Chapter 5

Yellowstone Cutthroat Trout

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Introduction

The Yellowstone cutthroat trout is more abundant and inhabits a greater geographical range than does any other nonanadromous subspecies of cutthroat trout (Varley and Gresswell 1988). The Yellowstone cutthroat trout was indigenous to the Snake River upstream from Shoshone Falls, Idaho, and the Yellowstone River above the Tongue River, Montana (Behnke 1992). Although there are some disagreements concerning the evolutionary history of cutthroat trout and various cutthroat trout subspecies (Behnke 1992; Stearley 1992; Stearley and Smith 1993), the most recent incursion of Yellowstone cutthroat trout into the Yellowstone River drainage is apparently related to the retreat of glacial ice approximately 12,000 years ago (Richmond and Pierce 1972). Individual populations of the Yellowstone subspecies have evolved numerous life history characteristics in response to the diverse environments in which they have been isolated since the last glacial retreat; human activities, however, have resulted in a substantial reduction in the historical distribution of this subspecies.

Life History Characteristics

Spawning patterns.—Yellowstone cutthroat trout spawn exclusively in running water, and there are three spawning patterns:

(1) Resident populations generally spawn within their home range in lotic systems. Fish may migrate, but spawners do not enter tributary streams. Kelly (1993) recorded movement of mature Yellowstone cutthroat trout in the Yellowstone River between Yellowstone Lake and the Upper Falls of the river (28 km). Approximately 52% of recaptured fish were collected in the segment where they were initially marked; 41% moved upstream, and 7% moved downstream. After emergence, fry may move either upstream or downstream or remain near the redd (Varley and Gresswell 1988).

(2) Fluvial populations migrate from streams and rivers into tributaries to spawn. This pattern has been documented in the Yellowstone River in Montana (Clancy 1988), several drainages in the Snake River in Idaho (Thurow et al. 1988), and in the Yellowstone River (below the Lower Falls) and Lamar River in Yellowstone National Park (Varley and Gresswell 1988). Juveniles may emigrate as fry or spend 1 to 3 years in natal tributaries before returning to the mainstem (Thurow et al. 1988; Varley and Gresswell 1988).

(3) Adfluvial populations live in lakes and ascend inlets or descend outlets to spawn. Although juveniles from most tributaries to Yellowstone Lake migrate to the lake shortly after emergence, some may remain in their natal stream for one or more years if the habitat is suitable (Varley and Gresswell 1988). Returns of marked fish suggested long-term (more than 2 years) lotic residency for some Yellowstone cutthroat trout that were spawned in Pelican Creek, a tributary of Yellowstone Lake (Gresswell et al., in press). Outlet spawning is less common, but has been documented in Yellowstone Lake (Ball and Cope 1961), Heart Lake (Varley and Gresswell 1988), and Pocket Lake (U.S. Fish & Wildlife Service, unpubl. data) in Yellowstone National Park. Fry move upstream to the lake after emergence, and this behavior appears to be heritable (Raleigh and Chapman 1971; Bowler 1975).

Homing by Yellowstone cutthroat trout spawners is believed to influence life history diversity through reproductive isolation (Gresswell et al., in press). Ball (1955) documented natal homing (return of adult spawners to the area of their birth) in Arnica Creek, a tributary of Yellowstone Lake. Repeat homing behavior (individual spawners returning to the same tributary in successive years; McCleave 1967) has been observed for adfluvial spawners from Yellowstone Lake (Cope 1957a; Jones et al. 1984) and fluvial spawners from the Yellowstone River in Montana (Clancy 1988) and the Blackfoot and South Fork Snake rivers in Idaho (Thurow et al. 1988). In-season homing was experimentally investigated when individual adults returned to a spawning area after dislocation (McCleave 1967; Jahn 1969; LaBar 1971).

Straying during the spawning migration is low. Between 1949 and 1955, 18,836 cutthroat trout from Yellowstone Lake were tagged as they entered Arnica, Chipmunk, Clear, Grouse, and Pelican creeks to spawn (Cope 1957a). Of 244 adults that returned to spawn in subsequent years, 97% were collected in the stream where they were originally tagged. In a separate study, Ball (1955) marked three groups of immature cutthroat trout in 1950 and 1951 as they migrated from Arnica Creek to Yellowstone Lake. Between 16 and 25% of these fish eventually returned to spawn in Arnica Creek, but none were recovered in the five other tributaries being monitored during that period. More recently, 23% of 42,229 cutthroat trout marked at Clear Creek in 1979 returned to spawn again, but only 1% of the marked fish were collected in Pelican or Cub creeks (Jones et al. 1985). Only 10 of 333 Yellowstone cutthroat trout tagged in tributaries to the Blackfoot River failed to return to the stream in which they were marked; nine of these fish strayed between two streams that entered the Blackfoot River 400 m apart (Thurow 1982).

Migration timing.—Substantial differences in migration timing have been documented for tributaries to Yellowstone Lake (Gresswell et al., in press). Physical characteristics of a drainage directly influence the hydrologic cycle in a basin (Morisawa 1968), and a strong relation between timing of spawning migrations of Yellowstone cutthroat trout and hydrographic stage and water temperature has been observed in tributaries to the lake (e.g., Ball and Cope 1961; Jones et al. 1990). Throughout the range of Yellowstone cutthroat trout, spawner abundance generally increases as water temperature rises and discharge decreases from spring runoff peak (Varley and Gresswell 1988; Byorth 1990; Thurow and King 1994). During the early portion of the spawning migration in Clear Creek, some fish have been observed repeatedly moving into and out of tributaries without spawning (USFWS, unpubl. data).

Yellowstone cutthroat trout generally spawn between March and August, and migrations begin when temperatures approach 5°C (Varley and Gresswell 1988; Byorth 1990; Thurow and King 1994). Although Yellowstone cutthroat trout spawners will enter tributaries prior to major increases in discharge, most fish migrate after the spring peak (Ball and Cope 1961; Jones et al. 1990; Thurow and King 1994). Daily upstream migrations increase to a peak in concordance with water temperature, usually between 1300 and 1700 hours (Byorth 1990; Jones et al. 1990). For 13 years between 1977 and 1992, maximum daily water temperature in Clear Creek, a tributary to Yellowstone Lake, ranged from 10 to 14.2°C on the date of peak spawning migration (USFWS, unpubl. data). In 1991, maximum daily water temperature in Pine Creek, a tributary to the South Fork Snake River, ranged from 16 to 20°C during the Yellowstone cutthroat trout spawning migration (Thurow and King 1994).

In most tributaries to Yellowstone Lake, Yellowstone cutthroat trout spawners remain in streams from 6 to 25 days (Varley and Gresswell 1988), but in some larger tributaries, adfluvial spawners may not return to the lake for many months (Jones et al. 1982). Males generally migrate into spawning tributaries earlier than do females and remain in spawning areas longer (Ball and Cope 1961). Emigration of postspawners is generally nocturnal while discharge is high during the early portions of the spawning migration, but most fish move during the day as the run progresses (Varley and Gresswell 1988).

Characteristics of spawning fish.—In tributaries to Yellowstone Lake, older and larger Yellowstone cutthroat trout migrate first (Ball and Cope 1961; Jones et al. 1990). Data suggest that older and larger individuals also migrate farther upstream (Cope 1957b; Dean and Varley 1974); this behavior has been noted for other fishes (Briggs 1955). Nevertheless, fish usually spawn earlier at lower elevation sites. Age, length, weight, and condition factors decline as the spawning migration progresses (Jones et al. 1990).

Mean age of spawners varies geographically. Thurow et al. (1988) reported that most resident fish in the upper Snake River in Idaho matured at age 4 or 5. Most Yellowstone cutthroat trout in Henrys Lake mature at age 3 (Thurow et al. 1988). Clancy (1988) considered fish age 3 and older as mature in the Yellowstone River between Corwin Springs and Springdale, Montana. Between 1987 and 1992, mean age for spawners at Clear Creek, a tributary to Yellowstone Lake, was 5.8 years (Gresswell et al., in press).

