Brown Trout (*Salmo trutta*): A Technical Conservation Assessment

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with life cycle model by David McDonald, Ph.D.[2]

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ACKNOWLEDGMENTS

AUTHOR'S BIOGRAPHY

Laura A. T. Belica received a M.S. degree in Zoology and Physiology from the University of Wyoming in 2003 (as L.A. Thel). Her research interests center around the ecology of fishes, hydrology, and watershed management, especially as they relate to the management of aquatic ecosystems and native fishes.

COVER PHOTO CREDIT

Brown trout (*Salmo trutta*). Photograph taken by Eric Engbretson. Used with permission.

SUMMARY OF KEY COMPONENTS FOR CONSERVATION OF BROWN TROUT

The brown trout (*Salmo trutta*) is native to Europe, North Africa, and West Asia, and since its introduction to North America in 1883, it is now found throughout southern Canada and much of the United States. Brown trout have been introduced into streams, rivers, reservoirs, and lakes and have been able to form self-sustaining populations in all of these environments. Non-native brown trout are thought to have replaced native inland cutthroat trout (*Oncorhynchus clarki*) in parts of their range, particularly in large rivers and lakes. Within the Rocky Mountain Region (Region 2) of the USDA Forest Service (USFS), brown trout are found in Colorado, Kansas, Nebraska, South Dakota and Wyoming, but are most widespread in Colorado and Wyoming. In those states of Region 2 where they occur, except for Kansas, brown trout are found in public waters providing recreational fisheries, including on many federal lands, such as several National Forest System, National Park System, and Bureau of Land Management lands.

Water management activities that alter stream flow during spawning and the sensitive early life stages can adversely affect naturalized brown trout populations. Land management practices may also degrade or reduce habitat and negatively affect populations. Fisheries management activities applied to brown trout are mostly designed to maintain or improve recreational trout fisheries. However, in areas where the preservation or restoration of native fish populations is a primary goal, removal of brown trout may be a component of native species recovery efforts. Brown trout tolerate annual fluctuations in fertility, but populations are sensitive to changes in absolute survivorship of young-of-year and changes in relative proportions of the younger age-classes in the population. If conditions that lower brown trout yearling recruitment or change the proportion of age-0 through age-2 fish in a population are sustained over several years, population age-structure, size, and biomass may be altered.

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EDITOR: Richard Vacirca, USDA Forest Service, Rocky Mountain Region

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INTRODUCTION

Goal

This conservation assessment of brown trout (*Salmo trutta*) (**Figure 1**) was performed for the Species Conservation Project for the Rocky Mountain Region (Region 2) of the USDA Forest Service (USFS) (**Figure 2**). An assessment on brown trout was included as part of the Species Conservation Project because it is a Management Indicator Species on several national forests in Region 2 and is highly valued as a recreational fishery by the public.

The assessment addresses the biology, ecology, and management of brown trout in North America, with emphasis on populations occurring in the states encompassed by or neighboring USFS Region 2. The assessment is intended to provide pertinent information regarding brown trout biology, ecology, and management to aid Forest planning and management activities. As the brown trout is a non-native game species that is actively managed for a variety of objectives, a synopsis of the present management of brown trout by management agencies within states encompassed by Region 2 is also

included in the assessment. However, the primary focus of the assessment is on the biology and ecology of the species, which is meant to synthesize the current state of knowledge with regard to brown trout throughout Region 2, in order to improve understanding of land management's potential effects on desired brown trout fisheries and to facilitate various management decisions. The scope and specificity of the information provided in the assessment is necessarily limited by the large geographic region encompassed by Region 2 and the complex array of fisheries management objectives that arise from the brown trout's status as a game species and its history as an introduced species.

Scope, Uncertainty, and Limitations

As a popular game species that has been introduced around the world, the brown trout has been the focus of much research. The information obtained regarding brown trout ecology and biology was primarily drawn from research conducted within Region 2, but some information was obtained from studies of populations beyond the region to provide a more comprehensive summary of the species' biology and ecology. Where possible, the assessment draws on information primarily

Figure 1. Brown trout (*Salmo trutta*). Photo taken by Mark Smith (Wyoming Game and Fish Department). Used with permission.
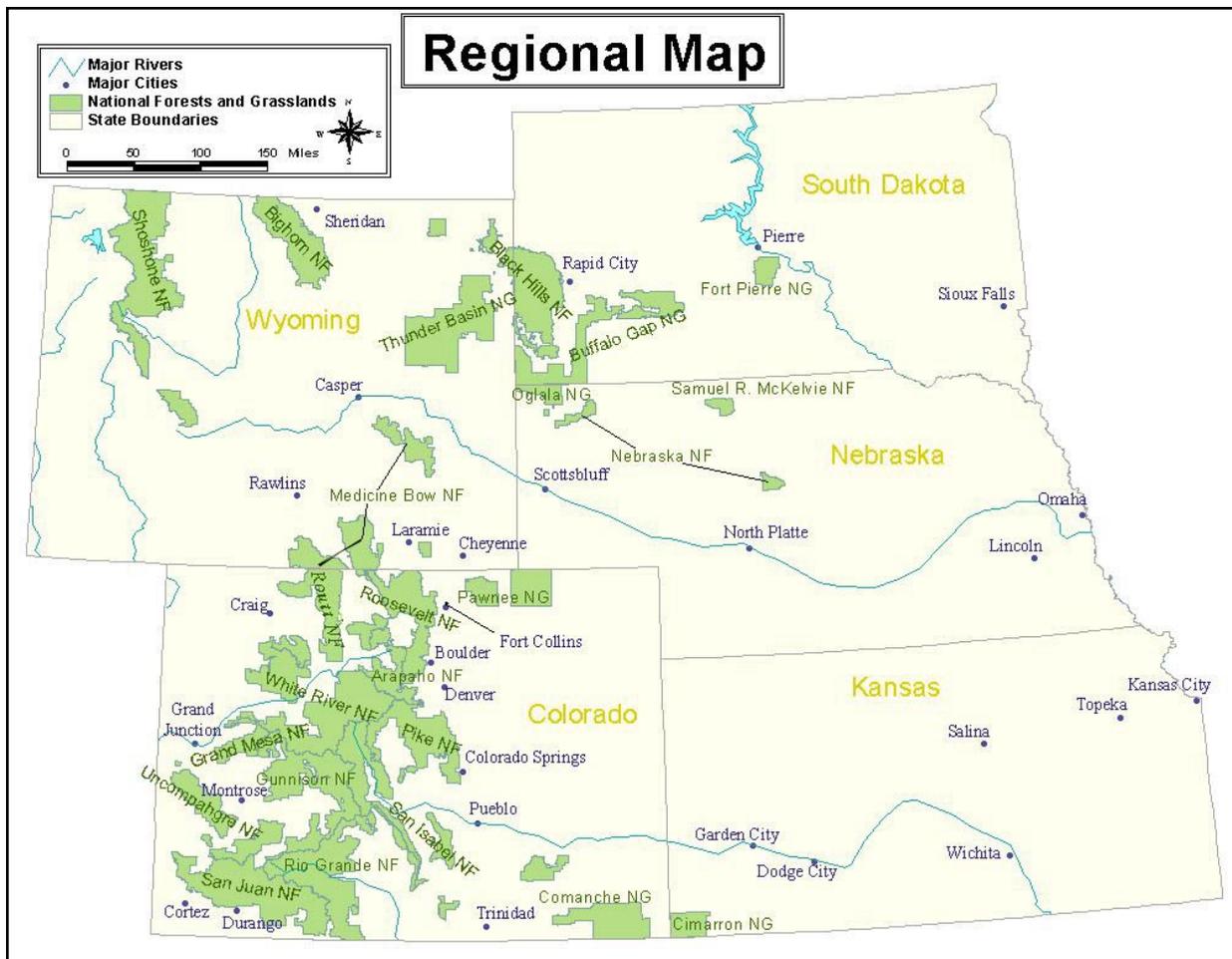
Figure 2. National forests and grasslands within USDA Forest Service, Rocky Mountain Region.

derived from studies of populations in North America, as different life-history forms of brown trout taken from different regions of its native range were introduced and have mixed together in North American waters for over 120 years. However, much of the research (basic biology and ecology) on the species has been conducted on populations occurring in its native range in Europe. Therefore, in a few cases, information from studies on populations occurring beyond North America was necessarily incorporated in the assessment. The information synthesized in this assessment is primarily drawn from published texts and peer reviewed articles in technical journals; theses, dissertations, and agency publications provided additional information.

Brown trout are a managed game species, and differences in water, land, and fisheries management over time and among locations have had various influences on populations occurring in Region 2. A comprehensive summary of the range of variation present among populations and management programs in the states encompassed by Region 2 was not feasible

for this assessment. Instead, this assessment emphasizes the biology and ecology of the brown trout, particularly for populations occurring in Region 2, which is hoped to provide managers with detailed knowledge of the species and its limiting factors that can be used as a resource when planning and evaluating various management activities. Where specific examples are summarized, they can only be considered representative of the specific time periods and localities referenced. Furthermore, interpretation and application of research findings from any specific population of brown trout occurring in Region 2 should be done with caution as many aspects of brown trout biology and ecology vary with environmental conditions, community composition, and the local history of land, water, and fisheries management.

This assessment endeavors to describe what is known of the species and the range of biological and ecological parameters documented for populations occurring in or around Region 2. It identifies gaps in knowledge of brown trout biology and ecology within

Region 2 that may impede effective management and that may be used to guide future investigations.

Web Publication and Peer Review

This assessment will be published on the USFS Region 2 World Wide Web site (www.fs.fed.us/r2/projects/scp/assessments/index.shtml). The assessment was peer reviewed by Peter McHugh, Ph.D. (Utah State University), a known expert in the salmonid group. His input has been incorporated into the final document.

MANAGEMENT STATUS AND NATURAL HISTORY

Management Status and Existing Regulatory Mechanisms

USDA Forest Service

Within USFS Region 2, the brown trout is designated as a Management Indicator Species and is used as an indicator of species viability at forest and project levels. They are used to 1) estimate effects of planning alternatives on fish and wildlife populations (36 CFR 219.9 (a) (1)) and 2) monitor the effects of management activities on species by evaluating population trends (36 CFR 219.9 (a) (6)).

State agencies

Except for Kansas, all states within Region 2 have naturalized, self-sustaining brown trout populations in many waters, and state agencies are primarily responsible for stocking hatchery-reared brown trout in some locations. Considered a sport fish, the brown trout is actively managed and harvested, but the regulatory mechanisms vary by state. In all states in Region 2, anglers are required to purchase a fishing license, and some states require trout permits (stamps). Specific information regarding licensing and permits can be found in the respective state's fishing regulation publications referenced below. Stocking continues to be a major component of brown trout management in several areas of the region. Unfortunately, it was not feasible to compile and summarize stocking records for brown trout throughout Region 2. Fisheries researchers and managers seeking information regarding brown trout populations on National Forest System lands are urged to obtain information on stocking histories for specific waters from the appropriate agency in their location.

The Colorado Division of Wildlife has designated the brown trout as a game fish. The statewide daily bag limit is four, and the possession limit is eight for any combination of trout, arctic charr, grayling, or salmon (except kokanee) (Colorado Division of Wildlife, 2006 Fishing Regulations and Property Directory: http://wildlife.state.co.us/Brochures). Where brown trout are found with cutthroat trout (*Oncorhynchus clarki*), special tackle regulations (artificial flies and lures) apply. More restrictive regulations that may be applied to trout in certain waters mainly include reduced bag and possession limits, immediate release requirements, minimum length limits, and tackle restrictions. Prohibition of fishing above USFS boundaries was also noted for a few streams as well as special regulations for gold medal fisheries occurring on National Forest System lands (2006 Fishing Regulations and Property Directory). Special regulations as they apply to specific locations in Colorado are too extensive to summarize here, but they are detailed in the 2006 Fishing Regulations and Property Directory. Special regulations also apply to Indian reservations, military lands, and Rocky Mountain National Park and can be obtained from the managing entities (2006 Fishing Regulations and Property Directory).

In Kansas, the predominate trout species is the rainbow trout (*Oncorhynchus mykiss*), which is stocked annually to provide a trout season from mid-October to mid-April (Kansas Department of Wildlife and Parks, 2006 Kansas Fishing Regulations Summary: http://www.kdwp.state.ks.us/news/fishing/fishing_regulations). Brown trout are thought to exist predominately in private waters (Cross and Collins 1995) and are designated as a sport fish (Kansas Department of Wildlife and Parks, 2006 Kansas Fishing Regulations Summary). The daily creel limit for trout is five, and the possession limit is 15; these restrictions apply throughout the state, including Fort Riley Military Reservation (Kansas Department of Wildlife and Parks, 2006 Kansas Fishing Regulations Summary and "Creel and Length Limits in Effect on Ft. Riley" accessed from http://www.riley.army.mil/Recreation/Outdoor/Fishing/).

In Nebraska, brown trout are designated as a sport fish, and except on specific waters where special regulations apply, the bag limit for trout is seven, and the possession limit is 14 fish (Nebraska Game and Parks Commission 2006 Fishing Guide: http://www.ngpc.state.ne.us). Information on special bag, possession, and length limits and tackle regulations are listed by waterbody in the Fishing Guide (Nebraska

Game and Parks Commission 2006 Fishing Guide: http://www.ngpc.state.ne.us). Special regulations that apply to trout populations include reduced bag limits and waters managed as total catch-and-release (Nebraska Game and Parks Commission, 2006 Fishing Guide: http://www.ngpc.state.ne.us).

In South Dakota, the statewide daily and possession limits for trout (in any combination with salmon, splake, herring, lake herring, and whitefish) is five and 10 fish respectively (South Dakota Department of Game, Fish, and Parks, 2006 Fishing Handbook: http://www.sdgfpinfo/Pulblications/FishingHandbook.pdf). For trout taken from the Missouri River, however, the possession limit is only five fish. For waters on the border of Nebraska and South Dakota, both the daily and possession limits for trout are seven fish (South Dakota Department of Game, Fish, and Parks, 2006 Fishing Handbook). In the Trout Management Area of the Black Hills, several streams and ponds are managed as catch-and-release for trout; elsewhere, the statewide regulations for trout (in combination with salmon, splake, etc.) apply, but only one trout longer than 14 inches may be included in the daily creel (South Dakota Department of Game, Fish, and Parks, 2006 Fishing Handbook).

In Wyoming, brown trout are considered a sport fish, and the statewide daily creel and possession limits are each six fish, in any combination of trout, salmon, and grayling, and only one fish can be larger than 20 inches (Wyoming Game and Fish Commission, 2006-2007 Wyoming Fishing Regulations: http://gf.state.wy.us/downloads/pdf/fish/fishregs.pdf). Special regulations apply to specific waters throughout the state and primarily consist of differences from statewide bag and possession limits (either more or less), minimum length limits, tackle restriction, and seasonal or annual closures of some waters to fishing; however, these regulations are too extensive to summarize here (2006-2007 Wyoming Fishing Regulations). Special regulations for waters on National Forest System land in Wyoming primarily include tackle restrictions (artificial flies and lures only) and the immediate release or reduced creel and possession limits for cutthroat trout and some seasonal closures to protect wildlife (2006-2007 Wyoming Fishing Regulations).

Biology and Ecology

Description and systematics

Taxonomy

The native range of the brown trout includes Europe, western Asia, and northern Africa (Page and Burr 1991, Behnke 2002). The species has been introduced around the world, into at least 24 countries, and it has formed self-sustaining populations in North and South America, New Zealand, Australia, Africa, and the headwaters of the Himalayas in Asia (Elliott 1994, Behnke 2002).

The name *Salmo trutta* was included in the 1758 publication of the "System of Nature" by Linnaeus in reference to the form of brown trout found in large rivers; the stream resident and sea-run forms of brown trout were distinguished as *S. fario* and *S. eriox* respectively (Bachman 1991, Elliott 1994, Behnke 2002). Linnaeus distinguished the lake inhabiting form of brown trout as *S. lacustris* (Behnke 2002). Eventually, resulting from the great variation in the appearance of populations throughout their native range, about 50 species of brown trout were described, but they have all since been consolidated into the single species *S. trutta* (Behnke 2002).

Brown trout were brought to North America in 1883 as a shipment of eggs from Baron von Behr, a German sportsman and president of the German Fish Culturist Association, to Fred Mather, a prominent fish culturist and representative of the U.S. Fish Commission at the 1880 Berlin Fish Cultural Exposition (Behnke 2002). The original shipment from Germany included 60,000 eggs of a large lake form of brown trout and 20,000 eggs of a form inhabiting streams. The eggs were distributed to hatcheries in New York and Michigan, and the surviving offspring were used as broodstock in American hatcheries (Behnke 2002). The first documented introduction of brown trout into public waters of the United States occurred in 1884 in Michigan (Behnke 2002). Several subsequent shipments of brown trout eggs from Germany, England, and Scotland included many of the species' life history forms found in western Europe (lake, sea-run, river, and

brook forms) (Behnke 2002). Fish hatcheries located throughout the United States participated in propagation and introduction of brown trout, and the original strains and life history forms became mixed in hatcheries and public waters (Behnke 2002). The rapid naturalization of brown trout and their success in forming self-sustaining populations throughout North America have been attributed in part to the increased genetic diversity of the mixed forms that were introduced (Behnke 2002). Brown trout are often referred to as German brown, von Behr, or Loch Leven trout in reference to some of the original stocks brought to America, but because of the subsequent mixing of stocks, the common names referring to particular strains are considered inappropriate (Baxter and Stone 1995).

Identification

Brown trout have an elongate, somewhat compressed body, with a thick, short caudle peduncle and a short to moderate head (Simpson and Wallace 1982, Baxter and Stone 1995). They have a rounded snout, a large mouth that extends to or beyond their eye, and teeth on their jaws, vomer, palatines, and tongue (Simpson and Wallace 1982, Page and Burr 1991, Baxter and Stone 1995). Their caudal fin is not forked, and its appearance is described as squarish with few to no dark spots (Simpson and Wallace 1982, Baxter and Stone 1995, Behnke 2002). Their adipose fin is small and slender and may have orange or red spots or an orange or red border (Bachman 1991).

The spotting patterns and body coloration of brown trout in North America are diverse due to their mixed ancestry (Bachman 1991, Behnke 2002). Spotting patterns range from many irregularly shaped spots profusely distributed to larger rounded spots more sparsely distributed on the body (Behnke 2002). Brown trout have red and brown-black spots on their head and body, but fish from lake or marine waters may lack red spots at some stage of their lives (Behnke 2002) and older individuals may not have red spots (Simpson and Wallace 1982, Bachman 1991). The spots may be surrounded by pale halos, often pink or gray (Simpson and Wallace 1982, Page and Burr 1991). The lack of dark spots (few to none) on the caudal fin is considered a distinguishing characteristic of the species (Bachman 1991, Behnke 2002). Brown trout do not have white edges on their pelvic or anal fins (Page and Burr 1991).

The body coloration of brown trout in streams is typically olive, brownish yellow, to dark brown dorsally. The sides of brown trout are commonly yellow-brown and may have a silver sheen, and their bellies are a lighter yellow or white (Page and Burr 1991). Brown trout inhabiting large lakes or marine waters are often silver and can have X-shaped marks dorsally (Bachman 1991, Page and Burr 1991). Brown trout living in clear streams have been described as having bright colors whereas in fish inhabiting lakes, found under ice in winter, or undergoing smoltification, the colors can be obscured by a silvery iridescence (Bachman 1991, Baxter and Stone 1995).

Brown trout have been variously reported to have 115 to 140 lateral scales, 9 to 11 dorsal fin rays, 9 to 11 anal fin rays, 14 to 17 gill rakers, 56 to 61 vertebrae, and usually 10 branchiostegal rays (Simpson and Wallace 1982, Page and Burr 1991, Baxter and Stone 1995). Some of these characteristics overlap with other species of salmonids such as Atlantic salmon (*Salmo salar*) and rainbow trout (Behnke 2002). Brown trout have 80 chromosomes while Atlantic salmon have only 56 to 58 and rainbow trout have only 58 to 64 (Bachman 1991, Behnke 2002).

Adult brown trout can attain lengths up to 103 cm (40.5 inches) (Page and Burr 1995), but maximum lengths vary among habitats. Brown trout in small streams with limited food resources may only reach lengths around 25 cm (10 inches), whereas in more productive streams or rivers and lakes adults may reach lengths of 35 to 76 cm (14 to 30 inches) (Bachman 1991, Behnke 2002). In Wyoming, brown trout usually attain lengths ranging from 30 to 46 cm (12 to 18 inches) (Baxter and Stone 1995).

Mature males and females show some sexual dimorphism. Mature males have a rounded (convex) anal fin whereas mature females retain the falcate (concave) anal fin characteristic of immature brown trout (Simpson and Wallace 1982, Bachman 1991, Page and Burr 1991). Males also tend to have larger and more flattened heads than females, and old breeding males may develop a hooked lower jaw, called a kype (Simpson and Wallace 1982, Bachman 1991, Page and Burr 1991).

Juvenile brown trout have 9 to 14 short and narrow dark marks along their sides, called parr marks, and a few red spots along their lateral lines (Page and Burr 1991). Fingerling brown trout in Wyoming have pink lateral spots with blue borders (Baxter and Stone 1995). Larval brown trout can be distinguished from larval rainbow, cutthroat, and brook trout (*Salvelinus fontinalis*) in the field by longer pectoral fins, dense pigmentation on the anterior margin of the lower jaw (larvae ≥ 22 mm total length [TL], 0.9 inches TL),

pigmentation on the caudal fin that tends to line distal principal rays (larvae ≥ 19 mm TL, 0.7 inches TL), and scattered pigmentation across the entire adipose fin (larvae ≥ 29 mm TL, 1.1 inches TL) (Martinez 1984). Brook trout and brown trout mesolarva may be distinguished by the bulbous yolks of brook trout and the elliptical shape of brown trout yolks and the presence of globules in the yolk of brown trout. However, Martinez (1984) cautioned that the elliptical shape of brown trout yolks may be an artifact of laboratory rearing, and rainbow and occasionally cutthroat trout have large globules in the yolk. Bacon (1954) reported that brown trout could be identified by their speckled abdomens, but Martinez (1984) did not observe speckled abdomens of any of larval brown trout she examined. Brown trout larvae have light pigment on the anterior margin of the dorsal fin while rainbow and cutthroat trout have bold pigment on the anterior margin of the dorsal fin (Bacon 1954, Martinez 1984).

Distribution and abundance

Range

The brown trout is native to Europe, northern Africa, and western Asia, and since its introduction to North America in 1883, it is now found throughout southern Canada and much of the United States (Page and Burr 1991). Currently there are self-sustaining populations in 40 of the 48 conterminous states of the United States (Behnke 2002).

Brown trout were first brought to the western plains and mountain states with introductions to South Dakota in 1886, Colorado in 1887, and Montana and Nebraska by 1889 (Bachman 1991). In all states encompassed by Region 2, except for Kansas, brown trout are found in public waters, including on many federal lands (e.g., National Forest System, BLM, and National Park System lands). Among the five states included in Region 2, this species is most widespread in Colorado and Wyoming.

In Colorado, brown trout are found in mountain and foothill streams and rivers flowing onto the plains of eastern Colorado and into the valleys of western Colorado (**Figure 3**; Colorado Division of Natural Resources http://wildlife.state.co.us/fishing).

Kansas has few waters suitable for trout year-round, and no self-sustaining populations of brown trout are found in the state (Cross and Collins 1995). Brown trout are not actively stocked in Kansas. Rainbow trout obtained from hatcheries are planted in some areas to provide seasonal trout fishing (Kansas Department of Wildlife and Parks, 2006 Fishing Regulations Summary), and occasionally brown trout become mixed with rainbow trout by the suppliers (Mosher personal communication 2006). Brown trout are most likely to be found in private waters in Kansas (Cross and Collins 1995).

Brown trout can be found in suitable cold water habitats (including lakes, reservoirs and streams) throughout Nebraska, primarily in the northern and western parts of the state, particularly in the Panhandle region to the west and along the Niobrara River drainage in the north (**Table 1**, **Figure 4**; Nebraska Fishing Guide; Regulations and Public Waters 2006). Brown trout are also found in the Platte River and its tributaries (Lynch and Roh 1996, Nebraska Fishing Guide; Regulations and Public Waters 2006).

In South Dakota, brown trout are predominately found in streams of the Black Hills, but they also occur in lakes and reservoirs throughout central and western South Dakota as well as some tailwaters of the Missouri River (Common Fishes of South Dakota Identification Guide obtained from http://www.sdgfp.info/Wildlife/ Education/CommonFishes, South Dakota Fishing and Hunting Guide obtained from http://www.travelsd.com/ outdoors/hunting/fhrequest.asp). Brown trout were introduced to the Black Hills in 1886 and are one of the primary managed species in the Black Hills National Forest, the majority of which is encompassed by the South Dakota Game Fish and Parks "Black Hills Trout Management Area" (**Figure 5**; South Dakota Department of Game, Fish, and Parks 2006 Fishing Handbook). In the Black Hills Trout Management Area, trout are stocked in waters where natural reproduction is too low to meet angler demand (McNenny Fish Hatchery: http://www.sdgfp.info/Wildlife/Fishing/ Hatcheries/McNenny/). South Dakota Game Fish and Parks stopped stocking brown trout in the Black Hills seven to eight years ago (Shearer personal communication 2006). In recent years, rainbow trout stocking in the Black Hills has increased in response to declining brown trout abundance, which is thought to be related to recent drought and the spread of an invasive diatom, *Didymosphenia geminata* (South Dakota Department of Game, Fish, and Parks 2005 and 2006 Fishing Handbooks).

In Wyoming, brown trout have formed self-sustaining populations in larger streams and rivers at lower elevations (Baxter and Stone 1995). This species is found in all the major drainages of Wyoming with the exception of the Great Divide Basin and the Little
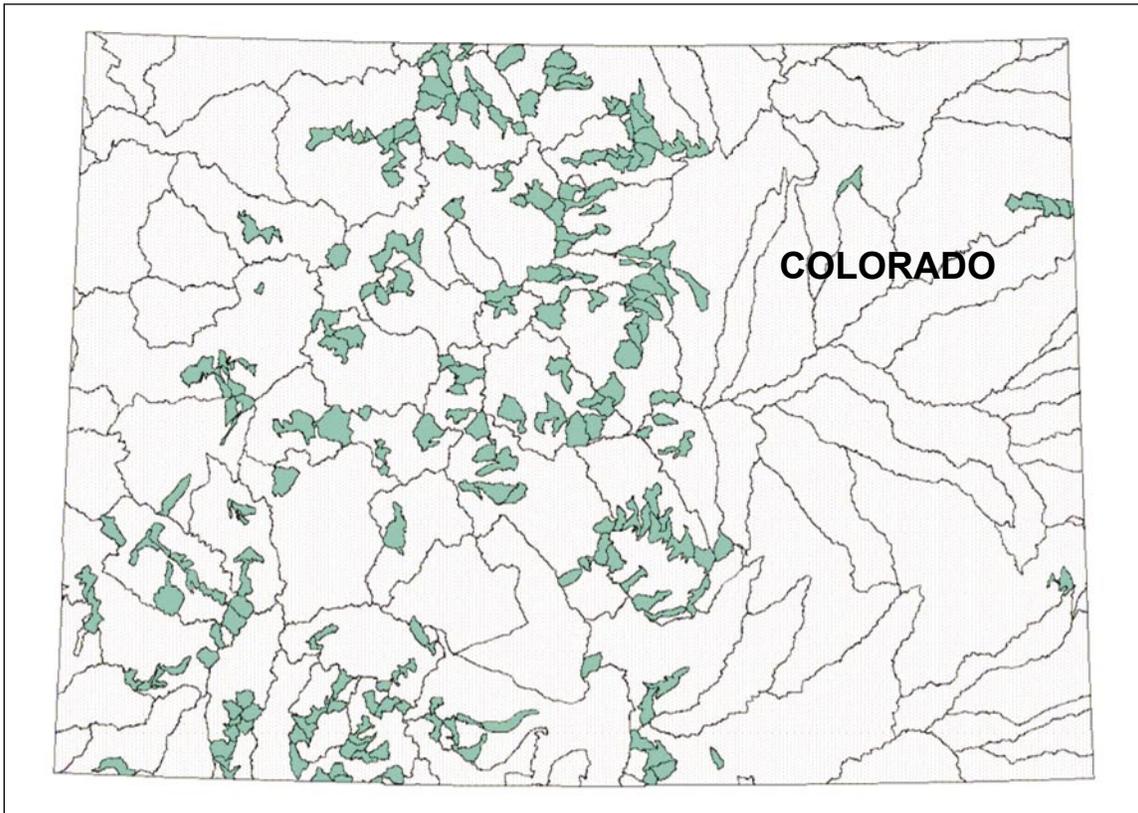
Figure 3a. Green shading indicates sub-watersheds where brown trout have been sampled.
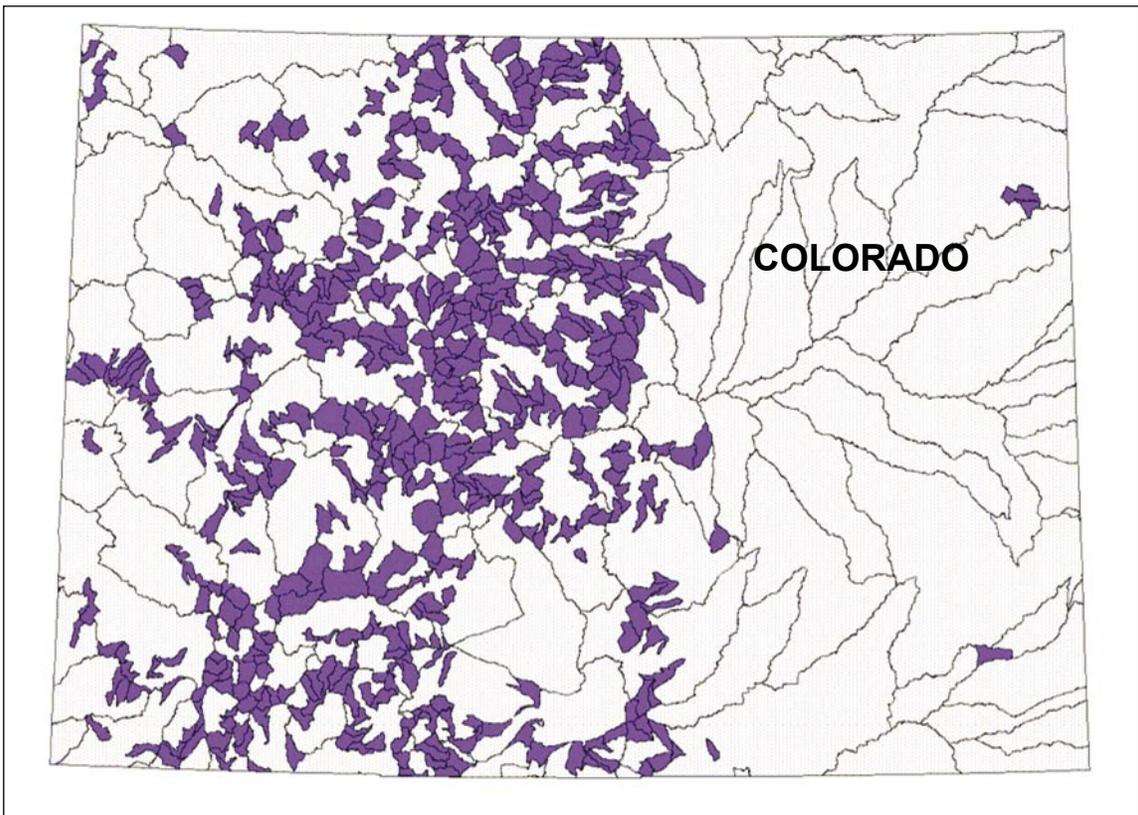
Figure 3b. Purple shading indicates sub-watersheds where brown trout have been stocked.

Figure 3. Brown trout distribution in Colorado by 6th level sub-watersheds displayed over 4th level sub-basins (USGS Hydrologic Cataloging Units) from 1985 to present. Maps were provided by Colorado Division of Wildlife and reflect both historic sampling (**Figure 3a**) and stocking (**Figure 3b**).

Table 1. Streams with known reproducing populations of brown trout in Nebraska. Recent information is limited and not included. Information was provided by Nebraska Game and Parks Commission (NGPC) District Fisheries Managers.

Stream	District	County
Sowbelly Creek	1	Sioux County
East Hat Creek	1	Sioux County
West Hat Creek	1	Sioux County
Soldiers Creek	1	Sioux and Dawes Counties
White River	1	Sioux and Dawes Counties
Niobrara River	1	Sioux and Dawes Counties
Dead Horse Creek	1	Dawes County
Chadron Creek	1	Dawes County
Big Bordeaux Creek	1	Dawes County
Little Bordeaux Creek	1	Dawes County
White Clay Creek	1	Sheridan County
Larabie Creek	1	Sheridan County
Sheep Creek	1	Sioux and Scottsbluff Counties
Tub Springs	1	Scottsbluff County
Dry Spottedtail	1	Sioux and Scotts Counties
Wet Spottedtail	1	Sioux and Scotts Counties
Winters Creek	1	Scotts County
Nine-Mile Creek	1	Scotts County
Bayard Drain or Stuckenhole Creek	1	Morrill County
West Wildhorse Creek	1	Morrill County
East Wildhorse Creek	1	Morrill County
Red Willow Creek	1	Morrill County
Long Pine Creek	2	Brown County
Plum Creek	2	Brown County
Fairfield Creek	2	Brown and Cherry Counties
Schlaegel Creek	2	Cherry County
Snake River	2	Cherry County
Gordon Creek	2	Cherry County
East Brank of Verdigre Creek	3	Antelope County
Steele Creek	3	Holt County
Louse Creek	3	Holt County

Missouri River Basin (Baxter and Stone 1995). The Wyoming Game and Fish Department and private groups also stock brown trout into lakes and reservoirs (Hubert and Guenther 1992, Wiley et al. 1993, 2006-2007 Wyoming Fishing Regulations). A map of brown trout distribution in Wyoming is provided in **Figure 6**.

Presently state agencies in Colorado, Nebraska, South Dakota, and Wyoming all maintain datasets containing information on brown trout distribution. The USFS Rocky Mountain Research Station, U.S. Geological Survey (USGS), Colorado State University, and multiple partners throughout the interior western United States are currently compiling a USFS Risk Assessment/Decision Support System dataset, which will be an additional source of information on brown trout distribution (Dunham personal communication 2006). Supported in part by funding from USFS Region 1, this dataset is being assembled from over 10,000 observations of occurrence of trout (e.g., native cutthroat, bull (*Salvelinus confluentus*), and rainbow trout, and non-native brook, brown, and rainbow trout) and environmental variables (e.g., stream width, air temperature, stream discharge, roads, valley morphology) related to fish distributions. The dataset was not publicly available at the time of publication of this assessment, but it is planned to be made available through a USFS or USGS website (contacts: J. Dunham,
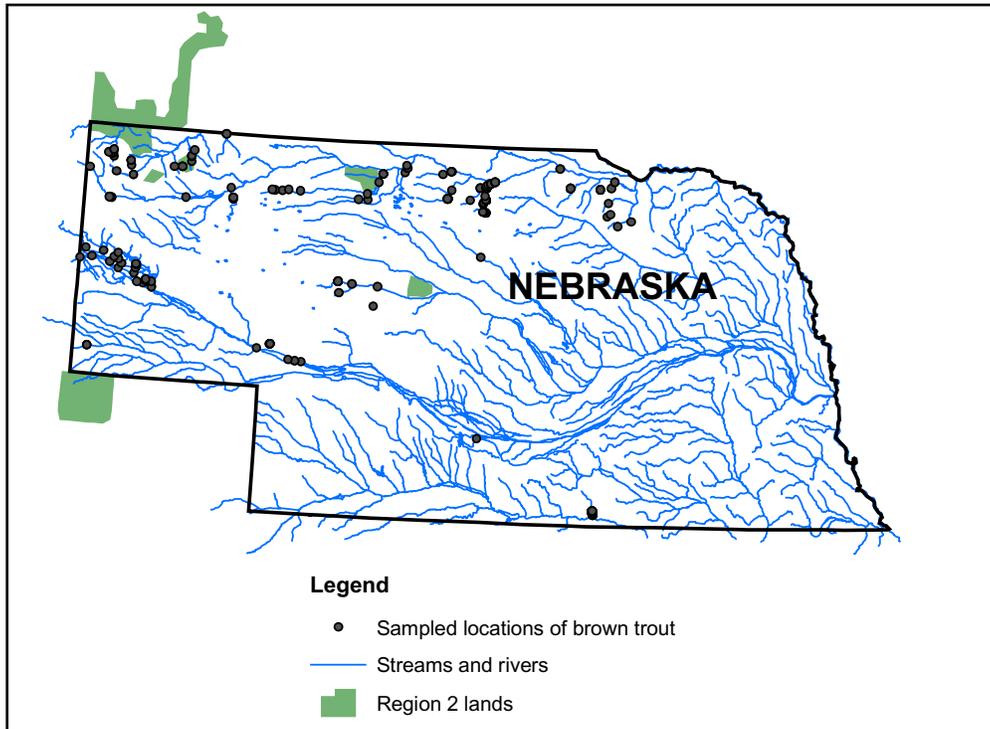
Figure 4. Brown trout collection locations in Nebraska provided by the Nebraska Game and Parks Commission. Data provided include collection locations that had been sampled from the 1970's to present, with the majority of locations sampled from the 1980's to present.
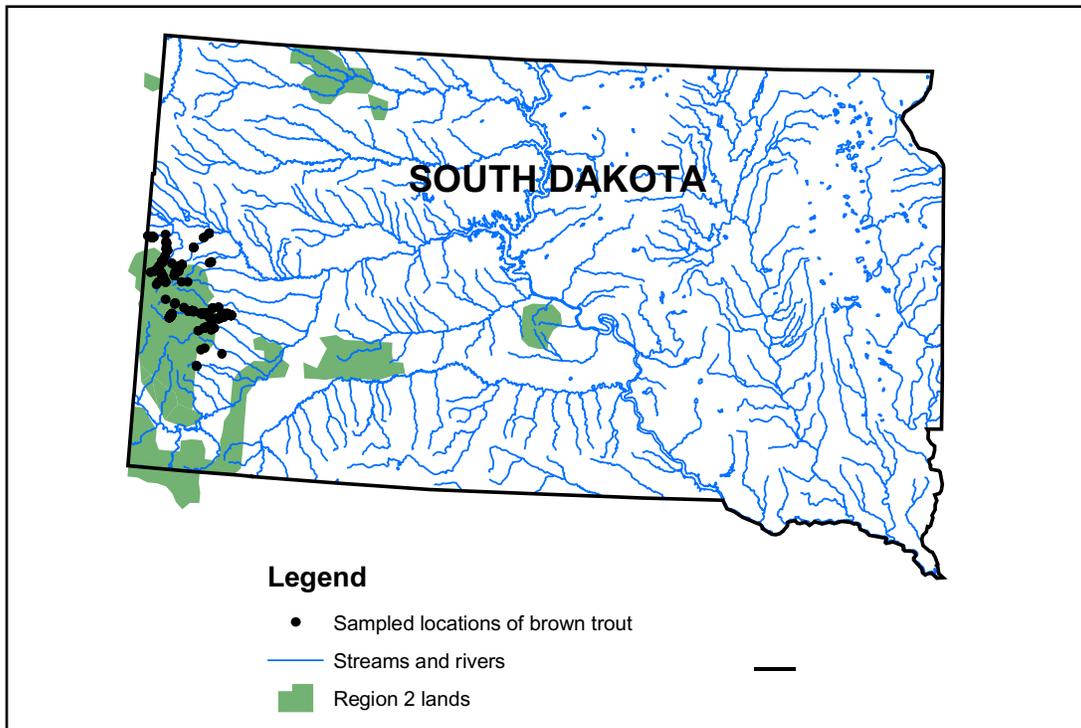
Figure 5. Brown trout collection locations in the Black Hills of South Dakota. Brown trout collection locations were provided by South Dakota Department of Game, Fish, and Parks and include sites that were sampled during the period from 1996 to 2006.
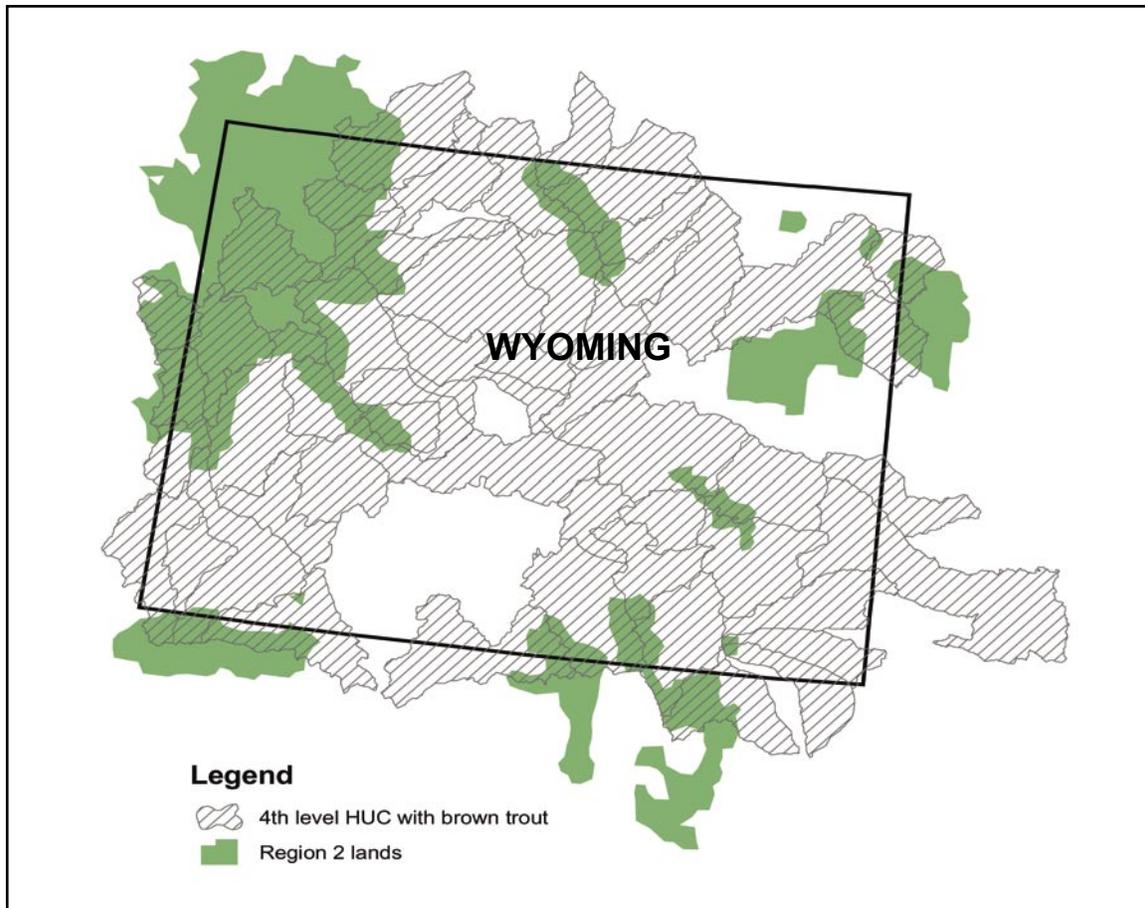
Figure 6. Brown trout distribution in Wyoming displayed by 4th level sub-basins (USGS Hydrologic Cataloging Units) based on database records provided by the Wyoming Game and Fish Department for the period 1996 to 2006. Please note: only database records that included location coordinates (e.g., UTM coordinates) were used to create the map; as a result, some sub-basins with brown trout may not be represented.

Aquatic Ecologist, USGS FRESC Corvallis Research Group and B. Rieman, Research Fisheries Biologist, USDA Rocky Mountain Research Station).

Abundance and population trends

The ability to evaluate patterns in abundance over time and among localities is a critical part of fisheries management (Ney 1999). When population estimates are collected over time for a single population, it provides valuable information on population trends, outcomes of management actions, and impacts of environmental changes (Ney 1999).

Differences in abiotic or biotic characteristics within or among systems or over time (Platts and Nelson 1988, Kwak and Waters 1997, Latterell et al. 1998) can influence brown trout population size, age structure, and biomass. In streams, the spatial variability in brown trout abundance can be significant (Kozel and Hubert 1989, Beard and Carline 1991). For instance, in a Pennsylvania stream, total densities of age-1+ brown trout ranged from 130 to 1304 fish per ha among 12 sample sections along a 35 km (21.7 mile) long stream (Beard and Carline 1991). Kozel and Hubert (1989) suggested that much of the variation in model predictions of trout biomass among study reaches was due to natural variation in habitat features associated with stream size and gradient.

Temporal fluctuations in brown trout abundance may make population trends difficult to discern. Platts and Nelson (1988) reported that brown trout abundance in a Utah stream varied considerably between years (maximum relative fluctuations of 754 percent and average relative fluctuations of 183 percent), but that fluctuations in biomass were comparatively low (maximum relative fluctuation of 287 percent and average relative fluctuation of 117 percent) and were attributed to the preponderance of mature fish in the

population. As a managed sport fish, the size of brown trout populations may also be influenced by angling and fisheries management activities that range from habitat improvements to stocking of brown trout alone or in combination with other salmonid species. Variation in angling pressure or stocking history among locations (Anderson and Nehring 1984, Vincent 1987) may add to the observed variability within and among populations of brown trout.

Surprisingly, few published population estimates for brown trout, and very few studies that had evaluated changes in brown trout populations over time to assess trends or response to various management practices were found in the literature review. However, many studies conducted within Region 2 have related trout abundance, or most frequently biomass (or standing stock), to habitat variables, and several models predicting trout biomass have been developed (see Binns and Eiserman 1979, Wiley and Dufek 1980, Anderson and Nehring 1984, Lanka et al. 1987, Scarnecchia and Bergersen 1987, Wesche et al. 1987, Kozel and Hubert 1989, Modde et al. 1991, Hogle et al. 1993, Hubert et al. 1996, Latterell et al. 1998). Although such models help to identify conditions that limit population biomass, they do not provide insight into other important aspects of populations such as size and age structures (Larscheid and Hubert 1992).

Unfortunately, for the purposes of this assessment, we found most studies reported estimates of population size or biomass for several trout species combined. Although combining trout species for analysis is useful for some objectives, it does not provide specific information needed to track changes in populations or changes in relative abundance among trout species found together over time (see Waters (1983) and Waters (1999) for an example of the changing relative abundance in trout species in one system over the long term). Additionally, ecological differences between trout species (e.g., variations in habitat use, activity patterns) are lost when density or biomass estimates are combined across species. Hubert et al. (1996) also noted that predictive models might have some bias if one trout species was predominant in the systems used in model development.

Although models relating trout density or biomass to physical habitat or flow characteristics may facilitate predictions of population trends in response to changing habitat conditions, other factors also may have significant influence on populations. For instance, Platts and Nelson (1988) found that natural population fluctuations could make trout population

trends difficult to discern, and Young (1994) suggested that fish movement patterns might account for much of the unexplained variability seen in fish-habitat models. Wright (1992) emphasized that fishing mortality, which is often not fully evaluated, can significantly affect populations, and Wesche et al. (1987b) found that fishing pressure was significantly correlated with brown trout standing stock in southeastern Wyoming streams. Beard and Carline (1991) stressed that habitat availability might not limit some brown trout populations as much as constraints on recruitment. Finally, few studies directly incorporated the effects of stocking on population estimates or provided details of stocking history of the system of study, even though variations in species and sizes of stocked fish and stocking rates among systems can have a range of impacts on naturalized trout population abundance and biomass (Vincent 1987).

