classic definition of a subspecies: that is, populations confined to a defined geographic region and clearly differing from all other subspecies of the species.

In taxonomy, the term polyphyletic subspecies has long been used to group populations of diverse ancestry that share common traits. Thus, the subspecies *O. m. newberrii* as applied to all Northern Great Basin redband trout is a polyphyletic subspecies. The common trait shared by all the Northern Great Basin redband trout that reflects their lacustrine evolutionary heritage is a higher number of gill rakers—typically two or three more gill rakers than found in *O. mykiss* outside this geographic region.

Trout populations living in large lakes with forage fishes commonly evolve specialized predator-prey relations under natural selection for hundreds or thousands of generations and attain a large size. Examples of this are the Lahontan Basin cutthroat trout of Pyramid Lake, the Bonneville Basin cutthroat trout of Bear Lake *O. c. utah*, the Kootenay Lake redband (or "Kamloops") trout, and the Upper Klamath Lake lacustrine form of redband trout (Behnke 1992, 2002). In the Northern Great Basin, the tui chub is the most common and ubiquitous forage fish. Suitable lacustrine habitat for redband trout has been present in the Harney, Warner Lakes, and Goose Lake basins, except during periodic droughts. These semi-continuous lakes have allowed redband trout to at least partially maintain their predator-prey evolutionary heritage. The Catlow, Fort Rock, and Chewaucan basins did not maintain suitable lacustrine environments after the last glacial epoch, but lakes did form in these basins from about 2,000 to 4,000 years ago during a "neoglacial" period. Allison and Bond (1983) reported trout fossils recovered from the present desert floor of the Fort Rock Basin (Fossil Lake) that were deposited when a lake covered the area during this neoglacial period. Although suitable lake environments would have occurred only sporadically in the Catlow, Fort Rock, and Chewaucan basins, tributary streams flowed to terminal marshes that contained tui chub, allowing migratory redband trout to continue their predator-prey interactions after the last glacial epoch. For example, when small redband trout (< 20 cm) enter the reservoir on Threemile Creek in the Catlow Basin, they feed on tui chub and grow rapidly. The average size of the redband trout that were collected for spawning was about 1.5 kg (Kunkel 1976; Kunkel and Hosford 1978).

The hereditary basis for a migratory adfluvial life history that requires a lacustrine environment obviously is not a fixed trait in Northern Great Basin redband trout. A fixed life history trait for migration to lakes in redband trout would have disappeared during drought periods when the shrunken lakes in the Harney, Warner, and Goose Lake basins became uninhabitable for salmonid fishes over several successive generations.

Much is yet to be learned about life history variation in the redband trout of the Northern Great Basin, but a "fluvial" type of life history, with extensive movement in larger streams might exist. For example, fluvial behavior in redband trout from the Donner und Blitzen River would allow for opportunistic migration to Malheur Lake when lake volume is sufficient. Similarly, in larger tributaries of the Goose Lake (e.g., Thomas and Cottonwood creeks) or Warner Lakes (Honey and Deep creeks) basins, migratory fluvial behavior can capitalize on opportunities to greatly increase habitat and forage when lake volumes increase. However, most populations of Northern Great Basin redband trout, especially in small streams isolated by physical or environmental barriers, can be considered as fluviatile. Only in the Upper Klamath Basin, where a continuous lacustrine environment has persisted since the Pliocene, have the true lacustrine or adfluvial form and the fluviatile form evolved to a degree that they can be distinguished from each other by diagnostic meristic traits.

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Evolutionary Diversity in Redband Trout

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Extended Abstract.—The evolutionary diversity of rainbow trout *Oncorhynchus mykiss* east of the Cascade Range, commonly called redband trout, has confused ichthyologists for nearly 150 years. These trout have persisted in a variety of habitats, including large river systems, streams above barrier waterfalls, and ancient, closed lake basins. They have been considered an undescribed species, cutthroat trout, or hybrids of rainbow and cutthroat trout (Behnke 1992). Currently, redband trout within large rivers east of the Cascades have been proposed as different subspecies (Behnke 1992), because they are morphologically and biochemically different from rainbow trout in coastal streams. The relationship of these subspecies to redband trout of Oregon's ancient desert lake basins has been unknown.

This paper examines the evolutionary ecology of rainbow and redband trout within large rivers and ancient lake basins. If ancient lake basins were long-term refuges for redband trout since Pleistocene or early times, endemic isolated populations may be unrecognized subspecies. Alternatively, if these habitats were colonized more recently, redband trout may represent populations of widely distributed inland subspecies from adjacent river systems.

Methods

We examined genetic differences among 11,400 rainbow trout from 243 locations in major basins throughout the Columbia River, northern Great Basin, and adjacent regions (Figure 1) at 28 enzyme encoding loci. We included two nonnative hatchery strains that typified cultured strains that have been widely released into western streams. Nested *G*-tests were used to test for differences among samples among and within major basins. The *G*-test statistic (*G*) divided by the degrees of freedom (df) was used to compare different geographical groups.

Results

Redband trout from different basins were as different from each other as they were from coastal rainbow trout (Figure 2). The major geographical genetic difference among rainbow trout, however, was associated with large river systems, rather than the east-west axis of the Cascade Range or isolation of individual basins. Four major genetic groups emerged from the analysis: (1) Columbia River populations; (2) populations from Goose Lake, Warner Lakes, and the Chewaucan Basin, which were biogeographically related to the Sacramento River (Minckley et al. 1986; Currens 1997); (3) populations from Upper Klamath Lake and River and the coastal Klamath Mountains; and (4) populations from pluvial lake basins in Oregon that were geographically and genetically intermediate between Columbia River and Klamath groups (Figure 2).

Each of the four major geographical groups included populations from different basins of distinctly different evolutionary lineages or subspecies (Figure 1, 2). Differences in allele frequencies among populations from different ba-

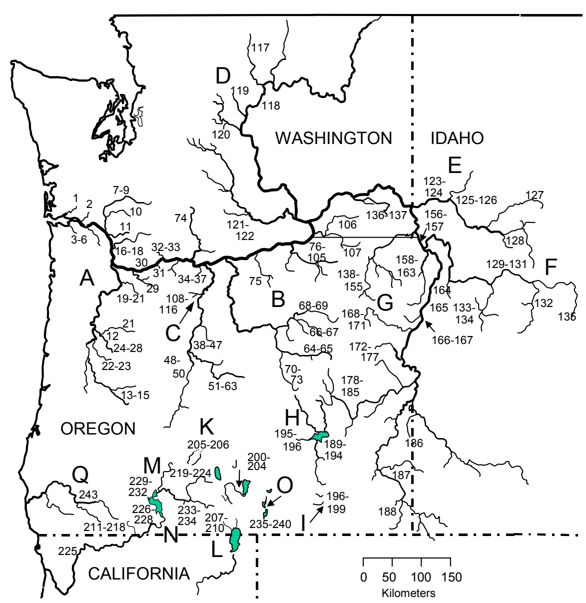

Figure 1.—Locations where rainbow trout were collected. Upper case letters indicate major groups: A, Lower Columbia River; B, Mid-Columbia River; C, White River; D, Upper Columbia River; E, Clearwater River; F, Salmon River; G, Snake River; H, Harney Basin; I, Catlow Valley; J, Chewaucan Basin; K, Fort Rock Basin; L, Goose Lake Basin; M, Upper Klamath Lake headwater populations; N, Upper Klamath River and Lake; O, Warner Valley; Q, Coastal Klamath Mountains.

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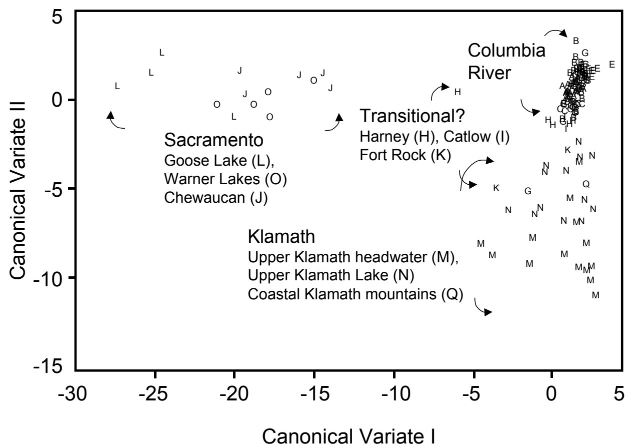

FIGURE 2.—Canonical variate analysis of allozyme variation among major evolutionary groups of rainbow trout. Letters correspond to groups in Figure 1.

sins ($G = 21881$; df = 396; G/df = 55.3) far exceeded differences within basins ($G = 23099$; df = 7458; G/df = 3.1). Major evolutionary lineages within the Columbia River group, for example, included both putative subspecies of redband and coastal rainbow trout, White River redband trout, and Harney Basin redband trout. The Klamath group included two major evolutionary lineages in Upper Klamath Lake and steelhead from coastal rivers of the Klamath Mountains province.

Discussion

Our results showed that redband trout include more major evolutionary lineages or subspecies than previously recognized. In isolated desert basins, we found distinct major lineages, but these were related to those in large river systems. Patterns of genetic diversity observed among redband trout would be expected from periods of isolation, fluctuations in abundance, and local extinctions interrupted by episodes of colonization and gene flow. This suggested a dynamic relationship between large rivers and ancient lakes. Isolation in ancient pluvial lake basins—which have filled, desiccated, and reformed many times (Antevs 1925; Mehringer 1977)—was a source of ecological and evolutionary diversity for redband trout. Large rivers provided long-term sources of stable aquatic habitat and intermittent dispersal of fish to peripheral areas. Fort Rock and Catlow Valley populations, which could not be unambiguously associated with a single major river system (Figure 2), illustrated this dynamic. Fort Rock redband trout reflected multiple hydrological connections and gene flow from lineages in different major river basins (Minckley et al. 1986; Currens 1997). Catlow Valley redband trout, which had very low levels of genetic diversity (Currens 1997), reflected greater geographical isolation from large rivers and genetic drift in small populations.

These results have important implications. Large river systems include both core production areas and peripheral habitats, such as isolated streams and lake basins. If resources are limited, protection of only core areas may conserve long-term production while jeopardizing unique races that evolved in peripheral habitats. Protection of genetically divergent groups may preempt protection of less divergent groups in core areas. Understanding how these fish survived and evolved in core and peripheral habitats, however, can help managers make informed choices.

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Loss of Genetic Variation in Redband Trout Isolated by Ancient and Recent Barriers

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Extended Abstract.—Ecological theory and observation indicate that isolated populations have a much greater risk of extinction than those that are not isolated (Diamond 1984). Most studies of isolated populations—usually on islands—implicate demographic, catastrophic, and genetic causes, including loss of genetic variation and inbreeding associated with founding events and small population sizes (Frankham 1998). Studies of genetic variation of many different kinds of organisms in island populations show that they have lower levels of genetic variation than mainland populations that are not isolated (Frankham 1997).

In Pacific salmon, populations are usually isolated by ancient geological barriers or recently constructed dams rather than by large bodies of water. Once-migratory populations are restricted to islands of habitat above these dams. Although construction of dams clearly reduced abundance of anadromous salmonids, impacts on isolated populations they created have not been well documented. Ecological and genetic theory predicts that these populations should lose genetic variation. Here we examine potential losses of genetic variation by comparing populations of redband trout *Oncorhynchus mykiss* (unique evolutionary lineages of rainbow trout) in free-flowing streams with those recently isolated by dams and those isolated by ancient geological barriers.

Methods

We measured genetic variation in populations of redband trout from the Deschutes, Snake, and Klamath Basins (Figure 1). In each basin, we examined fish from streams below impassable dams constructed during this century, streams above dams that once held anadromous fish, and streams that were isolated by ancient geological barriers. Areas of ancient isolation included the White River (Deschutes River basin), Harney Basin (Snake River basin), and Upper Klamath Lake tributaries (Minckley et al. 1986). Samples with evidence of introgression from introduced hatchery fish were not included. We tested the hypothesis that isolated populations had lower levels of genetic variation than populations not isolated, using *t*-tests on arcsin-transformed values of average heterozygosity and Wilcoxon–Mann–Whitney rank sum tests on the numbers of polymorphic loci, rare alleles, and alleles per locus in each population.

Results

In the Snake River, populations recently isolated above dams had lower levels of genetic variation than populations not isolated, for three of the four measures (Figure 2). Levels of genetic variation in recently isolated populations were similar to those above ancient barriers. In the Deschutes River, populations above dams had fewer numbers of rare alleles than those below dams, but we lacked statistical power to detect differences in other measures. In three of four measures, populations above ancient barriers had lower levels of variation than populations that were not isolated. In the Klamath Basin, patterns of genetic variation were more complex. Populations recently isolated above dams were not significantly different from those below. Populations in areas of ancient isolation had significantly fewer rare alleles and

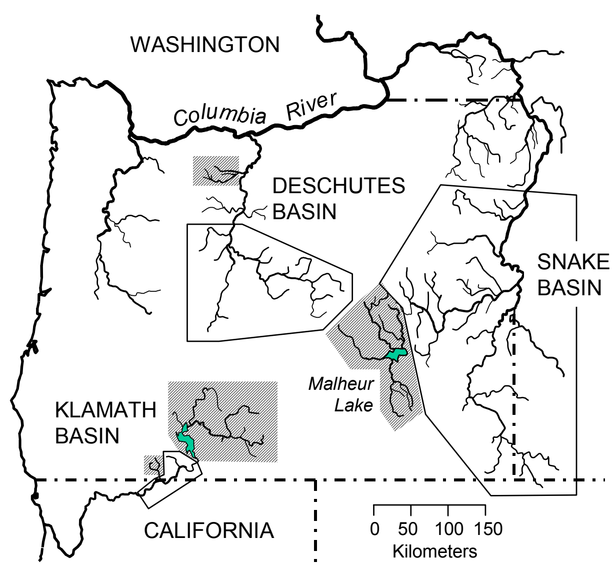

Figure 1.—Study area. Areas isolated by ancient barriers are shaded and those isolated by dams are shown in solid boxes. Samples were collected during 1984–1993 from 50 populations in the Snake River basin, 28 populations in the Deschutes River basin, and 26 populations in the Klamath River basin.

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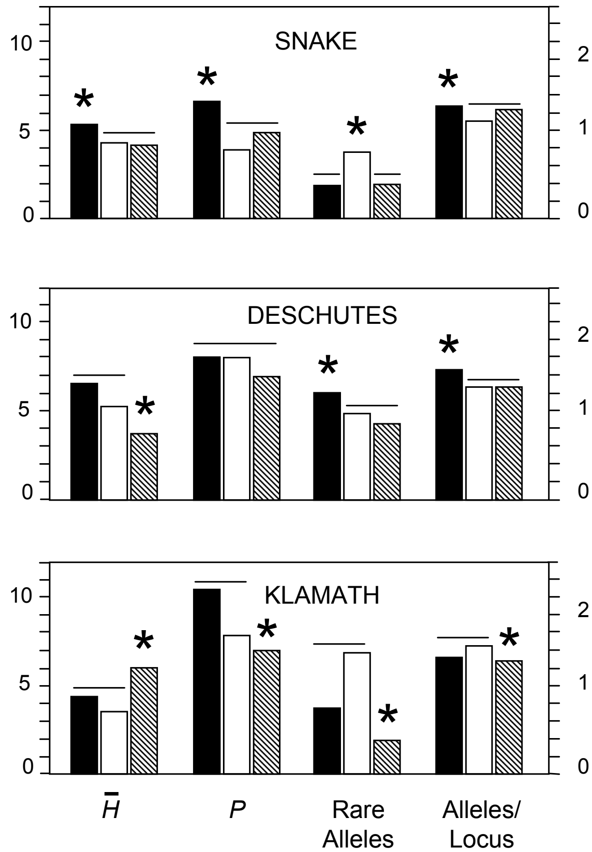

FIGURE 2.—Levels of genetic variation in populations not isolated (solid bars), populations isolated by dams (open bars), and populations above ancient barriers (shaded bars) at 28 enzyme encoding loci. Percent average heterozygosity ($\overline{H}$), number of polymorphic loci (*P*), and number of rare alleles are shown on the left abscissa; number of alleles per locus is on the right abscissa. Asterisks and horizontal bars indicate significant differences ($P < 0.05$) and lack of significant differences, respectively.

polymorphic loci than did those not isolated, but they also had higher levels of heterozygosity.

Discussion

Our studies of rainbow trout supported conclusions from other species that isolated populations have lower levels of genetic variation than those not isolated. These effects can be detected even in populations recently isolated by human activities. This was most obvious in the Snake River, where fish in some tributaries have been isolated by dams for nearly a century. As a consequence of a century of isolation, loss of habitat, and eradication by management agencies interested in stocking other strains of rainbow trout, native populations in these tributaries have apparently lost as much genetic variation as related populations isolated for thousands of years in the Harney Basin. Effects on recently isolated populations were less obvious in the Deschutes River, where main stem dams were closed only 30 years before these samples were collected.

Levels of genetic variation in the Klamath Basin reflected the more complex history of this basin. Although Upper Klamath Lake was at one time isolated from the lower Klamath River, overflows that breached this barrier forming the present upper Klamath River (Moyle 1976) would have provided opportunities for colonization and gene flow. High levels of endemism in Upper Klamath Lake (Minckley et al. 1986) also suggested that fish in this basin may have had long periods of stable habitat with fewer extinctions than in other isolated basins. Additionally, populations below dams have suffered recent declines in abundance, which may have resulted in lost genetic variation. This would confound our ability to infer changes in isolated populations.

Many of these interior basins are at the heart of country where redband trout have thrived (Behnke 1992). Our results indicate that human activities are taking a toll on these populations. Genetic variation is a vital sign of the long-term health of these populations. Ignoring these signs and their demographic and ecological implications will inevitably make conservation of these populations more difficult. Actions to increase population size by reconnecting islands of habitat will help stabilize losses and reduce risks of extinction.

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Redband Trout: Resilience and Challenge in a Changing Landscape
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Phenotypic Variation in Redband Trout

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Abstract.—The redband trout *Oncorhynchus mykiss* is a polymorphic species representing a primitive line of rainbow trout found east of the Cascade Mountain Range. In Oregon, different distinctive populations arose in the Columbia drainage and in the northern Great Basin (i.e., Catlow, Chewaucan, Fort Rock, Goose Lake, Harney-Malheur, Upper Klamath Lake). Some of the differences among populations are due to natural selection, but others may be due to ecophenotypic plasticity. Ecophenotypic plasticity is important because the current emphasis of the Endangered Species Act is to confer protection for genetically distinctive populations rather than distinctive phenotypes. We present evidence that phenotypic plasticity exists in redband trout of Oregon. We argue that unique ecophenotypic traits are important to preserve regardless of their origin, and that the criterion for evolutionary importance based only on genetically determined polymorphisms is incorrect.

The name redband evokes a particular image, a trout with a particular set of distinguishing characteristics associated with the high desert ecoregions of the Intermountain West. Although the group deserves much study, preliminary evidence suggests that the redband trout *Oncorhynchus mykiss* is polymorphic and cannot be easily stereotyped, because it is composed of a wide range of phenotypes expressing different behavioral and physiological traits, life histories, and morphologies (Behnke 2002; Gamperl et al. 2002; Rodnick et al. 2004). How various polymorphic states arose is not understood precisely. However, a discussion of the possibilities has tremendous bearing on conservation strategies. The objectives of this paper are to (1) discuss origins of polymorphism and how they relate to the Evolutionarily Significant Unit (ESU), (2) present evidence for the existence of phenotypic polymorphism in redband trout in Oregon, (3) describe unique characteristics of selected redband trout populations, and (4) discuss how conservation strategies should change to incorporate considerations of ecophenotypic plasticity in addition to measurement of genetic distances using molecular techniques.

Natural selection operates by winnowing unfit phenotypes from the population, and the phenotype is formed from the interaction of the environment with the genotype (Ehrlich and Holm 1963; Williams 1966). Therefore, polymorphic traits can arise within a species via three different means: addition of genes through mutation, deletion of genes (natural selection), or modification of gene expression (ecophenotypic plasticity). Thus, a species complex such as the redband trout, populations of which are dispersed over a broad geographical range and isolated from each other, may diverge because of (1) genetic drift due to founder effect or genetic bottlenecks caused by catastrophic events, (2) lowered outbreeding among populations, and (3) differences in selection pressures among populations.

Phenotypic Diversity

Natural selection is likely responsible for a wide diversity of redband trout phenotypes because of the rich array of habitats they have occupied across their natural range for millennia (Table 1). Some of the physical features that may have shaped phenotypic differences in redband trout are related to climate and climate shifts. For example, the pluvial and interpluvial periods in the Great Basin lasted for tens of thousands of years. As might be expected, some populations in the Great Basin may be better adapted for a xeric climate and higher temperatures that those that evolved in cold constant basins such as the Deschutes Basin. Indeed, recent findings suggest that redband trout in the Little Blitzen River and Bridge Creek are physiologically different in swimming stamina and metabolic power from that reported for other rainbow trout (Gamperl et al. 2002). In fact, Bridge Creek trout had greater metabolic power (ability to do work) above 24°C than at 12–14°C. Analysis of enzyme systems of these trout suggests that the Bridge Creek population is especially well adapted for anaerobic metabolism and life at higher temperatures (Rodnick et al. 2004). In contrast, the Metolius River is renowned because it is cold (approximately 12°C) year around. Its redband trout should be highly stenothermic and an interesting contrast to fish of the Malheur Lake basin.

How trout have adapted to high temperatures is uncertain. Clear experimental evidence for genetically based adaptation to high temperatures is lacking (Thorgaard et al. 2007, this volume). This uncertainty could be the result of a phenotypic

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TABLE 1.—Examples of phenotypic extremes of redband trout populations living in unusual habitats.

Stock, location	Phenotypic characteristic	Reference
Chino Creek, Nevada Swamp Creek, Oregon	Fish angled in 28.3°C water, actively feeding, not overly fatigued when released	Behnke (1992)
Deschutes River, Oregon	Resistance to *Ceratomyxa shasta*	Currens et al. (1997)
Klamath River (Keno reach), Oregon	Healthy populations of large (up to 60 cm) fish in reaches with 25–27°C.	Buchanan (1991)
Klamath River (Keno reach), Oregon	Populations exposed to pH of 9.2–9.6 for extended periods	Buchanan (1991)
Spring Creek (Klamath Basin), Oregon	Populations spawn in all months of year except September	Buchanan et al. (1990)
Goose Lake, Oregon and California	Adfluvial populations persist despite periodic drying of lake: complete in 1926 and 1992, and virtually dry 1929–1934	Federal Register (2000)
Donner und Blitzen River, Oregon	Populations experience diel water temperatures of 7.5–26.5°C	W. Hosford, ODFW (retired), personal communication

response, or it may reflect the difficulty in collecting unequivocal evidence of genetic influence. But genetically based adaptations remain a viable hypothesis and are the subject of current research (Thorgaard 2007, this volume).

Physical habitat that affects spawning also may have helped shaped redband trout phenotypes. Buchanan et al. (1990) counted fresh redds of spawning redband trout every 2 weeks throughout the year in Spring Creek, a tributary of the lower Williamson River and Klamath Lake. They found trout spawning in every month except September. The volcanic explosion of Mount Mazama about 7,700 years ago no doubt covered much of the spawning area in the upper Klamath Basin with dust and pumice. Spawning areas were probably extremely limited and Spring Creek has 300 cfs (8.5 m^3/s) of underwater upwelling sites. We believe that these extreme habitat conditions produced conditions for nearly constant spawning throughout the year, a very different pattern from other populations of *O. mykiss*, which spawn only during the spring. These are not the only examples of phenotypic extremes of *O. mykiss.* The high desert system has several and there are probably others yet to be described (Table 1).

Physical diversity of habitat is not the only driving force in natural selection. Redband trout have co-evolved with different faunal assemblages (Table 2) and biological interactions are a potent evolutionary force (McPeek 1996). Among the distinctive faunal assemblages with which they have evolved are those from Goose Lake, derived from the Pit River fauna of the Sacramento–San Joaquin system; the distinctive Klamath Lake fauna; the Deschutes Basin of the Columbia River fauna; and the isolated endorheic basins of the ancient Great Basin. Each faunal group imposed different types and intensities of interspecific interactions that probably resulted in different evolutionary pathways for the different populations of redband trout. For example, redband trout of the Great Basin evolved in the absence of the northern pike minnow *Ptychocheilus oregonensis*, a predatory minnow found in the Columbia Basin, whereas, redband trout of the Columbia River Plateau co-evolved with this species. The Goose lake redband trout evolved with the Pit roach *Lavinia* [=*Hesperoleucas*] *symmetricus mitrulus* and Goose Lake sucker *Catostomus occidentalis lacusanserinus,* fishes not found in other drainages in Oregon. Klamath redband trout evolved with the Klamath sucker complex and blue chub *Gila coerulea* and tui chub *Gila bicolor*, perhaps promoting the evolution of a piscivorous morph. Redband trout of the John Day Basin evolved with Chinook salmon *O. tschawytscha*, westslope cutthroat *O. clarkii lewisi*, and bull trout *Salvelinus confluentus.* Interspecific competition and niche segregation may have played a more significant evolutionary role in this system than in the Great Basin.

Differential immunity to diseases such as *Ceratomyxa shasta* among different populations results from the relative co-adapted history between parasite and host, and can reinforce differences between gene pools of salmonids (Buchanan et al. 1983). In fact, this type of interaction is one of the reasons that interbasin stock transfers in Oregon are regulated by a Native Fish Conservation Policy and a Hatchery Fish Management Policy. In a sense, differential immunity is an adaptation that one population can use to exert dominance over a competitor. Schroeder (2007, this volume) found that the native redband trout of the Deschutes River are resistant to *C. shasta,* but those isolated above the waterfalls of the White River, which drains into the Deschutes River, are susceptible. The original redband trout in the Metolius River, a tributary of the Deschutes, were presumably resistant. How-

TABLE 2.—Native fishes associated with redband trout from selected eastside basins of Oregon.

Basin	Common name	Scientific name
John Day	**redband trout (resident and anadromous)**	***Oncorhynchus mykiss ssp.***
	Pacific lamprey	*Lampetra tridentata*
	mountain whitefish	*Prosopium williamsoni*
	cutthroat trout	*O. clarkii lewisi*
	chinook salmon	*O. tshawytscha*
	bull trout	*Salvelinus confluentus*
	redside shiner	*Richardsonius balteatus*
	speckled dace	*Rhinichthys osculus*
	longnose dace	*R. cataractae*
	northern pikeminnow	*Ptychocheilus oregonensis*
	mountain sucker	*Catostomus platyrhynchus*
	bridgelip sucker	*C. columbianus*
	largescale sucker	*C. macrocheilus*
	torrent sculpin	*Cottus rhotheus*
	Piute sculpin	*C. beldingii*
Goose Lake	**Goose Lake redband trout**	***O. mykiss spp.***
	Pit–Klamath brook lamprey	*L. lethophaga*
	Goose Lake lamprey	*L. tridentata spp.*
	Goose Lake tui chub	*Gila bicolor thalassina*
	speckled dace	*R. osculus*
	Pit roach	*Lavinia* [*Hesperoleucas*] *symmetricus mitrulus*
	Goose Lake sucker	*C. occidentalis lacusanserinus*
	Modoc sucker	*C. microps*
	Pit sculpin	*Cottus pitensis*
Malheur	**Malheur redband trout**	***O. mykiss spp.***
	Mountain whitefish	*P. williamsoni*
	longnose dace	*R. cataractae*
	speckled dace	*R. osculus*
	redside shiner	*R. balteatus*
	tui chub	*G. bicolor spp.*
	Malheur mottled sculpin	*C. bairdii*
Lake Abert	**redband trout**	***O. mykiss spp.***
	speckled dace	*R. osculus*
	tui chub	*G. bicolor spp.*
Silver Lake	**redband trout**	***O. mykiss spp.***
	tui chub	*G. bicolor spp.*
	speckled dace	*R. osculus*
Catlow	**redband trout**	***O. mykiss spp.***
	tui chub	*G. bicolor spp.*
Warner	**redband trout**	***O. mykiss spp.***
	tui chub	*G. bicolor spp.*
	speckled dace	*R. osculus*
	Warner sucker	*C. warnerensis*

ever, years of stocking of susceptible hatchery rainbow trout led to introgression that left the Metolius River trout intermediate in resistance between hatchery trout and the Deschutes stock (Currens et al. 1997). Stocking of hatchery rainbow trout was discontinued in 1996, so natural selection should allow the pure redband trout genotype to persist in the Metolius. We have illustrated from these examples that polymorphic traits are likely to have evolved as a result of different selection pressures derived from biotic interactions.

Ecophenotypic plasticity is not as widely appreciated as is natural selection by fisheries managers as a mechanism resulting in polymorphism within a population. In contrast, systematists and evolutionary biologists understand such plasticity to be an important mechanism (Dobzhansky 1951; West-Eberhard 1989). The phenotype results from the additive interaction of the environment acting on the genome. This relationship can be expressed as follows:

Phenotypic variance = Environmental variance + Genetic variance + Interaction variance

Thus it is possible that fishes with different traits (physiological performance, shape, life histories) can result from the same genome. This plasticity may be especially important for the genus *Oncorhynchus*, which is tetraploid and in which large gene complexes are possible. Ecologically, this attribute is important because different phenotypes offer specialization, thereby reducing intraspecific competition (Dobzhansky 1951). Polymorphism expands the breadth of resource utilization and can buffer a population from disturbances. A species that can quickly respond developmentally to environmental cues will quickly adapt to uncertain and unpredictable environments. The rule of thumb is that ecophenotypic plasticity (i.e., phenotypic variance attributable to environmental variance) should dominate in uncertain environments, but natural selection should be more responsible for changes in phenotype where conditions change more slowly and predictably. Botanists have found that plants showing the highest phenotypic plasticity have low genetic heterozygosity and inhabit highly variable environments (West-Eberhart 1989).

It is not entirely clear how ecophenotypic plasticity is produced. Speculations are that there may be ontogenetic developmental switches, perhaps regulator genes or pleiotropic effects. However, there are many examples of its existence. The classic study was by Meyer (1987) on cichlids, where he discovered that he could take full sibs and obtain two drastically different morphs, fixed biters vs. suckers, by feeding them different diets. Ontogeny was important because the morphs could be reversed by switching diets up to 8.5 months of age, after which change would not result.

Ecophenotypic plasticity is a characteristic of salmonids. Preeminent among examples is the Icelandic Arctic charr *Salvelinus alpinus* in the Lake Thingvallavatn complex (Skúlason et al. 1989, 1996; Smith and Skúlason 1996). Four morphs are almost indistinguishable with respect to their genetic background. One morph is a small (7–22 cm), snail-eating charr that dwells in the interstitial spaces in the benthos. A second is a large (20–50 cm), epibenthic snail-eating charr. The other two morphs are adapted for the pelagic zone of the lake. They are more streamlined and have more gill rakers. One is a small (14–22 cm) zooplanktivore and the other is its predator, a large (25–60 cm) piscivore. It is important to note that the morphs are locally derived, that transplants of one morph can give rise to other morphs, and that ecophenotypic plasticity seems to follow the general rule. Lake Thingvallavatn is highly variable in food supply. In the Holarctic, *Coregonus–Prosopium* polymorphisms such as morphology of the jaw are associated with food habits (Svärdson 1979).

Other traits may be phenotypic responses to the environment. Life histories are highly plastic among salmonids and are influenced by growth rates (Thorpe 1987a, 1987b, 1989; Huntingford et al. 1988; Metcalfe 1993). For instance, fast growing coho salmon *O. kisutch* smolts mature early as jacks (Gross 1991; Gunnarsdóttir 1992). Precocial dwarfs are found repeatedly in the family Salmonidae, e.g., kokanee–sockeye salmon *O. nerka* and Atlantic salmon *Salmo salar* (Thorpe 1989). Anadromy may be an ecotypic polymorphic trait driven by growth rates of juvenile fishes (Thorpe 1989). The same might be said for "movers vs. stayers", the propensity for an adfluvial life style in some populations (Grant and Noakes 1987).

Management Implications

Why should fisheries managers be interested in phenotypic diversity? First, natural selection acts at the level of the individual or the phenotype (Dobzhansky 1951; Williams 1966). Therefore, phenotypes have selective value and are important in the evolution of the species. Second, unique phenotypes can be derived either through natural selection or through an ecophenotypic response to the environment. Presently, only genetic differences are used to identify populations as distinctive population segments (ESU), which fails to recognize an important second criterion, phenotypic differences (Healy and Prince 1995). Therefore, the risk is that certain important life history types will be ignored. The problem is that unique morphs may arise from early life history exposure to a unique habitat or sets of habitats. These habitats can be lost if the populations using them are not protected by the Endangered Species Act. Skúlason et al. (1989, 1996) argue that ecophenotypic plasticity is how adaptive radiation may proceed during its early stages, that different morphs will be spatially segregated, and traits may accrue that will eventually lead to reproductive isolation of the morphs. By definition then, unique phenotypes are evolutionarily significant despite the lack of genotypic differences.

We would expect ecophenotypic variation to be high in uncertain, unpredictable environments where variation occurs in recurrence intervals of natural disturbances (e.g., drought, flooding, fires) and in system productivity (e.g., ocean upwelling). Ecophenotypic variation may buffer the productivity of the population through uncertain times as well as allow exploitation of many different environments across wide spatial scales. In light of this, it is disturbing to witness the accelerating degree of habitat change across the landscape and to consider what this change will mean in terms of the loss of phenotypic diversity of our salmonids, especially redband trout. We need to modify our approach to Aquatic Diversity Areas in order to protect fishes (Li et al. 1995). We should identify unique phenotypes irrespective of the genetic background. The redband trout is a complex of populations with many phenotypes. It is our responsibility to protect them all. They are all evolutionarily significant.

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Redband Trout: Resilience and Challenge in a Changing Landscape
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Possible Approaches for Genetic Analysis of Temperature Adaptations in Redband Trout

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Abstract.—Although it has been widely assumed that the redband trout *Oncorhynchus mykiss* that live in desert streams have genetically based adaptations for high temperature, clear experimental evidence for this supposition is lacking and could be challenging to collect. The types of tests that could be conducted to test for such adaptations at the organismal, cellular, and biochemical levels are described. If evidence is found for such adaptations, their genetic control could then be examined. Approaches for analyzing the genetic control of differences in temperature response could include heritability studies and associations of measurable traits with candidate genes, possibly including the use of appropriate crosses involving clonal lines.

Some inland strains of rainbow trout *Oncorhynchus mykiss*, known as redband trout, are found in high desert streams, and investigators have proposed that these fish are adapted for high water temperatures (Behnke 1992; Zoellick 1999). This proposal is supported by the periodic elevation of temperatures in these streams above levels normally thought lethal in the rainbow trout species. The failure of introduced hatchery rainbow trout to displace these strains, after repeated introductions in some cases (Wishard et al. 1984), is also consistent with the idea that these redband trout populations harbor unique adaptations. The Rio Santo Domingo rainbow trout of Baja California previously have been proposed as being adapted to high water temperature (Needham and Gard 1959). Tolerance to hypoxia, as well as to high temperature, is likely to be important in adapting to such extreme environments (Vinson and Levesque 1994).

If redband trout do tolerate higher water temperatures than other rainbow trout, a fundamental question is the degree to which such adaptations are genetic or environmental in origin. Fish can acclimate to high temperatures by progressive exposures to increased temperature over time (Dyer et al. 1991; Logue et al. 1995). The degree of genetic or environmental basis for temperature adaptations (or other complex traits) is a complicated issue that requires raising fish with different genetic makeups (genotypes) in common environments and comparing their characteristics.

Questions about a genetic or environmental basis for temperature adaptations in redband trout, and of a genetic basis for adaptations in general, are important for several reasons. First, demonstrating a genetic basis for an adaptation provides an objective case for conservation. If animals from a particular population have a distinctive, inherited adaptation to a specific environment, they likely need to be conserved if the species is to occupy the habitat successfully. Although this adaptation might arise again independently in an introduced population, this is far from certain. Second, demonstrating a genetic basis for an adaptation and understanding the underlying mechanisms can contribute to basic information on the evolution and genetic control of important traits. Third, genetically based adaptations may have potential value in trout breeding programs. It could be easier to select for valuable traits (such as the ability to survive or grow quickly at high temperature) if we understand how the traits are controlled. Cold tolerance has been identified as an important trait for selection in tilapia (Behrends et al. 1990), and heat tolerance could similarly be of importance in extending the range of trout culture.

There are a number of possible tests for temperature adaptations in fishes. All involve examining different species or strains under a range of temperature conditions. These tests may be conducted at the organismal, cellular, or biochemical level. Rainbow trout are among the most well studied of fish species (Thorgaard et al. 2002) and present excellent opportunities for such studies.

Organismal Tests for Temperature Adaptations

The most obvious tests for temperature adaptations at the organismal level are thermal tolerance tests. One such test is a direct survival test, sometimes termed an "LD50" (lethal dose for 50%) study. The upper lethal temperature is known to be correlated to the preferred temperature in fish species (Tsuchida 1995). A related test, the "critical thermal maxima" or CTM test, relies on behavioral rather than survival endpoints for temperature tolerance (Peterson 1993; Bennett and Beitinger 1997; Smith and Fausch 1997). Lethal temperature and CTM appear to be highly correlated (Tsuchida 1995). Differences in temperature tolerance have been documented among salmonid species (Brett 1952; Lee and Rinne 1980; Elliott 1991). However, such trials on redband trout have not shown any difference in survival relative to hatchery rainbow trout strains (Sonski 1983). Redband trout from Threemile Creek (Oregon) used in that study may not be the strain most adapted to high temperatures, and temperatures in the stream are more moderate than in some other redband trout streams such as Chino Creek, Nevada (Behnke 1992). Gamperl et al. (2002) found no differ-

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ence in preferred temperature between two Oregon redband trout strains from streams with different thermal profiles.

Studies of organismal performance, such as growth rate, are another type of whole organismal test. Redband trout from Threemile Creek, Oregon, grown over a range of temperatures at the Bozeman Fish Technology Center in 1981 had significantly faster growth at 19°C than at 16°C (P. Dwyer, U.S. Fish and Wildlife Service, personal communication), which appears to be a different growth pattern than for other rainbow trout strains (Dwyer et al. 1981). Both thermal tolerance and performance studies are challenging to conduct properly because the temperature to which a fish has been acclimated influences its response to temperature.

Development rate is another organismal attribute that could be examined for temperature adaptations. For example, Tallman (1986) showed that the rate of development in chum salmon was dependent on the season of reproduction. One may therefore infer that differences in development rate among strains of salmonids incubated at a common temperature may reflect adaptation to the incubation environment of origin. Adaptations to temperature associated with development rate may be present in order to synchronize emergence of the fry to minimize predation (Godin 1982) or to maximize food availability. Development rate may be measured in a number of ways, including time to hatch, morphological analysis, or patterns of enzyme expression (Ferguson et al. 1985). The heritability of a trait (the proportion of the variation in the trait that is due to genetic factors) is measured by the degree to which relatives have a greater resemblance to each other than to unrelated individuals. (Gjerde 1993). Heritability (h^2) of hatching time ranged from 0.41 to 0.83 in pink salmon (Beacham 1988), and has been reported as high as 0.23 in rainbow trout (McIntyre and Blanc 1973). These relatively high values of h^2 in salmonids indicate that development rate is a quantitative trait upon which selection can have a large effect, thus producing local adaptations to temperature regimes. Significant differences in development rate also have been reported among hatchery strains of rainbow trout (Ferguson et al. 1985). Differences in development rate have been identified among clonal rainbow trout lines (Robison et al. 1999), and these differences have been exploited in mapping studies that have demonstrated that one particular chromosome region has an especially large effect on development rate. Taken together, these data indicate the potential for adaptation to local temperature regimes in rainbow trout. No data are available on development rates in redband trout. It is difficult to predict what development rate might be expected for these fish, as the embryos likely are developing at times when streams in which they live are still cool.

Meristic and morphometric analyses also may be useful in demonstrating temperature adaptation in fish. Variation in morphometric traits may reflect adaptation to particular environments (Hjort and Schreck 1982; Taylor and McPhail 1985; Beacham et al. 1988). Meristics and morphometrics, however, have both a genetic and an environmental component. For example, meristic counts are affected by temperature, such that the number of meristic elements is inversely related to development rate (Garside 1966; Lindsey et al. 1984; Beacham and Murray 1986). This effect also has been shown in clonal fish (Swain and Lindsey 1986). Beacham (1990) found that the heritability of meristic and morphological traits in chum salmon was quite high ($h^2 > 0.33$). Several studies have demonstrated that a significant interaction exists between genotype and environment when meristic traits are examined at multiple temperatures (Murray and Beacham 1989; Beacham 1990). These results suggest an adaptation to a specific temperature regime.

An additional indicator of adaptation to extreme temperatures is developmental stability. Developmental stability is commonly measured by scoring fluctuating asymmetry, which compares the number of bilateral meristic characters (Leary and Allendorf 1989). Fluctuating asymmetry has been suggested for use as an indicator of environmental stress (Valentine et al. 1973; Leary and Allendorf 1989). In chum salmon, increased temperatures resulted in increases in the observed levels of fluctuating asymmetry in three meristic characters (Beacham 1990). This result suggests that developmental stability, as measured by fluctuating asymmetry, could be a useful indicator of adaptation to high temperatures. Fish adapted to high temperatures might be expected to show less increase in fluctuating asymmetry in response to elevated temperatures during development than would fish not adapted to high temperatures.

Gamperl et al. (2002) recently examined swimming performance and metabolism of wild individuals sampled from two Oregon redband trout populations and found that individuals from the cooler stream had better performance at a low temperature (12°C), but that individuals from the two groups had similar performance at a high temperature (24°C). Because the fish were not reared in a common environment, it is not possible to conclude whether this phenotypic difference has a genetic basis.

Cellular and Biochemical Tests for Adaptation

If genetic evolution of thermal tolerance has occurred in redband trout, it likely has been associated with the regulation or modification of genes associated with normal cellular or biochemical function. Numerous cellular and biochemical assays exist that could be used to investigate adaptation to higher thermal tolerance in redband trout.

At the cellular level, the thermal tolerance of an organism could be assessed using cultured or isolated cells (Mosser et al. 1986; Goldspink 1995). The inactivation half-life of myofibril cells isolated from fish has been correlated to the temperature range to which a species was adapted (Goldspink 1995).

At the biochemical level, specific proteins or protein families are integral to the survival of organisms in variable environments (Powers et al. 1991). Foremost among these are the heat-shock family of proteins. Heat-shock proteins act as molecular chaperones, assisting in folding and assembly of other proteins or in the repair or degradation of damaged proteins (Parsell and Lindquist 1993). Both constitutive and inducible forms are found in all organisms and are crucial for cellular survival. The constitutive forms are found in cells under normal conditions. Their structure has been conserved throughout evolution, even maintaining a high degree of sequence similarity between forms in eukaryotes and prokaryotes. The inducible forms are expressed during times of stress, with heat being a major inducer. Inducible forms have shown diversity within and between species of fish, and may allow for evolution in changing environments (White et al. 1994; Norris et al. 1995).

The regulation of inducible heat-shock proteins could change in two ways to increase the thermal tolerance of an organism. First, the induction temperature of heat-shock proteins is closely related to the physiological optima of the organism (Dyer et al. 1991; Norris et al. 1995), and therefore an upward change in the induction temperature could provide protection against higher temperatures. This type of change could be important in redband trout because even if their upper tolerance has not changed, it is likely that they experience higher average temperatures and may have a higher preferred temperature. Secondly, the abundance of inducible heat-shock proteins has been correlated to increased survival time at a lethal temperature in fish and likely provides better protection at sublethal temperatures (Norris et al. 1995). Characterizing the inducible heat-shock proteins in rainbow and redband trout could provide insights into the role these proteins play in possible thermal tolerance of redband trout.

Another important biochemical adaptation is the ability of the muscles to efficiently contract over a range of temperatures. Coolwater fish such as carp can survive and maintain a high activity level over a wide range of temperatures. Carp express a different set of myosin genes at low versus high temperatures in order to maintain contractile force of the muscles over a wide range of temperatures (Goldspink 1995). Multiple copies of myosin genes exist in fish, but it is unknown if salmonids express alternate cold and warm isoforms. Given the tetraploid ancestry of salmonids (Allendorf and Thorgaard 1984), it is possible that redundant forms of this or other proteins have evolved different optimum temperatures. Such specialization of duplicated genes is a possible mechanism for the evolution of a thermal-tolerant salmonid.

Enzymes have been shown to be adapted to the ambient temperature of the fish species (Gelman et al. 1992). For example, Florida largemouth bass have enzymes more adapted to high temperature than do northern largemouth bass (Philipp et al. 1983). Gamperl et al. (2002) found some differences in enzyme activities between redband trout from two Oregon streams with different temperature profiles, but because the fish did not experience common environments it is not possible to conclude if the differences were genetic in origin or were environmentally induced. An additional test for adaptation among populations would be to sequence the DNA coding for enzyme loci and to test for non-synonymous substitutions. If the Ka (non-synonymous)/Ks (synonymous) ratio is greater than 1 (the neutral expectation), it indicates selection at that locus (Nei and Kumar 2000). Expression of different forms of enzymes can be another mechanism of temperature adaptation in fish (Lin and Somero 1995).

Additional physiological factors that may be important to the ability to withstand high temperatures include the composition of lipids in the cell, the proteins associated with this process (Hazel 1990; Logue et al. 1995), and overall levels of membrane fluidity (Hazel 1993). Lipid changes are involved in the development of temperature tolerance on an individual level and modulation of these responses could also be important on an evolutionary scale.

The demonstration of biochemically based adaptations in redband trout would provide a firm basis for their conservation and provide insights into the evolution of organisms faced with a changing environment. After performing organismal, cellular, or biochemical tests, we must determine whether there are statistically significant differences among the groups. If differences are found among groups that have been exposed to common environmental conditions, we can conclude that these differences are due to the genotypes.

Genetic Analysis of Differences

If a genetically based difference is found among groups (for example, a difference in temperature response between redband trout and other rainbow trout strains), the next question is, What is the genetic basis for the difference? Classically, the common view has been that differences in complex traits are likely to be related to many gene differences, and to be strongly influenced by the environment. Such "quantitative trait" differences usually have been examined by controlled mating designs in which individuals are produced with varying degrees of relatedness. Using these techniques, Meffe et al. (1995) demonstrated that temperature tolerance is a heritable trait in mosquitofish.

Recent developments in examining the genetic basis of differences include efforts to associate complex traits with particular genes or genetic markers. This approach of quantitative trait locus (QTL) analysis has become possible because of the ability to mark chromosomes in plants and animals using DNA technologies, and the realization that complex traits frequently are strongly influenced by a limited number of genes. DNA markers examined may be random in nature (Spruell et al. 1994; Olsen et al. 1996; Young et al. 1998) or may involve "candidate" genes that can be logically hypothesized to have a relation to the trait of interest (e.g., heat-shock genes for traits related to temperature response). Such studies currently are more advanced in plants and in some other animals than in fishes, but they are also beginning to be applied to fishes.

One approach for genetic analysis that has been quite successful in both plants and animals has been the use of inbred or homozygous lines (Burr and Burr 1991; Silver

TABLE 1.—Homozygous rainbow trout lines currently being propagated at Washington State University.

Line	Sex	Characteristics
Arlee	Male (YY)	Domesticated. Low nonspecific cytotoxic cell activity (Ristow et al. 1995).
Clearwater	Male (YY)	Semi-wild. Anadromous. Derived from wild steelhead, North Fork Clearwater R., Idaho in 1969 and propagated in freshwater at Dworshak National Fish Hatchery, Idaho before release and migration to the ocean. Six generations of freshwater captive rearing.
Hot Creek	Male (YY)	Domesticated.
Oregon State University	Female (XX)	Domesticated. Only fertile homozygous female line.
Swanson R.	Male (YY)	Semi-wild. Derived from wild rainbow trout on Kenai Peninsula, Alaska in the early 1980s. Three generations of full life cycle captive rearing.
Skookumchuck R.	Male (YY)	Semi-wild. Anadromous. Derived from wild steelhead, Skookumchuck R., Washington and propagated in a hatchery there before release and migration to the ocean
Klamath Lake	Male (YY)	Semi-wild. Derived from wild rainbow trout, Williamson R., Oregon (a tributary of Klamath Lake).

1995). Such lines have the advantage of uniformity in response over time and location. Important traits have been genetically analyzed using inbred or homozygous lines in a number of crop species (Burr and Burr 1991) and in mice (Silver 1995). It is possible to rapidly generate homozygous lines in rainbow trout and other fishes using chromosome set manipulation methods (Young et al. 1996). We are currently propagating seven clonal lines of rainbow trout and plan to use them to genetically analyze traits differing among the lines (Table 1).

Ultimately, our approach for genetic analysis of differences among the rainbow trout lines will be modeled on the approaches using homozygous lines that have already been used successfully with other systems (Silver 1995). If readily analyzed differences and sufficient numbers of genetic markers are available, it is possible to determine if differences among the lines are caused by a few major genes or many genes, and whether specific "candidate" genes are involved. The development of a genetic map of DNA markers for rainbow trout (Young et al. 1998; Sakamoto et al. 2000; Nichols et al. 2003) facilitates studies to map trait differences within the species. Differences in development rate among our rainbow trout clonal lines (Robison et al. 1999) have been genetically analyzed to demonstrate that some chromosome regions have especially large effects on differences among the lines (Robison et al. 2001). This leaves the question of which gene or genes within those regions are having these effects. Similar approaches could be used to genetically characterize temperature responses in redband trout. Quantitative trait loci associated with thermal tolerance have recently been identified in some crosses of rainbow trout (Perry et al. 2001), and these regions also might be tested for associations in controlled crosses involving redband trout.

The question of whether redband trout indeed have a genetically based adaptation to high temperature is still unresolved. We have outlined some of the possible approaches for investigating this important issue. In any case, it is clear that these are distinctive, native fish that merit protection in the challenging habitats where they survive.

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Effectiveness and Applicability of EMAP Survey Design in Status Review of Great Basin Redband Trout

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Extended Abstract—The redband trout *Oncorhynchus mykiss* ssp. occurs in interior basins of the Pacific Northwest. Oregon's Great Basin populations of redband trout persist in fragmented habitats that are a result of the area's geologic history, more recent hydrologic cycles of flood and drought, and anthropogenic disturbance. Concern about the status of these fish prompted the development of a new approach to accurately estimate the distribution, abundance, and biomass of resident redband trout in six geomorphically isolated basins of eastern Oregon (Table 1).

The large geographic area (42,000 km^2) of these basins and discontinuous distribution of fish in each basin was not conducive to population estimation methods based on *a priori* census of habitats (e.g. Hankin and Reeves 1988). Therefore, an alternative method that coupled accurate results at the individual basin scale with sample efficiency at a landscape scale was necessary. A sample design that combined statistical rigor with spatial distribution was developed and employed using procedures standardized by the U.S. Environmental Protection Agency's Environmental Monitoring and Analysis Program, or EMAP (Stevens and Olsen 2004).

Methods

Information on redband trout distribution was compiled from field biologists and was incorporated into a database that tracked source and type of data (field verified or professional opinion). This distribution was input into a Geographic Information System (GIS) and became the sampling universe for selecting sample sites (Figure 1). The GRTS (Generalized Random-Tessellation Stratified) design (Stevens and Olsen 2004) is a powerful survey design for stream networks because sites are selected in a spatially balanced array with variable probability of site selection across multiple basins—an approach that was developed by the Environmental Protection Agency for use in EMAP. Sites can be replaced if the selected sites cannot be visited, and post-stratification of sample sites is possible.

The goal of the study was to assess the status of redband trout by estimating the abundance of fish age 1 and older (designated age 1+) in each of the six basins, within 95% confidence intervals of $\pm$ 50%. A minimal sampling intensity of 35 sites per basin was chosen (210 for the six basins) based on levels of between-site variance in abundance estimates of age-1+ Great Basin redband trout from previous sampling (*Coefficient of Variation* as high as 150%, unpublished data J.M.D.). A base sample of 35 sites in each of the six basins was selected, with an "over sample" of 35 sites per basin to replace sites that could not be visited. Replacement sites were similar in location, size, elevation, and ownership to sites not sampled, to preserve the spatial balance (by selecting nearby sites) and to avoid introduction of possible bias.

We used a "local variance estimator" (Stevens 2003), which takes advantage of any spatial autocorrelations in the abundance of redband trout, to generate more precise estimates of variance than those obtained with the Horvitz-Thompson algorithm (1952). Uncertainty in estimates of total abundance also comes from sampling error of the fish survey method (electroshocking), although it is a minor component of the total variance in the population estimates.

Field sampling was done by two three-person crews that sampled an average of two sites per day. Each sample site was roughly located with topographic maps, after which the fine-scale proximity was determined with handheld GPS units. Sample reaches were enclosed with blocknets separated a distance of about 20 stream widths. Removal-depletion estimates of fish abundance were made within the netted reach of stream channel (Dambacher et al. 2001).

Results and Discussion

We sampled 185 sites in the six basins, representing about 1% of the stream distance occupied by redband trout. The estimated abundance of age-1+ redband trout was about 970,000 fish ($\pm$ 146,000 or 15%) (Table 1). Population estimates for age-1+ fish in individual basins ranged from 57,270 ($\pm$ 13%) in the Silver Lake basin, to 435,045 ($\pm$ 29%) in the

Table 1. —Population estimates of age-1+ Great Basin redband trout with 95% confidence limits (CL) expressed as percent of estimate.

Basin	Population estimate	± 95% CL
Silver Lake	57,270	13%
Lake Abert	149,103	30%
Goose Lake	98,409	26%
Warner Valley	171,715	28%
Catlow Valley	59,771	14%
Malheur Lakes	435,045	29%
Total	971,313	15%

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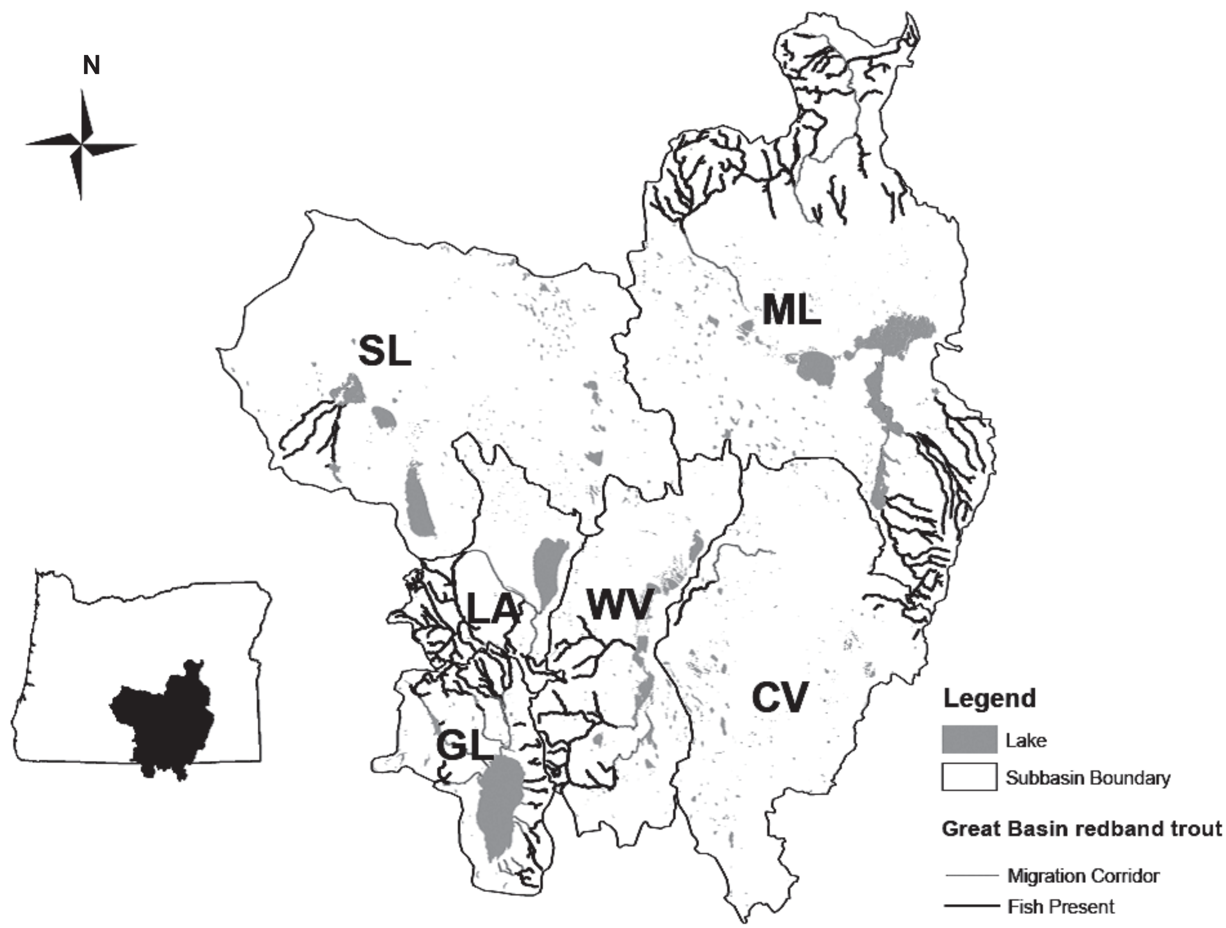

Figure 1.—Stream reaches identified in the mapping process as containing year-round rearing habitat (fish present category) for age-1+ redband trout. These stream reaches became the universe from which sample sites were selected. SL = Silver Lake; ML = Malheur Lakes; LA = Lake Abert; WV = Warner Valley; CV = Catlow Valley; GL = Goose Lake.

Malheur Lakes basin. The stream channel distance supporting year-round rearing for redband trout was estimated to be 2,167 km in the six basins (Figure 1), with another 1,017 km estimated to be used as migration corridor. A more detailed account of these estimates is available in Dambacher et al. (2001). Use of the local variance estimator reduced the 95% confidence interval an average of 30% for each basin compared to a simple random sample variance estimator.

A comprehensive query of data archives and professional opinion allowed us to approach a landscape assessment of an aquatic species within narrow time and financial constraints. Other landscape assessment techniques such as GAP (Kagan et al. 1999) require an extensive investment of time and resources in the development of data sets that may be used to model features of interest. The actual population assessment required a GIS approach for mapping and site selection, but would not have been reliable without the statistical tools developed for EMAP by EPA for the assessment of spatially balanced and randomly sampled sites. The GRTS sample design allowed us to maximize the statistical power of a relatively limited number of samples. The combination of all these tools made the spatial assessment of redband trout at a landscape scale possible and cost effective. The result was a novel approach to a common problem. This approach has the potential for broad application to species whose geographic distribution is widespread and discernible.

The sampling design was not suitable for examining fine-scale distribution of redband trout, because we sampled just 0.2 to 3.7% of the stream habitat in the six basins. A denser sample selection or census survey might have identified locally extirpated subpopulations or highlighted discontinuous distributions, although it was impractical at such a large scale. The decision by the U.S. Fish and Wildlife Service not to list Oregon's Great Basin redband trout as threatened or endangered was based partially on our estimated abundances of the fish in each of the six basins. Although the overall population of redband trout in the Great Basin may be considered viable, the vulnerability to extirpation of a spatially isolated subpopulation or a life history strategy within this widely distributed species may not be detectable with this survey design.

