

## Evolutionary Ecology of Redband Trout

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**Abstract.**—We examined genetic differences at 29 enzyme encoding loci among 10,541 rainbow trout *Oncorhynchus mykiss* from 240 collections throughout the species' range, including redband trout (i.e., several rainbow trout subspecies) in pluvial lake basins of the northern Great Basin that have had largely internal drainage with no connection to the Pacific Ocean. Differences among groups accounted for 29.2% of the genetic variation. Although we observed major genetic differences between coastal and inland groups (10.7%), which are currently considered to represent the major phylogenetic division in the species, we found that the greatest evolutionary divergence (19.7%) was related to persistence of three major river systems: the upper Sacramento, Klamath, and Columbia rivers. Genetic traits of redband trout from the northern Great Basin, where we found distinct subspecies or races, indicated that over millennia these pluvial habitats were sources of evolutionary diversity associated with large river systems rather than completely isolated refugia. However, redband trout did not constitute a distinct monophyletic group. Based on our data, redband trout of the Goose Lake, Warner Valley, and Chewaucan basins were distinct genetic races that were part of the diverse complex of Sacramento redband trout *O. mykiss stonei*. Harney Basin redband trout were a unique genetic race most closely associated with Columbia River redband trout *O. mykiss gairdneri*. White River and Fort Rock redband trout were associated with the Columbia River but showed allelic divergence comparable with that among other subspecies. Upper Klamath Lake rainbow trout included a previously unrecognized group associated with populations in the headwaters of the basin and a different subspecies from type locations for Upper Klamath Lake redband trout *O. mykiss newberrii* (i.e., Upper Klamath Lake and the upper Klamath River). The relationship of redband trout from the Catlow Valley to any of these other groups remained unresolved.

Long periods of stable aquatic habitat with episodes of isolation explain broad patterns of diversity in most North American freshwater fishes (Smith 1981). In contrast, regions with frequent geological or climatic disturbances may isolate fish populations, leading to allopatric differentiation, but high extinction rates associated with lack of stable aquatic habitats tend to prevent persistence and divergence of new species or subspecies (Smith et al. 2002). Fishes of the Pacific Rim, such as rainbow trout *Oncorhynchus mykiss*, have evolved in highly dynamic landscapes (McPhail and Lindsey 1986; Minckley et al. 1986). Because large parts of this region were sculpted by glacial, volcanic, and tectonic forces during Pleistocene and Recent times (McKee 1972; Porter 1983; Orr and Orr 2006), much of the present distribution and evolutionary diversity of these fishes may have been forged by chance extinctions, recolonizations, and relatively recent geographical isolation rather than long periods of adaptation in stable habitats. Patterns of genetic

diversity in rainbow trout—such as the differences among inland and coastal populations east and west of the Cascade Mountains (Allendorf 1975; Busby et al. 1996), southern California, and the Queen Charlotte Islands—can be explained by extinctions, isolation, and subsequent dispersal from different refugia during the last glacial period about 55,000 years before present (Okazaki 1984; Nielsen et al. 1994; McCusker et al. 2000).

Alternatively, evolutionary diversity in these fishes may reflect two sources of stable aquatic habitat that did persist: large river systems and large lakes. Present understanding of how rainbow trout persisted as a species and evolved in the dynamic landscape of the Pacific Northwest has not been informed by knowledge of the genetic diversity of fish isolated in ancient lake basins and their biogeographic relationship to large river systems. Both large river systems and large lakes existed during Pliocene to Recent times in the geographical range of rainbow trout. Three major rivers containing rainbow trout cut through the Cascade Range, for example, although this mountain range formed a major barrier to westward-draining streams from southern British Columbia to northern California as arc volcanics began 12–14 million years ago (Hammond 1979; Orr and Orr 2006). The northernmost river, the Columbia River, is the dominant river of

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Received June 24, 2008; accepted March 3, 2009  
Published online May 28, 2009

Cascadia, the Pacific Northwest region characterized by Cordilleran topography and habitats largely covered by glaciers during the Pleistocene (McKee 1972; Orr and Orr 2006). The southernmost river, the Sacramento River, drains interior basins and eastern slopes of the Cascades through the Pit and McCloud rivers (Orr et al. 1999). These large rivers apparently maintained most of their courses for at least the last 14 million years by cutting through lava dams, over waterfalls, and filled canyons and by capturing other streams (McKee et al. 1977; Swanson and Wright 1979; Orr and Orr 2006). Unlike the Columbia and Sacramento rivers formed during the late Miocene or Pliocene, the Klamath River, which is the smallest of the three rivers that currently breach the Cascade Range, was established when water levels in Upper Klamath Lake rose and spilled over volcanic divides of more recent origin to join the lower Klamath River as it cut its way westward through the older Klamath Mountains (Peacock 1931; Pease 1965; Moyle 2002). Before that, Upper Klamath Lake had no outlet to the ocean (Russell 1884; Hubbs and Miller 1948).

Lake basins also persisted despite disruptions to the landscape. Ancient lake basins containing fossilized trout in Miocene to Recent lake deposits (Taylor and Smith 1981; Allison and Bond 1983; Stearly 1989) still exist in the northern Great Basin where nonanadromous rainbow trout of unknown origin—commonly known as redband trout—occur. This region lies east of the Cascade Mountains and south of the Columbia River in Oregon's desert lake basins, which are mostly isolated from large continental river systems (Figure 1). The Fort Rock and Harney basins, which contain isolated Columbia and Snake River fish communities (Bisson and Bond 1971; Markle and Hill 2000), are just south of the Columbia River and were repeatedly disturbed by lava flows and volcanic ash after Miocene rift volcanics began (Piper et al. 1939; Axelrod 1968; Suppe et al. 1975). Five additional basins that contain rainbow trout, however—Upper Klamath Lake, Goose Lake, Chewaucan, Warner Valley, and Catlow Valley—are northwestern extensions of the Basin and Range physiographic province into the Pacific Northwest with different fish communities than those of Cascadia (Hubbs and Miller 1948; Minckley et al. 1986). These cold, arid basins, most of which are above 1,200-m elevation, have small streams and rivers originating in the surrounding mountains that drain to the lakes. Of these basins, only Upper Klamath Lake drains to the sea, although Goose Lake has overflowed into the Pit River in the headwaters of the Sacramento River during historical times (Hubbs and Miller 1948; Orr et al. 1999).

In these lake basins, Pleistocene glaciations that

reshaped much of western North America to the north were largely confined to local montane areas (Morrison 1965; Orr et al. 1999). Vast pluvial lakes formed during that period (Newberry 1871; Feth 1964; Snyder et al. 1964) from increases in precipitation, cooler temperatures, and reduced evapotranspiration rates (Morrison 1965; Mifflin and Wheat 1979). Larger lakes acted as regional amplifiers on local glaciation (Munroe et al. 2006). These lakes expanded habitat for fishes. Fluctuations of pluvial water levels in the northern Great Basin (Antevs 1925; Reheis 1999; Licciardi 2001), development of soils, and distribution of plant microfossils, dune activity, treelines, and peat formation (Morrison 1965; Mehringer 1977) indicated that climatic variability and associated environmental challenges to fishes during these times were no less than recent times.

The redband trout of the arid, isolated pluvial lake basins of Oregon, northern California, and interior Columbia River are morphologically diverse. This resulted in taxonomic confusion that persists to this day (reviewed in Behnke 1992). Phylogenetic studies of redband trout (Currens et al. 1990; Behnke 1992) concluded that they were rainbow trout with plesiomorphic traits also common to cutthroat trout *O. clarkii* that have been lost in the more widely distributed subspecies of coastal rainbow trout *O. mykiss irideus*. However, because redband trout shared no unique biochemical or morphological traits throughout their range (Wishard et al. 1984; Currens et al. 1990; Behnke 1992), considerable debate has occurred over the geographical origins of these fish and whether they represented ecophenotypes, multiple lineages resulting from vicariance of a widely distributed species, or an ancient single (but yet unsubstantiated) lineage of western trout. Behnke (1992) identified three nominal subspecies of redband trout: Columbia River redband trout *O. mykiss gairdneri*, which occurred east of the Cascades in the Columbia and Fraser rivers; Upper Klamath Lake redband trout *O. mykiss newberrii*; and Sacramento redband trout *O. mykiss stonei*, which he broadly applied to the diverse groups of redband trout of the Pit and McCloud rivers. The taxonomic relationship of the isolated redband trout of the Oregon desert lakes basins to these nominal subspecies and the role of these ancient lakes in the persistence of the species remained unknown. In this study, we use genetic data from redband trout in all major isolated basins and tributaries of the northern Great Basin and from anadromous and nonanadromous inland and coastal rainbow trout in the Columbia and Klamath River basins to examine the dynamics of Pleistocene habitats—glacial refugia, ancient lakes, and persistent large river systems—on the evolution of rainbow trout.

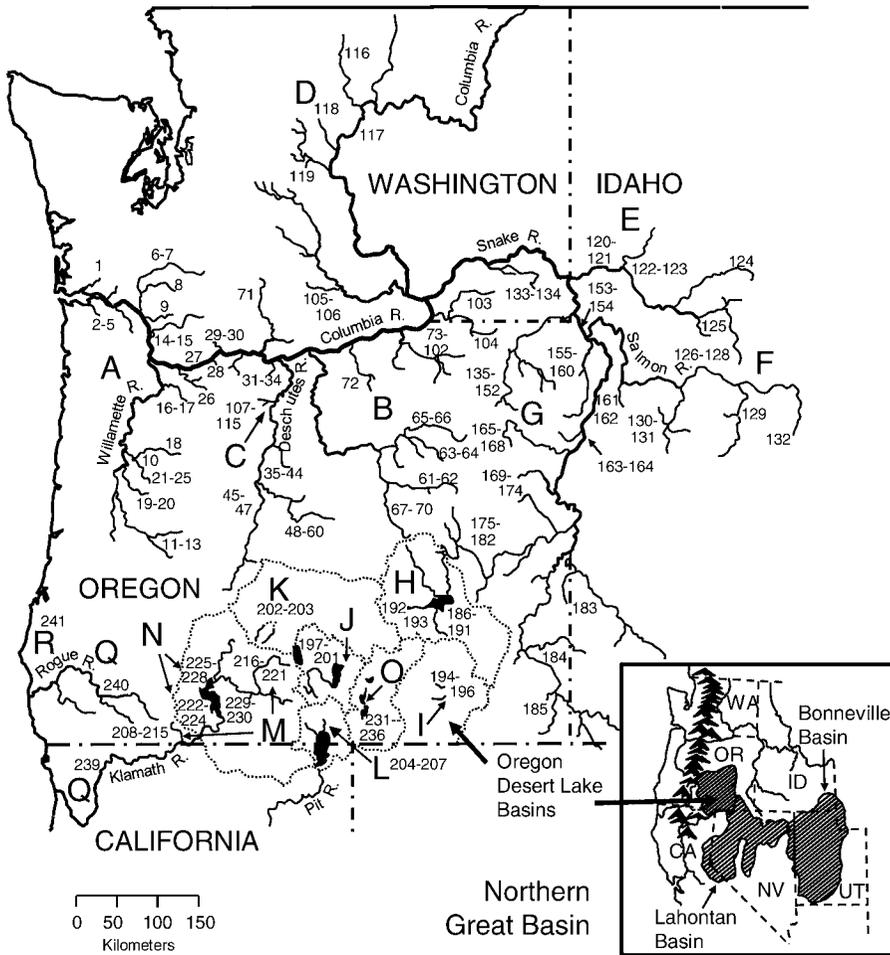


FIGURE 1.—Locations where samples of rainbow trout (including redband trout) were collected. Inset shows location of study area in the U.S. Pacific Northwest. Location numbers correspond to map numbers in Table 1. Uppercase letters A–Q indicate major evolutionary groups of rainbow trout–redband trout (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 Lake and upper Klamath River; O, Warner Valley; Q, coastal Klamath Mountains); uppercase letter R represents coastal cutthroat trout.