Given the lack of readily available data and the fact that compiling and analyzing brown trout data from the different management agencies and research institutions in the region was not feasible for this assessment, it was not possible to assess brown trout abundance or population trends across the region. In general, the fisheries researchers and managers with which the author spoke believed that brown trout populations were stable overall within Region 2. One exception is the Black Hills of South Dakota where recent drought and the spread of a diatom (*Didymosphenia geminata*) are thought to be contributing to the decline of some naturalized brown trout populations (South Dakota Department of Game, Fish, and Parks 2005 and 2006 Fishing Handbooks). In response to this decline, South Dakota Department of Game, Fish, and Parks has modified its stocking program and is stocking catchable-sized rainbow trout in waters not able to support naturalized brown trout populations (South Dakota Department of Game, Fish, and Parks 2005 and 2006 Fishing Handbooks).

In areas neighboring Region 2, several studies have documented fluctuations in brown trout populations that were attributed to natural variation and management practices. Platts and Nelson (1988) documented the temporal variability in abundance of a brown trout population in Utah; population estimates from ranged from 26 to 222 brown trout based on four pass electrofishing removal estimates from a 549 m (1,800 ft. or 0.34 mile) stream reach over a five year period. Corresponding brown trout biomass estimates ranged from 2.0 to 8.0 grams per meter (Platts and Nelson 1988). Vincent (1987) reported that the number and biomass of age-2+ naturalized brown trout in a

Montana river more than doubled four years after stocking of catchable-sized rainbow trout was ceased. In the same study, abundance and biomass of age-2+ brown trout decreased nearly 50 percent after stocking began in a previously unstocked tributary stream (Vincent 1987). A study of grazing effects on stream fish in a montane stream in northern New Mexico did not indicate that grazing affected fish populations; reported mean densities of brown trout ranged from 1 to 10 fish per 50 m (164 ft.) over four years, and biomasses ranged from 21 to 974 g per 50 m (164 ft.) in the study sections (Rinne 1988).

To provide a sense of the range of variation in brown trout populations throughout Region 2, the following section is a summary of reports of brown trout population density and biomass (standing stock or crop) found in published articles from systems within or near Region 2. The studies used different methods and measurement units and are provided as they were reported; they have not been converted for standardization. Readers are referred to the sources for more information.

Relative abundance and density estimates: Riley and Fausch (1992) reported the total number of brown trout collected in four-pass electrofishing and population estimates for several 250 m (820 ft.) long sampling reaches in two small northern Colorado mountain streams. Study sections on one stream were sampled during two successive years. Numbers of age-1 brown trout collected in four-pass electrofishing ranged from 31 to 167 fish, and corresponding population estimates ranged from 31 to 189 fish (Riley and Fausch 1992). Numbers of age-2+ brown trout collected in four passes ranged from 58 to 210 fish, and corresponding population estimates ranged from 58 to 213 fish (Riley and Fausch 1992). In another study in northern Colorado, Scarnecchia and Bergersen (1987) reported densities of brown trout greater than 151 mm (6 inches) TL ranging from 0.1 to 15.4 per 100 m^2 for ten small high elevation streams (2,146 to 3,139 m [7,040 to 10,300 ft.] above sea level).

In a section of the Rio Grande in southwestern Colorado, a reported population estimate for age-1+ brown trout in the Coller State Wildlife Area was 4,144 fish, and the density estimate for brown trout greater than 350 mm (14 inches) TL was 27 fish per ha (Shuler et al. 1994). Angling mortality in the area was low because anglers had to release fish less than 400 mm (16 inches) TL, and few brown trout reached that length by age-6 in that system (Shuler et al. 1994). Kruse et al. (1998) reported that densities of trout (including cutthroat, rainbow, brook, and brown trout) for 30 reaches of tributaries to the Greybull, Shoshone, and Clarks Fork rivers in northwestern Wyoming ranged from 0.002 to 0.426 trout per m^2.

Kozel and Hubert (1989) reported population estimates for brown trout over 100 mm (4 inches) TL in 24 reaches of 10 streams located on the Medicine Bow National Forest. Population estimates ranged from two fish (95% CI 1-3) to 96 fish (95% CI 75-117) for 200 m (656 ft.) long stream reaches.

In the lower Niobrara basin in Nebraska, only 2 percent of the fish collected from three streams over two years (1980-1981) were brown trout, despite stocking efforts and records that indicated several thousand fingerling brown trout had been planted in the years preceding and during the study period (Stewart 1985). Mean number of brown trout in three streams in the lower Niobrara basin over two years ranged from 0.125 to 3.143 per 100 m (328 ft.) long reaches (Stewart 1985), significantly lower than densities reported for other Nebraska trout streams which ranged from 13.8 to 224.7 fish per 100 m for brown and rainbow trout combined (Stewart 1985).

Biomass estimates: Several studies have estimated trout biomass in Region 2 streams. For brown trout longer than 100 mm (4 inches) TL, Kozel and Hubert (1989) reported standing stocks ranging from 0 to 190 kg per ha in 10 high-elevation streams (2,377 to 2,975 m above mean sea level) in the Medicine National Forest in southeastern Wyoming. For streams in the Missouri River and Colorado River drainages in Wyoming, Lanka et al. (1987) reported trout standing stock estimates ranging from 1.0 to 604.2 kg per ha (N = 65) in forested streams and 8.5 to 393.9 kg per ha (N = 26) in rangeland streams for both brook and brown trout combined.

Standing stocks of brown trout in one stream on the Medicine Bow National Forest, Wyoming were estimated for eight reaches during the 1970's and again for three years in the late 1980's after an increase in minimum flows. Estimated mean standing stock (pounds per mile) of brown trout for six study sites ranged from 56 (no data available for confidence intervals) to 635 (95% CI 547-742) during the 1970's (Harris et al.1991). In 1990, the last year of the second study, brown trout standing stock ranged from 213 (95% CI 194-232) to 818 (95% CI 711-925) pounds per mile among seven sites (five of the seven were used in the 1970's) (Harris et al. 1991).

In ten montane streams in northern Colorado, mid-summer biomass of trout (including combinations of brook, brown, cutthroat, and rainbow trout) ranged from 3.9 to 28.2 g per m^2 one year and from 4.0 to 26.2 g per m^2 the next year, with relative stream rankings similar between years (Spearman rank correlation r^2 = 0.79, P <0.01) (Scarnecchia and Bergersen 1987).

In the study designed to assess the response of a brown trout population to increased minimum flows in a stream in the Medicine Bow National Forest in southeastern Wyoming, Harris et al. (1991) reported mean biomass estimated for the period before increased minimum flow and annual biomass estimates for several years afterwards. Overall, the researchers found that brown trout standing stock increased in excess of natural fluctuation at only one site where deep water habitat for juvenile and adult fish increased (mean biomass pre-increase period ranged from 29 to 74 pounds per acre and the first year post-increase biomass ranged from 27 to 208 pounds per acre). The researchers noted the spatial variability in brown trout population responses to increased minimum flows. For instance, the only site where deep-water habitat increased was within 7.4 miles downstream of the dam. At sites located more than 7.4 miles downstream of the dam, tributary inflows mediated the impact of augmented minimum flows, and no significant increases in brown trout biomass was observed (Harris et al. 1991). For other sites within 7.4 miles downstream of the dam, the positive effects of increased minimum flows were thought to be offset by other limiting factors, particularly habitat (Harris et al. 1991).

Hubert and Guenther (1992) reported trout standing stocks ranging from 0.2 to 139.2 kg per ha in 22 reservoirs in Wyoming (reservoirs were less than 890 ha surface area at full pool and were located 1,253 to 1,366 m (4,110 to 4,481 ft.) above mean sea level). Reservoirs were stocked both by private interests and Wyoming Game and Fish Department with different combinations of fingerling brook, brown, cutthroat, and rainbow trout.

Activity and movement patterns

A range of activity patterns has been observed among brown trout populations. Contrasting reports of brown trout being most active diurnally, nocturnally, and during crepuscular periods have come from locations throughout North America and their global range. For example, Swift (1962) reported that brown trout in lakes were more active during the day, beginning with a increase in activity at dawn whereas Oswald (1978)

suggested that peak activity of brown trout in lakes was associated with dawn and dusk periods (as referenced by Clapp et al. 1990). Bachman (1984) observed stream-resident brown trout and found little difference in activity levels during daylight hours except for short peaks at dusk in early summer; however, no nighttime observations were made. Other researchers have reported that river and stream-inhabiting brown trout, including young-of-year (YOY), are most active at night (Clapp et al. 1990, La Voie and Hubert 1997, Young et al. 1997, Young 1999).

The variation in the diel activity patterns and habitat use observed among different brown trout populations is thought to result from multiple processes that influence population activity patterns (Railsback et al. 2005). Several researchers have suggested that the following factors influence activity patterns in salmonids:

❖ fish size, condition, and life-history stage

❖ variation in feeding success and predation risk with light level

❖ variation in metabolic rates with water temperature

❖ influence of habitat conditions on forage availability, feeding success, and cover availability

❖ intra-specific competition for food and habitat (Railsback et al. 2005).

Railsback et al. (2005) proposed that differences in diel activity patterns among populations in different locations or at the individual level can be explained by trade-offs among those factors. They also noted that while some species are specialized for either nocturnal or diurnal activity, other animals (such as brown trout) may not have inherent tendencies or traits; instead, activity patterns emerge from variations habitat conditions, population size structure, competitive conditions, temporal patterns of food availability, and other factors.

Movement patterns of brown trout also vary among populations. In their native range, brown trout have several distinct life history forms including stream residents and migrants that move into larger rivers, lakes, estuaries or the sea and return to streams to spawn. Inland populations of brown trout in North America have been documented to move a

range of distances with a few reports of lotic brown trout moving tens of kilometers between summer and winter habitats (Shetter 1968, Clapp et al. 1990, Young 1994), but in other systems, brown trout movements are more localized (Bachman 1984, Knouft and Spotila 2002). Most large-scale movements of brown trout are among seasonal habitats (i.e., from spring-summer foraging habitats to fall spawning or winter habitats), but large individuals can move considerable distances within seasonal ranges as well (Clapp et al. 1990, Young 1994).

It is difficult to generalize the activity and movement patterns of brown trout, so the following sections summarize several reports of the activity patterns and movements of brown trout in greater detail. Information on the Social patterns for spacing of brown trout is provided first, followed by information on activity and movement patterns. The information on activity patterns is divided into four main sections: adult activity patterns, foraging behavior, refuge use, and YOY activity patterns. Information on brown trout movement patterns for all age groups for which information was available is organized into three sections: diel movements and home ranges, seasonal and long-range movements, and dispersal movements of young and adults. Information from studies conducted on populations in Region 2 are emphasized, but reports from other locations are included where specific details were not available for Region 2 populations, and also to portray the range of variation that has been described for different populations.

Social patterns for spacing

Drift-feeding brown trout exhibit a linear dominance hierarchy in the wild, with older and larger fish having the highest ranks (Bachman 1984). Bachman (1984) observed brown trout behavior in a Pennsylvania stream over a three-year period and concluded that there was no clear correlation between the dominance rank of a brown trout and its position choice, feeding rate, agonistic encounter rate, or distance to cover. This would indicate that dominant individuals do not have preferential access to any particular best area. Rather than having discrete, exclusive territories that were defended, brown trout had overlapping home ranges and shared multiple feeding sites within the home ranges. Bachman (1984) remarked that if the occasional dominance contests between brown trout for a specific position within overlapping ranges were observed over a short time period, they could give the impression of territoriality. However, because brown trout used more than one feeding site and had overlapping home

ranges, there was no evidence to support the notion of territoriality defined as a "defended area that is nearly exclusively used and accessed by an individual within its home range" and in which territory holders have the advantage of prior residence in contests (Bachman 1984). Bachman (1984) suggested that the established dominance hierarchy in a brown trout population minimizes the energy expenditures of fish in the long term because individuals only occasionally engage in a dominance contest rather than constantly competing for drifting food items.

Bachman (1984) found the social structure of the drift-feeding brown trout population was very stable from year to year. Of 15 brown trout observed for the duration of the study, the highest ranked individual was never observed to lose an agonistic encounter in three years (Bachman 1984). Bachman (1984) noted that brown trout home ranges became smaller as fish aged and speculated that as fish grew larger their dominance ranking rose and they were less likely to be displaced from a particular foraging site, so that a smaller, less-energy consuming home range was required.

Bachman (1984) also observed that the home range of an individual brown trout did not change as it grew and became more dominant. When an older fish "disappeared," its range was taken over by YOY or yearlings. This would suggest that either the temporal and spatial variability of food in the stream was such that there were no areas that yielded food more consistently or in a substantially greater amount or that the fish could not detect the differences among locations (Bachman 1984). Agonistic interactions among brown trout were only observed at foraging sites, not within refuge sites, suggesting that at high population densities, foraging sites could become a limiting factor (Bachman 1984).

When hatchery-reared brown trout were introduced into the naturalized population in the Pennsylvania stream, agonistic encounters between the two groups were observed within 20 minutes (Bachman 1984). Wild fish initiated most agons, but there was no prior residence effect on the outcome of the contest, with about equal numbers of hatchery and wild fish winning contests (Bachman 1984). The largest and highest-ranking wild brown trout were able to dominate hatchery fish, but some hatchery fish were able to displace wild fish and establish themselves on foraging sites and appeared to integrate into the dominance hierarchy of the naturalized population.

The social pattern of spacing is more variable during the spawning period, but the size-related linear

dominance hierarchies described by Bachman (1984) are demonstrated with older and larger males typically dominating smaller males in contests for females. However, smaller "jack" males may sneak in to spawn with a female, despite the presence of a larger male. In some instances, male brown trout have been reported to defend redds being excavated by females (see Breeding biology section).

In winter, when feeding activity declines, brown trout have been observed to aggregate more (Cunjak and Power 1986, Heggenes et al. 1993). Reduced aggressiveness among brown trout of all age classes has been observed in winter and is thought to be an adaptation to minimize energy expenditures at cold temperatures (Heggenes et al. 1993, Vehanen et al. 2000). Cunjak and Power (1986) found that in winter, all age classes of brown trout congregated with brook trout, which were more abundant. The researchers suggested that the size of the aggregations could be related to habitat availability as the largest groups of trout were observed where pool habitat was limited (Cunjak and Power 1986).

The social patterns of piscivorous brown trout have not been studied as much as those of drift-feeding brown trout have. Behnke (2002) observed that although few stream resident brown trout transition to piscivorous diets and live beyond five years of age, those that do are the largest individuals in the stream and would have high ranks in dominance hierarchies of drift-feeding trout. Vehanen et al. (2000) suggested that the decline in brown trout aggressiveness at minimal current velocities observed by Gibson (1978) might reflect a switch in foraging tactics from sit-and-wait to cruising, since juvenile brown trout in lakes have been found to be cruising predators and have no territorial associations. Information on social patterns for spacing of brown trout in lakes and large rivers in western North America was not found in the literature review; however, brown trout are generally considered to be roving predators in those types of systems.

Diel activity patterns and behavior

Adult activity patterns and behavior: Bachman (1984) conducted an intensive study of naturalized brown trout diurnal activity patterns and behavior year-round in a fertile, high conductivity stream in Pennsylvania. Individually-identified fish were observed undisturbed from dawn to dusk in a large pool (90 m [295 ft.] long and 15.2 m [50 ft.] wide), over a period of three years (Bachman 1984). Brown trout spent 86 percent of daylight time in a sit-and-wait state,

searching the passing water column for food (using one to several precise foraging sites located in their home ranges) (Bachman 1984). They spent less than 14 percent of their foraging time in energetically costly activity, such as pursuing food, returning to foraging sites, changing positions, or engaging in agonistic encounters. Bachman (1984) concluded that the time spent in sit-and-wait states minimized the energy expended by the brown trout (as indicated by low tail beat frequencies). Agonistic encounters among brown trout were highest in May and June, corresponding with the months of highest feeding rates, but time of day did not have a significant effect on agonistic behavior; only water height had a significant positive effect on agonistic behavior (Bachman 1984). Bachman (1984) found that as brown trout aged, they spent less time pursuing food and an increased proportion of time in agonistic encounters. In general, brown trout became less active as they aged.

Whereas the brown trout observed by Bachman (1984), including the largest individuals, fed primarily from invertebrates in the fertile Pennsylvania stream, Clapp et al. (1990) followed the movements of eight very large (>400 mm [16 inches] TL) brown trout thought to be primarily piscivorous in a Michigan stream using radio telemetry over a period of 346 days. The typical activity pattern observed during the spring-summer period was one of inactivity during the day, when brown trout remained in cover, and active foraging at night. Beginning at dusk, brown trout moved away from the "home-site" (Clapp et al. 1990). They were active sporadically throughout the night and returned to cover near sunrise (Clapp et al. 1990). Clapp et al. (1990) observed that the daily foraging activity of brown trout appeared to be related to light level, food availability, and water temperature. The researchers found significant differences between hourly activity levels within and between months (see Foraging behavior section) and suggested that the daily cycle of foraging activity of large brown trout varies seasonally (Clapp et al. 1990).

In Wyoming streams, Young (1995) used radio telemetry to monitor brown trout (adults >250 mm [10 inches] TL) and observed that fish tended to occupy deep water, close to cover during daylight hours. Young (1999) reported that brown trout tended to be more active and to move greater distances during twilight and night hours than during the day. During twilight and night hours, a mean of 65 percent (±18 percent) and 63 percent (±13 percent) respectively of brown trout were active. In contrast, during the day a mean of 24 percent (±13 percent) brown trout were active.

Overall, brown trout were active an average of 11 hours of the diel cycle, with activity increasing after sunset and declining near sunrise (Young 1999). In an Idaho stream, Young et al. (1997) found that the proportion of active brown trout increased during crepuscular periods and at night. The diel movements of brown trout in the Idaho stream were described as predictable, with fish leaving daytime locations each evening and most returning to diurnal positions by 0800 the next morning (Young et al. 1997).

Shuler et al. (1994) evaluated brown trout distribution and microhabitat use during day and night at both high and low flows in 10 study sections of the Rio Grande in Colorado. The researchers found that the habitat associations of adults varied between night and day (see Habitat section); specifically, brown trout shifted to locations with higher water velocities at night. The authors suggested that brown trout were moving into mid-channel areas after sunset to feed from the increased invertebrate drift and then returning to lower velocity, inshore habitats late at night after feeding activity diminished (Shuler et al. 1994).

In summary, several researchers in or near Region 2 have found that lotic brown trout are more active during low-light periods, particularly dusk and early evening. Like other salmonids, brown trout are thought to be primarily visual feeders, but brown trout are considered to have better vision at low-light levels because their retinas contain a greater number of rod cells than other trout species, such as rainbow, cutthroat, and brook trout (Behnke 2002). The differences in daily activity patterns and behavior of brown trout have been attributed to a range of factors including predominant forage type (i.e., fish or invertebrates) and associated temporal fluctuations in forage availability, as well as differences in fish age/size, and water temperatures (Young 1999). Consequently, the range of variation in activity patterns among populations is likely to be large and related to local factors and population characteristics.

Foraging behavior: In the Pennsylvania stream studied by Bachman (1984), brown trout primarily fed on drift from foraging sites that were typically in front of or on top of a submerged rock from which fish had an unobstructed view of oncoming drift. These foraging sites had distinctively low water velocities (approximately 8 cm per s [0.26 ft. per s] in the area where the trout positioned their heads when using the sites). Based on the minimal tail beat frequencies of trout occupying the sites, Bachman (1984) concluded that little effort was required for trout to maintain their

positions despite swifter (up to 60 to 70 cm per s [2.0 to 2.3 ft. per s]) currents above. Because brown trout oriented themselves in foraging sites very precisely, only one fish could use a site at a time, but many sites were used by more than one brown trout during a day with different fish using the site in the same way (Bachman 1984). Most brown trout were found in one of several such sites day after day, and it was not uncommon to observe fish using many of the same sites for three consecutive years (Bachman 1984).

Bachman (1984) reported that brown trout become less active as they age, with the mean feeding rate declining with increasing age from 20.2 feeds per 15 minutes for age-1 fish to 5.6 feeds per 15 minutes for age-6+ fish. The proportion of surface and mid-water feeds remained approximately the same for all age groups and comprised the majority of brown trout feeding activity; only 7 to 13 percent of feeding was from the substrate (Bachman 1984). Total and mid-water feeding rates were significantly higher on sunny days, but they appeared to decrease as water temperature increased (Bachman 1984). Turbid conditions significantly depressed bottom-feeding rates only (Bachman 1984).

Bachman (1984) also reported that small fish fed in close proximity to, but always downstream of, larger fish and at a higher rate than the larger fish upstream and suggested that larger fish may have been passing up some items in the drift. Feeding rates of younger fish (age-1 to age-4) were higher (20.4 feeds per 15 minutes [SE = 2.1]) on days when an older fish (age-5+) was seen in the area than when older fish were not present (5.4 feeds per 15 min. [SE = 0.8]).

In the Pennsylvania stream, brown trout feeding rates varied from month to month; they were highest in spring, declined in July and August, and increased again in September and October (Bachman 1984). Brown trout fed from the surface and mid-water equally during the spring and summer, but in the fall, fish fed primarily from the mid-water (Bachman 1984). Brown trout were most mobile during spring, with movements among foraging sites highest in April and May compared to the rest of the year (Bachman 1984). Movements of younger fish (<age-4) were not correlated with size and age, but Bachman (1984) remarked that larger fish moved less frequently than younger fish. Movement rates were not significantly correlated with time of day, light intensity, water temperature, discharge levels, or turbidity.

Bachman (1984) concluded that the foraging behavior of brown trout was profoundly influenced

by the effect of water current on energy expended by fish as evinced by restricted home ranges of individuals (see below), the discrete nature of foraging sites within home ranges, and the large proportion of time fish spent stationary in foraging sites. The precise use of foraging sites allowed brown trout to sit-and-wait for passing drift items with a low energetic cost (Bachman 1984).

In the study of activity and movement patterns of presumably piscivorous brown trout in a Michigan river, Clapp et al. (1990) found that foraging activity was greatest in summer at night when brown trout moved into shallow riffles, deep pools, eddies, and side channels in search of prey. From June to August, brown trout were most active during low light periods, but variations in activity patterns were observed among summer months and were thought to be related to variations in food abundance (Clapp et al. 1990). In June, four daily peaks in foraging were observed, with greatest activity immediately after sunset followed by peaks in activity at 0100 hours, 0500 hours, and 1430 hours; trout were least active in the afternoon from 1600 to 1900 hours. In July, two peaks in foraging activity were observed, at midnight and before sunrise (0000 and 0500 hours respectively), with the midnight peak being the greatest level of foraging activity detected during the study. In August, no distinct peaks in daily activity were observed, with most brown trout active throughout much of the day, alternating between periods of higher and lower activity every 3 to 4 hours; however, a low point of activity was observed around 1100 hours (Clapp et al. 1990).

Young (1999) found that the activity patterns of adult brown trout in two Wyoming streams were not consistent with the typical foraging tactics of drift-feeding salmonids described by Bachman (1984). Instead, he observed brown trout "patrolling" home ranges mainly at night, moving among positions above and below their diurnal resting sites. Young (1999) suggested the foraging behavior reflected the exploitation of a patchily distributed and non-drifting food source such as fish, large invertebrates, or terrestrial invertebrates (Young 1999).

Winter foraging behavior: Although stream fish in temperate climates are typically considered less active during winter due to reduced metabolic demands and swimming abilities at cold-water temperatures (Cunjak and Power 1986, Cunjak 1996), some researchers have found that brown trout remain relatively active and continue to feed during winter even under harsh environmental conditions (Maciolek and Needham 1952). Because the native range of brown trout extends

north of the Arctic Circle, brown trout may be capable of alternate over-wintering strategies. Cunjak and Power (1986) observed that brown trout in an Ontario river exhibited reduced activity and decreased their energy expenditure by associating predominately with low velocity habitats. Maciolek and Needham (1952), on the other hand, found that brown trout in a mountain stream in California were active throughout the winter and fed regularly at all water temperatures (including 0 °C), at elevated discharges, and in "ice-laden" waters.

Maciolek and Needham (1952) reported on the effect of winter conditions on the feeding behavior of brown trout during the winter of 1950-1951 (November to April) in a stream in the Sierra Nevada Mountains (elevation 7,200 ft.). Brown trout were observed during the day, appearing in open sections of the stream in the morning after a few hours of sunlight (around 0830) when anchor ice that formed on cold nights would begin to break up (Maciolek and Needham 1952). Anchor ice break up was observed to increase discharge significantly, as water impounded by ice formations was released, and the increased flow disturbed the stream bed, dislodging substrates and invertebrates. Brown trout were observed feeding during and after the period of anchor ice break up, presumably on benthic invertebrates dislodged by the process, from around 0830 hours until 1530 hours, when temperatures and stream flows began to decrease (Maciolek and Needham 1952). Brown trout "seemed to disappear" in late afternoon when water temperatures began to decrease, and few fish were seen at night; however, trout kept in live cars in the stream at night for observation were described as being "far from sluggish" and able to avoid capture by hand "in the freezing, ice-laden waters" (Maciolek and Needham 1952). Brown trout were observed to surface feed during the winter when aerial insects were present, which usually occurred during periods of water temperatures of 2 to 6 °C (35 to 42 °F) (Maciolek and Needham 1952).

Refuge use: Bachman (1984) reported that brown trout abandoned foraging positions and moved towards the banks or cover when disturbed. In response to minor disturbances, such as a large bird flying over, brown trout usually darted away from their foraging sites and pressed their body to the substrate, where they remained motionless for several minutes before returning to the foraging site to resume feeding after 3 to 5 minutes (Bachman 1984). With repeated disturbance or when a "severe disruption" such as duck landing in the stream occurred, brown trout sought refuge in deep water or under cover of a bank, brush, or rock. On those occasions, brown trout would remain motionless in

the cover for 20 to 30 minutes before resuming their feeding position and activity. Multiple brown trout were observed to flee to the same cover and were not seen to feed, move, or engage in agonistic encounters while in the refuge (Bachman 1984).

Young (1995) observed that brown trout monitored with radio telemetry were more frequently associated with undercut banks after disturbance than any other type of cover. Young et al. (1997) remarked that because brown trout were less active during the day, and often concealed in cover, they were less likely to be displaced by disturbance from anglers (unlike rainbow trout observed), but when disturbed, brown trout would flee to nearby cover.

Maciolek and Needham (1952) noted that in winter, brown trout appeared to spend most of their time under shelf ice, undercut banks, or among willow roots and brush except while feeding from mid-morning to mid-afternoon.

Young-of-year activity patterns: Several studies have indicated that YOY brown trout habitat use varies over the diel cycle, leading researchers to suggest that their activity and behavior may vary between daylight and night hours. For instance, age-0 brown trout are less frequently observed in stream margin habitat during the day than at night. This may indicate cryptic behavior, with fish concealing themselves in cover during daylight, or it could reflect shifts in habitat use related to food abundance or predation avoidance (Harris et al. 1992, Griffith and Smith 1993, Hubert et al. 1994, La Voie and Hubert 1997, Roussel and Bardonnet 1999). Diurnal and nocturnal habitat associations of brown trout YOY during summer and fall have been particularly well-studied in Douglas Creek in the Medicine Bow National Forest (Harris et al. 1992, Hubert et al. 1994, La Voie and Hubert 1997), and the findings are summarized following.

In visual surveys, YOY brown trout have been observed in greater numbers in stream margin habitat at night than during the day (Harris et al. 1992, Hubert et al. 1994, La Voie and Hubert 1997). Harris et al. (1992) reported that age-0 brown trout used areas with higher current velocities and greater water depths during the day than at night. Similarly, Hubert et al. (1994) found that age-0 brown trout occupied positions closer to the stream edge at night than during the day. Hubert et al. (1994) suggested that at night, age-0 brown trout might move closer to the shore into stream margin habitats with lower current velocities and shallower depths, possibly to avoid predation by larger trout. However,

La Voie and Hubert (1997) determined from day and night electrofishing surveys that diel shifts in age-0 brown trout habitat associations were less consistent. There was no significant difference in depths used during the day and night by age-0 brown trout between July and August, but in September, fish were found at significantly greater water depths at night (La Voie and Hubert 1997). La Voie and Hubert (1997) also reported that age-0 brown trout were positioned significantly farther from shore during the day than at night in July, but no significant difference was observed between day and night positions in September. The researchers noted that more age-0 brown trout were always seen at night than during the day, regardless of habitat type. They suggested that fish could be remaining concealed in cover during the day within stream margins as suggested by Heggenes (1988a) or possibly, they were moving to locations where they were less visible during the day as suggested by Harris et al. (1992). Although the electrofishing surveys provided some evidence of diel shifts in habitat use by age-0 brown trout, the researchers remarked that the movement patterns and use of cover by young fish might be more complex than previously suggested.

Griffith and Smith (1993) investigated age-0 brown trout habitat use during winter in the South Fork of the Snake River in Idaho. The researchers found that age-0 brown trout were typically concealed during the day in the substrates of river margins at depths less than 0.5 m (1.6 ft.), and they estimated that between 61 and 66 percent of the fish emerged at night to swim in the water column in the same river margin habitat where they were concealed during the day. The authors suggested that the low-gradient river margin areas with large substrates provided suitable habitat for daytime concealment of age-0 trout and that they emerged at night, during the slightly warmer water temperatures, moving less than 1 m to feed on invertebrate drift (Griffith and Smith 1993). Griffith and Smith (1993) speculated that age-0 trout concealed in substrates did not emerge every night and that the frequency of emergence and activity levels would be related to water temperature and digestive rates. Age-0 brown trout habitat associations and behavior patterns would also be expected to vary in other systems with different winter environments, such as those with extensive surface and anchor ice conditions (Griffith and Smith 1993).

Experimental studies have provided additional insight into diel shifts in habitat use and the influence of predator presence on the behavior of age-0 brown trout. Habitat use patterns of age-0 brown trout soon after emergence were monitored in artificial stream

channels to assess the influence of food availability, predator presence, and the diel cycle on habitat use (Roussel and Bardonnet 1999). A diel pattern of habitat use was observed for age-0 brown trout in the control and food channels, with most fish using deep habitats during the day (mean 64 percent) and the shallower habitat located along the channel margins at night (mean 62 percent) (Roussel and Bardonnet 1999). Notably, in channels with predators (i.e., sculpin [*Cottus gobio*]), most age-0 brown trout concealed themselves in the substrate, and of those that did not, most used shallower margin habitat more than deeper water during both day and night (Roussel and Bardonnet 1999). The researchers suggested that the use of deeper water during the day even in the control channel, in which no food was distributed, indicated that the diel pattern of habitat use observed was an unlearned behavior possibly adapted to nocturnal predator avoidance, fluctuations in feeding activity related to light intensity, or avoidance of accidental downstream drift (Roussel and Bardonnet 1999).

Bardonnet and Heland (1994) also studied the habitat use of emerging brown trout in the presence and absence of potential predators (age-1+ trout and sculpin [*Cottus gobio*]). In the absence of predators, brown trout alevins were found in water 20 to 30 cm (8 to 12 inches) deep (Bardonnet and Heland 1994). When alevins emerged in the presence of predators, most remained cryptic, and when visible, most occupied the shallowest water, which was 10 cm (3.9 inches) in depth (Bardonnet and Heland 1994). Alevins were also observed in greater numbers during night and dusk hours than daylight and dawn hours (Bardonnet and Heland 1994) regardless of predator presence or absence. The presence of predators was found to increase the downstream movement of alevins by 20 percent, from 71.7 percent in the absence of predators to 92.5 percent with predators present (Bardonnet and Heland 1994). Alevins in the channel segment without predators were visible in greater proportions and more active than alevins in the channel with predators (Bardonnet and Heland 1994). Mean length and weight of alevins in the presence of predators were smaller, which suggested that their growth was reduced via reduced feeding activity (Bardonnet and Heland 1994). The researchers reported some evidence of alevins responding to predation threat with "risk-balancing," decreasing feeding activity at low levels of food availability and increasing activity (and hazard) when food levels are high (Fraser and Huntingford 1986 as referenced by Bardonnet and Heland 1994).

Movement patterns

Diel movements and home ranges: Bachman (1984) found that invertebrate-feeding brown trout (<330 mm [13 inches] TL) in a Pennsylvania stream had a restricted home range and daily movements. The mean home range of 53 brown trout was 15.6 m^2 (SE = 1.7) based on minimum-convex polygons encompassing 95 percent of sightings of individuals each year (Bachman 1984). Individuals remained faithful to the same area from year to year, and no fish had exclusive use of any home range with considerable overlap of the home ranges of neighboring brown trout (Bachman 1984). For instance, the home range of one brown trout was wholly within the home range of another, and both fish used one particular foraging site predominately. Within their home ranges, individual brown trout used from 1 to 32 foraging sites (mean = 6), making short quick movements to intercept food items in the drift or on the stream bed (Bachman 1984). Brown trout home ranges decreased during the second through fifth years of growth (age-1 to age-4). Bachman (1984) suggested that the increased size of fish as they aged increased their ability to maintain foraging site positions when challenged and consequently decreased their need to move among more foraging sites spread over a larger area. Bachman (1984) had little doubt that brown trout were thoroughly familiar with their home ranges, as they appeared to know the location of refuge sites and foraging sites and proceeded directly to them when disturbed or switching from one feeding site to another.

Knouft and Spotila (2002) monitored the movements of brown trout (roughly 200 to 500 mm [8 to 20 inches] FL) in another Pennsylvania stream with mark-recapture surveys and radio telemetry. They reported that overall, using pooled data, 95.5 percent of fish were recaptured or relocated within 800 m (2,625 ft. or 0.5 mile) of their initial capture location (Knouft and Spotila 2002). The researchers also reported that the ones that moved most, moved to adjacent sites, and those found further away were all age-1 or age-2 fish (Knouft and Spotila 2002). Distances moved by the age-1 and age-2 fish ranged from 275 to 1900 m (roughly 0.2 to 1.2 miles) from the June and August tagging period to December-January recaptures and from 375 to 1650 m (0.23 to 1.0 mile) to March-April recaptures (Knouft and Spotila 2002). The authors reported that the brown trout monitored with radio telemetry were typically found in the same areas in pools or under overhanging vegetation and usually displayed localized movements

of less than 6 m (19.7 ft.) (Knouft and Spotila 2002). The trout were only relocated weekly, and diel activity and movement patterns were not described.

Some studies have suggested that when brown trout switch to a piscivorous diet, they become more mobile, moving greater distances to meet resource needs (Shetter 1968, Clapp et al. 1990). Jenkins (1969) suggested that the large brown trout he observed were primarily piscivorous and had definite refuge positions and daily ranges for foraging (as referenced by Clapp et al. 1990). Clapp et al. (1990) found that very large, presumably piscivorous, brown trout were more mobile than the invertebrate-feeding population observed by Bachman (1984). Large brown trout (437 to 635 mm [17 to 25 inches] TL) moved an average of 239 m (784 ft.) between radio-telemetry relocations during the spring-summer period and an average of 3,103 m (1.9 miles) between relocations during the autumn-winter period (only 11 percent of variation in distance was attributable to length of time between relocations) (Clapp et al. 1990). After foraging movements at night, brown trout were observed to return to specific cover features each day (Clapp et al. 1990). Brown trout rotated among up to four specific home sites within their spring-summer ranges (Clapp et al. 1990). Typically, brown trout were observed spending 2 to 3 days at one home site before moving at night to a different one (Clapp et al. 1990). Home sites were separated by a mean distance of 386 m (1,266 ft. or 0.24 miles), but some were considerable distances apart (Clapp et al. 1990). One brown trout was observed traveling 3 km (1.9 miles) round trip on several occasions, moving 1.5 km (0.93 mile) upstream at night to forage and returning to a specific refuge site by morning (Clapp et al. 1990).

Young (1999) and Young et al. (1997) also found a high rate of diurnal site fidelity among adult brown trout. Observations of adult brown trout (mean = 340 mm [13.4 inches] TL, range = 264 to 467 mm [10.4 to 18.4 inches] TL) in two Wyoming streams (South French Creek and Hog Park Creek) showed that the first and last positions occupied by a brown trout during a diel cycle were within 10 m (32.8 ft.) of each other 84 percent of the time (Young 1999). Similar to the findings of Clapp et al. (1990), Young (1998) reported that brown trout tracked for more than one diel cycle often occupied different diurnal resting sites on different dates (mean = 3, range 2 to 5), but the home ranges used on different dates overlapped 83 percent of the time. Brown trout moved an average of 121 m (397 ft.) over the diel cycle, and the average home range was 41 m (134.5 ft.) for both streams and monitoring years (Young 1999). In an Idaho stream, the movement

patterns of large brown trout (mean = 494 mm [19.4 inches] TL, range = 342 to 622 mm [13.5 to 24.5 inches] TL) suggested that the trout used the same sites during the day for much of the year; more than 60 percent of brown trout were relocated within 100 m (328 ft.) of their first location (Young et al. 1997).

Using radio telemetry from mid-June to early December one year and from late September to early June the following year, Young (1994) monitored the movement patterns of brown trout (range = 250 to 530 mm [9.8 to 20.9 inches] TL) captured in another study of two montane streams in Wyoming (South French Creek and Douglas Creek). Young (1994) found that the majority (69 percent; n = 54) had home ranges greater than 50 m (164 ft.); home range was defined as the difference between a fish's most upstream and most downstream locations. In contrast to Bachman's (1984) finding that brown trout home range decreased as size increased, Young (1994) found that larger brown trout (>340 mm [13.4 inches] TL) had larger (410 m and 834 m [0.25 ft. and 0.52 mile) mean home ranges than smaller (<340 mm [13.4 inches] TL) brown trout, which had mean home ranges of 95 m and 28 m (312 ft. and 92 ft.). Young (1994) suggested that the difference in movement patterns among smaller and larger brown trout indicated that two different life-history strategies, river migrants and stream residents, existed in the population.

Using radio telemetry, Dare et al. (2002) described movement patterns in winter of 15 sub-adult brown trout in a regulated river in Wyoming, under variable discharge conditions. Brown trout moved frequently throughout the study and were observed at new locations 60 to 70 percent of the time during periods of higher discharge (Dare et al. 2002). As discharge decreased, movements decreased, but the trend was not statistically significant (Dare et al. 2002). Most brown trout moved less than 50 m (164 ft.), and no brown trout sub-adults were observed to move more than 500 m (1,640 ft.); only four of 15 sub-adults moved more than 300 m (984 ft.) from their initial location. Brown trout were described as making frequent short-distance movements characterized as "cruising" around a pool. In a preliminary study, "when discharge was relatively high and stable," brown trout were observed at new locations less frequently (30 to 40 percent of the time), leading the researchers to speculate that movement frequency was elevated during the flow manipulations in the study (Dare et al. 2002).

Seasonal and long-range movements: Bachman (1984) found that most brown trout in the Pennsylvania

stream used the same habitat year-round. In contrast, in a Michigan river, Clapp et al. (1990) tracked eight large brown trout for nearly a year and found that fish moved distances ranging from 370 to 33,420 m (0.23 to 20.8 miles). Brown trout appeared to use separate summer and winter ranges, with five of six individuals tracked during the fall-winter period moving 10 km (6.2 miles) upstream to slower and deeper river habitats that had been considered poor trout habitat previously due to warm temperatures in summer (Clapp et al. 1990). The researchers observed that most long-range movements by brown trout occurred during periods of high water (Clapp et al. 1990).

Young (1994) reported that brown trout movements in southeastern Wyoming streams were greater in the fall, presumably associated with spawning. Brown trout were observed migrating upstream during late summer and early fall; however, individuals moved upstream at different times, which confounded the statistical significance of the movement pattern (Young 1994). Young (1994) noted that brown trout tended to move downstream in winter and reported that no fish implanted with radio transmitters in the fall migrated out of the tributary during the winter. Of 13 brown trout implanted with transmitters in the fall, only five survived until April; all had moved downstream into a large beaver pond during the fall-winter period (sometime between mid October and late April), where they remained until early May (Young 1994). By mid-May, three of the larger brown trout left the tributary for the North Platte River, one moved 670 m (2,198 ft. or 0.4 mile) downstream, and the other died 284 m (932 ft.) downstream of the beaver pond (Young 1994). Young (1994) reported that the movements of brown trout were not significantly correlated with the available measures of water temperature or discharge, but the fish that left the streams for the river apparently left the tributaries during the high spring flows associated with snowmelt runoff. Based on the observations of brown trout movements, Young (1994) concluded that the larger brown trout in the study were river migrants that inhabited the warmer and more productive river during the summer, migrated into the tributaries to spawn and over winter, and returned to the river during high flows in spring; the smaller adult brown trout, on the other hand, were year-round stream residents.

Garrett and Bennett (1995) observed a similar pattern of seasonal movement of brown trout between a reservoir on the Pend Oreille River in Washington and two of its tributaries, with the difference that brown trout inhabiting the reservoir migrated into cooler tributary streams during early summer. Brown trout

left the reservoir when water temperatures increased above 19 °C by mid-July (Garrett and Bennett 1995). Distances moved from the reservoir into the streams ranged from 1.7 to 11.1 km (1 to 7 miles) (Garrett and Bennett 1995). The fish remained in the tributaries during the summer, gradually moving upstream (Garrett and Bennett 1995). When reservoir water temperatures cooled to below 19 °C in early September, no brown trout returned to the reservoir; they remained in the tributaries, presumably to spawn, as redds were seen in early November (Garrett and Bennett 1995). In early January, seven of 14 relocated brown trout had returned to the reservoir while the other seven remained in the tributaries (Garrett and Bennett 1995). Another group of brown trout had returned to the reservoir by early April, and an additional three were found in the reservoir at the mouth of one of the tributaries by mid-June (Garrett and Bennett 1995).

Other researchers have documented movements of brown trout into tributaries during summer when water temperatures in riverine habitats increase. Kaya et al. (1977) reported that brown trout moved out of the Firehole River in Yellowstone National Park into cooler tributaries before summer water temperatures in the river reached 24 °C. And although Young (1994) and Garrett and Bennett (1995) found some brown trout overwintering in tributaries after spawning, Meyers et al. (1992) reported brown trout moving more than 6 km downstream soon after spawning in a Wisconsin stream.

Long-range movements by brown trout in summer not associated with temperature refugia have also been observed. Young (1994) reported that two brown trout moved 3,002 and 4,614 m (1.9 and 2.9 miles) within a study stream over a period of 22 and 7 days respectively in summer. In the same study, another 19 brown trout implanted with radio transmitters in early summer were not relocated in the study streams, but two of the "missing" fish were found a month later in the North Platte River, 23 and 66 km (14.3 and 41 miles) from where they had initially been captured, and an angler caught a third 96 km (60 miles) downstream of its initial location a year later (Young 1994).

In summary, brown trout are capable of a range of movement patterns. Some studies have found little movement in some populations (Bachman 1984, Knouft and Spotila 2002) whereas others have observed long-range movements primarily related to seasonal shifts in habitat requirements (Kaya 1977, Clapp et al. 1990, Young 1994, Garrett and Bennett 1995). The movement patterns of brown trout populations appear to vary

among locations with differences in habitat quality and availability, life-history strategies, and foraging behaviors. Several studies have documented brown trout movements between summer and winter habitats, spawning movements, and movements to cool-water refugia in summer. Winter, summer, and spawning habitat requirements of salmonids are different, so seasonal movement is typically required (Cunjak 1996). Where the different required habitats are located in close proximity and sufficient availability, seasonal movements may be minimal or involve comparatively short distances (Bachman 1984, Cunjak 1996). However, seasonal shifts in habitat requirements can result in long distance movements of tens of kilometers (Clapp et al. 1990, Garrett and Bennett 1995), and as described by Young (1994), brown trout with different life history strategies may occupy the same habitat during much of the year but have widely ranging movement patterns.

Patterns of dispersal of young and adults

Dispersal patterns in populations of naturalized brown trout have been the subject of limited investigation in North America. Migratory forms of brown trout typically remain in their natal streams for one to several years before moving into lakes and rivers (Elliott 1994). The dispersal patterns of stream-resident brown trout likely vary among systems with habitat availability, population densities, and other conditions. Beard and Carline (1991) commented on the "prevailing notion that salmonids disperse widely from spawning areas and that all suitable habitat will eventually be filled" and referenced several studies (e.g., Shapovalov and Taft 1954, Chapman 1966, Allen 1969). However, the researchers pointed out that close associations between juvenile and adult salmonid densities and the spatial distribution of spawning habitat had been found for several species, including brown trout (Solomon and Templeton 1976 and Mortensen 1977 as referenced by Beard and Carline 1991), and this would indicate limited dispersal from natal areas. In systems where habitat is not a limiting factor (e.g., recruitment may be limited), there may be excess habitat available for juvenile and adult brown trout such that wide dispersal is not necessary.

In some stream systems, density-dependent emigration and mortality may regulate brown trout populations, and larger fry may have an advantage in establishing territories and surviving (Elliott 1994). However, in other systems, density does not appear to influence emigration or mortality rates among young brown trout very much. For instance, in two California

mountains streams, Jenkins et al. (1999) found that most age-1+ brown trout exhibited little net movement between spring and winter, and the emigrants that were observed in the study did not differ in size from the residents. They concluded that young brown trout mortality and emigration were independent of density in that system. Jenkins et al. (1999) suggested that the patterns they observed were more compatible with a local dominance hierarchy structure (e.g., Jenkins 1969, Nakamo 1995) rather than "a mosaic of exclusive territories from which losers or 'floaters' were ejected or doomed to die of starvation" (e.g., Mason and Chapman 1965, Grant and Kramer 1990).

Beard and Carline (1991) found that brown trout in their study area (a productive limestone stream in Pennsylvania) exhibited limited dispersal. They concluded that juvenile brown trout did not disperse far from natal areas based on several findings. First, age-1+ brown trout densities varied widely and were positively correlated with redd densities among sampling sections, and the variability in redd densities among sites appeared to be a function of differences in spawning habitat availability among stream sections (Beard and Carline 1991). Second, total densities of brown trout at different sampling sections were similar in summer (July and August) and post-spawning (December), which indicated that brown trout did not make extensive spawning movements in that stream (Beard and Carline 1991). The researchers believed that the wide variation in brown trout densities among stream sections was related to varying recruitment rates among locations, which in turn was a function of variations in spawning habitat, and that brown trout dispersal from spawning/natal sites was limited in the stream (Beard and Carline 1991).

Knouft and Spotila (2002) monitored the movements of brown trout in another Pennsylvania stream and reported that most were relocated within 800 m (0.5 mile) of their initial capture location. Of the fish that moved greater distances, most were age-1 or age-2 (Knouft and Spotila 2002), which may indicate some limited dispersal movements by young brown trout in some systems.

In streams with peak flows related to snowmelt runoff in spring and early summer, displacement of young brown trout by high discharge is a possible mechanism of dispersal. Heggenes (1988b) investigated the effect of elevated flows on young brown trout in a Norwegian stream and concluded that under normal conditions, brown trout with a mean length of at least 67 mm (2.6 inches) are not washed out or displaced by

sudden high flows if coarse substrates supplying cover and low-velocity microhabitats are present.

Dispersal of adult brown trout in river systems may be more extensive, but it has not been investigated directly. Clapp et al. (1990) and Young (1994) documented extensive movements by brown trout adults inhabiting rivers.

Habitat

In their native range, brown trout thrive in streams, rivers, and lakes, and anadromous forms are common. In Region 2, brown trout have been introduced into streams, rivers, reservoirs, and lakes and have been able to form self-sustaining populations in all of these habitat types.

Water temperature and oxygen content are thought to be primary factors influencing the successful introduction of brown trout. Naturalized populations have been established in locations with temperature regimes similar to those of the brown trout's native range (Elliott 1994). Survival temperatures of brown trout range from a lower limit of 0 °C to an upper limit of 25 to 30 °C, with the upper limit related to acclimation temperature (Elliott 1994). Brown trout are considered more tolerant of slightly warmer water temperatures than native North American trouts (Baxter and Stone 1995). Experiments have demonstrated that domesticated brown trout have more reserve energy and "scope of activity" than domesticated rainbow trout at temperatures approaching upper lethal limits (Bachman 1991). However, although brown trout can survive at warmer temperatures for short periods, their actual tolerance of warmer waters may be less than their reputation suggests (Bachman 1991).