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Distribution and Status of Redband Trout in the Interior Columbia River Basin and Portions of the Klamath River and Great Basins

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Abstract.—We summarized existing knowledge (circa 1996) of the potential historical range and the current distribution and status of non-anadromous interior redband trout *Oncorhynchus mykiss* ssp. in the U.S. portion of the interior Columbia River Basin and portions of the Klamath River and Great Basins. We estimated that the potential historical range included 5,458 subwatersheds and represented about 45% of the species' North American range. Two forms of interior redband trout were considered, those sympatric with steelhead *O. mykiss* ssp. and allopatric forms that evolved outside the range of steelhead. Data were compiled from existing surveys and expert opinions of over 150 biologists during the scientific assessment for the Interior Columbia River Basin Ecosystem Management Project (ICBEMP). We also predicted fish presence and status in unsampled areas, using statistical models to quantitatively explore relationships among redband trout status and distribution, the biophysical environment, and land management. Redband trout had the highest likelihood of being present or supporting strong populations in mid-size or smaller streams, of higher gradients, in highly erosive landscapes with steep slopes, with more solar radiation, and mean annual air temperatures less than 8–9ºC. Variables reflecting the degree of human disturbance within watersheds (road density, land ownership, and management emphasis) were also important. Redband trout remain the most widely distributed native salmonid in the ICBEMP assessment area and the second most widely distributed native fish, occupying 47% of the subwatersheds and 64% of their potential range. Sympatric redband trout are the most widely distributed of the two forms, present in an estimated 69% of their potential range. Despite their broad distribution, important declines in distribution and status are apparent from our analysis, although finer scale extirpations of redband trout populations were more difficult to quantify. Both forms of redband trout have narrower distributions and fewer strong populations than historical populations; neither form supported strong populations in more than 17% of their potential ranges. Habitat degradation, habitat fragmentation, and non-native species introductions are primary factors that have influenced status and distribution. Because of the likelihood of introgressive hybridization with introduced salmonids, actual status of some strong populations may be worse than suggested. Although much of the potential range has been altered, core areas remain for conserving and rebuilding more functional aquatic systems in order to retain the ecological diversity represented by redband trout. Protection of core areas critical to stock persistence and restoration of a broader matrix of productive habitats will be necessary to ensure the full expression of phenotypic and genotypic diversity in interior redband trout. We recognize the limitations of this database and acknowledge that estimates based on expert opinion and modeling involve inherent uncertainties. A more refined synthesis of redband trout distribution and status will require documentation, consistency, and rigor in sampling and data management that does not currently exist.

Rainbow trout *Oncorhynchus mykiss* are a widely distributed salmonid native to western North America. Little consensus exists on the taxonomic nomenclature for the groups. Currens et al. (2007, this volume) suggested the species should be segregated into at least four groups: (1) Columbia River populations; (2) populations from Goose Lake, Warner Lakes, and the Chewaucan Basin; (3) Upper Klamath Lake and River and coastal Klamath Mountain populations; and (4) populations from pluvial lake basins in Oregon. Other taxonomists have suggested three groups (Behnke 1992): (1) Coastal rainbow trout west of the Cascade/Sierra mountain divide; (2) Interior Columbia River redband trout upstream of Celilo Falls, including the Fraser and Athabasca rivers in Canada, the upper Klamath River Basin, and the

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isolated interior basins of Oregon; and (3) the Sacramento–San Joaquin redband trout. Although the systematics of redband trout are in dispute, genetic and physical characteristics support the view that these groups warrant subspecies recognition (Allendorf 1975; Utter and Allendorf 1977; Allendorf and Utter 1979; Allison and Bond 1983; Berg 1987; Stearley and Smith 1993).

Here we consider the interior redband trout native to the interior Columbia River Basin and portions of the Klamath River and Great Basins. Redband trout have two distinct life histories, anadromous (steelhead) and non-anadromous. In this paper, we confine our analysis to non-anadromous redband trout *O. mykiss* ssp.. Thurow et al. (2000) describe the distribution and status of steelhead *O. mykiss* ssp. in the same assessment area.

Interior redband trout exhibit broad phenotypic diversity including varying age-at-maturity, frequency and timing of spawning, seasonal timing and patterns of migration, longevity, habitat selection, temperature tolerance, and a host of other characteristics. Life histories of redband trout are variable. At least three forms have been described, including adfluvial and fluvial migratory forms and resident forms. Adfluvial redband trout (such as Kamloops rainbow trout) migrate from lentic waters to tributaries and were historically present in Canadian lakes, Crescent Lake, Washington and several isolated lake basins within the Northern Great Basin in Oregon (Moyle et al. 1989; Behnke 1992). Fluvial redband trout remain in flowing waters throughout their entire life cycle and inhabit streams ranging from low-order tributaries to large rivers, compared to resident forms that have more restricted movements. Because redband trout have persisted in a variety of biophysical settings, other life history adaptations may exist (*see* Thorpe 1994). Movement among habitats and populations may be an important mechanism for maintenance of genetic variability in populations (Leary et al. 1992) and for their persistence in variable environments (Rieman and Clayton 1997; Rieman and Dunham 2000). Local adaptation and selection for unique alleles resulting from isolation, however, may also be important to total genetic variability in the species (e.g., Lesica and Allendorf 1995; Gamperl et al. 2002). Introgressed forms of redband trout, hybrids with introduced cutthroat trout *O. clarkii* or coastal rainbow trout, have replaced native redband trout in some areas today (Currens et al. 1997; Neville et al. *in preparation*).

As a result of declines in abundance and distribution, the interior redband trout is considered a species of special concern by the American Fisheries Society (Williams et al. 1989) and in all states within the historical range, and is classified as a sensitive species by the USDA Forest Service (Forest Service) and USDI Bureau of Land Management (BLM). In 1994, the Kootenai River redband trout in northern Idaho and Montana was petitioned for listing under the Endangered Species Act of 1973 (ESA). The USDI Fish and Wildlife Service (USFWS) determined that listing was unwarranted because there was insufficient information to identify the Kootenai River population as a distinct population segment. A 1997 petition to the USFWS to list redband trout in the Catlow, Fort Rock, Harney, Warner Lakes, Goose Lake, and Chewaucan basins of eastern Oregon was also denied. Concerns for the persistence of other redband trout stocks in the interior Columbia River Basin have culminated in several listings under the ESA (www.nwr.noaa.gov/ESA-Salmon-Listings). The final rules list only anadromous forms because of inconclusive data regarding the relationship between steelhead and non-anadromous redband trout. Upper Columbia River steelhead were listed as endangered in 1997 and downgraded to threatened in 2006. Snake River Basin steelhead were listed as threatened in 1997, Lower Columbia River steelhead were listed as threatened in 1998, and Middle Columbia River steelhead were listed as threatened in 1999, with all three listings reaffirmed in 2006.

Despite concerns for the species persistence, the distribution and status of redband trout across their range are poorly defined. One goal of the Interior Columbia River Basin Ecosystem Management Project (ICBEMP) (Quigley and Arbelbide 1997) was a comprehensive evaluation of the status and distribution of fishes (Lee et al. 1997). In this paper we describe the potential historical range and the current (as of 1996) distribution and status of redband trout in the U.S. portion of the interior Columbia River Basin and portions of the Klamath River and Great Basins, hereafter referred to as the ICRB. We also describe 1996 conditions and consider factors likely to influence the species' future.

Methods

The ICBEMP confined our analysis to the United States portion of the interior Columbia River Basin east of the Cascade crest and portions of the Klamath River and Great Basins (Figure 1). The area includes over 58 million ha in Idaho, Montana, Nevada, Oregon, Washington, and Wyoming, of which 53% is administered by the Forest Service or BLM (Quigley et al. 1996). Lee et al. (1997) and Rieman et al. (1997b) provide detailed descriptions of the hierarchical system of subbasins, watersheds, and subwatersheds and the ecological reporting units we used. Topography was used to define subbasins averaging 356,500 ha surface area, watersheds averaging 22,800 ha, and subwatersheds averaging 7,800 ha (Figure 1). Subwatersheds were the smallest sample unit used in our analysis of fish distributions. These divisions follow the hierarchical framework of aquatic ecological units described by Maxwell et al. (1995). The study area also was subdivided into 13 broad geographical regions known as Ecological Reporting Units (ERUs) (Lee et al. 1997) (Figure 2). The ERUs were delineated based primarily on the distribution of potential vegetation types and broad zoogeographical boundaries to aquatic and terrestrial organisms.

Sympatric and allopatric forms of non-anadromous redband trout were assessed separately. We considered allo-

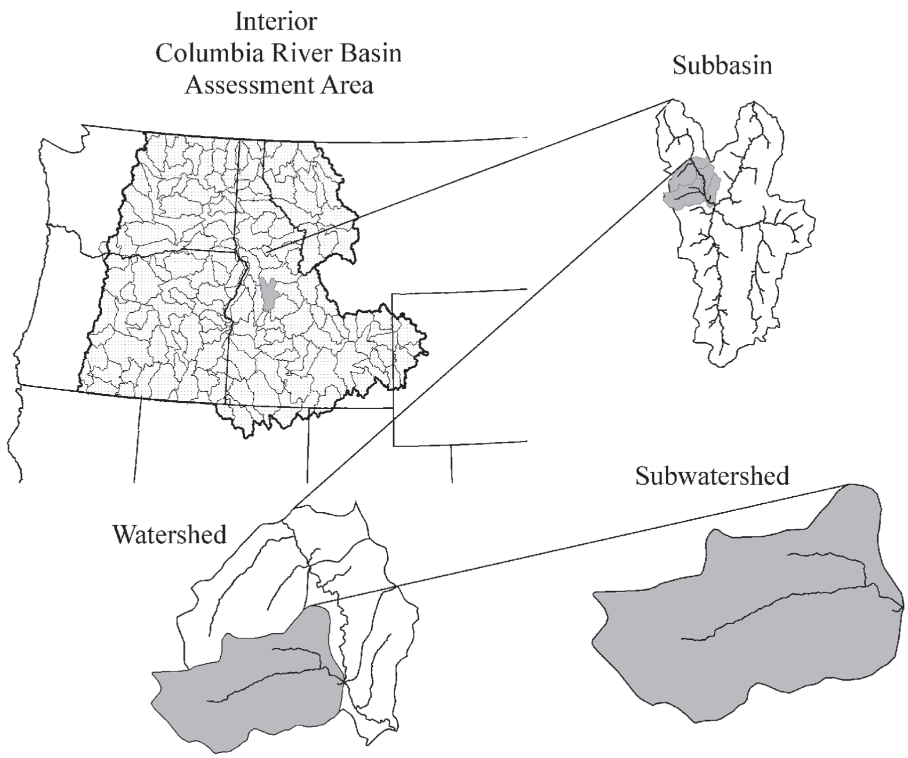

Figure 1.—The interior Columbia River Basin in the U.S. and portions of the Klamath River and Great Basins and the hierarchy of hydrologic units used in the analysis.

patric redband trout those that evolved outside the historical range of steelhead and assumed that this form was evolutionarily distinct from other redband trout because of isolation. We considered sympatric redband trout to be the non-anadromous form historically associated with steelhead. A non-anadromous form is likely to exist in sympatry with steelhead (Busby et al. 1996). Morphologically, anadromous and non-anadromous redband trout juveniles are indistinguishable, so we relied on knowledge of established barriers to anadromy to define the range for the allopatric form. The distribution of small populations of allopatric redband trout isolated from, but within the general range of steelhead (for example, above natural barriers in 2nd- and 3rd-order streams) was not addressed.

Known Status and Distribution

We held a series of workshops in 1995 and asked more than 150 biologists from across the ICRB to characterize the status and distribution of native salmonids including redband trout. Participants were asked to use existing information to classify the status of naturally reproducing populations in each subwatershed within their jurisdiction. If populations were supported solely by hatchery-reared fish, naturally spawning fish were considered absent. Biologists classified subwatersheds where fish were present as spawning or rearing habitat, overwintering or migratory-corridor habitat, or as supporting populations of unknown status. Subwatersheds supporting spawning and rearing were further classified as strong or depressed. Strong subwatersheds include those where: (1) all major life histories that historically occurred within the watershed are present; (2) numbers are stable or increasing, and the local population is likely to be at half or more of its historical size or density; and (3) the population or metapopulation within the subwatershed, or within a larger region of which the subwatershed is a part, probably contains at least 5,000 individuals or 500 adults. When no information was available to judge current presence or absence, the subwatershed was classified as status unknown. Because non-anadromous redband trout and juvenile steelhead were indistinguishable and the level of genetic or behavioral segregation between them is unknown (Busby et al. 1996), we classified the status of sympatric redband trout as unknown when steelhead were present. Unknown also was the default classification in the absence of survey responses or information from prior databases, or where there were conflicting responses between the survey and electronic databases that could not be resolved. We asked biologists to rely on biological characteristics and to not infer status from habitat or landscape information or presence of introduced fishes. Where possible, classifications were reviewed by others familiar with the area in question and we attempted to use only the most current information.

The resolution of our data may produce estimates of current distributions that are more optimistic than work based on stream reaches (Rieman et al. 1997b). Redband trout were considered present in the entire subwatershed if they occurred

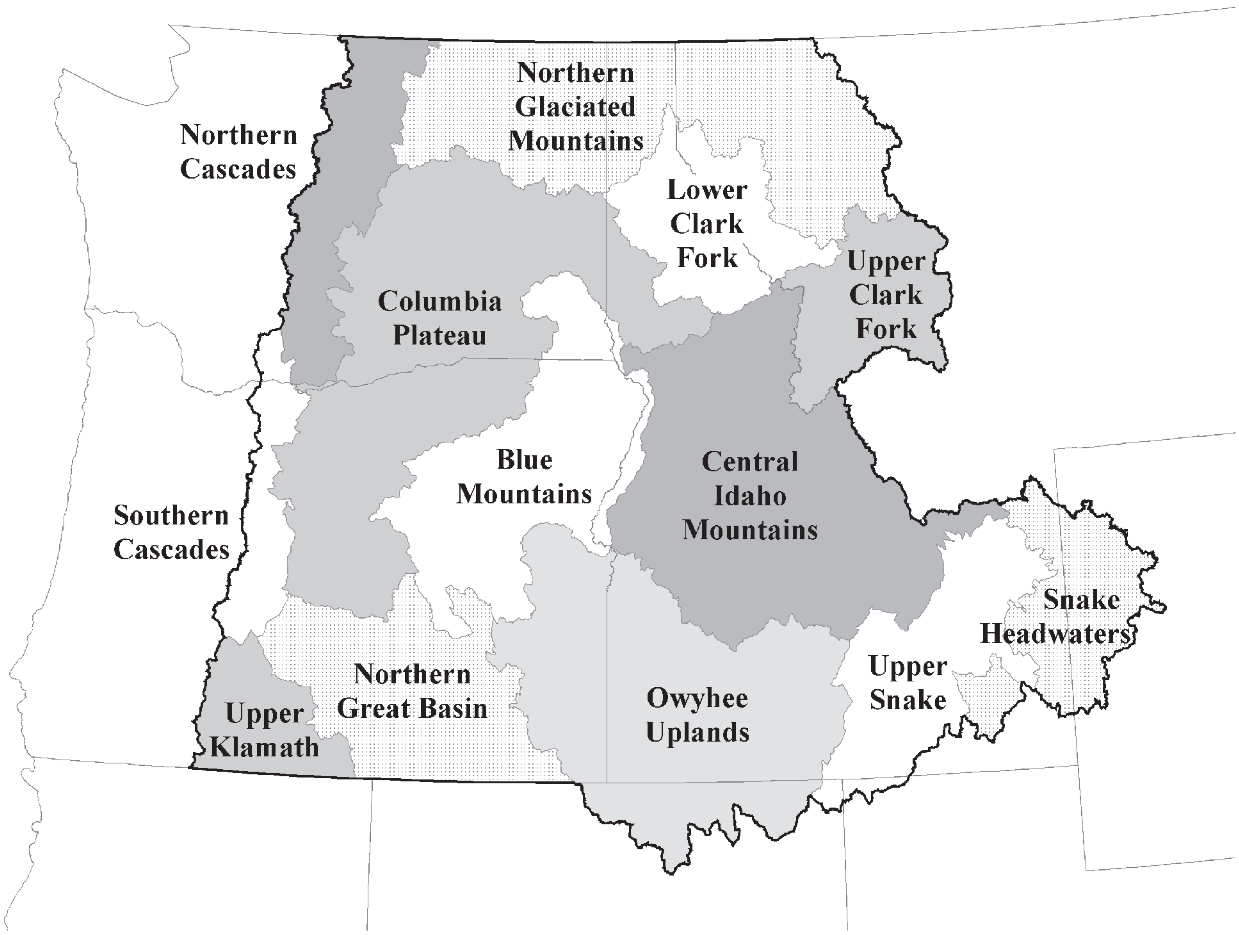

Figure 2.—Ecological reporting units (ERUs) used to summarize information across broad regions of similar biophysical characteristics in the interior Columbia River Basin in the U.S. and portions of the Klamath River and Great Basins, adapted from Lee et al. (1997).

anywhere within it. Because redband trout have the potential for extended movement and dispersal (Moyle et al. 1989), subwatersheds provide an appropriate sampling unit for a large-scale analysis. To minimize bias, distributions were based on the number of occupied subwatersheds.

Potential Historical Range

Potential historical ranges, hereafter referred to as potential ranges, were defined as the likely distributions in the ICRB prior to European settlement. Potential ranges were characterized from historical distributions in prior databases and augmented through published and anecdotal accounts. The potential range of all forms of redband trout included freshwaters west of the Rocky Mountains, extending from northern California to northern British Columbia, Canada (Figure 3). What may be a primitive form has been found in the Athabasca and Peace River drainages on the east flank of the Rocky Mountains (Carl et al. 1994). We did not consider the distribution of redband trout in Canada, but they are believed to have been present throughout the upper Columbia River Basin with the exception of the upper Kootenai River Basin above Kootenai Falls (Behnke 1992; E. Parkinson, British Columbia Ministry of Environment, personal communication). Redband trout were widely distributed and occupied most waters from the southern desert basins to the high mountain coniferous forests (Cope 1879, 1889; Jordan 1892; Gilbert and Evermann 1895; Jordan and Evermann 1896; Snyder 1908; Jordan et al. 1930; Behnke 1992). Hubbs and Miller (1948) and Behnke (1992) speculated that a wet cycle in the Pleistocene could have allowed redband trout to move from the Columbia River Basin to the upper Klamath River and several of the closed desert basins along the southern margin of Oregon.

We included all subwatersheds that were accessible as potential range based on known current and historical occurrences because redband trout can be highly mobile, moving through subwatersheds, watersheds, subbasins, and basins at different life stages seasonally (Moyle et al. 1989). Subwatersheds that were known to be historically isolated by barriers to movement were excluded from potential ranges. We recognize that, within subwatersheds, the potential range may be further restricted by elevation, temperature, and local channel features but did not attempt to define potential ranges at a finer resolution.

Figure 3.—Native range of interior redband trout in North America. Distributions outside the interior Columbia River Basin in the U.S. and portions of the Klamath River and Great Basins were adapted from Behnke (1992).

Predictive Models

We produced a set of predictions using statistical models, called classification trees (Breiman et al. 1984), that reflect the likelihood of redband trout presence, or the likely status of the population, within unsampled or unknown subwatersheds. Our objective was to generate a complete picture of the current distribution and status of redband trout by quantitatively exploring relationships among fish distribution, the biophysical environment, and land management. Lee et al. (1997) and Rieman et al. (1997b) provide a detailed description of classification trees and the fitting, cross-validation, and pruning routines. We summarized 28 variables with the potential to influence aquatic systems from more than 200 landscape variables available across the ICRB (Lee et al. 1997). Quigley and Arbelbide (1997) describe the variables and their derivations in detail. Rieman et al. (1997b) list the categorical and continuous variables we used to represent vegetative communities, climate, geology, landform and erosive potential, land management history, and relative intensity of human disturbance.

Two separate classification tree models were built for redband trout. In the first tree (Presence model), known status was reduced to a binomial variable by combining all presence calls (present-strong, present-depressed, or transient in migration corridor) into a single "present" call (Lee et al. 1997). A second tree (Status model) was constructed with a trinomial response to distinguish spawning and rearing areas (present-strong or present-depressed) from non-spawning areas. Present-strong and present-depressed were retained as two separate responses, while migration corridors and absence were combined into a third response as absent. Trees were used to estimate the probability of presence or absence of redband trout in subwatersheds classified as unknown and to predict status in subwatersheds classified as unknown or present-unknown. All estimates and predictions were limited to the potential range.

We summarized known and predicted status and distribution of redband trout across the ICRB. We estimated the percentage of the potential range currently occupied by comparing the number of occupied subwatersheds to the total subwatersheds in the potential range. Because areas supporting strong populations are potentially critical for short term persistence and long term recovery, we summarized subwatersheds supporting known or predicted strong populations and defined them as strongholds. We estimated the percentage of the potential and current range supporting strongholds by comparing subwatersheds with strongholds to the total number of subwatersheds in the potential and current ranges. We mapped distributions and strongholds using a geographic information system (GIS). To estimate the proportion of the current distribution in protected status, we summarized the number of occupied subwatersheds within National Park Service lands and in designated wilderness areas.

Results

Potential Historical Range

The potential range of redband trout included 77% of the ERUs and 73% of the subwatersheds in the ICRB (Tables 1, 2). This area includes 5,458 subwatersheds and represents about 45% of the species' North American range (Figure 3). The only major areas of the ICRB that did not support redband trout were the Snake River upstream from Shoshone Falls, tributaries to the Spokane River above Spokane Falls, Rocky Mountain basins in Montana excluding the Kootenai River, and portions of the northern Great Basin in Oregon (Figure 4). Only six subwatersheds were identified exclusively as corridors (Tables 1, 2). Sympatric redband trout were the most widely distributed form, occupying an estimated 59% of all subwatersheds and all but four ERUs (Table 1; Figure 4). Allopatric redband trout were less widely distributed, occupying an estimated 40% of all subwatersheds (Table 2; Figure 4).

Known Status and Distribution

Based on our synthesis, redband trout appear to have remained relatively widely distributed. We estimated that they were known to be present in 55% of the subwatersheds in the potential range (Tables 1, 2). Populations of redband trout remained in some portion of all ERUs in the potential range. Sympatric redband trout were believed present in 59% of the potential range (Table 1; Figure 4). Strong populations of the sympatric form were judged to be present in 5% of the potential range and 9% of the current range. Allopatric redband trout were estimated to be present in 40% of the potential range, with strong populations in 7% of the current range (Table 2; Figure 4).

Despite their broad occurrence, the distribution and status of redband trout was unclassified or unknown in many subwatersheds. About 27% of the sympatric redband trout potential range and 39% of the allopatric redband trout potential range was not classified (Tables 1, 2). Another 41% of the sympatric redband trout potential range and 23% of the allopatric redband trout potential range was judged to support redband trout, but too little information was available to evaluate status. As described above, our inability to differentiate juvenile steelhead and sympatric redband trout was a principal reason for the unknown status of sympatric redband trout.

Predictive Models

Two classification models were developed from 1,793 subwatersheds with complete fish status and landscape information. The Status model for classifying status of red-

Table 1.—Summary of classifications (number of subwatersheds) of occurrence and status for sympatric redband trout throughought Ecological Reporting Units of the study area.

				Status where present					
Ecological Reporting Unit	Total	Potential historical range	Total present	Strong	Depressed	Unknown	Transient in migration corridor	Absent	Unknown or no classification
Northern Cascades	340	292	222	5	4	213	0	7	63
Southern Cascades	141	125	107	25	38	44	0	19	4
Upper Klamath	175	35	8	0	0	8	0	0	27
Northern Great Basin	506	0	0	0	0	0	0	0	0
Columbia Plateau	1,089	796	398	23	94	278	3	148	250
Blue Mountains	695	643	534	35	69	427	3	23	86
Northern Glaciated Mountains	955	258	180	21	3	156	0	31	47
Lower Clark Fork	415	98	67	3	17	47	0	8	23
Upper Clark Fork	306	0	0	0	0	0	0	0	0
Owyhee Uplands	956	898	279	38	154	87	0	283	336
Upper Snake	301	0	0	0	0	0	0	0	0
Snake Headwaters	387	0	0	0	0	0	0	0	0
Central Idaho Mountains	1,232	1,051	693	66	146	481	0	43	315
Entire study area	7,498	4,196	2,488	216	525	1,741	6	562	1,151

Table 2.—Summary of classifications (number of subwatersheds) of occurrence and status for allopatric redband trout throughought Ecological Reporting Units of the study area.

				Status where present					
Ecological Reporting Unit	Total	Potential historical range	Total present	Strong	Depressed	Unknown	Transient in migration corridor	Absent	Unknown or no classification
Northern Cascades	340	48	31	0	0	31	0	2	15
Southern Cascades	141	0	0	0	0	0	0	0	0
Upper Klamath	175	140	36	0	10	26	0	0	104
Northern Great Basin	506	405	99	2	49	48	0	165	141
Columbia Plateau	1,089	254	67	1	62	4	0	62	125
Blue Mountains	695	52	40	13	26	1	0	10	2
Northern Glaciated Mountains	955	198	101	4	10	87	0	21	76
Lower Clark Fork	415	1	1	0	0	1	0	0	0
Upper Clark Fork	306	0	0	0	0	0	0	0	0
Owyhee Uplands	956	58	32	2	13	17	0	4	22
Upper Snake	301	0	0	0	0	0	0	0	0
Snake Headwaters	387	0	0	0	0	0	0	0	0
Central Idaho Mountains	1,232	106	93	13	2	78	0	1	12
Entire study area	7,498	1,262	500	35	172	293	0	265	497

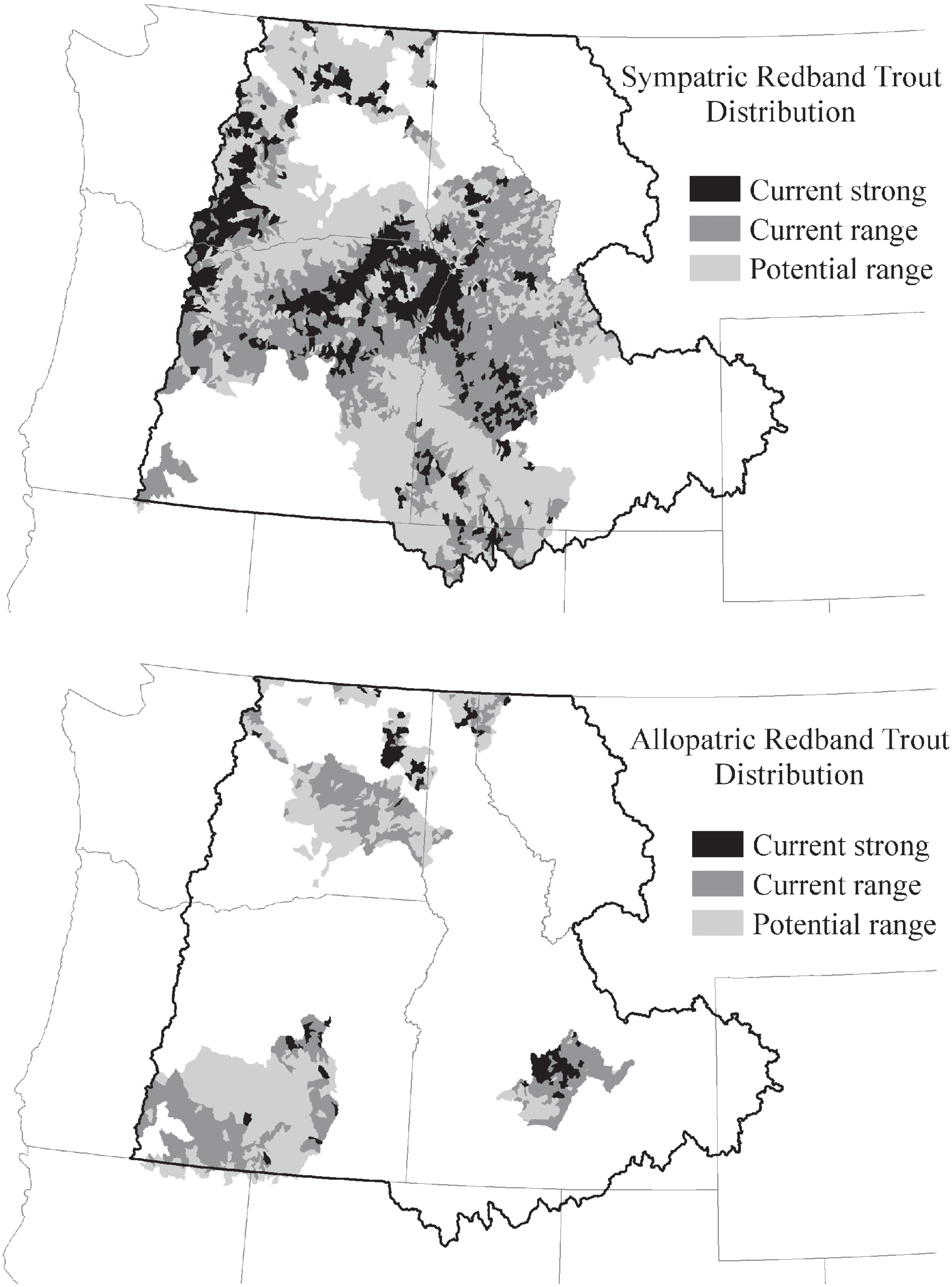

Figure 4.—The potential historical range, known and predicted current range, and known and predicted strong populations of sympatric redband trout (top) and allopatric redband trout (bottom) within the interior Columbia River Basin in the U.S. and portions of the Klamath River and Great Basins.

band trout in spawning and rearing areas (strong, depressed, absent) had an overall classification success rate of 76% and was most successful classifying absent (83%) followed by depressed (74%) and strong (58%) (Table 3). Nineteen variables were used in the model and five explained a major portion of the deviance (a measure of variation in categorical variables, Lee et al. 1997) (Table 4). Variables were: *management class* based on land ownership and management emphasis, *slope* was area-weighted average midslope based on 90 m digital elevation maps, *anadromous access* was accessible to anadromous fish (yes or no), *ecological reporting unit*, and *hucorder* was the number of upstream subwatersheds tributary to the subwatershed of interest. Redband trout were more likely to be present in spawning and rearing areas in mid-size or smaller streams within landscapes with steep slopes in certain ERUs. The relationship between redband trout status and anadromous access was less clear. As explained above, we considered the status of sympatric redband trout unknown when steelhead were present. Biologists were able to classify redband trout status in 119 subwatersheds with anadromous access, and redband trout had similar likelihood of being present (0.54) as absent (0.46) in spawning and rearing areas (Table 4). Variables potentially reflecting the degree of human disturbance within watersheds (management class) were also important. Redband trout were four times less likely to be present in spawning and rearing areas and more than five times less likely to be strong in subwatersheds within private and federal grazing lands and private agricultural lands compared to private and federal forest lands, moderately grazed Forest Service lands, or tribal lands (Table 4).

Table 3.—Cross classification comparison of predicted and reported status and occurrence of both forms of redband trout pooled across the study area. Tables represent comparisons for a model of status within spawning and rearing areas (top) and for presence and absence (bottom) across the potential historical range.

	Predicted status in spawning and rearing areas			
Reported status	Absent	Depressed	Strong	Total
Absent	688	134	9	831
Depressed	117	525	70	712
Strong	32	73	145	250

Misclassification error rate = 435/1,793 = 24%

	Predicted occurrence across range		
Reported occurrence	Absent	Present	Total
Absent	749	76	825
Present	255	713	968

Misclassification error rate = 331/1,793 = 18%

The second model had an overall classification success rate of 82% when limited to presence or absence (Table 3). Of the sixteen variables used in this model, five explained a major portion of the deviance: *mean annual precipitation* in mm; *base erosion index* representing relative surface erodability without vegetation; *mean annual solar radiation* based on topographic shading, latitude, and aspect; *ecological reporting unit*, and *mean annual air temperature* (Table 5). Redband trout were more likely to be present in subwatersheds with precipitation greater than about 38 cm, highly erosive landscapes, higher solar radiation, and mean air temperatures less than 8.7ºC (Table 5).

Overall, the patterns suggested by the classification models were consistent with our understanding of redband trout biology and habitat use. The frequency of physiographic and geophysical predictor variables within the models suggests that biophysical setting is an important determinant of redband trout distribution and habitat suitability. The importance of management class suggested a negative influential effect of human disturbance.

Based on these analyses we used the two models to estimate the probability of occurrence of sympatric redband trout in 1,151 subwatersheds that were previously unclassified and to predict status (strong, depressed, absent.) in those subwatersheds and an additional 1,741 subwatersheds where fish were present of unknown status (Table 1; Figure 5). We used the classification models to estimate the probability of occurrence of allopatric redband trout in 497 subwatersheds that were previously unclassified and to predict status in those subwatersheds and an additional 293 subwatersheds where fish were present of unknown status (Table 2; Figure 6).

Known and Predicted Status and Distribution

After combining the known and predicted subwatershed classifications, we estimated that sympatric and allopatric redband trout jointly occupy 47% of the ICRB and remain in 64% of their combined potential historical range (Figure 4; Tables 6, 7). Sympatric redband trout are the most widely distributed of the two forms; their estimated distribution includes 69% of the potential range (Tables 1, 6; Figure 4). The largest areas of unoccupied potential habitat include the Owyhee Uplands and Columbia Plateau. Allopatric redband trout are not as widely distributed and are currently estimated in 49% of the potential range (Tables 2, 7; Figure 4). Allopatric redband trout are least well distributed in the Northern Great Basin and Columbia Plateau, where they are believed absent in 71% of the potential range (Tables 2, 7).

Despite their broad distribution, relatively few strong redband trout populations were identified (Figures 5, 6). We estimated that 78% of the subwatersheds in the current range of sympatric redband trout supported spawning and rearing and 31% were classified as strong (Table 6). Strong populations were present in 17% of the potential range and 24% of the current range. Allopatric redband trout had fewer strong populations. We estimated that 94% of the subwatersheds in the current range of the allopatric form supported spawn-

Table 4.—The first 11 nodes of a classification tree for redband trout status (absent, depressed, strong) showing discriminating variables, sample sizes, splitting criteria, and frequency distributions within spawning and rearing areas in 1,793 subwatersheds used to develop the model. Nodes and accompanying data are hierarchical and represent the structure of a tree. The root node represents the complete distribution. The first split occurs at mngclus (management class, based on ownership and management emphasis) and produces nodes 2 and 3 that are further independently subdivided. Node 2 includes BLM (BR) and private (PR) grazed lands, Forest Service high impact lands with grazing (FH), and private agricultural lands (PA). Node 3 includes Forest Service moderately impacted and grazed lands (FG) and high impact lands with no grazing (FM), managed wilderness (FW), Forest Service and private forest lands (PF), and tribal lands (TL). Other variables included: slope (area weighted average midslope), eru (ecological reporting unit), hucorder (number of upstream subwatersheds), and anadac (access for anadromous fish). See Lee et al. (1997) for further information.

				Relative frequencies		
Node (Variable and criteria)	Sample size	Deviance	Modal class	Absent	Depressed	Strong
1) root	1,793	3578.0	A	0.4635	0.3971	0.1394
2) mngclus: BR, FH, PA, PR	1,254	2107.0	A	0.5981	0.3437	0.05821
4) slope < 9.9835	757	961.5	A	0.7411	0.2417	0.01717
8) eru: 4,7,10	464	460.5	A	0.8362	0.1487	0.01509
9) eru: 1,2,5,6,13	293	444.2	A	0.5904	0.3891	0.02048
5) slope > 9.9835	497	964.0	D	0.3803	0.4990	0.1207
10) hucorder < 144	460	887.5	D	0.3304	0.5391	0.1304
11) hucorder > 144	37	0.0	A	1.0000	0.0000	0.0000
3) mngclus: FG, FM, FW, PF, TL	539	1067.0	D	0.1503	0.5213	0.3284
6) anadac < No	420	716.6	D	0.0619	0.5857	0.3524
7) anadac > Yes	119	252.4	A	0.4622	0.2941	0.2437

Table 5.—The first 11 nodes of a classification tree for redband trout presence (P) or absence (A) showing discriminating variables, sample sizes, splitting criteria, and frequency distributions within 1,793 subwatersheds used to develop the model. Nodes and accompanying data are hierarchical and represent the structure of a tree. The root node represents the complete distribution. The first split occurs at pprecip (mean annual precipitation), node 2 is < 380.3 mm compared to node 3 that is >380.3 mm. These two nodes are further independently subdivided. Other variables included: baseero (base erosion index), solar (mean annual solar radiation), and mtemp (mean annual air temperature). See Lee et al. (1997) for further information.

Node (Variable and criteria)	Sample size	Deviance	Modal class	Absent	Present
1) root	1,793	2474.00	P	0.46010	0.53990
2) pprecip<380.296	840	1021.00	A	0.70360	0.29640
4) baseero<5.637	432	372.80	A	0.84490	0.15510
8) eru:2,5,6,7	99	126.00	A	0.66670	0.33330
9) eru:4,10	333	219.60	A	0.89790	0.10210
5) baseero>5.637	408	560.90	A	0.55390	0.44610
10) mtemp<8.707	254	349.50	P	0.44880	0.55120
11) mtemp>8.707	154	180.50	A	0.72730	0.27270
3) pprecip>380.296	953	1062.00	P	0.24550	0.75450
6) solar<277.231	258	357.40	A	0.51550	0.48450
7) solar>277.231	695	576.20	P	0.14530	0.85470

ing and rearing and 20% were classified as strong (Table 7). Strong populations were estimated in 9% of the potential range and 18% of the current range. Model predictions tended to be spatially correlated with known conditions. That is, predicted strong populations were more likely to occur in proximity to known strong populations and predicted depressed populations in proximity to known depressed populations (Figures 5, 6).

Of the 3,500 subwatersheds that supported either form of redband trout, about 10% were in protected status within National Park Service or designated wilderness (Tables 6, 7). About 9% of the 816 subwatersheds supporting strongholds for either redband trout form were in protected status. For sympatric redband trout, 12% of the present distribution and 10% of the strongholds were within lands of protected status (Table 6). The most secure portions of the distribution were found within the Central Idaho Mountains (25% of the current range and 15% of the strongholds in protected status), the Northern Cascades, and the Blue Mountains ERUs. For allopatric redband trout, less than 4% of the current range and less than 3% of the strongholds were within lands of protected status (Table 7). Subwatersheds supporting allopatric redband trout were secure only within the Northern Cascades ERU, where 55% of the current range and the one stronghold were in protected status.

Discussion

Limitations of our Approach

Our analysis has several important limitations. As de-

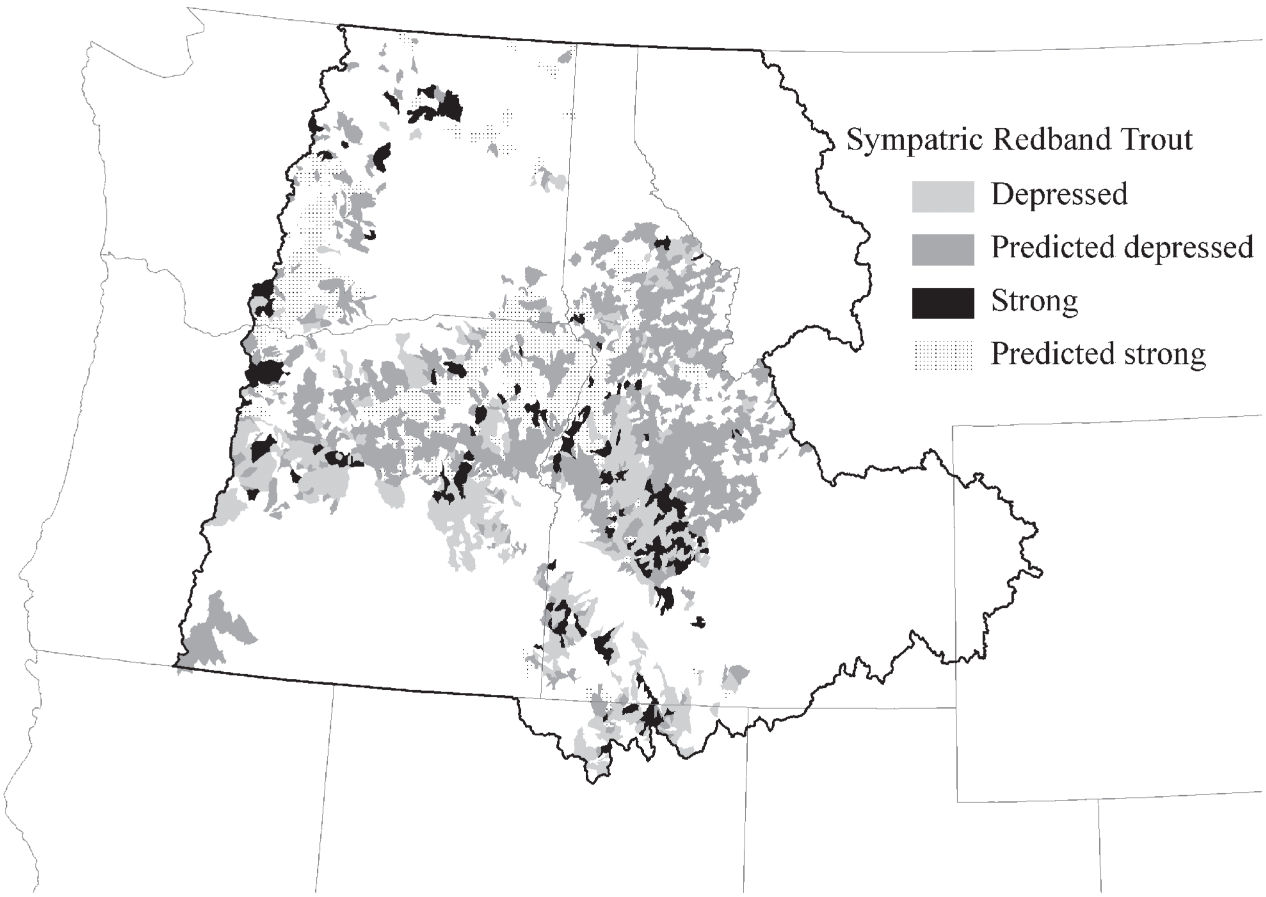

Figure 5.—Known and predicted classifications of status for sympatric redband trout within spawning and rearing areas in the interior Columbia River Basin in the U.S. and portions of the Klamath River and Great Basins.

scribed above, the ICBEMP (Quigley and Arbelbide 1997) mandated a comprehensive evaluation of the status and distribution of fishes within a clearly defined area. Consequently, we described the potential historical range and the current distribution and status of redband trout only within the interior Columbia River Basin and portions of the Klamath River and Great Basins, and omitted other important areas within the range of redband trout (i.e., in California and Canada).

Secondly, many of the "known" subwatershed classifications relied on expert opinion rather than actual surveys. We predicted fish presence and status in areas classified as "unknown," using statistical models to quantitatively explore relationships among redband trout status and distribution, the biophysical environment, and land management. As noted above, where possible, classifications were reviewed by others familiar with the area in question and we attempted to use the most current (circa 1996) information. Despite criteria for classification and review, an element of subjectivity remains in the data and inconsistencies in judgment undoubtedly occurred.

To explore potential errors associated with "expert-based" analyses, we summarized a 2001 attempt to update the 1995 classification. In 2001, a group of biologists were asked to review and update our classifications within a subset of the watersheds we addressed. Some of the biologists participated in our original 1995 workshops; others were new to the process. Criteria for classification and review were intended to be the same as in 1995. Deadlines required that the 2001 update be completed in a much shorter time than our original 1995 classifications. Results of the 2001 update suggested that the 1995 classifications for sympatric populations of redband trout and other native salmonids were similar. Notable inconsistencies were present in the classifications for allopatric redband trout, however, particularly in the number of "strong" populations. In 1995, 35 subwatersheds were classified as strong versus 126 similarly classified in 2001. Additional information provided in the 2001 update indicated that 60% of those changes were a result of new data and 25% of the changes were due to "errors" in the 1995 data. It was unclear, however, how many changes were a result of differing interpretations of the criteria and data between the two classifications. Conversations with participants in the 2001 update suggested that some of the upgrades from depressed to strong status were based on inferred population status from improvements in habitat quality as a result of management actions (e.g., following improvements in grazing management). Our 1995 criteria explicitly stated that status must not be inferred from habitat

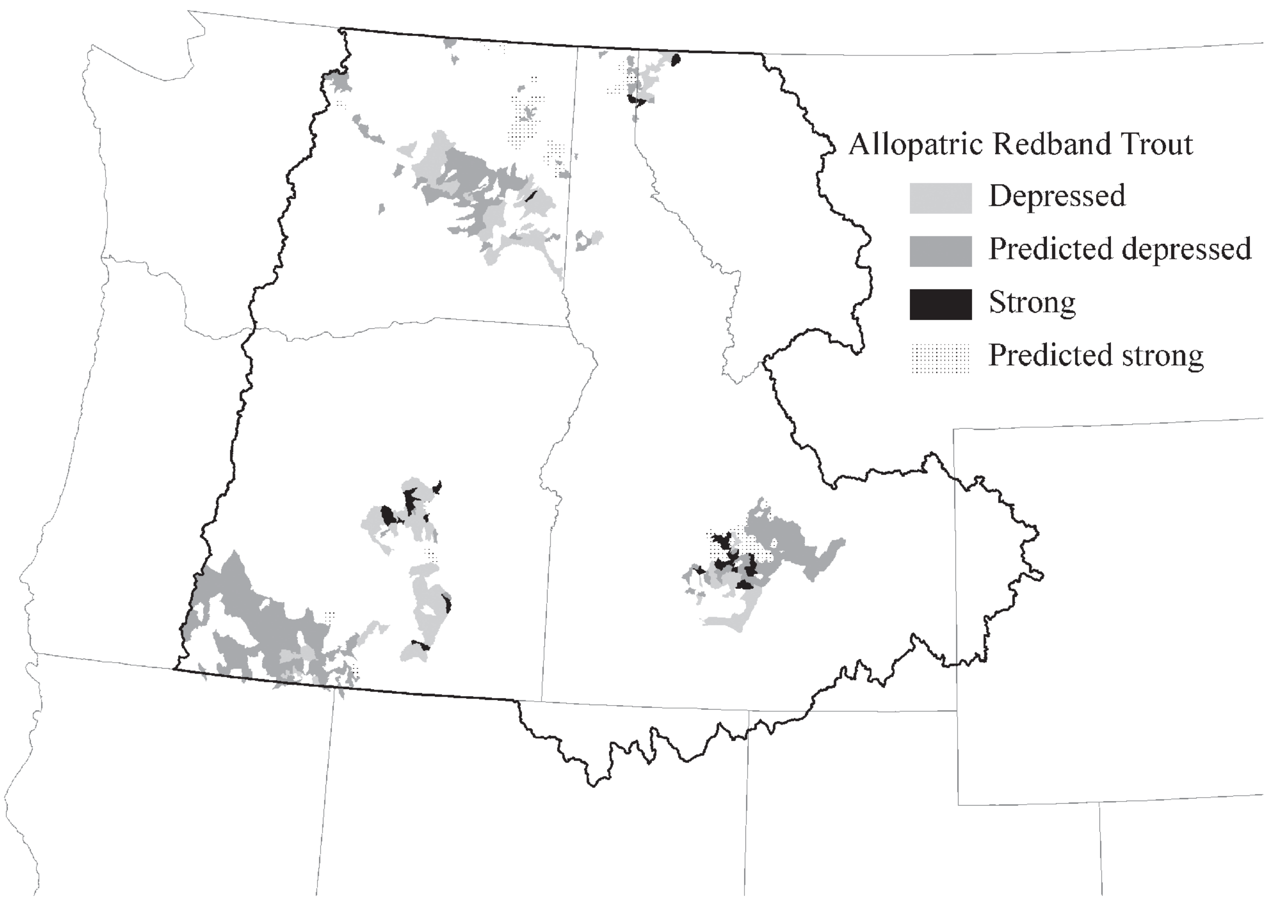

Figure 6.—Known and predicted classifications of status for allopatric redband trout within spawning and rearing areas in the interior Columbia River Basin in the U.S. and portions of the Klamath River and Great Basins.

conditions. No attempt was made to investigate the basis for such discrepancies or to resolve inconsistencies between the two classifications on a subwatershed by subwatershed basis.

The inconsistencies between the 1995 and 2001 classifications and the large number of subwatersheds classified as "unknown" are both symptomatic of the lack of quantitative information available for redband trout in the ICRB. Our analysis was the first comprehensive attempt to describe the broad scale distribution and status of redband trout in the ICRB. A more precise synthesis of species distributions will require consistent and rigorously maintained field surveys and data management protocols that at present simply do not exist at this scale of analysis. Other recent species surveys have used approaches similar to ours (e.g., Shepard et al. 2005); emerging research suggests that traditional sampling approaches also have important limitations (Peterson et al. 2005; Rosenberger and Dunham 2005; Thurow et al. 2006).

Status and Distribution

Redband trout were judged to be the most widely distributed native salmonid in the ICRB, occupying 64% of the combined potential range of the two forms. Some redband trout populations remained in portions of all the ERUs that are part of the potential range. Of 66 native fishes in the ICRB, redband trout were the second most widely distributed (Lee et al. 1997). Although redband trout remained distributed in much of their potential range, important declines in distribution and status are apparent from our analysis. We were unable to quantify extirpations of redband trout populations, however, because much of the potential range is too speculative. Attempts to quantify extirpations are further confounded because it is unlikely that redband trout occupied all reaches of all accessible streams.

The distribution of many redband trout populations was likely restricted by elevation, temperature, and local channel features. Mullan et al. (1992) suggested that some redband trout avoid water temperatures exceeding 22ºC (lower elevational limit) and that the distribution of steelhead may be restricted to stream reaches that exceed 1,600 annual temperature units (upper elevational limit). Platts (1974) similarly reported an upper elevational limit in the South Fork Salmon River; redband trout populations were not found above 2,075 m. In contrast, other redband trout forms in the southern margins of the range exhibit tolerance to high water temperatures (Kunkel 1976; Johnson et al. 1985; Behnke 1992; Zoellick 1999).

Table 6.—Summary of total known + predicted classifications (number of subwatersheds) for occurrence and status of sympatric redband trout in all subwatersheds and within "Protected" areas (National Park Service lands and designated wilderness) within the study area. The numbers predicted are based on the classification trees for redband trout within the range of summer steelhead and are shown in parentheses. Fifty-five subwatersheds classified as unknown did not have a prediction.

	Total known + predicted				Known + predicted within "Protected" areas	
Ecological Reporting Unit	Present	Strong	Depressed	Absent	Present	Strong
Northern Cascades	258 (36)	93 (88)	35 (31)	34 (27)	49 (1)	7 (5)
Southern Cascades	111 (4)	46 (21)	56 (18)	14 (0)	9 (0)	2 (0)
Upper Klamath	23 (15)	0 (0)	31 (31)	8 (8)	0 (0)	0 (0)
Northern Great Basin	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Columbia Plateau	457 (59)	73 (50)	305 (211)	339 (191)	0 (0)	0 (0)
Blue Mountains	579 (45)	249 (214)	241 (172)	64 (41)	50 (1)	38 (31)
Northern Glaciated Mountains	181 (1)	42 (21)	12 (9)	75 (44)	3 (0)	2 (2)
Lower Clark Fork	68 (1)	14 (11)	50 (33)	30 (22)	4 (0)	1 (0)
Upper Clark Fork	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Owyhee Uplands	336 (57)	54 (16)	213 (59)	513 (230)	2 (0)	2 (0)
Upper Snake	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Snake Headwaters	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Central Idaho Mountains	870 (177)	131 (65)	613 (467)	181 (138)	221 (67)	20 (13)
Entire study area[a]	2,883 (395)	702 (486)	1,556 (1,031)	1,258 (701)	338 (69)	72 (51)

[a] There were 7,498 subwatersheds in the study area and 4,196 in the potential range

Our analysis suggests that both forms of redband trout have more limited distributions and fewer strongholds than historically. Model results suggest it is unlikely that new population strongholds will be identified in areas spatially disjunct from known strongholds, because unknown areas generally have habitat conditions that are less likely to support populations than areas where observations were available (Lee et al. 1997). If redband trout are abundant, we generally know of their presence. Sympatric redband trout were known or predicted to be widely distributed in large patches of suitable habitat in the Northern Cascades, Blue Mountains, and Central Idaho Mountains. These watersheds represent the core of the sympatric distribution and appear to be relatively secure. Known or predicted populations in watersheds within the Southern Cascades, Upper Klamath, Owyhee Uplands, and Northern Glaciated Mountains were recently (since 1900) isolated from steelhead by dams. These latter populations appeared to be more fragmented in the remaining distribution. Allopatric redband trout within the Northern Great Basin, and portions of the Northern Glaciated Mountains, the Columbia Plateau, Central Idaho Mountains, and the Owyhee Uplands have been isolated from steelhead over geologic time. Remaining populations appeared to be severely fragmented and restricted to small patches of known or potential habitat. These areas likely represent a critical element of the evolutionary history for this species and a major challenge in conservation management. Introgression with introduced rainbow trout is potentially a serious but unevaluated threat for both redband trout forms.

Other status reviews in Idaho, Oregon, and Montana similarly report declines in redband trout populations (Moskowitz and Rahr 1994; Anonymous 1995; Kostow 1995; Perkinson 1995; Dambacher and Jones 2007, this volume; Gerstung 2007, this volume; Stuart et al. 2007, this volume). As described above, concern for the persistence of redband trout has increased efforts to conserve remaining populations. Our analysis and other work suggest that habitat degradation, habitat fragmentation, and introductions of non-native species and rainbow trout are primary factors that have influenced the status and distribution of redband trout and are likely to influence future species trends.

Factors Influencing Status and Distribution

Despite the limitations of the analysis, we believe that the general patterns provide some insight on redband trout. In general they appear to occupy a wide array of habitats, suggesting that they evolved over a wider range of environmental conditions than other native salmonids in the ICRB (Lee et al. 1997). Currens et al. (2007, this volume) suggest

Table 7.—Summary of total known + predicted classifications (number of subwatersheds) for occurrence and status of allopatric redband trout in all subwatersheds and within "Protected" areas (National Park Service lands and designated wilderness) within the study area. The numbers predicted are based on the classification trees for redband trout outside the range of summer steelhead and are shown in parentheses. Forty-nine subwatersheds classified as unknown did not have a prediction.

	Total known + predicted				Known + predicted within "Protected" areas	
Ecological Reporting Unit	Present	Strong	Depressed	Absent	Present	Strong
Northern Cascades	31 (0)	1 (0)	12 (12)	16 (14)	17 (0)	1 (0)
Southern Cascades	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Upper Klamath	111 (75)	0 (0)	112 (102)	15 (15)	2 (2)	0 (0)
Northern Great Basin	117 (18)	5 (3)	89 (40)	258 (93)	1 (0)	0 (0)
Columbia Plateau	72 (5)	1 (0)	120 (58)	182 (120)	0 (0)	0 (0)
Blue Mountains	42 (2)	15 (2)	27 (1)	10 (0)	0 (0)	0 (0)
Northern Glaciated Mountains	102 (1)	44 (40)	27 (17)	92 (71)	0 (0)	0 (0)
Lower Clark Fork	1 (0)	0 (0)	1 (1)	0 (0)	0 (0)	0 (0)
Upper Clark Fork	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Owyhee Uplands	39 (7)	2 (0)	23 (10)	19 (15)	0 (0)	0 (0)
Upper Snake	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Snake Headwaters	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Central Idaho Mountains	102 (9)	46 (33)	54 (52)	4 (3)	2 (0)	2 (2)
Entire study area[a]	617 (117)	114 (79)	465 (293)	596 (331)	22 (2)	3 (2)

[a] There were 7,498 subwatersheds in the study area and 1,262 in the potential range

that redband trout include more major evolutionary linkages or subspecies than previously recognized, which contributes to ecological and evolutionary diversity. Redband trout are often found in more extreme conditions than those associated with other salmonids. Populations in the southern margin of the ICRB inhabit turbid and alkaline waters with minimum temperatures near freezing and maximum temperatures from 25–29ºC (Kunkel 1976; Johnson et al. 1985; D. Buchanan, Oregon Department of Fish and Wildlife, personal communication). Behnke (1992) and Zoellick (1999) reported redband trout in tributaries to the Snake and Owyhee river basins tolerating maximum temperatures from 28 to 29ºC. Growth has been positively associated with temperature in forested streams (Mullan et al. 1992), and redband trout are often found in warmer waters than other salmonids. The apparent persistence of redband trout in some heavily disturbed basins might suggest that some populations are less strongly influenced by habitat disruption than other salmonids. If redband are more resistant, the loss of a population may be an indication of substantial habitat disruption. Persistence in a disturbed basin, however, could be influenced by several factors, including emigration of fish from adjacent areas or a time lag in population response (Rieman and Clayton 1997; Rieman and Dunham 2000).

Habitat degradation.—Anthropogenic disturbance has influenced redband trout status and distribution. We found no instances of a positive association with increased human disturbance. Although our models were not designed to test linkages between specific watershed characteristics and species status, variables reflecting the degree of human disturbance within watersheds (roads and management class) were useful predictors of redband trout status. A supplemental road analysis described in Lee et al. (1997) found decreasing likelihood of redband trout occupancy and a decreasing likelihood of strongholds if occupied, with increasing road density in forested landscapes. The lowest mean road density values were associated with strong population status. Redband trout status was negatively associated with increasing road density within forested, higher-elevation areas (Lee et al. 1997).

Work at finer scales has also described the result of habitat degradation. Interior redband trout habitats have been altered by a host of land use practices (Williams et al. 1989; Moskowitz and Rahr 1994; Anonymous 1995; Perkinson 1995). Diverting water for irrigation threatens many populations in the southern portion of the range through dewatering of stream reaches, loss of fish in unscreened diversions, blockage of migration corridors, and alteration of stream channels. The loss or conversion of riparian cover has been caused by grazing, timber harvest, mining, urbanization, and agriculture (Meehan 1991). Although removal of canopy by fire may benefit production in colder, high elevation streams

(Rieman et al. 1997a), in warmer and dryer environments the loss of riparian cover has been associated with excessive temperature and reduced abundance and production (Li et al. 1994; Tait et al. 1994). Channel alterations associated with attempts to control flooding, develop floodplains, and construct roads have been extensive and adversely affect stream hydraulics (Bottom et al. 1985), nutrient pathways (Schlosser 1982), invertebrate production (Benke et al. 1985), and fish production. In Idaho, unaltered stream reaches supported 8 to 10 times the densities of redband trout observed in altered channels (Thurow 1988). Habitat alterations may reduce the resilience and stability of the entire aquatic assemblage (Pearsons et al. 1992). Declines of fluvial forms in particular, have been most common in larger low-elevation streams that have historically been the focus of agricultural, residential, and other forms of development.

Fragmentation.—Many systems that support redband trout remain as remnants of what were larger, more complex, diverse, and connected systems. With the exception of the Central Idaho Mountains, the Blue Mountains, and the Northern Cascades, most of the important areas for redband trout exist as patches of scattered watersheds. Many are not well connected or are likely restricted to smaller areas than existed historically. Where watershed disturbances such as construction of dams, irrigation diversions, or other migration barriers result in loss of connectivity, remaining redband trout populations have been progressively isolated into smaller and smaller patches of habitat. Corridors that provide habitat for migration, rearing, and overwintering may be critical to the conservation of species where connections among population are important (Hanski and Gilpin 1991; Rieman and Dunham 2000). Such effects can be exaggerated by climate change. In the Goose Lake basin, Oregon, adfluvial redband trout find refuge in tributaries when the lake dries and recolonize the lake when it fills (Gerstung 2007, this volume; Tinniswood 2007, this volume). Factors that isolate tributaries from Goose Lake would increase the risk of extinction during dry cycles. The loss of genetic variability through genetic drift may be a particularly important factor in the more isolated watersheds in the southern range of redband trout (Wallace 1981; Berg 1987). The loss of spatial diversity in population structure and of the full expression of life-history pattern may lead to a loss of productivity and stability important to long term persistence (Lichatowich and Mobrand 1995).