Average size of Yellowstone cutthroat trout spawners is also variable. In Idaho, few fish less than 200 mm were mature, most fluvial spawners exceeded 275 mm, and mean length varied between 300 and 500 mm (Thurow et al. 1988). In the Yellowstone River in Montana, Clancy (1988) grouped fish over 300 mm as adults, and spawners from two tributaries to the river ranged from 322 to 368 mm in 1988 and 1989 (Byorth 1990). Benson and Bulkley (1963) found that Yellowstone Lake fish above 300 mm were mature, and most fish less than 250 mm were immature. Data collected since 1985 suggest that mean length of Yellowstone cutthroat trout spawners from individual tributaries to Yellowstone Lake ranged from 305 to 405 mm (USFWS, unpubl. data). In small subalpine lakes and streams Yellowstone cutthroat trout may mature between 100 and 130 mm.

Angler harvest can affect the mean age and length of Yellowstone cutthroat trout spawners (Gresswell and Varley 1988). At Clear Creek, mean age of Yellowstone cutthroat trout declined to 3.9 years in the mid-1960's when angler success (number of fish captured/hour) and mean length of captured fish were declining. Since restrictive regulations were implemented in the early 1970's, the average age in the spawning run has increased. Age 9 Yellowstone cutthroat trout have been collected annually in Clear Creek since the late 1970s; maximum age of spawners has increased to 11 years old. At LeHardy Rapids (Yellowstone River, approximately 6 km below Yellowstone Lake), annual monitoring demonstrated an increase in mean age from 3.7 years immediately following the implementation of catch-and-release regulations in 1973 to 6.1 years in 1986 and 1989 (Jones et al. 1992). Corresponding increases in length have been observed in both locations.

Thurow et al. (1988) reported that except for the Henrys Lake Hatchery migration, females were more abundant than were males in fluvial spawning populations sampled in Idaho. Male:female ratios varied from 0.37:1 to 0.17:1 in the Blackfoot River (Thurow 1982), and Moore and Schill (1984) reported a male:female ratio of 0.83:1 in the South Fork Snake River. Females are also more abundant in adfluvial spawning migrations in tributaries to Yellowstone Lake. Males often dominate the early portion of spawning migrations, but the proportion of males decreases as the spawning migration progresses (USFWS, unpubl. data). Between 1945 and 1953, mean male:female ratios for six tributaries ranged from 0.61:1 to 0.74:1 (Ball and Cope 1961). Estimates for 13 sample years between 1973 and 1992 at Clear Creek range from 0.52:1 to 0.75:1 (USFWS, unpubl. data).

An anomalous situation exists in the Yellowstone River below Yellowstone Lake. Since 1976, males have been more numerous than females in most annual dip-net samples from LeHardy Rapids. Male:female ratios were 0.73:1 and 0.79:1 in 1974 and 1975, but since 1976, the male:female ratio has dropped below 1.06:1 only three times (1982, 1986, and 1989). The mean male:female ratio between 1976 and 1991 was 1.35:1. Because these estimates are based on weekly surveys, they may not be directly comparable to male:female ratios obtained from fish traps. Yet samples at LeHardy Rapids are collected throughout the spawning migration, sample sizes are large, and methods have remained unchanged since 1974 (Jones et al. 1992). The 1973 change in angling regulations may explain this phenomenon.

The preponderance of males has been observed elsewhere. Byorth (1990) reported that males dominated the early portions of the spawning migration in Cedar Creek, but as the migration peaked the male:female ratio approached 1:1. Berg (1975) reported similar trends in Cedar Creek. Males were also more abundant in another Yellowstone River tributary, Tom Miner Creek, in 1988 and 1989. Male:female ratios in these fluvial spawning migrations may vary from other reported values because of differences in habitat and life history development, but the low number of spawners in the samples may influence results.

Spawning frequency.—Repeat spawning is common for Yellowstone cutthroat trout (Clancy 1988; Thurow et al. 1988; Varley and Gresswell 1988), but the prevalence of iteroparity can be affected by angler harvest (Varley and Gresswell 1988). Ball and Cope (1961) reported that first-time spawners composed up to 99% of spawning migrations in Yellowstone Lake during a period when angler harvest was greater than the estimated maximum sustained yield (325,000 trout; Benson and Bulkley 1963). But at least 23% of 42,229 Yellowstone cutthroat trout marked at Clear Creek in 1979 spawned again between 1980 and 1984 (Jones et al. 1985). Repeat spawners represented up to 15% of some resident and fluvial migrations in Idaho (Thurow et al. 1988). Thurow (1982) found that 93% of repeat spawners were females.

Additional spawning may be in either consecutive or alternate years (Thurow et al. 1988; Varley and Gresswell 1988). Using putative spawning erosion on scales, Bulkley (1961) concluded that consecutive-year spawners were more common in tributaries to Yellowstone Lake. At Clear Creek, however, spawners marked in 1979 returned most frequently in alternate years (1980–1984; Jones et al. 1985). Varley and Gresswell (1988) reported that alternate-year spawning was more common in populations at higher elevations. The pattern of repeat spawning is probably related to growth, parasitic infection, and other physiological factors (Ball and Cope 1961). In the Yellowstone River between Corwin Springs and Springdale, Yellowstone cutthroat trout that spawned during consecutive years consistently exhibited the slowest growth (Clancy 1987).

Based on recaptures of tagged fish, Ball and Cope (1961) reported that average instream mortality of Yellowstone cutthroat trout spawners was 48% in 5 tributaries of Yellowstone Lake between 1949 and 1953. Welsh (1952) reported that in 1951 and 1952, 28% of Yellowstone cutthroat trout spawners in Arnica Creek died near spawning sites and another 1% died before postspawning emigration was complete. At Clear Creek, estimates of instream mortality based on total counts of upstream and downstream migrants averaged 13% for 5 sample years (1977–1979, 1983, and 1984; Jones et al. 1985). In recent years, estimates of instream mortality at Clear Creek have increased (mean = 31% for 1987, 1988, 1991, and 1992; USFWS, unpubl. data) although the relative influence of changes in monitoring procedures and increased numbers of white pelicans *Pelecanus erythrorhynchos* has not been investigated.

Fecundity and early development.—Fecundity is related to length, weight, or age of fish (Bagenal 1978), and changes in mean length and age affect population fecundity (total number of eggs deposited by females; Bagenal 1978). Although relative fecundity (number of eggs/kg of female body weight; Bagenal 1978) has remained unchanged (2,633 eggs/kg; Jones et al. 1985), population fecundity at Clear Creek has risen from 6.2 million eggs in the 1950's to an average of almost 32 million eggs between 1975 and 1992 (USFWS, unpubl. data). Average fecundity of female Yellowstone cutthroat trout has risen in association with increases in mean length, and population fecundity remains high despite a decline in spawner abundance observed at Clear Creek in recent years (USFWS, unpubl. data).

Fecundity of Yellowstone cutthroat trout from Henrys Lake, Idaho, averaged 1,577 and 2,930 eggs/female (mean lengths of 319 mm and 518 mm; Thurow et al. 1988). Moore and Schill (1984) reported a mean fecundity of 1,413 eggs for females collected from the South Fork Snake River (mean length = 377 mm). At Clear Creek (Yellowstone Lake), the estimated mean fecundity for Yellowstone cutthroat trout in 1992 was 1,393 eggs/female (mean length = 394 mm; USFWS, unpubl. data).

Egg mortality of Yellowstone cutthroat trout in natural redds was estimated to range between 12 and 42% in 3 tributaries to Yellowstone Lake (Mills 1966); mortality was associated with inadequate water flow through gravel. Ball and Cope (1961) estimated 60–70% egg mortality. Angler wading may reduce survival; 83% of Yellowstone cutthroat trout eggs and pre-emergent fry were killed by twice-daily wading (Roberts and White 1992).

