The Yellowstone Lake Crisis: Confronting a Lake Trout Invasion

A Report to the Director of the National Park Service
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A Report to the Director of the National Park Service

Edited by John D. Varley and Paul Schullery

Yellowstone Center for Resources
National Park Service, Yellowstone National Park, Wyoming

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Trout paintings by Michael Simon
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THE LAKE YELLOWSTONE TROUT CRISIS
EXECUTIVE SUMMARY

Yellowstone Lake is home of the premier surviving inland cutthroat trout fishery in North America. This fishery is threatened with destruction by illegally introduced lake trout, which were discovered in 1994. The lake trout are known to exist in at least four and possibly as many as six age groups, proof of a relatively small but reproducing population (Fig. 1). The older age groups are now able to reproduce, and the lake trout population will almost certainly grow rapidly.

The discovery of these non-native lake trout in Yellowstone Lake caused great alarm among fisheries biologists throughout the greater Yellowstone area because of the lake trout’s reputation for displacing species such as cutthroat trout in other western lakes. Park administrators sought to verify the “doomsday” opinion of local biologists by arranging an assessment of the situation by United States and Canadian specialists in population dynamics and lake trout biology. The experts convened an information-sharing workshop in February 1995, and concluded that the lake trout population in Yellowstone Lake is likely to expand and cause precipitous decline in the cutthroat trout population. The majority view was that the cutthroat trout are likely to decline to 10-20% of present abundance. These percentages translate to a decline from an estimated 2.5 million trout of catchable size at present to 250,000-500,000 at some time in the foreseeable future.

Except for its strongholds in the upper Yellowstone River area, the Yellowstone cutthroat trout is imperiled. Human activities have already reduced its range to 15% of its historic distribution. The appearance of lake trout in Yellowstone Lake has ominous implications for the continued viability of the Yellowstone cutthroat trout as a subspecies.

The predicted decline of Yellowstone cutthroat trout will destroy the world-famous fisheries in the lake and its tributaries, including the storied fishery in the Yellowstone River between the lake and the Upper Falls; this latter fishery gained international prominence in the 1970s as the site of pioneering advances in catch-and-release fishing, and remains one of the world's premier destinations for trout fishermen. For nearly 150 years, the lake itself has developed its own superlative reputation as a “trout catchery.” Though a lake trout fishery will evolve in the lake consonant with the cutthroat decline, it will be a highly specialized fishery of interest only to a comparatively few anglers and will not occur at all on the rivers and streams. The replacement fishery will in no respect (ecologically, economically, or socially) replace the fisheries it destroys.

The cutthroat trout decline will also cause severe disruption in the food supply for two
species listed under the Endangered Species Act—the threatened grizzly bear and the endangered bald eagle—and will likewise affect many species of special concern, including the white pelican, otter, black bear, mink, osprey, and loon; an estimated 42 species of mammals and birds in all. Grizzly bear, white pelican, and osprey abundance at Yellowstone Lake, and perhaps other species as well, are all correlated with the abundance of Yellowstone Lake cutthroat trout. Because of pronounced differences in the habits and habitat uses of lake trout and cutthroat trout, the lake trout will not serve as a replacement food source for these affected species of mammals and birds.

In reviewing current fishery technologies, workshop participants concluded that there is little prospect that the lake trout can be eradicated from Yellowstone Lake. However, scientists from the Great Lakes region offered some hope that expansion of the lake trout population might be contained through an aggressive gill-netting program such as those used by commercial fishing operations in the Great Lakes. Following that lead, personnel from the National Park Service and the U.S. Fish and Wildlife Service’s Fishery Assistance Office at the park developed an action plan to initiate a control program. The program’s effectiveness depends on an understanding of where the lake trout populations are located in each season so that they can be netted without harming the cutthroat trout population.

Initial efforts will proceed based on knowledge that in the summer the lake trout generally inhabit deeper waters than do cutthroat trout. As understanding of the location and movements of both species is refined, program effectiveness will be increased. An important first step is to import Great Lakes technology as well as to obtain the additional financial resources and personnel needed to implement and maintain these emergency measures. There was a consensus view among the workshop biologists that only an aggressive lake trout control program would protect the cutthroat population and thus the ecological character of the entire Yellowstone Lake basin.

While the potential ecological losses are staggering, the potential economic losses can be summarized as equally immense. The 1994 value of the Yellowstone fisheries above the great falls, including the lake and its tributaries, is estimated at slightly more than $36 million. The cumulative 30-year value of the cutthroat trout sport fishery, assuming lake trout were absent, is estimated at more than a billion dollars ($1,080,000,000). Assuming lake trout are vigorously controlled, the consonant value declines to $685 million. If lake trout are not controlled, the value declines to $439,950,000. The last value represents a three-decade economic loss of $640 million, which can be considered the net economic effect of the illegal lake trout introduction if no actions are taken to control the species.

With lake trout control, at an estimated program cost of $9 million over 30 years, the effects of lake trout on the cutthroat trout population have a high probability of being ameliorated. The benefit-to-cost ratio for the lake trout control program is a favorable 27:1.

If the effects of lake trout on cutthroat trout are greater than projected by the experts, and the Yellowstone cutthroat trout becomes rare or nearly extinct, the cost of the destruction of all fish life in the lake and its tributaries (the start-from-scratch alternative for restoring the native fishery), and the subsequent reestablishment of the cutthroat trout population to its former condition is estimated to be $32-181 million.
Abstract: On July 30, 1994, lake trout (*Salvelinus namaycush*) were discovered in Yellowstone Lake, Yellowstone National Park, Wyoming, the core of the remaining undisturbed, natural habitat for the native Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*). Data from this and other lake trout caught subsequently by anglers and the U.S. Fish and Wildlife Service suggest lake trout have reproduced in Yellowstone Lake since at least 1989 and now number in the thousands, perhaps tens of thousands. A highly piscivorous, nonnative species, lake trout will probably thrive in Yellowstone Lake and reduce the lake’s cutthroat trout stocks substantially unless preventive management actions are taken.

Yellowstone Lake, Yellowstone National Park, Wyoming, is the core of the remaining undisturbed, natural habitat for the native Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*) (Varley and Gresswell 1988). During the past two decades in particular, fishery managers have used angling regulations to greatly reduce angler harvest, considered a principal human threat to the cutthroat trout stocks of Yellowstone Lake (Gresswell and Varley 1988). As a result, the stocks have recovered markedly from past overharvest and, to many managers, appeared safe from adverse human activities (Jones et al. 1993).

The perception of Yellowstone Lake as a secure refuge for Yellowstone cutthroat trout changed abruptly on July 30, 1994, when a lake trout (*Salvelinus namaycush*) was caught from the lake by an angler on a guided fishing trip. The fishing guide, aware that lake trout were not known to occur in Yellowstone Lake, immediately contacted National Park Service rangers. The angler and guide were interviewed, and the fish, 43 cm long, was given to park authorities. On August 5, a second lake trout (42 cm long) was caught under similar circumstances and given to park authorities.

A National Park Service press release dated August 11, 1994, described the discovery of lake trout in Yellowstone Lake; outlined ecological consequences that could result from establishment of this highly piscivorous, nonnative fish species; and offered a reward for information leading to the arrest and conviction of the person or persons responsible for illegally stocking the fish. Human culpability was assumed because natural movement of lake trout into Yellowstone Lake from other park waters in which they are found was not possible.

Extensive media coverage of the issue resulted in additional reports to the U.S. Fish and Wildlife Service (FWS) (technical advisors to the National Park Service) of lake trout captures from Yellowstone Lake. Two experienced anglers reported the capture on August 15, 1994, of three “roughly [46 cm] 18-inch” lake trout from Yellowstone Lake. Because the anglers believed the odor of fish might attract bears to their backcountry campsite, the putative lake trout were killed and returned to the lake. On August 20, a park visitor gave park authorities a photograph of herself holding a lake trout 43 cm long that she had caught from the lake July 21, 1994, and subsequently consumed. A fishing guide...
reported that a lake trout < 33 cm long was caught and kept by one of his clients in 1993. Two park employees, both experienced anglers, reported that they caught and returned to the lake a lake trout in the mid-1980s.

Although the evidence in late August 1994 indicated that lake trout were present in Yellowstone Lake, the origin of the lake trout population was not clear. Some people speculated that the lake trout caught by anglers in 1994 were part of a small group of fish illegally stocked into the lake as fingerlings only a few years earlier. Remarkably, a scenario similar to this was described in a fictional magazine article (Parks 1991) that had been brought to the attention of park authorities. Alternatively, it was possible that the lake trout caught by anglers had been produced in the lake from a founding parent stock that had been present there for many years.

