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Life-History Organization of Yellowstone Cutthroat trout (*Oncorhynchus clarki bouvieri*) in Yellowstone Lake

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Life-history organization of the cutthroat trout (*Oncorhynchus clarki*) may be viewed at various levels, including species, subspecies, metapopulation, population, or individual. Each level varies in spatial scale and temporal persistence, and components at each level continually change with changes in environment. Cutthroat trout are widely distributed throughout the western United States, occurring in such diverse environments as coastal rivers of the Pacific Northwest and interior streams of the Great Basin. During its evolution the species has organized into 14 subspecies with many different life-history characteristics and habitat requirements. Within subspecies, organization is equally complex. For example, life-history traits, such as average size and age, migration strategy, and migration timing, vary among individual spawning populations of Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*) in tributary streams of Yellowstone Lake. Understanding the effects of human perturbations on life-history organization is critical for management of the cutthroat trout and other polytypic salmonid species. Loss of diversity at any hierarchical level jeopardizes the long-term ability of the species to adapt to changing environments, and it may also lead to increased fluctuations in abundance and yield and increase the risk of extinction.

On peut déterminer le cycle vital de la truite fardée (*Oncorhynchus clarki*) au niveau de l'espèce, de la sous-espèce, de la métapopulation, de la population ou de l'individu. Chaque niveau varie à l'échelle spatiale et temporelle, et les composantes de chaque niveau évoluent continuellement en fonction de l'environnement. La truite fardée est répandue dans l'ouest des États-Unis, habitant des milieux aussi différents que les cours d'eau côtiers du Pacifique nord-ouest que les cours d'eau intérieurs du Grand Bassin. Au cours de son évolution, l'espèce s'est divisée en 14 sous-espèces dont les caractéristiques du cycle vital et les besoins en matière d'habitat varient. Au sein des sous-espèces, l'organisation est tout aussi complexe. Par exemple, les caractéristiques du cycle vital, comme la longueur et l'âge moyens, la stratégie migratoire et le moment de la migration, varient entre les populations de géniteurs de la truite fardée de Yellowstone (*Oncorhynchus clarki bouvieri*) peuplant les cours d'eau tributaires du lac Yellowstone. La gestion de la truite fardée et d'autres espèces de salmonidés formées d'un groupe de sous-espèces dépend de la compréhension des conséquences des perturbations anthropogènes de l'organisation du cycle vital. L'appauvrissement de la biodiversité à n'importe quel niveau hiérarchique compromet la capacité à long terme de l'espèce de s'adapter à un environnement changeant, et il peut aussi mener à des fluctuations accrues de l'abondance et du rendement, en plus d'accroître le risque d'extinction.

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For several decades scientists and conservationists have focused on the preservation of biodiversity in an attempt to curb increasing rates of environmental degradation and biological extinction (e.g., Noss 1990; Erwin 1991; Soulé 1991). In many cases, however, biodiversity has been defined exclusively in terms of species richness (Erwin 1991), while ecological function and the value of intraspecific diversity have often been ignored (Sinclair 1988; Varley and Gresswell 1988; O'Brien and Mayr 1991). Failure to recognize intraspecific variability is especially acute in the case of polytypic species that occupy diverse habitats (Brown et al. 1992; Rieman and McIntyre 1993).

Because fishes exhibit greater intraspecific phenotypic variation than other taxa (Allendorf et al. 1987), recognition

of this inherent variability is extremely important for maintaining biodiversity at the species level. Understanding variation at hierarchical levels below species is the focus of current research concerning the decline of anadromous salmonids. Healey (1986) reported that although individual species of Pacific salmon (*Oncorhynchus* spp.) can be characterized by certain life-history traits (e.g., age and size at maturity, fecundity, and mortality), there is extensive variation among and within populations of these species. Some researchers have suggested that life-history variation represents adaptation to spatial and temporal variation in environment (e.g., Schaffer and Elson 1975; Carl and Healey 1984; Beacham and Murray 1987), and correlations between genetic heritability and life-history traits have been observed

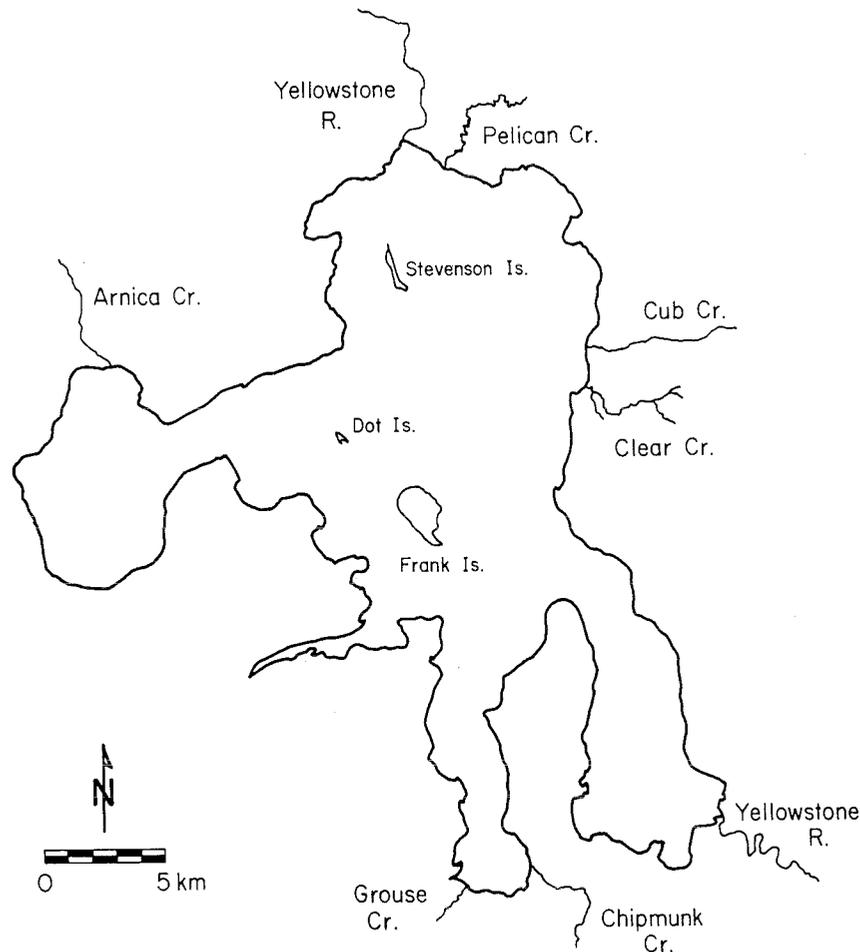


FIG. 1. Yellowstone Lake, Wyoming, and major tributaries.

(Carl and Healey 1984; Gharrett and Smoker 1993; Hankin et al. 1993).

A plethora of information is available about life-history variation among and within populations of anadromous salmonids (e.g., Murphy 1968; Beacham 1984; Taylor 1990), but less has been published about indigenous populations of nonanadromous forms. Jonsson and Sandlund (1979) discussed the relationship between environmental factors and life histories for isolated fluvial populations of brown trout (*Salmo trutta*) in Norway. In a large lake in Greenland, Riget et al. (1986) were able to differentiate three ecological forms of Arctic char (*Salvelinus alpinus*) using life-history characteristics. In the western United States, Cope (1957) reported life-history differences among populations of Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*) in Yellowstone Lake, and genetic divergence among isolated populations of Yellowstone cutthroat trout was investigated by Bulkley (1963).

We believe that the Yellowstone cutthroat trout in Yellowstone Lake provide an example of the importance of interpopulation life-history diversity to persistence. The objective of this paper is to synthesize information concerning spatial and temporal life-history variation of the Yellowstone cutthroat trout in Yellowstone Lake. We describe the organization of individual spawning populations in the lake basin and discuss the management implications of life-history variation among populations.

Yellowstone Lake

Yellowstone Lake is located at an elevation of 2357 m (Fig. 1). Surface area is 34 108 ha, and the shoreline length is 239 km (Kaplinski 1991). Kaplinski (1991) estimated a mean depth of 48.5 m and a maximum depth of 107 m. Vegetation in the drainage basin (261 590 ha; Benson 1961) is predominantly lodgepole pine *Pinus contorta* and sub-alpine meadows. A total of 124 tributaries to the lake have been identified; Yellowstone cutthroat trout have been observed spawning in 68 of these streams (Jones et al. 1987).

Growing season in the lake is short; from 1951 through 1986, an average of 205 ice-free days occurred annually (R. Gresswell, unpublished data). Diatoms dominate the phytoplankton community, but during periods of thermal stratification, blooms of *Anabaena flos-aquae*, a blue-green alga, are common (Benson 1961; Garret and Knight 1973). Zooplankton (*Diaptomus shoshone*, *Daphnia schøedleri*, and *Conochilus unicornis*) are the primary food of immature Yellowstone cutthroat trout (Benson 1961). Mature cutthroat trout feed on zooplankton, two amphipods (*Gammarus lacustris* and *Hyallela azteca*), and aquatic insect larvae found in the littoral zone (Benson 1961; Jones et al. 1990).

