Yellowstone Science

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Yellowstone Cutthroat Trout Conservation

Source and Date of Lake Trout Introduction

History of Lake Fish Hatchery


NPS/MIKE YOCHIM

Southeast arm of Yellowstone Lake.

Manipulated Ecosystems

My first job in Yellowstone was as a Youth Conservation Corps crew leader in the summer of 1993. For the last job of the season, our crew got to spend 10 days camping at Trail Creek, near the southeast arm of Yellowstone Lake. It was breathtaking to be on the lake in August. We felt thoroughly spoiled to be allowed to pass those long days in what appeared to be such a remote, pristine environment.

The next summer, news of the discovery that lake trout had been illegally introduced to the lake traveled quickly throughout the park's administrative offices in Mammoth Hot Springs. People were sad and angry, wondering who did it and how, and what would happen to the lake's native Yellowstone cutthroat trout. In this issue of *Yellowstone Science,* Andrew Munro et al.'s article reports on how they identified the source and date of the lake trout introduction in Yellowstone Lake. People continue to point out that Hiram M. Chittenden's 1903 history, *The Yellowstone National Park: Historical and Descriptive,* 4th ed., lists "10,000 yearling lake trout" as having been planted by the U.S. Fish Commission "in the Yellowstone River above the falls in 1890." An exhaustive search by John Varley of official records on translocations has found no indication that such a plant took place. But if it did, the introduction failed, as did others—Atlantic salmon were also planted in the lake and never seen again. According to writer and historian Paul Schullery, not a single lake trout appears in the official records of gillnetting and fish management work in the park between 1900 and 1990. However, highly credible observers have reported catching lake trout in Yellowstone Lake over the park's history. This may suggest early introductions of lake trout to the lake, resulting in a few reported catches. Regardless, studies such as Munro et al.'s indicate that the current lake trout crisis is the result of recent, successful introductions.

Yellowstone's fisheries have been tinkered with since at least 1881, the date of the earliest fish stocking in the park. Tom Olliff, the new Chief of the Yellowstone Center for Resources, considers Yellowstone's aquatic systems to be the park's "most disturbed" environments—not pristine at all. Also in this issue, Lee Whittlesey records the history of former fishery operations and the hatchery at Yellowstone Lake, which were part of park managers' early efforts to "improve" the fishery for the benefit of sportfishers. Although park management later moved away from manipulation toward protection of native species, today's ease and expansion of world travel and trade has brought with it the movement and proliferation of non-native species, and new concerns.

Invasive non-native species are now acknowledged worldwide to be a major threat to biodiversity; once introduced, efforts to control or eliminate them can be time-consuming and expensive. Prevention is the key. Yellowstone now spends roughly $400,000 annually just to *suppress* lake trout population growth. In the meantime, the lake's native Yellowstone cutthroat trout, which provide an important source of energy to at least 42 species of birds and mammals and have recently supported a $36 million annual sport fishery, also suffer from the effects of whirling disease and drought. In their article, Todd Koel et al. describe the efforts of the park's aquatic sciences program to conserve the park's native Yellowstone cutthroat trout in the face of these and other threats.

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on the cover
Yellowstone cutthroat trout, courtesy Mimi Matsuda.

NPS/JIM PEACO

Aerial view of the Yellowstone River delta.

FEATURES

DEPARTMENTS

NEWS & NOTES


NPS/BECKY WYMAN

2006 Winter Elk Count

The Northern Yellowstone Cooperative Wildlife Working Group conducted its annual, late winter classification of northern Yellowstone elk on March 23, 2006. Biologists traveled by helicopter to classify a total of 3,649 elk as bulls, cows, or calves in specified sampling areas throughout the northern winter range during the one-day survey. Northern Yellowstone elk winter between the northeast entrance of Yellowstone National Park and Dome Mountain/Dailey Lake in the Paradise Valley.

Estimated sex and age ratios for the population were 24 calves and 20 bulls per 100 cows. Calf ratios averaged 20 calves per 100 cows inside the park and 27 calves per 100 cows north of the park boundary. The overall ratio of 24 calves per 100 cows is higher than the late-winter ratios of 12–14 calves per 100 cows during 2002–2005, and within the range of 22–34 calves per 100 cows observed during the previous six years.

P.J. White, biologist for Yellowstone National Park, indicated, "The increase in recruitment this year probably reflects less predation by wolves and, in part, a decrease in antlerless elk harvest." An apparent disease outbreak reduced wolf numbers on the northern range by 40% during summer 2005. Also, Montana Fish, Wildlife and Parks significantly reduced antlerless elk permits for the Gardiner area late season elk hunt over the last five years, due primarily to four consecutive years of low recruitment.

Tom Lemke, biologist for Montana Fish, Wildlife and Parks, added, "Improved elk recruitment this winter is definitely good news, but it will probably take at least another good recruitment year to move back into a Standard Hunting Season package. However, this year's data on recruitment, harvest, migration size, and winter distribution may allow for a modest increase in antlerless permits within the existing Restrictive Season framework for the January 2007 Gardiner late hunt." Final elk permit quotas will be set by the Fish, Wildlife and Parks Commission in July 2006.

Due to a lack of snow cover and unusually windy conditions, the working group was unable to complete the annual winter trend count of northern Yellowstone elk during the typical period in late December or early January. Biologists attempted to conduct a count on March 22, 2006, but elk inside the park were widely distributed at higher elevations and in timbered areas, which made detection difficult and unreliable compared to previous winters. Thus, the count was considered poor and inaccurate, and results are not comparable to surveys during good conditions in previous years.

The working group, comprised of resource managers and biologists from the Montana Department of Fish, Wildlife and Parks; Yellowstone National Park; Gallatin National Forest; and U.S. Geological Survey–Northern Rocky Mountain Science Center, will continue to monitor trends of the elk population and evaluate the relative contribution of various components of mortality, including predation, environmental factors, and hunting. The Working Group was formed in 1974 to cooperatively preserve and protect the long-term integrity of the northern Yellowstone winter range for wildlife species by increasing our scientific knowledge of the species and their habitats, promoting prudent land management activities, and encouraging an interagency approach to answering questions and solving problems.

Yellowstone Late Winter Bison Population Estimate

The recently completed 2006 late winter bison population estimate is 3,500 bison.

Based on a late winter aerial survey, the estimate takes into account the 2005 late summer population estimate of 4,900 bison, known brucellosis risk management mortalities, and scientific estimates of over-winter mortality rates.

The population estimate is used to guide adaptive management strategies under the Interagency Bison Management Plan (IBMP). Specific management actions may be modified based on expected late winter population levels as corroborated by the annual late winter estimate.

During winter, 939 bison were removed from the wild bison population through capture operations at Stephens Creek, in accordance with the IBMP. This is the sixth winter the IBMP has been used to guide brucellosis risk management actions.

The IBMP is a cooperative plan designed to protect Montana's brucellosis-free status while allowing for the conservation of a viable, wild bison population. Protecting Montana's brucellosis-free status requires keeping bison from mixing with cattle grazing on land outside the park.

The five cooperating agencies operating under the IBMP are the National Park Service, the U.S. Forest Service, the Animal and Plant Health Inspection Service, the Montana Department of Livestock, and the Montana Department of Fish, Wildlife and Parks.

YS

Passages — Frederick Brown Turner

by Debra Patla and Charles R. Peterson
Herpetology Laboratory, Idaho State University

COURTESY OF DEBRA PATLA

Fred Turner, left, with his brother at the Lake Lodge study area, 1955.

Fred Brown Turner, 1927–2006

On February 6, 2006, Frederick Brown Turner passed away in Encinitas, California, at the age of 79. Dr. Turner was renowned for his groundbreaking work on amphibians in Yellowstone National Park in the 1950s.

The son of Lewis and Josephine Turner, Fred Turner was born on February 4, 1927, in Carlinville, Illinois. In 1943, when Lewis Turner was named Dean of the School of Forestry at Utah State University, the Turner family moved to Logan, Utah. Fred was quickly engaged in the western landscape when his father sent him to work on white pine blister rust control in Idaho.

At the age of 16, Fred enrolled as a freshman at Utah State University. He enlisted in the Air Force Reserve and was called to active duty in the summer of 1945. When he returned to civilian life in 1946, Fred enrolled at University of California–Berkeley and studied zoology. He received his master's degree in 1950, graduating with honors, and was elected to Phi Beta Kappa. Fred then took a job as instructor of botany at Illinois College.

Longing for the West, he sought summer employment as a ranger naturalist in Yellowstone National Park, and was assigned to work at Fishing Bridge in 1952. Fascinated by the frogs he encountered in the vicinity of "Soldier Creek" (now known as Lodge Creek), Fred conceived of investigating the structure and dynamics of the spotted frog population for a doctoral degree. For the following three years (1953–1955), he engaged in intensive research while simultaneously working for the park, compiling data collected in his free time with the assistance of his wife, Mabel. During those years, Fred also had the company of his brother, Lewis, who worked as a fishing guide out of West Thumb. Lewis helped Fred map the study area, and together the brothers enjoyed backpacking trips in some of the wildest parts of the park.

Fred received his PhD in Zoology from UC–Berkeley in 1957. His academic advisor was herpetologist Robert C. Stebbins, and their relationship extended to lifelong mutual admiration and professional contact. After a short stint as an instructor at Wayne State University, Fred accepted a position as a researcher at a UCLA laboratory, working at the Nevada Test Site on experimental research for the Atomic Energy Commission. Collaborating with colleagues he admired, and supported by unusually stable funding for fieldwork, Fred was gratified by a career that allowed him to conduct herpetological research in California, Nevada, and Utah. Fred retired from scientific work in 1986. He suffered deterioration of memory in his last few years, and was a resident of Silverado Senior Living Center in Encinitas when he died of complications due to pneumonia.

Fred Turner pioneered herpetology in Yellowstone in the 1950s, providing the park with its first checklist (1951) and guide (1955) of reptiles and amphibians. He wrote articles about his observations for Yellowstone's *Nature Notes*, and published his findings in scientific journals. Fred's PhD research on the Lake Lodge spotted frog population was published in *Ecological Monographs* in 1960. This study of population structure, growth rates, and spatial relationships (frog movements with respect to habitat features), remains one of the most comprehensive investigations ever completed for this species. Its value as the only detailed, historical study of an amphibian population in Yellowstone has only increased with time. Chuck and I feel very fortunate to have had Fred as a guide for several days in 1992 and 1993. His observations, along with his shock at the frog population decline, kindled our curiosity and inspired our research efforts. Through Fred's work in the Lake Lodge area, we can virtually observe a frog population of 50 years ago: how many frogs were present, what habitat they used, and how they moved from one area to another to meet their seasonal habitat requirements (see *Yellowstone Science,* winter 1999). Without Fred's painstaking work, it would be impossible to see the Lake Lodge frog population for what it actually is today: a remnant persisting in habitat altered by human activities and environmental change.

We have been inspired by Fred Turner's scientific understanding of amphibians, his delight and patience in prying out the secrets of their lives, his encouragement of our work, and his sorrow about amphibian declines. Walking in Fred's footsteps in Yellowstone, we are thankful for the legacy of his admirable work.

YS

Where Did They Come From?

Natural Chemical Markers Identify Source and Date of Lake Trout Introduction in Yellowstone Lake

Andrew R. Munro, Thomas E. McMahon, and James R. Ruzycki


NPS/PAT BIGELOW

Fisheries technician Brad Olszewski with a lake trout removed from a Yellowstone Lake spawning area.

EXOTIC SPECIES pose one of the most pervasive threats to fresh waters worldwide (Hall and Mills 2000; Rahel 2000; Kolar and Lodge 2002). Dramatic changes in species abundance and energy flow have been observed following the establishment of a single new species, even in large lakes (Zaret and Paine 1973; Vander Zanden et al. 1999). Although many exotic species have been intentionally introduced for commercial or recreational purposes, unauthorized transplants and invasions have also contributed substantially to exotic species expansion (McMahon and Bennett 1996; Fuller et al. 1999; Rahel 2000).

When an exotic species is first detected in a new location, questions about where it originated and when it was transplanted or invaded are frequently difficult to answer with confidence (Radtke 1995; McMahon and Bennett 1996; Hebert and Cristescu 2002). This uncertainty hinders possible management actions for avoiding future occurrences and, in some instances, raises questions as to whether a presumed invader is, in fact, native or has resided in the system longer than suspected but at low abundance (Kaeding et al. 1996; Waters et al. 2002). Recent investigations of freshwater zooplankton illustrate the utility of genetic markers as a forensic tool for studying invasion biology (Cristescu et al. 2001; Hebert and Cristescu 2002). In this paper, we demonstrate the use of natural chemical markers in fish otoliths to identify the probable source and date of introduction of an exotic fish species.

Exotic lake trout (*Salvelinus namaycush*) were discovered in Yellowstone Lake in 1994 (Kaeding et al. 1996). This 250,000-ha, high-elevation lake near the headwaters of the Yellowstone River drainage is one of the largest relatively intact lake ecosystems in the United States, and is the primary remaining habitat for Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*)

(Gresswell and Varley 1988). The clear, deep, cold waters and abundant prey base of Yellowstone Lake provide prime habitat for piscivorous lake trout, and by 1996 their population was estimated to be several thousand, including individuals as large as 91 cm in length (Ruzycki et al. 2003). Development of an abundant lake trout population was anticipated if left unchecked, with the resultant high predation pressure causing a significant decline in the Yellowstone cutthroat trout population (Varley and Schullery 1995; Ruzycki et al. 2003). Cutthroat trout generally evolved in the absence of competing top predators (Behnke 1992), and declines have been documented in several western North American lakes following lake trout introduction (Cordone and Frantz 1966; Marnell 1988; Donald and Alger 1993). Consequently, an aggressive lake trout removal program was initiated in Yellowstone Lake in 1995 to protect a valuable recreational fishery and the integrity of the lake's terrestrial and aquatic foodwebs, which are heavily dependent on cutthroat trout (Varley and Schullery 1995; Koel et al. 2003).

The origin of the lake trout in Yellowstone Lake is unknown. Although lake trout from the Great Lakes were introduced into Yellowstone National Park's Shoshone and Lewis lakes in the late 1800s and later spread to Heart Lake, these lakes are in the Snake River (Pacific) drainage, and lack connection to the Yellowstone River (Atlantic) drainage (Fig. 1) (Varley and Schullery 1983). Prior to 1994, no lake trout had been reported in Yellowstone Lake despite extensive population sampling and angler survey records dating back more than 50 years (Gresswell and Varley 1988; Kaeding et al. 1996). Based on the age and size of lake trout when they were discovered in 1994 (≤5 years and 43 cm), it was estimated that lake trout had reproduced in Yellowstone Lake since at least 1989, but when the original transplant occurred was unknown (Kaeding et al. 1996).

