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EFFECTS OF INTRODUCED LAKE TROUT ON NATIVE CUTTHROAT TROUT IN YELLOWSTONE LAKE

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Abstract. The establishment of a reproducing population of nonnative lake trout (*Salvelinus namaycush*) poses a serious threat to the integrity of the Yellowstone Lake ecosystem, particularly to the indigenous cutthroat trout (*Oncorhynchus clarki bouvieri*). We used standard fisheries techniques to quantify the population-level impact resulting from this introduction, while the U.S. National Park Service (NPS) developed a program to control their numbers. Lake trout diets, thermal history, growth, and size structure were incorporated into a bioenergetics model to estimate the predatory impact of introduced lake trout and to evaluate the effectiveness of the NPS lake trout control program. Population size structures were estimated from catches of fish in gill nets that were corrected for mesh size selectivity. Lake trout abundance was estimated using virtual population (cohort) analysis, and cutthroat trout abundance was estimated using hydroacoustics. Juvenile cutthroat trout were highly vulnerable to predation, and lake trout preyed on cutthroat trout that averaged 27–33% of their body length. Based on our model, an average piscivorous lake trout consumed 41 cutthroat trout each year. During 1996, the piscivorous lake trout population consumed an estimated 15 metric tons of cutthroat trout (129 000 fish) composing 14% of the vulnerable cutthroat trout production. The NPS removed nearly 15 000 lake trout from 1995 to 1999. Had these predators remained in Yellowstone Lake they would have consumed an estimated 23 metric tons of cutthroat trout (200 000 fish) during 1999 alone. If left unchecked, lake trout would clearly pose a serious threat to the long-term existence of the indigenous cutthroat trout. This analysis demonstrates the negative impact of an introduced predator in an ecologically isolated aquatic ecosystem.

Key words: bioenergetics model; cutthroat trout; indigenous species; introduced species; lake trout; Oncorhynchus clarki bouvieri; *predation;* Salvelinus namaycush; *species invasions; Yellowstone Lake, Wyoming.*

Introduction

Biological invasions are second only to habitat destruction as a cause of native species decline (Simberloff 2001). To conserve native species, managers and conservation biologists are increasing their efforts at eliminating or controlling introduced species (e.g., Kaiser 2001). A wide array of control methods for introduced species have been used, ranging from shooting and trapping to introducing biological control agents. However, before control efforts can be justified, and to facilitate public support for management actions, the negative impacts of introduced species should be demonstrated. Although many predator introductions were unintentional, many others were introduced to provide a recreational resource perceived to be lacking (e.g., Kaufman 1992). When such introduced species become established, a clientele often develops that exploits the resource and lobbies for maintaining the introduced species. Therefore, the challenge to conservationists is to demonstrate negative impacts before significant damage occurs to native communities, begin control measures while the introduced population is small, and act before a clientele becomes established. This challenge can be met by implementing a control program while simultaneously collecting data to evaluate and substantiate it.

Biological invasions are particularly devastating on islands. Species-poor island communities are susceptible to invasions (Loope and Mueller-Dombois 1989, Pimm 1989, Mauchamp 1997) and their native fauna can be particularly devastated by novel predators (e.g., Craig et al. 2000). Predators introduced to islands often confront few competitors and find many vulnerable prey species that evolved without predators (e.g., Kiesecker and Blaustein 1997, Fritts and Rodda 1998). Nevertheless, the small size and isolation of many islands may facilitate control of unwanted invaders.

Many lakes can be considered islands because they are isolated from other aquatic systems in a terrestrial

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landscape (Magnuson 1976). In North America, natural barriers have isolated lakes, creating island communities that have been largely closed since the last ice age (Magnuson 1991). The introduction of novel predators to lakes has had devastating consequences to indigenous fish fauna (e.g., Zaret and Paine 1973, Mills et al. 1994, Nyström et al. 2001). The consequences of a novel predator have perhaps been greatest in Lake Victoria, Africa, where predatory Nile perch (*Lates niloticus*) have been implicated in the possible extinction of hundreds of haplochromine cichlid species (Reinthal and Kling 1994, Goldschmidt 1996).

The 1994 discovery of introduced lake trout (*Salvelinus namaycush*) in Yellowstone Lake, Wyoming, raised considerable concern for the native fauna (Varley and Schullery 1995). Lake trout are large, long-lived fish predators that have been extensively introduced into waters outside their native range (Crossman 1995). Lake trout were introduced into Lewis and Shoshone Lakes, previously fishless lakes of Yellowstone National Park, Wyoming, during the 1890s (Varley and Schullery 1998) and subsequently spread downstream to Jackson and Heart Lakes through connecting rivers. Although on the other side of the continental divide from Yellowstone Lake, these waters were the likely source of the introduced lake trout because they are $<$30 km distant by road. Microchemistry analysis and aging of lake trout otoliths suggests they have been in Yellowstone Lake at least since the early 1980s (A. Munro, *unpublished data*). Lake trout are well adapted to cold, oligotrophic (nutrient-poor) lakes with extensive hypolimnia. Their large body size, longevity, iteroparity, high fecundity, large eggs, and independent embryos are attributes that contribute to their survival in harsh environments where recruitment can be variable (Evans and Olver 1995), especially when few reproductive individuals are present. This *K*-selected strategy, or bet-hedging, is adaptive when reproductive failures occur among years. Large body size also assures few predators for adults and often places this piscivore at the top trophic position in food webs (Vander Zanden and Rasmussen 1996).

A reproducing population of nonnative lake trout in Yellowstone Lake potentially poses a serious threat to the integrity of this ecosystem, particularly to indigenous cutthroat trout. Cutthroat trout (*Oncorhynchus clarki*) were once the dominant salmonid of interior waters of the western United States. Fourteen subspecies are recognized (Behnke 1992), but only four subspecies inhabit large lake ecosystems. The greatest abundance of genetically pure, lake-dwelling Yellowstone cutthroat trout (*O. c. bouvieri*) now exists only in the most undisturbed habitats of its former range in Yellowstone National Park, Wyoming (Varley and Gresswell 1988, Behnke 1992). Yellowstone National Park (YNP) includes 91% of the current range of the Yellowstone cutthroat trout subspecies and contains 85% of their historical lake habitat (Varley and Gresswell 1988, Gresswell 1995).

Yellowstone Lake cutthroat trout are predisposed to lake trout predation. In fish communities, predation risk is strongly related to predator gape limitation, so body size strongly influences prey vulnerability (Mittelbach and Persson 1998). To maintain large body sizes, large fish predators also require high caloric intake. In Yellowstone Lake, lake trout attain sizes two to three times larger than cutthroat trout. The largest lake trout captured in YNP exceeded 16 kg (Varley and Schullery 1998), and elsewhere lake trout have exceeded 36 kg (Scott and Crossman 1973). In contrast, cutthroat trout from Yellowstone Lake rarely exceed 2 kg. Cutthroat trout in Yellowstone Lake have also evolved over the past 10 000 yr without large piscine predators and are believed to lack adaptive behaviors to reduce predation (Behnke 1992).

Cutthroat trout play a significant role in the Yellowstone Lake ecosystem by providing an important trophic link to the terrestrial community. The influence of piscine nutrients on terrestrial ecosystems has been demonstrated for both lotic (Cederholm et al. 1989, Hilderbrand et al. 1999, Willson and Gende 2000) and lentic (Spencer et al. 1991) ecosystems. The shallow-water distribution and spawning migrations of cutthroat trout into tributary streams exposes them to many avian and mammalian predators that rely on these fish for protein (Swenson 1978, Gunther 1995, Schullery and Varley 1995). Significant reductions in their population would reduce migratory spawners and have cascading effects on the surrounding ecosystem (Spencer et al. 1991).