Yellowstone cutthroat trout and longnose dace (*Rhinichthys cataractae*) are native to Yellowstone Lake (Simon 1962). Three non-native fishes, reidside shiner (*Richardsonius balteatus*), lake chub (*Couesius plumbeus*), and longnose sucker

(*Catostomus catostomus*), have become established in the lake since the 1920s. An extensive fishery data base exists for cutthroat trout in Yellowstone Lake as a result of over four decades of field investigations. These data were collected primarily for monitoring the effects of angler harvest, but they also provide important information about distribution of life-history characteristics of Yellowstone cutthroat trout among spawning tributaries to the lake and changes that have occurred through time.

Pollution and land-use practices that degrade salmonid habitat in other parts of the United States have been limited in the Yellowstone Lake basin by U.S. National Park Service policies. Despite substantial habitat protection, however, Yellowstone cutthroat trout in Yellowstone Lake historically were subjected to the effects of non-native fish introductions, spawn-taking operations, commercial fishing, and intensive sport-fishery harvest (Gresswell and Varley 1988). As a result of some or all of these factors, abundance and average size and age of cutthroat trout in the Yellowstone Lake fishery declined after World War II to a low in the late 1960s. After angler harvest was reduced in the 1970s, numbers and average size increased; however, attendant effects of anthropogenic activities on life-history characteristics of cutthroat trout have not been assessed.

Life-history Organization of Cutthroat Trout: A Perspective

Life-history organization of cutthroat trout may be examined at various hierarchical levels, including species, subspecies, metapopulation, population, or individual (Fig. 2). A metapopulation is a group of local populations that are linked by movements of individuals among the populations (Hanski and Gilpin 1991). Each hierarchical level varies in spatial scale and in temporal persistence, and components of each level continually develop and evolve with changes in the level-specific environment (Warren and Liss 1980). Environment at each level is perceived as a spatial array that changes through time. Individual life-history characteristics may interpenetrate the hierarchy so that groups of local populations and metapopulations may share similar life histories.

Systematists disagree about the evolutionary history of cutthroat trout (Behnke 1992; Stearley 1992; Stearley and Smith 1993), but fossil evidence suggests that species of Pacific trout (including cutthroat trout) originated in the Miocene (Stearley and Smith 1993). Since then, cutthroat trout have diverged into 14 subspecies (Behnke 1988). Historical distribution of cutthroat trout subspecies included temperate rain forests of the Pacific Northwest, pluvial basins within the Great Basin, subalpine areas of the Rocky Mountains, and high-deserts of the Southwest. Habitats ranged from beaver ponds to large lakes (e.g., Pyramid Lake, Nevada), and from first-order tributaries to the Columbia River. Variation in life-history characteristics such as anadromy, iteroparity, and age at maturity reflect the diverse environments and selective factors affecting the evolution of the species (Gresswell 1988). Some cutthroat trout forms can be differentiated by susceptibility to angling (Dwyer 1990).

With the possible exception of the coastal cutthroat trout (*Oncorhynchus clarki clarki*), the Yellowstone cutthroat trout is more abundant and inhabits a greater geographical range than any other subspecies of cutthroat trout (Varley and Gresswell 1988). Yellowstone cutthroat trout were

indigenous to the Yellowstone River drainage in Montana and Wyoming and portions of the Snake River drainage in Wyoming, Idaho, Nevada, Utah, and possibly Washington (Behnke 1988). Numerous metapopulations of Yellowstone cutthroat trout evolved unique life-history characteristics in response to environmental changes and isolation that ensued following late Pleistocene glaciation. The Yellowstone Lake metapopulation (Fig. 2b) supported an extensive hatchery operation from 1899–1957 that led to the worldwide distribution of the subspecies. The metapopulation in Heart Lake co-evolved with seven other fish species (Smith and Kendall 1921; Varley and Schullery 1983), and piscivory is common in cutthroat trout in the lake. McBride Lake is small head-water lake; individuals in this metapopulation feed primarily on zooplankton, scuds, and aquatic insects. Yellowstone cutthroat trout from McBride Lake have been used to establish feral populations in small lakes and reservoirs in Montana (McMullin and Dotson 1988). The Yellowstone River below the Lower Falls supports a fluvial metapopulation of Yellowstone cutthroat trout that has persisted despite the introduction and establishment of non-native salmonids (Clancy 1988).

Anthropogenic activities, including habitat degradation, angler harvest, and non-native species introductions, have contracted the historical range of Yellowstone cutthroat trout. Lacustrine forms remain in approximately 85% of the historical range, but only about 10% of the original fluvial habitat is still occupied by genetically unaltered populations (Varley and Gresswell 1988). Range restriction resulted in the loss of life-history variation, especially of forms that were common to large rivers at lower elevation, such as the Yellowstone River near Miles City, Montana, and the Snake River above Shoshone Falls (Varley and Gresswell 1988).

Even in a single body of water, such as Yellowstone Lake, individual spawning populations of Yellowstone cutthroat trout differ in life-history characteristics associated with spatial and temporal environmental patterns (Gresswell and Varley 1988; Fig. 2c). On an areal basis, Yellowstone Lake represents almost 80% of the remaining historic lacustrine habitat of the Yellowstone cutthroat trout. Tributaries to the lake range from the upper Yellowstone River, a sixth-order river with an 110 000-ha drainage, to unnamed first-order streams with watersheds of less than 10 ha.

Spatial Variation of Cutthroat Trout Life Histories in Yellowstone Lake

Reproductive Isolation and Homing

Sinclair (1988) suggested that any behavior enhancing the retention of population members near the source of reproduction must ultimately be adaptive because it increases the probability of successful sexual reproduction. Although complete reproductive isolation among populations of Yellowstone cutthroat trout from spawning tributaries probably does not occur in the Yellowstone Lake drainage, there is substantial evidence of homing by adult spawners. We believe that the relative fidelity of individual spawning populations to specific tributaries supports the view that the assemblage of Yellowstone cutthroat trout in Yellowstone Lake should be considered a metapopulation. Local adaptation to specific environmental conditions in individual tributaries is evident, and concomitantly, there is evidence of movement (straying) among populations. Although occupation