In late August 1994 the FWS developed a plan of action that had as its goal the elimination of lake trout from Yellowstone Lake. This goal is consistent with National Park Service policy (NPS 1988) that directs the removal of nonnative organisms from the park when feasible, especially when they present threats to native organisms. Objectives of the plan were to (1) characterize the lake trout population, (2) locate potential lake trout spawning areas, (3) determine the origin of the lake trout, and (4) identify remedial actions. This report describes and interprets the data collected under Objectives 1 and 2.

**YELLOWSTONE LAKE AND CUTTHROAT TROUT**

Yellowstone Lake lies 2,356 m above mean sea level in east-central Yellowstone National Park. The lake has a surface area of 341 km², shoreline length of 239 km, mean depth of 48.5 m, and maximum depth of 107 m. A thermocline forms in July and may persist in mid-September at a depth of 10-20 m. The hypolimnion remains well-oxygenated during stratification. Phytoplankton standing crops are low and generally dominated by diatoms. Summer surface temperatures rarely exceed 18°C, and ice covers the lake from mid-December through May or early June (Benson 1961, Knight 1975, Kaplinski 1991).

Yellowstone cutthroat trout and longnose dace (*Rhinichthys cataractae*) are the native fishes of Yellowstone Lake, whereas longnose sucker (*Catostomus catostomus*), redside shiner (*Richardsonius balteatus*), and lake chub (*Couesius plumbeus*) are established, nonnative species. The minnow species inhabit only warm, vegetated bays and other littoral areas; cutthroat trout and longnose sucker are found throughout the lake (Benson 1961).

Yellowstone cutthroat trout are obligate stream spawners (Varley and Gresswell 1988). Approximately half of the lake’s 126 tributaries are known to be used for spawning by cutthroat trout from Yellowstone Lake. Cutthroat trout in Yellowstone Lake provide the most popular sportfishery in Yellowstone National Park (Jones et al. 1993), as well as food for grizzly bears, osprey, white pelicans, river otters, and other animals (Davenport 1974, Swenson 1978, Reinhart and Mattson 1990).

**PROCEDURES**

**Characterizing the Lake Trout Population**

Gill nets, set perpendicular to the lake shore in relatively shallow water in mid-September, have been used for more than two decades to monitor trends in cutthroat trout and longnose sucker populations in Yellowstone Lake (Jones et al. 1993). That traditional monitoring program continued in 1994, and its techniques were also generally used in the search for lake trout in deeper water during the remainder of the field season.
Gill nets used routinely are 38 m long, 1.8 m deep, and have five 7.6-m panels of 19, 25, 32, 38, and 51 mm mesh (bar measure) monofilament netting. For subsequent deepwater gill netting, these nets and others similar in construction but twice as long (i.e., two “monitoring” nets attached end-to-end) were used. Gill nets were set during the day and retrieved the next morning. Captured fish were measured to total length and weighed. Captured lake trout (and those provided by anglers) were frozen and retained for age-growth, sexual maturation, and other analyses.

Angling was also used in attempts to capture lake trout. Downriggers were used to troll a variety of lures at depths shown by sonar to be occupied by fish. Shallow trolling often accompanied deep trolling with downriggers. Most of the angling effort was expended in lake regions from which recreational anglers had captured lake trout.

**Locating Potential Lake Trout Spawning Areas**
Visual observation of substrates was used to locate potential lake trout spawning areas. Observers in a boat moving slowly along the lake shoreline, in water 2-7 m deep, recorded substrate characteristics on topographic maps.

**RESULTS**

**Gillnetting**
Altogether, 1,368 Yellowstone cutthroat trout, 630 longnose suckers, and 2 lake trout were caught in gill nets set in many regions of Yellowstone Lake (Fig. 1). Catch rates for cutthroat trout and longnose suckers were highest in shallow water and declined with increasing depth (Table 1). Few longnose suckers were found in water deeper than 30.5 m. Lake trout were caught in nets that had their shallow end in water about 36.6 m deep.

Range in lengths of individual cutthroat trout varied little with depth, although few age-1+ cutthroat trout (15-20 cm long) were caught in waters 15.2-30.5 m deep (Fig. 2). Ranges in lengths were similar for longnose suckers caught in waters 0-15.2 m and 15.3-30.5 m deep (Fig. 3). The lake trout caught in gill nets were 20 and 32 cm long.

**Angling**
Twenty Yellowstone cutthroat trout (32 -53 cm long) were caught by angling. Of these, seven were caught by downriggers at depths of 12.2-38.1 m; the remainder were caught at depths <6.1 m. No lake trout were caught. As many as four lures were fished simultaneously during the 59 hours spent fishing between September 7 and October 5, 1994.

**Analyses of Individual Lake Trout**
Analyses of scales revealed that the two lake trout (43 and 42 cm long) caught by the guided anglers were five years old, whereas the two
lake trout (32 and 20 cm long) caught in gill nets were four and two years old. The fish therefore were of the 1989, 1990, and 1992 year-classes, respectively (C. R. Bronte, National Biological Service, Ashland, Wis., pers. commun.).

Analyses of gonadal tissue from the two large lake trout revealed that both fish were male. However, opinions on stage of reproductive maturity differed between the two analysts who examined the histological preparations. Beth MacConnell (FWS, Bozeman, Mont., pers. commun.) indicated the fish were immature, whereas C. M. Kaya (Department of Biology, Montana State University, Bozeman, pers. commun.) saw evidence of early-stage spermatogenesis in both specimens. (The tissue preparations had been considerably distorted by freezing and thawing that occurred before tissue fixation.) Kaya also pointed out that brook trout (*Salvelinus fontinalis*) at a similar stage of gonadal development in June can spawn in October (Henderson 1962).

**Potential Spawning Habitat**
Visual observation revealed that cobble, rubble, or boulder substrates occur in many areas along the Yellowstone Lake shoreline (Fig. 4).

**DISCUSSION**
All of the lake trout reported caught by anglers in 1994 were approximately 43 cm long and might have been of one year-class produced in

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Table 1. Catch statistics for Yellowstone cutthroat trout, longnose suckers, and lake trout caught in 38- or 76-m-long gill nets in each of four ranges of water depth, Yellowstone Lake, fall 1994.

<table>
<thead>
<tr>
<th>Depth range (m)</th>
<th>No. of sets</th>
<th>Cutthroat trout</th>
<th>Longnose suckers</th>
<th>Lake trout</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>38 m</td>
<td>76 m</td>
<td>N</td>
<td>Catch rate&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>0–15.2</td>
<td>61</td>
<td>4</td>
<td>994</td>
<td>12.2</td>
</tr>
<tr>
<td>15.3–30.5</td>
<td>11</td>
<td>0</td>
<td>76</td>
<td>5.6</td>
</tr>
<tr>
<td>30.6–45.7</td>
<td>28</td>
<td>22</td>
<td>295</td>
<td>3.2</td>
</tr>
<tr>
<td>45.8–61.0</td>
<td>1</td>
<td>3</td>
<td>3</td>
<td>0.3</td>
</tr>
</tbody>
</table>

<sup>a</sup> Water depth at the shallow end of the gill net.
<sup>b</sup> Fish caught per 30.5 linear m of net.
<sup>c</sup> Gill nets entirely of 76 mm mesh netting.
Lake Trout Discovered

1989. If so, these fish recruited into the sportfishery at age 5, the minimum age of maturity in wild lake trout (Healey 1978). Whether the 1989 year-class embodies the first natural reproduction of lake trout in Yellowstone Lake is unknown. The presence of these fish and additional, younger lake trout suggests that lake trout have reproduced annually in Yellowstone Lake since at least 1989.

On the basis of a mark-recapture (in gill nets) experiment that included more than 49,000 marked, adult cutthroat trout, and extrapolation of areal densities of fish caught in purse seines set at many locations around the lake, Jones et al. (1980) concluded conservatively that there were 1-4 million catchable cutthroat trout (>35 cm long) in Yellowstone Lake in 1979. The total population of cutthroat trout would be much larger, perhaps by a factor of three or more. If cutthroat trout are equally abundant today, and they and lake trout are similar in their vulnerability to capture in gill nets, the approximate 1000:1 ratio of these fish in our gillnet catch suggests that lake trout number in the thousands, perhaps tens of thousands, in Yellowstone Lake.