Here, we report on the use of a bioenergetics model to estimate the population-level effects of lake trout on indigenous cutthroat trout. Bioenergetics models have been widely used by fisheries scientists to measure predatory impacts (Hansen et al. 1993) and have been applied to predatory fish introductions (Kitchell et al. 1997). However, we believe this is the first application of bioenergetics to simultaneously evaluate the impact of an introduced predator and a program to control their abundance. Although we applied this approach to an aquatic ‘‘island’’ system, the approach should also be useful to assess effects of predators introduced to terrestrial islands. We previously reported per-capita predatory consumption estimates for these lake trout (Ruzycki and Beauchamp 1997), but these were based on preliminary information and not expanded to include population-level impacts. Here, we present predation rates using lake-wide abundance estimates of both lake trout and cutthroat trout, coupled with expanded diet and age-structure information, and project this predatory impact into the future. The National Park Service (NPS) is conducting a lake trout removal program and needs to track its success, so we also report predation estimates for the lake trout removed from the population.

STUDY AREA

Yellowstone Lake (surface area 341 km^2) is located in east-central Yellowstone National Park, Wyoming (elevation 2356 m), near the headwaters of the Yellowstone River, and is isolated by large waterfalls just downstream of the outlet. The lake has a mean depth of 48 m and a maximum depth of 107 m (Kaplinski 1991). Ice cover typically occurs from mid-December through May, and a thermocline forms in July. Hypolimnetic waters below the thermocline remain well oxygenated during thermal stratification and summer surface temperatures rarely exceed 18°C (Benson 1961).

Although only two fish species are indigenous to Yellowstone Lake, four introduced species are now established. Yellowstone cutthroat trout and longnose dace (*Rhinichthys cataractae*) are indigenous (Simon 1962). Longnose sucker (*Catostomus catostomus*), redside shiner (*Richardsonius balteatus*), lake chub (*Couesius plumbeus*), and lake trout have been introduced. Longnose dace, redside shiner, and lake chub inhabit littoral regions, whereas cutthroat trout and longnose sucker are distributed throughout the lake (Gresswell et al. 1994). Lake trout have also been captured throughout the lake, but adult fish are most abundant in a large, western bay called West Thumb.

METHODS

To determine per-capita lake trout predation of cutthroat trout we used an age-structured bioenergetics modeling approach to estimate consumption by average individuals of each age class. Model inputs specific to Yellowstone Lake included predator diet composition, thermal history, and annual growth rates. Per-capita consumption was expanded to population-level consumption using the estimated age-structured abundance of the piscivorous portion of the lake trout population. We then compared this population-level predation to the estimated abundance of cutthroat trout and their population-level production of biomass. Another approach to estimating the predatory impact of lake trout would have been to monitor changes in the demographics of the cutthroat trout population. We chose bioenergetics modeling over this approach for several reasons. First, lake trout consumption estimates provided a direct measure of the impact on the cutthroat trout population without the confounding effects from other potential influences (e.g., angler exploitation, whirling disease, environmental factors). Second, modeling consumption by the more spatially limited and much smaller population of lake trout was logistically more feasible than monitoring the cutthroat trout population, which was much more numerous. Third, intensively sampling the cutthroat trout population would have potentially reduced the same population we were attempting to conserve. Fourth, the lake trout invasion was relatively recent and their influence on cutthroat trout demography at this early stage would likely not have been evident. Finally, we were able to maximize limited resources by collecting data to quantify the predatory impact, while concurrently helping to develop and implement the NPS lake trout control program.

Age and growth of lake trout and cutthroat trout

Age and annual growth for lake trout were estimated from annual growth increments on sagittal otoliths. Since we were interested only in average growth of fish from each year class, we used a standard regression technique allowing the intercept to differ from the origin (Campana 1990, DeVries and Frie 1996). We attempted to represent all ages by selecting 114 fish across the entire size range of fish captured with gill nets and received from anglers from 1996 to 1998. Our target was to represent each age class by a minimum of three individuals. To do this, we chose at least five fish from each of 14 50-mm length groups (200–850 mm). We used linear regression of total body length (TL, millimeters) as a function of otolith radius to convert average otolith size at each annulus to average length at annulus formation. The body lengths back-calculated using annuli delimited the minimum average length for each age class, whereas the maximum size was determined from the next annulus. Dissected otoliths were cleaned in bleach (sodium hypochlorite) to remove adhering tissue, rinsed in deionized water, and stored in 95% ethanol (Secor et al. 1991). The remainder of otolith preparation followed Casselman and Gunn (1992), except that otoliths were read directly rather than from acetate impressions. Annual growth increments of prepared otoliths were measured at 25–40 × magnification with an image analysis program (Leica Q500MC, Leica Microsystems, Bannockburn, Illinois, USA) and interpreted by consensus of two viewers. To estimate the size-at-age of lake trout for which we had insufficient otolith samples, we fit a von Bertalanffy growth curve to age groups that satisfied our minimum criteria. Parameters for the von Bertalanffy growth curve were determined using a least squares nonlinear regression model fit (SPSS 1997).

Age and annual growth for cutthroat trout were estimated from annual growth increments on scales from 1227 fish across the size range captured in gill nets from 1991 to 1998 (115–540 mm TL). Annuli were interpreted from images of acetate impressions of scales magnified using a microprojector (Lagler 1956). The remainder of age and growth methods for cutthroat trout were similar to those used for lake trout, except that a von Bertalanffy growth curve was not needed.

The abundance of fish in age classes was determined by developing age-frequency distributions of the lake trout and cutthroat trout populations. Length classes were converted to age classes as defined above. We used catches of fish in NPS gill nets from 1995 to 1998 to represent the lake trout and cutthroat trout populations. Effort from this netting was equivalent to 2604 overnight sets of 100-m nets. Nets were set at depths from 1–75 m throughout the lake during the ice-free season from late May through October. Because gill nets are highly selective for certain sizes of fish, we used a range of mesh sizes from 19–89 mm square measure. We adjusted for the size selectivity of each mesh size for each species separately following Hansen et al. (1997), except that we used Gaussian (normal distribution) functions instead of skew-normal probability density functions (J. R. Ruzycki, *unpublished data*). We also adjusted for unequal mesh-size effort by determining the proportion of effort for each mesh size relative to the most frequently used mesh size and by dividing individual mesh-size catches by this proportion. This method adjusts the estimated size distribution of fish populations based on individual mesh-size effort and vulnerability of the different sizes of fish in the population to the mesh sizes used for sampling (Hansen et al. 1997). All subsequent analyses used these adjusted catch rates of fish in gill nets.

Lake trout and cutthroat trout abundance and production

We used gill net catches to estimate lake trout population abundance by virtual population or cohort analysis (VPA) for a population subjected to a continuous fishery. We assumed that the oldest lake trout in the population was 23 yr of age, the oldest fish aged using otoliths. We used Pope's approximation (Pope 1972) and terminal F assumptions (Hilborn and Walters 1992) to model the fish abundance during the years from 1996 to 1999. To satisfy the assumptions of equal catchability and natural mortality among age groups, the analysis was restricted to adult fish (ages 6–23 yr; all ages hereafter are in years), and the gill net selectivity method was used to estimate the age-frequency distributions. We also had too few years with sufficient catches of juvenile fish for a VPA of lake trout <6 yr of age. We extrapolated the abundance of lake trout ages not fully catchable by the gear (ages 3–5) by multiplying the total number of lake trout aged 6–23 by the ratio of lake trout at ages 3–5 to ages 6–23 from the corrected age-frequency distribution. We then apportioned this abundance estimate into the three age classes (3–5) using this same corrected age-frequency distribution.

A hydroacoustics (sonar) survey was used to estimate the abundance of cutthroat trout throughout Yellowstone Lake between 3 and 6 August 1998. To adequately sample the entire cutthroat trout population, we stratified the lake into two zones: nearshore (0–40 m deep) and offshore or pelagic (>40 m deep). The survey was composed of 14 nearshore transects and 9 offshore transects. For nearshore zones, we continuously varied our sampling between the 4 and 40 m depth contours. Conventional line transects were used while sampling offshore regions. Single transects within strata were used as replicates for data analysis.