We used chemical analysis of otoliths ("ear stones" associated with hearing and balance, composed primarily of calcium carbonate and an organic matrix) to estimate where the lake trout originated and when they were transplanted into

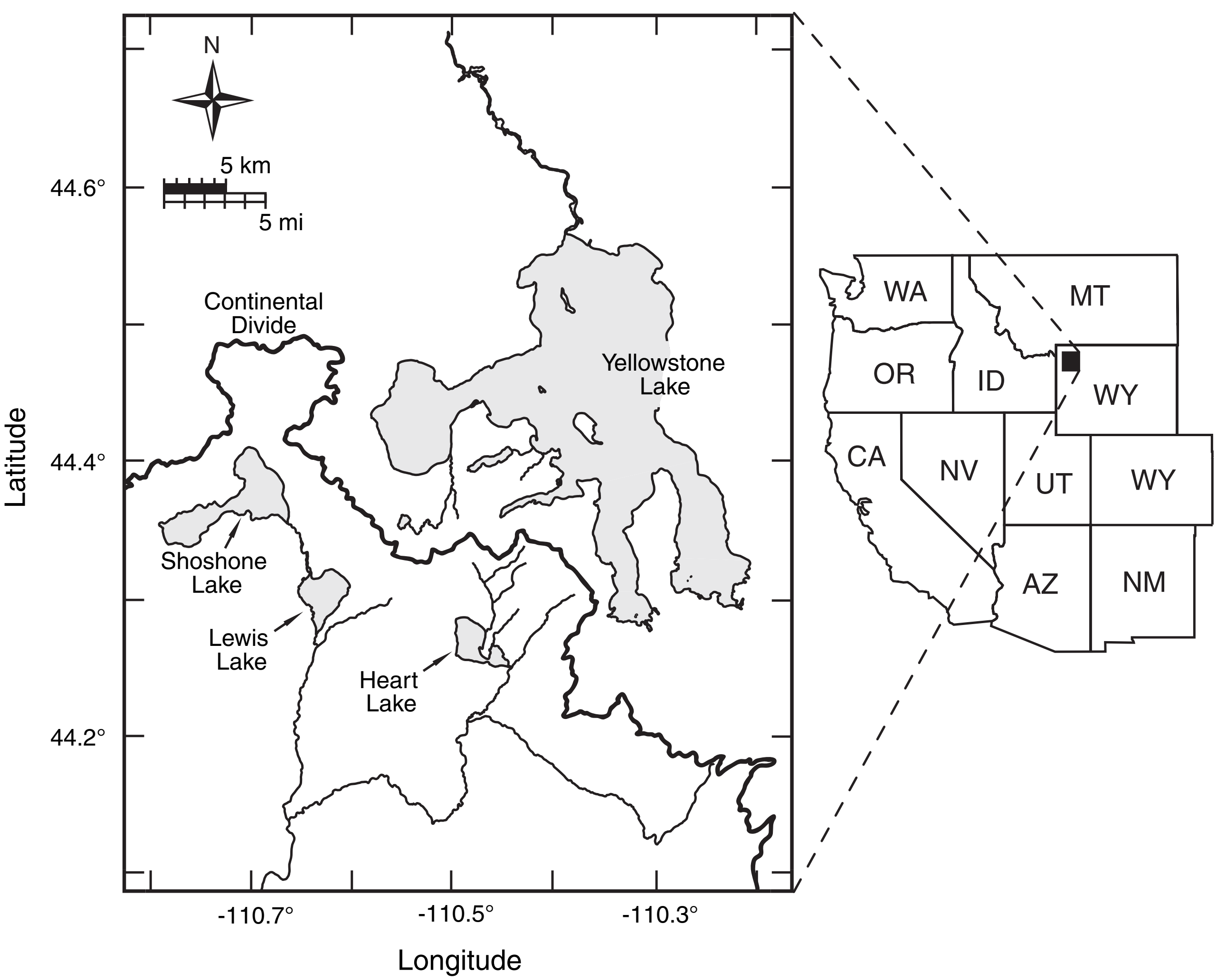

Figure 1. Map of the major lakes in the study area, Yellowstone National Park.

Group	Lake	*n*	Total length (mm) Median	Range	Age (years) Median	Range	Year-class range
Known-origin	Heart	10	490	327–691	15	8–22	1977–1991
	Lewis	10	503	416–949	14	9–26	1973–1990
	Yellowstone	10	720[a]	700–767	9	8–11	1988–1991
Suspected transplants	Yellowstone	20	805	765–890	18	10–32	1965–1987

[a]Length data were not available for five of the known-origin Yellowstone Lake fish.

Table 1. Summary of length, age, and year-class of the known-origin lake trout and suspected transplants collected from three lakes in Yellowstone National Park.

Yellowstone Lake. Because trace elements of ambient waters are incorporated into otoliths as a fish grows, analysis of natural chemical markers in otoliths can be used to reconstruct environmental history, including timing of movements and stock origins (Campana 1999; Limburg et al. 2001; Thorrold et al. 2001). However, to our knowledge, no one has used the elemental composition of otoliths to assess introductions of exotic species.

The strontium-to-calcium ratio (Sr:Ca) has been the most widely used marker in otolith composition studies because (i) of the strong correlation between otolith and ambient water ratios, (ii) strontium ions can substitute for calcium ions in the calcium carbonate ($CaCO_3$) of the otoliths, and (iii) Sr is more apt to reflect environmental concentrations than other elements owing to a lack of physiological regulation (Campana 1999). Organisms do not actively regulate Sr uptake like other essential elements (e.g., Ca, K, Na, P). However, because the uptake is through several membrane barriers (water – gills – blood – endolymph [fluid that bathes the otoliths] – otolith) the concentration is not the same as in the water; there is some discrimination. Although similar, Ca and Sr ions are physically and chemically different; Sr is larger and heavier. Furthermore, other physical and chemical factors can alter the incorporation of Sr into the otolith during crystal formation. However, as seen in Fig. 3, there is a relation between the ratio of the concentration of Sr and Ca in the source water and what is eventually incorporated into the otolith.

We compared the Sr:Ca ratios in otoliths from suspected transplants with those in (i) otoliths of lake trout from more recent year-classes, thought to have been spawned and reared in Yellowstone Lake, and (ii) otoliths of lake trout from Lewis and Heart lakes, the two most likely source lakes in Yellowstone National Park. We hypothesized that lake trout reared in a single lake would have similar otolith Sr:Ca ratios throughout their lives, from the early-growth zone near the nucleus to the outer edge. In contrast, we predicted that lake trout transplanted into Yellowstone Lake would have a significantly different chemical composition between the two zones, reflective of a change in environmental history, and that the Sr:Ca ratio of the early growth zone could be used to identify the probable source lake of the transplant. We further surmised that among suspected transplants, the timing of the change in Sr:Ca ratio in relation to the age of the fish could provide an estimated date of when transplantation had occurred.

Materials and methods

Otolith collection and preparation

Two groups of otoliths were analyzed for this study. The first group consisted of archived otoliths from lake trout that had been collected from Yellowstone Lake during early stages of the lake trout removal program in 1996 and 1997. It was surmised that the largest fish in these samples were likely some of the original fish transplanted to Yellowstone Lake, and smaller sizes were offspring of these suspected transplants. Twenty otoliths, 10 from each year, were randomly selected from among the 164 largest lake trout that constituted the suspected transplant group. These fish were >70 cm total length and comprised the upper 10 to 20% of length range of lake trout collected during 1996 and 1997 gillnet sampling (Table 1). The second group consisted of otoliths from lake trout of known origin: suspected offspring of the original founding population in Yellowstone Lake and lake trout of various ages from Heart and Lewis lakes (Table 1). Otoliths from this group were randomly selected from fish gillnetted in 1999 from all three lakes (n = 10 for each lake).

Otoliths were extracted, cleaned, and stored in polyethylene vials soon after collection. One otolith from each fish was sectioned, ground, and polished to expose the nucleus following the techniques of Secor et al. (1992). Prior to chemical analysis, otolith sections were ultrasonically cleaned in a series of baths of Milli-Q water, analytical-grade hexane, and analytical-grade methanol (<1 min each) to remove surface contaminants.

Otolith chemistry

Otolith chemical composition was measured with a Phi–Evans time-of-flight secondary ion mass spectrometer (ToF-SIMS) (Schueler 1992). For each otolith, ^{88}Sr and ^{44}Ca ion counts were measured at two sites, the early-growth zone

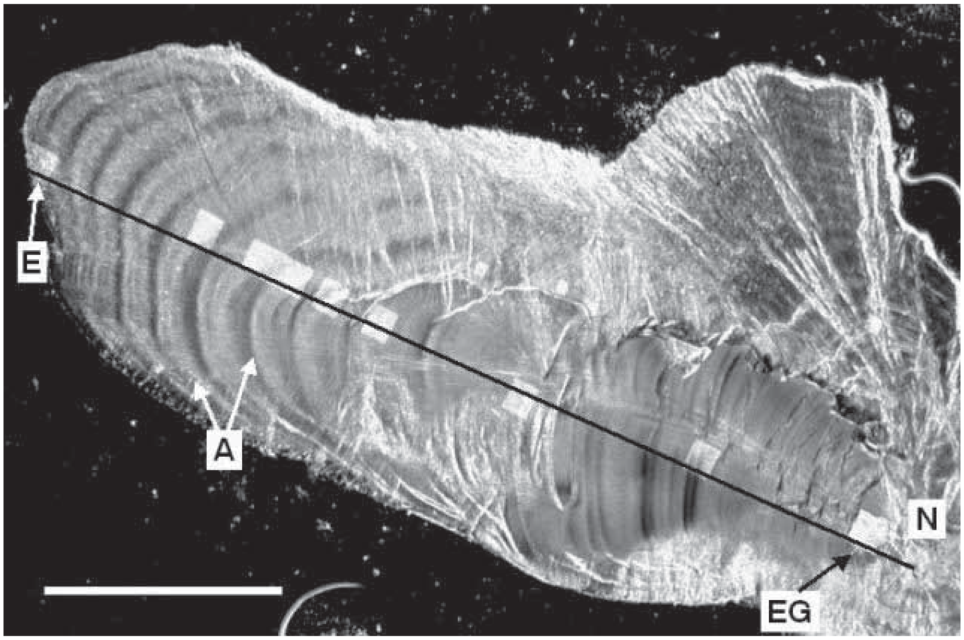

Figure 2. Transverse section of a lake trout otolith from a suspected transplant into Yellowstone Lake. Analysis sites for ^{88}Sr and ^{44}Ca ion counts were located in the early-growth zone (EG), near the nucleus (N), and the edge zone (E) in each otolith. Analyses along a transect were used to pinpoint the location of any temporal changes in Sr:Ca ratios. A, annuli. Scale bar = 0.5 mm.

near the nucleus and a zone near the outer edge (Fig. 2), and reported as Sr:Ca ratios. For a subset of otoliths from each group (suspected transplants into Yellowstone Lake, n = 5; offspring of transplants, n = 1; Heart Lake, n = 2; Lewis Lake, n = 1), additional ion counts were measured at three equidistant points between the early-growth and edge sample sites. If large changes were detected between adjacent sample sites, further sites were sampled to pinpoint the location of temporal changes in Sr:Ca ratio along the otolith axis (Fig. 2). Abrupt changes in Sr:Ca ratio have been correlated with rapid changes in water chemistry (e.g., Limburg et al. 2001). The date of a large change in Sr:Ca ratio, indicative of a movement to new waters, was estimated by comparing the location of the change on the otolith axis with the age of the fish at that time. Annuli were identified using aging criteria developed for lake trout otoliths by Sharp and Bernard (1988).

Water chemistry

Sr:Ca ratios of water from each of the three study lakes were measured to assess whether geochemical differences existed among the lakes, and the degree to which these differences were imparted to lake trout otoliths. Surface water samples were collected from Heart and Lewis lakes in 2000 (n = 4 per lake) following standard protocols (American Public Health Association 1998). Water was collected in 1-L polyethylene acid-washed bottles, and 100 mL of each sample was immediately filtered through a 0.45-µm-pore membrane filter into an opaque, acid-washed polyethylene bottle. Water samples were then preserved with 1 mL of analytical-grade concentrated nitric acid and refrigerated until analyzed. Yellowstone Lake water samples were collected at different depths in the water column in four areas of the lake (Southeast Arm, West Thumb, Mary Bay, and Stevenson Island) in 1997 (n = 30) and 1998 (n = 41) using a hydrobottle clean of trace metals (Balistrieri et al. In press). The water samples were filtered and preserved using the same methods described above. Total dissolved Sr and Ca concentrations (milligrams per liter) were measured with a Perkin-Elmer Sciex Elan 6000 inductively coupled plasma mass spectrometer (Lamothe et al. 1999) and converted to molar concentrations for calculation of the Sr:Ca ratio.

Statistical analyses

A type III mixed model analysis of variance (ANOVA) and Tukey's multiple comparison tests (SAS Institute Inc. 2000) were used to compare Sr:Ca ratios among known-origin lake trout from Heart, Lewis, and Yellowstone lakes. Lake and otolith zone (early growth and edge) were included as fixed factors, and individual fish, zone × fish interaction, and zone replication as random factors in the ANOVA. For all tests, significance was measured at $\alpha = 0.05$.

Nearest-neighbor discriminant analysis was used to determine the probable source of lake trout in Yellowstone Lake. In this type of analysis, each new observation is assigned to the group to which the majority of its nearest neighbors belong (Johnson 1998). Mean otolith Sr:Ca ratios for known-origin fish, weighted by number of sites sampled in each otolith zone, were used to construct the model. The Sr:Ca ratios from lake trout otoliths of suspected transplants were classified using the model developed for the known-origin data set.

Differences in lake water Sr:Ca ratio among the three study lakes were evaluated using a one-factor ANOVA, and Tukey's multiple comparison test was used to test for pairwise differences. Simple linear regression was used to assess the relationship between otolith and lake water Sr:Ca ratio. Only Sr:Ca data from the otolith edge zones were used to best match otolith composition with lake water composition at the times of sampling (within one year for Heart and Lewis lakes and two years for Yellowstone Lake).

Results

Lake water Sr:Ca ratios were significantly different among Heart, Lewis, and Yellowstone lakes, with differences in mean values among the lakes ranging from 160% to 270% (Fig. 3; Table 2). Tukey's multiple comparison tests indicated significant differences for all pairwise comparisons among the lakes. There was a significant linear relation between the otolith Sr:Ca ratios of known-origin lake trout and the lake water Sr:Ca ratios (Fig. 3). Although water samples from Lewis and Heart lakes were collected in a different year than were Yellowstone Lake samples, the small differences in lake water Sr:Ca between the 1997 and 1998 samples in Yellowstone Lake suggest that annual variation in water chemistry was minor compared to the among-lake differences (Table 2).

