

# Rainbow Trout (*Oncorhynchus mykiss*): A Technical Conservation Assessment



Prepared for the USDA Forest Service,  
Rocky Mountain Region,  
Species Conservation Project

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## **ACKNOWLEDGMENTS**

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## **COVER PHOTO CREDIT**

Photograph of rainbow trout (*Oncorhynchus mykiss*) by E.R. Keeley, used with permission.

# SUMMARY OF KEY COMPONENTS FOR CONSERVATION OF THE RAINBOW TROUT

## *Status*

The Rocky Mountain Region (Region 2) of the USDA Forest Service is beyond the native range of the rainbow trout (*Oncorhynchus mykiss*). Populations in Region 2 were established by introductions from hatcheries for recreation and market purposes, and it is not considered a federally or state threatened, endangered, or sensitive species (U.S. Fish and Wildlife Service; <http://endangered.fws.gov/>). Elsewhere in its native range, several populations of rainbow trout are federally listed as threatened or endangered. However, this is not likely to influence the status of populations in Region 2, where the species is common in streams and lakes and populations are maintained either through self-sustaining natural reproduction or through various levels of supplemental stocking of hatchery fish where self-sustaining populations do not occur. Natural or anthropogenic alteration of habitat may lead to declines in individual populations, as may changes in management practices intended to protect native species; otherwise, the rainbow trout should be considered secure within Region 2.

## *Primary Threats*

As noted above, there are no native stocks of rainbow trout in Region 2. Nonetheless, existing stocks in the Region face the potential for population declines under the influence of both natural and human threats that alter or destroy habitat. Addressed more specifically elsewhere in this assessment, these threats include, but are not limited to, reduction of stream discharge, and changes in water temperature, water quality, substrate, and food base. In addition, perpetuation of some existing populations and future development of new populations to support fishing demand will take place against a backdrop of concerns over conservation or recovery of native fishes and their habitats, which are documented in other assessments in this series. Such constraint was not in place when many of the existing rainbow trout populations were established.

## *Primary Management Elements, Implications and Considerations*

Rainbow trout in the Rocky Mountain Region are an introduced, nonnative species capable of occupying a wide array of habitats, feeding on virtually any type of nutritionally valuable organism, and hybridizing with native trout that may be the focus of recovery efforts. This ecological flexibility has allowed them to join native faunas throughout the United States and the world, where they often alter relationships among members of the receiving fauna.

Persistence of rainbow trout populations in Region 2 will depend on persistence of water quality and quantity sufficient to maintain the existing coolwater ecosystems they presently occupy. Populations presently maintained by stocking of catchable-size trout (in support of a “put-and-take” management strategy) or fingerlings (for a “put-grow-take” strategy) could be enhanced by providing additional spawning, fry, or juvenile habitat. Such actions could also reduce management costs by shifting the age and size of stocked fish toward earlier life history stages or by relying more on natural spawning.

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## INTRODUCTION

This assessment is one of many being produced to support the Species Conservation Project for the USDA Forest Service (USFS) Rocky Mountain Region (Region 2), which encompasses the national forests and national grasslands in Colorado, Kansas, Nebraska, South Dakota, and Wyoming. The rainbow trout (Salmonidae: *Oncorhynchus mykiss*; also called redband trout in some regions) is the focus of this assessment because it is a Management Indicator Species (MIS) on a number of national forests within Region 2. As an MIS, it serves as a barometer for species viability at the forest level. Management Indicator Species have two functions: 1) to estimate the effects of planning alternatives on fish and wildlife populations (Title 36, Code of Federal Regulations 219.19 [Planning - Ecological, social, and economic sustainability] (a) (1)); and 2) to monitor the effects of management activities on species via changes in population trends (36 CFR 219.19 (a) (6)). The primary goal of this assessment is to provide the USFS and other federal (e.g., Bureau of Land Management, U.S. Fish and Wildlife Service (USFWS), Bureau of Reclamation) and state agencies with information about the primary threats to naturally-reproducing rainbow trout populations in the wild as well as stocked (hatchery-raised) rainbow trout in designated recreational fisheries. This information will facilitate further evaluation of rainbow trout in Region 2, leading to decisions by the agency regarding its conservation and management status.

### Goal

Species conservation assessments produced as part of the Species Conservation Project are designed to provide forest managers, research biologists, and the public with a thorough discussion of the biology, ecology, conservation status, and management of certain species based on available scientific knowledge. The assessment goals limit the scope of the work to critical summaries of scientific knowledge, discussion of broad implications of that knowledge, and outlines of information needs. The assessment does not seek to develop specific management recommendations. Rather, it provides the ecological background upon which management must be based and focuses on the consequences of changes in the environment that result from management (i.e., management implications). We also summarize management practices or fisheries regulations that relate to rainbow trout of the states in Region 2. Given the present ubiquity of the animal in a wide array of aquatic environments, its origins and often persistence due to stocking of hatchery-reared

fish, and quite localized management directives in some cases, we do not attempt a catalog of locales, sources of fish, or regulations on a local scale within the states.

The primary foci of this report deal with rainbow trout biology, their possible interactions with sensitive native cutthroat trouts (*Oncorhynchus clarkia*) (e.g., greenback cutthroat trout (*O. c. stomias*), Colorado River cutthroat trout (*O. c. pleuriticus*), Yellowstone cutthroat trout (*O. c. bouvieri*), Rio Grande cutthroat trout (*O. c. virginalis*); **Figure 1**), and real or potential threats facing existing rainbow trout stocks within Region 2. This report should provide agencies with a better understanding of the rainbow trout and the sport fishing opportunities it provides or might provide under different management practices.

### Scope

The rainbow trout assessment examines the biology, ecology, conservation status, and management of this species with specific reference to the geographic and ecological characteristics of the USFS Rocky Mountain Region where possible. Although most of the massive literature on this species (a search of Cambridge Scientific Abstracts, June 2008, for references with ‘rainbow trout’ as keywords yielded 15,858 citations) originates from investigations outside the region, this document places that literature in the ecological and social contexts of the central Rocky Mountains. Similarly, this assessment is concerned with reproductive behavior, population dynamics, and other characteristics of rainbow trout in the context of the current environment rather than under historical conditions. The native environment of the species is considered in conducting the synthesis, but it is placed in a current context.

In producing the assessment, we reviewed refereed literature, non-refereed publications, research reports, and data accumulated by resource management agencies. Many of the references we used came from studies beyond Region 2, but the behavioral and ecological plasticity of rainbow trout make it likely that patterns seen elsewhere could appear under similar circumstances in the Region. Not all published materials should be considered equally reliable, so we have emphasized refereed literature in the assessment. Nonetheless, data not subjected to peer review (e.g., Natural Heritage Program records, NatureServe reports, various “gray literature” reports) were important in describing the geographic distribution and many other aspects of the biology of the species.





**Figure 1.** Native ranges of western trout species and subspecies in the western United States and Canada. From: The Western Native Trout Campaign, [www.westerntrout.org/trout/index.htm](http://www.westerntrout.org/trout/index.htm).

### ***Treatment of Uncertainty***

This assessment is based on information reported by a wide array of organizations and individuals. As such, the strength of the available information in terms of its accuracy and precision depends on many factors, including when work was done, prevailing concepts at that time, the experience of and resources (e.g., time, assistance, instrumentation) available to those collecting the information, the potential for doing manipulative experiments as opposed to relying entirely on observations made in field or laboratory, and the nature and quantity of detail desired by those driving a particular study. These and other factors compound the inherent uncertainty in living systems that traces to variability due to both biotic and abiotic influences on populations, communities, and ecosystems in a particular location.

The animal that is the subject of this assessment exhibits tremendous plasticity in its ability to deal with varied environmental demands and challenges in recent ecological time or much longer evolutionary time. Nonetheless, it is not difficult to summarize this variability into a general description of the norms of life for rainbow trout. Therefore, those establishing or managing stocks of rainbow trout outside of their normal range should understand something of the “normal” pattern as well as the potential variation that may be expressed in a particular location or stock.

### ***Application and Interpretation Limits of This Assessment***

Information used in this assessment was collected from studies that were conducted throughout the native and introduced geographical ranges of this species as



well as with a number of hatchery populations. Although most information should apply broadly throughout the range of the species, it is likely that certain life history parameters (e.g., growth rate, longevity, spawning time) will differ in different locales and along environmental gradients. Thus, information regarding conservation or management strategies for the species may pertain specifically to Region 2 and not apply to other portions of the species' range.

### ***Web Publication***

Species assessments in the Species Conservation Project are being published on the Region 2 World Wide Web site ([www.fs.fed.us/r2/projects/scp/assessments/index.shtml](http://www.fs.fed.us/r2/projects/scp/assessments/index.shtml)). Placing the documents on the Web makes them available to agency biologists and the public more rapidly than publishing them as reports. More important, Web publication facilitates revision of the assessment, which will be accomplished based on the guidelines established by Region 2.

### ***Peer Review***

Assessments developed for the Species Conservation Project have been peer reviewed prior to release on the Web. Peer review for this assessment was administered by the American Fisheries Society, employing recognized experts for this or related taxa. Peer review was designed to improve the quality of communication and to increase the rigor of the assessment.

## **MANAGEMENT STATUS AND NATURAL HISTORY**

### ***Existing Regulatory Mechanisms, Management Plans, and Conservation Strategies***

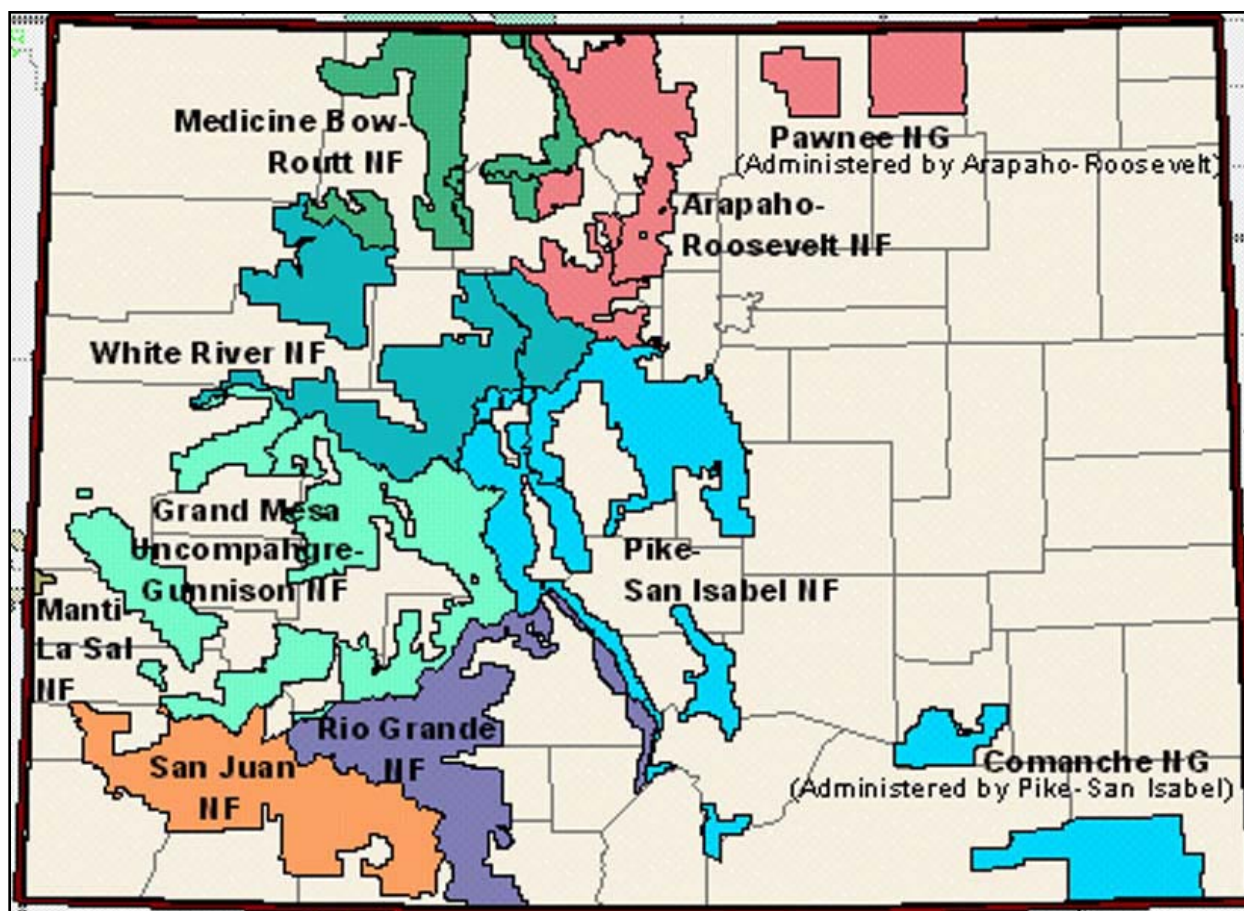
We developed state summaries from print and World Wide Web sources produced by individual states and by both Region 2 and national programs of the USFS. Links to maps for each state are on the USFS Roadless Area Conservation website (<http://roadless.fs.fed.us/>). Names of fishes follow Nelson (2006).

Colorado and Wyoming together contribute more than 90 percent of the total acreage (23,747,000 of 26,219,000 acres) of National Forest System Lands in Region 2. Collectively these states provide homes for at least 109 species and subspecies of fishes (this

number does not include several hybrids; Johnson and Nomanbhoy 2005).

Colorado contributes more than 66 percent of the acreage (14,490,000 of 26,104,000 acres) of National Forest System Lands in Region 2 (USDA Forest Service 2006) (**Figure 2a**). The diverse array of habitats contained in this area offers opportunities to catch roughly 80 species, subspecies, or hybrids of warm- and coldwater fish from 6,000 miles of rivers and streams (major rivers include portions of the Colorado, Rio Grande, Arkansas, and South Platte Rivers; <http://www.enchantedlearning.com>) and more than 2,000 lakes and reservoirs (<http://wildlife.state.co.us/Fishing/>, 2008). Included in this array of aquatic systems are waters on 13 national forests. All or much of the Arapaho, Grand Mesa, Gunnison, Medicine Bow (also see Wyoming, below), Pike, Rio Grande, Roosevelt, Routt, San Isabel, San Juan, Uncompahgre and White River national forests and a small portion of the Utah-centered Manti-La Sal National Forest's Moab Ranger District (administered by Region 4) and two national grasslands, the Comanche and Pawnee national grasslands.

As the agency primarily responsible for managing the state's fish resources, the Colorado Division of Wildlife (CDOW) operates 14 coldwater hatcheries or rearing units (15 if one includes the Mt. Ouray hatchery operated by Mt. Shavano Hatchery personnel) and two warmwater hatcheries. Two USFWS hatcheries supplement total Colorado hatchery output. In 2005, CDOW and USFWS hatcheries stocked more than 3.64 million catchable coldwater fishes (3.57 million of which were rainbow trout), 13.4 million fingerling coldwater fishes (6.07 million rainbow trout fingerlings), 54.5 million warmwater sport fishes, and almost 96,000 individuals of species considered at risk (Federal or State Endangered, Threatened or Special Concern) (U.S. Fish and Wildlife Service 2005). The daily bag limit for most salmonids, which includes rainbow trout, brown trout (*Salmo trutta*), brook trout (*Salvelinus fontinalis*), cutthroat trout (with several subspecies), California golden trout (*Oncorhynchus mykiss aguabonita*), lake trout (*S. namaycush*), splake (lake trout x brook trout hybrid), Arctic charr (*S. alpinus*), grayling (*Thymallus arcticus*), chinook salmon (*O. tshawytscha*), and kokanee (*O. nerka*; landlocked sockeye salmon), in aggregate is four, with the limit for possession being eight. Exceptions are limits of 10 for both brook trout less than 8 inches and kokanee. Statewide, 168 miles of Gold Medal streams (i.e., waters offering the greatest potential for trophy trout fishing) provide angling opportunities for large trout and are managed to ensure populations of big fish. There are many locale-specific



**Figure 2a.** National Forests and Grasslands of Colorado. From: <http://www.roadless.fs.fed.us/states/co/state3.shtml>.

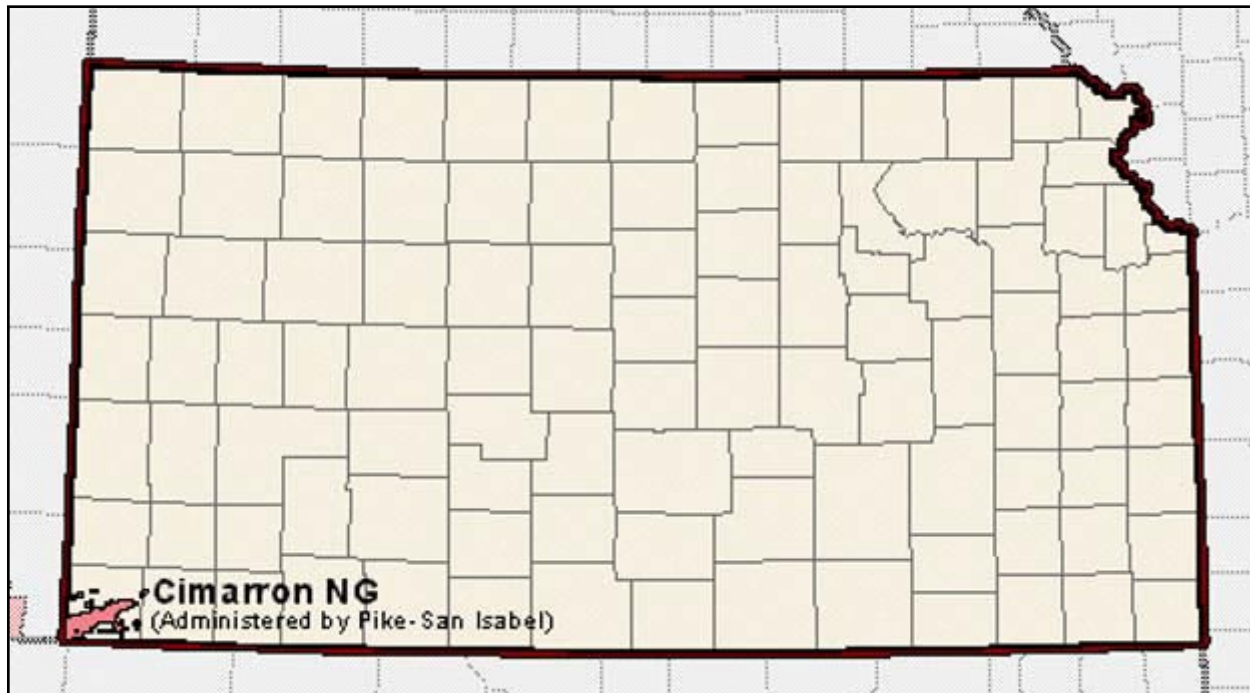
regulations as well; the pamphlet describing fishing regulations for 2008 includes 67 pages of specific regulations on fishing and other uses.

Regulations also disallow take of a number of threatened or endangered aquatic species, including bonytail (*Gila elegans*), Colorado pikeminnow (*Ptychocheilus lucius*), humpback chub (*G. cypha*), razorback sucker (*Xyrauchen texanus*), Arkansas darter (*Etheostoma cragini*), Rio Grande sucker (*Catostomus plebeius*), brassy minnow (*Hybognathus hanksoni*), common shiner (*Luxilus cornutus*), river shiner (*Notropis blennioides*), northern redbelly dace (*Phoxinus eos*), southern redbelly dace (*Phoxinus erythrogaster*), plains minnow (*Hybognathus placitus*), suckermouth minnow (*Phenacobius mirabilis*), lake chub (*Couesius plumbeus*), Arkansas River speckled chub (*Macrhybopsis tetranema*), greenback cutthroat trout and boreal toad (*Bufo boreas boreas*). To accommodate the growing number of cutthroat streams and lakes included in conservation and recovery actions for greenback cutthroat trout, CDOW has identified protected Cutthroat Conservation and Recreation waters

where fishing is by artificial flies and lures only, and all cutthroat must be returned to the water immediately.

CDOW provides a variety of fishing related programs such as a June weekend of free fishing for residents and non-residents, and Colorado residents 64 and older fish free. The state maintains lists of record fish of many species by weight and, for released fish taken by anglers participating in its Master Angler program, by length. Colorado's record rainbow trout was taken from Morrow Point Reservoir (Gunnison County) in 2003 by Lee Cox; it weighed 19 lbs. 10 oz. and was 34 inches long. However, a 40-1/4 inch fish caught and released by Tony Felicilda in the Taylor River would likely have exceeded the present weight record.

The Cimarron National Grassland is the only National Forest System property in Kansas, and its 108,000 acres make it the smallest System holding among the five Region 2 states (**Figure 2b**). Most of the 10,000 miles of streams and rivers in Kansas (major rivers include all or portions of the Kansas, Republican, Smoky Hill, Arkansas, and Missouri rivers; <http://www>



**Figure 2b.** National Forests and Grasslands of Kansas. From: <http://www.roadless.fs.fed.us/states/ks/state3.shtml>.

.enchantedlearning.com) are privately owned, and over 150,000 privately-owned farm ponds in Kansas provide outstanding fishing opportunities. There are also 24 large reservoirs, 40 state fishing lakes, and more than 200 community lakes.

The Kansas Department of Wildlife and Parks (KDWP) operates four hatcheries and a rearing pond to support stocking Kansas waters; there are no National Fish Hatcheries in Kansas. In 2005, Kansas hatcheries produced 74.6 million warmwater fishes, including bluegill (*Lepomis macrochirus*), channel catfish (*Ictalurus punctatus*), Colorado pikeminnow, grass carp (*Ctenopharygodon idella*), largemouth bass (*Micropterus salmoides*), paddlefish (*Polyodon spathula*), pallid sturgeon (*Scaphirhynchus albus*), redear sunfish (*L. microlophus*), sauger (*Sander canadensis*), saugeye (sauger x walleye hybrid), smallmouth bass (*M. dolomieu*), striped bass (*Morone saxatilis*), wiper (white bass [*M. chrysops*] x striped bass hybrid), and walleye (*S. vitreus*); other species reared in state hatcheries include crappie (*Pomoxis* spp.) and northern pike (*Esox lucius*) (U.S. Fish and Wildlife Service 2005). Special fishing-related programs offered by the KDWP are a trout program, an urban fishing program, the Fishing Forecast, and an up-to-date fishing report.

Kansas State hatcheries do not produce rainbow trout, but the KDWP does stock and manage this species

in selected waters throughout the state. Rainbow trout stocked in the Cimarron National Grassland are introduced to impounded waters or fishing pits. In the 1950's, the fishing pits were hand dug for the purpose of attracting waterfowl; they were later stocked with rainbow trout and other game fishes as recreational fishing interest increased (Chappell 2006). During the summer months, these fishing pits are stocked with channel catfish, bass, and grass carp (also known as white amur); rainbow trout from a hatchery near Boulder, Colorado are introduced in the fall to further diversify the angling experience and to provide a winter fishery (Progress and Management Report 2005, provided by Lowell Aberson). Planted trout rarely survive into the hot summer months because of high fishing pressures and high temperatures; the pits are isolated from the Cimarron River and thus are occasionally dry under drought conditions. The Kansas trout season runs from October 15 to April 15, with a daily creel limit of five trout and 15 total trout in possession. The state record rainbow trout, 9 lb. 5 oz. and 28-¼ inches long, was captured on a crappie jig in Lake Shawnee by Raymond Deghand on November 14, 1982.

USFS Region 2 manages 352,000 acres among three areas in Nebraska, the Nebraska and Samuel R. McKelvie national forests and the Ogallala National Grassland. The Nebraska Game and Parks Commission (NGPC) regulates fishing throughout the state.



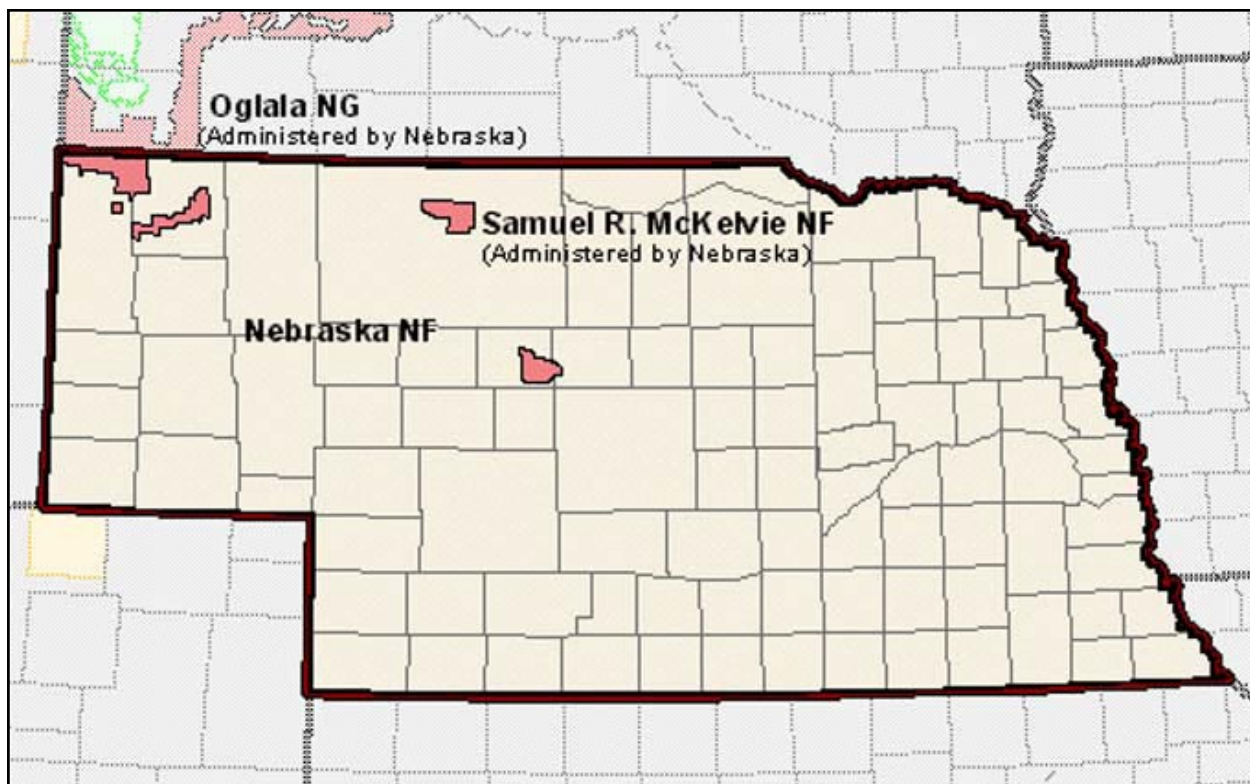
Nebraska is well known for its reservoir fishing. Lake McConaughy near Ogallala (30,000 acres when full), Lewis & Clark Reservoir on the South Dakota border (30,000 acres when full), and Harland County Reservoir in south-central Nebraska (13,500 acres when full) are the largest reservoirs in the state (**Figure 2c**). In addition, smaller irrigation reservoirs in western and central Nebraska and flood-control reservoirs in eastern Nebraska provide excellent fishing opportunities, as do many farm ponds and sand pits across the state. Nebraska also boasts over 1,300 natural lakes, most of them in the Sandhills in north-central Nebraska; however, many of these are surrounded by private land without regular public access (Nebraska Wildlife Federation: <http://www.nebraskawildlife.org/>). Nebraska anglers also fish a range of small streams in the northern and western parts of the state, as well as major rivers including portions of the Missouri, Niobrara, Platte, and Republican rivers.

While larger man-made waters, such as Lake Ogallala and the Sutherland Supply Canal, provide blue-ribbon rainbow trout fisheries, most of Nebraska's trout-supporting habitats flow through private land in the northern and western parts of the state. Private waters include, but are not limited to, flowing waters (excluding the Missouri River), private natural lakes,

privately constructed lakes, private sandpits, and private farm ponds. Thus, many quality trout fishing areas lack public access and require permission from landowners to enter.

More than 100 species of fish live in Nebraska, almost all of which can be identified with the Nebraska Game and Parks Commission's superb online and interactive Fish Identification Guide.

The Commission operates four fish hatcheries and one coldwater rearing station that produce warm-, cool-, and coldwater fish species for stocking in various sections of the state. There are no National Fish Hatcheries in Nebraska. Warm- and coolwater species commonly requested by regional managers include northern pike, muskellunge (*Esox masquinongy*), tiger musky (northern pike x muskellunge hybrid), walleye, largemouth bass, bluegill, channel catfish, white bass, crappie, bluegill x green sunfish (*Lepomis cyanellus*) hybrids, redear sunfish, and yellow perch (*Perca flavescens*); all of these are stocked as fingerlings, advanced fingerlings, or sub-adults. Hybrid species such as wiper (striped bass x white bass) are also popular with anglers who enjoy the aggressiveness and sport the hybrids provide. In 2005, Nebraska hatcheries produced almost 6.9 million fish, including roughly



**Figure 2c.** National Forests and Grasslands of Nebraska. From: <http://www.roadless.fs.fed.us/states/ne/state3.shtml>.

304,000 rainbow trout and 12,500 brown trout (U.S. Fish and Wildlife Service 2005). The remaining species and hybrids produced were black crappie (*Pomoxis nigromaculatus*), blue catfish (*Ictalurus furcatus*), bluegill, channel catfish, grass carp, hybrid striped bass (wiper), largemouth bass, muskellunge, northern pike, pallid sturgeon, rock bass (*Ambloplites rupestris*), sauger, walleye, white bass, and yellow perch.

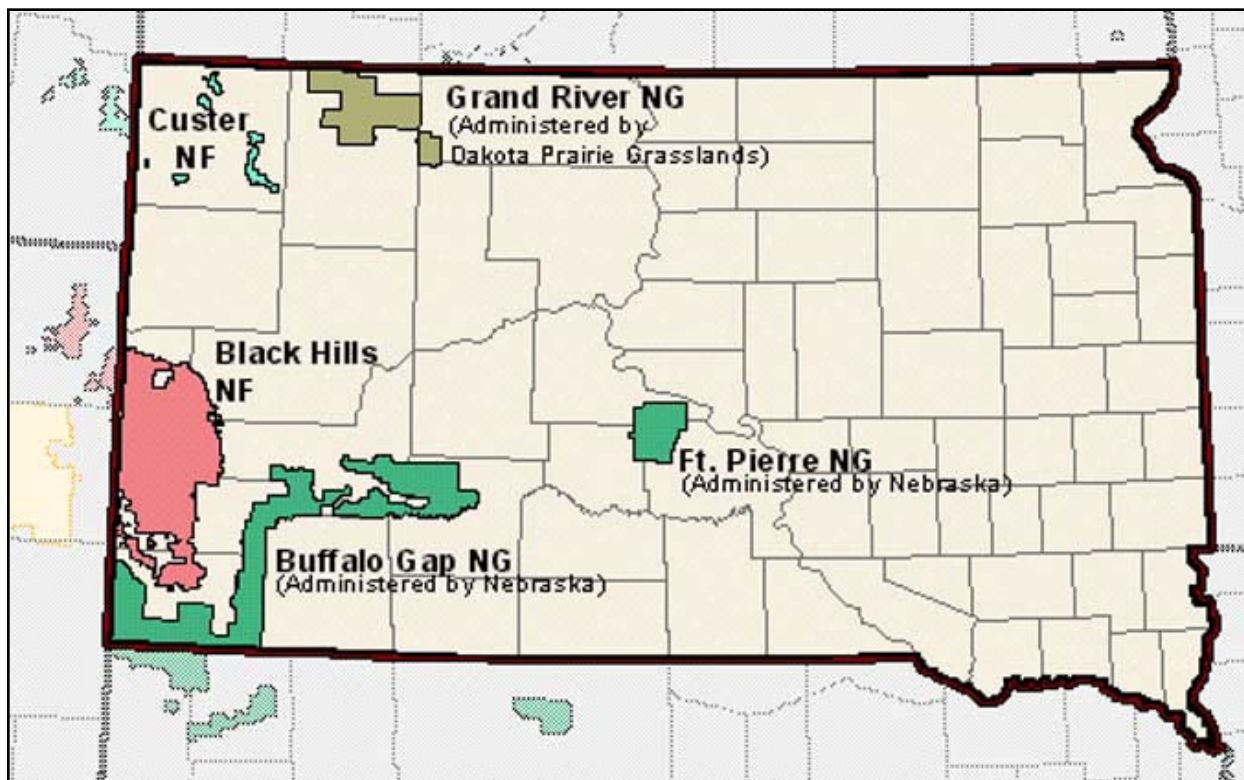
Although relatively few are produced in state hatcheries, rainbow trout are popular in Nebraska, and the NGPC stocks and manages coldwater trout fisheries throughout the state. Most trout are stocked as catchables (9 to 11 inches) and are placed in rivers, streams, and lakes to provide angling for both rural and urban fishing programs. The NGPC currently stocks rainbow trout at two popular put-and-take recreation areas (Two Rivers State Recreation site and Lake Ogallala), as well as in Panhandle ponds and pits. The daily bag and possession limits for trout (all species) are seven and 14, respectively.

While some quality trout fishing areas in Nebraska offer public access, many are private waters and can be accessed only through private waters management ([www.ngpc.state.ne.us](http://www.ngpc.state.ne.us)). The NGPC does provide assistance for private landowners in developing

and restoring trout habitats as well as in performing fish community assessments and private waters stocking programs. Furthermore, across the state, the NGPC has 1) improved aquatic habitat through an Aquatic Habitat Program funded in part by a state Aquatic Habitat Stamp, 2) been active in aquatic education programs, and 3) developed a Master Angler program that includes a special award for catch-and-release fishing. State size records are maintained for a wide array of species and hybrids, and in many cases, information is provided for previous as well as present records. The rainbow trout state record was harvested by Frank Aloy in 1975 on a nightcrawler bait; it weighed 14 lb. 2 oz.

Region 2 of the USFS manages three areas within South Dakota: the Black Hills National Forest and the Buffalo Gap and Fort Pierre national grasslands. The Custer National Forest and Grand River National Grasslands are administered by Region 1 of the Forest Service. The South Dakota Game and Fish Department (SDGFD) has primary responsibility for managing the state's fish resources.

South Dakota encompasses over 700,000 acres of public fishing waters, including 450 public fishing lakes and 10,000 miles of streams and rivers managed for recreational fishing (**Figure 2d**). Eight major tributary



**Figure 2d.** National Forests and Grasslands of South Dakota. From: <http://www.roadless.fs.fed.us/states/sd/state3.shtml>.

rivers (the largest include the Cheyenne, Missouri, James, and White rivers) and the Missouri River provide abundant fishing opportunities, as do the smaller streams from the Black Hills in the west to the Prairie Coteau in the east. In the western third of the state, the Black Hills offer 14 mountain lakes and more than 400 miles of streams containing brook, brown, and rainbow trout. On the surrounding prairie, reservoirs and more than 50,000 stock ponds (many on private land) also provide angling opportunity for largemouth bass, northern pike, and a variety of panfish. Most fishing is concentrated in Missouri River impoundments in the middle of the state and away from major population centers. Four massive dams on the Missouri River have created more than 900 square miles of open water, 3,000 miles of shoreline, and a world-class freshwater fishery. Prairie stock ponds ranging from 1 to 100 acres also dot the central part of South Dakota. More than 120 glacial lakes ranging in size from several acres to more than 17,000 acres occur in the northeastern part of the state. Southeastern South Dakota has more than 175 fishing lakes ranging in size from 3 to 29,000 acres; some of these are glacial lakes while many are manmade lakes constructed for water conservation and irrigation. Three major rivers course through the southeastern region as well: the Big Sioux River, the James River, and the Missouri River, which includes Lewis and Clark Lake, a 30-mile-long Missouri River reservoir.

The SDGFD lists 108 species of fishes (in 23 families) as occupants of South Dakota waters; 36 of these are listed as rare and thus of special concern. As support for its programs, the Department operates four fish hatcheries, one of them primarily a salmon (especially chinook) spawning and imprinting station. The USFWS also operates a National Fish Hatchery in the state where fish are reared for use in the Missouri River system. In 2005, state and Federal hatcheries produced more than 56 million fish (U.S. Fish and Wildlife Service 2005). Slightly less than 666,000 of these were coldwater species and hybrids, dominantly rainbow trout and fall chinook salmon, but also including brown trout, lake trout, and splake. The remaining warm- and coolwater fishes included black crappie, bluegill, largemouth bass, muskellunge, paddlefish, pallid sturgeon, smallmouth bass, walleye and yellow perch, and 54 million (96.7 percent) of these were walleye! Two years later, in 2007, South Dakota stocked almost 51 million fish. Lake trout, muskellunge, pallid sturgeon, and splake were no longer raised, and black bullhead, brook trout, fathead minnows, northern pike, and redear sunfish had been added. Coldwater fish were represented by 379,000 brook trout, brown trout,

chinook salmon, and rainbow trout while once again walleye dominated (98.7 percent) all stocked fish.