### Methods

We collected 240 samples of rainbow trout by electrofishing in the wild or seining at hatcheries from locations throughout Washington, Oregon, and Idaho, including all basins of the northern Great Basin where rainbow trout occurred (Figure 1; Table 1). Sampling locations for wild rainbow trout were chosen to avoid collecting introduced nonnative rainbow trout and admixtures with nonnative hatchery strains by reviewing available stocking records and interviewing local fishery biologists. Sampling in the wild included multiple reaches and multiple juvenile size-classes to minimize collections of siblings. Two nonnative

hatchery strains, Oak Springs and Cape Cod, which have been extensively released into many streams in Oregon and which are representative of other domesticated hatchery strains derived from coastal California populations and used in other states (Dollar and Katz 1964; Kinunen and Moring 1978), were included as a baseline to identify samples of undocumented nonnative populations and admixtures of nonnative and indigenous populations. In addition, 217 coastal cutthroat trout *O. clarkii clarkii* were collected from 12 locations in the Coquille River, Oregon, to serve as an outgroup.

Specimens were frozen immediately on dry ice and

TABLE 1.—Sample names, origins, and years of collection for rainbow trout (including redband trout; coastal cutthroat trout were used as the outgroup). Map numbers correspond to collection locations in Figure 1. Hatchery samples have the designation "strain." Origins of anadromous hatchery strains are from Howell et al. (1985). Evolutionary group codes are defined in Figure 1. Samples where temporal differences in allele frequencies were detected have one asterisk. Samples that showed evidence of introgression with nonnative hatchery strains have two asterisks. Life history forms are anadromous (A); nonanadromous (N); above natural barrier to anadromy (B); and above human-caused barrier to areas historically accessible to steelhead (D). Life stages are adult (A) and juvenile (J).

Evolutionary group code	Map number	Sample name	Collection year	River of origin	Major life history form using habitat	Life stage code
A	1	Grays River	1985	Grays River	A	J
A	2–3	Big Creek winter strain	1983, 1984	Big Creek	A	J
A	4–5	Eagle Creek winter strain*	1983, 1984	Big Creek	A	J
A	6	Cowlitz River late-winter strain	1983	Cowlitz River	A	J
A	7	Cowlitz River summer strain	1983	Washougal and Klickitat rivers	A	J
A	8	South Fork Toutle River	1985	Toutle River	A	J
A	9	Coweeman River	1985	Coweeman River	A	J
A	10	South Santiam summer strain	1985	Washougal and Klickitat rivers	A	J
A	11–12	Leaburg summer strain*	1984, 1985	Washougal and Klickitat rivers	A	J
A	13	McKenzie summer strain	1985	Washougal and Klickitat rivers	A	J
A	14–15	Skamania summer strain	1983, 1984	Washougal and Klickitat rivers	A	J
A	16–17	Eagle Creek winter strain*	1983, 1984	Clackamas River and Big Creek	A	J
A	18	Willamette River winter strain	1983	North Santiam River	A	J
A	19–20	Calapooia River	1983, 1984	Willamette River	A	J
A	21–23	Thomas Creek	1983–1985	South Santiam River	A	J
A	24–25	Wiley Creek*	1984, 1985	South Santiam River	A	J
A	26	Sandy River	1984	Sandy River	A	J
A	27	Hamilton Creek	1985	Hamilton Creek	A	J
A	28	Neal Creek	1985	Hood River	A	J
A	29–30	Wind River	1984, 1985	Wind River	A	J
B	31	Eightmile Creek no. 1	1993	Eightmile Creek	A	J
B	32	Eightmile Creek no. 2	1993	Eightmile Creek	A	J
B	33–34	Fifteenmile Creek	1983, 1984	Fifteenmile Creek	A	J
B	35	Bakeoven Creek	1984, 1985	Deschutes River	A	J
B	36	Buck Hollow Creek	1984, 1985	Deschutes River	A	J
B	37	Deschutes resident strain	1984, 1985	Deschutes River	N	J
B	38	Deschutes River	1984, 1985	Deschutes River	N	A
B	39	Lower Nena Creek	1984, 1985	Deschutes River	A	J
B	40	Mid-Nena Creek	1984, 1985	Deschutes River	N, B	J
B	41	Upper Nena Creek	1984, 1985	Deschutes River	N, B	J
B	42	Big Log Creek	1984, 1985	Trout Creek, Deschutes River	A	J
B	43	Lower East Foley Creek	1984, 1985	Trout Creek, Deschutes River	A	J
B	44	Upper East Foley Creek	1984, 1985	Trout Creek, Deschutes River	N, B	J
B	45–47	Deschutes summer strain*	1983–1985	Upper Deschutes River	A	J
B	48	Crooked River gorge	1993	Crooked and Deschutes rivers	N, D	J
B	49	Lower Crooked River	1993	Crooked and Deschutes rivers	N, D	J
B	50	Bowman Dam**	1993	Crooked and Deschutes rivers	N, D	J
B	51	Mckay Creek	1993	Crooked and Deschutes rivers	N, D	J
B	52	Ochoco Creek**	1993	Crooked and Deschutes rivers	N, D	J
B	53	Marks Creek	1993	Crooked and Deschutes rivers	N, D	J
B	54	Horse Heaven Creek	1993	Crooked and Deschutes rivers	N, D	J
B	55	Pine Creek	1993	Crooked and Deschutes rivers	N, D	J
B	56	Lookout Creek	1993	Crooked and Deschutes rivers	N, D	J
B	57	Howard Creek	1993	Crooked and Deschutes rivers	N, D	J
B	58	Fox Canyon Creek	1993	Crooked and Deschutes rivers	N, D	J
B	59	Deep Creek	1993	Crooked and Deschutes rivers	N, D	J
B	60	Deer Creek	1993	Crooked and Deschutes rivers	N, D	J
B	61–62	Deardorff Creek	1984, 1985	Main stem John Day River	A	J
B	63–64	Vinegar Creek	1984, 1985	Middle Fork John Day River	A	J
B	65	Granite Creek	1984	North Fork John Day River	A	J
B	66	Meadow Creek	1985	North Fork John Day River	A	J
B	67	Grasshopper Creek	1987	South Fork John Day River	N, B	J, A
B	68	South Fork headwaters	1987	South Fork John Day River	N, B	J, A
B	69	Izee Falls	1987	South Fork John Day River	N, B	J, A
B	70	Rockpile Ranch	1987	South Fork John Day River	A	J
B	71	White Creek	1984	Klickitat River	A	J
B	72	Willow Creek	1984	Willow Creek	A	J
B	73–74	North Fork Umatilla River	1992, 1994	Umatilla River	A	J
B	75–76	Buck Creek	1992, 1994	Umatilla River	A	J
B	77–78	Thomas Creek	1992, 1994	Umatilla River	A	J
B	79–80	South Fork Umatilla River	1992, 1994	Umatilla River	A	J

TABLE 1.—Continued.