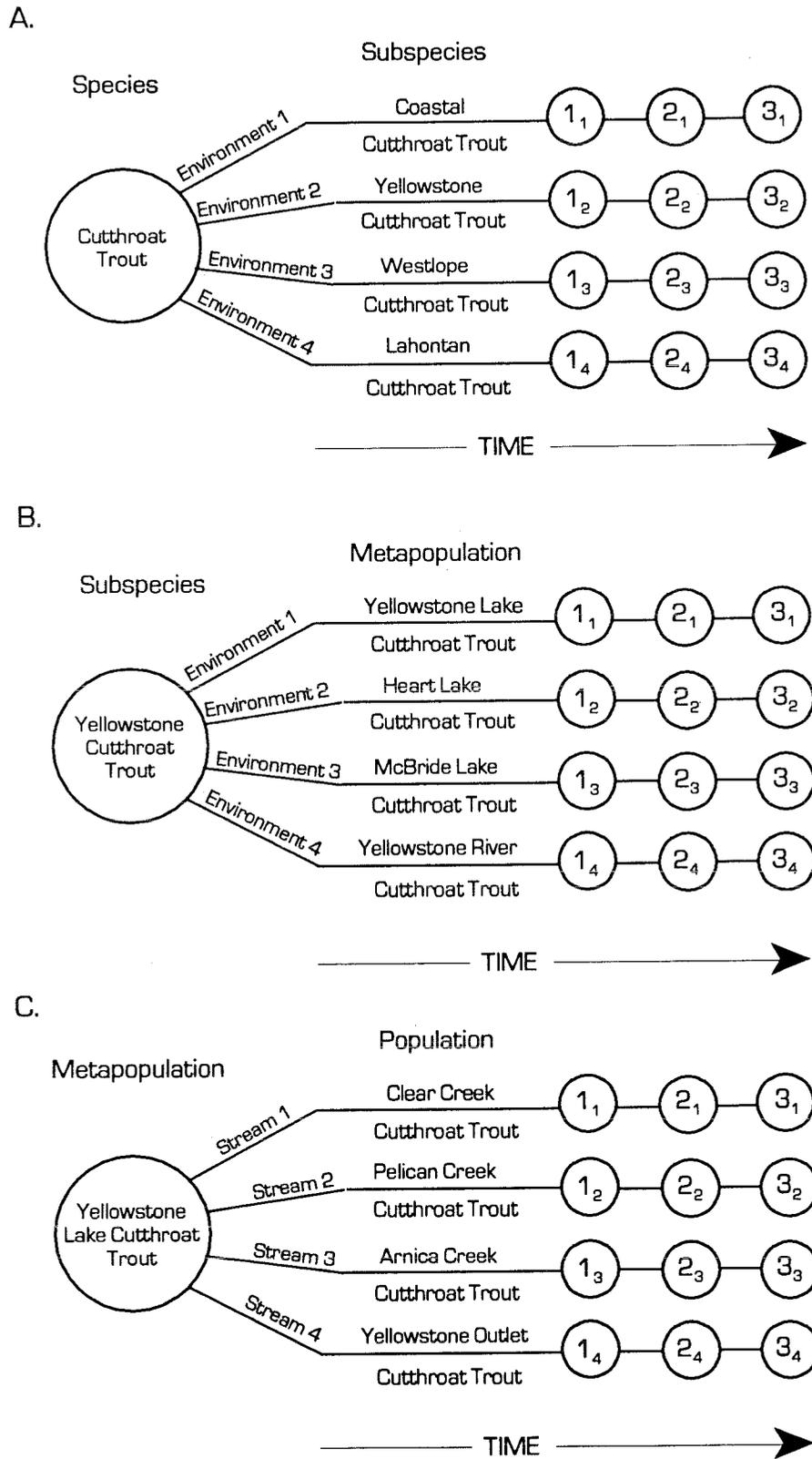


FIG. 2. A hierarchical view of life-history organization of the (a) cutthroat trout (*Oncorhynchus clarki*) species, (b) Yellowstone cutthroat trout (*Oncorhynchus clarki bowieri*) subspecies, and (c) Yellowstone Lake metapopulation of Yellowstone cutthroat trout. At each level in the hierarchy, subgroups adapt through time to changes in level-specific environment (adapted from Wevers 1994).

of diverse habitat patches in a spatially heterogeneous environment provides the basis for persistence individual populations, interpopulation movement is critical to the colonization of vacant habitat patches (temporal environmental

heterogeneity) and, ultimately, metapopulation persistence (Hanski 1991).

Ball (1955) documented natal homing (the return of adult spawners to the area of their birth) for Yellowstone cutthroat

trout in Yellowstone Lake. Three groups of immature Yellowstone cutthroat trout were fin clipped in 1950 and 1951 as they emigrated from Arnica Creek (Fig. 1) to Yellowstone Lake. Group estimates indicated that between 16 and 25% of the clipped fish survived to return to Arnica Creek as spawners, and none of the fish marked in Arnica Creek were recovered in five other lake tributaries being monitored between 1950 and 1954.

Repeat homing behavior (individual spawners returning to the same tributary in successive years; McCleave 1967) has been observed for spawners from Yellowstone Lake. Between 1949 and 1955, 18 836 Yellowstone cutthroat trout spawners were tagged in Arnica, Chipmunk, Clear, Grouse, and Pelican creeks (Cope 1957). Approximately 97% of 244 adults returning as repeat spawners were collected in the same stream in which they were originally marked. In a more recent study, at least 23% of 42 229 spawners marked at Clear Creek in 1979 returned to spawn again between 1980 and 1984; however, an average of about 1% of the marked fish were collected annually in Pelican Creek and Cub Creek (Jones et al. 1985).

Between 1949 and 1953, the proportion of repeat spawners that returned in consecutive years or alternate years varied among streams (Ball and Cope 1961). Based on the return of fish from individual tag groups, consecutive-year spawners were most abundant in Arnica Creek and Chipmunk Creek. The proportion of consecutive- and alternative-year spawners in Pelican Creek and Grouse Creek varied among years and tag groups. At Clear Creek, however, spawners marked in 1979 returned most frequently in alternate years (1980–84; Jones et al. 1985).

Meristic and morphological differences in populations of Yellowstone cutthroat trout historically derived from Yellowstone Lake reflect effects of reproductive isolation. Bulkley (1963) examined variation in spotting patterns, basibranchial teeth counts, and coloration as criteria for distinguishing populations. Samples from Yellowstone Lake tributaries (Arnica, Cub, Clear, Chipmunk, Grouse, and Pelican creeks) were compared with those collected from populations that had been separated from Yellowstone Lake for 13 yr (Creston National Fish Hatchery, Montana), 21 yr (Bear Creek), and approximately 8000 yr (Sedge Creek). Yellowstone cutthroat trout in Bear and Sedge creeks were isolated from Yellowstone Lake (and each other) by chemical and thermal barriers when the level of the lake dropped in the early Holocene (Kaplinski 1991); however, Bear Creek was stocked with 252 000 Yellowstone cutthroat trout from the Yellowstone Lake hatchery between 1921 and 1941 (Varley 1981). Based on basibranchial teeth and spotting counts, Sedge Creek and Bear Creek fish differed from one another and from the combined Yellowstone Lake sample and the hatchery sample, and there was evidence of divergence of the Creston hatchery sample from the Yellowstone Lake group. Because differences among populations in spotting pattern and basibranchial teeth number varied directly with time since isolation from Yellowstone Lake, Bulkley (1963) concluded that some degree of genetic change was involved.

In a study of serum-antigen variations among Yellowstone cutthroat trout from seven tributaries and the outlet of Yellowstone Lake, Liebelt (1969) identified at least five separate populations. Fish spawning in Clear, Columbine, and Cub creeks and the outlet were grouped together, but trout from Chipmunk, Grouse, and Pelican creeks and the

Yellowstone River inlet all formed unique populations. The isolation of Pelican Creek was attributed to differences in timing of the annual spawning migration, and geographical distance was suggested as a significant factor in the establishment of the other three isolated populations (Liebelt 1969).

Pattern of Spawning Migration

Yellowstone cutthroat trout spawn exclusively in fluvial environments (Varley and Gresswell 1988). Varley and Gresswell (1988) described four migratory spawning patterns for Yellowstone cutthroat trout: fluvial (fluvial residents dispersing locally within the area of the home range); fluvial–adfluvial (fluvial residents moving into tributaries to spawn); lacustrine–adfluvial (lacustrine residents moving into lake tributaries to spawn); and allacustrine (lacustrine residents moving into the outlet stream. The occurrence of all four patterns in the Yellowstone Lake drainage suggests local adaptation to diverse habitats.

The lacustrine–adfluvial migration pattern is most common in the lake drainage, but fluvial and allacustrine patterns have also been observed. For example, fluvial cutthroat trout from the Yellowstone River downstream from the Yellowstone Lake and allacustrine individuals from the lake spawn in the area of the Yellowstone River immediately below the Yellowstone Lake outlet. Tagging studies conducted from 1951 to 1953 suggested little interchange between these populations (Ball and Cope 1961), and recent tagging and marking studies support this conclusion (Kelly 1993). Mechanisms that maintain the putative separation of these two spawning populations have not been extensively investigated, but Ball and Cope (1961) reported temporal separation of the two groups in the spawning area. Fluvial spawning has also been observed in the upper reaches of Pelican and Clear creeks; fish in these areas are assumed to be fluvial residents that remain in these areas throughout their lives.

Yellowstone cutthroat trout spawn between April and August in tributaries of Yellowstone Lake (Ball 1955; Cope 1956, 1957; Jones et al. 1986). Although most individuals in a spawning population are initial spawners, iteroparity is common (Gresswell and Varley 1988). Larger adults generally enter the streams earlier and ascend farther up tributaries than smaller individuals (Cope 1957; Ball and Cope 1961). Ball and Cope (1961) reported that most spawners remain in the tributaries from 1 to 3 wk, and males stay longer than females. This pattern does vary, however, and in 1980, marking studies in Pelican Creek, the second-largest tributary of Yellowstone Lake, suggested that some spawners overwintered in the stream before returning to the lake.

Juvenile Emigration and Residence

Eggs hatch 25–49 d after deposition (278–365 Celsius temperature units, sum of mean daily temperatures above 0°C; Kelly 1993), and young fish emerge from the gravel approximately 2 wk later (Ball and Cope 1961; Mills 1966; Kelly 1993). Most emigrate to the lake within 2 mo of emergence, but some may remain in the natal stream for several years (Welsh 1952; Benson 1960). Immature Yellowstone cutthroat trout that overwinter in Clear, Cub, and Arnica creeks generally emigrate at age 1 or age 2 (Welsh 1952; Benson 1960; U.S. Fish and Wildlife Service, Yellowstone National Park, WY 82190, unpublished data). In Pelican Creek, however, the pattern is more complex. In 1980, all spawners

TABLE 1. Life-history traits of Yellowstone cutthroat trout spawners in six tributaries to Yellowstone Lake, 1950–61.

Stream	Mean spawner abundance ^b	Timing of spawning migration ^a		Mean male:female ratio ^c	Mean age (years) ^d	Mean length (mm) ^e
		Mean initiation (Julian date)	Mean duration (days)			
Pelican Creek	13 282	144	38	0.70:1	4.3	365
Cub Creek	3 793			0.77:1		
Clear Creek	8 938			0.70:1	4.4	378
Chipmunk Creek	8 378	147	56	0.72:1	4.7	391
Grouse Creek	7 362	153	53	0.70:1	4.6	385
Arnica Creek	3 818	131	80	0.65:1	4.3	363

^a1951–53 (Ball and Cope 1961).

^b1950–54, 1959, 1961 (Benson and Bulkley 1963).