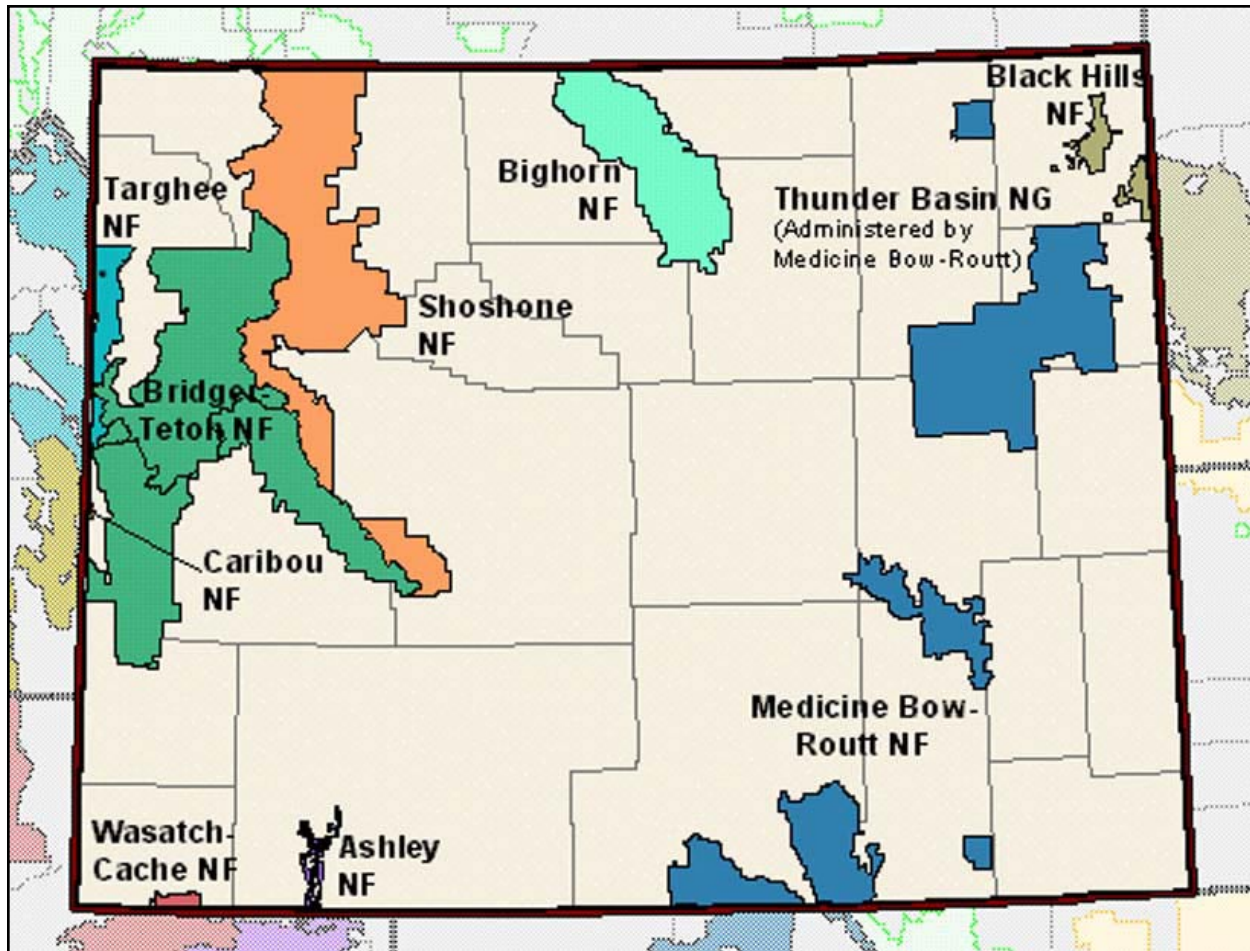
Clearly, rainbow trout have only regional importance in a state known for its diverse warmwater fisheries. Nonetheless, carefully crafted regulations governing the take of trout, salmon, and their relatives (e.g., splake, whitefish, lake herring) differ from place to place. For example, on the Missouri River, the daily bag and possession limits are five and 10, respectively; in Nebraska-South Dakota border waters, these limits are seven and seven; on western rivers, five and 10; and in the Black Hills, five and 10. In the Black Hills Trout Management Area, only one 14" or longer trout may be included in the daily creel, the SDGFD prohibits highgrading of any trout species, and several specific locations are catch and release only, with gear restricted to artificial lures only. South Dakota maintains state records for 62 species and hybrids. The state record rainbow trout was taken on July 4, 1980 from the Lake Oahe tailwaters by Tom Moore; it weighed 19 lbs. 4 oz.

Wyoming fishing opportunities on National Forest System lands in Region 2 span 5,365,500 acres of the Bighorn, Medicine Bow-Routt [also see Colorado, above], Shoshone, and portions of the Black Hills national forests and the Thunder Basin National Grassland (USDA 2006) (**Figure 2e**). The Ashley, Caribou-Targhee, Bridger-Teton, and Wasatch-Cache national forests are administered by Region 4 of the Forest Service. These areas provide excellent angling opportunities in a range of aquatic systems, including rivers, streams, alpine lakes, and reservoirs. Additional opportunities exist throughout the state. Major waterways include the Bighorn, Green, Belle Fourche, Powder, and North Platte rivers.

The Forest Service primarily manages aquatic habitat, while the Wyoming Game and Fish Department is responsible for managing fish populations on National Forest lands. The Wyoming Game and Fish Department provides quality fishing opportunities to the public, improves aquatic habitat for game and non-game fishes, and seeks to restore historic populations of native fishes. Management information and regulations (Wyoming Game and Fish Commission 2008a) are provided for five drainage areas in Wyoming:

- ❖ Area 1: Snake River, Salt River, Greys River, Hoback River, Gros Ventre River and Buffalo Fork River Drainages and all drainages west of the Teton and Snake River Ranges.





**Figure 2e.** National Forests and Grasslands of Wyoming. From: <http://www.roadless.fs.fed.us/states/wy/state3.shtml>.

- ❖ Area 2: Wind River, Bighorn River, Shoshone River, Clarks Fork and Yellowstone River Drainages.
- ❖ Area 3: the Niobrara River, Cheyenne River, Stockade-Beaver Creek, Sand Creek, Belle Fourche River, Little Missouri River, Little Powder River, Powder River, Tongue River, and Little Bighorn River Drainages.
- ❖ Area 4: Green River, Little Snake River, Bear River and Great Divide Basin Drainages.
- ❖ Area 5: North Platte River, Sweetwater River and South Platte River Drainages.

Although general regulations exist for segments of all these areas, there are many clearly-stated exceptions for segments of these various drainages, reflecting considerable care in managing local conditions. Such detail relies heavily on the angler to know both local

regulations and where she/he may be in what is often wild country.

The array of fishes identified as game fish and for which creel limits are established reflects the diversity of aquatic habitats encountered in Wyoming: largemouth, smallmouth, and rock bass (*Micropterus*, *Ambloplites*); bluegill, pumpkinseed, green sunfish, green sunfish-bluegill hybrid (*Lepomis*); crappie (*Pomoxis*); walleye and sauger (*Sander*); yellow perch (*Perca*); salmonids (including brook trout, brown trout, cutthroat trout, golden trout, lake trout, rainbow trout, salmon, splake, tiger trout, other trout hybrids; *Salmo*, *Oncorhynchus*, *Salvelinus*); whitefish (*Prosopium*); grayling (*Thymallus*); northern pike and tiger musky (*Esox*); catfish, bullheads, stonecats (*Ameiurus*, *Ictalurus*, *Noturus*, *Pylodictis*); ling/burbot (*Lota*); shovelnose sturgeon (*Scaphirhynchus*); and, freshwater drum (*Aplodinotus*). In 2005, Wyoming's public hatcheries produced 4.9 million fish (U.S. Fish and Wildlife Service 2005). Trout, kokanee, splake



and grayling constituted 3.8 million (78 percent) of that total, roughly 2 million of which were rainbow trout. Largemouth bass, northern pike, and walleye contributed less than 1.1 million of the total, and these were dominated by walleye (847,100). The vast majority of rainbow trout (almost 1.6 million) were produced for fingerling stocking, reflecting the state's long-standing move toward put-grow-take fisheries and establishment of self-sustaining populations (Wiley 2003a).

Historically, many of Wyoming's high mountain lakes were fishless due to isolation from lowland streams as a result of uplifting and glacial activity that formed these lakes (Wiley 2003b). Many high elevation lakes provide coldwater fish habitat and have been or are stocked and managed by the WGFD.

In 1999, the WGFD, after an extensive review process (described in Annear et al. 1999), shifted to a coldwater stream fishery ranking system based on quantifiable and readily available data from one relying on the highly subjective variables of aesthetics, accessibility, and productivity (**Table 1**). The revised system, based on estimated pounds of game fish per mile, ranks coldwater streams as blue-, red-, yellow-, and green-ribbon fisheries (in declining order of fish density), is far more informative and easier for the angle to understand than the implications or basis of the previous system.

In general, the creel limit in Wyoming for "trout" (combination of brown trout, cutthroat trout, grayling, golden trout, lake trout, rainbow trout, salmon, splake, tiger trout, and other trout hybrids) is 6, no more than one of which exceeds 20 inches. An exception is made for brook trout, for which the limit is 16, no more than six of which exceed 8 inches. The Wyoming rainbow trout state record was harvested by Frank Favazzo in 1969 in Burnt Lake, Sublette County; it weighed 23 lbs. and was 35-½ inches long.

## Biology and Ecology

### Systematics

Many names have been applied to rainbow trout since they were first described in 1792 (**Table 2**). The short history of this nomenclature provided here should serve management personnel in at least two ways. First, it should reduce confusion over the recent dynamics in the trout's scientific name and demonstrate how taxonomists work to have names indicate evolutionary relationships. Second, it will help newcomers to the field find important information about the species published under different names (especially *Salmo gairderi*).

The rainbow trout (*Oncorhynchus mykiss*) belongs to the Class Actinopterygii, Order Salmoniformes, and Family Salmonidae (including trout, salmon, char, whitefish, grayling). The earliest fossil salmonid, *Eosalmo driftwoodensis*, dates from roughly 50 million years ago and was described in 1977 from Eocene beds in British Columbia (Wilson and Li 1999). Within the family, the genera *Salmo* and *Oncorhynchus* diverged from a common ancestor during the Miocene 15 to 20 million years ago (mya), with *Oncorhynchus* in the North Pacific Ocean and *Salmo* in the North Atlantic Ocean. Toward the end of the Miocene (ca. 5 mya), *Oncorhynchus* evolved both salmon-like and trout-like species, with the latter giving rise to cutthroat and rainbow (or redband) lineages toward the end of the Pliocene (ca. 2 mya). Fossils from the ice ages and interglacial periods of the later Pliocene through the Pleistocene (2.5 million to 10,000 years ago) record members of the rainbow trout lineage as far south as southwestern Mexico (Behnke and Tomelleri 2002, Hendrickson et al. 2002). Of more immediate interest, however, and indicative of the incredible ecological flexibility of fishes in the rainbow trout lineage, are the recent discovery and rediscovery of several poorly known trout taxa in mountain drainages

**Table 1.** Wyoming Game and Fish state-wide trout stream classification system. (Annear et al. 1999)

Category	Percent of Stream Miles	Pounds of Sport Fish per Mile
Blue Ribbon	2.3	≥ 900
Red Ribbon	4.8	≥ 500 and < 900
Yellow Ribbon	46.1	≥ 100 and < 500
Green Ribbon	46.8	≥ 1 and < 100
Orange Ribbon	unknown	Any cool/warm water game fish present

**Table 2.** Scientific nomenclature for rainbow trout. (Modified from FishBase, 2006.)

<i>Salmo mykiss</i>	Walbaum, 1792	original combination
<i>Onchorynchus mykiss</i>	(Walbaum, 1792)	present valid name
<i>Onchorrhynchus mykiss</i>	(Walbaum, 1792)	misspelling
<i>Oncorhynchus myskis</i>	(Walbaum, 1792)	misspelling
<i>Parasalmo mykiss</i>	(Walbaum, 1792)	new combination
<i>Salmo penshinensis</i>	Pallas, 1814	junior synonym
<i>Salmo purpuratus</i>	Pallas, 1814	junior synonym
<i>Parasalmo penshinensis</i>	(Pallas, 1814)	junior synonym
<i>Salmo gairdneri</i>	Richardson, 1836	junior synonym
<i>Salmo gairdnerii</i>	Richardson, 1836	junior synonym
<i>Salmo gairdnerii gairdnerii</i>	Richardson, 1836	junior synonym
<i>Fario gairdneri</i>	(Richardson, 1836)	junior synonym
<i>Oncorhynchus gairdnerii</i>	(Richardson, 1836)	other
<i>Salmo rivularis</i>	Ayres, 1855	junior synonym
<i>Salmo gairdneri irideus</i>	Gibbons, 1855	junior synonym
<i>Salmo gairdnerii irideus</i>	Gibbons, 1855	junior synonym
<i>Salmo iridea</i>	Gibbons, 1855	junior synonym
<i>Salmo irideus</i>	Gibbons, 1855	junior synonym
<i>Trutta iridea</i>	(Gibbons, 1855)	junior synonym
<i>Salmo truncatus</i>	Suckley, 1859	junior synonym
<i>Salmo masoni</i>	Suckley, 1860	junior synonym
<i>Salmo kamloops</i>	(Jordan, 1892)	junior synonym
<i>Salmo rivularis kamloops</i>	(Jordan, 1892)	junior synonym
<i>Oncorhynchus kamloops</i>	Jordan, 1892	junior synonym
<i>Salmo gairdneri shasta</i>	Jordan, 1894	junior synonym
<i>Salmo gilberti</i>	Jordan, 1894	junior synonym
<i>Oncorhynchus mykiss nelsoni</i>	Evermann, 1908	junior synonym
<i>Salmo nelsoni</i>	Evermann, 1908	junior synonym
<i>Salmo irideus argentatus</i>	Bajkov, 1927	junior synonym
<i>Salmo kamloops whitehousei</i>	Dymond, 1931	junior synonym

The species was initially described in *Salmo*, a genus erected by Linnaeus for the Atlantic salmon. Subsequent names reflect the best estimates of relationships at the time. When authorities are given in parentheses, it indicates that the species was previously described by that author but with a different name.

of northwestern Mexico (states of Chihuahua, Sonora, Durango, Sinaloa; see [http://www.utexas.edu/tmm/tnhc/fish/research/truchas\\_mexicanas/](http://www.utexas.edu/tmm/tnhc/fish/research/truchas_mexicanas/) and <http://www.americanfishes.com/mexico/>).

The genus *Oncorhynchus* includes 10 or 11 species and about 30 subspecies worldwide (Nelson 2006). The name was first applied by Suckley in 1860 to the males (only) of pink salmon (*O. gorbuscha*), which was originally described as *Salmo gorbuscha* by Walbaum (1792). *Oncorhynchus* was, therefore, the earliest applicable genus when biologists recognized the distinct nature of Pacific salmon.

To understand the history of scientific names applied to rainbow trout, one must turn to the “Law of Priority” established in the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature 1999). With rare exception, this means that the earliest available name becomes the accepted name.

*Salmo*, erected by Linnaeus in 1758 for the Atlantic salmon, was the first valid name in the Family Salmonidae. The rainbow trout was originally named *S. mykiss* by Walbaum in 1792 from fish captured on the Kamchatka peninsula of Siberia (Behnke 1992).

Richardson subsequently applied the name *S. gairdneri* to steelhead (sea-run rainbow trout) collected from the Columbia River at Fort Vancouver in 1836 (McPhail and Lindsey 1970, Moyle 2002), considering them to be different from the Kamchatka fish. In 1855, Gibbons described juvenile steelhead from a tributary of San Francisco Bay as *S. irideus*. Because *S. gairdneri* had priority, *S. irideus* became invalid (a “junior synonym”) as a species name; it is, however, retained in the common name (*irid-*, G., rainbow) and as a subspecies name for Coastal rainbow trout (*Oncorhynchus mykiss irideus*). Subspecies represent geographic variants that exhibit somewhat distinct characteristics from other members of a species elsewhere, yet do not warrant elevation to full species status.

Similarities in morphology and life history characteristics between the western rainbow trout and the brown trout and Atlantic salmon of the eastern United States and Europe led to retention of Richardson’s name until 1989, when anatomical and molecular studies demonstrated closer affinities between rainbow trout and Pacific salmon (genus *Oncorhynchus*; Behnke and Tomilleri 2002) than with the eastern species of *Salmo*. Similarly, recognition that the Kamchatka trout and western North American rainbow trout, now more correctly included within the genus *Oncorhynchus*, did not warrant separate species status led to the reapplication of the law of priority and return to the earliest available species name (*mykiss*) and the emergence of the new combination, *Oncorhynchus mykiss*, as the valid name for rainbow trout.

### Species description

Salmonids can generally be distinguished by the presence of a fusiform body, forked tail, adipose fin (a fleshy fin without internal supports along the midline of the back between dorsal fin and tail), and an enlarged fleshy or scaly process (axillary scale or process) at the base of each pelvic fin (Moyle 2002, Nelson 2006). The closely related smelts (Osmeridae) also possess an adipose fin but lack the axillary process, while North American catfishes (Ictaluridae) possess an adipose fin but lack scales and have distinct barbels on the chin.

The body of a rainbow trout is usually elongate, becoming somewhat deeper and compressed in larger fish (Moyle 2002, Nelson 2006). The mouth is large and terminal, with the upper jaw usually extending to or beyond the rear margin of the eye. Teeth are borne on upper and lower jaws, vomer, palatines, and tongue. Adult rainbow trout tend to be silvery in background color, with black spots on the back as well as on the

dorsal, adipose, and caudal (tail) fins, and a band of pink to red along the sides. The back is often dark blue to brown, the lower sides and belly silvery white to light yellow. Coloration varies with habitat, size, and sexual condition. Stream residents and spawners tend to be darker, with more intense colors, while lake residents tend to be lighter, brighter, and more silvery. Juveniles often exhibit 5 to 13 dark, oval “parr marks” along the side and light tips to dorsal and anal fins. The fins (except the adipose) are supported by segmented, branched soft rays (no true spines); specific fin ray counts include: dorsal 10 to 12, caudal (tail) 19, anal 8 to 12, pelvic 9 to 10, and pectoral 11 to 17. Scales are small and easily removed, with 110 to 160 pored scales along the lateral line, 18 to 35 scale rows above the lateral line, and 14 to 29 rows below it. There are 9 to 13 branchiostegal rays.

### Salmonid life history characteristics

Conservation and management practices for salmonids must consider the complexity of life histories characteristic of these fishes, particularly when maintenance of self-sustaining populations is desired. The reason for such concern is simply that distinct life history stages must be considered as distinct ecological entities, each with its own habitat requirements, capabilities, tolerances, and ecological pressures. Failure to ensure availability of stage-specific habitats reduces the likelihood that self-sustaining populations may be established or maintained.

The life history stages of naturally reproducing trout and salmon, including rainbow trout, with definitions and general comments about their environments and characteristics, include:

**Egg** – laid in depressions (redds) dug in spawning gravels by females; potentially susceptible to predation by interstitial invertebrates; normal development requires free percolation of water through the surrounding gravel, or at least relatively high humidity (exposure of eggs in redd s did not greatly reduce viability or otherwise affect development of chinook salmon and steelhead eggs, provided temperatures were moderate and the substrate retained a moisture content of at least 4 percent (Reiser and White 1983)); fertilization to hatching time varies with water temperature but is about 370 degree days (ca. 100 days at 3.9 °C and 21 days at 14.4 °C [FAO Fisheries and Aquaculture Department, rainbow trout fact sheet]).

**Alevin/sac-fry** – hatchlings usually remain in the gravels two to four weeks depending on temperature (Raleigh et al. 1984, FAO Fisheries and Aquaculture Department, rainbow trout fact sheet) and rely on yolk for nutrition; highly susceptible to exposure, probably a result of very high surface/volume ratio, simple epithelium and lack of scales (exposure with associated desiccation causes high mortality among sac fry (Reiser and White 1983, Montgomery and Tinning unpublished)); susceptible to attack by interstitial invertebrates, fungi, microbes, etc.; transition from this stage to the next involves critical events, including movement of the young fish to the surface through interstitial spaces among the gravels, “swim-up” to gulp surface air and initially fill the gas bladder, movement to slow-moving water near shore, and initiation of exogenous feeding.

**Fry** – post-emergence, free-swimming, free-feeding stage; feed primarily on small invertebrates; generally occupy shallow, warm, still or low velocity waters near shore where they establish and defend territories (reviewed in Gerking 1994); variously mottled color patterns; susceptible to a variety of terrestrial and aquatic predators as well as competition from both salmonid and non-salmonid fishes (e.g., Hayes 1989; Gaudreault et al. 1986 described aggression between juvenile brook charr [*Salvelinus fontinalis*], and adult ninespine sticklebacks [*Pungitius pungitius*]); tendencies to move from cover at night may increase exposure to predators and stronger currents (see Fausch et al. 2001 regarding rainbow trout fry displacement in current; increases of as little as 4 to 14 cm per sec in water velocity displaced brown trout fry downstream at night [Heggenes 1988, Heggenes and Traaen 1988]); in streams, fry prefer shallower water and lower velocities than do other life stages of stream-dwelling trout; once fry move from natal gravels to rearing areas, they tend to exhibit three distinct genetically influenced movement patterns: downstream movement to a larger river, lake or to the ocean; upstream movement from an outlet river to a lake; local dispersal from natal spawning grounds to rearing areas (Raleigh et al. 1984).

**Parr/juvenile/fingerling** – sexually immature individuals larger than fry, usually with parr marks (dark, oval marks) along their sides; occupy and defend feeding territories in moving water

along sides of stream reaches or in eddies, but frequently move into shallow, slow-moving water at night; feed primarily on aquatic invertebrates and allochthonous drift; susceptible to a variety of predators and competitors depending on habitat; different species of salmonids may exhibit parr characteristics for one to several years, and parr marks may be retained by adults in small streams; “fingerling” is often used by managers and culturists concerned more with size than color patterns; in many salmonids, male fish of this age/size may mature sexually and use “sneak” tactics to spawn with adult females (this pattern is best known in Atlantic salmon (*Salmo salar*), chinook salmon, and some other salmon species [Montgomery et al. 1987]), but also occurs in steelhead and perhaps other rainbow trout stocks (Schmidt and House 1979) and may have significance for reproductive biology of naturally spawning populations in Region 2.

**Smolt** – juvenile steelhead or salmon moving or preparing to move downstream to the sea; transition usually accompanied by increased silvering of the body with near-obliteration of previous colors and parr marks, enlargement of pectoral and other fins, and increased forking of the tail; entry into sea water involves changes in ion exchange pumps in gills and other physiological adjustments; some rainbow trout in lakes and reservoirs lack a physiological smolt stage, but exhibit movements and life history similar to steelhead. (e.g., juvenile rainbow trout migrate from natal streams to lake or reservoir, instead of ocean, for rearing [Raleigh et al. 1984]).

**Adult** – reproductive or potentially reproductive fish; occupy wider ranges of stream or lake habitats than fry or parr; feed on aquatic invertebrates, drift, and occasionally small fish; like parr and fingerlings, are susceptible to a variety of predators and competitors depending on habitat, size, etc.

## Distribution and abundance

All populations of rainbow trout in Region 2 have been established through stocking of fish from their native range (**Figure 3**) or from hatchery stocks whose origins trace to animals taken from the native range. The native range of *Oncorhynchus mykiss* includes cool waters of the Pacific Rim, from northern Baja California to eastern Asia as far south as the Amur River and Sakhalin Island, although these southern



**Figure 3.** Native distribution of rainbow trout in the United States. Green – current distribution, red, historic distribution NatureServe 2006.

records may be due to straying by steelhead (the sea-run form of rainbow trout) from well-established Kamchatka Peninsula populations (Fishbase 2006). In North America, rainbow trout are native to Pacific coast streams from the Kuskokwim River, Alaska, south to northern Baja California, upper Mackenzie River drainage (Arctic basin), Alberta, and British Columbia, and endorheic basins of southern Oregon (**Table 3**; Page and Burr 1991).

#### Population trends (local, regional, and rangewide)

The range and population sizes of rainbow trout are declining in various parts of their native range while expanding in other areas due to stocking (NatureServe 2006). For example, within their native range, steelhead populations from Southern California and the Upper Columbia River are listed as Endangered, while those from the Central and South-Central California Coast, Snake River Basin, Lower Columbia River, California Central Valley, Upper Willamette River (winter run),

and Middle Columbia River are Threatened. Even the McCloud River redband trout, the fish from which most modern hatchery stocks have been derived, is a candidate for listing under the Endangered Species Act.

In stark contrast to the declines of many native rainbow trout stocks is the continuing expansion of their range by introductions throughout the world; this may be regarded as global in its present distribution (Fishbase 2006). As noted elsewhere in this assessment, rainbow trout, particularly derivatives of the McCloud River redband trout from California (Hedgpeth 1991), have been reared in hatcheries since the middle of the 19th century. Fish from those hatcheries have been distributed into coolwater systems in North America (**Figure 4**), South America, Europe, Asia, Africa, and Australia, as well as a number of smaller, non-continental land masses (e.g., New Zealand; MacCrimmon 1971). In Canada, the rainbow trout occur outside British Columbia from the Avalon Peninsula of Newfoundland, across the southern portions of the provinces from Nova Scotia to Ontario, north to central Manitoba, to northern

**Table 3.** Original ranges and subspecies considered within *Oncorhynchus mykiss*.

**Rainbow trout of coastal basins**

Kamchatkan rainbow trout *Oncorhynchus mykiss mykiss*\*  
Coastal rainbow trout *Oncorhynchus mykiss irideu*\*

**Rainbow trout of the mid- and upper Columbia and Fraser River basins**

Columbia River redband trout *Oncorhynchus mykiss gairdneri*\*

**Redband trout native to six internal basins of the Northern Great Basin, plus the Upper Klamath Lake basin**

Redband trout of the Northern Great Basin *Oncorhynchus mykiss newberrii*

**Redband trout of the northern Sacramento River basin**

Sacramento redband trout *Oncorhynchus mykiss stonei*

**Three subspecies of trout native to the Kern River basin**

California golden trout *Oncorhynchus mykiss aquabonita*  
Kern and Little Kern golden trout *Oncorhynchus mykiss gilberti*  
Upper Klamath redband trout *Oncorhynchus mykiss newberrii*

**Rainbow-like trout native to Baja California and the Rio Yaqui, Rio San Lorenzo, and Rio del Presidio drainages of Mexico (tributaries to the Gulf of California).**

Baja California rainbow trout *Oncorhynchus mykiss nelsoni*

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\*taxa that include sea-run (anadromous) trout. The term steelhead is often applied to anadromous forms of *Oncorhynchus mykiss*, but is not endorsed by Nelson, et al. 2004. (From Behnke 1992, 2002)

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Alberta, and in the Yukon. No other coolwater sport and food fish has experienced such a purposeful expansion of range.

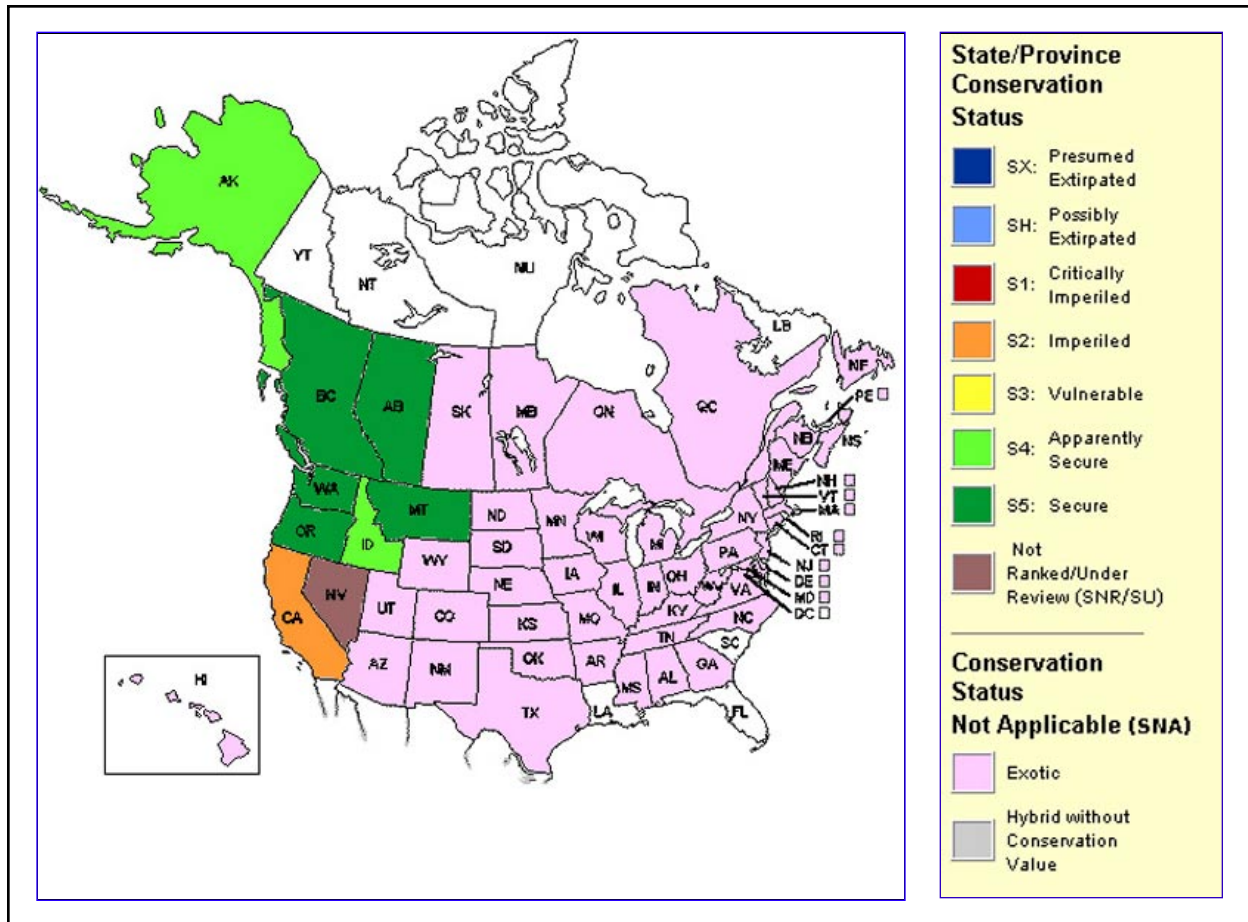
**Activity patterns**

Much is known about the activity patterns of wild, self-reproducing, and introduced rainbow trout. Some aspects of their behavior are described in greater detail elsewhere in this assessment (e.g., sections on feeding, reproduction). Here we focus on movements, particularly of adults, at various scales.

Rainbow trout are primarily diurnally active, with feeding peaks normally during crepuscular periods. During the day, they tend to remain within a confined area of a stream or lake, but may move from areas of low to high food density or from rapidly flowing water with higher food supply to resting areas with reduced flow. Because of such behavior, stream-dwelling trout have often been considered to be sedentary and to have relatively small home ranges (Mellina et al. 2005, Rio Grande SCP2005). However, recent studies demonstrate that long range movements are common in stream-dwelling trout and that experimental and observational bias have favored recording of sedentary behavior, with

insufficient sampling of wide-ranging individuals. Fish exhibit both types of behavior (Mellina et al. 2005), with the importance and timing of environmental cues as well as the genetic influences (Behnke 1992) in promoting movement varying from stream to stream. Thus, both sedentary and movement types of behavior are likely to be found within any given population, although the frequency of these behaviors varies considerably among streams and among individual fish as they alter their responses to changing conditions. In British Columbia, for example, movement by stream-dwelling trout was stimulated by decreases in dissolved oxygen levels and/or by increases in sedimentation during road construction (Mellina et al. 2005).

An additional pattern of movement common to rainbow trout and many other species of salmonids (e.g., Pacific and Atlantic salmon, brook trout, brown trout, Arctic charr) is migration to and from oceans, lakes, or other distant locations in streams. Such migrations may take fish to richer feeding areas in oceans or lakes or to areas with more suitable or abundant spawning substrates. Rainbow trout that undertake such migrations to the sea have been termed steelhead, and genetically based differences in behavior of anadromous and stream-dwelling trout have enabled



**Figure 4.** Distribution and conservation status of rainbow trout in the United States. NatureServe 2006.

both lineages to coexist without hybridizing (Behnke 1992). Coastal cutthroat trout, coastal rainbow trout, inland redband trout (rainbow trout), and rainbow trout coexist by maintaining reproductive isolation by choosing different preferred habitats throughout all life stages (Behnke and Tomelleri 2002). The longest known spawning migrations by native steelhead trout returning to their natal grounds to spawn extended from the almost 1,600 km from the sea to the upper Columbia River, British Columbia, and to the upper Snake River near Twin Falls, Idaho. Both these runs have been largely blocked by dams, with accompanying major declines or extirpation of native sea-run fish and an apparent loss of genetic variation once present in such fish.

Because native stream-dwelling trout, like most other non-anadromous trout, generally lack a strong hereditary basis for directed movement (Behnke 1992), migrations of landlocked fish between streams and lakes are often attributed to fish stocked from populations derived from steelhead. In such populations, long-range movement occurs regularly, is directional between two

or more well separated habitats, and a large fraction of the population participates (Mellina et al. 2005).

Migrations are initiated by spatial changes in stream or lake conditions as well as by seasonal effects on behavior of fish. For example, in Nebraska, nonnative rainbow trout of Lake McConaughy migrate 145 km or more upstream in the North Platte River to suitable tributaries for spawning (Behnke and Kloppel 1975, Behnke 1992). In spring, a relatively large lakeward migration is followed by a period of restricted movements throughout the summer and autumn, followed by movements to overwintering habitats.

Adults are not the only life history stage to move. Increased temperatures in spring will initiate movements by juveniles from streams to lakes. Lentic habitats often provide greater thermal stability and abundant food and habitat resources needed for growth and survival. In the summer months, trout primarily focus on feeding, and this behavior determines their distribution in streams and lakes; in the winter, fish focus on overwintering in larger, deeper areas (Mellina et al. 2005).



Hatchery (catchable and subcatchable) fish may also influence movements of wild trout in streams. Stocking densities and rates of removal of hatchery trout by anglers will influence wild and stocked trout movements. The effects of hatchery fish on wild trout populations is of special importance to managers (Behnke and Tomelleri 2002) because while stocked fish compete for all the same resources as do wild trout, they can have lower reproductive success in nature and then be lost from the gene pool in as little as two generations (Skaala et al. 1990). Artificial density created by stocking should be neither high nor long lasting to minimize stress and/or displacement of wild trout populations (Behnke 1992).

## Habitat

Rainbow trout pass through several distinct life history stages (egg, alevin or sac fry, free-swimming fry, juvenile, adult), each with its own habitat requirements. Insufficiency or absence of habitat for any of the early life history stages will obviously depress recruitment into later stages.

Four general types of required habitat may be linked to the various stages of trout life history: spawning habitat, nursery or rearing habitat (including egg incubation, fry, and juvenile habitats), adult habitat, and overwintering habitat (Behnke 1992). For the purpose of this assessment and to better aid in management decisions, trout habitat has been broken down into the following six sections:

- ❖ Spawning habitat
- ❖ Egg incubation habitat
- ❖ Fry habitat
- ❖ Juvenile habitat
- ❖ Adult habitat
- ❖ Overwinter habitat

Rainbow trout are typically spring spawners, but spawning time differs in various locations, elevations, and among different hatchery-reared and various hybrid strains. Several factors are addressed separately in the following descriptions of suitable habitat for various life stages, but the reader should keep in mind that fish must respond to the combined effects of multiple physical, chemical, and biological variables in their respective environments. In self-sustaining populations, fish encounter all the important factors in a suitable, but usually not optimum, range of conditions capable of supporting each life history stage. The combination of factors should be of particular interest to managers since the mix sets the carrying capacity for that stream, and that capacity can be altered if one or more of the factors is altered (Bjornn and Reiser 1991).

## Spawning habitat

Spawning success is directly related to water quantity and quality, substrate composition, area of suitable substrate, and cover (**Table 4**). The number of spawning sites directly relates to the availability of suitable habitat. The amount of suitable stream substrate for spawning tends to increase with stream order (Bjornn and Reiser 1991).

**Streamflow:** Streamflow regulates the amount of spawning area available and water over gravel beds. As the snow pack melts in the spring, rivers rise and inundate additional spawning habitat. Flows may continue to increase to the point that velocities become too high for spawning and scour (see below) ensues, such that high streamflow then outweighs the benefits of increased water levels. High waters can decrease stream productivity, and thus relationships between flow and suitable substrate become important tools for managers. The USFWS developed an instream flow incremental

**Table 4.** Spawning habitat for western trout and kokanee salmon. (Adapted from Reiser and Bjornn 1979, Schuett-Hames and Pleus 1996, Morris and Caverly 2004, and Larsen (no date).)

Species	Water depth (m)	Water velocity (m/s)	Substrate size per (cm)	Ave. Size of Redd (m <sup>2</sup> )	Recommended Area Per Spawning Pair (m <sup>2</sup> )
Kokanee	0.061	0.2 - 0.7	small gravel*	—	—
Steelhead	0.244	0.4 - 0.9	0.5 - 10.2	4.4 - 5.3	17.6 - 21.2
Rainbow	0.244	0.5 - 0.9	0.5 - 5.1	0.2	0.8
Cutthroat	0.061	0.1 - 0.7	0.5 - 10.2	0.1 - 0.9	0.5 - 4.5
Brown	0.244	0.2 - 0.6	0.5 - 7.6	0.5	2
Small-bodied salmonids**	0.1	moving	0.8 - 6.4	—	1

\*Morris and Caverly 2004.

\*\*Schuett-Hames and Pleus 1996 – includes: resident rainbow, cutthroat, kokanee, brown, brook, bull trout and Dolly Varden.

methodology (IFIM) to estimate the amount of suitable habitat (Bjornn and Reiser 1991).

**Temperature:** Rainbow trout are able to spawn in temperatures ranging from ~2 to 20.0 °C (36 to 68 °F; Raleigh et al. 1984, Bjornn and Reiser 1991), but spawning is generally initiated when water temperature exceeds 6 to 7 °C (42 to 44 °F) regardless of geographic area (Behnke 2002). In wild, self-sustaining rainbow trout populations, spawning is often triggered when the fish move from colder to warmer waters of river or lake tributaries. Rainbow trout that spawn in lakes with inlet and outlet streams may spawn as much as one month earlier in the outlet than the inlet due to temperature differences (Raleigh et al. 1984). Spawning date and temperature vary considerably among hatchery strains of rainbow trout, so managers can stock fish that spawn under sets of conditions that maximize the survival of the offspring. Artificial propagation has placed an emphasis on developing fall spawners, thus enabling hatcheries to produce size-specific rainbow trout year round (Behnke 2002). For example, spring-spawning strains tend to spawn when water warms sufficiently to allow normal embryo development. Fall-spawning trout must allow sufficient time for their embryos to reach a critical stage of development before the water becomes too cold (Bjornn and Reiser 1991).

**Space:** Larger fish dig larger redds, and poor quality or insufficient spawning habitat may force females to make several redds. The density of redds depends largely on the area of suitable habitat for spawning; the number, size and behavior of spawners; and the area required for each redd. The average area of a redd with a single egg pocket is ~0.2 m<sup>2</sup>.