Acoustic data were collected during daylight with a Model 241 echosounder (Hydroacoustic Technology, Seattle, Washington, USA) with two 200 kHz split-beam transducers each positioned 0.5 m below the surface. To enumerate fish near the surface a 6°-transducer was aimed horizontally (i.e., side-looking, 8° below horizontal), enabling us to sample fish 10–50 m from the boat and from the water's surface to 8–12 m deep. To enumerate fish at greater depths, a 15°-transducer was aimed vertically and sampled fish at depths >8 m (down-looking, Yule 2000). The down-looking and side-looking threshold was set at 0.2 and 0.44 volts, respectively, which allowed detection of fish targets exceeding −55 dB (~100 mm TL). To collect simultaneous data from the two transducers, we used a fast-multiplexing technique where sound waves alternated between the side- and down-looking channels.

Densities of acoustic targets were expanded to estimate lake-wide fish abundances by areal and volumetric expansion within the two strata. Side-looking population estimates were calculated by multiplying average density within the sampled volume by surface-water volumes of the near- and offshore zones. Population estimates from the side-looking transducer within a stratum were later converted to estimates per unit lake surface area, because these are most commonly reported. Sample volume for the down-looking transducer increases with depth. A simple solution to correct for increasing sample volume with depth is to convert fish detected to density at the surface. For example, at 4 m deep, the area of the cone equals 1 m^2 using the 15°-transducer. Therefore, a fish detected 4 m deep equals one ''weighted'' fish (1 fish/m^2). At 20 m, the cone area is 5.3 m^2, and one fish detected at this depth is equivalent to 0.19 fish/m^2 at the surface (i.e., 1/5.3). Fish densities at the surface were estimated by summing weighted fish. Surface area and volume for each 10-m stratum were calculated from a digitized bathymetric map (Yellowstone National Park, Spatial Analysis Center, Wyoming, USA) adapted from Kaplinski (1991).

Because hydroacoustic technology does not identify fish species, acoustic targets were assigned to species using results from gill nets set along the bottom in nearshore zones, and mid-water trawling and vertical gill nets deployed in the limnetic waters of offshore zones. For nearshore zones, we used gillnetting designed to measure distribution of both lake trout and cutthroat trout. Sixteen sample sites were randomly chosen from a total of 280 potential sites. Each site was sampled with a gang of six monofilament gill nets designated as the sample unit. Small-variable-mesh nets and large-variable-mesh nets were paired and set overnight at three depth strata (3–10 m, 15–25 m, and 30–50 m). Large-mesh nets (3.3 m deep, 68.6 m long) consisted of five, 13.7 m long panels of different mesh size (57-, 64-, 70-, 76-, and 89-mm bar measure netting). Similarly, small-mesh nets (2 m deep, 76 m long) consisted of five equal panels of 19-, 25-, 32-, 38-, and

51-mm bar measure netting. One small-mesh and one large-mesh net were set at each of the three depth strata. For offshore zones, 26 trawl tows were conducted during three nights concurrent with hydroacoustics sampling. The trawl opening was 3 m wide and 7 m deep, and was fitted with a cod-end mesh of 5 mm. The trawl was lowered to a specified depth, opened, towed at 1.0 m/s for 20–35 min, closed, and brought back to the surface. In addition, vertical gill nets (2.1 m wide, 27.4 m deep) were suspended from the surface in water exceeding 35 m deep. At each of three sites, a gang of three gill nets each composed of a single mesh size (13-, 19-, or 25-mm bar measure netting) were set on two consecutive days (24 h for each set). Fish captured were identified to species and measured (TL). Hydroacoustic targets were assigned to species after stratifying by zone and using proportions of species in catches within size groups caught in nets. Because neither gillnetting nor hydroacoustic efforts adequately sampled cutthroat trout <100 mm TL, this portion of the population was not included in our analysis.

Biomass production by age classes of cutthroat trout vulnerable to lake trout predation was estimated by first determining the size range of cutthroat trout (64–365 mm TL) in the diets of 418 lake trout (320–850 mm TL) captured in the gill nets and in additional netting used for the NPS control program. To convert length measures (TL) to mass (M_{CT}, grams), we used a length/mass relationship developed using all cutthroat trout (size range = 131–508 mm TL) captured in our gill nets from Yellowstone Lake during 1997:

$$M_{\mathrm{CT}} = 0.000033\mathrm{TL}^{2.77} \qquad (1)$$

($r^2 = 0.92$, $n = 1920$). Age class abundance for cutthroat trout was estimated by applying the proportion represented by each age class (ages 2–6) from the age-frequency distributions developed from the adjusted gill net catches to the hydroacoustic abundance estimate. Biomass for each age class was then calculated as the product of mean body mass (g) and abundance. Production (P_{CT}, metric tons per year) was estimated as

$$P_{\mathrm{CT}} = G \times B \qquad (2)$$

where G is the instantaneous rate of growth (natural log of the ratio of final to initial mass), and B is the mean biomass (metric tons) of each age class (Ney 1993). Initial and final masses for each age class were determined from the scale analysis and length/mass regression.

Seasonal and ontogenetic diets of lake trout

We examined the diets of lake trout collected by gill nets during May through October 1996–1999. Fish captured in the nets were placed on ice, and stomachs were removed for later analysis. Prey items were identified and separated by taxon, blotted, and weighed. When possible, partially digested fish prey items were identified by external body or bone morphology. Total lengths for all intact cutthroat trout in the diets of lake trout predators were measured. Original TL at ingestion for partially digested cutthroat trout was converted from measured vertebral column length (VL), and standard length (SL) using regression equations derived from a sample of 30 preserved cutthroat trout specimens (125–235 mm TL; Ruzycki and Beauchamp 1997). To describe seasonal shifts in food preference, we divided the ice-free season into three periods based on thermal stratification of the lake (see *Lake trout consumption rates*).

Female lake trout fecundity

We estimated size-specific female lake trout fecundity (eggs per kilogram) to project the future growth of an expanding lake trout population. We collected 11 female lake trout (size range = 481–805 mm TL) at spawning grounds during September and October 1996. Mature gametes were dissected from each female and subsampled volumetrically using three replicates. After estimating the average number of eggs/L, the total volume of each female's eggs was then measured and converted to number of eggs per kilogram body mass. Nonlinear regression was used to develop a relationship between female body mass and number of eggs.

Lake trout consumption rates

For model simulations, individual lake trout diet composition was calculated as proportions of total diet by wet mass. Seasonal changes in diet composition were examined by dividing the ice-free season into three periods: prestratification, 15 May to 15 July; stratified, 16 July to 20 September; and poststratification, 21 September to 31 October. Data from the poststratification period was used to model the remainder of the ice-free season (November–December). We collected no diet information for the ice-covered season, so we estimated winter diets by linear interpolation from poststratification to prestratification proportions.

Because temperatures experienced by lake trout strongly influence their physiological energetics, we measured vertical temperature profiles bi-weekly (once every two weeks) at a central location in Yellowstone Lake during the ice-free season from June through October 1998 and 1999 using a thermistor lowered at 1–5-m intervals through the water column. For the remainder of the year, we measured vertical temperature profiles using a vertical array (1, 3, 5, 10, 15, 20, 30, and 40 m depths) of thermistors that recorded temperatures at 1-h intervals. Bi-weekly mean temperatures were then calculated to provide similar time intervals as the ice-free measurements. Depths inhabited by lake trout were determined from catches of fish in NPS gill nets set at depths from 5–75 m. Because of ontogenetic shifts in lake trout depth distributions, lake trout thermal history was modeled separately for the three age

TABLE 1. Energy density estimates (J/g wet mass) of individual predator and prey items used for bioenergetics simulations.