Eggs generally hatch in 25–49 days (310 Celsius temperature units, sum of mean daily temperatures above 0°C), and juveniles emerge from the gravel 2 weeks later (Ball and Cope 1961; Mills 1966; Kelly 1993). Juveniles often move to shallow, slow-flowing areas, and migratory individuals soon begin to emigrate (Varley and Gresswell 1988). Although young-of-the-year Yellowstone cutthroat trout are locally numerous in the Yellowstone River below Yellowstone Lake, fish less than 250 mm are not common (Schill and Griffith 1984; Kelly 1993). Kelly (1993) reported that numbers of young-of-the-year fish declined over 90% within 25 days after peak emergence in 1990 and 1991. Few juveniles were observed, and most were found in the segment between Sulfur Caldron and the Upper Falls.

Thurow et al. (1988) reported that in many drainages in Idaho, fry migrate downstream shortly following emergence, whereas juvenile Yellowstone cutthroat trout do not emigrate from some tributaries for 1 to 3 years. Both patterns have been observed in tributaries to Yellowstone Lake (Benson 1960; Gresswell et al., in press) and in the Yellowstone River drainage in Montana (Byorth 1990). Welsh (1952) suggested that the distance from redd to stream mouth directly influenced the length of time that fry remained in tributaries to Yellowstone Lake; those in the upper reaches of Arnica Creek often remained in the stream over winter. Thurow et al. (1988) reported a density-dependent downstream migration related to the abundance of suitable habitat.

Growth.—Growth of Yellowstone cutthroat trout is variable and dependent on population and environmental conditions. Growth rate generally increases as elevation decreases. Thurow et al. (1988) reported that migratory stocks grow faster than do nonmigratory stocks because of the greater growth potential in higher-order mainstem reaches. Thurow et al. (1988) reported that growth of individuals in migratory populations is greatest following emigration from natal areas and prior to maturity.

Males generally grow faster than do females in Henrys Lake (Irving 1955) and Yellowstone Lake (Bulkley 1961; USFWS, unpubl. data). The largest individuals sampled in Yellowstone Lake were males, but Varley and Gresswell (1988) suggested that this may be due to greater longevity rather than to faster growth. Recent information from Yellowstone Lake and Clear Creek indicates that many large (over 450 mm) individuals are immature (USFWS, unpubl. data). In an environment where the annual growing season is short, somatic growth may be encouraged by postponement of maturity and the associated demands of gonadal development.

In the Blackfoot River and Willow Creek drainages, Idaho, Yellowstone cutthroat trout reach 8 or 9 years of age, lengths greater than 600 mm, and weights from 2 to 4 kg (Thurow et al. 1988). Maximum size in Yellowstone Lake is somewhat lower (over 500 mm and 1.5 kg), but Yellowstone cutthroat trout in Heart Lake, Yellowstone National Park, can exceed 5 kg. Eight species of fish evolved in Heart Lake, and Yellowstone cutthroat trout are believed to be highly piscivorous in this lacustrine environment.

Varley and Gresswell (1988) summarized "typical" back-calculated lengths for Yellowstone cutthroat trout from Carlander (1969): age 1, 100 mm; age 2, 180 mm; age 3, 240 mm; age 4, 310 mm; age 5, 370 mm; age 6, 410 mm. Similar values for growth of Yellowstone cutthroat trout from Yellowstone Lake for 20 years between 1969 and 1992 were obtained: age 1, 60 mm; age 2, 140 mm; age 3, 240 mm; age 4, 310 mm; age 5, 350 mm; age 6, 390 mm; age 7, 420 mm; age 8, 450 mm; age 9, 470 mm (USFWS, unpubl. data). Many other data are available (Irving 1955; Laakso 1956; Laakso and Cope 1956; Bulkley 1961; Benson and Bulkley 1963; Irving 1979; Thurow 1982; Moore and Schill 1984; Corsi 1988; Shepard 1992; USFWS, unpubl. data).

Age analysis for Yellowstone cutthroat trout has primarily relied on the use of fish scales. Scales form when fish are approximately 41 to 44 mm in Yellowstone Lake (Brown and Bailey 1952; Laakso and Cope 1956). Laakso and Cope (1956) validated the use of scales up to age 2. The authors found that some fish did not form an annulus until the end of the second year of growth, and criteria to distinguish "normal" and "retarded" scale formation in the Yellowstone Lake watershed were established. Laakso (1955) maintained that criteria for establishing age at first annulus (on scales) in the Yellowstone Lake drainage have general applicability, but the universality of this hypothesis has not been determined.

The frequency of normal scales appears to be related to growth rate (Laakso 1955). In a review of populations throughout the range of the Yellowstone cutthroat trout, Lentsch and Griffith (1987) reported that the lack of a first-year annulus was related to temperature within the natal stream. They suggested that when accumulated Celsius temperature units were 720 or fewer, all fish lacked an annulus at the end of the first season of growth. All fish formed an annulus if the Celsius temperature units were 1,500 or greater.

Habitat Relations

Yellowstone cutthroat trout occupy diverse habitats. Lacustrine populations inhabit waters from the size of small beaver ponds to large lakes (e.g., Yellowstone Lake, 35,400 hectares). Varley and Gresswell (1988) reported that populations were historically common in large rivers such as the Snake River above Shoshone Falls, Idaho (mean annual flow, 156 m^3/s), and the Yellowstone River near Miles City, Montana (mean annual flow, 321 m^3/s). In contrast, Yellowstone cutthroat trout can be found in first-order tributaries with mean widths of 1 m and discharge as low as 0.06 m^3/s.

Yellowstone cutthroat trout are well adapted to cold, harsh environments. Data reviewed by Carlander (1969) suggested optimum water temperatures between 4.5 and 15.5°C for the subspecies. Dwyer and Kramer (1975) reported the maximum "scope for activity" at 15°C (difference between maximum and minimum metabolic rates) for a sample of cultured cutthroat trout (age 1+). Yellowstone cutthroat trout collected from Yellowstone Lake under 1 m of ice were actively feeding in water 0 to 4°C (Jones et al. 1979). Populations exist in streams in Yellowstone National Park with summer maxima between 5 and 8°C (Jones et al. 1979). Isolated populations in alpine and subalpine areas overwinter for up to 8 months in small streams with low temperatures and extreme ice conditions (Varley and Gresswell 1988).

Although Yellowstone cutthroat trout are currently associated with cold water habitats, Varley and

Gresswell (1988) reported that water temperatures within portions of the historical range exceeded 26°C. Most of these large-river, warm-water populations have been extirpated, yet several populations have been documented in geothermally heated streams in Yellowstone National Park with an ambient water temperature of 27°C (Varley and Gresswell 1988). Yellowstone cutthroat trout apparently survive under these extreme conditions by locating thermal refugia. Kelly (1993) suggested that cutthroat trout were excluded from Alum Creek, a tributary to the Yellowstone River in Yellowstone National Park, because summer water temperatures often exceeded 22°C.

Yellowstone cutthroat trout tolerate a broad range of chemical conditions. Varley and Gresswell (1988) reported that the subspecies has been collected from waters in Yellowstone National Park with total dissolved solids ranging from about 10 to 700 mg/L. They speculated that conditions were more variable in the historical range (e.g., waters in the Bighorn River drainage, Wyoming, have total dissolved solids exceeding 2,000 mg/L; U.S. Geological Survey, unpubl. data). Alkalinity is relatively low (mean = 64 mg $CaCO_3$/L) in most areas of Yellowstone National Park, but waters in the upper Snake River basin exceed 150 mg $CaCO_3$/L (Thurow et al. 1988). Mean alkalinity for three tributaries used by fluvial spawners from the Yellowstone River in Montana ranged from 46 to 378 mg $CaCO_3$/L (Byorth 1990). Although populations of Yellowstone cutthroat trout have been documented in waters with pH from about 5.6 to over 10.0, none have been observed where pH is below 5.0 (Varley and Gresswell 1988). Kelly (1993) reported that unsuitable water quality precluded survival of Yellowstone cutthroat trout in three tributaries to the Yellowstone River in Hayden Valley, Yellowstone National Park; these streams are characterized by widely fluctuating pH resulting from poor buffering capacity.