Non-native species introductions.—Redband trout are part of a native community that includes cottids, catostomids, cyprinids, and salmonids including westslope cutthroat trout *O. clarkii lewisi*, bull trout *Salvelinus confluentus*, mountain whitefish *Prosopium williamsoni*, steelhead, and Chinook salmon *O. tshawytscha* (Lee et al. 1997). The Columbia River basin harbors 52 native freshwater species. Thirteen of these natives are endemic to the system (Hocutt and Wiley 1986). The introduction and expansion of nonnative species has influenced redband trout. Displacement may occur through competition, predation, and hybridization (Fausch 1988; Leary et al. 1993) and by introduction of diseases (Nehring and Walker 1996). About 50 non-native species have been introduced within the range of redband trout (Lee et al. 1997). At least 25 foreign species (not native to U.S.) have been introduced in Idaho, Oregon, Washington, and Montana, and 67 native species have been transplanted to systems where they are not indigenous (Fuller et al. 1999). Introduced rainbow trout, brook trout *S. fontinalis*, and brown trout *Salmo trutta* are widely distributed in lowland and alpine lakes and streams. Introduced rainbow trout were reported in 78% of the watersheds in the ICRB (Figure 7), and brook trout in about 50% (Lee et al. 1997), making them the most widely distributed fishes in the ICRB. Brown trout were found in 23% of the watersheds (Lee et al. 1997). Many other salmonids have been introduced outside their natural range and hatchery-reared forms have also been widely stocked. These include Lahontan *O. c. henshawi*, Yellowstone *O. c. bouvieri*, and westslope cutthroat trout; interior redband trout and coastal forms of rainbow trout; Chinook and coho salmon *O. kisutch*; kokanee *O. nerka*; and steelhead.

The effects of introductions on genetic integrity of redband trout have not been thoroughly assessed. Because of the potential for genetic introgression, we suspect that our assessment of strong populations may be optimistic. The long history of stocking rainbow trout within the ICRB, and the proclivity for redband trout and rainbow trout to hybridize (Allendorf et al. 1980; Wishard et al. 1984; Berg 1987; Currens et al. 1990; Leary et al. 1992; Moskowitz and Rahr 1994; Anonymous 1995; Williams et al. 1996), support concerns about the distribution and status of the original redband trout genotype. Introgressive hybridization is viewed as one of the most pervasive problems in the management of other non-anadromous native salmonids (Allendorf et al. 2001, 2004) and may be a serious threat to many fishes in general (Campton 1987). The effects may include a loss of fitness and a loss of genetic variability important to long-term stability and adaptation in varying environments.

Information is also lacking on the factors influencing the spread of diseases from fish introductions. Whirling disease (caused by *Myxobolus cerebralis*) has emerged as an issue of controversy and concern for its potential effects on wild redband trout populations in the western U.S. (Hulbert 1996). Although several ecological factors appear to influence disease epidemics, these relationships are not clearly defined. Nehring and Walker (1996) suggest that without a disease sampling protocol, whirling disease effects can be masked by other factors including angler harvest and other sources of natural mortality. The authors suggest that rainbow trout are among the most susceptible salmonids to mortality caused by whirling disease.

Conservation and Restoration Opportunities

To conserve the ecological diversity represented by the many life history patterns of redband trout, we suggest it will be critical to (1) conserve remaining healthy popula-

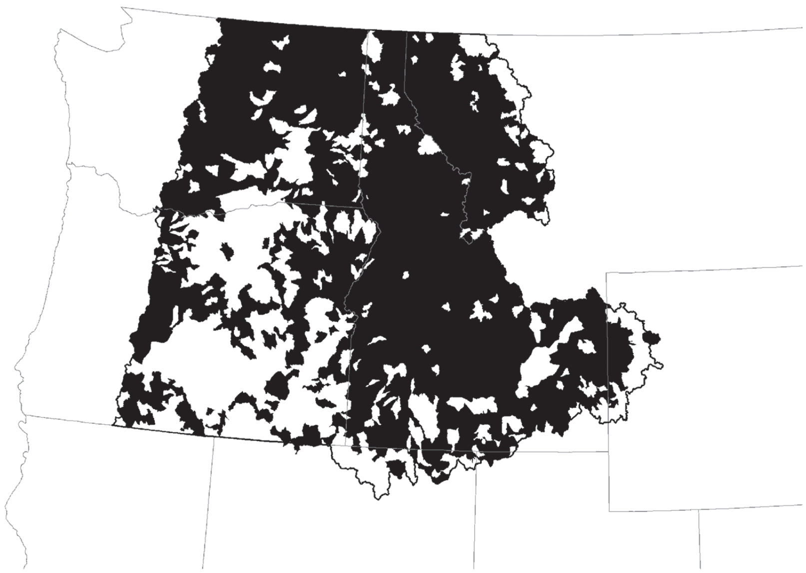

Figure 7.—Current range of introduced rainbow trout in the interior Columbia River Basin in the U.S. and portions of the Klamath River and Great Basins by watershed.

tions, (2) conserve unique populations, and (3) restore a broader mosaic of productive habitats. A general consensus of aquatic conservation strategies is that conservation and rehabilitation should focus first on the best remaining examples of biological integrity and diversity (Moyle and Sato 1991; Reeves and Sedell 1992; Doppelt et al. 1993; Frissell et al. 1993; Rieman and McIntyre 1993; Lee et al. 1997). Though the historical distribution and status of redband trout has declined, key areas remain for rebuilding and maintaining more functional aquatic systems. We suggest that core areas for conservation can be represented by subwatersheds supporting strong populations and locally adapted populations with unique phenotypic or genotypic characteristics.

Subwatersheds that support strong populations likely represent a fortuitous balance of habitat quality, climatic and geologic constraint, and geographic location that effectively minimize cumulative threats (Thurow et al. 1997). Where migratory life-history forms remain, the occurrence of strongholds may also indicate the relative integrity of a larger system of watersheds. Strongholds are more likely to serve as sources for the support of weak or at-risk populations, refounding of locally extinct populations, or refounding of habitats made available through restoration (Schlosser and Angermeier 1995).

Isolated and locally adapted populations, particularly those on the margins of the species range, may represent a disproportionate part of the total genetic variability in species (Scudder 1989; Lesica and Allendorf 1995). Although the large variation in morphological characteristics of redband trout has discouraged firm taxonomic boundaries within the group (Behnke 1992), researchers report genetic differentiation among populations, particularly in allopatric forms within isolated basins (Berg 1987; Currens et al. 2007, this volume). Isolated populations may represent evolutionarily distinct lineages and important components of the genetic variability of the species. Examples include redband trout native to Upper Klamath Lake, Oregon desert basins (Malheur, Catlow, Fort Rock, Chewaucan, Warner Lake, and Goose Lake), Idaho's Wood River, and the Kootenai River in Idaho and Montana. Unique characteristics of some isolated redband trout, lacustrine fish in Upper Klamath Lake for example (Behnke 1992; Hemmingsen and Buchanan 1993), suggest that some populations may warrant identification as separate evolutionary units or subspecies (Williams et al. 1989).

Although protection of core areas including strongholds and unique populations is critical, it will not be sufficient. Such reserves will never be large or well distributed enough to maintain biological diversity (Franklin 1993). Because redband trout are relatively broadly distributed, recovery of habitats outside core areas will be essential to secure more strong populations representative of the broad diversity of the species and its life history patterns. Achieving this goal will require the maintenance or rehabilitation of a network of well-connected, high-quality habitats that support a diverse assemblage of native species, the full expression of potential life histories and dispersal mechanisms, and the genetic diversity necessary for long-term persistence and adaptation in a variable environment.

Management of federal lands will have a major influence on the success of conservation and restoration efforts. About 55% of the distribution of redband trout occurs on federal land (Lee et al. 1997). Fifty-six percent of the strongholds occur on Forest Service and BLM lands. Small portions of the current range of redband trout are on lands managed under protected status. About 10% of the subwatersheds in the current range and 9% of the strongholds are secure within National Park Service lands or designated wilderness. The most secure portions of the distribution were found within the Central Idaho Mountains, the Northern

Cascades, and the Blue Mountains ERUs.

In addition to the need for watershed restoration and more ecologically compatible land use policies, conservation and restoration of redband trout populations will need to address the effects of non-native species introductions. In some cases, introductions of non-native trout continue and could be curtailed to avoid effects on native redband trout. Recently, concern about the effects of introductions on wild salmonids and the costs of hatchery programs have caused many state agencies to restrict stocking of non-native species to areas that will not support naturally reproducing salmonid populations (Van Vooren 1994). In many cases, however, non-native fishes are established and many are desirable to anglers. As a result, removal may be infeasible or socially unacceptable (Lee et al. 1997). Where non-native species are well established, containment of the potential effects of these forms may be the only reasonable goal.

Importantly, conserving and restoring healthy populations of non-anadromous redband trout may also be critical to the persistence or restoration of some steelhead stocks. Although the relationship between the two forms is not well understood (Busby et al. 1996), there is evidence that some progeny of non-anadromous forms migrate to sea and some progeny of steelhead remain in freshwater (Shapovalov and Taft 1954; Burgner et al. 1992; Olsen et al. 2006). Steelhead confined above barriers adopt a non-anadromous lifestyle appropriate to the habitats available (Moffitt and Bjornn 1984). Mullan et al. (1992) also reported that steelhead progeny in very cold streams residualized and adopted a non-anadromous life history but suggested that these fish retained the ability to produce anadromous offspring. Mullan et al. (1992) reported that blockage of the Methow River by a dam for 14 years exterminated coho salmon but not steelhead. If sympatric redband trout have the potential to refound steelhead, that has application for the recovery of unique populations of steelhead eliminated by human-caused barriers. The maintenance of such distinct life histories may be an adaptation to variable environments (Gross 1991). For example, in watersheds that were periodically blocked by stochastic events, sympatric redband trout populations that retained the ability to produce anadromous progeny would have been able to refound steelhead. Perhaps in recognition of this potential, the National Marine Fisheries Service (NOAA) stated that it believed non-anadromous redband trout could help buffer extinction risks to an anadromous population and believed available evidence suggested that resident rainbow trout should be included in listed steelhead Evolutionary Significant Units (ESUs) in certain cases (Federal Register 62[August 18, 1997]:43937–43954). Since 1997, however, NOAA has reversed its position and only steelhead are currently included in the ESA listing (www.nwr.noaa.gov/ESA-Salmon-Listings).

Conversely, losses of steelhead may pose serious consequences for sympatric redband trout. Steelhead may facilitate gene flow between the two forms, and if this flow is eliminated, non-anadromous forms may diverge (Currens et al. 2007, this volume). The questions regarding phenotypic diversity and life history plasticity between steelhead and redband trout forms might be addressed in a series of field experiments. For example, redband trout populations above barriers and within the range of steelhead might be supplemented with nutrients to accelerate growth followed by monitoring of out-migrants. Conversely, steelhead might be introduced into a trout-barren stream within the range of redband trout and monitored for production of out-migrants and adaptation to freshwater residence. Olsen et al. (2006) observed that because it is possible that steelhead and redband trout may be restored from each other, both forms should be conserved.

Conclusions

Redband trout and are the most widely distributed native salmonid in the ICRB, and populations of both sympatric and allopatric forms appear to be relatively secure in some ERUs. Despite their broad distribution, local extirpations and important declines have occurred; both forms have more limited distribution and fewer strongholds than historically. Habitat degradation and fragmentation and the pervasive introduction of non-native species suggest that further declines are likely. Focused conservation and restoration efforts will be necessary to retain the remarkable ecological diversity expressed by redband trout.

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Benchmarks and Patterns of Abundance of Redband Trout in Oregon Streams: a Compilation of Studies

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Abstract.—This work summarizes pre-1998 studies of population abundance of stream resident redband trout *Oncorhynchus mykiss* ssp. in Oregon, and compares basin-level surveys of habitat and fish populations in streams of two ecoregions. Interquartile values of density and biomass were used to develop benchmarks of high, moderate, and low abundance. Comparison among Crooked River streams (Blue Mountain ecoregion) showed large differences in population abundance associated with watershed characteristics such as elevation, flow, temperature, land use, and disturbance history. Comparisons among Catlow Valley streams (High Desert ecoregion) found redband trout to be concentrated in discrete reaches associated with high spring flow or in narrow canyon reaches with riparian zones that were not intensively grazed by cattle. These reaches could possibly function as population refugia. Populations of redband trout in Catlow Valley streams were severely depressed during the time of sampling. Degraded stream habitat, drought conditions, and system connectivity appeared to be important factors associated with their status and recovery.

Estimates of fish populations are commonly conducted to monitor population status and trends and to compare treatment effects between populations. Although the rainbow trout *Oncorhynchus mykiss* is one of the most-studied fishes in Oregon streams, very little research has been done on resident populations in central and eastern Oregon, where they are recognized as a distinct subspecies known as redband trout (Currens 1997). Redband trout occur in five major ecoregions in central and eastern Oregon (Figure 1). Their environments are typically arid and range from montane forests to desert shrub and grasslands. Knowledge is particularly lacking about general factors affecting the distribution and abundance of redband trout throughout these widely diverse environments and, at a more basic level, about what constitutes relatively high or low population abundance. In this paper we summarize pre-1998 studies of population abundance of stream resident redband trout in Oregon, from which we develop abundance benchmarks. In addition, comparative surveys of habitat and fish populations in streams in the Crooked River and Catlow Valley basins will be used to demonstrate basin-level effects on the distribution and abundance of redband trout.

Methods

Compilation of abundance estimates.— Abundance estimates (density and biomass) of age-1 and older redband trout (hereafter designated as $\geq$ age-1) were compiled from pre-1998 published and unpublished studies from central and eastern Oregon (Table 1). Age-class designations were typically putative, being determined by length frequency of sampled fish, but were sometimes more precisely determined by scale analysis. Only studies of stream-resident populations with abundance reported in terms of habitat area were considered. Those with densities reported in lineal terms, such as fish per lineal meter or mile, were excluded. In studies with sample sites that had wetted channel lengths less than 30 times the channel width, multiple sites were averaged to a single estimate at the reach or stream level. Estimates of age-0 fish were omitted to avoid their large variation in between- and within-year abundance. Interquartile values for density and biomass were used to delineate benchmarks for low, moderate, and high levels of abundance.

Stream surveys.—Two sets of stream habitat surveys are summarized in this report to provide a comparison of between- and within-stream patterns of redband trout abundance. Stream habitat and fish population surveys were con-

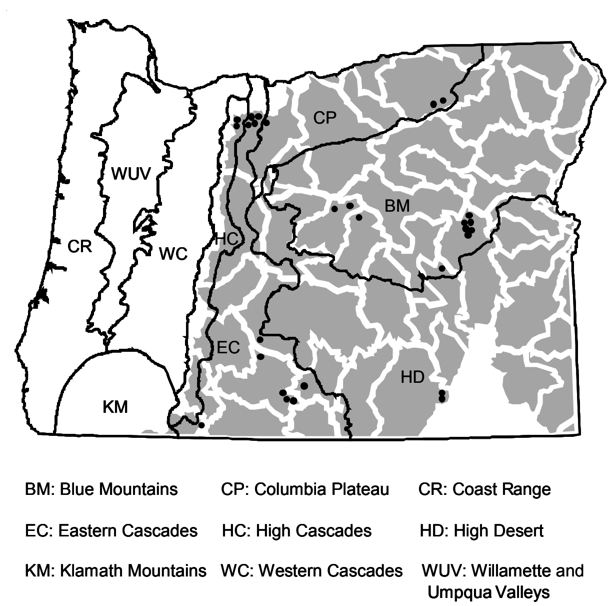

Figure 1.—Major drainages (shaded areas) with historic populations of redband trout and Oregon ecoregions. Ecoregions depicted here are the major ones designated by Clarke et al. (1991), except the High Cascades ecoregion, which is a subregion of the Western Cascades. Filled circles denote location of one or more sites from which abundance data were collected (Table 1).

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TABLE 1.—Data sources for redband trout abundance estimates in streams of central and eastern Oregon.

Data source	Number of estimates fish/m^2	Number of estimates g/m^2
Osborn 1968	3	0
Kunkel 1976	5	6
ODFW et al. 1985	44	44
ODFW unpublished data[a]	30	0
Total	82	50

[a] Population estimates from 1991 to 1995, Aquatic Inventory Project, Corvallis.

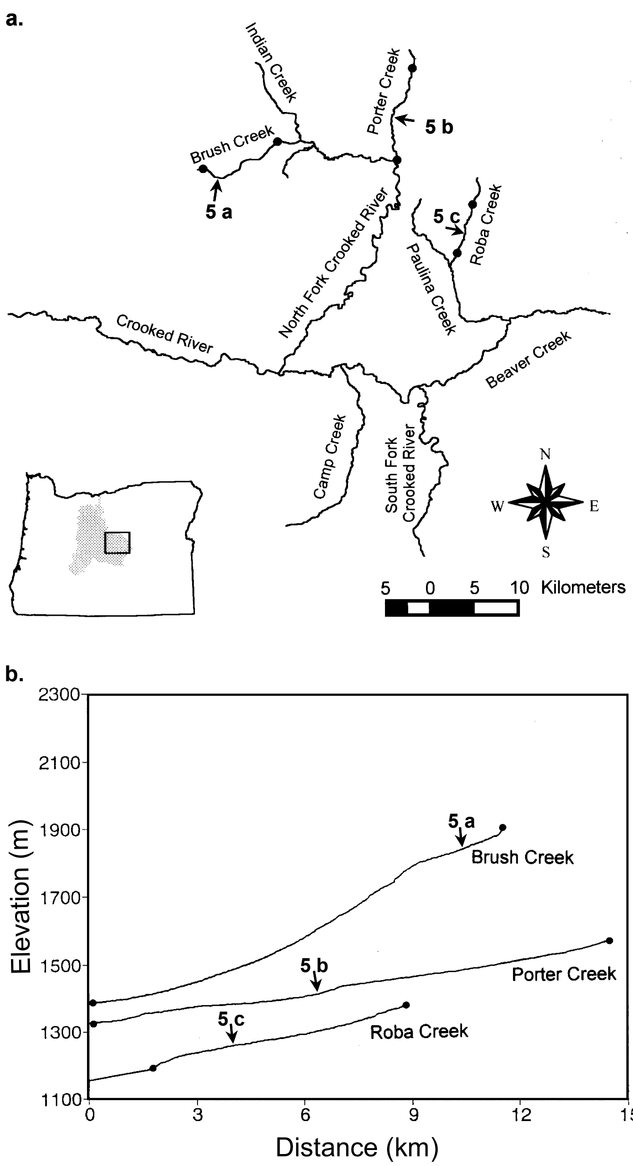

FIGURE 2.—(a) Streams surveyed in the Crooked River basin, Blue Mountain ecoregion, with (b) longitudinal profile. Filled circles denote survey limits; arrows denote location of photographs in Figure 5.

ducted by the Aquatic Inventory Project, Oregon Department of Fish and Wildlife (ODFW), in the Blue Mountain and High Desert ecoregions. Blue Mountain streams were surveyed in the Crooked River basin during the summers of 1991–1993, when there was a drought throughout Oregon (1985–1994). High Desert streams were surveyed in the Catlow Valley basin in 1995, the year following the end of the drought.

Stream habitat was surveyed and fish population abundance was estimated in three streams in the Crooked River basin (Figure 2) deemed to represent high, moderate, and low habitat quality (A. Stuart, ODFW, personal communication). Sampling occurred over three successive years: Porter Creek in 1991 (moderate quality habitat), Brush Creek in 1992 (high quality), and Roba Creek in 1993 (low quality). Stream habitat was quantified with methods of Moore et al. (1997). Estimates of total fish population were made by removal-depletion techniques with backpack electroshockers and blocknets. Streams were stratified into pool and fast-water habitat types and systematically sampled (Hankin and Reeves 1988). Separate estimates of fish abundance were calculated for each habitat type using formulas from Bohlin (1981).

Three streams were inventoried in 1995 (Figure 3) as part of a separate effort to gather information for conservation planning in the Catlow Valley basin (Dambacher and Stevens 1996). In Three Mile Creek, fish population estimates were made with removal-depletion techniques. In Home and Skull creeks only presence-absence sampling was conducted, which consisted of single-pass electroshocking

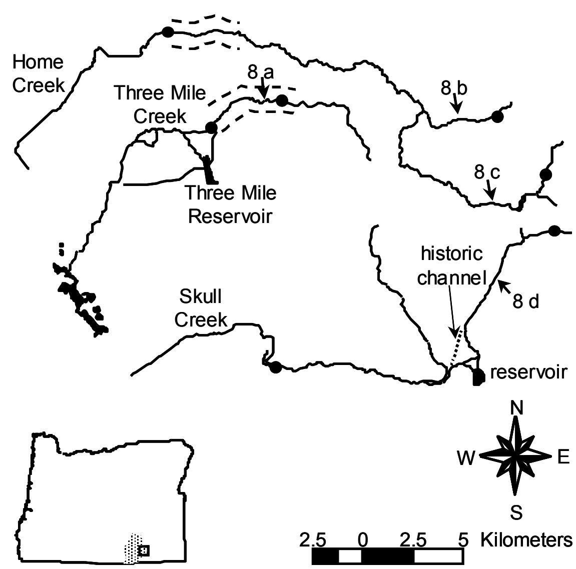

FIGURE 3.—Streams surveyed in Catlow Valley, High Desert ecoregion. Filled circles denote survey limits. Downstream limits of survey are at canyon openings near the east rim of Catlow Valley. Parallel sets of dashed lines denote stream reaches within narrow canyons; arrows denote location of photographs in Figure 8.

without blocknets in three pool and three fast-water habitat types at each sample site. Sample sites were arrayed throughout stream systems to describe the distribution of each fish species. In Home and Skull creeks, capture data from presence-absence sampling were used to infer crude levels of relative abundance, where < 0.01 captured fish/m^2 was used to distinguish a low level from higher levels. Presence-absence sampling was conducted in Skull Creek again in 1997.

Results

Abundance summary and benchmarks

A 100-fold difference between the lowest and highest abundances of ≥ age-1 redband trout was reported in the reviewed studies (Figure 4). Density averaged 0.014 fish/m^2 and ranged between 0.0069 and 0.65 fish/m^2. Biomass averaged 4.2 g/m^2 and ranged between 0.14 and 21 g/m^2. The overall mean weight of ≥ age-1 fish was 30 g and ranged between 13 and 123 g.

Benchmarks of abundance were developed from interquartile values of fish density and biomass (Table 2). The boundary values for low density and biomass were roughly one-third of those for high levels.

Crooked River basin

Watershed characteristics, land-use intensity, and disturbance history differed greatly among the three streams surveyed in the Crooked River basin, which represented a broad spectrum of watershed and stream habitat conditions (Tables 3 and 4). Brush Creek had the highest elevation, the highest flow, the lowest stream temperature, and the lowest level of cattle grazing or timber harvest. Its riparian vegetation appeared to be near its full potential (Figure 5a), with an overstory of large conifers and an understory of small hardwoods and perennial grasses. In contrast, Roba Creek had the lowest elevation and flow, the highest stream temperature, and high levels of cattle grazing and timber harvest. This stream had recently experienced a flash flood, which, after extensive logging of its headwaters, left the channel incised into freshly scoured banks and with degraded riparian conditions (Figure 5c). Conditions in Porter Creek were generally intermediate to Brush and Roba creeks in terms of instream habitat, riparian conditions, and disturbance history. Although Porter Creek historically had a riparian canopy of mature cottonwoods, few remained at the time of the survey; many appeared decadent and many more had fallen (Figure 5b). Recruitment of young cottonwoods was lacking and evidently suppressed as a result of grazing by cattle. Although the three streams differed markedly in watershed characteristics and land use (Table 3), they were similar in measures of instream habitat (Table 4). Brush Creek

TABLE 2.—Benchmarks of abundance for ≥ age-1 redband trout taken from interquartile values of 82 estimates of density and 50 estimates of biomass compiled from pre-1998 studies of central and eastern Oregon streams (Table 1).

Abundance level	fish/m^2	g/m^2
Low	≤ 0.059	≤ 2.0
Moderate	0.060–0.19	2.1–4.9
High	≥ 0.20	≥ 5.0

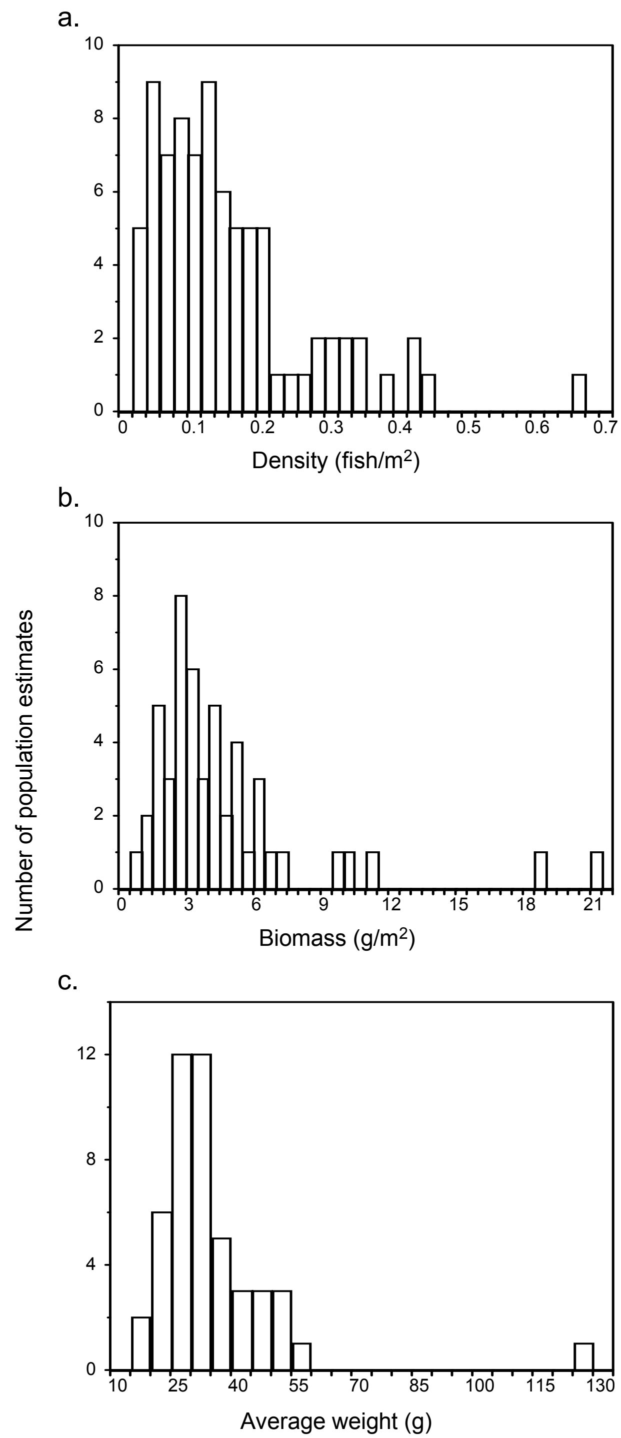

FIGURE 4.—Frequency distribution of ≥ age-1 redband trout (a) density, (b) biomass, and (c) average weight, summarized from published and unpublished estimates (Table 1) of Oregon stream populations.

TABLE 3.—Watershed characteristics of three Blue Mountain streams, Crooked River basin, Oregon.

Stream	Year surveyed	Basin area	Mid-basin elevation	Stream flow[a] (m^3/s)	Maximum water temperature[a] July 1993	Relative intensity cattle grazing	Relative intensity timber harvest	Disturbance history
Brush Cr.	1992	20 km^2	1,600 m	0.04	16°C	low	low	none recently noted
Porter Cr.	1991	40 km^2	1,400 m	0.01	21°C	high	moderate	1991 channel drying
Roba Cr.	1993	30 km^2	1,200 m	0.003	24°C	high	high	1991 flood, 1992 channel drying

[a] Measured at lower limit of stream habitat survey (Figure 3) in July 1993.

had greater bank stability than the other two streams, but also had high levels of fine sediments. Levels of shade, large wood, and pool habitat were mixed among the streams.

Speckled dace *Rhinichthys osculus* occurred with redband trout in all three of the sampled streams. Brook trout *Salvelinus fontinalis* were present in Brush Creek, and the mountain sucker *Catostomus platyrhynchus* in Roba Creek (Figure 6). The upstream distribution of brook trout in Brush Creek was limited by a small falls, as was the distribution of speckled dace in Porter Creek. Dry channel reaches at the time of sampling caused gaps in the distribution of redband trout in Porter Creek. A similar gap in redband trout distribution in Roba Creek occurred in a reach that had been dry the previous summer.

Although available habitat (wetted area) for redband trout in the three streams differed by no more than a factor of 1.6, there was a 20-fold difference in the density of ≥ age-1 fish (Figure 7). Basin area was not correlated with habitat availability or fish population size (Table 3). The smallest basin, Brush Creek, had the greatest amount of available habitat and the largest population of redband trout. Based on the abundance benchmarks in Table 2, densities of ≥ age-1 redband trout were high in Brush Creek, moderate in Porter Creek, and low in Roba Creek. The high density of redband trout in Brush Creek occurred along with many ≥ age-1 brook trout, resulting in a combined density of 0.66 ≥ age-1 salmonids/m^2.

Catlow Valley basin

Habitat overview.—Habitat surveys in Catlow Valley streams (Figure 3) revealed conditions of moderate habitat quality in Three Mile Creek and in a few reaches of Home Creek, but low habitat quality in all of Skull Creek and in the greater portion of Home Creek. Specific values of habitat conditions are not presented in this report but are summarized in detail by Dambacher and Stevens (1996). Habitat quality, as defined by pool habitat, substrate, bank stability, and riparian conditions (Platts 1991), appeared to be severely reduced in reaches exposed to intensive cattle grazing. Such reaches (e.g., Figure 8b–d) were conspicuously lacking in riparian vegetation, had up to 90% actively eroding stream banks, and were inundated by fine sediments (> 40% in riffle substrates). The best habitat occurred in narrow canyon reaches in the lower portions of Three Mile (Figure 8a) and Home creeks. These reaches were incised into the eastern edge of the Catlow Rim (Figure 9), where remote and difficult access has prevented intensive grazing by cattle. Here dense thickets of alder and chokecherry bordered the streams, boulder substrate and riparian vegetation stabilized stream banks, and large springs maintained cool stream temperatures. The majority of flow in Three Mile Creek comes from a large spring midway through the canyon. Below the canyon reach, streamflow is diverted into Three Mile Reservoir (Figure 3). Skull Creek lacks a narrow canyon (Figure 9), and all channel reaches were severely impacted and degraded from intensive grazing by cattle. Its

TABLE 4.—Habitat characteristics of three Blue Mountain streams in the Crooked River basin, Oregon, from 1991 to 1993, ODFW stream habitat surveys.

Stream	Percent actively eroding banks	Percent shade	Large wood debris volume (m^3/100m)	Percent riffle fines	Percent pool area	Wetted channel width (m)
Brush Cr.	4	57	14	38	15	3.5
Porter Cr.	15	49	not estimated[a]	13	11	1.5
Roba Cr.	38	63	9	33	25	2.0

[a] Generally observed to be lower than levels in Roba Creek.

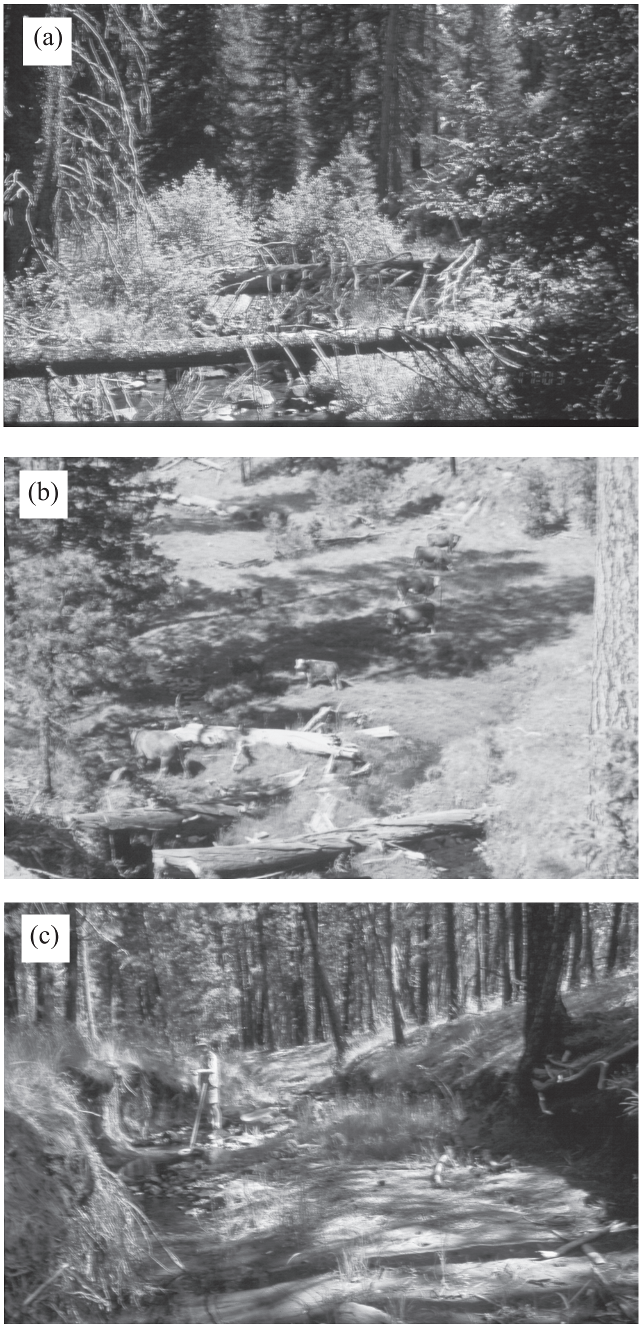

FIGURE 5.—Upstream views of (a) Brush Creek (1992), (b) Porter Creek (1991), and (c) Roba Creek (1993), Crooked River basin. Locations are shown in Figure 2.

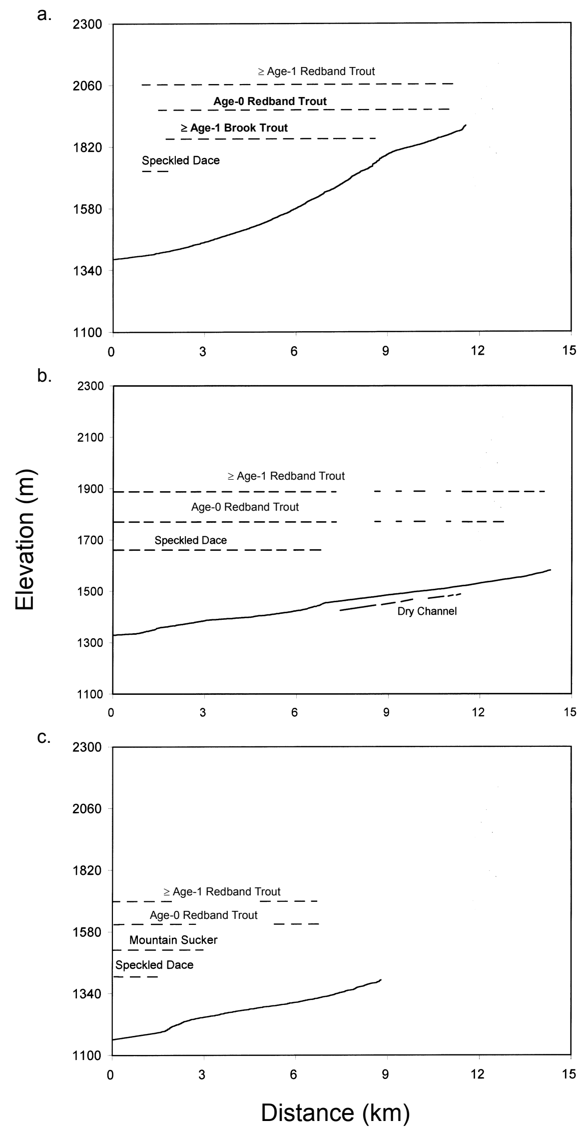

FIGURE 6.—Longitudinal profile and distribution of fishes in (a) Brush Creek, (b) Porter Creek, and (c) Roba Creek. Distribution gaps in Porter Creek are channel segments that were dry during the survey, and in Roba Creek are over a channel section that was wetted during the survey but dry the previous year.

headwaters were bounded by moderately sloped hillsides, and its lower portion had a gentle gradient within an open valley. Below its headwaters, Skull Creek was diverted into a ditch, around a broad meadow, and into a reservoir. From there it flowed back into its natural stream channel below the meadow (Figure 3). The headwaters of Skull Creek had areas of spring inflow, but these were heavily impacted by cattle grazing (Figure 8d).

Three Mile Creek.—Redband trout have historically occurred in Three Mile Creek and Three Mile Reservoir, the latter of which has an abundant population of Catlow tui chub *Gila bicolor* ssp. Redband trout commonly enter the reservoir after a year of stream life and become large (> 50 cm) from feeding on tui chub (Kunkel 1976). During the mid-1970s, Kunkel estimated the population of redband trout in Three Mile Reservoir to be as high as 890 fish, with nearly 250 adults spawning, primarily at age 3, in the section of Three Mile Creek between its irrigation diversion and springs. The stream population of ≥ age-1 fish between the diversion and springs was estimated to be as high as 1,700, with a density as high as 1.5 fish/m^2. This is an extraordinarily high density (Figure 4) and corresponds with an excep-

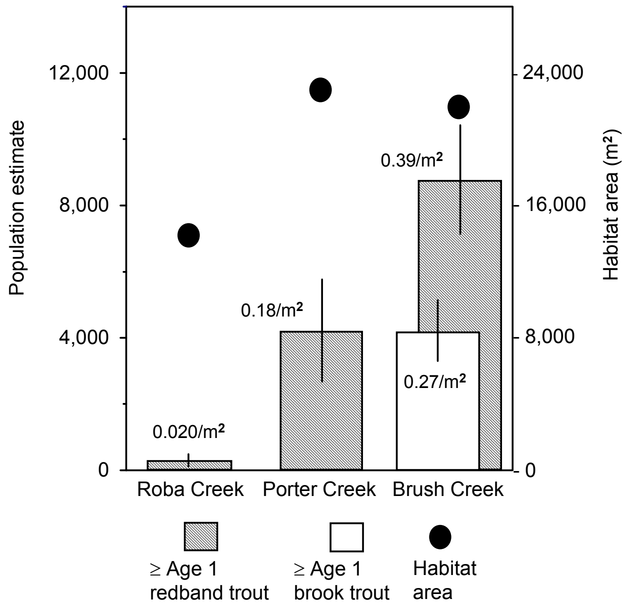

FIGURE 7.—Population estimates (with 95% confidence intervals as vertical lines), habitat area, and density of ≥ age-1 salmonids in three streams of the Crooked River basin, Blue Mountain ecoregion.

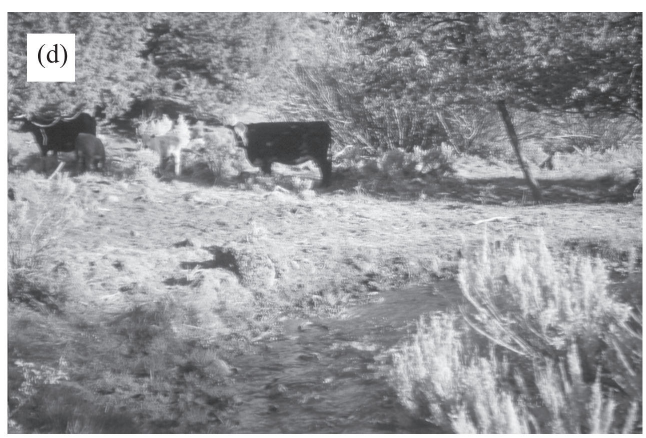

FIGURE 8.—Photographs of Catlow Valley streams, in (a) canyon reach of Three Mile Creek (1994) that has limited access for cattle, (b) area of spring inflow in Home Creek tributary (1995), (c) intensively grazed reach in Home Creek (1995), and (d) intensively grazed reach in Skull Creek where redband trout were found in 1997. Locations are shown in Figure 3; (a) and (b) are upstream views; (c) and (d) are downstream views.

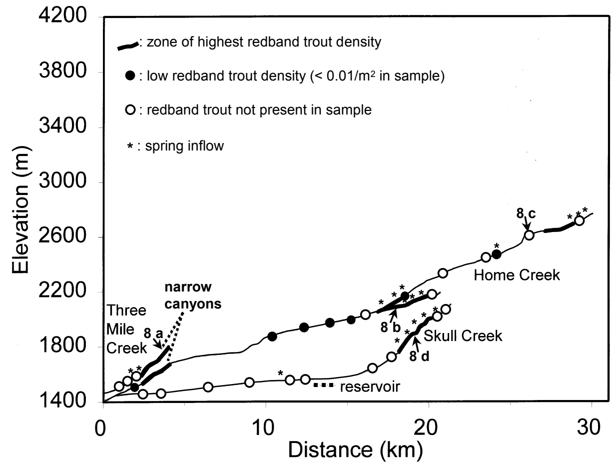

FIGURE 9.—Longitudinal profile of three Catlow Valley streams, High Desert ecoregion, with distribution and relative abundance of redband trout from 1995 and 1997 electrofishing sampling. Arrows denote location of photographs in Figure 8. In general, reaches with the highest densities of redband trout were associated with narrow canyons or with large amounts of spring inflow.

tional level of production (17.2 $g \cdot m^{-2} \cdot yr^{-1}$), which stands as some of the highest ever reported in a small stream (Kunkel 1976).

A change in the schedule of irrigation diversions in the early 1990s is suspected to have interrupted the migration of fish between the reservoir and Three Mile Creek (W. Bowers, ODFW, personal communication). An abundant population of tui chub was found in the reservoir in 1993, but no redband trout were found (unpublished data, W. Bowers, ODFW). In 1995 we found no redband trout in Three Mile Creek between the diversion and the springs, despite intensive population sampling (multiple-pass electroshocking with blocknets), although an estimated 265 ≥ age-1 fish (95% confidence interval ± 41%) were found upstream of the springs. The above-springs reach had only marginal habitat, with puddled flow between pools and dry riffles. Tui chub were abundant in the reservoir in 1997, but again no redband trout were found (Dambacher and Burke 1997).

Home Creek.—Redband trout in Home Creek were concentrated in a narrow canyon reach and two reaches associated with heavy spring flow (Figures 8b and 9). Redband trout were absent or in low abundance in all other reaches, especially where intensive cattle grazing caused severe degradation to stream habitat (Figure 8c). Age-0 fish were particularly concentrated near spring inflows in the headwaters and in a tributary.

Skull Creek.—We found no redband trout in Skull Creek in 1995 using a presence-absence sampling approach. Tui chub were relatively abundant in a low gradient reach downstream of the reservoir (Dambacher and Stevens 1996). Prior to these surveys, the reservoir had been drawn down for repair, and fish populations in the reservoir were eliminated by repeated episodes of drying. Although it was suspected that redband trout might have been extirpated from Skull Creek (Dambacher and Stevens 1996; Howell 1997), repeat sampling in 1997 found redband trout within a 3.0-km headwater reach (Dambacher and Burke 1997). Sixteen fish were captured in multiple sample sites that covered 6% of the length of this reach.

Presuming no clandestine reintroductions in 1996, redband trout in Skull Creek were likely not extinct in 1995, however their abundance was so low as to be undetected by relatively intensive sampling. Sampling in 1995 had encompassed all of the 3.0-km headwater reach occupied by redband trout in 1997, as well adjacent upstream and downstream reaches. Thirteen percent of the length of the 3.0-km reach was sampled as discrete habitat units of pools and riffles in a series of sample sites. In addition, the majority of pools and pocket-pool habitats between these sites were spot-checked for fish presence by electroshocking.

Evidence suggests that poor survival might be a contributing factor to the status of the Skull Creek population. Based on length-age relationships previously established from Home and Three Mile creeks (Kunkel 1976; Dambacher and Stevens 1996), 15 of the 16 fish captured in Skull Creek in 1997 were either age 0 or not yet hatched at the time of the 1995 sampling. In 1997, one was age 0 (1997 cohort), 14 were age 2 (1995 cohort), and only one was age 4 or 5 (1992 or 1993 cohort).

In 1997, the density of ≥ age-1 fish captured in Skull Creek by presence-absence sampling was 0.06 fish/m^2. Assuming that sampling caught no less than half of the actual population (a conservative assumption given that catchability for electrofishing in small streams is typically greater than 0.5, unpublished data JMD), then the density of the 1997 population was likely no higher than 0.12 ≥ age-1 fish/m^2. This range in density (0.06–0.12 ≥ age-1 fish/m^2) corresponds to a moderate level of abundance (Table 2). Thus, by crude extrapolation of these densities into the wetted area of the 3.0 km reach, the total population of ≥ age-1 redband trout in Skull Creek in 1997 could have been around 250 to 500 fish.

Discussion

Density and biomass estimates of ≥ age-1 redband trout summarized here are similar to those reported for other rainbow trout populations that are anadromous or resident (Platts and McHenry 1988; Bjornn and Reiser 1991). Our summaries carry the value of not being mixed with age-0 densities (as in Platts and McHenry 1988), and for their being from relatively large sections of stream channel (> 30 channel widths long). As a consequence, they should indicate differences between stream or reach-level abundance, and not merely differences between types of habitat such as pools and riffles.

The three Blue Mountain streams showed wide variation in redband trout abundance that was associated with watershed-level characteristics such as flow and temperature, which in these examples were independent of basin size. Differences in abundance were also likely heightened by a legacy of drought and floods. Although negative impacts to stream habitat from intensive cattle grazing and timber harvest were apparent, it was not possible to determine even relative effects of these two practices on fish populations due to confounding watershed-level factors. Although these comparisons were not intended to rigorously evaluate effects of land use and habitat quality on redband trout, they nonetheless highlight the important context that watershed characteristics can provide to studies of stream fish populations (Dunham and Vinyard 1997). Furthermore, they emphasize the need for an experimental approach, such as a before-after-control-impact (BACI) design, to investigate land-use effects on fish populations.

General patterns of distribution and abundance of redband trout differed greatly between streams in the Crooked River and Catlow Valley basins. In the Crooked River basin the distribution of redband trout was relatively continuous, except for localized channel drying, and major patterns of abundance were more apparent between than within streams. Conversely, populations of redband trout in streams of Catlow Valley were concentrated in relatively discrete reaches that had locally favorable rearing conditions—such as spring inflows or narrow canyons—and were at a low abundance or absent in the majority of habitat elsewhere. Riparian zones are characteristically fragile in arid environments. The degraded condition of habitat in the majority of stream channels in Catlow Valley during these surveys (Figure 8) illustrated the familiar consequence of intensive grazing by cattle in riparian zones (Platts 1991).

Assuming that these patterns of abundance can be generalized to other systems, important considerations for the conservation of redband trout are suggested. In the Blue Mountains, redband trout might be extirpated from streams with the poorest habitat quality and highest disturbance, such as Roba Creek. However, since these stream systems are well connected to one another (Figure 2), at least seasonally, colonization could readily ensue from basins such as Brush Creek, with rearing environments that are more stable and of higher quality and capacity. Conversely, colonization from adjacent basins in the High Desert is often precluded by isolation of streams (Figure 3). Thus identification and protection of local refugia within each stream system are of central importance. High Desert streams represent some of the harshest rearing environments endured by redband trout, and conditions could have approached “worst-case” during the 1985–1994 drought cycle. Narrow canyon and spring inflow reaches (Figure 9) could function as refugia for the stream populations during adverse conditions. These areas may thus represent critical habitat for persistence of redband trout and have the potential to serve as sources of fish to colonize adjacent reaches. As such, they warrant special consideration for protection and restoration.

Based on the size-class distribution of the limited number of fish sampled in Skull Creek in 1997, we speculate that reproduction may have been successful only infrequently. Although a cohort of fish was represented from 1995, limited reproduction apparently occurred in 1994 and 1996, and only a single age-0 fish was found to represent the 1997 cohort. Age-0 fish were apparently difficult to detect in this reach in 1995, but there is less uncertainty about the lack of age-1 and age-3 fish in the 1997 sampling, as electrofishing efficiency is much higher for these larger fish. Moreover, identical sampling gear and effort in other Catlow Valley streams documented a wide range of abundance for both age-0 and ≥ age-1 redband trout (Dambacher and Stevens 1996). Thus it seems unlikely that the observed pattern in Skull Creek was a consequence of sampling bias.

Given the possiblity of episodic reproduction, it is remarkable that ≥ age-1 redband trout in Skull Creek could increase in 2 years from an undetectable level to a moderate level of abundance. However, this example also illustrates an important limitation in the use of fish density alone to rate the status of a population. In Skull Creek a moderate density was exhibited by a population that had a limited distribution (3.0 km), a limited population size (likely < 500 fish), possibly a discontinuous age-class structure, and severely degraded habitat. These factors are of overriding importance in determining the status of a population (Van Horne 1983).

The status of the stream and reservoir populations in Three Mile Creek appears dire. Absence of fish between the diversion and springs is puzzling, as habitat conditions in this reach are some of the most favorable in all of Catlow Valley (Dambacher and Stevens 1996), and this reach has historically supported record levels of abundance and production (Kunkel 1976). Kunkel found this reach of stream to support both stream-resident and adfluvial life histories. It is surprising that a failure of the reservoir population, presumably from a loss of connectivity, would have such a dramatic effect on the stream-resident population. This result raises the question: is the reproductive capacity of the stream-resident life history dependent on the presence of the adfluvial life history?

The adfluvial life history of redband trout is an important component of this species’ adaptation to arid inland environments and is in need of basic research. The phenomenon of population collapse and colonization could be ideally studied in the stream and reservoir system of Three Mile Creek, as the scale is small and relatively easy to study. This system is highly productive and therefore likely to respond quickly to recovery efforts. Furthermore, the system could represent a microcosm of larger basins that have experienced collapses of the adfluvial life history, such as the Goose Lake and Warner Valley basins.

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Redband Trout: Resilience and Challenge in a Changing Landscape
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Gene Flow between Resident and Anadromous Rainbow Trout in the Yakima Basin: Ecological and Genetic Evidence

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Abstract.—We examined ecological and genetic evidence to determine the potential for gene flow between resident rainbow trout and anadromous steelhead *Oncorhynchus mykiss* in the Yakima River basin. Electrofishing, trapping, radio telemetry, redd surveys, and snorkeling were used to determine the spatial and temporal distribution of spawning *O. mykiss*. Steelhead had a smaller spatial spawning distribution than rainbow trout, but it was entirely within the range of rainbow trout spawning areas. Furthermore, the spawning time of rainbow trout and steelhead was positively related to elevation, and no differences in timing were detected between forms ($P > 0.05$). In addition, we observed many instances of interbreeding between rainbow trout and steelhead. Genetic evidence from starch gel electrophoresis also suggested that rainbow trout and steelhead interbreed. Rainbow trout were genetically indistinguishable from sympatric steelhead collected in the North Fork of the Teanaway River. In addition, estimates of hatchery and wild fish admixtures in naturally produced *O. mykiss* suggested that hatchery rainbow trout had previously spawned with steelhead and that hatchery steelhead had previously spawned with rainbow trout. We speculate that the magnitude of gene flow between rainbow trout and steelhead may vary spatially and temporally, depending in part on the number of anadromous steelhead that spawn within an area or year and on the number of steelhead offspring that rear and mature entirely within freshwater.

Oncorhynchus mykiss may possess the most diverse life-history patterns of any of the Pacific salmonid species. Much of the variation can be attributed to the migrational tendencies that have been observed within the species. One dominant life-history form of *O. mykiss* (steelhead) rears in fresh water, migrates to the ocean, and then returns to spawn in fresh water (Shapovalov and Taft 1954; Withler 1966; Wydoski and Whitney 1979; Behnke 1992; Peven et al. 1994). The other dominant life-history form of *O. mykiss* (rainbow trout) spends its entire life in fresh water (Wydoski and Whitney 1979; Behnke 1992). Within each dominant life-history form there is additional variation in migrational tendencies. For instance, some steelhead will migrate annually between the ocean and freshwater up to five times in order to spawn (Shapovalov and Taft 1954); some steelhead may rear in fresh water for up to 7 years before migrating to the ocean (Peven et al. 1994), and some offspring of steelhead may mature in fresh water without migrating to the ocean (Shapovalov and Taft 1954; Mullan et al. 1992a; Viola and Schuck 1995). Some rainbow trout are extremely sedentary, whereas others migrate considerable distances, particularly as juveniles during the spring and as adults before spawning (Bartrand et al. 1994). It is unclear whether ecological or genetic factors are responsible for the expression of the variation in migrational tendencies within *O. mykiss*, but both factors are probably influential. One mechanism that may influence the expression of intermediate migrational tendencies, or a mixture of such tendencies, is interbreeding between steelhead and rainbow trout (Moring and Buchanan 1978).

There is considerable uncertainty whether resident and anadromous *O. mykiss* interbreed (Busby et al. 1996). Both forms are found together throughout much of their range and spawn primarily during the spring (Rounsefell 1958; Scott and Crossman 1973; Wydoski and Whitney 1979). However, rainbow trout spawn at other times, particularly in spring-fed streams and in streams that have had hatchery stocking (Biette et al. 1981). Although rainbow trout and steelhead generally spawn at similar times and places, little is known about fine-scale spatial and temporal differences (*see* Neave 1944; Shapovalov and Taft 1954). High spatial and temporal overlap in spawning among rainbow trout and steelhead increases the potential for these forms to interbreed.

Genetic comparisons of rainbow trout and steelhead collected within a basin reveal differences in *O. mykiss* that are correlated with geography. In general, rainbow trout and steelhead collected from similar geographic locations are more genetically similar to each other than to rainbow trout and steelhead collected from different geographic locations (Busby et al. 1996). For example, rainbow trout and steelhead collected in the Columbia Basin east of the Cascade mountains are more similar to each other than to rainbow trout and steelhead collected west of the Cascades (Allendorf 1975). At a smaller scale, in the Deschutes River basin, Currens et al. (1990) found that there were significant differences in allozyme frequencies between rainbow trout collected above a barrier falls and *O. mykiss* collected below the falls. These fish from below the falls were probably a combination of rainbow trout and steelhead. Somewhat con-

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trary to the theory that rainbow trout and steelhead share the same gene pool, Campton and Johnston (1985) found that rainbow trout in the upper Yakima Basin were primarily an admixture of hatchery and native rainbow trout despite the stocking of hatchery steelhead into the basin. Furthermore, Neave (1944) found significant differences between average scale counts of rainbow trout and steelhead collected from the same place in the Cowichan River basin, British Columbia. He believed that these differences were genetically based, which suggests the two forms were not interbreeding. We know of no published studies that have compared the genetic structure of wild rainbow trout and steelhead that were collected from populations spawning in sympatry.

Determination of interbreeding between rainbow trout and steelhead has important management implications. As early as 1944, and most likely before, Neave (1944) suggested that rainbow trout and steelhead should be managed as different species in order to protect both forms. More recently, the National Marine Fisheries Service is considering whether to include rainbow trout as part of a steelhead evolutionarily significant unit (ESU) (Busby et al. 1996; NMFS 1996). If interbreeding between rainbow trout and steelhead occurs frequently, then rainbow trout might be considered part of a steelhead ESU. Furthermore, the abundance of rainbow trout may influence whether a steelhead ESU is worthy of protection by the federal government. Thus, depending on whether rainbow trout and steelhead interbreed and on the abundance of rainbow trout, an ESU may or may not receive federal protection.

The purpose of our study was to determine the potential for gene flow between resident and anadromous forms of *O. mykiss* in the Yakima River basin. We did this by determining the spatial and temporal overlap of spawning, comparing the genetic similarity of rainbow trout and steelhead collected from the same area, and by examining allozyme data for resident x anadromous matings, using hatchery fish as genetic markers.

Study Area

The Yakima Basin drains an area of 15,941 km^2 of south-central Washington, entering the Columbia River near Richland, Washington. Major subbasins of the Yakima River include the Satus, Toppenish, Naches, and upper Yakima (Figure 1). It is estimated that almost 100% of *O. mykiss* spawners in the Satus and Toppenish subbasins are steelhead (Hubble 1992; J. Hubble, Yakama Nation, personal communication), but less than 1% of *O. mykiss* spawners in the upper Yakima Basin are steelhead (WDFW, unpublished data). The proportion of *O. mykiss* that spawn in the Naches subbasin as steelhead is believed to be intermediate between Satus/Toppenish and the upper Yakima River. The lower boundary of the upper Yakima Basin is Roza Dam, which was constructed in 1939. Prior to 1987, fish could not ascend the fish ladder to pass upstream of Roza Dam when the reservoir pool was low. Low pool typically occurred during the winter. During 1987 a modification was made to the fish ladder that allowed fish to pass the dam when the reservoir pool was low. Rainbow trout located upstream of Roza Dam are abundant and provide Washington's best wild stream-trout fishery (Krause 1991; Probasco 1994). The Naches subbasin has several irrigation diversions that span the entire channel width. The Satus subbasin has no dams.

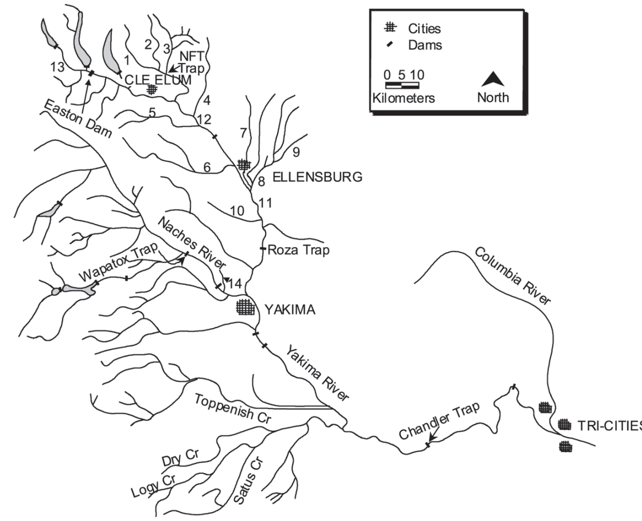

FIGURE 1.—Map of the study area. Numbers refer to study locations in the upper Yakima Basin (1–West Fork of the Teanaway River, 2–Middle Fork of the Teanaway River, 3–North Fork of the Teanway River, 4–Swauk Creek, 5–Taneum Creek, 6–Manastash Creek, 7–Wilson Creek, 8–Cherry Creek, 9–Badger Creek, 10–Umtanum Creek, 11–sections 1-3 of the Yakima River, 12–section 4-6 of the Yakima River, 13–section 7 of the Yakima River, 14–Buckskin Creek).