Prey item	Surrogate	Energy density (J/g)	Reference
Amphipods	Amphipoda	4427†	Cummins and Wuycheck (1971)
Chironomids	Chironomidae	2742†	Cummins and Wuycheck (1971)
Zooplankton	*Daphnia* spp.	3812‡	Luecke and Brandt (1993)
Leeches	Hirudinae	4743§	Hanson et al. (1997)
Unidentified invertebrates	···	3931‖	Calculated as an average of identified invertebrates
Fish eggs	*Salvelinus namaycush*	5699¶	Stewart et al. (1983)
Unidentified fish	*Oncorhynchus mykiss*	5764§	Hanson et al. (1997)
Cutthroat trout	*Oncorhynchus mykiss*	5764§	Hanson et al. (1997)
Longnose sucker	*Perca flavescens*	4186§	Hanson et al. (1997)
Lake trout	*Salvelinus namaycush*	5699¶	Stewart et al. (1983)

groups (3–4, 5–8, and 9–23) used to describe lake trout diets.

We used the Hanson et al. (1997) bioenergetics modeling program to develop a model for the lake trout population of Yellowstone Lake. This model solves an energy balance equation by constraining ration levels by the observed growth endpoints that are specific to the population of interest (Kitchell et al. 1977). The physiological parameters for lake trout were taken from Stewart et al. (1983). Model runs began on 1 June and ended 31 May. Ice cover typically breaks up on Yellowstone Lake near 1 June. We hypothesized that lake trout growth accelerated during this period, thus creating a new annulus on their otoliths. Predator and prey energy densities were derived from literature sources (Table 1). Because information was unavailable for energy content of several prey species, surrogates were used. Ten percent of invertebrate prey biomass was assumed indigestible after Stewart et al. (1983).

Because male and female lake trout differ in both their maturity schedules and percent of body mass invested into gonadal tissue, we simulated spawning in the model separately for males and females using data collected from lake trout captured during the 1996–1998 spawning seasons. Simulations incorporated maturity schedules (most male lake trout mature at age 4 and females mature at age 7), gonadal to total individual biomass ratios (males = 3.3%, females = 14.3%), and the population sex ratio (64% males; J. R. Ruzycki, *unpublished data*). Maturity schedules and the population sex ratio were determined from fish captured in gill nets throughout the season. Further, after individuals mature in Yellowstone Lake, females spawn only every other year, whereas males spawn yearly. Frequency of spawning was determined by examining the gonads of all lake trout captured during the spawning season. To simulate mass loss from spawning, we therefore subtracted 2.1% (3.3 × 0.64) of body mass for fish ages 4–6 and 4.7% ([3.3 × 0.64] + [14.3 × 0.36 × 0.5]) for fish ≥7 yr of age each year on 1 October, which corresponds to peak spawning time.

Separate model simulations were run for each age class (ages 3–23) of lake trout. To convert length (TL) to mass (M_{LT}, grams) for lake trout, we used a length/mass relationship from lake trout (185–854 mm TL) captured in Yellowstone Lake from 1997 to 1999:

$$M_{\mathrm{LT}} = 0.000019\mathrm{TL}^{2.89} \tag{3}$$

($r^2 = 0.95$, $n = 7161$). Individual model consumption estimates for an average fish of each age class (kilograms per year) were expanded to population-level consumption using the 1996 VPA abundance estimate (ages 6–23) and the age-frequency distribution (ages 3–5). Consumption by all age classes was then summed to estimate total population consumption.

Control program evaluation

We evaluated the effectiveness of the NPS lake trout control program by estimating the number of cutthroat trout that would have been consumed by the netted lake trout had they been left in the population. To simulate mortality and growth for the proportion of the population represented by netted fish captured during 1996–1998, we applied annual survival and growth rates for each subsequent year after they were removed from the population. Survival rates for adult lake trout (ages 6–16) and cutthroat trout (ages 2–10) were computed from a catch curve using the adjusted gill net data from 1995 to 1998 (Van Den Avyle 1993). To convert the biomass of cutthroat trout eaten per year to number eaten per year, we divided the biomass consumed by each lake trout age class by the average body mass (g) of cutthroat trout found in their diets (see *Methods: Lake trout consumption rates*).

We projected to the year 2035 the future potential impact on cutthroat trout by a controlled, an uncontrolled, and an uncontrolled and expanding age 3–23 lake trout population. We present these projections not to predict the actual biological outcome, but to show a range of possible outcomes. Declining trends in the lake trout population with control were estimated using the difference in our VPA estimates from 1996 and 1999 and assuming that this decline would continue for another four years (2000–2003). We assumed this decline was reasonable because removal efforts during this period will likely equal or exceed 1999 efforts.

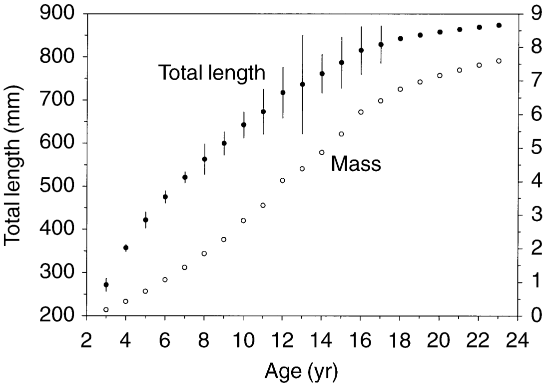

FIG. 1. Sizes (total length, mm; mass, kg) at age (yr) of lake trout sampled from Yellowstone Lake, Wyoming. Sizes at ages 3–17 were determined from measurements of otoliths. Sizes at ages 18–23 were determined using a von Bertallanfy growth curve. Error bars indicate 95% confidence intervals.

Because the lake trout population in Yellowstone Lake is recently established (Keading et al. 1996; A. Munro, *unpublished data*) and expanding, we assumed that no density-dependent declines in growth or survival had yet occurred, so that removal efforts would not result in compensatory responses. We then assumed that the lake trout population would remain stable at this controlled level from 2003 to 2035 due to sustained removal efforts.

Increases in the lake trout population without control were estimated using the same 1996–1999 VPA estimates, except that fish removed annually from the population during the control program were added back to the population estimates for the years 1996–1999. We then estimated annual survival of this uncontrolled lake trout population using the catch curve method based on our 1996 catches, which represent the lake trout population before significant removal efforts were initiated. All lake trout cohorts were allowed to grow and recruit to the next age class based on this unexploited survival estimate. For each year of the simulation, each new age 3 cohort was assumed to equal that of the 1996–1999 average. This estimate does not incorporate increases in natural spawning production and is therefore conservative.

Finally, we estimated an uncontrolled lake trout population that is expanding its reproductive potential by utilizing the extensive spawning substrates throughout the entire lake basin. Beginning with the uncontrolled population, we simulated an expanding population by allowing the population to grow without density dependence by incorporating estimates of female fecundity (see above) and annual survival rates. Egg-to-age-1 annual survival rate ($S = 0.0043$) was taken from Shuter et al. (1998), whereas survival rates for older age classes were estimated using a catch curve. These projections were then compared to our estimates of the 1998 lake-wide population and production estimates of vulnerable cutthroat trout (ages 2–6). All statistical analyses were computed using Sigma Stat software (SPSS 1997).

RESULTS

Age and growth of lake trout and cutthroat trout

The oldest lake trout aged using otoliths (23 yr) measured 858 mm TL, and the smallest lake trout (aged 2 yr) measured 123 mm TL. Sagittal otolith radius (O_r, millimeters) was positively related to lake trout TL at capture as follows:

$$\mathrm{TL} = 583.2(O_r) - 234.7 \qquad (4)$$

($r^2 = 0.95$, $n = 114$, $P < 0.001$). We restricted this and subsequent analyses to the size and age range of fish in our sample (ages 2–23; Campana 1990). For this analysis, lake trout size at age increased from 271 mm TL (0.18 kg) at age 3 to 828 mm TL (6.4 kg) at age 17 (Fig. 1). For lake trout, the von Bertalanffy growth function fit to the otolith size-at-age data was

$$l_t = 903(1 - e^{-0.144(t+0.70)}) \qquad (5)$$

($r^2 = 0.99$, $n = 114$, $P < 0.001$), where l_t is total length (mm) at time t (yr). Using this equation, an age 23 lake trout is 873 mm TL (7.6 kg; Fig. 1), and maximum attainable body size is 903 mm TL (7.9 kg) for the Yellowstone Lake population (Van Den Avyle 1993).