Otolith Sr:Ca ratios of known-origin lake trout were also significantly different among the three lakes (Fig. 4). Mean otolith Sr:Ca ratios of Yellowstone Lake lake trout were significantly different from lake trout otolith Sr:Ca ratios from Heart Lake and Lewis Lake. Differences in otolith Sr:Ca ratios between lake trout from Lewis and Heart lakes were not significant at the $\alpha = 0.05$ level. However, the Sr:Ca ratio for Lewis Lake fish was strongly influenced by one fish with a Sr:Ca ratio much greater than that observed in the other nine fish sampled (Fig. 4). When this outlier was removed, the pairwise difference in otolith Sr:Ca ratios between Lewis Lake and Heart Lake lake trout was highly significant.

Otolith Sr:Ca ratios between the early-growth and edge zones among known-origin lake trout from each lake varied little (Fig. 4), the average difference ranging from 0.1 to 5.3%, despite a wide range in the age of fish sampled (8–26 years) (Table 1). Variation of Sr:Ca ratios obtained from multiple sampling within a sample site on the otolith was also low, averaging 3.92% ($n = 25$). Accordingly, there was no significant interaction between lake and otolith zone as factors in the ANOVA. Additional samples taken between the early-growth and edge zones also revealed consistent Sr:Ca ratios across the otolith growth axis among lake trout sampled from different lakes (Fig. 5). Nearest-neighbor discriminant analysis correctly classified 90 to l00% of lake trout into their home lake (Table 3).

In sharp contrast with lake trout of known origin, 18 of 20 suspected transplants, ranging from 13 to 32 years of age at the time of their collection in 1996 and 1997, exhibited substantial increases (mean = 256%) between the early-growth

Lake	Year	*n*	Mean (SD)
Heart	1999	4	2.40 (0.23)
Lewis	1999	4	1.53 (0.71)
Yellowstone	1997	30	3.92 (0.10)
	1998	41	4.01 (0.14)

Table 2. Lake water Sr:Ca ratios (mmol·mol^{-1}) from Heart, Lewis, and Yellowstone lakes, Yellowstone National Park.

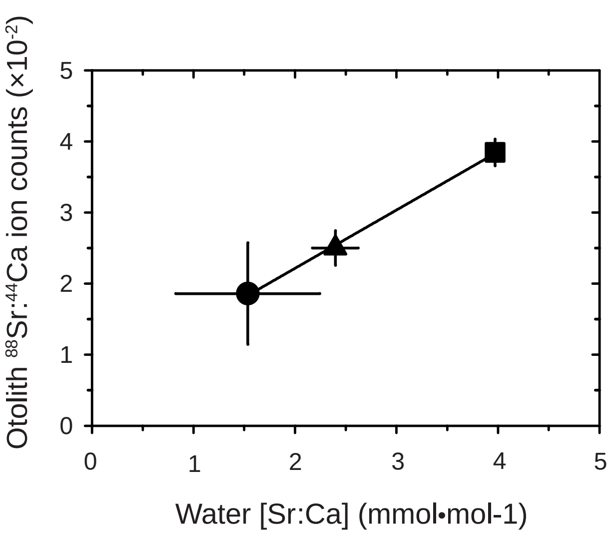

Figure 3. Relation between mean lake water Sr:Ca ratios and mean otolith edge Sr:Ca ratios of lake trout from Heart (▲), Lewis (●), and Yellowstone (■) lakes. The solid line denotes fitted linear regression.

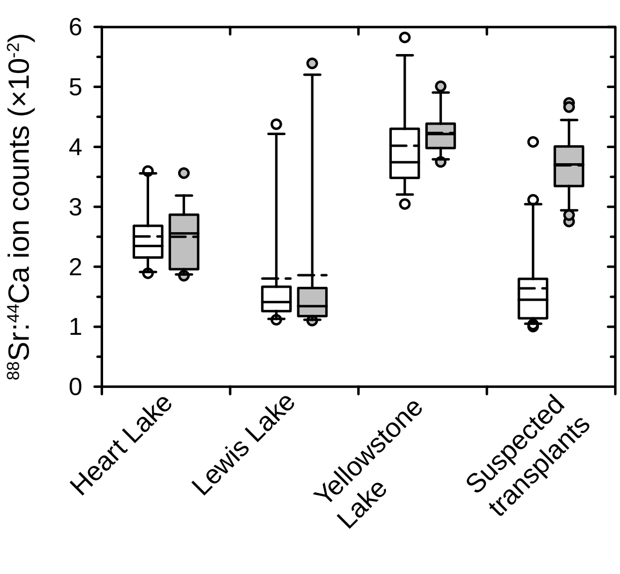

Figure 4. Comparison of Sr:Ca ratios of known-origin lake trout otoliths and otoliths of suspected transplants. Two zones were analyzed for each otolith: early-growth (open boxes) and edge zones (shaded boxes) for both known-origin lake trout from Heart, Lewis, and Yellowstone lakes ($n = 10$ per lake) and suspected transplants gillnetted from Yellowstone Lake ($n = 20$). Boxes show the mean Sr:Ca ratios (broken line), median (central solid line), first and third quartiles (box edges), and individual outliers (circles) outside the 10th and 90th percentiles (whiskers).

	% classification into lake		
	Heart	Lewis	Yellowstone
Known-origin			
Heart	100	0	0
Lewis	0	90	10
Yellowstone	0	0	100
Suspected transplants			
Early growth	5	90	5
Edge	20	0	80

Note: Cross-validation results for the known-origin lake trout calibration data set (*n* = 10 fish per lake) were used to assess classification accuracy. Early-growth and edge zones of the otoliths from the group of suspected transplants captured in Yellowstone Lake (*n* = 20) were classified into one of the three lakes. The probable origin of lake trout in Yellowstone Lake was based on the early-growth-zone Sr:Ca ratios of suspected transplants.

Table 3. Classification of lake trout into probable source lakes.

and edge zones (Fig. 4). Eighty percent of the edge zones of suspected transplants were classified by the discriminant model as Yellowstone Lake, whereas 90% of the Sr:Ca ratios measured in the early-growth zone were classified as Lewis Lake (Table 3). This percentage increased to 100% if the two fish that had similar early-growth and edge zone Sr:Ca ratios were excluded from the classification analysis. Sampling along the otolith axis of a random subset (*n* = 3) of lake trout exhibiting the abrupt shift in Sr:Ca ratio revealed that Sr:Ca ratio increases occurred within a short period (Fig. 6). The increase in Sr:Ca ratios was estimated to occur in 1989 for two fish (Figs. 6a and 6b) and in 1996 for one fish (Fig. 6c) of the subset sampled. The other two fish, representing the lake trout with similar early-growth and edge zone Sr:Ca ratios, showed little variation in Sr:Ca ratios along the otolith axis (Figs. 6d and 6e). These fish were the youngest in the group of suspected transplants (ages 10 and 11).

Discussion

Our work demonstrates that otolith chemical composition can be used to identify a probable source and date of exotic species introductions. Water chemistry differed significantly among the three large lakes we studied, and these differences were directly imparted to lake trout otoliths. The low variation in Sr:Ca ratios of known-origin lake trout along the otolith axis from the early-growth to the edge zone, despite a wide range of ages, established that lake trout from each lake lived in a similar water chemistry throughout their lives. This temporal and spatial stability in otolith chemical signatures was reflected by the high discriminatory power to classify lake trout by their home lake based on unique otolith Sr:Ca ratios. These findings corroborate previous work demonstrating (i) a strong association between chemical composition of water and otolith chemistry (Bath et al. 2000; Wells et al. 2003), and (ii) that source waters, even in freshwater environments, can be identified with a moderate-to-high degree of precision based on otolith chemical composition (Thorrold et al. 1998; Wells et al. 2003). Both attributes of otoliths are important in determining stock origins, and our findings indicate that this is particularly relevant for exotic species where stock origin is frequently unknown.

Unlike known-origin lake trout, the large and rapid change in Sr:Ca ratio along the otolith axis of suspected transplants demonstrates that these fish experienced a rapid change in water chemistry. The magnitude of the change in otolith Sr:Ca ratio among suspected transplants (256% increase) mirrors that shown by anadromous fish migrating from freshwater to seawater. For example, Limburg (1995) found that otolith Sr:Ca ratios of age-0 American shad (*Alosa sapidissima*) increased by 250 to 620% during movement from freshwater to seawater. Such a large and rapid change in otolith chemistry among lake trout from older year-classes supports the hypothesis that lake trout were transplanted to Yellowstone Lake. All

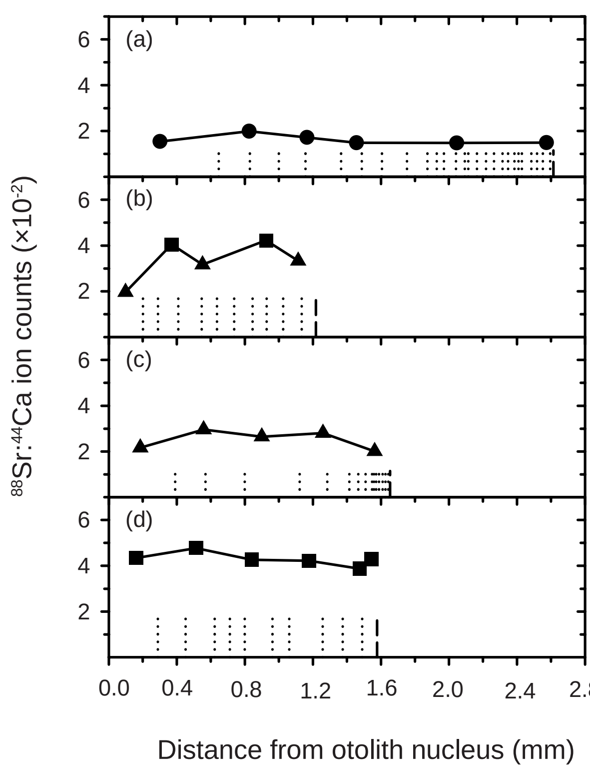

Figure 5. Patterns of Sr:Ca ratios along the otolith axes of four known-origin lake trout from (*a*) Lewis Lake (26 years, 949 mm), (*b*) Heart Lake (10 years, 481 mm), (*c*) Heart Lake (15 years, 490 mm), and (*d*) Yellowstone Lake (10 years, 767 mm). Analysis sites were classified by discriminant analysis: Lewis Lake (●), Heart Lake (▲), and Yellowstone Lake (■). The dotted lines show the location of annuli and the broken line the otolith edge.

Yellowstone Lake lake trout from younger age-classes, ≤11 years (1986 estimated year-class and later) at the time of collection in 1996–1999, had similar early-growth and edge zone Sr:Ca ratios, indicating a constant environmental history. In contrast, all lake trout from older year-classes had a marked increase in Sr:Ca ratios between the early-growth and edge zones, indicating that these fish had reared in waters of distinctly different water chemistry during their life-span. These results therefore support the assertion that initial transplanting and natural reproduction of lake trout in Yellowstone Lake likely occurred during the mid- to late l980s (Kaeding et al. 1996). Although our sample size was not large enough to pinpoint the exact number and timing of transplants, Ruzycki et al.'s (2003) estimate of 298 lake trout >10 years old in 1996 (year-class 1986 and earlier) suggests that a rather large number of individuals were transplanted. Moreover, the dating of the abrupt shifts in otolith chemistry as occurring in 1989 and 1996 suggests that multiple transfers may have occurred.

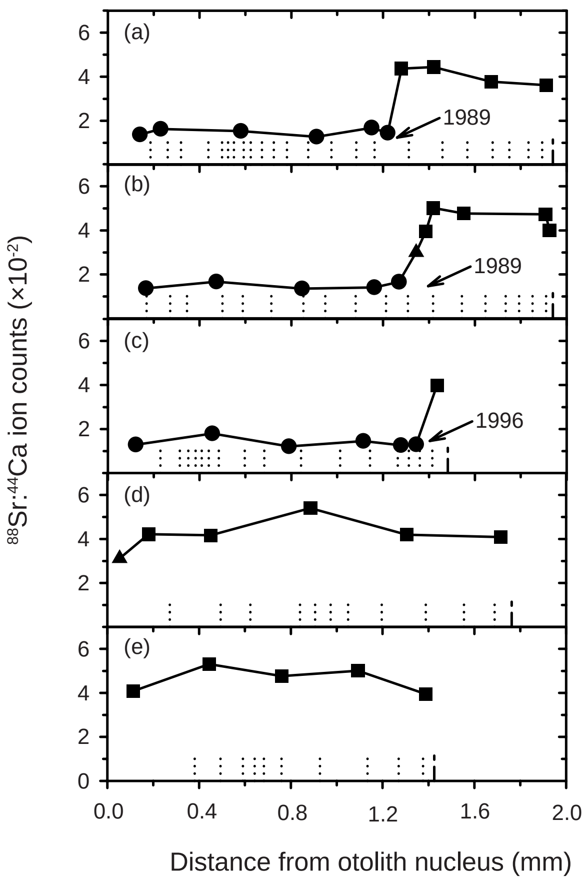

Figure 6. Patterns of Sr:Ca ratios measured along the otolith axes of five lake trout from the group of suspected transplants collected from Yellowstone Lake: (*a*) 23 years, 832 mm, (*b*) 18 years, 850 mm, (*c*) 16 years, 768 mm, (*d*) 11 years, 782 mm, and (*e*) 10 years, 765 mm. Three of the fish show a rapid increase in Sr:Ca ratios corresponding to transplant dates of 1989 (Figs. 6*a* and 6*b*) and 1996 (Fig. 6c), whereas the two youngest fish (Figs. 6*d* and 6e) show little variation in Sr:Ca ratios, suggesting that they had lived in Yellowstone Lake throughout their lives. Analysis sites were classified by discriminant analysis: Lewis Lake (●), Heart Lake (▲), and Yellowstone Lake (■). The dotted lines show the location of annuli and the broken line the otolith edge. Arrows mark the estimated year that the increase in Sr:Ca ratios occurred.

The classification of 90% of the early-growth-zone Sr:Ca ratios of the suspected transplants into Lewis Lake by discriminant analysis suggests that of the two lakes considered to be the most probable source lakes within Yellowstone National Park, Lewis Lake is the likely source of transplanted lake trout. Unlike Heart Lake, Lewis Lake is accessible by road, which may have facilitated the unauthorized transfer of lake trout into Yellowstone Lake.