Some studies have found that brown trout growth is constrained at water temperatures below 4 °C and above 19.5 °C (Elliott 1994), and brown trout are reported to be most active and grow best at temperatures between 12.6 and 15.4 °C (Bachman 1991). Garrett and Bennett (1995) reviewed reports of optimum and preferred temperatures of brown trout, and they noted much variation: one report of brown trout growth and activity being maximized at 13.3 to 23.9 °C, and other reports of brown trout temperature preferences of 11 to 14 °C or 12.4 to 17.6 °C (Garrett and Bennett 1995). Garrett and Bennett (1995) found that brown trout left a reservoir for cooler tributary streams when reservoir temperatures reached 19 °C. This was consistent with another observation of brown trout in Lake Ontario being found in temperatures ranging from 8 to 18 °C but never above 20 °C (Nettles et al. 1987 as referenced by Garrett and Bennett 1995). Lee and Rinne (1980) compared critical thermal maxima of five trout species found in the southwestern United States, including brown trout, and they found no significant differences among them. Critical thermal maxima of brown trout acclimated at 10 °C was 28.96 °C ± 0.41 °C, and when acclimated at 20 °C, it was 29.85 °C ± 0.58 °C, but under fluctuating temperature regimes, lethal temperatures were lower (21 to 27 °C) (Lee and Rinne 1980).

Rahel and Nibbelink (1999) found that the distribution of brown trout in southeastern Wyoming was related to stream size and mean July air temperatures. The geographic range of brown trout was positively associated with mean July air temperatures of 19 to 22 °C, and within that thermal zone, brown trout were more likely to occur in large streams (>4 m (13.1 ft.) wetted width) than in small streams. Brown trout probability of occurrence was high in large streams within the moderate thermal zone of 19 to 22 °C, intermediate in small streams in the moderate thermal zone or large streams in the warm thermal zone of >22 °C, and low in other categories.

Isaak and Hubert (2004) found a non-linear relationship between trout biomass (including brown trout) and mean July-August stream water temperatures in southwestern Wyoming. Trout biomass peaked around mean July-August water temperatures of 12 °C, and biomass fell to near zero at mean July-August water temperatures of 3 °C and 21 °C, producing a dome-shaped curve relationship between biomass and temperature (Isaak and Hubert 2004). Sympatric populations of cutthroat trout and brown trout occurred in areas with mean stream temperatures greater than 9 °C, but at lower mean stream temperatures, trout populations were comprised of cutthroat trout and brook trout, and no brown trout were found. Isaak and Hubert (2004) noted that although many studies have documented the relationship between trout populations and temperature, the nature of the relationship (positive or negative associations) depends on which portion of the thermal range is sampled. For instance, studies that indicate a negative relationship between population size and temperature for trout may result from research locations near the southern margin of species' ranges or the comparative ease of collecting data in more accessible downstream portions of watersheds with warmer water temperatures (Isaak and Hubert 2004). In contrast, studies of high-elevation trout populations or those located near northern margins

of species' ranges have reported positive relationships between temperature and population size (Isaak and Hubert 2004).

Optimal and limiting temperature ranges during the summer growing season have received most attention, but temperatures during other periods can also influence brown trout populations. For instance, Kaya (1977) reported that brown trout gonadal maturation, and consequently reproductive success, was impaired in warmer waters of a geothermally-heated stream in Yellowstone National Park, and winter water temperatures during the period of egg development can significantly influence recruitment (see Breeding biology section). The temperature range for brown trout egg development is considered to be approximately 0 to 15 °C (Elliott 1994). Stonecypher (1992) found reduced survival of brown trout embryos incubated at 2 °C, and Reiser and Wesche (1979) documented the freezing of brown trout eggs buried in the substrates of a Wyoming stream. In contrast, elevated temperatures during the winter incubation period may be detrimental to brown trout reproduction. Live trout eggs collected from redds in the warm-water (13.3 °C) section of a geothermally-heated stream during mid-December yielded no brown trout; all were identified as rainbow trout when they later hatched in the laboratory (Kaya 1977). Kaya (1977) found the ratio of YOY brown trout to rainbow trout from the stream was 1:7.7 consistent with the conclusion that brown trout reproduction was impaired at elevated temperatures (Kaya 1977).

Similar to other salmonids, brown trout have higher requirements for water oxygen content than many other fish species. Free-swimming brown trout can tolerate a minimum oxygen concentration of 5.0 to 5.5 mg per L, but an 80 percent saturation level is considered optimal (Crisp 1989, Elliott 1994). Assuming adequate flow of water across the eggs, minimum water oxygen concentration requirements for brown trout eggs are thought to be similar to those of closely related species, around 1 mg per L at 5.5 °C and 7 to 10 mg per L at 10 to 17 °C (Elliott 1994). However, minimum oxygen requirements are mediated by factors such as water temperature, fish metabolism, and embryo development stage, and oxygen availability is influenced by other environmental variables such as oxygen demands of sediments or aquatic vegetation (Crisp 1989).

Brown trout are fairly tolerant of a wide range of pH, occurring in waters with pH ranging from 4.95 to 8.0 or higher (Bachman 1991) with an upper lethal limit of 9.2 (Crisp 1989). Brown trout may have problems with osmoregulation at pH levels around 4.5, and if elevated concentrations of aluminum occur with low pH (pH of 4.5 to 5.5), survival may be reduced (Crisp 1989). The alkalinity level, an index of water fertility, considered desirable for trout culture is between 80 and 200 mg per L, with 120 to 400 mg per L considered optimal for fish growth (Stickney 1991 and Piper et al. 1982 as referenced by Pender and Kwak 2002).

Brown trout require a range of habitats to complete their life cycle. In addition to suitable habitats during the summer growing season, they require suitable spawning nursery/rearing, and winter habitats. Following is information regarding adult brown trout habitat use during summer in lotic and lentic environments, spawning habitat requirements, winter habitat, and YOY and juvenile brown trout habitat use.

Habitat use - streams and rivers

Brown trout are often the predominant trout found at lower elevations in cold and cool-water streams and rivers of the Rocky Mountain Region, and they are thought to be more tolerant of the less favorable environments in lower reaches of stream systems than rainbow and cutthroat trout (Simpson and Wallace 1982, Baxter and Stone 1995). Given the range of factors that affect habitat use and distribution, it is difficult to define precisely the habitat preferences of brown trout across broad geographic regions. However, several models of brown trout habitat associations in streams and rivers have been developed or tested in Region 2 and have identified important components of brown trout habitat.

Wesche et al. (1987) tested the ability of the U.S. Fish and Wildlife Service Habitat Suitability Index Model (HSI Model) to predict brown trout standing stock in streams in southeastern Wyoming. Thirteen of the 18 variables included in the HSI model were tested. Five HSI model variables were not tested because data were unavailable. The variables not tested included maximum water temperature during embryo development, average velocity over spawning areas during spawning and embryo development periods, average size of substrate in spawning areas, and annual maximum and minimum pH (Wesche et al. 1987). Wesche et al. (1987) tested an additional 25 habitat variables for correlation with brown trout standing stock. Two of the HSI variables and seven of the 25 additional variables tested were significantly correlated with brown trout standing stock (Wesche et al. 1987). These variables included measures of flow regime, shade, depth variation, water velocity, water velocity

variation, proportion of rubble substrate, trout cover, late summer stream flow, and stream flow variation (Wesche et al. 1987).

Kozel and Hubert (1989) compared the applicability of several trout habitat assessment models (e.g., Binns and Eiserman 1979, Wesche 1980, Lanka et al. 1987) on small trout streams at high elevations (>2,375 m (7,792 ft.) above mean sea level) in the Medicine Bow National Forest in southeastern Wyoming. The streams used were located in 15 watersheds that had not been subject to extensive logging, mining, overgrazing, road construction, or upstream diversion or water storage structures (Kozel and Hubert 1989). Of all of the habitat variables included in the various models, those that were found to most influence trout standing stocks were width to depth ratio, abundance of overhead bank cover, average stream width, and level of late summer stream flow (Kozel and Hubert 1989). Habitat features such as the abundance of submerged aquatic vegetation, the degree of bank erosion, and the variation in annual stream flow were found to be of less importance to trout standing stock in the relatively unimpacted, small, high-elevation streams (Kozel and Hubert 1989). The authors noted that some of the variables might be more important in larger streams at lower elevations that were included in the development of some of the tested models (Kozel and Hubert 1989).

Larscheid and Hubert (1992) found that the size structure of brown trout populations in montane streams in the Medicine Bow National Forest was related to the position of the study reach in the watershed, channel gradient, and composition of the salmonid community. Most adult brown trout were smaller in size in mid-elevation, moderate-gradient, forested reaches where they occurred with brook trout (Larscheid and Hubert 1992). More large brown trout were found in lower portions of the watersheds in meadows or rangeland stream reaches in the foothills that had low gradients, meandering channels, deep trench pools with abundant overhanging banks and no other species of trout were present (Larscheid and Hubert 1992). As gradient increased, the proportion of quality-sized (defined as >250 mm [9.8 inches] TL) brown trout decreased, and reaches with few quality-size brown trout were significantly different in gradient and riparian features from those with abundant quality-size brown trout (Larscheid and Hubert 1992). Five variables were correlated with the proportion of quality-size brown trout. Abundant quality-sized brown trout were found in reaches with high standing stocks of brown trout as well as high conductivity and alkalinity (chemical features

indicative of high biological productivity) (Larscheid and Hubert 1992). The proportion of quality-size brown trout was negatively related to overhanging vegetation and overhanging vegetation with deep water. The authors suggested that water temperatures and lack of suitable pool habitat limited brown trout at higher elevations, whereas low-gradient reaches with abundant undercut banks, deep pools, and aquatic vegetation provided more favorable conditions (Larscheid and Hubert 1992).

Modde et al. (1991) investigated the relationship between stream habitat and brown trout biomass in streams of four different land types in Black Hills National Forest. The land types represented were those containing the major stream fisheries in the Black Hills and included crystalline canyon, gently dipping plateau, moderately rolling uplands, and limestone canyon. Most stream morphometric and water quality variables (20 of 24 variables) differed among land type associations, with the exception of mean depth, bank undercut, bank water depth, and nitrate concentration, which were not significantly different among land type associations. Brown trout biomass was greatest in pool habitat and in the limestone canyon land type association, which had the highest area percentage of pools (the authors reported the pool to riffle plus rapid ratio as "1.59"). The researchers found the highest biomass of brown trout relative to habitat availability was in plunge pools. Biomass of brown trout relative to habitat availability was intermediate in trench and dammed pools and lowest in lateral scour pools. Brown trout biomass in higher velocity habitats was always relative low. The researchers also observed that brown trout biomass was greater than brook trout in all land type associations and habitat types except for lateral scour pools, which was the habitat type most used by brook trout. Similar to research findings in southeastern Wyoming, Modde et al. (1991) found that brown trout biomass was greater in the two land forms with deeper and wider streams (i.e., the moderately rolling uplands and limestone canyons).

Young (1995) investigated brown trout diurnal habitat use with radio telemetry in two streams in southeastern Wyoming and found significant differences between habitats used by brown trout and those available in both streams. Overall, brown trout tended to occupy deep water in edge secondary habitat types closer to cover and stream banks than expected by chance (Young 1995). Available habitat differed between streams and influenced what habitats were used in each stream (Young 1995). For instance, one of the streams had abundant beaver, and brown trout disproportionately used beaver-created habitats despite

the availability of much woody debris. In contrast, beaver were largely absent in the other stream, and brown trout occupied habitats with coarse woody debris extensively (Young 1995). Based on the habitat use patterns observed in the two streams, Young (1995) suggested that brown trout might select bank-associated habitats, especially those created by beaver, over debris habitats.

Brown trout used areas with current velocities similar to those reported elsewhere: mode near bottom 12.2 to 20.7 cm per s (0.4 to 0.7 ft. per s), mode near surface 18.9 to 35 cm per s (0.6 to 1.1 ft. per s), and a mean near bottom 26.7 cm per s (0.9 ft. per s) (Young 1995). However, 63 percent of the time, the current velocity could not be measured because fish were occupying positions under banks or cover, but currents were presumed to be very low in those areas. In locations where velocity was measurable, there was no significant difference in mean water velocity between used and available habitats with two exceptions: side channels in one stream and the measurements of water velocity 10 cm (3.9 inches) from the substrate in the other stream (Young 1995). Young (1995) found that differences in water velocities between used and available habitats were inconsistent and suggested that when not feeding on invertebrate drift, brown trout were focusing on habitat characteristics unrelated to water velocity, such as overhead cover. Young (1995) also noted that brown trout might have been selecting cover types that locally reduced water velocities.

Using a combination of snorkeling and angling techniques, Shuler et al. (1994) investigated diurnal and nocturnal differences in brown trout association with different types of boulder structures in a section of the Rio Grande, Colorado. The researchers found significant differences in trout distribution among boulder structure types between day and night. At night, adult trout used single boulder and wing dam structures less than they did during the day, and they used mid-channel clusters or areas without structures more (Shuler et al. 1994). Most adult brown trout used areas 33 to 69 cm (1.0 to 2.3 ft.) deep (Shuler et al. 1994). Adults shifted to locations with higher mean water velocities at night (range = 21 to 83 cm per s [0.7 to 2.7 ft per s) compared with day (Shuler et al. 1994). Trout not associated with boulder structures were located at similar depths and velocities during the day as those associated with structures were, but at night, fish not using structures were found in areas of higher water velocities (Shuler et al. 1994). During day and night, similar proportions of trout held positions near natural bank cover (Shuler

et al. 1994). The researchers concluded that boulder structures provided important habitat with lower velocities and often deeper water than areas without structures (Shuler et al. 1994).

Use of cover: As discussed in the Activity and movement patterns section, some populations of brown trout are most active diurnally whereas others are more nocturnal. Different populations have been found to be more or less associated with cover in different studies, in part related to the activity patterns of the population and when the surveys were conducted. For instance, Bachman (1984) reported that the drift-feeding brown trout in a Pennsylvania stream infrequently used overhead cover. Age-2 brown trout were located in the open 83 percent of the time between the hours of 0900 and 1900 (Bachman 1984). Bachman (1984) also reported that as brown trout aged, they were less likely to be seen, but home ranges not wholly contained within the observation area and the cryptic coloration of the fish were considered the causes of less frequent sightings. Overall, the probability of seeing an individual brown trout in the stream during daylight hours ranged from a low of 0.64 in April and May to a high of 0.81 in November (Bachman 1984).

Other researchers have reported that overhead cover is a key component of brown trout habitat use. Clapp et al. (1990) noted that nocturnally-active brown trout spent most of their daylight hours associated with specific cover sites, and daytime resting sites were areas with low water velocities (<10 cm per s [0.33 ft. per s]), logs or overhanging cover, silt substrates, and water depths greater than 30 cm (11.8 inches). Young et al. (1997) also reported that brown trout were most often associated with cover during the day. Wesche et al. (1987) found that the proportion of overhead bank cover in sampling reaches explained the greatest amount of variation in trout standing stock between sites in Wyoming streams (brown trout comprised 61 to 100 percent of the trout populations at the study sites). Wesche et al. (1987) concluded that in small streams, the amount of overhead bank cover available strongly influenced the amount of trout that the stream could support. Deep-water cover areas were important cover for brown trout in larger streams, with mean discharges greater than 2.75 m^3 per s (Wesche 1980), but not in smaller streams (Wesche et al. 1987).

In addition to reducing the visibility of a fish, some types of cover provide refuge from swift currents. Bachman (1984) described how brown trout precisely used rocks to minimize their energetic

expenditure while waiting for food items to drift by (see Foraging behavior subsection of Activity and movement patterns section).

Shuler et al. (1994) evaluated adult and juvenile trout (rainbow and brown trout) microhabitat use during the day and night at both high and low flows in sections of the Rio Grande, Colorado in which three types of boulder habitat structures had been placed: single boulders, mid-channel clusters shaped to be concave downstream, and bank deflectors (or wing dams). The channel was wide (mean width = 55 m [180 ft.]), was primarily composed of low-gradient riffles and runs with small to large cobble substrates, and had been "devoid" of boulders and woody debris aggregations prior to habitat enhancement (Shuler et al. 1994). Stream reaches with boulder structures had habitats with lower velocities and often deeper water than reaches without boulder structures (Shuler et al. 1994). The researchers found that wing dams provided current velocity refuges up to 30 m (98 ft.) downstream while the mid-channel structures did not influence current velocities over as great a distance (Shuler et al. 1994). Results suggested that water velocity and cover influenced brown trout feeding site selection and that the boulder structures augmented habitat availability by providing more locations that were energetically favorable for brown trout (Shuler et al. 1994).

Shuler et al. (1994) found a high proportion of adult and juvenile trout located near some form of cover during the day (88 and 84 percent, respectively) and at night (84 and 86 percent, respectively). Most adult trout not using boulder structures occupied positions close to a natural form of cover (80 percent during the day, and 66 percent at night) (Shuler et al. 1994). Similarly, most juvenile trout not using boulder structures were found associated with a natural form of cover (89 percent during the day, and 91 percent at night) (Shuler et al. 1994). At high flows, trout moved closer to shore to areas with slower currents as the velocity refuges downstream from mid-channel structures decreased (Shuler et al. 1994). Wing dams in particular were found to provide important habitat to adult brown trout during day and night and under high and low flow conditions (Shuler et al. 1994). Based on observations of brown trout avoiding deep, mid-channel areas with swift currents and no cover and of trout moving into shallower, inshore areas when the velocity refuges downstream of mid-channel boulder structures were reduced in size at high flows, Shuler et al. (1994) concluded that depth was an important factor to adult brown trout.

Habitat use - reservoirs and lakes

Fewer studies of brown trout habitat associations in reservoirs and lakes were found in the literature review than for streams and rivers in United States. However, it was not possible to perform a comprehensive literature review of brown trout because of the enormous amount of published material on the species, so some information on brown trout habitat associations pertinent to lakes and reservoirs may have been missed.

Habitat use of brown trout in lakes and reservoirs is likely to vary broadly from year to year and from location to location, but shifting to cooler waters in summer is the general pattern that has been reported. Nettles et al. (1987) observed brown trout in Lake Ontario moving from near-shore areas in late spring when water temperatures exceeded 18 °C and inhabiting cooler waters associated with the thermocline for the duration of the summer.

Barwick et al. (2004) studied brown trout habitat use and temperature, dissolved oxygen, and depth preferences in a large reservoir in the southeastern United States during the summer when suitable habitat was most limited. The reservoir brown trout preferred water temperatures in the range of 7.5 to 21.9 °C (mean = 12.5 °C; mode = 11.0 °C) during the months of July and August and temperatures in the range of 8.8 to 12.0 °C (mean = 10.2 °C; mode = 9.5 °C) in September (Barwick et al. 2004). They used areas with significantly different dissolved oxygen concentrations between months in the summer. Dissolved oxygen concentrations ranged from 4.2 to 10 mg per L, and both the mean and mode of dissolved oxygen in habitats used decreased from July to September (Barwick et al. 2004). Similarly, the depths used differed significantly over the course of the summer; the range of depths used was 14 to 54 m (46 to 177 ft.), with brown trout using deeper depths in late summer (Barwick et al. 2004).

In comparison, rainbow trout in the reservoir selected cooler water temperatures and greater depths than brown trout, but both species generally exhibited preferences for water 20 °C or cooler and containing 5.0 mg per L or more of dissolved oxygen (Barwick et al. 2004). Barwick et al. (2004) noted that both brown trout and rainbow trout used areas of the reservoir with abundant standing timber, which may indicate that brown trout in lentic environments prefer cover. Other researchers investigating trout habitat use in

the reservoir, however, had not observed the same association with standing timber. Barwick et al. (2004) suggest that in some years the cool-water strata are not thick enough to intersect with the standing timber. No differences in diel preferences of brown trout were observed (Barwick et al. 2004).

Overall, Barwick et al. (2004) found that brown trout habitat preferences were comparable to those reported by other researchers for the months of July and August, but brown trout in their study selected cooler temperatures and deeper depths in September than was noted in previous studies. Differences were attributed to inter-annual variations of cool-water strata in the reservoir and between reservoirs (Barwick et al. 2004).

Spawning habitat

In streams, brown trout prefer to spawn in areas with faster currents and gravel substrates. Brown trout inhabiting lakes or large rivers usually move into tributary streams to spawn (Elliott 1994). In lakes without suitable tributary stream habitat, brown trout can spawn along "the stony, wave-washed shores" (Elliott 1994). Factors influencing brown trout spawning site selection at the microhabitat scale are not precisely known, but a number of variables have been examined in several studies. Factors such as water depth, current velocity, water temperature, dissolved oxygen concentrations, and groundwater inflow have been found to influence redd site selection by brown trout in some systems (Elliott 1994).

In a study conducted within Region 2, in mountain streams of southwestern Wyoming, brown trout redd sites were found within a fairly narrow range of water depths and current velocities (Grost and Hubert 1990). However, water depths and current velocities associated with brown trout redd sites vary across their range and with female size (Grost and Hubert 1990). Salmonids reportedly do not spawn in water shallower than their body depth (Crisp and Carling 1989 as referenced by Grost and Hubert 1990).

Grost and Hubert (1990) described the physical characteristics of redd sites constructed by 20 to 40 cm (8 to 16 inches) TL brown trout in the Medicine Bow Mountains of southeastern Wyoming. They found brown trout using water depths of 12 to 18 cm (4.7 to 7 inches) disproportionately to their availability, and no redds were constructed in water less than 6 cm (2.4 inches) or greater than 30.5 cm (12 inches) deep. Brown trout constructed redds in sites with current velocities between 24 and 37 cm per s (0.8 and 1.2 ft. per s) in greater proportion to their availability, whereas current velocities between 0 and 12 cm per s (0 and 0.4 ft. per s) were used less relative to their availability. Grost and Hubert (1990) found no indication of redd site selection based on substrates as substrate types were used in proportion to their availability; the predominant substrates in the study reach were particles 26 to 75 mm (1 to 3 inches) in diameter, and subdominant substrate size classes were 76 to 300 mm (3 to 12 inches) and 7 to 25 mm (0.3 to 1 inch) in diameter (Grost and Hubert 1990). Overall, redd site selection was greatest for water depths of 12 to 18 cm (4.7 to 7.0 inches) and velocities of 24 to 37 cm per s (0.8 to 1.2 ft. per s) (Grost and Hubert 1990). Avoidance was greatest for water depths less than 6 cm (2.4 inches) and velocities of 0 to 12 cm per s (0 to 0.4 ft. per s) (Grost and Hubert 1990).

Before increased minimum flow requirements were implemented, Reiser and Wesche (1977) had described the physical characteristics of brown trout redds in the same study area. Depending on location, the autumn flow conditions were estimated to be 1.5 to 2.0 times less than those observed by Grost and Hubert (1990). Grost and Hubert (1990) compared their findings with those of Reiser and Wesche (1977) and found the characteristics of brown trout redd sites to be similar in both studies. Mean current velocity over brown trout redds, during the previous lower flow conditions was 31 cm per s (1.0 ft. per s), and the current velocity frequency distributions were "nearly identical" between the two studies (Grost and Hubert 1990). Water depths over the redds were similar, with depths ranging from 12.3 to 18.3 cm (4.8 to 7.2 inches) most frequently used in both studies (Grost and Hubert 1990). However, before minimum flow requirements were implemented, the range of depths of redd sites was broader; after flow was increased, the range narrowed and shifted slightly towards deeper waters (Grost and Hubert 1990).

A study of brown trout redd sites in a Michigan stream found that brown trout always spawned in areas with gravel substrates (Hansen 1975). The influence of groundwater inflow on brown trout redd site selection was more complex. Brown trout redd density was the same in areas with and without groundwater inflow (Hansen 1975). Of the redds located in areas with groundwater inflow, brown trout were primarily found in areas of the stream bed that had an intermediate mix of ground and surface water (Hansen 1975). Brown trout appeared to avoid constructing redds in zones with undiluted groundwater inflow or low dissolved oxygen (Hansen 1975). Hansen (1975) reported that if surface and groundwater temperatures differed during the spawning period, brown trout avoided all

of the warmest areas of the stream bed, and when surface and groundwater temperatures were similar during spawning, brown trout avoided areas with low dissolved oxygen levels. In general, brown trout tended to select sites with intermediate mixing of ground and surface water and avoided sites with low dissolved oxygen (Hansen 1975).

Hansen (1975) suggested that whether groundwater inflow was beneficial or detrimental to embryo development depended on the interaction of several factors and would differ among systems. For instance, in a system with permeable gravels, redd sites located in areas with groundwater and surface water mixing had higher and more stable temperatures and adequate dissolved oxygen (Hansen 1975). However, if dissolved oxygen supply was marginal (whether from less permeable gravels, low oxygen in surface water, or low hydraulic gradients), then the addition of warmer groundwater could cause mortality by increasing embryo oxygen demand when supply was insufficient (Hansen 1975). Whether or not early hatching resulting from warm groundwater inflows was beneficial to a population would be related to other factors that affect emerging trout (e.g., timing of seasonal floods, food availability at different temperatures, predation) (Hansen 1975). Hansen (1975) suggested that a main benefit of groundwater in redds was a "wide range in hatching dates that provides some insurance against a major stress of short duration eliminating an entire year's crop."

Winter habitat use - streams and rivers

Cunjak (1996) discussed the critical characteristics of winter habitat of stream fish, with many examples from research on brown trout. Cunjak (1996) regarded the availability of suitable winter habitat as the primary factor regulating stream fish populations in winter, as time spent feeding and in agonistic encounters is thought to decline at low water temperatures. In general, habitats that minimize energy expenditure and provide protection from predation and adverse physiochemical conditions, such as ice, low oxygen, and fluctuations in flow, are considered suitable winter habitat for lotic brown trout (Cunjak and Power 1986, Cunjak 1996). In particular, adult brown trout tend to associate with deeper waters with lower current velocities and some type of cover in winter.

Low current velocities and cover are important components of brown trout winter habitat. Use of specific stream habitat types varies among systems and reaches with differences in availability, discharge,

temperature, groundwater inflows, and ice dynamics (Griffith and Smith 1993, Young 1994, Cunjak 1996, Dare et al. 2002). Brown trout have been reported to use various types of cover in winter, including stream substrates, woody debris, undercut banks, shelf ice, aquatic vegetation, backwaters and side channels, and deep pools.

Small age-0 brown trout have been found to use cobble and boulder substrates as winter habitat, and age-1 brown trout have been observed using woody debris (see Young-of-year winter habitat section). Adult brown trout often use deep pools as winter refuge (Cunjak and Power 1986, Young 1994, Dare et al. 2002). However, deep water is not always suitable winter habitat; in some systems, frazil ice can accumulate in pools, reducing volume substantially and increasing water velocities in the remaining area of the pool (Cunjak 1996). Similarly, pools that freeze over completely may not be suitable habitat if they become deoxygenated (Cunjak 1996). Other pool-like habitats such as backwaters and beaver ponds can provide deep, large, low current velocity habitats suitable for over-wintering stream fishes; however, Cunjak (1996) noted that their value as winter habitat for stream fish has been under-appreciated in the past. Young (1994) reported that both stream-resident and river-migrant brown trout over wintered in a deep beaver pond in a mountain stream in southeastern Wyoming.

Cunjak and Power (1986) studied brown and brook trout winter habitat use in a river in Ontario and found that the trout used habitats with slower water velocities and greater overhead cover in the winter than they did in the summer. In winter, trout were observed in pools, slow reaches of runs, or along stream margins, but they were rarely observed holding positions in mid-stream, in riffles, or at the heads of pools, which were typical of summer feeding stations. Brown trout tended to occupy deeper water but similar water velocities as brook trout where they occurred together. Winter habitat use varied among study sites and age groups, but positions selected by trout were consistent with the notion of energetic cost minimization (Cunjak and Power 1986).

Cunjak and Power (1986) reported the depth, current velocity, and cover characteristics of winter habitat used by age-1+ brown trout at two sites. Depths used ranged from 29 to 68 cm (11.4 to 26.8 inches) (mean = 53.4 cm [21.0 inches]) at one site and 31 to 150 cm (12.2 to 59.0 inches) (mean = 75.6 cm [29.8 inches]) at the other. Focal velocities used at the two sites ranged from 1.5 to 18.0 cm per s (0.05 to 0.59 ft.

per s) (mean = 5.7 cm per s [0.19 ft. per s]) and 1.5 to 43.0 cm per s (0.05 to 1.41 ft. per s) (mean = 16.0 cm per s [0.52 ft. per s) respectively. Use of cover by the age-1+ brown trout at each site was 100 percent and 88.9 percent, respectively.

Dare et al. (2002) reported on the winter habitat associations of sub-adult brown trout in a regulated river in Wyoming at different discharge levels. The sub-adult brown trout used greater than average water depths and slower than average water velocities, particularly pools with abundant cover (Dare et al. 2002). Brown trout used boulders, deep water, and vegetation as cover, but deep-water cover was the most frequently used cover type (Dare et al. 2002). Boulders were used as cover predominantly in riffle and run habitats whereas deep water was the primary form of cover used in pool habitats (Dare et al. 2002).

As discharge decreased, the habitats used by the sub-adult brown trout increased in availability (Dare et al. 2002). For instance, a decline in discharge resulted in reduced current velocities in run habitats (<30 cm per s [<1 ft. per s]) while depths remained greater than 0.75 m (2.5 ft.) such that runs became suitable, deep-water cover habitats with low current velocities (Dare et al. 2002). The researchers found that pools in the river provided stable environments under variable discharge conditions and were preferred by resident salmonids (Dare et al. 2002). Dare et al. (2002) also observed that more trout moved from runs to pools than vice versa.

In a mountain stream in California, Maciolek and Needham (1952) found brown trout were active during the day in winter, but when water temperatures decreased late in the day the fish retreated to cover; typically shelf ice that had formed along stream margins. The researchers also reported that trout that had occupied small side channels in summer and fall left them for the main channel in winter and only occasionally used the side channels on warm winter days (Maciolek and Needham 1952).

Ice effects: Fisheries researchers have long recognized the importance of surface, frazil, and anchor ice formation and their effects on streamfish habitats in winter (Maciolek and Needham 1952, Cunjak 1996). Factors such as snowfall, winds, and air temperature significantly influence stream conditions and ice dynamics in winter, which in turn influence trout habitat use and over-winter survival. Variability in winter flow regimes and ice dynamics among streams and differences in local hydraulics and physical structure within streams may explain much of the variation in trout winter habitat use that have been reported (Cunjak 1996).

Maciolek and Needham (1952) found that ice dynamics influenced the behavior, activity patterns, and habitat use of brown trout inhabiting a California mountain stream (see Activity and movement patterns and Food habits sections). Brown trout have been observed to use surface ice as cover, whether it forms along the edges of streams only as shelf ice or covers the entire width of the stream (Maciolek and Needham 1952, Young 1995). Sub-surface ice, frazil and anchor ice, can disrupt discharge and decrease habitat availability. Maciolek and Needham (1952) described how diel cycles of anchor ice formation and break-up resulted in fluctuating discharge levels by alternately impounding water and then releasing it, and in the process significantly disturbed the streambed. On one occasion, the anchor ice formations caused trout mortality when water flow to side channels were blocked leaving trout stranded as the remaining water drained into the porous substrates (Maciolek and Needham 1952). Frazil ice that forms hanging ice dams can decrease pool habitat. In one study, a brown trout in a pool was observed moving away from an area influenced by a hanging ice dam to part of the pool where a small spring entered and frazil ice had not accumulated (Brown et al. 2000).

Groundwater influence: Cunjak and Power (1986) found that lotic brown and brook trout aggregated near areas of groundwater inflow in winter. Unlike brook trout, which selected positions close to groundwater sources, brown trout distanced themselves slightly from the warmer temperatures found at sources of groundwater inflow, selecting positions downstream where temperatures were cooler but remained above freezing (Cunjak 1996). Cunjak (1996) speculated that brown trout may have selected positions downstream of groundwater sources because the warmer water temperatures (5 to 7 °C) found closer to the groundwater inflows may have increased metabolic rates or because of other habitat preferences (e.g., depth, cover) in combination with the proximity to groundwater inflows, which mediated ice formation.

Young-of-year habitat use

Brown trout spend their first year of life in their natal habitat, usually a stream (Elliott 1994). Age-0 brown trout require low velocity habitats (Chapman and Bjornn 1969 as referenced by Anderson and Nehring 1985). In montane streams with flow regimes in which high spring flows occur after age-0 brown trout emerge from the gravel, age-0 brown trout require low current

habitats, often shallow stream margin or backwater areas (Anderson and Nehring 1985, Hubert et al. 1994). Studies conducted in experimental channels indicate that age-0 brown trout are vulnerable to displacement at higher current velocities (Ottoway and Clarke 1981), and elevated discharge during the post-emergence period has been linked to low recruitment (Anderson and Nehring 1985).

Age-0 brown trout habitat use has been the focus of several studies in Douglas Creek, a mountain stream in southeastern Wyoming. Douglas Creek was altered by railroad tie drives and gold mining in the late nineteenth and early twentieth centuries and a reservoir upstream of the study section that operated under minimum flow requirements of 0.16 m^3 per s at the time of the study (La Voie and Hubert 1996). Age-0 brown trout were found primarily concentrated in low gradient meadow reaches of the stream (channel slope <1.0 percent) with riparian vegetation composed of grasses, sedges, and willows (Harris et al. 1992). The study area had a wide, shallow channel (mean wetted width of 8 m [26 ft.], thalweg depth of 0.5 m [1.6 ft.]) with predominantly gravel and cobble with silt in backwaters and along shore of pools.

Hubert et al. (1994) reported that over 90 percent of age-0 brown trout in the low gradient reaches of Douglas Creek were found in lateral habitats including stream margins, backwater pools, and secondary channel pools. Age-0 brown trout were most frequently found in stream margin habitats (60 percent) followed by backwater pools (33 percent), and none were found in riffle or trench pool habitats (Hubert et al. 1994). Current velocities in the lateral habitats were low, in early summer (range = 0 to 16 cm per s [0 to 0.52 ft. per s]), and 55 percent of age-0 brown trout were observed at current velocities of 0 cm per s (0 ft. per s) (Hubert et al. 1994). Depths used by age-0 brown trout in early summer ranged from 1 to 32 cm (0.4 to 12.6 inches) and velocities from 0 to 18 cm per s (0 to 0.6 ft. per s) (Harris et al. 1992). Median depth used by age-0 brown trout was 4 to 5 cm (1.6 to 2.0 inches) in early summer (Hubert et al. 1994).

Hubert et al. (1994) observed that age-0 brown trout were more frequently observed in backwater pools in June (61 percent) than in July when they were most frequently found in stream margins (80 percent). Stream flow was constant between months during the study, and the authors attributed the shift in habitat use to age-0 brown trout using a wider range of current velocities and occupying positions further from the stream edge as they grew (Hubert et al. 1994).

La Voie and Hubert (1996) investigated age-0 brown trout habitat use during late summer (mid-August to mid-September) in Douglas Creek. Three types of stream margin habitat were distinguished: backwaters, pool margins, and riffle margins. The authors expected that as they grew, age-0 brown trout would use deeper water, faster currents, larger substrates, and positions further from the shore in late summer than in early summer (La Voie and Hubert 1996).

La Voie and Hubert (1996) found that age-0 brown trout continued to use water depths in riffle and backwater habitats in late summer similar to those reported by Hubert et al. (1994) during early summer. In pool margins, age-0 brown trout moved into deeper water in August and September (La Voie and Hubert 1996). Hubert et al. (1994) had found that the median water velocity used by age-0 brown trout in June and July was 0 cm per s (0 ft. per s), whereas La Voie and Hubert (1996) found median water velocity used in late summer was 0 cm per s (0 ft. per s) in backwaters, 2 to 7 cm per s (0.07 to 0.23 ft. per s) in pool margins and 2 to 6 cm per s (0.07 to 0.20 ft. per s) in riffle margins. In late summer, age-0 brown trout distance from the shore varied among the three stream margin habitat types. Age-0 brown trout observed in riffle margins tended to be closer to the shore than those found in pool margins, and the positions of fish in backwaters were more variable (La Voie and Hubert 1996). The authors concluded that the anticipated shifts in habitat use did not occur among all habitat types. Age-0 brown trout in pools were found in deeper, faster water further from shore during late summer, whereas fish in riffle margins were found in greater current velocities but not at greater depths or further from shore (La Voie and Hubert 1996). No temporal trends in water depth, substrate use, or distance from the shore were observed for age-0 brown trout occupying backwater habitats, but there was some indication that fish used backwater areas closer to main channel currents more during late summer (La Voie and Hubert 1996).

Other researchers have reported that age-0 salmonids move into deeper, faster waters as they grow during their first summer (Kennedy and Strange 1982, Cunjak and Power 1986, Hillman et al. 1987 as referenced by La Voie and Hubert 1997), but that pattern was not observed in Douglas Creek. La Voie and Hubert (1997) found no significant difference in the lengths of age-0 brown trout captured from stream margin or main channel habitats, but they remarked that most fish greater than 66 mm (2.6 inches) in length were found in the main channel, whereas most fish less than 45 mm (1.8 inches) in length were found in stream margin

habitat, suggesting that as age-0 brown trout grew, they shifted from shallow, low current stream margin habitat into deeper waters with greater current velocities. La Voie and Hubert (1997) noted that age-0 brown trout growth "virtually ceased in late summer" in Douglas Creek, resulting from the low water temperatures of the high elevation stream (2,613 m [8,573 ft.]), and that the age-0 brown trout were smaller at the end of their first summer than sizes reported for other populations. The authors suggested that in high-elevation montane streams, age-0 brown trout might not grow large enough their first year to shift to swifter and deeper waters (La Voie and Hubert 1997).

Nehring and Anderson (1993) investigated limiting habitats of brown and rainbow trout in 11 Colorado streams of varying elevation, size, and discharge. They observed habitat preferences of more than 350 age-0 trout (both species combined) over two field seasons and developed depth and velocity habitat suitability curves for two- to four-week-old brown and rainbow trout fry (**Table 2**; Nehring and Anderson 1993).

In larger river systems, age-0 brown trout have been found to be primarily associated with margin habitat as well. In Arkansas, in several tailwaters on the White River, age-0 brown trout were typically found within 1 to 3 m (3.3 to 6.6 ft.) of the bank, at shallow depths, in low current velocities, and in close proximity to cover (Pender and Kwak 2002). Other habitat variables, such as dissolved oxygen concentration, temperature, substrate particle size, bank distance, and depth and cover distance of microhabitats, varied among sites, but all fell within or near the values generally considered suitable (Pender and Kwak 2002).

Pender and Kwak (2002) provide a detailed summary of the range of depths, current velocities, temperatures, and particularly types of cover with which age-0 brown trout were associated in the tailwaters.

Cover: Young-of-year brown trout utilize a variety of cover types. Stream substrates, aquatic vegetation, and woody debris have been found to be important cover types used by age-0 brown trout in many different systems (Hubert et al. 1994, Pender and Kwak 2002, McRae and Diana 2005). For instance, in a Wyoming stream 89% of age-0 brown trout were found associated with rocks, aquatic vegetation, or woody debris cover that provided current refuge and overhead cover (Hubert et al. 1994).

Age-0 brown trout used rocks that provided current refuge as cover most frequently (47%) in Douglas Creek, Wyoming (Hubert et al. 1994). Gravel and other larger stream substrates have been found to be primary sources of cover for age-0 and yearling brown trout in several studies (Heggenes 1988b, Griffith and Smith 1993, Hubert et al. 1994). Because brown trout spawn in areas with predominately gravel and cobble substrates, age-0 brown trout are naturally associated with larger stream substrates if they do not move far after emergence. The small age-0 brown trout are able to conceal themselves in the substrates and use the interstitial spaces as cover from predators and refuge from high flows (McRae and Diana 2005). La Voie and Hubert (1997) found age-0 brown trout 36-75 mm (1.4-3 inches) TL were frequently concealed in cobble interstices during the day and emerged at night. In tailwaters, Pender and Kwak (2002) observed age-0 trout descending into crevices in the gravel substrates as current velocity increased during periods of dam

Table 2. Normalized (0.0-1.0) frequency distribution of depth and velocity preferences of two- to four-week-old rainbow and brown trout fry in Colorado streams. Reproduced from Nehring and Anderson (1993).

Depth (cm)	Normalized frequency	Velocity (cm/s)	Normalized Frequency
0.00	0.00	0.00	1.00
3.05	0.40	3.05	0.45
6.10	1.00	6.10	0.37
9.15	1.00	9.15	0.28
12.19	1.00	12.19	0.10
15.24	1.00	15.24	0.04
18.29	0.30	18.29	0.03
21.34	0.20	21.34	0.02
24.38	0.14	24.38	0.01
27.43	0.14	27.43	0.00
30.48	0.00	30.48	0.00

water release. The ability of age-0 brown trout to use different types of substrates as cover is likely related to their size, with smaller individuals able to use smaller substrates more effectively than larger individuals. Griffith and Smith (1993) speculated age-0 brown trout were restricted to larger substrates than smaller age-0 cutthroat trout in an Idaho river.

Aquatic vegetation has been found to be an important source of cover for age-0 trout in other studies and has been positively correlated with trout densities in some systems (Kocik and Taylor (1996) and Maki-Petays et al. (1997) as referenced by McRae and Diana (2005)). DeVore and White (1978) reported 80% of age-0 brown trout used substrate, aquatic vegetation, or woody debris as concealment (as referenced by Hubert et al. 1994). Gosse and Helm (1981) found age-0 brown trout were associated with macrophyte beds and MacCrimmon et al. (1990) found the amount of macrophytes influenced the abundance of age-0 brown trout at the habitat scale (as referenced by Hubert et al. 1994). In addition to providing cover from predators, aquatic vegetation is associated with increased production of aquatic macroinvertebrates (Egglishaw and Shackley 1977), which juvenile trout prey upon (Jowett 1992 as referenced by McRae and Diana 2005). In a Michigan river and its tributaries, McRae and Diana (2005) found that percent gravel substrate and percent emergent vegetation accounted for 62 percent of the variance in densities of age-0 brown trout. McRae and Diana (2005) speculated that the decline in brown trout densities below a dam on the river could be related to the decreased occurrence of emergent vegetation below the dam and the resulting reduction in habitat available for age-0 brown trout.

In tailwaters in Arkansas, age-0 brown trout of the same size class were associated with different cover types at different sites (Pender and Kwak 2002). Age-0 brown trout cover preference appeared to vary with their size and local environmental characteristics. For instance, age-0 brown trout less than 65 mm (2.6 inches) TL were most frequently associated with woody debris at one site, cobble at another, and submersed vegetation at a third site (Pender and Kwak 2002). At the same sites in the same respective order, larger age-0 brown trout (>65 mm [2.6 inches] TL) were most frequently associated with bank vegetation at the first site, submersed vegetation at the second, and woody debris at the third site (Pender and Kwak 2002).

Vehanen et al. (2000) investigated age-0 and age-1 brown trout use of different types of cover in relation to seasonal variations in water temperature and fluctuating

flow levels in artificial flumes. Four types of cover were available to the fish: velocity cover only; velocity cover with visual isolation from other fish; velocity, visual, and overhead cover; and overhead cover alone. Experiments were conducted in late summer, winter, and early summer at water temperatures of 13.2 to 13.7 °C, 1.7 to 1.8 °C, and 14.6 to 14.9 °C, respectively.

Vehanen et al. (2000) found that brown trout cover preferences varied seasonally and suggested that the young brown trout used cover differentially in order to minimize energy expenditure and predation risk at low temperatures, to maximize foraging efficiency in summer, and to minimize energy expenditure in increased flows. The researchers reported most young brown trout aggregating in velocity shelters in winter and preferring shelters with both visual isolation and overhead cover (Vehanen et al. 2000). Young brown trout also selected lower current velocities in winter than they did in summer, suggesting energy-minimizing behavior (Vehanen et al. 2000). The authors suggested that although energy demands are reduced at low water temperatures, the burst swimming ability is also reduced; this may explain preferences for increased cover at cold temperatures (Vehanen et al. 2000). In late summer, young brown trout used cover types that only provided current refuge more than cover types that provided current refuge in addition to visual isolation or overhead cover or a combination of the three (Vehanen et al. 2000). The authors speculated that cover that only provides current refuge is most efficient during foraging and that during the summer growing season when water temperatures are higher, there is a trade-off between reduced visual contact with drift items and the protection from types of cover that provide visual isolation and overhead cover (Vehanen et al. 2000).

Young-of-year winter habitat: Several researchers have observed age-0 (YOY) salmonids using interstitial spaces in stream substrates as winter habitat. Bjornn (1971) reported that YOY of two salmonid species entered interstitial spaces when stream temperatures dropped to 4-6 °C. Rimmer et al. (1983) found that when water temperatures fell below 10 °C in autumn, the visible population of Atlantic salmon YOY decreased by 92 to 98 percent.

Griffith and Smith (1993) studied winter habitat use of age-0 brown trout and age-0 and age-1 cutthroat trout in the South Fork of the Snake River in Idaho. They found that age-0 trout of both species were restricted to shallow river margin habitat and typically remained concealed in the substrates at depths less than 0.5 m (1.6 ft.) within 1 m (3.3 ft.) of the shoreline during

the day. The researchers recounted that age-0 trout collected during electrofishing surveys were "shaded pitch black" when emerging from concealment (Griffith and Smith 1993). Cobble, around 20 cm (7.9 inches) in diameter, was the smallest substrate in which age-0 trout were found concealed. Estimates of age-0 brown trout density ranged from 0 to 0.5 fish per meter of bank and varied along the margin habitats of the study area with substrate size. The researchers speculated that age-0 cutthroat trout were able to use the interstitial spaces smaller than the spaces brown trout could use because of the former's smaller size (Griffith and Smith 1993). Greatest densities of age-0 trout were found in clean boulder bank habitats, and estimated maximum densities approached 500 fish per 100 m^2 near the end of the winter season. The authors did not include woody debris habitats in their study, but they remarked that age-0 trout density in woody debris habitats could be even greater based on other researchers finding cutthroat and brown trout at 2 to 4 times greater densities in woody debris than in boulder habitat (Schrader and Griswold 1992 as referenced by Griffith and Smith 1993).

La Voie and Hubert (1997) monitored age-0 brown trout habitat use in a mountain stream in southeastern Wyoming from later summer until late fall. Up to three days prior to ice formation in the stream, no significant change in the relative abundance of age-0 brown trout was observed in visual surveys. The researchers concluded that a shift to winter habitat had not occurred despite the decrease in the diurnal range of water temperature to 2.5 to 7.5 °C (La Voie and Hubert 1997). The authors reported that many age-0 brown trout continued to be observed at night when water temperatures were as low as 5 °C, which suggested that water temperatures were not yet low enough to force all of the age-0 brown trout in the stream into the interstitial spaces in the substrate (La Voie and Hubert 1997).

During winter in an Ontario river, age-0 brown trout used depths ranging from 30 to 63 cm, mean 46.2 cm, (11.8 to 24.8 inches, mean 18.2 inches) and 26 to 55 cm, mean 43.1 cm, (10.2 to 21.7 inches, mean 17.0 inches). Age-0 brown trout were found at mean focal velocities of 4.7 cm per s, range 1.5 to 9.5 cm per s (mean 0.15 ft. per s, range 0.05 to 0.31 ft. per s) and 2.2 cm per s, range 1.5 to 4.5 cm per s (mean 0.07 ft. per s, range 0.05 to 0.15 ft. per s), and all were "associated beneath cover" at each site (Cunjak and Power 1986). No brown trout were found overwintering beneath rocks, which the researchers thought might be related to differences in climate, temperature, discharge, and ice dynamics among systems, and the authors suggested that fish inhabiting systems with more

variable conditions in winter might remain more active and overwinter in stream substrates (Cunjak and Power 1986). The researchers also noted that in the Ontario river other taxa including cyprinids, crayfish, and frogs were seen overwintering in gravels and that competition for suitable shelter may influence juvenile brown trout behavior (Cunjak and Power 1986).