Evolutionary group code	Map number	Sample name	Collection year	River of origin	Major life history form using habitat	Life stage code
B	81–82	Camp Creek	1992, 1994	Umatilla River	A	J
B	83–84	North Fork Meacham Creek	1992, 1994	Umatilla River	A	J
B	85–86	Upper Meacham Creek	1992, 1994	Umatilla River	A	J
B	87–89	Lower Squaw Creek	1992–1994	Umatilla River	A	J
B	90–91	McKay Creek**	1992, 1994	Umatilla River	A	J
B	92–93	East Birch Creek	1992, 1994	Umatilla River	A	J
B	94–95	Pearson Creek	1992, 1994	Umatilla River	A	J
B	96–97	West Birch Creek	1992, 1994	Umatilla River	A	J
B	98–99	East Fork Butter Creek	1992, 1994	Umatilla River	A	J
B	100	Bingham Springs	1983	Umatilla River	A	J
B	101–102	Umatilla summer strain*	1984, 1992	Umatilla River	A	J
B	103	Touchet River	1985	Walla Walla River	A	J
B	104	Walla Walla River	1985	Walla Walla River	A	J
D	105–106	Satus Creek	1983, 1984	Yakima River	A	J
C	107	Lower White River**	1984	White River	N, B	J, A
C	108	Lower Tygh Creek**	1984	White River	N, B	J, A
C	109	Upper Tygh Creek	1984	White River	N, B	J, A
C	110	Jordan Creek**	1984	White River	N, B	J, A
C	111	Little Badger Creek	1984	White River	N, B	J, A
C	112	Threemile Creek	1984	White River	N, B	J, A
C	113	Rock Creek**	1984	White River	N, B	J, A
C	114	Gate Creek	1984	White River	N, B	J, A
C	115	Barlow Creek	1984	White River	N, B	J, A
D	116	Fawn Creek	1984	Methow River	A	J
D	117	Wells summer strain	1983	Columbia River above Priest Rapids	A	J
D	118	Mad River	1984	Entiat River	A	J
D	119	Peshastin Creek	1985	Wenatchee River	A	J
E	120	Mission Creek	1985	Clearwater River	A	J
E	121	Big Canyon Creek	1985	Clearwater River	A	J
E	122	Dworshak summer strain	1985	North Fork Clearwater River	A	J
E	123	Hagerman summer strain	1985	North Fork Clearwater River	A	J
E	124	Fish Creek	1985	Lochsa River	A	J
E	125	Meadow Creek	1985	Selway River	A	J
F	126	Sheep Creek	1985	Salmon River	A	J
F	127	Chamberlain Creek	1985	Salmon River	A	J
F	128	Horse Creek	1985	Salmon River	A	J
F	129	Indian Creek	1985	Middle Fork Salmon River	A	J
F	130	Johnson Creek	1985	South Fork Salmon River	A	J
F	131	Secesh River	1985	South Fork Salmon River	A	J
G	132	Sawtooth strain	1985	Snake River, above Hells Canyon	A	J
G	133–134	Tucannon River	1984, 1985	Tucannon River	A	J
G	135–136	Fly Creek	1983, 1984	Grande Ronde River	A	J
G	137	Limber Jim Creek	1983	Grande Ronde River	A	J
G	138	Sheep Creek	1984	Grande Ronde River	A	J
G	139	Chicken Creek	1984	Grande Ronde River	A	J
G	140	Meadow Creek	1992	Grande Ronde River	A	J
G	141	Ladd Creek	1992	Grande Ronde River	A	J
G	142	Wallowa summer strain	1984	Snake River	A	J
G	143–144	Wallowa River	1983, 1984	Grande Ronde River	A	J
G	145–146	Lostine River	1983, 1984	Grande Ronde River	A	J
G	147	Broady Creek	1992	Grande Ronde River	A	J
G	148	Horse Creek	1992	Grande Ronde River	A	J
G	149	Jarboe Creek	1992	Grande Ronde River	A	J
G	150	Little Lookingglass Creek	1992	Grande Ronde River	A	J
G	151	Mottet Creek**	1992	Grande Ronde River	A	J
G	152	Swamp Creek	1992	Grande Ronde River	A	J
G	153	Cook Creek	1992	Snake River	N, B	J, A
G	154	Cherry Creek	1992	Snake River	N, B	J, A
G	155	Gumboot Creek	1983, 1984	Imnaha River	A	J
G	156–157	Grouse Creek	1983, 1984	Imnaha River	A	J
G	158–159	Big Sheep Creek	1983, 1984	Imnaha River	A	J
G	160	Imnaha summer strain	1984	Imnaha River	A	J
G	161	Niagara summer strain	1985	Snake River, above Hells Canyon	A	J
G	162	McGraw Creek	1990	Snake River	N, B	J, A
G	163	Conner Creek**	1992	Pine Creek	N, D	J
G	164	North Pine Creek	1992	Pine Creek	N, D	J
G	165	Big Creek	1992	Powder River	N, D	J

TABLE 1.—Continued.

Evolutionary group code	Map number	Sample name	Collection year	River of origin	Major life history form using habitat	Life stage code
G	166	Indian Creek	1990	Powder River	N, D	J
G	167	Summit Creek	1992	Powder River	N, D	J
G	168	Sutton Creek	1992	Powder River	N, D	J
G	169	Dixie Creek	1991	Burnt River	N, D	J
G	170	Last Chance Creek	1990	Burnt River	N, D	J
G	171	Lawrence Creek (above)	1991	Burnt River	N, B	J
G	172	Lawrence Creek (below)	1991	Burnt River	N, D	J
G	173	South Fork Dixie Creek	1991	Burnt River	N, D	J
G	174	Snow Creek	1990	Burnt River	N, D	J
G	175	Black Canyon Creek**	1988	Malheur River	N, D	J
G	176	Cottonwood (Bully Creek)**	1988	Malheur River	N, D	J
G	177	Cottonwood Creek	1989	Malheur River	N, D	J
G	178	Hog Creek	1991	Malheur River	N, D	J
G	179	South Fork Indian Creek**	1989	Malheur River	N, D	J
G	180	Dinner Creek	1988	Malheur River	N, D	J
G	181	Calf Creek**	1991	Malheur River	N, D	J
G	182	North Fork Squaw Creek	1991	Malheur River	N, D	J
G	183	Carter Creek	1989	Succor Creek	N, D	J
G	184	Dry Creek	1989	Owyhee River	N, D	J
G	185	West Little Owyhee River	1991	Owyhee River	N, D	J
H	186	Deep Creek	1993	Blitzen River	N, B	J, A
H	187	Indian Creek	1993	Blitzen River	N, B	J, A
H	188	Bridge Creek	1989	Blitzen River	N, B	J, A
H	189	Krumbo Creek**	1989	Blitzen River	N, B	J, A
H	190	Mud Creek	1989	Blitzen River	N, B	J, A
H	191	Smyth Creek	1988	Smyth Creek	N, B	J, A
H	192	Upper Sawmill Creek	1993	Silver Creek	N, B	J, A
H	193	Lower Sawmill Creek	1993	Silver Creek	N, B	J, A
I	194	Home Creek no. 1	1993	Home Creek	N, B	J, A
I	195	Home Creek no. 2	1993	Home Creek	N, B	J, A
I	196	Upper Home Creek	1993	Home Creek	N, B	J, A
J	197	Augur Creek	1992	Chewaucan River	N, B	J, A
J	198	Dairy Creek	1992	Chewaucan River	N, B	J, A
J	199	Bear Creek	1992	Chewaucan River	N, B	J, A
J	200	Elder Creek	1992	Chewaucan River	N, B	J, A
J	201	Witham Creek	1992	Chewaucan River	N, B	J, A
K	202	Bridge Creek	1993	Bridge Creek	N, B	J, A
K	203	Buck Creek	1993	Buck Creek	N, B	J, A
L	204	Beaver Creek	1993	Goose Lake	N, B	J, A
L	205	Camp Creek	1993	Goose Lake	N, B	J, A
L	206	Cox Creek	1993	Goose Lake	N, B	J, A
L	207	Thomas Creek	1993	Goose Lake	N, B	J, A
M	208	Beaver Creek	1989	Jenny Creek	N, B	J, A
M	209	Fall Creek**	1989	Jenny Creek	N, B	J, A
M	210	Jenny Creek no. 1**	1989	Jenny Creek	N, B	J, A
M	211	Jenny Creek no. 2	1989	Jenny Creek	N, B	J, A
M	212	Johnson Creek no. 1	1989	Jenny Creek	N, B	J, A
M	213	Johnson Creek no. 2	1989	Jenny Creek	N, B	J, A
M	214	Shoat Springs**	1989	Jenny Creek	N, B	J, A
M	215	Willow Creek**	1989	Jenny Creek	N, B	J, A
M	216	Deming Creek	1987	Sprague River	N, D	J, A
M	217–218	Paradise Creek	1987, 1990	Sprague River	N, D	J, A
M	219–221	Williamson River no. 1	1987, 1990	Upper Williamson River	N, D	J, A
N	222	Klamath River	1987	Klamath River	N, D	J, A
N	223–224	Spencer Creek	1987, 1990	Klamath River	N, D	J, A
N	225	Rock Creek	1987	Klamath Lake	N, D	J, A
N	226	Wood Creek	1990	Klamath Lake	N, D	J, A
N	227–228	Spring Creek	1987, 1992	Lower Williamson River	N, D	J, A
N	229–230	Trout Creek	1987, 1990	Sprague River	N, D	J, A
O	231	Honey Creek no. 1	1993	Honey Creek	N, B	J, A
O	232	Honey Creek no. 2	1993	Honey Creek	N, B	J, A
O	233	North Fork Deep Creek	1993	Deep Creek	N, B	J, A
O	234	Deep Creek	1993	Deep Creek	N, B	J, A
O	235	Willow Creek no. 1	1993	Deep Creek	N, B	J, A
O	236	Willow Creek no. 2	1993	Deep Creek	N, B	J, A
P	237	Cape Cod strain	1985	McCloud River, California, and related hatchery strains	N	J

TABLE 1.—Continued.

Evolutionary group code	Map number	Sample name	Collection year	River of origin	Major life history form using habitat	Life stage code
P	238	Oak Springs strain	1985	McCloud River, California, and related hatchery strains	N	J
Q	239	Bogus Creek	1990	Klamath River	A	J
Q	240	Soda Creek	1989	Rogue River	A	J
R	241	Coastal cutthroat trout	1991	Coquille River	N	J

stored at  $-20^{\circ}\text{C}$  or  $-80^{\circ}\text{C}$ . Procedures for protein electrophoresis were those of Aebersold et al. (1987). The 29 allozyme loci (and corresponding International Union of Biochemistry Enzyme Commission enzyme numbers) examined were: *ADA-1\** (3.5.4.4); *ADH\** (1.1.1.1); *sAH\** (4.2.1.3); *CK-A1\** and *CK-A2\** (2.7.3.2); *GPI-A\**, *GPI-B1\**, and *GPI-B2\** (5.3.1.9); *G3PDH-1\** and *G3PDH-2\** (1.1.1.8); *mIDHP-1\**, *mIDHP-2\**, and *sIDHP-1,2\** (1.1.1.42); *LDH-B2\** and *LDH-C\** (1.1.1.27); *sMDH-A1,2\** and *sMDH-B1,2\** (1.1.1.37); *mMEP-1\**, *sMEP-1\**, and *sMEP-2\** (1.1.1.40); *PEP-A\**, *PEP-B1\**, *PEP-C\**, and *PEP-D1\** (3.4.-.-); *PGM-2\** (5.4.2.2); and *sSOD-1\** (1.15.1.1). Data for the two nonnative hatchery samples and samples from the lower Deschutes River were published in Currens et al. (1990) but were included here with revised nomenclature and allele designations. Log-likelihood ratio tests (*G*-test) were used to test for goodness of fit to Hardy–Weinberg expectations to detect potential Wahlund effects within samples associated with population subdivision and to test for allelic homogeneity among samples using StatXact (Mehta and Patel 2003) with Monte Carlo estimates of *P*-values and sequential Bonferroni correction for multiple comparisons (Rice 1989). Samples (all individuals from a collection location) with frequency distributions at *ADA-1\**, *LDH-B2\**, *sSOD-1*, and number of scales in the lateral series that were similar to nonnative hatchery strains or intermediate between nonnative hatchery strains and indigenous populations (Campton and Johnston 1985; Currens et al. 1997) were removed from further analysis. Samples collected from locations where cutthroat trout and rainbow trout co-occurred were analyzed for potentially misidentified cutthroat trout and hybrids (Campton and Utter 1985; Campton 1987), and any such individuals were removed.