Change in Sr:Ca ratios with age or maturation (ontogenetic or physiologic effects) is a possible alternative explanation to the transplant hypothesis. However, an age- or maturation-induced Sr:Ca ratio increase was unlikely given that lower Sr:Ca ratios would be expected in the early-growth zone among all lake trout. Further, the pattern of increased Sr:Ca ratio was only observed in suspected transplants and not in the early-growth zone or among younger age groups of other lake trout sampled from Yellowstone Lake or from any of the lake trout sampled from Heart and Lewis lakes, which varied greatly in age.

Another possible explanation for the increase in Sr:Ca ratios in the otoliths of the suspected transplant group of lake trout is temporal or spatial variation in lake water Sr:Ca ratios of Yellowstone Lake. The large increase in otolith Sr:Ca ratios in 1989 observed in some lake trout from the suspected transplant group coincided with the intense wildfires in Yellowstone National Park in 1988 that altered dissolved ion concentrations of some streams in Yellowstone National Park (Minshall et al. 1997). Although Sr was not measured, other dissolved ions in the lake showed only minor changes in concentration, and Lathrop (1994) and Theriot et al. (1997) found no evidence for significant changes in water chemistry resulting from the 1988 wildfires; therefore, temporal changes in water chemistry seem unlikely to account for the 256% increase in otolith Sr:Ca ratios for Yellowstone Lake lake trout. Yellowstone Lake has many hydrothermal vents that may be a source of local enrichment of Sr and Ca (Balistrieri et al. In press). However, we found that lake water Sr:Ca ratios varied little (<3.5%) with depth or among lake subbasins; therefore, it is also unlikely that the increase in otolith Sr:Ca ratios was a result of fish inhabiting different areas within Yellowstone Lake with different Sr:Ca ratios.

There are two important caveats when assessing the implications of this study. First, the long life-span of lake trout facilitated a long-term retrospective analysis of their environmental history. Detection of unique chemical marks would have been more difficult in species with higher turnover rates or with extensive migrations between waters of differing chemical signatures. Second, although Lewis Lake was identified as the source lake for transplanted lake trout with a high degree of probability, not all ambient waters have unique Sr:Ca signatures (Gillanders et al. 2001; Wells et al. 2003; Munro 2004). Therefore, we cannot eliminate the possibility that lake trout were transplanted from some other lake with Sr:Ca ratios similar to those of Lewis Lake. In future studies, use of isotopes or other elements in addition to Sr could enhance the accuracy of identifying source waters (Kennedy et al. 2002; Wells et al. 2003).

There is growing appreciation for just how extensive introductions of exotic species have been, and the formidable problem they present for aquatic ecosystem management (Hall and Mills 2000; Rahel 2000; Kolar and Lodge 2002). For instance, in Montana alone, 375 cases of unauthorized introductions of fishes of 45 different species have been documented in 224 different waters (Vashro 1995). Detection of an exotic species often poses questions about when the invasion occurred and the geographic origin of the exotic, but few tools have been available to answer them (McMahon and Bennett 1996; Hebert and Cristescu 2002; Waters et al. 2002). Better knowledge of where exotic species originated and the relative risks they pose is essential for the design of educational and regulatory programs to stem the tide of future unauthorized introductions (McMahon and Bennett 1996; Kolar and Lodge 2002). Genetic markers have recently been shown to be a useful forensic tool for studying invasion biology (Cristescu et al. 2001; Hebert and Cristescu 2002; Waters et al. 2002). Our study demonstrates how chemical analysis of otoliths can provide a novel forensic tool to estimate geographic origin and timing of exotic fish introductions. Because both chemical and genetic analysis techniques have distinct advantages and limitations (Cristescu et al. 2001; Thorrold et al. 2001; this study), a combination of both tools could provide important insights into the study of invasion biology.

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Acknowledgements

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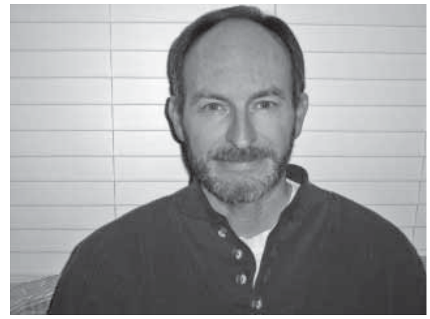

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Construction of the Lake fish hatchery building in 1928.

PHOTO COURTESY NPS, YELLOWSTONE NATIONAL PARK, C.A. LORD, YELL 20798-1

Of Fairies' Wings and Fish

Fishery Operations and the Lake Fish Hatchery in Yellowstone

Lee H. Whittlesey

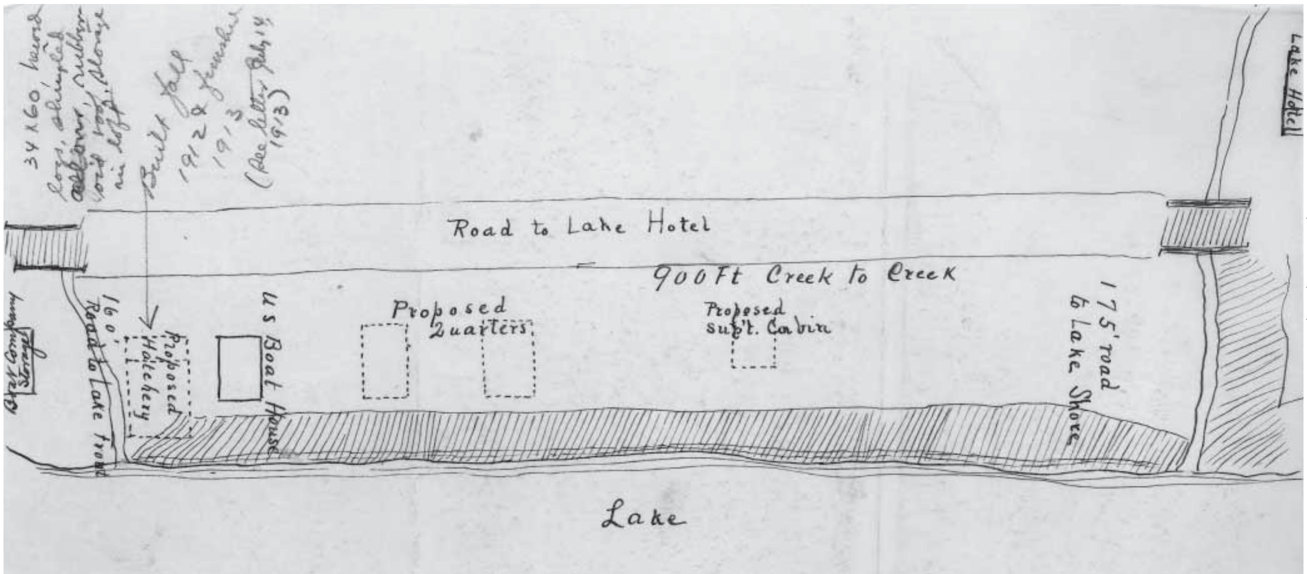
"…for I have been unable to live in the beauty of Yellowstone without feeling the touch of fairies' wings as they flitted from flower to flower."

—Howard Back, The Waters of Yellowstone With Rod and Fly, *1938*

WITH THOSE POETIC WORDS, angler/writer Howard Back gave us the background for his love of fish and fishing in Yellowstone National Park. The park was a place where his imagination could combine with his love of angling to imbue him with the desire to share the magic of fishing and the beauty of park lakes and streams with readers. In his 1938 book, Mr. Back wrote of park beauty and fishing tips while also discussing some history of the Yellowstone fishery.

This fishery history begins in 1870, with the explorations and writings of the Washburn–Langford–Doane expedition. Historian Paul Schullery has chronicled it in his article, "Their Numbers Are Perfectly Fabulous."[1] While members of the Washburn party were not the first to fish in Yellowstone—archeological evidence indicates that American Indians fished there long ago, and that later fur trappers or prospectors may also have done so—party members of 1870 were the first to write about it.

Following the Washburn party, fishing in Yellowstone was a continuous activity. In the 1870s, Hayden survey members wrote quite a lot about fish and fishing, and both the Earl of Dunraven in 1874 and General William Strong in 1875 experienced angling in the park. A glance at issues of *Forest and Stream* magazine from 1874 to 1890



W.T. THOMPSON TO LLOYD BRETT, AUGUST 5, 1912, YNPA

Hand-drawn map showing locations of existing and proposed buildings, 1912.

reveals numerous pieces written about fish and fishing in the new park.[2]

Early officials were inclined to try to "improve" the park's fishery. The earliest fish stocking in Yellowstone National Park occurred in 1881, when Superintendent P. W. Norris moved some native trout from Trout Lake to nearby ponds, probably the small lakes known today as Buck Lake and Shrimp Lake. Norris also talked about introducing non-native carp into park waters, dreaming of making modifications to the fishery even before he had the personnel or money to do so.[3] Investigators from the U.S. Fish Commission—David Starr Jordan, Barton W. Evermann, and S. A. Forbes—began the stocking of park lakes and streams with exotic trout, and they all produced government reports (1889–1893) about the park's fishery.[4]

After 1900, park officials under the U.S. Army began to develop the Yellowstone fishery program, deciding to officially tinker with the fish and their habitats. Although manipulating fish populations of park lakes and streams began in earnest in 1889, when the U.S. Fish Commission decided to stock various fishless waters, no shipping of Yellowstone fish eggs to locations outside the park began until 1901.[5] Fishery management operations at Yellowstone Lake began at West Thumb shortly after 1900, and from 1901 to 1953, Yellowstone National Park was the largest single source of wild cutthroat trout eggs in the United States.[6] An 1898 suggestion by Captain J. B. Erwin that a fish hatchery be established in the park had, according to a person who worked at the 1920s hatchery, "far reaching effects [that] would forever alter the natural state of the Park."[7]

Support for fish hatcheries permeated the thinking of just about all nature managers in those days. "It was believed," declared fish historians John Varley and Paul Schullery, "that nature often needed human 'help' to make fisheries better."[8] Or as another fishery expert noted, the purpose of fish hatcheries in Yellowstone was "to assist nature with a job she had been doing adequately for thousands of years."[9] Managers believed that fish should be heavily stocked in all available waters in order to have the best possible sportfishing ("the best possible campfire meal," as Varley put it), and they believed that fish eggs should be harvested and shared in great numbers with other locations around the nation and the world. They also believed that the supply of trout might someday dwindle due to fishing pressure. "The hatcheries are maintained," explained Hugh Smith and William Kendall in 1921, "for the purpose of keeping up the supply of [cutthroat] trout."[10] Finally, managers believed that many fish eggs were lost naturally and that such "unfortunate" events could and should be prevented.[11]

In accordance with these theories, the U.S. Bureau of Fisheries (part of the Department of Commerce), made an initial egg taking on May 15, 1901, at West Thumb.[12] Mr. D. C. Booth, superintendent of the national fish hatchery at Spearfish, South Dakota, conducted this operation, assisted by four U.S. Army soldiers.[13] To support this activity, workmen erected a hatchery building on Little Thumb Creek in 1903, and enlarged it in 1906 and 1912.[14]

Park fishery operations were limited to the West Thumb area until 1909, when a small cabin and hatching troughs were erected at Clear Creek and egg collecting was performed at Cub Creek.[15] Fishery workers eventually set up fish traps at numerous streams and lakes and established other small hatcheries at Soda Butte, Trout Lake, and Grebe Lake.[16]

But what was to become the center of the park's fish culture operation for the next 40 years was planned for a location at Yellowstone Lake. In 1912, W. T. Thompson, superintendent of Yellowstone's fishery operations, asked the Commissioner of Fisheries for permission to erect four buildings on the shore of Yellowstone Lake one-half mile west of the Lake Hotel. A log house was all that was "here now," opined Thompson, along with "a few open air [fish] troughs subject to depredation by the bears." He regretted that "the men cook and eat in the open." Thompson asked for a 30' × 60' hatchery, a central storehouse, a mess building with quarters in it, and a cabin/office for himself.[17] He needed these facilities, explained one of Thompson's supervisors, "in order to facilitate fish cultural operations in the Yellowstone Park and extend its present field operations."[18]

A month later, Thompson was pleased to learn that the Department of the Interior had authorized construction of his requested buildings. The buildings "will all be located on the narrow strip of lake front," he noted definitively, "betwixt the very small creek into which the Lake Hotel sewers drain [Hotel Creek] and the next small creek S.W. [Hatchery Creek] on the banks of which our boat house and temporary hatchery now stand." Thompson concluded, "the hatchery building will be located between the present boat house and the creek." He included a hand-drawn map for the files that showed the locations of the current and proposed buildings.[19]

Workmen commenced construction on these buildings and completed them in 1913—a hatchery (34' × 60'), a mess hall, a bunkhouse, and a shop. Laborers installed a small dam and pipeline to ensure an adequate water supply to the complex, and erected new fish troughs. The complex soon boasted 26 double and 2 single troughs, each with eight compartments of about 14' × 18' each. Each trough could hold 500,000 fish eggs.[20] In 1914, workmen added a bungalow and a four-horse barn at the complex.[21] "The workings of the plant have become a matter of interest to so many tourists," proclaimed the park superintendent that year, "as to require at times the services of one of the attendants constantly in showing them around."[22]

Thompson's buildings apparently were not built well, for park officials were describing the hatchery building at Lake as old and decrepit by the late 1920s. Yellowstone was now under the management of the recently established National Park Service (NPS), and park officials took steps in 1928 to build another hatchery. Workmen erected most of the new building that summer and added interior details in 1929, so that the main building was ready for occupancy in 1930. Also erected that summer were a new bunkhouse and mess house. These buildings were of frame and log construction of the type then being approved by the Landscape Division of the NPS.[23]

The new hatchery building was 42' × 108' and contained an office for the hatchery superintendent, a main room of 42' × 68' for hatching and packing eggs, and an aquarium room "with seven large tanks" containing native park fish so that the public could view them at a lower level through glass windows.[24] A balcony, accessible via a stairway at the front of the building, allowed visitors to look down on workers at the hatching troughs without permitting entrance to the room. Workmen soon "wrecked" the old hatchery building, which was described as "very unsightly and in a very poor state of repair." "All in all," declared a report on the project, "the [new] hatchery building is one of the most modern in the western part of the country, with a capacity of about 25 million or more eggs per year."[25] Superintendent Roger Toll's monthly report for July 1929 was even more emphatic, stating that "37 men are working [on the new building], and by the end of the season, the Lake Fish Hatchery will then be the finest and most up-to-date hatchery in the United States."[26]

The burgeoning hatchery complex also included three new rectangular rearing ponds about 75 yards west of the

The purpose of fish hatcheries in Yellowstone was "to assist nature with a job she had been doing adequately for thousands of years."

NPS, YELLOWSTONE NATIONAL PARK, YELL 30040

Old Lake fish hatchery. 1928.