Spawning streams are most commonly perennial with groundwater and snow-fed water sources; gradient is usually below 3% (Varley and Gresswell 1988). Varley and Gresswell (1988) reported that the use of intermittent streams for spawning is not widely documented, but spawning has been observed in intermittent tributaries to Yellowstone Lake. In these streams fish spawn during spring runoff, and fry emigrate in July and August, prior to stream desiccation. Although many fry and some adults may become stranded as discharge drops, Varley and Gresswell (1988) suggested that spawning in intermittent streams may provide a reproductive advantage over nonindigenous fall-spawning salmonids that have been introduced throughout the range of the Yellowstone cutthroat trout.

Varley and Gresswell (1988) suggested that Yellowstone cutthroat trout spawn wherever optimum temperature and substrate are found, but this may be an oversimplification. Cope (1957b) reported that forest cover had little effect on the distribution of redds in tributaries to Yellowstone Lake, and spawners did not always congregate in areas with the greatest concentration of spawning gravel. Thurow and King (1994) noted that in Pine Creek, Yellowstone cutthroat trout spawners selected different sites for spawning in 1991 and 1992; severe drought in 1992 would have caused dewatering at sites used the previous year. The authors emphasized the importance of other physical cues, such as water velocity, for locating redds in areas with a high probability of hatching success and fry survival. Water depth is correlated with water velocity, and this variable may also provide an important physical cue.

Varley and Gresswell (1988) reported that optimum size for gravel in Yellowstone cutthroat trout spawning areas is 12–85 mm in diameter. In 11 redds from Cedar Creek, Byorth (1990) estimated approximately 74% (by weight) gravel (2–63.5 mm in diameter) and 17% cobble (63.5–256 mm in diameter). Yellowstone cutthroat trout in Pine Creek spawned in areas where substrate was less than 100 mm in diameter (Thurow and King 1994). Approximately 60% of the substrate was in the 16- to 64-mm size-class, 15% was in the 6.4- to 16-mm size-class, and 20% was less than 6.4 mm in diameter. Thurow and King (1994) found no significant change in composition of undisturbed substrate near redds from the start to the end of incubation.

Mean size of 66 redds measured by Thurow and King (1994) was 1.58 m long by 0.60 m wide; redds encompassed an area of approximately 1 m^2. Yellowstone cutthroat trout spawned in water 9 to 55 cm deep in Pine Creek, but over 80% of the redds were at depths between 10 and 30 cm deep (Thurow and King 1994). Average depth of redds in Pine Creek was 20 cm beside the pit and 21 cm upstream from the pit. In a smaller tributary (Cedar Creek), Byorth (1990) reported that 86% and 75% of Yellowstone cutthroat trout redds were constructed at depths of 9.1 to 15.2 cm in 1988 and 1989. Mean depth of redds in Cedar Creek was approximately 12 cm in both years.

Water velocities within 5 cm of completed redds were 16 to 73 cm/s in Pine Creek, and the average was 42 cm/s beside the redd and 46 cm/sec upstream from the redd (Thurow and King 1994). Mean current velocity at redds in Cedar and Tom Miner creeks averaged approximately 24 cm/s and 38 cm/s (Byorth 1990). Velocities ranged from 0 to 68 cm/s in Cedar Creek, but most redds were found at velocities between 16 and 27 cm/s. Water velocity was 14–71 cm/s near redds in Tom Miner Creek (Byorth 1990).

Thurow and King (1994) observed superimposition of redds, generally laterally or immediately downstream of existing redds. Byorth (1990) reported superimposition of redds in Cedar and Tom Miner Creeks, and superimposition has been documented in tributaries to Yellowstone Lake (Mills 1966). Thurow and King (1994) suggested that because most eggs were deposited in the center of the upstream edge of the tailspill, redd superimposition that is located laterally or downstream of the tailspill may not disturb the eggs.

In streams, fry generally seek areas of low velocity (Varley and Gresswell 1988). Yellowstone cutthroat trout fry in Cedar and Tom Miner creeks used similar habitat. Mean depth of locations used by fry in both streams was approximately 11 cm (range 3–24 cm; Byorth 1990). Water velocities were also similar (3 and 5 cm/s for Cedar and Tom Miner creeks), and approximately 50% of fry were located where velocities exceeded 2 cm/s (Byorth 1990). Stream substrate at sites used by Yellowstone cutthroat trout fry differed between the two streams; these differences probably reflected differences in available substrate materials (Byorth 1990).

In late winter (March–April) at water temperatures ranging from 4 to 7°C, Griffith and Smith (1993) found juvenile Yellowstone cutthroat trout concealed in water shallower that 0.5 m within 1 m of the wetted perimeter of the stream. Of seven sites sampled in the South Fork Snake River, 87% of the fish captured were age 0 Yellowstone cutthroat trout, 2% were age 1 Yellowstone cutthroat trout, and 11% were brown trout (Griffith and Smith 1993). Density of age 0 Yellowstone cutthroat trout increased as the substrate size of unembedded cover increased. From 61 to 66% of the juvenile trout in concealment emerged at night (Griffith and Smith 1993).

Adfluvial fry usually begin emigration soon after emergence, but some may overwinter in the natal stream. After emigration from natal streams, fry congregate in shallow water along the shoreline prior to movement into deeper water (Gresswell and Varley 1988). Apparently in Yellowstone Lake most juveniles (through age 2) are pelagic (Gresswell and Varley 1988). Plankton are abundant in these areas, and the vast size of the pelagic area provides protection from predation by larger individuals.

Adfluvial Yellowstone cutthroat trout move into the littoral zone after maturation and apparently remain there throughout the year (Gresswell and Varley 1988). A shift in food preference is associated with the shift in habitat, and the proportion of larger macroinvertebrates in the diet increases (Benson 1961). Mature individuals are especially prominent during spawning migrations as they travel along the shoreline to tributaries. Because most angler use is focused on the shallow, near-shore areas, older and larger Yellowstone cutthroat trout are vulnerable to angler harvest. Scarcity of juvenile Yellowstone cutthroat trout (through age 2) in the angler catch is assumed to be associated with their residence in pelagic areas (Gresswell and Varley 1988).

Biotic Interactions

Except where barriers limited access (e.g., Waha Lake, Idaho, and Crab Creek, Washington), rainbow trout have replaced the Yellowstone cutthroat trout in the Columbia River Basin below Shoshone Falls on the Snake River (Behnke 1992). The falls may have been formed 30,000 to 60,000 years ago during the Bonneville floods (Malde 1965), or as recently as 14,500 years ago (Oviatt et al. 1992). Above the falls, Yellowstone cutthroat trout evolved with 10 other fish species (Thurow et al. 1988). In Yellowstone National Park, seven of these fishes were historically sympatric with Yellowstone cutthroat trout in the Heart Lake drainage (Jordan 1891; Smith and Kendall 1921; Dean and Varley 1974). On the east side of the Continental Divide only longnose dace were historically sympatric with the Yellowstone cutthroat trout above the Upper Falls of the Yellowstone River (Benson and Bulkley 1963). Below the falls, mountain whitefish, mottled sculpin, longnose sucker, white sucker, and longnose dace were all historically found in the Yellowstone River (Clancy 1988); the white sucker, however, has not been collected in Yellowstone National Park (Varley and Schullery 1983).

There are many predators in the range of the Yellowstone cutthroat trout. Birds may have the greatest effect on populations in the Yellowstone Lake drainage. The size of fish selected and biomass consumed per day vary among bird species (Davenport 1974; Swenson 1978; Swenson et al. 1986). Estimated total biomass of cutthroat trout consumed by birds near Yellowstone Lake was 117,100 and 83,800 kg for 1973 and 1974 (Davenport 1974).