Non-endemic hatchery rainbow trout and steelhead have been heavily stocked in the Yakima Basin since the early 1940s (Campton and Johnston 1985). Between 1950 and 1980, 3,400,000 rainbow trout and 830,000 juvenile steelhead were stocked into the Yakima Basin from non-endemic hatchery populations (Campton and Johnston 1985). Between 1981 and 1994, about 966,000 rainbow trout and 1,268,500 steelhead were stocked into the Yakima Basin from endemic and non-endemic hatchery sources (Washington Department of Fish and Wildlife stocking records). Most of the hatchery rainbow trout stocked into the Yakima Basin were derived from northern California. Hatchery steelhead smolts stocked into the Yakima Basin were derived mainly from fish native to the Washougal and Klickitat rivers (Skamania strain) (Crawford 1979; Campton and Johnston 1985). These hatchery populations are genetically distinguishable from each other and from *O. mykiss* in the Yakima Basin (Campton and Johnston 1985; Pearsons et al. 1994). Non-endemic hatchery populations contain alleles that are not found in endemic Yakima River populations, and alleles common to hatchery and endemic populations are found in different frequencies (Phelps and Baker 1994). These differences are largely due to the source locations of hatchery strains (e.g., coastal areas). Trout from these areas are known to be genetically different from inland *O. mykiss* (Campton and Johnston 1985).

Methods

Ecology.—Sexual maturity and time of spawning were estimated in seven sections of the mainstem of the Yakima River between Roza Dam and Easton Dam and in 35 study sections in 13 tributaries of the upper Yakima River (Figure 1). The seven mainstem sections were numbered from 1 at the lowest to 7 at the highest elevation. Elevations above sea level at the midpoint of the sections ranged from 390 to 701 m in the mainstem and from 446 to 847 m in the tributaries. Adult steelhead were distinguished from adult rainbow trout by their larger size (> 51 cm FL) and location of capture (e.g., upstream trap). Their identity was often verified from scale pattern analysis. Electrofishing was used to collect rainbow trout for determination of maturity in the upper Yakima River and its tributaries from February through June during 1990 to 1993. Sample sizes were usually 10 to 30 adult-sized rainbow trout per section per survey, for a total of 30 to 90 rainbow trout per tributary per survey. In each tributary, a sample was collected with a back-pack electrofisher in a low, middle, and high elevation stream section. In the mainstem, a driftboat electrofisher was used to collect fish at least once per month from February until June. Fish were anesthetized and checked for spawning condition by gently squeezing the abdomen with thumb and forefinger to see if ova, milt, or resorbing fluids could be extruded. Sexually mature fish were defined to be those that exuded either milt or ova; they were further classified as ripe or spent.

The peak time of rainbow trout spawning was determined by calculating the time at which the greatest percentage of adult rainbow trout were sexually mature. The percentage of sexually mature rainbow trout was calculated as follows. First, the minimum adult size for each tributary stream and mainstem section was estimated to be the fork length of the smallest sexually mature rainbow trout collected during the sampling period (Martin et al. 1994). All others that were equal to, or greater than the minimum length were considered adult size and were defined as "potential" adults. The percentage of sexually mature rainbow trout was calculated by dividing the number of mature rainbow trout in a given sample by the number of "potential" adults.

The peak time of spawning activity was identified using an Open Quasi Cubic Spline method (Manugistics Corporation 1992) and then locating the highest points on the curve. The spline method uses a fifth-order polynomial interpolation to smooth small data sets. We used this smoothing to facilitate location of peaks. Peaks were not interpreted if sample size was less than eight adult-sized fish or if the percentage of sexually mature rainbow trout was less than 16%. The estimated peak time of spawning for each stream section was then compared to elevation at the midpoint of the section to determine if a relationship existed between rainbow trout spawn timing and elevation.

The spawn timing of steelhead was determined using a variety of field methods between 1990 and 1993, such as observations of redds, bankside observations, snorkeling, trapping, electrofishing, and radio telemetry. Panel or picket weir traps were used to trap fish in Wilson, Cherry, Umtanum, Swauk, and Taneum creeks. Spawning times and locations of radio-tagged steelhead were determined from a report by Hockersmith et al. (1995). Redds with fish on or near them were observed by helicopter on April 30, 1991. Bankside and snorkeling observations of steelhead were made throughout the study period. If an adult steelhead was collected by electrofishing or observed in a tributary after March 1, it was assumed to be a spawner at the time of sampling and information on spawning time and location was recorded. Steelhead that spawn in upper Yakima River tributaries frequently enter, spawn, and exit tributaries over a short time (Hockersmith et al. 1995).

Simple regression was used to describe the relationship between spawn timing and elevation for both rainbow trout and steelhead. Multiple regression and *t*-tests were used to compare the slopes and intercepts of regressions for rainbow trout and steelhead.

Hatchery steelhead "smolts" were released into the North Fork Teanaway subbasin annually between the spring of 1991 and 1994 and were examined for sexual maturity and gender. Approximately 150 steelhead from an average release number of 31,155 were examined at the time of release. In addition, hatchery steelhead juveniles and residuals were captured throughout the spring and summer in the North Fork Teanaway subbasin and examined for sexual maturity and gender. These fish were collected by electrofishing and trapping (weirs and screw traps).

Genetics.—Three genetic analyses were performed to determine if gene flow occurred between rainbow trout and steelhead. First, naturally produced sympatric rainbow trout and steelhead juveniles were collected from the North Fork of the Teanaway River and their allele frequencies were compared. Similarities in allele frequencies are an indication that the rainbow trout and steelhead interbreed. Rainbow trout were collected between 1991 and 1993 by electrofishing and angling. Steelhead smolts were collected in a downstream migrant trap during 1991. Second, naturally produced steelhead adults were collected throughout the Yakima Basin and were genetically examined for introgression with hatchery rainbow trout. Third, naturally produced rainbow trout adults were collected throughout the upper Yakima Basin and were genetically examined for introgression with hatchery steelhead.

To avoid mixes of steelhead and rainbow trout in the samples, specific guidelines were used to classify naturally produced rainbow trout and steelhead at the time of collection (see classification above). Only fish that were classified as naturally produced rainbow trout or steelhead were used in the analyses. Fish were classified as rainbow trout if they were < 51 cm, had characteristic coloring and morphology, and if they were sexually mature at the time of collection. Sexual maturity was determined based on the examination of gonads or the exuding of milt or ova. Precociously mature offspring of steelhead parents would be classified as rainbow trout under these criteria. Hatchery-produced rainbow trout were excluded from the samples. Rainbow trout were classified as "hatchery" if they had eroded fins and wavy fin rays. Juvenile fish were classified as steelhead if they had typical smolt characteristics and if they were captured in a downstream migrant trap or by electrofishing in areas without rainbow trout, such as in the Satus or Toppenish subbasins (Hubble 1992; J. Hubble, Yakama Nation, personal communication). Typical smolt charactistics that we used to classify steelhead included silvery coloration, lack of visible parr marks, easy loss of scales, torpedo shape (relatively thin), and dark band on the caudal fin. Hatchery-produced steelhead were excluded from the samples if they had clipped adipose or ventral fins, eroded fins, or wavy fin rays.

Naturally produced steelhead smolts that were used to determine introgression with hatchery rainbow trout were collected between 1989 and 1994. Downstream migrant traps were used to collect steelhead smolts from the Naches subbasin, upper Yakima Basin, and from the Yakima River at Prosser. Steelhead smolts were collected by electrofishing in the Satus and Toppenish subbasins. Naturally produced rainbow trout were collected between 1990 and 1993 in seven mainstem sections of the upper Yakima River and 10 of its tributaries. Rainbow trout were collected by electrofishing, angling, and trapping.

The collected fish were either dissected in the field (most adult specimens) or frozen whole at ultra-low temperatures (–80°C) and transported on dry ice to the Washington Department of Fish and Wildlife's Genetics Laboratory. Muscle, heart, eye, and liver tissues were dissected from each fish and placed into 12 x 75-mm plastic culture tubes. Electrophoresis followed the methods of Aebersold et al. (1987). The electrophoretic protocol, enzymes screened, and alleles observed during this study are described in Phelps et al. (1994). Genetic nomenclature follows the conventions of Shaklee et al. (1990).

A chi-square goodness of fit test was used to compare allozyme data between rainbow trout and steelhead collected in the North Fork of the Teanaway River. Hatchery admixtures were estimated using the program ADMIX (Long 1991). The ADMIX program calculates maximum likelihood estimates of the percentage of the genes that are contributed from hypothetical ancestral parental sources. Stated another way, ADMIX yields admixture proportions that are the best estimates of combinations of hypothetical parental sources. Results can indicate the degree of past breeding events if (1) the putative parental source information is correct, (2) their frequencies are reasonably close to what they would have been at the time the admixture occurred, and (3) there was opportunity for admixture. All of these conditions seem reasonable for our data. Because wild and introduced hatchery fish in the Yakima Basin are so different genetically, intermediate allele frequencies should indicate past breeding events. Three potential parental sources were used in the analysis: wild *O. mykiss*, hatchery rainbow trout, and hatchery steelhead (Table 1). "Wild" is defined as the naturally produced population that would be present in the Yakima Basin in the absence of interbreeding with non-endemic hatchery fish. Potential parental sources for wild *O. mykiss* were determined by examining allele frequencies of fish from the Satus and Teanaway subbasins; these fish were presumed to be representative of wild *O. mykiss*. Allele frequencies for steelhead produced at the Skamania Hatchery were used for the potential parental source of hatchery steelhead. Allele frequencies for rainbow trout produced at the Goldendale Hatchery were used for the potential parental source of hatchery rainbow trout. Some allele frequencies of potential parental sources were adjusted up or down if the "unknown population" was outside of the ranges of potential parental sources. This "adjustment" was necessary in order for the program to run.

Gametic disequilibrium analysis was used to determine whether rainbow trout collections contained a mixture of distinct gene pools or recent mixtures of gene pools (Nei and Li 1973; Waples and Smouse 1990; Phelps et al. 1994). In our samples, we had the ability to find significant gametic disequilibrium due to the presence of "pure" hatchery and "pure" wild rainbow trout, recent interbreeding of hatchery

TABLE 1.—Allele frequencies of potential parental sources used in admixture analyses. Sources for wild *O. mykiss* were from Satus and Teanaway subbasins, hatchery rainbow trout from Goldendale Hatchery, and hatchery steelhead from Skamania Hatchery.

Locus and Allele	Allele Frequency of Parental Source		
	Wild *O. mykiss*	Hatchery Rainbow	Hatchery Steelhead
*ADA-1*100*	1.00	0.25	1.00
*sAH*100*	0.80	1.00	0.97
*ALAT*100*	0.96	1.00	0.94
*CK-A1*100*	1.00	0.94	1.00
*GAPDH-3*100*	0.96	1.00	1.00
*bGLUA*100*	1.00	0.67	1.00
*mIDHP-2*100*	1.00	0.63	0.99
*sIDHP-2*72*	0.30	0.05	0.32
*LDH-B2*100*	0.50	1.00	0.82
*LDH-C*100*	1.00	0.90	1.00
*sMDH-B2*83*	0.00	0.55	0.01
*MPI*100*	0.90	1.00	1.00
*mSOD*100*	0.90	1.00	1.00
*sSOD-1*152*	0.05	0.36	0.24
*sSOD-1*38*	0.05	0.00	0.00
*TPI-3*100*	0.96	1.00	0.99
*ADH*100*	1.00	1.00	0.96
*GPI-A*100*	1.00	1.00	0.94
*G3PDH-1*100*	1.00	0.99	0.84
*sMEP-1*100*	1.00	1.00	0.94
*PEPA*100*	1.00	1.00	0.98
*PEPD-1*100*	1.00	1.00	0.91

and wild rainbow trout, or mixtures of rainbow trout cohorts that were genetically dissimilar (our samples were pooled among years). Failure to detect significant disequilibrium in collections would suggest that either parental gene pools have introgressed and represent one gene pool, or sample sizes were insufficient (Nei and Li 1973). We did not examine the steelhead collections because some of these were from traps that collected multiple stocks of steelhead. Otherwise, gametic disequilibrium analysis was performed on the same data that were used in the ADMIX analysis.

Results

Ecology

The spatial and temporal overlap of rainbow trout and steelhead spawning was very high. Except for one steelhead that spawned in a high elevation tributary that we did not electrofish, sexually mature rainbow trout were collected in all areas where steelhead spawned. However, rainbow trout spawned over a much larger geographic area than did steelhead. Rainbow trout spawned throughout all sampled reaches of the upper Yakima River basin. Rainbow trout spawned in tributaries and mainstem areas, and sexually mature individuals were collected at elevations between 375 and 1,061 m. Steelhead also spawned in tributaries and mainstem areas but spawned at elevations between 375 and 896 m.

Rainbow trout and steelhead spawned at similar times during the spring. Spawning generally began in February and continued through June. The earliest date that sexually mature rainbow trout were collected was February 1, and the latest date for spring spawners was June 28. Some sexually mature fish were also collected during fall sampling in some locations but not during the summer (Pearsons et al. 1996). Our analysis was restricted to spring spawning. Steelhead spawning occurred between February 28 and July 2.

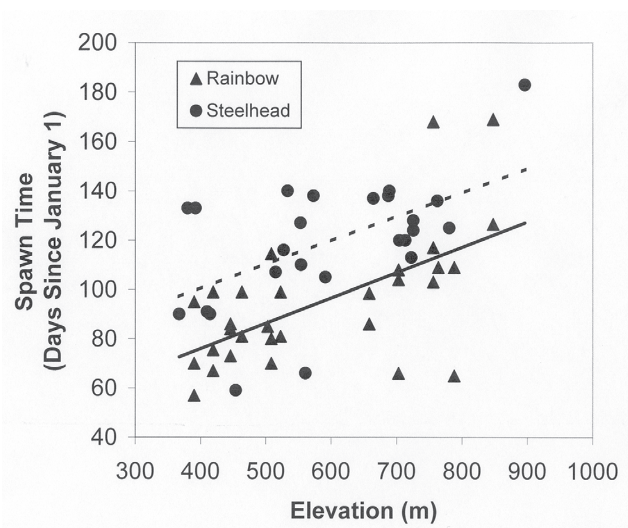

FIGURE 2.—Peak of spawning time for rainbow trout and spawning time of steelhead relative to elevation in the upper Yakima River basin. Regression lines are also presented (top line–steelhead, bottom line–rainbow trout).

Spawn timing of both rainbow trout and steelhead was positively related to elevation (Figure 2):

$$\text{PSTRBT} = 0.103 \cdot (\text{E}) + 34.8 \ (n = 30, r^2 = 0.37, P < 0.05)$$

$$\text{STSTH} = 0.098 \cdot (\text{E}) + 61.1 \ (n = 28, r^2 = 0.30, P < 0.05).$$

Where PSTRBT is the peak of spawn timing of rainbow trout measured in days since January 1, STSTH is the time of steelhead spawning in days since January 1, and E is the elevation measured in meters. There was no statistical difference in the intercepts ($t = 0.142$, $P = 0.89$) or slopes ($t = 0.978$, $P = 0.33$) of regressions between the peak of rainbow trout spawning and steelhead spawning.

We probably underestimated the duration of time that sexually mature rainbow trout were present because sexually mature fish were often collected during the first and last sampling period. However, sexually mature rainbow trout were rarely collected during other sampling activities in the summer, although some sexually mature rainbow trout have been collected in Badger, Wilson, and Cherry creeks and the Middle Fork of the Teanaway River during the fall.

We have observed many instances of suspected breeding between rainbow trout and steelhead. In 1992 a ripe female steelhead was trapped while migrating into Umtanum Creek and later was recaptured "spent" while migrating back downstream. This occurred near the peak of rainbow trout spawning activity in the creek. No other steelhead were observed to have entered the creek through the trap that year. In 1990, a spent female steelhead was collected adjacent to her redd in association with several ripe male rainbow trout. No other steelhead were collected in Umtanum Creek during 1990 despite intensive sampling. In 1995, one female steelhead was observed with mature rainbow trout on a redd in Buckskin Creek (tributary to the lower Naches River). Again, no male steelhead were captured in an adult migrant trap located below the redd. Lastly, many precocious hatchery steelhead have been observed in the North Fork Teanaway Basin. Up to 4.0% of hatchery steelhead released were sexually mature males. Less than 0.1% of precocious hatchery steelhead encountered during all sampling activities were females. Some precocious hatchery steelhead have been collected after they have spawned and others have been observed spawning with rainbow trout in the North Fork Teanaway subbasin.

Genetics

Genetic data supported the hypothesis that rainbow trout and steelhead were interbreeding where they were found in sympatry. Rainbow trout were genetically indistinguishable from steelhead collected in the North Fork of the Teanaway River ($X^2 = 54.99$, df = 43, $P = 0.104$). Except for the Satus and Toppenish subbasins, steelhead were estimated to be an admixture of hatchery rainbow trout, hatchery steelhead, and wild steelhead (Table 2). This result suggests that some steelhead have spawned with hatchery rainbow trout sometime

TABLE 2.—Admixture analysis of parental source (Long 1991) for Yakima Basin steelhead stocks. Smolts were collected by electrofishing or trapping. One standard error of the point estimate is shown in parentheses.

			Potential parental sources (%)		
			Hatchery		Wild
Location	Years	*n*	Rainbow	Steelhead	Yakima River
			Satus Creek subbasin		
Dry Creek	1989, 1991	153	2 (1)	0	98 (1)
Logy Creek	1990–1991	186	1 (0.3)	0	99 (0.3)
Satus Creek	1990–1991, 1994	263	2 (1)	0 (1)	98 (1)
			Toppenish Creek subbasin		
Toppenish Creek	1990, 1994	172	0 (0.5)	0	100 (0.5)
			Naches River subbasin		
Wapatox trap	1989–1991	366	6 (1)	4 (2)	90 (3)
			Upper Yakima Basin		
Roza trap	1989–1990	175	16 (2)	6 (3)	78 (3)
N.F. Teanaway trap	1991	25	9 (4)	11 (9)	80 (10)
			Yakima River (composite)		
Chandler trap	1989, 1994	373	11 (2)	3 (2)	86 (2)
Yakima Hatchery	1991	40	5 (2)	44 (10)	52 (10)

in the past. Conversely, with the exception of Wilson and Cherry creeks and the mainstem Yakima River above the Ellensburg Town Diversion, rainbow trout were estimated to be an admixture of hatchery rainbow trout, hatchery steelhead, and wild rainbow trout (Table 3). Again, this result further indicates that some rainbow trout and steelhead spawned together.

The estimated percentage of hatchery admixture among *O. mykiss* varied with location and life-history type. The percentage of hatchery rainbow trout alleles detected in rainbow trout samples was negatively related to elevation (Figure 3). However, the percentage of hatchery steelhead alleles detected in rainbow trout was unrelated to elevation. The highest percentage of hatchery rainbow trout admixture in steelhead samples in subbasins of the Yakima Basin was found in the upper Yakima Basin (16%), followed by the Naches (6%), Satus (2%), and Toppenish (0%) subbasins (Table 2). Rainbow trout had higher percentages of hatchery admixtures than did steelhead (Tables 2 and 3).

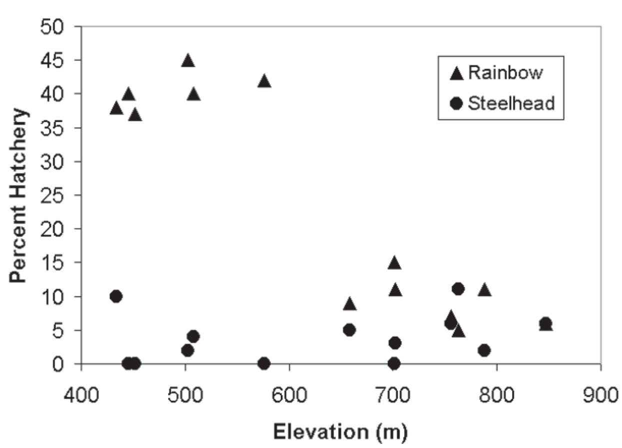

FIGURE 3.—Percentage of non-endemic hatchery rainbow trout and steelhead alleles found in naturally produced rainbow trout collected in the upper Yakima River basin.

Gametic disequilibrium analyses generally indicated that gene pools of parental sources were mixed through interbreeding. In other words, most of the rainbow trout collections (8 of 12) were not separate populations of non-endemic hatchery and wild fish but rather mixed populations of hatchery and wild fish. Those collections that were in disequilibrium were Wilson Creek, Cherry Creek, Manastash Creek, and the Middle Fork of the Teanaway River ($P < 0.05$). These collections were probably not in equilibrium because they contained samples with recent hatchery admixtures or were from pooled samples. Wilson Creek is the last stream location in the upper Yakima Basin that is still stocked with non-endemic rainbow trout, and some of these trout probably disperse into nearby Cherry Creek.

Discussion

Ecological and genetic evidence indicates that rainbow trout and steelhead in the Yakima Basin interbreed when in sympatry. Interbreeding between the two life-history forms may occur in a variety of ways. For example, the following

TABLE 3.—Admixture analysis of parental source (Long 1991) for upper Yakima Basin rainbow trout. Mature (ripe or spent) adults were collected by electrofishing. One standard error of the point estimate is shown in parentheses.

			Potential parental sources (%)		
			Hatchery		Wild
Location	Years	*n*	Rainbow	Steelhead	Yakima River
			Tributaries		
Wilson[a]	1990–1993	74	40 (3)	0	60 (3)
Cherry[a]	1990–1991	12	37 (5)	0	63 (5)
Badger	1991–1992	45	45 (7)	2 (5)	53 (8)
Umtanum	1990–1993	102	40 (7)	4 (6)	56 (8)
Taneum	1990–1992	59	11 (4)	2 (4)	87 (5)
Swauk	1990–1992	64	11 (2)	3 (3)	86 (3)
Manastash	1991–1992	69	9 (3)	5 (4)	86 (5)
M.F. Teanaway	1991–1993	86	5 (2)	11 (6)	84 (6)
W.F. Teanaway	1991–1993	72	7 (2)	6 (4)	87 (4)
N.F. Teanaway	1991–1993	55	6 (3)	6 (6)	88 (7)
			Mainstem		
Sections 1–3	1990–1992	108	38 (4)	10 (6)	52 (6)
Sections 4–6[a]	1990–1992	52	42 (4)	0	58 (4)
Section 7	1991–1992	14	15 (3)	0	85 (3)

[a] did not use *PEPD-1*100* for the estimate

crosses may occur: female steelhead x male rainbow trout, male steelhead x female rainbow trout, residual female steelhead (offspring of steelhead x steelhead mating) x male rainbow trout, residual male steelhead (offspring of steelhead x steelhead mating) x female rainbow trout, female steelhead x anadromous male rainbow trout (offspring of rainbow x rainbow trout mating) and male steelhead x anadromous female rainbow trout (offspring of rainbow x rainbow trout mating). All of the interbreedings that we observed that involved an anadromous adult were between female steelhead and male rainbow trout. At Waddell Creek, California, Shapovalov and Taft (1954) observed that female steelhead were very often accompanied by male rainbow trout during spawning. Only rarely were resident females observed with steelhead during spawning. Furthermore, as in other salmonids, male rainbow trout may successfully spawn with female steelhead, even in the presence of male steelhead, by sneak spawning (Shapovalov and Taft 1954; Hutchings and Myers 1985; Foote and Larkin 1988; Wood and Foote 1996). The sex ratio of anadromous steelhead may also be skewed toward females when large proportions of male offspring residualize (Thorpe 1987; Peven et al. 1994). A high proportion of anadromous females would increase the potential for female steelhead to spawn with male rainbow trout, particularly if anadromous male steelhead were scarce. This has been shown to occur in other salmonids (Jonsson 1985; Myers and Hutchings 1987).

Precocious male steelhead that do not migrate to the ocean may also spawn with female rainbow trout. We know of no studies that have definitively documented residualized precocious steelhead in natural populations below barriers. However, Mullan et al. (1992a) provide evidence to suggest that "steelhead" at high elevations are thermally fated to a resident life history. Humans have created self-sustaining populations of residualized steelhead in locations above impassable barriers. It is well documented that hatchery-reared populations of steelhead produce numerous precocious male steelhead (Tipping et al. 1995; Viola and Schuck 1995) that can spawn with female steelhead (Viola and Schuck 1995). Spawning between precocious males and anadromous females has also been documented in other salmonids (Myers and Hutchings 1987; Mullan et al. 1992b).

The amount of gene flow in the upper Yakima Basin may be artificially high due to low escapement of steelhead and a high number of rainbow trout. For example, three instances of gene flow between rainbow trout and steelhead occurred when only one female steelhead had ascended a stream that contained many mature rainbow trout. If the steelhead was to spawn in that stream it had to spawn with a rainbow trout or with another species. In addition, steelhead in the upper Yakima Basin collected at Roza Dam had the highest estimated percentage of hatchery rainbow trout ancestry, which further supports the contention that interbreeding may be artificially high in the upper Yakima Basin. Other explanations for the relatively high percentage ancestry of hatchery rainbow trout in steelhead in the upper Yakima Basin are also possible. For example, the number of hatchery rainbow trout stocked, or their survival and reproductive success, may have been higher in the upper Yakima Basin than in other areas of the basin. Unfortunately, we do not have the data that could be used to eliminate either of the explanations. Roza Dam was a probable contributor to the reduction in steelhead abundance, and to the ecological release of rainbow trout in the absence of strong anadromous fish runs

(Campton and Johnston 1985). The high proportion of spawning steelhead found in the Satus and Toppenish subbasins might be more representative of a natural population in the Yakima Basin.

We speculate that the magnitude of gene flow between rainbow trout and steelhead may vary spatially and temporally. If steelhead are in low enough numbers that they have difficulty finding steelhead mates, then there is a higher probability that they will spawn with rainbow trout if rainbow trout are present in spawning condition. Thus, in times or locations that experience low steelhead spawning escapements and that have sympatric rainbow trout populations, the extent of interbreeding could be relatively high. However, in times or locations with high steelhead spawning escapements and/or low numbers of sympatric rainbow trout, interbreeding could be relatively low. Interbreeding may be high when conditions that promote maturation of steelhead in fresh water are good. This might occur when growing conditions in fresh water are poor (Mullan et al. 1992a) or good (Thorpe 1987).

Results from our work suggest that endemic rainbow trout in the Yakima Basin should be included within a steelhead ESU because the two forms are not reproductively isolated when in sympatry. In fact, rainbow trout may be a good source of natural genes if steelhead are extirpated or if wild steelhead are excessively admixed with hatchery steelhead. Indeed, rainbow trout located in high elevation areas of the upper Yakima Basin could have a more natural complement of genes than steelhead spawning in the upper Yakima Basin. However, breeding between rainbow trout and steelhead poses genetic risks to steelhead. Interbreeding between hatchery admixed rainbow trout and steelhead may decrease the long-term fitness of steelhead due to loss of adaptation. In the upper Yakima Basin, this may occur at relatively low elevations, where hatchery admixtures of rainbow trout are high.

Acknowledgments

This paper is dedicated to Steve Phelps, who was a champion of wild fish conservation. He died in December 1999 and is greatly missed by his friends and the natural resources he cherished. We are very thankful to the people and entities that have helped bring this work to fruition. We especially thank Steve Leider, who was instrumental in helping in the initial design of the field work, provided administrative and intellectual support, and reviewed the manuscript. Bill Hopley also provided administrative support during the writing of this manuscript. Craig Busack and Carl Schreck provided excellent comments that improved the manuscript. Jim Olson, Marcia Fischer, Andrew Murdoch, John Long, Greg Strom, and Karin Wieland helped with the field work and data entry. Bruce Baker assisted with the genetic analyses. Craig Busack suggested the ADMIX program for our analysis and Jeffrey Long, National Institutes of Health, supplied us with the ADMIX program. Finally, thanks are extended to Anne Marshall, who reran some of Steve's genetic analyses and updated tables. This work could not have been completed without the funding provided by Bonneville Power Administration to the Yakima Species Interactions Studies under contract DE-BI79-96BP64878.

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Redband Trout: Resilience and Challenge in a Changing Landscape
Oregon Chapter, American Fisheries Society, 2007

Redband Trout in the Deschutes and White Rivers, Oregon

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Abstract.—Redband trout *Oncorhynchus mykiss* were studied in the lower Deschutes River in 1971–1988, and in the White River in 1983 and 1984 above a barrier waterfall located 3.4 km upstream of its confluence with the Deschutes River. Deschutes redband trout are genetically similar to those found east of the Cascade Mountains in the Columbia River basin, whereas White River redband trout are genetically unique and represent a different major evolutionary group among redband trout. Within the lower Deschutes River basin, redband trout occupy a wide range of habitats with vast differences in rearing conditions. Habitats include small spring-fed streams with low water temperatures, small streams with low summer flow and high water temperatures, and large rivers, of which the White River is the only glacial water in the lower Deschutes River basin. Deschutes redband trout are more abundant than those in the White River and are resistant to *Ceratomyxa shasta*, to which White River redband trout are susceptible. Within the White River basin, abundance of redband trout generally decreased with increased elevation. Redband trout may have been displaced or reduced in abundance by nonnative brook trout *Salvelinus fontinalis* in some upper White River tributaries where the habitat apparently favors brook trout. Redband trout in the upper White River, which is highly turbid during glacial melt, mainly fed on terrestrial invertebrates, whereas those in the lower river primarily fed on aquatic invertebrates. Although many positive measures have been taken to protect redband trout and their habitat in the lower Deschutes River basin, threats to populations remain from activities such as rail transport of hazardous materials along the Deschutes River, timber harvest and road construction, and stocking of hatchery rainbow and brook trout in the White River basin.

The Deschutes River below the Pelton–Round Butte hydroelectric complex is renowned for its fisheries on resident and anadromous *Oncorhynchus mykiss*. These fisheries are important for recreational users of the river and for tribal ceremonial and subsistence fishers. The Oregon Department of Fish and Wildlife (ODFW) conducted studies on population characteristics and life history of resident redband trout, and on effects of angling regulations in the lower Deschutes River in 1971–1988 (Schroeder and Smith 1989). A second study of redband trout was conducted in 1983–1984 in the White River, a tributary to the Deschutes River that is blocked to upstream fish passage 3.4 km from the confluence with the Deschutes by a series of waterfalls (ODFW et al. 1985). In addition, investigators from Oregon State University conducted studies on the stock characteristics of Deschutes and White River redband trout (Currens 1987; Currens et al. 1990; Currens 1997). This paper summarizes important findings of these studies and presents information to illustrate the life history and habitat diversity of redband trout in the lower Deschutes River basin.

Study Area

Redband trout in the Deschutes River basin were studied in the lower 161 km of the Deschutes River below the Pelton–Round Butte hydroelectric dam complex (lower Deschutes River), and in the White River, a tributary of the lower Deschutes River (Figure 1). The Deschutes River basin covers approximately 27,200 km^2 of central Oregon, of which the White River drains about 1,100 km^2. The White River is the second largest tributary of the lower Deschutes River. These study rivers flow through a mixture of public, tribal, and private lands. Much of the river frontage is public, administered by Bureau of Land Management, U.S. Forest Service, or State of Oregon. The remainder is either Warm Springs Indian Reservation or private property. Both rivers have been designated as National Wild and Scenic Rivers, and the lower Deschutes River has been designated as a State Scenic Waterway.

From its source at Little Lava Lake in the Cascade Mountains, the Deschutes River flows east and north, entering the Columbia River 330 km from the Pacific Ocean. The lower Deschutes River lies within the Columbia Plateau ecoregion (Omernik 1987). Westside tributaries (including the White River basin) extend into the Cascades ecoregion, and eastside tributaries extend into the Blue Mountains ecoregion. The lower Deschutes River flows through a narrow, winding canyon that drops from an elevation of 425 m to 50 m. Sherars Falls is a 5-m drop located 71 km upstream of the mouth of the Deschutes (Figure 1). The falls may have historically impeded upstream migration of redband trout but probably was not a barrier, especially at high flow when water would have cascaded down basalt ledges around the sides of the falls. A fishway constructed in the 1940s facilitated passage at the falls.

The White River originates at White River Glacier on the southeastern slopes of Mt. Hood and flows 80 km east to its confluence with the Deschutes River (Figure 1). Elevation of the White River drops from 2,100 m to 225 m. The upper river flows through a glaciated U-shaped valley before entering a deeply incised canyon that cuts through a basalt-capped plateau. In the Tygh Valley area the river flows

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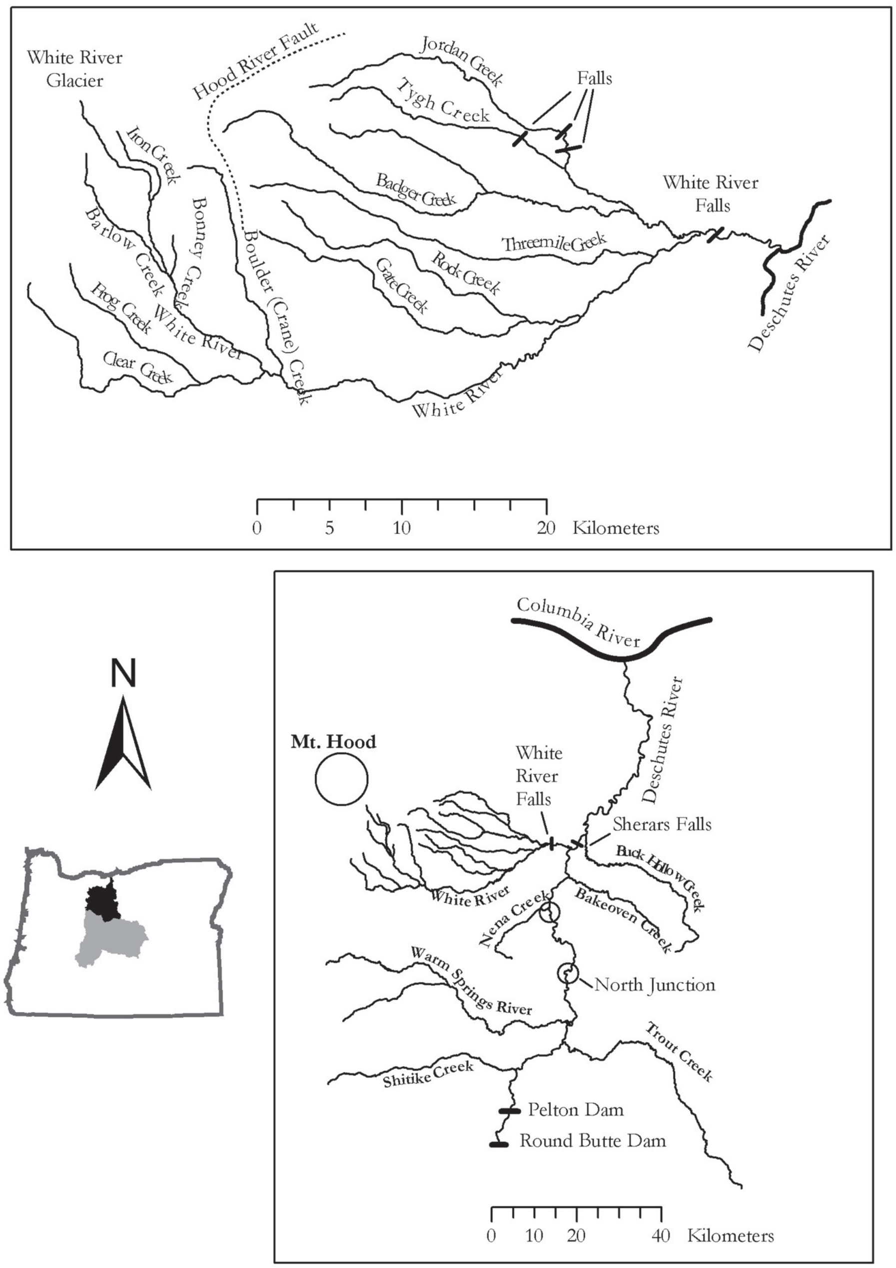

FIGURE 1.—Maps of the lower Deschutes River and the White River study areas. The shaded area of the inset indicates the Deschutes River basin, with the black shading designating the basin area downstream of the Pelton–Round Butte hydroelectric dams.

through a wide valley floor before plunging over a series of three barrier waterfalls (43 m, 8 m, and 6 m) and flowing another 3.4 km through a narrow canyon to the Deschutes River. The White River basin can be divided into three hydrologic areas: (1) main stem, the only water that is glacially influenced, (2) tributaries originating on the east slope of the Hood River Fault (e.g., Tygh, Badger, Rock, and Threemile creeks), and (3) tributaries originating on the west slope of the Hood River Fault (e.g., Boulder Creek) or on the east slope of the Cascade crest (e.g., Clear and Barlow creeks) (Figure 1).

Methods

Morphology, Genetics, and Disease Resistance.—Redband trout were collected for genetic and morphological analyses from one area in the lower Deschutes River (mature resident fish) and from nine areas in the White River basin. Juvenile *O. mykiss* were collected in tributaries of the Deschutes River where steelhead spawn and rear. Hatchery redband trout derived from the Deschutes River population were sampled from Oak Springs Hatchery. Genetic and morphological analyses were conducted by methods described in Currens (1987) and Currens et al. (1990).

Susceptibility to *Ceratomyxa shasta* (a myxosporean parasite) of wild redband trout from the White River was studied by holding 100 White River redband trout for 3 weeks in the Deschutes River, which is a known source of *C. shasta* (Ratliff 1981, 1983), along with 20 fish of a known susceptible strain of rainbow trout (Roaring River strain) as controls. In an ancillary experiment, 100 Roaring River rainbow trout were held for 3 weeks in the lower White River above the falls. After exposure, fish were transported live to the Fish Disease Laboratory in Corvallis and reared in pathogen-free water at 12°C. Mortalities were removed daily and examined by ODFW pathologists for *C. shasta* spores (Ratliff 1983). After 81 days at the laboratory, the survivors were killed and examined for spores.

Life History and Ecology.—In the lower Deschutes River, we captured redband trout in areas 5.0–6.5 km long using electrofishing gear mounted in a driftboat. We sampled each side of the river in a study section separately, and both sides generally were sampled on the same day. We held captured fish in a livebox and processed them at intervals of 0.8 km or 1.6 km (work stations). Redband trout were tagged during 6–9 sample trips with individually numbered Floy® tags to estimate abundance. Tagged redband trout were transported upstream in a jet boat for release in quiet water about one-half the distance between work stations. The low occurrence of fish recaptured two or more times during a sampling season (1% of tagged fish) compared to those recaptured a single time (14% of tagged fish) indicated good mixing of tagged and untagged fish (Schroeder and Smith 1989). Scale analysis of tagged and untagged fish indicated that tagging did not have a significant effect on growth (Schroeder and Smith 1989).

Effects of angling regulations on abundance of Deschutes redband trout in the Nena Creek and North Junction areas (Figure 1) were evaluated in the 1980s (Schroeder and Smith 1989). Estimates of abundance were calculated with the Schnabel mark-and-recapture method (Ricker 1975) for three size groups of redband trout in the lower Deschutes River that generally corresponded with age-2, age-3, and age-4 and older fish. Because of low recapture rates on small fish, abundance was estimated only for redband trout $\geq$ 19 cm. Migration and growth of redband trout also were evaluated from recoveries of tagged fish. In addition, the capture of tagged fish by anglers or in traps at Pelton Dam and at Warm Springs National Fish Hatchery in the lower Warm Springs River was used to evaluate migration of redband trout in the lower Deschutes River basin.

A limited study of food habits was conducted in the lower Deschutes River in 1976. Fish were collected 1 d/month for a year, usually at midmonth and midday, and stomachs were removed. Stomach contents were identified, enumerated, and weighed. In the White River, we collected data on food availability (insect drift) and food use (stomach contents) in August and September 1984 during a study of the effects of glacial conditions on redband trout. Drift nets (20 x 30 cm) were spaced on a riffle from the bank to the thalweg. Nets were set with 2.5 cm remaining above the water surface to catch adult aquatic and terrestrial insects. We collected most drift samples for 1 h at dusk. To study the food use of redband trout, we removed the stomachs of fish collected from the areas where drift nets were set. Contents of drift nets and stomachs were sorted and identified, and each taxon was counted and weighed.

We collected data on abundance, migration, and distribution of redband trout in the White River with electrofishing gear. All sites were sampled with backpack electrofishers, except a 3.4-km reach of the lower White River where we used a boat electrofisher. Fish sampling in the tributaries differed in 1983 and 1984. Tributaries were extensively sampled without block nets in 1983 to determine distribution and relative abundance of fish in the basin. Fewer sites were intensively sampled in 1984, when we used block nets and multiple-pass removal methods (Zippin 1958; Seber and Whale 1970) to estimate numerical and biomass density. Effects of glacial conditions on redband trout were assessed by information on fish abundance, substrate composition, and food availability and use. Redband trout were sampled at two sites in the White River during glacial melt, and in Barlow Creek, a nonglacial tributary in the upper basin. We recorded sample time, number of fish, fork length, and weight. In addition, substrate samples were collected at these sites with a freeze-core sampler.

Results and Discussion

Stock Characteristics

Mature redband trout in the Deschutes River are locally called “redsides” because most have a bright red stripe along the lateral line that extends onto the operculum. Faint yellow or orange coloration often occurs on the underside of the mandible, similar to that seen in cutthroat trout *O. clarkii*. Spotting of Deschutes redband trout ranges from large black spots on the entire dorsal surface to relatively few spots confined to the dorsal surface of the caudal area. Redband trout in the White River are generally heavily spotted and do not exhibit the degree of red coloration seen in Deschutes redband trout. Coloration on the underside of the mandible was not observed in White River redband trout.

Currens et al. (1990) concluded that wild redband trout in the lower Deschutes River basin belong to an inland group of *O. mykiss* associated with the Columbia and Fraser rivers east of the Cascade Mountains. General characteristics of this inland group are high frequencies of the lactate dehydrogenase *LDH-B2*76* allele and little variation at the superoxide dismutase *sSOD-1** locus (Allendorf and Utter 1976). However, White River redband trout exhibited very low frequencies of *LDH-B2*76* (Currens et al. 1990), suggesting distinct differences between redband trout in the lower Deschutes River and those in the White River (Figure 2). Genetic analyses also indicated greater genetic differentiation in redband trout of the White River basin than in *O. mykiss* in tributaries of the lower Deschutes River (Currens 1987).

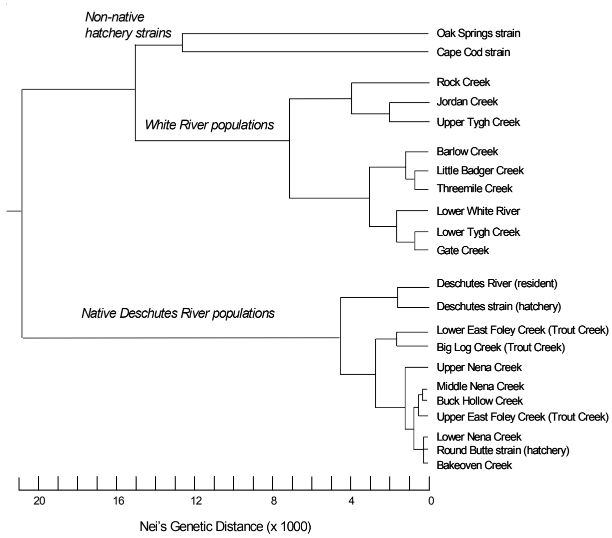

FIGURE 2.—Phenogram of biochemical similarity of two forms of native redband trout in the Deschutes River basin and nonnative hatchery strains (from Currens et al. 1990). Deschutes River samples were juvenile *O. mykiss* from streams used by steelhead, except mature resident fish from the main stem and hatchery strains from Oak Springs Hatchery (Deschutes resident strain) and Round Butte Hatchery (Deschutes steelhead strain).

Genetic analyses of redband trout collected from 13 major basins in Oregon, Washington, and Idaho indicated that redband trout in the White River represent a major evolutionary group, sharing similarities with redband trout from Chewaucan, Fort Rock, Catlow Valley, and Harney basins (Currens 1997). White River redband trout may represent an ancestral lineage of *O. mykiss* that invaded inland basins after the last glacial period (Currens et al. 1990). Behnke (1992) hypothesized that native cutthroat trout were replaced by an ancestral form of inland redband trout that entered the Columbia River watershed during or just before the last major glacial advance (30,000–50,000 years ago). Similarities between redband trout in the White River and Fort Rock basins suggest that an ancestral form of *O. mykiss* invaded the White River during a period when the Fort Rock and Deschutes River basins were connected—before late Pleistocene lava flows separated the drainages (Currens et al. 1990). Isolation of White River redband trout above the falls would have prevented them from acquiring traits that evolved in other inland redband trout of the Columbia and Fraser rivers (Currens et al. 1990). The amount of genetic divergence between the more primitive forms and more recent forms of redband trout (e.g., frequencies of *LDH-B2*76*) suggests that they have been isolated for perhaps 30,000 years (Behnke 1992).

Within the lower Deschutes River, genetic differences were detected between mature resident redband trout sampled in the main stem and juvenile *O. mykiss* from other Deschutes tributaries that are used by steelhead (Currens 1987). Because resident redband trout were sampled from only a single area of the lower Deschutes River, questions remain about differentiation among redband trout in different areas of the main stem.

Resident redband trout in the lower Deschutes River have meristic counts that also place them with other populations east of the Cascade Mountains, although they represented some of the lowest counts for the inland group (Currens et al. 1997). Mature redband trout collected in the main-stem Deschutes River have fewer scales and more pyloric caecae (average of about 50) than White River redband trout and juvenile *O. mykiss* from other Deschutes tributaries that are used by steelhead (Currens 1987). Basibranchial teeth were present in a small percentage of Deschutes and White River redband trout (Currens 1987). Although the morphology of redband trout differed between the Deschutes and White rivers, White River redband trout had similar morphological characteristics (Currens 1987) despite the wide range of thermal and hydrological habitats they occupy.

Although hatchery rainbow trout were stocked in the lower Deschutes River until 1978, redband trout in the main stem were genetically and morphologically different than hatchery strains (Currens 1987). Introgression between wild redband trout and hatchery rainbow trout in the lower Deschutes River would have been unlikely because the hatchery fish were susceptible to *C. shasta* (Ratliff 1983) and probably would not have survived to spawn.

Samples of redband trout from four locations in the White River basin showed intermediate genetic and morphological characteristics between those of coastal and inland populations, suggesting some level of introgression with introduced hatchery fish (Currens et al. 1990). These samples were collected in areas where nonnative rainbow trout had been stocked (the lower White River and Jordan, Rock, and lower Tygh creeks). However, the adenosine deaminase *ADA-1*85* allele was not detected in any White River population (Currens et al. 1990), despite its common presence in nonnative hatchery strains that were stocked in the basin. This allele was also common in hybridized redband trout populations in the Metolius River (Currens et al. 1997). Although hatchery rainbow trout had been stocked in some areas of the White River basin for 50 years at the time of this study (1984), introgression with wild fish may have been limited for several reasons. First, the hatchery fish stocked in the White River basin were fall-spawning stocks, whereas wild redband trout spawned in the spring, therefore minimizing direct interbreeding between wild and newly stocked hatchery fish. Spawning conditions in the fall also may have prevented successful reproduction of hatchery fish because of low water in the tributaries where hatchery fish were stocked, or because of high loads of glacial sediment in the main stem during fall rains. In addition, the reproductive potential of hatchery fish in the lower main stem is decreased because of mortality (natural and harvest) and downstream migration past the falls. The catch of hatchery rainbow trout by boat electrofishing gear in a 3.4-km reach above the falls decreased from 1.0 fish/min in July 1984, shortly after a group of hatchery fish was stocked, to < 0.1 fish/min in Oc-

TABLE 1.—Infection frequencies from *Ceratomyxa shasta* in White River redband trout and in hatchery rainbow trout exposed to waters of the Deschutes and White rivers, 24 May–20 June 1984 (from ODFW et al. 1985).

Exposure location	Stock	Mean water temperature (°C)	Number exposed	Infection frequency (%)
Deschutes River	Roaring River[a]	13	20	95
Deschutes River	White River	13	100	93
White River	Roaring River[a]	11	100	0

[a] Known susceptible stock.

tober. During the time that a migrant trap was operated below the falls (28 April–28 June 1984), an estimated 233 hatchery rainbow trout migrated over the falls, representing about 12% of the fish that had been stocked above the falls.

Disease Resistance

Within the lower Deschutes River basin, the resistance of redband trout populations to infections caused by *C. shasta*, a myxosporean parasite, depends on whether the fish evolved in the presence of the parasite. Redband trout in the Deschutes River are resistant to infections caused by *C. shasta* (Johnson 1975), which is present in the Deschutes River and has been in high abundance in the past (Ratliff 1981, 1983). In contrast, White River redband trout held in the Deschutes River had high levels of *C. shasta* infection (Table 1). A susceptible stock of rainbow trout held in the lower White River above the falls did not have any infections (Table 1), indicating that the parasite was absent in this part of the watershed. Although native salmonids in the Deschutes basin are usually resistant to *C. shasta* (Buchanan et al. 1983; Ratliff 1983; Currens et al. 1997), native redband trout in the White River lack resistance, apparently because they did not evolve with *C. shasta* and because they have been reproductively isolated from the resistant redband trout in the Deschutes River. Interbreeding between resistant and susceptible stocks can result in intermediate levels of resistance (Hemmingsen et al. 1986; Wade 1986; Currens et al. 1997), indicating heritability of resistance.

Life History and Ecology—Deschutes River

Species composition.—Redband trout share the lower Deschutes River with a wide range of other native species. In addition to summer steelhead and spring and fall races of Chinook salmon *O. tshawytscha*, the river also supports large populations of mountain whitefish *Prosopium williamsoni* and suckers *Catostomus columbianus* and *C. macrocheilus*. Data collected in the lower Deschutes River in 1975 (standardized by the recapture rate of redband trout) suggested that whitefish were almost six times as abundant as redband trout and suckers were twice as abundant (Schroeder and Smith 1989).

Other native species found in the lower Deschutes River include bull trout *Salvelinus confluentus*, Pacific lamprey *Lampetra tridentata*, northern pikeminnow *Ptychocheilus oregonensis*, dace (*Rhinichthys* spp.; *R. cataractae* common), cottids (*Cottus* spp.; *C. beldingii and C. rhotheus* common), redside shiner *Richardsonius balteatus*, and chiselmouth *Acrocheilus alutaceus*. Uncommon species include coho salmon *O. kisutch* and sockeye salmon O. *nerka*. Low numbers of nonnative fish also have been captured in the river.

Distribution and Abundance.—Redband trout are distributed throughout the lower 160 km of the Deschutes River, although abundance is higher upstream of Sherars Falls (Figure 1), which is not a complete barrier to migration. Density of redband trout ≥ 19 cm in several sample areas upstream of Sherars Falls averaged about 1,000 fish/km (Schroeder and Smith 1989). Densities ranged from 400 to 1,600 fish/km, with an average 95% confidence interval of ± 24% of the estimate. Limited sampling downstream of Sherars Falls indicated that the density of redband trout was only 30% of that above the falls (Schroeder and Smith 1989). The Deschutes River below Sherars Falls has higher water temperature and lower quantity of spawning gravel than the river above the falls. These factors and the influence of glacial sediment from the White River could make the Deschutes River below Sherars Falls less productive for redband trout than the river above the falls.

The annual abundance of Deschutes redband trout generally fluctuated in a similar manner in two study areas above Sherars Falls (Figure 3). The abundance of redband trout in the Nena Creek area increased after angling regulations were changed to a 30.5-cm minimum size limit in 1979 (Figure 3). Effects of the regulation change were most noticeable in redband trout ≥ 25 cm, which increased almost four times in

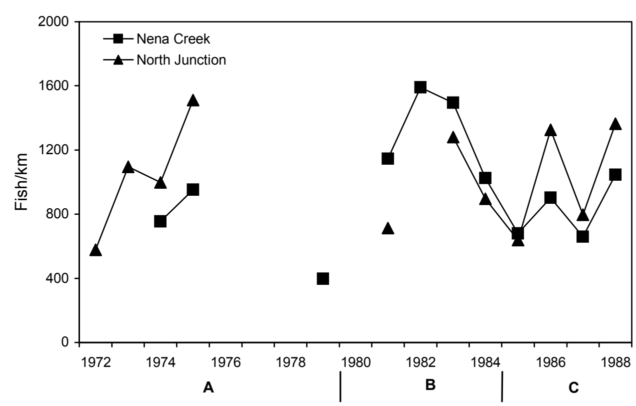

FIGURE 3.—Abundance of redband trout ≥ 19 cm in two study areas of the Deschutes River, 1972–1988 (from Schroeder and Smith 1989). Catch restrictions were: **A** = Nena Creek: 6 fish ≥ 15.2 cm (6 in.), only 3 ≥ 30.5 cm (12 in.); North Junction: 2 fish ≥ 30.5 cm, **B** = both areas: 2 fish ≥ 30.5 cm, **C** = both areas: 2 fish 25.4–33.0 cm (10–13 in.).

the Nena Creek area compared to a slight decrease (10%) in the North Junction control area (Schroeder and Smith 1989). Angling regulations in both areas were changed to a slotted size limit in 1985. Subsequently, the abundance of redband trout < 31 cm decreased in both areas (40 and 22% at Nena Creek and North Junction, respectively). The abundance of fish ≥ 31 cm decreased slightly (10%) at Nena Creek after the regulation change, whereas the abundance of these fish increased 40% at North Junction (Schroeder and Smith 1989).

Spawning.—Most Deschutes redband trout spawned between April and July, with first-time spawners being 3 or 4 years of age and averaging 30–33 cm in length. Their fecundity averaged 1,300–1,500 eggs. Mature fish composed about 30% of the population of redband trout 25.0–30.9 cm, and increased to 75% in fish ≥ 31 cm. Within the population of mature fish, about half were repeat spawners, although the time between spawning for some fish was 2 to 3 years (Schroeder and Smith 1989).

Some redband trout spawned at the same time and in the same general locations as steelhead (Schroeder and Smith 1989). Spawning surveys below Pelton Dam also showed slight overlap in timing of spawning between redband trout and steelhead, but a segregation of spawning habitat based on differences in microhabitat characteristics of redds (Zimmerman and Reeves 2000). Primary spawning gravels in the main stem are found around islands, in side channels, and in areas close to shore that are protected from high flows. The quantity of suitable spawning gravel is greatest immediately below Pelton Reregulating Dam and substantially decreases downstream (Huntington 1985). Little information has been collected on the use of tributaries by Deschutes redband trout for spawning and rearing. However, Currens (1987) reported that *O. mykiss* collected in small, unisolated tributaries of the lower Deschutes River mostly were juveniles < 2 years of age. They were genetically differentiated from resident redband trout in the main stem, and exhibited low levels of allelic heterogeneity indicative of gene flow among tributary populations, suggesting that these tributaries are primarily used by steelhead.

Age and Growth.—Scale analysis and tag recoveries indicated that many redband trout ≥ 25 cm were 5–7 years old, with some fish living to 10 years (Schroeder and Smith 1989). On average, redband trout in the lower Deschutes River grow about 8–11 cm per year in their first 3 years of life, and annual growth slows to 1–3 cm as more fish reach maturity.

Maturity and size influence the growth of redband trout in the lower Deschutes River. Immature redband trout in the Deschutes River grew faster than mature fish (Table 2). The difference in growth among stages of maturity within a size group was significant ($P < 0.05$) except for fish < 19 cm ($P = 0.14$). Growth may be limited in mature redband trout because food consumed in the early spring would be used for gonadal development, and food consumed in the summer would be used to regain body condition after spawning. However, food consumption by redband trout > 25 cm was found to decrease in late summer and autumn after a peak in spring and early summer (Schroeder and Smith 1989). Even if fish remain immature, growth slows as they become larger (Table 2).

Food Habits.—The primary diet of redband trout in the lower Deschutes River was insects, mainly Ephemeroptera, Plecoptera, Trichoptera, and Diptera (Schroeder and Smith 1989). Immature aquatic insects were generally a larger part of the redband trout diet than adult insects, except during spring and early summer, when Plecoptera and Ephemeroptera adults composed a major portion of the diet. Some redband trout consumed fish (whitefish and sculpins), fish eggs (primarily whitefish), snails, and crayfish.

Migration.—Recoveries of tagged fish suggest that most redband trout ≥ 19 cm do not move great distances within the lower Deschutes River (Schroeder and Smith 1989). However, studies of Deschutes redband trout were not designed to measure migration of fish and results should be viewed with caution (*see* Gowan et al. 1994). Of the tags returned by anglers or recovered in traps (average of 333 tags recovered from each of four different study areas above Sherars Falls), 77% were within the original tagging areas of 5.0–6.5 km, 12% were upstream, and 11% were downstream. Tagging generally occurred in early spring and returns from anglers occurred in summer and fall. Of the fish that did migrate, the median distances of upstream and downstream movement were 18 and 13 km, respectively. Within the tagging areas (5.0–6.5 km long), 72% of the recaptured fish were caught on the same bank of the river within 1.6 km of where they were tagged and released 1–4 years earlier. The remainder of recaptured fish had moved across the river within 1.6 km of where they were tagged and released (18%) or had moved upstream or downstream (10%).

Migration of redband trout between two study areas 16 km apart (Figure 1) was estimated during an extensive tag-

TABLE 2.—Mean annual growth (SE, *n*) of tagged redband trout in the Deschutes River in four size groups and three stages of maturity (from Schroeder and Smith 1989). The stage of maturity was determined at the time of capture and at the time of subsequent recapture.

Maturity between capture	Mean annual growth by size group (cm)			
and recapture	< 19.0	19.0–24.9	25.0–30.9	≥ 31.0
Immature to immature	8.2 (0.63, 33)	5.4 (0.20, 159)	3.4 (0.18, 152)	2.8 (0.35, 57)
Immature to mature	5.8 (2.87, 3)	4.4 (0.29, 72)	2.9 (0.14, 147)	1.8 (0.15, 122)
Mature to mature		1.9 (0.55, 15)	0.9 (0.14, 86)	0.8 (0.10, 270)

ging program in the 1980s by expanding recoveries of tagged fish by the estimated proportion of the population that was tagged (Schroeder and Smith 1989). An estimated 9 redband trout per year migrated upstream from the Nena Creek area to the North Junction area, representing 0.3% of the Nena Creek population. The downstream migration from North Junction to Nena Creek averaged 2 redband trout per year, which was just 0.05% of the North Junction population. However, some tagged fish could have migrated between areas during the year before returning to their original area. Redband trout in these two study areas exhibited differences in life history (size and age at maturity, percentage of repeat spawners, annual mortality), suggesting influence of different environments, influence of differential harvest, or presence of local populations (Schroeder and Smith 1989). Additional work could determine if these life history differences have persisted and if they are related to low migration rates between areas.

Migration of redband trout in the lower Deschutes River is interesting because the river supports both resident and anadromous races of *O. mykiss*. Currens (1987) found that resident redband trout in the main stem were genetically differentiated from and more reproductively isolated than *O. mykiss* sampled in tributaries used by steelhead. His analysis also suggested that these groups had been reproductively isolated for a long period. In a recent study, analysis of Sr/Ca ratios in otoliths indicated that all adult steelhead (n = 20) were progeny of steelhead females and all adult redband trout (n = 38) were progeny of resident redband trout (Zimmerman and Reeves 2000). These data and the continued presence of the two races in the lower Deschutes River suggest distinct separation and reproductive isolation of resident and anadromous *O. mykiss*.

Life History and Ecology—White River

Species Composition.—The White River basin has a low diversity of native fish species (ODFW et al. 1985). The only native species in the basin besides redband trout are cottids (*C. beldingii* and *C. confusus* tentatively identified, other cottid species also may be present), mountain whitefish, and longnose dace. Cottids are well distributed throughout the basin. Mountain whitefish appeared to be limited to the lower 8 km of the White River above the falls and longnose dace were found only in Threemile Creek below a reservoir. Northern pikeminnows and suckers were not found in the White River basin, although they are abundant in the Deschutes River. In addition, no bull trout were found in the White River basin. Brook trout were found only in the upper basin. Hatchery rainbow trout have been introduced into the main stem, a few tributaries, and several lakes and small reservoirs in the basin. However, during surveys of the basin, hatchery rainbow trout were captured only in the lower White River, where their estimated abundance was < 10% that of wild redband trout.