Sedimentation and ice dynamics may influence YOY trout use of stream substrates as winter cover. For instance, in systems where sediment deposition is high and ice forms along stream margins, trout were observed to use substrates located towards mid-channel areas where less deposition occurred and substrates were less embedded (Cunjak 1996). Other habitats used in winter by YOY trout may include aquatic vegetation, side channel and backwater ponds, and pools behind beaver dams (Griffith and Smith 1993, Cunjak 1996).

Juvenile habitat use

Juvenile brown trout may remain in streams, transitioning to deeper habitats as they grow (Bachman 1991), or they may move into lakes or larger rivers during their second or third year of life where they become sexually mature (Elliott 1994). Heggenes (1988b) found that yearling brown trout distribution in a Norwegian stream was negatively related to shallow habitats, less than 5 cm (2 inches) deep and positively related to habitats with depths of 10 to 25 cm (3.9 to 9.8 inches). Brown trout yearlings did not exhibit an obvious preference for water velocity except that they avoided the areas with the slowest currents (<5 cm per s [0.16 ft. per s]) (Heggenes 1988b). Yearling brown trout were associated with substrates 64 to 256 mm (2.5 to 10.0 inches) in diameter, which was not significantly different from those used by older fish (Heggenes 1988b). Yearling brown trout avoided areas with no cover and demonstrated a "slight" avoidance of habitats with the highest percentage of cover, mainly areas of undercut banks (Heggenes 1988b).

Shuler et al. (1994) found most juvenile brown trout in the Rio Grande in Colorado using similar depths (range 27 to 57 cm [10.6 to 22.4 inches]) during the day and night. Juvenile trout used slightly faster water at night, with mean current velocities of habitats used of 9 to 45 cm per s (0.3 to 1.5 ft. per s) during the day and 3 to 45 cm per s (0.1 to 1.5 ft. per s) at night, but the difference was not statistically significantly (Shuler et al. 1994). Of juvenile trout not associated with boulder structures, 89 percent used areas with natural cover during the day and 91 percent at night (Shuler et al. 1994). Juvenile trout used mid-channel

boulder clusters and natural bank cover more than other boulder structures at night than during the day, but they demonstrated a preference for wing-dams and an avoidance of single boulders at night (Shuler et al. 1994). As with adult trout, wing-dams were important to juveniles day and night and under high and low flows (Shuler et al. 1994).

In winter, Griffith and Smith (1993) did not find any age-1+ brown trout concealed in river margin substrates, indicating that juvenile brown trout may be too large to occupy those habitats by their second winter. Cunjak and Power (1986) reported that age-1+ brown trout tended to occupy deeper and faster water than age-0 brown trout in an Ontario river, and like age-0 brown trout, age-1+ fish demonstrated a preference for positions beneath cover.

Food habits

Like other trout, brown trout feed primarily on aquatic invertebrates, terrestrial insects, and small fish. The diets of brown trout have been described as "diversified," and their food habits range broadly with variation in size and age, spatial and temporal variability in food availability, behavior, and habitat characteristics (Simpson and Wallace 1982, Bachman 1991, Baxter and Stone 1995, Bridcut and Giller 1995).

Although diet variability among brown trout populations is well known and is easily attributed to differences in environments and food availability, comparisons of population feeding patterns and foraging strategies are further complicated by intra-population variability (Bridcut and Giller 1995). Bridcut and Giller (1995) examined diet variability of brown trout at different spatial and temporal scales and found significant variation in feeding patterns of brown trout over time at multiple scales: among sub-populations, between groups occupying different habitats (e.g., pools versus riffles), and among individuals. In general, the researchers found that brown trout occupying pools tended to have higher diet specialization than those predominately associated with riffles; however, over time individual brown trout displayed both feeding strategies within single habitats (Bridcut and Giller 1995). As found in other studies, seasonal differences in food availability also significantly influenced brown trout diets at the individual, habitat group, and sub-population levels. The researchers suggested that intraspecific dominance hierarchies (see Social patterns for spacing section) play a role in the diverse diets of individual brown trout within a population. Specifically, competition among brown trout for the optimal

diet results in greater variability among individuals (Bridcut and Giller 1995). For instance, dominant fish successfully compete for optimal feeding positions and consequently better access to food resources, whereas the diets of subordinate fish will be more influenced by the degree of competition arising from spatial and temporal variability in food availability (Bridcut and Giller 1995).

During the first two years of life, brown trout feed primarily on aquatic invertebrates and small fish of various species (Simpson and Wallace 1982). Recently emerged fry feed on zooplankton and other small invertebrates (Bachman 1991). As age-0 brown trout develop and grow, and are better able to maintain position in faster currents, they may move into deeper and swifter waters and begin to feed on terrestrial and aquatic insects (Bachman 1991).

Detailed information regarding the feeding habits of age-0 brown trout from research conducted in a mountain stream in southwestern Wyoming follows. Age-0 brown trout were not found to move away from stream margin habitats into deeper and faster waters by the end of their first summer (La Voie and Hubert 1994). However, in the study stream, drifting invertebrates were available in greater densities in the stream margin habitats used by age-0 trout than in the main channel (La Voie and Hubert 1994). Feeding rates of age-0 brown trout generally coincided with variations in drift densities, with the abundance of food items in fish stomachs increasing with the density of drifting invertebrates after sunset (La Voie and Hubert 1994). In August, diel variation in the density of drifting invertebrates was not evident, and similarly no variation in the abundance of invertebrates in age-0 brown trout stomachs was observed throughout the diel cycle (La Voie and Hubert 1994). In September, densities of drifting invertebrates increased after sunset, and an associated increase in the abundance of invertebrates in age-0 brown trout stomachs was observed (La Voie and Hubert 1994). The researchers concluded that age-0 brown trout fed throughout the day and likely increased their feeding after dark in response to increases in the density of drifting invertebrates (La Voie and Hubert 1994).

Age-0 brown trout displayed preferences for particular food items, as the composition of drifting invertebrates and those found in their stomachs were not strongly related and in general there was little apparent relation between the two (La Voie and Hubert 1994). In August, age-0 brown trout had positive electivity indices for Ephemeroptera during each of six sampling periods

throughout a diel cycle (La Voie and Hubert 1994). In August, age-0 brown trout additionally had a positive electivity index for zooplankton at night (La Voie and Hubert 1994). No other invertebrate groups were found to have positive electivity indices in August (La Voie and Hubert 1994). In September, positive electivity indices were observed for several groups including zooplankton and Ephemeroptera, which remained important, but Chironomidae larvae and adults also had positive electivity indices coinciding with an increase in their availability in the drift (La Voie and Hubert 1994). Other food items available to age-0 brown trout included Trichoptera and Plecoptera larvae, Elmidae larvae and adults, and terrestrial insects.

La Voie and Hubert (1992) found that the mean lengths of the invertebrates in age-0 brown trout stomachs increased with trout size class (size classes spanned 21 to 65 mm [0.8 to 2.6 inches] TL in 5 mm [0.2 inch] increments) and that there was low variability in the size of prey taken within each length group, indicating that age-0 brown trout are selective for particular sizes of prey (La Voie and Hubert 1992). The smallest age-0 brown trout (21 to 25 mm [0.8 to 1 inch] TL), consumed primarily zooplankton followed by Diptera (mostly Chironomidae larvae) (La Voie and Hubert 1992). Age-0 brown trout 26 to 35 mm [1 to 1.4 inches] TL) consumed primarily Diptera, particularly Chironomidae larvae and pupae and Simulidae larvae, and fish larger than 36 mm (1.4 inches) TL consumed primarily Ephemeroptera nymphs (La Voie and Hubert 1992).

La Voie and Hubert (1992) noted that the study area was downstream of an impoundment, which had likely increased the availability of zooplankton in the stream. Other researchers have found that zooplankton is an important component of age-0 brown trout diets downstream of lakes and reservoirs (Nilsson 1957 and Crisp et al. 1978 as referenced by La Voie and Hubert 1992). In streams without lentic waters upstream, other researchers had found diets of smaller age-0 brown trout (<26 mm [1 inch] TL) are composed mainly of Chironomidae larvae (McCormack 1962 as referenced by La Voie and Hubert 1992). The authors speculated that the increased availability of zooplankton in their study area may have allowed the smallest age-0 brown trout to utilize smaller prey than typically available in an un-impounded stream, and consequently the variation in size of prey with size of age-0 trout may have been more apparent in that stream than would be expected in others (La Voie and Hubert 1992).

Pender and Kwak (2002) reported on the food habits of age-0 brown trout in several tailwaters of an Arkansas river. Differences in invertebrate food availability were found among the different tailwater sites with benthic invertebrate densities varying significantly between sites. Age-0 brown trout feeding intensity, measured by stomach fullness, was similar among sites, and at all sites, they displayed strong positive selection for Diptera of various life stages, and particularly for Chironomidae larvae (Pender and Kwak 2002). Large age-0 brown trout additionally positively selected Isopoda, Amphipoda, and Gastropoda at several locations. Age-0 brown trout expressed strong negative selection for Rotifera, Oligochaeta, and Hydroida, but the authors noted that those items might have been digested more rapidly and been underrepresented in the samples (Pender and Kwak 2002).

Aquatic invertebrates are the primary component of diets of smaller adult brown trout, but larger adults are thought to incorporate more fish in their diets. Brown trout begin incorporating fish into their diets around 130 to 160 mm (5.1 to 6.3 inches) TL (Mittlebach and Persson 1998, Museth et al. 2003), with the largest adults switching to predominately piscivorous diets at lengths around 350 mm (13.8 inches) (Clapp et al. 1990). Lake-inhabiting brown trout in Europe were reported to start feeding on fish at 130 to 160 mm (5.1 to 6.3 inches) TL, around age 2 or older, but fish comprised less than 10 percent of their diet at that size range (L'Abee-Lund et al. 1992 as referenced by Mittlebach and Persson 1998). In a Michigan stream, the stomachs of brown trout 76 to 152 mm (3 to 6 inches) in length contained 100 percent invertebrates whereas stomachs of 152 to 254 mm (6 to 10 inches) long brown trout contained 93 percent invertebrates and 7 percent fish by volume (Stauffer 1977 as referenced by Clapp et al. 1990). Another study in Michigan found that diets of brown trout larger than 305 mm (12 inches) consisted of 25 percent invertebrates and 75 percent fish by weight (Alexander 1977 referenced by Clapp et al. 1990).

However, water fertility can influence food availability and consequently fish diets (Kwak and Pender 2002). In very productive streams, resident brown trout have been observed to feed mainly on aquatic insects (Bachman 1991). In a productive stream in Pennsylvania, the diets of all size classes of brown trout (size range was 100 to 410 mm [4 to 16 inches] TL) were almost entirely composed of insects from the drift, followed by crayfish and smaller species of fish such as sculpin and dace (Bachman 1991).

In other systems, different food items may have greater importance in brown trout diets (Bachman 1991). For instance, in streams with abundant aquatic vegetation, crustaceans such as isopods and amphipods may be as or more important than insects (Bachman 1991). In some systems, snails and mollusks have been found to comprise a large component of brown trout diets (Bachman 1991). Other animals have also been found to be a part of brown trout diets, including leeches, frogs, salamanders, and rodents (Bachman 1991).

Brown trout can be opportunistic feeders and more general in their food habitats or they can tend toward specialization. Differences between specialist and generalist food habitats among brown trout have been attributed to differences in genetics and environmental factors experienced by populations (Bachman 1991). With the exception of extremely productive systems that produce dense populations of aquatic invertebrates, most larger brown trout (>310 mm [12.2 inches] TL) inhabiting larger streams, rivers, and lakes are thought to switch from a diet composed predominately of invertebrates to one comprised mainly of fish and crayfish (Bachman 1991).

In a Rocky Mountain stream in southwestern Colorado, Allan (1978) found that brown trout ranging in length from 68 to 295 mm (2.7 to 11.6 inches) (mean = 153 mm [6 inches] TL) and weights from 2.7 to 253.0 g (mean = 35 g) primarily fed on aquatic insects. Brown trout diets included Ephemeroptera, Plecoptera, Trichoptera, Diptera, and Coleoptera as well as terrestrial invertebrates and non-insect aquatic invertebrates such as Oligochaeta and Acari. Drifting invertebrates are thought to be more visible to salmonids, and brown trout were found to feed more upon the surface drift of emergent and terrestrial insects (Allan 1978). Allan (1978) reported that brown trout fed most heavily on the Ephemeroptera prey in the drift, but in a lesser proportion than expected based on the availability of Ephemeroptera in the drift and benthos. Brown trout consumption of Ephemeroptera was related to their diel availability, comprising 66.7 percent of items in brown trout stomachs at night when they were most abundant in the drift. Brown trout also consumed prey items from the benthos (including taxa that were considered "relatively large but rare"), emerging aquatic insects, and terrestrial items more frequently than their availability from the drift and benthos. Allan (1978) also compared the mean size of a species of mayfly present in the drift with the mean size of individuals consumed by brown trout and found brown trout selecting significantly larger individual

mayflies. Brown trout stomachs contained food items throughout the 24-hour cycle, but the number of food items was greatest in the afternoon (1300, 1700 hours) and evening (1900, 2300 hours) (Allan 1978).

Kaeding and Kaya (1978) investigated differences in trout diets and growth between geothermally altered and unaltered sections of the Firehole River in Yellowstone National Park. In the geothermally altered section, stream productivity and invertebrate abundance was greater than in unaltered sections upstream. In the unaltered upstream section, brown trout fed predominately on the most numerically abundant taxa: Trichoptera, followed by Plecoptera, Ephemeroptera, Coleoptera, and Diptera (Kaeding and Kaya 1978). In the warmer and more productive geothermally-altered stream section, brown trout fed primarily on the numerically dominant food items: Diptera, snails (*Physa* sp.), Ephemeroptera, and to a lesser extent on Trichoptera, Odonata, and Amphipoda (Kaeding and Kaya 1978). Plant matter was also commonly found in brown trout stomachs from the geothermally altered stream section (Kaeding and Kaya 1978). Fish were infrequently consumed by trout in either section of the river (despite trout in the altered section attaining lengths exceeding 300 mm [11.8 inches] in their third year of life); however, trout eggs were commonly found in the stomach contents of trout in fall and early winter (Kaeding and Kaya 1978).

Marrin and Erman (1982) reported on the summer diets of brown trout in a subalpine reservoir in California. They found that non-piscivorous brown trout, generally less than 300 mm (11.8 inches) TL, fed primarily on limnetic invertebrates. Food items found in non-piscivorous brown trout stomachs included Daphnia, Chironomidae larva, Diptera pupae, and other aquatic and terrestrial insects as well as detritus, algae, and aquatic plants (Marrin and Erman 1982). Larger brown trout and rainbow trout in the reservoir became piscivorous around 300 mm (11.8 inches) TL and fed primarily on fish and crayfish and a lesser amount on Chironomidae larvae and Diptera pupae (Marrin and Erman 1982). Detritus and algae or aquatic plants were also found in the stomachs of the piscivorous trout (Marrin and Erman 1982).

Brown trout appetite, measured as voluntary feeding, has been found to vary with water temperature in experimental studies (Elliott 1975). Brown trout appetite was greatest between temperatures of 13.3 and 18.4 °C, decreased rapidly at temperatures above 18.4 °C, and declined slowly at temperatures from 13.3 to 6.6 °C (Elliott 1975). Brown trout feeding was described as

erratic at water temperatures below 6 °C and above 19 °C (Elliott 1975). Based on the experimental results coupled with a previously derived relationship for daily caloric requirements, Elliott (1975) suggested that at water temperatures between 3.8 and 18.4 °C, brown trout may be able to meet metabolic demands and daily maintenance requirements by feeding to satiation in one meal, but that above temperatures of 19 °C trout would lose weight due to a decreased appetite coupled with increased activity and metabolic rates.

Elliott (1975) also found that trout weight affected the time to satiation, with large brown trout requiring more time to reach satiation. The brown trout in the experiment ranged in weight from 8 to 358 g, and the larger fish often required more than 60 minutes of feeding to be satiated. Elliott (1975) found that brown trout of all sizes required 1 to 5 seconds to "handle" food (obtain and swallow), and the success rate of capture ranged from 1 to 30 food items per minute. The size of the food item and of the trout did not affect the handling time or the success rate, and as a result larger trout (>100 g [0.22 lbs.]) that required more food also required more time to satiate their appetites (Elliott 1975). Elliott (1975) also noted that different caloric and nutritional composition of different food items, coupled with their variable digestibility, affects the relationship between trout weight, temperature, time to satiation, and ability to meet daily caloric requirements.

Bachman (1984) observed naturalized brown trout feeding from the stream surface, water column, and substrates in a Pennsylvania stream. Bachman (1984) reported that brown trout took only one second to intercept items in the drift or to capture organisms on the bottom from their stationary foraging sites. However, during a surface feed, it took the fish longer, about 6 seconds, to return to their foraging site because the current swept the fish farther downstream (Bachman 1984). Bachman (1984) assessed the energetic costs of brown trout feeding from the surface versus the water column or substrate and concluded that the energetic costs of feeding from the surface were greater. However, Bachman (1984) also observed that when brown trout fed from the surface while maintaining position in the current, their feeding rates increased.

The metabolic rate of fish in the wild is considered to be greater than metabolic rates of fish in laboratory conditions, and investigators have used a value twice that of the metabolic demand at a resting state to represent the requirements of brown trout in the wild (Elliott 1975). With all the variations possible (e.g., nutritional values of different food items, fish size,

energy requirements at different water temperatures and current velocities), estimating brown trout dietary requirements is considered difficult at best. Elliott (1975) suggested that in the wild, brown trout appetite might in part be regulated by the ration required for daily metabolic demands and maintenance, so that trout eat enough to satisfy their energy demands.

Winter food habits: Brown trout are thought to feed less actively in winter than during other times of year when water temperatures and metabolic demands are greater. Elliott (1975) found that brown trout appetites decreased and feeding activity became erratic at water temperatures below 6 °C. Researchers have suggested that in winter, stream fish feed primarily to sustain the minimum level of metabolic activity required considering the reduction of metabolic rates in cold water and the negligible growth that occurs during the season (Cunjak 1996).

However, other researchers have found that brown trout feed actively in winter, and aquatic invertebrate abundance and biomass in streams can be relatively high in winter, especially in streams with winter-growing species, as comparatively fewer aquatic insects emerge in winter and therefore remain in the stream at various stages of development (Maciolek and Needham 1952, Cunjak 1996). Maciolek and Needham (1952) investigated the availability of invertebrates and the diets of naturalized brown trout during winter in a California mountain stream, and they found that benthic invertebrate availability remained high and brown trout continued to feed actively. Several hatches of aquatic invertebrates were observed during a winter that was considered warmer than usual when water temperatures were 4 °C (40 °F) or greater (Maciolek and Needham 1952).

Maciolek and Needham (1952) reported that black flies (Simuliidae) and midges (Chironomidae) hatched throughout the winter whereas stoneflies of the genera *Nemoura* and *Capnia* hatched in late January in abundance and mayflies (Ephemeroptera) and micro-caddis adults (Hydroptilidae) began emerging in late March. Terrestrial Dipterans and Lepidopterans were also found in the stream samples during the study (Maciolek and Needham 1952). Aquatic Oligochaetes were the most abundant taxon during the winter and comprised about 10 percent of the drift and benthic food available to trout (Maciolek and Needham 1952). However, relative abundances of insect orders were found to vary considerably among seasons and years. For instance, Maciolek and Needham (1952) compared invertebrate samples collected in the winter of 1951

with some collected in February of 1942, and they found notable differences in relative abundance of different insect orders, particularly for Ephemeroptera, Trichoptera, Diptera, Coleoptera, and Oligochaeta.

Maciolek and Needham (1952) reported "the greatest number of drifting foods was always available during periods of peak flow" associated with anchor ice break up from late morning to early afternoon, and brown trout were observed feeding only during and following peak flows. The researchers found some correlation between the availability of organisms (from drift and benthic samples combined) and percent composition by number in stomach contents, but comparisons based on percentages by weight had little correlation (Maciolek and Needham 1952). The naturalized brown trout were found to ingest fewer but larger invertebrates than the introduced hatchery rainbow trout in the stream (Maciolek and Needham 1952). Brown trout consumed proportionately more caddis fly larvae, whereas rainbow trout consumed proportionately more midge and black fly larvae (Maciolek and Needham 1952). Over the entire winter period, Dipterans represented only 12.4 percent of the total available benthic invertebrates, but they were consumed in greater proportions by both rainbow trout (54.9 percent) and brown trout (31.6 percent) (Maciolek and Needham 1952). The researchers compared trout feeding habits during periods when the stream was "ice-laden" versus those for the entire winter on average and found that more Trichoptera, Ephemeroptera, and Plecoptera were consumed by trout during cold periods with subsurface ice accumulation (frazil and anchor ice) whereas more Diptera, Coleoptera, and Oligochates were ingested over the entire course of the winter (Maciolek and Needham 1952). One brown and one rainbow trout had eyed trout eggs in their stomachs; the researchers suggested that anchor ice formation during extremely cold weather likely disturbed the spawning gravels and led to the release of the eggs into the current (Maciolek and Needham 1952). The researchers believed that the rarity of trout eggs in trout stomachs indicated that anchor ice caused minimal egg disturbance, but they also noted the winter of 1951 was considered relatively mild. The researchers also reported finding one 610 mm (24 inches) long female brown trout that had eaten another trout about 152 mm (6 inches) long (Maciolek and Needham 1952).

Maciolek and Needham (1952) did not specify species, but reported digestive rates of trout that were force fed mayfly and stonefly nymphs and Oligochates and returned to a live car in the stream. At least 50 percent of each type of food item was digested after 14 hours at water temperatures between 0 and 2 °C (32 and 35 °F) (Maciolek and Needham 1952). The researchers noted that trout had been observed feeding at colder temperatures in the stream and were even caught by hook and line in ice-laden water at 0 °C (Maciolek and Needham 1952). Furthermore, of 100 specimens of trout, only four in total (three of which were brown trout) had empty or trace amounts of food in their stomachs (Maciolek and Needham 1952). The researchers reported that very few trout seen or captured during the winter appeared to be in poor condition and that only seven of the 53 dead trout found in their study section between November and April were naturalized brown trout, the rest were hatchery rainbow trout (Maciolek and Needham 1952). Based on their observations, Maciolek and Needham (1952) concluded that low water temperatures did not limit feeding of trout in the mountain stream in winter.

Breeding biology

Brown trout are iteroparous; spawning only occurs during the breeding season each year, but individuals can spawn several times during their life. The proportion of repeat spawners in a population of brown trout likely varies among populations and years. For instance, the proportion of repeat spawners in a year varied from 5 to 69 percent for several populations of sea-run brown trout in Norway (Elliott 1994). In some populations of stream-resident brown trout, individuals may spawn each year once they mature, but because stream residents typically have shorter life spans (most around five years), they still may only have the opportunity to spawn a few times during their life.

Brown trout prefer to spawn in fast-water sections of streams with gravel substrates (see Spawning habitat section). Lake and river-dwelling brown trout will usually move upstream into tributaries to spawn (Simpson and Wallace 1982, Elliott 1994). However, if no suitable tributaries are available, brown trout in lakes can spawn along rocky shores (Elliott 1994).

Brown trout, like other salmonids, are brood hiders and bury their eggs in the substrate (Moyle and Cech 2000). Females excavate a depression by swimming on their sides and stirring up the substrate with their tails (Elliott 1994, Behnke 2002). The excavated areas and the accompanying mound of displaced substrates downstream are usually oval-shaped and are called redds. Redd construction may occur over a period of several days as the female enlarges the redd. Female brown trout have been observed "probing" the excavated depression (pit) with their anal fin, and the

behavior has been suggested to be a female's way of assessing the readiness of the redd (Bachman 1991).

Redd preparation gains the attention of males that compete to fertilize the eggs (Behnke 2002). A number of males may compete for dominance prior to spawning, with one male chasing away competitors, or a number of males may court a female simultaneously (Bachman 1991, Behnke 2002). Sometimes a single male attends a female, and both fish protect the redd site during its preparation (Simpson and Wallace 1982), with the male guarding the redd site while the female periodically rests (Bachman 1991). Jack males, small-bodied males that sneak into redds to release their sperm simultaneously with a larger male that is mating with a female, are common among brown trout (Elliott 1994, Moyle and Cech 2000). Often jack males are stream residents that sneak in on mating pairs of larger lake, river, or sea-run brown trout that have migrated into a stream to spawn (Elliott 1994).

During the spawning act, the female brown trout presses her anal fins to the substrate releasing her eggs over the depression while the male(s) close alongside the female shed their sperm (Bachman 1991, Elliott 1994). The female then moves a little upstream and digs another depression, which displaces the substrate downstream covering the eggs just deposited (Elliott 1994). The female may lay more eggs in that depression and repeat the spawning process several times, each time moving slightly upstream to bury the deposited eggs. A single redd may contain several such "egg pockets" within a mound of displaced substrate, which is called the tailspill (Elliott 1994).

Brown trout redds in a stream in the Medicine Bow National Forest of southeastern Wyoming were described as follows by Grost et al. (1991). Average redd size was 150 cm (59 inches) in length (range = 70 to 259 cm [27 to 102 inches]). Eggs were most frequently found in the front section of the tailspill, but eggs were found throughout the redds, with most redds having multiple egg pockets. Substrate composition in the egg pockets was correlated with substrates outside of redds, indicating that the composition of the streambed affects the egg pocket composition. The researchers found that substrate composition in the egg pockets of brown trout redds had a greater frequency of occurrence of large particles (>50 mm [2 inches]) than other locations within the redd, suggesting that larger particles may be important in egg pocket structure and are potentially sought by brown trout. Substrate samples of redds revealed that brown trout removed particles less than 6.3 mm (0.25 inch) in diameter from egg pockets and particles less than 3.4 mm (0.13 inch) in diameter from tailspills during redd construction.

Depth of egg burial has been positively correlated with female length in many populations of brown trout (Elliott 1994). Mean egg depth of a population of small-bodied stream resident brown trout was 4 cm (1.6 inches) (Elliott 1994). In contrast, mean egg depth of a population of large-bodied sea-run brown trout was 17.5 cm (6.9 inches) (Elliott 1994). Average depth of eggs in brown trout redds in the Medicine Bow Mountains of Wyoming was consistent with that reported for brown trout of similar size in Great Britain (Grost et al. 1991). Grost et al. (1991) found eggs of moderately-sized female brown trout (20 to 40 cm [8 to 16 inches] TL) buried between 2 and 23 cm (0.8 and 9.0 inches) below the substrate surface, but most frequently they were found 9 to 12 cm (3.5 to 4.7 inches) deep. Eggs buried more deeply are thought to be less susceptible to washout by spates (Elliott 1994), and they may be less susceptible to disturbance by anchor-ice dynamics (Maciolek and Needham 1952). All nests, regardless of depth, require adequate water flow through the eggs to ensure adequate oxygen and removal of metabolic products, such as ammonia, or egg mortality may be increased (Elliott 1994).

Redd superimposition, the construction of a redd over an existing redd, has been observed in several studies of brown trout (Grost and Hubert 1990, Beard and Carline 1991, Essington et al. 1998). Redd superimposition by brook and brown trout in some streams has been attributed to high densities of fish on spawning grounds and limited availability of suitable habitat (Essington et al. 1998). Beard and Carline (1991) observed brown trout redd superimposition rates of 50 to 90 percent in a Pennsylvania stream, and they attributed this to the limited availability of high quality spawning habitat (Essington et al. 1998). Curry and Noakes (1995) attributed the high rate of redd superimposition they observed among spawning brook trout to high population density (Essington et al. 1998). In a southeastern Wyoming mountain stream, Grost and Hubert (1990) estimated brown trout redd superimposition rates of 20 to 30 percent, indicating that spawning habitat was not severely limited.

Essington et al. (1998) suggested that other factors may influence redd superimposition rates among brook and brown trout populations. In a Minnesota stream, the researchers observed a redd superimposition rate of 34 percent among female brown trout, but neither female abundance nor habitat availability were significantly correlated with redd superimposition (Essington et

al. 1998). Essington et al. (1998) found that female brook trout demonstrated a preference for spawning on existing redd sites in a field experiment. The experiment consisted of observing the redd site selections of female brook trout returning to the spawning ground after having been disturbed during the initial stages of redd construction. Researchers denied the female brook trout access to the redds they had initiated by covering them with cobbles, but redds constructed by other females and artificial redds constructed by the researchers were available to the returning females. Of five returning female brook trout, three selected an existing natural redd site, and one selected an artificially constructed redd; only one of the five females initiated redd construction on an unused site (Essington et al. 1998). Essington et al. (1998) concluded that brook trout females exhibit some preference for spawning on existing redd sites. The researchers suggested that the presence of an existing redd made a site more attractive for spawning, possibly because existing redds are easier to excavate (reducing energetic costs), repeated use of redds removes more sediment and improves embryo survival, or because redd superimposition destroys the eggs of competitors (Essington et al. 1998).

Spawning season

The timing of the brown trout spawning period is related to photoperiod and water temperature and varies with latitude and elevation across their range (Elliott 1994). Spawning periods in the Northern Hemisphere have been documented to occur from October to March (Elliott 1994). Brown trout spawning in North America tends to occur sometime between late summer and early winter, typically when water temperatures decrease to around 7 °C (45 °F) and the days begin to shorten (Behnke 2002). In the western United States, brown trout spawn in fall, usually from October through December (Simpson and Wallace 1982).

In the Medicine Bow Mountains of southeastern Wyoming, brown trout spawned in October at elevations ranging from 2,700 to 3,100 m (8,858 to 10,171 ft.) above mean sea level (MSL) (Grost et al. 1991). In the tailwaters of the White River in Arkansas, at a lower latitude and elevation, brown trout spawning season began in mid-October and lasted through late November (Pender and Kwak 2002). Spawning periods of brown trout inhabiting cold-water sections of a geothermally influenced stream in Yellowstone National Park were not discernibly different from spawning periods of brown trout found in a warm water section; however, the brown trout inhabiting the warm water section of the stream had much lower reproductive success (Kaya 1977).

In Wisconsin, notable differences in spawning timing were observed between stocked and naturalized populations of brown trout (Stefanik and Sandheinrich 1999). The median date of redd formation (date by which 50 percent of the redds observed during the spawning period had been constructed) was 10 days earlier for stocked than for naturalized brown trout (Stefanik and Sandheinrich 1999). Hatchery-reared salmonids have been known to exhibit earlier spawning timing due to selection in the hatchery environment. For instance, in the Wisconsin study, the timing of brown trout spawning in one hatchery occurred one month earlier than that of naturalized populations in local streams due to exposure to an artificial photoperiod (Stefanik and Sandheinrich 1999). Whether the brown trout stocked are hatchery reared from wild fish or hatchery reared from hatchery brood stocks may influence the spawning timing of stocked fish in streams as spawning timing is considered a heritable trait in salmonids (Stefanik and Sandheinrich 1999). In streams with naturalized populations of brown trout that are also stocked, the distribution of spawning activity during the breeding season can be bimodal and may reflect differences in spawning timing between the two groups (Stefanik and Sandheinrich 1999). Stefanik and Sandheinrich (1999) observed single peaks in brown trout spawning activity in streams that had not been stocked in at least six years, and they suggested that the spawning period of stocked fish may shift towards that of naturalized populations over time.

Autumn low flows and drought conditions can influence spawning timing of lake and river-inhabiting brown trout, which may congregate at the mouths of tributaries awaiting flow increases to migrate upstream to spawning grounds (Bachman 1991). If low flows persist into the spawning season, trout may move all at once into a stream to spawn after an increase in flow (such as from a heavy rain), and the breeding period may only last a few days rather than several weeks (Bachman 1991).

Incubation period

The rate of brown trout egg development is inversely related to water temperature, with longer incubation periods required at cooler water temperatures (Stonecypher 1992, Stefanik and Sandheinrich 1999). The temperature range for brown trout embryo development is thought to be between 1.4 to 15.0 °C

(Humpesch 1985 as referenced by Stonecypher 1992) although the low end of the range may be closer to 0 °C (Elliott 1994). Typical incubation periods vary across the range of brown trout with variations in water temperature regimes. In Idaho, brown trout eggs develop and hatch in a period of approximately two to four months (Simpson and Wallace 1982). In a mountain stream in California, brown trout reportedly spawn in November and December, and eggs begin to hatch in early January, but peak emergence of fry does not occur until May and June (Jenkins et al. 1999). Brown trout eggs fertilized in October in a mountain stream in southeastern Wyoming (stream elevation ranged from 2,700 to 3,100 m [8,858 to 10,171 ft.] above MSL) were reported to have not yet hatched during redd sampling in April (Grost et al. 1991). In tailwaters of the White River in Arkansas where brown trout spawned in October and November, fry emergence began in late February, one of the earliest emergence timings reported for brown trout in North America (Pender and Kwak 2002).

In Montana, brown trout fry emergence timing and water temperatures during the incubation period were monitored in two tributaries of the upper Clarks Fork River (Reiser et al. 1998). In late November, water temperatures were 3.2 °C at one site and 0.1 °C at the other (Reiser et al. 1998). From late November until March, water temperatures rarely exceed 2.5 °C, and from December to late February, temperatures were often close to 0 °C (Reiser et al. 1998). In early March, water temperatures began increasing in one stream from 1.8 to 9.2 °C by the first week in April. At the other stream site, water temperatures increased from 0.9 to 5.5 °C over the same period (Reiser et al. 1998). Fry first emerged from the colder site during the last days of April when water temperatures were about 7 °C, whereas at the site with warmer waters, fry emerged weeks earlier. Based on brown trout spawning in late October to early November in that system, an estimated 600 thermal units were required for brown trout fry emergence to commence (1 Thermal unit (TU) = 1 °C above freezing (0 °C) for a period of 24 hours) (Reiser et al. 1998).

Embody (1934) reported that brown trout egg incubation periods to 50 percent hatch ranged from 34 to 148 days at mean water temperatures ranging from a high of 11.24 °C to a low of 1.89 °C, respectively. Stonecypher (1992) investigated the relative time required for brown trout embryos to reach the "eyed" stage at three different water temperatures (2, 4, and 7 °C) and at one of four different acclimation rates. The brown trout used in the study were from Soda

Lake, located near Pinedale, Wyoming, and they were spawned in late October (Stonecypher 1992). Brown trout incubated at 7 °C reached the eyed stage in a mean period of 35 days, those incubated at 4 °C reached the eyed stage in 75 days on average, and those held at 2 °C developed to the eyed stage in about 115 days on average.

Crisp (1981) compared different models of the relationship between water temperature and incubation rates for brown trout (using the data published Embody (1934)), but also used the models to extrapolate incubation periods at the lower temperatures of 0 °C and 1 °C. Although the extrapolation to lower temperatures was acknowledged as not statistically sound, Crisp (1981) believed that it was worthwhile considering the paucity of available data on the influence of near zero temperatures on salmonid incubation rates, despite the exposure of eggs of fall/winter spawners to low temperatures in the wild. By extrapolating brown trout egg incubation temperatures to 1 °C and 0 °C, Crisp (1981) found that the incubation period of brown trout eggs increased by weeks; from about 151 days at a mean temperature of 2 °C to 178 to 179 days at a mean temperature of 1 °C and 211 to 213 days at a mean temperature of 0 °C.

However, Crisp (1981) noted that the incubation periods of salmonid eggs kept at constant temperatures were longer (eggs developed slower) than those of eggs kept at ambient temperatures that fluctuated about a mean consistent with the constant temperature. Crisp (1981) commented on the need for more data on hatching times at lower water temperatures as well as determination of the relationship between temperatures and mortality rates. Crisp (1981) reported that incubation periods could vary at least ±10 percent from the mean within a species resulting from factors such as variations in eggs (both from a single female and among females) and water temperature fluctuations.

In addition to stream water temperature regimes and differences among eggs, other factors may influence brown trout embryo development rates. Young et al. (1990) found that as geometric mean particle size of substrates in egg pockets were reduced, the peak of brown trout fry emergence occurred earlier, but the duration of the emergence period was prolonged. Young et al. (1990) suggested that substrate composition in egg pockets may influence aspects of embryo development and emergence timing.

Hansen (1975) suggested that the variability in the hatching dates of brown trout embryos in a

Michigan stream resulted from the high variability in water temperatures among and within redd sites resulting from the spatially variable mixing of ground and surface waters in the streambed. Water temperatures of the redds ranged from 0 to 8 °C, and eggs survived in all redds (Hansen 1975). Redds located in areas of the streambed without groundwater inflow were colder, and water temperatures within the redds closely tracked the temperature fluctuations of the surface water (Hansen 1975). Redds in streambed zones with greater groundwater inflows had consistently higher and less variable temperatures, and eggs hatched earlier (Hansen 1975). Hansen (1975) speculated that the variability in hatching dates within and among redds may benefit the population by ensuring different dates of emergence and therefore minimizing the adverse impacts of stochastic events that may occur during the fry emergence period.

Fertility and survivorship

The reproductive success rate of brown trout in terms of the number of young surviving to reproduce is low. Although brown trout have high fecundity and produce large numbers of eggs, their offspring experience high mortality rates, particularly during the early life stages. In general, survivorship and fertility rates for fish are inversely related to fecundity, i.e. fishes with high fecundity tend to have low fertility (Moyle and Cech 2000).

In brief, many factors influence the reproductive success of brown trout populations, and survivorship rates vary greatly among populations and years. Spawning success can be diminished by factors that influence the fertility of sexually mature adults in addition to environmental conditions (e.g., flow fluctuations, lack of suitable habitat). Developing embryos receive some protection by being buried in stream substrates, but embryos remain susceptible to adverse environmental conditions such as redd dewatering, sedimentation, and predation. Brown trout larvae remain in the redds for several weeks after hatching as they continue to develop. Larvae in the redds are vulnerable to the same threats as eggs, but additional mortality occurs from the failure of some individuals to transition from endogenous feeding on yolks to exogenous feeding on live prey. Mortality rates are thought to be particularly high during the few weeks after brown trout fry emerge from redds. For instance, during the post-emergence period, survivorship rates as low as 3 percent have been reported for brown trout (Pender and Kwak 2002). Mortality during the post-emergence period is caused primarily by starvation and predation. As survivors grow, mortality rates decline

significantly. Some researchers have suggested that survivorship during the post-emergence period has the greatest influence on brown trout yearling recruitment and therefore year-class strength in subsequent years (Elliott 1994). Other researchers consider the period from egg deposition up to emergence as the more critical period in salmonid life history (McNeil and Ahnell 1964 as referenced by Pender and Kwak 2002). The specific stage during which most mortalities occur may differ among populations, systems, and years with variations in environmental and other conditions. The mortality rate of brown trout during the first year influences yearling recruitment and affects the age structure of brown trout populations.

The following sections describe, in detail, factors that have been found to influence the potential reproductive success of brown trout, including the fecundity of individuals and populations and factors affecting spawning success. Research on the relationship between brown trout female size and fecundity is presented in greater detail in the Population demography section. Brown trout survival from the incubating embryo stage through their first year are discussed under the heading Ecological influences on survival and reproduction in the Population demography section.

Fecundity: Fecundity, the number of eggs in the ovaries of a female fish, is the most commonly used measure of reproductive potential in fisheries since it is relatively easy to measure (Moyle and Cech 2000). Many factors can affect fecundity, and differences in fecundity among brown trout populations have been variously attributed to variations in genetic stock, growth rates, food availability, stream fertility, metal concentrations, and other environmental factors such climate (McFadden et al. 1965, Bagenal 1969b, Lobon-Cervia et al. 1997, Jonsson and Jonsson 1999, Pender and Kwak 2002).

In general, fecundity tends to increase with fish size, with larger fish producing more eggs than smaller fish (both in absolute numbers of eggs produced and relative to body size), indicating that the energetic investment in egg production is greater in larger members of the species (Moyle and Cech 2000). The exponential relationship between size and fecundity in females is especially true for species like brown trout that spawn just once a year and produce large numbers of eggs (Moyle and Cech 2000). In contrast, the reproductive potential of male fish usually increases linearly with size throughout its life.

Many researchers have found a relationship between the size, age, and condition of female brown trout and the number of eggs produced (Elliott 1994). However, the relationship between the size of eggs produced by a female and female size is variable in brown trout. A positive correlation has been found between the size of the egg and the size of the fry produced, and because larger fry are thought to have a survival advantage, there has been much interest in the relationship between the number of eggs produced by a female and the mean size of eggs produced (Bagenal 1969a, Ojanguren et al. 1996). The influence of female size, age, and condition on fecundity and egg size has been investigated throughout the native and introduced range of brown trout (McFadden et al. 1965, Taube 1976, Bagenal 1969b, Lobon-Cervia et al. 1997, Jonsson and Jonsson 1999).

Several researchers have found that larger brown trout females tend to produce more and typically larger eggs (Taube 1976, Elliott 1994, Ojanguren et al. 1996). For instance, in a Michigan population, Taube (1976) found that fecundity varied greatly among females of similar sizes and ages, but still found that the egg number was positively correlated with both female size and age. Taube (1976) also found a positive correlation between the female's size and age and the mean size of the eggs, with larger and older fish producing larger eggs (based on measurements of rehydrated eggs that had been preserved in formalin), but there was much variability among individual fish. Ojanguren et al. (1996) also found that the size of eggs produced by individual females varied greatly, but still found that egg sizes were positively correlated with maternal body size in females of the same age and from the same population.

When differences in female size are accounted for, some researchers have found evidence of a trade-off between the number and size of eggs produced. For instance, slower growing females have been found to produce fewer, but larger, eggs than faster growing females (Bagenal 1969b, Lobon-Cervia et al. 1997). In laboratory experiments, better fed female brown trout not only grew faster, but a greater proportion were mature and they produced significantly more and smaller eggs than poorly fed females (Bagenal 1969b). Although poorly fed brown trout females produced fewer eggs, the eggs were larger, particularly based on dry weight comparisons (Bagenal 1969b). Notably, eggs with more dry material also tended to contain less water (Bagenal 1969b). Bagenal (1969b) reported that survival of fry derived from larger eggs was significantly greater than survival of fry from small eggs and suggested that larger egg size compensated for lower fecundity (numbers of eggs) in the survival of the progeny. Bagenal (1969b) stressed the need to determine egg size by dry weights or chemical composition because the size and mass of eggs is affected by variation in water content, and egg water content typically increases as the spawning period is approached.

In other studies of European populations of brown trout, several researchers have suggested a trade-off between egg size and number of eggs produced. In Norway, Jonsson and Jonsson (1999) found that both fecundity and wet egg mass increased with fish size (somatic mass) for both anadromous and freshwater resident brown trout. However, once differences in fish size were accounted for, an apparent trade-off between the number eggs produced and egg size was observed both within and among populations. For example, in a population of hatchery-reared brown trout, there was a negative correlation between the number of eggs and egg mass, and among similarly sized female brown trout from different populations, the researchers found that egg mass was greater, but egg number was lower, among females from populations in southern Norway (58° N latitude) compared with females from middle Norway (63° N latitude) (Jonsson and Jonsson 1999). The researchers suggested that the gonadal investment of brown trout from the two latitudes was similar but resulted in fewer larger eggs in the south where warmer water temperatures were thought to increase metabolic demands of embryos and thus make larger eggs more advantageous (Jonsson and Jonsson 1999). The researchers also reported that females that had spawned in previous years produced heavier eggs than first time spawners did (Jonsson and Jonsson 1999).

In Spain, researchers compared different sub-populations of stream-resident brown trout and found that fecundity and egg size increased with female length, but when the effect of length was accounted for, there was an inverse relationship between fecundity and egg size (Lobón-Cerviá et al. 1997). The researchers also found that slow growing females from a less productive stream site developed fewer eggs than faster growing trout from more productive sites (Lobón-Cerviá et al. 1997). Females from a site with intermediate growth rates produced intermediate numbers of eggs (Lobón-Cerviá et al. 1997). A similar pattern was observed in the inter-annual variations in egg size and fecundity at one site, with females having high fecundity with small eggs one year and low fecundity and larger eggs another (Lobón-Cerviá et al. 1997).

Researchers have continued to investigate interactions between female size, age, and condition and fecundity and egg size in brown trout. Pender and Kwak (2002) compared the fecundity of brown trout from different tailwaters along an Arkansas river and found females from one site with poorer body condition had both fewer and smaller eggs than similarly sized females in better condition at other sites.

Brown trout fertility can also be influenced by environmental factors that affect gamete production, such as water quality. Warm water temperatures adversely affected brown trout gonadal maturation and reproduction in a section of the Firehole River downstream of geothermal features in Yellowstone National Park (Kaya 1977). Only 52 percent of brown trout sampled in the warm-water section of the stream matured during the seasonal maturation period from mid-August to late November, in contrast to 100 percent of the brown trout sampled from a cold-water section upstream of the geothermal features (Kaya 1977). In contrast, rainbow trout were found predominately in the warm section of the stream, and 79 percent of the adults had mature gonads during the same sampling period (Kaya 1977).

Elevated concentrations of metals in water can adversely affect salmonid health, and several metals are known to affect fish reproduction negatively (Farag et al. 1995, Pender and Kwak 2002). For instance, exposure to high concentrations of copper (Cu) has been found to affect fish growth and reproduction (Farag et al. 1995), and cadmium and lead have been reported to affect fish reproduction as well (Lam 1983 and Moore and Ramamoorthy 1984 as referenced by Pender and Kwak 2002). Other metals and contaminants may have negative effects on fish reproduction directly or indirectly, by negatively affecting invertebrate populations, fish physiological processes, or fish growth.

Spawning disruptions: Nelson (1986) attributed the low reproductive success of a population of brown trout downstream from a dam on a Montana river mainly to the disruption of spawning caused by flow fluctuations during peak spawning activity. Ironically, the flow fluctuations resulted from requests by the Montana Department of Fish, Wildlife, and Parks for lower dam releases to facilitate fish surveys downstream and "once the practice was discontinued, yearling stocks improved dramatically" (Nelson 1986).

Nelson (1986) used a simple analytical approach consisting of comparing plots of yearling recruitment to plots of flow magnitude and variation to examine the relationships between discharge and the spawning, incubation, and rearing stages of brown trout year classes over a 14-year period. Yearling recruitment was categorized into three classes: poor (39 to 164 yearlings per 1967 m [1.2 miles]), fair (333 to 646 yearlings per 1967 m), and good (864 to 1255 per 1967 m). Nelson (1986) found that large flow fluctuations preceding or during peak spawning activity were associated with poor recruitment of yearling brown trout. Flow fluctuations correlated with poor recruitment consisted of discharge decreases of 54 to 75 percent that were either preceded or followed by increases in discharge of 80 to 369 percent, with the fluctuations occurring over periods of 3 to 23 days. Flow magnitudes during the incubation and rearing stages were examined for correlations with yearling recruitment, but no relationships were evident (Nelson 1986).