^c1950, 1952–53 (Ball and Cope 1961).

^d1953–55 (Benson and Bulkley 1963).

^e1953–55, 1958–59 (Bulkley 1961).

migrating upstream (22 293) were marked with fin clips, but 51% of 32 777 downstream migrants (excluding young-of-the-year) were unclipped. Although there are several possible explanations for the large proportion of unclipped fish, multiyear residency is suggested for at least some of these fish because approximately 49% of 2 503 unclipped fish, ranging in total length from 110 to 480 mm, had not spawned.

Raleigh and Chapman (1971) investigated stream temperature, water source, and “innate factors” in relation to migration of fry (young-of-the-year) from incubation areas into Yellowstone Lake. They concluded that movements of fry upstream from the lake outlet (assumed progeny of allacustrine spawners) and downstream from lake tributaries (assumed progeny of lacustrine–adfluvial spawners) were innately controlled responses to environmental stimuli. In a similar study, Bowler (1975) concluded that genetic factors controlled movement of inlet and outlet spawners, but rheotactic acclimation could significantly alter the response of inlet fry. Fry from the outlet area displayed an altered response (downstream movement) when tested in a water source different from the one used for incubation and acclimatization. Although fluvial spawners from the Yellowstone River and allacustrine spawners from Yellowstone Lake both spawn in the outlet area, all fish collected in these studies were presumed to be from allacustrine sources (Raleigh and Chapman 1971; Bowler 1975).

Initiation and Duration of Spawning

Distinct temporal patterns for the spawning migrations in Arnica, Chipmunk, Clear, Grouse, and Pelican creeks during the 1940s and 1950s were identified by Cope (1957). Ball and Cope (1961) reported mean date of spawning initiation and duration of the spawning migration in four of these streams from 1951 through 1953 (Table 1). Statistical analysis (ANOVA, Newman–Keuls multiple-means comparison) of these data reveals significant differences ($p \leq 0.05$) in the mean date of spawning initiation between Arnica Creek (May 10) and Grouse Creek (June 1). Furthermore, mean duration of the spawning migration in Arnica Creek (80 d) differed significantly ($p \leq 0.05$) from Pelican, Chipmunk, and Grouse creeks (38, 53, and 56 d, respectively).

Abundance, Size, and Age of Spawners

Abundance, mean length, and mean age estimates for cutthroat trout spawning in six tributaries of Yellowstone Lake were collected sporadically between 1950 and 1961 (Table 1). The mean number of fish (13 282) ascending Pelican Creek for seven sample years (1950–54, 1959, 1961) was significantly greater (ANOVA, Newman–Keuls multiple-means comparison; $p \leq 0.05$) than all other streams in the subset. Cub and Arnica creeks had the lowest mean estimates (3793 and 3818 fish, respectively).

Differences in mean length of Yellowstone cutthroat spawners sampled in five tributaries were statistically significant (ANOVA, Newman–Keuls multiple mean comparison; $p \leq 0.05$). Spawners from Chipmunk Creek (391 mm) and Grouse Creek (385 mm) were largest, and those sampled in Arnica and Pelican creeks (363 and 365 mm, respectively) were the smallest. Mean age of spawners for the period between 1953 and 1955 varied from 4.3 yr in Arnica Creek to 4.7 yr at Chipmunk Creek (Table 1); however, differences among streams were not statistically significant (ANOVA, $p = 0.15$).

Male:Female Ratio and Fecundity

The observed male:female ratio for Yellowstone cutthroat trout in a combined sample from 1950, 1952, and 1953 varied from 0.65:1 (Arnica Creek) to 0.77:1 (Cub Creek); observed ratios were identical (0.70:1) for cutthroat trout from Clear, Grouse, and Pelican creeks during this period (Table 1). Differences among streams were not statistically significant (ANOVA, $p = 0.95$).

Cope (1957) used estimates of relative fecundity (number of eggs per unit weight; Bagenal 1978) to compare the size of cutthroat trout eggs among streams. Samples were collected at the Yellowstone Hatchery from 1941 through 1952 (Cope 1957). Differences in slope for regressions of the number of eggs (dependent variable) and ovary weight (independent variable) were statistically significant for Chipmunk, Grouse, and Pelican creeks. Based on these results, Cope (1957) suggested that the relationship between egg size and ovary weight was specific to Yellowstone cutthroat trout from each of the three streams.

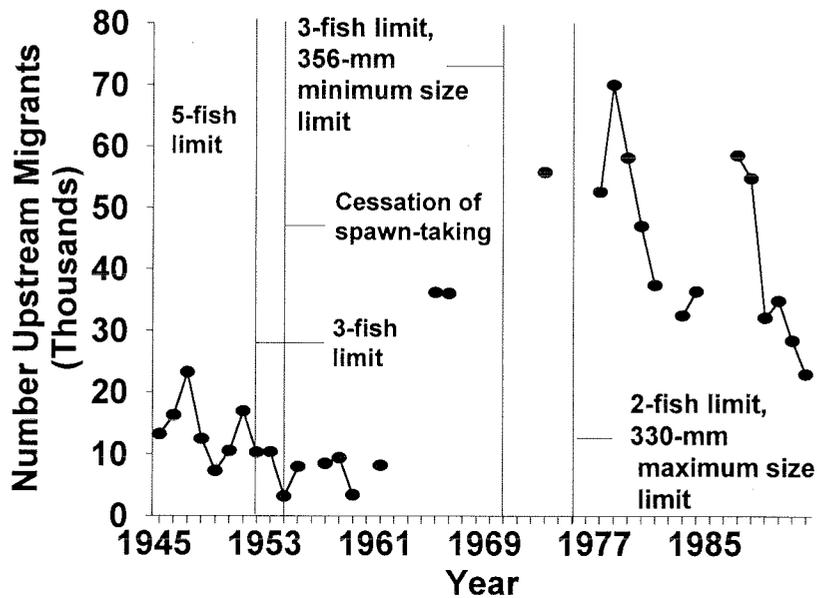


FIG. 3. Counts of Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*) spawners at Clear Creek, Yellowstone Lake, under various management scenarios, 1945–92.

Temporal Variation in Life Histories of Cutthroat Trout in Yellowstone Lake

Information describing the spawning population of Yellowstone cutthroat trout in Clear Creek from 1945 to 1992 provides an example of temporal variation in life histories associated with two major anthropogenic activities in the Yellowstone Lake drainage, the hatchery operation and the sport fishery. From 1899 to 1957 over 818 million eggs were collected from Yellowstone cutthroat trout spawners entering tributaries to Yellowstone Lake (Varley 1979). Clear Creek was one of the larger tributaries that were blocked annually for spawn-taking purposes. Mature Yellowstone cutthroat trout congregate in the littoral zone in association with spawning migration and for feeding. Because the majority of angler use is concentrated in the littoral zone, this life-history trait may increase the vulnerability of mature fish to angling (Gresswell and Varley 1988). Immature individuals (through age 2) are not common in the angler catch.

At Clear Creek the number of spawning cutthroat trout declined from a mean of approximately 16 000 between 1945 and 1948 to 3353 spawners in 1954 (Benson and Bulkley 1963). Abundance in Clear Creek increased following implementation of a three-fish (any size) creel limit and the closure of the hatchery and subsequent cessation of spawn taking (Fig. 3). Counts between 1957 and 1961 averaged 7300 spawners annually (Gresswell and Varley 1988), but by the mid-1960s, the number of spawners averaged approximately 36 000 fish annually. After the cessation of spawn-taking activities, the number of Yellowstone cutthroat trout rose despite an increase in the mean number of fish harvested from Yellowstone Lake from 224 000 (1950–53) to 318 000 annually (1954–65).

Following a series of regulations that reduced angler harvest, the number of spawning Yellowstone cutthroat trout continued to increase. A 356-mm minimum-size limit was implemented in 1970. The daily creel limit was three fish until 1973 when it was reduced to two fish. In 1975, a two-fish,

330-mm maximum-size limit was imposed. After the adoption of this regulation, annual harvest dropped to a mean of approximately 71 000 Yellowstone cutthroat trout for the period between 1983 and 1992. Since 1977, annual counts of spawning cutthroat trout at Clear Creek have remained above levels observed in the 1950s (Fig. 3); however, recent declines (1990–92) suggest the influence of factors other than angler harvest on annual variation in spawner abundance.

Mean length of spawning Yellowstone cutthroat trout in Clear Creek averaged approximately 369 mm for the period from 1953 to 1955 (Fig. 4). Annual estimates of mean length increased to an average of 389 mm for the 1957–61 period. As harvest expanded from the late 1950s through the early 1960s, however, mean length of spawners in Clear Creek declined to an average of 365 mm for 1966 and 1967. Since the two-fish, 330-mm maximum-size regulation was instituted in 1975, annual estimates of mean length have risen above previous high measurements and currently average approximately 399 mm (1988–92).