NPS, YELLOWSTONE NATIONAL PARK, DAUM, YELL 30043

New Lake fish hatchery. 1928.

new building on nearby Hatchery Creek. The ponds were 112', 108', and 98' long and each 5' wide. Workers stocked the ponds with small fry (young fish), which were held there and fed before being planted in park waters. "This improvement," explained Toll, "is a decided advantage in the propagation of fish at the Yellowstone Lake plant, as previously it was necessary to plant fish direct from the hatchery which resulted in serious loss."[27]

East of the new building, workmen built an exhibit pond, 65' long × 5' wide, where mature fish could be kept for viewing.[28] A new bunkhouse and messhouse were located nearby. The bunkhouse, completed in 1930, was 86' × 27', with a recreation room, a bathroom, and 15 individual rooms for employees. The messhouse, constructed in 1929 and 1930, was 56' × 24', with a large dining room, kitchen, pantry, and living quarters for the cook. A small woodshed built at the rear of the mess house was 15' × 20' in size.

A donation of $15,000 by William E. Corey of Pittsburgh, Pennsylvania, in October 1926 made this hatchery construction possible. The Bureau of Fisheries matched these funds, so that the final result was to "enable the Bureau to properly handle fish propagation and planting in Yellowstone National Park."[29] After the buildings had been extant for approximately 10 years, NPS officials ordered the Bureau of Fisheries regional director to paint all new buildings at Lake a gray-green color, and to include the existing fish hatchery buildings in that order.[30] During 1928–1930, the Bureau of Fisheries also reconditioned and extended its nearby boat dock, from which three 33-foot launches and several smaller boats operated during summer months.[31]

Little is known about the history of the boathouses at Lake that supported the hatchery buildings. There was a boathouse of some sort at the Lake hatchery in 1912, but a more substantial one was apparently built in 1930—probably one of the two that are still there today. Assistant Superintendent M. S. Daum stated in 1929 that two buildings remained to be erected at the new hatchery, including a new boathouse to be built on the "end of the dock on the site of the old fish hatchery."[32] This boathouse appeared in the park's 1941 master plan, but nothing else about it has been found.

A note in the history card file of the Yellowstone Research Library, compiled in the 1920s by Superintendent Horace Albright, states that an old boathouse was torn down and replaced at Lake in 1926, but it is not known which boathouse this was.[33] It may have been the second of the two boathouses that are still there. A photo taken about 1928 that appears in Frank H. Tainter's and Bill Tanner's "Fish Culture in Yellowstone National Park The Early Years: 1901–1930," shows a piece of the boathouse next to the "old" Lake fish hatchery. The caption reads, "to the left is the boat house which was still in existence in 1986."[34]

The completion of the Lake hatchery and boathouse complex gave the park fishery operation the shot in the arm that it needed in order to function efficiently for the next 25 years. Activities continued to include the planting of both native and non-native fish in park streams as well as the collection and export of large numbers of trout eggs. Howard Back described the process in 1938:

> *The hatchery at Lake Junction on Yellowstone Lake confines itself to the stripping of cutthroat trout, and large demands for these fish are satisfied from this origin. The Park, in return for supplying the eyed ova, has a first call on the hatched fish to the extent of its own requirements. The Lake Junction hatchery, which is open to the public, and which you [the visitor] certainly ought to visit, is fed from traps on eleven different streams which run into the lake. In 1937 an all-time record—in fact a world record—for one hatchery was set. No less than forty million eyed ova were handled and passed out in good condition to the feeding hatcheries, almost one hundred per cent arriving in a perfect state at their destination, so skilled is the work of dispatch.… I confess that my mind boggles at the thought of forty million trout.*[35]

During the period 1930–1957, the National Park Service gradually changed some of the earlier policies that manipulated natural conditions in the park. It thus made substantial strides in fishery science and ecosystem management toward the "natural regulation" philosophy that is in place today. For example, in 1936 the NPS decreed that no exotic fish were to be planted in waters that contained only native fish, wider distribution of exotic fishes was to be prohibited, artificial improvements on lakes and streams were to be avoided, exotic fish food was to be prohibited, fishless waters might be best left fishless, and propagation of native fish was to be encouraged to the greatest possible extent.[36]

In 1949, the NPS sought the advice of a team of fishery research biologists from the U.S. Fish and Wildlife Service on how egg-taking operations might be affecting the ecology of the Yellowstone Lake fishery. As early as 1953, these biologists recognized that egg-taking and restocking were not necessary to maintain the fishery. "In fact," noted Phillip Sharpe, "they found [that] the excessive removal of eggs was detrimental to reproduction." The hatchery program, it was learned, posed an actual threat to the lake's cutthroat trout population.[37]

Thus in the 1950s, NPS officials dramatically curtailed manipulative park fishery operations. The last substantial collection of eggs from Yellowstone fish occurred in 1953, and the last fish stocking for the benefit of anglers occurred in 1955. The NPS closed all park fish hatcheries in 1957, and made plans to return the entire park fishery to its original, self-sustaining basis. In 1961, the Interior Department's Bureau of Sport Fisheries and Wildlife replaced the advisory fishery research biologists it had stationed at Yellowstone with workers who began long-term research on all park waters to learn about the fishery and develop monitoring to aid management. Fisheries management was shifting toward general research and protection of native species and away from artificially "aiding" the fishery. Worries about angler pressure on waters and the idea of returning live fish to the water (catch-and-release fishing) were also becoming primary considerations.[38]

"[T]hey found [that] excessive removal of eggs was detrimental to reproduction." The hatchery program, it was learned, posed an actual threat to the lake's cutthroat trout population.

Where does the Lake hatchery stand in the history of the Yellowstone fishery and in the history of fish hatcheries across this nation, and how does the history of the Yellowstone fishery play into the history of other fisheries around the United States? The answers are straightforward, according to one fish historian. In the history of the Yellowstone fishery, the Lake hatchery stands tall. Its building was central to Yellowstone fishery operations for 25 years (1930–1955), and today it is the only physical remnant of Yellowstone's long history of active fishery manipulation. In regard to the country at large, it is important—if painful—to note that the Lake fish hatchery, just like other hatcheries that produced fish destined to become harmful exotics when they arrived at their destinations, "was the source of many, many harmful infestations of Yellowstone cutthroat trout beyond the park waters."[39] For instance, Yellowstone cutthroats from the Lake hatchery were often introduced into waters populated by westslope cutthroats vulnerable to such non-native competition. The hatchery may also have been detrimental to the park's own Yellowstone cutthroat trout population. Though they were native to the park, hatchery-reared cutthroat were not necessarily returned to the same park waters from which they had originated. In any aquatic environment, one potential result of such actions can be the loss of genetic information in fish subpopulations historically associated with a natal stream. For example, the 60 or so active spawning streams that feed into Yellowstone Lake are subject to local, environmental variations that might have affected their natal cutthroat subpopulations in the long term. Had the hatchery operations not scrambled those natural distinctions, the subpopulations might have been better suited to deal with stressors such as invasive species and drought.[40]

None of that makes the old fish hatchery building at Lake any less historically important, but it has much deteriorated. While the surrounding buildings in the complex have continued to be used as park housing, for many years the main hatchery building has been used only for storage. The building commemorates a time in the national parks when natural processes were subordinated to the will of humans, and the story of what went on there in the history of Yellowstone fishery operations is fascinating indeed. For although buildings may not stimulate our imaginations in the way that fish do, they are part of the cultural resources that supported the park's natural resources—the "freshwater wilderness" celebrated by John Varley and Paul Schullery that is an integral part of the larger Yellowstone wonderland. It was this freshwater wilderness that so long ago caused fisherman Howard Back to imagine gossamer-garbed fairies "flitting from flower to flower" in accompaniment to the dance of his fly rod on Yellowstone waters.

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Endnotes

[1] Paul Schullery, "Their Numbers Are Perfectly Fabulous: Sport, Science, and Subsistence in Yellowstone Fishing, 1870," *Annals of Wyoming* 76 (Spring 2004):6–18. Whether he likes it or not, Schullery is today considered by many to be the foremost expert on the history of fishing in America.

[2] The 1871 Hayden survey is well treated and cited in Marlene Deahl Merrill, *Yellowstone and the Great West* (Lincoln: University of Nebraska Press, 1999), who also cites Hayden's 1872 and 1878 reports. Dunraven's fishing is in Windham T. Wyndham-Quin, Fourth Earl of Dunraven, *The Great Divide: Travels in the Upper Yellowstone in the Summer of 1874* (London: Chatto and Windus, 1876), while Strong's is in William A. Strong *in* Richard A. Bartlett, ed., *A Trip to the Yellowstone National Park in July, August, and September, 1875* (Norman: University of Oklahoma Press, 1968). Sarah Broadbent's index to *Forest and Stream* magazine is housed at the Yellowstone National Park Research Library (hereafter YRL) and her master's thesis on the subject is at both Montana State University and Yellowstone. *See also* John D. Varley and Paul Schullery, *Freshwater Wilderness: Yellowstone Fishes and Their World* (Yellowstone National Park: Yellowstone Library and Museum Association (hereafter YLMA), 1983); Paul Schullery, "Edward in Wonderland: Yellowstone Recollections of an Angling Great," *American Fly Fisher* 29 (Winter 2003):2–12; John D. Varley, "A History of Fish Stocking Activities in Yellowstone National Park Between 1881 and 1980," U.S. Fish and Wildlife Service, Information Paper No. 35, January 1, 1981, YRL; John Byorth, "Trout Shangri-La: Remaking the Fishing in Yellowstone National Park," *Montana the Magazine of Western History* 52 (Summer 2002):38–47; and Mary Ann Franke, "A Grand Experiment: One Hundred Years of Fisheries Management in Yellowstone," two parts, *Yellowstone Science* 4(4) (Fall 1996):2–7; 5(1) (Winter 1997):8–13.

[3] Norris's mention of his trout stocking activities as well as his interest in stocking carp in some park waters are in P. W. Norris, *Fifth Annual Report of the Superintendent of the Yellowstone National Park,* December 1, 1881, 30–32.

[4] The Evermann and Jordan studies are cited in John D. Varley and Paul Schullery, *Yellowstone Fishes: Ecology, History, and Angling in the Park* (Mechanicsburg, Pa.: Stackpole Books, 1998), while the Forbes study is S. A. Forbes, "A Preliminary Report on the Aquatic Invertebrate Fauna of the Yellowstone National Park, Wyoming." Pages 207–258 *in* U.S. Fish Commission, Bulletin 11, Vol. XI for 1891 (Washington, D.C.: Government Printing Office, 1893).

[5] The stocking of park lakes and stream with exotic fish—brown, brook, lake, and rainbow trout—had huge effects on the ecosystem, as these fish suddenly inhabited many miles of formerly fishless streams. They also competed with the natives for food and spawning space and in some cases interbred with natives to dilute or destroy native genotypes.

[6] B. B. Arnold, "A Ninety-Seven Year History of Fishery Activities in Yellowstone National Park, Wyoming," 10, unpublished manuscript, U.S. Department of Interior, Bureau of Sport Fisheries and Wildlife, Division of Fishery Services, March 19, 1967, YRL. James R. Simon stated in 1939 that from Yellowstone Lake and Yellowstone River "more clean [cutthroat trout] eggs are now taken than from all other waters in the United States combined." Simon, *Yellowstone Fishes* (Yellowstone National Park: YLMA, 1939), 8. Currently missing from the park library and archives—and thus from this paper—are the Fishery Annual Reports, 1901–1953, which, if they could be found, would explain much history to us.

[7] Frank H. Tainter and Bill Tanner, "Fish Culture in Yellowstone National Park, the Early Years: 1901–1930," 4, unpublished manuscript, 1987, YRL. Erwin's original suggestion for a hatchery is in James B. Erwin, *Report of the Acting Superintendent of the Yellowstone National Park to the Secretary of the Interior, 1898* (Washington, DC: GPO, 1898), 12.

[8] Varley and Schullery, *Yellowstone Fishes*, 94.

[9] F. Phillip Sharpe, *Yellowstone Fish and Fishing* (Yellowstone National Park: YMLA, 1970), 10.

[10] Hugh M. Smith and William C. Kendall, *Fishes of the Yellowstone National Park*, Bureau of Fisheries Document No. 904 and Appendix III to the Report of the U.S. Commissioner of Fisheries for 1921 (Washington, DC: GPO, 1921), 6. There is also a 1915 edition of this book that was less complete.

[11] Smith and Kendall (*Fishes,* 6) gave the reasoning behind this theory in the following paragraph: "The questions naturally arise, why not let the trout run up the creeks and spawn naturally? Why not permit the eggs to hatch in the manner intended by nature and let the young remain for awhile in the water where they were born and then run back to the lake at the proper time? These questions, which will, no doubt, be asked by many thoughtful park visitors, afford an opportunity to indicate one way in which it is possible to *improve on nature* and to point out why in the Yellowstone National Park, as elsewhere, *it is desirable or necessary for the fish-culturist to go to nature's assistance*" (emphasis added).

[12] Arnold ("Ninety-Seven Year History," 10) refers to this site as "West Thumb Creek," possibly present-day Big Thumb Creek, but it is more likely that the stream was present Little Thumb Creek where officials built the hatchery a few years later. Howard Back explained the egg-taking process in his 1938 book: "fish are trapped as they run up-stream and stripped of a large part of their spawn, which is then hatched out.… This hatching is done in two stages. In the local hatchery the eggs are ripened until they reached the stage known as 'eyed ova,' which means that through the transparent skin of the egg you can perceive the black spot of the embryo fish's developed eye. At this stage they are dispatched to 'feeding hatcheries,' where they are brought to full development. They are then and from there redistributed as fry, under the direction of the Bureau of Fisheries, to the points where they are most needed." Back, *The Waters of Yellowstone With Rod and Fly* (New York: Lyons Press, 2000), 24.

[13] Arnold, "Ninety-Seven Year History," 10. The operation is mentioned in John Pitcher, *Report of the Acting Superintendent of the Yellowstone National Park to the Secretary of the Interior, 1901* (Washington: GPO, 1901), 5. Booth removed an estimated one million fish eggs from Yellowstone Lake this first year. *See also* R. J. Fromm, "An Open History of Fish and Fish Planting in Yellowstone National

Park," unpublished report, 1940, YRL vertical files.

[14] Archive Document 6887, 1906, Yellowstone National Park Archives (hereafter YNPA), says the fish hatchery building erected at West Thumb in 1903 by the Department of Commerce was a frame structure with a main portion of 20' × 28' and rear (hatchery) portion of 22' × 36', located one and one-half miles north of the West Thumb soldier station. A map drawn by hand onto the text of this document shows the new hatchery on "Fisheries Creek," apparently present Little Thumb Creek. Also built was a barn 22' × 28' and an office/storage building 20' × 30'. Permission to construct these buildings is in documents 6888, 6889, 6890, and 7323, all 1906. Thus it appears that the hatchery was built in 1903 and additional buildings were constructed in 1906. Document 6886 is a 1906 map that shows the site, which appears to be a bit farther north than the one and one-half miles figure given in document 6887. The 1906 map shows the buildings on what appears to be present Little Thumb Creek. Document 5924 describes work done on the West Thumb hatchery in 1906.