Similar to the VPA abundance estimates, the age-frequency distribution of the lake trout population, estimated from corrected gill net catches, indicated a greater number of young adults (ages 4–6) compared to older age classes (Fig. 2A). The estimated age-frequency distribution of the relatively short-lived cutthroat trout was dominated by fish age 2–6 (Fig. 2B).

Lake trout abundance and cutthroat trout production

We estimated the abundance of age 3–5 lake trout at 8300 fish and age 6–23 lake trout at 2998 fish in 1996, prior to substantial removals by the NPS lake trout control program. In 1999, after the removal of 14 469 age 3–23 fish by the NPS during 1995–1998, the population was estimated at 4800 age 3–5 and 1740 age 6–23 lake trout. The age 6–23 portion of the lake trout population was dominated by younger age classes with fish ages 6–9 accounting for 65% of the total (Table 2). We estimated the cutthroat trout population in 1998 at 1.74 million (95% CL; 1.21 and 2.27 million) fish >100 mm TL. Production by this population was an estimated 196 metric tons/yr. Seventy two percent (142 metric tons/yr) of this production was by age classes 2–5.

Diets of lake trout

We apportioned lake trout into three age categories (3–4, 5–8, and 9–23) based on ontogenetic shifts in the proportion of cutthroat trout in their diets. Young lake trout diets were dominated by invertebrates, but

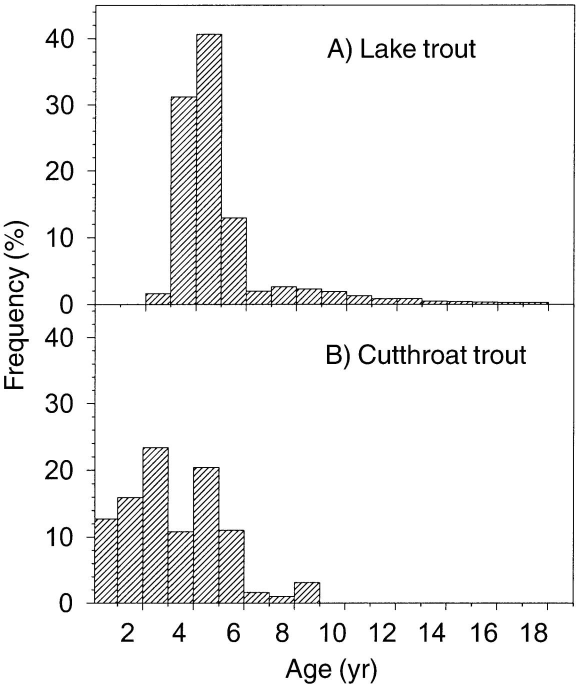

FIG. 2. Age-frequency distributions for (A) age 3–18 lake trout and (B) age 1–9 cutthroat trout captured in Yellowstone Lake. The lake trout and cutthroat trout distributions are from fish captured in gill nets from 1996 to 1999 and from 1997 to 1998, respectively, and are corrected for gill net mesh selectivity.

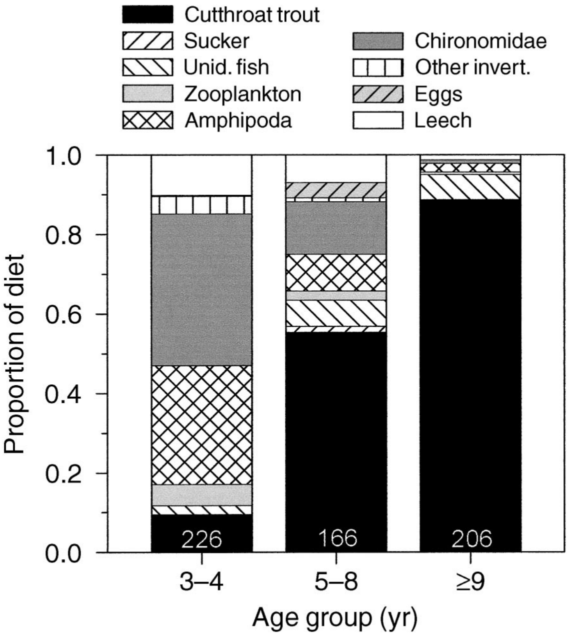

FIG. 3. Annual diet composition (calculated as proportion of diet by wet mass) of three age groups of lake trout. Diet categories include: cutthroat trout, longnose sucker (sucker), unidentified fish (unid. fish), zooplankton, Amphipoda, Chironomidae, Hirunidae (leech), other invertebrates (other invert.), and lake trout eggs (eggs). Sample sizes for non-empty stomachs examined in each age category are shown near the bottom of the histogram.

fish prey items became increasingly important as lake trout grew (Fig. 3). Proportions of cutthroat trout in the diet differed significantly among age groups of lake trout (Kruskal-Wallis ANOVA on Ranks: $H = 272.8$; df $= 2$; $P < 0.001$). Invertebrates composed 83% of the annual diets of age 3–4 lake trout, whereas fish prey represented $>$60% of the diet for age 5–8 lake trout (421–563 mm TL). The diets of lake trout ≥9 yr of age ($>$600 mm TL) were dominated (95%) by fish prey. Most fish eaten were cutthroat trout. Except for large adults, lake trout exhibited seasonal shifts in prey selection (Fig. 4). During the ice-free season, age 3–4 lake trout shifted from a spring diet dominated by amphipods to an autumn diet composed largely of chironomids. Age 5–8 lake trout increased the proportion of cutthroat trout in their diets from 30% in spring to 77% in autumn, whereas larger lake trout ate predominately cutthroat trout (81–98%) throughout the year.

Female lake trout fecundity

The relative fecundity (eggs per kilogram body mass) of female lake trout increased with body size. Female lake trout fecundity (F_{LT}; number of eggs) was positively related to female body mass (m; kg) as follows:

$$F_{\mathrm{LT}} = 0.03m^{1.48} \qquad (6)$$

($r^2 = 0.88$, $n = 11$, $P < 0.0001$).

Lake trout consumption rates

When lake trout reached 320 mm TL, they began preying on cutthroat trout (Fig. 5), and diets showed

TABLE 2. Abundance estimates for 18 age classes of lake trout during 1996–1999 for the Yellowstone Lake population as calculated from a virtual population analysis (Hilborn and Walters 1992). Abundance estimates for ages 3–5 and total estimated abundance are also shown for each year.

	Age (yr)																		
Year	3–5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	Total
1996	8300	788	695	590	396	231	123	59	41	21	16	12	10	3	2	3	3	2	3	11 298
1997	8352	601	706	601	480	327	171	75	28	12	3	5	2	1	0	0	1	0	2	11 367
1998	6925	351	517	576	421	288	189	96	47	19	4	0	2	0	0	0	0	0	0	9 434
1999	4800	105	228	423	376	263	160	102	50	16	13	2	0	2	0	0	0	0	0	6 540