Such numbers of lake trout are too large to be explained hypothetically by an introduction of fingerling lake trout a few years ago. Instead, large numbers and multiple year-classes of lake trout indicate reproduction in Yellowstone Lake. When the founding stock of parent lake trout began to reproduce is unknown, as is the reproductive history of their progeny. Lake trout in Yellowstone Lake were unknown to park authorities prior to 1994 because the population of catchable-size lake trout was much smaller, the few anglers who caught lake trout did not bring the fish or other substantial evidence to park authorities, and traditional monitoring programs were designed to sample...
cutthroat trout in shallow water in early fall (when lake trout are likely to be in deep water because the lake has not yet undergone temperature destratification).

Lake trout are capable of rapid population increase (Curtis 1990) and are likely to thrive in Yellowstone Lake unless preventive management actions are taken. Lake temperatures and water quality are ideal for lake trout, and substrates ostensibly suitable to lake trout spawning (areas of cobble and rubble with little or no fine sediments [Thibodeau and Kelso 1990, Edsall et al. 1992]) occur at many locations. Reproduction by the 1989 year-class of lake trout in Yellowstone Lake could rapidly increase the population.

The extent that the cutthroat trout population of Yellowstone Lake might be reduced by lake trout competition or predation is unknown but potentially substantial. Macroinvertebrate foods of cutthroat trout and longnose sucker (Benson 1961, Benson and Bulkley 1963) also are eaten by young lake trout (Elrod 1983, Elrod and O’Gorman 1991), and cutthroat trout and longnose suckers themselves would be food for juvenile and adult lake trout. Individual lake trout in Yellowstone Lake grow slowly, similar to lake trout in nearby (10 highway km) Lewis Lake, where the species was introduced officially in 1890, and an abundant population has developed (Jones et al. 1983). This suggests that competition for food already occurs among lake trout and other fish species in Yellowstone Lake.

Predation on cutthroat trout by lake trout might become especially significant in Yellowstone Lake because, as our data suggest, many cutthroat trout, including young fish, occupy deep water, the habitat of lake trout. In contrast, the other potential prey species, longnose sucker, occurs primarily in shallow water.

Introduced lake trout have been implicated in the extinction of Lahontan cutthroat trout (O. c. henshawi) in Lake Tahoe (Cordone and Frantz 1966). Benson et al. (1961) stated that introduced lake trout eliminated native cutthroat trout in several large, deep lakes in the Rocky Mountain region but provided no supportive data. In Heart Lake, Yellowstone National Park, the native Yellowstone cutthroat trout may have declined markedly after lake trout of unknown origin became established (Dean and Varley 1974). In Jackson Lake, Wyoming, substantial decline in the native Yellowstone cutthroat trout accompanied colonization of the lake by lake trout (Behnke 1992). Lake trout also have been shown to eliminate native bull trout (S. confluentus) in lakes (Donald and Alger 1993).

In Yellowstone Lake, the lake trout is a potential keystone predator (sensu Paine 1966), an organism that greatly influences ecosystem processes as a result of its feeding activity. Among the ecosystem processes likely to be affected by lake trout is energy flow from the aquatic to the terrestrial ecosystem. Today, this energy transfer includes Yellowstone cutthroat trout eaten by grizzly bears, white pelicans, river otters, ospreys, and other terrestrial animals. Because cutthroat trout spawn in tributaries and use other shallow-water habitats during other times of the year in Yellowstone Lake, they are vulnerable to such predation. In contrast, the habits of lake trout make them almost entirely unavailable to terrestrial predators.

ACKNOWLEDGMENTS
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Lake Trout Discovered
EDITORS'S NOTE: UPDATE ON LAKE TROUT SITUATION THROUGH JUNE, 1996

During the summers of 1995 and 1996, additional data was gathered on lake trout in Yellowstone Lake. Experimental gillnetting conducted by the U.S. Fish and Wildlife Service has yielded several hundred additional lake trout from 7 inches up to 32 inches (12.5 lbs.)

National Park Service staff received angler reports of nearly 100 additional lake trout, most caught by anglers from the lake shore. Most of these fish were in the 16-19 inch size range, with several ranging up to 23 inches. Lake trout were comparatively common along the shore and in surface waters until the middle of July when they moved to deep water.

Both the numbers and the distribution of these lake trout serve to strengthen the prevailing opinion that the situation is grave and alarming. It is now clear that there are many lake trout of a variety of age classes in the lake, and that one or more age class is capable of spawning. It is likewise clear that the fish are distributed throughout the lake, as these fish were caught in many locations. The situation is, if anything, more troubling than previously imagined.
Yellowstone Lake is the last great refuge of the once widespread Yellowstone cutthroat trout, \textit{Oncorhynchus clarki bouvieri}. Though heavily exploited by recreational and commercial fishing between 1890 and 1970, recent changes in fishing regulations have restored robust numbers and population structure (Gresswell and Varley 1988). Yellowstone Lake and its tributaries and outlet stream have become world-renowned as examples of intensively used yet healthy fisheries (Varley and Schullery 1983), and the potential effects of an illegally introduced population of lake trout, \textit{Salvelinus namaycush}, therefore causes considerable anxiety among managers, scientists, and the public.

All the roles played by cutthroat trout in the lake’s ecosystem have not been examined, but many have, and the accumulated information allows cautious predictions of the consequences of a collapse of the cutthroat trout population. For example, we know there are 42 species of mammals and birds that are known or suspected of using cutthroat trout for food in the Yellowstone Lake area (Table 1). These mammals and birds take all ages of fish, in all parts of the lake and in the tributary streams. Their predation on living trout is best known (e.g., osprey) but the consumption of carcasses of migratory salmonids, particularly in spawning streams, has been shown to be ecologically significant (Cederholm et al. 1989). This consumption, or scavenging, is apparently quite complex, and may reach quite far into the terrestrial food chain.

We cannot look into the future and say that any of these bird or mammal species would themselves be extirpated as a consequence of the collapse of cutthroat trout population, but knowing the importance of the native trout to these species, we must assume that some of them would be seriously diminished, if not imperiled.

Ecologists have noted the extraordinary precision of resource partitioning among predators on the Yellowstone Lake cutthroat trout (Davenport 1974, Varley and Schullery 1983). The many avian and mammalian predators who depend wholly or in part upon this resource are surprisingly specialized in the size of the fish they take, with the result that fish of all ages are subjected to predation, and are therefore of importance to some or several predators. Thus any alteration of the age structure of the trout population will begin to have effects on some predators before it affects others, but eventually, as the trout population declines, all predators will be affected.

A LAST STRONGHOLD OF YELLOWSTONE CUTCROUT AT RISK

When white settlers first began colonizing the western United States there were probably 14 subspecies of cutthroat trout (\textit{Onchorhynchus clarki} spp.) in various levels of abundance (Behnke 1979). After several centuries of civilized “progress,” two subspecies are extinct and eight of the remaining groups are listed by the American Fisheries Society (1989) as endangered, threatened, or of special concern. In this sad history of neglect and extermination, the preservation of two subspecies, the coastal cutthroat trout (\textit{O. clarki clarki}), and Yellowstone cutthroat trout (\textit{O. clarki bouvieri}), gave the public some cause for celebration. But then
Table 1. Checklist of birds and mammals known or suspected to utilize Yellowstone cutthroat trout as a food source in the Yellowstone Lake drainage.

<table>
<thead>
<tr>
<th>Species</th>
<th>Known</th>
<th>Suspected</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Mammals:</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Water shrew</td>
<td>Sorex palustris</td>
<td>X</td>
</tr>
<tr>
<td>Masked shrew</td>
<td>Sorex cinereus</td>
<td>X</td>
</tr>
<tr>
<td>Dusky shrew</td>
<td>Sorex monticolus</td>
<td>X</td>
</tr>
<tr>
<td>Deer mouse</td>
<td>Perimyscus maniculatus</td>
<td>X</td>
</tr>
<tr>
<td>Red squirrel</td>
<td>Tamiasciurus hudsonicus</td>
<td>X</td>
</tr>
<tr>
<td>Uinta chipmunk</td>
<td>Tamias umbrinus</td>
<td>X</td>
</tr>
<tr>
<td>Flying squirrel</td>
<td>Glaucomys sabrinus</td>
<td>X</td>
</tr>
<tr>
<td>Muskrat</td>
<td>Ondatra zibethicus</td>
<td>X</td>
</tr>
<tr>
<td>Ermine</td>
<td>Mustela erminea</td>
<td>X</td>
</tr>
<tr>
<td>Longtailed weasel</td>
<td>Mustela frenata</td>
<td>X</td>
</tr>
<tr>
<td>Mink</td>
<td>Mustela vison</td>
<td>X</td>
</tr>
<tr>
<td>Marten</td>
<td>Martes americana</td>
<td>X</td>
</tr>
<tr>
<td>Striped skunk</td>
<td>Mephitis mephitis</td>
<td>X</td>
</tr>
<tr>
<td>Otter</td>
<td>Lutra canadensis</td>
<td>X</td>
</tr>
<tr>
<td>Wolverine</td>
<td>Gulo gulo</td>
<td>X</td>
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<td>Badger</td>
<td>Taxidea taxus</td>
<td>X</td>
</tr>
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<td>Coyote</td>
<td>Canis latrans</td>
<td>X</td>
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<tr>
<td>Bobcat</td>
<td>Lynx rufus</td>
<td>X</td>
</tr>
<tr>
<td>Cougar</td>
<td>Felis concolor</td>
<td>X</td>
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91% of the remaining range of the Yellowstone cutthroat trout is located in Yellowstone National Park, and practically all of that is in the Yellowstone Lake and River (Fig. 1, Varley and Gresswell 1988). The report by McIntyre (this volume) now causes us considerable concern for the fate of these cutthroat trout in their last major stronghold.