[15] Arnold, "Ninety-Seven Year History," 11. Fromm ("An Open History," 14) says that D. C. Booth reported in 1909 that the West Thumb station was the "greatest collecting center for [cutthroat trout] in the United States."

[16] Smith and Kendall (*Fishes*, 5–6, 10) stated that "in 1921, a permanent hatchery was erected on Soda Butte Creek, which had been the site of a field hatchery for a number of years." That same year, officials established a "small hatchery" at Fish Lake, now called Trout Lake.

[17] W. T. Thompson to Commissioner of Fisheries, June 25, 1912, *in* file 50, item 45 (letter box 23), YNPA.

[18] Benjamin S. Cable to Secretary of Interior, July 10, 1912, *in* file 50, item 45 (letter box 23), YNPA. *See also* C. A. Thompson to Lloyd Brett, July 12, 1912, in same file.

[19] W. T. Thompson to Lloyd Brett, August 5, 1912, and hand-drawn map, *both in* file 50, item 45 (letter box 23), YNPA. *See also* Arnold, "Ninety-Seven Year History," 11, and Yellowstone National Park museum collection photos 6858 and 6859.

[20] Tainter and Tanner, "Fish Culture," 21, 30–31; Arnold, "Completion dates and improvement of buildings used for fish culture and management during 1901–1951," *in* "Ninety-Seven Year History," 22. The superintendent's annual report for 1913 elaborated as follows: "A hatchery building 34 by 60 feet was constructed of hewed logs, shingled over to present an attractive appearance, on the site near the outlet of Yellowstone Lake selected and approved by the department [of Interior and Commerce] last year. This building is furnished with modern equipment. The loft was finished and used during the past season as quarters for the employees and will be available for storage use after other contemplated buildings are constructed. This building furnishes room for apparatus with a capacity for eyeing 30,000,000 [fish] eggs. A small dam was built across the [Hatchery] creek about 400 feet upstream from it, and water supply for the work is drawn from this pond through a 12-inch wooden stave pipe." Lloyd Brett, *Report of the Acting Superintendent of the Yellowstone National Park to the Secretary of the Interior, 1913* (Washington: GPO, 1913), 9.

[21] Tainter and Tanner, "Fish Culture," 31.

[22] Lloyd Brett, *Report of the Acting Superintendent of the Yellowstone National Park to the Secretary of the Interior, 1914* (Washington: GPO, 1914), 13.

[23] National Park Service, "Final Construction Report on Account 777, Donation in the Amount of $15,000 for Construction in Connection with Furthering Fish Propagation at Lake Yellowstone in Yellowstone National Park. Appropriation 4 X 470 National Park Service, Donations," [1], unpublished manuscript with photographs, 1928–1930, *in* file of same name as this document, box N-40, YNPA. *See also* M. F. Daum, "Report on the Construction of the Lake and Mammoth Fish Hatchery Season of 1929," file number 164, [1929], YRL vertical files.

[24] Tainter and Tanner ("Fish Culture," 34) give these sizes as 48' × 108' and 48' × 68', respectively.

[25] "Final Construction Report on Account 777," [1]–2. Inconsistently, the 1929 annual report of the Bureau of Fisheries gave the inside measurement of the building as 38' × 108' 6". C. F. Culler, "Annual Report Fiscal Year 1929 and Season of 1929 Yellowstone Park Station," 20, unpublished Bureau of Fisheries report in box N-41, YNPA.

[26] Roger W. Toll, *Monthly Report of the Superintendent,* July 1929, 12, YRL.

[27] *Ibid*. Similar rearing ponds were built at Mammoth Hot Springs near the present old powerhouse, but their existence was short-lived. These ponds were abandoned in 1934, when they proved unsatisfactory in function. Chester Lindsley, *The Chronology of Yellowstone* (unpublished bound manuscript, YRL, no date), 306.

[28] *Ibid*.

[29] Daum, "Report on the Construction," 3; "Final Construction Report on Account 777," 4.

[30] Paul Brown to Fred Foster, January 17, 1940, *in* file "620-30 Fish Hatchery Part 2, January 1, 1940 to December 31, 1943," box D-157, YNPA.

[31] *Ibid*. Inconsistently, the 1929 annual report of the Bureau of Fisheries gave the measurement of the mess hall as 21' × 58', with dining room 20' × 21', kitchen 12' × 21', two bedrooms each 10' × 11', one storeroom 10' × 11', and bathroom 5' × 6'. Inconsistently, this same report gave the measurement of the "dormitory" as 24' × 83', containing a recreation room 15' × 24', sixteen individual rooms of 8' × 10', with a four-foot hall running through the center of the building. C. F. Culler, "Annual Report Fiscal Year 1929 and Season of 1929 Yellowstone Park Station," 20, unpublished Bureau of Fisheries report in box N-41, YNPA.

[32] Daum, "Report on the Construction," 3. For mention of the 1912 "U.S. Boat House," see hand-drawn map, August 17, 1912, *in* file 50, item 45 (letter box 23), YNPA.

[33] History Card File, "Lake—Boathouse," YRL. These white typed cards with orange separators are marked "History Cards" and are located in the wooden file cabinet next to the librarians' workroom, Yellowstone Heritage and Research Center, Gardiner, Montana.

[34] Tainter and Tanner, "Fish Culture," 40.

[35] Back, *Waters of Yellowstone*, 24–25.

[36] Fromm, "An Open History," 28.

[37] Sharpe, *Yellowstone Fish and Fishing*, 11–12; Mary Ann Franke, "A Grand Experiment (Part II)," 8. Adds Franke, "Although some fry were returned to the lake, the eggs were scrambled, mixing together distinctive genotypes. In addition, the reduced escape of spawners had combined with fishing pressure to cause the virtual collapse of spawning migrations in some [tributary] streams." *See also* O. B. Cope, "The Yellowstone Fishery Investigations from Their Inception to the Present," unpublished paper, U.S. Fish and Wildlife Service, no date (1952), YNPA.

[38] Franke, "A Grand Experiment (Part II)," 1, 8. The Annual Project Technical Reports, produced by the U.S. Fish and Wildlife Bureau of Sport Fisheries from 1962 through at least 1992, have added thousands of pages to our knowledge of Yellowstone National Park streams, lakes, and rivers.

[39] E-mail, Paul Schullery to author, February 15, 2006.

[40] Ibid.

Conserving Yellowstone Cutthroat Trout for the Future of the GYE

Yellowstone's Aquatic Sciences Program

Todd M. Koel, Patricia E. Bigelow, Philip D. Doepke, Brian D. Ertel, and Daniel L. Mahony

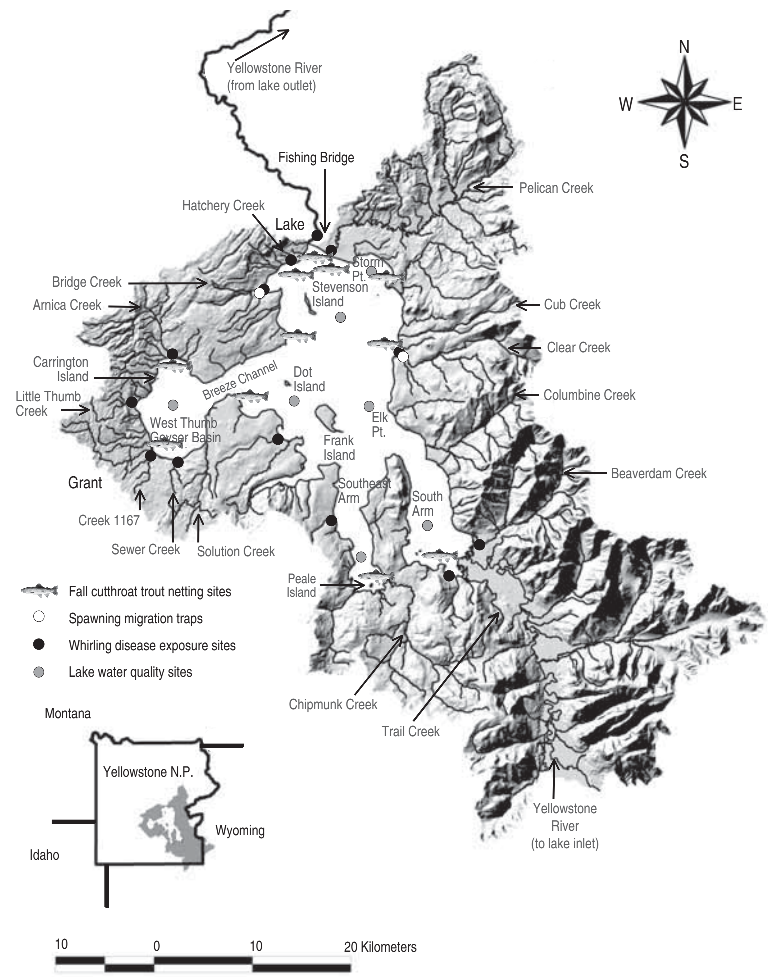


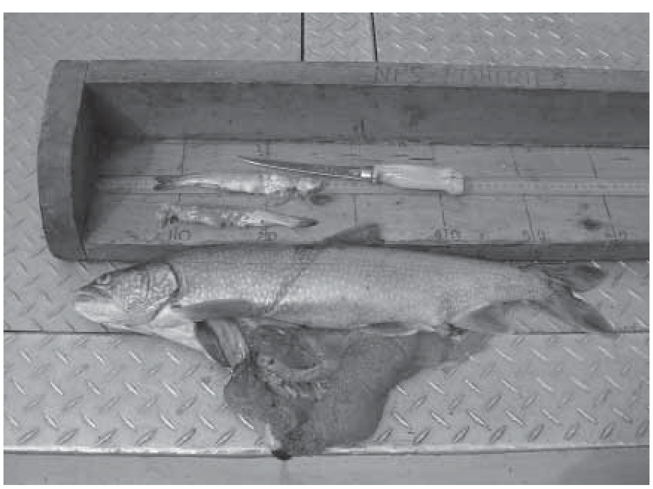
Figure 1. Yellowstone Lake and several major tributary drainages within Yellowstone National Park.

THE LARGEST inland cutthroat trout population in the world is the adfluvial Yellowstone cutthroat trout (YCT; *Oncorhynchus clarki bouvieri*) population of Yellowstone Lake. These fish have great ecological, economic, and historical significance, and they were noted by early explorers of the lake area for their beauty and abundance (Schullery and Varley 1995; Gresswell and Liss 1995; Doane 1871). This subspecies is important for maintaining the integrity of the Greater Yellowstone Ecosystem, arguably the most intact naturally functioning ecosystem remaining in the lower 48 United States. Grizzly bears (*Ursus arctos*), bald eagles (*Haleaeetus leucocephalus*), and many other avian and terrestrial species use YCT as an energy source (Swenson et al. 1986; Gunther 1995; Schullery and Varley 1995).

However, in streams throughout Yellowstone National Park and elsewhere in the natural range of Yellowstone cutthroat trout, populations have been compromised by introgression with non-native rainbow trout (*O. mykiss*) or other cutthroat trout subspecies (Behnke 2002; Koel et al. 2004). Recently, the population has also been exposed to three other potential stressors, including non-native lake trout (*Salvelinus namaycush*; Kaeding et al. 1996), the exotic parasite *Myxobolus cerebralis* (the cause of whirling disease; Koel et al., in press), and a drought that has persisted throughout the intermountain West, 1998–2004 (Cook et al. 2004).

In addition to the stream system, Yellowstone Lake and its drainages provide a great variety of environmental conditions for the native cutthroat trout (Figure 1). At 34,000 ha, Yellowstone Lake is the largest lake above 2,000 m elevation in North America. Of the 124 tributaries flowing into the lake, 68 have been used by spawning cutthroat trout (Jones et al. 1987; Gresswell et al. 1997). Geothermal features occur throughout much of Yellowstone Lake (Morgan et al. 2003). Unfortunately, the very presence of these many unique and variable environments may increase the vulnerability of this system to invasion by non-native and exotic species such as lake trout, *M. cerebralis,* and possibly others in the future.

Contemporary research points to non-native species as the greatest threat to cutthroat trout of the intermountain West (Gresswell 1995; Kruse et al. 2000; Dunham et al. 2004). Prior to Euro-American manipulation, Yellowstone Lake cutthroat trout existed for approximately 10,000 years (since glacial recession) in sympatry with only one other fish species, the longnose dace (*Rhinichthys cataractae*; Behnke 2002). Now, longnose suckers (*Catostomus catostomus*), lake chubs (*Couesius plumbeus*), redside shiners (*Richardsonius balteatus*), and lake trout are also present in the lake system due to introductions. Non-native lake trout would not be a suitable ecological substitute for cutthroat trout in the Yellowstone Lake system because they are inaccessible to most consumer species. Lake trout tend to occupy greater depths within the lake than do cutthroat trout. Lake trout remain within Yellowstone Lake at all life stages and they do not typically enter tributary streams, as do cutthroat trout. Evidence from other, similar systems, suggests that introduced lake trout will result in the decline of cutthroat trout (Cordone and Franz 1966; Dean and Varley 1974; Behnke 1992). Bioenergetics modeling suggests that an average-sized mature lake trout in Yellowstone Lake will consume 41 cutthroat trout per year (Ruzycki et al. 2003).


BARB ROWDEN

Bioenergetics research suggests that each lake trout in Yellowstone Lake has the potential to consume 41 cutthroat trout or more each year.

The cutthroat trout of Yellowstone Lake and its tributaries have remained genetically pure due to isolation provided by the lower and upper falls of the Yellowstone River, located 25 km downstream from the lake outlet near Canyon. The genetic purity of these fish makes them extremely valuable. With the recent invasions by lake trout and *M. cerebralis,* the park is placing a high priority on preservation and recovery of YCT. Following the guidance of a lake trout expert advisory panel (McIntyre 1995), the NPS has used gillnetting to determine the spatial and temporal distribution of lake trout within Yellowstone Lake. The efforts have led to a long-term lake trout removal program for the protection of YCT in this system (Mahony and Ruzycki 1997; Bigelow et al. 2003). In addition, there are many other activities that the park conducts for the conservation of native YCT, including long-term monitoring, research on whirling disease, and environmental planning that will lead to the restoration of stream populations in the northern range. This article will describe trends in YCT abundance and size, examine the impacts of lake trout on bears and anglers, and describe results of efforts to suppress lake trout population growth within Yellowstone Lake.