**Water depth and velocity:** Females typically choose spawning sites at water depths greater than 18 cm with greater than average velocities (e.g., 48 to 91 cm per s). Velocities are measured at the upstream edge of the redd because that point is believed to most closely approximate conditions before the redd was constructed and thus reflects the depth and velocity selected by the fish (Bjornn and Reiser 1991). Water velocity is important for successful spawning because faster water delivers well-mixed and oxygenated water to the redd, and it must be fast enough to penetrate and move through the interstices of the redd. Continuous flow of water through the egg pocket is critical for delivering sufficient oxygen to embryos, removing metabolic waste products, and keeping the substrate free from silt so fry can emerge from interstices (Raleigh et al. 1984, Workman et al. 2004). Water depth is important because water must remain deep enough to support the

spawning adults and to cover the redd when fry emerge (Workman et al. 2004).

**Substrate:** Rainbow trout are primarily stream spawners and generally require tributary streams with gravel substrates in riffle areas for successful reproduction (Raleigh et al. 1984). The suitability of gravel substrate for spawning is directly related to fish size (Bjornn and Reiser 1991, Raleigh et al. 1984, Workman et al. 2004). In general, substrate particles must be large enough to enable successful alevin emergences from the redd (Workman et al. 2004). The female generally selects a redd site in gravel substrates located at the head of a riffle or on the downstream edge of a pool. The redd is constructed by the female and is typically longer and deeper than her greatest body depth (Raleigh et al. 1984). During redd construction and spawning, streambed particles are displaced so that fertilized eggs can be deposited in one or several “egg pockets.” Depths of egg pockets will vary according to the size of the female and local substrate conditions, but on average they range from ~0.08 m for small fish (characteristic of most stream spawners) to ~0.20 m for large individuals (e.g., the size of sea-run steelhead; Schuett-Hames et al. 1996). Redd construction reduces the amounts of fine sediment and organic matter in the pockets where eggs are deposited. Once spawners deposit eggs and sperm, the females cover the eggs with hydraulically-displaced particles (Bjornn and Reiser 1991).

**Cover:** Trout may arrive at spawning grounds weeks or months before they are ready to spawn, so sufficient cover creates an environment where fish are less vulnerable to disturbance and predation for extended periods of time. Cover for rainbow trout waiting to spawn may include, but is not limited to, overhanging vegetation, undercut banks, submerged vegetation, submerged objects such as logs and rocks, floating debris, deep water, and areas of turbulence and/or high turbidity (Bjornn and Reiser 1991).

**Streams, tributaries, rivers, lakes, and reservoirs:** Rainbow trout spawn almost exclusively in streams (Raleigh et al. 1984). Lakes and reservoirs with no inlet or outlet streams generally limit, and in most cases inhibit, reproducing populations of rainbow trout. Rainbow trout in lakes and reservoirs with inlet and outlet streams are thought to have similar life history as steelhead (sea-run rainbow trout) without the smolt life stage.

Trout production is typically most successful in streams with a pool-to-riffle ratio of approximately 1:

1. While trout habitually spawn in both permanent and intermittent tributaries, the latter (including rivers below dams whose discharge fluctuates drastically over short periods) tend to expose redds and either stress or kill eggs and especially alevins. Trout will readily utilize intermittent streams if competition for redd sites is too high in permanent streams (Erman and Hawthorne 1976).

#### *Nursery habitats – egg incubation and fry rearing*

The habitat requirements of embryos during incubation are quite different than those of spawning adults because successful incubation and emergence of fry depend on precise combinations of extragravel and intragravel chemical, physical, and hydraulic variables. Dissolved oxygen, water temperature, biochemical oxygen demand of material carried in the water and deposited in the redd, substrate size, fine sediment, channel gradients, channel configuration, water depth, surface water discharge, velocity, porosity of gravel in the redd and surrounding streambed and the velocity of the water through the redd are important variables that determine incubation success and thus reproductive success (Bjornn and Reiser 1991). The period of egg incubation begins at the end of spawning and normally lasts 30 to 100 days, with the duration at a particular location largely dependent on temperature (Raleigh et al. 1984).

**Streamflow:** Above-substrate streamflow is usually less significant during egg incubation than percolation of water through the gravels surrounding egg pockets to provide oxygen and remove wastes. The most significant exception to this occurs during seasonal spates associated with periods of rapid snowmelt or heavy seasonal rains that can displace streambed gravels in the redd (see section on Scour below).

**Dissolved oxygen:** Eggs are generally most vulnerable to hypoxic conditions during early stages of development (Bjornn and Reiser 1991). Salmonids incubating at low dissolved oxygen levels are weak, small, and slower to develop and have an increased frequency of abnormalities.

**Temperature:** Incubation time and success varies inversely with temperatures. Rainbow trout eggs can withstand temperature extremes of ~35 to 61 °F (~1.6 to 16 °C), but temperatures of 45 to 50 °F (~7 to 10 °C) yield the highest survival rates among embryos. In general, the higher the temperature, within the acceptable range, the faster the rate of development and

thus shorter incubation period and time to emergence (Raleigh et al. 1984).

**Water depth and velocity:** Depth is not expected to be a limiting factor for egg incubation as long as the eggs are moist during incubation, and egg pockets are submerged from the time of hatching until the fry emerge (Raleigh et al. 1984).

**Substrate:** The redd environment is most favorable right after construction and may change little or drastically depending on weather, streamflows, other spawning trout, and other fish in the area. Porosity is highest right after the redd is constructed and declines over time as the interstitial spaces acquire fine sediments (Bjornn and Reiser 1991). Normally, particles should be >1 cm in diameter to permit adequate percolation for successful embryonic development (Raleigh et al. 1984). Egg densities in natural redds are typically lower than those in artificial culture facilities (Bjornn and Reiser 1991).

**Cover:** Cover is not thought to be a limiting factor for egg incubation; in fact, spawning gravels are more likely to occur away from quiet or slowly flowing waters near shorelines where deposition of fine sediments occurs (Raleigh et al. 1984).

#### *Fry habitat*

Fry absorb most or all of the contents of their yolk sac at a length of roughly 35 to 40 mm, 3 to 4 months after hatching. They then move through the interstices of gravels surrounding the egg pocket to the substrate surface and to shallow, low-velocity (and usually relatively warm) water along the shore. Fry inhabit low velocity water and protective cover typically found along the margins of streams and in spring seeps, side channels, backwaters, and small tributaries (Behnke 1992).

For the purpose of this assessment, we recognize fry habitat as that occupied during the period from emergence from spawning gravel to the time when they become juveniles at approximately 4 months post-emergence (Raleigh et al. 1984).

**Temperature:** There appears to be almost no variation in the critical thermal maximum (temperature at which animal loses control of normal orientation and swimming performance) for rainbow trout at sizes of ~4 to >30 cm (reviewed in Rodnick et al. 2004). During summer periods, fry tend to occupy temperatures averaging 13 to >19 °C, depending on local conditions.

However, their shallow, near-shore habitats may experience considerable short-term (daily) fluctuations in temperature, as they are particularly susceptible to changes in air temperature, insolation, and other conditions that influence shallow, slow-moving waters. Growth rates during this phase, as during the subsequent juvenile phases when there are similarly no nutrient or energy expenditures for reproductive activity (Cunjak and Green 1986), are highly temperature dependent. For example, (Raleigh et al. 1984) cites a growth rate at 10 °C that was ten times greater than at 3 °C, values that indicate a  $Q_{10}$  of ~27, far greater than the  $Q_{10}$  values of 2 to 3 recorded for most biological functions [ $Q_{10}$  is a factor by which the rate of a biological function increases when the temperature is raised by ten degrees C; it is calculated as  $Q_{10} = R_2/R_1^{10/t_2-t_1}$ , where  $t_2 > t_1$ ]. This difference was likely exaggerated by a test temperature near the lower limit of their tolerance;  $Q_{10}$  values increased for metabolic rates of larger rainbow trout as they neared their critical thermal maximum (Rodnick et al. 2004).

**Water depth and velocity:** Fry occupy shallower water and lower velocities than stream rainbow trout of any subsequent life stage. Fry typically occupy depths ranging from 25 to 50 cm, and will utilize velocities less than 30 cm per sec, but they prefer velocities less than 8 cm per sec. Fry are especially vulnerable to being washed away outside their preferred range of velocities and survival decreases dramatically with increased velocity. Predictably, fry are more apt to be swept away in the event of a flood (Behnke 1992). As the fish grow, they move into faster, deeper waters (Raleigh et al. 1984).

**Substrate:** Fry substrates typically range from mud and silt to bedrock and cobble. Bustard and Narver (1975) reported that fry substrate was most closely associated with particles ranging from 10 to 25 cm in diameter, but this will vary considerably depending on habitats available. As noted above, fry establish feeding territories that vary with size, population density, visibility, and food density (Imre et al. 2004; Keeley 2002, 2003); in an experimental system, Imre et al. (2004) measured mean territories of approximately 80 to 160 cm<sup>2</sup>, but others have suggested the range may be as great as 15 cm<sup>2</sup> to 1 m<sup>2</sup> (Brown 2003). Keeley (2003) demonstrated that population self-thinning (a decline in population density apparently not due to predation or other local deaths) occurred in young-of-the-year steelhead as they grew under constant food conditions.

**Cover:** After hatching and during the first months of life, cover is critical for successful rearing to take

place, thus few fry can be found more than 1 m from cover. Types of cover include, but are not limited to, aquatic vegetation, woody and other debris, and the interstices between rocks. Raleigh et al. (1984) noted that coarse-grained substrate is used for cover.

### *Juvenile habitat*

While the size of juvenile rainbow trout may vary depending on local conditions, here we include individuals that range in length from ~4 to 20 cm (~1.8 to 7.9") or from ~4 months of age to sexual maturity (typically at age 2). Variables that factor into juvenile habitat preferences and use include substrate, cover, depth, velocity, temperature, size, and activity of the individual trout, intra- and interspecific interactions, season, and stream location (Raleigh et al. 1984). Thus, juveniles explore and occupy a wide range of habitats as they grow and mature.

**Streamflow:** As noted above, as fry grow and enter their juvenile stage, they move into deeper and more swiftly flowing water that offers greater complexity of cover for larger fish and larger and more diverse food supplies. There is a strong correlation between year class abundance and flow regimes, with a strong positive correlation between year class abundance and lower than normal flows (Behnke 1992). This probably reflects greater availability and stability of fry rearing habitat as much as availability of slower water for juveniles moving into deeper habitat.

**Temperature:** Temperature preferences of juveniles vary considerably, in part due to changes related to age and acclimation temperature (Raleigh et al. 1984). As they grow, juveniles move into deeper and swifter water more characteristic of that occupied by adults. In general, however, they should thrive at mean summer temperatures in which adults thrive and grow (~10 to 18 °C).

**Water depth and velocity:** Once rainbow trout reach 12.5 to 15 cm, survival rates increase, and at this stage, they will relocate to riffle areas where territories are established in deeper waters such as pools (Behnke 1992). Velocity preferences of juvenile rainbow trout vary widely as they are dependent partially on individual activity, whether the fish is stationary (resting) or swimming (feeding, exploring). Other factors affecting velocity preferences in juvenile fish are season and flow. Juveniles occupy a wide range of depths depending on their activity and geographic location (Raleigh et al. 1984).

**Substrate:** Undercut banks are used for establishing territories, but juvenile rainbow trout commonly associate with more exposed areas over gravel, cobble, and near boulders. When stationary, juveniles have demonstrated a preference for gravel over cobbles and boulders, and they encounter silt and sand during random swimming and when resting or foraging in side channels or nearshore habitats (Raleigh et al. 1984).

**Cover:** A cover area of 15 percent of total stream area or greater is adequate for juveniles to avoid predators and to provide resting grounds (Raleigh et al. 1984). Cover may be found instream or on the streamside. In the water, cover includes submerged vegetation, debris piles, woody debris, logs, boulders, and other objects that provide protection or alter local current flow patterns. Streamside cover may be provided by overhanging vegetation, undercut banks, and other objects that hang over the water (Raleigh et al. 1984). When cover provides shade, it probably also enhances visibility of exposed prey and reduces the ability of predators to see the lurking juvenile (Helfman 1981).

#### *Adult habitat*

Rainbow trout are considered adults when they reach sexual maturity at age 2 or 3 or when they attain lengths of ~20 cm (~8.0"), a size when many are capable of maturing given the proper conditions (Raleigh et al. 1984).

**Streamflow:** There is a direct relationship between annual streamflow and the quality and amount of available trout habitat. At low water levels, undercut banks, large portions of instream cover and desired shoreline habitats may be exposed, while at very high water levels excellent habitats may be in deep water or inordinately strong currents (Behnke 1992). The most critical period is usually during base flow, the lowest flows of late summer to winter. Base flows 50 percent or more of the average annual daily flow are ideal for maintaining quality trout habitat, while base flows of 25 to 50 percent are considered fair, and below 25 percent are considered poor (Raleigh et al. 1984).

**Temperature:** Summer temperatures of 10 to 18 °C are optimal for stream-dwelling trout (Behnke 1992). As water temperatures increase, dissolved oxygen levels decrease, and this may be detrimental or lethal to the fish if levels drop substantially. Rainbow trout can survive at suboptimal dissolved oxygen levels, but not without a cost and subsequent behavioral or

physiological changes that may jeopardize their health. For example, low dissolved oxygen can result in altered swimming speed, a decline in growth rates, reduced fecundity, and even constrain spawning. Temperature and dissolved oxygen levels influence depth distribution of trout in various environments (Raleigh et al. 1984).

**Space:** The space required for individual territories largely depends on the total suitable space available. The complexity of the habitat along with food availability and the presence of predators all determine what part of the available suitable space fish use. As wild trout age and grow in size, the amount of space required for territorial needs increases.

**Water depth and velocity:** Stream trout typically live at depths of 0.3 m or greater and in areas where slow waters for resting are available. Fast waters are also used by adult rainbow trout because strong currents dislodge, suspend, and carry food. Trout often forage by holding station in eddies or other locations with reduced current adjacent to swift water, moving into the swift current to intercept prey. Fish occupy a wide range of depths depending on their activity (e.g., resting vs. foraging; Raleigh et al. 1984).

**Substrate:** Adult trout are less constrained to specific substrates than smaller life history stages. As indicated in other sections here, they range widely in lakes, rivers and streams, and at various times in their adult lives, they can occupy all but the shallowest of marginal habitats. Key components of river substrate for adults are large structure (e.g., boulders, woody debris) that diversifies local instream flow patterns to produce microhabitats differing in velocity and cover, and pools and undercut banks that provide quiet refuges.

**Cover:** The addition of three-dimensional cover, present in both instream and streamside areas and providing extra depth, preferred substrate, overhanging vegetation, submerged vegetation, undercut banks, instream objects (i.e. debris piles, woody debris, logs, large rocks), increases the complexity of the space available and thus the carrying capacity (Bjornn and Reiser 1991, Behnke 1992, Raleigh et al. 1984). A cover area of 25 percent of the total stream area or greater is suitable for adult rainbow trout. (Raleigh et al. 1984).

**In streams, tributaries, rivers, lakes, and reservoirs:** Rainbow trout populations that successfully reproduce in lakes with inlet and outlet streams typically spend two summers in a stream and two summers in a lake before they are considered mature (Raleigh et al.

1984). Pools provide resting areas and refuge from adverse conditions and are thus inhabited throughout the year by adult and juvenile stream rainbow trout (Raleigh et al. 1984).

### *Overwinter habitat*

The amount of adequate overwintering habitat is a major factor limiting salmonid densities, often more so than the amount of summer-rearing habitat. The key features of winter habitat for juvenile salmonids appear to be substrate, cover, and lower water velocity. These features are affected by natural processes, especially those related to watershed characteristics such as gradient, geology, and hydrologic regime, as well as land use practices.

**Streamflow:** The effect of stream discharge on winter habitat varies with geography. In contrast to the Pacific Northwest, where heavy winter rainfall generates spates with potential for scouring, sedimentation, and washout of fish (Morgan and Hinojosa no date), streams in the more arid Rocky Mountain Region are likely to experience low flow and greater threat to fish of stranding or formation of anchor ice during winter. Mitro et al. (2003) found a relatively tight correlation between abundance of age 0+ rainbow trout and river discharge in the second half of winter (15 Jan-31 Mar) in the Snake River, Idaho, possibly indicating greater availability of complex streamside habitat at higher flows.

**Temperature:** Cooling of water as winter approaches stimulates movements of trout to overwintering habitat. Such movements tend to be downstream to areas with greater winter flow, deeper pools, or more groundwater discharge (Morgan and Hinojosa no date). Winter stream temperatures of greatest concern are, of course, those near, at, or occasionally below freezing (0 °C, 32 °F). Supercooling (temperatures <0 °C) in freshwaters can occur where water movements or other phenomena inhibit formation of surface ice cover. Under such conditions, ice can form on and in the substrate, freezing fry and juvenile fish, or it can form highly abrasive free-floating ice crystals (frazil ice; Simpkins et al. 2000).

**Water depth and velocity:** For adult fish, overwinter survival is directly related to the availability of deep water with low current velocity and protective cover typically found in deep pools with large boulders or deep beaver ponds (Behnke 1992). Stream resident

trout fry commonly overwinter in shallow areas of low velocity near the stream margin.

**Substrate and cover:** Fry and small juveniles of rainbow trout and steelhead preferentially inhabit areas with coarse substrate (i.e., gravel, cobble, woody debris), tend to take refuge in the interstices of these substrates during the day, and emerge into the water column at night where they may feed (Bustard and Narver 1975, Hillman et al. 1987, Simpkins 1997, Morgan and Hinojosa no date). In the interior of British Columbia, steelhead or rainbow trout occupied rock crevices or large substrata, often associated with riprap-stabilized banks (Swales et al. 1986). In streams with large amounts of large woody debris, juvenile salmonids experience higher overwinter survival than in streams with less (Murphy et al. 1984a in Morgan and Hinojosa no date). If sufficient cover occurs locally, rainbow trout may not move downstream during or preceding winter (Raleigh et al. 1984).

### *Food habits*

Rainbow trout are opportunistic feeders, and their primary food items depend in part on the stage of life history as well as the habitat occupied (**Table 5**). Although no comprehensive list of foods ingested is attempted here, one can expect these fish to feed on items characteristic of the benthos (organisms associated with the substrate or with other solid materials like woody debris), the water column (drift in streams and zooplankton and nekton in lakes), and surface (animals that have fallen into the water or are swimming). Fry restricted to quiet waters feed on small insects and other invertebrates, including nematodes, amphipods, cladocerans, and many types of both terrestrial (e.g., adult Coleoptera, Diptera, Formicidae, larval Lepidoptera) and aquatic insects (e.g., larvae and pupae of midges, black flies, caddisflies; beetles, crane flies, soldier flies, mayflies, stoneflies) (Fishbase 2006).

Diets of juvenile and adult trout are even more diversified, with a wide assortment of terrestrial and aquatic insects, other aquatic invertebrates including nematodes, leeches, annelids, gastropod and other mollusks, and benthic and planktonic crustaceans (cladocerans, isopods, amphipods, shrimps, crayfish), both small ray-finned fishes and brook lampreys, fish eggs and larvae, detritus, benthic algae (Fishbase 2006), and even an occasional lizard (Lintermans 1992), mouse (Merz 2002), or bat (Y. Bernstein, personal

**Table 5.** Known foods of rainbow trout. (Lintermans 1992, Kerr and Lasenby 2000, Merz 2002, Fishbase 2006; Montgomery, Bernstein, William Leibfried, personal observations.)

<b>Algae</b>	<b>Snails and other mollusks</b>
<i>Cladophora</i>	
<i>benthic diatoms</i>	
<b>Detritus</b>	<b>Fishes</b>
	unidentified fish eggs and larvae
	Alewife
	American smelt
<b>Nematodes</b>	Bloater chub
	Bluegill
<b>Leeches</b>	Brook lamprey
	Brook trout
<b>Annelids</b>	Brown bullhead
	Fathead minnow
<b>Aquatic insects</b>	Five spined stickleback
dragonflies	Green sunfish
damselflies	Johnny darter
chironomid midges - larvae & pupae	Largemouth bass
simuliid black flies - larvae & pupae	Longfin smelt
rhyacophilid caddisflies - larvae & pupae	Nine spined stickleback
hydropsychid caddisflies - larvae	Prickly sculpin
dytiscid beetles	Rainbow trout
haliplid beetles	Redside shiner
dipteran craneflies	Slimy sculpin
dipteran soldierflies	Sockeye salmon
ephemeropteran (including baetid) mayflies	Speckled dace
plecopteran stoneflies	Threadfin shad
	Three-spined stickleback
	Yellow perch
<b>Terrestrial insects</b>	<b>Reptiles</b>
adult Coleoptera	Southern water skink (Australia)
Diptera	
Formicidae	
larval Lepidoptera	
<b>Aquatic crustaceans</b>	<b>Mammals</b>
amphipods (Gammarus)	mouse
cladocerans	bat
isopods	
shrimps	
crayfish	

observation). Detritus and benthic algae may reflect incidental ingestion with animal prey, but trout may also derive meaningful nutrition from partial digestion of these materials or epiphytic organisms (e.g., diatoms) that grow attached to them (W. Leibfried and Montgomery unpublished).

Clearly, rainbow trout are likely to feed on any organisms of potential—or perceived—nutritional value. Knowledge of trout feeding behavior and ecology will enhance assessment of potential nutritional resources and their utility in nature.



Rainbow trout are visual and particulate (ingesting individual items) feeders, and thus usually concentrate their feeding activity during daylight or crepuscular periods (dawn, dusk) or at night when downwelling light is sufficient to silhouette prey against a light background (Tippetts and Moyle 1978, Rogers et al. 1984, Angradi and Griffith 1990). Inherent periodicity in feeding is most evident where food is consistently available; trout feed most heavily at dawn or dusk in hatchery self-feeding systems (Boujard and Leatherland 1992, Chen et al. 2002). The actual foraging periods of individuals or a particular stock are likely to vary, however, in response to prey availability, predator pressures, seasonal changes in behavior, and other ecological factors, and may well be modified by short-term learning (Riehle and Griffith 1993, Warburton 2003). For example, Tippetts and Moyle (1978) attributed unusually high epibenthic foraging in the McCloud River to turbid conditions that interfered with drift feeding in adult rainbow trout.

The ability to respond to changes in availability of prey over relatively short periods is significant because trout influence the drifting patterns and densities of some prey. For example, mayfly nymphs avoid drifting during the day in the presence of rainbow trout, and are probably detecting trout through chemical means (Douglas et al. 1994). Trout may experience extended periods of low food availability, but food-deprived fish often exhibit hyperphagia and considerable compensatory growth following such stressful periods (Jobling and Koskela 1996).

Feeding territories of fry and juvenile trout may influence several aspects of trout ecology relevant to management (Gerking 1994). First, territories may be interspecific and thus bring introduced rainbow trout into conflict with native species. Conflict may lead to physical damage, reduces foraging time, and likely increases stress hormone levels. Second, territory size tends to increase with body size, declining food density and reduced current. Territoriality can lead (a) to displacement of subordinate individuals (Gilmour 2005) to habitats where they are more likely to be transported downstream and suffer higher mortality or (b) to status as “floaters,” non-territorial animals that experience lower food intake and other density-dependent pressures. Such territories become potentially important regulators of population size.

Feeding behavior of adult rainbow trout differs from that of fry and juveniles. Unlike territorial juveniles, adults in streams tend to occupy home ranges with multiple foraging and refuge sites. Trout

remain somewhat passive at foraging sites and move from them to intercept drifting or other prey. An adult rainbow trout will move among such locations and displace subordinate individuals in the process, usually with little overt aggression, in a manner characteristic of a local dominance hierarchy. Periods of foraging at these sites will also be interspersed with periods in refuge sites in quiet waters beneath undercut banks or rocky ledges.

Significant differences in foraging behavior may also occur between wild and domesticated trout. Hybrids between wild and domesticated trout experience reduced survival in nature, apparently because of increased risk-taking without a simultaneous improvement in predator avoidance behavior. Domesticated rainbow trout are reared in the absence of predators and must compete for food thrown on the water surface. Hatcheries may therefore select against predator avoidance, although this is not the only possible explanation for this altered behavior. Selection for rapid growth under reduced predation pressure may shift the optimal trade-off between energetic gain and mortality risk in favor of “high gain-high risk” phenotypes. Genes for predator avoidance may no longer contribute to fitness and may decrease in frequency or drift into fixation. Furthermore, selection for large body size in the absence of predators will favor risk-prone and/or risk-indifferent foragers relative to more risk-averse individuals (Johnsson 1992).

### Breeding biology

Rainbow and other western trout and salmon evolved primarily in the flowing water of small streams to large rivers, where they feed primarily on drifting invertebrates and small fishes. Pacific salmon, as well as some rainbow trout inhabiting coastal streams and rivers, evolved an anadromous habit as well. These fish spend variable numbers of juvenile years in the river, migrate to sea where rich marine foods support growth to large size, and return to spawn in their natal streams. Spawning habitat varies considerably among species and between sea-run (steelhead) and riverine rainbow trout.

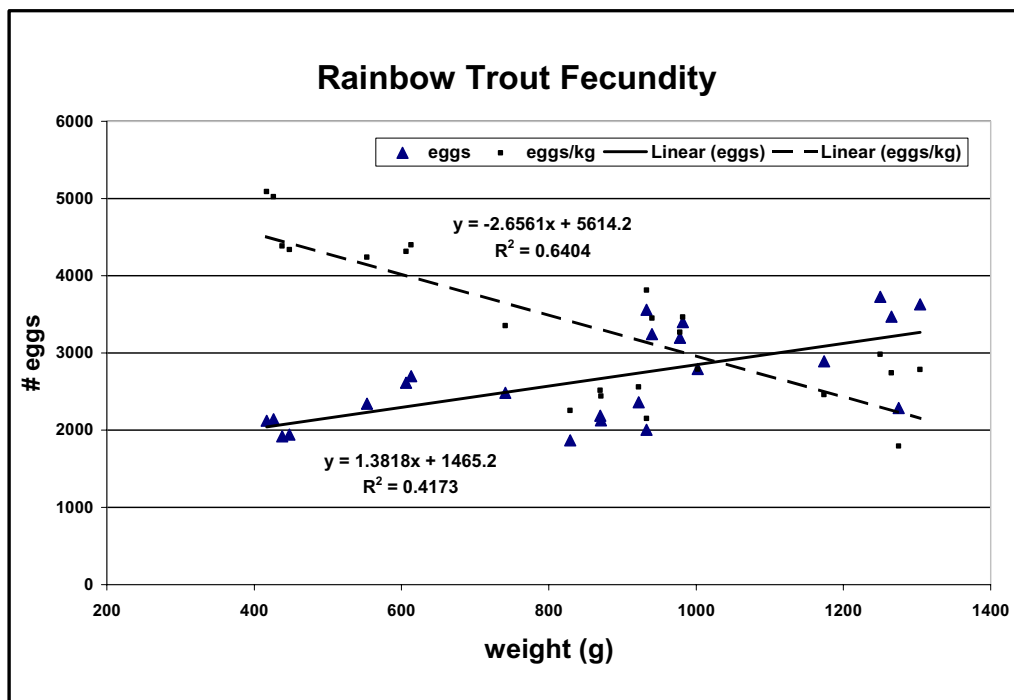
During reproductive periods, a female digs a depression in rocky (normally gravel or small cobble) substrate with strong lateral flexions of her tail, all the while being attended and defended by a male. Digging also suspends and displaces fine sediments. Spawning involves simultaneous release of gametes by female and male, after which the female digs upstream of the initial depression, displacing gravel downstream to bury

eggs laid there. This produces a single, buried “egg pocket.” The female then begins excavation of another spawning depression. One to several egg pockets may be laid within a single nest area, termed a redd. Female fecundity varies with size (**Figure 5**). Eggs are aerated by flow of water through the interstices of the gravel. Time to hatching is temperature dependent. Hatchlings (sac-fry or alevins) possess large yolk sacs that support early growth. When most of the yolk is absorbed, the fish move to the surface and to shallow, slow-moving water along stream edges and begin the free-living, exogenous-feeding stages of their lives.

Although much less studied than in some other species (e.g., Atlantic salmon), rainbow trout are among a variety of salmonids whose small males exhibit “sneak” or “satellite” mating tactics when in competition for spawning opportunities with large attending males (Montgomery 1983, Montgomery et al. 1987, Esteve 2005). Satellites may be parr or small adults, both of which sacrifice additional growth by channeling nutrients and energy into elaboration of testes. These fish remain inconspicuous but near an actively digging female, do not court, and dart in to emit milt (spermatozoa and accompanying fluids) only when the female and larger attending male begin to spawn. Both parr and small adult fish are fertile,

fertilize variable proportions of eggs laid, and thereby competitively reduce the reproductive success of the dominant male.

The continued artificial selection of rainbow trout in hatcheries has enabled this species to express elevated growth rates compared to those observed in natural populations or self-sustaining populations established in the past. If recently stocked fish grow to unusually large size and exhibit the expected proportional increase in fecundity (**Figure 5**), they might competitively exclude the smaller and lower-fecundity previous residents. Biro and others (2004) suggest that greater body size potentially achieved by fish exhibiting elevated growth rates may not increase fitness because of increased risk of predation associated with increased feeding required to achieve and maintain the large body. Domesticated rainbow trout are selected for rapid growth and early maturity, characteristics often accompanied by a short life span, and they did not outgrow wild trout in a predator-free lake. Trade-offs between growth and mortality rates appear to be associated with variations among populations rather than within populations (Biro et al. 2004). Few domesticated rainbow trout survive more than one year in the wild after reaching sexual maturity (at approximately age 1 year) and therefore may normally



**Figure 5.** Rainbow trout fecundity related to weight. Lines represent linear regressions of total eggs per female (solid line) and eggs/kg per female (dashed line). Data combined from Blom and Dabrowski 1995, Gall and Gross 1978, and Su et al 1997.

spawn once or not at all. Most wild western trout will first spawn at ages 2 to 4 years. Fecundity of western rainbow trout is greatly influenced by environment as well as heredity, and will ultimately influence the age and size at first spawning (Behnke 1992).

## Demography

### *Genetic characteristics and concerns*

Genetic analyses indicate that the salmonids arose via autotetraploidy during matings between members of the same species (vs. allotetraploidy due to interspecific hybridization). As a result, whitefishes, graylings, trout, and salmon possess four sets of chromosomes (tetraploid condition) instead of the more common two sets characteristic of diploid organisms. The formation of new taxa via tetraploidy has been studied extensively in some groups (e.g., higher plants), and the additional genetic material may have supported the rapid evolution within the salmonids.

Among populations of rainbow trout, chromosome number varies, indicating considerable dynamism in chromosomal rearrangements (e.g., fusions, fissions) through the evolutionary history of the species. The diploid ( $2n$ ) chromosome number of rainbow trout ranges from  $2n = 58$  to  $2n = 64$ , but all share the same number of chromosome arms (104; Thorgaard 1983). Fish with the most common chromosome number,  $2n = 58$ , appear to represent the ancestral condition for populations exhibiting higher  $2n$  numbers and presently range from Russia to coastal California (Phillips et al. 2005). Deviation of a population from the widespread  $2n = 58$  may suggest origins of stocked fish in areas beyond the core native range of the trout.

Ryman and Utter (1987) produced a valuable early compilation of information on salmonid genetics and the discipline's relevance to fisheries management. That volume identified key concerns that remain today, including issues with genetic variation in wild and hatchery stocks, inbreeding effects, hybridization and introgression, and gene frequency shifts under the influence of genetic drift and directional selection.

The greatest management problems with genetics of rainbow trout relate to limited genetic variation in small wild populations or hatchery stocks and associated inbreeding depression (loss of vigor, viability, fecundity, etc., related to loss of genetic variation due to homozygosity). Specific concerns relevant to management of rainbow trout populations include:

- ❖ Population-wide genetic variation may be reduced due to inbreeding (hatcheries) or small population bottlenecks, where the few animals to survive and reproduce carry only a fraction of the total genetic variation in an original larger population. This tends to reduce flexibility of responses to altered environmental conditions and to increase susceptibility to other threats. For example, recent studies of California golden trout indicate that lake populations experienced reductions in genetic diversity due to a series of bottlenecks and then suffered introgressive hybridization with hatchery-reared and stocked rainbow trout (Gold and Gold 1976, Cordes et al. 2006).
- ❖ Heterozygosity may be reduced (and thus homozygosity increased), so that for many genes an individual possesses only one allele at that gene. Higher heterozygosity has been correlated with increased disease resistance (Ferguson and Drahushchak 1990), better condition (Danzmann et al. 1988), and developmental stability (Leary et al. 1985) in rainbow trout.
- ❖ Introgressive hybridization may lead to disruption of highly evolved gene complexes in particular locales and thus reduce fitness for animals occupying these locales. The fidelity of salmonids to spawning in natal streams has led to stocks highly adapted to specific sites (e.g., Marnell et al. 1987, ) and to genetic divergence among fish from different geographic locations (e.g., Docker and Heath 2003, Novak et al. no date). Several genetic studies demonstrate introgressive hybridization between rainbow trout and other salmonids (especially various cutthroat stocks and subspecies - see below; Young et al. 2001; Campbell et al. 2002).
- ❖ Hatchery rearing may intentionally or unintentionally select for traits that enhance success in hatcheries but produce fish that perform poorly in the wild, in part because novel hatchery environments contribute to genetic divergence from a wild phenotype (Johnsson 1992). Miller et al. (2004) demonstrated drastically reduced survival from hatching to age 1+ of hatchery rainbow trout compared to naturalized (wild, but previously established from stocked fish)

fish (Miller et al. 2004). Sundstrom et al. (2004), working with brown trout, found that hatchery-reared fish were more bold than wild fish and that bold fish tended to become socially dominant. In fact, effects of hatchery rearing may be even more pervasive than commonly recognized. Marchetti and Nevitt (2003) recorded differences in eight brain measurements between hatchery reared and wild rainbow trout, with components of hatchery fish brains consistently smaller than those of wild fish. The brain areas affected are known to influence such key activities as predator avoidance, growth and gaining access to appropriate mates.

#### *Additional concerns with hybridization*

Rainbow trout in waters of Region 2 provide many recreational fishing opportunities, yet they also create problems by hybridizing with native cutthroat subspecies, thereby threatening the genetic integrity of cutthroat trout (Madeira et al. 2005, Ross 1997, Shepard et al. 1997). This contrasts with coastal cutthroat and native rainbow trout because they have evolved in sympatry (Hitt et al. 2003) and have maintained reproductive isolation.

Both rainbow trout and cutthroat trout spawn in the spring, react similarly to environmental cues that initiate spawning (Behnke 2002), and thereby create an opportunity for gene flow between the two species (Kershner et al. 1997). In fact, Behnke (2002) suggests that when rainbow trout are introduced in waters where native cutthroat populations exist, hybridization is the likely outcome. Cutthroat trout tend to occupy colder habitats than do other *Oncorhynchus* species, but all other requirements for reproductive success and threats to their existence are similar to rainbow trout (Behnke 2002). Hitt and others (2003) recorded introgression hybridization between native westslope cutthroat and planted rainbow trout, and concluded that hybridization was spreading rapidly in an upstream direction but might be reduced by erecting physical barriers. Kruse et al. (2001) believe that reliance for long-term conservation on Yellowstone cutthroat trout populations isolated in headwater streams was unwise due to small sizes of populations that made them more susceptible to genetic drift (change in allele frequencies that occurs entirely from chance) or unpredictable environmental conditions.

As noted above, native trout populations, including cutthroats, often appear to have adaptive gene complexes that ‘fit’ the fish to local conditions. When disrupted by nonnative rainbow genes, this compromises the ability of native fish stocks to thrive in their local environments.

The decline of native cutthroat species (Varley and Gresswell 1988, Kershner et al. 1997, Ross 1997, Henderson et al. 2000, Kruse et al. 2000, Hitt et al. 2003), and in some cases the local disappearance of a distinctive cutthroat phenotype, is often attributed to introgressive hybridization between introduced rainbow trout and native cutthroat species in Region 2. Nonetheless, hybrids between native cutthroat and hatchery rainbows can produce large fish that meet angler satisfaction (Ross 1997, Behnke 2002). Such use of hybrids may appeal to agencies because the fish exhibit accelerated growth rates to larger size than either parental species. For example, Montana stocked rainbow x cutthroat hybrids in Ashley Lake through at least August 2006; the lake produced the 30-pound, 4-ounce world record “cutbow” in 1982. There is also a psychological value in creating “new” organisms and therefore providing anglers with the opportunity to fish for a new kind of prey (Ross 1997).

Often associated with hybridization is partial or complete sterility. Stocking with sterile animals ensures no reproduction and thus no hybridization or natural recruitment, but problems generated by higher densities and heavier competition may persist.

#### *Social patterns for spacing*

Like many fishes, rainbow trout exhibit a variety of social systems depending on age and size, population density, availability and type of habitat, food availability, and experience. Fry in appropriate habitat will, as noted above, establish feeding territories. These territories may be defended against conspecifics as well as other species, and their size fluctuates with food density. At low population densities, juveniles and adults may defend territories or, particularly in the case of locally dominant adults, move among multiple feeding and resting sites in a home range, simply displacing subordinate fish from locations preferred by the larger animal. At higher densities or in restricted habitat, juveniles and small adults, including recently stocked hatchery fish, often form aggregations in the water column near shore or in other areas of slowly flowing water.

## Pattern of dispersal of young and adults

Dispersal of young begins, as noted elsewhere, by recently emerged fry moving to quiet near-shore locations where they establish feeding territories. Individuals incapable of winning and holding a territory or other site for persistent occupation will normally be displaced to suboptimal habitat. Fry and juveniles in such circumstances may be flushed from their initial site of occupancy by strong currents, particularly at night when their visual orientation and ability to hold station is compromised. In a somewhat similar fashion, juveniles and adults move preferentially downstream during the winter in order to find deeper and more persistent habitats for overwintering. Spring may see spread of fish from downstream to upstream habitation and, for mature fish, spawning sites. During spring, summer and into fall, many trout remain restricted in their movements, moving tens to a few hundred meters. Others may move several kilometers.