We used four different analyses to examine geographical and phylogenetic patterns of variation among rainbow trout. We tested for statistically significant variation among different groups with a four-level analysis of molecular variance (AMOVA) and calculated separate fixation indices ( $F_{ST}$ ) for each

regional group using Arlequin 3.1 (Excoffier et al. 2005) with 1,000 permutations. We compared two different phylogeographic scenarios of rainbow trout evolution: (1) inland versus coastal rainbow trout (the refugia–dispersal hypothesis) and (2) divergence of rainbow trout associated with the three major rivers and ancient lakes of this study (the habitat hypothesis). For the latter analysis, samples from the northern Great Basin lake basins were assigned to Columbia, Klamath, or Sacramento River systems based on zoogeographical and geological evidence from Hubbs and Miller (1948) and Minckley et al. (1986). Within major phylogeographic lineages, we examined differences among rainbow trout of different geographical regions and differences among local aggregations within regions. Rainbow trout above ancient barriers in the White River, a tributary of the Deschutes River in the mid-Columbia River region (Figure 1), were considered a separate geographical group because of evidence that they were disjunct from redband trout of the northern Great Basin (Currens et al. 1990). To visualize major patterns of geographical variation within and among groups and identify loci that contributed most to the differences, we used canonical variates analysis (CVA) of arcsine–square-root-transformed allele frequencies using BMDP software (Dixon et al. 1990). In addition, we examined genetic similarity among major evolutionary groups by constructing a majority-rule consensus dendrogram from matrices of genetic distance values (Cavalli-Sforza and Edwards 1967) and the neighbor-joining tree algorithm (Saitou and Nei 1987) using PHYLIP 3.6 (Felsenstein 2007) and 1,000 bootstrapped data sets. Phenetic analyses, which use similarity or distance measures calculated from frequency data, may suggest phylogenetic relationships when genetic similarity reflects evolutionary descent, but they are unable to account for potential homoplasies that can occur from gene flow or genetic drift. To examine the robustness of the genetic distance analyses, we examined patterns of character evolution among major evolutionary groups of rainbow trout under the criterion of parsimony (Kluge and Farris 1969; Farris 1970) using the GLOBAL and MUL-

PARS branch-swapping algorithms in PAUP software (Swofford 2003). Character trait analysis is appropriate for inferring phylogenies when gene flow among lineages is minimal (Swofford et al. 1996), but it can also identify homoplasies that may indicate gene flow among lineages (Buth 1984; Hillis et al. 1996). Each locus was considered a character, and different combinations of alleles represented different character states (Buth 1984). Geographical groups of rainbow trout that had unique combinations of character states were considered major evolutionary groups. Coastal cutthroat trout constituted the outgroup. Character states were unordered in rainbow trout, except for *CK-A1\**. Structure divergence of *CK-A1\** and *CK-A2\** in rainbow trout (but not in cutthroat trout) was assumed to be derived from an earlier isolocus (Allendorf and Thorgaard 1984). A majority-rule consensus tree (majority > 0.6) was constructed from all equally parsimonious cladograms.

### Results

Genetic differences documented among the 10,541 rainbow trout in this study were based on 96 alleles segregating at 29 loci. Of these, 16 loci had an average frequency of the most common allele of 0.95 or less: *ADH\**, *sAH\**, *G3PDH-1\**, *GPI-B1\**, *mIDHP-1\**, *mIDHP-2\**, *sIDHP-1,2\**, *LDH-B2\**, *sMDH-B1,2\**, *sMEP-1\**, *sMEP-2\**, *PEP-A\**, *PEP-B1\**, *PEP-C\**, *PGM-2\**, and *sSOD-1\**. The *ADA-1\** locus was an important diagnostic locus for identifying introgression with exotic hatchery strains (Currens et al. 1997) but otherwise was not informative. Only *CK-A2\** was monomorphic in all samples. No collections deviated from Hardy–Weinberg equilibrium after correcting for multiple comparisons and removing samples that showed evidence of introgression with nonnative domesticated rainbow trout strains. Out of the 240 samples chosen to minimize collecting from populations where introgression with domesticated rainbow trout strains might have occurred, only 18 collections showed evidence of introgression (Table 1). Likewise, although allele frequencies of rainbow trout from a location could have changed over the duration of this study, only 7 of 43 collections (8 from hatcheries and 35 from wild locations) showed significant temporal variation and six of these were from hatchery samples (Table 1). Consequently, we treated each collection of fish from a location as a single sample in subsequent analyses.

Four major genetic groups of rainbow trout emerged from analysis of geographical variation: (1) Columbia River populations; (2) populations from Goose Lake, Warner Valley, and the Chewaucan Basin; (3) populations from Upper Klamath Lake and the coastal

Klamath Mountains; and (4) populations from pluvial lake basins in Oregon that were geographically and genetically intermediate between the Columbia River and Klamath River groups (Figure 2). The CVA indicated that major evolutionary divergence among rainbow trout included in this study occurred between redband trout from Goose Lake, Warner Valley, and Chewaucan basins and redband trout from all other collections (Figure 2). This difference along CVA axis I (Figure 2) explained 69% of the observed variation in these data. Variation at *GPI-B1\**, *PEP-B1\**, *PEP-A\**, and *sSOD-1\** contributed most to differences between Goose Lake–Warner Valley–Chewaucan Basin redband trout and other rainbow trout. Redband trout in these basins usually had high frequencies of *GPI-B1\*138*, which was absent from collections in most other basins. Likewise, *PEP-B1\*69* was common in Goose Lake and Chewaucan Basin redband trout, but it occurred at low frequencies or was absent in rainbow trout or redband trout from other basins. In contrast, *PEP-A\*111* was absent in Goose Lake, Warner Valley, Chewaucan Basin, Fort Rock, and Catlow Valley redband trout, but it occurred at low levels in all other collections. High and sometimes moderate frequencies of *sSOD-1\*152* occurred in Goose Lake, Warner Valley, and some Harney Basin redband trout, although it was rare among rainbow trout and redband trout in other areas (Table 2).

Major allelic differences also occurred between rainbow trout from the Columbia River and those from Upper Klamath Lake and the Klamath River (Figure 2). Collections from Harney, Fort Rock, and Catlow Valley basins were intermediate between populations from the Columbia River and those from Upper Klamath Lake and the Klamath River. These differences, illustrated by CVA axis II (Figure 2), explained 15% of the observed allelic variation. Redband trout collected from the Upper Klamath Lake headwater sites had moderate frequencies of *sAH\*112*, an allele that was absent in all collections except those from the upper Klamath River, Fort Rock, and Warner Valley, where it was rare. Collections from Upper Klamath Lake headwater locations, upper Klamath River and Upper Klamath Lake, and coastal Klamath Mountains generally also had greater variation at *mIDHP-2\** and *PEP-C\** than Columbia River populations. In contrast, frequencies of *sIDHP-1,2\*72* were lower in coastal and lower Klamath River rainbow trout groups (Table 2).

The two major axes of the CVA did not show a prominent evolutionary break between redband trout and rainbow trout east and west of the Cascade Mountains, respectively. Geographical divergence at *LDH-B2\**, which has been considered evidence of inland and coastal subspecies (Allendorf 1975; Oka-

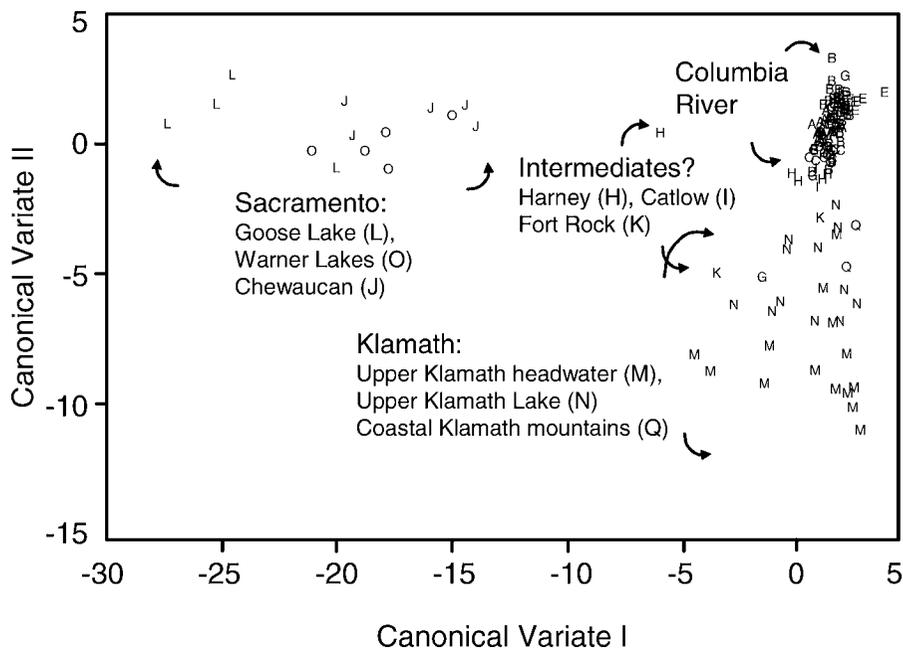


FIGURE 2.—Canonical variates analysis of allozyme variation among 16 major evolutionary groups of rainbow trout (including redband trout). Twelve alleles entered into the analysis: *ADH*\*65, *sAH*\*112, *GPI-B1*\*138, *mIDHP-2*\*144, *sIDHP-1,2*\*72, *LDH-B2*\*76, *sMDH-B1,2*\*83, *PEP-A*\*100, *PEP-A*\*111, *PEP-B2*\*69, *PEP-C*\*100, and *sSOD-1*\*152.

zaki 1984; Behnke 1992) was primarily limited to populations in the Columbia River system (Table 2). Inland redband trout from the middle and upper Columbia River and from the Clearwater, Salmon, and Snake rivers were characterized by high frequencies of *LDH-B2*\*76, but the allele was absent or rare in other populations east of the Cascades, including redband trout collected from the White River, Goose Lake, Upper Klamath Lake headwaters, and Klamath River. Similarly, only low to moderate frequencies occurred in redband trout east of the Cascades in Chewaucan, Warner Valley, Harney, Catlow Valley, and Fort Rock basins and in coastal rainbow trout west of the Cascades in the lower Columbia River populations (Table 2).