Methods

Yellowstone National Park's Fisheries and Aquatic Sciences program employs a multi-faceted approach to YCT monitoring and conservation, consisting of fish trapping, netting, visual assessment, voluntary angler reporting, aggressive lake trout removal, and whirling disease research. A brief description of each of those aspects follows.

Cutthroat trout spawning migration traps. The NPS has monitored the Yellowstone cutthroat trout spawning population by counting upstream-migrating adults at Clear Creek and Bridge Creek since 1945 and 1999, respectively. From May to July each year, YCT are counted at permanent weirs as they move upstream from Yellowstone Lake to spawn. Until 1998, all fish were trapped and manually enumerated. Since then, electronic counters have been used.

Cutthroat trout fall netting assessment. Within Yellowstone Lake, cutthroat trout population abundance and length structure have been assessed by netting conducted during September of each year since 1969. Multi-mesh-size (experimental) gillnets (38.0 m length, 7.6 m graduated mesh panels of 19, 25, 32, 38, and 51 mm) are placed in sets of five nets perpendicular to the shoreline overnight, in shallow water (0–5 m depth), at 11 sites throughout Yellowstone Lake (Jones et al. 1977).

Cutthroat trout spawning visual surveys. Visual surveys for cutthroat trout and bear activity have been conducted annually since 1989 on 9–11 tributaries located along the western side of Yellowstone Lake between the Lake and Grant Village developed areas (Reinhart 1990; Reinhart et al. 1995). Spawning reaches were initially delineated on each tributary, and the standardized reaches are walked in an upstream direction once each week from May through July. The observed cutthroat trout are counted, and the weekly activity by black bears (*U. americanus*) and grizzly bears is estimated by noting the presence of scat, parts of consumed trout, fresh tracks, and/or bear sightings.

Angler report card information. Since 1979, angler effort and success have been assessed via a report card distributed to each angler who purchases a special use permit for fishing (Jones et al. 1980). Information on the waters fished, time spent, and species and sizes of fish caught by anglers is obtained. Annually, approximately 4,000 anglers (5% of all anglers) have voluntarily completed and returned cards to the park's fisheries program.

Lake trout removal program. Gillnetting has been used to suppress lake trout in Yellowstone Lake each year since 1994. Spatially, the gillnet locations have been concentrated in the lake's West Thumb, where lake trout densities have been found to be highest. Through the years of the program, however, both lake trout and gillnetting have expanded outward to include the lake's main basin and, to a lesser extent, its southern arms. Small-mesh (19–44 mm mesh size) gillnets are placed on the lake bottom in water typically 40–65 m deep. Gillnets are 300 m length, set in gangs of six contiguous nets (1,800 m total length each), typically for more than seven days. During the open water season (late May–late October), up to 16 km of gillnet are in place fishing for lake trout.

The mature lake trout of Yellowstone Lake begin congregating near known spawning locations in late August each year. The removal program targets these fish until early October, when spawning is typically completed. The locations targeted in the fall, including Breeze Channel, Carrington Island, Geyser Basin, and Solution Creek, are gillnetted using shallow-set (0–20 m depth), large-mesh gillnet (51–70 mm mesh size) sets of short duration (typically one day) to reduce mortality of any YCT bycatch. In 2004, boat-mounted electrofishing was also used to remove spawning lake trout and kill deposited eggs in shallow waters (<5 m depth) at night.

Whirling disease prevalence and severity. The prevalence of *M. cerebralis* within Yellowstone Lake was determined by examination of juvenile and adult YCT mortalities from the fall netting assessment and lake trout removal program, 1998–2003. Screening of these fish occurred initially by the pepsin trypsin digest (PTD) method, where the heads of fish suspected of carrying the disease were chemically broken down and the resulting material was examined for the presence of myxospores (Andree et al. 2002). Samples were also tested by the nested polymerase chain reaction (PCR) technique to confirm the presence of *M. cerebralis* DNA (Andree et al. 1998).

The prevalence and severity of *M. cerebralis* within 15 tributaries and the Yellowstone River (lake inlet and lake outlet) was determined by use of YCT sentinel fry exposures, 1998–2003 (Koel et al. in press). In each cage (1 m height, 0.5 m diameter, and constructed of 5 mm galvanized wire mesh), 60–80 cutthroat trout fry (25–50 days post-hatch) were exposed for a 10-day period, July–September. Following the exposures, fry were held in aquaria for an additional 90 days at 10–13°C to allow for parasite development prior to being sacrificed. The PCR technique (Andree et al. 1998) was used to test for the presence of *M. cerebralis*. Histological examination was conducted on fry from *M. cerebralis*-positive exposures to determine the severity of infection. Severity was ranked on a scale of 0 (no infection) to 5 (most severe infection) for each fry examined (Baldwin et al. 2000).

Trends in Cutthroat Trout Abundance

Shortly after the establishment of Yellowstone National Park as the world's first national park in 1872, the fishery was widely publicized in national and local newspapers, as well as

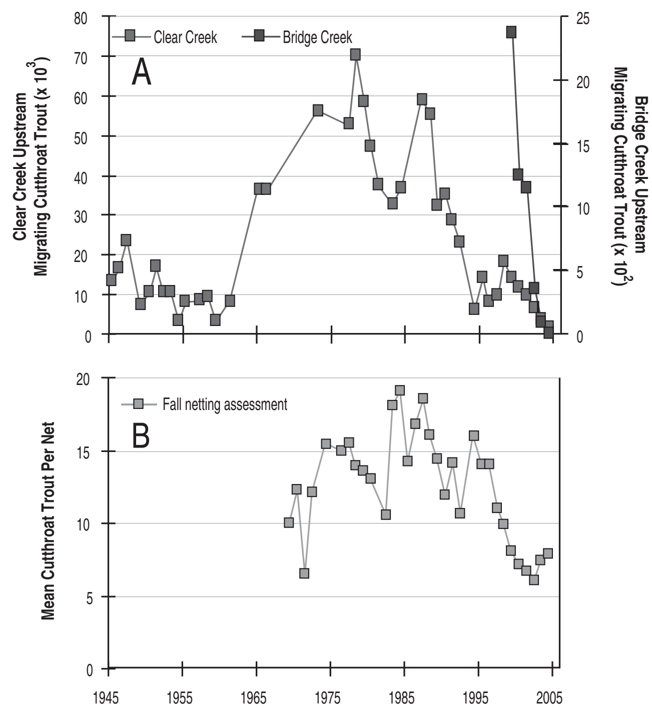


Figure 2. Number of upstream-migrating cutthroat trout counted at Clear Creek (1945–2004) and Bridge Creek (1999–2004) spawning migration traps (A), and mean number of cutthroat trout collected per net during the fall netting assessment on Yellowstone Lake, 1969–2004 (B). Note differences in scale between Clear Creek and Bridge Creek data.

in periodicals such as *Forest and Stream* and *American Angler.* Anglers began visiting the lake, its tributary streams, and the Yellowstone River in great numbers, and the U.S. Fish Commission began looking for ways to propagate and distribute the cutthroat trout of Yellowstone Lake to locations across North America (Varley and Schullery 1998). The result was the development of a federally operated fish culture facility on the north shore of Yellowstone Lake. From 1900 to 1956, more than 818 million YCT eggs were removed for use in other waters, mostly outside Yellowstone National Park (Varley 1981; Varley and Gresswell 1988). The cutthroat trout also were subject to a great amount of angling pressure, and were commercially fished to provide food for visitors until 1919, a few years after the creation of the National Park Service (NPS). Evidence of a cutthroat trout population decline during the mid-1900s resulted in the closure of the egg-taking operations and implementation of increasingly restrictive angling regulations (Varley 1983; Gresswell and Varley 1988).

Impacts of historical egg-taking operations and liberal angler harvest regulations for Yellowstone Lake cutthroat trout were observed in counts of upstream-migrating fish at Clear Creek. Only 3,161 cutthroat trout ascended Clear Creek in 1954, just two years prior to the cessation of fish culture operations on Yellowstone Lake (Varley and Schullery 1998; Figure 2). With angling restrictions, the number rebounded during the 1960s and 1970s to 70,105 YCT in 1978 (Jones et al. 1979). Although there was variation among years, the increasing trend in cutthroat trout abundance within Yellowstone Lake was also indicated by the fall netting assessment. An average of 10.0 fish per net were caught by this assessment in 1969, and 19.1 fish per net were caught in 1984.

Since the late 1980s, however, there has been a significant decline in the Yellowstone Lake cutthroat trout population. The number of upstream-migrating cutthroat trout counted at Clear Creek was 1,438 during 2004. This count was down from 3,432 in 2003, and 6,613 in 2002, and was the lowest count since 1954. The fish counting station operated on Bridge Creek, a small northwestern tributary, indicated that only a single fish migrated upstream during 2004. The number of spawning cutthroat trout in recent years has declined by more than 50% annually in Bridge Creek, and has decreased by more than 99% since counts began in 1999, when 2,363 cutthroat trout ascended the stream to spawn. The decline was also evident in the results of the fall netting assessment, where an average of 15.9 cutthroat trout per net were caught in 1994, and only 6.1 per net were caught in 2002. Prior to 2003, the reduction in catch by the fall netting program averaged 11% per year since 1994, the year lake trout were first discovered in Yellowstone Lake. During 2003–2004, however, the fall netting assessment provided some of the first indications that the cutthroat trout population may be responding positively to efforts to remove non-native lake trout. An average of 7.4 fish per net were caught in 2003, and 7.9 fish per net were caught in 2004.

Trends in Cutthroat Trout Length

Length-frequency data from the fall netting program from 1997 to 2004 indicated an increase in length (>325 mm) and reduction in numbers of adult YCT in Yellowstone Lake (Figure 3). In 2004, fewer fish between the lengths of 325 and 425 mm were collected than in earlier years. Historically, most cutthroat trout sampled in spawning tributaries such as Clear Creek were in this size range (Jones et al. 1993). Despite this, an apparent increase in numbers of juvenile cutthroat trout (100–325 mm) has been noted in recent years

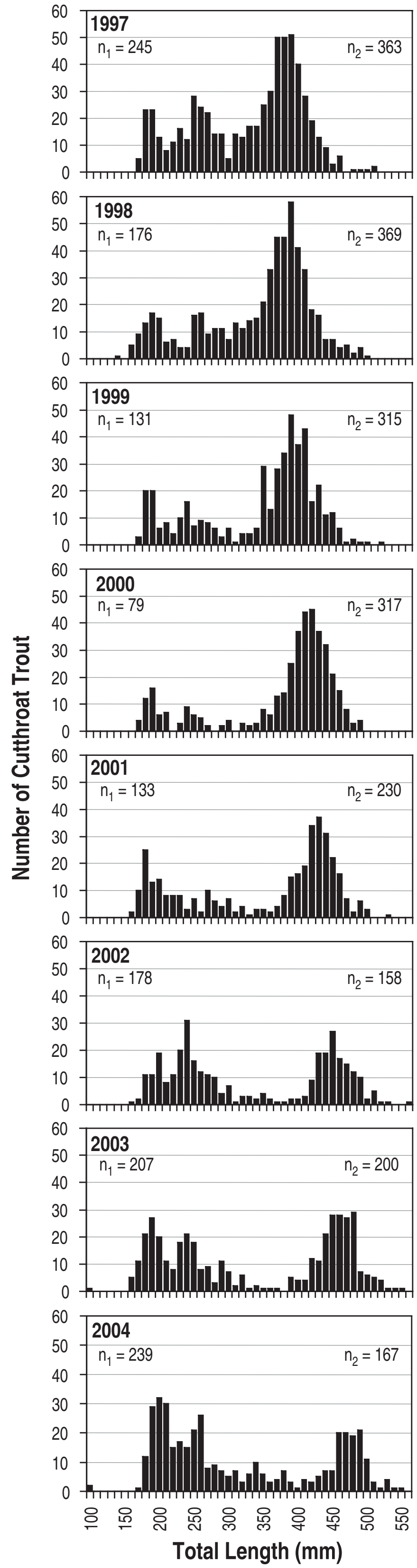


Figure 3. Length-frequency distributions of cutthroat trout collected during the fall netting assessment on Yellowstone Lake with total number of trout <325 mm (n_1) and >325 mm (n_2), 1997–2004.

(2002–2004). Many of these juveniles have been collected in the southern arms of Yellowstone Lake, which may act as refuges for YCT due to the low numbers of lake trout and low incidence of *M. cerebralis* in these areas (see below; Koel et al. 2004).

Influence on Cutthroat Trout Consumers

Bears. Upstream-migrating cutthroat trout within Yellowstone Lake tributaries historically have served as a significant source of energy for black bears and grizzly bears in the lake area (Reinhart and Mattson 1990). The average number of cutthroat trout observed each week during spawning visual surveys of 9–11 tributaries (1989–2004) has declined to the point where few trout have been observed in recent years (Figure 4). In fact, only 35 cutthroat trout were seen on spawning reaches of the nine streams surveyed over a period of eight weeks in 2004. A similar trend was observed in use of these streams by black bears and grizzly bears. It was apparent that few bears used these tributaries, as bear activity was only evident a total of eight times during 2004. By comparison, the visual surveys of spawning cutthroat trout documented activities by bears 50 times in 1991. These results suggest a trophic-level cascade (Spencer et al. 1991), possibly resulting from the introduction of non-native and exotic species into this pristine ecosystem (Reinhart et al. 2001). Bears may have been forced to use other energy sources in the region during the spring spawning period when they previously relied on cutthroat trout.

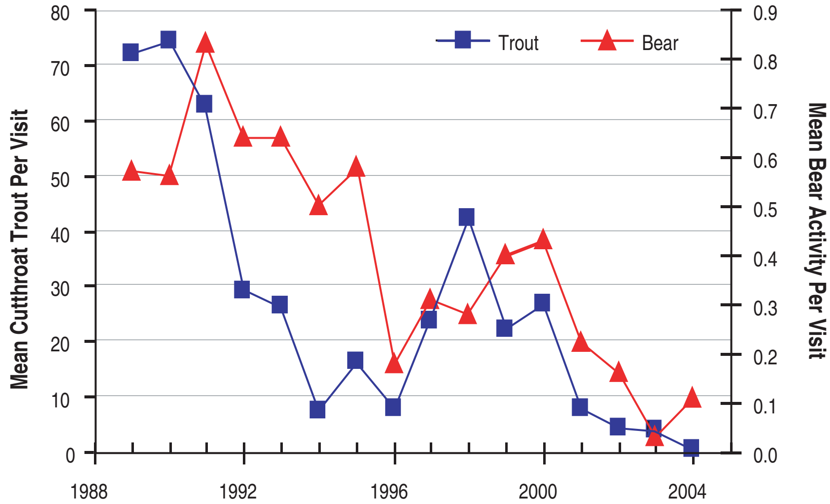


Figure 4. Mean number of cutthroat trout and mean activity by black bears and grizzly bears observed during weekly spawning visual surveys of 9–11 tributaries located along the western side of Yellowstone Lake between Lake and Grant, 1989–2004.

