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Estimates of Predator Consumption of Yellowstone Cutthroat Trout (*Oncorhynchus clarki bouvieri*) in Yellowstone Lake

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ABSTRACT

We estimated consumption of Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*) by resident terrestrial predators and human anglers to place into context the potential predatory impact of exotic lake trout (*Salvelinus namaycush*) in Yellowstone Lake, Yellowstone National Park, Wyoming, USA. Estimates of consumption rates of piscivorous birds and mammals from the literature were combined with recent estimates of abundance of these predators in the park. Angling mortality was estimated by creel surveys from park management records. Results from a demographic model were used to estimate population size and age distribution of the cutthroat trout population. We estimated that terrestrial predators consumed approximately 7% of the trout population in the lake; angler mortality represented only 1-4% of the adult population. Piscivorous birds accounted for most (99%) of predator mortality, which was focused largely on juvenile trout. American white pelicans *(Pelecanus erythrorhynchos)* and grizzly bears (*Ursus arctos*) ate an estimated 5% of the adult trout spawning in streams. Depending on the ultimate size of the lake trout population, predation by introduced lake trout is expected to increase juvenile mortality by 13-67%. Consumption of young adult cutthroat trout by a large population of lake trout would effectively increase angling mortality by 50%. The resulting decline in the native cutthroat trout population is projected to have a significant effect on piscivorous birds, mammalian carnivores, and anglers in Yellowstone National Park.

INTRODUCTION

The recently discovered occurrence of lake trout (*Salvelinus namaycush*) in Yellowstone Lake, Wyoming, is expected to pose a significant threat to the survival of the Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*) (Kaeding et al. 1996). Introduced lake trout have been implicated in the declines of native fish faunas across North America (Benson et al. 1961, Cordone and Frantz 1966, Dean and Varley 1974, Donald and Alger 1993), and fisheries managers and biologists fear that predation by adult lake trout will eventually lead to the collapse of the cutthroat trout population (McIntyre 1995), which represents the largest remaining population of the subspecies (Gresswell 1995). Because the cutthroat trout is the dominant fish in the system in terms of abundance and biomass, terrestrial predators such as white pelicans *(Pelecanus erythrorhynchos)*, ospreys (*Pandion haliaetus*), and grizzly bears (*Ursus arctos*) are also likely to suffer significantly from a decline in the Yellowstone Lake cutthroat trout population. The demise of the Yellowstone Lake population is expected to have a substantial negative effect on the recreational

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sports fishery as well, which has been valued at more than $36 million annually (Varley and Schullery 1995). The lake trout is unlikely to replace cutthroat trout in either the current recreational fishery or the diets of most predators because it occupies deeper waters of the lake and spawns in the lake, not streams.

To date, research aimed at understanding and managing the lake trout problem has focused on the predatory impact of lake trout on cutthroat trout in Yellowstone Lake (Ruzycki and Beauchamp 1997). However, it may be difficult to assess adequately the relative effects of lake trout without some estimate of natural mortality rates. We developed a matrix demographic model of the Yellowstone Lake population to examine the possible consequences of lake trout in the system (Stapp and Hayward in press). As part of this study, we sought to estimate mortality of cutthroat trout by natural predators and by human anglers in order to provide some ecological context for the potential effects of lake trout. Here, we apply our model results and published information on consumption rates and abundance of predators in the Yellowstone Lake ecosystem to estimate annual natural mortality of different age classes of cutthroat trout. We also compare natural and human angling mortality to our estimates of mortality from lake trout predation.

METHODS

Gresswell and Varley (1988) and Varley and Gresswell (1988) reviewed the ecology and management history of the cutthroat trout population in Yellowstone Lake. The lake is deep and oligotrophic and, at 35,000 ha, is the largest high-elevation lake in North America. The Yellowstone cutthroat trout is the only native salmonid and, until the discovery of lake trout, co-existed in the lake with longnose suckers (*Catostomus catostomus*) and two introduced minnows. Thus, the Yellowstone Lake population presumably evolved in the absence of native predatory fishes (Varley and Schullery 1996). Since the inception of Yellowstone National Park, human exploitation of the fishery has been extensive. A significant decline in abundance of cutthroat trout occurred in the 1960s, which park officials attributed to several decades of overharvest and spawn-taking operations (Varley and Gresswell 1988). Beginning in the 1970s, fishing was restricted on both the lake and along tributaries. The recovery of the population to a large, stable size and near-historical age distribution has been attributed to the successful implementation of these regulations.