Distribution and Abundance.—Wild redband trout in the White River basin above White River Falls are widely distributed in the main stem and in all major tributaries. They are also found above barrier waterfalls in several tributaries, particularly in Jordan and Tygh creeks.

The habitat types inhabited by redband trout in the White River basin are highly diverse. The White River is a glacial stream that seasonally has high levels of sediment (suspended and bedload) when White River Glacier melts. The upper part of the watershed is montane, forested habitat and the lower watershed is sagebrush–juniper–ponderosa pine habitat, with a cottonwood riparian community in the Tygh Valley area. The range of mean maximum water temperatures in summer was 9–15°C in the upper river and 14–19°C in the lower river. Tributaries flowing from the east slope of the Hood River Fault (Figure 1) start in montane, forested habitat and end in sagebrush–juniper–ponderosa pine habitat. Maximum water temperatures in the summer ranged from 11°C in upper reaches of these streams to 25°C in lower Tygh Creek. Tributaries in the upper White River basin are mostly in montane, forested habitat with low maximum temperatures in summer (range of 9–12°C).

Wild redband trout (age 1 and older) in the White River basin generally were more abundant in sites below 900 m than in high elevation sites (Figure 4), suggesting productivity is higher in low-elevation waters. Conductivity in the White River and its tributaries was higher at low elevations (80–86 μS/cm) than at high elevations (42–66 μS/cm), and conductivity in the White River basin was lower than that in the Deschutes River (range 100–160 μS/cm). The density of redband trout in a 3.4-km section just upstream of White River Falls was about 350 fish/km in 1984.

Brook trout were found in three tributary watersheds (Clear, Boulder, and Barlow) of the upper White River, downstream of lakes where they have been stocked (ODFW et al. 1985). However, brook trout were not found in Badger Creek downstream of lakes where they are present. Allopatric populations of brook trout were found in the upper reaches of Clear and Frog creeks during 1983 surveys, with a zone of sympatry downstream of these sites (Figure 5). The lower

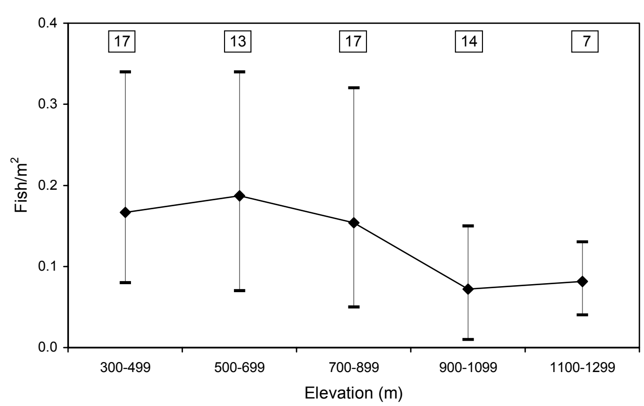

FIGURE 4.—Mean and range of densities (fish/m^2) of age-1 and older redband trout (> 8 cm) caught with electrofishing gear in White River tributaries, August–September 1984. Number of sample sites is given in boxes (data source: ODFW et al. 1985).

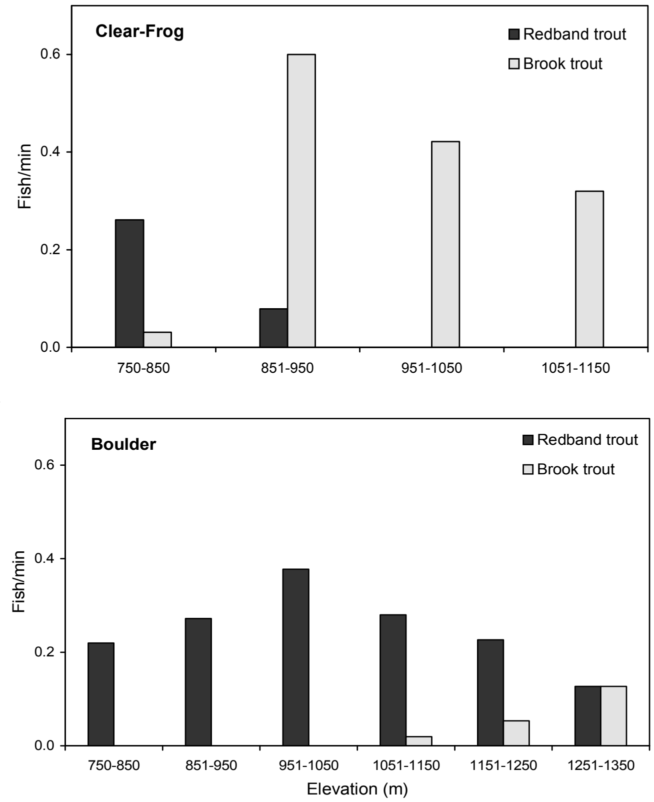

FIGURE 5.—Catch rate (fish/min) by electrofishing of redband and brook trout ≥ 5 cm in elevational reaches of Clear, Frog, and Boulder creeks, August–September 1983 (data source: ODFW et al. 1985).

reach of Clear Creek was predominantly redband trout. A higher percentage of brook trout was found in the downstream reach of Clear Creek in 1984 (26%) than in 1983 (7%), and a few redband trout were found in the upper reach of Clear Creek in 1984. Brook trout were well established in the upper reach of Boulder Creek (Figure 5) in 1983 and 1984 surveys. The only other tributary with brook trout was Barlow Creek, where small numbers were found in the lower reach, above and below a small tributary of lower Barlow Creek (Green Lake Creek) where brook trout were allopatric. Small numbers of brook trout also were found in the White River in 1984 near the confluence with Barlow Creek.

Studies have reported that redband trout are the superior competitor and that brook trout are not common in interior Pacific streams where steelhead and redband trout are indigenous (reviewed in Fausch 1988). In contrast, brook trout apparently have displaced redband trout in the upper areas of Clear and Frog creeks (Figure 5). An alternate explanation is that redband trout were naturally absent in the upper reaches of these streams. However, redband trout were distributed into the upper reaches of other White River tributaries where brook trout were absent or in low numbers. In addition, the average catch of fish in sympatric sites or in allopatric brook trout sites was greater than the average catch of redband trout in sample sites of lower Clear Creek where redband trout were predominant (Table 3), indicating adequate production potential in the upper reaches of these streams. Brook trout also may have displaced some redband trout in the upper area of Boulder Creek (Figure 5 and Table 3). However, the abundance of redband trout might be naturally low at the high elevations of upper Boulder Creek, and brook trout may be occupying habitat niches to which they are adapted. Redband trout in upper Boulder Creek were found at higher elevations than redband trout in other upper White River tributaries. The catch of redband trout remained relatively high (0.24 fish/min) in the upper reaches of Badger, Jordan, and Gate creeks at elevations similar to the uppermost sites of Boulder Creek.

In other studies, brook trout occupied the upstream reaches of streams where low water temperature and velocity may have conferred a competitive advantage to brook trout and limited the upstream migration of rainbow trout (reviewed in Fausch 1988). Water temperatures in upper White River tributaries generally were similar (Table 3). The areas where brook trout were most abundant had lower gradient and more pool habitat than the areas where redband trout predominated or were allopatric (Table 3). These data suggest that brook trout have a competitive advantage over redband trout in stream sections where low-velocity pools are available, and that lack of pool habitat in high gradient areas may limit the downstream distribution of brook trout. For example, high gradient and the low percentage of pools in upper Badger Creek (Table 3) may have prevented brook trout from becoming established in that stream.

Questions about range expansion or contraction of brook trout cannot be answered, because surveys of White River tributaries are lacking before 1983–1984 and surveys in 1997–1999 were not extensive enough to determine species distribution (U. S. Forest Service, unpublished data). Brook trout may be persisting in Clear, Boulder, and Barlow creeks because of continued stocking into some lakes of these watersheds. However, brook trout may be self-sustaining in some tributaries. Brook trout were last stocked in Frog Lake at the head of Frog Creek in 1956, yet brook trout were abundant in Frog Creek over several size groups in 1984 and juvenile fish were found in 1998 (U.S. Forest Service, unpublished data). Brook trout could migrate into Frog Creek from Clear Creek, although they were last stocked in Clear Lake in 1989. An allopatric population of brook trout was found in 1983 in Green Lake Creek, a small tributary that drains Green Lake and enters lower Barlow Creek from the west. Green Lake had been stocked with brook trout just three times in 1953–1955. Additional surveys in tributaries of the upper White River would provide important information on the status of redband trout, and could provide information on the interactions between redband and brook trout.

Age and Growth.—Scale analysis indicated that most of the redband trout collected in the White River basin were 1–3 years old, with some up to 5 years old. Sampling was more extensive in tributaries than in the main stem, which could influence these results. Although the tributaries represent almost 75% of the stream length that supports fish in the

Table 3.—Relative catch by electrofishing (fish/minute) of redband and brook trout ≥ 5 cm and habitat characteristics in samples sites of White River tributaries, 1983–1984 (data source: ODFW et al. 1985).

	Upper White River tributaries			
Parameter	Clear-Frog	Boulder	Other[a]	Badger Creek[b]
Catch (fish/min)				
Redband trout	0.26	0.27	0.36	0.18
Sympatric[c]	0.42 (0.18)	0.30 (0.11)		
Brook trout	0.54			
Gradient				
Redband trout	5.7	3.5	3.2	4.7
Sympatric	2.2	2.0		
Brook trout	1.8			
Pool area (%)				
Redband trout	41	41	40	35
Sympatric	51	51		
Brook trout	65			
Water temperature (°C)				
Mean maximum	11.8	12.8	11.8	13.4
Mean minimum	7.5	7.5	6.9	7.9

[a] Barlow, Bonney, and Iron creeks and an unnamed tributary downstream of Bonney Creek.
[b] Above 800 m in elevation.
[c] Combined catch of redband and brook trout, with catch of redband trout in parentheses.

basin, younger fish might disproportionately rear in the tributaries. The mean annual growth of redband trout in the lower White River in their first 2 years (11.9 cm and 6.2 cm, respectively) was significantly greater ($P < 0.05$) than the first 2 years of growth (8.1 cm and 3.4 cm, respectively) in all other locations of the basin.

Scales from redband trout > 30 cm in the lower White River, showed that first spawning was generally at age 3 (61% of the sample) or age 4 (31%), and at 30–33 cm, similar to that in the Deschutes River. White River redband trout in the lower river showed continued growth after maturity, based on a small sample of scales (n = 21), which contrasts with little growth after maturity seen in Deschutes redband trout. Studies linking fish growth to energy intake and loss have shown a decrease in trout growth in midsummer because food consumption was inadequate to meet metabolic demands (*see* Railsback and Rose 1999). Although data are limited, scales of age-3 and older redband trout in the lower White River showed a substantial increase in growth in summer, suggesting a sustained level of food consumption. In contrast, Deschutes redband trout > 25 cm consumed less food in the summer than in the spring. A bioenergetics model found that growth was affected primarily by food consumption, which reflected factors such as water temperature, flow, and trout density (Railsback and Rose 1999).

Glacial Influences.—Redband trout residing in the White River are exposed to large amounts of glacial sediment when White River Glacier is actively melting (usually August and September). Redband trout continued to be found in the upper main stem even when the levels of bedload and suspended sediment were very high. However, the catch of redband trout in the upper river decreased by 50% from August to September, when glacial melt was at its peak (Figure 6). The catch of redband trout in nearby Barlow Creek decreased 22% in September whereas catch in the lower river increased 37%. These data suggest that some redband trout in the upper main stem moved downstream to areas less affected by glacial melt, but apparently did not move into a nearby tributary.

During glacial melt the average load (Mg/d) and maximum concentration (g/L) of suspended sediment is about 65 times greater in the upper White River (908 Mg/d and 53 g/L) than in the lower river (14 Mg/d and 0.8 g/L) (U.S. Department of the Interior, Bureau of Reclamation and Geological Survey, unpublished data). Bedload transport of sediment in the upper river was estimated at 458 Mg/d dur-

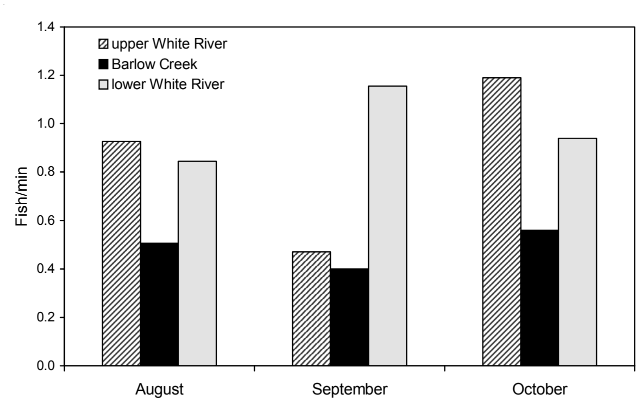

FIGURE 6.—Catch rate (fish/min) by electrofishing of redband trout ≥ 5 cm in two sections of the White River (glacial) and in Barlow Creek (nonglacial tributary), August and September 1984. Sediment load from glacial melt was highest in the upper White River in September (data source: ODFW et al. 1985).

ing a period of active melt (U.S. Department of the Interior, Bureau of Reclamation, unpublished data). Fall and winter rain flushes deposits of glacial sediment from the upper river and increases the suspended sediment load in the lower river to an average of 1,628 Mg/d with concentrations as high as 57.8 g/L (U.S. Department of the Interior, Geological Survey, unpublished data).

Redband trout in the White River also would have been exposed to large influxes of sediment during historic periods of volcanic activity of Mount Hood. For example, about 200 years ago collapse of a lava dome produced lahars that flowed the length of the White River and inundated large portions of Tygh Valley (Scott et al. 1997). Lahars (also called volcanic debris flows or mudflows) carry large amounts of sediment and can form when hot gases rapidly melt glaciers or when heavy rain saturates volcanic deposits. The amount of sediment carried by lahars is illustrated by an event in 1984 when a small lahar flowed from the crater of Mount St. Helens and produced a sediment load of 135,000 Mg/d with concentrations of almost 83 g/L (Dinehart 1997).

Glacial sediment increases the amount of fine material in the substrate and subsequently lowers the production and availability of aquatic invertebrates. The percentage of fines and sand (< 1.0 mm) in the top 10 cm of substrate was much higher in the upper river (35%) than in the lower river (3%), or in lower Barlow Creek (5%)—a nonglacial tributary of the upper White River (ODFW et al. 1985). During glacial melt, drift samples in the upper river were composed equally of aquatic and terrestrial insects, whereas samples in the lower river were almost exclusively (99%) aquatic invertebrates (ODFW et al. 1985). However, redband trout that continued to reside in the upper main stem during peak glacial melt were able to maintain their body condition, evidently by feeding predominantly on terrestrial insects. Almost 80% of the diet (by weight) of redband trout in the upper White River was terrestrial insects during a period of glacial melt, whereas terrestrial insects in the lower river composed less than 1% of the diet (ODFW et al. 1985).

Conclusions

Redband trout in the lower Deschutes River basin represent a rich diversity of genetics and life histories, including resident and anadromous forms and ancestral populations in the White River basin. These populations also illustrate the use of widely different habitats by resident redband trout, including a large river populated by anadromous steelhead, a glacial river, small streams with high summer temperatures and low flow, and montane streams with low summer temperatures. Redband trout in these varied habitats may have acquired unique adaptations for surviving in their environments.

In many respects, the prospects for redband trout in the lower Deschutes River basin have improved in recent decades. Riparian areas have received more protection by federal, state, and tribal managers. The inaccessible nature and public or tribal ownership of much of the lower Deschutes River basin has protected many miles of rivers and streams from development or overuse. In the lower Deschutes and White rivers, angling for redband trout has become increasingly restricted and stocking of hatchery rainbow trout has ceased. However, continued vigilance will be necessary to protect redband trout populations and their habitats. Although habitat in the main stem of the Deschutes River is relatively stable, questions remain about long-term effects of dams on riverine habitat downstream. In addition, threats to habitat remain from runoff from agricultural land and transport of chemicals and toxic materials on a railroad that runs along the bank of the river for almost 140 km. Examples of activities in the White River basin that have degraded redband trout habitat include water withdrawals for irrigating agricultural land and timber harvest with its associated road construction.

Redband trout in the lower Deschutes River have long received special attention from fish managers and researchers, and have gained special recognition and support from the public. Although redband trout in the White River basin represent an important lineage in the evolution of redband trout, I believe they have yet to receive the level of consideration from land and fish managers commensurate with their importance to the diversity of redband trout east of the Cascades. With the exception of the Wild and Scenic River status for the main stem, no watersheds within the basin have been accorded special protection by land managers to protect the unique White River redband trout. Stocking of hatchery rainbow trout into streams ended in 1994, but hatchery rainbow and brook trout continue to be stocked into lakes of the watershed. In recent years, triploid hatchery trout have been stocked into lakes, under the assumption that induced triploidy would reduce detrimental effects on wild redband trout if the hatchery fish migrate out of lakes into streams. Although brook trout have apparently established self-reproducing populations in some streams, continued stocking into lakes increases the risks that brook trout may displace redband trout in streams downstream of lakes.

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Redband Trout: Resilience and Challenge in a Changing Landscape
Oregon Chapter, American Fisheries Society, 2007

Redband Trout Investigations in the Crooked River Basin

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Abstract.—We characterized life history information of redband trout *Oncorhynchus mykiss* in the Crooked River basin, a major tributary of the Deschutes River in Oregon. We describe the historical activities that have impacted redband trout, including fish management and land and water management. Then we focus on two major objectives: the first is a description of populations including distribution, relative abundance, life history (spawn timing, age and growth), species assemblage, and genetics. Second, we discuss habitat conditions and population status. Crooked River redband trout comprise a diverse collection of populations that have been fragmented and isolated by numerous large and small irrigation dams, and a few natural barriers. Portions of the main stem are largely inhospitable to trout during the summer months due to dewatered reaches or high summer temperatures. Spawning occurs from early spring to early summer. Young-of-the-year typically reach 40–90 mm by fall. Length frequency distributions in four tributary basins of the main stem in July indicated age-1 fish average 74–98 mm, and age-2 fish average 124–147 mm. Density of fish in small tributary streams ranged from 0.01 to > 2.64 fish/m^2. Streams with high summer temperatures (> 21°C) tend to support densities less than 0.5 fish/m^2. Redband trout in the main-stem Crooked River were larger than their counterparts in tributaries. Young-of-the-year redband trout were typically 60–100 mm, while age-1, age-2, age-3, and age-4 trout were estimated at 119, 206, 237, and 300 mm, respectively. Abundance of redband trout > 180 mm in the main-stem Crooked River below Bowman Dam ranged from 516 to 5,140 fish/km. Preliminary genetic analyses indicate that Crooked River trout belong to the redband trout evolutionary line but have diverged from other redband trout groups. At least three genetically unique populations were found in the basin and tended to be geographically clustered. Some populations in the Ochoco Creek system and lower Crooked River areas showed low to moderate levels of hatchery introgression, probably due to a combination of chemical treatment projects and high levels of past hatchery stocking.

The Crooked River basin historically supported two native salmonid species: resident (redband trout) and anadromous (summer steelhead) forms of *Oncorhynchus mykiss*, and spring Chinook salmon *O. tshawytscha*. Anadromous steelhead and Chinook salmon were extirpated by construction of Bowman Dam on the Crooked River at rkm 112 in 1961, and by termination of passage efforts in 1968 at the Pelton–Round Butte hydroelectric dam complex on the Deschutes River, just downstream of its confluence with the Crooked River. Very little is known about redband trout, the sole remaining native salmonid in the Crooked River basin. Recently, fish managers and biologists initiated studies to delineate distribution and population status in the basin, and conducted habitat inventories of streams flowing through U.S. Forest Service (USFS) land of the Ochoco National Forest.

Studies were conducted by personnel from the Oregon Department of Fish and Wildlife (ODFW) and USFS, commencing in 1989. Goals of the studies were to obtain information on the life history and status of redband trout in the Crooked River basin and, ultimately, to assist resource managers in conserving redband trout and their habitat. The first objective was to focus on life history information, including distribution and relative abundance of redband trout in numerous streams throughout the basin. Additional information was collected on species assemblages, life history characteristics (spawning time, age, and growth), and genetics (hatchery introgression and diversity of populations within and outside the basin). The second major objective was to assess the present status of redband trout, including habitat conditions, to identify potential limiting factors. The information in this study will assist resource managers in conserving redband trout and their habitat.

Study Area

The Crooked River is the largest and easternmost tributary of the Deschutes River, encompassing a watershed of approximately 14,000 km^2 (Figure 1). The river flows through a variety of geological formations and plant communities, ranging from narrow basalt canyons to a wide agricultural valley. The Crooked River is composed of two major tributaries: the North Fork Crooked River arising in

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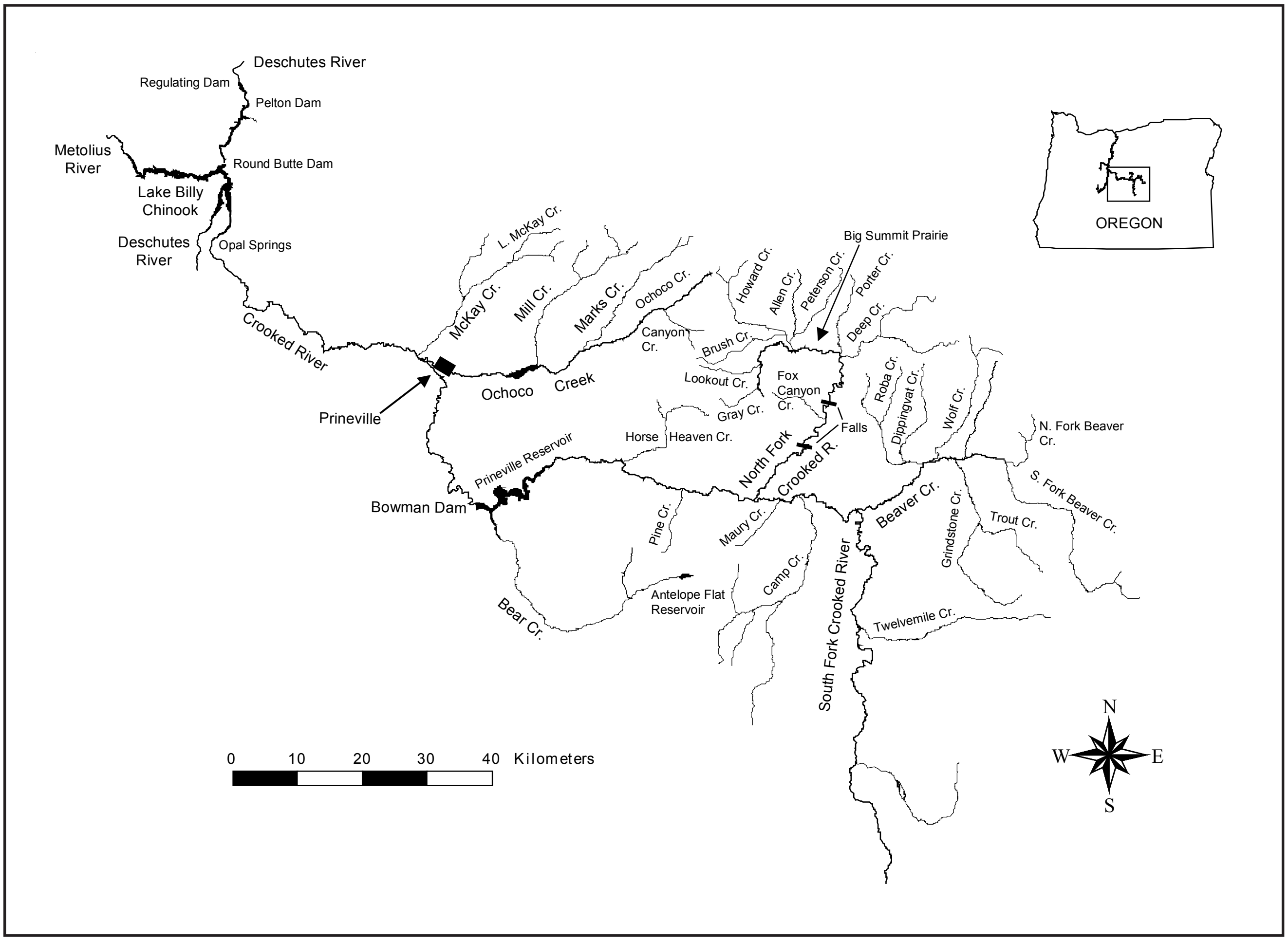

FIGURE 1.—The Crooked River basin in central Oregon.

the Ochoco Mountains and the South Fork Crooked River arising from springs in the high desert plateaus of the southeast portion of the basin. From their confluence, the main stem generally flows east to west until reaching Prineville Reservoir (rkm 112) impounded by Bowman Dam. Bowman Dam discharges regulated releases of water during the irrigation and non-irrigation season into the river below. The river flows out of the reservoir and joins the Deschutes River at Lake Billy Chinook, which was formed in 1964 by Round Butte Dam on the Deschutes River at rkm 177. Other major tributaries include Beaver (rkm 200), Ochoco (rkm 74), and McKay (rkm 72) creeks.

The Crooked River basin is an arid watershed with average annual precipitation ranging from 25–30 cm at lower elevations to 75–100 cm at higher elevations in the Ochoco Mountains. Low elevation floodplains and valleys are primarily occupied by irrigated agriculture. Vegetation at transitional elevations includes sagebrush *Artemisia* spp. and western juniper *Juniperus occidentalis*. Vegetation at upland and high elevations includes ponderosa pine *Pinus ponderosa*, lodgepole pine *P. contorta,* and mixed conifer forests of Douglas-fir *Pseudotsuga menziesii*, white fir *Abies concolor*, and western larch *Larix occidentalis*.

At high elevations, much of the Crooked River basin is rolling hills. At transitional and low elevations, portions of the main stem and the North and South Fork Crooked River carve deep canyons through the central Oregon desert. Generally, land ownership is split evenly between public and private lands, with public lands administered by the USFS and the Bureau of Land Management.

In addition to redband trout, other indigenous fishes of the Crooked River basin include mountain whitefish *Prosopium williamsoni*, sculpin *Cottus* spp., northern pikeminnow *Ptychocheilus oregonensis*, longnose dace *Rhinichthys cataractae*, speckled dace *R. osculus,* largescale sucker *Catostomus macrocheilus,* bridgelip sucker *C. columbianus,* and chiselmouth *Acrocheilus alutaceus.* Introduced game species include brook trout *Salvelinus fontinalis*, brown trout *Salmo trutta*, largemouth bass *Micropterus salmoides*, smallmouth bass *M. dolomieu*, brown bullhead *Ameiurus nebulosus*, black crappie *Pomoxis nigromaculatus*, and bluegill *Lepomis macrochirus.* Numerous strains of rainbow trout from other watersheds have also been introduced.

Historical Background

A review of historical events and management provides context and a reference for comparing present habitat conditions and population status. Historical background information was collected from unpublished ODFW reports, a review of Oregon State Game Commission and Fish Commission annual reports from the 1940s through 1960s, and information collected at the Crook County Historical Society. In addition, Buckley (1992) summarized historical conditions reported by early explorers, including the Peter Skene Ogden fur trapping expedition, and military expeditions. Nehlsen (1995) described changes in land and water use in the Crooked River basin from the turn of the 20th century, and the construction of the Pelton–Round Butte dam complex that ultimately led to the demise of anadromous fish in the Crooked River basin.

Historical accounts by early explorers and military expeditions documented dramatically different habitat conditions in the Crooked River basin than those found today (Buckley 1992). Early explorers described the Crooked River basin as having abundant riparian vegetation and adequate supplies of grass, water, and firewood. The banks and floodplain of the Crooked River were described as, "covering the entire valley bottom, with a dense growth of willow trees that in some areas had to be cut away to facilitate travel". One expedition described Crooked River tributaries in late June 1859 as, "all the principal streams and their tributaries are pebbly bottomed and skirted with willows, some of them from four to six inches in diameter, affording good fuel, and the waters are generally sweet and icy cold" (U.S. Congress 1860). Another military expedition near the mouth of Maury Creek (rkm 185) described the Crooked River in late July as, "Pine, birch, and cedar. Grass on hills. Coarse grass on narrow bottomlands - alkaline soil - Good running stream 30 ft wide 1 ft deep in middle. Good rocky bottom, with plenty of fish" (Andrews 1860). The rivers and streams were described as being abundant with native fish including rainbow trout, summer steelhead, and Chinook salmon (Crook County Historical Society 1981). In 1826 Peter Ogden, an early Hudson Bay fur trapper, found an Indian weir used to capture anadromous fish at the junction of the North Fork and South Fork Crooked River (Buckley 1992).

Historical records indicate that stream incision occurred in the basin around 1885–1903 (Buckley 1992). Decline of instream habitat coincided with a period of intense cattle and sheep grazing throughout the basin. Concurrently, a commercial fishery that almost entirely blocked upstream migration of anadromous fish was in operation from 1880 to 1900 (Davidson 1953). By 1912, reaches of the main-stem Crooked River were completely dry in the summer because of water diversions (USGS 1914). Preliminary surveys of fish distributions were not conducted until the 1950s, at least 50 to 70 years after extensive portions of the Crooked River basin had been severely degraded, dewatered, or blocked by dams or diversions. Descriptions of the main-stem Crooked River in the 1950s indicated that during late winter and spring, salmonids migrated the entire length of the river. However, water diversions in the center sections made habitat unsuitable during the summer (OSGC 1951). Some tributaries, however, still provided habitat suitable for trout. "Resident populations are considered to be sufficient in magnitude to provide fair fishing for the few anglers that frequent these waters" (OSGC 1951).

In the past 50 years, land and water management activities have further contributed to alteration and fragmentation of native fish habitat in the Crooked River basin. Reduction or loss of flow and mortality of juvenile fish have been caused by new unscreened diversions, while sedimentation and loss of gravels have been caused by depositing fill in channels or removing substrate from channels. Construction of large and small impoundments for irrigation storage created additional impassable barriers for native fish. Extensive seasonal and year-long livestock grazing in upland and riparian areas, and extensive logging and road construction on private and public lands caused reduction of important streamside riparian habitat and likely exacerbated the effects of channel alteration by changing the timing and amount of peak runoff (Nehlsen 1995).

Numerous chemical treatment projects using rotenone were conducted from the mid-1950s to the late 1980s to treat flowing and standing water bodies (OSGC 1951, 1958, 1962, 1969; Herrig 1964). The objective was to remove species such as northern pikeminnow and suckers, which were thought to compete with trout for food and space, and in some instances, to prey on eggs or juvenile trout. A substantial portion of the main-stem Crooked River, the South Fork Crooked River, and Ochoco Creek were treated with rotenone for removal of these species (Figure 2). In 1960, the Crooked River above Prineville Reservoir was treated in preparation for the completion of Bowman Dam. The treatment project included 96 km of the main stem and 50 km of tributaries, including the North and South Fork Crooked River, and Camp, Horse Heaven, Sanford, and Bear creeks (Figure 2; OSGC 1962). In 1963, the lower Crooked River was treated with rotenone from rkm 91 (21 km below Bowman Dam) to Smith Rock State Park (rkm 37), and included the lower 6 km of Dry Creek (Figure 2; Herrig 1964). Following the 1963 treatment project, the river was stocked with fingerling and legal-sized trout. In 1957, Ochoco Reservoir and 400 km of named streams and tributaries in the watersheds of Ochoco, Marks, and Mill creeks were chemically treated (Figure 2; OSGC 1958). In addition, another 320 km of unnamed streams, irrigation ditches, and marsh were treated during this project. Millions of fish including suckers, northern pikeminnow, goldfish (*Carassius auratus*), and sculpin were killed, as well as redband trout, hatchery rainbow trout, brown bullhead, and crappie. A 1968 treatment of Ochoco reservoir and 80 km of tributaries killed (in order of abundance) suckers, dace, rainbow trout, and sculpin (OSGC 1969).

Exotic fish species were introduced to provide addition-

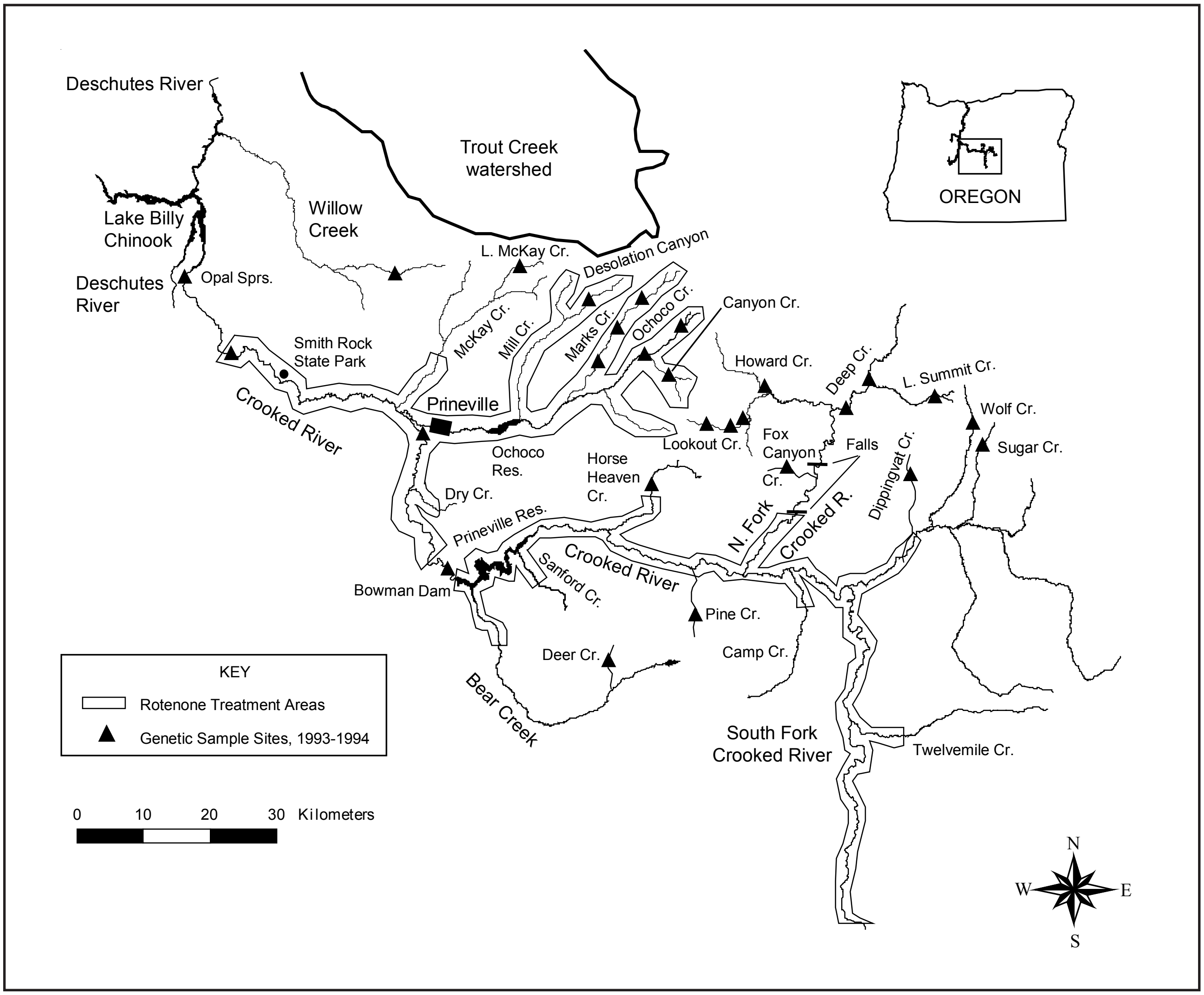

FIGURE 2.—Map of chemical treatment projects and genetic sample collections in the Crooked River basin.

al angling opportunities in the basin and included largemouth and smallmouth bass, crappie, and brook and brown trout (OSGC 1951, 1958, 1962, 1969). Nonnative stocks of hatchery rainbow trout fingerlings and yearlings were planted sporadically in streams and reservoirs throughout the basin from the 1920s to the mid-1980s (ODFW, unpublished reports). The combination of chemical treatments, which caused direct mortality, and the introduction of exotic species and hatchery rainbow trout, which caused competition or predation, likely led to further impacts to redband trout in the basin.

The management philosophy of fish and wildlife managers in the Crooked River basin since the mid-1980s has shifted from stocking of hatchery rainbow trout to protection and restoration of native fish and their habitats. The Oregon Fish and Wildlife Commission adopted the Wild Fish Management Policy (ODFW 1992), which emphasized protection and management of wild native fish species over exotic species. The policy recommended release of hatchery fish for sport and commercial fisheries only where they were compatible with wild fish. Fish managers in the Crooked River basin quickly adopted this policy and stocked hatchery fish in lakes or reservoirs only where intensive recreational fishing occurred and the potential for competing or breeding with native redband trout was limited. In addition, managers emphasized the protection and restoration of native fish habitat. This has included reconnecting fragmented stream reaches through construction of passage facilities at barriers, screening water diversions, and constructing streamside riparian fences and livestock pasture systems that encourage recovery of riparian and upland areas.

Methods

Fish distribution and upstream limits in tributaries were determined by visual observations and electrofishing. In tributaries, the upstream limit of redband trout presence was determined by linearly sampling pools and riffles with pocket pools. An upstream point or limit was determined by the presence of an impassable barrier or by the absence of redband trout within approximately 400 m upstream of the last observed fish. Some distributions were based on visual observations of redband trout recorded in unpublished historical ODFW Physical and Biological surveys from the 1970s. Most watersheds in the Crooked River system were comprehensively surveyed for the presence of redband trout, with the exception of South Fork Crooked River and Beaver Creek, Bear Creek, and Camp Creek watersheds.

We used backpack electrofishers to estimate relative abundance and species composition in small streams by randomly sampling 5- to 100-m lengths of streams, depending on the width of the stream. Block nets were placed at upstream and downstream ends of the reach. Generally, two to three thorough passes were made in an attempt to capture most of the fish present. Streams generally were sampled in July and August during low flows, when most fish resided in pools. Captured fish were identified to species, measured for total length, and released near the capture site. The length and width of sample sites were measured to estimate relative abundance (fish/m^2).

Fish were collected in the main-stem Crooked River below Prineville Reservoir using a driftboat-mounted electroshocker. We attempted to capture all species of fish observed in the first pass and only redband trout in subsequent passes. All fish were identified to species (genus for sculpins), and fork length of redband trout was measured. All redband trout > 180 mm were marked with a caudal fin punch to calculate a population estimate using a Schnabel mark-and-recapture estimate (Ricker 1975). The mark-and-recapture estimate for each year the study was conducted was calculated over the entire size class of redband trout larger than 180 mm. Captured fish ranged from 70 to 500 mm in length. Marked fish were moved upstream approximately 0.4–0.8 km above the capture site to keep them within the sample reach. Both sides of the river were sampled, although boating hazards limited our ability to sample all areas effectively. In a 3-day consecutive sampling effort in April 1989, using two passes each day for a total of six passes, 559 redband trout > 180 mm were captured and marked in an 8-km reach immediately below Bowman Dam (rkm 104–112). A second 8-km reach was sampled downstream from the mouth of McKay Creek (rkm 64–72) on a fourth day, but only 11 redband trout were captured. From 1993 to 1995, 5,001 redband trout > 180 mm were captured and marked in a 3-km reach below Bowman Dam (rkm 109–112). This reach was sampled the third week of June each year for a 3- to 5-day consecutive period with two passes each day. A second 2-km reach (rkm 88–90) was sampled in 1993, where only 31 redband trout > 180 mm were captured and marked.

We measured lengths of redband trout in small streams from April to October to estimate age and growth. Length-frequency histograms were constructed to delineate age-0, age-1, age-2, and age-3 and older trout. Scale samples were collected from redband trout in Allen (North Fork Crooked River tributary) and McKay creeks to assess the age of fish and to serve as a reference for growth rates of fish in tributaries. Scale samples were also collected from redband trout in the main-stem Crooked River below Bowman Dam to assess age and growth.

Migration of fish in the main-stem Crooked River below Bowman Dam was assessed by a tagging and movement study. In 1989, concurrent with the mark-recapture work, 535 redband trout that were not given a caudal punch were tagged with individually numbered anchor tags (Floy Tags, Seattle Washington). Information on individual growth and movement was gathered from fish that were later recaptured by anglers.

Spawning surveys were conducted on USFS lands in early May to late June 1994 in tributaries of Ochoco, McKay, and North Fork Crooked River. In the main-stem Crooked River, we noted redds and ripe or spawned female redband trout when electrofishing in April 1989 and June 1993–1995.

Information on redband trout genetics was assessed from two independent studies. Redband trout were collected from 21 sites throughout the basin (Figure 2). Fish were captured, flash frozen on dry ice, and sent to genetics laboratories at Oregon State University (OSU) or Washington Department of Fish and Wildlife (WDFW) for allozyme analysis. In one study, redband trout were collected in streams where hatchery rainbow trout had been stocked and in streams with no history of stocking (Currens 1994). In a second study, redband trout were collected from 10 populations that were either completely or partially isolated from the rest of the basin by manmade or natural barriers (Phelps et al. 1996). Both studies used procedures for allozyme electrophoresis described in Aebersold et al. (1987). Genetic variation was examined at 43 loci at the OSU laboratory, whereas the WDFW laboratory analyzed 79 loci, with 60 loci chosen for enzyme activity. The WDFW laboratory concurrently analyzed samples from nine locations in the Deschutes River basin and samples from a commonly used hatchery strain (Cape Cod stock crossed with rainbow trout originating from coastal northern California).

Hatchery stocking records of rainbow trout were compiled from the early 1920s to 1995 for the streams where wild fish were collected for genetic analysis, and for nearby streams from which hatchery fish could have migrated and interbred with wild redband trout. The history of chemical rotenone projects from the 1950s to the late 1980s was compiled by location to document the extent of this management practice in the Crooked River basin (Figure 2).

Indicators of habitat quality and complexity that were evaluated on streams within USFS lands included water temperature, stream shading, and large woody debris (LWD). Water temperatures during the summer low flows were collected with recording thermographs such as TempMentor® (Ryan Instruments, Redmond, Washington) or dataloggers such as Hobo® Temp (Onset Instruments, Pocasset, Massachusetts). Water temperature was recorded from June to October during 1994 and 1995 in streams on USFS lands. Maximum temperature (7-d running average) was used in the analysis, based on Oregon water temperature standards (ODEQ 1995). Data were compared with the state water temperature standard of 64°F (17.8°C) for the Crooked River basin.

Fish habitat data were collected on USFS streams using methods developed by Grover et al. (1992). Average shade was determined using solar pathfinders, with readings taken at 30.5-m intervals along the stream thalweg. We counted LWD in four size classes based on length and diameter at the small end. Size categories for wood were from the stream survey protocol of USFS Region 6 (USFS 1993).

During stream surveys and other sampling activities, we noted streams with low flows, dewatered reaches, extremely poor riparian and instream conditions, and passage barriers. A comprehensive summary of water diversions was compiled in 1990 that documented all diversions in the basin for irrigation, hydroelectric, or domestic use (ODFW, unpublished report).

A team of federal, state, and tribal fish biologists determined the status of redband trout populations in the Crooked River Basin. Populations in watersheds were ranked as strong, depressed, absent, or unknown based partially on population characteristics described in Rieman et al. (1997). In addition to information on relative abundance of redband trout, status also considered species assemblages, including presence or abundance of nongame and introduced species, and habitat conditions.

Results

Distribution

Redband trout were documented throughout most major watersheds in the basin, from headwater streams high in the Ochoco Mountains downstream to Lake Billy Chinook. However, the abundance of redband trout varied considerably throughout the basin, and in some watersheds they were completely absent. Some populations were isolated by seasonally dewatered sections of streams and rivers. A detailed map of redband trout distribution in the Crooked River basin was summarized on a GIS map and is available at offices of the ODFW Prineville Field Station and USFS Ochoco National Forest.

Hatchery-reared Deschutes River redband trout (identified by fin clips) were the only redband trout found in surveys of the South Fork Crooked River. Remnant populations of redband trout may still exist in headwater streams, but lack of access to private lands prevented surveys of these areas.

Small, isolated populations of redband trout were found on USFS land in headwater tributaries of Beaver and Camp creeks, while headwater tributaries of Ochoco and McKay creeks, and the North Fork Crooked River supported low to moderately abundant populations of redband trout. In downstream reaches, on private lands where flows were reduced by irrigation withdrawal and riparian areas were more degraded, fish populations were composed almost exclusively of nongame species. For example, no redband trout were found in the middle and lower reaches of Camp Creek. Grindstone Creek and the lower reaches of its tributary, Trout Creek, were surveyed in the summer of 1995 and no redband trout were found. Remnant populations of redband trout may exist in headwater reaches of these streams, but lack of access on private lands precluded surveys of these reaches.

Redband trout were captured during inventory and creel surveys in Lake Billy Chinook. Although these fish could be from the Metolius or Upper Deschutes River, some Crooked River fish may have adopted an adfluvial life history strategy. However, an artificial barrier at Opal Springs limits migration to 1 km above the reservoir.

TABLE 1.—Relative densities (fish/m^2) of redband trout (all age classes) in tributary streams of the Crooked River basin on lands of Ochoco National Forest, 1990–1994.

Watershed	Stream	Date	Fish/m^2
Ochoco	Canyon	August 1992	2.6
	Ochoco	August 1992	2.7
	Marks	August 1992	0.3–0.8
	Mill	July 1991	< 0.1–0.1
North Fork Crooked R	N.F. Crooked R.	July 1990	< 0.1
	Gray	July 1994	0.1
	Lookout	August 1991	0.8
	Brush	August 1991	1.4
	E. Fork Howard	July 1991	0.5–0.7
	W. Fork Howard	July 1991	1.0
	Howard	July 1991	0.8
	Porter	August 1992	0.4
Beaver	Dippingvat	August 1992	1.0
	Roba	August 1992	0.2

Abundance

Relative abundance of native redband trout in tributary streams of the Crooked River ranged from 0.01 to almost 3 fish/m^2 (Table 1). An abundant population of redband trout was found in the Crooked River immediately below Bowman Dam, where discharge from the hypolimnion of the reservoir supplies cold water to the river. The temperature of water released from the dam ranged from 4 to 12°C throughout the year. The abundance of trout > 180 mm ranged from 516 to 5,143 trout/km (Table 2). Redband trout and whitefish were the dominant fish species in this section of river.

At rkm 91 on the lower Crooked River, approximately

TABLE 2.—Abundance (fish/km) of redband trout > 180 mm determined by mark-and-recapture estimates of fish captured by boat electrofishing in the Crooked River below Bowman Dam, 1989, 1993–1995. CI = confidence interval.

Year	Reach	Fish/km	(95% CI)
1989	rkm 104–112	516	364–786
1993	rkm 109–112	1,431	1,049–2,007
1994	rkm 109–112	5,143	4,296–6,277
1995	rkm 109–112	3,811	3,263–4,512

80% of the streamflow is diverted into a canal from mid-April to mid-October. In 1993, abundance of redband trout > 180 mm decreased from 1,430 fish/km above the diversion to approximately 80 fish/km below the diversion. The fish community was a mixture of nongame species, whitefish, and redband trout. Thirteen kilometers below this diversion, a second major diversion reduced summer flows in the Crooked River to < 1 m^3/s. Through the lower Crooked River valley, from rkm 80 to approximately rkm 29, redband trout were scarce and probably well below 80 fish/km. Based on visual observations, anecdotal information from angling reports, and nonstatistical samples, we believe the abundance of redband trout increases dramatically below rkm 29, where several springs add cold, clean water to the river.

Species Composition

Fish species assemblages were primarily or exclusively redband trout in headwater streams with good to excellent riparian conditions and low water temperatures. The exceptions were Brush, Lookout, and Allen creeks, which also had small populations of naturally reproducing brook trout, progeny of hatchery fish stocked in the late 1920s. In headwater reaches of North Fork Crooked River tributaries such as Brush, Lookout, Allen, and Porter creeks, redband trout was the exclusive or primary species, with the percentage of nongame species increasing as sampling progressed downstream. In the upper reaches of the North Fork Crooked River above Big Summit Prairie, the species assemblage was composed of about 20% redband trout and 80% dace. Downstream of Deep Creek, redband trout composed < 1% of the fish sampled in the North Fork Crooked River. Nongame fish upstream of Lower Falls on the North Fork Crooked River were dace and bridgelip suckers, while additional nongame species below the falls included northern pikeminnow, chiselmouth, and largescale sucker.

Redband trout were very sparse in the main-stem Crooked River above Prineville Reservoir, where habitat is characterized by a deeply incised stream channel, very low summer flows, and high water temperatures. In 1966, dace constituted the majority of the fish found in the Crooked River from Prineville Reservoir to the North Fork Crooked River, with much of the remainder comprising suckers, chiselmouth, and northern pikeminnow. Smallmouth bass, brown bullhead, and a few redband trout were noted at sample sites immediately above the reservoir and at the mouth of the North Fork.

Redband trout and mountain whitefish were the predominant fish species in the 21-km reach below Bowman Dam. It is unknown why redband trout were the predominant species in 1989 and the population subsequently shifted to approximately equal percentages of redband trout and whitefish by 1993–1995, while in the same time period trout abundance increased substantially. Below a diversion canal at rkm 91, the fish community is a mixture of nongame species, whitefish, and redband trout (Table 3).

Age and Growth

Young-of-the-year redband trout were observed from early July to mid-August in headwater tributaries of Ochoco Creek and in the North Fork Crooked River. The smallest redband trout we observed were age-0 fish (25–60 mm in July). The size of the larger fry in July (> 50 mm) suggested that first emergence occurred in late May or early June. The average size of redband trout in the Ochoco Creek watershed was slightly larger than that in other tributaries, probably because of lower elevations and slightly higher water temperatures. By September, the length of most age-0 fish ranged from 60 to 100 mm and averaged 76 mm. However, a few age-0 fish were as small as 41 mm.

Mean lengths of redband trout collected in tributaries averaged 74–98 mm at age 1 and 124–147 mm at age 2. The oldest fish estimated from scale analysis was age 6 (280 mm); however, larger fish up to 355–455 mm have been observed in other sampling in tributaries, which suggests that redband trout may live longer than 6 years of age. Age from scales may be conservative because scale-margin erosion limits accurate reading of annuli.

The age composition of redband trout collected after a fish kill in McKay Creek in August 1996 was 75% age 0, 12% age 1, 11% age 2, and 2% age 3 and older. However,

TABLE 3.—Species composition (%) of fish captured during the first pass of electrofishing in the lower Crooked River, 1989, 1993–1995. Rb = redband or rainbow trout, Wf = mountain whitefish, BrB = brown bullhead, SB = smallmouth bass, LSu = largescale sucker, BSu = bridgelip sucker, Clm = chiselmouth, Npm = northern pikeminnow, Cot = sculpins, D = dace.

Year	Rb	Wf	BrB	SB	LSu	BSu	Clm	Npm	Cot	D
					Bowman Dam reaches					
1989[a]	96	4	0	0	0	0	0	0	0	0
1993[b]	49	49	1	< 1	0	0	0	< 1	< 1	0
1994[b]	40	59	0	0	0	< 1	0	0	1	0
1995[b]	52	48	0	0	0	< 1	0	0	< 1	0
					Valley Reaches					
1989[a]	20	54	0	0	7	2	6	11	0	0
1993[b]	16	51	0	1	28	1	0	0	0	2

[a] Bowman Dam reach = rkm 104–112; Valley reach = rkm 64–72.
[b] Bowman Dam reach = rkm 109–112; Valley reach = rkm 88–90.

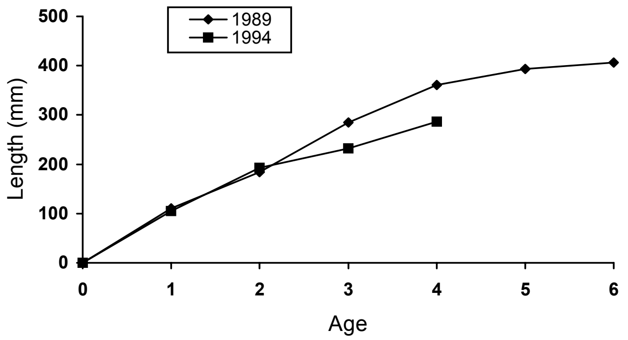

FIGURE 3.—Back-calculated total length (mm) at annulus formation of redband trout captured by electrofishing in the Crooked River (rkm 104–112), 1989 and 1994.

the number of fish collected at sample sites could have been reduced by scavengers during the 2 days between the fish kill and the survey.

No observations were made on size or timing of emergence of age-0 redband trout in the main-stem Crooked River below Bowman Dam. However, the length of age-0 fish salvaged from a diversion canal in October ranged from 60 to 140 mm. In the Crooked River below Bowman Dam, back-calculated lengths at annulus formation of age-1 to age-4 redband trout were 119, 206, 237, and 300 mm, respectively (Borgerson 1994). Scales collected from redband trout in April 1989, when densities were approximately 10% of 1994 densities, showed back-calculated lengths at annulus formation of 116, 193, 299, 379, 413, and 426 mm, respectively, for fish of age 1 to age 6 (Figure 3). Maximum age of redband trout in the main stem estimated from scales was 5 to 6 years. In 1989 and 1994, larger fish were captured whose scales were too regenerated to determine age and whose size suggested that some fish live longer than 6 years. Anglers have reported landing redband trout up to 610 mm.

Movement

Of the 41 tags recovered by anglers from redband trout tagged in 1989, most fish either remained in the 8-km sample area (41%) or migrated 2–8 km (32%), mostly downstream. Four fish (10%) migrated 16–24 km downstream within 2 months of being tagged. Anglers did not report the location of the fish caught for the remaining 7 fish (17%). All fish were tagged in 1989; anglers returned tags for 2 years, with the last tag reported in May 1991. Thirty-five tags were returned in 1989, five in 1990, and one in 1991. Some fish could have migrated out of the study area and back between the time they were tagged and the time they were recovered by anglers. We could not determine if a tagged fish had moved upstream or downstream within the 8-km sample area due to the lack of precision in tagging and recapture locations.

Spawning

Spawning surveys in tributaries of Ochoco Creek and North Fork Crooked River indicated that spawning occurred from late April through mid-June. Surveys in early May to early June in Mill Creek indicated some redband trout had already spawned, with the most recent redds completed by early June. Redds were found in Little McKay Creek in late May. In tributaries of the North Fork Crooked River, upstream of Big Summit Prairie and in the Deep Creek watershed, active redd building was observed in late May and early June. Although these surveys were preliminary, redband trout in tributaries appear to spawn primarily from early May to mid-June. In the Mill and McKay tributaries, ripe males were observed in early April, suggesting that these redband trout might spawn earlier, possibly due to higher water temperatures at lower elevations. However, ripe males may not accurately indicate time of spawning.

In the main-stem Crooked River below Bowman Dam, spawned redband trout and redds were observed by biologists from mid-April to late June. Anglers have reported spawning fish as early as February and March. A 1961 survey of the Crooked River from Bowman Dam to Prineville documented “two salmonid redds” in mid-February, which would have been from summer steelhead or redband trout.

Genetic Analysis

Genetic analysis showed that redband trout in the Crooked River basin belong to the inland rainbow trout, or redband trout, evolutionary line (Currens 1994). All fish had allele frequencies at *LDH-B2** and *sSOD-1** similar to other redband trout east of the Cascade Mountains. Samples from nine locations, some of which were from isolated populations, revealed an allele (*GPI-A*87*) previously undocumented in redband trout collected in other watersheds of the Deschutes River basin. The frequency of this allele suggests that the Crooked River redband trout may have diverged from other redband trout groups (Currens 1994). Phelps et

TABLE 4.—Hatchery introgression (%) in redband trout collected from 15 streams in the Crooked River basin (Figure 2) (Currens 1994; Phelps et al. 1996).

Watershed	Stream or section	Introgression (%)
Beaver	Dippingvat	0
	Sugar	11
	Wolf	1
North Fork Crooked River	Lookout	5
	Fox Canyon	6
	Deep	5
	Howard	5
	Little Summit	4
Crooked River	Pine	0
	Horse Heaven	< 1
	Below Bowman Dam	11
Ochoco	Ochoco	18
	Canyon	11
	Marks	32
	Desolation Canyon	0

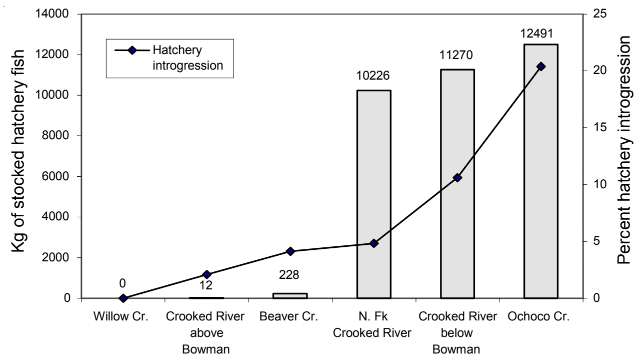

FIGURE 4.—Total weight (kg) of stocked hatchery trout (bars with total kg above), and average hatchery introgression (%) by watershed, Crooked River basin.

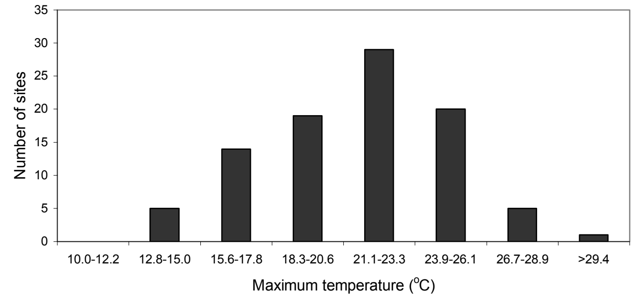

FIGURE 5.—Maximum water temperature (°C, 7-d running average) for 93 sites in streams of the Ochoco National Forest, 1994–1995.

al. (1996) also reported new allelic variation at four loci.

Overall, Crooked River redband trout had low levels of hatchery introgression (Table 4). However, populations in the lower Crooked River basin, including the reach below Bowman Dam, and Ochoco, Marks, and Canyon creeks (Figure 2), had introgression levels of 11–32%. These fish had a frequency of the *LDH-B2*100* allele that was intermediate between nonnative hatchery rainbow trout and wild populations of redband trout in the Crooked River basin (Currens 1994). Generally, the level of introgression was higher in streams where more hatchery fish had been stocked (Figure 4).

Genetic distance was used to compare similarity among populations in the two independent studies, each of which showed three to four general geographic groups within the Crooked River basin (Table 5). However, both studies found populations that did not group with proximate populations. For example, Currens (1994) found that the Deep Creek population did not group with other streams in the immediate vicinity, while Phelps et al. (1996) found that the Deep Creek fish were geographically grouped with nearby streams. Currens (1994) found that redband trout from most main-stem sites grouped with samples from mid Crooked River tributaries with the exception of a sample from Bowman Dam, which grouped with samples from the Ochoco–McKay watersheds and upper Bear Creek (Table 5). Phelps et al. (1996) reported that fish from Sugar Creek in the upper basin (Beaver Creek watershed) grouped with fish from streams in the Ochoco Creek watershed, which is relatively low in the Crooked River basin (Figure 2). This might be the result of a sampling error, such as mislabeling of samples. In addition, Phelps et al. (1996) grouped redband trout from two Deschutes basin populations that are geographically closer to lower Crooked River with the mid Crooked River and Beaver Creek populations (Table 5). Phelps et al. (1996) also identified an anomalous population of redband trout in Desolation Canyon above a natural barrier in the Mill Creek watershed (Figure 2), which was different than populations in the Ochoco–McKay watersheds or than in all other streams in the basin. This result could be affected by sampling from a small population or by collecting a non-representative sample from the population. Conversely, because these fish are isolated above a barrier, results may indicate a real difference in this population. Some of the findings in the genetic

TABLE 5.—Major geographic groupings of redband trout in the Crooked and Deschutes river basins, Oregon, based on genetic analyses from two different studies. Streams in italics indicate exceptions to the geographic grouping or samples from Deschutes basin.