## Limiting factors

A wide array of limiting factors has been noted in preceding sections. Habitat for any of the major life history stages is crucial. The amount of available spawning habitat will limit the number of eggs that are likely to complete development. Insufficient fry habitat will result in high mortality of this stage and reduced recruitment of juveniles and, subsequently, adults. Food supply may also be restricted due to low reproductive success of food organisms or suppression of food availability through predation by rainbow trout or other fishes. Negative interactions with other species may include competition with conspecifics or other species, cannibalism by larger trout, predation by both aquatic and terrestrial organisms, and parasitism and disease, all touched on in more detail below.

## Predators

Given the diversity of habitats occupied by rainbow trout during their various life stages, they are potentially susceptible to virtually any predator that feeds underwater or on fish occupying shallow, near-shore, or near-surface environments (**Table 6**; Tabor and Wurtsbaugh 1991, Lovvorn et al. 1999, Zimmerman 1999, Kerr and Lasenby 2000 and references therein, Laake et al. 2002, Gard 2005). Thus, managers should make independent assessments of likely predators based on the behavior of predators in the area of concern rather than on existing reports of animals known to take rainbow trout. This approach would, for example, add both snakes that forage in or adjacent to stream systems

and are known to eat fishes, including some species of water (*Natrix*) and garter (*Thamnophis*) snakes, and predatory invertebrates to lists of likely predators (**Table 6**). Similarly, estimates of the intensity of threats from predators should be based on the densities and predatory tactics of predators relative to the habitat and behavior of different trout life history stages. Fry in shallow nearshore waters, for example, are more likely to be attacked by snakes, wading birds, and giant water bugs or crayfish than later life history stages, while adult trout in lakes or higher order streams with open canopy will be more susceptible to raptors than wading birds.

## Competitors

Competition is frequently cited as an important factor controlling size of animal and plant populations, yet its existence is more often inferred than demonstrated through controlled experiment (Connell 1980, Weber and Fausch 2003). The lack of resource overlap between two species, for example, may reflect either (a) no competition for that resource or (b) the result of intense competition and competitive exclusion by one species of another.

Nonetheless, patterns consistent with competitive interactions among animals (e.g., local extinctions; displacement in space, time, or food use; fragmentation of once continuous populations; altered patterns of behavior; different size distributions or condition in and out of areas where competition occurs) appear commonly throughout the expanded range of rainbow trout. Depending on the circumstances, competition may be expressed through direct interaction or conflict between individuals over a resource ("contest" competition) or through "exploitation" competition where both use the same resource but differ in their volume or efficiency of use. Although competitive interactions may be asymmetric (affecting one of the competing animals or life history stages more than the other), both competitors suffer negative effects such as reduced access to a resource or physical damage from direct conflict.

Furthermore, the nature and severity of competitive effects may differ with taxonomic relationship of the interacting animals; intense competition is more likely between closely- than distantly-related species (Ross 1986). Species that may compete with rainbow trout are taxonomically diverse (**Table 7**), but most detailed research has focused on competition between conspecifics (other rainbow trout) or between rainbow trout and other salmonids. This reflects the expectation that broad similarities in habitat use, feeding patterns,



**Table 7.** Recent reports of known, likely and unlikely competitors of rainbow trout.

Species	Common name	Reference
<b><i>Known or likely:</i></b>		
<b><u>Salmonidae</u></b>		
<i>Oncorhynchus clarki henshawi</i>	Lahontan cutthroat trout	Peacock and Kirchoff 2004
<i>O. kisutch</i>	coho salmon	Bonar et al. 2005
<i>O. masou</i>	masou salmon	Morita et al. 2004
<i>O. mykiss</i>	rainbow trout, steelhead	Hayes et al. 2004
<i>O. nerka</i>	kokanee	Schneidervin and Hubert 1987
<i>Salmo salar</i>	Atlantic salmon	McKenna and Johnson 2005
<i>Salmo trutta</i>	brown trout	Scott and Irvine 2000, Hayes 1987
<i>Salvelinus fontinalis</i>	brook trout (brook charr)	Lohr and West 1992
<i>Salvelinus leucomaenis</i>	white-spotted charr	Morita et al. 2004
<i>Thymallus thymallus</i>	grayling	Honsig-Erlenburg 2001
<b><u>Cyprinidae</u></b>		
<i>Gila atraria</i>	Utah chub	Schneidervin and Hubert 1987
<i>Lepidomeda vittata</i>	Little Colorado spinedace	Robinson et al. 2003
<i>Ptychocheilus grandis</i>	Sacramento pikeminnow	Reese and Harvey 2002
<i>Rhinichthys osculus</i>	speckled dace	Robinson et al. 2003
<i>Richardsonius balteatus</i>	reidside shiner	Reeves et al. 1987
<b><u>Catostomidae</u></b>		
<i>Catostomus catostomus</i>	longnose sucker	Trojnar and Behnke 1974
<i>C. commersoni</i>	white sucker	Schneidervin and Hubert 1987
<i>C. discobolus</i>	bluehead sucker	Robinson et al. 2003
<b><u>Percidae</u></b>		
<i>Perca flavescens</i>	yellow perch	Fraser 1978
<b><u>Gasterosteidae</u></b>		
<i>Gasterosteus aculeatus</i>	threespine stickleback	Vamosi 2003
<b><u>Galaxiidae</u></b>		
<i>Galaxias brevipinnis</i>	koaro	Kusabs and Swales 1991
<b><u>Other vertebrates</u></b>		
[Not specified]	frogs	Jackson et al. 2004
<i>Ambystoma tigrinum</i>	tiger salamander	Olenick and Gee 1981
<b><u>Invertebrates</u></b>		
<i>Euastacus spp.</i>	Australian spiny crayfish	Jackson et al. 2004
<b><i>Unlikely:</i></b>		
<b><u>Anguillidae</u></b>		
<i>Anguilla bengalensis</i>	African mottled eels	Butler and Marshall 1996
<b><u>Cyprinidae</u></b>		
<i>Clinostomus funduloides</i>	rosyside dace	Rincon and Grossman 1998
<b><u>Salmonidae</u></b>		
<i>O. tshawytscha</i>	chinook salmon	McMichael and Pearsons 1998
<i>Salmo trutta</i>	brown trout	Lucas 1993
<i>Salvelinus fontinalis</i>	brook trout	Strange and Habera 1998



**Table 7 (concluded).**

Species	Common name	Reference
<i>Ambloplites ariommus</i>	shadow bass	Fenner et al. 2005
<i>Lepomis macrochirus</i>	bluegill sunfish	Fenner et al. 2005
<i>Micropterus dolomieu</i>	smallmouth bass	Fenner et al. 2005
<i>M. salmoides</i>	largemouth bass	Shrader and Moody 1997
<b><u>Other vertebrates</u></b>		
<i>Aonyx capensis</i>	Cape clawless otters	Butler and Marshall 1996

The list is not exhaustive, but includes reports from locales in North America, Europe, Japan, Australia and New Zealand to emphasize the diversity of real or suspected competitors. Because competitive interactions affect both competing taxa, this also indicates where rainbow trout may impose competitive pressures on other species.

their possession of both highly similar and yet species-specific patterns of behavior and communication. For example, in staged contests between juvenile steelhead and coho salmon, steelhead tended to display more than coho, larger fish chased more while small fish displayed more, and the larger fish won consistently independent of species (Young 2003). When rainbow trout were pitted against juvenile Atlantic salmon, resident fish always outperformed challengers, regardless of species (Volpe et al. 2001). This was consistent with McKenna and Johnson's (2005) assessment that rainbow trout and juvenile Atlantic salmon occupied similar ecological niches in Lake Ontario drainages, but the competitive effects of the trout apparently declined with increasing temperature (Coghlan 2005). Rainbow trout were also competitively superior to white-spotted charr (*Salvelinus leucomaenis*), but not the sympatric masou salmon in Japan (Hasegawa 2004, Morita et al. 2004).

Ecological and behavioral similarities across salmonid taxa extend to reproductive activity as well as the more commonly addressed feeding and habitat. Interference-competition involving redd superimposition of brown and rainbow trout (Hayes 1987) limited spawning success of both species (egg deposition to fry emergence: 2.1 percent for rainbow trout, 0.2 percent for brown trout). Late spawning rainbows experienced the highest spawning success. Spring-spawning rainbow trout superimposed 13 percent and 3 percent of native, fall-spawning Dolly Varden (*Salvelinus malma*) and white-spotted charr in a small stream in Hokkaido, Japan.

As inferred by the list of real or potential competitors of rainbow trout (**Table 7**), the nature of interspecific competitive interactions faced by rainbow trout is likely to include both contest and exploitative forms of competition. Many of these interactions lead to concerns over the fate of native fishes, including several cyprinoids and various subspecies of cutthroat trout in

the western United States. However, these interactions are not always negative. Nilsson and Northcote (1981) describe how apparent habitat displacement of cutthroat trout by rainbow trout resulted in more piscivory and a higher growth rate by cutthroat trout. Similarly, rainbow trout are not always the winners in competitive interactions. Schneidervin and Hubert (1987) proposed that competition for food among rainbow trout, introduced kokanee, Utah chub (*Gila atraria*) and white sucker (*Catostomus commersoni*) in Flaming Gorge Reservoir contributed to limited stocking success of the trout.

The nature of competition is such that studies tend to focus on the interactions of species and often overlook subtle influence of environment on competition or the secondary effects that competitive stress may exert on the general health of interacting species. For example, competitive interactions of rainbow trout with various fishes may be weakened in warm waters. On the basis of little dietary overlap between trout and three native warmwater fishes (smallmouth bass, shadow bass, bluegill sunfish), Fenner et al. (2005) doubted that competition for food occurred. Steelhead held with Sacramento pikeminnow exhibited much poorer growth at 20 to 23 °C, when pikeminnow initiated more interactions with trout, than at cooler temperatures (15 to 18 °C) (Reese and Harvey 2002). Similarly, steelhead dominated steelhead/redside shiner interactions at low (12 to 15 °C), but not high (19 to 22 °C), temperatures (Reeves et al. 1987), but even these relationships can be complex. In aquarium and stream tank experiments, small, subordinate steelhead escaped damage from dominant steelhead by joining groups of shiners (Tinus and Reeves 2001).

Furthermore, competitive interactions and the status resulting from them may generate physiological effects in rainbow trout that are difficult to detect but that may reduce their performance or viability in

nature. For example, Li and Brocksen (1977) recorded increased variance in routine metabolism, growth rate, consumption rate, and growth efficiency with increased density, all likely due to intraspecific competition. Subordinate rainbow trout had higher rates of sodium uptake across the gill than dominant fish (Sloman et al. 2004), apparently due to changes in gill permeability that resulted in higher throughput of water and increased sodium efflux. Such changes may increase susceptibility to ion regulatory challenges and increase metabolic cost of ion regulation. Subordinate animals may avoid competition with dominant fish by shifting feeding and activity cycles, behaviors involving the pineal and its hormone melatonin. Social stress affects circulating melatonin (Larson et al. 2004).

### Parasites and disease

Rainbow trout may harbor a wide array of parasites, but few appear to exert strong impacts on fish in Region 2. Buchmann et al. (1995) found published reports of 169 taxa of parasites from rainbow trout worldwide, including representatives of seven major animal groups: Monogenea - monogenetic trematodes (single host in the life cycle), Digenea - digenetic trematodes (more than one host in the life cycle), Cestoda - tapeworms, Nematoda - roundworms, Acanthocephala - thorny-headed worms, Crustacea - copepods and their relatives, and Hirudinea - leeches. These same major categories have also been recorded from Region 2, as have representatives of additional groups including bacteria, fungi, ciliates, flagellates, myxozoans (cause of whirling disease, the greatest concern to fish managers in the western United States and elsewhere), and microsporidians (**Table 8**).

Clearly, the diversity of potential parasites is high. Nonetheless, the simple presence of a parasite in Region 2 may not be a cause for alarm, but the potential for transmission to rainbow trout increases with occurrence of a parasite in cool waters or in other species of salmonid fishes and their relatives (e.g., golden, brown and cutthroat trout, mountain whitefish). On the other hand, infection by parasites such as the causative agent of whirling disease, *Myxobolus cerebralis*, may have massive economic and practical impacts, with destruction of large numbers of fish and/or closure of a hatchery until it is subsequently certified as parasite-free. Similarly, rates of transmission to and among rainbow trout in the wild are likely to be much lower than among hatchery fish held in high-density rearing facilities, although whirling disease in particular may wreak havoc on wild stocks of trout (see below). Finally, visually obvious parasites in fish taken by anglers, even

if those parasites have no effect on tissue quality and pose no threat to humans, may generate problems ranging from declines in the number of licenses sold to negative media reports.

It behooves fisheries personnel to develop at least a fundamental understanding of the major categories of fish parasites, including the means to identify them, their basic life cycles, the maladies they may cause, and best practices for preserving samples for subsequent accurate identification by trained professionals. Even armed with such knowledge, a manager's options for control or elimination of many parasites are highly constrained. Effective treatments are often unknown, and existing chemical safety regulations limit the number of compounds allowed for treatments of fishes intended for human consumption or of water that may be released into the environment. Additional information on regulations about, and compounds potentially available for, treatment of parasites and other fish diseases may be found in Nickum et al. (2004) and on the website for the U.S. Fish and Wildlife Service (2005) Aquatic Animal Drug Approval Partnership Program (<http://www.fws.gov/fisheries/aadap/ACCESS/states.html>).

As noted previously, the greatest parasitic threat to rainbow trout in Region 2 at present is whirling disease. Caused by a metazoan, *Myxobolus cerebralis*, the disease affects stream-dwelling salmonids in the northeastern and western United States. Infected fish may have a darkened tail, twisted spine, or deformed head (shortened, twisted jaws). Young fish may also swim erratically (whirl). While other diseases and even genetic conditions can cause these signs as well, managers should request immediate reports of any fish exhibiting such symptoms.

The life cycle of the parasite requires two hosts (**Figure 6**): a fish and an annelid worm. Larval *Myxobolus cerebralis* colonize the head and spinal cartilage of fingerling trout, reproduce rapidly, damage cartilage, and place pressure on the nervous system. Damage to the skeletal and nervous systems cause the fish to swim erratically, often uncontrollably in circles, making them particularly susceptible to predators and interfering with their ability to feed. When an infected fish dies, large numbers of *M. cerebralis* spores (each about the size of a red blood cell) are released into the water and settle in sediments. Spores are subsequently eaten by *Tubifex tubifex*, a segmented (annelid) worm that lives in fine sediments. Spores then transform into an active, infective larval stage termed a triactinomyxon that is released into the water. Triactinomyxon larvae float in the water until they contact a fish host, renewing

**Table 8.** Examples of major groups and genera of parasites recorded from rainbow trout or other salmonids. (Becker and Brunson 1967, Buttner and Hamilton 1976, Ching 1984, Weekes and Penlington 1986, Woo and Wehnert 1986, Dick et al. 1987, Szalai and Dick 1988, Bates and Kennedy 1990, Dies 1990, Buchmann et al. 1995, Mitchum 1995, Buchmann and Bresciani 1997, Varley and Schullery 1998, Pottinger and Day 1999, McKinney et al. 2001, Choudhury et al. 2004, Gieseke et al. 2006, FAO Fisheries and Aquaculture Department (no date).)

<b>Bacteria</b>	<b>Digenean trematodes</b>
<i>Aeromonas</i> (golden trout)	<i>Apophallus</i> (brook trout)
	<i>Clinostomum</i>
<b>Fungi</b>	<i>Crepidostomum</i> (brook trout)
<i>Ichthyophonous</i>	<i>Diplostomum</i>
<i>Saprolegnia</i> (brown trout)	<i>Tylodelphys</i>
<b>Ciliates</b>	<b>Cestodes</b>
<i>Amphiphrya</i>	<i>Bothriocephalus</i>
<i>Apiosoma</i>	<i>Corallobothrium</i>
<i>Capriniana</i>	<i>Diphyllbothrium</i> (cutthroat trout)
<i>Chilodonella</i>	<i>Ligula</i>
<i>Epistylis</i>	<i>Proteocephalus</i> (cutthroat trout)
<i>Ichthyophthirius</i>	
<i>Trichodina</i>	<b>Acanthocephala</b>
<i>Trichodinella</i>	<i>Acanthocephalus</i>
	<i>Neoechinorhynchus</i>
<b>Flagellates</b>	<i>Pomphorhynchus</i>
<i>Costia</i>	
<i>Cryptobia</i>	<b>Nematodes</b>
<i>Hexamita</i>	<i>Capillaria</i> (cutthroat trout)
<i>Ichthyohodo</i>	<i>Truttaedacnitis</i>
	<i>Capillaria</i> (cutthroat trout)
<b>Microsporidia</b>	<i>Contracaecum</i>
<i>Loma</i>	<i>Cystidicola</i>
<i>Nucleospora</i>	<i>Eustrongylides</i>
<b>Myxozoa</b>	<b>Parasitic Crustacea</b>
<i>Henneguya</i> (mountain whitefish)	<i>Argulus</i> (unidentified salmonid)
<i>Myxobolus</i>	<i>Ergasilus</i>
<i>Tetracapsula</i>	<i>Lernaea</i>
	<i>Salmincola</i> (cutthroat trout)
<b>Monogenean trematodes</b>	<b>Leeches</b>
<i>Dactylogyrus</i>	unidentified genus (cutthroat trout)
<i>Eubothrium</i>	<i>Piscicola</i>
<i>Gyrodactylus</i> (cutthroat trout)	
<i>Proteocephalus</i>	
<i>Tetraonchus</i> (mountain whitefish)	
<i>Triaenophorus</i>	

Taxonomy as presented in original source. Photographs of a wide variety of the Wyoming parasites on host fishes are available at: <http://gf.state.wy.us/downloads/ppt/parasitesofwyomingfishes.ppt> and <http://gf.state.wy.us/downloads/pdf/parasitesofwyomingfishes.pdf>.

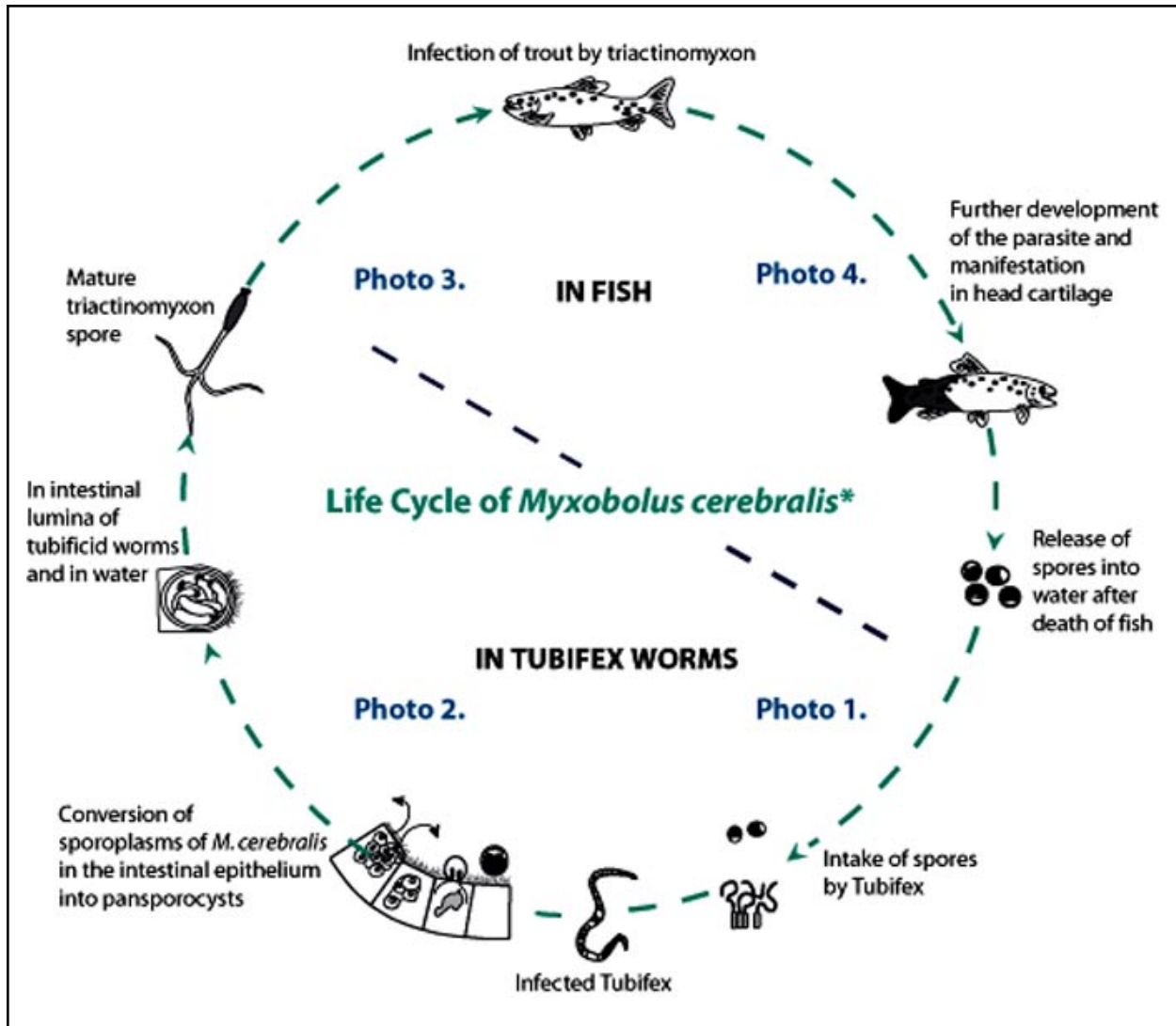


Figure 6. Life cycle of the whirling disease parasite. Matbouli et al. 1992 .

the cycle. At present, once established in a stream, the parasite cannot be eradicated, nor can its worm host, without potentially damaging the ecosystem. Whirling disease has no known human health effects.

Until the 1990's, *Myxobolus cerebralis* was primarily a problem in hatchery settings, but that changed rapidly (Gilbert and Granath 2003). In drainage basins where *M. cerebralis* has been detected, wild rainbow trout populations have declined in both Montana (Vincent 1996, Baldwin et al. 1998) and Colorado (Nehring and Walker 1996). For example, from 1978 to 1991, Montana's Madison River supported a stable wild trout fishery (Vincent 1996). Rainbow trout populations plummeted, however, from 3,300 fish per mile estimated in 1991 to 300 per mile in 1995 along a 56-mile section of the river (D. Vincent personal communication cited in Rognlie and Knapp

1998). Similar declines have been reflected in poor recruitment in the Middle Park sections of the Colorado River, which previously supported high densities of age-0 rainbow trout (Nehring and Thompson 2001 cited in Sipher and Bergerson 2005). The parasite can also be spread in its spore form by birds and humans (particularly boaters and anglers) and their equipment.

*Myxobolus cerebralis* appears capable to infect all salmonid fishes, but susceptibility to infection differs among species (Table 9). Gilbert and Granath (2003) noted that although rainbow trout are most susceptible to disease, the parasite is able to infect numerous species of salmonid fishes, including sockeye salmon, golden trout, cutthroat trout, brook trout, bull trout (*Salvelinus confluentus*), steelhead, chinook salmon, Atlantic salmon, and brown trout. All subspecies of cutthroat trout and the mountain whitefish are also quite

**Table 9.** Susceptibility to whirling disease among species of salmonids found in Region 2.

Species	Common Name	Susceptibility Code
<i>Oncorhynchus mykiss</i>	Rainbow trout	3
<i>Oncorhynchus mykiss</i>	Steelhead	3
<i>Oncorhynchus clarki bouveri</i>	Yellowstone cutthroat	2
<i>Oncorhynchus clarki lewisi</i>	West slope cutthroat	2
<i>Oncorhynchus clarki pleuriticus</i>	Colorado River cutthroat	2
<i>Oncorhynchus clarki virginalis</i>	Rio Grande cutthroat	2
<i>Oncorhynchus clarki stomisa</i>	Greenback cutthroat	2
<i>Salvelinus fontinalis</i>	Brook Trout	2
<i>Salvelinus confluentus</i>	Bull trout	1
<i>Salvelinus namaycush</i>	Lake trout	0 S
<i>Salmo trutta</i>	Brown trout	1
<i>Prosopium williamsoni</i>	Mountain whitefish	2 S

Based on laboratory or natural exposure to *Myxobolus cerebralis* at vulnerable life stages. Susceptibility: 0 = resistant, no spores develop; 1 = partial resistance, disease rare and develops only when exposed to very high parasite doses; 2 = susceptible, clinical disease common at high parasite doses, but greater resistance to disease at low doses; 3 = highly susceptible, clinical disease common; S = susceptibility is unclear (conflicting reports, insufficient data, lack of *M. cerebralis* confirmation). Modified from: Whirling Disease Initiative, Montana Water Center, Montana State University, Bozeman, Montana 59717; <http://whirlingdisease.montana.edu/about/transmission.htm>.

susceptible. In recent years, however, considerable interest has focused on rainbow trout strains, particularly the Hofer strain from Germany, that exhibit reduced susceptibility to the parasite. Susceptibility to infection also depends on the age of the fish (**Table 10**). Young individuals whose cartilaginous skeletons have not been fully replaced by bone are particularly susceptible.

Whirling disease has not been detected in Kansas, Nebraska, or South Dakota (Whirling Disease Initiative website, <http://whirlingdisease.montana.edu/default.asp>). There is no monitoring for the disease in Kansas because trout fishing is a put-and-take fishery using certified whirling-disease-free private hatchery fish. Nebraska conducts a monitoring program for state and private hatchery fish that are exported. In South Dakota, importation and transportation of potential carriers of the disease are regulated, and all hatcheries are screened annually for the disease.

Whirling disease has been known from Colorado since 1987 (Colorado Division of Wildlife 2008). In

Colorado, it occurs in all coldwater drainages except the Animas and North Republican rivers. In 1998, 11 of Colorado's 16 hatcheries were contaminated by the parasite, but due to eradication efforts by the CDOW, by December 2004 just six were still considered positive for the parasite. The state imposes fish health inspections on public and private hatcheries and fish culture facilities, requires a fish health disease certification on imported fish, has an extensive whirling disease research program, and instituted a policy in 2000 that calls for the cessation of stocking of any WD-positive trout into any waters with self-sustaining salmonid fish populations.

Whirling disease was first detected in Wyoming in 1988 (Wyoming Game and Fish Department 2008b), and as recently as April 2008, whirling disease was discovered in one of the state hatcheries and in fish recently transferred from that hatchery to two other rearing stations (Wyoming Game and Fish Department press release, 1 April 2008). Managers have moved rapidly to identify possible infections elsewhere in the

**Table 10.** Relationship between life history stage of a fish and the likelihood that stage may transmit whirling disease.

Life history stage	Source of parasite & parasite stage	Likelihood of detection
Eggs*	No	Not applicable
Fry, alevins	Yes – immature parasite stages	Low to high
Juveniles, adults	Yes – spores	Moderate to high

\*assumes disinfection and no transfer of water or material that might carry the parasite. Modified from: Whirling Disease Initiative, Montana Water Center, Montana State University, Bozeman, Montana 59717; <http://whirlingdisease.montana.edu/about/transmission.htm>.

hatchery system, and have moved plans for renovation of the affected hatchery to the top of the priority list. State regulations forbid release of live fish or fish eggs without the consent and supervision of the WYGFD or transport of live fish or live fish eggs from the water of capture.

## Symbiosis

The term symbiosis describes relatively stable relationships between two (or more) species. The concept in its simplest form encompasses mutualism, where both organisms benefit from the interaction; commensalism, where one benefits and the other is not harmed; and parasitism, where one benefits and the other is harmed. Excluding parasites (addressed elsewhere in this assessment) and gastrointestinal microbes recorded from rainbow trout (e.g., see Cahill 1990, Huber et al. 2004), we are aware of a single symbiosis (an apparent commensalism) involving rainbow trout. Small steelhead will take refuge in groups of redband shiner (*Richardsonius balteatus*) to escape competitive attacks from larger steelhead (Tinus and Reeves 2001).

## MANAGEMENT AND CONSERVATION

### *Conservation Status of Rainbow Trout in the Rocky Mountain Region*

As noted elsewhere, rainbow trout are not native to any of the Region 2 states. The International Commission on Zoological Nomenclature (1999) does not list rainbow trout. NatureServe (2006) ranks the species as secure (G5). Two subspecies (California golden trout and Inland redband trout and redband steelhead (*Oncorhynchus mykiss gairdneri*)) have been introduced into Colorado, with the former also introduced to Wyoming; NatureServe (2006) ranks for the golden and redband subspecies are G5T1 and G5T4, respectively, in their native ranges.

### *Potential Threats to Trout Populations*

Resource managers face a difficult balancing act in the western United States, where rare native species concerns and now-wild rainbow trout management may conflict with constituent-driven trout stocking programs. Wild rainbow trout may displace native cutthroat stocks and at the same time are displaced or otherwise compromised by hatchery trout introductions. In turn, hatchery rainbow trout have introduced whirling and other diseases and parasites

to both hatcheries and natural waters. Thus, although attention in what follows focuses on human and other natural threats, several types of threats derive from the various trout stocks themselves.

Rainbow trout fishery declines, and in some cases collapses, have been attributed to increased human activity that has directly altered the original coldwater habitats of this group of fishes. Some examples of human activities directly affecting fisheries are hydropower development, forest management, livestock grazing, road development, logging, and mining (Everest et al. 1989).

Work directed at maintaining healthy trout fisheries result in a variety of secondary benefits, including improved water quality, mitigation of droughts and floods, increased groundwater replenishment, improved wildlife habitat, improved recreational opportunities, increased cycling and movement of nutrients, maintenance of biodiversity, and increased economic values (from recreation and tourism, real estate, and water availability; [www.tu.org](http://www.tu.org)).

Rainbow trout and other fishes require complex aquatic habitats and healthy riparian zones to establish and maintain reproducing populations. Both aquatic and riparian habitats have been declining because of increased human activity over the last several decades. For example, excessive sedimentation due to agricultural, mining, road-building, logging, and other activities reduces primary and invertebrate production (a major portion of trout diets), destroys submerged aquatic vegetation (important for cover), and fills crevices and rocky interstices (refuges for small fish and eggs). While the following list of threats to rainbow trout is not comprehensive, it does include topics of particular relevance to Region 2.

#### Anthropogenic disturbance

#### *Agriculture*

Many activities associated with rangeland management and farming activities adjacent to flowing or standing waters will affect fish habitats directly or indirectly. Fortunately, these effects can be reversed to varying degrees given careful thought and planned habitat management (Bowers et al. 1979).

**Irrigation:** In 2000, agricultural irrigation accounted for approximately 90 percent of Colorado's total annual water consumption; values for other Region 2 states were Kansas – 56 percent, Nebraska

– 71 percent, South Dakota – 71 percent, and Wyoming – 87 percent (USGS, <http://water.usgs.gov/watuse>). Particularly relevant to fisheries managers is the fact that control of and priority for use of available water varies across states and usually rests in the hands of entities other than state or federal resource management agencies (also see section on Outdated Water Rights Systems below). Examples from Region 2 states include Colorado - Division of Water Resources, Water Conservation Board, Ground Water Commission, Department of Public Health and Environment (Water Quality Control Division); Kansas - Department of Water Resources, Department of Health and Environment (Bureau of Water); Nebraska - Department of Natural Resources, Department of Environmental Quality (Water Quality Division); South Dakota - Department of Environment and Natural Resources; Wyoming - State Engineer, Department of Environmental Quality. Furthermore, legislation may influence water management practices directly. For example, legislation in Colorado makes adherence to various “best management practices” for irrigation voluntary (e.g., Waskom 1994), and while application of better irrigation management and technology increases, motivation to make such improvements tends to be constrained by practical (e.g., time and effort constraints, perceived sufficiency of available water) or economic concerns (Bauder et al. 1999).

Irrigation and irrigation practices have long affected rainbow trout and other fishes in a variety of ways (Clothier 1953a reviewed in Der Hovanisian 1995). Particularly problematic are irrigation canals with high flow rates compared to those of the source stream (high flow ratios). These conditions may be influenced by placement of intakes adjacent to wing dams, on curves of rivers, or near other types of diversions that increase current velocity, inject fish into canals, or inhibit return to the source river (with greatest influence on young or small fish; Der Hovanisian 1995). Fish moving downstream and young-of-the-year fish are often drawn into headgates while fish moving to upstream spawning or other sites have difficulty passing irrigation diversions and are often swept into irrigation canals (Anonymous 2003). Extensive cover, including areas where pools form, also increases losses as fish take refuge as water levels drop rather than return to the source stream (Der Hovanisian 1995).

Secondary and age- or size-specific effects exert considerable influence on irrigation-related loss. High population density and proximity to spawning areas increase the likelihood that rainbow trout and other fishes will be entrained into the canals; young-of-the-

year trout constitute major fractions of fish observed or dying in canals. Irrigation withdrawals can also disrupt spawning, increase siltation, increase water temperatures above tolerable levels, and increase local population densities and density-dependent interactions (e.g., competition, predation; see Der Hovanisian 1995). In portions of the Snake River and its major tributaries, reservoirs and irrigation diversions have resulted in reduced streamflows, degraded water-quality conditions, loss of habitat, and proliferation of non-native, warmwater species of fish (Maret 1995 in Clark et al. 1998).

**Cattle grazing:** Grazing, particularly on public lands controlled by the USFS and other federal and state agencies, has become a tremendously contentious issue in the western United States. As an internet search for sites dealing with public lands grazing will verify, many believe that damage caused by cattle grazing to aquatic and terrestrial systems on these lands represents a failure of management agencies to protect valuable natural resources while artificially perpetuating an industry romanticized for more than a century in literature and film.

Insofar as fishes and fisheries are concerned, uncontrolled grazing along streams, ponds, and wetlands leads to excessive disturbance of naturally occurring banks as well as damage to structures placed by various stream enhancement projects (Binns 2004; [www.ngpc.state.ne.us](http://www.ngpc.state.ne.us)), and will cause root bound trees to collapse. Trees provide fish with cover and food, as well as keep the water cool. As banks erode, there is an increased level of silt in the water that can suffocate eggs as well as abrade fish gills (Giuliano 2006). Changes to vegetation adjacent to watercourses, from plowing pastures, planting and harvesting farm crops, or replacing a forest with a pasture, directly affect available resting and hiding cover and increase water temperatures. Grazing activities have led to major declines in both native and nonnative trout species throughout Region 2.

The Federal grazing fee, which applies to Federal lands in 16 western states on public lands managed by the Bureau of Land Management (BLM) and the USFS, is adjusted annually and is calculated by using a formula originally set by Congress in the Public Rangelands Improvement Act of 1978. These 16 states include all Region 2 states as well as Arizona, California, Idaho, Montana, Nevada, New Mexico, North Dakota, Oklahoma, Oregon, Utah, and Washington. Under this formula, as modified and extended by a presidential Executive Order issued in 1986, the grazing fee cannot

fall below \$1.35 per animal unit month (AUM); also, any fee increase or decrease cannot exceed 25 percent of the previous year's level. An AUM is the amount of forage needed to sustain one cow and her calf, one horse, or five sheep or goats for one month. The grazing fee for 2008 is \$1.35 per AUM, the same level as it was in 2007. The figure is adjusted each year according to three factors: current private grazing land lease rates, beef cattle prices, and the cost of livestock production. In effect, the fee responds to market conditions, with livestock operators paying more when conditions are better and less when conditions decline. Without the requirement that the grazing fee cannot fall below \$1.35 per AUM, the 2008 fee would have dropped below one dollar per AUM because of declining beef cattle prices and increased production costs from the previous year.

#### *Logging for timber and for water*

Logging activities reduce intragravel dissolved oxygen concentrations because stream temperatures increase after the riparian canopy is removed; logging also increases fine sediment concentrations (Bjornn and Reiser 1991). Some Colorado state officials have advocated logging state and national forests to increase the amount of water available for use in streams rather than for feeding dense trees in high elevations. Research has shown that between 25 and 40 percent of the watershed forest would need to be cut to produce the desired increase in water yield. The increase would come in wet years where there is more than enough water, and reservoirs would need to be constructed to catch the water for future need. Logging for water would ultimately be catastrophic for local stream fisheries due to increases in sediment and muddy waters, loss of woody debris that provides important trout habitat, and increases in water temperature due to decrease in shade ([www.tu.org](http://www.tu.org)).

#### *Mining*

Hard rock mine waste, which is believed to be the single largest polluter in the United States, contaminates over 40 percent of the headwaters of western watersheds. There are nearly 500,000 abandoned mines across the west. In Colorado alone, there are 20,299 abandoned mine sites and approximately 1,300 miles of adversely affected waters ([www.tu.org](http://www.tu.org)). Elevated concentrations of arsenic, cadmium, copper, lead, and zinc near mines or in affected waters may be fatal to fishes as they cause hypertrophy, degeneration and necrosis of epithelial cells that support normal gill function (Farag et al. 2003).

#### *Roads, road construction, stream channelization, population fragmentation*

The use of roads and construction of new roads or other development projects adjacent to streams have serious implications to fisheries due to habitat degradation. Roads and developments constructed in valleys take advantage of relatively flat topography and gentle valley gradients; thus, they also generally lie near or along streams and rivers. Problems arise when the width of a valley becomes restricted as this frequently leads to roads that occupy, realign, encroach on, and cross stream channels (Ruediger and Ruediger no date). Affected stream segments are generally shorter than before alteration, with higher gradients, swifter currents, larger grain substrata over the long term (construction and subsequent bank or hillside erosion will increase sediment load), few slow-moving backwaters, and reduced riparian communities. Banks may be stabilized by riprap, eliminating undercut bank refuges, and road crossings may impede or halt upstream movements of fishes, leading to population fragmentation (Dunham et al. 1997). In general, habitat complexity is much reduced, and both spawning and rearing habitat for rainbow trout and other salmonids are largely eliminated in the affected sections. Road construction also leads to release of toxic chemicals associated with cement and phenolic compounds from road surfacing compounds (Crisp 1993).

Managers should expect surprises in the nature of developments that can influence aquatic ecosystems and fisheries. For example, whitewater parks are becoming popular in Region 2. One website (<http://www.ripboard.com/community/whitewaterpark.shtml>) lists 11 such parks in Colorado with another four planned or under construction in Colorado; one whitewater park is in Wyoming. Basic features of whitewater park construction suggest considerable local impact on trout fisheries and water quality. These parks use boulders set in cement to mimic natural river features such as waves and holes with associated plunge pools, fast flowing water in mid-channel areas, and lateral and mid-channel eddies (McGrath 2003). Individual instream structures may create different hydraulic features during low, medium, or high flow conditions. Stream bank stabilization, re-grading and terracing, footpath construction, and terraced riparian revegetation are common in park design.