We constructed a demographic matrix model for the cutthroat trout population in Yellowstone Lake (Stapp and Hayward in press). Parameters in our model included vital rates (age-specific survival and fecundity) calculated from earlier studies from the lake and nearby waters, and from recent unpublished data collected as part of monitoring studies conducted by the Park Service to track trends in the lake's cutthroat trout population (Jones et al. 1987-1990). In addition to providing information on the growth rate of the population and insights into the relative importance of different life stages in understanding population growth, our model allowed us to calculate the stable age distribution, defined as the proportionate representation of different age classes in the population under the vital rates specified in our model. These results indicated that approximately 90% of the population is of Ages 3 and younger, 3% of Age 4, 2% of Age 5, and 2% of Ages 6 and older, using the age-length categories for Yellowstone cutthroat trout provided by Gresswell (1995). We combined the stable age distribution and a Park Service estimate of 3.5 million trout ≥350 mm (Age 5+) in Yellowstone Lake (range 1-4 million; Jones et al. 1980) to estimate the number of cutthroat trout in each age class and the total population size in the lake. These estimates were used to estimate the proportion of different life stages consumed by predators and removed by anglers. We emphasize that our projections of predator consumption and changes in the size of the cutthroat trout population are based on results of a relatively simple, deterministic model with restrictive assumptions. A model incorporating density-dependent population growth and dynamic predator-prey relationships between cutthroat trout and their predators would likely refine these estimates.

We used published estimates of rates of energy and/or trout consumption by predators and the abundance of associated predator populations to estimate annual consumption of Yellowstone cutthroat trout. We focused on vertebrate species that we expected would be the most important natural predators (piscivorous birds, grizzly bears). We did not consider other vertebrates (e.g., black bears, *Ursus americanus*; river otters, *Lutra canadensis*; dippers, *Cinclus mexicanus*) that are known to prey on cutthroat trout, but for which we lacked adequate data to assess population size, consumption rates, or relative use of stream and lake areas. We also assessed the potential effects of human anglers by estimating fishing mortality (including hooking mortality from catch-and-release anglers) using creel survey reports from Yellowstone Lake anglers (Jones et al. 1990).

Estimates of the amount of biomass or energy consumed by predators were converted to numbers of fish as follows. We first estimated the size and mass of adult, spawning and juvenile trout. The average lengths (mass) of adult and spawning trout were 312 mm (320 g) and 353 mm (468 g), respectively, based on results of gill net sampling (Jones et al. 1990) and spawner surveys (Gresswell et al. 1997) and a length-mass regression for lentic populations of inland cutthroat trout (Kruse and Hubert 1997). We used the stable age distribution from our model and average lengths for juvenile trout to calculate a weighted average for body length (97 mm). However, because this value was outside the range of the published length-mass regression, we assumed an average mass of 20 g for Ages 1-3. Energy consumption estimates were converted to fish biomass by assuming 5.38 KJ/g wet mass of cutthroat trout and 90% assimilation efficiency (Pritchard and Robbins 1990).

Grizzly bears

Grizzly bears are found throughout the park, but the activity of many bears is concentrated around Yellowstone Lake tributaries and other spawning streams during the June-July spawning period (Reinhart and Mattson 1990). Because of the omnivorous food habits of grizzly bears, cutthroat trout may be a relatively small component of the annual diet, but trout may be an important source of energy and protein in spring, particularly for reproductive females. The concentrated nature of trout prey in streams, however, tends to concentrate bear activity, increase rates of encounter between females with dependent young and solitary males near spawning streams, and leads to higher cub mortality (Mattson and Reinhart 1995). The intensive use of spawning streams, especially those near Yellowstone Lake, also brings bears closer to human activity, which may pose a risk to park visitors and increase bear deaths from motor vehicle accidents and removals by park staff. Thus, cutthroat trout seem to play an important and complex role in the natural history of Yellowstone grizzlies.