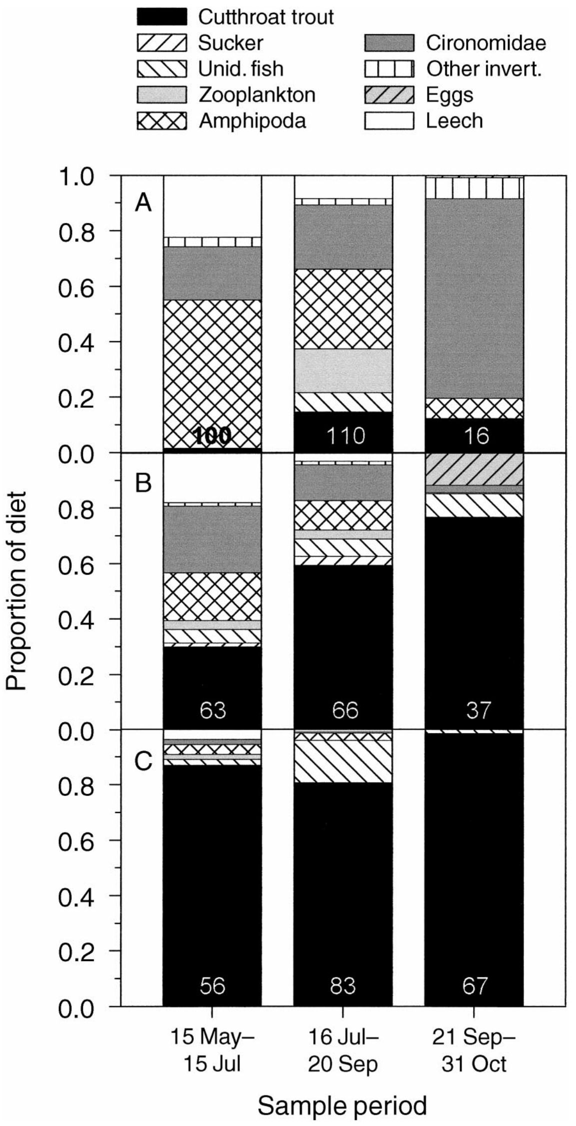

FIG. 4. Diet composition (calculated as proportion of diet by wet mass) of three age classes of lake trout (A, age 3–4; B, age 5–8; C, age 9–23) during three periods of the ice-free season. Diet categories include: cutthroat trout, longnose sucker (sucker), unidentified fish (unid. fish), zooplankton, Amphipoda, Chironomidae, Hirunidae (leech), other invertebrates (other invert.), and lake trout eggs (eggs). Sample sizes for non-empty stomachs examined in each age group during each season are shown near the bottom of the histograms.

lake trout primarily ate small cutthroat trout from 65 to 365 mm TL. Total length of cutthroat trout (CT_{TL}) prey in diets of lake trout was positively related to lake trout TL (LT_{TL}) where:

$$CT_{TL} = 0.36(LT_{TL}) - 27.5 \tag{7}$$

($r^2 = 0.29$, $n = 418$, $P < 0.001$). Although lake trout consumed cutthroat trout from 11 to 57% of their body length ($\bar{x} = 32\%$), 90% of cutthroat trout prey were between 20 and 45% of the length of their lake trout predator.

Based on gill net catches and concurrent measurements of temperature profiles, lake trout demonstrated ontogenetic shifts in their thermal history. Fish <5 yr of age were primarily juveniles that inhabited deep water and hence had a cold thermal history (Fig. 6). Throughout the year, fish age 5–8 began switching to piscivory, were found at shallower depths, and enhabited relatively warm temperatures during summer months compared to the other two age groups. Age 9–23 adults inhabited intermediate depths near the thermocline for much of the year. We have no information on depth distribution of lake trout from Yellowstone Lake during winter months. However, we modeled the largest, most piscivorous fish at slightly shallower depths compared to smaller sizes due to their piscivorous, sight-feeding behavior. Therefore, these fish were estimated to inhabit colder temperatures than younger fish because colder water is found nearer the surface during the ice-covered season.

Model simulations indicated that the lake trout population consumed large numbers of cutthroat trout in Yellowstone Lake. Young lake trout consumed a variety of prey taxa, but cutthroat trout dominated consumption as the predators grew (Table 3). Cutthroat trout made up 8% of annual consumption by ages 3–4, 60% for ages 5–8, and 79% for ages 9–23. Increasing energetic demands due to increasing body size also influenced the biomass of cutthroat trout consumed by individual lake trout. Annual estimated consumption of cutthroat trout by individuals in each age class of lake trout ranged from 0.17 to 8.3 kg/yr (Fig. 7). Based on

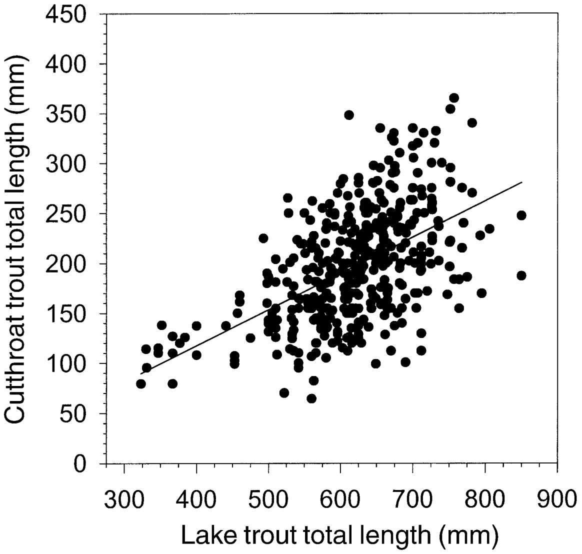

FIG. 5. Total length of cutthroat trout prey in the diets of lake trout predators across a range of total lengths captured during 1996–1999. The solid line is a least-squares linear regression equation fit to the data (see *Results: Lake Trout Consumption Rates*).

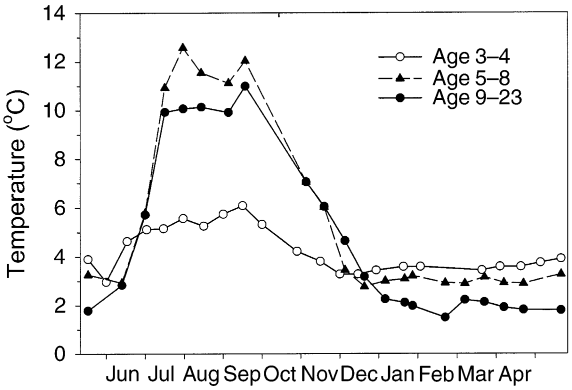

FIG. 6. Estimated annual thermal history (°C) of three age classes of lake trout used for bioenergetics simulations.

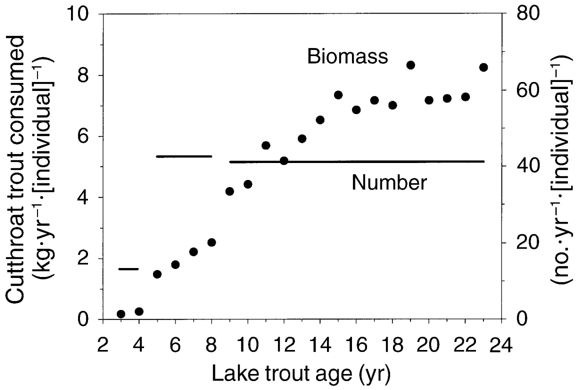

FIG. 7. Bioenergetics simulation estimates of biomass (kg; solid circles) of cutthroat trout consumed per lake trout each year by 21 age classes of lake trout captured in Yellowstone Lake. Average number of cutthroat trout consumed per predator each year by three age classes of lake trout (age 3–4; age 5–8; age 9–23) is also illustrated as horizontal lines extending through the represented ages.

the mean size of cutthroat trout in their diets, age 3–4, age 5–8, and age 9–23 lake trout consumed an average of 13, 42, and 41 cutthroat trout of average size each year, respectively (Fig. 7). Over a 23-yr life-span in Yellowstone Lake, a lake trout would consume an estimated 1066 cutthroat trout.

Control program evaluation

The NPS lake trout removal program has saved a large number of cutthroat trout from predation. During 1996, the estimated lake trout population (≥3 yr of age) consumed 522 000 cutthroat trout from 65–365 mm TL. During 1999, four years after the NPS control program began, the estimated consumption by lake trout declined to 302 000 cutthroat trout. The 14 469 lake trout removed from 1996 to 1998 by this control program would have consumed more than 750 000 cutthroat trout during this period. Moreover, without the control program, the unexploited lake trout population would have consumed an estimated 684 000 cutthroat trout during 1999 alone.

An unexploited lake trout population would also

TABLE 3. Annual consumption (kg/yr) by an estimated population of 12 300 age 3–23 lake trout during 1996 as estimated by bioenergetics simulations.