Currens (1994)	Phelps et al. (1996)
North Fork Crooked River watershed	
Fox Canyon, Howard, Lookout	Fox Canyon, Howard, Lookout, Deep, Little Summit
Ochoco–McKay watersheds	
Marks, Ochoco, Little McKay, *Deer, Lower Crooked River (at Bowman Dam)*	Marks, Ochoco, Canyon, *Sugar*
	Desolation
Crooked River below North Fork–Beaver Creek watershed	
Pine, Horse Heaven, *Deep*,	Pine, Horse Heaven, Dippingvat, Wolf, *Trout and Willow creeks (Deschutes basin)*
Lower Crooked River (at Opal Springs, below Prineville, near Prineville)	Lower Crooked River below Bowman Dam, *Deschutes River (above Lake Billy Chinook)*

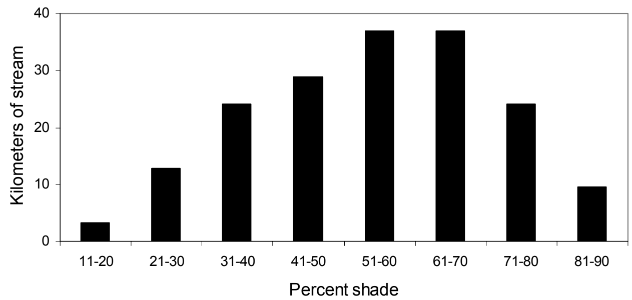

FIGURE 6.—Stream surface shading (%) measured by solar pathfinder for 176 km of streams on lands of the Ochoco National Forest, 1994–1995.

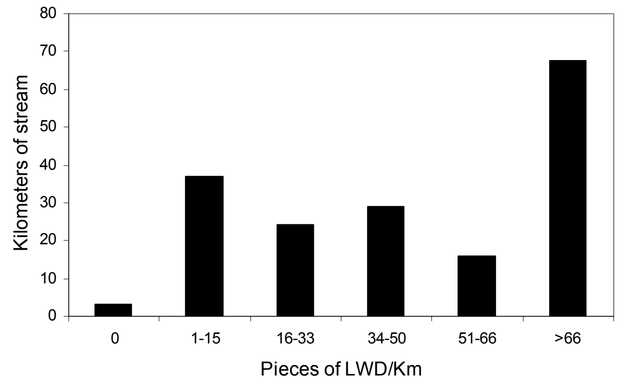

FIGURE 8.—Density of large woody debris (LWD/km) in 176 km of streams on the Ochoco National Forest, 1994–1995.

analyses could have been influenced by the eradication or near-eradication of redband trout populations in some streams because of chemical treatment projects and the subsequent recolonization of these streams.

Habitat Condition

Habitat surveys on USFS lands indicated that many streams had high summer water temperatures, suboptimal shading, and lack of large wood. Many streams did not meet the Oregon water temperature standard of 64°F (17.8°C) (Figure 5). Of the 93 sites measured, the 7-d running average for maximum temperature exceeded the standard in 80% of the sites, of which 28% had maximum temperatures above 75°F (23.9°C). In general, water temperature increased downstream from source areas, sometimes very rapidly.

Of the 176 km of streams surveyed, only 6% met or exceeded the USFS stream standard of > 80% shading (Figure 6). Almost 40% of the surveyed sections of streams had < 50% shade. In general, low levels of shading result in higher water temperatures and subsequently lower redband trout densities. In the Crooked River basin, streams with high summer water temperatures and poor habitat conditions supported lower densities of redband trout (Figure 7).

Large woody debris (LWD) is an important measure of habitat complexity and is often associated with pool formation and bank stability. In general, higher trout densities are found in streams with more LWD. The USFS adopted an interim standard of two pieces of LWD per 30.5 m of stream (66 pieces/km). The Inland Native Fish Strategy (USFS 1995) amended Forest Plans in the Columbia River basin to establish a density standard of > 12 pieces/km with sizes of > 30 cm in diameter and > 10.6 m in length. Of the 176 km of stream surveyed on USFS lands, 38% met the original forest plan standard (Figure 8). Of the total wood counted, only 24% met the minimum size standard specified by the Inland Native Fish Strategy, and nearly half was small brush < 6 m long (Figure 9).

On private lands, water withdrawal for irrigation is the major factor affecting fish populations. Diversions reduce flows or dewater reaches during the summer and are associated with seasonal or permanent dams that make fish passage difficult or impossible. Over 700 out-of-stream water rights were documented in the Crooked River basin. All mainstem reaches and many tributary reaches have water rights that exceed the capacity of the stream (Table 6). Although instream water rights were filed on 30 streams, they are junior to existing out-of-stream water rights, and flows are generally inadequate to meet the existing water rights.

Barriers contribute to fragmentation of fish populations and their habitat. Large manmade passage barriers include the Pelton–Round Butte Project, with three major hydroelectric dams, and Ochoco and Prineville Reservoirs, two

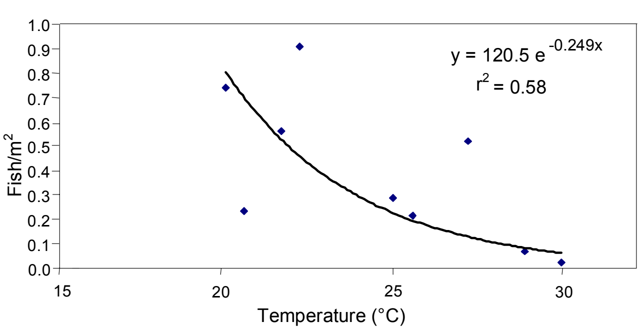

FIGURE 7.—Relationship between density (fish/m^2) of redband trout (all age classes) and maximum water temperatures (°C) in small streams of the Crooked River basin, 1994–1995.

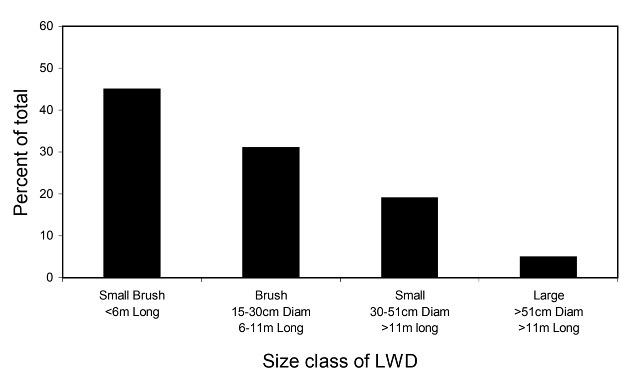

FIGURE 9.—Frequency of size classes of large woody debris (LWD) in 176 km of streams on the Ochoco National Forest, 1994–1995.

TABLE 6.—Appropriated water withdrawals and recommended minimum flow (m^3/s) during summer months for selected stream reaches in the Crooked River basin.

	Flow (m^3/s; ft^3/s in parentheses)	
Watershed	Withdrawal	Recommended
Bear Creek	0.62 (22)	0.08 (3)
South Fork Crooked R.	1.95 (69)	0.11 (4)
North Fork Crooked R.	5.04 (178)	0.71 (25)
Ochoco Creek	2.83 (100)	0.28 (10)
Beaver Creek	3.48 (123)	0.42 (15)

large irrigation projects. Over 60 partial and complete barriers from storage dams were documented in the main stem, North Fork and South Fork Crooked River, and on most of the tributaries. The only remaining flowing waters in the basin that have few barriers are some of the tributaries on USFS lands; however, many of these have dams for livestock watering ponds, or impassable road culverts.

Population Status

Population status of redband trout was determined by summarizing data on presence and abundance for different watersheds in the Crooked River basin. Redband trout inhabited most major watersheds and tributaries in the basin. However, relative abundance appeared to be directly related to quality of habitat, which ranged from excellent to very poor. Streams with good to excellent habitat generally had redband trout densities > 1 fish/m^2. Streams with poor habitat had lower abundance of fish, generally < 0.5 fish/m^2. In many cases, streams had a mix of habitat quality; the reaches with good habitat conditions supported moderate to high abundances of redband trout, while the reaches with poor habitat conditions had lower abundances of redband trout. Where habitat was in good condition, populations exhibited a mix of diverse age classes, from young-of-the-year fish to mature fish up to 6 years old. Tributaries with degraded riparian conditions, poor instream habitat conditions, and high summer water temperatures had low densities of redband trout and often had missing cohorts. These streams also had a higher proportion of nongame fish.

Redband trout were present in watersheds or areas of watershed that represent 45% of the basin. However, strong populations of redband trout were present in only 7% of the basin, either in headwater areas or in the Crooked River immediately downstream of Bowman Dam or immediately upstream of Lake Billy Chinook (Figure 10). In the remainder of the basin, redband trout populations were classified as depressed or absent in 37% and 22% of the basin, respectively. The status of redband trout in 34% of the basin is unknown, primarily in the southern and eastern parts of the basin, where access to streams on private land was limited. Because most of these streams lack high quality habitat, we assume that redband trout populations are depressed or absent in this part of the basin.

In the spring or in years with good summer flow, redband trout occupied stream reaches that became dry or intermittent in late summer or in drought years. For example, when Peterson Creek was surveyed in a year with normal flows, redband trout were found 3.2 km upstream of their recorded upper limit. This indicated that redband trout were able to recolonize a section of stream after flows returned and adequate habitat was reestablished in a previously dry section.

Species assemblages showed an increase of nongame fish and a substantial decrease of redband trout where streams were severely degraded and had high summer water temperatures. Several tributaries that drain the eastern and southern portions of the basin, including the South Fork Crooked River and Beaver, Grindstone and Camp creeks, contained almost exclusively nongame fish species such as dace and suckers, which are more tolerant of high summer water temperatures. Although it is not possible to accurately document historic distribution of redband trout in these watersheds, the historic descriptions of vegetation by early explorers and military expeditions suggest that these streams likely would have supported more abundant populations of native salmonids.

Discussion

Population and Life History Information

Despite the degraded condition of habitat in the basin and management practices of the past (e.g., chemical treatment of streams), abundance and growth of redband trout are similar to other streams and rivers in central and eastern Oregon. In the smaller tributary streams of the Crooked River, redband trout had comparable growth to that reported by

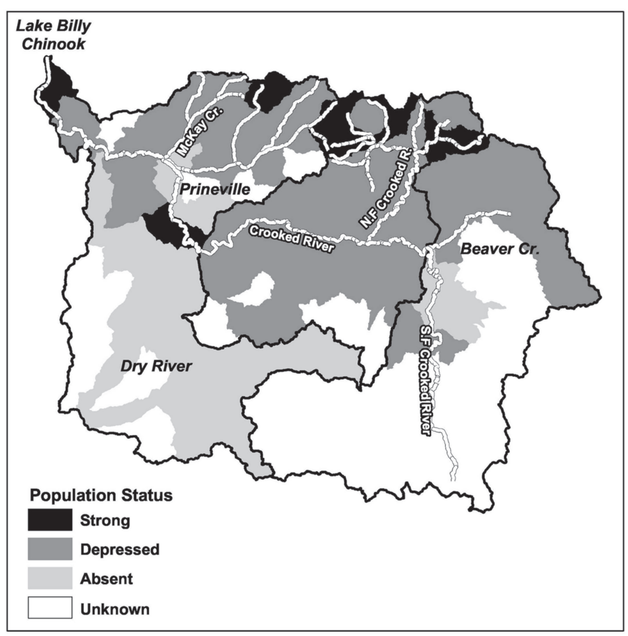

FIGURE 10.—Population status of redband trout populations in the Crooked River basin, Oregon, 1993. Labels indicate general watersheds or geographic areas.

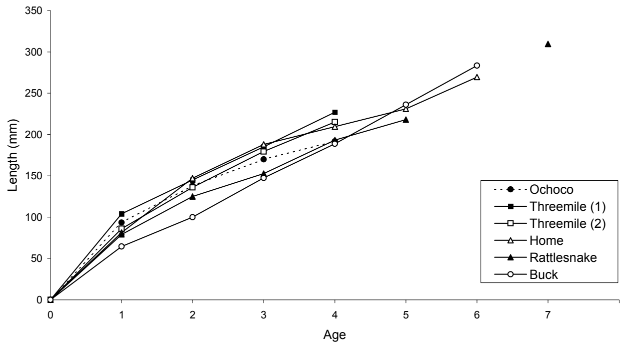

FIGURE 11.—Mean length of redband trout at ages 1–8 in small streams of Ochoco Creek (Crooked River basin), and Threemile, Home, Rattlesnake and Buck creeks (southeast Oregon, from Kunkel 1976).

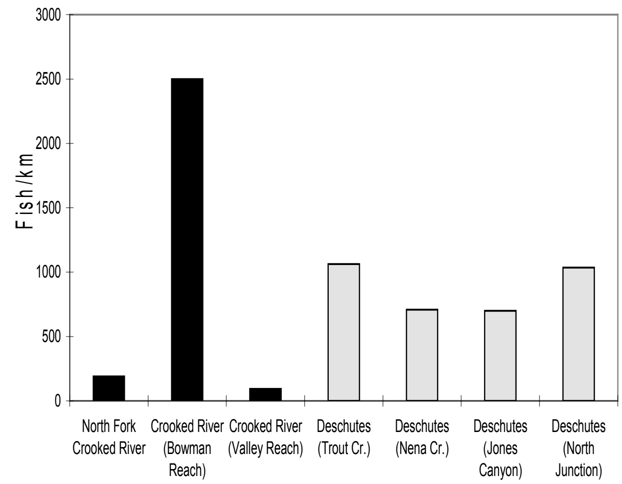

FIGURE 13.—Relative abundance of redband trout in the Crooked (solid bars) and Deschutes rivers, Oregon (light bars); Deschutes River data are from Schroeder and Smith (1989).

Kunkel (1976) for populations in southeastern Oregon streams (Figure 11). Densities of redband trout age 2 and older in tributaries were mostly lower than those reported by Kunkel (1976) (Figure 12). The density of redband trout in small streams of the Crooked River basin was low in streams with high water temperature and poor habitat quality.

Streams in the Crooked River basin have the potential to support large populations of redband trout where suitable water temperature and good quality habitat exist. For example, the Crooked River below Bowman Dam, where release of cool water provides good quality habitat, supports densities of redband trout that are at least twice that of several reaches in the Deschutes River (Figure 13), which is a nationally renowned "blue ribbon" fishery because of the abundance and size of its redband trout (Schroeder and Smith 1989). Redband trout in the main-stem Crooked River had comparable or slower growth than fish from Deming, Spring, and Spencer creeks of the Klamath River basin (Buchanan et al. 1990; Borgerson 1992) or than redband trout in the Deschutes River (Schroeder and Smith 1989) (Figure 14). Lower growth rates of redband trout in 1994 than in 1989 in the main-stem Crooked River may be related to the higher abundance of fish in 1994.

Until the past decade, redband trout were thought to live 3 years before they spawned and died (Hosford and Pribyl 1983). Recent work (Buchanan et al. 1990; Borgerson 1991, 1992) has shown that redband trout in the Klamath and Blitzen River basins live longer than 3 years and may spawn repeatedly. Redband trout in both small and large streams of the Crooked River basin were found to live to at least 6 years of age and sometimes older (ODFW, unpublished data).

Hatchery introgression in Crooked River redband trout populations was relatively low (Currens 1994; Phelps et al. 1996), although hatchery rainbow trout have been widely stocked in the basin since at least the 1940s. Two varieties of domestic hatchery rainbow trout were widely used in the basin from 1960 through the 1990s. Earlier stocking records did not identify the hatchery stock used in the 1940s and 1950s, although they were likely a domestic hatchery stock such as Cape Cod. Stocking of hatchery fish before the 1940s also may have occurred without documentation. The early method of stocking hatchery fish was to sporadically plant large numbers of very small fish (i.e. 440 fish/kg), which probably resulted in minimal numbers of hatchery fish reaching maturity to spawn with wild fish. However, stocking oc-

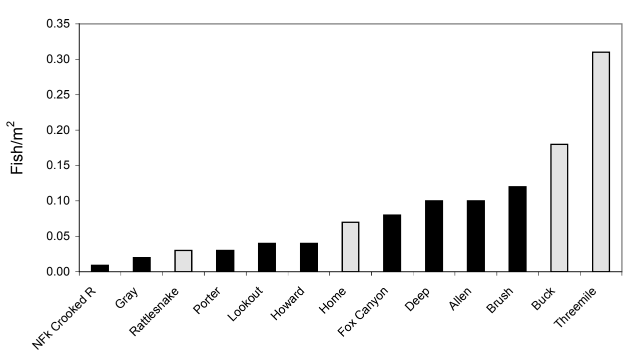

FIGURE 12.—Density (fish/m^2) of redband trout age 2 and older in the Crooked River basin (solid bars) and in four streams in southeast Oregon (light bars; from Kunkel 1976).

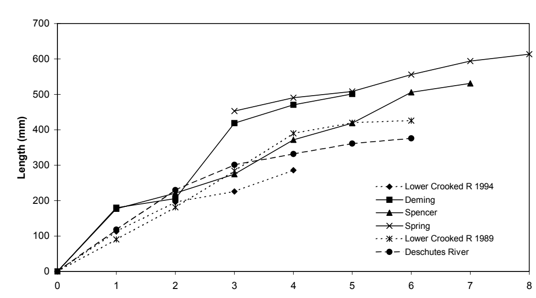

FIGURE 14.—Mean length at ages 1–8 of redband trout from larger streams in central and south-central Oregon. Deschutes River data are from Schroeder and Smith (1989); Klamath River tributary data are from Buchanan et al. (1990) and Borgerson (1992).

curred in streams with small populations of resident redband trout. Therefore, even a few hatchery fish reaching maturity could have had a large effect on these small populations. The nearly total eradication of redband trout in entire stream reaches from widespread chemical treatment projects in the basin and the subsequent stocking of hatchery fish would have increased the opportunity for competition and for interbreeding between hatchery fish and a greatly reduced population of redband trout.

Crooked River redband trout showed relatively high levels of genetic variability when compared to other redband trout populations, but variability within populations was significantly less than populations of redband trout in other basins. Redband trout in the Crooked and upper Deschutes basins had among the highest level of gene diversity (16.1%) of redband trout populations studied to date (Currens 1994; Phelps et al. 1996). Populations of redband trout in the Kootenai River basin also had a gene diversity of 16% determined from allozyme data (Knudsen et al. 2002). However, the level of gene diversity in other populations of redband trout has been considerably lower, including populations in the lower main-stem Deschutes (7.5%) and the White (5.6%) rivers (Currens 1987), and in the upper Snake River, Idaho (8.8%; Wishard et al. 1984).

Angler harvest appeared to have little impact on redband trout populations in the tributaries of the Crooked River basin. In 1996, the Oregon Fish and Wildlife Commission adopted a statewide minimum size of 203 mm (8 in.) for harvest of all resident trout. Most fish in tributary streams do not reach this size until they are age 4 or older. Although exploitation of redband trout in tributaries is unknown, < 5% of a population in most streams would exceed the minimum legal size. This suggests that the size regulation results in a de facto catch-and-release fishery in these streams. However, most redband trout in the main-stem Crooked River reach the minimum size of 203 mm by age 2, which would allow a larger proportion of the population to be harvested compared to populations in the tributaries.

Habitat Condition and Population Status

The effect of water temperature on wild trout is complex, and includes factors such as maximum and minimum temperature, diel fluctuation, and the duration that temperature remains above physiological limits. The presence of thermal refugia at the microhabitat level may allow fish to occupy streams that otherwise are too warm. Nonetheless, data presented in this paper indicate that long reaches of stream within the Crooked River basin had poor quality habitat for redband trout. Redband trout are generally known to be better adapted to high water temperatures than other salmonids (Behnke 1992). For example, Dickson and Kramer (1971) reported that the greatest activity of rainbow trout occurred from 15 to 20°C (59 to 68°F), and Raleigh et al. (1984) identified the upper incipient lethal temperature for adult rainbow trout to be 25°C (77°F). Lee and Rinne (1980) reported a Critical Thermal Maximum temperature of 29.4°C (84°F) for rainbow trout. In contrast, Behnke (1992) has recorded redband trout in Nevada actively feeding at 30°C. Redband trout in Three Mile Creek in the Catlow Valley (an Oregon desert basin), showed optimum growth efficiency at water temperatures > 19°C (Behnke 1992). Redband trout collected from a wild Oregon population and exposed to increasing water temperatures in a Texas hatchery exhibited increases in growth at temperatures up to 24°C, but a cessation of feeding at 25°C (Sonski 1983). Fingerlings gained more weight when held at 20°C than at either 15 or 22°C. However, Sonski (1983) felt that diseases in hatchery populations might remain chronic at temperatures > 20°C. From these studies, maximum summer temperatures of approximately 20°C may be the upper limit for populations of Crooked River redband trout to be classified as "healthy". Redband trout populations in the Crooked River basin are probably depressed at temperatures > 23°C (73°F).

Our results suggest that most streams in the Crooked River basin are too warm to support healthy redband trout populations. Only 36% of the streams monitored in the Crooked River basin had maximum water temperatures below 20°C. The maximum water temperature in over 40% of the monitored streams exceeded 23°C, at which we would classify the population as depressed. All of these monitored streams were on the Ochoco National Forest and probably represent the best remaining habitat in the basin, because they generally are more shaded and are at higher elevations than the rest of the basin.

In addition to negative effects on individual fish, high water temperatures also affect fish communities. As water temperature increases, intraspecific competition may cause shifts in community structure within redband trout streams. Reeves et al. (1987) observed that redside shiners (*Richardsonius balteatus*) out-competed steelhead juveniles when water temperatures reached 19–22°C. A similar process may occur in streams within the Crooked River basin. At two sites in Mill Creek, we noted that the species assemblage shifted from predominantly redband trout and sculpins to predominantly dace as water temperature increased (ODFW, unpublished data). The species composition at a site where water temperature was 19°C was 28% redband trout, 45% sculpins, and 27% dace. At a downstream site where the water temperature was 23°C, dace constituted 88% of the fish sampled, while 6% were redband trout and 4% were sculpins.

A second factor influencing trout populations in the basin is habitat simplification. A study of three streams in the nearby John Day River basin found that physically complex streams were more stable than simple habitats, and that effects of floods on native fish assemblages were greater in simplified stream reaches than in more complex reaches (Pearsons et al. 1992). Trout, sculpins, and dace in more complex habitats were more resistant to effects of floods and more resilient after floods.

Complex habitats have been characterized as containing pools > 1 m deep, with coarse sediment and cover from vegetation or undercut banks. In heavily forested areas, the density and location of large wood has proven a useful indicator of complexity. Cordova (1995) found that 63% of the pools were formed by 11% of the pieces of LWD he measured. The density of LWD as a factor in pool formation was more important in moderately constrained and unconstrained channels than in highly constrained channels. In addition, larger sizes of LWD were significantly more likely to form pools than small sizes of LWD. We found a lack of deep pools and a paucity of LWD, particularly large-sized wood, in surveys of headwater streams in the Crooked River basin. Low density of LWD in streams within the basin contributes to reduced habitat complexity and fish production.

In general, habitat complexity of streams in the Crooked River basin has decreased because undercut streambanks, structure created by LWD, and beaver dams have been lost as a result of land management activities and development. Because habitat complexity has been lost, many streams have become incised and isolated from their floodplain, similar to conditions observed in Camp Creek (Buckley 1992).

Although redband trout currently occupy an estimated 75% of their historic range, their abundance is apparently at a fraction of historic levels. Many streams, particularly in the southeast portion of the basin, may have lost native redband trout because of habitat degradation, reduced flows, and high water temperatures. Strong populations of redband trout are now found in only 7% of the basin, including two short reaches of the main-stem Crooked River: the Wild and Scenic River section below Bowman Dam and the lower Crooked River upstream of Lake Billy Chinook. Both of these reaches have abundant, cold water. In the reach below Bowman Dam, hypolimnetic water from Prineville Reservoir greatly increases flow and cools the river. In the section just upstream of Lake Billy Chinook, flow increases almost 20 fold from the input of natural springs that also significantly lower water temperatures.

The remaining strong populations of redband trout are located in headwater streams on the Ochoco National Forest. All strong populations are found on federally managed land. Many of the most productive fishery habitats were historically located in low gradient reaches of the main-stem Crooked River and its major tributaries. These areas were also the first places settled and developed in the basin and currently represent some of the most degraded habitats. For example, native redband trout and summer steelhead historically were present in the South Fork Crooked River and Twelvemile Creek, a major tributary. Summer steelhead were extirpated after 1964 by passage barriers downstream. Redband trout may have been eliminated from these streams because of habitat degradation, including silting of spawning beds, and because of a chemical treatment project in early 1981. In our surveys of this sub-basin, we found only hatchery redband trout (Deschutes stock), which are stocked annually, and found no evidence of natural reproduction.

Most reaches of the North Fork and main-stem Crooked River are in a degraded condition, with low flows and high summer temperatures. These areas support densities of redband trout < 300 fish/km. In stark contrast, the tailrace reach below Bowman Dam supports very high densities of redband trout, indicating a tremendous capacity to produce native salmonids where good quality habitat is present (e.g., adequate flow throughout the year and water temperatures below 15°C during the summer). Since 1989, abundance of redband trout in 21 km of the lower Crooked River below Bowman Dam has shown a 10-fold increase from approximately 520 to 5,200 fish/km. We believe this is attributable to increases in winter flow from uncontracted storage in the reservoir. Prior to 1989, when very little stored water was available to augment flows, the river was often as low as 0.3 m^3/s. Since 1989, the Bureau of Reclamation has released from 0.8 to 2.1 m^3/s through the winter storage season. We believe that the historic abundances of redband trout in major streams such as the North Fork and South Fork Crooked River, and the main stem upstream of Prineville Reservoir, were significantly higher than those currently observed, and that they may have approached the densities seen in the Crooked River below Bowman Dam.

The geographic genetic similarities among redband trout in the Crooked River basin are consistent with the metapopulation concept (Rieman and McIntyre 1993). We theorize that historically the main-stem Crooked River was a "source" population for populations in tributary watersheds. Currently, vast reaches of the main-stem Crooked River, with the exception of the 21-km reach below Bowman Dam, have severely reduced populations of redband trout. In addition, severe habitat degradation and numerous partial and complete barriers on the main stem and tributaries have fragmented populations, many of which are now completely isolated from each other. Populations with extremely low abundance, in streams with marginal habitats, and with little or no exchange of genetic material, have a high risk of extinction (Rieman and McIntyre 1993). Fragmentation and isolation of populations may eliminate life history forms and reduce survival, growth, and resilience. These effects can increase the risk of extinction.

Conclusion

Redband trout populations are depressed throughout most of the Crooked River basin, especially in the central and lower portions of the basin. With increasing settlement and development, redband trout populations have declined in distribution and abundance within the Crooked River basin. Land and water management practices over the last 120 years have resulted in a decline in riparian condition, river channel morphology, water quality and quantity, and subsequent declines or extirpation of native fish populations.

Our study clearly indicates the difference in redband trout density, abundance, and population structure between degraded habitat and good habitat. When streams are returned to higher flows, riparian functions are protected, and complex habitat is created, redband trout rebound remarkably well. However, the current conditions of most streams in the

Crooked River basin are degraded, and fish habitat and production are substantially diminished from historical times. Loss of riparian vegetation, along with subsequent effects on channel morphology and stability, have negatively impacted redband trout populations in many streams. The most important factors limiting redband trout production in the basin are probably low flows or dewatered reaches of streams and high summer water temperatures. Withdrawals of water from streams and removal of riparian vegetation that shades streams have increased summer water temperatures outside the normal range of variability.

Harvest appears to have had little impact on fish populations, and further restrictions to angling opportunity will make little difference in the status and health of populations, particularly in tributaries. Future management to improve the health of redband trout in the Crooked River basin must focus on protecting and restoring habitat, restoring stream flows, protecting the remaining genetic variability, preventing the extirpation of isolated populations, reducing hatchery introgression, and reintroducing native redband trout into streams where they have been extirpated. Considerable effort will be necessary to work with local, state, and federal governments, and private landowners to accomplish additional protection and restoration.

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Adaptive Management for Klamath Lake Redband Trout

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Abstract.—The upper Klamath River basin trout fishery consistently produces redband trout *Oncorhynchus mykiss* that exceed 4.5 kg. It is among the finest trout fisheries in the United States. The redband trout of the upper Klamath River basin have evolved in harsh environmental conditions and may be uniquely adapted to the habitats found in Upper Klamath and Agency lakes. These redband trout also have developed behavioral and life history characteristics that enable them to inhabit the highly eutrophic waters of the Klamath Basin. The management of Klamath Lake redband trout has evolved from the early 1920s, when large numbers of hatchery trout were stocked to supplement consumptive recreational fisheries, to the 1990s, when natural production, habitat protection and enhancement, and conservative angling regulations were used to provide for trophy redband trout fisheries. This evolution in management resulted from evaluating hatchery trout stocking programs and collecting information on stock-specific disease resistance, life history, and genetics. In addition, changes were made in Oregon Department of Fish and Wildlife trout management policies that emphasized the importance of native fish. Fish managers should continue to collect new information critical for sound, biologically based management of redband trout, and to incorporate this information into management plans.

The native rainbow trout *Oncorhynchus mykiss* that inhabits Klamath Lake is considered a redband trout, and is sometimes listed as a subspecies *O. m. newberrii* (Behnke 1992). In addition to the lacustrine redband trout that migrates from Klamath Lake to the Williamson and other rivers, populations of redband trout are also found in small tributaries. Although little is known about their life history, Behnke (1992) suggested that the tributary populations might represent a resident stream form of redband trout.

Although Klamath Lake is usually mentioned as a single body of water, it consists of two lakes (Upper Klamath and Agency) connected by a 2.4-km waterway (Figure 1). The waters of Upper Klamath and Agency lakes are naturally eutrophic and produce an abundant supply of zooplankton, insects, and fish (Bond et al. 1968; Eilers et al. 2004). Klamath Lake redband trout grow to a large size because of ample food in the lakes. Their adfluvial life history allows them to take advantage of this abundant food by migrating from spawning streams to rear in the lakes. Because redband trout grow to become trophy-sized fish in just a few years, they are the most prized sport fish in the upper Klamath River basin. The largest redband trout recorded in the Klamath Lake fishery was caught in 1956, and measured 86.4 cm (34 in) and 11.3 kg (25 lb). One redband trout, found dead in a spawning tributary to the lakes, measured 94.0 cm (37 in) and would have been close to 13.6 kg (30 lb) prior to spawning. Thousands of anglers fish the waters of the upper Klamath River basin every year in search of trophy redband trout. Angling is open all year on the lakes, but the highest catch rates of redband trout occur in the spring to early summer and in the fall. The fishery on the Upper Klamath and Agency lakes is considered a mixed-stock fishery because the lakes are common rearing areas for multiple stocks of adfluvial redband trout. Fly anglers also pursue the trophy fish in tributary streams such as the Williamson, Sprague, and Wood rivers (Figure 1). These streams offer some of the best fly fishing in the United States and have been featured on national television and in magazine articles.

The upper Klamath River basin has a long history of fish management dating back to the early 1900s, when fishery managers first stocked hatchery trout into the waters of the basin. Many fish managers have since applied their craft in the basin with varying degrees of success. This paper will review the past management of the adfluvial stocks of redband trout in the upper Klamath River basin and will describe how changes came about in their management. Adfluvial populations of redband trout in the basin include populations in the Williamson River (lower and Kirk Springs reaches), Spring Creek, Wood River, and lower Sprague River (Figure 1) (Kostow 1995). Additional stock diversity may exist in redband trout populations in other tributaries of Klamath Lake, but the genetics and life histories of these populations have yet to be studied. Information on the biology and life history of redband trout stocks in the upper Klamath River basin also will be discussed as it relates to the management of this species. Much of the information presented in this paper is found in annual, monthly, and special reports of the Klamath Fish District, Oregon Department of Fish and Wildlife (ODFW) and in Klamath Basin Fish Management plans.

The Upper Klamath River Basin

Many unique fishes are found in the Klamath River basin because of its history of long periods of geological isolation. During the Pleistocene Epoch, the upper Klamath River basin was once dominated by a large pluvial lake called Lake Modoc. Lake Modoc covered an estimated 283,900 ha and stretched from what is now Tule Lake, California, to Fort Klamath, Oregon (Dicken 1980). Upper Klamath and

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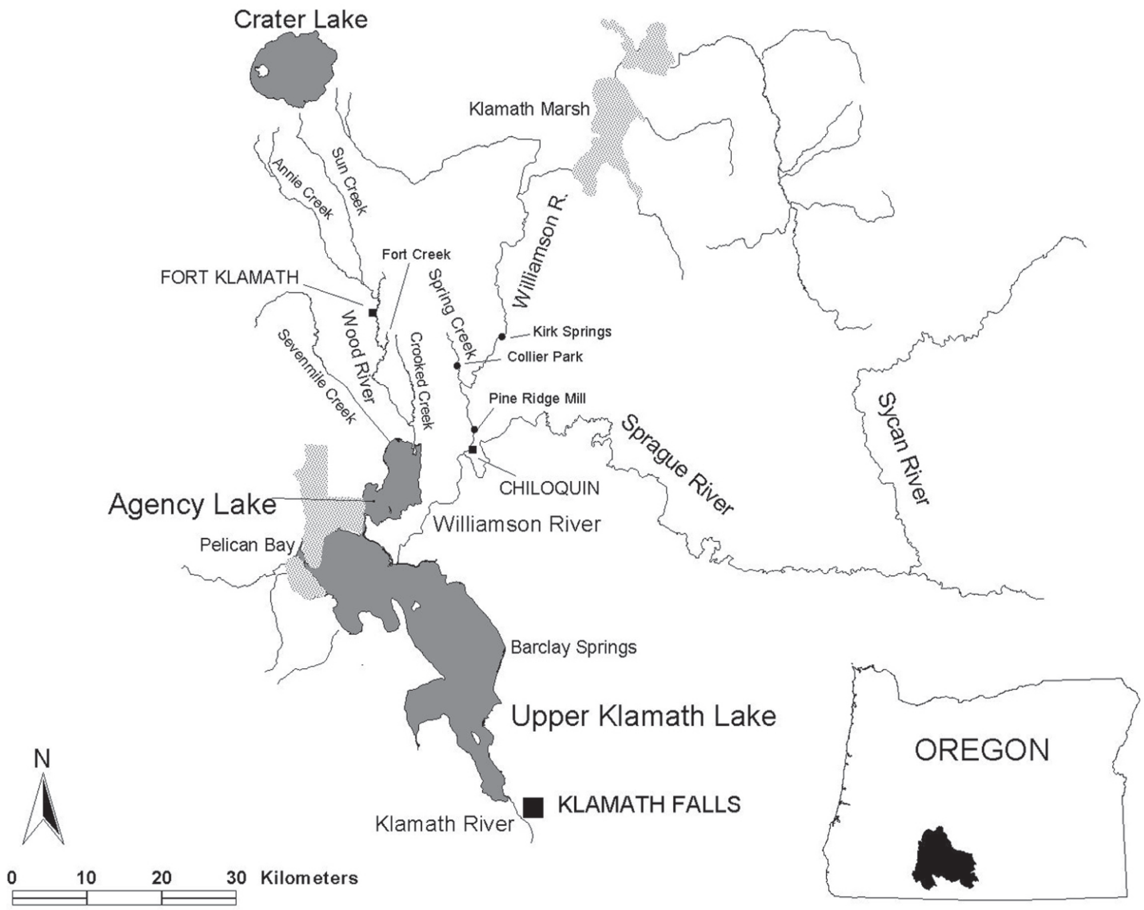

FIGURE 1.—Map of the Wood and Williamson River drainages in the upper Klamath River basin, Oregon. Light shaded areas represent hardstem bulrush–cattail marsh habitat.

Agency lakes are the largest remnants of this ancient lake and currently cover 32,900 and 3,500 ha, respectively, at maximum lake elevation of 1,263 m (USACE 1978). The level of the lake is regulated by Link River Dam, constructed in 1921 on a natural lava dam near the town of Klamath Falls. Both lakes, although large in surface area, are relatively shallow, with an average depth of about 2.5 m.

The watershed basin for the lakes encompasses an area of about 9,800 km^2. The major tributaries of Agency Lake are Sevenmile Creek, Wood River and its tributaries Fort and Crooked creeks (Figure 1), and numerous small springs along the west side of the lake. The Williamson River and its main tributary, the Sprague River, supply most of the inflow to Upper Klamath Lake. Smaller tributaries and springs also enter Upper Klamath Lake.

Although upper Klamath and Agency lakes are naturally eutrophic because of their shallow depths, deep sediments, and phosphorus-rich volcanic soils in the watershed, nutrient and sediment loading to the lakes have increased over the last century and have led to its current state as a hypereutrophic system (Eilers et al. 2004). Levels of phosphorus delivery to the lakes have increased from activities in the watershed such as logging, grazing, and irrigated agriculture (Miller and Tash 1967; Eilers et al. 2004). An additional source of phosphorus is from decomposition of soils in drained wetlands (Snyder and Morace 1997; Bradbury et al. 2004). Wind action can resuspend the fine lake sediments, further increasing the loading of phosphorus in the lakes (Bond et al. 1968; Laenen and LeTourneau 1996). Extensive blooms of *Aphanizomenon flos-aquae*, a blue-green alga, correspond to large seasonal increases in total phosphorus and adversely impact water quality and fisheries in the lakes. The dynamics of the algal bloom have resulted in extended periods of elevated pH, low dissolved oxygen, and toxic levels of ammonia (Bortleson and Fretwell 1993; Kann and Smith 1999; Perkins et al. 2000). These extended periods of poor water quality during summer months have caused chronic stress in fishes and resulted in fish kills (Scoppettone and Vinyard 1991; Kann and Smith 1999; Perkins et al. 2000).

Life History and Distribution of Adfluvial Redband Trout

The biology and life history of adfluvial redband trout in the upper Klamath River basin have not been extensively investigated. We do have some knowledge of when and where adult redband trout spawn, but this information is limited to some of the larger spawning tributaries such as the Williamson and Wood rivers and Spring Creek. The adfluvial redband trout populations of the upper Klamath River basin utilize tributaries for adult holding and spawning, and for early juvenile rearing. Little information is known about juvenile life history of adfluvial redband trout. Juvenile redband trout are thought to spend up to 1 year rearing in tributaries before migrating to the lakes where they rear until maturity. Research has shown that redband trout first spawn generally at age 3 and, depending on the stock, may spawn in consecutive years up to age 8 (Borgerson 1991).

The major spawning tributaries for adfluvial redband trout in the upper Klamath River basin are the Williamson, lower Sprague, and Wood rivers and Spring Creek (Figure 1). The lower Williamson River below Klamath Marsh, and its main tributaries Spring Creek and the Sprague River, support the largest populations of redband trout in the upper Klamath River basin. The Kirk Springs area of the lower Williamson River (Figure 1), is one of two main redband trout spawning areas in the river; the other being the 3.2 km reach downstream of Spring Creek. Spring Creek, a major tributary of the lower Williamson River, has a flow of about 8.5 m^3/s (300 ft^3/s) of clear, cold water (4.4°C). Although Spring Creek is only 3.2 km long, it provides good spawning and rearing habitat, which has been improved with the addition of spawning gravel and large wood. The Wood River is a low gradient stream that flows 27 km from its spring source to Agency Lake. Redband trout spawn in the upper 3.2 km of the river.

Late summer fish kills that sometimes occur in Upper Klamath Lake usually involve large numbers of Lost River (*Deltistes luxatus*) and shortnose (*Chasmistes brevirostris*) suckers, and blue (*Gila coerulea*) and tui (*G. bicolor*) chubs, although some adult redband trout also have been found. Few juvenile redband trout are found during the fish kills, but moribund and dead juveniles are quickly lost to bird predation. In addition to direct mortality, long periods of poor water quality increase stress on fish and can have sublethal effects that reduce fitness (Perkins et al. 2000). Therefore effects on redband trout might be greater than that measured by counts of dead fish. Large fish kills were documented in 1995–1997, with 1997 being most severe for redband trout (Perkins et al. 2000). Redds counted in Spring Creek (Table 1) did not significantly change ($P = 0.87$) from 1991–1995 to 1996–2001, suggesting that fish kills in the lake did not have a direct effect on number of redband trout spawners. Periods of poor water quality that result in large fish kills of suckers and chubs may not cause high mortality of adult redband trout if the trout migrate out of Upper Klamath Lake early or move into cool-water refuges such as springs in Pelican Bay (Figure 1). Another possibility is that overlap in age classes of redband trout may buffer effects of mortality on the number of spawners, especially if conditions that lead to fish kills in the lake are infrequent.

Historical Management of Klamath Lake Redband Trout

The evolution of redband trout management in Klamath Lake and its tributaries has resulted largely from the collection of information by biologists who have worked in the upper Klamath River basin. This information has been used to develop new fish policies and plans that will guide the management of redband trout in the upper Klamath basin for years to come. In reviewing the historical management of Klamath Lake redband trout, it is important to remember the political and social atmosphere in which fishery biologists were working during their employment. Options for future management of native trout populations are often limited by the management decisions that were made during the past century and their consequences. Choosing the future direction of fish management will require an understanding of the historical changes that have shaped present-day trout populations (Buchanan et al. 1989).

Redband trout management in the upper Klamath River basin had its beginnings in the late 1920s, when hatchery

Table 1. Counts of redband trout redds in two sections of Spring Creek and in 5 km of the Williamson River below Spring Creek, 1974–2001. Redd counts were conducted at approximately 2-week intervals. Redd counts in Spring Creek started in November of the previous year. Redds were counted in the Williamson River in September after the river cleared of tannic runoff from Klamath Marsh.

	Spring Creek			
Year	Gabion (near mouth)	Collier Park	Total	Williamson River
1974				43
1975				99
1976	62	302	364	117
1977	36	294	330	170
1978	80	124	204	123
1979	49	230	279	61
1980	67	151	218	112
1981	86	180	266	105
1982	76	95	171	
1983	84	128	259	
1984	131	128	259	
1985	148	131	279	
1986	245	228	473	
1987	284	182	466	
1988	238	233	471	
1989	209	365	574	
1990	253	316	569	
1991	232	250	482	83
1992	274	326	600	161
1993	315	312	627	113
1994	328	354	682	146
1995	356	207	563	113
1996	292	276	568	171
1997	303	258	561	96
1998	346	394	740	
1999	366	147	513	
2000				153
2001	359	256	615	

trout were first stocked into Klamath Lake and its tributaries. The principal management activities for trout fisheries in Upper Klamath and Agency lakes from the late 1920s through the 1960s were the stocking of hatchery trout to provide recreational fisheries and the monitoring of fisheries with creel surveys. Stocking records of ODFW report large numbers of hatchery trout released into the lakes and tributaries from 1928 to 1963. The cumulative totals of hatchery trout stocked in the lakes during this period were 12 million rainbow trout and 400,000 brook trout *Salvelinus fontinalis*. Total numbers of hatchery trout stocked into tributaries were 4.8 million rainbow trout of various strains, 1.5 million brook trout, 280,000 steelhead *O. mykiss*, and 27,500 cutthroat trout *O. clarkii*.

The majority of hatchery trout stocked in the basin were released as unfed fry until 1960. One reason fish were released at this life stage was because high survival was assumed to occur in the highly productive lakes. Another reason larger fish were not released in the early years was that hatchery practices such as disease treatment and nutrition had not advanced to the point of successfully rearing larger fish. In the early 1960s, Arthur Gerlach (ODFW Klamath District fish biologist, 1957–1967) observed a decline in the numbers of trout taken in the sport fishery. Consequently, changes were made in the management of the lakes to increase the numbers and size of trout available to the recreational fishery. These changes included increasing the numbers of fingerling trout (5–10 cm) and swim-up fry released into the lakes. From 1961 to 1962, the numbers of hatchery trout released in the lakes increased for fingerlings (55,220 to 201,000) and for swim-up fry (539,500 to 2.3 million). Stocking times and locations also were modified to increase survival. Release times were changed from summer to winter to avoid releasing hatchery trout into marginal habitat caused by poor water quality. Location of release changed from general lake releases to releases into Barclay Springs, along the eastern shore of Upper Klamath Lake (Figure 1). The cool spring water in Barclay Springs provided better water quality than that in the lake, and it was believed that better water quality would provide excellent rearing conditions for fry releases and would increase survival. Angling regulations were adopted for the lakes that protected larger fish by limiting the daily bag limit to two trout ≥ 51 cm (20 inches).

Surveys of the important spawning tributaries also were conducted to determine what measures could be taken to increase natural reproduction. These surveys showed that small dams blocked most of the major spawning tributaries and that pumice sand covered the spawning areas. Surveys also revealed major losses of wetlands around the lakes, reduction of trout rearing habitat because of dredging in the lower sections of the Wood and Williamson rivers, and severe impacts to stream habitat in the upper watersheds of the basin because of poor forestry and agricultural practices.

Because of these findings, Gerlach concluded that the hatchery program for the Upper Klamath and Agency lakes was going to be important for the maintenance of the trout fishery. The increased stocking program also was seen as necessary to supplement any natural reproduction. A conclusion of the management program was that trout stocking should continue until such time that the natural production in the lakes could sustain the recreational trout fishery.

Managers noted some success following the increase in the numbers of hatchery trout stocked. In 1963, the proportion of small fish increased in the catch, but the total number of fish caught was low. The low catch was attributed to small numbers of anglers participating in the fishery. In 1964, managers observed that the numbers of trout taken by anglers in both lakes increased considerably, with the average size ranging from 36 to 46 cm. A group of 125,000 marked fingerlings were released in the lakes in 1963. Although the number of trout caught seemed correlated with increased numbers of stocked trout, few marked fish were caught in the fishery; none in 1963 and five in 1964, with an average length of 36 cm. It was becoming increasingly apparent that even though hatchery releases in the lakes had increased, the increase in trout production could not be attributed to increased levels of stocking.

Management in the 1970s continued to use hatchery releases as a strategy to supplement fish production and to increase the numbers of trout available in the recreational fishery. However, the trout stocking program was refined during this period. The fishery management plan called for annual stocking of 50,000–60,000 legal rainbow trout in streams and 550,000 fingerlings into Upper Klamath and Agency lakes. Concerns were frequently expressed that despite increases in hatchery releases, hatcheries were not keeping up with demand. Additional marking programs were initiated to evaluate the trout stocking program and to determine if changes in the hatchery stocking program were successful in increasing trout production.

Studies conducted in the early 1970s to evaluate success of trout stocking in Upper Klamath Lake concluded that a release of 310,000 fingerling trout in Upper Klamath Lake contributed < 0.4% to the trout fishery. These results added to the increasing evidence that rainbow trout stocked in the upper Klamath River basin did not survive to contribute to recreational fisheries. Fishery managers also recognized that because the stocks of rainbow trout released into waters of the basin were not indigenous, they did not exhibit survival and growth rates, or contribute to the fisheries as well as indigenous stocks of redband trout, which have adapted to the high summer pH and temperatures characteristic of waters in the upper Klamath River basin.

One of the early studies that helped shape management of the redband trout in the Williamson River was a 1972 study that evaluated the redband trout fishery in a 6.4-km section of the Williamson River south of the town of Chiloquin. The objectives of this study were to determine anglers' opinion of management of the fisheries and to document redband trout harvest in the river. The study, through its marking program, also provided information on redband trout movement within the Williamson River and in Upper Klamath Lake. Findings from this study showed that the overall catch rate of redband trout in the lower Williamson River was 0.77 fish/angler and 0.29 fish/hr. Anglers considered a trophy fish to be ≥ 51 cm (20 inches), and wanted a quality rather than a consumptive fishery. As a result of this study, special angling regulations were enacted for portions of the lower Williamson River that included a bag limit of two fish > 30.5 cm (12 inches) and a gear restriction of lures and flies only. Additionally, stream rehabilitation projects were initiated in the Williamson River in 1974 to improve habitat for redband trout.

Shifts in management philosophy started to take place and were conveyed in a 1974 report by Wendell Stout (ODFW Klamath District fish biologist, 1967–1977) in which he stated: "Major emphasis in the Klamath Basin will be directed to the protection and enhancement of resident game fishes presently established." The management goals in 1974 for redband trout in the upper Klamath River basin were to (1) maintain the maximum healthy population of redband trout in all waters capable of trout production in the basin; (2) maintain and, where practical, enhance the present quality of angling experience in terms of productive angling for large fish in all waters providing this opportunity; (3) prevent any further loss or deterioration of redband trout habitat; (4) improve stream habitat; and (5) assure public access to all desirable fishing areas.

Problems in achieving these management goals were identified and actions were taken. Physical stream surveys were conducted in areas critical to natural production of redband trout to assess the location and extent of land use practices damaging fish habitat. These surveys were important for the identification of critical habitat for redband trout and physical factors limiting natural production. For example, lack of spawning and rearing areas were identified as limiting factors for populations of native redband trout in Spring Creek. In 1975, a gabion was placed across the mouth of Spring Creek and gravel was placed above it to provide spawning habitat. Wood was also added to the creek to provide juvenile rearing habitat. Adult redband trout were observed spawning in the introduced gravel within months of placement. Additional gravel was placed in the 1980s in Spring Creek at the gabion and upstream near Collier Park (Figure 1).

We compared counts of redds in years when surveys were conducted in Spring Creek and the Williamson River to assess use of placed gravel and potential shifts in spawning distribution. The average number of redds in Spring Creek significantly increased ($P < 0.01$) from 277 in 1976–1981 to 583 in 1991–1997 (Table 1). However, of the two survey sections in Spring Creek, the average number of redds in the gabion section increased almost five-fold ($P < 0.01$), from 63 to 300, while the average number of redds in the Collier Park section increased only about 30%, from 213 to 283 ($P = 0.08$). The lack of significant change in the upper section could have been a consequence of the introduced gravel moving downstream. Concern was raised that the increase in redds in Spring Creek could have resulted if redband trout that would have spawned in the main stem of the Williamson River below Spring Creek were now spawning in Spring Creek. Because of this concern, index counts in the Williamson River from Spring Creek to Pine Ridge Mill (Figure 1) were resumed in 1991 (after having been stopped in 1982). The average number of redband trout redds was not significantly different ($P = 0.98$) between 1976–1981 (115) and 1991–1997 (126) (Table 1). Redds were counted in the Williamson River in September, several months after redband trout spawned, because the river is discolored from tannic runoff out of Klamath Marsh until late summer. Therefore, counts of redds in any given year may include redds that were made and counted in the previous year, if the older redds remain visible because winter and spring flows were not high enough to move gravel. Although this bias may affect the exact number of redds in a given year, it is unlikely to affect comparisons between the two 6–7 year periods.

During the late 1970s and early 1980s, major changes were made in trout management in Oregon and in the upper Klamath River basin because of new ODFW management policies and plans, and the discovery of *Ceratomyxa shasta* in Klamath Lake (*see below*). Policies and management plans adopted by the Oregon Fish and Wildlife Commission (OFWC) included the Wild Fish Management Policy in 1978, and a statewide trout plan (ODFW 1987). These policies and plans guided fish management toward sustaining the diversity and abundance of native fish. Protection and enhancement of wild stocks was given first and highest consideration in fish management. The new policies and plans also provided guidance in addressing diversity in angling opportunities within the constraints of species biology, distribution, and abundance.

A new fish management plan for Upper Klamath and Agency lakes was adopted by the OFWC in 1981. This plan incorporated the newly developed ODFW Wild Fish Management Policy and called for management of the fisheries with wild trout only. No hatchery fish have been stocked in Upper Klamath and Agency lakes since 1979. In addition, stocking of all streams (except for Spring Creek) was discontinued after 1991, when the Wood River and Sevenmile Creek were last stocked.

The discovery of *C. shasta* in Upper Klamath Lake played a key role in determining the management of redband trout in the upper Klamath River basin. In 1979, *C. shasta* was determined to be the cause of death in 40 small rainbow trout in Upper Klamath Lake at Barclay Springs. This important discovery helped explain why hatchery trout survival was so poor in Klamath Lake. The majority of exotic rainbow trout stocked into Upper Klamath Lake were susceptible to and likely killed by *C. shasta.* As a result of detecting *C. shasta* in Upper Klamath Lake, stocking of rainbow trout in Upper Klamath and Agency lakes and all its tributaries (excluding Spring Creek) was terminated. The hatchery fish released into Spring Creek are a domesticated stock of coastal rainbow trout and have very poor survival in the main stem of the Williamson River because they are susceptible to *C. shasta* that is present in the river. The hatchery rainbow trout stocked in Spring Creek provide a put-and-take fishery in summer, when numbers of wild redband trout are low. No hatchery rainbow trout were found in Spring Creek during studies when adults were trapped (Buchanan et al. 1990, 1991; Hemmingsen et al. 1992). Kirk Springs redband trout were used in the early 1990s to start a strain of hatchery redband trout. These fish were used in Spring Creek to replace the Cape Cod hatchery rainbow trout, but were difficult to catch. Some of these fish migrated to the Williamson River and Upper Klamath Lake and returned as adult spawners. For example, of the redband trout captured in Spring Creek in December 1992–May 1993, 267 were wild fish and 27 were hatchery fish (identified by adipose fin clips) that had been stocked in previous years (Hemmingsen and Buchanan 1993). This program was subsequently dropped because of the failure to meet the primary objective of a put-and-take fishery and because of potential negative impacts on wild redband trout. The stocking of hatchery rainbow trout (Cape Cod strain) was then reinstated.

Research studies were conducted by the Native Trout Project of the ODFW Fish Research Section in 1989–1994. These studies added information critical to the sound biological management of redband trout stocks in the upper Klamath River basin. Studies revealed that the redband trout of Upper Klamath Lake were unique in terms of life history characteristics, meristics, disease resistance, and allozyme variation. Studies on the resistance of redband trout to *C. shasta* within the upper basin found that the infective stage of *C. shasta* exists in the lower Williamson River and Upper Klamath Lake (Buchanan et al. 1989). Although *C. shasta* was not detected in Spring Creek, juvenile redband trout from the creek were resistant. However, these juvenile fish are progeny of adults that are exposed to *C. shasta* in the Williamson River and possibly in Upper Klamath Lake. *C. shasta* was absent from the Williamson River upstream of Klamath Marsh, and most of the juvenile redband trout from this area were susceptible when exposed to *C. shasta* (Buchanan et al. 1989).

Research findings also showed that redband trout in the upper Klamath River basin represent a unique and highly divergent evolutionary line (Buchanan et al. 1990), and that genetic differences existed between populations of redband trout in headwater streams and those associated with Upper Klamath Lake (Buchanan et al. 1994). A comparison between the life history characteristics of adult redband trout in Spring Creek and those at Kirk Springs showed significant differences in spawn timing and duration, and in the size of adult spawners (Buchanan et al. 1991; Hemmingsen et al. 1992; Hemmingsen and Buchanan 1993), although the two populations are genetically similar (Buchanan et al. 1994). In addition, tagging studies supported the hypothesis that redband trout populations from these two areas are reproductively isolated from each other, despite the absence of a physical barrier between the two spawning sites (Buchanan et al. 1991; Hemmingsen et al. 1992; Hemmingsen and Buchanan 1993). Redband trout from Spring Creek are genetically distinct from those in the Wood River, although fish from both populations are thought to spend some of their life in the Klamath Lake complex. Based on allele frequencies, Wood River redband trout grouped more closely with headwater groups than with other populations associated with Upper Klamath Lake, but they did share some similarities with the Upper Klamath Lake populations (Buchanan et al. 1994).

Future Management of Klamath Lake Redband Trout

The Klamath River Basin Fish Management Plan (ODFW 1997) was developed with information about past management of Klamath Lake redband trout, life history characteristics and biology of redband trout in the basin, and ODFW fish management policies. This plan was developed with the intent of optimizing recreational use of the fish resources in the upper Klamath River basin for present and future generations, while conserving the integrity of the native fish fauna. The principal consideration in developing this management plan was compliance with the ODFW Wild Fish Management Policy (ODFW 1992) and the statewide trout plan (ODFW 1987). These documents guide management toward sustaining diversity and abundance of the native trout in Oregon.

The guiding principles for redband trout management in Upper Klamath and Agency lakes, and all tributaries contributing redband trout production to the rearing populations in the lakes, include the following: (1) management of fish resources must consider potential ecological consequences; (2) maintenance or restoration of indigenous species is of foremost importance and is the guiding principle for this plan; and (3) no management direction proposed in the plan is expected to have significant detrimental effects on any indigenous species.

The key objectives of the plan are to maintain protection of genetic diversity, adaptiveness, and abundance of redband trout in the waters of the basin, and to provide for diverse angling opportunities by providing for consumptive and recreational fisheries on redband trout where they occur in these waters. Proposed management alternatives for Klamath Lake redband trout call for natural production and management for trophy fisheries.

Summary

Management of redband trout in the upper Klamath River basin has progressed from the early 1920s, an era when hatchery fish were released in attempts to increase fish production, to the 1990s, when the uniqueness of endemic stocks of redband trout and habitat protection and enhancement are paramount for producing trophy trout fisheries. This progression happened because fish managers incorporated the results of biological studies of redband trout to develop policies and management plans that recognized the importance of native fishes and natural production. Although management goals and objectives have changed through time, the current management of Klamath Lake redband trout is designed to preserve these unique stocks of fish for the enjoyment of present and future generations of anglers and the general public.

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Redband Trout: Resilience and Challenge in a Changing Landscape
Oregon Chapter, American Fisheries Society, 2007

Adfluvial Life History of Redband Trout in the Chewaucan and Goose Lake Basins

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Abstract.—The life history of redband trout in the Chewaucan and Goose Lake basins includes an adfluvial form, fish that migrate as juveniles to rear in lacustrine habitats before returning to streams for spawning. The adfluvial life history was studied in 2000 and 2001 with a combination of trapping, radio tagging, and scale analysis. Peak migration of juvenile redband trout in the Chewaucan River occurred in late March to late April. In Thomas Creek (Goose Lake basin) catch of juvenile fish was highest in mid May. Upstream migration of adult fish began as early as January in the Chewaucan River and began in early March in Thomas Creek. Spawning in both basins occurred from late March to June, and adult fish began migrating downstream as early as mid April. In the Chewaucan Basin, 86% of the spawning occurred in Dairy and Elder creeks and in the main stem of the Chewaucan River. In the Goose Lake basin, 79% of the spawning occurred in Thomas Creek. Scale analysis indicated that repeat spawning was common in adfluvial redband trout, although 40–80% of the radio-tagged fish died after spawning. The average length of radio-tagged fish was greater than that of all upstream migrants, and the tagged fish may have been predominantly repeat spawners. Age-3 and age-4 redband trout represented 76% and 86% of adults in the Goose Lake and Chewaucan basins, respectively. Passage problems at irrigation diversions for adults migrating upstream and downstream, and for juveniles migrating downstream were documented in both basins. Of the radio-tagged adult fish migrating downstream after spawning, 94% and 71% were diverted into irrigation ditches in the Chewaucan River and Thomas Creek, respectively. The adfluvial life history has persisted despite periodic drought and loss of lacustrine habitat, and degradation of freshwater habitats. Irrigation diversions continue to affect adfluvial migration of juvenile and adult redband trout in both basins, but ongoing cooperation with landowners and planned projects should alleviate many of the passage problems. For example, substantial improvements in fish passage have occurred recently in the Chewaucan River with construction of fish ladders at all diversion dams, removal of one of the diversion dams, and installation of a fish screen on the largest of the three irrigation ditches.