Radiotelemetric studies suggest that at least 44 different grizzly bears feed on Yellowstone Lake spawners (Reinhart and Mattson 1990). Because female bears were located near spawning streams 1.65 times more frequently than males (Mattson and Reinhart 1995), we estimated that 27 females and 17 males typically forage in the lake's spawning streams. Approximately 37% of females near streams had dependent young (Mattson and Reinhart 1995), so we assumed that 10 of the 27 females had cubs.

We calculated daily energy expenditure using Mattson's (1997) estimates for active male and female grizzlies. Energy consumption of female bears with young was assumed to be four times that of solitary, non-reproductive females. The diet of bears was assumed to be 90% cutthroat trout (Mattson and Reinhart 1995) for a typical spawning period (47 days; Gresswell et al. 1997). We also assumed that all trout consumed were spawners from the lake and not permanent stream residents.

Piscivorous birds

At least 15 species of piscivorous birds live near Yellowstone Lake and its tributaries and thus depend to some degree on cutthroat trout (Dean et al. 1975). Some species such as eared grebes (*Podiceps nigricollis*) and California gulls (*Larus californicus*) consume primarily juvenile fish, whereas larger birds such as American white pelicans and common mergansers (*Mergus merganser*) feed on adults and spawners (Dean et al. 1975). Davenport (1974) estimated population sizes and daily trout consumption of 12 species of piscivorous birds on Yellowstone Lake in 1973 and 1974. We used this information, combined with more recent estimates of population sizes, to estimate annual mortality of trout due to bird predation. We assumed that trout were susceptible to avian predators for 135 d each year (15 May - 30 September).

Two of the most important avian predators on cutthroat trout have been studied intensively in Yellowstone National Park. Because of their consistent abundance and the large amount of fish biomass they consume, American white pelicans are the most important predators on adult cutthroat trout (Varley and Schullery 1996). Diem and Pugesek (1994) estimated an average population size of 546 adults and 214 juveniles on the Molly Islands, the largest breeding congregation in Yellowstone Lake. Adult pelicans consumed 0.85 kg of fish per day (Davenport 1974), whereas nestlings consumed 1.2 kg/d (MacMahon and Evans 1992) until fledging (67 d; Johnsgard 1993). We assumed that adults fed on spawning fish during the 47-d spawning period and adult fish for the remainder of the summer. Ospreys are not as abundant as pelicans but they are dependent on cutthroat trout. On average, 43 adult ospreys foraged on Yellowstone Lake in 1974 (Davenport 1974, Swenson 1978). Based on information provided by Swenson (1979), we assumed that there are 17 active nests on the Lake each year and an average of 0.67 young fledged per active nest. Approximately 93% of the diet of ospreys was cutthroat trout, most (89.5%) of which were smaller than 350 mm (Swenson 1978). Adult and nestling ospreys consumed 0.40 kg/d and 0.62 kg/d (45-d nestling period), respectively (Dean et al. 1975). We used the distribution of prey sizes provided by

Swenson (1978) to partition consumption of trout into juvenile (Age 1-3) and Age 4 life stages.

Less information was available regarding rates of trout predation and productivity of the other 13 avian piscivores in the Yellowstone Lake population. We estimated trout consumption by young birds of these species by assuming that developing young would require a proportion (28%) of total adult consumption intermediate between that calculated for pelicans (43%) and ospreys (14%).

Human anglers

In combination with hatchery operations, human angling was implicated in the decline of the lake's cutthroat trout population during the middle of the century. On average, more than 300,000 trout were removed annually by anglers between 1955 and 1965, when creel limits were still relatively high and there was no limit on the size of trout taken (Gresswell and Varley 1988). Recovery of the population since the 1980's has been attributed largely to the change in fishing regulations in 1975 to reduce harvest and protect spawning-age trout (Gresswell and Varley 1988). Landing and creel rates, and the age distribution in both creel surveys and gill net sampling have remained relatively constant since 1980. Furthermore, older age classes (Ages 9 and 10) are discovered in increasing numbers in spawning runs (Keading et al. 1995). These data suggest that the Yellowstone Lake trout population has been relatively stable in recent years.