Nelson (1986) suggested that the rapid flow fluctuations and associated changes in water depths and velocities downstream of the dam interfered with spawning site selection or the successful completion of the spawning act. Brown trout had been found to select a limited range of water depths and current velocities in a previous study in the area, and Nelson (1986) speculated that rapid fluctuations in flow might have made it difficult for brown trout to select suitable spawning sites. Nelson (1986) referenced another study by Hamilton and Buell (1976) in which flow changes reportedly had an adverse effect on salmonid spawning success via untimely egg release, failure to fertilize eggs, failure to cover eggs, and disrupted fish abandoning the spawning area and failing to return. Other studies have reached differing conclusions regarding the impact of flow fluctuations during spawning on the reproductive success of salmonids. Nelson (1986) referenced two studies of spawning Chinook salmon (*Oncorhynchus tshawytscha*) below a Columbia River dam that reported conflicting findings (Bauersfeld 1978 and Chapman et al. 1982). Bauersfeld (1978) found that flow fluctuations adversely affected salmon reproductive success, but Chapman et al. (1982) were unable to confirm those findings based on their observations at the same location (Nelson 1986). Chapman et al. (1982) and Stober (1982) reported that spawning salmon displaced by flow fluctuations returned to complete spawning when flows stabilized (Nelson 1986). However, Nelson (1986) noted that semelparous salmon might be more likely to return to spawning grounds after disturbance than iteroparous brown trout would. Nelson (1986) acknowledged that because of limited data and the analytical approach used, it could not be conclusively proved that flow fluctuations during spawning period

resulted in low recruitment of brown trout. Instead, the role of flow fluctuations during the spawning period should be considered among the complex interactions that can affect the reproductive success of brown trout (Nelson 1986).

In a more recent study of brown trout populations in tailwaters, Pender and Kwak (2002) observed that high discharges from dams during the spawning period affected spawning timing and habitat selection of brown trout. The researchers observed brown trout abandoning redd construction in response to increasing flows, but they also observed fish returning to spawning grounds and reinitiating spawning once flows stabilized. Brown trout redds constructed near river margins during high flows were dewatered when flows decreased and waters receded (Pender and Kwak 2002). The low densities of age-0 brown trout at one of the tailwaters in the study were suggested to be related to the high water releases that had persisted throughout the spawning period (Kwak and Pender 2002).

Poor water quality may also disrupt spawning. Woodward et al. (1995) recounted a study by Saunders and Sprague (1967) in which the introduction of copper and zinc repulsed Atlantic salmon ascending a tributary to spawn. Woodward et al. (1995) found that brown trout in an experimental chamber avoided water that contained metals (e.g., cadmium, copper, lead, zinc) that simulated ambient metals concentrations of water in the Upper Clark Fork River in Montana (Woodward et al. 1995). Brown trout also displayed an avoidance response when water pH was reduced (Woodward et al. 1995).

Egg fertilization rates: Fertilization rates of salmonid eggs in the wild are difficult to estimate but could be high. McFadden et al. (1965) reported fertilization rates often exceeding 90 percent for salmonids, and a similarly high rate was reported for New Zealand brown trout by Hobbs (1937). Salmonid embryo survival to hatching is also thought to be high, around 80 percent, under favorable temperature and water flow conditions during the incubation period (McFadden et al. 1965).

Population demography

Spatial characteristics of populations and genetic concerns

Several researchers have noted gradients in salmonid distributions in western North American streams with brook trout and cutthroat trout predominating in the headwaters, and brown trout or rainbow trout in mid- and lower elevation stream sections or larger river habitats (Moore et al. 1991, Rahel and Nibbelink 1999, Quist et al. 2004, McHugh and Budy 2005). However, as an introduced species, the spatial and genetic characteristics of brown trout populations are related not only to the species' ecology and zoogeography, but also reflect historic and current management activities.

The genetic characteristics of naturalized and brood stock populations of brown trout in Region 2 have been the subject of limited research. Genetic variation provides potential for evolutionary flexibility, which is important in allowing stocks to adapt to changing conditions (Alexander and Hubert 1995). Because brown trout were introduced to western states over 100 years ago and brood stocks have evolved in hatcheries over that time period, there is no information on the original genetic diversity or understanding of how hatchery practices and selection for traits have influenced the genetic characteristics of different brown trout populations (Alexander and Hubert 1995). In a review of the history and analysis of the genetic variation of Wyoming salmonid broodstocks, Alexander and Hubert (1995) reported that Wyoming Game and Fish Soda Lake brown trout brood stock had high genetic diversity compared with seven other stocks for which information was available at the time.

Brown trout produced from broodstocks are used to supplement natural recruitment of wild populations, in put-and-take, or put-and-grow-and-take fisheries in some systems in Region 2. Alexander and Hubert (1995) noted that because the Wyoming brown trout broodstock had high genetic diversity, the survival rates of fish introduced to the wild were likely favorable. The researchers also cautioned that because the genetic diversity of naturalized populations of brown trout are not understood, managers should be aware that stocking in areas with wild populations may facilitate loss of genetic diversity within wild populations (Alexander and Hubert 1995). For example, in Norway, after hatchery-reared brown trout that were introduced into two streams with wild brown trout successfully spawned with the wild fish, the genetic contribution of the hatchery fish to the wild population was estimated to be 19.2 percent and 16.3 percent based on samples of age-0 trout (Skaala et al. 1996). Many factors affect the reproductive interactions of hatchery and wild populations of brown trout and therefore the success of their offspring and degree of genetic introgression, including relative physiological condition of the two stocks, differences in size and growth rates between

stocks, differences in behaviors, and acclimation period of hatchery fish (Skaala et al. 1996).

There is less concern regarding the genetic impacts of hatchery brown trout on naturalized brown trout populations in waters with low natural recruitment rates in Region 2. In lakes, reservoirs, tailwaters, or streams with low rates of recruitment where brown trout are planted for put-and-take or put-and-grow-and-take fisheries, the genetic variation of the brood stocks used is "of little concern as long as the stocked fish are pleasing to anglers and return to the creel is at a satisfactory rate" although "genetic variation may be important for survival, growth, longevity, and catchability of stocked fish" (Alexander and Hubert 1995).

Brown trout hybridize with their closest relative Atlantic salmon, and natural hybrids of brown trout X Atlantic salmon are a common concern in the fishes' native range in Europe. Brown trout X brook trout hybrids, called "tiger trout," have been produced artificially, but there are few reports of natural hybrids between the two species occurring in western North America (Brown 1966, Allan 1977), despite their overlapping spawning seasons and reports of members of the two species engaging one another on the spawning grounds. Brown trout X brook trout hybrids are considered short-lived and infertile (Sorensen et al. 1995). No reports of natural brown trout hybridization with lake trout (*Salvelinus namaycush*) or bull trout (*S. confluentus*) were identified in our literature review.

Life history characteristics

Life history and demographic characteristics of brown trout populations vary with differences in several factors including temperature regimes, food availability, population density, and habitat. Life history characteristics of populations are also influenced by stochastic catastrophic events and the combined influences of land, water, and fishery management practices. Fisheries management practices in particular contribute to much variability in the characteristics of brown trout populations, particularly through stocking programs, fishing regulations, habitat improvements, flow regulations, and management of other species in the assemblage. Brown trout populations are also differentially influenced by angling pressure.

Providing a synthesis of the basic life history characteristics (e.g., growth rate, maximum size, age of maturity, life expectancy, population age structure, fecundity) of brown trout populations in Region 2 was not feasible because of the limited amount of

published information available and the broad range of environments and variety of management practices that have been applied to populations within Region 2. Identifying specific information on the demographic characteristics of naturalized populations of brown trout in Region 2 from a literature review proved difficult as many studies in the past combined trout species together for analysis or were understandably more concerned with reporting overall production (standing stock and biomass) than specific demographic parameters of populations such as age of maturity, fertility, and mortality rates. A summary of the life history characteristics of brown trout (primarily from in and around Region 2) follows. Land, water, and fisheries management practices that affect characteristics of brown trout populations are discussed in later sections (see Potential threats section).

Age and growth: The primary factors that affect brown trout growth rates are water temperature regimes, food availability, current velocities, habitat availability, and density (Preall and Ringler 1989, Elliott 1994, Jenkins et al. 1999), but variations in growth rates within and among brown trout populations may also have a significant genetic component. For instance, the relationship between female size and growth rate with egg size and offspring growth rate likely has a genetic component in addition to being influenced by environmental factors (Ojanguren et al. 1996). The genetic characteristics of naturalized populations of brown trout in the western United States are not well understood (Alexander and Hubert 1995), and consequently, the possible influence of differences in genetic characteristics on growth rates among populations is largely unknown.

In most North American streams, brown trout usually live five or six years and reach maximum lengths of 25 to 30 cm (10 to 12 inches) (Behnke 2002). In streams of limited productivity, brown trout may rarely live longer than four years or attain sizes larger than 25 cm (10 inches) (Behnke 2002). A few individuals in a population of stream residents may significantly extend their life span and attain larger sizes by shifting to a piscivorous diet. Stream-resident brown trout are typically larger than 310 mm (12.2 inches) TL when they switch to a predominately fish diet (Bachman 1991), and once they switch, they experience rapid growth and can extend their life span to 10 to 12 years (Behnke 2002). Brown trout inhabiting rivers and lakes, where food supplies are more abundant, usually reach much larger sizes, 35 to 76 cm (14 to 30 inches), and have longer life spans (5 to 12 years in rivers, and up to 15 years or more in lakes) (Behnke 2002).

Brown trout grow fastest during their first few years of life, after which growth rates decline steadily for several years before stabilizing for older age classes (Simpson and Wallace 1982), unless individuals switch from an insectivorous diet to a piscivorous diet and experience rapid growth at older ages (Behnke 2002). Generally, typical growth rates of brown trout are considered to be around 10 cm (4 inches) per year for the first three years of life after which growth slows to roughly 5 cm (2 inches) per year (Simpson and Wallace 1982). In one report of seasonal growth increments for age-0 brown trout, age-0 trout reached mean lengths of 6.6 cm (2.6 inches) during late summer of their first year, 9.5 cm (3.7 inches) their first winter, and 10.4 cm (4.1 inches) by early summer of their second year (age-1) (Vehanen et al. 2000). Mean lengths of brown trout age-0 through age-5+ in a Michigan river population were reported as 8.0 cm, 18.0 cm, 27.1 cm, 34.9 cm, 43.5 cm, and 48.0 cm respectively (3.1, 7.1, 10.7, 13.7, 17.1, and 18.9 inches, respectively) (Fausch and White 1981), reflecting the pattern of decreased growth rate after the first several years of life.

Few estimates of length-at-age or mean annual growth increments for brown trout populations in or around Region 2 were found in the literature review. Based on previous reports, including length-frequency data by other researchers, Wolf et al. (1990) roughly estimated length-at-age for a population of relatively small and slow-growing stream brown trout in southwestern Wyoming. Wolf et al. (1990) estimated that brown trout reached 5.1 cm (2 inches) by the end of their first summer and 10.2 to 12.7 cm (4 to 5 inches) by the end of their second summer. Unpublished research by Wesche (1972) indicated that maximum brown trout age in the stream was 5 years based on scale analysis; however, it was thought that otolith analysis might have produced greater maximum age estimates (Wolf et al. 1990).

In a study of electrofishing impacts on trout growth, Thompson et al. (1997a) reported mean annual growth increments for "shocked" and "unshocked" age-3, and age-4 and age-5 (combined) brown trout in the Rio Grande in Colorado. Mean annual growth increments were 67.5 mm (2.7 inches) for shocked and 71.7 mm (2.8 inches) for unshocked age-3 brown trout (Thompson et al. 1997a). For age-4 and age-5 fish combined, mean annual growth increment was 41.3 mm (1.6 inches) for shocked and 52.6 mm (2.1 inches) for unshocked brown trout (Thompson et al. 1997a).

Beyond Region 2, Puckett (1951) reported the average calculated total length (in inches) at each scale annulus for brown trout taken from the West Gallatin River in Montana. The following mean lengths-at-age reported by Puckett (1951) have been converted into centimeters for consistency: age-1 fish were 9.4 cm (3.7 inches), age-2 fish were 22.4 cm (8.8 inches), age-3 fish were 33.5 cm (13.2 inches), age-4 fish were 40.4 cm (15.9 inches), and age 5 fish 48.8 cm (19.2 inches).

Population density and environmental factors have been found to influence growth rates of brown trout. Although some researchers have proposed that the growth of YOY stream resident brown trout is largely independent of population density because early mortality and emigration reduces density to the carrying capacity (Elliott 1994), Jenkins et al. (1999) found that age-0 brown trout size was negatively related to trout density in two mountain streams in California. Jenkins et al. (1999) reported that the relationship between trout density and mean individual mass of age-0 brown trout at the end of their first growing season was consistently negative, suggesting density-dependent growth. Indications of an inverse relationship between body mass and population density have been reported for adult stream resident brown trout as well (Dunham and Vinyard 1997). However, density effects on growth may be difficult to detect from observational data, particularly when data are collected at small spatial scales, if insufficient information is collected to evaluate interannual variations in growth, or in systems with relatively high fish densities that result in a growth-density relationship with a flat slope (Jenkins et al. 1999).

Environmental factors that have been suggested to influence age-0 brown trout growth rates include shortened growing seasons at high elevations and water and habitat quality. La Voie and Hubert (1997) reported that growth of age-0 brown trout had practically ceased by late summer in a high elevation stream in southwestern Wyoming. In June, age-0 brown trout had a mean length of 26 mm (1 inch) TL, and in July, mean length was 39 mm (1.5 inches) TL in the same stream (Harris et al. 1992). By September, age-0 brown trout had reached a mean size of 55.8 mm (2.2 inches) TL, but growth had slowed significantly. By October, mean size of age-0 brown trout was 56.0 mm TL, indicating that between September and October growth was minimal (La Voie and Hubert 1997). For an Idaho stream, Maret et al. (1993) reported reduced larval brown trout growth in reaches that were warmer, had lower dissolved oxygen concentrations, and poorer water quality (related to agricultural land uses) compared to larval growth in an un-impacted, colder, upstream site with higher mean concentrations of dissolved oxygen.

Griffith and Smith (1993) observed differences in the mean sizes and condition factors of age-0 brown trout associated with three different types of winter habitat in the South Fork of the Snake River, Idaho, but sample sizes were very small.

Environmental conditions also influence growth rates of older age classes of fish. Kaeding and Kaya (1978) found that differences in water temperature and stream productivity resulted in large differences in growth rates and lengths-at-age for all age classes of brown trout located in two sections of the Firehole River in Yellowstone National Park. The researchers aged brown trout from a geothermally-influenced section of the stream that was more productive and had water temperatures typically 10 °C greater than a section upstream of the geothermal feature (Kaeding and Kaya 1978). Brown trout at the uninfluenced sampling station had one season of growth annually from April or May through August, whereas those from the geothermally-influenced station had two annual growth periods, one from February to early July and then a shorter growth period in early fall of about two months (Kaeding and Kaya 1978). Brown trout hatched sooner at the geothermally-influenced station, grew considerably more their first year, and remained substantially larger at every age than fish from the upstream station (Kaeding and Kaya 1978). Unfortunately, the length-at-age estimates and age frequency distribution from the influenced station represented brown trout combined with rainbow trout and was compared to the estimates for brown trout alone from the uninfluenced station. For rainbow and brown trout combined in the geothermally-influenced section, the length frequency distribution indicated that age-0 trout ranged in size from 11 to 17 cm (4.3 to 6.7 inches) TL, age-1 trout ranged from 21 to 31 cm (8.3 to 12.2 inches) TL, age-2 trout ranged from 32 to 40 cm (12.6 to 15.7 inches) TL, and age-2+ trout were greater than 40 cm (15.7 inches) TL (Kaeding and Kaya 1978). In contrast, at the uninfluenced station, age-0 brown trout ranged in size from 2 to 4 cm (0.8 to 1.6 inches) TL, and by age-3, most were still less than 20 cm (7.9 inches) TL (Kaeding and Kaya 1978).

Differences in survival and growth rates of stocked "domestic" and "wild" strains of brown trout have also been observed. In a field performance test in Wisconsin, stocked brown trout fingerlings and yearlings that were first-generation from naturalized fish (called wild-strain) were compared to hatchery strains (domestic-strain) (Avery et al. 2001). The wild-strain fish had comparable growth and superior survival rates to the domestic-strain fish in two different rivers (Avery et al. 2001). The wild-strain brown trout matched the growth rate of the domestic-strain in a moderately fertile stream, but the domestic-strain brown trout maintained their initial size advantage (Avery et al. 2001). In a more fertile stream, the wild-strain growth rate exceeded that of the domestic-strain, and the initial size advantage of the domestic-strain was reduced (Avery et al. 2001). Survival among the wild-strain brown trout was also significantly greater, 1.3 to 4.5 times higher than the domestic-strain during the first year, and 4 to 42 times higher after two years (Avery et al. 2001).

Notably, stocked trout have been found to impact growth and survival of naturalized populations of brown trout in some systems adversely (Vincent 1987). Vincent (1987) found that stocking catchable-sized rainbow trout did not have an apparent adverse impact on brown trout during their first 18 months of life, but it was correlated with reduced growth rates of age-1+ brown trout. Stocking catchable-sized rainbow trout was also found to decrease the abundance and biomass of age-2+ brown trout by 49 percent in one stream (Vincent 1987).

Knowledge of age and growth of brown trout populations within Region 2 is limited by the lack of published data. Growth rates and lengths achieved by brown trout populations likely vary widely among different populations across Region 2 given the spatial and temporal variability in environmental factors, differences in trout population density among locations, and variations in feeding behavior, diets, and activity patterns among populations. Several bioenergetic models predicting brown trout growth have been developed and tested, particularly for drift-feeding individuals, and many studies have investigated factors influencing brown trout growth in natural settings. Reviewing the many models and studies was beyond scope of the assessment, but interested readers can find many publications on the topic.

Weight-length relationships: The relationship between fish length and weight can be used as measure of the variation of the weight of a fish from the expected weight based on its length, providing an indication of an individuals "well-being" or "fatness" (Anderson and Neumann 1996). Allan (1978) estimated a weight-length relationship for brown trout from a mountain stream in southwestern Colorado (stream elevation was 2820 m [9252 ft.]). Thirty-two brown trout ranging in size from 6.8 to 29.5 cm (2.7 to 11.6 inches) in length (mean = 15.3 cm [6.0 inches]) and with weights ranging from 2.7 to 253.0 g (p.006 to 0.558 lbs.; mean = 35.0

g [0.077 lbs.]) were used for the estimate: W = 0.0081 L$^{3.07}$ (r^2 = 0.995), where W is weight in grams and L is length in centimeters (Allan 1978).

Thompson et al. (1997a) estimated body condition of brown trout in three rivers in Colorado, the Rio Grande, the Arkansas River, and the Dolores River. They estimated Fulton's condition factor K = (W/L^3)*10^5, where W is fish weight in grams, L is fish length in millimeters, and 10^5 is a scaling factor. Mean condition factor (K) for brown trout in the three rivers are provided in **Table 3**.

Puckett (1951) reported the coefficient of condition for brown trout in the West Gallatin River in Montana. Coefficient of condition was calculated for individual fish using the formula C = (W*10^5)/L^3, where W = weight in pounds and L = total length in inches (Puckett 1951). Mean condition factors for each age group were reported. For brown trout age-1 C = 40.1 (n = 5), age-2 C = 36.8 (n = 26), age-3 C = 35.9 (n = 43), age-4 C = 34.0 (n = 27), and age-5 C = 37.0 (n = 1) (Puckett 1951).

Nehring (1991) assessed the effect of introduced *Mysis relicta* (opossum shrimp) escapement from two Colorado reservoirs on brown trout growth and condition downstream and found that mysid escapement positively influenced brown trout growth within 5 km of reservoir outlets. Length-Weight regressions were developed and used to compare trout growth and condition before and after mysid introduction to the systems, and the estimated coefficients for different sites and years are reported in Nehring (1991).

More generally, Behnke (2002) reported that brown trout found in small streams reached sizes of 25 to 30 cm (10 to 12 inches) and 227 to 340 g (8 to 12 oz.) whereas those in rivers and lakes reached sizes of

35 to 76 cm (14 to 30 inches) and 0.45 to 5.4 kg (1 to 12 lbs.).

Age of maturity: Age of sexual maturity is related in part to the environment that the population inhabits (Moyle and Cech 2000). Where the environment is favorable and adult survival is high, age of first reproduction may be delayed (Moyle and Cech 2000). In contrast, populations inhabiting unfavorable environments may reproduce at younger ages (Moyle and Cech 2000). In less predicable environments, where adult survival probabilities are low, natural selection favors females that reproduce as soon as possible (Moyle and Cech 2000). The relationship between environment and age at reproduction is evident among the lake and stream-dwelling forms of brown trout in Europe (Moyle and Cech 2000). A brown trout population inhabiting a productive and predictable lake environment grew to a large size and delayed breeding until age-5 to age-7 whereas a population from a less productive and predictable stream grew more slowly, and matured at earlier ages, age-3 to age-5 (Alm 1949 as referenced by Moyle and Cech 2000).

Generally, stream-resident brown trout mature as early as age-2 or age-3, with males usually maturing before females (Bachman 1991, Elliott 1994). However, brown trout have been found to mature at younger ages. In a Michigan river, a third of age-1 males collected before and during the spawning period were mature, and a few age-2 females were mature (Taube 1976). For the same population, the proportion of mature females per age-class continued to lag one year behind that of the males until age-4, when all males and females examined were mature (Taube 1976). By length group, males also matured at smaller sizes than females. Taube (1976) reported that 35 percent (n = 12) of males 152 to 176 mm (6 to 7 inches) in length were mature whereas no females (n = 6) were mature at those lengths.

Table 3. Estimated body condition of brown trout exposed and not exposed to electrofishing in three Colorado rivers, the Rio Grande, the Arkansas, and the Dolores. The researchers estimated Fulton's condition factor K=(W/L^3)*10^5, where W is fish weight in grams, L is fish length in millimeters, and 10^5 is a scaling factor. Reproduced from Thompson et al. (1997).

River, year	Total length (cm)	Shocked brown trout		Unshocked brown trout	
		Mean *K* (SE)	N	Mean *K* (SE)	N
Dolores, 1993	35-48	1.122 (0.0287)	12	1.150 (0.0159)	70
Dolores, 1994	29-50	1.031 (0.0258)	11	1.082 (0.0105)	109
Arkansas, 1993	27-38	0.987 (0.0141)	63	1.008 (0.0042)	657
Arkansas, 1994	22-36	0.970 (0.0101)	116	1.097 (0.0110)	157
Rio Grande, 1993	24-44	0.962 (0.0104)	79	0.982 (0.0102)	83

In a survey of a population in a mountain stream in Wyoming, 31 percent of 563 brown trout greater than 150 mm (6 inches) in length were sexually mature (Grost et al. 1990). Males and females were not distinguished, but the majority of mature brown trout were between 200 and 400 mm (8 and 16 inches) long (Grost et al. 1990). The smallest length class with mature fish was 176 to 200 mm (7 to 8 inches), of which 6 percent were considered mature. All brown trout longer than 326 mm (12.8 inches) were sexually mature (**Table 4**; Grost et al. 1990).

Size and fecundity relationships: Fecundity, the number of eggs in the ovaries of a female fish, is the most commonly used measure of reproductive potential in fisheries since it is relatively easy to measure (Moyle and Cech 2000). Fecundity tends to increase with fish size, with larger fish producing more eggs than smaller fish, both in absolute numbers of eggs produced and relative to body size, indicating that the energetic investment in egg production is greater in larger members of the species (Moyle and Cech 2000). The exponential relationship between body size and fecundity in females is especially true for species, such as the brown trout, that spawn just once a year and produce large numbers of eggs (Moyle and Cech 2000). In contrast, the reproductive potential of male fish usually increases linearly with size throughout their life.

Fecundity varies greatly among life-history forms of brown trout. Elliott (1994) reported that while a 15 cm (6 inches) long stream resident female may only produce 100 eggs, a 50 cm (20 inches) long sea-run female brown trout may produce 2,000 eggs. Brown trout fecundity also varies among waters and among females within a population (Taube 1976, Jonsson and Jonsson 1999, Moyle and Cech 2000). Several researchers have suggested that food availability influences much of the variability in brown trout fecundity (Taube 1976, Bachman 1991). In general, when food resources are abundant and exceed requirements for growth and maintenance, fish can produce more and larger eggs; those conditions can exist in very productive systems or when population levels are low and there is little intra-specific competition (Moyle and Cech 2000).

Taube (1976) counted the complete egg complement of 90 female brown trout collected between August 31 and November 5 from the Platte River of Michigan. The smallest mature female (193 mm [7.6 inches] TL, age-1) had the fewest eggs (107), and the second largest female (462 mm [18.2 inches] TL, age-4) had the most eggs (2,419). Mean number of eggs of female brown trout length class groups (25 mm [1 inch]) increment classes ranging between 202 and 472 mm (8 and 18.6 inches) ranged from 241 eggs for the smallest size group to 1,737 eggs for the largest size group (**Table 5**). Taube (1976) noted that the greatest increase in egg number occurred from age-3 to age-4 brown trout (**Table 6**).

Although Taube (1976) found positive correlations between female length and number of eggs as well as female age and number of eggs, he observed that fecundity was highly variable among females in all size and age groups. For instance, in five females 345 to 353 mm (13.6 to 13.9 inches) TL with ages ranging from age-2 to age-4, egg counts ranged from 584 to 1,255 (Taube 1976). Similarly, the mean size of the eggs from the same five females was variable (mean egg diameters ranged from 3.9 to 4.7 mm [0.15 to 0.18 inch]). Despite the variability among similarly sized and aged females, Taube (1976) found statistically significant relationships between brown trout fecundity and age and length and developed the following regression equations to predict the number of eggs, N, from total length or age: $N = 7.3$ (total length [mm]) $- 1498.8$ and $N = 353.3$ (age group) $- 155.7$.

Similar to Elliott (1994), Taube (1976) described a large difference in fecundity between different life history forms of brown trout. Female brown trout that had spent one to two growing seasons in Lake Michigan had 1.5 to 5 times more eggs than river residents (Taube 1976). Adjusting for differences in size between the lake and river females, the lake females still produced 1.5 to 2.4 times as many eggs as the river inhabitants (Taube 1976).

Taube (1976) measured the mean diameter of eggs (preserved in 10 percent formalin for two to four months then soaked in water for three days prior to measuring) and reported mean egg diameters ranging from 3.7 to 4.3 mm for length classes 202 to 227 mm (8 to 9 inches) TL to 355 to 472 mm (14 to 18.6 inches) TL respectively (**Table 5**). By age, mean egg diameters ranged from 3.8 to 4.5 mm (0.15 to 0.18 inch) for age-1 to age-5 females (**Table 6**). However, it was unknown if all the measured eggs had reached their ultimate size since spawning typically occurred in October and November and females were collected from late August through early November (Taube 1976). The mean diameter of the eggs of four of five lake brown trout were larger than those of the largest river brown trout, ranging from 5.1 to 5.4 mm (0.20 to 0.21 inch) in diameter (Tauble 1976). Other researchers have reported similarly large egg diameters, ranging from 4.9

Table 4. Estimated length frequency distribution of mature brown trout in Douglas Creek, Wyoming. "Average percent mature in each length class was derived from Avery (1985)." Reproduced from Grost and Hubert (1990).

Length class (cm)	Average percent mature	Number of fish sampled	Estimated number of mature fish
15.0-17.5	0	190	0
17.6-20.0	6	111	7
20.1-22.5	31	98	30
22.6-25.0	68	51	35
25.1-27.5	86	45	39
27.6-30.0	88	24	21
30.1-32.5	91	7	6
32.6-35.0	100	15	15
35.1-37.5	100	12	12
37.6-40.0	100	5	5
40.1-42.5	100	1	1
42.6-45.0	100	2	2
45.1-47.5	100	0	0
47.6-50.0	100	1	1
50.0	100	1	1

Table 5. Number and size of eggs of female brown trout in relation to age for population in the Platte River, Michigan. Reproduced from Taube (1976).

	Egg counts		Egg measurements	
Length (mm)	Number of fish	Mean number of eggs with 95% confidence limits	Number of fish	Mean egg diameter (mm) with 95% confidence limits
202-227	8	241 ± 42	7	3.7 ± 0.3
228-252	14	295 ± 39	14	3.8 ± 0.1
253-278	18	452 ± 58	12	4.2 ± 0.1
279-303	18	522 ± 66	15	4.2 ± 0.1
304-328	11	681 ± 126	7	4.4 ± 0.2
329-354	8	936 ± 238	6	4.3 ± 0.3
355-472	12	1737 ± 267	9	4.3 ± 0.3

Table 6. Number and size of eggs of female brown trout in relation to age for population in the Platte River, Michigan. Reproduced from Taube (1976).

	Egg counts		Egg measurements	
Age group	Number of fish	Mean number of eggs with 95% confidence limits	Number of fish	Mean egg diameter (mm) with 95% confidence limits
I	4	279 ± 207	3	3.8 ± 0.9
II	41	493 ± 79	32	4.1 ± 0.1
III	26	766 ± 216	20	4.1 ± 0.2
IV	10	1382 ± 477	7	4.3 ± 0.2
V	1	1601	1	4.5

to 5.6 mm (0.19 to 0.22 inch), for lake-inhabiting brown trout (L'Abée-Lund and Hindar 1990 as referenced by Mittelbach and Persson 1998).

Other reports of brown trout egg size from outside of Region 2 are consistent with Taube's (1976) findings for the Michigan population. In tailwaters of the White River in Arkansas, mean diameters of brown trout eggs ranged from 3.82 to 4.50 mm (0.15 to 0.18 inch) (Pender and Kwak 2002). In the Firehole River in Yellowstone National Park, the number of female brown trout over 310 mm (12.2 inches) TL with eggs with diameters greater than 4 mm (0.16 inch) peaked in October (Kaya 1977).

Summary of matrix analysis of population demographics for stream resident brown trout

Matrix demographic models facilitate the assessment of critical transitions in a species' life history. A primary purpose of the analysis is to assess and identify the critical stages in the life history of a species that may have a major impact on its population dynamics. A matrix demographic analysis was performed for a theoretical population of stream resident brown trout and is presented in the **Appendix** of this document.

Information on vital rates for stream-resident brown trout populations in Region 2 was extremely limited, and better data are needed for a more robust analysis. The values used in the analysis were drawn from research performed in Region 2 when possible, and supplemented with reports of brown trout fecundity and survival rates from research conducted elsewhere. Fecundity values for different age-classes represented in the model were estimated using the equation provided by Taube (1976). The proportion of reproductively mature individuals in each age-class was based on Grost et al. (1990). Survival rates of eggs to hatch was based on a laboratory study performed by Stonecypher (1992), and survival rate of age-0 fish post-emergence was based on an estimate from Elliott (1994). Survival of age-1+ fish was based on age ratios developed from the length frequency distribution reported by Grost et al. (1990). The model consisted of six stages, representing age-0 to age-5 brown trout as life stages, with a self-loop at the age-5 stage to represent age-5+ fish. Age-5+ fish were assumed to have a low constant survival probability from year to year. The model did not account for an increase in female fecundity with size beyond age-5 (i.e., the number of eggs produced remained constant after age-5). A 1:1 female to male sex ratio was assumed for the model.

The matrix analysis indicated that the absolute survival rate of age-0 brown trout has a major impact on population dynamics. This result is not unexpected for brown trout given their high fecundity but low fertility, and it is consistent with findings that brown trout populations are sensitive to annual variations in survival of age-0 fish (see following section: Ecological influences of survival and reproduction). The analysis also indicated that proportional changes in the survival rates of young age classes, through age-2, can have major impacts on population dynamics. This result in part reflects that in the data used, the majority of female fish did not reach reproductive maturity until age-2.

The matrix analysis underscores the need for better data on brown trout populations and vital rates for brown trout populations in North America generally and in Region 2 in particular. Given the importance of age-0 survival to the population dynamics of brown trout, better estimates of brown trout fertility in the wild and survival rates of the earliest life history stages are imperative to improving the accuracy and relevance of the analysis. With better data, several model refinements would be possible. For example, data from longer term studies of wild populations would provide a range of the natural variability in brown trout vital rates, which could be used to assess the impact of stochastic fluctuations on populations. Similarly, density-dependent effects on population dynamics could be assessed with a better dataset. Another major model refinement would be to incorporate better the impact of large females that switch to piscivory and can dramatically increase both their life span and fecundity. A few large female fish in a population may have a significant impact on population dynamics and persistence, especially in the context of stochastic fluctuations. Similarly, extending the analysis to fluvial and lentic populations of brown trout or systems where fluvial or lentic adults spawn in tributaries containing stream resident populations would enhance the understanding of the range of populations dynamics that different types of brown trout populations experience in Region 2.

Ecological influences on survival and reproduction

Brown trout are well adapted for many environments, as has been demonstrated by their successful introduction to suitable cold-water systems worldwide. They feed on a wide range of invertebrates, and their diets vary among systems with differences in food availability. As brown trout grow larger, their diets are increasingly supplemented by small fish, and by becoming piscivorous, they can attain large sizes and

long life spans. In many stream systems, brown trout are the dominant aquatic predator and usually have few competitors. Where brown trout have been introduced, they have had detrimental impacts on native fauna, and in many systems in North America, they have displaced or completely replaced native salmonids (Behnke 2002). Other introduced salmonids in Region 2, such as rainbow trout, have diets similar to that of brown trout, but their habitat use and activity patterns differ slightly, which may explain how sympatric populations have persisted in the region (see Competition section).

Mortality of adult brown trout is caused by predation, parasitism, and adverse environmental conditions. Piscivorous birds and mammals and other fish prey on brown trout, but as a game fish, angling may be the predominant form of predation in some systems. Salmonids are affected by a number of parasites in North America that can affect survival and reproduction (see Parasites section), and diseases can decimate trout populations. Jenkins et al. (1999) reported an early summer "epidemic" that resulted in 30 to 67 percent mortality of brown trout in a mountain stream. However, brown trout are resistant to whirling disease, an introduced parasite that can decimate populations of trout native to North America (see Parasites section).

Annual mortality of adult brown trout may be greatest in winter, particularly in streams where suitable habitat is limited and in years when winter conditions are severe (Cunjak 1996). Some studies have found over-winter mortality rates of resident salmonids in excess of 65 percent (Cunjak 1996). Maciolek and Needham (1952) reported that the brown trout population of a California mountain stream decreased an average of 60 percent during winter over a four-year period. In severe winters, ice and snow are thought to cause most of the mortality of stream fish (Maciolek and Needham 1952). Slater (1944) reported several hundred trout were killed when a snow-bank collapsed into a rearing pond (as referenced by Maciolek and Needham 1952). Jenkins et al. (1999) commented that winter mortality for all size classes of brown trout in two mountain streams in California ranged from "negligible to nearly virtually total, depending on meteorological events."

Particularly in the mountainous high elevation streams of Region 2 where winter conditions can be severe, a lack of suitable over-winter habitat may limit brown trout populations. Several researchers have identified beaver ponds, back waters, and off channels pools as important over-wintering habitat for brown trout (Young 1995, Cunjak 1996), and other beaver-influenced habitats are preferred cover for brown trout in summer (Young 1995). Systems with beaver populations and natural flow regimes are more likely to provide the complex array of habitats that brown trout and other salmonids require (Cunjak 1996).

Brown trout combine relatively high fecundity with a moderate to long life span, and this has helped the species establish itself, persist, and even thrive in a range of environments (Moyle and Cech 2000). The longer life span of brown trout allows mature fish to spawn multiple years, and consequently populations are less sensitive to periods of poor reproduction than shorter-lived species of salmonids such as brook trout (Bachman 1991). Jenkins et al. (1999) suggested that the relationship between brown trout growth rates and population density contributes to population regulation. During periods of low population densities (e.g., after catastrophic events), high growth rates may facilitate the rapid recovery of populations via increased fecundity. In contrast, under high density conditions, lower growth rates and poorer individual condition may result in decreased fecundity of adults and poor recruitment from increased mortality of age-0 trout.

The reproductive strategy of brown trout involves minimal parental care, but because eggs are deposited in redds and covered with substrates, developing embryos are somewhat protected. Egg predation by other fish is considered to be less of a threat to species that construct redds or nests compared to open substrate spawners, but early life stages of brown trout are susceptible to predation by benthic macroinvertebrates and mortality from other environmental factors (e.g., fluctuating discharge, redd sedimentation, low dissolved oxygen concentrations). The survival rates of early life stages of brown trout can be highly variable among locations and years because of the range of factors affecting their survival. For example, a study in a Pennsylvania stream found significant variation in brown trout embryo survival among stream sections in one year, but not in another year (Beard and Carline 1991). Notably, survival rates were most variable in stream sections where overall survival was lowest (Beard and Carline 1991). Despite the vulnerability of immobile brown trout embryos and larvae in redds, in some systems, mortality rates are thought to be highest for age-0 brown trout during the post-emergence period. Mortality during the early life stages of brown trout is considered a key population regulator, and ecological influences on survival of early life stages are discussed in detail in the following sections.

Terms used for early life-stages: Several common terms are often used in the salmonid literature

to distinguish different phases in the early life history of salmonids in the weeks following hatching and are used for convenience (or as used by the authors of the research being summarized) in this assessment. The term alevin refers to hatched larvae that still rely on their yolk sacs for food and remain in the redds within the interstitial spaces of the stream substrate, a life stage that lasts several weeks (Elliott 1994). The term fry describes a short transition phase of several weeks after the young fish have emerged from the gravel (often referred to as "swim-up") and transition to feeding exogenously as the remains of their yolk sacs are exhausted (Elliott 1994). The terms embryo, larvae, age-0, or YOY are used consistent with their common use in the literature and in the rest of this document.

Survival of embryos and larvae: Because brown trout are brood hiders, the fertilized eggs and developing embryos are relatively protected by being buried in stream substrates. However, mortality during the incubation stage can be high. Adequate water flow through the egg pockets of redds is required to provide adequate dissolved oxygen and remove metabolic wastes from developing embryos. Alterations of water flow, temperature, and dissolved oxygen concentrations during the incubation stage can lower survival rates of brown trout embryos. Predation by aquatic invertebrates and fish and sub-surface ice formation are other causes of mortality during the incubation period.

Temperature: Under optimal conditions, the survival rates of brown trout embryos are high. In a laboratory study of artificially fertilized eggs, brown trout embryo survival rate to the eyed stage was 94 percent for eggs fertilized and incubated at 7 °C (Stonecypher 1992). For eggs fertilized at 7 °C and then acclimated at four different rates to incubation temperatures of 4 °C and 2 °C, the mean survival rates of brown trout embryos were 79 and 53 percent, respectively (Stonecypher 1992). Mean percent survival rates to the swim-up stage were 85, 72, and 49 percent for embryos incubated at temperatures of 7 °C, 4 °C, and 2 °C, respectively (Stonecypher 1992). Mortality of brown trout embryos occurred throughout the incubation period, but rates tended to be higher during the first 40 days of development, particularly at incubation temperatures of 2 °C (Stonecypher 1992).

However, winter water temperatures in the wild can be much more severe. Reiser and Wesche (1979) reported nearly complete mortality of brown trout eggs placed in Vibert boxes and buried 15 cm (6 inches) deep in substrates of artificial redds in locations where water depth was 12 to 20 cm (4.7 to 7.9 inches). Only 0.5 to 3.4 percent (mean = 1.95 percent) of eggs survived (Reiser and Wesche 1979). The researchers found no correlation between water depth or water velocity and egg survival. They suggested that extremely low water temperatures and *in situ* freezing were the main causes of egg mortality, indicating that freezing of redds may be an important factor in the Rocky Mountain West where winter water temperatures can remain at very low levels for long periods (Reiser and Wesche 1979).

Flow regime: Fluctuating flows during spawning and incubation periods are one of the first regulators of trout year-class strength (Anderson and Nehring 1985). Variations in discharge between spawning and incubation periods can have differing impacts on brown trout recruitment. Under low flows, spawning habitat is reduced, and brown trout may spawn in mid-channel areas that are not suitable habitats under higher flow conditions that may follow. Conversely, if spawning occurs during high flows, redds may be dewatered as the stream width is reduced under subsequent low flow conditions. Where flow regimes have been altered by water management activities, the resulting flow regime may adversely affect reproductive success of brown trout. In a study of the effects of variable discharge on trout populations in Colorado streams, Nehring and Anderson (1993) identified fluctuations in spawning habitat or discharge between egg deposition and hatching during the winter months as critical limitations on brown trout recruitment at three sites.

Elevated discharges may adversely affect brown trout populations through other mechanisms as well. High flows may move substrates and displace or damage embryos and larvae (Jensen and Johnsen 1999). Increased sediment transport associated with high discharge can result in increased sedimentation and accumulation of fines in redds, reducing oxygen availability to embryos or preventing emergence (Jensen and Johnsen 1999). Spina (2001) found YOY brown trout densities were inversely related to peak discharge during the incubation period (measured as maximum discharge between January 1 and March 31) in an 11-year study of a brown trout population in the southern Sierra Nevada range. Spina (2001) cautioned that while low recruitment may not have been caused by high discharges alone, stream managers should be mindful of possible impacts of high flows on incubating trout eggs.

Other studies have found that high discharge events do not always result in decreased survival of age-0 brown trout and that low discharges can also adversely affect reproductive success of salmonids (Lobón-Cerviá

1996, Davies 1991 as referenced by Spina 2001). Flow reductions during the incubation period can result in redd dewatering and high mortality of eggs. However, temporary reductions in discharge may not be as detrimental as sustained reductions, as salmonid eggs in redds have been found to be somewhat tolerant of temporary dewatering. A few studies have reported high rates of hatching success of salmonid eggs that had been dewatered from one to five weeks experimentally in artificial redds as well as in natural redds in streams (Hobbs 1937, Becker et al. 1983, and Reiser and White 1983 as referenced by Nelson 1986). However, alevins may be much more susceptible to dewatering of redds, and dramatic increases in alevin mortality have been associated with short periods of redd dewatering. Nehring and Anderson (1993) recounted a report by Becker et al. (1982) in which salmonid alevins exposed to a daily one-hour period of dewatering experienced 97 percent mortality. Becker et al. (1983) demonstrated that a one time dewatering of salmonid redds for 6 hours resulted in 99 percent mortality of intra-gravel alevins (as referenced by Nehring and Anderson 1993). Nehring and Anderson (1993) suggested the near failure of one brown trout year class resulted from dewatering that occurred in April when brown trout larvae were still in the gravel. In that study, minimum daily flow levels in April were 66 percent lower than flow levels during the brown trout spawning period the preceding autumn (Nehring and Anderson 1993).

Relatively stable discharges from the spawning period through incubation and fry emergence may be key to the reproductive success of brown trout, particularly in regulated rivers in Region 2. Anderson and Nehring (1985) found that age-0 brown trout recruitment was good in the South Platte River, Colorado during the three years of the study with suitable flows throughout the brown trout spawning and incubation periods. Nehring and Anderson (1993) regressed the absolute differences in spawning flows and spawning habitat between October and March against age-1 brown trout density at a site on the Colorado River and found the correlations were highly negative. The researchers observed a similar pattern in which winter flow reductions appeared to have an adverse effect on yearling brown trout recruitment on the Taylor River in Colorado. Nehring and Anderson (1993) reported that the brown trout population in the Taylor River increased an average of 63 percent when reservoir discharge was stabilized during the brown trout spawning-incubation period compared to years when releases were not stabilized. The researchers concluded that flow stability from egg deposition in October-November through

hatching in April was critical to brown trout year class recruitment (Nehring and Anderson 1993).

Sedimentation of redds and dissolved oxygen concentration: Increased sediment load in streams can result in sediment deposition within redds and adversely affect the survival of brown trout embryos during the incubation period by altering chemical and physical characteristics (e.g., dissolved oxygen concentration, intergravel water velocity, interstitial pore space, water temperature) (Young et al. 1990). Grost et al. (1991) found that fine sediments naturally accumulated in the egg pockets of brown trout redds as the winter incubation progressed in a mountain stream in Wyoming. A higher percentage of two fine-particle size classes, 0.85 mm and 0.42 mm diameter, were found in egg pocket samples collected in winter months compared to those collected in fall just after spawning (Grost et al. 1991). These two size classes were found to be most detrimental to salmonid embryo and alevin survival in another study (Reiser and White 1988 as referenced by Grost et al. 1991). Egg pockets appeared to be particularly susceptible to fine sediment accumulation as substrate composition in other areas of the redd did not differ significantly between fall and winter samples (Grost et al. 1991).

In a laboratory study of the effects of fine sediments on brown trout survival to emergence, Young et al. (1990) found that as the particle size of sediments increased, the proportion of fry surviving to emergence increased. Maret et al. (1993) evaluated the effects of sediment and other types of non-point source pollution on brown trout embryo survival in Idaho streams. They found a significant inverse relationship between percent of fine sediment and brown trout survival to emergence and a significant positive relationship between intergravel dissolved oxygen (IGDO) saturation and brown trout survival to emergence (Maret et al. 1993). A weak inverse relationship between percent of fine sediments and IGDO was also found (Maret et al. 1993).

In the same study, the researchers reported that IGDO and percent oxygen saturation levels were significantly less at locations affected by agricultural pollutants than at a control location, with up to 40 percent of the IGDO measurements below 6.0 mg per L (the proposed water quality criterion at the time for salmonids) at the impacted sites (Maret et al. 1993). Brown trout embryo survival to emergence at the control station ranged from 18 to 83 percent and averaged 48 percent (Maret et al. 1993). Brown trout embryo

survival at impacted sites ranged from 0 to 9 percent, 0 to 54 percent, and 0 to 44 percent, and averaged 4, 17, and 14 percent at the three sites respectively. Brown trout embryo mortality was highest during the pre-eyed stage, and the authors suggested that it was because embryos at that stage have not developed a circulatory system and rely on diffusion for oxygen (Maret et al. 1993). Brown trout embryo survival to emergence increased greatly with mean IGDO concentrations above 8.0 mg per L and 70 percent oxygen saturation (Maret et al. 1993). Maret et al. (1993) suggested that the major factor in brown trout embryo mortality might have been sediment reducing intergravel water velocities and consequently IGDO. However, the researchers also noted that other factors that were not measured, such as oxygen demand of the sediments and decaying eggs, might have caused dissolved oxygen concentrations to fall below necessary levels (Maret et al. 1993). The researchers recommended future studies that would consider how the biochemical oxygen demand of sediments in combination with reduced exchange with oxygenated surface water might affect IGDO in egg pockets.

Predation: Brown trout embryos and larvae are susceptible to predation because of their small size and immobility. The egg-embryos and larvae (alevins) are small enough to be preyed on by benthic invertebrates, but benthic-feeding fishes are more commonly noted as a concern, particularly suckers and sculpin. Several researchers have found that sucker and sculpin predation on trout eggs and alevins is not a significant source of mortality, and some have suggested that although some predation does occur, viable eggs buried in the redds are relatively protected (Holey et al. 1979, Moyle 2002, Pender and Kwak 2002). Maciolek and Needham (1952) suggested that the few brown trout eggs they found in the stomachs of rainbow and brown trout adults during a winter diet analysis had been disturbed from redds and released into the stream current by anchor ice dynamics. In their study of the effects of sediment and other types of non-point source pollution on brown trout embryo survival, Maret et al. (1993) concluded that the 18 to 83 percent survival rate of brown trout to emergence at the control site indicated other factors such as predation by macroinvertebrates and disease accounted for embryo mortality.

Because "hatched" brown trout larvae remain in redds and continue to develop while being sustained by their yolk sacs, they are exposed to similar threats as the incubating egg-embryos. However, additional factors may cause mortality at the alevin stage. As discussed above, alevins in redds may be more vulnerable to dewatering than embryos. Additionally, alevins can be trapped in redds and prevented from emerging by sedimentation (Jensen and Johnsen 1999). Another factor affecting brown trout survival at the alevin stage is the adequacy of their yolk resource in sustaining them until they finish development and switch to live prey. Larger eggs produce larger alevins with a greater yolk resource, improving their probability of survival as they have a longer period to find adequate exogenous food resources (Elliott 1994). Bagenal (1969b) found that brown trout fry derived from larger eggs survived longer than those from small eggs did. Larger alevins may also be vulnerable to predation by macroinvertebrates for a shorter period than smaller individuals are.