This subspecies is worthy of preservation in its own right; it is part of the planet’s biodiversity. But there are many other reasons for preserving this trout population. The cutthroat trout is a celebrity among the trout family (e.g., Trotter 1987) due to its popularity with sport fishermen. As an all-around sport fish it has few peers: it grows to a fairly large average size, is highly vulnerable to sport fishing, even by novice anglers, and it has high susceptibility to repeated catches when released (Varley 1984, Gresswell and Liss 1995). Cutthroat trout, more than any other trout species, is the archetype of western trout fishing. These traits are also the reasons that it is so vulnerable to overexploitation and the main reason so many of the cutthroat subspecies are declining.

All of this is very important, of course, but the Yellowstone cutthroat trout is also important in the fabric of something very much larger: the ecosystem in which it lives. It is this dimension we explore here.

**Other Fishes**

For the past 10,000 years or so, only the longnose dace (*Rhinichthys cataractae*) shared Yellowstone Lake with the native cutthroat (Varley and Schullery 1983). As a result of the activities of modern humans, the Yellowstone cutthroat trout now share Yellowstone Lake with several other introduced fish species: redside shiners (*Richardsonius balteatus*), longnose sucker (*Catostomus catostomus griseus*), lake chub (*Couseus plumbeus*), and most recently, lake trout (*Salvelinus namaycush*).

Prior to the advent of the lake trout, the survival of the native cutthroat trout did not appear to be affected by the nonindigenous newcomers. In fact, cutthroat trout are occasionally known to feed heavily on some of these fish (Brown 1974). The effects of a collapse of the cutthroat trout population on these other species is not known, nor is the effect of lake trout predation on these species predictable. We can speculate that lake trout might prey heavily on the sucker because both are hypolimnetic (deep-dwelling, bottom-oriented) species, but all age and size groups of all species (including cutthroat trout) would be potentially vulnerable to lake trout predation.
predation, depending upon their preferred habitats.

**BIRDS**

We know or suspect that a minimum of 20 bird species in the Yellowstone Lake ecosystem (Table 1) have evolved using the cutthroat trout as a primary or significant source of food. The species diversity is as complex as it is fascinating. The stream-dwelling dipper (*Cinclus mexicanus*), for instance, is an efficient predator of trout fry as they emerge from the gravel and migrate lakeward. Based on this fact, we can speculate about the effect no cutthroat spawners, or greatly diminished spawning activity, might have on this species. What follows are short case histories of the bird species we have the most knowledge of, and the potential effects of the lake trout disruption.

The bald eagle (*Haleaeetus leucocephalus*) is widely thought of as a predominantly fish-eating species, but studies in Yellowstone show that only about 25% of its diet is fish (Davenport 1974, Swenson et al. 1986), and only about half of the fish it eats are trout (Davenport 1974). This does not mean that trout are unimportant to the bald eagle, of course; its status over the past several decades has often been precarious, and any change or reduction in its food base, especially protein- and fat-rich fish, could be critically significant. As well, some of its other prey, especially waterfowl, are themselves in part dependent upon fish, and so in effect the eagle's reliance on fish is higher than might appear from an examination only of its immediate prey. Davenport (1974) estimated that the daily consumption of fish per bald eagle was 0.09 lb. per day. Lake trout are not expected to be vulnerable to bald eagle predation.

The osprey (*Pandion haliaetus*) lives almost entirely on fish, and most of the fish are trout (Fig. 2). Yellowstone Lake and River host numerous breeding pairs of ospreys. Swenson (1978) found that 93% of the fish bones identified near osprey nests were from trout, and the rest were from Longnose suckers. Longnose suckers may have been overrepresented in this sample because their bones are heavier and more likely to endure and be found. Swenson (1978) also determined these birds selectively preyed on cutthroat trout about 11 inches in length. Davenport (1974) estimated that ospreys averaged 0.88 lb. of fish per day on Yellowstone Lake. Because they live at a far greater depth than cutthroat trout, lake trout will hardly ever be available to ospreys. After several decades of struggle, osprey are doing relatively well in Yellowstone National Park (Fig. 3), but past experience indicates their susceptibility to stress.

White pelicans (*Pelecanus occidentalis*) are among the most-studied species of animals in Yellowstone National Park (Fig. 4, Diem and Condon 1967). The nesting colony in Yellowstone is the only known colony in an American national park, and is the highest elevation colony known anywhere (Fig. 5). In 1994, a record 739 white pelican nests were initiated on the Molly Islands, but nesting success was low (T. McEneaney, NPS, pers. commun., 1995). In 1922, Ward estimated that virtually all of the pelican diet in Yellowstone Lake was trout, but since then the introduction
several recent studies that indicate that white pelicans consume 2 to 4 pounds of fish per day. Davenport (1974) estimated that 72% of the diet of great blue herons (Ardea herodias) around Yellowstone Lake was trout, and that they consumed an estimated 1.93 lb. of food each per day. While the population of herons is relatively small (several dozen) the birds average about 1,000 “heron-use days” in the course of the summer season. Unlike many species of fish-eating animals, but like the pelicans, herons take fish of many sizes, from 2 to 16 inches in length. Lake trout are not expected to be vulnerable to herons.

The common merganser (Mergus merganser), though not as large or glamorous as the above-named species, may in some years actually consume more fish than any of them because the population is fairly large (400-800 birds, 62,000 use-days) and they spend a long season on the lake (Davenport 1974). Davenport (1974) estimated that mergansers averaged 1.0 lb. of trout eaten per day.

and proliferation of the longnose sucker has probably shifted the percentage of non-salmonids consumed to some extent. Pelicans fish in shallow water for trout and suckers between 6 and 16 inches, and it is unlikely lake trout will be vulnerable in this way to the birds in the future. Davenport (1974) summarized


According to Davenport’s (1974) estimate of trout consumption in 1973 and 1974, the California gull \((Larus\ californicus)\), whose population was estimated between 1,400 and 2,000 (160,000 bird-days use) and whose diet is 50% trout, consumed as much trout as did pelicans. The eared grebe \((Podiceps\ caspicus)\), whose numbers ranged from 2,500 to 3,000 (100,000 bird-days use) depended entirely upon trout for its diet, and consumed 0.31 lb. per day. The common loon \((Gavia\ immer)\) and the caspian tern \((Hydroprogne\ caspia)\), occur in smaller numbers (15 and 35, respectively) but both depend entirely upon trout for their food, and consume 1.91 and 0.7 lb. of food per day (Davenport 1974). Other bird species that eat trout include the Barrow’s goldeneye \((Bucephala\ islandica)\), bufflehead \((Bucephala\ albeola)\), and belted kingfisher \((Megaceryle\ alcyon)\). None of the above species are expected to utilize lake trout because of the fish’s deep water habits.

Double-crested cormorants \((Phalacrocorax\ auritus)\) are another prominent fish-eater on Yellowstone Lake (Fig. 6). Cormorants apparently consume few trout, and may not have inhabited the lake at all until after the introduction of longnose suckers (Davenport 1974). If cormorants are profundal predators, as a diet of suckers suggests, they may consume lake trout in Yellowstone Lake. It is not known if the presence of lake trout, who will themselves prey on longnose suckers, will enhance or decrease cormorant population size.

All of the above species of birds, with the possible exception of the cormorant, prey on fish within a few feet of the surface of Yellowstone Lake, along the lake shoreline, or in the shallower waters of the lake’s tributaries.
and outlet stream. Cutthroat trout, who prefer these same habitats, are thus vulnerable to this predation. Lake trout spend almost all of their lives at depths too great to be reached by these predators. In the event of a collapse of the cutthroat trout population and an increase in the lake trout population, the lake trout are not expected to provide a replacement prey.