The AMOVA supported the observation that inland versus coastal differences did not explain the major evolutionary differences among rainbow trout. Overall, differences among groups accounted for 29.2% of genetic variation that we observed (Table 3). Differences among rainbow trout and redband trout associated with large persistent river systems explained more of this variation (19.7%) than did the geographical isolation of coastal and inland groups (10.7%).

Among basins, distinct patterns also emerged from analysis of the differences among collections within basins (Table 3). The  $F_{ST}$  values for differences among

collections within basins ranged from 0.001 in the Salmon River basin to 0.1692 for the Upper Klamath Lake basin. Resident populations associated with habitats in lake basins contributed more to the among-population diversity within river systems than did populations in river basins with anadromous or migratory populations (represented in these data primarily by Columbia River populations). Within Columbia River basins with anadromous populations (Table 1), for example,  $F_{ST}$  ranged from 0.001 to 0.0409. In the Snake River, where resident populations were created when anadromous populations were isolated by dams over the last 100 years,  $F_{ST}$  was 0.07152. In contrast,  $F_{ST}$  for basins of the northern Great Basin ranged from 0.06309 to 0.1381, except for Goose Lake ( $F_{ST} = 0.03449$ ), where tributary-spawning redband trout have migratory life histories that use the lake for rearing during high water years and return to different tributaries to spawn. Finally, further analysis of the Upper Klamath Lake basin revealed that an important source of the genetic structure within that basin could largely be explained by the presence of two geographic groups: one associated with the lower parts of streams draining into Upper Klamath Lake redband trout, and another associated with populations isolated by ancient waterfalls in Jenny Creek and the

TABLE 2.—Mean allele frequencies for key loci ( $\theta_{\text{regions}} > 0.02$ ) and alleles, total number of samples ( $N$ ), and number of populations examined for rainbow trout within different regions or groups (group codes A–I are defined in Figure 1). Frequencies are not listed for *ADH*\*-50; *ADH*\*-123; *ADH*\*-59; *sAH*\*123; *G3PDH*-1\*80; *GPI*-B1\*152; *GPI*-B1\*130; *GPI*-B1\*25; *mIDHP*-1\*-520; *mIDHP*-2\*83; *sIDHP*-1,2\*116; *sIDHP*-1,2\*58; *LDH*-B2\*113; *sMDH*-B1,2\*116; *sMDH*-B1,2\*70; *sMDH*-B1,2\*92; *sMDH*-B1,2\*120; *sMDH*-B1,2\*124; *sMEP*-1\*107; *PEP*-A\*93; *PEPB*-1\*83; *PEPB*-1\*50; *PEP*-C\*92; *PGM*-2\*-10; *sSOD*-1\*187.

Variable or locus	Allele	A	B	C	D	E	F	G	H
$N$		2,230	3,865	266	286	389	537	1,688	195
Populations		20	52	5	4	6	6	41	7
Locus:									
<i>ADH</i> *	-100	1.000	0.979	1.000	0.995	1.000	1.000	0.995	0.890
	-65	0.000	0.001	0.000	0.000	0.000	0.000	0.000	0.006
	-78	0.000	0.017	0.000	0.005	0.000	0.000	0.005	0.104
<i>sAH</i> *	100	0.926	0.825	0.670	0.761	0.679	0.711	0.857	0.926
	85	0.061	0.164	0.328	0.216	0.317	0.231	0.138	0.018
	72	0.014	0.010	0.002	0.023	0.004	0.076	0.005	0.045
	112	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>G3PDH</i> -1*	-100	0.922	0.991	0.992	0.983	0.999	1.000	0.983	0.994
<i>GPI</i> -B1*	100	0.991	0.990	1.000	1.000	1.000	0.994	0.998	0.981
	138	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.019
	145	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>mIDHP</i> -1*	100	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	-280	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>mIDHP</i> -2*	100	1.000	0.988	1.000	1.000	1.000	1.000	0.998	0.895
	144	0.000	0.012	0.000	0.000	0.000	0.000	0.002	0.105
<i>sIDHP</i> -1,2*	100	0.665	0.674	0.736	0.635	0.640	0.633	0.722	0.730
	42	0.155	0.129	0.037	0.180	0.145	0.187	0.112	0.005
	121	0.015	0.007	0.002	0.004	0.002	0.006	0.003	0.032
	72	0.165	0.189	0.224	0.181	0.213	0.175	0.164	0.187
<i>LDH</i> -B2*	100	0.772	0.404	0.996	0.305	0.285	0.279	0.364	0.844
	76	0.226	0.594	0.004	0.687	0.715	0.713	0.634	0.156
<i>sMDH</i> -B1,2*	100	0.900	0.979	0.987	0.976	0.996	0.984	0.984	0.913
	83	0.084	0.010	0.008	0.009	0.000	0.005	0.009	0.016
	78	0.000	0.002	0.000	0.000	0.000	0.000	0.001	0.000
<i>sMEP</i> -1*	100	0.902	0.994	0.998	0.875	1.000	1.000	0.997	0.936
	83	0.098	0.005	0.002	0.000	0.000	0.000	0.003	0.009
<i>PEP</i> -A*	100	0.981	0.922	0.982	0.938	0.716	0.941	0.913	0.998
	111	0.017	0.065	0.018	0.062	0.280	0.056	0.043	0.002
<i>PEPB</i> -1*	100	0.994	0.975	1.000	1.000	1.000	0.998	0.997	0.989
	134	0.005	0.017	0.000	0.000	0.000	0.002	0.002	0.000
	69	0.001	0.006	0.000	0.000	0.000	0.000	0.001	0.011
<i>PEP</i> -C*	100	1.000	1.000	1.000	1.000	1.000	1.000	0.998	1.000
	110	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.000
<i>PGM</i> -2*	-100	1.000	0.981	0.992	0.997	0.994	0.997	0.998	0.987
	-120	0.000	0.013	0.008	0.003	0.006	0.003	0.002	0.013
<i>sSOD</i> -1*	100	0.669	0.944	0.987	0.934	0.942	0.920	0.945	0.910
	152	0.331	0.032	0.013	0.013	0.020	0.011	0.022	0.009
	38	0.000	0.023	0.000	0.053	0.038	0.070	0.033	0.000

headwaters of streams and rivers draining into Klamath Lake (Table 1).

Geographical distribution of different allelic combinations also indicated consistent patterns of differences among major evolutionary groups associated with the Columbia, Klamath, and Sacramento rivers (Figure 3). Patterns of character evolution were represented by 29 equally parsimonious cladograms. In all cladograms, rainbow trout associated with Upper Klamath Lake, the Klamath River, and the Rogue River (a coastal river in the Klamath Mountain Province) represented a monophyletic lineage. Likewise, in all cladograms, Columbia River populations formed a monophyletic group. In 27 of 29 cladograms, the presence of *sAH*\*72 and

*G3PDH*-1\*80 alleles in both Columbia River and Harney Basin major evolutionary groups suggested a common ancestry. In contrast, no cladograms suggested that coastal rainbow trout of the lower Columbia River, Klamath River, and the Klamath Mountain Province were a single lineage that was a sister group of all inland and northern Great Basin redband trout groups, which is what would have been expected if extant rainbow trout diversity reflected divergence of coastal and inland lineages associated with Pleistocene isolation and dispersal from refugia east and west of the Cascade Mountains.

The character state analysis also showed a close evolutionary relationship between the Goose Lake–

TABLE 2.—Extended.

Variable or locus	I	J	K	L	M	N	O	P	Q
<i>N</i>	45	98	50	81	256	222	91	157	85
Populations	3	5	2	4	7	6	6	2	2
Locus:									
<i>ADH</i> *	0.918	0.945	0.867	0.908	0.987	0.882	0.935	0.997	0.886
	0.082	0.055	0.096	0.083	0.013	0.118	0.042	0.000	0.114
	0.000	0.000	0.038	0.008	0.000	0.000	0.023	0.003	0.000
<i>sAH</i> *	1.000	0.897	0.867	0.993	0.541	0.909	0.924	0.978	0.955
	0.000	0.103	0.100	0.007	0.118	0.033	0.062	0.022	0.045
	0.000	0.000	0.000	0.000	0.000	0.003	0.008	0.000	0.000
	0.000	0.000	0.033	0.000	0.341	0.055	0.006	0.000	0.000
<i>G3PDH-1</i> *	1.000	1.000	1.000	1.000	1.000	0.967	1.000	0.908	1.000
<i>GPI-B1</i> *	1.000	0.418	0.974	0.065	0.975	0.972	0.412	1.000	1.000
	0.000	0.582	0.026	0.935	0.000	0.000	0.556	0.000	0.000
	0.000	0.000	0.000	0.000	0.025	0.028	0.032	0.000	0.000
<i>mIDHP-1</i> *	1.000	0.979	1.000	0.996	1.000	1.000	0.915	1.000	1.000
	0.000	0.021	0.000	0.004	0.000	0.000	0.085	0.000	0.000
<i>mIDHP-2</i> *	1.000	0.989	0.992	1.000	0.946	0.994	0.957	1.000	0.956
	0.000	0.011	0.008	0.000	0.054	0.006	0.043	0.000	0.038
<i>sIDHP-1,2</i> *	0.562	0.645	0.765	0.735	0.796	0.900	0.758	0.691	0.864
	0.077	0.029	0.050	0.014	0.028	0.065	0.110	0.143	0.101
	0.000	0.051	0.021	0.017	0.015	0.001	0.006	0.033	0.000
	0.361	0.275	0.165	0.234	0.158	0.033	0.126	0.133	0.036
<i>LDH-B2</i> *	0.902	0.851	0.913	0.986	0.996	1.000	0.785	1.000	0.977
	0.098	0.149	0.088	0.014	0.001	0.000	0.215	0.000	0.023
<i>sMDH-B1,2</i> *	1.000	0.962	0.977	0.978	0.956	0.952	0.881	0.831	0.938
	0.000	0.038	0.019	0.018	0.010	0.007	0.103	0.169	0.009
	0.000	0.000	0.000	0.000	0.024	0.008	0.000	0.000	0.000
<i>sMEP-1</i> *	0.944	1.000	1.000	1.000	1.000	1.000	1.000	0.916	0.969
	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.084	0.031
<i>PEP-A</i> *	1.000	1.000	0.962	0.988	0.890	0.888	0.970	0.990	0.951
	0.000	0.000	0.000	0.000	0.093	0.107	0.000	0.003	0.037
<i>PEPB-1</i> *	0.989	0.562	0.923	0.343	0.937	0.972	0.929	1.000	0.928
	0.000	0.000	0.000	0.000	0.004	0.020	0.000	0.000	0.042
	0.011	0.438	0.077	0.657	0.059	0.008	0.071	0.000	0.029
<i>PEP-C</i> *	1.000	1.000	1.000	1.000	0.976	0.947	1.000	1.000	0.969
	0.000	0.000	0.000	0.000	0.014	0.053	0.000	0.000	0.031
<i>PGM-2</i> *	0.983	0.975	0.983	0.981	0.918	0.944	0.996	0.903	1.000
	0.000	0.025	0.017	0.007	0.082	0.046	0.004	0.097	0.000
<i>sSOD-1</i> *	0.844	0.963	0.942	0.463	0.896	0.838	0.796	0.714	0.808
	0.156	0.037	0.058	0.537	0.104	0.162	0.204	0.286	0.160
	0.000	0.000	0.000	0.000	0.028	0.000	0.000	0.000	0.031

Chewaucan Basin–Warner Valley complex of redband trout, although the relationships were not completely resolved (Figure 3). In all, 25 of 29 cladograms supported a close evolutionary relationship between Warner Valley and Goose Lake, a disjunct part of the

Sacramento River basin. In the other four cladograms, shared presence of *sMDH-A1,2\*37* indicated a common ancestry of Chewaucan Basin and Goose Lake redband trout, with Warner Valley redband trout as the only immediate sister group.