Mean age of Yellowstone cutthroat trout spawning in Clear Creek dropped to a low of 3.9 yr in the mid-1960s concomitant with increasing harvest (Fig. 5). In 1973, only about 6% of the fish sampled were age 6 and over. Since then, mean age has risen substantially, and between 1987 and 1992, mean age for spawners in Clear Creek averaged 5.8 yr. Age-9 Yellowstone cutthroat trout were collected at Clear Creek annually during this period. There is no simple explanation for the observed changes. Increased longevity resulting from decreased angler harvest may have led to an increase in the number of times an individual fish spawned, but delayed maturity could have produced similar results.

Changes in mean length and age have affected the population fecundity of spawners at Clear Creek. Although relative fecundity appears to be unchanged, the current reproductive potential averages almost 32 million eggs annually (Jones et al. 1985). This represents a 500% increase over estimates from the 1950s (6.2 million eggs).

Iteroparity has apparently increased in Clear Creek since the 1950s. Ball and Cope (1961) reported that only 1.22% of

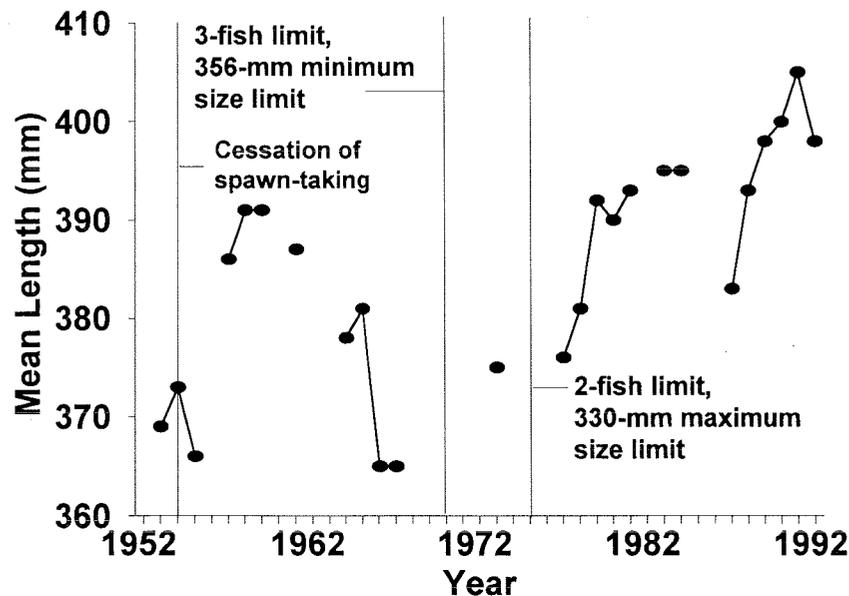


FIG. 4. Mean lengths of Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*) spawners entering Clear Creek, Yellowstone Lake, under various management scenarios, 1953–92.

spawning Yellowstone cutthroat trout in Yellowstone Lake were repeat spawners. A mean instream-mortality estimate (five streams over a 5-yr period, 1950–54) of 48.1% indicated that many spawners died after spawning. Returns of marked fish at Clear Creek during the 1980s suggest that a minimum of 23% of fish that spawned in 1979 returned to spawn at least once (Jones et al. 1985), and repeat spawners were collected up to 5 yr after they were originally marked. During five sample years from 1977 through 1984, mean instream-mortality estimated from total upstream and downstream counts in Clear Creek was 12.9%. In recent years, estimates of instream mortality at Clear Creek have increased (mean = 30.8% for 1987, 1988, 1991, and 1992; U.S. Fish and Wildlife Service, Yellowstone National Park, WY 82190, unpublished data); however, the relative influence of changes in monitoring procedures and presence of increased numbers of white pelicans (*Pelecanus erythrorhynchos*) has not been investigated.

Discussion

Except where barriers limited access, rainbow trout (*Oncorhynchus mykiss*) replaced Yellowstone cutthroat trout in the Columbia River Basin below Shoshone Falls on the Snake River (Behnke 1992) sometime after the falls were formed. Citing Malde (1965), Behnke (1992) suggested that the formation of Shoshone Falls occurred 30 000 – 60 000 yr ago during the Bonneville Flood; however, recent information suggests that this event dates to approximately 14 500 yr ago (Oviatt et al. 1992). At the same time, the Yellowstone subspecies was forced out of high-elevation environments by Pleistocene glaciation. The most recent incursion of Yellowstone cutthroat trout to the Yellowstone River drainage is related to the retreat of glacial ice that occurred about 12 000 yr ago (Richmond and Pierce 1972).

This set of events suggests that the Yellowstone cutthroat trout were reduced to low abundance and greatly restricted range during the late Pleistocene and that current genetic structure of the subspecies was significantly affected by this

geographical range constriction. Allozyme data support the occurrence of a geologically recent genetic bottleneck in the Yellowstone subspecies. In a survey of 10 Yellowstone cutthroat trout populations over a broad geographical range, Loudenslager and Gall (1980) reported that only 8% of the genetic diversity was due to divergence among populations. In a broader context, Allendorf and Leary (1988) compared divergence within eight nonanadromous salmonids, and the Yellowstone cutthroat trout was the only form with low genetic divergence among local populations.

There are inconsistencies in the taxonomy of cutthroat trout, however. Although the Yellowstone and west-slope (*Oncorhynchus clarki lewisi*) subspecies have been isolated from each other for 1–2 million yr (Allendorf and Leary 1988; Behnke 1988) and allozyme data suggest that west-slope cutthroat trout may be a distinct species (Allendorf and Leary 1988), morphologically the two subspecies remain undifferentiated (Allendorf and Leary 1988). Alternatively, life-history traits of spawning populations of Yellowstone cutthroat trout within the Yellowstone Lake drainage suggest phenotypic variation that may imply local adaptation, but allozyme divergence is low compared with that observed among populations of westslope cutthroat trout (D.K. Shiozawa and R.N. Williams, Department of Zoology, Brigham Young University, Provo, UT, unpublished data).

One exception to this generality was detected in genetic divergence of Yellowstone cutthroat trout from Sedge Creek (R.N. Williams, R.F. Leary, and D.K. Shiozawa, Clear Creek Genetics, Meridian, ID, unpublished data). This population has been reproductively isolated for thousands of years, and heterozygosity and allelic diversity were substantially lower within the Sedge Creek population than in other populations of Yellowstone cutthroat trout. Samples of cutthroat trout from Sedge Creek and Yellowstone Lake revealed substantial allozyme divergence (Nei's $D = 0.046$) compared with levels commonly observed among other Yellowstone cutthroat trout populations (Nei's $D = 0.003$); however, no evidence of divergence of mitochondrial DNA between Sedge Creek and Yellowstone Lake populations was apparent.

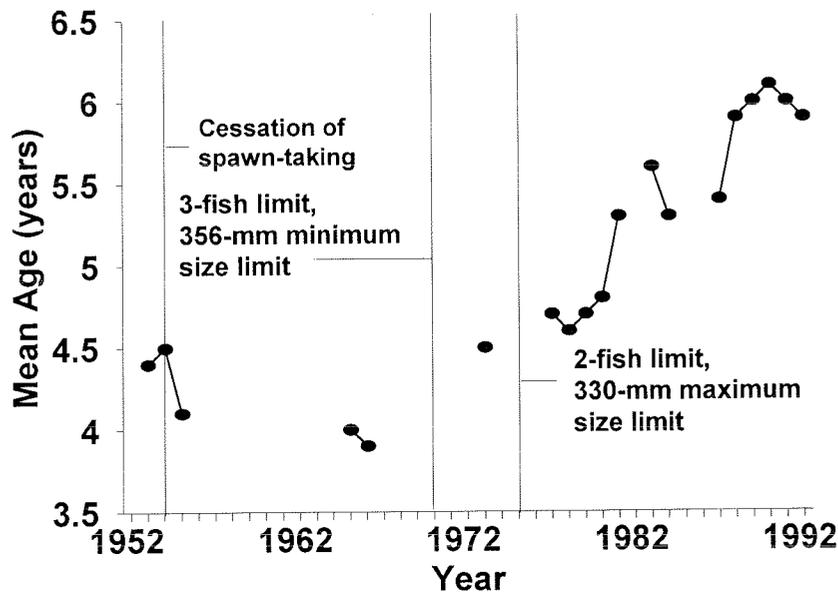


FIG. 5. Mean age of Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*) spawners entering Clear Creek, Yellowstone Lake, under various management scenarios, 1953–92.

These examples underscore difficulties that arise in the management and conservation of polytypic taxa such as the cutthroat trout. Lack of genetic divergence (based on solely on molecular analysis) could suggest that local adaptations are simply phenotypic responses to environmental variability and not the basis for conservation of local populations. Allendorf and Leary (1988) concluded, however, that lack of divergence at allozyme loci is not indicative of the absence of important interpopulation genetic differences. Considering efforts to preserve genetic diversity, Echelle (1991) cautioned that no single measure of variation should be considered exclusively. Identifying life-history differences between populations can provide important information concerning local adaptation and the relationship among life-history organization and specific aspects of the environment. Documentation of life-history differentiation is necessary to provide management support for the protection of unique life-history types in the absence of documented allozyme divergence.