Post-emergence survival of young-of-year: Emergence of brown trout fry from the redd is a shift in habitat use that is accompanied by a transition from yolk reliance to feeding on live prey (Stefanik and Sandheinrich 1999). The post-emergence period is considered a critical time in the survival of brown trout and mortality after emergence can be extremely high. Mortality rates greater than 90 percent have been reported for recently emerged brown trout fry (Elliott 1994). In a 20-year study of a population of brown trout in England, Elliott (1994) found that the critical period of fry mortality varied among year-classes from 33 to 70 days post-emergence. In some systems, fry mortality during the post-emergence period is density dependent and inversely related to egg abundance (Elliott 1994). In other systems, density dependent factors appear less important (Pender and Kwak 2002), or a combination of density dependent and independent factors is thought to regulate age-0 brown trout survival in accordance with annual variability in factors such as trout abundance and flow regimes (Latterell et al. 1988, Jenkins et al. 1999). Jenkins et al. (1999) suggested high mortality during very early life stages may be a more important mechanism of population regulation in systems with anadromous populations of brown trout (e.g., Black Brow's Beck as described by Elliott 1994) in which population fecundity is not related to local food availability. Therefore, the number of offspring can easily exceed the carrying capacity of stream rearing habitats. After the critical post-emergence period, mortality rates decline and are thought to be primarily density independent. Factors that influence survival rates of YOY brown trout include the size of fry, food availability, intra- and inter-specific competition, predation, habitat availability, and disturbances such as flow variability.

Impacts of increased stream flow on fry survival during the post-emergence period have received much

research attention. High flows can displace brown trout fry downstream, reduce the amount of suitable rearing habitat, decrease food availability, and increase competition for territory and food (Latterell et al. 1988). Several studies have suggested that high flows during the emergence and post-emergence period negatively affect survival of age-0 brown trout. However, variations in the timing, magnitude, and duration of spring-summer high flows related to snowmelt runoff in Region 2 vary considerably among systems and years, and consequently there is much variability in the extent of the impact on brown trout populations. Similarly, for regulated rivers, the differences in flow releases among dams and years have variable impacts on brown trout recruitment depending in part on the timing, magnitude, duration, and frequency of releases.

The susceptibility of age-0 brown trout to displacement by high flows has been related to body size in addition to body condition, water temperature, flow timing, and the availability of refuges from currents. Anderson and Nehring (1985) suggested that high flows soon after fry emergence (i.e., before fry have reached a size that enables sustained swimming) can be the most detrimental to trout recruitment in Colorado systems. Once age-0 trout reach an adequate size, they are thought to be less vulnerable to high mortality from flow increases, except in extreme events such as flash floods (Anderson and Nehring 1985).

In a flume study, Vehanen et al. (2000) found that increased flows displaced age-0 brown trout, especially after their first exposure to high flows. In experiments, the highest proportion of age-0 brown trout were displaced in winter when water temperatures were low; reduced swimming ability was thought to be a primary factor (Vehanen et al. 2000). Age-1 brown trout were more easily displaced by high flows in spring than age-0 trout were during late summer at similar temperatures (Vehanen et al. 2000). The authors speculated that age-1 brown trout in early spring were in poorer condition (therefore less resistant to displacement) than yearling brown trout at the end of the summer growth period (Vehanen et al. 2000). Heggenes (1988b) found that induced peak flows in a small stream in Norway did not displace brown trout (mean length $\geq$ 67 mm [2.6 inches] TL) and suggested that young brown trout were able to use coarse stream substrates as micro-refuges from increased currents. Similarly, Jensen and Johnsen (1999) reported that spring floods did not significantly increase mortality of age-1+ brown trout.

Anderson and Nehring (1985) evaluated the impacts of spring and summer discharge levels on brown trout fry below a reservoir on the South Platte River of Colorado. Brown trout fry emerge from late March to early April in the South Platte River, and discharge levels during April and May were thought to regulate year-class strength (Anderson and Nehring 1985). The researchers found that brown trout year-class strength was significantly correlated with peak discharge in spring, and recruitment was lowest during three years when discharge from an upstream reservoir rose quickly in spring and was sustained at a high level through mid-summer (Anderson and Nehring 1985). Similarly, elevated discharge from snowmelt runoff in early summer reduced recruitment of fall spawning brook and brown trout in mountain streams in Colorado (Latterell et al. 1988). The magnitude and duration of high flows in the streams were inversely related to brown trout recruitment; however, the researchers were not able to evaluate the effects of peak flow timing on brown trout recruitment due to data limitations (Latterell et al. 1988).

An indirect impact of high flows on age-0 brown trout is a reduction of food availability. Allen (1951 as reported by Jensen and Johnsen 1999) observed reduced growth of brown trout following a heavy spate due to mortality of invertebrates. Jensen and Johnsen (1999) found that unlike sympatric Atlantic salmon, the growth of brown trout in a river in Norway was not reduced in years with high spring flows. They speculated that this was because brown trout fed more on terrestrial insects, the supply of which was unaffected by floods (Thomas 1962, Egglishaw 1967 as referenced by Jensen and Johnsen 1999).

In their native range, age-0 brown trout have been found to be less susceptible to high spring flows associated with snowmelt runoff after emergence, and one study suggested that water temperatures during brown trout emergence might be an important factor in determining fry mortality. Jensen and Johnsen (1999) studied the effect of peak spring floods on survival and growth of juvenile Atlantic salmon and brown trout in a Norway river. The river had a flow regime similar to that of the Rocky Mountain streams with characteristically low winter flows followed by a rapid increase in discharge associated with snowmelt runoff in spring (May-June), followed by low discharges summer and smaller spates in autumn (September/October) (Jensen and Johnsen 1999). In the study, brown trout and Atlantic salmon typically hatched and emerged from the gravel during the periods of high spring discharges (Jensen and Johnsen 1999). Interestingly, Jensen and Johnsen (1999) found that age-0 brown trout survival was not significantly affected by discharge during the egg stage

or after emergence. Instead, low discharges during the alevin stage and high water temperatures at emergence positively influenced brown trout year-class strength. The researchers remarked that even though brown trout are better adapted to low temperatures than Atlantic salmon are, in cold years low water temperatures during emergence apparently limited brown trout recruitment (Jensen and Johnsen 1999). Jensen and Johnsen (1999) suggested that cold water temperatures may reduce age-0 brown trout survival by negatively affecting initial feeding success and swimming performance. The study found that increased age-0 brown trout mortality was not limited to years with extreme floods, and since it occurred during years with more "modest flows," water temperatures during emergence may significantly affect brown trout recruitment (Jensen and Johnsen 1999).

As discussed previously, several studies have indicated that larger sized eggs result in larger larvae in salmonids, and larger fry are thought to have a comparative advantage over smaller fry for survival. Larger body size is thought to contribute to improved swimming performance, reduced predation risk, and increased feeding ability.

Researchers have found that brown trout fry from larger eggs grow faster and perform better in swimming stamina experiments. Ojanguren et al. (1996) found that egg size (based on dry weights) accounted for most of the variance in mean fry length 52 and 90 days after hatching, and fry fork length positively influenced swimming endurance of brown trout fry. Ojanguren et al. (1996) also observed that swimming stamina after a six-day starvation period was reduced minimally for larger brown trout fry whereas the stamina of smaller fry was notably diminished. Brown trout fry size has also been correlated with water temperature during incubation. Stonecypher (1992) found that brown trout embryos incubated at lower temperatures (2 ° and 4 °C) had greater lengths and weights than embryos incubated at 7 °C, but initial egg sizes were not determined in the study. Stonecypher (1992) recounted that in other studies, salmonid eggs incubated at lower temperatures produced longer larvae, but that greater weights of the larvae were related to initial egg size.

It is thought that the improved swimming abilities of larger fry also increases their ability to escape predation (Ojanguren et al. 1996). Larger body size may diminish predation risk by reducing the number of potential predators; for example, some invertebrate predators may not be able to handle and subdue a larger brown trout fry (Ojanguren et al. 1996). Larger brown trout fry may grow out of the smaller and more vulnerable size classes more quickly as growth rates of brown trout fry have also been positively correlated with initial size (Ojanguren et al. 1996).

Visual acuity increases with fish size and may contribute to improved feeding success of larger brown trout fry (Ojanguren et al. 1996). Larger sized fry may have greater reserves and therefore more time to adapt successfully to exogenous feeding (Elliott 1994). Larger brown trout fry may also be more resilient to periods of starvation than smaller fry are (Ojanguren et al. 1996). Larger fry may also have a competitive advantage in systems where survival is density dependent and competition for territories is important; however, other factors, such as prior residence and individual differences in aggressiveness, also influence the outcome of contests (Elliott 1994, Ojanguren et al. 1996).

In many systems, the specific combination of factors that contribute to high age-0 brown trout mortality is likely to vary from year to year and among locations. For example, Pender and Kwak (2002) speculated that several factors interacted and contributed to low age-0 brown trout densities at one of their tailwater study sites. The researchers found that age-0 brown trout densities were lower in the tailwater where females had lower fecundity and smaller egg sizes, but they noted that the site was also significantly less productive than other tailwaters and had the lowest invertebrate densities and highest sculpin densities observed. Although there was no evidence to suggest that sculpins were preying on age-0 brown trout, the researchers noted that a comparison of invertebrates (identified to the family level) found in sculpin and age-0 brown trout stomachs indicated similarity in their diets, suggesting that inter-specific competition may have also contributed to low age-0 brown trout densities at the site (Pender and Kwak 2002).

Spatial characteristics of populations

Metapopulation dynamics and spatial characteristics, such as sources and sinks, for naturalized populations of brown trout have not been the subject of intense study in North America. Similarly, the sensitivity of naturalized brown trout populations to habitat fragmentation and population isolation has not received as much research attention as for native salmonids. One study reported brown trout entrainment in irrigation canals in western Wyoming; however, the researcher found that brown trout were able to navigate out of the canal and back into the mainstem of the river (Roberts 2004).

Stream-resident brown trout appear to have small home ranges during non-migratory periods, but they may move significant distances in response to seasonal shifts in habitat requirements (see Activity and movement patterns section). Fluvial brown trout apparently have larger home ranges even during non-migratory periods and require access to tributaries for spawning and refuge habitats (see Activity and movement patterns section). Consequently, connectivity within stream systems is likely important to the persistence of naturalized brown trout populations.

Brown trout invasion of headwater habitats has not been as well investigated as invasions by brook trout in Region 2, but brown trout may have replaced many native salmonid populations in the region historically (Behnke 2002, McHugh and Budy 2005). Introduced trout, such as brown trout, are considered threats to native aquatic fauna (Dunham et al. 2004), and fisheries management practices that sustain or augment brown trout populations may have detrimental impacts on native fauna in some locations. Adams et al. (2001) described how stocking high mountain lakes to meet recreational fishing demands can facilitate the invasion of headwater stream networks by introduced trout and threaten remaining populations of native salmonids which tend to be concentrated in fragmented headwater refuges protected from downstream invasions of introduced salmonids by physical or biological barriers. Adams et al. (2001) suggested that managers consider the effects of geography on invasions when prioritizing efforts to protect or rehabilitate native species.

Limiting factors

As one of the most successfully and widely introduced fish species in the world that has established self-sustaining populations that have persisted over 100 years in many environments throughout Region 2, brown trout populations do not appear to be severely restricted by limiting factors. As discussed in previous sections, brown trout populations in Region 2 may be most limited by factors that affect reproductive success and yearling recruitment, such as:

❖ spawning and rearing habitat availability (Nehring and Anderson 1993)

❖ alteration of natural hydrographs or fluctuating flows during the spawning, incubation, or emergence periods (Anderson and Nehring 1985, Nehring and Anderson 1993)

❖ degraded habitats or water quality (Eaglin and Hubert 1993, Maret et al. 1993).

However, because brown trout tend to be longer lived than some trout species and are iteroparous, one weak year class will not drastically reduce the spawning population (Jensen and Johnsen 1999). If adverse conditions continue for several years, then they could be detrimental to brown trout populations.

Factors such as food and habitat availability (including winter habitats) can limit abundance and biomass of adult brown trout (Modde et al. 1991, Cunjak 1996) or indirectly affect reproductive success through reduced condition and fecundity of females (Pender and Kwak 2002). In systems where long distance movements between key habitats are required (e.g., spawning, winter refuge), features that hinder or preclude movements may become limiting factors (Cunjak 1996).

Water and land management practices that denude water or habitat quality, result in habitat loss, or alter flow regimes are most likely to adversely affect brown trout populations (Anderson and Nehring 1985, Eaglin and Hubert 1993, Maret et al. 1993). Natural disturbances, such as extended drought or other factors like the invasive diatom (*Didymosphenia geminata*), may also constrain some populations, as seen in some locations in the Black Hills National Forest (South Dakota Department of Game, Fish, and Parks 2005 and 2006 Fishing Handbooks, Environmental Protection Agency Region 8 Aquatic Nuisance Species: http://www.epa.gov/Region8/water/monitoring/didymosphenia.html).

Factors limiting the further geographic expansion of brown trout populations in Region 2 likely include natural geographic or anthropogenic barriers to movements and differences in water conditions and habitat availability associated with elevation gradients. In downstream lowland sections of drainages, the distribution of brown trout probably is most limited by their inability to survive high summer water temperatures (Rahel and Nibbelink 1999).

In contrast, reduced presence of brown trout in high elevation headwater streams is thought to be related to a variety of factors including lack of suitable habitats and low winter water temperatures during embryo incubation periods (Larscheid and Hubert 1992, Rahel and Nibbelink 1999, McHugh and Budy

2005). In Region 2 headwater streams, which are most commonly dominated by brook trout or cutthroat trout, researchers have found that brown trout remain superior competitors, even at low water temperatures, compared to the other two trout species (Taniguchi et al. 1998, McHugh and Budy 2005). Reduced competitive abilities of brown trout compared to other trout species at cooler temperatures is not thought to be a significant factor in explaining the upstream distributional limits of brown trout observed in the Rocky Mountain Region.

Rahel and Nibbelink (1999) suggested that colder water temperatures associated with higher elevation headwaters may favor the smaller-bodied and shorter-lived brook trout bioenergetically compared to brown trout, which grow larger, live longer, and reproduce later. The shallower waters associated with headwaters may also favor smaller-bodied species, such as the brook trout, since suitable habitat for larger fish like brown trout may be more limited, especially spawning areas as the depth of spawning habitats has been related to fish size in salmonids (Rahel and Nibbelink 1999).

In New Zealand, research suggests that brown trout distribution is limited by the availability of suitable habitats and that flow variations coupled with stream bed instability (in gravel-bed rivers with braided channels) restricted brown trout invasion of some systems (McIntosh 2000). In Australia, brown trout were found to be more vulnerable to periodic droughts resulting in stream drying and high water temperatures, exhibiting much higher mortality than native fishes (Closs and Lake 1996 as referenced by McIntosh 2000). In the western United States, McHugh and Budy (2005) suggested that the downstream limit of native cutthroat trout distribution in mountain stream systems was determined by the presence of brown trout and their interactions with them, whereas the upstream range of brown trout was limited by abiotic factors, including reduced reproductive success of brown trout at high elevations with cold water temperatures during embryo incubation periods.

Cold water temperatures during the winter incubation period of brown trout may be a significant factor in explaining the reduced numbers of brown trout observed at higher elevations in the Rocky Mountain Region. Stonecypher (1992) reported much reduced survival of brown trout embryos incubated at water temperatures of 2 °C, and Reiser and Wesche (1979) documented the freezing of brown trout eggs buried in the substrates of a southeastern Wyoming stream. Museth et al. (2003) attributed the poor recruitment of brown trout in a sub-alpine Norwegian lake one year

to a preceding "unusually cold and snow-poor winter" that "caused bottom freezing in the nursery streams." In a Pennsylvania stream in which habitat availability was in excess of the trout population level, the spatial distribution of brown trout was highly correlated with the distribution of spawning grounds, and brown trout dispersal from the natal areas was minimal (Beard and Carline 1991). If brown trout dispersal from natal habitats Region 2 streams follows a similar pattern, then the lack of brown trout in some headwater stream reaches may indicate poor reproductive success in those areas.

Community ecology

Because brown trout have been introduced to a variety of aquatic habitats, the variations in community ecology are numerous. In Region 2, brown trout are found primarily in mountain and foothill streams where fish assemblages include native and introduced salmonids, cyprinids, catostomids, and cottids (sculpins). For example, in ten mountain streams in Colorado, brown trout either were the only trout or they occurred with rainbow trout, and trout comprised most of the fish biomass; the remaining fish biomass consisted of catostomids, cyprinids, and cottids (Nehring and Anderson 1993). The ten Colorado streams were described as typically consisting of two to six nongame species in addition to the trout, including white sucker (*Catostomus commersoni*), longnose sucker (*C. catostomus*), bluehead sucker (*C. discobolus*), and flannelmouth sucker (*C. latippinnis*), longnose dace (*Rhinichthys cataractae*), speckled dace (*R. osculus*), or mottled sculpin (*Cottus bairdi*) (Nehring and Anderson 1993). Brown trout were found in similar stream communities in southwestern Wyoming in the Salt River basin with up to seven other fish species, including cutthroat trout (*Onchorhyncus clarki*), Paiute sculpin (*C. beldingi*), longnose dace, mountain sucker (*Catostomus platyrhynchus*), leatherside chub (*Sniderichthys copei*), and speckled dace; they were also found in depauperate assemblages in which the only other fishes were cutthroat trout and Paiute sculpin (Quist et al. 2004).

In cool-water lowland systems in Region 2 (e.g., larger streams, rivers, reservoirs, and tailwaters), brown trout are often part of fish assemblages that include a variety of native species in addition to other introduced sport fishes and forage species. In rivers and reservoirs, brown trout may be part of fish assemblages that also include other salmonids, percids, ictalurids, esocids, gadids (specifically burbot), native and introduced cyprinids and catostomids, and introduced forage fishes

(e.g., mooneyes, herrings) (Gipson and Hubert 1991, Baxter and Stone 1995, Marsh and Douglas 1997, Miranda 1999). Brown trout, along with several other species of trout, have been introduced into many alpine lakes in the western United States, many of which originally lacked trout or were completely fishless (Dunham et al. 2004).

As a non-native species, brown trout can have numerous effects on the communities into which they have been introduced. Dunham et al. (2004) described the range of impacts that non-native trout introductions have had on headwater ecosystems of western North America. These effects can be profound and wide-ranging and may include species extirpations, alteration of ecosystem productivity and nutrient cycling, dispersal of pathogens and diseases, and many additional indirect effects on ecosystems. The decline of many native fish populations, particularly of native salmonids, as well as amphibians and invertebrates, has been attributed to introductions of non-native trout (Fuller et al. 1999, Townsend 2002, Dunham et al. 2004). For example, research in New Zealand has shown that brown trout have a range of impacts on ecosystems, from affecting the behavior of grazing invertebrates to altering the distribution of large carnivorous invertebrates, displacing native fish, enhancing algal biomass and altering algal species composition (via their effects on invertebrates), and affecting primary production and nutrient flux (Townsend 2002). There is much information on the impacts of introduced trout in general and several species in particular (see Dunham et al. 2004 for many references in North America). The following sections discuss the role of brown trout in aquatic communities as predators, competitors, and prey and the parasites to which they are susceptible.

Predation by brown trout

Brown trout are carnivorous, and in many systems, they prey predominately on invertebrates, but fish become an increasingly important component of the brown trout diet as they grow larger. Brown trout begin incorporating fish into their diets around 130 to 160 mm (5.1 to 6.3 inches) TL (Mittlebach and Persson 1998, Museth et al. 2003), with the largest adults switching to predominately piscivorous diets at lengths around 350 mm (13.8 inches) TL (Clapp et al. 1990).

Garmen and Nielsen (1982) quantified the magnitude of stocked brown trout consumption of nongame fish in a Virginian stream. Most larger brown trout (>280 mm [11 inches] TL) were piscivorous, but consumption of fish by smaller trout (<280 mm

[11 inches] TL) was negligible in the Virginia stream (Garmen and Nielsen 1982). Garmen and Nielsen (1982) found that the larger brown trout consumed primarily small suckers, minnows, sculpin, and darters, and the three most frequently consumed fish species were consumed in proportion to their combined abundance (Garmen and Nielsen 1982). Brown trout consumption of fish increased in later summer and early fall with the increasing availability of age-0 fish. Over the duration of the summer (May through August), large brown trout (initial stocking density of 12.5 g per m^2) were estimated to consume 5,254 fish in a 300 m (984 ft.) stream section (Garmen and Nielsen 1982). Garmen and Nielsen (1982) reported that brown trout consumed fish ranging in size from 25 to 110 mm (1 to 4.3 inches) TL, and a large proportion (38 percent) were 25 to 50 mm (1 to 2 inches) long, consistent with the length frequency distribution of age-0 fishes.

Garman and Nielsen (1982) proposed that the introduction of brown trout to streams had particularly adverse effects on nongame fish for several reasons, including their reduced vulnerability to angling and increased over-winter survival compared to other trout, their quick adaptability to diverse native foods, and their more piscivorous diet than some native trouts. The authors suggested that the potential impacts of continuous piscivory from self-sustaining brown trout populations (or in systems where over-winter survival of stocked fish is high) could include a decrease in nongame fish biomass, an increase in brown trout production, and possible extirpation of nongame species (Garmen and Nielsen 1982).

Marsh and Douglas (1997) investigated predation by introduced fishes, including brown trout, on native fish species in the Little Colorado River. Unfortunately, only two brown trout digestive tracts were examined in the study, so the extent of their impact on native species could not be assessed. The one brown trout for which food items could be identified was reported to have fed mostly on terrestrial insects (20 percent) and fish (20 percent) followed by fish eggs (10 percent) (Marsh and Douglas 1997).

Brown trout also influence fish assemblage composition by preying upon the young of other salmonids. They appear to feed much more intensively on the YOY of other salmonids than on their own (Alexander 1977 as referenced by Fausch and White 1981). Alexander (1979 as referenced by Latterell et al. 1998) reported that predation by large brown trout accounted for 33 to 58 percent of age-0 brook trout mortality in a Michigan stream. Latterell et al. (1998)

reported adult brown trout abundance was correlated with reduced recruitment of yearling brook and brown trout in a study of six mountain streams in Colorado. Where populations of native cutthroat trout are found with brown trout, more research regarding the potential predatory effect of brown trout on cutthroat trout has been recommended (McHugh et al. *in press*). McHugh et al. (*in press*) suggested that brown trout predation on cutthroat trout is likely. The researchers did not find definitive evidence of brown trout predation on cutthroat trout, but they did report an indication of trophic level differentiation, with brown trout having higher trophic position than cutthroat trout, based on a combination of diet and stable isotope analyses (McHugh et al. *in press*).

Piscivory by large brown trout has been implicated as a cause for low returns on stocked salmonid fingerlings in lentic systems as well (Marrin and Erman 1982, Stuber et al. 1985, Tabor and Wurtsbaugh 1991). In Colorado, low creel returns on stocked fingerling rainbow trout in a reservoir was in part attributed to predation by large resident brown trout (Stuber et al. 1985). At the time, brown trout were estimated to comprise 40 percent of the assemblage and had a mean length of 342 mm (13.5 inches). The researchers found that 40 to 60 percent of brown trout stomachs contained remains of fingerling rainbow trout over the study period (Stuber et al. 1985).

In a sub-alpine lake in Norway, brown trout were found to prey heavily on an introduced minnow during its spawning season (Museth et al. 2003). Minnows were found in 9 percent of brown trout 160 to 299 mm (6.3 to 11.8 inches) TL and 20 percent of brown trout $\geq$ 300 mm (11.8 inches) TL during the minnow spawning period (Museth et al. 2003). In samples collected after the minnow spawning period, the observed frequency of minnows in brown trout stomachs fell to 1.4 percent and 0.8 percent in the 160 to 299 mm (6.3 to 11.8 inches) TL and $\geq$ 300 mm (11.8 inches) TL size classes, respectively (Museth et al. 2003). The researchers estimated that brown trout consumed the majority (90 percent) of their annual consumption of the minnows during the minnows' spawning period, which accounted for approximately 60 percent of the annual loss in biomass of the sexually mature component of the minnow population (Museth et al. 2003).

Brown trout are known to feed on a variety of organisms and consequently have affected numerous native aquatic fauna, particularly in systems that historically lacked fish predators (Garman and Nielsen 1982, Bradford et al. 1998). Brown trout have been found to have detrimental impacts on non-fish native taxa, especially in headwater systems that were initially fishless (Bradford et al. 1998, Dunham et al. 2004). In a study of alpine lake assemblages in the Sierra Nevada mountains of California, Bradford et al. (1998) found that several native taxa (especially those that were large, mobile, or conspicuous), such as tadpoles, microcrustaceans, and several species of epibenthic or limnetic macroinvertebrates, that were common in alpine lakes without trout were rare or absent in lakes with trout. In particular, tadpoles rarely occurred in lakes with trout. Tadpoles were found in just one of 18 lakes with trout, despite the presence of adult frogs at some of the lakes (Bradford et al. 1998). Similarly, macroinvertebrate species richness was reduced in lakes containing trout (Bradford et al. 1998). The authors concluded that the introduction of trout to the alpine lakes had "profound effects on the structure and composition of faunal assemblages."

Other impacts of brown trout on communities may result from their size-selectivity for prey or the prey's response to their presence. Brown trout have been reported to be selective of prey types and sizes. Several reports document brown trout preferentially consuming larger individuals of several species of invertebrates in greater proportions than their abundance (Newman and Waters 1984, Hubert and Rhodes 1992) and consuming small-bodied or YOY fishes (Garmen and Nielsen 1982, Museth et al. 2003). The feeding selectivity of trout may affect prey growth rates, habitat use, and population structures, but the impacts may be difficult to discern in observational studies (Garmen and Nielsen 1982, Newman and Waters 1984, Pecarsky et al. 2002, Museth et al. 2003, Townsend et al. 2003).

Competitors

Brown trout have been widely introduced throughout Region 2, and in many locations, they occur with other native and introduced trout. Competition by introduced trout is considered a factor in the decline and extirpation of populations of native cutthroat trout in Region 2 (Behnke 2002), and brown trout have been able to displace and contribute to the decline of brook trout populations in their native range (Fausch and White 1981, Bachman 1991, Behnke 2002). In some locations, brown trout populations overcame native fish populations so rapidly that the native fish were extirpated (Behnke 2002).

Compared to native North American trout, brown trout are considered more resistant to angling, with rainbow, brook, and cutthroat trout considered

increasingly easier to catch (Behnke 2002). Observers of rainbow, brook, and brown trout in an aquarium characterized brown trout as more wary, remaining near the bottom and feeding less frequently, than the other trout species (Bachman 1991). Bachman (1991) remarked that the wariness of brown trout might explain its reputation as being harder to catch than other trout. Additionally, brown trout vision is better adapted for low light conditions than other trout; their retinas contain more rod cells, which may enhance their feeding success in dim light (Behnke 2002).

In systems with highly variable conditions (e.g., floods, ice dynamics), fish populations are affected by perturbations that may contribute to changes in relative species abundance and interactions (Fausch and White 1981). Waters (1983) suggested that floods and accompanying habitat loss that decimated a brook trout year-class contributed to the decline of the brook trout population and coincident expansion of brown trout in one stream. Cunjak (1996) speculated that in streams where winter habitat is a limiting factor, interspecific competition among salmonids could be severe.

Competition with brook trout: Brown trout have displaced brook trout from many systems in the native range of brook trout (Behnke 2002). In western North America, where brook trout are also an introduced species, a similar pattern of apparent brook trout displacement by brown trout has been observed. Several studies in montane areas of Region 2 have found that brook trout are typically predominant in headwater sections and brown trout are predominant in downstream sections at lower elevations (Kozel and Hubert 1989, Rahel and Nibbelink 1999). The distributional pattern of the two species within stream systems has been correlated with a number of inter-related factors including gradients in water temperature, stream size, stream slope, and elevation (Fausch and White 1981, Rahel and Nibbelink 1999). Fausch and White (1981) noted that because such environmental factors are correlated with one another, the distribution of the species cannot be attributed to any single factor, and the differential susceptibility of the two species to angling and predation is likely to contribute to the dynamics between sympatric populations.

Some combination of competitive interactions for habitats (e.g., feeding, resting, spawning) as well as for mates likely contributes to the observed distributional pattern in systems where the species are sympatric (Fausch and White 1981, Sorensen et al. 1995, Rahel and Nibbelink 1999, Grant et al. 2002). The relative competitive advantage of the two species can be influenced by factors such as size, age, stream size, habitat conditions, or the environmental adaptations of different populations (Fuller et al. 1999).

Fausch and White (1981) found that brown trout dominated brook trout in competition for scarce resting positions in a Michigan stream. Brook trout use of resting positions expanded to include more favorable sites when brown trout were removed from the study area, but because sufficient feeding positions were available, competition for feeding sites was not evident (Fausch and White 1981). In the Black Hills National Forest, Modde et al. (1991) found both brook trout and brown trout preferred pool habitats, but brook trout were more often found in lateral scour pools, which brown trout used less frequently than other pool types, suggesting that some type of negative interaction between brook and brown trout was occurring.

Fausch and White (1986) found that brook trout and brown trout competed in the same dominance hierarchy structure (as referenced by McRae and Diana 2005), which may explain Larscheid and Hubert's (1992) findings in mid-elevation reaches of a Wyoming stream where brook and brown trout co-occurred. Larscheid and Hubert (1992) reported that brook trout had an enhanced size structure and attained larger sizes in mid-elevation reaches (compared with headwater reaches) and suggested that larger brook trout were able to effectively compete with brown trout in mid-elevation reaches of the stream, but that small brook trout could be excluded from the optimal mid-elevation habitats. Larscheid and Hubert (1992) suggested that in lower elevation stream reaches, brown trout were completely dominant and able to exclude brook trout.

Rahel and Nibbelink (1999) noted that several researchers have found that brown trout are behaviorally dominant over brook trout at warmer water temperatures (Fausch and White 1981, Waters 1983), but in high-elevation streams with colder water, the competitive advantage may shift to brook trout (Fausch 1989). However, Taniguchi et al. (1998) found that brook trout did not have the competitive advantage at 3 °C in an experimental stream (as referenced by Rahel and Nibbelink 1999). Rahel and Nibbelink (1999) suggested that the cold water temperatures associated with higher elevation stream reaches in Region 2 may favor brook trout bioenergetically or that brook trout reproduction may be more successful than brown trout in small headwater habitats because brook trout mature at a smaller body size and can spawn in shallower waters.

Reproductive interactions between the two species are also thought to contribute to the displacement of brook trout by brown trout. Several studies have reported that the spawning seasons and habitats of brook and brown trout overlap and redd superimposition and heterospecific spawning between the species has been observed (Sorensen et al. 1995, Grant et al. 2002). No isolating reproductive behaviors were observed between brook and brown trout in the wild (Grant et al. 2002), and reproductive interactions between the two species are thought to be more detrimental to brook trout for several reasons. Brook trout spawn earlier and their redds are more likely to be disturbed by later spawning and larger brown trout, which construct deeper redds (Sorensen et al. 1995). Additionally, male brook trout are more likely to waste effort courting larger brown trout females than smaller brook trout females (Sorensen et al. 1995). Furthermore, because brook trout tend to be smaller than brown trout, male brown trout have the advantage with females of both species (Sorensen et al. 1995). Finally, because brook trout are shorter-lived than brown trout and may only spawn once, brook trout populations are more vulnerable to successive years of poor reproduction (Bachman 1991, Sorensen et al. 1995).

Competition with rainbow trout: Several researchers have demonstrated that the diets of brown and rainbow trout are similar and broadly overlap (Marrin and Erman 1982, Behnke 2002), suggesting that competition between the species could occur where food or foraging sites are limited. Brown trout were dominant over rainbow trout, and both species used similar habitats in streams in the southeastern United States (Gatz et al. 1987). Rainbow trout used all preferred habitat types less in sympatry than in allopatry (Gatz et al. 1987). Water velocity and related variables were the most important habitat factors to rainbow trout, followed by cover and water depth (Gatz et al. 1987). The researchers suggested that brown trout were behaviorally dominant and habitat limited, with the result that rainbow trout were forced to shift their habitat use (Gatz et al. 1987).

However, in several rivers in Region 2, the two species are often found together in equivalent numbers (Behnke 2002). Behnke (2002) suggested that large rivers provide adequate habitat complexity for both species and noted that where populations of brown trout and rainbow trout successfully coexist, they have similar diets and growth rates. In other systems, differences in activity patterns, foraging behavior, or specific habitat preferences may reduce competition between brown trout and rainbow trout (Young et al.

1997, Behnke 2002). For instance, Young et al. (1997) found differences between brown and rainbow trout activity patterns and home range sizes in an Idaho stream. In general, rainbow trout were more mobile, moving greater distances, and were generally more active during the day than brown trout (Young et al. 1997). Behnke (2002) suggested that brown trout tend to associate more with cover along the stream banks while rainbow trout occupy mid-channel habitats.

Because rainbow trout and cutthroat trout are spring spawners, competition with brown trout for spawning habitat is not a factor. However, because age-0 brown trout emerge from redds earlier than spring-spawning trout, they are larger and may be better able to compete for food and habitat (Wang and White 1994).

Competition with cutthroat trout: Extirpations and declines of cutthroat trout populations throughout western North America have been attributed to overfishing, habitat destruction, and the effects of non-native species introductions (Wang and White 1994, McHugh and Budy 2005). The adverse impacts of brown trout on cutthroat trout have not received as much attention as those of brook trout and rainbow trout (Wang and White 1994, McHugh and Budy 2005). Non-native brown trout have replaced cutthroat trout in parts of their range, particularly in large rivers and lakes (Fuller et al. 1999, Behnke 2002). For instance, brown trout are considered partly responsible for the near extinction of Lahnotan cutthroat trout in Lake Tahoe in the 1940's and were introduced into Flaming Gorge Reservoir to control populations of Utah chub (McAffee 1966 and Teuscher and Luecke 1996 as referenced by Fuller et al. 1999).

Several researchers have suggested that brown trout displacement of cutthroat trout in streams is probably more common than previously thought (Wang and White 1994, McHugh and Budy 2005). Kershner (1995 as referenced by Shrank 2004) reported that Bonneville cutthroat trout (*Oncorhynchus clarki utah*) declined in streams stocked with brook trout, brown trout, or both. Wang and White (1994) recounted the observations of low rates of overlap between brown trout and cutthroat trout populations in Montana compared to the amount of overlap of rainbow and brook trout with cutthroat trout, and they suggested that the low degree of overlap between brown trout and cutthroat trout indicated that brown trout could displace cutthroat trout. Wang and White (1994) further speculated that Yellowstone cutthroat trout (*O. clarki bouvieri*) might be more competitive than other subspecies of cutthroat since Yellowstone cutthroat

populations overlapped more frequently with brown trout than westslope cutthroat trout (*O. clarki lewisi*) in the Montana research.

Only a few researchers have directly assessed competition between brown trout and cutthroat trout. Wang and White (1994) investigated microhabitat use and agonistic behavior between similarly sized age-1 wild brown trout and age-1 hatchery reared greenback cutthroat trout (*Oncorhynchus clarki stomias*) in experimental stream channels. The researchers reported that the brown trout were more aggressive than similarly sized greenback cutthroat trout, initiating more interspecific and intraspecific agonistic interactions and 92 percent of the observed attacks (Wang and White 1994). When placed in groups of cutthroat trout, single brown trout were able to dominate all fish, even larger cutthroat trout (Wang and White 1994). In the experiments, brown trout displaced greenback cutthroat from energetically favorable sites in pools and near food sources, but in the absence of brown trout, cutthroat trout shifted to a wider range of microhabitats, including more favorable sites (Wang and White 1994). In contrast, habitat use of brown trout changed little in the presence of cutthroat trout (Wang and White 1994). The researchers suggested that brown trout possessed an inherent competitive ability, not just a size advantage, over cutthroat trout.

More recently, McHugh and Budy (2005) reached the same conclusion that brown trout were superior competitors compared to cutthroat trout. McHugh and Budy (2005) investigated whether temperature-mediated competition between brown and cutthroat trout explained the distribution of trout species along elevational stream gradients in western mountain systems. Condition and growth rates were compared among groups of Bonneville cutthroat trout and brown trout in allopatry and sympatry reared in stream enclosures distributed along a 45 km (28 miles) section of a mountain stream in Utah (McHugh and Budy 2005). Asymmetric competition between the species was found, with brown trout adversely affecting cutthroat trout performance at all temperatures (McHugh and Budy 2005). Brown trout condition was not negatively impacted by cutthroat trout at any temperature; in fact, brown trout performed better in sympatry than allopatry, suggesting that for brown trout, intraspecific competition was more intense (McHugh and Budy 2005). In related research, the same authors found other evidence of brown trout competition with cutthroat trout. They reported that based on stable isotope tissue patterns analysis, the diets of the two species overlapped and cutthroat trout dietary habits shifted in response to brown trout presence (McHugh and Budy 2006, McHugh and Budy *in press*).

The researchers concluded that the downstream limit of cutthroat trout distribution in mountain stream systems was determined by the presence of brown trout and their interactions with them, whereas the upstream range of brown trout was limited by abiotic factors, specifically by reduced reproductive success of brown trout at high elevations with cold water temperatures during embryo incubation periods (McHugh and Budy 2005).

Competition with stocked trout: Hatchery brown trout have been found to be at a competitive disadvantage with naturalized brown trout for numerous reasons including their lower stamina, reduced tolerance of thermal change, unfamiliarity with natural features, higher susceptibility to angling, and inappropriate behavior (e.g., inefficient foraging, excessive movement, faulty habitat selection, tameness, and increased aggressiveness) (Wang and White 1994). Bachman (1984) reported that hatchery-reared brown trout introduced into a Pennsylvania stream moved more, engaged in more agonistic encounters, and ate less than the naturalized brown trout.

Despite the disadvantage of hatchery-reared compared to naturalized brown trout, stocking streams with catchable-sized trout has been found to have detrimental impacts on naturalized brown trout populations and has been related to decreased survival and growth rates. Vincent (1987) reported that naturalized brown trout population size increased, biomass increased, and mortality rates decreased after stocking of catchable rainbow trout stopped in two Montana streams. Bachman (1984) remarked that naturalized brown trout displayed signs of stress after the introduction of hatchery brown trout and that although large naturalized brown trout were able to win agonistic encounters with hatchery trout, the bouts were frequently much longer than those observed among naturalized brown trout.

Competition with non-game fishes: Non-game fishes have often been considered a significant source of competition for food resources in trout fisheries, and programs to reduce non-game fish abundance in order to improve trout production remain an important component of fisheries management (Wydoski and Wiley 1999). In some systems, particularly reservoirs, non-native non-game "forage" fishes have been introduced to augment game fish production, and accidental introductions of non-native non-game fish

have become a problem in some areas (Wydoski and Wiley 1999). Increasing concern for native non-game fishes over the years has resulted in several studies of diet overlap and the potential competition between brown trout and several native non-game fishes. Several studies have found that native non-game fish have little diet overlap with brown trout or potential to affect brown trout adversely via competition.

Marrin and Erman (1982) investigated summer diet overlap and potential competition between brown and rainbow trout and a native minnow and sucker in a subalpine California reservoir. The researchers reported minimal dietary overlap between the mainly limnetic-feeding trout and the benthic-feeding Tahoe sucker (*Catostomus tahoensis*) (Marrin and Erman 1982). The native cyprinid in the reservoir, the tui chub (*Gila bicolor*), was limnetic-feeding, like the trout (Marrin and Erman 1982). However, the researchers reported that the trout were more selective feeders (i.e., they focused on larger species of zooplankton) than the tui chub, and food resources were sufficiently partitioned to avoid competition between the species (Marrin and Erman 1982). Furthermore, once the trout reached a piscivorous size (>300 mm [11.8 inches] TL), both of the non-game fishes became trout prey (Marrin and Erman 1982).

Marrin and Erman (1982) found low levels of food niche overlap of rainbow and brown trout combined with the native sucker and minnow in July and August, but not in October. The increased diet overlap between trout and the native sucker and minnow in October was attributed the trout switching from diets composed of equal amounts of Dipteran pupae and zooplankton to one dominated by zooplankton while at the same time the suckers increased their consumption of zooplankton (Marrin and Erman 1982). The diet shifts of the species corresponded to reduced densities of benthic invertebrates in early fall, particularly in Dipteran densities (Marrin and Erman 1982). The researchers also noted that in October, 62 percent of trout ceased feeding, along with about a third of the non-game fish (Marrin and Erman 1982). They concluded that competition from native suckers could only affect trout adversely if the suckers were able to remove enough Chironomid larvae from the substrate to limit the number of emergents available to trout (Marrin and Erman 1982). The authors believed that scenario was unlikely since they found no evidence that suckers affected the density of Chironomidae or other taxa important to trout diets (Marrin and Erman 1982). The limnetic feeding tui chub had a higher diet overlap with trout, but they were almost exclusively planktivorous and therefore did not

significantly compete with trout for Diptera and surface insects (Marrin and Erman 1982). The native minnow had gill rakers adapted for small prey, which allowed them to feed less selectively on zooplankton than the trout (Marrin and Erman 1982). Marrin and Erman (1982) speculated that the only way the trout could be adversely impacted by exploitative competition from tui chub was if crustacean zooplankton were the only available food resource and the more numerous minnow population was able to harvest most of the large Daphnia preferred by trout.

Gipson and Hubert (1991) reported that body condition of rainbow trout in small Wyoming reservoirs was inversely related to the abundance of non-salmonid fishes. Hubert and Guenther (1992) assessed the effect of non-salmonid fishes and chemical and physical features of reservoirs on trout standing stocks in 22 Wyoming reservoirs. The researchers found non-salmonid fish abundance and total dissolved solids accounted for most of the variation in trout standing stocks ($R^2 = 0.56$), with non-salmonid fish abundance negatively related and total dissolved solids positively related to trout standing stocks (Hubert and Guenther 1992). The majority of the non-salmonid fishes found in the reservoirs were white suckers, longnose suckers, and yellow perch (*Perca flavescens*) (Hubert and Guenther 1992). Hubert and Guenther (1992) suggested that the results indicated potential competition between trout and non-salmonid fishes in Wyoming reservoirs. However, the results may have been somewhat complicated by differences in stocking practices among reservoirs; for instance, the authors noted that fisheries managers had learned which reservoirs were most productive through experience and consequently stocked those reservoirs with larger numbers of trout (Hubert and Guenther 1992).

Ruetz et al. (2003) reviewed the ecological debate regarding the competitive interactions between trout and sculpin in streams. Brocksen (1968) suggested that sculpin and trout are competitors, but Moyle (1977) disagreed with the suggestion, questioning the study design based on a literature review that indicated there was little evidence to support the notion of competition between trout and sculpin. Researchers have noted that diet overlap is often used as evidence for or against competition for food resources between trout and sculpin, even though diet overlap alone is considered insufficient evidence (Moyle 1977, Crowder 1990 as referenced by Ruetz et al. 2003). Trout and sculpin have different morphologies and foraging modes. For instance, sculpin lack a gas bladder and are associated with the benthos, primarily feeding from the stream substrate by using their lateral line system in addition

to vision to detect prey (Ruetz et al. 2003). In contrast, trout, which mainly rely on visual cues, are able to exploit prey drifting on the surface of the water and in the water column, and feed from the benthos (Ruetz et al. 2003). As a result, trout have more potential food resources than sculpin (Ruetz et al. 2003).

Ruetz et al. (2003) studied the potential for slimy sculpin (*Cottus cognatus*) competition with juvenile brown trout for food resources in field experiments. They specifically investigated whether the differences between the two species of fish might lead to predator facilitation, in which the foraging strategy of one predator causes prey to be more vulnerable to another, but they found no evidence of predator facilitation. Slimy sculpin growth was lowest in the presence of brown trout whereas brown trout growth was not strongly affected by presence of slimy sculpin (Ruetz et al. 2003). The researchers concluded that the results supported Moyle's (1977) assertion that sculpin do not diminish trout production in most circumstances (Ruetz et al. 2003). The researchers further suggested that results of their study indicated that brown trout is the superior competitor and more likely to impact sculpin adversely than to be negatively affected by sculpin (Ruetz et al. 2003). Although other researchers have found that when fish densities were held constant among different combinations of brown trout and sculpin (*C. gobio*), growth rates did not vary regardless of the presence or absence of the other species, suggesting that intraspecific and interspecific competition were similar in strength (Dahl 1998, Fausch 1998 as referenced by Ruetz et al. 2003).

Differences among systems, species, and relative densities of trout and non-game fish may result in different interactions between brown trout and non-game species. For instance, Pender and Kwak (2002) suggested competition between age-0 brown trout and Ozark sculpin could be a factor in Arkansas River tailwater sites with low invertebrate densities and high sculpin densities. Pender and Kwak (2002) reported that some components of age-0 brown trout and sculpin diets overlapped, but the sculpin diets were broader than age-0 trout diets and the amount of diet overlap varied among sites. In addition, the researchers noted that diet overlap was assessed by comparing taxa at the family level, which can obscure differences (Pender and Kwak 2002).

Predation of brown trout

Brown trout are considered more difficult to catch, by anglers and other predators, than other trout are (Fausch and White 1981, Behnke 2002). They are preyed upon by a number of piscivores, including mammals, birds, and other fish. Common mammalian and avian predators include anglers, river otter, mink, mergansers, great blue heron, pelican, and kingfisher. Young (1995) observed seven potential brown trout predators around a mountain stream in Wyoming, and reported that predators killed five of the study fish. Although Young (1995) did not list the predators observed, he stated that five were avian species and two were mammalian, including mink and presumably anglers.

Few studies have assessed the impact of predators on brown trout, particularly in winter, but mink, river otter, and mergansers have been found to be effective fish predators in winter (Cunjak 1996). Brown trout may be especially susceptible to endothermic predators in winter where suitable winter habitat is limited and brown trout aggregate in large numbers in the available habitat (Cunjak 1996). However, in other systems, predation during winter may not influence brown trout winter mortality. In a mountain stream in California during winter, no piscivorous animals or their tracks were observed, leading the researchers to conclude that predation did not significantly affect the trout population (Maciolek and Needham 1952).

Brown trout eggs and larvae are susceptible to predation while in the redds, particularly by benthic macroinvertebrates. Fish predation on incubating trout eggs is thought to be rarer, but benthic-feeding fishes, such as sculpin and sucker, have been considered potential salmonid egg-predators (Holey et al. 1979, Pender and Kwak 2002). By being buried in stream substrates, salmonid eggs are usually well protected from predaceous fish, and fish predation on eggs is thought to occur primarily when redds have been disturbed by other forces (e.g., anchor ice dynamics, scouring flows) (Maciolek and Needham 1952, Holey et al. 1979). Pender and Kwak (2002) noted that studies documenting sculpin predation on trout eggs and larvae were typically conducted "under artificial conditions." In their investigation of Ozark sculpin (*Cottus hypselurus*) diets in an Arkansas tailwater, they found no evidence of sculpin predation on brown trout eggs (Pender and Kwak 2002). In other systems with different species of sculpin that have evolved with native trout, egg and larvae predation may be more likely, but the depth of brown trout egg pockets would probably still provide substantial protection to developing embryos and larvae from benthic-feeding fishes.

Parasites and diseases

A number of parasites and diseases affect brown trout throughout its range in western North America. While much of the knowledge on parasites and diseases affecting trout has come from aquaculture, several studies have been conducted on the parasites and diseases that brown trout encounter in nature in western North America (Schisler et al. 1999, de la Hoz and Budy 2004). It was not feasible to review the extensive literature concerning fish pathology to determine the full range of parasites and diseases that brown trout encounter in the freshwater systems of Region 2, but there are numerous articles and books regarding salmonid pathogens in addition to several expert fish pathologists in Region 2 that should be consulted for specific information.