Aside from localized displacement, it is not known what the overall effect of cutthroat trout declines will be on bear populations, as bears of this region are also threatened by the decline of whitebark pine (*Pinus albicaulis;* Mattson and Merrill 2002). Despite this threat to important food sources, the status of the grizzly bear population in the Greater Yellowstone Ecosystem is currently considered to be stable to increasing. The grizzly bear population has increased from an estimated 136 bears in 1975, when it was listed as a threatened species, to at least 431 bears in 2004 (Haroldson and Frey in press). In addition, grizzly bears have expanded their range by 48% over the last two decades (Schwartz et al. 2002). On November 17, 2005, the U.S. Fish and Wildlife Service proposed to remove the Greater Yellowstone Ecosystem population of grizzly bears from the threatened species list (USFWS 2005).

Anglers. Yellowstone National Park has long been a destination for anglers from around the world. Historically, more than one-third of visiting anglers fished Yellowstone Lake. In recent years, estimates derived from returns of angler report cards have suggested that anglers on Yellowstone Lake experienced a decline in the number of cutthroat trout caught per hour from 2.0 in 1998 to 0.8 in 2004 (Figure 5), while lake trout caught per hour increased from 0.0 in 1998 to 0.1 in 2004. In addition, the average length of cutthroat trout caught by anglers on Yellowstone Lake increased from 370 mm in 1995 to 448 mm in 2004. The decline in numbers of YCT caught by anglers has been even more significant on Pelican Creek, the lake tributary where *M. cerebralis* infection has been most severe (see below). There, the number of cutthroat trout caught per hour declined from 2.5 in 1979 to 0.3 in 2003. Since 2001, regulations have required that YCT be immediately released unharmed. Angling on the Pelican Creek drainage was completely closed in 2004 in an attempt to slow the dispersal of *M. cerebralis* to other park waters.

Lake Trout Removal Program a Decade after Discovery

Since the discovery of lake trout in Yellowstone Lake in 1994 (Kaeding et al. 1996), efforts to counteract this non-native species have intensified. The NPS gillnetting program has removed >100,000 lake trout since 1994 (Figure 6). The gillnetting effort has increased in recent years to an average of 10 times that of 1999. In 2004, a total of 26,634 lake trout were removed using 15,781 effort units (one effort unit = 100 m of net set over one night). Catch rate has declined since 1998, when an average of 5.5 lake trout per unit of effort were caught. In 2004, catch per unit effort (CPUE) for lake trout remained low (1.69) but was slightly higher than that of 2001–2003.

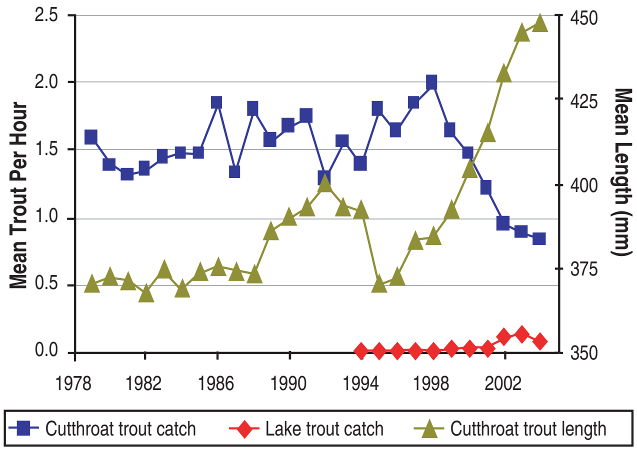


Figure 5. Angler-reported catch rate for cutthroat trout and lake trout, and the average length of cutthroat trout caught by anglers from Yellowstone Lake, 1979–2004.

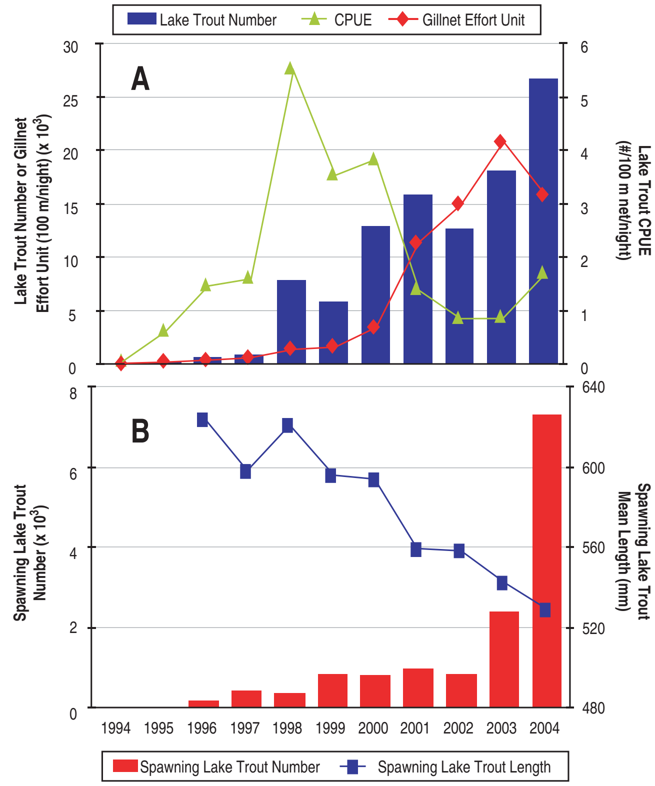


Figure 6. Number of lake trout removed, gillnet units of effort (1 unit = 100 m of net/night) used, and lake trout catch per unit of effort obtained by the lake trout removal program on Yellowstone Lake during the entire gillnetting season, 1994–2004 (A). Number and mean length of mature lake trout removed near spawning locations (Breeze Channel, Carrington Island, Geyser Basin, and Solution Creek) on Yellowstone Lake during late August–early October, 1996–2004 (B).

Avoiding bycatch of cutthroat trout has been a challenge for the lake trout removal program. Initially, the bycatch was very high: 6.6 cutthroat trout for every lake trout netted in 1995. This high bycatch was in part due to the higher densities of cutthroat trout and lower densities of lake trout that occurred within Yellowstone Lake during the mid-1990s. Since then, gillnetting protocols have been improved to reduce bycatch while maximizing removal of lake trout. Gillnets are now consistently set very deep (40–65 m depth), except during lake trout spawning periods. Since 1998, the bycatch has been 0.1 cutthroat trout or less for each lake trout netted.

As the lake trout population has grown and expanded in recent years, spawning fish have become a focal point for the removal program. In 2003, an additional lake trout spawning location was identified near the West Thumb Geyser Basin. This area, along with areas near Carrington Island, Solution Creek, and Breeze Channel, has been gillnetted since 1996. The total number of spawning lake trout caught by gillnetting was 2,371 in 2003 and 7,283 in 2004. An additional 1,063 spawning lake trout were removed by electrofishing in 2004. The average length of spawning lake trout removed near spawning areas has decreased each year. The recent decline in the annual lakewide catch rate of lake trout and the annual reduction in the average length of sexually mature fish are positive indications that the removal program is exerting measurable mortality on this population.

Lake trout densities in the West Thumb remain high, and a serious threat to YCT. Model simulations have suggested that the YCT population might have declined by 60% or more within 100 years if the lake trout population was permitted to grow uncontrolled (Stapp and Hayward 2002). Cutthroat trout abundance indices suggest that a decline of that magnitude (or greater) has already occurred. The NPS will continue to investigate new methods to target the lake trout population. In particular, using hydroacoustics, underwater cameras, and high resolution (1 m) bathymetry, the NPS is currently delineating and characterizing known lake trout spawning areas (all presently in the West Thumb), to predict where new spawning areas may be pioneered in the lake basin. These potential spawning areas will be closely monitored and targeted for lake trout removal if fish begin to use them in the future.

Whirling Disease and Drought as Additional Threats

Myxobolus cerebralis was discovered in Yellowstone Lake in 1998 among juvenile and adult cutthroat trout (Koel et al. in press). Examination of gillnetting mortalities has since confirmed the presence of the parasite throughout Yellowstone Lake, with highest prevalence existing in the northern region of the lake, near known infected streams (see below; Koel et al. 2004). Although the widespread presence of this harmful parasite in the lake is disturbing, the discovery of *M. cerebralis* spores in adult fish each year suggests that at least some cutthroat trout are surviving initial *M. cerebralis* infection.

By 2001, cutthroat trout sentinel fry exposures confirmed the presence of *M. cerebralis* in three important spawning streams: Pelican Creek, Clear Creek, and the Yellowstone River downstream from the lake outlet near Fishing Bridge (Koel et al. in press). Since then, sentinel exposures in the Yellowstone River upstream of the lake inlet and 13 other spawning tributaries have failed to detect the presence of the parasite. The impacts of *M. cerebralis* have been most severe in Pelican Creek, where few wild-reared fry have been observed in recent years (2001–2004). Cutthroat trout sentinel fry exposures in this tributary have indicated that >90% of the fry were infected with *M. cerebralis,* with an average severity (by histological examination) of >4 on a scale of 0 (no infection) to 5 (most severe infection; Koel et al. 2004).

Consistent, annual counts of upstream-migrating adult cutthroat trout have not been made in Pelican Creek in recent years, but records exist from an historic weir that was previously used to enumerate spawning fish from 1964 through 1981 (Jones et al. 1982). Netting near the location of the weir (near the tributary mouth) for upstream-migrating adults in 2002–2004 indicated that the spawning cutthroat trout population of Pelican Creek, which in 1981 was nearly 30,000 fish, has been essentially lost. With a drainage area of 17,565 ha, Pelican Creek is the second largest tributary to Yellowstone Lake in terms of discharge.

Drought in the intermountain West since 1998 may have impacted cutthroat trout populations due to increased water temperatures and a reduction in peak stream flows (USGS 2004). In many cases, flows in tributary streams have become sub-terminal near the lake, flowing through large sand and gravel bars. This disconnect of tributary streams from the lake has been occurring during mid-summer and fall, when cutthroat trout fry would typically be outmigrating to Yellowstone Lake. Biologists have consistently noted cutthroat trout fry that are stranded in isolated side channels and pools in seasonally disconnected tributaries. Although cutthroat trout have existed in the Yellowstone Lake ecosystem since glacial recession (Behnke 2002), and evolved in the face of great variation in thermal and other environmental regimes, the current drought is occurring during a period when the cutthroat trout are also impacted by lake trout predation and *M. cerebralis*.

Conclusions

Our results identify long-term impacts of lake trout and *M. cerebralis* on cutthroat trout in Yellowstone Lake and the Greater Yellowstone Ecosystem. Even with the Yellowstone National Park fisheries program dedicated to the preservation and recovery of the Yellowstone Lake cutthroat trout population, it appears to be in peril. In addition, two important cutthroat trout consumers, the black bear and grizzly bear (icons for Yellowstone National Park and highly sought by millions of visitors each year), are using cutthroat trout spawning streams much less frequently. Yellowstone National Park anglers, a third of whom fish Yellowstone Lake, also have experienced a significant reduction in catch.


NPS/TODD KOEL

Columbine Creek, at its mouth along the eastern shore, disconnected from Yellowstone Lake in August 2004.

Of great interest to park managers is the timing and original source of lake trout that were illegally introduced to Yellowstone Lake. Research on the microchemistry (Sr:Ca ratios) of otoliths has suggested that a lake trout introduction likely occurred in the late 1980s (Munro et al. 2005; and this issue of *YS*). These results suggest that lake trout existed in Yellowstone Lake for at least five years prior to being reported to the NPS by an angler. The otolith microchemistry, as well as comparative DNA analyses, has provided evidence that the lake trout origin was Lewis Lake (Stott 2004; Munro et al. 2005), a lake within the park that was intentionally stocked with lake trout from Lake Michigan in 1890 (Varley 1981). To date, it remains unknown exactly how the lake trout were introduced to Yellowstone Lake.

At present, a mandatory kill regulation is in place for all lake trout caught on Yellowstone Lake, and the NPS asks anglers each year to assist with the lake trout removal effort in this way. The Yellowstone Lake situation represents a unique case in which anglers are solicited to fish for lake trout without the desire to preserve the fishery. In NPS requests for angler support, it is made clear that the goal is removal of as many lake trout as possible and suppression of the population for the purpose of cutthroat trout conservation.

Because lake trout in Yellowstone Lake are known to prey on the native YCT (Ruzycki et al. 2003), the removal of >100,000 lake trout has reduced predation on this important population. The lake trout removal program on Yellowstone Lake represents a test case for the development of similar programs to preserve native salmonids in the intermountain West. For example, lake trout removal is currently being experimentally conducted on Lake Pend Oreille in northern Idaho, and is being considered for Lake McDonald of Glacier National Park and Swan Lake of northwestern Montana.

The cumulative effects of lake trout and *M. cerebralis* have put stress on the Yellowstone Lake cutthroat trout population during a period of intense drought in the intermountain West. The cutthroat trout population size of this system was once considered to be in the millions; however, current abundance indices suggest that only a fraction of that population exists today. The potential for lake trout control and rehabilitating historical cutthroat trout abundance are yet to be achieved. Relatively low CPUE and an annual decrease in the size of sexually mature fish are indicators that the removal program is exerting pressure on this lake trout population. A continued focus on lake trout removal will be required into the future if cutthroat trout are to persist in Yellowstone Lake at a level allowing the overall integrity of the Greater Yellowstone Ecosystem to be maintained.

Author's note: Monitoring of YCT at Clear Creek has continued since this paper was prepared and originally published. During 2005, 917 YCT were counted moving upstream into Clear Creek to spawn. This count is the lowest ever recorded at this trap, with records dating back to 1945. Although the invasion of Yellowstone Lake by lake trout and the whirling disease parasite has certainly taken its toll, we remain hopeful that recent snowpack and resulting higher stream flows will benefit YCT and assist in a rebound of this ecologically important population.

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From the Archives

NPS, YELLOWSTONE NATIONAL PARK, YELL 1949

A group of Lake Hotel employees gathered for a photo after a successful day's fishing on Yellowstone Lake in 1901. Today every cutthroat trout seems precious, but back then anglers had the luxury of large kills, and often the fish were thrown away after the picture was taken.

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NPS/MIKE YOCHIM

The Yellowstone River south of Yellowstone Lake.

Coming this summer, *Yellowstone Science* features an interview with John Varley.

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