TABLE 3.—Analysis of molecular variance for rainbow trout of the three major river systems and basins of Cascadia and the northern Great Basin. All sources of variation were significant ( $P < 0.0001$ ) based on 1,000 permutations.

Source of variation	df	Sum of squares	Variance components	Percent variance
Among major river systems	2	670.47	0.2100	19.70
Among basins within major rivers	12	1,398.85	0.0774	7.27
Among populations within basins	162	819.97	0.0232	2.18
Within populations	20,909	15,788.87	0.75512	70.85

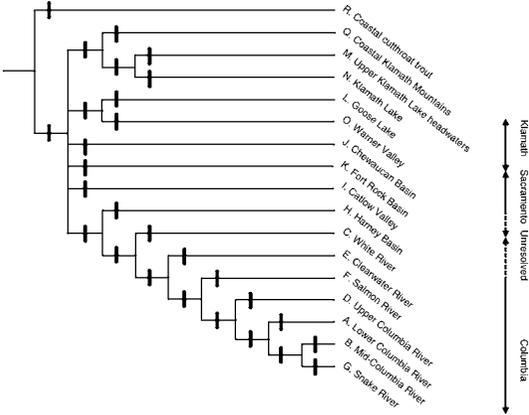


FIGURE 3.—Consensus cladogram of 29 equally parsimonious trees for rainbow trout (including redband trout) based on allozyme characters; coastal cutthroat trout were used as the outgroup (letters correspond to sample locations in Figure 1). Bars indicate gain or loss of characters. A complete table of character state changes at each node is available in Currens (1997) or from the authors.

The inability of the character analysis to unambiguously identify relationships of Chewaucan Basin, Catlow Valley, and Fort Rock redband trout probably reflected different groups evolving similar allele

combinations independently or undocumented traits that might indicate a recent common ancestor. Catlow Valley redband trout, for example, had allelic combinations for *mMEP-1\** and *mIDHP-2\** that were similar to those in Goose Lake and Warner Valley. Similarly, Fort Rock redband trout expressed allelic combinations involving *sAH\*112*, which were characteristic of Upper Klamath Lake groups (Table 2; Figure 3). Whether these were homoplasies or suggested common ancestries that could be resolved by additional data was not possible to determine from this analysis.

Evolutionary relationships based on genetic distance analyses (Figure 4) supported the major geographical patterns of allelic frequency divergence identified by CVA (Figure 2) and cladistic analysis (Figure 3), with a few differences. Redband trout collected from Upper Klamath Lake and the Upper Klamath Lake headwater locations grouped with coastal rainbow trout from the Klamath Mountain Province, although the bootstrap value was not as large as for other major lineages. Similarly, Goose Lake, Warner Valley, and Chewaucan Basin redband trout formed a single group. Columbia River redband trout (not including White River redband trout) and Harney Basin redband trout also formed a genetically similar group. Within the Columbia River, inland redband trout were a distinct cluster from lower Columbia River rainbow trout.

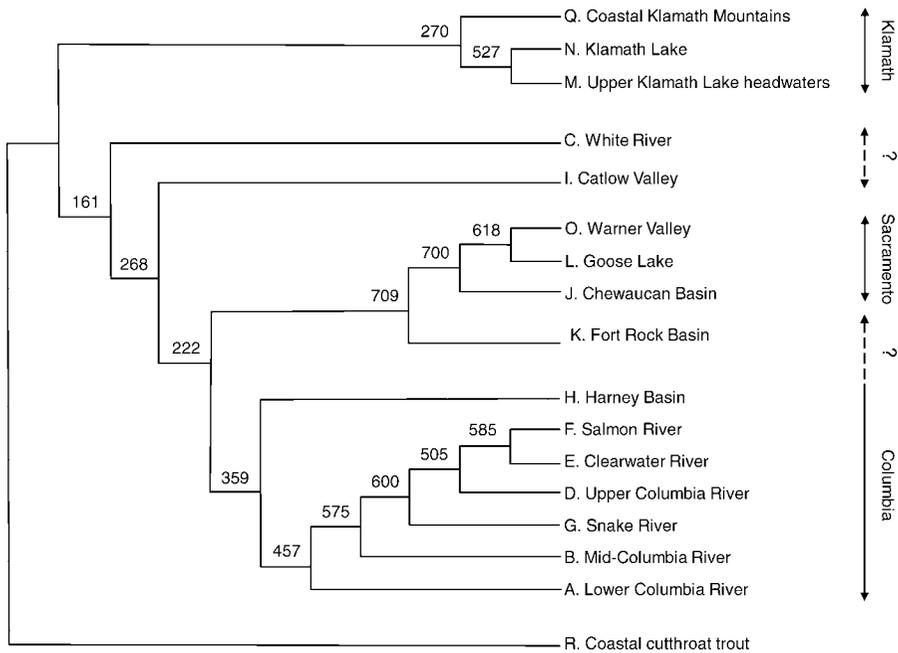


FIGURE 4.—Consensus dendrogram of evolutionary relationships of rainbow trout (including redband trout) based on the neighbor-joining method and Cavalli-Sforza-Edwards chord distances (letters correspond to sample locations in Figure 1; coastal cutthroat trout were used as the outgroup). Numbers at nodes show bootstrap values based on 1,000 repetitions.

White River redband trout, which we previously identified as distinct from all other Columbia River populations and more like northern Great Basin redband trout in the Fort Rock Basin (Currens et al. 1990), were also distinct in this analysis. Redband trout from Fort Rock Basin, however, were genetically more similar to Goose Lake, Warner Valley, and Chewaucan Basin redband trout. Fort Rock had Pleistocene and earlier connections with the Columbia River before it was isolated (Allison 1940, 1979; Allison and Bond 1983) that apparently did not exist for Goose Lake, Warner Valley, and Chewaucan Basin, but geographical patterns of vicariance in these redband trout may be obscured by homoplasies identified by the character analysis.

### Discussion

Patterns of genetic diversity in this study showed evolutionary continuity around three major river systems that breached the crest of the Cascade Range: the upper Sacramento River, the Klamath River, and the Columbia River. This strongly suggested that large river systems must have provided long-term sources of stable, diverse aquatic habitat that allowed rainbow trout to persist and evolve in the dynamic landscape of Pleistocene and Recent times. Large pluvial lake basins also persisted during this time. The genetic relationships between endemic redband trout of pluvial lake basins of the northern Great Basin and redband trout of the upper Sacramento, Klamath, and Columbia rivers indicated that during the Pleistocene or even more recently, these habitats were probably sources of ecological and evolutionary diversity between large rivers and large lakes rather than completely independent habitats. In contrast, genetic differences in allozyme traits between coastal and inland forms of rainbow trout may be more localized than previously acknowledged. Although the hypothesis that isolation and dispersal from different glacial refugia is useful to explain inland versus coastal differences within river systems (e.g., Allendorf 1975; Okazaki 1984; Behnke 1992), it may need to be expanded to account for persistence of other lineages. Rainbow trout from coastal southern California streams, for example, which were a distinctly different major evolutionary lineage from coastal rainbow trout of Cascadia (Nielsen et al. 1994; Busby et al. 1996), may be evidence of one of several Pleistocene refugia that supported the persistence and evolution of rainbow trout and redband trout around large river systems.

#### *Phylogeny of Redband Trout*

Based on our data, redband trout are a polyphyletic group that includes multiple subspecies and genetic

races. Therefore, the term “redband trout” can be used to refer to the fine-scaled rainbow trout indigenous to waters east of the Cascade Mountain range, but it otherwise conveys little information about the taxonomy or unique adaptations of these fish. No cladistic or neighbor-joining trees (Figures 3, 4) indicated that rainbow trout of these regions shared a common lineage distinct from coastal populations, such as those in the lower Columbia River, coastal Klamath Mountains, or domesticated rainbow trout strains. Inland redband trout of the Columbia River, for example, represented a different lineage than redband trout of the northern Great Basin. Similarities among these groups mostly reflected either retention of primitive morphological or allozyme traits that have been lost in other groups (Currens et al. 1990; Behnke 1992) or independent evolution of the same trait. Likewise, although many of these groups occupied alpine, arid environments, there is little evidence to indicate they shared a common origin for unique physiological or behavioral adaptations (e.g., tolerance for warm water) that might be expected given the rigors of those environments (Vinson and Levesque 1994; Rodnick et al. 2004; Feldhaus 2006).

However, Behnke (1992) argued for the integrity of a more restricted Great Basin redband trout lineage based largely on shared primitive morphological and allozyme traits. He hypothesized that these reflected an early invasion of the northern Great Basin from the south and subsequent isolation. In our analyses, the neighbor-joining tree showed weak support for a common group of redband trout from interior basins of Oregon (Goose Lake, Warner Valley, Chewaucan Basin, and Fort Rock), with White River and Catlow Valley redband trout as divergent groups. The clustering largely reflects similar frequencies of *LDH-B2\*100* among these groups (Table 2). In the cladistic analyses, however, this characteristic was less informative about evolutionary relationships because the analysis attempted to account for symplesiomorphies (Currens et al. 1990) or homoplasies arising from genetic drift or episodic gene flow. Our analyses, for example, revealed that although different groups either lack or have low frequencies of *LDH-B2\*76* (Table 2), some have simply retained the ancestral state with cutthroat trout (e.g., coastal rainbow trout or exotic hatchery strains) while others have independently lost the allele (e.g., Upper Klamath Lake redband trout; Figure 3). No unique derived traits defined redband trout of the northern Great Basin. Consequently, the relationships of some of these groups in Figure 4 remained unresolved.