We used our model to evaluate the possible impact of human angling as a source of mortality for trout. We used results of volunteer creel surveys from 1985-1989 (Jones et al. 1990) to estimate the number of trout removed from Yellowstone Lake by anglers each year. Total human-related mortality was calculated by adding an additional 8-10% mortality from hooking injuries for fish that were landed and released. Current fishing regulations permit anglers to keep two fish <330 mm in length. Because trout measuring <250 mm are not completely recruited into the fishery and are presumably kept less often by anglers (mean length of fish creeled = 312 mm; Jones et al. 1990), an individual trout may be vulnerable to direct human mortality for only a single year (Jones et al. 1990), at approximately Age 4. We compared the number of fish removed from this age class by anglers to our estimate of abundance of Age 4 trout in Yellowstone Lake.

RESULTS AND DISCUSSION

Based on the stable age distribution from our demographic model, we estimated that 5.2% of the population was ≥350 mm in length (Age 5+). Combining this information with the park's estimate of 3.5 million trout in Ages 5 and older, we estimated a total population size of 67.7 million fish, with a range of 19.3 - 77.4 million. Some 61 million of these are juveniles (Age 1-3) and 6.6 million were considered adults (Age 4+).

Effects of terrestrial predators and anglers

Using our estimates of annual mortality from natural vertebrate predators and human anglers, we estimated that terrestrial vertebrates consume approximately 7% (6 - 24%) of the total trout population each year (Table 1). Piscivorous birds account for 99% of predator mortality, most (94%) of which was directed at juvenile age classes. Human anglers and grizzly bears each take $\leq$0.1% of the total population and approximately 2% of the adult age classes that they prey upon. Combined, human and vertebrate predators killed an estimated 345,650 adult trout (Age 4+), representing approximately 5% of the adult population. Predators also consumed approximately 5% of the estimated spawners from Yellowstone Lake tributaries.

Predators accounted for a relatively small proportion of the total estimated mortality of Yellowstone Lake cutthroat trout. We estimated annual mortality rates of 63% and 52% of juvenile and adult cutthroat trout, respectively, based on data in Ball (1955) and creel survey data from the Park fishery (Stapp and Hayward in press). If our estimates of survival rates and predator consumption are reasonable, terrestrial predators and human anglers are directly responsible for 12% (range: 10 - 49%) and 10% (9 - 35%), respectively, of annual mortality on juvenile and adult trout. These results suggest that we have either underestimated predation by these sources or that other factors are responsible for most of the mortality of cutthroat trout in this system. For example, other terrestrial or aquatic predators may have a larger impact than expected. Alternately, abiotic factors and disease may be the most important sources of mortality for Yellowstone cutthroat trout.

Our estimates of predation by avian predators are considerably lower than those reported for salmonids in other systems. Piscivorous birds consumed 20-24% of annual production of brown and brook trout in Michigan streams (Alexander 1979). Similarly, White (1957) calculated that mergansers consume more than 67%

Table 1. Estimates of annual mortality of Yellowstone Lake cutthroat trout from terrestrial predators and anglers. Estimates of proportion of fish population consumed is based upon a model-derived stable age distribution and a population estimate of 67.7 million fish (Stapp and Hayward in press). Values in parentheses are consumption estimates for the range of population sizes of the cutthroat trout population (range: 19.3 - 77.4 million trout).

Predator	Life stage/age class eaten	Total number eaten/yr	% of stage eaten/yr	% of total fish population eaten
Grizzly bears	stream spawners	20,910	1.59 (1.40 - 5.58)	0.03 (0.03 - 0.11)
Piscivorous birds[a]	juveniles (Age 1-3)[b]	4,438,120	7.26 (6.36 - 25.39)	6.55 (5.73 - 22.92)
	adults (Age 4+)[c]	211,200	3.21 (2.81 - 11.22)	0.31 (0.27 - 1.09)
	stream spawners[d]	46,390	3.54 (3.10 - 12.38)	0.07 (0.06 - 0.24)
Human anglers[e]	young adults (Age 4)	67,150	2.18 (1.90 - 7.61)	0.10 (0.09 - 0.35)
Total predator mortality		4,783,770		7.07 (6.18 - 24.74)