Although white pelicans were estimated to remove 350,000 Yellowstone cutthroat trout (approximately 105,900 kg) annually in the 1920's (based on population estimates of 500 to 600 pelicans; Ward 1922), Davenport (1974) argued that the estimate of 3.6 kg fish/pelican/day was high. Using an estimate of 1.3 kg fish/pelican/day, she estimated that biomass of Yellowstone cutthroat trout consumed by white pelicans was approximately 16,800 kg (195 pelicans) and 34,500 kg (400 pelicans) in 1973 and 1974 (Davenport 1974).

Grizzly bears (*Ursus arctos horribilis*) and bald eagles (*Haliaeetus leucocephalus*) also commonly feed on Yellowstone cutthroat trout (Mealey 1980; Swenson et al. 1986; Reinhart 1990). Swenson et al. (1986) found that during the breeding season (April-August), Yellowstone cutthroat trout accounted for approximately 23% of the diet of bald eagles in Yellowstone Lake, the Yellowstone River and their tributaries above Upper Falls, and Lewis, Shoshone, and Heart lakes. Eagles consumed Yellowstone cutthroat trout almost exclusively during the peak spawning period in Yellowstone Lake (May-July, Ball and Cope 1961; USFWS, unpubl. data), switching to flightless birds as fish became less available. In the Snake River and its major tributaries from the mouth of Lewis Lake to the mouth of the Henrys Fork, cutthroat trout composed about 8% of their diet, but the exact proportion of Yellowstone cutthroat trout cannot be estimated because this included the range of the Snake River fine-spotted cutthroat trout (unnamed subspecies of cutthroat trout occurring in the Snake River between Jackson Lake and Palisades Reservoir; Behnke 1992).

Thurow et al. (1988) cited McMasters (1970) and Thurow (1982) to support their contention that Yellowstone cutthroat trout were opportunistic feeders that consume preferred food items according to availability. Behnke (1992) suggested that Yellowstone cutthroat trout are generally more piscivorous than westslope cutthroat trout. In migratory populations in Idaho, growth increased coincident with a shift from insectivory to piscivory following emigration from the tributaries (Skinner 1985). Because Yellowstone cutthroat trout in Heart Lake (Snake River drainage, Yellowstone National Park) evolved with seven other fishes, piscivory may have been favored among mature cutthroat trout. Perhaps the fewer indigenous fishes explains why piscivory is rare in Henrys Lake and Yellowstone Lake (Irving 1955; Benson 1961; Jones et al. 1990).

Juvenile Yellowstone cutthroat trout in the pelagic area of Yellowstone Lake feed primarily on zooplankton including *Daphnia shøedleri* and *Diaptomus shoshone* (Benson 1961). Mature Yellowstone cutthroat trout move into the littoral zone and remain there throughout the year feeding on zooplankton, larger crustaceans (primarily *Gammarus lacustris* and *Hyalella azteca*), and aquatic insects (Benson 1961; Gresswell and Varley 1988; Jones et al. 1990).

One exception to the limited piscivory in Yellowstone Lake was observed during weir monitoring of the annual Yellowstone cutthroat trout spawning migration in Pelican Creek. Approximately 33% of stomach samples collected from Pelican Creek in 1972 (n=27) and 1973 (n=69) contained fish (Dean and Varley 1974). Of 65 fish identified from stomach samples, 64 were redside shiners and 1 was a longnose dace; spawning migrations of these two fishes are believed to roughly coincide with cutthroat trout. Although redside shiners were routinely netted and released below the trap, relations between handling and piscivory below the weir were not investigated. It is possible that the observed predation by cutthroat trout in Pelican Creek may be an artifact of trapping.

Sixty-four parasitic species are associated with cutthroat trout (Hoffman 1967; Heckmann and Ching 1987), and 18 of these have been collected from Yellowstone cutthroat trout from Yellowstone Lake (Heckmann 1971; Heckmann and Ching 1987). In 1956 and 1957, 55–60% of 10,700 fish from Yellowstone Lake tributaries had parasites (Cope 1958). The prevalence of parasites elsewhere is not well documented (Woodbury 1934; Bangham 1951; Hoffman 1967).

Perhaps the most infamous of the parasites associated with Yellowstone cutthroat trout is the tapeworm found in Yellowstone Lake. There is disagreement about the taxonomy of this tapeworm (Otto and Heckmann 1984). Recent work suggests that two species, *Diphyllobothrium ditremum* and *Diphyllobothrium dendriticum*, are present instead of the single previously identified species *Diphyllobothrium cordiceps* (Heckmann and Ching 1987). Infestation rates are high (46–100%; Woodbury 1934; Bangham 1951; Post

1971; Heckmann and Ching 1987). Effects on mortality rates have not been assessed. Hall (1930) speculated that stunting and diminished egg production were possible, but this has never been substantiated. Some individuals may contain over 400 plerocercoids (Heckmann 1971), but many individuals exhibiting a high level of parasitism often remain vigorous (Post 1971).

The aesthetics of dense infestations of tapeworms appear to be the major concern of anglers (Linton 1891; Post 1971), but there is some evidence that human infections are possible (Heckmann and Ching 1987). Many anglers from Yellowstone Lake historically responded by discarding parasitized fish. In one survey in July 1959, 7,500 fish were counted in garbage cans near Yellowstone Lake. During 4 random days in July 1978, only 9 Yellowstone cutthroat trout were found in almost 300 bags of garbage from 2 campgrounds; expansion of these results yielded an estimate of 300 discarded fish for the 2 campgrounds during the month (Jones et al. 1979). The difference in counts is believed to be associated with reduced infection rates in younger fish that now constitute the legal harvest. The white pelican is a host of the tapeworm (Linton 1891), and during the 1920's, there was support for a plan to destroy pelican eggs on the rookery to reduce the bird population and (hypothetically) the incidence of tapeworms (Varley and Schullery 1983).

Other parasites may be numerous. Parasitic copepods, *Lepeophtheirus salmonis*, *Lernaeopoda bicauliculata*, *Salmincola edwardsii*, and *Salmincola* sp. (Heckmann and Ching 1987), are found on gills, fins, and points of fin insertion. Cope (1958) reported that highest infestation density was at the point of fin insertion. Leeches, *Piscicola salmositica* and *Illinobdella* sp. (Heckmann and Ching 1987), occur on the outside of the body, but there does not appear to be a preferred area (Cope 1958).

One species of eye fluke, *Diplostomum baeri buccelentum*, occurred in all 25 Yellowstone cutthroat trout collected from Yellowstone Lake in 1985 by Heckmann and Ching (1987). Dwyer and Smith (1989) found metacercariae of eye flukes thought to be *Diplostomum baeri buccelentum* in 6 of 10 Yellowstone cutthroat trout from Yellowstone Lake. Eye flukes cause diplostomatosis or eye fluke disease of fishes, and the effect on visual acuity depends on the density of worms (Heckmann and Ching 1987). Severe infections may affect feeding ability and ultimately growth.

Infestation characteristics varied with location, sex, and season. Among spawning migrations in five tributaries, parasite infestation rates appeared to be higher in Arnica Creek than in other tributaries (Cope 1958). Cope (1958) also found that males had more parasitic copepods, females harbored more leeches, infestation rates decreased through time, and fewer downstream migrants were parasitized than were upstream migrants. Yellowstone cutthroat trout in Clear Creek were an exception to this seasonal generalization; the greatest incidence of leeches was during the latter portion of the migration. Since 1978, however, data from Clear Creek suggest higher infestation in the early portion of the migration (USFWS, unpubl. data).

Little is known about disease in naturally reproducing populations of Yellowstone cutthroat trout. The causative agent for furunculosis, *Aeromonas salmonicida*, has been isolated from individuals collected from the Yellowstone River below Yellowstone Lake (USFWS, unpubl. data). MacConnell and Peterson (1992) reported proliferative kidney disease in a population of Yellowstone cutthroat trout in a remote reservoir in Montana, but this was the first substantiated occurrence of the disease in a feral population of cutthroat trout.