#### *Aquatic hitchhikers/nuisance organisms*

The ecological balance of waters in western states has been compromised by introductions and/or



accidental arrivals of a number of organisms, some of which have been specifically identified as “aquatic nuisance species” (ANS). Collectively, the five Region 2 states have identified at least 29 species as such, including one alga (“didymo” - *Didymosphenia geminata*), nine flowering plants [saltcedar, *Tamarix* spp., is included due to its influence on riparian communities], a freshwater jellyfish (*Craspedacusta sowerbyi*), the rusty crayfish (*Orconectes rusticus*), six molluscs, 10 fishes, and the American bullfrog (*Rana catesbaiana*). Although some species (e.g., American bullfrog) occur in all five states, no species is recognized as present (and thus ANS) on more than three state lists, reflecting a desire by states to identify those organisms most likely to cause or have the potential to cause damage to existing aquatic communities. Some state lists also include species not yet recorded from that state, particularly if they have been reported from adjacent or nearby states or are known to be rapidly expanding their range. For example, hydrilla (*Hydrilla verticillata*) was listed as not yet occurring in Colorado and Kansas, as were giant salvinia (*Salvinia molesta*) for Colorado, rusty crayfish for Kansas, New Zealand mudsnail for Kansas and South Dakota, quagga mussel from Colorado and Wyoming, and round goby (*Neogobius melanostomus*) and ruffe (*Gymnocephalus cernuus*) from Kansas.

Of the 29 species listed, only one might be viewed as a success story for control. The rusty crayfish was introduced into a Wyoming pond, but it was subsequently removed by state officials at considerable cost to both the state and the company that imported the prohibited species (<http://gf.state.wy.us/downloads/pdf/RegionalNews/RKrustycrayfish.pdf>). However, considerable effort at both state and federal levels is being directed at public education about particularly vagile and invasive species (e.g., Eurasian watermilfoil (*Myriophyllum spicatum*), zebra mussel (*Dreissena polymorpha*), round goby (*Neogobius melanostomus*)), how to identify them and how to control their accidental spread (see websites for: USDA National Invasive Species Information Center, <http://www.invasivespeciesinfo.gov/>; USGS Nonindigenous Aquatic Species program, <http://nas.er.usgs.gov/>; US Fish and Wildlife Service Aquatic Nuisance Species program, <http://www.fws.gov/Contaminants/ANS/ANSContacts.cfm>; the 100th meridian initiative, <http://www.100thmeridian.org/>; the intergovernmental Aquatic Nuisance Species Task Force, <http://www.anstaskforce.gov/default.php>).

## Energy development

The BLM and the USFS are proposing unprecedented levels of gas, oil, and coal bed methane exploration and extraction on public lands, with possible severe impacts on crucial fish and wildlife habitats throughout Montana, Wyoming, Colorado, Utah, and New Mexico. The White House has placed an emphasis on domestic energy production as a matter of national security. Trout Unlimited and other conservation organizations believe that short-term energy production should not result in diminished long-term productive capabilities of lands and water that sustain us in a variety of ways. Protection of critical fish habitat and migratory corridors should remain a priority as responsible energy production takes place ([www.tu.org](http://www.tu.org)).

## Chemical pollution

Effluent from a wide array of domestic, agricultural, and industrial sources can affect trout and other aquatic biota (Crisp 1993).

- ❖ Organic materials such as domestic sewage, farm slurry, silage liquor, and various industrial effluents create high demand for microbial oxygen; this in turn depletes dissolved oxygen levels in the water, which stresses fish and may be lethal.
- ❖ Increases in suspended solids can influence the fish at all stages: redds can be choked by the silt; if interstices are filled, alevins cannot “swim up” and are asphyxiated; suspended solids and silt affect the sight-feeding ability of rainbow trout and can abrade gill membranes.
- ❖ Toxic materials found in effluent can poison fish or result in high oxygen demand, but they can also affect fish indirectly through their effects on suspended solids and siltation.
- ❖ Inorganic fertilizers and other nutrients commonly wash off the land in large quantities, result in eutrophication (enrichment) of streams, and can support growth of toxic blue-green algae in lake environments; effluent discharge may be consistent and or sporadic and result in drastic impacts on food availability for fish.

- ❖ Effluent can have drastic effects on pH, which in turn may alter animal physiology, solubility of organic and inorganic compounds, and other aspects of ecosystem function.
- ❖ Heated effluent affects water temperature, altering dissolved oxygen concentrations in the receiving waters.
- ❖ Concern is growing rapidly over endocrine disruptors in effluent from population centers (Gray et al. 2000); such compounds trace to a variety of drugs used for birth control and other purposes, are active at very low concentrations (making detection difficult), and may affect vertebrate animal maturation and gender and thereby influence the potential for successful spawning in fish and amphibian populations.

### *Dams*

Dams cause discontinuities in stream and river systems, thereby changing long- and short-term stream discharge patterns and permanently altering riverine ecosystems. These discontinuities disrupt gene flow among previously interbreeding populations, setting the stage for loss of genetic diversity through selection and drift, and interfere with or eliminate movements within the system, especially dispersal of young fish and migration to feeding or spawning sites (Gillette et al. 2005). Ecological conditions in reservoirs behind dams are unlike those to which stream fishes are adapted, but they do meet habitat and spawning requirements of a wide array of often predatory fishes adapted to standing or slowly flowing waters. Failure of natural reproduction in trout populations influenced by dams may require hatchery introductions to support sport fisheries. These effects are most obvious, if not most pronounced, in the Columbia River, where salmon abundance is 5 to 10 percent of pre-dam levels due to loss of habitat and access to spawning sites, increased mortality of migrating smolts in reservoirs and dam turbines, and reliance on hatchery fish to support fisheries (Behnke 1998). Dams are common in Region 2 states; in fact, Kansas has the second highest number of dams in the United States (Gillette et al. 2005).

### *Excessive harvest*

Some declines of rainbow trout in healthy fisheries have been associated with over-harvest (Everett 1973, Binns 2004), including depletion of stocks of naturally reproducing rainbow trout in Region 2, with lower fish

densities leading to supplemental stocking. Such fishing pressures can dilute the benefits of other management actions set in place to increase trout biomass.

Although it may sound like a *non sequitur*, even catch-and-release practices may result in excessive harvest. For example, in catch-and-release waters, individual Yellowstone cutthroat trout may be captured multiple times (Kershner et al 1997). While catch-and-release clearly reduces immediate mortality, each capture, handling, and release event generates stress and increases susceptibility to a variety of other factors that may lower vitality or survival and thereby functionally generate harvest beyond what is immediately obvious. Bartholomew and Bohnsack (2005) calculated an average 20 percent post-release mortality for rainbow trout, but estimate this would rise to roughly 50 percent with three catch-and-release events and to near 70 percent with five such events. Initial surprise at such high mortality figures declines in light of Meka's (2004) demonstrations of the effects of hook structure, landing time, and angler experience on structural damage to rainbow trout in a catch-and-release system. Meka and McCormick (2005) also described significant, sublethal physiological responses to these same variables.

### *Changes in water temperature*

Changes in water temperature may exert particularly strong impacts on fishes in thermally well-mixed stream environments (Myrick 1999, Myrick and Cech 2000). At present, short-term changes often result from natural or anthropogenic reductions in stream flow or reduction of riparian canopies that lead to more rapid and extensive warming or cooling depending on the season. Contributors to these changes include drought, water withdrawals, dam operations, and a variety of near-stream development activities.

Present-day managers, however, must address likely long-term effects of increasing temperatures. Predictions relevant to how global warming may affect Region 2 states include (Glick 2006, U.S. Environmental Protection Agency 2008):

- ❖ Increased atmospheric temperature will increase frequency of drought and fires, increase evaporation, and change precipitation patterns.
- ❖ Heavier precipitation in some areas will increase risks of flooding, expand floodplains, increase variability of stream flow, increase velocity during high flow periods, increase

erosion, and reduce water quality and aquatic system health.

- ❖ Droughts, changing patterns of precipitation and snowmelt, and increased evaporation will change availability of water for drinking, and may result in increased competition for water from agriculture, industry, and energy production sectors.
- ❖ Altered precipitation and reduced snowpack will change hydrographs (e.g., timing of peak flows, available water) and thus change water flow to and size of lakes, streams, and wetlands.
- ❖ As waters warm, existing species will be replaced by species adapted to the warmer water, disrupting aquatic system health and allowing non-indigenous and/or invasive species to become established, with particularly severe impacts on high-elevation, coldwater species.
- ❖ Warmer waters will make hypoxia more common, foster harmful algal blooms, and change the toxicity of some pollutants.

Managers should view these concerns and predictions as relevant to planning now. Consider quotes from Field et al. (2007) in the Environmental Protection Agency report: "...[s]pring and summer snow cover has decreased in the U.S. west...", "...[t]he fraction of annual precipitation falling as rain (rather than snow) increased at 74% of the weather stations studied in the western mountains of the U.S. from 1949 to 2004...", "[t]hreats to reliable supply are complicated by the high population growth rates in western states where many water resources are at or approaching full utilization...", and "...streamflow has decreased by about 2% per decade in the central Rocky Mountain region over the last century." Although somewhat dated, conservative estimates by O'Neal (2002; based on several modeled scenarios for continued global warming) suggest loss of 4 to 20 percent of trout and salmon habitat by 2030, 7 to 31 percent by 2060, and 14 to 36 percent by 2090, depending on fish species and model.

#### *Outdated water rights systems*

Competition for water can be intense, particularly in many of the western states. At the time of this publication, the most recent summary of water usage

by states is for 2000 (USGS 2008). Specific usages identified in this state-by-state report include public supply (i.e., water released to public or private water suppliers who then pass it on to a variety of users), domestic, irrigation, livestock, aquaculture, industrial, mining, and thermoelectric power.

The doctrine of prior appropriation (also "Colorado Doctrine") drives water rights in the western states. This doctrine states that while no person may own the water, individuals, municipalities, and corporations may use it for beneficial purposes (state details below). This prior appropriation system allows water users to construct works in arid regions to move water over long distances to where the water is needed and provides for assignment of a water use priority date. Since the investment to construct works to move water long distances is considerable, it was and continues to be important to protect that investment. The first to use (appropriate) the water establishes a water right by diverting water and putting it to a beneficial use; this first use provides the user with the senior water right. During periods of low water availability, senior rights take precedent over any junior rights and must be fully satisfied before junior rights are met. This and the early view that "beneficial uses" meant domestic, municipal, agricultural, or industrial uses led to needs for recreation and wildlife being relegated to very weak positions. All Region 2 states adhere to this doctrine.

**Colorado:** Colorado surface water law (State Constitution, Article XVI, and Colorado Revised Statutes) is based upon the doctrine of prior appropriation or "first in time - first in right", and the priority date is established by the date the water was first put to a beneficial use. A modified form of prior appropriation governs the establishment and administration of groundwater rights (Ground Water Management Act of 1965). What constitutes beneficial use in Colorado is not specified in statute, but previous categories have included natural resource uses such as Aesthetics and Preservation of Natural Environments, Fisheries, Minimum Flow, Recreation, Wildlife Watering and Wildlife Habitat. [Source: Bureau of Land Management, National Science and Technology Center, Western States Water Laws, Colorado Water Rights Fact Sheet, <http://www.blm.gov/nstc/WaterLaws/colorado.html>.]

**Kansas:** Kansas is a "prior appropriation state" in regard to water rights, as spelled out in the state's water appropriation act (KSA 82a-701). It has been illegal since 1978 to use water for any purpose, other than domestic use, without either holding a vested right

or receiving a permit to appropriate water from the Division of Water Resources. This applies to ground and surface water on both private and public property. [Source: Northwest Kansas Groundwater Management District No. 4, <http://www.gmd4.org/law.html>; also, <http://www.ksda.gov>.]

**Nebraska:** The State of Nebraska Constitution (Article XV-6: *Right to divert unappropriated waters*) establishes the doctrine of prior appropriation as the primary determinant of water rights. The Article specifies that highest priority is given to “domestic purposes,” followed by “agricultural purposes” and subsequently “manufacturing purposes.” Of relevance to fisheries managers is an associated Annotation (5. Miscellaneous) that notes the term “divert” does not prohibit nondiversionary appropriations, such as instream flow uses.

**South Dakota:** The Dakota territorial legislature enacted legislation in 1881 establishing a procedure to “locate” surface water rights, and later (1907) the state legislature affirmed the doctrine of prior appropriation. In 1955, legislation made use of ground water also subject to the doctrine of prior appropriation. [Source: South Dakota – Department of Environment and Natural Resources, [http://www.state.sd.us/denr/des/waterrights/wr\\_history.htm](http://www.state.sd.us/denr/des/waterrights/wr_history.htm).]

**Wyoming:** Wyoming’s first surface water laws were enacted in 1875, and more comprehensive laws were adopted along with the state constitution in 1890 (Jacobs et al. 2003). Water rights in Wyoming, as in most of the western states, are regulated by priority and based on the “doctrine of prior appropriation.” Preferred uses of both surface and ground water, in order, are (1) drinking water for both humans and livestock, (2) water for municipal purposes, (3) water for steam engines and general railway use; water for cooking, laundering, bathing, and refrigerating (including the manufacturing of ice); water for steam and hot-water heating plants, steam power plants, and (4) water for industrial purposes (Jacobs et al. 2003).

### *Instream flow*

As human populations and the volume and complexity of their demands grow, concerns over the availability of water for aquatic systems and the recreational benefits they provide also grow (see Gillilan and Brown 1997 for background; Brown 2003). The response by resource management agencies has been to seek “instream flow” rights and allocations that guarantee, or at least increase the likelihood of,

retention of sufficient water in waterways to support normal aquatic ecosystem functions. Water allocations are the purview of the states, which differ in the agencies allocating water rights, acceptance and support of instream flow allocations, and approaches to allocation of ground water vs. surface water (Tellman no date).

- ❖ The **Colorado** Water Conservation Board oversees the instream flow program in Colorado, and acquires instream flow rights through either a new application process or by acquiring established, senior water rights (Merriman and Janicki no date). They also have an active instream flow monitoring and protection program for established water rights. Groundwater and surface water allocation systems are integrated so that impacts on one type of water may affect granting of rights to another type of water (Tellman no date). Water rights may be bought and sold. Where there is no unappropriated water, this system makes room for newcomers without harming previous rights holders.
- ❖ **Kansas** water use is directed by the Kansas Water Plan, developed by the Kansas Water Office and approved by the Kansas Water Authority. The state defines minimum desirable streamflows, and the Chief Engineer withholds from appropriation that amount of water needed to maintain minimum desirable streamflow (K.S.A. 82a-703(b)). The state also can limit permitted withdrawals to ensure that environmental flow needs are met even in times of drought, and can purchase water rights on over-appropriated waterways in order to establish minimum environmental flows. Kansas has a unified water appropriation system. Permit approval in certain areas is subject to minimum streamflow requirements.
- ❖ **Nebraska’s** instream flow law, overseen by their Department of Natural Resources, is among the most restrictive in the West (Zellmer no date). Instream flow waters must come from unappropriated sources, inhibiting sources from donations or purchase. Unappropriated water must be available to provide the approved flow at least 20 percent of the time. Only the Game and Parks Commission and 23 Natural Resource Districts (no individuals) may own an instream flow right. Instream flows may

be appropriated “to maintain the existing recreational uses or needs of existing fish and wildlife species,” and so may not cover enhancements. Finally, an instream flow may only be granted if the demonstrated benefit outweighs economic and social considerations (e.g., recharge for municipal water systems, water quality maintenance, etc.). Individuals may change the purpose of their water right to instream flows, but fear of losing a water right to the state may deter such conversions. Nebraska is the only Region 2 state to treat groundwater and surface water as legally separate systems (Tellman no date).

- ❖ **South Dakota** does not appear to have a specific instream flow program, but has approved water rights for what amounts to instream flow on several occasions (Gillilan and Brown 1997). Among the types of uses requiring a permit are “Recreation use” and “Fish and wildlife propagation” ([http://www.state.sd.us/denr/des/waterrights/wr\\_permit.htm](http://www.state.sd.us/denr/des/waterrights/wr_permit.htm)); while the term “propagation” is somewhat unusual in this context, these recognized uses should cover instream flow needs. Permits for water use are reviewed and awarded by the Water Management Board and Chief Engineer, South Dakota Department of Environment and Natural Resources, and while they operate separate groundwater and surface water allocation systems, they explicitly unify criteria and priorities for allocation.
- ❖ **Wyoming** has been assessing and acquiring instream flow allocations for more than 30 years, and is presently working under the guidance of a 5-year water management plan (Annear and Dey 2006). The Game and Fish Department selects stream segments on which to file for a right. The Water Development Commission then applies for the appropriation following a hydrologic study to determine if instream flow can be provided from unappropriated natural flow of the stream or if storage water will be needed for part or all of the instream use. That study is supplied to the State Engineer, who conducts a public hearing and decides whether to approve, approve with modifications, or reject the application. Wyoming regulates groundwater and surface

water separately, but explicitly integrates them in the allocation process (Tellman no date). The presumption is that waters are not connected unless proven otherwise.

#### *Fish stocking in wilderness and other protected areas*

Of the five Region 2 states, only Kansas has no land designated as wilderness, and only two wilderness areas occur in each of Nebraska (12,429 acres; 0.03 percent of state acreage) and South Dakota (77,570 acres; 0.16 percent state acreage; see [wilderness.net](http://wilderness.net) for statistics and maps). Nonetheless, anglers fish for rainbow trout in Soldier Creek, Soldier Creek Wilderness Area, Nebraska National Forest, and in South Dakota’s Black Hills National Forest, which encompasses the Black Elk Wilderness Area. In contrast, each of Colorado and Wyoming contain more than 3 million acres of wilderness that constitutes more than 5 percent of the land area in each state, predictably focused on high altitude sections of the Rocky Mountains. The USFS administers all of the wilderness area in Wyoming and roughly 93 percent of the wilderness acreage in Colorado; the remainder is administered by the BLM, the National Park Service, and the U.S. Fish and Wildlife Service.

Because relatively few fishes colonized mountain watersheds of the western United States after the last glaciation, approximately 95 percent of roughly 16,000 high elevation lakes were historically fishless. Native and nonnative sport fish have been introduced into many historically fishless lakes in these areas (over 60 percent of these high mountain lakes have been stocked; Pilliod and Peterson 2001), creating conflicts between managing natural ecosystems and providing opportunities for recreation (Knapp et al. 2001, Wiley 2003b). Such conflicts grow naturally from state desires to develop, expand, and manage remote or wilderness fisheries (section 4(d)(8) of the 1964 Wilderness Act; P.L. 88-577) and federal mandates to protect the biological integrity of wilderness (Pilliod and Peterson 2001, Wiley 2003b, USDA Forest Service 2007). For example, the USFS policy regarding fisheries management in wilderness specifies no stocking of exotic species and places highest priority for stocking on Federal threatened or endangered indigenous species (species occurring naturally in the area), followed in order by other indigenous species, threatened or endangered native (to the United States) species, and other native species. These guidelines relegate rainbow trout to the lowest priority category.

Another policy (USDA Forest Service 2007) directs the USFS to “stock barren waters only after determining that the scientific and research values of such barren waters will not be eliminated from a wilderness...” Fish introductions into previously fishless lakes have affected lake nutrient cycling, algal dynamics, and the invertebrate fauna, and in many areas these introductions have caused declines in resident amphibians (Knapp et al. 2001). However, many of these effects followed establishment of self-sustaining populations stocked before wilderness-related concerns arose (Wiley 2003b). In any event, once likely effects of fish stocking have been identified within a wilderness, managers should be able to target specific lakes for protection or restoration without overly compromising fishing opportunities in remote and environmentally pristine areas (Pilliod and Peterson 2001).

#### Natural disturbance

##### *Drought*

Low flows significantly alter and limit trout habitat in streams. In addition, low flows deposit silt, fill interstices between rocks and gravel, and limit availability of invertebrate foods for trout, thus influencing both wild and stocked fish. During drought, juvenile habitat is often reduced significantly, forcing these fish to occupy adult habitats where

they are more vulnerable to predators and less able to compete for food. Flushing flows, if they occur or can be produced from reservoir releases, can clean substrates of accumulated silt and provide habitat for macroinvertebrate prey of trout.

##### *Fire*

Recent large and sometimes catastrophic fires in the western states, including some in Region 2, have attracted considerable public concern over the effects on land, timber, terrestrial wildlife, structures, and human life. Clearly, decades of fire suppression have contributed to the frequency and severity of such fires (Donovan and Brown 2007). The less easily observed inhabitants of aquatic systems receive less attention, yet aquatic ecosystems often suffer severe post-fire impacts.

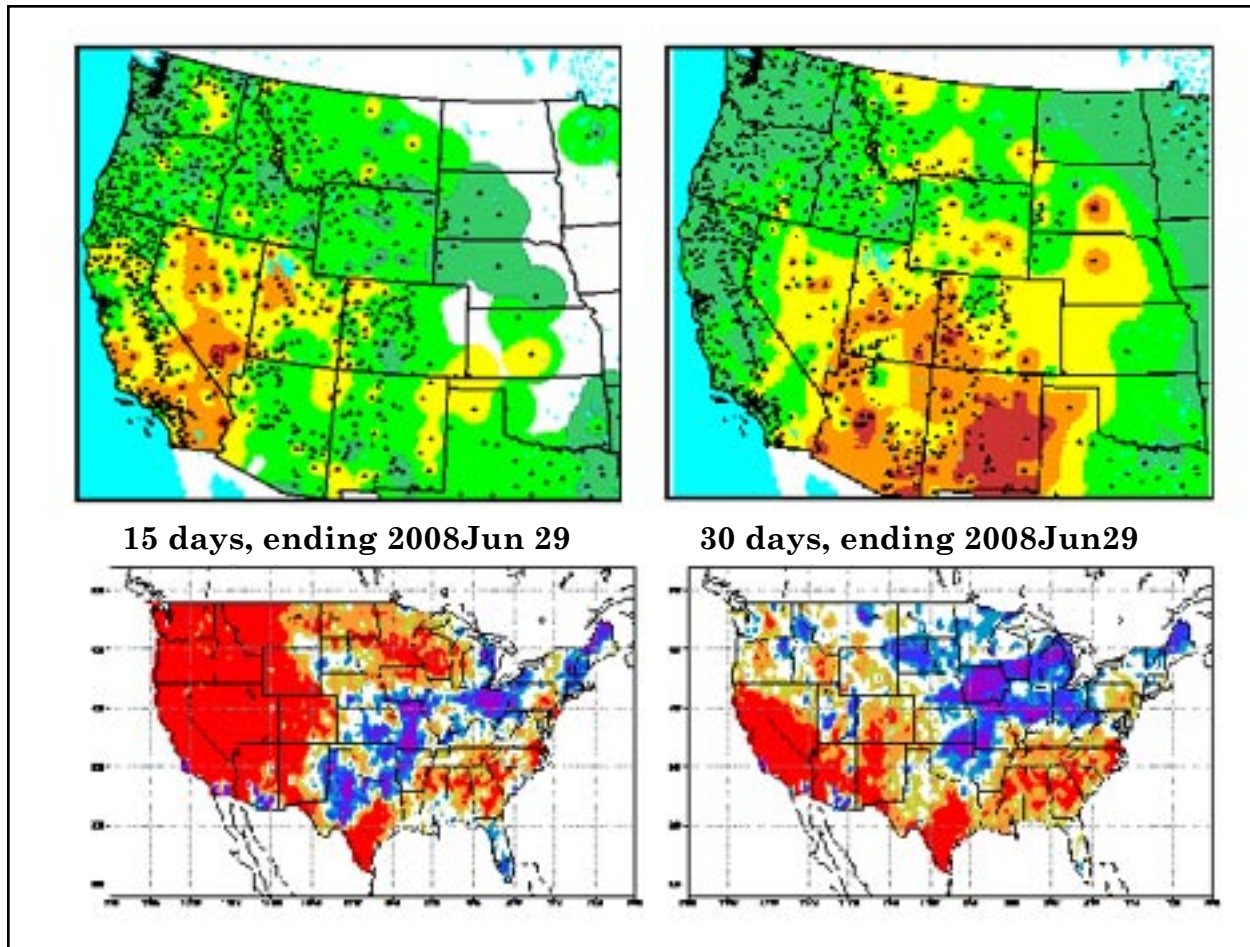
Fire is common in the Rocky Mountain area in general (**Table 11**) and sufficiently common in all Region 2 states to suggest potentially widespread impact on virtually any waters in those states. This is particularly evident from a map of wildfire danger in the United States (**Figure 7**). In 2005 alone, for example, there were 28 large fires ( $\geq 100$  acres in timber,  $\geq 300$  acres in grasslands, or fire with Type 1 or Type 2 Incident Management Team assigned) in Colorado, 16 in Kansas, one in Nebraska, seven in South Dakota,

**Table 11.** Federal and non-Federal fires in the Rocky Mountain area, 2007.

Agency Type	Agency	<u>Human</u>		<u>Lightning</u>		<u>WFU*</u>		<u>Total</u>	
		Fires	Acres	Fires	Acres	Fires	Acres	Fires	Acres
<b><u>Federal</u></b>	BIA	920	27,646	187	2,139	0	0	1,107	29,785
	BLM	73	1,687	531	15,264	8	121	612	17,072
	FWS	15	1,598	7	133	0	0	22	1,731
	NPS	8	308	28	9	2	1	38	318
	USFS	154	411	367	43,132	10	107	531	43,650
<b><u>State</u></b>	CO	1,706	9,562	1,226	8,524	0	0	2,932	18,086
	KS	2,440	24,835	112	1,672	0	0	2,552	26,507
	NE	687	7,826	114	12,475	0	0	801	20,301
	SD	520	27,305	507	153,094	0	0	1,027	180,399
	WY	364	14,457	233	14,602	0	0	597	29,059
<b><u>Other</u></b>	Other	4	3,533	1	0	0	0	4	3,533
<b><u>RMA Total</u></b>	Total	6,891	119,168	3,313	251,044	20	229	10,223	370,441

Fires occurring on Federal agency lands are listed only for those agencies. State figures represent all Non-federal fires in the respective state (as reported to the USFS Regional Office’s State and Private Forestry staff).

WFU\* - Wildland Fire Used for Resource Benefit - naturally ignited fires managed to accomplish specific pre-stated resource management objectives in predefined geographic areas outlined in Fire Management Plans. Data for WFU fires are not included in columns for lightning-caused fires. Source: Rocky Mountain Area and Coordination Center 2007 Annual Report, National Interagency Fire Center, Boise, Idaho.



**Figure 7.** Fire threats and drought in the western United States. Upper panels: forecast fire danger class for (A) 25 May 2006 and (B) 7 July 2008. Light green areas indicate Moderate danger; yellow, orange and red indicate High, Very High and Extreme danger, respectively. Lower panels: Drought conditions in the 48 contiguous states, averaged over 15- and 30-day periods in June 2008. Source: Rocky Mountain Area Coordination Center of the National Interagency Fire Center, Boise, Idaho (fire danger maps are updated daily).

and nine in Wyoming (total 61; Rocky Mountain Area and Coordination Center, 2005 Annual Report, of the National Interagency Fire Center, Boise, Idaho).

Aquatic resource managers should take active interest in all stages of response to potential or real fire. Personnel of Region 2 continue to treat forests to reduce fire danger, including mechanical removal of fuels, prescribed burns, and control of naturally ignited fires in ways that meet existing fire management objectives. Such labor intensive and expensive programs are long-term efforts; in FY 2005, Region 2 treated 149,486 acres, 57 percent (85,691 acres) of which were in wildland-urban interface zones (USDA Forest Service Region 2 Fiscal Year 2005 Fuels Treatment Accomplishment Report, February 2006). Fire should therefore be considered a potential threat to almost any aquatic system beyond urban areas. Even methods to

reduce fire danger may exert negative impacts on local stream systems.

Species with narrow habitat requirements that occur in fragmented populations or in highly degraded or lower order (e.g., 1<sup>st</sup> and 2<sup>nd</sup> order) systems are probably most vulnerable to fire and fire-related disturbance. However, fishes demonstrably affected by wildfire in the southwestern United States from 1989-2003 included five non-natives (brook, brown, and rainbow trout, green sunfish, yellow bullhead) and 13 natives (Gila trout, three suckers, and nine cyprinid minnows) representing an array of habitat requirements and abundances (Rinne 2004).

Immediate effects of fire may include potentially lethal increases in water temperature, particularly in small, shallow waters exposed to severe fire conditions.

Hitt and others (2003), cited in Cilimburg and Short 2005) reported an 8-hr period where water temperatures were 14 °C greater than in a nearby unburned stream. Similarly, changes in water chemistry may include large spikes in nitrate, phosphate, and ammonium due to diffusion of smoke into stream water and ash inputs (Cilimburg and Short 2005). If water temperatures rise, oxygen levels are also likely to drop. Fish kills are not uncommon.

There are longer term impacts as well (Cilimburg and Short 2005). Temperatures in smaller streams may remain unusually high if the riparian and forest canopy has been removed. Flow volume invariably increases, particularly in areas with steep terrain, and may lead to restructuring of stream substrata and changes in normal seasonal patterns of discharge. Debris, ash, and other sediment inputs increase, with the potential for increased turbidity, lower primary productivity, and suffocation. Fish that survive may move from the affected areas to avoid chemical and other alterations to their habitat (Cilimburg and Short 2005). Debris flows following an Arizona fire created new barriers to fish movements (Rinne and Carter 2002), potentially inhibiting recolonization of affected stream reaches.

The USFS commonly employs timber harvest projects in areas struck by fires. These efforts allow for the economical recovery of the burned timber, provide work for nearby communities, and accelerate restoration of forest vegetation within the burned areas. Nonetheless, these efforts actually slow forest recovery (Karr et al. 2004) through compaction and chemical alteration of soils, removal of organic and inorganic nutrients, increasing erosion and stream sedimentation, eliminating shade trees for regenerating plants, etc.

*Scour (extracted from Schuett-Hames et al. 1996)*

Developing eggs and alevins of rainbow trout are vulnerable to scouring that causes mechanical shock, crushing, entrainment of the fish with moving gravel, or release of eggs and larvae into above-substrate current. Both biological and physical factors affect the vulnerability of redds to scour. Large females tend to deposit eggs at greater depth than do smaller fish, reducing the probability of scour. Spring-incubating salmonids, such as most rainbow and cutthroat trout, are vulnerable where snow melt produces peak flows in late spring or early summer, but late fall or winter rainfall will be particularly damaging to winter-incubating populations of rainbow trout. Construction of redds removes smaller particles, coarsens the substrate, and

raises resistance to scouring; loosening of the bed during spawning may lower this same resistance. Long interludes between storm events also enhance stability of the bed. Activities and events that can destabilize the stream bed and lead to severe and chronic scour include removal or displacement of large woody debris due to stream clean out after logging, urban development, removal of debris jams to improve fish passage, and floods or debris flows. Other factors that increase the likelihood or severity of scour include increased storm water runoff from impervious surfaces associated with urban development, timber harvest in areas susceptible to rain-on-snow runoff events, increased supply of coarse sediment due to upstream landslides, and stream channelization projects. Timber harvest, roads, mining operations, and urban development accelerate erosion, and stream side vegetation is sometimes removed or disturbed by timber harvest, urban development, and agriculture, and grazing operations.

### *Predation*

As noted above, rainbow trout are targets of a wide array of predators. Williams and others (1997) documented rainbow trout susceptibility to predation by a large bull trout population in the lower and Lake Billy Chinook (Williams et al. 1997). Cutthroat trout are believed to provide a key food source for at least 28 species of birds and mammals (Williams 2002). In Yellowstone National Park, a team of researchers followed a sow bear with cubs and concluded they averaged 100 fish per day for 10 days. It is further believed that pelicans in Yellowstone National Park get the majority of their nourishment from cutthroat trout, consuming as many as 300,000 pounds in a season. Cormorants and pelicans greatly increased their take of trout after 10 to 16 cm fish were stocked in the North Platte River, Wyoming, and they may have taken up to 80 percent of trout stocked in 1994 (Derby and Lovvorn 1997, Lovvorn et al. 1999).

Such reports focus on later life history stages (fingerlings and larger) of rainbow trout and other salmonids, but managers should also consider sources of predation on the eggs and fry. Both round goby (*Neogobius melanostomus*; listed as a potential nuisance species by Kansas, but not recorded from Region 2 yet) and sculpins (*Cottus* spp.; residents in all Region 2 states) penetrate interstitial spaces in cobble and gravel redds to prey on salmonid eggs and fry (Chotkowski and Marsden 1999, Jonas et al. 2005). Salmonid eggs may be particularly sensitive to attack immediately following spawning, as the female covers the redd; mature male Atlantic salmon parr feed



actively on just-spawned eggs (Montgomery et al. 1987). Invertebrates may also be threats to eggs and sac fry. Brown and Diamond (1984) described predation on rainbow trout eggs by two stoneflies (Plecoptera), a phantom crane fly (Diptera), a caddisfly (Trichoptera), and a gammarid amphipod.

### ***Management of Rainbow Trout in Region 2***

#### **Implications and potential conservation elements**

Rainbow trout are not presently of conservation concern, but various populations may ultimately suffer environmental, anthropogenic, and political threats. Long-term drought cycles, perhaps amplified by global warming, may reduce volume and consistency of flow in stream systems and potentially lead to warming of water in reservoirs or lakes. While acquisition of primary water rights to maintain stream flow is advisable, history suggests that costs would be considerable and competition from extraction-dependent users would be intense. Populations of greatest value should be identified, and alternative approaches to maintaining water supply to those populations should be explored.

Human population expansion, accompanied by destructive development of land, is inevitable. Region 2 personnel should be integrally involved, where possible, in planning for development in areas around, and particularly upstream, of National Forest System lands. Riparian corridors and forest buffers along streams should reduce sediment and pollutant inputs from building and roads that would do damage locally and downstream. Such protections could well enhance property values if accompanied by educational efforts explaining their importance to stream ecology and emphasizing that enhanced biodiversity contributes to the “living-near-nature” experience.

The major political threat to persistence of some rainbow trout populations appears to be mandates associated with the ESA and related legislation at state or federal levels. Native fishes in the arid western United States have a dismal record of recovery even after responsible agencies have committed tremendous energy and resources to recovery efforts. Rainbow trout are implicated as contributors to declines of native species, and their removal from designated critical habitat for native fishes will certainly appear in recovery plans for a variety of salmonid and non-salmonid species. This threat may grow as additional species are listed at national and state levels.

#### **Rainbow and native fishes**

Since their introduction into waters outside their native range, rainbow trout have displaced native species in Region 2 and elsewhere from their historic range by means of competition, predation, and other detrimental influences, including hybridization and introgression (Ross 1997). Pritchard and Crowley (2006) identify the primary threat to long-term persistence of Rio Grande cutthroat trout as the presence of non-native trout. Non-native trout, particularly rainbow trout, are either stocked or occur in self-sustaining populations in the majority of waters that historically supported Rio Grande cutthroat trout.

Kruse et al. (2000) surveyed most of the streams that might harbor Yellowstone cutthroat trout outside Yellowstone National Park. Genetically pure Yellowstone cutthroat trout occupied only 27 (26 percent) of 104 streams surveyed, and only 30 percent of 822 km of the perennial streams that contained trout. Henderson et al. (2000) tracked spawning movements of rainbow, Yellowstone cutthroat, and rainbow-Yellowstone cutthroat hybrid trout in the South Fork Snake River, and they discovered considerable spatial and temporal overlap of spawning sites in rainbow and Yellowstone cutthroat trout. Hybrid trout genes surveyed were dominated (64 percent) by rainbow trout markers.

Colorado River cutthroat trout were historically common in the upper Green River and Colorado River watersheds, but they now occupy less than 1 percent of their previous range. However, the amount of this restriction due to rainbow trout versus brook trout or other fishes is unclear. Special management status for this fish has been sought in Colorado, Wyoming, and Utah (Kershner et al. 1997).

Outside of Region 2, the westslope cutthroat trout (*Oncorhynchus clarki lewisi*) occupies less than 5 percent of its historic range within the upper Missouri River drainage in Montana (Shepard et al. 1997), and hybridization and introgression are well-established between coastal cutthroat trout and anadromous rainbow trout (Young et al. 2001). Perhaps the most disturbing development in the widespread concerns over interactions of rainbow trout with cutthroat trout focuses on Colorado’s greenback cutthroat trout. Originally listed as Federally Endangered, this fish was downlisted to Threatened status and eventually considered for removal from listing on the basis of dedicated and extensive recovery efforts by the Colorado Division of Wildlife to establish naturally

reproducing populations. Recently, however, Metcalf et al. (2007) reported molecular evidence demonstrating that many of the putative pure strains of greenback trout developed through Colorado Division of Wildlife efforts were actually descendents of Colorado River cutthroat trout stocked a century ago. Metcalf et al. (2008) recently demonstrated hybridization between rainbow trout and greenback cutthroat trout and Colorado River cutthroat trout populations. It appears that greenback trout populations are a greater cause for concern than previously thought.

Hybridization may also be a threat facing some populations of westslope cutthroat trout (Hitt et al. 2003). Westslope cutthroat trout and rainbow trout naturally occur in sympatry over a portion of their ranges (**Figure 1**), so reproductive isolating mechanisms likely evolved between the two species in these areas. Consistent with that expectation, hybridization between the two species is thought to be rare, but small amounts of introgression are detectable by molecular genetic methods.

Campton and Kaeding (2005) recently commented on a recommendation that only “nonhybridized” populations be considered for protection under the Endangered Species Act (ESA). They note that any population with detectable traces of introgression would be excluded from ESA and eligible for eradication, and they point out a biological dichotomy between “(1) the need to conserve the genetic resources of an imperiled species in which introgression has occurred and (2) the need to eliminate hybridization threats posed by introduced taxa.” In their response to Campton and Kaeding (2005), Allendorf et al. (2005) defined a nonhybridized or pure population as one having less than 1 percent introgression with either rainbow trout or any other subspecies of cutthroat trout, and urged that policies and guidelines should be developed on a species-by-species case. They concluded that USFWS has two opposing policies for dealing with hybridized populations of cutthroat trout, and that the USFWS is not relying on the best data available to address the threat of hybridization to westslope cutthroat trout (Allendorf et al. 2005). This concern is certainly not restricted to westslope cutthroat trout. Of the 14 named and unnamed cutthroat subspecies, two are extinct while other species are of special concern (Williams 2002).