Age class (yr)	Cutthroat trout	Sucker	Unid. fish	Amph.	Chiro.	Leech	Zoop.	Other invert.	Lkt eggs	Total
3	27	0	3	103	146	34	9	15	0	338
4	770	0	101	2805	4015	931	270	423	0	9 315
5	6093	129	681	747	1114	584	186	52	593	10 179
6	1269	27	142	156	232	121	39	11	123	2 118
7	1382	30	154	170	252	131	42	12	133	2 307
8	1339	29	149	164	244	126	41	12	129	2 234
9	1577	0	79	31	14	19	0	0	0	1 720
10	969	0	49	19	8	12	0	0	0	1 057
11	664	0	33	13	6	8	0	0	0	724
12	293	0	15	6	3	3	0	0	0	320
13	230	0	12	5	2	3	0	0	0	251
14	132	0	7	3	1	2	0	0	0	144
15	112	0	6	2	1	1	0	0	0	122
16	76	0	4	2	1	1	0	0	0	84
17	65	0	3	1	1	1	0	0	0	71
18	21	0	1	0	0	0	0	0	0	23
19	17	0	1	0	0	0	0	0	0	18
20	22	0	1	0	0	0	0	0	0	24
21	22	0	1	0	0	0	0	0	0	24
22	15	0	1	0	0	0	0	0	0	17
23	23	0	1	0	0	0	0	0	0	26
Total	15 118	214	1446	4228	6039	1979	586	525	978	31 114

Notes: Diet categories included: cutthroat trout, longnose sucker (sucker), unidentified fish (Unid. fish), Amphipoda (Amph.), Chironomidae (Chiro.), Hirudinae (Leech), zooplankton (Zoop.), other invertebrates (Other invert.), and lake trout eggs (Lkt eggs). Total consumption by age classes and diet categories is also shown.

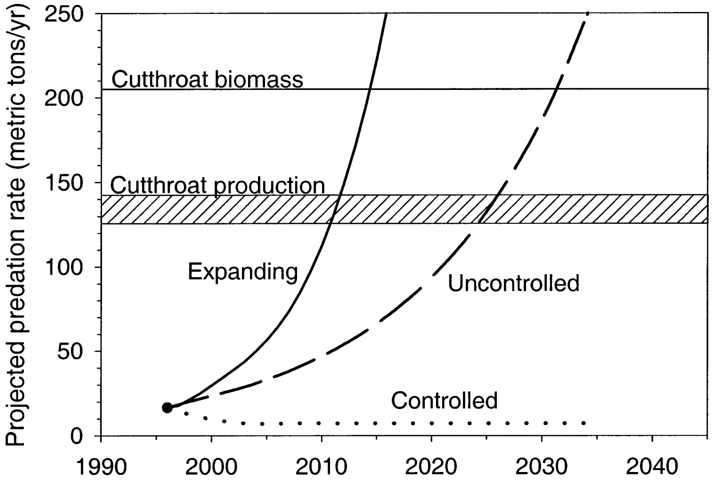

FIG. 8. Projected annual predation rate of cutthroat trout by lake trout (1996–2035) with (controlled) and without (uncontrolled) population control efforts and for an uncontrolled lake trout population that was assumed to expand exponentially throughout the lake basin (expanding). Predation with control was calculated as a 50% decline in the lake trout population every four years from 1996 to 2003 and then maintained at the 2003 level. Predation without control from 1996 to 2035 was modeled at the same increasing rate as that calculated for years 1996–1999 if no control measures were enacted. Cutthroat trout production was assumed to range between the production by the 1998 estimated population of vulnerable age classes (ages 1–4; top of hatched bar) and production minus 1990s annual human exploitation (bottom of hatched bar). Biomass (metric tons) of the 1998 estimated population of vulnerable age classes (ages 1–4) of cutthroat trout is also shown.

have the potential to consume an increasing proportion of the cutthroat trout production. During 1996, lake trout consumed 10% of the annual production by the vulnerable portion of the cutthroat trout population. By 1999, lake trout consumption was reduced to 7% of annual production. Without the NPS control program, lake trout would have consumed more than 21 metric tons or 15% of the vulnerable cutthroat trout production during 1999. Finally, all the lake trout removed from 1996 to 1998 would have consumed 31 metric tons of cutthroat trout prior to 1999 if they had been left in the population.

Projection of the lake trout population, and their consumption, into the future indicated that lake trout have the potential to impose a substantial predatory demand on cutthroat trout within 25 yr. By the year 2002, the uncontrolled and the uncontrolled expanding lake trout populations were projected to be similar at 26 000 and 30 400 fish, respectively. By the year 2030, however, the uncontrolled expanding population was projected at slightly >1.8 million fish while the uncontrolled population remained at slightly <30 000 fish. During this same period, but with sustained control similar to 1999 efforts, the controlled lake trout population was projected to remain at 3500 fish. Subsequently, the controlled lake trout predation rate was projected to remain low at 6 metric tons/yr or 4.2% of the estimated 1998 cutthroat trout production (Fig. 8). Without control, and given the estimated 1996–1999 reproductive potential, annual lake trout predation was projected to equal annual cutthroat trout production by 2025 and exceed cutthroat trout biomass by 2033. Without control and with potential expansion throughout the lake, annual lake trout predation was projected to exceed annual cutthroat trout production by 2012 and exceed cutthroat trout biomass by 2015.

DISCUSSION

When lake trout were first discovered in Yellowstone Lake in 1994, it was anticipated that they would have a substantial impact on the indigenous cutthroat trout population (Varley and Schullery 1995, Kaeding et al. 1996). Lake trout have been implicated in the decline of native cutthroat trout populations in several western North American lakes (Cordone and Frantz 1966, Marnell 1988, Behnke 1992), so our results are not surprising. However, we provide the first population-level quantitative assessment of a lake trout invasion for western North America. Analogous bioenergetics approaches to quantify ecological effects by introduced predators have been applied to Nile perch in Lake Victoria (Kitchell et al. 1997), and chinook (*Oncorhynchus tshawytscha*) and coho (*O. kisutch*) salmon in the Laurentian Great Lakes (Stewart et al. 1981), providing needed information for management decisions. Our evaluation should provide resource managers added justification to sustain their control efforts to preserve the remaining cutthroat trout population in Yellowstone Lake.

Few cutthroat trout are invulnerable to the largest lake trout predators in Yellowstone Lake. Although the average cutthroat trout consumed by lake trout was 32% the predator's body length, lake trout are capable of capturing prey at least half their body length (Fig. 5). Similar results have been reported for lake trout in other systems (Yule and Luecke 1993). The largest lake trout captured during 1996–1999 was 914 mm TL, which should be able to eat cutthroat trout up to 450 mm TL. The largest cutthroat trout captured during the same period was 567 mm TL, but most of the population was <450 mm TL. Therefore, few cutthroat trout will be invulnerable to predation, especially if large lake trout are not controlled.

Our modeling simulations indicate that predation by lake trout can substantially reduce the cutthroat trout population. Before control of large lake trout began in 1996, these predators were already consuming >500 000 cutthroat trout/yr, a level few populations of native cutthroat trout in western North American lakes could withstand. In Bear Lake, a 282-km^2 lake in northeast Utah and southeast Idaho, Ruzycki et al. (2001) estimated the age 2 and older Bonneville cutthroat trout (*O. clarki utah*) population at only 31 000 fish. We know of no other published abundance estimates for cutthroat trout populations in other large lakes of western North America, and Yellowstone Lake is the last remaining large western lake dominated numerically by cutthroat trout. Yellowstone Lake represents the core of the remaining, relatively undisturbed natural habitats for this species. Spawning habitat within the watershed is extensive (Gresswell et al. 1997) and has not been significantly altered by deforestation. Because of limited human disturbance, production by the Yellowstone Lake cutthroat trout population is large, which may enable this population to persist with moderate predator control. Despite this resilience, introduced lake trout will increasingly regulate the cutthroat trout population if control measures prove ineffective.