Reasons for Concern

Yellowstone cutthroat trout were historically found in the Yellowstone River drainage in Montana and Wyoming and in the Snake River drainage in Wyoming, Idaho, Utah, Nevada, and probably Washington (Varley and Gresswell 1988; Behnke 1992). Human activities and angler harvest have resulted in widespread extirpation of populations of this subspecies. Varley and Gresswell (1988) estimated that genetically unaltered populations of Yellowstone cutthroat trout occupy 10% of the historical stream habitat (2,400 km) and about 85% of the historical lacustrine habitat (38,500 hectares). Presently, 91% of the current range of Yellowstone cutthroat trout lies within the boundary of Yellowstone National Park (Gresswell and Liss, in press).

In contrast to declines of other cutthroat trout subspecies, the decline of Yellowstone cutthroat trout has been well documented. In a summary of the distribution of Yellowstone cutthroat trout in Montana, Hadley (1984) reported a continued loss of Yellowstone cutthroat trout populations from a previous assessment by Hanzel (1959). More recently, biologists estimated that the subspecies historically occupied approximately 4,800 and 15,100 km of streams in Montana and Wyoming (Yellowstone Cutthroat Trout Working Group 1994). Habitat suitability for Yellowstone cutthroat trout was not verified for all locations identified in Wyoming, thus these may be overestimates. Approximately 965 km of stream in Montana and 4,700 km in Wyoming were assumed to currently support Yellowstone cutthroat trout. These estimates may also be inflated because populations are introgressed in 42–50% of the current habitat in Montana, and there is no information available concerning the genetic purity of Yellowstone cutthroat trout populations in Wyoming (YCTWG 1994). Considering only genetically unaltered populations in Montana, it appears that only 10% of the historical range (stream km) in that state still sustains Yellowstone cutthroat trout. Assuming similar conditions in Wyoming, estimates of the current range by Varley and Gresswell (1988) may be realistic but not encouraging. Significantly, 54% of the existing fluvial habitat of Yellowstone cutthroat trout supports introduced salmonids, e.g., brown trout and brook trout, that are potential competitors or predators.

Population declines and extirpations have been greatest in low-elevation, high-order (3 or larger) streams (Hanzel 1959). These areas have historically been the focus of most human activities including agriculture and resource extraction. Additionally, abundant access in low-elevation areas has encouraged angler harvest and nonnative species introductions. Remoteness of high-elevation portions of the native range probably contributed to the preservation of remaining populations, and in much of this area, public ownership has provided habitat protection that is lacking in lower elevations (Varley and Gresswell 1988).

Causes of the Decline

Hybridization resulting from introductions of rainbow trout, nonnative subspecies of cutthroat trout, or nonindigenous stocks of Yellowstone cutthroat trout is the primary cause of the decline and extirpation of Yellowstone cutthroat trout throughout its historical range (Allendorf and Leary 1988; Varley and Gresswell 1988). Hybrids between rainbow trout and Yellowstone cutthroat trout are developmentally successful, and progeny may appear as morphological and meristic intermediates between parental types or virtually identical to a single parental type (Ferguson et al. 1985). Consequently, it is virtually impossible to verify genetic integrity with morphological data alone. Nuclear allozymes and mtDNA haplotypes, however, have proven useful for detecting hybridization (Leary et al. 1987; Forbes and Allendorf 1991).

In the upper Snake River drainage, hybridization with rainbow trout has resulted in the virtual disappearance of Yellowstone cutthroat trout in the Henrys Fork Snake River (Griffith 1988) and lower portions of the Blackfoot, Portneuf, and Teton rivers (Varley and Gresswell 1988). In Montana, virtually all drainages where rainbow trout have been stocked in the historical range of Yellowstone cutthroat trout now support hybrid populations of the two species (Hanzel 1959). Allendorf and Leary (1988) reported evidence of hybridization and introgression in 8 of 16 samples from tributaries to the Yellowstone River in Montana. Because these tributaries were selected at random, Allendorf and Leary (1988) asserted that the results were a reliable representation of hybridization in the Yellowstone River drainage.

Reproductive isolation between Yellowstone cutthroat trout and rainbow trout has apparently prevented hybridization in some areas. Wishard et al. (1980) examined Yellowstone cutthroat trout populations from four tributaries to the upper Blackfoot River and found no evidence of hybridization with rainbow trout. In these drainages, Yellowstone cutthroat trout spawn in May and June in headwater reaches, and rainbow trout of hatchery origin typically spawn from winter through spring in lower reaches of the drainage (Thurow 1982). A similar situation has been observed in the Yellowstone River below the Lower Falls.

Snake River fine-spotted cutthroat trout have been introduced in many waters originally containing Yellowstone cutthroat trout, but the extent of hybridization is unknown, in part because hybrids are difficult to recognize. Introgression resulting from the introduction of mixed stocks of Yellowstone cutthroat trout is also common (Allendorf and Leary 1988). Yellowstone Lake was once the largest source of cutthroat trout in the world, and over 818 million eggs were gathered from Yellowstone Lake tributaries between 1899 and 1957 (Varley 1979). Many of the resulting fry were returned to the lake (Gresswell and Varley 1988; Varley and Gresswell 1988). At the metapopulation level, Gresswell and Varley (1988) suggested that planting fry in the lake and its tributaries led to the potential mixing of up to 68 historically distinct genetic entities.

Non-salmonid species are commonly indicted as competitors of salmonid species, but it does not appear that the introduction of longnose suckers, redside shiners, and lake chubs into Yellowstone Lake has affected Yellowstone cutthroat trout (Gresswell and Varley 1988). Marrin and Erman (1982) found evidence of competition between brown trout and rainbow trout in Stampede Reservoir, California, but competition between trout and the tui chub or Tahoe sucker was "unlikely." Niche separation, both spatial and temporal, may reduce the incidence of competition in these examples. Although competition may be substantial in different environments, it would probably be greatest between species with similar niches.

Introduction of brown trout and rainbow trout to the Madison River in Yellowstone National Park was followed by the extirpation of indigenous westslope cutthroat trout and fluvial Arctic grayling (Jones et al. 1981), but Yellowstone cutthroat trout are still abundant in sections of the Yellowstone River where they are sympatric with brown trout and rainbow trout (Clancy 1988). In some Idaho streams where Yellowstone cutthroat trout are sympatric with brown trout and brook trout, cutthroat trout persist if habitat has not been degraded and angler harvest is not extreme (Thurow et al. 1988). The consequences of the recent unauthorized introduction of lake trout into Yellowstone Lake are unknown.

Griffith (1988) reported that cutthroat trout are less likely to coexist with brook trout than with other nonnative salmonids even in undisturbed habitats, and Yellowstone cutthroat trout have been extirpated from most areas in Yellowstone National Park where brook trout have been introduced (Gresswell 1991). Mechanisms for replacement are unknown (Griffith 1988; Thurow et al. 1988). Competitive exclusion has probably been cited most frequently, and niche overlap may be greater between Yellowstone cutthroat trout and brook trout than between these fishes and other salmonid species.

Alternatively, species replacement (Griffith 1988) may often explain the extirpation of Yellowstone cutthroat trout. MacPhee (1966) reported that brook trout were less vulnerable to angling than were cutthroat trout. In a section of the Yellowstone River in Montana where special regulations have been imposed (catch-and-release for cutthroat trout; four fish less than 330 mm and one fish greater than 559 mm for brown trout and rainbow trout), the incidence of hooking scars was greater for Yellowstone cutthroat trout than for brown trout or rainbow trout (Shepard 1992). Differential mortality imposed by angler harvest could contribute to the eventual dominance of the least susceptible group. Once cutthroat trout have been replaced by another salmonid, the situation is generally irreversible without human intervention (Moyle and Vondracek 1985).

Human activities such as dam construction, water diversions, grazing, mineral extraction, road construction, and timber harvest have substantially degraded lotic environments (Meehan 1991), including portions of the historical range of Yellowstone cutthroat trout. Angler wading can also be a significant source of disturbance (Roberts and White 1992). Human activities have resulted in barriers to migration, reduced flows, sediment deposition, groundwater depletion, streambank instability, erosion, and pollution. Efforts to curtail human activities and restore degraded stream segments are increasing, but habitat degradation continues at an alarming rate.