#### Tools and practices

A wide array of methods exists for managing populations of salmonid fishes (see review in Pritchard and Cowley 2005), especially rainbow trout. Some methods (e.g., extensive genetic analysis) are likely to

see greater use with the many native fishes of the West for which there is concern. Nonetheless, to meet the needs of management, rainbow trout must be subject to population and, as more self-sustaining populations are developed, demographic monitoring and analyses. Habitat, including concerns about instream flow during critical periods, remains an issue as well. Habitat quality indices based on readily measured habitat variables may simplify rapid evaluation of existing habitat over the range of the trout, as long as they take habitat requirements of all life stages into account.

#### *Rainbow trout as a Management Indicator Species*

Ecosystem management has become a driving concept underlying natural resource management in the United States. Ideally, population and habitat monitoring of many species within an ecosystem over extended periods would provide managers with indications of ecosystem health. Such time- and labor-intensive study is, however, beyond the capability of existing state or federal programs. Faced with such constraints, responsible agencies often monitor the fate of one or a few species that may be indicators of the health of an ecosystem or species of concern (“target species” below).

Selection of such Management Indicator Species (MIS) has been directed and guided by the National Forest Management Act of 1976 (NFMA; as amended in several subsequent years). Population dynamics of such species are expected to reflect the effects of management activities on important members of a given biota. The NMFA recognizes that MIS may be drawn from:

- ❖ endangered and threatened plant and animal species,
- ❖ species with special habitat needs that may be influenced by management activities,
- ❖ commonly hunted, fished, or trapped species,
- ❖ non-game species of special interest, and
- ❖ other plants or animals selected because their population dynamics may indicate effects of management activities on other species or on water quality.

Implicit in the concept of indicator species is that indicator dynamics reflect dynamics of other

ecologically similar species (e.g., guild members), and habitat of the indicator species should overlap extensively with those of all other guild members (Block et al. 1987).

There remains considerable concern over the validity and utility of use of MIS as predictors of ecosystem responses and over how they should be selected. At least three categories of indicator species have emerged, functions of which should be considered as Region 2 National Forests and Grasslands develop or modify their own lists of indicators. The term “indicator species” is applied to species used to assess the magnitude of anthropogenic disturbance (ecosystem health), to monitor population trends in other species, and to locate areas of high regional biodiversity (Caro and O’Doherty 1999, Caro 2000). “Umbrella species” describes those used to delineate the type of habitat or size of area for protection; these are often species with large home ranges that encompass larger populations of species with small home ranges. “Flagship species” are those species used to attract public attention, raise awareness, or attract funding to a conservation cause. Despite the NFMA focus on indicator species, each of these functions will be important to National Forest System lands.

Should rainbow trout be used as MIS in Region 2? The answer may vary among forests and grasslands, and likely among locations within individual jurisdictions, for utility of the trout as an indicator must be related to explicitly defined criteria that are in accord with assessment goals (Landres et al. 1988). There are both pros and cons to use of rainbow trout as MIS in Region 2 (partial lists; based in part on Landes et al. 1988, Caro and O’Doherty 1999, Caro 2000, Caro et al. 2005), including:

**Pros:**

- ❖ rainbow trout are not of special concern in Region 2 states, so permitting requirements for research and monitoring should be less stringent than with listed target species;
- ❖ rainbow trout are frequently common, allowing large samples to be collected for monitoring studies, with associated reductions in error for estimated population sizes and length/weight relationships, as well as more robust data across different size and life history classes;

- ❖ large populations allow sacrifice of individuals for physiological or compositional testing that might indicate elevated stress (e.g., stress hormones) or other indicators of declining health (e.g., low lipid levels) not evident from simple length/weight measurements;
- ❖ rainbow trout are likely to be more available for relevant experimental manipulations in laboratory and field to elucidate relationships between types and intensity of environmental disturbance and demographic changes;
- ❖ rainbow trout are widespread in Region 2, so an initial assessment of the effects of various environmental conditions may be achieved rapidly through comparisons among locations differing in key environmental variables.

**Cons:**

- ❖ one reason rainbow trout are widely successful is their ability to tolerate varied environmental conditions; sensitive target species could easily be harmed or lost before managers could detect a response to changing conditions in rainbow trout populations;
- ❖ relatively slow development and maturation rates, relatively low fecundity, and sufficient mobility to allow relatively long distance avoidance movements may make vertebrate animals less useful for detecting the influence of environmental degradation than non-vertebrate organisms;
- ❖ ideally, responses of indicator and target species should be similar, but data demonstrating this relationship are difficult to acquire, particularly when conditions differ among communities at different locations;
- ❖ demographic parameters are likely to vary considerably among populations of rainbow trout based on origin of the population (e.g., recently stocked vs. established), identity of the strain, pure vs. hybrid, etc.; such will either demand many studies to demonstrate similar responses of indicator and target species or will reduce the accuracy of predictions of response at one location when the indicator-target relationship was developed at another location;

- ❖ environmental change may exert either density-dependent or -independent effects; in either case, small or isolated populations of target species are likely to suffer genetic and other effects more severely than large or widely-connected populations of indicator species.

Landres et al. (1988) suggest that reliance on a MIS should occur only when other assessment options are unavailable. Implicit in this recommendation is the suggestion that such reliance should be considered a transitional step. As information grows about community composition and function and the biology of individual species within that community, capability to model community and ecosystem responses more precisely will grow.

### *Management approaches*

Rainbow trout must be viewed as permanent residents of Region 2 ponds, lakes, streams, and rivers. Unfortunately, a continuing management conflict pits their negative impacts on native species against their widespread acceptance as a sport and food fish. Clearly, none of the following tactics will fit all habitats and desires, and habitat or fish population manipulations will always take place against a backdrop of constituent, agency, and governmental demands and conditions.

1. Identify locations best suited for at least four management approaches:
  - a. complete protection (no take) of native species in their historically native habitat
  - b. native-only sport fisheries
  - c. mixed native/rainbow trout fisheries
  - d. moderate to high intensity rainbow trout fisheries.

Areas of complete protection (1a) serve, in part, as sources of species-specific genetic diversity and essentially pure stocks for reestablishing or supplementing native fish populations. This is particularly likely if a population is sufficiently large to avoid loss of genetic diversity from genetic drift and if native habitat is sufficiently healthy to avoid unusual selection pressures.

Areas open to native-only sport fishing (1b) provide another repository of genetic diversity, and they have the potential to attract anglers interested in an unusual fish and an unusual sport fishing experience. Such programs should be supplemented with public education

programs that inform about the native species, declining populations, management efforts, and related topics.

Mixed-species fisheries (1c) provide another somewhat unusual consumptive use and educational opportunity, but with less constraining habitat conditions that may allow better fishery returns per unit time.

Finally, exclusive or near-exclusive dependence on rainbow trout (1d) may be required to support more intensive fisheries or those in degraded habitat. The ecological flexibility of rainbow trout and readily available public and private hatchery systems combine to make rainbow trout the ideal coldwater fish to support a wide array of sport fishing demands not met by more constraining conditions involving native species.

2. Evaluate and improve habitat, as necessary, so that it will support habitat requirements of all trout life history stages (see Habitat section above). If self-reproducing populations can be established through habitat improvement, it will reduce costs associated with stocking or allow limited hatchery resources to be directed to fisheries that require stocking.
3. Where stocking of rainbow trout is required (e.g., ponds in Cimarron National Grassland, irrigation canals, some reservoirs), identify genetic strains with the best performance for conditions in the area targeted for stocking.
4. Consider isolating species, subspecies, and strains from gene exchange with other groups. For example, native-only populations restricted to headwater streams above natural or artificial barriers to upstream movement would be protected against natural colonization from below, but could nonetheless contribute juveniles to fisheries in areas downstream. Where some natural reproduction occurs, similar isolation of specific strains of rainbow trout that perform particularly well under local environmental or fishery conditions may help to retain desired characteristics for longer periods than if they were mixed with other rainbow trout strains or potentially hybridizing species.
5. Consider developing the most productive (to the angler) fishing opportunities at points

closest to primary access, and accompany those efforts with improved support facilities that would tend to concentrate angling pressures from casual anglers in those areas.

6. Diversify angling regulations and programs with respect to, at least, gear, bag limits, and available species, for these influence angler perceptions of the quality of fishing experiences, whether or not they have an impact on managers' biological objectives. For example, fly/lure-only or catch-and-release restrictions communicate an agency's desire to develop excellent fisheries for the experienced angler. Reduced bag limits may affect overall take very little, but they will allow more anglers to approach the 'golden' limit, perceived (as in par for golf) as an indicator of personal fishing expertise. Improved and safe access for children to local waters with put-take fisheries benefit individuals and families not otherwise drawn to outdoor sports. Collectively, diversifying fishing opportunities serves a diverse angling public and trumpets the sensitivity of agencies to diverse constituent needs, desires, and conditions.
7. Educate anglers and visitors in ways that are more visual, auditory, and kinesthetic than one can find in the usual magazines, brochures, and static displays at many visitor centers. Static displays at agency offices and visitor centers could be replaced by touch-screen or trackball controlled computers that link directly to existing attractive and information-rich web sites for National Forest System lands and state resource management agencies. Links to professional quality photographs and videos on these web sites could be supplemented with short (<3 to 5 minute), topically focused videos or podcasts produced at very low cost by students and their teachers from high schools and colleges. This would be inexpensive, involve local communities, be highly visible to local media, expand availability of visually enticing introductions to natural and human resources, take advantage of readily available modern technology and students conversant with that technology, increase the breadth of resident and tourist audiences for agency programs, and free up agency Information and Education employees for

more substantive projects. These products could be downloaded from web sites, or for quite nominal costs, they could be loaded onto CDs or DVDs for free or very low cost distribution. Some agencies could also partner more extensively with sportsmens' or conservation organizations, with the latter hosting frequent rural fishing clinics or aquatic habitat renovation work days.

#### *Roles of hatcheries in fisheries and conservation*

Fishes have been introduced into North American waters since at least the 1840's, with widespread distribution of Pacific salmon and trout since at least the 1870's (Ross 1997, Mills et al. 1993, Pister 2001). In many locales, stocking of hatchery fishes has enhanced the condition of both sport and commercial fisheries resources and provided greatly expanded fishing opportunities not supported by natural fish production. However, stocked fish have not always been beneficial, but have contributed to widespread decline and sometimes extinction of native species, altered ecosystem function, and been vectors for the introduction of parasites and disease (Miller et al. 1989, Williams et al. 1989, Richter et al. 1997, Lightfoot 2004).

Thus, hatchery programs and desires to conserve wild native resources can come into strong conflict over proposed management actions (Finlayson et al. 2005). For example, naturalized populations of rainbow trout compete or hybridize with native cutthroat populations throughout Colorado and Wyoming, yet there is considerable interest in conserving these naturalized populations to meet angler satisfaction. Such competing management goals make it difficult to satisfy angler demand while protecting native fish populations and naturalized fish populations simultaneously. Nonetheless, modern hatcheries continue a tradition of attracting considerable public support. They provide a visible and esthetically pleasing example of an agency's attempts to serve constituents by enhancing fishing opportunities where they have been reduced by human alterations to the land or where such opportunities simply did not exist.

Issues relating to hatcheries and stocking are not restricted to concerns about the fate of native species. Epifanio (2000) surveyed the 50 states for their involvement in coldwater fisheries and problems that affected those fisheries. Forty-seven respondent states managed such fisheries, 38 of which indicated that the primary barriers to establishing and

maintaining self-sustaining populations related to habitat. The implications of this finding contrasted sharply with budgets of state management agencies that deemphasized habitat-related programs while pouring many resources into hatcheries and stocking programs.

Clearly, habitat protection and enhancement benefit development of fisheries for native and introduced species, assist with conservation of threatened taxa, and facilitate development of self-sustaining populations of introduced fishes, which may, in turn, reduce reliance on hatchery fish. The USFS and all Region 2 states are active in aquatic habitat research, recovery, and enhancement, reflecting important shifts in concerns about and emphasis on the links between healthy ecosystems and healthy fisheries.

**Approaches to stocking hatchery trout:** A major responsibility of fish managers is to see that the waters of the state are not overstocked or that stocked fish do not otherwise negatively affect existing fish stocks or native fish populations (Wiley et al. 1993, Ross 1997). Nonetheless, unpredicted heavy angler harvest can deplete fish populations, causing agencies to turn to a range of compensatory mechanisms to deter the impacts of excessive harvest (Ross 1997). Under these and other circumstances, constituent desires – and sometimes demands – may outweigh biological considerations. For example, Flaming Gorge Reservoir has experienced times when food supply was low and competition from nongame fishes was high, so rainbow trout stocking was not justified economically. Nonetheless, stocking continued due to high public demand (Wiley et al. 1993).

**Hatchery fishes:** Although rainbow trout are the focus of this assessment and are the most successfully reared and distributed of any coldwater fish worldwide, they are only one of many fishes important to hatchery and fisheries programs in the Rocky Mountain Region (**Table 12**). Rainbow trout rose to dominance in coldwater hatchery programs because of their ease of culture, ability to tolerate a wide variety of physical, chemical, and biotic conditions in receiving waters, and ability to grow to relatively large size (a fact that has also made them valuable for laboratory experiments benefiting from larger fish than animals like goldfish and guppies). During the first half of the 20th century, development of hatchery-rearing systems for rainbow trout resulted in rapid development of federal, state, and tribal rearing facilities throughout the United States and other nations, with accompanying introduction of these fish into many ecosystems and faunas.

With the advent of concern for declining native species driven by the Endangered Species Act and its precursors, as well as the growth in techniques for hybridization (see examples in **Table 12**) and genetic manipulation of fishes, hatchery functions have diversified to include rearing of native species for recovery efforts and special hybrids or strains suitable for introductions into waters with particular habitat conditions or fishing demands. In some cases, these efforts have reduced production capabilities for rainbow trout and/or led to improved methods for intensified culture of trout.

As noted elsewhere in this assessment, hatchery fish are selected for rapid growth in the absence of predators, conditions not common in the wild (Biro et al. 2004). Stocked rainbow trout tend to have lower survival rates than wild trout in nature (**Table 13**), in part because they are more vulnerable to predation and may contribute little to reproduction in the wild (Miller et al. 2004). Nonetheless, hatchery fish introduced to waters for put-grow-take and put-and-take fisheries where native and naturalized populations already reproduce will compete for food resources. Thus, while hatchery fish have reduced fitness due to low survival and reproduction, they bring increased competition to native and naturalized populations of the same or other species and ultimately result in negative consequences on resident trout. Continued stocking and inbreeding might also disrupt adaptations of naturalized and native fish to local conditions (Miller et al. 2004).

The enduring controversy between wild trout management and hatchery trout management appears to be a social problem more than a biological problem, for at the heart of the controversy lie obvious moral and economic implications. Early in the 1900's, the conventional wisdom was that hatchery stocking of large numbers of fry was essential for maintaining trout abundance, even where wild populations often existed and were reproducing successfully. A general belief developed over time that hatchery trout can provide good fishing anytime, ignoring the fact that, given good habitat, natural rainbow trout reproduction produces a surplus of young sufficient to eventually recruit into and support even an intense fishery.

This faith in hatcheries and stocking has been deeply entrenched in both fisheries personnel and anglers (Behnke 2004). Derisley Hobbs (1948, cited in Behnke 2004) studied the effectiveness of stocking young trout in New Zealand streams. He argued, and was largely ignored, that the number of young trout

**Table 12.** Fishes raised in Region 2. Data from online state and Federal sources 2006.

Species/hybrids	# hatcheries (state/fed)	Family	Genus	species (subspecies/strain/hybrid)
rock bass	1/0	Centrarchidae	<i>Ambloplites</i>	<i>rupestris</i>
largemouth bass	7/1	Centrarchidae	<i>Micropterus</i>	<i>salmoides</i>
black crappie	2/1	Centrarchidae	<i>Pomoxis</i>	<i>nigromaculatus</i>
bluegill	6/1	Centrarchidae	<i>Lepomis</i>	<i>macrochirus</i>
bluegill hybrids	1/0	Centrarchidae	<i>Lepomis</i>	(bluegill x green sunfish)
panfish [NS]	1/0	Centrarchidae	[NS]	[NS]
red ear sunfish	2/0	Centrarchidae	<i>Lepomis</i>	<i>microlophus</i>
smallmouth bass	2/1	Centrarchidae	<i>Micropterus</i>	<i>dolomieu</i>
sunfish hybrids	2/0	Centrarchidae	<i>Lepomis</i>	[NA]
grass carp	3/0	Cyprinidae	<i>Ctenopharyngodon</i>	<i>idella</i>
northern pike	3/0	Esocidae	<i>Esox</i>	<i>lucius</i>
muskellunge	3/0	Esocidae	<i>Esox</i>	<i>masquinongy</i>
tiger muskellunge	1/0	Esocidae	<i>Esox</i>	(n. pike x muskellunge)
hybrid muskellunge	1/0	Esocidae	<i>Esox</i>	(tiger?)
blue catfish	1/0	Ictaluridae	<i>Ictalurus</i>	<i>furcatus</i>
channel catfish	6/0	Ictaluridae	<i>Ictalurus</i>	<i>punctatus</i>
palmetto bass	1/0	Moronidae	<i>Morone</i>	[NA]
striped bass	2/0	Moronidae	<i>Morone</i>	<i>saxatilis</i>
striped bass hybrids	1/0	Moronidae	<i>Morone</i>	[NA]
white bass	1/0	Moronidae	<i>Morone</i>	<i>chrysops</i>
wiper	4/0	Moronidae	<i>Morone</i>	(white x striped bass)
sauger	3/0	Percidae	<i>Sander</i>	<i>canadensis</i>
saugeye	2/0	Percidae	<i>Sander</i>	[NA]
walleye	9/1	Percidae	<i>Sander</i>	<i>vitreus</i>
walleye/sauger hybrid	1/0	Percidae	<i>Sander</i>	[NA]
yellow perch	4/0	Percidae	<i>Perca</i>	<i>flavescens</i>
paddlefish	2/1	Polyodontidae	<i>Polyodon</i>	<i>spathula</i>
Bear River (Bonneville) cutthroat trout	3/0	Salmonidae	<i>Oncorhynchus</i>	<i>clarkii</i> (utah)
Colorado River cutthroat trout	2/0	Salmonidae	<i>Oncorhynchus</i>	<i>clarkii</i> (pleuriticus)
cutthroat trout (subsp. /strain unid.)	1/0	Salmonidae	<i>Oncorhynchus</i>	<i>clarkii</i>
Snake River cutthroat trout	6/2	Salmonidae	<i>Oncorhynchus</i>	<i>clarkii</i> (bouvieri)
Yellowstone cutthroat trout	4/0	Salmonidae	<i>Oncorhynchus</i>	<i>clarkii</i> (bouvieri)
Eagle Lake rainbow trout	6/0	Salmonidae	<i>Oncorhynchus</i>	<i>mykiss</i> (aquilarum?)
Fall rainbow trout	3/0	Salmonidae	<i>Oncorhynchus</i>	<i>mykiss</i>
Firehole rainbow trout	2/0	Salmonidae	<i>Oncorhynchus</i>	<i>mykiss</i>
rainbow trout	8/4	Salmonidae	<i>Oncorhynchus</i>	<i>mykiss</i> (subsp. /strain unid.)
kokanee salmon	5/0	Salmonidae	<i>Oncorhynchus</i>	<i>nerka</i>
chinook salmon	4/1	Salmonidae	<i>Oncorhynchus</i>	<i>tshawytscha</i>
brown trout	10/2	Salmonidae	<i>Salmo</i>	<i>trutta</i>
brook trout	5/0	Salmonidae	<i>Salvelinus</i>	<i>fontinalis</i>
lake trout	3/2	Salmonidae	<i>Salvelinus</i>	<i>namaycush</i>
splake	5/0	Salmonidae	<i>Salvelinus</i>	(brook x lake)
grayling	3/0	Salmonidae	<i>Thymallus</i>	<i>arcticus</i>

state (n = 23) and federal (n = 6) hatcheries. Not an exhaustive list. [NA] - not applicable; [NS] - not specified.



**Table 13.** Post-stocking survival rates for rainbow trout stocked in North American waters. (Modified from Kerr and Lasenby 2000; additional information and sources listed therein)

Waterbody	Life Stage Stocked	Time from Release	Survival Rate (%)
<b><u>Lakes</u></b>			
East Fish Lake (Michigan)	—	6 months (October-April)	86%
Fox Lake (Minnesota)	Fingerlings	4 months	37%
Little Bass Lake (Minnesota)	Fingerlings	4 months	11%
Little Shell Lake (Minnesota)	Fingerlings	4 months	18%
McCall & Muerlin Lakes (Minnesota)	Fingerlings	4 months	0%
Quemado Lake (New Mexico)	Fry	Time required to achieve 7.5 in length	9.2%
Misc. prairie lakes (North Dakota)	—	1 month	15-54%
Misc. lakes (Michigan and Wisconsin)	Age I (yearling)	5 months	32-60%
	Age II	5 months	15-19%
Misc. lakes (Colorado)	—	—	20-60%
<b><u>Reservoirs</u></b>			
Porcupine Reservoir (Utah)	Fingerlings	14 months	6.5-7.6%
Unnamed Reservoir (Utah)	Fingerlings	—	39-55% (1987)
	Fingerlings	—	19-25% (1988)
<b><u>Ponds</u></b>			
Fuller Pond (Michigan)	—	6 months (fall-spring)	50%
	—	6 months (spring-fall)	10%
<b><u>Streams/rivers</u></b>			
Convict Creek (California)	Large (2.8-3.7 ) fingerlings	89-151 days	46.6%
	Small (1.3-1.7 ) fingerlings	89-151 days	44.2%
Flint Creek (Montana)	Catchables	6 weeks (summer)	83%
		Overwinter	68%
Fool Creek (Wyoming)	—	1 year (1974-1975)	41.6-48.5%
Little Missouri River (Arkansas)	—	5 months	3-10%
Platte River drainage (Nebraska)	Fingerlings	4-6 months	3.6-54.1%
Taylor Creek (California)	Fingerlings	1 month	10.6%
Three Streams (Tennessee)	Fall fingerlings	5 months	1-3%
	Spring yearlings	3 months	2-7%

reared in hatcheries was insignificant compared to the number of young trout produced naturally. Allen (1951) subsequently supported Hobbs' conclusions about the futility of adding hatchery trout where young wild trout were abundant. Although Allen's findings did not convince fishery managers to stop stocking, they did cause wild trout managers in the United States to change from stocking fry and fingerlings to stocking catchable trout (Behnke 2004). This shift has also influenced public attitudes; for the past 40 years, for example, Trout Unlimited has tried to shift the focus from put-and-take fisheries dependent on stocking catchable trout to an emphasis on wild trout management.

**Uses of hatchery fishes - introduction of nonnative species:** Introductions of species such as rainbow trout, brown trout, largemouth bass, striped bass, walleye, and a number of other species and hybrids (Table 12) to new geographic areas to enhance fishing opportunities have been viewed as successes by many game and fish agencies across the country (Ross 1997). In contrast, conservation biologists argue that nonnative fish introductions have been irreversibly deleterious to the fragile fish communities of the arid West (see chapters in Minckley and Deacon 1991), and Richter et al. (1997) concluded that introductions of exotic species were the greatest threat to the native aquatic fauna of the western United States. As noted elsewhere in this

assessment, likely impacts of nonnative species include increased intra- and interspecific competitive and predatory pressures as well as occasional introductions of new parasites and disease. Recovery efforts for native cutthroat trout in Region 2 have also been compromised by hybridization with stocked rainbow trout that has led to reduction, and in some cases loss, of locally adapted gene complexes in native populations (Kershner et al. 1997, Hendrickson et al. 2003).

**Uses of hatchery fishes - establishing self-sustaining fish populations in new reservoirs and ponds:**

Reservoir and pond construction has been on the rise since the beginning of the 20th century (Ross 1997). Maintaining long-term, high quality conditions in such systems can be a challenge, as they often undergo rapid ecological succession with its accompanying changes in community productivity, composition, and structure. These changes can lead to boom-and-bust cycles in fish communities, where some species thrive under certain conditions and decline as those conditions change. In general, warmwater species (e.g., largemouth and smallmouth bass, crappie and sunfish, yellow perch, catfish), when managed with the correct predator-prey balance, commonly establish self-sustaining populations in reservoirs and ponds. Coldwater species, like trout, are less likely to form self-sustaining populations, in part due to their requirements for clean gravel spawning substrates preferably swept by currents that are not characteristic of most reservoir and pond systems (Ross 1997). Such substrates may occur in tributaries or in reservoirs with excellent water quality and little sedimentation. In the Cimarron National Grassland, rainbow trout are stocked in winter, and fish not harvested are not expected to live through the hot summer months (Chappell 2006).

**Uses of hatchery fishes - supplementing populations:**

Supplemental stocking has become an integral part of management of numerous salmonid populations, both in and out of Region 2. Supplemented populations may have been depleted by overharvesting, habitat deterioration, loss of migratory pathways from dam construction, and various other factors. Although supplemental stocking is initiated to improve the abundance of the depleted stock, stocking is often continued after stock recovery has been accomplished to satisfy increased angler demand (Ross 1997). As noted elsewhere in this assessment, supplemental stocking does not enhance the self-sustaining capacity of wild populations, but it remains a popular approach to address depleted populations or to stimulate or support increased angling pressure.

A relatively recent development for supplemental stocking is introduction of sterile triploid rainbow trout. Perhaps the best known cases of stocking of sterile fishes comes from widespread use of triploid grass carp, a species occurring in each of the Region 2 states, for aquatic weed control. However, sterile triploid rainbow trout are also appearing in fisheries in some western states. Sterility ensures they will not hybridize with resident fishes or establish naturally reproducing populations. In addition, they tend to exhibit rapid growth and often attain large size; the Washington state record, almost certainly a triploid fish, weighed 29.6 pounds. Although we found no reference to federal or state programs that stock triploid rainbow trout in Region 2, there are at least two private hatcheries producing or rearing these fish in the Region, and they are stocked into at least one private Colorado fishing lake. Other western states stocking triploid rainbow trout include Utah, Idaho, and Washington.

**Fisheries supported by stocking - put-and-take fisheries:**

Put-and-take fisheries are designed to provide anglers with fishing opportunities when self-sustaining populations cannot be established. Trout are the most common coolwater fishes introduced because they are popular among anglers, can be reared to catchable size more quickly and at lower cost than other popular sport fishes, and can be grown and available year round (Ross 1997). Even though catchable trout are more expensive to raise, they cost less per fish creel than subcatchable trout because so few of the latter return compared to the number planted (Wiley et al. 1993). A reasonable expectation of return to anglers for a successful stocking program would be at least 50 percent of stocked fish (Wiley 2003a).

There are several reasons agencies turn to put-and-take fisheries.

1. Catchable trout can be stocked to meet heavy short-term angling demands in areas that cannot sustain self-reproducing populations. For example, trout may be stocked in the spring when angling pressures are on the rise but where waters will be too warm in the summer months to support a coldwater trout fishery.
2. Fishing can be provided to areas of dense human populations where waters may be polluted or simply not satisfactory to maintain long-term fisheries (Ross 1997). Focused urban fishing programs exist in, at least,

Kansas, Nebraska, and Colorado (as part of the latter state's "Fishing is Fun" program, which involves local communities in a three-way partnership with the Colorado Division of Wildlife and Federal Sportfish Restoration Act monies).

3. Hatchery trout may shift angling pressures away from wild populations by steering anglers toward catchables stocked in the same water system (Ross 1997).
4. Angler satisfaction, at least for less experienced anglers, may be high with put-and-take fisheries because stocked fish are easier to harvest than wild fish.

Programs that stock catchable trout aim to satisfy recreational demand, stimulate sales of fishing licenses, and generate excise taxes from purchase of fishing equipment and boat fuels. These latter revenues provide a major source of funding for most state fisheries management programs, and by their very nature, they are intended for support of enhanced fishing opportunities and not simply for conservation of wild resources (Ross 1997). This can lead to conflicts of interest among management personnel or agencies, depending on their perceived mandates or responsibilities. For example, the highest numbers of hybrids between rainbow trout and Colorado River cutthroat trout were found in streams that were most recently exposed to stocking (Kershner et al. 1997). Such put-and-take fisheries with nonnative species have the potential to damage fragile populations of native fishes, even to the point of local extinction, and they ignore alternative approaches, such as development of special native-species fisheries that could attract considerable angler interest while satisfying conservation objectives.

**Fisheries supported by stocking - put-grow-and-take fisheries:** Put-grow-and-take fisheries help meet the demand of anglers who seek to harvest fish that resemble wild populations. Naive stocked fry or fingerlings that survive face the same pressures as wild trout do as they mature to catchable size, and therefore they behave more like wild trout and provide anglers with a more natural fishing experience. These fish are less costly to rear than catchables and may therefore reduce program costs if survival to catchable size is high (Ross 1997). Wiley (2003b) believed that stocking catchable trout was a success if return to anglers was  $\geq 1$  pound for each pound of fish stocked in streams (for trout 1.25-8" in length, 1300-5 per pound) and 1 pound

per pound stocked in standing waters (trout stocked 1.25-5", 1300-20/lb).

**Fisheries supported by stocking - tailwater and two-story fisheries:** Tailwater fisheries occur downstream of dams where cold, clear water is released from the hypolimnion of the reservoir. Because sediment loads are low in hypolimnetic waters and downstream fine sediments are often displaced during heavy releases, gravel, cobble, and bedrock substrates are often exposed and available for colonization by highly productive algae and invertebrates. These organisms, supported in part by the frequently nutrient-rich hypolimnetic waters, may allow development of robust trout fisheries (McKinney et al. 1999, Simpkins and Hubert 2000). Stocked rainbow trout often can survive to reproductive age, create self-sustaining populations, and grow to large size, but extreme winter conditions may lead to high overwinter mortality (Ross 1997, Annear et al. 2002).

Two-story fisheries occur in lakes or reservoirs that stratify, providing a warmwater fishery in the epilimnion and a cool- or coldwater fishery in the hypolimnion. For example, Colorado's Eleven Mile Reservoir on the South Platte River contains rainbow, cutthroat, rainbow-cutthroat trout hybrids, kokanee salmon, and small populations of brown and mackinaw (lake) trout, as well as warmwater species such as yellow perch, northern pike, walleye, and smallmouth bass (Gerlich 2001). Problems may arise if there is insufficient forage for one of the two fisheries or if seasonal destratification (as in shallow lakes or reservoirs) produces intolerable conditions for certain species in the community. The former circumstance occurs with striped bass in Lake Powell on the Arizona-Utah border, for example, where small striped bass grow rapidly on a gizzard shad (*Dorosoma cepedianum*) diet in the epilimnion but large bass move to a hypolimnion that lacks sufficient forage to maintain strong growth or condition. This led to a recommendation that rainbow smelt (*Osmerus mordax*), native to the north Atlantic and north Pacific, be introduced to serve as a hypolimnetic forage fish for striped bass (see comments and historical review in Minckley 1991).

**Fisheries supported by stocking - "reclaimed" systems:** Reclaimed fisheries for trout are those where management agencies remove existing fishes and replace them with trout in support of a put-grow-take fishery or establishment of a self-sustaining population. The rationale for such treatments usually focuses on removal of predators and/or potentially competitive

or otherwise undesired “nuisance” species, leaving the waters free for development of trout fisheries. Rotenone or antimycin are the most common ichthyocides used to remove species present. Because treated waters lack most potential predators or competitors, small subcatchable trout should experience excellent survival and keep program costs low (Ross 1997).

Reclaiming systems for trout fisheries can create sustainable fisheries in waters perceived to need rehabilitation. However, managers must carefully assess the presence or absence of native fishes and develop objectives and methods with great care. A rotenone treatment of the Green River in preparation for developing a trout fishery in Flaming Gorge Reservoir affected native fish populations in more than 800 km of the river and its tributaries and well downstream of the target area (Holden 1991).

**Urban fisheries:** Although not applicable to management of rainbow trout in Region 2 national forests and grasslands, regional managers should be aware of the growing application of stocked rainbow trout to existing urban waters in a variety of U.S. cities. Of the five states of the Rocky Mountain Region, Kansas and Nebraska have well-developed urban fishing programs at this time, and there has been recent approval for such a program in Colorado as part of their “Fishing is Fun” program. In Kansas, 77 lakes are currently stocked with 3/4- to 1 1/2-pound channel catfish, hybrid sunfish, and wipers every few weeks from April through September (<http://www.kdwp.state.ks.us>). This program serves all Kansas metro areas with populations exceeding 40,000 that have public fishing waters. Garden City provides the only urban program close to a Region 2 facility (Cimarron National Grassland). Nebraska’s Urban Fishing Program (UFP) (<http://www.ngpc.state.ne.us>) currently lists about 75 potential program sites in 55 cities across Nebraska, with sites added as the Nebraska Game and Parks Commission’s Aquatic Habitat Program works to improve lake and pond habitat in conjunction with the Nebraska Environmental Trust Fund and the Nebraska Department of Environmental Quality. Catchable size channel catfish and trout are stocked to provide fishing opportunities to more anglers. In some lakes, stocking frequency has been increased to meet demand, and additional fish species have been stocked to diversify opportunity in a few locations. While the Nebraska UFP works primarily on smaller (<100 acres) lakes and city park ponds, streams and rivers flowing through urban areas may also be included in program activities in the future. Finally, Colorado’s Wildlife Commission recently approved a resolution to promote urban fishing access. “Fishing is

Fun” applications for funding from urban communities will receive high priority.

These types of programs share several somewhat distinctive characteristics compared to management schemes in more natural waters. Urban fishing programs introduce catchable size fish into existing lakes and ponds found in parks and other areas of human population centers. Because such systems frequently experience considerable seasonal temperature variation, urban programs in the western states stock trout in the cool periods and catfish or other warmwater species in warmer periods. This and frequent and often widely publicized stocking schedules ensure year-round fishing opportunity and virtually guarantee intense fishing pressure and high public visibility. States differ in the funding sources for such programs and the sources of fish for stocking. In some cases, a state fishing license allows access to both urban and rural fishing opportunities while in other states (e.g., Arizona) a separate license is required for urban fishing. Similarly, in some states, stocked fish are produced in state hatcheries while in others (e.g., Arizona) stocked fish are purchased from commercial suppliers. Minimum size of fish may be designated, and a few much larger fish are often added to each load of fish to increase attractiveness to anglers.

Such programs have many benefits. When managed properly, they bring considerable positive visibility to agencies from segments of the population often not knowledgeable about natural resources or their management, clearly demonstrating an agency’s concern for all of their various constituencies. In addition, urban sites add a valuable and different dimension to existing inner-city or suburban recreation opportunities, and they tend to bring a diverse array of people together. They also have been used effectively for special youth fishing programs where children learn about resources and management and are taught to fish, often using agency equipment.

**Factors influencing survival and reproduction of stocked fish:** Many factors influence the return rate of stocked trout (Kerr and Lasenby 2000). Attempts to establish reproducing and eventually self-sustaining populations should consider factors listed elsewhere in this assessment as necessary for successful reproduction as well as survival and growth of all life history stages. When fish are stocked into waters where life expectancy is short due to intense angling pressure or marginal conditions, constraints are relaxed because rainbow trout exhibit greater tolerance for many water quality variables (e.g., salinity, pH, temperature) than

many other salmonids. Nonetheless, factors affecting post-stocking success should be considered. Four factors, each discussed below in detail, include habitat sufficiency, stocking practices, emigration of stocked fish, and anglers.

**Habitat sufficiency - physical habitat:** As noted elsewhere, habitat requirements differ among life history stages. While types of habitat required for spawning and rearing through the fry stage may be a concern only when attempting to establish an actively reproducing population, stocking of subcatchables and catchables should occur where they can form aggregations in deep pools or disperse into more complex cover and feed sufficiently to support survival.

**Habitat sufficiency - water quality:** The chemistry (e.g., salinity, osmolarity, dissolved oxygen) of receiving waters should be similar to that of hatchery or transport water. Hatchery fish have failed to survive in waters where total dissolved solids vary greatly from hatchery to receiving waters. Lakes and streams, particularly in urban areas, receive a variety of chemical pollutants. Low dissolved oxygen levels in waters that are warm, polluted, or otherwise have high levels of respiratory activity may be tolerable for post-emergent life history stages, but they may slow development, cause premature or delayed hatching of eggs, and lead to reduced size of hatchling sac fry (Bjornn and Reiser 1991).

**Habitat sufficiency - water temperature:** Receiving waters should have temperatures similar to hatchery or transport water temperatures. Significant temperature shock during stocking may alter responsiveness, swimming ability, or other behavioral functions in the short term and affect physiological functions in the long term as the animal acclimates to the new temperature. Given the many effects of temperature on fishes, in-stream temperature regulation is a common management issue. Stream temperature can be altered by removal of stream bank vegetation, withdrawal and return of agricultural water from irrigation, releases from cold and deep or warm and near-surface waters of reservoirs, and cooling of nuclear and other power plants (Bjornn and Reiser 1991).

**Habitat sufficiency - water quantity:** Fish should be stocked into streams where extreme fluctuations in discharge, either natural or regulated, are unlikely or where sufficient habitat (e.g., deep pools for summer and winter refuge, cover, refuges from strong currents) remains during normal seasonal extremes of flow. Changes in flow regime directly affect

wetted area of the streambed, water velocity, suspended solids, and the rates and locations of bed scour and sediment deposition (Crisp 1993); all of these may affect survival of one or more life history stages. High and low seasonal flows and ice appear to limit survival and return of subcatchable trout more than catchable trout. Trout in shallow standing waters (i.e., shallow lakes, ponds) are susceptible to high temperatures and accompanying low dissolved oxygen during summer periods, while complete winter ice cover may lead to hypoxic and even anoxic conditions and winter fish kills. Artificial aeration or water circulation may overcome both conditions to various degrees.