The presence and extent of the life-history diversity in Yellowstone Lake may be important, regardless of the mechanisms that control it. Numerous studies suggest that life-history variation has adaptive significance in other polytypic fish species (e.g., Healey 1986; Taylor 1991; Hankin et al. 1993; Quinn and Unwin 1993), and phenotypic plasticity can be a key component of evolutionary change (Thompson 1991). Although genetic differentiation is apparently low among Yellowstone cutthroat trout, the documented life-history variation suggests a strong adaptability to disparate environments. Den Boer (1968) submitted that diversity is directly related to the probability of long-term population persistence; in a spatially and temporally heterogeneous environment, spreading risk through maintenance of natural diversity is critical. Diversity provides a means of buffering environmental change at all levels of differentiation (i.e., within a species, subspecies, metapopulation, and population), and therefore, management activities that impinge on the natural variation in a polytypic taxon may eventually reduce the capacity for survival of the taxon as a whole.

From an evolutionary standpoint, local adaptation provides an important means to exploit a wide variety of habitats. A metapopulation comprises numerous locally adapted populations. At any point in time, some populations may be declining in abundance while others are becoming established or increasing (Hanski and Gilpin 1991). These opposing processes of extinction and colonization determine the trajectory of metapopulation persistence. For a metapopulation to persist, the rate of population extinctions must not exceed the rate of colonization. From this perspective, local populations within a metapopulation have important functional value in metapopulation persistence regardless of their genetic or phenotypic uniqueness.

The relative integrity of the cutthroat trout metapopulation structure in Yellowstone Lake may have influenced recovery of the fishery when constraints imposed by angler harvest diminished. Management policies of the U.S. National Park Service contributed to the pristine condition of the Yellowstone Lake watershed and spawning and rearing habitats and, consequently, to the integrity of the cutthroat trout metapopulation. The uneven effects of angling also supported the structure of the metapopulation. Because angler effort and harvest were not spread evenly throughout the lake (Benson and Bulkley 1963), it is likely that some of the spawning populations were relatively unaffected by harvest. Additionally, some life-history types (e.g., those with early spawning migration or extended stream residence) within heavily impacted populations may have persisted.

A wide range of life-history diversity occurs among cutthroat trout populations spawning in tributaries of Yellowstone Lake. These differences are spatially distributed among the spawning populations, and temporal variation within the Clear Creek spawning populations coincided with changes in management strategies. Life-history variation in the Yellowstone Lake drainage is reflective of diversity that has been documented at the subspecies and species level (Gresswell 1988).

Of the life-history characteristics examined, abundance and mean length of spawners and timing (i.e., initiation, duration, and peak) of annual spawning migrations appear to

be the most variable in the Yellowstone Lake drainage. Male:female ratio was similar among streams, and although some annual variation has been noted, no temporal trends have been identified. Differences in mean age among spawners from various tributaries were not significant when data collected from six streams during the 1950s was compared; however, these data may have been affected by changes in population structure resulting from anthropogenic activities during that period. For example, mean age of spawners at Clear Creek increased almost 2 yr after cessation of spawn taking and reductions in harvest during the 1970s.

Life-history organization of spawning populations of cutthroat trout in Yellowstone Lake is complex, but evidence suggests a relationship with spatial and temporal aspects of the environment. Preliminary investigation of basin-level environmental variables and life-history parameters obtained from 27 tributaries between 1985 and 1987 suggests that elevation, aspect, and drainage area are correlated with the date of spawning migration initiation and mean length of cutthroat trout spawners in individual tributaries (R. Gresswell, unpublished data). Elevation, aspect, and drainage area are among physical characteristics of drainages that directly influence flow and peak discharge (Morisawa 1968), and the timing of spawning migrations appears to be directly related to hydrographic stage and water temperature (e.g., Ball and Cope 1961; Jones et al. 1990). Relationships between spawning migrations and hydrographic pattern thus suggest one possible link between habitat variation and life-history diversity in the Yellowstone Lake drainage.

Habitat complexity of Pelican Creek may explain migration patterns such as extended residence in the stream 3 or 4 yr after emergence or spawning adults that remain in the stream for months or years before emigration. Pelican Creek has a mainstem length of over 53 km and at least 125 first-order tributaries. Hydrothermal springs that are locally numerous in some of the tributaries to Pelican Creek may provide refuges for overwintering fish. Additionally, resident populations of fluvial Yellowstone cutthroat trout have been observed in Pelican Creek. Apparently, many of the life-history types occurring throughout the Yellowstone Lake drainage are present in Pelican Creek alone.

Temporal variation of life-history traits at Clear Creek is strongly associated with changes in fishery management. Because increases in the number of spawners at Clear Creek after the cessation of spawn-taking activities occurred while angler harvest was increasing, it is probable that spawn-taking operations contributed to previous reductions in spawner abundance. Alteration of the historical gene pool or reduction in the number of cutthroat trout allowed to proceed upstream to spawn naturally may have contributed to this decline. Similar effects from hatchery introductions have been documented for a wide range of salmonids in North America (Evans and Willox 1991; Krueger and May 1991), and the negative effects of hatchery supplementation is a principal consideration in the conservation of dwindling wild populations (Ryman and Laikre 1991; Waples 1991)

Declines in mean length and age of spawning Yellowstone cutthroat trout at Clear Creek during the 1960s may be associated with fish harvest by anglers in Yellowstone Lake. Alterations observed in the structure of the Clear Creek population are probably representative of the magnitude of change that has occurred in other lacustrine-adfluvial spawning populations in Yellowstone Lake, and data collected from

spawning cutthroat trout at Pelican and Cub creeks during the late 1970s and early 1980s suggest similar responses to reduction in harvest (Jones et al. 1979, 1983). Patterns from the Yellowstone Lake fishery are consistent with effects of harvest predicted by population theory (Nikolskii 1969) and with observations from commercial fisheries (Christie 1972; Larkin 1977; Ricker 1981). Resulting reductions of mature fish in a population can drastically reduce the reproductive capacity, especially within late-maturing and iteroparous life-history types (Ricker 1963). Less abundant forms are at increased risk of extirpation or extinction (Nelson and Soulé 1987).

There is little evidence that the introduction of non-native fishes has negatively affected Yellowstone cutthroat trout in Yellowstone Lake (Gresswell and Varley 1988). Some diet overlap has been identified, but spatial interaction is low among these fishes. It is fortuitous that non-native salmonids have not become established in the drainage because similarities in habitat requirements and life-history traits common to this family of fishes often result in intense interspecific competition (e.g., Marrin and Erman 1982; Griffith 1988). Additionally, hybridization with rainbow trout could potentially result in the extirpation of the indigenous Yellowstone cutthroat trout genome in Yellowstone Lake.

Attempts to accommodate continued increases in visitation to Yellowstone National Park may eventually threaten the integrity of the Yellowstone Lake ecosystem and ultimately, the cutthroat trout metapopulation in the lake. Development of visitor facilities at Lake Village, Bridge Bay, Fishing Bridge, and Grant Village has included a substantial road system. Road culverts have reduced access to adfluvial spawners in some tributaries, and at least two culverts totally block annual spawning migrations (Dean and Varley 1974; Jones et al. 1986). Disturbance of spawners, trampling of eggs in redds (Roberts and White 1992), and angling mortality (Gresswell and Varley 1988) are perturbations associated with the presence of visitors in the vicinity of spawning streams. Additionally, human presence may alter use patterns of natural predators, affecting both predator and prey populations (Swenson 1975; Reinhart 1990). This is especially important because of the frequent occurrence of endangered species including grizzly bears (*Ursus arctos horribilis*) and bald eagles (*Haliaeetus leucocephalus*) in the Yellowstone Lake drainage. Alteration of natural fire regimes, especially in the developed areas, has also occurred in the drainage. Although individual activities such as these may not appear to have substantial effects on the persistence of the cutthroat trout in the Yellowstone Lake drainage, the synergistic and cumulative effects of human presence should be considered in all future management decisions. Each individual spawning population is important in the spatiotemporal mosaic of populations and life-history types that form the Yellowstone Lake metapopulation and ultimately to the persistence of this complex assemblage.