Although there are no dams on the Yellowstone River in the historical range of the Yellowstone cutthroat trout, numerous impoundments in the Snake River have altered historical fish migration patterns. Spawning and rearing areas have been isolated in the Blackfoot, Portneuf, South Fork Snake, Teton, Henrys Fork Snake, and main-stem Snake rivers (Thurow et al. 1988). Below dams, spawning and rearing habitats are limited, and altered discharge patterns compound problems downstream (Thurow et al. 1988). Elle and Gamblin (1993) suggested that reduced winter flows below a dam on the South Fork Snake River resulted in significant mortality of age 0 Yellowstone cutthroat trout.

Culverts can also alter or totally block fish migration (Belford and Gould 1989), and culverts are widespread throughout the range of the Yellowstone cutthroat trout. Belford and Gould (1989) reported that Yellowstone cutthroat trout could not pass through a culvert on Cedar Creek, a tributary to the Yellowstone River in a section where population densities are limited by the availability of spawning habitat (Clancy 1988). Several culverts on tributaries to Yellowstone Lake reduce access to adfluvial spawners, and at least two culverts totally block annual spawning migrations (Dean and Varley 1974; Jones et al. 1986).

Water diversions have been significant in the decline of Yellowstone cutthroat trout in Montana (Hadley 1984). Clancy (1988) found that population density of Yellowstone cutthroat trout in the Yellowstone River was greatest in the vicinity of tributaries that supported spawning migrations. Byorth (1990) documented loss of spawning habitat for Yellowstone cutthroat trout in three tributaries to the Yellowstone River where water was diverted annually. Irrigation withdrawals often prohibited fluvial migrations into Reese Creek, a tributary to the Yellowstone River on the north boundary of Yellowstone National Park, prior to water-rights adjudication (Jones et al. 1990). In Idaho, the Blackfoot, Henrys Fork Snake, Portneuf, Raft, Teton, and mainstem Snake rivers and Willow Creek are seriously affected by irrigation removals (Thurow et al. 1988). Degraded water quality and unscreened irrigation ditches contribute to the problems associated with water diversions (Johnson 1964; Clancy 1988; Thurow et al. 1988; Byorth 1990).

Effects of livestock grazing on riparian habitats are well documented (Gresswell et al. 1989; Platts 1991). In the range of the Yellowstone cutthroat trout, Thurow et al. (1988) reported that intensive livestock grazing has caused degradation of riparian areas and subsequent stream bank sloughing, channel instability, erosion, and siltation. Alterations are broadly distributed on private and public lands throughout the upper Snake River basin in Idaho and Wyoming (Binns 1977; Thurow et al. 1988). Clancy (Montana Department of Fish, Wildlife, and Parks, pers. commun.) suggested that habitat deterioration resulting from livestock grazing in the Yellowstone River drainage was less of a threat to indigenous populations of Yellowstone cutthroat trout than hybridization and dewatering.

The influence of mineral extraction on Yellowstone cutthroat trout in Idaho has been primarily within the Blackfoot River drainage. Phosphate mines in that area are associated with increased sedimentation (Thurow et al. 1988). An abandoned gold mine in the headwaters of Soda Butte Creek (near Cooke City, Montana, upstream from Yellowstone National Park) caused extensive pollution through the 1960's (Jones et al. 1982). In Yellowstone National Park, fish populations were low, and anglers had minimal success (Arnold and Sharpe 1967). Reclamation of the tailings site reduced the input of pollutants and led to improvements in the fishery during the last two decades (Jones et al. 1982). A planned expansion of mining near Cooke City poses a renewed threat to the Yellowstone cutthroat trout population in Soda Butte Creek (Jones et al. 1992).

Yellowstone cutthroat trout are extremely vulnerable to angling, and angler harvest has contributed to substantial declines in population abundance throughout the historical range of the subspecies (Binns 1977; Hadley 1984; Gresswell and Varley 1988; Thurow et al. 1988). Schill et al. (1986) estimated that individuals in the Yellowstone River between Yellowstone Lake and Sulphur Caldron were captured an average of 9.7 times during the 108-day angling season. Many tagged Yellowstone cutthroat trout were captured two or three times in a single day (Schill et al. 1986). Although high catchability is important to most anglers, it may lead to substantial declines in abundance if the harvest is not restricted (Gresswell and Liss, in press).

Examples from Yellowstone National Park have special relevance because anthropogenic habitat alterations have been minimal. In Yellowstone Lake, measures of abundance and population structure of Yellowstone cutthroat trout suggested substantial deviation from historical levels as harvest increased through the 1950s. By 1968, landing rate and average size of captured fish declined to unprecedented levels (Gresswell and Varley 1988). These changes happened under a creel limit of only three fish per day; angler effort during this period reached 15.8 angler-hours/ha (Varley and Gresswell 1988). Similar effects were noted on populations in the Yellowstone River (Fishing Bridge-Upper Falls) and Lamar River. Following implementation of special regulations, these populations exhibited significant increases in mean length and generally stable landing rates despite continued increases in angler effort (Gresswell and Varley 1988; Gresswell and Liss, in press).

Outside of Yellowstone National Park, effects of angler harvest have been similar. The mean length and the proportion of spawners greater than 380 mm declined substantially between 1973 and 1983 in Cedar Creek. During that period angling regulations allowed the daily harvest of 5 Yellowstone cutthroat trout (only one over 457 mm). Beginning in 1984, regulations for Yellowstone cutthroat trout in the Yellowstone River for approximately 80 km downstream from the Park boundary were changed to catch-and-release. Clancy (1988) reported an increase in the proportion of Yellowstone cutthroat trout larger than 299 mm in that section of river since the implementation of the no-harvest regulation and Shepard (1992) suggested that density increased where recruitment of Yellowstone cutthroat trout was adequate (Shepard 1992). The proportion of Yellowstone cutthroat trout longer than 405 mm had not increased significantly by 1991 (Shepard 1992).

Thurow et al. (1988) suggested that angler harvest had contributed to the decline of Yellowstone cutthroat trout in the upper Snake River basin. Special regulations including size limits and adjustments of angling-season length have been implemented on the South Fork Snake and Blackfoot rivers to reduce the effect of angler harvest. A regulation specifying a 2-fish limit and release of Yellowstone cutthroat trout between 250 and 405 mm resulted in an increase in older and larger fish in the South Fork Snake River (Heise to Palisades Dam) after 3 years (Thurow et al. 1988). In the Blackfoot River, however, a reduced harvest (3-fish limit) without size restrictions did not accomplish management goals (Thurow et al. 1988).

There is some evidence that historical egg-taking was detrimental to individual spawning populations. Spawning runs were blocked annually in some larger tributaries (Gresswell and Varley 1988). Annual spawner counts in Clear Creek dropped from approximately 16,000 between 1945 and 1948 to 3,353 in 1953 (Benson and Bulkley 1963). After egg-taking ceased in 1953, the number of Yellowstone cutthroat trout spawners rose to an average of 7,300 annually between 1957 and 1961 (Gresswell and Varley 1988). By the mid–1960's spawner counts had reached an average of 36,000 annually, despite concurrent increases in angler harvest in the lake (Gresswell et al., in press).

Current Management

Yellowstone cutthroat trout have been designated as a "Species of Special Concern-Class A" by the American Fisheries Society (Johnson 1987), and this status has been officially recognized by the Montana Department of Fish, Wildlife, and Parks (YCTWG 1994). The subspecies is also recognized as a species of special concern in Idaho and managed accordingly. Both the Northern and Rocky Mountain regions of the USDA Forest Service consider the Yellowstone cutthroat trout a sensitive species (YCTWG 1994). Though the Yellowstone cutthroat trout has not been given a formal status in Wyoming, the subspecies has influenced management activities in recent years (YCTWG 1994; R. Wiley, Wyoming Game and Fish Department, pers. commun.). In Yellowstone National Park, indigenous species, including the Yellowstone cutthroat trout, receive priority in management decisions.