Our model simulations can be used to assess the effectiveness and necessity of the NPS lake trout control program. Three years after the control program began, lake trout consumption of cutthroat trout had been reduced by an estimated 43%. Without control measures, lake trout predation of cutthroat trout during 1999 would have increased an estimated 32% over 1996 levels. If the lake trout population was allowed to grow at this pace, assuming constant recruitment, consumption of vulnerable cutthroat trout (ages 1–4) would represent more than half of cutthroat trout production in 13 yr and would exceed production in 25 yr (Fig. 8). If lake trout expand their population by using the extensive spawning and rearing habitat available throughout the lake, our simulations indicate that lake trout predation rates would exceed annual cutthroat trout production in 11 yr, less than half the amount of time. This approach assumes a stable age distribution and current predator–prey dynamics that do not include density dependence. More accurate projections of predatory effects into the future will require estimating functional and numerical responses of these predators. However, it is likely that lake trout predatory effects would accelerate with their population growth, at least until density-dependent effects occur through the depletion of the lake trout's principle prey, cutthroat trout.

Without a control program removing the largest predatory size classes of lake trout, more of their population would likely become piscivorous, accelerating negative effects on the native cutthroat trout. The abundance and age structure of the unexploited lake trout population prior to 1996 suggests a recently established population dominated by younger age classes. In the absence of control, however, the population age structure would likely become dominated by older, more predatory individuals. Predation of larger, reproductive cutthroat trout would be accelerated because larger lake trout are capable of ingesting larger prey. This elevated predation of older cutthroat trout would limit their reproductive capacity, thus reducing their population's resilience to predation.

Although we had no information on lake trout diets for cold-water periods, it is unlikely that our estimates of cutthroat trout consumed by lake trout are inaccurate enough to alter our conclusions. Our model simulations indicated that <30% of annual consumption of cutthroat trout by lake trout occurred during this period, so if lake trout completely switched to alternate prey, we could have overestimated consumption of cutthroat trout by nearly 30%. However, the only significant alternative fish prey available to lake trout are longnose suckers and smaller lake trout, which were only a minor component of lake trout diets during the cold-water period for which we had data. Invertebrates are another alternative prey source, but lake trout in other western North American lakes consume similar or smaller proportions of invertebrate prey during winter months, because they either do not shift their diets or shift to a diet dominated by fish prey (Yule and Luecke 1993, Thiede 1997, Ruzycki et al. 2001).

During 2000, the NPS captured 12 792 lake trout in their control program. This catch is considerably greater than our 1999 population estimate of 6500 age 3–23 fish. Although this discrepancy raises doubts about our virtual population estimate, recruitment of younger fish likely accounts for much of the difference. Our 1999 estimate was for only age 3 and older lake trout. Catches in 2000 were dominated by younger fish (P. Bigelow, *personal communication*), including many fish that were age 2 in 1999 and not included in our 1999 estimate. During this period, younger age classes of lake trout were likely still expanding. Age 2 fish in 1999 were spawned as eggs in the fall of 1996 (age 0 in 1997), the first year that spawning concentrations of lake trout were discovered in Yellowstone Lake. The NPS control program likely had only partial success at controlling reproduction during these years, so recruitment was probably substantial. Despite a decline in older lake trout from 1996 to 1999, large year classes of young fish likely recruited to sizes vulnerable to gill nets and increased gill net catches of lake trout in subsequent years.

The detrimental effects of the lake trout introduction in Yellowstone Lake may extend beyond their direct influence on the cutthroat trout population. Cutthroat trout play a significant role as both predator and prey in the Yellowstone Lake ecosystem, and provide an important trophic link to the terrestrial community for as many as 42 avian and mammalian predators and scavengers (Schullery and Varley 1995). For example, grizzly bears (*Ursus horribilus*) feed extensively on cutthroat trout during spawning runs in Yellowstone Lake tributaries (Reinhart and Mattson 1990), and cutthroat trout are an important high-quality food source (Gunther 1995). Osprey (*Pandion haliaetus*) feed almost exclusively on cutthroat trout in the Yellowstone Lake drainage, capturing fish that swim near the surface (Swenson 1978). In contrast, because lake trout inhabit relatively deep water, reproduce within the lake, and grow to much larger body sizes, they would not provide the same trophic link to the terrestrial environment, even if they replaced cutthroat trout biomass within the lake.

Lake trout are not the only introduced threat to cutthroat trout persistence. Whirling disease, caused by the parasitic protozoan *Myxobolus cerebralis*, was discovered in Yellowstone Lake cutthroat trout in 1998 (NPS, *unpublished data*) and threatens the high productivity of cutthroat trout that may enable their resilience to the lake trout threat. Human exploitation also affects cutthroat trout. Although past overexploitation was halted in 1975 (Gresswell and Varley 1988), angling regulations from 1976 to 2000 still allowed harvesting of fish <330 mm TL. During 1997–1999, anglers removed 40 000–50 000 cutthroat trout each year (NPS, *unpublished data*) in the same size range preyed on by lake trout. A catch-and-release-only regulation was established in 2001 for all native fishes in Yellowstone National Park, which should reduce angling mortality to low levels.

The invasion of Yellowstone Lake and the consequent impacts by predatory lake trout are not unique. Introductions of predatory fish have had profound effects on indigenous lake fauna throughout the world (e.g., Zaret and Paine 1973, Mills et al. 1994, Reinthal and Kling 1994, Hrabik et al. 1998). However, unlike earlier reports, we have provided a quantitative assessment of the nonnative predator's population-level impact and projected it into the future to demonstrate their potential to influence the Yellowstone Lake ecosystem. Kitchell et al. (1997) used a similar bioenergetics approach to explore the interactions between introduced Nile perch, native fishes, and human influences in Lake Victoria to support management actions. Our intent here was to not only document the effects of lake trout, but to also provide much needed scientific evidence in support of managers' commitment to control lake trout in Yellowstone Lake. Faced with the consequences of no action and recognizing the costs and effort associated with substantive action, the NPS acted quickly and initiated a maintenance control program with limited direct evidence of the lake trout's influence on cutthroat trout (Varley and Schullery 1995). Evidence presented here has already been used to support continuing the control program and as a measure of its effectiveness.

Until recently, the effects of fish introductions have been poorly studied (Moyle 1985, Allendorf 1991) despite sometimes devastating consequences to indigenous fauna. Fortunately, increasing attention is being directed at the detrimental effects of fish introductions throughout the world (e.g., Crowl et al. 1992, Mills et al. 1993, Reinthal and Kling 1994, Hrabik et al. 1998, Nyström et al. 2001). In North America, lake trout have been widely introduced to benefit human recreation (Crossman 1995), but the ecological consequences of these introductions were poorly understood. Recently, increasing attention is being given to indigenous fishes and their associated economic values (e.g., Gresswell and Liss 1995). The quantitative results presented here should provide much needed data for the preservation of native fishes, particularly cutthroat trout, as they face increasing perturbations from invasions and other anthropogenic influences.

Our results may also hold important lessons for the management of invaders in other ecosystems. The invasion ecology of lakes is similar to island ecosystems (Magnuson 1976, 1991), which have been particularly devastated by invasions of novel predators (e.g., Fritts and Rodda 1998). Eradication of introduced animals has also been most successful on islands because reinvasions are less likely than on mainland sites (Craig et al. 2000). We have demonstrated the potential impact of a novel predator on an isolated community during the early stages of the invasion and have provided a measure of success for the program designed to control them. This information is often needed to confront public opposition to conservation programs. Rapidly developing support for conservation programs is crucial to avoid developing a ''clientele'' for the introduced organism. Control is also most feasible during early stages of an invasion (Manchester and Bullock 2000), so early action is prudent even in the absence of quantitative proof of predator effects. Most importantly, our approach of controlling introduced predator numbers while concurrently developing information about their effects simultaneously addresses each of these biological and sociological management issues. Using this bioenergetics modeling approach to quantify the detrimental effects of introduced predators and validating a program to control them should be useful when applied to invasion events in many ecosystems.

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