Redband trout *Oncorhynchus mykiss* were studied in the Chewaucan and Goose Lake basins, with a primary focus of obtaining information about the adfluvial life history in these basins and about juvenile life history in the Chewaucan River. Very little is known about redband trout in the Chewaucan Basin. Redband trout historically used the lower Chewaucan Marsh for rearing, thus establishing adfluvial populations (Bowers et al. 1999). The adfluvial life history in the Chewaucan was considered extinct in a 1990s status report (Kostow 1995). However, adfluvial redband trout were documented in 1996, following the construction of Rivers End Reservoir in 1994 (Ed Now, Oregon State Police, personal communication). Adfluvial redband trout in the Goose Lake basin spawn in several Oregon and California tributaries, although little information is available on the adfluvial life history prior to 1977. Adfluvial redband trout appeared to be numerous in the Goose Lake basin in 1978 (ODFW, unpublished data), but none were observed in Oregon streams from 1982 to 1997. In California, adfluvial redband trout were not seen after 1989 (Moyle et al. 1995). Runs of adfluvial redband trout appeared again in Oregon and California streams in 1997–1999 (Gerstung 2007, this volume).

Redband trout from populations in the basins of Goose Lake, Chewaucan, and Warner Lakes were genetically similar, and generally were more differentiated from redband trout in the Fort Rock and Catlow basins (Currens 1997). Berg (1987) also found that Goose Lake redband trout were most closely related to the Warner Lake redband trout. The glucose-6-phosphate isomerase 138 allele (GPI-B1*138) occurred in frequencies of 45–100% in redband trout of the Goose Lake, Chewaucan, and Warner Lakes basins (Berg 1987; Currens 1997), and was very rare or absent in other *O. mykiss* populations.

This study was undertaken to collect information on redband trout in the Chewaucan and Goose Lake basins that would aid in management, conservation, and recovery of the species. The specific objectives were to: (1) collect life history information on juvenile and adult redband trout in both basins, including timing and age of migration, use of fluvial and lacustrine habitats, and timing and distribution of spawning; (2) identify passage problems for juvenile and adult redband trout; and (3) document the abundance, migration timing, size, and age of outmigrant juvenile redband trout in the Chewaucan Basin.

Study Area

The Chewaucan and Goose Lake basins lie within the northern part of the Basin and Range physiographic province. These basins generally are characterized as closed basins; that is, they are internally drained with no outlet to the ocean. However, during the Pleistocene Epoch, some of these lakes reached high levels and had temporary access to large rivers flowing to the Pacific Ocean. During periods of high water levels, redband trout in these basins probably developed adaptations for a lacustrine life history (Behnke 1992).

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Chewaucan Basin

The Chewaucan River originates at the confluence of Dairy and Elder creeks, which begin on Gearhart Mountain and Deadhorse Rim, and flows 85 km to Lake Abert (Figure 1). The basin covers about 700 km^2. Lake Abert is an alkali lake that likely has been inhospitable for redband trout for hundreds of years. During the Pleistocene Epoch, pluvial Lake Chewaucan covered the Summer Lake, Lake Abert, and Chewaucan Marsh areas. It covered an estimated area of 1,244 km^2 and reached an elevation of about 1,380 m (Allison 1982). For comparison, the elevation at the town of Paisley is 1,340 m.

A century of livestock grazing has occurred in the Chewaucan River watershed and reached a peak in the early 1900s. An assessment of the upper watershed documented grazing permits in 1909 for 110,000 sheep and 26,000 cat-

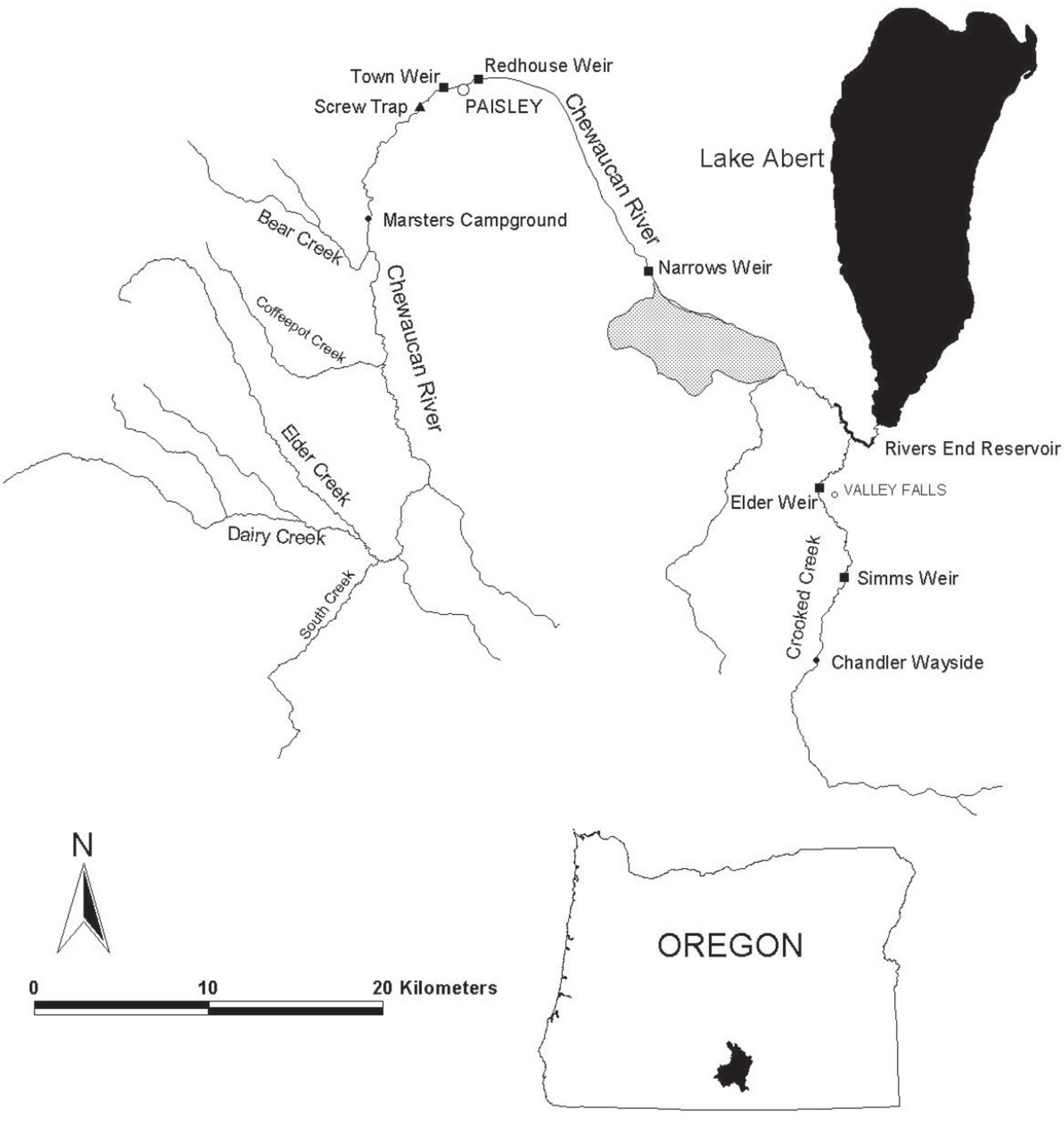

Figure 1.—Map of the Abert Lake basin with weir and screw trap locations. Stippled shading shows general area of Chewaucan Marsh.

tle and horses on Fremont National Forest lands (Peets and Friedrichsen 1999). The numbers had dropped to 78,000 sheep and 11,000 cattle and horses by 1929, but the habitat in the watershed was classified as severely degraded. As an example, a tributary of Coffeepot Creek was described as having severe bank erosion and downcutting because the vegetation was so scarce (Peets and Friedrichsen 1999). The degraded habitat in the watershed caused by overgrazing was further impacted by drought in the late 1920s to mid 1930s. The numbers of sheep dropped to 31,200 by 1959 and sheep grazing ended in the basin in the 1960s. The number of cattle increased slightly to 12,400 in the 1950s and 1960s, and is currently about 12,500 in the upper watershed.

The mean monthly flow of the Chewaucan River ranges from a high of about 14 m^3/s (500 cfs) in May to a low of 1 m^3/s (30 cfs) in September. At the confluence of Dairy and Elder creeks, the Chewaucan River is a low gradient, meandering stream with gravel substrate and riffle-pool sequences. As the river continues north, it flows through a canyon reach that is characterized by moderately steep gradient, cobble substrate, and rapids and runs with irregularly spaced pools. A small section of the river upstream of Marsters Campground is entrenched and dominated by cobbles, in part because of riprap and other bank protection structures installed by the U. S. Forest Service to protect a trail bridge and picnic area. The river empties into the basin that held the Pleistocene Lake Chewaucan and flows through the Chewaucan Marsh, a large wetland area that has been impacted by ditching and draining for agricultural use. Two major floods have occurred within the last century, resulting in high flows of about 180 m^3/s (100-year event) in 1964–65 and 195 m^3/s (500-year event) in 1997.

Rivers End Reservoir begins at approximately rkm 1.6 (Figure 1), with a maximum surface area of 2.6 km^2 and a maximum depth of 5.4 m. Adfluvial redband trout from Rivers End Reservoir have been unable to reach spawning grounds of the Upper Chewaucan River and tributaries because of three impassable barriers: Narrows, Redhouse, and Paisley Town weirs (Figure 1). Fish passage has been recently provided at all three weirs, allowing adfluvial redband trout to reach the upper watershed. Elder Weir on Crooked Creek remains an upstream barrier for fish migrating out of Rivers End Reservoir (Figure 1).

In addition to redband trout, the two other fish species native to the Chewaucan basin are the speckled dace *Rhinichthys osculus* and tui chub *Siphateles oregonensis* [*Gila bicolor*]. Redband trout and speckled dace are the only native species thought to occur in the mainstem Chewaucan River. Redband trout are also found in Crooked Creek along with tui chub. Although Harris (2000) described the tui chub as extirpated from the Chewaucan River and tributaries (except Crooked Creek), some tui chub were captured in the Chewaucan River screw trap in 2000. Hatchery rainbow trout were stocked in the Chewaucan watershed from 1928 to 1998. Stocking was ceased because of concerns about introgression and competition with native redband, and because of low angler harvest of hatchery fish (Bowers et al. 1999). Brook trout *Salvelinus fontinalis* were introduced into the basin in 1930 at Dairy Creek and are present in the upper watershed, but are seldom observed in the lower reaches of the Chewaucan River.

Goose Lake Basin

Goose Lake is a large, hypereutrophic and turbid lake (Johnson et al. 1985) in Lake and Modoc counties of south central Oregon and northeastern California (Figure 2). Goose Lake covers about 360 km^2 at an elevation of 1,437 m (4,716 ft) when it is full (Phillips and Van Denburgh 1971), with an average depth of about 2.5 m and a maximum depth of 7.3 m (GLFWG 1994). During the Pleistocene Epoch, Goose Lake covered an estimated area of about 950 km^2 and reached an elevation of about 1,525 m (Conaway 2000).

Water quality measured in Goose Lake in June and September 1993 found salinity levels of 1.0–1.7 ppt and pH of 9.0–9.8 (GLFWG 1994). The range of water temperatures at the bottom of the lake was 16–23°C. Goose Lake has gone dry 10 times in the last two centuries (1851,1852, 1926, 1929–1934, 1992), and was almost dry in 1924–1925 and 1986–1991. In recorded history, Goose Lake has overflowed into the North Fork of the Pit River in 1868 and 1881 (GLFWG 1996).

Irrigation dams that create passage problems in the Thomas Creek watershed include Garret, Taylor, Utley, 70 Ranch, Gover, Cox-Bauers, Camp Creek, and Camp Creek Culvert (Figure 3). Possible passage problems exist at other culverts and stream headcuts. The Garret weir has a concrete-step fish ladder and Utley, Gover, and Ranch 70 weirs have portable Denil steep-pass ladders (Clay 1995). The Gover weir has a rotary drum fish screen on the irrigation canal.

Tributaries of Goose Lake in Oregon include 660 km of perennial streams and 900 km of intermittent or ephemeral streams (GLFWG 1996). The primary Oregon streams that historically supported adfluvial redband trout are Dry, Drews, Cottonwood, Thomas, Crane, Cogswell, Kelley, and Pine creeks (Figure 2). Within the Thomas Creek watershed, adfluvial redband trout also used Augur, Camp, Cox, and Bauers creeks. The California streams that historically had adfluvial redband trout are upper Pine, Cottonwood, Willow, (including its tributary, Buck Creek), Lassen, and Davis creeks (Figure 2). The lower reaches of several of these streams have been channelized and diverted and are no longer directly connected to the lake. The primary focus of this study was the Thomas Creek watershed.

Other native fish found in the Goose Lake basin in addition to redband trout are the Goose Lake sucker *Catostomus occidentalis lacusanserinus*, Modoc sucker *C. microps,* Goose Lake lamprey *Lampetra tridentata* ssp., speckled dace, Goose Lake tui chub *S. thalasinnus* [*Gila bicolor thalassina*], Pit roach *Lavinia* [*Hesperoleucus*] *symmetricus*

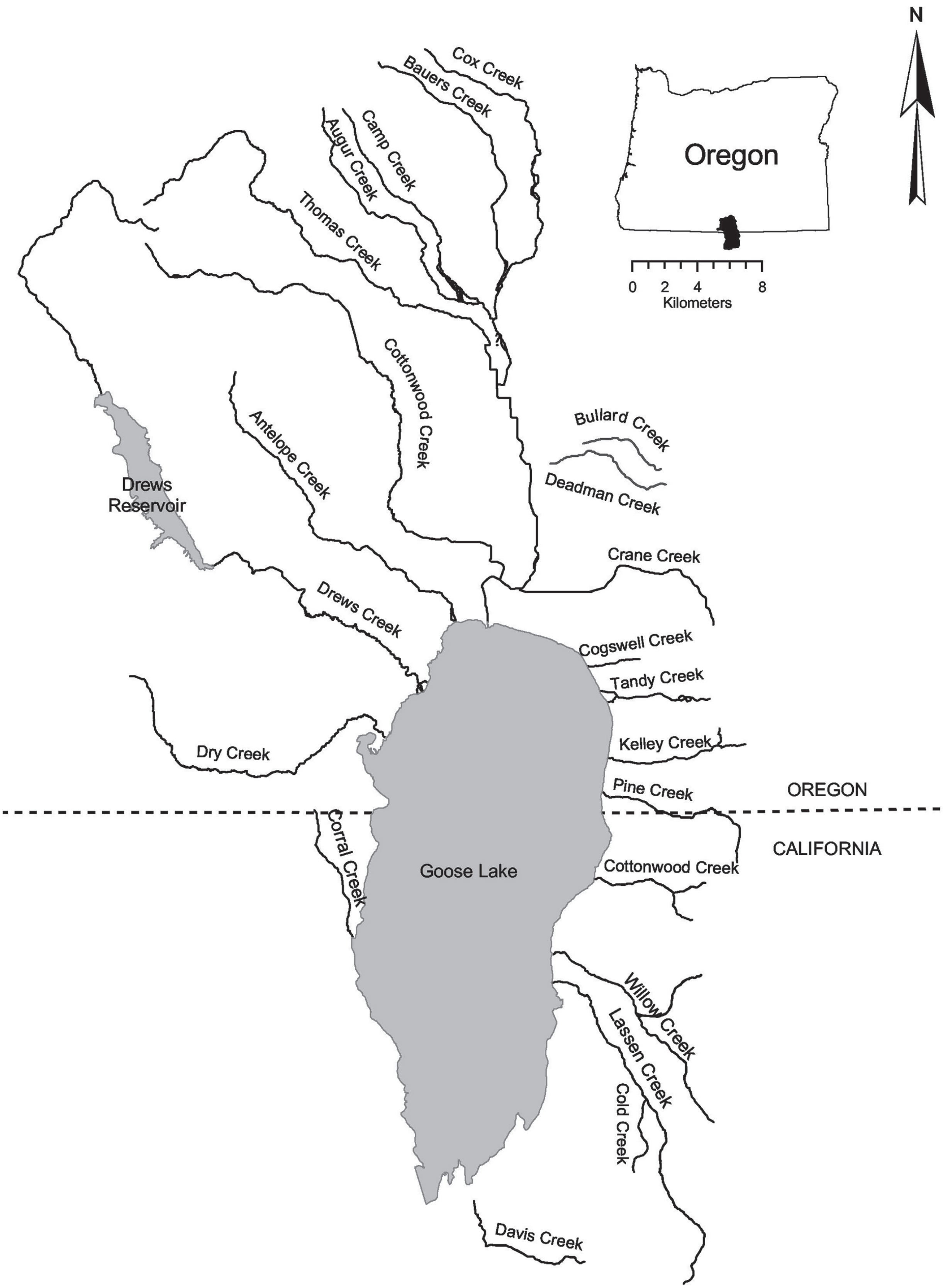

Figure 2.—Map of the Goose Lake basin.

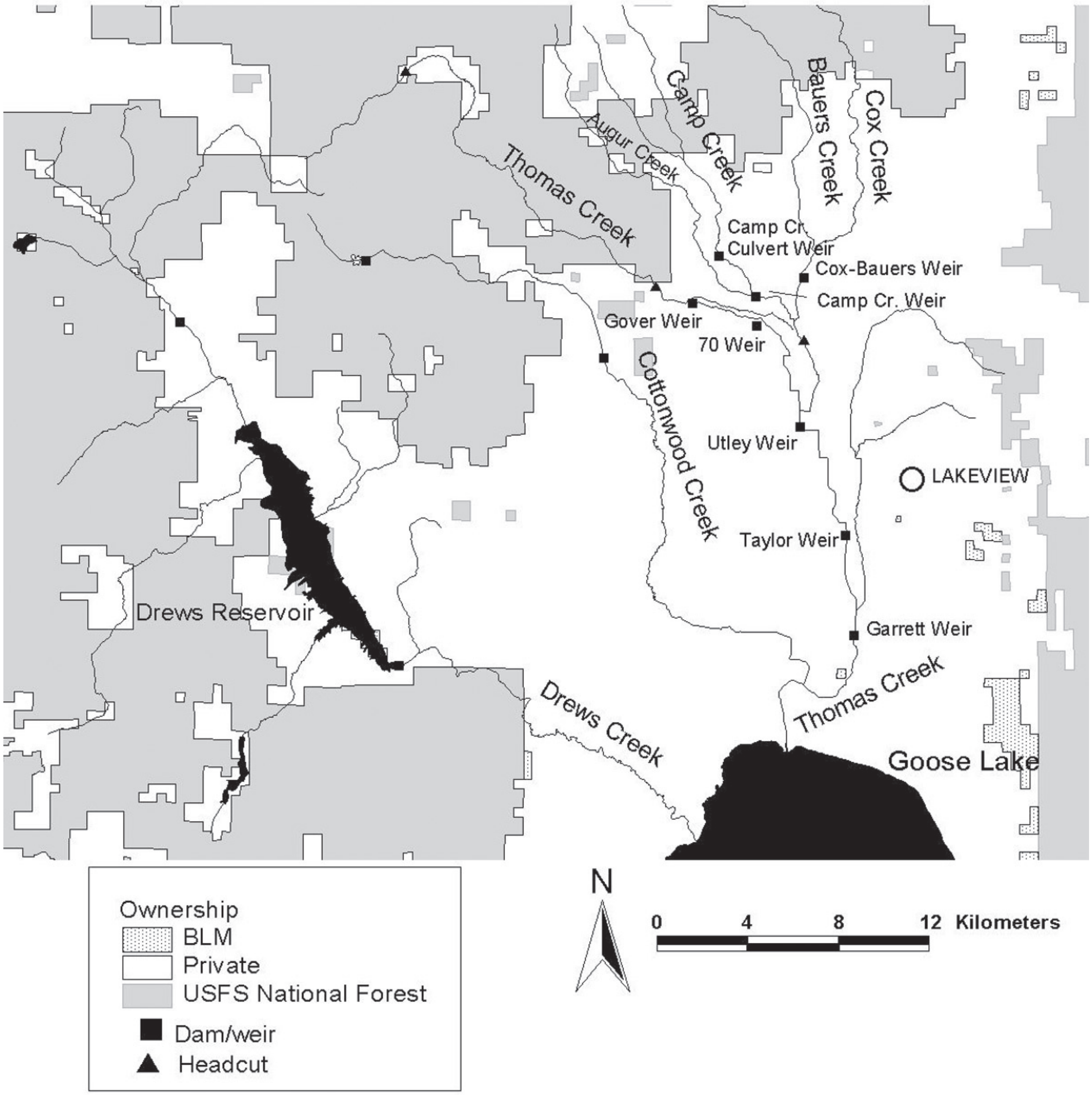

Figure 3.—Locations of weirs and headcuts in the watersheds of Thomas and Drews creeks.

mitrulus, Pit sculpin *Cottus pitensis*, and Pit-Klamath brook lamprey *L. lethophaga*.

Methods,

Chewaucan Basin

Redband trout were captured with hoop nets, seines, or hook-and-line. Hoop nets were set in Rivers End Reservoir in February and March 2000 and in April 2001, and in the Chewaucan River (rkm 16) in April 2001. Seining occurred in Crooked Creek (Elder weir) in March and April 2000. Hook-and-line sampling occurred in the Chewaucan River at the Narrows weir (rkm 26) in March 2000. A trap was built at the Narrows weir in 2001 and was operated in March–May but no redband trout were caught.

We inserted radio tags in some of the captured adfluvial redband trout, and other redband trout were released without radio tags. Anesthetized fish were measured, weighed, and scales were collected. Redband trout were put on a surgery cradle and kept in anesthetic solution for surgical implantation of tags. Radio transmitters were inserted through an incision made in the ventral area above the pelvic fin to the left of the midventral line. The incision was closed with three independent absorbable sutures or Appose® stainless steel staples. A veterinary surgical adhesive (Vet Bond™)

was placed on the incision after surgery in 2001. An antibiotic was applied to the incision and fish were placed in a recovery tub. Lotek™ (model MBFT-5) transmitters were used in fish 33–43 cm and ATS (Advanced Telemetry Systems) transmitters (model 5955) were used in redband trout > 43 cm.

We used a Telonics™ TR2/TS1 scanning receiver and a Lotek™ STR 1000 receiver to track fish on the ground every other day during their upstream and downstream migrations. Tracking from an airplane occurred weekly from April through June, then monthly through September. Locations of spawning areas, passage problems, and refuge areas were determined with global positioning satellite (GPS) units.

Redband trout caught and tagged in the Chewaucan River were transported in an oxygenated tank to the upper Chewaucan River above Paisley (rkm 46) and released in a large pool. Fish caught and tagged at Elder Weir in Crooked Creek were released above the weir, or were transported about 5 km upstream and released. One redband trout caught and tagged at Rivers End Reservoir in 2001 was released above Paisley and the others were released in the reservoir.

A 1.5-m rotary screw trap was fished in the Chewaucan River (rkm 47.5) upstream of Paisley (Figure 1) from 5 March to 30 June 2000 and 15 March to 25 June 2001 to capture migrating redband trout. The trap operated 7d/week and redband trout were given a day-specific fin clip on Monday–Friday. The trap was not checked on Saturdays and Sundays, and fish were accumulated in the live box of the trap. Anesthetized fish were measured (fork length, mm), weighed (g), and scales were collected. Fish recovered for up to 1 hour before being released upstream or downstream of the trap, but not in the same pool as the trap.

Estimates of trap efficiency were computed by releasing up to 25 fin-clipped redband trout per day upstream of the trap approximately 0.5 km. Trap efficiency (E) was determined by the equation:

$$E = R / M$$

where R is the number of recaptured redband trout and M is the number of fin-clipped fish released. The estimated number of migrating redband trout (N) was then calculated weekly by the equation:

$$N = C / E$$

where C is the total number of unmarked redband trout captured in the trap. Confidence intervals for the estimated number of migrants were determined by the equation:

$$95\%\ CI = 1.96 \times \text{sqrt}(V)$$

where V is the variance as determined by the bootstrap method using 1,000 iterations (Thedinga et al. 1994).

Goose Lake Basin

Adfluvial redband trout were captured with hook and line at the Utley weir (rkm 21) in Thomas Creek (Figure 3). Radio tags were inserted in redband trout captured in March and April 2000 and in March 2001. Tagging technique was similar to that used in the Chewaucan River. Redband trout were released above the Utley weir after tagging.

Redband trout were also captured with seines in Thomas Creek at the Utley weir and in a bypass trap at the Gover weir in Thomas Creek (Figure 3). The Gover weir is constructed in May each year, and interrupts downstream passage except for available spill. The bypass trap was operated in 1999–2001. Juvenile fish could also bypass Gover weir in May via a Denil steep pass that was installed in 2000 and 2001 for passage of adult fish. However, once the steep pass was blocked in early June, all downstream migrants were caught in the bypass fish trap. The bypass trap was operated May–mid November 2000 and May–mid August 2001, and was sampled weekly. We enumerated and measured (fork length, mm) all juvenile and adult redband trout and measured a subsample of redband trout fry. Scales were collected from adult redband trout. In addition to the sampling in Thomas Creek, redband trout were captured with a seine in Pine Creek in 2001.

Results

Chewaucan Basin

We captured 151 adfluvial redband trout in the Chewaucan River, Crooked Creek, and Rivers End Reservoir in 2000 and 2001, and inserted radio tags in 41 of these fish (Table 1). The size range of adfluvial redband trout captured in the Chewaucan River (hoop net and hook-and-line), Crooked Creek, and Rivers End Reservoir was 127–660 mm (Figure 4).

The upstream migration of redband trout in the Chewaucan River, as determined by their capture at the Narrows Weir (rkm 26), began in January (Figure 5), similar to that seen in the late 1990s. Spawning occurred in early to late spring, and the first adult redband trout returned downstream to Rivers End Reservoir on April 21 (Figure 5). In Crooked Creek, adult redband trout were captured at the Elder Weir in late March, but they were very ripe and likely had been in Crooked Creek for 2 to 3 weeks. Spawning in Crooked Creek occurred in early March to mid April, and the first adult redband trout returned to Rivers End Reservoir on April 4 (Figure 5).

Of the 34 redband trout tagged and released above Paisley, spawning locations were documented for 22 fish: 9 in

Table 1.—Number of adfluvial redband trout captured in the Chewaucan River basin, and number of fish tagged with radio tags, 2000–2001.

			Number	
Year	Location (rkm)	Method	Captured	Tagged
2000	Rivers End Reservoir (3.2)	hoop net	10	2
2001	Rivers End Reservoir (3.2)	hoop net	3	1
2000	Chewaucan River (25.6)	hook and line	26	14
2001	Chewaucan River (16.0)	hoop net	49	19
2000	Crooked Creek (3.2)	seine	47	5
2000	Chewaucan River (47.5)	screw trap	2	0
2001	Chewaucan River (47.5)	screw trap	14	0

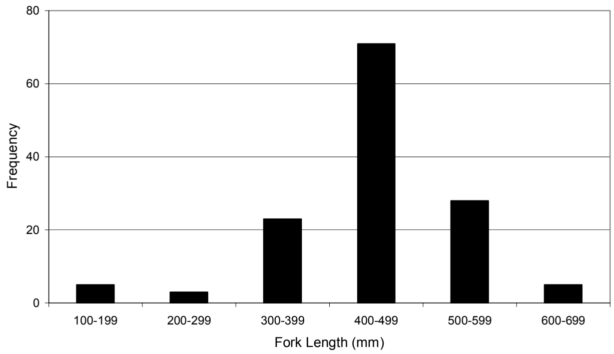

Figure 4.—Length frequency of adfluvial redband trout (n = 135) captured in Crooked Creek (Elder weir, rkm 3), Chewaucan River (rkm 16 and 26), and Rivers End Reservoir, 2000–2001.

Elder Creek, 3 in Dairy Creek, 3 in Bear Creek, and 7 in the Chewaucan River (Figure 6). The average distance traveled by tagged redband trout was 66 km in 2000 and 40 km in 2001, and the maximum distance was 146 km in 2000 and 103 km in 2001. We documented just one spawning redband trout in Crooked Creek above Elder weir, but several spawning fish and redds were seen below the weir.

Two redband trout that were tagged in Rivers End Reservoir in 2000 migrated to the Narrows weir in late March and spent 1 month at the weir but were unable to pass. Only one adult redband trout was able to migrate downstream past Town, Redhouse, and Narrows weirs and reach Rivers End Reservoir. Fifteen other redband trout were diverted into irrigation ditches during their downstream migration. In the Chewaucan River, almost 80% of the tagged redband trout eventually died an average of 45 d after spawning or after reaching their uppermost migration point (average of 70 d after release). Of the 27 mortalities, 10 died near their uppermost migration point and 17 died after migrating an average of 36 km downstream. In Crooked Creek two of the five tagged fish died, one 28 d after spawning and one after returning to the reservoir 70 d after release.

Most adfluvial redband trout in the Chewaucan River were age 3 or age 4, with mean lengths of about 440–500 mm (Table 2). The age-2 fish in the Chewaucan River were captured in Rivers End Reservoir, and scales from these fish suggested good growth during the winter of 1999–2000. Most of the redband trout seined at Elder Weir in Crooked Creek were age 3 or age 4, and were generally smaller at ages 2–5 than those captured in the Chewaucan River or Rivers End Reservoir (Table 2). Some age-1 redband trout were captured in Crooked Creek and were likely downstream migrants. The single age-2 fish captured in Crooked Creek was silvery and also may have been migrating downstream.

Redband trout spawners that were captured in the Chewaucan River were most commonly age 3 (57%) or age 4 (37%), with the remainder evenly divided between age 2 and age 5. We were unable to determine the age of the largest redband trout captured (660 mm) because the scales were regenerated. Scale analysis indicated that iteroparity is common in adfluvial redband trout. Thirty-six percent of the fish sampled in the Chewaucan River (n = 44) had spawned at least once before, and three consecutive spawning checks were seen in five of the fish from age 3 to age 5. In Crooked Creek, 27% of adfluvial redband trout (n = 11) had spawned before, but no more than two spawning checks were seen in any of the scales.

Scale analysis of adult redband trout indicated that the most common age of the downstream migrating redband trout was age 1 in the Chewaucan River (64%) and Crooked Creek (68%). The other migrants were mostly age 2 (34% and 30% in the Chewaucan River and Crooked Creek, respectively), with just 2% of the fish migrating at age 3. The majority of redband trout spent 2 years rearing in Rivers End Reservoir before spawning (69% and 80% for Chewaucan River and Crooked Creek, respectively), followed by 3 years and 1 year.

The catch of redband trout in the Chewaucan River screw

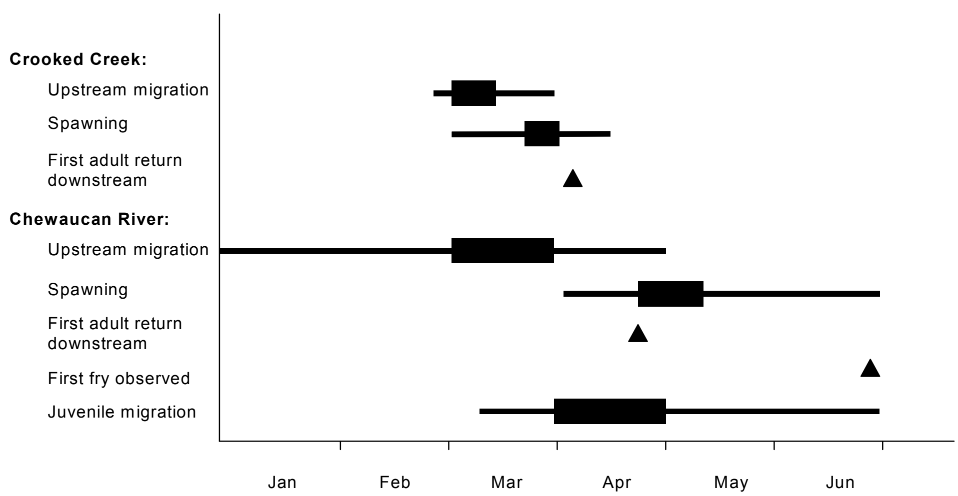

Figure 5.—Timing of adult redband trout migration and spawning in the Chewaucan River and Crooked Creek, and timing of fry observation and juvenile migration in the Chewaucan River. Blocks indicate periods of peak occurrence and triangles indicate time of first occurrence.

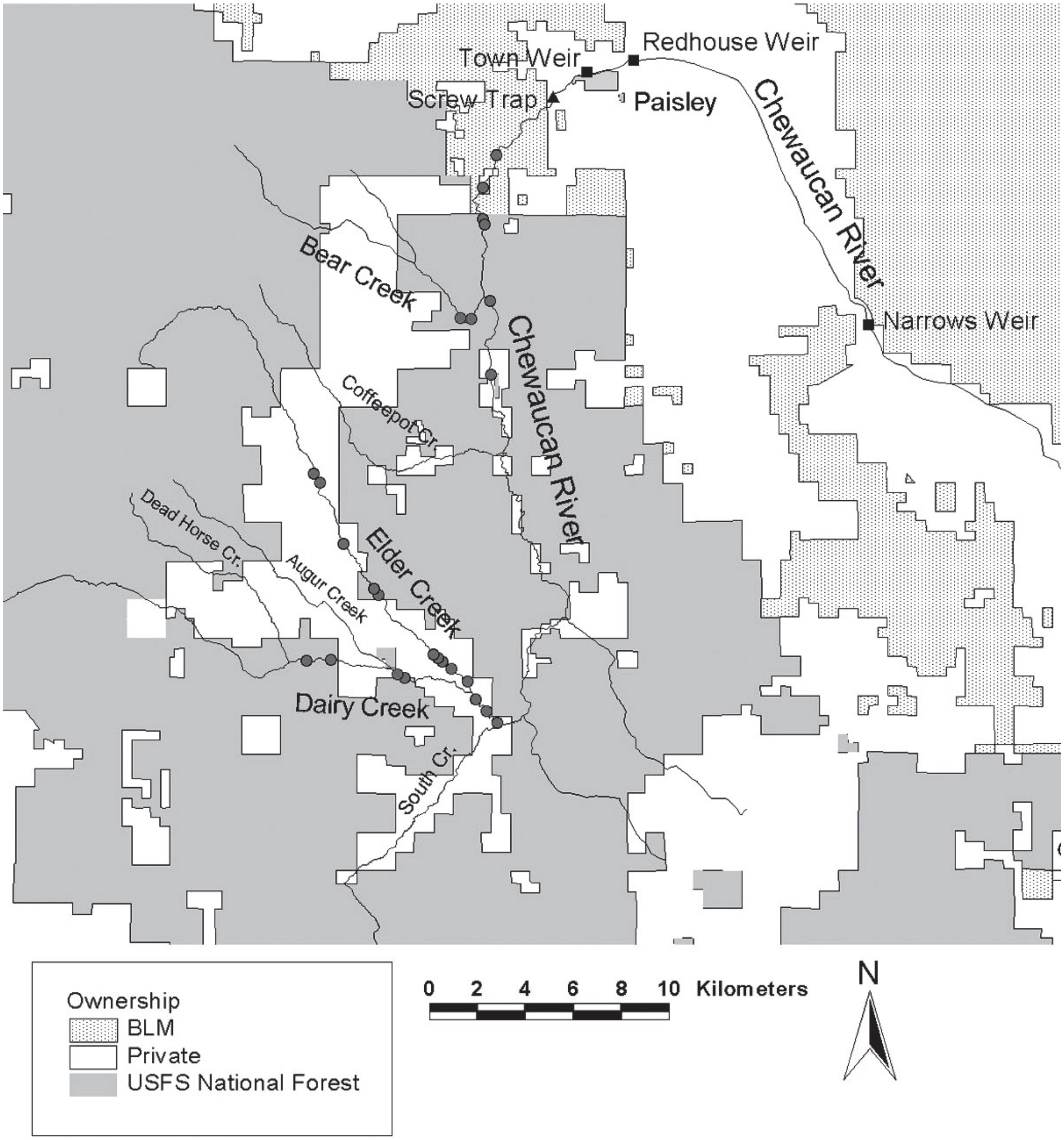

Figure 6.—Spawning locations (circles) of radio tagged adfluvial redband trout in the Chewaucan River basin, 2000–2001.

trap was almost exclusively age-1–age-3 juvenile migrants (1,875 fish), with small numbers of fry (11) or adult fish (16). The estimated number of downstream migrants was 10,699 (± 2,447) in 2000 and 5,404 (± 932) in 2001. Trap efficiency was lower in 2000 (12%) than in 2001 (19%). Although the peak catch of redband trout occurred in late March in both years, the peak number of migrants occurred in late April in 2000 based on the expanded estimates of catch. Scale analysis of juvenile redband trout captured in the screw trap suggested the most common migrants were age 1 or age 2, similar to that seen in analysis of adult scales. The length of age-1 migrants was smaller in 2000 than in 2001 (Figure 7).

Goose Lake Basin

We captured 132 adfluvial redband trout in Thomas Creek and inserted radio tags in 39 fish (Table 3). The size range of the adfluvial redband trout was 305–635 mm (Figure 8).

Table 2.—Mean fork length (mm) and 95% confidence interval of age-2–age-5 adfluvial redband trout captured in the Chewaucan River (rkm 16 and 26) and in Rivers End Reservoir, 1997–2001, and in Crooked Creek (rkm 3), 2000. Lengths back-calculated from scales.

	Age			
	2	3	4	5
Chewaucan River				
Mean length (+ 95% CI)	337 (28)	442 (11)	501 (5)	529 (19)
Sample size	5	47	53	14
Crooked Creek				
Mean length (+ 95% CI)	231	386 (23)	435 (31)	500 (49)
Sample size	1	18	19	3

The mean length of tagged redband trout was 519 mm (range 413–610 mm) in 2000 and 532 mm (range 448–635 mm) in 2001. The mean weight of redband trout in 2001 was 1,826 g (range 947–3,228 g). Weight was not measured in 2000. We also captured 24 redband trout in Pine Creek (Table 3).

The upstream migration of adfluvial redband trout in Thomas Creek, as determined by their capture at Utley weir, began in early March and ended in late May (Figure 9), when no redband trout were captured or seen jumping at the weir. Most diversion weirs are constructed in early to late May and impede upstream migration. Spawning occurred from late March to early June (Figure 9) in water temperatures of 8–11°C. Adult redband trout returned to Goose Lake in mid April and early May (Figure 9). Migrating redband trout fry were captured in a fish trap at Gover Weir in Thomas Creek (rkm 31) in June and July (Figure 9).

Of the 39 tagged redband trout, 79% spawned in Thomas Creek, and six of these spawned above the headcut at rkm 32 (Figure 10). The remaining six fish spawned in the Camp or Augur watersheds (Figure 10). The average migration distance was 22–23 km, and the maximum distance was

Table 3.—Number of adfluvial redband trout captured in the Goose Lake basin, and number of fish tagged with radio tags, 2000–2001.

			Number	
Year	Location (km)	Method	Captured	Tagged
2000	Thomas Creek (20.9)	hook and line	49	20
2001	Thomas Creek (20.9)	hook and line	30	19
2001	Thomas Creek (20.9)	seine	33	0
2000	Thomas Creek (30.4)	bypass trap	2	0
2001	Thomas Creek (30.4)	bypass trap	18	0
2001	Pine Creek (1.0)	seine	24	0

42 km in 2000 and 54 km in 2001, exclusive of travel to and in Goose Lake. In 2001, the adfluvial run of redband trout appeared larger than in 2000. The catch of redband trout for radio-tagging took 1 week in 2001 compared to 4 weeks in 2000, and the catch of downstream-migrating adult fish was much higher in 2001 than in 2000 (Table 3). Redband trout also were observed in Pine Creek in 2001 for the first time in approximately 10 years.

Six redband trout were able to negotiate irrigation weirs and return to Goose Lake (four in 2000 and two in 2001). These fish were found throughout Goose Lake, but were difficult to locate because of the high conductivity (> 3,000 µS/cm) and the size of the lake. Fifteen other redband trout were diverted into irrigation ditches during their downstream migration, with most problems caused by Taylor, Camp Creek Culvert, Utley, and 70 weirs. Upstream migration was impeded at headcuts in Thomas (rkm 32.2) and Camp creeks, and at the Cox-Bauers and Utley weirs. The Cox Flat headcut (rkm 57) was a complete barrier to upstream migration. Based on migration of tagged redband trout, upstream or downstream passage was evidently not a problem at the Garret or Gover weirs (Figure 10). The mortality of tagged

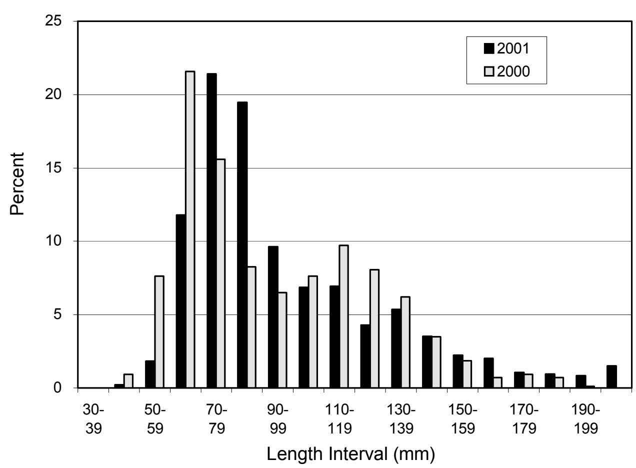

Figure 7.—Length frequency of juvenile redband trout captured in a rotary screw trap in the Chewaucan River, 2000–2001.

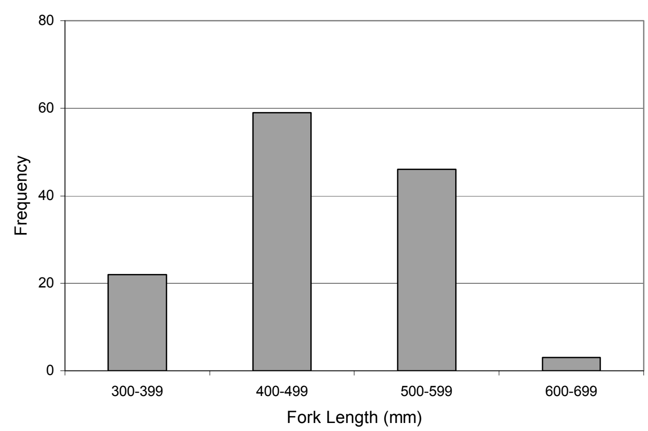

Figure 8.—Length frequency of adfluvial redband trout captured in Thomas Creek (Utley and Gover weirs) with hook and line, seine, and downstream fish trap in spring, 2000–2001.

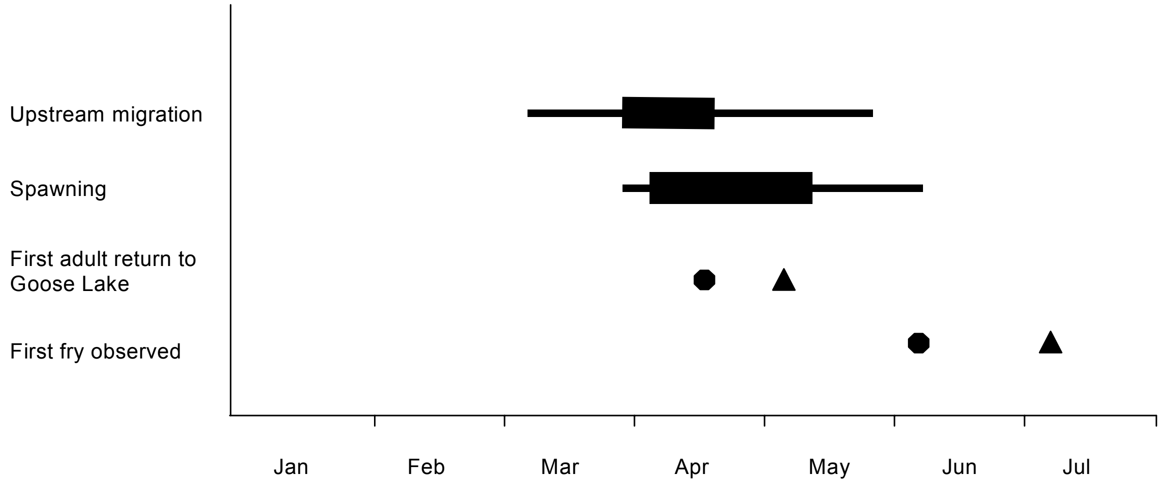

Figure 9.—Timing of adult redband trout migration and spawning, and fry observation in Thomas Creek and Goose Lake. Blocks indicate period of peak occurrence. Triangles indicate time of first occurrence of fry in 1999 and adult return to Goose Lake in 2000, and circles indicate first occurrence of fry in 2000 and 2001 and adult return to Goose Lake in 2001.

redband trout was 62%, and occurred an average of 26 d after spawning and 49 d after release. Of the 24 mortalities, 7 died near their uppermost migration point and 17 died after migrating an average of 7 km downstream.

Most adfluvial redband trout in the Goose Lake basin were age 3 or age 4, with mean lengths of 425–490 mm (Table 4). Redband trout first spawned at ages 2–5, with most occurring at age 3. Scale analysis indicated that iteroparity is common in adfluvial redband trout redband trout in the Goose Lake basin and that they generally spawn every year once they begin to spawn. Thirty-three percent of the fish captured in Thomas Creek (n = 44) had spawned at least once before, with three spawning checks seen in four fish and four spawning checks seen in one fish. One radio-tagged redband trout that had spawned in 2000 returned in 2001. This fish was age 4 in 2000 and did not grow between 2000 (578 mm) and 2001 (565 mm). Most of the juvenile redband trout in the Goose Lake basin migrate at age 1 (48%) or age 2 (48%), with a few migrating at age 3 (4%). Analysis of 143 scales showed that most of the adfluvial redband trout spent 1 (27%) or 2 (56%) years in Goose Lake before spawning, with the remainder spending 3 (8%) or 4 (1%) years in the lake. The fish that spent 4 years in the lake was the second largest redband trout captured in Thomas Creek (610 mm).

Table 4.—Mean fork length (mm) and 95% confidence interval of age-2– age-5 adfluvial redband trout captured in Thomas Creek (rkm 21), 1997–2001. Lengths back-calculated from scales.

	Age				
	2	3	4	5	6
Mean length (+ 95% CI)	339 (41)	425 (21)	490 (16)	533 (33)	615 (28)
Sample size	12	39	49	14	2

Redband trout fry were most abundant during the month of August in 1999, with the first fry observed on 6 July (Figure 9). In 2000 and 2001, the first redband trout fry were observed in early June, with a peak in mid to late June. The abundance of juvenile redband trout was highest in mid May in 2000 and 2001 (Figure 9). Few juvenile fish were caught in 1999.

Discussion

Adfluvial redband trout have persisted in the Chewaucan basin after being considered extinct in a statewide review of wild fish (Kostow 1995). The adfluvial life history likely developed during the Pleistocene Epoch when pluvial Lake Chewaucan formed in the closed Lake Abert and Summer Lake basins. After the climate shifted and the large lake disappeared, the adfluvial life history probably depended on ponded wetlands of Chewaucan Marsh. European settlement of the valley brought habitat changes that negatively affected adfluvial redband trout, including development of irrigation dams, draining of wetlands, and overgrazing of uplands. A habitat project that created a small reservoir was completed at Rivers End Ranch in 1994 near the mouth of the Chewaucan River. In 1996, large redband trout were observed at the Narrows weir (E. Now, Oregon State Police, personal communication). During the present study, migrating redband trout were caught on their upstream migration, passed above barriers, and almost half of the radio-tagged fish migrated at least 34 km to spawn. Therefore, the reservoir appears to be providing the necessary "lake" habitat for adfluvial redband trout. The migratory fish reside in Rivers End Reservoir and migrate upstream in the early spring to the Narrows weir on the Chewaucan River. Although the reservoir appears to be providing habitat that is essential for the adfluvial life history, the future of this life history is uncertain because of passage barriers to upstream and down-

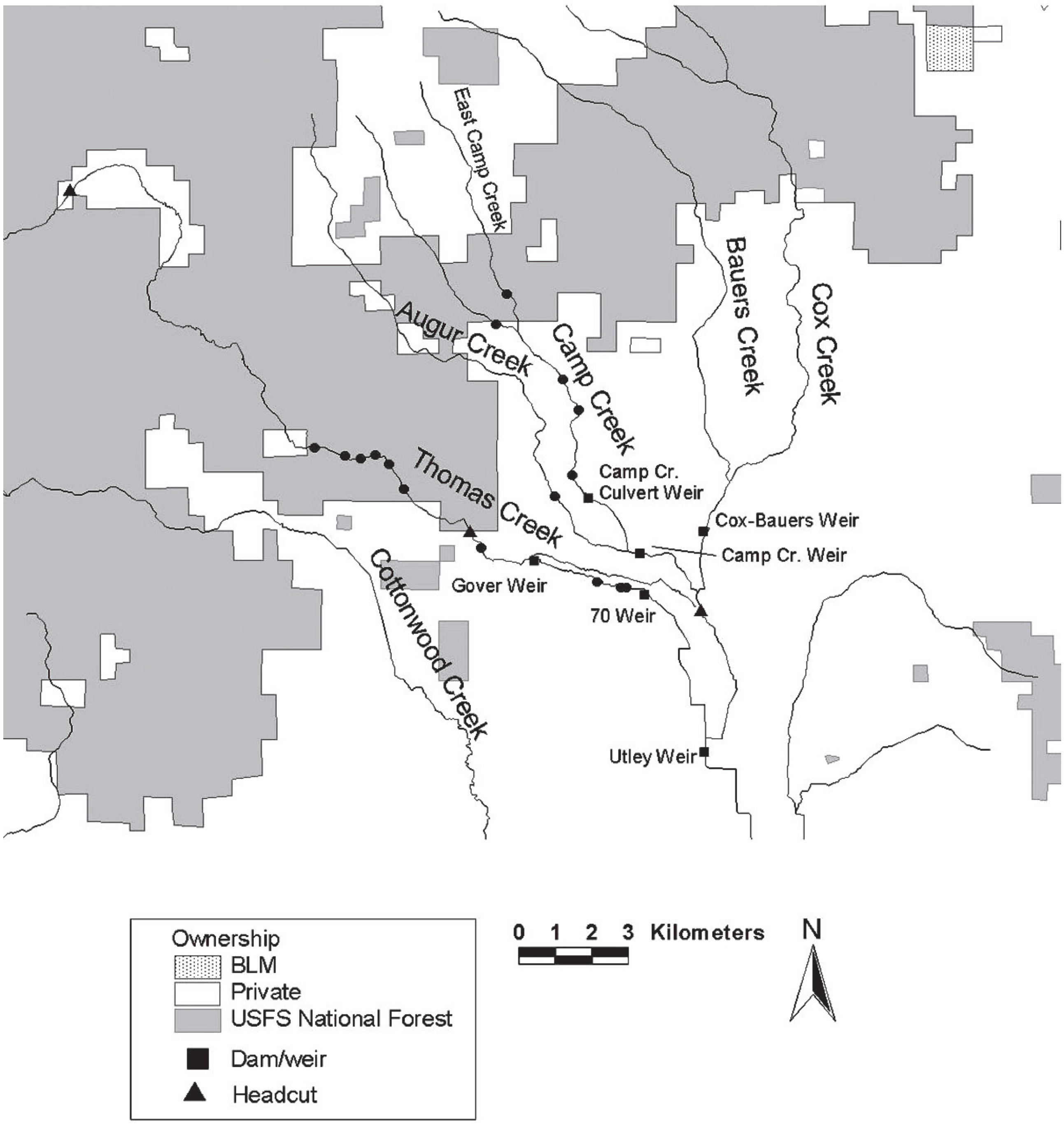

Figure 10.—Spawning locations (circles) of radio-tagged adfluvial redband trout in the Thomas Creek watershed, Goose Lake basin, 2000–2001.

stream migration. Recent construction of fish ladders at permanent irrigation dams in the lower Chewaucan River should provide passage to the upper watershed for adult fish. The largest irrigation diversion at the Paisley Town Weir was recently removed, the diversion intake for the large irrigation ditch was modified to minimize impacts on migrating redband trout, and a fish screen was installed to divert downstream migrants (juvenile and adult fish) back to the river. Irrigation ditches at the Narrows and Redhouse weirs are currently not screened to protect juvenile fish migrating downstream or adult fish returning to the lower river. However, Ducks Unlimited has recently secured $250,000 for fish screens on the Chewaucan River. Screening could be completed as early as 2008 for the Narrows Weir and 2009 for the Redhouse Weir.

Access to and from spawning areas in the Chewaucan River and Crooked Creek is limited by several irrigation diversion dams. We documented that at least one redband trout was able to return to the reservoir after spawning in the Chewaucan River, but most of the other adults became trapped in irrigation ditches and eventually died. Although some weirs in the basin are in place all year, overflow usually occurs during spring flow and can provide the opportunity for juveniles to pass downstream. Therefore, passage for juvenile migrants is dependent on the magnitude and timing of flow during early spring. Juvenile migration in the Chewaucan River peaks in late March–late April, when high flows can occur, but flow usually peaks in May. Even in high flows, some juveniles are diverted into unscreened irrigation ditches. Similar passage problems exist at Elder weir in Crooked Creek, although adult redband trout may be able to migrate upstream in low flow through an irrigation canal.

The upper Chewaucan watershed is an important spawning area for adfluvial redband trout. The highest number of spawners in 2000 and 2001 occurred in Elder Creek, with high numbers also occurring in Dairy Creek or in the Chewaucan River below the confluence of Dairy and Elder creeks. At present, homing of adfluvial redband trout to natal areas is not known. A study of redband trout (50–200 mm) in three sections (825 m) of Elder Creek indicated that 93–98% of these fish moved < 90 m (Osborn 1968), and suggested that redband trout in Elder Creek might not contribute to populations in the lower sections of the watershed. However, the peak migration of juvenile redband trout in the Chewaucan River (from trap catches) occurred from late March through late April. In contrast, Osborn (1968) studied movement in Elder Creek from June to September or November, well after peak migration of juvenile redband trout. Our data also indicate Elder Creek is an important spawning area for adfluvial redband trout, and if these fish were homing to their natal stream, then redband trout from Elder Creek would contribute significantly to the redband trout that rear in the Chewaucan River and Rivers End Reservoir.

In the Goose Lake basin, use of the lake by adfluvial redband trout was limited during the extended drought in 1986–1992, and ultimately was lost when Goose Lake dried in October 1992 (Bowers et al. 1999; Gerstung 2007, this volume). Scale data collected in 1997 indicated that redband trout recolonized the lake in 1994 and began returning to Thomas Creek in 1996. Tributary streams provide important refugia during drought periods for the adfluvial life history. The most important tributary for adfluvial redband trout currently is Thomas Creek, especially a 6-km reach (rkm 26–32) that accounted for 69% of all documented spawning in the watershed and that previously had been considered a migration corridor. Within this area, the largest concentration of spawners occurred in a 1-km reach (Weast property, rkm 29–30) where two springs occur, which provides high quality habitat during the summer. The concentration of spawning redband trout downstream of rkm 32 is probably because of higher water temperatures upstream of the springs and difficult passage at a high gradient headcut.

In contrast, a 1970 creel survey indicated that Bauers Creek was the best angling stream in the basin, and Cox and Bauers creeks were identified as the most important spawning streams in 1977 (ODFW, unpublished data). A survey of 35 randomly selected sites in Goose Lake basin streams in Oregon and California in 1999 found that the average density of juvenile redband trout was higher in Bauers Creek than in the other sampled streams, although one site in Camp Creek had the highest density (ODFW, unpublished data). In this study, no adult fish with radio tags migrated to Cox or Bauers creeks. Although habitat in Bauers Creek is still in good condition, long-term passage problems may affect access to the stream. A headcut on Camp Creek just downstream of Cox Creek might confuse upstream migrating redband trout and a culvert weir on Cox Creek may impede passage.

Scale analysis indicated that repeat spawning was common in adfluvial redband trout, but 40–80% of the radio-tagged fish died after spawning, about one-third near the spawning area and two-thirds on a return migration downstream, either below barriers or in irrigation ditches. Because the average length of fish given radio tags was greater than the average length of all upstream migrants, the radio-tagged fish may have been predominantly repeat spawners, which likely have higher post-spawning mortality. Although most mortality of radio-tagged fish occurred well after their release (5–10 weeks), handling and tagging fish on their spawning migration may have contributed to the eventual mortality in these fish.

Information collected in the Goose Lake basin indicated that female redband trout have a higher survival after spawning than males. Of the repeat spawners, over 80% were females. Most of the radio-tagged redband trout that returned to Goose Lake after spawning were females. In contrast, male redband trout stayed longer in the creeks near the spawning areas, which would make it difficult to return to Goose Lake because of low flow and installation of irrigation dams. In Pine Creek, all the spawned redband trout captured in June were females that had regained physical condition and had returned to a silvery color. Of the spawned redband trout seined at the Utley weir in May, females were in much better condition than males.

Iteropariety is generally less common in male salmonids (Behnke 1992; Schwanke 2002), in part, because competition for mates carries a physiological cost and males remain at spawning sites longer (Willson 1997; Schwanke 2002). Male rainbow trout in Alaska began their post-spawning migration to a lake later than females (Schwanke 2002), and similar results were reported for lacustrine brown trout in Norway (Rustadbakken et al. 2004).

Adfluvial redband trout in the Chewaucan and Goose Lake basins grow quickly, with age-3 fish averaging 442 and 425 mm, respectively. For comparison, the average length of age-3 redband trout in the Williamson River of the Klamath basin was 445–461 mm (Buchanan et al. 1990). The high rates of growth are attributable to use of suitable lacustrine-type habitat by the redband trout. Rivers End Reservoir evidently provides this habitat for adfluvial redband trout in the Chewaucan basin, and Goose Lake provides essential habitat during years when snowpack is adequate to keep the lake accessible for redband trout. However, as previously mentioned, adfluvial redband trout encounter passage barriers to and from the lacustrine habitat.

Life history strategies appear to be similar in the Goose Lake and Chewaucan basins, but some small differences in life history have been identified by scale analysis. Age-3 and age-4 redband trout comprised the majority of adult fish, representing 76% and 86% of adults in the Goose Lake and Chewaucan basins, respectively. The oldest redband trout identified by scale analysis were age 5 in the Chewaucan Basin and age 6 in Thomas Creek of the Goose Lake Basin, although total age can be difficult to determine in repeat spawners. By comparison, redband trout in the Williamson River (Kirk Springs) can live to 6 years (Buchanan et al. 1990), in Threemile Creek to 7 years (Kunkel 1976), and in Spring and Spencer creeks to 8 years (Buchanan et al. 1989, 1990, 1991; Borgerson 1992). The relatively short life span of redband trout in the Goose Lake and Chewaucan basins may be attributable to harsh conditions such as periodic droughts, high water temperatures and lack of coldwater refugia during summer, and occasional winter kills in the shallow lake or reservoir.