Concerned management agencies in Wyoming and Montana recently developed a draft interagency management guide for the Yellowstone River basin (YCTWG 1994). The guide formalized management strategies for the Yellowstone cutthroat trout in the Yellowstone River basin and clarified the direction of management for the subspecies. Supporters of the plan included the American Fisheries Society, Bureau of Land Management, Crow Indian Tribe, Greater Yellowstone Coalition, Montana Association of Conservation Districts, the National Park Service, Trout Unlimited, USDA Forest Service, and the USDI Fish and Wildlife Service.

Special status provided to indigenous populations of Yellowstone cutthroat trout is critical to the fish's persistence. Current management emphasizes populations sustained by natural reproduction and by stocking (Varley and Gresswell 1988; YCTWG 1994). Both management approaches include strategic elements involving genetic integrity, habitat management, and harvest regulation (Varley and Gresswell 1988).

Efforts to identify genetically unaltered populations of Yellowstone cutthroat trout are important. In the Yellowstone River drainage, both in Yellowstone National Park and outside the Park in Montana, genetic sampling has been pursued vigorously in recent years. Most management agencies require positive genetic identification before protecting populations of Yellowstone cutthroat trout, so this work is critical to the persistence of the subspecies (Varley and Gresswell 1988). Additionally, the value of protecting and genetically restoring introgressed populations of Yellowstone cutthroat trout where genetic purity is greater than 97% was officially recognized in the interagency management guide for the Yellowstone River basin (YCTWG 1994).

To maintain genetic integrity of indigenous populations of the Yellowstone cutthroat trout, Montana, Idaho, and Wyoming have modified their stocking guidelines. Management of fluvial fisheries in Montana emphasizes wild trout populations, and stocking in lotic systems was terminated in 1974 (Vincent 1987). In Idaho, stocking in the upper Snake River basin is restricted to waters that do not support viable populations of genetically unaltered Yellowstone cutthroat trout. In areas that still receive nonnative fish introductions, tactics to prevent introgression are being investigated (Thurow et al. 1988).

The use of piscicides to remove undesirable fishes to protect indigenous species from hybridization and competition with other salmonid species has been infrequent (Rinne and Turner 1991). In Colorado and Montana this technique has been successfully used to protect and reestablish indigenous cutthroat trout populations. In Yellowstone National Park, brook trout were removed from Arnica Creek, a tributary to Yellowstone Lake that supports an annual migration of adfluvial Yellowstone cutthroat trout (Gresswell 1991). Renovation eliminated potential competition and predation in Arnica Creek and prevented the invasion of the lake and other tributaries by brook trout. Although removal of nonnative species may be critical for protecting and reintroducing Yellowstone cutthroat trout in some areas, it is extremely expensive and difficult to achieve; the preferred alternative is to avoid nonnative species introductions.

Varley and Gresswell (1988) suggested that habitat management includes protection, enhancement, and improvement. Protection of habitat may be the most cost-effective form of habitat management. Although improvement is associated with both degraded and relatively pristine habitats, enhancement is generally synonymous with restoring degraded habitats. Opportunities for habitat restoration are widespread, and this activity may significantly affect the persistence of Yellowstone cutthroat trout in their historical range. The USDA Forest Service has recently increased efforts to identify areas of critical habitat for the Yellowstone cutthroat trout in the Greater Yellowstone Ecosystem (B. May, Gallatin National Forest, pers. commun.). Critical habitat will be prioritized for protection and restoration projects.

Modifying culverts is one aspect of habitat enhancement that is often overlooked, but this type of restoration may provide substantial benefits in areas where production is limited. Clancy and Reichmuth (1990) described a detachable fishway that was inexpensive, portable, and durable. Belford and Gould (1989) documented an increase in the number of Yellowstone cutthroat trout spawners ascending a modified culvert in Cedar Creek. They developed guidelines for installing new culverts and identifying culverts that require velocity-reduction devices to allow passage. Wooden baffles were installed in four culverts on two tributaries to Yellowstone Lake in 1976 (Jones et al. 1977). Observations suggest improved passage through these culverts, but effects have not been rigorously evaluated.

Water diversion continues to be a critical aspect of habitat management for the Yellowstone cutthroat trout; unfortunately, it is also one of the most contentious. Attempts have been made to establish fish and wildlife sustenance as a "beneficial use" of flowing water in western states (Varley and Gresswell 1988). In Montana, the Department of Fish, Wildlife, and Parks was recently granted the legal right to lease water rights from agricultural interests, but the use of this strategy has been limited.

Riparian habitats have received increasing management attention since the late 1970's (Platts and Rinne 1985). In recent years, many grazing strategies have been evaluated (Meyers 1989; Platts 1989), and successful techniques are being implemented on many public lands. Improved riparian management may be the most critical habitat issue facing fishery managers in areas where natural flow regimes are unaffected by water diversions.

Gresswell (1990) defined special regulations as number limits, size limits, and terminal gear specifications, used singly or collectively, to reduce angler harvest. Season length and fishing season opening date are important auxiliary mechanisms that can be used to protect vulnerable spawning aggregations. Currently, these regulations are being broadly applied within the present range of the Yellowstone cutthroat trout to maintain indigenous and introduced populations. A combination of size limits and daily creel and possession limits are being used in Yellowstone National Park. Catch-and-release regulations are the most common, but in some areas maximum- (only fish below a specified size may be kept) and minimum-size (only fish above a specified size may be kept) limits are used in conjunction with a 2-fish creel limit. In Idaho, harvest of Yellowstone cutthroat trout on the South Fork Snake River from Heise to Palisades Dam is limited to 2 fish; fish between 203 and 406 mm must be released (Elle and Gamblin 1993). Reduced angling seasons and harvest limits (2 to 3 fish) are being considered for Henrys Lake and the Blackfoot River (Thurow et al. 1988). Yellowstone cutthroat trout are protected either by catch-and-release or 2-fish slot limits in Montana, and in Wyoming, 2-fish (any size) and 2-fish slot limits have been implemented for most indigenous populations. In 1994 the catch-and-release regulation in Montana was extended to include all streams and rivers in the Yellowstone River basin upstream from Springdale, Montana, to the Yellowstone National Park boundary (YCTWG 1994).

Research Needs

The relation between life history variation and environmental characteristics merits investigation, as do age-specific habitat needs. Identifying large-scale habitat factors that influence distribution, dispersal, and recolonization of Yellowstone cutthroat trout is also crucial for evaluating the effects of current land-use activities and anticipated global climate change.

Knowledge of life history diversity (and whether it has a genetic basis) is critical to protecting the remaining populations of Yellowstone cutthroat trout. Varley and Gresswell (1988) suggested that the greatest threat to the subspecies was the continued loss in genetic variability represented by unique local populations. Considering efforts to preserve genetic diversity, Echelle (1991) cautioned that no single measure of diversity, e.g., mtDNA, meristics, or life history variation, should take precedence over other forms of information. Identifying differences among populations can provide important information concerning local adaptation and the relation between life history organization and specific aspects of habitat.

To understand the natural capacity of the Yellowstone cutthroat trout, it is important to evaluate life history strategies and organization in areas where the effects of human activities can be minimized. Most information concerning Yellowstone cutthroat trout has focused on maintaining angler harvest, thus there are relatively few data on undisturbed populations. Often, angler harvest has been neglected in research design despite its influence. Although there are abundant data from Yellowstone Lake describing Yellowstone cutthroat trout life history during the 1950's, this was a period when the influence of cultured fish and angler harvest was at a maximum. Also, research is needed to assess the indirect effects of angling, such as redd trampling and bank erosion.

Long-term monitoring is integral to understanding the variation in Yellowstone cutthroat trout populations and relations between habitat and climatic variation. Such monitoring is essential for determining the effects of angler harvest and long-term habitat changes.

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