All analyses indicated that coastal rainbow trout from the Klamath Mountains were more closely related

to other Klamath River populations than to coastal rainbow trout from the lower Columbia River. Likewise, all analyses indicated that Columbia River rainbow trout were distinct from those in other major river systems. However, neither the cladistic nor genetic distance analyses provided a definitive phylogeny. Rather, cladistic and genetic distance analyses emphasized different aspects of the persistence and evolution of rainbow trout in these river systems. Where there may have been opportunities for reticulate evolution as different parts of these river systems became accessible to different groups, results of cladistic analysis may be better interpreted as anagenic trajectories rather than simple phylogenies. In contrast, where there was evidence of long-standing geographical isolation, the patterns may indicate historical patterns of vicariance. For example, within the clade associated with the present Columbia River basin (excluding the White River) where there may have been opportunities for gene flow, the gains and losses of alleles associated with different geographical groups (Figure 3) may not entirely reflect historical patterns of vicariance. However, the correlation between the geological history of Harney Basin, Fort Rock Basin, and the White River and the differentiation of their fishes (Bisson and Bond 1971; Allison 1979; Currens et al. 1990) supported a very early divergence of the isolated redband trout of these areas from redband trout of the Columbia River.

#### *Biogeography of Major Groups*

Redband trout from Goose Lake, Pit River, Warner Valley, and Chewaucan Basin represented dispersal and divergence of upper Sacramento River redband trout into Oregon. Many investigators have recognized faunal and physiographic evidence for considering Goose Lake a disrupted part of the upper Sacramento River (Russell 1884; Snyder 1908a; Hubbs and Miller 1948). Native fish fauna of Goose Lake were typical of Sacramento River assemblages (Minckley et al. 1986; Moyle 2002). Additionally, Berg (1987) noted close genetic similarities between redband trout in the Pit River, a tributary of the upper Sacramento River, and redband trout in Goose Lake, which has overflowed into the Pit River in historical times. Until recently, evidence for considering Warner Valley and Chewaucan Basin as part of the upper Sacramento River system was limited. Fish assemblages in both basins were dominated by three widely distributed, persistent species—tui chub *Gila bicolor* complex, speckled dace *Rhinichthys osculus*, and redband trout—that have been largely indistinguishable morphologically from forms in other basins. The presence of California roach *Hesperoleucus symmetricus* in Warner Valley, if

indigenous, would be additional strong evidence of connection to the Sacramento River, where the species is endemic (Hubbs and Miller 1948; Minckley et al. 1986; Moyle 2002). Minckley et al. (1986) also suggested a close relationship between Warner suckers *Catostomus warnerensis* of Warner Valley and Modoc suckers *Catostomus microps* of the Pit River, although they presented few data. Recent mitochondrial and microsatellite DNA studies of tui chub, however, supported a shared evolutionary history between the Pit River, Goose Lake, and Warner Valley because the basins were found to share a distinct species, the Goose Lake tui chub *G. thalassinus* (formerly recognized as subspecies *G. bicolor thalassinus*; Harris 2001). Tui chub in Chewaucan Basin, however, were distinct and thought to be another allopatric species, although the genetic similarities to Goose Lake and Warner Valley tui chub compared with other northern Great Basin populations suggested some historical gene flow (Harris 2001; Chen et al. 2009).

Our results provided additional support for the biogeographical relationship among fishes in these basins based on genetic characteristics of redband trout. Genetic data from this study demonstrated geographical differences among redband trout and close association between forms from Goose Lake and Warner Valley and more limited association with fish from the Chewaucan Basin (Figures 3, 4). Presence of *mIDHP-1\*280* in only Goose Lake, Warner Valley, and Chewaucan Basin redband trout, presence of *sMDH-A1,2\*37*, and unusually high frequencies of *GPI-B1\*138* in these populations provided strong support for association of these basins (Table 2). Allelic frequencies at *PEP-A\**, *PEP-B1\**, and *sSOD-1\** also indicated similarities among these groups that distinguished them from other groups of rainbow trout. In addition, our unpublished analyses of Berg's (1987) data from Goose Lake, McCloud River, and Pit River redband trout and our samples using loci common to both studies showed strong genetic similarities between Goose Lake, Warner Valley, and Chewaucan Basin redband trout and those in the McCloud and Pit rivers. Based on our data, we concluded that Goose Lake, Warner Valley, and Chewaucan Basin redband trout should be considered part of the diverse Sacramento redband trout complex, although the relationship of Chewaucan Basin redband trout needs further resolution. The presence of alleles that characterize Chewaucan Basin redband trout, such as *sMDH-A1,2\*37* and *GPI-B1\*138*, at low frequencies in redband trout from Upper Klamath Lake and Fort Rock basins, respectively, may indicate multiple connections with different basins.

Klamath rainbow trout consisted of populations from

coastal Klamath Mountain streams (Rogue and Klamath rivers below the dams) and streams associated with Upper Klamath Lake basin. This was not unexpected. Other evidence suggested that coastal Klamath Mountain streams that are presently separated from the Klamath River were biogeographically and evolutionarily related. Rainbow trout from this region had a unique karyotype (Thorgaard 1983). Coastal steelhead (anadromous rainbow trout) from Klamath Mountains Province, which included the Rogue and Klamath rivers, formed a geographical genetic cluster that was distinct from coastal populations to the north or south based on allozyme data (Busby et al. 1996). The Rogue River also contained a closely related form of the Klamath smallscale sucker *Catostomus rimiculus*, which was endemic to the lower Klamath River (Snyder 1908b; Minckley et al. 1986; Moyle 2002).

Within Upper Klamath Lake basin, however, major allelic differences existed between (1) redband trout found in the small streams and lower reaches of rivers associated with Upper Klamath Lake and (2) redband trout associated with Jenny Creek, which were isolated above ancient waterfalls, and those in headwaters of Sprague and Williamson rivers ( $F_{ST} = 0.1692$ ,  $P < 0.0001$ ). Abrupt changes in allele frequencies in collections from the Sprague River indicated a geographical boundary near Trout Creek. The divergence of these groups within the Upper Klamath Lake basin is greater than the divergence between inland and coastal forms ( $F_{ST} = 0.107$ ) over all the collections in this study. Behnke (1992) also noted morphological differences between redband trout with adfluvial life histories associated with Upper Klamath Lake and those with riverine life histories in the headwaters of the Sprague River; he attributed the differences to adaptation to different environments. Upper Williamson River, Sprague River, and Jenny Creek redband trout were also susceptible to infection by the myxozoan parasite *Ceratomyxa shasta*, whereas Upper Klamath Lake and Klamath River forms, which co-occur with the parasite (Stocking and Bartholomew 2007), were resistant (Oregon Department of Fish and Wildlife, unpublished data). The shared traits of these headwater redband trout with those isolated behind the Jenny Creek barrier waterfall, estimated to be 5 million years old (Hohler 1981), suggested that this evolutionary lineage represents a previously more widely distributed lineage that was present before Upper Klamath Lake overflowed to establish connections with the Klamath River, thereby opening an avenue for colonization from the lower river. No subspecific name currently exists for the redband trout in the headwaters of the Upper Klamath Lake basin, but both morphological data and our genetic data showed that they were

not the same group as the Upper Klamath Lake redband trout that occurred where the first specimens of the *O. mykiss newberrii* subspecies were collected.

The evolutionary relationship between coastal rainbow trout that currently use the Klamath River accessible to steelhead and those redband trout that may have become established in the streams associated with Upper Klamath Lake and the upper Klamath River, where type specimens of Upper Klamath Lake redband trout were collected (Girard 1856), remained unclear. We observed much greater differences between the resident redband trout of headwater streams of the Upper Klamath Lake basin and those associated with Upper Klamath Lake than we did between rainbow trout from coastal Klamath River sites, considered to be coastal rainbow trout, and the nonanadromous rainbow trout from the streams where Upper Klamath Lake redband trout were thought to occur. Allozyme techniques did not allow us to compare genetic characteristics of the original collections of Upper Klamath Lake redband trout with our collections. Snyder (1931) indicated, based on interviews, that steelhead and other Pacific salmon may have once used streams above Upper Klamath Lake. If future genetic work shows that the nonanadromous redband trout associated with Upper Klamath Lake are more closely related to coastal steelhead, it would strengthen our hypothesis that this group evolved from fishes that accessed Upper Klamath Lake after it overflowed into the Klamath River and that an older form of redband trout still exists in headwaters and above barriers. Alternatively, if future investigations based on analysis of Upper Klamath Lake redband trout type specimens show that extant redband trout of Upper Klamath Lake represent *O. mykiss newberrii* and that these fish are different from steelhead in the lower Klamath River, it would support Behnke's (1992) conclusion that both redband trout and coastal steelhead once used the Klamath River.

Columbia River rainbow trout included all the major evolutionary groups within the extant Columbia River and Harney basins (Figures 2, 3). Although they are currently isolated and have diverged from inland redband trout of the Columbia River (Figures 3, 4), Harney Basin redband trout were almost certainly linked to Columbia River populations in the past, probably through multiple hydrographic connections with Snake River or mid-Columbia River tributaries (Piper et al. 1939; Bisson and Bond 1971). Most fish of Harney Basin are typical Columbia or Snake River species (Snyder 1908a; Minckley et al. 1986; Markle and Hill 2000), although Hubbs and Miller (1948) hypothesized that substantial isolation had led to four or five endemic subspecies.