**Mammals**

With the exception of grizzly bears, the use of cutthroat trout by mammals has not received the amount of study attention birds have received; yet a surprising number of mammal species—22—are known or suspected of using cutthroat trout as a primary or significant food item (Table 1). For species like otters there is little doubt of the potential impact of lake trout. Observers on Yellowstone Lake have reported they seem to be able to catch cutthroat trout at will. The deep-dwelling lake trout will certainly be less available and accommodating. What follows are short discussions and some speculation on the effect of lake trout on our best-known mammal species.

Though the historical record is sketchy due to the shortage of observers and changing patterns of human use (Skinner 1927, Whittlesey 1988, Schullery 1991), it is assumed that prior to the creation of Yellowstone National Park, grizzly bears (*Ursus arctos*) preyed heavily on spawning cutthroat trout in the tributary streams of Yellowstone Lake. During the extended period of open-pit garbage dumps in Yellowstone (roughly 1890-1970), when increasing numbers of bears devoted much of their attention to feeding at these concentrated food sources, relatively few reports were made of bears feeding on these spawning runs, a notable exception being bears that discovered easy concentrations of fish at spawner collection weirs operated by hatchery managers. By the 1960s, when the first ecological study of Yellowstone grizzly bears was undertaken, the Yellowstone Lake cutthroat trout population was severely depressed and garbage feeding by bears was at its height (Schullery 1992). The Craighead research team observed no feeding by grizzly bears on spawning trout in the 1960s (J. Craighead, pers. commun., 1984).

In the late 1960s, a general overhaul of park fishing regulations allowed the cutthroat trout population to begin a rapid recovery, with concurrent increase in grizzly bear activity along spawning streams (Fig. 7). Yellowstone Lake has 124 tributaries, at least 59 of which are known to have cutthroat trout spawning runs. Surveys in 1974 and 1975 revealed bear activity on 17 streams, and clear evidence of bear fishing on 11 (Hoskins 1975). Surveys in 1985-1987 revealed that 93% of the streams now had evidence of bear activity, and 61% “had conclusive evidence of bear fishing” (Fig. 8, Reinhart and Mattson 1990). An estimated minimum of 44 bears used these spawning runs in 1987 (Reinhart and Mattson 1990), and sometimes this use was substantial; Yellowstone Grizzly Foundation researchers observed an adult female grizzly bear maintain an average harvest of 100 fish per day (average fish weight = 1.3 lbs) for 10 days (S. French, pers. commun., 1989).
Black bears (*Ursus americanus*) also fish these spawning streams, though they are not observed as often as are grizzly bears. Most use of spawning runs has been by grizzly bears, but Reinhart and Mattson (1990) noted that “black bear use of streams was also increasingly common, progressing from the east shore to the west shore.” The presence of grizzly bears on a stream apparently deterred black bears from fishing more.

Gunther (1995) noted that “cutthroat trout are an important, high quality food source for grizzly bears that have home ranges adjacent to Yellowstone Lake. Unlike cutthroat trout, lake trout do not move up tributary streams to spawn, but spawn within the lake at depths making them unavailable to many terrestrial predators such as grizzly bears.” It is not possible to quantify the effects of this loss of an important nutritional source with much precision, but those effects will obviously be substantial.

Unlike the bears, the river otter (*Lutra canadensis*) is “almost entirely carnivorous” (Streubel 1989), and has been a commonly observed denizen of the lake since the park’s earliest history. As predators in Yellowstone Lake, they are trout specialists but are also thought to eat longnose suckers. It is not known whether a shift of biomass in the lake from cutthroat to lake trout will have an effect on otters, but given the observed vulnerability of the cutthroat trout to otters, we suspect the shift will be negative.

The above-described birds and mammals are the best-known consumers of Yellowstone cutthroat trout, because we have research data in hand on them. But there are many more species who are known or assumed (either from local anecdotal information or from the scientific literature) to use these fish (Table 1). In all, some 42 species of birds and mammals are known or suspected to depend on the Yellowstone cutthroat trout to some extent. The list could undoubtedly be extended with the inclusion of reptiles, amphibians, invertebrates, bacteria, and fungi. It is obvious from the above discussion and from Table 1 that the Yellowstone cutthroat trout is the central, or keystone, species in the Yellowstone Lake ecosystem, and that its decline or disappearance would have disastrous consequences for much of the remaining animal life.
LITERATURE CITED


Socioeconomic Values Associated with the Yellowstone Lake Cutthroat Trout

By John D. Varley and Paul Schullery

The study of the social and economic dimensions of fish and wildlife in our country is a relatively young discipline, even for sport species harvested or otherwise of great interest to people, but especially when applied to nonconsumptive activities such as wildlife viewing or hearing. We know, for example, that wildlife observation is “the single most important activity” for 94% of Yellowstone National Park visitors (Duffield 1992), eclipsing even the storied geysers. From this information, we can conclude that wildlife viewing is socially valuable. A dollar valuation for this enormously important activity, however, has never been established. Though fish viewing has seldom been held in the same esteem as wildlife observation, the social significance of a robust population of nonharvested cutthroat trout recently became obvious to park managers. In recent years, cutthroat trout viewing at Fishing Bridge and LeHardys Rapids (Fig. 1), for instance, attracted more than a third of a million visitors, about 10% of the total annual park visitation (Gresswell and Liss 1995). What is particularly surprising is that in Yellowstone National Park, an area famous for its trout fishing, the nonconsumptive fish viewing public exceeds the total number of anglers (Fig. 2).

Social and Economic Values

Fish and wildlife are recognized as having several types of economic values besides those associated with their direct consumption (e.g., hunting, trapping, or fishing harvest). These values include use value, which is how much an individual is willing to pay to enjoy wildlife, either firsthand, or through some media; option value, which is how much an individual is willing to pay just to ensure that the wildlife exists in case the individual some day may choose to go view it; existence value, which is how much an individual is willing to pay just to know that an animal continues to thrive in the wild; and bequest value, which is how much an individual is willing to pay to know that an animal will survive for the enjoyment of future generations (Swanson et al. 1994). Except for wolf recovery, whose future regional net economic impact is on the order of $43 million a year (Duffield 1992), these values have not up to now been computed for any species in the Yellowstone Lake ecosystem, but are quite high in other nature reserves (Swanson et al. 1994).

Fig. 1. LeHardys Rapids, where cutthroat trout are frequently visible during their spawning run, has become a significant visitor attraction emphasizing a nonconsumptive use of the fishery. NPS photo.

Though wolf recovery analyses and data from other reserves may by suggestive, or even compelling, nontraditional economic values remain poorly considered and frequently neglected, merely because they have not been as well quantified as have many other types of resources. For example, if the existence value of the grizzly bear to all Americans and all other people with a concern for wildlife were to be calculated, it would at least seriously compete with the better-known values of many other traditionally recognized resources, and in fact might...
exceed them. An example given by Duffield et al. (1987) concluded that stream fisheries in Montana compared favorably economically with marketed resources such as timber, coal, or grazing. The current plight of the Yellowstone Lake cutthroat trout, with its consequences for many other species of wildlife, is an excellent example of why more analyses of these values are needed. Until now, no attempt has been made to estimate at least some of the lost spiritual, scientific, or recreational values should the Yellowstone Lake cutthroat trout population be reduced or destroyed.

**Significance of the Yellowstone Lake Ecosystem**

Yellowstone Lake, the waters tributary to it, and its outlet downstream to the Upper Yellowstone Falls are the most popular and heavily used fisheries in the park (Fig. 3), together supporting more than 264,000 cutthroat trout “catches” annually and almost 50% of the total parkwide fishing interest. Yellowstone Lake has more than 100 tributary streams and a half-dozen lakes in its immediate watershed within the park boundary. It must be emphasized that fish populations and fishing in the tributary streams (e.g., Pelican Creek, Upper Yellowstone River) and in the world-famous section of the Yellowstone River between Fishing Bridge and the Upper Yellowstone Falls will be as severely affected by lake trout as will Yellowstone Lake.