Generally, fish pathogens exist in all freshwater systems, and healthy fish can withstand occasional exposure and even harbor pathogens (Strange 1996). Under particular conditions, fish can become diseased, and growth, reproduction, and survival can be affected (Strange 1996). The interaction of several factors such as degraded water quality (e.g., sedimentation, low dissolved oxygen), pollutants, high fish density, poor fish condition, and other environmental factors that promote pathogens contribute to infections in fish populations (Strange 1996). Fish kills in wild fish are usually caused by adverse environmental conditions whereas mortality related to serious disease outbreaks are more commonly found in fish culture situations (Strange 1996).

Some diseases that affect brown trout in Region 2 include a range of gill ectoparasites (documented by Schisler et al. 1999), plestophera and epitheliocytis parasites (as reported by Kershner 1995 and cited by Schrank 2004), and bacterial diseases such as furunculosis (caused by *Aeromonas salmonicida*), enteric redmouth (caused by *Yersinia ruckeri*), and bacterial kidney disease (caused by *Renibacterium salmoninarum*) (Mitchum 1982). Diseases such as bacterial kidney disease are endemic in some naturalized populations of trout, including brown trout, in Region 2 (Mitchum et al. 1979), and naturalized fish can infect stocked fish (Mitchum and Sherman 1981). The transfer of bacterial kidney disease from a naturalized population of brook trout to recently stocked hatchery brook, brown, and rainbow trout was documented in a small lake and stream system in southeastern Wyoming (Mitchum and Sherman 1981). Mitchum and Sherman (1981) also reported trout in southwestern Wyoming infected with two common bacteria, *A. hydrophila* and *Pseudomonas*

fluorescens, which can cause disease in fish under high stress conditions. Viruses such as infectious pancreatic necrosis affect young trout (Strange 1996), and other viruses have been found in brown trout in the United States (Hendrik et al. 1991). Hatcheries screen fish for parasites and diseases and have regulations regarding stocking diseased fish. However, regulations vary, and some common parasites, such as *Aeronomonas* spp. (bacteria) or *Ichthyopthirius multifilia* (a protozoan), may accompany stocked fish (Heidinger 1999).

Whirling disease, caused by the parasitic protozoan *Myxobolus cerebralis*, can have devastating effects on trout populations (Baldwin et al. 1998), but brown trout are considered to have "partial resistance" in which "clinical disease is rare and develops only when exposed to very high parasite doses" (**Table 7**). Although brown trout are somewhat resistant, rainbow and cutthroat trout are more susceptible, and the presence of whirling disease in Region 2 waters is of particular concern for fisheries managers in the region (Thompson et al. 1999).

Whirling disease became a concern in Region 2 in the late 1980's when the parasite was first found in Colorado in 1987 and Wyoming in 1988 (The Whirling Disease Foundation, http://www.whirling-disease.org/). Whirling disease has not been detected in the trout fishery in the Black Hills of South Dakota, or in Nebraska and Kansas (The Whirling Disease Foundation, http://www.whirling-disease.org/). All states in Region 2, except Kansas, monitor state hatcheries and private fish culture facilities for the parasite (The Whirling Disease Foundation, http://www.whirling-disease.org/). Kansas reportedly does not monitor for whirling disease because all trout are obtained from certified whirling disease-free private hatcheries for put-and-take fisheries (The Whirling Disease Foundation, http://www.whirling-disease.org/). In Colorado, whirling disease is found in all cold-water watersheds except the Animas and North Republican rivers and is impacting trout populations in the following rivers: Cache la Poudre, Colorado, Dolores, Fryingpan, Gunnison, Middle Fork of South Platte, South Platte, Rio Grande, and Roaring Fork (The Whirling Disease Foundation, http://www.whirling-disease.org/). In Wyoming, the parasite has been detected in the following waters: North Platte, South Fork Shoshone, Salt, Yellowstone, Fire Hole, Big Laramie, Little Laramie, North Fork Popo Agie, Jakey's Fork, East Fork, New Fork, and Green rivers and Fontenelle Reservoir and Yellowstone Lake (The Whirling Disease Foundation, http://www.whirling-disease.org/).

Table 7. Susceptibility of salmonid species to whirling disease (*Myxobolus cerebralis*). "Scale of 0-3 or S: 0=resistant, no spores develop; 1=partial resistance, clinical 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)." Reproduced from the Whirling Disease Initiative, http://whirlingdisease.montana.edu/about/transmission.htm.

Genus	Species	Common name	Susceptibility
Oncorhynchus	*mykiss*	Rainbow trout	3
	mykiss	Steehead trout	3
	clarki	Cutthroat trout	2
	c. bouveri	Yellowstone cutthroat	2
	c. lewisi	Westslope cutthroat	2
	c. pleuriticus	Colorado River cutthroat	2
	c. virginalis	Rio Grande cutthroat	2
	c. stomias	Greenback cutthroat	2
	tshawytscha	Chinook salmon	2
	nerka	Sockeye salmon	3
	keta	Chum salmon	3
	gorbuscha	Pink salmon	1 S
	masu	Cherry salmon	1 S
	kisutch	Coho salmon	1
Salvelinus	*fontinalis*	Brook trout	2
	malma	Dolly Varden	1 S
	confluentus	Bull trout	1
	namaycush	Lake trout	0 S
Salmo	*salar*	Atlantic salmon	2 S
	trutta	**Brown trout**	**1**
Prosopium	*williamsoni*	Mountain whitefish	2 S
Thymallus	*thymallus*	European grayling	2 S
	arcticus	Artic grayling	0
Hucho	*hucho*	Danube salmon	3

Several studies have evaluated the distribution *Myxobolus cerebralis*-infected waters, and although the transfer of infected fish has often been the suspected mechanism of introduction, several studies have suggested that environmental factors (e.g., climate, watershed geomorphology, geology), and water quality and temperature may play a role in the variations in the distribution of the parasite and impacts on wild trout populations (Baldwin et al. 1998, Modin 1998, Thompson et al. 1999, de la Hoz and Budy 2004). Once introduced to a region, whirling disease can spread via fish and wildlife movements and human activities (Whirling Disease Initiative, http://whirlingdisease.montana.edu/about/transmission.htm). For instance, in Colorado a private fish hatchery operator was convicted recently of planting *Myxobolus cerebralis* infected trout in Colorado, New Mexico, and Utah waters (Whirling Disease Initiative Newsletter, January 2006). Ongoing research has also demonstrated that two life stages of the parasite (the triactinomyxon and myxospore stages) can be transferred by anglers' waders and wading boots (preliminary research results by Oregon State University researchers Paul Reno and David Latremouille as reported in the Whirling Disease Initiative Newsletter, January 2006). Research investigating the differential effects of whirling disease on different species, subspecies, and strains of salmonids continues (Ryce et al. 2001). Investigations of differences among strains of the tubifex worm (*Tubifex tubifex*) (the parasites other obligate host), which have exhibited variations in resistance to the parasite, are also underway (El-Matbouli et al. 1999, Dubey et al. 2005 as referenced by the Whirling Disease Initiative Newsletter, January 2006).

Envirogram of ecological relationships

Envirograms are dendrograms that depict the ecological relationships that influence the survival and reproductive success of a species (Andrewartha and Birch 1984). Envirograms consist of a centrum and a web, which together are used to represent all of the major ecological relationships important to a species (Andrewartha and Birch 1984). The centrum consists of the factors that directly affect the species and has four components: resources, malentities, predators, and mates (Andrewartha and Birch 1984). The web represents environmental factors that affect the species indirectly via their influence on the centrum components (Andrewartha and Birch 1984).

An envirogram for brown trout was developed based on the literature review performed for this species assessment (**Figure 7**). The envirogram attempts to summarize the major ecological relationships that influence the survival and reproductive success of brown trout in Region 2, and it reflects the information presented in this assessment. The resources component of the envirogram focuses on brown trout food and habitat and the major factors that can influence their availability. The malentities component of the envirogram depicts factors that can adversely affect brown trout populations, including natural and human disturbances of streamflow, habitat, or water quality. The mates component primarily focuses on spawning habitat availability, but also factors that influence survival of the early life stages, up to fry emergence. The predators component summarizes the ecological factors that influence the effect of various types of predators on brown trout populations, including human, animals, and parasites.

The envirogram depicts some of the major ecological relationships of brown trout in Region 2. However, the ecology of brown trout is complex, and

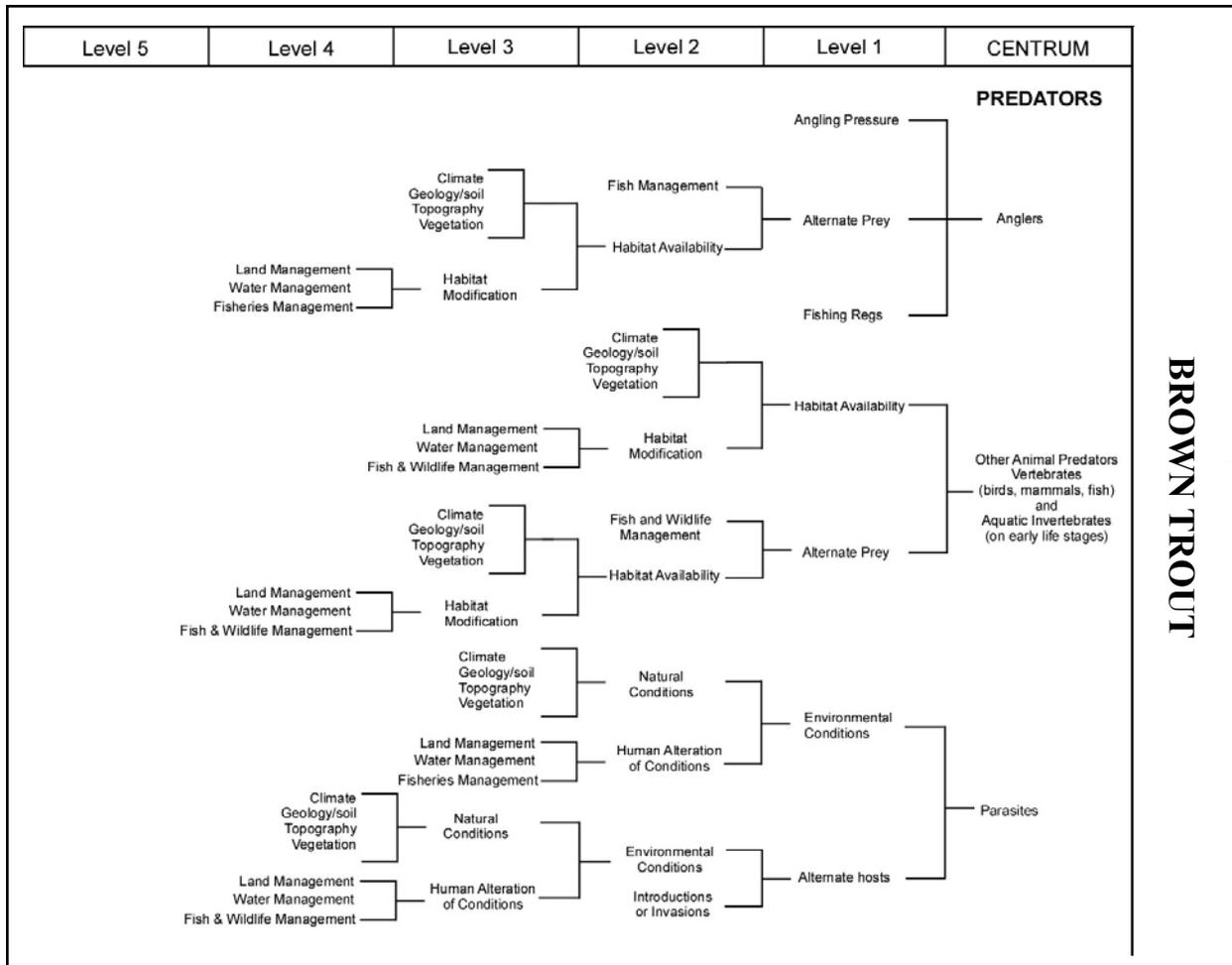**Figure 7a.** Resources envirogram of the brown trout.

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Figure 7b. Predators envirogram of the brown trout.

the primary factors affecting a population's reproductive success and survival can vary greatly among systems in Region 2 with differences in community composition, environmental conditions, and land, water, and fisheries management activities. The envirogram is not comprehensive, in the sense that not all the ecological connections that may influence brown trout populations in Region 2 are represented in detail. For example, brown trout populations in Yellowstone National Park occurring downstream of geothermal influences have been found to have poor reproductive success due to the effects of elevated water temperatures on brown trout gonadal development, among other factors. While this an important finding that is reported in the Fertility section of the assessment, the relationship between brown trout gonadal development and elevated water temperatures is not explicitly represented in the envirogram as it was not considered to be a major factor in the reproductive success of the majority of brown trout populations inhabiting cold and cool waters in Region 2. Similarly, in the interest of

simplicity some relationships are not fully developed. For example, in the predator component, there is a link between the impact of anglers on brown trout and angling pressure, but the factors that influence angling pressure are not outlined. Managers and biologists concerned with brown trout populations are urged to use the envirogram as a starting point to be refined and expanded on with the more detailed information presented in the assessment and specific knowledge of the system or population of interest.

CONSERVATION CONCERNS

Extrinsic Threats

Potential threats

Brown trout are well adapted for a variety of cold-water environments, and self-sustaining populations occur throughout much of the United States. While
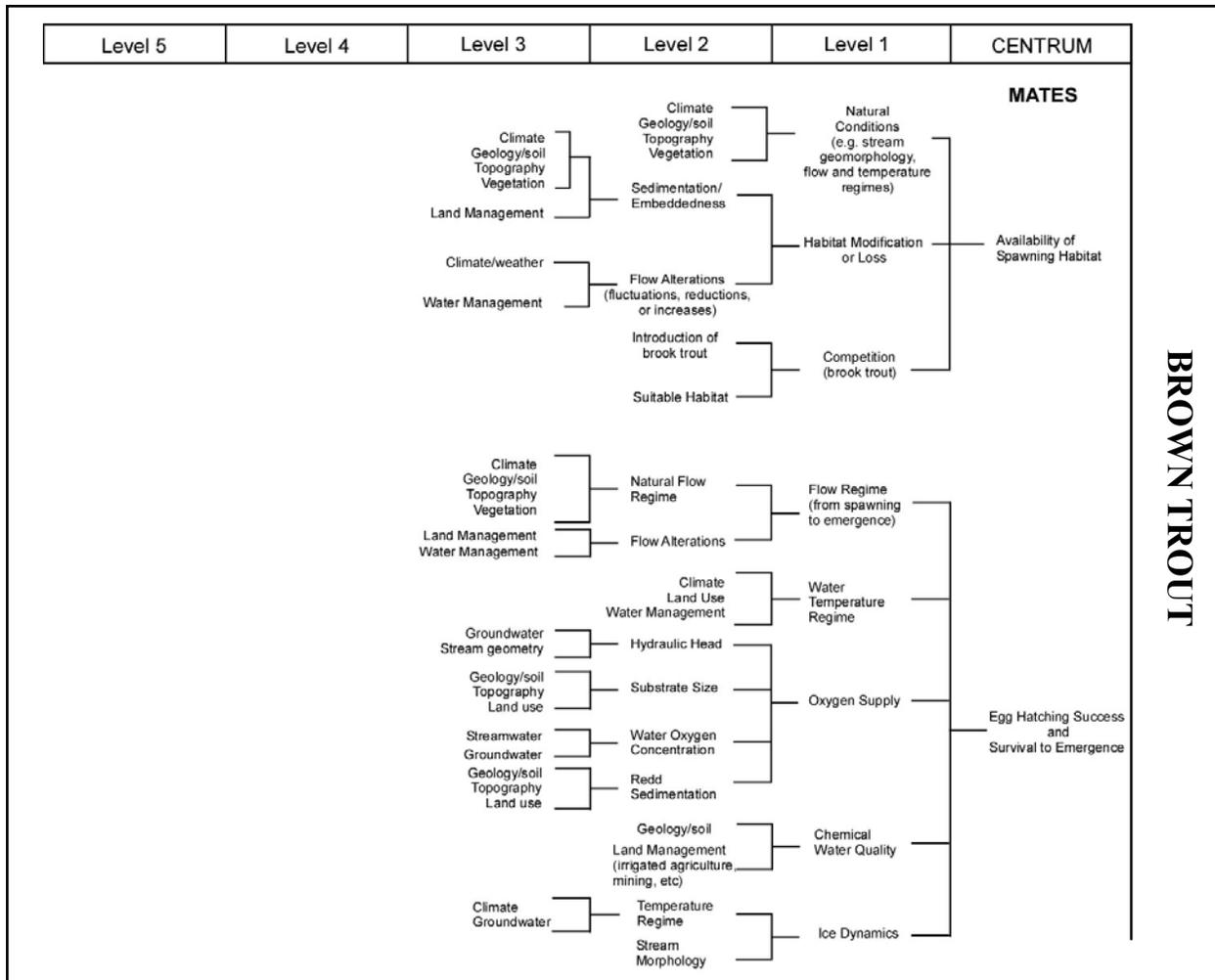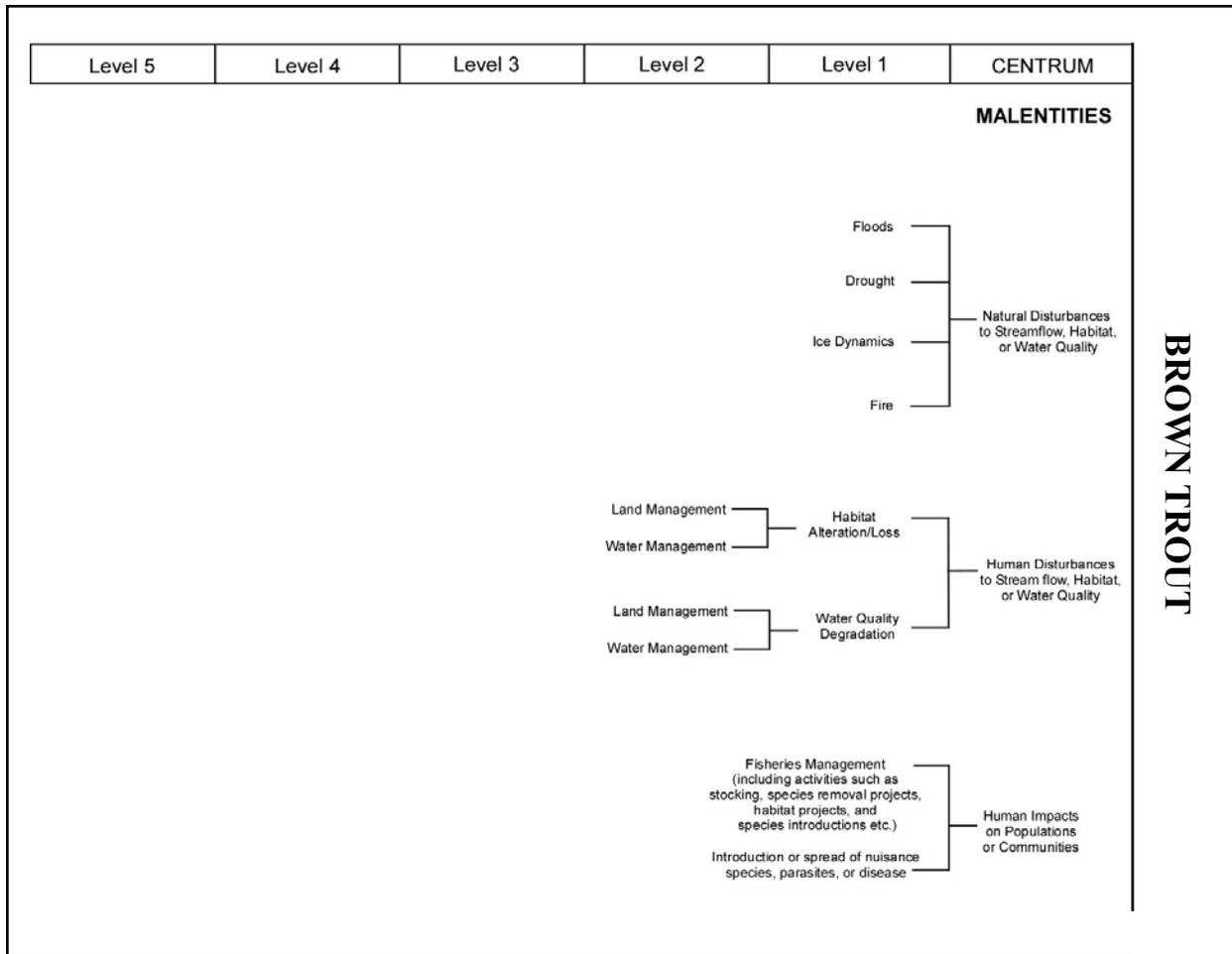
Figure 7c. Mates envirogram of the brown trout.

this species tolerates annual fluctuations in fertility, population growth rates are particularly sensitive to changes in absolute survivorship of YOY. If conditions that lower brown trout yearling recruitment are sustained over several years, then population size, structure, and biomass may be altered.

Typical periodic natural disturbances, such as floods and fires, are not thought to threaten the persistence of brown trout unless human activities have altered flow regimes, water quality, or landscapes in a way that augments the detrimental effects of natural disturbances. Water management activities that alter stream flow during spawning, incubation, and the sensitive early life history stages can adversely affect naturalized brown trout populations. Land management practices may also degrade or reduce habitat and can negatively affect populations. Of the myriad of fisheries management activities applied to brown trout, most are designed to maintain or improve recreational trout fisheries. However, in areas where the preservation or restoration of native fish populations is a primary goal, removal of brown trout may be a component of native species recovery efforts.

It is noteworthy that many water, land, and fisheries resources throughout the Rocky Mountains have been subjected to a range of intensive management activities historically. Many stream systems have been impacted by resource extraction or management practices that alter channel geomorphology or have deleterious effects on aquatic biota. For instance, Douglas Creek, a stream in the Medicine Bow National Forest that contains a well-studied brown trout population, has been impacted by timber harvest, tie-driving, gold mining, reservoir construction, transbasin water diversion, and grazing (Wolf et al. 1990, Harris and Hubert 1991) not to mention species introductions. Although the following sections discuss potential threats to brown trout from water, land, and fisheries management activities and

Figure 7d. Malentities envirogram of the brown trout.

natural disturbances separately, in many systems a number of impacts from past or current activities may occur in combination.

Water management

Dams and their associated alteration of natural flow regimes downstream have numerous effects on fish, and their impacts are well known. Detrimental impacts of dams on brown trout populations downstream have been attributed to fluctuating flows during the reproductive period and early life history stages (Anderson and Nehring 1985, Nelson 1986, Nehring and Anderson 1993, Pender and Kwak 2002).

In regulated systems, water management practices should be considered in the context of the local hydrologic regime and fish assemblage (Cunjak 1996). Fluctuating flows during the fall spawning period can influence spawning timing and habitat selection by brown trout (Pender and Kwak 2002). Spawning

sites selected under variable flow conditions may be unsuitable after dam releases and flows have stabilized, resulting in redd dewatering or fry emergence in swift water, mid-channel habitats (Anderson and Nehring 1985). Nehring and Anderson (1993) suggested that brown trout reproduction could be highly successful in regulated rivers, even in years of average or below average water discharge, as long as reservoir discharge did not exhibit rapid or extreme fluctuations. High releases after the sensitive post-emergence stage has passed are not considered as damaging (Nehring and Anderson 1993).

The potential impacts of flow alterations in winter on brown trout populations include changes in habitat availability and stream ice dynamics (Cunjak 1996). Winter is considered a difficult period for adult trout since discharge is typically at its lowest level and habitat availability and food may be reduced (Dare et al. 2002). Adult brown trout in regulated rivers may be resilient to short-term decreases in discharge in

winter, provided ample pool habitat is available, as the hypolimnetic releases from upstream reservoirs can dampen fluctuations in water temperature and prevent ice formation in regulated rivers (Dare et al. 2002). However, in smaller streams ice formation is more likely, and further reductions of streamflow (for instance for snowmaking in alpine ski operations) can result in accelerated ice formation, block fish movements, and change habitat availability for immobile eggs and fry (Cunjak 1996). Maciolek and Needham (1952) reported that many adult rainbow and brown trout died in a mountain stream when subsurface ice accumulation precluded water flow into a side channel and stranded trout. Additionally, water withdrawal from streams in winter may reduce accumulated thermal units and adversely impact fishes not well adapted for activity or development at freezing temperatures, particularly near the limits of their range (latitudinal or altitudinal) (Cunjak 1996).

In some systems where much of stream discharge is allocated for other uses, sustained low flows or dewatering may be a concern during the summer when agricultural demands for water tend to be higher (Covington and Hubert 2003). The potential detrimental effects of severely reduced streamflow on trout include reducing habitat, limiting food resources, impeding movement, and increasing summer water temperature or decreasing water quality (Covington and Hubert 2003). For trout inhabiting reservoirs, drawdowns may affect reservoir productivity, trout habitat availability, predator-prey or competitive interactions, reproductive success, and trout abundance (Hubert and Guenther 1992).

Sediment sluicing, the practice of opening dam gates to remove sediments accumulated behind lowhead diversion structures, can cause elevated concentrations of suspended solids several kilometers downstream for hours (Bergstedt and Bergersen 1997). Bergstedt and Bergersen (1997) found that sluicing resulted in "sediment concentrations and durations sufficient to cause behavioral, sublethal, and lethal responses in salmonids" in a Wyoming river. The researchers found that the mean condition of the salmonid assemblage, which included brown trout, was significantly greater upstream of the diversion structure than it was downstream (Bergstedt and Bergersen 1997). Detrimental effects of high suspended solids concentrations were found in internal and external examinations of mountain whitefish (*Prosopium williamsoni*) and included abnormal gills, mild fin erosion, and elevated hematocrit levels, which can be a sign of acute stress (Bergstedt and Bergersen

1997). Adverse effects of suspended solids on stream fish include mortality, reduced growth rates, reduced resistance to disease, abnormal embryo development (eggs and larvae), alteration of behavior and movement patterns, and a reduction of food items (Bergstedt and Bergersen 1997). The researchers found that salmonids moved less above the dam (mean = 1.8 km [1.1 mile]) than they did below (mean = 4.3 km [2.7 miles]), and they suggested that this may be due to an avoidance response to the sluicing or because visual cues that aid fish in maintaining position were lost (Bergstedt and Bergersen 1997).

Connectivity among stream, river, and lake habitats is important where brown trout populations rely on tributary streams for spawning habitat, cool-water refugia, or over-winter habitat. For example, one reservoir population of brown trout was found to use tributary streams both as cool-water refugia in summer (because the reservoir did not become stratified and provide suitable summer habitat) and for spawning (Garrett and Bennett 1995). Barriers to movements such as impassible culverts and diversion dams could impede brown trout movements with negative effects on self-sustaining brown trout populations. Because brown trout spawn in autumn during low flow conditions, high current velocities are not as likely to impede passage through culverts (Bedford and Gould 1989), but lack of adequate water flow or poorly maintained structures (e.g. debris accumulations) may hamper brown trout passage during low flow conditions in late summer and early autumn. A review of the literature on barriers to brown trout movement was beyond the scope of this assessment, but some research has been conducted on brown trout passage through highway culverts (Belford and Gould 1989) and fish ladders retrofitted for irrigation diversion structures (Schmetterling et al. 2002).

Land management

The effects of forestry, grazing, and agricultural practices as well as road construction on salmonid fishes and their habitat have been the subject of much research (see Meehan 1991 for a start). Land uses such as timber harvest, grazing, and roads can augment sediment delivery to streams and pose threats to fish populations if erosion rates and sediment delivery to streams are not managed. Increased sediment delivery to streams, whatever the source, tends to reduce trout habitat by resulting in less diverse physical habitats, decreased water quality, denuded spawning substrates, and reduced availability of deep pools (Hicks et al. 1991) and may be associated with decreased trout

standing stock in affected reaches (Harris et al. 1991, Eaglin and Hubert 1993).

Within Region 2, Eaglin and Hubert (1993) assessed the influence of logging and road construction on stream substrates and standing stocks of trout in the Medicine Bow National Forest in Wyoming. The 28 study reaches evaluated in the study represented the range of stream sizes and the extent of logging in the area (Eaglin and Hubert 1993). Mean channel slopes of study reaches ranged from 1.5 to 4.0 percent and were in drainages where clearcut logging had occurred between 1964 and 1984 (Eaglin and Hubert 1993). Study reaches were selected to ensure no confounding effects from water diversion structures upstream, beaver dams, historic tie driving activities, or past mining activities (Eaglin and Hubert 1993). Culvert density (measured as roads crossing watercourses) of the study reaches ranged from 0.0 to 5.1 culverts per km^2, road density ranged from 0.0 to 2.6 km per km^2, and the proportion of the drainage logged ranged from 1.5 to 25.3 percent (Eaglin and Hubert 1993).

Eaglin and Hubert (1993) found that the proportions of logged land and culvert density were each positively correlated to the amount of fine substrates and substrate embeddedness in stream reaches (Eaglin and Hubert 1993). Bankfull width was also significantly related to substrate embeddedness and amount of fine sediments (Eaglin and Hubert 1993). Furthermore, culvert density was negatively related to trout standing stocks (Eaglin and Hubert 1993). Together bankfull width and culvert density accounted for variation in trout standing stock in a multiple regression model (r^2 = 0.34, p = 0.006) with trout standing stock inversely related to both variables (Eaglin and Hubert 1993). The cumulative effects of logging and road construction appeared to impact trout standing stocks (Eaglin and Hubert 1993). The researchers also noted that sediment delivery into streams was likely increased by the number of times that roads crossed water courses and that roads, especially those that ran downhill, could serve as ephemeral channels for water and sediment during snowmelt runoff or thunderstorms (Eaglin and Hubert 1993).

Sedimentation that embeds stream substrates can denude or decrease brown trout spawning habitat. Beard and Carline (1991) observed that brown trout females appeared unsuccessful in excavating redds in embedded substrates downstream from a tributary with a high silt load. Embedded substrates also reduce YOY trout access to interstitial spaces (Mullner et al. 1998), which may serve as cover from predation (Hubert et al. 1994),

refuge from high flows (Heggenes 1988b), or over-winter habitat (Griffith and Smith 1993, Cunjak 1996).

Sediment deposition within redds can adversely affect the survival of brown trout eggs and alevins by altering chemical and physical characteristics such as dissolved oxygen concentration, intergravel water velocity, interstitial pore space, and water temperature (Young et al. 1990). Because brown trout spawn in the fall and the embryos develop slowly at low water temperatures, they are susceptible to the accumulation of sediment over months, especially in high elevation locations with protracted incubation periods where eggs are deposited in October and fry may not emerge until late spring. Brown trout survival to emergence is positively correlated with measures of mean particle size of redd substrates; as particle size increases, the proportion of fry surviving to emergence increases (Young et al. 1990). Young et al. (1990) found that as geometric mean particle size of redd substrates decreased, peak emergence of brown trout fry occurred earlier and the emergence interval was prolonged, indicating that substrate composition may affect other aspects of brown trout fry emergence.

In addition to sediment load, land use affects other aspects of water quality that can influence brown trout reproductive success. In an Idaho watershed with irrigated agriculture and grazing, best management practices (BMPs) were implemented to reduce non-point source pollutants. Although suspended solids were reduced by up to 78 percent and bacteria, nutrient, and turbidity levels decreased, the improvements in water quality were not adequate to restore trout reproductive success (Maret et al. 1993). The poor reproductive success of brown trout in the stream was attributed to insufficient dissolved oxygen levels in the stream water (Maret et al. 1993). The researchers speculated that organic sediments with high oxygen demands may have accounted for the reduced dissolved oxygen concentrations in trout redds and noted that stream bank erosion, irrigation returns, and small trout hatcheries in tributaries may have continued to contribute large amounts of suspended sediments, organic sediments, and phosphorus to the water despite the implementation of BMPs in the watershed.

Increased sediment loads from land use activities can also reduce stream habitat complexity by filling deep, low velocity habitats, such as pools and back waters, and by reducing cover (Wesche et al. 1987, Cunjak 1996). Preservation of diverse stream habitats is important to cold-water fishes that utilize a variety of habitats to complete their life cycle. Stream channels

exposed to increased sediment loads become wider and shallower, and as a result, they are more conducive to ice accumulation, which may further constrain habitat availability in winter (Cunjak 1996). In some systems in the Rocky Mountain Region, some historic activities have altered stream physical habitat complexity. For instance, stream channels used in tie drives were altered historically and remain wider and shallower, and they typically provide little instream cover for fish (Harris et al. 1991).

Intact riparian vegetation is considered important in mediating stream bank erosion, maintaining stream habitat complexity, and providing instream cover for fish (Wesche et al. 1987, Cunjak 1996, Covington and Hubert 2000). Riparian vegetation provides cover to fish in the form of overhanging vegetation, but it also promotes woody debris recruitment and the formation of undercut banks (Wesche et al. 1987, Covington and Hubert 2000). Additionally, in headwater streams, summer water temperatures are correlated with solar incidence, so land management practices that result in the removal of riparian vegetation can lead to increased water temperatures and could be detrimental to cold-water fishes (Hicks et al. 1991). Water temperatures in excess of about 19 °C (66 °F) have been associated with reduced growth rates of brown trout (Elliott 1994).

The effects of land management activities that alter the timing or intensity of peak flows or base flow conditions are similar to the effects described for water management practices that alter natural flow regimes. Potential adverse impacts of altered flows from land use practices include decreasing the reproductive success of brown trout during the spawning, incubation, or post-emergence periods. Increased runoff can also deliver excess sediment, nutrients, or pollutants to streams. In areas were cool groundwater inputs are the primary source of stream flow, such as trout streams in the lower Niobrara River basin in Nebraska, lowering base flows from groundwater withdrawal can also result in increased water temperatures in summer and contribute to lowered trout survival (Stewart 1985).

Contemporary and historic mining activities pose additional threats to stream fishes. The primary impacts of mining are increased erosion and sediment delivery to streams and impacts to water quality from acidic or toxic leachates (Nelson et al. 1991). The impacts of mining largely depend on type of material being mined, processing practices, and the age of the mine since regulations have changed over time.

Mining has occurred throughout the Rocky Mountains for over 100 years, and elevated concentrations of heavy metals are found some stream systems (Farag et al. 1995, Clements and Rees 1997). Heavy metals affect benthic invertebrate communities in streams by reducing abundance and species richness and altering community composition (Clements and Rees 1997). Heavy metals can have detrimental impacts on fish populations. Reduced biomass, population density, and survival observed in some brown trout populations have been attributed to metals contamination (Marr et al. 1995, Clements and Rees 1997). A comprehensive summary of the effects of mining on brown trout populations in Region 2 was not possible for this assessment. Nelson et al. (1991) provide an excellent review of the effects of mining on salmonids and their habitats, and interested readers are urged to consult the literature for additional information.

The effect of heavy metals on the physiology of brown trout and other salmonids has been investigated in the Clarks Fork River in Montana where overall salmonid abundance and biomass is reduced, but the brown trout is the predominant species present (Marr et al. 1995a, Marr et al. 1995b, Farag et al. 1995). Farag et al. (1995) found significantly elevated concentrations of several metals (i.e., copper, arsenic, cadmium) in brown trout tissues and other evidence of metals exposure including lipid peroxidation, microscopic copper inclusions, increased Metallothionein (a metal binding protein) concentrations, and significantly higher concentrations of lead in brown trout stomachs. The researchers did not observe effects of metal exposure on size or growth of brown trout, but sample sizes were small and fish were not aged (Farag et al. 1995). However, laboratory studies have related cooper exposure to reduced growth in rainbow and brown trout (Dixon and Sprague 1981a and 1981b as referenced by Farag et al. 1995), and increased tissue levels of arsenic, cadmium, and lead have been linked to decreased survival and growth of rainbow and brook trout (Cockrell and Hilton 1988, Benoit et al. 1976, Holcombe et al. 1976 as referenced by Farag et al. 1995).

Stream fish exposure to heavy metals from non-point sources is influenced by hydrologic events, and there are three main forms:

❖ chronic exposure to elevated concentrations during spring snowmelt runoff

❖ chronic exposure to comparatively low concentrations during winter low flows

❖ episodic exposure related to storm events in which pulses of extremely high concentrations of metals are accompanied by decreases in water pH and hardness (Marr et al. 1995a).

Toxicity of heavy metals to fish can be enhanced by acidic runoff from stream bank and floodplain sediments, which increase the biologically available forms of some metals. Heavy metals can persist in stream environments for long periods in contaminated sediments and be released during high flows or ice break-up, even after point sources of pollutants are remediated (Clements and Rees 1997). Acid mine drainage from tunnels or events such as failures of tailing ponds can release contaminants in lethal amounts in headwaters and decimate fish populations (Moore et al. 1991). Moore et al. (1991) concluded that "marsh systems may slow metals transport, but they do not necessarily completely stop downstream contamination of the food web by the most mobile of the metals."

The effects of heavy metals on brown trout in the wild are difficult to assess, in part because other variables that differ between metals impacted and unimpacted sites confound comparisons. In a section of the Arkansas River affected by metals contamination, Clements and Rees (1997) found that cadmium, copper, and zinc levels were elevated in the river water, in dominant invertebrate prey, and in brown trout gill and gut tissues. However, the metal concentrations in brown trout kidney and liver tissue, the organs that store and regulate metals in the body, were greater at the less impacted upstream station than at the downstream site (Clements and Rees 1997). Although metals contamination altered the benthic macroinvertebrates community at the downstream impacted site (the community shifted towards metal-tolerant taxa), prey abundance was not reduced, and brown trout size and condition factors were significantly greater at the metals-impacted downstream site compared to the upstream site (Clements and Rees 1997). Bioaccumulation of metals in fish are known to be influenced by feeding habits, water temperature, water hardness, and fish size, in addition to metal concentrations in water and food items (Clements and Rees 1997). The researchers suggested that the greater prey abundance downstream and the accompanying flexibility of brown trout diets, coupled with the slightly warmer temperatures at the downstream site, mediated the adverse effects of metals contamination on brown trout (Clements and Rees 1997).

Thunderstorms can temporarily increase metal levels, when surface runoff from streamside mine wastes reaches the channel, with potentially lethal effects on fish (Marr et al. 1995a). In a laboratory study that simulated variations in water quality in the Clark Fork River during storm events, Marr et al. (1995a) found that brown trout juveniles and fry were adversely affected by episodic and continuous metal exposure. The researchers found differences between brown trout and rainbow trout in their response to episodic exposure to a mixture of metals (i.e., zinc, copper, lead, cadmium). Brown trout were more sensitive than rainbow trout when water hardness and pH remained constant, but under conditions of depressed water hardness and pH, similar to those produced by runoff related to thunderstorms, brown trout were less sensitive to elevated metals than rainbow trout were (Marr et al. 1995a). Differences in the physiological response of brown and rainbow trout appeared to explain the relative resilience of brown trout to metals toxicity (Marr et al. 1995a). The researchers speculated that reduced pH associated with stormflow increases brown trout tolerance of metals, and provides some protection that compensates for their increased sensitivity to metals caused by reductions in water hardness (Marr et al. 1995). Among age classes, there was little difference between brown trout fry and juveniles during pulsed exposures, but fry were more sensitive to continuous exposure than juveniles (Marr et al. 1995a). In related research, juvenile brown trout physiologically acclimated to sub-lethal concentrations of metals, but acclimation was found to have metabolic costs that resulted in reduced growth, which the researchers suggested could also adversely impact reproductive potential (Marr et al. 1995b). Consequently, within a stream system, variations in the magnitude, duration, and frequency of runoff events can differentially affect trout species, age-classes, and population responses to toxicants (Marr et al. 1995a).

Acid mine drainage (AMD) is caused by the oxidation of sulfide minerals through the erosion of mine spoils. Although most commonly associated with coal mining, AMD also occurs where pyrite (FeS2) occurs including in granitic mineral deposits in the western United States (Nelson et al. 1991). Streams that receive acid mine drainage are usually characterized by low pH, high conductivity, and high metal and sulfate concentrations (Henry et al. 1999). Acid mine drainage from tunnels, runoff from tailing piles, or events such as leakage from or failures of tailing ponds, can release contaminants in lethal amounts and decimate fish populations (Moore et al. 1991, Nelson et al. 1991). An array of toxic metals may be dissolved in AMD streams: aluminum, iron, manganese, zinc, copper, arsenic, and lead. Streams with AMD can impact

otherwise unaffected streams into which they flow by creating acid mixing zones that are typified by areas of rapidly changing pH and precipitation of the metals that were dissolved in the acidic discharge (Henry et al. 2001). Moore et al. (1991) found that concentrations of some metals (in bioavailable forms) persisted kilometers downstream of headwater contaminant sources in a Montana river. Although the concentration of contaminants in solute form decreased over shorter distances via precipitation or adsorption and many particulate contaminants were entrained in marshes, cadmium and zinc remained bioavailable over several kilometers of the river (Moore et al. 1991).

The adverse effects of low pH on stream fishes include mortality, reduced growth rate, reproductive failure, skeletal deformities, and increased exposure to toxic metals (Nelson et al. 1991). In salmonids, poor recruitment rates of young age-classes have been related to acidic discharge, and studies have shown that alevins are particularly susceptible to low pH conditions (Nelson et al. 1991). Streams severely affected by AMD (pH <3.5) are usually fishless, whereas less severely affected streams (pH = 4.5-6.0) may have low fish diversity and abundance (Henry et al. 1999). Acidification has also been linked to elimination or declines in aquatic invertebrate populations and changes in the composition of invertebrate assemblage towards more acid-tolerant taxa affecting the food available to fishes (Nelson et al. 1991). The effects of acidification are not limited to the stream receiving the acidic discharge; at the confluence of a stream with AMD and an unaffected stream, fish mortality may be increased in mixing zones where toxic metals precipitate from the acidic water and may accumulate on fish gills (Henry et al. 2001).

Brown trout may reduce their exposure to metal by avoiding stream sections with elevated metals concentrations and reduced pH (Woodward et al. 1995). Avoidance behavior may explain the reduced abundance or distribution of brown trout in some areas (Woodward et al. 1995). For example, brown trout distribution in a section of the Shoshone River, Wyoming appeared to indicate avoidance of a stream section based on water chemistry characteristics, specifically an area downstream of a geothermal spring containing hydrogen sulfide (H_2S) (Dare et al. 1991).

Fisheries management

Although the direct impacts of fisheries management and anglers on brown trout cannot be overlooked, they are too numerous and diverse to address in detail for brown trout populations in Region 2 in this assessment. In addition to the original introduction of brown trout to the area, the main effects of fisheries management and anglers on brown trout populations in Region 2 include stocking, habitat improvement projects, harvest regulations, angling pressure, and harvest. Tools and practices of fisheries management and research may also have some detrimental effects on brown trout populations. Several researchers in Region 2 and elsewhere have found that electrofishing can cause injury and reduce growth rates in brown trout (Kocovsky et al. 1997, Thompson et al. 1997a, 1997b). In areas where management objectives are to restore or protect populations of native cutthroat trout or other native species, removal of brown trout has been a component of fisheries management (see Harig et al. 2000 regarding greenback cutthroat trout). Similarly, brown trout removal may be necessary in efforts to protect important conservation stocks of cutthroat trout or to facilitate the expansion of cutthroat trout populations in some situations (McHugh and Budy 2005, McHugh and Budy 2006). The effects of fisheries management activities on naturalized brown trout populations are briefly discussed in the following sections.

Stocking effects: In the past, brown trout and other fish introductions were made primarily by federal and state management agencies and less commonly through accidental releases and "well intentioned anglers" (Wingate 1991). In recent years, stocking of brown trout has declined, and many naturalized populations have been left to persist without augmentation (Behnke 2002). In a few areas of Region 2, brown trout continue to be planted to meet angler demands (see Distribution section). While stocking can have a multitude of impacts on aquatic communities, including naturalized brown trout populations as well as other taxa (see Community ecology section), it is conducted for the social and economic benefits provided to anglers and communities (Wingate 1991). With the increased awareness of the impacts of stocking introduced species, such as brown trout, on native trout and other fauna, there have been more recommendations in recent years that fisheries managers consider the impact of brown trout on native species in decisions regarding future stocking (McHugh and Budy 2006).

Stocking hatchery-reared brown trout in areas with naturalized populations also has detrimental effects on the "wild" brown trout that several researchers have remarked on over the years. Bachman (1984) observed that the introduction of the hatchery-reared brown trout appeared to stress naturalized brown trout and that

the hatchery fish engaged naturalized brown trout in agonistic encounters for feeding sites. These encounters lasted longer than what is typical of naturalized brown trout and led to exhaustion in naturalized fish that were involved in successive bouts. Bachman (1984) also observed that hatchery-reared brown trout moved constantly, fed less, and changed position more frequently than naturalized brown trout, and as a result, few survived over winter to the following year.

Vincent (1987) found that brown trout population size and biomass more than doubled four years after the cessation of stocking catchable-sized hatchery rainbow trout in a Montana river. Decreases in age-2+ brown trout numbers and biomass were seen when stocking of catchable-sized rainbow trout was initiated in a previously unstocked stream in Montana (Vincent 1987). Vincent (1987) also reported that mean annual growth of all age-1+ brown trout was reduced during years with stocking compared to years when no stocking occurred, particularly during winter and among yearlings and age-2 fish.

Stocking of catchable-sized rainbow trout also raised the mortality rates in naturalized brown trout populations for several years, until the population stabilized at a lower level, at which time the mortality rate was similar to the prestocking level (Vincent 1987). Stocking appeared have greater adverse effects on adult brown trout than on the young, with no significant changes in number between stocking and non-stocking years found for age-0 and yearling brown trout (Vincent 1987). Vincent (1987) also reported that the negative impacts of stocking appeared to negate the potential positive of effects of favorable water years on the naturalized brown trout populations during the study. Notably, the brown trout population appeared to recover quickly after stocking cessation, reaching peak biomass after two years, whereas naturalized rainbow trout biomass was still increasing four years after stocking stopped (Vincent 1987).

In systems where the number of available feeding sites determines the carrying capacity of the stream, the addition of hatchery-reared, catchable-sized trout may disrupt the linear dominance hierarchy established by naturalized brown trout, and thus create stresses that may effectively reduce the system's carrying capacity (Vincent 1987). Furthermore, the introduction of hatchery fish may increase naturalized brown trout susceptibility to angling since hatchery fish tend to be more active and appear to increase the activity of naturalized trout and affect their activity patterns (Vincent 1987).

Habitat improvements: Stream habitat restoration or enhancement projects are typically designed to increase the carrying capacity for trout by augmenting the availability of cover (Wesche et al. 1987). Assessments of the efficacy of trout habitat enhancement projects have been conducted in Region 2 (e.g., Shuler et al. 1994 or the "Compendium of trout stream habitat improvement projects done by the Wyoming Game and Fish Department, 1953-1998" available from http://gf.state.wy.us/habitat/aquatic/compendium/index.asp). However, some researchers have pointed out a few shortcomings or unforeseen effects of some habitat enhancement projects.

In order to promote self-sustaining populations and reduce the need for stocking, several researchers have suggested that habitat enhancement projects should address other habitat deficiencies that may be limiting populations in a system, such as winter or rearing habitats (Cunjak 1996, McRae and Diana 2005). Cunjak (1996) cautioned that habitat enhancement projects that focus on summer habitat availability might improve trout production beyond the carrying capacity that winter habitats can support in streams. Cunjak (1996) suggested that habitat simulation models and instream flow methodologies should incorporate winter habitat requirements and ice dynamics. McRae and Diana (2005) recommended that if suitable rearing habitats are limited, managers should direct their efforts towards enhancing rearing habitat to augment growth and survival of stocked fingerlings and to promote the potential for a self-sustaining population. Other studies have found that increasing the amount of gravel substrate can improve the natural recruitment of brown trout (Meyers et al. 1992, Mesick 1995 as referenced by McRae and Diana 2005), which can reduce the need for expensive put-and-take fisheries (McRae and Diana 2005). Some studies have found that angling success rates for brown trout decrease at water temperatures exceeding 19 °C, reducing angler satisfaction, and recommend habitat management objectives that prevent water temperatures in excess of 19 °C, including preventing practices that increase water temperature such as flow removal in summer and removal of streamside vegetation that provides shade (McMichael and Kaya 1991). Another consideration in enhancement projects is that work to improve angler access (e.g., clearing stream side brush) can change flow and sediment dynamics, alter habitats, reduce

rearing habitats for age-0 fish, and reduce overall fish abundance in impacted reaches (Cunjak 1996). The full complement of habitats required by different life stages as well as the inherent variability within and among streams should be considered to improve the efficacy of habitat enhancement projects (Cunjak 1996).