Scale analysis and trap catches indicate most redband trout in the Chewaucan River migrate to the more productive lacustrine-type habitat at age 1, similar to that found for redband trout in Threemile Creek (Kunkel 1976) and in Spencer Creek (Buchanan et al. 1989, 1990, 1991; Borgerson 1992). In contrast, juvenile redband trout in the Goose Lake basin generally migrate at age 2. Because Rivers End Reservoir supports a large population of potential predators such as largemouth bass *Micropterus salmoides* and brown bullhead *Ameiurus nebulosus*, age-1 migrants to the reservoir would seem to be more vulnerable to predation than an older age migrant. However, age-1 redband trout could be rearing in productive habitat below the screw trap before migrating into Rivers End Reservoir at age 2.

The adfluvial life history of redband trout in the northern Great Basin is a component of the diversity of the species and contributes to the resilience of populations. This life history arose during the Pleistocene, when the closed basins contained large lakes, and has persisted through periodic drought and loss of lacustrine habitat. More recently, populations of redband trout have been affected by habitat alterations such as diversion of water from streams, channelization of streams, and drainage of wetlands. Although tributary streams provide refuge that enables this life history to persist, habitat in the tributaries has been degraded by land use practices. The potential listing of redband trout under the federal Endangered Species Act in the 1990s raised awareness of the species and initiated efforts to conserve and recover populations. These efforts have led to passage improvements at irrigation diversions and other conservation measures on private and public lands.

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Redband Trout: Resilience and Challenge in a Changing Landscape
Oregon Chapter, American Fisheries Society, 2007

Status and Management of Three Groups of Redband Trout in Northeastern California

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Abstract.—Three distinct groups of undescribed rainbow trout *Oncorhynchus mykiss* occur in northeastern California and are currently referred to as the Warner Valley, Goose Lake, and McCloud River redband trout. The Warner Valley redband trout, primarily found in the Warner Valley basin in south-central Oregon, is also represented by two small populations in California tributaries. The populations in both states have been severely depleted by habitat degradation and were impacted by a series of recent droughts that nearly dried up the Warner Valley lakes. California management efforts have been limited to genetic analysis, population and habitat surveys, and livestock exclusion fencing. The Goose Lake redband trout is endemic to the harsh alkaline environment of Goose Lake. The population has fluctuated because of periodic lake desiccation, and has seriously declined since the early 1900s, largely because of impassible irrigation diversion dams on spawning tributaries and degraded rearing habitat. Goose Lake dried up in 1992 and was subsequently recolonized with stream-dwelling redband trout from its tributaries after the lake refilled. Significant runs of spawning redband trout were observed in the most suitable tributaries in 1998–2001. Actions to protect Goose Lake redband trout include improvement of fish passage and rearing habitat in tributaries, seasonal angling closures to protect spawners, and cessation of stocking nonnative rainbow trout. McCloud River redband trout historically occurred throughout the drainage of the upper McCloud River above the impassable Middle McCloud Falls. The most genetically pure populations are now limited to about 10% of their historic habitat because of displacement by and introgression with introduced trout and because of low summer flows, especially in drought years. Management efforts have focused on genetic analysis, fish population and habitat surveys, and protecting and improving trout habitat. The stocking of nonnative rainbow trout has been terminated.

Northeastern California waters support three distinct groups of undescribed interior rainbow trout *Oncorhynchus mykiss*, currently referred to as redband trout (Berg 1987; Behnke 1992, 2007, this volume; Currens 1997; Nielsen et al. 1999). The three groups are (1) the Warner Valley redband trout, found in the California headwaters of two tributaries to Oregon's Warner Valley drainage (Figure 1); (2) the Goose Lake redband trout, endemic to the Goose Lake basin and the upper Pit River (into which Goose Lake occasionally flows) within the Sacramento River drainage (Figure 2); and (3) the McCloud River redband trout, which is endemic to the upper McCloud River drainage above the impassable Middle McCloud Falls, also within the Sacramento River drainage (Figure 3). Information regarding these three groups of redband trout was collected by fisheries personnel from the California Department of Fish and Game (CDFG); Oregon Department of Fish and Wildlife (ODFW); U.S. Forest Service (USFS) consisting of the Modoc, Fremont, and Shasta–Trinity National Forests; U.S. Fish and Wildlife Service (USFWS); U.S. Bureau of Land Management (BLM); and University of California at Davis (UCD). Much of the information collected since 1992 has been coordinated by the Goose Lake Fishes Working Group (GLFWG) and the Upper McCloud River Redband Trout Core Group (UMRTCG). Both groups are composed of representatives from the previously mentioned state and federal agencies and institutions, and representatives from local governments, landowners, and non-profit organizations. The working groups were established to develop conservation strategies through a collaborative process.

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Taxonomic Relationship among Groups

The taxonomic status of the redband trout in California remains uncertain and is subject to considerable debate; thus, no formal actions have been taken to establish new taxa. The following discussion summarizes data on taxonomic status.

After conducting an extensive allozyme analysis of rainbow trout samples collected throughout California, Berg (1987) concluded that there are three lineages that have been independently derived from a "coastal rainbow-like" common ancestor and are now each genetically distinct enough to warrant recognition as subspecies. Berg (1987) found the Goose Lake trout to be most closely related to the redband trout of the Warner Valley drainage. Bagley (1997) conducted studies independently using mitochondrial and microsatellite (DNA) analysis of California redband trout populations and found the Goose Lake and Warner Valley populations to be distinct from each other, with the McCloud River populations being most distinct. Currens (1997) found some genetic similarities between redband trout in the Goose Lake basin and the Chewaucan River basin, and speculated that there may have been an ancient hydrologic connection between Oregon's Thomas Creek, the largest and most northerly tributary to Goose Lake, and the headwaters of the Chewaucan River. A few miles of low relief topography currently separate the two headwaters. A past linkage would have allowed fish populations in the two drainages to intermingle. Currens also notes that the Warner Valley redband trout differs in many respects from redband trout in the neighboring Goose Lake, Chewaucan, and Catlow basins. This is not surprising, considering that these basins may have been isolated from each other since the last pluvial period, more than 9,000 years ago (Behnke 1992, 2007, this volume). In general, redband trout in Goose Lake, Warner, and Chewaucan basins are most closely related to each other and are more differentiated from redband trout in the nearby Fort Rock and Catlow basins (Currens 1997; Behnke 2007, this volume).

Using microsatellite (DNA) analyses of California redband trout populations, Nielsen et al. (1999) contend that the McCloud River redband trout shares a close association with the Goose Lake redband, the Little Kern golden trout *O. mykiss aguabonita*, and the rainbow trout of Rio Santo Domingo in northern Baja California, suggesting "a vicariant distribution of microsatellite diversity throughout the southern range of this species." Like Goose Lake and the upper McCloud rivers, the Little Kern River is currently isolated from the Sacramento–San Joaquin river system by impassable barriers, and the Rio Santo Domingo now flows into the Pacific Ocean only during rare flood events.

Legal Status

The legal status of the Warner Valley, Goose Lake, and McCloud River redband trout is in a state of flux. All three groups of redband trout had been candidates for listing under the federal Endangered Species Act. Continued candidate status was determined by USFWS not to be warranted at this time in view of current cooperative efforts among state and federal agencies and landowners to improve the status of each of these redband trout groups (Rhew 2007, this volume).

The McCloud River and Goose Lake redband trout are still listed by the CDFG as Species of Special Concern (CDFG 2001), and all three redband groups are on the USFS Sensitive Species List. These classifications do not provide statutory protections, but instead are intended to call attention to the plight of the species and to the need to take management action to halt their decline.

Warner Valley Redband Trout

Historic Distribution and Genetics

The Warner Valley redband trout historically occurred in suitable lakes and streams throughout the Warner Valley drainage (Figure 1) within southeastern Oregon (Belsky 1997; USDI 1997). The headwaters of most tributaries still support redband trout, and two of these tributaries, Dismal Creek and the South Fork of Twelvemile Creek, originate in California (Figure 1).

Genetic analysis of tissues from redband trout collected from the California portion of Dismal Creek and the South Fork of Twelvemile Creek indicates that these populations do not appear to be of hatchery origin and share characteristics with redband trout from Goose Lake and from other Warner Valley populations (Gall et al. 1982; Bagley 1997). Further genetic testing has been proposed to clarify the presence of Warner Valley redband trout in northeastern California.

Status and Management

Information on the status of Warner Valley redband trout is limited to that collected during spot sampling by electrofishing and to visual observations of habitat condition. Dismal Creek is in relatively good condition and supports an abundance of small trout within the Dismal Swamp region near the stream headwaters (P. Chappell, CDFG, 2001, personal communication). In 1990, ODFW found good redband trout numbers in the Oregon portion of Dismal Creek and in the upper reaches of Deep Creek, which is located downstream (Figure 1). Most of the upper Deep Creek drainage is on public land within Fremont National Forest. In contrast, the majority of the California portion of the South Fork Twelvemile Creek is situated on private or BLM lands and supports only a sparse population of redband trout. Much of the stream habitat is in poor condition due to siltation, loss of riparian vegetation, and high water temperatures. Livestock exclusion fencing has been established with limited success (P. Chappell, CDFG, 2001, personal communication).

Redband trout are moderately abundant in the upper reaches of the North Fork Twelvemile Creek in Oregon (Figure 1) (C. Edwards, ODFW, 2001, personal communication). Redband trout populations in the lower Twelvemile Creek and confluent Twentymile Creek in Oregon were relatively robust during 1995–1998, a period of good streamflow. Low streamflow and high water temperatures in 1999 resulted in a significant decline in the redband trout population. Redband trout populations in other portions of the Warner Valley drainage, with the exception of the upper Honey Creek drainage, also appear to be very depressed (Belsky 1997).

Adfluvial redband trout formerly occurred in all of the 11 interconnected lakes within the Warner Valley of Oregon. Populations would expand during wet cycles and decline during dry periods. All of the lakes nearly dried up in 1992 (Kostow 1995). Some recolonization occurred in Hart and Crump Lakes, the largest and most upstream of the Warner Valley lakes (Figure 1), during the 1994–1998 wet cycle. However, a dry cycle that started in 1999 nearly eliminated the recovering population (C. Edwards ODFW, 2001, personal communication). Other lakes in the Warner Valley are now less suitable for redband trout because they dry up more frequently. Many of the stream habitats within the Warner Valley drainage, which were a recolonization source of redband trout for the Warner Valley lakes, have been seriously damaged by poorly managed livestock grazing and by irrigation diversions that block fish migration out of the lakes and severely reduce streamflows below the diversions (USDI 1997).

The draft Recovery Plan for the threatened and rare native fishes of the Warner Basin and Alkali Basin (USDI 1997)

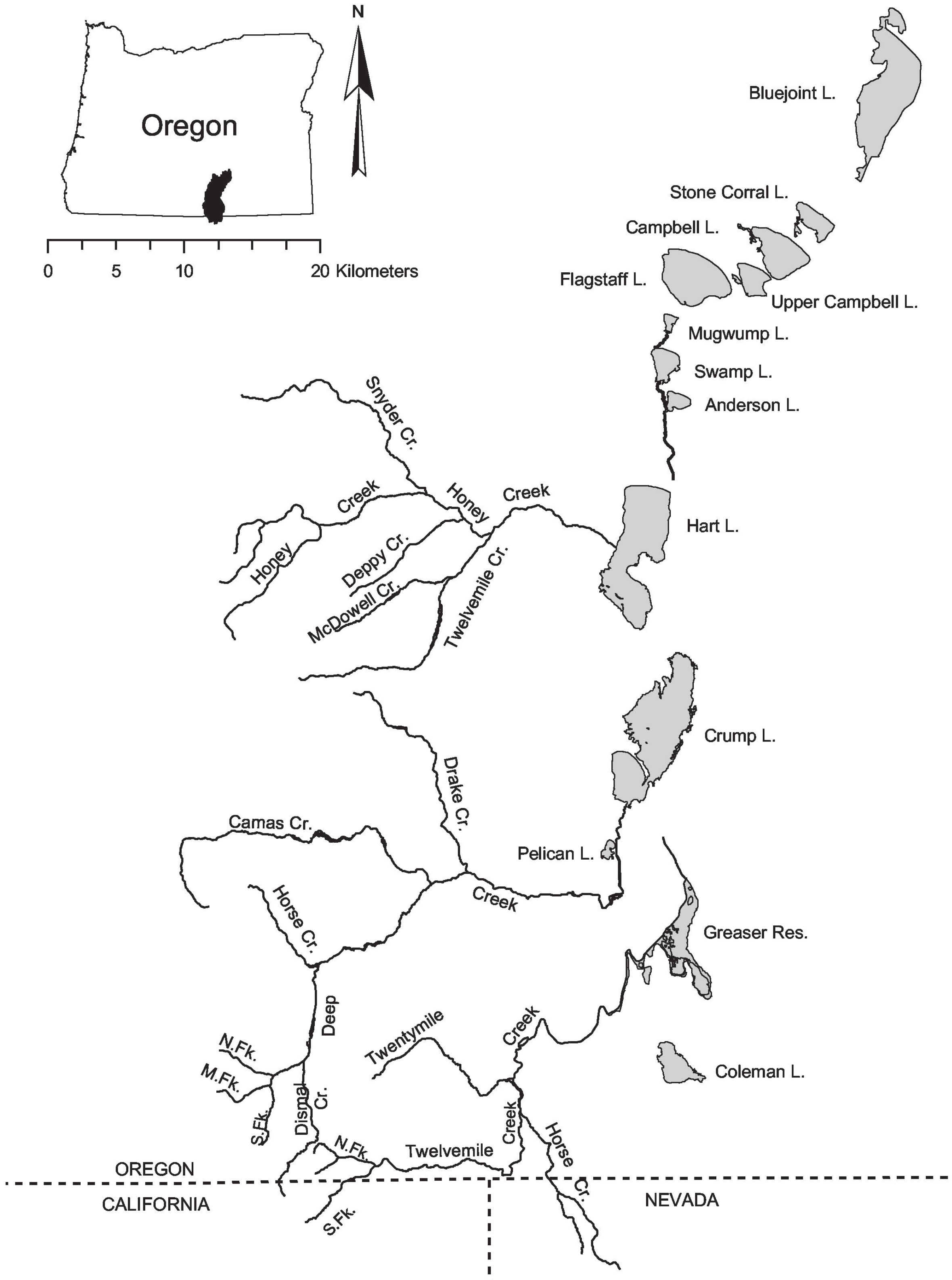

FIGURE 1.—Map of the Warner Valley drainage.

recommends provisions for protecting and improving habitat for the federally threatened Warner sucker *Catostomus warnerensis,* which occupies much of the range of the Warner Valley redband trout. The redband trout presumably would benefit from improved land and water management practices directed toward recovering the listed Warner sucker.

Goose Lake Redband Trout

Historic Distribution and Genetics

Goose Lake redband trout are endemic to Goose Lake and most of its larger tributaries (Figure 2). Redband trout that are genetically and morphologically similar also occur in tributaries to the upper reaches of the Pit River south of Goose Lake (Berg 1987; Behnke 2007, this volume). During historic wet periods, Goose Lake overflowed into the Pit River and flowed downstream towards the Sacramento River; the last overflow occurred in 1881 (CVRWQCB 1966). Pit River Falls is a 12-m high waterfall immediately below the confluence of Pit River and Fall River that currently isolates the Goose Lake and upper Pit River fish fauna from the remainder of the Sacramento River drainage.

Goose Lake has an immense surface area (37,230 ha when full), and is shallow (1.2–2.4 m average depth), very turbid (transparency generally 10–20 cm), and highly alkaline, with an alkalinity of 700 mg/L, expressed as calcium carbonate, measured during the summer of 1966 (CVRWQCB 1966). In addition, the pH is high, typically above 9, and levels of total dissolved solids are very high, ranging from 800 to 2,600 mg/L and increasing when lake volume decreases (CVRWQCB 1966). Summer water temperatures are moderately high, often reaching 22°C and occasionally as high as 26°C. Stratification is of short duration when it occurs. Eight species of fish are native to the lake basin (Moyle and Daniels 1982; Moyle et al. 1995), including the Goose Lake redband trout, Goose Lake tui chub *Gila bicolor thalassina,* Goose Lake sucker *Catostomus occidentalis lacusanserinus*, Pit roach *Lavinia* [*Hesperoleucus*] *symmetricus mitrulus*, Pit sculpin *Cottus pitensis*, Goose Lake lamprey *Lampetra tridentata* ssp., Pit-Klamath brook lamprey *Lampetra lethophaga*, and speckled dace *Rhinichthys osculus*. Exotic fish species established in tributaries to Goose Lake have not been observed in the lake, evidently unable to cope with the water conditions of the lake.

Goose Lake once abounded with redband trout despite the harsh environment. Evermann (1897) described Goose Lake as a water "that teemed with large silvery and black spotted trout." They were still numerous enough during the 1920s to support a commercial fishery centered in Lakeview, Oregon (USDA 1981a). Because of high lake turbidity, sport fishing for Goose Lake trout has been confined to the larger lake tributaries, where annual spring spawning migrations formerly sustained local fisheries for large redband trout. For example, the ODFW reported a catch of 111 trout over 40 cm long from Thomas Creek during May of 1977. Sixteen tributary streams, with over 640 linear stream kilometers of perennial habitat, flow into Goose Lake (GLFWG 1996). Long-time residents claim that most of these tributaries formerly supported runs of spawners from the lake. Recent surveys reveal that fewer tributary systems are still accessible to spawners because of impassable irrigation diversion dams (Tinniswood 2007, this volume). Accessible tributaries include Lassen and Willow creeks within California, and Thomas, Drews, Crane, and Dry creeks within Oregon (Figure 2). Stream surveys show that headwater reaches of most Goose Lake tributaries still support resident populations of Goose lake redband trout (GLFWG 1996).

As of 1997, the USFS, CDFG, and ODFW had conducted 19 biological and 15 habitat surveys in Goose Lake tributaries. In addition, six allozyme analyses have been conducted on redband trout from Thomas, Cox, Camp, Crane, Willow, and Lassen creeks (all tributaries to Goose Lake) (Figure 2), and on Joseph, Parker, Pine, and East creeks (all tributaries to the upper Pit River). Results appear in unpublished reports by Gall et al. (1982), and in the dissertations of Berg (1987) and Currens (1997). In addition, redband trout in Pine, Cottonwood, Davis, and Lassen creeks (Figure 2) were sampled for DNA analysis and results appear in Bagley (1997).

Status and Management

Goose Lake redband trout populations probably have always fluctuated widely, expanding during wet periods and declining during dry periods. Lake populations undoubtedly were eliminated during 1851–1852, 1926, 1929–1934, 1976–1977, and 1990–1992, when Goose Lake dried up or nearly dried up (GLFWG 1996). Apparently Goose Lake has been repeatedly recolonized after these dry periods with redband trout from its numerous tributaries.

Quantitative data on population trends of redband trout in Goose Lake do not exist. Because no sport fishery exists in the lake, an assessment of the population with creel surveys was not possible. Sampling Goose Lake by gill net has been too sporadic to provide population estimates or trends. The recorded observations of migrating and spawning redband trout in Goose Lake tributaries remain as the only available indicator of relative trout abundance in Goose Lake. However, only sporadic spot observations of spawners have occurred in tributaries, and no weir or fish ladder counts have been conducted. Because lake tributaries are usually too high and turbid during spring spawning migration to make quantitative estimates, spawning run assessments are typically derived from brief observations of migrating redband trout as they attempt to ascend barriers, or of spawning fish in shallow tributaries.

Available information on run size is confined to qualitative characterizations such as "small", "fair", "good", "large", or "significant". A large run might consist of perhaps a few hundred up to a few thousand spawners per tributary, whereas a small run might consist of only a few fish (C. Edwards, ODFW, 2001, personal communication). Runs of spawners

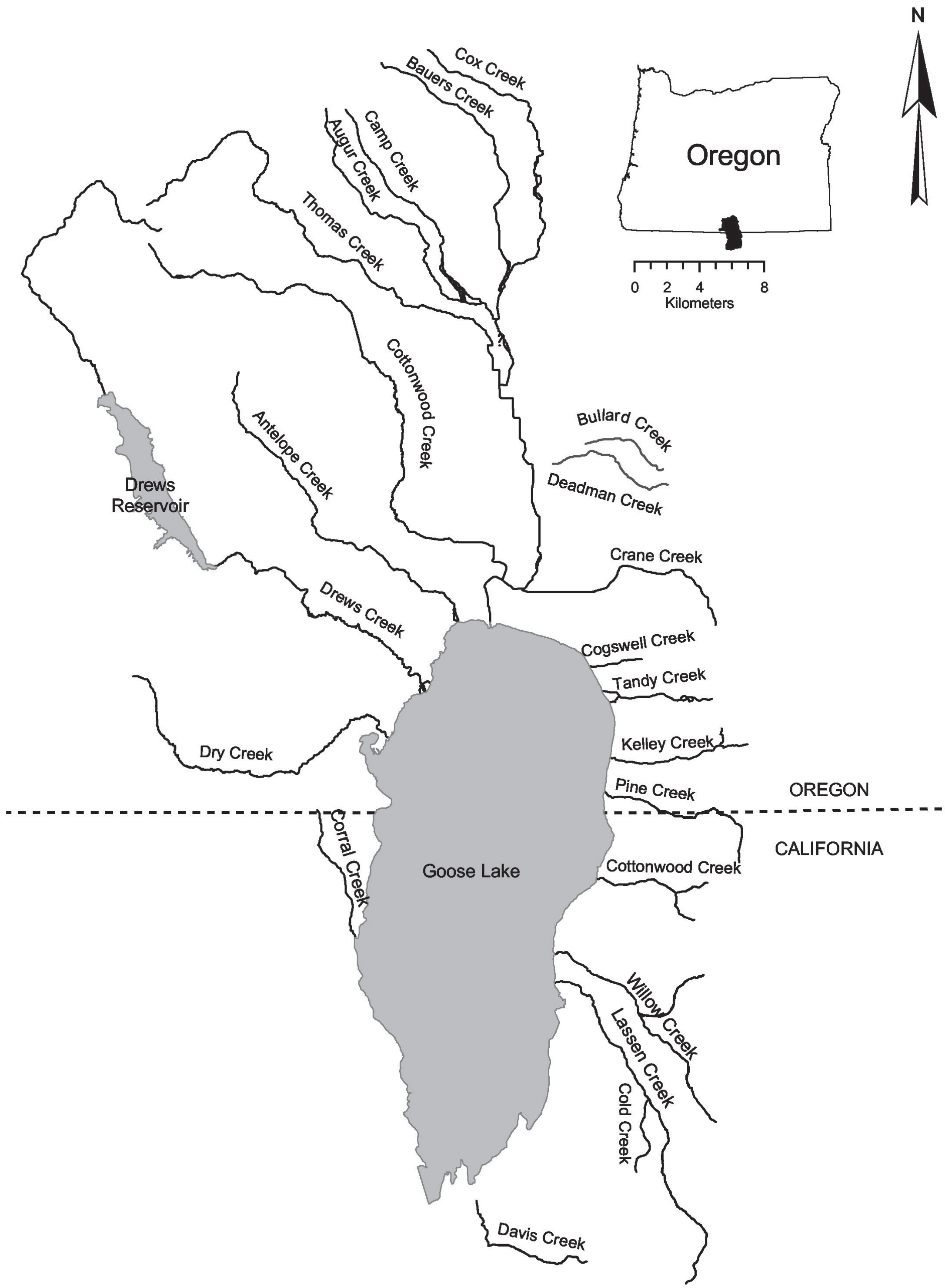

FIGURE 2.—Map of the Goose Lake drainage.

reported from Oregon tributaries were good during the 1950s and early 1960s, fair during the 1970s, and unnoticeable or absent between 1981 and 1996 (C. Edwards, ODFW, 2001, personal communication). In California, significant runs of spawners occurred in Willow Creek until it was blocked by a dam in 1969 and in Lassen Creek until 1987, when water levels in Goose Lake had declined to the extent that the lake was no longer suitable for trout. The lake virtually dried up in 1992, then refilled by 1995. During this period, recolonization of the lake with redband trout from tributaries had commenced, and by 1997 a small run of spawners was observed in Lassen Creek. Substantial runs were observed in

Lassen Creek from 1998 through 2001. During 2000 and 2001, spawning runs were also observed in other California tributaries where they had not been observed for decades, including Willow, Pine, and Cottonwood creeks (P. Chappell, CDFG, 2001, personal communication). Obstructions on Cottonwood and Pine creeks confined most spawners to the lower reaches of these tributaries. For the first time since 1981, runs of spawners were also observed in the late 1990s in Oregon tributaries, including Thomas, Crane, Drews, Kelley, and Dry creeks. The greatest numbers were observed in Thomas Creek and suitable tributaries (C. Edwards, ODFW, 2001, personal communication). A series of years with near normal to above normal runoff were likely responsible for the expansion of the Goose Lake trout population. A dry period that began in 1999 resulted in low tributary streamflows and a decline in the water level of Goose Lake.

The rate and magnitude of recolonization of Goose Lake with redband trout may be changing along with the frequency of lake desiccation. Significant recolonization of the lake did not occur for at least 9 years following desiccation in 1977 and for 7 years following desiccation in 1992. The recolonization rate is likely related to the relative abundance of redband trout in tributary streams and to the occurrence of very high streamflows needed to flush the largely resident redband trout down to the lake.

During the 19^{th} and early 20^{th} centuries, when redband trout were reputed to be very abundant in Goose Lake, 74 years passed between the desiccation of 1852 and that of 1926. During the next 74 years the lake dried up on three occasions. The last two were only 19 years apart, indicating that the climate may be becoming drier. The desiccation frequency also may have been accelerated by the diversion of water from tributaries for irrigation. Records show that the average annual inflow of 250,000 acre-feet (308 million cubic meters) of water to Goose Lake is reduced through diversions for irrigation by a mean of 85,000 acre-feet annually (CVRWQCB 1966; CVRWQCB 1996).

Habitat damage and obstructions on most spawning tributaries undoubtedly have had a major effect on redband trout abundance in Goose Lake and its tributaries. Many of the former spawning tributaries to Goose Lake remain blocked by impassible road culverts and diversion dams. The lower reaches of most lake tributaries are dewatered or nearly so during the irrigation season, and few irrigation diversions are screened. Upstream spawning and nursery habitat has been degraded by stream channelization, road construction, logging, mining, and livestock grazing—the latter being the most extensive. Nonnative brown trout have largely displaced redband trout in several tributaries, notably Pine Creek and portions of Davis Creek.

Management efforts in California include enforcement of seasonal closures and zero bag limit regulations on Goose Lake tributaries to protect spawning redband trout and their offspring. The stocking of nonnative trout in Goose Lake and tributaries has been prohibited since the early 1980s. The improvement and maintenance of fish passage continues to be a high priority in the more significant spawning tributaries, such as Willow, Lassen, and Pine creeks. A flood-damaged irrigation diversion dam in Willow Creek was rebuilt and equipped with a fish ladder in 1987, and modifications are planned that would improve fish passage under varying flows. In Lassen Creek a culvert under Highway 395 has been equipped with baffles to facilitate fish migration, structures have been placed in the stream channel to help redband trout ascend irrigation diversion structures, and two diversion ditches have been screened (P. Chappell, CDFG, 2001, personal communication). Beaver dams are periodically breached when they obstruct upstream fish migration. These efforts appear to be producing results. For example, large runs of Goose Lake redband trout spawners were observed in Willow Creek during 1999 and 2000, the first significant runs since 1969. Spawning run size in Lassen Creek was also unusually large during this period.

Efforts also have been made to improve redband trout spawning and rearing habitat in Willow and Lassen creeks. In both creeks, effects of cattle grazing in stream corridors have been reduced by fencing riparian pastures and by installing structures to control streambank erosion. Structures to improve pool habitat have been installed in the primary spawning and nursery reaches of Lassen Creek. Visual surveys and fish population samples indicate that stream habitat is gradually improving. During 1994, electrofishing and snorkel surveys of 13 km of Lassen Creek (including Cold Creek, its principal spawning tributary) revealed that redband trout were very abundant. Their population was estimated to be about 13,000 redband trout (1,000 trout/km), mostly 40 to 200 mm in fork length (Hendricks 1995). A similar survey was conducted in 6.4 km of nearby Willow Creek in 1994 and produced a population estimate of only 3,500 redband trout (547 trout/km) of the same size range as Lassen Creek (Hendricks, unpublished data). Since there had not been recent spawning runs from the lake into either Lassen or Willow creeks, the redband trout observed during the 1994 survey were probably stream resident fish. The redband trout population in Willow Creek is much smaller than in Lassen Creek because trout habitat in Willow Creek is not as abundant and has been severely degraded by irrigation diversions and heavy cattle grazing along stream banks. Downstream movement of resident redband trout from Goose Lake tributaries plays an essential role in recolonization of the lake after periodic desiccation; thus, tributary habitat quality is critical.

Significant runs of redband trout spawners from Goose Lake had not been observed in Oregon tributaries for a 15-year period from 1981 to 1996. The recovery of Goose Lake redband trout spawning runs in Oregon tributaries had been hampered by inadequate fish passage at diversion dams as well as by inadequate streamflow. A program was initiated in Oregon tributaries in 1992 to improve fish passage and stabilize stream banks. To date, fish passage in Oregon tributaries has been improved on Thomas, Dry, Drews, Crane, and Kelley creeks, which facilitated the migration of redband trout spawners from Goose Lake that were observed in large numbers between 1988 and 2001 (C. Edwards, ODFW, 2001, personal communication).

Because of concerns about losses of Goose Lake redband trout and other endemic fishes resulting from low streamflows and the desiccation of Goose Lake during the 1987– 1992 drought, the Goose Lake Fishes Working Group was formed in 1992 to develop a Goose Lake Fishes Conservation Strategy Plan. The plan was completed in 1996 (GLFWG 1996) and established a framework for developing watershed-level management plans and actions needed to prevent the need for listings under the Federal or California Endangered Species Act. As a result, the following tasks have been or will be pursued: site-specific angling closures; fish distribution and fish population surveys; habitat surveys including baseline monitoring; emergency responses to new droughts; improvement of fish passage for upstream migrating adult and downstream migrating juvenile fish; improved management and restoration of stream habitat through cooperative improvements and development of corrective actions in land management practices; research on life histories, habitat requirements, and nonnative fish introductions; genetic analysis to determine taxonomic status and extent of hybridization; and public outreach and information sharing.

The Conservation Strategy Plan does not specifically address water control in the Goose Lake basin, although water removal has had a major effect on streamflow and fish passage in tributaries. Implementation of a modified strategy that addresses water diversion operations and that emphasizes watershed habitat conditions and fish passage could result in increased numbers of redband trout in Goose Lake and its tributaries. For example, the timing of installation and removal of diversion dam boards is critical to upstream and downstream passage for Goose Lake redband trout (Moyle et al. 1995). A change in the operation of diversion dams could be accomplished without modifying existing water rights. Adult redband trout migrate from the lake to stream spawning areas during late March and early April, and juveniles (typically 1 to 2 years old) migrate to the lake in spring during high flows (Tinniswood 2007, this volume). Early placement of diversion dam boards can thus prevent either the upstream movement of adults or the return of spawned-out adults and juveniles back to Goose Lake. Agreements with landowners are needed to coordinate timing of board placements in diversion structures. In instances where boards are in place before spawners have completed their migration, the installation of portable aluminum fish ladders has been effective in passing adult fish, provided that excess water is allowed to flow down the ladder rather than over the dam. In the Thomas Creek drainage some progress has been made to alter the timing of dam board installation or provide alternate passage (C. Edwards, ODFW, 2001, personal communication). Additional fish screens are needed at irrigation structures on most Goose Lake tributaries to prevent diversion of juvenile fish into agricultural fields. As of 2001 only a few fish screens had been installed (P. Chappell, CDFG, 2001; C. Edwards, ODFW, 2001, personal communications).

McCloud River Redband Trout

Historic Distribution and Genetics

In 1872, while establishing a federal egg-taking facility at Baird Station on the McCloud River, Livingston Stone reported the presence of a fine-scaled resident trout characterized by a broad, nearly scarlet band. He called them "red-banded trout" (Hoopaugh 1974). Much later, Wales (1939) documented the presence of highly colored trout in several tributaries of the upper McCloud River and speculated that they were golden trout that must have been stocked. McCloud River redband trout are limited to the upper McCloud River drainage above the impassable Middle McCloud Falls. McCloud River redband trout historically occupied up to 96 km of stream habitat during good water years, including about 58 km in 17 tributaries (Figure 3).

Between 1970 and 1995, numerous trout from the McCloud River drainage were collected and examined by taxonomists and geneticists using meristic, morphometric, allozyme, chromosomal, and microsatellite DNA analysis. A consensus developed that the highly colored trout found in the McCloud River above an impassable falls (Middle Falls) was a unique form of rainbow trout, which was most closely related to the Volcano Creek golden trout *O. m. aguabonita* of the Southern Sierra Nevada (Schreck and Behnke 1971; Miller 1972; Gold 1977; Behnke 1992). The trout were given the name redband trout after Stone's "red-banded trout" (Hoopaugh 1974). Subsequent allozyme analyses of trout samples collected from McCloud River tributaries above and below Middle Falls and from golden-like trout of the Kern River drainage indicated that redband trout from the McCloud River above the falls differed significantly from those below, and that both populations were significantly different from those of the Kern River drainage and Goose Lake (Gall et al. 1982; Berg 1987). Using mitochondrial and nuclear DNA analysis of McCloud and Kern River rainbow or golden trout samples, Bagley (1997) concluded that the McCloud River redband trout and Kern River golden trout may represent independent lineages that became isolated from the coastal rainbow trout of the Sacramento–San Joaquin drainage by long-term barriers. McCloud River redband trout also differ significantly from redband trout of interior Oregon basins.

Status and Management

Distribution and abundance of redband trout in the McCloud drainage have been reduced because of low summer flows, especially during droughts, introduction of brown *Salmo trutta* and brook *Salvelinus fontinalis* trout, stocking of and introgression with hatchery rainbow trout, and stream sedimentation. The largest redband trout populations occur in the middle reaches of the mainstem McCloud River and in Tate Creek, its largest tributary (Figure 3). During late summer, and especially during poor water years, the amount

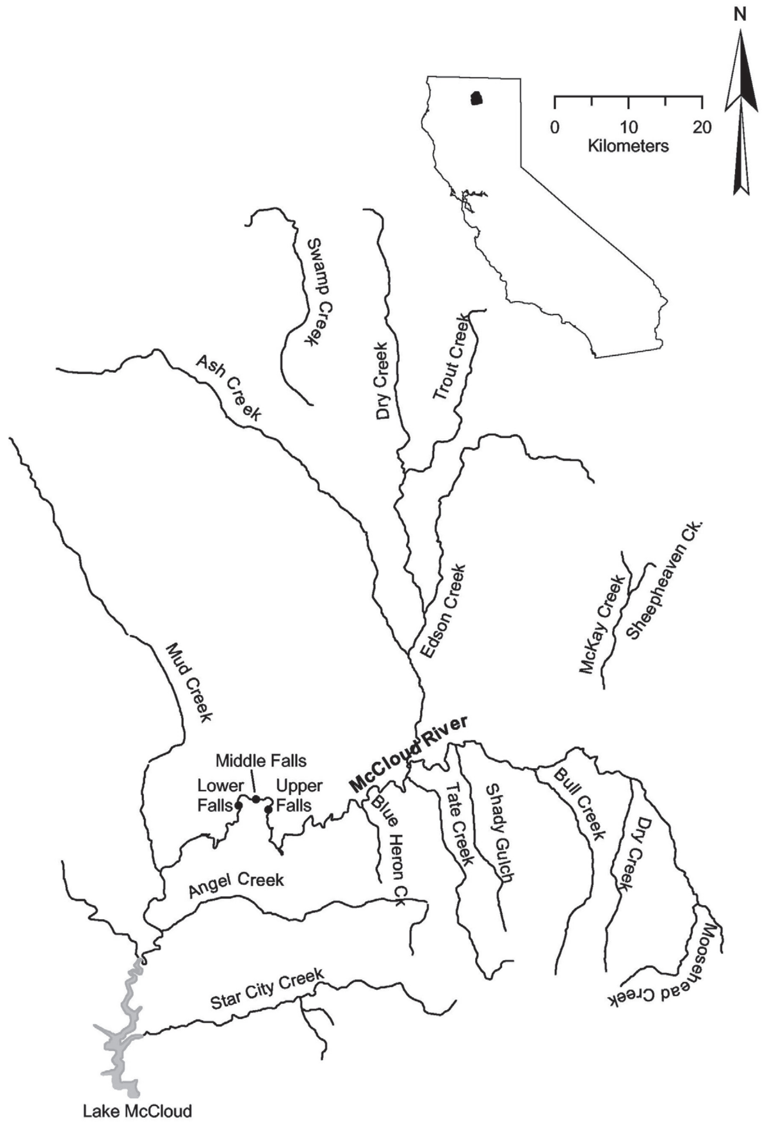

FIGURE 3.—Map of the upper McCloud River drainage.

of perennial habitat for redband trout decreases significantly in the upper McCloud drainage as major reaches of the main stem and lower reaches of most tributaries become intermittent or flows become entirely subsurface. The amount of stream habitat with adequate summer flow in the upper McCloud River drainage is about 96 km in good water years. Based on visual observations and spot electrofishing, the total population (exclusive of young-of-year) is roughly 15,000 redband trout in good water years. During the drought of 1987–1992, the amount of habitat with adequate flow decreased to 37 km, and the numbers of redband trout dropped to about 5,000. Sheepheaven, Swamp, Trout, and Edson creeks contain about 12 km of habitat (Figure 3) that supports about 4,000 redband trout (exclusive of young-of-year) during good water years. The amount of occupied habitat decreased during the 1987–1992 drought and the population declined to fewer than 2,000 redband trout.

Because much of the upper McCloud River drainage is covered with porous volcanic rock, most streams lose water through percolation as they flow downstream. The water eventually reappears as several large-volume springs in the McCloud River canyon, nearly 3 miles downstream of Middle Falls. Protecting the small amount of water that remains in the stream channels during periods of low streamflow is important for protecting the redband trout populations. Fortunately, little water is currently used for residential or agricultural development in the McCloud River drainage because most of the land is in federal ownership (USFS) or in large private ownership that is zoned for forestry purposes. However, zoning of the private lands could change in the future.

Introduced brown and brook trout have become established in the main stem of the McCloud River and in about 70% of the tributaries. Redband trout have been nearly displaced from 11 km of the main stem and have been entirely displaced from 13 km of habitat in five tributaries.

Nonnative hatchery rainbow trout (Shasta strain) were stocked as yearlings for decades in the McCloud River and its larger tributaries. Allozyme analysis has been conducted on redband trout sampled in the upper McCloud River and in Tate, Moosehead, Bull, Sheepheaven, Edson, Swamp, and Trout creeks in order to determine the extent of introgression with nonnative rainbow trout (Gall et al. 1982; Berg 1987). These rainbow trout appear to have hybridized with redband trout in the river and tributaries that flow from the south directly into the river (Berg 1987, 1994). In addition, microsatellite DNA data have been obtained from redband trout collected in the upper McCloud River and in Moosehead, Dry, Bull, Shady Gulch, Blue Heron, Sheepheaven, Edson, Swamp, and Trout creeks. However, results of these analyses were inconclusive with respect to the magnitude of introgression with nonnative rainbow trout (Nielsen et al. 1996, 1999), and further DNA analysis using additional microsatellite markers for nonnative rainbow trout will be needed.

Redband trout in tributaries that flow into the McCloud River from the north (Sheepheaven, Swamp, Trout, and Edson creeks) are less likely to have introgression with hatchery rainbow trout than populations in tributaries flowing from the south. The north tributaries have not been stocked with hatchery fish, with the exception of Trout Creek, and flows in these tributaries seldom reach the river except during brief periods of extreme runoff. Trout Creek was stocked regularly until 1976, when it was chemically treated and restocked with redband trout from Sheepheaven Creek, which was thought to be the purest population of McCloud redband trout. Redband trout from Sheepheaven Creek were also stocked in 1972 and 1974 into Swamp Creek, a nearby fishless stream where a small population of redband trout has become established.

Stocking of hatchery rainbow trout in the main stem upper McCloud River was terminated in 1994 in response to the designations of McCloud redband trout as a sensitive species by USFS and as a threatened species candidate by USFWS. In addition, the stocking practice violated California Fish and Game Commission policy, which states: "Hatchery trout will not be stocked in waters where they may compete or hybridize with trout which are threatened, endangered, or species of special concern." Anglers became very concerned with the cessation of stocking "catchable-sized" trout, and timberland owners feared potential new land-use restrictions. In response, a Redband Trout Working Group, consisting of representatives from the CDFG, USFS, USFWS, local government, timberland owners, and angling groups, was formed to engage in a collaborative effort to develop a conservation agreement. The conservation agreement focuses on actions to reduce the need to list the upper McCloud River redband trout under the Endangered Species Act and was completed in 1998 (CDFG and Shasta–Trinity National Forest 1998). Under terms of the agreement, nonnative rainbow trout will no longer be stocked in the upper McCloud River drainage.

The management of redband trout habitat on USFS land continues to be guided by the Comprehensive Habitat Management Plan for the Redband Trout (USDA 1981b), the Shasta–Trinity National Forest Land and Resources Management Plan (USDA 1995), and the Redband Trout Conservation Agreement (CDFG and Shasta–Trinity National Forest 1998). Measures have been taken on federal and private lands to reduce soil erosion and stream sedimentation. For example, USFS and private timberland owners have added crushed rock and other materials to road surfaces, have improved road drainage systems, and have improved road crossings at streams to reduce the delivery of sediments from the road network into streams. Livestock, which have damaged stream banks and riparian vegetation in the past, have been largely fenced from sensitive portions of Trout, Edson, and Sheepheaven creeks, and grazing standards have been improved in much of the remainder of the upper McCloud River drainage.

The USFS has acquired, by land exchange, a key inholding on Trout Creek and nearly all of the privately owned stream frontage on the upper McCloud River above Middle Falls to facilitate both redband trout protection and recreation management. Stream surveys, including habitat typing, have been completed on most river tributaries, and fish population inventories have been completed for Sheepheaven, Edson, Swamp, and Trout creeks and in three sections of the mainstem McCloud River.

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Redband Trout and the Endangered Species Act

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Abstract.—Redband trout *Oncorhynchus mykiss* and the Endangered Species Act (ESA) have been linked since 1982, when the fish first appeared as a candidate species. Petitions to list populations of redband trout under the ESA were filed with the U.S. Fish and Wildlife Service (USFWS) in 1994, 1995, and 1997. USFWS found that the listing action requested in the first two petitions was not warranted; therefore, they received no further processing. Action on the 1997 petition to list redband trout in the Great Basin was held up for over 2 years because of a backlog that was created by a 1995 budget cut. It has since been reviewed, and a decision that listing was not warranted was issued in 2000. A series of budget and policy decisions in 1995 and 1996 resulted in changes to the procedures and categories used to assign a species to the status of candidate for listing as threatened or endangered under the ESA. Federal legislation in 1995 rescinded $1.5 million in the USFWS budget that was to be used for listing activities and created a large backlog of pending listing actions. Subsequently in 1996, USFWS eliminated several categories under which a species could be assigned candidate status. The remaining category for candidate status is used for species that are judged to warrant listing as threatened or endangered, but the listing is precluded by higher priority needs. Five populations of redband trout (four in Oregon) had been assigned to Category 2 status (insufficient information to proceed with a proposed rule) by USFWS in their published candidate lists from 1982 to 1994. When the policy was changed in 1996, 23 fish species in Oregon were dropped as candidates for listing, leaving bull trout *Salvelinus confluentus* as the sole fish species in Oregon remaining on the list. Since 1996, bull trout have been removed from the candidate list and listed as threatened. At present, no fish species in Oregon are on the candidate list. Although USFWS no longer maintains an extensive list of candidate species, it continues to promote actions for nonlisted species.

Although the specific taxonomy and phylogenetic relationships among various forms of rainbow trout *Oncorhynchus mykiss* have not been resolved, rainbow trout from coastal river systems have been recognized as having significant differences from rainbow trout inhabiting rivers east of the Cascade Mountains that are commonly known as redband trout (Currens et al. 1990; Behnke 1992; Currens 1997). Redband trout are considered to be a more primitive form of rainbow trout than the coastal populations, and therefore evolutionarily intermediate between an ancestral "cutthroat-like" species and the coastal rainbow trout. In general, redband trout possess characteristics that are closer to cutthroat trout than to rainbow trout, such as presence of a faint orange cutthroat mark under the jaw; presence of vestigial basibranchial teeth in some fish; pronounced white or yellow tips on dorsal, anal, and pelvic fins; higher scale counts; fewer pyloric caecae; and elliptical rather than rounded parr marks (Behnke 1992).

The U.S. Fish and Wildlife Service (USFWS) administers the Endangered Species Act (ESA) of 1973 as amended (16 U.S.C. 1531 *et seq.*) for freshwater fish species, subspecies, and populations. Policy changes in 1996 affected the method used to identify species as candidates for listing under the ESA, and the manner used to process petitions to list species. These policy changes affected the status of redband trout under the ESA and the processing of petitions to list redband trout.

Listing Process and Candidate Species

USFWS must take several steps to process petitions requesting that a species be added or removed from the list of threatened or endangered species under the ESA. First, USFWS must publish a 90-day finding indicating whether or not a petition presents substantial information that the petition action is warranted, such as decline in abundance or distribution, and loss of or threats to habitat. If the petition is found to have substantial information, USFWS will continue to process the petition, following a prescribed order based on assigned priority for listing actions, and will publish a 12-month finding that the listing is warranted or not warranted. If the petition cannot be processed immediately because listing action is precluded by other higher priority actions, the species is assigned candidate status. Further action on the possible species listing will occur after other higher priority listing actions are processed. If the petition is found to have insufficient evidence that a listing may be warranted, no further action is taken.

Section 4 of the ESA identifies the process and factors to be considered when evaluating species for listing or a change in their listing status. In addition to other information about the status of a species, a substantial finding for a petitioned action must also show that the taxonomic unit requested for listing meets the requirements of a distinct vertebrate population segment (DPS) as defined by USFWS policy (Federal Register 1996a). This policy relies on three elements to determine the validity of a potential DPS: discreteness, significance, and conservation status. A population segment meets the criteria for discreteness if it satisfies either of two conditions: (1) it is markedly separated from other populations of the same taxon as a consequence of

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physical, physiological, ecological, or behavioral factors; or (2) it is delimited by international governmental boundaries within which differences in control of exploitation, habitat management, conservation status, or adequate regulatory mechanisms exist. After a population is determined to be discrete, evidence of its significance is evaluated, which may consider, but is not limited to, the following: (1) persistence in an ecological setting that is unusual or unique for the taxon, (2) loss of the population would result in a significant gap in the range of the taxon, (3) representative of the only surviving natural occurrence of a taxon that may be more abundant elsewhere as an introduced population outside its historic range, or (4) marked genetic difference from other populations of the species. If the population meets the identified criteria, it must then be evaluated for status as threatened or endangered under the ESA.

Prior to 1996, the definition of a candidate species was any species being considered by the Departments of Interior or Commerce for listing as an endangered or threatened species under the ESA, but which had not been the subject of a proposed rule (Federal Register 1982). Several categories were contained within the candidate status. Category 1 candidates were species for which USFWS had on file sufficient information indicating that the species warranted listing under the ESA, but that its listing was precluded by the need to process higher priority listing actions (warranted but precluded). Category 2 candidates were species for which USFWS had information indicating that the species may be in need of the protections of the ESA, but did not have sufficient information to proceed with a proposed rule to list. Category 3 was basically a classification that removed species from candidate status for one of three reasons. Category 3a species were those believed to have gone extinct. Category 3b species were those that had undergone taxonomic revision and were no longer believed to be taxonomically distinct. Category 3c species were those that had been found to be more abundant than previously believed, or were not presently subjected to threats sufficient to warrant their listing.

Redband Trout Petitions

USFWS has received three petitions for listing populations of redband trout. The first petition, received in April 1994, requested listing of the Kootenai River redband trout (Federal Register 1995a). The second petition, received in April 1995, requested listing of desert redband trout above Brownlee Dam and below Shoshone Falls on the Snake River (Federal Register 1995b). USFWS found that the requested listings were not warranted because insufficient information was provided to demonstrate that these redband trout populations represented distinct population segments and were therefore a listable entity. The 90-day finding on the second petition stated that USFWS accepted the taxonomic system proposed by Behnke (1992) and recognized redband trout east of the Cascade Mountains as *O. m. gairdneri.* This contrasted to previous designations by the USFWS, which identified redband trout east of the Cascade Mountains as *O. m. gibbsi*, and did not include the state of Washington as part of the identified range.

A third petition, received in September 1997, requested listing of the Great Basin redband trout in southern Oregon, northern California, and northwest Nevada. The petition was evaluated for possible emergency listing action and was then put on hold because of the backlog in processing listing actions that was created by passage of Public Law 104-6 (*see below*). The petition was subsequently reviewed in 1998–1999 and a finding that listing was not warranted was issued in 2000 (Federal Register 2000a). In the 90-day finding for Great Basin redband trout (Federal Register 1998b), USFWS also initiated study of the distribution and abundance of interior redband trout, with a range defined as east of the crest of the Cascade Mountains in the Columbia/Snake, Klamath, and Sacramento River systems. In a press release following the 12-month finding on Great Basin redband trout, USFWS anticipated that the review would be completed in 2 to 4 years.

Budget and Policy Decisions of 1995 and 1996

The U.S. Congress passed Public Law 104-6 in April 1995, which, among other things, rescinded $1.5 million from the USFWS budget for listing activities and prohibited use of remaining funds for processing final listing determinations for species or critical habitat. At the time of this moratorium, USFWS had proposed rules to list 243 species and had identified 182 species as candidates waiting further processing. Additionally, USFWS continued to receive petitions for listing actions. Therefore, the moratorium created a backlog of listing actions that awaited processing after funding was restored in April 1996. On 16 May 1996, USFWS published final guidance on restarting listing actions that included a five-tier procedure for setting priorities: (1) prepare and process emergency listings; (2) continue to prepare and process outstanding proposed rules based on their listing priority; (3) prepare and process new proposed rules for species facing high magnitude threats and screen petitions for emergency action; (4) prepare and process new proposed listings for species facing moderate or low-magnitude threats, final decisions on proposed reclassifications and delistings, and administrative findings for petitions; and (5) prepare and process critical habitat determinations and new proposed reclassifications or delistings (Federal Register 1996c). The first priority in the latest listing priorities published by USFWS (Federal Register 1999b) remains the processing of emergency listings, and the other three priorities (in order) are to process final decisions on proposed listings, resolve the conservation status of candidate species, and process 90-day or 12-month administrative findings on petitions. Actions on critical habitat designations were no longer given priority with the other listing actions and were to be conducted under a separate budget item.

At the same time that USFWS was dealing with the backlog of listing actions, it initiated a change in the way it listed species as candidates for listing. The policy change was initiated because USFWS felt that the Category 2 list added to "confusion about the conservation status of these taxa" (Federal Register 1996b). In addition, USFWS stated that the need for a species of concern list was "beyond implementation of the Endangered Species Act", that using the old Category 2 list as a species of concern list was "inappropriate", and that lists maintained by other governmental and non-governmental entities had "vastly superior information" than that maintained by USFWS (Federal Register 1996d). Under the revised policy of 1996, USFWS limited candidate status to those species for which it has sufficient information to list as endangered or threatened, but issuing proposed rules for listing is precluded by other listing activity. Therefore, the candidate status is now analogous to the previous definition of a Category 1 candidate (warranted but precluded). All other species were removed from the candidate list, and Categories 2 and 3a–3c were eliminated (Federal Register 1996b).

Effects of Policy Change on Candidate Species

Redband trout first received candidate status in the Animal Candidate Notice of Review (NOR) of 1982, when they were assigned Category 2 status (Federal Register 1982). The range of redband trout was listed as California, Oregon, Idaho, and Nevada. In the 1991 NOR, four specific populations of redband trout were identified as candidates: (1) Catlow Valley, Oregon; (2) Goose Lake, Oregon and California; (3) McCloud River, California; and (4) Warner Valley, Oregon (Federal Register 1991). In addition, all other redband trout populations that had been identified in the 1982 review were given candidate status under the label of "interior redband trout" and their range was changed from the 1982 review by adding Montana and omitting California. All redband trout in the 1991 review were assigned Category 2 status. No other redband trout populations were added or removed from candidate status through the 1994 review (Federal Register 1994). Because the 1996 change in USFWS policy for identifying candidate species eliminated all but those in Category 1, all Oregon redband trout populations on the candidate list prior to 1996 were removed. Within the identified range of redband trout, the only population identified as a candidate species in the revised 1996 policy was the McCloud River redband trout (Federal Register 1996b). These fish were later removed in 2000 because a Conservation Agreement was believed to have reduced the threats to these fish (Federal Register 2000b).

USFWS listed 24 candidate fish species in Oregon prior to the 1996 policy change (Table 1). After the policy change, the bull trout *Salvelinus confluentus* was the only candidate species in Oregon, but it has since been removed from the candidate list and was listed as threatened in 1998 (Federal Register 1998a). Two Oregon fish species appeared in the USFWS 2002 NOR (Federal Register 2002a): coastal cutthroat trout *O. clarkii clarkii* (proposed threatened) and Dolly Varden *S. malma* (proposed threatened under a "similarity of appearance" provision because of their physical similarity to the listed bull trout). Coastal cutthroat trout were later withdrawn from proposed listing because it was more abundant than previously believed and because of reduced threats (Federal Register 2002b).

Species, subspecies, or populations that appeared on the former list of candidate species had been assigned a level of conservation importance by various agencies (especially at the federal level). For example, the U.S. Forest Service (USFS) maintains a list of sensitive species that is used to evaluate compliance of USFS actions with the National Forest Management Act (NFMA, 16 USC 1600 *et seq*.). This list was originally drawn from the USFWS candidate list of Category 1 and 2 species. Among other things, USFS policy requires that national forests be managed in a manner that provides for a diversity of plant and animal communities. With the elimination of multiple candidate species categories, questions were raised about the effect this would have on lists of taxa maintained by federal agencies. In response to this issue, USFWS stated that many federal agencies such as USFS, Bureau of Land Management, and Department of Defense were working with The Nature Conservancy's Heritage Program to evaluate all the species and subspecies appearing on their sensitive species lists (Federal Register 1996d). The Heritage Program ranks species and subspecies on the basis of rarity, such as number of extant populations. USFWS also stated that efforts such as these should

TABLE 1.—Oregon fishes identified as candidate species in 1994.

Common name	Scientific name
Green sturgeon	*Acipenser medirostris*
Jenny Creek sucker	*Catostomus rimiculus* ssp.
Goose Lake sucker	*C. occidentalis lacusanserinus*
Klamath largescale sucker	*C. snyderi*
Malheur mottled sculpin	*Cottus bairdii* ssp.
Margined sculpin	*C. marginatus*
Slender sculpin	*C. tenuis*
Alvord chub	*Gila alvordensis*
Catlow tui chub	*G. bicolor* ssp.
Summer Basin tui chub	*G. bicolor* ssp.
Sheldon tui chub	*G. bicolor eurysoma*
XL Spring tui chub	*G. bicolor oregonensis*
River lamprey	*Lampetra ayresi*
Goose Lake lamprey	*L. tridentata* ssp.
Pacific lamprey	*L. tridentata*
Pit roach	*Lavinia symmetricus mitrulus*
Westslope cutthroat trout	*Oncorhynchus clarkii lewisi*
Catlow Valley redband trout	*O. mykiss* ssp.
Goose Lake redband trout	*O. mykiss* ssp.
Warner Valley redband trout	*O. mykiss* ssp.
Interior redband trout	*O. mykiss gibbsi* [a]
Umpqua Oregon chub	*Oregonichthys kalawatseti*
Millicoma dace	*Rhinichthys cataractae* ssp.
Bull trout	*Salvelinus confluentus*

[a] Recognized by USFWS as *O. m. gairdneri* in 1995 per Behnke (1992)

result in a "more comprehensive list" than their previous list of candidate species. The State of Oregon also maintains a list of sensitive vertebrates through the Oregon Natural Heritage Program at Oregon State University, which may be sufficient to maintain conservation focus on the species, subspecies, and populations that formerly were listed on the USFWS candidate list. However, funding at the state level remains uncertain and may jeopardize the comprehensive focus of the program.

Another issue raised with changes in the candidate policy was the value of the Category 2 list as a tool in land use planning for identifying species at risk. USFWS responded that these types of purposes were far broader than the purposes of the ESA, and that numerous other federal laws such as NFMA and the Federal Land Management Planning Act have broad mandates to protect biodiversity.

A policy was developed by USFWS and National Marine Fisheries Service for conservation agreements that recognize the benefit of providing early conservation efforts for "proposed and candidate species, and species likely to become either proposed or candidate species in the near future" (Federal Register 1999a). In addition, a policy was developed to evaluate conservation efforts when making listing decisions based on the certainty of implementation and effectiveness of such efforts (Federal Register 2003). These two policies are intended to promote early conservation efforts and to provide guidance on evaluating how effective these efforts will be to conserve species.

Several conservation agreements have been completed for species of concern including the Colorado River cutthroat trout *O. clarkii pleuriticus*, the McCloud redband trout, and the Catlow Valley redband trout and tui chub *Gila bicolor* ssp. Although these conservation agreements are relatively young and have yet to be tested by factors such as prolonged drought and water shortages or changes in land ownership, it is hoped that they will promote the continued recognition and support for the conservation of species of concern by the public, land management agencies, and regulatory agencies. If so, there should be few effects from the lack of a USFWS species watch list.

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Epilogue

When I first started working on this project back in 2001, I didn't think that I had much of a background on the biology of redband trout. Then I realized that my student Chuck Osborn and I had worked on the fish back in the 1960s. We thought the fish in Elder Creek, in the Chewaucan drainage, were just rainbow trout (I do remember that they looked quite different from rainbows I was used to seeing). Little did I know.

Which brings me to someone who did know. I would like to dedicate my effort on this project to Carl Bond, whose lifelong study of Oregon fishes has been an inspiration to generations of students and colleagues alike. Among other things, Carl has left us with a challenge regarding redband trout. From his extensive work on Klamath Lake he is quite familiar with the relationship of the redband trout and the tui chub, and with the importance of the chub as a forage fish for many populations of redbands. He tells a story that ought to be investigated. It is his view that tui chubs contain thiaminase, a powerful enzyme that results in thiamine deficiency and consequent mortality in many species of fishes. This phenomenon may well be behind the failure of some coastal strains of rainbow trout stocked in Diamond Lake during the period when the chub was abundant. In contrast, hatchery redbands of the Williamson River strain stocked in the lake during that period were more successful.

Thiaminase is known to be present in the alewife, among other species, and has been a problem in the restoration of lake trout in the Great Lakes. The enzyme affects early embryonic development and may significantly reduce early survival. It seems that those populations of redband trout that evolved in association with the tui chub, usually in a lacustrine environment, developed resistance to this enzyme. Further investigation of the adaptation that allows some redband trout to survive a diet of tui chubs would be a real contribution to understanding their biology.

This book has taken a long time to produce. There were many reasons, but one substantial one was my halting familiarity with the complexity of page layout in the form of Pagemaker®. More than once I was tempted to throw in the towel. Thanks to the good works of Judy Radovsky in the Printing Department at OSU, I was brought back from the brink. And Judy rescued our project again at the 11th hour, just as we were going to press. This book would not exist without her gracious assistance.

Finally, for those of you who revel in finding typos or editorial inconsistencies, we plead guilty, but leave you with the epigram that heads the Style Manual of the American Fisheries Society:

"*A foolish consistency is the hobgoblin of little minds*."
— Ralph Waldo Emerson

JIM HALL