In 1994, 237,700 angler days were reported on all parkwide waters, and 78,169 (33% of the parkwide total) of those were spent on Yellowstone Lake (Kaeding et al. 1995). Extrapolating from data and interpretations for the Yellowstone Lake ecosystem presented in Varley et al. (1976) and the 1994 sport fishery data from Kaeding et al. (1995), we estimate the 1994 use on the Yellowstone River between the falls and the lake at 33,500 (14%) angler days, and the lakes and streams flowing into Yellowstone Lake at 3,400 (1.4%) angler days. Thus, we can estimate about 115,069 angler days, which in the past have been totally supported by cutthroat trout, to be in some way jeopardized by the advent of lake trout in this ecosystem.

The U.S. Fish and Wildlife Service annual reports for the past several decades have quantified extremely high levels of angler satisfaction with the fishing experiences produced by the Yellowstone Lake ecosystem. For example, in 1994, more than two-thirds of all anglers landed one or more cutthroat trout per outing, and those fish averaged more than 15 inches in length. Seventy-eight percent of the anglers responding to questionnaires reported satisfaction with their angling experience (Kaeding et al. 1995). Most fishermen and fishing writers speak of these kinds of angling adventures in superlatives.

There are accepted ways to derive an economic value for sport fisheries and we have done that here to underscore the importance of exactly what is at risk in the Yellowstone Lake ecosystem. To a great extent we have followed the method and calculations of Duffield et al. (1987), a part of which is known as a regional Travel Cost Model (TCM). The TCM approach is recommended by both the Water Resources Council (1979, 1983) and the U.S. Department of the Interior (1986) as a preferred technique. Another technique reported by Duffield et al. (1987) focuses on angler expenditure data per trip, sometimes called the “trickle-down model.”
wild trout fishery with a hatchery-supported fishery would cost $281,200 annually. He further estimated, based on actual hatchery production costs, that each wild cutthroat trout was worth $72.63 over the span of its projected three-year catchable life. Varley (1984) concluded that to recreate a fishery supported solely by hatchery fish equal to the Yellowstone River could not likely be done because the costs per fish were too high for any public agency to bear, or for anglers to tolerate paying for.

No specific economic analysis has been conducted of angler benefits or expenditures on the Yellowstone River, but calculations have been made for similar, close-by waters in the state of Montana and Wyoming. The economic data generated from fisheries in the two states are fairly comparable. For the sake of simplicity and relevance to the present, we have used Montana’s figures. The 1987 study by Duffield et al. calculated total recreational value per day for many Montana waters. Based on a reported travel cost of $.36 per mile, the statewide average for all stream fisheries was $135.38, but the data on the “blue-ribbon” Yellowstone River in Montana was higher, amounting to $276.74. Using the 1994 estimate of use on the Yellowstone River downstream from Fishing Bridge of 33,500 angler days, and Montana’s calculation for their portion of the Yellowstone, yields a 1994 value of $9,270,800 for this portion of the Yellowstone River.

It is worth noting that among all Montana streams, those nearest Yellowstone National Park (Upper Yellowstone, Upper Yellowstone tributaries, Madison, Madison tributaries) had the highest values per day in the state.

Yet another significant measure of economic value of fisheries is angler expenditure per outing. Duffield et al. (1987) calculated that total angler expenditure per day for Montana residents on streams was $29.45. For nonresidents the daily expenditure on streams was $153.61. Yellowstone Park fishermen are essentially all

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**Fig. 3.** The cutthroat trout population of the Yellowstone River (between Fishing Bridge and the Upper Falls) is threatened by the lake trout invasion, because these cutthroats spend the winter in the lake and are therefore vulnerable to predation. This river fishery is world-famous as the site of pioneering work in special regulations, and would be severely reduced in quality if the lake trout thrive in Yellowstone Lake. NPS photo.
nonresidents in terms of their expenditures and so the angler expenditure for the Yellowstone River equates to $5,145,900.

**YELLOWSTONE LAKE TRIBUTARY STREAMS AND LAKES**
The rivers, streams and lakes tributary to Yellowstone Lake are often cited by fishermen and writers as notable fisheries in their own right. Well-known streams such as the Upper Yellowstone River (above the lake), Thorofare Creek, Pelican Creek, plus literally dozens of others, and lakes such as Alder, Trail, Riddle and Sylvan, are expected to be seriously affected by the introduction of lake trout in Yellowstone Lake. Almost all of these fisheries are significantly tied to the fortunes of the cutthroat trout of Yellowstone Lake, mostly because of the annual spawning migrations from the “mother lake,” and the resultant redistribution of trout biomass. Using the economic factors detailed above, plus the Duffield et al. (1987) figures for lakes in the “Madison [River] Area” near Yellowstone Park, we estimate the total recreational value per day for these fisheries to be on the order of $809,700.

In terms of the average nonresident angler expenditure per day, an additional $365,300 can be added to the annual value of the fisheries associated with the lakes and streams tributary to Yellowstone Lake.

**YELLOWSTONE LAKE FISHERY**
The Yellowstone Lake fishery has been considered peerless since it was discovered by modern anglers in the middle of the last century. Since its popularity with Euroamericans began, literally tens of millions of cutthroat trout have been harvested, although catch-and-release regulations in recent years have reduced that harvest to fewer than 100,000 annually (Fig. 5).

We have estimated the value of the Yellowstone Lake fishery in several ways. In the first model, we have used Varley’s (1984) figures from the

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**Fig. 4.** Each wild cutthroat trout in the famous “catch-and-release” water of the Yellowstone River between Fishing Bridge and the Upper Falls has a calculated recreational value of about $72.00. NPS photo.
Yellowstone River catch-and-release section on the value of each catchable cutthroat trout, and the estimate quoted in McIntyre et al. (this volume) on the number of catchable trout in the lake to compute an average “catchable stock.” Thus, the estimate of 2.5 million catchable cutthroat trout in the lake with a nominal value of $72.63 per fish yields a value of $181,575,000 for the current catchable stock in terms of “replacement or duplication value” and “avoided fish hatchery costs.”

Using the Montana valuation figures (Duffield et al. 1987) for total recreational value, we project that the 1994 estimates of 78,169 angler days spent on Yellowstone Lake, and a value of $194.74 per angler day, yield an estimated value of $15,222,600 for that year. Using the figures calculated by Duffield et al. (1987) for average nonresident expenditure on quality lakes near Yellowstone Park an additional figure of $5,257,600 can be estimated.

**ECONOMIC VALUE OF THE YELLOWSTONE LAKE ECOSYSTEM**

Based upon the above figures for the Yellowstone River, Yellowstone Lake, and the tributaries to the lake, summed to a grand total, we conservatively estimate that the nominal one year (1994) economic value of the sport fisheries in the Yellowstone Lake ecosystem is $36,021,900.

The effect of lake trout on the Yellowstone Lake ecosystem has been projected out over a 30-year horizon, so given the following assumptions, we can project the economic effect over the next three decades. We assume 1) no lake trout control is implemented, and 2) the demise of the cutthroat trout occurs as predicted by McIntyre et al. (this report). We also factored in the expectation that during the decline of cutthroat trout, lake trout will offer a replacement sport fishery at least on par with the Lewis Lake lake trout fishery in the park. Given these assumptions, we project that in 30 years (2024) the Yellowstone Lake ecosystem sport fisheries will decline from the 1994 value of $36,000,000 to an annual value of $8,492,300.

Consequently, the cumulative 30-year value of the cutthroat trout sport fishery assuming the introduction of lake trout had not occurred is estimated at more than a billion dollars ($1,080,000,000). The consonant value assuming lake trout populations are vigorously controlled and do not exceed 20-30% of the trout biomass in the lake is $685,000,000. If no significant lake trout control is carried out and their population approaches 70-80% of the trout biomass, the 30-year value of the sport fishery is expected to decline to $439,950,000. This last scenario represents a three decade economic erosion of $640 million, which we consider the long-term net economic effect of the introduction of lake trout if park managers fail to take action.

Further, if the surge of lake trout is greater than projected and the decline in cutthroat trout is worse than expected, and this results in the cutthroat trout population becoming extinct or nearly so at the end of 30 years, we estimate that the total ecological restoration of the cutthroat trout in Yellowstone Lake, its outlet stream, and its tributaries, would have a one-time cost of a minimum of $31,250,000, or a multiple year “replacement-in-kind” of $181,575,000. If the cutthroat decline was severe enough, the subspecies may warrant listing under the Endangered...
Species Act, which would increase the restoration costs cited above.

By any measure it is obvious that saving the native ecosystem would be the desired course of action on both biological and economic grounds. Elsewhere in this volume, a lake trout control program is presented that uses a combination of sport angler exploitation and intensive, large-scale gillnetting and trapping to significantly suppress their population. This type of program, which would have to be carried out indefinitely (assuming no technological breakthroughs occur), would cost approximately $300,000 per year (30 years = $9,000,000). Thus, the lake trout control program and preservation of as much of the cutthroat trout fishery as possible would result in a highly favorable benefit:cost ratio of 27:1.