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References

- ALLENDORF, F.W., AND R.F. LEARY. 1988. Conservation and distribution of genetic variation in a polytypic species, the cutthroat trout. *Conserv. Biol.* 2: 170-184.
- ALLENDORF, F.W., N. RYMAN, AND F.M. UTTER. 1987. Genetics and fishery management: past, present, and future, p. 1-20. *In* N. Ryman and F.M. Utter [ed.] Population genetics and fishery management. Washington Sea Grant Program, University of Washington Press, Seattle and London.
- BAGENAL, T.B. 1978. Aspects of fish fecundity, p. 75-101. *In* S.D. Gerking [ed.] Ecology of freshwater fish production. John Wiley & Sons, New York, NY.
- BALL, O.P. 1955. Some aspects of homing in cutthroat trout. *Proc. Utah Acad. Sci. Arts Lett.* 32: 75-80.
- BALL, O.P., AND O.B. COPE. 1961. Mortality studies on cutthroat trout in Yellowstone Lake. U.S. Fish Wildl. Serv. Res. Rep. 55: 62 p.
- BEACHAM, T.D. 1984. Age and morphology of chum salmon in southern British Columbia. *Trans. Am. Fish. Soc.* 113: 727-736.
- BEACHAM, T.D., AND C.B. MURRAY. 1987. Adaptive variation in body size, morphology, egg size, and developmental biology of chum salmon (*Oncorhynchus keta*) in British Columbia. *Can. J. Fish. Aquat. Sci.* 44: 244-261.
- BEHNKE, R.J. 1988. Phylogeny and classification of cutthroat trout. *Am. Fish. Soc. Symp.* 4: 1-7.
- BEHNKE, R.J. 1992. Native trout of western North America. *Am. Fish. Soc. Monogr.* 6: 275 p.
- BENSON, N.G. 1960. Factors influencing production of immature cutthroat in Arnica Creek, Yellowstone Park. *Trans. Am. Fish. Soc.* 89: 168-175.
- BENSON, N.G. 1961. Limnology of Yellowstone Lake in relation to the cutthroat trout. U.S. Fish Wildl. Serv. Res. Rep. 56: 33 p.
- BENSON, N.G., AND R.V. BULKLEY. 1963. Equilibrium yield management of cutthroat trout in Yellowstone Lake. U.S. Fish Wildl. Serv. Res. Rep. 62: 44 p.
- BOWLER, B. 1975. Factors influencing genetic control in lakeward migrations of cutthroat trout fry. *Trans. Am. Fish. Soc.* 104: 474-482.
- BROWN, L.R., P.B. MOYLE, W.A. BENNETT, AND B.D. QUELVOG. 1992. Implications of morphological variation among populations of California roach *Lavinia symmetricus* (Cyprinidae) for conservation policy. *Biol. Conserv.* 62: 1-10.
- BULKLEY, R.V. 1961. Fluctuations in age composition and growth rate of cutthroat trout in Yellowstone Lake. U.S. Fish Wildl. Serv. Res. Rep. 54: 31 p.
- BULKLEY, R.V. 1963. Natural variation in spotting, hyoid teeth counts, and coloration of Yellowstone cutthroat trout. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. 460: 11 p.
- CARL, L.M., AND M.C. HEALEY. 1984. Differences in enzyme frequency and body morphology among three juvenile life history types of chinook salmon (*Oncorhynchus tshawytscha*) in the Nanaimo River, British Columbia. *Can. J. Fish. Aquat. Sci.* 41: 1070-1077.
- CHRISTIE, W.J. 1972. Lake Ontario: effects of exploitation, introductions, and eutrophication on the salmonid community. *J. Fish. Res. Board Can.* 29: 913-929.
- CLANCY, C.G. 1988. Effects of dewatering on spawning by Yellowstone cutthroat trout in tributaries to the Yellowstone River, Montana. *Am. Fish. Soc. Symp.* 4: 37-41.
- COPE, O.B. 1956. Some migration patterns in cutthroat trout. *Proc. Utah Acad. Sci. Arts Lett.* 33: 113-118.
- COPE, O.B. 1957. Races of cutthroat trout in Yellowstone Lake. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. 208: 74-84.
- DEAN, J.L., AND J.D. VARLEY. 1974. Fishery Management Investigations, Yellowstone National Park. Tech. Rep. 1973. Bureau of Sport Fisheries and Wildlife, Yellowstone National Park, Wyoming. 170 p.
- DEN BOER, P.J. 1968. Spreading of risk and stabilization of animal numbers. *Acta Biotheor.* 18: 165-194.
- DWYER, W.P. 1990. Catchability of three strains of cutthroat trout. *N. Am. J. Fish. Manage.* 10: 458-461.
- ECHELLE, A.A. 1991. Conservation genetics and genic diversity in freshwater fishes of western North America, p. 141-153. *In* M.L. Minckley and J.E. Deacon [ed.] Battle against extinction: native fish management in the American West. The University of Arizona Press, Tucson, AZ.
- ERWIN, T.L. 1991. An evolutionary basis for conservation strategies. *Science (Wash., DC)* 253: 750-752.
- EVANS, D.O., AND C.C. WILLOX. 1991. Loss of exploited, indigenous populations of lake trout, *Salvelinus namaycush*, by stocking of non-native stocks. *Can. J. Fish. Aquat. Sci.* 48: 134-146.
- GARRETT, P.A., AND J.C. KNIGHT. 1973. Limnology of the West Thumb of Yellowstone Lake, Yellowstone National Park. Final Rep. (Contract 2-101-0387). Montana State University, Bozeman, MT.
- GARRETT, A.J., AND W.W. SMOKER. 1993. Genetic components in life-history traits contribute to population structure, p. 197-202. *In* J.J. Cloud and G.H. Thorgaard [ed.] Genetic conservation of salmonid fishes. Plenum Press, New York, NY.
- GRESSWELL, R.E. [ED.] 1988. Status and management of interior stocks of cutthroat trout. *Am. Fish. Soc. Symp.* 4: 140 p.
- GRESSWELL, R.E., AND J.D. VARLEY. 1988. Effects of a century of human influence on the cutthroat trout of Yellowstone Lake. *Am. Fish. Soc. Symp.* 4: 45-52.
- GRIFFITH, J.S., JR. 1988. Review of competition between cutthroat trout and other salmonids. *Am. Fish. Soc. Symp.* 4: 134-140.
- HANKIN, D.G., J.W. NICHOLAS, AND T.W. DOWNEY. 1993. Evidence for inheritance of age of maturity in chinook salmon (*Oncorhynchus tshawytscha*). *Can. J. Fish. Aquat. Sci.* 50: 347-358.
- HANSKI, I. 1991. Single-species metapopulation dynamics: concepts, models and observations. *Biol. J. Linn. Soc.* 42: 17-38.
- HANSKI, I., AND M. GILPIN. 1991. Metapopulation dynamics: brief history and conceptual domain. *Biol. J. Linn. Soc.* 42: 3-16.
- HEALEY, M.C. 1986. Optimum size and age at maturity in Pacific salmon and effects of size-selective fisheries, p. 39-52. *In* D.J. Meerburg [ed.] Salmonid age at maturity. *Can. Spec. Pub. Fish. Aquat. Sci.* 89.
- JONES, R.D., R. ANDRESEK, D.G. CARTY, R.E. GRESSWELL, D.L. MAHONY, AND S. RELYA. 1990. Fishery and aquatic management program in Yellowstone National Park. Tech. Rep. 1989. U.S. Fish and Wildlife Service, Yellowstone National Park, WY. 284 p.
- JONES, R.D., P.E. BIGELOW, R.E. GRESSWELL, L.D. LENTSCH, AND R.A. VALDEZ. 1983. Fishery and aquatic management program in Yellowstone National Park. Tech. Rep. 1982. U.S. Fish and Wildlife Service, Yellowstone National Park, WY. 216 p.
- JONES, R.D., D.G. CARTY, R.E. GRESSWELL, K.A. GUNTHER, L.D. LENTSCH, AND J. MOHRMAN. 1985. Fishery and aquatic management program in Yellowstone National Park. Tech. Rep. 1984. U.S. Fish and Wildlife Service, Yellowstone National Park, WY. 189 p.
- JONES, R.D., D.G. CARTY, R.E. GRESSWELL, C.J. HUDSON, L.D. LENTSCH, AND D.L. MAHONY. 1986. Fishery and aquatic management program in Yellowstone National Park. Tech. Rep. 1985. U.S. Fish and Wildlife Service, Yellowstone National Park, WY. 204 p.
- JONES, R.D., D.G. CARTY, R.E. GRESSWELL, C.J. HUDSON, AND D.L. MAHONY. 1987. Fishery and aquatic management program in Yellowstone National Park. Tech. Rep. 1986. U.S. Fish and Wildlife Service, Yellowstone National Park, WY. 201 p.
- JONES, R.D., J.D. VARLEY, D.E. JENNINGS, S.M. RUBRECHT, AND R.E. GRESSWELL. 1979. Fishery and aquatic management program in Yellowstone National Park. Tech. Rep. 1978. U.S. Fish and Wildlife Service, Yellowstone National Park, Wyoming. 311 p.
- JONSSON, B., AND O.T. SANDLUND. 1979. Environmental factors and life histories of isolated river stocks of brown trout (*Salmo trutta m. fario*) in Søre Osa River system, Norway. *Env. Biol. Fish.* 4: 43-54.
- KAPLINSKI, M.A. 1991. Geomorphology and geology of Yellowstone Lake, Yellowstone National Park, Wyoming. M.S. thesis, Northern Arizona University, Flagstaff, AZ. 82 p.
- KELLY, B.M. 1993. Ecology of Yellowstone cutthroat trout and evaluation of potential effects of angler wading in the Yellowstone River. M.S. thesis, Montana State University, Bozeman, MT. 100 p.
- KRUEGER, C.C., AND B. MAY. 1991. Ecological and genetic effects of salmonid introductions in North America. *Can. J. Fish. Aquat. Sci.* 48: 66-76.
- LARKIN, P.A. 1977. An epitaph for the concept of maximum sustained yield. *Trans. Am. Fish. Soc.* 106: 1-11.
- LIEBELT, J.E. 1969. A serological study of cutthroat trout (*Salmo clarki lewisi*) from tributaries and the outlet of Yellowstone Lake. *Proc. Mont. Acad. Sci.* 29: 31-39.
- LOUDENSLAGER, E.J., AND G.A.E. GALL. 1980. Geographic patterns of protein variation and subspeciation in cutthroat trout, *Salmo clarki*. *Syst. Zool.* 29: 27-42.
- MALDE, H.E. 1965. The Snake River plain, p. 255-264. *In* H.E. Wright and D.G. Frey [ed.] The Quaternary of the United States. Princeton University Press, Princeton, NJ.
- MARRIN, D.L., AND D.C. ERMAN. 1982. Evidence against competition between trout and nongame fishes in Stampede Reservoir, California. *N. Am. J. Fish. Manage.* 2: 262-269.
- MCCLEAVE, J.D. 1967. Homing and orientation of cutthroat trout (*Salmo*