[a] Includes fish consumption by adult and nestling birds. Except for American white pelicans and ospreys, consumption by nestlings was estimated as 28% of adult consumption.
[b] Species include, in order of biomass of trout consumed: eared grebe, California gull, common merganser, Caspian tern (*Sterna caspia*), Barrow's goldeneye (*Bucephala islandica*), common loon (*Gavia immer*), bufflehead (*Bucephala albeola*), belted kingfisher (*Ceryle alcyon*), and double-crested cormorant (*Phalacrocorax auritus*).
[c] American white pelican, osprey, and bald eagle (*Haliaeetus leucocephalus*).
[d] American white pelican.
[e] Yellowstone Lake creel survey, mean number creeled plus hooking mortality, 1985-1989.

of salmon smolt production. Ruggerone (1986) concluded that ring-billed gulls (*Larus delawarensis*) alone consumed 2% of spring migration of juvenile salmon (*Oncorhynchus* spp.) and steelhead (*Salmo gairdneri*). Elson (1962) found that removal of kingfishers and, especially, mergansers resulted in a five-fold increase in survival of stock parr of Atlantic salmon compared to areas where these predators were present. We speculate that differences in predation rates between our results and those of previous studies may reflect the unique conditions of our system; many of these earlier studies focused on hatchery-reared juveniles in stream populations where encounter rates and susceptibility to predators may be higher than for native trout in a large lake such as Yellowstone Lake. Obviously, any estimate of predatory impact will be influenced significantly by the reliability of estimates of the size and age distribution of the trout population and of predator population densities. The range of our estimate of the size of the Yellowstone Lake population was wide (Table 1), but even assuming the smallest population size (19.3 million trout), our estimates imply that terrestrial predators may have a relatively minor impact (<25%) on the Yellowstone Lake population.

Based on these results, we speculate that abundance of cutthroat trout is not driven by mortality from terrestrial predators or human angling, at least not at current harvest levels or predator densities. Additionally, because of the current large size of the Yellowstone Lake population, it seems unlikely that the carrying capacity of the environment for predators is determined by abundance of cutthroat trout. Other factors (e.g., the availability of nesting habitat or alternate prey, intraspecific territoriality, or encounters with humans) may set the upper limit on the size of most predator populations in the park. It is also important to recognize, however, that, although terrestrial predators may not be an important mortality factor for cutthroat trout, a significant decline in trout abundance may have a dramatic effect on population persistence of many of these species, which depend on cutthroat trout for most of their nutritional and energetic intake during some portion of their life. Thus, while the effects of a drop in cutthroat trout numbers may be subtle for species with mixed diets (e.g., grizzly bears, otters), species such as pelicans, ospreys, and other piscivorous birds may experience population declines that mirror or are more drastic than those observed in the cutthroat trout population as a whole.

Potential effects of lake trout

A significant decline in the cutthroat trout population has been projected in the event that a large population of lake trout were to become established in Yellowstone Lake (McIntyre 1995). To minimize the impact of introduced lake trout, the Park Service implemented a large-scale gill-netting program in 1996, encouraged recreational fishing for lake trout, and initiated research to estimate the predatory impact of lake trout on cutthroat trout. These studies suggest that each large (>300 mm) lake trout consumes, on average, 59 cutthroat trout each year, and that 95% of the cutthroat trout eaten are two- and three-year-old juveniles (100-270 mm; Ruzycki and Beauchamp 1997). Based on these consumption estimates, a population containing 10,000 large lake trout would consume 590,000 cutthroat trout each year. A future population of 50,000 lake trout, which would not be unreasonable for a lake the size of Yellowstone Lake, would consume 2.95 million cutthroat trout. Assuming that most mortality from lake trout is concentrated on juvenile age classes and that natural mortality rates remain the same (Table 1), a relatively small population of lake trout would increase mortality of juvenile trout by 13%. Increased predation on juvenile cutthroat trout may be critical to the survival of the lake population because of the importance of survival of young trout to asymptotic population growth in our demographic model (Stapp and Hayward in press). If the lake trout population were to grow unchecked, predation on juvenile and adult cutthroat trout would increase by 67% above the current natural level. This scenario would then likely result in a 60% or greater reduction in the size of the cutthroat trout population within 100 years.