Through this brief presentation of social and economic dimensions of lake trout invasion, we have attempted to add a useful perspective on some of the values at risk. Though we were only able to speculate about option, existence, and bequest values, it is clear to us they would be substantial if those figures were available. However, by any measure the angler-use projections, while partially presumptive, demonstrate a resource of extraordinary scope, quality, and value. The fishery at risk is held in great esteem by the public and is very valuable to the local and regional economy. The Yellowstone Lake cutthroat trout population fits the definition of extraordinary significance: in their own right because they are now an imperiled subspecies, for the fishing experience they provide, on behalf of the charismatic wildlife species they feed, for the scientific laboratory they are a part of, and for the economic bonanza they provide the region.

**Literature Cited**


INTRODUCTION
Lake trout (Salvelinus namaycush) were captured in Yellowstone Lake, Yellowstone National Park in 1994. Lake trout are not indigenous to the lake and their predatory habits are perceived to be a threat to the native Yellowstone cutthroat trout (Oncorhynchus clarki bouvieri) and to all other aquatic and terrestrial species that depend on the presence of a robust population of cutthroat trout. As part of an action plan to address the problem, administrators of Yellowstone National Park convened a team of scientists to help characterize the threat to the cutthroat trout and to identify and judge the potential effectiveness of management actions to reduce that threat.

The team met in Gardiner, Montana, in February 1995. Members were selected so that as a whole the team had demonstrated capacity for objective analysis and broad experience with cutthroat trout, lake trout, population biology, management techniques, and management strategies. This is a report of their findings and judgments.

PARTICIPANTS AND PROCEEDINGS
Participants included Frederick Binkowski (Milwaukee, Wisconsin), Theodore Bjornn (Moscow, Idaho), Jon Erickson (Jackson, Wyoming), Robert Gresswell (Corvallis, Oregon), Michael Healey (Vancouver, British Columbia), Leo Marnell (Glacier National Park, Montana), John McIntyre (Boise, Idaho, Chairman), Reginald Reisenbichler (Seattle, Washington), Bruce Rieman (Boise, Idaho), James Selgeby (Ashland, Wisconsin), and James Vashro (Kalispell, Montana). Additional information was provided by David Donald (Regina, Saskatchewan) and Robert Behnke (Ft. Collins, Colorado), who were unable to attend the meeting.

The team was directed to an exploration of the available information concerning fish community dynamics in Yellowstone Lake and in other lakes where lake trout have been introduced. Based on these discussions and on their personal experience and background, each member judged the likelihood that lake trout can be eliminated from Yellowstone Lake, the likelihood that the lake trout population can be controlled, and the expected percent loss in the cutthroat trout population with and without suppression of lake trout. Team members were also asked to identify potentially useful management methods and to judge the potential effectiveness of each. Finally, they were asked to describe information needed to address the problem and to monitor the result of actions that may be taken by the National Park Service (NPS).

PROGNOSIS
The team concluded there is only a slight chance that lake trout can be eliminated from Yellowstone Lake (Fig. 1A), but they all judged there to be at least a 50% chance that substantial
control of lake trout population’s expansion was feasible (Fig. 1B).

If the lake trout population is not suppressed, most participants judged the loss of cutthroat trout from present levels would equal or exceed 50% within the next 20 years (Fig. 2A). They judged that suppression of the lake trout population might limit that loss to less than 30% of present levels (Fig. 2B).

In the absence of some action to limit lake trout, most team members judged the number of cutthroat trout would be reduced by 70% or more within 100 years (Fig. 2C). The expectation of loss in 100 years with lake trout suppression was variable, but five of eight respondents judged that it may be possible to limit the loss of cutthroat trout to 10-20% of present levels (Fig. 2D).

It is not a foregone conclusion that lake trout population will cause a catastrophe for the cutthroat trout. One participant concluded that even with no suppression of lake trout, cutthroat trout are likely to be reduced only by 20% in the short term (Fig. 2A) or the long term (Fig. 2C). Most concluded otherwise, however, and judged that protection of a robust population of cutthroat trout may require aggressive action on the part of NPS managers to suppress lake trout.

Suppression of the lake trout population was judged possible, and the cutthroat trout population remaining within 100 years may be 2 to 4 times as large as is likely if the lake trout are not suppressed.

**POSSIBLE CONTROL METHODS**

The following methods for suppressing the lake trout population were identified by the team or were otherwise brought to its attention. Options that received no more than a 0.5 chance of success by half or more of the team members are described first. Methods judged likely to be more effective are described second.

**Status Quo Angling**

Present angling regulations include killing any captured lake trout and reporting the catch to park authorities. Most team members judged that the present sport fishery of Yellowstone...
Lake had less than a 50% chance of effectively limiting the lake trout population. The present open season, no-limit regulations for lake trout will continue to raise public awareness and provide an additional monitoring tool.

**Killing Lake Trout Embryos**

This proposal included covering spawning areas with polyethylene sheeting, or with screens to collect and subsequently destroy spawn, killing developing embryos with toxicants or smothering (e.g., sand), use of mechanical removal methods (e.g., suction dredge), or use of concussion to destroy embryos. Locating and covering all of the potential spawning areas did not seem to be a viable strategy for Yellowstone Lake. The majority of the team judged there to be less than a 30% chance that any of these alternatives is a viable method for suppressing lake trout in Yellowstone Lake.

**Provide Cover for Juvenile Cutthroat Trout**

The proposal was to construct artificial cover near the outlet of major spawning tributaries to protect cutthroat trout fry as they enter the lake. None of the participants judged this tool as having a chance for success of even 20%. The additional cover was thought to be as likely to provide cover for waiting predators, including lake trout, as well as for migrating cutthroat trout fry.

**Release Sterile Sea Lampreys in Yellowstone Lake**

Discussion of this proposal included an acknowledgment that there is no source of sterile sea lamprey. Further, there is concern that use of such a tool cannot be applied without causing additional risk to cutthroat trout and other endemic species. No participant gave this proposal more than a 10% chance for successful control of lake trout at the present time.

**Attract Lake Trout to Sound or Chemicals**

Experimental evidence exists that fish can be attracted to sound and to chemicals (including pheromones), captured, and removed. Given
the absence of evidence that large numbers of lake trout could be attracted from substantial distances, the team judged that there was no more than a 30% chance of success with sound or chemical attractants.

**Trap-net**
More than half the team members judged the use of trap-nets to have at least a 40% chance of successfully suppressing the lake trout population. The main disadvantage of the method is high expense of operation.

**Long-line Fishing**
Nine participants judged that long-line fisheries would have only between 10 and 30% chance of success in controlling lake trout abundance. One participant judged long-line fishing to have a 60% chance for success. Disadvantages of the method include the need for use of cut-baits, and this technique is more labor intensive than netting and trapping techniques.

**Use of Divers or Remotely Operated Vehicles to Kill Lake Trout**
These methods offer little hope for success in killing large numbers of lake trout. No respondent judged that even a 30% chance for success exists.

**Supplementation of Cutthroat Trout Population**
Increasing the number of cutthroat trout in Yellowstone Lake by stocking hatchery-reared cutthroat trout was viewed as only contributing to an even greater food supply for lake trout. No respondent judged supplementation to have more than a 20% chance of reducing the perceived risk to the cutthroat trout population in Yellowstone Lake.

**Stocking “Buffer Species”**
The general conclusion was that the effects of adding new species to the lake community were too unpredictable. Most team members judged this proposition to have only a 10% chance of successfully diverting the lake trout’s dietary habits and reducing risk for cutthroat trout.

**Use of Chemical Toxicants**
There was no support for use of chemical treatment of Yellowstone Lake to eliminate the lake trout. Disadvantages include the non-selectivity of potential chemicals and the infeasibility of treating such a large lake.

**Use of “Judas Fish”**
The proposal was to obtain and sterilize male lake trout from Lewis Lake. These males would then be fitted with radio or ultrasonic transmitters and released in Yellowstone Lake where they would help to locate the spawning grounds. The team judged that such ventures might be useful but should begin with fish captured from Yellowstone Lake.

**Use of Sterile Male Lake Trout**
The proposal was to stock large numbers of sterile males according to protocols developed for insect pest control. The ensuing discussion generally discounted the proposal because the needed technology for fish has not been developed.

The following methods were judged to have at least a 50% chance of being successful in reducing lake trout abundance by more than half of the respondents.