Population management through regulations: Fisheries managers use angling regulations and population, community, habitat manipulations to enhance or protect a fishery for the benefit of the users (Noble and Jones 1999). A synopsis of current regulations for the states encompassed by Region 2 is included in the Management Status and Existing Regulatory Mechanisms section. Certain waters are managed specifically, but in many areas, general regulations for trout apply. Variations in environments, habitats, communities, and fisheries management activities and regulations among systems, combined with differences in angling pressure among locations, can result in array of impacts on brown trout populations.

Lack of knowledge or understanding of fishing regulations is related to angler compliance levels and can significantly affect the attainment of management objectives (Noble and Jones 1999). Compliance with regulations can be difficult to promote, and the effects of non-compliance on a fish population are difficult to identify (Gigliotti and Taylor 1990, Noble and Jones 1999). Regulations and harvest can affect various aspects of population demographics, such as population age-structure, population reproductive potential, and mortality rates. Regulations, in combination with angling pressure and angler compliance levels, can have significant impacts on game fish populations (Gigliotti and Taylor 1990) because the mortality rate of a population of game fish is comprised of natural mortality, hooking or handling mortality, and legal and illegal catch mortalities (Wright 1992).

Wright (1992) suggested that the first step in managing trout populations in situations where abundance is low should be to determine what factors are limiting trout production, specifically whether carry capacity is limited by the existing habitat or if overfishing may be occurring. Wright (1992) also pointed out that in the past, some studies evaluating the effects of habitat availability or land management practices on fisheries have overlooked the impacts of fishing mortality and differential angling pressure among sites on results.

Temporal variation in habitat use and spatial variation of habitats within systems means that trout require adequate connectivity between summer, spawning, and winter habitats and that special regulation areas should be of adequate size to encompass the range of a population's habitat use (Clapp et al. 1990, Cunjak 1996). Fisheries managers should also consider the range of movement of the trout population when they establish special regulation areas (Clapp et al. 1990, Wright 1992, Cunjak 1996). For example, Clapp et al. (1990) found that a blue-ribbon fishing area utilized by large brown trout during spring and summer in a Michigan river would have to be around 5 km (3.1 miles) long to encompass the average spring-summer range of the fish. The researchers also observed that brown trout moved 10 km (6.2 miles) upstream to overwinter in habitat that was considered marginal for trout during summer (Clapp et al. 1990). Within Region 2, Young (1994) noted that special regulations protected spawning age trout in the North Platte River; but that once brown trout left the river for spawning in tributaries, they could be harvested by anglers.

Electrofishing effects: Electrofishing is one of the most common methods for sampling fish populations that reside in fluvial environments. Researchers have found that electrofishing can injure fish and result in behavioral changes, reduced growth rates, and lower survival rates (see Kocovsky et al. 1997, Thompson et al. 1997a, 1997b for references to specific research). For instance, Thompson et al. (1997a) evaluated the long-term effects of electrofishing on growth and body condition of brown trout in several Colorado streams and found that age-4+ brown trout that had been electrofished the year before had reduced growth rates in one stream and reduced body condition in another stream, compared to fish that had not been electrofished.

Within Region 2, several studies have been conducted to assess the effects of electrofishing injuries on fish populations. Thompson et al. (1997b) assessed the immediate effects of boat-mounted and "walk" electrofishing (using a shore-based unit) on brown trout in several rivers in Colorado, and Kocovsky et al. (1997) evaluated the long-term effects of annual three-pass backpack electrofishing on brown trout in a Colorado stream.

Thompson et al. (1997b) found that 18 to 52 percent of brown trout collected by boat electrofishing and 27 to 38 percent captured by walk electrofishing

had spinal injuries. Most of the injured fish (also including rainbow trout) had spinal injuries classified as least severe, and only 2.1 percent or less of the fish had the most severe types of spinal injuries (Thompson et al. 1997b). Internal hemorrhage injuries were observed in 24 to 45 percent of brown trout collected by boat electrofishing and 12 to 30 percent of brown trout collected by walk electrofishing (Thompson et al. 1997b). The researchers reported that fish length was significantly related to the probability of injury and suggested that fish in better condition may be more susceptible to injury as they may have more powerful muscle contractions (Thompson et al. 1997b).

Kocovsky et al. (1997) reported that after six to eight years of backpack electrofishing, injury rates of brown trout were 6.9 percent, based on external examinations. Based on X-rays and necropsy, Thompson et al. (1997b) found that rainbow trout were more susceptible to injury from electrofishing than brown trout were. When evaluating fish injury rates over longer terms, Kocovsky et al. (1997) found longnose suckers had the highest injury rates followed by brown trout, rainbow trout, and finally brook trout, but because fish were evaluated only externally for injury, actual injury rates were likely underestimated. Trout populations increased or remained stable over the study period, suggesting that repeated electrofishing did not adversely affect populations (Kocovsky et al. 1997). Kocovsky et al. (1997) also noted that the high mobility rates of some fish (specifically brook trout in their study) could obscure population effects of electrofishing injury in "spatially dynamic" populations.

Natural disturbances and climate change

It is unclear how sensitive brown trout populations are to particular natural disturbances, but existing land and water management practices at the time of the disturbance may have a role in augmenting or reducing the negative impacts of natural disturbances. Variations in geology, topography, climate, vegetation cover, and the sequence and severity of the disturbances would also affect the impacts of natural disturbances on brown trout and other members of cold-water fish assemblages.

Forest fires can be detrimental to fish populations by increasing mortality rates due to changes in water temperature and chemistry (Minshall and Brock 1991, Rinne 1996). Extreme degradation of water quality from toxic slurry or ash flows after fires causes high mortality among streamfish (Rinne 1996). Fire suppression methods may also cause fish mortality. Minshall and

Brock (1991) reported that the inadvertent release of fire retardant (ammonium phosphate) on a stream resulted in almost total trout mortality in the affected section. After fire, increased erosion and higher peak and total discharge from burned hillslopes can degrade stream water quality and fish habitat (Minshall and Brock 1991). Runoff is likely to be more flashy, and variations in the timing and magnitude of flows may negatively affect stream biota that are unable to adjust, resulting in decreased biotic diversity and production (Minshall and Brock 1991). Populations of aquatic invertebrates can be markedly reduced post fire, and recovery to pre-fire density and diversity can be slow (Rinne 1996). As watershed recovery progresses, biotic productivity may increase with increased algal and invertebrate production that is beneficial to fish (Minshall and Brock 1991). However, an extreme precipitation event may trigger debris flows from burned slopes or mobilize sediment from ephemeral channels and result in elevated suspended sediment concentration in streams and fish mortalities several years after fire (Bozek and Young 1994). The extent of fire impact on brown trout populations would depend on numerous factors:

- ❖ the spatial characteristics of the fire relative to the distribution of brown trout in the watershed

- ❖ the size of the burn area

- ❖ burn intensity

- ❖ the weather after the fire, which affects erosion and streamflow

- ❖ the availability of downstream or other refugia for fish

- ❖ stream connectivity and the potential for recolonization of fire-affected reaches by fish from unaffected areas (Minshall and Brock 1991, Rinne 1996).

Winter conditions, particularly stream ice dynamics, can adversely affect brown trout populations. Relatively few studies have been conducted on populations of brown trout in winter in environments similar to those experienced in Region 2. In a winter study of a California mountain stream, Maciolek and Needham (1952) concluded that brown trout "fared quite well, for ice conditions that caused a small initial winter mortality, later offered fish cover and food." However, Maciolek and Needham (1952) continued that it was "probable that lower temperatures, more

continuous cold weather, heavy snowfalls, or a combination of these would have a more drastic effect on fish and other stream life." A study of brown trout in Norway attributed low recruitment one year to a preceding cold, dry winter that resulted in subsurface ice formation in brown trout spawning streams (Museth et al. 2003). Because winter conditions and related brown trout mortality rates are likely to vary from year to year and location to location, severe winter conditions and ice dynamics alone are unlikely to present a serious threat to brown trout populations unless sustained for a number of years or in combination with other detrimental impacts on the population.

Several researchers have investigated the potential impact of climate warming on trout populations in the western United States (Keleher and Rahel 1996, Rahel et al. 1996, Jager et al. 1999). In general, changes in temperature regimes (Keleher and Rahel 1996), coupled with hydrologic changes (Jager et al. 1999) associated with climate change, have the potential to fragment populations of trout as the amount of suitable habitat in downstream reaches is reduced. Jager et al. (1999) suggested that interactions between hydrologic and temperature effects may combine to form nonlinear threshold population responses to climate change. Jager et al. (1999) also suggested that hydrologic changes that could affect trout mortality or reproductive success have effects (e.g., redd dewatering, scouring) that should be considered in addition to temperature effects such as summer starvation, lethal high temperatures, or incubation temperatures.

Jager et al. (1999) found that brown trout were more susceptible to redd scouring when the hydrologic regime was shifted from one of peak flows in early summer to rain-on-snow events in winter, but they noted that the adverse impacts were not as great as expected. Jager et al. (1999) commented that traits such as thermal tolerance, growth, maturation, and spawning timing would be important in population response to the effects of climate warming, and they noted Kaya's (1977) findings that in a geothermally-heated stream, rainbow trout delayed spawning to fall while brown trout did not delay spawning and experienced abnormal gonadal maturation at elevated water temperatures.

Trout population responses to climate warming are likely to vary among locations. For instance, local groundwater inputs may mediate temperature effects on egg incubation, and prey availability may mediate summer starvation in some locations (Jager et al. 1999). Isaak and Hubert (2004) suggested that trout population response to climate warming may be "context specific" if populations exhibit a non-linear response to temperatures across a broad range. For example, in situations in which warm temperatures are currently limiting, populations would move upstream and become more fragmented as suggested by Rahel et al. (1996). In contrast, where cold temperatures were limiting, populations could expand into previously unoccupied areas (Isaak and Hubert 2004). McHugh and Budy (2005) pointed out that although brown trout invasions of montane stream systems may have slowed since their introduction, if cold water temperatures have limited brown trout invasion upstream, then climate warming could enable brown trout to expand their distributions upstream. Several studies have focused on the effects of temperature increases on trout populations, but fewer studies have considered other impacts of climate change on coldwater fishes, such as changes in local hydrologic regimes (Jager et al. 1999). For example, the typical hydrologic regime of high elevation areas in which annual peak flows are associated with snowmelt runoff in spring could shift to winter due to rain-on-snow events in a climate change scenario. Such shifts in timing of peak flows could significantly affect fall-spawning brown trout (Jager et al. 1999). A better understanding of spatial variation in temperatures within systems as well as the effects of climate warming on local hydrologic regimes is needed to better predict the effects of climate warming on particular species of management concern (Jager et al. 1999, Isaak and Hubert 2004).

Biological Conservation Status

Abundance and distribution trends

An assessment of the abundance and distribution trends of brown trout in Region 2 was not feasible due to the amount of information needed to establish trends for such a widespread and intensively managed species and because much of the data has not been compiled or is not easily accessible. Compared to past practices, stocking rates of brown trout have been reduced in many areas (Behnke 2002). For instance, many stream populations within Wyoming are self-sustaining, and trout stocking is mainly conducted to provide angling opportunities in lakes and reservoirs (Wyoming Game and Fish Commission 2006-2007 Wyoming Fishing Regulations). Yet brown trout continue to be stocked in four of the five states encompassed by Region 2, which suggests that brown trout abundance and distribution are not declining in the region except perhaps in areas where naturalized populations are in decline and supplemental stocking has ceased. Only one such example was encountered in Region 2, in the Black Hills of South

Dakota where brown trout stocking ceased several years ago and naturalized populations appear to be in decline (South Dakota Department of Game, Fish, and Parks 2006 Fishing Handbook). However, there maybe other examples in the region.

Intrinsic vulnerability

Brown trout are widely distributed throughout North America and are well adapted to the range of cold- and cool-water habitats that they occupy. Brown trout have life history characteristics and a reproductive strategy that is well suited for the stream systems they occupy in much of Region 2. However, brown trout populations are sensitive to conditions that lower reproductive success and survivorship of YOY brown trout, particularly anthropogenic activities that reduce habitat or alter stream flows. Brown trout are carnivores, and invertebrates and small fish are the primary components of their diet. They have been found to be superior competitors compared to other common trouts in Region 2, native inland cutthroat trout (Wang and White 1994, McHugh and Budy 2005) and non-native brook trout (Fausch and White 1981) and rainbow trout (Gatz et al. 1987). Brown trout are also less susceptible to whirling disease than other trouts found in Region 2. As a result, the distribution of other trout species may be negatively influenced by the presence of brown trout (Kozel and Hubert 1989b, Modde et al. 1991, Larscheid and Hubert 1992, Wang and White 1994, Harig et al. 2000, McHugh and Budy 2005).

Information Needs and Management of Brown Trout in Region 2

Implications and potential management elements

The brown trout is an exotic game fish species that is important component of recreational fisheries in Region 2. Brown trout have clear value as a sport fish and have been a component of aquatic ecosystems in Region 2 for over 100 years; however, they can also have detrimental impacts on native fauna. Given the complex ecosystem and socioeconomic role of brown trout and the broad geographical scale of Region 2, a generalized discussion of implications and management elements for the species is not possible. Instead, the following sections consist of general recommendations for population monitoring that would improve the knowledge and information available to resource managers and researchers in the region, regardless of specific management objectives.

One general recommendation is that the effects of various management activities that may affect brown trout populations, whether related to land, water, or fisheries management, be considered in conjunction as part of the research, planning, or management process. In Region 2, there is a long history of land and water resource use and fisheries management, and consequently many systems are influenced by a combination of factors that together can have significant and complex effects on brown trout populations and the ecosystems they inhabit.

Additionally, because the brown trout is an exotic species that can have negative effects on native fauna, the impact of brown trout, and brown trout management activities, on special status species (i.e., federally threatened and endangered species, Region 2 sensitive species, management indicator species) should be considered where appropriate.

Tools and practices

Inventory and monitoring of populations

As a sport fish, the distribution of brown trout in states encompassed by Region 2 is well known compared to many non-game species, and inventorying populations on Region 2 lands is likely unnecessary in many cases. However, in locations where there has been a gap in sampling of many years, or in areas where stocking of brown trout was once common and has since ceased, inventorying current brown trout populations would be useful.

The ability to evaluate patterns in abundance over time and among localities is a critical part of fisheries management and provides valuable information on population trends, outcomes of management actions, and impacts of environmental changes (Ney 1999). As an important game fish and as a management indicator species on some Region 2 forests, brown trout population surveys have been conducted on some National Forest System lands, often with the cooperation of state agencies. In some cases, state agencies or national forests have established long-term monitoring programs for trout populations (including brown trout) or are currently developing monitoring plans.

One example of a trout assemblage monitoring approach is being developed for the Medicine Bow National Forest. The species comprising the trout assemblage (i.e., brook, brown, rainbow) are considered together as a management indicator species on the

forest. The assemblage monitoring approach (rather than species-specific) was selected so that the entire forest area would be represented despite differences in trout species distribution along elevational gradients (Eaglin personal communication 2006). The Medicine Bow National Forest trout monitoring program will include conducting population estimates and collecting additional information on demographic characteristics (e.g., length frequencies, age structure) (Eaglin personal communication 2006). Population estimates and sampling will be performed at sites selected using a randomization method (being developed) within 7th-level watershed units (Eaglin personal communication 2006). The data collected as part of the monitoring program will provide information needed to assess changes in abundance and distribution as well as to identify concerns to be addressed in specific studies, such as low recruitment or habitat concerns (Eaglin personal communication 2006).

Where monitoring programs have not been initiated or considered, establishing long-term monitoring programs for populations of brown trout at a few locations would provide basic, but still needed, information on the population characteristics and dynamics of brown trout in Region 2 and aid in forest management and planning activities.

In addition to providing baseline data needed to evaluate or predict the impacts of various land and water management practices, establishing long-term monitoring programs at different sites in Region 2 may yield additional insights on how variations in abiotic and biotic characteristics among systems affect brown trout populations across the region. Long-term population datasets, when correlated with hydrologic and environmental conditions and variation, would be useful in assessing the impacts of various natural disturbances and climate change scenarios on brown trout abundance and distribution.

Long-term population monitoring is also necessary to understand the range of natural fluctuations in naturalized brown trout populations in Region 2 so that effects of management activities or environmental changes can be interpreted. Platts and Nelson (1988) cautioned that natural variability in some trout populations might make it impossible to discern correctly the effects of various management activities in many short-term studies. For example, Harris et al. (1991) assessed the effects of a minimum flow increase on a brown trout population and were able to account for the natural variability in the population because

several years of pre- and post- flow increase data had been collected.

Because the brown trout is a sport fish, researchers and population monitoring efforts should not ignore the influence of fisheries management activities and angling pressure on population characteristics and dynamics. Variations in angling pressure and stocking practices among locations and over time may add to the observed variability within and among populations of brown trout (Anderson and Nehring 1984, Vincent 1987). Wright (1992) emphasized that fishing mortality can significantly affect trout populations, and Wesche et al. (1987b) found that fishing pressure was significantly correlated with brown trout standing stocks in southeastern Wyoming streams. The effects of stocking and angling pressure should be considered in population estimates, and monitoring programs should incorporate available information on stocking rates and angling pressure when possible.

Population monitoring programs could also improve the understanding of brown trout ecology and be helpful in determining limiting factors to populations in the Rocky Mountain Region. Population monitoring of brown trout may also prove useful in efforts to protect populations of native cutthroat trout, or other species of concern, from invasion by brown trout, especially where land and water use activities may alter flow regimes, physical habitats, water quality, or water temperature regimes in a manner that might facilitate the expansion of brown trout populations into headwater systems.

Similarly, it would be beneficial to monitor trout assemblages and to assess the population trends of different trout species in sympatry. In the past, many studies have combined population and biomass estimates across trout species, but tracking population trends of species occurring in sympatry separately would provide insights into the interactions among trout species and also help to explain different patterns in relative species abundance observed among locations or over time. For example, Waters (1983) followed the populations of brook and brown trout in a Minnesota stream in a long-term study and was able to identify the environmental events and ecological mechanisms that contributed to the near total replacement of brook trout by brown trout in the stream over a 15-year period. Population information (i.e., age-structure, length frequencies, biomass, population size estimates) collected over longer periods coupled with data on environmental and habitat conditions near the distributional limits of brown trout in Region 2 systems may also help to

answer specific questions such as why brown trout are not often found in headwater systems in Region 2.

In areas where brown trout population monitoring programs have not been initiated previously, consideration should be given to selecting streams that have been previously surveyed, to build on existing data sets, or in areas of particular interest to managers or researchers. In order for comparisons to be made among systems or for a single population over time, sampling effort should be consistent and precisely measured. Consistency in sampling effort includes standardization of sampling gear types, specifications, and operation as well as sampling similar habitat types at similar times of year, and under similar weather and water conditions (Ney 1999). An additional consideration for establishing trout population monitoring programs is that trout may be patchily distributed within streams, so that population estimates from small reaches may not be sufficient to extrapolate to longer reaches accurately (Hankin and Reeves 1988 as referenced by Harig et al. 2000). Stratified random sampling based on habitat or systematic sampling of streams has been recommended as alternatives (Doloff et al. 1993 as referenced by Harig et al. 2000).

Population and habitat management

Brown trout populations are found in a wide range of habitats, and many models have been developed to aid trout fishery managers. Models can be used to predict trout abundance and biomass from environmental conditions and habitat characteristics, to identify factors that limit populations, to assess the effects of environmental changes on populations, and to direct management efforts. For instance, models can help managers to identify where trout populations may be limited by climate, habitat, altered flow regimes, or poor water quality, etc. as well as indicate management interventions such as habitat enhancement, minimum flow implementation, or harvest regulations. Models also have the potential to assist in the evaluation of the potential threat of brown trout to native taxa in some systems (Fausch et al. 2001, McHugh and Budy 2006).

In areas where native aquatic fauna are imperiled, consideration should be given to the effects of brown trout in species conservation and recovery plans. Some populations of brown trout may have to be managed to protect other species of interest. Potential management actions that may be necessitated in those situations could include:

❖ preventing the expansion of brown trout populations into certain areas

❖ removing brown trout from locations where important populations of imperiled species occur

❖ assessing the potential threat of brown trout to native taxa or particular systems prior to stocking actions (McHugh and Budy 2006).

Because brown trout require a variety of habitats to complete their life cycle, ensuring that adequate habitat complexity is maintained for different life stages and seasonal needs is important. Much research has been conducted on the effects of various land and water management practices on salmonids and their habitats. In Region 2, where brown trout are found in a variety of environments, the knowledge of agency personnel and fisheries researchers familiar with the local characteristics and conditions of aquatic ecosystems is valuable. Evaluating habitat conditions, for all life stages and seasons, in systems where habitat may be limiting or where management activities may affect habitat provides important information to fisheries and resource management. Similarly, determining the annual movement patterns and range of brown trout in the different types of systems they inhabit in Region 2 would provide useful information on populations and habitat requirements, especially for populations that may move between rivers and lakes and tributaries or cross national forest boundaries.

Information needs

The brown trout has been a popular research subject, as is evident from the length of this assessment. The literature review performed for this assessment primarily focused on information pertaining to populations in Region 2, or western North America, and could not be comprehensive given the tens of thousands of publications pertaining to brown trout. As a result, the few information gaps identified primarily concern specific aspects of brown trout ecology in the Rocky Mountain Region and detailed knowledge of its population dynamics and impacts on aquatic communities within Region 2.

Information concerning the fecundity, fertility, mortality rates, growth rates, population age-structure, and sex ratios is limited orlacking for Region 2 populations. This information is critical to improving

the understanding of brown trout ecology and population dynamics in the region, especially considering the broad range of environments this species inhabits. Detailed demographic data collected over long time periods would help to answer many of the questions that remain about the ecology of brown trout in the western United States and its impact on native species and communities.

Similarly, with a few notable exceptions, relatively little information on brown trout activity, movement patterns, and feeding habitats in Region 2 was found in the literature review. Activity and movement patterns for populations of brown trout in lakes, reservoirs, and rivers in Region 2 are particularly limited. Information regarding the food habits of brown trout in different types of Region 2 ecosystems is also limited and the effects of piscivorous brown trout on native fish species in the region are poorly understood. Given the range of environments this species inhabits in Region 2, the adverse impacts it can have on native species, and its potential to invade new habitats under changing climatic conditions, a more complete understanding of the range of activity and movement patterns and feeding habitats of brown trout in Region 2 would be useful.

The impacts of natural and anthropogenic disturbances on salmonid species historically have received far more attention than for many non-game species. However, additional research directed towards the effects of specific conditions in Region 2 that may limit populations (e.g., flow regimes in regulated systems, drought, winter ice dynamics) would be beneficial. A better understanding of the ecology of brown trout in Region 2 would help to mitigate adverse impacts of management activities on brown trout fisheries or alternatively, be helpful in protecting sensitive populations of native fauna from brown trout population expansions.

An additional information need includes improved knowledge of brown trout distributions at local scales and its overlap with other streamfish species, particularly species of concern in Region 2. This information, coupled with knowledge of brown trout ecology and population responses to environmental fluctuations, would improve the understanding of its current influence on aquatic ecosystems and fauna as well as aid in the prediction of future population trends and distributional changes that may occur with changing climatic and environmental conditions in the region (Jager et al. 1999, Fausch et al. 2001, McHugh and Budy 2005). Determining the key factors that have limited the

expansion of brown trout populations in Region 2 is critical to understanding its invasive potential under altered climatic or environmental conditions.

Data on brown trout occurrence and relative abundance have been collected by state and federal agencies as well as university researchers, but much of the data has not been compiled or published in easily accessible formats. The information gaps that currently exist regarding brown trout distribution and population trends in Region 2 could be addressed by a cooperative effort among agencies and institutions to compile and evaluate existing data. Such an undertaking would involve an enormous effort but would benefit fisheries research and resource management efforts throughout the region. For streams or watersheds of particular interest to managers or researchers, additional efforts to compile and synthesize data regarding environmental characteristics or information pertaining to the land, water, and fisheries management histories could provide information needed to better understand many aspects of the ecology of brown trout in the region as well as the short and long-term impacts of various land, water, and fisheries management practices on aquatic ecosystems.

One such effort is currently underway for the Intermountain Region, but the associated analyses primarily concern the interactions between non-native brook trout and native cutthroat trout. A similar effort focused on brown trout would have much benefit, as the impact of brown trout on native cutthroat trout (and other fishes) has received comparatively less attention in the region over the years. The following description of the project, the USFS Risk Assessment/Decision Support System Dataset, was obtained from the co-PIs: J. Dunham of the USGS and B. Rieman of the USFS.

The USDA Forest Service Rocky Mountain Research Station, U.S. Geological Survey, and Colorado State University are collaborating with numerous partners throughout the interior western United States to assemble existing data on the presence of trout and environmental variables related to fish distributions. The work is supported in part by funding from USFS Region 1. The dataset includes over 10,000 observations of occurrence of trout, native and introduced, to the region (including inland cutthroat subspecies, brook trout, rainbow trout, bull trout, and brown trout). Environmental variables such as stream width, air temperatures, stream discharges, roads, valley morphology, and a variety of others are under consideration for inclusion in statistical models focused on predicting occurrence of native cutthroat trout and non-native brook trout. One of the main objectives of the

analysis is to understand conditions under which native cutthroat trout and non-native brook trout may coexist. Results from the work will be useful in decisions about management actions to control undesirable impacts of non-native brook trout and in providing managers and researchers with a broad view of potential factors that contribute to persistence of native cutthroat trout in the face of invasions by non-native trout.

Aquatic ecosystems in Region 2 continue to change with changing land, water, and fisheries management activities as well as with unanticipated alterations of the biota related to the spread of introduced species or pathogens such as whirling disease. Long-term monitoring programs, coupled with research on the effects of changing conditions, are needed to understand the impacts of particular changes as they occur. For example, currently in the Black Hills National Forest, the spread of the diatom *Didymosphenia geminata* appears to be having a deleterious effect on naturalized brown trout populations (Hirtzel personal communication 2006). Research is needed to identify the cause for the spread of the diatom and the nature of its impacts on brown trout and the rest of the aquatic community. *Didymosphenia geminata* has become a nuisance species in many aquatic ecosystems in the western United States, including several in Colorado and in the Black Hills of South Dakota (U.S. Environmental Protection Agency, Region 8 Aquatic Nuisance Species: http://www.epa.gov/Region8/water/monitoring/didymosphenia.html), and it may become a concern elsewhere in Region 2.

Although the "hot" topics in fisheries research change over the years, collecting information on the "basics" of brown trout and other stream fishes over the long term remains important to understanding the observed changes in aquatic ecosystems over time. The accessibility of the data collected is equally important. Improved access to data, whether via publication in agency reports, journals, or other methods, is needed to continue to advance the understanding of brown trout biology and ecology in Region 2.

DEFINITIONS

Age structure – the age distribution of a population.

Alevin – a newly hatched salmonid, still reliant on the yolk sac for food; it remains in the redd for a period of several weeks.

Allopatry – occurring in different geographical areas, having non-overlapping distribution ranges, or occurring in isolation.

Anadromous – reproducing in freshwater, but spending much of the life cycle in marine environments; ascending rivers from the ocean to breed.

Anthropogenic – relating to or resulting from the influence of humans on nature.

Anchor ice – ice formed on streambed substrates.

Benthic – relating to or occurring at the bottom of a body of water.

Carrying capacity – the maximum biomass of a population that a defined area can support over time.

Connectivity – referring to the pathways that allow fish to move about a stream drainage and to recolonize areas after local extinctions have occurred; dams and road culverts often interrupt the connectivity of a drainage.

Demographic – pertaining to the study of population statistics, changes or trends based on variables such as fertility, mortality, and migration.

Dendrogram – a branching diagram representing a hierarchy of categories.

Embryo – a vertebrate during the stages of development prior to birth or hatching.

Environmental fluctuations – changes in habitat conditions such as temperature, salinity, oxygen concentration, or the amount of water flowing in a stream.

Fecundity – the number of ova produced by a female fish.

Fertility – the birth rate of a population.

Fingerling – commonly refers to small in size, young, immature fish (up to around 10 cm in length).

Fluvial – relating to or inhabiting a river.

Fry – an early life stage of a salmonid, after the alevin stage, consisting of a short transition phase of several weeks after the young fish have emerged from the gravel and transition to feeding exogenously as the remains of their yolk sacs are exhausted.

Habitat connectivity – refers to the degree to which organisms can move throughout the area or system of interest.

Habitat suitability index model – a model based on suitability indices formulated from variables that affect the life cycle and survival of a species, referred to as an HSI model.

Hybridization – refers to the cross between individuals of different species and the production of hybrid offspring.

Interstitial – relating to or situated in the interstices, the small space between things.

Invertebrates – animals without backbones, such as insects and crustaceans.

Iteroparous – repeated reproduction, e.g. fish that can spawn multiple times in their life.

Larvae – plural of larva, the early, immature form of an animal that at hatching is fundamentally unlike its parent and must change to assume the adult characters. Used in this document in reference to newly hatched fish and also immature invertebrates.

Lentic – standing or slow-flowing water habitats, such as lakes, ponds, or reservoirs.

Limnetic – relating to or inhabiting the open water of a body of freshwater.

Lotic – running water habitats, such as streams and rivers.

Macroinvertebrate – invertebrates large enough to be seen with the naked eye, greater than 0.5 mm in size.

Malentities – factors that can harm or kill the species; other organisms can be malentities if they harm or kill the species of interest, but unlike predators, malentities do not benefit from harming or killing the species of interest.

Meristic character – an anatomical feature that can be counted, such as the number of spines on the dorsal fin or the number of scales along the lateral line of a fish; frequently used to identify fish species using a taxonomic key.

Metapopulations – spatially isolated populations that function as independent populations but that can exchange occasional individuals; this exchange allows extirpated populations to become re-established.

Microhabitat – the specific combination of habitat elements in the place occupied by a fish for a specific use such as feeding, spawning, resting etc.

Morphometric character – an anatomical feature that can be measured, such as the length of various body parts or ratios of body parts; used to identify fish species using a taxonomic key.

Non-game species – an animal species that is not harvested for recreational or commercial purposes.

Piscivorous – feeding on fishes.

Polymorphic – existence of a species in many different forms independent of the variations of sex.

Recruitment – the number of individuals hatched in any year that survive to a particular size or age, such as age-1 or reproductive size.

Salmonid – member of the family Salmonidae.

Semelparous – breeding only once in a lifetime, e.g. fish that spawn once and then die.

Stochastic – random.

Sympatry – occurring in the same area, occupying the same geographical range, or having overlapping ranges of distribution.

Tailwater – the area immediately below a dam, where the river water is typically cooler and more nutrient rich.

Taxa – plural of taxon, a taxonomic group or entity.

Vital rates – demographic characteristics such as birth rate, fecundity, and survival rates that determine the growth rate of a population.

Yearling – an age-1 fish.

Young-of-year – fish hatched in a given calendar year, an age-0 fish, abbreviated YOY.

Year class – the year in which a fish hatched.

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APPENDIX

## *Matrix Analysis of Population Demographics for Brown Trout*

Life cycle graph and model development

Matrix demographic models facilitate assessment of critical transitions in the life history of a species. A key first step is to create a *life cycle graph*, from which to compute a *projection matrix* amenable to quantitative analysis using computer software (Caswell 2001). The life history data for brown trout described by Taube (1976), Grost et al. (1990), Stonecypher (1992), and Elliott (1994) provided the basis for a stage-classified life cycle graph that has six stages (**Figure A1**). The first five stages are age-specific (age-classes) while the sixth includes all fish in their sixth year or later. From the life cycle graph, we conducted a matrix population analysis assuming a birth-pulse population with a one-year

census interval and a post-breeding census (Cochran and Ellner 1992, McDonald and Caswell 1993, Caswell 2001). Computations were done with a *Mathematica™* program written by D.B. McDonald, based on algorithms in Caswell (2001). Beyond this introductory paragraph, rather than using an age-indexing system beginning at 0, as is the norm in the fisheries literature, we use stage-based indexing beginning at 1 (first-year, second-year, etc.) (**Table A1**). Note that the breeding pulse comes at the end of each one-year census interval. Individuals are therefore larger when breeding than when they were censused in that stage (almost a year earlier).

In order to estimate the vital rates for brown trout (**Table A2**), we used the following criteria:

❖ the life history had six stages, with a self-loop on the sixth stage denoting a low constant probability of survival for the very largest fish
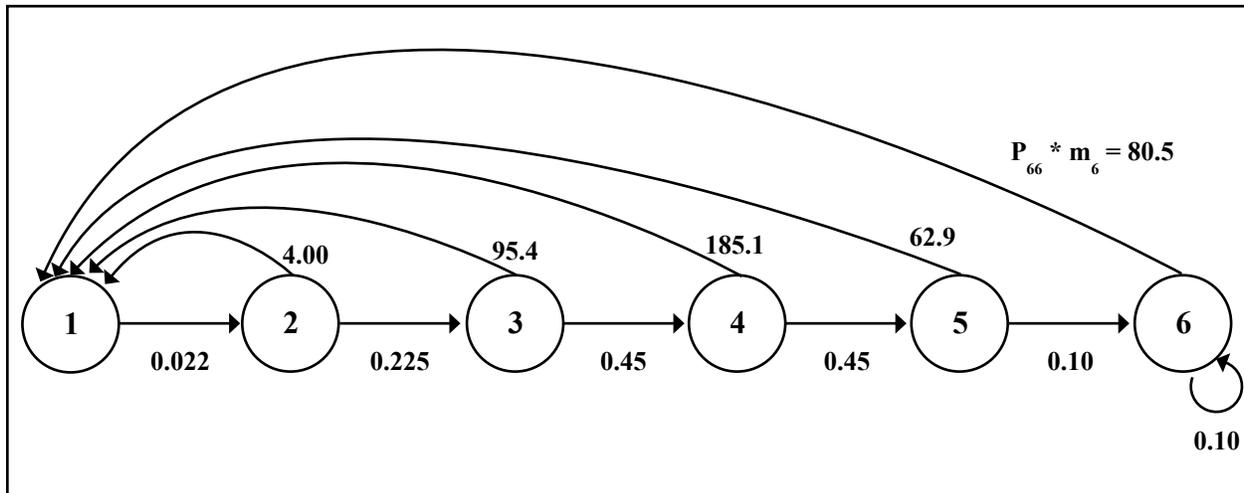
Figure A1. Life cycle graph for brown trout, consisting of circles (*nodes*), describing stages in the life cycle and *arcs*, describing the *vital rates* (transitions between stages). The horizontal arcs are survival rates (e.g., first-year survival, P_{21} = 0.022). The remaining arcs, pointing back to Node 1, describe fertility (e.g., P54* m4). Each of the arcs corresponds to a cell in the matrix of **Figure A2**. The self-loop on Node 6 denotes constant low survival for fish in their sixth year and older.

Table A1. Relationship between conventional fisheries age categories, life cycle stage, weighted mean size of stage and size range for stage, for brown trout (after Taube 1976 and Grost et al. 1990).

Age (fisheries convention)	Stage	Proportion mature	Female eggs
0	1	0.00	0
I	2	0.18	18
II	3	0.77	212
III	4	0.91	411
IV	5	1.00	629
V	6	1.00	805

Table A2. Vital rates for brown trout, used as inputs for projection matrix entries of **<u>Figure A1</u>** and **<u>Figure A2</u>**.

Vital rate (fertility or survival)	Numerical value	Description
m_2	17.8	Number of female eggs produced by a second-year female
m_3	212.1	Number of female eggs produced by a third-year female
m_4	411.4	Number of female eggs produced by a fourth-year female
m_5	628.8	Number of female eggs produced by a fifth-year female
m_6	805.4	Number of female eggs produced by a sixth-year female
P_{21}	0.0216	First-year survival
P_{32}	0.225	Second-year survival
P_{43}	0.45	Third-year survival
P_{54}	0.45	Fourth-year survival
P_{65}	0.1	Fifth-year survival
P_{66}	0.1	"Older adult" survival

- ❖ the proportion of each stage that was reproductively mature was based on Grost et al. (1990); Stage 1 = 0; Stage 2 = 0.18; Stage 3 = 0.77; Stage 4 = 0.91; and 1.0 thereafter

- ❖ egg production (m_i) by stage was estimated from the equation in Taube (1976): *Eggs = 353.3 x AgeGroup - 155.7*, where *AgeGroup* is traditional fisheries age designations (Age 0, Age 1, etc.)

- ❖ survival through the first year (P_1) had three components: egg survival to hatch was estimated as 0.72 based on lab rearing results from Stonecypher (1992); survival post-hatch was estimated at 0.05 based on Elliott (1994), with a decrement for survival in the wild of 0.6; the (arbitrary) 0.6 value also had the property of yielding a λ of very nearly 1.0; the compound value for P_{21} therefore became 0.72*0.05*0.6 = 0.0216

- ❖ survival data were estimated from age ratios developed from the length frequency distribution reported in Grost et al. (1990); this yielded approximate "prime-of-life" survival rates of 0.45 ($= P_{43}, P_{54}$) and survival from Stage 5 on of 0.10 ($= P_{65}, P_{66}$).

Because the model assumes female demographic dominance, the egg number used was half the published value, assuming a 1:1 sex ratio. We also made a final and major assumption that the long-term value of λ (population growth rate) must be near 1.0. This final assumption allowed us to solve for the major unknown, the difference in survival in the wild vs. under the conditions of Stonecypher (1992) and Elliott (1994),

using the characteristic equation (McDonald and Caswell 1993).

The model has two kinds of input terms: P_{ij}, describing survival rates, and m_i, describing fertilities (**<u>Table A2</u>**). **<u>Figure A2a</u>** shows the symbolic terms in the projection matrix corresponding to the life cycle graph, and **<u>Figure A2b</u>** gives the corresponding numeric values. Note also that the fertility terms (F_i) in the top row of the matrix include a term for offspring production (m_i) as well as a term for the survival of the mother (P_i) from the census (just **after** the breeding season) to the next birth pulse almost a year later. Based on the estimated vital rates used for the matrix, λ was 1.007. This should not be taken to indicate a stationary population (i.e., a population of constant size) because the value was used as a target toward which to adjust estimated fertility rates and was subject to the many assumptions used to derive all the transitions. Therefore, the value of λ should not be interpreted as an indication of the general well-being or stability of the population. Other parts of the analysis provide a better guide for any such assessment.

Sensitivity analysis

A useful indication of the state of the population comes from the sensitivity and elasticity analyses. **Sensitivity** is the effect on λ of an **absolute** change in the vital rates (a_{ij}, the arcs in the life cycle graph [**<u>Figure A1</u>**] and the cells in the matrix, **A** [**<u>Figure A2</u>**]). Sensitivity analysis provides several kinds of useful information (see Caswell 2001, pp. 206-225). First, sensitivities show how important a given vital rate is to λ, which Caswell (2001, pp. 280-298) has shown to be a useful integrative measure of overall fitness. One can therefore use sensitivities to assess

Stage	1	2	3	4	5	6
1		$P_{32} * m_2$	$P_{43} * m_3$	$P_{54} * m_4$	$P_{65} * m_5$	$P_{66} * m_6$
2	P_{21}					
3		P_{32}				
4			P_{43}			
5				P_{54}		
10					P_{65}	P_{66}

Figure A2a. Symbolic values for the cells of the projection matrix. Each cell corresponds to one of the arcs in the life cycle graph of **Figure A1**. The top row is fertility, with compound terms describing survival of the mother (P_{ij}) and egg production (m_i). Empty cells have zero values and lack a corresponding arc in **Figure A1**. Note that the matrix differs from a strictly age-classified (Leslie) matrix because of the entry in the bottom right, corresponding to the self-loop on the sixth node in the life cycle graph.

Stage	1	2	3	4	5	6
1		4.001	95.44	185.13	62.88	80.54
2	0.022					
3		0.225				
4			0.45			
5				0.45		
6					0.1	0.1

Figure A2b. Numeric values for the projection matrix.

Figure A2. The input matrix of vital rates, **A** (with cells a_{ij}) corresponding to the brown trout life cycle graph (**Figure A1**). a) Symbolic values. b) Numeric values.

the relative importance of the survival (P_i) and fertility (F_i) transitions. Second, sensitivities can be used to evaluate the effects of inaccurate estimation of vital rates from field studies. Inaccuracy will usually be due to paucity of data, but it could also result from use of inappropriate estimation techniques or other errors of analysis. In order to improve the accuracy of the models, researchers should concentrate additional effort on accurate estimation of transitions with large sensitivities. Third, sensitivities can quantify the effects of environmental perturbations, wherever those can be linked to effects on age-specific survival or fertility rates. Fourth, managers can concentrate on the most important transitions. For example, they can assess which stages or vital rates are most critical to increasing λ of endangered species or the "weak links" in the life cycle of a pest.

Figure A3 shows the "possible sensitivities only" matrix for this analysis. While one can calculate sensitivities for non-existent transitions, these are usually either meaningless or biologically impossible (e.g., the sensitivity of λ to moving backward in age, from Stage 3 to Stage 2). In this analysis, the sensitivity of λ to changes in first-year survival (13.5; 89.6 percent of total) is overwhelmingly the most important key to population dynamics.

Stage	1	2	3	4	5	6
1		0.006	0.001	0.001	0	0
2	13.5					
3		1.19				
4			0.299			
5				0.044		
6					0.025	0.003

Figure A3. Sensitivities matrix, **Sp** (remainder of matrix is zeros). Only values that correspond to non-zero arcs in the life cycle graph are shown. The transition to which λ of brown trout is overwhelmingly sensitive is first-year survival (89.6 percent of total sensitivity).

Elasticity analysis

Elasticities are the sensitivities of λ to **proportional** changes in the vital rates (a_{ij}). The elasticities have the useful property of summing to 1.0. The difference between sensitivity and elasticity conclusions results from the weighting of the elasticities by the value of the original vital rates (the a_{ij} arc coefficients on the graph or cells of the projection matrix). Management conclusions will depend on whether changes in vital rates are likely to be absolute (guided by sensitivities) or proportional (guided by elasticities). By using elasticities, one can further assess key life history transitions and stages as well as the relative importance of reproduction (F_i) and survival (P_i) for a given species. It is important to note that elasticity as well as sensitivity analysis assumes that the magnitude of changes (perturbations) to the vital rates is small. Large changes require a reformulated matrix and reanalysis.

Elasticities for brown trout are shown in **Figure A4**. The λ of brown trout was most elastic to changes in survival over the first three years (the three combined represent 68.8 percent of the total elasticity), followed by the fertility of Stages 3 and 4. Overall, survival transitions accounted for approximately 71 percent of the total elasticity of λ to changes in the vital rates. Survival rates, particularly at early ages, are the demographic parameters that warrant most careful monitoring in order to refine the matrix demographic analysis.

Other demographic parameters

The **stable stage distribution** (SSD; **Table A3**) describes the proportion of each stage in a population at demographic equilibrium. Under a deterministic model, any unchanging matrix will converge on a population structure that follows the stable stage distribution, regardless of whether the population is declining, stationary, or increasing. Under most conditions, populations not at equilibrium will converge to the SSD within 20 to 100 census intervals. For brown trout at the time of the post-breeding annual census (late autumn through late spring), eggs should represent 97.1 percent of the population. Second-year fish (hatched the previous breeding season) should constitute 72.9 percent of the non-egg population. **Reproductive values** (**Table A4**) can be thought of as describing the "value" of a stage as a seed for population growth relative to that of the first (newborn or, in this case, egg) stage (Caswell 2001). The reproductive value is calculated as a weighted sum of the present and future reproductive output of a stage discounted by the probability of surviving (Williams 1966). The reproductive value of the first stage is, by definition, always 1.0. For example, a fourth-year

Stage	1	2	3	4	5	6
1		0.025	0.13	0.11	0.02	0.002
2	0.29					
3		0.26				
4			0.13			
5				0.02		
6					0.002	0

Figure A4. Elasticity matrix, **E** (remainder of matrix is zeros). The λ of brown trout is most elastic to changes in survival over the first three years (Cells e_{21}, e_{32}, e_{43}), followed by survival at later ages. As with the sensitivities, changes in the fertility transitions have relatively little effect on λ.

Table A3. Stable Stage Distribution (right eigenvector). Because first-year fish (eggs) numerically dominate the population at the time of the census, the proportion of fish excluding eggs are shown in parentheses for Stages 2 to 5.

Stage	Description	Proportion (excluding eggs)
1	Eggs	0.971
2	Second-year females	0.021 (0.729)
3	Third-year females	0.005 (0.163)
4	Fourth-year females	0.002 (0.073)
5	Fifth-year females	0.001 (0.032)
6	Sixth-year females	0.000 (0.004)

Table A4. Reproductive values for females. Reproductive values can be thought of as describing the "value" of a stage as a seed for population growth, relative to that of the first (egg) stage, which is always defined to have the value 1.

Stage	Description	Proportion (excluding eggs)
1	First-year females (eggs)	1
2	Second-year females	46.6
3	Third-year females	191.0
4	Fourth-year females	215.6
5	Fifth-year females	71.2
6	Sixth-year females	88.8

female is "worth" approximately 216 eggs, the peak in this life cycle. The cohort generation time for brown trout is 3.5 years (SD = 0.8 years).

Potential refinements of the models

Clearly, better data on survival and fertility rates from Region 2, especially in the first few years of life, would increase the relevance and accuracy of the analysis. The present analysis should be considered as at best only an approximate guide to the forces acting on the demography of brown trout in Region 2. Further, data from natural populations on the range of variability in the vital rates would allow modeling of the impact of stochastic fluctuations. For example, time series based on actual temporal or spatial variability would allow construction of a series of "stochastic" matrices that mirrored actual variation. One advantage of such a series would be the incorporation of observed correlations between variations in vital rates. Using observed correlations would incorporate forces that we did not consider. Those forces may drive greater positive or negative correlation among life history traits.

Other potential refinements include incorporating density-dependent effects. At present, the data appear insufficient to assess reasonable functions governing density dependence. Another refinement would be to incorporate the small proportion of individuals in stream resident populations that become piscivorous at around age-4 or age-5 and consequently extend their life span, attaining larger sizes and greater fecundity. A similar refinement would include extending the analysis to include the larger, longer-lived, and more fecund river resident fish that are found spawning in tributaries along with stream residents in some drainages in Region 2. Presently, the data are insufficient to address the influence of the individuals in a population that switch to piscivority on population dynamics.

Summary of major conclusions from matrix projection models

❖ the major purpose of the matrix model is to assess critical stages in the life history (e.g., juvenile vs. adult survival, fertility vs. survival) rather than to make (often unwarranted) predictions about population growth rates, population viability, or time to extinction; because the data are scanty, the model also provides preliminary guidance on which vital rates should be the focus of any future monitoring efforts

❖ first-year survival accounts for 89.6 percent of total "possible" sensitivity; any absolute changes in this vital rate will have major impacts on population dynamics

❖ survival through the first three years accounts for 68.8 percent of the total elasticity; proportional changes in early survival will have major impacts on population dynamics

❖ the shift in emphasis between the sensitivity analysis (first-year survival) and the elasticity analysis (survival through the third year) indicates that it may be useful to understand whether variation is generally absolute (small but absolute changes) vs. proportional; regardless, survival through the first three years of life is clearly a critical feature of the population dynamics of brown trout.

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