Assuming that lake trout predation, angling mortality, and natural mortality are additive, it seems plausible that predation by lake trout may substantially reduce the availability of cutthroat trout for terrestrial predators. Considerable attention has been directed at the possible impact on the resident grizzly bear population (e.g., Wuerthner 1998), but the most immediate and dramatic effect would likely be on piscivorous birds, which depend on juvenile cutthroat trout (Table 1). In comparison, grizzly bears have a broad diet and some ability to switch among foods (Mattson 1997, Mattson et al. 1991). Moreover, although adult cutthroat trout currently represent only 1% of the diet of lake trout in the lake (Age 4 trout; Ruzycki and Beauchamp 1997), a large population of lake trout would consume approximately 34,000 adult, catchable cutthroat trout, which would be equivalent to a 50% increase in angling mortality. A reduction in the abundance of these younger trout would presumably be translated into fewer spawners, and less prey for stream-based predators, and, as suggested earlier, a dramatic decline in the Yellowstone Lake cutthroat trout population.

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LITERATURE CITED

Alexander, G. R. 1979. Predators of fish in coldwater streams. Pp. 153-170 in: Predator-prey systems in fisheries management (H. Clepper, ed.). Sport Fishing Institute, Washington, DC.

Ball, O. P. 1955. Some aspects of homing in cutthroat trout. Proceedings of the Utah Academy of Science, Arts, and Letters 32:75-80.

Benson, N. G., J. R. Greeley, M. I. Huish, and J. H. Kuehn. 1961. Status of management of natural lakes. Transactions of the American Fisheries Society 90:218-224.

Cordone, A. J., and T. C. Frantz. 1966. The Lake Tahoe sport fishery. California Fish and Game 52:240-274.

Davenport, M. B. 1974. Piscivorous avifauna on Yellowstone Lake, Yellowstone National Park. U. S. D. I. National Park Service, Yellowstone National Park, WY.

Dean, J. L., and J. D. Varley. 1974. Annual project report - 1973. Fishery management Program, Yellowstone National Park.

Dean, J. L., J. D. Varley, and R. E. Gresswell. 1975. Annual project report - 1974. Fishery management Program, Yellowstone National Park.
Diem, K. L., and B. H. Pugesek. 1994. American white pelicans at the Molly Islands, in Yellowstone National Park: Twenty-two years of boom-and-bust breeding, 1966-1987. Colonial Waterbirds 17:130-145.
Donald, D. B., and D. J. Alger. 1993. Geographic distribution, species displacement, and niche overlap for lake trout and bull trout in mountain lakes. Canadian Journal of Zoology 71:238-247.
Elson, P. F. 1962. Predator-prey relationships between fish-eating birds and Atlantic salmon. Fisheries Research Board of Canada Bulletin No. 133.
Gresswell, R. E. 1995. Yellowstone cutthroat trout. Pp. 36-54 in: Conservation assessment for inland cutthroat trout (M. Young, ed.). U.S.D.A. Forest Service, General Technical Report RM-GTR-256, Fort Collins, CO.
Gresswell, R. E., W. J. Liss, G. L. Larson, and P. J. Bartlein. 1997. Influence of basin-scale physical variables on life history characteristics of cutthroat trout in Yellowstone Lake. North American Journal of Fisheries Management 17:1046-1064.
Gresswell, R. E., and J. D. Varley. 1988. Effects of a century of human influence on the cutthroat trout of Yellowstone Lake. American Fisheries Society Symposium 4:45-52.
Johnsgard, P. A. 1993. Cormorants, darters, and pelicans of the world. Smithsonian Institution Press, Washington, DC.
Jones, R.D., R. Andrascik, D. G. Carty, E. M. Colvard, R. Ewing, W. R. Gould, R. E. Gresswell, D. L. Mahony, T. Olliff, and S. E. Relyea. 1990. Annual project technical report for 1989. Fishery and Aquatic Management Program, Yellowstone National Park, National Park Service.
Jones, R.D., D. G. Carty, R. Ewing, R. E. Gresswell, E. D. Koch, D. L. Mahony, and J. L. Mohrman. 1989. Annual project technical report for 1988. Fishery and Aquatic Management Program, Yellowstone National Park, National Park Service.
Jones, R.D., D. G. Carty, R. E. Gresswell, C. J. Hudson, and D. L. Mahony. 1987. Annual project technical report for 1986. Fishery and Aquatic Management Program, Yellowstone National Park, National Park Service.
Jones, R.D., D. G. Carty, R. E. Gresswell, and D. L. Mahony. 1988. Annual project technical report for 1987. Fishery and Aquatic Management Program, Yellowstone National Park, National Park Service.
Jones, R.D., R. E. Gresswell, D. E. Jennings, S. M. Rubrecht, and J. D. Varley. 1980. Annual project technical report for 1979. Fishery and Aquatic Management Program, Yellowstone National Park, National Park Service.
Kaeding, L. R., G. D. Boltz, and D. G. Carty. 1996. Lake trout discovered in Yellowstone Lake threaten native cutthroat trout. Fisheries 21:16-20.
Kaeding, L. R., D. G. Carty, D. L. Mahony, G. Boltz, and S. A. Anderson. 1995. Annual project technical report for 1994. Fishery and Aquatic Management Program, Yellowstone National Park, National Park Service.
Kruse, C. G., and W. A. Hubert. 1997. Proposed standard weight (W_s) equations for interior cutthroat trout. North American Journal of Fisheries Management