**Directed Angling (Fig. 3A)**
This option included use of anglers experienced in catching lake trout. Cut bait, echo location, ice fishing, and other approaches known to be effective in catching lake trout would be used.

**Lake-wide Gillgetting (Fig. 3B)**
Commercial fisheries in the Great Lakes can effectively harvest and depress targeted stocks of lake trout. Locations and movements of lake trout tend to be predictable, thus making the fish
vulnerable to such fishing. Removal of large fish is an effective means of limiting lake trout reproduction because they do not mature until attaining a body length of 15 to 18 inches. Net fisheries should be able to avoid cutthroat trout for the most part by fishing when lake trout and cutthroat trout are separated by depth, and where together, by targeting lake trout that are larger than cutthroat trout.

**Capture on Spawning Grounds (Fig. 3C)**
This method includes location of lake trout spawning grounds through use of radio or ultrasonic tagging, and use of intensive netting or other techniques to capture or destroy the congregated fish.

**Conclusions**
Based on these results, the team concluded that use of mechanical removal methods, either gillnetting or some combination of gillnetting and trapping is likely to provide the greatest success in controlling lake trout abundance. Initial control measures can be initiated in 1995 field season along with an experimental gillnetting program for obtaining the information needed to improve the effectiveness of the program. Adaptive management strategies to incorporate new information and understanding on a continuing basis. Some of the reviewed methods or other ideas may become useful in the future, either by themselves or in combination with other methods.

Control of the lake trout population is likely to require a perpetual effort. In the short term, the lake trout population is expected to continue expanding limited by the effectiveness of the control effort. In the long term, the lake trout population presumably will tend to stabilize at a level also dictated by the effectiveness of the control program. The effort (including costs and other resources) needed to control the lake trout population at that level can then be estimated. A carefully developed and managed lake trout control program can provide the information needed to evaluate its success.

**Information Needs**
The team concluded that most information needed to implement an effective program can be obtained by initiating an aggressive
The Yellowstone Lake Crisis

experimental gillnetting program for lake trout and refining the existing monitoring program for cutthroat trout. Elaborate and expensive new program elements are not needed over and above the gillnetting program. Primary information needs are data to assess the status (abundance indices and distribution in space and time) of the lake trout and to monitor impacts on Yellowstone cutthroat trout. Accurate information to assess abundance trends of cutthroat trout is most important. Present gill-netting, creel census, and census methods in spawning streams need to be refined to enable cohort and catch-curve analyses. Extensive surveys of spawning streams combined with intensive investigation of three spawning streams in separate locations around the lake would help to improve the present database. Information needed to monitor lake trout abundance and to develop their population dynamics (age-determination, mortality, recruitment, spawning dynamics, diet) and growth rates was considered the next most important task.

Appropriate locations and time periods for the most effective removal of lake trout without further harming cutthroat trout are unknowns. Accordingly, adaptive management must be seen as an integral component of the lake trout control program.

Depth distribution may be the most appropriate criterion for separating cutthroat trout and lake trout because considerable overlap in their size distributions is expected in Yellowstone Lake. Almost no cutthroat trout are found at depths greater than 30 m, and lake trout may prefer depths near 40-60 m. These criteria can be used to begin a control program, and target depths can be verified from netting, tagging, and radio tracking. Captured lake trout might be fitted with radio tags to facilitate locating the spawning grounds. As information comes available to show the most effective sizes, locations, and seasons for use of nets, an increasingly aggressive program can be developed to control lake trout abundance.

Additional information to assess the source and reproductive success of the lake trout in Yellowstone Lake, to describe the genetic structure of the cutthroat trout metapopulation, and to partition sources of cutthroat trout mortality were also identified as important for understanding the dynamics of the system, but not as critical to the immediate need as the information described earlier.

Summary

1. Although there is a slight chance that lake trout will not threaten the Yellowstone Lake cutthroat trout, chances are high that lake trout cannot be eliminated and will seriously reduce the cutthroat trout population in Yellowstone Lake.

2. The probability that lake trout abundance can be limited by initiating an aggressive control program using mechanical means of removal is high, but there is little chance that lake trout can be eliminated. Consequently, a long-term commitment is required to maintain control lake trout abundance.

3. The cutthroat trout population is likely to be reduced whether or not the lake trout are suppressed, but suppression of lake trout may reduce the expected loss of cutthroat trout by 50% or more.

4. Most information needed to increase the effectiveness of initial control measures can be obtained from the control program itself. Some modification of the present monitoring program is required to enable detection of changes in the cutthroat trout population.
A DRAFT PLAN OF ACTION FOR CONTROLLING EXPANSION OF THE LAKE TROUT POPULATION IN YELLOWSTONE LAKE

by Tom Olliff

INTRODUCTION
In the absence of complete knowledge of the behavior and habits of lake trout in Yellowstone Lake, we intend to develop a program for limiting their expansion based on available knowledge coupled with careful monitoring and application of adaptive management strategies. Control will begin by gillnetting at depths where cutthroat trout do not occur, and secondarily by experimental gillnetting designed primarily to gain information on lake trout distribution in space and time. Monitoring provides the basis for assessing the success or failure of alternative management actions and provides the basis for making real-time adjustments needed to help reduce deleterious effects in the cutthroat trout population.

Our long-term goal is to develop and maintain a program for controlling lake trout abundance that will limit the loss of cutthroat trout to less than 20% of present levels. Proposed levels of effort may be initially too conservative or excessive, but rigorous application of adaptive management will enable us to make appropriate adjustments as the program develops in subsequent years.

We identify the fact that additional resources are needed if our present fishery program is to remain intact. We have, however, elevated the perceived crises caused by the lake trout to our most important problem for fishery investigations. If we cannot successfully secure the additional funding required for this effort, we will redirect existing resources for aquatic ecosystem work to the following program.

1995 OBJECTIVES
1. We will attempt to secure $50,000 of new funding to finance the 1995 experimental program.

2. We will take action to secure a permanent addition of $300,000/year to base funding for the fishery program to maintain the control program.

3. Present monitoring efforts for cutthroat trout were designed only to detect long-term changes in the population and must be supplemented to attain the desired result. The cutthroat trout population needs to be monitored at a level of rigor that will provide the statistical sensitivity needed to detect changes in abundance in a timely manner. Consequently, we will expand spawning ground surveys to all important spawning streams, and increase the intensive monitoring presently conducted only at Clear Creek to three runs by including two additional tributaries.

4. We want to prevent existing lake trout from attaining spawning size. We will accordingly move aggressively to remove as many lake trout from deep water as time and personnel permit.

5. We will develop a suitable index for monitoring lake trout abundance in Yellowstone Lake. Data from Objectives (4) and (6) will help to attain this objective.

6. We will improve our effectiveness in removing lake trout. This objective requires that we develop an understanding of lake trout...
OBJECTIVES FOR 1996
1. We will attempt to secure permanent funds (estimated at $300,000/year) added to our base funding to maintain the control program.

2. We will maintain an expanded spawning ground survey on all important spawning streams, and intensively monitor runs in three important tributaries.

3. We will continue preventing as many lake trout as we can from attaining spawning size by gillnetting in deep water and other locations where it is shown from work in 1995 Objective (5) and 1996 Objective (4) that lake trout can be captured without harming cutthroat trout. We will continue work and analysis to develop a suitable index for monitoring lake trout abundance in Yellowstone Lake.

4. We will continue to improve our effectiveness in removing lake trout via an experimental gill-netting program designed to assess where and when lake trout can be effectively captured without harming cutthroat trout. The objective includes description of lake trout age-structure, mortality, recruitment, and behavior.

OBJECTIVES FOR 1997
1. We will maintain an expanded spawning ground survey on all important spawning streams, and intensively monitor runs in three important tributaries.

2. We will continue efforts to prevent as many lake trout as we can from attaining spawning size by gillnetting in deep water and other locations where it is shown from work in 1995 Objective (5) and 1996 Objective (4) that lake trout can be captured without harming cutthroat trout. We will continue to develop a suitable index for monitoring lake trout abundance in Yellowstone Lake.

3. We will continue to improve our effectiveness in removing lake trout via an experimental gill-netting program designed to assess where and when lake trout can be effectively captured without harming cutthroat trout. The objective includes description of lake trout age-structure, mortality, recruitment, and behavior.

4. To the extent that by 1997 adaptive management has enabled us to redirect resources and personnel to some additional endeavors, we will initiate studies to locate spawning locations and to assess spawning success for lake trout, to describe the structure of the cutthroat trout metapopulation, and to partition the sources of mortality for cutthroat trout.
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