**Habitat sufficiency - productivity of receiving waters:** Receiving waters must have sufficient food standing crops to support introduced trout over the short term and sufficient primary production (or allochthonous input in lower order streams; Vannote et al. 1980) and secondary production to ensure a sufficient trout food supply in the long term. Strong seasonality of insect and other trout food production and the frequently accompanying curtailed growing season at high altitudes and high latitudes should be considered in developing stocking strategies for trout.

**Habitat sufficiency - resident stocks of trout or other competing or predatory fishes:** As noted elsewhere, interactions of rainbow trout with resident fishes, particularly in Colorado and Wyoming with extensive coolwater habitat and established native and introduced faunas, may take several forms. Susceptibility to resident predators will be highest shortly after stocking when new animals are disoriented, stressed, naïve, and concentrated in a small area. Competition for fundamental resources such as food, feeding sites, and refuge or resting sites may be most intense immediately after stocking, occur at any time of year, be intra- or interspecific, and be either exploitative or contest in nature. For example, some of Wyoming's waters lack an adequate food supply to support wild populations, and management strategies recognizing this have proven successful at providing a decent fishery (Wiley et al. 1993). Predictably, subcatchable trout suffer lower survival under such conditions, leading managers to conclude that subcatchables should only be stocked into lakes where density of piscivorous species is low and competition for food with non-game species is light. In contrast to the recurring and complex nature of competition over resources required for all size groups of trout, competition for spawning sites and mates will be seasonal, potentially intense, contest in nature, and involve both conspecifics and other salmonids.

**Habitat sufficiency - hatchery conditions:**

Hatchery rearing practices will influence physiological, anatomical, and behavioral traits of rainbow trout. Hatchery diets support rapid growth and generally good condition and nutritional status. Body composition may change with altered diet over the short term (Gelineau et al. 2002, Yamamoto et al. 2002), and body composition may influence performance of interest to managers (e.g., overwinter survival, swimming performance; Gregory and Wood 1998). As noted elsewhere, purposeful and accidental selection can alter several other performance variables.

**Habitat sufficiency - genetic strain:**

Intense artificial selection has produced a variety of rainbow trout strains, each with characteristics intended to enhance performance in specific ecological or hatchery conditions (and probable unintended characteristics resulting from selection associated with high density rearing) (Myrick 1999, Myrick and Cech 2000). Traits of rainbow trout that exhibit genetic influence include physiological characteristics (growth, disease/parasite resistance, age at maturation), behavioral traits (movements, swimming ability, general ease of handling, general activity and feeding rates), and traits influenced by an animal's physiology, behavior, and ecology (e.g., survival, catchability, and contributions to fisheries) (Kerr and Lasenby 2000, Valente et al. 2001). For example, ten years of spawning-date manipulations produced a trout that spawned over 60 days in advance of its original date (Gall 1998), expanding the time of year when eggs or fingerlings can enter the production system and respond to a year-round market demand for rainbow trout (Siitonen and Gall 1989).

**Habitat sufficiency - transport stress:**

Fish arriving at a stocking site have undergone a series of stressful conditions that should be minimized when possible (Dunlop et al. 2004). Capture at the hatchery generally involves concentration in raceways with a seine or other barrier that leads to increased fright, decreased inter-individual distance, and increased abrasion. Fish may be moved to transport tanks by net, mechanical suction, or conveyor, all accompanied by exposure, additional abrasion, and eventual immersion into water that may differ in temperature and composition to the original raceway. Transport extends the period of stress and may increase its severity due to vibration and dense packing of fish. Finally, stocking places stressed animals through yet another sequence of handling and introduction into an extremely foreign environment.

**Stocking practices - note on stocking**

**terminology:** Various agencies have applied an array of stocking prescriptions, so managers seeking to compare published alternatives face potential confusion from the variety of terms used to describe stocked fish (**Table 14**; Kerr and Lasenby 2000). These terms include number of individuals, age (e.g., young-of-the-year, Age I, Age II, yearling), body size (e.g., fingerling, catchable, subcatchable, total (TL) or fork length (FL), number of fish per pound), and life history stage (see section in this assessment). Interpretation of stocking data may require managers to develop algorithms that allow at least approximate transformations among various quantitative descriptors.

**Stocking practices - time of stocking:**

In general, spring or early summer stocking, when stocked fish encounter periods of rich food supplies and survivors can explore habitat and insert themselves into existing social systems, generates higher rates of return than fall stocking does (Kerr and Lasenby 2000). Wiley et al. (1993) suggested that subcatchables, if stocked in streams at all, should be stocked immediately after spring runoff to avoid subjecting these fish to excessive and turbid flows and to take advantage of rich spring and early summer foods to support rapid growth. Subcatchables stocked in fall exhibited low survival and return; fewer than 10 percent of the catchable trout stocked in the fall returned, and these generally did not survive to the second season. Similarly, where there are multiple stockings in the same location during a fishing season, returns tend to be greater with early-season than with late-season stocking.

**Stocking practices - size at stocking:**

Small trout are more susceptible to predation or competition from larger fish than larger trout are. For example, comparison of return rates for catchable trout in lakes (47 percent) and streams (27.5 percent) with return rates for subcatchable trout of 8 percent in lakes and 6 percent in streams indicated that subcatchables did not meet management standards for return rates in a Wyoming system (Wiley et al. 1993). In Crystal Reservoir, stocked catchable trout had return rates of almost 90 percent, probably because larger trout escape predation more successfully than smaller trout, fewer fish need rely on a limited food supply, and anglers keep and report larger fish rather than practice catch-and-release with small fish.

**Stocking practices - number of trout stocked and stocking rates:** Stocking rates vary considerably

**Table 14.** Summary of rainbow trout stocking rates reported in various North American jurisdictions.

Water body	Age/size category	Per acre - Per ha	Per meter or mile
<b><u>Ponds</u></b>			
	fry	350-1000	
	fingerlings	200-500	
<b><u>Lakes</u></b>			
	fry	1500	16,000-64,000/mi shoreline
	fingerlings	30-150	200/mi shoreline
	yearlings	2-150	100-350/mi shoreline
	subcatchables	20-30	
	catchables	10, 150-300	
	“fish”	25-75	
<b><u>Streams</u></b>			
	fry		450/m
	fingerlings	100-200	60/m
	yearlings	50-100, 50-150	30/m, 15/m

Extracted from Kerr and Lasenby 2000. For more focused specific recommendations incorporating measures of fishing effort and biological productivity in Wyoming, readers should see Wiley 2003b.

among different jurisdictions according to desired yield, survival, desired mean weight per fish in the catch, competing species, habitat type, size of trout available, expected fishing pressure, fish abundance in the receiving water, and productivity of the system (**Table 14**). While there are no universally applicable guidelines for trout stocking, Kerr and Lasenby (2000) provide an extensive list of approaches used to determine the number and size of rainbow trout to be stocked in various North American standing and flowing waters. In some cases, relatively simple data sets can direct stocking tactics. Hubert et al. (1996), for example, developed a model based on percent cover, elevation, late summer wetted stream width and channel gradient to calculate predicted mean biomass (PMB) of trout supportable by Wyoming streams, information potentially valuable in determining subsequent stocking practices. Regardless of the approach used to determine stocking densities, there is always a potential for overstocking. Mortality rates of hatchery-reared rainbow trout may increase substantially with an increase in stocking density (Kerr and Lasenby 2000).

**Emigration of stocked fish:** Movements of recently stocked fish from targeted recipient waters may interfere with achievement of management objectives. In their review of rainbow trout stocking programs, Kerr and Lasenby (2000) list factors that have been demonstrated to influence post-stocking movements of trout, including water quantity (elevated discharge or flooding, reductions in water levels) and quality (water temperatures, formation of frazil ice, pollution),

stocking practice (density, especially overstocking), and characteristics of stocked fish (genetic strain).

**Anglers:** Anglers vary considerably in their primary motivations for fishing and thus in their potential impact on trout populations and their likelihood to fish local vs. remote waters or stocked vs. wild fish. “Social anglers” enjoy time spent with friends and/or family while “nature anglers” are most interested in enjoying the outdoors. For the “relaxation anglers,” fishing provides an opportunity to escape everyday pressures and relax as opposed to the “excitement anglers” for whom fishing provides an opportunity for excitement. “Food anglers” are primarily motivated by the opportunity to bring fish home to eat, and “sports anglers” seek to catch a trophy fish, become a proficient angler, or compete with other anglers in fishing tournaments.

### ***Information Needs***

As previous sections of this assessment verify, many aspects of the biology of rainbow trout in nature are well documented, as are topics relating to rainbow trout hatchery production, introductions outside their range, impact on native species, and various aspects of their physiology, genetics, cell biology, and diseases. In general, the biological information necessary to develop strong management plans is available. The major issues appear to relate more to interspecific conflicts with native species, education of constituents, and creativity in management practices than to insufficient knowledge



about rainbow trout biology. There are several key needs for additional information that would ease development of management practices consistent with modern ecosystem management and conservation biology.

1. As indicated elsewhere, evidence indicates that introduced rainbow trout have exerted negative impacts on native salmonids and other fishes. In many cases, the actual nature (e.g., predation, competition) and intensity of the impacts is unclear; simple overlap in resource use or a species of concern recorded from a trout stomach are insufficient to establish the type or level of threat. While most managers rarely possess the luxury of time to perform laboratory or field experiments, urging (and funding) such studies by agency research personnel, interns, students, or college and university faculty could provide managers with much-needed tools. For example, demonstration of competition virtually requires carefully designed experiments, yet Weber and Fausch (2003) found few studies sufficiently rigorous to test for presence of competition between wild and stocked salmonids. Similarly, descriptions of diets based on stomach or intestinal contents may be misleading without measures of food availability (e.g., standing stock, periodicity of availability) or periodicity and frequency of feeding.
2. Reassessment of stocking programs could lead to greater efficiency in management of both hatcheries and fish in the wild. Stocking programs thought to be necessary when begun may lead to expectation of their continuance by constituents even though they are unnecessary. For example, Montana stopped stocking brown trout and rainbow trout in a section of the Madison River where these fish were long established (Vincent 1987, Williams 2002). Within four years, numbers of fish three years of age and older increased by 942 percent. Such experiments may meet with angler resistance if not accompanied by educational programs.
3. In some systems, stocking catchable size trout is not justifiable nor does it create value. Low intensity fisheries on mountain streams, for example, may well be supported by natural reproduction and growth of trout, eliminating the need for any stocking. Even

where supplementation is desired, natural productivity of many aquatic environs could support put-grow-take fisheries dependent on fingerling or fry stocking.

4. As additional wild trout restoration efforts are developed, educational programs directed at anglers and outfitters should be developed and distributed widely. These should be assessed to see if they prevent situations where anglers sabotage these efforts with illegal stocking (Williams 2002) or reduce charges that agencies are trying to put outfitters out of business with protective programs like catch-and-release that, in the long run, create sustainable fisheries and enhanced fishing opportunities. The restoration of cutthroat trout in Yellowstone Lake and catch-and-release regulations generated \$36 million for local business owners in 2002. The value of these actions in Yellowstone Lake was later compromised by an illegal stocking of lake trout, a large predator capable of virtually eliminating cutthroat trout from the system (Williams 2002).
5. Efforts should be continued to understand, educate, and work with both consumptive and non-consumptive users about conservation and management needs and tactics. Such efforts must incorporate the literature on learning styles of constituents and produce educational instruments to match those learning styles. Conflicts with constituents may arise when interested parties (e.g., individuals, non-governmental organizations) do not understand the problem at hand or the methods available to managers for dealing with that problem that are practical and both biologically and cost effective.

Rainbow trout are unusual among western fishes in that their widespread distribution through many types of habitats, their visibility to both consumptive and non-consumptive users, and their nonnative status virtually ensure constituent and political involvement in what for most other fishes would be biological decisions. In addition to being central in the native-vs.-nonnative conflict, they also figure heavily in the economics of sport fishing and aquatic habitat support. The average angler spends over \$1,200 per year on the sport, contributing an estimated \$116 billion overall to the economic output in the United States. The fishing industry supports over one million jobs and

over \$30 billion in wages, generating more revenues than large corporations like Nike, Ford, or Microsoft ([www.sdgifp.info](http://www.sdgifp.info)). As recruitment of new hunters declines (Flather and Hoekstra 1989) and interest in fishing increases, agency focus may change. Resident angler participation exceeded hunter participation in Colorado, Wyoming, Nebraska, and Kansas; hunting

participation exceeded angling participation in South Dakota (U.S. Fish and Wildlife Service 2006). Although millions of dollars are spent each year on native cutthroat and other native fish restoration efforts, rainbow trout will hold a critically important position in state resource management well into the near future.

## REFERENCES

- Allen, K.R. 1951. The Horokiwi Stream: a study of a trout population. New Zealand Marine Department Fisheries Bulletin 10:1-238.
- Allendorf, F.W., R.F. Leary, N.P. Hitt, K.L. Knudsen, M.C. Boyer, and P. Spruell. 2005. Cutthroat trout hybridization and the U.S. Endangered Species Act: one species, two policies. *Conservation Biology* 19(4):1326-1328.
- Angradi, T.R. and J.S. Griffith. 1990. Diel feeding chronology and diet selection of rainbow trout (*Oncorhynchus mykiss*) in the Henry's Fork of the Snake River, Idaho. *Canadian Journal of Fisheries and Aquatic Sciences* 47: 199-209.
- Annear, T., S. Wolff, R. Wiley, R. Keith, K. Johnson, P. Mavrikakis, and C. Meyer. 1999. Modification of the Wyoming Game and Fish Department's system for classifying stream fisheries. Wyoming Game and Fish Department, Fish Division, Administrative Report. 8 pp.
- Annear, T.C. and P.D. Dey. 2006. Water Management Unit Five-Year Plan; 2006 to 2010. Wyoming Game and Fish Department Administrative Report, AW-SW-EP1-540. 40 pp. Available at: <http://gf.state.wy.us/downloads/pdf/Fish/5yearplan2006.pdf>.
- Annear, T.C., W. Hubert, D. Simpkins, and L. Hebdon. 2002. Behavioural and physiological response of trout to winter habitat in tailwaters in Wyoming, USA. *Hydrological Processes* 16:915-925.
- Anonymous. 2003. Aquatic habitat priorities, Upper Bighorn River Corridor. Wyoming Game and Fish Department, 6 pp. Available at: <http://gf.state.wy.us/downloads/pdf/Priorities/Cody/CYAHPriority9.pdf>.
- Anonymous. 2006. Proposal to develop muskellunge broodstock to maintain current tiger muskie program In Washington. Washington Department of Fish and Wildlife. Available at: [http://wdfw.wa.gov/hab/sepa/06047\\_proposal.pdf](http://wdfw.wa.gov/hab/sepa/06047_proposal.pdf).
- Baldwin, T.J., J.E. Peterson, G.C. McGree, K.D. Staigmiller, E.S. Motteram, C.C. Downs, and D.R. Stanek. 1998. Distribution of *Myxobolus cerebralis* in salmonid fishes in Montana. *Journal of Aquatic Animal Health* 10:361-371.
- Bartholomew, A. and J.A. Bohnsack. 2005. A review of catch-and-release angling mortality with implications for no-take reserves. *Reviews in Fish Biology and Fisheries* 15:129-154.
- Bates, R.M. and C.R. Kennedy. 1990. Interactions between the acanthocephalans *Pomphorhynchus laevis* and *Acanthocephalus anguillae* in rainbow trout: testing an exclusion hypothesis. *Parasitology* 100:435-444.
- Bauder, T., R. Waskom, M. Frasier, and D. Hoag. 1999. Irrigation best management practices: what are Colorado producers using? Colorado State University in cooperation with the Colorado Department of Agriculture and the Colorado Department of Public Health and Environment. Available at: <http://www.cde.state.co.us/artemis/ag/AG85019INTERNET.pdf>.
- Becker, C.D. and W.D. Brunson. 1967. *Diphyllbothrium* (Cestoda) infections in salmonids from three Washington lakes. *Journal of Wildlife Management* 31:813-824.
- Behnke, R.J. 1992. Native trout of western North America. American Fisheries Society Monograph 6, Bethesda, MD. 275 pp.
- Behnke, R.J. 1998. About trout: do we learn from history? *Trout* 1998 (Spring):55-57.
- Behnke, R.J. 2004. About trout: wild trout, hatchery trout and the sad story of Derisley Hobbs. *Trout* 2004 (Summer): 59-60.
- Behnke, R.J. and J.R. Tomelleri. 2002. Trout and salmon of North America. The Free Press, New York, NY. 384 pp.
- Binns, N.A. 2004. Effectiveness of habitat manipulation for wild salmonids in Wyoming streams. *North American Journal of Fisheries Management* 24:911-921.
- Binns, N.A. and F.M. Eiserman. 1979. Quantification of fluvial trout habitat in Wyoming. *Transactions of the American Fisheries Society* 108:215-228.

- Biro, P.A., M.V. Abrahams, J.R. Post, and E.A. Parkinson. 2004. Predators select against high growth rates and risk-taking behaviour in domestic trout populations. *Proceedings of the Royal Society B: Biological Sciences* 271: 2233-2237.
- Bjornn, T.C. and D.W. Reiser. 1991. Habitat requirements of salmonids in streams. *American Fisheries Society Special Publication* No. 19:83-138.
- Block, W.M., L.A. Brennan, and R.J. Gutiérrez. 1987. Evaluation of guild-indicator species for use in resource management. *Environmental Management* 11:265-269.
- Blom, J.H. and K. Dabrowski. 1995. Reproductive success of female rainbow trout (*Oncorhynchus mykiss*) in response to graded dietary ascorbyl monophosphate levels. *Biology of Reproduction* 52:1073-1080.
- Bonar, S.A., B.D. Bolding, M. Divens, W. Meyer. 2005. Effects of introduced fishes on wild juvenile coho salmon in three shallow Pacific Northwest lakes. *Transactions of the American Fisheries Society* 134:641-652.
- Boujard, T. and J.F. Leatherland. 1992. Demand-feeding behaviour and diel pattern of feeding activity in *Oncorhynchus mykiss* held under different photoperiod regimes. *Journal of Fish Biology* 40:535-544.
- Bowers, W., B. Hosford, A. Oakley, and C. Bond. 1979. Wildlife habitats in managed rangelands - The Great Basin of southeastern Oregon native trout. USDA Forest Service, Pacific Northwest Forest and Range Experiment Station, General Technical Report PNW 084.
- Brown, A.F. and M. Diamond. 1984. The consumption of rainbow trout (*Salmo gairdneri* Richardson) eggs by macroinvertebrates in the field. *Freshwater Biology* 14:211-215.
- Brown, L.R. and A.M. Brasher. 1995. Effect of predation by Sacramento squawfish (*Ptychocheilus grandis*) on habitat choice of California roach (*Lavinia symmetricus*) and rainbow trout (*Oncorhynchus mykiss*) in artificial streams. *Canadian Journal of Fisheries and Aquatic Science* 52:1639-1646.
- Brown, T.C. 2003. Water availability and recreational opportunities. Pages 299-314 in M.B. Baker, P.F. Ffolliott, L.F. DeBano, and D.G. Neary, editors. *Riparian areas of the southwestern United States: hydrology, ecology, and management*. Lewis Publishers, New York, NY. 408 pp.
- Buchmann, K. and J. Bresciani. 1997. Parasitic infections in pond-reared rainbow trout *Oncorhynchus mykiss* in Denmark. *Diseases of Aquatic Organisms* 28:125-138.
- Buchmann, K.A. Uldal, and H.C. Lyholt. 1995. A checklist of metazoan parasites from rainbow trout (*Oncorhynchus mykiss*). *Acta Veterinaria Scandinavica* 36:299-318.
- Bustard, D.R. and Narver, D.W. 1975. Preferences of juvenile coho salmon (*Oncorhynchus kisutch*) and cutthroat trout (*Salmo clarki*) relative to simulated alteration of winter habitat. *Journal of Fisheries Research Board Canada* 32:681-687.
- Butler, J.R.A. and B.E. Marshall. 1996. Resource use within the crab-eating guild of the upper Kairezi River, Zimbabwe. *Journal of Tropical Ecology* 12:475-490.
- Buttner, J.K. and R.W. Hamilton. 1976. *Ergasilus* (Copepoda:Cyclopoida) infestation of coho and chinook salmon in Lake Michigan. *Transactions of the American Fisheries Society* 105:491-493.
- Cahill, M.M. 1990. Bacterial flora of fishes: a review. *Microbial Ecology* 19:21-41.
- Campbell, M.R., J. Dillon, M.S. Powell. 2002. Hybridization and introgression in a managed, native population of Yellowstone cutthroat trout: genetic detection and management implications. *Transactions of the American Fisheries Society* 131:364-375.
- Campton, D.E. and L.R. Keading. 2005. Westslope cutthroat trout, hybridization, and the U.S. Endangered Species Act. *Conservation Biology* 19(4):1323-1325.
- Caro, T. 2000. Focal species. *Conservation Biology* 14:1569.
- Caro, T., J. Eadie, and A. Sih. 2005. Use of substitute species in conservation biology. *Conservation Biology* 19: 1821.

- Caro, T.M. and G. O'Doherty. 1999. On the use of surrogate species in conservation biology. *Conservation Biology* 13:805.
- Chappell, Andrew. 2006. Wildlife Biologist, Rocky Mountain Region, U.S. Forest Service. Personal communication.
- Chen, W.-M., M. Naruse, and M. Tabata. 2002. Circadian rhythms and individual variability of self-feeding activity in groups of rainbow trout *Oncorhynchus mykiss* (Walbaum). *Aquaculture Research* 33: 491-500.
- Ching, H.L. 1984. Description of *Neoechinorhynchus salmonis* sp. n. (Acanthocephala: Neoechinorhynchidae) from freshwater fishes of British Columbia. *Journal of Parasitology* 70:286-291.
- Chotkowski, M.A. and J.E. Marsden. 1999. Round goby and mottled sculpin predation on lake trout eggs and fry: field predictions from laboratory experiments. *Journal of Great Lakes Research* 25:26-35.
- Choudhury, A., T.L. Hoffnagle, and R.A. Cole. 2004. Parasites of native and nonnative fishes of the Little Colorado River, Grand Canyon, Arizona. *Journal of Parasitology* 90:1042-1053.
- Cilimburg, A. C., and K. C. Short. 2005. Forest fire in the U. S. Northern Rockies: a primer. Retrieved *July 13 2006* from <http://www.northernrockiesfire.org>.
- Claramunt, R.M., J.L. Jonas, J.D. Fitzsimons, and J.E. Marsden. 2005. Influences of spawning habitat characteristics and interstitial predators on lake trout egg deposition and mortality. *Transactions of the American Fisheries Society* 134:1048-1057.
- Clark, G.M., T.R. Maret, M.G. Rupert, M.A. Maupin, W.H. Low, and D.S. Ott. 1998. Water quality in the Upper Snake River Basin, Idaho and Wyoming, 1992-95: U.S. Geological Survey Circular 1160. Available at: <http://water.usgs.gov/pubs/circ1160>.
- Clothier, W.D. 1953. Fish loss and movement in irrigation diversions from the West Gallatin River, Montana. *Journal of Wildlife Management* 17:144-158.
- Coghlan, S.M. 2005. Atlantic salmon restoration in the southern Lake Ontario watershed: evaluating anthropogenic, bioenergetic, and competitive constraints (Abstract from unpublished Ph.D. dissertation). *Dissertation Abstracts International Part B: Science and Engineering* 65(10):4910.
- Colorado Division of Wildlife. 2006. Colorado fishing 2006: fishing regulations & property directory, 85 pp.
- Colorado Division of Wildlife. 2008. Whirling disease. Available at: <http://wildlife.state.co.us/Research/Aquatic/WhirlingDisease>.
- Connell, J.H. 1980. Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos* 35:131-138.
- Cordes, J.F., M.R. Stephens, M.A. Blumberg, and B. May. 2006. Identifying introgressive hybridization in native populations of California golden trout based on molecular markers. *Transactions of the American Fisheries Society* 135:110-128.
- Crisp, D.T. 1993. The environmental requirements of salmon and trout in freshwater. *Freshwater Forum* 3:176-202.
- Cunjak, R.A. 1996. Winter habitat of selected stream fishes and potential impacts from land-use activity. *Canadian Journal of Fisheries and Aquatic Sciences* 53 (Supplement 1):267-282.
- Cunjak, R.A. and J.M. Green. 1986. Influence of water temperature on behavioural interactions between juvenile brook charr, *Salvelinus fontinalis*, and rainbow trout, *Salmo gairdneri*. *Canadian journal of zoology* 64(6):1288-1291.
- Danzmann, R.G., M.M. Ferguson, and F.W. Allendorf. 1988. Heterozygosity and components of fitness in a strain of rainbow trout. *Biological Journal of the Linnean Society* 33:285-304.
- Dellefors, C. and J.I. Johnsson. 1995. Foraging under risk of predation in wild and hatchery-reared juvenile sea trout (*Salmo trutta* L.). *Nordic Journal of Freshwater Research Drottningholm* 70:31-37.
- Der Hovanisian, J.R. 1995. Trout stream enhancement studies: synopsis of information on irrigation diversion fish loss. Idaho Department of Fish and Game, Fisheries Technical Reports, Vol. 101, Article 10. 15 pp.

- Derby, C.E. and J.R. Lovvorn. 1997. Predation on fish by cormorants and pelicans in a cold-water river: a field and modeling study. *Canadian Journal of Fisheries and Aquatic Science* 54:1480-1493.
- Dick, T.A., M.H. Papst, and H.C. Paul. 1987. Rainbow trout (*Salmo gairdneri*) stocking and *Contracaecum* spp. *Journal of Wildlife Diseases* 23:242-247.
- Dies, K. 1990. Leech infestations in trout. *Canadian Veterinary Journal* 31:119.
- Dillon J.C., D.J. Schill, and D.M. Teuscher. 2000. Relative return to creel of triploid and diploid rainbow trout stocked in eighteen Idaho streams. *North American Journal of Fisheries Management* 20:1-9.
- Docker, M.F. and D.D. Heath. 2003. Genetic comparison between sympatric anadromous steelhead and freshwater resident rainbow trout in British Columbia, Canada. *Conservation Genetics* 4:227-231.
- Donovon, G.H. and T.C. Brown. 2007. Be careful what you wish for: the legacy of Smokey Bear. *Frontiers in Ecology and the Environment* 5:73-79.
- Douglas, P.L., G.E. Forrester, and S.D. Cooper. 1994. Effects of trout on the diel periodicity of drifting in baetid mayflies. *Oecologia* 98:48-56.
- Dunham, J.B., G.L. Vinyard, and B.E. Rieman. 1997. Habitat fragmentation and extinction risk of Lohantan cutthroat trout. *North American Journal of Fisheries Management* 17:1126-1133.
- Dunlop, R.A., P.R. Laming, and T.E. Smith. 2004. The stress of four commercial farming practices, feeding, counting, grading and harvesting, in farmed rainbow trout, *Oncorhynchus mykiss*. *Marine and Freshwater Behaviour and Physiology* 37:179-192.
- Epifanio J. 2000. The Status of Coldwater Fishery Management in the United States: An Overview of State Programs. *Fisheries* 25(7):13-27.
- Erman D.C. and V.M. Hawthorne. 1976. The quantitative importance of an intermittent stream in the spawning of rainbow trout. *Transactions of the American Fisheries Society* 105:675-681.
- Esteve, M. 2005. Observations of spawning behaviour in Salmoninae: *Salmo*, *Oncorhynchus* and *Salvelinus*. *Reviews in Fish Biology and Fisheries* 15:1-21.
- Everest, F.H., G.H. Reeves, and J.R. Sedell. 1989. Salmonid habitat: new beginnings through enhancement, but not without uncertainty, risk and failure. *In: Wild Trout, Steelhead and Salmon in the 21<sup>st</sup> Century*. Pacific Northwest Forest and Range Experiment Station, Corvallis, OR.
- Everett, G.V. 1973. The rainbow trout *Salmo gairdneri* (Rich.) fishery of Lake Titicaca. *Journal of Fish Biology* 5: 429-440.
- FAO Fisheries and Aquaculture Department, Cultured Aquatic Species Information Programme. No date. Rainbow trout fact sheet. Available at: [http://www.fao.org/fishery/culturedspecies/Oncorhynchus\\_mykiss](http://www.fao.org/fishery/culturedspecies/Oncorhynchus_mykiss).
- Farag, A.M., D. Skaar, D.A. Nimick, E. MacConnell, and C. Hogstrand. 2003. Characterizing aquatic health using salmonid mortality, physiology, and biomass estimates in streams with elevated concentrations of arsenic, cadmium, copper, lead, and zinc in the Boulder River Watershed, Montana. *Transactions of the American Fisheries Society* 132:450-467.
- Fausch, K. D., Y. Taniguchi, S. Nakano, G.D. Grossman, and C.R. Townsend. 2001. Flood disturbance regimes influence rainbow trout invasion success among five Holarctic regions. *Ecological Applications* 11:1438-1455.
- Fenner, D.B., M.G. Walsh, and D.L. Winkelman. 2005. Diet overlap of introduced rainbow trout and three native fishes in an Ozark stream. Pages 475-482 *in* M. Nickum, P. Mazik, J. Nickum, and D. MacKinlay, editors. *Propagated Fish in Resource Management*. American Fisheries Society Symposium Vol. 44, 640 pp.
- Ferguson, M.M. and L.R. Draushchak. 1990. Disease resistance and enzyme heterozygosity in rainbow trout. *Heredity* 64:413-417.

- Field, C.B., L.D. Mortsch, M. Brklacich, D.L. Forbes, P. Kovacs, J.A. Patz, S.W. Running, and M.J. Scott. 2007. North America. *In*: M.L. Parry, O.F. Canziani, J.P. Palutikof, P.J. van der Linden, and C.E. Hanson, editors. 2007. Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY.
- Finlayson, B., W. Somer, D. Duffield, D. Propst, C. Mellison, T. Pettengill, H. Sexauer, T. Nesler, S. Gurtin, J. Elliot, F. Partridge, and D. Skaar. 2005. Native inland trout restoration on National Forests in the western United States: time for improvement? *Fisheries* 30:10-17.
- Fishbase, 2006. A global information system on fishes. Available at: <http://www.fishbase.org/home.htm>.
- Flather, C.H. and T.W. Hoekstra. 1989. An analysis of the wildlife and fish situation in the United States: 1989-2040. General Technical Report RM-178. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO. 146 pp.
- Fraser, J.M. 1978. The effect of competition with yellow perch on the survival and growth of planted brook trout, splake, and rainbow trout in a small Ontario lake. *Transactions of the American Fisheries Society* 107:505-517.
- Gall, G. 1998. Designing fish breeding programs: Why is aquaculture so far behind? Abstract from World Aquaculture Society meeting, Louisiana State University, Baton Rouge, LA.
- Gall, G.A.E. and S.J. Gross. 1978. Genetic studies of growth in domesticated rainbow trout. *Aquaculture* 13:225-234.
- Gard M. 2005. Variability in flow-habitat relationships as a function of transect number for PHABSIM modeling. *River Research and Applications* 21(9):1013-1019.
- Gaudreault, A., T. Miller, W.L. Montgomery, and G.J. FitzGerald. 1986. Interspecific interactions and diet of sympatric juvenile brook charr, *Salvelinus fontinalis*, and adult ninespine sticklebacks, *Pungitius pungitius*. *Journal of Fish Biology* 28:133-140.
- Gelineau, A., V. Bolliet, G. Corraze, and T. Boujart. 2002. The combined effects of feeding time and dietary fat levels on feed intake, growth, and body composition in rainbow trout. *Aquatic Living Resources* 15:225-230.
- Gerking, S.D. 1994. *Feeding ecology of Fish*. Academic Press Inc., San Diego, CA. 416 pp.
- Gerlich, G.W. 2001. Eleven Mile Reservoir Fishery Management Plan. Colorado Division of Wildlife, NE Aquatic Section. 25 pp.
- Gieseker, C.M., S.G. Serfling, and R. Reimschuessel. 2006. Formalin treatment to reduce mortality associated with *Saprolegnia parasitica* in rainbow trout, *Oncorhynchus mykiss*. *Aquaculture* 253:120-129.
- Gilbert, M.A. and W.O. Granath, Jr. 2003. Whirling disease of salmonid fish: life cycle, biology, and disease. *Journal of Parasitology* 89:658-667.
- Gillette, D.P., J.S. Tiemann, D.R. Edds, and M.L. Wildhaber. 2005. Spatiotemporal patterns of fish assemblage structure in a river impounded by low-head dams. *Copeia* 5:539-549.
- Gillilan, D.M. and T.C. Brown. 1997. *Instream flow protection: seeking a balance in western water use*. Island Press, Washington, D.C. 417 pp.
- Gilmour, K.M., J.D. DiBattista, and J.B. Thomas. 2005. Physiological causes and consequences of social status in salmonid fish. *Integrative and Comparative Biology* 45:263-273.
- Giuliano, W.M. 2006. Should I fence the streams, ponds, and wetlands in my pastures? *Rangelands* 28:29-31.
- Glick, P. 2006. Fueling the fire: global warming, fossil fuels and the fish and wildlife of the American west. National Wildlife Federation. 30 pp. Available at: <http://www.nwf.org/globalwarming/pdfs/FuelingtheFire.pdf>.
- Gold, M.F. and J.R. Gold. 1976. Golden trout in trouble. *Natural History* 85: 74-84.



- Gray, T.P.R., S. Jobling, S. Morris, C. Kelly, S. Kirby, A. Janbakhsh, J.E. Harries, M.J. Waldock, J.P. Sumpter, and C.R. Tyler. 2000. Long-term temporal changes in the estrogenic composition of treated sewage effluent and its biological effects on fish. *Environmental Science and Technology* 34:1521-1528.
- Gregory, T.R. and C.M. Wood. 1998. Individual variation and interrelationships between swimming performance, growth rate, and feeding in juvenile rainbow trout (*Oncorhynchus mykiss*). *Canadian Journal of Fisheries and Aquatic Sciences* 55:1583-1590.
- Hasegawa, K., T. Yamamoto, M. Murakami, and K. Maekawa. 2004. Comparison of competitive ability between native and introduced salmonids: evidence from pairwise contests. *Ichthyological Research* 51:191-194.
- Hayes, J.W. 1987. Competition for spawning space between brown (*Salmo trutta*) and rainbow trout (*S. gairdneri*) in a lake inlet tributary, New Zealand. *Canadian Journal of Fisheries and Aquatic Sciences* 44:40-47.
- Hayes, J.W. 1989. Social interactions between 0+ brown and rainbow trout in experimental stream troughs. *New Zealand Journal of Marine and Freshwater Research* 23:163-170.
- Hayes, S.A., M.H. Bond, C.V. Hanson, and R.B. MacFarlane. 2004. Interactions between endangered wild and hatchery salmonids: can the pitfalls of artificial propagation be avoided in small coastal streams? *Journal of Fish Biology* 65 (suppl. 1):101-121.
- Hedgpeth, J. 1991. The passing of the salmon. Pages 52-60 in A. Lufkin. *California's salmon and steelhead, the struggle to restore an imperiled resource*. University of California Press, Berkeley, CA.
- Heggenes, J. 1988. Physical habitat selection by brown trout (*Salmo trutta*) in riverine systems. *Nordic Journal of Freshwater Research* 64:74-90.
- Heggenes, J. and T. Traaen. 1988. Downstream migration and critical water velocities in stream channels for fry of four salmonid species. *Journal of Fish Biology* 32:717-727.
- Helfman, G.S. 1981. The advantage to fish of hovering in the shade. *Copeia* 1981:392-400.
- Henderson, R., J.L. Kershner, and C.A. Toline. 2000. Timing and location of spawning by nonnative wild rainbow trout and native cutthroat trout in the South Fork Snake River, Idaho, with implications for hybridization. *North American Journal of Fisheries Management* 20:584-596.
- Hendrickson, D.A., H. Espinosa-Pérez, L.T. Findley, W. Forbes, J.R. Tomelleri, R.L. Mayden, J.L. Nielsen, B. Jensen, G. Ruiz-Campos, A. Varela-Romero, A.M. Van Der Heiden, F. Camarena, and F.J. García de León. 2002. Mexican native trouts: a review of their history and current systematic and conservation status. *Reviews in Fish Biology and Fisheries* 12:273-316.
- Hillman, T. W., J. S. Griffith, and W. S. Platts, 1987. Summer and winter habitat selection by juvenile chinook salmon in a highly sedimented Idaho stream. *Transactions of the American Fisheries Society*. 116:185-195.
- Hitt, N.P., C.A. Frissell, C.C. Muhlfeld, and F.W. Allendorf. 2003. Spread of hybridization between native westslope cutthroat trout, *Oncorhynchus clarki lewisi*, and nonnative rainbow trout, *Oncorhynchus mykiss*. *Canadian Journal of Fisheries and Aquatic Sciences* 60:1440-1451.
- Hobbs, D.F. 1948. Trout fisheries in New Zealand. New Zealand Marine Department, Wellington, Fisheries Bulletin No. 9. 175 pp.
- Hodgson, J.R., C.J. Hodgson, and S.M. Brooks. 1991. Trophic interaction and competition between largemouth bass (*Micropterus salmoides*) and rainbow trout (*Oncorhynchus mykiss*) in a manipulated lake. *Canadian Journal of Fisheries and Aquatic Sciences* 48:1704-1712.
- Holden, P.B. 1991. Ghosts of the Green River: impacts of Green River poisoning on management of native fishes. Pages 43-54 in W.L. Minckley and J.E. Deacon, editors. *Battle against extinction: native fish management in the American West*. University of Arizona Press, Tucson, AZ.
- Honsig-Erlenburg, W. 2001. Distribution and threat of grayling (*Thymallus thymallus*) in Carinthia (Austria). *Verhandlungen der Gesellschaft für Ichthyologie* 2:49-57.