17:784-790.
Mattson, D. J. 1997. Use of ungulates by Yellowstone grizzly bears *Ursus arctos*. Biological Conservation 81:161-177.
Mattson, D. J., and D. P. Reinhart. 1995. Influences of cutthroat trout (*Oncorhynchus clarki*) on behavior and reproduction of Yellowstone grizzly bears (*Ursus arctos*), 1975-1989. Canadian Journal of Zoology 73:2072-2079.
Mattson, D. J., B. M. Blanchard, and R. R. Knight. 1991. Food habits of Yellowstone grizzly bears, 1977-1987. Canadian Journal of Zoology 69:1619-1629.
McIntyre, J. D. 1995. Review and assessment of possibilities for protecting the cutthroat trout of Yellowstone Lake from introduced lake trout. Page 28-33 in: The Yellowstone Lake crisis: Confronting a lake trout invasion (J. D. Varley and P. Schullery, eds). Report to the Director of the National Park Service, National Park Service, Yellowstone National Park.
McMahon, B. F., and R. M. Evans. 1992. Nocturnal foraging in the American white pelican. Condor 94:101-109.
Pritchard, G. T., and C. T. Robbins. 1990. Digestive and metabolic efficiencies of grizzly and black bears. Canadian Journal of Zoology 68:1645-1651.
Mattson. 1990. Bear use of cutthroat trout spawning streams in Yellowstone National Park. International Conference on Bear Research and Management 8:343-350.
Ruggerone, G. T. 1986. Consumption of migrating juvenile salmonids by gulls foraging below a Columbia River dam. Transactions of the American Fisheries Society 115:736-742.
Ruzycki, J. R., and D. A. Beauchamp. 1997. A bioenergetic modeling assessment of the lake trout impact in Yellowstone Lake. Pages 127-133 in: Wild Trout IV (R. Hamre, ed.). Trout Unlimited and Federation of Fly Fishers, Fort Collins, CO.
Stapp, P., and G. D. Hayward. In press. Effects of an introduced piscivore on native trout: Insights from a demographic model. Biological Invasions.
Swenson, J. E. 1979. Factors affecting status and reproduction of ospreys in Yellowstone National Park. Journal of Wildlife Management 43:595-601.
Swenson, J. E. 1978. Prey and foraging behavior of ospreys on Yellowstone Lake, Wyoming. Journal of Wildlife Management 42:87-90.
Varley, J. D., and R. E. Gresswell. 1988. Ecology, status, and management of the Yellowstone cutthroat trout. American Fisheries Society Symposium 4:13-24.
Varley, J. D., and P. Schullery. 1996. Yellowstone Lake and its cutthroat trout. Pp. 49-73 in: Science and ecosystem management in the National Parks (W. L. Halvorson and G. E. Davis, eds.). University of Arizona Press, Tuscon, AZ.
Varley, J. D., and P. Schullery. 1995. Socioeconomic values associated with the Yellowstone cutthroat trout. Pages 22-27 in: The Yellowstone Lake crisis: Confronting a lake trout invasion (J. D. Varley and P. Schullery, eds.). Report to the Director of the National Park Service, National Park Service, Yellowstone National Park.

White, H. C. 1957. Food and natural history of mergansers on salmon waters in the Maritime Provinces of Canada. Fisheries Research Board of Canada Bulletin No. 16.

Wuerthner, G. 1998. A fish story. National Parks May/June:24-27.

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