Although isolated redband trout in the White River and those in interior Fort Rock basin have diverged significantly from all other groups associated with the Columbia River, their persistence also reflected the long-term stability of rainbow trout habitat associated with the Columbia River. Pliocene and Pleistocene fossils of Pacific salmon (Cavender and Miller 1972; Allison and Bond 1983), geological evidence of outflow to the Deschutes River (Allison 1940, 1979), and the close evolutionary relationship of Fort Rock redband trout to White River redband trout (Currens et al. 1990) supported a long-standing biogeographical relationship with the Columbia River. However, the homoplasies reflected by the uncertainty in assigning Fort Rock Basin redband trout unambiguously to a lineage (Figures 3, 4) also indicated the importance of intermittent hydrological connections to different basins. Unlike other studies (Wilmot 1974), we detected low frequencies of *LDH-B2\*76* in Fort Rock redband trout, which could indicate previous connections to the Columbia, Klamath, or Sacramento River system. Expression of the *sAH\*112* allele in Fort Rock redband trout, however, was good evidence of limited gene flow from Upper Klamath Lake basin populations. This allele was abundant in headwater collections from Upper Klamath Lake basin but absent in Columbia River rainbow trout (Table 2). Geographically, the closest populations to Fort Rock redband trout were in headwaters of the Sprague River of Upper Klamath Lake basin, which were separated from Fort Rock streams by a low wetland divide at Sycan Marsh. This corridor between the two basins may also have allowed dispersal of tui chub and speckled dace (Hubbs and Miller 1948; Minckley et al. 1986). The presence of fossil suckers *Chasmistes batrachops* in Fort Rock Basin and extant shortnose suckers *Chasmistes brevirostris* in Upper Klamath Lake (Minckley et al. 1986) also suggested episodic association between the basins. The considerable genetic differences between White River and Fort Rock redband trout and the inland redband trout of the Columbia River—such as these groups' low frequencies of *LDH-B2\*76*, which characterizes inland Columbia River redband trout (Table 2), and the long period of current isolation from other redband trout—suggested that these redband trout may represent a different subspecies.

More than any other group, Catlow Valley redband trout appeared decoupled from any major river system. Genetically, Catlow Valley redband trout were more similar to Fort Rock and Harney Basin redband trout than to fish from other basins (Figures 2–4), which may indicate a Columbia River association. Although other studies failed to detect the *LDH-B2\*76* allele (Wilmot 1974; Wishard et al. 1984) in Catlow Valley redband

trout, we detected low frequencies of the allele, which was abundant in the upper Columbia River populations and also occurred in Sacramento River populations (Berg 1987). Hubbs and Miller (1948) proposed that an overflow of pluvial Lake Catlow into Harney Basin gave tui chub access to Catlow Valley. This was dismissed by Minckley et al. (1986) because the gradient would have been too precipitous for tui chub, but it may not have been too steep for redband trout. Hubbs and Miller (1948) did not consider the distribution of rainbow trout because they assumed that all rainbow trout were introduced. In contrast, these data suggested that the fish were indigenous redband trout. Extinctions, genetic drift, and limited opportunity for immigration as a result of the basin's isolated location and lack of large, persistent or interconnected streams may have obscured relationships to major river systems. Like Chewaucan and Warner Valley basins, Catlow Valley did not adjoin a major river basin. Unlike the other two basins, which had complex networks of internal rivers and streams draining mountainous regions, Catlow Valley restricts rainbow trout to the fate of three short, independent creeks (Hubbs and Miller 1948; Minckley et al. 1986; ODFW 2005) that would have limited population size and gene flow and increased potential for genetic drift and allele extinction. Only two other fish species—tui chub and speckled dace—have persisted in the basin (Minckley et al. 1986). This low species diversity may also reflect lack of long-term aquatic stability and ecological diversity. The relationship between Catlow Valley redband trout and existing nominal subspecies remains unresolved.

Our analyses suggested that over many millennia, the small streams and rivers associated with pluvial lake basins were sources of ecological and evolutionary diversity for rainbow trout within large river systems rather than unique, isolated habitats leading to new species or extinction of rare species. Evidence of dynamic hydrological connections among basins apparently led to persistent habitat for rainbow trout associated with larger rivers despite (and sometimes because of) Pleistocene climates and glaciation. This may explain why large river systems were a greater source of evolutionary diversity in our data than isolation and dispersal from inland or coastal Pleistocene refugia. Speciation by peripheral isolation (Mayr 1963; Brooks and McLennan 1991) would have depended on isolation that was strong enough to allow novel traits to become established and habitat that was stable enough to prevent extinctions. However, climatic variability, as indicated by geologic evidence of fluctuating pluvial water levels (Antevs 1925; Mifflin and Wheat 1979; Licciardi 2001), glaciations, and

volcanic disruptions (Pease 1965), almost certainly at times reduced the amount of stable habitat locally and resulted in local extinctions in these pluvial lake basins. For the fishes that could exploit the opportunities, the same variability would have provided episodic opportunities and avenues for recolonizations to occur (e.g., Reheis 1999) and expanded habitat separated by long periods of isolation. One likely explanation for homoplasies in our data, for example, was that they reflected rare, episodic immigration and gene flow with populations in nearby large river systems. These episodes would have helped maintain species cohesion at the scale of large river systems while allowing divergence of geographical races and subspecies. Genetically, the process of isolation, extinction, and recolonization of peripheral populations in basins sets up an age distribution at the level of populations (or drainages) within large river systems that would have tended to increase the degree to which genetic variance is partitioned among populations (McCauley 1991), while providing a buffer against extinction of all populations in the system. For many Great Basin species, geographic isolation and lack of stable aquatic habitats caused by climatic variability and tectonism may indeed have led to high extinction rates and lower species diversity (Smith 1981; Smith et al. 2002). The ability of the rainbow trout, however, to adapt its life history to a variety of habitats may have allowed these fish to persist and diversify by exploiting available habitat that was not available to other fishes.

The capacity for partial migration, or in salmonids the tendency of individuals and populations to express a variety of migratory life histories ranging from anadromy to adfluvial migrations to little or no migration (Hendry et al. 2004), is one such adaptation. Partial migration allows salmonids to respond to changing environmental conditions (Jonsson and Jonsson 1993; Kaitala et al. 1993). Although habitat or behavioral differences may promote spatial and temporal isolation of sympatric migratory forms in some streams (Zimmerman and Reeves 2000; McMillan et al. 2007), most studies demonstrated that where sympatric migratory forms can occur, gene flow was much greater among the different life history forms than among spawning aggregations in different streams (Docker and Heath 2003; Olsen et al. 2006; McPhee et al. 2007), indicating that these are different life history strategies that occur within populations. In the dynamic environment of Cascadia and the northern Great Basin, this adaptation allowed progeny of steelhead that became isolated above barriers by landslides, lava flows, tectonic activity, or dams to survive as resident rainbow trout without anadromy. Evidence of this is the presence of nonmigratory redband trout above

dams in streams that were once accessible to steelhead (Table 1). Likewise, in the Oregon desert lake basins, this adaptation allowed redband trout to (1) cross low divides into other basins during episodically high water levels or through stream capture; (2) migrate to large lakes that formed during wet periods and grow to sizes that increased fecundity by an order of magnitude, which may have decreased demographic risks of extinction; (3) recolonize streams where local extinctions may have occurred; and (4) survive in small headwater streams during warmer climates and droughts when lakes dried.

### *Conservation Implications*

This study has implications for conservation and management of rainbow trout. First, despite mismanagement and neglect, many streams still contain indigenous populations. Our analyses revealed unique geographical races and potentially unnamed subspecies that are important management units for conservation. Under the evolutionarily significant unit (ESU) concept (Waples 1991), most of the major groups we have described would be considered as distinct ESUs. Busby et al. (1996), for example, identified similar evolutionary lineages in the Columbia, Klamath, and Sacramento rivers where steelhead occur. The redband trout of the White River, Fort Rock, Harney Basin, Catlow Valley, Chewaucan Basin, Warner Valley, Goose Lake, and Upper Klamath Lake would also meet the criteria for distinct ESUs. Although stocking and subsequent introgression with exotic hatchery strains threatened this diversity for most of the last half of the 20th Century, management agencies discontinued this practice by the mid-1990s (ODFW 2005).

Even more important may be the recognition that unless large river systems and pluvial lake basins are managed to promote connectivity of habitats, human intervention will be increasingly necessary to maintain only a fraction of the current genetic diversity and distribution within and among these ESUs; however, such intervention would be difficult. Redband trout are presently missing from 71% of their potential range in northern Great Basin and Columbia Plateau, strong populations occur in 9% of their potential range, and only 3% of their strongholds are within lands where their habitats are protected (Thurow et al. 2007). One of the major threats to unique redband trout groups in the northern Great Basin is habitat fragmentation and the associated demographic and genetic risks of isolation in small streams. In the Harney Basin, for example, redband trout in different streams were once interconnected by migrating to shared rearing areas in Harney and Malheur lakes and returning to streams to spawn. Currently, of the 10 streams containing redband

trout, only one contains a spawning aggregation with the adfluvial life history once shared by most populations throughout the northern Great Basin. Most streams in this basin and in other basins no longer provide passage to the lakes because of artificial barriers, reduced streamflows, degraded habitat and water quality, and introduction of exotic predators. In the Warner Valley, the three streams that historically provided access to large lakes do so only rarely if at all. Similar conditions apply to all three streams with redband trout in Fort Rock Basin, three of the four redband trout streams in the Chewaucan Basin, and nearly half of the 13 redband trout streams in Goose Lake basin. Adfluvial life histories are still common only in streams associated with Upper Klamath Lake (ODFW 2005).

The effects of these habitat changes on partial migration may explain the pattern of  $F_{ST}$  values that we observed. In Columbia River streams, where anadromous rainbow trout are common, and in Goose Lake, where the redband trout still express adfluvial life histories,  $F_{ST}$  values were less (0.001–0.049 and 0.034, respectively) than in basins where habitat changes restrict the range of partial migration, indicating that gene flow and genetic effective population sizes increased with expression of more migratory life histories. For example, in the Snake River tributaries used by steelhead until dams were constructed over 100 years ago,  $F_{ST}$  (0.072) was larger than in areas where anadromy still occurred, suggesting that loss of the anadromous life history has increased isolation among local aggregations. In isolated streams of the northern Great Basin, where both anthropogenic and longer-term climatic changes have greatly restricted migratory life histories and isolated different groups,  $F_{ST}$  values were greatest (0.063–0.138). Overall, our results suggest that restoration of connectivity among streams and lakes to allow redband trout the full range of migratory adaptations that they have evolved over millennia to face environmental challenges will provide the most robust opportunity for their continued persistence and evolution.

#### Acknowledgments

We are grateful for the inspiration of Carl Bond, Oregon ichthyologist and Professor Emeritus of Fisheries at Oregon State University; the many district fishery biologists of the Oregon Department of Fish and Wildlife who helped with this research, especially Dave Buchanan and Alan Hemmingsen; and the Department of Fisheries and Wildlife at Oregon State University, which supported this publication with an award from the Thomas G. Scott Fund.

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