- Huber, I., B. Spanggaard, K.F. Appel, L. Rossen, T. Nielsen, and L. Gram. 2004. Phylogenetic analysis and in situ identification of the intestinal microbial community of rainbow trout (*Oncorhynchus mykiss*, Walbaum). *Journal of Applied Microbiology* 96:117-132.
- Hubert, W.A., T.D. Marwitz, K.G. Gerow, N.A. Binns, and R.W. Wiley. 1996. Estimation of potential maximum biomass of trout in Wyoming streams to assist management decisions. *North American Journal of Fisheries Management* 16:821-829.
- Imre, I., J.W. Grant, and E.R. Keeley. 2004. The effect of food abundance on territory size and population density of juvenile steelhead trout (*Oncorhynchus mykiss*). *Oecologia* 138:371-378.
- International Commission on Zoological Nomenclature. 1999. *International Code of Zoological Nomenclature*, Fourth Edition. The International Trust for Zoological Nomenclature, London.
- Jackson, J.E., T.A. Raadik, M. Lintermans, and M. Hammer. 2004. Alien salmonids in Australia: impediments to effective impact management, and future directions. *New Zealand Journal of Marine and Freshwater Research* 38:447-455.
- Jacobs, J.J., P.T. Tyrrell, and D.J. Brosz. 2003. Wyoming water law: a summary. Report B849R, University of Wyoming Agricultural Experiment Station. Available at: <http://seo.state.wy.us/PDF/b849r.pdf>.
- Jacobsen, L. 2005. Otter (*Lutra lutra*) predation on stocked brown trout (*Salmo trutta*) in two Danish lowland rivers. *Ecology of Freshwater Fish* 14:59-68.
- Jensen, B., G.R. Campos, A.V. Romero, A. van der Heiden, F. Camarena, and F.J.G. de Leon. 2002. Mexican native trouts: a review of their history and current systematic and conservation status. *Reviews in Fish Biology and Fisheries* 12:273-316.
- Jepsen, N., S. Pedersen, and E. Thorstad. 2000. Behavioural interactions between prey (trout smolts) and predators (pike and pikeperch) in an impounded river. *Regulated Rivers: Research & Management* 16:189-198.
- Jobling, M. and J. Koskela. 1996. Interindividual variations in feeding and growth in rainbow trout during restricted feeding and in a subsequent period of compensatory growth. *Journal of Fish Biology* 49:658-667.
- Johnson, B. and N. Nomanbhoy. 2005. An eField Guide to Western Fishes -- Colorado and Wyoming. Copyright 2005, Colorado State University. <http://taurus.cnr.colostate.edu/projects/cofishguide/index.cfm>.
- Johnsson, J.I. 1992. Growth and foraging behaviour in juvenile rainbow trout (*Oncorhynchus mykiss*). Goteborgs Universitet (Sweden); 0904; 27 p.
- Johnsson, J.I. 1993. Big and brave: size selection affects foraging under risk of predation in juvenile rainbow trout, *Oncorhynchus mykiss*. *Animal Behaviour* 45:1219-1225.
- Jonas, J.L., R.M. Claramunt, J.D. Fitzsimons, J.E. Marsden, and B.J. Ellrott. 2005. Estimates of egg deposition and effects of lake trout (*Salvelinus namaycush*) egg predators in three regions of the Great Lakes. *Canadian Journal of Fisheries and Aquatic Science* 62:2254-2264.
- Jordan, D.S. 1963. The genera of fishes and a classification of fishes. Reprinted by Stanford University Press, Stanford, CA. [Originally published 1917-1920 and 1923.]
- Kansas Department of Wildlife and Parks. 2008. Kansas Fishing Regulations Summary. 41 pp. Available at: [http://www.kdwp.state.ks.us/news/fishing/fishing\\_regulations](http://www.kdwp.state.ks.us/news/fishing/fishing_regulations).
- Karr J.R., J.J. Rhodes, G.W. Minshall, F.R. Hauer, R.L. Beschta, C.A. Frissell, and D.A. Perry 2004. The effects of postfire salvage logging on aquatic ecosystems in the American west. *BioScience* 54(11):1029-1033.
- Keeley, E.R. 2003. An experimental analysis of self-thinning in juvenile steelhead trout. *Oikos* 102:543-550.
- Kerr, S.J. and T.A. Lasenby. 2000. Rainbow trout stocking in inland lakes and streams: An annotated bibliography and literature review. Fish and Wildlife Branch, Ontario Ministry of Natural Resources, Peterborough, Ontario. 220 pp. + appendices. Available at: <https://ozone.scholarsportal.info/bitstream/1873/8329/1/10290369.pdf>.

- Kershner, J.L., C.M. Bischoff, and D.L. Horan. 1997. Population, habitat, and genetic characteristics of Colorado River cutthroat trout in wilderness and nonwilderness stream sections in the Uinta Mountains of Utah and Wyoming. *North American Journal of Fisheries Management* 17:1134-1143.
- Knapp, R.A., P.S. Corn, and D.E. Schindler. 2001. Fish stocking impacts to mountain lake ecosystems. The introduction of nonnative fish into wilderness lakes: good intentions, conflicting mandates, and unintended consequences. *Ecosystems* 4:275-278.
- Kruse, C.G., W.A. Hubert, and F.J. Rahel. 2000. Status of Yellowstone cutthroat trout in Wyoming waters. *North American Journal of Fisheries Management* 20:693-705.
- Kruse, C.G., W.A. Hubert, and F.J. Rahel. 2001. An assessment of headwater isolation as a conservation strategy for cutthroat trout in the Absaroka Mountains of Wyoming. *Northwest Science* 75:1-11.
- Kusabs, I.A. and S. Swales. 1991. Diet and food resource partitioning in koaro, *Galaxias brevipinnis* (Guenther), and juvenile rainbow trout, *Oncorhynchus mykiss* (Richardson), in two Taupo streams, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 25:317-325.
- Laake, J.L., P. Browne, R.L. DeLong, and H.R. Huber. 2002. Pinniped diet composition: a comparison of estimation models. *Fishery Bulletin* 100:434-447.
- Landres, P.B., J. Verner, and J.W. Thomas. 1988. Ecological uses of vertebrate indicator species: a critique. *Conservation Biology* 2:316-328.
- LaRoche, A.L. and B. Garland. 1980. Environmental extremes and native brook trout populations in southeastern United States. Trout Unlimited and Federation of Fly Fishermen.
- Larsen, R.E. No date. Fishery habitat: 1) living space and reproductive requirements. University of California Cooperative Extension, University of California, Davis. Fact Sheet No. 26.
- Larson, E.T., S. Winberg, I. Mayer, O. Lepage, C.H. Summers, and O. Overli. 2004. Social stress affects circulating melatonin levels in rainbow trout. *General and Comparative Endocrinology* 136:322-327.
- Leary, R.F., F.W. Allendorff, and K.L. Knudsen. 1983. Developmental stability and enzyme heterozygosity in rainbow trout. *Nature* 301:71-72.
- Leary, R.F., F.W. Allendorff, K.L. Knudsen, G.H. Thorgaard. 1985. Heterozygosity and developmental stability in gynogenetic diploid and triploid rainbow trout. *Heredity* 54:219-225.
- Li, H.W. and R.W. Brocksen. 1977. Approaches to the analysis of energetic costs of intraspecific competition for space by rainbow trout (*Salmo gairdneri*). *Journal of Fish Biology* 11:329-341.
- Lightfoot, G. 2004. Triploid trout in native trout waters: Phase 1-literature review and recommendations for Phase 2. *Trout News* 38:25-26.
- Lintermans, M. 1992. Predation on *Eulamprus tympanum* by rainbow trout. *Herpetofauna* 22:34-35.
- Lohr, S.C. and J.L. West. 1992. Microhabitat selection by brook and rainbow trout in a Southern Appalachian stream. *Transactions of the American Fisheries Society* 121:729-736.
- Lovvorn, J.R., D. Yule, and C.E. Derby. 1999. Greater predation by double-crested cormorants on cutthroat versus rainbow trout fingerlings stocked in a Wyoming river. *Canadian Journal of Zoology* 77(12):1984-1990.
- Lucas, M.C. 1993. Food interrelationships between brown trout, *Salmo trutta* L., and rainbow trout, *Oncorhynchus mykiss* (Walbaum), in a small put-and-take stillwater fishery. *Aquaculture and Fisheries Management* 24:355-364.
- MacCrimmon H.R. 1971. World distribution of rainbow trout (*Salmo gairdneri*). *Journal of Fisheries Research Board Canada*. 28(5):663-704.
- Madeira, M.J., B.J. Gomez-moliner, and A.M. Barbe. 2005. Genetic introgression on freshwater fish populations caused by restocking programmes. *Biological Invasions* 7:117-125.

- Marchetti, M.P. and G.A. Nevitt. 2003. Effects of hatchery rearing on brain structures of rainbow trout, *Oncorhynchus mykiss*. *Environmental Biology of Fishes* 66:9-14.
- Maret, T.R. 1995. Water-quality assessment of the upper Snake River Basin, Idaho and western Wyoming-- summary of aquatic biological data for surface water through 1992: U.S. Geological Survey Water-Resources Investigations Report 95-4006, 59 pp.
- Marnell, L.F., R.J. Behnke, and F.W. Allendorf. 1987. Genetic identification of cutthroat trout (*Salmo clarki*) in Glacier National Park, Montana. *Canadian Journal of Fisheries and Aquatic Sciences* 44:1830-1839.
- Matbouli M.E., T. Fischer Scherl, and R.W. Hoffmann. 1992. Annual Review of Fish Diseases, p. 392. Available from The Whirling Disease Initiative at <http://whirlingdisease.montana.edu/about/lifecycle.htm>.
- McGrath, C.C. 2003. Potential effects of whitewater parks on in-stream trout habitat. Report prepared for: Recreational Engineering and Planning, Inc., Boulder, CO. 12 pp. Available at: <http://www.wwparks.com/Web%20fish%20report.pdf>.
- McKenna, J.E. and J.H. Johnson. 2005. Juvenile rainbow trout production in New York tributaries of Lake Ontario: implications for Atlantic salmon restoration. *North American Journal of Fisheries Management* 25:391-403.
- McKinney, T., D.W. Speas, R.S. Rogers, and W.R. Persons. 1999. Rainbow trout in the Lee's Ferry recreational fishery below Glen Canyon Dam, Arizona, following establishment of minimum flow requirements. Final Report to U.S. Bureau of Reclamation, Grand Canyon Monitoring and Research Center, Flagstaff, AZ. Arizona Game and Fish Department, Phoenix, AZ. Cooperative Agreement No. 1425-97-FC-40-22690.
- McKinney, T., T. Robinson, D.W. Speas, and R.S. Rogers. 2001. Health assessment, associated metrics, and nematode parasitism of rainbow trout in the Colorado River below Glen Canyon Dam, Arizona. *North American Journal of Fisheries Management* 21:62-69.
- McMichael, G.A. and T.N. Pearsons. 1998. Effects of wild juvenile spring chinook salmon on growth and abundance of wild rainbow trout. *Transactions of the American Fisheries Society* 127:261-274.
- McPhail, J.O. and C.C. Lindsey. 1970. Freshwater fishes of northwestern Canada and Alaska. *Bulletin of the Fisheries Research Board of Canada* 173. 381 pp.
- Meka, J.M. 2004. The influence of hook type, angler experience, and fish size on injury rates and the duration of capture in an Alaskan catch-and-release rainbow trout fishery. *North American Journal of Fisheries Management* 24:1309-1321.
- Meka, J.M. and S.D. McCormick. 2005. Physiological response of wild rainbow trout to angling: impact of angling duration, fish size, body condition, and temperature. *Fisheries Research* 72:311-322.
- Mellina, E., S.G. Hinch, K.D. MacKenzie, and G. Pearson. 2005. Seasonal movement patterns of stream-dwelling rainbow trout in north-central British Columbia, Canada. *Transactions of the American Fisheries Society* 134: 1021-1037.
- Merriman, D. and A.M. Janicki. No date. Colorado's instream flow program – how it works and why it's good for Colorado. Available at: [cwcb.state.co.us/NR/rdonlyres/6333F3FC-E2F8-4E7E-9BD3-690FCC4285D1/0/FinalRiparianAssocPaper.pdf](http://cwcb.state.co.us/NR/rdonlyres/6333F3FC-E2F8-4E7E-9BD3-690FCC4285D1/0/FinalRiparianAssocPaper.pdf).
- Merz, J.E. 2002. Seasonal feeding habits, growth, and movement of steelhead trout in the lower Mokelumne river, California. *California Fish and Game* 88: 95-111.
- Metcalf, J.L., V.L. Pritchard, S.M. Silvestri, J.B. Jenkins, J.S. Wood, D.E. Cowley, R.P. Evans, D.K. Shiozawa, and A.P. Martin. 2007. Across the great divide: genetic forensics reveals misidentification of endangered cutthroat trout populations. *Molecular Ecology* 16:4445-4454.
- Metcalf, J.L., M.R. Siegle, and A.P. Martin. 2008. Hybridization dynamics between Colorado's native cutthroat trout and introduced rainbow trout. *Journal of Heredity* 99:149-156.
- Miller, L.M., T. Close, and A.R. Kapuscinski. 2004. Lower fitness of hatchery and hybrid rainbow trout compared to naturalized populations in Lake Superior tributaries. *Molecular Ecology* 13:3379-3388.

- Miller, R.R., J.D. Williams, and J.E. Williams. 1989. Extinctions of North American fishes during the past century. *Fisheries* 14:22-38.
- Mills, E.L., J.H. Leach., J.T. Carleton, and C.L. Secor. 1993. Exotic species in the Great Lakes: history of biotic crises and anthropogenic introductions. *Journal of Great Lakes Research* 19:1-54.
- Minckley, W.L. 1991. Native fishes of the Grand Canyon region: an obituary? Pages 124-155 *in* Colorado River Ecology and Dam Management. Committee to Review the Glen Canyon Environmental Studies, Water Science and Technology Board, National Research Council. 288 pp.
- Minckley, W.L. and J.E. Deacon, editors. 1991. Battle against extinction: native fish management in the American west. University of Arizona Press, Tucson, AZ. 517 pp.
- Mitchum, D.L. 1995. Parasites of fishes in Wyoming. Pub. 116, Wyoming Game and Fish Department. 304 pp.
- Mitro, M.G., A.V. Zale, and B.A. Rich. 2003. The relation between age-0 rainbow trout (*Oncorhynchus mykiss*) abundance and winter discharge in a regulated river. *Canadian Journal of Fisheries and Aquatic Sciences* 60: 135-139.
- Montgomery, W.L. 1983. Parr excellence. *Natural History* 92(6):58-67.
- Montgomery, W.L., G.E. Goslow, Jr., K.B. Staley, and J.R. Mills. 1987. Alternative mating behaviors of male Atlantic salmon (*Salmo salar*), with special reference to mature male parr. Pages 232-238 *in* W. Matthews and D. Heins, editors. *Evolutionary and Community Ecology of North American Stream Fishes*. University of Oklahoma Press, Norman, OK.
- Montgomery, W.L. and K. Tinning. 2006. Impacts of fluctuating water levels on eggs and fry of rainbow trout in the Colorado River below Glen Canyon Dam, Arizona. Unpublished manuscript.
- Morgan, A. and F. Hinojosa. No date. Winter habitat utilization by juvenile salmonids: a literature review. Northwest Indian Fisheries Commission, Olympia, WA. 26 pp.
- Morita, K., J.I. Tsuboi, and H. Matsuda. 2004. Methodological insights: the impact of exotic trout on native charr in a Japanese stream. *Journal of Applied Ecology* 41:962-972.
- Morris, A.R. and A. Caverly. 2004. 2003-2004 Seton and Anderson Lakes kokanee assessment. British Columbia Conservation Foundation and Ministry of Water, Land and Air Protection. Kamloops, British Columbia. Available at: [http://www.bchydro.com/bcrp/projects/docs/bridge\\_river/03SE04.pdf](http://www.bchydro.com/bcrp/projects/docs/bridge_river/03SE04.pdf).
- Moyle, P.B. 2002. Inland fishes of California, revised and expanded. University of California Press, Berkeley, CA. 502 pp.
- Myrick, C. 1999. Temperature, genetic, and ration effects on juvenile rainbow trout (*Oncorhynchus mykiss*) bioenergetics. Dissertation Abstracts International Part B: Science and Engineering [Diss. Abst. Int. Pt. B - Sci. & Eng.]. Vol. 60, no. 2, p. 433. Aug 1999.
- Myrick, C.A. and J.J. Cech, Jr. 2000. Temperature influences on California rainbow trout physiological performance. *Fish Physiology and Biochemistry* 22:245-254.
- Narum, S.R., C. Contor, A. Talbot, and M.S. Powell. 2004. Genetic divergence of sympatric resident and anadromous forms of *Oncorhynchus mykiss* in the Walla Walla River, U.S.A. *Journal of Fish Biology* 65:471-488.
- NatureServe. 2006. NatureServe Explorer: An online encyclopedia of life [web application]. Version 4.7. NatureServe, Arlington, VA. Available <http://www.natureserve.org/explorer>.
- Nebraska Game and Parks Commission. 2008. 2008 Nebraska Fishing Guide, Regulations and Public Waters. 56 pp. Available at: <http://www.ngpc.state.ne.us/fishing/guides/fishguide/fishguide.asp>.
- Nehring, B. and P.G. Walker. 1996. Whirling disease in the wild: the new reality in the intermountain west. *Fisheries* 21:28-30.
- Nehring, R.B. and K.G. Thompson. 2001. Impact assessment of some physical and biological factors in the whirling disease epizootic among wild trout in Colorado. Colorado Division of Wildlife, Special Report Number 76.

- Nelson, J.S. 2006. Fishes of the world, 4th ed. Wiley, Hoboken, NJ. 601 pp.
- Nickum, J.G., H.L. Bart, Jr, P.R. Bowser, I.E. Greer, C. Hubbs, J.A. Jenkins, J.R. MacMillan, J.W. Rachlin, J.D. Rose, P.W. Sorensen, and J.R. Tomasso. 2004. Guidelines for the Use of Fishes in Research. American Fisheries Society, Bethesda, MD.
- Nilsson, N-A. and T.G. Northcote. 1981. Rainbow trout (*Salmo gairdneri*) and cutthroat trout (*S. clarki*) interactions in coastal British Columbia lakes. Canadian Journal of Fisheries and Aquatic Science 38:1228-1246.
- Novak, M.A., J.L. Kershner, and K.E. Mock. No date. Molecular genetic investigation of Yellowstone cutthroat trout and finespotted Snake River cutthroat trout. A report in partial fulfillment of agreement # 165/04, State of Wyoming, Wyoming Game and Fish Commission Grant Agreement.
- Olenick, R.J. and J.H. Gee. 1981. Tiger salamanders (*Ambystoma tigrinum*) and stocked rainbow trout (*Salmo gairdneri*): potential competitors for food in Manitoba pothole lakes. Canadian Field-Naturalist 95:129-132.
- O'Neal, K.O. 2002. Effects of global warming on trout and salmon in U.S. streams. Defenders of Wildlife, Pacific Fishery Management Council, Washington, D.C.
- Page, L.M. and B.M. Burr. 1991. A field guide to freshwater fishes. Houghton Mifflin, Boston, MA. 432 pp.
- Parkhurst, J.A., R.P. Brooks, and D.E. Arnold. 1992. Assessment of predation at trout hatcheries in central Pennsylvania. Wildlife Society Bulletin 20:411-419.
- Peacock, M.M. and V. Kirchoff. 2004. Assessing the conservation value of hybridized cutthroat trout populations in the Quinn River drainage, Nevada. Transactions of the American Fisheries Society 133:309-325.
- Pettersson, J., J.I. Johnsson, and T. Bohlin. 1996. The competitive advantage of large body size declines with increasing group size in rainbow trout. Journal of Fish Biology 49:370-372.
- Phillips, R.B., M.R. Morasch, P.A. Wheeler, and G.H. Thorgaard. 2005. Rainbow trout (*Oncorhynchus mykiss*) of Idaho and Alaskan origin (2n = 58) share a chromosome fusion relative to trout of California origin (2n = 60). Copeia 2005:661-664.
- Pilliod, D.S. and C.R. Peterson. 2001. Local and landscape effects of introduced trout on amphibians in historically fishless watersheds. Ecosystems 4:322-333.
- Pister, E.P. 2001. Wilderness fish stocking: history and perspective. Ecosystems 4:279-286.
- Pritchard, V.L. and D.E. Cowley. 2006. Rio Grande cutthroat trout (*Oncorhynchus clarkii virginalis*): a technical conservation assessment. USDA Forest Service, Rocky Mountain Region. Available at: <http://www.fs.fed.us/r2/projects/scp/assessments/riograndecutthroattrout.pdf>.
- Raleigh, R.F., T. Hickman, R.C. Solomon, and P.C. Nelson. 1984. Habitat suitability information: rainbow trout. USFWS-BSP, Fort Collins, CO.
- Reese, C.D. and B.C. Harvey. 2002. Temperature-dependent interactions between juvenile steelhead and Sacramento pikeminnow in laboratory streams. Transactions of the American Fisheries Society 131:599-606.
- Reeves, G.H., F.H. Everest, and J.D. Hall. 1987. Interaction between reidside shiner (*Richardsonius balteatus*) and the steelhead trout (*Salmo gairdneri*) in western Oregon: the influence of water temperature. Canadian Journal of Fisheries and Aquatic Sciences 44:1603-1613.
- Reiser, D.W. and T.C. Bjornn. 1979. Habitat Requirements of Anadromous Salmonids. In: Meehan, W.R., Technical Editor. Influence of Forest and Rangeland Management on Anadromous Fish Habitat in the Western United States and Canada. USDA Forest Service General Technical Report PNW-96. 54 pp.
- Reiser, D.W. and R.G. White. 1983. Effects of complete redd dewatering on salmonid egg-hatching success and development of Juveniles. Transactions of the American Fisheries Society 112:532-540.
- Richter, B.D., D.P. Braun, M.A. Mendelson, and L.L. Master. 1997. Threats to imperiled freshwater fauna. Conservation Biology 11:1081-1093.

- Riehle, M.D. and J.S. Griffith. 1993. Changes in habitat use and feeding chronology of juvenile rainbow trout (*Oncorhynchus mykiss*) in fall and the onset of winter in Silver Creek, Idaho. *Canadian Journal of Fisheries and Aquatic Sciences* 50: 2119-2128.
- Rincon, P.A. and G.D. Grossman. 1998. The effects of rainbow trout (*Oncorhynchus mykiss*) on the use of spatial resources and behavior of rosyside dace (*Clinostomus funduloides*). *Archiv fur Hydrobiologie* 141:333-352.
- Rinne, J. N. and C. Carter. 2002. Short-Term Effects of Wildfires on Fishes in the Southwestern United States. Management Implications. Proceedings Symposium, Effects of Fire on Wildlife, San Diego, California. Dec 2002.
- Robinson, A.T., S.D. Bryan, and M.G. Sweetser. 2003. Habitat use by nonnative rainbow trout, *Oncorhynchus mykiss*, and native Little Colorado spinedace, *Lepidomeda vittata*. *Environmental Biology of Fishes* 68:205-214.
- Rodnick K.J., A. K. Gamperl, K. R. Lizars, M. T. Bennett, R. N. Rausch, and E. R. Keeley. 2004. Thermal tolerance and metabolic physiology among redband trout populations in south-eastern Oregon. *Journal of Fish Biology* 64(2):310-335.
- Rogers, S.C., D.W. Church, A.H. Weatherley, and D.G. Pincock. 1984. An automated ultrasonic telemetry system for the assessment of locomotor activity in free-ranging rainbow trout, *Salmo gairdneri*, Richardson. *Journal of Fish Biology* 25:697-710.
- Rognlie, M.C. and S.E. Knapp. 1998. *Myxobolus cerebralis* in *Tubifex tubifex* from a whirling disease epizootic in Montana. *Journal of Parasitology* 84:711-713.
- Ross, M.R. 1997. Fisheries conservation and management. Prentice Hall, Upper Saddle River, NJ. 374 pp.
- Ross, S.T. 1986. Resource partitioning in fish assemblages: a review of field studies. *Copeia* 1986:352-388.
- Ruediger, R. and W. Ruediger. No date. The effects of highways on trout and salmon rivers in the western U.S. 9 pp. Available at: [http://www.dot.state.fl.us/EMO/sched/Trout\\_Streams.pdf](http://www.dot.state.fl.us/EMO/sched/Trout_Streams.pdf).
- Ryman, M. and F. Utter. 1987. Population genetics and fishery management. University of Washington Press, Seattle, WA. 420 pp.
- Schmidt S.P. and E.W. House. 1979. Precocious sexual maturation development in hatchery-reared and laboratory maintained male steelhead trout (*Salmo gairdneri*). *Journal of Fisheries Research Board Canada*. 36: 90-93.
- Schneidervin, R.W. and W.A. Hubert. 1987. Diet overlap among zooplanktophagous fishes in Flaming Gorge Reservoir, Wyoming-Utah. *North American Journal of Fisheries Management* 7:379-385.
- Schuett-Hames, D. and A. Pleus. 1996. Literature review & monitoring recommendations for salmonid spawning habitat availability. Northwest Indian Fisheries Commission, TFW-AM-9-96-002. Available at: <http://www.nwifc.org/tfw/documents/sha01.pdf>.
- Schuett-Hames, D., B. Conrad, A. Pleus, and K. Lautz. 1996. Literature review and monitoring recommendations for salmonid spawning gravel scour. TFW Ambient Monitoring Program, 82 TFW-AM-9-96-001.
- Scott, D. and J.R. Irvine. 2000. Competitive exclusion of brown trout *Salmo trutta* L., by rainbow trout *Oncorhynchus mykiss* Walbaum, in lake tributaries, New Zealand. *Fisheries Management and Ecology* 7:225-237.
- Serezli, R. 2004. Spawning time, fecundity and hatchery performance of rainbow trout (*Oncorhynchus mykiss*) broodstocks in the Eastern Black Sea region. Ph.D. Dissertation. Graduate School of Natural and Applied Sciences, Karadeniz Technical University, Trabzon, Turkey. (ABSTRACT: [http://www.fbe.ktu.edu.tr/fbe\\_eng/tezler/balikcilik/doktora/99-/di455.html](http://www.fbe.ktu.edu.tr/fbe_eng/tezler/balikcilik/doktora/99-/di455.html)).
- Shepard, B.B., B. Sanborn, L. Ulmer, and D.C. Lee. 1997. Status and risk of extinction for westslope cutthroat trout in the Upper River Basin, Montana. *North American Journal of Fisheries Management* 17:1158-1172.
- Shrader, T. and B. Moody. 1997. Predation and competition between largemouth bass and hatchery rainbow trout in Crane Prairie Reservoir, Oregon. Information report 97-1, Oregon Department of Fish and Wildlife, Portland, OR.

- Siitonen, L. and G.A.E. Gall. 1989. Response to selection for early spawn date in rainbow trout, *Salmo gairdneri*. *Aquaculture* 78:153-161.
- Simpkins, D. G. 1997. Winter movements and habitat use by small rainbow trout in the Big Horn River, below Boysen Reservoir, Wyoming. Master's thesis. University of Wyoming, Laramie.
- Simpkins, D.G. and W.A. Hubert. 2000. Drifting invertebrates, stomach contents, and body conditions of juvenile rainbow trout from fall through winter in a Wyoming tailwater. *Transactions of the American Fisheries Society* 129:1187-1195.
- Simpkins, D.G., W.A. Hubert, and T.A. Wesche. 2000. Effects of fall-to-winter changes in habitat and frazil ice on the movements and habitat use of juvenile rainbow trout in a Wyoming tailwater. *Transactions of the American Fisheries Society* 129:101-118.
- Sipher, C.R. and E.P. Bergersen. 2005. The effects of whirling disease on growth and survival of Snake River cutthroat and Colorado River rainbow trout fingerlings. *Journal of Aquatic Animal Health* 17:353-364.
- Skaala, O., G. Dahle, K.E. Joerstad, and G. Naevdal. 1990. Interactions between natural and farmed fish populations: information from genetic markers. *Journal of Fish Biology* 36:449-460.
- Sloman, K.A., G.R. Scott, D.G. McDonald, and C.M. Wood. 2004. Diminished social status affects ionoregulation at the gills and kidney in rainbow trout (*Oncorhynchus mykiss*). *Canadian Journal of Fisheries and Aquatic Sciences* 61:618-626.
- South Dakota Game, Fish, and Parks. 2008. South Dakota 2008 Fishing Handbook. 56 pp. Available at: <http://www.sdgifp.info/Publications/FishingHandbook.pdf>.
- Strange, R.J. and J.W. Habera. 1998. No net loss of brook trout distribution in areas of sympatry with rainbow trout in Tennessee streams. *Transactions of the American Fisheries Society* 127:434-440.
- Su, G.-S., L.-E. Liljedahl, and G.A.E. Gall. 1997. Genetic and environmental variation of female reproductive traits in rainbow trout (*Oncorhynchus mykiss*). *Aquaculture* 154:113-122.
- Sundstrom, L.F., E. Petersson, J. Hojesjo, J.I. Johnsson, and T. Jarvi. 2004. Hatchery selection promotes boldness in newly hatched brown trout (*Salmo trutta*): implications for dominance. *Behavioral Ecology* 15:192-198.
- Swales, S., R.B. Lauzier, and C.D. Levings, C.D. 1986. Winter habitat preferences of juvenile salmonids in two interior rivers in British Columbia. *Canadian Journal of Zoology*. 64:1506-1514.
- Szalai, A.J. and T.A. Dick. 1988. Helminths of stocked rainbow trout (*Salmo gairdneri*) with special reference to *Clinostomum complanatum*. *Journal of Wildlife Diseases* 24:456-460.
- Tabor, R.A. and W.A. Wurtsbaugh. 1991. Predation risk and the importance of cover for juvenile rainbowtrout in lentic systems. *Transactions of the American Fisheries Society* 120:728-738.
- Taniguchi, Y., K.D. Fausch, and S. Nakano. 2002. Size-structured interactions between native and introduced species: can intraguild predation facilitate invasion by stream salmonids? *Biological Invasions* 4:223-233.
- Taniguchi, Y., Y. Miyake, T. Saito, H. Urabe, and S. Nakano. 2000. Redd superimposition by introduced rainbow trout, *Oncorhynchus mykiss*, on native charrs in a Japanese stream. *Ichthyological Research* 47:149-156.
- Tellman, B. No date. Why has integrated water management succeeded in some states but not in others? Available at: [http://www.ucowr.siu.edu/updates/pdf/V106\\_A2.pdf](http://www.ucowr.siu.edu/updates/pdf/V106_A2.pdf).
- Thelen, G.C. and F.W. Allendorf. 2001. Heterozygosity-fitness correlations in rainbow trout: effects of allozyme loci or associative overdominance? *Evolution* 55:1180-1187.
- Thorgaard, G.H. 1983. Chromosomal differences among rainbow trout populations. *Copeia* 1987:650-662.
- Tinus, C.A. and G.H. Reeves. 2001. Redside shiner (*Richardsonius balteatus*) shoals provide a behavioral competitive refuge for subordinate juvenile steelhead trout (*Oncorhynchus mykiss*). *Canadian Journal of Fisheries and Aquatic Sciences* 58:319-324.



- Tippetts, W.E. and P.B. Moyle. 1978. Epibenthic feeding by rainbow trout (*Salmo gairdneri*) in the McCloud River, California. *Journal of Animal Ecology* 47:549-559.
- Trojan, J.R. and R.J. Behnke. 1974. Management implications of ecological segregation between two introduced populations of cutthroat trout in a small Colorado lake. *Transactions of the American Fisheries Society* 103: 423-430.
- USDA Forest Service. 2004. Eyerly fire salvage project, Sisters Ranger District, Deschutes National Forest, Jefferson County, Oregon. EPA number: 040301F: 623.
- USDA Forest Service. 2006. Land Area Report. Available at: <http://www.fs.fed.us/land/staff/lar/>.
- USDA Forest Service. 2007. Forest Service Manual, FSM 2300 - Recreation, Wilderness, and Related Resource Management. Chapter 2320 - Wilderness Management. 55 pp. Available at: [http://www.wilderness.net/NWPS/documents/FS/FS\\_wilderness\\_policy.doc](http://www.wilderness.net/NWPS/documents/FS/FS_wilderness_policy.doc).
- U.S. Environmental Protection Agency. 2008. Climate Change. Available at: <http://www.epa.gov/climatechange/>.
- U.S. Fish and Wildlife Service. 2005. Public Aquaculture Production Database. Available at: <http://www.fws.gov/fisheries/aadap/ACCESS/states.html>.
- U.S. Fish and Wildlife Service and U.S. Census Bureau. 2006 National Survey of Fishing, Hunting, and Wildlife-Associated Recreation. 168 pp. Available at: <http://www.census.gov/prod/www/abs/fishing.html>.
- U.S. Geological Survey. 2008. Water use in the United States. Available at: <http://water.usgs.gov/watuse>.
- Valente, L.P., P. Saglio, L.M. Cunha, and B. Fauconneau. 2001. Feeding behaviour of fast- and slow-growing strains of rainbow trout, *Oncorhynchus mykiss* (Walbaum), during first feeding. *Aquaculture Research* 32:471-480.
- Vamosi, S.M. 2003. The presence of other fish species affects speciation in threespine sticklebacks. *Evolutionary Ecology Research* 5:717-730.
- Vannote, R.L., G.W. Minshall, K.W. Cummins, J.R. Sedell, and C.E. Cushing. 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* 37:130-137.
- Varley, J.D. and R.E. Gresswell. 1988. Ecology, status and management of the Yellowstone cutthroat trout. Pages 13-24 in R.E. Gresswell, editor. Status and management of interior stocks of cutthroat trout. American Fisheries Society, Symposium 4, Bethesda, MD.
- Varley, J.D. and P. Schullery. 1998. Yellowstone fishes: ecology, history, and angling in the park. Stackpole Books. 160 pp.
- Vincent, E.R. 1987. Effects of stocking catchable-size hatchery rainbow trout on two wild trout species in the Madison River and O'Dell Creek, Montana. *North American Journal of Fisheries Management* 7:91-105.
- Vincent, E.R. 1996. Whirling disease and wild trout: the Montana experience. *Fisheries* 21:32-33.
- Volpe, J.P., B.R. Anholt, and B.W. Glickman. 2001. Competition among juvenile Atlantic salmon (*Salmo salar*) and steelhead (*Oncorhynchus mykiss*): relevance to invasion potential in British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences* 58:197-207.
- Warburton, K. (2003) Learning of foraging skills by fish. *Fish and Fisheries* 4:203-215.
- Waskom, R.M. 1994. Best management practices for irrigation management. 1994. Bulletin #XCM-173, Colorado State University Cooperative Extension in cooperation with Colorado Department of Agriculture. 17 pp. Available at: <http://www.ext.colostate.edu/Pubs/crops/xcm173.pdf>.
- Weber, E.D. and K.D. Fausch. 2003. Interactions between hatchery and wild salmonids in streams: differences in biology and evidence for competition. *Canadian Journal of Fisheries and Aquatic Sciences* 60:1018-1036.
- Weekes, P.J. and B. Penlington. 1986. First records of *Ligula intestinalis* (Cestoda) in rainbow trout, *Salmo gairdneri*, and common bully, *Gobiomorphus cotidianus*, in New Zealand. *Journal of Fish Biology* 28:183-190.
- Wiley, R.W. 2003a. Planting trout in Wyoming high-elevation wilderness waters. *Fisheries* 28:22-27.

- Wiley, R.W. 2003b. Trout stocking guidelines for Wyoming fisheries. Wyoming Game and Fish Department, Fish Division, Administrative Report. 15 pp.
- Wiley, R.W., R.A. Whaley, J.B. Satake, and M. Fowden. 1993. Assessment of stocking hatchery trout: A Wyoming perspective. *North American Journal of Fisheries Management* 13:160-170.
- Williams, J.E., J.E. Johnson, D.A. Hendrickson, S. Contreras-Balderas, J.D. Williams, M. Navarro-Mendoza, D.E. McAllister, and J. E. Deacon. 1989. Fishes of North America endangered, threatened, or of special concern: 1989. *Fisheries* 14:2-20.
- Williams, R.N., R.F. Leary, and K.P. Currens. 1997. Localized genetic effects of a long-term hatchery stocking program on resident rainbow trout in the Metolius River, Oregon. *North American Journal of Fisheries Management* 17: 1079-1093.
- Williams, T. 2002. Trout are wildlife, too. *Audubon* 104:36-47.
- Wilson, M.V.H. and G-Q. Li. 1999. Osteology and systematic position of the Eocene salmonid *Eosalmo driftwoodensis* Wilson from western North America. *Zoological Journal of the Linnean Society* 125:279-311.
- Woo, P.T.K. and S.D. Wehnert. 1986. *Cryptobia salmositica*: Susceptibility of infected rainbow trout, *Salmo gairdneri*, to environmental hypoxia. *Journal of Parasitology* 72:392-396.
- Workman, R.D., D.B. Hayes, and T.G. Coon. 2004. Spawning habitat selection by rainbow trout in the Pere Marquette River, Michigan. *Journal of Great Lakes Research* 30:397-406.
- Wyoming Game and Fish Commission. 2008a. Wyoming Fishing Regulations 2008-2009. 32 pp. Available at: <http://gf.state.wy.us/fish/fishing/fishregs.pdf>.
- Wyoming Game and Fish Commission. 2008b. Wyoming Game and Fish Wildlife Forensics and Fish Laboratory. Available at: <http://gf.state.wy.us/services/lab/index.asp>.
- Yamamoto, T., T. Shima, H. Furuita, and N. Suzuki. 2002. Influence of dietary fat level and whole-body adiposity on voluntary energy intake by juvenile rainbow trout *Oncorhynchus mykiss* (Walbaum) under self-feeding conditions. *Aquaculture Research* 33:715-723.
- Young, K.A. 2003. Evolution of fighting behavior under asymmetric competition: an experimental test with juvenile salmonids. *Behavioral Ecology* 14:127-134.
- Young, K.A. 2004. Asymmetric competition, habitat selection, and niche overlap in juvenile salmonids. *Ecology* 85: 134-149.
- Young, W.P., C. Ostberg, P. Keim, and G.H. Thorgaard. 2001. Genetic characterization of hybridization and introgression between anadromous rainbow trout (*Oncorhynchus mykiss* irideus) and coastal cutthroat trout (*O. clarki clarki*). *Molecular Ecology* 10:921-929.
- Zellmer, S.B. No date. Instream flow legislation. Available at: <http://watercenter.unl.edu/WRRI/WaterResearch/ZellmerInstreamFlows.pdf>.
- Zimmerman, M.P. 1999. Food habits of smallmouth bass, walleye, and northern pikeminnow in the lower Columbia River Basin during outmigration of juvenile anadromous salmonids. *Transactions of the American Fisheries Society* 128:1036-1054.

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