- clarki*) in Yellowstone Lake, with special reference to olfaction and vision. *J. Fish Res. Board Can.* 24: 2011–2044.
- MCMULLIN, S.L., AND T. DOTSON. 1988. Use of McBride Lake strain Yellowstone cutthroat trout for lake and reservoir management in Montana. *Am. Fish. Soc. Symp.* 4: 42–44.
- MILLS, L.E. 1966. Environmental factors and egg mortality of cutthroat trout (*Salmo clarki*) in three tributaries of Yellowstone Lake. M.S. thesis, Colorado State University, Fort Collins, CO. 67 p.
- MORISAWA, M. 1968. Streams their dynamics and morphology. McGraw-Hill, New York, NY. 175 p.
- MURPHY, G.I. 1968. Pattern in life history and the environment. *Am. Nat.* 102: 391–403.
- NELSON, K., AND M.E. SOULÉ. 1897. Genetical conservation of exploited fishes, p. 345–368. *In* N. Ryman and F.M. Utter [ed.] Population genetics and fishery management. Washington Sea Grant Program, University of Washington Press, Seattle and London.
- NIKOLSKI, G.V. 1969. Theory of population dynamics as the biological background for rational exploitation and management of fishery resources. Oliver and Boyd, Edinburgh. 323 p.
- NOSS, R.F. 1990. Indicators for monitoring biodiversity: a hierarchical approach. *Conserv. Biol.* 4: 355–364.
- O'BRIEN, S.J., AND E. MAYR. 1991. Bureaucratic mischief: recognizing endangered species and subspecies. *Science (Wash., DC)* 251: 1187–1188.
- OVIATT, C.G., D.R. CURREY, AND D. SACK. 1992. Radiocarbon chronology of Lake Bonneville, eastern Great Basin, USA. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* 99: 225–241.
- QUINN, R.T., AND M.J. UNWIN. 1993. Variation in life history patterns among New Zealand chinook salmon (*Oncorhynchus tshawytscha*) populations. *Can. J. Fish. Aquat. Sci.* 50: 1414–1421.
- RALEIGH, R.F., AND D.W. CHAPMAN. 1971. Genetic control in lakeward migration of cutthroat trout fry. *Trans. Am. Fish. Soc.* 100: 33–40.
- REINHART, D.P. 1990. Grizzly bear habitat use on cutthroat trout spawning streams in tributaries of Yellowstone Lake. M.S. thesis, Montana State University, Bozeman, MT. 128 p.
- RICHMOND, G.M., AND K.L. PIERCE. 1972. Surficial geologic map of the Eagle Peak quadrangle, Yellowstone National Park, Wyoming. *Misc. Geol. Invest. Map I-637*. U.S. Geological Survey, Washington, DC.
- RICKER, W.E. 1963. Big effects from small causes: two examples from fish population dynamics. *J. Fish Res. Board Can.* 20: 257–264.
- RICKER, W.E. 1981. Changes in the average size and average age of Pacific salmon. *Can. J. Fish. Aquat. Sci.* 38: 1636–1656.
- RIEMAN, B.E., AND J.D. MCINTYRE. 1993. Demographic and habitat requirements for conservation of bull trout. *USDA For. Serv. Gen. Tech. Rep. INT-302*.
- RIGET, F.F., K.H. NYGAARD, AND B. CHRISTENSEN. 1986. Population structure, ecological segregation, and reproduction in a population of Arctic char (*Salvelinus alpinus*) from Lake Tasersuaq, Greenland. *Can. J. Fish. Aquat. Sci.* 43: 985–992.
- ROBERTS, B.C., AND R.G. WHITE. 1992. Effects of angler wading on survival of trout eggs and pre-emergent fry. *N. Am. J. Fish. Manage.* 12: 450–459.
- RYMAN, N., AND L. LAIKRE. 1991. Effects of supportive breeding on the genetically effective population size. *Conserv. Biol.* 5: 325–329.
- SCHAFFER, W.H., AND P.F. ELSON. 1975. The adaptive significance of variations in life history among local populations of Atlantic salmon in North America. *Ecology* 56: 577–590.
- SIMON, J.R. 1962. Yellowstone fishes. Yellowstone Interpret. Ser. 3. Yellowstone Library and Museum Association, Yellowstone National Park, WY. 49 p.
- SINCLAIR, M. 1988. Marine populations. Washington Sea Grant Program, University of Washington Press, Seattle and London. 252 p.
- SMITH, H.M., AND W.C. KENDALL. 1921. Fishes of the Yellowstone National Park. *Bur. Fish. Doc. 904*. U.S. Department of Commerce, Washington, DC. 30 p.
- SOULÉ, M.E. 1991. Conservation: tactics for a constant crisis. *Science (Wash., DC)* 253: 744–750.
- STEARLEY, R.F. 1992. Historical ecology of Salmoninae, with special reference to *Oncorhynchus*, p. 622–258. *In* R.L. Mayden [ed.] Systematics, historical ecology, and North American freshwater fishes. Stanford University Press, Stanford, CT.
- STEARLEY, R.F., AND G.R. SMITH. 1993. Phylogeny of the Pacific trouts and salmon (*Oncorhynchus*) and genera of the family Salmonidae. *Trans. Am. Fish. Soc.* 122: 1–33.
- SWENSON, J.E. 1975. Ecology of the bald eagle and osprey in Yellowstone National Park. M.S. thesis, Montana State University, Bozeman, MT. 146 p.
- TAYLOR, E.B. 1990. Phenotypic correlates of life-history variation in juvenile chinook salmon *Oncorhynchus tshawytscha*. *J. Anim. Ecol.* 59: 455–468.
- TAYLOR, E.B. 1991. A review of local adaptation in Salmonidae, with particular reference to Pacific and Atlantic salmon. *Aquaculture* 98: 185–207.
- THOMPSON, J.D. 1991. Phenotypic plasticity as a component of evolutionary change. *Trends Ecol. Evol.* 6: 246–249.
- VARLEY, J.D. 1979. Record of egg shipments from Yellowstone fishes, 1914–1955. *Inf. Pap. 36*. U.S. National Park Service, Yellowstone National Park, WY. 44 p.
- VARLEY, J.D. 1981. A history of fish stocking activities in Yellowstone National Park between 1881 and 1980. *Inf. Pap. 35*. U.S. Nat. Park Service, Yellowstone National Park, WY. 93 p.
- VARLEY, J.D., AND R.E. GRESSWELL. 1988. Ecology, status, and management of the Yellowstone cutthroat trout. *Am. Fish. Soc. Symp.* 4: 13–24.
- VARLEY, J.D., AND P. SCHULLERY. 1983. Freshwater wilderness: Yellowstone fishes and their world. Yellowstone Library and Museum Association, Yellowstone National Park, WY. 133 p.
- WAPLES, R.S. 1991. Genetic interactions between hatchery and wild salmonids: lessons from the Pacific Northwest. *Can. J. Fish. Aquat. Sci.* 48: 124–133.
- WARREN, C.E., AND W.J. LISS. 1980. Adaptation to aquatic environments, p. 15–40. *In* R.T. Lackey and L. Nielsen [ed.] Fisheries management. Blackwell Scientific Publications, Oxford.
- WELSH, J.P. 1952. A population study of Yellowstone blackspotted trout (*Salmo clarki*). Ph.D. thesis, Stanford University, Stanford, CA. 180 p.
- WEVERS, M.J. 1994. Life history and evolutionary adaptation of Pacific salmon and its application in management. Ph.D. thesis, Oregon State University, Corvallis, OR. 128 p.